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PHYLOGENY OF THE NAUTILOIDEA

(FILOGENEZA ŁODZIKÓW)

BY

JERZY DZIK

(WITH 72 TEXT-FIGURES AND 47 PLATES)

WARSZAWA — KRAKÓW 1984

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JERZY DZIK

PHYLOGENY OF THE NAUTILOIDEA

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A semiquantitative method of the phylogeny reconstruction is applied to study of fossil Nautiloidea. Morphology of calcareous deposits, appearing first in the phragmocone of the baltoceratid Ellesmeroceratina, supports a concept of their secretion from the cameral liquid. This model explains either the lack of both types of deposits in Ellesmeroceratina with the siphon retreating from the older parts of the phragmocone (as indicated by formation of diaphragms), and the lack of cameral deposits in the Endoceratina, whose long septal necks prevented an effective exchange of cameral liquid between the siphuncle and camerae. The baltoceratid *Cochlioceras* was ancestral to both the Endoceratina, which originated before the earliest Arenigian with elongation of the septal necks, and the Orthoceratina, which originated with a shift of the siphuncle from a ventral to central position in the phragmocone. The Discosorida evolved before the Llandeilian from unidentified, endogastrically curved. breviconic ellesmeroceratids probably through a swelling of the connecting ringsl They developed radial lamellae in the siphuncle and a complexly shaped adult shell aperture but the general shape of their endogastrically curved, compressed shell persisted until their extinction. The Oncoceratida evolved before the latest Arenigian from exogastrically curved Ellesmeroceratina. They differ from the ancestors of the Tarphyceratida in having a short body chamber. Oncoceratids do not differ from the Discosorida in structure of the connecting rings. The Actinoceratida evolved from some as-yet-unknown Late Arenigian sactoceratid Orthoceratina. The radial structure of siphuncular deposits, recognized commonly as typical of the actinoceratids, also occurs in some Orthoceratina (*Clinoceras*), whereas there are no radial blocks in the siphuncle of some Actinoceratina (*Eushantungoceras*). The Lituitina evolved from Late Arenigian Orthoceratina with a relatively breviconic shell, and elongated spetal necks. They are characterized by connecting rings disappearing during ontogeny and/or by the narrow ventral sinus of the shell aperture. The main trend in their evolution was toward an exogastric shell with a deep apertural sinus, the coiling of which begins in the juvenile stages. It is suggested that Llandeilian *Centrocyrtoceras* is the earliest representative of the Nautilida, and links them with kionoceratid Orthoceratina. The retractor attachment scar typical of the Nautilida appeared only in the Silurian *Lechtritrochoceras* (*Kosovoceras*) due to a shift of the main attachment area from the ventral to lateral sides of the shell. The large protoconch appeared in the main nautilid stock as late as the Carboniferous. A modified systematics of the subclass Nautiloidea is proposed. 137 nautiloid species, mostly from the Paleozoic and Mesozoic of Poland, are described and/or illustrated. The following new taxa are erected: Lituitina, new suborder; Oncotoceratidac, new family; Weberoceratidae, new family; Arionoceratidae, new family; *Cochlioceras roemeri* sp. nov.: *Lysagoraceras kielcense* sp. nov.: and *Gonatocyrtoceras longissimum* sp. nov.

Key words: Cephalopoda, Nautiloidea, evolution, taxonomy, ontogeny, functional morphology, Ordovician, Devonian, Carboniferous, Triassic, Jurassic, Poland, Bohemia, erratic boulders.

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FILOGENEZA ŁODZIKÓW

Streszczenie. — Opracowanie zawiera rozważania na temat pokrewieństw filogenetycznych Nautiloidea oraz ilustracje fotograficzne i rysunkowe 137 gatunków łodzików (w tym 3 nowe), głównie z paleozoiku i mezozoiku Polski. Poza gatunkami spoza Polski i z bałtyckich głazów narzutowych zilustrowano gatunki łodzików z następujących odsłonięć: ordowik — Mójcza koło Kielc, Międzygórz koło Sandomierza; sylur — Prągowiec koło Łagowa, Bełcz koło Opatowa; dewon — Jabłonna koło Daleszyc, Łagów Świętokrzyski, Kielce-Kadzielnia, Dębnik koło Krakowa, Dzikowiec Kłodzki; karbon — Zalas (Orlej) koło Krakowa, Dąbrowa Górnicza; trias — Wolica koło Chęcin, Ligota Samborowa; jura — Łapiguz koło Łukowa, Lasocin koło Małogoszcza, okolice Chęcin, Działoszyna, Iłży i Ogrodzieńca; kreda — Annopol koło Sandomierza, Kazimierz nad Wisłą. Formalnej rewizji taksonomicznej poddano gatunki łodzików opisane przez GÜRICHA (1897) z dewonu Świętokrzyskiego i przez ROEMERA (1862) z ordowickich głazów narzutowych okolic Oleśnicy. W oparciu o rekonstrukcję filogenezy łodzików, dokonaną przy użyciu sformalizowanej metody uwzględniającej dane stratygraficzne, zaproponowano zmodyfikowaną klasyfikację podgromady Nautiloidea. Przedstawione rezultaty badań pociągające za sobą zmiany dotychczasowej interpretacji filogenezy i systematyki łodzików sprowadzają się do następujących wniosków: (1) w ewolucji Endoceratina następował wzrost rozmiarów muszli embrionalnej, zaś najpierwotniejsze łodziki miały rozwój larwalny podobny jak amonity; (2) złogi syfonalne i komorowe we fragmokonach pierwotnych łodzików są skutkiem znacznie intensywniejszej niż u dzisiejszych gatunków wymiany płynu komorowego pomiędzy syfonem i komorami powietrznymi — złogi nie występują we fragmokonach łodzików z diafragmami w syfonie, nie ma złogów komorowych we fragmokonach endocerasów, u których światło syfonu oddzielone jest od komór powietrznych nieporowatymi kołnierzykami septalnymi; (3) rzędy Discosorida i Oncoceratida nie różnią się między sobą strukturą syfonu, lecz pierwotnym kierunkiem zagięcia muszli, endogastrycznym (jak u większości Ellesmeroceratina) u Discosorida, a egzogastrycznym (jak u Tarphyceratida) u Oncoceratida; (4) Lituitina subordo nov. wywodzą się z Orthoceratina; ich najpierwotniejsza grupa, Sinoceratidae, (czyli tzw. „Leurocycloceratidae"), cechuje się pierścieniami łączącymi syfonu ulegającymi przyżyciowej destrukcji; (5) Nautilida wyodrębniły się już w środkowym ordowiku z Orthoceratina o podłużnie prążkowanych, zagiętych muszlach.

CONTENTS

INTRODUCTION

The subclass Nautiloidea includes all ectocochliate cephalopods except for the ammonoids, i.e. except exogastric, longiconic forms with a narrow, ventral siphuncle and a primitive developmental pattern (subspherical, small protoconch; planktonic larva). This diagnosis is exclusive instead of inclusive and hence, disputable in logical terms. A better diagnosis, however, is hard to come by, because of the insufficient understanding of the anatomy of fossil Nautiloidea. In fact, all attempts to divide the Nautiloidea into only a few subunits stemmed from an assumption of the preponderant diagnostic value of often one anatomic structure, e.g. muscle attachment scars (MUTVEI 1964 *b*) or siphuncular deposits (SHIMANSKY and ZHURAVLEVA

1961). Later observations have demonstrated a considerable variability in those structures even within low-rank taxa, and a relatively high constancy in the basic "Bauplan". In my opinion there is no need to distinguish more than three widely accepted cephalopod subclasses: Nautiloidea, Ammonoidea, and Coleoidea.

Only a single nautiloid genus, with five species or subspecies, has persisted to the present; it ranges from Southern Australia to the Philippines (STENZEL 1964; HOUSE 1973). The Paleozoic nautiloids differ from the present *Nautilus* not only in shell morphology but also in internal structure; for example, they possess an operculum (TUREK 1976, 1978; HOLLAND *et al.* 1978) that may have functioned as jaws (DZIK 1981), as in the ammonoids. There is little certainty that all fossil nautiloids were tetrabranchiate. Unfortunately, the few comments on nautiloid soft body structures are either mistaken (EHRENBERG 1942), or doubtful (FLOWER 1955, ZEISS 1968). Therefore the only way to determine nautiloid evolution is to analyse the shell structure through time.

Fossil nautiloids have been known since the very inception of paleontology; indeed they attracted much attention in the classics. The greatest contribution to our knowledge of the morphological variation among fossil nautiloids was made by BARRANDE (1865—1877). The accuracy of the illustrations (also in the case of siphuncular structures) has been so great that BARRANDE'S work has remained valid so much so that its appearance was followed by long-term stagnation in nautiloid paleontology. BARRANDE'S monograph includes descriptions and illustrations of more than 1.500 nautiloid species derived mostly from the Ludlovian and Přidolian, and subordinately from the Llanvirnian, Wenlockian, Siegenian, and Eifelian of Bohemia. BARRANDE'S species concept is typological as in most contemporaneous papers. BARRANDE neglected in general both intrapopulation and ontogenetic variation.

My estimate of the actual number of the nautiloid species in the Ordovician to Devonian of Bohemia is 130. BARRANDE'S estimate of more than 10 times more this number is due not only to neglect of ontogenetic and intrapopulation variability (especially large among the Oncoceratida), but also to his practice of distinguishing species on poorly or fragmentarily preserved specimens. The majority of BARRANDE'S species are not confined to any stratigraphic interval; they are morphotypes attributable to various, not necessarily interrelated species. From a purely theoretical point of view (see BRETSKY and BRETSKY 1978), the presence of a dozen hundreds of Silurian nautiloid species, representative of a more or less coherent ecological group at a high trophic level, is incompatible with the present view of ecosystem complexity, especially concerning the Early Paleozoic communities.

Nonetheless, some students assumed that BARRANDE'S species were too inclusive and split them into additional typological species with reliance on exclusive the illustrations instead of studying actual specimens (e.g. FOERSTE 1926, FLOWER and TEICHERT 1957). It has also become a rule rather than an exception to erect new genera on BARRANDE'S illustrations; to my knowledge, the original material has not been revised before the recent studies by Czech authors (HORNÝ 1956, 1965; MAREK 1971; TUREK 1972, 1975, 1976).

Shell morphology and larval development of the Ordovician nautiloids of the Baltic region were analysed by HOLM (1885, 1895, 1896, 1897, 1898, 1899) whose work on the Silurian forms has been supplemented by MUTVEI (1957, 1962, 1964). The Ordovician and Silurian nautiloids of this area were also studied by REMELE (1880—1881, 1882, 1886, 1890), LINDSTRÖM (1890), SCHRÖDER (1891), STRAND (1935) and SWEET (1958, 1959). Rich undescribed material is housed at Naturhistoriska Riksmuseet, Stockholm. The Early Paleozoic nautiloids of the Baltic region, in fact equal the Bohemian forms as source material for the reconsideration of nautiloid systematics and phylogeny. Other Early Paleozoic nautiloid faunas are comparatively poorly known even though extensively studies and described (e.g. BALASCHOV 1962, BARSKOV 1972; BLAKE 1882; CHEN and LIU 1974; FLOWER 1946, 1964*a*; MIAGKOVA 1967; SERPAGLI and GNOLI 1977; TEICHERT and GLENISTER 1952; ULRICH *et al.* 1942; 1943, 1944; WILSON 1961).

The present-day understanding of the non-nautiloid nautiloids is well illustrated by the two most widely accepted reference classifications of the Nautiloidea: "Treatise on Invertebrate Paleontology" and "Osnovy Paleontologii" and the consequent variation in nautiloid systematics. A good example is the generic diagnoses of spindle-shaped Oncoceratida. In the "Treatise" SWEET (1964: 300) followed the systematics of FLOWER (1938). According to him, the genus *Acleistoceras* is characterized by "maximum diameter in anterior part of phragmocone", *Anglicornus* by "maximum gibbosity slightly in front of posterior end of body chamber", *Blastocerina* by "greatest gibbosity in adapical third of body chamber", *Eleusoceras* by "greatest gibbosity posterior of body chamber", *Micronoceras* by diameter "enlarging to body chamber mid-length", *Ovoceras* by diameter "expanding adorally beyond adapical part of body chamber", and *Verticoceras* by "greatest gibbosity in adapical part of body chamber". A single specimen resembling type species of the genus *Acleistoceras*, *A. olla* (SAEMANN, 1854), however, passes in ontogeny the stages supposedly diagnostic of the other genera listed. Similarly, the juvenile stages of beet-shaped *Pachtoceras bogoslovskyi* ZHURAVLEVA, 1972, were referred by ZHURAVLEVA (1972) to the new genus *Platyconoceras* diagnosed by its funnel-shaped shell; and the name *Vertorhizoceras* designates simply juveniles of *Devonocheilus* and *Ukhtoceras*. Ontogenetic stages of aperture constriction are also commonly used for diagnoses of various genera and species. It would seem that the only way of generic assignment of a species under study is to erect a new genus, which is indeed the common practice. ZHURAVLEVA'S (1972) monograph of the Devonian Discosorida includes 66 new genera. An extreme case is given by several papers by FLOWER (1936 to 1976) where virtually each specimen, irrespective of its state of preservation, is designated as the type specimen of a new species or genus, and the diagnoses of which do commonly not point to any difference relative to other taxa. One is therefore unable to recognize the difference between, say, *Discoceras perornatus* and *Plectolites costatus* based on closely similar specimens collected from the same bed (FLOWER 1968).

According to FLOWER and TEICHERT (1957), TEICHERT (1964), and ZHURAVLEVA (1972, 1974) the orders Discosorida and Oncoceratida differ in the thickness of their connecting rings. Nonetheless, the connecting ring is much thicker in typical representatives of the Oncoceratida, e.g. *Oonoceras* (fig. 15c) and *Oocerina s.l.* (MIAGKOVA 1967) than in most discosorids. Yet this is the only reason why ZHURAVLEVA (1972, 1974) transfers to the order Discosorida most forms ascribed previously to the Oncoceratida. Consider, for example, the genus *Edenoceras* MIAGKOVA, 1967, from the Llandoverian of Siberia; it was placed in the Discosorida although it shows no significant difference from the genus *Osbornoceras* from the Llandoverian of North America, which has remained in the Oncoceratida.

It seems unreasonable to regard the orthoceratids and actinoceratids as superorders or subclasses, because there are taxa (e.g. *Helenites*, *Buchanoceras*, *Cyrtactinoceras*) assigned by various authors either to the former, or to the latter group although they are neither evolutionary intermediates, nor secondary homeomorphs.

This study presents an alternative way to erect some tens of new genera for nautiloid material collected in the Lower Paleozoic of Poland as would seem inevitable using previous taxonomic methods. I believe that the best way to determine supraspecific interrelationships among fossil nautiloids is to propose testable models of the course of their evolution.

This paper does not pretend to be a revision of fossil nautiloids described elsewhere. Even in the case of collections that I was able to examine, such a revision was impossible because of the lack of sufficient data regarding distribution of collected materials in the particular geological sections. In most cases additional collecting is needed to obtain samples that might be a basis for taxonomic revision. The aim of this paper is to discuss present knowledge of the course of evolution of the Nautiloidea and to propose provisional schemes of their phylogeny on the basis of available data. Some taxonomic conclusions regarding supraspecific systematics of nautiloids are also presented.

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Abbreviations and terminology:

ZPAL — Zakład Paleobiologii, Polska Akademia Nauk, Warsaw, Poland
IG — Instytut Geologiczny, Warsaw, Poland
NM — Narodni Muzem, Prague, Czechoslovakia
UWR — Instytut Geologii, Uniwersytet Wrocławski. Wrocław, Poland
MGUW — Muzeum Geologiczne, Uniwersytet Warszawski, Warsaw, Poland
MZ — Muzeum Ziemi, Polska Akademia Nauk, Warsaw, Poland
ZMS — Zakład Młodych Struktur, Instytut Nauk Geologicznych, Polska Akademia Nauk, Cracow, Poland
siphon — fleshy tissue surrounded by the siphuncle
siphuncle — (here used as synonymous with ectosiphuncle) tube surrounding siphon, including septal necks, connecting rings and calcareous deposits inside
spiculum — apical part of siphon constricted by siphuncular deposits
siphuncular deposits — calcareous deposits secreted against connecting rings and septal necks of the siphuncle during the life of animal
cameral deposits — calcareous deposits secreted against original walls of camerae during the life of animal
brevicone — conch characterized by high whorl expansion rate
longicone — conch characterized by low whorl expansion rate
depressed — descriptive of whorl or conch with lateral diameter larger than dorsoventral
compressed — descriptive of whorl or conch with lateral diameter smaller than dorsoventral
diaphragm — imperforate calcareous partition crossing siphuncle, secreted by siphon
septum — imperforate calcareous partition crossing phragmocone, secreted by mantle
endogastric — descriptive of conch curved in manner placing infundibulus on concave side
exogastric — descriptive of conch curved in manner placing infundibulus on convex side
sample — group of specimens taken from single layer of rock (or several layers not differing significantly in the composition of fossil assemblage and time of deposition)
population — group of animals of the same species living in the same area
biological species (= biospecies) — group of populations coexisting in time and not isolated genetically
temporal species (= chronospecies) — arbitrarily cut part of continuum of biospecies in time

MATERIAL

The present study is based on collections of fossil nautiloids from the Paleozoic and Mesozoic of Poland and observations of various museum collections from other countries, as well as on data from the literature. The main sources of the material are as follows:

1. A considerable part of the investigated nautiloid collection derived from erratic boulders

of Baltic origin scattered all over Poland. The age of the boulders was usually determined after their conodont faunas (Dzik 1976, 1978). The most abundant nautiloid associations came from the cherrish-red limestones of the *Paroistodus originalis* Zone (Volkhovian, Arenigian), glauconitic limestones of the *Eoplacognathus pseudoplanus* Zone (Kundan, Llanvirnian), blue-grey organodetritic limestones of the *Eoplacognathus foliaceus* to *E. reclinatus* Zones (Lasnamägian, Llanvirnian) and the *Eoplacognathus robustus* to *E. lindstroemi* Zones (Uhakuan, Llandeilo), graptolitic limestones (Early Ludlovian), and *Beyrichia* limestones (Přidolian). Less abundant nautiloid associations have been collected from the boulders of other Ordovician through Devonian stratigraphic intervals.

2. Ordovician to Devonian nautiloids have also been collected in the Holy Cross (Świętokrzyskie) Mts in central Poland, but abundant nautiloid faunules occur there only in a few exposures. Well preserved pelagic nautiloids, often with the apical part of a shell, were found in the Early Ludlovian graptolitic shales at Prągowiec gorge by Łagów. An ecologically similar faunule occurs in shales of the Late Givetian Świętomarz Beds at Śniadka by Bodzentyn. Late Frasnian strata of Płucki by Łagów yielded another nautiloid faunule. A very large collection including several distinct nautiloid species has been taken from the Early Famennian (*Cheiloceras* Zone) limestones and marls at the Kadzielnia quarry, Kielce. A nautiloid faunule equivalent both in age and in composition occurs at the left wall of Dule gorge, Łagów. From the opposite wall of Dule gorge (this exposure has for long been investigated by paleontologists; Sobolew 1912, Schönenberg 1952), an abundant and diverse nautiloid faunule has been collected. The nautiloids occur with ammonoids in a few calcareous intercalations within a shaly set. All these beds are assigned to a single ammonoid zone (*Platyclymenia* Zone) but differ, nevertheless, considerably in the composition of the cephalopod and conodont assemblages. A large assemblage was collected bed-by-bed from a trench at Jabłonna near Daleszyce. The faunule ranges in age throughout the whole Famennian but most nautiloids are representative of the *Cheiloceras* and *Platyclymenia* Zones; the beds are numbered consecutively as by Wolska (1962).

3. Some nautiloids have been collected from the Late Famennian (*Wocklumeria* Zone) limestones of Dzikowiec by Nowa Ruda, Sudeten (Ebersdorf of German authors).

4. I studied also a large collection of nautiloids from the Early Carboniferous (Visean) of the Orlej quarry near Cracow and Gałęzice near Chęciny, collected by Dr. Stanisław Czarniecki and housed at the Institute of Geological Sciences of the Polish Academy of Sciences, Cracow.

5. In addition, I studied the materials housed at the museums of the Geological Institute, Warsaw, and the Wrocław University. The latter two collections include not only specimens from Poland but also well preserved nautiloids from the Carboniferous of Great Britain and Belgium, the Devonian of Germany, the Silurian of Bohemia, the Ordovician of China, the Permian of Sumatra, and the Triassic of Pakistan.

6. During my 1976 stay in Moscow, I was able to examine a rich nautiloid collection under the care of Dr. P. A. Zhuravleva in Paleontological Institute. This collection includes specimens from the Ordovician and Silurian of Siberia (described in part; see Zhuravleva 1957, 1962), and from the Devonian all over the Soviet Union (described in part; see Zhuravleva 1972, 1974, 1979). I looked also at the collection under the care of Dr. I.S. Barskov (Moscow University), including specimens from the Ordovician of Siberia (undescribed) and from the Ordovician to Silurian of Kazakhstan (described in part; see Barskov 1959, 1971).

7. Especially important observation come from my studies on Barrande's collection housed at the Narodní Museum, Prague; this collection includes several thousands of excellently preserved nautiloid specimens. The only information usually provided is the name of the outcrop and the stratigraphic attribution in Barrande's original terms. There is no certainty that a homogeneous fossil assemblage occurs in an exposure referred to in such vague terms; much caution is required about inferred range of variation of the component species. However, from

the exposures that have persisted, most cephalopod-bearing beds are actually thin and rather distinct (Dr. V. TUREK, personal communication). Most of the collections come from the Ludlovian Kopanina Formation and the Přidolian Přidoli Formation. The faunules from the Llanvirnian Šárka Formation, the Siegenian Koněprusy Limestone, and the Eifelian Choteč Limestone and Třebotov Limestone are probably homogeneous, too. Only a minor part of the collection derived from other strata. The range of variation of the supposed nautiloid species is more or less constant all over the area investigated by Barrande.

8. The Mesozoic nautiloids investigated in the present study, and illustrated partly in this paper, have been collected from the Anisian of the Holy Cross Mts, the Ladinian of Upper Silesia, the Bathonian of Łęczyca, the Callovian of the Holy Cross Mts and Łuków, the Oxfordian of the Holy Cross Mts and Polish Jura Chain, the Valanginian of Tomaszów Mazowiecki, the Albian of Annopol, and the Maastrichtian of Kazimierz on Vistula.

9. After manuscript of this study was submitted to the editor I have been able to examine rich nautiloid collections of the Naturhistoriska Riksmuseet, Stockholm. Some of the observations made at that time were introduced into the text and phylogenetic concepts were verified.

PROBLEM AND METHODS

To consider all thus far erected nautiloid species in a study of nautiloid evolution would be equivalent to a reconstruction of fanciful "evolutionary" trends each confined to a state of preservation, ontogenetic stage, and/or a portion of the intrapopulation variability range. One has therefore to determine clearly the criteria of selection of the basic paleontologic data. A considerable number of nautiloid species erected on material which is in my opinion unidentifiable to the specific or even generic rank, have been excluded. The main information which I wished to extract from the remaining basic observations was the intrapopulation variability. When following this approach to paleontology, the keystone problem is the relationship of an assemblage of conspecific fossils derived from a single bed to the original population structure of living organisms. Several authors discussed this problem from the ecological viewpoint (e.g. STANTON 1976, PETERSON 1976, THAYER 1977, DZIK 1979). I shall therefore consider only the implications of a transformation of the original population structure for the feasibility of a biometrical recognition of co-occurring species.

An assemblage of conspecific fossils differs from the original population of living organisms first of all in the age structure. A sample of a living population reflects the contribution of particular ontogenetic stages to the total biomass of the population; in contrast, a sample of a fossil assemblage reflects the mortality distribution over particular ontogenetic stages (see DZIK 1979). Hence, a fossil assemblage gives an overestimate of those stages, most commonly the juvenile ones, which suffered the highest mortality. The mortality pattern may vary over the area inhabited by freely migrating organisms. This is reflected by a variation in the contribution of particular ontogenetic stages to coeval fossil assemblages recorded in more or less distant localities. Consider for example the Callovian cephalopods from Łuków (detached block of Baltic origin; MAKOWSKI 1952) and Lasocin (Holy Cross Mts; SIEMIĄTKOWSKA-GIŻEJEWSKA 1974). Juvenile nautiloids and ammonoids predominate at Łuków, while adults make up the majority of the Lasocin assemblage.

This difference in the very nature of a fossil assemblage and the original population of living organisms may be amplified by post-mortem sorting depending upon the hydrodynamic properties of fossil remains. The fossilization biases do not significantly affect the feasibility of a biometrical recognition of co-occurring fossil species. Every valid taxonomic procedure requires a comparability of the investigated specimens and hence their ontogenetic equivalence, which has nothing in common with a change in proportion of particular ontogenetic stages in a sample. Only adult individuals have been considered in the present study, whereas juvenile specimens have contributed to the analysis of frequency distribution of ontogeny-independent characters. Apertural modification has been recognized as the criterion for nautiloid maturity. An increase in septal density and an onset of muscle attachment scars reflect a growth inhibition that may or may not be indicative of maturity. It is to be kept firmly in mind that the rate of apertural constriction may vary among assemblages of conspecific fossils, and one may often be unable to recognize whether an isolated specimen is mature or immature.

The preceding discussion holds only under the condition that the effects of evolution are insignificant within a single fossil assemblage. These effects are indeed negligible in all the investigated assemblages, as judged from the associated conodonts whose rate of evolution was certainly greater during the Early Paleozoic than that of the nautiloids. The structure of a fossil assemblage may also be biased by migration of various populations of living organisms during the formation of the respective rock bed; a multimodal frequency distribution of at least a single character is however to be expected if the migrating populations did significantly differ from one another.

The nature of nautiloid fossil assemblages was considerably affected by post-mortem transportation of empty shells floating with currents. Shells of the Recent *Nautilus pompilius* are transported over a distance of some thousands of kilometers outside the inhabited area (STENZEL 1964; HOUSE 1973). Coeval nautiloid fossil assemblages can therefore be expected to be indistinguishable in composition among adjacent localities, unless the localities were separated due to a peculiar pattern of shoreline or currents. Hence, one may claim that some nautiloid collections derived from erratic boulders of the same lithology and conodont age are to be considered as a single homogeneous sample.

One may thus conclude that the basic observations analysed in the present study are representative of nautiloid populations. The limits of a sample of the single species within a fossil assemblage have been set according to the morphological homogeneity of a group of fossils or the morphological discontinuity relative to associated groups. Unfortunately, available assemblages are too small in number to be statistically tested for homogeneity and hence, all conclusions are based upon a qualitative analysis of the recorded frequency distributions of morphological characters.

It must be noted that each nautiloid species has its own range of intrapopulation variability. As a rule tightly coiled Recent (MIRANO 1977; STUMBUR 1975) and Mesozoic (TINTANT 1969*b*) Nautilida are much less variable than Palaeozoic breviconic Discosorida and Oncoceratida (see figs 19-21). Some oncoceratid species, for example Devonian *Lysagoraceras kielcense* sp.n., significantly differ, however, even from their congeners in the range of intrapopulation variability.

The morphological information of a specimen typical of a population is presented in pictogram, showing the essential characters to be compared among the investigated populations. The pictograms have been arranged as composite diagrams according to the criteria discussed below. The characters presented in the pictograms include shell outline and ornamentation, as well as siphuncle position and structure. If the range of intrapopulation variability in a particular character exceeds the difference between species, that character has been eliminated. Consequently, only a few pictograms contain data on chamber length, septal convexity, and sutural form. The pictographic method allows the presentation of much information in a small figure. It also allows to consider all available information, whether or not the range of variability in a morphological feature can be determined for all investigated populations.

The pictograms have been arranged in diagrams each provided with a time axis (see figs 3, 7, 12, 14, etc.). The main criterion for arranging the pictograms in a diagram has been the continuity of all morphological transformations along the time axis. Where the fossil record of a nautiloid group is very incomplete, I organized pictograms into isochronous morphological lineages. The single criterion for construction of these lineages was the maximal continuity of the morphological gradient along a hypothetical axis of morphological transformations normal to the time axis. The only criterion for ordination of the data has been the continuity of morphological changes, while the previous systematic position has been entirely disregarded.

Phylogenetic trees are most commonly reconstructed intuitively or numerically (e.g. with use of the Advanced Wagner Computer Program; see COLLIER 1971). The adequacy of numerical methods may actually be doubtful. The numerical approach to phylogenetic reconstruction requires an a priori assumption of either equality, or hierarchy in the diagnostic value of the considered phenetic characteristics (ABDUL-RAZZAQ 1973; see also HARPER 1976 for review). Furthermore, the ranges of characters themselves are chosen subjectively. The pictographic method is planned to overcome the troubles associated with numerical methods of phylogeny reconstruction, as well as to introduce the time dimension as an important parameter. Neither subjective recognition, nor a priori valuation of characters is required; to the contrary, an organism is treated in "holistic" terms, as an integrated construction. Morphological characters are recognized and valuated only a posteriori and exclusively for taxonomic purposes. Those characters undergoing distinct directional evolutionary changes are recognized as taxonomically diagnostic. Stratigraphic data, neglected by the majority of formal methods of the phylogeny reconstruction, are here used in the same way as in "stratophenetic approach" of GINGERICH (1979).

A model of the course of nautiloid phylogeny represented by pictographic diagram is a working hypothesis to be subsequently tested by new empirical evidence. To claim that two heterochronous populations, represented each by a fossil sample, are part of a single phyletic lineage implies that morphologically intermediate populations occurred temporally between them. The occurrence of a population intermediate in time and in morphology between one of the two and a population representative of another evolutionary lineage is therefore indicative of the implausibility of the previously accepted phylogenetic model; an alternative model is then to be proposed (cf. HARPER 1976). If more than one phylogenetic model can be proposed to account for empirical data, the criterion is given by Occam's Razor; the most plausible is the model assuming the least incompleteness of the fossil record and hence, the least number of hypothetical intermediate morphological stages. Such a model is also characterized by higher degree of falsifiability.

PRINCIPLES OF TAXONOMIC NOMENCLATURE

Sets of populations recognized according to the above procedure of phylogenetic reconstruction are, in a sense, systematic units. To determine the range and rank of the recognized nautiloid taxa, I have taken into account their species diversity and morphological variability, as well as the principle of monophyly, defined below, and, to a minor extent, required that a taxon should be clearly diagnosed, i.e., its members should be easily identifiable. I have not placed systematic boundaries at gaps in the fossil record because this inevitably leads to instability in the definition of taxa brought about by future advances in the study of their evolution. The only exception is for the provisional subdivision of the order Nautilida.

The definition of monophyly here used is modified after ASHLOCK (1971). I assume that all taxa are monophyletic in the sense that a taxon must comprise evolutionary lineages derived from a single ancestral population with the latter population included. In other words, the lower boundary of a supraspecific taxon is traced below the separation of the earliest two temporally concurring species assigned to the taxon.

I use the term "ancestral population" instead of "ancestral species" because of the inconsistency in the use of the term "species" in paleontology and zoology. Only a few authors distinguish between the concept of chronospecies, cut out arbitrarily from a continuous evolutionary lineage, and the isochronous biospecies that are most commonly objectively recognizable. Both the concepts of paleontological species and biospecies are aspects of the only biological reality, evolutionary sequences of arrays of populations, each array being delimited by the continuity of genetic interflow among the constituent populations. In temporal species, spatial variation among the constituent populations is most commonly neglected; with biospecies, temporal change is neglected. Use of either concept in paleontology introduces some elements of "philosophy" or interpretation of the significance of fossil materials. The basic data for the study of organic evolution are therefore derived from fossil samples rather than from fossil species, as the latter represent subjectively biased observations on populations attributable to real evolutionary continua. A fossil sample represents the population of living organisms from which it is derived, the temporal extension of a population is neglected. Thus a paleontological taxon can be delimited by setting only a few arbitrary boundaries between populations successive in time, namely at the base of the considered taxon and at the bases of its descendant taxa; this is consistent with the so-called classical evolutionary method (CEM: BOCK 1973, STEINECK and FLEISHER 1978).

The nature of paleontological taxa is considerably influenced by the relationship of the principles of paleontological to zoological taxonomy. Paleontologists implicitly assume the validity of these principles but the consequent taxonomic concepts are only exceptionally found applied in practice. No doubt that the standard is to be looked for in the traditional zoological taxonomy. A zoological taxon of supraspecific rank must include at least a single subunit. Boundaries between supraspecific zoological taxa reflect either a morphological gap between clusters of species (this is so especially in numerical taxonomy), or an arbitrary decision of the authors. The combination of the principle of monophyly with the principles of zoological taxonomy, referred by definition to a single time plane, inevitably implies some unequivocal principles of paleontological taxonomy (DZIK 1976: 396-397). A paleontological taxon of supraspecific rank has thus to include at least a single species at each time plane within its stratigraphic range, then it is equivalent to a zoological taxon; it has to include also all the ancestral species (populations) along with the latest common ancestor, and a number of descendant species dependent upon the range of coeval taxa of the same rank. A paleontological supraspecific taxon has to include more subtaxa than a zoological taxon of the same rank. Even with the incompleteness of the fossil record taken into account, the latter requirement is only exceptionally met in paleontological practice. The number of species in a paleontological taxon is often seemingly comparable to that of a zoological taxon of the same rank even though the paleontological taxon is actually monospecific at each time plane. This is achieved through arbitrarily cutting out a portion of a single evolutionary lineage. In turn, a monospecific zoological taxon occurs as an exception rather than as a rule.

The adjustment of the principles of paleontological taxonomy to those accepted in zoology does not imply that the boundaries and taxonomic ranks of paleontological taxa will come to be more objective. The boundaries between zoological taxa coincide with morphological or biological gaps, while there are no such gaps in paleontology (the concept of macroevolution put forth by some authors is not discussed here). A boundary between paleontological taxa coincides usually with a gap in the fossil record as known at the very moment of the erection of the taxa, but it tends with time to become a real boundary between coexistent species. When the range and taxonomic rank of a systematic unit are accepted to be wholly arbitrary, one has to indicate clearly the criteria applied to establish a taxonomic classification. Neither numerical taxonomy, nor cladistics may provide us with satisfactory criteria, as already discussed by several authors (see STEINECK and FLEISHER 1978 for review). I believe that it is more reasonable and convenient to base a taxonomic classification upon the paleontological tradition. A new systematics proposed for an organic group should then adjust to the standard provided by an as widely accepted and stable subsystem as possible. Note however that, judging from the number of papers intended exclusively to revise entirely previous taxonomic classifications (most commonly through splitting), there are no stable systematic patterns today.

In my revision of the nautiloid systematics, I have accepted the order Nautilida and the best known of its subunits for the standards of the range of nautiloid orders, suborders, and families. Owing to the work by Kummel (1953 to 1964), Wiedmann (1961), and Tintant (1969 to 1974) who took into account intrapopulation variability, this is certainly the best known order of the Nautiloidea, especially in the Mesozoic.

PHYLOGENY AND CLASSIFICATION

Order **Endoceratida** Teichert, 1933

Diagnosis. — Primitive Nautiloidea with wide, ventral, cylindrical siphuncle, and straight to endogastrically curved shell. Some forms inconsistent in a single character with this diagnosis (e.g. *Bactroceras, Beekmanoceras*) are assigned to the Endoceratida according to their direct phylogenetic relationship.

Suborder **Ellesmeroceratina** Flower, 1950

Diagnosis. — Short septal necks and thick connecting rings.

Remarks. — The Ellesmeroceratina differ from descendent Endoceratina exclusively in the length of the septal necks and the planktonic larval stage. They differ from the Oncoceratida and Discosorida in their cylindrical siphuncle; from the Orthoceratida in the ventral siphuncle; from the Tarphyceratida and Nautilida in their straight or endogastrically curved shell.

Phylogeny (fig. 2). — The oldest known nautiloid is *Plectronoceras cambria* (Walcott, 1913) from the Late Cambrian (*Tsinania* Zone) of northern China (Ulrich *et al.* 1944, Yochelson *et al.* 1974). Specific distinction of the coeval forms *P. liaotungense* Kobayashi, 1935, from Manchuria and *P. huaibeiense* Chen, Tsou and Qi, 1979, from northern China is questionable. All thus far collected specimens of *Plectronoceras* are juveniles ranging from 1 to 3 mm in diameter (Ulrich *et al.* 1944). Such a small size of the apical portion of the shell suggests a planktonic mode of larval life (Dzik 1981). The shell of *Plectronoceras* is considerably curved endogastrically, at least in juvenile stages. None of the specimens has been preserved with the connecting rings.

New data come from the well preserved nautiloids from the Fengshan Formation, northern China (Chen *et al.* 1979). These authors are of the opinion that the nautiloid-bearing middle part of the Fengshan Formation is approximately equivalent to the Late Franconian, below the Gasconadian of North America. 54 species representing 29 genera have been distinguished in the Fengshan nautiloid fauna. Only three of them are sufficiently well documented to be accepted. These are: *Multicameroceras zaozhuangense* (Chen and Qi, 1979) with rather short, endogastrically curved shell and considerably swollen connecting rings, *Ellesmeroceras elongatum* (Zou and Chen, 1979) with straight to a little exogastrically curved shell and cylindrical siphuncle; and *Eburoceras jiagouense* Zou and Chen, 1979, closely related to, if non conspecific with, *E. elongatum*. Other taxa recognized by Chen *et al.* (1979) can not be distinguished from one or another of the three. Additional work, however, may prove their specific distinctness.

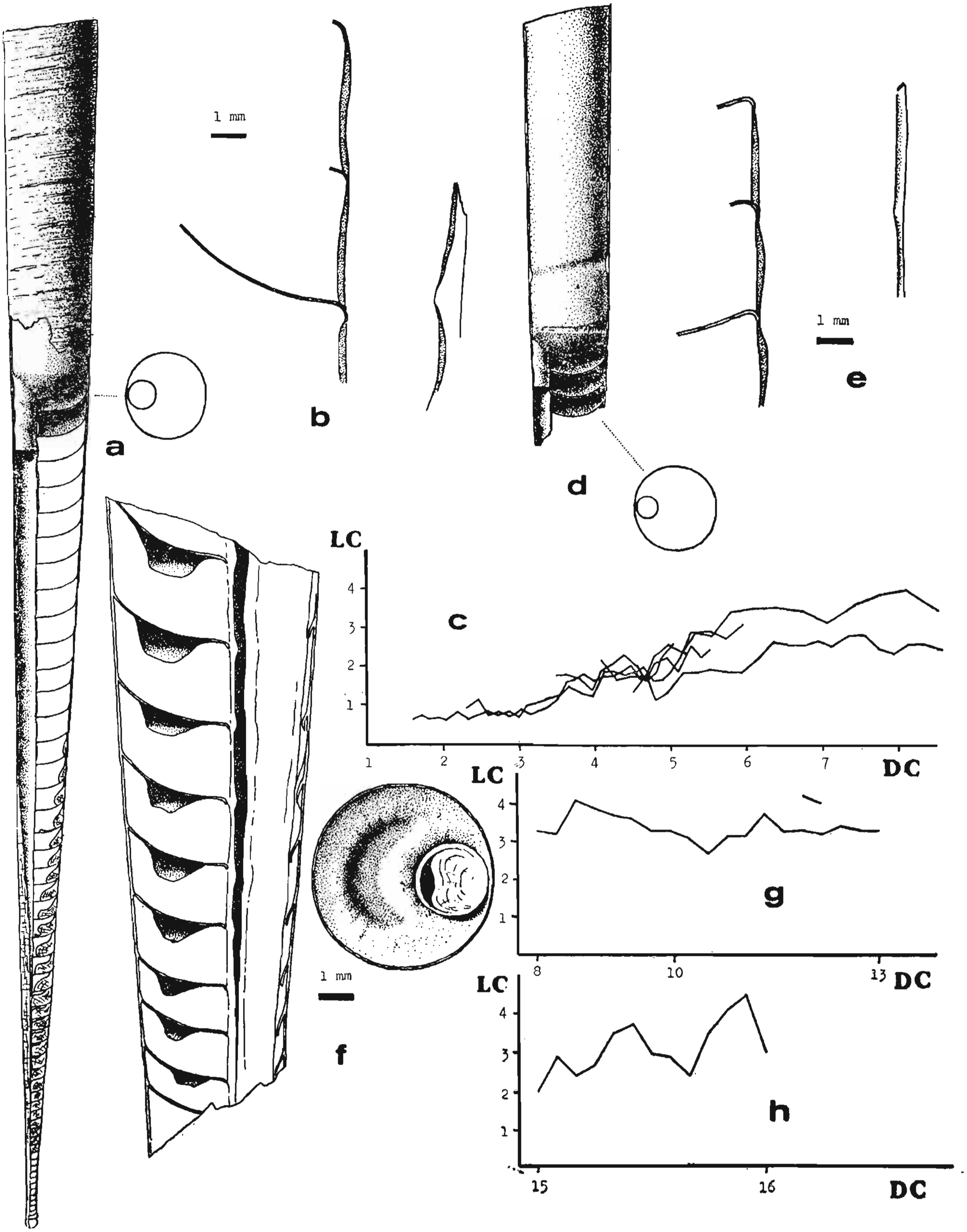
Multicameroceras is preceded by fragmentary specimens of *Plectronoceras* within the Fengshan Formation. The two genera are no doubt closely related. The available data do not clearly indicate any diagnostic difference, since the two genera were erected for specimens of different ontogenetic stages. It is, however, noteworthy that in *Multicameroceras* the connecting rings change in outline during ontogeny; at the late juvenile stages the rings are almost cylindrical in shape. This is consistent with the ontogenetic development of the siphuncle in *Palaeoceras*, as presented by FLOWER (1964*a*). *Palaeoceras mutabile* can then be recognized as a transitional evolutionary stage between the *Plectronoceras-Multicameroceras* lineage and the typical ellesmeroceratids. CHEN *et al.* (1979) claimed a phylogenetic relationship of *Multicameroceras* (= *Protactinoceras*) to the Actinoceratina. This hypothesis is implausible because of the occurrence of diaphragms in the siphuncle and the absence of calcareous deposits in the phragmocone of *Multicameroceras*, as well as the hiatus between occurrences of *Multicameroceras* and its homeomorphic actinoceratins. The other two nautiloids from the Fengshan Formation show characters typical of the Tremadocian Ellesmeroceratidae, namely a long and compressed shell with cylindrical siphuncle.

Their close relatives occur in the Late Cambrian San Saba Limestone, Texas, time equivalent to the Fengshan Formation. These are *Eremoceras primum* (FLOWER, 1964) with its siphuncle attached to the shell wall, and *Palaeoceras mutabile* FLOWER, 1954, with siphuncle somewhat distant from the shell wall and connecting rings swollen at the juvenile stages. FLOWER (1964) described several other species from the material from the same locality, which he claimed varied in the structure of the siphuncle as well as in the extent and direction of shell curvature. In my opinion, these forms may represent the intrapopulation variability of *P. mutabile.*

The above discussed Cambrian forms may have given rise to some distinct evolutionary lineages of compressed, typical ellesmeroceratids known mostly from the lowermost Tremadocian (see FLOWER 1964 ULRICH *et al.* 1944, MALINOWSKAYA 1964). The latter group includes orthoconic forms with shell of variable elongation and siphuncle attached to or somewhat distant from the shell wall (fig. 2). One may postulate that this group is ancestral to nautiloids with a slightly endogastrically curved, terminally tapering, smooth (*Albertoceras*) or annulate shell (*Walcottoceras*) (FLOWER 1964*a*).

The Late Tremadocian Ellesmeroceratidae are poorly known. The species *Ellesmeroceras tchunense* BALASCHOV, 1962, with rather narrow siphuncle considerably distant from the shell wall, has been recorded in limestones of the Chunsky horizon on the Podkamiennaya Tunguska river, Siberia, time-equivalent to the North American Jeffersonian (Late Tremadocian). Such a position of the siphuncle is also found in *Apocrinoceras talboti* TEICHERT and GLENISTER, 1954, from the Early Arenigian Emanuel Limestone, Australia, and *Rudolfoceras cornuoryx* (WHITFIELD, 1886) from the Arenigian Fort Cassin Limestone, Vermont; the former species differs from *E. tchunense* in its swollen connecting rings and circular shell section, while the latter has a short shell with circular cross section. Position of siphuncle is probably nothing more than convergence and both *A. talboti* and *R. cornuoryx* may rather be related to the baltoceratid or protocycloceratid Ellesmeroceratina characterized by their circular shell section.

The Baltoceratidae may have evolved from "*Pachendoceras*" *huzzahense* (ULRICH and FOERSTE, 1931) from the Early Tremadocian Gasconade Dolomite of Missouri (FLOWER 1964*a*). Unfortunately, the latter species is very poorly known. It resembles other ellesmeroceratids in having well developed diaphragms but its somewhat depressed shell resembles the Baltoceratidae. FLOWER (1964*a*) interpreted one of the specimens illustrated by ULRICH *et al.* (1944, pl. 61: 4) as an apical part of the shell, whereas it is actually three times as wide as the conspecific specimens shown on the same plate. The somewhat later form "*Robsonoceras*" *robsonensis* (WALCOTT, 1924), (FLOWER 1964*a*), does not significantly differ from either "*Rioceras*" *nondescriptum* FLOWER, 1964, from the Late Tremadocian El Paso Limestone, New Mexico, or "*Metabaltoceras*" *fusiformise* FLOWER, 1964, from the Late Arenigian Fort Cassin Limestone, New York. All these forms, as well as some dozens of related species described by ULRICH *et al.* (1943) and FLOWER (1964*a*) may be closely related to an evolutionary branch of the genus *Cochlioceras*. One can hardly demonstrate their distinctness from the latter at the present state of knowledge of their morphology and of the type species of *Cochlioceras*.



The Baltoceratidae are the best studied in the Baltic area, due mostly to Holm (1897, 1898) and Mutvei (1957). The most common baltoceratid species is *Cochlioceras burchardi* (Dewitz, 1879) from the Lasnamägian (Llanvirnian). It displays (fig. 1d) a moderately wide siphuncle situated close to the shell wall (Dewitz 1880, Mutvei 1957). This marginal position of the siphuncle results in the formation of a ventral lobe of the suture; this lobe is rather variable in shape (pl 1: 2-4). *C. burchardi* evolved probably from *C. avus* (Holm, 1897) (pl. 1: 1) from the Kundan (Balaschov 1955) at the Arenigian/Llanvirnian boundary, with the siphuncle somewhat distant from the shell wall and hence, without the ventral lobe (fig. 1e; pl. 1: 1). There is considerable variability in sutural form even within a single phragmocone. Both *C. burchardi* and *C. avus* are representatives of the main evolutionary lineage of the genus *Cochlioceras*. An interesting form, *C. roemeri* sp.n., has been found in the Volkhovian (Late Arenigian) to Lasnamägian (Llanvirnian) strata of the Baltic area. It shows a fairly wide siphuncle somewhat removed from the shell wall. The large material collected from erratic boulders permitted the recognition of well developed cameral and siphuncular deposits in *C. roemeri* (fig. 1a, b, f; pl. 1: 5-9); poorly preserved siphuncular deposits had also been recognized in the Late Arenigian baltoceratids from North America (Flower 1964*a*).

C. roemeri shows siphuncular and cameral deposits indistinguishable from those recorded in the most primitive Orthoceratida (Hook and Flower 1976, 1977), and the type of its siphuncular deposits is considered ancestral to that of the Endoceratina. No apical part of the shell of the type species of *Cochlioceras* has thus far been investigated. One may, however, assume that calcareous deposits occur quite commonly in the baltoceratid siphuncle and/or camerae, since all phragmocone fragments of *C. roemeri* and primitive representatives of the genus *Orthoceras* less than 5 mm in diameter contain both types of deposits.

The morphology and structure of siphuncular and cameral deposits in primitive nautiloids is well known (Mutvei 1964, Fischer and Teichert 1969, Ristedt 1971). Much diagnostic value is usually ascribed to the morphology of siphuncular deposits (Mutvei 1954*b*, Kolebaba 1974, Stanley and Teichert 1976). All investigated siphuncular and cameral deposits are closely similar in microstructure, indicating similarity in the mode of secretion. They grew up in the form of successive aragonite layers, resembling in this respect inorganic dripstones. Siphuncular deposits were supposed to be either of mesodermal origin (Flower 1955), or secreted by the siphonal epithelium (Mutvei 1964). They are in direct contact with the connecting rings and septal necks so that the former interpretation is to be rejected; mesodermal secretion seems implausible in any mollusks. Cameral deposits were thought to be either secreted by a hypothetical cameral mantle (e. g. Shimansky and Zhuravleva 1961, Teichert in Fischer and Teichert 1969, Kolebaba 1974) or deposited from the cameral liquid (e. g. Fisher in Fisher and Teichert 1969). Mutvei (1964*b*) refuted cameral deposits formation during life, but this opinion is unacceptable because of the regular and widespread occurrence of these structures. The absence of connecting rings has not been demonstrated in any nautiloid but even assuming that the connecting rings underwent perforation in the adult stages of some nautiloids, their cameral deposits do not differ in structure from those associated with normally developed connecting rings; hence, there is no need to claim a difference in their formation. Furthermore, cameral deposits occur also in belemnite phragmocones whose function has thus far been beyond any doubt (Jeletzky 1966). To assume that phragmocone chambers were filled entirely with soft tissues is to deny their hydrostatic function (cf. Westermann 1977). Such a hypothesis is also incompatible with data on the mode of secretion of the septa (see Kulicki 1979). I contend, therefore, that Fishers's (in Fisher and Teichert 1969) interpretation is the best. Siphuncular and cameral deposits were precipitated from the cameral liquid produced by the siphonal epithelium. As a rule massive siphuncular and cameral deposits are associated in the apical part of nautiloid shells. The only exception is in the

Fig. 1

Cochlioceras roemeri sp. n.; *a* Reconstruction of the shell, boulder E-252 (see pl. 1: 5, 7-9), Rozewie, Poland; *b* section through the siphuncle; *c* relative growth of air chamber length (LC) and shell diameter (DC) in a sample from the *E. reclinatus* Zone, Lasnamägian; *f* reconstruction of a shell fragment, ZPAL N/001 (pl. 1: 6), erratic boulder of red limestone, Volkhovian (?), Rozewie, Poland. *Cochlioceras burchardi* (Dewitz, 1880); *d* Reconstruction of the shell, after the sample from the boulder E-149 (see pl. 1: 2-4), *E. reclinatus* Zone, Lasnamegian, Międzyzdroje, Poland; *g* relative growth of air chamber length and shell diameter in the same population. *Cochlioceras avus* Eichwald, 1860; *e* Section through a siphuncle, ZPAL N/016 (pl. 1: 1), boulder E-060, *A. variabilis* Zone, Kundan, Mochty, Poland; *h* relative growth of air chamber length and shell diameter in the same specimen.

endoceratids with massive siphuncular deposits but without any cameral deposits. It is noteworthy that the endoceratid elongate septal necks almost completely separate the siphon from the chambers, preventing effective cameral-liquid exchange except of removal of the liquid from the last chambers, similarly as in Recent *Spirula* and *Nautilus* (see COLLINS *et al.* 1980).

Apart from the endoceratids, all nautiloids displaying siphuncular deposits show also cameral deposits. Moreover, the secretion of siphuncular deposits began at the septal necks in all nautiloids except for the Endoceratina. In fact, this was the only region in the siphon where the interflow of the cameral liquid was hampered. The rate of aragonite deposition from the liquid was therefore here the highest. In most nautiloids the siphuncular and cameral deposits are better developed at the ventral side of the shell, which may be due to a gravitational accumulation of the liquid. All the above evidence contributes to a coherent interpretation of the siphuncular and cameral deposits as effects of aragonite deposition from the cameral liquid; deposition began within the siphuncle and after penetration of the liquid through the porous connecting rings continued into the chambers. It means, however, that exchange of the cameral liquid in the phragmocones of early Nautiloidea was much more intense than in Recent *Nautilus*.

This interpretation accounts for the structural resemblance between the nautiloid siphuncular and cameral deposits; where the connecting rings disappeared secondarily, a distinct boundary has disappeared betweeen them (COLLINS 1969; SWEET 1958; figs 50, 51, 53). Deposits are widely variable even within a single phragmocone, (see fig. 34), although their general structural pattern remains constant throughout a higher taxon. Form and growth rate of siphuncular deposits are variable even within a single segment. The supposed traces of blood vessels in nautiloid cameral deposits (FLOWER 1941*c*, KOLEBABA 1974) have been considered as evidence for a cameral mantle. These authors apparently refer to an analogy with blood vessels in the brachiopod mantle or those visible on belemnite rostra. Even disregarding the functional implausibility of a cameral mantle, one can point to the occurrence of channel and rib systems in inorganic calcareous dripstones, which indicate the flow direction. There is no significant difference between the latter structures and those recorded in the nautiloid chambers. The pattern of surface channels in cameral deposits may thus provide us with important information on the flow direction of cameral liquids.

The above explanation for the nautiloid intraphragmocone deposits indicates also that weakly developed apical deposits may well be devoid of any functional significance; they appear to be the byproduct of some peculiarities in the calcium carbonate metabolism, as well as result of functional degeneration of the apical part of the phragmocone. The structure of siphuncular and cameral deposits is therefore beyond genetical control; rather, it reflects the physiological and environmental conditions. This would account for the variation in structural details associated with the constancy in general structural pattern. Consequently, the diagnostic value of both siphuncular and cameral deposits is diminished (but not denied), while their significance for functional and other biological analyses is increased.

The supposedly bactritid affinities of the genus *Bactroceras* (= *Eobactrites*) are disputable. Some species (?) attributable to this genus are known from the Llanvirnian of Sweden (HOLM 1898), Norway (SWEET 1958), and Bohemia (BARRANDE 1868). During the Llanvirnian, some *Bactroceras* were probably increasing the length of the air chambers and the depth of septa, possibly an adaptation to pelagic life (cf. WESTERMANN 1980). Chamber length, however, is highly variable in these nautiloids. The only ellesmeroceratid protoconch known to date belongs to *Bactroceras*; it was originally described by BARRANDE (1868, p. 247: 26—28; see also DZIK 1981: fig. 1*a*) from siliceous concretions of the Llanvirnian Šárka Formation at Osek by Beroun, Bohemia, and assigned to *Tretoceras parvulum*. Its identity with *Bactroceras sandbergeri* (BARRANDE, 1868), occurring commonly in those strata, is strongly indicated. Its narrow, marginal siphuncle begins asymmetrically at the wall of the spherical embryonic shell and runs along the ventral wall of the shell (DZIK 1981). The form of the body chamber is unknown. *Bactroceras* (= *Eobactrites*) is homeomorphic with the Devonian genus *Bactrites*; it differs from the latter in its simple aperture, larger-sized embryonic shell, and probably also in the pattern of the retractor muscles.

Siphuncular and cameral deposits occur also in the family Protocycloceratidae (see FLOWER 1964). This is a poorly known ellesmeroceratid group of uncertain range. Most thus far described protocycloceratids (ULRICH *et al.* 1944) are represented by very poorly and fragmentarily preserved specimens. Shell annulation alone can hardly be considered sufficient for the familial distinction of an taxon; this feature has appeared independently in the evolution of various nautiloid groups. The best preserved protocycloceratids were described by HOOK and FLOWER (1977) from two Early Arenigian formations of New Mexico, Texas, and Utah. The nautiloid fauna of the Florida Mountain Formation is very closely related, if not identical, to that of the Wahwah Limestone. Both faunas include mostly primitive orthoceratids (supposedly two species) and annulated ellesmeroceratids. I believe that, from the biological viewpoint, only two groups of annulated forms can be distinguished among the numerous species and genera proposed by HOOK and FLOWER (1977). "*Rhabdiferoceras planiseptatum*" has a rather wide, ventral siphuncle close to the shell wall, and unusually weakly convex septa; "*Rudolfoceras keadyi = Kyminoceras kottlovskii*" shows a narrower siphuncle displaced further away from the shell wall. These names are probably junior synonyms of previously described species (see ULRICH *et al.* 1944, FLOWER 1964). Some other protocycloceratids may also be present in these strata but the available data are insufficient for their recognition. Both mentioned forms show siphuncular and cameral deposits like those in the associated orthoceratids. The variability in siphuncular deposits, which served as the basis for erection of some new nautiloid genera by HOOK and FLOWER (1977), does not appear to be greater than in a single species of *Orthoceras* (figs 33—34). The adapical part of the protocycloceratid shell illustrated by HOOK and FLOWER (1977, pl. 19: 3) is less than 1.5 mm in diameter. Thus the larval shell resembles closely that of the orthoceratids.

The family Bathmoceratidae characterized by its elongated and straight shell and the peculiar thickening of the connecting rings which intrude into the siphuncle, probably evolved from some primitive baltoceratids. Its oldest and most primitive known species is *Eothinoceras americanum* ULRICH, FOERSTE, MILLER and UNKLESBAY, 1944, which is probably conspecific with *E. maitlandicum* TEICHERT and GLENISTER, 1954, from the Early Arenigian of Australia. The adult form of this species may have been described under the name *Proterocameroceras brainerdi* TEICHERT and GLENISTER, 1954. Connecting rings with elongate triangular section are typical of *Eothinoceras*, for which a subgeneric rank within *Bathmoceras* seems to be sufficient. Concerning this feature, *Eothinoceras* is intermediate between the typical ellesmeroceratids with thick connecting rings and more advanced species representative of the genus *Bathmoceras*. In *Bathmoceras s.s.*, the connecting rings between septa are so thick that they take the form of elongate tongues in longitudinal section (HOLM 1889, BARRANDE 1868, BALASCHOV 1955, SWEET 1958, CHEN and LIU 1974). The connecting rings of bathmoceratid siphuncle are also considerably thickened in the segments near the living chambers; they intrude the living chambers. This indicates different origin and function of the siphuncular structures between *Bathmoceras* and other nautiloids. An attempt to derive the siphuncular deposits from thickened connecting rings (FLOWER 1944, 1976) is incompatible with their mode of growth, microstructure, and time sequence.

The most successful lineage of the Ellesmeroceratina has proved to be the family Bassleroceratidae which includes forms with somewhat exogastrically curved shell. According to FLOWER (1964, 1976), the oldest Bassleroceratidae occur in the Demingan (Late Tremadocian) but the oldest reliable records are from the Early Arenigian (TEICHERT and GLENISTER 1954). The bassleroceratids appear to occur in the Tremadocian, since they are considered ancestral to the Late Tremadocian Tarphyceratida. FLOWER (1976) included the Bassleroceratidae in the order Tarphyceratida which appears disputable. To recognize whether bassleroceratids are tarphyceratid relatives, the length of the living-chamber and the siphuncular structure have to be known. As judged from the single known specimen, *Bassleroceras annulatum* TEICHERT and GLENISTER, 1954 from the Early Arenigian Emanuel Limestone, Australia, displays a short living chamber which places it close to the oldest representatives of the Oncoceratida. Unfortunately, the structure of its siphuncle remains unknown. Some intermediate forms between Bassleroceratidae and Oncoceratida occur in the Middle Kundan of Öland.

Apocrinoceras talboti TEICHERT and GLENISTER, 1954, known from a single small shell fragment from the Emanuel Limestone, has swollen connecting rings. This may suggest relationship to the order Discosorida (or possibly to the Oncoceratida, since we know little about shell curvature in this species). A similar, yet undescribed, species occurs in Middle

Kundan of Öland, Sweden. The weak exogastric curvature of the Late Cambrian *Palaeoceras mutabile* and its relatives from China is regarded as a doubtful criterion for its relationship to the Bassleroceratidae (see Flower 1964, Chen *et al.* 1979*a*,1979b). The weakly endogastric or exogastric curvature of the primitive nautiloids was probably of little adaptive value, as suggested by the high intrapopulation variability in various Silurian and Devonian oncoceratids.

A fairly rich ellesmeroceratid assemblage, including markedly coiled brevicones, was described by Flower (1964*a*) from the Early Tremadocian Smith Basin Limestone of New York. Flower distinguished ca. 30 species in this assemblage but I believe that there are only four biospecies present, i.e. *Ellesmeroceras* (= *Ectenolites*) *penecilin* (Flower, 1964) with long and straight shell, *Eremoceras progressum* (Flower, 1964) with short and straight shell, *Walcottoceras praenuntium* (Flower, 1964) with annulate and slightly endogastrically curved shell, and *Oneotoceras infundibulum* (Flower, 1964) with short and considerably endogastrically curved shell. A revision of the topotype material is needed.

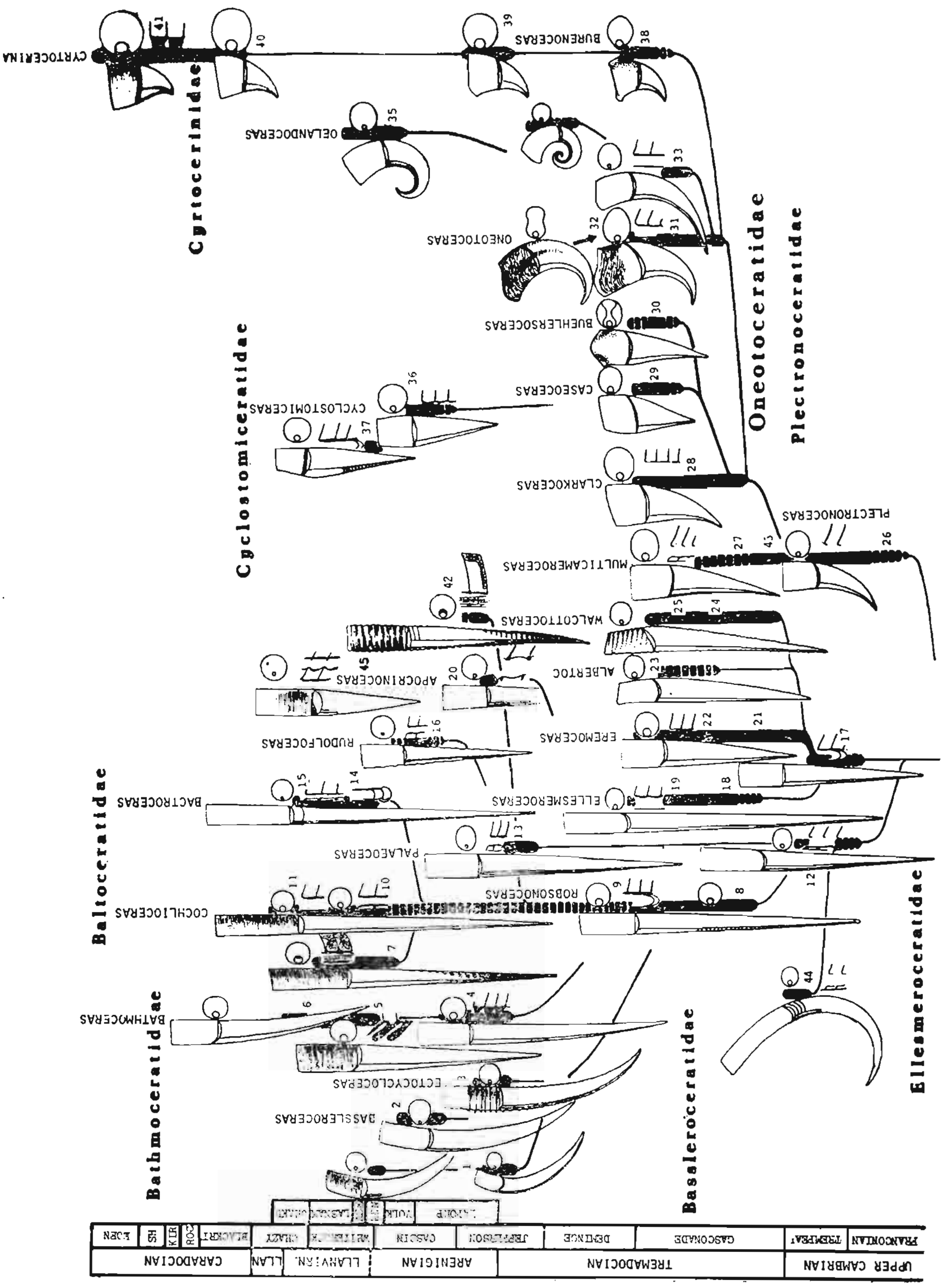
The ellesmeroceratid genus *Oneotoceras* is here placed in the Oneotoceratidae fam. n. This family includes several homeomorphs of the Discosorida and Endoceratina. The best preserved assemblage of the primitive, Early Tremadocian oneotoceratids was described by Flower (1964) from the Tanyard Formation, Texas, mostly on the basis of non-oriented polished sections of single specimens. Flower distinguished ca. 30 biospecies but only two seem to be sufficiently substantiated, i.e. *Oneotoceras* (= *Barnesoceras*) *clavatum* (Flower, 1964) with rather short and endogastrically markedly curved shell, and *Oelandoceras* (= *Woosteroceras*) *spirale* (Flower, 1964) with longer and slightly curved shell. Non-oriented phragmocone sections described under the generic names *Muriceras* and *Microbaltoceras* may belong to *O. spirale*. The smallest of these sections are less than 1 mm in diameter (Flower 1964*a*: pl. 15: 1, pl. 14: 1-3), indicating that the protoconch of *O. spirale* was not larger than that of typical orthoceratids, bactritids, or ammonoids.

Most known Ordovician oneotoceratids have been described from single, poorly preserved, and doubtfully dated specimens (Ulrich *et al.* 1943, Flower 1964*a*). The early stages of their evolution can therefore be reconstructed only tentatively using some morphological trends

Fig. 2

Hypothetical phylogenetic relationships among members of the suborder Ellesmeroceratina; 1 *Bassleroceras annulatum* Teichert and Glenister; 2 *Bassleroceras acinacellum* (Whitfield), *B. perseus* (Billings), *Copiceras erectum* UFM and U; 3 *Ectocycloceras catalinae* Teichert and Glenister, *Kyminoceras foresti* Teichert and Glenister; 4 *Eothinoceras americanum* UFM and U, *E. maitlandi* Teichert and Glenister,? *Proterocameroceras contrarium* Teichert and Glenister; 5 *Bathmoceras complexum* Barrande, *B. linnarsoni* Angelin and Lindström; 6 *Bathmoceras norvegicum* Sweet; 7 *Cochlioceras roemeri* sp. n. (fig. 1a-c, f; pl. 1: 5-10); 8 *Pachendoceras huzzahense* UFM and U; 9 *Robsonoceras robsonense* (Walcott); 10 *Cochlioceras avus* Eichwald (fig. 1e, h; pl. 1: 1); 11 *Cochlioceras burchardi* (Dewitz) (fig. 1d, g; pl. 1: 2-4); 12. *Palaeoceras mutabile* Flower, *Balkoceras gracile* Flower, *Anhuiceras elongatum* Zou and Chen; 13 *Ellesmeroceras tchunense* Balaschov; 14 *Bactroceras avus* Holm; 15 *Bactroceras angustisiphonatum* (Rüdiger); 16 *Rudolfoceras cornuoryx* (Whitfield); 17 *Ectenolites primus* Flower; 18 *Ellesmeroceras scheii* Foerste, *Stemtonoceras elongatum* Ulrich and Foerste, 19 *Ectenolites subgracilis* Ulrich and Foerste; 20 *Apocrinoceras talboti* Teichert and Glenister; 21 *Ellesmeroceras progressum* Flower; 22 *Eremoceras syphax* (Billings); 23 *Albertoceras walcotti* Ulrich and Foerste; 24 *Walcottoceras monsense* (Walcott); 25 *Rudolfoceras praenuntium* Flower; 26 *Plectronoceras cambria* (Walcott), *P. liaotungense* Kobayashi; 27 *Multicameroceras multicameratum* (Kobayashi), *Wanwanoceras peculiare* Kobayashi, *Sinoeremoceras wanwanense* (Kobayashi); 28 *Boreoceras washburni* Miller and Youngquist, *Dakeoceras normale* Ulrich and Foerste, *Clarkoceras newtonwinchelli* (Clarke); 29 *Caseoceras contractum* UF and M; 30 *Buehlersoceras compressum* UF and M; 31 *Barnesoceras clavatum* Flower, *Levisoceras mercurium* (Billings); 32 *Oneotoceras loculosum* (Hall); 33 *Woosteroceras spirale* Flower, 34 *Beekmanoceras priscum* Ruedemann; 35 *Oelandoceras haelluddenense* Foerste = *O. byrunense* Foerste = *O. kristdalense* Foerste; 36 *Cyclostomiceras cassinense* (Whitfield); 37 *Pictetoceras eichwaldi* (Verneuil); 38 *Burenoceras pumilum* Ulrich and Foerste, *Conocerina brevis* Ulrich and Foerste; 39 *Cumberloceras buttsi* UF and M; 40 *Cyrtocerina typica* Billings; 41 *Cyrtocerina madisonensis* Miller, *C. crenulata* Flower; 42 *Protocycloceras lamarcki* (Billings), *Rhabdiferoceras planiseptatum* Hook and Flower; 43 *Eburoceras jiagouense* Zou and Chen; 44 *Sinoeremoceras zaozhuangense* Chen and Qi; 45 *Apocrinoceras* (?) sp. n.

within the family. The Oneotoceratidae may have derived from either *Plectronoceras* and *Multicameroceras*, with short, incurved shell, or *Eremoceras* with short straight shell. The latter possibility may be supported (and the former refuted) by the occurrence of swollen con-



necting rings in *Multicameroceras* (BALASCHOV 1962, CHEN *et al.* 1979). The Plectronoceratidae and Cyclostomiceratidae probably were less well adapted to pelagic life than the Ellesmeroceratidae and Baltoceratidae.

A small group of orthoconic inflated nautiloids is known from the Late Arenigian to Early Llanvirnian. It includes *Cyclostomiceras cassinense* (WHITFIELD, 1886) from the Fort Cassin Limestone of Vermont (ULRICH *et al.* 1943), and *Pictetoceras eichwaldi* (VERNEUIL, 1845) from the Kundan of Estonia. The morphology and internal structure of the latter species have been investigated by MUTVEI and STUMBUR (1971). I disagree with their reconstruction of *Pictetoceras* emphasizing the very large protoconch typical of the nautiloids with larval development entirely within an egg capsule. The available data on the apical parts of the ellesmeroceratid shell suggest a small planktonic larva, similarly as in ammonites (see ERBEN *et al.* 1968); and even if the larva of *Pictetoceras* developed within an egg capsule, the latter could not be as large as shown in MUTVEI and STUMBUR'S (1971) reconstruction.

The only Late Ordovician undoubted representative of the Ellesmeroceratina is *Conocerina* (FLOWER 1946, 1952*a*) commonly considered to be related to the Bathmoceratidae because of its considerably thickened connecting rings (FLOWER 1964). In my opinion, the morphological gap between the bathmoceratids and *Conocerina* is much too large to accept this hypothesis. *Conocerina* probably evolved from the Early Ordovician Oneotoceratidae with very short shell; however, any more precise comparison among these forms is impossible because of the unknown structure of their siphuncles (fig. 5). There are in the Arenigian of China (CHEN 1976) nautiloids with considerably curved but rather long shell, as well as with connecting rings resembling those of *Conocerina.*

Irianoceras antiquum KOBYASHI and BURTON, 1971, from New Guinea which was interpreted as an ancient representative of the Ellesmeroceratina (KOBAYASHI and BURTON 1971), is actually the phragmocone of a (?) Jurassic belemnite.

Proposed systematics. — In this and following chapters, the format of the "Treatise on Invertebrate Palaeontology" has been applied, i.e. the name of the type species follows the generic name; the lack of author's name means that the type species was designated in the same paper as the genus.

Ellesmeroceratidae KOBAYASHI, 1934

[= Balkoceratidae FLOWER, 1964; Yanheceratidae CHEN and QI, 1979]

Straight to a slightly curved, long, compressed shell.

Palaeoceras FLOWER, 1954; *P. mutabile*

[= *Balkoceras* FLOWER, 1964]

Siphuncle somewhat displaced from the shell wall; juvenile connecting rings swollen.

Ellesmeroceras FOERSTE, 1921; *E. scheii*

[= *Ectenolites* ULRICH and FOERSTE, 1936; *Stemtqnoceras* ULRICH and FOERSTE, 1936; *Tanycameroceras* CHEN and QI, 1979; *Eoectenolites* CHEN and QI, 1979; *Anhuiceras* ZOU and CHEN; 1979; *Dongshanoceras* ZOU and CHEN, 1979; *Eodiaphragmoceras* CHEN and QI, 1979; *Eoclarkoceras* CHEN and QI, 1979; *Weishanhuceras* CHEN and QI, 1979; *Aethoₗoxoceras* CHEN and QI, 1979; *Archendoceras* CHEN and QI, 1979]

Straight to slightly curved, elongated shell with marginal cylindrical siphuncle.

Eburoceras ZOU and CHEN, 1979; *E. jiagouense*

[= *Pseudendoceras* CHEN and ZOU, 1979; *Paraplectronoceras* QI and CHEN, 1979; *Yanheceras* CHEN and ZOU, 1979]

Long, endogastrically markedly curved shell; close to *Ellesmeroceras*.

Eremoceras HYATT, 1884; *Cyrtoceras syphax* BILLINGS, 1865

Relatively short shell.

Albertoceras ULRICH and FOERSTE, 1936; *A. walcotti*

Endogastrically slightly curved shell with tapering living chamber.

Walcottoceras ULRICH and FOERSTE, 1936; *Endoceras* (?) *monsensis* WALCOTT, 1924

Like *Albertoceras* but with annulated shell.

Baltoceratidae KOBAYASHI, 1935

Long, straight shell with circular cross section.

Robsonoceras ULRICH and FOERSTE, 1936; *Ellesmeroceras robsonensis* WALCOTT, 1924
[= *Pachendoceras* ULRICH and FOERSTE, 1936]
Relatively long shell, diaphragmate siphuncle.

Cochlioceras EICHWALD, 1860; *Orthoceras avus* EICHWALD, 1857
[= *Rioceras* FLOWER, 1964; *Metabaltoceras* FLOWER, 1964; *Protobaltoceras* TROEDSSON, 1937]
Relatively wide siphuncle with orthoceratid-like siphuncular deposits.

Bactroceras HOLM, 1898; *B. avus*
[= *Eobactrites* SCHINDEWOLF, 1932]
Narrow siphuncle.

Protocycloceratidae KOBAYASHI, 1935

Straight to endogastrically slightly curved, annulated shell with well developed siphuncular and cameral deposits.

Protocycloceras HYATT, 1900; *Orthoceras lamarcki* BILLINGS, 1859
[= *Catoraphiceras* ULRICH and FOERSTE, 1936; *Amsleroceras* HOOK and FLOWER, 1977; *Rangeroceras* HOOK and FLOWER, 1977; *Veneficoceras* HOOK and FLOWER, 1977; *Bakeroceras* HOOK and FLOWER, 1977; ? *Vassaroceras* ULRICH, FOERSTE, MILLER and UNKLESBAY, 1944]
Elongated shell with relatively wide siphuncle.

? ***Apocrinoceras*** TEICHERT and GLENISTER, 1952; *A. talboti*
Swollen connecting rings.

Ectocycloceras ULRICH and FOERSTE, 1936; *Orthoceras catalinae* BILLINGS, 1865
[= ? *Rudolfoceras* ULRICH, MILLER, FOERSTE and UNKLESBAY, 1944]
Relatively short shell with narrow siphuncle.

? ***Kyminoceras*** TEICHERT and GLENISTER, 1954; *K. foerstei*
[= ? *Diastoloceras* TEICHERT and GLENISTER, 1954]
Elongated shell, narrow cylindrical siphuncle.

Bathmoceratidae HOLM, 1889

Straight to slightly curved, long shell; thick connecting rings intruding the siphuncle.

Bathmoceras BARRANDE, 1867; *Orthoceras complexum*
[= *Eothinoceras* ULRICH, FOERSTE, MILLER and UNKLESBAY, 1944]

?Bassleroceratidae ULRICH, FOERSTE, MILLER AND UNKLESBAY, 1944

Elongated exogastrically curved shell with relatively narrow siphuncle.

Bassleroceras ULRICH and FOERSTE, 1936; *Orthoceras perseus* BILLINGS, 1865
[= ? *Dyscritoceras* ULRICH and FOERSTE, 1936; *Leonardoceras* FLOWER, 1968]
Shell compressed.

Plectronoceratidae KOBAYASHI, 1935

Endogastrically curved, compressed shell.

Plectronoceras ULRICH and FOERSTE, 1933; *Cyrtoceras cambria* WALCOT, 1913 (poorly known)

Multicameroceras KOBAYASHI, 1935; *Ellesmeroceras* (?) *multicameratum* KOBAYASHI, 1931
[= *Sinoeremoceras* KOBAYASHI, 1933; *Wanwanoceras* KOBAYASHI, 1933; *Protactinoceras* CHEN and QI, 1979; *Lunanoceras* CHEN and QI, 1979; *Recteseptoceras* TSOU and CHEN, 1979; *Physalactinoceras* CHEN and QI, 1979; ? *Jiaguoceras* CHEN and TSOU, 1979]
Relatively short, endogastrically slightly curved shell, wide siphuncle with considerably swollen connecting rings (cylindrical at adult stages).

Oneotoceratidae new family

Relatively short, compressed, endogastrically curved shell with cylindrical siphuncle.

Clarkoceras RUEDEMANN, 1905; *Piloceras newtonwinchelli* CLARKE, 1897
[= *Dakeoceras* ULRICH and FOERSTE, 1931; *Boreoceras* MILLER and YOUNGQUIST, 1947]
Short, compressed, endogastrically slightly curved shell.

Caseoceras ULRICH, FOERSTE and MILLER, 1943; *C. contractum*
Very short, almost straight shell.

Buehlersoceras ULRICH, FOERSTE and MILLER, 1943; *B. compressum*
Almost straight shell with laterally constricted aperture.
Oneotoceras ULRICH, 1926; *Cyrtoceras loculosum* HALL, 1861
[= ?*Levisoceras* FOERSTE, 1925; *Barnesoceras* FLOWER, 1964]
Endogastrically markedly curved, compressed shell.
Oelandoceras FOERSTE, 1932; *O. haelluddense*
[= ?*Beekmanoceras* ULRICH and FOERSTE, 1936; *Meikeloceras* FLOWER, 1971; *Woosteroceras* FLOWER, 1964]
Markedly curved or loosely coiled shell, with ovate cross section.
Burenoceras ULRICH and FOERSTE, 1931; *B. pumilum*
[= ?*Cumberloceras* ULRICH, FOERSTE and MILLER, 1943]
Very short, markedly curved shell with laterally constricted aperture.

Cyrtocerinidae FLOWER, 1946

Very short shell; thick connecting rings intruding into siphuncle.
Cyrtocerina BILLINGS, 1865; *C. typica*
?***Tangshanoceras*** CHEN, 1976; *T. endogastrum*

Cyclostomiceratidae FORSTE, 1925

Short, straight shell with circular cross section.
Cyclostomiceras HYATT in ZITTEL, 1900; *Gomphoceras cassinense* WHITFIELD, 1886
[= *Pictetoceras* FOERSTE, 1926; *Paracyclostomiceras* CECIONI, 1953]

Suborder **Endoceratina** TEICHERT, 1933

Diagnosis. — Very long septal necks coming close to or even intruding the preceding septum; cylindrical, ventral siphuncle filled in its apical part with diaphragms and/or calcareous deposits of "cone-in-cone" structure (endocones).

Remarks. — Long septal necks make the Endoceratina different from their ancestral Ellesmeroceratina as well as from all the other primitive nautiloids. The complete separation of the siphon from the chambers by the imperforate neck made cameral-liquid exchange probably difficult, causing the absence of cameral deposits.

Phylogeny (fig. 7). — The Endoceratina show rather vaguely defined morphological patterns and large intrapopulation variability in virtually all phenetic characters useful for taxonomic purposes. Most authors neglected this variability which resulted in an extreme taxonomic splitting of this group (see ULRICH *et al.* 1943, 1944; FLOWER 1952, 1958, 1964*b*, 1971; BALASCHOV 1968). MUTVEI (1964) was the first to realize the intrapopulation variability in the form of the siphuncular deposits of the endoceratids from the Baltic area but his observations have thus far remained neglected by other authors. MUTVEI's results are confirmed by my work on the endoceratids derived from Early Ordovician erratic boulders well dated by conodonts (see fig. 3b-j). There is variation not only in the endocones, but also in the length of septal necks (fig. 3k-l) and camerae (fig. 3n), as well as in siphuncle position. Research on endoceratid populations appears then as the only means to recognize their taxonomy and phylogeny.

The main diagnostic characters of the Endoceratina are their long septal necks and hence, the evolution of the necks is the key to endoceratid origin and phylogenetic relations. Neck length certainly was important for the mechanisms controlling cameral liquid exchange. In fact, other shell characters making the Endoceratina distinct among the Nautiloidea are to a considerable extent induced by the neck elongation. Long necks are known also in some modern cephalopods (*Aturia, Spirula*); liquid exchange in these cephalopods (exemplified by *Nautilus*) is of little importance (COLLINS *et al.* 1980; WARD and MARTIN 1978).

According to Flower (1964*a,b*), the ancestor of the Endoceratina is *Pachendoceras huzzahense* ULRICH and FOERSTE, 1931, from the Early Tremadocian Gasconade Dolomite of Missouri. The structure of its siphuncle is unknown but the siphuncular nucleus ends paraboloidally (ULRICH *et al.* 1944; pls 61, 64) suggestive of deeply concave diaphragms or even endocones. The endocones are probably at least in part related in origin to diaphragms, as indicated by the continuity between diaphragms and endocone layers in the primitive endoceratids (FLOWER 1964*b*: pl. 4: 14, 16; COLLINS 1971; TEICHERT and CRICK 1974); *Pachendoceras* may then represent the ancestral stage in endocone evolution. Other details in shell structure of that species have been discussed above. *Cotteroceras compressum* ULRICH and FOERSTE, 1936, from the Early Arenigian Cotter Dolomite of Missouri, resembles *Pachendoceras* in the structure of its spiculum, and may actually be its close relative. The phylogenetic relationship of both *Cotteroceras* and *Pachendoceras* to the Endoceratina can hardly be reliably evaluated, as there are no data available on the structure of their siphuncle. In fact, siphuncular deposits occur also in the typical Baltoceratidae. It is a matter of arbitrary decision whether these two forms will be assigned to the Ellesmeroceratina or to the Endoceratina, as the phylogenetic relationship between the two suborders appears unquestionable. *Proendoceras annuliferum* (FLOWER, 1941) from the Beekmantown of New York has been also placed in the Endoceratina. It is based on a fragment of nautiloid phragmocone with typically ellesmeroceratid siphuncular structure, found in a thin section taken from the Middle Tremadocian Beekmantown Limestone of New York (FLOWER 1941, 1953). It has been shown above that siphuncular deposits occur also in the ellesmeroceratids and hence, there is no reason to assign this species to the Endoceratina. The systematic position of the genus *Proterocameroceras* attributed traditionally to the Endoceratina also appears disputable. The oldest known representative of the genus, *Proterocameroceras sibiricum* BALASCHOV 1955, from the Tremadocian/Arenigian boundary of Siberia (BALASCHOV 1962), displays a very thick connecting rings and its septal neck attains only one third of chamber length. Its siphuncular deposits are much more strongly developed at the ventral side of the shell, and may actually resemble those of *Cochlioceras*. The type species *P. brainerdi* (WHITFIELD 1886) from the Arenigian Fort Cassin Limestone of Vermont, shows siphuncular deposits of typically endoceratid structure (ULRICH *et al.* 1944). Considerably elongate septal necks occur in *Loxochoanella warburtoni* TEICHERT and GLENISTER, 1954, and *Hemichoanella canningi* TEICHERT and GLENISTER, 1954, from the Early Arenigian Emanuel Limestone, Australia. The septal necks attain half chamber length (TEICHERT and GLENISTER 1954), just as in *Talassoceras kumyschtagense* BALASCHOV, 1960, from an imprecisely dated locality in Siberia. *Loxochoanella warburtoni*, *Thylacoceras kimberleyense*, and *Hemichoanella canningi* may actually represent different ontogenetic stages of a single species. Neck curvature would then have increased in ontogeny. The above discussed forms can be regarded as evolutionary intermediates between the Ellesmeroceratina and Endoceratina.

Unquestionable endoceratids with septal necks reaching each the preceding septum have been reported from the Early Arenigian upwards. The Latorpian Emanuel Limestone, Australia, yielded some primitive endoceratids, described by TEICHERT and GLENISTER (1954) under the generic names *Anthoceras*, *Lobendoceras*, *Ventroloboceras*, and *Notocycloceras*, but were so closely interrelated that as to belong possibly to a single species. A revision of the topotype material is needed. These forms show a straight, rather long, transversally annulated shell with marginal wide siphuncle. There is a deep lobe in the suture at the wall contact of the siphuncle. These forms, clustered around *Anthoceras decorum* TEICHERT and GLENISTER, 1954, may be ancestral to the other Endoceratina. The smallest shell diameter, recorded from the Emanuel Limestone, is 3.3 mm. Some species from Asia (BALASCHOV 1960, 1962) are also attributed to *Anthoceras*.

There are some forms in the Kundan (Early Llanvirnian) of the Baltic area and in the El Paso Limestone, New Mexico, that seem to be closely related to the Australian species *A. decorum*. BALASCHOV (1968) recognized three genera with seven species among the nautiloids from the Late Kundan. These shells are externally indistinguishable, transversely annulated and longitudinally striated, with variable cross section of the siphonal spiculum. In ZPAL collection there are specimens with spiculum intermediate in cross section between BALASCHOV's genera, which I collected from the coeval erratic boulders (fig. 4a-f, pl. 7-8) as well as from the Sukhrumägi section by Tallinn, Estonia. Presumably, one deals here with the single population of the species *Anthoceras vaginatum* (SCHLOTHEIM, 1820) exhibiting great variability in spiculum form, in close analogy to species described by MUTVEI (1964). The replacement of the specific name "*vaginatum* SCHLOTHEIM, 1820" by a new one cannot be justified by either the rules of ICZN or paleontological practice, despite lack of illustrations in SCHLOTHEIM's original paper. There is no ambiguity in its actual meaning. *A. vaginatum* is atypical of orthoconic nautiloids in its constancy in sutural undulation (fig. 7b). Its suture resembles the Early Arenigian Australian forms but is somewhat more complex. The specimens of *A. vaginatum* derived from boulder ZPAL E-079 show a slightly endogastrically curved shell (fig. 4, pl. 3: 7-8). The sample size is too small to determine whether this is an endmember of intrapopulation variability range, or an indication of phylogenetic relationship to *Cyrtendoceras estoniense* FOERSTE, 1932 (BALASCHOV 1962*b*). The latter species, described probably from the Late Kundan or Aserian, may or may not be a distinct taxon, and its revision is needed. "*Endocycloceras*" *gracile* FLOWER, 1964, from the El Paso Limestone, New Mexico (FLOWER 1964), is a little older than the above discussed forms but it is externally indistinguishable from them; whereas the only known specimen, from which FLOWER described this species and attributed it to the Ellesmeroceratina, has no internal structures preserved. A trend towards endogastrical coiling of the shell is well expressed in *Cyrtendoceras schmidti* HOLM, 1892, probably collected from the Aserian. Its siphuncular structure and cross section indicate close relationship to *A. vaginatum.* An endmember of this evolutionary lineage is represented by *Cyrtendoceras hircus* HOLM, 1892, from the Lasnamägian (Late Llanvirnian), with compressed, almost gyroconic shell (see HOLM 1892, FOERSTE 1932).

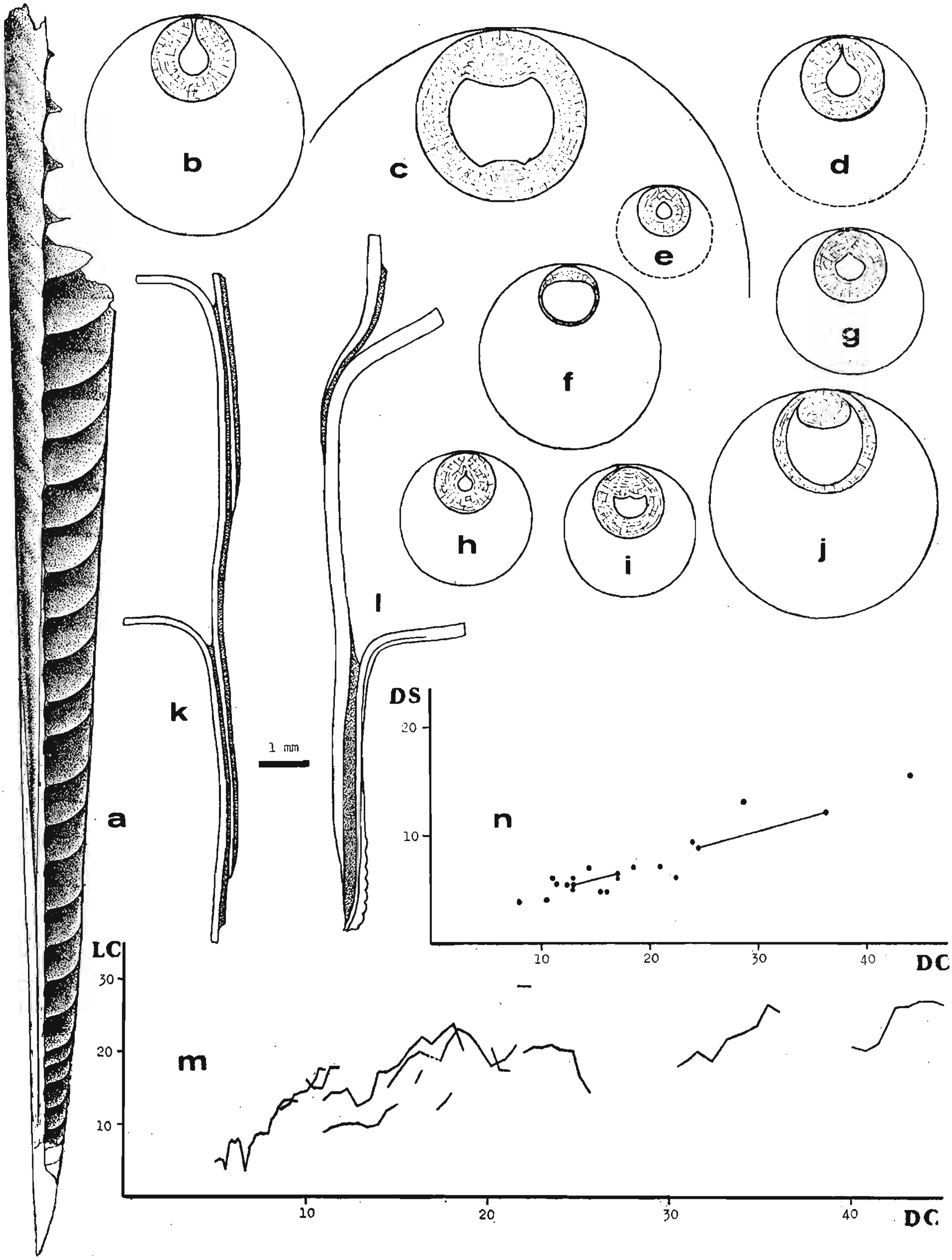
The endogastrically curved piloceratid shell resembles externally *Cyrtendoceras* but this morphological affinity is due to convergence rather than phylogenetic relationship. This is indicated by the completeness of the trend to increase shell curvature in *Cyrtendoceras* lineage above discussed, as well as by different shell proportions in the early Piloceratidae. Despite their long septal necks (ULRICH *et al.* 1944), the Piloceratidae resemble in their short and compressed shell the *Clarkoceras*-like ellesmeroceratids rather than the ancestral endoceratids with long shell of circular section. And yet the Piloceratidae appeared earlier than the typical Endoceratida, the oldest known piloceratid species, *Bisonoceras coniforme* FLOWER, 1964, occurs in the Middle Tremadocian. Furthermore, the Piloceratidae differ from the typical Endoceratina in their blunt spiculum indicative of the close relationship of the endocones to diaphragms (FLOWER 1964, ULRICH *et al.* 1943). One can, therefore, not reject the hypothesis that long septal necks arose independently in two lineages derived from distinct ellesmeroceratid groups: the typical Endoceratina and the Piloceratidae. In addition to *Bisonoceras*, early in occurrence but advanced in shell curvature, the Piloceratidae include also some weakly curved forms reported mostly from the Cassinian (Arenigian) of North America. There is a large number of established piloceratid taxa but these are most commonly of little biological value, as they have been erected on isolated siphuncular deposits. The best known piloceratid sample including complete specimens is from the Fort Cassin Limestone of Vermont (ULRICH *et al.* 1943). *Cassinoceras explanator* (WHITFIELD, 1886) (= *C. grande* ULRICH and FOERSTE, 1938), shows a large compressed shell with blunt apex suggestive of larval development within a large egg.

If the Piloceratidae were descendants of the typical Endoceratina, the transitional group may be the Manchuroceratidae with straight shell circular in cross section, and wide, bluntly ending siphuncle (BALASCHOV 1968, CHANG 1965, CHEN 1976, CHEN and LIU 1977, KOBAYASHI 1977). The considerable variation observed in the spiculum of the Manchuroceratidae probably reflects intraspecific variability. This group is probably related to the primitive endoceratids through the somewhat more slender *Coreanoceras.* To recognize their phylogenetic relationships, however, more data on their shell structure and variability are needed.

An isolated position within the Endoceratina is occupied by the Intejoceratidae reported thus far exclusively from Siberia. I was able to study the Intejoceratidae collected by Dr. F. A. ZHURAVLEVA (Paleontological Institute, Moscow). These are nautiloids with wide, subcentral siphuncle and conical, moderately elongated shell. There is an ontogenetic increase in the relative siphuncle diameter. As judged from the preserved fragments, the shell apex is rather pointed (fig. 7: 13). There is no specimen with well preserved siphuncle which results in divergent opinions on the length of the septal necks (BELASCHOV 1962); there is little doubt, however, that these necks are rather short. The most characteristic feature of the intejoceratids is the nature of their siphuncular deposits. These are composed of radial plates, preserved in the form of flat calcite crystals running along and intruding the siphuncle. A secondary, diagenetic modification of this structure cannot be refuted. The intejoceratids have been reported only from isolated localities attributable to the Vichorevsky horizon (*Intejoceras, Evencoceras, Bajkaloceras*) or the Krivoluksky horizon (*Padunoceras*), but hardly referrable at the moment to the European or North American stratigraphic standards. They range probably from the Early Arenigian to Late Llanvirnian. The oldest known intejoceratid assemblage, collected at Rožkovo village on Angara (BALASCHOV 1962), includes forms variable in the thickness of the endocone plates. The assemblage was attributed to some species of the genera *Intejoceras* and *Bajkaloceras*, but should probably be considered as a single population. The irregular segmentation of the vertical plates in "*Bajkaloceras*" is probably secondary, as judged from their irregular formation and diagenetic fracturing. "*Padunoceras*" *rugosaeforme* BALASCHOV, 1960, is probably the youngest known species of *Intejoceras*; its specific distinctness can hardly be evaluated, as the description is based on an isolated siphuncle. FLOWER'S (1976) assessment that *Padunoceras* and *Evencoceras* are typical endoceratids close to *Rossoceras* (? = *Proterovaginoceras*) is precarious. FLOWER did not demonstrate that "*Rossoceras*" has longitudinal plates in the siphuncle; furthermore, the siphonal position within the shell is unknown since the species has been erected on a single isolated siphuncle. Such plates can, however, develop by recrystallization as exemplified by the formation of similar structures due to silicification (TEICHERT and CRICK 1974, WADE 1977*b*).

The core of the suborder Endoceratina consists of the family Endoceratidae including all the typical ortho- and longiconic endoceratids. The main diagnostic character for endoceratid species and genera is the structure of the embryonic shell. Unfortunately, it has been recognized in only a few species. Other characters such as spiculum form or septal neck length, are so variable within a single species that they can be of taxonomic value only after their intrapopulation variability is known.

In the Baltic area, the Endoceratidae appeared in the Latorpian (Early Arenigian) together with neritic limestone facies. The oldest forms are known from some shell fragments unidentifiable specifically described as *Dideroceras leetsense* BALASCHOV, 1968. The endoceratids become common in the Volkhovian. Some fragmentary, poorly preserved, only insignificantly differing in morphology endoceratid specimens have been reported from the Volkhovian of Estonia and Leningrad region (BALASCHOV 1968). They show longer air chambers than the Latorpian forms. The oldest specific name applied to the Volkhovian endoceratids is *Endoceras glauconiticum* HEINRICHSON, 1935. Abundant endoceratids occur in erratic boulders attributable to the "untere rothe Vaginatenkalk" which is time equivalent to the Volkhovian. These boulders, derived probably from the central part of the Ordovician epicontinental sea basin (maybe from Västergotland, Sweden), contain an abundant pelagic fauna like those typical of all cephalopod limestones throughout the fossil record. The endoceratid species found in these boulders does not differ from the Estonian material of *Dideroceras glauconiticum* (see HEINRICHSON 1935, BALASCHOV 1968). *D. glauconiticum* has a moderately long shell with long air camerae (pl. 2). The length of the septal necks is one third of camera length but highly variable (fig. 3k-1). The siphuncle is variable in diameter (fig. 3b-j). The spiculum is most commonly drop-like in cross-section; calcification commenced at the dorsal and lateral



sides. A small proportion of specimens with spiculum invaginated ventrally or both dorsally and ventrally, occurs in a population of *D. glauconiticum* collected from a single boulder of the *P. originalis* Zone (sheet from the Opatów cloister, Holly Cross Mts, collection of Professor J. SAMSONOWICZ, IG). The spiculum is here lunate or H-shaped in cross section (fig. 3c, i, j). This fits well with MUTVEI's (1964) observations on the wide variability in spiculum form in the endoceratids. I have not found any apical shell parts in *D. glauconiticum*. The narrowest siphuncular fragment is 1.8 mm in diameter (pl. 2: 7). "*Nanno*" *pygmaeum* (HOLM, 1897, from the Grå Vaginatumkalk (Kundan, hence younger than *D. glauconiticum*), is the only known apical part of the endoceratid siphuncle with equally small non-camerate protoconch. *D. glauconiticum* may have a protoconch of *Suecoceras*-type, that is with camerae beginning at the very apex, as well. Regardless of the structural details, the larval shell of *D. glauconiticum* is certainly much smaller than in later endoceratids. I have found several specimens out of the known variability range of *D. glauconiticum* in boulders of the same lithology. One of these shows an unusually elongate spiculum with deep, dorsal invagination (fig. 3j; pl. 3: 6); this may be an extreme endmember. Another endoceratid specimen shows an unusually narrow siphuncle with long, cylindrical, *Suecoceras*-like septal necks (fig. 5f; pl. 4: 4). This phragmocone may be related to "*Nanno*" *fistula* HOLM, 1896, from the Grå Vaginatumkalk. Its dating is vague, it is not younger than Aserian, possibly Kundan, time-equivalent to the Grå Vaginatumkalk.

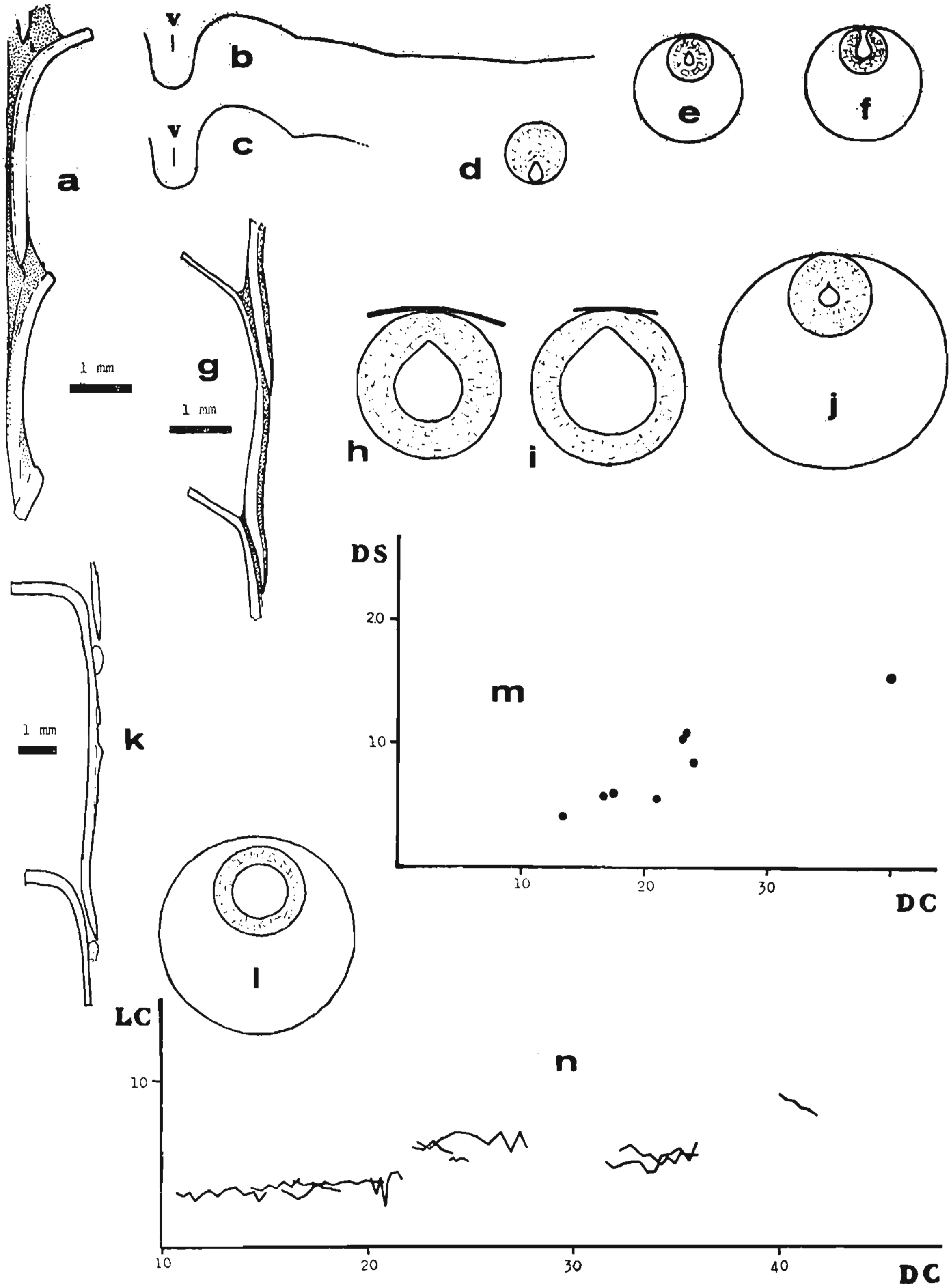
The wide-siphunculate form Endoceratidae gen. et sp. indet. TEICHERT and GLENISTER, 1954, from the Volkhovian Gap Creek Formation, Australia, may be closely related to *D. glauconiticum*. Erratic boulders of the *A. variabilis* Zone (Early Kundan) contain an endoceratid sample (6 specimens) with relatively short septal necks (only slightly overlapping with the preceding segment), much shorter air chambers than in *D. glauconiticum*, and spiculum circular in cross section (fig. 4k-n; pl. 3: 3-5). They do not differ in camera length from *Cameroceras lasnamaense*, as described by BALASCHOV (1968). The other characters do not differ from other *Cameroceras* and *Endoceras*. "*Cameroceras lasnamaense*" from the Early Kundan gave probably rise to *Endoceras incognitum* SCHRÖDER, 1881, with still shorter camerae and larger apical angle, recorded from the Lasnamägian to Aserian. As illustrated by HOLM (1897), only *Suecoceras*-type protoconchs (*S. dux*, *S. recurvum*) occur in the endoceratids recorded in the Röd Lituitkalk (Aserian), similar in shell outline to *E. incognitum*; these protoconchs are more distinctly separated from the post-larval shell than in *Suecoceras papilla*. The species from the Röd Lituitkalk is probably ancestral to later typical species of *Endoceras* as well as to the wide-siphunculate *Endoceras damesi* DEWITZ, 1880 (? = *Palaeocyclendoceras eichwaldi* BALASCHOV, 1968). A lineage with wide siphuncle off the shell wall branched in the Middle Caradocian from the typical *Endoceras* lineage. This group is widely but superficially known. It persisted along with the main *Endoceras* group up to the end of the Ordovician. There are also some earliest Silurian endoceratids (BLAKE 1882). The *Endoceras* species resemble very closely the ellesmeroceratid genus *Cochlioceras* in the pattern of pedal retractors (SCHRÖDER 1881).

The earliest endoceratid species with septal necks reaching to mid-length of the preceding neck is probably "*Nanno*" *fistula* HOLM, 1896, from the Kundan or Volkhovian. In the Late Kundan, this group is represented by *Dideroceras wahlenbergi* FOORD, 1887, with spiculum

Fig. 3

Dideroceras glauconitum (HEINRICHSON, 1935); *P. originalis* Zone, Volkhovian; *a* Reconstruction of apical part of the phragmocone; b-j section through apical part of a shell, ×2; *b* ZPAL N/032 (pl. 2:6), boulder E-222, Międzyzdroje, Poland; *c* IG 8. II. 256; *d* ZPAL N/031, boulder E-116, Rozewie, Poland; *e* IG 8. II. 256a; *f* ZPAL N/040, boulder E-228, Międzyzdroje; *g* ZPAL N/039 (pl. 2: 5), same boulder; *h* ZPAL N/033, boulder E-116, Rozewie; *i* ZPAL N/030 (pl. 2: 3) same boulder; *j* ZPAL N/087, boulder E-104, Międzyzdroje; *k-l* section through siphuncle; *k* IG 8. II. 256b; *l* IG 8. II. 264 (pl. 2: 9); *m* relative growth of air chamber length (LC) and shell diameter (DC) in a population; *n* relative growth of siphuncle diameter (DS) and shell diameter (DC).

highly variable but most commonly ovate in cross section (MUTVEI 1964). Closely related forms, like "*Schmidtoceras kundense* BALASCHOV, 1968", occur in erratic boulders as well as in Estonia (fig. 4g-j; pl. 3: 1-2). Their spiculum is most commonly drop-like in cross section (5 specimens from the erratic boulders), showing an affinity to *D. glauconiticum*.



The genus *Suecoceras*, including forms with very slender shell, long septal necks, and inflated embryonic shell with camerated apical part (fig. 5a; pl. 4: 1), appears for the first time in the Aserian (HOLM 1897, BALASCHOV 1968). It evolved probably from *D. glauconiticum*; its long camerae and deep septa are suggestive of a similar mode of life (cf. WESTERMANN 1980). All the investigated specimens from the erratic boulders of Poland, as well as from Estonia and the Leningrad region (BALASCHOV 1968) have spiculum with ovate cross section (fig. 8a; pl. 4: 2-5). Protoconch of *S. holmi* PATRUNKY, 1926 exceed 11 mm in diameter (HOLM 1897; NEBEN and KRUEGER 1971; pl. 4: 5 in this paper).

"*Orthoceras*" *novator* BARRANDE, 1868 recorded by BARRANDE (1868, 1877) from the Llanvirnian Šarka Formation of Bohemia differs from Baltic endoceratids and orthoceratids in very wide subcentral siphuncle. Its poor preservation precludes taxonomic identification. One may only suppose that it was related to *Suecoceras*, whose siphuncle was sometimes considerably distant from the shell wall, or to the Siberian intejoceratids.

"*Nanno*" *fistula* HOLM, 1896, may be ancestral to the genus *Proterovaginoceras* with very long septal necks covering entirely each the preceding siphuncular segment. "*Nanno*" *pygmaeum*, "*Nanno*" *fistula*, and *Proterovaginoceras bellemnitiforme* HOLM, 1885, probably belong to a single lineage with a trend towards increased protoconch size. In the latter species, known from the Aserian of Baltic region (HOLM 1897; BALASCHOV 1968), the protoconch diameter ranges from 18.0 to 22.5 mm (mean 20.1; measured 16 specimens from the collection of Naturhistoriska Riksmuseet, Stockholm). Closely related form from the Folkeslunda limestone of Öland (Lasnamägi) shows range of variability of the protoconch size from 25.0 to 29.0 mm.

FLOWER (1955*a*, 1955*b*, 1958, 1971, 1974, 1976) described an abundant endoceratid fauna from the Whiterockian (equivalent to Late Volkhovian to Early Uhakuan; Llanvirnian) and Chazyan (Late Uhakuan to Early Kukrusean; Late Llanvirnian to Llandeilo) of North America. He established several species and genera based mostly on isolated siphuncle and shell fragments and, hence, insufficiently documented. The large variability observed in cross section of the spiculum certainly reflects intraspecific variability. Several species and genera (e.g. *Williamsoceras*, *Cacheoceras*, *Kiotoceras*, *Najaceras*) have been erected on single specimens collected from isolated exposures. The available data on the septal necks are scarce but suggest the occurrence of both *Endoceras* (short necks, e.g. *Trinitoceras* from the Whiterockian, *Chazyoceras* from the Chazyan) and *Proterocameroceras* (long necks, e.g. *Najaceras* from the Whiterockian, *Emmonsoceras* from the Chazyan). All these endoceratids show a *Nanno*-type protoconch with its apical part filled entirely with siphuncle. The best known protoconch species, *Nanno novemboracum* RUEDEMANN, 1906, from the Chazyan Valcour Limestone (FLOWER 1941, 1955*a*, 1958), possibly identical to *N. aulema*, co-occurs with the phragmocones *Vaginoceras oppletum* RUEDEMANN, 1906, with slightly overlapping septal necks, thick connecting rings, and spiculum with drop-like cross section. *Nanno* is therefore not synonymous with *Proterovaginoceras*. It should be considered either as synonymous with *Endoceras*, or taxonomically distinct. The

Fig. 4

Anthoceras vaginatum (SCHLOTHEIM, 1820); *a* Section through a siphuncle, ZPAL N/023, boulder E-079, *E. pseudoplanus* Zone, Kundan, B IIIγ, Mochty, Poland; *b* septal suture, ZPAL N/022 (pl. 3: 7), same boulder; *c* septal suture, ZPAL N/017 (pl. 3: 8), *A. variabilis* Zone (?), B IIIβ; *d* section through a siphuncle, ZPAL N/023, boulder E-079 (see above); *e* section through apical part of shell, ZPAL N/021, same boulder; *f* section through apical part of a shell, ZPAL N/022 (pl. 3: 7), same boulder. *Dideroceras kundense* (BALASCHOV, 1968); *g* Section through a siphuncle, IG 137. II. 43 (pl 3: 3), erratic boulder, Kundan (?), Świebodzice, Poland; *h* section through a siphuncle, ZPAL N/063a; boulder E-079, Mochty, Poland, *E. pseudoplanus* Zone, Kundan, B IIIγ; *i* section through an isolated siphuncle, ZPAL N/063b, same boulder; *j* section through a shell, ZPAL N/062, same boulder. *Dideroceras wahlenbergi* (FOORD, 1887); *k* Section through a siphuncle, ZPAL N/045 (pl. 3: 4), boulder E-096, *A. variabilis* Zone, Kundan, B IIIβ, Zgierz, Poland; *l* section through shell of the same specimen; *m* relative growth of siphonal diameter (DS) and shell diameter (DC) in a sample from erratic boulder, *A. variabilis* Zone; *n* relative growth of air chamber length (LC) and shell diameter in the same sample.

endoceratids maintained a large embryonic shell ("*Foerstellites*") up to the very end of their stratigraphic range. Specimen of *Rossiceras* from the Late Ordovician of Kallholn, Sweden from the collection of Naturhistorska Riksmuseet, Stockholm has embryonic shell 22.5 mm in diameter.

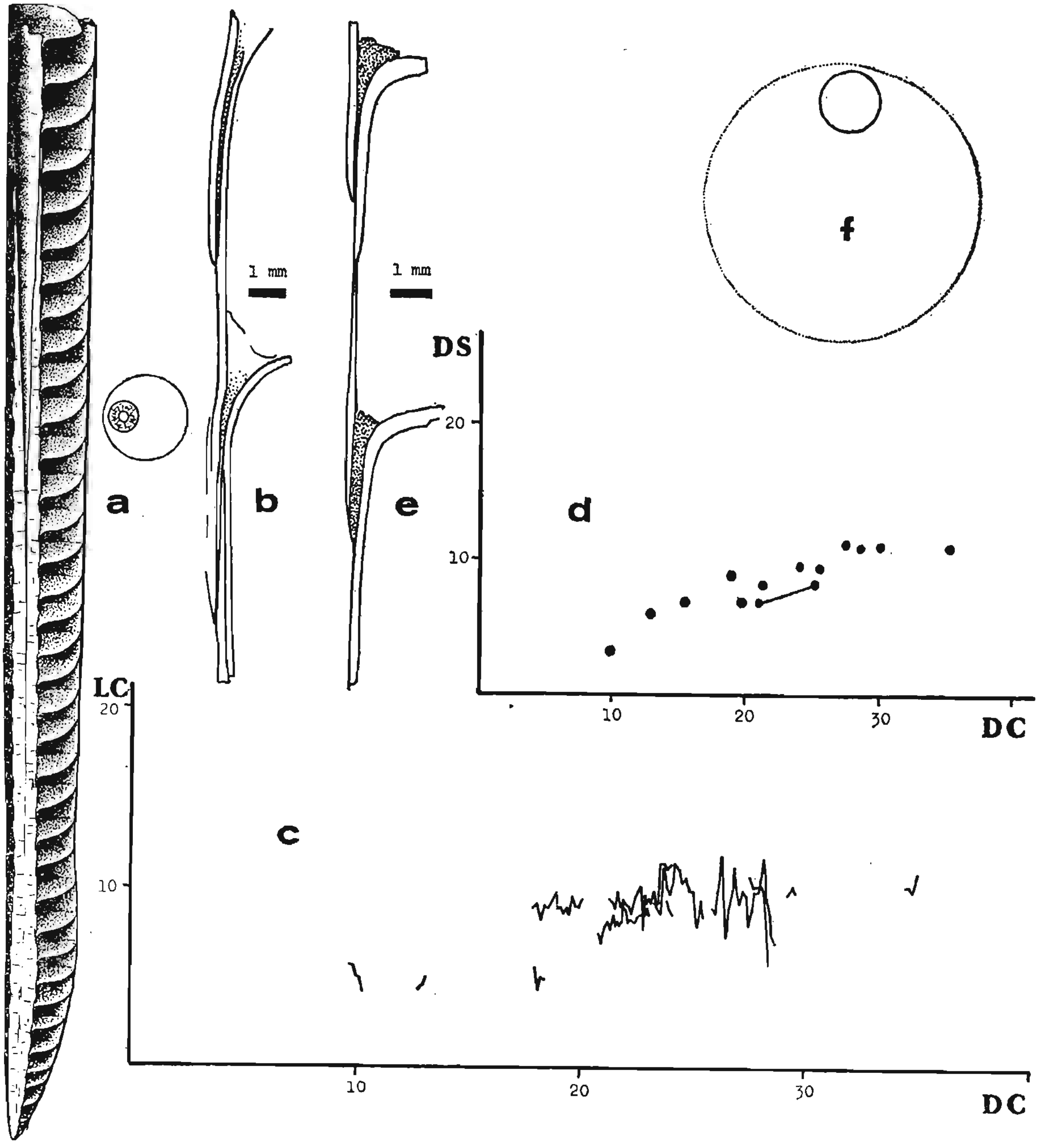


Fig. 5

Suecoceras holmi (PATRUNKY, 1926); *a* Reconstruction of longitudinal section through apical part of the shell, mostly from the specimen ZPAL N/071 (pl. 4: 3); *b* section through a siphuncle, ZPAL N/079, erratic boulder, Orłowo, Poland; *c* relative growth of air chamber length and shell diameter in a population from the *E. reclinatus* Zone; *d* relative growth of siphuncle diameter (DS) and shell diameter (DC) in the same population. *Suecoceras* (?) sp.; ZPAL N/083 (pl. 4: 4), dark-cherrish limestone with iron oolites, Volkhovian or Kunda Stage (?); *e* section through the siphuncle; *f* reconstruction of section through the shell (see pl. 4: 4).

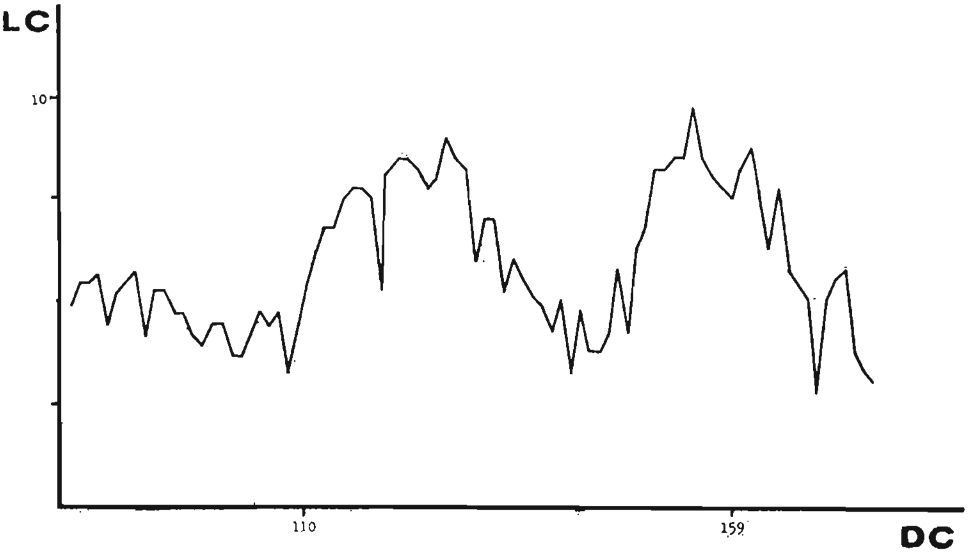


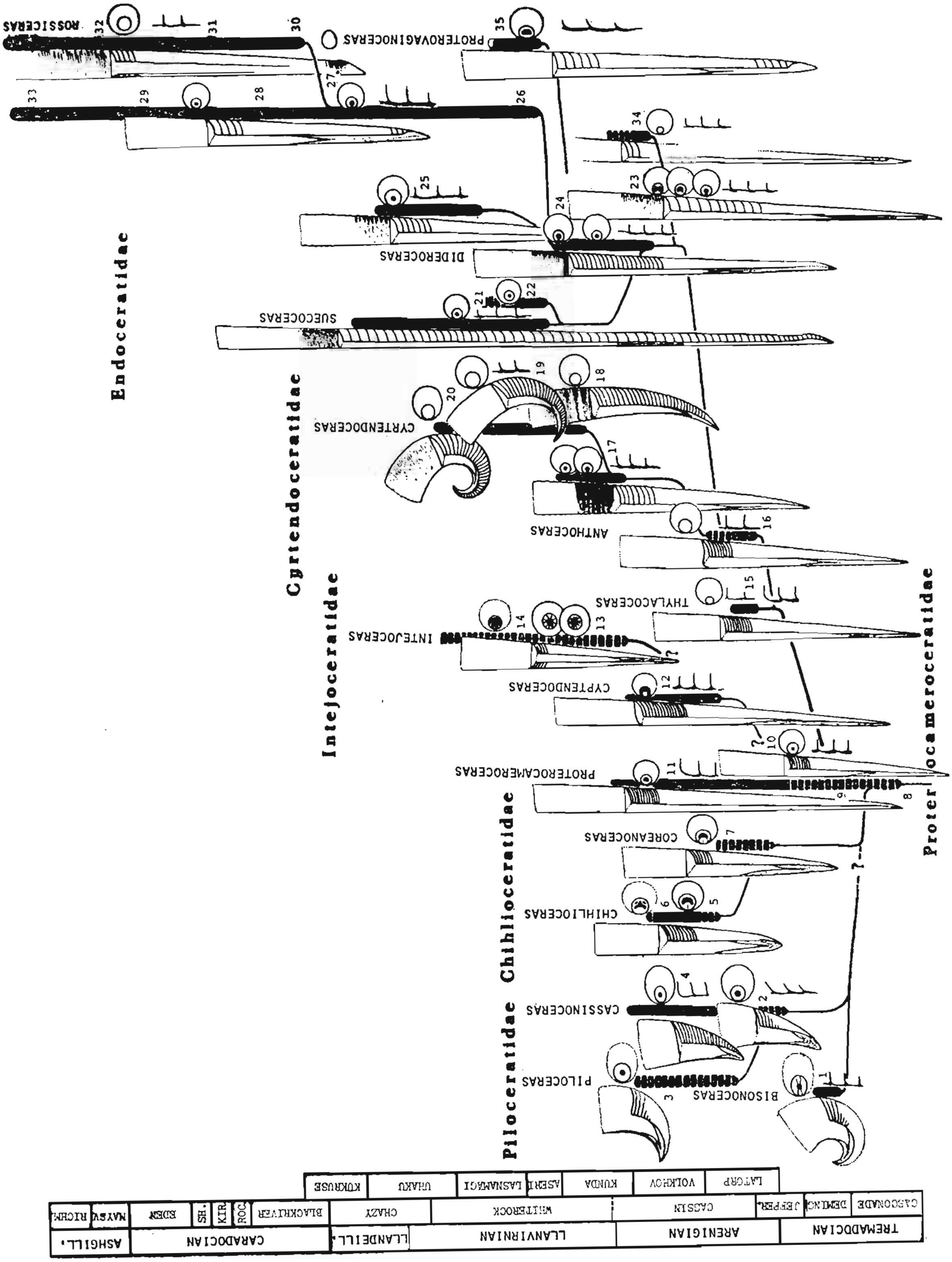
Fig. 6
Ontogenic growth in air chamber length in "*Cameroceras alternatum* FLOWER, 1968"; after FLOWER 1968*b*, pl. 3: 7; Black River Limestone, St. Raymond, Quebec.

There is without doubt an evolutionary trend towards increased protoconch size in the Endoceratina. The ancestral protoconch was probably a spherical embryonic shell associated with an cylindrical larval shell, typical of the ancestral Ellesmeroceratina. One can not say whether the larval development became confined to an egg capsule prior to or after the evolutionary formation of long septal necks. The endoceratid ova containing more and more yolk must have finally attained some centimeters in length and over 30 millimeters in diameter. Those large eggs must have been laid in small numbers and within a specialized egg capsule. One can hardly imagine how this could be done without some complex behavioral adaptations including an appropriate attachment or concealment of the eggs, and possibly also development of parental care. One may conclude that the Endoceratina differed from their associated Orthoceratida in their reproductive strategy; the latter nautiloids were producing a large number of planktonic eggs, while the former were laying only a few very large eggs.

The course of endoceratid ontogeny can be tentatively inferred from the length of the camerae. I am referring to a pattern of camera length in single shells, common among the Ordovician orthoconic nautiloids, as exemplified by *Dideroceras glauconiticum* (fig. 3) and the associated *Geisonoceras* sp. (fig. 33d). This pattern consists in a slight increase in septal density every 200 mm in shell length. My own data from the erratic boulders may be disputable but the pattern is very clearly shown by "*Cameroceras alternatum* FLOWER, 1968" (diagnosed by irregular spacing of septa in the only known specimen) showing three distinct cycles in spacing over the total distance of 580 mm. The specimen increases from 110 up to 159 mm in shell diameter between the two last peaks in septal density. The observed undulations may reflect a biological rhythm, controlled by either spawning, or seasonal changes. Neither the rate of cephalopod shell formation of some 200 mm per year, nor the cephalopod life span of a few years seem to be unacceptable (see MARTIN *et al.* 1979; COLLINS *et al.* 1980). The seasonal rather than spawning control of the recorded rhythm is suggested by the occurrence of the discuseed pattern also at the juvenile stages, whereas sexual maturity is usually attained by mollusks only after completion of the shell.

The weight of the siphuncular deposits is not sufficient for a hydrostatic equilibrium of the endoceratid shell. The absence of interconnection between the siphonal tissue and the chambers made impossible any efficient exchange of the cameral liquid in the endoceratid phragmocone.

The camerae must therefore have been filled up with a constant proportion of air and cameral liquid; the shell probably maintained a horizontal position. The cameral-liquid exchange goes on very slowly also in Recent *Nautilus* without having any significant effect on the animal's ability to move vertically (WARD 1979; COLLINS *et al.* 1980). The absence of intense exchange



of the cameral liquid has caused the complete lack of cameral deposits in the Endoceratina. In this respect Endoceratina differ significantly from other early nautiloids.

Proposed systematics. —

?Proterocameroceratidae Kobayashi, 1937

Orthocones with well developed endocones and short septal necks; arbitrarily assigned to the Endoceratina.

Proterocameroceras Ruedemann, 1905; *Orthoceras brainerdi* Whitfield, 1886
[= ?*Paraendoceras* Ulrich and Foerste in Foerste, 1936; *Proendoceras* Flower, 1955; *Loxendoceras* Collins, 1971; *Clitendoceras* Ulrich and Foerste, 1936]
Long spiculum.

?***Pachendoceras*** Ulrich and Foerste, 1936; *Cameroceras huzzahense* Ulrich and Foerste, 1931
[= ?*Cotteroceras* Ulrich and Foerste, 1936; *Dartonoceras* Flower, 1964]
Wide-angular endocones (diaphragms ?); possibly synonymous to *Robsonoceras* (Baltoceratidae).

?***Cyptendoceras*** Ulrich and Foerste, 1936; *C. ruedemanni*
Siphuncular deposits exclusively at the ventral side of shell; possibly attributable to the Baltoceratidae.

Piloceratidae Miller, 1889

Compressed brevicones with wide-angular endocones passing into diaphragms.

Piloceras Salter in Murchison, 1859; *P. invaginatum*
Endogastrically curved shell; poorly known.

Bisonoceras Flower, 1964; *B. coniforme*
[= *Disphenoceras* Flower, 1964]
Considerably endogastrically curved shell; poorly known.

Cassinoceras Ulrich and Foerste, 1936; *Piloceras explanator* Whitfield, 1886
Very short, almost straight shell.

Cyrtendoceratidae Hyatt in Zittel, 1900

Long, straight to endogastrically curved shell with septal necks elongated but not reaching the preceding septum

Thylacoceras Teichert and Glenister, 1952; *T. kimberleyense*
[= *Hemichoanella* Teichert and Glenister, 1954; *Loxochoanella* Teichert and Glenister, 1954; *Lebetoceras* Teichert and Glenister, 1954; *Talassoceras* Balaschov, 1960; ?*Loxochoanella* Teichert and Glenister, 1954]
Straight and smooth shell with narrow siphuncle and septal necks reaching approximately to mid-length of preceding chamber.

Fig. 7

Hypothetical phylogenetic relationships among members of the suborder Endoceratina; 1 *Bisonoceras corniforme* Flower; 2 *Cyrtendoceras carnegiei* Teichert and Glenister; 3 *Piloceras invaginatum* Salter; 4 *Cassinoceras explanator* (Whitfield); 5 *Manchuroceras wolungense* Kobayashi; 6 *Chihlioceras nathani* Grabau; 7 *Coreanoceras kemipoense* Kobayashi; 8 *Pachendoceras huzzahense* Ulrich and Foerste; 9 *Proendoceras annuliferum* (Flower); 10 *Paraendoceras jeffersonense* Ulrich and Foerste; 11 *Proterocameroceras brainerdi* (Whitfield), *Clitendoceras saylesi* Ulrich and Foerste; 12 *Cotteroceras compressum* Ulrich and Foerste; 13 *Intejoceras angarense* Balaschov, *Bajkaloceras angarense* Balaschov; 14 *Padunoceras rugosaeforme* Balaschov; 15 *Thylacoceras kimberleyense* Teichert and Glenister, *Hemichoanella canningi* Teichert and Glenister, *Lebetoceras oepiki* Teichert and Glenister; 16 *Anthoceras decorum* Teichert and Glenister, *Lobendoceras emanuelense* Teichert and Glenister; 17 *Anthoceras vaginatum* (Schlotheim) = *Paracyclendoceras cancellatum* (Eichwald) = *Paracyclendoceras compressum* Balaschov = *Protocyclendoceras balticum* Balaschov = *Protocyclendoceras iruense* Balaschov = *Lobocyclendoceras kundense* Balaschov = *L. buchi* (Lesnikova) (fig. 4a-f; pl. 3: 7-8); 18 *Cyrtendoceras remelei* Foerste, *Cyclocyrtendoceras estoniense* (Foerste); 19 *Endoceras* (*Cyrtocerina*) *schmidti* Holm; 20 *Cyrtendoceras hircus* (Holm); 21 *Suecoceras holmi* Patrunky (fig. 5a-d; pl. 4: 1-7); 22 *Suecoceras barrandei* (Dewitz); 23 *Dideroceras glauconiticum* (Heinrichson) (fig. 3a-n; pl. 2: 1-9); 24 *Dideroceras wahlenbergi* (Foord) (fig. 4k-n, pl. 3: 4-6), *Schmidtoceras kundense* (Balaschov) (fig. 4g-j; pl. 3: 1-3); 25 *Endoceras damesi* Dewitz, *Palaeocyclendoceras eichwaldi* Balaschov; 26 *Endoceras incognitum* Schröder (pl. 3: 9), *Cameroceras lasnamaense* Balaschov; 27 *Chazyoceras valcourense* Flower, *Vaginoceras oppletum* Ruedemann, *Nanno aulema* Ruedemann, *Nanno novemboracum* Ruedemann; 28 *Endoceras proteiforme* Hall, *Vaginoceras multitubulatum* (Hall), *Nanno kingstonense* Whiteaves; 29 *Cameroceras vertebrale* Eichwald, *Cameroceras trentonense* Conrad; 30 *Rossiceras idaverense* Balaschov; 31 *Endoceras abundum* (Miller); 32 *Rossiceras hasta* (Eichwald), *Endoceras megastoma* Eichwald; 33 *Foerstellites faberi* (Foerste); 34 *Nanno fistula* Holm; 35 *Proterovaginoceras bellemnitiforme* (Holm).

Anthoceras Teichert and Glenister, 1954; *A. decorum* Teichert and Glenister, 1954
[= *Ventroloboceras* Teichert and Glenister, 1954; *Lobendoceras* Teichert and Glenister, 1954; *Notocycloceras* Teichert and Glenister, 1954; *Paracyclendoceras* Balaschov, 1968; *Protocyclendoceras* Balaschov, 1968; *Lobocyclendoceras* Balaschov, 1968; *Cyclocyrtendoceras* Balaschov, 1968; ?*Catoraphiceras* Ulrich and Foerste, 1936]

Straight to slightly endogastrically curved, annulated shell with long septal necks reaching proximity of preceding septum.

Cyrtendoceras Patrunky, 1926; *Endoceras* (*Cyrtocerina*) *hircus* Holm, 1892

Considerably endogastrically curved shell.

Chihlioceratidae Grabau, 1922

[= Manchuroceratidae Kobayashi, 1935]

Straight, short shell with circular section and blunt apex.

Chihlioceras Grabau, 1922; *C. nathani*
[= *Manchuroceras* Ozaki, 1927; *Yehlioceras* Shimizu and Obata, 1937; *Kerkoceras* Chen and Liu, 1974]

Bluntly ending siphuncle.

Coreanoceras Kobayashi, 1932; *C. kemipoense*

Pointed siphuncle.

Intejoceratidae Balaschov, 1960

[= Padunoceratidae Balaschov, 1960; Bajkaloceratidae Balaschov, 1962]

Subcentral siphuncle with endocones split into radial plates.

Intejoceras Balaschov, 1960; *I. angarense*
[= *Evencoceras* Balaschov, 1960; *Padunoceras* Balaschov, 1960; *Bajkaloceras* Balaschov, 1962]

Endoceratidae Hyatt, 1883

[= Emmonsoceratidae Flower, 1958; Najaceratidae Flower, 1976; Allotrioceratidae Flower, 1955]

Long and straight shell with septal necks intruding the preceding necks.

Dideroceras Flower in Flower and Kummel, 1950; *Endoceras Wahlenbergi* Foord, 1887

Embryonic shell with chambers probably beginning at apex; moderately long shell.

Suecoceras Holm, 1896; *Endoceras barrandei* Dewitz, 1880

Embryonic shell with chambers beginning at apex; very long shell.

Endoceras Hall, 1847; *E. proteiforme*
[= *Vaginoceras* Hyatt, 1883; *Cameroceras* Conrad, 1842; *Nanno* Clarke, 1894; *Chazyoceras* Flower, 1958; *Palaeocyclendoceras* Balaschov, 1968; *Trinitoceras* Flower, 1976]

Embryonic shell without chambers in apical part; septal necks intruding a little in preceding neck.

Proterovaginoceras Ruedemann, 1905; *Nanno belemnitiformis* Holm, 1885
[= *Lamottoceras* Flower, 1955; *Meniscoceras* Flower, 1941; *Allotrioceras* Flower, 1955; *Mirabiloceras* Flower, 1955; *Rossoceras* Flower, 1964; *Williamsoceras* Flower, 1964; *Najaceras* Flower, 1971; *Kiotoceras* Flower, 1971; *Ignoceras* Flower, 1976; *Cacheoceras* Flower, 1976; *Perkinsoceras* Flower, 1976; *Emmonsoceras* Flower, 1958]

Embryonic shell without chambers in apical part; septal necks very long, covering entirely the preceding neck.

Rossiceras Balaschov, 1961; *Endoceras hasta* Eichwald, 1860

Close to *Endoceras* but with siphuncle away from shell wall.

Chisiloceras Gortani, 1934; *C. marinelli*

[needs revision]

Order **Tarphyceratida** Flower, 1950

Diagnosis. — Exogastrically coiled shell with elongated body chamber, cylindrical siphuncle, and large protoconch.

Remarks. — The Tarphyceratida resemble in morphology some Oncoceratida and Nautilida, but differ in their elongated body chamber, ornamentation, and siphuncular structure. Homeomorphs may occur.

Phylogeny (fig. 12). — The oldest Tarphyceratida are known from the Tremadocian of North America. This, however, does not necessarily indicate that the tarphyceratids originated in the North American epicontinental sea, as the Tremadocian nautiloid faunas from other continents are very poorly known. According to FLOWER (1964), the tarphyceratid genus *Aphetoceras* occurs already in the Demingan (Middle Tremadocian). The oldest described specimens, however, come from the Jeffersonian (Late Tremadocian). The true tarphyceratids are, nonetheless, older than the earliest record of the Bassleroceratidae, while the latter are thought to be transitional from the Ellesmeroceratina to Tarphyceratida (see FLOWER 1976). Typical representatives of the genus *Bassleroceras* from the Cassin Limestone are known exclusively by the adoral part of their shell; they may actually be shell fragments of some uncoiled tarphyceratids, even though their large size makes them different from *Aphetoceras*. *Bassleroceras annulatum* TEICHERT and GLENISTER, 1954, from the latest Jeffersonian or Early Cassinian Emanuel Formation, resembles the Oncoceratida in its small size and short (?) body chamber (TEICHERT and GLENISTER 1954: pl. 1: 17-18). No bassleroceratid is known to have a body chamber as elongated as in *Aphetoceras*, while the problematic forms with equally elongated body chamber may be attributed to *Aphetoceras* as well. Regardless of whether the known Bassleroceratidae make up a transitional evolutionary stage between the Ellesmeroceratina and Tarphyceratida, the phylogenetic relationship of the two orders through some bassleroceratid-like forms appears certain (FLOWER 1976). All recorded Late Tremadocian tarphyceratids show a ventral siphuncle with thick connecting rings and a loosely coiled (more tightly at the juvenile stages), elongated shell (ULRICH *et al.* 1942). Completely uncoiled tarphyceratids (*Aphetoceras*) have been recorded not only from the Late Tremadocian of North America, but also from the Early Arenigian Emanuel Limestone of Australia (TEICHERT and GLENISTER 1954) and the Early Kundan of the Baltic area (HOLM 1899, NEBEN and KRUEGER 1971). The Baltic species *Aphetoceras proteus* (HOLM, 1899) was studied by HOLM (1899) who described its siphuncular structure. NEBEN and KRUEGER (1971, pl. 18: 6) illustrated under the name *Tragoceras falcatum* a complete specimen. The North American Early Arenigian (i.e. Cotter Formation) representatives of *Aphetoceras* with rather tightly coiled initial whorls (e.g. *A. evolutum* ULRICH, FOERSTE, MILLER and FURNISH) may be ancestral to the Baltic species *Tragoceras falcatum* (SCHLOTHEIM, 1820) (fig. 8; pl. 5: 2-3). The latter species has been known for long from the latest Kundan and Aserian of Estonia and erratics, and extensively described (SCHLOTHEIM 1820, SCHRÖDER 1891, BALASCHOV 1953, MUTVEI 1957, STUMBUR 1962) but its early development has remained poorly recognized. BALASCHOV (1953) described under the name *Planctoceras arciforme* the early developmental stages of some shells, associated with adoral shell fragments indistinguishable from *T. falcatum*. The specimens were collected from the Late Kundan of Estonia, the strata typical of *T. falcatum*. They resemble also rather closely "*Falcilituites*" *decheni* REMELE, 1882 from the Middle Kundan (REMELE 1882, NEBEN and KRUEGER 1971) which differs from *T. falcatum* in slightly wider whorls. The considerable differences in size of the living chamber of *T. falcatum* with preserved scars of muscle attachment (MUTVEI 1957) may be due to a periodic growth inhibition related to an increase in mortality rate, as is the case in *Estonioceras* (see below). "*Bentoceras rubeli*" (STUMBUR 1962) belongs probably to *T. falcatum*. The specimen described by STUMBUR (1962) displayed more loosely coiled initial whorls than *T. decheni*. The youngest record of *Tragoceras* is "*Aserioceras purtsensis*" from the Aserian of Estonia (STUMBUR 1962). "*Estonioceras*" *subcostatum* ANGELIN, 1880 from the Kundàn probably also belongs to this genus.

Numerous tarphyceratids with tightly coiled initial whorls and uncoiled last whorl have been reported from the Cassinian (Arenigian) of North America. They may be arranged according to shell robustness. *Plectoceras manitouense* FLOWER, 1952, from the Manitou Limestone, and *Alaskoceras sewardense* (FLOWER, 1941) of unknown geological age, are most closely related to *T. subcostatum* in number of whorls and shell size. They are linked with the massive *Eurystomites kellogi* (WHITFIELD, 1886) group through *Tarphyceras clarkei* RUEDEMANN, 1906, from the Cassin Limestone of New York, and its close relatives from some other localities (see Ulrich *et al.* 1942). The endmember of this morphocline is the huge *Clytoceras capax* Ulrich, Foerste, Miller and Furnish, 1942, from the Powell Formation of Arkansas, with rapidly expanding whorls.

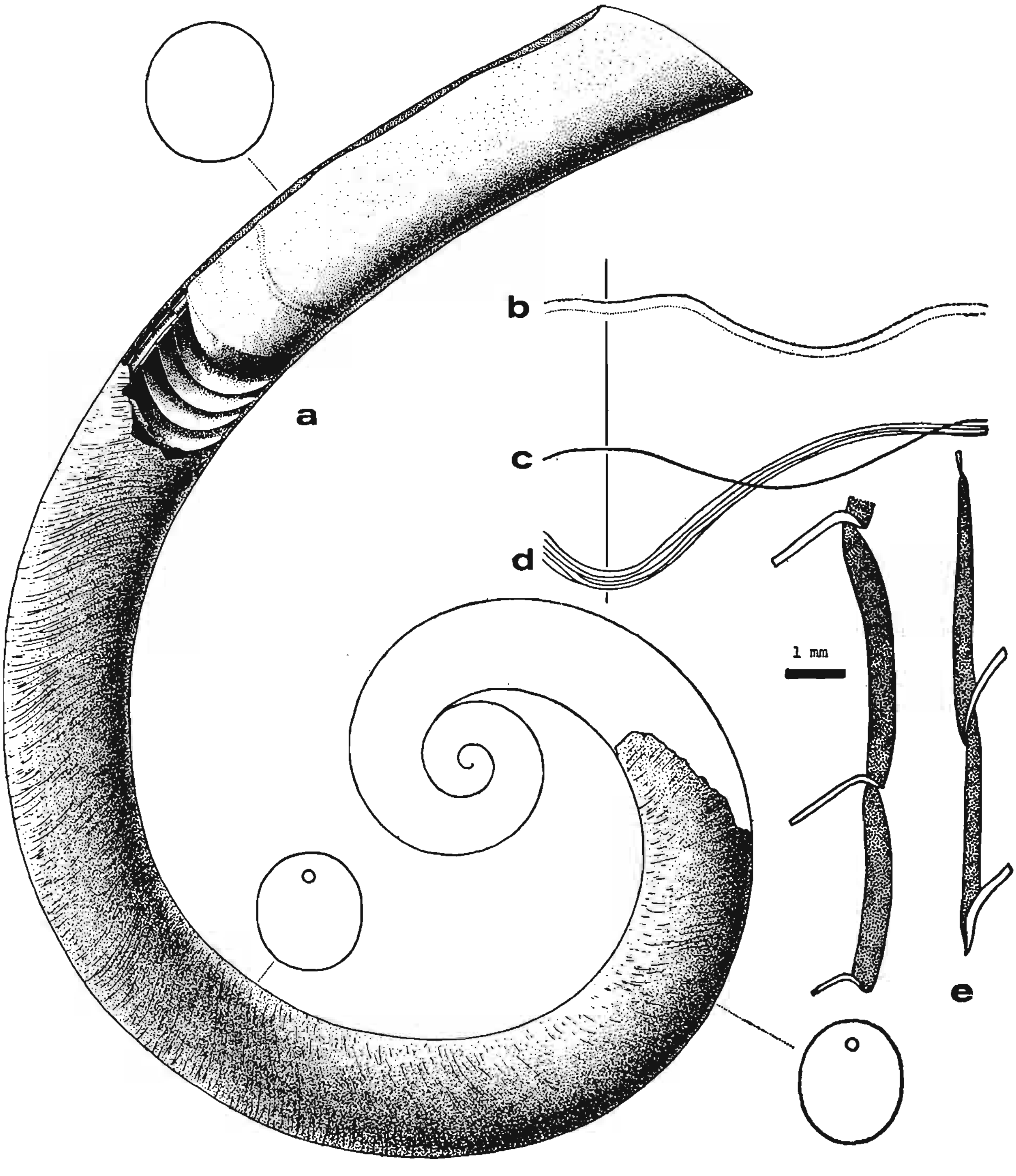


Fig. 8
Tragoceras falcatum (Schlotheim, 1820); *E. pseudoplanus* Zone, Late Kundan; *a* Reconstruction of the adult shell, *b* pedal muscle attachment scar, ZPAL N/090 (pl. 5: 3); erratic boulder, Mochty, Poland; *c* septal suture of the same specimen: *d* growth lines in the same specimen; *e* longitudinal section through a siphuncle, ZPAL N/089 (pl. 5: 2), boulder E-079, Mochty

The genus *Estonioceras*, abundant in the Baltic area, may be a relative of the American *Tarphyceras*. Its distinctive feature among the Tarphyceratidae is the transversely discoidal section of the initial whorls. *Estonioceras* is confined to the Late Kundan of Estonia (SCHRÖDER 1882; MUTVEI 1957; BALASCHOV 1953, 1955, 1962; STUMBUR 1959), the Middle Kundan of Sweden and erratic boulders (NEBEN and KRUEGER 1971). Several species described from these strata vary in shell size and cross section, the latter being also ontogeny dependent (see SCHRÖDER 1881, MUTVEI 1957). *Estonioceras* presents however a case where the criteria applied commonly to recognize maturity of a cephalopod shell are insufficient. There are multiple peaks in septal density as well as groups of pedal muscle attachment scars in a single shell. This is well exemplified by the specimen presented in pl. 5 : 1 with distinct pedal muscle attachment scars at phragmocone mid-length and in the body chamber. Nevertheless, this is an immature specimen. One may conclude that pedal muscle scars appear owing to inhibition of growth, no matter whether it is caused by the achievement of maturity, or unfavourable environmental conditions, or some physiological disturbances. The latter two possibilities may account for an increase in mortality rate related to growth inhibitions. *Estonioceras ariense* (see SCHRÖDER 1882, BALASCHOV 1962) with uncoiled last whorl represents probably the mature shell of *E. lamellosum* (HISINGER, 1837). One may thus claim that there is only a single described species of *Estonioceras* in the Baltic area.

Plectroceras jason (BILLINGS, 1859) (? = *Avilionella multicamerata* RUEDEMANN, 1906) from the Chazyan (Llandeilian) and *P. robertsoni* (HALL, 1861) from the Blackriveran (Early Caradocian) of North America (see WILSON 1961, COLLINS 1879) evolved probably from *Tarphyceras*. Related forms have also been recorded from China (CHANG 1964). An interesting group of very small tarphyceratids is represented by *Shumardoceras complanatum* (SHUMARD, 1863) from the Jefferson City and the Theodosia formations of Missouri (ULRICH *et al.* 1942), *Moreauoceras milleri* CULLISON, 1944, and *Pilotoceras brunei* CULLISON, 1944, both from the underlaying Rich Fountain Formation (CULLISON 1944).These few specimens may represent a single, monospecific lineage. An undescribed species from Siberia (Podkamiennaya Tunguska, Baykit village) of similar age, as judged from the associated conodonts, shows most generalized morphology. It matches the North American species in shell outline, subventral siphuncle, and fine oblique annulae. Its elliptic whorl section seems to be a primitive character. It seems to me precarious to attribute the tree American species to distinct genera.

All the forms discussed above show a ventral to subventral siphuncle as characteristic of the family Tarphyceratidae, including most Early Ordovician tarphyceratids. In turn, tarphyceratids with subdorsal siphuncle prevail in the Middle to Late Ordovician. The siphuncle is never marginal and lies actually rather close to center in various forms. Its displacement to the shell center and further dorsally does therefore not require any far-reaching reorganization of shell architecture. A somewhat more central position of the siphuncle is the only difference between *Centrotarphyceras seelei* (WHITFIELD, 1886) from the Fort Cassin Limestone of Vermont and *Tarphyceras*. The assignment of *C. seelei* and some related problematic species to a genus distinct from *Tarphyceras* (ULRICH *et al.* 1942) seems to me unjustified. *Barrandeoceras natator* (BILLINGS, 1859) from the Chazyan (Llandeilian) may have evolved from *C. seelei*. Its siphuncle is central also in the juvenile stages (ULRICH *et al.* 1942). As shown below, the Uranoceratidae cannot have evolved from *Barrandeoceras*, or any other Tarphyceratida. The species *B. natator* is then the only representative of the Barrandeoceratidae and Barrandeoceratina are so closely affiliated to *Centrotarphyceras* that there is no reason to distinguish it at so high a taxonomic rank. Therefore, *Barrandeoceras s.s.* is here assigned to the family Tarphyceratidae.

Curtoceras eatoni (WHITFIELD, 1886) from the Fort Cassin Limestone of Vermont, is morphologically transitional between the Tarphyceratidae with subcentral siphuncle and the Trocholitidae with dorsal siphuncle. It differs from *Centrotarphyceras seelei* in its smaller shell and the siphuncle location dorsally of whorl center. Half of the last whorl is uncoiled, as in most tarphyceratids.

The siphuncle is even more dorsal and the shell is more involute in *Trocholitoceras walcotti* HYATT, 1894, from the Fort Cassin Limestone. *Litoceras adamsi* FLOWER, 1968, described from numerous specimens from the Pogonip Formation, Nevada, may have evolved from *Trocholitoceras*, whereas its relationship to the type species of the genus *Litoceras* seems doubtful. In fact, the siphuncle is ventral of the whorl center in *Litoceras versutum* (BILLINGS, 1865) (= *L. whiteavesi* = *L. calciferum* = *Nautilus avus* BARRANDE, 1870) from the St. George Beds of New Foundland (ULRICH *et al.* 1942). Similar forms have also been recorded from the Antelope Valley Limestone in Nevada (FLOWER 1968). The systematic position of *Plectolites incipiens* (BARRANDE, 1870), widespread in the Whiterockian (Llanvirnian) of North America, has thus far remained enigmatic. An large assemblage of well preserved specimens probably attributable to *P. incipiens* has been described under the names *Discoceras perornatus* FLOWER, 1968, and *Plectolites costatus* FLOWER, 1968, from the Antelope Valley Limestone. *P. incipiens* shows a massive, somewhat involute shell, more or less typical in outline of the *Trocholitoceras-Litoceras* group. Its distinctive characters consist in the oblique, transverse ribs passing into keels and widely spaced, longitudinal striae. The ornamentation resembles very closely Baltic representatives of the much younger genus *Discoceras*. This is probably why FLOWER (1968*a*) attributed one of his specimens to a new species of *Discoceras*; however, neither the illustrations, nor the text provide us with sufficient information to justify the placing of virtually indistinguishable specimens in two genera (one of them new), and the erection of two new species.

In spite of the similarity of ornamentation between *Plectolites* and *Discoceras*, one can hardly recognize the nature of the relationship between the American and Baltic trocholitids and discoceratids. All Baltic species of *Discoceras* show a distinctly evolute shell with relatively low expansion rate of the whorls, and a uncoiled adoral part of the living chamber. In fact, *Plectolites incipiens* resembles "*Litoceras*" *adamsi* in shell outline, and the two species may

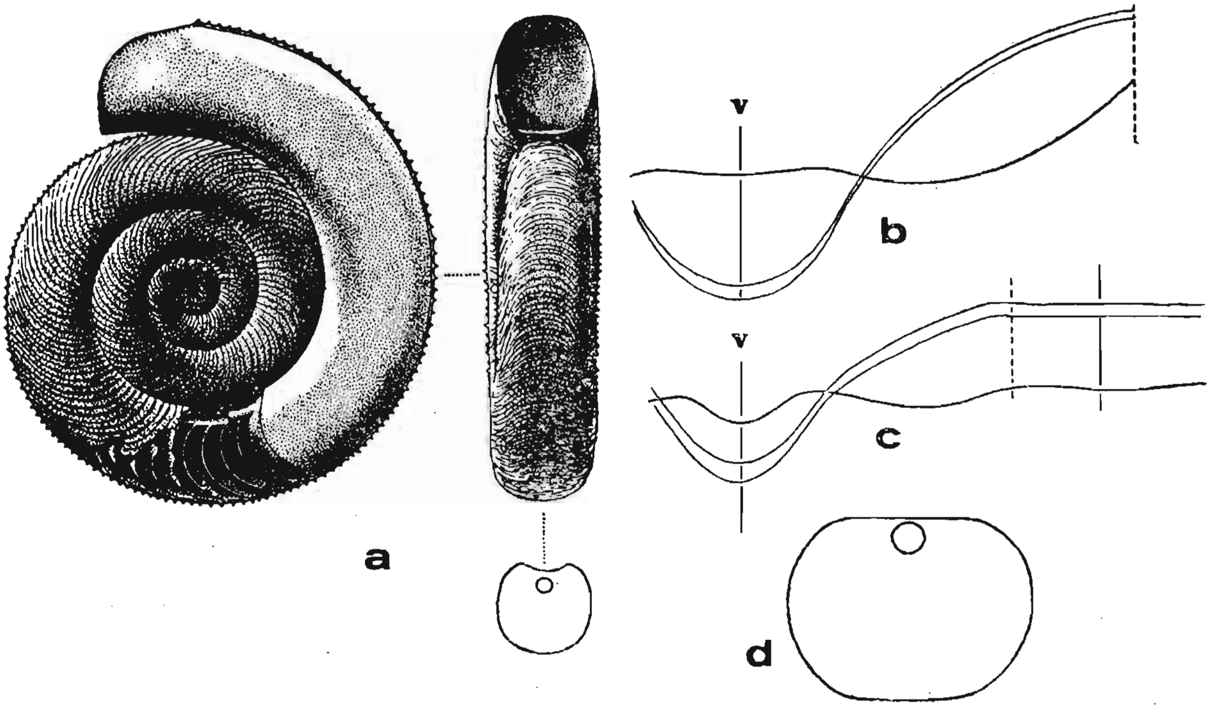


Fig. 9

Discoceras sp.; ZPAL N/098 (pl. 6: 4), boulder E-212, Oanduan (dated after the occurrence of *Icriodella superba*); *a* Reconstruction; *b* septal suture and growth lines. *Discoceras antiquissimum* (EICHWALD, 1845); IG 139. II. 7 (pl. 7: 1), erratic boulder, latest Caradocian or Ashgillian (dated after the lithology), Zawidowice, Poland; *c* septal suture and growth lines; *d* whorl cross section.

represent a taxon unrelated to *Discoceras*; this may be either a subgenus of *Trocholitoceras* or a distinct genus.

In the Middle Kundan of Öland, Västergotland, and Dalarna yet undescribed robust tarphyceratid occurs, which may be related to *Litoceras*. It is characterized by rather involute, compressed shell with subquadrate whorl section, ornamented by low transverse ribs and distinct growth lines. Siphuncle position is not visible on none of the few specimens in the collections of Naturhistoriska Riksmuseet, Stockholm, so its relationship remains obscure.

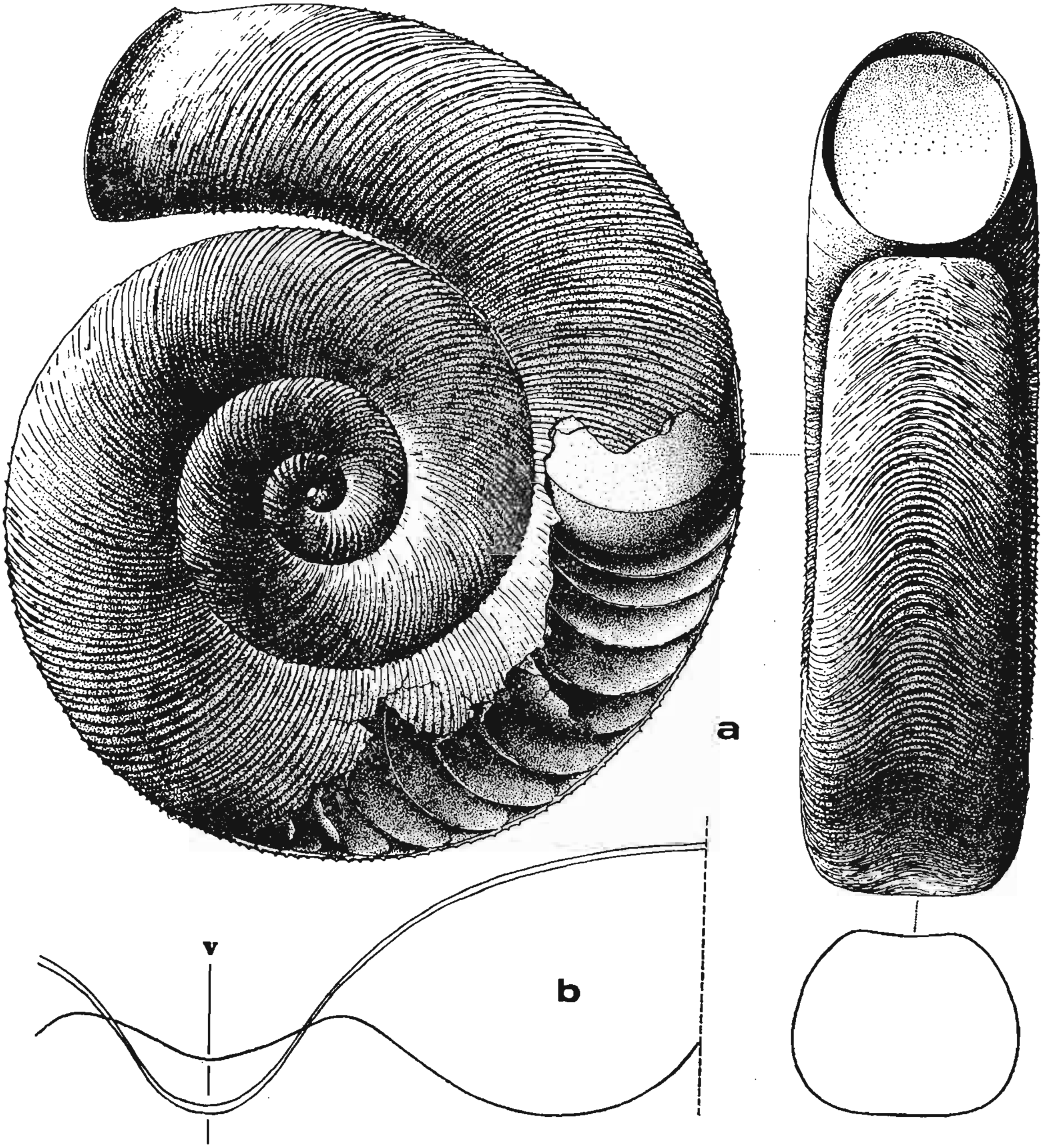


Fig. 10
Discoceras roemeri (STRAND, 1934); ROEMER's original material (see pl. 6: 5-6), latest Caradocian or Ashgillian, Zawidowice; *a* Reconstruction of the adult shell; *b* septal suture and growth lines.

The oldest records of *Discoceras s.s.* are in the *Ogygiocaris* Shales of Norway (Sweet 1958), of Lasnamägian age (Llanvirnian). These are evolute forms with slowly expanding whorls subsquare in cross section (SWEET 1958). They resemble the tarphyceratids rather than the American trocholitids in external view. The shell ornamentation consists of oblique growth lines intercalated with conspicuous lamellae. The lamellae are relatively widely spaced and occur at the edge of prominent ribs, recognizable also at an internal mould in descendant species (STRAND 1935, STUMBUR 1959, CHEN and LIU 1974); this is apparent i.a. in *Discoceras antiquissimum* (pl. 7: 1). Beginning with the Llandeilian, an independent lineage appears without the transverse lamellae. These forms are often placed in a distinct genus, *Schroederoceras*. The oldest representative of this group is probably *Discoceras arcuatum* (LOSSEN, 1860) from the Llandeilian of Norway (SWEET 1958). Supposedly, *D. bandonis* REMELE, 1880, belongs also to this lineage (see NEBEN and KRUEGER 1971). Concerning the morphology of muscle scars, the Ashgillian species *D. angulatum* (SAEMANN, 1850) appears to be the best known form (MUTVEI, 1957). The pattern of the scars differs considerably from that in *Trocholites* (see below) with the scars better developed ventrally. There is much better affinity in this respect to *Estonioceras*. However, the paired retractor scars are more distinct in *Discoceras* than in *Estonioceras*. I propose nevertheless to separate *Trocholites* and *Discoceras* at the familial or at least subfamilial level. A large number of *Discoceras* species have been described from the Late Caradocian to Ashgillian (figs 9-10). A review and discussion of those species is given by STRAND (1934) and SWEET (1958). *Discoceras* was also split into several genera based on the whorl section (STUMBUR 1962). It is, however, to be kept in mind that most specimens collected from the Late Ordovician of the Baltic area are poorly preserved and deformed. The drawings of the whorl sections are commonly far from reliable. Furthermore, we know close to nothing on intrapopulation and intraspecific variability in particular species. I believe therefore that one is unable at the moment to reconstruct particular evolutionary lineage within the Discoceratidae, new family.

Discoceratids have also been reported from the Llandoverian of England (BLAKE 1882), Wenlockian of North America (FOERSTE 1925), and Gotland, and possibly Late Silurian of Australia (ETHERIDGE 1905).

Rich and well preserved collection of unnamed discoceratids from the Slite Beds (Wenlockian) of Gotland is housed at Naturhistoriska Riksmuseet, Stockholm. They are of rather uniform size (approximately 70 mm in diameter) but considerably vary in distribution of transverse ribs. One population, known from Othem, is characterized by peculiar course of shell ontogeny. Earliest stages are closely coiled, with delicate ornamentation with growth lines. After reaching diameter of approximately 19 mm shell begins loosely coiled. Whorls contact themselves at diameter about 47 mm, but adult living chamber is again uncoiled.

Curtoceras teres (EICHWALD, 1840) from the Aserian of Estonia is the oldest known Baltic tarphyceratid with subcentral siphuncle. The ornamentation of its shell, with regularly distributed delicate ribs and compressed evolute shell, suggests relationship with younger species of *Discoceras*, differing only in the dorsal siphuncle.

I also believe that there are similar to discoceratids forms in the Late Ordovician of China (see CHEN and LIU 1974). "*Discoceras*" *kazakhstanense* BARSKOV, 1972, from the Late Caradocian of Kazakhstan, show a very small shell, resembling *Trocholites* rather than *Discoceras*. This is probably a distinct genus with poorly known phylogenetic relationships.

The Late Ordovician North American genus *Wilsonoceras* with large evolute shell (MILLER 1932*b*) may be related to *Discoceras*. The genus *Trocholites* occurs both in the Baltic area and in North America. Its oldest species is probably *T. depressus* (EICHWALD, 1840) recorded in the *Ogygiocaris* Shales (Lasnamägian, Llanvirnian) of Norway (SWEET 1958), in the Lasnamägian of Estonia (STUMBUR 1960*b*), and in Sweden. Most of its records from erratic boulders are dated as Uhakuan (*Eoplacognathus robustus* and *E. lindstroemi* Zones). Virtually every mature specimen shows a different shell size and apertural outline (see REMELE 1880, SCHRÖDER 1891, NEBEN and KRUEGER 1971, fig. 14 and pl. 6 in this paper), which indicates considerable intrapopulation variability. Nonetheless, all specimens resemble the Early Ordovician *Trocholitoceras* in shell outline, and *Hardmanoceras* (see CHEN 1976, KOBAYASHI 1959) in shell size. The ancestors of *Trocholites* are therefore to be looked for among the latter two genera. The mature shell attains its largest size (up to 64 mm in diameter) in *Trocholites hospes* (REMELE, 1880) common in the Folkeslunda limestone (Lasnamägian of Öland) and in erratic boulders of of the same age (NEBEN and KRUEGER 1971). *T. macrostoma* SCHRÖDER, 1891, much smaller and less involute, with compressed shell, occurs with *T. hospes*. Species of this genus resemble each other in shell size, while varying in mature whorl section and aperture outline. The whorls are depressed, and the aperture flares in *T. contractus* SCHRÖDER, 1882, from the *E. robustus* Zone, Uhakuan (fig. 14a, e; pl. 6: 1). In turn, the whorls are rounded in section and the aperture is triangularly constricted in *T. orbis* SCHRÖDER, 1882, from the *E. reclinatus* Zone (Lasnamägian and earliest Uhakuan) (fig. 11f-j; pl. 6: 2-3). In contrast to the patern displayed by all other Tarphyceratida, the two species show the best developed muscle attachment scars in the adumbilical, dorsal part of the whorl (fig. 11). This demonstrates clearly

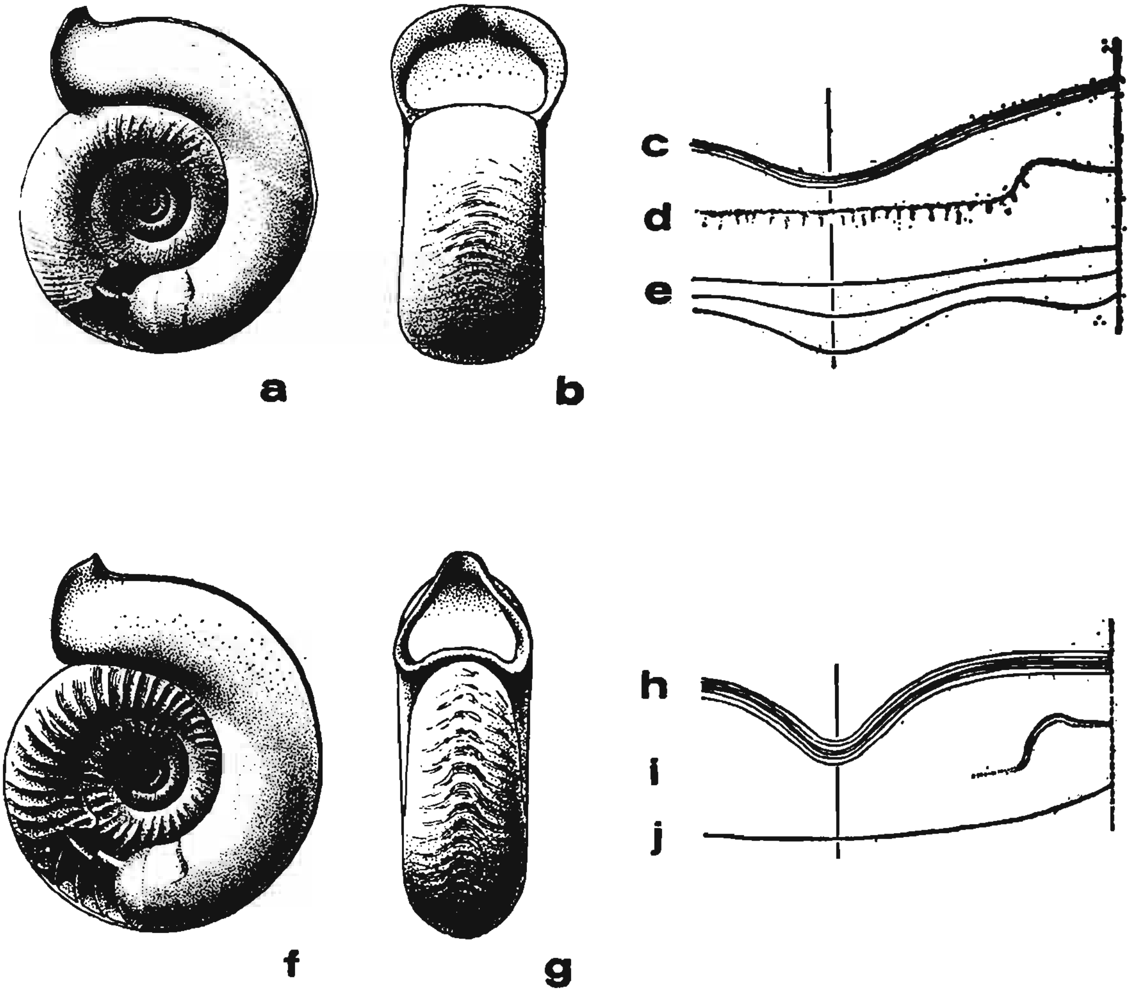


Fig. 11
Trocholites contractus SCHRÖDER, 1891; ZPAL N/091 (pl. 6: 1), boulder E-240, *E. robustus* Zone, Uhakuan, Stężyca, Poland. *a-b* reconstruction of adult shell; *c* growth lines; *d* pedal muscle attachment scar; *e* variation in the septal suture. *Trocholites orbis* SCHRÖDER, 1891; ZPAL N/092 (pl. 6: 3), boulder E-254, *E. lindstroemi* Zone, Uhakuan, Międzyzdroje; *j-g* Reconstruction of the shell; *h* growth lines; *i* pedal muscle attachment scar; *j* septal suture.

that the pattern of pedal muscle scars has not so great diagnostic value, as claimed by Mutvei (1964). I propose nonetheless to recognize *Trocholites* and its related involute genera as a distinct family. *Trocholites* has also been reported from the Chazyan (Llandeilian) Valcour Limestone of New York. Some new species have been erected by Flower (1943*b*) for those specimens but the original descriptions and illustrations do not allow one to say whether or not the American forms differ from the Baltic ones. The youngest known representative of the genus is from the latest Caradocian (Strand 1934).

A morphologically unique tarphyceratid group (*Weberoceras*, *Paradiscoceras*) related to the Trocholitidae and Discoceratidae occurs in the Late Ordovician of Kazakhstan (Barskov 1972). These are small shells resembling *Hardmanoceras* in outline but more compressed, with a somewhat uncoiled adapertural part of the living chamber, and a dorsal siphuncle. Their uniqueness among the Tarphyceratida consists in the absence of a ventral sinus of the growth lines. This group is considered to be a distinct family, Weberoceratidae new family (fig. 12). The additional material, thus far undescribed, is under the care of Dr. L. S. Barskov (Moscow University).

The tarphyceratid larval development is fairly uniform throughout the order and hence, gives little information on the course of evolution of the Tarphyceratida (Stumbur 1959, 1960). The larva developed probably within an egg capsule. The eggs were variable in size, depending upon the adult size.

Proposed systematics.—

Tarphyceratidae Hyatt, 1894

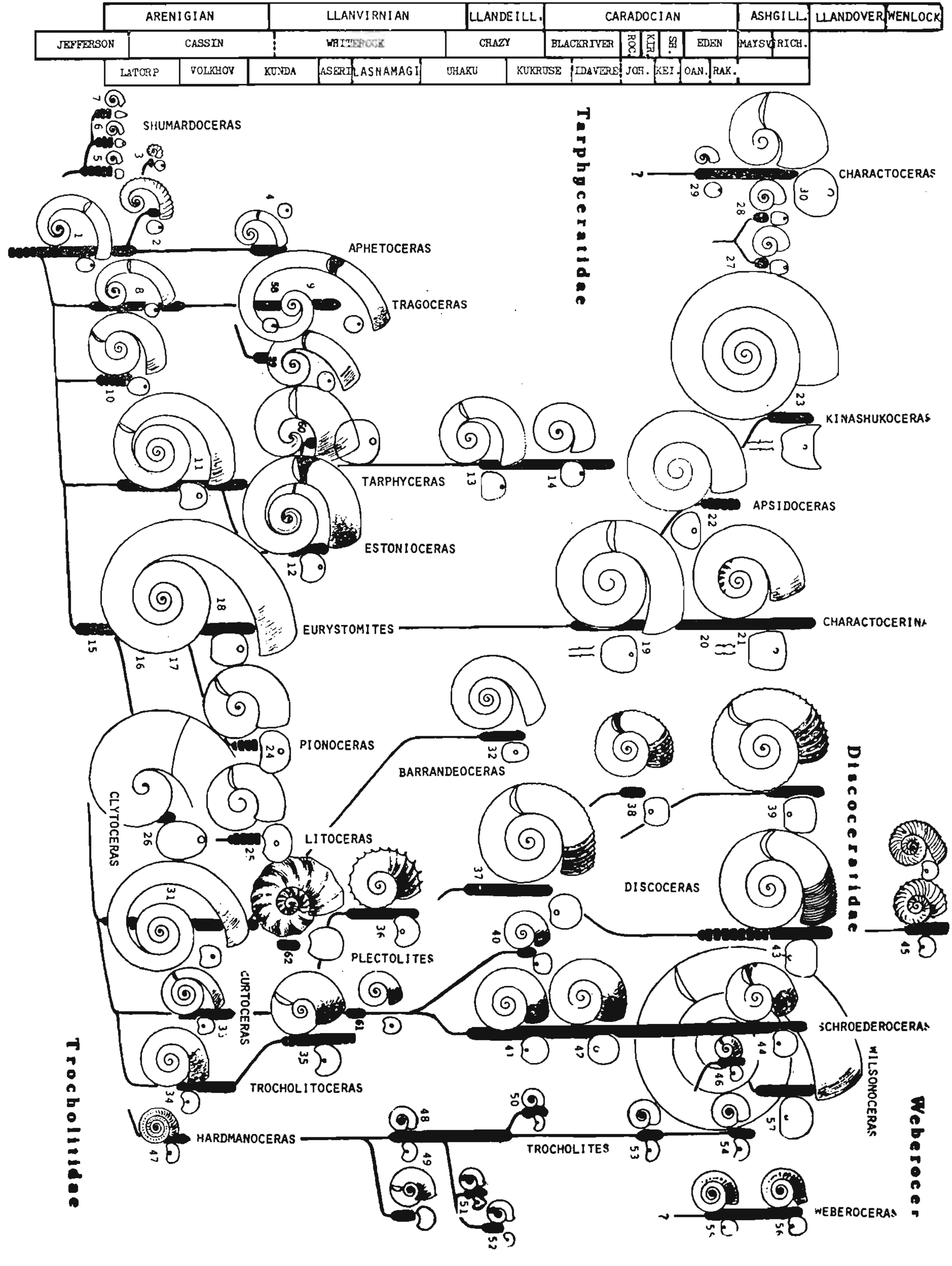
[= Estonioceratidae Hyatt, 1900; Plectoceratidae Hyatt 1900; Apsidoceratidae Hyatt, 1884; Barrandeoceratidae Foerste, 1925]

Shell evolute, undivided muscle scars best developed ventrally, siphuncle ventral to central.

Fig. 12

Hypothetical phylogenetic relationships among members of the order Tarphyceratida Flower, 1950; 1 *Aphetoceras subcostulatum* UFM and F; 2 *Aphetoceras delectans* Teichert and Glenister; 3 *Aethoceras caurus* Teichert and Glenister; 4 *Estonioceras proteus* Holm; 5 *Moreauoceras milleri* Cullison; 6 *Shumardoceras complanatum* (Shumard); 7 *Pilotoceras brunei* Cullison; 8 *Aphetoceras evolutum* UFM and F, *Pycnoceras rotundatum* UFM and F; 9 *Tragoceras falcatum* (Schlotheim) (fig. 8a-e; pl 5: 2-3); 10 *Plectoceras manitouense* Flower, *Alaskoceras sewerdense* (Flower); 11 *Tarphyceras clarkei* Ruedemann; 12 *Estonioceras lamellosum* (Hisinger) (pl. 5: 1); 13 *Plectoceras jason* (Billings), *Avilionella multicamerata* (Ruedemann); 14 *Plectoceras robertsoni* (Hall), *P. carletonense* Foerste, *Campbelloceras clochense* Collins; 15 *Campbelloceras tuelli* Miller and Cullison; 16 *Campbelloceras virginianium* (Hyatt); 17 *Pionoceras vokesi* UFM and F; 18 *Eurystomites kelloggi* (Whitfield), *Cycloplectoceras miseri* UFM and F; 19 *Chidleynoceras chidleyense* Foerste, *Fremontoceras cooperi* Foerste; 20 *Charactocerina eximia* Sweet and Miller; 21 *Charactocerina leithi* Nelson; 22 *Apsidoceras elegans* Troedsson; 23 *Kinashukoceras churchillense* Nelson; 24 *Pionoceras pomponium* (Billings); 25 *Litoceras versutum* (Billings) = (?) *L. calciferum* (Billings), *L. whiteavesi* Hyatt, *Nautilus avus* Barrande; 26 *Clytoceras capax* UFM and F; 27 *Tarphyceras morkokense* Balaschov; 28 *Tarphyceras excentricum* Balaschov; 29 *Vasalemmoceras tolerabile* Stumbur; 30 *Charactoceras baeri* (Meek and Worthen), *Ch. estonicum* Strand; 31 *Centrotarphyceras yellvillense* UFM and F, *C. seelei* (Whitfield); 32 *Barrandeoceras natator* (Billings); 33 *Curtoceras eatoni* (Whitfield); 34 *Trocholitoceras walcotti* Hyatt; 35 *Litoceras adamsi* Flower; 36 *Plectolites decipiens* (Barrande) = *Discoceras perornatum* Flower = *Plectolites costatus* Flower; 37 *Discoceras depressum* Sweet, *D. boreale* Sweet; 38 *Discoceras ievesense* (Balaschov), *D. vesenbergense* (Balaschov); 39 *Discoceras antiquissimum* (Eichwald) (Text-fig. 9c-d; pl. 7: 1); 40 *Curtoceras kerstovense* Balaschov; 41 *Schroederoceras arcuatum* (Lossen); 42 *Schroederoceras rarospira* (Eichwald), *S. bandonis* (Remele); 43 *Discoceras roemeri* Strand (Text-fig. 10a-b; pl. 6: 5-6), *D. saemanni* (Hyatt); 44 *Schroederoceras angulatum* (Saemann), *S. hyatti* Strand; 45 *Craftonoceras graftonense* (Meek and Worthen); 46 *Discoceras kazakhstanense* Barskov; 47 *Hardmanoceras lobatum* Teichert and Glenister; 48 *Trocholites depressum* (Eichwald); 49 *Trocholites hospes* (Remele); 50 *Trocholites ruedemanni* Flower; 51 *Trocholites orbis* Schröder (Text-fig. 11f-i; pl. 6: 2-3); 52 *Trocholites contractus* Schröder (text-fig. 11a-e; pl. 5: 4, 6: 1); 53 *Trocholites ammonium* Conrad; 54 *Trocholites nakholmensis* (Kjerulf); 55 *Paradiscoceras orientale* Barskov; 56 *Weberoceras mariannae* Barskov; 57 *Wilsonoceras mccharlesi* (Whiteaves), *W. squawcreekense* Miller, *W. bighornense* Miller; 58 *Tragoceras decheni* (Remele); 59 *T. subcostatum* (Angelin); 60 *Estonioceras* sp. n.; 61 *Curtoceras teres* (Eichwald); 62 Gen. et sp. indet.

Aphetoceras HYATT, 1894; *A. americanum*
[= ?*Aethoceras* TEICHERT and GLENISTER, 1954]
Completely uncoiled, small shell.



Tragoceras Remele, 1880; *Orthoceratites falcatus* Schlotheim, 1820

[= *Bentoceras* Stumbur, 1962; *Aserioceras* Stumbur, 1962; *Pycnoceras* Hyatt, 1894; ?*Falcilituites* Remele, 1886]

Compressed shell with tightly coiled 2-3 initial whorls, and uncoiled successive ones.

Tarphyceras Hyatt, 1894; *T. praematurum*

[= ?*Plectoceras* Hyatt, 1894; *Centrotarphyceras* Ulrich and Foerste, 1936]

Like *Tragoceras* but shell more massive with shorter coiled part.

Estonioceras Noetling, 1883; *Lituites lamellosus* Hisinger, 1837

[= *Remeleceras* Hyatt, 1894; *Eichwaldoceras* Balaschov, 1955]

Close to *Tarphyceras* but initial whorls with lateral keels.

Barrandeoceras Hyatt, 1884; *Nautilus natator* Billings, 1859

Externally similar to *Tarphyceras*; centrally situated siphon.

Eurystomites Schröder, 1891; *Nautilus kelloggi* Whitfield, 1886

[= *Cycloplectoceras* Ulrich, Foerste, Miller and Furnish, 1942; ?*Campbelloceras* Ulrich and Foerste, 1936]

Large shell, uncoiled last whorl with subsquare section, and ventral siphuncle.

Charactocerina Foerste, 1935; *Eurystomites plicatus* Whiteaves, 1896

[= ?*Chidleynoceras* Shimizu and Obata, 1935; *Fremontoceras* Foerste, 1935]

Close to *Eurystomites* but with trapezoidal whorl section, and slightly swollen connecting rings.

Apsidoceras Hyatt, 1884; *Gyroceras* (*Lituites*) *magnificum* Billings, 1857

Whorls triangular in cross section; poorly known.

Kinashukoceras Nelson, 1962; *K. churchillense*

Shell with concave, sharp-edged venter.

Pionoceras Ulrich, Foerste, Miller and Furnish, 1942; *Nautilus pomponius* Billings, 1865

Large, completely coiled shell with flattened whorls and subventral siphuncle.

Litoceras Hyatt, 1883; *Nautilus versutus* Billings, 1865

Like *Pionoceras* but subventral siphuncle.

Clytoceras Ulrich, Foerste, Miller and Furnish, 1942; *C. capax*

Very large, rapidly expanding, compressed shell with ventral siphuncle.

Shumardoceras Ulrich and Foerste, 1936; *Lituites complanata* Shumard, 1863

[= *Moreauoceras* Cullison, 1944; *Pilotoceras* Cullison, 1944]

Very small, completely coiled shell with compressed whorls and constricted aperture.

?***Charactoceras*** Foerste, 1924; *Trochoceras*? *baeri* Meek and Worthen, 1865

[= *Vasalemmoceras* Stumbur, 1962]

Possibly attributable to the Uranoceratidae.

Discoceratidae new family

Evolute shell with dorsal siphuncle, uncoiled adapertural part of the last whorl, and ventral muscle scars.

Curtoceras Ulrich, Foerste, Miller and Furnish, 1942; *Lituites eatoni* Whitfield, 1886

Small shell with considerably uncoiled adapertural part of the last whorl.

Discoceras Barrande, 1867; *Clymenia antiquissima* Eichwald, 1842

[= *Graftonoceras* Foerste, 1925; *Sweetoceras* Stumbur, 1962]

Large shell with a somewhat uncoiled end of living chamber; growth lines and transverse lamellae.

Schroederoceras Hyatt, 1894; *Lituites angulatus* Saemann, 1852

[= ?*Rectanguloceras* Stumbur, 1962]

Like *Discoceras* but only growth lines.

?***Wilsonoceras*** Foerste, 1929; *Trochoceras mccharlesi* Whiteaves, 1890

Very large shell with uncoiled living chamber.

Trocholitidae Chapman, 1857

Involute shell may be uncoiled at aperture, dorsal siphuncle, muscle scars in umbilical part of body chamber.

?***Hardmanoceras*** Teichert and Glenister, 1952; *H. lobatum*

Small shell with depressed whorls, ribs parallel to growth lines.

Trocholitoceras Hyatt, 1894, *T. walcotti*

Large, smooth, involute shell with relatively shallow umbilicus.

Plectolites Flower, 1968; *P. costatus*

Large, involute shell, transverse ribs passing into lamellae.

Trocholites Conrad, 1838; *T. ammonius*

Small, involute shell, growth lines and inconspicuous ribs.

Weberoceratidae new family

Small, evolute shell with dorsal siphuncle, uncoiled adapertural part of the last whorl, growth lines without ventral sinus.

Weberoceras BARSKOV, 1972; *W. mariannae*
[= ?*Paradiscoceras* BARSKOV, 1972]

Order **Discosorida** FLOWER, 1950

Diagnosis. — Endogastrically curved, compressed shell with ventral siphuncle and inflated connecting rings.

Remarks. — The Discosorida differ from the Endoceratida in considerably inflated connecting rings, and from the endogastrically curved representatives of the Oncoceratida in compressed shell.

Phylogeny (fig. 14). — Endogastrically curved, breviconic nautiloids with wide siphuncle with inflated connecting rings appeared first in the Llandeilian of North America (FLOWER and TEICHERT 1957) and Europe (SWEET 1958). Of those early forms, only the European species *Strandoceras strandi* SWEET, 1958, seems to be related to the Caradocian Discosorida. The genus *Ruedemannoceras*, recorded in the Chazy Limestone of New York and Vermont (FLOWER and TEICHERT 1957), Cephalopod Shale of Norway (SWEET 1958), and erratic boulders attributable to the Backsteinkalk (NEBEN and KRUEGER 1971: pl. 30; *Cyrtoceras* sp.), widely differs from the proper Discosorida in its subcentral siphuncle and depressed shell. Its assignment to the Discosorida is questionable and it may be related to the Orthoceratida (e.g. *Cyrtactinoceras*). In turn, *Madiganella magna* TEICHERT and GLENISTER, 1952, from Australia and *Ulrichoceras beloitense* FOERSTE, 1928, from North America are very closely related to *Ruedemannoceras boycii* (WHITFIELD, 1886); the available data do not support their generic distinction. FLOWER and TEICHERT (1957) claim that *Ruedemannoceras*, descended directly from *Plectronoceras* and is ancestral to all discosorids. Neither the position of its siphuncle, nor the stratigraphic position substantiate this opinion.

I believe that the ancestral discosorid is *Protophragmoceras* (= *Strandoceras*) *strandi* (SWEET 1958) from the Cephalopod Shale of Norway. There is a wide stratigraphic gap (two stages) between *P. strandi* and morphologically similar ellesmeroceratids and hence, one can not point to any ellesmeroceratid form as its ancestor. Inflated connecting rings occur in two ellesmeroceratid species erected on single, fragmentary specimens; the orthoconic *Apocrinoceras talboti* TEICHERT and GLENISTER, 1954, from the Early Arenigian Emanuel Limestone of Australia, and supposedly the slightly endogastric *Clelandoceras rarum* FLOWER, 1964, from the Arenigian Cassin Limestone of North America. The latter species may be ancestral to *Protophragmoceras*. A phylogenetic inference from a single oblique polished section through a poorly preserved specimen is obviously to be taken with caution. FLOWER (*in* FLOWER and TEICHERT 1957) erected also the genus *Glenisteroceras*, based on a single fragment of a poorly preserved nautiloid shell from the Fort Cassin Formation, and assigned all the above mentioned forms with inflated connecting rings to his new family Apocrinoceratidae. Inflation of connecting rings, especially when as slight as in the forms under discussion, does not prove phylogenetic relationship.

The Ordovician species of *Protophragmoceras* have been recorded exclusively from the Baltic area. A few poorly preserved specimens attributable probably to this genus have been reported from the Early Caradocian (NEBEN and KRUEGER 1971). I found a rather well preserved specimen with unusually densely spaced septa in an erratic boulder dated, after the occurrence of *Chasmops wrangeli* (SCHMIDT), as the Idaverean-Jõhvian (Early Caradocian) (pl. 7: 2). The considerable curvature of this small shell, and the outline of the living chamber suggest its relationship to *P. murchisoni* (BARRANDE, 1886) but the large time gap makes this doubtful. Of the Ashgillian forms described from Estonia (TEICHERT 1930) and Norway (STRAND

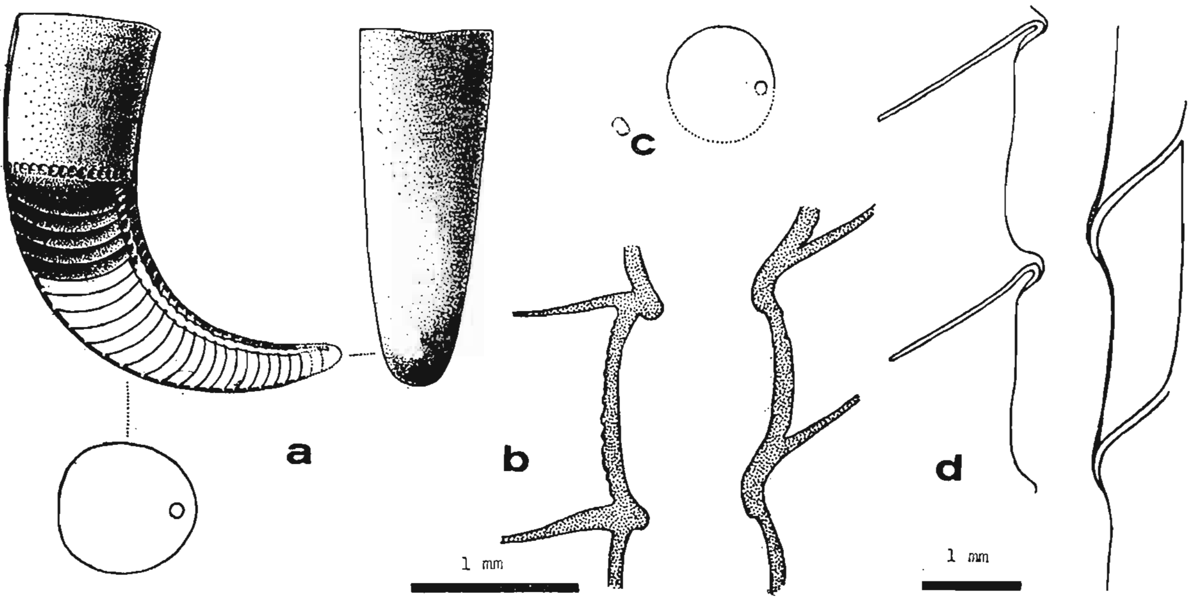


Fig. 13
Flowerites sobolewi nom. n.; ZPAL N/103 (pl. 7: 3), *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland. *a* Reconstruction of the adult shell, × 1.3, *b* longitudinal section through the siphuncle. *Flowerites* vel *Devonocheilus* sp. (cf. *F. austrirhiphaeus* Zhuravleva, 1972), ZPAL N/101 (pl. 7: 6), *Cheiloceras* Zone, Famennian, Jabłonna, bed J. 6, Holy Cross Mts. *c* section through the phragmocone, *d* longitudinal section through the siphuncle.

1934), two species are doubtless valid. *Protophragmoceras tyriense* Strand, 1934, has a compressed, curved shell with relatively long living chamber, and resembles the Late Silurian *P. neutrum* (Barrande, 1886). *P. sphynx* (Schmidt, 1858) with massive, weakly curved shell almost circular in cross section (pl. 7: 6) seems to be rather isolated. I know of no Early Silurian representatives of *Protophragmoceras*. Apart from the Scandinavian species of this genus, the only records are from the Ludlovian of Bohemia. There are some specimens in Barrande's collection at the Narodní Muzeum, Prague, attributable to two species, *P. neutrum* and *P. murchisoni*, each showing a rather narrow range of morphological variability, and differing in shell size and coiling. One of the specimens of *P. murchisoni* shows a terminal constriction at the aperture without any change in apertural outline. All other of Barrande's species assigned by Flower and Teichert (1957) to *Protophragmoceras*, as well as those erected by Flower after Barrande's illustrations, are based on specimens easily attributable to one or the other former species. *Phragmoceras beaumonti* Barrande, 1866, placed by Flower in the genus *Protophragmoceras*, appears to be a juvenile of *Phragmoceras broderipi* Barrande, 1866. *Protophragmoceras nonnulum* Zhuravleva, 1972, from the Borszczów Beds (Gedinnian) of the Podolia is a shell fragment of the associated species *Endoplectoceras podolicum* Zhuravleva, 1972. The genus *Endoplectoceras* differs from *Protophragmoceras* in its long, spiralic shell. It probably derived from the *P. neutrum* lineage. The oldest representative, *E. secula* (Barrande, 1865), occurs in the Ludlovian (?) of Bohemia. The poorly preserved specimen was described under the name *Antigyroceras spirale* by Barskov (1972) from Kazakhstan, while it probably belongs to this genus.

The *P. murchisoni* lineage probably gave rise to the most unique and persistent discosorid lineage: the Phragmoceratidae. These include markedly compressed, short shells with the aperture covered at maturity except for two moderately-sized, opposed openings. The smaller, siphonal opening certainly contained the funnel. The other one must thus have contained the head with tentacles. Some early specimens show a medial depression in the swelling around the head opening (Hedström 1917, pl. 4), corresponding to an unknown organ. The drop-like shell section, aperture elongation, and position of the openings comprise unequivocal evidence of the mode of locomotion. The animal moved normally to the shell long axis, with head and tentacles directed anteriorly, oppositely to position of funnel. A phragmocone fragment from the Llandoverian of Siberia (Miagkova 1967) may be the oldest record of the genus *Phragmoceras*. The genus has been reported mostly from the Wenlockian to Ludlovian (?) of North America (Foerste 1929, 1930, 1936; Foerste and Savage 1927). Most North American specimens, as well as those from the Wenlockian to Ludlovian of England (Blake 1882), and Wenlockian of Gotland, are poorly preserved. The richest and best preserved collections of *Phragmoceras* come from the Hemse Beds (Early Ludlovian) of Gotland (Hedström 1917) and coeval erratic boulders (Noetling 1883), and from the Ludlovian Kopanina Formation of Bohemia (Barrande 1865, 1877). There is morphologic variability at each locality, including adult size. The largest specimens are twice as large in diameter as the smallest ones. Sexual dimorphism may be superimposed on the intrapopulation variability, but one can not recognize any distinct classes in adult size or shell outline without biometrics (at least in the Barrande's and Naturhistoriska Riksmuseet collections). The variability of *Phragmoceras* contributed to the erection by various authors of a large number of species within samples taken from single localities. In my opinion, the absence of any morphological discontinuities between these supposed taxa indicates that all are part of the intrapopulation variation. There are only two unquestionable species in the Barrande's collection; namely, *P. imbricatum* with relatively elongate shell of circular section, and *P. broderipi* with considerably curved, compressed shell. *T. broderipi* is probably junior synonym of *P. arcuatum* Sowerby, 1839, from England. As judged from the excellent illustrations by Hedström (1917), the specimens from Gotland belong to three species different from their Bohemian congeners, showing a similar variation at a more advanced evolutionary level (in spite of their older age). These species are *Ph. lamellosum* Hedström, 1917, with spirally coiled shell, *Tubiferoceras proboscideum* (Hedström, 1917) and questionable *Ph. dentatum* Hedström, 1917.

The larval development took place within an egg capsule in *Phragmoceras*, as in all the other discosorids. In *Ph. broderopi* the protoconch approximates 8 mm in diameter, it shows a distinct "cicatrix" (cf. Erben and Flajs 1976) and growth lines over its entire surface. One may therefore claim that the egg was also approximately 8 mm in size. Hedström (1817) and Barrande (1877) have illustrated several apical parts of discosorid shells. The caecum is slightly elongate and attached tightly to the ventral shell surface (Hedström 1917: pl. 8: 3). Septal distance increases as a linear function of shell length.

Phragmoceras has well developed siphuncular deposits which are confined to the septal necks. They have mostly the form of a ring with indistinct radial grooves and split completely into radial lamellae if strongly developed (pl. 7: 4). Their radial nature has thus far not been recognized, even though Barrande presented, under the name *P. beaumonti*, a juvenile specimen of *P. broderipi* with excellently preserved radial lamellae (Barrande 1866, pl. 165: 26; the structure is much more clearly visible in the specimen than in the drawing). Flower (*in* Flower and Teichert 1957) assigned that specimen to the genus *Protophragmoceras*, and recognized the radial lamellae for "festooned deposits". Their radial structure was first recognized by Zhuravleva (1972) who correctly derived the Late Devonian *Bolloceras* (split by her into the genera *Pseudobolloceras*, *Nucites*, *Pseudophragmoceras*, and *Taxyceras*) from *Phragmoceras*, while their Middle Devonian congeners were placed in the order Oncoceratida. The family Taxyceratidae Zhuravleva, 1972, includes endogastric discosorids with elongate aperture along with some typical oncoceratids. Their only feature in common is the occurrence of radial deposits. I studied the material from both the Middle Devonian Hlubočepy Limestone of Bohemia and the Late Devonian of the Russian Platform. The nautiloids collected from the Hlubočepy Limestone are poorly preserved and deformed as a rule. The fauna is nonetheless so abundant that one is able to recognize BARRANDE'S fifteen species described from Hlubočepy as a single monospecific population. These species formed the basis for the erection of three distinct genera: *Bolloceras*, *Metaphragmoceras*, and *Paraconradoceras* (FOERSTE 1926; FLOWER 1938). The holotype of the type species of *Bolloceras* is the only undeformed specimen in the BARRANDE'S collection from Hlubočepy. The siphuncular structure displayed by *B. rex* (BARRANDE, 1865) *s. l.* has not been described in detail; its only known feature is the radial lamellar structure of the deposits. The species ?*Pseudophragmoceras arcanus* ZHURAVLEVA, 1972, described from juvenile specimens from the Emsian of the Northern Urals, is probably a *Bolloceras*. The shell curvature in both *B. arcanum* and *B. rex* is suggestive of their derivation from the *Phragmoceras arcuatum-Ph. labiosum* lineage. Stratigraphically higher *Bolloceras* has been recorded from the Frasnian and Famennian of central Russia (ZHURAVLEVA 1972). The latter material includes a few poorly preserved and incomplete specimens resembling the Bohemian ones, even though possibly with more strongly curved shell; and, in my opinion, does not substantiate the erection of six new species, four new genera, and one new family (ZHURAVLEVA 1972). Some poorly preserved specimens of *Bolloceras* have also been reported from North America (FLOWER 1938).

The Phragmoceratidae resemble the Gomphoceratidae with short, slightly endogastrically curved shell, divided aperture, and well developed radial lamellae in the siphuncle over its entire length. The Gomphoceratidae are widespread in the Silurian of North America (FLOWER 1943, FOERSTE 1928) and Europe (BARRANDE 1865, 1866; MUTVEI 1964). The ancestral form of the gomphoceratid aperture is probably shown by *Conradoceras conradi* BARRANDE, 1865, from the Late Ludlovian Kopanina Formation of Bohemia. In BARRANDE'S original collection, *C. conradi* is represented by a few specimens, taken from three localities, distinctive for their small size. The terminal aperture resembles the immature aperture of *Octamerella*, and the generic distinctness of *Conradoceras* seems to be questionable. In fact, this may be an extreme variety of concurring *O. callistoma*. The mature aperture of *O. callistoma*, known also from the Slite beds of Gotland, is divided into several pairs of sinuses decreasing ventrally in size, the dorsalmost two are much larger than the others. The position of the funnel opening indicates that the mode of locomotion was similar to, but probably less efficient than in *Phragmoceras*. However, the openings for the head and tentacles pointed vertically downwards, which suggests a different feeding habit. The population known from the Slite beds of Gotland, probably conspecific with Bohemian *Tetrameroceras rimosum* BARRANDE, 1865, shows very high variability in the form of mature aperture. It ranges from two pairs of narrow slits to *Octomerella*-like, with three pairs of lateral sinuses.

There are only two pairs of fissure-like sinuses in *Tetrameroceras bicinctum* (? = *T. rimosum*) from the Ludlovian Kopanina Formation of Bohemia and Hemse beds of Gotland, and in *T. pavidum* from the Přidolian of Bohemia. This may also be the case in *Hemiphragmoceras pusillum*, the type species of the genus, erected on poorly preserved specimens, much idealized in BARRANDE'S drawings (1865, pl. 52: 1-9).

The dorsal pair of apertural sinuses is indistinctly subdivided in *Gomphoceras panderi* (BARRANDE, 1865). In *G. panderi* the siphuncle shifts from a ventral to subcentral position, and the connecting rings change in ontogeny from inflated to cylindrical. *G. obovatum* SOWERBY, 1839, from the Ludlovian of England (BLAKE 1882) seems indistinguishable from *G. panderi*. It is associated with *G. pyriforme* SOWERBY, 1839, and differs from the latter only in preservation. *G. pyriforme* is the type species of the genus *Gomphoceras* SOWERBY, 1839, and by implication of the family Gomphoceratidae PICTET, 1854. My opinion is that it is conspecific with *G. obovatum* and probably also with *Hexameroceras panderi* (BARRANDE, 1865). I propose to retain the traditional names *Gomphoceras* (older, subjective synonym of *Hexameroceras* and *Codoceras*) and Gomphoceratidae (older synonym of Hemiphragmoceratidae). The poor preservation of the holotype of *G. pyriforme* is not considered sufficient cause for rejection of the name *Gomphoceras*, as supplementary topotypes have been described. *Pristeroceras timidum* RUEDEMANN, 1925, described from very poorly preserved specimens from the Late Silurian Syracuse Formation of New York (SWEET and LENTZE 1956) may also be junior synonym of *G. panderi.*

The phylogenetic relations of the Devonian forms with weakly curved shell and simple aperture (*Wadeoceras* TEICHERT, 1939, and *Polyelasmoceras* TEICHERT and GLENISTER, 1952, from Australia; *Urtasymoceras* ZHURAVLEVA, 1972, from the Southern Urals; and *Archiacoceras* FOERSTE, 1926, from Germany) have thus far remained unclear. I assign them to the Discosorida because of their endogastric, compressed shell. When considered jointly as the family Archiacoceratidae, they range from the Siegenian ("*Brachydomoceras*" *erectum* TEICHERT and GLENISTER, 1952) up to the Early Famennian (*Wadeoceras australe* TEICHERT, 1939). Their lamellae along the entire siphuncle, make them similar to the Gomphoceratidae, but some oncoceratids show the same structure. The European species *Archiacoceras subventricosum* (d'ARCHIAC and VERNEUIL, 1842) is unique among the archiacoceratids in its considerably inflated connecting rings (FLOWER 1943; CRICK and TEICHERT 1979). As judged from a mature phragmocone, collected at Gerolstein and housed at the University of Wrocław UWR 2006 and specimens illustrated by CRICK and TEICHERT (1979), *Archiacoceras* resembles the Ordovician Discosoridae in shell shape.

The systematic position of the genus *Flowerites* ZHURAVLEVA, 1972, is also unclear. It includes two Famennian undoubted species distant in age from any possible discosorid ancestors. Other species placed in this genus by ZHURAVLEVA (1972) have been erected on juvenile specimens of slightly endogastric oncoceratids. The genus may indeed have evolved from such oncoceratids (e.g. *Devonocheilus*), while its shell compression is a secondary feature. This hypothesis may be supported by the succession of the species. A single phragmocone with weakly endogastrically curved shell and little depressed to circular in section (pl. 7: 6; fig. 13c-d) has been found in the lower part of the *Cheiloceras* Zone (Famennian) at Jabłonna. This specimen may be assigned to *Flowerites austrirhiphaeus* ZHURAVLEVA, 1972, but its affinity to the oncoceratid genus *Devonocheilus* recorded thus far only in the Frasnian cannot be rejected. *F. austrirhiphaeus* may then be intermediate between the Frasnian *Devonocheilus* and *F. sobolewi* nom. nov. known from the *Platyclymenia* Zone of Łagów (pl. 7: 3-4; fig. 13a). The latter species is homeomorphic with the Ordovician-Silurian genus *Protophragmoceras.*

FLOWER and TEICHERT (1957) assigned to the Discosorida a large number of exogastric, depressed nautiloids which are here attributed to the order Oncoceratida. The order Discosorida was understood even more widely by ZHURAVLEVA (1972). In both cases the diagnostic feature of the order was the "thick connecting rings". The taxon delimited in this way is polyphyletic. Connecting ring thickness changes rather rapidly in evolution, as is illustrated by the Ellesmeroceratina. Relatively thick connecting rings occur even among the typical oncoceratids. Furthermore, a large number of Bohemian Silurian nautiloids assigned by FLOWER to the Discosorida show actually thin connecting rings. MUTVEI (1964) noted that the complex structure of connecting rings described by FLOWER reflects a post-mortem recrystallization. The supposed thick connecting ring (FLOWER and TEICHERT 1957; fig. 6, pl. 11) consists mostly of siphuncular and cameral deposits. The actual connecting ring can hardly be identified. The considerable development of siphuncular deposits (polyptychocones) is also not diagnostic because such structures arose independently in several high-rank taxa, the Endoceratina, Orthoceratida, and Oncoceratida. As understood by FLOWER and TEICHERT, the order Discosorida is a heterogeneous group of bulgy nautiloids associated with shallow-water (see WESTERMANN 1973) facies. It includes various forms attributable to both the proper Discosorida and Oncoceratida, due to homeomorphy instead of close phylogenetic relationship. The primitive oncoceratids and discosorids are separated by a wide morphological gap. This gap, however, tended to decrease in the course of the evolution. One may suppose that the basic difference between the two orders is in the structure of the soft body, but the relevant data are unfortunately very scarce (see Sweet 1959).

The discosorid cameral deposits have usually only the form of a thin layer covering the siphuncle; while the siphuncular deposits are developed virtually over the entire length of the siphuncle, making up a solid layer apically (Flower and Teichert 1957). This suggests rather poor exchange of the cameral liquid confined to the earliest chambers. This may be related to the supposed shallow-water, bottom dependent life (Flower and Teichert 1957; Westermann 1973).

Proposed systematics.—

Discosoridae Teichert, 1931

[= Cyrtogomphoceratidae Flower, 1940]

Brevicones with marginal siphuncle and simple mature aperture.

Protophragmoceras Hyatt, 1900; *Cyrtoceras murchisoni* Barrande, 1866
[= *Strandoceras* Flower, 1946]

Considerably curved shell with living chamber of constant diameter.

Endoplectoceras Foerste, 1926; *Trochoceras secula* Barrande, 1865
[= *Antigyroceras* Barskov, 1972]

Like *Protophragmoceras* but with longer, coiled shell.

Cyrtogomphoceras Foerste, 1924; *Oncoceras magnum* Whiteaves, 1890

Slightly curved shell with tapering living chamber.

Konglungenoceras Sweet, 1959; *K. norvegicum*

Like *Cyrtogomphoceras* but with considerably curved shell.

Discosorus Hall, 1852; *D. conoideus*

Robust, slightly curved brevicones with tapering living chamber.

Phragmoceratidae Hyatt, 1900

[= Bolloceratidae Zhuravleva, 1962; Taxyceratidae Zhuravleva, 1972]

Brevicones with T-shaped, elongate aperture and radial siphuncular deposits.

Phragmoceras Broderip, 1839; *P. arcuatum* Sowerby, 1839

Fig. 14

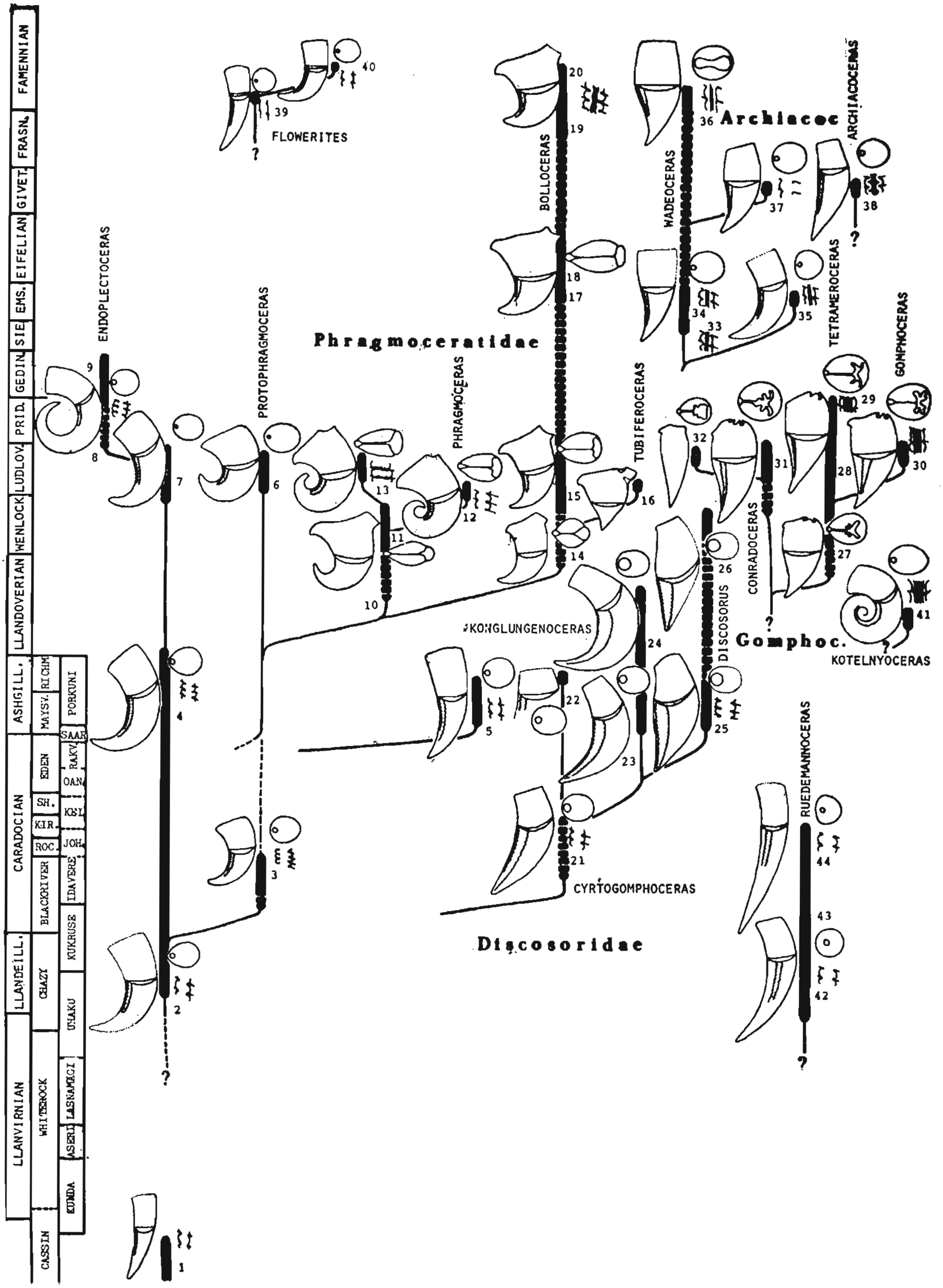
Hypothetical phylogenetic relationships among members of the order Discosorida Flower, 1950. 1 *Clelandoceras rarum* Flower, 2 *Strandoceras strandi* Sweet; 3 *Protophragmoceras* sp. (pl. 7: 2); 4 *Protophragmoceras tyriense* Strand; 5 *Protophragmoceras sphynx* (Schmidt); (pl.7: 7); 6 *Protophragmoceras murchisoni* (Barrande); 7 *Protophragmoceras neutrum* (Barrande) = *P. barrandei* Flower, *P. virgula* (Barrande), *P. conspicuum* (Barrande), *P. obliquum* Flower; 8 *Endoplectoceras secula* (Barrande), *Antigyroceras orientale* Barskov; 9 *Endoplectoceras podolicum* Zhuravleva = = *Protophragmoceras nonnulum* Zhuravleva; 10 *Phragmoceras* sp. Miagkova; 11 *Phragmocerina lineolata* Whiteaves; 12 *Phragmoceras lamellosum* Hedström; 13 *Phragmoceras broderipi* Barrande (pl.7: 5), *P. beaumonti* Barrande; 14 *Phragmoceras nelsonense* Parks; 15 *Phragmoceras arcuatum* Sowerby, *P. labiosum* Barrande; 16 *Tubiferoceras proboscideum* (Hedström), *T. sauvagei* Foerste, *T. vantutti* Foerste and Savage; 17 *Pseudophragmoceras arcanum* Zhuravleva; 18 *Bolloceras rex* (Barrande) = *Metaphragmoceras verneuilli* (Barrande), *Paraconradoceras rigescens* (Barrande); 19 *Taxyceras audax* Zhuravleva = *Pseudobolloceras necopinum* Zhuravleva, *Bolloceras hartii* Flower; 20 *Pseudophragmoceras moderatum* Zhuravleva = *Nucites implicatus* Zhuravleva; 21 *Cyrtogomphoceras baffinense* Foerste; 22 *Diestoceras* sp. Sweet; 23 *Cyrtogomphoceras* cf. *thompsoni* Foerste (Sweet 1955); 24 *Konglungenoceras norvegicum* Sweet; 25 *Cyrtogomphoceras dowlingi* (Foerste); 26 *Discoceras austini* Foerste; 27 *Tetrameroceras faberi* Flower; 28 *Hemiphragmoceras pusillum* (Barrande), *Tetrameroceras bicinctum* (Barrande); 29 *Phragmoceras pavidum* Barrande; 30 *Hexameroceras panderi* (Barrande) = *Codoceras indomitum* (Barrande), *Gomphoceras pyriforme* Sowerby, *Pristeroceras timidum* Ruedemann; 31 *Octamerella callistoma* (Barrande), *Hexameroceras byronense* Foerste; 32 *Conradoceras conradi* (Barrande); 33 *Brachydomoceras erectum* Teichert and Glenister; 34 *Macrodomoceras hewitti* Teichert and Glenister, *Pectinoceras subtrigonum* (M'Coy); 35 *Polyelasmoceras aduncum* Teichert and Glenister; 36 *Wedeoceras australe* Teichert; 37 *Urtasymoceras urtasymense* Zhuravleva; 38 *Archiacoceras subventricosum* (d'Archiac and Verneuil); 39 *Flowerites austrirhipaeus* Zhuravleva; 40 *Flowerites ellipticus* (Sobolev) (pl. 7: 3-4); 41 *Kotelnyoceras arcticum* Balaschov; 42 *Ruedemannoceras boycii* (Whitfield); 43 *Madiganella magna* Teichert and Glenister; 44 *Ulrichoceras beloitense* Foerste. For alternative interpretation of *Flowerites* and *Kotelnyoceras* see fig. 29. *Ruedemannoceras* may be attributable to the Orthoceratina.

Curved shell with poorly developed siphuncular deposits confined to septal necks.

Tubiferoceras Hedström, 1917; *Phragmoceras proboscideum*

Very short shell; head opening of aperture separated with shelf.

Bolloceras Foerste, 1926; *Phragmoceras rex* Barrande, 1865



[= *Metaphragmoceras* Flower, 1938; *Paraconradoceras* Foerste, 1926; *Pseudophragmoceras* Zhuravleva, 1972; *Pseudobolloceras* Zhuravleva, 1972; *Taxyceras* Zhuravleva, 1972; *Nucites* Zhuravleva, 1972]

Like *Phragmoceras* but with well developed radial lamellae along entire siphuncle.

Kotelnyoceras Balaschov, 1979; *K. arcticum*

Tightly coiled shell.

Gomphoceratidae Pictet, 1854

[= Hemiphragmoceratidae Foerste, 1926]

Slightly curved brevicones with mature aperture composed of paired sinuses.

Gomphoceras Sowerby, 1839; *G. pyriforme*

[= *Hexameroceras* Hyatt, 1883; *Codoceras* Hyatt, 1900; *Pristeroceras* Ruedemann, 1925]

Aperture with two pairs of head sinuses; dorsal sinuses indistinctly subdivided.

Tetrameroceras Hyatt, 1884; *Phragmoceras bicinctum* Barrande, 1865

[= *Hemiphragmoceras* Hyatt, 1900]

Aperture with two pairs of head sinuses.

Conradoceras Foerste, 1926, *C. pseudoconradi* = *Phragmoceras conradi* Barrande, 1865

[= *Octamerella* Teichert and Sweet, 1962]

Aperture with several pairs of head sinuses.

Archiacoceratidae Teichert, 1939

[=Polyelasmoceratidae Shimansky, 1958]

Slightly curved brevicones with simple mature aperture; siphuncular deposits radial lamellar.

Archiacoceras Foerste, 1926; *Phragmoccratites subventricosum* d'Archiac and Verneuil, 1842

[= *Polyelasmoceras* Teichert and Glenister, 1952]

Relatively long shell.

Wadeoceras Teichert, 1939; *W. australe*

[= *Brachydomoceras* Teichert and Glenister, 1952; *Macrodomoceras* Teichert and Glenister, 1952; *Urtasymoceras* Zhuravleva, 1972; *Pectinoceras* Teichert and Glenister, 1952]

Inflated brevicone.

Incertae sedis

Flowerites Zhuravleva, 1972; *F. austrirhiphaeus*

Homeomorph of *Protophragmoceras*; possibly descendant of *Devonocheilus* (Oncoceratida).

Ruedemannoceras Flower, 1940; *R. boycii*

[= *Franklinoceras* Flower, 1957; *Madiganella* Teichert and Glenister, 1952; *Ulrichoceras* Foerste, 1928]

Somewhat depressed shell with subcentral siphuncle; possibly related to *Cyrtactinoceras* (Orthoceratida).

Order Oncoceratida Flower, 1950

Diagnosis. — Mostly exogastrically curved shells, ventral siphuncle with inflated connecting rings and short living chamber.

Remarks. — Some advanced oncoceratid groups may show a secondarily slightly endogastrically curved shell with central siphuncle and/or concave connecting rings.

Phylogeny (figs. 17, 18, 27, 32). — Tracing a boundary between the Oncoceratida and Ellesmeroceratina is a difficult task. The siphuncular structure cannot serve as a single criterion because not all ellesmeroceratids show a cylindrical siphuncle, and not all have a thicker connecting ring than in the oncoceratids. More diagnostic value may be attributed to the length of a living chamber. The oldest known oncoceratids occur in the Middle Kundan (Latest Arenigian) of Öland, Sweden. These yet undescribed forms are closely related to another species from Folkeslunda limestone of Öland (Llanvirnian) and erratic boulders of the same age (fig. 18a-b; pl. 9: 1). The single juvenile specimen from erratic boulder differs from later representatives of *Oonoceras* exclusively in its small shell and marginal siphuncle. Although the microstructure of the connecting ring cannot be recognized because of recrystallization, one may claim that its considerable thickness (fig. 15b) is only partly due to the occurrence of cameral deposits. If this interpretation is valid, the form under discussion would indeed appear morphologically intermediate between the Ellesmeroceratina and Oncoceratida in shell outline, marginal position of the siphuncle, and the considerable thickness of the connecting rings. It differs from *Bassleroceras annulatum* TEICHERT and GLENISTER, 1954 from the Early Arenigian Emanuel Limestone, Australia, in its larger-sized and more curved shell with supposedly the same length of the living chamber (see TEICHERT and GLENISTER 1954). Some undescribed Baltic species fill the gap between these forms. One may thus claim that the Oncoceratida derived from exogastric ellesmeroceratids of the genus *Bassleroceras*. Unfortunately, none of the Arenigian specimens of *Bassleroceras* shows a complete living chamber; it may be short in *B. perseus* (BILLINGS), the type species of the genus (see ULRICH *et al.* 1944). This contradicts a close relationship between the Bassleroceratidae and Tarphyceratidae, as claimed by FLOWER (1976). The Early Ordovician Tarphyceratida differ from *Oonoceras* in their very long living chamber. The proper systematic position of *Bassleroceras* cannot be determined without revision of the North American collections.

The shell outline of *Oonoceras* sp. from the Baltic Llanvirnian (fig. 15) persisted in a more or less the same form to the end of the Silurian (fig. 15c; pl. 8: 2). However, the pre-Ludlovian record is very scanty. The few specimens from the Late Ordovician of North America (FLOWER 1946) are so fragmentary and poorly preserved that their attribution to *Oonoceras* is disputable. BARSKOV (1972) described under the names *Miamoceras longum* and *Tschingizoceras tschingizense* some Late Ordovician nautiloids from Kazakhstan which probably belong to *Oonoceras*. I believe that *Neoceras pumilum* MIAGKOVA, 1967, from the Llandovery of Siberia, and *Laureloceras cummingsi* FLOWER, 1943, from the Wenlockian Laurel Limestone of North America, are also congeneric with *Oonoceras*. The largest material showing the morphological variation of *Oonoceras* has been collected from the Ludlovian Kopanina Formation and the Přidolian of Bohemia. *O. acinaces* BARRANDE, 1866, the type species of the genus, shows a long shell with short living chamber without constriction of its adapertural part. The shell is initially more curved than in its adult part. In my opinion, the topotype population of *O. acinaces* recorded from Dlauha Hora includes also *Cyrtoceras sociale*, *C. plebeium*, *C. elongatum*, and *C. hoernesi*. To determine species ranges also of other localities, much detailed work is needed. BARRANDE'S species are clearly heterogeneous, based upon morphological similarity of widely different forms at a certain ontogenetic stage (e.g. *Cyrtoceras circumflexum*). The morphological variation consists in the length of apical coiling (a complete whorl in the extreme case) as well as in the prominence of ornamentation produced by irregular growth lines. Neither of these characters permits recognition of distinct classes that might reflect biospecies. The Přidolian specimens collected at Karlštein show in average more coiled juvenile stage, but, because of the lack of adult stages comparable to those of the Ludlovian population, one is unable to say whether or not these are conspecific populations. The connecting rings are fairly slender in the juveniles of *O. acinaces*, but they change in outline during ontogeny. The adult connecting rings are rather thick (fig. 15c) which confirms the supposed primitive state of the genus.

The genus *Zitteloceras* recorded mostly from the Early Caradocian of Canada, seems to be related to *Oonoceras*. In spite of rather abundant records, its shell shape is poorly known. It resembles *Oonoceras*, as well as the associated but more advanced *Richardsonoceras*, in its considerably curved shell with supposedly non-tapering adult living chamber (see FOERSTE 1928, WILSON 1961). The shell is circular in cross section, and dorsally somewhat flattened. Its most characteristic feature is the shell ornamentation produced by conspicuous, transverse lamellae, almost straight at the shell surface but undulated at the free margin (see STEELE and SINCLAIR 1971). Such ornamentation occurs also in a shell fragment described under the name *Crenuloceras giganteum* from the Late Llanvirnian Antelope Valley Limestone (FLOWER 1968, pl. 23: 12). The large size of the latter differs from *Zitteloceras*; there, however, are no data on the internal structure allowing its reliable assignment to the Cephalopoda. Nevertheless,

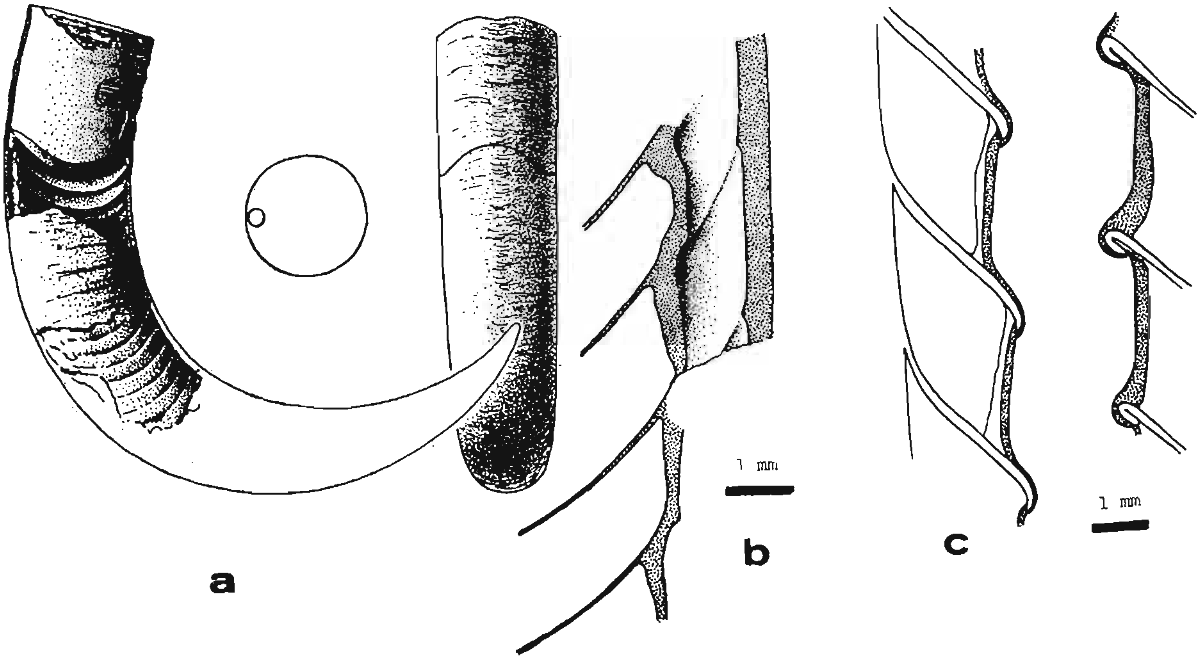


Fig. 15
Oonoceras sp.; ZPAL N/101 (pl. 9: 1), boulder E-138, *E. foliaceus* Zone, Lasnamägian, Międzyzdroje, Poland. *a* Reconstruction of the shell; ×1.3; *b* longitudinal section through the siphuncle. *Oonoceras acinaces* (Barrande, 1866); ZPAL N/108 (pl. 8: 2), borehole Parczew IG 10, depth of 1230 m, Ludlovian (?); *c* Longitudinal section through the siphuncle.

Flower erected a new genus solely on the basis of this specimen. According to Flower (1975: 144), further findings of congeneric specimens are indicative of its trocholitid (Tarphyceratida) affinities. The earliest known representative of *Zitteloceras* is thus the Chazyan species *Z. praecedens* Flower, 1952, its youngest congener is *Z. hintzi* (Foerste, 1910) from the Ashgillian of North America (Flower, 1946).The latter species does not significantly differ from the Early Caradocian form *Z. hallianum* (d'Orbigny, 1850). Large number of species assigned to *Zitteloceras* have been described from the Early Caradocian of Ontario (Wilson 1961) and New Foundland (Flower, 1952*a*), as well as from the Ashgillian of Ohio (Flower 1946) and England (Teichert 1940); their distinctiveness is disputable.

The Silurian *Hercocyrtoceras* is closely related to *Zitteloceras*. *Hercocyrtoceras* occurs in the Wenlockian of Quebec and Gotland and the Late Silurian of Bohemia, well known due to Barrande (1866) and Horný (1965). Its shell shape is identical to *Zitteloceras*, whereas the structure of its thick-walled siphuncle resembles that in *Oonoceras* (see Horný 1965); the siphuncular structure of typical representatives of *Zitteloceras* has remained unknown. The youngest species of the genus is *Hercocyrtoceras* (*Corbuloceras*) *corbulatum* (Barrande, 1866), from the Přidolian of Karlštein near Prague. The peculiar shell ornamentation in *Hercocyrtoceras* suggests that this is a form transitional between the Ordovician *Zitteloceras* and the Early Devonian *Rutoceras*. The affinity of the Devonian Rutoceratidae s.s. to the former two genera is so striking that their phylogenetic relationship is in little doubt. The only difference consists in a considerable elongation of the loosely coiled shell of the Devonian rutoceratids; there is a close resemblance in shell section and ornamentation, as well as in siphuncular structure (Collins 1969). The Rutoceratidae *s.s.* are here understood to include only longitudinally ribbed forms. They are rather poorly known (see e.g. Holzapfel 1879; Whitborne 1892; Whiteaves 1891). Apart from the work by Collins (1963) on *Rutoceras eifeliense* (d'Archiac and Verneuil), there has been no modern research on this group. A shell fragment with preserved siphuncle attributable to *Hindeoceras* sp. (pl. 9: 2) found in the Givetian Skały Formation at Świętomarz, the Holy Cross Mts,. Poland, confirms the hypothesis that the Rutoceratidae are related to *Hercocyrtoceras*. Because of the scarcity of the available data, rutoceratid evolution is poorly known. In addition to gyroconic forms, the Rutoceratidae include also some orthoconic to cyrtoconic genera. *Cartersoceras*, resembling very closely *Hindeoceras* (= *Tetranodoceras*) in shell ornamentation, may be secondarily orthoconic. In turn, the shell of *Aphyctoceras* is much more finely ornamented with low longitudinal ribs and transverse annulations; this genus has been reported from the Eifelian of Novaya Zemla (ZHURAVLEVA 1974) and the Givetian of Germany (HOLZAPFEL 1897). This supposed descendant of the *Zitteloceras-Hercocyrtoceras* lineage links the typical rutoceratids with *Capricornites* which lacks any longitudinal ribs; the latter genus has been recorded from the Emsian of the Urals (ZHURAVLEVA 1974) and from the Eifelian of Bohemia (BARRANDE 1865). The Bohemian species *Capricornites annulatum* (BARRANDE, 1865) found in the dark limestones at Lochkov (G-g_1 in BARRANDE's terms, probably the Choteč Limestone) shows excellently preserved retractor muscle scars (BARRANDE 1865, pl. 44: 4-7) with a metameric pattern typical of the Oncoceratida.

The genus *Ptenoceras* is commonly attributed to the Rutoceratidae, but it resembles also the nautiloid family Uranoceratidae and its systematic position is far from being established. *Ptenoceras alatum* (BARRANDE, 1865), known from abundant and excellently preserved specimens from neptunian dykes in the Siegenian Koněprusy Limestone of Bohemia (pl. 42: 2), has a loosely coiled, depressed shell. Beginning with the second whorl, periodic lateral "auricles" appear on the shell, resembling funnel-shaped endings of the ribs in *Rutoceras*, as well as the spines in *Hercoceras*. The oncoceratid affinities of *Ptenoceras* are suggested by the muscle scar pattern recorded from *Doleroceras resimum* ZHURAVLEVA, 1972, from the Early Eifelian of the Urals. The shell shape of *D. resimum* resembles closely that of *Ptenoceras alatum*. Lateral spines occur at the adapertural part of the living chamber in *P. resimum*, resembling the "auricles" of *P. alatum*. The retractor scar is metamerically subdivided in *P. resimum*, as in typical oncoceratids; furthermore, there are two predominant ventral scars, which resemble those of the Ordovician (SWEET 1959) and Llandovery (MIAGKOVA 1967) oncoceratids. The scar belt is shifted adaperturally at the ventral side. The affinity in muscle scar pattern, however, can not be regarded as a proof for the position of *Ptenoceras* and *Doleroceras* in the Oncoceratida. Such a metameric muscle scar pattern arose also independently in *Discoceras* (Tarphyceratida) and *Pictetoceras* (Ellesmeroceratina). In fact, such a pattern may also have derived from the pattern typical of *Uranoceras* (Nautilida). The main evidence for the supposed oncoceratid affinity of *Ptenoceras* was supplied by BARRANDE (1865, pl. 44: 15-16) who described radial lamellae in the siphuncle of *Ptenoceras*. I re-examined the specimen illustrated by BARRANDE, as well as several others, and found no trace of radial, lamellar siphuncular structures. The Rutoceratidae have thus far been considered ancestral to, and placed in the Nautilida. Their morphology and stratigraphic position clearly contradict this hypothesis.

A very small oncoceratid species with straight and depressed shell occurs in the Ludlovian Kopanina Formation of Bohemia and in the Hemse beds of Gotland. It has been described by BARRANDE (1866, pl. 148: 16-23) from Bohemia under the names *Cyrtoceras castor* and *C. pollux*. It resembles in external morphology the bactritids but differs from the latter group in its inflated connecting rings, short living chamber, and densely spaced septa, all characteristic of the oncoceratids. This is probably a new genus, possibly related to *Oonoceras*.

The genus *Richardsonoceras* derived probably from *Oonoceras* through further shortening and coiling of the shell. This relationship is suggested by shell morphology of the oldest known representative of *Richardsonoceras*, *R. fallax* (BILLINGS, 1857) = *R. simplex* (BILLINGS, 1857), from the Early Caradocian of Canada (WILSON 1961). A large sample of this species has been described under various specific and generic names from the type formation, permitting reconstruction of the complete shell. The shell is considerably curved in the initial stages, and the

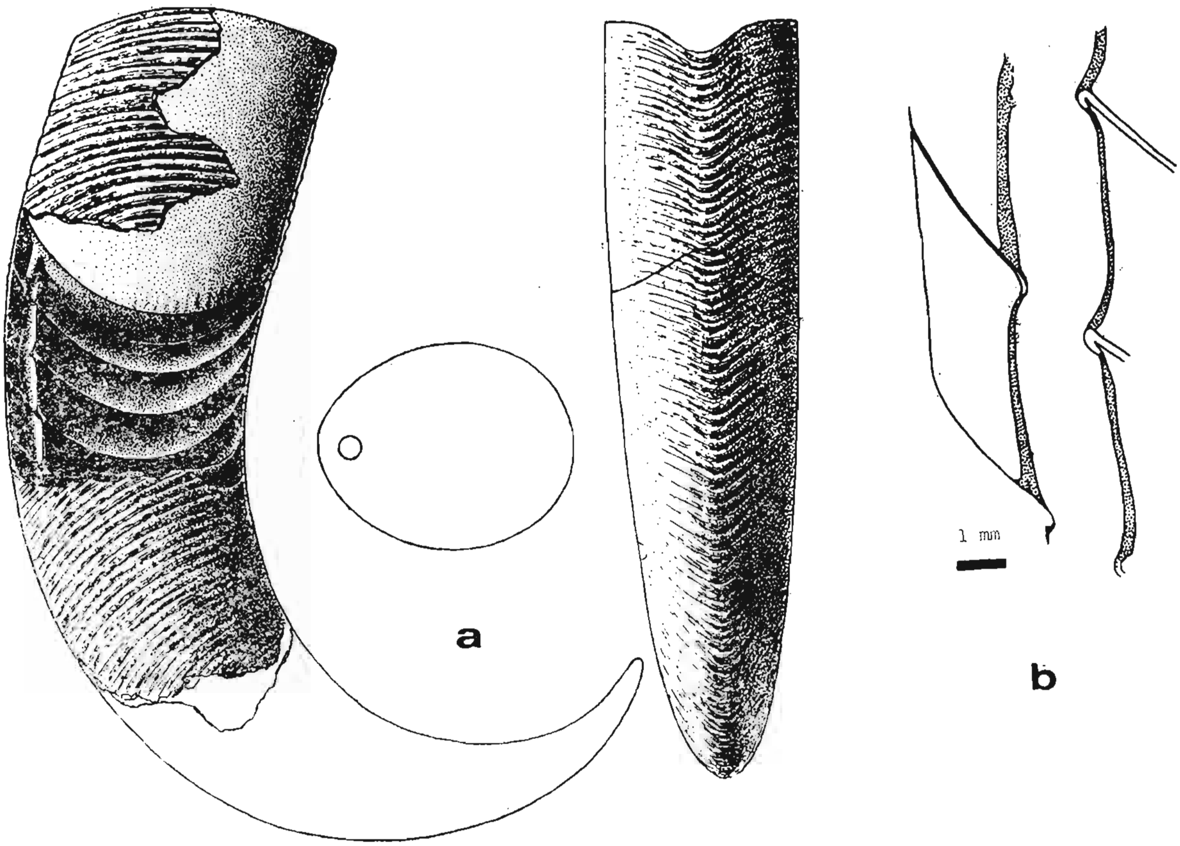


Fig. 16
Richardsonoceras sinuososeptatum (Flower, 1861); UWR 3230s (pl. 8: 1); paratype, erratic boulder, Ashgillian (?), Zawidowice, Poland. *a* Reconstruction of the subadult shell; *b* longitudinal section through the siphuncle.

mature shell shows a complete whorl. The living chamber is short, with transverse aperture, almost cylindrical adaperturally. The siphuncular structure is not known in detail but, as judged from well preserved silicified specimens described under the generic name *Loganoceras*, differs little from *Oonoceras* (see Steele and Sinclair 1971). In spite of the taxonomic splitting, the variability of the total sample is relatively small. Some specimens of *Richardsonoceras* have also been reported from the Late Ordovician of the Baltic area (Romer 1861, Strand 1935). They are shorter than *R. fallax*, which distinguishes them from *Oonoceras* but makes them closer to various Silurian forms assigned here to *Richardsonoceras* (fig. 16; pl. 9: 1). The taxonomy of this Baltic *Richardsonoceras* involves complex nomenclatural problems discussed below (see p. 188). The only preserved specimen of Roemer (pl. 9: 1) is a phragmocone mould with traces of coarse ornamentation. The pattern of growth lines indicates a deep funnel sinus (fig. 16). The siphuncle structure is typical of the primitive oncoceratids (fig. 16). In turn, "*Beloitoceras*" *heterocurvatum* Strand, 1935, is much smaller with distinctly tapering final chamber. The available material is too scarce to assess if there is one or two species. Strand (1935) defined his species very broad, to include also endogastric forms separated later by Sweet (1959) as a distinct species *Parryoceras strandi*. The Bohemian Silurian oncoceratids illustrate that a single population may indeed include both exo- and endogastric forms; however, this is rather not the case of *B. heterocurvatum*.

The richest collections of relatively breviconic, considerably coiled oncoceratids attributable to *Richardsonoceras* come from the Late Silurian of Bohemia. The enormous morphological variability of them presents a serious taxonomic problem. The hundreds of specimens collected from various localities of the Kopanina Formation and assigned by BARRANDE to 35 species present a morphological continuum, from slender forms close to *Oonoceras acinaces* ("*Cyrtoceras baculoides*"), through massive, considerably coiled ones ("*C. patulum*", "*C. haueri*"), to short and strongly coiled ones attributable probably to a new genus. One can hardly distinguish any morphological classes in the continuum presented in fig. 17. Even when only two species are distinguished, *Richardsonoceras patulum* (BARRANDE, 1866) and *R. haueri* (BARRANDE, 1886), one can not be sure that these are true biospecies. There is a variation in initial coiling and shell expansion rate, as well as in ornamentation (irregular growth lines). Fossil population sampled at different localities vary in shell robustness, and prominence of ribs produced by growth.

The wide range of intrapopulation variability recorded from *Richardsonoceras* in the Bohemian Silurian is rather surprising. An explanation can be found in some mechanism of shell growth and their relations to environmental factors. The external morphology of the nautiloid shell results, as in most other mollusks, from secretory activities of the mantle margin. Ontogenetic changes in shell shape are therefore caused mostly by a change in the shape and size of the mantle margin. The size of the mantle margin depends on the size of the living chamber, and by implication on the soft body weight. The growth of the mantle margin in diameter is rarely strictly linearly correlated with the rate of marginal accretion (i.e. the growth of shell in length). Usually the rate of shell diameter increase is low at the early juvenile stages, rapidly increasing at the subadult stages, and declining again at the final ontogenetic stages. This growth pattern of shell is common to most nautiloids but it is much more easily recognizable in brevicones than in longicones. It is especially well exemplified by the beet-like shell outline in breviconic oncoceratids (fig. 27 and pl. 15: 1).

The comparison of the actual changes in the rate of increase of shell diameter relative to the growth of shell in length, in two species with widely differing shell shape, *Richardsonoceras patulum* (pl. 8: 3) and *R. haueri* (pl. 8: 4), indicates that a difference in the patterns of these changes is of little diagnostic value. The irregular changes observed in *R. patulum* (fig. 35b) suggest an extrinsic, environmental influence. More favourable environmental conditions, permitting a higher rate of increase in body weight, may considerably modify the shell geometry. The observed differences between *R. haueri* and *R. patulum* (fig. 24) may thus be of accidental nature. There is little doubt, however, that the ontogenetic pattern recorded in *Lysagoraceras* sp. (pl. 14: 8; fig. 24c) is strongly genetically controlled.

A difference in growth rate between the dorsal and ventral shell sides also is among the controlling factors of nautiloid shell shape, resulting in spiral coiling. RAUP (1967) and BAYER (1978) reduced the variation in outline of spirally coiled ammonoid shells to a variation in growth rate of the radius of shell spiral. The latter author assumed also that a spiral form is among the characters programmed by the mollusk genome and presented differential equations to describe the effects of extrinsic disturbance on phenotypic accomplishment of the genetic program (i.e., the logarithmic spiral). In my opinion, the radius of a spiral is of little biological meaning especially in loosely coiled forms with whorls not-attached to one another. I believe that a difference in growth rate between the shell sides is the only cause for the spiral coiling of a shell.

The above discussed phenomena bear on some troublesome taxonomic problems. Taken for granted the non-linear (in relation to length) nature of a shell diameter increase in ontogeny, the apical angle is without any diagnostic value if it is not referred to a particular ontogenetic stage. The changes in shell coiling or inflation may also be without any taxonomic value because they may depend upon extrinsic, environmental factors, or reflect a weak (if any) correlation in time among various factors controlling shell ontogeny.

In the Late Silurian of Bohemia some forms occur with short and very strongly curved shell, probably related to *Richardsonoceras*. The shell coiling may have induced a change in cross section of the adult shell, which is circular to slightly depressed in the group under discussion. Large specimens supposedly representative of a single species, "*Cyrtoceras*" *tardum* Barrande, 1886, occur abundantly in the Wenlockian (?) of Dvorce and the Přidolian of Karlštein. Barrande himself erected 19 species on the material from Dvorce, conspecific with or closely related to "*C.*" *tardum*. Large shells of "*C.*" *tardum* occur with very similar but small shells of "*C.*" *circumflexum* at Karlštein. Further research is needed to learn whether this is sexual dimorphism. The specific identity of related forms from other localities with "*C.*" *tardum* remains thus far uncertain.

The genus *Osbornoceras* from the Llandoverian of North America (Foerste 1936) and Siberia closely resemble the above discussed Bohemian forms, except for its T-shaped aperture. A Siberian species resembles the type species so closely that their distinction may be questioned; nevertheless, it was originally described under a separate generic name, *Edenoceras hiliferum* Miagkova, 1967, and assigned to the order Discosorida. This demonstrates the ambiguity in ordinal diagnoses of the Oncoceratida and Discosorida. This ambiguity is partly due to very poor knowledge of the genus *Oncoceras*, nominative of the entire order.

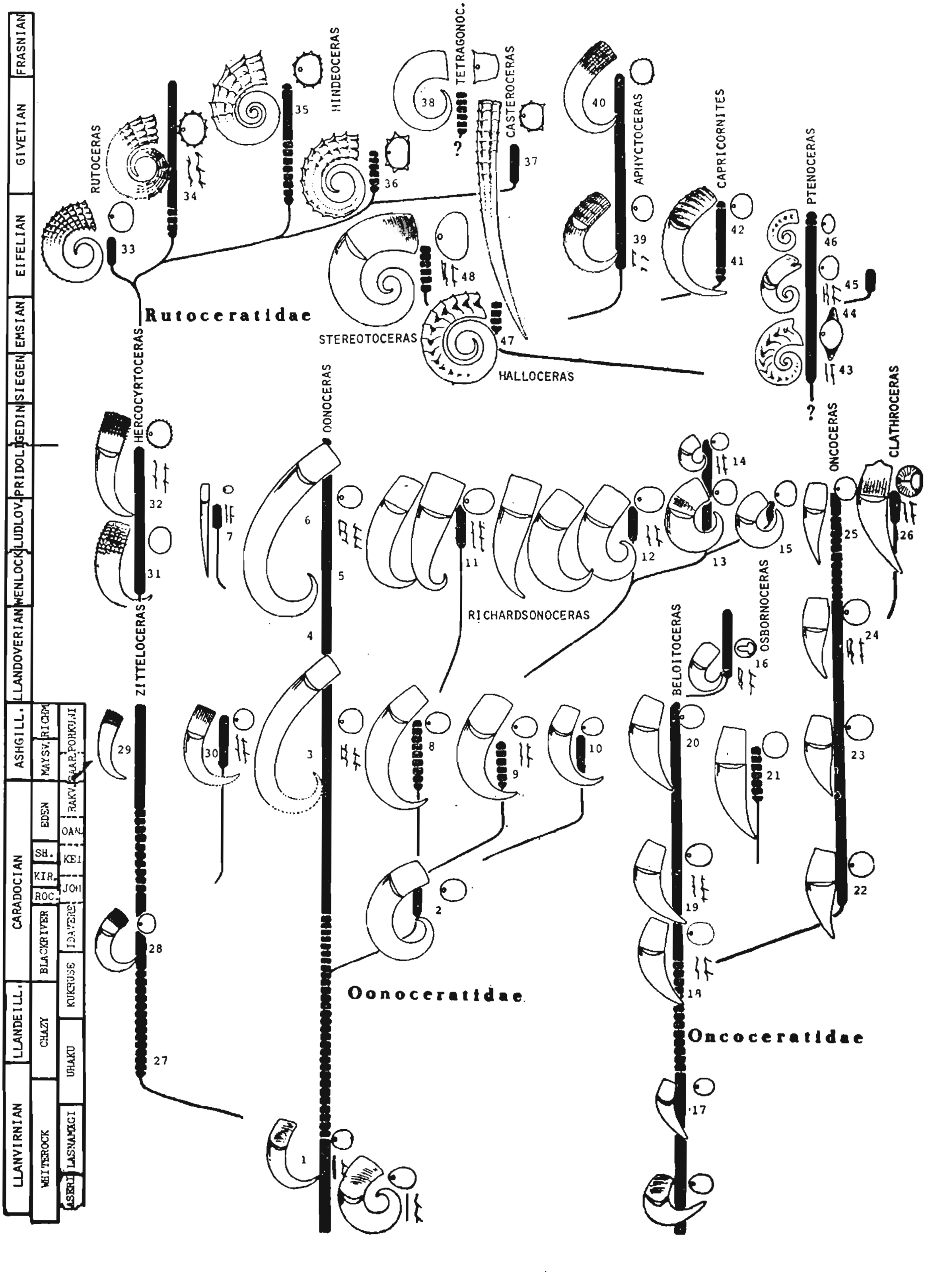
The genus *Oncoceras*, as well as the whole family Oncoceratidae, is characterized by short, weakly curved, bulgy shell and has been recorded mostly from the Ordovician of North America. Poor preservation and vague descriptions of the material have resulted in much taxonomic confusion in the Oncoceratidae.

The oldest described representative of the family is *Leonardoceras parvum* Flower, 1968, known from a single poorly preserved specimen from the Late Llanvirnian Antelope Valley Limestone. Very similar, much better preserved specimens occur in the Middle Kundan of Öland. The only difference from later, typical species of *Beloitoceras* is in their smaller shells. *Beloitoceras stoermeri* Sweet, 1958, from the Early Caradocian Lower *Chasmops* Limestone, Norway, appears as the only Ordovician oncoceratid with well known internal structure. Its relatively wide siphuncle shows little inflated connecting rings, especially at the ventral side. The best preserved oncoceratid shell outline is shown in material from the Early Caradocian of Canada. A large number of oncoceratid species have been described from those strata (Wilson 1961), of which only two species seem to be well founded. *Beloitoceras isodorum* (Billings, 1865) has a more strongly curved, slightly compressed shell closely resembling the ancestral oncoceratids. *Oncoceras constrictum* Hall, 1847, shows an almost straight, very inflated shell.

Fig. 17

Hypothetical phylogenetic relationship among members of the families Oonoceratidae, Oncoceratidae, and Rutoceratidae. 1 *Oonoceras* sp. (fig. 15a, b; pl. 9: 1); 2 *Richardsonoceras simplex* (Billings), *Loganoceras regulare* (Billings); 3 *Miamoceras longum* Barskov, *Tschingizoceras tschingizense* Barskov; 4 *Neoceras pumilum* Miagkova; 5 *Laureloceras cumingsi* Flower; 6 *Oonoceras acinaces* (Barrande) (fig. 15c; pl. 8: 1), *Shuranoceras dolmatovi* Barskov; 7 *Cyrtoceras castor* Barrande; 8 *Richardsonoceras xiushuanense* Chen and Liu; 9 *Richardsonoceras sinuososeptatum* (Roemer) (fig. 16a, b; pl. 8: 1); 10 *Beloitoceras heterocurvatum* Strand; 11 *Richardsonoceras patulum* (Barrande) (pl. 8: 3; 9: 3); 12 *Richardsonoceras haueri* (Barrande) (pl. 8: 4); 13 *Cyrtoceras tardum* Barrande; 14 *Cyrtoceras circumflexum* Barrande; 15 *Cyrtoceras inflexens* Barrande; 16 *Osbornoceras swinnertoni* Foerste, *Edenoceras hiliferum* Miagkova; 17 *Leonardoceras parvum* Flower; 18 *Beloitoceras stoermeri* Sweet; 19 *Beloitoceras isodorum* (Billings), *B. pandion* (Hall); 20 *Beloitoceras amoenum* (Miller), *Neumatoceras gibberosum* Foerste; 21 *Miamoceras shideleri* Flower; 22 *Oncoceras constrictum* Hall; 23 *Oncoceras arlandi* Flower; 24 *Oratoceras sibiricum* Zhuravleva; 25 *Talattoceras inflatum* Miagkova = *T. crenatum* Miagkova; 26 *Clathroceras sulcatum* (Barrande); 27 *Zitteloceras praecurrens* Flower; 28 *Zitteloceras hallianum* (d'Orbigny); 29 *Zitteloceras hintzi* (Foerste), *Ringoceras praecurvum* Strand; 30 *Piersaloceras gageli* Teichert, *Zitteloceras costatum* Teichert; 31 *Hercocyrtoceras amator* (Billings); 32 *Corbuloceras corbulatum* (Barrande); 33 *Rutoceras jason* (Hall), *Goldringia cyclops* (Hall); 34 *Gyroceras tredecimum* (Phillips), *Rutoceras eifeliensis* (d'Archiac and Verneuil) (see pl. 9: 2); 35 *Hindeoceras canadense* (Whiteaves); 36 *Tetranodoceras transversum* (Whiteaves); 37 *Casteroceras alternatum* (Hall); 38 *Tetragonoceras gracile* (Whiteaves); 39 *Aphyctoceras parvulum* (Kuzmin), *A. ujense* Zhuravleva; 40 *Kophinoceras acutecostatum* Sandberger, *K. wesfalicum* Holzapfel; 41 *Capricornites rhiphaeus* Zhuravleva; 42 *Gyroceras annulatum* Barrande; 43 *Ptenoceras alatum* (Barrande); 44 *Rutoceras eospinosum* Zhuravleva; 45 *Doleroceras resimum* Zhuravleva; 46 *Pleuroncoceras nodosum* (Bronn); 47 *Halloceras undulatum* (Vanuxem); 48 *Stereotoceras oppletum* Flower. For alternative interpretation of *Ptenoceras* group see fig. 60.

The lineages represented by these two species occur throughout the Late Ordovician (FLOWER 1946). The *Beloitoceras* lineage seems to have ended in the Ashgillian. In turn, some poorly known and infrequent Silurian forms may be representative of *Oncoceras*. The species described by ZHURAVLEVA (1964) under the name *Oratoceras sibiricum*, and by MIAGKOVA (1967) under



the names *Talattoceras inflatus* and *T. crenatus* from the Llandoverian of Siberia, shows a siphuncular structure indistinguishable from that of *Beloitoceras stoermeri*, and a shell outline very close to *Oncoceras constrictum*. "*Cyrtoceras*" *cyclostomum* BARRANDE, 1866, from the Ludlovian of Bohemia, is probably the last representative of the *Oncoceras* lineage; unfortunately, the siphuncular structure is unknown in this species. The taxonomic position of *Clathroceras sulcatum* (BARRANDE, 1865) from the Ludlovian of Bohemia and Scotland is unclear. It resembles *Oncoceras* in its external morphology but its aperture is constricted, and the large shell is longitudinally ribbed.

An important group of compressed, bulgy oncoceratids are those with considerably inflated, subspherical connecting rings. Most representatives of this group were assigned by FLOWER and TEICHERT (1957) to the order Discosorida, because of their laminar siphuncular deposits (polyptychocones) and supposedly thick connecting rings. The typically discosorid connecting ring is thin and hence, its thickness can not indicate relationship to the Discosorida. Furthermore, the connecting ring structures thougth to be characteristic of the group under discussion, well preserved in Ordovician *Faberoceras* (FLOWER and TEICHERT 1957, pl. 11: 2) and Devonian *Alpenoceras* (see MAREK 1976, pl. 2: 5), are heterogeneous. The connecting rings recorded in *Alpenoceras* do not differ in thickness from other oncoceratids, or from typical discosorids. In the specimen illustrated by MAREK (1976), the connecting rings are preserved as a thin layer reaching the septum in proximity of considerably bent septal necks, and are widely different in microstructure from the adjacent layers. In turn, the connecting ring is marked by a thin and dark line in the section through a specimen of *Faberoceras*. The layers supplementing the connecting rings at the chamber side were certainly cameral deposits, as indicated by their continuation at the proximal surface of septa; they are therefore not homologous to connecting rings. The connecting ring is associated with large, laminar siphuncular deposits clearly radial in pattern (SCHINDEWOLF 1941, MAREK 1976). The structure of siphuncular deposits is also of little significance for phylogenetic relationships of this group.

According to FLOWER and TEICHERT (1957), the Westonoceratidae, the oldest family of this group, are secondarily exogastric descendants of a discosorid *Ulrichoceras*. Derivation of the Westonoceratidae from *Ulrichoceras* would require an inversion of shell curvature and a shift of the siphuncle from subcentral to ventral position. The succession of forms that might contribute to the supposed *Ulrichoceras*-Westonoceratidae lineage does not corroborate this hypothesis. Exogastric oncoceratids with inflated connecting rings, which may be rather closely related to the Westonoceratidae (fig. 18), occur already in the Chazyan (Llandeilian); coeval with the genus *Ruedemannoceras* which is closely related to *Ulrichoceras* (the latter two genera are to be attributed to the Orthoceratida rather than to the Discosorida). The missing link between the oonoceratids and westonoceratids may be *Hemibeloitoceras* (= *Metephippioceras*) *lobatum* BALASCHOV, 1962, from the Krivoluksky horizon (equivalent to the Chazyan and Llandeilian) of Siberia. This is a rather poorly known longicone, weakly curved with relatively wide, marginal siphuncle (BALASCHOV 1962). The oldest known North American westonoceratid is *Sinclairoceras haha* FLOWER, 1952, from the Blackriveran (Early Caradocian) Simard Limestone, Quebec. *Simardoceras simardense* FLOWER, 1957, and *Teicherticeras sinclairi* FLOWER, 1957, described from single specimens from the Simard Limestone, are probably conspecific with *S. haha*. This species may be ancestral to the other North American Late Ordovician westonoceratids. The family may also include some poorly known forms from the Late Ordovician of the Baltic area (STRAND 1934, TEICHERT 1930). Some westonoceratid genera show a very peculiar shell form, e.g. *Westonoceras* with its living chamber imbedded into the phragmocone (NELSON 1963). Only a single westonoceratid lineage, evolved probably from the genus *Winnipegoceras*, trespassed the Ordovician/Silurian boundary. It includes considerably curved forms with very wide siphuncle (*Tuyloceras*) recorded from the Wenlockian Ekwan Limestone of Canada and its approximate time equivalents (FLOWER and TEICHERT

1957). These forms may resemble the Llandoverian discosorid genus *Konglungenoceras* in the adaptive type, as indicated by their similarly wide siphuncle and curved shell outline. The *Glyptodendron* group, attributed by FLOWER and TEICHERT (1957) to the Discosorida and thought to be somewhat related to the Westonoceratidae, seems to belong to the Uranoceratidae (Nautilida).

A peculiar group of small Silurian nautiloids clustered around the genus *Inversoceras* may be related to the westonoceratid genus *Antiphragmoceras*. They resemble the latter genus in their compressed, originally exogastric shell and aperture with distinct dorsal sinus, but the time hiatus is large. The dorsal sinus, so well developed in the Trimeroceratidae, occurs in a rudimentary form in various nautiloids, e.g. *Phragmoceras* (Discosorida; see HEDSTRÖM 1917), *Gonatocyrtoceras* (Oncoceratida). The specialized aperture and small shell make the difference between *Inversoceras* and *Antiphragmoceras*. An alternative phylogenetic interpretation relating the Trimeroceratidae to *Mandaloceras* (depressed shell with radial lamellar structure of the siphuncle) seems to be less justified. The Trimeroceratidae have been reported from the Silurian of North America (FLOWER 1943*b*), China (CHEN 1976), Bohemia (BARRANDE 1865) and Gotland (non described). The best preserved Bohemian material is confined to the Ludlovian Kopanina Formation. The collection is moderately large and includes individuals of probably three species: *Inversoceras perversum* BARRANDE, 1865, with exogastric shell and a pair of lateral sinuses in the mature aperture; the related but orthoconic *Trimeroceras staurostomum* (BARRANDE, 1865); and *Pentameroceras mirum* (BARRANDE, 1865) with two pairs of lateral sinuses in the aperture. In the Halla Beds of Gotland population of new trimeroceratid species occurs showing variability in aperture constriction from *Trimeroceras* to *Pentameroceras* shape. *I. perversum* shows very high but continuous variation in shell curvature which makes unreasonable its subdivision into the species erected by FOERSTE (1926) from BARRANDE'S illustrations. There is also no evidence for sexual dimorphism as claimed by FOERSTE (1926). The trimeroceratids may have given rise to *Katageioceras rarum* ZHURAVLEVA (= *Turoceras totense* ZHURAVLEVA) known exclusively from juveniles collected in the Emsian of the Urals (ZHURAVLEVA 1972).

"*Richardsonoceras*" *nikiforovae* BALASCHOV, 1962, from the Ashgillian of Siberia, probably evolved from *Hemibeloitoceras lobatum*, the main difference being in the much more curved shell of the former species. In turn, "*R.*" *nikiforovae* may be ancestral to a nautiloid group reported mostly from the Silurian of Bohemia, clustered around the genus *Oxygonioceras* (fig. 16). The morphological affinity consists not only in siphuncular structure and position and shell shape, but also in the somewhat sharp-edged venter of the shell. The latter character is not conclusive for phylogenetic reconstruction because it occurs also in some other oncoceratids, e.g. *Richardsonoceras*. The conjunction of the above mentioned features may indicate that *Digenuoceras latum* (FOERSTE, 1929) known from a few specimens from the Ashgillian of North America (SWEET and MILLER 1958), is also related to the group of *Oxygonioceras*. There is no reliable record of this group between the Ashgillian and Ludlovian. In the Ludlovian Kopanina Formation, Bohemia, it is represented by at least three distinct species. *Oxynoticeras oxynotum* (BARRANDE, 1865), known from a few specimens collected from the exposures at Lochkov and Kosoř, shows a flat, tightly coiled shell with sharp ventral fastigation. The adult shell diameter ranges from 62 (Kosoř) up to 103 mm (Lochkov) indicating considerable intraspecific variability. Its close relative, *O. priscum* (BARRANDE, 1865), known after a rich collection derived from various localities, and described under a dozen specific names, approximates *O. oxynotum* in shell size but the shell is less compressed and the venter more rounded. The adult shell diameter ranges from 53 ("*T. aequale*", Lochkov) up to 120 mm (Kosoř). There is also variation in shell asymmetry and cross section. The co-occurrence of these two highly varying species, raises the question of their specific distinction. Basing on BARRANDE'S original material, one can not trace a boundary between *O. oxynotum* and *O. pris-*

cum. Furthermore, "*Trochoceras speciosus*" and "*T. regale*", differing in the whorl expansion rate, may also be distinct species. Similar spectrum of morphotypes is known also from the Slite and Hemse beds of Gotland. *Oxygonioceras* may include *Trochoceras tortuosum* (Sowerby, 1839) from the Early Ludlovian of England (Blake 1882).

Cyrtoceras alinae Barrande, 1868, here tentatively assigned to the genus *Digenuoceras* (pl. 9: 4) may be related to *Oxygonioceras* even though its shell is only weakly curved. *D. alinae* includes probably Barrande's 42 species described from various localities of Kopanina formation. Its whorl section and siphuncular structure are indistinguishable from those of *Oxygonioceras*, while the intraspecific variability consists only in shell curvature, that ranges from almost orthoconic (pl. 9: 4) to cyrtoconic (1/2 whorl) ("*Cyrtoceras concors*"). I have not found any morphologic discontinuities within the range of these forms, which might indicate more than a single biospecies. The peculiar *S.* (?) *discoideum* (Barrande, 1866), from the Přidolian of Karlštein, may be related to *B. alinae.* It shows a short, very strongly curved, compressed shell with fastigate ventral side (pl. 9: 4).

It is difficult to determine the ancestors of another Bohemian Silurian oncoceratid group included here in the genus *Rizosceras.* These forms have breviconic, bulgy shell with weakly curved initial part, simple mature aperture, and inflated connecting rings. The apical angle changes considerably during ontogeny. The shell expands at first rather slowly but much more rapidly later; finally, it becomes almost cylindrical with the adult living chamber (pl. 15: 1). Simultaneously, the connecting rings change from elongate to very inflated. My study of the material collected by Barrande, failed to determine the range of intrapopulation variability in *Rizosceras.* The point is that there is morphological continuity between exogastrically and weakly endogastrically curved apical parts of the shells. The rate of shell expansion is also variable. The continuity cannot be regarded as reflecting evolution because the endmembers co-occur commonly within short stratigraphic interval. As judged from the Barrande's original material, only two species of *Rizosceras* can justifiably be recognized in the Ludlovian Kopanina Formation; these are: *R. quasirectum* (Barrande, 1866) with relatively long, endogastric shell with variable cross section (this species includes probably also "*Cyrtoceras forte*" and "*C. esuriens*"), and *R. intermedium* (Barrande, 1866) with either exogastric, or straight, or weakly endogastric, bulgy shell. The latter species was split by Barrande into 63 species attributed to the genera *Orthoceras* and *Cyrtoceras.* Later on, two genera, *Rizosceras* and *Danaoceras*, were erected on the original material (Foerste 1926; Flower, 1957). The supposed radial lamellar structure of the siphuncle in "*Danaoceras danai*" (Barrande 1866, pl. 171: 7) cannot be seen in the original specimen. Most of Barrande's species are not morphotypes but merely different states of preservation and deformation of conspecific specimens. The range of intrapopulation variability in the Přidolian of Karlštein is smaller than in conspecific older populations; the Přidolian population is predominated by almost orthoconic specimens (pl. 15: 1). This may also be an artifact of the smaller sample size, as Barrande described only 12 species from Karlštein. The Karlštein population is also dominated by compressed forms, even though shells with almost circular section are also present. The group considered may also include juvenile specimens described under the name *Protophragmoceras* (?) *boreale* from the Wenlockian of North America (Foerste and Savage 1927), as well as those from the Gedinnian of Podolia attributed to *Turoceras schnyrevae* (Zhuravleva, 1959).

In my opinion, both the structure and ontogeny of the siphuncle and the shell outline indicate the descent of *Sthenoceras aduncum* (Barrande, 1866) from the Koněprusy Limestone, from the Silurian *Rizosceras intermedium* (note that Barrande's original age attribution is F_2 instead of e_2 which indicates clearly that the type horizon is Siegenian instead of Silurian, as was claimed by Flower and Teichert (1957) who erected *Sthenoceras* exclusively on the illustrations given by Barrande). Barrande described also a few other, supposedly conspecific specimens from the Koněprusy Limestone. Some of these present initial parts of the shell indistinguishable from their counterparts found in Silurian *Rizosceras*. FLOWER and TEICHERT (1957) attributed *S. aduncum* to the Discosorida and derived it from some Ordovician species of *Protophragmoceras*. The Ashgillian species *P. sphynx* resembles indeed *S. aduncum* in the shell outline, but the stratigraphic gap covers the whole Silurian and, moreover, the discosorids related to *Protophragmoceras* never show any ontogenetic change in the shell expansion rate as recorded in *Sthenoceras* and *Rizosceras*. The hypothesis that there is a direct phylogenetic relationship between *R. intermedium* and *S. aduncum* therefore to be more plausible; in fact, it is corroborated not only by the stratigraphic sequence, but also by similarity in the mechanisms controlling shell growth. Then, there is also no reason to attribute the North American and European Givetian genus *Alpenoceras* to the Discosorida (see MAREK 1976). *Alpenoceras* is almost indistinguishable from *Discoceras* and *Sthenoceras* in shell shape (FLOWER and TEICHERT 1957), while it differs in its considerably developed siphuncular deposits. The deposits of *Alpenoceras* resemble those shown by the bulgy discosorids; they display however a radial pattern (SCHINDEWOLF 1941, MAREK 1976) similar to that recorded in the Ordovician *Faberoceras*. The species of *Alpenoceras* are very poorly known and one can not determine their number.

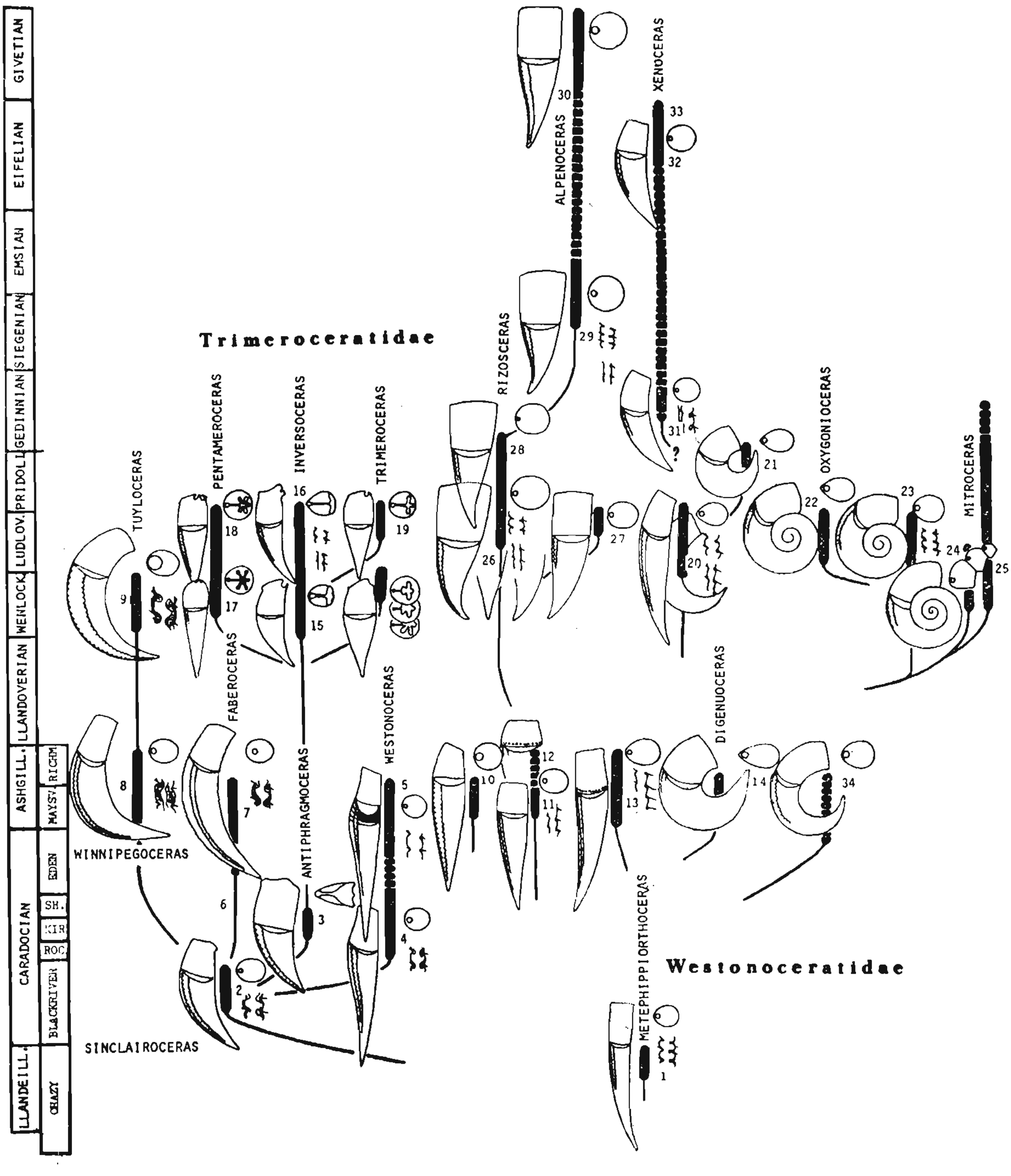
The systematic position of trochospirally coiled Silurian forms described under the name *Mitroceras* (= *Foersteoceras*) is also unclear. They have first been described from poorly preserved specimens from the Wenlockian of North America (RUEDEMANN 1925). The siphuncular structure is unknown, even though the connecting rings are certainly inflated. A single incomplete specimen found in an erratic boulder of the Beyrichienkalk (pl. 15: 6) may belong to *Mitroceras*, as its poorly preserved marginal siphuncle shows inflated rings. Presumably, *Mitroceras* should be placed close to *Oxygonioceras*.

Shell depression is a secondary feature in the Oncoceratida. It developed rather late independently in some distinct lineages. The family Devonocheilidae is here meant to include depressed, bulgy, relatively breviconic forms with weakly developed radial structures in the siphuncle. The oldest records of the Devonocheilidae are from the Wenlockian and Ludlovian of North America and Baltic region. Unfortunately, described species (FOERSTE 1924, 1926, 1930, 1934; FOERSTE and SAVAGE 1927) are as a rule very poorly preserved, and the siphuncular structure remains unknown in all but one species. The geological setting is also unfavourable because the species are described from specimens of various localities with different geological age. One cannot determine the number of species and their interrelationships without revision of the original material. One may, however, claim that at least four distinct devonocheilid species are present in that fauna: *Grimsbyoceras genuiflexum* FOERSTE, 1934, with considerably curved, bulgy shell; the best known *Amphicyrtoceras orcas* (HALL, 1862) (? = = *Streptoceras janus* BILLINGS, 1866) with exogastric, bulgy shell with triangular, constricted aperture and narrow, marginal siphuncle (FOERSTE 1926); *Grimsbyoceras clitum* (BILLINGS, 1866), very closely related if not conspecific with the former species, displaying a relatively elongate shell; and *Galtoceras arcticameratum* (HALL, 1852) with long and slender shell (FOERSTE 1934). The genus *Chadwickoceras* FOERSTE, 1930, with straight and very bulgy shell may be their close relative.

In the Slite beds of Gotland undescribed species of Devonocheilidae occurs similar in shape to *Gonatocyrtoceras*. Another undescribed species from the Högklint Limestone is characterized by rather elongated shell.

I do not know any unquestionable devonocheilids from the Bohemian Silurian. In fact, "*Cyrtoceras*" *obesum* BARRANDE, 1866, with some supposedly conspecific forms, and "*C.*" *inflectens* BARRANDE, 1866, both from the Ludlovian of Bohemia, are the only two that resemble in shell outline the Devonocheilidae but their siphuncular structure remains unknown. "*C.*" *obesum* is known exclusively from juvenile specimens, whereas "*C.*" *inflectens* may well be related to some considerably curved oonoceratids. The oldest unquestionable representative of the Devonocheilidae in the Paleozoic of Bohemia is *Gonatocyrtoceras heteroclytum* (BARRANDE,

1866) from the Siegenian Koněprusy Limestone, Bohemia. It is represented by several specimens with very small bulgy shell with constricted subtriangular aperture; its isolated living chamber described by BARRANDE under the name *Gomphoceras* ? *semiclausum* was elevated by FLOWER (1947) to the rank of a distinct genus, *Cayugoceras*, and attributed to the Discosorida. This species may have evolved from the American *Streptoceras janus*. The successor in the same evolutionary lineage is *Gonatocyrtoceras nostras* ZHURAVLEVA, 1972 (= *G. inamoenum*), from the Early Eifelian of the Urals. The latter species, known after three specimens, shows a more slender shell than *G. heteroclytus*, which makes it close to *S. janus* as well as to later devonocheilids. Possibly, the very small size and bulgy shape of the shell of *G. heteroclytum* are related



to peculiar environmental conditions of the Koněprusy Limestone reefs. Apart from the American form "*Naedyceras*" *gibbosum* Flower, 1945, attributable possibly to *Gonatocyrtoceras*, and "*Sophoceras*" *strenuum* Zhuravleva, 1972 (= *Stroggyloceras altaicum*, *Elaphoceras inclemens*), known from three specimens collected in the Late Frasnian of the Altai, all other species of *Gonatocyrtoceras* occur in the Early Famennian of Europe. The lineage of *G. strenuum*, distinctive in its dorsal flattening correlated with considerable curvature of the shell, continues in "*Selenoceras*" *subterraneum* Zhuravleva, 1972, from the Famennian *Platyclymenia* Zone of the Urals. There is another evolutionary lineage in the Famennian, probably derived from *G. nostras*, a representative of which is *G. holzapfeli* (Sobolew, 1912) found in the *Platyclymenia* Zone at Łagów, the Holy Cross Mts, Poland (fig. 18; pl. 12: 1-6). The latter species occurs at Łagów with *G. guerichi* (Sobolev, 1912) and is indistinguishable in the juvenile stage (see fig. 20; pl. 13: 1-5). A comparison of the reconstructed adult, typical specimens (figs. 19, 20) illustrates great differences so that specific identification in this material should be no problem; yet the distinction of the two species is uncertain. The intrapopulation variabilities are so large that no two specimens in the investigated collection are identical. Variation is seen in all characters that may be of any taxonomic value, i.e. coiling and shell expansion (pls. 12-13), as well as adult shell size (fig. 19e), living chamber shape (fig. 19c-d), and aperture form. I have divided, rather arbitrarily, that Łagów material of *Gonatocyrtoceras* into two species because the difference between the endmembers of the whole spectrum of forms seems to be too great for single species. They include a large variety of morphs differing in adult size by a factor of two or more (see pl. 13). The available data, however, do not allow the conclusion that sexual dimorphism accounts for the variability recorded. A congeneric species, *Gonatocyrtoceras longissimum* sp.n., with very long shell and laterally constricted aperture (fig. 21 and pl. 11) occurs in the *Cheiloceras* Zone of the Holy Cross Mts. The material collected from Kadzielnia, as well as from different limestone facies of Jabłonna indicates very large intrapopulation variability in shell curvature and living chamber length. The adult shell sizes within these populations again differ by a factor of more than two.

"*Tritonoceras*" *chernovi* Zhuravleva, 1972, described from a single specimen from the Early Frasnian of the Urals, may be the ancestor of *G. guerichi*; according to Zhuravleva the diagnostic feature of the new genus is phragmocone asymmetry, which I consider teratologic. The only subadult specimen does not permit even specific separation of *T. chernovi* from *G. guerichi*. "*Elaphoceras*" *quaietum* Zhuravleva, 1972, known after two specimens from the Late Frasnian of Timan, may also belong to *G. guerichi*. This may also be the case of *Cyrtoceras platygaster* Born, 1912, from the Early Famennian and *Gyroceras halli* Wedekind, 1908, from the *Cheiloceras* Zone of the Harz Mountains.

Fig. 18

Hypothetical phylogenetic relationships among members of the family Westonoceratidae *s. l.* 1 *Hemibeloitoceras lobatum* Balaschov = *Metephippiorthoceras helenae* Zhuravleva; 2 *Sinclairoceras haha* Flower; 3 *Antiphragmoceras ulrichi* Foerste; 4 *Teicherticeras hussei* Foerste; 5 *Westonoceras manitobense* (Whiteaves); 6 *Faberoceras saffordi* Flower; 7 *Faberoceras multicinctum* Flower; 8 *Winnipegoceras laticurvatum* (Whiteaves); 9 *Tuyloceras percurvatum*, ? *Iowoceras southhamptonensis* Foerste and Savage; 10 *Landeroceras prolatum* (Miller); 11 *Danoceras breve* Strand; 12 *Diestoceras* sp. Sweet, 1959, *D. brevidomum* Foerste; 13 *Parryoceras euchari* Sweet and Miller, *Lykholmoceras norvegiae* Strand; 14 *Digenuoceras latum* (Foerste); 15 *Inversoceras dayi* Foerste; 16 *Inversoceras perversum* (Barrande); 17 *Pentameroceras cumingsi* Flower, *P. rarum* Foerste and Savage, *P. byronense* Foerste, *Stenogomphoceras chadwicki* Foerste, *Eotrimeroceras jupiteriense* Foerste; 18 *Pentameroceras mirum* (Barrande); 19 *Trimeroceras staurosum* (Barrande); 20 *Digenuoceras* (?) *alinae* (Barrande) (pl. 9: 4); 21 *Digenuoceras* (?) *discoideum* (Barrande) (pl. 9: 5); 22 *Oxygonioceras oxynotum* (Barrande); 23 *Oxygonioceras priscum* (Barrande) (pl. 15: 4); 24 *Mitroceras gebhardi* (Hall); 25 *Foersteoceras turbinatum* (Hall); 26 *Rizosceras indocile* (Barrande) = *Danaoceras danai* (Barrande) (see pl. 15: 5); 27 *Rizosceras quasirectum* (Barrande); 28 *Rizosceras intermedium* (Barrande) (pl. 15: 1); 29 *Sthenoceras aduncum* (Barrande); 30 *Alpenoceras ulrichi* (Foerste), *A. eifeliense* (Schindewolf); 31 *Xenoceras oncoceroides* Flower; 32 *Wissenbachia orthogaster* (Sandberger and Sandberger); 33 *Tumidoceras lentum* Flower; 34 *Richardsonoceras nikiforovae* Balaschov.

Slender devonocheilids with simple aperture probably appeared first in the American Silurian. Their ancestor may be poorly known *Galtoceras arcticameratum* (Hall, 1852) from the Wenlockian Guelph Dolomite (Foerste 1934). The Ludlovian form *Worthenoceras racinense*

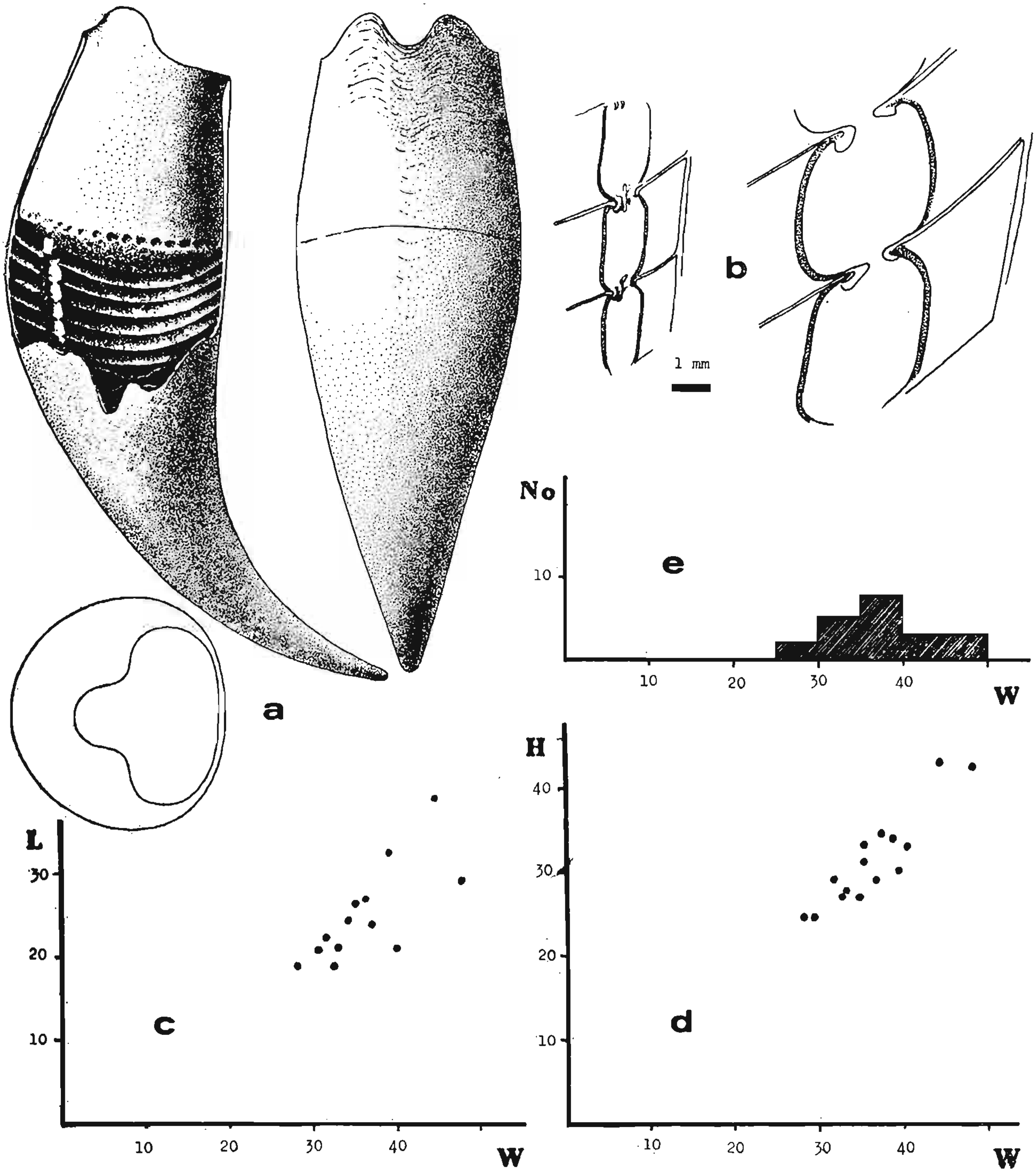


Fig. 19

Gonatocyrtoceras holzapfeli (Sobolev, 1912); *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 12: 1-6); *b* longitudinal section through a siphuncle close to the apex and at the mid-length of a phragmocone, ZPAL N/323; *c* plot of mature living chamber length (L) against width (W); *d* plot of adult living chamber height (H) against width (W); *e* width-frequency-distribution of adult living chambers.

Foerste, 1934, may be junior synonym of *G. arcticameratum*. Supposedly, the successor of this group is "*Cyrtoceras*" *bryozoon* Barrande, 1866, from the Eifelian Choteč Limestone of Bohemia. Unfortunately, neither the aperture, nor the siphuncular structure has been preserved in the only known specimen of the latter species and hence, one can hardly be certain of its systematic position; it resembles *Gonatocyrtoceras longissimum* in shell outline. The successor in the lineage under discussion may be *Cyrtospyroceras reinmanni* Flower, 1938, from the Givetian of New York. The only known specimen is poorly preserved, lacking the living chamber, which makes its definite identification impossible. The supposed shell annulation is probably an artifact caused by corrosion. The slender devonocheilids appear abundantly only in the Famennian. A large and excellently preserved sample of *Chrysoceras tumidum* Zhuravleva, 1972 (= *Ch. reticulatum*, *Ch. incompertum*, *Ch. inconcussum*, *Ch. coactum*, *Plagioceras incelebratum*, *Athanatoceras praecipuum*, *A. decorum*, *Brevicoceras nitidum*, *Exochoceras enucleatum*, *E. depressum*, *E. efferum*, *E. invocatum*, *E. commodum*, *E. nonnulum*, *E. ratum*, *E. varum*, *Pelagoceras lautum*, *P. mendicum*), is known from the Early Famennian

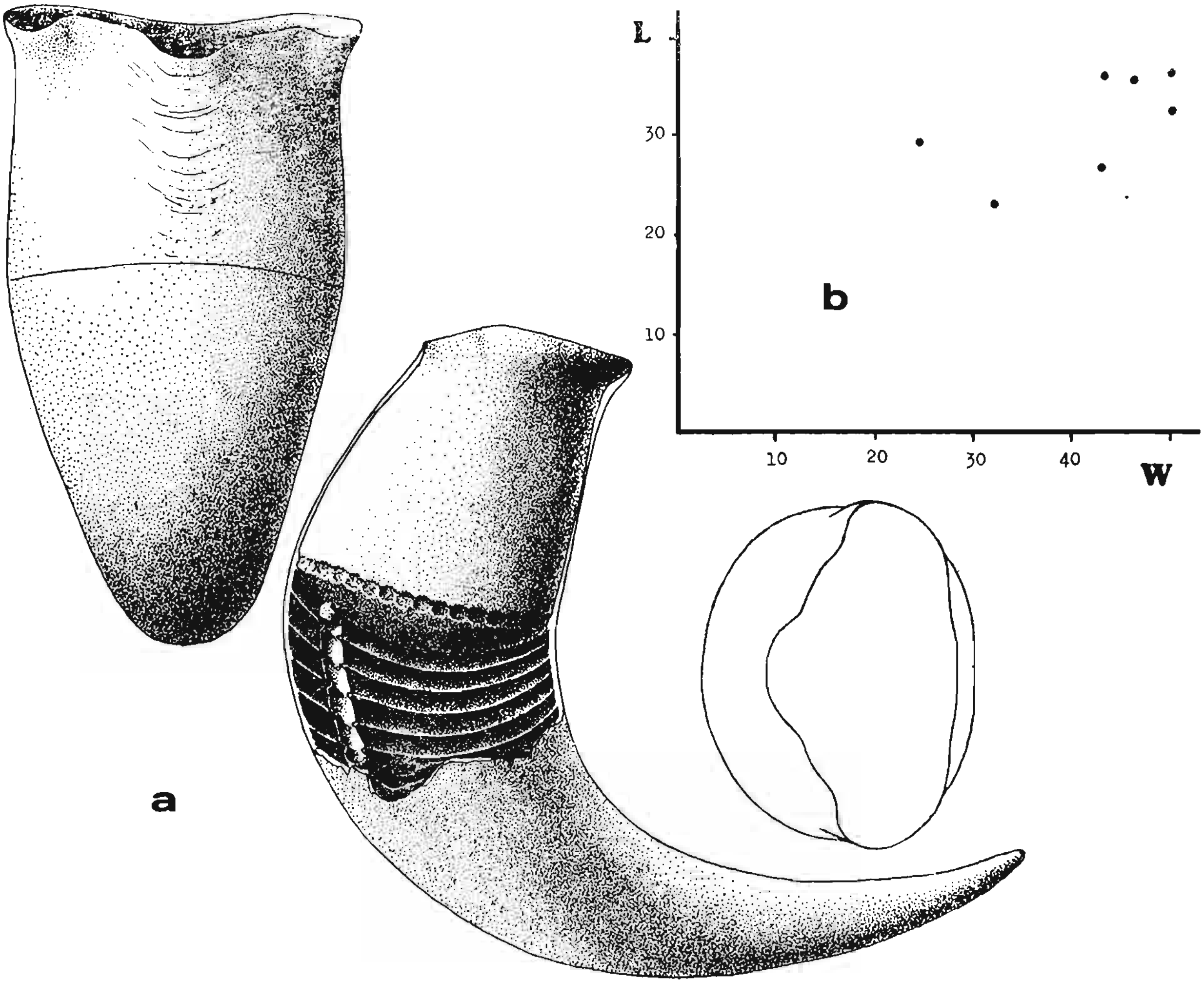


Fig. 20
Gonatycyrtoceras guerichi (Sobolev, 1912); *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 13: 1-5); *b* plot of adult living chamber length (L) against width (W).

Platyclymenia Zone of the southern Urals. As in other oncoceratids, the intrapopulation variability exists mostly in shell shape that ranges from almost orthoconic to a 1/2 whorl gyroconic (*Athanatoceras praecipuum*).

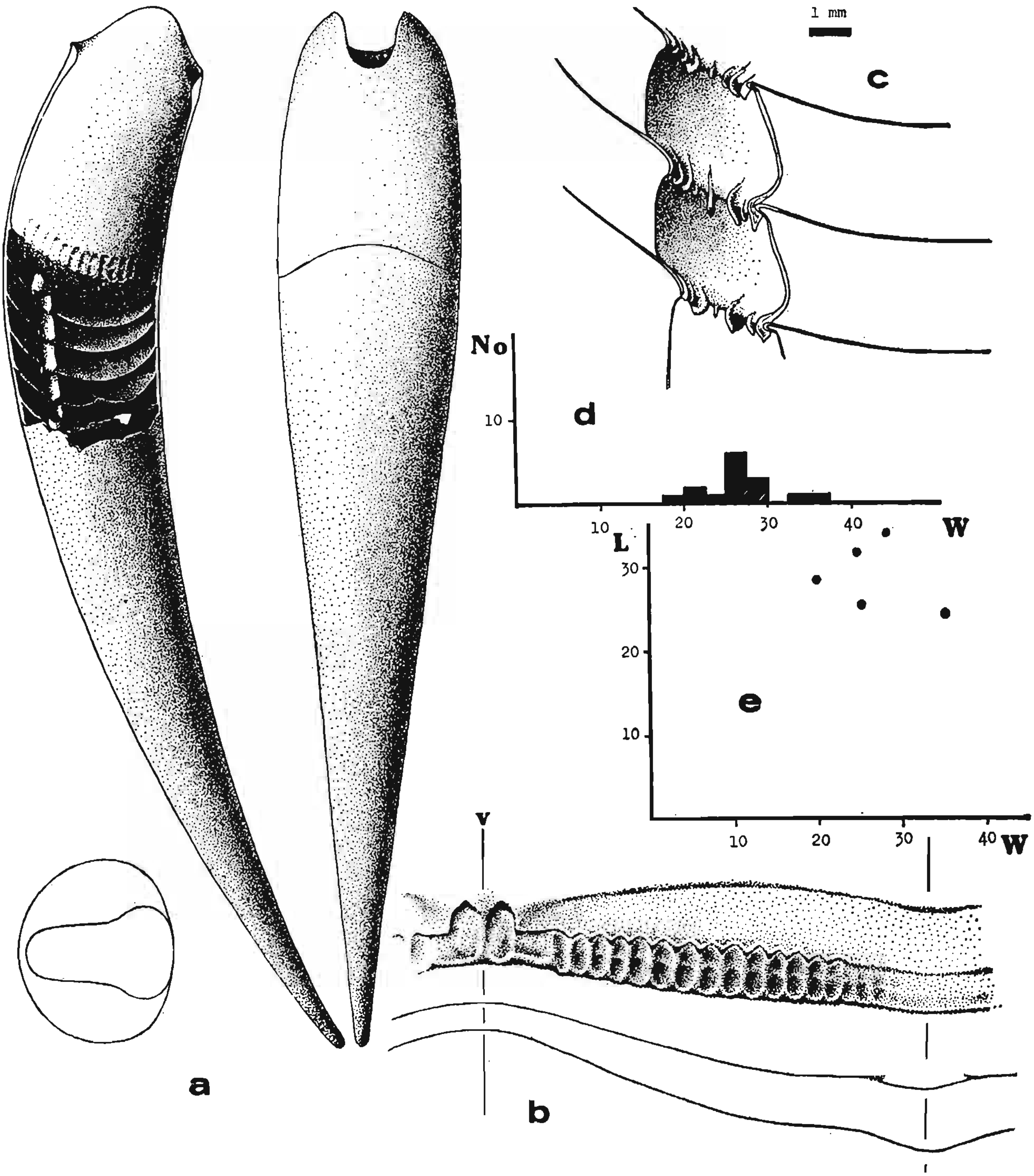


Fig. 21

Gonatocyrtoceras longissimum sp. n.; *Cheiloceras* Zone, Famennian, Kielce-Kadzielnia, Poland; *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 11: 1-7); *b* pedal retractor scar and variation in septal suture; *c* longitudinal section through a siphuncle, ZPAL N/237, Jabłonna; *d* width-frequency-distribution of adult living chambers; *e* plot of adult living chamber length (L) against width (W).

Devonocheilids with simple adult aperture occur abundantly in the Famennian of Poland. *Lysagoraceras kielcense* sp. n. with strongly curved, small shell (fig. 22; pl. 10: 1-4) is found in the Famennian *Cheiloceras* Zone at Jabłonna. Its intrapopulation variability is very small relative to other oncoceratids. Presumably, three devonocheilid species occur in slightly younger strata (*Platyclymenia* Zone) at Łagów. *L. lagoviense* (GÜRICH, 1896) has a relatively long shell, almost straight at the juvenile stages but considerably curved in the living chamber; its intrapopulation variability is considerable (fig. 23; pl. 10: 5-9). The smallest and largest adults

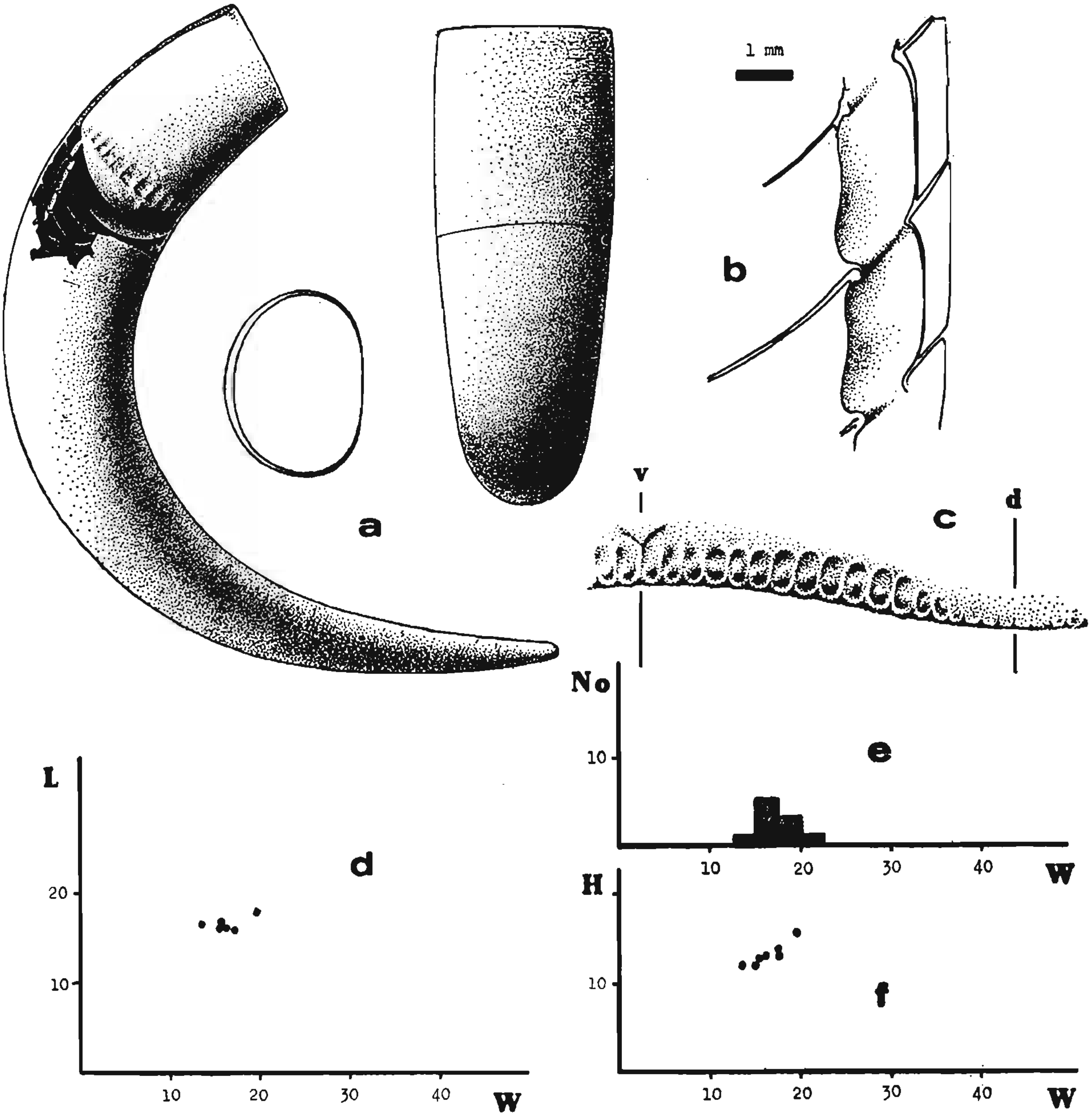


Fig. 22

Lysagoraceras kielcense sp. n.: *Cheiloceras* Zone, Famennian, Jabłonna, Holy Cross Mts, Poland; *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 10: 1-4); *b* longitudinal section through a siphuncle, ZPAL N/120; *c* pedal retractor scar; *d* plot of adult living chamber length against width; *e* width-frequency-distribution of adult living chambers; *f* plot of adult living chamber height against width.

differ in size by a factor of more than three, but the scarcity of material does not allow one to recognize whether this is sexual dimorphism, or specific heterogeneity.

There are several examples indicating that the time correlations among various ontogenetic processes are far from strong in the Nautiloidea, perhaps due to physiological primitiveness of the nautiloids. This is demonstrated first of all by the extremely large intrapopu-

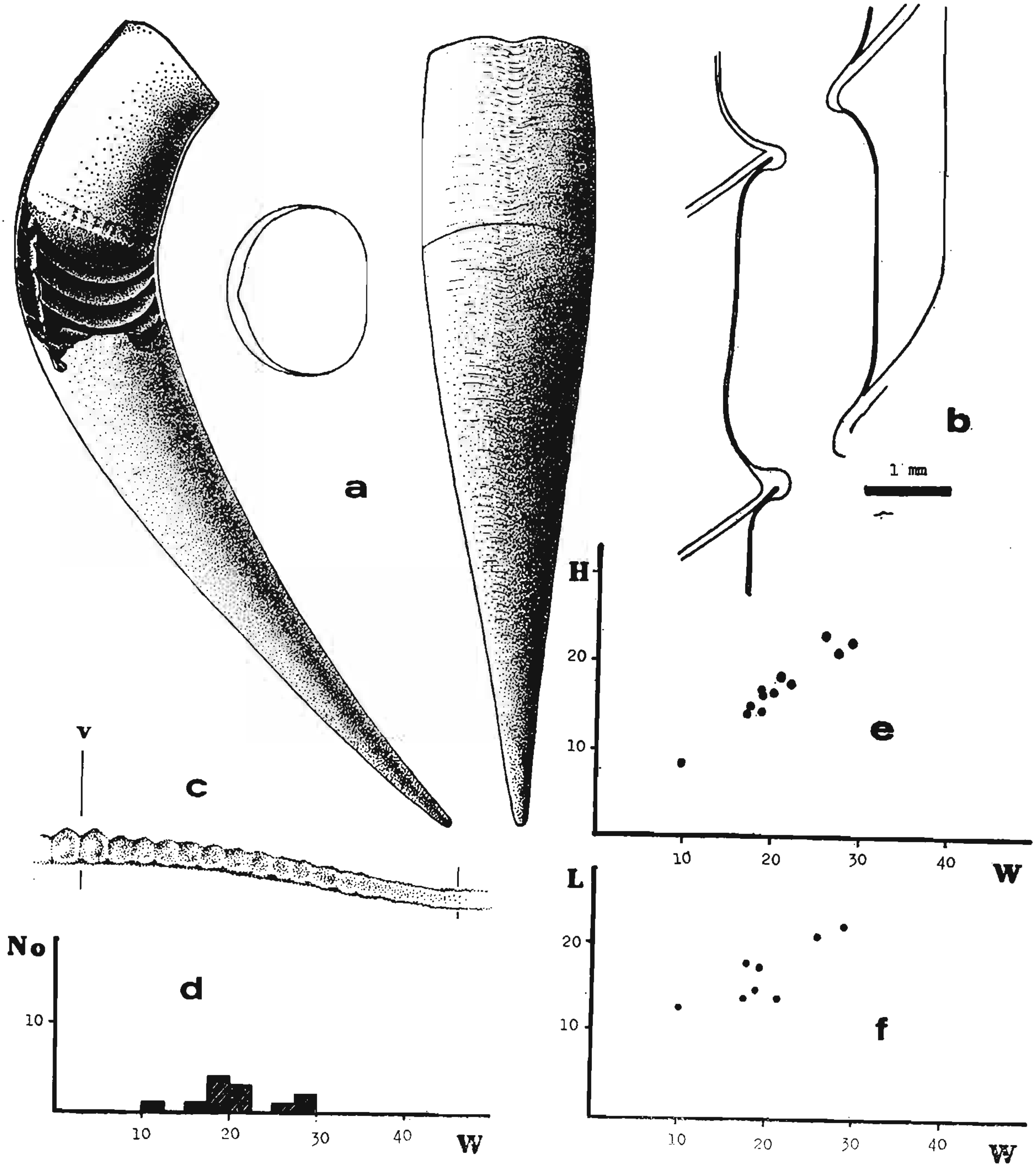


Fig. 23

Lysagoraceras lagoviense (GÜRICH, 1896); *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 10: 5-9); *b* longitudinal section through a siphuncle, ZPAL N/147; *c* muscle scar; *d* width-frequency-distribution of mature living chambers; *e* plot of mature living chamber of height (H) against width (W); *f* plot of mature living chamber length (L) against width (W).

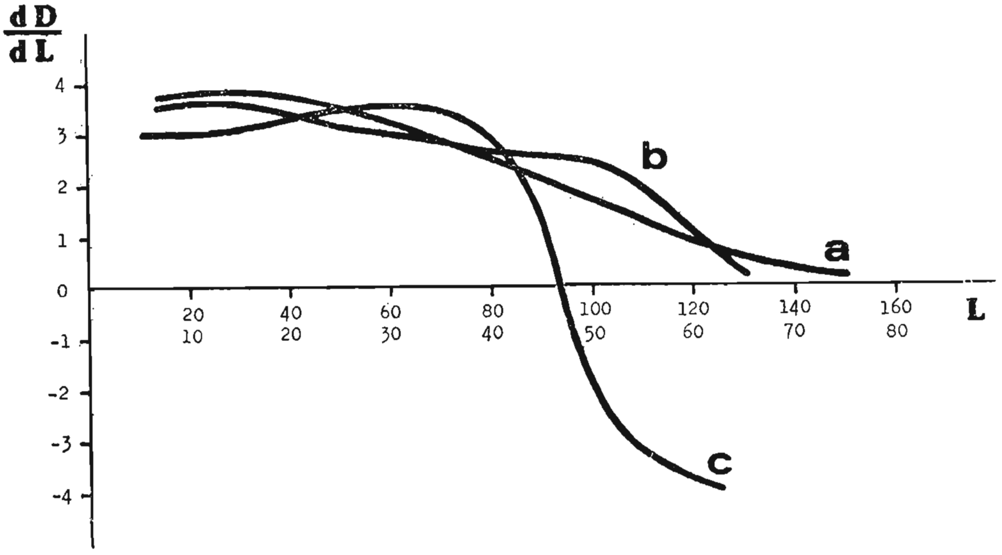


Fig. 24

Relative growth of shell diameter increase $\left(\frac{dD}{dL} = \mathrm{tg}\alpha\right)$ and shell length (L); *a Richardsonoceras hauseri* (Barrande, 1865) (pl. 8: 4); *b R. patulum* (Barrande, 1865) (pl. 8: 3); *c Lysagoraceras* sp. (lower scale) (pl. 14: 8).

lation variability in size of the adult nautiloid shell, suggestive of a variation in the rate of ontogenetic accomplishment of the genetic program. The weaker curvature of the shell in smaller adults of *Lysagoraceras lagoviense* than in the larger ones suggests lack of time correlation (synchronization) between the changes in shell diameter and coiling. The observed variation may indicate that physiological factors dampening the rate of diameter increase started to act earlier in ontogeny than those controlling shell coiling. In the extreme case of the smallest individuals, the former process may have been considerably advanced while the latter just began (fig. 24; pl. 14: 8). *L. subfusiforme* (Münster, 1840) (fig. 25; pl. 14: 1-4, 6), reported also from the *Cheiloceras* Zone of the Harz Mountains (Wedekind 1908, Schönenberg 1952), differs from *L. lagoviense* in its orthoconic adult shell. Some specimens, especially those incomplete, can not be unequivocally assigned to one or the other species but *L. subfusiforme* is probably a true biospecies. Its intrapopulation variability is very large (fig. 25c-e) but the homogeneity of the population seems to be established. Similar, possibly conspecific populations have also been recorded from the coeval strata of the Urals (Zhuravleva 1972). The abundant, most commonly well preserved specimens were the basis for erection of numerous new species and genera, all of them fall within the range of intraspecific variability, comparable to that recorded in the populations from Harz and the Holy Cross Mountains. Thus, I consider the Zhuravleva's names *Andreioceras incolume*, *A. reticulatum*, *A. pertinax*, *Vertorizoceras erraticum*, *Xiphoceras obtusum*, *Ropaloceras mugodzharicum*, *R. commune*, *R. implicatum*, *R. illicitum*, *Nipageroceras rhiphaeum*, *Kadaroceras inausum*, *Metrioceras desertum*, *Stagonites miser*, *Lysagoraceras separatum*, *Deinoceras pubes*, and *D. notabile* as junior synonyms of *L. subfusiforme*. An endmember of the morphological series in shell inflation and coiling occurs also at Łagów. Its straight to slightly endogastric, very inflated shell resembles very closely *L. subfusiforme* in the apertural outline. The generic assignment of this species is problematic, I attribute it tentatively to *Lysagoraceras*. It may be conspecific with ?*Anglicornus erraticus* Zhuravleva, 1972, from the *Platyclymenia* Zone of Kazakhstan. Such an interpretation should, however, be treated with caution because of the great geographic distance; the more so since Zhuravleva based her species on a single specimen. In turn, the approximate time equivalence of the records seems to be the only reason to assign the specimen from Kazakhstan to the genus *Anglicocornus* erected by Flower and Caster (1935) on a single, unidentifiable, deformed

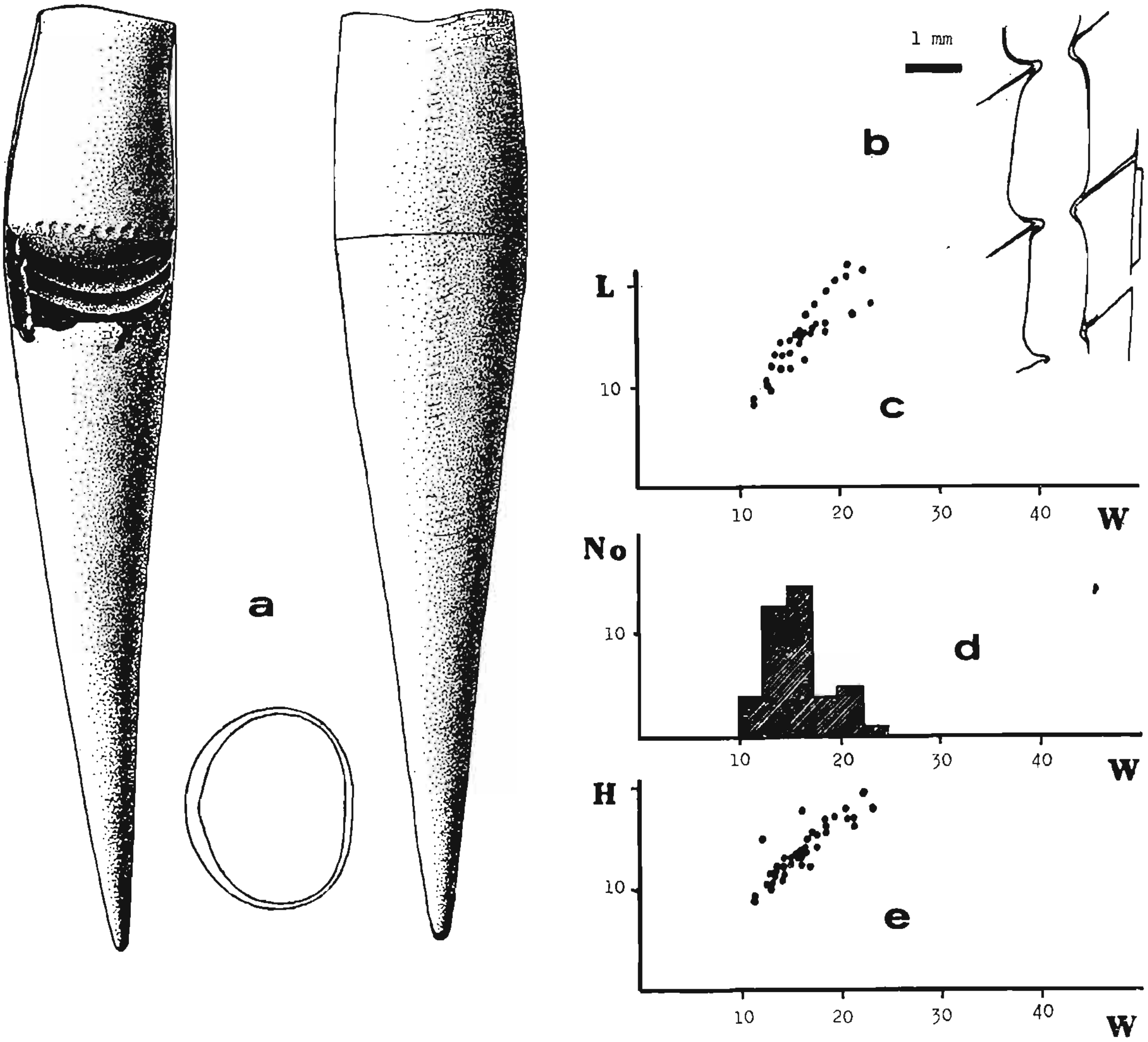


Fig. 25

Lysagoraceras subfusiforme (Münster, 1840); *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts., Poland; *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 14: 1-6); *b* longitudinal section through a siphuncle, ZPAL N/181; *c* plot of adult living chamber length (L) against width (W); *d* width-frequency-distribution of adult living chambers; *e* plot of adult living chamber height (H) against width (W).

and corroded specimen; note that another specimen from Flower and Caster's locality, preserved even more poorly, is the type of the genus *Blastocerina*.

The genera *Devonocheilus* and *Ukhtoceras*, both with straight to slightly curved shell with constricted aperture, have thus far been reported exclusively from the Late Devonian of Europe. The somewhat exogastric shell is certainly a primitive feature in this group. One can not be certain of direct ancestors of the group, possibly *Ovoceras oviforme* (Hall, 1860) from the Givetian Cherry Valley Limestone of North America (Flower 1938), or *Taskanoceras boreum* Zhuravleva, 1972, from the Emsian of Siberia. If this is the case, this lineage can be traced backwards to *Chadwickoceras fusiforme* Foerste, 1930, from the Wenlockian of North America. The species *Ukhtoceras uchtense* (Holzapfel, 1899) (= *U. angustiangulare*, *U. quietum*, *U. opinatum*, *U. gregarium*, *U. pignus*, *U. neocopinatum*, *U. heckeri*, *Vertorizoceras timanicum*, *V. rapidum*, *V. scapus*, *V. cautum*, *Chuticeras usitatum*, *Jaregoceras timanicum*, *J. gutta*, *Pancornus nativus*, *Stagonites tenuiculus*. *Ungulites komiensis*), known from abundant and well preserved

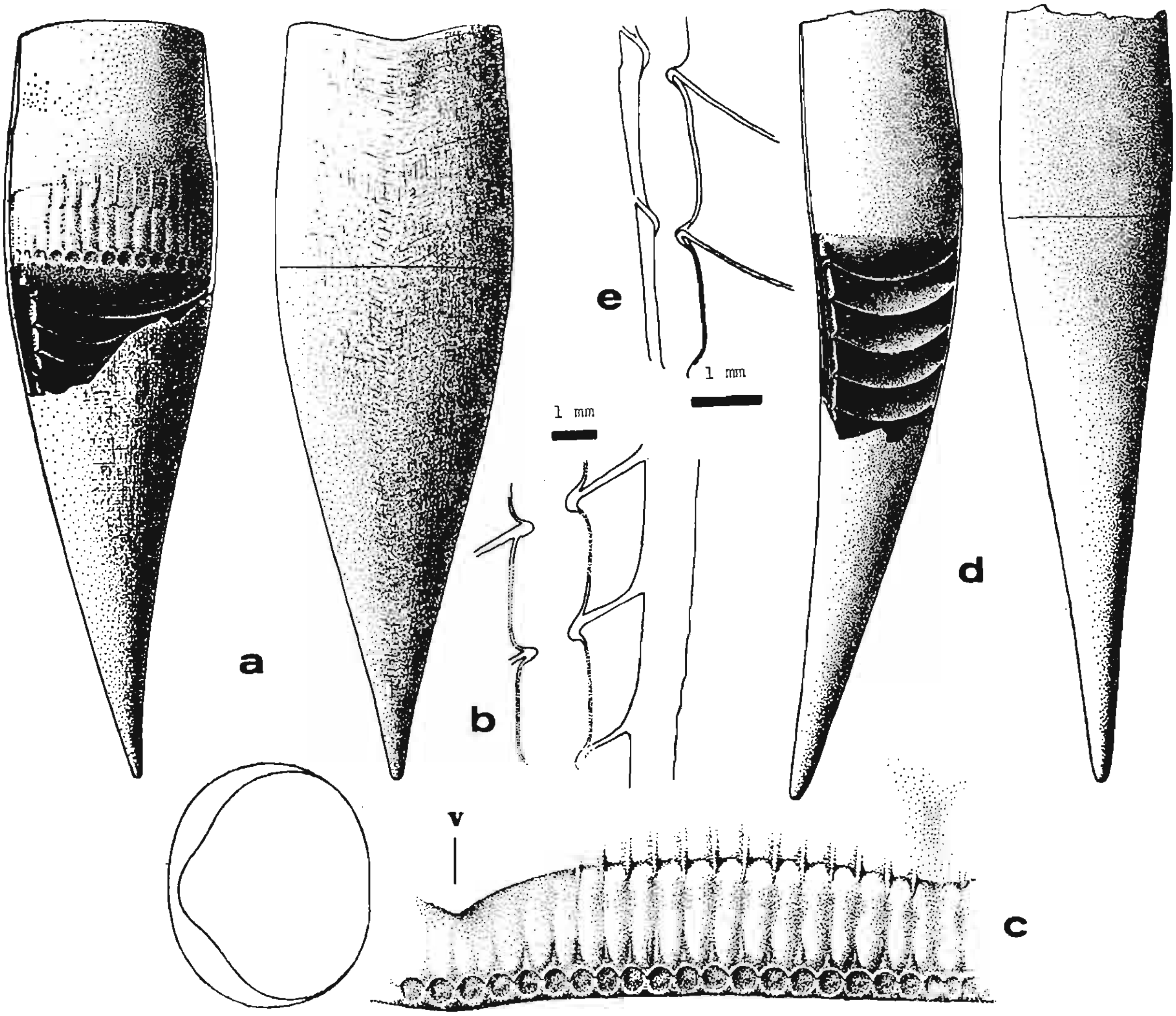


Fig. 26

Lysagoraceras (?) cf. *erraticum* (ZHURAVLEVA, 1972); ZPAL N/208 (pl. 14: 5), *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland; *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 14: 5, 9-10); *b* longitudinal section through the siphuncle; *c* pedal retractor scar. *Devonocheilus* (?) sp.; ZPAL N/331 (pl. 14: 7), *Wocklumeria* Zone, Famennian, Dzikowiec, the Sudetes, Poland, *d* Reconstructed adult shell in lateral and ventral views; *e* longitudinal section through its siphuncle.

specimens from the Early Frasnian of Timan, shows a fusiform, slightly exo- or endogastric, or (most commonly) orthoconic shell. Its constricted aperture is T-shaped in the adults. Its direct descendant is "*Carotites*" *procerus* ZHURAVLEVA, 1972 (= ?*Flowerites asiaticum*, *Carotites dzharailensis*, *C. longidomus*, *Vertorizoceras subitum*), from the Famennian *Platyclymenia* Zone of Kazakhstan. *U. ukhtense* co-occurs in the Early Frasnian of Timan with *Devonocheilus timanicus* (HOLZAPFEL, 1899) (= *D. inops*, *D. reticulatus*, *D. tenuiculus*, *D. usensis*, *D. admirandus*, *D. verus*, *D. alimbetus*, *Vertorizoceras ivanovi*, *Flowerites breviconus*, *Synetoceras immidiatum*) showing a considerably endogastric shell, relatively slender at the juvenile stages but more bulgy in its adult part, with only slightly constricted, triangular adult aperture (ZHURAVLEVA 1972). *Devonocheilus* may also continue in the Famennian. A fragment of endogastric phragmocone (pl. 7: 6) found in the *Cheiloceras* Zone at Jabłonna, the Holy Cross Mts., Poland, may belong to *Devonocheilus*. A specimen (fig. 26-e; pl. 14: 7) from the latest Famennian *Wocklumeria* Zone of Dzikowiec (Ebersdorf of German authors), the Sudetes, may be its congener. *Flowerites* perhaps evolved from *Devonocheilus*. It includes two species: *F. austrirhiphaeus* Zhuravleva, 1972, from the *Platyclymenia* Zone of the Urals, and *F. sobolewi* nom. nov. from the same zone of Łagów, the Holy Cross Mts. (fig. 13). *Devonocheilus* resembles

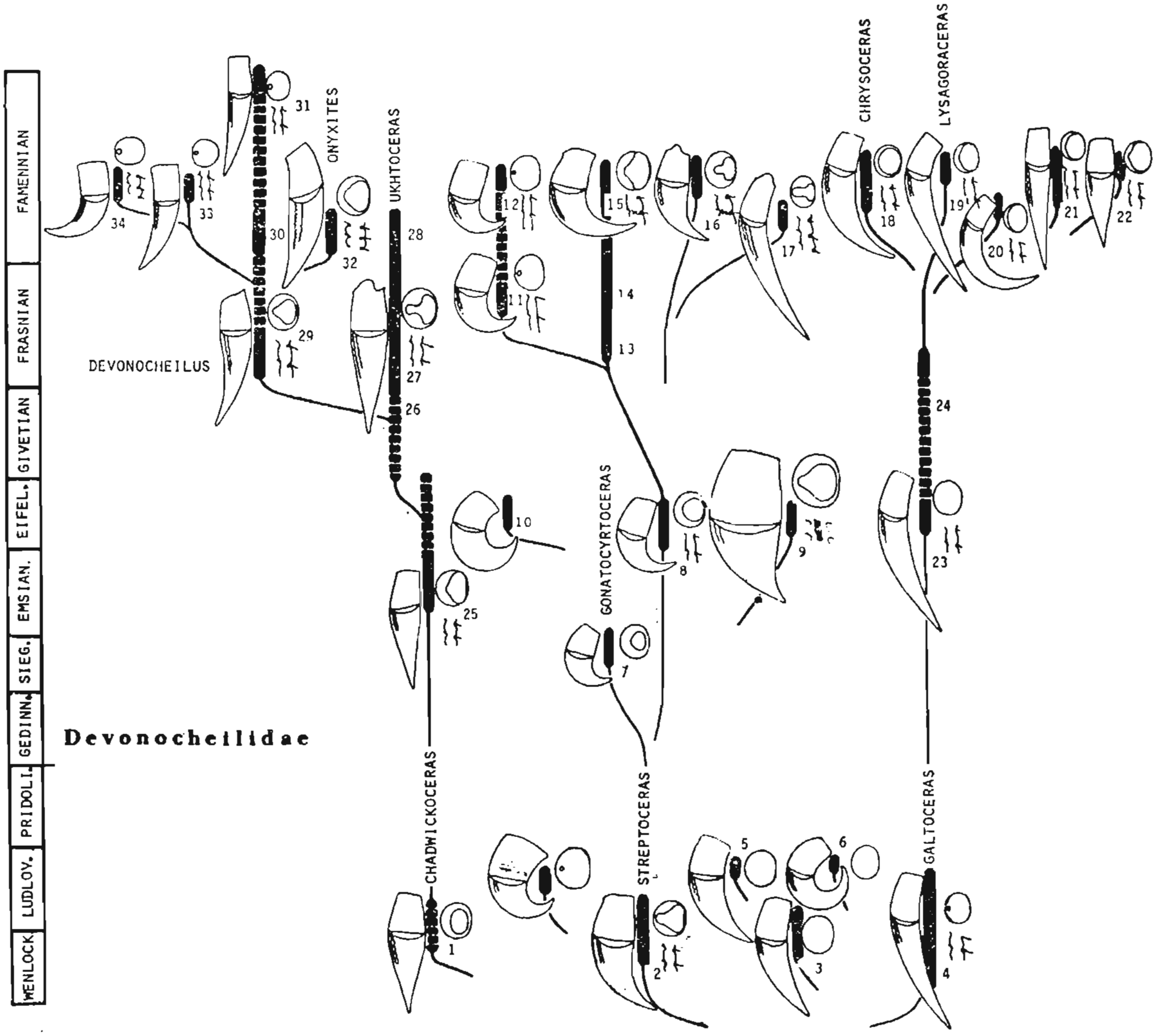


Fig. 27

Hypothetical phylogenetic relationships among members of the family Devonocheilidae Zhuravleva, 1972, *s. l.* 1 *Chadwickoceras fusiforme* Foerste; 2 *Streptoceras janus* Billings, *Amphicyrtoceras orcas* (Hall); 3 *Grimsbyoceras clitus* (Billings); 4 *Galtoceras arcticameratum* (Hall), *Worthenoceras subfusiforme* Foerste, *W. racinense* Foerste; 5 *Cyrtoceras obesum* Barrande; 6 *Cyrtoceras inflectens* Barrande; 7 *Gonatocyrtoceras heteroclytum* (Barrande) = *Cayugoceras semiclausum* (Barrande); 8 *Gonatocyrtoceras nostras* Zhuravleva; 9 *Paracleistoceras devonicans* (Barrande); 10 *Naedyceras gibbosum* Flower; 11 *Sophoceras strenuum* Zhuravleva; 12 *Selenoceras subterraneum* Zhuravleva; 13 *Tritonoceras chernovi* Zhuravleva; 14 *Elaphoceras quaietum* Zhuravleva; 15 *Gonatocyrtoceras guerichi* (Sobolew) (fig. 20a, b; pl. 13: 1-5); 16 *Gonatocyrtoceras holzapfeli* (Sobolew) (fig. 19a-e; pl. 12: 1-6); 17 *Gonatocyrtoceras longissimum* sp. n. (fig. 21a-c; pl. 11: 1-7); 18 *Chrysoceras tumidum* Zhuravleva; 19 *Lysagoraceras lagowiense* (Gürich) (fig. 23a-f; pl. 10: 5-9); 20 *Lysagoraceras kielcense* sp. n. (fig. 22a-c; pl. 10: 1-4); 21 *Lysagoraceras subfusiforme* (Münster) (fig. 25a-e; pl. 14: 1-6); 22 *Anglicornus*? *erraticus* Zhuravleva (see fig. 26a-c; pl. 14: 5-11); 23 *Cyrtoceras bryozoon* Barrande; 24 *Cyrtospyroceras reinmanni* Flower; 25 *Taskanoceras boreum* Zhuravleva; 26 *Poterioceras obesum* Holzapfel; 27 *Ukhtoceras uchtense* (Holzapfel); 28 *Carotites procerus* Zhuravleva; 29 *Devonocheilus timanicus* (Holzapfel); 30 *Flowerites vel Devonocheilus* sp. (pl. 7: 6); 31 *Devonocheilus* (?) sp.; 32 *Onyxites inversus* (Wenjukoff), 33 *Flowerites austrirhiphaeus* Zhuravleva; 34 *Flowerites ellipticus* (Sobolew) (pl. 7: 3-4). For alternative interpretation of *Flowerites* see fig. 16. *Paracleistoceras devonicans, Cyrtoceras obesum,* and *Cyrtoceras inflectens* are here assigned only tentatively.

especially the former species, differing in the non-constricted mature aperture of *F. austrirhiphaeus*. The other species is either homeomorphic with, or a descendant of *Protophragmoceras* (Discosorida). A phylogenetic relationship between *Flowerites* and *Devonocheilus* is suggested, in spite of the compressed, considerably endogastrically curved shell of the former, by their stratigraphic proximity. *Onyxites inversus* (WENJUKOFF, 1866) (= *O. depressus*, *O. conveniens*, *O. poculus*, *Manyoceras losiense*, *Radoceras reconditum*, *Draconoceras geniculatum*), from the Early Famennian of central Russia (ZHURAVLEVA 1972), is another descendant of *Devonocheilus*.

There are two types of radial-lamellar siphuncular structure in the Oncoceratida, similar to those recorded in the discosorid families Phragmoceratidae and Gomphoceratidae. (1) The morphologically more primitive form is characterized by ovate blades encircling the septal neck. The blades (lamellae) are closely related in origin to septal necks and neck elongation results necessarily in elongation of the lamellae. Distinction of the lamellae depends, as a rule, upon inflation of the connecting rings; they are very indistinct in juveniles with cylindrical rings (FLOWER 1943; see also the siphuncular structure in *Gonatocyrtoceras*). (2) In some oncoceratids with considerably elongate connecting rings, the lamellae are nonetheless very prominent and persistent from one septal neck to another. This is the other type of oncoceratid radial-lamellar siphuncular structure but intermediate morphological forms also occur. It was pointed out above that the occurrence of lamellae in a siphuncle cannot be considered as the main diagnostic feature but monophyletic nautiloid groups nevertheless exist with constant radial-lamellar structure of the siphuncle. Two of these groups, the Poterioceratidae and Jovellaniidae, discussed below, are ranked arbitrarily as families.

The oldest known nautiloid species with siphuncular structure of the first type (blades only on septal necks) is *Valcouroceras bovinum* FLOWER, 1943, from the Chazyan (Llandeilian) of New York and Vermont (FLOWER 1943*b*). In addition to the type species, *Valcouroceras* includes also some other topotype species erected on specimens with poorly known internal structure (FLOWER 1943*a*). Their distinction, as well as that of the genus *Eorizoceras* resembling the juveniles of *Valcouroceras*, may be disputable. *Valcouroceras* resembles closely in the shell outline and connecting rings *Beloitoceras*, from which it may have evolved. The shell is considerably exogastrically curved at the early developmental stages, but later almost straight. The cross section is subcircular. *V. bovinum* presumably shows a considerable intrapopulation variability. The only morphological difference from *Beloitoceras*, indicating the origin of a new evolutionary lineage, is the occurrence of radial lamellae in the siphuncle of *Valcouroceras*. The Ordovician evolution of this group is very poorly known because of the poor understanding of the internal structure of most Ordovician oncoceratids.

The next-younger nautiloid species with radial lamellae confined to the septal necks is *Diestoceras indianense* (MILLER and FABER, 1894) from the Late Ordovician of Indiana. It has an almost straight, very bulgy shell with circular section. *Diestoceras* is homeomorphic with the Late Devonian genus *Pachtoceras*, but their relation is questionable because there are no intermediates in age. Silurian oncoceratids with similar siphuncular structure and shell outline have been recorded exclusively in Bohemia.

The Bohemian Poterioceratidae *s. l.* always show a constricted, T-shaped aperture, and the trend to shifting of the siphuncle from ventral to centro-dorsal position. The abundant material from the Wenlockian, Ludlovian, and Přidolian strata in the vicinity of Prague demonstrates clearly a wide intrapopulation variability along with a tendency to produce local varieties. The variability consists mostly in shell size and ornamentation. The shell expansion rate was very variable in ontogeny, supposedly because influence of variable environmental conditions. This is most clearly visible in the specimens collected at Dvorce (Wenlockian?). The figures given by BARRANDE to present those growth irregularities were the basis of the genus *Vespoceras* FLOWER (in FLOWER and TEICHERT 1957). As judged from my own research on BARRANDE'S collection in the National Museum, Prague, the material under discussion includes only 8 to 9 biospecies. The form closest in morphology to the ancestral genus *Diestoceras* is "*Cinctoceras*" *robustum* (BARRANDE, 1865) (= *Vespoceras cingulatum*) known from some specimens found at Kosoř (? Kopanina Formation, Ludlovian). This species shows a relatively elongate shell and ventral siphuncle. FLOWER (*in* FLOWER and TEICHERT 1957) considered it to be congeneric with "*C.*" *imperiale* with subdorsal siphuncle, only because of the irregular ornamentation. "*C.*" *robustum* may be related to "*Umbeloceras*" *incola* (BARRANDE, 1865) (= ?*U. spei, Ovocerina mumia*) collected at Lochkov. The latter species shows a smaller, more bulgy shell with fissure-like mature aperture. Actually, "*U.*" *incola* may be a variety of "*C.*" *robustum.* This lineage persists also in the Přidolian, represented by an abundant sample of the species "*Mandaloceras*" *simplex* (BARRANDE, 1865). Fourteen species of "*Gomphoceras*" distinguished by BARRANDE in the collection from Karlštein, are probably conspecific with "*M.*" *simplex.* The latter species differs from "*C*" *robustum* in its siphuncle being a little away from the venter of the shell, and its aperture showing a medial dorsal sinus. A similar form was reported by KISIELIEV and BALASCHOV (1968) under the name *Umbeloceras tumescens.* The Gedinnian phragmocones described under the names *Rizoceras podolicum* BALASCHOV, 1968, and *Metarizoceras sinkovense* BALASCHOV, 1968, may also belong to the same group of species.

Mandaloceras verneuilli (BARRANDE, 1865) from Lochkov, including also some other of BARRANDE's species erected on the material from Lochkov, shows a subcentral siphuncle and weakly endogastrically curved shell similar in outline to that of "*C.*" *robustum.* "*Ovocerina*" *marsupium* (BARRANDE, 1865) known from Zadni Kopanina (? Kopanina Formation, Ludlovian) differs from *M. verneuilli* in its slightly exogastrically curved shell. In some individuals of this species peculiar irregularities in gas-chamber length have been recorded (BARRANDE 1865, pl. 83: 6, 9). This evolutionary lineage may also continue into the Přidolian but this is uncertain because of the poor preservation of its supposed representatives from Karlštein. The largest and most spectacular Bohemian poterioceratid specimens are "*Cinctoceras*" *imperiale* (BARRANDE, 1865), which has a subdorsal siphuncle and a shell outline close to that of "*C*" *robustum.*

All the above discussed species are closely interrelated. The ranges of their variability overlap and hence, their separation is often arbitrary. Similar range of variability is shown by populations of gomphoceratids from Slite and Hemse beds of Gotland. They supposedly resulted from a local adaptive radiation of a group of rather immobile benthos-related organisms with ontogenetic development lacking the stage of a pelagic larva. There is no need to erect a distinct genus for each of these species (see FLOWER and TEICHERT 1957), and to establish a new family. In my opinion, these Bohemian forms belong to a single genus, *Mandaloceras* HYATT, 1900. A poorly known species of this genus, characterized by a subventral siphuncle and a peculiarly ornamented, longitudinally striated shell, has been recorded from the Gascons Formation, Canada (FOERSTE 1936).

A subdorsal siphuncle occurs not only in some Silurian species of *Mandaloceras* but also in some Devonian Poterioceratidae. *Laumontoceras laumonti* (BARRANDE, 1865), known exclusively from a phragmocone fragment from the Siegenian (?) of France, may be related to *Mandaloceras*, but their stratigraphic and paleozoogeographic proximity appears thus far as the only evidence in support of this hypothesis. The Middle and Late Devonian forms differ from those discussed above in their open mature aperture, while the similar position of the siphuncle may reflect convergence rather than phylogenetic relationship.

A large stratigraphic gap covering the entire Early Devonian occurs in the fossil record of the evolution of the Poterioceratidae *s. l.*, with ventral siphuncle. Some forms occur in the Eifelian Třebotov Limestone of Bohemia that may belong to this group, but any reliable phylogenetic interpretation is impossible because of poor preservation. In fact, "*Gomphoceras*" *senex* BARRANDE, 1865, with constricted (?) aperture, straight, bulgy shell circular in cross section, and supposedly weakly inflated connecting rings with radial lamellae, is the only Bohemian Eifelian species reliably placed in the Poterioceratidae *s. l.* BARRANDE (1865) based several species on externally similar specimens collected from the Třebotov Limestone but these are unidentifiable. Equally poorly preserved are most specimens collected from various Middle Devonian localities in North America (FLOWER 1938). The data presented by FLOWER do not demonstrate that the Middle Devonian North American poterioceratids represent more than a single species, *Acleistoceras olla* (SAEMANN); but this does not imply that their monospecificity is proved. In addition to several forms reported by FLOWER (1938) and FOERSTE (1927), *A. olla* may also be represented by somewhat better preserved specimens of Devonian oncoceratids described by FAGERSTRÖM (1961) and ULRICH *et al.* (1943). Their internal structure remains very poorly known. The only available information on their siphuncular structure is a section through a specimen figured by FLOWER (1938, pl. 1: 1) under the name *Brevicoceras pompeyense.* The section presents radial lamellae and inflated connecting rings as typical for the family. It significantly differs, however, from a schematic section through the siphuncle of the type species of the genus *Acleistoceras* (see SWEET 1964). The specimen under discussion may be congeneric (conspecific ?) with a phragmocone described by FLOWER (1938) under the name *Cyrtogomphus curvatus.* The taxonomy of the North American Devonian Poterioceratidae cannot be verified until new, better preserved material is collected and investigated. One may, however, suppose that *A. olla* and possibly also *Ovoceras oviforme* (HALL, 1860) are ancestors of later Poterioceratidae known mainly from Europe. The exogastric curvature and ventral

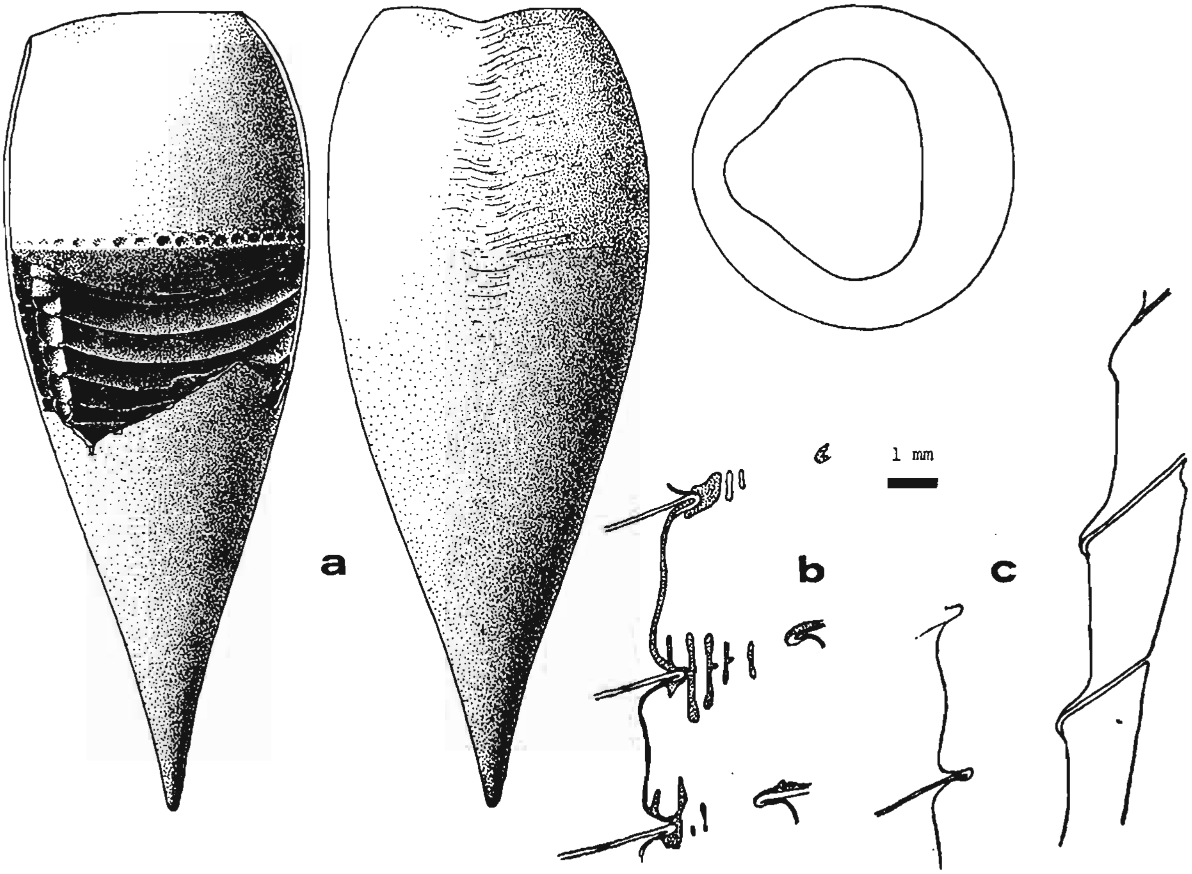
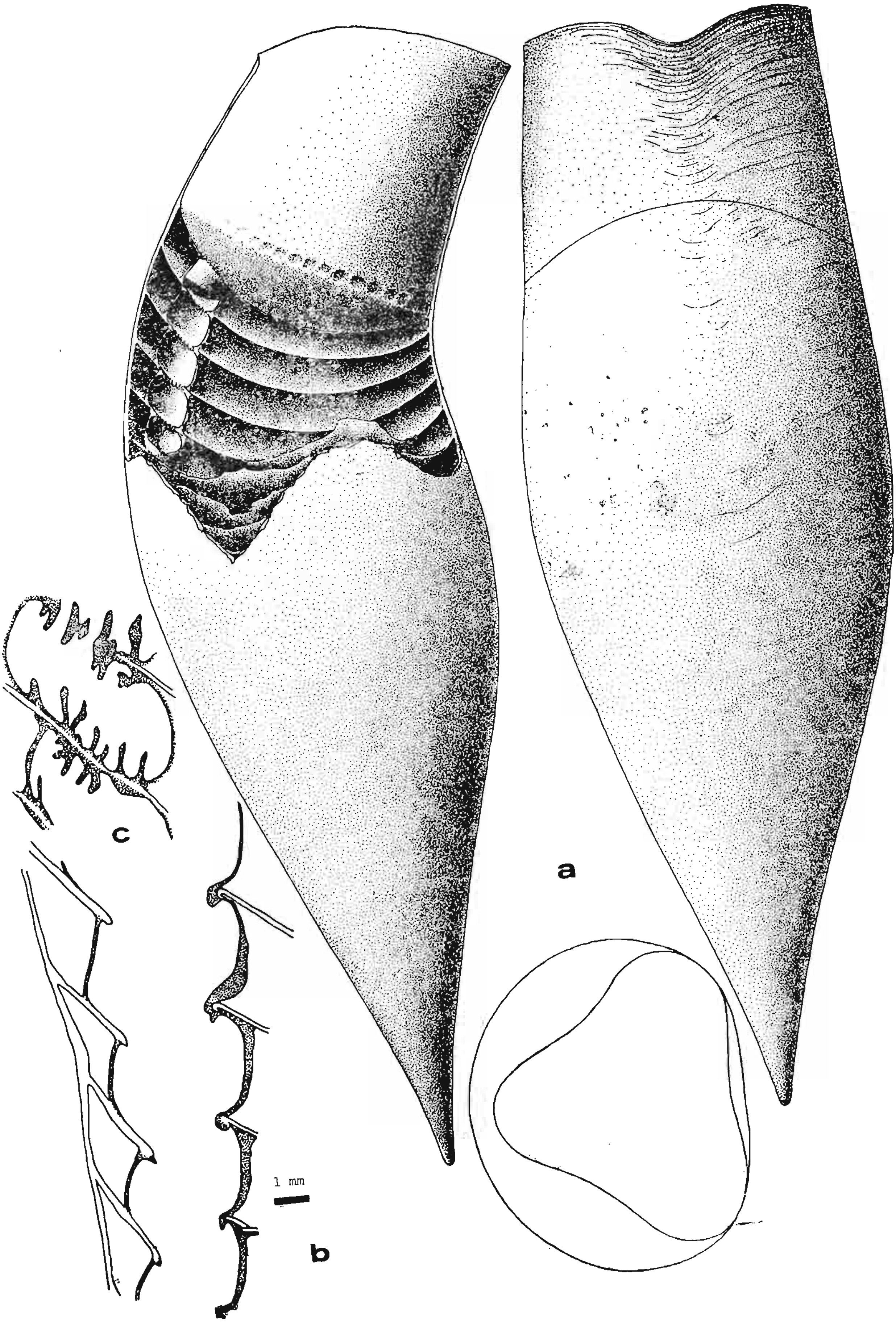


Fig. 28

Pachtoceras abbreviatum (GÜRICH, 1901); *Cheiloceras* Zone, Famennian, Kielce Kadzielnia, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 16: 3-5); *b, c* longitudinal section through a siphuncle, *b* ZPAL N/386 (pl. 16: 5); *c* ZPAL N/388 (pl. 16: 4)


c
a
1 mm
b

siphuncle of *Acleistoceras* are suggestive of its primitiveness. In turn, its weakly constricted, triangular aperture resembles the Late Devonian genus *Pachtoceras* characterized by a orthoconic and bulgy shell. *Apioceras inflatum* Quenstedt from the Late Givetian of Gerolstein, and *Sycoceras ficus* (Roemer, 1850) from the Frasnian of Adorf may be the earliest species of *Pachtoceras*. This genus (attributed by Zhuravleva 1972 to the order Discosorida) has been reported from some Late Devonian localities on the Russian Platform, Timan, and Holy Cross Mts., but the actual number of its species can hardly be determined because of considerable intrapopulation variability and generally poor preservation. The oldest of these populations occurs in the Domanikovaia svita (Middle Frasnian) of Timan, and belongs to *Pachtoceras* (*Raphanites*) *bogoslovskyi* (Zhuravleva, 1972) (= *Platyconoceras patella*, *Stagonites pacatus*, *S. zilimensis*, *Therioceras tumidum*, *T. procurvum*, *T. lautum*). The specimens are excellently preserved and show a bulgy shell with strongly constricted terminal aperture. The well developed funnel sinus in the aperture indicates that this species is related to *Apioceras inflatum*. A specifically unidentifiable population of *Pachtoceras* (pl. 16: 1-2, 8) occurs in the Late Frasnian at Płucki by Łagów (the Holy Cross Mts, Poland). Very similar forms occur also in the Early Famennian *Cheiloceras* Zone at Kadzielnia (Kielce, Poland). The Polish populations resemble very closely those from Timan in shell outline and average dimensions as well as in siphuncular structure (see fig. 28a-c and pl. 16: 3-5, and Zhuravleva 1972, pl. 5: 2-3). Further, a population of *Pachtoceras* with an average mature shell size (pl. 16: 6-7) twice as great as at Kadzielnia, has been recorded from coeval strata at Jabłonna (the two localities are 20 km apart). The ranges of intrapopulation variability observed at Kadzielnia and Jabłonna can not be treated biometrically because of specimen fragmentation, but there is little doubt that they overlap in part. The siphuncle shifts gradually from the venter during the ontogeny of *Pachtoceras*; the larger specimens from Jabłonna thus show a more central siphuncle. These morphological differences may merely reflect a difference in environment, causing development of local varieties. Specimens of *Pachtoceras* recorded from the *Cheiloceras* Zone of the central Russian Platform and described by Zhuravleva (1972) may all belong to the type species of the genus, *P. rotundum* (Pacht). Single specimens supposedly belonging to *Pachtoceras* have also been reported from the Early Frasnian of Kazakhstan (*Kitatites insidosus* Zhuravleva, 1972) and the Famennian (?) of Novaya Zemla (*Pachtoceras hyperboreum* Zhuravleva, 1972).

The phylogenetic interpretation of *Almaloceras abaeratum* Zhuravleva, 1974 (= *Mnemoceras galithkyi*, *Lychnoceras occultum*, *Corysoceras karatauense*, ? = *Mimolychnoceras zolkinae*) from the Late Famennian of Karatau, Kazakhstan, presents a serious problem. This species resembles very closely the above discussed species of *Pachtoceras* in shell outline, aperture, and siphuncle. However, *A. abaeratum* shows radial lamellae extended over the entire connecting ring as in the family Jovellaniidae. The only form with supposedly similar shell outline and siphuncular structure is *Paracleistoceras devonicans* (Barrande) from the Eifelian Třebotov Limestone of Bohemia. This species is known exclusively from very poorly preserved specimens with scarcely recognizable internal structure, and may actually be related to the genus *Gonatocyrtoceras* (Devonocheilidae). The stratigraphic gap separating the records of *Paracleistoceras* and *Almaloceras* is also too wide to admit their close phylogenetic relationship as certain. In my opinion, the radial lamellae could be secondarily elongated in *Almaloceras* whose derivation from *Pachtoceras* appears plausible to me. Similar relationships may also be claimed for *Evlanoceras evlanense* (Nalivkin, 1947) (= *Cyclopites abundans* Zhuravleva,

Fig. 29

Evlanoceras (?) *kontkiewiczi* (Gürich, 1896); *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 19: 1-3); *b* tangential section through a siphuncle, ZPAL N/367 (pl. 19: 2); *c* sagittal section through the same siphuncle.

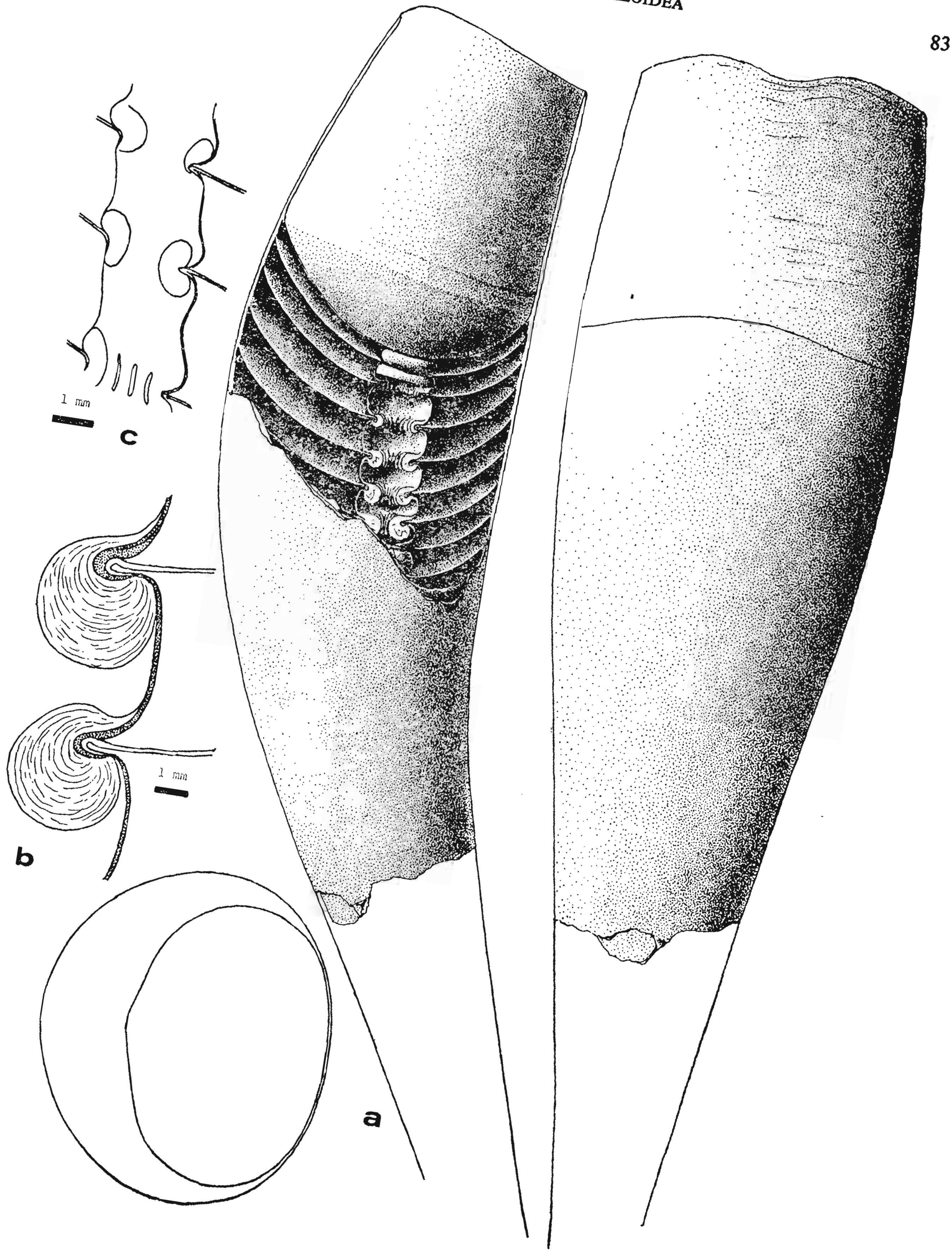
1972, *Paraevlanoceras compressum* ZHURAVLEVA, 1972) from the Late Frasnian of central Russia. The latter species is known from numerous but much deformed specimens and hence, its shell shape is uncertain. According to ZHURAVLEVA (1972), the adult shell of *E. evlanense* was endogastrically curved and that of *Cyclopites abundans*, in my opinion conspecific, straight. I re-examined the original material and believe that *E. evlanense* has a weakly exogastrically curved shell, trilobate terminal aperture, and radial lamellae continuous between septal necks. It remains uncertain, whether *Evlanoceras* is related to the Jovellaniidae, close to *Paracleistoceras*, or to *Pachtoceras* or *Acleistoceras*. This problem becomes even more complex after considering *Evlanoceras* (?) *kontkiewiczi* (GÜRICH, 1896), externally similar to *E. evlanense* (fig. 29). The only specimen with recognizable siphuncular structure (fig. 29b-c and pl. 19: 2) shows a siphuncle indistinguishable from that of typical *Pachtoceras* (unfortunately, this specimen is not curved at the living adult chamber and, hence, its identification is disputable). Furthermore, the early stages of *E.* (?) *kontkiewiczi* resemble very closely those of *Pachtoceras*, especially as observed in the population from Jabłonna. *Pachtoceras* occurs in the Holy Cross Mts. exclusively in the *Cheiloceras* Zone, whereas *Evlanoceras* (?) *kontkiewiczi* is confined to the *Platyclymenia* Zone, supporting their close phylogenetic relationship.

The recognition of shell morphology and siphuncular structures in *Pachtoceras* has much bearing on the phylogenetic interpretation of the Carboniferous representatives of *Poterioceras*. Most important is the siphuncular shift from a marginal to subventral during the ontogeny of *Pachtoceras*. This means that adult shells of *Pachtoceras* have the siphuncle situated between the shell center and ventral side, just as in *Poterioceras*. The Early Carboniferous species of *Poterioceras* (see FOORD 1898, CRICK 1905, SHIMANSKY 1968) present a morphological sequence ranging from orthoconic, bulgy forms virtually indistinguishable from the Late Devonian *Pachtoceras*, namely *Poterioceras lagenale* (KONINCK) from the Tournaisian, up to relatively narrow forms with strongly exogastrically curved initial part of the shell, namely *P. apicale* FOORD, 1896, from the Visean. *Poterioceras* differs from *Pachtoceras* only in its juvenile subcentral siphuncle. It reflects probably an acceleration of mentioned shift of the siphuncle away from the shell wall in ontogeny. Presumably there is no difference in siphuncular structure between *Poterioceras* and *Pachtoceras*. SHIMANSKY (1968) described sections through the siphuncle of *Poterioceras* under the names *Calchasiceras* sp. (SHIMANSKY 1968, pl. 10: 5) and ? *Paracleistoceras* sp. (SHIMANSKY 1968, pl. 11: 3). These specimens show distinct radial lamellae in the siphuncle.

The shift of the poterioceratid siphuncle away from the venter happened not only in *Mandaloceras* and *Poterioceras*, but also in *Mecynoceras*. The Early Famennian strata of the central Russian Platform yield abundant individuals of *Mecynoceras rex* (PACHT, 1858) with straight shell inflated in the final part of the adult phragmocone, and simple, non-constricted adult aperture. The siphuncular structures are very poorly preserved, but one may claim that they undergo an ontogenetic change from elongate, straight necks with radial lamellae continuous over the entire connecting ring to considerably curved necks with radial lamellae confined to them. There is no single undeformed specimen in the rich collection of this species investigated by ZHURAVLEVA (1972) and hence, there is no reason to erect the new genus and species *Paramecynoceras fixum* on the laterally compressed specimens. The shells were probably circular in their original cross section and the present variation in shell shape resulted from variously oriented deformations.

Fig. 30

Mecynoceras (?) *polonicum* (GÜRICH, 1896); *Cheiloceras* Zone, Famennian, Poland. *a* Reconstructed adult shell in lateral and ventral views, and the outline of its aperture (see pl. 17: 3); *b* longitudinal section through a siphuncle, ZPAL N/381 (pl. 17: 2), Kielce-Kadzielnia; *c* longitudinal section through a juvenile siphuncle, ZPAL N/234, Jabłonna, bed J. 6, Holy Cross Mts.


1 mm
c
b
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a

A successive stage in the evolutionary shift of siphuncular position is represented by *Mecynoceras* (?) *polonicum* (GÜRICH, 1896) from the Early Famennian *Cheiloceras* Zone of Poland. Its spindle-shaped, slightly curved shell shows a simple aperture and subdorsal siphuncle (fig. 30). The siphuncle displays very strongly developed radial lamellae which appear even in the penultimate septal neck (pl. 17: 2). The lamellae fill the siphuncle almost entirely in the apical part of a shell but contact the siphuncular wall only in proximity of the aperture. The phylogenetic relations of both *M. rex* and *M.* (?) *polonicum* are unclear. The latter species resembles *Phragmoceras bulbosum* SANDBERGER from the Middle Devonian of Germany, which shows, however, a different shell outline. In turn, *Laumontoceras laumonti* (BARRANDE) is known exclusively from a phragmocone fragment and should probably be regarded as closely related to *Mandaloceras* with T-shaped aperture. *Mecynoceras* evolved probably from *Acleistoceras*. The evolutionary trend consists of a migration of the siphuncle from subventral to subdorsal position, similar to that in the *Mandaloceras* lineage. The genus *Aktjubocheilus* from the Famennian *Platyclymenia* Zone of the Urals (ZHURAVLEVA 1972, 1974) may be a descendant of *M. rex*.

The Oncoceratida with radial lamellae developed over the entire connecting rings have been recorded from strata coeval to those yielding the oldest known specimens of *Valcouroceras*. The earliest known representative of this group is *V.* ? *holtedahli* SWEET, 1957, from the Cephalopod Shale (Uhakuan?, Llandeilian) of Norway. The only described specimen, a phragmocone fragment, resembles both *Beloitoceras* and *Valcouroceras* in its siphuncular structure, and its main distinctive feature is the occurrence of continuous lamellae in the siphuncle. *Minganoceras subturbinatum* (BILLINGS, 1857) from Quebec is supposedly a little younger than *V.* ? *holtedahli*. Its siphuncular structure resembles *Valcouroceras* but the lamellae are much more strongly developed and cover partly the connecting ring (FLOWER 1946). The systematic position of this species, known from a single fragment, can not be established; the considerably depressed shell suggests, however, relation to *Augustoceras shideleri* FLOWER, 1946, from the Late Ordovician Leipers Formation of Kentucky. The latter species shows indeed very distinct, evenly developed radial lamellae and a considerably depressed shell. FLOWER (1946*a*) described from the Late Ordovician of Ohio numerous shell fragments under various specific names of *Augustoceras* and *Manitoulinoceras* (FLOWER 1946*a*). They resemble very closely *A. shideleri* and their distinction seems doubtful to me. An abundant nautiloid assemblage with virtually the same siphuncular structure has also been reported from the Llandoverian of Siberia (MIAGKOVA 1967). These shells differ from those discussed above in their circular to slightly compressed cross section, whereas they vary in shell curvature and elongation. I am unable to determine the species diversity of this assemblage which was doubtless much overestimated by MIAGKOVA. Possibly, this is a single conspecific population of *Hiregiroceras costulatum* MIAGKOVA, 1967, with a very high intrapopulation variability. It is noteworthy that this unquestionable oncoceratid displays much thickened connecting rings, which character is claimed by FLOWER and TEICHERT (1957) and ZHURAVLEVA (1972) to be diagnostic of the Discosorida. At least two oncoceratid species with continuous radial lamellae in the siphuncle occur in the Silurian of Bohemia. One of these, *Oocerina lentigradum* (BARRANDE, 1866), known from a single specimen, resembles the American *Augustoceras shideleri* in the depressed shell. The remaining forms, known from numerous but fragmentary specimens, have compressed shells as in the Siberian species *Hiregiroceras costulatum*. The best preserved specimen representative of this group has been described from Wenlockian (?) under the name *Cyrtoceras strangulatum* BARRANDE, 1866, and shows a considerably curved shell. Possibly, the shell fragments collected in the same exposure and described under the names *Projovellania athleta* (BARRANDE, 1866) and *Mixosiphonoceras desolatum* (BARRANDE, 1866) are conspecific with *C. strangulatum*, but I am unable to ascertain this without seeing the original specimens. Very similar shell fragments have also been recorded from the Wenlockian to Ludlovian strata of Sardinia (*Galtoceras sardoum* and *Oocerina abdita*; see Serpagli and Gnoli 1977), as well as in China (LAI 1965).

Abundant nautiloid material resembling *O. lentigradum* has been described by SIEMIRADZKI (1906), HERITSCH (1930*b*), ZHURAVLEVA (1961, 1974), and BALASCHOV (1968) from the Gedinnian Czortków and Borszczów Beds in Podolia. I investigated the rich collection in the care of Dr. ZHURAVLEVA, and believe that it belongs to a single species with moderate intraspecific variability consisting mostly in shell curvature and also in shell cross section (slightly depressed to weakly compressed); the shell is always more curved ventrally than dorsally. The aperture has commonly a weakly developed ventral sinus of widely variable depth. There is no morphologic gap between any two morphotypes. The Podolian material was the basis of two new genera and nine new species attributed to four genera (ZHURAVLEVA 1974). The differences between these "species" commonly reflect a difference in preservation or ontogenetic stage. One can not recognize the nature of the difference between *Jovellania podolica* (SIEMIRADZKI, 1906) and the Bohemian *Oocerina lentigradum*, since the latter is known from a single specimen; that specimen is much smaller than most Podolian forms but its shell outline is almost identical to typical *J. podolica*. *J. buchi* (de VERNEUIL, 1850) from the Siegenian (?) of France may also belong to this evolutionary lineage. The differences observed between the above discussed Late Ordovician, Silurian, and Early Devonian forms do not substantiate their assignment to distinct genera but the systematic revision of the original material is needed.

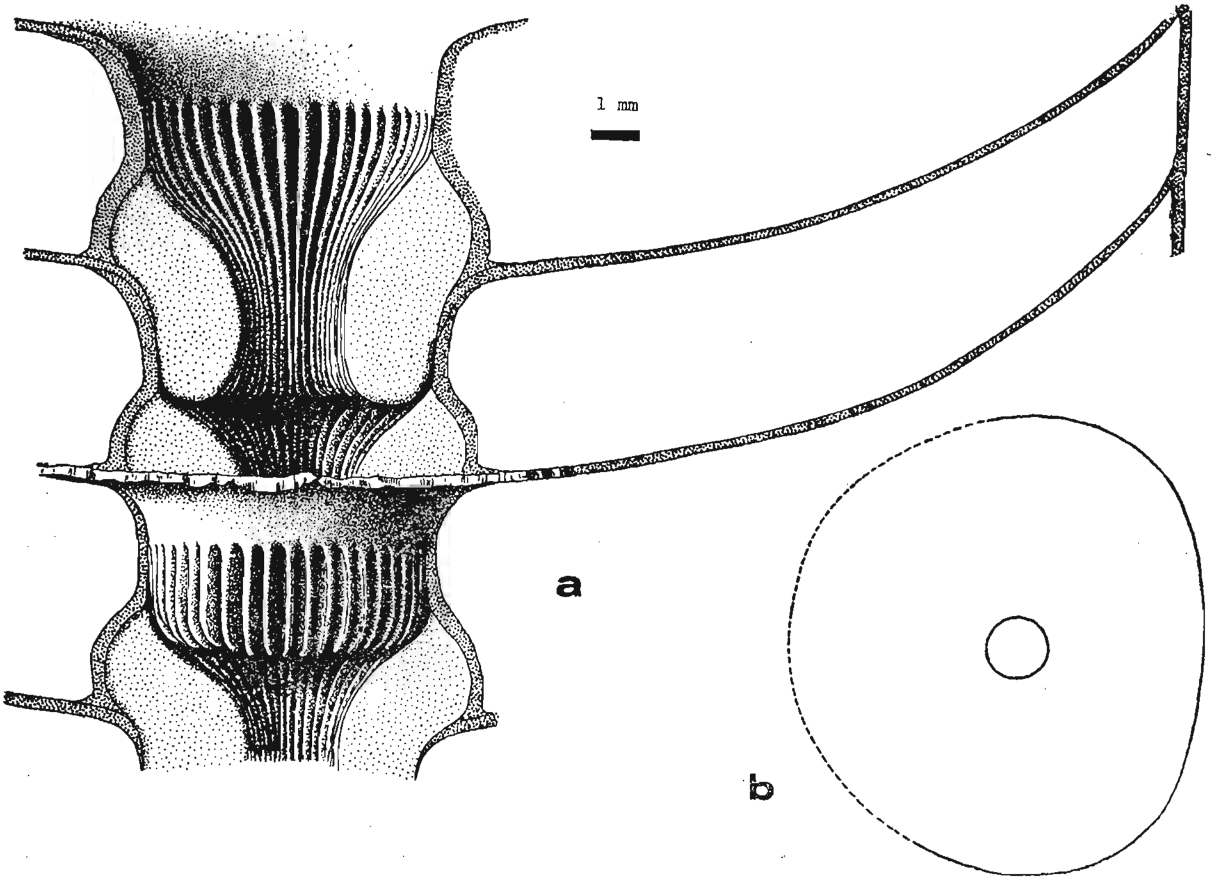


Fig. 31
Balashovia (?) *vel Mecynoceras* sp.; *Cheiloceras* Zone, Famennian, Holy Cross Mts, Poland; *a* Reconstruction of the siphuncular structure, Jabłonna (see pl. 18: 1); *b* cross section of the phragmocone, left wall of Dule gorge, Łagów (see pl. 18: 2-3).

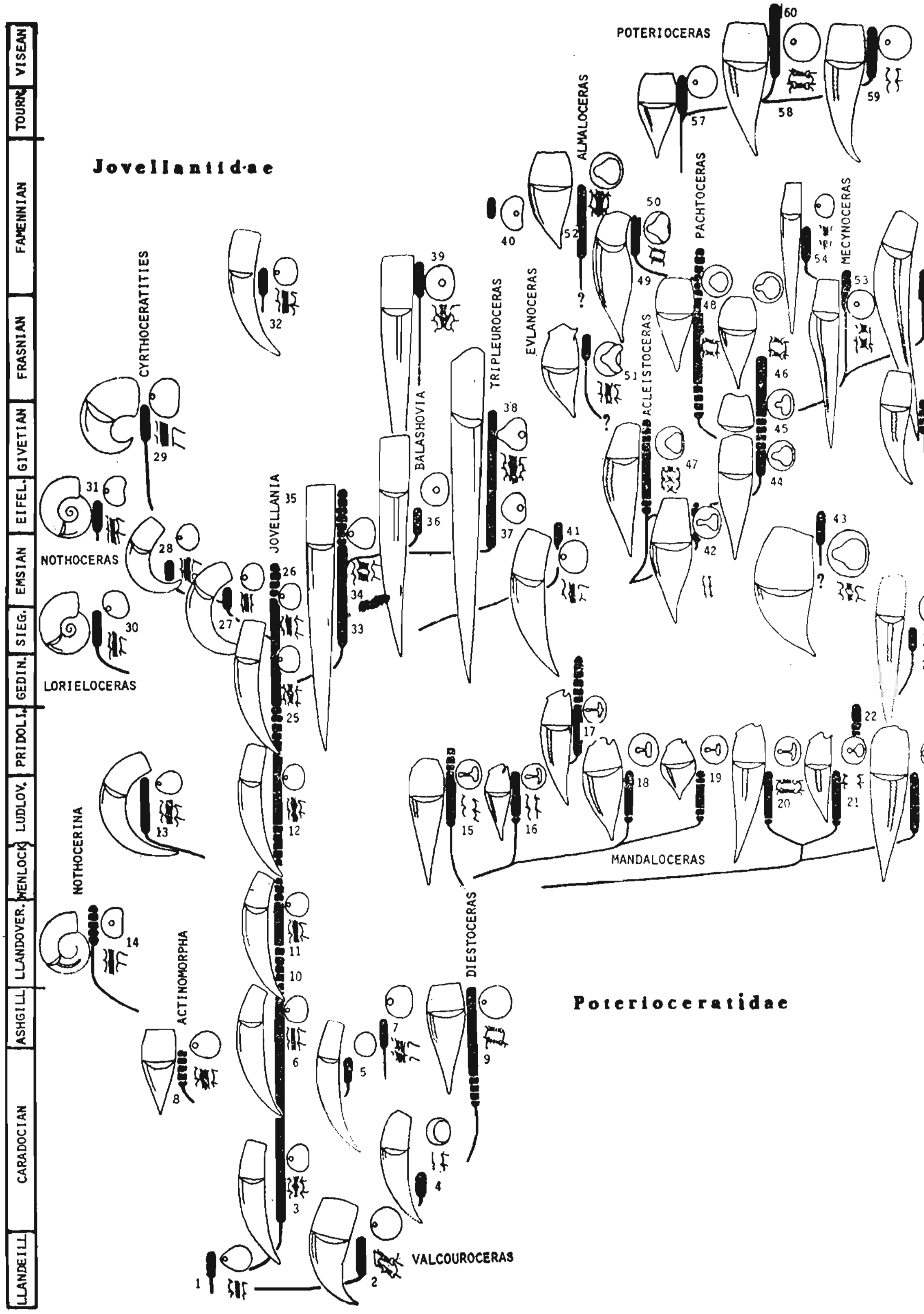
The position of *Cyrtoceratites depressus* (Bronn, 1833) from the Late Givetian of Germany is unclear. Its considerably curved shell and continuous radial lamellae in the siphuncle (Dechaseaux 1941, Schönenberg 1953) resemble those of the above discussed forms but it differs from them in its concave connecting rings and very rapidly expanding shell; its living chamber is unknown. There is a well preserved phragmocone of *C. depressus* at the Wrocław University (UWR 2108), which resembles in outline *Cranoceras alatum* Holzapfel, 1897.

A nautiloid group with longiconic shell, triangular in cross section, occurs in the Early to Middle Devonian, presenting a morphological sequence ranging from ventral (as in *Jovellania*) to dorsal position of the siphuncle. Its distinctive features is the weakly curved, considerably elongate septal neck. Possibly, "*Mixosiphonoceras*" *norvegicum* Strand, 1953, known from two phragmocone fragments from the Late Ordovician of Norway, belongs to this group, as indicated by its siphuncular structure. Its direct relationship with the Devonian forms is, however, disproven by the total absence of Silurian forms. The oldest known representative is *Jovellania jovellani* (Verneuil, 1852) from the Siegenian (?) of France (Dechaseaux 1941). It is followed by "*Mixosiphonoceras*" *boreale* Kuzmin, 1965, from the Late Emsian of Novaya Zemla (Kuzmin 1965, Zhuravleva 1974). Both species have a ventral siphuncle, whereas the externally similar *Balaschovia salairica* (Balaschov, 1955) and *B. borea* Zhuravleva, 1974, from the Eifelian of Kazakhstan and Novaya Zemla, respectively, have a central siphuncle. All these species are alike in siphuncular structure. In turn, a dorsal siphuncle is present in a poorly known species from the Eifelian of Bohemia and Poland, *Tripleuroceras archiaci* (Barrande, 1868). The scarce specimens of this species found in the Třebotov Limestone, Bohemia, permit reconstruction of the shell shape. It was large, slowly expanding in width, ovate-triangular in

Fig. 32

Hypothetical phylogenetic relationships among members of the families Poterioceratidae, Jovellaniidae, and Nothoceratidae; 1 *Valcouroceras? holtedahli* Sweet; 2 *Valcouroceras bovinum* Flower; 3 *Minganoceras subturbinatum* (Billings); 4 *Broeggeroceras contractum* Sweet; 5 *Broeggeroceras? elongatum* Sweet; 6 *Augustoceras shideleri* Flower, *A. kulunbulakense* Barskov, *A. lobatum* Barskov; 7 *Mixosiphonoceras norvegicum* Strand; 8 *Anthomorpha pupa* Flower; 9 *Diestoceras indianense* (Miller and Faber); 10 *Blakeoceras llandoveri* (Blake); 11 *Hiregiroceras costulatum* Miagkova; 12 *Oocerina lentigradum* (Barrande), *Galtoceras? sardoum* Serpagli and Gnoli = (?) *Oocerina abdita sensu* Serpagli and Gnoli; 13 *Cyrtoceras strangulatum* Barrande, *Projovellania athleta* (Barrande), *Mixosiphonoceras desolatum* (Barrande); 14 *Nothocerina rara* Barskov; 15 *Cinctoceras robustum* (Barrande) = *Pseudogomphoceras rigidum* (Barrande), *Vespoceras cingulatum* (Barrande); 16 *Umbeloceras incola* (Barrande) = (?) *U. spei* (Barrande), *Ovocerina mumia* (Barrande) (see pl. 15: 2); 17 *Mandaloceras simplex* (Barrande); 18 *Gomphoceras microstoma* Barrande; 19 *Gomphoceras capitatum* Barrande, 20 *Mandaloceras verneuilli* (Barrande) = (?) *M. bohemicum* (Barrande); 21 *Ovocerina marsupium* (Barrande) = (?) *O. alphaeus* (Barrande); 22 *Mandaloceras haueri* (Barrande), *Vespoceras vespa* (Barrande), *V. perplexans* Flower; 23 *Cinctoceras imperiale* (Barrande), *C. agassizi* (Barrande), *C. singulare* (Barrande); 24 *Laumontoceras laumonti* (Barrande); 25 *Jovellania podolica* (Siemiradzki); 26 *Jovellania buchi* (Verneuil); 27 *Cyrtoceras grohmanni* Dahmer; 28 *Turnoceras novosemelicum* (Kuzmin) = (?) *Nectoceras semelicum* Nalivkin *in* Zhuravleva; 29 *Cyrthoceratites depressus* (Bronn); 30 *Lorieloceras lorieli* (Barrande); 31 *Nothoceras bohemicum* Barrande = (?) *Anomaloceras anomalum* (Barrande); *Nothoceras roussanovi* Kuzmin; 32 *Conostichoceras hardmanni* Teichert; 33 *Jovellania jovellani* (Verneuil); 34 *Mixosiphonoceras boreale* Kuzmin; 35 *Coelocyrthoceras ventralissimum* (Sandberger and Sandberger); 36 *Balashovia salairica* (Balaschov), *B. boreale* Zhuravleva; 37 *Tripleuroceras archiaci* (Barrande) (pl. 20: 1-4); 38 *Tripleuroceras triangulare* (d'Archiac and Verneuil) (pl. 19: 4, 20: 2); 39 *Balashovia* (?) *vel Mecynoceras* sp. (fig. 31a-b; pl. 18: 1-3); 40 *Kijoceras clarum* Zhuravleva; 41 *Blakeoceras empiricum* (Barrande); 42 *Gomphoceras senex* Barrande; 43 *Paracleistoceras devonicans* (Barrande); 44 *Ovoceras oviforme* (Hall); 45 *Apioceras inflatum* Quenstedt; 46 *Raphanites bogoslovskyi* Zhuravleva; 47 *Acleistoceras olla* (Saemann), *Exocyrtoceras minutum* Flower, *Brevicoceras casteri* Flower, *Eleusoceras nicholsi* Flower, *Aleoceras gracile* Flower, *Cyrtogomphus curvatus* Flower, *Hipparionoceras iowaense* Flower 48 *Pachtoceras? rotundum* (Pacht): 49 *Pachtoceras abbreviatum* (Gürich) (fig. 28a-c; pl. 15: 3, 16: 1, 3-7); 50 *Evlanoceras? kontkiewiczi* (Gürich) (fig. 29a, b; pl. 19:13); 51 *Evlanoceras evlanense* (Nalivkin): 52 *Almaloceras abaeratum* Zhuravleva; 53 *Mecynoceras rex* (Pacht); 54 *Aktjubochellus anaticula* Zhuravleva; 55 *Phragmoceras bulbosum* Sandberger; 56 *Mecynoceras* (?) *polonicum* Gürich (fig. 30a-c; pl. 17: 1-4); 57 *Poterioceras lagenale* (Koninck); 58 *Calchasiceras ventricosum* (Mc Coy); 59 *Poterioceras fusiforme* (Sowerby), *P. latiseptatum* Foord, *Meloceras apicale* Foord, *P. arcuatoseptatum* Foord, *Welleroceras liratum* Miller and Furnish; 60 *Poterioceras oviforme* Shimansky = *P. cuneatus* Shimansky.

cross section; the siphuncle had continuous radial lamellae and elongate, straight septal necks. This reconstruction is supported by poorly preserved specimens from the Eifelian of Jurkowice, Poland (pl. 20: 1 and 3-4). A more advanced species, *T. triangulare* (ARCHIAC and VERNEUIL,



1841), occurs in the Eifelian of Germany (SANDBERGER and SANDBERGER 1856) and the Givetian of Poland (pl. 19: 4, pl. 20: 2). It resembles *T. archiaci* in shell outline and size, but differs in its triangular cross section and the conspicuous ribs at the apical part of the shell (pl. 20: 2). As indicated by the growth lines well preserved on a specimen collected at Miłoszów, Holy Cross Mts., Poland (pl. 19: 4), the aperture shows a gently rounded, shallow dorsal sinus and ovate lateral lobes oblique to the septal sutures, with convexity opposite to them, and forming a sharp ventral sinus. The transverse juvenile annulations run parallel to the growth lines. The wide siphuncle has the same structure as in the above discussed species. No representative of the genus *Balaschovia* has been reported from the Frasnian, but a possible descendant occurs in the Early Famennian *Cheiloceras* Zone of the Holy Cross Mts. It is known from fragmentary specimens and one can not determine the shell outline of a mature individual. As judged from the size of a mature (?), presumably incomplete living chamber (pl. 18: 3), this was a large form with ovate triangular cross section (fig. 31b) and siphuncular structure only insignificantly different from those of *Balaschovia* and *Tripleuroceras* (see pl. 18: 1, 3 and fig. 31a). The material is too incomplete to substantiate erection of a new species. This form may actually be related to *Mecynoceras*. The juveniles of *Mecynoceras* show straight dorsal septal necks, a feature which might well extend in phylogeny over the adult stages.

Proposed systematics.—

Oonoceratidae HYATT, 1900

Long, compressed, exogastrically curved to coiled shell with ventral siphuncle lacking any radial structures; short, cylindrical living chamber.

Oonoceras HYATT, 1884; *Cyrtoceras acinaces* BARRANDE, 1866
Long shell strongly curved at the initial stages.
Richardsonoceras FOERSTE, 1952; *Cyrtoceras simplex* BILLINGS, 1857
[= *Loganoceras* FOERSTE, 1932; ? *Ankyloceras* ZHURAVLEVA, 1974; *Almaloceras* ZHURAVLEVA, 1974]
Relatively short shell loosely coiled at the initial stages.

Rutoceratidae HYATT, 1884

Curved to coiled shell with longitudinal spines or costae formed by frills.

Zitteloceras HYATT, 1884; *Cyrtoceras hallianum* d'ORBIGNY, 1850
[= ? *Ringoceras* STRAND, 1935; *Piersaloceras* TEICHERT, 1930]
Curved shell with strongly developed undulating lamellae at shell surface.
Hercocyrtoceras FOERSTE, 1927; *Oncoceras amator* BILLINGS, 1866
[= *Corbuloceras* HORNY, 1965]
Like *Zitelloceras* but with lamellar undulations forming longitudinal ribs.
Rutoceras HYATT, 1884; *Cyrtoceras jason* HALL, 1879
[= *Goldringia* FLOWER, 1945]
Loosely coiled shell ornamented with transverse, undulating lamellae
Hindeoceras FLOWER, 1945; *Cyrtoceras canadense* WHITEAVES, 1891
[= ?*Tetranodoceras* FLOWER, 1936, nom. oblit.; *Centrolitoceras* FLOWER, 1945]
Like *Rutoceras* but with lamellar undulations forming longitudinal ribs.
?***Tetragonoceras*** WHITEAVES, 1891; *T. gracile*
Poorly known.
Casteroceras FLOWER, 1936; *Cyrtoceras alternatum* HALL, 1879
Close to *Hindeoceras* but with straight shell.
Aphyctoceras ZHURAVLEVA, 1974; *Rutoceras parvulum* KUZMIN, 1966
Curved, annulated shell with low, longitudinal ribs.
Capricornites ZHURAVLEVA, 1974; *C. rhiphaeus*
Curved, annulated shell with growth lines only.
?***Stereotoceras*** FLOWER, 1950; *S. oppletum*
[= ?*Gonionaedyceras* FLOWER, 1945; *Gyronaedyceras* FLOWER, 1945; *Anamesoceras* ZHURAVLEVA, 1978]
Large, loosely coiled, strongly depressed shell with growth lines only.
?***Halloceras*** HYATT, 1884; *Cyrtoceras undulatum* VANUXEM, 1842
Poorly known.

?Ptenoceras Hyatt, 1894; *Gyroceras alatum* Barrande, 1865
[= *Pleuroncoceras* Flower, 1950; *Dissidoceras* Zhuravleva, 1972]
Loosely coiled shell with transverse lamellae forming prominent lateral wings.

Oncoceratidae Hyatt, 1884

Short, compressed, bulgy shell with ventral siphuncle lacking radial lamellae.

Beloitoceras Foerste, 1924; *Oncoceras pandion* Hall, 1861
[= *Neumatoceras* Foerste, 1935; *Leonardoceras* Flower, 1968]
Considerably curved, compressed shell.

Oncoceras Hall, 1847; *O. constrictum*
[= *Miamoceras* Flower, 1946; *Talattoceras* Miagkova, 1967; *Oratoceras* Zhuravleva, 1964]
Weakly curved shell with subcircular cross section.

Osbornoceras Foerste, 1936; *O. swinnertoni*
[= *Edenoceras* Miagkova, 1967]
Very strongly curved shell with constricted, T-shaped aperture.

?Clathoceras Foerste, 1926; *Phragmoceras sulcatum* Barrande, 1865
Weakly curved shell with circular cross section and constricted aperture.

Westonoceratidae Teichert, 1935

Exogastric, compressed brevicones, ventral siphuncle with laminar siphuncular deposits.

Metephippiorthoceras Zhuravleva, 1957; *M. helenae*
[= *Hemibeloitoceras* Balaschov, 1962]
Long, weakly curved shell.

Sinclairoceras Flower, 1952; *S. haha*
Short, curved shell with tapering final chamber.

Westonoceras Foerste, 1924; *Cyrtoceras manitobense* Whiteaves, 1890
[= *Teicherticeras* Foerste, 1933; *Landeroceras* Foerste, 1935]
Long and straight shell with adult phragmocone terminally inflated.

Faberoceras Flower, 1946; *F. multicinctum*
Gently curved, relatively long shell with centro-ventral siphuncle.

Winnipegoceras Foerste, 1928; *Cyrtoceras laticurvatum* Whiteaves, 1895
Strongly curved, fusiform shell.

Tuyloceras Foerste and Savage, 1927; *T. percurvatum*
Like *Winnipegoceras* but with very wide siphuncle.

Mitroceras Hyatt, 1894; *Trochoceras gebhardi* Hall, 1852
[= *Foersteoceras* Ruedemann, 1925]
Trochospirally coiled shell.

Digenuoceras Foerste, 1935; *Oxygonioceras ? latum* Foerste, 1929
[= *?Parawestonoceras* Zhuravleva, 1972]
Poorly known.

Oxygonioceras Foerste, 1925; *Trochoceras oxynotum* Barrande, 1877
Tightly, mostly trochospirally coiled shell.

Rizosceras Hyatt, 1884; *Orthoceras indocile* Barrande, 1866
[= *Danaoceras* Foerste, 1926; *Sthenoceras* Flower, 1957]
Slightly exo- to endogastrically curved, bulgy shell with simple aperture and relatively narrow siphuncle.

Alpenoceras Foerste, 1927; *A. ulrichi*
Like *Rhizosceras*, but with wide siphuncle.

?Xenoceras Flower, 1952; *X. oncoceroides*
[= *?Wissenbachia* Foerste, 1926; *?Tumidoceras* Flower, 1949]
Exogastric shell, ventral siphuncle with radial lamellae.

Devonocheilidae Zhuravleva, 1972

[= Entimoceratidae Zhuravleva, 1972; Ukhtoceratidae Zhuravleva, 1972]
Depressed, fusiform shell with ventral siphuncle; radial lamellae absent or weakly developed, confined to septal necks.

Galtoceras Foerste, 1934; *Cyrtoceras arcticameratum* Hall, 1852
[= *Grimsbyoceras* Foerste, 1934; *?Worthenoceras* Foerste, 1930]
Elongate, exogastric shell; poorly known, possibly synonymous with *Streptoceras*.

Streptoceras Billings, 1866; *S. janus*
[= *Amphicyrtoceras* Foerste, 1924; *Austinoceras* Foerste, 1934; *Rhomboceras* Foerste, 1934]

Short, exogastric shell with constricted aperture of triangular outline.

Chadwickoceras FOERSTE, 1930; *C. fusiforme*
[= ?*Taskanoceras* ZHURAVLEVA, 1972]

Straight to slightly curved, bulgy shell with considerably dorso-ventrally flattened aperture.

Ukhtoceras ZHURAVLEVA, 1972; *Gomphoceras uchtense* HOLZAPFEL, 1899
[= *Carotites* ZHURAVLEVA, 1972; *Vertorizoceras* ZHURAVLEVA, 1972; *Chuticeras* ZHURAVLEVA, 1972; *Jaregoceras* ZHURAVLEVA, 1972; *Pancornus* ZHURAVLEVA, 1972; *Ungulites* ZHURAVLEVA, 1972]

Slightly exo- to endogastrically curved brevicone with narrow, ventral siphuncle and constricted terminal aperture.

Devonocheilus SHIMANSKY, 1962; *Phragmoceras timanicum* HOLZAPFEL, 1899
[= *Synetoceras* ZHURAVLEVA, 1972]

Endogastric brevicone with narrow, ventral siphuncle.

Onyxites ZHURAVLEVA, 1972; *O. onerosus*

Like *Devonocheilus* but with considerable inflated connecting rings.

Gonatocyrtoceras FOERSTE, 1926; *Cyrtoceras heteroclytum* BARRANDE, 1866
[= *Sophoceras* ZHURAVLEVA, 1972; *Selenoceras* ZHURAVLEVA, 1972; *Tritonoceras* ZHURAVLEVA, 1972; *Elaphoceras* ZHURAVLEVA, 1972]

Strongly exogastrically curved, bulgy shell; narrow, ventral siphuncle with weakly developed radial lamellae; constricted terminal aperture with deep funnel sinus.

Chrysoceras ZHURAVLEVA, 1972; *C. reticulatum*
[= *Plagioceras* ZHURAVLEVA, 1972; *Athanatoceras* ZHURAVLEVA, 1972; *Exochoceras* ZHURAVLEVA, 1972; *Physioceras* ZHURAVLEVA, 1972; *Pelagoceras* ZHURAVLEVA, 1972; *Aipetoceras* ZHURAVLEVA, 1972]

Like *Gonatocyrtoceras* but with simple aperture.

Lysagoceras SCHÖNENBERG, 1952; *L. angustum* (= *Cyrtoceras lagowiense* GÜRICH, 1896)
[= *Andreioceras* ZHURAVLEVA, 1972; *Xiphoceras* ZHURAVLEVA, 1972; *Ropaloceras* ZHURAVLEVA, 1972; *Nipageroceras* ZHURAVLEVA, 1972; *Kadaroceras* ZHURAVLEVA, 1972; *Metrioceras* ZHURAVLEVA, 1972; *Stagonites* ZHURAVLEVA, 1972; *Deinoceras* ZHURAVLEVA, 1972; ? *Entimoceras* ZHURAVLEVA 1972; ?*Cyrtospyroceras* FLOWER, 1938]

Shell long, straight to curved in its living chamber, with simple aperture.

Trimeroceratidae HYATT, 1900

Straight to exogastrically curved, bulgy shell with ventral siphuncle, and constricted aperture with dorsal sinus

?***Antiphragmoceras*** FOERSTE, 1925; *A. ulrichi*

Considerably compressed shell with constricted aperture triangular in outline.

Inversoceras HEDSTRÖM, 1917; *Phragmoceras perversum* BARRANDE, 1865

Curved shell with T-shaped terminal aperture.

Trimeroceras HYATT, 1884; *Gomphoceras staurostomum* BARRANDE, 1865
[= *Eotrimeroceras* FOERSTE, 1928]

Straight and bulgy shell with aperture cruciform in outline.

Pentameroceras HYATT, 1884; *Gomphoceras mirum* BARRANDE, 1865
[= ?*Stenogomphoceras* FOERSTE, 1930]

Terminal aperture with two pairs of lateral sinuses.

Poterioceratidae FOORD, 1888

[= Acleistoceratidae FLOWER, 1950; Brevicoceratidae FLOWER, 1941; Diestoceratidae FOERSTE, 1926; Valcouroceratidae FLOWER, 1945]

Exogastric to secondarily endogastric, bulgy shell with circular to depressed cross section; ventral to secondarily central or subdorsal siphuncle with inflated connecting rings and strongly developed radial lamellae confined to septal necks.

Valcouroceras FLOWER, 1943; *V. bovinum*
[= *Eorizoceras* FLOWER, 1943; *Graciloceras* FLOWER, 1943]

Exogastric shell with circular cross section, ventral siphuncle with well developed radial lamella.

Diestoceras FOERSTE, 1924; *Gomphoceras indianense* MILLER and FABER, 1894

Straight and bulgy shell with ventral, wide siphuncle.

Pachtoceras FOERSTE, 1926; *Gomphoceras rotundum* PACHT, 1858
[= *Raphanites* ZHURAVLEVA, 1972; *Platyconoceras* ZHURAVLEVA, 1972; *Therioceras* ZHURAVLEVA, 1972; ?*Kitatites* ZHURAVLEVA, 1972; ?*Dynatoceras* ZHURAVLEVA, 1972]

Devonian homeomorph (?) of *Diestoceras*.

Poterioceras MCCOY, 1844; *Orthoceras fusiformis* SOWERBY, 1829
[= *Calchasiceras* SHIMANSKY, 1957; *Welleroceras* MILLER and FURNISH, 1938; *Culullum* SHIMANSKY, 1968]

Like *Pachtoceras* but with centro-ventral siphuncle with gently curved septal necks.

Mandaloceras Hyatt, 1900; *Gomphoceras bohemicum* Barrande, 1865
[= *Vespoceras* Flower, 1957; *Ovocerina* Flower, 1947; *Cinctoceras* Flower, 1957; ?*Laumontoceras* Foerste, 1926]
Slightly endo- to exogastrically curved shell with constricted, T-shaped aperture and ventral to centro-dorsal siphuncle.
Acleistoceras Hyatt, 1884; *Apioceras olla* Saemann, 1854
[= *Brevicoceras* Flower, 1938; *Aletoceras* Flower, 1938; *Eleusoceras* Flower, 1938; *Exocyrtoceras* Flower, 1938; *Micronoceras* Flower, 1938; *Verticoceras* Flower, 1938; *Cyrtogomphus* Flower, 1938; ?*Hipparionoceras* Flower, 1945; ?*Ovoceras* Flower, 1936; ?*Anglicoceras* Flower and Caster, 1935 (= *Blastocerina* Flower and Caster, 1935]
Close to *Pachtoceras* but with more elongate shell.
Mecynoceras Foerste, 1926; *Gomphoceras rex* Pacht, 1858
[= ?*Aktjubocheilus* Zhuravleva, 1972]
Long, fusiform shell with terminally inflated phragmocone; subventral to subdorsal siphuncle and simple aperture.

Jovellaniidae Foord, 1888

?***Evlanoceras*** Zhuravleva, 1972; *Pachtoceras evlanensis* Nalivkin, 1947
Bulgy shell with ventral siphuncle and constricted, trilobate aperture.
[= Oocerinidae Teichert, 1939; Manitoulinoceratidae Shimansky, 1956; Tripleuroceratidae Foerste, 1926; ?Cyrtoceratidae Chapman, 1857]
Radial lamellae continuous from one septal neck to the next.
Jovellania Bayle, 1879; *Orthoceratites buchi* de Verneuil, 1850
[= *Oocerina* Foerste, 1926; *Augustoceras* Flower, 1946; *Manitoulinoceras* Foerste, 1926; *Kidleynoceras* Foerste, 1924; *Paraoocerina* Zhuravleva, 1961; *Herkimeroceras* Foerste, 1926; *Hiregiroceras* Miagkova, 1967; *Moyerocanoceras* Miagkova, 1967; *Pachyceras* Miagkova, 1967; *Rhytidoceras* Miagkova, 1967; *Xyloceras* Miagkova, 1967; *Anonymoceras* Zhuravleva, 1974; *Mixosiphonoceras* Hyatt, 1900; *Minganoceras* Foerste, 1938; ?*Perimecoceras* Foerste, 1926]
Elongate, slightly exogastric, weakly depressed to compressed shell with ventral siphuncle.
?***Coelocyrtoceras*** Foerste, 1926; *Cyrtoceras ventralissimum* Sandberger and Sandberger, 1872
Poorly known.
Balashovia Zhuravleva, 1974; *Tripleuroceras salairicum* Balaschov, 1955
Long and straight shell with triangular cross section and central siphuncle.
Tripleuroceras Hyatt, 1884; *Orthoceras archiaci* Barrande, 1868
[= ?*Kijoceras* Zhuravleva, 1972]
Like *Balashovia* but with dorsal siphuncle.
?***Paracleistoceras*** Foerste, 1926; *Phragmoceras devonicans* Barrande, 1865
[= *Blakeoceras* Foerste, 1926; *Poteriocerina* Foerste, 1926; *Turnoceras* Foerste, 1926; *Conostichoceras* Foerste, 1926]
Large, bulgy shell with ventral siphuncle; poorly known.
Almaloceras Zhuravleva, 1974; *A. abaeratum*
[= *Corysoceras* Zhuravleva, 1974; *Mimolychnoceras* Zhuravleva, 1974; *Lychnoceras* Zhuravleva, 1974; *Mnemoceras* Zhuravleva, 1974]
Weakly curved, bulgy shell with ventral siphuncle.
?***Cyrtoceratites*** d'Archiac and Verneuil, 1842; *Cyrtocera depressa* Bronn, 1835
Strongly exogastrically curved, short shell, ventral siphuncle with concave connecting rings; poorly known.
?***Actinomorpha*** Flower, 1943; *A. pupa*
Straight, breviconic shell with ventral, wide siphuncle.

Nothoceratidae Fischer, 1882

Long, coiled shell with radial lamellae continuous from one septal neck to the next one.
Nothoceras Barrande, 1856; *N. bohemicum*
[= *Anomaloceras* Hyatt, 1884]
Planispirally coiled shell with ventral siphuncle.
Lorieloceras Foerste, 1926; *Trochoceras lorieli* Barrande, 1870
Trochospirally coiled shell with ventral siphuncle.
Nothocerina Barskov, 1972; *N. rara*
Coiled shell with central siphuncle.

Order Orthoceratida Kuhn, 1940

Diagnosis. — Straight to weakly curved shell originally with subcentral siphuncle. In some extreme forms, shell may be short (*Mariceras*) or exogastrically spirally coiled (*Lituites*), and siphuncle ventral (Bactritidae) or dorsal (?) (*Mariceras*).

Suborder **Orthoceratina** KUHN, 1940

Diagnosis. — Straight to weakly curved shell with narrow, subcentral siphuncle (marginal ventral siphuncle in the Bactritidae).

Phylogeny (figs 39, 42, 49). — The only difference between the orthoceratids and the baltoceratid ellesmeroceratids is in the subcentral siphuncle of the former group. Cameral and siphuncular deposits in *Orthoceras* (figs 33-35) and *Cochlioceras* (Baltoceratidae) (fig. 1) are indistinguishable. The widespread opinion that there are no cameral and siphuncular deposits in *Cochlioceras* and *Orthoceras* follows mainly from poor knowledge of their apical shell parts. I have collected well preserved material from erratic boulders and found that all the orthoceratid adult shell fragments less than 5 mm in diameter show well developed siphuncular and cameral deposits. The occurrence of both deposits is also a rule rather than an exception among the baltoceratids (FLOWER 1964, HOOK and FLOWER 1976). Typical representatives of *Cochlioceras* with well developed calcareous deposits occur in the Baltic area at least since the Volkhovian to Lasnamägian. The larval shell of *Cochlioceras* remains unknown but the observed shell fragments of *C. roemeri* at less than 2 mm in diameter indicate that it was small in size. One may suppose that it was like that of a close relative of *Cochlioceras*, *Bactroceras* (= *Eobactrites*) *sandbergeri* from the Llanvirnian of Bohemia, i. e. composed of a spherical apical part approximating 2 mm in diameter and a distinct cylindrical living chamber (DZIK 1891); hence, similar to the larval shell typical of *Orthoceras*. The evolutionary transition from *Cochlioceras* to the Orthoceratidae consisted thus exclusively in a shift of the siphuncle from a subventral to subcentral position, while all the other shell characters remained virtually the same.

The ancestral orthoceratid morphology may well be represented by the shells described by FLOWER (1962) from the El Paso Limestone, New Mexico, under the name *Buttsoceras novomexicanum*, and by HOOK and FLOWER (1976) from the Wahwah Limestone, Utah, under the name *Tajaroceras wardae*. Slight morphological differences between specimens collected from the two localities reflect probably mainly a difference in preservation and ontogenetic stage of the shells; the specimens figured by FLOWER (1962) are larger than the others and hence, show relatively shorter chambers and a narrower siphuncle. The range of intraspecific variability of *Tajaroceras novomexicanum* seems comparable to that recorded in *Cochlioceras roemeri* and *Orthoceras*. The siphuncular deposits of *T. novomexicanum* are indistinguishable in structure from those of *C. roemeri*, while the cameral deposits are better developed at the shell wall in the former species than in the latter. *T. novomexicanum* is probably of Cassinian (Late Arenigian) age; hence, it is older than the known typical orthoceratids. It is noteworthy that in the Florida Mountain Formation of Texas and New Mexico occur nautiloids conspecific with *T. wardae* but with diaphragmate siphuncle (HOOK and FLOWER 1977, pl. 6: 19, pl. 10: 6). This corroborates the hypothesis of a close phylogenetic relationship between the orthoceratids and endoceratids. *Michelinoceras primum* FLOWER, 1962, described from the El Paso Limestone based on single non-oriented section, may actually be either an obliquely cut baltoceratid, or a representative of the *Buttsoceras*. The considerable diameter of its siphuncle precludes its assignment to *Michelinoceras*. *Buttsoceras adamsi* (BUTTS, 1926) from the Odenville Limestone, Alabama (FLOWER 1962) shows a narrower siphuncle and may be more evolutionarily advanced than the above discussed forms. It may be conspecific with one or another of the Baltic species of *Orthoceras*. One may suppose that it is conspecific with *Wardoceras orygoforme* HOOK and FLOWER, 1977, from the Wahwah Limestone of Utah. These conclusions should be verified by a systematic revision of the original collections.

In the Baltic area, the orthoceratids appear in great abundance in the Volkhovian. Despite this one can not recognize the actual number of species because of the small diagnostic value of the phragmocone fragments found most commonly. The most distinct and common form, possibly conspecific with the Aserian "*Orthoceras*" *nilssoni* BOLL, 1857 *sensu* TROEDSSON in

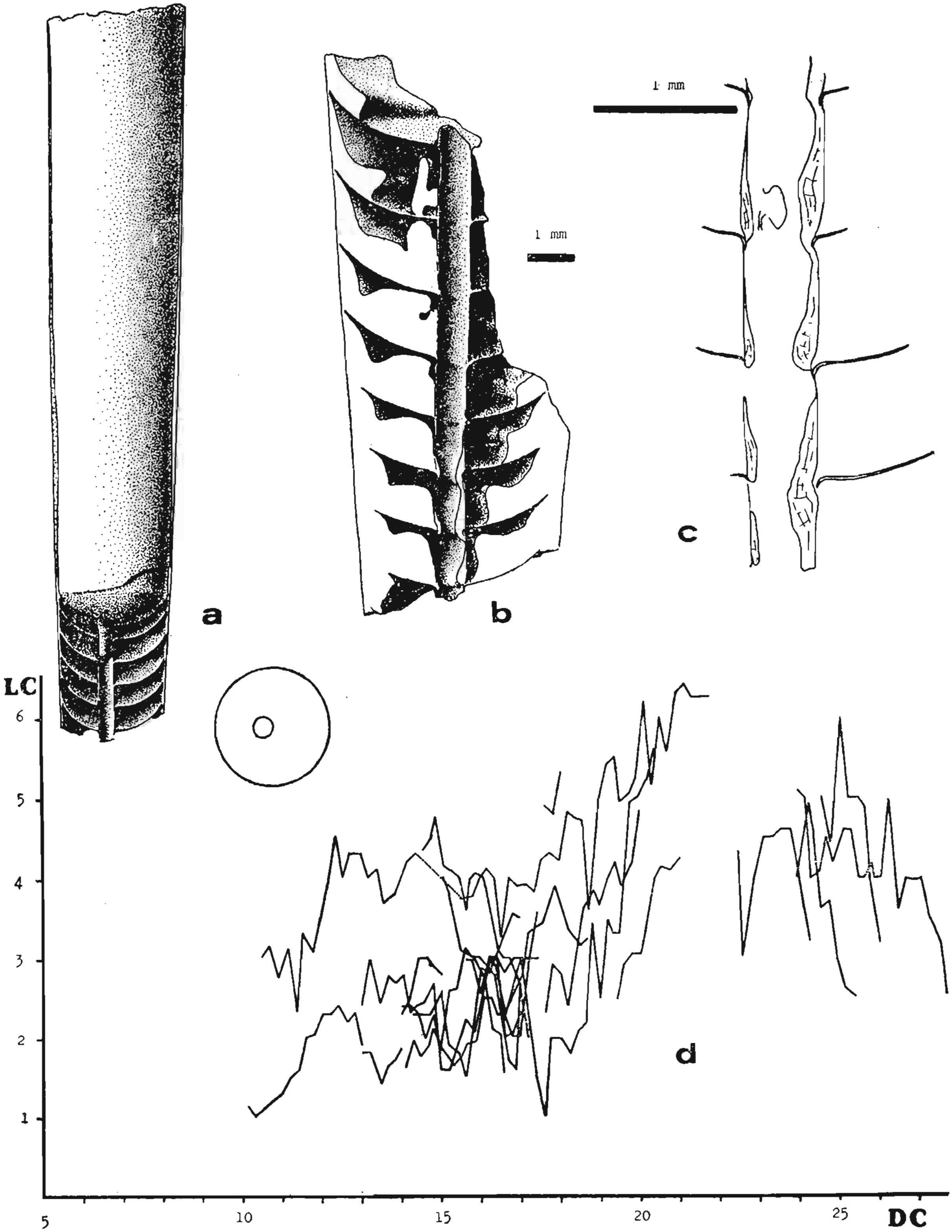
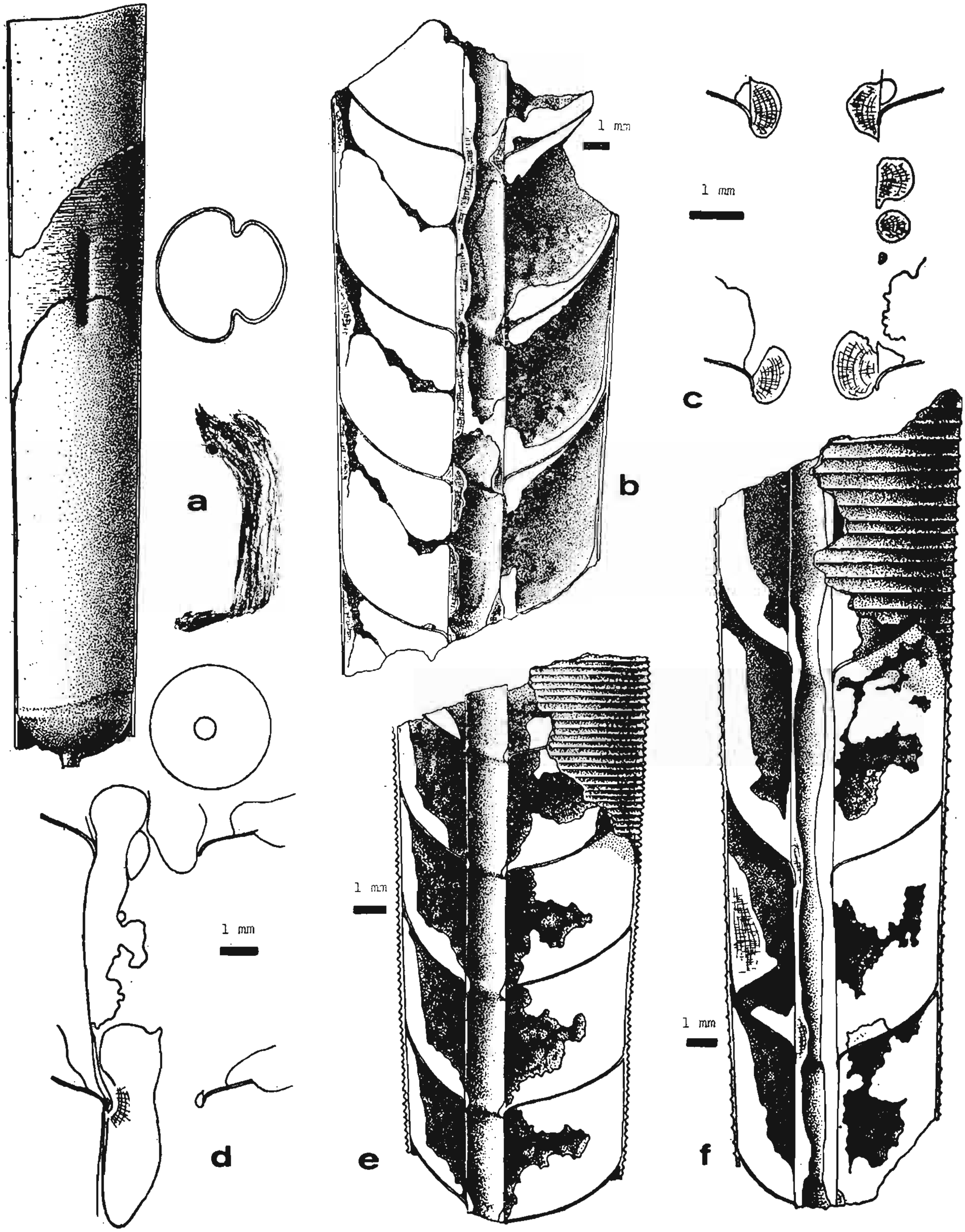


Fig. 33

Geisonoceras sp.; erratic boulders of Baltic origin *P. originalis* Zone, Volkhovian; *a* Reconstruction of the adult living chamber (see pl. 21: 10); *b* reconstruction of a phragmocone fragment with calcareous deposits, ZPAL N/405 (pl. 21: 6), boulder E-116, Rozewie, Poland; *c* section through the siphuncle of the same specimen; *d* a relative growth of air chamber length (IC) and shell diameter (DC), most specimens derived from two erratic boulders.

coll. shows a smooth, relatively short shell with narrow and central siphuncle (fig. 33). As judged from a few fragmentarily preserved adult living chambers, it does not show any apertural modifications. This species should therefore be attributed to the genus *Michelinoceras* or *Geisonoceras*. Apart from this most common Baltic orthoceratid species, erratic boulders

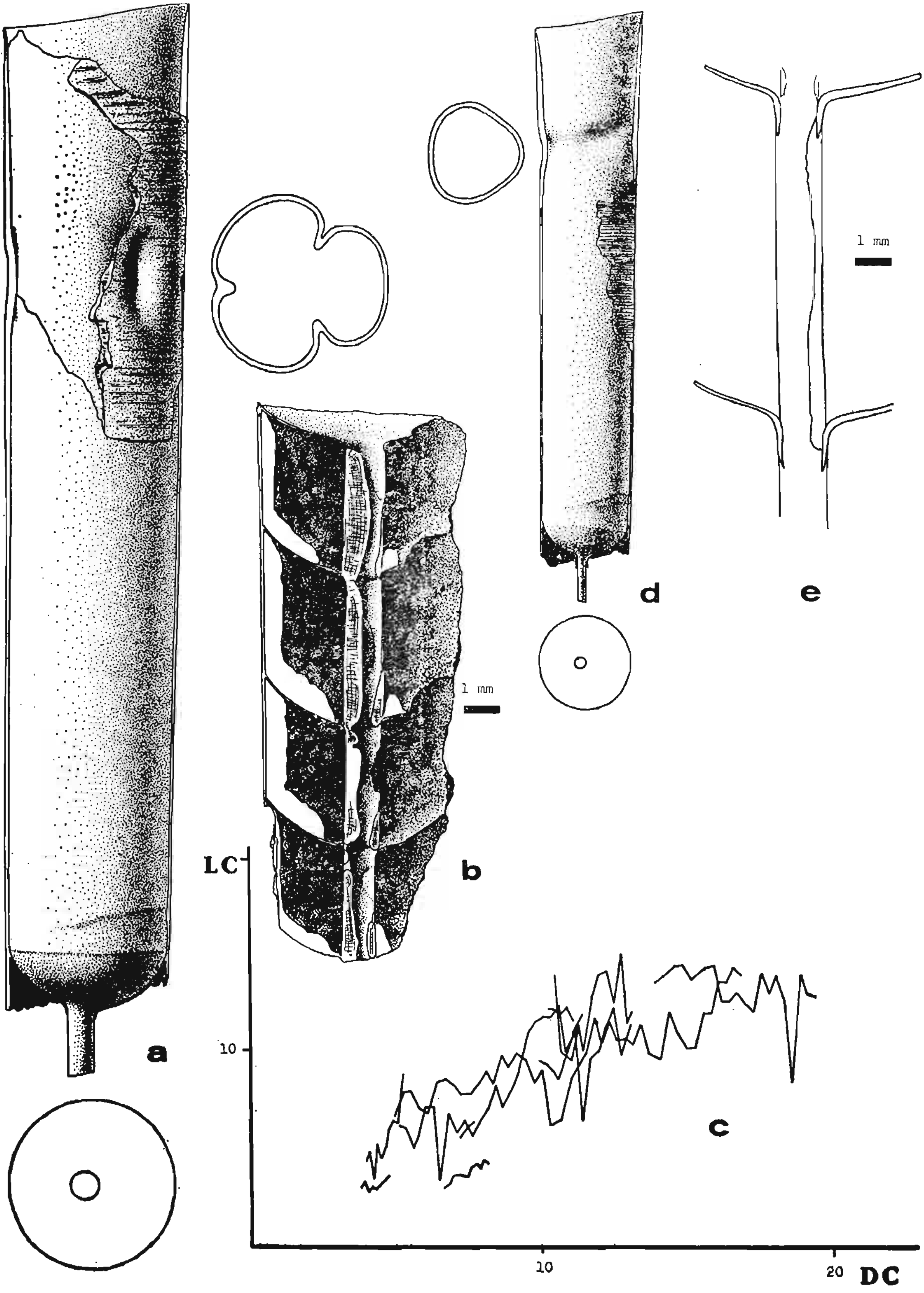


attributable to the *P. originalis* Zone yield also orthoceratids with long, ornamented shell with wide, eccentric siphuncle. Their adult shells are much smaller than those discussed above (pl. 29: 1, 4), and correspond in size to the earliest peak in septal density in *Geisonoceras* sp. (fig. 33d). Because of a variation in growth-line density at the shell surface, I assign these forms arbitrarily to the species *O.* cf. *nilssoni* Boll, 1857 *sensu* Neben and Krueger, 1971, and *O. wahlenbergi* Boll, 1857; howeve-, these two may merely be conspecific morphotypes. The finely striated form, *O. wahlenbergi* (fig. 34e), ranges from the base of the Volkhovian to the top of the Kundan. The more coarsely ornamented form, *O.* cf. *nilssoni* (fig. 34f), ranges from the Late Volkhovian to Early Kundan. True *O. nilssoni*, characterized by large shell, more quickly expanding on adult stage, occurs in the Aserian.

The Llanvirnian orthoceratids are much better known (Troedsson 1932) than their older relatives. Three species of *Orthoceras*, distinguishable exclusively by their adult living chambers, occur in the *Orthoceras* limestones of the Aserian, Lasnamägian, and Uhakuan. The main difference between these species is the presence or absence of peculiar depressions in the wall of the adult living chamber. The most generalized species, *O. scabridum* Angelin, 1890, occurring in the Folkeslunda Limestone, shows a slightly constricted adult living chamber (fig. 38d). Diameter of adult chambers ranges among the 34 specimens in the collection of Naturhistoriska Riksmuseet, Stockholm, from 13.5 to 19.0 mm (mean 16.7). There are only two dorsolateral depressions in *O. bifoveatum* Noetling, 1884, expressed in the form of longitudinal internal nodes (fig. 34a). In *O. regulare* Schlotheim, 1820, an additional ventral depression appears, shallower than the dorsolateral ones (fig. 35a). These peculiar depressions have nothing in common with apertural thickening of the shell widespread among the Mollusca. They were produced by the mantle margin long before achievement of maturity and shifted gradually in ontogeny to one third length of the adult living chamber. Thus, they could not be related to any particular organ, and were certainly not muscle attachment scars. They are most likely analogous to apertural teeth in some land snails, even though they differ from the latter structures in the mode of formation. The mantle margin must have turned its parts inside during the formation of the depressions. The considerable development of a depression at the ventral side of shell in *O. regulare* suggests that either the funnel was lacking, or the traditional interpretation of shell sides is incorrect. Retractor scars are arranged in the form of a ring at the base of the living chamber in *O. regulare* and *O. scabridum*, and better developed at the dorsal than at the opposite side; shell orientation is based on the apertural slope (Mutvei 1957). *O. scabridum* is the only one among the three species that can be identified from its phragmocone; because of its very narrow siphuncle (fig. 35e).The other two species are almost indistinguishable in their adult parts of phragmocones, whereas their adapical parts of phragmocones bearing calcareous deposit can hardly be attributed to adult living chambers; one would need a specimen almost a meter in length to do this with certainty. The adapical shell parts are therefore only tentatively identified as attributable to the associated mature specimens of *O. regulare* and *O. bifoveatum*; phragmocones with cameral deposits better developed at the convex side of a septum are here assigned to *O. bifoveatum*. The calcareous deposits are widely variable in

Fig. 34

Orthoceras bifoveatum Noetling, 1879; *a* Reconstruction of the adult living chamber, mostly after the specimen ZPAL N/431 (pl. 22: 9), boulder E-239, *E. reclinatus* Zone, Lasnamägian, Garcz, Poland. *Orthoceras* cf. *bifoveatum* Noetling, 1879; *b* Reconstruction of a phragmocone fragment, ZPAL N/427, boulder E-085, *E. lindstroemi* Zone, Uhakuan, Mochty; *c* section through a siphuncle, ZPAL N/426 (pl. 22: 8), same boulder; *d* section through a siphuncle, ZPAL N/428, Kundan (?), Zgierz, Poland. *Orthoceras "wahlenbergi* Boll, 1857" *e* Reconstruction of a fragment of the phragmocone, from the specimen ZPAL N/415 (pl. 21: 5), boulder E-117, *A. variabilis* Zone, Kundan, B III β , Rozewie, Poland. *Orthoceras "nilssoni* Boll, 1857"; *f* Reconstruction of a phragmocone fragment from the specimen ZPAL N/417 (pl. 22: 2), boulder E-186, Volkhovian, Międzyzdroje, Poland.


a
b
1 mm
LC
10
10
20
DC
c
d
e
1 mm

form, just as in the other orthoceratids, and are of little diagnostic value. Balaschov (1957) described from the Kundan an excellently preserved apical part of a shell supposedly attributable to the genus *Orthoceras*. It shows a considerably inflated, subspherical apex. In my opinion, there is no need to recognize *O. bifoveatum* as representating a distinct genus (see Balaschov 1956).

The adult living chamber of *Ctenoceras schmidti* Noetling, 1884, known from Aserian of Estonia and Baltic erratic boulders, displays three depressions indistinguishable from those typical of *O. regulare* (see Neben and Krueger 1973). These structures are so unique among the Nautiloidea that a close mutual relationship of the two species is beyond any doubt. They differ in size (diameter of adult living chamber of *C. schmidti* ranges from 12.5 to 14.0 mm), ornamentation, curvature and position of siphuncle (more close to convex side in *C. schmidti*).

The genus *Orthoceras*, with its peculiar morphology of the living chamber, did probably not leave any descendants. The Late Ordovician and Silurian orthoceratids evolved rather from some primitive forms with simple living chamber, like Aserian *Geisonoceras* (?) *nilssoni* (Boll, 1857).

Michelinoceras michelini (Barrande, 1866), known from some fragmentary specimens from the Ludlovian of Bohemia, is the only species unquestionably attributable to the genus. A crushed adult living chamber stored at the University of Wrocław (pl. 25: 7) may also be assigned to *M. michelini*. Numerous apical shell parts have been attributed to *M. michelini*, resembling very closely those of *Plagiostomoceras* (see Ristedt 1965, Kisieliev 1975). When compared to the only known larval shell of *Orthoceras* (see Balaschov 1957), they show a very small-sized subspherical apex. The lectotype of *M. grande* (Meneghini, 1857) from the Wenlockian of Sardinia, recognized for a senior synonym of *M. michelini* (Serpagli and Gnoli 1977), shows actually a much wider siphuncle than the latter and may rather represent the genus *Columenoceras*. Some Late Devonian forms with very long, transversely striated shell (pl. 28: 1-11) may have evolved from the orthoceratid branch under discussion. I collected a fairly rich material from the *Wocklumeria* Zone at Dzikowiec, the Sudetes. It includes some specimens with relatively small shell diameter and phragmocone proportions close to *M. michelini*, as well as some wider individuals with more densely spaced septa and more rapidly expanding shell (cf. pl. 28: 2, 9). The sample size is too small to determine whether or not these are distinct biospecies. Almost indistinguishable longiconic forms from the Early Carboniferous are commonly described under the generic name *Mitorthoceras* (see Gordon 1962, 1964*a*, 1964*b*).

The genus *Geisonoceras* differs from *Michelinoceras* in its more rapidly expanding, most commonly large shell with relatively wide siphuncle. It evolved probably directly from non-specialized Early Ordovician representatives of the family Orthoceratidae. Its oldest unquestionable record is *G. kureikense* Miagkova, 1967, from the Llandovery of Siberia, the best known species of the genus. The subspherical apex of its larval shell is relatively large; it is twice as great as that of *M. michelini* but at the same time, half as large as that of "*Psilorthoceras chaubetae*" from the Wenlockian and "*Caliceras capillosum*" from the Ludlovian (Ristedt 1968, Kolebaba 1975). These size relationships reflect probably the egg sizes. The shape of the embryonic shell of *G. kureikense* (see Miagkova 1967) indicates that this may be the ancestor

Fig. 35

Orthoceras regulare Schlotheim, 1820; *a* Reconstruction of the adult living chamber, based on the specimen ZPAL N/445 (pl. 23: 4), boulder E-237, *E. reclinatus* Zone, Lasnamägian, Garcz near Kartuzy. *Orthoceras* cf. *regulare* Schlotheim, 1820; *b* Reconstruction of a phragmocone fragment, ZPAL N/448 (pl. 23: 2), boulder E-141, *E. reclinatus* Zone, Lasnamägian, Międzyzdroje; *c* relative growth of air chamber length and shell diameter in a sample from erratic boulders of the grey *Orthoceras* limestone (Lasnamägian to Uhakuan). *Orthoceras scabridum* Angelin, 1880; *d* Reconstruction of the adult living chamber based on the specimen ZPAL N/456 (pl. 24: 1), boulder E-145, *E. reclinatus* Zone, Lasnamägian, Międzyzdroje; *e* section through a siphuncle, same specimen.

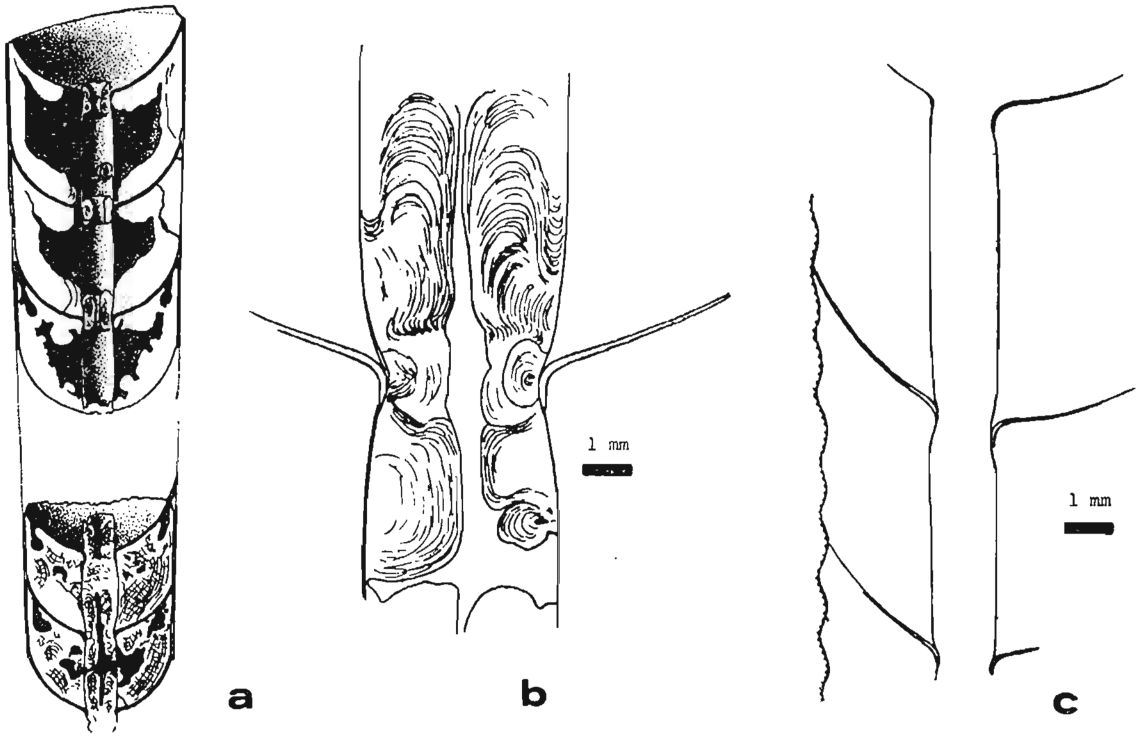


Fig. 36
Columenoceras agassizi (Barrande, 1866); ZPAL N/461 (pl. 25: 8), Late Silurian, borehole Parczew IG 10, depth of 1235 m, Poland; *a* Longitudinal section through a fragment of the phragmocone; *b* longitudinal section through the siphuncle. *Columenoceras* cf. *duponti* (Barrande, 1866); ZPAL N/470 (pl. 25: 3), Early Ludlovian, erratic boulder from Orłowo, Poland; *c* longitudinal section through the siphuncle.

for the latter two species which are actually attributable to the genus *Arionoceras* and hence, discussed below. The apical part of the shell of *G. rivale* (Barrande, 1866), the type species of *Geisonoceras*, is unknown even though the species has been described from many individuals recorded in the Ludlovian of Bohemia and other regions (Babin 1966, Serpagli and Gnoli 1977). *G. rivale* attains a considerable shell size and shows a relatively wide siphuncle and highly variable shell ornamentation, even in a single individual. Ring-like siphuncular deposits are fairly variable in morphology and as a rule confined to the septal necks. This morphological variation was the basis for the erection of several species and genera from specimens probably conspecific with *G. rivale*. The shell morphology is simple and hence, the range of intraspecific variability can not be precisely determined.

Columenoceras columen (Barrande, 1866) from the Ludlovian of Bohemia is a close relative of *G. rivale*. It shows a fairly wide siphuncle with siphuncular deposits biscuit-like in longitudinal section (fig. 36 and pl. 25: 8), and an annulated apical part of the shell (Barrande 1868). It may be conspecific with "*Orthoceras*" *agassizi* Barrande, 1866, ranging up to the Eifelian. *Columenoceras duponti* (Barrande, 1866) with shell annulation extending over the adult stages may be a distinct species. *Acrosphaerorthoceras gregale* Ristedt, 1968, described originally from the apical part of a shell, shows a shell ornamentation very similar to that in *C. duponti* (see Ristedt 1968, 1971; Serpagli and Gnoli 1977). Its characteristics includes an unusually small, mucronate embryonic shell and a weakly inflated larval shell, which makes it similar to *Hemicosmorthoceras laterculum* Ristedt, 1968. Erratic boulders of Early Ludlovian age contain apical parts of shells of the *Hemicosmorthoceras* type (pl. 25: 10) associated with phragmocones attributable to *Columenoceras* (pl. 25: 2-3). One can hardly identify the two species from fragmentary specimens, while they probably co-occur also in the Ludlovian of Poland (fig. 36a-b and pl. 25: 1, 3, 8). *C. duponti* may also be conspecific with or at least closely related to *Pseudocycloceras karagandense* BARSKOV, 1959, with similar shell ornamentation and siphuncular deposits resembling the primitive orthoceratids. This problem, however, cannot be solved with a single shell fragment including only a few chambers (see BARSKOV 1959, 1977).

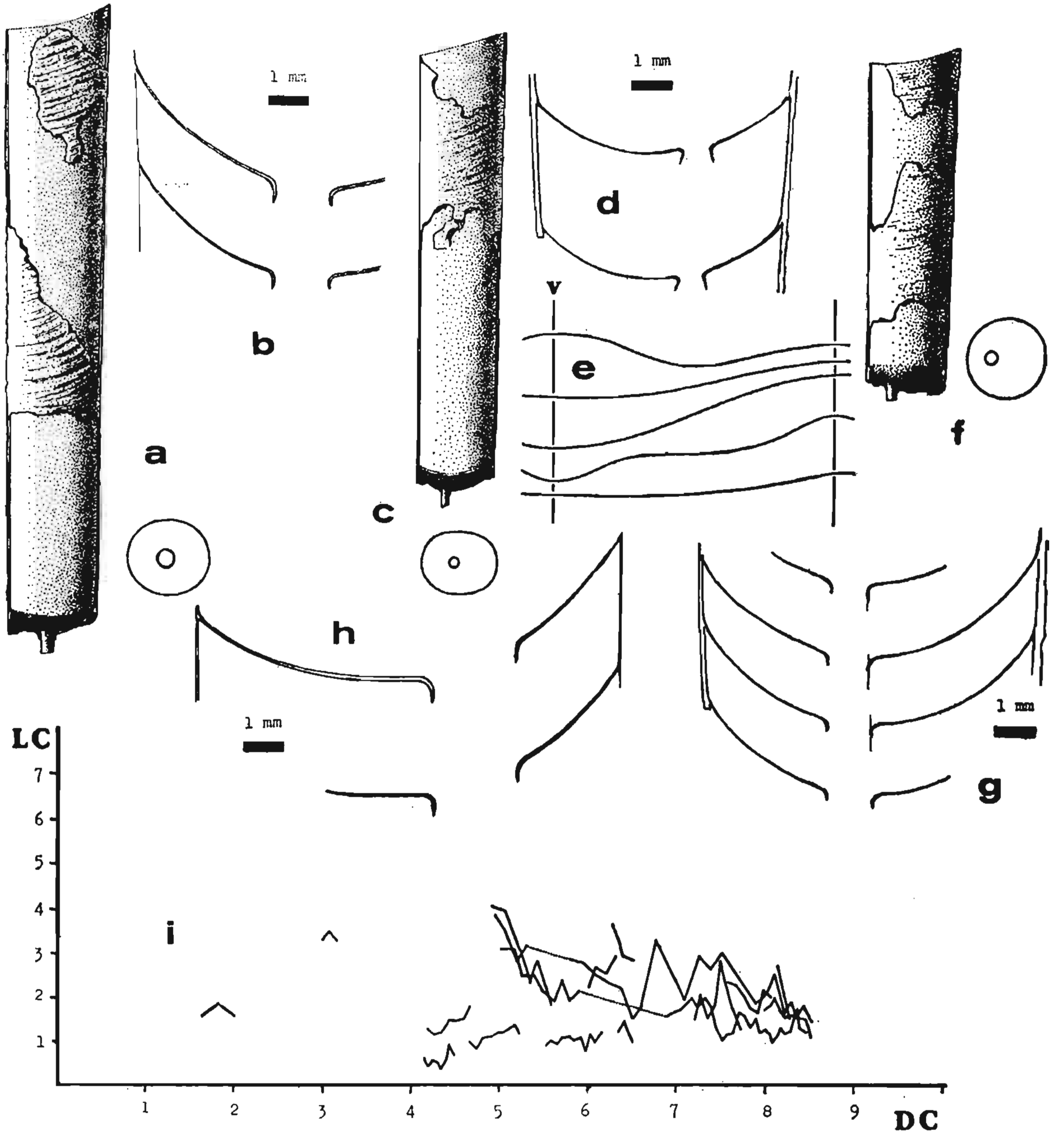


Fig. 37

Plagiostomoceras cf. *angustum* (HOLZAPFEL, 1895); Late Frasnian, Płucki, Holy Cross Mts, Poland; *a* Reconstruction of the living chamber; *b* longitudinal section through a siphuncle, ZPAL N/516. *Plagiostomoceras* aff. *angustum* (HOLZAPFEL, 1895); Early Famennian, Jabłonna, Holy Cross Mts, Poland; *c* Reconstruction of the living chamber; *d* longitudinal section through a siphuncle, ZPAL N/552, bed J. 11; *e* variation in the septal suture (equally variable is the siphuncle position); *i* relative growth of camerae length and shell diameter. *Bogoslovskya* sp.; *Platyclymenia* Zone, Famennian, Łagów-Dule, Holy Cross Mts, Poland; *f* Reconstruction of the living chamber; *g* longitudinal section through a siphuncle, ZPAL N/561 (pl. 28: 12). *Plagiostomoceras* sp.; ZPAL N/531 (pl. 23: 4), Early Famennian, Jabłonna, bed J. 18, Holy Cross Mts, Poland; *h* longitudinal section through the siphuncle.

A peculiar nautiloid lineage beginning with *Jangziceras sichuanense* LAI, 1964, from the Wenlockian of China (LAI 1964, 1965; CHEN and LIU 1974) may be related to the above discussed forms. *J. sichuanense* resembles *Columenoceras* in shell outline but its siphuncle is much wider and eccentrically situated, and the siphuncular deposits are confined to the septal necks and occur only at ventral side forming blocks isolated from one another. Nautiloid shells almost indistinguishable in siphuncular structure but shorter, have been recorded from the Eifelian of Novaya Zemla (KUZMIN 1965) and Canada (COLLINS 1969).

An evolutionary trend towards decreasing siphuncle width, appears in a lineage beginning with *Plagiostomoceras*. This genus ranges at least from the Wenlockian to Eifelian and differs from the *Michelinoceras* lineage in its compressed shell, subventral siphuncle, and dorsal apertural lobe. *Plagiostomoceras* and *Protobactrites*, closely related if not identical forms, are known mostly from the Ludlovian of Bohemia. Typical species are *Plagiostomoceras pleurotomum* (BARRANDE, 1866), with long dorsal apertural lobe and variable shell ornamentation with transverse step-form striae (rugae), and *Protobactrites styloideum* (BARRANDE, 1866) with smooth shell (this may be the effect of preservation) and a more ventral siphuncle. The generic distinction of these two species is disputable but there is no need to replace the widely used name *Plagiostomoceras* with its senior synonym *Protobactrites*; however, the decision of the International Commission of Zoological Nomenclature is needed. *Plagiostomoceras* has also been recorded from the Wenlockian of Sardinia (SERPAGLI and GNOLI 1977), the Ludlovian of the Holy Cross Mts. (pl. 26: 1-12), the Early Devonian of Australia (TEICHERT and GLENISTER 1952), and the Eifelian of Novaya Zemla (KUZMIN 1965). The apical part assigned by RISTEDT (1968) to *Protobactrites* resembles that of *Michelinoceras*. In addition to typical forms showing a considerably compressed shell, ventral siphuncle, and distinct apertural lobe, there are also some Silurian and/or Devonian species attributable to the *Plagiostomoceras* group, although different in one or another feature from the mode. Among them, "*Orthoceras*" *ganimedes* BARRANDE, 1866, from the Přidolian of Karlštein, Bohemia, shows oblique rather than arched growth lines and a subcentral siphuncle.

Apical parts of nautiloid shells have been found in the Late Givetian of the Holy Cross Mts. with siphuncle position and shell cross section typical of the genus *Plagiostomoceras*, but also associated with considerably inflated, ovate apex (pl. 27: 6-7) resembling some bactritids (ERBEN 1960, CLAUSEN 1968).

The Famennian nautiloid fauna of the Holy Cross Mts. includes forms resembling externally typical representatives of *Plagiostomoceras* but with only somewhat oblique aperture (fig. 37a) or circular cross section of the shell (fig. 37f). I do not erect new species from these materials because of insufficient knowledge (unknown is the outline of the apical part of shell, the structure of the siphuncle, etc.). Possibly, these specimens are conspecific with some previously erected species known exclusively from specimens unidentifiable at the species level (i. e. *Arkonoceras arkonense* FLOWER, 1938; „*Orthoceras*" *angustum* HOLZAPFEL, 1895). The Polish forms may also be conspecific with various apical parts shell from the Late Frasnian of Germany assigned by CLAUSEN (1968) to several new species, as well as with numerous species of the genera *Bogoslovskya* and *Plagiostomoceras* described from the Devonian of the Urals (ZHURAVLEVA 1978*b*).

The phylogenetic position of "*Orthoceras*" *cardiolae* GÜRICH, 1896, described on the material collected in the Holy Cross Mts. (pl. 27: 10-13) is unclear. Some specimens resemble *Plagiostomoceras* in phragmocone outline but show a very wide siphuncle situated between the shell center and ventral side (fig. 37h). This indicates that the *Plagiostomoceras* lineage might have given rise to the aberrant Visean species *Haruspex latisiphonatus* SHIMANSKY, 1968. It is known merely from a single fragment of the juvenile (?) phragmocone exhibiting an unusually wide siphuncle. No siphuncular structures have been preserved and hence, one cannot reject the possibility that *H. latisiphonatus* is related to *Jangziceras* (*Folioceras*), but the latter assumption would require a wider stratigraphic gap. The main evolutionary lineage of *Plagiostomoceras* may be represented in the Namurian by "*Euloxoceras* sp. A" (GORDON 1964) from Arkansas. A very well known species from the Artiniskian of the Urals, *Shikhanoceras sphaerophorum* SHIMANSKY, 1954, may also be related to *Plagiostomoceras*, even though one cannot reject the hypothesis that it is related to *Michelinoceras* (*Mitorthoceras*). It shows an inflated larval shell, a slightly compressed shell with almost simple aperture, and a somewhat eccentric siphuncle. The structural simplicity of the orthoconic orthoceratids and the diagnostic significance of poorly preservable characters (larval shell, terminal aperture) result in the virtually impossible specific identification of these fossils. The phylogenetic position of most thus far described forms also remains far from recognized, in spite of the existing complex systematics.

The shell morphology (especially the dorsal elongation of the aperture, and the shell compression), the siphuncle position and structure, and the form of the larval shell (ERBEN 1960, 1965) are all indicative of a phylogenetic relationship of the Bactritidae to *Plagiostomoceras*. The morphological affinity in larval-shell shape between the Early Devonian genus *Cyrtobactrites* (see ERBEN 1960, 1965) and the Silurian genus *Parasphaerorthoceras* (RISTEDT 1968) is notable. The oldest known bactritids, differing from the *Plagiostomoceras*-*Protobactrites* group in their marginal ventral siphuncle, appear in the latest Silurian (TERMIER and TERMIER 1950). Nonetheless, the primitive bactritids are known mostly from the Middle to Late Devonian (ERBEN 1960, CLAUSEN 1968). Their specific characters consists mostly in aperture form and shell cross section. Although the shell section imposes some changes in the septal suture, as in *Plagiostomoceras*, the suture is commonly recognized as an important diagnostic feature among the bactritids (ERBEN 1960, 1964, SHIMANSKY 1962; CLAUSEN 1968; MAPES 1979).

There are three distinct bactritid species in the Famennian of the Holy Cross Mts., supposedly representative of lineages separated from each other in the Middle Devonian. One cannot indicate their relations to previously known bactritids because of poor knowledge of the latter forms. The most primitive one of the three, i. e. the closest to the ancestral bactritids, is *Lobobactrites* sp. (fig. 38a) showing a moderately developed apertural lobe, compressed shell, and coarse ornamentation. The septal suture has shallow lateral lobes but the available material is too scarce to permit recognition of intrapopulation variability. A related but more specialized form is *L. carinatus* (MÜNSTER, 1840) with apertural dorsal rostrum and shell ornamentation with sharp, step-like transverse ribs (see also BABIN and CLAUSEN 1967); the suture has lateral lobes. The third species is poorly known; its distinctive feature is the circular cross section of its shell. It may be related to the genus *Bactrites s. s.*, from the type species of which it differs in its longer shell (fig. 38e). *Pseudobactrites* from the Early Devonian of Bohemia and France (ERBEN 1960) is unique among the orthoconic bactritids in its aperture with two pairs of lateral lappets separated by deep sinuses. This aperture resembles indeed *Lituites*, while considerably differing from both *Bactrites* and *Lobobactrites* (it may however have evolved from that typical of the primitive representatives of *Lobobactrites*). A similar aperture is also shown by exogastric *Cyrtobactrites* from the Emsian of Germany (ERBEN 1960). A less specialized aperture but at the same time a more curved, exogastric shell is shown by *Anetoceras arduennense* (STEINIGER, 1856) from the Early Emsian of Hunsrück (ERBEN 1960, 1962). *Metabactrites formosus* BOGOSLOVSKY, 1972, from the Emsian of the Urals, *Kokenia tenuissima* CHLUPAČ and TUREK, 1977, and *K. obliquecostata* HOLZAPFEL, 1895, from the Late Givetian of Bohemia and Germany. All these species are based on single ontogenetic stages and preservations incompatible with one another. They, nevertheless, show so much affinity to each other that one cannot trace any taxonomic boundary of generic rank. *A. arduennense* is commonly regarded as the earliest ammonoid. The boundary between the subclasses Nautiloidea and Ammonoidea traced within this group of species is somewhat too ambiguous. In my opinion, the phylogenetic development of the exogastric shell in the lineage *Lobobactrites*-*Cyrtobactrites*-*Kokenia* (*Anetoceras*) should delimit nautiloid-ammonoid boundary. Consequently, the genera

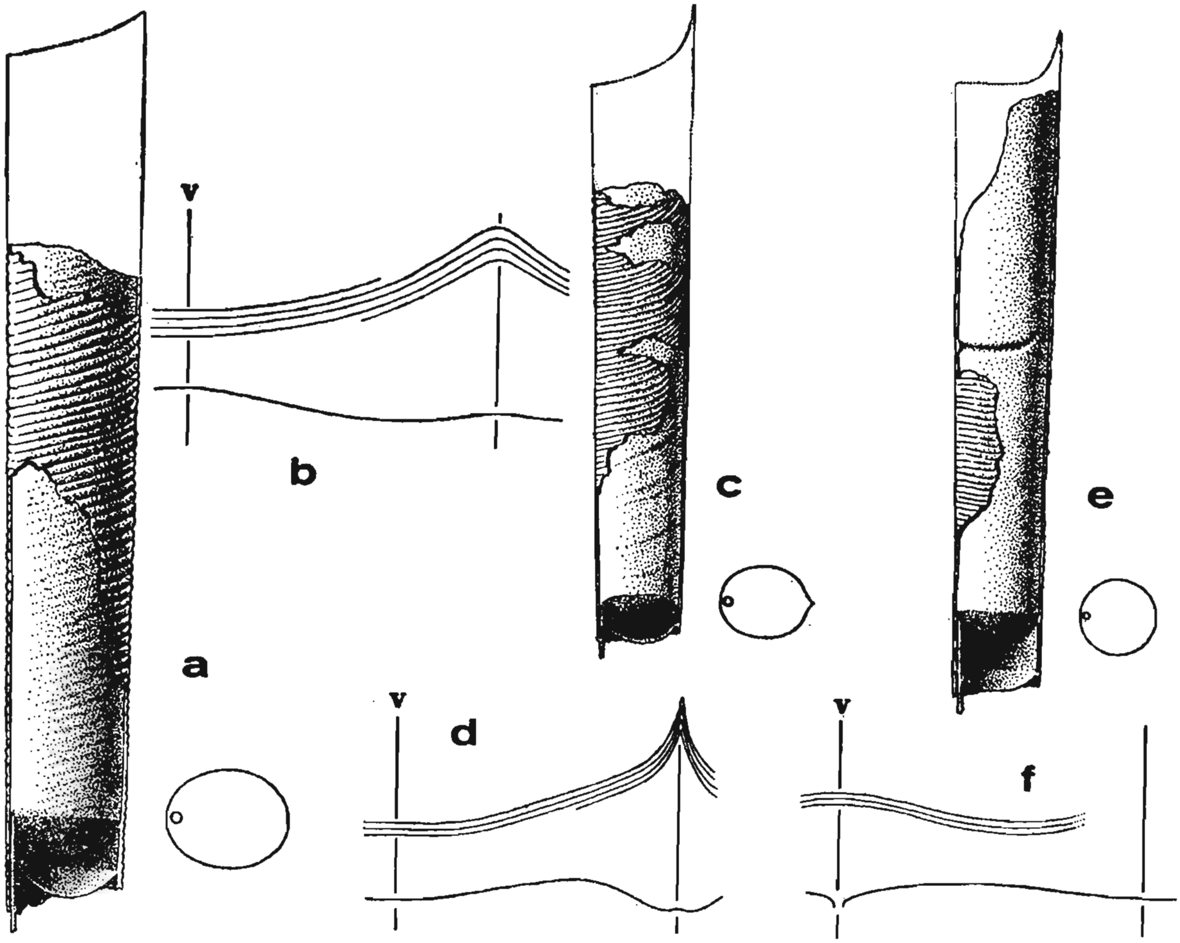


Fig. 38
Lobobactrites sp.; *Cheiloceras* Zone, Famennian, Jabłonna, Holy Cross Mts, Poland; *a* Reconstruction of the living chamber (see pl. 28: 5), ×2; *b* septal suture and growth lines. *Lobobactrites carinatus* (MÜNSTER, 1840); same horizon and locality; *c* reconstruction of the living chamber (see pl. 28: 3-4); *d* septal suture and growth lines. *Bactrites* sp.; same horizon and locality; *e* Reconstruction of the living chamber (see pl. 28: 6); *f* septal suture and growth lines.

Cyrtobactrites and *Kokenia* (? = *Metabactrites*, *Anetoceras*) are to be assigned to the ammonoid family Anetoceratidae.

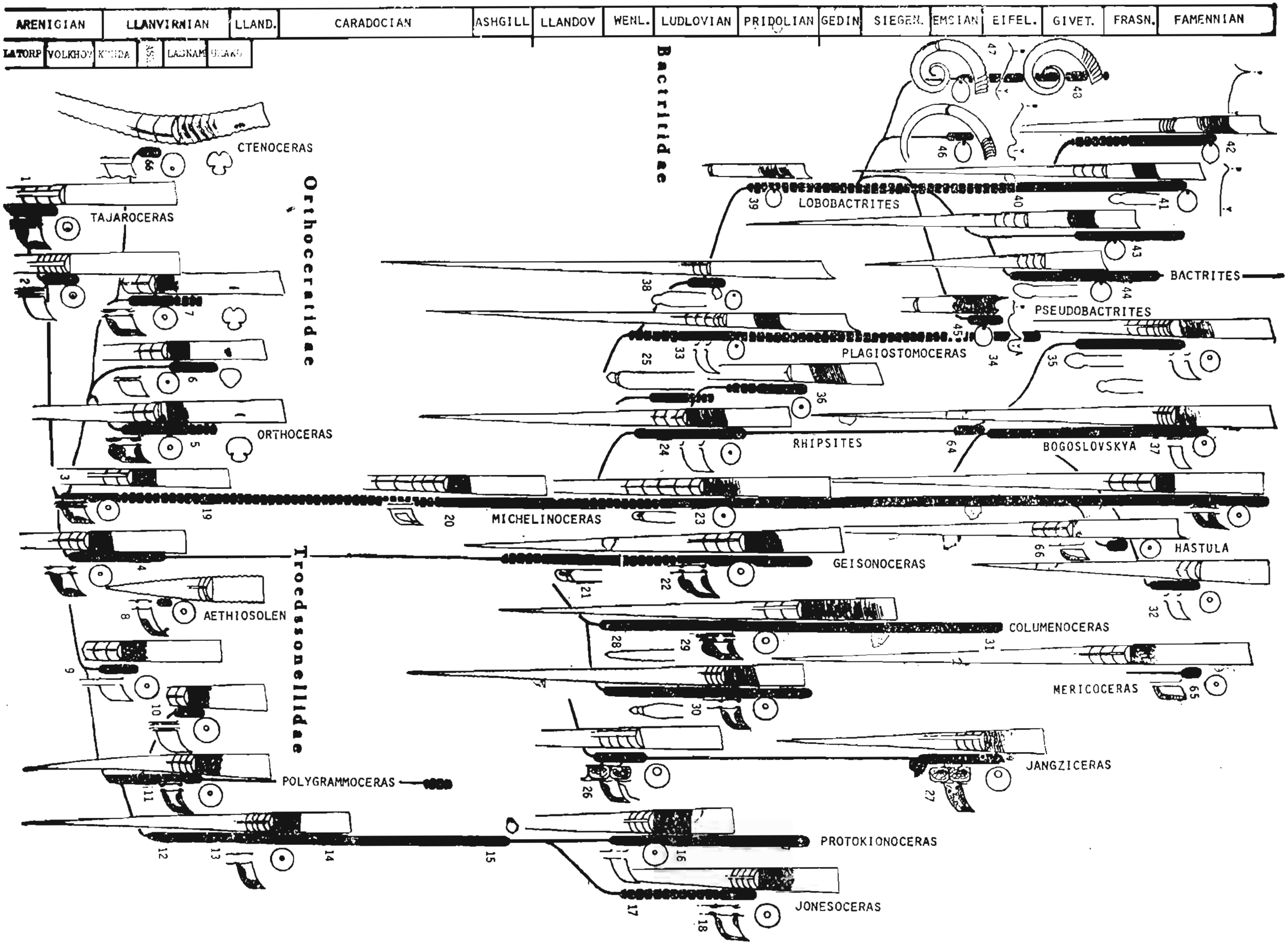
Some bactritid lineages continued also in the Carboniferous. The most primitive one persisted up to the end of the Permian, and possibly even up to the Late Triassic (*Dillerites shastensis* GORDON, 1966). The genus *Ctenobactrites* with sharp dorsal apertural incision appeared in the Early Namurian. Its Early Carboniferous representative, *C. inhonorus* SHIMANSKY, 1968, shows merely a shallow depression in the dorsal apertural lobe, but its Late Carboniferous descendant, *C.* sp. SHIMANSKY, 1968 displays the aperture typical in outline of the Permian species of *Ctenobactrites* (see SHIMANSKY 1954, 1968). MAPES (1979) presented recently a monograph on the North American Carboniferous bactritids. Every bactritid assemblage of distinct geological age is therein described under a separate specific name. Furthermore, the species recognized within a single bed are typological in nature, as intrapopulation variability is never taken into account. In my opinion, none of these new bactritid taxa is sufficiently well documented. Their distinctness from the previously described American, European (SCHMIDT 1951), and Uralian species (SHIMANSKY 1954, 1968) remains to be demonstrated. *B. sinuosum* MAPES, the only species differing in morphology from the other North American Carboniferous bactritids, was based on a single specimen. The peculiar undulation of the septal suture variable even within this single phragmocone, may well reflect some developmental irregularities or be an endmember of intrapopulation variability (see fig. 37e). The taxonomic value of the form of the wrinkle layer and septal spacing has been much overestimated by Mapes (see fig. 33d). When compared to non-bactritid nautiloids, one cannot substantiate the claim that the protoconch shape is a diagnostic feature of familial rank, and that slight displacement of the siphuncle away from the shell wall is an ordinal diagnostic character. On the other hand, Mapes allows for an extremely wide intraspecific variability in the morphology of the embryonic shell (see *Orbobactrites girtyi* Mapes, 1979; p. 24: 8, 11); in fact, specimens with both spherical and hemispherical protoconch are assigned to a single species (unless this is a lapsus calami).

The most important descendant of the Bactritidae is certainly *Eobelemnites caneyense* Flower, 1945 from the Early Namurian Fayetville Shale, Arkansas (Flower and Gordon 1959, Gordon 1964*a*), together with some other possibly conspecific forms from more or less coeval localities. They resemble typical bactritids in the phragmocone cross-section, and ***Lobobactrites carinatus*** in the aperture shape. The only but extremely important difference from the bactritids is in the occurrence of calcareous deposits secreted from the outside in the apical part of the shell, i. e. in the presence of a rostrum. ***Eobelemnites*** is therefore to be considered at the oldest known representative of the Coleoidea.

Neither the timing nor the mode is known of the evolution of the covering of the bactritid shell with manle. *Eobelemnites* shows a well developed rostrum, while its ancestors with mantle covered shell probably did not produce such extra-phragmocone deposits. The rostrum functioned as a counterweight to the phragmocone buoyancy; it could develop owing to the appearance of the mantle cover, but the buoyancy could not have been the cause for mantle cover development. The mantle cover must be explained in other ways than buoyancy mechanisms. Some free-living gastropods may provide us with an analogy. The formation of the mantle cover must been preceded by a loss of the shell's protective function and an expansion of the soft body outside the shell aperture. From a formal standpoint, the boundary between the subclasses Nautiloidea and Coleoidea is most plausibly traced to the appearance of an external mantle covering the shell. The occurrence of external mantle is reflected by a shell smoothness or very fine ornamentation. To recognize this, one needs excellently preserved material. One may claim that typical bactritids, coarsely ornamented and with very long living chamber, did not have any mantle covering the shell. An external mantle may, however, have occurred in the breviconic Devonian representatives of the genus *Bactrites* known exclusively from moulds, e. g. in *B. subconicus*. Anyway, the boundary between the Nautiloidea and Coleoidea may be found in the *Bactrites-Eobelemnites* lineage.

The Permian family Parabactritidae probably includes primitive coleoid phragmocones and its relationships to the true Bactritidae (see Erben 1964) is questionable. The position of some Carboniferous species with a considerable apical angle (8-10°) assigned by Mapes (1979) to the families Parabactritidae and Sinuobactritidae is problematic. The morphology of the apical part of their shell suggests a close relation to the bactritids, but a peculiar longitudinal ornamentation of their very apex is remarkable (Mapes 1979, pl. 27: 11). The continuity of this ornamentation beyond the protoconch may indicate that the larval development occurred within an egg capsule (as in the Kionoceratidae). One may also suppose that the longitudinal ribs present a rudimentary rostrum secreted from the outside. In fact, the coeval belemnites show rostra with a similarly ornamented surface (Flower and Gordon 1959). A solution to this problem is needed prior to the ultimate assignment of the Parabactritidae *sensu* Mapes, 1979, to either the Bactritidae *s. l.*, or the Probelemnitidae. At present, there is no reason to establish a distinct family Parabactritidae for these Carboniferous forms.

Longitudinal striation of the shell appeared independently in various nautiloid groups. The diagnostic value of this feature has been much overestimated, especially owing to the com-


ARENIGIAN
LLANVIRNIAN
LLAND.
CARADOCIAN
ASHGILL
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EMSIAN
EIFEL.
GIVET.
FRASN.
FAMENNIAN
LATORP
VOLKHOV
LASNAM
Orthoceratidae
Bactritidae
Troedssonellidae
CTENOCERAS
TAJAROCERAS
ORTHOCERAS
AETHIOSOLEN
POLYGRAMMOCERAS
MICHELINOCERAS
GEISONOCERAS
LOBOBACTRITES
BACTRITES
PSEUDOBACTRITES
PLAGIOSTOMOCERAS
RHIPSITES
BOGOSLOVSKYA
HASTULA
COLUMENOCERAS
MERICOCERAS
JANGZICERAS
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Fig. 39 a

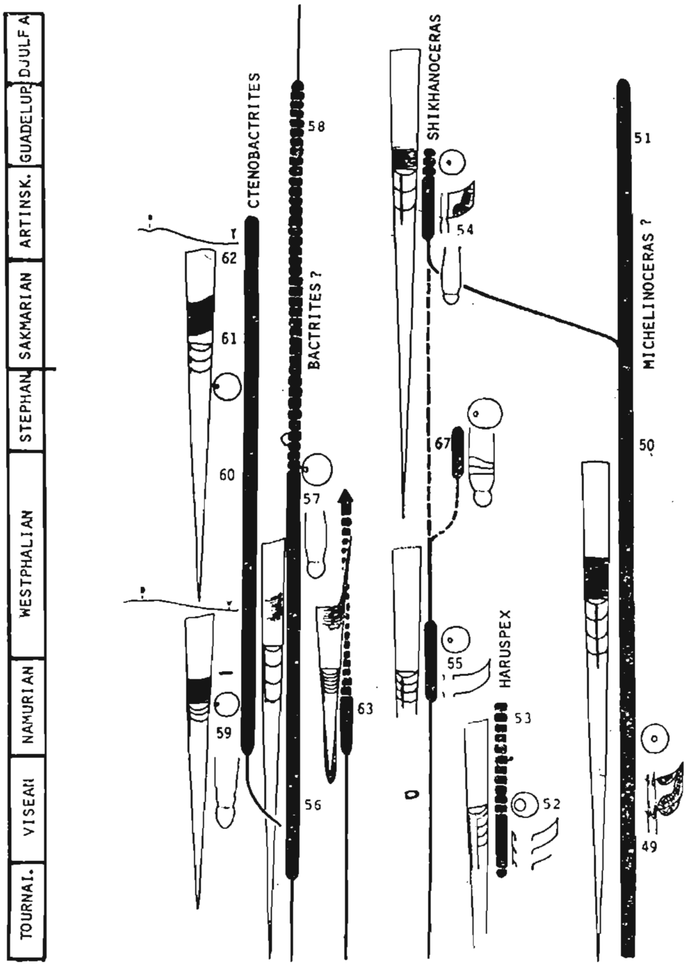


Fig. 39b

Hypothetical phylogenetic relationships among members of the families Orthoceratidae, Troedssonellidae, and Bactritidae and their relation to the Anetoceratidae (Ammonoidea) and Aulacoceratidae (Coleoidea); 1 *Tajaroceras wardae* Hook and Flower = *Buttsoceras novemexicanum* Flower; 2 *Buttsoceras adamsi* (Butts); 3 *Orthoceras "nilssoni* Boll" (fig. 34f; pl.22: 1-5); 4 *Geisonoceras* sp. (fig.33a-d; pl. 21: 6, 10); 5 *Orthoceras bifoveatum* Noetling (fig. 31a-b; pl. 22: 8-10); 6 *Orthoceras scabridum* Angelin (fig. 36d, e; pl. 24: 1-2, 6-8); 7 *Orthoceras regulare* Schlotheim (fig. 35a; pl. 22: 7, 22: 1-4); 8 *Aethiosolen whittingtoni* Flower; 9 *Protobactrites delicatulum* Troedsson; 10 *Troedssonella endoceroides* (Troedsson); 11 *Polygrammoceras lineatum* (Angelin); 12 *Kionoceras acutum* (Angelin); 13 *Kionoceras valcourense* Flower; 14 *Kionocuras laqueatum* (Hall), *Protokionoceras strandi* Troedsson; 15 *Protokionoceras isotelorum* Strand; 16 *Kionoceras laxias* (Hall), *K. studenitsense* Balaschov; 17 *Protokionoceras anticostiense* Foerste; 18 *Jonesoceras jonesi* (Barrande); 19 *Bactroceras chinense* Lai, *Michelinoceras toquimense* Flower; 20 *Eosomichelinoceras huananense* Chen; 21 *Geisonoceras kureikense* Miagkova; 22 *Geisonoceras rivale* (Barrande) = *Harrisoceras vibraeyi* (Barrande) (see pl. 24: 3-5); 23 *Michelinoceras grande* (Meneghini) = *Kopaninoceras jucundum* (Barrande) (pl. 25: 10); 24 *Plagiostomoceras gruenewaldti* (Barrande); 25 *Parasphaerorthoceras acurratum* Ristedt; 26 *Jangziceras sichuanense* Lai; 27 *Orthoceras selmenevense* Foerst, *Folioceras segmentatum* Collins; 28 *Neosichuanoceras columinum* Chen; 29 *Columenoceras columen* (Barrande), *Acrosphaerorthoceras gregale* Ristedt; 30 *Orthoceras duponti* Barrande, ?*Pseudocycloceras karanglense* Barskov, *Hemicosmorthoceras laterculum* Ristedt; 31 *Columenoceras agassizi* (Barrande) (fig. 36a, b; pl. 25: 1-8); 32 *Plagiostomoceras* (?) *cardiolae* (Gürich) (pl. 27: 10-13); 33 *Plagiostomoceras pleurotomum* (Barrande) (pl. 26: 1-13), ?*Hemicosmorthoceras semiannulatum sensu* Serpagli and Gnoli; 34 *Plagiostomoceras calvicense* Kuzmin; 35 *Plagiostomoceras angustum* (Holzapfel) (fig. 37a-c, i; pl. 27: 1-9), *P. devingtalae* Zhuravleva; 36 *Orthoceras ganimedes* Barrande; 37 *Bogoslovskya* sp. (fig. 37f; pl. 28: 10, 12), *B. perspicua* Zhuravleva, ?*Sphaerorthoceras effrenatum* Ristedt; 38 *Protobactrites styloideum* (Barrande); 39 *Bactrites* sp. Termier and Termier, 40 *Lobobactrites ellipticus* (Frech); 41 *Lobobactrites* sp. (fig. 38a, b; pl. 28: 5); 42 *Lobobactrites carinatus* (Münster) (fig. 38c; d; pl. 28: 3, 4, 8); 43 *Bactrites subflexuosus* (Münster); 44 *Bactrites subconicus* (Sandberger); 45 *Pseudobactrites peneaui* Ferronière, *P. bicarinatus* Erben; 46 *Cyrtobactrites sinuatus* Erben, *C. asinuatus* Erben; 47 *Metabactrites formosum* Bogoslovsky; 48 *Kokenia obliquecostata* Holzapfel, *K. tenuissima* Chlupač and Turek; 49 *Mitorthoceras perfilosum* Gordon (see pl. 28: 1-2); 50 *Orthoceras unicamera* Smith; 51 *Bitaunioceras bitauniense* Haniel, *B. coahuilense* Miller and Youngquist; 52 *Haruspex latisiphonatus* Shimansky; 53 Gen. et sp. indet. Shimansky; 54 *Shikhanoceras sphaerophorum* Shimansky; 55 *Euloxoceras* sp. A Gordon; 56 *Bactrites steinhaueri* (Sowerby) (see fig. 38e. f; pl. 28: 6-7), *B. carbonarius* Smith; 57 *Bactrites longicameratus* Shimansky; 58 *Bactrites mexicanus* Girty; 59 *Ctenobactrites inhonorus* Shimansky; 60 *Ctenobactrites* sp. Shimansky; 61 *Ctenobactrites mirus* Shimansky; 62 *Ctenobactrites costatus* Shimansky; 63 *Eobelemnites caneyense* Flower, *Hematites barbarae* Flower and Gordon, *Palaeoconus bakeri* Flower and Gordon, *Bactritomimus ulrichi* Flower and Gordon, *B. girtyi* Flower and Gordon; 64 *Rhipsites attenuatus* Zhuravleva; 65 *Mericoceras karagandense* Zhuravleva, *Stiloceras reticulatum* Zhuravleva; 66 *Ctenoceras schmidti* Noetling; 67 *Sinuobactrites wewokensis* Mapes.

mon practice of erecting new taxa on ornamented shell fragments with unknown internal structure. Most nautiloid groups including longitudinally ornamented orthoconic forms are artificial. I believe that only a single lineage including longitudinally striated forms evolved directly from the Orthoceratidae. Its oldest known representative is "*Protobactrites*" *delicatulum* TROEDSSON, 1932, from the Llanvirnian of the Baltic area. Besides its weak ornamentation, the species does not differ from the associated orthoceratids. TROEDSSON (1932) described a large number of longitudinally striated orthoconic forms from the Baltic Ordovician but additional research is needed to determine the actual species diversity of this fauna. TROEDSSON did not consider the intrapopulation variability and hence, some of his species are morphotypes. Much discussion was focused on *Troedssonella endoceroides* (TROEDSSON, 1932) thought to be distinctive in its well developed siphuncular deposits fused into a solid structure. However, these deposits are commonly fused among the orthoceratids (figs. 34-35 and pl. 25: 9) and highly variable even in a single phragmocone. There is no reason to assign an especially important position in nautiloid phylogeny to *Troedssonella* (see SWEET 1964, FLOWER 1975) known from a single fragmentary specimen closely resembling the associated species. I propose to include all of these Baltic Ordovician, finely striated orthocones in *Perigrammoceras*. These forms may have given rise to *Protokionoceras*, characterized by its shell ornamented with distinct longitudinal ribs. The oldest representative of the latter genus is "*Kionoceras*" *valcourense* FLOWER, 1952, from the Chazyan (Llandeilian) of New York. Having erected some new species on barely distinguishable specimens collected from a single exposure, FLOWER (1952*a*) writes: "Here four species can be recognized, except of course by those who insists that there may be only one species of a genus in a population". Related forms have been reported from the Late Ordovician of the Baltic area (TROEDSSON 1932) and from the Silurian of the Podolia (BALASCHOV 1975). *Jonesoceras jonesi* (BARRANDE, 1866) from the Ludlovian of Bohemia may also be referred to the group under discussion. It shows a densely longitudinally striated shell with simple, relatively wide siphuncle with typically orthoceratid siphuncular deposits. "*Virgoceras*" *cancellatum* FLOWER, 1945, from the Wenlockian Laurel Limestone of New York has nothing in common with the type species of the genus *Virgoceras*, which may be synonymous with *Geisonoceras rivale*. *V. cancellatum* should be transferred to the genus *Jonesoceras*. *Mericoceras karagandense* ZHURAVLEVA, 1978, from the Famennian of Kazakhstan, shows a finely longitudinally striated shell homeomorphic with the Ordovician troedssonellids but it may have evolved from *Michelinoceras* as well.

The European Silurian pelagic faunas include as an important component a nautiloid group characterized by relatively short, most commonly straight shell with narrow, cylindrical siphuncle. This group is here recognized as a distinct family Arionoceratidae fam. nov. It is morphologically coherent and includes more or less complete sequences reflecting the course of the phylogeny. The oldest representative of the Arionoceratidae may be *Arionoceras* (*Joldagiroceras*) *gyratum* MIAGKOWA, 1967, from the Llandoverian of Siberia. The arionoceratids may have branched from the primitive breviconic Orthoceratidae already during the Ordovician and the boundary between the two families may appear less clear-cut after further research.

There are two distinct species of *Arionoceras* in the Ludlovian of Bohemia and the Baltic area, differing in their siphuncular width and shell size and slenderness. The larger and supposedly more primitive (this is suggested by its resemblance to *A. gyratum* in the width of siphuncle) *A. arion* (BARRANDE, 1868), was claimed by BARSKOV (in BARSKOV and KISSELOV 1970) to show septa without necks. After having investigated BARRANDE's original material and an additional collection from the Bohemian Silurian (pl. 30: 5-7), I am of the opinion that this is an artifact of the preservation of BARSKOV's specimens. In fact, well preserved phragmocones of *A. arion* show short septal necks like those observed in other orthoceratids with simple siphuncle. SERPAGLI and GNOLI (1977) claim that *A. arion* is a junior synonym of *A. affine* (MENEGHINI, 1857) described from the Wenlockian of Sardinia. *A. affine* co-occurs in Sardinia

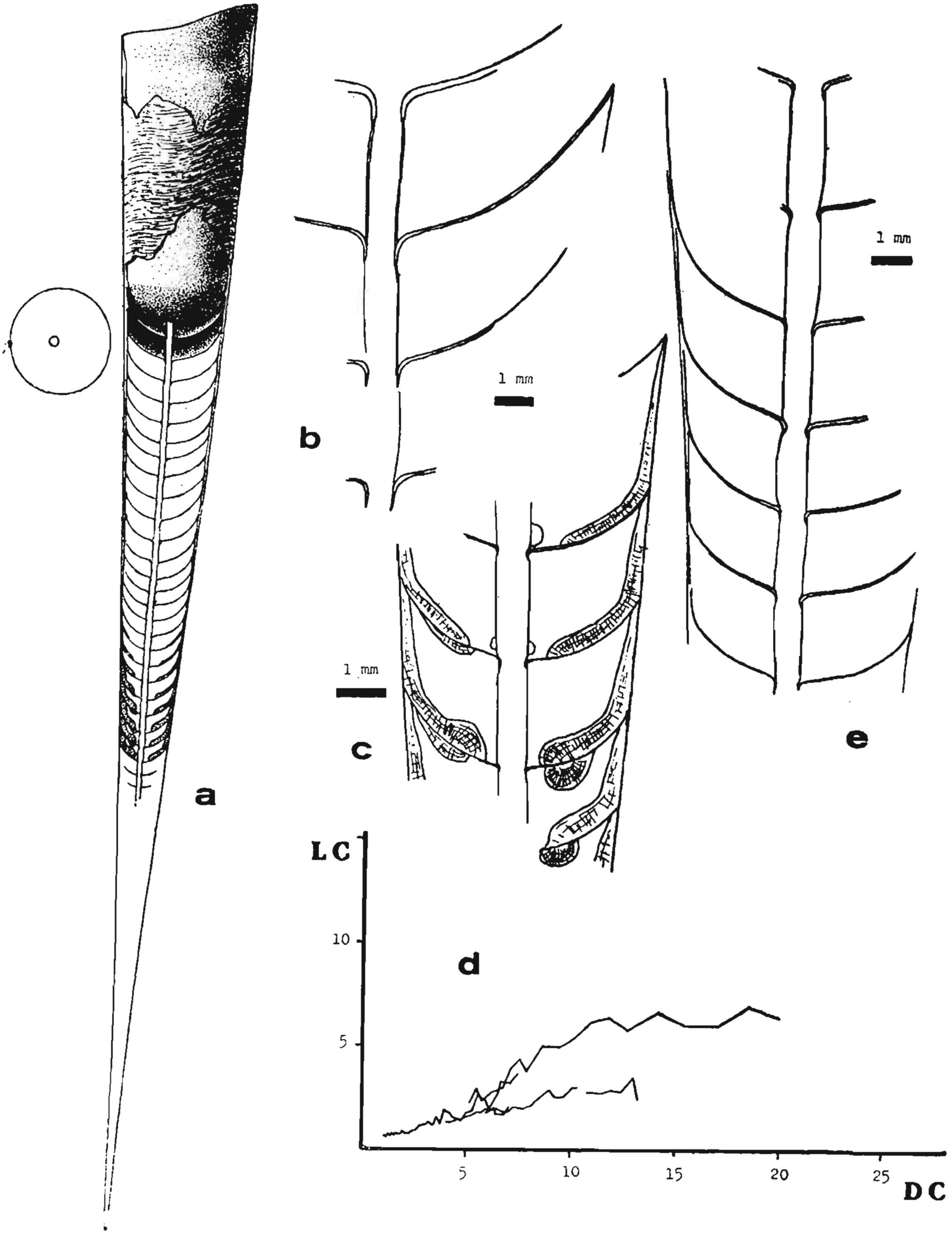


Fig. 40

Arionoceras valens (Barrande, 1868); Ludlovian, Poland; *a* Reconstruction of the adult specimen (see pl. 29: 4-5); *b* longitudinal section through a siphuncle, ZPAL N/661 (pl. 29: 4), erratic boulder of the graptolite limestone, Rozewie; *c* frontal section through a siphuncle, ZPAL N/662 (pl. 29: 3) boulder of the same lithology and locality; *d* relative growth of phragmocone chamber length (LC) and shell diameter (DC), in a Baltic population (erratic boulders of the graptolite limestones); *e* medial section through a phragmocone, ZPAL N/659, borehole Białopole IG, depth of 1670.7 m.

with *A. submoniliforme* (MENEGHINI, 1857); the two species show much affinity in their external morphology but the latter shows a larger ovate elongate protoconch. These species are almost indistinguishable in outline of the apical part of their shell from *Caliceras capillosum* (BARRANDE, 1866) as described by KOLEBABA (1975) from the Ludlovian of Bohemia. In fact, a juvenile phragmocone of *C. capillosum* can hardly be distinguished from the equivalent growth stages of *A. arion* and *A. submoniliforme*. Slight differences in separation of the embryonic shell cannot provide sufficient basis to distinguish orthoceratid species and genus, because this feature is usually highly variable in the Orthoceratida. One is unable to say which of the MENEGHINI'S species is synonymous with *A. arion* without an additional of the topotype material. The species *A. arion*, *A. affine*, and *A. submoniliforme* are known only from uncomparable developmental stages.

The other Bohemian Silurian representative of *Arionoceras*, *A. valens* (BARRANDE, 1868), shows a siphuncle much narrower than in the type species of the genus. Its living chamber is unusually variable in length. A sample found in erratic boulders attributable to the Early Ludlovian graptolite limestone of the Baltic area, seems to be conspecific with the Bohemian population of *A. valens*. In spite of considerable variability in shell ornamentation and apical angle, all the forms from the erratic boulders are placed in a single species (fig. 40 and pl. 29: 3-8). In boulder ZPAL E-036, an apical part of shell close in morphology to *A. submoniliforme* (pl. 29: 6) has been found associated with *A. valens*. It is to be noted that growth lines reflecting probable diurnal increments run independently of transverse ribs at the shell of surface *A. valens* (pl. 29: 8). This may be explained as a variation in growth of the conchioline periostracum in a pocket of the mantle producing the growth lines; whereas the ribs result from subsequent crumpling of the periostracum fixed by a secretion of the prismatic layer. This hypothesis is confirmed by the occurrence of wrinkles here and there at the margin of ribs. The periodic pattern in spacing of the transverse ribs may reflect inhibition in growth during the secretion of a septum (see also DZIK 1981).

"*Cyrtoceras*" *mirum* BARRANDE, 1866, from the Ludlovian to Přidolian of Bohemia, may be closely related to the species of *Arionoceras*. It shows a short, exogastric shell with very long living chamber. Similar but very poorly preserved nautiloids occur also in the Siegenian to Eifelian of Bohemia.

"*Orthoceras*" *fluminese* MENEGHINI, 1857 (pl. 30: 7), attributed by SERPAGLI and GNOLI (1977) to *Orthocycloceras*, differs from the type species of that genus, *O. alayense* (BARSKOV, 1972), in its narrow siphuncle and rapidly expanding apical part of the shell. It seems to be more closely related to *Arionoceras* than to *Orthocycloceras*.

There are also longitudinally striated arionoceratids. A morphological sequence has been recorded from the Ludlovian to Přidolian of Bohemia in the mode of development of a peculiar longitudinal ornamentation. "*Orthoceras*" *sericatum* BARRANDE, 1868, resembles *A. arion* in shell outline but its shell is finely reticulated with growth lines and longitudinal striae. *Vericeras ambigena* (BARRANDE, 1874) from the Ludlovian displays distinct longitudinal ribs (KOLEBABA 1977), while its apex is indistinguishable from that of *Arionoceras*. In *Parakionoceras striatopunctatum* (BARRANDE, 1868), the shell surface is covered with fine longitudinal furrows divided into several punctae like those in the gastropod genus *Actaeon*. *Parakionoceras originale* BARRANDE, 1868, which is the endmember of this morphological sequence, shows a shell ornamented with less densely spaced but more distinct longitudinal furrows. The furrows split the outer layer of the shell into stripes lense-like in cross section and hence, there are ribs of the inner layer corresponding in position to the furrows in the outer layer. Where the outer layer is removed, the ornamentation is therefore quite different from the external one (pl. 29: 1). According to KOLEBABA (1977) the peculiar shell ornamentation of *Parakionoceras originale* developed from a bending of longitudinal lamellae, which produced longitudinal channels below shell surface. The mode of development of the longitudinal ornamentation is well recognized during the ontogeny of *P. originale* (pl. 29: 1). It suggests a phylogenetic relationship of this group to the Llandoverian *A.* (*Joldagiroceras*) *gyratum* (MIAGKOVA, 1967).

The systematic position of the genus *Choanoceras*, known from a few Ordovician to Silurian specimens, remains unclear. The diagnostic characteristics include a conical outline of the septa, depressed, exogastric shell, and variably inflated connecting rings. The slow evolution of the septal outline, diagnostic of the genus, is well illustrated in the fossil record. Presumably, the oldest representative of this evolutionary lineage is *Montyoceras arcuatum* FLOWER, 1941, from the Llandeilian Valcour Limestone of New York. Various coeval forms described under different names were also ascribed to this group by FLOWER (1941, 1961) but they may actually be representatives of the genus *Clinoceras* unrelated to *Choanoceras*. *Ecdyceras sinuiferum* FLOWER, 1941, resembles *Sphooceras* in morphology but any reliable phylogenetic interpretation is impossible because of its poor preservation. According to FLOWER (1941), *Montyoceras* evolved from some forms close to *Clinoceras*. This, however, disregards its exogastric shell, different outline of connecting rings, and siphuncle position; the shell of *Clinoceras* is endogastrically (?) curved, and the septal necks are considerably curved even at the juvenile stages. The choanoceratid shell structure is so poorly known that one cannot point to their ancestors. *Montyoceras* is indistinguishable from later species of *Choanoceras* in its shell outline but its septal suture is still very primitive. Conical septa are displayed by *Choanoceras imitans* FLOWER, 1952, from the Early Caradocian Platteville Dolomite of Illinois. *Hadoceras septicurvatum* STRAND, 1932, from the Ashgillian of Norway may also be referred to the same evolutionary lineage. *Choanoceras mutabile* LINDSTRÖM, 1890, from the Ludlovian of Gotland shows extremely conical septal outline. *Redpathoceras clarki* FLOWER, 1943, from the Early Caradocian Leray Limestone of Quebec, is known from a single specimen described so vaguely that its systematic position cannot to be determined with certainty.

The Choanoceratidae are commonly recognized as ancestors of the Acoceratidae (see MILLER 1932, FLOWER 1941, FURNISH and GLENISTER 1964). This interpretation is based upon septal modifications being present, even though differing in both families. It is also corroborated by an affinity in muscle scar pattern between *Choanoceras* (see FLOWER 1952*a*) and *Billingsites* (see SWEET 1959*b*). The branching must have happened prior to the modification of septal curvature. The choanoceratid shell is depressed, whereas the typical ascoceratid shell is compressed; hence, an evolution in shell section must have also taken place. Both evolutionary trends are well illustrated in the fossil record (MILLER 1932; FLOWER 1941, 1963). The oldest representative of the Ascoceratidae, *Probillingsites*, appears in the Early Caradocian (SWEET 1958) preceded by a primitive choanoceratid *Montyoceras*. *Probillingsites* shows almost unmodified septal curvature and a depressed shell, like that recorded in *Montyoceras*. *Probillingsites*, characterized by only a slight adapertural displacement of the dorsal side of the septa gave in the Ashgillian rise to *Billingsites*, the latter genus showing a few last air chambers extended at the dorsal side of the living chamber. The Ordovician ascoceratids have been split into a large number of species (MILLER 1932; FLOWER 1941, 1946), in spite of the very poor preservation of most specimens. The existing taxonomy is so complicated that without a re-examination of the type materials one can do little more than claim an outline phylogeny.

The Upper Ordovician species of *Billingsistes* show a shell subcircular to very weakly depressed in cross section (see NEBEN and KRUEGER 1973, pl. 13: 1-2). *Lindstroemoceras dolium* (LINDSTRÖM, 1890) (= *Ascoceras cochleatum* LINDSTRÖM) from the Early Wenlockian Visby Marl of Gotland resembles very closely the preceding *Billingsites* in shell section except for the slight compression in the former. This species is known from a few specimens and, in my opinion should not be recognized as representative of a distinct genus. Most data on variability in the ascoceratid shell outline and internal structure have been supplied by the materials collected in the Ludlovian of Bohemia (BARRANDE 1865) and Gotland (LINDSTRÖM 1890). I believe that there are four ascoceratid species in the Ludlovian Kopanina Formation, Bohemia. These are: *A. buchi* Barrande, 1865, with relatively bulgy, coarsely ornamented shell; *A. kayserlingi* Barrande, 1865, with rather finely, transversely ribbed shell; *A. bohemicum* Barrande, 1865, with relatively large and bulgy, smooth shell; and *A. gracile* Barrande, 1865, with elongate shell and modified terminal aperture. The mature specimens of *A. bohemicum* from Kosoř range from 21 to 52 mm in shell diameter. A similar range of intrapopulation variability is shown by all the four species. The variation is often great and, hence, one cannot define precisely the ranges of particular species. Possibly, certain of the four ascoceratid species are merely varieties of the others. All other specific names introduced by Barrande (1865) are synonymous with one or another of these four. There are at least three species of *Ascoceras* in the Ludlovian Hemse Beds of Gotland, two of them conspecific with *A. bohemicum* and *A. gracile*. Third one, *A. manubrium* Lindström, 1890 differs from *A. gracile* only in larger size of adult shells (fig.41). Lindström (1890) recognized twelve species in his collection, but these are rather morphotypes than biospecies. In fact, almost the whole collection was taken from a single lithostratigraphic unit and, if we assume a similar intrapopulation variability as in the Bohemian ascoceratids, there are at most three species differing in shell slenderness and adult size.

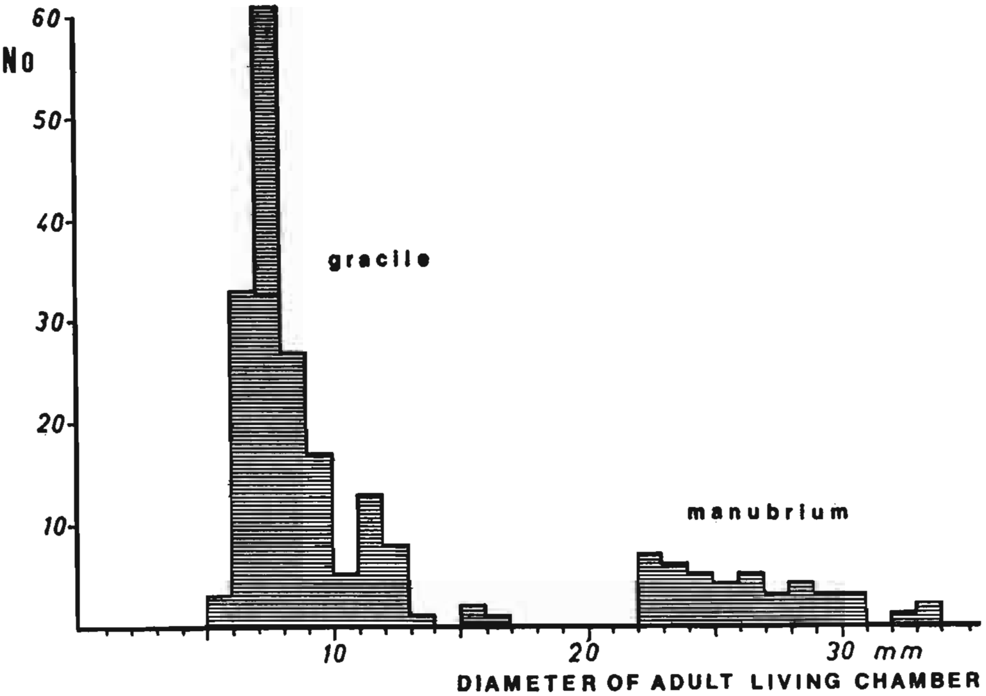


Fig. 41
Size-frequency distribution in the sample of *Ascoceras gracile* group from the Hemse Beds, Gotland. Based on specimens housed at Naturhistoriska Riksmuseet, Stockholm.

The apical part of the shell of *Ascoceras* was described by Lindström (1890) from the Ludlovian Hemse beds of Gotland. The embryonic shell was a little less than 2 mm in diameter, which indicates a considerable size of the egg. The larval shell is much inflated (Lindström 1890, pl. 1: 34-35). The juvenile stages resemble very closely those observed in the orthoceratids; the shell is subcircular in cross section, with a narrow, cylindrical siphuncle situated between the shell center and ventral side (Lindström 1890). The shell outline changes rapidly at the base of the mature living chamber, the latter being considerably swollen. This points to a considerable effect of genetic controls upon the complicated shell ontogeny because the shell was produced by the mantle margin and the mature shell's new adaptive function (buoyancy) could be accomplished only after the completion of growth. Mature living chambers are rather commonly found without any camerae ("*Aphragmites*", recorded in most Bohemian species; BARRANDE 1865) which demonstrates that the camerae were produced only after achievement of a certain size and shape of the shell. Specimens with modified aperture showing a dorsal lappet and lateral sinuses have been reported from both Bohemia and Gotland under the name *Glossoceras*. Their shell outline is almost indistinguishable from that observed in the associated gracile ascoceratids. In fact, they may be conspecific with the latter and represent their final ontogenetic stages.

I refute the supposition that the ascoceratid phragmocone underwent truncation during ontogeny (see FLOWER 1941, FURNISH and GLENISTER 1964). In the Ludlovian Hemse beds of Gotland, complete specimens of *Ascoceras* occur as frequently as those of the associated orthoceratids. Post-mortem truncation of the shell at the base of the living chamber was obviously facilitated by the shell shape. Furthermore, a separation of the living chamber from the phragmocone may well occur during removal from the rock; the absence of ascoceratid phragmocones from the BARRANDE'S collection indicates that this was commonly the case; isolated living chambers with the air chambers lacking have also been commonly found (BARRANDE 1865, pl. 94: 20-27); were this the result of truncation, living organisms must have lacked any hydrostatic apparatus. I cannot imagine any mechanism resulting in shell truncation, since only a narrow siphon occurred in the broken off phragmocone, the position of which made impossible its mechanical contribution to the truncation. I cannot imagine any extrinsic factor that could truncate a shell at a particular moment during ontogeny without affecting the animal itself.

There is only a single species of *Ascoceras* in the Přidolian of the Baltic area and Bohemia (pl. 29: 1), supposedly a descendant of *A. bohemicum*.

All the above discussed orthoceratids have subcylindrical to cylindrical connecting rings. Inflation of the connecting rings, e. g. in the Ascoceratidae, was due to inhibition in shell growth in length. Those forms with shells most rapidly increasing in length (this can be estimated from the air-chamber length) show also the most near-cylindrical siphuncle. Inflation of connecting rings and the rate of shell increase in length are negatively correlated. *Clinoceras* gave, however, rise to a large branch of the Orthoceratida characterized by a considerable inflation of the connecting rings throughout ontogeny. The oldest slightly breviconic orthoceratids (*Geisonoceras* sp. from the Volkhovian of the Baltic area; fig. 33) display slightly swollen connecting rings and the Early Llanvirnian species of *Clinoceras* show moderately inflated rings, hence, there is no morphological discontinuity. The evolutionary transition from *Orthoceras* to *Clinoceras* probably involved chiefly a shortening of both the living chamber and the phragmocone, and an increase in egg size. In the Baltic area *Clinoceras* ranges from the Kundan to the Caradocian. The type species of the genus, *C. dens* MASCKE, 1876, was described from a specimen from an erratic boulder of probably Late Llanvirnian age. Unfortunately, the holotype seems to have disappeared, and its illustration has been much idealized. Erratic boulders of Baltic origin found in northern Poland yield nautiloid specimens resembling very closely that one figured by MASCKE (1876). The difference consists in their almost straight growth lines and the apertural constriction being visible only at a mould, while it appears at the shell surface in MASCKE's figure; this may well reflect an idealization of the illustration rather than an actual morphological difference. The apertural constriction increases in distinctiveness during ontogeny and present the most distinctive character of *C. dens* relative to its descendants (fig. 43; pl. 32: 1-6). The shell of *C. dens* is depressed and the apical siphuncle and chambers are filled with deposits (fig. 43e). The siphuncular deposits are variable in structure; it is noteworthy that a radial pattern may occur, as commonly recognized as a diagnostic feature of the Actinoceratida. The specific distinction of *O. masckei* DEWITZ, 1880 (see NEBEN and KRUEGER

1971), described from the coeval erratic boulders is disputable. Shell fragments indistinguishable from *C. dens* have been commonly recorded throughout the Paleozoic. In spite of the erection of the genus *Clinoceras* a hundred years ago, none of these specimens was attributed to it; instead, several new genera and species have been designated, a phylogenetic tree was constructed (Flower 1938) showing a variation in preservation and siphuncular structure among a few

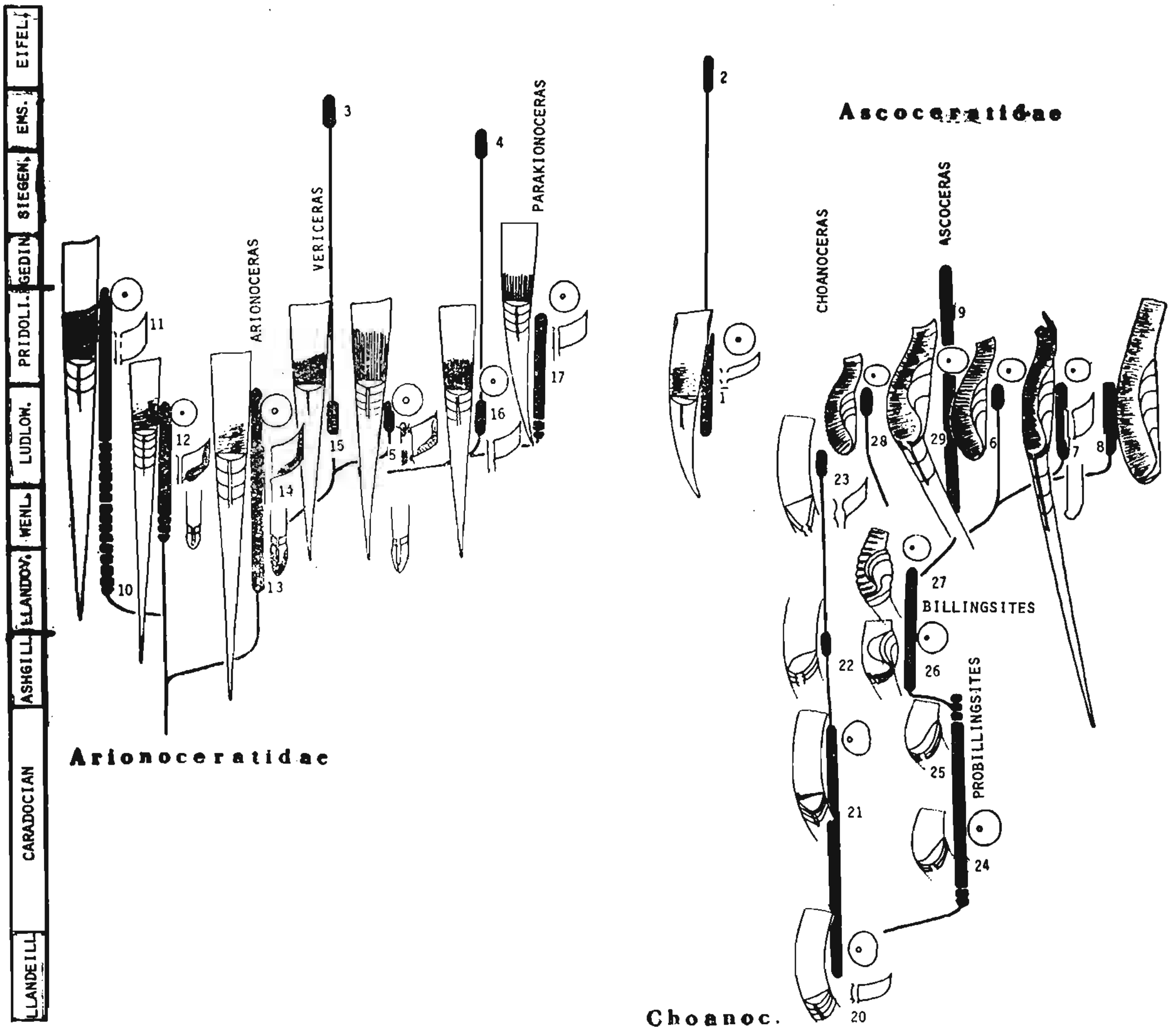


Fig. 42

Hypothetical phylogenetic relationships among members of the families Arionoceratidae, Choanoceratidae, and Ascoceratidae; 1 *Cyrtoceras mirum* Barrande; 2 *Orthoceras pastinaca* Barrande; 3 *Parakionoceras concinnum* Zhuravleva, *P. superfluum* Zhuravleva; 4 *Parakionoceras arctorhiphaeum* Zhuravleva; 5 *Vericeras ambigena* (Barrande); 6 *Ascoceras keyserlingi* Barrande; 7 *Glossoceras gracile* Barrande, *Parascoceras fistula* (Lindström); 8 *Ascoceras manubrium* Lindström; 9 *Ascoceras murchisoni* Barrande (see pl. 16: 2; 29: 11); 10 *Tambegiroceras moyerocanum* Miagkova; 11 *Arionoceras fluminese* (Meneghini) (pl. 30: 7); 12 *Arionoceras valens* (Barrande) (fig. 40a-e; pl. 29: 1-10), *A. affine* (Meneghini); 13 *Joldagiroceras gyratum* Miagkova; 14 *Arionoceras arion* (Barrande) (pl. 30: 5-6), *A. submoniliforme* (Meneghini), *Psilorthoceras chaubetae* Ristedt, *Caliceras capillosum* (Barrande); 15 *Orthoceras sericatum* Barrande; 16 *Parakionoceras striatopunctatum* (Barrande), 17 *Parakionoceras originale* (Barrande) (pl. 29: 1-2; 30: 3-3-4); 18 *Ecdyceras foerstei* Flower; 19 *Sphooceras truncatum* (Barrande) (pl. 31: 5-7); 20 *Montyoceras arcuatum* Flower, *Ecdyceras sinuiferum* Flower; 21 *Choanoceras imitans* Flower; 22 *Hadoceras septocurvatum* Strand; 23 *Choanoceras mutabile* Lindström; 24 *Probillingsites* sp. Sweet; 25 *Probillingsites pronis* Miller and Youngquist; 26 *Billingsities deformis* (Eichwald), *B. canadensis* (Billings), *Schuchertoceras anticostiense* (Billings); 27 *Lindstroemoceras dolium* (Lindström) = *Ascoceras cochleatum* Lindström; 28 *Aphragmites buchi* Barrande; 29 *Ascoceras bohemicum* Barrande.

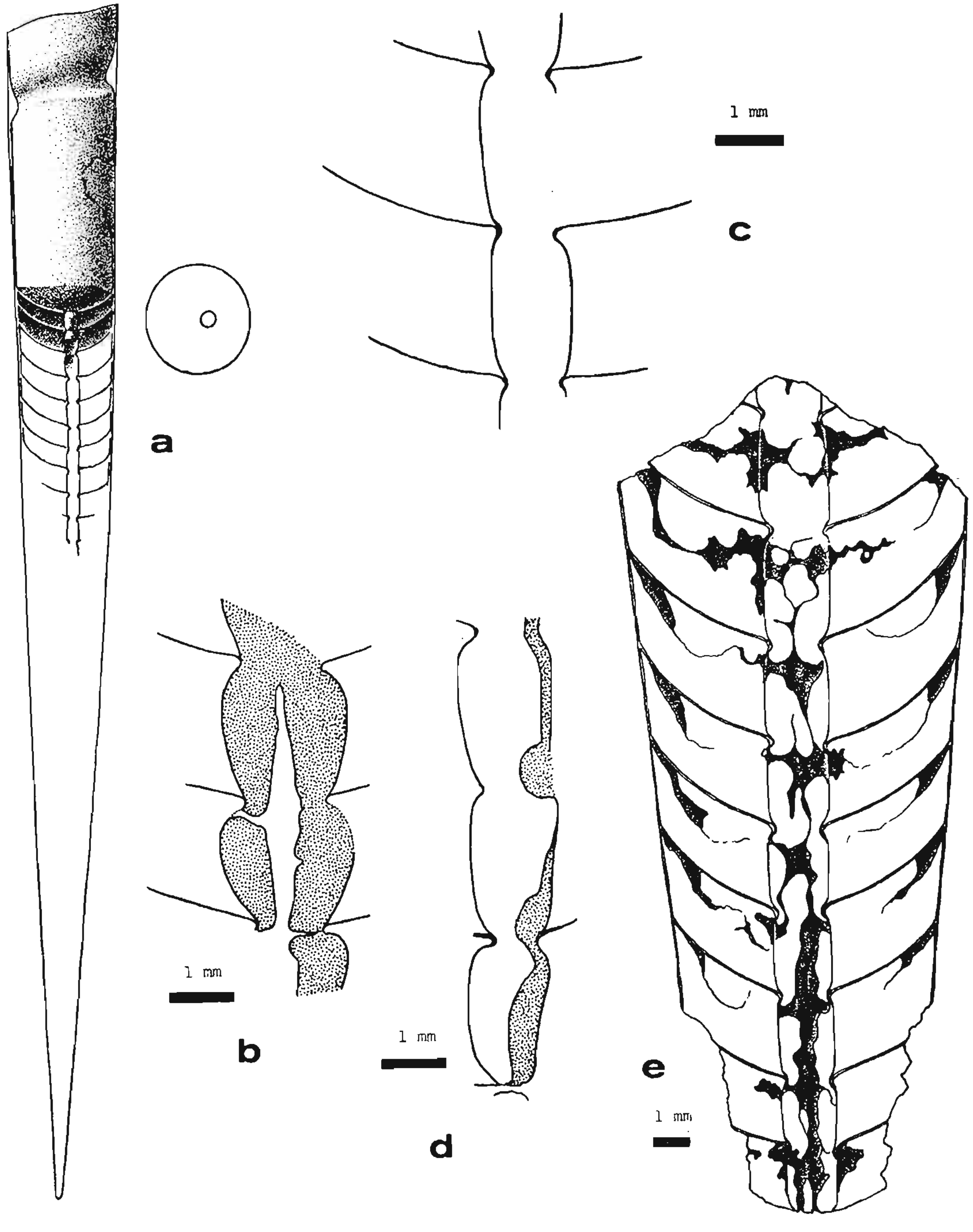


Fig. 43

Clinoceras cf. *dens* Mascke, 1876; *a* Reconstruction of the adult shell, apertural outline from the specimen ZPAL N/698 (pl. 32: 1), boulder E-215, *E. foliaceus* Zone Lasnamägian, Mochty; *b* longitudinal section through a siphuncle, ZPAL N/700, same boulder; *c* longitudinal section through a siphuncle, ZPAL N/692 (pl. 32: 3), boulder E-134, Uhakuan (?), Wieżyca; *d* section through a siphuncle, ZPAL N/699 (pl. 32: 2), erratic boulder, Lasnamägian (?), Zgierz; *e* reconstruction of a phragmocone fragment, ZPAL N/691; probably *Raniceps* limestone, Middle Kundan, Häludden, Öland, Sweden.

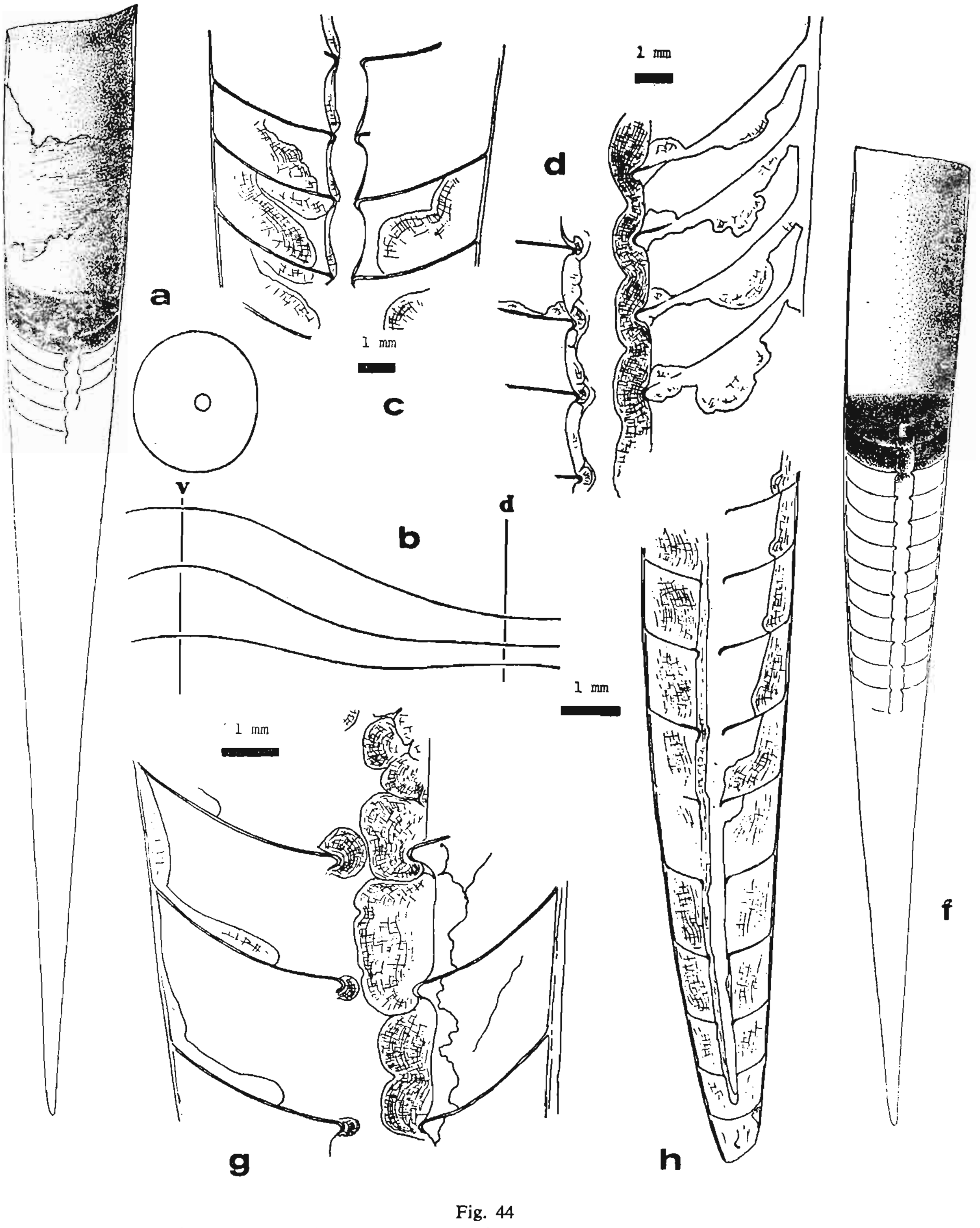


Fig. 44

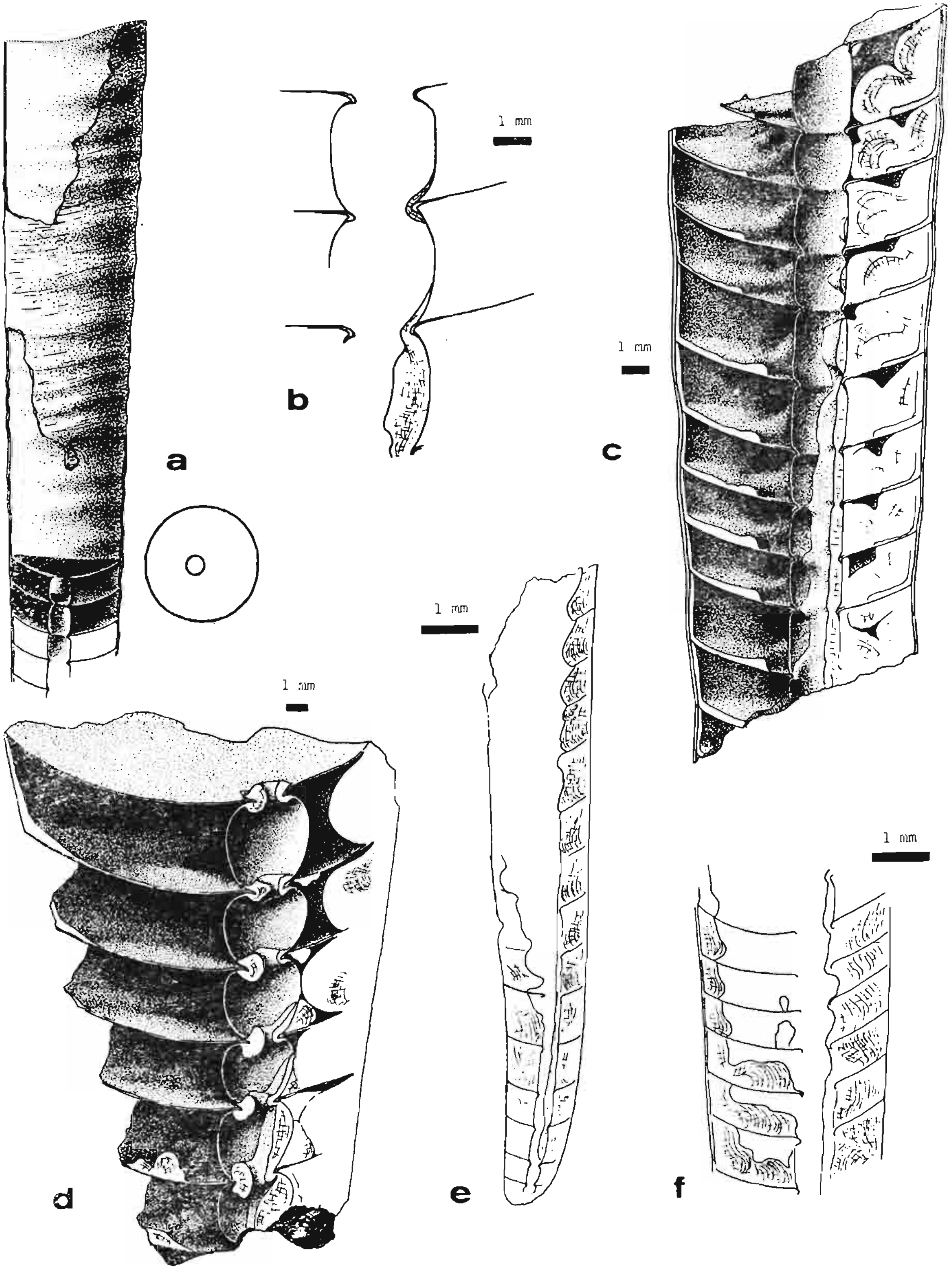
Clinoceras muensteri (WEDEKIND, 1908); *a* Reconstruction of the adult specimen, mostly after the specimen ZPAL N/717 (pl. 33-10), *Platyclymenia* Zone, Famennian, Łagów-Dule; *b* variation in septal suture in the population from Łagów-Dule; *c* longitudinal section through a phragmocone, ZPAL N/710 (pl. 33: 6), *Manticoceras* Zone, Frasnian, Płucki. *Clinoceras* (?) sp.; *d* Longitudinal section through a phragmocone, ZPAL N/741 (pl. 33: 2), *Cheiloceras* Zone, Famennian, Jabłonna, bed J. 9. *Clinoceras* sp.; *e* Visean (D_2), Orlej quarry by Zalas, near Cracow; *f* Reconstruction of the adult specimen (living chamber shape from the specimen UWR 1859 (pl. 34: 8), Caroline seam, Upper Silesia, Namurian); *g* longitudinal section through a phragmocone, ZMS A. I. 70/03; *h* apical part of a shell with damaged apex (non-medial section at the earliest two chambers), ZMS A. I. 70/01.

species rather than the evolution of the whole group. There is considerable variation in morphology of the siphuncular deposits even within a single phragmocone but their structure was, nonetheless, commonly considered as a feature diagnostic of genera, and even an evolutionary pattern was distinguished (BARSKOV 1968). Actually, the species of *Clinoceras s. l.* resemble rather closely one another and show considerable intrapopulation variability and consequently, a specific identification of single, especially juvenile, specimens is virtually impossible. Most erected species and genera need detailed revision with the intra population variability taken into account. In ZPAL and ZNS collections there are some hundreds of specimens of *Clinoceras* ranging in age from Ordovician through Carboniferous but I am often unable to point to any characters permitting an unequivocal distinction between the Ordovician and Carboniferous forms. Possibly, the outline of the adult living chamber and the size of the larval shell will prove to be diagnostic but these structures are found only infrequently.

In spite of the widespread and abundant occurrence of *Clinoceras*, only a few species can be recognized as well founded, i. a. Silurian "*Orthoceras*" *decipiens* BARRANDE, 1866, from the Ludlovian Kopanina Formation of Bohemia. This species may, however, be representative of a distinct evolutionary lineage, characterized by a more inflated siphuncle and larger shell, and leading to *Dnestroceras podolicum* (SIEMIRADZKI, 1906) from the Gedinnian Czortków Beds of the Podolia (fig. 47a-b and pl. 37: 1). A rich collection of complete specimens of *Clinoceras muensteri* (WEDEKIND, 1917) has been taken from the Early Famennian limestones (*Cheiloceras* to *Platyclymenia* Zones) of the Holy Cross Mts. (fig. 44a-c and pl. 33: 1, 4-11). This species shows considerable variation in suture as well as in shell length and shape. ZHURAVLEVA (1978*b*) did not take into account the intrapopulation and intraspecific variability of the Famennian clinoceratids from the Urals and Kazakhstan and erected a dozen new species and genera. A very similar, hardly identifiable species occurs in the Visean to Namurian of the Upper Silesia and Cracow area (fig. 44f-h and pl. 34: 3-8). An especially rich collection including also apical parts of the shell has been taken from the Orlej quarry. The specimens from Orlej vary in the from of connecting rings ranging from weakly to strongly convex. One cannot, however, reject a possibility that the collection includes also another species, externally indistinguishable from the former. No doubt, the associated slender shells with curved larval shell and smaller apex (fig. 45e-f and pl. 34: 2) belong to a specifically distinct form. The available data do not permit distinction of the latter species from the Late Carboniferous *Pseudorthoceras knoxense* (MCCHESNEY, 1859) (see FISHER and TEICHERT 1969) as well as from the Permian *Uralorthoceras tzvetaevae* SHIMANSKY, 1954. The three forms may represent a single evolutionary lineage, which may include *Pseudocyrtoceras acus* (KONINCK, 1880) from the Tournaisian (SCHINDEWOLF 1943) as well as several other poorly known Early Carboniferous forms.

Another form of the apical part of the shell is exhibited by *Dolorthoceras tenuifilosum* GORDON, 1964, from the Namurian Fayetteville Shale of Arkansas. Its simple, parabolic apex is indicative of phylogenetic relationship to Permian *Dolorthoceras stiliforme* SHIMANSKY, 1954, and Triassic *Trematoceras elegans* (MÜNSTER, 1841). Besides a questionable bactrid lineage ending with *Dillerites*, this is the longest-persisting group of orthoconic nautiloids. The Triassic orthoceratids are widely but poorly known. A large number of species have been erected but the actual species diversity of this group seems to be low. The Early Triassic forms (KIPARISOVA 1961) do not significantly differ from the Late Triassic ones (MOJSISOVICS 1873-1902). These are gracile longicones resembling very closely *Michelinoceras* in external view. The morphology of their apical part (known thus far exclusively in the species of the genus *Trematoceras*; BÜLOW 1915) is indicative of their descent from the above discussed Carboniferous and Permian forms.

No doubt that *Proteoceras perkinsi* (RUEDEMANN, 1906) (see FLOWER 1955), from the Chazyan (Llandeilian) of New York is a close relative of *Clinoceras dens*. Its bulgy, endogastrically (?) curved shell and subdorsal (?) siphuncle with ontogenetical decrease of inflation of the connecting rings and of distance from the shell wall, are indicative of its more advanced position relative to *C. dens*. *P. perkinsi* is known only from phragmocone fragments (FLOWER 1955) and hence, one cannot compare it reliably to other forms. The available data suggest its close affinity to *Cyrtactinoceras rebelle* (BARRANDE, 1866), from the Ludlovian of Bohemia and the



Baltic area (fig. 45d and pl. 33: 3). The adult living chamber of the latter species shows a slightly constricted aperture and a distinct, broad retractor attachment scar at the more convex side (the scar is invisible in the illustrations given by Barrande (1866, pl. 164: 10-12). In addition to the shell outline, *Cyrtactinoceras* (= *Proteoceras*) differs from *Clinoceras* in its cameral deposits being mostly confined to the shell wall rather than to the septa. In fact, *Cyrtactinoceras* resembles *Spyroceras* rather than other clinoceratids in the structure and pattern of the cameral deposits. This may also suggest similar life habits of these two genera.

As judged from the shell outline and ontogenetic change in position of the siphuncle, the lineage of *Cyrtactinoceras* may also be related to the Late Ordovician forms *Whiteavesites winnipegense* (Whiteaves, 1892) and *Whitfieldoceras mumiaeforme* (Whitfield, 1882). The latter two species may also be related to the family Actinoceratidae, as indicated by their large shell. These two interpretations are not incompatible each with other. The Actinoceratidae are almost certainly polyphyletic. The Actinoceratidae resemble the other actinoceratids exclusively in their large larval shell, whereas the shell section and ontogeny, the position of siphuncle, and to a certain degree the nature of cameral deposits connect the genus *Actinoceras* and its relatives with the genus *Cyrtactinoceras*.

Some Silurian species differing from *Clinoceras* in their longitudinally striated, considerably curved shell have been assigned to the genus *Lyecoceras*. Mutvei (1957) erected two species of *Lyecoceras* from the Ludlovian Hemse Beds of Gotland; the species differ in shell section and prominence of ornamentation but their intrapopulation variability remains unknown. Almost indistinguishable and presumably conspecific forms occur in the Ludlovian of Bohemia, e. g. "*Orthoceras*" *araneosum* Barrande, 1866. More strongly curved and distinctly longitudinally striated Bohemian specimens may be representative of an evolutionary lineage derived from the typical *Lyecoceras*.

Much discussion was focused on the systematic position of the family Sactoceratidae including forms with a shell shape as in *Clinoceras*, but at the same time with strongly inflated connecting rings. Shimansky (1962) attributed this nautiloid group to the Actinoceratoidea. Teichert (1964) included these forms in the actinoceratid family Ormoceratidae. The sactoceratids, however, show no radial pattern of siphuncular deposits typical of the Actinoceratina, and their relatively small embryonic shell militates against their derivation from the typical Actinoceratina. In turn, all the available data on their shell structure are suggestive of a direct relationship to *Clinoceras*. The oldest known representative of this group, *Tunguskoceras tunguskense* (Balaschov, 1962) from the Krivoluksky horizon (Llandeilian) of Siberia, has a shell indistinguishable in size, outline, and ornamentation from *Clinoceras*. The only difference is in the considerable inflation of the connecting rings in *T. tunguskense*. Very similar, but most commonly incomplete, forms have also been recorded in the Ordovician to Silurian of North America, Siberia, and Europe (Zhuravleva 1957, Flower 1957, Kobluk and Hall 1976, Aronoff 1978). In spite of their narrower siphuncle, they were usually assigned to various actinoceratid genera. The best known representative of this nautiloid group is *Sactoceras richteri* (Barrande, 1866) reported from the Ludlovian of Bohemia (Barrande 1866), Sardinia (Serpagli and Gnoli 1977), and Lithuania (Saladzhius 1966). Its shell is ornamented exclusively with growth lines. The associated species "*Orthoceras*" *cuvieri* Barrande, 1865, is almost indistinguishable from *S. richteri* in the shell outline and siphuncular structure but its

Fig. 45

Eridites (?) sp.; erratic boulders of the Beyrichienkalk, Přidolian, Orłowo; *a* Reconstruction of the living chamber, mostly from the specimen ZPAL N/751 (pl. 32: 9); *b* longitudinal section through a siphuncle, ZPAL N/753; *c* reconstruction of a phragmocone fragment, ZPAL N/742 (pl. 32: 4). *Cyrtactinoceras* sp.; ZPAL N/761 (pl 33: 3), erratic boulder of Baltic origin, Early Ludlovian (?), Orłowo, Pomerania; *d* reconstruction of a fragment of the phragmocone. *Pseudorthoceras* cf. *striolatum* (Meyer, 1832); Visean (D_3), Orlej quarry, Zalas near Cracow; *e* Apical part of a shell, ZMS A. I. 70/45; *f* longitudinal section through a phragmocone; (see also pl. 34: 1-2).

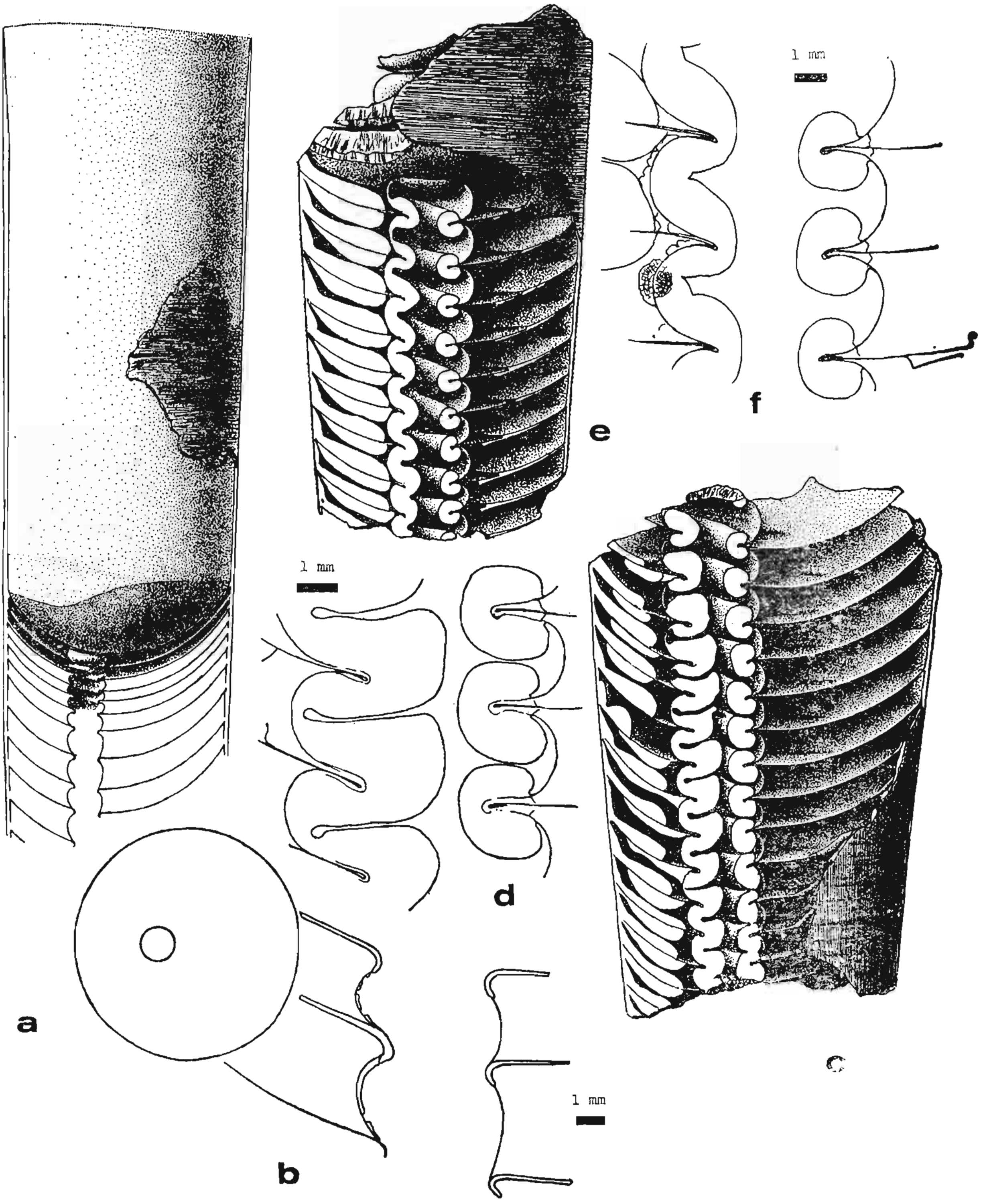


Fig. 46

Dnestroceras podolicum (Siemiradzki, 1906); ZPAL N/432 (pl. 37: 1); Czortków beds, Gedinnian, Jagielnica, Podolia, Ukraine); *a* Reconstruction of the living chamber; *b* section through the siphuncle. *Satoceras danicum* (Teichert, 1934); ZPAL N/800 (pl. 37: 7), erratic boulder of the Beyrichienkalk, Přídolian, Zgierz; *e* Reconstruction of a fragment of the phragmocone; *f* section through the siphuncle. *Sactoceras* (?) sp. ex gr. *Orthoceras cuvieri* (Barrande, 1868); ZPAL N/801 (pl. 37: 3), erratic boulder of the Beyrichienkalk, Přídolian, Garcz by Kartuzy, Pomerania; *c* Reconstruction of a fragment of the phragmocone; *d* section through the siphuncle.

shell surface is longitudinally striated. In erratic boulders of Ludlovian or Přidolian age there are two species corresponding in shell ornamentation to the two Bohemian forms, but with much more inflated connecting rings (fig. 46 and pl. 37). At the moment one cannot say whether *O. cuvieri* evolved from *Sactoceras* through appearance of longitudinal striation, or from *Lyecoceras* through inflation of siphonal segments.

Dnestroceras podolicum (SIEMIRADZKI, 1906) (= *D. incertum* ZHURAVLEVA, 1961 = *D. seretense* BALASCHOV, 1968) from the Gedinnian Czortków Beds of the Podolia may be a relative of *Sactoceras*. It displays a large straight shell with eccentric siphuncle with the segments inflated a little less than in *Sactoceras*. Its siphuncular deposits overlap with the connecting ring and do not significantly differ from those observed in other pseudoorthoceratids or sactoceratids (ZHURAVLEVA 1961). A mature specimen collected at Jagielnica in Podolia (fig. 46a-b, pl. 37: 1) provides us with an example of ontogenetic change in the septal suture. The suture is initially straight but a deep and wide lobe appears gradually at the siphonal side. This reflects probably the outline of retractor scar unfortunately invisible on the specimen. This is evidence for the diagnostic insignificance of the orhoceratid sutural line. This is rather inconsistent with high adaptive value of the shape of nautiloid septa suggested by WESTERMANN (1973, 1977).

The evolutionary lineage derived from *Sactoceras* supposedly persisted throughout the Devonian but its fossil record is very poor and unreliable. It may be represented by *Buchanoceras graviventrum* TEICHERT and GLENISTER, 1952, from the Siegenian of Australia; *Arpaoceras raphaeli* ZHURAVLEVA, 1962, from the Famennian (?) of Armenia; and *Macroloxoceras magnum* FLOWER, 1957, from the Famennian Chaffee Limestone of Colorado. The Carboniferous "actinoceratids" probably branched from this lineage. The systematics of the Carboniferous "actinoceratids" is very complicated (see SCHINDEWOLF 1943, LAI 1964*b*, SHIMANSKY 1968, TURNER 1951, GORDON 1964) but it has little in common with the species diversity of this group. Most species have been distinguished by slight differences in the siphuncular structure, although on the one hand inflation of connecting rings is highly variable during ontogeny and within a single population, and on the other hand, virtually indistinguishable adult stages may be associated with widely differing embryonic shells (SCHINDEWOLF 1943). I believe that one is unable to identify a single specimen with broken-off apical part of the shell. SCHINDEWOLF (1943) investigated the Visean to Namurian "actinoceratids" of Silesia and found that adult phragmocone parts of the *Rayonnoceras* type are associated with two different types of the apical part, which he recognized as diagnostic of the genera *Pseudactinoceras* and *Carbactinoceras*. *Pseudactinoceras* (= *Campyloceras*, see SWEET 1964) displays a narrow apical siphuncle increasing gradually in diameter; hence, there is a continuous ontogenetic transition from the larval phragmocone of *Clinoceras* type to the adult one of *Rayonnoceras* type. The other type of embryonic shell is characterized by a wide apical siphuncle; actually the siphuncle fills almost entirely the apical part of phragmocone in width, but its subdivision into intervals corresponding to the chambers is still discernible (fig. 47). Such specimens were described by SCHINDEWOLF under the generic name *Carbactinoceras*, but GORDON (1964*a*, pl. 3: 4-6) assigned them to *Rayonnoceras*. New species erected by SCHINDEWOLF for apical parts of the shell are most probably synonymous to various, previously known species described for adult individuals. One needs both the adult shell with living chamber, and its apical part to identify a form at the specific level. *Rayonnoceras* has been attributed to the Actinoceratida because of the radial pattern of its siphuncular deposits (MUTVEI 1964, GORDON 1964). However, a similar pattern is also shown by some typical orthoceratids, whereas *Rayonnoceras* differs considerably from the typical Actinoceratina. Its relatively narrow apical siphuncle suggests that the large embryonic shell evolved independently of the Actinoceratida. One may suppose that *Sactoceras*, *Pseudactinoceras*, and *Rayonnoceras* reflect an evolutionary trend towards size increase of the egg, even though the latter remains smaller than in the Ordovician Actinoceratina. A phylogenetic relationship of *Rayonnoceras* to the Pseudorthoceratidae and Sactoceratidae is in my

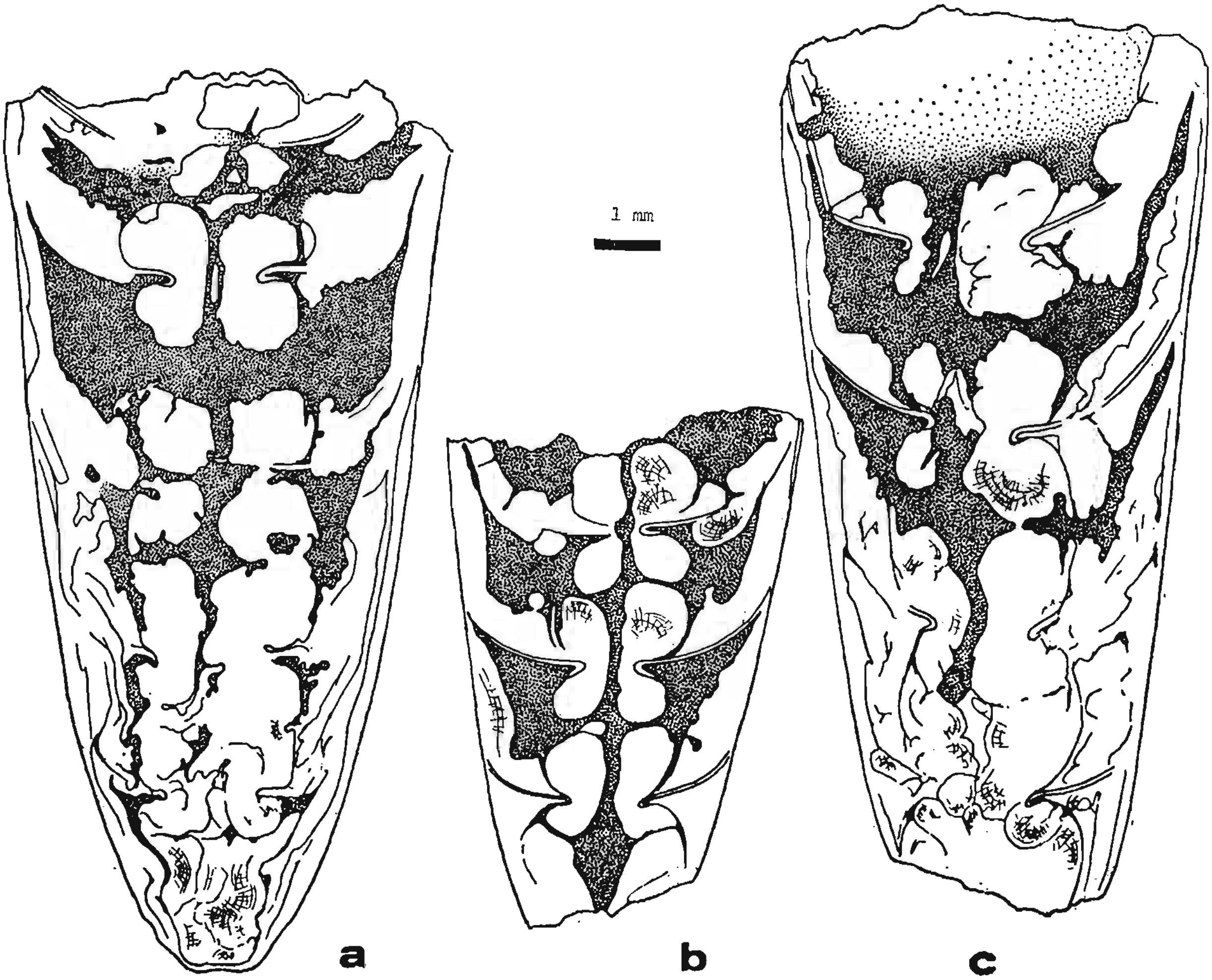


Fig. 47
Rayonnoceras sp.; apical part of shell; Visean (D_2), Orlej quarry, Zalas near Cracow; *a* Frontal section, ZMS A. I. 70/69; *b* frontal section, ZMS A. I. 70/68; *c* medial section, ZMS A. I. 70/67.

opinion without doubt. *Rayonnoceras* is the last representative of the Orthoceratina with inflated siphuncle. It persisted up to the end of the Namurian.

Shell annulation occurs rather commonly among the Orthoceratida. This is a fairly persistent character and hence, it may be of much diagnostic value. Among the oldest annulated descendants of the Pseudorthoceratidae is *Tofangoceras pauciannulatum* KOBAYASHI, 1972 (? = "*Protocycloceras*" *krivolukense* BALASCHOV, 1962). The best studied material comes from the Krivoluksky Horizon (Llandeilian) of Siberia (BALASCHOV 1962). Its distinctive shell annulation occurs on every few chambers, even at the juvenile stages. Shell annulation appears to be related to septa formation in the other annulated orthoceratids and hence, an annulation occurs usually at each phragmocone chamber. Such forms commonly occur in Baltic erratic boulders attributable to the Late Llandeilian to Early Caradocian (pl. 34: 5), and in the Early Caradocian of Norway (SWEET 1958: "*Ctenoceras schmidti* NOETLING, 1884"). Some fragments of adult living chambers collected from the erratic boulders indicate that the aperture is modified as in the Silurian *Cyrtocycloceras urbanum* (BARRANDE, 1866), without any lateral depressions. It seems to me very likely that the Late Silurian species of *Cyrtocycloceras* are descendants of so meant "*C. schmidti*".

A shell ornamentation very similar to that observed in *Cyrtocycloceras* is present in *Paraphragmites ascoceroides* FLOWER, 1943 (= *P. gomphoceroides* FLOWER, 1943) from the Silurian Stonehouse Formation of Nova Scotia. A phylogenetic relationship of *P. ascoceroides* to *Cyrtocycloceras* is nonetheless disputable because of the very short living chamber and spindle-shaped shell in the former. The shell outline and siphuncular structure of *P. ascoceroides* may in turn indicate a relation to *Cyrtactinoceras*. In spite of a distinct lobe at the convex side of the aperture and a sinus at the concave side (this is clearly seen in the pattern of growth lines; FLOWER 1943, pl. 40: 4-5), FLOWER claims that the shell of *Paraphragmites* is exogastrically curved. If this is correct, all the orthoceratids would be exogastric.

Fine longitudinal striation at the shell surface of *Cyrtocycloceras* permitted further evolution towards a distinct longitudinal striation to ribbing. The oldest annulated and longitudinally striated form is *Stereospyroceras champlainense* FLOWER, 1955, from the Chazyan (Llandeilian) of Vermont. Its only known specimen is fragmentary. The oldest unquestionable records of this group are in the Blackriveran (Early Caradocian) of North America (WILSON 1961) and in the coeval strata of Norway (SWEET 1958). Somewhat more robust forms with short and weakly curved shell with relatively sharp longitudinal ribs and flattened annulations are representative of the lineage of *Gorbyoceras*. Its Early Caradocian (Wilson 1961) and Ashgillian species (FLOWER 1946*a*) show evenly spaced annulations over the shell. There is no reason to erect as many species in this group as was done by FLOWER (1946*a*). A descendant of this lineage is "*Cyrtoceras*" *pugio* BARRADE, 1868, from the Ludlovian of Bohemia. There is no annulation on the juvenile part of its shell, only a longitudinal striation. The annulation appears at a shell diameter of some 5 mm; it becomes more and more flat with age but nonetheless, it persists over the shell in length (BARRANDE 1866, pl. 156: 18, 22). In contrast, shell annulation develops exclusively in the early stages of shell growth in a closely related species from the Siegenian of Bohemia, "*Orthoceras*" *pulchrum* BARRANDE, 1866, which shows, however, considerable intrapopulation variability.

Some widespread lineages of annulated orthoceratids arose during the Ordovician from *Gorbyoceras*. *G. textumaraneum* (ROEMER, 1861) from the Late Ordovician erratic boulders of Baltic origin shows sparsely distributed, prominent longitudinal ribs (fig. 48d and pl. 35: 4-6). It may be conspecific with *Spyroceras alternestriatum* STRAND, 1935, from the Ashgillian of Norway. The genus *Kionoceras* is characterized by a coarse longitudinal ornamentation and a disapearance of shell annulation in the adult stages. Presumably, it is represented in the Ludlovian of Bohemia by only two species, *K. bronni* BARRANDE, 1868, with relatively densely spaced ribs, and *K. doricum* (BARRANDE, 1868), with coarser shell ornamentation. The latter species occurs also in erratic boulders of Přidolian age (Beyrichienkalk) in the Baltic area (pl. 36: 3-5). The juvenile shell of *Kionoceras* resembles *Gorbyoceras* in ornamentation; the siphuncular and cameral deposits resemble those of *Orthoceras* (fig. 48d). A channel parallel to the siphuncle occurs in a specimen belonging to *Kionoceras* (pl. 36: 5). This is probably a post-mortem boring by a sipunculid (?) worm. Such structures have been interpreted as an "additional siphuncle" considered as diagnostic of the genus *Tretoceras* (see FLOWER 1976). COLLINS (1967) noted that the "siphuncle" described by FLOWER (1961) from a specimen of *Ecdyceras* may be a worm boring in the endocones of an endoceratid.

Kionoceras may have given rise to "*Spyroceras*" *karpinskyi* ZHURAVLEVA, 1962, from the Eifelian of the Urals. The latter species has a straight, relatively long shell annulated in its apical part and ornamented with sparse longitudinal ribs; it is unique in its growth lines running as deep sinuses between the ribs, suggesting that the aperture was provided with sharp teeth set onto the ribs. The siphuncle is subcylindrical. *Kionoceras arcticum* BALASCHOV, 1959, from the Middle Devonian of Tajmyr Peninsula is poorly known but it may be a link between the Silurian and Carboniferous species of *Kionoceras*.

Forms with elongated, annulated and longitudinally striated orthoconic shell have a long

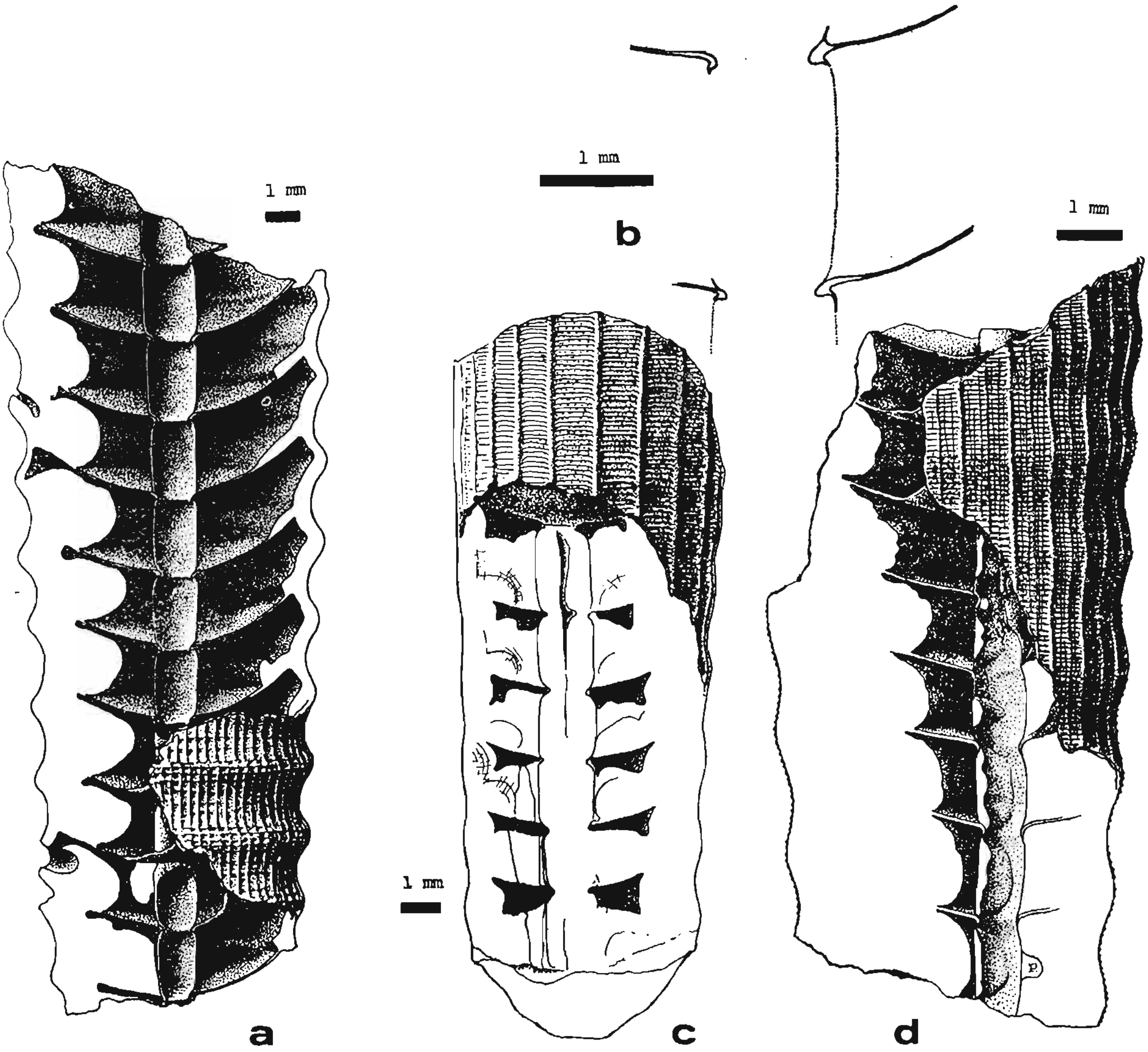


Fig. 48
Spyroceras senckenbergi TEICHERT, 1930; ZPAL N/780 (pl. 35: 5), boulder E-082, *A. ordovicicus* Zone, Ashgillian, Orłowo, Pomerania; *a* Reconstruction of a fragment of the phragmocone; *b* longitudinal section through the siphuncle. *Kionoceras* cf. *doricum* (BARRANDE, 1868); ZPAL N/789 (pl. 36: 5), erratic boulder of the Beyrichienkalk, Přidolian, Międzyzdroje; *c* Reconstruction of a fragment of the phragmocone. *Gorbyoceras* sp.; ZPAL N/778 (pl. 36: 1), boulder E-264, Ashgillian (?), Międzyzdroje, Wolin Island; *d* Reconstruction of a fragment of the phragmocone.

evolutionary history. The oldest known species of this group is *Spyroceras arcuoliratum* (HALL, 1874) from the Early Caradocian of North America. It appears to be conspecific with a number of morphologically almost indistinguishable forms described under different names (see WILSON 1961, STEELE and SINCLAIR 1971), but their interrelationships cannot be determined with certainty because of their unknown internal structure. In the Late Ordovician of the Baltic area this lineage is represented by *Spyroceras senckenbergi* TEICHERT, 1930 (fig. 48 and pl. 35: 5 in this paper), which differs from *S. arcuoliratum* in its more distinct annulation and transverse, simple aperture. These characters may reflect an evolutionary advancement of *S. senckenbergi* because they make it similar to its Silurian and Devonian descendants, whereas *S. arcuoliratum* resembles in this respect "*Ctenoceras schmidti*" (*sensu* SWEET 1958). The best known Silurian representatives of this lineage are "*Dawsonocerina*" *caelebs* (BARRANDE, 1874) from the Ludlovian, and "*D.*" *omega* (BARRANDE, 1874) from the Přidol'an, both of Bohemia (HORNY 1956). These are actually heterochronous conspecific populations rather than distinct species. Both resemble very closely *S. senckenbergi*. Finely striated species of the genus *Spyroceras* are widespread in the Devonian but are so poorly known that one cannot recognize any evolutionary trends within this group. The scarce data on their internal structure (fig. 46; COLLINS 1969), confirm a close relationship of the Devonian forms to the earlier ones. The youngest records of *Spyroceras* are from the Famennian (pl. 36: 2, 7). Some species of *Spyroceras* differ from their congeners in their flat longitudinal ribs (pl. 36: 4). An extreme example of this modification of the longitudinal ornamentation is "*Anaspyroceras*" *pseudocalamiteum* (BARRANDE, 1866) from the Late Silurian to Siegenian of Bohemia. Its longitudinal ribs are in form of erect lamellae, whereas the juvenile shell resembles *Spyroceras* in its reticulate ornamentation (RISTEDT 1968).

Erratic boulders of the Beyrichienkalk yield abundant specimens of orthoconic forms resembling the annulated orthoceratids in their siphuncular structure, but with a smooth, only weakly annulated shell (fig. 45a-b and pl. 32: 4-9). They may be conspecific with *Eridites astrovae* ZHURAVLEVA, 1961, known from fragmented and poorly preserved specimens from the Ludlovian of the Podolia. The systematic position of *E. astrovae* is unclear. Perhaps it gave rise to the Emsian *Rhabdites comprendus* ZHURAVLEVA, 1978.

The Devonian annulated orthoceratids are so poorly known that one cannot recognize their relationship to their Carboniferous morphological counterparts. There are various longitudinally ribbed forms in the Early Carboniferous that resemble very closely the Silurian species of *Kionoceras* (see FOORD 1897, SHIMANSKY 1968, TURNER 1954, NEWELL 1936). The Tournaisian to Visean *Kionoceras gesneri* (MARTIN, 1843), most closely related to typical representatives of this genus, resembles also very closely the Late Carboniferous *Kionoceras* sp. (see NEWELL 1936) and the Early Permian *K. serenum* SHIMANSKY, 1954. One may suppose that the lineage of *Kionoceras* persisted at least from the Silurian through the earliest Permian. The cylindrical siphuncle of the Late Paleozoic species of *Kionoceras* may, however, suggest their phylogenetic independence of the Silurian ones. The Early Carboniferous longitudinally ribbed forms present a morphological sequence ranging from *K. gesneri* with straight shell, through *Cyrtothoracoceras tuberculatum* (McCOY, 1844) with curved but similarly ornamented shell, to *Cornuella ornata* (EICHWALD, 1840) with annulated shell showing tubercles at the intersection of longitudinal ribs and annulations (SHIMANSKY 1968).

Remarkable evolutionary trends are shown by the Cycloceratidae, characterized by their annulated shell without any longitudinal ornamentation at the adult stages. The apical parts of cycloceratid shells are distinctly longitudinally striated but this ornamentation gradually disappears during ontogeny (GORDON 1960, 1964; pl. 34: 11 in this paper). This may indicate a phylogenetic relationship to the longitudinally striated kionoceratids. The oldest, very incomplete, records of the Cycloceratidae are in the Eifelian (ZHURAVLEVA 1978) and Famennian (pl. 34: 12; FLOWER and CARTER 1935). More abundant materials showing the morphological variation of the group have been derived from the Visean and Namurian (pl. 34: 7, 11; GORDON 1960, 1964*a*; SHIMANSKY 1968). In spite of a large number of thus far recognized species, the Cycloceratidae appear to be rather weakly variable. Typical representatives of *Cycloceras* (probably congeneric with *Reticycloceras*) are almost indistinguishable from the Silurian *Cyrtocycloceras* in shell outline and internal structure. The ancestral cycloceratid lineage probably persisted to the latest Permian (pl. 35: 1-2; SHIMANSKY 1965, TEICHERT and KUMMEL 1973), while the morphological evolution consisted mostly in a shift of the siphuncle nearer to the shell wall. The outline of the aperture, as reflected by the growth lines and annulations is rather diverse and possibly will prove to be of great diagnostic value. The cycloceratid evolution and taxonomy are very poorly known. An important evolutionary trend is towards a progressively shorter shell. The early stage of this evolutionary process is represented by *Cryptocycloceras* *bestia* SHIMANSKY, 1968, from the Late Carboniferous of the Urals, as well as by some similar forms from the Early Carboniferous of other areas (pl. 35: 3). A still shorter and straight shell is characteristic of *Brachycycloceras subquadratum* SHIMANSKY, 1968, from the Visean to Namurian of the Urals (SHIMANSKY 1968; SHIMANSKY and ZHURAVLEVA 1961, pl. 8: 9); very similar forms have also been reported from North America (GORDON 1964*a*, 1964*b*). *Brachycycloceras* shows an aperture slightly undulated in outline. A peculiar nautiloid lineage that started with *Mariceras*? sp. A GORDON, 1964, and some related forms from the Namurian Fayetteville Shale of Arkansas (GORDON 1964*a*, pl. 15: 12), supposedly derived from *Brachycycloceras*. This lineage is characterized by its considerably curved, very short shell with narrow siphuncle situated closely to the convex side; it persisted up to the Early Permian. The last character typical of breviconic orthoceratids, never occurs among the Nautilida to which order the group under discussion has thus far been attributed. Derivation of this group from either *Cornuella*, *Navis*, or *Brachycycloceras* is possible.The latter relationship seems to me most likely even though far from being demonstrated. The fossil record of the evolution leading from the Namurian "*Mariceras*" to the Early Permian *Scyphoceras* is rather poor. The richest described collection of *Scyphoceras* was taken from the Artiniskian of the Urals (RUZHENTSEV and SHIMANSKY 1954). A large number of new species and genera have been erected on this collection, but in my opinion, there may well be only a single species of *Scyphoceras* in the Early Permian of the Urals. The Early Permian *Scyphoceras dionysii* RUZHENTSEV and SHIMANSKY, 1954, resembles the Late Carboniferous *Tetrapleuroceras karpinskyi* SHIMANSKY, 1949, in the considerably curved, almost gyroconic juvenile shell ("*Scyphoceras*", "*Venatoroceras*") associated with a bulgy and almost straight adult shell ("*Dentoceras*"). The species of *Scyphoceras* supposedly show considerable intrapopulation variability. This nautiloid group has also been reporterted, although under different names, from North America (FLOWER 1963).

FURNISH, GLENISTER and HANSMAN (1962, 1964) claim that at maturity *Brachycycloceras* discarded its apical part, a similar concept as that of shell truncation in *Sphooceras* and the Ascoceratidae. I believe that the evidence presented by FURNISH, GLENISTER and HANSMAN does not substantiate their interpretation. The observed preservation and internal structure of the shell do not significantly differ from those recorded in other nautiloids.

Elongated and annulated nautiloid shells resembling *Cycloceras* but attributed to various genera, are widespread in the Late Permian (FLIEGEL 1901, SHIMANSKY 1965, TEICHERT and KUMMEL 1973, SCHRÉTER 1974). Relatively high variation in annulation density as commonly observed at a single locality, is to be interpreted as intrapopulation variability. The shape of the adult living chamber (SHIMANSKY 1965) as well as the shell ornamentation are indistinguishable from those of the Early Carboniferous species of *Cycloceras* (= *Reticycloceras*). The main difference is in a more eccentrical position of the siphuncle (pl. 35: 2) in the Late Permian forms. I question if this suffices for erection of the genus (subgenus ?) *Lopingoceras*.

Proposed systematics.—

Orthoceratidae M'COY, 1844

[= Michelinoceratidae FLOWER, 1945; Geisonoceratidae ZHURAVLEVA, 1959; Folioceratidae COLLINS, 1962]

Long and straight, transversally ornamented shell with inflated embryonic part, and long living chamber, subcentral siphuncle; connecting rings cylindrical to at most a little inflated.

Tajaroceras HOOK and FLOWER, 1976; *T. wardae* (? = *Buttsoceras novomexicanum* FLOWER, 1962)

[= *Wardoceras* HOOK and FLOWER, 1977; *Enigmoceras* HOOK and FLOWER, 1977; ?*Buttsoceras* ULRICH and FOERSTE, 1933]

Wide, subcentral siphuncle.

Orthoceras BRUGUIÈRE, 1789; *Orthoceratites regularis* SCHLOTHEIM, 1820

[= *Bifoveoceras* BALASCHOV, 1956]

Short, longitudinal depressions at the surface of the mature living chamber.

Ctenoceras NOETLING, 1884; *C. schmidti*

Close to *Orthoceras* but annulated and slightly curved shell.

Michelinoceras Foerste, 1932; *Orthoceras michelini* Barrande, 1866
[= *Mitorthoceras* Gordon, 1960; *Geisonoceroides* Flower, 1939; *Bitaunioceras* Shimizu and Obata, 1935; ?*Sphaerorthoceras* Ristedt, 1968; *Mimogeisonoceras* Zhuravleva, 1978; ?*Geisonocerella* Zhuravleva, 1978]

Narrow, central siphuncle; long and simple living chamber.

Geisonoceras Hyatt, 1844; *Orthoceras rivale* Barrande, 1866
[= *Harrisoceras* Flower, 1936; ?*Pleurorthoceras* Flower, 1962; *Kopaninoceras* Kisieliev, 1970]

Relatively wide siphuncle with a little inflated connecting rings; relatively short living chamber; elongated embryonic shell.

Fig. 49

Hypothetical phylogenetic relationships among members of the families Pseudorthoceratidae, Sactoceratidae, Cycloceratidae, Kionoceratidae, Greenlandoceratidae, and Tripteroceratidae; 1 *Clinoceras dens* Mascke (fig. 43a-c; pl. 32: 1-7), *C. masckei* Dewitz; 2 *Proteoceras perkinsi* (Ruedemann); 3 *Tunguskoceras tunguskense* (Balaschov); 4 *Tofangoceras pauciannulatum* Kobayashi, *Protocycloceras krivolukense* Balaschov; 5 *Stereospyroceras champlainense* Flower; 6 "*Ctenoceras schmidti*" *sensu* Sweet (pl. 34: 5); 7 *Monomuchites decrescens* (Billings), *M. costalis* Wilson; 8 *Cyrtocycloceras urbanum* (Barrande) (pl. 34: 9-11); 9 *Orthoceras kendalense* Blake *sensu* Siemiradzki, 10 *Dawsonoceras annulatum* Balaschov; 11 *Dawsonoceras barrandei* Horný; 12 *Dawsonoceras obsoletum* (Barrande); 13 *Gorbyoceras tetrauense* Wilson; 14 *Gorbyoceras duncanae* Flower; 15 *Gorbyoceras textumaraneum* Roemer (pl. 35: 4, 6)., 16 *Cyrtoceras pugio* Barrande; 17 *Orthoceras pulchrum* Barrande, *O. patronus* Barrande; 18 *Orthoceras bronni* Barrande; 19 *Kionoceras doricum* (Barrande) (pl. 36: 3, 5); 20 *Spyroceras senckenbergi* Teichert (fig. 46a, b; pl. 35: 5); 21 *Cedarvilleoceras porkunense* Balaschov; 22 *Dawsonocerina caelebs* (Barrande); 23 *Dawsonocerina omega* (Barrande); 24 *Spyroceras thoas* (Hall); 25 *Spyroceras crotalum* (Hall); 26 *Spyroceras karpinskyi* Zhuravleva; 27 *Anaspyroceras pseudocalamiteum* (Barrande); 28 *Orthoceras tubicinella* Sowerby; 29 *Whitfieldoceras mumiaeforme* (Whitfield), *Whiteavesites winnipegense* (Whiteaves); 30 *Cyrtactinoceras rebelle* (Barrande) (fig. 45d; pl. 33. 3); 31 *Paraphragmites ascoceroides* Flower; 32 *Eridites astrovae* Zhuravleva; 33 *Eridites* (?) sp. (fig. 45a-c; pl. 32: 4, 5, 8, 9); 34 *Orthoceras decipiens* Barrande, *Gordonoceras bondi* Teichert and Glenister, *Allanoceras inusitatum* Barskov; 35 *Dnestroceras podolicum* (Siemiradzki) = (?) *D. incertum* Zhuravleva (fig. 47a, b; pl. 37: 1); 36 *Buchanoceras graviventrum* Teichert and Glenister, *Orthoceras pallidum* Barrande; 37 *Orthonybyoceras covingtonense* (Foerste and Teichert), *Ormoceras kiaeri* Sweet; 38 *Sactoceras richteri* (Barrande), *Hellenites formosus* (Zhuravleva), *Siberioceras shimanskyi* Zhuravleva; 39 *Sactoceras danicum* (Teichert) (fig. 47c, f; pl. 37: 5-7); 40 *Podoliceras giganteum* Balaschov, *Lyecoceras gotlandense* Mutvei, *Orthoceras araneosum* Barrande; 41 *Lyecoceras longistriatum* Mutvei; 42 *Cyrtoceras trilby* Barrande; 43 *Cyrtoceras lepidum* Barrande; 44 *Striatoceras striatum* (Troedsson) = *Greenlandoceras lineatum* (Troedsson); 45 *Stromatoceras eximium* Teichert and Glenister, *Metastromatoceras formosum* Zhuravleva; 46 *Sactoceras elegantulum* Zhuravleva; 47 *Orthoceras cuvieri* Barrande; 48 *Sactoceras* (?) aff. *cuvieri* (Barrande) (fig. 47, c, d; pl. 37: 2, 3); 49 *Allumettoceras paquettense* Foerste; 50 *Murrayoceras murrayi* (Billings); 51 *Tripteroceras hastatum* (Billings); 52 *Mongoceras angustum* Miagkova, *Kionoceras muyagirum* Miagkova; 53 *Spyroceras arcuoliratum* (Hall); 54 *Isorthoceras sociale* (Hall); 55 *Macroloxoceras magnum* Flower, *Arpaoceras raphaeli* Zhuravleva; 56 *Spyroceras* cf. *crotalum* (Hall) (pl. 36: 2, 7); 57 *Spyroceras* sp.; 58 *Kionoceras gesneri* (Martin), *Dolorthoceras kionoideum* (Schmidt); 59 *Kionoceras* sp. Newell; 60 *Cyrtothoracoceras tuberculatum* McCoy; 61 *Cornuella ornata* (Eichwald); 62 *Neocycloceras obliquum* Flower and Caster, *Cycloceras* sp. (pl. 34: 7-12); 63 *Cycloceras dombarense* Shimansky; 64 *Brachycycloceras subquadratum* Shimansky, *B. washingtonense* Gordon, *Scyphoceras* sp. cf. *Scyphoceras caessator* (Hall and Whitfield) *sensu* Gordon (see also pl. 35: 3); 65 *Mariceras* sp. Gordon, "corallite-like nautiloid" Shimansky; 66 *Brachycycloceras normale* Miller, Dunbar and Condra; 67 *Tetrapleuroceras karpinskyi* Shimansky, *Neptunoceras sakmarense* Shimansky; 68 *Cryptocycloceras bestia* Shimansky, 69 *Cycloceras laevigatum* (McCoy) *sensu* Shimansky; 70 *Scyphoceras dionysii* Ruzhentsev and Shimansky, *Mariceras ferum* Ruzhentsev and Shimansky, *Venatoceras verae* Ruzhentsev and Shimansky, *Dentoceras magnum* Ruzhentsev and Shimansky; 71 *Clinoceras muensteri* (Wedekind) (Text-fig. 44a-c; pl. 33: 1-1); 72 *Clinoceras* sp. (fig. 44 f, h; pl. 34: 3-8); 73 *Psiaoceras hesperis* Eichwald, *Antonoceras balaschovi* Shimansky; 74 *Navis oneraria* Shimansky; 75 *Dolorthoceras incisum* Gordon, *D. tenuifilosum* Gordon, *Pseudorthoceras stonesense* Gordon; 76 *Pseudorthoceras striolatum* (Meyer) (fig. 45 e, f; pl. 34: 1-2); 77 *Pseudorthoceras comatum* Schmidt, ?*Tripteroceroides margaritae* Shimansky; 78 *Mooreoceras* sp. B Gordon; 79 *Pseudactinoceras promiscum* Schindewolf; 80 *Rayonnoceras solidiforme* Croneis, *R. fayettevillense* Croneis, *Carbactinoceras torleyi* Schindewolf (fig. 48a-c; pl. 38: 1); 81 *Rayonooceras fainae* Shimansky; 82 *Loxoceras breyni* (Fleming); 83 *Dolorthoceras stiliforme* Shimansky; 84 *Pseudorthoceras knoxense* (McChesney); 85 *Uralorthoceras tzvetaevae* Shimansky; 86 *Reticycloceras croneisi* Gordon, *R. girtyi* Gordon, *R. peytonense* Gordon; 87 *Lopingoceras lopingense* (Stoyanov), *L. orientale* (Flügel) (pl. 35: 1-2), *Neocycloceras obliqueseptatum* (Waagen); 88 *Kionoceras serenum* Shimansky; 89 *Pythonoceras boreum* Zhuravleva; 90 *Spyroceras suave* Zhuravleva; 91 *Pseudokionoceras nikolaevi* Zhuravleva; 92 *Rhabdites compressus* Zhuravleva; 93 *Nebroceras imaginarium* Zhuravleva, 1978.

Columenoceras BARSKOV, 1960; *Orthoceras columen* BARRANDE, 1866
[= *Neosichuanoceras* CHEN and LIU, 1977; ?*Pseudocycloceras* BARSKOV, 1959; *Tambegiroceras* MIAGKOVA, 1967; ?*Hemicosmorthoceras* RISTEDT, 1968; ?*Acrosphaerorthoceras* RISTEDT, 1968; ?*Parasphaerorthoceras* RISTEDT, 1968; *Vajgachites* ZHURAVLEVA, 1978]

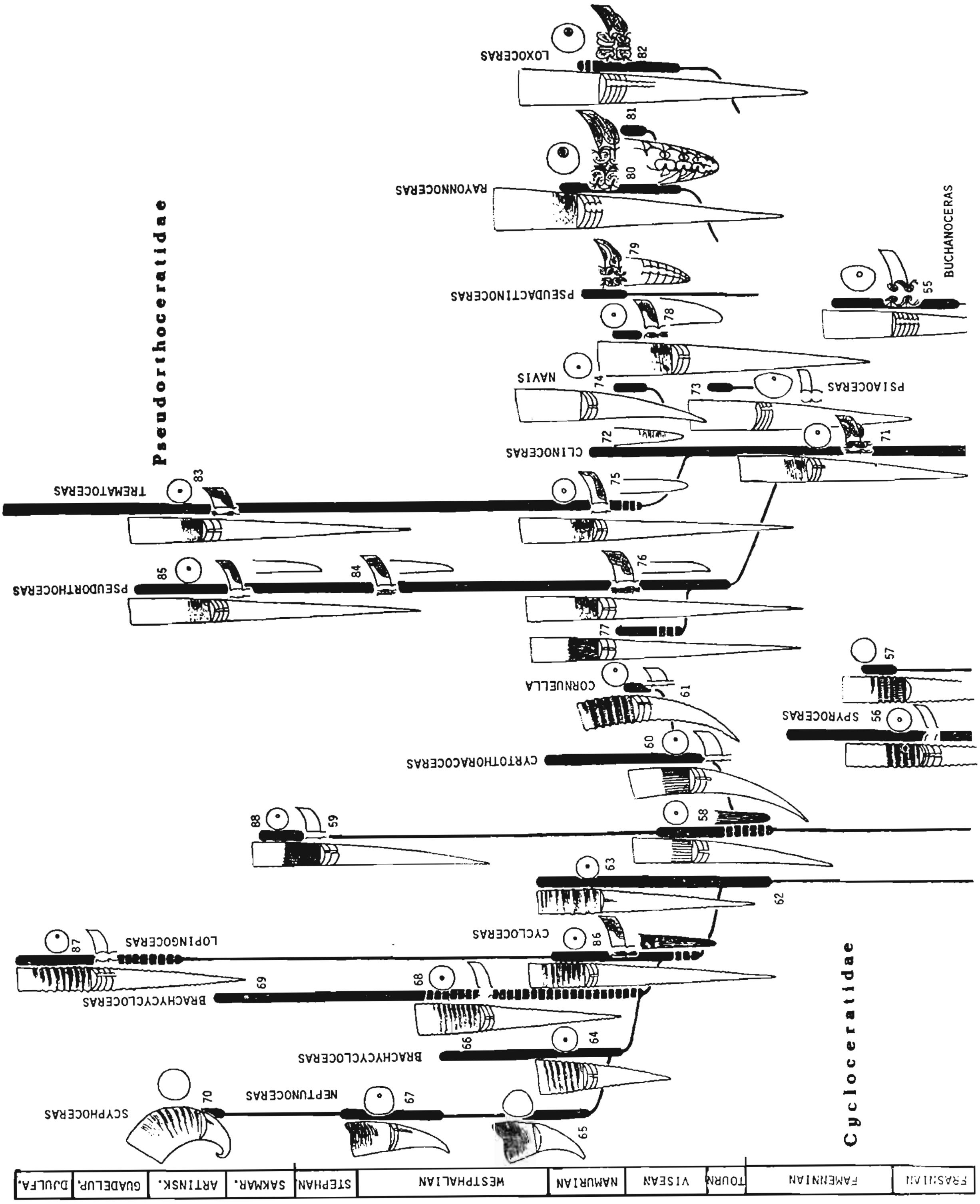


Fig. 49a

Long shell, densely annulated in its apical part; small-sized, mucronate embryonic shell and inflated larval (?) shell. *Plagiostomoceras* TEICHERT and GLENISTER, 1952; *Orthoceras pleurotomum* BARRANDE, 1866
[= ?*Protobactrites* HYATT, 1900; *Arkonoceras* FLOWER, 1945]

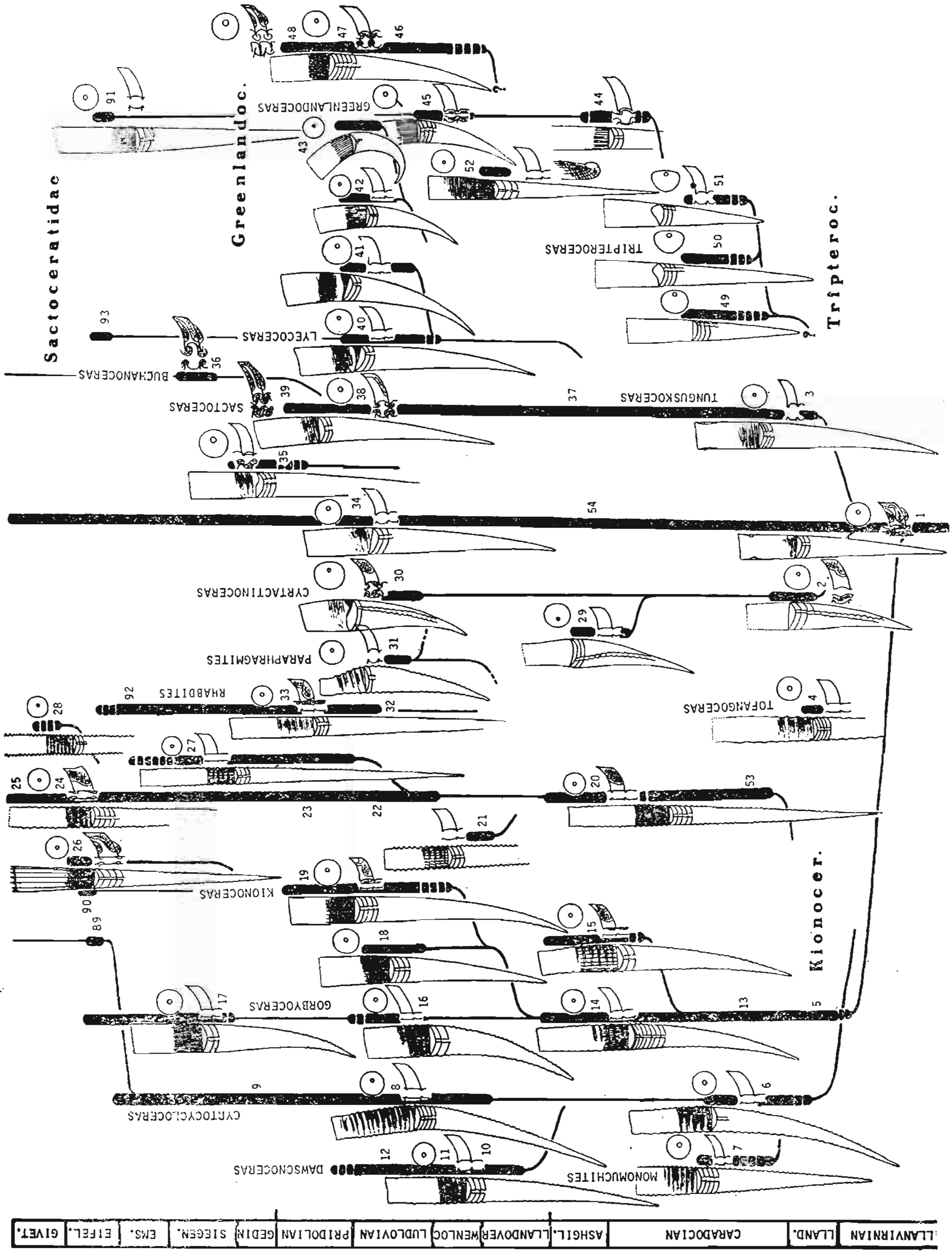


Fig. 49b

Long and compressed shell with centro-ventral siphuncle and long dorsal apertural lobe.

Haruspex SHIMANSKY, 1968; *H. latisiphonatus*

Like *Plagiostomoceras* but with very wide siphuncle.

Jangziceras LAI, 1964; *J. sichuanense*
[= *Folioceras* COLLINS, 1969; ?*Sichuanoceras* CHANG, 1963]

Wide, centro-ventral siphuncle with siphuncular deposits in form of ventral blocks.

?***Tofangoceras*** KOBAYASHI, 1927; *T. pauciannulatum*
[= *Sigmocycloceras* KOBAYASHI, 1934; *Cyclobuttsoceras* CHEN, 1976]

Shell annulations spaced much more sparsely than septa.

Bogoslovskya ZHURAVLEVA, 1978; *B. perspiqua*

Shell outline as in *Michelinoceras* but with subventral siphuncle as in *Plagiostomoceras.*

Rhipsites ZHURAVLEVA, 1978; *R. attenuatus*

Related to *Plagiostomoceras* but with very weakly developed apertural lobe.

Hastula ZHURAVLEVA, 1978; *H. subtilis*

Related to *Michelinoceras* but with dorsal apertural lobe.

Shikhanoceras SHIMANSKY, 1954; *S. sphaerophorum*

Weakly compressed shell with inflated larval shell, and simple aperture, and subcentrical, narrow siphuncle.

Troedssonellidae KOBAYASHI, 1938

Straight, longitudinally ornamented shell with cylindrical siphuncle.

Polygrammoceras FOERSTE, 1928; *P. twenhofeli*
[= *Troedssonella* KOBAYASHI, 1935]

Fine longitudinal striation; relatively narrow siphuncle with weakly inflated connecting rings.

Protokionoceras GRABAU and SHIMER, 1910; *Orthoceras medullare* HALL, 1868

Sparsely spaced longitudinal ribs and fine transverse striation; subcylindrical siphuncle.

Jonesoceras BARSKOV, 1960; *Orthoceras jonesi* BARRANDE, 1874

Densely spaced longitudinal striation and wide, tubular siphuncle.

Mericoceras ZHURAVLEVA, 1978; *M. karagandense*
[= *Stiloceras* ZHURAVLEVA, 1978]

Long and straight shell with fine longitudinal striation and narrow, cylindrical siphuncle.

Bactritidae HYATT, 1884

Long and straight shell with subspherical embryonic shell, narrow, ventral siphuncle, and aperture with conspicuous dorsal lobe.

Bactrites SANDBERGER, 1843; *B. subconicus*

Relatively short shell with circular cross section.

Lobobactrites SCHINDEWOLF, 1932; *Bactrites ellipticus* FRECH, 1897

Long, compressed shell with wedge-like dorsal apertural lobe.

Pseudobactrites FERRONIÈRE, 1921; *P. bicarinatus*

Aperture with deep lateral, ventral, and dorsal sinuses.

Ctenobactrites SHIMANSKY, 1951; *C. costatus*

Dorsal apertural lobe with medial incision.

Arionoceratidae new family

Relatively short shell, straight to slightly curved (most commonly endogastrically) with circular cross section, narrow, cylindrical, central siphuncle.

Arionoceras BARSKOV, 1970; *Orthoceras arion* BARRANDE, 1868
[= *Psilorthoceras* RISTEDT, 1968; *Caliceras* KOLEBABA, 1976]

Straight and smooth shell.

Vericeras KOLEBABA, 1977; *Orthoceras ambigena* BARRANDE, 1874

Fine longitudinal ribbing.

Parakionoceras FOERSTE, 1928; *Orthoceras originale* BARRANDE, 1868

Short, slightly curved shell with ornamentation of laterally bent, longitudinal lamellae.

Choanoceratidae MILLER, 1932

Depressed, exogastric shell; subventral siphuncle with inflated connecting rings; septa conical.

Montyoceras FLOWER, 1941; *M. arcuatum*

Septa parabolic.

Choanoceras LINDSTRÖM, 1890; *C. mutabile*

Septa conical.

Ascoceratidae Barrande, 1867

Exogastric shell with inflated mature living chamber constricted at dorsal side by septa; subventral siphuncle with inflation of connecting rings changing in ontogeny.

Probillingsites Foerste, 1928; *P. welleri*
[= ?*Shamattawaceras* Foerste and Savage, 1927]
Depressed shell with slightly convex few last sutures.

Billingsites Hyatt, 1884; *Ascoceras canadense* Billings, 1857
[= *Schuchertoceras* Miller, 1932; *Lindstroemoceras* Miller, 1932]
Several last camerae dorsally extended, short mature living chamber with subcircular cross section.

Ascoceras Barrande, 1847; *A. bohemicum* Barrande, 1865
[= *Glossoceras* Barrande, 1865; *Aphragmites* Barrande, 1865; *Parascoceras* Miller, 1932]
Compressed, elongate mature living chamber; several last camerae dorsally extended.

Pseudorthoceratidae Flower and Caster, 1935

[= Clinoceratidae Flower, 1946; Sactorthoceratidae Flower, 1946; Hebetoceratidae Flower 1941; Mysterioceratidae Sweet, 1964; Stereoplasmoceratidae Kobayashi, 1934; Proteoceratidae Flower, 1962; Paraphagmitidae Flower, 1935]

Smooth, depressed, straight to endogastrically (?) curved shell; siphuncle between center and convex side, moderately inflated connecting rings.

Clinoceras Mascke, 1876; *C. dens*
[= *Mysterioceras* Teichert and Glenister, 1953; *Stereoplasmoceras* Grabau, 1922; *Isorthocera*, Flower, 1962; *Sactorthoceras* Kobayashi, 1934; *Allanoceras* Barskov, 1959; *Gordonoceras* Teichert and Glenister, 1952; *Palmeroceras* Flower, 1939; *Anastomoceras* Flower, 1939; *Adnatoceras* Flower, 1939; *Bradfordoceras* Flower and Caster, 1935; *Cayutoceras* Flower, 1939; *Ninkiangoceras* Lai, 1965; ?*Arazdajanites* Zhuravleva, 1978; ?*Probatoceras* Zhuravleva, 1978; *Paramooreoceras* Zhuravleva, 1978; *Plenoceras* Zhuravleva, 1978; *Passaloceras* Zhuravleva, 1978; *Tartaroceras* Zhuravleva, 1978; *Xyloceras* Zhuravleva, 1978, *non* Miagkova, 1967]
Straight to slightly curved, relatively short shell with straight, evenly expanding apical part.

Navis Shimansky, 1968; *N. oneraria*
Short, considerably curved shell; poorly known.

Cyrtactinoceras Hyatt, 1900; *Cyrtoceras rebelle* Barrande, 1866
[= *Proteoceras* Flower, 1955; ?*Whitfieldoceras* Foerste, 1932; *Whiteavesites* Foerste, 1932]
Short, curved, bulgy shell; considerably inflated connecting rings (the inflation decreasing in ontogeny), siphuncle shifting in ontogeny from shell wall towards center.

Pseudorthoceras Girty, 1911; *Orthoceras knoxense* McChesney, 1859
[= *Uralorthoceras* Shimansky, 1954; *Mooreoceras* Miller, Dunbar and Condra, 1933; ?*Euloxocera* Miller, Dunbar adn Condra, 1933]
Long and straight shell with slender, curved apical part.

Trematoceras Eichwald, 1851; *Orthoceratites elegans* Münster, 1841
[= *Dolorthoceras* Miller, 1931]
Long, straight shell with straight, parabolically ending apical part.

Rhabdites Zhuravleva, 1978; *R. compressus*
[= ?*Skleroceras* Zhuravleva, 1978; ?*Eridites* Zhuravleva, 1961]
Long, transversally striated and shallowly annulated shell.

Sactoceratidae Troedsson, 1926

[= ?Loxoceratidae Hyatt, 1900; Pseudactinoceratidae Schndewolf, 1943; Carbactinoceratidae Schindewolf, 1943]
Large, mostly straight shell; very strongly inflated connecting rings.

Sactoceras Hyatt, 1884; *Orthoceras richteri* Barrande, 1867
[= *Orthonybyoceras* Shimizu and Obata, 1935; *Podoliceras* Balashov, 1968; *Helenites* Zhuravleva, 1962; ?*Climacoceras* Chen, 1976]
Moderately-sized shell with considerably curved septal necks.

Tunguskoceras Zhuravleva, 1957; *Sactoceras tunguskense* Balaschov, 1955
Moderately-sized, straight shell with rather gently curved septal necks.

Buchanoceras Teichert and Glenister, 1952; *B. graviventrum*
[= ?*Macroloxoceras* Flower, 1957; *Arpaoceras* Zhuravleva, 1962; *Dorkadoceras* Zhuravleva, 1978]
Gently curved septal necks; poorly known.

Pseudactinoceras Schindewolf, 1943; *P. promiscuum*
[= ?*Campyloceras* McCoy, 1844]

Apical part of shell curved; apical part of the siphuncle as in *Clinoceras*, adult connecting rings inflated, with considerably curved septal necks.

Mstikhinoceras SHIMANSKY, 1961; *M. mirabile*

Poorly known.

?***Loxoceras*** MCCOY, 1844; *Orthoceras breyni* FLEMING, 1828

Siphuncle filling almost entire width of apical camerae; siphuncular deposits with distinct radial blocks.

Rayonnoceras CRONEIS, 1926; *R. solidiforme*

[= *Carbactinoceras* SCHINDEWOLF 1935; ?*Paraloxoceras* FLOWER, 1939]

Resembling *Loxoceras* but with siphuncular deposits less distinctly subdivided, in bilateral pattern.

?***Psiaoceras*** SHIMANSKY, 1957; *Gomphoceras hesperis* EICHWALD, 1860

[= ?*Antonoceras* SHIMANSKY, 1957]

Shell considerably flattened on siphonal side, with relatively narrow siphuncle.

Greenlandoceratidae SHIMIZU and OBATA, 1935

Longitudinally striated shell; narrow siphuncle with weakly inflated connecting rings.

Lyecoceras MUTVEI, 1957; *L. gotlandense*

[= *Nebroceras* ZHURAVLEVA, 1978]

Finely striated, weakly curved shell.

Greenlandoceras SHIMIZU and OBATA, 1935; *Sactoceras lineatum* TROEDSSON, 1926

[= *Striatoceras* SHIMIZU and OBATA, 1935; *Stromatoceras* TEICHERT and GLENISTER, 1952; *Metastromatoceras* ZHURAVLEVA, 1957; ?*Eostromatoceras* CHEN, 1976; ?*Pseudokionoceras* ZHURAVLEVA, 1978]

Shell ornamented with coarse, longitudinal ribs; inflated connecting rings.

Tripteroceratidae FLOWER, 1941

[= Allumettoceratidae FLOWER, 1945]

Short, depressed shell with triangular cross section; siphuncle with inflated connecting rings; situated close to the flattened side of the shell; homeomorphic with *Psiaoceras*.

Tripteroceras HYATT, 1884; *Orthoceras hastatum* BILLINGS, 1857

[= *Allumettoceras* FOERSTE, 1926]

Cycloceratidae HYATT, 1900

[= Brachycycloceratidae FURNISH, GLENISTER and HANSMAN, 1964; Scyphoceratidae RUZHENTSEV and SHIMANSKY, 1954; Neptunoceratidae SHIMANSKY, 1956; Dawsonoceratidae FLOWER, 1962; ?Eskimoceratidae SHIMIZU and OBATA, 1935]

Annulated shell with slightly inflated connecting rings; longitudinal ornamentation confined to juvenile stages.

Cyrtocycloceras FOERSTE, 1936; *Cyrtoceras urbanum* BARRANDE, 1866

[= ?*Anaspyroceras* SHIMIZU and OBATA, 1935; *Aclisoceras* ZHURAVLEVA, 1978]

Long, weakly curved shell.

Dawsonoceras HYATT, 1884; *Orthocera annulata* SOWERBY, 1818

Transversally undulated lamellae.

Cycloceras MCCOY, 1844; *Orthocera annularis* FLEMING, 1815

[= *Reticycloceras* GORDON, 1960; *Neocycloceras* FLOWER and CASTER, 1935; *Lopingoceras* SHIMANSKY, 1962; *Pythonoceras* ZHURAVLEVA, 1978]

Juvenile shell with longitudinal ribs.

Brachycycloceras MILLER, DUNBAR and CONDRA, 1933; *B. normale*

[= *Cryptocycloceras* SHIMANSKY, 1968]

Short, straight to slightly curved shell with circular cross section.

Neptunoceras SHIMANSKY, 1949; *N. sakmarense*

[= *Tetrapleuroceras* SHIMANSKY, 1949]

Short and curved shell with trapezoid cross section.

Scyphoceras RUZHENTSEV and SHIMANSKY, 1954; *S. dionysi*

[= *Mariceras* RUZHENTSEV and SHIMANSKY, 1954; *Venatoroceras* RUZHENTESV and SHIMANSKY, 1954; *Dentoceras* RUZHENTSEV and SHIMANSKY, 1954; *Sorinoceras* FLOWER, 1963]

Very short shell strongly curved in early stages.

?***Paraphragmites*** FLOWER, 1943; *P. ascoceroides*

Very short, bulgy shell decreasing terminally in diameter.

?***Aethiosolen*** FLOWER, 1968; *A. whittingtoni*

Short and straight shell; relatively wide siphuncle with weakly inflated connecting rings.

?Monomuchites WILSON, 1961; *M. costalis*
[= *Eskimoceras* TROEDSSON, 1926]
Short, densely annulated shell with annulation spacing equal to chamber length.

Kionoceratidae HYATT, 1900

[= Spyroceratidae SHIMIZU and OBATA, 1936]
Annulated and longitudinally ribbed shell with weakly inflated connecting rings.

Gorbyoceras SHIMIZU and OBATA, 1936; *Orthoceras gorbyi* MILLER, 1894
[= *Stereospyroceras* FLOWER, 1955; *?Metaspyroceras* FOERSTE, 1932]
Relatively short, weakly curved shell, shallowly annulated entirely.

Kionoceras HYATT, 1884; *Orthoceras doricum* BARRANDE, 1868
[= *Mimetoceras* ZHURAVLEVA, 1978]
Resembling *Gorbyoceras* but with annulation confined to apical part of shell, and with coarse ribbing.

Cyrtorthoracoceras TURNER, 1954; *Cyrtoceras tuberculatum* MCCOY, 1844
Curved, non-annulated shell with coarse longitudinal ribs.

Cornuella SHIMANSKY, 1968; *Cycloceras ornatum* EICHWALD, 1860
Resembling *Cyrtothoracoceras* but with coarse annulation.

Spyroceras HYATT, 1884; *Orthoceras crotalum* HALL, 1861
[= *Dawsonocerina* HORNY, 1956; *Cedarvilleoceras* SHIMIZU and OBATA, 1935; *Perigrammoceras* FOERSTE, 1924; *Leurocycloceras* FOERSTE, 1928 (type species only); *Raphiceras* ZHURAVLEVA, 1978; *Ryspoceras* ZHURAVLEVA, 1978; *?Plagiocycloceras* ZHURAVLEVA, 1978; *Daedaloceras* ZHURAVLEVA, 1978]
Long, straight, annulated and longitudinally striated shell.

Suborder **Lituitina** new suborder

Diagnosis. — Subcentral, cylindrical siphuncle with long septal necks. Exogastric coiling of the apical part of shell, extended in phylogeny over later ontogenetic stages; funnel sinus narrow and deep, except in the most primitive forms.

Remarks. — The Lituitina differ from homeomorphic representatives of the Tarphyceratida and Nautilida in their narrow apertural sinus constricted by lateral lappets, and the funnel sinus. The boundary between the Lituitina and Orthoceratina is traced rather arbitrarily, as the genus *Rhynchorthoceras* and whole family Sinoceratidae may be assigned to the suborder Orthoceratina as well as to the Lituitina.

Phylogeny (fig. 55). — The Ordovician lituitids range in shell shape from almost straight to tightly coiled. The dominant opinion is presently that the coiled forms are primitive and that the Lituitina are descendants of the Tarphyceratida (SWEET 1964, FLOWER 1976*a*). However SCHINDEWOLF (1942, see SWEET 1958) derived the Lituitina from the Orthoceratida and claimed that the ancestral lituitids were orthoconic. SWEET (1958) reviewed the stratigraphic succession of the early lituitids and demonstrated that SCHINDEWOLF'S hypothesis is incompatible with the record.

The keystone problem in the phylogenetic interpretation of the Lituitina is the age attribution of erratic boulders of Baltic origin that yielded most described representatives of this group. The crucial data have been derived from red neritic limestones of the *Paroistodus originalis* Zone (Volkhovian BIIβ, Late Arenigian). The only representative of the Lituitina that occurs in boulders of the Volkhovian age is *Rhynchorthoceras* aff. *beyrichi* (REMELE, 1880) (fig. 50a-c; pl. 1, 6). It resembles its congeners in its weakly exogastrically curved shell and subventral siphuncle. There is no funnel sinus, at least in the juvenile stages. *R.* aff. *beyrichi* shows relatively short septal necks, which contrasts to its later congeners with known siphuncular structure. The next-younger lituitid species is *Holmiceras kjerulfi* (BRØGGER, 1882) from the *Asaphus* Shale or lower *Endoceras* Limestone of Norway (SWEET 1958) time equivalent to the Early Kundan (latest Arenigian). The apical part of its shell is curved. According to SWEET (1958), it presents at most a single loosely coiled whorl but this is probably an overestimate, as suggested by the protoconch size of known Lituitina.

The new data on the stratigraphic distribution of the Lituitina seem thus to corroborate SCHINDEWOLF's hypothesis (1942, see SWEET 1958). Additional evidence is given by a comparison of the siphuncular structure in the sinoceratids (fig. 53) and the lituitids (figs. 50-52). These two groups are unique among the nautiloids in that their connecting rings underwent destruction while the organism was still alive, as well as in their interconnected siphuncular and cameral deposits (HOLM 1885, SWEET 1958).

There has been much controversy about the functional interpretation of the phragmocones assigned to the family "Leurocycloceratidae". These forms are distinctive in their continuous cameral and siphuncular deposits and the absence of preserved connecting rings. The septal necks are long, indicating a cylindrical form of the siphuncle. Unfortunately, the type species of the genus *Leurocycloceras* and, by implication, of the whole family, *L. raymondi* FOERSTE, 1928, was described from an isolated living chamber. The ornamentation makes impossible its reference to any of its congeners or members of the family. This specimen may actually be corroded and deprived of a longitudinal ornamentation and belong to a species of the genus *Spyroceras* (= *Dawsonocerina*). The nautiloids with "*Leurocycloceras*"-like structure never show shell annulations. I propose to attribute the forms assigned thus far to the Leurocycloceratidae, exclusive of the type species of *Leurocycloceras*, to the family Sinoceratidae.

The absence of connecting rings from the sinoceratid phragmocones was the basis of the assumption (FLOWER 1941*c*, FISHER and TEICHERT 1969, KOLEBABA 1974) of a cameral mantle in the Sinoceratidae. This idea was extended to encompass all the nautiloids with cameral deposits (see FISHER and TEICHERT 1969) even though most nautiloids show normally developed connecting rings hindering the soft body from direct contact with the hypothetical cameral mantle. Furthermore, cameral deposits occur also in belemnite phragmocones. The hypothesis of cameral mantle implies a difference in phragmocone function between the Paleozoic nautiloids and Recent cephalopods and hence, necessitates a rejection of phragmocone homology between these groups. The calcareous deposits are usually confined to the apical part of the phragmocone and hence, are to be regarded as a gerontic structure; an apex filled up with deposits could not function as an active hydrostatic organ. A destruction of the connecting rings, like that recorded in the Sinoceratidae, was without any crucial functional significance; the more so since their wall probably was very thin and organic in structure. Having no wall, the siphon may nonetheless act efficiently and the cameral liquid may produce a solid secondary layer at the septal walls and necks.

The affinity in phragmocone structure between the Sinoceratidae and Lituitidae may not be of much biological significance but is, nonetheless, indicative of a phylogenetic relationship. All known typical sinoceratids are much younger in geological age than *Rhynchorthoceras* aff. *beyrichi*. The latter species is also more primitive in the length of septal necks (fig. 50b-c). One may thus conclude that *Rhynchorthoceras* evolved directly from the Orthoceratidae, whereas the other Sinoceratidae are its descendants or close relatives. The former hypothesis is supported by the much longer septal necks observed in later species of *Rhynchorthoceras* (fig. 50d-e) postdating *R.* aff. *beyrichi* but preceding the genus *Sinoceras* and other typical sinoceratids. *Sinoceras* appears to be so close to *Rhynchorthoceras* both in morphology and in stratigraphic position that one may consider it as a descendant of the latter. The position of the other sinoceratids remains unclear. In fact, one can not reject the possibility that septal necks underwent elongation also in another lineage derived from the Orthoceratidae. The orthoconic lituitids placed in *Rhynchorthoceras* persisted up to the Llandeilian (SWEET 1958, REMELE 1880, 1882). *Sinoceras s. s.* differs from *Rhynchorthoceras* in its straight shell with central siphuncle and its ornamentation consisting of irregular growth lines. Its stratigraphic range is rather poorly known (YÜ 1930, CHEN and LIU 1974). There are some specimens of *Sinoceras chinense* (FOORD, 1888) from J-tschang, China, at the Wrocław University. The associated limestone yielded a conodont species, *Dapsilodus viruensis* (FÅHRAEN), ranging from the Llaneiilian

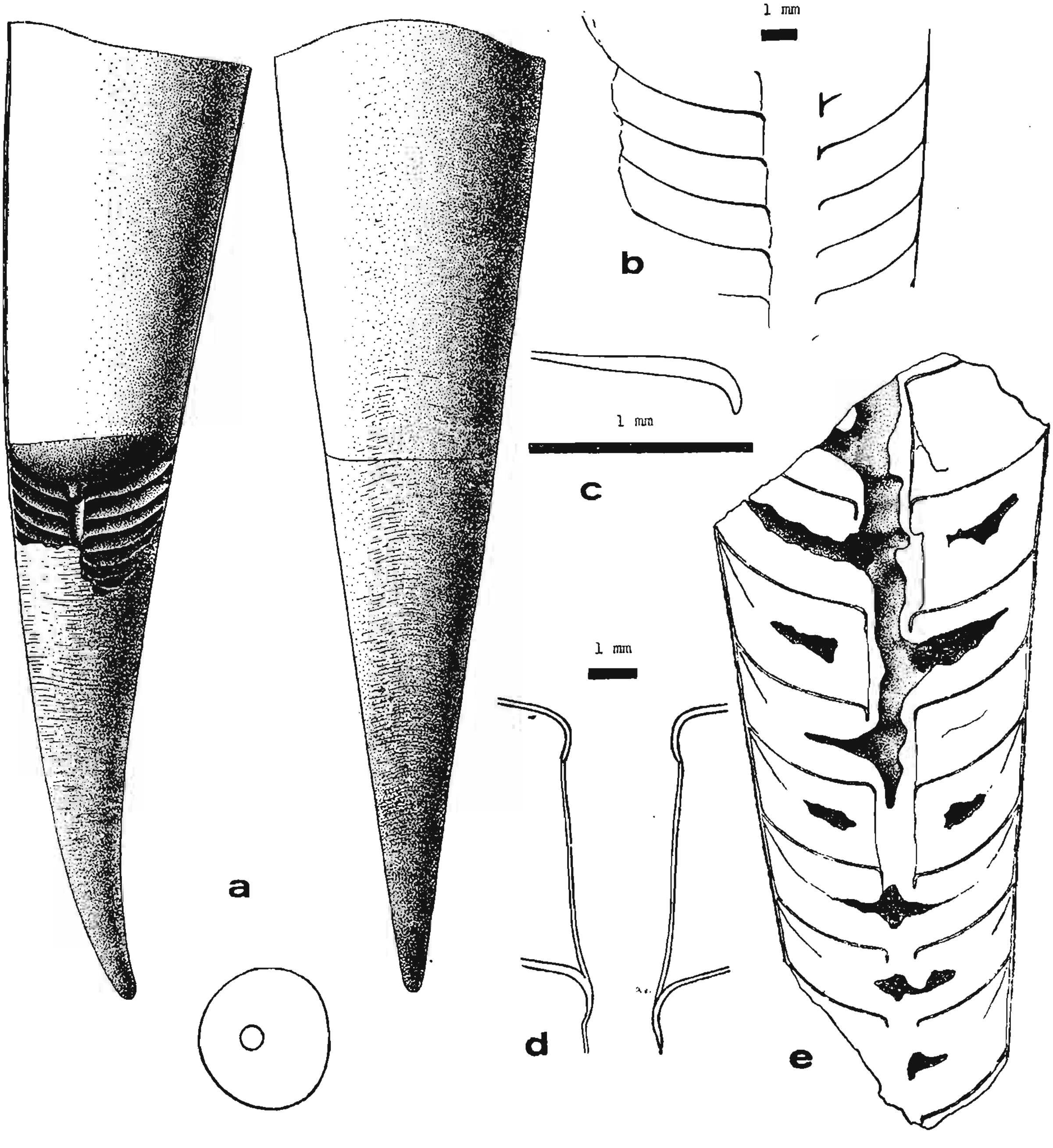


Fig. 50

Rhynchorthoceras aff. *beyrichi* (REMELE, 1880); erratic boulder, *P. originalis* Zone, Volkhovian, Opatów, Poland; *a* Reconstruction of the juvenile shell, mostly from the specimen IG 8. II. 260 (pl. 39: 1); *b* section through a phragmocone, IG 8. II. 254 (pl. 39: 5); *c* septal neck, same specimen. *Rhynchorthoceras conicum* (HISINGER, 1827); *d* Longitudinal section through a siphuncle, ZPAL N/820, boulder E-229, Kundan (?), Rozewie; *e* reconstruction of a phragmocone fragment, ×2, ZPAL N/882 (pl. 39: 3), boulder E-224, Aserian, Rozewie.

up to the end of the Ordovician in the Baltic area. *Tyrioceras kjerulfi* STRAND, 1934, may be placed in the same nautiloid group. It is known, however, from an isolated living chamber only, so that its phylogenetic relations cannot be recognized.

The systematic classification of the Silurian "*Leurocycloceras*" is rather complex but nevertheless, the genus is very poorly known because most species are based upon unidentifiable shell fragments (FLOWER 1941, FOERSTE 1928a). The youngest in time of this group are "*L.*" *superplenum* COLLINS, 1969, in the Siegenian of Canada, and *Sinoceras riphaeum* ZHURAVLEVA, 1978, in the Eifelian of the Urals. "*L.*" *superplenum* supposedly had a long and smooth shell like that described from the Ludlovian of Bohemia under the name "*Orthoceras*" *evanescens* BARRANDE, 1866. Much better known is another Silurian genus, *Murchisoniceras*, showing

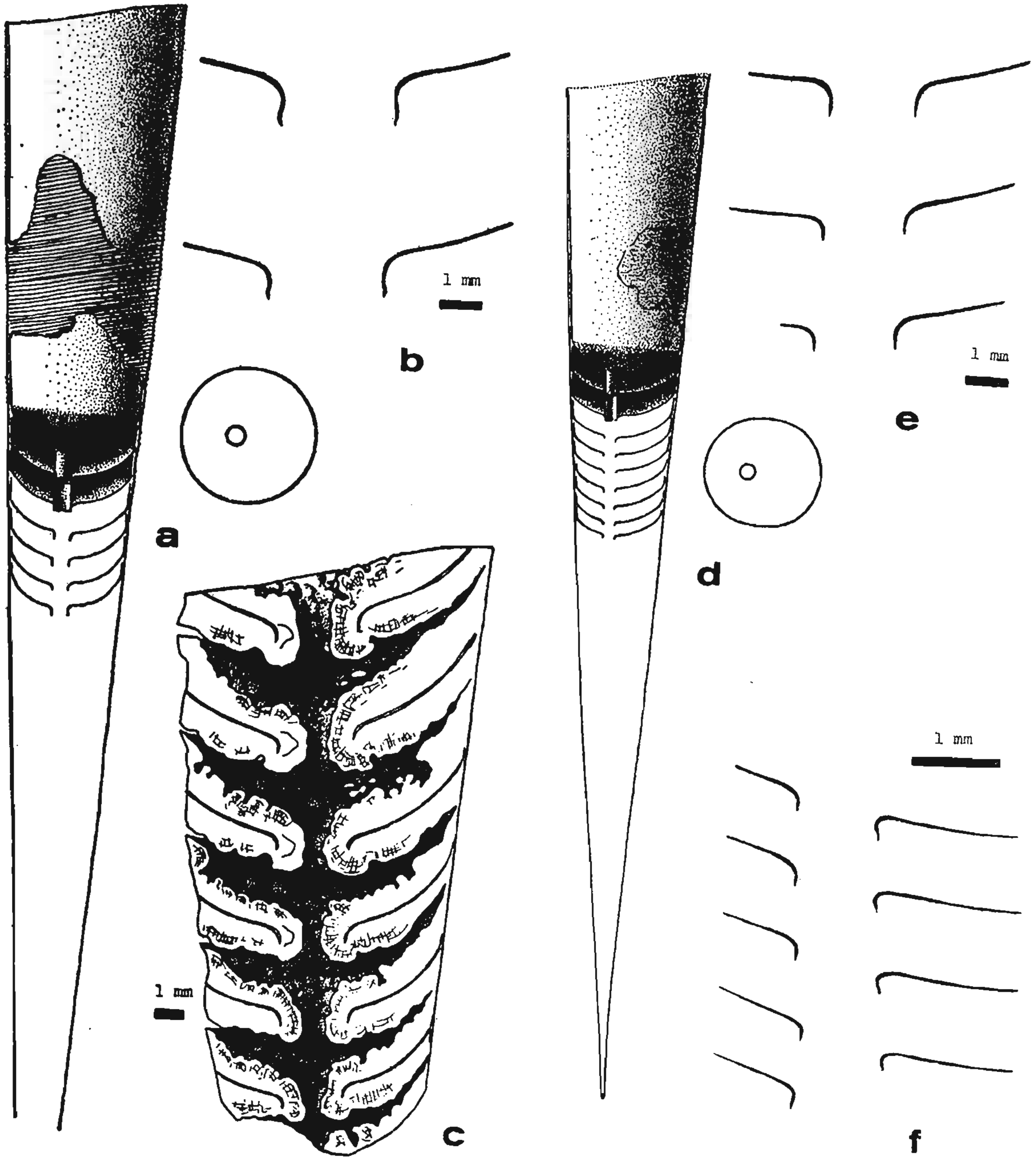


Fig. 51

Murchisoniceras aff. *murchisoni* (BARRANDE, 1868); erratic boulders of the Beyrichienkalk, Přidolian, Poland; *a* Reconstruction of the juvenile living chamber; *b* section through a siphuncle, ZPAL N/687 (pl. 30: 1), Rozewie, *c* reconstruction of a phragmocone fragment, ZPAL N/683 (pl. 31: 4), Wieżyca. *Murchisoniceras* cf. *obsolescens* (BARRANDE, 1868); Přidolian, erratic boulders, Poland; *d* Reconstruction of the juvenile specimen; *e* section through a siphuncle, ZPAL N/678, Orłowo; *f* section through a siphuncle, ZPAL N/679 (pl. 31: 2), Międzyzdroje.

a compressed, relatively short shell with septa spaced more densely and septal necks shorter than in "*Leurocycloceras*". The latter two characters may be interrelated. In the Bohemian Ludlovian, *Murchisoniceras* is represented by two species, *M. murchisoni* (BARRANDE, 1866) with large, weakly compressed shell, and *M. obsolescens* (BARRANDE, 1866) with smaller and more compressed shell. *M. murchisoni* shows deposits of the "*Leurocycloceras*" type, while the nature of the deposits in *M. obsolescens* remains unknown.The evolutionary lineage of *M. obsolescens* may be continued by *M. taeniale* (BARRANDE, 1866) from the Přidolian of Bohemia. Both the lineages have also been recorded in the Přidolian erratic boulders in the Baltic area (fig. 51). *Mariceras pragense* KOLEBABA, 1974, the morphology of which is considered by KOLEBABA as an evidence for the existence of a cameral mantle, is in my opinion based upon juvenile shell fragments attributable to *Murchisoniceras*.

The enigmatic species *Sphooceras truncatum* (BARRANDE, 1868), reasonably recognized as the only member of a distinct family, resembles *Murchisoniceras* in its compressed shell and relatively long septal necks. Since the original work of BARRANDE appeared (1868), this species is widely considered as undergoing shell truncation in ontogeny (FLOWER 1962, SWEET 1964). All specimens show a blunt apex and very short phragmocone including only a few air chambers. The ovate apical part of the shell is smooth, except for indistinct growth lines like those recorded on the adult shell. It is distinguished by a prominent growth-line (pl. 31: 5-7). A corroded apex reveals the underlying layer of shell wall exhibiting an ornamentation very similar to that observed at the cephalopod wrinkle layer. A more intense corrosion reveals the microstructure of secondary deposits filling up the apex. The deposits consist of fine radial lamellae interconnected through lateral anastomoses, showing thus a microstructure analogous to that observed in the cameral deposits of *Arthrophyllum* (see BABIN 1966). A comparison of the apical deposits of *S. truncatum* to those present in the embryonic shell of similarly preserved *Psilorthoceras capillosum* (KOLEBABA 1975, pl. 2: 2) corroborates this interpretation. The mould of the apical deposits of *Sphooceras* is usually regarded as a truncational callus. This is however incompatible with the shell morphology of *Sphooceras*. In fact, one can hardly imagine so regular a pattern of regeneration of the apex, even taken for granted the existence of a cameral mantle. One can not suggest any reasonable mechanism of shell truncation (this is also the case with the Ascoceratidae).

The apical part of the shell of *Sphooceras* appears to be a protoconch, an interpretation supported by the lack of any broken off orthoceratid shell fragments that might be referred to *Sphooceras*. However, if we assume that the interpretation of the apex as a protoconch of *Sphooceras* is correct, another question arises. If the entire ovate apical part of the shell is an embryonic shell, the egg must have been greater in size than the mature shell aperture! Since this could not be the case, the larva must have developed outside of its egg capsule; it must have resembled a cap-like snail in morphology because it could not have been provided with a functional phragmocone. A short adult shell with parabolic apex was certainly of much hydrodynamic advantage. Ontogenetically, the septal necks became more and more curved in outline, siphonal segments probably increased in inflation, but this cannot be ascertained because their wall is never preserved (pl. 31: 6).

Sphooceras has thus far been recorded in the Ludlovian of Bohemia and Gotland. The inclusion of a Silurian nautiloid from the Podolia in this genus (KISIELIEV and BALASCHOV 1968, BALASCHOV 1975) is a misinterpretation. In turn, "*Ecdyceras*" *foerstei* FLOWER, 1946, from the Ashgillian Arnheim Formation of Kentucky could be assigned to *Sphooceras*, but not with certainty because the only known specimen is very poorly preserved.

The structure of the cameral deposits observed in *Gorgonoceras*, *Arthrophyllum*, *Coralloceras*, and *Exopoceras* may indicate a phylogenetic relationship of these genera to *Murchisoniceras* and *Sphooceras*. The four genera are, however, so poorly known that one can only speculate (note that the structure of cameral deposits may lack any diagnostic value). The genus *Exo-*

poceras, described by Stanley and Teichert (1976) from fragmentary and poorly preserved material, shows (as judged from a schematic reconstruction by these authors) a siphuncle similar to that observed in *Orthoceras* and hence, quite different from that typical of *Gorgonoceras*

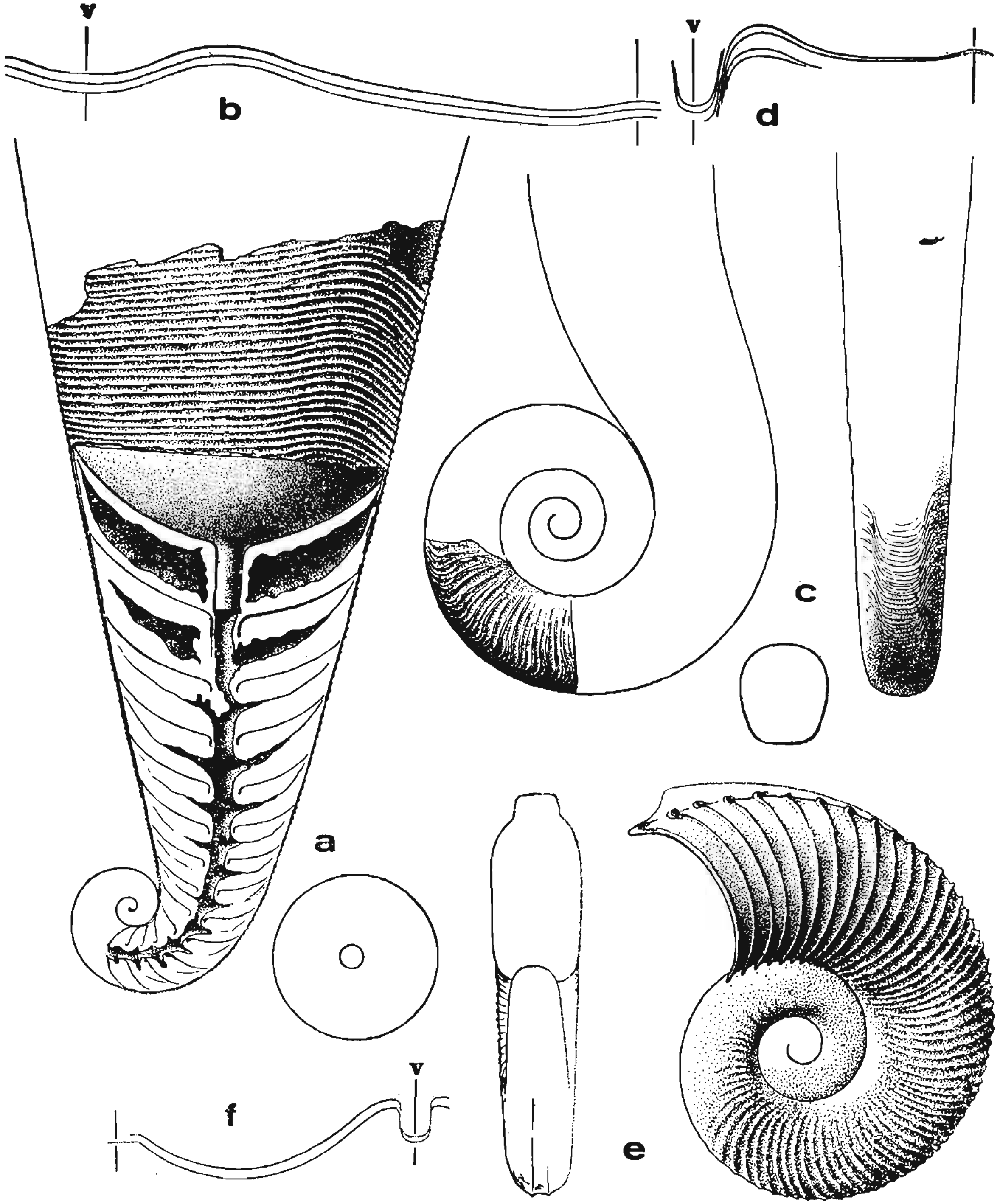


Fig. 52

Ancistroceras torelli (Remele, 1880); boulder E-085, *E. lindstroemi* Zone, Uhakuan, Mochty by Warsaw, Poland; *a* reconstruction of apical part of adult shell (see pl. 40: 1-2); *b* growth lines. *Lituites (Angelinoceras) latum* Angelin, 1880; erratic boulder, Aserian (?), Zgierz; *c* Reconstruction of a shell, ZPAL N/833 (pl. 40: 3), spiral part after Neben and Krueger (1971); *d* growth lines. *Cyclolituites* sp. (?); IG 8. II. 196 (pl. 38: 3-4), *Orthis sandstone*, Kundan (?), Międzygórz by Sandomierz, Poland, *a* Reconstruction of the shell, *f* growth lines.

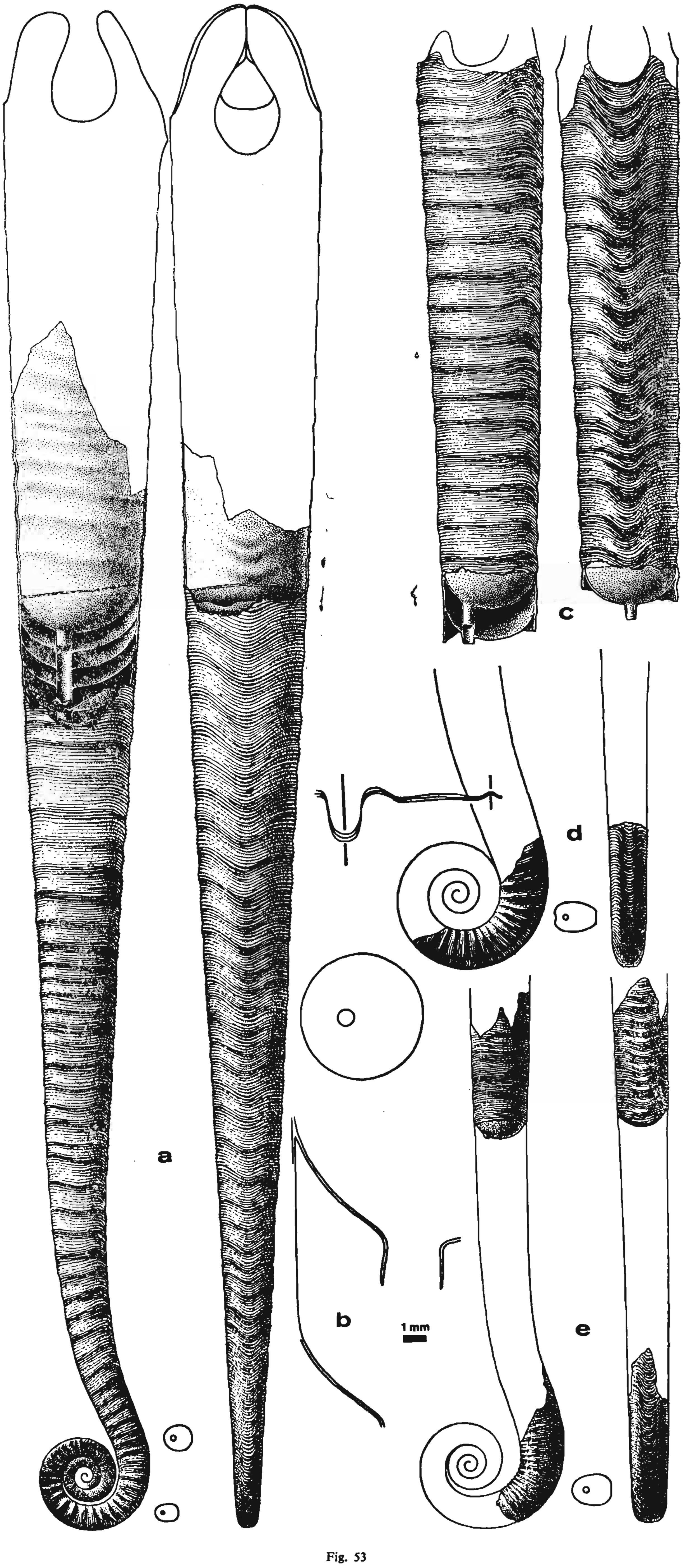


Fig. 53

Lituites cf. *lituus* (Montford, 1808); boulder E-236, *E. robustus* Zone, Garcz by Kartuzy; *a* Reconstruction of the adult specimen, based on the specimen ZPAL N/851 (pl. 41: 1). *Lituites discors* Holm, 1891; *E. reclinatus* Zone, Lasnamägian; *a* Longitudinal section through a siphuncle, ZPAL N/840 (pl. 40: 5), boulder E-149, Międzyzdroje; *e* reconstruction of initial part of the shell, after fragmentary specimens collected mostly from the boulder E-252 inset — shell ornamentation after the specimens ZPAL N/838 (pl. 40: 7) and N/834 (pl. 40: 10). *Lituites perfectus* Wahlenberg, 1840; *E. lindstroemi.* Zone, Uhakuan; *c* Reconstruction of the adult living chamber, from the specimen ZPAL N/841 (pl. 41: 4), boulder E-231, Garcz by Kartuzy; *d* reconstruction of initial part of the shell and the growth lines, from the specimen ZPAL N/839 (pl. 41: 5), erratic boulder, Orłowo.

(see ZHURAVLEVA 1961). The radial lamellar structure of its cameral deposits may be an artifact of fossilization, as suggested by the somewhat analogously preserved siphuncular structures of some actinoceratids (TEICHERT and CRICK 1974, WADE 1977) and endoceratids (BALASCHOV 1960). *Coralloceras* (?) *lithuanica* SALADZHIUS, 1966, is a corroded shell fragment of *Murchisoniceras*.

Holmiceras bennetti FLOWER, 1975, from the Whiterockian (? Kundan) Table Head Limestone, New Foundland, appears to be closely related to the oldest lituitid species with curved apical shell part, *H. kjerulfi*. The apical part of shell of *H. bennetti* presents probably a complete whorl of fairly small diameter. These two forms are also closely related to *Lituites praecurrens* HOLM, 1891, from the Grå Vaginatumkalk (Middle Kundan) of Öland. The group under discussion is intermediate in morphology between and supposedly ancestral to the genera *Ancistroceras* (with very wide shell) and *Lituites* (with slender shell). Species of *Ancistroceras* are widespread in the Baltic area but most of their records are in poorly dated erratic boulders (REMELE 1880, NEBEN and KRUEGER 1971). The well dated records are confined to the Lasnamägian and Uhakuan (SWEET 1958). Only two species can justifiably be distinguished in that stratigraphic interval, *Ancistroceras undulatum* (BOLL, 1857) and *A. torelli* (REMELE, 1880), differing mostly in the size of the coiled part of the shell and in shell expansion rate. The apical part of the shell described under the name *Cyclolituites kjerulfi* SWEET, 1958, may be assigned to *A. undulatum*. In fact, it does not display any feature indicative of its evolutionary advancement, which might justify its attribution to the genus *Cyclolituites*, while the shell diameter resembles very closely that of apical parts of *A. undulatum*.

The genus *Lituites* is represented in the Baltic area by several successive species. Their close stratigraphic relationships suggest that they belong, at least in part, to a continuous evolutionary lineage (SWEET 1958). However, the available morphological data are insufficient to permit recognition of evolutionary trends or demonstration of evolutionary continuity (fig. 54). More detailed research is needed to determine whether the Baltic *Lituites* comprise a single evolutionary lineage or allopatrically arisen migrants from other areas.

Relatively breviconic "*Holmiceras*" *praecurrens* (HOLM, 1891) from the Middle Kundan is succeded by *Lituites* (*Angelinoceras*) *latum* ANGELIN, 1880 from the Segerstad Limestone (Aserian). This species, probably conspecific with *L. hageni* REMELE, 1880, shows considerable variability in the size, whorl section, and whorl expansion rate of the coiled initial part of the shell. Diameter of coiled shell of *L. latum* ranges from 37.0 mm to 51.5 mm (collections of the Naturhistoriska Riksmuseet, Stockholm) and significantly exceeds diameter of corresponding shell parts of other lituitids. Shape of the shell aperture strongly changes between coiled and straight parts of the shell — deep ventral sinus almost completely disappears. Adult shell is rather robust (JAANUSSON and MUTVEI 1953); a shape of its aperture is unknown. The growth lines change during ontogeny of *L.* (*Angelinoceras*) just as in *L.* (*Lituites*). The two subgenera resemble each other also in shell cross section and position of the siphuncle. Thus, the only difference between them is in size of the coiled part of shell (fig. 54). I believe that it is not sufficient reason for their separation at the genus level. The latest record of supposed *L.* (*Angelinoceras*) is in the Llandeilian of Norway (SWEET 1958).

L. tornquisti HOLM, 1891, from the uppermost Segerstad Limestone (Aserian) is the earliest representative of *Lituites s. s.* It exhibits two pairs of well developed lateral lappets at the adult aperture (HOLM 1891; JAANUSSON and MUTVEI 1953). The successive form is *L.* (*Trilacinoceras*) *discors* HOLM, 1891, from the lower Seby limestone (Lasnamägian) characterized by more elongated adult shell (HOLM 1891). *L. discors* is succeeded in the upper Seby limestone by *L. lituus* MONTFORD, 1808, with larger adult shell (g. 53a and pl. 41: 1-3; NOETLING 1882; NEBEN and KRUEGER 1971). The latter species displays a distinct dorsal sinus at the mature aperture. This is the only basis for separation *L. discors* and *L. lituus* between different genera by SWEET (1958). Population of *L. lituus* from the upper Seby limestone of Öland shows a range

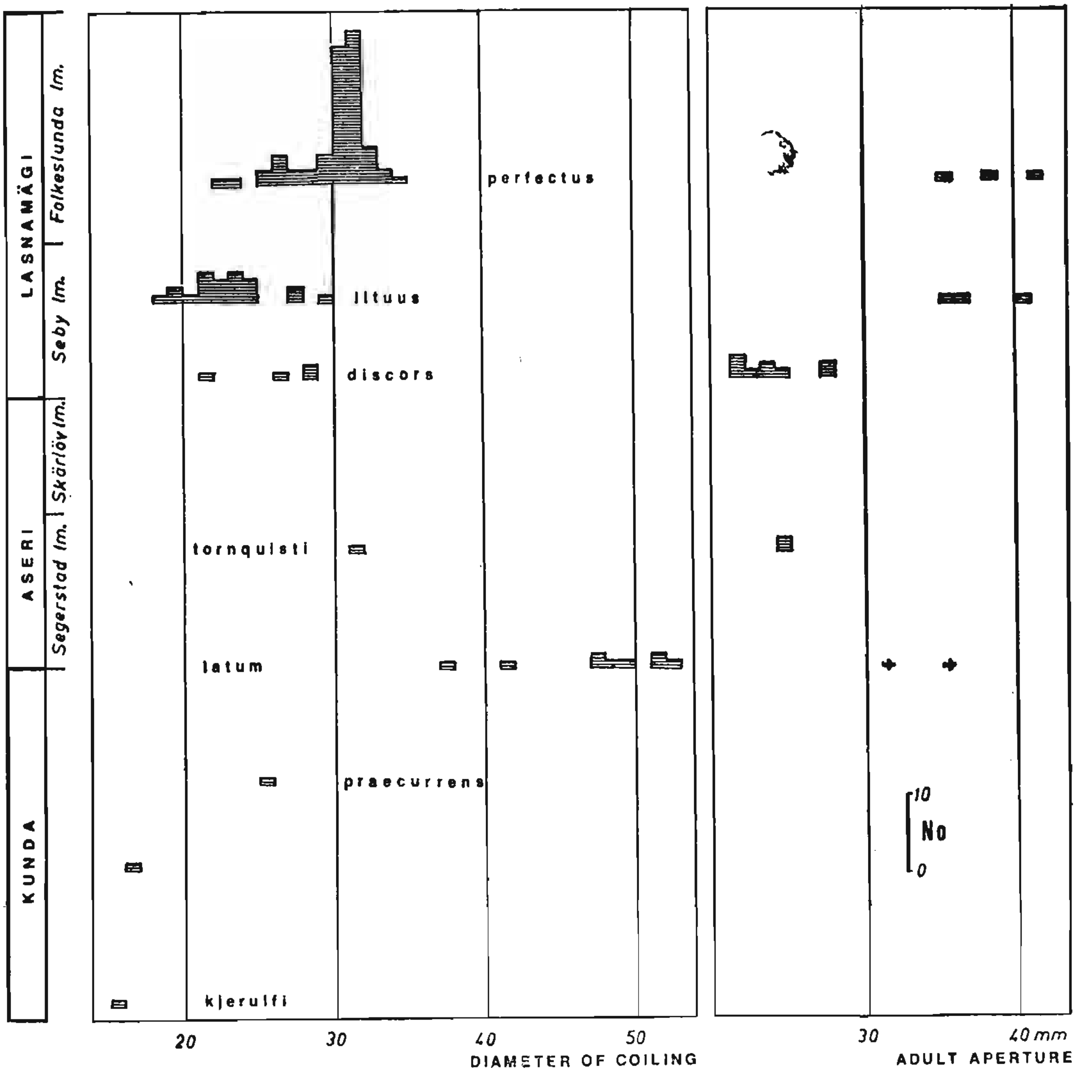
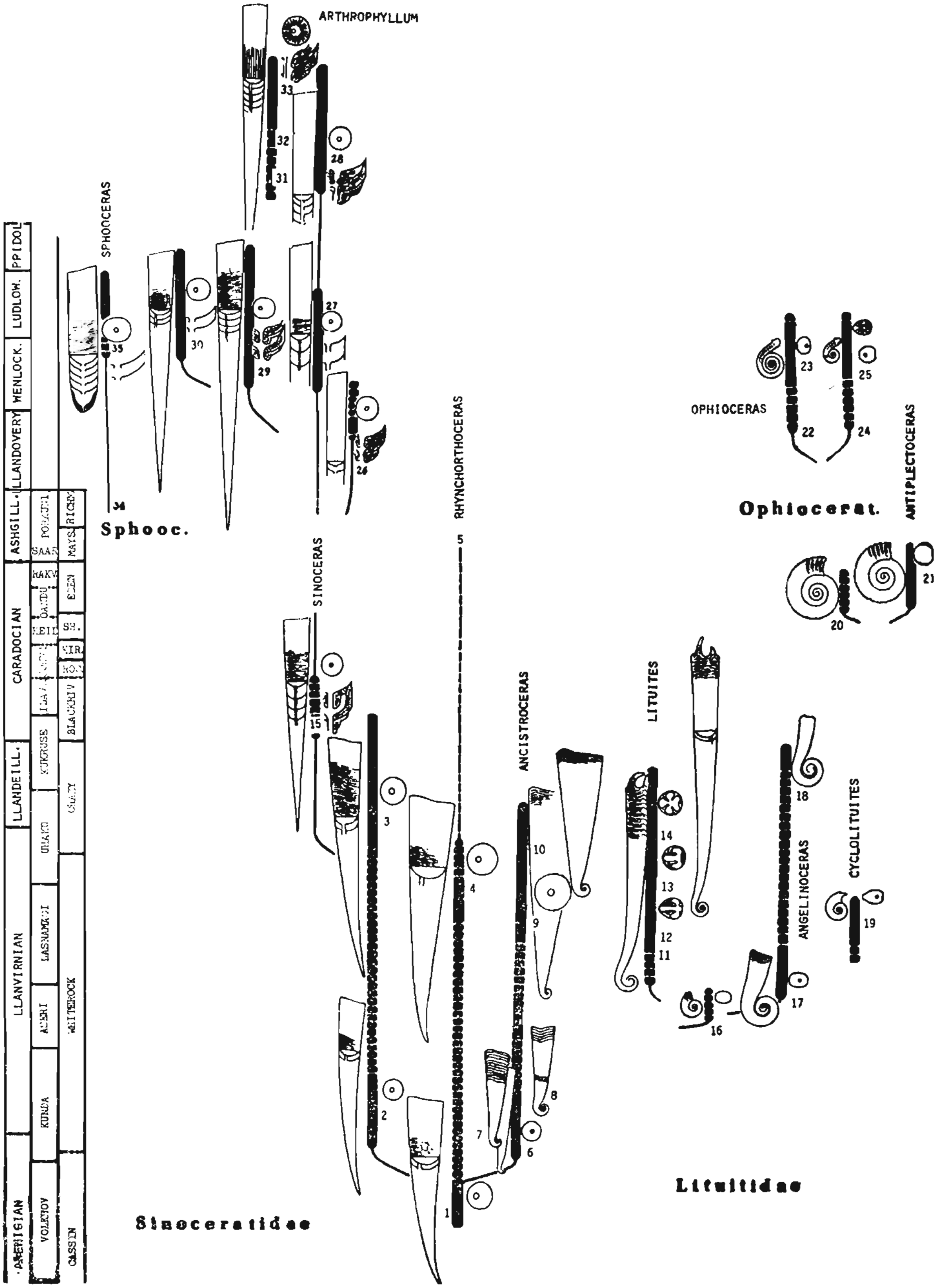


Fig. 54
Size-frequency distribution in the samples of *Lituites* species from Sweden. Based on specimens housed at Naturhistoriska Riksmuseet, Stockholm.

Fig. 55
Hypothetical phylogenetic relationships among members of the suborder Lituitina; 1 *Rhynchorthoceras* aff. *beyrichi* (Remele) (fig. 50a-c; pl. 39: 1, 5); 2 *Rhynchorthoceras conicum* (Hisinger) (fig. 50d, c; pl. 39: 3, 4); 3 *Rhynchorthoceras helgoyense* Sweet; 4 *Rhynchorthoceras beyrichi* (Remele), *R. zaddachi* Mascke (pl. 39: 6, 7); 5 *Tyrioceras kjerulfi* Strand; 6 *Holmiceras kjerulfi* (Brøgger); 7 *Holmiceras bennetti* Flower; 8 *Lituites praecurrens* Holm; 9 *Ancistroceras undulatum* Boll, *Cyclocliuites kjerulfi* Sweet; 10 *Ancistroceras torelli* (Remele) (fig. 51a, b; pl. 40: 1-2); 11 *Lituites tornquisti* Holm; 12 *Trilacinoceras discors* (Holm) (fig. 52b, c; pl. 40: 4-10), *T. norvegicum* Sweet; 13 *Lituites lituus* (Montford) (fig. 52a; pl. 41: 1-3); 14 *Lituites perfectus* Wahlenberg (fig. 52c, d; pl. 41: 4, 5); 15 *Sinoceras chinense* Foord; 16 *Cyclolituites americanus* (Hyatt); 17 *Angelinoceras hageni* (Remele) = *A. latum* (Angelin) (fig. 51c, d; pl. 40: 3); 18 *Angelinoceras* sp. Sweet; 19 *Cyclolituites lynnensis* (Kjerulf), *C. lynceus* Holm, *C. applanatum* Remele; 20 *Antiplectoceras shamttavaense* (Parks); 21 *Antiplectoceras askerense* Strand; 22 *Ophidioceras welleri* Foerste; 23 *Ophioceras rudens* Barrande = = *O. rota* Lindström; 24 *Ophioceras simplex* Barrande = *O. reticulatum* Angelin; 25 *Ophidioceras wilmingtonense* Foerste; 26 *Leurocycloceras brucense* (Williams), *L.* cf. *niagarense* Foerste; 27 *Orthoceras evanescens* Barrande; 28 *Leurocycloceras superplenum* Collins; 29 *Murchisoniceras murchisoni* (Barrande) (fig. 53a-c; pl. 30: 1, 2; 31: 1, 4), *Mariceras pragense* Kolebaba; 30 *Murchisoniceras obsolescens* (Barrande) (fig. 53d, f; pl. 31: 2), *Orthoceras taeniale* Barrande; 31 *Esopoceras sinuosum* Stanley and Teichert, *Lamellorthoceras gracile* Termier and Termier; 32 *Arthrophyllum kahlbergense* Dahmer, *Coralloceras coralliforme* (Le Maitre); 33 *Gorgonoceras visendum* Zhuravleva; 34 *Ecdyceras foerstei* Flower; 35 *Sphooceras truncatum* (Barrande).

of variability in the diameter of coiled shell parts from 21.0 to 27.0 mm (mean 23.7 mm, S = = 1.99, 11 specimens from the collection of Naturhistoriska Riksmuseet measured). The youngest known species of *Lituites*, *L. perfectus* WAHLENBERG, 1818, from the Folkeslunda



limestone (fig. 52c-d and pl. 41: 4-5; HOLM 1891; SWEET 1958) shows range of variability of this character overlapping with *L. lituus* (from 22.5 mm to 35.5 mm, 37 specimens measured) but they differ significantly in mean value (30.3 mm, S = 3.09). Standard deviations do not overlap (fig. 54) so it is sufficient for separation of temporal subspecies or species according to the rule proposed by DZIK and TRAMMER (1980).

As judged from the oscillations observed in camerae length in phragmocones of orthoconic nautiloids (figs 3m, 6, 33d), which can be regarded as seasonal, the rate of shell increase in length approximates 20 cm per year. There are indeed some 350 growth lines per 20 cm shell length interval in *Lituites*, but it would be presumptuous to consider this result as sufficient evidence without corroboration from more comprehensive investigations.

The genus *Cyclolituites* shows a completely coiled adult shell. The species *C. lynnensis* (KJERULF, 1865), *C. applanatus* (REMELE, 1880), and *C. lynceus* (HOLM, 1891), all described from the Lasnamägian of the Baltic area, can hardly be recognized as distinct. In turn, *C. kjerulfi* SWEET, 1958, appears to be the apical part of *Ancistroceras*. *C. americanus* HYATT, 1894, from the St. George Beds of New Foundland (FLOWER 1975), also seems to be an immature specimen; it is probably attributable to *Angelinoceras*, which is consistent with its stratigraphic position (? Kundan). In turn, a problematic fossil from the *Orthis* sandstone of Międzygórz by Sandomierz, Poland (fig. 52e-f, pl. 38: 3-4), may be assigned to *Cyclolituites*. However, this classification must be treated with caution because of the absence of preserved septa and its early age (? Early Kundan). In fact, one can hardly reject the possibility that this is a *Angelinoceras* or even a bellerophontid monoplacophoran.

The Ophioceratidae show an almost completely coiled adult shell. They resemble the Lituitidae in shell ornamentation as well as in their aperture with two ventrolateral lappets and a deep funnel sinus. In addition to a few Silurian species, this group may also include *Antiplectoceras* from the Upper Ordovician of North America (FOERSTE and SAVAGE 1927), Norway (STRAND 1935), and Siberia (BALASCHOV 1962). The most complete known specimen of *Antiplectoceras* differs from the Silurian species of *Ophioceras* exclusively in its larger shell. The genus *Ophioceras* is known from the Silurian of North America (FOERSTE 1930), China (CHEN and LIU 1974, "*Systrophoceras circulare*"), Gotland (LINDSTRÖM 1895), Poland (TOMCZYKOWA 1958), and Bohemia (BARRANDE 1865, TUREK 1972). I was able to examine the rich ophioceratid collection of Barrande, mostly from the Ludlovian of Bohemia and stored at the Narodní Muzeum, Prague. *Ophioceras rudens* (BARRANDE, 1865) and *O. simplex* (BARRANDE, 1865), differing in shell size, position of siphuncle, and whorl number. It is noteworthy that the ophioceratids described by LINDSTRÖM (1895) from the coeval strata of Gotland also belong to only two species, each possibly conspecific with a Bohemian form. This is also the case with the North American ophioceratids.

Proposed systematics. —

Sinoceratidae SHIMIZU and OBATA, 1935

[= Leurocycloceratidae *sensu* SWEET, 1964; ?Lamellorthoceratidae TEICHERT, 1961]

Straight to weakly curved shell with subcentral siphuncle and weakly developed ventral funnel sinus.

Rhynchorthoceras REMELE, 1881; *Lituites Breynii* BOLL, 1857
[= ?*Tyrioceras* STRAND, 1934]

Slightly exogastric shell with ventro-central siphuncle.

Sinoceras SHIMIZU and OBATA, 1935; *Orthoceras chinense* FOORD, 1888
[= *Leurocycloceras* auctorum (*non L. raymondi* FOERSTE, 1928])

Shell with circular section and very long septal necks.

Murchisoniceras BABIN, 1966; *Orthoceras murchisoni* BARRANDE, 1865

Short and compressed shell with relatively short septal necks.

Arthrophyllum BEYRICH, 1950; *Orthoceratites crassum* ROEMER, 1843
Lamellorthoceras TERMIER and TERMIER, 1950; *L. vermiculare*

Gorgonoceras Zhuravleva, 1961; *G. visendum*
Coralloceras Zhuravleva, 1962; *Orthoceras coralliforme* Le Maitre, 1950
Esopoceras Stanley and Teichert, 1976; *E. sinuosum*
All these genera very poorly known; deposits as in *Murchisoniceras* but radial in structure.

Sphooceratidae Flower, 1962

Very short, straight, compressed shell with very large-sized protoconch (?), and cameral deposits with radial microstructure.
Sphooceras Flower, 1962; *Orthoceras truncatum* Barrande, 1868

Lituitidae Philips, 1848

Apical part of shell coiled; deep funnel sinus on juvenile coiled stage.
Lituites Bertrand, 1763; *Orthoceras lituum* Montford, 1808
[= *Holmiceras* Hyatt, 1894; *Angelinoceras* Hyatt, 1894; *Trilacinoceras* Sweet, 1958; *Asymmetroceras* Chen and Liu, 1974]
Long and straight shell with coiled apical part; mature aperture with two pairs of lappets.
Cyclolituites Remele, 1886; *Lituites applanatum* Remele, 1880
Completely coiled, compressed shell.
Ancistroceres Boll, 1857; *Lituites* (*Ancistroceras*) *undulatum* Boll, 1857
[= *Nevadoceras* Flower, 1968]
Rapidly expanding shell with coiled apical part.

Ophioceratidae Hyatt, 1894

Long shell almost entirely coiled (except for the adapertural part); deep funnel sinus delimited by short lappets.
Ophioceras Barrande, 1865; *O. simplex*
Antiplectoceras Foerste and Savage, 1927; *Discoceras* (?) *shamattawaense* Parks, 1915

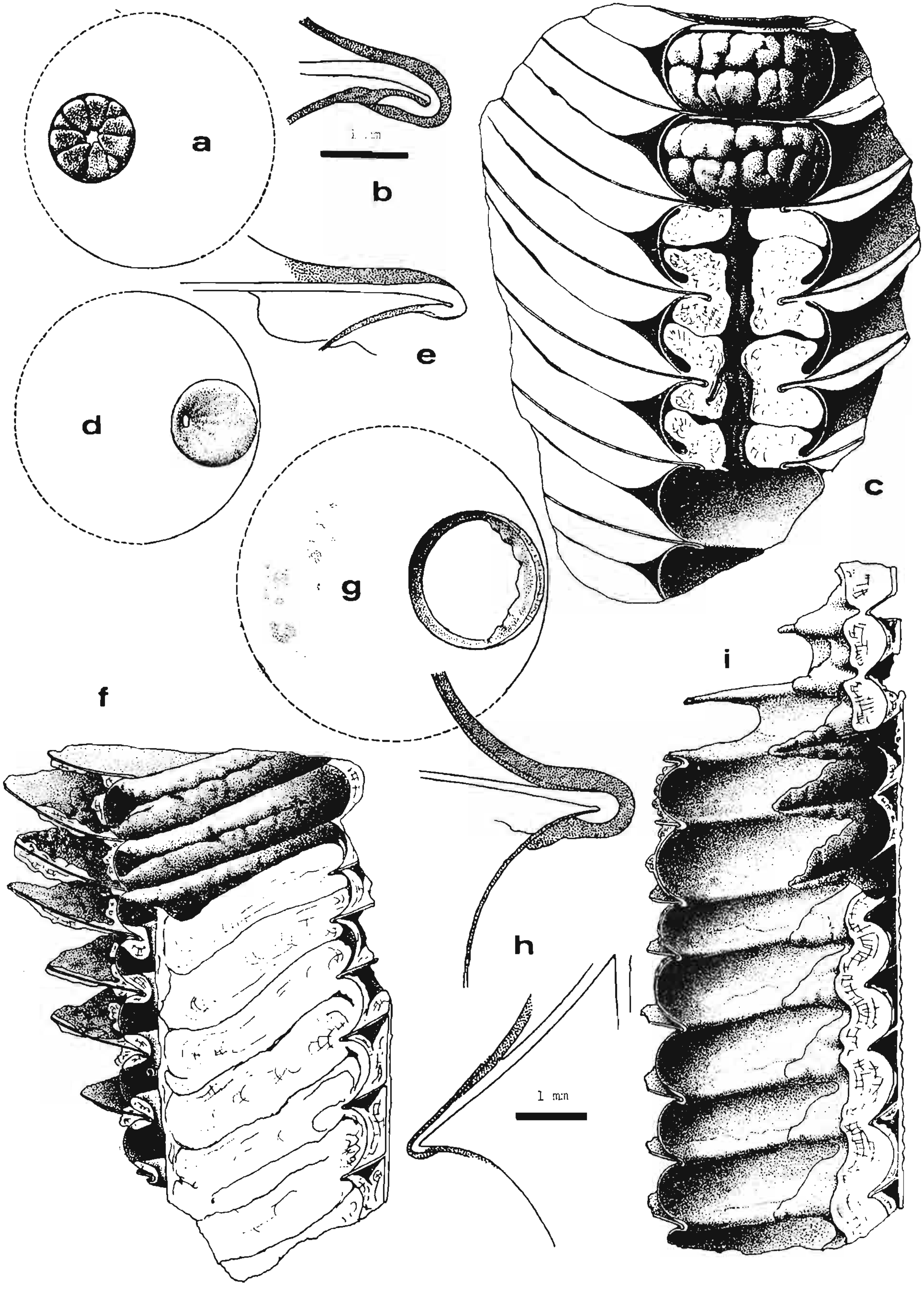
Suborder **Actinoceratina** Teichert 1933

Diagnosis. — Siphuncle with considerably inflated connecting rings and well developed deposits subdivided into radial blocks; protoconch exceeding 10 mm in diameter; long and straight shell with siphuncle between shell center and ventral (?) side.

Remarks. — The Actinoceratina differ from the orthoceratid families Pseudorthoceratidae and Sactoceratidae exclusively in protoconch size and consequent minimum diameter of the siphuncle. Presumably, this is a polyphyletic group.

Phylogeny (fig. 57). — The oldest known Actinoceratina occur at the Arenigian/Llanvirnian boundary (Kundan in the Baltic area, Whiterockian in North America). A typical actinoceratid form of that age is *Ormoceras* (*Adamsoceras*) *holmi* Troedsson, 1926, from the Late Kundan (B IIIγ). Most specimens attributed to this species show gently curved septal necks (Mutvei 1964, Balaschov 1955) but this character is variable even in a single phragmocone (see Troedsson 1926). One may therefore claim that a specimen found in an erratic boulder of red coloured *Orthoceras* limestone supposedly of the Kundan age, showing very strongly curved septal necks (fig. 56a-c, pl. 38: 7), should also be assigned to *O. holmi*. The opposite endmember of the range of morphological variation may be represented by *Ormoceras schmidti* Balaschov, 1955, known from two phragmocone fragments with relatively narrow siphuncle. The variation in shell diameter in the Actinoceratina from the Late Kundan suggests that the inflation in their connecting rings decreased during ontogeny, as in most sactoceratids and younger actinoceratids. The variation in curvature of septal necks is partly of ontogenetic, and partly of intrapopulation nature.

A more or less coeval representative of the Actinoceratina from the Table Head Limestone, New Foundland, was known to Barrande (1870, pls. 432-433). Flower (1968, 1976) split this sample into seven species which seem to differ mostly in preservation. This may be a single population attributable to *Cyrtonybyoceras haesitans* (Billings, 1857), differing from *C. holmi*


a
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1 mm
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1 mm

in the curved apical part of its shell and the wide siphuncle situated close to the convex side of the shell.

The actinoceratid fauna from the *Palliseria* Zone of the Antelope Valley Limestone, Nevada, was split by Flower (1968) into fourteen species assigned to several genera. As judged from his illustrations, the range of variation in siphuncular structure does not exceed that recorded in the Baltic population of *O. holmi*. The curvature of septal necks changes even in a single individual (see Flower 1968, pl. 4: 7, pl. 5: 4, etc.). The preservation is so poor that shell cross section cannot be used as a diagnostic feature. The only actinoceratid from Nevada which certainly is distinct morphologically is *Adamsoceras attenuatum* Flower, 1968, known from an incomplete oblique section through the shell. It resembles, however, the Baltic *O. schmidti* and its specific distinction may also be questioned. Flower (1968) distinguished the Early Ordovician forms attributed previously to *Ormoceras* as the genus, *Adamsoceras*, on their connecting rings being thicker than in all other Actinoceratina (Mutvei 1964). One cannot agree with this opinion because the siphuncular structure of typical Silurian representatives of *Ormoceras* is unknown. Also, a slight difference in inflation of the connecting rings (Flower 1968) does not suffice to establish a new genus.

There are also actinoceratids in the Late Llanvirnian of North America (Flower 1952, 1968) and Baltic area (Balaschov 1955), but their poor preservation makes their certain classification impossible. *Ormoceras kiaeri* Sweet, 1958, shows a siphuncle too narrow to be attributed to the Actinoceratina; it is a sactoceratid. *Ormoceras* is widespread in the North American Caradocian where its best known species is *O. allumettense* (Billings, 1857) from the Leray-Rockland Beds of Quebec (Wilson 1961). Some Early Devonian forms (Collins 1969) may also be attributed to *Ormoceras*, as judged from their resemblance to numerous but only superficially known Late Ordovician and Silurian forms. If we assume that the figure given by Collins (1969, fig. 8) is reliable and the connecting rings are thick in a Devonian representative of *Ormoceras*, siphuncular structure is maintained constant in this lineage since the Early Ordovician through the Devonian. Various sactoceratids have also been assigned to *Ormoceras*, but they can be recognized from their much narrower siphuncle; in fact, the siphuncle is never less than 1 cm in diameter even in the apical part of actinoceratid shells.

I do not know of any reliable record of the apical part of the shell of *Ormoceras*. The species "*Orthoceras*" *docens* Barrande, 1868, from the Ludlovian to Přidolian (?) of Bohemia, resembles *Ormoceras* in shell structure but the siphuncle inflation indicative of the apical proximity appears at a shell diameter equal to the mature shell of *Ormoceras* (see Barrande 1868, pl. 250: 1-8), pointing to a very large protoconch. This character and the absence of radial subdivision of the siphuncular deposits may indicate that "*O*". *docens* represents a distinct evolutionary lineage. In addition to "*O.*" *docens*, Barrande (1868) erected also some other species close to *Ormoceras* ("*O.*" *steiningeri*, "*O.*" *billingsi*, "*O.*" *rude*) which may be conspecific with "*O.*" *docens*. However, this cannot be demonstrated without knowledge of the apical part of their shells. *Kaliceras subcentraticum* Chen and Liu, 1974, from the Silurian of China, resembles very closely *Ormoceras* in structure of the apical part of its shell but it is much smaller. In turn,

Fig. 56

Ormoceras cf. *holmi* Troedsson, 1926; ZPAL N/814 (pl. 38: 7), erratic boulder, Kundan (?), Orłowo; *a* Reconstruction of the cross section; *b* septal neck; *c* reconstructed longitudinal (non-medial) section through the phragmocone; note exposed siphuncular deposits in the upper two, dissected deposits in the central three rings, and the absence of deposits from the lower rings. *Eushantungoceras kiaeri* (Teichert, 1934); ZPAL N/812 (pl. 38: 5), erratic boulder, Ludlovian (?), Orłowo; *d* Reconstruction of the shell cross section; *e* septal neck; *f* reconstructed longitudinal section through the siphuncle, note non-dissected siphuncular deposits in the upper two segments. *Eushantungoceras* sp.; ZPAL N/813 (pl. 38: 6), erratic boulder of Ostseekalk, Caradocian, Mochty; *g* Reconstruction of the shell cross section; *h* dorsal and ventral septal necks; *i* reconstructed median section through the siphuncle, note non-dissected siphuncular deposits in two segments.

"*Orthoceras*" *stokesi* Barrande, 1868, from the Ludlovian of Bohemia, shows a wide siphuncle indicative of its actinoceratid assignment, along with siphuncular deposits of pseudorthoceratid type, i. e. extended widely at the connecting rings.

Various ormoceratids have been reported from the East Asia (Kobayashi 1958, 1959; Lai 1965; Chang 1965; Wade 1977; Chen 1975) but their fragmentary state and imprecise dating make impossible the recognition of their phylogenetic relationships. In fact, they do not significantly differ from their relatives from other regions.

Both the stratigraphic succession and morphological analysis of early actinoceratids indicate that the most primitive forms displayed a straight to weakly exogastric shell with moderately-sized protoconch and siphuncle situated between the shell center and convex side; their connecting rings were inflated. Their ancestors are therefore to be looked for among the Sactoceratidae, the latter group being a morphological link between the Ormoceratidae and Pseudorthoceratidae. The earliest actinoceratids are coeval with representatives of the pseudorthoceratid genus *Clinoceras* (fig. 43e), while the Sactoceratidae appeared only in the Llandeilian. One may thus conclude that the actual ancestor of the Actinoceratina is still missing. To recognize the phylogenetic position of the Actinoceratina, one has to know the direction of shell curvature and siphuncle orientation, as well as the pattern of muscle scars and the primitive protoconch form. An opposite orientation of the pseudorthoceratid and actinoceratid shells has been traditionally accepted. The Pseudorthoceratidae show a projected part of the aperture at the siphonal (convex) side of the shell and hence, this side is commonly regarded as dorsal. However, such characteristics are considered as indicative of the ventral side of shell in *Rhynchorthoceras*. In spite of the lack of any data on the apertural outline in the Actinoceratina, the siphonal side of their shell is recognized as the ventral one. *Ormoceras* (*Adamsoceras*) shows relatively thick connecting rings. This, however, does not disprove its relationship to the Orthoceratina because a similar structure occurs also in the lituitid genus *Ancistroceras*. A phylogenetic relationship of the Actinoceratina to the Orthoceratina seems to me much more likely than its alternative relation to the Ellesmeroceratina. An evolutionary transition from the Ellesmeroceratina to Actinoceratina would require a central shift of the siphuncle, inflation of the connecting rings, and development of siphuncular deposits. Hence, an orthoceratid evolutionary stage would have been passed through. Collins (1976) claimed that the Actinoceratina evolved from the Ellesmeroceratina through a new form found in the Arenigian of Turkey. As judged from its brief description, the latter form is a baltoceratid with elongate septal necks indicative of a relation to the lineage leading to the Endoceratina. In fact, slight growth of siphuncular deposits at the septal necks does not indicate phylogenetic relation to the Actinoceratina. The Late Cambrian plectronoceratids with considerably inflated connecting rings ("Protactinoceratida" of Chen *et. al.* 1979) are separated from the earliest Actinoceratina by a large stratigraphic hiatus and differ from the latter in their ventro-marginal, diaphragmate siphuncle with no calcareous deposits.

The actinoceratid fauna of the Krivoluksky horizon in Siberia (Zhuravleva 1959, Balaschov 1962), time equivalent to the Chazyan (Llandeilian), is of crucial significance for recognition of the evolution of the Actinoceratina. That fauna includes abundant forms with wide siphuncles intermediate in morphology between the genera *Ormoceras* (especially "*Wutinoceras*" *planiseptatum* Flower, 1968) and *Armenoceras*. In spite of the relatively narrow range of morphological variation, this fauna was split by Balaschov (1962) into a dozen or so species. In my opinion, *Armenoceras lenaense* Balaschov, 1962, is the only well founded species in that fauna. Distinctness of *Metarmenoceras sibiricum* Zhuravleva, 1959 (*non* Balaschov, 1962), characterized by its gently curved septal necks, is doubtful. The considerable width of siphuncle and the outline of septal necks of *A. lenaense* are suggestive of a phylogenetic relationship to the genus *Actinoceras*, but the evidence is far from being unequivocal. The fauna of the Krivoluksky horizon includes also the earliest representative of the Sactoceratidae, namely *Tunguskoceras tunguskense* ZHURAVLEVA, 1959. *Tunguskoceras* differs from the associated actinoceratids in its much smaller shell and narrower siphuncle. There are no data on protoconch morphology of *A. lenaense* and hence, one cannot say whether this is a distinct evolutionary lineage derived from *Tunguskoceras*, or an ormoceratid. The latter hypothesis may be corroborated by the maintenance of constant siphuncle width towards the shell apex.

Later representatives of the genus *Armenoceras* show a wide, ventral siphuncle with considerably curved septal necks and may be descendants of *A. lenaense*. Their attribution to various species is questionable because of the fragmentary state of the specimens. The best known forms of this group occur in the Late Caradocian to Ashgillian of North America and Greenland (BARRANDE 1866, pl. 237; TROEDSSON 1926; FOERSTE and TEICHERT 1930). Apical parts of the shell of *Armenoceras* or its relative are assigned to the genus *Selkirkoceras* (see FOERSTE 1929). The earliest siphuncular segment is very wide in "*Selkirkoceras*" occupying the width of the shell. The shell is strongly depressed.

Typical representatives of *Armenoceras* have siphuncular deposits surrounding the septal neck, leaving in the center a free space for the siphonal soft tissue. However, there are some actinoceratids resembling *Armenoceras* in siphuncular structure, but with eccentrical pattern of the deposits, i. e. marginal dorsal (?) position of the siphon. The earliest forms of this group occur in the Llandeilian (*Nybyoceras holmi* SWEET, 1958; *Actinoceras* cf. *caneyense sensu* BALASCHOV, 1962). This evolutionary lineage may also be represented by a fragmentary specimen found in an erratic boulder of the Ostseekalk (see fig. 56g-i and pl. 38: 6). Its wide siphuncle makes unequivocal evidence for its assignment to the Actinoceratina. The position of the siphuncle and the shape of septal necks are typical of the armenoceratids. However, the siphuncular deposits, developed mostly at the ventral side, are most subdivided into radial blocks; there are also no free spaces (perispatia) between deposits of neighboring septal necks. Contrary to most Actinoceratina, the siphuncular deposits are most strongly developed between the septa, just as they are in the Pseudorthoceratidae. This structure is an example of how far from unequivocal is any diagnosis of the suborder Actinoceratina, and how close in morphology are the Actinoceratina and Pseudorthoceratidae.

Similarly developed siphuncular deposits, eccentric and only indistinctly subdivided into radial blocks, occur also in *Eushantungoceras pseudoimbricatum* (BARRANDE, 1870) and *E. kiaeri* (TEICHERT, 1934) from the Early Ludlovian of Baltic area (see MUTVEI 1964; BARRANDE 1866, pl. 237: 8-10; CHERNS 1981), Podolia (SIEMIRADZKI 1906, KISIELIEV and BALASCHOV 1968), Bohemia (BARRANDE 1866, 1870), and the Urals (BALASCHOV 1971). Despite the structure of the siphuncular deposits, *Eushantungoceras* resembles *Armenoceras* in the structure of its shell and siphuncle. The apical part of its shell is poorly known. The smallest shell fragment of the Ludlovian species *E. pseudoimbricatum* (= "*O.*" *exoticum* BARRANDE, 1866, pl. 216: 12; pl. 38: 8 in this paper) has a weakly endogastric shell with relatively narrow siphuncle with only slightly decreasing diameter towards the apex. As judged from the shell outline, the protoconch can be estimated as less than 2 cm in size. Another specimen illustrated by BARRANDE (1866, pl. 233: 7) shows a somewhat inflated siphuncle which might suggest proximity of the shell apex, but the shell size is actually much greater than in *O. exoticum.* The protoconchs of the Late Ordovician Asian actinoceratids described by KOBAYASHI (1937) correspond in size to the least diameter of the siphuncle recorded in *Eushantungoceras.* A dorso-marginal position of the siphon inside the siphuncle appears clearly in medial sections through those shells, which corroborates the hypothesis that the Ordovician armenoceratids with eccentric siphuncular deposits are related to the Silurian ones.

The most peculiar actinoceratid group is the Gonioceratidae with leaf-like, depressed shell with sharp lateral edges resembling the orthoceratid family Tripteroceratidae. Their relationship to the Ormoceratidae is suggested by the shell shape of *Ellinoceras septicurvatum* BALASCHOV, 1960, from the Early Ordovician of Siberia. In fact, *Ellinoceras* has a siphuncle of the *Ormoceras* type but its shell is depressed and the septal suture is considerably folded with a bipartite ventral sinus. While the sutures of the Gonioceratidae and *Ellinoceras* can be derived from a hypothetical common ancestor, their evolutionary development due to a convergence of independent lineages also appears plausible. The record of *Ellinoceras* is imprecisely dated and one can not say whether its morphological primitiveness is consistent with its age. The first unquestionable representative of the Gonioceratidae is *Lambeoceras* (*Hoeloceras*) *helgoyense* (SWEET, 1958) from the Llandeilian of Norway. Its siphuncle shows typically gonioceratid septal necks, the shell is considerably depressed, and the septal suture has a deep ventral sinus (SWEET 1958). *L. helgoyense* may thus be ancestral to the later species of *Lambeoceras* and *Gonioceras*. *Lambeoceras askeri* (SWEET, 1958) from the Early Caradocian of Norway presents already a form typical of the genus. *Lambeoceras* is widespread in the Late Ordovician of North America (LEITH 1942, TROEDSSON 1926, FLOWER 1968). It persisted up to the end of the Ashgillian but underwent evolutionary change in the shape of the septal necks. *Gonioceras* is widespread in the Chazyan (Llandeilian) to Middle Caradocian of North America (FLOWER 1943*b*, 1957, 1968; WILSON 1961). Fragments have also been reported from the Urals (BALASCHOV 1964) and China (CHEN 1976). Numerous erected species of this genus vary mostly in the preservation of the type specimens (see FLOWER 1943, WILSON 1961), whereas the leaf-like shell outline is common to all of them. The apical part of the shell shows a moderately-sized protoconch (WILSON 1961) greatly differing from typical Actinoceratina. The siphuncle shows rapidly expanding early connecting rings and hence, its adapical part is fusiform in outline.

Various Carboniferous orthoceratids with considerably inflated rings are also commonly referred to the Actinoceratina. SCHINDEWOLF (1943) demonstrated that very similar adult forms may have widely differing ontogenies. The largest protoconchs in this group are found in the genera *Rayonnoceras* (= *Carbactinoceras*) (SCHINDEWOLF 1942, GORDON 1964*a*) and *Loxoceras* (SHIMANSKY 1968), both from the Early Carboniferous. However, these protoconchs never exceed 6 mm in diameter. Hence, the two genera are much less advanced in this respect than the Ordovician actinoceratids. It seems to me unlikely that protoconch size decreased considerably in the course of actinoceratid evolution. If these Carboniferous forms were descendants of the Early Paleozoic Actinoceratina, their ancestors should be looked for among the most primitive groups. A wide stratigraphic hiatus between the known Early Devonian and Early Carboniferous actinoceratid-like forms makes a relationship of *Rayonnoceras* and *Loxoceras* to the Sactoceratidae equally plausible as the above presented hypothesis. *Loxoceras* resembles *Ormoceras* in the structure of the siphuncular deposits and hence, their close relationship is likely. In turn, *Rayonnoceras* largely differs in structure of the siphuncular deposits from the typical actinoceratids. The radial subdivision of the deposits is indistinct, whereas their bilateral symmetry is very clear. Several pairs of semilunate blocks are separated by a medial free space (MUTVEI 1964). There is also a bilateral-symmetrical pattern in distribution of the cameral deposits interpreted thus far as traces of the soft body (SHIMANSKY 1964, fig. 7; 1968, pl. 16: 4). The first form with siphuncular structure resembling that in *Rayonnoceras* is *Metarmenoceras ? meneghinii* SERPAGLI and GNOLI, 1977, from the Wenlockian or Ludlovian of Sardinia. It differs from typical representatives of *Rayonnoceras* in its elongated slender shell. A similar siphuncular structure is also shown by some Early Devonian forms known exclusively from shell fragments (FLOWER 1940, BABIN 1966, COLLINS 1969). However, the stratigraphic hiatus separating them from the Visean species of *Rayonnoceras* is too large to allow certainty about their phylogenetic relationship. Furthermore, these Early Devonian nautiloids may or may not belong to the Actinoceratina.

WADE (1977*a*, *b*) described in detail the siphuncular structure in some actinoceratids from the Middle Ordovician of Australia, and erected a new genus, *Georgina*, indistinguishable from *Actinoceras* in its septal necks and position of the siphuncle but with very complex siphuncular deposits. These deposits consist of radial blocks growing out of a septal neck and surrounding the aperture of the septum, and of symmetrical blocks attached to the connecting ring and intruding wedge-like between the radial blocks. The spatial distribution of these two systems of radial blocks indicates their twofold formation. The siphuncular deposits were first produced at the septal necks (analogous to the previously known anctinoceratids; MUTVEI 1964), and the retreating soft tissues subsequently produced deposits filling up the space occupied earlier by the siphuncle. The symmetrical nature of the secondary blocks cannot be explained at the moment. Possibly, it reflects a distribution of either secretion centers, or invaginations of siphonal epithelium. WADE (1977*a*) recognized these Australian forms as representatives of an endemic family, Georginiidae, because of the complex structure of their siphuncular deposits. One may, however, suppose that the uniqueness of that structure reflects mostly the poor preservation and insufficient knowledge of the actinoceratid siphuncular deposits. In fact, in some well preserved specimens of *Actinoceras*, they are indistinguishable in structure from those recorded in *Georgina* (see e. g. WILSON 1961, pl. 18: 1-3). The other georginiid genus, *Mesaktoceras*, is known from an isolated siphuncle and may actually belong to the Ormoceratidae.

Proposed systematics. —
Note that the family Sactoceratidae here assigned to the Orthoceratina, may equally be placed in the Actinoceratina. This would ensure the monophyletic nature of the Actinoceratina, but the only difference between the Actinoceratina and Orthoceratina would then consist of the more strongly inflated connecting rings in the former suborder.

Polydesmiidae KOBAYASHI, 1940

Wide, central siphuncle with gently curved septal necks.
Polydesmia LORENZ, 1906; *P. canaliculata*
Long, gently curved septal necks, inflated connecting rings.
Ordosoceras CHANG, 1959; *O. sphaeriforme*
[= *Meitanoceras* CHEN and LIU, 1974]
Connecting rings inflated only in their adoral parts.

Ormoceratidae SAEMANN, 1853

[= Deiroceratidae SHIMANSKY, 1954; Loxoceratidae HYATT, 1900]
Shell circular in section, with cubcentral siphuncle of moderate diameter; siphuncular deposits subdivided into thick radial blocks.
Ormoceras STOKES, 1840; *O. bayfieldi*
[= *Adamsoceras* FLOWER, 1957; *Wutinoceras* SHIMIZU and OBATA, 1935; *Linormoceras* KOBAYASHI and MATUMOTO, 1942; *Jeholoceras* KOBAYASHI and MATUMOTO, 1942; *Elrodoceras* FOERSTE, 1924; ?*Loxoceras* MCCOY, 1844; *Mesowutinoceras* CHEN, 1976; *Mesaktoceras* WADE, 1977]
Straight shell with relatively small protoconch, thick (?) subspherical connecting rings.
Cyrtonybyoceras TEICHERT, 1933; *Orthoceras haesitans* BILLINGS, 1857
Exogastrically curved apical part of the shell; wide, subventral siphuncle.
Deiroceras HYATT, 1884; *Orthoceras python* BILLINGS, 1857
Long and straight shell with elongate connecting rings.

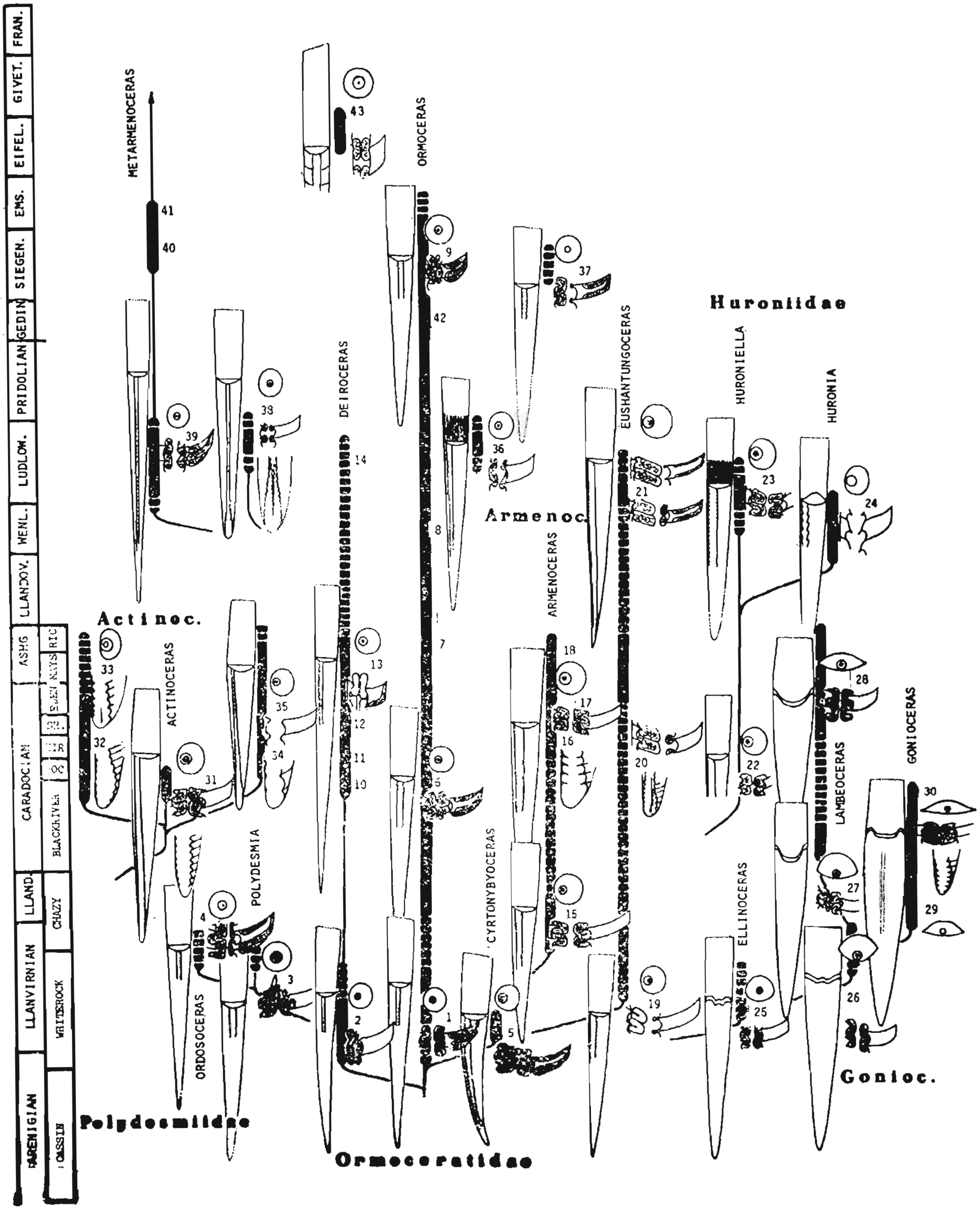
Armenoceratidae TROEDSSON, 1926

[= Discoactinoceratidae KOBAYASHI, 1978]
Shell circular to somewhat depressed in section, eccentrical, wide siphuncle with considerably curved septal necks.
Armenoceras FOERSTE, 1924; *Actinoceras hearsti* PARKS, 1915
[= *Discoactinoceras* KOBAYASHI, 1927; *Nybyoceras* TROEDSSON, 1926; *Selkirkoceras* FOERSTE, 1929]
Siphuncular deposits growing uniformly up around the septal necks.
Eushantungoceras SHIMIZU and OBATA, 1935; *Orthoceras imbricatum* BARRANDE, 1866
[= *Kaliceras* CHEN and LIU, 1974; *Parahelenites* CHEN and LIU, 1974; *Selenoplax* CHERNS, 1981;
Siphuncular deposits confined mostly to the ventral side.

Actinoceratidae Saemann, 1853

Depressed shell with eccentrical siphuncle, ontogenetically decreasing in diameter inflation of connecting rings; septal necks weakly curved.

Actinoceras Bronn, 1895; *A. bigsbyi*
[= ?*Metactinoceras* Zhuravleva, 1959; *Paractinoceras* Hyatt, 1900; *Kochoceras* Troedsson, 1926]



Huroniidae Foerste and Teichert, 1930

Eccentrical siphuncle with septal necks turned upwards and attached to the adapical wall of the septum.

Huronia Stokes, 1824; *H. bigsbyi*

Long siphuncular segments.

Huroniella Foerste, 1924; *Huronia inflecta* Parks, 1915

Rather short siphuncular segments.

Gonioceratidae Hyatt, 1884

[= Ellinoceratidae Balaschov, 1962]

Depressed, laterally angulate shell, with deep ventral sinus of the septal suture.

Ellinoceras Balaschov, 1960; *E. septicurvatum*

Ovate cross-section, strongly undulated septal suture with narrow ventral sinus; poorly known.

Lambeoceras Foerste, 1917; *Gonioceras lambii* Whiteaves, 1891

[= *Hoeloceras* Sweet, 1958]

Depressed, relatively elongate shell.

Gonioceras Hall, 1847; *G. anceps*

Flat, very wide shell with prominent lateral lobes of the septal suture.

? Carbactinoceratidae Schindewolf, 1942

Straight shell with circular section; subventral siphuncle with distinctly bilateral-symmetrical siphuncular deposits.

Rayonnoceras Croneis, 1926; *R. solidiforme*

[= *Carbactinoceras* Schindewolf, 1952]

Metarmenoceras Flower, 1940; *M. bilaterale*

Order Nautilida Agassiz, 1847

Diagnosis. — Exogastrically coiled, moderately elongated shell with narrow, originally subcentral siphuncle (but ventral in *Centroceras*, and dorsal in *Aturia*); larval development within an egg capsule, without planktonic larval stage.

Remarks. — The nautiloid systematics is far from being satisfactory; it is precarious to distinguish taxa of higher than familial rank. For practical purposes, I assign the Early Paleozoic nautiloids to the suborder Centroceratina, the Late Paleozoic and Triassic ones to the suborder Tainoceratina, and the post-Triassic forms to the suborder Nautilina. These suborders cannot be unequivocally diagnosed because of frequent evolutionary convergence.

←

Fig. 57

Hypothetical phylogenetic relationships among members of the suborder Actinoceratina; for Carboniferous forms of unclear systematic position see fig. 51; 1 *Adamsoceras holmi* (Troedsson) (fig. 56a-c; pl. 38: 7); 2 *Ormoceras schmidti* Balaschov, *Adamsoceras attenuatum* Flower; 3 *Polydesmia canaliculata* Lorenz; 4 *Ordosoceras sphaeriforme* Chang; 5 *Cyrtonybyoceras heasitans* (Billings), 6 *Ormoceras allumettense* (Billings), 7 *Ormoceras lambei* Foerste, 8 *Ormoceras bayfieldi* (Stokes), *Elrodoceras indianense* (Miller), *E. abnorme* (Hall), 9 *Ormoceras* sp. Collins; 10 *Deiroceras kindlei* Foerste; 11 *Aluveroceras levense* Balaschov; 12 *Deiroceras python* (Hall) 13 *Deiroceras remotiseptatum* (Hall) 14 *Orthoceras memor* Barrande, *Deiroceras amanti* Heritsch 15 *Armenoceras lenaense* Balaschov, *Metactinoceras sibiricum* Zhuravleva 16 *Selkirkoceras tyndallense* Foerste, *S. cuneatum* Foerste 17 *Armenoceras arcticum* Troedsson; 18 *Nybyoceras bekkeri* Troedsson, *Armenoceras holtedahli* Strand; 19 *Nybyoceras holmi* Sweet, *Actinoceras* cf. *caneyense* Balaschov; 20 *Armenoceras ventrosiphonatum* Kobayashi, *A. elegans* Endo *sensu* Balaschov; 21 *Eushantungoceras pseudoimbricatum* (Barrande) (pl. 38: 8) = *E. imbricatum*, *E. uralicum* Balaschov, *Armenoceras kiaeri* Teichert (fig. 56d-f pl. 38: 5); 22 *Discoactinoceras mutiplexum* Kobayashi; 23 *Huroniella cochleata* (Schlotheim); 24 *Huronia bigsbyi* Foerste; 25 *Ellinoceras septicurvatum* Balaschov; 26 *Hoeloceras helgoyense* Sweet; 27 *Hoeloceras askeri* Sweet; 28 *Lambeoceras lambei* (Whiteaves); 29 *Gonioceras chaziense* Ruedemann; 30 *Gonioceras anceps* Hall; 31 *Actinoceras bigsbyi* Bronn, *A. margaritae* Flower, *A. billingsi* Foerste; 32 *Actinoceras paquettense* Foerste and Teichert; 33 *Kochoceras cuneiforme* Troedsson, *Actinoceras insulaenigrae* Strand; 34 *Floweroceras boreale* Miller and Youngquist; 35 *Paractinoceras canadense* (Whiteaves), *Leurorthoceras hanseni* Foerste; 36 *Orthoceras stokesi* Barrande; 37 *Orthoceras puzosi* Barrande; 38 *Orthoceras docens* Barrande, *O. billingsi* Barrande, *O. rude* Barrande, *O. steiningeri* Barrande; 39 *Me armenoceras meneghinii* Serpagli and Gnoli; 40 *Metarmenoceras bilaterale* Flower; 41 *Rayonnoceras* sp. Collins; 42 *Ormoceras seretense* Balaschov, 1968; 43 *Zeravshanoceras priscum* Zhuravleva.

Suborder **Centroceratina** FLOWER 1950

Phylogeny (fig. 59). — A group of finely longitudinally striated, loosely coiled nautiloids, supposedly all attributable to a single biospecies *Centrocyrtoceras vagrans* (BILLINGS 1857), occurs in the Blackriveran (Early Caradocian) of Canada (FOERSTE 1933, WILSON 1961). These forms appear to be rather closely related to the genus *Uranoceras* ranging from the Late Ordovician (MUTVEI 1957) upwards. Their morphological affinity with *Uranoceras* consists not only in the shell outline and longitudinal striation but also in the subcentral siphuncle with weakly inflated connecting rings. *C. annulatum* (HALL, 1847) from the Trenton of New York (FOERSTE 1933) is intermediate in age between *C. vagrans* and the earliest representative of *Uranoceras*, *U. longitudinale* (ANGELIN, 1880). The origin of *Centrocyrtoceras* and *Uranoceras* is unclear. The two genera are traditionally considered as related to *Barrandeoceras*, a typical tarphyceratid, even though they differ from the latter in shell ontogeny, ornamentation, length, and coiling, as well as aperture shape and siphuncular structure. In fact, they show much more affinity with cyrtoconic, longitudinally striated, and annulated kionoceratids (Orthoceratida). The relationship of *Centrocyrtoceras* and *Uranoceras* to the Kionoceratidae is also suggested by the juvenile ornamentation of the earliest representative of *Centrocyrtoceras*, *C. percinatum* FOERSTE, 1933, from the Chazyan (Llandeilian), which consists of longitudinal ribs and transverse shell annulations. The muscle scars recorded from *Uranoceras longitudinale* (ANGELIN, 1880) from the Ashgillian Boda Limestone, Sweden (MUTVEI 1957) resemble very closely those observed in the Ascoceratidae (see FLOWER 1952*a*, SWEET 1958) but this can hardly be regarded as evidence for their phylogenetic relationship. A similar pattern of muscle scars occurs in most exogastrically curved nautiloid attributable to various systematic groups, including the Tarphyceratidae (see MUTVEI 1957). In turn, *Centrocycloceras* lacks an apertural sinus pointing to its close relationship to the Orthoceratida.

Some poorly known species of *Uranoceras* have been recorded in the Wenlockian of North America (FOERSTE 1925). The available data do not allow the distinction from one another of several Silurian American species attributed to the genera *Uranoceras*, *Cliftonoceras*, and *Cumingsoceras* (see FOERSTE 1925, FLOWER and TEICHERT 1957). They are also indistinguishable from *Uranoceras uranum* (BARRANDE, 1866) from the Ludlovian of Bohemia. The latter species shows a massive, compressed, loosely coiled shell ornamented with growth lines and very fine, longitudinal striae; its connecting rings are considerably inflated, but the septal necks are at most indistinctly curved, and the septa intrude inside the siphuncle as in *Dawsonoceras* (Orthoceratina).

An Late Ordovician coiled relative of *Uranoceras* is *Charactoceras*. Its shell is more tightly coiled than in *Uranoceras*; actually, its whorls contact each other and have a concave dorsum. This genus is known from poorly recognized species from the Late Ordovician of North America (FOERSTE 1924, TROEDSSON 1926, SWEET and MILLER 1956, and others) and the Baltic area ("*Trochoceras*" sp. of Strand 1935). Some tightly coiled nautiloid shells ornamented exclusively with growth lines, which resemble *Charactoceras*, were also reported from the Silurian and Devonian (BARRANDE 1865, HERITSCH 1930). The most abundant and best preserved material has been collected from the Ludlovian to Přidolian of Bohemia. Some "species" erected by BARRANDE on this material appear to represent populations successive in age and closely related in phylogeny. "*Nautilus*" *sternbergi* BARRANDE, 1865, with flat, evolute shell, occurs in the Ludlovian Kopanina Formation at Lochkov. "*N.*" *bohemicus* BARRANDE, 1865, from the Přidoli Formation of Karlštein, shows a more involute shell (pl. 42: 1). Finally, "*N.*" *tyrannus* BARRANDE, 1865 (= "*N*" *sacheri*), from Lochkov preserved in limestones differing in lithology from those containing "*N.*" *sternbergi*, is intermediate in morphology between the latter and "*N.*" *bohemicus*. This may reflect a continuous evolutionary transition, which is rather unusual in the fossil record of nautiloid evolution. The larval shell of *N. bohemicus* is large (pl. 42: 1) and there is little doubt that the embryo developed entirely within an egg capsule.

The Middle Devonian North American forms attributed to *Rhadinoceras*, *Wellsoceras*, and *Heracloceras* may be representative of the above evolutionary branch. The best known species of that group, *Rhadinoceras atlas* FLOWER and GORDON, 1972, is almost indistinguishable in shell outline from *Charactoceras*. Either *Uranoceras*, or *Centrocyrtoceras* could have given rise to the Lechritrochoceratidae, a group of Silurian loosely coiled nautiloids with subcentral siphuncle and shell ornamented with longitudinal striae and transverse ribs. The latter group is represented in the Wenlockian and Ludlovian of North America by several species, poorly known because of the preservation, attributed to the genera *Bickmorites*, *Jolietoceras*, and *Lechritrochoceras* (see FOERSTE 1925, 1926, 1936). They appear to be closely related to the lechritrochoceratids from the Silurian of Gotland and Bohemia represented by abundant and excellently preserved specimens. The oldest recorded lechritrochoceratids in Bohemia are some fragmentary specimens from the Llandoverian (TUREK 1976), but a great majority of known specimens were collected in the Ludlovian to Přidolian. The Late Silurian Bohemian lechritrochoceratids have been split into some tens of species and genera (BARRANDE 1865; TUREK 1975, 1976). I was able to examine the original material stored at the National Museum, Prague, as well as undescribed material of closely related forms from Gotland at the Naturhistoriska Riksmuseet, Stockholm, and I believe that the actual number of species of the Uranoceratidae *s. l.* in the Late Silurian of Bohemia was greatly overestimated (by a factor of 2-3 or even more) by BARRANDE and TUREK. The Lechritroceratidae display a considerable intrapopulation variability in prominence of ornamentation and shell coiling. In my opinion, only six evolutionary lineages are recognizable in the Bohemian material, each equivalent to a distinct genus as erected previously. These biospecies make up a morphologically coherent group, with transverse ribbing as their common shell character and are separated by a morphological gap from smooth-shelled *Uranoceras uranum*.

Inclytoceras inclytum (BARRANDE, 1865) (= *Lechritrochoceras disjunctum*) from the Ludlovian Kopanina Formation resembles *Uranoceras* in shell outline. Its loosely coiled, breviconic shell is ornamented with transverse ribs and striae, and indistinct, sparsely spaced longitudinal striae (TUREK 1976). It resembles in shell morphology *Peismoceras optatum* (BARRANDE, 1865) from time equivalent strata, while differing in the more slender shell with distinct dense longitudinal striation, and somewhat ventral siphuncle in the latter species. *P. optatum* may be conspecific with *P. pulchrum* from the Wenlockian Motol Formation and *P. mirandum* from the Přidolian, as well as with an English form, *Catyrephoceras giganteum* (BLAKE, 1882). *Magdoceras signatulum* from the Ludlovian Kopanina Formation shows a more tightly coiled, short, asymmetrical shell with distinct but sparse longitudinal striation. In shell ornamentation and brevity, *M. signatulum* resembles *I. inclytum*. There is a considerable intrapopulation variability in the prominence of ornamentation in *M. signatulum*. This was the basis for the recognition of several morphotype species (see TUREK 1976) assigned originally to *Lechritrochoceras*, namely *L. disjunctum*, *L. hoernesi*, *L. placidum*, *L. turgescens*, and *L. trochoides*. As defined by BARRANDE (1865), some of these species are heterogeneous because they are partly synonymous with *L. inclytum*, *M. signatulum* could have given rise to *Sphyradoceras clio* (HALL, 1861) from the Emsian of North America. *Calocyrtoceras cognatum* (BARRANDE, 1865) from the Ludlovian Kopanina Formation has commonly been attributed to the Orthoceratida because of its uncoiled shell. However, its shell ornamentation and cons derable curvature make it closely related to the Uranoceratidae *s. l.* BARRANDE's collection includes two samples of *C. cognatum* described under different names. The population from Lochkov shows a more strongly curved shell than the population from Kosoř. Presumably, the two populations are heterochronous because the distance between the localities is too small to have prevented the shells from post-mortem mixing. The uncoiling of shell of *C. cognatum* migth be a secondary modification.

Systrophoceras arietinum (BARRANDE, 1865) from the Ludlovian Kopanina Formation differs greatly from the above discussed forms. It has a much more longiconic shell than other uranoceratids, without longitudinal ornamentation. The siphuncular structure and position are unknown. The shell ornamentation and outline of *S. arietinum* is indicative of the phylogenetic relationship of *Systrophoceras* to the Nautilida. Some shell fragments similar to *S. arietinum* were also recorded from the Siegenian (*Trochoceras anomalum* BARRANDE, 1865, pl. 27: 8-19) and Eifelian (*Gyroceras fritschi* BARRANDE, 1877, pl. 517).

The Silurian Uranoceratidae *s. l.* present a continuous spectrum in muscle scar pattern, ranging from ventral position of the main part of the retractor scar, as in *Uranoceras*, to lateral position (TUREK 1976). The latter pattern, prevalent in the Bohemian uranoceratids, is typical of Carboniferous (see FOORD and CRICK 1890, SWEET 1958) and later Nautilida (see MUTVEI 1957), while it is unknown in other nautiloids. This points to the crucial significance of the Uranoceratidae *s. l.* for the determination of the origin of the Nautilida. From this view, the genus *Lechritrochoceras* (including *Kosovoceras*) appears to be especially interesting. It appeared in the Wenlocian in North America (FOERSTE 1926) but its best known representatives occur in the Ludlovian of Bohemia (TUREK 1975). The Bohemian species of *Lechritrochoceras* resemble the above discussed genera *Inclytoceras* and *Peismoceras*, except for their small adult shell. They are highly variable in shell ornamentation; in fact, they range from almost smooth to transverse ribbed and tuberculate, with longitudinal striation being their common characteristic. TUREK (1975) erected several species on this variation in shell ornamentation, although one cannot recognize any morphological discontinuities, and TUREK himself (1975: 35) noted a gradual increase in the proportion of tuberculate specimen in population of younger age. I believe that this is a monospecific evolutionary lineage with the populations varying greatly in shell ornamentation; the evolutionary trend was towards a ventro-lateral tuberculation. In fact, such tubercles are typical of the Middle Devonian species of *Lechritrochoceras* (see HOLZAPFEL 1895, WHIDBORNE 1892). The pattern of pedal retractor scars in *Lechritrochoceras* is indistinguishable from that of typical other Nautilida. As indicated by a distinct longitudinal striation, subcentral siphuncle, small embryonic shell, and wide umbilicus, *Lechritrochoceras* is a direct relative of the Tournaisian trigonoceratids (Nautilina); the stratigraphic gap is not very wide because *Lechritrochoceras* ranges at least up to the top of the Givetian. This is why I am of the opinion that all forms descendant from *Uranoceras* should be placed in the Nautilida rather than in the Tarphyceratida.

Two loosely coiled nautiloid species from the Siegenian Koněprusy Limestone, Bohemia, were traditionally regarded as ancestral to the Nautilida. Their common feature is a ventromarginal siphuncle, distinguishing them from both the Uranoceratidae *s. l.* and typical Nautilina. The larger species, *Trochoceras davidsoni* BARRANDE, 1865, resembles very closely in shell outline and ornamentation *Lechritrochoceras* (*Kosovoceras*) *sandbergeri* (BARRANDE, 1865) from the Late Silurian. The difference consists in the shell of *T. davidsoni* being larger, with ventral siphuncle, and without longitudinal striation. The dominant trend in the Silurian evolution of *Lechritrochoceras* is towards a reduction of longitudinal shell ornamentation and a development of tubercles (TUREK 1975). Thus, *Trochoceras* appears to represent a further stage in this evolutionary trend. Various lechritrochoceratids show a subventral siphuncle, and *Peismoceras* displays even a ventral one. Hence, the position of siphuncle does not differ fundamentally *Trochoceras* and *Lechritrochoceras*. One may therefore suppose that *Trochoceras* evolved directly from a Silurian *Lechritrochoceras*. The systematic position of the other Siegenian species, *Ptenoceras alatum* (BARRANDE, 1865) (pl. 42: 2), is much less clear, as discussed above (p. 57).

Some possible descendants of *Trochoceras* occur in the Eifelian of Hlubočepy, Bohemia. *T. tardum* BARRANDE, 1865, known from very poorly preserved specimens (BARRANDE 1865, pl. 26), appear to be a close relative of *T. davidsoni*. The genera *Adelphoceras* and *Homoad-*

elphoceras, erected on very poorly preserved and supposedly conspecific specimens, can not be placed in any known nautiloid group. As judged from moulds, their shell has two rows of tubercles, which is unusual among the trochoceratids; these may thus be rutoceratids. BARRANDE (1870, pl. 459) figured *A. bohemicum* with a T-shaped aperture, but there is no distinct aperture on the original specimen stored at the Narodní Muzeum, Prague, and hence BARRANDE'S reconstruction is incorrect. *Hercoceras mirum* (BARRANDE, 1854) is well known from several, poorly preserved, specimens. Its tightly coiled shell, very long lateral spines, and peculiar adult aperture (BARRANDE 1865, pl. 42: 3-5) are indicative of its considerable evolutionary advancement. It is associated with very similar, but, at maturity, uncoiled shells of *Gyroceras nudum* BARRANDE, 1865, intermediate in morphology between *Hercoceras* and *Trochoceras*.

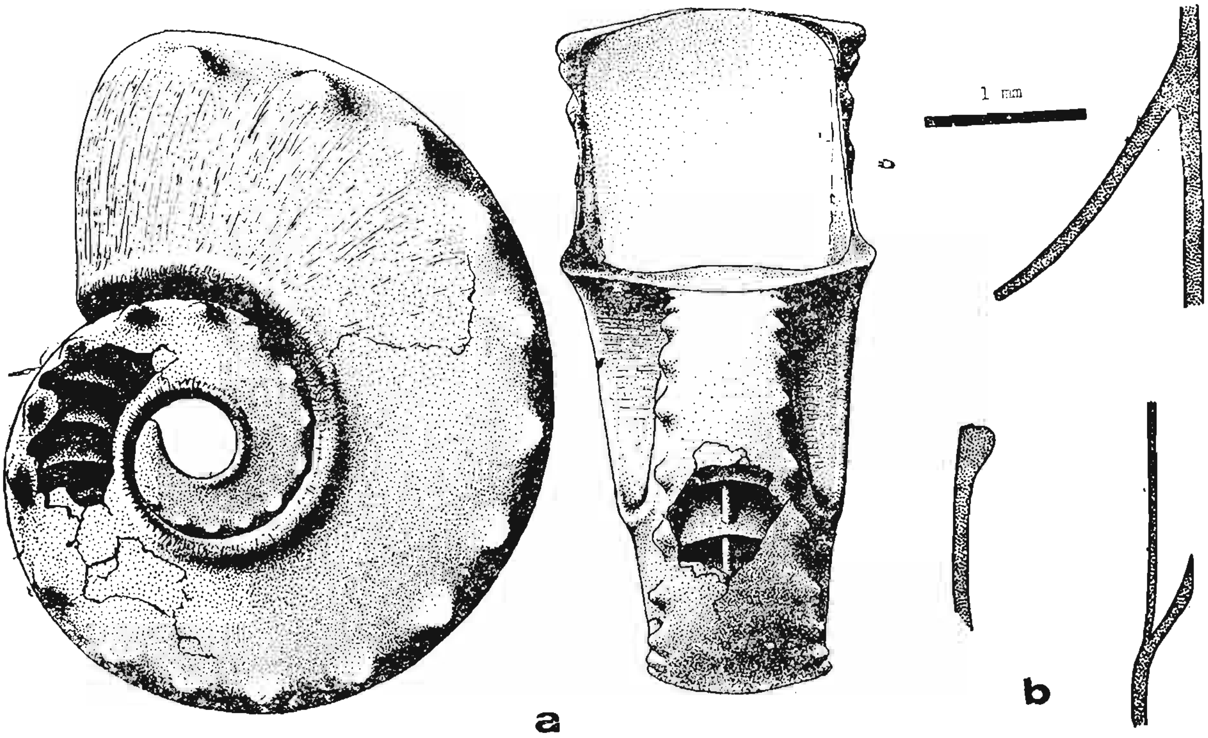


Fig. 58
Centroceras tetragonum (d'ARCHIAC and VERNEUIL, 1842); Świętomarz beds, Late Givetian, Śniadka by Bodzentyn, Holy Cross Mts, Poland; *a* Reconstruction of the subadult shell; *b* section through ventral part of a septum (minimum distance of the siphuncle from the ventral wall equals to the length of that part of the septum close to the wall) and through a siphuncle fragment, ZPAL N/818 (pl. 42: 3-4).

Some juvenile shells from the Emsian to Eifelian of the Urals and Novaya Zemla (KUZMIN 1965, ZHURAVLEVA 1974) may be related to *Hercoceras*. Presumably, they are ancestral to another poorly known Eifelian form, *Nassauoceras subtuberculatum* SANDBERGER and SANDBERGER, 1852, from Germany. *N. subtuberculatum* shows a depressed, subtrapezoidal whorl cross section and ventrolateral tubercles (SANDBERGER and SANDBERGER 1852). It may be ancestral to *Centroceras tetragonum* (d'ARCHIAC and VERNEUIL, 1842) from the Late Givetian of North Caucasus, Eifel, and the Holy Cross Mts. (pl. 42: 3-4; fig. 58). *C. tetragonum* shows a more compressed shell than *N. subtuberculatum*, and a dorsolateral rib. An even more compressed shell is displayed by *Strophiceras binodosum* SANDBERGER and SANDBERGER, 1852, from the Late Givetian of Germany and *Centroceras marcellense* (VANUXEM, 1842) from the Cherry Valley Limestone, North America (FLOWER 1952*b*). *C. marcellense* and *C. tetragonum* are indistinguishable from each other at the juvenile stages, but the adult tubercles are ventral on *C. marcellense* and lateral on *C. tetragonum*. The Famennian species *Carlloceras garlandense* Flower and Caster, 1935, is very poorly known but this may be descended from *Centroceras.*

Proposed systematics. —

„*Cyrtoceras*" *alternans* Tietze, 1870 from the Famennian of Dzikowiec in the Sudetes may represent a conservative trochoceratid lineage, which preserved depressed coils till the end of the Devonian. The only specimen of this species (see Tietze 1870: pl. 17:18) has been probably lost during World War II.

Uranoceratidae Hyatt, 1900

[= Centrocyrtoceratidae Kobayashi, 1934]

Finely longitudinally striated, loosely coiled, massive shell; subcentral siphuncle with inflated connecting rings; primitive forms annulated at the juvenile stages.

Uranoceras Hyatt, 1884; *Cyrtoceras uranum* Barrande, 1866
[= *Cliftonoceras* Flower, 1957; *Glyptodendron* Claypole, 1878; *Cumingsoceras* Flower, 1950]
Non-annulated shell with oblique aperture.

Centrocyrtoceras Foerste, 1926; *Cyrtoceras annulatum* Hall, 1847
[= *Paquettoceras* Foerste, 1933]
Annulated shell with aperture with lateral sinuses.

Lechritrochoceratidae Flower, 1950

[= ?Nephriticeratidae Hyatt, 1894]

Longitudinally striated and transversally ribbed shell with subventral, narrow siphuncle.

Bickmorites Foerste, 1925; *Lituites bickmoreanus* Whitfield, 1885
[= *Gasconsoceras* Foerste, 1936; *Savageoceras* Foerste, 1930]
Large-sized, rather long, loosely coiled shell.

Jolietoceras Foerste, 1925; *J. senescens*
Juvenile shell loosely coiled, adult shell straight.

Systrophoceras Hyatt, 1894; *Trochoceras arietinum* Barrande, 1865
Slowly expanding, loosely coiled shell ornamented exclusively with growth lines and transverse ribs.

Lechritrochoceras Foerste, 1926; *Trochoceras desplainense* McChesney, 1860
[= *Leurotrochoceras* Foerste, 1926; *Trochodictyoceras* Foerste, 1926; *Kosovoceras* Turek, 1975; ?*Dartoceras* Foerste, 1936]

Fig. 59

Hypothetical phylogenetic relationships among members of the suborder Centroceratina; 1 *Centrocyrtoceras vagrans* (Billings) = (?) *Centrocyrtoceras bondi* (Safford), *Paquettoceras allumettense* Foerste; 2 *Uranoceras longitudinale* (Angelin); 3 *Cliftonoceras quadratum* Flower, *Cumingsoceras elrodi* (White), *Uranoceras hercules* (Winchell and Marcy); 4 *Uranoceras uranum* (Barrande); 5 *Charactoceras baeri* (Meek and Worthen), *C. estonicum* Teichert; 6 *Nautilus sternbergi* Barrande, *N. tyrannus* Barrande, *N. sacheri* Barrande; 7 *Heracloceras*? *bohemicum* (Barrande) (pl. 42: 1); 8 *Heracloceras inelegans* (Meek); 9 *Wellsoceras columbiae* (Whitfield); 10 *Rhadinoceras cornulum* (Hall); 11 *Rhadinoceras atlas* Flower and Gordon; 12 *Jolietoceras senescens* Foerste; 13 *Bickmorites bickmoreanus* (Whitfield); 14 *Systrophoceras arietinum* (Barrande); 15 *Leurotrochoceras aeneas* (Hall), *Lechritrochoceras desplainense* (McChesney); 16 *Kosovoceras sandbergeri* (Barrande), 17 *Kosovoceras nodosum* (Barrande); 18 *Calocyrtoceras cognatum* (Barrande); 19 *Inclytoceras inclytum* (Barrande); 20 *Peismoceras* sp. Turek; 21 *Peismoceras pulchrum* (Barrande); 22 *Peismoceras optatum* (Barrande), *P. mirandum* (Barrande); 23 *Magdoceras signatulum* (Barrande); 24 *Sphyradoceras clio* (Hall); 25 *Trochoceras davidsoni* (Barrande); 26 *Adelphoceras bohemicum* Barrande, *Homoadelphoceras devonicans* (Barrande), *Trochoceras tardum* Barrande; 27 *Trochoceras vicaryi* Holzapfel, *T. pulcherrimum* Whidborne; 28 *Hercoceras mirum* Barrande; 29 *Adeloceras kakvense* Zhuravleva; 30 *Bastindoceras aculeatum* (Kuzmin), *Threaroceras inexpectans* Flower; 31 *Centroceras tetragonum* (d'Archiac and Verneuil) (text-fig. 58a, b; pl. 42: 3-4); 32 *Strophiceras binodosum* (Sandberger and Sandberger); 33 *Centroceras marcellense* (Vanuxem); 34 *Carlloceras garlandense* Flower and Casters; 35 *Ptenoceras alatum* (Barrande) (pl. 42: 2); 36 *Doleroceras resimum* Zhuravleva; 37 *Pleuroncoceras nodosum* (Bronn); 38 *Halloceras undulatum* (Vanuxem), 39 *Gyroceras submamillatum* Whiteaves; 40 *Lyrioceres simpsoni* (Nottleroth); 41 *Nephriticerina cornulum* Flower and Gordon; 42 *Nephriticerina alpenensis* Foerste, 43 *Homaloceras planatum* Whiteaves, 44 *Tetragonoceras gracile* Whiteaves, 45 *Nephriticeras bucinum* (Hall), *Beaupleuroceras incipiens* Williams, *Endoplanoceras gomphus* Flower. For alternative interpretation of *Ptenoceras* group see fig. 20.

Small shell with slightly constricted aperture and advolute whorls (contacting one with another); ventro-lateral tubercles in later species.

Sphyradoceras HYATT, 1884; *Trochoceras clio* HALL, 1861

[= *Magdoceras* TUREK, 1976; *Inclytoceras* TUREK, 1976; ?*Calocyrtoceras* FOERSTE, 1936]

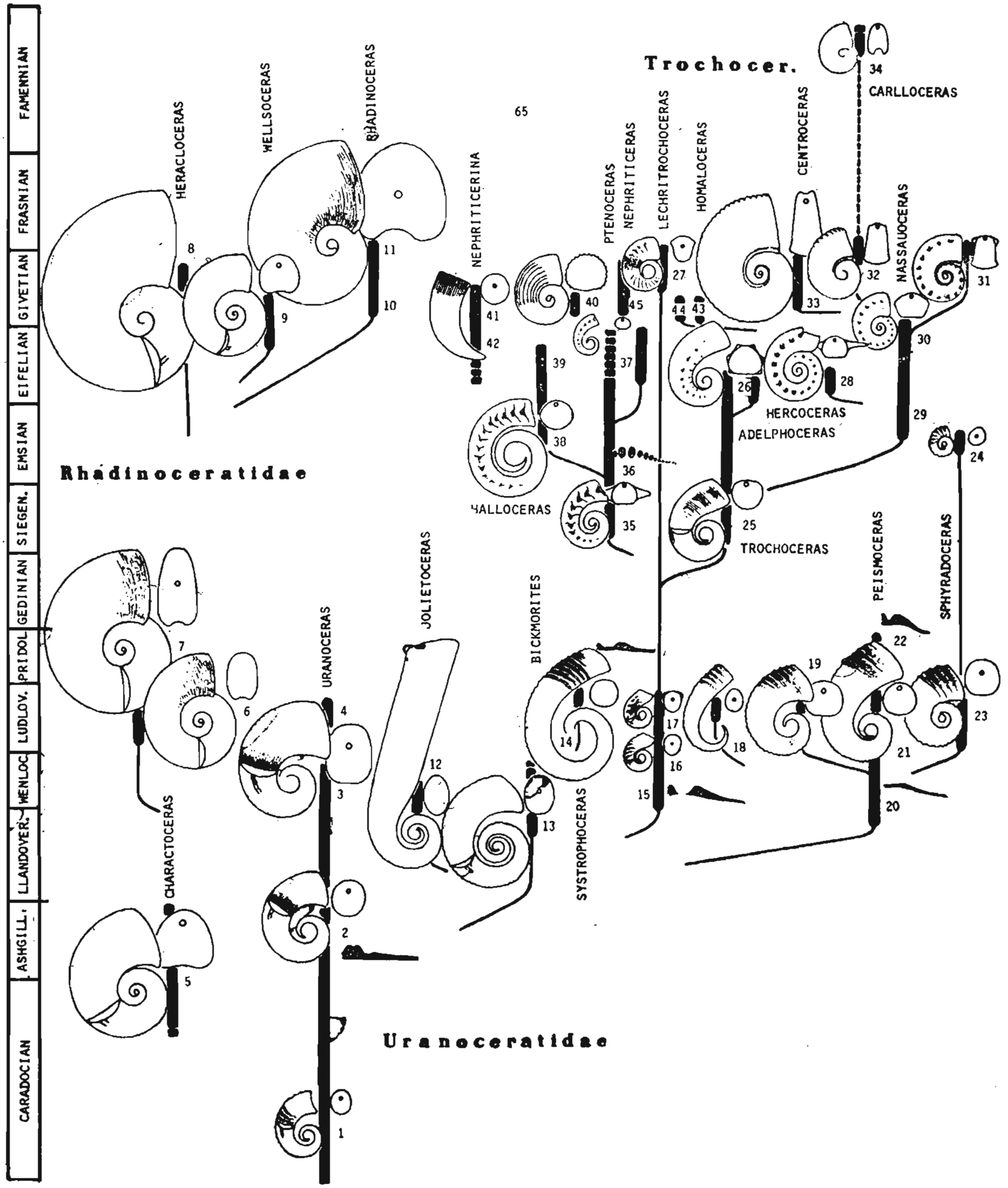
Short, strongly ornamented shell with subcentral siphuncle; shell ranging from uncoiled to trochospiral.

Peismoceras HYATT, 1894; *Trochoceras optatum* BARRANDE, 1865

[= ?*Catyrephoceras* FOERSTE, 1926]

Like *Sphyradoceras* but with subventral siphuncle.

?***Nephriticeras*** HYATT, 1884; *Nautilus bucinum* HALL, 1860



[= *Beaupleuroceras* WILLIAMS, 1935; *Endoplanoceras* FLOWER, 1938; *Lyrioceras* FOERSTE, 1927]
Short and tightly coiled shell with distinct longitudinal striae and weak transverse ribs.

?***Nephriticerina*** FOERSTE, 1927; *N. alpenensis*
Very short, weakly curved shell with longitudinal striation only.

Rhadinoceratidae HYATT, 1900

Massive, tightly coiled shell with subcentral siphuncle, ornamented exclusively with growth lines.

Charactoceras FOERSTE, 1924; *Trochoceras? baeri* MEEK and WORTHEN, 1865
Robust shell with uncoiled ultimate whorl; subventral siphuncle with inflated connecting rings; close to *Uranoceras*.

Rhadinoceras HYATT, 1894; *Nautilus cornulum* HALL, 1876
Massive shell with central siphuncle.

Heracloceras TEICHERT, 1940; *Gyroceratites* (*Nautilus*?) *inelegans* MEEK, 1871
Like *Rhadinoceras* but with compressed shell.

Wellsoceras FLOWER, 1940; *Gyroceras columbiense* WHITFIELD, 1882
Long and evolute shell.

Trochoceratidae ZITTEL, 1884

[= Centroceratidae HYATT, 1900; Tetragonoceratidae FLOWER, 1945]

Shell ornamented with growth lines, tubercles, spines, or alae; ventral siphuncle.

Trochoceras BARRANDE, 1848; *T. davidsoni* BARRANDE, 1865
Loosely coiled, smooth shell with ventro-lateral row of tubercles.

Hercoceras BARRANDE, 1865; *Gyroceras mirum* BARRANDE, 1854
[= *Anomaloceras* HYATT, 1884; *Spanioceras* ZHURAVLEVA, 1974; *Adeloceras* ZHURAVLEVA, 1974; *Megaloceras* ZHURAVLEVA, 1974]
Tightly coiled shell with lateral spines or tubercles, constricted mature aperture.

Nassauoceras MILLER, 1932; *Nautilus subtuberculatus* SANDBERGER and SANDBERGER, 1852
Like *Hercoceras*, in need for revision.

Centroceras HYATT, 1884; *Goniatites marcellensis* VANUXEM, 1842
Tightly coiled shell with trapezoidal cross section, ornamented with ventro-lateral tubercles and dorso-lateral ribs.

Homaloceras WHITEAVES, 1896; *H. planatum*
Like *Centroceras*, but with loosely coiled shell.

Carlloceras FLOWER and CASTER, 1935; *C. garlandense*
Poorly known, in need for revision.

?***Ptenoceras*** HYATT, 1894; *Gyroceras alatum* BARRANDE, 1865, see also p. 89.
?***Doleroceras*** ZHURAVLEVA, 1972; *D. resimum*
?***Adelphoceras*** BARRANDE, 1870; *A. bohemicum*
?***Halloceras*** HYATT, 1884; *Cyrtoceras undulatum* VANUXEM, 1842
?***Anepheleceras*** ZHURAVLEVA, 1974; *Halloceras torulosum* KUZMIN, 1966
?***Dzhinsetoceras*** ZHURAVLEVA, 1978; *D. irregulare*

Suborder uncertain
"Superfamily **Aipoceratoidea**"

There is a group of Early Carboniferous Nautilida with spirally coiled, very large but short shell and ventro-marginal siphuncle (fig. 60). They differ greatly from the associated Nautilida in shell proportions and siphuncle position. One can also hardly assume that any centroceratid genera were their ancestors. Their relationship to the Nautilida is nonetheless suggested by the pattern of pedal retractor scar in *Solenocheilus* (see FOORD and CRICK 1890). This Early Carboniferous group, commonly regarded as a distinct superfamily, the Aipoceratoidea, includes two evolutionary branches that may or may not be phylogenetically interrelated. The Aipoceratidae display an evolute and considerably compressed shell. Their mature aperture, known exclusively from *Asymptoceras*, is laterally constricted; whereas the adult aperture of Solenocheilidae has elongate lateral alae in the form of conspicuous spines. The solenocheilid shell is involute, with depressed whorls. The Aipoceratidae resemble somewhat the Devonian genera *Rhadinoceras* and *Centroceras* in shell shape, but their phylogenetic relationship appears to be unlikely because

Rhadinoceras has a subcentral siphuncle, while *Centroceras* display a conspicuous shell ornamentation consisting of tubercles and ribs. The Aipoceratidae appear to be related to *Geitonoceras lucidum* (ZHURAVLEVA, 1974, from the Early Famennian of Kazakhstan (ZHURAVLEVA 1974) and perhaps from the Late Famennian of the Sudetes (see TIETZE 1870: p. 17:19). An almost complete, thus far undescribed specimen of this species, under the care of Dr. F. A. ZHURAFLEFA (Paleontological Institute, Moscow) resembles *Aipoceras* in shell outline. Supposedly, its protoconch was very large. As indicated by shell shape (weakly curved), siphuncle structure, and whorl section, *Geitonoceras* may be related to the Early Devonian Oncoceratids, but this hypothesis cannot be confirmed at the moment.

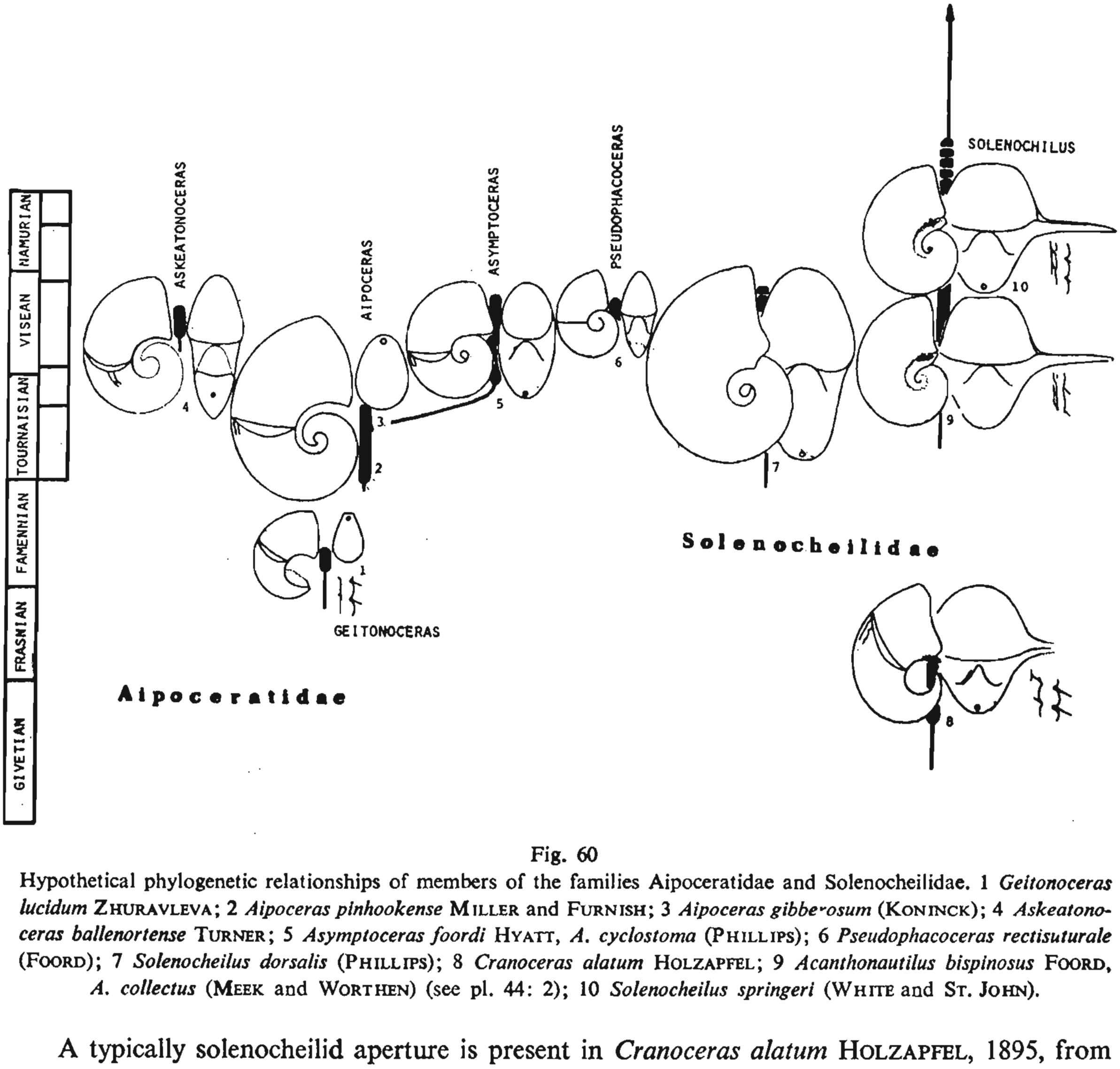


Fig. 60

Hypothetical phylogenetic relationships of members of the families Aipoceratidae and Solenocheilidae. 1 *Geitonoceras lucidum* ZHURAVLEVA; 2 *Aipoceras pinhookense* MILLER and FURNISH; 3 *Aipoceras gibbeosum* (KONINCK); 4 *Askeatonoceras ballenortense* TURNER; 5 *Asymptoceras foordi* HYATT, *A. cyclostoma* (PHILLIPS); 6 *Pseudophacoceras rectisuturale* (FOORD); 7 *Solenocheilus dorsalis* (PHILLIPS); 8 *Cranoceras alatum* HOLZAPFEL; 9 *Acanthonautilus bispinosus* FOORD, *A. collectus* (MEEK and WORTHEN) (see pl. 44: 2); 10 *Solenocheilus springeri* (WHITE and ST. JOHN).

A typically solenocheilid aperture is present in *Cranoceras alatum* HOLZAPFEL, 1895, from the Late Givetian of Germany. Its siphuncle (SCHÖNENBERG 1952) resembles *Solenocheilus*, while its loosely coiled shell may be considered primitive. However, it differs from the Solenocheilidae in the very short living chamber.

The above data suggest that the Aipoceratoidea are much more closely related to the Oncoceratidae than to the Nautilida. However, in my opinion it is more reasonable to retain the Aipocerataceae in the Nautilida until their systematic position is known.

Pseudophacoceras rectisuturale (FOORD, 1900) attributed by TURNER (1968) to the Liroceratidae, and *Askeatonoceras ballynortense* TURNER, 1966, attributed by TURNER to the Phacoceratidae, resemble both the Aipoceratidae in their large, evolute shell with triangular whorl cross section. However, *Askeatonoceras* shows an arched septal suture and a subcentral siphuncle, in contrast to other aipoceratids. The systematic position of *Askeatonoceras* and *Pseudophacoceras* remains uncertain.

Proposed systematics. —

Aipoceratidae HYATT, 1883

Compressed shell with ventro-marginal siphuncle, laterally constricted mature aperture, and large protoconch.

?*Geitonoceras* ZHURAVLEVA, 1974; *G. lucidum*
Loosely coiled shell with angulate venter.
Aipoceras HYATT, 1884; *Gyroceras gibberosum* de KONINCK, 1880
Loosely coiled shell with whorls ovate in cross section.
Asymptoceras RYCKHOLT, 1852; *Nautilus cyclostomus* PHILLIPS, 1836
Tightly coiled shell with constricted aperture and whorls; ovate whorl section.
?***Askeatonoceras*** TURNER, 1968; *A. ballynortense*
Loosely coiled shell with subcentral siphuncle and triangular whorl section.
?***Pseudophacoceras*** TURNER, 1966; *Phacoceras*? *rectisuturale* FOORD, 1900
Tightly coiled shell with triangular whorl section.

Solenocheilidae HYATT, 1893

Shell dorsally depressed, with lateral spines at mature aperture.
Solenocheilus MEEK and WORTHEN, 1870; *Nautilus (Cryptoceras) springeri* WHITE and St. JOHN, 1868
[= *Acanthonautilus* FOORD, 1896]

Suborder **Tainoceratina** SHIMANSKY, 1957

Phylogeny (figs. 62, 65, 67). — There are no spirally coiled nautiloids in the Frasnian to Famennian which might link the Middle Devonian with the Carboniferous Nautilida. The only known specimen of *Carlloceras garlandense* FLOWER and CASTER, 1935, a poorly preserved fragment of a juvenile whorl from the Famennian, resembles rather closely the Givetian genus *Centroceras* but differs strongly from later forms. This stratigraphic gap in the fossil record of the Nautilida is associated with a morphological discontinuity between their Middle Devonian and Lower Carboniferous representatives. There is little doubt that this is not an evolutionary discontinuity but one can hardly point to any lineages that may have linked the Uranoceratidae *s. l.* with the Tainoceratina. The subgenus *Lechritrochoceras* (*Kosovoceras*) ranging from the Silurian to Givetian (TUREK 1975, WHIDBORNE 1885, HOLZAPFEL 1895), may be the most plausible ancestor to the Early Carboniferous Nautilida. It resembles the Tournaisian to Visean Tainoceratina in its small evolute shell ornamented with longitudinal striae and transverse ribs, with moderately-sized protoconch and subcentral siphuncle, and especially in the lateral position of its muscle scar (TUREK 1975) as in the post-Devonian Nautilida (see MUTVEI 1957, SWEET 1959b).

The Tournaisian (Kinderhookian) Nautilida are widespread but only superficially known (KONINCK 1880, MILLER and GARNER 1953, GUTSCHICK and TRECKMAN 1957, SHIMANSKY 1968). Most species show a loosely coiled, longitudinally ornamented shell, but there are also some tightly coiled forms. The loosely coiled forms present a morphological spectrum in whorl section ranging from reverse ovate, through ventrally depressed and concave, to reverse triangular (*Choteauoceras americanum* (MILLER and FURNISH, 1939), *Rineceras*, *Tribolоceras*, and *Trigonoceras*, respectively). *C. americanum* appears the most primitive form among the known Carboniferous Nautilida. This is suggested by its stratigraphic position, its marginal position in the morphologic spectrum, and its considerably resemblance to *Lechritrochoceras* (*Kosovo-

ceras) *pulcherrimum* (WHIDBORNE, 1892), the closest Devonian relative of the Early Carboniferous Nautilida. The loosely coiled Nautilida occur almost exclusively in the Early Carboniferous. The only other record of such forms is from the Early Permian of the Urals; they resemble in morphology the Early Carboniferous ones (RUZHENTSEV and SHIMANSKY 1954), but can hardly be considered as relatives because of the wide stratigraphic gap. Curved species of the genera *Cyrtothoracoceras* and *Cornuella* resemble the loosely coiled Early Carboniferous Nautilida in their shell ornamentation (see TURNER 1954, SHIMANSKY 1968), and their assignment to the Orthoceratida may indeed be questioned.

The tightly coiled Tournaisian and Visean Nautilida also present a morphologic spectrum which is linked with their loosely coiled relatives; this indicates homogeneity of the family Trigonoceratidae as understood in the present paper. Unfortunately, adult shells of tightly coiled Tournaisian forms remain unknown and hence, one cannot determine which ontogenetic stages are represented by the specimens described. The collection stored at the University of Wrocław includes a specimen of *Vestinautilus konincki* (d'ORBIGNY, 1850) closely resembling that one figured by KONINCK (1880), with shell ontogeny typical of most Early Carboniferous Tainoceratina. The whorl diameter is rather small in the earliest ontogenetic stages, which indicates that the protoconch was less than 2 mm in diameter. The first whorl is ornamented with distinct longitudinal ribs and striae which gradually disappear leaving only three lateral ribs at the apertural end of the second whorl. Later on in ontogeny, the outer rib disappears and the venter becomes convex instead of concave. These ontogenetic trends suggest that the adult shell of *V. konincki* resembles in section *Subvestinautilus crassimarginatus* (FOORD, 1900) known from large specimens from the Visean of Great Britain. *S. crassimarginatus*, as well as its Visean and Namurian relatives, lacks a concave venter in the juvenile stages (TURNER 1954). One may suppose that the ontogenetic stage with convex venter shifted backwards in ontogeny in the course of evolution, completely removing from ontogeny the stage with concave venter. However, this interpretation has not been demonstrated. Shell morphology of the Tournaisian Nautilida is too poorly known to permit recognition of their phylogenetic relationships. The Visean Trigonoceratidae *s. l.* may as well have evolved from forms other than *V. konincki*.

Juveniles of various species of the Namurian to Westphalian genus *Endolobus* resemble very closely juveniles of *Subvestinautilus* (see GORDON 1964a). They show distinct longitudinal striae and lateral ribs disappearing in ontogeny. The adult shell of *Endolobus* has an ovate whorl section; it is ornamented exclusively with growth lines (GORDON 1964*a*, pl. 9: 1). Juvenile specimens described under names *Knightoceras*, *Valhallites*, and *Edaphoceras* (see GORDON 1964*a*, SHIMANSKY 1968) may belong to various species of *Endolobus*. As indicated by the shell ontogeny, *Endolobus* may have evolved from *Subvestinautilus* through a further shift backward in ontogeny of the disappearance of longitudinal ribbing and angulate whorl section. Some species of *Endolobus* show undulations of the lateral whorl edges, which may become transformed into tubercles persisting to the adult stages (MURPHY 1976). A similar evolutionary change took place, independently and much earlier, in another lineage derived from *Subvestinautilus*, that one leading to *Temnocheilus*. Visean *Temnocheilus coronatum* (McCOY, 1844) resembles very closely *Subvestinautilus* in its shell outline, and the undulation of its internal edges is the only difference (see FOORD 1900, 1903; TURNER 1954). The lineage of *Temnocheilus* is commonly regarded as ranging to the end of the Carboniferous but detailed investigations are needed to determine its true stratigraphic range. This is because lateral tubercles may develop from transverse ribs as well, indicating the possibility of homeomorphy. The evolutionary development of lateral tubercles from transverse ribs in *Lechritrochoceras* (*Kosovoceras*) has been illustrated by TUREK (1975). One may suppose that most tuberculate shell ornamentations in Late Paleozoic Nautilida developed only from transverse ribs. This type of ornamentation is widespread among the Cephalopoda, resulting in the common occurrence of parallel evolution and convergence. This considerably hampers the deciphering of the evolutionary pathways.

The first Carboniferous species of the Nautilida with a coiled and distinctly transverse ribbed shell is *Celox erratica* SHIMANSKY, 1967 (?=*Gzheloceras antiquum*, *G. striatum*) from the Visean of Kazakhstan. Its shell is relatively bulgy and involute, ornamented with longitudinal striae and low transverse ribs. The shell shape suggests close relationship to the earliest involute liroceratids. *C. erratica* may have evolved from a bulgy representative of *Vestinautilus*, such as *V.* pinguis KONINCK, 1880, or *Potoceras dubium* HYATT, 1894. Unfortunately, the adult shell of *C. erratica* remains unknown, *C. erratica* supposedly gave rise to *Gzheloceras memorandum* SHIMANSKY, 1967, from the Namurian of Kazakhstan. The latter species is a little more evolute than *C. erratica.* It is ancestral to the lineage of *Ghzeloceras* which, in turn, appears to be ancestral to most groups of post-Early Carboniferous ribbed Nautilida. The relatively massive longitudinal ribbing of *C. erratica* and *G. memorandum* (see SHIMANSKY 1967, pl. 6: 4-5) along with transverse ribs support the hypothesis that these are ancestral also of *Tylonautilus nodiferus* (ARMSTRONG, 1866), a peculiar ornamented form widespread in the Namurian (GORDON 1964*a*, SHIMANSKY 1967). Presumably, *Tylonautilus* is a monospecific genus because the observed differences among "species" other than *T. nodiferus* do not justify their specific distinction. *T. nodiferus* differs from *C. erratica* and its relatives in the concave venter resembling very closely *Vastinautilus konincki.* Furthermore, the ornamentation of *Tylonautilus* can be very easily derived from that typical of *V. konincki.* In spite of the absence of any Visean intermediates, one cannot reject the hypothesis that *Tylonautilus* evolved from *V. konincki*, while *C. erratica* represents a secondary branch of that lineage.

Tylonautilus may have given rise to the genus *Tainoceras* recorded from the Late Carboniferous upwards. Their phylogenetic relationship is indicated by the concave venter and longitudinal arrangement of tubercles in *Tainoceras*; the tubercles are more prominent and less numerous than in *Tylonautilus.* The lineages of *Tainoceras* is poorly documented in the fossil record, namely in the Early Permian (MILLER and KEMP 1947, CHAO 1954), latest Permian (TEICHERT and KUMMEL 1973, SCHRÉTER 1977), and earliest Triassic (SHIMANSKY 1968). *Trematodiscus klipsteini* MOJSISOVICS, 1873, from the Late Triassic of the Alps, resembles in morphology the Paleozoic representatives of *Tainoceras* and may be the last member of that evolutionary lineage.

Gzheloceras memorandum from the Early Namurian of Kazakhstan probably gave rise to *G. faticanum* SHIMANSKY, 1967, from the Late Namurian of the Urals, which has a more evolute shell with the tubercle-like ventro-lateral parts of the ribs. This slight change in ornamentation marks the origin of a large nautiloid group usually described under the generic names *Pleuronautilus* and *Metacoceras.* Their taxonomy is very poorly understood; the range and actual number of species can hardly be recognized because of the fragmentary state of most specimens and the lack of data on intrapopulation variability. I believe that this group is unrelated to the genus *Pleuronautilus*, which is characterized by ventro-lateral longitudinal ribs. *Metacoceras* should be restricted to forms with subtrapezoidal whorl section, which probably branched from the group under discussion. The generic name *Pseudotemnocheilus* appears to be more appropriate for the group considered. The type species *P. posttuberculatus* (KARPINSKY, 1874), is well known from the material collected from the Artinskian of the Urals. RUZHENTSEV and SHIMANSKY (1954) distinguished several species, assigned partly to *Pseudotemnocheilus*, and partly to *Metacoceras*, in the collection taken from strata that yielded also *P. posttuberculatus.* I did not examine the original material but the illustrations of RUZHENTSEV and SHIMANSKY (1954) suggest that all species represent various ontogenetic stages in a conspecific population with relatively low variation. The most complete specimen is the holotype of "*Metacoceras kruglovi*" (RUZHENTSEV and SHIMANSKY 1954, pl. 5: 4a-b). The adult shell is evolute, without ribs but with conspicuous ventro-lateral spines projected laterally; the whorl section is reverse trapezoidal with rounded umbonal margins. The protoconch is conical in outline, up to 3 mm in diameter (Ruzhentsev and Shimansky 1954, pl. 3: 6). The larval shell is distinctly ornamented, weakly curved, up to 10 mm in length, ending with a distinct constriction. In the Late Carboniferous of North America, there are some forms with very long spines (Tucker 1977), closely related to *P. posttuberculatus.* They may be ancestral to the Permian species *Cooperoceras texanum* Miller, 1945, known from silicified specimens from the Glass Mts, Texas (Miller and Youngquist 1949).

The genus *Metacoceras*, characterized by its wide and angulate shell section, and recorded from the Namurian and Westphalian of Poland (Korejwo 1969, 1974; Korejwo and Teller 1972; Bojkowski 1979) among others, may be a descendant of *Pseudotemnocheilus*, but this remains to be demonstrated. Some morphologically intermediate species have been recorded (see Hyatt 1891; Miller *et al.* 1933; Delepine 1937; Kummel 1953, 1960; Unklesbay 1962). The pedal retractor scar of *Metacoceras* (see Sweet 1959*b*) is typical of the Nautilida. The Late Permian forms described from Hungaria by Schréter (1974) under the name of *Tirolonautilus* may actually belong to *Metacoceras.* According to Kummel (1953), the Triassic genus *Mojsvaroceras* is a descendant of *Metacoceras.*

Various Permian and Triassic Nautilida with laterally ribbed shells have been attributed to the genus *Pleuronautilus.* I believe that this is a polyphyletic taxon including several evolutionary lineages that branched independently from *Gzheloceras.* The range of the genus should then be restricted to the branch including the type species. This lineage is unique among the ribbed Nautilida in showing ventrolateral ribs or rows of tubercles. The earliest known representative of *Pleuronautilus s. s.* is "*Sholakoceras*" *bisulcatum* Ruzhentsev and Shimansky, 1954, from the Sakmarian of the Urals. It is known from a single juvenile specimen but the well

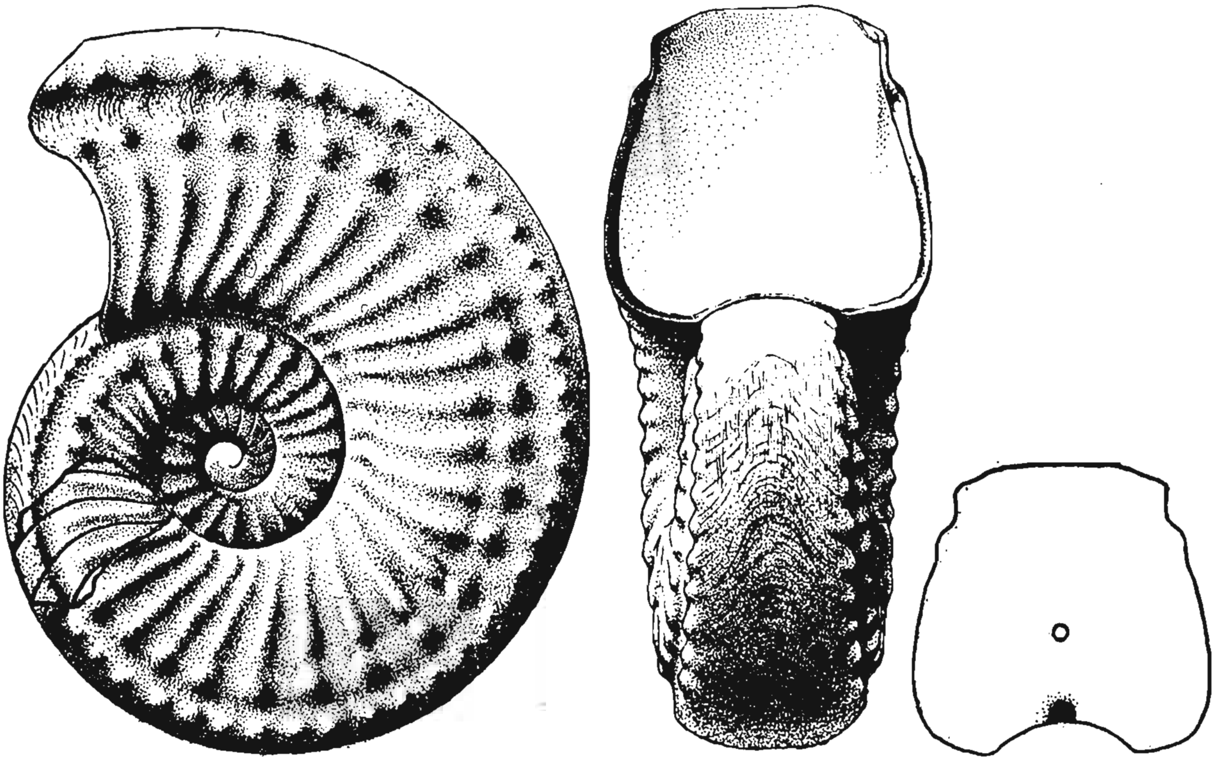
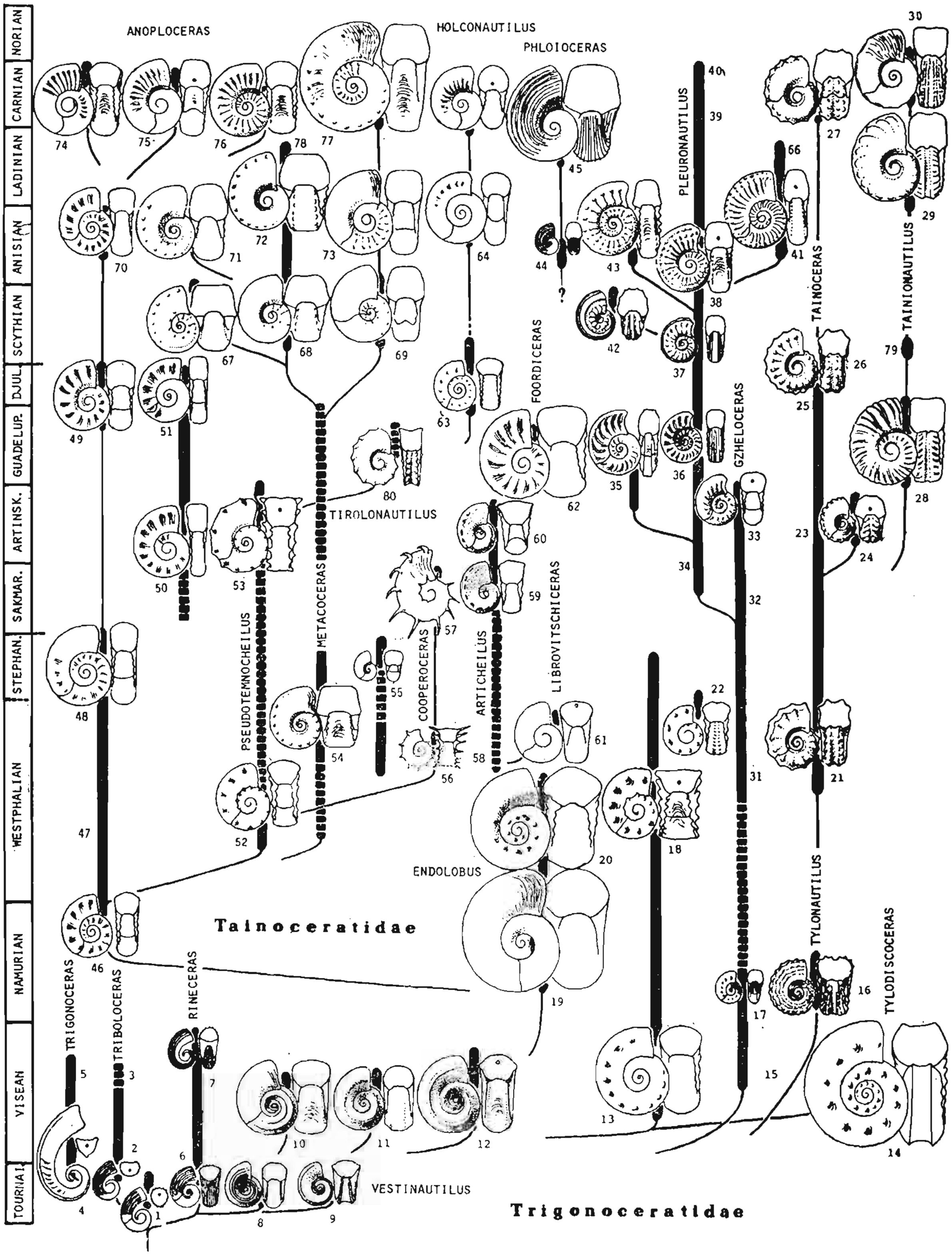


Fig. 61

Pleuronautilus trinodosus Mojsisovics, 1882; MGUW 5/6/35, pl. 43: 8, Anisian, Młodzawy by Skarżysko-Kamienna, Poland; reconstruction of the shell.

developed ventro-lateral edges make its assignment to *Pleuronautilus* very likely. This genus may also include some North American Leonardian species attributed by MILLER and YOUNGQUIST (1949) to *Foordiceras*. There are two evolutionary lineages of *Pleuronautilus* in the Permian. One of these is represented by "*Tangshiashanites*" *marginalis* CHAO, 1954, from the Artinskian



of China, with flat shell resembling closely "*S.*" *bisulcatum*. The other is represented by *Pleuronautilus sumatrensis* Fliegel, 1901 (= *P. loczyi* Fliegel, 1901) from the Guade'upian of Sumatra Island (pl. 43: 1-2). *P. sumatrensis* may be ancestral to *P. kokeni* Frech, 1905, from the earliest Triassic of the Salt Range, Pakistan (pl. 43: 3). The latter species has outer ribs split into rudimentary tubercles as typical of later, Triassic representatives of the genus. It displays also two pairs of well developed ventro-lateral ribs, and longitudinal striation. This ornamentation may be considered as ancestral to that observed in the type species, *P. trinodosus* Mojsisovics, 1882, from the Anisian (pl. 43: 8), as well as to the peculiar ornamentation recorded in *P.* (*Ussurinautilus*) *amurensis* Kiparisova, 1961, from the Scythian of Pacific coast of North Asia. *P.* (*U.*) *amurensis* shows a very involute shell with transverse ribs confined to the adumbilical part of the whorls, and ventro-lateral ribs developed much more strongly than in its congeners. There are three species of *Pleuronautilus* in the Anisian of the Alps, differing from each other mostly in the prominence of particular elements of the ornamentation (see Mojsisovics 1882, Hauer 1896); these are: *P. trinodosus*, *P. mosis*, and *P. ornatus*. They are typically Alpine faunal elements but they were recorded also from the Anisian of the Holy Cross Mts (fig. 61 and pl. 43: 8; Łuniewski 1923). *Pleuronautilus s. s.* is widespread in the Triassic (Kummel 1953, Chen 1976) and persisted up to the Carnian (Mojsisovics 1873).

A serious problem is posed by the systematics of the Early Carboniferous Grypoceratidae. This is a widely variable group characterized by their discoidal adult shell and peculiar, angulate

Fig. 62

Hypothetical phylogenetic relationships among members of the families Trigonoceratidae and Tainoceratidae; 1 *Chouteauoceras americanum* (Miller and Furnish); 2 *Triboloceras serratum* (Koninck) (see pl. 44: 6); 3 *Triboloceras kazakhstanense* Shimansky; 4 *Nautiloceras aigokeros* (Münster); 5 *Trigonoceras paradoxicum* (Sowerby); 6 *Rineceras propinquum* (Koninck); 7 *Rineceras alapayevskense* Kruglov; 8 *Nautilus pinguis* Koninck; 9 *Vestinautilus konincki* (d'Orbigny); 10 *Vestinautilus paucicarinatus* (Foord); 11 *Vestinautilus cariniferus* (Sowerby); 12 *Subvestinautilus crassimarginalis* (Foord); 13 *Temnocheilus coronatus* (McCoy); 14 *Tylodiscoceras unicum* Miller and Collison; 15 *Celox erratica* Shimansky; 16 *Tylonautilus nodosocarinatus* (Roemer); 17 *Gzheloceras memorandum* Shimansky; 18 *Temnocheilus bellicosus* (Morton); 19 *Nikenautilus beleutensis* Shimansky, *Endolobus clorensis* Collison, *E. spectabilis* (Meek and Worthen), *Knightoceras oxylobatum* Miller and Downs (see also pl. 44: 3); 20 *Endolobus ortoni* (Whitfield); 21 *Tainoceras quadrangulum* (McChesney); 22 *Tainoceras murrayi* Miller and Unklesbay, *T. monilifer* Miller, Dunbar and Condra; 23 *Tainoceras clydense* Miller and Kemp, *T. hunanense* Chao; 24 *Hunanoceras globosum* Chao; 25 *Tainoceras* sp. Teichert and Kummel; 26 *Tainoceras* sp. 2 Shimansky; 27 *Trematodiscus klipsteini* Mojsisovics; 28 *Tainionautilus transitorius* (Waagen); 29 *Thuringionautilus jugatonodosus* (Zimmermann); 30 *Trematodiscus rectangularis* (Hauer); 31 *Gzheloceras nikitini* (Tzvetaeva); 32 *Gzheloceras sholakense* Ruzhentsev and Shimansky; 33 *Gzheloceras uralense* Ruzhentsev and Shimansky, *Rhiphaeoceras venustum* Ruzhentsev and Shimansky; 34 *Sholakoceras bisulcatum* Ruzhentsev and Shimansky, *Foordiceras gregarium* (Miller); 35 *Tangchiashanites marginalis* Chao; 36 *Pleuronautilus sumatrensis* Fliegel (pl. 43: 1-2); 37 *Pleuronautilus kokeni* Frech (pl. 43: 6); 38 *Pleuronautilus trinodosus* Mojsisovics (pl. 43: 8); 39 *Palaskensis* Kummel, *P. cornaliae* (Stoppani); 40 *Pleuronautilus lepsiusi* Mojsisovics; 41 *Pleuronautilus mosis* Mojsisovics; 42 *Pleuronautilus* (*Ussurinautilus*) *amurensis* Kiparisova; 43 *Temnocheilus ornatus* Hauer, *T. triserialis* Hauer; 44 *Trachynautilus subgemmatus* Mojsisovics; 45 *Phloioceras gemmatum* (Mojsisovics); 46 *Gzheloceras faticanum* Shimansky, *partim*; 47 *Gzheloceras tacitum* Shimansky; 48 *Gzheloceras maklai* Shimansky; 49 *Metacoceras doroshamense* Shimansky, *M. dorsoarmatum* Abich, *Pleuronautilus dzhulfensis* Shimansky; 50 *Pleuronautilus linchangense* (Yin); 51 *Pleuronautilus* sp. indet. 1 Teichert and Kummel; 52 *Temnocheiloides acanthicus* (Tzvetaeva) (see also pl. 44: 4); 53 *Pseudotemnocheilus posttuberculatus* (Karpinsky); 54 *Metacoceras mcchesneyi* Murphy; 55 *Parametacoceras bellatulum* Miller and Owens; 56 *Cooperoceras milleri* Tucker; 57 *Cooperoceras texanum* Miller; 58 *Mosquoceras tschernyschevi* (Tzvetaeva); 59 *Mosquoceras simense* Ruzhentsev and Shimansky; 60 *Articheilus luxuriosum* Ruzhentsev and Shimansky; 61 *Librovitschiceras atuberculatum* (Tzvetaeva); 62 *Foordiceras goliathum* (Waagen), 63 *Temnocheilus* sp. indet. Teichert and Kummel, *Syringonautilus vagus* Shimansky; 64 *Holconautilus semicostatus* (Beyrich); 65 *Holconautilus ramsaueri* (Hauer); 66 *Pleuronautilus cornaliae* (Stoppani); 67 *Enoploceras newelli* Kummel; 68 *Mojsvaroceras frechi* Kummel; 69 *Phaedrysmocheilus subaratus* (Kayserling), *Pleuronautilus idahoensis* Kummel; 70 *Pleuronautilus pichleri* (Hauer), *P. distinctus* Mojsisovics; 71 *Temnocheilus augusti* Mojsisovics; 72 *Mojsvaroceras neumayri* (Mojsisovics); 73 *Pleuronautilus ventricosus* Hauer, *P. polygonius* Hauer, *Temnocheilus binodosus* Hauer; 74 *Encoiloceras superbum* (Mojsisovics); 75 *Anoploceras ampezzanum* (Lorezt); 76 *Pleuronautilus gaudryi* (Mojsisovics), *P. tibeticus* Mojsisovics; 77 *Enoploceras wulfeni* Mojsisovics; 78 *Temnocheilus cassianus* Mojsisovics, *Mojsvaroceras turneri* Kummel; 79 *Tainionautilus trachyceras* Frech.

juvenile ornamentation. A large number of species are based on juvenile specimens found in a few localities representing a narrow stratigraphic interval, namely the Visean to Early Namurian (see FOORD 1900, TURNER 1966, SCHMIDT 1957, SHIMANSKY 1967). This suggest considerable intraspecific variability. On the other hand, one can hardly say which specimens are juveniles and which are adults. The domatoceratids may also display an ammonoid-like sexual dimorphism, with small ornamented males and large smooth-shelled females. Consequently, it is impossible to decipher details of the domatoceratid evolution, or even to recognize the number of evolutionary lineages.

The Grypoceratidae appear to be a homogeneous group, closely related to the primitive Trigonoceratidae. The richest material of the Grypoceratidae comes from the Visean of Scotland and Ireland (FOORD 1900). This material is so variable and diverse in species that there is little doubt that the family must have branched and diversified earlier, at least during the Tournaisian (fig. 62). The species *Epidomatoceras planotergatus* (McCOY, 1844), possibly identical with some congeneric species erected by TURNER (1965), was especially important for the further evolution of the Grypoceratidae. If one assumes that the ontogeny of *Epidomatoceras*, typical of the whole family, recapitulates the phylogeny, certain phylogenetic relationships of the domatoceratids are suggested. The initial whorl in *Epidomatoceras* is distinctly longitudinally striated (DELEPINE 1937; TURNER 1954; KUMMEL 1964, fig. 313: 5); resembling the adult shell of the most primitive grypoceratids. The second whorl is subquadratic in section, with sharp ventro-lateral and dorso-lateral edges, as in the adult (?) shell of *Mesochasmoceras* and its relatives. The adult shell of *Epidomatoceras* (up to 200 mm in diameter) is ornamented with growth lines only and ovate in whorl section. There are very few data on the ontogeny of *Domatoceras*, but one may claim that the evolutionary trend to shift growth stages backwards in ontogeny, widespread in the Nautilida, took place also in the lineage of *Epidomatoceras* and *Domatoceras*.

The genus *Domatoceras* was represented by numerous evolutionary lineages very early in its history, in the Early Westphalian; the morphological variation existed at that time mostly in adult shell size and coiling. This branch persisted more or less unchanged up to the Permian (SHIMANSKY 1965, 1967; RUZHENTSEV and SHIMANSKY 1954; KUMMEL 1953; TEICHERT and KUMMEL 1973). One of its component lineages, which started with *Domatoceras gigas* (TZVETAEVA, 1888) from the Namurian (?) of Moscow region (KALANDADZE 1961, SHIMANSKY 1967) and supposedly included representatives of the genera *Titanoceras* and *Kummeloceras*, is characterized by a very large shell (over 300 mm in diameter) with weakly concave venter. The latest Permian species (see TEICHERT and KUMMEL 1973), *Pseudotitanoceras armeniacum* (ABICH, 1878), and the Scythian species *Germanonautilus montpelierensis* KUMMEL, 1953, link *Domatoceras* and the Middle Triassic representatives of the genus *Germanonautilus*. In fact, *G. dolomiticus* (Quenstedt, 1849) abundant in the Anisian of the Holy Cross Mts, Poland (fig. 63 and pl. 43: 7) appears to be especially close to "*Titanoceras*". Its shell is massive and relatively evolute, with concave venter. Its funnel-like umbilicus differs from the later *G. bidorsatus* (SCHLOTHEIM, 1820), and contributes to the affinity of *G. dolomiticus* to the Permian domatoceratids. *G. bidorsatus* is widespread in the Ladinian of Poland and Germany. Its shell is wider than in *G. dolomiticus*, with prominent dorso-lateral edges somewhat constricting the umbilicus (fig. 64; MUNDLOS 1971). If this is a descendant of *G. dolomiticus*, these two species should be considered as an evolutionary lineage confined to the epicontinental Central-European sea (but see FRANZ 1903). Another evolutionary branch of *Germanonautilus*, which could have evolved independently from *G. montpellierensis* occurs in the Triassic of the Alps and Andes. Its members are characterized by bulgy shells with very narrow umbilicus. Its earliest typical representative is *G. furlongi* SMITH, 1914, from the Anisian (KUMMEL 1953), while *G. schloenbachi* (MOJSISOVICS, 1873) from the Carnian is its last member.

The oldest recorded calcified jaws, very important for deciphering the evolution of nautiloid anatomy, are associated with *Germanonautilus*. Calcified upper beaks (*Rhyncolithes hirundo*) and lower beaks (*Conchorhynchus avirostris*) of nautiloid jaw commonly occur in the Ladinian of Germany (Ruffe 1962, Müller 1963*a*, *b*). They are usualy associated with *G. bidorsatus*, but their occurrence also in ceratite living chambers was regarded by Schmidt-Effing (1972) as evidence for their assignment to the Ammonoides. The latter interpretation seems unlikely, because ammonoid jaws differ in structure from nautiloid jaws, even if calcified (Lehmann *et al.* 1980), whereas the complex *O. avirostris-R. hirundo* does not significantly differ from calcified jaws of extant *Nautilus* (see Saunders *et al.* 1978). The absence of any other calcified nautiloid jaws from the Triassic and earlier periods may suggest that *G. bidorsatus* is representative of the main evolutionary lineage linking the Paleozoic Tainoceratina and the post-Triassic Nautilina. This corroborates the above hypothesis that *Germanonautilus* derived from *Domatoceras* rather than *Metacoceras* (see Kummel 1953), because a close relative of *Domatoceras*, the genus *Syringonautilus*, appears to be ancestral to the Jurassic Nautilida (see Kummel 1953*b*, 1956). *Syringonautilus* differs from its relatives, *Domatoceras* and *Grypoceras*, in its longitudinally ornamented shell with oval whorl section. Its distinction from *Cenoceras*, with which

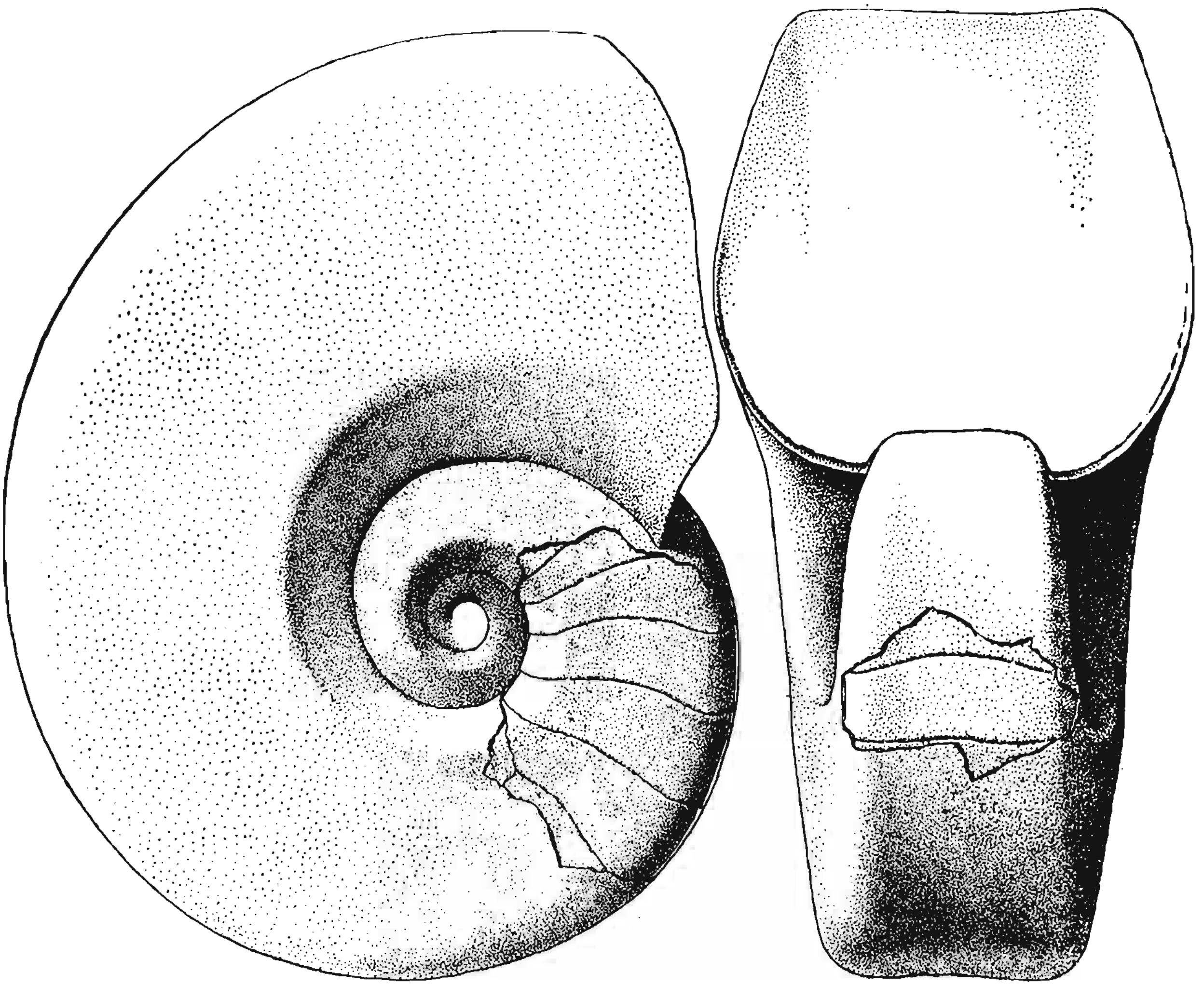


Fig. 63

Germanonautilus dolomiticus (Quenstedt, 1849); *Lima striata* beds, Anisian, Wolica, Holy Cross Mts, Poland; reconstruction of the adult shell, ×0.66, mostly from the specimen ZPAL N/855 (see also pl. 43: 7).

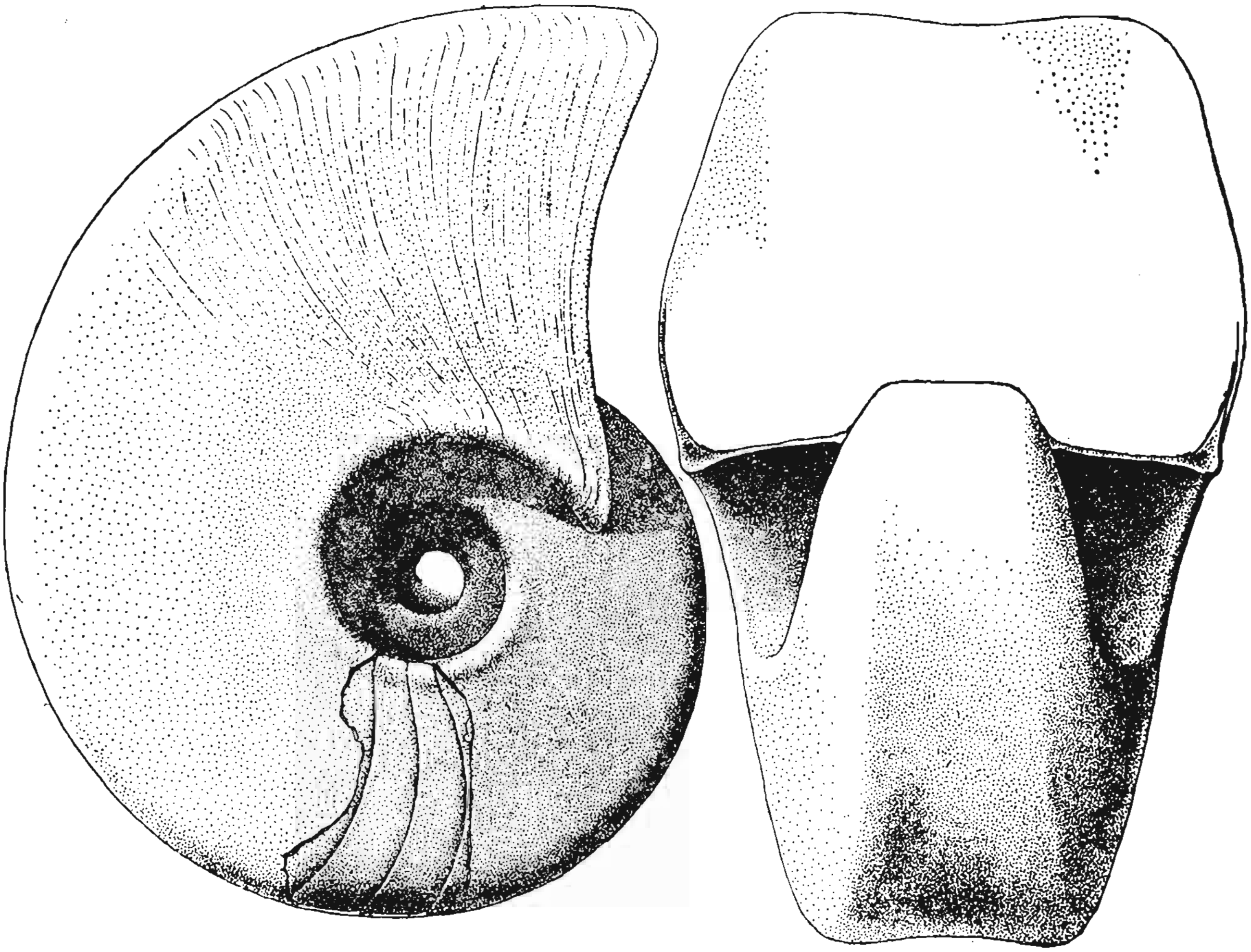


Fig. 64

Germanonautilus bidorsatus (SCHLOTHEIM, 1820), Wilkowice beds, Early Ladinian (Fassanian), Ligota Samborowa; Opole Silesia, Poland; reconstruction of the adult shell, ×0.66, mostly from the specimen ZPAL N/859.

it occurs from the Carnian upwards, seems to be questionable. This is also the case with Triassic species of the two genera. There are no data on morphology of the Early Triassic species of *Syringonautilus*, which makes impossible the precise recognition of its ancestral forms (KUMMEL 1953). The occurrence of an aberrant form of the related genus *Syringoceras*, characterized by its ventral siphuncle, in the Scythian of Primorie (KIPARISOVA 1960) may suggest that the lineage of *Syringonautilus* branched from the group of *Domatoceras* and *Grypoceras* during the Permian. The species *Menuthionautilus kieslingeri* COLLIGNON, 1933, with a cosmopolitan range (KUMMEL 1953*c*; KIPARISOVA 1960, 1961), may be an involute relative of *Syringoceras*.

The evolutionary continuity and close structural affinity between the Paleozoic Tainoceratina and extant *Nautilus* are demonstrated also by the structure of the radula. Excellenty preserved nautiloid radulae described from the Late Carboniferous Francis Creek Shale, Illinois, under the names *Palaeocadmus herdinae* SOLEM and RICHARDSON, 1975, and *P. pohli* SAUNDERS and RICHARDSON, 1979, resemble closely the radulae of extant *Nautilus*. Unfortunately, their generic position is unknown. Even if they would be assigned to a lineage ancestral to *Nautilus* (Domatoceratidae ?), other Paleozoic nautiloids must have displayed a radula similar in structure to "*Palaeocadmus*".

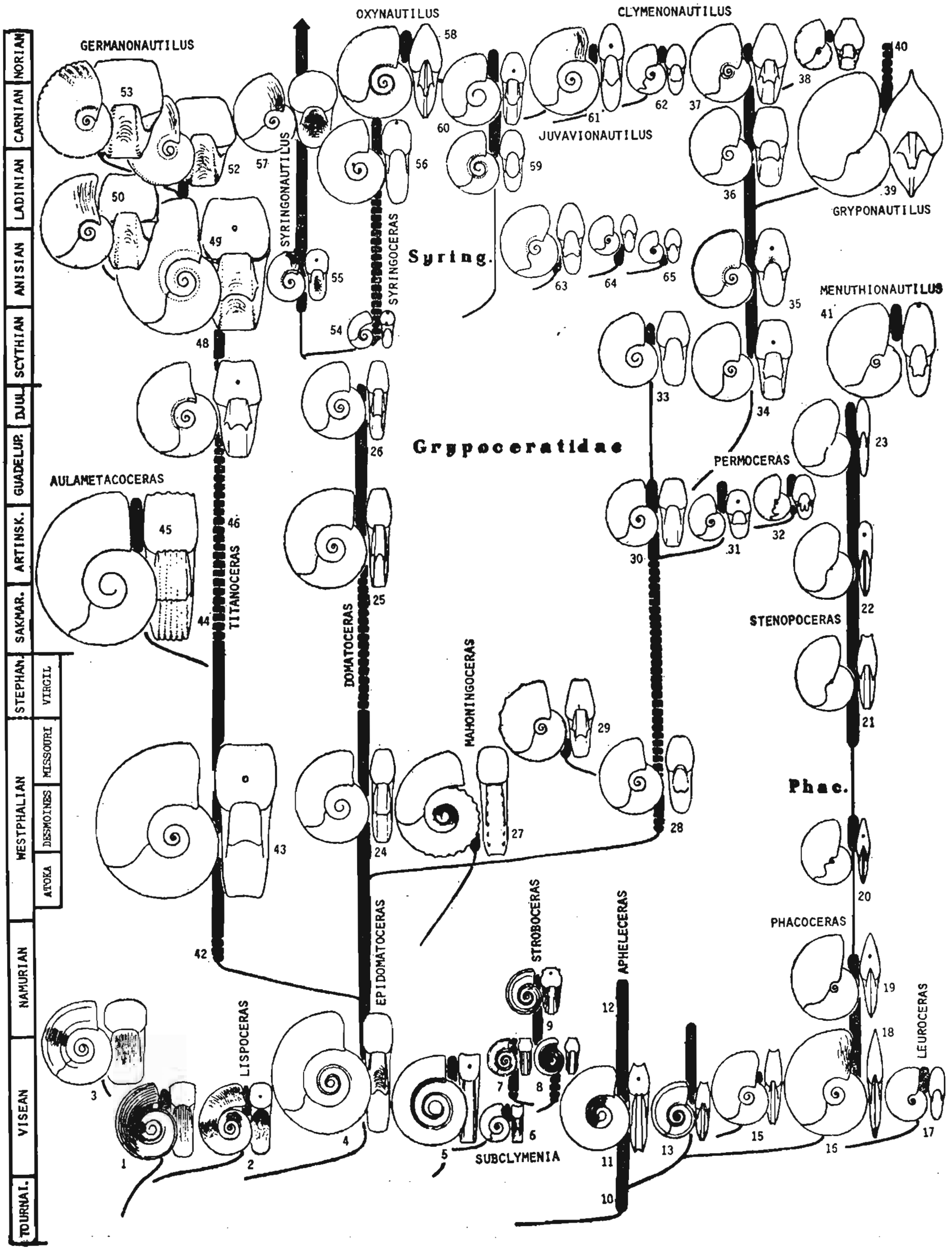
Strongly ornamented, small shells of various species of *Stroboceras* resemble very closely the juvenile shell of *Epidomatoceras* and its relatives (TURNER 1965). One may even attempt to trace a homology between particular longitudinal ribs and striae found in forms assigned by TURNER (1965) to the genera *Epidomatoceras*, *Stroboceras*, *Catastroboceras*, and *Pseudocatastroboceras*. In spite of a rich literature on *Stroboceras s. l.* (SCHMIDT 1956, TURNER 1965, MILLER and GARNER 1953, SHIMANSKY 1967) supplemented by a collection from the Visean of Cracow region (fig. 66c, d; pl. 42: 5-7, pl. 43: 4-5, pl. 44: 2), I am unable to determine whether these are adult specimens or juveniles of some externally dissimilar forms. Possibly, the type specimen of *Pseudocatastroboceras pulense* TURNER, 1965, is a mature shell. There are two species of *Stroboceras* in the Visean strata at Orlej quarry by Cracow, Poland, *S. duplicatum* SCHMIDT, 1951 (fig. 66d and pl. 43: 4-5) and *S. humerosum* SCHMIDT, 1951 (fig. 66f and pl. 42: 5-7). Both species show considerable variability, especially the shell ornamentation in *S. duplicatum*. Several species of *Stroboceras s. l.* were erected by TURNER (1965) on specimens derived from various localities and stratigraphic intervals, which makes recognition of their intrapopulation variability ranges impossible. One may, nonetheless, claim that at least some of those species (e. g. *Catastroboceras kilbridense*, *C. thornliebankense*, *Pseudocatastroboceras prestwichi*, *P. sholverense*) may fall within the range of intraspecific variability of *S. humerosus*. In fact, even *S. humerosus* itself may represent an end-member of intraspecific variation of one or another earlier described species. Such taxonomic problems cannot be solved, nor can a distinction be achieved between intrapopulation variability and evolutionary change, without revision of the original materials. Anyway, nothing can be accomplished by splitting these forms into many species attributed to various genera.

The juvenile specimens described from the Middle Visean of New South Wales under the name of *Vestinautilus* sp. (BROWN *et al.* 1964) may also be close to *Epidomatoceras* or some related genera, whereas *Knightoceras* sp. from these strata possibly represents the juvenile shell of *Temnocheilus* or *Vestinautilus* (*Subvestinautilus*).

There is no doubt that *Stroboceras* is related to *Aphelceceras*, the latter genus being characterized by a discoidal shell with concave venter; delimited by ribs, *Epistroboceras stubblefieldi* TURNER, 1954 from the Middle Visean of the Isle of Man (TURNER 1954) is intermediate in morphology between *Stroboceras* and *Apheleceras*. *A. mutabile* (MCCOY, 1844) from the Visean of Ireland (pl. 42: 8) differs from *E. stubblefieldi* mostly in the much larger initial whorl. The taxonomic value of this difference cannot be evaluated at the moment. The two forms under discussion may represent conspecific populations or distinct evolutionary grades within a single lineage. Unfortunately, there are no data on intrapopulation variability in the size of the initial whorl among the Carboniferous Nautilida.

The next stage of evolutionary flattening of the shell, which began in *Apheleceras*, may be represented by *Phacoceras oxystomum* (PHILLIPS, 1836) from the Visean (DELEPINE 1939, TURNER 1966, SHIMANSKY 1967). This is suggested by the angular juvenile venter in the lineage of *Phacoceras*, especially in its late representatives (SHIMANSKY 1967). The genera *Phacoceras*, *Epiphacoceras*, *Pseudostenopoceras*, and *Stenopoceras* appear to be members of a single evolutionary lineage displaying a trend to increasing shell involution and changing septal suture. Middle Visean *P. oxystomum* shows a relatively evolute shell with arched suture. *Epiphacoceras trochlea* (ROEMER, 1860) from the Late Visean is much more involute, with undulating suture (SCHMIDT 1951, TURNER 1966). *Pseudostenopoceras lenticulare* SHIMANSKY, 1967, from the Early Namurian and *P. rouilleri* (KONINCK, 1878) from the Early Westphalian have obvolute shells with increased undulation of the suture (SHIMANSKY 1967). Taking into account this evolutionary trend and also an increase in shell bulging and extension of ventral angularity over later ontogenetic stages, the genus *Stenopoceras* can be derived from *P. rouilleri*. *Stenopoceras* is represented by a few species ranging from the latest Carboniferous to the end of the Permian (HYATT 1891, MILLER 1932, MILLER and THOMAS 1936, CHAO 1940, MILLER and YOUNGQUIST 1949).

The Paleozoic Nautilida with bulgy and involute shell probably are monophyletic in origin (fig. 65). They appear to be linked to some bulgy species of *Vestinautilus* (*Subvestinautilus*), by the Visean form *Coloceras bistriale sensu* Foord, 1900 (? = *Potoceras dubium* Hyatt, 1894, see pl. 44: 5). The relationship of the latter to *Vestinautilus* is indicated by its lateral ribs, whereas its ovate whorl section resembles a smooth-shelled species from the Early Carboni-



ferous of Nova Scotia (KUMMEL 1964), *Diodoceras avonensis* (DAWSON, 1868). *D. avonensis* may have given rise to the evolutionary lineage of the genus *Peripetoceras* recorded from the Early (GORDON 1960) and Late Carboniferous (SHIMANSKY 1967, TUCKER and MAPES 1978, TUCKER *et. al.* 1978), and Permian (RUZHENTSEV and SHIMANSKY 1954; TICHY 1975). The last representative of this lineage of nom-ornamented, evolute nautiloids is *Peripetoceras freieslebeni* (GEINITZ, 1843) from the Guadelupian (?) of England (KUMMEL 1964).

Another evolutionary branch characterized by well developed lateral ribs, which resembles *Potoceras dubium*, started with *Liroceras bistriale* (PHILLIPS, 1836) from the Visean (fig. 66a-b and pl. 43: 5; TURNER 1954). *Liroceras* was recorded also in the Westphalian of Upper Silesia (PŘIBYL and RUŽIČKA 1954). Its best known species is "*Coloceras*" *milleri* NEWELL, 1936, from the Late Missourian Farley Limestone of Kansas. The juvenile shells of the Namurian species of *Liroceras* show a coarse longitudinal ornamentation (GORDON 1964*a*) indicative of a relationship to the Trigonoceratidae. *Liroceras* may have given rise to the Permian *Condraoceras*, Triassic *Paranautilus*, and possibly also *Coelogasteroceras*, the latter genus ranging from the Namurian to Lower Permian (GORDON 1964*a*) and characterized by a ventral furrow.

The above discussed bulgy and involute Nautilida show a transverse, straight septal suture, which is correlated with the uniformly rounded whorl section. In turn, the genus *Stearoceras* displays a suture with weak ventral undulation (GORDON 1964*a*), which suggests relationship to an important evolutionary lineage that started with *Ephippioceras clitellarium* (SOWERBY,

Fig. 65

Hypothetical phylogenetic relationships among members of the families Grypoceratidae, Syringonautilidae (? = Cenoceratidae), and Phacoceratidae; 1 *Vestinautilus semiglaber* FOORD, *Triboloceras formosum* FOORD; 2 *Thrincoceras hyatti* FOORD, *Discitoceras leveilleanum* (KONINCK), *Lispoceras trivolve* HYATT, *Maccoyoceras discors* (MCCOY), *Discitoceras costellatum* (MCCOY), *Pararineceras luidi* TURNER; 3 *Thrincoceras depressum* HYATT; 4 *Epidomatoceras planotergatum* (MCCOY), 5 *Mesochasmoceras latidorsatum* (MCCOY), *Mesochasmoceras mutabile* (MCCOY) (pl. 42: 7), 6 *Subclymenia evoluta* (PHILLIPS), 7 *Stroboceras humerosum* (SCHMIDT) (fig. 66f; pl. 42: 5, 6), *S. subsulcatum* (PHILLIPS), *Catastroboceras quadratum* (FLEMING), *Pseudocatastroboceras rawsoni* (INGLIS), *etc.*; 8 *Stroboceras duplicatum* SCHMIDT (fig. 66d, e; pl. 43: 3, 4; 44: 1); 9 *Stroboceras hartti* (DAWSON); 10 *Apheleceras disciforme* (MEEK and WORTHEN); 11 *Apheleceras hibernicum* (FOORD and CRICK); 12 *Apheleceras arkansanum* GORDON; 13 *Epistroboceras stubblefieldi* TURNER, *E. sulcatum* (SOWERBY); 14 *Subclymenia ornata* SHIMANSKY; 15 *Diorugoceras planidorsatum* (PORTLOCK); 16 *Phacoceras oxystomum* (PHILLIPS); 17 *Liroceras applanatum* HYATT; 18 *Epiphacoceras trochlea* (ROEMER); 19 *Pseudostenopoceras lenticulare* SHIMANSKY; 20 *Pseudostenopoceras rouilleri* (KONINCK), *P. solare* SHIMANSKY; 21 *Stenopoceras abundum* MILLER and THOMAS; 22 *Stenopoceras dumblei* (HYATT); 23 *Stenopoceras* sp.; 24 *Domatoceras umbilicatum* (HYATT); 25 *Plummeroceras plummeri* KUMMEL; 26 *Domatoceras parallelum* (ABICH), *Virgaloceras noduliferum* (REED); 27 *Mahoningoceras subquadrangulare* (WHITFIELD); 28 *Domatoceras inostranzevi* (TZVETAEVA); 29 *Domatoceras gardi* MURPHY; 30 *Permodomatoceras trapezoidale* RUZHENTSEV and SHIMANSKY; 31 *Neodomatoceras rarum* RUZHENTSEV and SHIMANSKY; 32 *Permoceras bitauniense* (HANIEL); 33 *Grypoceras brahmanicum* (GRIESBACH), *G. hexagonum* (DIENER); 34 *Grypoceras bidorsatoides* KUMMEL, *G. aemulans* KUMMEL, *G. ussuriense* KIPARISOVA; 35 *Grypoceras whitnei* (GABB), *Nautilus quandrangulus* BEYRICH, *N. privatus* MOJSISOVICS; 36 *Grypoceras buriji* KIPARISOVA; 37 *Grypoceras mesodicum* (HAUER); 38 *Gryponautilus cooperi* SMITH; 39 *Gryponautilus galeatus* (MOJSISOVICS), *G. ananiensis* POPOV, *G. suessi* MOJSISOVICS, *G. involutum* KIESLINGER; 40 *Indonautilus kraffti* MOJSISOVICS, *I. bambanagensis* (MOJSISOVICS); 41 *Menuthionautilus kieslingeri* COLLIGNON, *M. korzichi* KIPARISOVA, 42 *Domatoceras gigas* (TZVETAEV), 43 *Titanoceras ponderosum* (MEEK), *Domatoceras mosquense* (TZVETAEV), *D. podolskense* (TZVETAEV), *D. magister* SHIMANSKY, *Mosquoceras teschernyschevi shimanskyi* KALANDADZE, 44 *Kummeloceras* sp. SHIMANSKY, 45 *Aulametacoceras mackeei* MILLER and *Unklesbay*, 46 *Kummeloceras sibiricum* SHIMANSKY, 47 *Pseudotitanoceras armeniacum* (ABICH), *Domatoceras gracile* SHIMANSKY, 48 *Germanonautilus montpelierensis* KUMMEL; 49 *Germanonautilus dolomiticus* (QUENSTEDT) (fig. 63; pl. 43: 7); 50 *Germanonautilus bidorsatus* (SCHLOTHEIM) (fig. 64), *Tumidonautilus pertumidus* (ARTHABER); 51 *Germanonautilus furlongi* SMITH, *G. johnstoni* KUMMEL, *Nautilus salinarius* MOJSISOVICS, *N. tintoretti* MOJSISOVICS; 52 *Germanonautilus bruenneri* (HAUER); 53 *Germanonautilus schloenbachi* (MOJSISOVICS); 54 *Syringoceras praevolutum* KIPARISOVA; 55 *Syringonautilus lilianus* (MOJSISOVICS), *S. carolinus* (MOJSISOVICS); 56 *Syringoceras evolutum* (MOJSISOVICS); 57 *Syringonautilus bullatus* MOJSISOVICS, *Germanonautilus brooksi* SMITH, *Cenoceras trechmanni* (KUMMEL); 58 *Oxynautilus acutus* (HAUER); 59 *Nautilus longobardious* MOJSISOVICS; 60 *Juvavionautilus subtrapezoidale* MOJSISOVICS, *J. trapezoidale* (HAUER); 61 *Juvavionautilus haterophyllus* (HAUER); 62 *Clymenonautilus ehrlichi* (MOJSISOVICS); 63 *Nautilus palladi* MOJSISOVICS; 64 *Nautilus cancellatus* HAUER; 65 *Syringonautilus bosnensis* (HAUER).

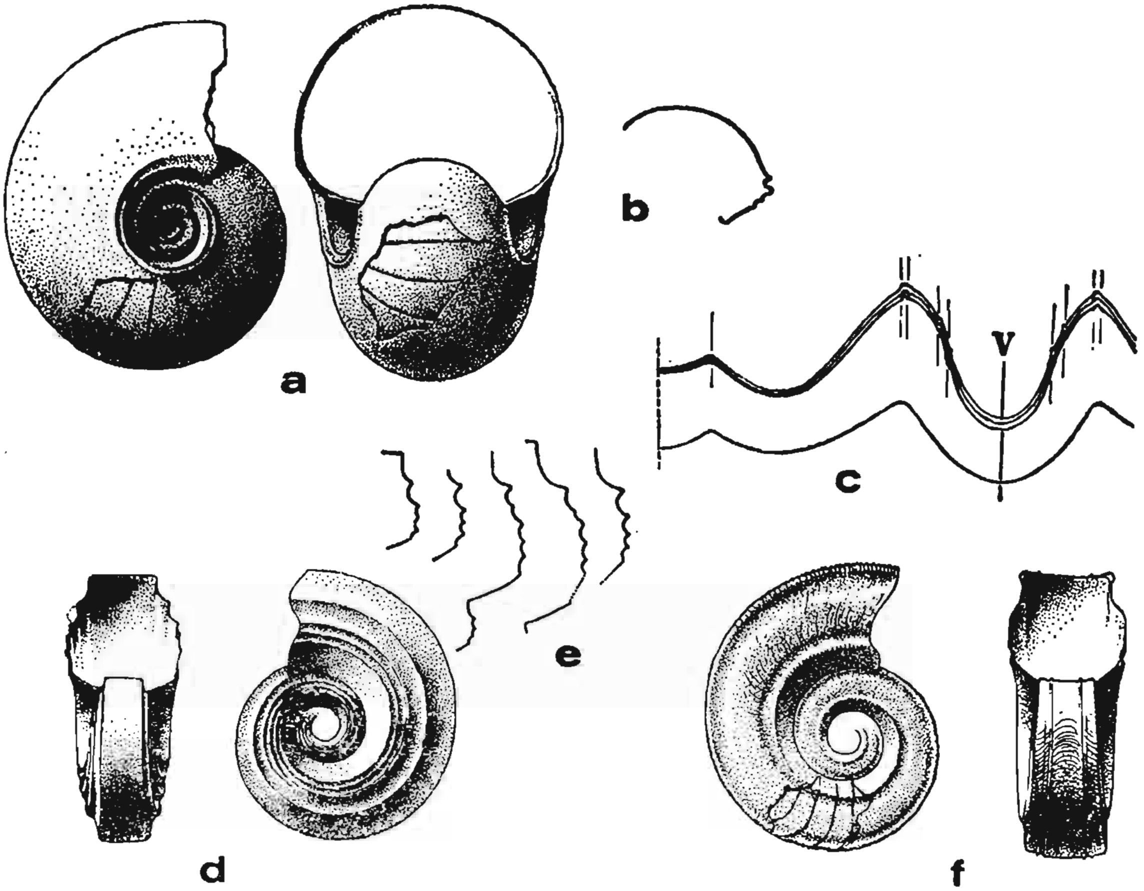


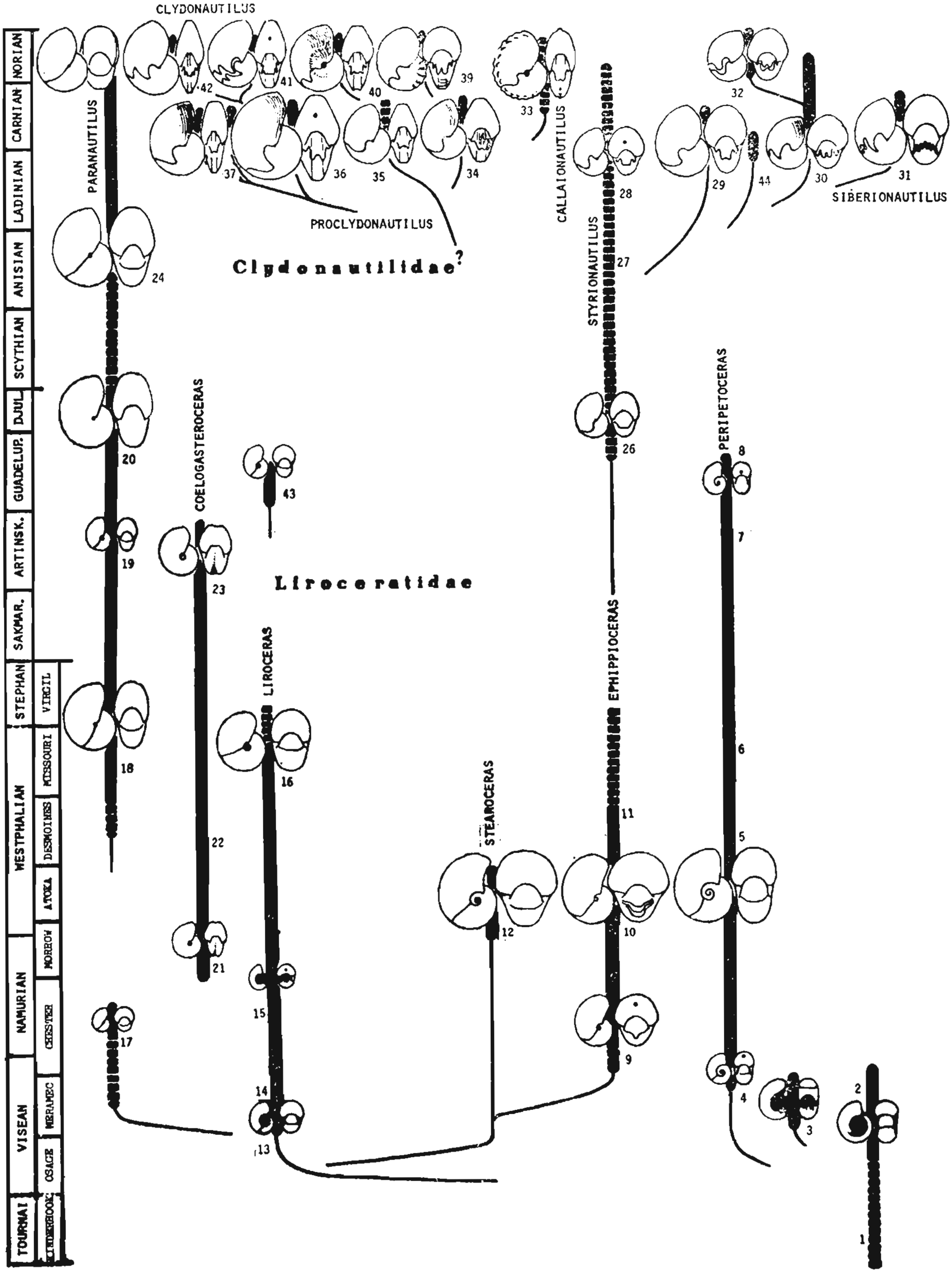
Fig. 66

Liroceras bistriale (Phillips, 1836); Visean (D_2), Orlej quarry, Zalas near Cracow, Poland; *a* Reconstruction of the subadult shell, from several specimens; *b* cross section of a whorl (see pl. 43: 5), ×2. *Stroboceras humerosus* (Schmidt, 1951); same horizon and locality; *c* Growth lines and the septal suture; *f* reconstruction of the subadult shell, from several incomplete specimens (pl. 43: 3, 4). *Stroboceras duplicatum* Schmidt, 1951; same horizon and locality; *d* Reconstruction of the subadult shell, from several incomplete specimens; *e* variation in the lateral ornamentation (twice enlarged) (see pl. 44: 1).

Fig. 67

Hypothetical phylogenetic relationships among members of the families Liroceratidae and Clydonautilidae; 1 *Nautilus pinguis* Koninck; 2 *Coloceras bistriale* (Phillips *sensu* Foord), *Potoceras dubium* Hyatt (see also pl. 44: 5), 3 *Planetoceras globatum* (Sowerby); 4 *Diodoceras avonensis* (Dawson); 5 *Peripetoceras fischeri* Shimansky, *P. wewokense* Tucker, Mapes and Aronoff; 6 *Peripetoceras* sp. Shimansky, *P. bridgeportense* Tucker and Mapes; 7 *Peripetoceras asselense* Ruzhentsev and Shimansky; 8 *Peripetoceras freieslebeni* (Geinitz); 9 *Ephippioceras clitellarium* (Sowerby); 10 *Ephippioceras ferratum* (Cox), *Megaglossoceras glicki* Gordon; 11 *Megagloglossoceras montgomeriensis* (Worthen); 12 *Stearoceras gibbosum* (Hyatt), *S. smithi* Gordon, *Knightoceras parvulum* Unklesbay; 13 *Liroceras fornicatum* Shimansky; 14 *Liroceras bistriale* (Phillips) (fig. 66a, b; pl. 43: 5); 15 *Liroceras bicostatum* Gordon, *Bistrialites bimembris* Shimansky; 16 *Liroceras dubium* Miller and Unklesbay, *L. liratum* (Girty), *Coloceras milleri* Newell; 17 *Liroceras ruzhentsevi* Shimansky; 18 *Condraoceras primum* Miller, Lane and Unklesbay; 19 *Condraoceras ellipsoidale* Ruzhentsev and Shimansky; 20 *Paranautiluus* cf. *peregrinus* (Waagen); 21 *Coelogasteroceras gracile* Gordon; 22 *Coelogasteroceras coxi* Gordon; 23 *Coelogasteroceras mexicanum* Girty; 24 *Paranautilus smithi* Kummel, *Nautilus pseudobrembranus* Assmann; 25 *Paranautilus simonyi* (Hauer), *P. modestus* (Mojsisovics), *Sibyllonautilus fergusoni* Kummel; 26 *Styrionautilus* sp. Shimansky; 27 *Styrionautilus* sp. Kummel; 28 *Styrionautilus styriacus* (Mojsisovics); 29 *Proclydonautilus triadicus* (Mojsisovics); 30 *Proclydonautilus goniatites* (Hauer); 31 *Siberionautilus multilobatus* Popov; 32 *Proclydonautilus spirolobus* (Dittmar); 33 *Callaionautilus turgidus* (Kieslinger); 34 *Clydonautilus sauperi* (Hauer); 35 *Proclydonautilus griesbachi* (Mojsisovics); 36 *Cosmonautilus dilleri* Hyatt and Smith; 37 *Cosmonautilus shastensis* Smith; 38 *Cosmonautilus pacificus* Smith; 39 *Proclydonautilus gasteroptychus* (Dittmar); 40 *Gonionautilus quenstedti* (Hauer); 41 *Clydonautilus noricus* (Mojsisovics); 42 *Gonionautilus securis* (Bitter); 43 *Alexandronautilus abichi* (Kruglov); 44 *Proclydonautilus ursensis* Smith.

1840), (see Roemer 1861*b*; Delepine 1937, Shimansky 1967). *Ephippioceras* ranges to the Late Namurian (Gordon 1964), where it is replaced with *Megaglossoceras* beginning with the Early Westphalian; the latter shows a wider ventral saddle (Shimansky 1967, Gordon 1964*a*). Most



data on this group are based on poorly preserved and fragmentary specimens, which makes detailed study of the evolution impossible.

In addition to *Paranautilus*, there is in the Triassic another lineage of involute nautiloids, namely that of the genus *Styrionautilus*, known since the latest Permian (Shimansky 1965). *Styrionautilus*, is indistinguishable from *Paranautilus* in its shell shape but its considerably undulating septal suture suggests relationship to *Megaglossoceras*. The fossil record between the Late Permian species of *Styrionautilus* and its Late Triassic congener, *S. styriacus* (Mojsisovics, 1873) is very scarce (Kummel 1953). Kummel (1953) claimed that *Styrionautilus* began the great radiation of Late Triassic involute nautiloids with complex suture which are attributed to the family Clydonautilidae. Out of this group, the genus *Proclydonautilus* appears to be closest to the ancestral *Styrionautilus*. It can, however, be divided into two subgroups widely different in shell ontogeny and whorl section. One of these, close to *S. styriacus* and characterized by an ovate section of the juvenile as well as adult whorls, includes *P. triadicus* (Mojsisovics, 1873), *P. ursensis* Smith, 1927, and *P. goniatites* (Hauer, 1849) from the Carnian, and *P. spirolobus* (Dittmar, 1868) from the Norian. This subgroup may have given rise to *Siberionautilus multilobatus* Popov, 1951, from the Carnian of Siberia. The other subgroup includes the type species of *Proclydonautilus*, *P. griesbachi* (Mojsisovics, 1896) and other species with trapezoidal juvenile whorls, which are usually assigned to the genus *Cosmonautilus*. The two species' groups hitherto assigned to *Proclydonautilus* resemble each other closely in their adult shell, but their markedly different shell ontogenies suggest different evolutionary origins. Whorl section and suture observed in the group of *P. griesbachi* permit the hypothesis that this group gave rise to the Norian species of *Gonionautilus* and *Clydonautilus*. However, a phylogenetic relationship of the genera Proclydonautilus *s. s.*, *Clydonautilus*, and *Gonionautilus* to *Styrionautilus*, as claimed by Kummel (1953), appears to be less likely than their derivation from *Gryponautilus* (Grypoceratidae). Therefore, I propose to place the group of *P. triadicus* in the genus *Styrionautilus*, and to transfer *Styrionautilus* along with its descendant *Siberionautilus* to the family Liroceratidae *s.l.*

Proposed systematics. —

Trigonoceratidae Hyatt, 1884

Loosely coiled or evolute shell with lateral ribs and wide whorl cross section.

Triboloceras Hyatt, 1884; *Gyroceras serratum* Koninck, 1844
[= *Rineceras* Hyatt, 1893; *Chouteaucceras* Miller and Garner, 1953]
Loosely coiled shell with longitudinal ribs.

Trigonoceras McCoy, 1844; *Orthocera paradoxica* Sowerby, 1825
Loosely coiled shell with ventro-lateral and dorsal ribs.

Vestinautilus Ryckholt, 1852; *Nautilus konincki* d'Orbigny, 1850
[= *Subvestinautilus* Turner, 1954; *Potoceras* Hyatt, 1894]
Evolute shell with 1-3 lateral ribs.

Lispoceras Hyatt, 1893; *L. trivolve*
[= *Discitoceras* Hyatt, 1884; *Pararineceras* Turner, 1954; *Thrincoceras* Hyatt, 1893; *Maccoyoceras* Miller, Dunbar and Condra, 1933]
Evolute shell with numerous longitudinal ribs.

Temnocheilus McCoy, 1844; *Nautilus (Temnocheilus) coronatus*
Evolute shell with a single lateral rib split into tubercles.

Endolobus Meek and Worthen, 1865; *Nautilus spectabilis* Meek and Worthen, 1960
[= *Edaphoceras* Hyatt, 1884; *Knightoceras* Miller and Owen, 1934; *Valhallites* Shimansky, 1959]
Lateral ribs disappearing on the adult stages.

Tylodiscoceras Miller and Collinson, 1950; *T. unicum*
Evolute shell with lateral tubercles and ventral furrow.

Phacoceratidae Shimansky, 1962

Flat shell with venter delimited by sharp edges at least at the juvenile stages.

Apheleceras Hyatt, 1884; *Nautilus (Discites) disciformis* Meek and Worthen, 1873

[= *Epistroboceras* Turner, 1954; *Diorugoceras* Hyatt, 1893]
Evolute shell with concave venter.
Phacoceras Hyatt, 1884; *Nautilus oxystomus* Phillips, 1836
[= *Epiphacoceras* Turner, 1966; *Pseudostenopoceras* Shimansky, 1967]
Flat shell with sharp venter; shell involution increasing in the course of the evolution.
Stenopoceras Hyatt, 1893; *Phacoceras dumblei* Hyatt, 1891
Involute shell with deep umbilicus and flat venter with sharp edges.
?Leuroceras Hyatt, 1893; *L. applanatum*
Involute shell with rounded venter.

Tainoceratidae Hyatt, 1882

[= Rhiphaeoceratidae Ruzhentsev and Shimansky, 1954; Mosquoceratidae Ruzhentsev and Shimansky, 1954]
Evolute shell with lateral transverse ribs sometimes transformed into tubercles or spines.
Gzheloceras Ruzhentsev and Shimansky, 1954; *G. uralense*
[= *Celox* Shimansky, 1967]
Whorl ovate in section, with lateral ribs confined to the mid-flank.
Anoploceras Hyatt, 1900; *Nautilus wulfeni* Mojsisovics, 1873
[= *Encoiloceras* Hyatt, 1900; *Holconautilus* Mojsisovics, 1902]
Like *Gzheloceras* but with somewhat longer lateral ribs.
Tylonautilus Pringle and Jackson, 1928; *Nautilus (Discites) nodiferus* Armstrong, 1866
Tubercles at intersection of numerous longitudinal ribs with lateral transverse ribs.
Tainoceras Hyatt, 1883; *Nautilus quadrangulus* McChesney, 1860
[= *Hexagonites* Hayasaka, 1947; *Neotainoceras* Zhao, Liang and Zheng, 1978]
Shell with concave venter; some longitudinal rows of tubercles.
Tainionautilus Mojsisovics, 1902; *Nautilus transitorius* Waagen, 1879
[= *Thuringionautilus* Mojsisovics, 1902]
Shell with numerous transverse ribs reaching to narrow ventral furrow.
Seironautilus Zhao, Lian and Zheng, 1978; *S. nodosus*
[= *Eulomacoceras* Zhao, Liang and Zheng, 1978; *Clavinautilus* Zhao, Liang and Zheng, 1978; *Liometacoceras* Zhao, Liang and Zheng, 1978; *Paratainonautilus* Zhan, Liang and Zheng, 1978]
Close to *Tainionautilus* but with incipient ventral tubercles.
Pleuronautilus Mojsisovics, 1882; *P. trinodosus*
[= *Sholakoceras* Ruzhentsev and Shimansky, 1954]
Lateral ribs split ventraly into longitudinal rows of tubercles which may be transformed into longitudinal ribs.
Pseudotemnocheilus Ruzhentsev and Shimansky, 1954; *Nautilus posttuberculatus* Karpinsky, 1874
[= *Temnocheiloides* Shimansky, 1967]
Flat shell with transverse ribs ending in ventro-lateral tubercles.
Cooperoceras Miller, 1945; *C. texanum*
Like *Pseudotemnocheilus*, but with long ventro-lateral spines.
Metacoceras Hyatt, 1883; *Nautilus (Discites) sangamonensis* Meek and Worthen, 1861
[= *Enoploceras* Hyatt, 1900; *Parametacoceras* Miller and Owen, 1934; *Phaedrysmocheilus* Shimansky and Erlanger, 1955; *Mojsvaroceras* Hyatt, 1883]
Shell with dorso-lateral edges and ventro-lateral tubercles; whorl section wide trapezoidal.
Articheilus Ruzhentsev and Shimansky, 1954; *A. luxuriosum*
[= *Mosquoceras* Ruzhentsev and Shimansky, 1954; *Leonardocheilus* Ruzhentsev and Shimansky, 1954]
Shell with ventro-lateral tuberculate ribs; whorl section reverse-trapezoidal.
?Librovitschiceras Shimansky, 1957; *Nautilus atuberculatus* Tzvetaeva, 1888
?Foordiceras Hyatt, 1893; *Nautilus goliathus* Waagen, 1879
Tirolonautilus Mojsisovics, 1902; *Nautilus crux* Stache, 1877

Grypoceratidae Hyatt, 1900

[= *Permoceratidae* Miller and Collinson, 1953]

Shell section trapezoidal, smooth in the adult stages.
Epidomatoceras Turner, 1954; *Nautilus planotergatum* McCoy, 1836
[= *?Mesochasmoceras* Foord, 1900; *Pseudocatastroboceras* Turner, 1965; *Paradomatoceras* Delepine, 1937; *Catastroboceras* Turner, 1965]
Juvenile whorls angular and ornamented, adult whorls with ovate section and smooth.
Domatoceras Hyatt, 1891; *D. umbilicatum*

[= *Plummeroceras* KUMMEL, 1953; *Virgaloceras* SCHINDEWOLF, 1954; *Permodomatoceras* RUZHENTSEV and SHIMANSKY, 1954]

Flat, evolute shell with high trapezoidal whorl section.

Titanoceras HYATT, 1884; *Nautilus ponderosus* MEEK, 1873
[= *Kummeloceras* SHIMANSKY, 1967; *Pseudotitanoceras* SHIMANSKY, 1965]

Very large shell with subsquare whorl section.

Aulametacoceras MILLER and UNKLESBAY, 1942; *A. mackeei*

Like *Titanoceras*, but venter ornamented with longitudinal ribs.

Germanonautilus MOJSISOVICS, 1902; *Nautilus bidorsatus* SCHLOTHEIM, 1832
[= *Tumidonautilus* DIENER, 1915]

Weakly involute shell with wide trapezoidal whorl section.

Grypoceras HYATT, 1883; *Nautilus mesodicus* QUENSTEDT, 1845
[= *Neodomatoceras* RUZHENTSEV and SHIMANSKY, 1954]

Involute, flat shell with subtrapezoidal whorl section.

Gryponautilus MOJSISOVICS, 1902; *Nautilus galeatus* MOJSISOVICS, 1873
[= *Indonautilus* MOJSISOVICS, 1902]

Obvolute shell with keeled venter in the adult stages.

Permoceras MILLER and COLLINSON, 1953; *Nautilus* (*Aganides*) *bitauniensis* HANIEL, 1925

Involute, flat shell, septal suture with deep ventral and lateral sinuses.

?Neostenopoceras ZHAO, LIANG and ZHENG, 1978; *N. guangdeense*

Poorly known.

Subclymenia d'ORBIGNY, 1849; *Goniatites evolutus* PHILLIPS, 1836

Evolute shell with concave venter delimited by sharp edges; septal suture with lateral sinuses.

Stroboceras HYATT, 1884; *Gyroceras hartti* DAWSON, 1868

Evolute shell ornamented with numerous longitudinal ribs; whorl section subtrapezoidal with flat venter delimited by sharp edges.

Mahoningoceras MURPHY, 1974; *Nautilus* (*Gyroceras?*) *subquadrangularis* WHITFIELD, 1882

Close to *Epidomatoceras*, but with ventro-lateral tubercles.

Clydonautilidae HYATT, 1900

[= Gonionautilidae KUMMEL, 1950

Involute shell with deep umbilicus, whorl section subtrapezoidal; septal suture with deep lateral sinuses.

Callaionautilus KIESLINGER, 1924; *C. turgidus*

Poorly known.

Proclydonautilus MOJSISOVICS, 1902; *Nautilus griesbachi* MOJSISOVICS, 1896
[= *Cosmonautilus* HYATT and SMITH, 1905]

Ovate lateral lobe of septal suture.

Clydonautilus MOJSISOVICS, 1882; *Nautilus noricus* MOJSISOVICS, 1873
[= *Gonionautilus* MOJSISOVICS, 1902]

Sharp-ended main lateral sinus supplemented with additional ventro-lateral sinuses.

Syringonautilidae MOJSISOVICS, 1902

Longitudinally striated, evolute shell with ovate to fastigate section.

Syringonautilus MOJSISOVICS, 1902; *Nautilus lilianum* MOJSISOVICS, 1882
[= *?Cenoceras* HYATT, 1884]

Whorl section subquadratic to ovate; subcentral siphuncle.

Syringoceras HYATT, 1894; *Ammonites? granulosostriatum* KLIPSTEIN, 1843

Like *Syringonautilus*, but with ventral siphuncle.

Juvavionautilus MOJSISOVICS, 1902; *Nautilus heterophyllus* HAUER, 1849

Whorl section ovate triangular.

?Oxynautilus MOJSISOVICS, 1902; *Nautilus acutum* HAUER, 1846

Weakly involute shell with keeled venter and triangular whorl section.

Clymenonautilus HYATT, 1900; *Nautilus ehrlichi* MOJSISOVICS, 1873

Like *Juvavionautilus*, but septal suture with sharp-ended lateral lobe.

?Menuthionautilus COLLIGNON, 1933; *Nautilus* (*Menuthionautilus*) *kieslingeri*

Involute flat shell with ovate whorl section, ventral siphuncle.

?Phloioceras HYATT, 1884; *Nautilus gemmatum* MOJSISOVICS, 1878
[= *Trachynautilus* MOJSISOVICS, 1902]

Shell ornamented with numerous longitudinal ribs.

Liroceratidae MILLER and YOUNGQUIST, 1949

[= Ephippioceratidae MILLER and YOUNGQUIST, 1949; Siberionautilidae POPOV, 1951]

Involute and bulgy shell with ovate whorl section.

Peripetoceras HYATT, 1894; *Nautilus freieslebeni* GEINITZ, 1843
[= *Diodoceras* HYATT, 1900]
Relatively evolute and flat shell.

Coelogasteroceras HYATT, 1893; *Nautilus canaliculatus* COX, 1858
Shell with narrow umbilicus and shallow ventral furrow.

Stearoceras HYATT, 1893; *Endolobus gibbosus* HYATT, 1891
Wide shell with narrow umbilicus.

Paranautilus MOJSISOVICS, 1902; *Nautilus simonyi* HAUER, 1849
[= *Condraoceras* MILLER, LANE and UNKLESBAY, 1947]
Obvolute but relatively flat shell.

Liroceras TEICHERT, 1940; *Coloceras liratum* GIRTY, 1911
[= *Bistrialites* TURNER, 1954]
Homeomorphic with *Paranautilus*.

Ephippioceras HYATT, 1884; *Nautilus ferratus* COX, 1858
[= *Megaglossoceras* MILLER, DUNBAR and CONDRA, 1933]
Wide shell, septal suture with ventral saddle.

Styrionautilus MOJSISOVICS,1902; *Nautilus styriacus* MOJSISOVICS, 1873
Septal suture with trapezoidal ventral saddle and rounded lateral lobes.

Siberionautilus POPOV, 1951; *S. multilobatus*
Septal suture with additional ventro-lateral lobes.

Suborder **Nautilina** AGASSIZ, 1847

Phylogeny (fig. 71). — An outline phylogeny of the post-Triassic nautiloids was presented by KUMMEL (1965), WIEDMANN (1961), and TINTANT (1969). The data on the Cretaceous Nautilina were reviewed by SHIMANSKY (1975). The post-Triassic nautiloids are relatively well known, although the species concept implicit in various papers may be disputable. Below, I shall discuss only the most important episodes in the evolutionary history of this group.

The Jurassic species of *Cenoceras* (see PIA 1915) show a continuous evolutionary transition from the Triassic representatives of *Syringonautilus* (see MOJSISOVICS 1882). According to KUMMEL (1959), *Cenoceras* evolved from *Syringonautilus* through an increase in shell involution. The Anisian *S. lilianus* (MOJSISOVICS, 1882) has a relatively evolute, flat shell. Its Carnian successor, *S. bullatus* (MOJSISOVICS, 1882), shows a more bulgy and involute shell; whereas the species *C. treichmanni* (KUMMEL, 1953) has been assigned to *Cenoceras* merely because of its slightly narrower umbilicus. The boundary between *Syringonautilus* and *Cenoceras* has therefore been traced arbitrarily. At the present moment, one cannot give diagnoses of the two genera which would clearly separate them from each other, because the ranges of their morphological variations overlap. The assignment of *Syringonautilus* and *Cenoceras* to distinct families also is disputable.

The type species of *Cenoceras*, *C. intermedius* (SOWERBY, 1816), differs from *C. trechmanni* in its even narrower umbilicus. As understood by KUMMEL (1954, 1956) and TINTANT and COURBOULEIX (1974), the genus *Cenoceras* includes forms widely variable in whorl section, shell involution, and ornamentation. In my opinion, it is more reasonable to restrict the range of the genus to longitudinally striated forms with ovate whorls. *Cenoceras* then becomes a senior subjective synonym of *Syringonautilus*. In turn, such species as *C. excavatus* (SOWERBY, 1826) or *C. araris* (DUMORTIER, 1869), ornamented exclusively with growth lines, should be recognized as a distinct genus, *Ophionautilus*. The latest representative of the main evolutionary lineage of *Cenoceras* is *C. calloviense* (OPPEL, 1858) (? = *N. rollieri* LOESCH, 1914) from the Late Callovian to Early Oxfordian (fig. 69 an pl. 45: 3, 4). The longitudinal striation typical of the genus becomes less and less distinct in the ontogeny of this species, but nonetheless persists to the last whorl. Both the striation and the ovate whorl section of *C. calloviense* indicate its close relationship to typical representatives of *Cenoceras*, while distinguishing it from *Paracenoceras s. s.* One may therefore claim that *Paracenoceras* evolved from some other species of *Cenoceras*.

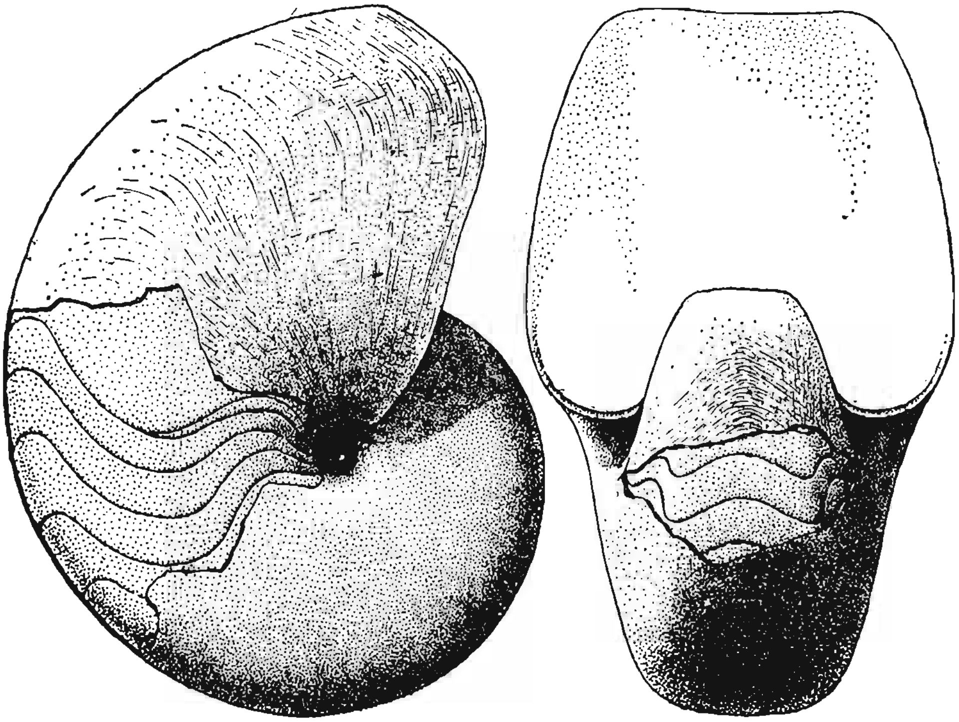


Fig. 68

Cenoceras calloviense (OPPEL, 1858); Late Callovian, Łapiguz near Łuków, Poland; reconstruction of the adult shell mostly after the specimen MGUW (6/7/1 (pl. 45: 4); note incomplete las septum.

TINTANT (1969*b*) claimed that there is a sexual dimorphism, with *C. blakei* (JEANNET, 1951) as the macroconch, and typical *C. calloviense* as the microconch. However, the evidence presented by TINTANT is unconvincing. As judged from the increase in density of growth lines, only a single specimen figured by TINTANT (1969*b*, pl. 11: 1) is mature. Actually, this is the largest specimen in TINTANT'S collection, with concave venter delimited by sharp edges. The mature specimens of *C. calloviense* found at Łuków, Poland (fig. 68 and pl. 45: 3, 4), as well as at Papilé, Lithuania (KRENKEL 1915, pl. 23: 1-2), show invariab'y a much smaller shell with the last whorl ovate in cross section. Possibly, the specimens regarded by TINTANT (1969*b*) as microconchs are conspecific with *C. calloviensis*, but the absence from Łuków and Popielany of any forms that could be recognized as macroconchs makes this hypothesis untenable. In my opinion, it is more likely that the angulate species *O. blakei* interpretes as á macroconch actually belongs to a distinct evolutionary lineage, namely one leading to the genus *Paracenoceras*. Mature specimens of the Oxfordian species *P. hexagonum* (SOWERBY, 1826) (? = *Nautilus giganteus* d'ORBIGNY, 1842; see KUHN 1936) are distinctly angulate with a concave venter (fig. 69), whereas the juvenile shell resembles *Cenoceras* in outline (pl. 45).

An extremely involute shell ornamented as in typical *Cenoceras* is *C. simillissimum* (FOORD and CRICK, 1890) from the Early Jurassic of England (KUMMEL 1956). This may be the ancestor of the genus *Eutrephoceras* derived by KUMMEL (1956) and WIEDMANN (1961) from *Cenoceras*. However, the shell shape and straight septal suture of *Eutrephoceras* resemble those of the Triassic liroceratid, *Paranautilus*. In fact, *Cenoceras chilense* (HUPPÉ, 1854) from the Early Jurassic may link the Norian species *Paranautilus simonyi* (HAUER, 1849) and later, Jurassic species of *Eutrephoceras* (see KUHN 1939). The absence of data on Rhaetian nautiloids cannot be considered as evidence for the extinction of all nautiloids at the end of the Norian, except for a single evolutionary lineage of the genus *Cenoceras*. Some other Jurassic nautiloid lineages also may have started in the Triassic. The genus *Eutrephoceras* is regarded as ancestral to all Cretaceous nautiloids (KUMMEL 1956, WIEDMANN 1961). However, the available data do not permit demonstration of evolutionary transitions from *Eutrephoceras* to any other genus. *Eutrephoceras* persisted in Australia up to the end of the Miocene (CHAPMAN 1914); hence, it preceded in that area the extant genus *Nautilus*. However, there is no morphologic affinity between the Miocene representatives of *Eutrephoceras* and Recent *Nautilus* (STENZEL 1964). Most thus far described species of *Eutrephoceras* are in need of critical revision, as they may differ from one another chiefly in preservation and distortion of the type specimens (see WIEDMANN 1961, SHIMANSKY 1975).

Undulated septal suture appeared independently in various nautiloid lineages. This is also the case with the Nautilina. The oldest example with such an undulation among the Nautilina is "*Pseudaganides*" *kochi* (PRINZ, 1906) from the earliest Jurassic. Its flat shell is close to *Cenoceras araris*, and there is no reason to suppose that it is related to typical species of *Pseudaganides* known, according to MARCHAND and TINTANT (1971), since the Aalenian. *O. calloviense* also shows a suture (fig. 68) very close to that of *Pseudaganides*. However, the earliest typical representatives of *Pseudaganides* differ from *C. calloviensis* in their concave venter being delimited by sharp edges (TINTANT 1971). The ancestor of *Pseudaganides* is therefore to be looked for among such forms as *C. blakei*. As biometrically demonstrated by TINTANT (1971), species of *Pseudaganides* display considerable intrapopulation variability. *Pseudaganides* occurs abun-

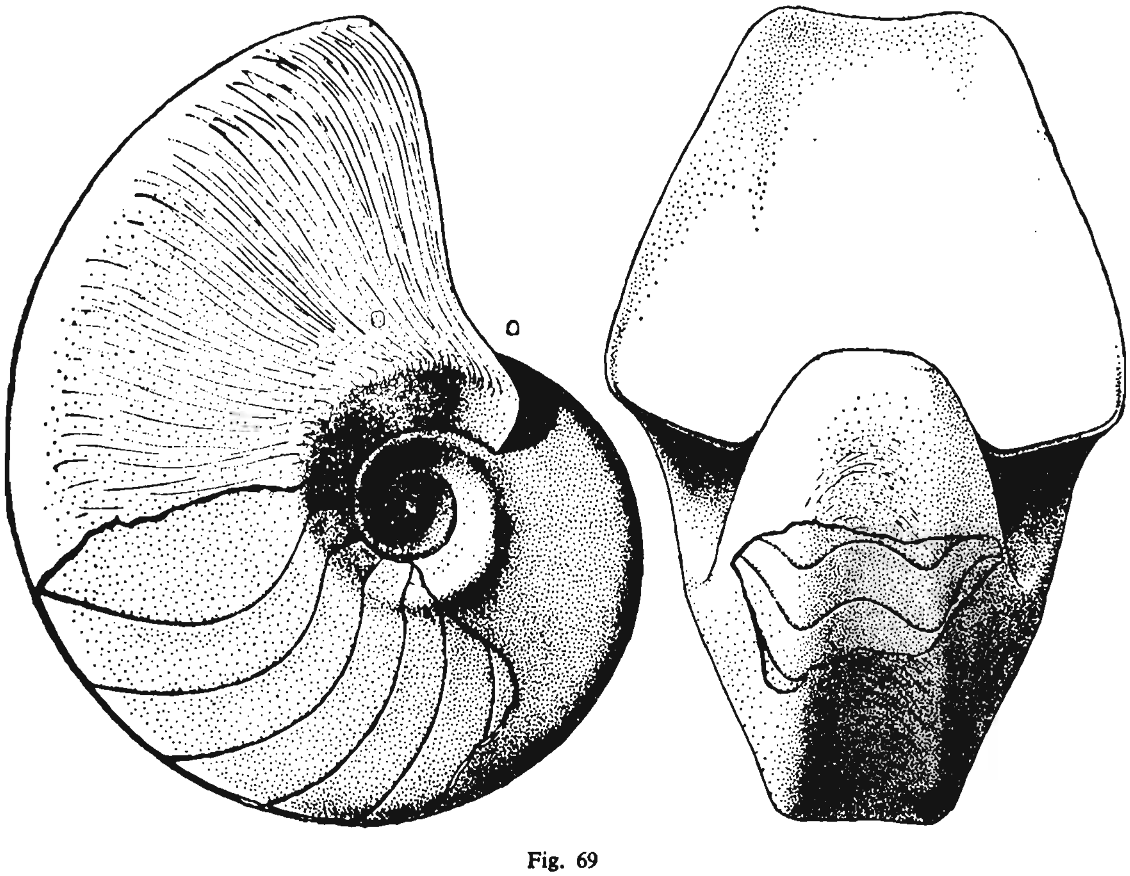


Fig. 69
Paracenoceras hexagonum (SOWERBY, 1826); *Idoceras planula* Zone, Late Oxfordian, Bukowa Góra, southern margin of the Holy Cross Mts, Poland; reconstruction of the shell, ×0.66 mostly after the specimen ZPAL N/863.

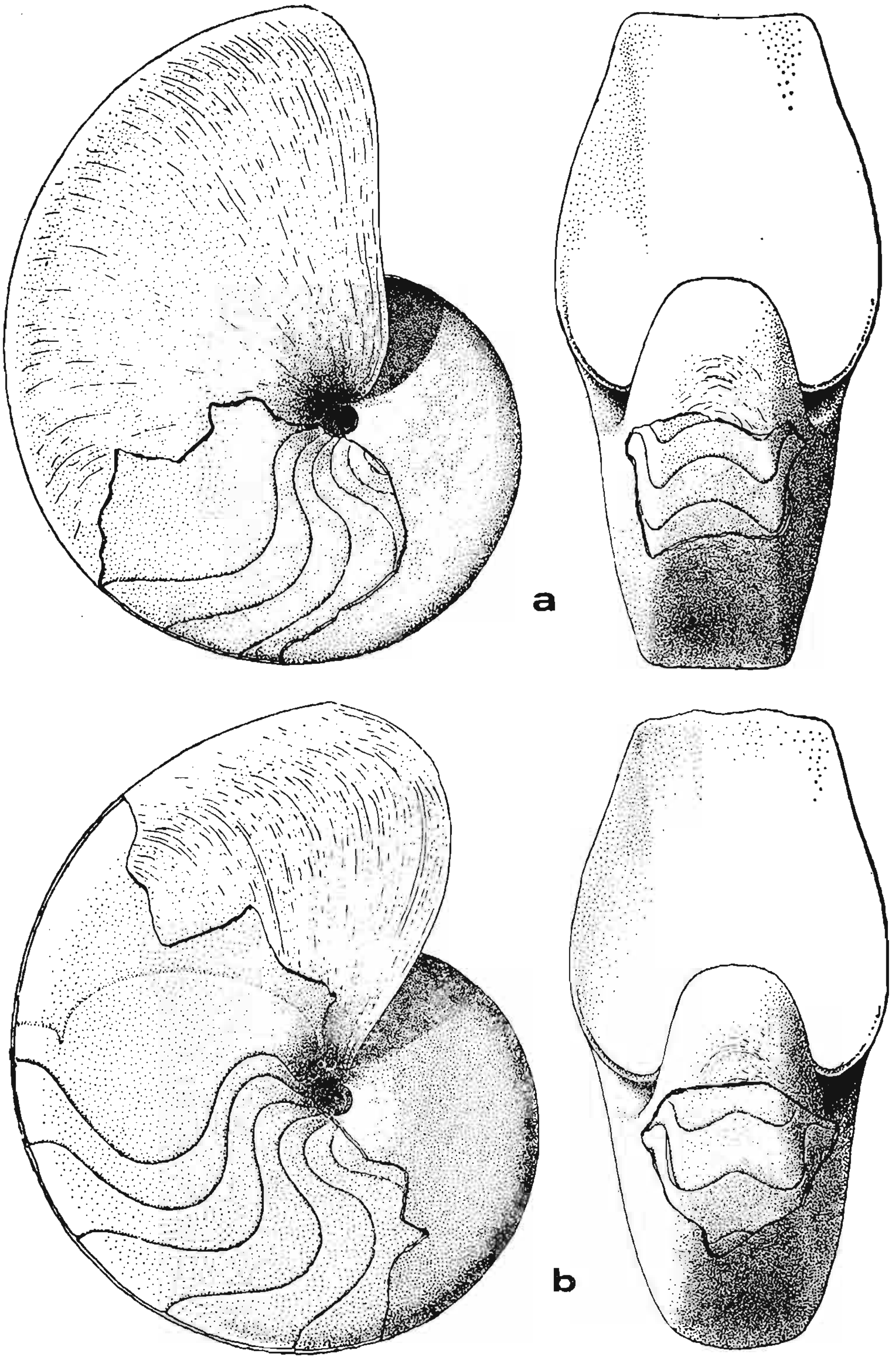


Fig. 70

Pseudaganides sp.; Late Callovian, Lasocin, southern margin of the Holly Cross Mts, Poland; *a* Reconstruction of the adult shell (see pl. 46: 1). *Pseudaganides aganiticus* (SCHLOTHEIM, 1820); *Perisphinctes bifurcatus* Zone, Oxfordian, Tokarnia, southwestern margin of the Holy Cross Mts, Poland. *b* Reconstruction of the adult shell, mostly from the specimen ZPAL N/890 (pl. 47: 5); the arched line at the surface of the living chamber may represent the outline of the pedal retractor scar, but this may be an artifact as well.

dantly in Poland, ranging from the Late Callovian through Early Kimmeridgian. Its Late Callovian representatives differ sharply from the succeeding forms in their slightly concave venter being delimited by ribs (fig. 70a and pl. 45: 1). In turn, they resemble *P. frickensis* JEANNET, 1948, from the Early Callovian of France. The Early Oxfordian to Early Kimmeridgian Polish populations have a slightly convex venter and relatively deep undulation of the suture (fig. 70b); however, there is a considerable intrapopulation variability in lobe depth (pl. 46), and no evolutionary trend towards increasing undulation can be discerned. The investigated material was collected from the southern margin of the Holy Cross Mts and from the Częstochowa Upland. These two regions were at that time marginal parts of a single narrow basin and, therefore, the occurrence of more than one species of *Pseudoganides* in this collection appears to be unlikely. One may claim that the observed variation is intrapopulation variability. Some other species of *Pseudaganides* (see LOESCH 1914), therefore, seem to be too narrowly defined. Forms indistinguishable in shell morphology from the Oxfordian-Kimmeridgian species *P. aganiticus* (SCHLOTHEIM, 1820) occur in France at least since the Bathonian (MARCHAND and TINTANT 1971). Thus, *P. aganiticus* from the Early Oxfordian of Poland did not evolve from the Late Callovian *P.* sp.

Very deep and pointed lobes occur in the suture of *Pseudonautilus geinitzi* (OPPEL, 1868) from the Tithonian to Berriasian (SHIMANSKY 1975). This is a descendant of *Pseudaganides*, with the Early Tithonian species *Pseudonautilus* (*Bavarinautilus*) *eurychoros* SCHAIRER and BARTHEL, 1977, being an intermediate evolutionary stage. The latter species does not have pointed lobes and ovate whorls and, hence, its assignment to *Pseudonautilus* is unjustified. Its external shell shape resembles very closely that of *P. aganiticus*, and its sutural undulation exceeds only a little the range of intrapopulation variability observed in the Early Kimmeridgian populations of the latter species (cf. pl. 46; SCHAIRER and BARTHEL 1977, pl. 12). Hence, there is no need to establish a new subgenus. *P. eurychoros* is known from two incomplete specimens co-occurring in the Early Tithonian Korallenkalk of Laisacker with equally rare specimens of *Pseudaganides schneidi* (LOESCH, 1912). This raises the question of the specific distinctness of *P. eurychoros.*

The genus *Cymatoceras* is linked with *Cenoceras* by a fairly complete morphological sequence of successive forms. *Procymatoceras subtruncatum* (MORRIS and LYCETT, 1850) from the Bajocian of England (KUMMEL 1956) displays an obvolute shell ornamented on the adult stages exclusively with irregular growth lines. A similar large form occurs also in the Bajocian of Łęczyca, Central Poland (pl. 45: 1). The involute shell, the septal suture and the weakly angulate whorl section are indicative of derivation of these forms from some involute representatives of *Cenoceras*. The evolutionary transition from *Cenoceras* should have consisted in the reduction of the longitudinal striation, as in some other lineages descendant of *Cenoceras*. The irregular growth lines per se cannot be regarded as sufficient evidence for the phylogenetic relationship of *Procymatoceras* to *Cymatoceras*. However, *P. subtruncatum* probably gave rise to *Paracymatoceras mondegoense* TINTANT, 1971, from the Early Callovian of Spain, and *Procymatoceras boulardi* TINTANT, 1969, from the Middle Callovian of Spain, both of which resemble Cretaceous species of *Cymatoceras* in their shell ribbing. The latter two species resemble each other in shell shape, while the suture of *Paracymatoceras mondegoense* resembles that of evolutionarily advanced species of *Cenoceras* (e. g. *C. calloviense*). *Paracymatoceras ibericum* TINTANT, 1971, from the Late Oxfordian of Spain, and *P. asper* (OPPEL, 1868) from the Tithonian of Štramberk, Moravia (TINTANT 1969*a*) present successive stages in the evolution of cymatoceratid ornamentation. Note, however, that TINTANT (1969) is of the opinion that the genera *Procymatoceras*, *Paracymatoceras*, and *Cymatoceras* are not closely related. Typical Early Cretaceous species of *Cymatoceras* display an ornamentation consisting of distinct densely spaced, sometimes bifurcating ribs (SHIMANSKY 1975). The juvenile shell of *C. bifurcatum* (OOSTER, 1858) from the Early Cretaceous is longitudinally striated (SHIMANSKY and ZHURAVLEVA 1961, pl. 13: 6), which corroborates the hypothesis that *Cymatoceras* derived from *Cenoceras*. The ornamentation of *Cymatoceras* increased in coarseness during the Cretaceous, which resulted in evolution of a descendant genus, or subgenus, *Syrionautilus* (see Shimansky 1975). *C.* (*Syrionautilus*) *libanoticus* (Foord and Crick, 1890) is the only fossil nautiloid found with its calcified jaws *in situ* (Kummel 1956, Saunders *et al.* 1978); the jaws do not differ from those of extant *Nautilus*. Later species of *Cymatoceras* are characterized by very large initial chambers of the phragmocone (pl. 47: 8; Shimansky 1975), much larger than in any other Nautilina, including genus *Nautilus* (Davis and Mohorter 1973).

Shell ornamentation is independent of growth lines in the Barremian to Aptian species *Eucymatoceras plicatum* (Fitton, 1835), supposedly a descendant of Early Cretaceous *Cymatoceras*. Its ribs run obliquely, as in some divaricate bivalves.

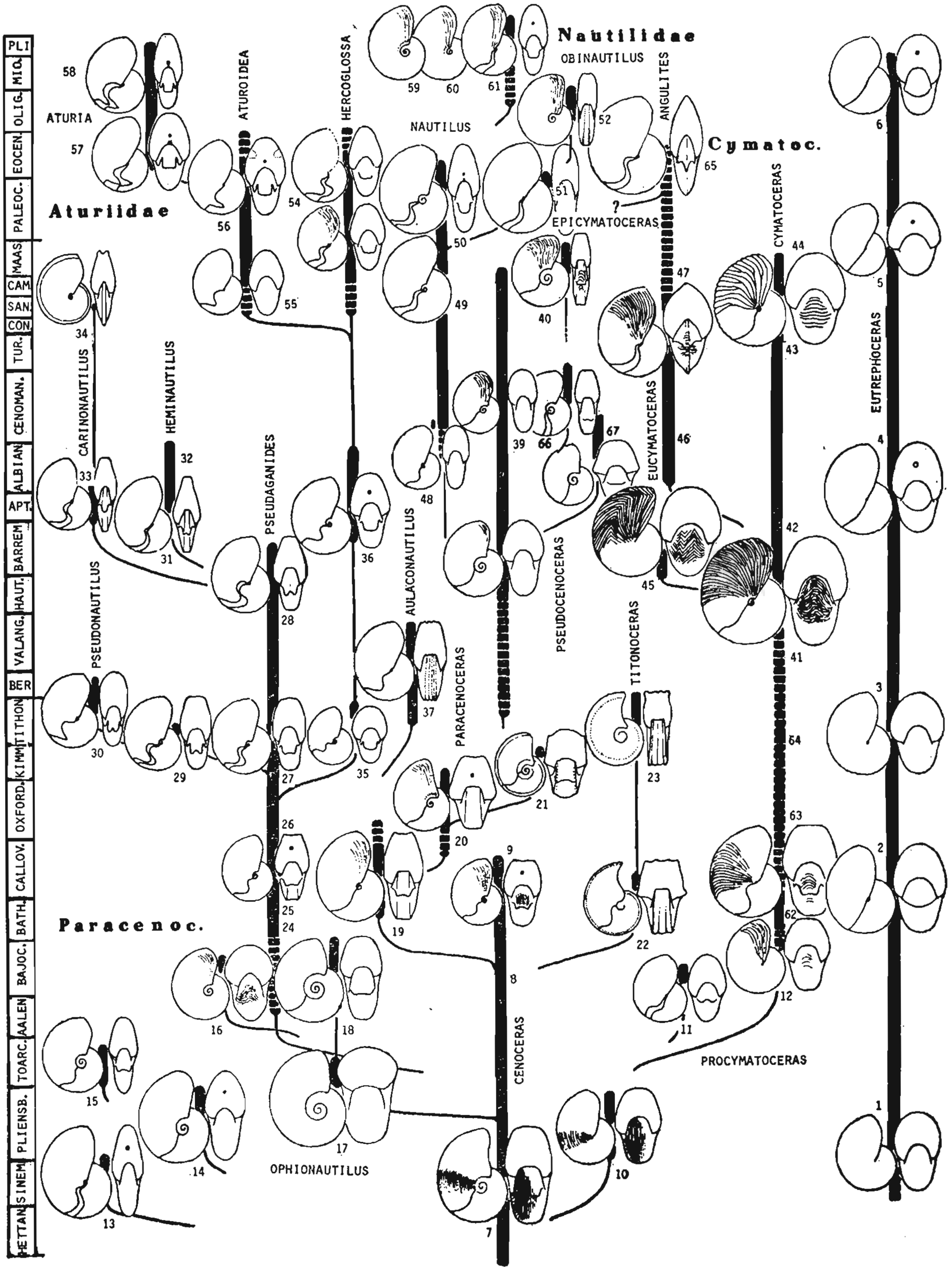
Deltocymatoceras leiotropum (Schlüter, 1876) from the Emscherian of Germany has a keeled venter. It is related to *Cymatoceras* (see Wiedmann 1961). Kummel (1956, 1964) and Shimansky (1975) regarded the difference between *D. leiotropum* and *Angulites triangularis* (Montford, 1802), known from a mould of Cenomanian age, as indicative of familial rank, but, in fact, the two forms do not differ significantly in any observable character. There are in the Late Cretaceous and Paleogene various involute nautiloids with angulate venter, which are assigned to the genera *Deltonautiloides* and *Teichertia*. Out of this group, the best known form is the Eocene species *Teichertia prora* Glenister, Miller and Furnish, 1956, showing a keel already at the second whorl (Glenister *et al.* 1956). Taxonomy and phylogeny of this group are unclear.

Some Early Cretaceous nautiloids appear to be closely related to the Jurassic representatives of *Pseudaganides*. *Xenocheilus ulixis* Shimansky and Erlanger, 1955, from the Hauterivian of Crimea (Shimansky 1975), may be a direct descendant of *Pseudaganides*. In turn, *Palelialia*

Fig. 71

Hypothetical phylogenetic relationships among members of the suborder Nautilina. 1 *Cenoceras chilense* (Huppé); 2 *Eutrephoceras montanense* Kummel; 3 *Eutrephoceras cyclotum* (Oppel); 4 *Eutrophoceras clementinum* (d'Orbigny); 5 *Eutrephoceras desertorum* (Quaas) (pl. 47: 6); 6 *Nautilus balcombensis* Chpman; 7 *Cenoceras striatum* (Sowerby); 8 *Cenoceras inornatum* (d'Orbigny); 9 *Cenoceras calloviense* (Oppel) (fig. 68; pl. 45: 3-4); 10 *Cenoceras similissimum* (Foord and Crick); 11 *Nautilus glaber* Foord and Crick; 12 *Procymatoceras subtruncatum* (Morris and Lycett), (pl. 45: 1); 13 *Hercoglossoceras kochi* (Prinz); 14 *Cenoceras araris* (Dumortier), *C. arariforme* (Pia), *C. adneticum* (Pia); 15 *Cenoceras beirense* Tintant and Courbouleix; 16 *Cenoceras excavatum* (Sowerby); 17 *Cenoceras austriacum* (Hauer), *C. schwalmi* (Prinz); 18 *Ophionautilus burtonensis* (Foord and Crick); 19 *Paracenoceras welmae* Jeannet; 20 *Paraceonoceras hexagonum* (Sowerby) (fig. 69; pl. 45: 2); 21 *Somalinautilus antiquus* (Daque); 22 *Aulaconautilus bicarinatus* Jeannet, *Cymatonautilus julii* (d'Orbigny), *C. mojsisovicsi* (Neumayr), *C. collignoni* Tintant; 23 *Titonoceras zitteli* Retowski; 24 *Pseudaganides crassisinuatus* (Crick); 25 *Pseudaganides subbiangulatus* (d'Orbigny); 26 *Pseudaganides kutchensis* (Waagen), *P. aganiticus* (Schlotheim) (fig. 70b; pl. 46: 6-7; 47: 1-5); 27 *Pseudaganides schneidi* (Loesch); 28 *Xenocheilus ulixis* Shimansky; 29 "*Pseudonautilus* (*Bavarinautilus*)" *eurychoros* Schairer and Barthel; 30 *Pseudonautilus geinitzi* (Oppel); 31 *Heminautilus saxbii* (Morris); 32 *Heminautilus rangei* (Huppé); 33 *Carinonautilus lacerdae* (Villanova); 34 *Carinonautilus ariyalurensis* Spengler; 35 *Nautilus stromeri* Loesch, ?*Paracymatoceras asper* (Oppel); 36 *Palelialia karpinskyi* (Karakasch), *Pseudaturoidea forbesiana* (Blanford); 37 *Aulaconautilus sexcarinatus* (Pictet), *A. druzczici* Shimansky; 38 *Pseudocenoceras campichei* (Karakasch), *Cymatoceras picteti* (Karakasch); 39 *Pseudocenoceras largilliertanum* (d'Orbigny); 40 *Epicymatoceras vaelsense* (Binckhorst); 41 *Cymatoceras pseudoelegans* (d'Orbigny); 42 ?*Anglonautilus undulatus* (Sowerby); 43 *Cymatoceras bifidum* Shimansky, ?*Cimomia tenuicostata* Glenister, Miller and Furnish; 44 *Syrionautilus libanoticus* (Foord and Crick) (pl. 47: 8); 45 *Eucymatoceras plicatum* (Fitton); 46 *Deltoidonautilus triangularis* (Montford); 47 *Deltocymatoceras leiotropis* (Schlüter); 48 *Cimomia schroeteri* Wiedmann; 49 *Deltoidonautilus* sp. Shimansky; 50 *Teichertia similis* Shimansky, *T. imitator* Shimansky; 51 *Cimomia burtini* (Galeotti); 52 *Obinautilus pulcher* Kobayashi; 53 *Hercoglossa danica* (Schlotheim); 54 *Hercoglossa orbiculata* (Tuomey); 55 *Aturoidea schweinfurthi* (Quaas); 56 *Aturoidea parkinsoni* (Edwards); 57 *Aturia alabamensis* (Morton); 58 *Aturia aturi* (Basterot), *A. angulata* (Conrad), *A. cubaensis* (Lea); 59 *Nautilus scrobiculatus* (Solander); 60 *Nautilus macromphalus* Sowerby; 61 *Nautilus pompilius* Linné; 62 *Paracymatoceras mondegoense* Tintant; 63 *Paracymatoceras ibericum* Tintant; 64 *Paracymatoceras asper* (Oppel); 65 *Teichertia prora* Glenister, Miller and Furnish; 66 *Pseudocenoceras fittoni* (Sharpe); 67 *Pseudocenoceras archiacianum* (d'Orbigny) (pl. 47: 9, 10).

karpinskyi (Karakasch, 1907) from the Barremian of Crimea differs both from *Pseudaganides* and *Xenocheilus* in the absence of a ventral lone, so that it resembles the genus *Hercoglossa*. *P. karpinskyi* probably evolved from "*Nautilus*" *stromeri* Loesch, 1914, from the Tithonian



of Štramberk, Moravia. Thus, *Hercoglossa* may be a descendant of *Pseudaganides.* Their resemblance in the undulation of the septal suture would then not be homeomorphy, as usually interpreted (KUMMEL 1956, MARCHAND and TINTANT 1971), but be due to phylogenetic relationship. *Hercoglossa* gave rise to a rather complete evolutionary lineage leading to the Tertiary genus *Aturia* ranging up to the Miocene. In addition to its complex suture, *Aturia* is also characterized by its dorsal siphuncle and very long septal necks. The siphuncle is dorsal throughout ontogeny (STURANI 1959). According to JUNG (1966), most "species" of *Aturia* represent actually two coeval species, namely *A. aturi* BASTEROT, 1825, and *A. cubaensis* (LEA, 1841) (see MILLER and FURNISH 1956, ANTUNES 1966).

The extant genus *Nautilus* (see HIRANO 1977), including five species or subspecies living in the area around the Philippines and Australia, was derived by KUMMEL (1956) and WIEDMANN (1961) from *Eutrephoceras.* In fact, some species of the latter genus preceded *Nautilus* in Australia (CHAPMAN 1914, MCGOWRAN 1959) but, nevertheless, they cannot be considered as related to the extant species of *Nautilus.* The most involute species of the latter, and hence the closest to *Eutrephoceras, N. pompilius* MONFORD, 1808 widely differs from *Eutrephoceras* in its septal suture (STENZEL 1964) even in the juvenile stages (DAVIS and MOHORTER 1973). The suture resembles in turn that of the genus *Cimomia,* related closely to *Hercoglossa.* "*Deltoidonautilus*" *haughti* (OLSSON, 1928) from the Eocene of Chile (MILLER and DOWNS 1950) resembles very closely *N. pompilius* in shell shape and suture, and may be its direct ancestor. *Cimomia* was recorded also in the Eocene of Australia (MCGOWRAN 1959). The septal suture is not described in congeners of *N. pompilius,* but these are more evolute than the latter and, hence, seeming unlikely more closely related to *Eutrephoceras.* The systematic position of *Nautilus praepompilius* SHIMANSKY, 1957, from the Paleogene of Kazakhstan, cannot be recognized at the moment. Similar forms the European and North American Tertiary were attributed to *Eutrephoceras* (see PALMER 1961, SCHULTZ 1976*a*, *b*).

Taxonomic assignment of fossil calcified beaks of the nautiloid jaw should greatly contribute to our knowledge of the biology of fossil nautiloids, because there is a correlation between beak form and diet in extant cephalopods. Those extant Octopoda feeding upon shelled benthos display much more massive beaks than pelagic squids feeding upon fish.

The oldest records of calcified beaks of the nautiloid jaw are from the Ladinian (MÜLLER 1963*a*, *b*), where they are associated with *Germanonautilus bidorsatus.* Both the lower and upper beak of that Triassic nautiloid resemble very closely in outline those of the extant species of *Nautilus* (see SAUNDERS *et al.* 1978). The working edge of the Triassic beaks is more strongly "ornamented" than in *N. pompilius,* and appears to resemble in function the ribbed beaks of *N. macromphalus* (see SAUNDERS *et al.* 1978). In spite of this resemblance, the Triassic rhyncholites differ markedly from their later counterparts, mostly in the apical ornamentation of the upper beak and in its parabolic outline. The posterior boundary of calcification is convex in the Triassic form *Rhyncholites hirundo,* which is the basis of the claim that it is representative of the evolutionary lineage leading to *Nautilus.* There are rhyncholites with posterior edge convex (form genus *Rhyncholites*) in the Jurassic through Tertiary (TEICHERT and SPINOSA 1971). They are somewhat variable in shape but their general outline remains more or less constant and close to that observed in *Nautilus.* A group with very sharp beak and relatively small posterior part (form genera *Arcuatobeccus* and *Scaptorhynchus*) branched off during the Tertiary and persisted up to the Miocene. The only record of a fossil rhyncholite *in situ* is from *Cymatoceras* (*Syrionautilus*) *libanoticus* from the Late Cretaceous. That rhyncholite does not significantly differ in outline from *N. pompilius* (see SAUNDERS *et al.* 1978). One may thus suppose that typical *Rhyncholites* should be characteristic of the lineages of *Nautilus* and *Cymatoceras* with their common ancestor included. The nautiloid phylogeny is too poorly known to allow the setting of precise boundaries for this group. However, Tertiary representatives of *Rhyncholites* probably belong to the associated genera *Eutrephoceras* and/or *Cimomia* (see WARD and COOPER 1972). The stratigraphic range of *Scaptorhynchus*-like forms is consistent with the range of considerably specialized representatives of the lineage of Aturoidea and *Aturia*. The relative complexity of their septal suture and their shell compression are commonly regarded as adaptations to pelagic life. The morphologic affinity of jaws to those of the squids is entirely consistent with this interpretation. One may conclude that, contrary to *Cymatoceras*, *Aturia* fed mainly upon soft-bodied nektonic and planktonic organisms.

Most Jurassic and Cretaceous rhyncholites (form genus *Rhynchoteuthis*) show an angulate posterior boundary of calcification (pl. 47: 7). Because of this difference from the jaw of *Nautilus*, they were excluded from Nautiloidea. Since the time ammonoid and belemnite jaws were found, the latter interpretation seems to be untenable. Various subgroups are recognized within the rhyncholite group of *Rhynchoteuthis*. The form genera *Rhynchoteuthis*, *Hadrocheilus*, *Globosobeccus*, and others with moderately sharp, triangular beak (GĄSIOROWSKI 1973, DIENI 1975) resemble the form genus *Rhyncholites*; they range from the Early Jurassic to Late Cretaceous. Two other lineages may be derived from the main one. One of these is characterized by very wide parabolic beaks (form genus *Gonatocheilus*), the other by very sharp and elongate beaks (form genus *Leptocheilus*). Both lineages range from the Late Jurassic to Early Cretaceous (DIENI 1975).

To assign rhyncholites of the *Rhynchoteuthis* group to specified nautiloid shell taxa is a difficult task. If adaptation in rhyncholites parallels changes in shell morphology, this can nonetheless be attempted. The rhyncholites *Leptocheilus* resembles *Scaptorhynchus* assigned above to *Aturia*. Therefore, they can be expected to belong to forms resembling *Aturia* in shell morphology. There is a form almost homeomorphic with *Aturia* in the Late Jurassic to earliest Cretaceous, namely *Pseudonautilus*. If this assignment is correct, the rhyncholites ancestral to *Leptocheilus* (that is *Palaeoteuthis* and *Rhynchoteuthis*) are to be attributed to the ancestor of *Pseudonautilus*, the genus *Pseudaganides*. The progressive specialization in rhyncholite morphology in the group of *Globosobeccus* and *Palaeoteuthis* through *Leptocheilus* may parallel the specialization in septal suture recorded in *Pseudaganides* (see MARCHAND and TINTANT 1971). If the *Rhynchoteuthis* group is assigned to *Pseudaganides* and *Cenoceras*, the wide rhyncholites *Gonatocheilus* are to be attributed to bulgy-shelled *Paracenoceras*.

The above hypothetical assignment of rhyncholites to nautiloid shells obviously is only a tentative interpretation.

Proposed systematics. —

The present understanding of the phylogeny of the Nautilina does not permit the construction of coherent systematics, or even to present unequivocal diagnoses of the families. The systematics presented below arose from an attempt to fit the previous systematics (KUMMEL 1956, 1964) to the probable phylogeny. The main taxonomic criterion is the ontogeny of whorl cross section and shell ornamentation.

Paracenoceratidae SPATH, 1927

[= Pseudonautilidae SHIMANSKY and ERLANGER, 1955; Heminautilinae SHIMANSKY, 1962]

Shell longitudinally striated at least at the juvenile stages, with undulated septal suture and trapezoidal to ovate (in specialized forms) whorl section.

Cenoceras HYATT, 1884; *Nautilus intermedius* SOWERBY, 1816

Shell longitudinally striated at the adult stages, with ovate trapezoidal whorl section.

Ophionautilus SPATH, 1927; *Nautilus burtonensis* FOORD and CRICK, 1890
[= ?*Hercoglossoceras* SPATH, 1927; ?*Procymatoceras* SPATH, 1927]

Shell smooth at the adult stages, with ovate whorl section.

Paracenoceras SPATH, 1927; *Nautilus hexagonus* SOWERBY, 1826

[= *Somalinautilus* SPATH, 1927]
Shell smooth, with adult angulate trapezoidal whorl section.

Titonoceras RETOWSKI, 1894; *T. zitteli*
[= *Cymatonautilus* SPATH, 1927]
Shell with ventro-lateral ribs and aperture with deep lateral sinuses.

Pseudaganides SPATH, 1927; *Nautilus kutchensis* WAAGEN, 1873
[= *Xenocheilus* SHIMANSKY and ERLANGER, 1955]
Shell smooth, with considerably undulated septal suture and adult trapezoidal whorl section.

Aulaconautilus SPATH, 1927; *Nautilus sexcarinatus* PICTET, 1867
Like *Pseudaganides* but with longitudinal furrows on venter.

Pseudonautilus MEEK, 1876; *Nautilus geinitzi* OPPEL, 1868
Involute shell with ovate whorl section; pointed lateral lobes on septal suture.

?***Heminautilus*** SPATH, 1927; *Nautilus saxbii* MORRIS, 1848

?***Carinonautilus*** SPENGLER, 1910; *C. ariyalurensis*

Cymatoceratidae SPATH, 1927

[= Eutrephoceratidae MILLER, 1951]

Involute shell with ovate whorl section; adult whorls with coarse transverse ornament; juvenile whorls longitudinally striated in primitive forms.

Procymatoceras SPATH, 1927; *Nautilus subtruncatus* MORRIS and LYCETT, 1850
Similar to *Cenoceras* but with irregular transverse ornamentation.

Paracymatoceras SPATH, 1927; *Nautilus asper* OPPEL, 1868
Intermediate between *Procymatoceras* and *Cymatoceras*.

?***Eutrephoceras*** HYATT, 1894; *Nautilus dekayi* MORTON, 1834
Bulgy and smooth shell with straight septal suture.

Cymatoceras HYATT, 1884; *Nautilus pseudoelegans* d'ORBIGNY, 1840
[= *Syrionautilus* SPATH, 1927]
Shell ornamented with coarse transverse ribs; septal suture weakly undulated.

Eucymatoceras SPATH, 1927; *Nautilus plicatus* FITTON, 1835
Shell ornamented with oblique ribs producing a zigzag pattern.

?***Deltoidonautilus*** SPATH, 1927; *Nautilus sowerbyi* SOWERBY, 1843
[= *Deltocymatoceras* KUMMEL, 1956; ?*Teichertia* GLENISTER, MILLER and FURNISH, 1956]
Close to *Cymatoceras* but with ventral keel.

Nautilidae BLAINVILLE, 1825

[= Hercoglossidae SPATH, 1927]

Smooth shell with ovate whorl section and considerably undulated septal suture without ventral lobe.

Hercoglossa CONRAD, 1866; *Nautilus orbiculatum* TUOMEY, 1856
[= ?*Palelialia* SHIMANSKY, 1955]
Involute shell with considerably undulated septal suture with rounded lobes.

Nautilus LINNÉ, 1758; *N. pompilius*
[= *Cimomia* CONRAD, 1866]
Like *Hercoglossa* but suture with shallow lobes.

?***Pseudocenoceras*** SPATH, 1927; *Nautilus largilliertanus* d'ORBIGNY, 1840
Shell flat and relatively evolute.

Aturiidae CHAPMAN, 1857

Shell involute, smooth, with subdorsal siphuncle; undulated septal suture with pointed lateral lobe but without ventral lobe.

Aturoidea VREDENBURG, 1925; *Nautilus parkinsoni* EDWARDS, 1849

Aturia BRONN, 1838; *Nautilus aturi* BASTEROT, 1825

Incertae sedis

Epicymatoceras KUMMEL, 1956

Cymatonautilus SPATH, 1927

Obinautilus KOBAYASHI, 1954

PATTERNS IN NAUTILOID EVOLUTION

The general pattern of nautiloid phylogeny was presented recently by TEICHERT (1969), ZHURAVLEVA (1972), and FLOWER (1976). Phylogenetic trees of these authors are partly incompatible with one another because of a considerable variation in definition of high-rank taxa among the authors. Particular structures or evolutionary lineages were only exceptionally discussed. Nevertheless, all those reconstructions are to a large extent similar one to another, as well as to the above presented models. The main differences between the present paper and the previous work concern the relationship of exogastric forms to the Discosorida, the origin of the Lituitina and Actinoceratina, and the origin and early evolution of the Nautilida.

According to the earlier (DZIK 1981) presented hypothesis, the ancestors of the Nautiloidea are to be looked for among the Early to Middle Cambrian hyoliths with shell circular in cross section (i.e. the Circothecida) and uncalcified operculum. The size of the smallest shell fragments of the Late Cambrian to Early Ordovician Ellesmeroceratina is less than 1 mm in diameter, which indicates that the larva was small-sized. This demonstrates that the mode of ontogeny typical of the Orthoceratida and Ammonoidea is primitive for the Cephalopoda. Primitive nautiloids may also exhibit a planktotrophic embryonic development.

The main problem in models attempting to account for the origin of the Cephalopoda is in the formation of the phragmocone. My solution to this problem (DZIK 1981) starts with the functional significance and ontogenetic development of the phragmocone. I assume that the phragmocone is related both in origin and function to some adaptation of the larva of ancestral pre-cephalopods to produce a bubble of light liquid to buoy up the shell of the veliger in water. The planktonic mode of life was gradually extended in the course of evolution over later ontogenetic stages, with larger shell, which required an increase in the volume of the hydrostatic apparatus. The pressure of secreted liquid pushed the viscera forwards, but the viscera left in the back a septum produced by the entire surface of the mantle. Only a strand of soft tissue stemming from the attachment of the larval pedal retractor muscle did not shift forward. This tissue strand was the only part of the animal body retaining contact with the liquid and, hence, it began to function as an organ of liquid exchange and finally transformed into the siphuncle. Strong development of the cameral and siphuncular deposits in the early nautiloids with wide non-diaphragmate siphuncle indicates much more intense cameral liquid exchange than in extant cephalopods.

The changes in frequencies of particular groups of the Nautiloidea through time were discussed by TEICHERT and KUMMEL (1964) who considered the number of genera described from particular stratigraphic intervals. Consequently, their results reflected mostly views of various paleontologists on the generic ranges (and definition of taxa) among the Nautiloidea. Nautiloid evolution appeared to begin with explosive radiation in the Early Ordovician (an artifact of the work by several splitters who investigated the Ordovician faunas), followed by a rapid decline during the Late Paleozoic and Mesozoic (effected by the biological approach to the Nautilida by KUMMEL and others). With this traditional approach, every paper splitting supraspecific taxa considerably affects the pattern of evolution, even though it may not give any new real data. In an attempt to avoid subjective biases, I used the number of reconstructed evolutionary lineages in particular to construct the diagrams presented in fig. 72. I did so in order to distinguish between coeval biospecies (or a time section through the whole evolutionary lineages) and arbitrarily recognized temporal species (= chronospecies or fragments of evolutionary lineages). Otherwise, the species diversity of rapidly evolving groups could be overestimated because the number of temporal species per time unit is much greater in rapidly than in slowly evolving groups.

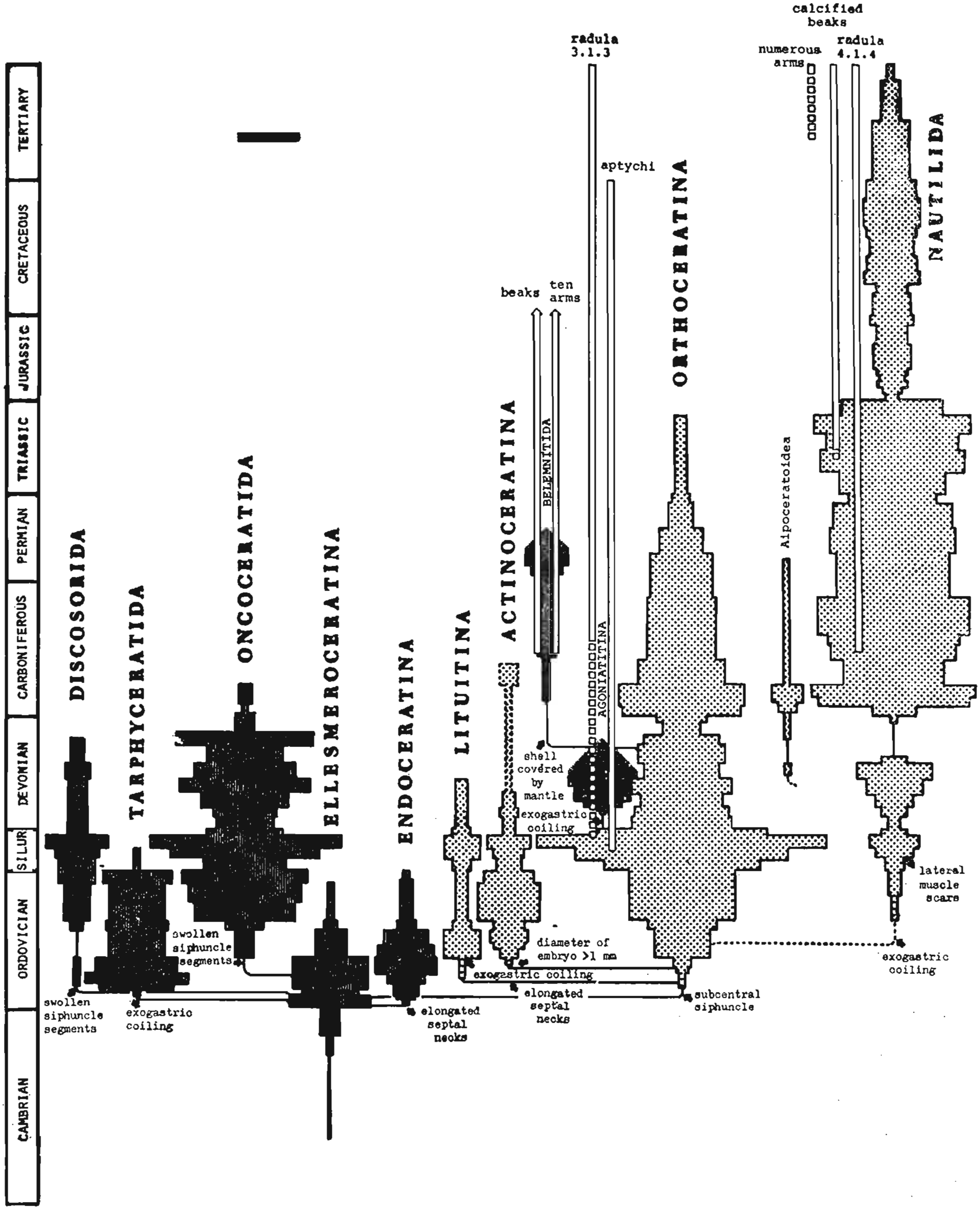


Fig. 72

Phylogenetic relationships among large groups of the Nautiloidea, and their relation to the other cephalopod subclasses. Width of a clade reflects the species richness at a time plane (1 mm, monospecific evolutionary lineage), with unquestionably distinct species taken into account only. Blank vertical bars indicate the fossil record of particular body structures (hypothetical occurrences marked by dashed lines). Black arrows indicate evolutionary events which permit definition of taxa. Dotted are derivatives of the Orthoceratina, originally with subcentral siphuncle; hachured are derivatives of the Ellesmeroceratina, originally with ventral siphuncle; grey-colored are the early evolutionary stages of the Ammonoidea and Coleoidea.

The pattern obtained of nautiloid evolution differs from those presented by TEICHERT and KUMMEL (1964) and FLOWER (1976). The results obviously are still biased. The Late Silurian peak in nautiloid diversity is an artifact of BARRANDE'S (1865—1877) work on the rich nautiloid fauna from the Silurian of Bohemia. Similar causes effected the peaks in the Visean and the Late Triassic. Further research should smooth the clades which will then become drop-like in shape (actually, this can already be recognized).

Beginning with the Early Ordovician, the Nautiloidea maintained approximately constant numbers of adaptive types, which were, however, realized each by various groups successive in time. The frequency of homeomorphy among the Nautiloidea may indicate that they occupied more or less the same width of ecospace through time. Competition was mostly between nautiloid groups. An evolutionarily vigorous group, the Ammonoidea, branched from the Nautiloidea during the Devonian and occupied a many niches utilized previously by the nautiloids. This ecological reorganization may account for the relatively variable compositions of the Devonian nautiloid faunas. After the Devonian, only the specialized Orthoceratida were affected by considerable competitive pressure and, indeed, underwent a sharp decline in diversity during the Late Paleozoic. Only a few lineages of planktonic (?) longiconic and orthoconic nautiloid occurred in the Permian and Triassic. A stable species diversity was achieved in the Early Carboniferous by the spirally coiled Nautilida, the only order of Nautiloidea (apart from the Orthoceratida) surviving the Middle Carboniferous. The constancy in species diversity of the Nautilida from the Early Carboniferous to the end of the Triassic (fig. 73) is striking, especially since it was maintained in spite of an intense evolution that changed the proportions of various subgroups among the Nautilida. This indicates that the Nautilida occupied a certain part of the ecospace and lived free of competitive pressure by other organisms. The state of "species equilibrium" (see BRETSKY and BRETSKY 1976) was achieved by communities including the nautiloids of the Devonian-Carboniferous boundary or a little later. The Late Triassic disturbance of that equilibrium and the succeeding variation in species diversity of the nautiloids up to their almost total extinction in the Pliocene supposedly were caused by ecological expansion of some competitors, possibly the teleostean fish.

DESCRIPTION OF NEW AND INADEQUATELY KNOWN SPECIES

Family **Baltoceratidae** KOBAYASHI, 1935

Cochlioceras EICHWALD, 1860

Type species: *C. avus* EICHWALD, 1860

Cochlioceras roemeri sp. n.

(fig. 4a-c and pl. 1: 5-10)

?*Proterocameroceras gdovense* BALASCHOV, 1968; BALASCHOV 1968, p. 92, pl. 1: 2-5, *partim* (non holotype, pl. 1: 1).

Holotype: ZPAL N/010, pl. 1: 9a-b.

Type horizon and *locality*: *Eoplacognathus reclinatus* Zone, Lasnamägian, Late Llanvirnian; erratic boulder of Baltic origin, Rozewie, northern Poland.

Derivation of the name: In honour of Karl Ferdinand von Roemer (1818—1891), in recognition of his work on erratic boulders.

Diagnosis. — Ventral siphuncle up to one third of the shell in diameter, filled with deposits in its apical part; siphuncular deposits in form of massive rod at ventral side, with flat rings at septal necks; cameral deposits well developed.

Remarks. — *C. roemeri* sp. n. does not differ externally from its congeners. Its uniqueness consists in its much wider siphuncle. It differs from *C. burchardi* also in its siphuncle lying a little away from the shell wall and, consequently, in its straight septal suture. Any comparison to the siphuncular structure of other congeneric species is impossible because of lack of data.

A similar siphuncular structure was recorded among the American baltoceratids (FLOWER 1964).

Occurrence. — *C. roemeri* sp. n. occurs rather commonly in erratic boulders of the *E. reclinatus* Zone (Folkeslunda Limestone), but never in association with its coeval congener, *C. burchardi*. Provided that the specimens assigned by BALASCHOV (1968) to *Proterocameroceras gdovense* (except for the holotype supposedly being the apical part of a shell of *Dideroceras*) belong to *C. roemeri*, the latter species occurs also in the *E. reclinatus* Zone of Estonia. The conspecificity of "*P. gdovense*" and *C. roemeri* is indicated by the shell shape and presumably also the structure of siphuncular deposits (see BALASCHOV 1968, pl. 1: 2v). One specimen was found in a boulder indistinguishable in lithology from those of the *Paroistodus originalis* Zone (untere rote Vaginatenkalk; Volkhovian); anyway, this specimen cannot be younger than the Kundan.

Family uncertain

Flowerites ZHURAVLEVA, 1972

Type species: *F. austrirhiphaeus* ZHURAVLEVA, 1902

Flowerites sobolewi nom. n.

(fig. 16a-b and pl. 7: 3-4)

Cyrtoceras ellipticum n. sp.; SOBOLEW 1912, pl. 5, pl. 2: 5a-b.
non Cyrtoceras ellipticum LOSSEN, 1860, p. 27, pl. 1:3.

Holotype: SOBOLEW 1912, pl. 2: 5a-b (probably stored at the Charkov University).

Type horizon and locality: *Platyclymenia* Zone, Famennian; Łagów-Dule, the Holy Cross Mts, Poland.

Diagnosis. — After SOBOLEW: "Horn-like curved shell elliptic in cross section, with the long axis running dorso-ventrally. Shell smooth, with indistinct transverse striation. Longitudinal ribs discernible in moulds. Air chambers low. Siphuncle at the inner (concave) side."

Remarks. — SOBOLEW (1912) figured one relatively large but incomplete specimen. Some additional specimens collected by myself confirm the correctness of this diagnosis. The "longitudinal ribs discernible in moulds" of SOBOLEW are the attachment scars of retractor muscles. The dorsal (convex) side of the shell is a little flattened, whereas the ventral side is parabolic in outline. The living chamber is cylindrical without any significant terminal modifications, with a ventral rudimentary funnel sinus. The connecting rings are recrystallized. There are no deposits. The intrapopulation variability consists in shell size and coiling.

The phylogenetic relations of this species are unclear. It may be a descendant of *Protophragmoceras* (Silurian; Discosorida) or *Devonocheilus* (Late Devonian; Oncoceratida).

Family **Oonoceratidae** RUEDEMANN, 1906

Richardsonoceras FOERSTE, 1932

Type species: *Cyrtoceras simplex* BILLINGS, 1857

Richardsonoceras sinuososeptatum (ROEMER, 1861)

(fig. 19a-b and pl. 9: 1a-d)

Orthoceras sinuoso-septatum; ROEMER 1861, pl. 7: 6a-b (?), pl. 6: 3a-c.
?*Beloitoceras heterocurvatum* n. sp.; Strand 1934, pl. 10: 8a-b, 9a-b (*non* pl. 10: 10-11).

Paratype: specimen UWR 3230s (pl. 7: 6a-b in ROEMER 1961), pl. 9: 1a-d in this paper; lectotype (pl. 6: 3a-c in ROEMER 1861) probably lost.

Type horizon and locality: Probably Ashgillian, erratic boulder of Baltic origin, Zawidowice by Oleśnica, Poland.

Emended diagnosis. — Relatively short, exogastrically curved conchs with almond-shaped cross section, ventral side sharp, and thick growth lines, the latter being arched in outline and running obliquely, forming a sharp sinus at the ventral side.

Remarks. — ROEMER (1861) erected the species *C. sinuososeptatum* from two fragmentary specimens, one of which (figured in the present paper) was exogastrically curved, while the other was almost straight. When erecting the new species *B. heterocurvatum*, diagnosed to include both endogastrically and exogastrically curved forms, STRAND (1934) included only the exogastrically curved specimen of ROEMER and designated the other specimen as the holotype of *C. sinuososeptatum*. SWEET (1959*a*) subsequently restricted the range of *B. heterocurvatum* to exogastric forms only, and erected a new species, *Parryoceras strandi*, for the endogastrically curved specimen of STRAND. Two exogastrically curved specimens figured by STRAND differ widely in the size of their mature living chamber (32 and 21.5 mm in diameter). ROEMER's only preserved specimen attains 32 mm in diameter of immature phragmocone, which resembles the holotype of *B. heterocurvatum*. There is a close resemblance also in the aperture outline, as judged from the traces of growth lines discernible on the mould of the phragmocone. As illustrated by STRAND, the mature living chamber of *B. heterocurvatum* declines in diameter adaperturally, as in the type species of the genus. The holotype of *B. heterocurvatum* agrees with the paratype of *C. sinuososeptatum* in the shape of connecting rings. One may thus suppose that the specimens are conspecific.

The specimen illustrated in the present paper is the only preserved original of *C. sinuososeptatum*. The other specimen figured by ROEMER was lost during World War II. Its true specific assignment cannot be demonstrated but, due to the imprecision of ROEMER's drawings, there is no certainty that the two specimens belonged to distinct species. To solve this problem, the holotype of *R. sinuososeptatum* is needed.

Family **Devonocheilidae** ZHURAVLEVA, 1972

Lysagoraceras SCHÖNENBERG, 1952

Type species: *L. angustum* SCHÖNENBERG, 1952 (= *Cyrtoceras lagowiense* GÜRICH, 1896)

Lysagoraceras lagowiense (GÜRICH, 1896)

(fig. 26a-f and pl. 10: 5-9)

Cyrtoceras lagowiense sp. n.; GÜRICH 1896, pp. 322-323, pl. 13: 9a-b.
Cyrtoceras angustum sp. n.; GÜRICH 1896, pp. 324-325, pl. 12: 4a-d.
Poterioceras wedekindi n. sp.; SOBOLEW 1912, p. 5, pl. 4: 3a-b.
Poterioceras cf. *latum* WEDEKIND; SOBOLEW 1912, p. 5, pl. 4: 4a-b, pl. 5: 2a-b.
?*Poterioceras frechi* n. sp.; SOBOLEW 1912, p. 5, pl. 6: 2a-b.
Lysagoraceras angustum n. sp.; SCHÖNENBERG 1952, pp. 394-399, figs. 13-14 and pl. 26: 4.
Holotype: specimen UWR 3228s (pl. 13: 9a-b in GÜRICH 1896), pl. 10: 7 in this paper.

Emended diagnosis. — Elongated almost straight shell in the juvenile stages, but strongly exogastrically curved beginning with the end of the mature phragmocone.

Remarks. — *L. lagowiense* differs from the associated species *L. subfusiforme*, which it resembles most closely, in its considerably curved terminal part of the mature shell. It resembles *Gonatocyrtoceras longissimum* sp. n. in shell shape, but differs from the latter in its simple mature aperture and marginal position of the siphuncle which is also smaller in diameter. The holotype of the type species of *Lysagoraceras* is a juvenile specimen of an unidentifiable slender nautiloid species. The only species with such a juvenile form recorded at Dule, where SCHÖNENBERG's (1952) specimen was collected, is *L. lagowiense*. It seems to me unlikely that SCHÖNENBERG's (1952) specimen is representative of a species with unknown adult shell, and I propose to treat *L. lagowiense* as the type species of the genus.

Variability. — There is variation in size of the mature shell, which may be correlated with the extent of adapertural shell curvature (fig. 26d and pl. 10: 8-9). As a rule, the smaller a specimen, the less curved is its shell; in extreme small specimens *L. lagowiense* can hardly be distinguished from *L. subfusiforme*. There is also considerable variation in the length of the mature living chamber (fig. 26f), which may be correlated with a variation in the apical angle. Shell cross section is relatively constant in *L. lagowiense* (fig. 26e), but this feature is of very little diagnostic value.

Occurrence. — The unquestionable records of the species are confined to the exposure Dule at Łagów, Poland, which belong in the *Platyclymenia* Zone (*marginifera* Zone in conodont zonation). All the specimens were found in a black, compact limestone but I am unable to point out their precise position in the section.

Lysagoraceras kielcense sp. n.

(fig. 25a-f and pl. 10: 1-4)

Holotype: ZPAL N/111, pl. 10: 1.
Type horizon and locality: Jabłonna (Kawczyn) by Daleszyce, Holy Cross Mts, Poland; bed J. 6, *Cheiloceras* Zone.

Diagnosis. — Long shell, strongly exogastrically curved over its entire length, with considerably flattened dorsal side.

Remarks. — *L. kielcense* is sharply different in shell shape from all associated species. It resembles *Chrysoceras timidum* from the Famennian of the Urals (ZHURAVLEVA 1972) in its shell curvature but differs in its much more slender, smaller and compressed shell.

Variability. — *L. kielcense* is unique among the thus far investigated Oncoceratidae in its very narrow range of intrapopulation variability. The variation consists mostly in shell curvature and shape, and the size of the mature shell (fig. 25d-f).

Occurrence. — The species has thus far been recorded exclusively in a trench at Jabłonna, Holy Cross Mts, Poland. It occurs in beds J. 6 to J. 9 of the *Cheiloceras* Zone (see WOLSKA 1967).

Gonatocyrtoceras FOERSTE, 1926

Type species: *Cyrtoceras heteroclytum* BARRANDE, 1866 (= *Cayugoceras semiclausum* (BARRANDE, 1865))

Gonatocyrtoceras longissimum sp. n.

(fig. 24a-e and pl. 11: 1-7)

?*Cyrtoceras* (?) *elongatum* n. sp., GÜRICH 1901, p. 354, Sig. 5.
cf. *Stereotoceras canadense* FLOWER; SCHÖNENBERG 1952, pp. 388-394, figs. 11-12, pl. 27: 1 (*non* pl. 27: 2).
Holotype: ZPAL N/223, pl. 11: 5a-d.
Type horizon and locality: Jabłonna (Kaczyn) by Daleszyce, Holy Cross Mts, Poland; bed J. 7, *Cheiloceras* Zone.

Diagnosis. — Long, weakly curved shell with siphuncle situated between the shell center and venter; aperture laterally constricted and the plane of funnel sinus situated normally to the depressed head part of peristome.

Remarks. — *G. longissimum* widely differs from its congeners in its long shell with considerably laterally constricted aperture. Its phragmocone fragments resemble *Lysagoraceras* in external view, but differ in the siphuncle lying away from the venter. *G. longissimum* differs from its relatives also in the separation of the ventral pair of retractor muscle scars. This is a primitive feature reported thus far from Ordovician (SWEET 1959) and Llandoverian (MIAGKOVA 1967) representatives of the Oncoceratida. However, this could be owing to the considerable length of the living chamber.

Variability. — There is a very wide intrapopulation variability in the collections from Jabłonna and Kadzielnia. It consists mostly in the size of the mature shell (fig. 24d), the length of the mature living chamber (fig. 24e), and shell curvature (pl. 11: 1-2, 4-6). The shape of the aperture obviously is ontogeny-dependent.

Occurrence. — The species has thus far been recorded only from the *Cheiloceras* Zone at Kadzielnia and Jabłonna (beds J. 6 to J. 7). The specimens from Jabłonna are smaller in average.

Gonatocyrtoceras holzapfeli (SOBOLEW, 1912)

(fig. 22a-d and pl. 12: 1-6)

Poterioceras Holzapfeli n. sp.; SOBOLEW 1912, p. 8, pl. 5: 1.
?*Poterioceras ventratum* n. sp.; SOBOLEW 1912, p. 6, pl. 4: 1-2.
Cyrtoceras aff. *bilineatum* SANDBERGER; SOBOLEW 1912, p. 5, pl. 3: 1.
Poterioceras? *obesum* HOLZAPFEL; SCHÖNENBERG 1952, pp. 380-384, figs 8-9, pl. 26: 1-2.
Holotype: SOBOLEW 1912, pl. 5: 1 (probably stored at the Charkov University).
Type horizon and locality: *Platyclymenia* Zone, Famennian; Łagów-Dule, Holy Cross Mts, Poland.

Emended diagnosis. — Bulgy, weakly exogastrically curved shell with mature living chamber declining in transverse diameter; aperture with deep ventral sinus and a pair of ventral lappets.

Remarks. — *G. holzapfeli* differs from its congeners in its more weakly curved shell (in average) and supposedly also in the outline of the mature aperture.

Variability. — There is great variation, mostly in shell curvature and the shape of the living chamber (length, cross section, and narrowing). The boundary between *G. holzapfeli* and *G. guerichi* is indistinct and there are specimens that can hardly be identified (e. g. pl. 12: 1).

Occurrence. — The species occurs at Dule in association with *Paratornoceras lentiforme* and *Cheiloceras lagowiense*.

Gonatocyrtoceras guerichi (SOBOLEW, 1912)

(fig. 23a-b and pl. 13: 1-5)

Poterioceras Gürichi n. sp.; SOBOLEW 1912, p. 5, pl. 2: 6a-b.
?*Gyroceras halli* n. sp.; WEDEKIND 1908, p. 626, pl. 65: 2.
?*Cyrtoceras platygaster* n. sp.; BORN 1912, p. 591, pl. 20: 1a-b.
cf. *Stereotoceras canadense* FLOWER; SCHÖNENBERG 1952, pl. 27: 2a-b (only).
Tritonoceras chernovi sp. nov.; ZHURAVLEVA 1972, pp. 196-197, pl. 22: 1-2.
Elaphoceras conspectum sp. nov.; ZHURAVLEVA 1972, pp. 198-199, pl. 23: 3-4.
Elaphoceras quietum sp. nov.; ZHURAVLEVA 1972, pp. 199-200, pl. 23: 1-2.
Elaphoceras timanicum sp. nov.; ZHURAVLEVA 1972, pp. 200-201, pl. 23: 5.
Holotype: SOBOLEW 1912, pl. 2: 6a-b (probably stored at the Charkov University).
Type horizon and locality: *Platyclymenia* Zone, Famennian; Łagów-Dule, Holy Cross Mts, Poland.

Emended diagnosis. — Bulgy, exogastrically curved shell with mature living chamber decreasing adaperturally in dorsoventral diameter but expanding in width (as measured normally to dorsoventral diameter).

Remarks. — The juveniles of *G. guerichi* and *G. holzapfeli* are indistinguishable. On the average, *G. guerichi* is much more curved than *G. holzapfeli*, especially in the adapical part of the mature living chamber. Typical specimens of the two species differ in their apertural form, but there are also intermediates and hence, their specific distinction is uncertain. The form of the mature living chamber is unique and in fact, I am unaware of any similar specimens of unquestionably different species.

Variability. — There is very wide intrapopulation variability in shell size and shape, and also in the curvature of septa.

Occurrence. — The topotype population from Dule is the only one recorded from Poland. The specimens from the Famennian of the Harz which are referred to in the synonymy are very poorly preserved and their conspecificity with *G. guerichi* is uncertain. As judged from the three specimens thus far known, all from the Lower Frasnian of the Arctic Urals, *Tritonoceras chernovi* ZHURAVLEVA, 1972, does not significantly differ from *G. guerichi*. *G. guerichi* does not differ from five specimens, all from the Upper Frasnian of Timan, assigned by ZHURAVLEVA (1972) to three species of *Elaphoceras*. All forms can thus represent a single evolutionary lineage.

Family **Poterioceratidae** FOORD, 1888

Evlanoceras ZHURAVLEVA, 1972

Type species; Pachtoceras evlanensis NALIVKIN, 1947

Evlanoceras (?) *kontkiewiczi* (GÜRICH, 1896)

(fig. 29a-c and pl. 19: 1-3)

Cyrtoceras kontkiewiczi sp. n.; GÜRICH 1896, pp. 323-324, pl. 12: 2a-b.
Poterioceras abbreviatum? GÜRICH; SOBOLEW 1912, p. 5, pl. 6: 1.
Cyrtoceras n. sp. SOBOLEW 1912, p. 5, pl. 3: 2.
Holotype: specimen UWR 3227/s (pl. 12: 2 in GÜRICH 1896), pl. 19: 3 in the present paper.
Type horizon and locality: ?*Platyclymenia* Zone, Famennian; Psiarnia (Kielce), Poland.

Emended diagnosis. — Large, bulgy, depressed shell with non-tapering laterally mature living chamber; shell initially straight but curved exogastrically slightly before the mature living chamber.

Remarks. — The species is known only from shell fragments and hence, the reconstruction presented above is tentative. The exogastrically curved terminal part of the shell differs from related species of *Pachtoceras*. The siphuncular structure is discernible in a single juvenile specimen from Łagów (fig. 30b-c and pl. 19: 2), which differs from other members of the population in its more densely spaced septa; its conspecificity with *E.* (?) *kontkiewiczi* is uncertain.

Variability. — As judged from the few specimens known, the range of intrapopulation variability is rather narrow.

Occurrence. — The species has been recorded from the *Platyclymenia* Zone of Psiarnia (GÜRICH's only specimen) and Łagów, Holy Cross Mts, Poland.

Mecynoceras FOERSTE, 1926

Type species: *Gomphoceras rex* PACHT, 1858

Mecynoceras (?) *polonicum* (GÜRICH, 1896)

(fig. 31a-b and pl. 17: 1-4, pl. 18: 2)

Cyrtoceras polonicum n. sp.; GÜRICH 1896, pp. 321-322, pl. 12: 3.
Poterioceras polonicum GÜRICH; SOBOLEV 1912, p. 5, pl. 1: 12a-b.
Holotype: specimen UWR 2109 (pl. 12: 3 *in* GÜRICH 1896), pl. 17: 1 in the present paper.
Type horizon and locality: *Cheiloceras* Zone, Famennian; Łagów-Dule, Holy Cross Mts, Poland.

Emended diagnosis. — Slightly exogastrically curved shell with siphuncle situated somewhat dorsally of center; radial lamellae developed only at septal necks; connecting rings inflated.

Remarks. — *M.* (?) *polonicum* differs from its closest relative, *M. rex*, in the centro-dorsal siphuncle with considerably inflated rings, more streamlined shell, and the weakly exogastric curvature. Some juvenile shell fragments from Jabłonna (ZPAL N/234, 235) possibly attributable to *M.* (?) *polonicum* are indicative of considerable changes in siphuncular structure during ontogeny. The outline of juvenile connecting rings (fig. 31c) shows more resemblance to *M. rex* than does the adult form; the juvenile rings are much more elongate than the adult ones and, as judged from the poorly preserved specimens, the radial lamellae extend also on the connecting rings.

Occurrence. — The species has been recorded from the Early Famennian *Cheiloceras* Zone of Kadzielnia, Jabłonna, and Łagów (Intumescenskalk of GÜRICH), as well as from coeval strata of the Żbik gorge by Dębnik, Cracow area, Poland.

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PALAEONTOLOGICAL INDEX

Systematic names cited only are indicated by *italic*, and names accompanied by descriptions are indicated by roman letters.

Numerals which indicate the page, on which the species is cited only, are standard; numerals, which indicate pages with descriptions, are **bold**.

Numerals denoted with asterisks (*) indicate pages with figures.

ERRATA

Page	Line		For	Read
	from top	from bottom		
3		20	ringsl	rings.
6		3	studies	studied
7	1		non-nautiloid	non-nautilid
8	12		revived	reviewed
11		13	of a specimen	on a specimen
12	7		Wagner	Wagner Tree
39		20	tree	three
43	2 and 12		fig. 14	fig. 11
52		5	*Wedeoceras*	*Wadeoceras*
57		25 and 26	*P. resimum*	*D. resimum*
58	2		Flower, 1861	Roemer, 1861
65	11		*Discoceras*	*Discosorus*
67	10		fig. 18	fig. 19
		7	*staurosum*	*staurostomum*
76		2	*ellipticus* (Sobolew)	*sobolewi* nom. n.
90	23		*Lysagoceras*	*Lysagoraceras*
91	7		*Anglicoceras*	*Anglicornus*
	Title: **Jovellanidae** Foord, 1888 (line 11 from top) should be placed after line 13.			
100		12	parts shell	shell parts
129	20		*Isorthocera*	*Isorthoceras*
	34		*Euloxocera*	*Euloxoceras*
145	23		most	not
151	21		Lechritroceratidae	Lechritrochoceratidae
187		14	fig. 4	fig. 1
188	17		fig. 16	fig. 13
		9	fig. 19	fig. 16
189		3 and 23	fig. 26	fig. 23
190	1 and 2		fig. 26	fig. 23
	9 and 19		fig. 25	fig. 22
		5 and 22	fig. 24	fig. 21
191	2		fig. 22	fig. 19
	19		fig. 23	fig. 20
192	2		*Pachtoceras* Foerste, 1926	*Evlanoceras* Zhuravleva, 1972
	3		*Gomphoceras rotundum* Pacht, 1858	*Pachtoceras evlanensis* Nalivkin, 1947
	4		*Pachtoceras*	*Evlanoceras*
	5 and 17		fig. 30	fig. 29
	26 and 37		fig. 31	fig. 30

J. Dzik, ***Phylogeny of the Nautiloidea***
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PLATES

J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

Unless otherwise stated specimens are illustrated in natural size

PLATE 1

Page

Cochlioceras avus (EICHWALD, 1860) 16

1. Phragmocone in lateral (a) and ventral (b) views, ZPAL N/o16; erratic boulder E-080, *Amorphognathus variabilis* Zone, Middle Kundan (B III β), Zakroczym, Poland.

Cochlioceras burchardi (DEWITZ, 1880) 16

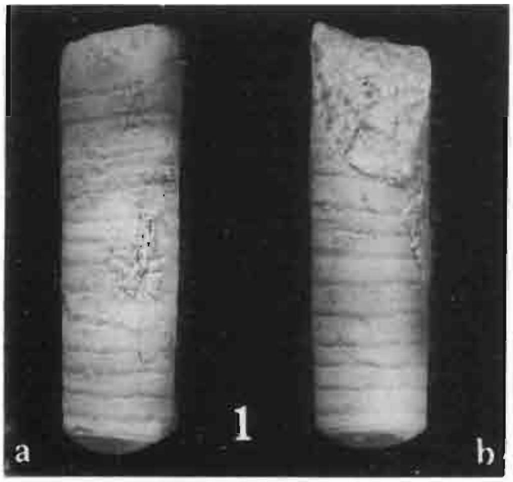
Erratic boulder E-149, *Eoplacognathus reclinatus* Zone, Lasnamägian, Międzyzdroje, Poland.

2. Adult living chamber in ventral (a) and lateral (b) views, ZPAL N/013.
3. Subadult specimen in lateral view; note the siphuncle; ZPAL N/015; erratic boulder E-149.
4. Subadult living chamber in ventral (a) and lateral (b) views, ZPAL N/014; boulder E-149.

Cochlioceras roemeri sp. n. 187

Erratic boulder E-252, *E. reclinatus* Zone, Lasnamägian, Rozewie, Poland; ×2.
(except figs. 6, 8)

5. Medial section through adapical part of a phragmocone, ZPAL N/004.
6. Medial section through adapical part of a phragmocone, ZPAL N/001; supposedly Volkhovian, Rozewie, Poland; ×3.
7. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/009.
8. Medial section through a phragmocone, ZPAL N/011; erratic boulder E-262, *E. reclinatus* Zone, Lasnamägian, Międzyzdroje, Poland.
9. Medial section through a phragmocone (a, b), holotype, ZPAL N/010; x 2.
10. Medial section through a phragmocone, ZPAL N/006; note small diameter of the apical part.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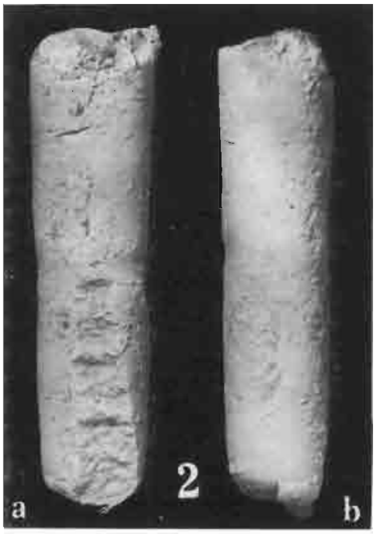
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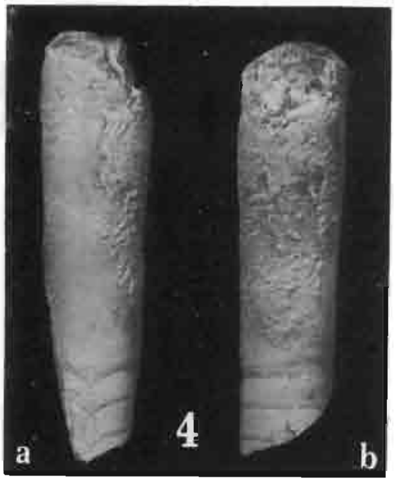
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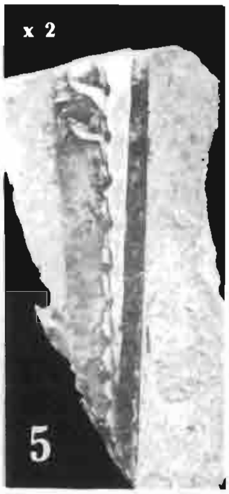
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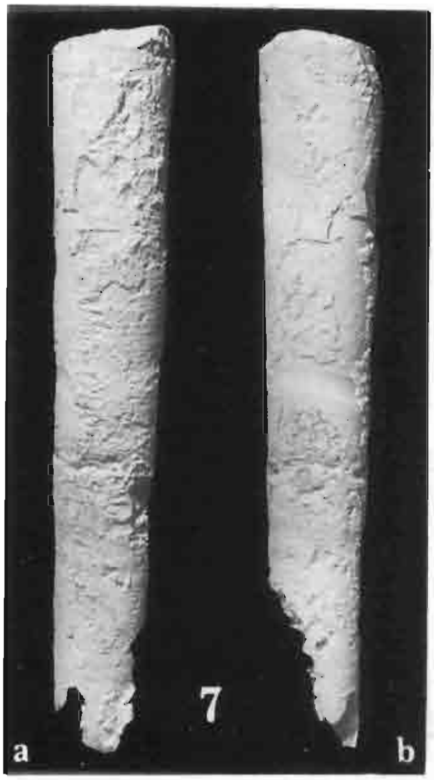
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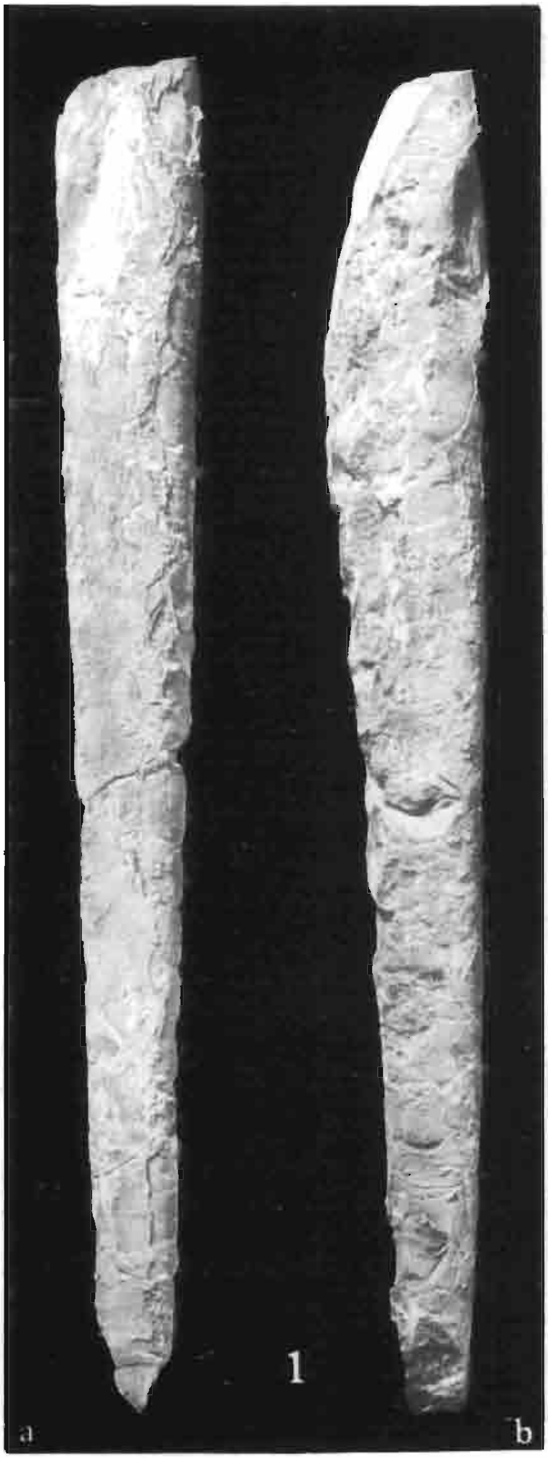
J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 2

	Page
Dideroceras glauconiticum (HEINRICHSON, 1935)	28

Paroistodus originalis Zone, Volkhovian, erratic boulders, Poland

1. Phragmocone in ventral (a) and lateral (b) views, ZPAL N/025; boulder E-116, Rozewie.
2. Medial section through a phragmocone, IG 8. II. 265; Opatów.
3. Transverse section through a phragmocone at the mid-length of the specimen, ZPAL N/030; boulder E-116, Rozewie.
4. Medial section through a phragmocone, IG 8. II. 267; Opatów.
5. Medial section through spiculum of a phragmocone, ZPAL N/039; boulder E-228, Międzyzdroje.
6. Transverse section through a phragmocone at the mid-length of the spiculum, ZPAL N/032; boulder E-116, Rozewie.
7. Medial section through spiculum of a phragmocone, ZPAL N/094; boulder E-116, Rozewie.
8. Medial section through spiculum and shell of a phragmocone, IG 8. II. 258a; Opatów.
9. Phragmocone in ventral view, IG 8. II. 264; Opatów.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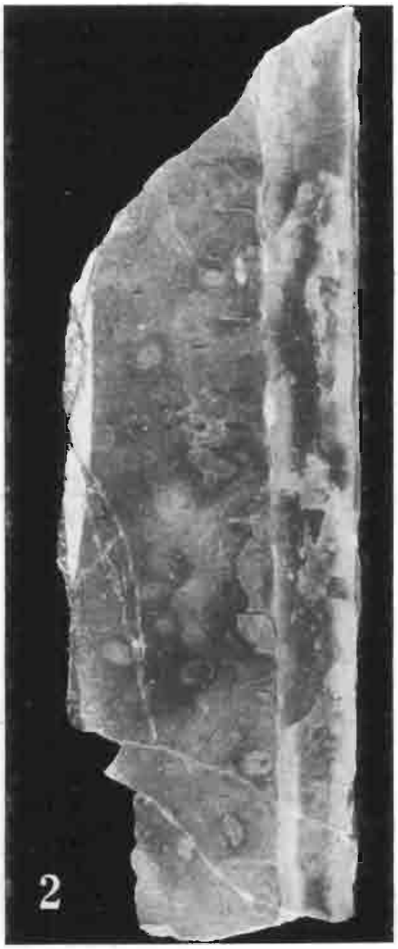
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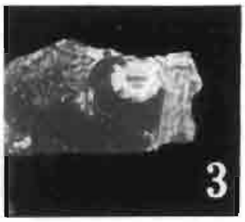
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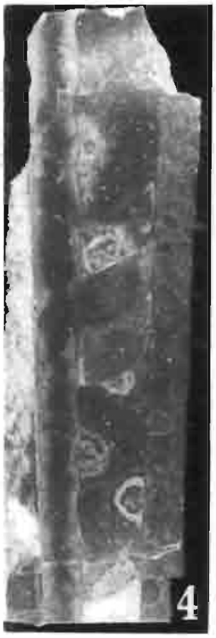
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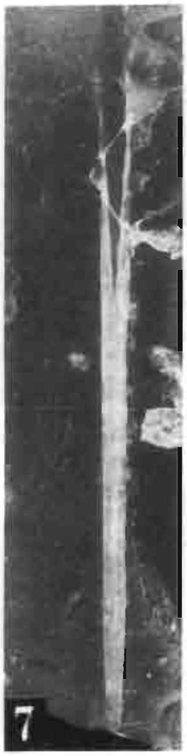
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 3

	Page
Dideroceras kundense (BALASCHOV, 1968)	31

Eoplacognathus pseudoplanus Zone, Late Kundan, erratic boulders, Poland

1. Isolated spiculum in lateral view, ZPAL N/066; Rozewie.
2. Spiculum in lateral view, ZPAL N/065; erratic boulder E-079, Mochty.
3. Phragmocone in ventral (a) and lateral (b) views, IG 137. II. 43; Świebodzice.

Dideroceras wahlenbergi (FOORD, 1887) 31

Amorphognathus variabilis Zone, Late Kundan, erratic boulders, Poland

4. Two sections through spiculum of a phragmocone (a, b), ZPAL N/045; erratic boulder E-089, Zgierz.
5. Longitudinal section through a phragmocone, ZPAL N/047; Zgierz.
6. Longitudinal (a) and transverse (b) section through a siphuncle, ZPAL N/087; Zgierz.

Anthoceras vaginatum (SCHLOTHEIM, 1820) 31

Eoplacognathus pseudoplanus Zone, Late Kundan, erratic boulders, Poland

7. Phragmocone in lateral (a) and ventral (b) views, ZPAL N/022; erratic boulder E-079, Mochty.
8. Phragmocone, ZPAL N/017; lithology indicative of the Kundan, Rozewie.

Endoceras incognitum SCHRÖDER, 1881 34

9. Phragmocone in ventral view, ZPAL N/060; erratic boulder E-081, *E. foliaceus* Zone Lasnamägian, Mochty, Poland.


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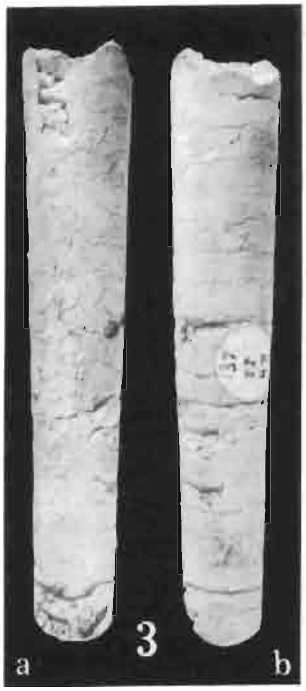
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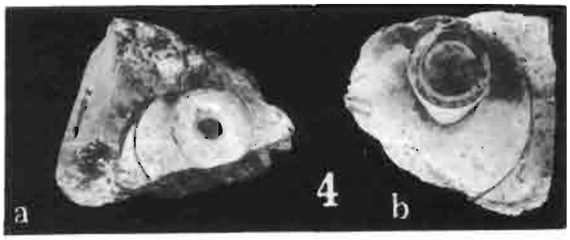
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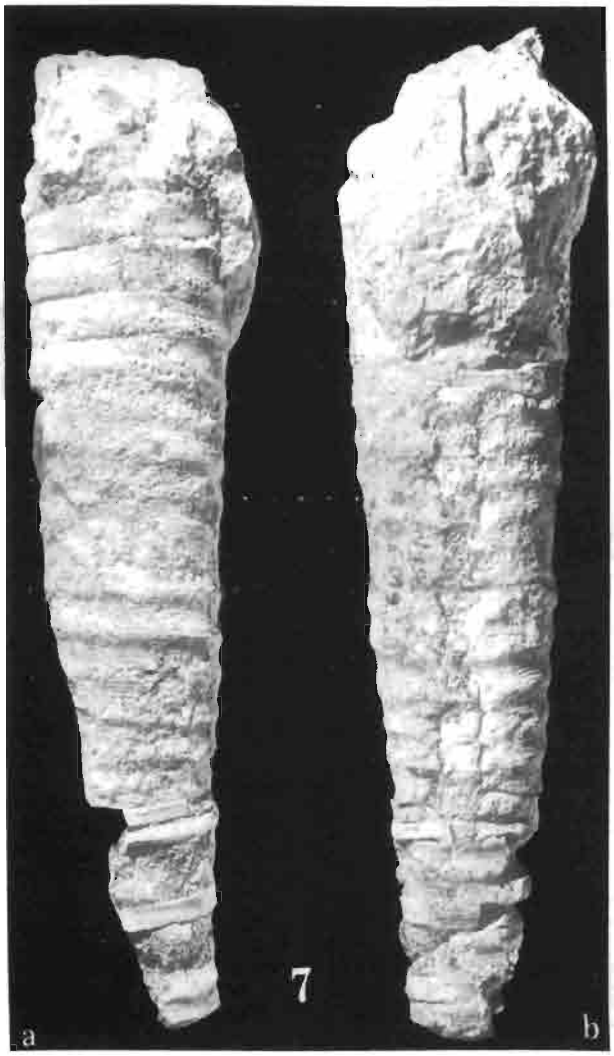
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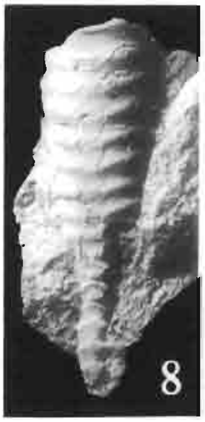
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 4

Page

Suecoceras holmi PATRUNKY, 1929 32

Eoplacognathus reclinatus Zone, Lasnamägian, erratic boulders, Poland

1. Phragmocone in ventral view (a, b), ZPAL N/070; erratic boulder E-138, Międzyzdroje; a ×0.5.
2. Phragmocone, ZPAL N/069; same boulder note the siphuncle and spiculum.
3. Longitudinal (a) and transverse (b) section through the apical part of inflated larval shell, ZPAL N/071; erratic boulder E-132; ×2.
6. Phragmocone in ventral view, ZPAL N/074; Mochty.
7. Phragmocone in ventral view, ZPAL N/075; Zgierz.

Suecoceras (?) sp. 32

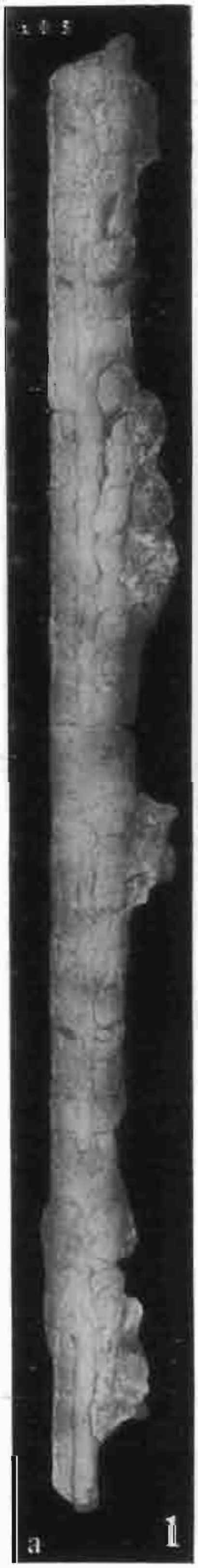
4. Ventral side of a phragmocone fragment, ZPAL N/083; lithology indicative of the Volkhovian to Aserian; Orlowo Poland; note the sectioned siphuncle.

Suecoceras (?) sp. 34

5. Phragmocone in ventral view, ZPAL N/085; *E. pseudoplanus* Zone, earliest Llanvirnian, borehole Stadniki IG 1 (depth of 1187 m), Poland; note ornamentation on the preserved shell fragments.

Suecoceras sp. 34

9. Phragmocone, UW 5/4/74, Mójcza Limestone, *E. reclinatus* Zone, Llanvirnian, Mójcza near Kielce, Poland.
8. Medial section through apical part of a shell, ZPAL N/912, erratic boulder E-275, *E. foliaceus* Zone, Lasnamägian, Szczecin, Poland.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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 5

Page

Estonioceras lamellosum (HISINGER, 1837) 45

1. Subadult complete specimen in apertural (a), ventral (b) and lateral (c) views, MGUW 6/6/31; note retractor muscle scars; *Eoplacognathus pseudoplanus* Zone, Late Kundan, Estonia (locality unknown).

Tragoceras falcatum (SCHLOTHEIM, 1820) 38

Eoplacognathus pseudoplanus Zone, Late Kundan or Early Aserian, erratic boulders, Mochty, Poland

2. Incomplete phragmocone in lateral (a) and ventral (b) views, ZPAL N/089; erratic boulder E-079.
3. Adult specimen in lateral view (b) and its living chamber in ventral view (a), ZPAL N/090.

Trocholites contractus SCHRÖDER, 1891 43

4. Juvenile specimen, lateral (a) and ventral (b) views, ZPAL N/872; erratic boulder E-274, Międzyzdroje, Poland; × 2.


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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 6

Page

Trocholites contractus SCHRÖDER, 1891 43

E. robustus Zone, Uhakuan, erratic boulder E-240, Stężyca, Poland

1. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/091.

Trocholites orbis SCHRÖDER, 1891 43

E. lindstroemi Zone, Uhakuan, erratic boulders, Poland

2. Small adult specimen in lateral view, ZPAL N/094; erratic boulder E-254, Rozewie.
3. Adult specimen in lateral (a) and apertural (b) views, ZPAL N/092; erratic boulder E-140, Międzyzdroje.

Discoceras sp. 40

Oanduan (?), erratic boulder E-212, Mochty, Poland

4. Adult (?) specimen in lateral (a) and ventral (b) views, ZPAL N/098.

Discoceras roemeri STRAND, 1934 41

Ashgillian (?), erratic boulders, Zawidowice, Poland

5. Adapertural part of adult living chamber in ventral (a) and lateral (b) views, UWR 3186a.
6. Subadult specimen in lateral (a) and apertural (b) views, UWR 1695a; ROEMER'S (1852, pl. 6: 26) original specimen.

Gen. et sp. indet. 42

Idaverean or Johvian, erratic boulder E-241, Gołubie, Poland

7. Specimen in lateral (a) and ventral (b) views, ZPAL N/097.

Schroederoceras sp. 45

Late Caradocian, erratic boulder, Zgierz, Poland

8. Specimen in lateral (a) and dorsal (b) views, ZPAL N/096.


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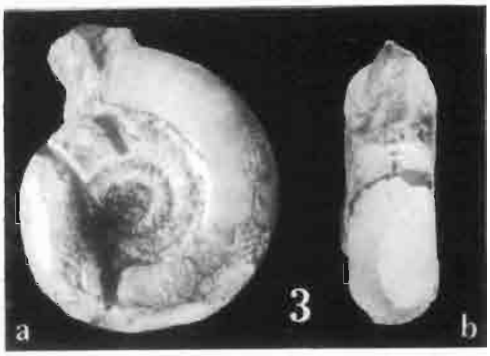
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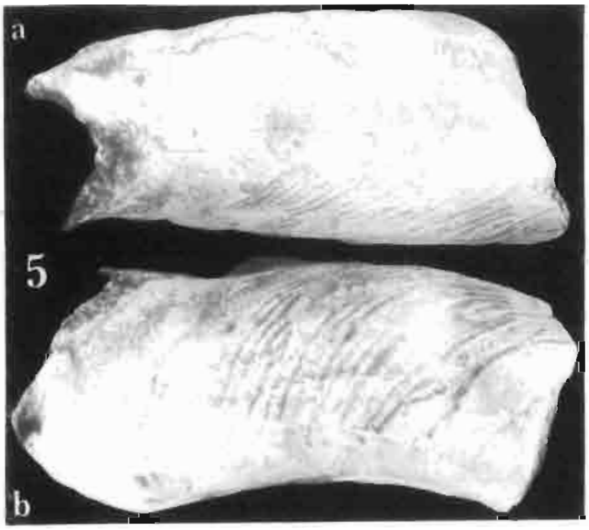
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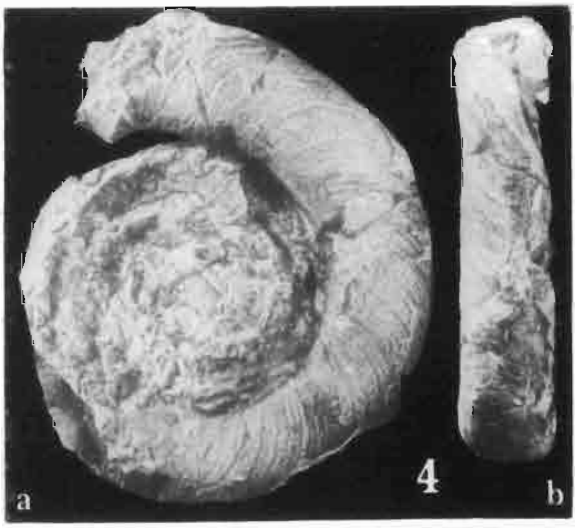
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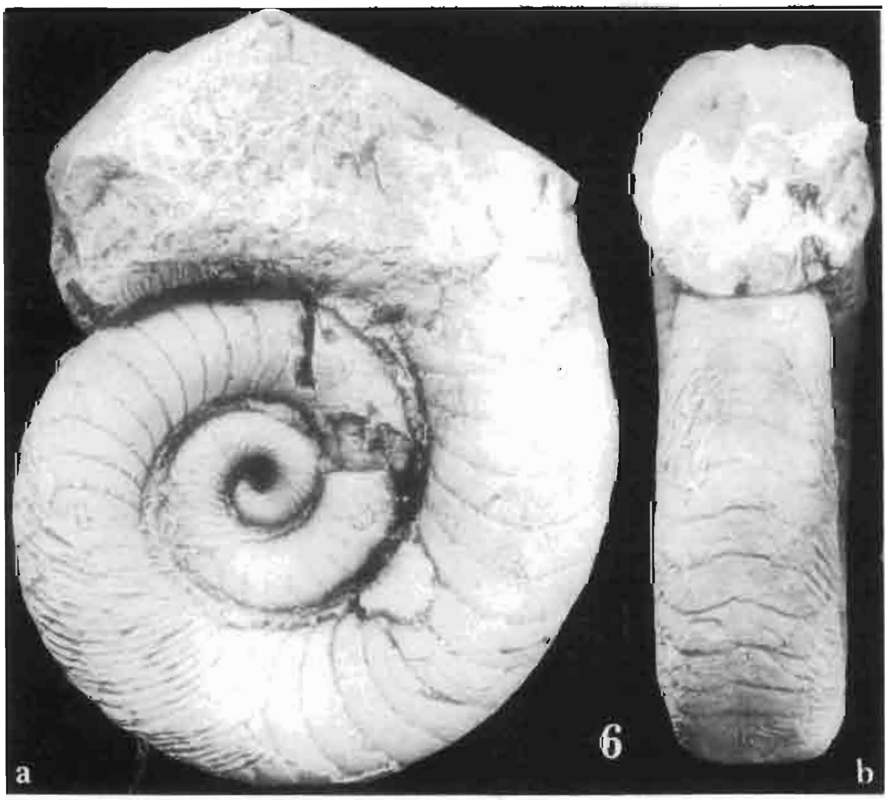
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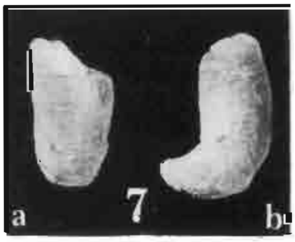
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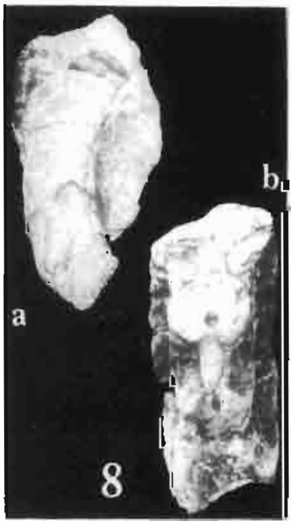
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 7

Page

Discoceras antiquissimum (EICHWALD, 1845) 45

1. Living chamber in lateral (a) and septal (b) views, IG 139. II. 7; Ashgillian (?), erratic boulder, Zawidowice, Poland; probably ROEMER'S (1852, pl. 6: 2f) original specimen.

Protophragmoceras sp. 53

2. Specimen in lateral (a) and ventral (b) views, ZPAL N/099; Idaverean or Johvian, erratic boulder E-241, Gołubie, Poland; also 2 × enlarged exposed part of its siphuncle (b).

Flowerites sobolewi nom. n. 188

Platyclymenia Zone, Famennian, Łagów-Dule, Poland

3. Medial section through and adult specimen, ZPAL N/103.
4. Adult specimen in dorsal (a) and lateral (b) views, ZPAL N/102.

Phragmoceras broderipi (BARRANDE, 1863) 53

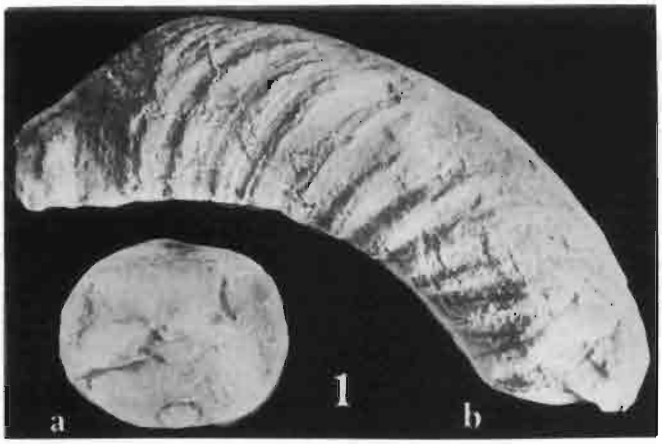
5. Medial section through an adult specimen, UWR 3231s; Kopanina Formation, Ludlovian, Lochkov, Bohemia; also its 2× enlarged siphuncle (b) with radial pattern of the siphuncular deposits.

Flowerites vel *Devonocheilus* sp. 75

6. Medial section through a phragmocone, ZPAL N 101, *Cheiloceras* Zone, bed J. 6, Jabłonna, Poland.

Protophragmoceras sphynx (SCHMIDT, 1858) 53

7. Phragmocone in lateral view (b) and its medial section (a), ZPAL N/100; Ashgillian (?), boulder E-090, Zgierz, Poland.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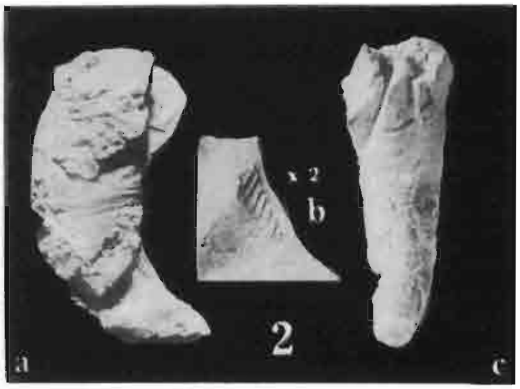
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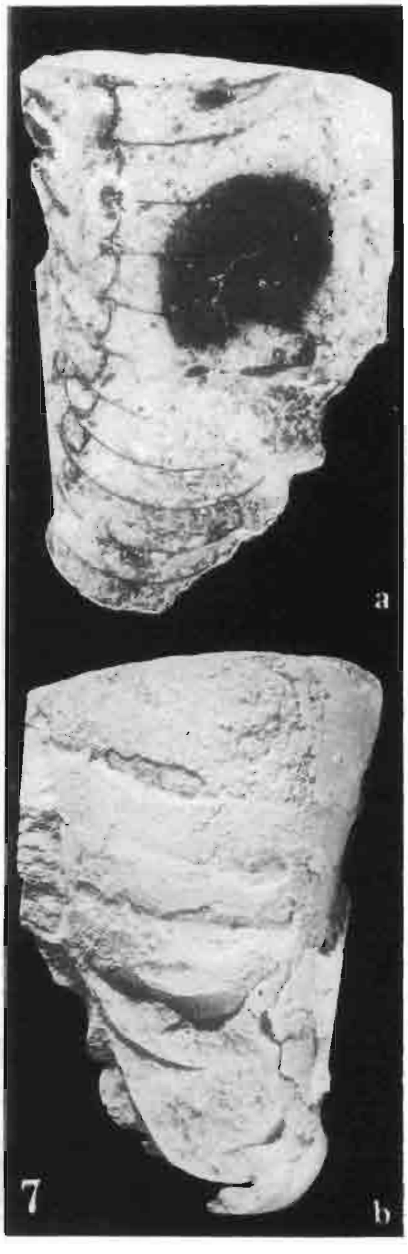
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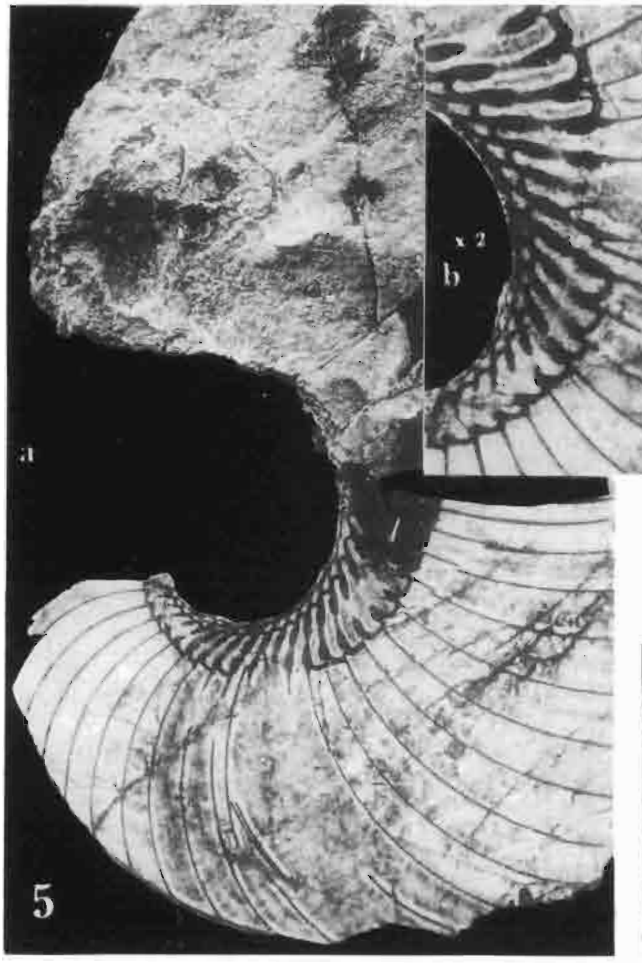
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 8

Page

Richardsonoceras sinuososeptatum (ROEMER, 1861) 188

1. Phragmocone of a subadult specimen in ventral (a), lateral (b), and adapertural (c) views, and its medial section (d), UWR 3230s; paratype; Ashgillian (?), erratic boulder, Zawidowice, Poland.

Oonoceras acinaces (BARRANDE, 1866) 56

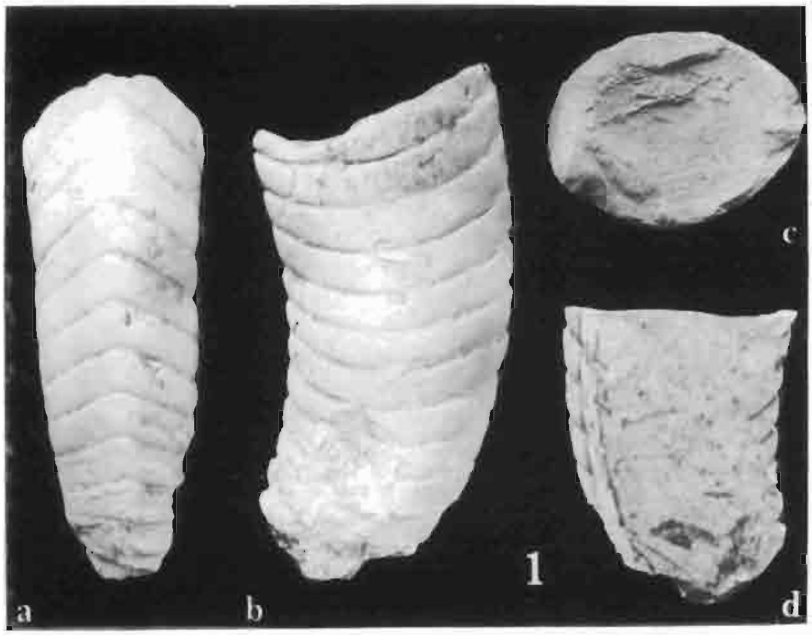
2. Adult specimen in lateral view, ZPAL N/108; Ludlovian (?), borehole Parczew IG 1 (depth 1230 m), Poland.

Richardsonoceras patulum (BARRANDE, 1866) 73

3. Adult specimen in ventral (a) and lateral (b) views, NM L-10099; BARRANDE's (1866, pl. 110: 1-6) original specimen; Kopanina Formation, Ludlovian, Zmrzlik, Bohemia.

Richardsonoceras haueri (BARRANDE, 1866) 73

4. Adult specimen in lateral view; BARRANDE's (1866, pl. 119: 10-12) original specimen; Kopanina Formation, Ludlovian, Zmrzlik, Bohemia.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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 9

	Page
Oonoceras sp.	56

1. Complete juvenile specimen in lateral (a) and ventral (b) views, ZPAL N/107; *E. foliaceus* Zone, Lasnamägian, boulder E-138, Międzyzdroje, Poland.

Hindeoceras sp.	61

2. Phragmocone fragment in septal (a) and dorsal (b) views, ZPAL N/354; also 2 × enlarged longitudinal section through its siphuncle (c); Skały beds (Eifelian Givetian boundary), Świętomarz, Poland.

Richardsonoceras patulum (BARRANDE, 1866)	73

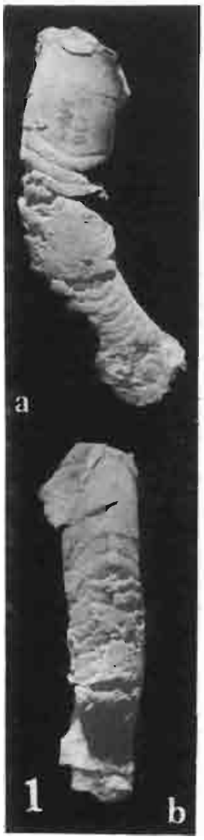
3. Longitudinal section through a specimen, NM L-10096 (*Cyrtoceras fraternum* in BARRANDE, 1866, pl. 109: 26-27); Kopanina Formation, Ludlovian, Lochkov, Bohemia.

Digenuoceras (?) *alinae* (BARRANDE, 1866)	66

4. Adult specimen in ventral (a) and lateral (b) views, NM L-10134; BARRANDE'S (1866, pl. 135: 13-19) original specimen; Kopanina Formation, Ludlovian, Lochkov, Bohemia.

Digenuoceras (?) *discoideum* (BARRANDE, 1866)	66

5. Adult specimen in ventral (a) and lateral (b) views, NM L-504; BARRANDE'S (1866, pl. 135: 5-8) original specimen; Přidolian, Karlštein, Bohemia.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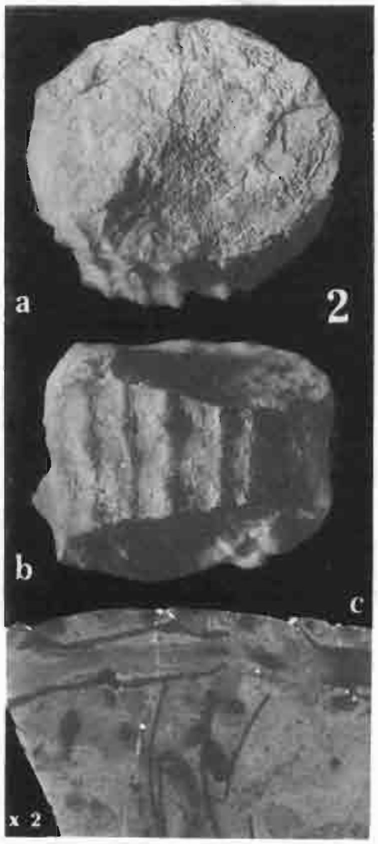
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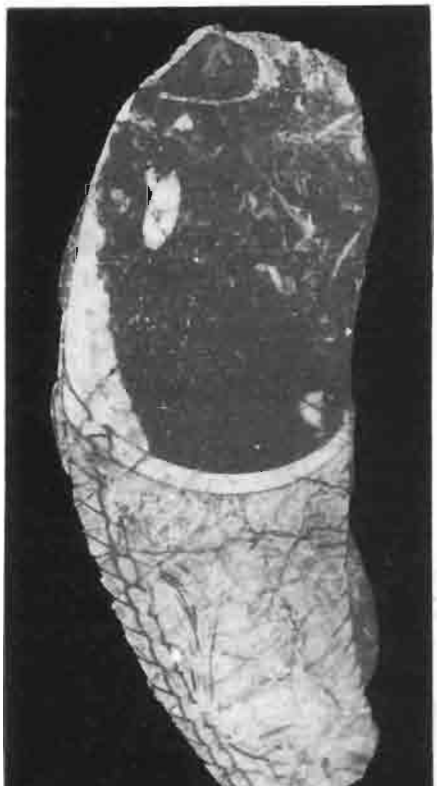
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 10

Page

Lysagoraceras kielcense sp. n. 190

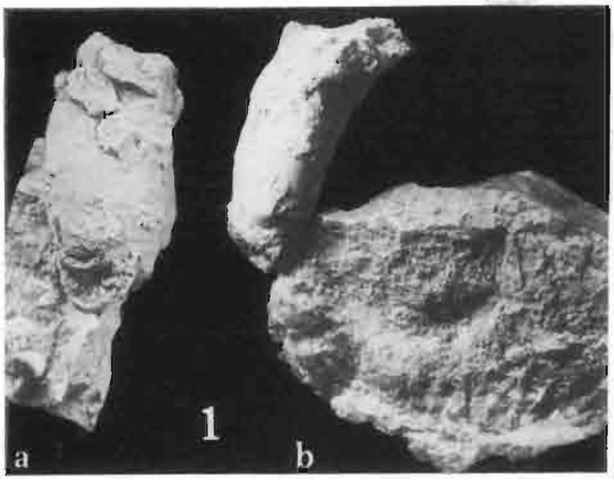
Cheiloceras Zone, Famennian, Jabłonna, Poland

1. Adult specimen in ventral (a) and lateral (b) views, holotype, ZPAL N/111; bed J. 6.
2. Longitudinal section through a specimen, ZPAL N/120; bed J. 9.
3. Mature living chamber in lateral (a) and ventral (b) views, ZPAL N/113; bed J. 6
4. Phragmocone of an adult specimen in lateral (a) and dorsal (b) views, ZPAL N/122; bed J. 6.

Lysagoraceras lagowiense (GÜRICH, 1896) 189

Platyclymenia Zone, Famennian, Łagów-Dule, Poland

5. Phragmocone in ventral (a) and lateral (b) views, ZPAL N/143.
6. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/144.
7. Adult specimen in lateral (a) and ventral (b) views, UWR 3228s; holotype, GÜRICH's (1896) original specimen.
8. Adult specimen in ventral (a) and lateral (b) views, ZPAL N/128.
9. Very small adult specimen in ventral (a) and lateral (b) views, ZPAL N/151.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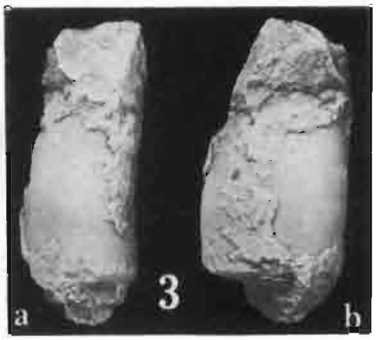
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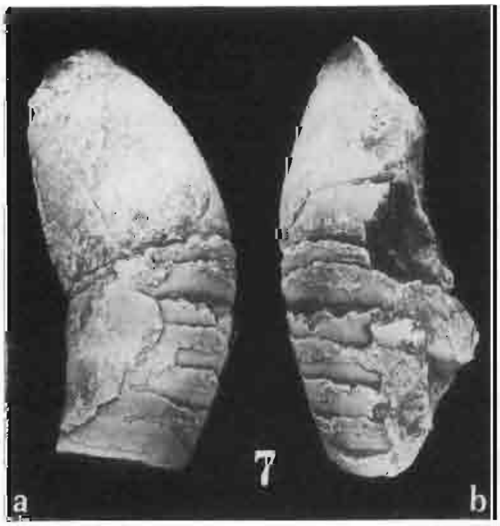
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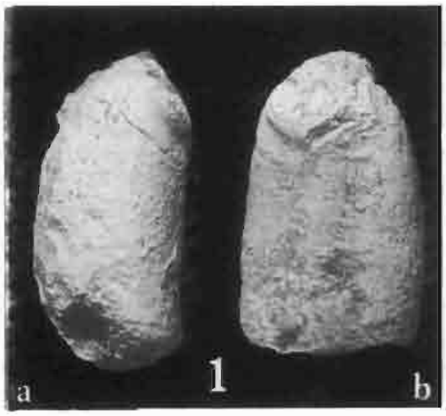
J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 11

Page

Gonatocyrtoceras longissimum sp. n. 190
Cheiloceras Zone, Famennian, Poland

1. Adult living chamber in lateral (a) and dorsal (b) views, ZPAL N/224; bed J. 6, Jabłonna.
2. Adult living chamber in ventral (a) and lateral (b) views, specimen from the burned collection of the Geological Institute, Warsaw; supposedly Kadzielnia.
3. Longitudinal section through a phragmocone, ZPAL N/237; Jabłonna; ×2.
4. Adult living chamber in lateral (a), dorsal (b), and septal (c) views, specimen from the burned collection of the Geological Institute, Warsaw; supposedly Kadzielnia.
5. Adult specimen in ventral (a), lateral (b), dorsal (c), and septal (d) views, ZPAL N/223, holotype; bed J. 7, Jabłonna.
6. Adult specimen in dorsal (a) and lateral (b) views, ZPAL N/227; Kadzielnia.
7. Longitudinal section through a phragmocone, ZPAL N/301; Kadzielnia; ×2.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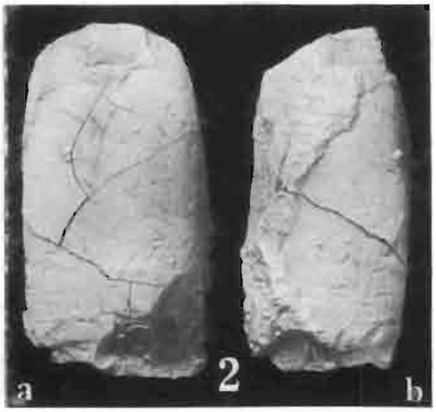
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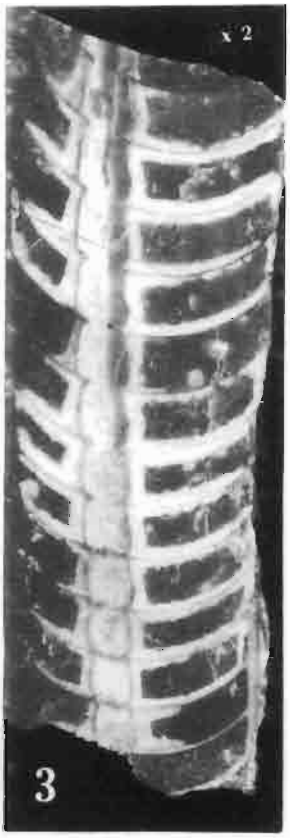
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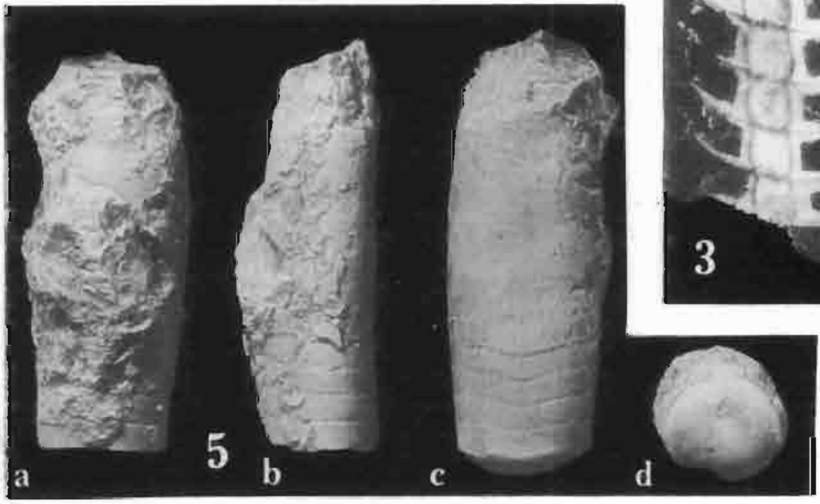
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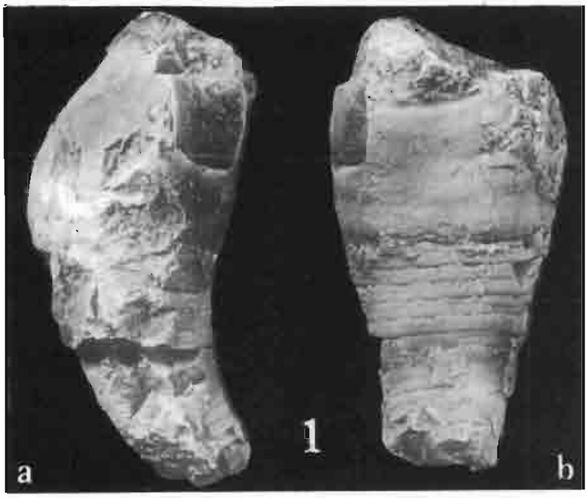
J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 12

Page

Gonatocyrtoceras holzapfeli (Sobolew, 1912) 191
Platyclymenia Zone, Famennian, Łagów-Dule, Poland

1. Subadult specimen in lateral (a) and dorsal (b) views, ZPAL N/319.
2. Adult specimen in lateral (a) and dorsal (b) views, ZPAL N/331.
3. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/320.
4. Subadult specimen in lateral (a), dorsal (b), and septal (c) views, ZPAL N/321.
5. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/317.
6. Adult specimen in lateral (a) and ventral (b) views, coll. Prof. H. Makowski.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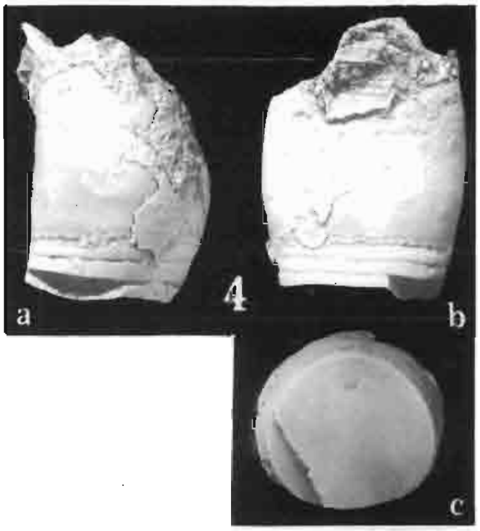
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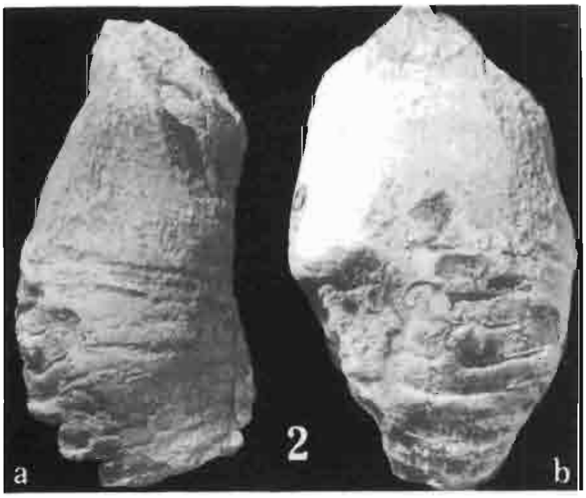
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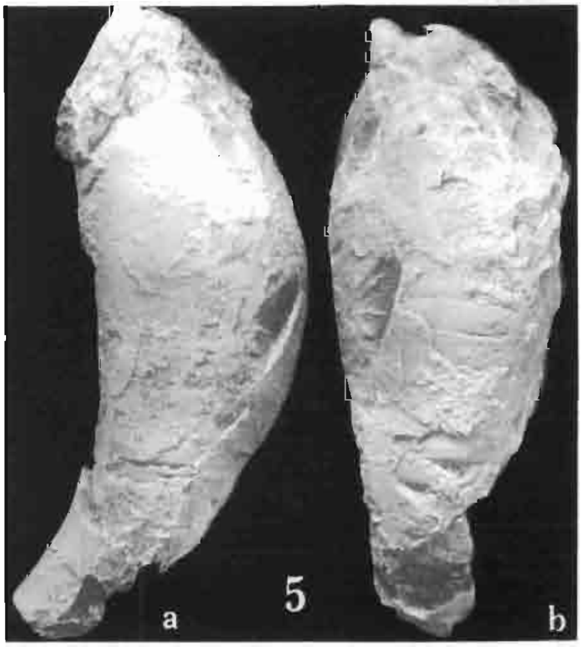
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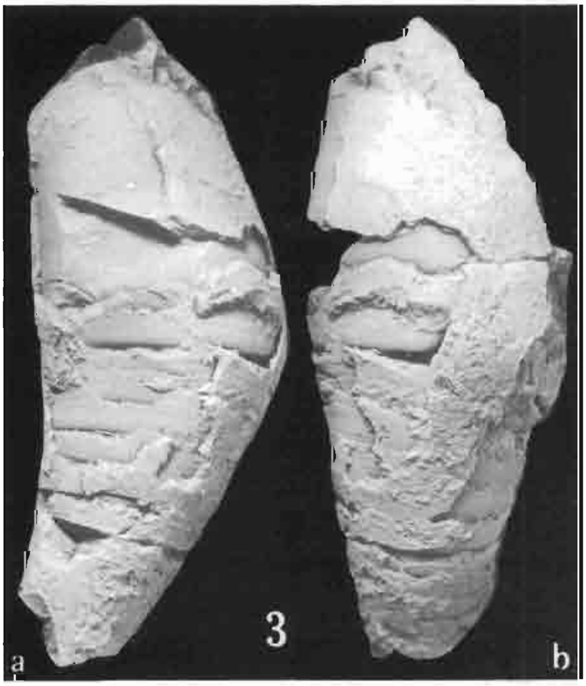
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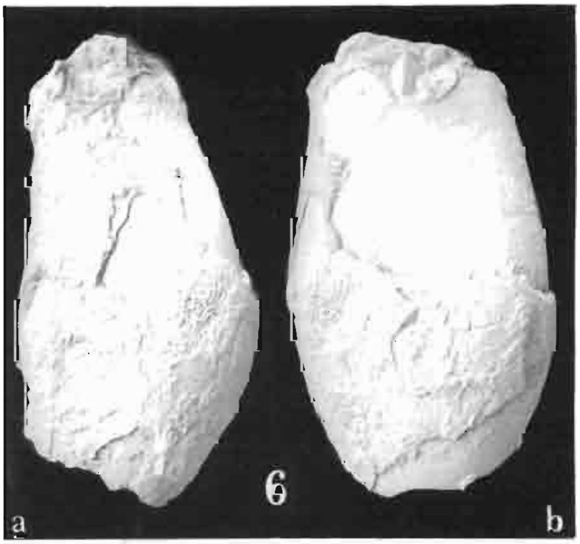
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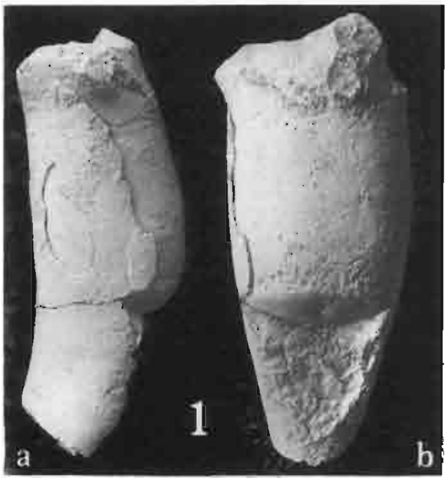
J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 13

Page

Gonatocyrtoceras guerichi (Sobolew, 1912) 191
Platyclymenia Zone, Famennian, Łagów-Dule, Poland

1. Very small adult specimen in lateral (a) and ventral (b) views, coll. Prof. H. Makowski
2. Large phragmocone in lateral (a) and dorsal (b) views, ZPAL N/335.
3. Longitudinal section through a phragmocone, ZPAL N/323.
4. Adult living chamber in lateral (a), ventral (b), and septal (c) views, ZPAL N/333.
5. Adult specimen in lateral (a) and ventral (b) views, coll. Prof. H. Makowski.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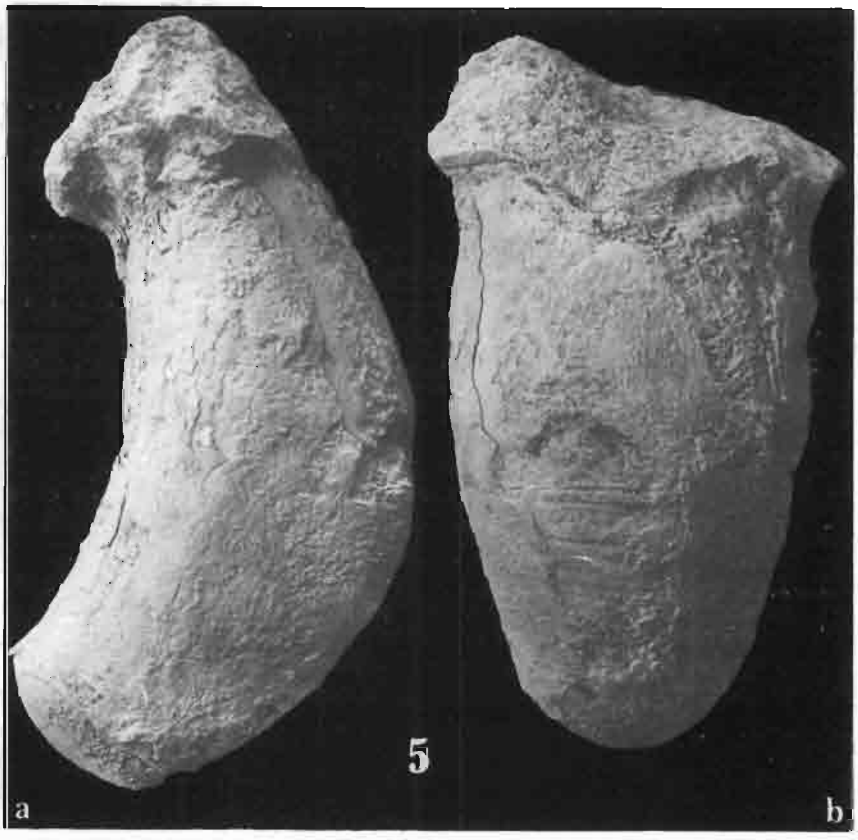
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 14

Page

Lysagoraceras subfusiforme (MÜNSTER, 1840) 74
Platyclymenia Zone, Famennian, Łagów-Dule, Poland

1. Adult specimen in lateral (a) and dorsal (b) views, ZPAL N/164.
2. Adult specimen in lateral view, ZPAL N/180.
3. Adult specimen in lateral view, ZPAL N/187.
4. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/163.
6. Adult living chamber in dorsal (a), lateral (b) and septal (c) views, ZPAL N/168; ×2.

Lysagoraceras (?) cf. *erraticum* (ZHURAVLEVA, 1972) 75
Platyclymenia Zone, Famennian, Łagów-Dule, Poland

5. Adult specimen in dorsal (a) and lateral (b) views, ZPAL N/208.
9. Very small specimen in dorsal (a) and lateral (b) views, ZPAL N/202.
10. Adult specimen in lateral (a) and dorsal (b) views, ZPAL N/210.

? *Devonocheilus* sp. 75

7. Adult specimen in lateral (a) and dorsal (b) views, ZPAL N/341; *Wocklumeria* Zone, Late Famennian, Dzikowiec, Poland.

Lysagoraceras sp. 73

8. Adult specimen in ventral (a) and lateral (b) views, ZPAL N/214; bed J. 7; *Cheiloceras* Zone, Famennian, Jabłonna, Poland; ×2.

Lysagoraceras (?) sp. (cf. *erraticum* ZHURAVLEVA, 1972) 75
Platyclymenia Zone, Famennian, Jabłonna, Poland

11. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/212; bed J. 26.


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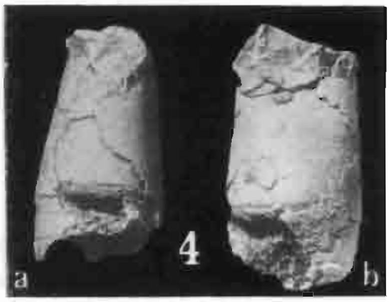
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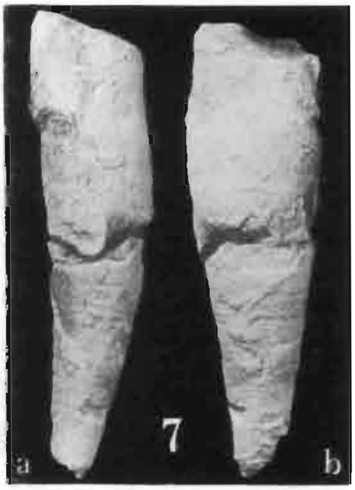
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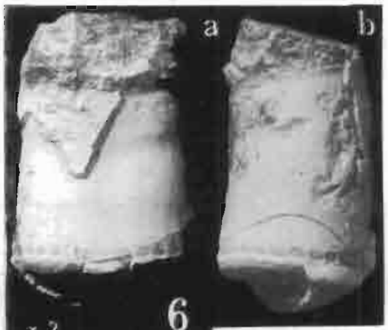
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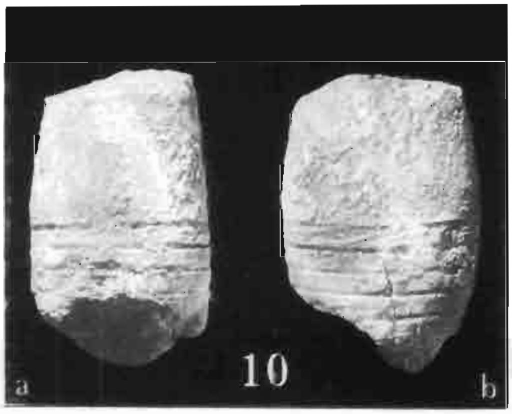
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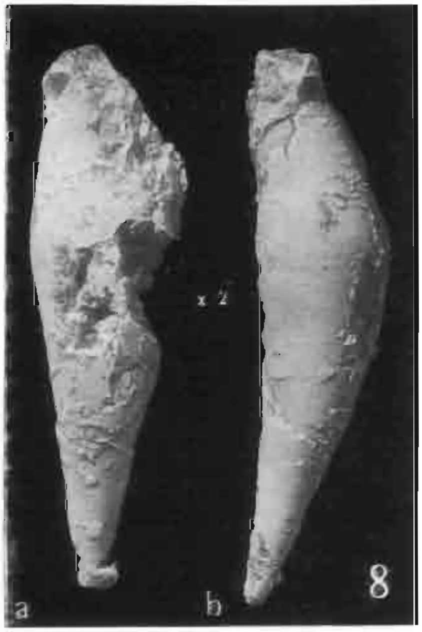
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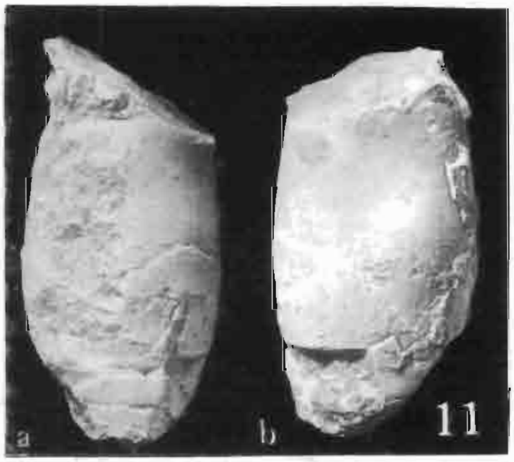
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 15

Page

Rizosceras intermedium (BARRANDE, 1865) 66

1. Adult specimen in lateral (a) and dorsal (b) views, **NM L-10263**; BARRANDE's (1885, pl. **150**: 22-25) original specimen; Přidolian, Karlštein, Bohemia.

Mandaloceras (?) sp. 87

2. Longitudinal section through a specimen, **ZPAL N/343**; Wenlockian (?), boulder E-164 (with *Poleumita angulatum* (WAHLENBERG)), Orłowo, Poland.

Pachtoceras (?) sp. 87

3. Specimen in lateral (a) and septal (b) views and its 2× enlarged longitudinal section (c), **ZPAL N/344**; Skały beds (Eifelian/Givetian boundary), Świętomarz, Poland.

Oxygonioceras priscum (BARRANDE, 1865) 66

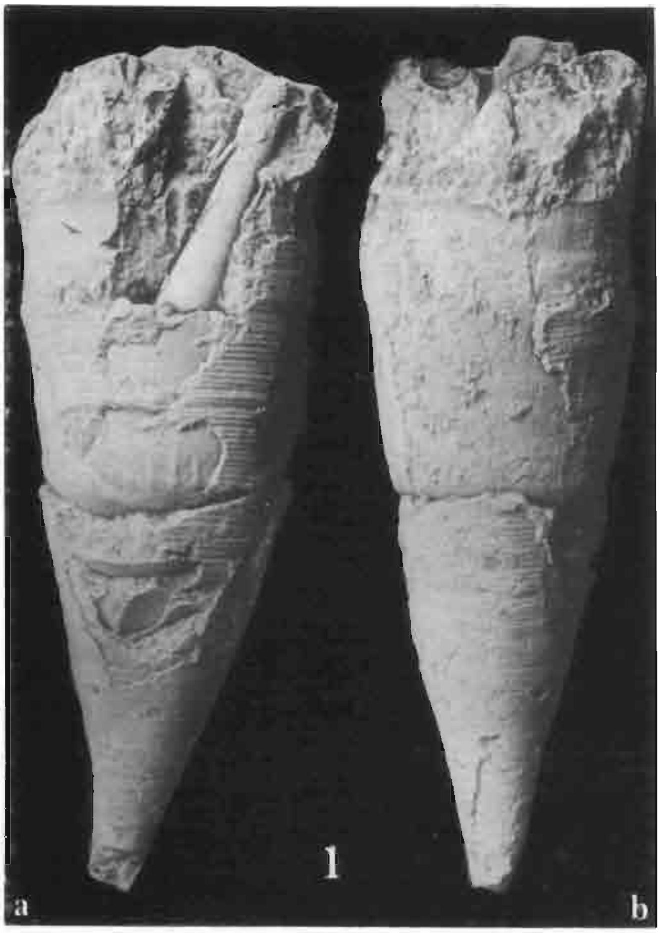
4. Adult specimen in apertural (a) and lateral (b) views, **NM L-140**; BARRANDE's (1865, pl. 15: 16-19) original specimen; Kopanina Formation, Ludlovian, Lochkov, Bohemia.

Rizosceras sp. 66

5. Compressed specimen, **ZPAL N/345**; Ludlovian, Prągowiec by Łagów, Poland.

Mitroceras (*Foersteoceras*) or *Lorieroceras* sp. 65

6. Specimen in adapertural view, **ZPAL N/342**; boulder of Beyrichienkalk, Pridolian, Zgierz, Poland.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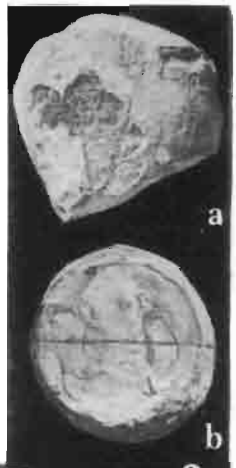
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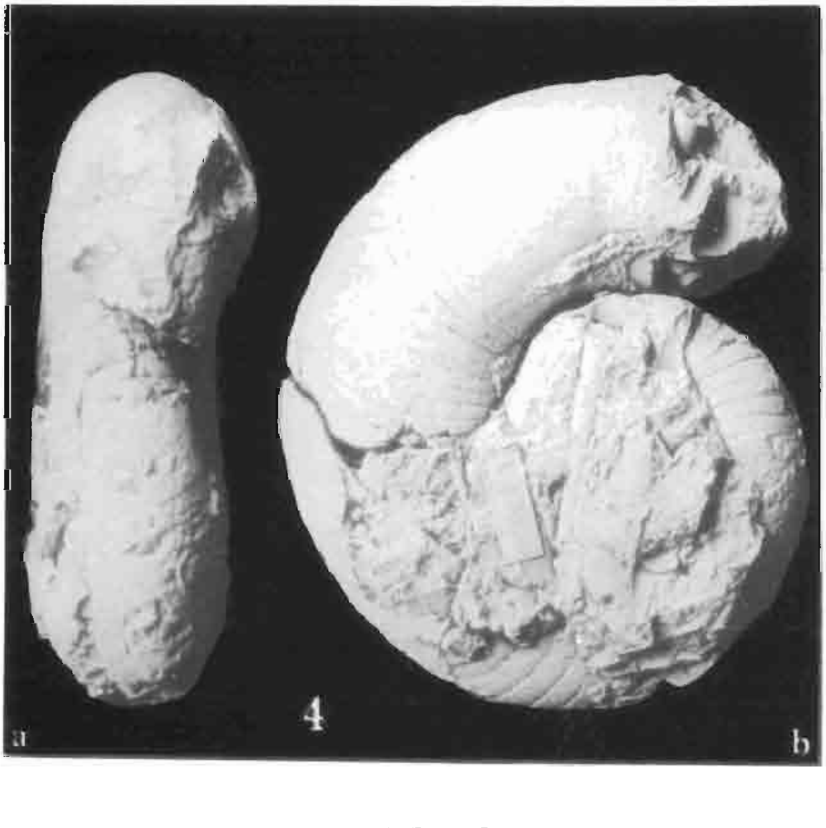
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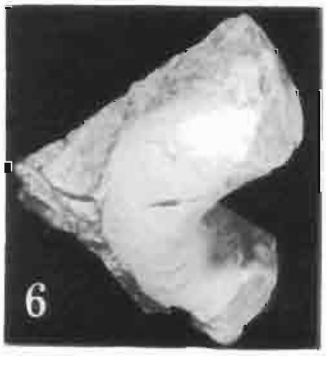
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 16

	Page
Pachtoceras sp.	87

Late Frasnian, Płucki by Łagów, Poland

1. Adult specimen in lateral (a) and ventral (b) views, ZPAL N/392.
8. Subadult specimen in lateral (a), dorsal (b) and septal (c) views, ZPAL N/389.

Pachtoceras abbreviatum (GÜRICH, 1901)	79

Cheiloceras Zone, Early Famennian, Kadzielnia, Poland

3. Adult specimen in ventral (?) view, ZPAL N/385.
4. Adult specimen in ventral (a), lateral (b), and septal (c) views, ZPAL N/388.
5. Longitudinal section through a specimen, ZPAL N/386.

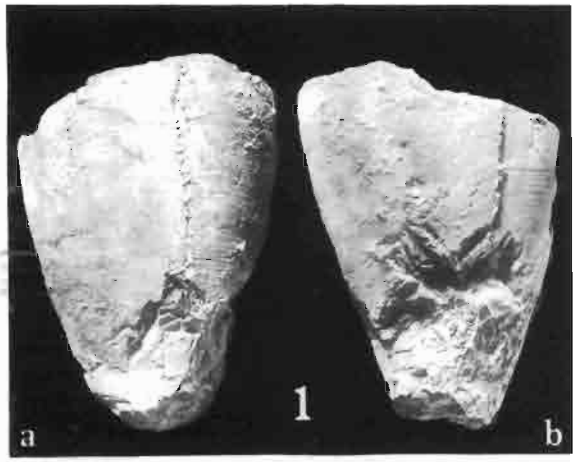
Ascoceras sp.	112

2. Adult specimen in lateral (a) and dorsal (b) views, ZPAL N/913; erratic boulder E-284, Ludlovian, Suwałki, Poland

cf. Pachtoceras abbreviatum (GÜRICH, 1901)	79

Cheiloceras Zone, Early Famennian, Jabłonna, Poland

6. Specimen in dorsal view, ZPAL N/364; bed. J. 8.
7. Longitudinal section through a specimen, ZPAL N/359; bed J. 11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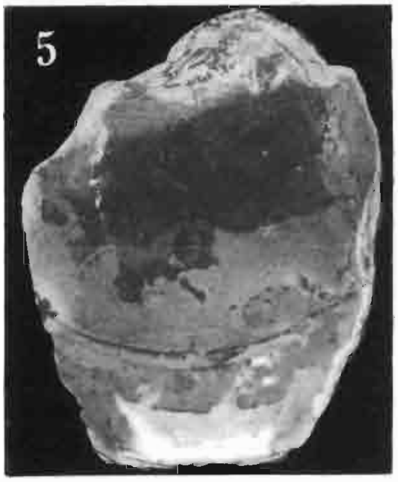
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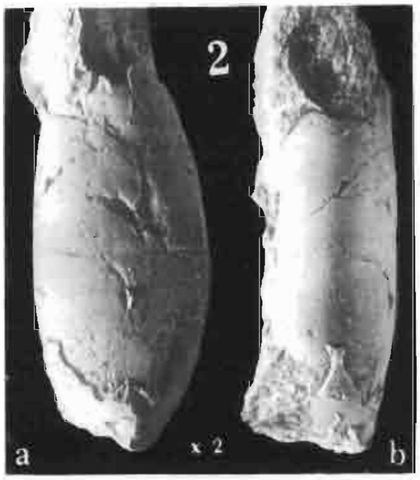
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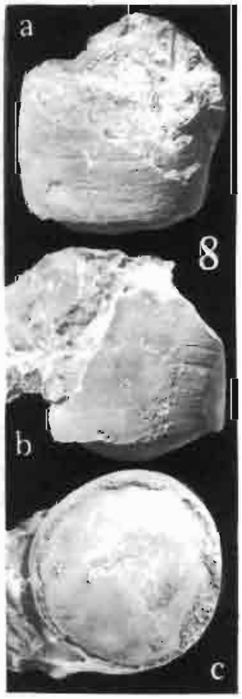
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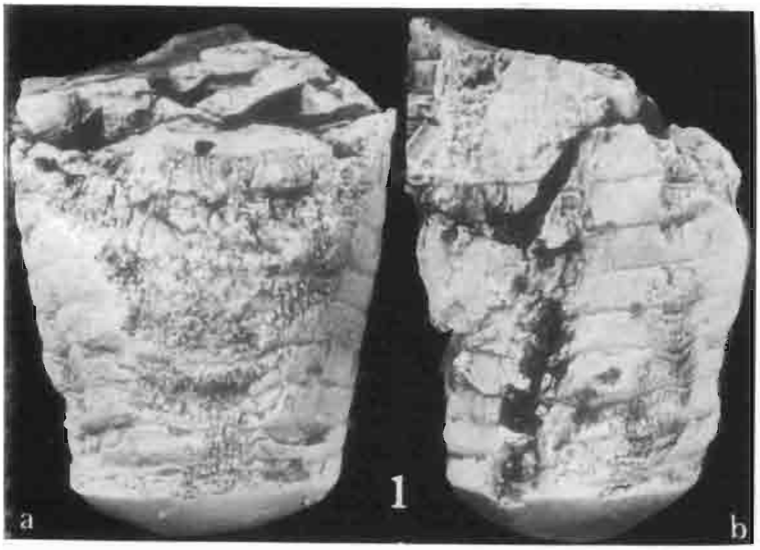
J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 17

Page

Mecynoceras (?) *polonicum* (Gürich, 1896) 192
Cheiloceras Zone, Early Famennian, Poland

1. Holotype in ventral (a) and lateral (b) views, UWR 2109 (Gürich 1896, pl. 12: 3a-b); Łagów, probably left wall of Dule gorge (labelled as Intumescens Stufe).
2. Longitudinal section through a specimen, ZPAL N/381; Kadzielnia.
3. Adult specimen in dorsal (a) and lateral (b) views, ZPAL N/382; Kadzielnia.
4. Two oblique sections through a specimen, ZPAL N/356; Dębnik, Żbik gorge, Cracow region.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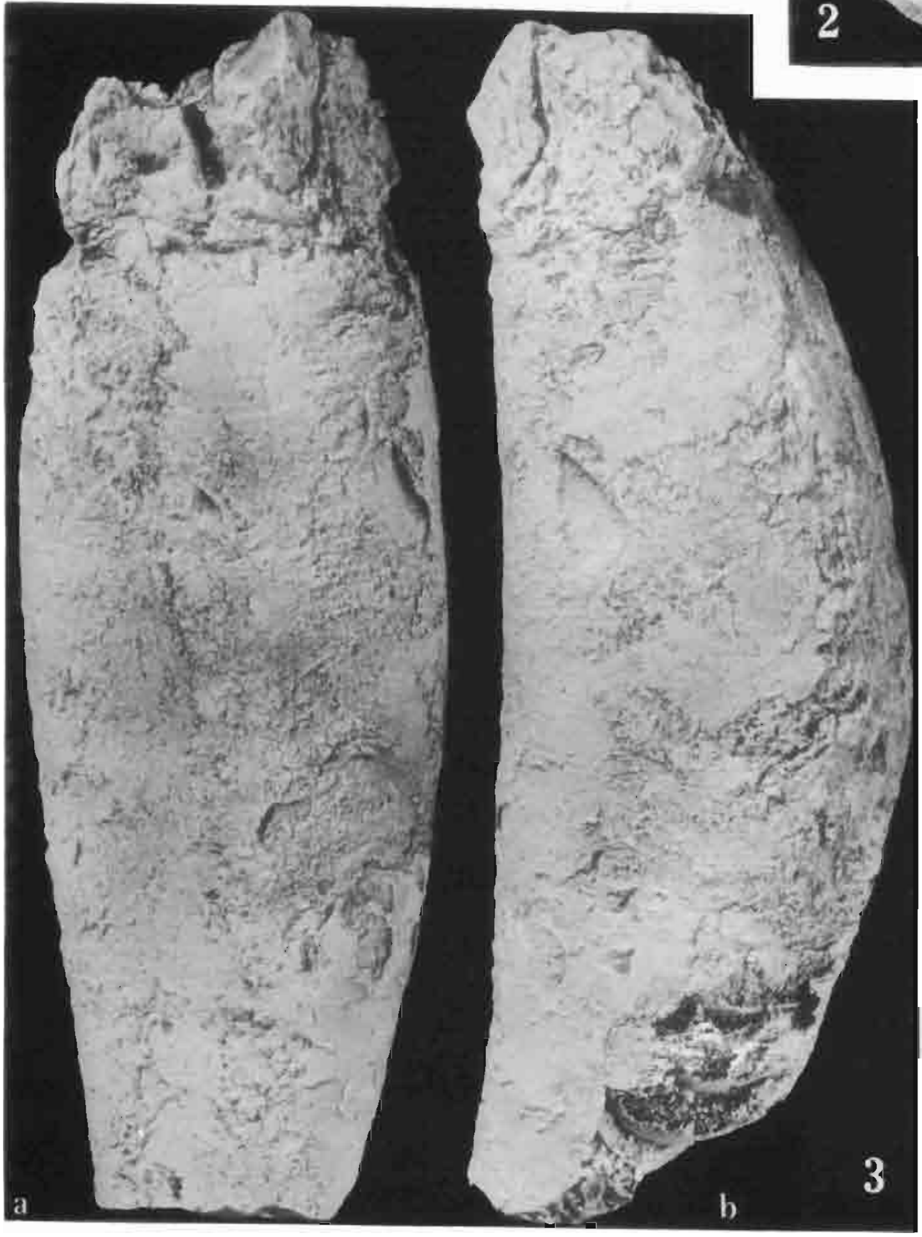
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 18

Page

Balaschovia (?) vel *Mecynoceras* sp. 85

Cheiloceras Zone, Early Famennian, Poland

1. Longitudinal section through a specimen, ZPAL N/351; bed J. 11, Jabłonna.
3. Longitudinal sagittal section through a phragmocone (b), and the associated living chamber in dorsal view (a), ZPAL N/353; Łagów, left wall of Dule gorge.

Mecynoceras (?) *polonicum* (GÜRICH, 1896) 192

Cheiloceras Zone, Early Famennian, Łagów — left wall of Dule gorge, Poland

2. Adult living chamber in dorsal (a) and septal (b) views, and medial section through a phragmocone (c), ZPAL N 395.


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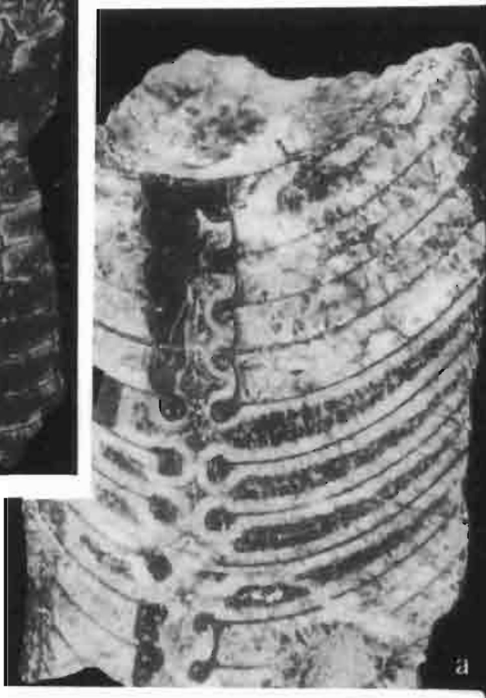
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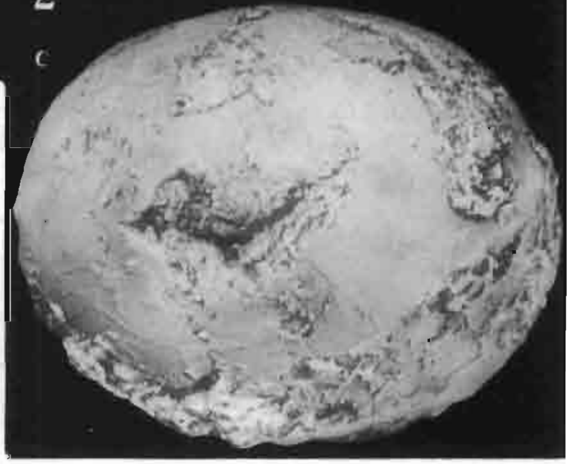
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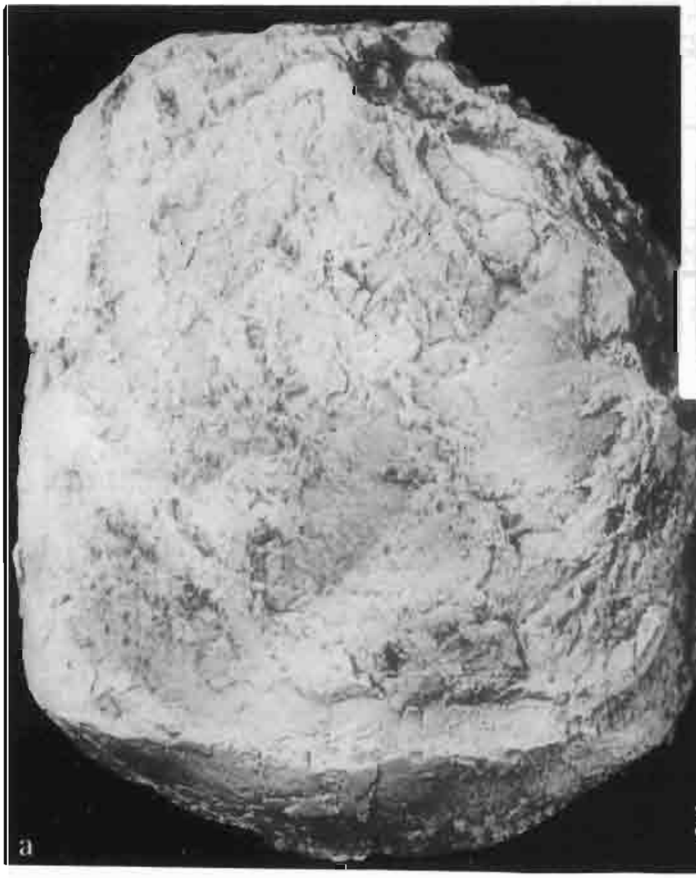
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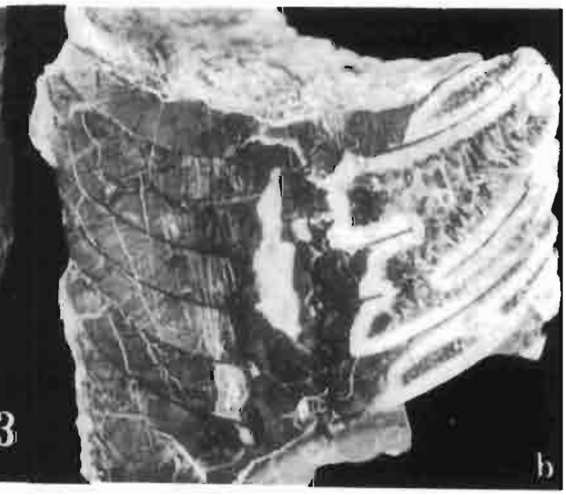
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 19

Page

Eylanoceras (?) *kontkiewiczi* (GÜRICH, 1896) 192

Platyclymenia Zone, Early Famennian, Poland

1. Incomplete adult phragmocone in lateral view, coll. Prof. H. MAKOWSKI; Łagów-Dule.
3. Subadult (?) specimen in lateral view, ZPAL N/367; Łagów-Dule.
3. Holotype in ventral view, UWR 3227a (GÜRICH 1896, pl. 12: 2a-b); Psiarnia, Kielce.

Tipleuroceras (?) *triangulare* (d'ARCHIAC and VERNEUIL, 1842) 87

4. Phragmocone in dorsal (b) lateral (d), and septal (c) views, ZPAL N/350; also its 2× enlarged longitudinal section (a); Givetian (?), Miłoszów by Rudki, Poland.


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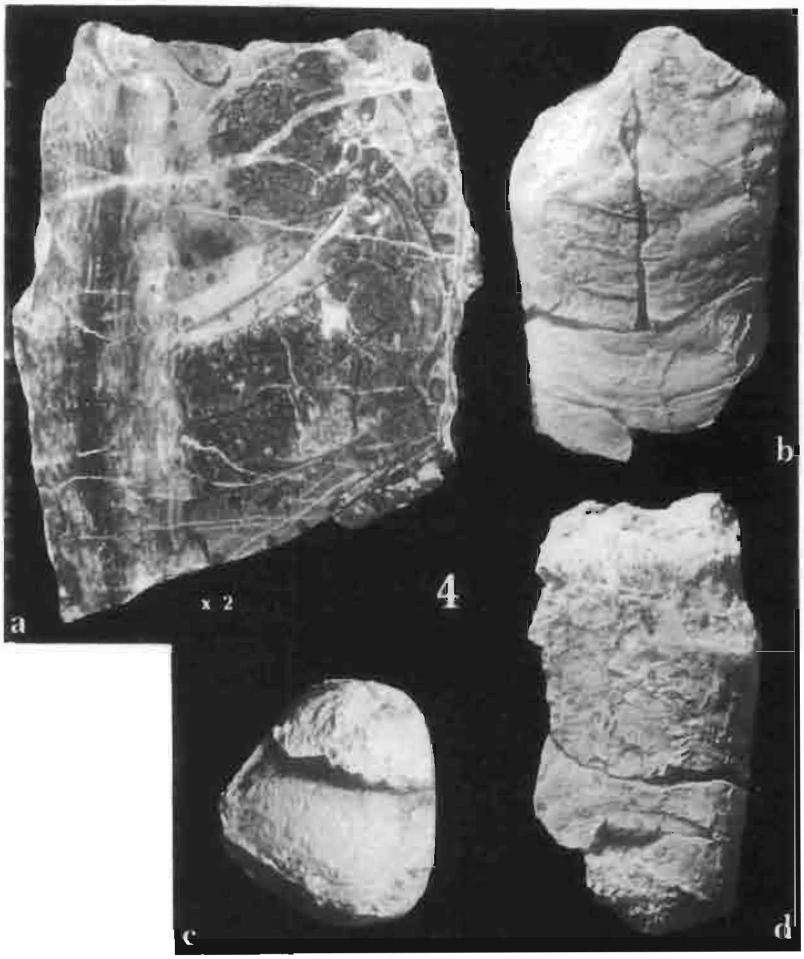

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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 20

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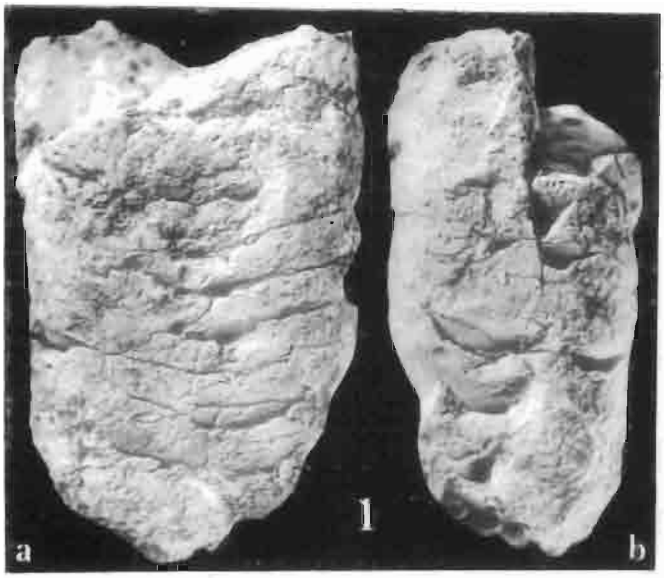
Tripleuroceras cf. *archiaci* (BARRANDE, 1868)	87

Eifelian, Jurkowice by Opatów, Poland

1. Phragmocone in dorsal (a) and lateral (b) views, ZPAL N/348.
3. Phragmocone in dorsal view, ZPAL N/347.
4. Adult compressed phragmocone, ZPAL N/346.

Tripleuroceras triangulare (d'ARCHIAC and VERNEUIL, 1842)	87

2. Phragmocone in dorsal (a) and lateral (b) views, ZPAL N/349; Givetian (?), Zbrza by Morawica, Poland.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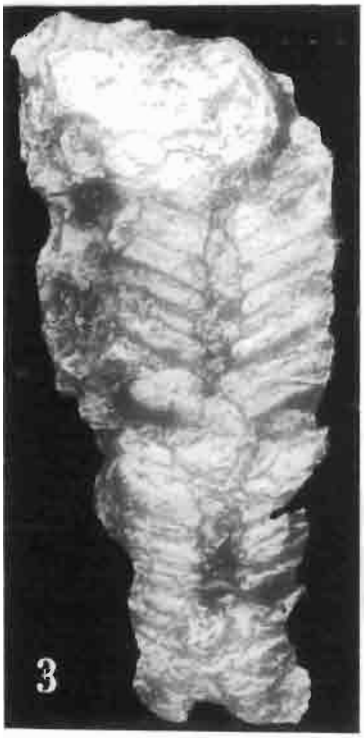
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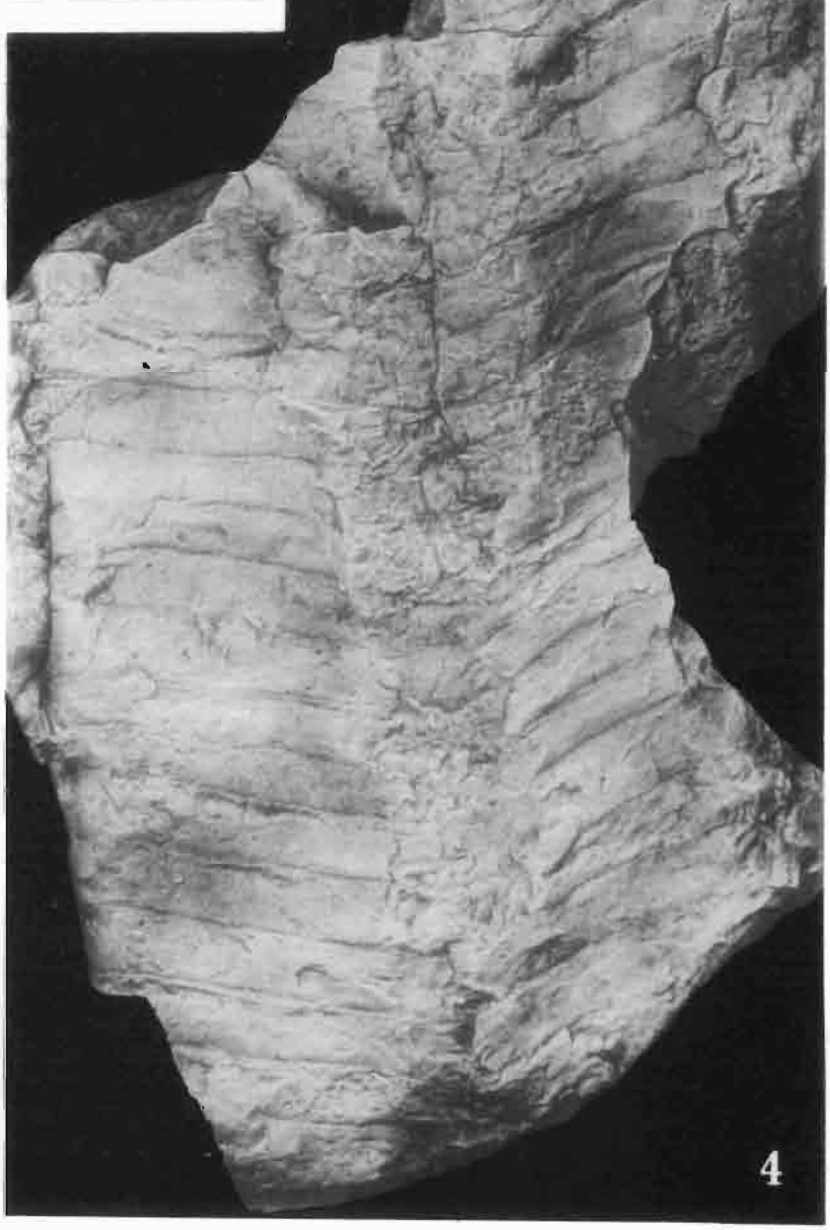
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 21

Page

Orthoceras "wahlenbergi BOLL, 1857" 94

Volkhovian, erratic boulders of Baltic origin, Poland

1. Longitudinal section through an adult specimen, ZPAL N/408; *P. originalis* Zone, boulder E-227, Rozewie.
2. Possible representative of the species, IG 8. II. 261; *P. originalis* Zone, Opatów.
3. Longitudinally broken adult phragmocone, ZPAL N/40; *Paroistodus originalis* Zone, erratic boulder E-251, Wejherowo.
4. Adult specimen, IG 8. II. 363; *P. originalis* Zone, Opatów.
5. Phragmocone ZPAL N/415; *Amorphognathus variabilis* Zone, erratic boulder E-117, Rozewie.
7. Phragmocone ZPAL N/414, also a 2× enlarged part of its shell (b); Early Volkhovian, boulder E-186, Międzyzdroje.
8. Specimen ZPAL N/40/; Kundan (?) erratic boulder E-228, Międzyzdroje; ×2.

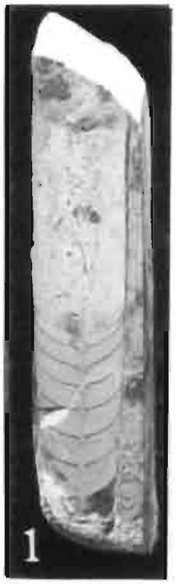
Geisonoceras sp. (aff. *O. nilssoni sensu* ANGELIN, 1880) 93

Volkhovian, *P. originalis* Zone, erratic boulder E-116, Rozewie, Poland

6. Longitudinal section through adapical part of a phragmocone, ZPAL N/405; ×2.
10. Adult specimen, in lateral view (a) and medial section through a phragmocone (b); ZPAL N/395.

Paracleistoceras (?) sp. 87

9. Transversely broken siphuncle (a) and its lateral surface (b); MZUW 676; horizon and locality unknown; both ×2.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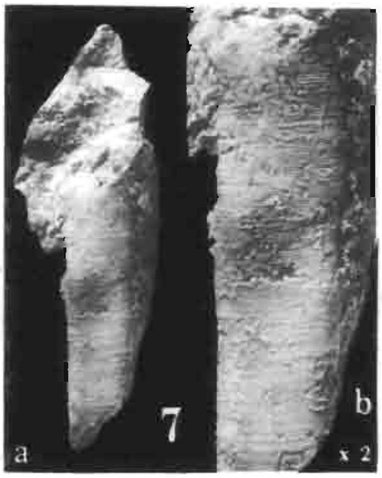
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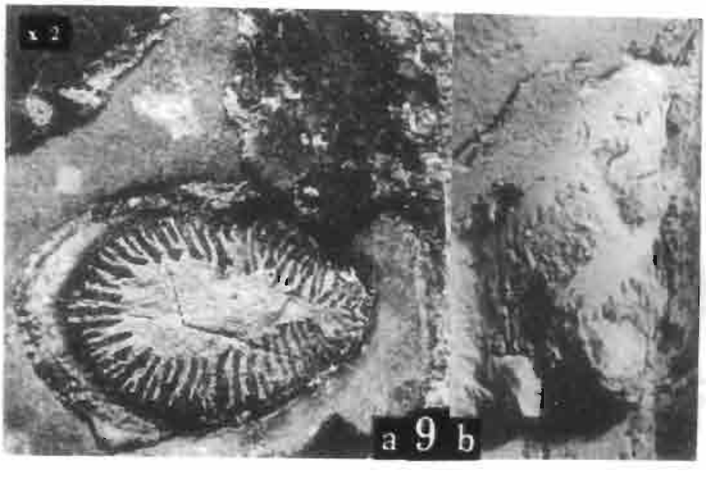
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a 9 b

J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

Plate 22

Page

Orthoceras "nilssoni BOLL, 1857" 94

Arenigian, erratic boulders of Baltic origin, Poland

1. Longitudinal section through a phragmocone, ZPAL N/420; boulder E-225, *E. pseudoplanus* Zone, Kundan, Rozewie; ×2.
2. Longitudinal section through a phragmocone, ZPAL N/417; boulder E-186, Early Volkhovian, Międzyzdroje; ×2.
3. Fragment of a living chamber, ZPAL N/421; boulder E-040, *A. variabilis* Zone?, Kundan, Zgierz.
4. Phragmocone, ZPAL N/416; boulder E-186, Early Volkhovian, Międzyzdroje; 2× enlarged shell fragment.
5. Longitudinal section through a phragmocone, ZPAL N/423; ×5 enlarged fragment, boulder E-040, Volkhovian (?), Zgierz.

Michelinoceras (?) sp. 104

6. Apical part of shell; Ludlovian, Valentin Törl, Carnian Alps, Austria; ×40.

Orthoceras cf. *regulare* SCHLOTHEIM, 1820 97

7. Longitudinal section through a phragmocone, ZPAL N/434; erratic boulder, Llanvirnian, Orłowo, Poland; ×2

Orthoceras cf. *bifoveatum* NOETLING, 1884 94

8. Frontal cross section of a phragmocone (a), ZPAL N/426; Llanvirnian, boulder E-085, *E. lindstroemi* Zone, Mochty, Poland; also an 5× enlarged fragment (b).

Orthoceras bifoveatum NOETLING, 1884 94

Lasnamägian, erratic boulders of Baltic origin, Garcz, Poland

9. Fragment of a mature living chamber in ventral (a) and dorsal (b) views, ZPAL N/431, *E. reclinatus* Zone, boulder E-239.
10. Longitudinal section through a phragmocone, ZPAL N/443; boulder E-236, *E. robustus* Zone.


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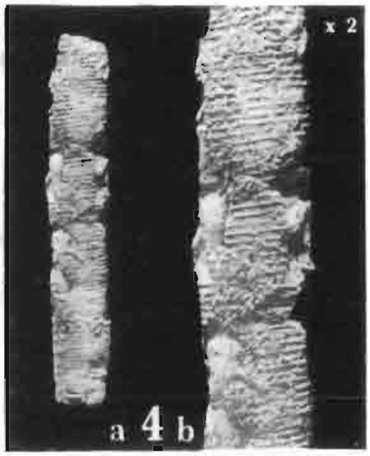
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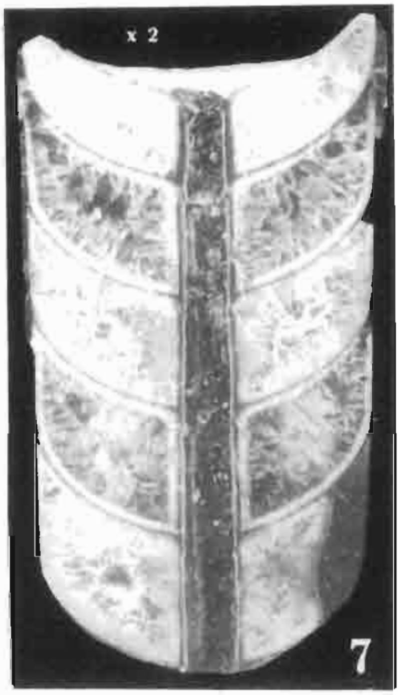
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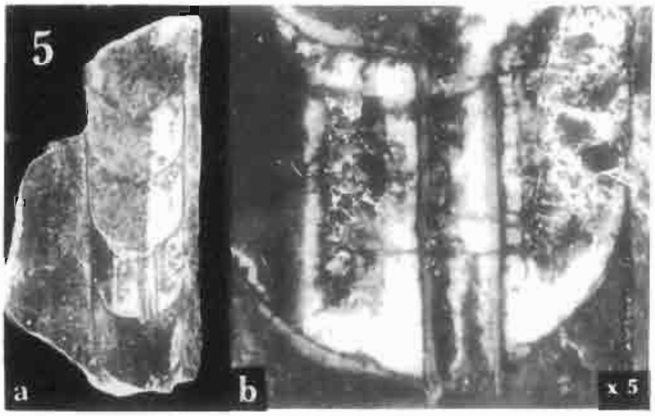
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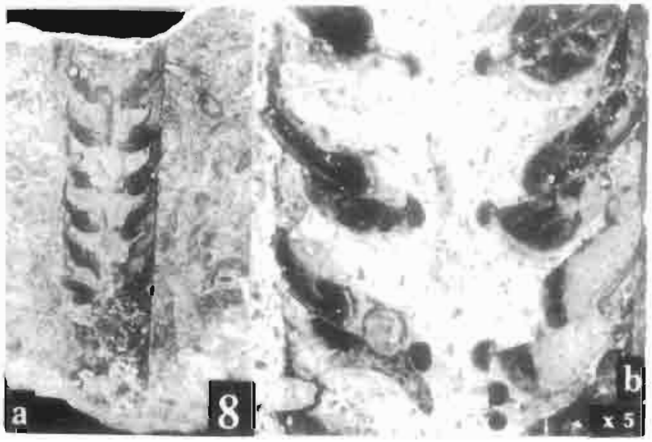
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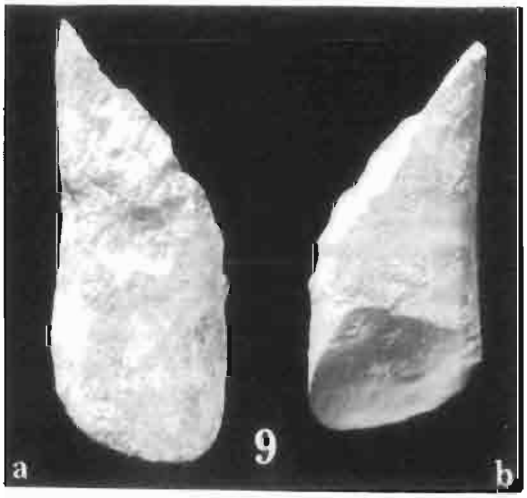
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 23

Page

Orthoceras cf. *regulare* SCHLOTHEIM, 1820 96

Lasnamägian and Uhakuan, erratic boulders of Baltic origin, Poland

1. Longitudinal section through a phragmocone, ZPAL N/437; boulder E-144, *E. lindstroemi* Zone, Uhakuan, Orłowo; ×2.
2. Phragmocone in lateral view (a) (c 0.5), ZPAL N/448; erratic boulder E-141, *E. reclinatus* Zone, Lasnamägian, Międzyzdroje; note: a part of the specimen in natural size (c), broken section through its adult part in natural size (b), and enlarged polished section through the adapical part (d).
3. Phragmocone in lateral (a) and ventral (b) views, ZPAL N/417; erratic boulder E-236, *E. robustus* Zone, Garcz.

Orthoceras regulare SCHLOTHEIM, 1820 96

4. Fragment of an adult living chamber in ventral (a) and dorsal (b) views, ZPAL N/445; boulder E-237; *E. reclinatus* Zone, Lasnamägian, Garcz, Poland.


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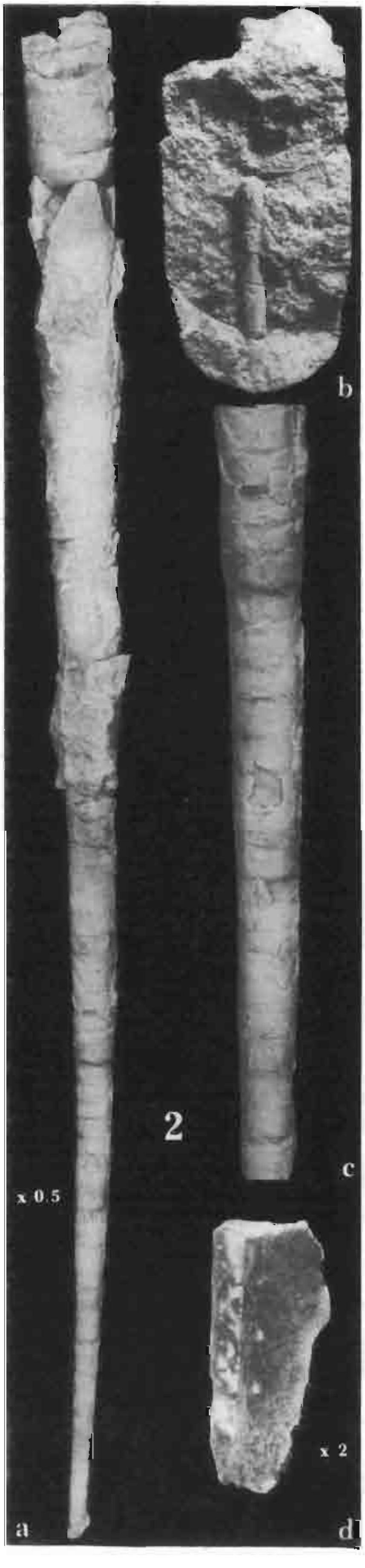
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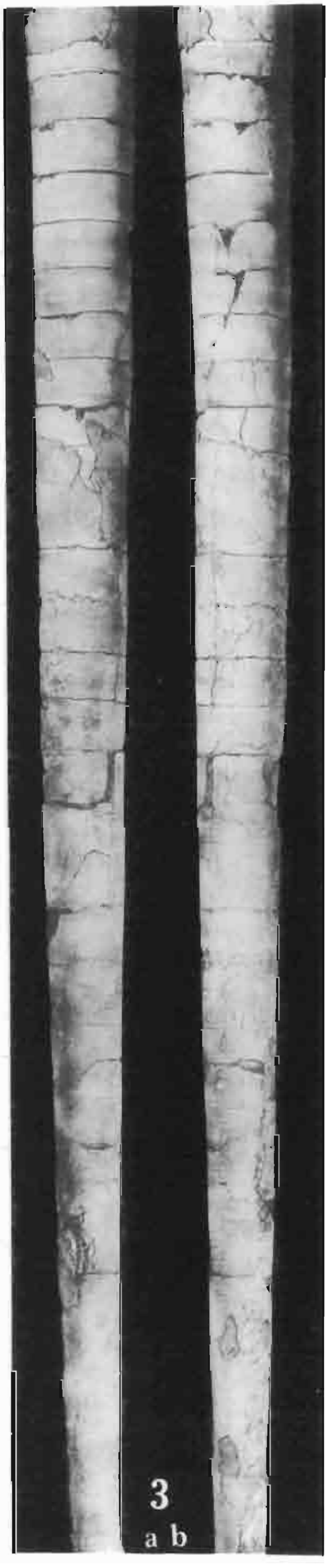
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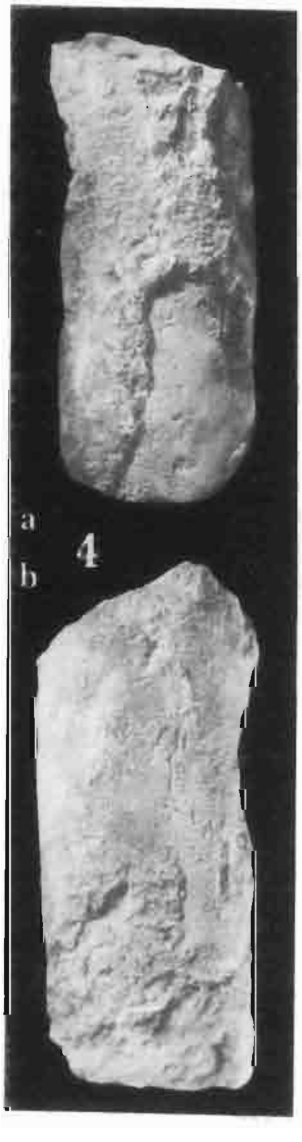
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 24

Page

Orthoceras scabridum ANGELIN, 1880 96

Lasnamägian *E. reclinatus* Zone, erratic boulder of Baltic origin, Poland

1. Adult specimen in dorsal (a) and both lateral views (b, c), ZPAL N/456; erratic boulder E-145; Międzyzdroje.
2. Adult living chamber in ventral (a) and lateral (b) views, ZPAL N/457; erratic boulder E-143, Międzyzdroje.
7. Juvenile living chamber, ZPAL N/455; erratic boulder E-145, Międzyzdroje.
8. Adult living chamber in ventral (a) and dorsal (b) views, UWR 3200; boulder from Lower Silesia.
6. Phragmocone, ZPAL N/454; boulder E-252, Rozewie.

Geisonoceras sp. 94

3. Living chamber in ventral view, ZPAL N/459; Late Silurian, borehole Białopole IG (depth of 1670.7 m), Poland.
4. Phragmocone in lateral view (a) and its medial section (b), IG 1316. II. 8; upper Siedlce beds, Ludlovian, borehole Gołdap, Poland.
5. Longitudinal section through a siphuncle, ZPAL N/460; erratic boulder, probably Early Ludlovian, Orłowo, Poland; ×5.


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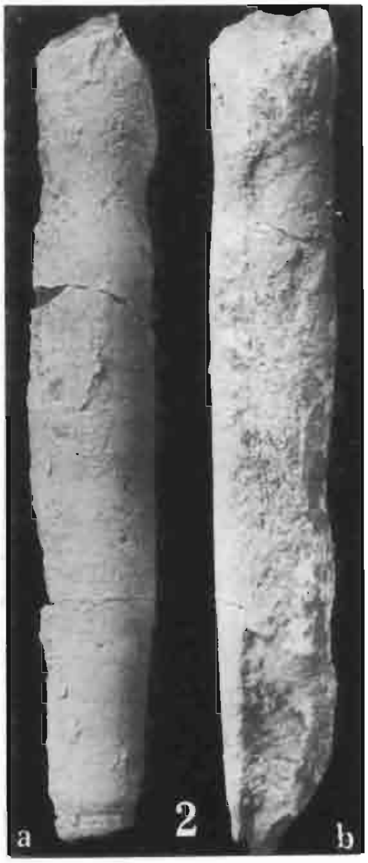
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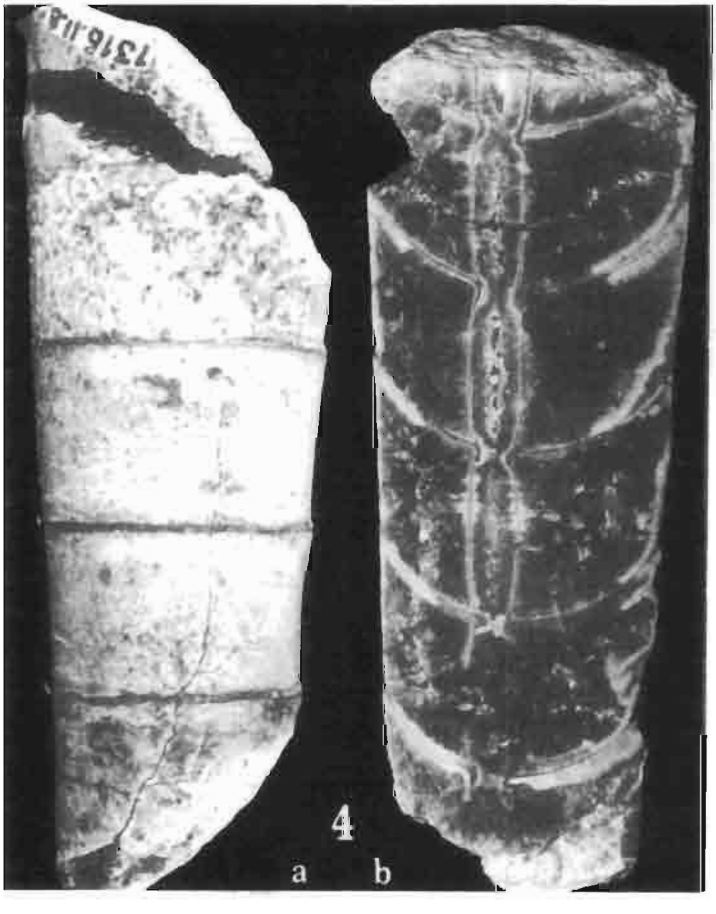
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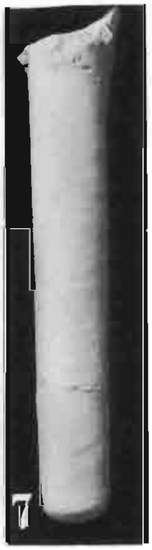
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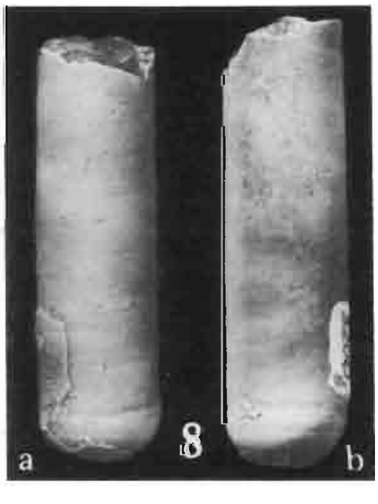
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J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 25

Page

Columenoceras agassizi (Barrande, 1866) 98

Ludlovian, Poland

1. Specimen ZPAL N/468; Prągowiec by Łagów.
2. Specimen ZPAL N/469; erratic boulder of graptolite limestone, Orłowo.
3. Longitudinal section through a phragmocone, ZPAL N/470; same boulder as above; × 5.
4. Specimen ZPAL N/464 (a) and its 2× enlarged part (b); Prągowiec by Łagów.
5. Phragmocone, ZPAL N/466; same locality as above.
6. Specimen ZPAL N/463; same locality as above.
7. Apical part of a shell ("*Hemicosmorthoceras*" sp.) possibly attributable to the species, ZPAL N/673; boulder E-258, graptolite limestone, Rozewie; × 5.
8. Phragmocone in external view (a) and its longitudinal section (b), ZPAL N/461; borehole Parczew IG 10 (depth of 1235 m).

Gen. et sp. indet. ("*Dissidoceras*") 106

9. Longitudinal section through a phragmocone, ZPAL N/462; Přidolian, Karlštein by Prague, Bohemia; × 2.

Michelinoceras sp. 104

10. Adult (?) living chamber in lateral view (with venter to the right), UWR 2049; Kopanina Formation, Ludlovian, Koněprusy by Beroun, Bohemia.


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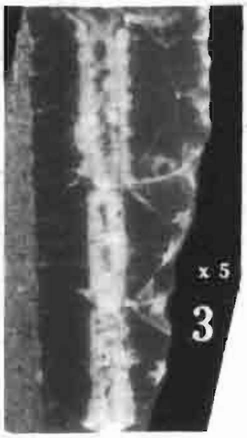
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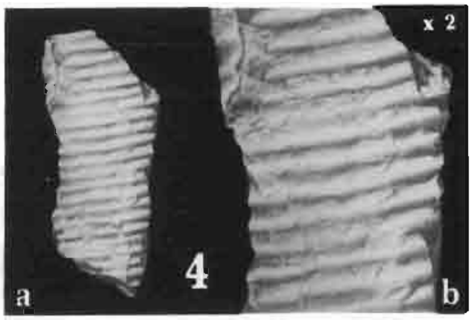
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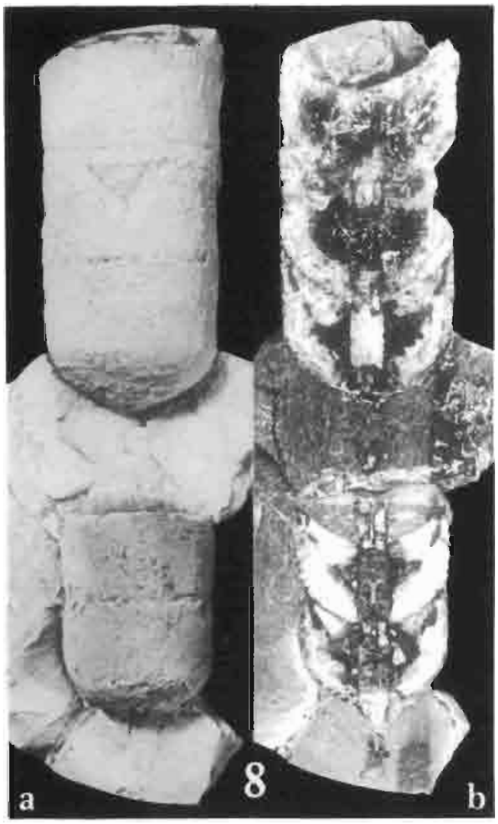
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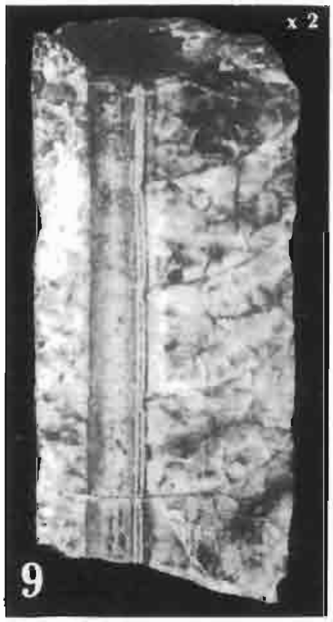
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J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 26

Page

Plagiostomoceras cf. *pleurotomum* (BARRANDE, 1866) 104

Early Ludlovian, Prągowiec by Łagów, Poland
(except for figs. 7-8)

1. Apical part of a shell, ZPAL N/479; ×5.
2. Apical part of a shell, ZPAL N/483; ×5.
3. Deformed specimen in oblique view (a), ZPAL N/475; also its 2× enlarged part (b).
4. Aperture of compressed adult specimen in ventral (?) view, ZPAL N/474.
5. Adapical part of a phragmocone, ZPAL N/493; ×2.
6. Fragment of a compressed shell, ZPAL N/471.
7. Apical part of a shell, ZPAL N/869; erratic boulder E-036, Międzyzdroje; ×5.
8. Longitudinal section through a specimen, ZPAL N/484; borehole Białopole IG (depth of 1670.7 m); ×2.
9. Two fragments of a phragmocone, ZPAL N/472; ×2.

Arionoceras (?) sp. 107

10-13. Opercula ("*Aptychopsis*"), ZPAL N/494, N/496, N/498, N/500; Ludlovian, Prągowiec by Łagów, Poland; ×2.


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x 5
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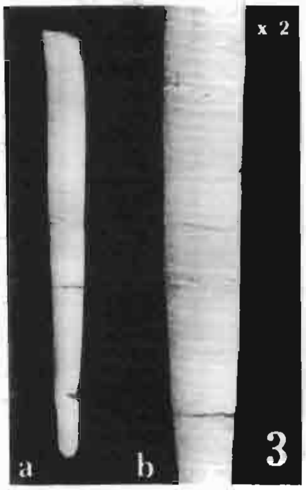
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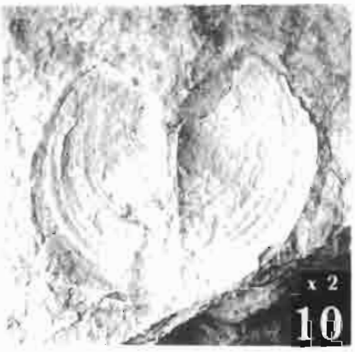
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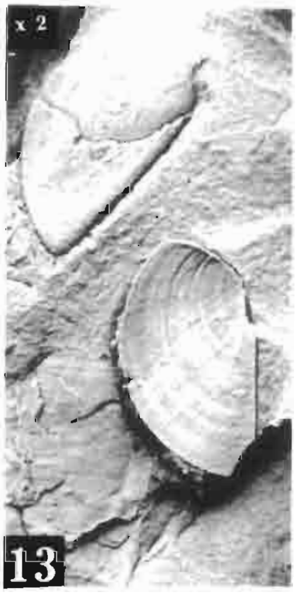
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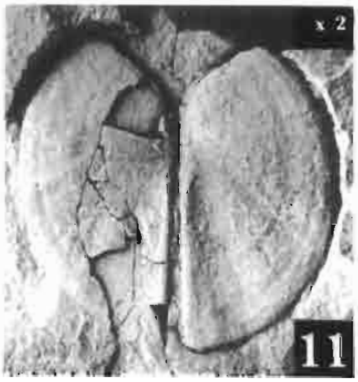
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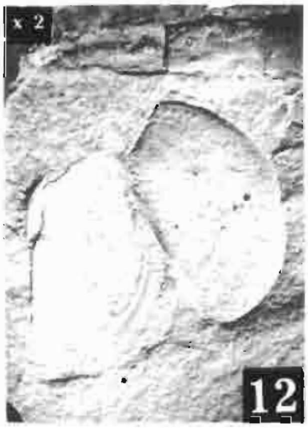
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 27

Page

Plagiostomoceras cf. *angustum* (HOLZAPFEL, 1895) 100

1. Apical part of a shell with inflated embryonic part supposedly broken off, ZPAL N/509; Late Frasnian, Płucki by Łagów, Poland; ×5.
2. Fragment of an adult living chamber (a, b), ZPAL N/511; same locality as above.
3. Adult (3) living chamber in dorsal (a) and lateral (b) views, ZPAL N/529, Early Frasnian, Rokiczany Dół by Dębnik near Cracow, Poland.
5. Longitudinal, slightly oblique section through a phragmocone, ZPAL N/551; Early Famennian, bed J. 7, Jabłonna, Poland; note the variation in chamber length.

Plagiostomoceras angustum (HOLZAPFEL, 1895)? 100

6. Apical part of a shell, ZPAL N/504; Late Givetian, Świętomarz beds, Śniadka by Bodzentyn, Poland; ×5.
7. Specimen ZPAL N/502; same locality as above; ×5.

Plagiostomoceras aff. *angustum* (HOLZAPFEL, 1895) 98

8. Living chamber in ventral (?) (a) and lateral (b) views, ZPAL N/532; Early Famennian, bed J. 8, Jabłonna, Poland.
9. Subadult specimen in ventral (a) and lateral (b) views, ZPAL N/541;

Plagiostomoceras sp. 98

4. Longitudinal section through a phragmocone ZPAL N/531; Early Famennian, bed J. 18, Jabłonna, Poland.

Plagiostomoceras (?) *cardiolae* (GÜRICH, 1896) 100
Famennian, Poland

10. Longitudinal section through a phragmocone, ZPAL N/510; *Platyclymenia* Zone, Łagów-Dule.
11. Longitudinal section through a phragmocone, ZPAL N/578; *Cheiloceras* Zone, Jabłonna, bed J. 11; ×2.
12. Specimen ZPAL N/577; *Cheiloceras* Zone, Jabłonna, bed J. 7; ×2.
13. Adult specimen in ventral (?) (a), septal (c), and lateral (b) views, ZPAL N/566; *Platyclymenia* Zone, Łagów-Dule.


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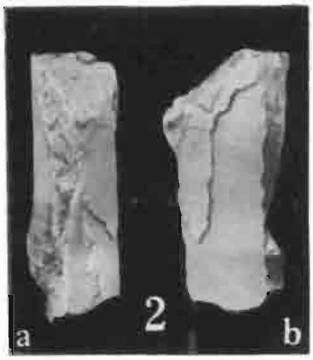
1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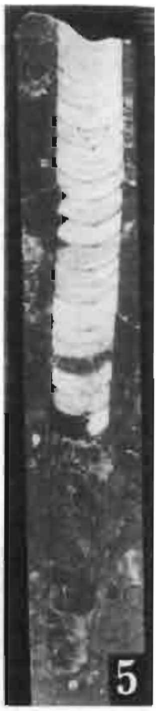
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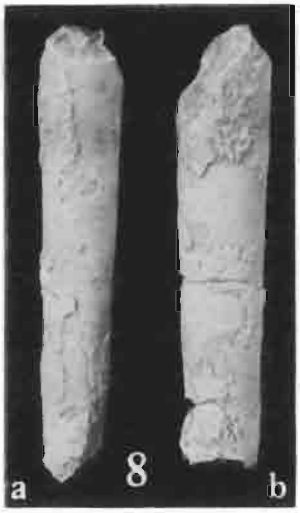
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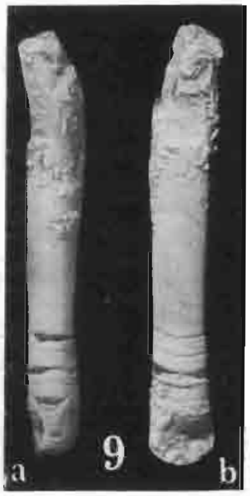
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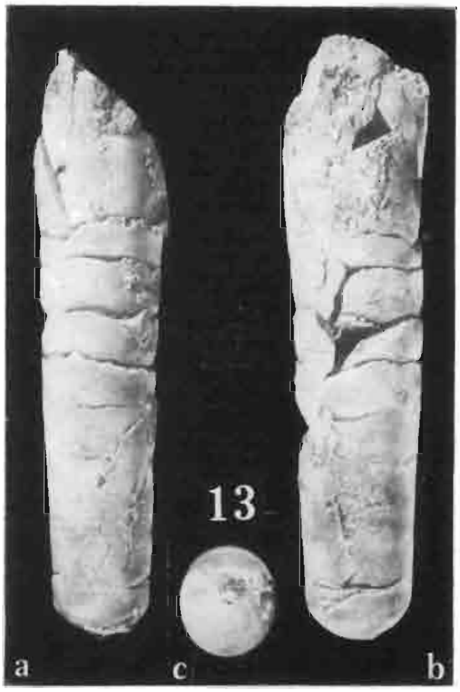
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J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 28

Page

Michelinoceras sp. 104

Late Famennian, *Wocklumeria* Zone, Dzikowiec, Poland (except for fig. 11)

1. Phragmocone ZPAL N/598; ×2.
2. Longitudinal section through a phragmocone, ZPAL N/599; ×2.
9. Phragmocone in septal (c) and lateral (b) views and its longitudinal section (a), IG 139. II. 50. (*Orthoceras crassus* A. Römer of Tietze 1870: pl. 16:17)
11. Specimen in lateral (a) and ventral (b) views, ZPAL N/585; Lower Famennian, *Cheiloceras* Zone, Jablonna, bed J. 16, Poland.

Bogoslovskya sp. 99

Famennian, Poland

10. Phragmocone fragment in septal and lateral views, ZPAL N/558; *Cheiloceras* Zone, Jabłonna, bed J. 11
12. Adult specimen in ventral (a), septal (c), and lateral (b) views, ZPAL N/561; *Platyclymenia* Zone, Łagow-Dule.

Bactrites sp. 102

Early Famennian, Jabłonna, Poland

6. Subadult specimen, ZPAL N/655; bed J. 11.
7. Fragmentary specimen in ventral view, ZPAL N/653; bed J. 15.

Lobobactrites carinatus (Münster, 1840) 102

Famennian, Poland

3. Living chamber in dorsal view, ZPAL N/629; Jabłonna, bed J. 3; ×2.
4. Adult specimen in dorsal and lateral views, ZPAL N/630; Jabłonna, bed J. 3; ×2.
8. Juvenile specimen in dorsal (a) and lateral (b) views, UWR 1961s (Gürich's (1896) original specimen); *Platyclymenia* Zone, Łagów-Dule.

Lobobactrites sp. 102

5. Adult specimen in dorsal (a) and lateral (b) views, ZPAL N/638; Famennian, Jabłonna, bed J. 5, Poland; ×2.


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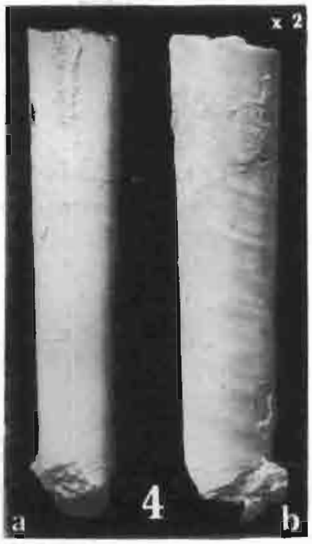
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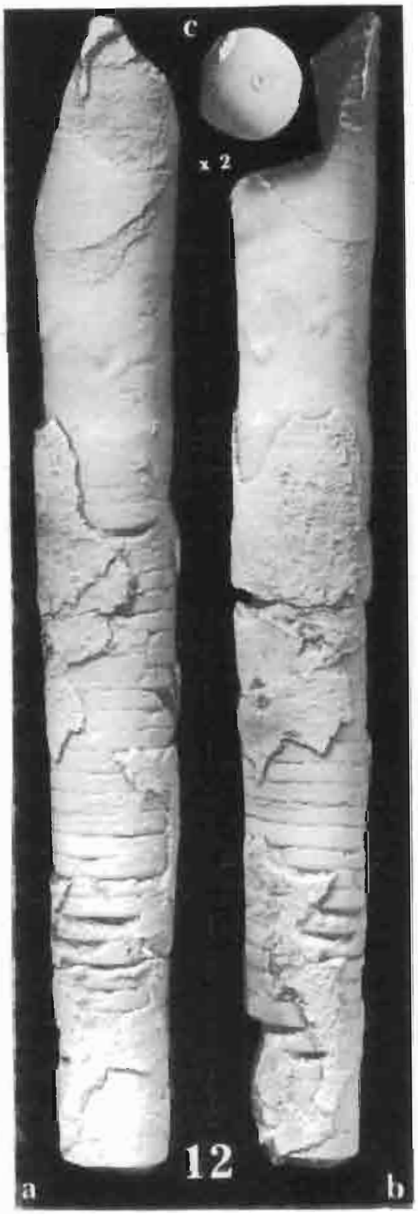
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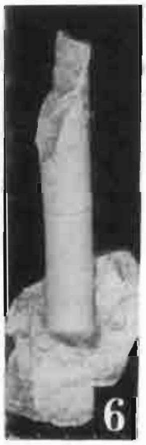
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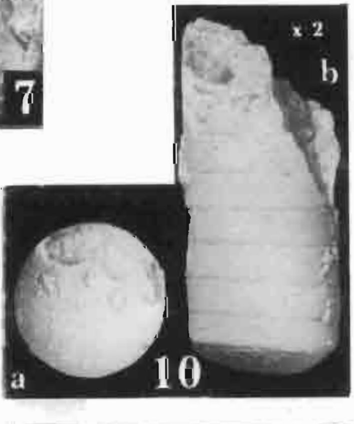
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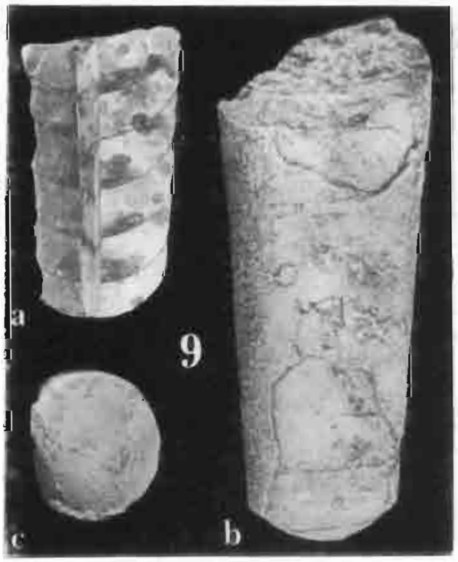
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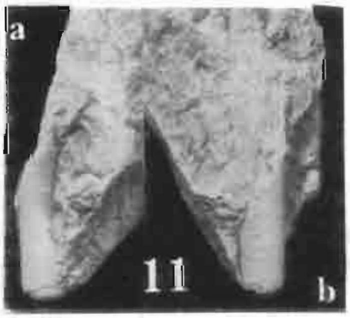
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 29

Page

Parakionoceras originale (BARRANDE, 1868) 112
Early Ludlovian, boulder E-036, Międzyzdroje, Poland

1. Juvenile specimen, ZPAL N/868; note the ontogenetic change in the ornamentation; ×5.
2. Apical part of a shell possible attributable to the species, ZPAL N/869a; ×5.

Arionoceras valens (BARRANDE, 1868) 108

3. Longitudinal section through a phragmocone, ZPAL N/662; erratic boulder of graptolite limestone, Early Ludlovian, Rozewie, Poland.
4. Section through a complete living chamber, ZPAL N/661; erratic boulder of graptolite limestone, Rozewie, Poland.
5. Living chamber in lateral (a) and dorsal (?) (b) views, ZPAL N/663; erratic boulder of graptolite limestone, Wejherowo, Poland.
6. Apical part of a shell, ZPAL N/870; boulder E-036, Ludlovian, Międzyzdroje, Poland.
7. Living chamber in lateral (a) and ventral (b) views, ZPAL N/665; erratic boulder similar in lithology to E-036, Garcz by Kartuzy, Poland.
8. Subadult living chamber in lateral (a) and ventral (b) views, ZPAL N/867; also enlarged (×5) ornamentation of the shell (c); boulder E-036, Międzyzdroje, Poland.
9. Crushed phragmocone possibly attributable to the species, with remains of a coloured ornamentation (?); borehole Chłapowo IG (depth of 1039 m), Late Ludlovian, Poland.

Arionoceras cf. *valens* (BARRANDE, 1868) 108

10. Phragmocone in external view (b) and its longitudinal section (a), IG 1316. II. 1; borehole Bartoszyce, Poland, Ludlovian.

Ascoceras cf. *murchisoni* (BARRANDE, 1865) 111

11. Specimen in lateral (a) and dorsal (b) views, ZPAL N/690; boulder E-086, Pridolian, Orłowo, Poland.


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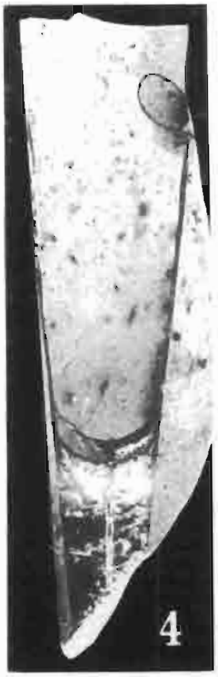
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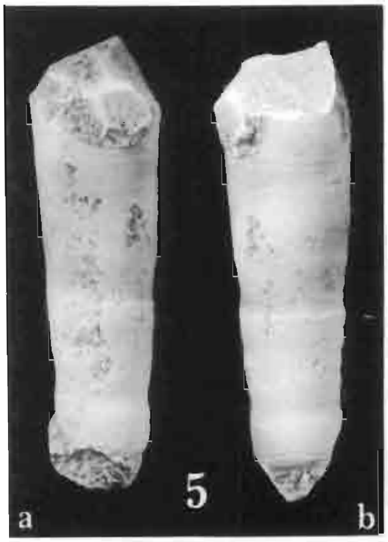
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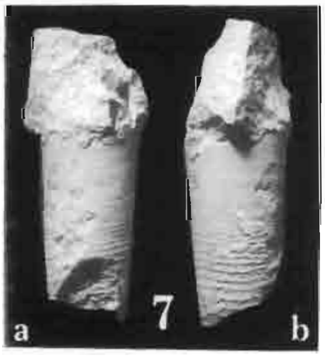
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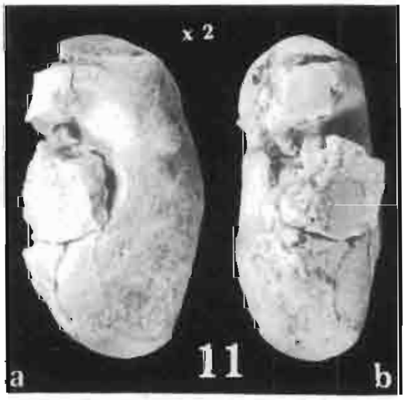
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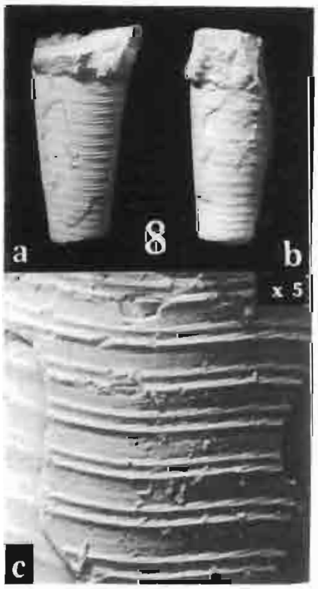
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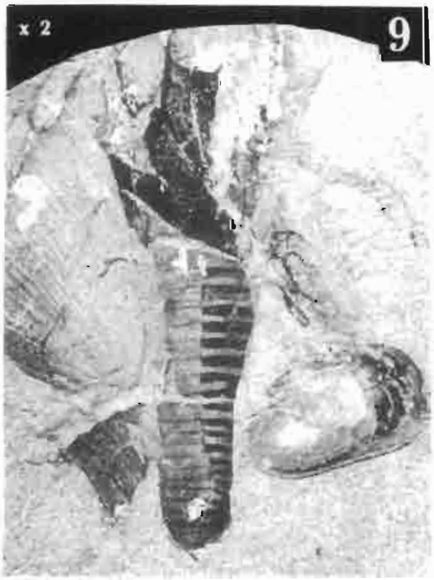
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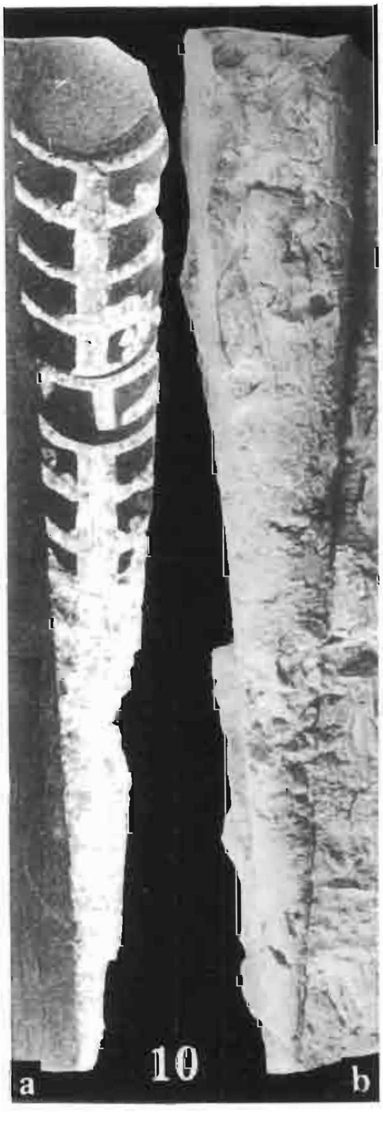
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 30

Page

Murchisoniceras aff. *murchisoni* (BARRANDE, 1868) 134
Přidolian, erratic boulders of Baltic origin, Poland

1. Phragmocone in lateral view (a) and its medial section (b), ZPAL N/687; Beyrichienkalk, Garcz by Kartuzy.
2. Subadult specimen in lateral view, ZPAL N/688; Beyrichienkalk, Orłowo.

Parakionoceras originale (BARRANDE, 1868) 112
Ludlovian, Poland

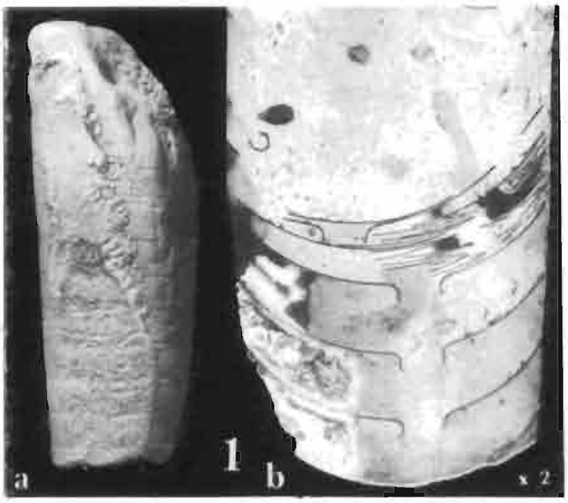
3. Compressed specimen, IG 318. II. 161; Pobroszyn by Opatów.
4. Compressed shell fragment, ZPAL N/853; Prągowiec by Łagów.

Arionoceras arion (BARRANDE, 1868) 112

5. Longitudinal section through a phragmocone, ZPAL N/660; Přidolian, Karlštein by Prague, Bohemia.
6. Subadult specimen in lateral (a) and ventral (b) views, UWR 3232s; Ludlovian, Kopanina Formation, Koněprusy by Beroun, Bohemia.

Arionoceras fluminese (MENEGHINI, 1857) 112

7. Living chamber in lateral (a) and ventral (b) views, IG 137. II. 40; Přidolian, Karlštein by Prague, Bohemia.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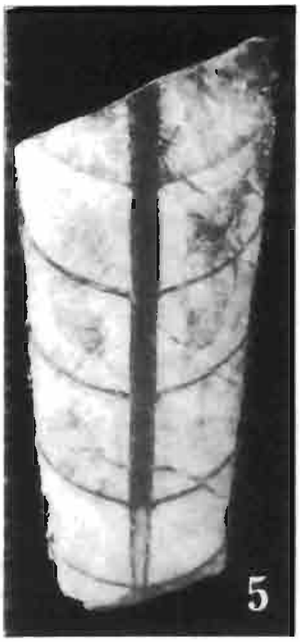
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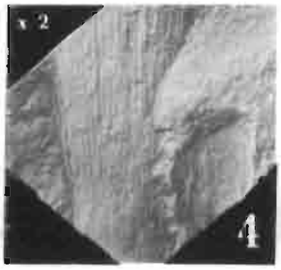
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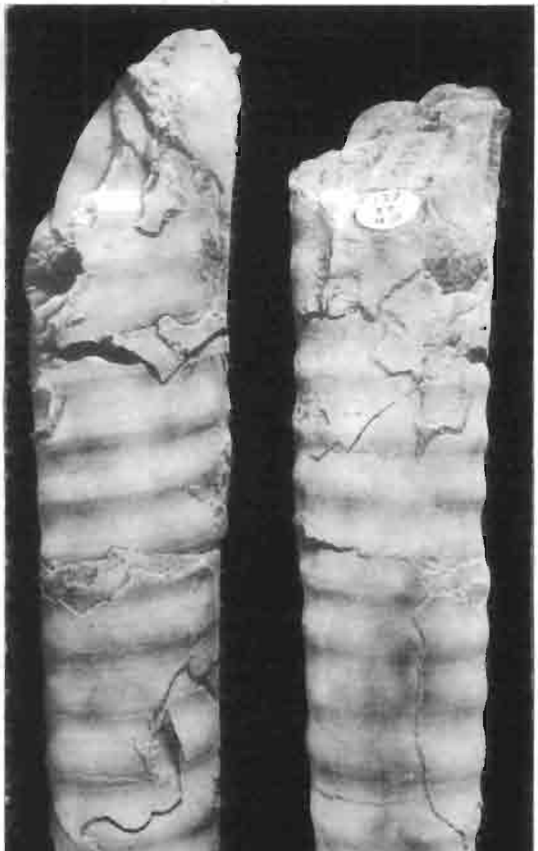
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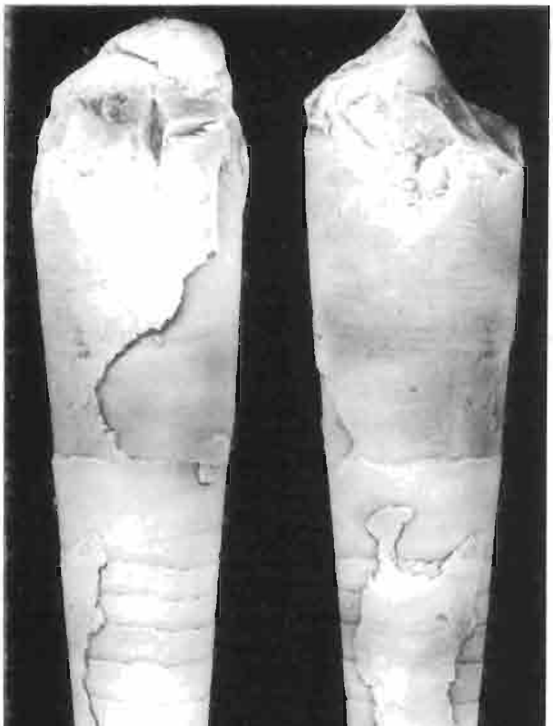
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J. Dzik: PHYLOGENY OF THE NAUTILOIDEA

PLATE 31

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Murchisoniceras aff. *murchisoni* (Barrande, 1868) 134
Přidolian, erratic boulders of Baltic origin, Poland

1. Longitudinal section through a specimen, ZPAL N/680; Orlowo.
4. Medial section through a phragmocone, ZPAL N/683; Wieżyca.

Murchisoniceras cf. *obsolescens* (Barrande, 1868) 134

2. Specimen in dorsal (?) (a) and lateral (b) views; ZPAL N/679: erratic boulder, Přidolian, Międzyzdroje, Poland.

Murchisoniceras sp. 134

3. Longitudinal section through a phragmocone, ZPAL N/676; erratic boulder, Early Ludlovian of graptolite limestone, Rozewie, Poland.

Sphooceras truncatum (Barrande, 1868) 135
Ludlovian, Kopanina Formation, Bohemia

5. Specimen in apical (c), lateral (b), and ventral (a) views, NM L 9186 (Barrande 1868, pl. 342: 2); Butovice.
6. Medial section through a phragmocone, NM L 9199 (Barrande 1868, pl. 343: 15); Lochkov.
7. Specimen in dorsal (a) and lateral (b) views, NM L 9201 (Barrande 1868, pl. 343: 17); Zmrzlik, *Cromus beaumonti* horizon.


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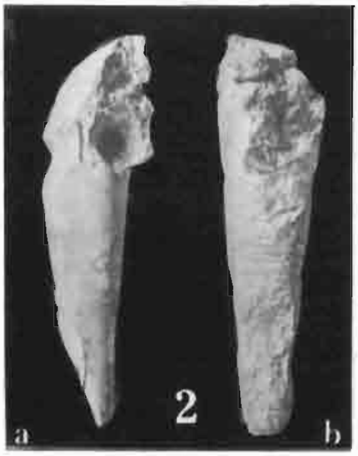
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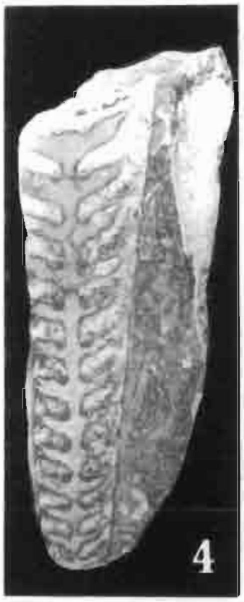
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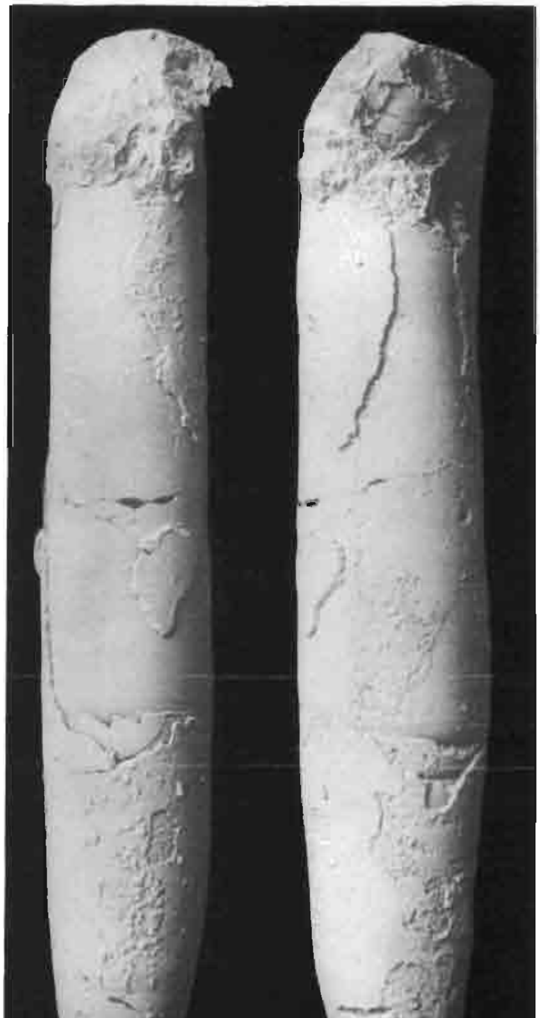
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PLATE 32

Page

Clinoceras cf. *dens* (MASCKE, 1876) 113
Llanvirnian, erratic boulders of Baltic origin, Poland

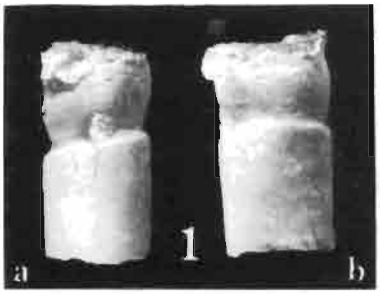
1. Apertural part of a mature living chamber in lateral (a) and ventral (?) (b) views, ZPAL N/698; boulder E-215, *E. foliaceus* Zone, Lasnamägian, Mochty by Warsaw.
2. Partly cut phragmocone in lateral view, ZPAL N/699; erratic boulder, supposedly Lasnamägian, Zgierz, Poland.
3. Juvenile specimen in lateral (a) and dorsal (?) (b) views and section through a phragmocone, ZPAL N/692; boulder E-134, Uhakuan, Wieżyca, Poland.
6. Adult living chamber in lateral (a) and ventral (b) views, ZPAL N/695; boulder E-102, Uhakuan or Kukrusean, Zgierz, Poland.

Clinoceras sp. 113

7. Adult specimen, ZPAL N/702; erratic boulder E-255, Caradocian, Międzyzdroje, Poland

Eridites (?) sp. 116
Přidolian, erratic boulders of Beyrichienkalk, Poland

4. Longitudinal medial section through a phragmocone, ZPAL N/742; Orłowo; note a phragmocone of *Murchisoniceras* sp. on the right.
5. Longitudinal section through a phragmocone, ZPAL N/757; Orłowo.
8. Medial section through a phragmocone, ZPAL N/754; boulder E-243, Stężyca.
9. Phragmocone in lateral (a) and ventral (?) (b) views, ZPAL N/751; also a 2× enlarged fragment of its dorsal side (c); Orłowo.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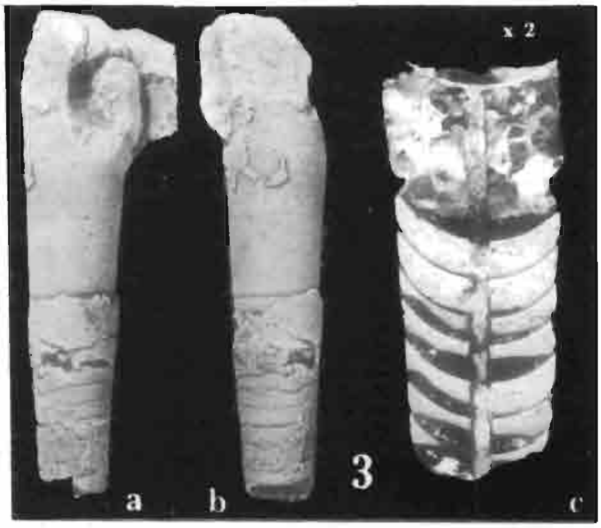
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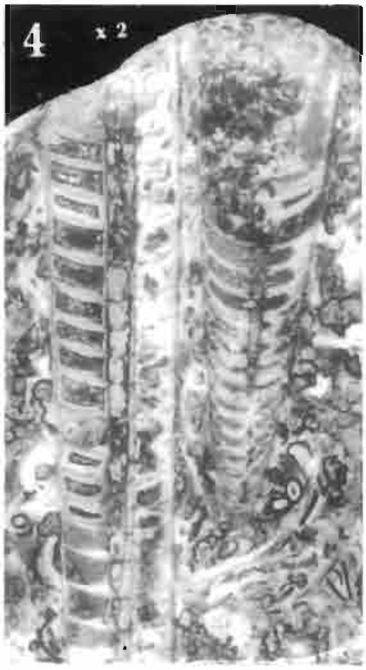
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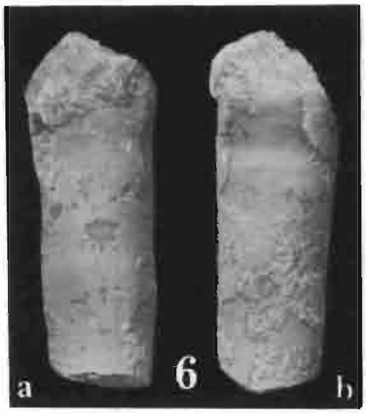
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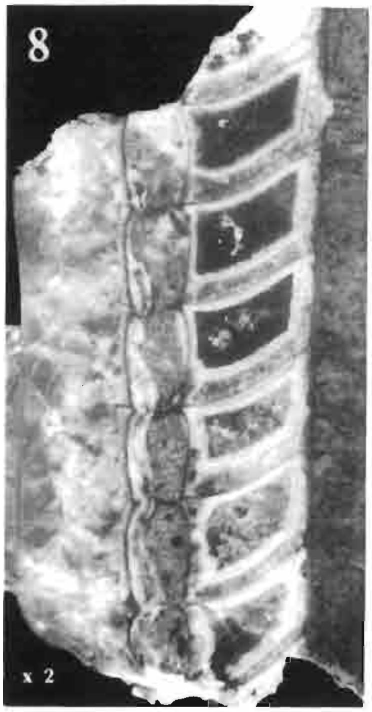
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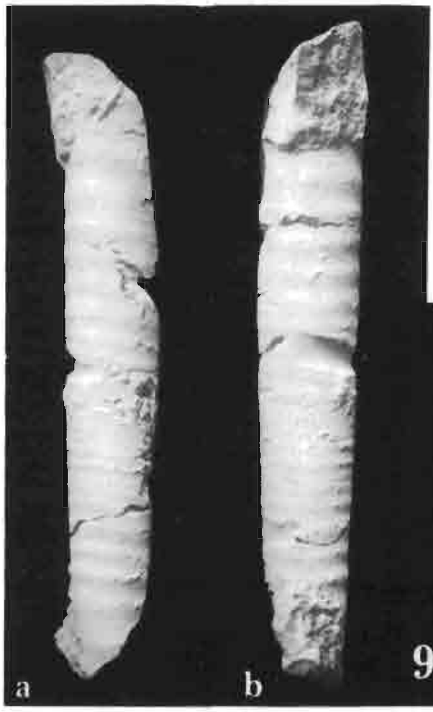
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 33

Page

Clinoceras muensteri (WEDEKIND, 1908) 114

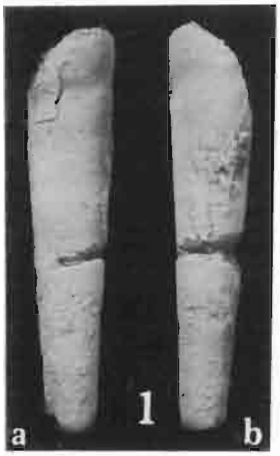
1. Juvenile specimen in lateral (a) and ventral (?) (b) views, ZPAL N/720; *Platyclymenia* Zone, Łagów-Dule, Poland.
4. Medial section through a phragmocone, ZPAL N/712; Early Famennian, *Palmatolepis crepida* Zone, Żbk gorge by Debnik near Cracow, Poland.
5. Phragmocone in ventral (?) (a) and lateral (b) views, ZPAL N/727; *Cheiloceras* Zone, Famennian, Jabłonna, bed J. 15, Poland.
6. Longitudinal section through a phragmocone, ZPAL N/710; *Manticoceras* Zone, Late Frasnian, Płucki, Poland.
7. Medial section through a phragmocone, ZPAL N/724; *Platyclymenia* Zone, Famennian, Łagów-Dule, Poland.
8. Subadult specimen in lateral (a) and dorsal (b) views, ZPAL N/719; same horizon and locality as above.
9. Phragmocone in lateral (a) and ventral (?) (b) views, ZPAL N/721; same horizon and locality as above.
10. Adult specimen in lateral (a) and dorsal (?) (b) views, ZPAL N/717; same horizon and locality as above.
11. Longitudinal section through a phragmocone, UWR 2119 (*Orthoceras* aff. *planiseptato* SANDBERGER in GÜRICH 1896, pl. 13: 6a-b); probably Late Frasnian or Early Famennian, Kielce-Karczówka, Poland.

Clinoceras (?) sp. 114

2. Medial section through a phragmocone, ZPAL N/741; *Cheiloceras* Zone, Famennian, Jabłonna, bed J. 9, Poland

Cyrtactinoceras sp. 116

3. Medial section through a phragmocone, ZPAL N/761; erratic boulder, Early Ludlovian (?), Orłowo, Poland.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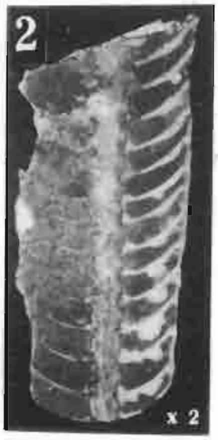
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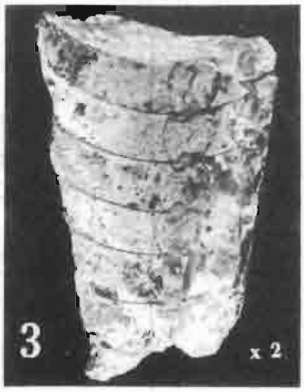
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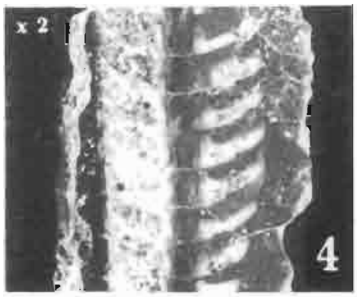
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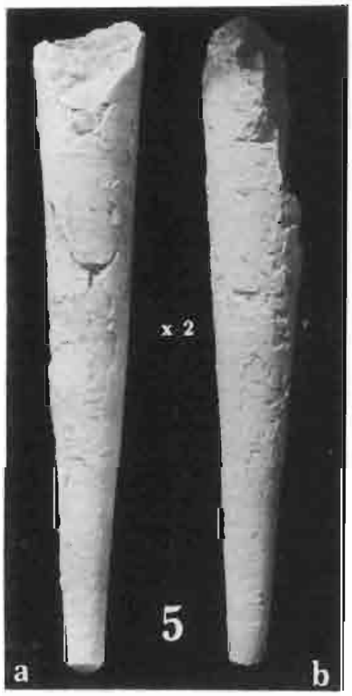
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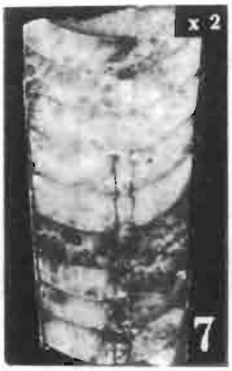
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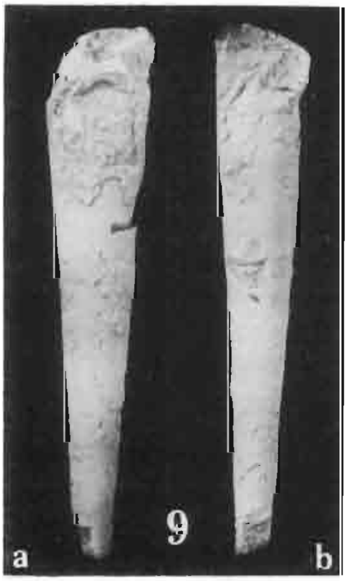
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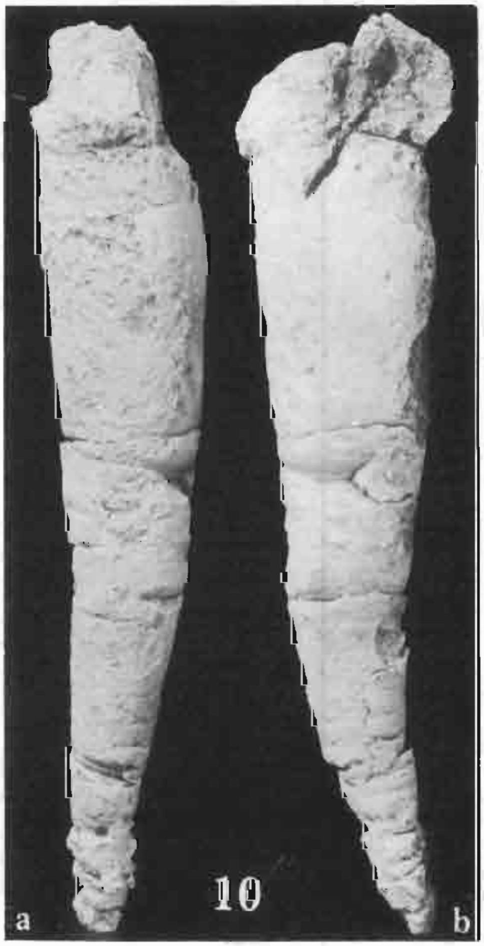
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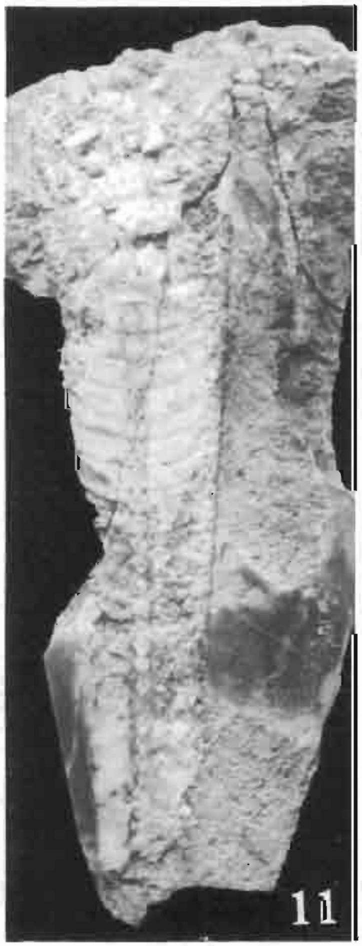
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PLATE 34

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Pseudorthoceras striolatum (MEYER, 1831) 114

Visean (D_2), Orlej quarry, Zalas near Cracow, Poland

1. Phragmocone. ZMS A.I.70/47.
2. Apical part of a shell, ZMS A.I.70/46.

Clinoceras sp. 114

3. Apical part of a shell. ZMS A.I.70/41: Visean, Orlej quarry, Poland.
4. Phragmocone, ZMS A.I.70/04; same horizon and locality as above.
6. Phragmocone in dorsal (?) (a) and lateral (b) views. UWR 1859A; Namurian, Caroline mine, Upper Silesia, Poland.
8. Adult living chamber in lateral (a), ventral (?) (b), and septal (c) views, UWR 1859B; same horizon and locality as above. (*Orthoceras* sp. of ROEMER 1863)

Cyrtocycloceras (?) sp. 127

5. Phragmocone fragment in dorsal (?) (a) and lateral (b) views. ZPAL N/765; also 2× enlarged (c); erratic boulder E-177, Kukrusean (?), Orlowo, Poland.

Cycloceras sp. 127

7. Aperture of a mature living chamber, ZMS A.I.70/88; Visean. Orlej quarry, Poland.
13. Living chamber in lateral (a) and dorsal (?) (b) views, UWR 1858s; Namurian, "Königsgrube", Upper Silesia, Poland. (*Orthoceras undatum* of ROEMER 1863)
14. Apical part of a shell, ZMS A.I.70/48; Early Namurian, Dąbrowa Górnicza, Poland.
15. Phragmocone fragment in ventral (?) view, ZMS A.I.70/78; same horizon and locality as above.

Cycloceras (?) sp. 127

12. Specimen ZPAL N/779; *Clymenia* or *Wocklumeria* Zone, Famennian. Jabłonna, Poland.

Cyrtocycloceras sp. 127

9. Specimen in external view (b) and longitudinal section (a). ZPAL N/774; erratic boulder. Přidolian (?), Orlowo, Poland.
10. Specimen in lateral (b) and dorsal (c) views, ZPAL N/777; also a 5× enlarged part of the shell (a); erratic boulder of Beyrichienkalk, Přidolian, Orlowo, Poland.
11. Apical part of a shell, ZPAL N/866; erratic boulder E-036, Early Ludlovian, Międzyzdroje, Poland; note the hemispherical embryonic shell, larval shell ornamented with growth lines, and annulated post-larval shell.


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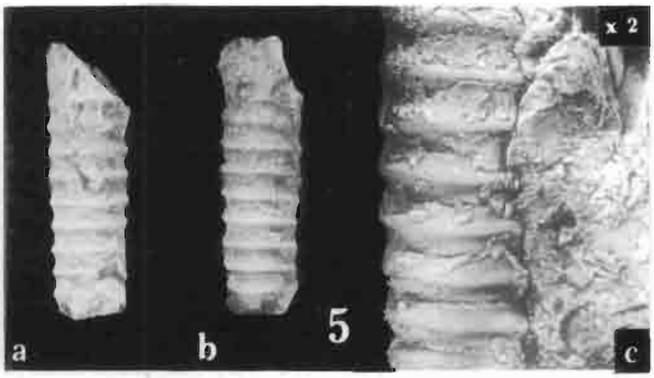
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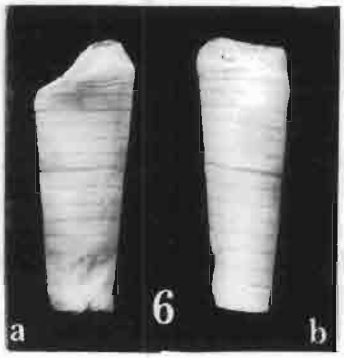
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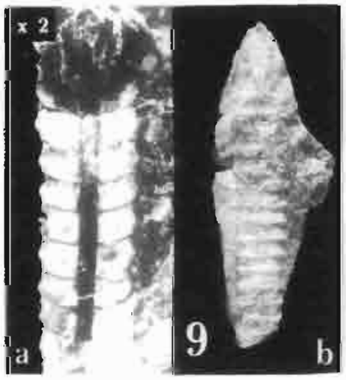
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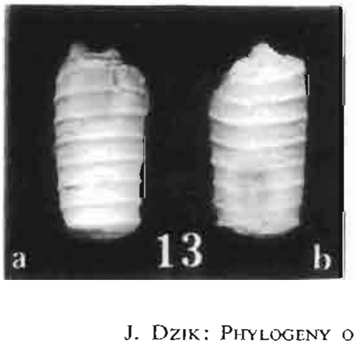
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PLATE 35

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Lopingoceras orientale (FLIEGEL, 1901) 127
Guadalupian, Padang, Sumatra Island

1. Phragmocone in lateral (a), dorsal (b), and ventral (c) views, UWR 2259s, holotype.
3. Longitudinal section through a phragmocone, UWR 2258s, paratype.

Brachycycloceras sp. (*O. calamus* de KONINCK?) 127

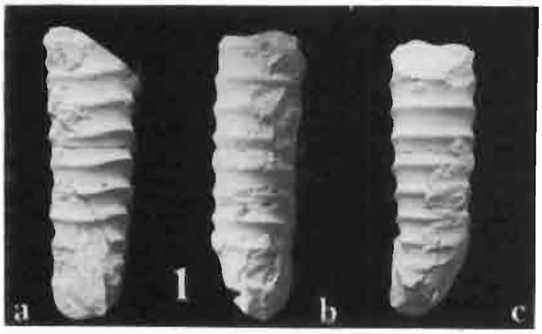
2. Specimen in lateral (a), dorsal (b), and ventral (c) views, UWR 2256s; Visean, Visé, Belgium.

Gorbyoceras textumaraneum (ROEMER, 1861) 127
Ashgillian (?), erratic boulders, Zawidowice by Oleśnica, Poland

6. Specimen in dorsal (?) (a) and lateral (b) views, UWR 1464s, holotype.
4. Holotype of *Orthoceras clathrato-annulatum* ROEMER, 1861 (a-c); UWR 1985s, possibly attributable to the species, but without any traces of ornamentation.

Spyroceras senckenbergi TEICHERT, 1934 127

5. Phragmocone fragment in external view (a) and longitudinal section (b), ZPAL N/780; also an enlarged ornamented shell fragment (c); erratic boulder E-082, *A. ordovicicus* Zone, Ashgillian, Orlowo, Poland.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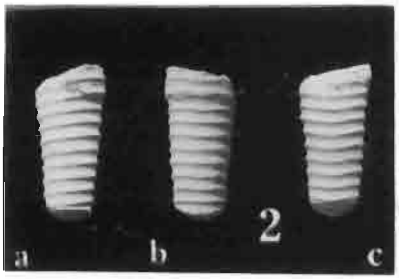
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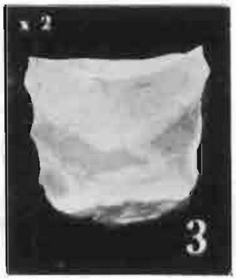
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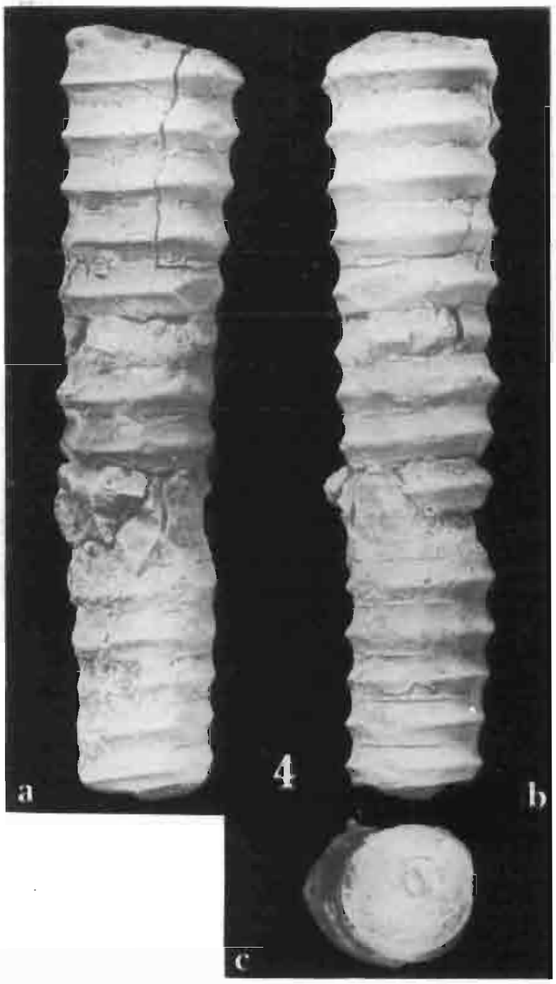
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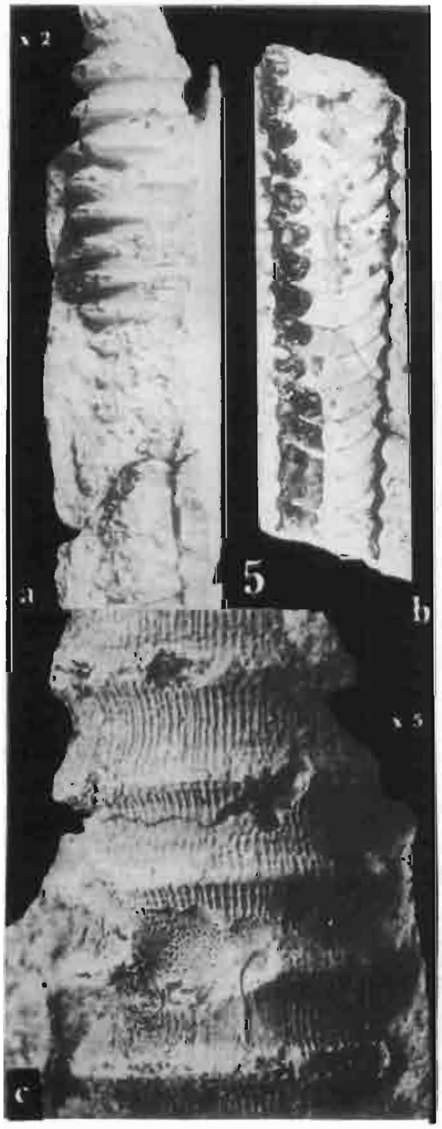
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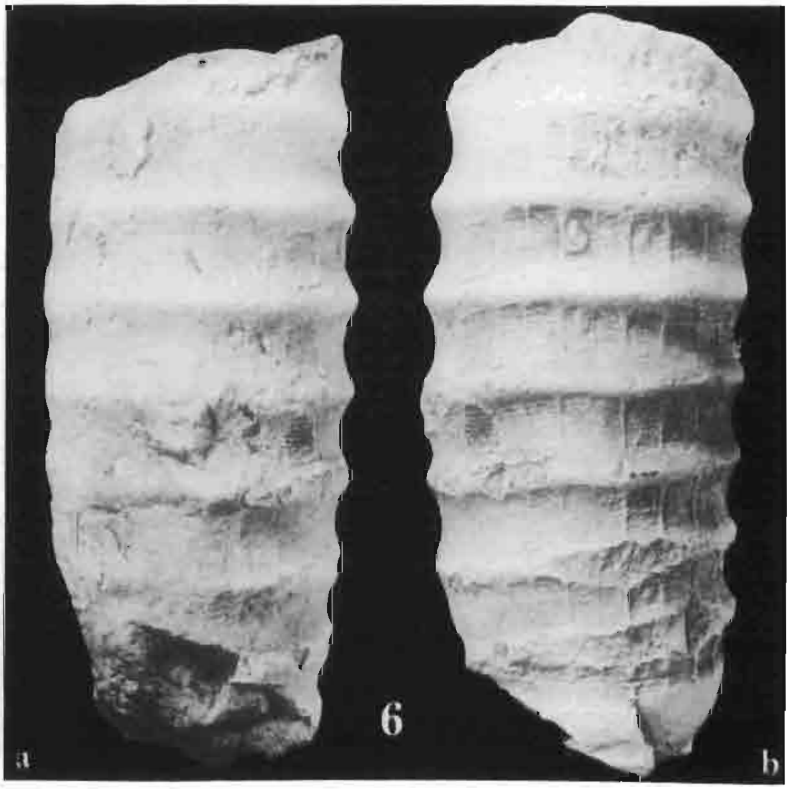
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PLATE 36

Page

Gorbyoceras sp. 122

1. Phragmocone in dorsal view (a) and its 5× enlarged portion. ZPAL N/778; boulder E-264, Ashgillian (?), Międzyzdroje, Poland.

Spyroceras cf. *crotalum* (HALL, 1861) 127

Platyclymenia Zone, Famennian, Jabłonna, bed J. 26, Poland

2. Longitudinal section through a phragmocone, ZPAL N/783.
7. Fragment of adult living chamber, ZPAL N/781; note traces of very fine longitudinal striation.

Spyroceras sp. 127

4. Shell fragment, UWR 1763; Early Famennian (?), "Hauptkalk", Dzikowiec by Nowa Ruda, Poland. (*Orthoceras calamiteum* MÜNSTER of TIETZE 1870: pl. 16:15).

Kionoceras cf. *doricum* (BARRANDE, 1868) 121

Erratic boulders of Beyrichienkalk, Přidolian, Poland

3. Juvenile specimen in ventral (?) (a) and lateral (b) views, ZPAL N/785; Rozewie.
5. Phragmocone fragment in external view (a) and its frontal cross section (b), ZPAL N/789; Międzyzdroje; note a boring by sipunculid (?) worm parallel to the siphuncle.

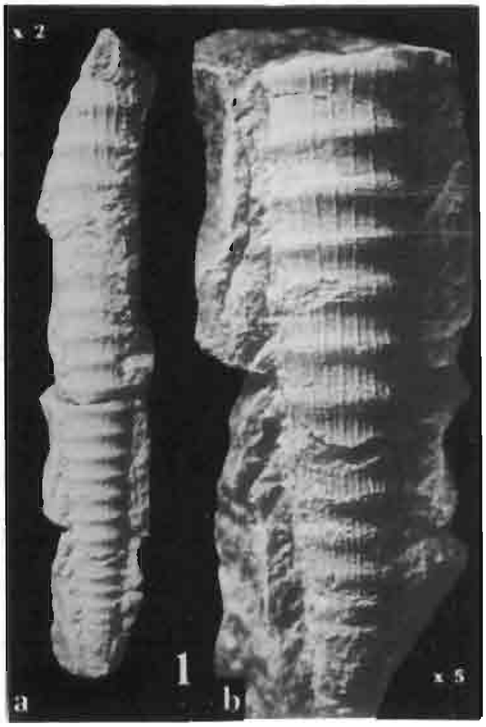
Gen. et sp. indet. (possibly oncoceratid) 127

6. Basal part of a living chamber in ventral (?) (a), dorsal (?) (c), and septal (b) views, ZPAL N/784; Late Ludlovian, Bełcz by Opatów, Poland.

Sactoceras sp. 118

Erratic boulders of Beyrichienkalk, Přidolian, Zgierz, Poland

8. Specimen ZPAL N/791; note its peculiar ornamentation.
9. Longitudinal, frontal section through an isolated siphuncle, ZPAL N/792.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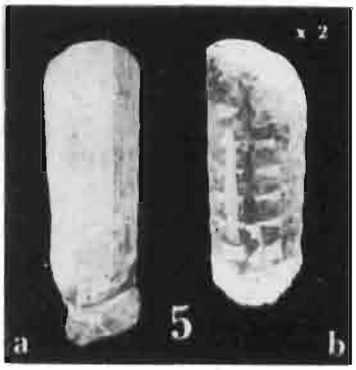
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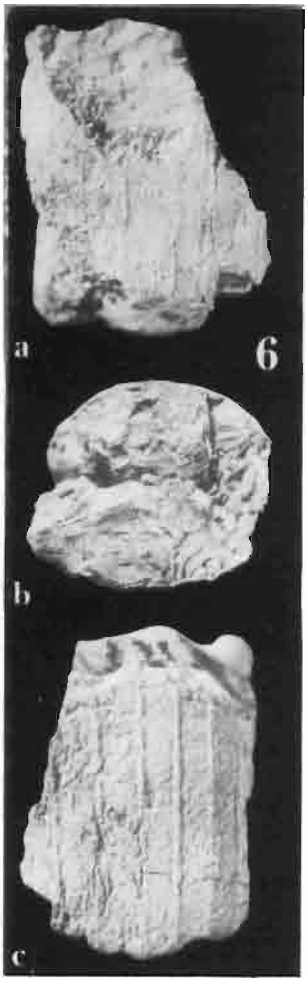
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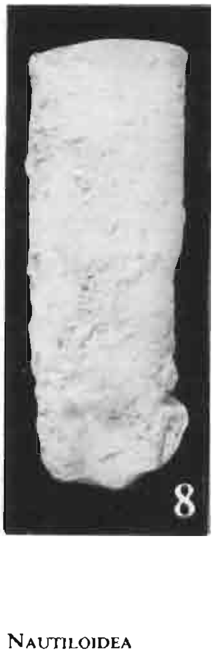
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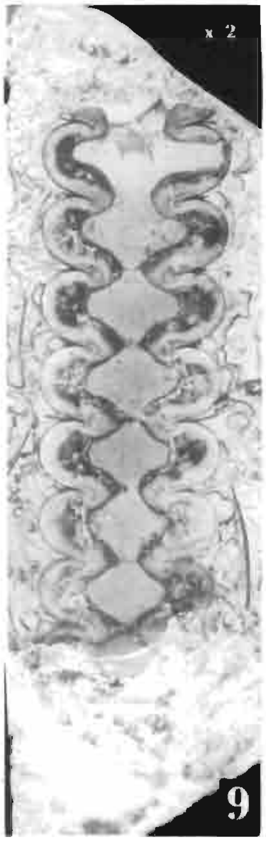
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PLATE 37

Page

Dnestroceras podolicum (SIEMIRADZKI, 1906) 118

Czortków beds, Gedinnian, Jagielnica, Podolia, Ukraine

1. Adult specimen in dorsal (?) (a) and lateral (b) views and 2× enlarged medial section through its phragmocone (c), ZPAL N/432; note ontogenetic change in septal suture.

Sactoceras (?) sp. ex gr. *Orthoceras cuvieri* BARRANDE, 1868 118

Erratic boulders of Beyrichienkalk, Přidolian, Poland

2. Phragomocone fragment in external view, ZPAL N/802; Mochty by Warsaw; note fine longitudinal striation.
3. Medial section through a phragmocone, ZPAL N/801; Garcz by Kartuzy.

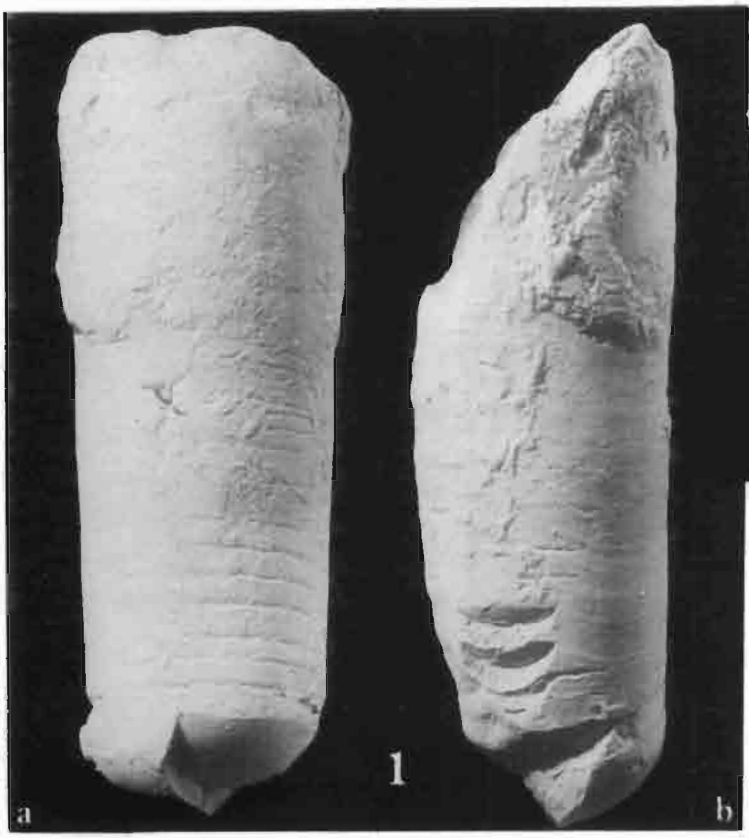
cf. *Balticoceras discors* (EICHWALD, 1840) 127

4. Specimen ZPAL N/815 in ventral (a), lateral (b) and septal (c) views; erratic boulder E-024, Oanduan (?), Zgierz, Poland.

Sactoceras danicum (TEICHERT, 1934) 118

Erratic boulders of Beyrichienkalk, Přidolian

5. Fragment of an adult (?) living chamber, ZPAL N/799; Orłowo, Poland.
6. Longitudinal section through a phragmocone, ZPAL N/796; Orłowo, Poland; note calcareous deposits at the outer surface of the connecting rings.
7. Longitudinal section through a phragmocone, ZPAL N/800; Zgierz, Poland.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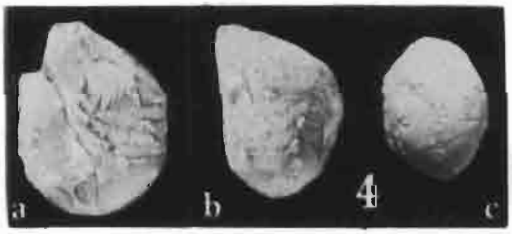
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PLATE 38

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Rayonnoceras sp. 120

1. Specimen ZMS A.I.70/59; Visean, Orlej quarry by Zalas near Cracow, Poland.
2. Specimen in ventral (?) (a) and lateral (b) views, UWR 1859; Namurian, Caroline mine, Upper Silesia, Poland. (*Orthoceras dilatatum* KONINCK of ROEMER 1863).

Cyclolituites (?) sp. 136

Orthis sandstone, Kundan (?), Międzygórz by Sandomierz, Poland

3. Specimen in lateral view, IG 8. II. 196.
4. Latex cast of external mould.

Eushantungoceras kiaeri (TROEDSSON, 1934) 142

5. Medial section through a siphuncle, ZPAL N/812; Early Ludlovian (?), erratic boulder from Orlowo, Poland.

Eushantungoceras sp. 142

6. Medial section through a siphuncle, ZPAL N/813; erratic boulder of Ostseekalk, Late Caradocian, Mochty by Warsaw, Poland.

Eushantungoceras pseudoimbricatum (BARRANDE, 1866) 142

8. Medial section through the holotype of *Orthoceras exoticum* BARRANDE (1866, pl. 216: 11-14), NM L 14349; Kopanina Formation, Ludlovian, Kosoř, Bohemia.

Ormoceras cf. *holmi* TROEDSSON, 1926 142

7. Oblique section through a specimen, ZPAL N/814; erratic boulder, Middle Kundan (?), Orlowo, Poland.


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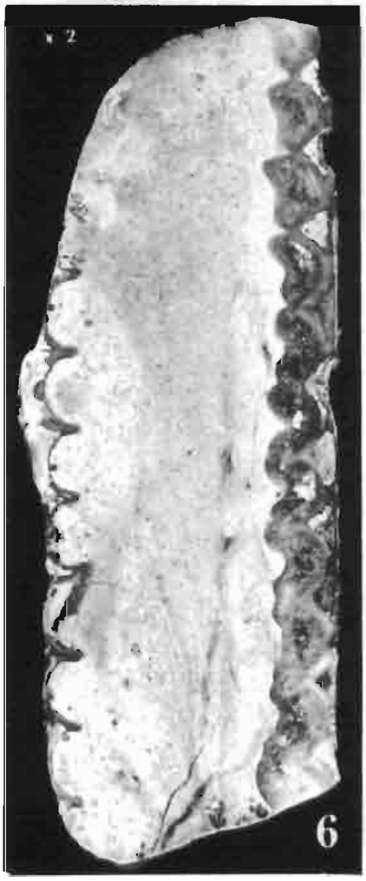
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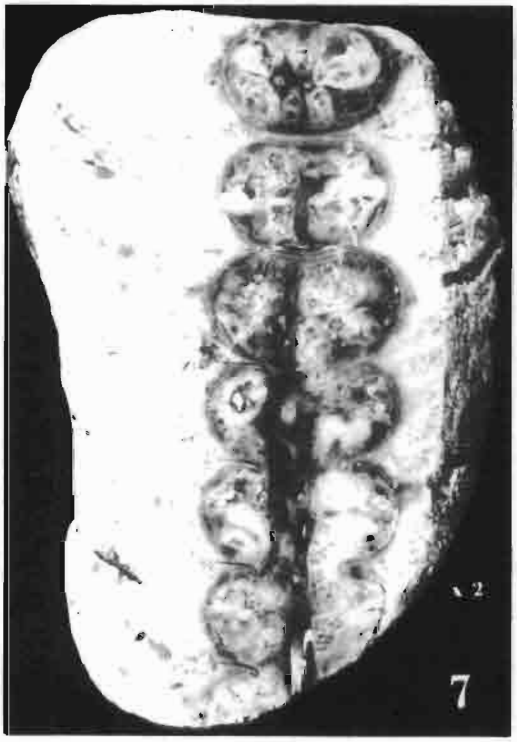
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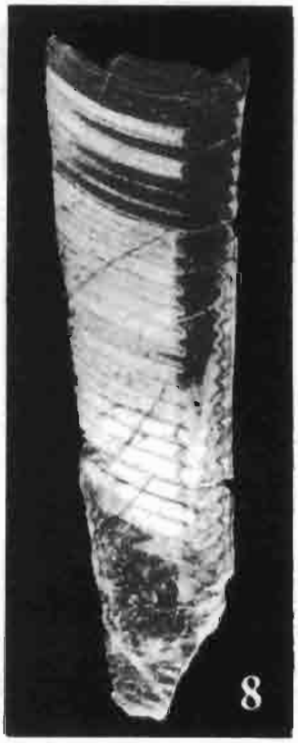
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PLATE 39

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Rhynchorthoceras aff. *beyrichi* (REMELE, 1880) 133
P. originalis Zone, Volkhovian, erratic boulder (?), Opatów, Poland

1. Phragmocone in lateral (a), ventral (b), and dorsal (c) views, IG 8. II. 260.
2. Phragmocone in ventral view, IG 8. II. 254.

Rhynchorthoceras sp. 133

2. Longitudinal section through a phragmocone ZPAL N/824; Lasnamägian (?), erratic boulder from Orłowo, Poland.

Rhynchorthoceras conicum (HISINGER, 1827) 133
Llanvirnian, erratic boulders, Poland

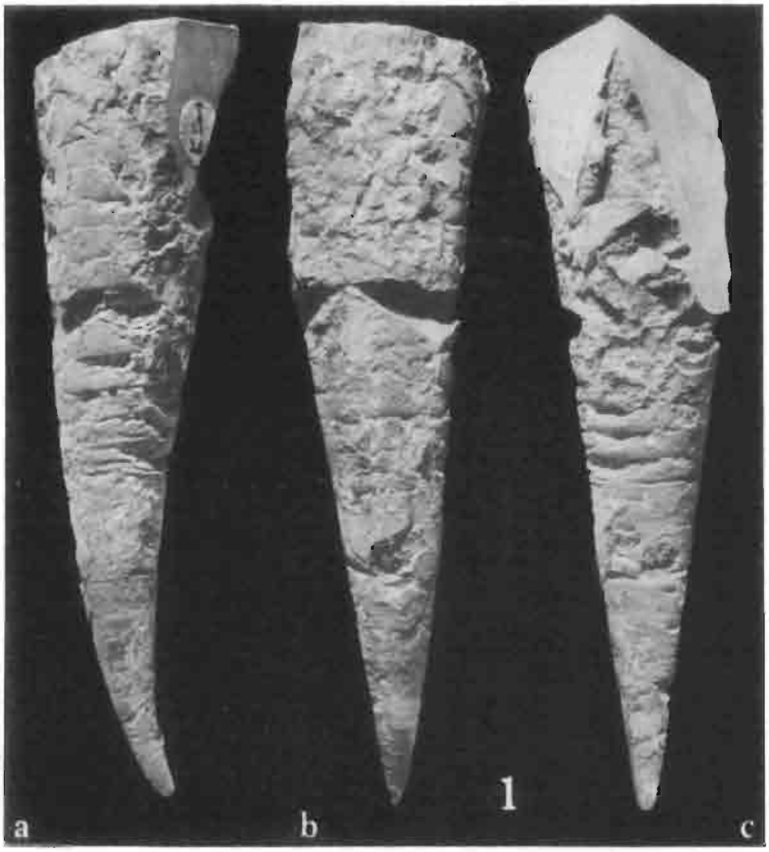
3. Longitudinal section through apical part of a phragmocone, ZPAL N/822; boulder E-224, Aserian, Rozewie.
4. Phragmocone in ventral (a), and lateral (b) views, ZPAL N/825; boulder E-260, *E. foliaceus* Zone, Lasnamägian, Międzyzdroje.

Rhynchorthoceras zaddachi MASCKE in REMELE, 1880 139
E. reclinatus Zone, Lasnamägian, Międzyzdroje, Poland

6. Medial section through a phragmocone, ZPAL N/828; boulder E-263.
7. Medial section through a specimen, ZPAL N/829; boulder E-259.

Ancistroceras torelli (REMELE, 1880) 136

8. Coiled part of a shell, ZPAL N/830; boulder E-085, *E. lindstroemi* Zone, Uhakuan, Mochty.
9. Phragmocone, ZPAL N/914; boulder E-279, Lasnamägian, *E. reclinatus* Zone, Międzyzdroje.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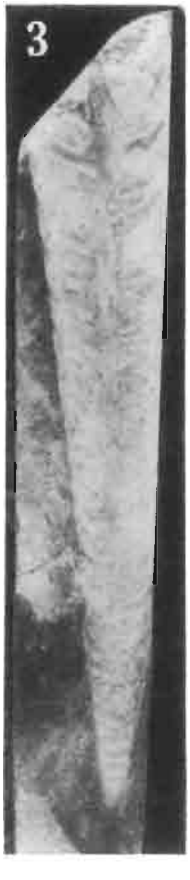
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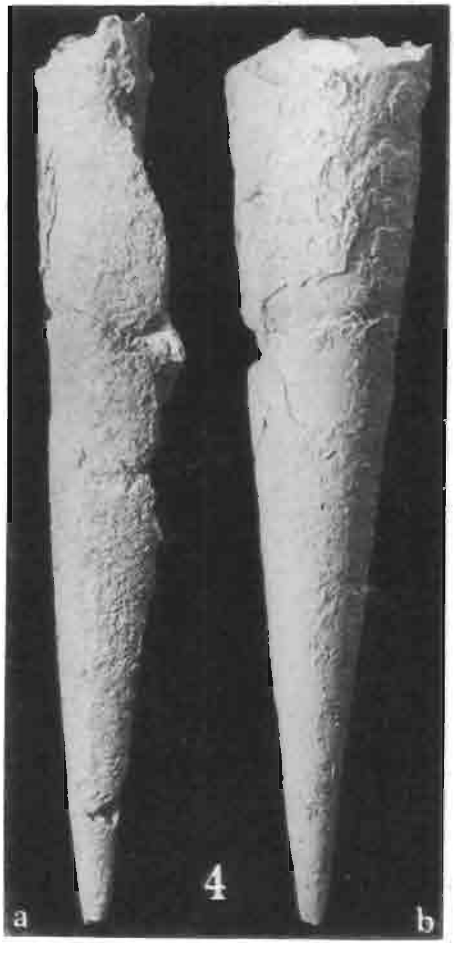
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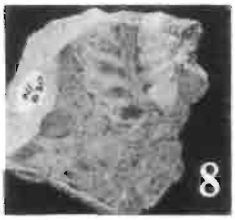
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PLATE 40

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Ancistroceras torelli (REMELE, 1880) 136

E. Lindstroemi Zone, Uhakuan, boulder E-085, Mochty by Warsaw, Poland

1. Specimen in lateral (a) and dorsal (b) view, ZPAL N/832.
2. Medial section through a specimen, ZPAL N/831.

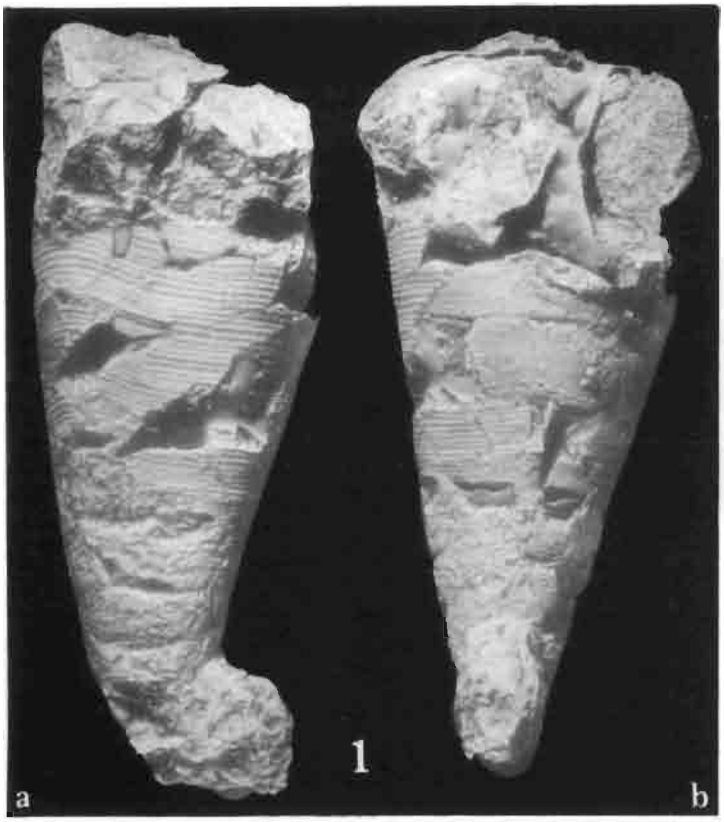
Lituites (*Angelinoceras*) *latus* ANGELIN, 1880 136

3. Specimen in lateral (a) and ventral (b) views, ZPAL N/833, (?) Kundan, erratic boulder, Zgierz, Poland.

Lituites discors HOLM, 1891 136

E. reclinatus Zone, Lasnamägian, erratic boulders of Baltic origin, Poland

4. Specimen in lateral (a) and oblique (b) ventral views, ZPAL N/842; boulder E-143, Rozewie.
5. Medial section through a specimen ZPAL N/840; boulder E-149, Międzyzdroje.
6. Medial section through a specimen ZPAL N/835; boulder E-252, Rozewie.
7. Specimen in lateral (a) and ventral (b) views, ZPAL N/838; erratic boulder, Orłowo.
8. Specimen in lateral view, ZPAL N/837; boulder E-252, Rozewie.
9. Specimen in lateral view, ZPAL N/836; same boulder as above.
10. Specimen in lateral (a) and dorsal (b) views, ZPAL N/834; boulder E-145, Międzyzdroje.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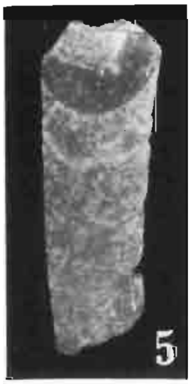
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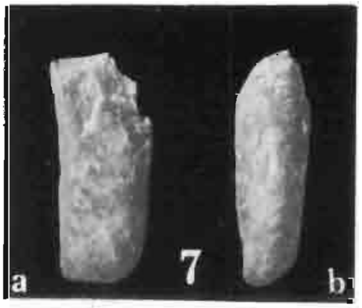
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PLATE 41

	Page
Lituites lituus (MONTFORD, 1808)	137

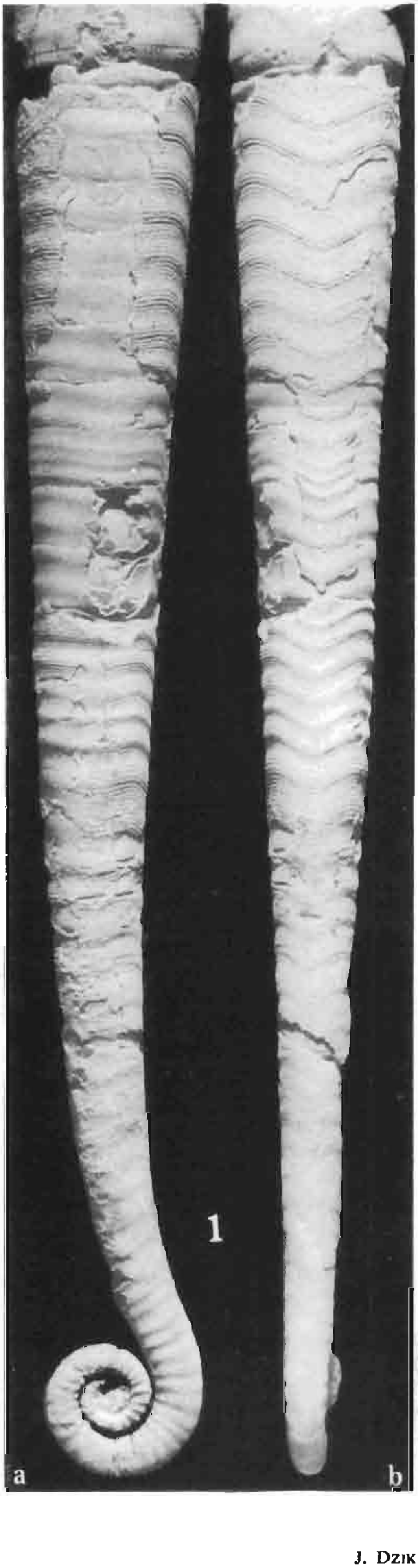
E. robustus Zone, Uhakuan, boulder E-236, Garcz by Kartuzy, Poland

1. Specimen in lateral (a) and ventral (b) views, ZPAL N/851.
2. Specimen in lateral view, ZPAL N/850.
3. Specimen in lateral (a) and ventral (b) views, ZPAL N/847

Lituites perfectus WAHLENBERG, 1840	137

E. lindstroemi Zone, Uhakuan, erratic boulders of Baltic origin, Poland

4. Adult living chamber in lateral (a) and ventral (b) views, ZPAL N/841; boulder E-231, Garcz by Kartuzy.
5. Specimen in lateral (a) and ventral (b) views, ZPAL N/839; also its 3× enlarged fragment (c); Orlowo.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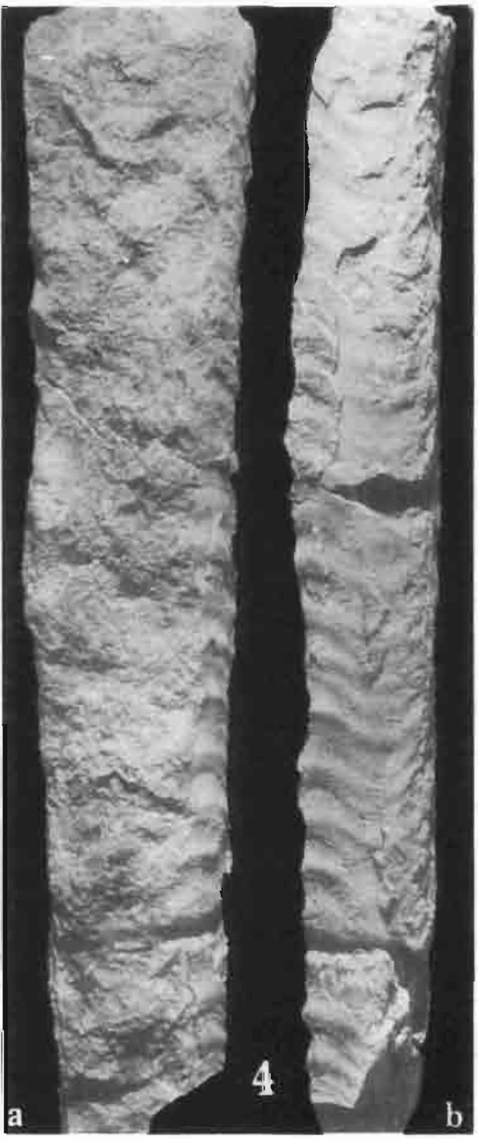
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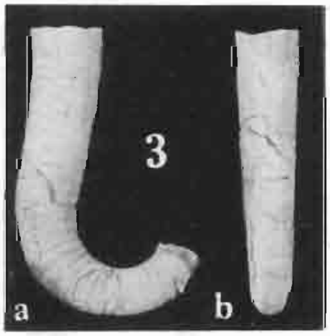
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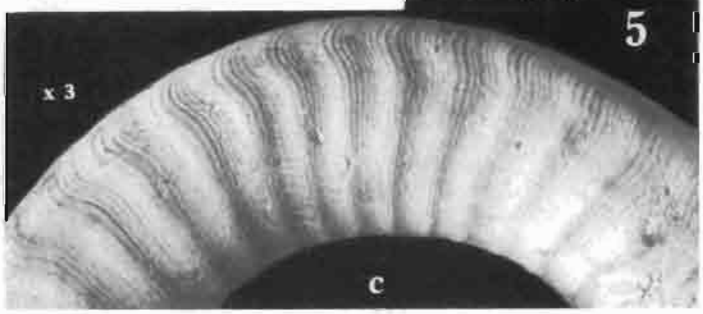
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 42

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Heracloceras (?) *bohemicum* (BARRANDE, 1865) 155

1. Juvenile specimen, IG 137. II. 46 in lateral (a) and ventral (b) views, also 2× enlarged protoconch (c); Přidolian, Karlštein by Prague, Bohemia.

Ptenoceras alatum (BARRANDE, 1865) 155

2. Specimen in lateral (a) and dorsal (b) views, UWR 3066s; note the absence of alae from the earliest ontogenetic stages; Siegenian, Koněprusy Limestone, Mnenany by Prague, Bohemia.

Centroceras tetragonum (d'ARCHIAC and VERNEUIL, 1842) 153

Late Givetian, Świętomarz beds, Śniadka by Bodzentyn, Poland

3. Protoconch and the first whorl in lateral (a) and ventral (b) views, also 2× enlarged (c), ZPAL N/818.
4. Fragment of a subadult phragmocone in lateral (a) and umbilical (b) views, ZPAL N/817.

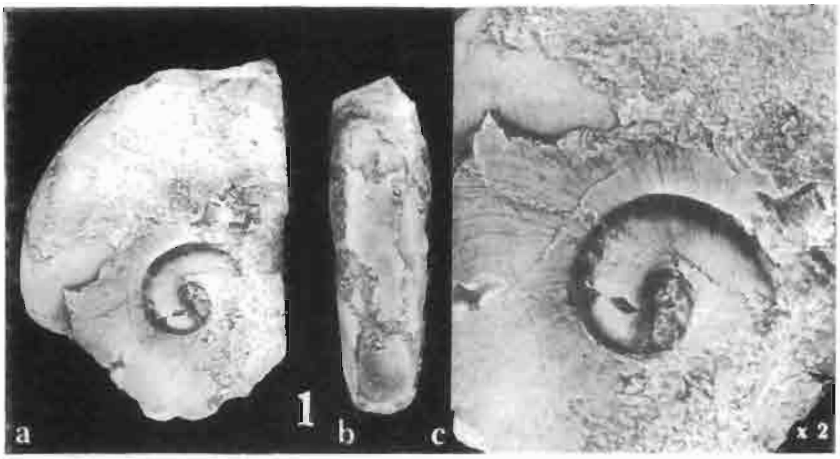
Stroboceras humerosum (SCHMIDT, 1951) 170

Visean (D_2), Orlej quarry by Zalas near Cracow, Poland

5. Deformed complete specimen, ZMS A.I.70/109.
6. Fragment of ventral side of a phragmocone, ZMS A.I.70/118.

Mesochasmoceras (?) *mutabile* (McCOY, 1844) 168

7. Specimen UWR 2237s; note its wide umbilical perforation, smooth shell surface, and complete living chamber with the aperture preserved; Visean, Kildare, Ireland.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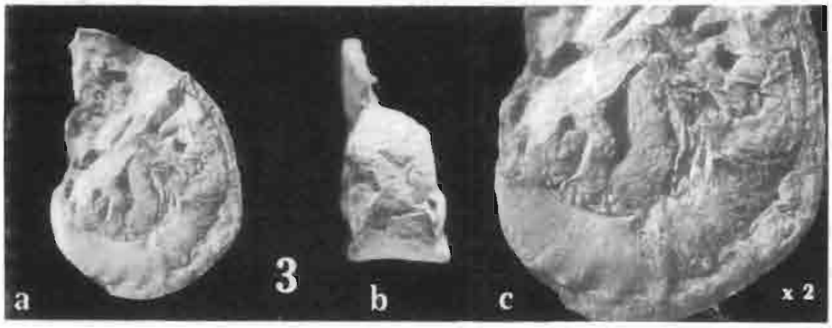
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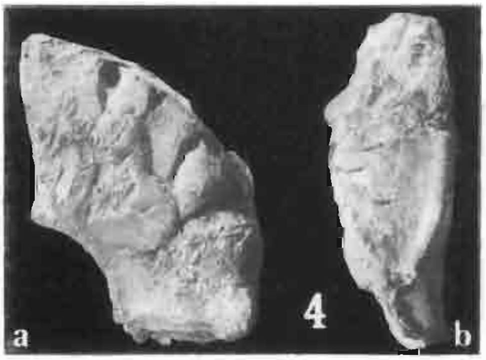
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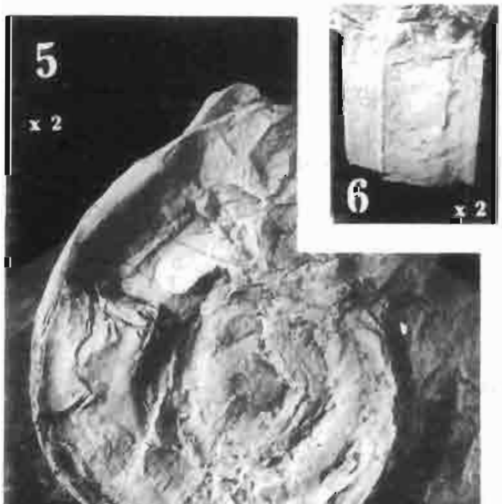
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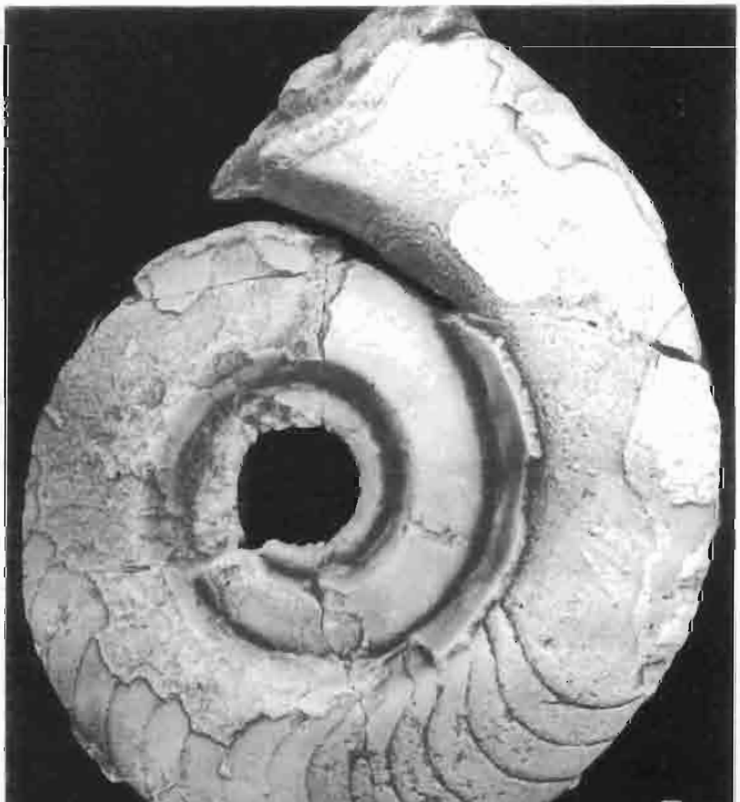
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PLATE 43

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Pleuronautilus sumatrensis (FLIEGEL, 1901) 162
Guadelupian, *Veerbekina* Zone, Padang, Sumatra Island

1. Subadult living chamber in lateral (a) and ventral (b) views, UWR 2330 (holotype of *P. loczyi* FLIEGEL, 1901).
2. Juvenile living chamber in lateral (a) and ventral (b) views, UWR 2458, holotype.

Stroboceras duplicatum SCHMIDT, 1951 170
Visean (D_2), Orlej quarry, Zalas near Cracow

3. Specimen ZMS A.I.70/122.
4. Specimen ZMS A.I.70/129.

Liroceras bistriale (PHILLIPS, 1836) 170

5. Specimen ZMS A.I.70/131, Visean (D_2), Orlej quarry, Zalas, Poland.

Pleuronautilus kokeni FRECH, 1905 162

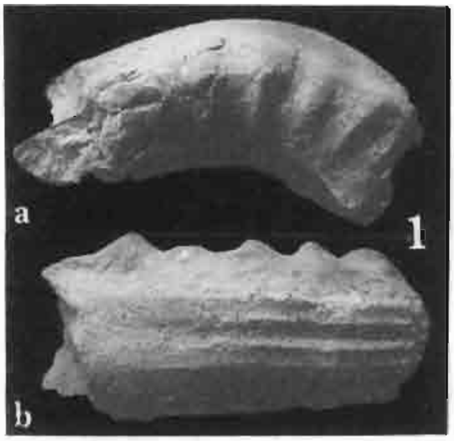
6. Juvenile phragmocone in lateral (a) and ventral (b) views, UWR 3229s; Scythian, *Koninckites volutum* Zone, Salt Range, Pakistan.

Germanonautilus dolomiticus (QUENSTEDT, 1849) 165

7. Juvenile specimen in apertural (a) and lateral (b) views, ZPAL N/856, Middle Anisian (Pelsonian), *Lima striata* beds, Wolica, Poland.

Pleuronautilus trinodosus MOJSISOVICS, 1882 161

8. Phragmocone in septal (a) and lateral (b) views, MGUW 5/6/35; perhaps ŁUNIEWSKI's second (not illustrated) original specimen of *P. mosis*?; Middle Anisian (Pelsonian), Młodzawy by Skarżysko-Kamienna, Poland.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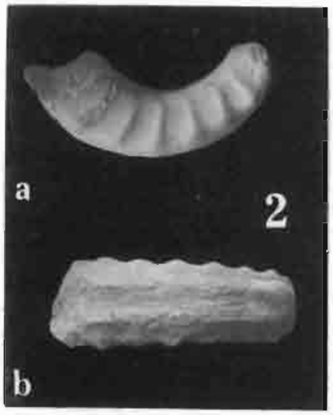
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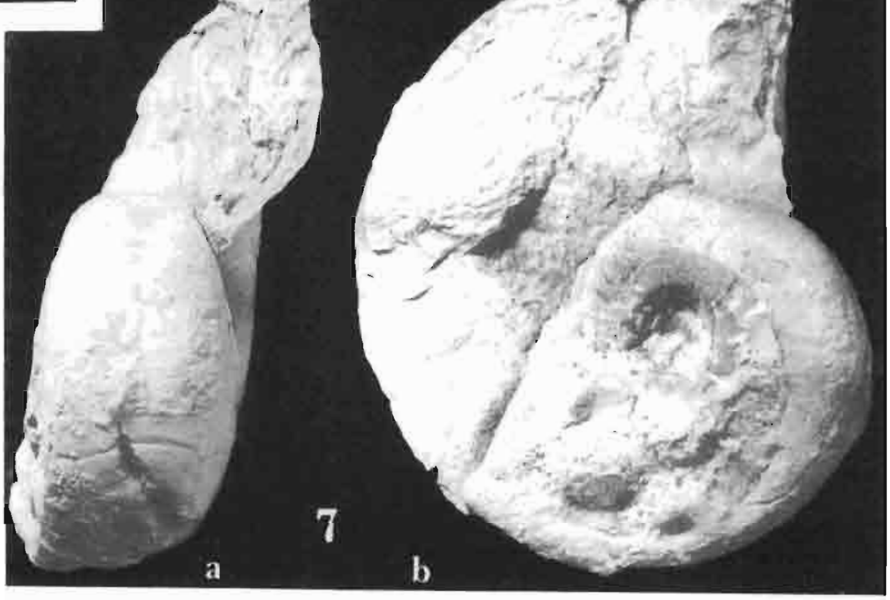
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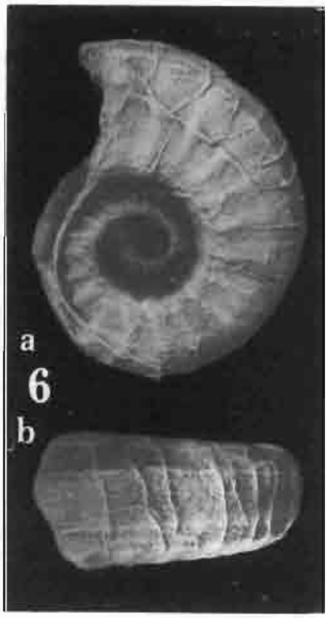
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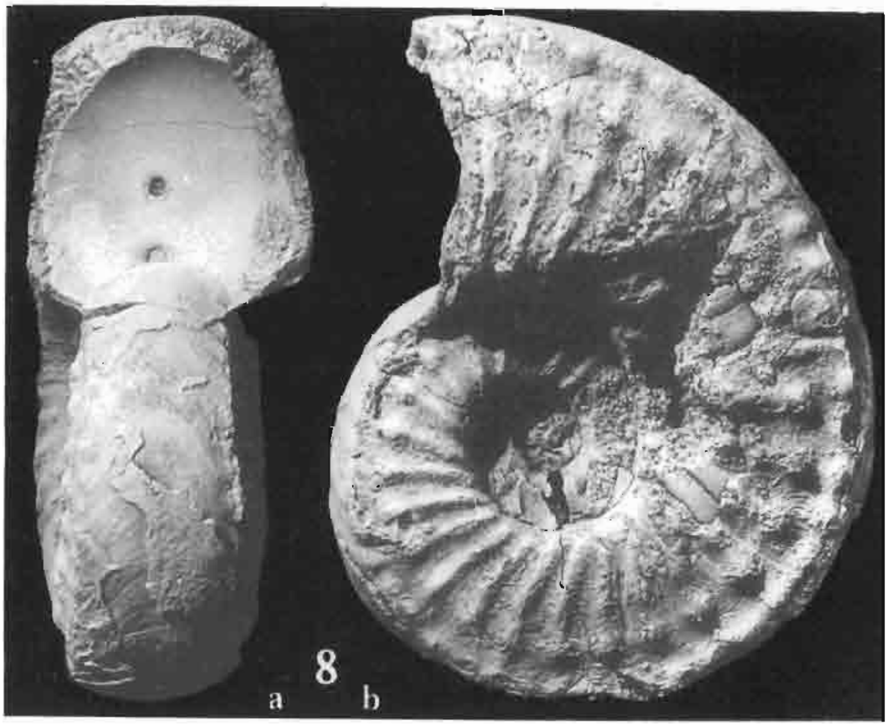
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 44

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Stroboceras duplicatum (SCHMIDT, 1951) 170

1. Specimen in lateral (a) and ventral (b) views, ZMS A.I.70; Late Visean (Go_a), Gałęzice, Poland; × 2.

Acanthonautilus ? sp. 157

2. Juvenile specimen in lateral (a) and ventral (b) views, ZMS Late Visean (GO_a), Gałęzice, Poland; × 2.

Endolobus ? sp. 162

3. Juvenile specimen in lateral (a) and ventral (b) views, ZMS; Late Visean (GO_a), Gałęzice, Poland; × 2.

Pseudotemnocheilus sp. 162

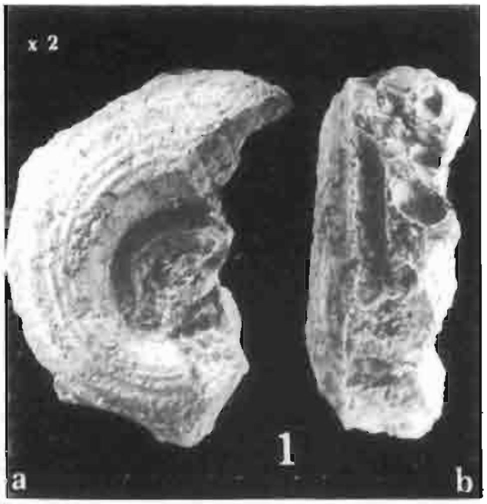
4. Specimen in lateral (a) and ventral (b) views, ZMS; Late Carboniferous or Early Permian, Treskelodden beds, Hyrnefjellet C5, Spitsbergen; × 2.

Potoceras ? sp. 171

5. Specimen in lateral and apertural views, ZMS; Late Visean (Go_a), Gałęzice, Poland; × 2.

Triboloceras sp. 162

6. Specimen in lateral (a) and dorsal (b) views, ZMS; Late Visean (Go_a), Gałęzice; × 2.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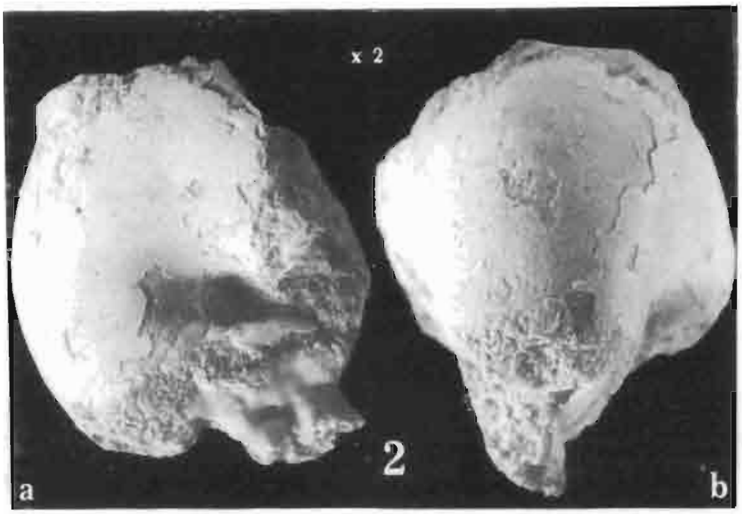
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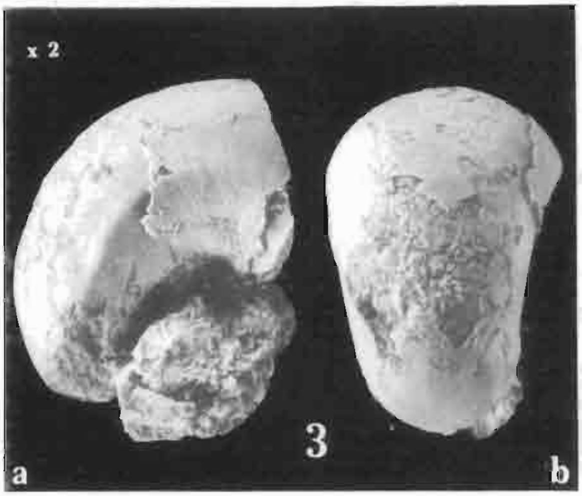
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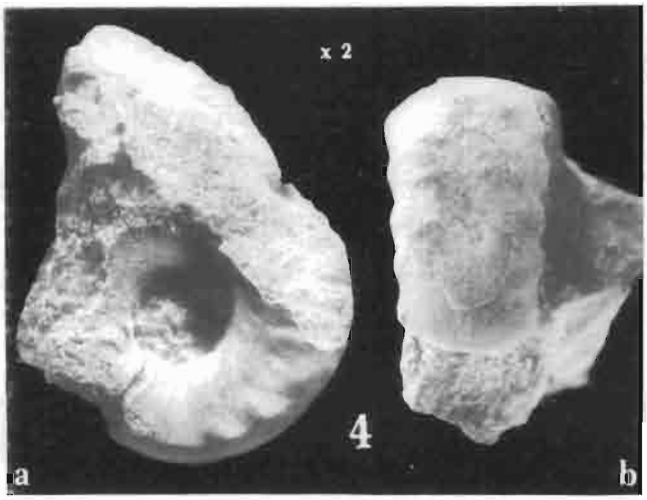
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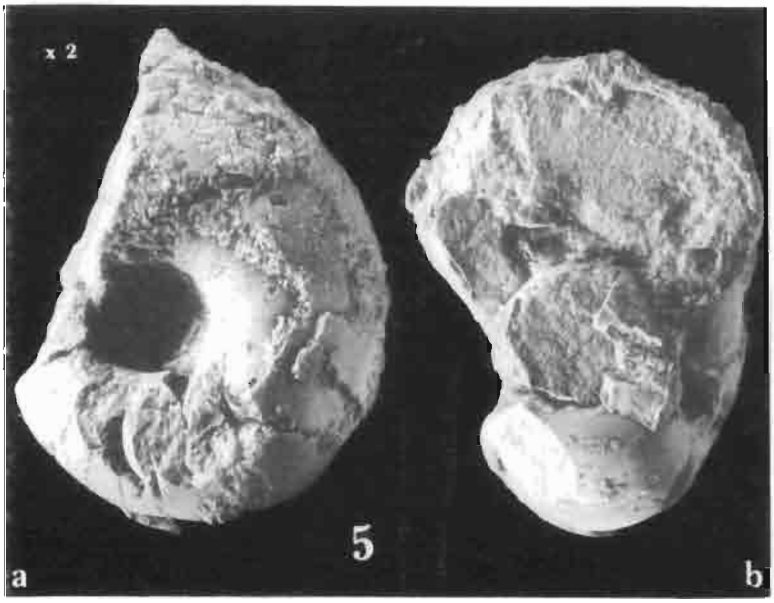
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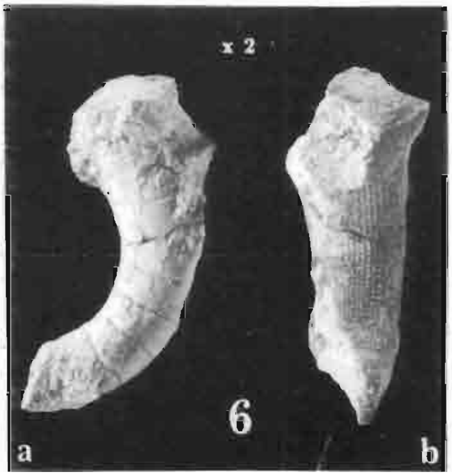
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 45

Page

Procymatoceras sp. 181

1. Inner whorl in lateral (a) and ventral (b) views, ZPAL N/861; *Parkinsonia ferruginea* Zone, Bajocian, Łęczyca, Poland.

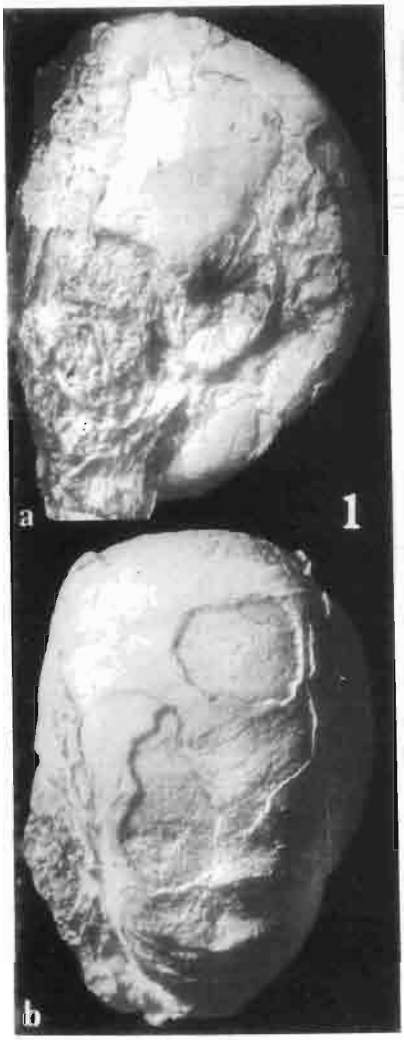
Paracenoceras hexagonum (SOWERBY, 1826) 177

2. Juvenile specimen in lateral (a) and abapertural (b) views, ZPAL N 864; Early Kimmeridgian, Błaziny by Iłża, Poland.

Cenoceras calloviense (OPPEL, 1867) 176

Late Callovian, Łapiguz by Łuków, Poland

3. Juvenile specimen in lateral (a) and apertural (b) views, ZPAL N/874.
4. Adult specimen in lateral (d) and ventral (c) views, MGUW 6·7/1; also its 2× enlarged first whorl in lateral (a) and ventral (b) views.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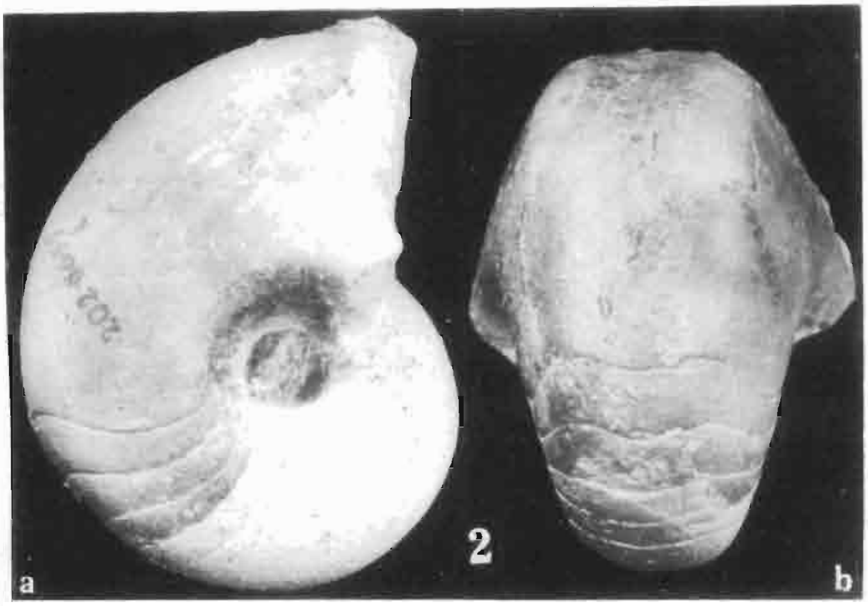
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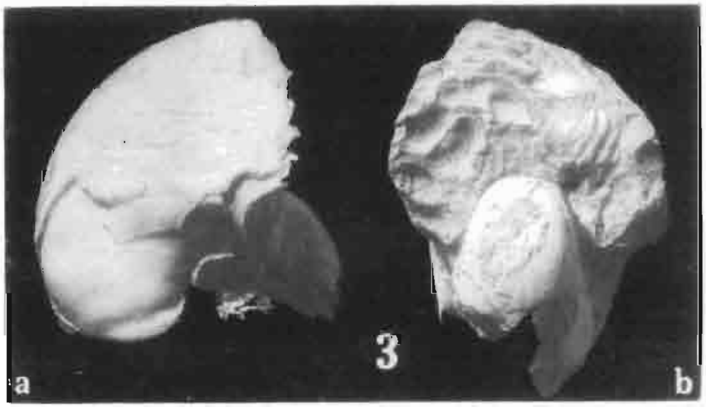
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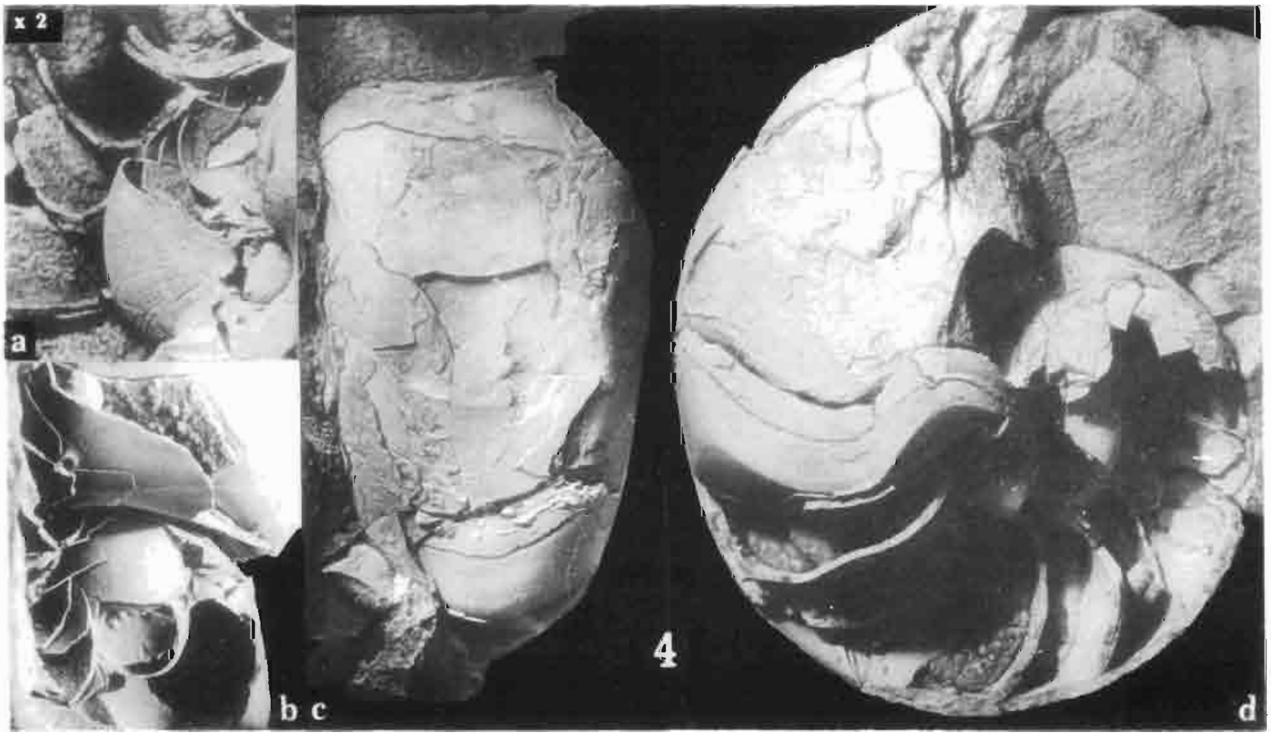
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PLATE 46

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Pseudaganides sp. 178

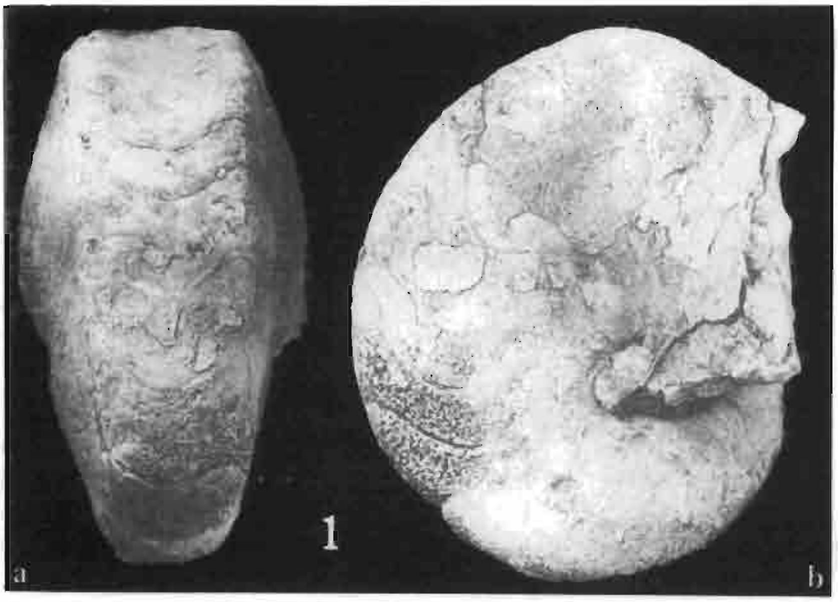
1. Adult specimen in ventral (a) and lateral (b) views, ZPAL N/885; Late Callovian, Lasocin, Poland.
2. Phragmocone in adapertural and lateral views, ZPAL N/884; same horizon and locality.
3. Silicified adult phragmocone in lateral (a) and septal (b) views, ZPAL N/880; Middle Callovian, Mnin, Poland.
4. First whorl in septal (a) and lateral (b) views, ZPAL N/881; same horizon and locality.

"*Rhynchoteuthis*" sp. 183

5. Calcified part of an upper beak in dorsal view, ZPAL N/910; Tithonian, Rogoźnik by Nowy Targ, Poland.

Pseudaganides aganiticus (SCHLOTHEIM, 1820) 178
Late Oxfordian, Poland

6. First whorl in lateral view, coll. Dr. A. WIERZBOWSKI (UW); *Idoceras planula* Zone; Patrzyków-Garbacze by Działoszyn; note ontogenetic development of the ornamentation.
7. Adult specimen in adapertural (a) and lateral (b) views, coll. Dr. A. WIERZBOWSKI, *Epipeltoceras bimammatum* Zone, Bobrowniki Kapitulne by Mierzyce.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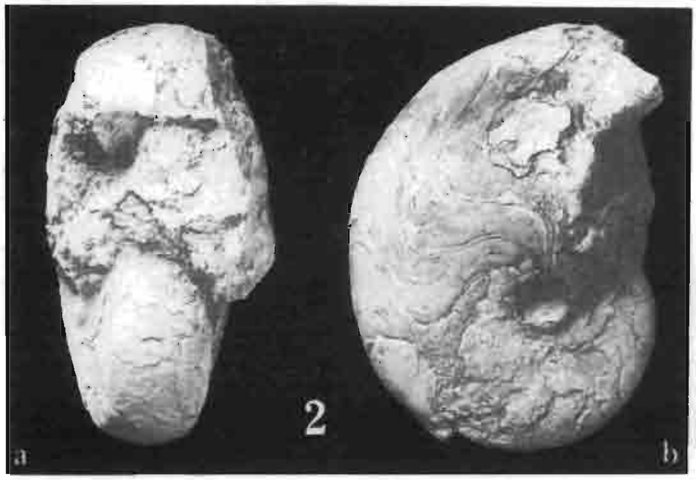
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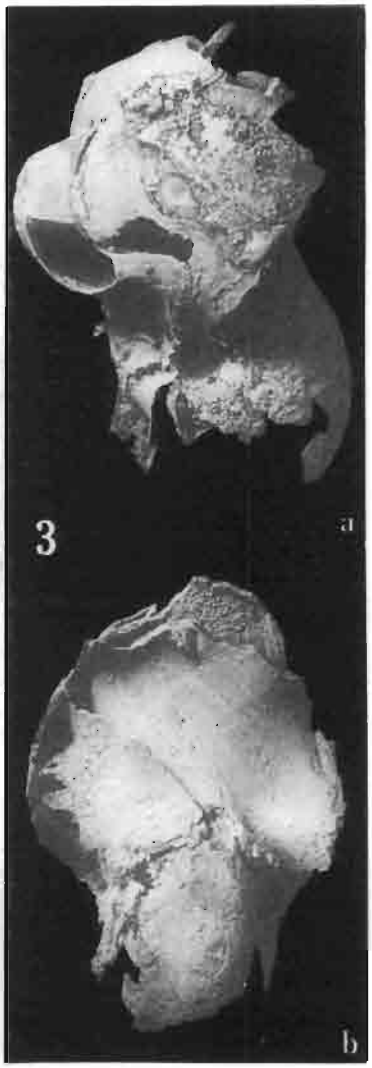
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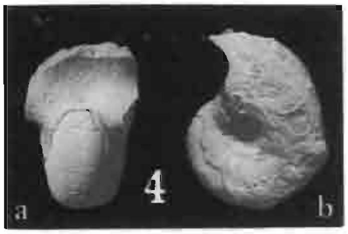
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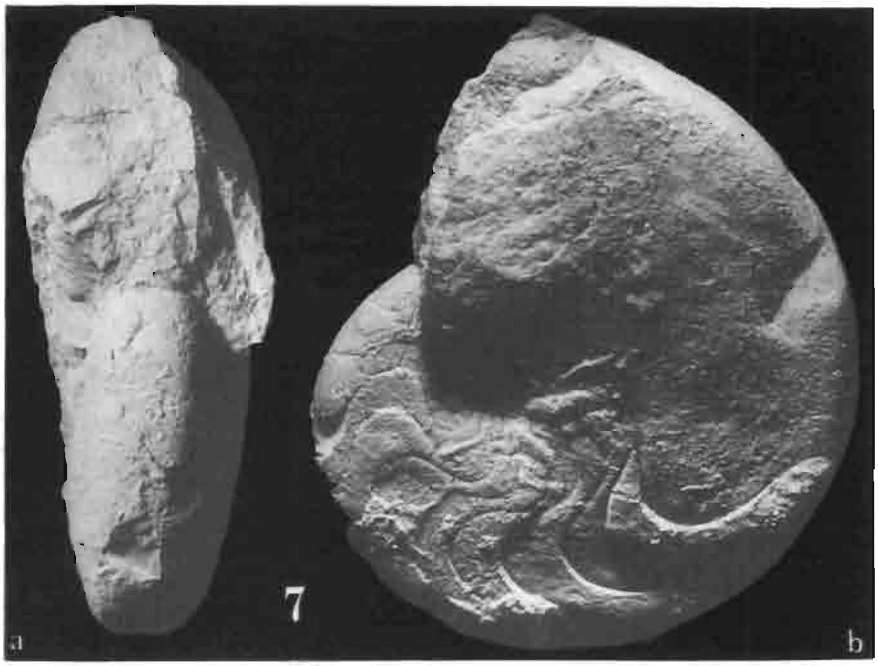
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J. DZIK: PHYLOGENY OF THE NAUTILOIDEA

PLATE 47

Page

Pseudaganides aganiticus (SCHLOTHEIM, 1820) 178

1. Juvenile specimen, ZPAL N/892; *Perisphinctes bifurcatus* Zone, Wola Morawicka, Poland.
2. Juvenile specimen in lateral (a) and apertural (b) views, coll. dr. A. WIERZBOWSKI; *Idoceras planula* Zone, Late Oxfordian, Działoszyn (outcrop 113 in WIERZBOWSKI's collection), Poland.
3. Juvenile phragmocone in lateral (a) and septal (b) views, ZPAL N/889; Early Oxfordian, Kłobuck, Poland.
4. Juvenile specimen, ZPAL N/891; Early Oxfordian, Działoszyn, Poland.
5. Adult specimen, ZPAL N/890; *P. bifurcatus* Zone, Oxfordian, Tokarnia by Chęciny, Poland

*Eutrephoceras sublaevigatum (*d'ORBIGNY, 1840*)* 181

6. Juvenile phragmocone in lateral and ventral views, coll. Dr. R. Marcinowski; Late Albian, Annopol by Sandomierz, Poland.

"*Rhynchoteuthis*" sp. 183

7. Specimen in ventral and dorsal view, ZPAL N/894; Barremian (?), Prałkowce by Przemyśl, Poland.

Cymatoceras (*Syrionautilus*) sp. 181

8. First whorl in lateral view, ZPAL N/899; note the large size of the first chamber; Maastrichtian, Kazimierz n. Wisłą, Poland.

Pseudocenoceras archiacianum (d'ORBIGNY, 1840) 181

Early Cenomanian, Annopol by Sandomierz, Poland

9. Juvenile specimen in lateral (a) and septal (b) views, ZPAL N/905.
10. Juvenile phragmocone in lateral and ventral views, coll. Dr R. MARCINOWSKI (UW).


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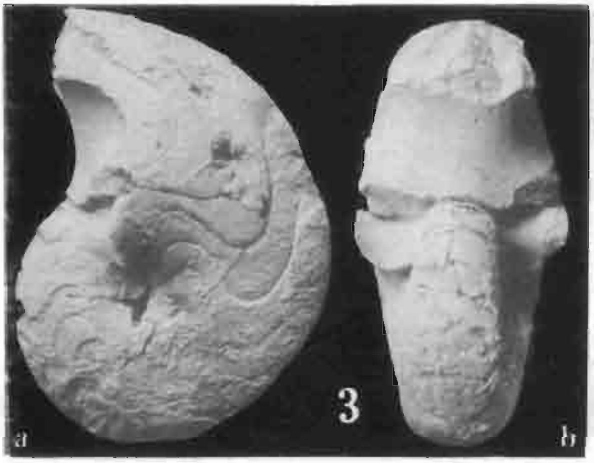
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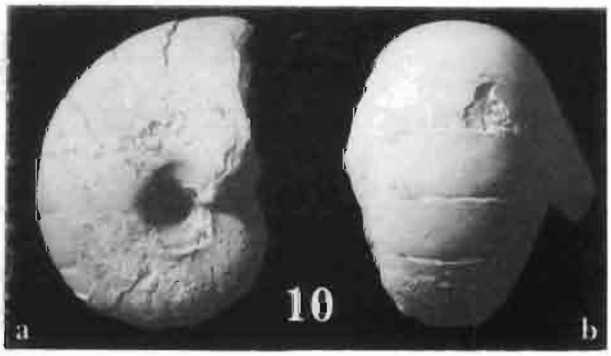
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