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**Part 2**

**ABSTRACTS**

## HEMIOPLITID AMMONOIDS FROM THE AUSTRAL BASIN OF PATAGONIA, ARGENTINA

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The recent finding of a beautifully preserved ammonite fauna in the Austral basin of Southern Patagonia, Argentina sheds light on the origin, evolutionary trends, and palaeobiogeographic distribution of the genus *Hemihoplites* Spath, 1922.

Two species were already known from Patagonia: *Hemihoplites ploskiewiczi* and *H. varicostatus*. The former is a small species with subrectangular to compressed whorl and fine, flexuous ribbing and has been included in the *Favrella americana* assemblage zone (late early to early late Hauterivian). The second one is a medium sized species with subrectangular to subquadrate whorl, flexuous ribbing bifurcate in inner whorls and simple on outer whorls. It has been found in beds with *Protaconeceras patagoniense* (*Favrella wilckensi* assemblage zone, late Hauterivian) and *Hatchericeras* spp. (*H. patagonense* assemblage zone, early-middle Barremian) (Riccardi and Aguirre-Urreta, 1989). Both species show sexual dimorphism. A third species, reported here for the first time, corresponds to *Hemihoplites feraudianus* (d'Orbigny), type species of the genus. Several specimens recovered from a single bed shows a total coincidence with the modern descriptions of this species regarding size, whorl section, and ornamentation (Delanoy, 1990, 1997). This species is also represented by a dimorphic pair. No other ammonites have been recorded with this species, but it can be placed in the Late Barremian (*Feraudianus* zone of Europe).

*Hemihoplites* is recorded in the recent edition of the "Treatise" as Upper Hauterivian-Barremian and its presence in older rocks of Southern Patagonia as recorded by Riccardi and Aguirre-Urreta (1989) has been overlooked (Wright, 1996) or dismissed as unlikely (Delanoy, 1990).

The early appearance of *Hemihoplites* in Southern Patagonia led some authors to question the age of the *Favrella americana*, *F. wilckensi* and *Hatchericeras patagonense* faunas (Delanoy, 1990). However, the recent discovery of *Hemihoplites feraudianus* permits to postulate a long history of this genus in the Austral basin, with an evolutionary trend towards increasing body size and coarser ribbing.

The sudden appearance of *Hemihoplites feraudianus* in the European late Barremian also prompts to the proposal of an immigration to the Tethyan region and casts doubts on the proposed origin of *Hemihoplites* from the late Hauterivian genus *Pseudothurmannia* (Wright, 1996) or from *Emericiceras* of the *barremense* group (Delanoy, 1990).

DELANOY, G., 1990. Données nouvelles sur l'espece-index *Hemihoplites feraudianus* (d'Orb., 1841)(Ammonoidea, Ancyloceratina). - C.R. Academie Sciences Paris 310, Série II, 661-666.

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WRIGHT, C.W., 1996. Cretaceous Ammonoidea. In: R.L. Kaesler: Treatise on Invertebrate Paleontology, Part L, Mollusca 4 Revised, 362 pp. Geological Society of America and University of Kansas Press.

## TYPES OF LOBE LINE DEVELOPMENT OF THE MIDDLE TRIASSIC AMMONOIDEA OF THE BOREAL AREA

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Four-lobed (VL:ID) or, more rare, five-lobed (VLU:ID) prime suture has been established by the authors to be characteristic for the majority of the Middle Triassic ammonoidea of Boreal region. Representatives of families Longobarditidae, Nathorstiidae, Tsvetkovitidae, Parapopanoceratidae, Ptychitidae, Beyrichitidae, Ussuritidae have prime sutures of the first type, Proarcestidae and Cladiscitidae - of the second type. Main types of lobe line development of the Middle Triassic Ammonoidea are:

1. Bilateral displacement of umbilical lobes, with the even lobes being displaced to the external side, the odd lobes - to the internal side of the whorl. Typical formula is  $(V_1V_1)LU^1U^2U^4..U^3I(D_1D_1)$ . Families Longobarditidae, Nathorstiidae and Tsvetkovitidae.
2. Bilateral displacement of umbilical lobes, with the odd lobes being displaced to the external side, the even lobes - to the internal side of the whorl. Typical formula is  $(V_1V_1)LU^1U^3..U^2I(D_1D_1)$ . Family Parapopanoceratidae.
3. Formation of umbilical lobes on the external side of the whorl and additional internal lateral lobes - on the internal side of the whorl, according to the formula:  $(V_1V_1)LU^1U^2U^3..II^2I^1(D_1D_1)$ . Family Ptychitidae.
4. Fission of the internal lateral lobe (I) on the early and middle ontogenesis stages after formation of the first umbilical lobe ( $U^1$ ) on the external side of the whorl. Typical formula is  $(V_1V_1)LU^1I_1:I_d(D_1D_1)$ . Family Ussuritidae.
5. The lobe line is developed according to the fourth type, but new lobes  $I_1$ ,  $I_2$ ,  $I_3$  etc. are forming from the saddle dividing the wings of the lobe (I) after its fission. Typical formula is  $(V_1V_1)LU^1I_1I_2^3...I_4^1I_d(D_1D_1)$ . Family Beyrichitidae.
6. A peculiar type of the lobe line development has been discovered for the Middle and Late Triassic Arcestidae having five-lobed prime suture. The development of the genus *Nevadisculites* studied by the authors from the Middle Anisian of Nevada occurs primarily by fission of the lobe (I) followed by formation of umbilical and additional internal lateral lobes, with first of them being displaced to the external side and the second - to the internal side of the whorl according to formula: VL:U:ID - VLU:ID - VLU:I<sub>1</sub>I<sub>1</sub>D -  $(V_1V_1)LUU^1U^2:(I_{1-2}I_{1-2})I_1I^1(D_1D_1)$ . Analogous type of development is characteristic for the Carnian *Proarcestes*. The only distinction is that an adventive lobe occurs at the early stage (0.8 - 1 whorl) on the top of the saddle V/L and disappears at the stage of 1.3 - 1.5 whorls. Both genera *Nevadisculites* and *Proarcestes* are included by the authors into the Family Proarcestidae. It is suggested that some Triassic Ammonoidea, due to the presence of five-lobed prime suture, should be excluded from the order Ceratitida having four-lobed prime suture. Triassic Ammonoidea having five-lobed prime suture join into the order Arcestida Vavilov, 1992.

# STATOLITH SHAPE AS AN INDICATOR OF THE LIFE STYLE IN RECENT AND EXTINCT DECAPOD CEPHALOPODS

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Squids and sepoids are decapod cephalopods having the unique jet propulsive locomotion which is characterized by a rhythmic change of linear acceleration. We have found that under acceleration, the statolith (gravity stone) may deviate around the three mutually perpendicular axes running through its rotation center and therefore may induce endolymph flows within the cavity of the equilibrium organs (statocysts). This finding re-considers the theory of the statocyst function in decapods. As the statoliths play an important role in detection of various types of accelerations, their general morphology is different in pelagic and demersal decapods (Fig.1). Pelagic squids (both nektonic and planktonic species) live in an environment without physical obstacles, and therefore have mainly 'rocket-like' movement. Demersal

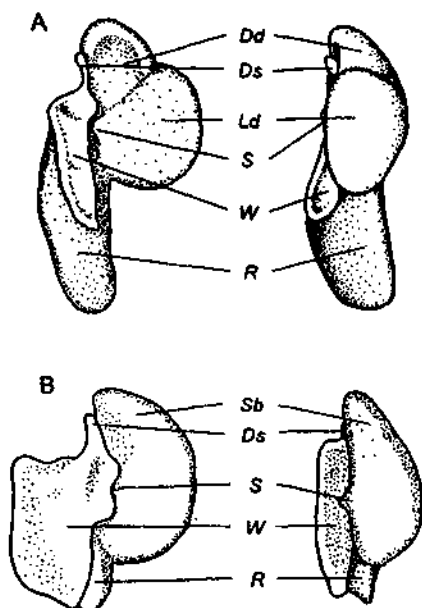


Fig.1. Statoliths of the near-bottom squid *Berryteuthis magister* (A) and pelagic squid *Moroteuthis robusta* (B). Lateral (left) and anterior (right) views. Dorsal (Dd) and lateral (Ld) domes, dorsal spur (Ds), statolith body (Sb), spur (S), wing (W) and rostrum (R).

sepoids and near-bottom squids either have to land on or to take off from the bottom, and negotiate bottom obstacles. Peculiarities in the statolith shape and size of demersal decapods (their relative total statolith length is considerably greater than that of pelagic species) make their statoliths more movable around the transversal axis than those of pelagic squids. Such a mobility provides a greater sensitivity to accelerations of the animal during both gliding and pitching. The oar-like rostrum of the demersal decapod statolith provides a greater sensitivity during rolling at low accelerations. Distinct separation of the statolith body into dorsal and lateral domes provides separation of endolymph flows in the corresponding channels during pitching and yaw, respectively. Thus, peculiarities of the statolith shape in demersal decapods give them greater sensitivity to low angular accelerations in all possible planes compared to those of pelagic species. Peculiarities of the statolith shape in pelagic species (especially long and wide wing achieving the rostrum tip and short sharpened rostrum)

make these statoliths hardly movable around both longitudinal and transversal axes that considerably diminish the sensitivity of these animals to angular accelerations in pitching and rolling planes. In pelagic squids, the statolith monitors mainly the strength and frequency of jet propulsions during linear movement. Thus, our findings make it possible to re-construct the life style and movement patterns of recent and (most important) extinct decapods using statolith shape features, and to re-consider evolutionary connections between different decapod groups.

# THE TAXONOMIC POSITION AND BIOSTRATIGRAPHIC VALUE OF THE GENUS *PSEUDOCRIOCERATITES* EGOIAN, 1969 (LYTOCERATINA) IN ROMANIA

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In describing his genus *Pseudocrioceratites*, Egoian (1969, p. 172) stated that it includes only two species: *P. pseudoelegans* EGOIAN and *P. rotundus* EGOIAN, both of them Clansayesian in age. Nevertheless, this group of cephalopods, characterised by a crioceratic appearance, but with typical lytoceratic suture, is also represented in the Barremian (by two new Romanian species and, possibly, by the incompletely defined *Pseudocrioceras stentor* ANDERSON), in the lower Aptian (by another Romanian species), and in the Albian time span (by *Crioceras* cf. *Munieri* DOUVILLE, 1916, non SARASIN & SCHONDELMAYER, 1901).

In this acception, the genus displays a very near to *Crioceratites emerici* LEVEILLE costume (except for the septate tubercles), and the suture with a very large, bifid lateral lobe and an also large, tending to be cruciform, internal lobe. On this basis, the genus is here interpreted as being an uncoiled representative of typical Lytoceratina, similarly to the related genus *Acantholytoceras* SPATH, 1923.

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## THE CLASSIC ANISIAN (MIDDLE TRIASSIC) AMMONOID LOCALITIES OF THE SOUTHERN ALPS, AND THEIR SIGNIFICANCE FOR THE DEFINITION OF THE ANISIAN SUBDIVISIONS

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The development of the standard scale for the Anisian Stage (Middle Triassic) has been a matter of debate since the last century. The Anisian Stage was defined in the Western Tethys, and its meaning and subdivisions were strongly influenced by ammonoid rich localities of Southern and Northern Alps, as well as Hungary. Many problems came out because of: (1) lack of bed-by-bed data, (2) restricted stratigraphic extent and scarce overlap of some type-localities, or (3) historical localities with condensed faunas, (4) direct correlations influenced also by taxonomical problems. For these reasons the number and the composition of the biozones of the Middle to Upper Anisian (Pelsonian and Illyrian Substages) is not yet well defined.

In the last 10 years seven classical and new localities in the Southern Alps have been bed-by-bed investigated in order to define the details of the Pelsonian-Illyrian faunal succession. The studied sections include Dont (Dolomites), Cimego (Giudicarie) that are the two type localities of the Pelsonian Substage and of the *Binodosus* Zone, and Stabol Fresco section, that is the most representative for the Illyrian Substage and the *Trinodosus* Zone in the original definitions. Adanà and Peschiera (Giudicarie), Menna and Lenna (Brembana Valley) were also taken into consideration.

All the sections were bed-by-bed directly correlated by guide ammonoids. In particular the most important result is the new direct correlation of Dont and Stabol Fresco sections.

The first ammonoid level of Stabol Fresco section, providing a rich *Bulogites* fauna, is correlated with level R of Dont section, that is some 2 m below the classic *binodosus* fauna. New fossiliferous levels have been found at Dont 2.5 m above the layers providing the *binodosus* fauna. The new fossil bearing beds record the FO of the bivalve *Daonella* followed by the occurrence of *Megaceratites*, *Lanceoptychites* and *Paraceratites* s.s. These taxa, typical of the *trinodosus* fauna, occur in the same sequence in the middle-upper part of Stabol Fresco section, some 50 m above the *Bulogites*-rich level. At Stabol Fresco, in between the last *Bulogites* level and the typical *trinodosus* fauna there is a rich fauna dominated by ceratitids of the group of *C. cimeganus* Mojsisovics, 1882. This fauna is not recorded at Dont where at the top of the *binodosus*-bearing level a lithologic change underlined by glauconite suggests a hiatus. Moreover faunal analysis of the *binodosus*-bearing leads to suggest a condensation.

The cross correlation of the studied sections are summarized in a composite range chart that notably differs from recent literature. As a consequence a new biostratigraphic scale for the Pelsonian-Illyrian is proposed.

## **EVALUATION OF CONSTRUCTIONAL DIFFERENCES IN JURASSIC AMMONITE SHELLS AND NAUTILUS**

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Modern *Nautilus* has served as a model in understanding the construction and function of the ammonite phragmocone. In the early Upper Jurassic of Madagascar a nautiloid that is essentially like modern *Nautilus* occurs together with the representatives of the three orders of the ammonites, *Lytocerotina*, *Phyllocerotina*, and *Ammonitina*. All these are preserved without changes in their mineral shell structure, and in part, with their siphuncular tube well preserved. The different features of shell that resulted from septum formation, chamber sheet attachment, siphonal-tube construction, muscle attachment and internal living chamber coatings (wrinkle layer, callus layer) are well preserved, while some organic layers have disappeared during early diagenesis, that resulted in no shell crushing due to compaction. The features interpreted in the light of new data that we have collected in our most recent studies on chambered cephalopods in Hamburg, Berlin, and Hanover give new insights into ammonite paleobiology.

## THE MIDDLE JURASSIC AMMONITE *KHERAICERAS* SPATH FROM THE INDIAN SUBCONTINENT

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*Kheraiceras* Spath has a near circumglobal distribution except for subboreal and is marked by a 'bio-event' (radiatio) especially during the Late Bathonian and Early Callovian time. Such 'bio-events' may blur the distinction of faunal provincialism and cut across geographic boundaries and thus help in establishing regional standard chronostratigraphy and interprovincial correlation. The present study reports six *Kheraiceras* species from the Indian subcontinent (Kutch, India and Baluchistan, Pakistan) including three new species. They are *Kheraiceras cosmopolitum* (Parona and Bonarelli), *K. bullatum* (D'Orbigny), *K. cf. hannoveranum* (Roemer), *K. spathi* n.sp.A and *K. noetlingi* n.sp.

Biostratigraphic potentialities of *Kheraiceras* are also explored. Dimorphism is well understood in the genus; but specific dimorphic pairs are poorly known. At least in three instances, matching of pairs has been firmly established and two new microconchs and one macroconch still lack their partners. Microconchs are of great help in species discrimination, biozonation and understanding evolution.

## PHYLOGENY AND SYSTEMATICS OF THE WOCKLUMERIINA (AMMONOIDEA, CLYMENIIDAE, MIDDLE TO LATE FAMENNIAN)

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In one of his classic monographs, Schindewolf (1937) described the ammonoid biostratigraphy of the latest Famennian (Wocklum-Stufe, Upper Devonian VI) which is based to a large extent on the rapid evolution of clymeniids with strange triangular coiling, also known, for example, in some Carboniferous goniatites. Trigonal whorls were thought to have evolved in three parallel lineages, two of which terminated abruptly during the sudden mass extinction associated with the global Hangenberg Event.

Since Schindewolf's work, new rich faunas with triangular clymeniids have been described from SW England, Algeria, South China, Russia, Kazakhstan, Thuringia, and Poland. These records, a revision of German collections (> 1.500 specimens), and new collections from Morocco, the Rhenish Massif, and Oklahoma allow a re-evaluation of systematics and phylogeny. Neo- and lectotypes had to be selected for all German taxa and there are new species of *Synwocklumeria* and *Kielcensia*. Intermediate Russian and Polish taxa show that Wocklumeriidae with ventral lobe were derived from open umbilicate Parawocklumeriidae (Korn 1992). Both groups form a natural systematic unit (Wocklumeriaceae) characterized by three apomorphies: 1. triangular coiling of at least early stages, 2. weak to strong constriction of straight whorl parts, and 3. the dorsal lobe is divided or reduced. Heterochronic processes played a major role in phylogeny. *Parawo. paradoxa*, *Epiwo. applanata*, *Wo. sphaeroides*, and *Kielcensia bohdanoviczi* represent iterative hypermorphic end-members, partly with re-activated ancestral conch features such as evolute and rotund coiling. Intraspecific dimorphism in the latter two species is documented by micromorphic specimens with shortened triangular ontogenetic stages. Heterochronic speciation (miniaturisation) may have been in progress just before the sudden extinction caused by the Hangenberg anoxic event. Large intraspecific variability of shell parameters in some species, slowly expanding longidomic whorls, deep protective constrictions, and the reduction of the ocular sinus indicate a suprabenthonic (demersal) lifestyle of Wocklumeriaceae. Triangular coiling can be interpreted as an attempt to shift the centre of mass and aperture downwards in order to optimize seafloor feeding during long phases of growths.

Shells features and sutural patterns support Schindewolf's idea of an origin of Wocklumeriaceae in Hexaclymeniidae although both groups are separated by a record gap. Glatziellidae, Pachyclymeniidae and Biloclymeniidae are regarded as further hexaclymeniid side-branches. All clymeniids with primarily wide and later subdivided ventral lobe are assigned to the suborder Wocklumeriina. Gonioclymeniids with narrow ventral lobes were derived from Platyclymeniidae. This confirms the dissolution of the traditional Gonioclymeniina (Korn 1992) and requires a re-definition of the Clymeniina.

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**ARTERIAL HEMOLYMPH SUPPLY IN THE BRANCHIAL HEARTS OF THE CUTTLEFISH  
*SEPIA OFFICINALIS* L. (CEPHALOPODA, DIBRANCHIATA)**

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The circulatory system of dibranchiate cephalopods includes the systemic heart, the paired branchial hearts and autonomously contractile vessels (Fiedler & Schipp, 1987; Wells & Smith, 1987). In the respiratory part of the venous system mainly the branchial hearts are responsible for pumping the deoxygenated hemolymph into the gills. There, the oxygenation of the respiratory pigment hemocyanin takes place. In octopods the average oxygen content in the arterial hemolymph is 3.3 vol %, whereas in the dichotomous branching of the vena cava, which supplies the branchial hearts with hemolymph, the oxygen content is only 0.4 vol % (Johansen & Lenfant, 1966) and may approach zero during hypoxic excursions (Houlihan et al., 1982).

Concerning the moderate oxygen supply of the branchial heart Driedzic (1985) proposed that it primarily operates anaerobically. However, the demonstration of arterial vessels running to the muscular rind of the branchial heart of *Octopus* (Wells & Smith, 1987), and the comparable enzyme profile of systemic and branchial heart (Driedzic et al., 1990), indicate an independent oxygen supply of this organ.

For the further elucidation of the existence of an arterial vascularization in the branchial hearts of *Sepia officinalis* L., tracer experiments were carried out on semi-adult animals of both sexes caught in the Bassin d'Arcachon (France). After in-situ injection of 1 ml Indian Ink (0.1% in seawater) into one of the auricles, the capacious organ complex composed of systemic heart, auricles, gills, renal appendages, branchial hearts and branchial heart appendages was removed. Tissues were investigated by histological methods.

Marked vessels coming from the connective tissue at the base of the branchial hearts were mainly localized at the dorsal surface of the organs by macroscopical observations. They form a ramifying mesh directly beneath the epithelium; some of these vessels run through the muscular wall up to the branchial heart appendages. The light microscopical studies revealed that the vessels of the inner folded epithelium in the branchial heart appendages are also filled up with tracer particles. In the extended lumen of the branchial hearts no tracer was found. After control injection of the Indian Ink solution into the vena cephalica, tracer particles were detected in the lumen of the organs but not in the ramifying vessels mentioned above.

The presented morphological study verify that the branchial hearts and even their appendages are supplied with oxygenated hemolymph from the systemic heart via a well-developed arterial vascularization - similar to the coronary system as described for the heart of most vertebrates.

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## VARIABILITY AND TAXONOMY OF *MAENECERAS* (GONIATITIDA, SPORADOCERATIDAE) FROM THE EARLY FAMENNIAN OF SOUTHERN MOROCCO

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The Sporadoceratidae are one of the most successful and longest-ranging Famennian ammonoid family with global distribution in (sub-)tropical areas. At the base of the classical Upper Nehden-Stufe (do IIß = Upper Devonian II-G), the oldest genus of the family, *Maeneceras*, descended from *Cheiloceras* (*Puncticeras*) *lagowiense* by the insertion of shallow lobes in the ventral (A<sub>2</sub>-lobe) and dorsal (U-lobe) saddles. More than a dozen early Famennian (Nehden-Stufe) species have been named which are said to be distinguished by shell parameters, constrictions (internal shell thickenings), and by the shape and depths of sutural elements. Similar species (*Maeneceras ungeri* Group) occur higher in the Famennian (UD III-V) but are all characterized by spiral ornament as in many Carboniferous goniatites and they will be placed in a new genus.

In order to clarify the taxonomic status and variability of early maeneceratids, a large population (nearly 300 specimens) from a single bed low in UD II-G at Hassi Nebech (southern Tafilalet, Anti-Atlas) has been used for morphometric investigation. Apart from usual shell parameters (whorl height and width, apertural height), the number and extent of mould constrictions per whorl and the relative proportions between the two adventitious lobes have been measured. There is moderate variation in whorl expansion rates but larger variation can be seen in whorl width. A number of specimens reach values as in the lectotype of *M. rotundum* (Wedekind) but there is only a slight separation of thicker and more compressed specimens.

The analyses of mould constrictions confirms the former idea that these follow growth stages with distinctive patterns. From 10 to 50 mm diameter, the number of constrictions increases constantly from between 2 and 3 to between 5 and 8 per whorl. In early stages, constrictions are complete but they gradually terminate on the lower or outer flanks in subsequent whorls. From ca. 60 mm diameter, constrictions are reduced drastically which suggests that protection against shell-breaking predators became irrelevant at late maturity. Clearly, taxa based on the number and course of constriction only, cannot be regarded as valid.

Previous studies showed that the second A-lobe became deeper during phylogeny, culminating in species such as *M. milleri* and *M. acutolaterale* where the rounded A<sub>2</sub> is as deep or deeper than A<sub>1</sub>. The investigated assemblage shows no relationship between size and depth of A<sub>2</sub> which suggests that forms with various degrees of septal folding were present contemporaneously. A histogram displays a small group with extremely shallow A<sub>2</sub> sensu *M. nuntio*, a majority group with A<sub>2</sub>/A<sub>1</sub> ratio between 16 and 28 % as in *M. subvaricatum*, and a slightly separated second peak between 32 and 40 % (trend towards *M. latilobatum*). The population studied gives no clear distinction of biological species; continuing morphological separation in successive faunas yet has to be shown. However, the subsequent introduction of additional morphological features such as spiral ornament only in the main group with A<sub>1</sub> < 30 % A<sub>2</sub> leaves the possibility that the single bed studied documents an episode of maeneceratid speciation in progress.

## THE ORIGIN AND EVOLUTION OF THE FAMILY DESHAYESITIDAE STOYANOW, 1949

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The family *Deshayesitidae* represents the important stage of the Early Cretaceous ammonite evolution. The subdivision of the Lower Aptian deposits practically in all the continents of the Earth is based on interrelations within some genera and species associations of this family. Morphology of the shell and evolution of suture of the European, Caucasian and Turkmenian deshayesitids have been revised. As a result, we propose the new concept of some generic taxa of the Deshayesitidae. *Deshayesites* Kasansky, 1914 - rather compressed, with flat or slightly convex flanks, subtriangular sections with a broad arched venter, strong ribs, sigmoidal primaries and branching or intercalated secondaries (1 or 2). No distinct tubercles. Suture formula -  $VU11^2:I^1D$ ; lobes I,  $I^2$  - on the flanks. Type-species: *Ammonites deshayesi* (Leymerie in d'Orbigny, 1842), Lower Aptian, France (Paris Basin). It includes about 40 species. *Paradeshayesites* Kemper, 1967 - different size of shell, very involute, whorls high, triangulate with flat flanks and arched venter; ribs dense, fine with bullates in the base and bundles, primaries bifurcate and trifurcate, secondaries 4 to 7-9. Suture formula -  $VU11^2 I^3 :I^1 D$ , lobes I,  $I^2$  - on the flanks. Type-species: *Hoplites laeviusculus* (von Koenen, 1902), Lower Aptian, tenuicostatus Zone, North-West Germany. It includes about 20 species. *Obsoleticeras* Bogdanova & I.Mikhailova, gen. nov. - high, quickly rising whorls with oval sections, early whorls with rare ribs, later with loosening of sculpture. Suture formula with broad shallow elements, lobes I,  $I^2$  - on the flanks. Type-species: *Prodeshayesites obsoletus* Casey, 1964, Lower Aptian, fissicostatus Zone, obsoletus Subzone, England (Surrey). It includes 5 species.

On the whole, the Deshayesitidae consists of the genera: *Turkmeniceras* Tovbina, 1962, *Deshayesites* Kasansky, 1914, *Paradeshayesites* Kemper, 1967, *Obsoleticeras* gen. nov., *Dufrenoyia* (Burckhardt Ms) Kilian & Reboul, 1915, *Burckhardtites* Humphrey, 1949 and probably, *Neodeshayesites* Casey, 1964 and *Kuntziella* Collignon, 1962. The type of suture-development of the last two genera is still unknown.

The Deshayesitidae derived from the Heteroceratidae. The Deshayesitidae has unsteady quinque-lobate primasuture -  $VUU^1 ID$ . To the end of the first whorl lobe  $U^1$  disappeared and the suture formula is  $VUID$ . It is the same as in the adult Heteroceratidae. Then the fifth lobe arose on the second whorl, but it is the new lobe  $I^1$  in the saddle  $I/D$ . In the evolution of the Deshayesitidae the umbilical part of the shell began to stretch out with involution of whorls and the umbilical part of suture began to incise:  $VUU^1 ID - VUID - VUI:I^1 D - VU11^2 :I^1 D - VU11^2 I^3 :I^1 D$ .

## **YOLK SAC MORPHOLOGIES IN CEPHALOPOD EMBRYOS**

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The basic pattern of embryogenesis is rather uniform throughout the class Cephalopoda. Depending on the specific ovum size, which may vary from less than 1 mm to about 30 mm, the organ-forming part (called the "embryo cap", or the "embryo proper") of the epibolic gastrula covers a larger (in small eggs) or smaller part (in large eggs) of the animal hemisphere of the uncleaved yolk mass. The rest of the gastrula forms an envelope for the yolk that remains outside the embryo cap and becomes the so-called outer yolk sac.

The overall shape of the yolk mass at early embryonic stages varies among systematic groups of cephalopods, from nearly globular to elongate/oval, to a certain degree also as a function of egg size. At advanced stages of organogenesis, the outer yolk sac becomes increasingly distinct due to a constriction of the brachial and cephalic zone of the embryo proper; an exception are some teuthoid squids (especially the Ommastrephidae), in which the outer yolk sac remains rudimentary. Starting out from a roughly globular form, the outer yolk sac may subsequently take on a different shape in the embryos of certain taxa.

The portion of the yolk mass lying inside the embryo proper is called the inner yolk sac and yolk neck (the latter connects the inner with the outer yolk sac). Whereas the yolk neck is a simple strand, which is more or less strongly compressed by the organs of the head, the inner yolk sac takes on a shape that is only partly due to simple "moulding" by the surrounding organs. There seems to be a shift of partial pressure between the outer and the inner yolk sac at late embryonic stages, and the final shape of the inner yolk sac is also influenced by the morphogenetic processes shaping the whole visceral complex of the embryo. More or less distinctive morphologies of the inner yolk sac can be recognized; for example, a peculiar "four finger" pattern appears in sepiolid embryos.

In a strictly functional perspective, the various yolk sac morphologies can be viewed as different modes of yolk storage during the developmental phase that leads to hatching. In most cephalopods, the newly hatched young can survive some time without food (from a few days to several weeks, depending on the juvenile physiology and ecology). Under normal conditions, the embryonic nutrient remaining in the inner yolk sac of the hatchling is resorbed independently from the onset of digestive processes that are induced by capture and ingestion of prey. This coexistence of lecithotrophy and active feeding is due to the morphological and physiological separation of the embryonic and post-embryonic alimentary organs; the actual duration of this concomitancy is partly conditioned by the volume of the yolk reserve, which in turn depends largely on the yolk storage capacity of the visceral mass.

This paper views evolutionary variation in developmental morphology of cephalopod "yolk organs" against the background of some pervasive functional constraints in yolk absorption.

## DWARF CEPHALOPODS: CONDITIONS OF REPRODUCTION AT SMALL SIZE

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The oldest fossils supposed to represent a cephalopod (*Plectronoceras* of the Upper Cambrian) are chambered shells measuring 15-20 mm in length. Thus the body size was in the same range as the adult size of the smallest living cephalopods, *Idiosepius pygmaeus*. Only slightly larger are some dwarf sepiids (e. g. *Sepia pulchra*, *Metasepia* spp.), the smallest sepiolids (*Sepiolo* spp.), some loliginid squids (*Pickfordiateuthis* spp.) and members of several pelagic squid families, some octopods (e. g. *Octopus micropyrsus* among the bottom-living forms; dwarf males in the pelagic *Argonauta*, *Tremoctopus*, *Ocythoe*).

A common biological feature of very small cephalopod species is a life-span of less than one year, with a minimum of about 3 months in *Idiosepius*. (The life span of dwarf males in pelagic octopods is unknown). The small adult size of the females, along with their short life-span, limits individual fecundity. The adaptive responses to this limitation vary widely among species or groups; the most striking difference appears in the respective egg sizes. In *Idiosepius pygmaeus*, the ovum measures about 1 mm in diameter, whereas in *Octopus micropyrsus*, it measures 8-10 mm in length, 4-5 mm in width. In both cases, however, maturation and release of eggs is prolonged; i. e. this terminal reproduction tends to multiple spawning.

During embryonic development, a very large part of the yolk mass stored in the ovum is used for the production of embryonic cell complexes and for the subsequent formation of functional organs. But some yolk remains in the so-called inner yolk sac; its volume is a function of (1) the speed of yolk absorption during late embryonic stages, and (2) the point of time when hatching actually occurs. The only species in which the young hatch without a yolk reserve are medium-sized octopods producing very large eggs (*Octopus maya*, *Eledone moschata*). Hatchlings of *E. moschata* can survive for 2 to 3 weeks without food, i. e. the early juvenile metabolism can function according to the adult "emergency program" (using muscular proteins as an energy source). This is an exceptional capacity for an early juvenile metabolism.

Adult size may be attained rapidly when hatchlings are relatively large due to strong embryonic growth based on a large amount of yolk in the egg (e. g. *Octopus micropyrsus*). However, *Idiosepius* shows that even small eggs giving rise to small hatchlings permit rapid growth to adult size, within a very short life-span.

A comparative analysis of all cephalopod embryos large and small suggests one generalization: embryogenetic mode and juvenile design require a minimal ovum size above 0.5 mm. This generalization is essential for any hypothesis on the likely reproductive mode of the earliest cephalopods, which were dwarfs.

The focus of this paper is on biological aspects of size limitations in the evolution of cephalopods, with special emphasis on the secondary size reductions that must have occurred, and on their functional limits.

# **PARALLEL BIOZONATION IN THE UPPER CALLOVIAN AND THE LOWER OXFORDIAN BASED ON THE PELTOCERATINAE SUB-FAMILY (AMMONITINA, ASPIDOCERATIDAE)**

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## **Biozonation in the Upper Callovian and in the Lower Oxfordian**

Ammonite biozonation in the Upper Callovian is based on two standard scales: (1) in the Sub-Boreal province two sub-families of Boreal origin are utilised (Kosmocerotinae and Cardiocerotinae); (2) in the Sub-Mediterranean province the scale is mixed, with some index fossils of Tethyan origin (Reineckeinae, Pseudoperisphinctinae or Peltocerotinae) while others are of Boreal origin (Cardiocerotinae). In the Lower Oxfordian, zonation for the Sub-Boreal province is reliant, barring exceptions, on the Cardiocerotinae. As these may be rare or absent in the Mediterranean province, it is essential to have a scale based exclusively on taxa of Tethyan origin. The first subdivisions based either on the Perisphinctidae or on the Taramelliceratinae are incomplete.

## **Interest of the Peltocerotinae subfamily**

Revision of the Aspidoceratidae family (Bonnot 1995, Courville & Bonnot 1998) shows that the Peltocerotinae allow a more complete subdivision. This sub-family occurs in the Sub-Mediterranean province right at the base of the Upper Callovian and remains comparatively abundant through to the top of the Lower Oxfordian. The Peltocerotinae are well defined by their ontogenesis and sexual dimorphism. Three characters constitute reliable criteria for identification: (1) the medium position of the rib bifurcation point on the sides (macroconchs and microconchs), (2) presence or absence of an intermediate ornamental stage between costulate and tuberculate stages (macroconchs), and (3) the morphology of the latero-ventral tubercles (macroconchs). These characters have made it possible to define or redefine twelve palaeospecies, with macroconch and microconch, divided into two genera (Peltoceras and Peltocerotoides).

## **Conclusion**

Their relative abundance, their wide geographical distribution and their rapid evolution mean that some species of Peltocerotinae can be used as index fossils for a biochronological scale at the resolution of the sub-zone or even the horizon. We propose a scale based on Peltocerotinae alone in the Upper Callovian and the Lower Oxfordian. This scale is particularly useful when index fossils of Boreal origin are rare or absent.

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## **CEPHALOPOD ACCUMULATIONS LINKED TO CONDENSATION EPISODES IN THE JURASSIC OF THE SUBBETIC (SOUTHERN SPAIN) AND IN THE SILURIAN OF THE CARNIC ALPS (AUSTRIA)**

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Cephalopod accumulations of the Subbetic Jurassic are linked to three main episodes of reduced net sedimentation : (1) Pliensbachian, (2) Lower-Middle Jurassic and (3) Middle-Upper Jurassic. Lower and/or upper surfaces of cephalopod beds usually coincide with stratigraphic discontinuities. These beds are discontinuous and of variable thickness, which indicates that the sea bottom was irregular at that time. Except for the Middle-Upper Jurassic discontinuity, a varied invertebrate fauna (bryozoa, brachiopods, gastropods, crinoids, serpulids, corals) occurs together with cephalopod remains. A typical feature is the presence of limonitic crusts which may appear either encrusting the discontinuity surface or coating the remains of cephalopods. In this last case, encrusters (mainly serpulids) can be found within the laminae.

A study of the particular preservation of the nautiloid cephalopod fauna within the condensed Lower Silurian sequences from the Cellon and Rauchkofel Boden sections in the Carnic Alps has highlighted interesting similarities with cephalopod preservation in Jurassic sequences in Spain. The beds are separated by thin laminated iron-rich layers or 'crusts' within which the nautiloids are sometimes apparently preserved. Iron-rich coatings and infillings of the fauna are common in certain levels. Concentrations of juvenile and equidimensional articulate brachiopods, nautiloids and small gastropods alternating with the nautiloid beds occur from about mid-way to the top of the sequence. Levels of trace fossils (*Thalassinoides-chondrites*) are also seen. Several gaps in sedimentation have been noted in recent studies on the sections which may reflect eustatic sea -level changes in an overall shallow water environment.

Cephalopods are the most conspicuous elements of the association and provide essential clues about taphonomic processes (reworking, dissolution, encrustation). Within each bed, cephalopods typically exhibit different taphonomic signatures, which allow differences to be inferred in the number of reworking events, from 3-4 to none (judging also from the polarity of geopetal infillings of the chambers). The depositional environment was relatively high energy and this caused fossil remains to be exhumed, transported and, to a minor extent, fragmented. Burial at shallow depths (centimetres) within the sediment caused dissolution and, probably, coating of the fossil remains with limonitic laminae. Some fossils were affected by several of such cycles. Fossils, whether they were coated or not, were finally trapped in small depressions developed in the former topography ; the levelling process culminated when normal pelagic sedimentation was restored. Further diagenetic processes of stylolitic dissolution modified the original appearance of the discontinuities and, probably, originated characteristic stratiform ferruginous crusts.

# REGULATION OF COILING IN PLANISPIRAL AMMONITES, INFERRED FROM CASES OF INFESTATION IN VIVO BY EPIZOANS

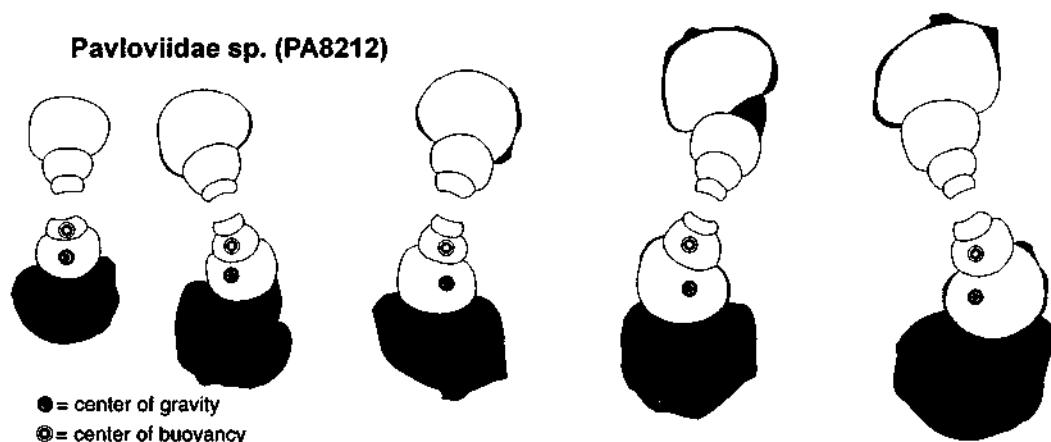
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In morphology, abnormalities can be considered as natural experiments which may aid in unravelling morphogenetic processes. This is of special interest in fossils, in which experimentation is not possible. Rare instances of planispiral Jurassic ammonites which were infested by epizoans during life show abnormalities in their coiling pattern, which may decipher the rules followed by ammonites during coiling.

When epizoans settled near or at the venter of the ammonite, the subsequently grown whorl partially went over and surrounded the epizoan in following the shortest path. The whorl then deviated from the previous symmetry plane and this caused the centres of gravity and, to a lesser extent, of buoyancy, to deviate accordingly. The ammonite now floated with the regularly coiled part of the shell inclined opposite to the deviated whorl (scheme, centre left). Since the animal kept the aperture forming a permanent angle with the vertical, during later growth the whorl crossed the venter of the previous whorl and passed on the other side periodically when trying to coil in a new plane (scheme, centre to right views). The scheme shows successive



sections at 90° of an ammonite before (left) and after infestation on its left side. Epizoans which were placed ventrally caused the subsequently grown whorl to detach from and re-attach to the previous whorl. The reconstruction of apertural orientations (taking ribs as old apertures) during all this process indicates that this parameter remained constant and is consistent with a free-floating life style. Two ammonites coiled trochospirally due to epizoans which settled on one side and which caused the shell to be permanently inclined. In order to keep the apertural orientation constant, the whorl remained displaced permanently towards the side opposite to the epizoan. This caused a slight trochospiral coiling.

In summary, planispiral ammonites needed two basic inputs to regulate their coiling geometry: (1) a constant apertural orientation during growth and (2) a permanent attachment to the previous whorl. Therefore, they were mainly based on equilibrium buoyancy.

## **PALAEOBIOGEOGRAPHY AND MIGRATION IN THE LATE CRETACEOUS BELEMNITE FAMILY BELEMNITELLIDAE**

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During the Cenomanian, the lowermost stage of the Upper Cretaceous, belemnites had a tripartite distribution. The family Belemnitellidae Pavlow inhabited the North Temperate Realm, the family Dimitobelidae Whiteaves inhabited the South Temperate Realm, and the family Belemnopseidae Naef inhabited the Tethyan Realm. The latter family became extinct in the Middle Cenomanian, and, consequently, belemnites had a bipolar distribution during the remaining part of the Late Cretaceous.

The belemnitellids, which include nine genera and two subgenera, appeared in the Lower Cenomanian, some way above the base of the substage, and became extinct at the Maastrichtian-Danian boundary. The dimitobelids appeared in the Aptian and disappeared in the lower Maastrichtian.

The belemnitellids were distributed in the North American (NAP) and North European (NEP) palaeobiogeographical Provinces of the North Temperate Realm, in addition to the northern margin of the Tethyan Realm in Europe. The NEP includes the Central European, Central Russian and Baltoscandian Subprovinces. The centre of evolution and dispersal lay in the NEP, which extends from Northern Ireland in the west to the Ural Mountains and beyond in the east.

The belemnitellids invaded the Tethyan Realm at least nine times, first in the Upper Cenomanian and later from the Upper Santonian to the Upper Maastrichtian. Species of five genera and two subgenera occur in this realm, and the majority of these are conspecific with those from the NEP. The belemnitellids immigrated at least six times into the NAP, first in the Middle Turonian and later from the Coniacian to the Upper Maastrichtian. Species of essentially two genera occur in the NAP, and these are endemic, with a few exceptions. More than a score migrations have been recognized within the subprovinces of the NEP.

The palaeobiogeographical distribution and migration patterns of the belemnitellids were to a certain extent controlled by eustatic sea-level changes, cool or warm climatic phases and competition, but the cause of several migration events cannot be satisfactorily explained at present.

A few examples are mentioned below. The genus *Praeactinocamax* invaded NV Europe twice during the Cenomanian coincidently with rapid rises of sea-level and cool climatic phases: *P. primus* in the Middle Cenomanian and *P. plenus* in the Upper Cenomanian. The latter even invaded the Tethyan Realm. In the Turonian, the belemnitellids retreated northwards in Europe, and entered, via a northern route, the NAP for the first time, probably due to a warming peak in the lowermost Turonian. The parallel evolution of the *Gonioteuthis* stock in the Central European Subprovince and the *Goniocamax-Belemnitella* stock in the Central Russian Subprovince during the Middle Coniacian to Early Campanian, a period of about 6-7 million years, was probably due to mutual competition.

## PHYLOGENY AND TAXONOMY OF THE BOREAL ANISIAN FAMILY CZEKANOWSKITIDAE

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The entire history of the Czekanowskitidae from its first appearance up to the extinction took place in the East Boreal region. Most probably the early Anisian genus *Groenlandites* (Grambergiidae) is the ancestor of the family. The first highly variable Czekanowskitid *Praeczekanowskites tumaefactus* appeared in a hypermorphic way by changing the shape of the last whorl from suboxyconic with a sharp venter to platyconic having usually a rounded venter. The genus *Praeczekanowskites* was the ancestor of two different genera. The middle ontogenetic stages of *P. planus* are comparable with the phenotype of the thin, involute, feebly ornamented genus *Timites* originated from the planus - group in a pedomorphic way. *P. tumaefactus* shows all characteristic features of the oldest *Czekanowskites* (*Cz. rieberi*), but the latter species differs by the appearance of a flattened venter with distinct ventral shoulders (hypermorphosis) on the terminal ontogenetic stages.

*Czekanowskites* s.s. unites very variable species with conch shapes from thin involute suboxycones to wide semievolute subcadicones. The next step in this phylogenetic line is the genus *Arctohungarites* s.s..

Contrary to *Czekanowskites* this genus has an invariable conch, usually thin involute platycones, ornamented only on the terminal part of the body chamber. The youngest species of *Arctohungarites* (*A. kharaulakhensis*, *A. trapezoidalis* etc.) differ from *Arctohungarites* s.s. by an essentially more evolute adult conch. For this group the new name *Boreiohungarites* is proposed.

From *Boreiohungarites* evolved the genus *Stannakhites* having a variable shape of shell, differing from *Czekanowskites* by the presence of a wide umbilicus in all modifications of the shell. The genus *Epiczekanowskites* usually is interpreted as a synonym of *Czekanowskites*, but it is separated from the last *Czekanowskites* by a distinct stratigraphic hiatus (3 zones). More probably *Epiczekanowskites* is descendant from *Arctohungarites* and originated as a result of deviation, i.e. morphological changes (appearance of rough ornamentation) on the middle ontogenetic stages. As a result of the family's taxonomic revision a new detailed biostratigraphic scheme of the Uppermost Lower Anisian and Middle Anisian, including 14 discrete biostratons, is proposed.

# SCAVENGING OR PREDATION: MISSISSIPPIAN GONIATITE ACCUMULATIONS IN CARBONATE CONCRETION HALOS AROUND *RAYONNOCERAS* (ACTINOCERIDA) BODY CHAMBERS FROM ARKANSAS

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Zangerl et al. (1968) and Quinn (1977) described from the Mississippian (Fayetteville Formation – Chesterian) of Northern Arkansas the occurrence of large numbers of goniatites in carbonate concretion halos surrounding collapsed body chambers of the actinocerid nautiloid *Rayonnoceras*. Both Zangerl et al. and Quinn speculated these accumulations are the stomach contents of the *Rayonnoceras*. An alternate accumulation hypothesis is that the goniatites died while scavenging because of the lack of oxygen and/or the concentration of poisonous gasses produced by bacterial decomposition of the *Rayonnoceras* carcass. To test which hypothesis is more correct; five concretion halos were cut into 2 to 4 cm thick slabs. All reasonably complete goniatite specimens (n = 743) on the slabs were measured for their maximum apparent diameter with the presence or absence of the body chamber and the angular relationship of the conch to the bedding being noted. Crushed ammonoids on the concretion surface which could have been introduced at a later time were eliminated from the data. The data were then compared to carbonate concretions containing numerous ammonoids from the Triassic of Canada and the Middle Carboniferous of England and Ireland.

The *Rayonnoceras* halo concretions have a great variation in the apparent diameters of the goniatites (min. 1.0 mm to a max. of 34.0 mm) with the mean average apparent diameter being 11.3 mm. Almost all the specimens are missing part or all of their body chambers, and ammonitella are almost completely absent. Overall, the cephalopod diversity is low. Most of the goniatites are randomly oriented to the bedding. In the comparative concretions, the ammonoids are mostly aligned parallel to the bedding, have low to high diversity, and most ammonoids retain most of their body chambers with the goniatite apparent diameter distribution conforming to reasonable survivorship curves.

Based on the number of specimens with missing body chambers, the significant deviation from a reasonable survivorship curve, the limited diversity, and the random conch orientation to bedding, we conclude that the goniatites around the body chambers are the last meal of the *Rayonnoceras*. Thus, these goniatite accumulations represent the only known occurrence where there is evidence that nautiloids have preyed on ammonoids.

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## PITS IN INTERNAL MOLDS OF CEPHALOPODS

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House, in 1960, described a number of Devonian ammonoids from the Emsian, Eifelian, and Givetian of the United Kingdom, North Africa, and Germany that have more-or-less regularly arranged pits in the internal molds. In 1983, Chlupáč and Turek reported similar pits also in Devonian anarcestines, but from what then was called Czechoslovakia. We have observed comparable pits in some ammonoids and in a bactritoid from the Devonian of Morocco. In addition, we have observed pits in a bactritoid and in some goniatites from the Carboniferous. House concluded that the pits are the result of pearl-like mounds that formed on the interior surface of the body-chamber of the ammonoid in life. He attributed the pearl-like mounds to pathologic responses to foreign particles that entered between the body of the cephalopod and the conch and that the particles apparently were restricted in their adapical movement by an unknown soft-part structure, which also resulted in the configuration of the mounds (and, hence, of the pits). The individual pits in the Devonian ammonoids are somewhat similar to those in the internal molds of Toarcian (Early Jurassic) ammonoids of Germany attributed to pearl formation by Keupp (1986).

Other pits in internal molds of ammonoid cephalopods have been reported. Some of these seem to be normal features of the taxa involved (for example, the lateral pits in *Agathiceras suessi* from the Permian, those in *Dunbarites rectilateralis* from the Carboniferous, and those in adolescent individuals of the Permian genus *Popanoceras*). Davis (1972) described and figured small pits that occur in the internal molds of some mature representatives of the Permian genera *Adrianites*, *Texoceras*, and *Waagenoceras*.

As House and Chlupáč & Turek clearly recognized, not all pits in the internal molds of cephalopods are the same. Interpretational evidence includes: the number, size, shape, and arrangement of the pits; the distribution of the pits with respect to one another and to the peristome, sutures, growth-lines, umbilicus, venter, plane of symmetry, and other features of the conch; the relationship of the pits to the ontogeny of the cephalopod; the presence and frequency of occurrence both within and among cephalopod taxa; the configuration of each pit with respect to the adjacent portions of the internal mold and to the overlying shell-wall, if preserved; and geologic and stratigraphic occurrence.

On the basis of analysis of a collection of some 20,000 hematite and calcite internal-molds of Lower through Upper Devonian cephalopods (mostly ammonoids) from Morocco, we conclude that biological pitting in internal molds is relatively uncommon in all units, with less than one percent of the specimens showing these features. However, some units in the Devonian of Morocco have yielded significantly more specimens with such pitting than have others. We agree with House that the pits were formed by pearl-like mounds on the inner surface of the conch. However, we conclude that some of these mounds are the product of parasite infestations and subsequent irritation of the mantle of the cephalopod during life. Different parasites seem to have produced different sizes, shapes, and arrangements of mound-structures, which vary among taxa of cephalopods and among specimens within a given taxon.

## **EARLY SHELL ONTOGENY IN BACTRITIDS AND ALLIED TAXA : COMPARATIVE MORPHOLOGY, SHELL WALL ULTRASTRUCTURE, AND PHYLOGENETIC IMPLICATION**

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Early ontogeny appears to be important for phylogeny, but in many groups of fossil cephalopods the initial part of the shell is not known. This paper is based on SEM studies of exceptionally well preserved juvenile shells of bactritoids, orthoceroids and ammonoids from the Upper Carboniferous-Lower Permian of the Southern Ural Mountains. In addition, the shell wall ultrastructure of initial portions of the shell of different taxa of Mesozoic ammonoids and coleoids was examined and compared with that in bactritoids.

Bactritoids are characterised by a marginal siphuncle. However, they initially have a submarginal siphuncle that migrates to the ventral position in the first 2 or 3 chambers. The protoconch is globular or egg-shaped with a boss-like primordial dome on the apex, often marked by a ring of modified ornament. There is no cicatrix on the apex of the protoconch. The shell wall is prismatic. The nacreous layer first appears immediately before the primary constriction near the fourth or fifth septum and soon becomes the dominant layer with a subordinate outer prismatic layer. There is no primary varix. The ornament of the initial portion of the shell, if it is present, disappears immediately before the primary constriction. The constriction, with the appearance of the nacreous layer and disappearance of ornament, is thought to represent the end of the embryonic shell, as in the ammonoids (Doguzhaeva, 1996a-c).

In orthocerids, with central siphuncle, the protoconch is cup-shaped and shows a cicatrix. A nacreous layer appears in the shell wall a short distance from the apex. The primary varix is absent. The cicatrix is known to be present in *Nautilus* (Arnold, 1988), orthocerids (Ristedt, 1971; Blind, 1988) and actinocerids (Ristedt, 1971; Doguzhaeva & al., 1996, 1998).

In respect of early shell ontogeny the bactritoids, ammonoids, belemnoids and spirulids stand apart from orthocerids, actinocerids and nautilids. The features which separate them are : 1) a protoconch that is larger than the next chamber, usually separated from the phragmocone, lacking a cicatrix and a nacreous layer (the first branch); on the contrary the protoconch is cap-shaped, sometimes smaller than the next chamber and possesses a cicatrix, nacreous layer appears at very early ontogenetic stage near the apex (the second group).

The bactritoids are distinguishable from ammonoids by lack of a primary varix and an interruption in the shell wall near the primary constriction; prominent features of all ammonoid groups. The bactritoids are thus considered as a separate taxon of the same rank as the ammonoids. However the data do not disprove the origin of ammonoids from the bactritoids but rather confirm it. The latter is also true for the phylogenetic relationship of the bactritoids and coleoids. In respect of shell wall ultrastructure there are no obstacle to believing that the bactritoids were the ancestors of the coleoids.

## ROSTRUM AND PHRAGMOCONE STRUCTURES IN THE LOWER CARBONIFEROUS COLEOID *HEMATITES* AND ITS TAXONOMIC ASSIGNMENT

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Flower and Gordon (1959) and Gordon (1965) considered *Hematites* as a belemnite. Jeletzky (1966, p.20) following the conclusions of Abel (1916) erected the new Order Aulacocerida and assigned *Hematites* to the order. However, he did not formally include this taxon in his classification. Flower and Gordon noted that the apical portions of the phragmocone had been removed prior to rostrum formation.

The conotheca lacks ventral or dorsal crests, growth lines and traces of proostracum, which Jeletzky considered important ordinal characteristics of the Aulacocerida. In *Hematites* the conotheca has been somewhat altered and it is unlike the conotheca in belemnites. There seems to be six layers from inside to outside: 1) A thin lamellar layer, 2) A thick columnar nacreous-like layer, 3) A thin nacreous? layer, 4) A thin layer with an outer spherulitic surface, 5) A thin layer with inclined lamellae, and 6) A thin layer with an inner spherulitic surface. Two specimens show that the body chamber was short equal to about 1.5 chambers in length. The ridged rostrum has the following significant morphological features: (1) Each ridge crest is covered by a row of filled pits separated by partitions. The pit-channels can be traced through the entire rostrum thickness. The narrow interspaces between the ridges extend to the conotheca. In some respects these ridge and pit structures are comparable to those on the external proostracum surface of the belemnite *Megateuthis* (see Doguzhaeva et al., herein), and that these surfaces served as the mantle attachment area. Thus, the mantle on *Hematites* was probably attached to the entire rostrum, whereas the rostrum in belemnites did not serve as an attachment function, 2) In all but one *Hematites* specimen the early phragmocone is missing, and the broken end is plugged with the central rod structure which is composed of parallel longitudinal carbonate rods that begins at the broken apical end of the phragmocone and continues to the apical end of the rostrum. This structure is exposed in the depression at the apical end of larger rostra, and everywhere else, it is covered by the radial rostral structure, 3) The thin, terminal edge of the rostrum on the conotheca forms a sinuous contact that includes a pronounced broadly U-shaped ventral sinus, and there is a suggestion of broad lappets in the lateral position. The ventral edge of the rostrum of one specimen extends farther orad than the dorsal edge.

Thus, *Hematites* differs from all other younger rostrum-bearing coleoids assigned by Jeletzky to the Aulacocerida by having a relatively short body chamber, a conotheca with a unique shell construction that is without growth lines and dorsal and ventral crests. The well-developed rostrum also has a number of unique structural features. Given these unique features, we are uncertain if the diagnosis of Jeletzky for the order Aulacocerida should be emended to accommodate *Hematites*, or if an entirely new order should be established to accommodate this primitive coleoid.

## STRUCTURE OF THE PRO-OSTRACUM AND MUSCULAR MANTLE IN BELEMNITES

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The pro-ostracum of belemnites has been explained as a remnant of the dorsal wall of the body chamber of the ectocochlean ancestors (Naef, 1922; Jeletzky, 1966). A different view, mentioned by Naef (1922) as less probable, considered the pro-ostracum as a new structure unrepresented in the ancestors. On our view the pro-ostracum of belemnites represents a remnant of the ridged rostrum of the aulacocerid ancestors. The belemnite rostrum would therefore have appeared as a new structure as Jeletzky (1966) believed. Fossilized muscular mantle showing crisscross pattern of the tunic of collagen fibres was previously described in *Belemnotheutis* (Kear & al. 1992), which is in some respects is anormal belemnite.

This paper investigates the pro-ostracum and the conotheca with the SEM in *Megateuthis* (M. Jurassic) and *Mesohibolites* (L. Cretaceous). We can show from imprints on the conotheca of *Megateuthis* the presence of typical coleoid mantle including the tunic with intersecting collagen fibres. This is the first record from typical belemnites of muscular mantle structure as known from living coleoids. Remains of the mantle are recorded in *Passaloteuthis* (L. Jurassic) as well.

In *Megateuthis* the pro-ostracum occupies about half the circumference of the shell at the anterior end of the phragmocone (Naef, 1922, Fig.73). A broad median field is flanked by narrow hyperbolar zones. The median field shows forwardly convex growth lines. It has a weak median ridge and one or more lateral ridges on each side. The hyperbolar zones bear flattened longitudinal ridges which converge forwards and are separated by narrow grooves. These carry regularly-spaced transverse pits forming a pattern comparable to that on the rostrum of *Hematites* (see Doguzhaeva et al., herein). The inner surface shows a feather-like pattern unrelated to that seen on the dorsal surface. A narrow central area is bounded by weak ridges. Areas lateral to the "feather" structure show a longitudinal pattern with subsidiary transverse elements. It looks similar to *Cylindroteuthis* (Naef, 1922, Fig. 87). The muscular mantle was attached to the sides of the pro-ostracum. Between the intersecting collagen fibres there are numerous irregular pits and traces of thin fibrous structure. In longitudinal shell section the pro-ostracum is represented by a distinct rather thin layer between the nacreous layer of the conotheca and the rostrum. This layer is irregularly mineralized, with a high organic content. Besides the nacreous layer the conotheca includes an inner spongy prismatic layer.

The outer surface of the pro-ostracum in *Mesohibolites* is similar to that of *Megateuthis*; it shows a broad median field with convex growth lines and narrower hyperbolar zones with longitudinal ribs. In section the layer which seems to represent the pro-ostracum is situated between the nacreous layer and rostrum.

## MORPHOMETRIC ANALYSES OF PARATORNOCERATIDS (GONIATITIDA) FROM THE EARLY FAMENNIAN OF SOUTHERN MOROCCO

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Large collections of ammonoids from single beds can be used for detailed morphometric analyses. They give insights into intraspecific variabilities within or between assemblages, allow the distinction of closely related taxa, or enable the recognition of chronomorphoclines in evolution. Statistical results affect taxonomy, stratigraphy, autecological interpretation, and the question of migrational events versus phyletic gradualism.

Two systematically excavated populations from the basal *Maeneceras* Zone (Upper Devonian II-G) of Dar Kaoua (Tafilalt) have been investigated to clarify the intraspecific variability in oxyconic members of the Dimeroceratidae (paratornoceratids s.l.). Measurements of more than 270 specimens showed that the successive faunas belong to two distinct species of *Acrieroceras*, each with narrow but partly identical fields of variation of shell parameters such as whorl height, apertural height, whorl and umbilical width. In both taxa, the relative whorl width decreases constantly with size but *Acri. n.sp.* from Bed H is significantly more compressed and on average larger than *Acri. falciculatum* Becker of Bed J. Juveniles can be distinguished by narrower umbilici and the lack of ribbing in the latter. The new species is close to forms previously identified as compressed morphotypes of *Paratornoceras lentiforme* but shows weakly developed shell thickenings which may form star-like mould constrictions around the umbilicus. Biphase allometric growths is expressed in both species up to ca. 10 mm diameter by a rapid ontogenetic change from three early evolute, depressed whorls to mature compressed, oxyconic stages.

The restricted shell variability suggests a strict selection on conch growth as can be expected from active swimmers. The razor-sharp acute venters gave good streamlining, whilst the irregular shell thickenings indicate that regular contact with shell-breaking predators still occurred, perhaps during regular descents to the seafloor. The morphological change from longidomic ancestral *Praemeroeras* with convex growth lines to mesodomic paratornoceratids with secondary small ocular sinus probably reflects an evolutionary transition from suprabenthonic (demersal) to fully pelagic lifestyle at maturity. This radiation took place after the sudden extinction of thinly oxyconic tornoceratids. It can be argued that both homoemorphic groups occupied the same principal ecological niche which had become vacant after the Upper Condros Event.

The size distribution of the two population indicates that both species lived permanently in the region of the Tafilalt Platform. There is no evidence of dimorphism. Shell growth did not stop with a maximum size after reaching maturity (at 15-25 and 20-40 mm diameter) but continued throughout life. This explains a minority of very large individuals with identical whorl expansion which measure up to more than twice the size as the majority of specimens. Since the more advanced *Acri. n. sp.* is the older of the two species, both probably represent immigrants that dominated the southern Moroccan shelf occasionally and alternatively after the somewhat earlier main phase of paratornoceratid evolution (*Paratornoceras* Zone, UD II-F).

## PHYLOGENY OF THE "POST-TRIASSIC" NAUTILOIDS

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The „Post-Triassic“ nautiloids (mostly systematized as suborder Nautilina) form a well-known systematic unit within the Nautiloidea which ranges from the beginning of the Jurassic to Recent. Triassic representatives of *Cenoceras* lack the characters outlined below and are therefore excluded from the suborder Nautilina. However, the monophyly of suborder Nautilina has still to be demonstrated. Within a phylogenetic analysis that uses data from about half of the described genera two subunits of the „Post-Triassic“ nautiloids are recognizable which can be demonstrated to be monophyletic; the family or superfamily Nautilidae/oidea Rafinesque-Schmalz, 1815 (incl. Cenoceratidae, Cymatoceratidae pars (?), Heminautilidae, Paracenoceratidae, Pseudaganididae, Pseudonautilidae) and the Aturiidae/oidea Chapman, 1857 (incl. Eutrephoceratidae, Hercoglossidae).

The family/superfamily Nautilidae/oidea is characterized by comparatively large embryonic conchs (minimum 1.5 cm in diameter in small species), 5 septa, and slightly curved embryonic conch which usually leaves a large „umbilical“ gap.

The family/superfamily Aturiidae/Aturioidea has small embryonic conchs (max. 1.0 cm in diameter), tightly coiled embryonic conchs leaving only a very small „umbilical“ gap.

A character that is unique within these two groups compared with other „Pre-Jurassic“ nautiloids and that is shared only by these two units has not yet been found. It might be that these two lineages independently crossed the Triassic/Jurassic.

Plesiomorphic characters that are presumably present in both groups are: an extremely yolk-rich development compared with the Neocephalopoda (Sphaerorthocerida, Bactritida, Ammonoidea, Coleoidea), a radula with 13 elements (known since Carboniferous), calcified beaks (since Triassic, probably Permian), „many“ arms, funnel with two folds, pin hole eye, 4 gills a.o., to mention just the more important features.

Within the family/superfamily Aturiidae/Aturioidea we have again two lineages, the family/subfamily Eutrephoceratidae/inae with almost straight sutures, and the Aturiidae/Aturiinae with a tendency to increase the folding of the sutures.

The units within the (super-)family Nautilidae/oidea can be characterized by conch form and moderate ornamentation. The Recent genera *Nautilus* and *Allonautilus* form an independent off-shoot that is easily characterized by several unique features (e.g. 7 septa at hatching, „protoseptum“)

The ancestor of the Nautilina (or ancestors, if not monophyletic) may have derived from a Triassic nautiloid group with smooth conchs such as the Syringonautilidae.

## THE DATA RETRIEVAL SYSTEM NAUTILOIDEA (DRSN)

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The Data Retrieval System Nautiloidea is a look-up system for students working systematically and taxonomically about fossil nautiloids based on HTML. For every taxon a data file was created that can be accessed via an index. It is not a genuine data base system. However, the pages can easily be retrieved via the Internet.

It is intended to cover the entire system of the Nautiloidea. Presently more than 10000 taxa of the species group (species, subspecies, varieties, mutations), about 1700 taxa of the genus group (genera and subgenera), and 270 taxa of the family group (incl. superfamilies, families, subfamilies, tribes and subtribes) are recorded. How many of these taxa are actually valid is still unknown considering the poor knowledge of most groups of the Nautiloidea

Each taxon of the species is treated in the following way: original binomen and author(s), present attribution, synonymies, derivation of name, types (holotype, lectotype, who designated the lectotype, ect.), material (repository of types and other material), occurrences (type locality, type horizon, other stratigraphic and geographic occurrences), original descriptions and figures, present taxonomic status, comments, contributors. Taxa of the genus group include: name of the genus and author(s), synonymy, type species (mode of type species designation), stratigraphic range and geographic occurrences, diagnosis, original descriptions, attributed species, present taxonomic status, comments, contributor(s)

The data sets of the taxa of the family group contain the following points: name of the taxon and author(s), synonymies, type genus, stratigraphic range and geographic occurrences, diagnosis, original descriptions, attributed genera, present taxonomic status, comments and contributor(s).

According to my estimates the number of taxa of the family and genus group is fairly complete (probably more than 99%), whereas the number of taxa of the species group may have reached the 90-95% level.

The DRSN is combined with the most complete bibliography that has been compiled. Papers were systematically looked through and all mentioned taxa were included in the synonymy lists. All nomenclatorial actions (e.g. type designations, corrections etc.) are included in the respective data sets. This time-consuming work often revealed nomenclatorial and systematic changes. About 200 unrecognized homonymies on species level, and about 10 unrecognized homonymies on genus level emerged. On the other hand, many preoccupied names were replaced more than once. The number of assigned species of many genera was compiled for the first time, resulting in unwildly numbers of species for some well-known genera (e.g. *Michelinoceras* contains at the moment about 160 species). The extent of many families was also compiled for the first time since the time of the „Treatise“.

At the moment, of course, most data sets of the species level are almost empty except for the names. However, the Post-Devonian nautiloids (about 2000 species, 200 genera) are covered more in detail. The taxa of the genus group and family group usually contain much more information. It is hoped that in a few years all taxa of the Nautiloidea are accessible with the above indicated details via the Internet (or CD-ROM).

## **TAPHONOMY OF AMMONITE CONDENSED ASSOCIATIONS. JURASSIC EXAMPLES FROM CARBONATE PLATFORMS OF IBERIA**

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Condensed associations of ammonites show different features in shallow environments in relation to deep environments. The degree of taphonomic condensation in recorded associations reaches the highest values in shallow epicontinental platforms, but not in deep basins. However, the degree of taphonomic heritage (estimated by the ratio of reelaborate elements in the whole assemblage) can reach 100% in both cases. The degree of packing of ammonite remains and the stratigraphical persistence display smaller values in shallow than in deep environments.

Condensed associations from deep environments usually contain taphonic population of type 1, composed of monospecific shells showing unimodal and asymmetric distribution of size-frequencies, with positive skew. These populations have a high proportion of microconchs and the shells of juvenile individuals are predominant, whilst shells of adult individuals are scarce. In deep environments, phragmocones are normally filled by sediment, and concretionary internal moulds display disarticulation surfaces and fractures with acute margins. Pyritic ammonites are common in certain deep environments.

On the other hand, in shallow environments, taphonic populations are usually of type 2 or 3, those of type 1 being not represented. Taphonic populations of type 2 are composed of mono- or polyspecific shells showing unimodal and normal distribution of size-frequencies, with high kurtosis. Populations of this second type have a low proportion of microconchs and the shells of juvenile individuals are scarce, whilst the shells of adult individuals are common. Taphonic populations of type 3 are composed of polyspecific shells showing uni- or polymodal and asymmetric distribution of size-frequencies, with negative skew. Shells of juvenile individuals are absent, microconchs are very scarce and shells of adult individuals are predominant in taphonic populations of this last type. In shallow environments, hollow ammonites (*i.e.*, shells showing no sedimentary infill in the phragmocone) are abundant, reelaborate internal moulds show high values of roundness and sphericity as well as common biogenic borings, and pyritic ammonites are scarce.

## TRIMARGINIA AND TRIMARGINITES (AMMONOIDEA) FROM THE IBERIAN BASIN

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South Tethyan or Arabian ammonites among NW European faunas occur in several episodes from Pliensbachian to Callovian time. Larval or pseudolarval dispersal is the most probable spreading process; however, such a requisite is not sufficient for establishing a true adult interbreeding population. *Trimarginia sinaitica* ARKELL is known from the Upper Bajocian of Sinai. The occurrence of Middle Jurassic *Trimarginia* ARKELL in Sicily, Spain and Normandy has been interpreted as a consequence of Arabian ammonite arrivals in European areas. An Upper Bathonian specimen of *Trimarginia* has also been reported from Switzerland also: *T. sylviae* MANGOLD & GYGY (M). In the case of NW European assemblages, the arrival by drifted shells (*i.e.*, taphonomic dispersal) appears as the most probable dispersal process. However, Iberian populations of *T. iberica* FERNÁNDEZ-LÓPEZ (M+m) are formed by monospecific assemblages, including juvenile specimens, representing true interbreeding, biological populations, rather than the result of occasional larval dispersal away from the living area of the species.

Representatives of the Oxfordian genus *Trimarginites* ROLLIER include the middle Oxfordian, Transversarium Zone species *Trimarginites arolicus* (OPPEL) (M) - *T. stenorhynchus* (OPPEL) (m), and the upper Oxfordian, Bimammatum Zone *T. trimarginatus* (OPPEL) (M), the presumable microconch representatives being still usually assigned to the species *T. stenorhynchus* (OPPEL) (m). The species *T. arolicus* appears restricted to the middle-upper part of the Transversarium Zone (Luciaeformis to Rotoides Subzone) and comprises abundant, mostly juvenile individuals, pointing to their interpretation as components of true biological populations inhabiting the Iberian Basin. The record of *T. trimarginatus* (OPPEL), at the Bimammatum Zone, much scarcer and formed mainly by adult individuals, points at them as components of allochthonous assemblages, formed by drifted shells from distant and deeper areas.

Iberian representatives of Bajocian *Trimarginia* and Oxfordian *Trimarginites* show many similarities in morphology and population structure. However, they have been respectively referred to the families Oppeliidae (DOUVILLÉ, 1890) and Haploceratidae (ZITTEL, 1884). According to the taphonomic data, a habitat of epicontinental platform for the Iberian representatives of *Trimarginia* and *Trimarginites* is proposed here. Both taxonomic groups may represent adaptive radiations from populations belonging to the family Lissoceratidae (DOUVILLÉ, 1885) of shelfal or oceanic basins.

## ORGANISMS IN BODY CHAMBERS OF FOSSIL CEPHALOPODS

Fraaye, René H.B.

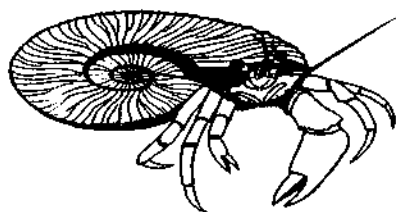
Oertijdmuseum, Bosscheweg 80, NL-5283 WB Boxtel, The Netherlands

In 1841 Mary Anning drew H. Strickland's attention to some black substances in the interior of Liassic ammonites from Lyme Regis, UK. She considered them to be inksacs of the ammonite animals. Strickland (1845) described Mary Anning's and some other specimens from the British Liassic and concluded them to be appendages and / or aptychi. Since then fossils occurring in cephalopod body chambers have received only scant attention.

In 1997, Jäger & Fraaye listed all previous data on stomach contents of ammonites and described in detail the diet of the Toarcian ammonite *Harpoceras falciferum* from the Posidonienschiefer of southern Germany. New data on the diet of the contemporary ammonite genera *Dactylioceras*, *Hildoceras*, *Phylloceras* and *Lytoceras* are now under study; preliminary results will be presented. Westermann's (1996) model of *Dactylioceras* as a planktonic drifter seems applicable to juveniles but probably not to adults. *Hildoceras* fed on organisms or parts of organisms lacking hard tissues. Large *Phylloceras* and *Lytoceras* probably were the producers of the phosphatic coprolites full of fish remains.

An ammonite inquilinistic mode of life has been reported for smaller ammonites (Matsumoto & Nihongi, 1979) and for decapods and fishes (Fraaye & Jäger, 1995a, b). Many newly collected specimens substantiate the view that the inquiline use of cephalopod shells by arthropods was a common and important co-evolutionary phenomenon in marine ecosystems from the Ordovician to at least the Eocene.

The first *in ammonite* occurrence of a hermit crab from the Early Cretaceous of Speeton, England is presented. This new find suggests that palaeontologists have looked in the wrong class of the "Mesozoic real estate market" and throws new light on the evolution of Cretaceous pagurids.



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## PASSENDORFER'S MIDDLE JURASSIC AMMONITES FROM THE HIGH TATRAS

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In the 1930's Edward PASSENDORFER, eminent Polish palaeontologist and geologist with life-long admiration of the Polish Tatras, published two important papers on Bathonian ammonites from the Tatras. He has continued collection works in the localities for decades, and this resulted in an extensive material, which is still kept at the University of Warsaw.

We revised the collection, identifying the original specimens described and figured by PASSENDORFER, and we visited the most important locality: Wielka Swistówka. The field studies indicate that most of the fossils (mainly ammonites, nautiloids, belemnites, brachiopods) came from a single condensation horizon sandwiched between Upper Triassic shallow-water carbonate and Upper Jurassic pelagic limestone. The ammonite bed is a 8--12 cm thick ferruginous limestone with a some centimetres stromatolitic layer in its lower part and a very fossiliferous upper part, where the (commonly fragmented) fossils are embedded together with angular limestone extraclasts and stromatolitic oncoids.

The composition of the ammonite fauna indicates Submediterranean affinity, with strong Tethan influence: 1/3 of the total fauna is represented by phylloceratids, and the most common ammonitid groups are perisphinctids e.g. *Procerites*, *Choffatia*), prohecticoceratids, oppeliids (*Oxycerites*, *Paraecotraustes*), tulitids (*Bullatimorphites*) and cadomitids (*Cadomites*). The systematic evaluation of the fauna proved the presence of several stratigraphically diagnostic forms: e.g. *Thraxites thrax* STEPHANOV, *Prohecticoceras ochraceum* ELMI, *Bullatimorphites eszterensis* (BÖCKH), B. (*Sphaeroptychius*) spp. and the richly represented *Cadomites bremeri* TSERETELI. These species indicate the topmost part of the Middle Bathonian, i.e. the Bremeri Zone. However, the taphonomic phenomena, and the presence of some younger elements (e.g. macrocephalitids) in the fauna may suggest reworking and thus a younger age for the formation of the fossil bed.

The occurrence of the fauna (in stromatolitic condensation level) and the stratigraphic position of the fossiliferous bed (appearance with considerable hiatus below and a shorter temporal lack above) suggest sequential setting similar to other Middle Jurassic ammonite beds in the wider palaeogeographic area: e.g. the early Bathonian of Swinitza (Southern Carpathians, Romania) and the Middle Callovian of Villány (South Hungary).

## AMMONOIDEA OF THE MANGYSHLAK LOWER TRIASSIC

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The Tyururpin Group yields a rich fossil assemblage of different faunal groups: ammonoids, nautiloids, bivalves, brachiopods, gastropods, etc.

Three sections of the Upper Olenekian have been studied in detail: northern slope of the Karatauchik Ridge, near the Dolnaya Well, thickness ~ 880m; northern slope of the Western Karatau Ridge, Dzhikansai sai, near the Shair Village, thickness ~ 1, 150 m and in the Kumshoky and Karashek Mountains, ~ 150 km SE of Karatau, thickness ~ 830 m. Layer-by-layer ammonoid collection enabled to specify the scheme of biostratigraphic subdivision earlier proposed by T.V.Astakhova (1960) and A.A.Shevyrev (1968, 1990). The following levels were established (in ascending order): Beds with *Dorikranites*, Beds with *Tirolites longilobatus*, Beds with *Columbites*, and Beds with *Stacheites*.

Beds with *Dorikranites*, easily recognizable throughout the Mangyshlak, are also traced in Tuarkyr and on the Mt. Bolshoe Bogdo. In the majority of the Mangyshlak sections these Beds are represented only by one or two species of the genus *Dorikranites*. In Tuarkyr and on the Mt. Bolshoe Bogdo the *Dorikranites bogdoanus* species occurs together with *Tirolites cassianus*.

In the overlying Beds with *Tirolites longilobatus*, along with the endemic ammonoid genera, the Alpine species *Tirolites cassianus* is also recorded throughout the section interval. Joint occurrence of the latter with *Dorikranites* in sections of the Mt. Bolshoe Bogdo and Tuarkyr enables to distinguish the Zone *Tirolites cassianus*, comprising Beds with *Dorikranites* and Beds with *Tirolites longilobatus*, in Mangyshlak. However, the lower boundary of the considered zone in the Mangyshlak sections is not paleontologically characterized due to the lack of ammonoids in the deposits, underlying the Beds with *Dorikranites*. Zone *Tirolites cassianus* in Mangyshlak is considered as an age equivalent of the Zone *Tirolites cassianus* in the Alps, Czechoslovakia, Bulgaria, Beds with *Tirolites* in Idaho.

Higher Beds with *Columbites*, noted for a rich diversity of ammonoids, are correlated with the Zone *Neocolumbites insignis* in Southern Primorye, Zone *Columbites costatus* in China, Beds with *Columbites* in Idaho, Beds with *Tirolites* – *Columbites* of the Salt Range, *parisianus* subzone in Japan.

Beds with *Stacheites* in Mangyshlak correspond to the Zone *Tirolites carniolicus* in Yugoslavia, Zone *Subcolumbites multiformis* in Southern Primorye, *Subcolumbites* beds of Afghanistan, Albania, Chios, Nevada, *Prohungarites* Beds in Idaho, Beds with *Procarnites* – *Letophyllites* in China, Beds with *Tozericeras pakistanum* in the Salt Range and *perrinismithi* subzone in Japan.

# THE TERMINAL REGION OF THE MALE GENITAL TRACT IN CEPHALOPOD SYSTEMATICS: A REVISED TERMINOLOGY, AND AN ILLUSTRATION OF INTRAGENERIC VARIATION WITHIN ONE GENUS OF OCTOPUS

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Characterizing cephalopod genera has long proved a difficult task: the genus *Octopus* Cuvier, for example, currently includes 112 species (e.g. SWEENEY & ROPER, 1998) but included among these are members of probably at least five other genera, which can be distinguished (in part at least) by the morphology of the male genital tract. However, although it is widely accepted that the morphology of the terminal region of the male genital tract is a species-specific characteristic, this region has rarely been described in sufficient detail to clarify the distinctions, and in systematic descriptions is typically included as a small part of a standard diagram illustrating the entire dissected male reproductive system.

Current work on redescrptions of octopus species in the Indo-Pacific has included a morphological study of the terminal region of the male reproductive tract in several different genera of the recent Octopodidae. A revised terminology for the terminal structures of the male reproductive tract is proposed, including several previously undescribed anatomical features. Work on 8 species within one particular genus (containing a total of 15 species) is the main focus of this presentation, with examples drawn from other, poorly known genera and one new genus.

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## BIOLOGY AND BIOGEOGRAPHY OF THE MIDDLE OXFORDIAN AMMONITES OF THE SUBGENUS *PLATYSPHINCTES*: A NEW EVIDENCE FROM POLAND

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After Tintant in 1961 created the ammonite genus *Platysphinctes* no other findings of forms allied to that genus were recorded. The original material used by Tintant (1961), however, provided only a fragmentary insight into biology and stratigraphic range of *Platysphinctes*.

The first records of the genus *Platysphinctes* in Poland give a new information on the biogeographic distribution of *Platysphinctes*. The representatives of *Platysphinctes* appear in the sections of the Polish Jura Chain, in non-condensed limestone succession, within a thin horizon of the uppermost part of the Plicatilis Zone (Middle Oxfordian). The collection represents monospecific population of *Perisphinctes* (*Platysphinctes*) *perplanatus* Tintant. Microconchs are for the first time recognized within this species and also within the subgenus *Platysphinctes*. Adult, lappeted microconchs range in final diameter from 45 mm to 77 mm. Macroconchs reach final diameter of about 120 mm or even more. In the adult macroconchs the terminal part of the body-chamber is almost completely smooth while the microconchs have never reached this stage of growth. The aspect of shell of the juvenile micro- and macroconchs is similar. It is characterised by moderately evolute to evolute way of coiling of whorls, by oval, rectangular or close to trapezoidal whorl-section and by numerous constrictions (3-4 on the last whorl of the adult microconchs and 3-5 in macroconchs). At an early stage of micro- and macroconch's growth ribs regularly bifurcate, later in ontogeny intercalatory ribs appear on the ventral side, whereas the bifurcations become occasionally alternated with paradischizotomous or even bidichotomous furcation. After each constriction the intercalatories increase in number and the points of furcation become less distinct.

Specimens of *Perisphinctes* (*Platysphinctes*) *perplanatus* occur in the Plicatilis Zone where also the representatives of the subgenus *Liosphinctes* Buckman are present. According to the new evidence, however, the suggestion of Brochwicz-Lewiński (1972) who considered *Platysphinctes* as a microconch of *Liosphinctes* seems to be an oversimplification.

The horizon where *Platysphinctes* are present, reflects the event of short-term invasion of ammonites from the Mediterranean Province to the area of the Polish Jura Chain, as indicated by the occurrence in that interval of such Mediterranean forms as *Perisphinctes* (*Kranaosphinctes*) *cyrilli* Neumann and *P. (K.) gyrus* Neumann.

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**OCTOPUS VULGARIS (CEPHALOPODA: OCTOPODIDAE) GAMETOGENESES: A HISTOLOGICAL APPROACH TO THE VERIFICATION OF THE MACROSCOPIC MATURITY SCALES.**

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Knowledge of the maturation process is vital to the understanding of reproduction biology and the relationship between spawning stock and recruitment. There are various gonadal maturity scales for cephalopods. A correct and widely applicable scale would be of great value for studying cephalopod life cycles. The purpose of the present study was to validate, using histological methods, the macroscopic maturity scale used for *Octopus vulgaris*. The changes in testes and ovaries during sexual maturation permitted the determination of six different histological stages for spermatogenesis and seven for oogenesis. The relative frequencies of these stages in each of the categories of the maturity scale, were calculated. By comparing these frequencies along with the macro-morphological changes, it was possible to follow closely the single cycle development of the gonads. The study also provided evidence to suggest that *Octopus vulgaris* is an intermittant spawner.

## **THE EVOLUTION OF THE OCTOPODA**

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The Octopoda can be derived from Coleoidea with 10 arms. Their evolution can be demonstrated by allometric growth and reduction of the middle field of the gladius.

The evolution of the coleoid gills is reconstructed. A loliginid basic type can be stated. The gills of the modern octopods represent a modification of this type. The gills of the fossil Plesiotheuthidomorpha still show the basic type of the Coleoidea. Therefore they are the stem lineage representatives of the vampyromorphoids.

# ORGANIZATION AND REORGANIZATION OF THE MAIN NERVE CORD IN UNTREATED AND REGENERATING TENTACLES OF THE CEPHALOPOD *SEPIA OFFICINALIS* L.

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The regeneration of treated arms and tentacles of cephalopods was proved in studies on *Ommastrephes bartrami* Lesueur (Murata et al 1981) and on *Architeuthis dux* Steenstrup (Aldrich F A & Aldrich M M 1968) which are similar to the one presented on *Sepia officinalis* L.. Macroscopic examinations on *Sepia officinalis* L. capability of regenerating its tentacles (Hielscher B et al 1996) reveal a completely new shape which might be divided into six separate stages: protrusion of the central main nerve cord, scarring of the wounded tissue, formation of a semicircular bud at first, later developing into a cone-like shape and finally the formation of suckers. These findings correspond with those of another study on the regeneration of the arms of *Sepia* (Féral J P 1979).

The centrally and axially running main nerve cord in the tentacle is formed of an inner neuropil and a cortex. Inside this cortex can be found the tractus cerebrotentacularis consists of two fibres of different thickness, one on the oral the other on the aboral side of the nerve cord. Enzyme histochemical slide examinations performed by means of glyoxylic acid induced fluorescence on 25 day- old regenerates indicated the presence of catecholamines primarily in the main nerve cord. This corresponds with other findings demonstrating the presence of catecholamines in the nervous system of *Sepia* (Kling G 1984).

The use of confocal laser scanning microscopy (clsm) permits a nearly complete characterization of the neural network in the untreated tentacle as well as detailed descriptions of the neuronal organization during the regenerative phases in treated tentacles. For incubation antibodies against – amongst others - serotonin (5-HT) and FMRFamid were used, for marking the fluorescence a second antibody. The nervous network of a untreated tentacle consists of the main nerve cord and six fibres arranged peripherally. In a regenerated stump of a treated tentacle there are no serotonin fluorescences during the first two phases of regeneration (0. – 20. day).

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## PALEOBIOGEOGRAPHY AND RELATIONSHIP OF SOUTH AMERICAN HETTANGIAN (LOWER JURASSIC) AMMONITES.

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In the uppermost Triassic (Late Rhaetian) of South America only the cosmopolitan genus *Choristoceras* is found which probably persisted - like in North America - to the first appearance of the Psilocerataceae. Most authors postulate for the Psilocerataceae a monophyletic origin from the Phyllocerataceae which survived in the open seas of that time, the critical period across the Triassic/Jurassic boundary. The basal Jurassic ammonite layer in northern Peru yielded specimens of *Psiloceras* which are characterized by a steep umbilical wall with a distinct umbilical border, showing great similarity with phylloceratacean genera, especially with *Rhacophyllites*. The suture line is that of *Psiloceras tilmanni* with a flat umbilical wall and the innermost whorls show the typical „Knötchenstadium“ which does not exist in Triassic ammonites. *P. tilmanni* probably is the oldest species of *Psiloceras* and was also found in North America but does not exist in northwestern Europe or in the Alps. The oldest species of *Psiloceras* found in these areas are comparable with species which occur in Chile above horizons with *P. tilmanni*. The adult suture line of these species is less complicated compared to the sutures found in *P. calliphylum* from the Alps, but it is similar to that of *P. psilonotum* from northwestern Europe. These differences probably were caused by different habits and ecology. Complexity of the suture line in epicontinental seas had no longer the importance as under pelagic conditions of an open ocean. It is striking that similar species are appearing in different Hettangian epicontinental seas (northwestern Europe, North and South America) which were not directly interconnected. This may be explained only by repeated immigrations from the open ocean. The genus *Caloceras* was not shown to exist in South America. This genus is more frequent in northwestern Europe than in the Alps and the evidence in North America is doubtful. Above biozones with different species of *Psiloceras* follow horizons with *Kammerkarites* which evolved from *Psiloceras*. *Kammerkarites* is frequent in the Tethyan Realm but is also found in northwestern Europe, North America and northeastern Asia. *Discamphiceras* derived from *Kammerkarites* and is frequent in the Middle Hettangian of South America. This genus is not found in northwestern Europe but in North America and the Tethyan Realm. Again the South American species have a less complicated suture line. The upper part of the Middle Hettangian is characterized by the mainly Tethyan genera *Laqueoceras* and *Sunrisites*. The Late Hettangian genus *Schlotheimia* by most authors is derived from *Saxoceras*, a genus which is frequent in northwestern Europe but which was not found in South America. The source of *Schlotheimia* could also be the Tethyan genus *Storhoceras* which is also found in South America, and transitional species between this genus and *Schlotheimia* exist. *Schlotheimia* is less frequent in South America than in northwestern Europe. Abundant is *Badouxia*, an endemic genus for North and South America. The Tethyan genera *Paracaloceras* and *Pseudetaomoceras* are represented by species which in part are comparable with species from North America and the Alps. Species of *Angulaticeras* are similar to those appearing in the Alps, northwestern Europe and North America.

Phylloceratina and Lytoceratina are much less frequent than Ammonitina but they are sporadically found also in North America. The phylloceratid genera *Nevadophyllites*, *Fergusonites* and *Phylloceras* and the lytoceratid genera *Eolytoceras* and *Ectocentrites* were identified. Both suborders are lacking in northwestern Europe. The connections between the Jurassic Pacific and the adjacent epicontinental seas of North and South America probably were better than between the Tethys and northwestern Europe.

## **TELESCOPING IN ORTHOCONIC NAUTILOIDS: AN INDICATION OF HIGH OR LOW ENERGY HYDRODYNAMIC REGIME ?**

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The phenomenon of telescoping in nautiloids has been widely accepted as an indicator of a high energy depositional environment in the Cephalopod Limestone facies. However, the actual mechanism of how it occurs is not clearly understood. It is hoped by studying the frequency and taphonomic preservation of these telescoped specimens both in the field and in thin section to determine whether it is really (a) a high energy factor or (b) a dissolution factor of the shell material itself due to prolonged exposure on the sea bottom thereby giving a very different environmental interpretation. The majority of specimens studied are from the Silurian of the Carnic Alps. Examples are also illustrated from the Silurian of the Prague basin and Morocco.

It has been noted that smaller orthoconic shells accumulated within the body chambers of larger cones and these appear to be randomly oriented within the sedimentary infill of the latter. The smaller cones in some cases have also penetrated the most adoral part of the siphuncle and sometimes form a plug as sediment infilling the body chamber is restricted in its infiltration of the siphuncle by these obstructions. The smaller cones invariably display geopetal structures which seem to reflect the position of the larger enclosing cone as it was deposited on the seafloor. This may reflect a slow accumulation of the smaller cones within the larger more immobile cone as deposition took place.

In thin section rare specimens have been observed with smaller cones telescoped within the phragmocone of the larger specimen. The septa of the smaller cones are intact however, those of the larger enclosing cone show dissolution effects and are in some cases no longer preserved. This may reflect long term exposure on the seafloor of the larger cone which with time becomes infilled with sediment and smaller elements of the fauna including smaller orthocones. Evidence of breakage of septa due to high energy penetration of smaller cones into the phragmocone appears to be rare and fragmented septa within the phragmocone have not been noted in thin sections of the material from the Carnic Alps.

The observations presented of the telescoping phenomenon may reflect local hydrodynamic conditions but it is important to note that environmental interpretations other than high energy are possible.

## SEXUAL DIMORPHISM IN THE GENUS *PSEUDOTHURMANNIA*.

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When it appeared that the holotype of *Ammonites angulicostatus* of d'Orbigny (1842) – lost for a long time but recently refound by Busnardo – does not correspond to the idea of how the genus *Pseudothurmannia* should look like when it was introduced by Spath (1923), the wisest thing to do is to maintain the current concept of the genus as it has been since Lapeyre (1974) proposed a 'lectotype of *Pseudothurmannia angulisostata* (d'Orbigny)'. Since Hoedemaeker (1994) considered this supposed 'lectotype' conspecific with *Pseudothurmannia ohmi* (Winkler), the latter species is proposed (Hoedemaeker, 1994) as the type of the genus *Pseudothurmannia*. This proposal will be sent to the ICZN. *Pseudothurmannia* is now considered a crioceratitid of which each rib bears a small ventrolateral clavus and of which the whorls are in touch with each other or even slightly overlapping.

Ropolo (1995) showed that among the crioceratitids the macroconchs are criocone, whereas the microconchs are ancylocone. Macro- and microconchs almost do not differ in size, only the size of the spiral part differs. In *Pseudothurmannia*, however, the whorls of both macroconchs and microconchs are in touch with each other or slightly overlapping, but differ markedly in size. So it appears that when the crioceratitids return to normal coiling, the difference in size between the sexual dimorphs also returns.

On this poster will be shown several species (or subspecies) of *Pseudothurmannia* each with their sexual dimorphs.

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# ONE OF THE MANY PROBLEMS: TAXONOMY OF THE COMMON SILURIAN NAUTILOID CEPHALOPOD "*ORTHOCERAS BULLATUM*" J de C. SOWERBY

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British Silurian nautiloid cephalopods, now under revision, are numerous, of interest in terms of palaeoecology and palaeobiogeography, and potentially biostratigraphically significant. Unfortunately they are frequently poorly preserved. In the graptolitic facies they are seen as flattened moulds; in the siltstones or sandstones of the shelf facies they tend to be broken, and infilled so as to be without preservation of internal structures. Good preservation is seen in some limestones but is uncommon. "*Orthoceras bullatum*" J de C. Sowerby though usually seen as distinctive fragmentary compressed moulds, ornamented and of characteristic proportions, is probably the commonest of all British species, particularly in the upper (Ludfordian) stage of the Ludlow Series. Consideration of it provides a good example for discussion of taxonomic problems and their possible solution.

In the form *Orthoceras bullatum* var *pictonense* McLearn, from Arisaig Nova Scotia, it was assigned by Rousseau Flower (1943) to Foerste's (1928) genus *Polygrammoceras*, of which several species from Anticosti were described. This genus was defined as having longitudinal ornament finer and without the fluting of *Kionoceras*. *Polygrammoceras* has been included, for example in the *Treatise of Invertebrate Paleontology*, in the Subfamily Kionoceratinae.

My experience has now shown that by examining all available material it is sometimes possible to find a rare vital clue to internal structure, which is crucial if phylogenetically reasonable taxonomy is to be suggested, without that suspicion of homeomorphy which perhaps excessively surrounds the use of readily available ornamentation. The type specimen of *O. bullatum* illustrated in Murchison's *Silurian System* of 1839 (plate 5, figure 29) reveals the siphuncle in part of the phragmocone.

Curiously, Blake's illustration (1882, plate 12, figure 4) omits the relevant part of the specimen. The segments of the siphuncle are somewhat expanded, as indeed they are in some of the Anticosti examples. Of the 369 specimens of "*Orthoceras*" *bullatum* that I have examined, a single example from the Much Wenlock Limestone of Ledbury, Herefordshire, which has been cut longitudinally and polished, reveals not only the external surface but internally annulosiphonate deposits developed towards the apical end.

Fortunately, this was the second example figured by Blake (1882, plate 12, figure 5) and is reasonably to be regarded as a paratype. Flower (1962) discussed the difficulty that many orthocones appear to have empty siphuncles until suitable preservation of a more apical region of the shell reveals their development there.

Thus the common problem of generic assignment is reasonably solved in this case by the name *Polygrammoceras* but the diagnosis of this genus in the *Treatise* must be modified to allow for the presence of siphuncular deposits. *Kionoceras* itself appears in some specimens to be similarly endowed. This was noted by Flower (1962), is mentioned with caution in the *Treatise*, and is seen in some of Barrande's illustrations. Thus the notion of the Subfamily Kionoceratinae, with genera separated particularly in terms of ornament, begins to appear somewhat more robust.

## THE PHYLOGENY OF PHARCICERATIDS AND THEIR RELATIVES (AMMONOIDEA, ANARCESTIDA; LATE GIVETIAN TO MIDDLE FRASNIAN)

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The oldest pharciceratids (Middle Devonian III-A), *Ph. amplexum* and *Ph. tridens*, are still rather simple-lobed, widely umbilicate and have broad and depressed, slowly expanding, longidomic whorls. It seems that they were derived from tubby *Afromaenioceras* by heterochronic processes, resulting in an extension of evolute early ontogenetic maenioceratid stages whilst the second umbilical lobe shifted towards the flank, leaving space for additional lobes around the umbilicus. The subsequent main lineage of evolution (Pharciceratidae) is characterized by a gradual proliferation of umbilical lobes whilst conchs became more involute and compressed. *Stenopharciceras* (entering in MD III-B) includes open umbilicate species with more than four flank lobes, *Synpharciceras* (MD III-C) comprises involute taxa with seven to eight flank lobes, and in the basalmost Frasnian (UD I-A) *Neopharciceras* there are as many as 10-14 flank lobes. Within *Stenopharciceras* there are side-branches which may deserve taxonomic distinction. In *Steno. lunulicosta*, for example, the number of lobes increased whilst the shell became rather serpenticonic.

Another branch from *Stenopharciceras* led to the compressed Petteroceratidae with third ventral lobes. Two new species from the MD III-E of Morocco give evidence for morphological change within the suboxyconic *Petteroceras*. *Pett. n.sp. I* has less lobes than *Pett. errans*, *Pett. n. sp. II* is more advanced, rather involute and thin. *Pett. feisti* from UD I-A of the Montagne Noire shows that the group survived just into the basalmost Upper Devonian. It is unclear whether the extremely rare involute *Meropharciceras* with rounded venter belongs to the same lineage or whether it branched off independently from early neopharciceratids.

Contemporaneously with youngest maenioceratids (MD II-D), the first species of a second multilobed group, the Eobeloceratidae, appeared in North Afrika. Members are characterized by faster expanding, mesodomic and compressed shells. Early stages are typically ribbed and there is a wide mid-flank saddle as in homoemorphic Frasnian Koenenitidae. *Mzerrebites* with rounded venter resembles *Koenenites* but lacks the pointed first ventral lobe. In *Mz. erraticus* (MD III-B), the outer flank lobe is unusually enlarged. The open umbilicate Gen. nov. I ("*Timanites meridionalis* Gp.", MD III-C) increased the number of lobes and developed oxyconic venters. This trend continued in the involute Gen. nov. II ("*Ph. taouzensis* Gp.", MD III-D) and there was a significant size increase. *Eobeloceras* represents a poorly known gigantic convolute side-branch. A third new genus ("*Ph. kayseri* Gp.") has flattened rather than acute venters.

Since the most primitive member of the strongly ribbed mostly Frasnian Triainoceratidae, the serpenticonic *Tamarites*, has a much simpler suture than *Maenioceras*, the ancestry of the family remains enigmatic. Ribbing was also found in evolute early stages of early Pharciceratidae. Multilobed Frasnian genera such as *Komioceras* and *Devonopronorites* have phylogenetic affinities with the Koenenitidae whilst *Nordiceras* evolved in parallel with beloceratids from Acanthoclymeniidae.

## WHAT MOLECULAR TOOLS TELL US ABOUT OCTOPODS SYSTEMATICS ?

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Octopods systematics is still controversial and in spite of important efforts, numerous problems remain. There are nomenclatural confusions in all the geographical areas and a lot of « species complexes » are unresolved. The many inadequately described taxa and the largely single character based classification are serious handicaps for improving the current Octopods classification. To reform the systematics and to give it well-built foundations, it is necessary to begin a complete review of the group by redefining the lowest classification taxa. The genus *Octopus* which represents at least 60% of the Octopoda species must be first examined. But taking into account that the separation of the family Octopodidae into three subfamilies may not be correct, the sample studied have to be enlarged to all the Octopodidae genera.

The aim of the present work is to use molecular phylogeny as a complementary approach to bring more information about the Octopods relationships. The phylogenetic analyses are based on the 3' end of the 16S rRNA gene (500 bp) and the third sub-unit of the cytochrome oxidase gene (700 bp) at the level of both DNA and protein sequences. Phylogenetic trees were calculated under three algorithms : Neighbor-Joining, Maximum of Parsimony and Maximum Likelihood. The data were also submitted to Bootstrap tests. The usefulness and the resolution scale of the two mitochondrial markers used will be discussed. The sample studied covers a broad spectrum of the Octopoda classification including : several individuals of the cosmopolitan *Octopus vulgaris* from various geographical areas, several *Octopus* species complexes (Macropus complex, Aegina complex, etc...) and other genera of the Octopodinae, a large sample of Eledoninae species, the two more important genera of the subfamily Bathypolypodinae (*Bathypolypus* and *Benthoctopus*) and members of other families. The results obtained confirm the paraphyly of the Octopodidae. Different research directions for finding discriminant characters are proposed. The *Octopus* genus is shown to be a catch-all genus and must be recentered to fewer species. The Octopodinae genera have to be reexamined all together and it seems necessary to redefine them. A large portion of the current *Octopus* species will be included in these restored taxa. The same conclusions can be drawn for the two other subfamilies examined : Bathypolipodinae and Eledoninae.

The analyses presented highlight that the Octopod classification will view major changes over the next ten years and probably might be completely reshaped. And molecular phylogeny will actively participate to these large modifications. Molecular tools help morphologists to determine discriminant characters by confirming or not their hypotheses and by bounding monophyletic groups. So it is necessary to develop active collaborations between molecular biologists and morphologists.

## LATE CRETACEOUS AMMONITE FAUNAS OF THE MAASTRICHTIAN TYPE AREA

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Although Kennedy's (1987) revision of ammonites from the type Maastrichtian has greatly improved our knowledge of these faunas, the stratigraphic ranges of most taxa are still comparatively poorly known. This is particularly unfortunate since we do now have a very detailed lithostratigraphy and well-correlatable ecozonal subdivisions based on bioclasts, benthic forams and ostracods. Moreover, we have a much better understanding of K/T boundary phenomena, as well as a sequence stratigraphic interpretation and a preliminary strontium isotope stratigraphy for the type Maastrichtian.

New ammonite material collected during recent fieldwork and recognised in private collections, comprises quite a number of taxa not previously recorded from the area. Notable recent additions include *Hauericeras* cf. *rembda* (Forbes 1846), *Pachydiscus haldensis* (Schlüter 1867), *P. subrobustus* (Seunes 1892), *Menuites terminus* (Ward & Kennedy 1993), *Patagiosites* sp., *Placenticeras* cf. *bidorsatum* (Roemer 1841), *Neancyloceras?* *phaleratum* (Griepenkerl 1889), *Baculites vaalsensis* Kennedy & Jagt 1995, *B. knorriani* Desmarest 1817, *Trachybaculites columna* (Morton 1834), *Scaphites gibbus* Schlüter 1872, *Hoploscaphtes* n. sp. (aff. *waagei/angmartussutensis*) and *Jeletzkytes dorfi* Landman & Waage 1993.

Concerning ammonite preservation in the Maastricht Formation, it may be noted that: 1 - generally speaking, ammonites are rare, with the exception of local acmes in baculitid and scaphitid distribution; 2 - ammonites are either absent from, or (extremely) poorly preserved in, the non-indurated portions in the sequence. Only under special conditions (e.g. silicification, rapid burial) have ammonites been preserved in these strata; naturally, such occurrences influence the species' range considerably. In combined lithostratigraphic sections, one illustrating the Haccourt/Maastricht/Geulhem area, the other the Heerlen/Vijlen/Aachen area, all ammonite taxa known to date are listed. Their stratigraphic ranges are calibrated against belemnite zones, and palaeobiogeographic implications of these faunas are briefly discussed.

In addition, the proposed ammonite index for the base of the Maastrichtian, *Pachydiscus neubergicus* (von Hauer 1858), is recorded for the first time from subunit 6 of the Vijlen Member (Gulpen Formation), as exposed in the Haccourt-Lixhe area (NE Belgium). Correlations with northern Germany using belemnites suggest these specimens to be of *cimbrica* Zone age (= late Early Maastrichtian).

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## BIOMECHANICS AS A TEST OF FUNCTIONAL PLAUSIBILITY: TESTING THE ADAPTIVE VALUE OF TERMINAL-COUNTDOWN HETEROMORPHY IN CRETACEOUS AMMONOIDS

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'Terminal countdown' heteromorphy (Seilacher and Gunji 1993), in which the onset of the new mode of growth signals the imminent end of skeletal accretion, is common among Cretaceous ammonoids. Most often represented in ammonoids by a shaft-and-hook-shaped body chamber, this strategy combines determinate growth with the development of novel form. The terminal countdown, like any determinate-growth strategy, can be viewed as a trade-off between continued growth and specialized adult form (with which further growth is incompatible). In theory, the adult morphology should be distinctly optimized to the adult life mode in order to make the trade-off evolutionarily 'worthwhile' (Klinger 1981; Seilacher and Gunji 1993).

But what is the adult life mode to which this morphology is apparently so specialized? Several hypotheses have been advanced over the past century for the function of this shaft-and-hook morphology, centering recently around arguments of hydrostatic stability. Kakabadzé and Sharikadzé (1993) and Monks and Young (1998) propose that the shaft-and-hook body chamber hydrostatically *destabilized* the shell, allowing the nekto-benthic heteromorph ammonoid multiple stable orientations. Here I present results of buoyancy-based biomechanical and analytical tests of this hypothesis.

These authors propose two mechanisms by which attitude might be actively controlled during life. Kakabadzé and Sharikadzé (1993) grant ammonoids the ability to control the placement of fluid and gas in the phragmocone, while Monks and Young (1998) allow for mobility of a small ammonoid soft body within the body chamber. These authors find that their mechanisms afford the heteromorph ammonoid up to 110° of attitude lability. Among these models' flawed assumptions is the placement of the (animal+shell)'s center of mass at the center of mass of the soft body. Using life-size models, I show that the buoyancy contributions of soft body and shell material are of the same order of magnitude. Thus the spatial distribution of shell material must be taken into account in buoyancy/attitude calculations. Along similar lines, the distribution of gas and liquid in the phragmocone is found to have little effect on attitude for most morphologies. However, a small, dense, mobile soft body might provide sufficient change of attitude to allow contact with the benthos, especially considering the added weight of the aptychus.

Biomechanics can be the key to testing functional hypotheses. By ruling out the mechanical plausibility of even end-member morphodynamic effects, we can explicitly test functional hypotheses of adaptation. Thanks to the constraint of neutral buoyancy, ammonoids provide strong tests of functional hypotheses for accretionary morphologies. Future work on biostratinomy, ontogeny, geochemistry, and epibiosis will clarify the relationship of T-C heteromorphy to alternate hypotheses of life mode. The adaptive function of heteromorphy in Cretaceous terminal-countdown forms remains equivocal, but certainly less open to debate.

## MUSCLE ATTACHMENT AND MANTLE-RELATED FEATURES IN UPPER CRETACEOUS *BACULITES* FROM THE UNITED STATES WESTERN INTERIOR

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*Baculites* from the Upper Cretaceous of the United States Western Interior commonly occur in flood abundance in early diagenetic concretions in shale intervals such as the Campanian Pierre Shale. Pristine aragonite preservation is widespread, while internal moulds and partially exfoliated specimens show a series of features that give clues as to muscle and mantle attachment between animal and shell. These are rare, and most conspicuous in adult body chambers and adjacent phragmocone, while features may be absent in the majority of co-occurring specimens in a single concretion. Structures present include a bilobed dorsal muscle scar and a single ventral scar at the adapical end of the body chamber. Rare individuals show repeated scars at the adapertural end of the adult phragmocone; others show a clear set of drag marks associated with the scar(s), as well as elsewhere on the surface of moulds, recording the adapertural migration of the tissues. Internal moulds of body chambers may bear a longitudinal groove or grooves associated with muscle scars, that corresponded to ridges on the inner surface of the shell. Problematic adaperturally concave traces on the flanks of partially exfoliated moulds may possibly reflect sites of weaker mantle attachment. Predated *Baculites* with massive damage to the shell, followed by repair and a return to near-normal shell growth, as well as recovery from parasitism(?) or pathological mantle growth, demonstrate the regenerative properties of the ammonite mantle.

## INJURIES – A KEY TO UNDERSTANDING LIFE MODES OF AMMONOIDS

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Comparative studies of the different types of regenerated injuries, which had been resulted from predatory interactivities, and their positions along the aperture of Mesozoic ammonoids (Early to Middle Triassic, Jurassic) allow to distinguish taxa with demersal modes of life and taxa which lived predominantly within the free water column, respectively. The main predators at the bottom were pincers-bearing crustaceans and in some cases also pycnodontid fishes, while predominantly different kind of fishes attacked free swimming ammonoids. A bimodal distribution (Fig.1) of same types of injuries caused by crustaceans along the aperture exhibits information about attacks during active as well as resting phases of these ammonoid animals, proving their demersal life style (KEUPP, 1997). From analogous types of injuries and their similar distribution patterns on the shell, a more or less bottom related life mode of Middle Triassic ptychitids is postulated as well as for the longidome Jurassic morphotypes with simple bifurcating ribs [e.g. *Dactylioceras* (Lower Toarcian) and several perisphinctids (Upper Jurassic)]. In contrast, the normal distribution of injury positions at the aperture, for example of Liassic harpoceratids, presumingly mostly caused by fish-attacks, indicates epipelagic life style. The often observed cases of multiple attacks on the same ammonoid specimen always with the same configuration of shell breakage and same position of injuries on the shell can be interpreted to hint at a stable habitat stationarity of both the predator and the ammonite.

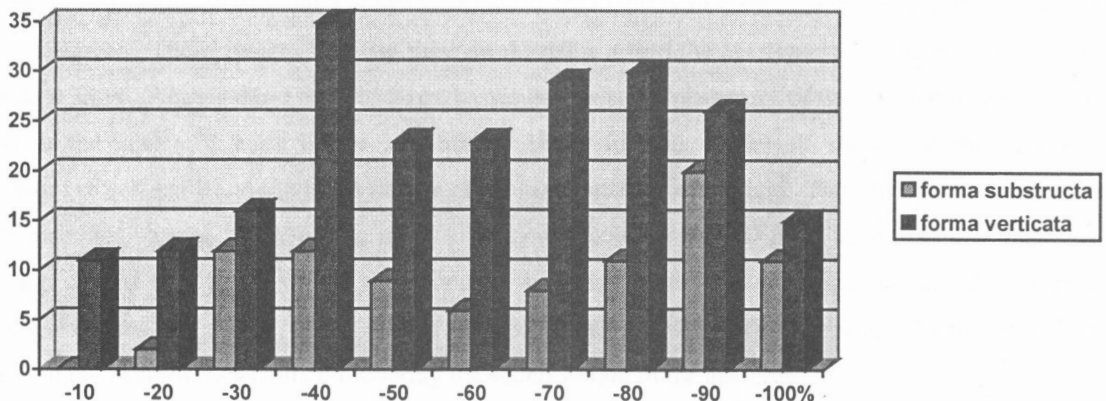


Fig.1: The localisation of injuries along the aperture (0% = edge of the umbilicus, 50% = middle of the whorl, 100 % = ventral median line) mostly caused by crustacean-ammonite interactivities of 315 injured specimens of *Orthosphinctes* from Late Jurassic (Lower Kimmeridgian) of Hartmannshof/Southern Germany exhibit a bimodal distribution pattern.

### References:

Keupp, H. (1997): Paläopathologische Analyse einer Population“ von *Dactylioceras athleticum* (SIMPSON) aus dem Unter-Toarcium von Schlaifhausen/Oberfranken.- Berliner Geowiss. Abh., E 25: 243-267

## AMMONOID PALAEOBIOGEOGRAPHY - THE *PSEUDOSCHLOENBACHIA* PARADOX.

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The ammonoid genus *Pseudoschloenbachia* is common in the late Santonian of South Africa and Madagascar and as a whole, has a virtually world-wide distribution. However, in the early Campanian in Madagascar, *Pseudoschloenbachia* s.s. disappears and is replaced by taxa which are regarded as chronologically derived subgenera of the nominal genus. Here, *Pseudoschloenbachia* s.l. occurs in abundance, comprising about 80% (8000 specimens) of the total ammonoid fauna. In contrast, only five specimens are known from Zululand, none from Pondoland, and perhaps less than a dozen from other parts of the world. Reasons for the sudden proliferation of *Pseudoschloenbachia* s.l. in the early Campanian of Madagascar, coincident with the sudden decline of the genus in the rest of the world remain enigmatic.

## SIZE CLASSES IN A DEVONIAN AMMONOID FROM THE MIDDLE DEVONIAN CHERRY VALLEY LIMESTONE OF NEW YORK STATE, U. S. A.

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The agoniatites in the Cherry Valley Limestone (Middle Devonian) of New York State, U.S.A. occur in discrete beds throughout their range. This and the lack of small juveniles preserved in these beds have led workers to suggest that the agoniatites represent periodic immigrants into the area during times of transgression. Before a viable reproducing population could become established they suffered a mass mortality event.

One of these beds, possibly the most extensive, is well exposed at the Seneca Stone Quarry as a large bedding plane exposure. It was originally thought that such an exposure would be ideal to study the population structure of the agoniatites. Unfortunately most of the specimens were lying oblique to the bedding surface and/or weathered in such a way as to make accurate measurements impossible.

A much smaller bed had been collected previously and is in public view in the New York State Museum, Albany.

It is the lower surface of a slab of the Cherry Valley Limestone, measuring ~ 1.6 m x 2.0 m. The slab contains 43 specimens of Agoniatites vanuxemi in lateral view, of which 39 were measureable. The following measurements were made: total diameter, the accompanying whorl height, phragmocone diameter, whorl height at the end of the phragmocone, and body chamber angle. Septal angles were also measured where possible.

Phragmocone diameter was considered a more constant measure of size because the body chamber measurements suggested that none of the specimens were complete. A size frequency histogram of phragmocone diameter (N=25) indicated the presence of three discrete size classes. Size classes in ammonoids have been used to suggest two things: sexual dimorphism and the presence of different age groups in a population. Sexual dimorphism is discounted here based on the lack of evidence of maturity. There are no adult apertural modifications known in Agoniatites, leaving septal approximation as the only evidence of maturity. In the 18 specimens where septal angles were measured, only four showed any indication of a decrease in septal spacing and in three of these it was slight. In none of the smaller sized individual was there any evidence of septal approximation.

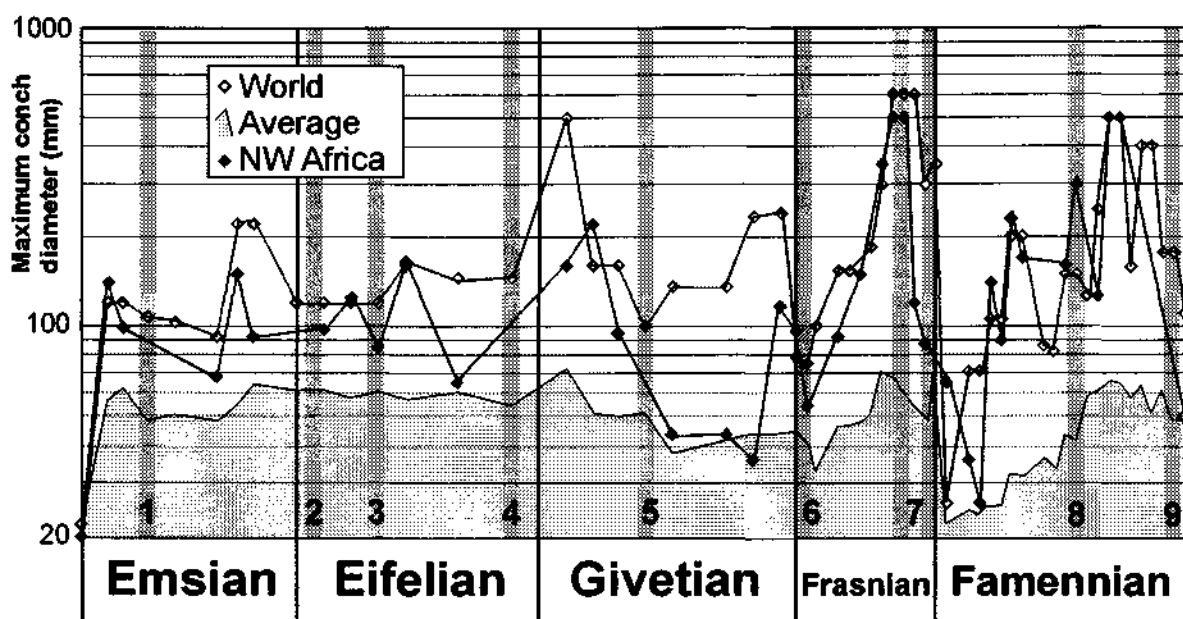
It is concluded from this that the three size classes present in this sample represent different age classes in the population of Agoniatites vanuxemi, possibly three annual cohorts. The smallest and presumably youngest individuals were subadults. The largest and presumably oldest individuals were probably near maturity since a few of them were beginning to experience the slow down in growth inferred from septal approximation. Smaller juveniles probably lived elsewhere, as suggested by their absence. Only upon reaching a certain size and age did they enter the adult habitat.

## DEVONIAN AMMONOID BIOMETRY AND GLOBAL EVENTS - PRELIMINARY RESULTS

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Devonian ammonoids from Morocco attract attention because of various reasons. One is the impressive size of some specimens, especially of Late Devonian species (e. g. of the genera *Manticoceras*, *Carinoceras*, *Gonioclymenia*, etc.) which attain conch diameters of more than 50 centimetres. Data of more than 1000 Devonian ammonoid species which are sufficiently treated in palaeontological literature were assembled. The maximum values of the diameters of these species were measured, extracted from various literature and from the database GONIAT (KULLMANN & KORN 1996).



Minima and maxima in ammonoid conch size of the three graphs (representing the world average, world maximum and NW Africa maximum through the Devonian) strikingly correlate with each other. The minima largely coincide with major global transgressive events (1-Daleje, 2-Chotec, 4-Kacák, 5-Taghanic, 6-Frasne, 7-Kellwasser, and 9-Hangenberg Event Levels). Maxima are present at the positions of the Upper Kellwasser Level (7) and of the *Annulata* Black Shales (8). An additional Event level can be recognised in the course of the graphs (3). It was described by JOHNSON et al. (1985) as transgression Id and happened in the *costatus* Zone (Eifelian). In the eastern Anti-Atlas (Morocco) it correlates with hiatuses/ facies changes in several localities and with the simultaneous appearance (pers. comm. M. KAZMIERCZAK, Tübingen) of various conodont and ammonoid species (e. g. *Subanarcestes macrocephalus*).

Global eustatic and climatic changes during the Devonian obviously influenced the growth of ammonoids, but the precise effect of facies changes on the size of the ammonoids is still unclear.

JOHNSON, J. G., KLAPPER, G. & SANDBERG, C. A. 1985. Devonian eustatic fluctuations in Euramerica. *Geol. Soc. Am. Bull.*, **96**, 567-587. Boulder.

KULLMANN, J., & KORN, D. 1996. GONIAT, Version 2.60 (13,5 MB). Universität Tübingen.

# AMMONOID SUCCESSION IN DEVONIAN SECTIONS OF NORTHWEST AFRICA

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The significance of the Northwest African, and of the Moroccan Devonian sedimentary successions in particular, is caused by several conditions, of which the marvellous exposures and rich fossil content are worth mentioning. Despite the rich ammonoid occurrences, however many of the index species used for the global ammonoid zonation of the Devonian (BECKER in WEDDIGE 1997) are either extremely rare or even unrecorded. For instance, only 16 of the 59 index species were found in the fossiliferous and well exposed Ouidane Chebbi section at the eastern margin of the Anti-Atlas. Six of these species were only surface collected specimens. Similar ratios have been recognised in most of the other ammonoid-bearing localities in Northwest Africa (BECKER & HOUSE 1994), and many other well-investigated exposures yielded even

fewer stratigraphically important species. Mainly caused by "stroboscopic" occurrence of index ammonoids, the global zonation is therefore hardly applicable in the Devonian succession of Northwest Africa. Therefore we work on an ammonoid stratigraphy for Northwest Africa which is based on the most characteristic and abundant genera and species of this region. Only partially, these regional stratigraphical units resemble the genozones established by BECKER (in WEDDIGE 1997).

The figure displays the stratigraphical ranges of 33 selected index species on which a new stratigraphical scheme can be established. It contains species which show overlapping duration (bars) as well as species which have been collected from one single horizon (dot).

BECKER, R. T. & HOUSE, M. R. 1994. International Devonian goniatite zonation, Emsian to Givetian, with new records from Morocco. Courier Forschungsinstitut Senckenberg, Willi ZIEGLER Festschrift II, 169, 79-135. Frankfurt a. M.

WEDDIGE, K. & al. 1996. Devon-Korrelationstabelle. Senckenbergiana lethaea, 76 (1/2), 267-286. Frankfurt a. M.

DEVONIAN	FAMENNIAN	<i>Acutimitoceras intermedium</i> <i>Wocklumeria sphaeroides</i> <i>Parawocklumeria paradoxa</i> <i>Kalloclymenia subarmata</i> <i>Gonioclymenia speciosa</i> <i>Endosiphonites muensteri</i> <i>Sporadoceras orbiculare</i> <i>Platyclymenia annulata</i> <i>Maeneceras biferum</i> <i>Acrimeroceras falciculatum</i> <i>Cheiloceras subpartitum</i> <i>Falcitornoceras falciculum</i> <i>Phoenixites frechi</i>
	FRASNIAN	<i>Crickites holzapfeli</i> <i>Beloceras tenuistriatum</i> <i>Mesobeloceras kayseri</i> <i>Triainoceras costatum</i> <i>Koenenites lamellosus</i>
	GIVETIAN	<i>Petteroceras errans</i> <i>Pharciceras tridens</i> <i>Maenioceras terebratum</i> <i>Sellagoniatites discoides</i> <i>Agoniatites obliquus</i>
	EIFELIAN	<i>Agoniatites vanuxemi</i> <i>Cabrieroceras plebeiforme</i> <i>Subanarcestes macrocephalus</i> <i>Pinacites jugleri</i> <i>Foordites veniens</i>
	EMSIA	<i>Anarcestes lateseptatus</i> <i>Sellanarcestes wenkenbachi</i> <i>Latanarcestes noeggerathi</i> <i>Mimagoniatites fecundus</i> <i>Erbenoceras advolvans</i>

## FROM PLINY TO WALCH - 1700 PIONEERING YEARS OF AMMONOID RESEARCH

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Ammonite conchs attracted humans long before they became objects of scientific interest. For instance they were appreciated in Late Palaeolithic cultures, when decorative specimens were drilled through the umbilicus and used as beads. The first written documentation of interest in ammonites was probably by the Roman naturalist C. Plinius Secundus (23-79 A.D.), who in the 37th and last volume of his "Historia naturalis" stated briefly: "The Hammonis cornu is among the holiest gems of Ethiopia, it is golden in colour and shows the shape of a rams horn; one assures that it causes fortune-telling dreams."

Fossils were quite correctly interpreted by the Arabian-Persian physician and philosopher ibn Sina (lat. Avicenna; 980-1037), who, in a section on stones in his Kitâb al-Shifâ' (The book of the remedy), said that: "... If what is said concerning the petrification of animals and plants is true, the cause of this [phenomenon] is a powerful mineralising and petrifying virtue which arises in certain stony spots ...".

Around the year 1255, the Dominican monk Albertus Magnus wrote his "De mineralibus", quoting ibn Sina, but at the same time decorating his descriptions of properties of stones by numerous fantastic stories. Albert described the "Draconites" (the "snakestone"), a term borrowed from Pliny, which most probably referred to an ammonite: "I myself have seen in Swabia in Germany a stone [...] and it had a pale-coloured [stripe] around it, and a very beautiful picture of a serpent on it." It is interesting that ammonites up to the late 17th century were quite often regarded as petrified snakes.

It took then more than 300 years, until Conrad Gesner (1565) for the first time figured ammonites, e.g. an amaltheid specimen. Despite the fact that his contemporary Pierre Belon had already (1551) published an often copied figure of a *Nautilus* shell together with its septa and siphuncle, the cephalopod origin of ammonites remained undiscovered for a long period. Even towards the end of the 17th century, the ammonite nature was still under discussion. Robert Hooke compared ammonites with Recent *Nautilus* and reached the conclusion that ammonites are not only of organic origin but also widely resemble *Nautilus* (posthumously published in 1705).

With the delayed broad acceptance of Steno's concept (1669) of the distinction of organic fossils and minerals, from the beginning of the 18th century ammonites were interpreted as fossil sea shells, of which the living animals had not yet been discovered. A landmark in ammonite research is the comprehensive classification scheme given by Johann Jacob Scheuchzer (1716), a physician of Zurich better known to the scientific public for his interpretation of a large fossil salamander as "Homo diluvii testis" ("the victim of the universal deluge"), and for his monumental "Physica sacra".

The following 50 years were characterised by innumerable reports of ammonites from many different regions, and cope with questions regarding preservation and distribution of these fossils. The most opulent of these books is J.E.I. Walch's "Naturgeschichte der Versteinerungen", the "18th century Treatise of Invertebrate Palaeontology", published in five volumes between 1768 and 1773.

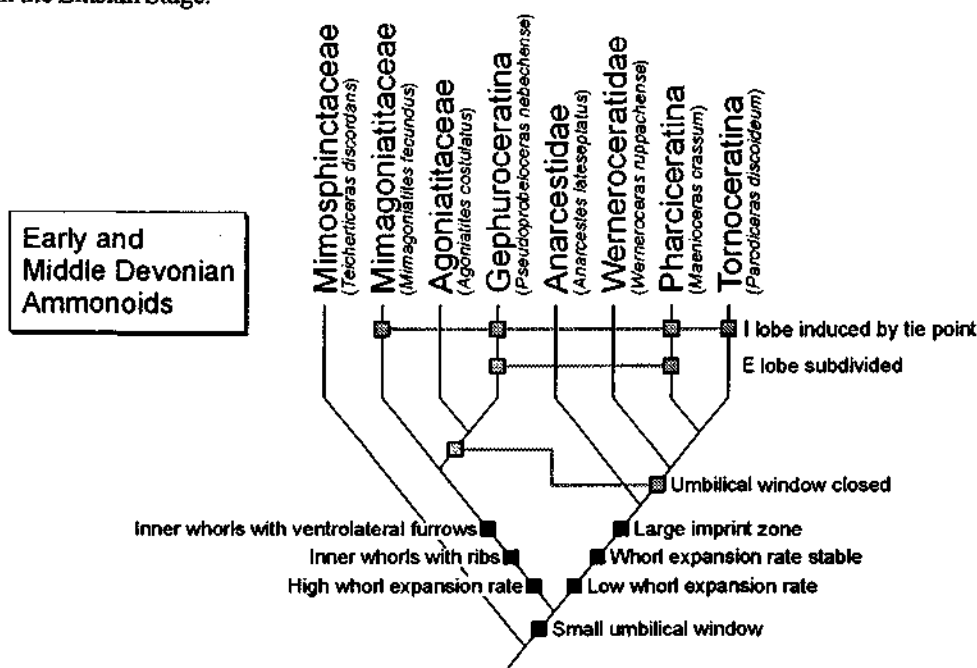
## PHYLOGENY OF EARLY AND MIDDLE DEVONIAN AMMONOIDS

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Cladistic analyses of Devonian ammonoids have not yet been achieved, although these fossils display a considerably large set of characters that would justify the application of such a method. To unravel the phylogenetic relationships of these forms, simultaneous stratophenetic and cladistic analyses were made, whose results partly support the scheme introduced by Erben (1964), but contradict in other respects.

The application of the two methods is based on characteristics regarding the coiling (whorl expansion rate, width of imprint zone, whorl cross section, and umbilical width), the septal apparatus (number and shape of lobes and their influence on septal geometry), and the ornamentation (growth lines and ribs). A new classification scheme is proposed in which the oldest ammonoids (order Agoniatitida) is subdivided into four suborders: Agoniatitina (paraphyletic), Gephuroceratina (monophyletic), Anarcestina (paraphyletic), and Pharciceratina (monophyletic). The suborders Gephuroceratina and Pharciceratina are regarded as independent phylogenetic lineages. The first are derived from agoniatitid ammonoids and the latter from anarcestids. Separation of the two units happened already in the Emsian Stage.



A separate analysis on the base of higher taxa which probably derived from the superfamily Mimocerataceae was made for the ammonoids of the Late Emsian, Eifelian and Givetian Stages. The most parsimonious cladogram, based on 18 informative characters, shows a separation of two independent evolutionary lineages of agoniatitid and anarcestid ammonoids. The analysis leads to the conclusion that the anarcestid ammonoids are distinguished from the agoniatitids by their very low whorl expansion rate which is stable during ontogeny and by their wider imprint zone of succeeding whorls. The closing of the umbilical window in the Emsian ammonoids and tridentation of the external lobe in gephuoceratids as well as pharciceratids are regarded as homoplasies.

ERBEN, Heinrich K. (1964): Die Evolution der ältesten Ammonoidea (Lieferung I). - Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 120 (2): 107-212, fig. 1-15, pl. 7-10; Stuttgart.

## AMMONOID FAUNAS FROM THE DEVONIAN AND EARLY CARBONIFEROUS OF THE CARNIC ALPS

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Devonian and early Carboniferous ammonoids have been known from several localities in the region of the Plöckenpass of the Carnic Alps since primary work was reviewed by Frech in the last century. Schindewolf revised Frech's collection and records of Kayser and Gortani and Von Gaertner added new records and described some sequences. This report is based largely on new collecting. No Lower Devonian records have been confirmed in this work. Middle Devonian records are sparse but include the anarcestids.

The Frasnian is well represented with faunas collected mainly by von Gaertner near the Wolayer Glacier including, *Ponticeras*, *Trimanticoceras*, *Maternoceras*, *Manticoceras*, *Probeloceras*, and *Beloceras* and aulacornoceratids but no evidence for terminal Frasnian faunas. The early Famennian Nehdenian is represented by *Cheiloceras* (*Torleyoceras*), *Cheil.* (*Cheil.*) and *Polonoceras*. Hembergian faunas are more varied and include *Platyclymenia*, *Rectoclymenia*, *Falciclymenia*, and the goniatites *Prolobites*, *Pseudoclymenia*, *Sporadoceras*, *Maeneceras*, *Lobotornoceras* and prionoceratids. The *Clymenia* Stufe is well developed at Grosser Pal and Casera Malpasso with the clymenid genera *Clymenia*, *Ornatoclymenia*, *Cyrtoclymenia*, *Cymaclymenia*, *Falciclymenia*, *Kosmoclymenia*, *Gonioclymenia*, *Sellaclymenia* and *Progonioclymenia*. Associated goniatites are *Discoctlymenia*, *Alpinites*, *Gondolfoceras*, *Maeneceras* and *Mimimitoceras*. They indicate the presence of the *acuticosta* and *ornata* Zones. Faunas match closely those of the Rhenish Massif but there is a high percentage of miniature forms. For example, the *Cl. laevigata* Group reaches only 40 mm in diameter in the Carnic Alps but more than 160 mm in the Rhenish Massif. Limestones of the *Wocklumeria* Stufe in sections at Grüne Scheid, Grosser Pal and Casera Malpasso yield *Kalloctlymenia*, *Finiclymenia*, *Sphenoclymenia*, *Wocklumeria*, *Parawocklumeria*, *Glatziella*, *Postglatziella*, *Kosmoclymenia*, *Linguaclymenia* and *Cymaclymenia* as well as the goniatites *Mimimitoceras* and *Balvia*. Early and late divisions are represented and the faunal composition is identical with equivalents in the Rhenish and Thuringian Massifs and Sudetans but lower in species diversity.

The Devonian-Carboniferous boundary is well exposed at Grosser Pal and Grüne Scheid (Korn 1992). The Hangenberg Event is represented by an unfossiliferous bed of marl. The latest Devonian *prorsum* Zone as well as the basal Carboniferous *acutum* Zone are represented by characteristic faunas, the latter with *Acutimitoceras*, *Gattendorfia* and *Eocanites*. Late Tournaisian goniatite faunas occur at three places in the Plöckenpass area with the genera *Merocanites*, *Muensteroceras* and *Ammonolepsites*.

# COLEOIDEA OF THE BOHEMIAN CRETACEOUS BASIN (CZECH REPUBLIC, EUROPE).

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Upper Cretaceous coleoids are represented by two different cephalopod groups - belemnites (Belemnitida Gray, 1849) and teuthid cephalopods (Teuthida Naef, 1916) in the Bohemian Cretaceous Basin (BCB). Belemnites: *Praeactinocamax plenus* (Blainville) occurs in the Late Cenomanian (Metoicoceras geslinianum Zone). The Plenus Cold Event (which enabled migration of this species into this area) was recently established for the BCB. Both the variability and possible sexual dimorphism are discussed for this species. *P. bohemicus* (Stolley) and *P. aff. bohemicus* are described from the latest Turonian (the base of the Teplice Formation of the Czech local stratigraphical scale). These species show affinities to belemnites from Greenland and North America however no relationship to belemnites from the Russian Platform. *Goniocamax lundgreni* (Stolley) is reported from the Middle Coniacian (Cremnoceramus crassus Zone) in the BCB.

Stage	Substage	Belemnites - No. of species			Teuthids - No. of species			
		1	2	3	1	2	3	4
Coniacian	upper							
	middle	■						
	lower							
Turonian	upper	■	■					
	middle				■			
	lower				■	■	■	■
Cenomanian	upper	■						
	middle							
	lower							

Fig. Coleoids diversity and the relation between belemnites and teuthids appearances in the Bohemian Cretaceous Basin (Czech Republic).

Teuthids: Occur in the Lower and Middle Turonian boundary interval in the BCB. Five genera (three of them new) and six and/or seven species are described on the basis of recent taxonomical re-evaluation of old collections. The radiation and diversification of this group is marked in the upper part of the Lower Turonian through lowermost Middle Turonian in the BCB. One of recently established genus probably represents a new family too. *Glyphiteuthis* sp. cf. *G. minor* is retained in the open nomenclature with respect to some differences from *G. minor* Fritsch. Appearance and radiation of teuthids in the upper Lower Turonian and Middle Turonian is possibly associated with the Late Cenomanian through Lower Turonian palaeoclimatical, ecological changes, belemnites local extinction and their areas reduction in the Central Europe.

## **SHELL - LOSS DUE TO PREDATION. - EFFECTS ON AMMONOIDS BUOYANCY.**

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The buoyancy regulation is one of the key functions for the evolutionary success of cephalopods. Ontogenetic and unexpected changes in buoyancy are dynamically adjusted by the osmotically driven hydrostatical apparatus. Evidences for its efficiency in buoyancy regulation in ammonoids are known from measurements of epizoans (HEPTONSTALL 1970) or from architecture of phragmocone/sipho (WEITSCHAT & BANDEL 1991). These investigations suggest that ammonoids had a much more effective buoyancy regulation than recent *Nautilus*. However, quantitative buoyancy calculations exist only for the compensation of an unexpected weight increase (HAPTONSTALL 1970). The compensation of sudden weight-loss, as occurring in context with shell-loss due to predation, may serve as an indicator for the buoyancy-apparatus efficiency. The current investigation focuses on the maximum of tolerable shell-loss in Mesozoic ammonoids. For this investigation, ammonites with significant shell loss were used that show later repair of the injury, thus indicating that the shell loss was not lethal and that the animal survived. On the basis of the volume equation of RAUP & CHAMBERLAIN (1961) after MOSELEY, the weight of the shell can be calculated. Knowing this, it is possible to calculate the relative weight-loss to the whole shell and therefore to compare the weight-loss. It can be shown that ammonoids tolerated sudden weight-loss 4 times more than the recent *Nautilus*.

To compensate weight-loss, both ammonoids and nautiloids had, after the recent understanding, to refill some liquid into the phragmocone. The amount of these liquid is shown in the table:

genus	max. shell loss in %	max. liquid refill in % phrag. – volume
Harpoceras	14	9
Dactylioceras	11	8
Nautilus	4*	2*

\*data based on WARD (1986)

Although the emptying mechanism is basically understand (GREENWALD et al. 1982), we did not understand anything about the refill of liquid into the phragmocone. The results of the current investigation suggests a much higher ability to refill liquid into the phragmocone in ammonoids than in *Nautilus*.

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The siphonal epithelium.- Journal of Morphology, 172:5-22; London

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RAUP, D.M. & CHAMBERLAIN, J.A.Jr. 1967. Equations for volume and center of gravity in ammonoid shells. Journal of Paleontology, 41 (3): 566-574; Tulsa

WARD, P. D. 1986. Rates and Processes of Compensatory Buoyancy Change in *Nautilus macromphalus*. – Veliger, 28 (4): 356-368; Berkeley

## A MAJOR PHYLLOCERATID-LYTCERATID FAUNAL TURNOVER IN THE LOWER JURASSIC

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Knowledge of earliest Jurassic phylloceratid and lytoceratid ammonites is hampered by the widespread absence of Tethyan Hettangian to Lower Sinemurian pelagic ammonite bearing rocks. Those present are often condensed, containing several ammonite zones within less than 1m of sediment and characterized by minor or major gaps between the zones (e.g. Northern Calcareous Alps). The most prominent hiatus within the Austrian Alps but probably also in other Alpine Mediterranean areas is present around the Hettangian-Sinemurian boundary and especially in the lower part of the latter. During this interval all Hettangian phylloceratids (*Paradasyceras*, *Nevadaphyllites*, *Fergusonites*, *Togaticeras*, "*Geyeroceras*" s.l.) are replaced by well known long ranging Liassic respectively Jurassic forms (*Phylloceras*, *Partschiceras*, *Calaiceras*, *Geyeroceras*, *Juraphyllites*). The same happens with the Lytocerataceae where *Pleuroacanthites*, *Eolytoceras* and *Analytoceras* are followed by a wealth of "true" lytoceratid genera such as *Trachyphyllites*, *Lytoceras* s. str. *Holcolytoceras*, *Aegolytoceras*, *Lytotropites* and *Adnethiceras*. The rapidity of the faunal replacement is difficult to assess due to insufficient sequential data. The indirect cause may have been a major sea level rise in the Tethyan realm which is documented by the common onset of the pelagic ammonitico rosso facies above many shallow water areas (drowned Triassic carbonate platforms) in (Upper) Sinemurian time.

## TRIASSIC AMMONOIDS AND THE HIMALAYAS

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The Himalayas represent the most complete tropical Triassic Ammonoid record within a single geographic region, and the importance of the Himalayas (including the Salt-Range) for Triassic Ammonoid biostratigraphy is similar to the one of Western Europe for the Jurassic. Of currently 35 discriminated standard zones, all except the youngest are known by diagnostic faunas. Due to the continuous record and an appropriate sedimentation rate the region will have growing importance in the near future as one of the primary study sites for high-resolution subdivisions (subzones p.p. horizons). Historically, it was the stratotype region for the biostratigraphic definition of the base of the Triassic epoch and by this of the Mesozoic era. Its extraordinary importance for Tethyan Lower Triassic ammonoid subdivisions is still valid (Guex 1978, Krystyn & Orchard 1996).

From palaeoecologic viewpoint the well documented sealevel changes and the general shallowing of the Upper Triassic sediment series of the Himalayas (Garzanti et al 1995) may provide plenty of information concerning live habitat of ammonites and their adaptation to changing environments whenever they will be studied in context. For example the evolutionary patterns of the *Tibetitidae* (Krystyn 1982) as the pioneering and very early group of pseudoceratitic ammonites could be seen as a direct or indirect response to the changing water depth of the Upper Triassic Himalayan shelf.

Another important topic is the still unsolved question of (sexual) dimorphism in Triassic Ammonoids (Davis et al. 1996). For a meaningful distinction of antidimorphic pairs in species collections of autochthonous shells are strictly necessary. The Himalayas are one of the rare Tethys areas where autochthonous faunas are available in larger quantities. Pelagic ammonoid faunas of the Tethys are usually of Hallstatt-type and completely unsuitable because they form condensed lag deposits and/or current induced shell concentrations. Krystyn 1982 describes from the Nepalese Himalayas two morphologies of mature individuals in the Upper Triassic genera *Jovites* and *Tropijuvavites* which differ in shell shape and ripping strength. They could form a case of sexual dimorphism different from the Jurassic one but otherwise similar to that of recent cephalopods.

# **MORPHOLOGY OF THE EARLY WHORLS OF GONIATITES FROM THE CARBONIFEROUS BUCKHORN ASPHALT (OKLAHOMA) WITH ARAGONITIC PRESERVATION**

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We investigated the morphology of the early whorls of goniatites from the Upper Carboniferous Buckhorn Asphalt (Oklahoma). The specimens show aragonitic preservation. They probably all belong to a single species or several closely related species. The ammonitella is approximately 0.8 mm in diameter. The initial chamber is wide and is covered by the first whorl of the ammonitella. The outer surface of the ammonitella is smooth without any trace of ornamentation or growth lines. In contrast, growth lines occur on the postembryonic shell. The initial chamber terminates in a thickened flange. There is an elongate muscle scar on the inner surface of the initial chamber just behind the flange. The wall of the initial chamber consists of three layers, the outermost of which is the dorsal wall of the next whorl. The wall of the ammonitella also consists of three layers: an inner prismatic layer representing the mural part of the proseptum and subsequent septa, a middle granular layer representing the wall proper of the ammonitella, and a very thin outer prismatic layer. The ammonitella wall is covered by the dorsal wall of the next (postembryonic) whorl. The wrinkles on the dorsal wall first appear near the apertural margin of the ammonitella. The wrinkles do not extend to the umbilical seam. The proseptum and second septum are closely spaced in median cross-section. The proseptum is prismatic and the second septum is nacreous. The morphology of these ammonitellas is similar to that of the ammonitellas of Mesozoic ammonoids with the exception that there is no ornamentation on the ammonitella in goniatites. This similarity in morphology implies a consistent mode of formation of the ammonitella.

## THE ULTRASTRUCTURE OF THE DORSAL SHELL WALL OF MESOZOIC AMMONOIDS

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Ultrastructure of the dorsal shell wall at the postembryonic stage was studied and compared in some genera of Mesozoic ammonoid suborders: *Lytoceratina* (*Tetragonites*); *Phylloceratina* (*Phyllopachyceras* and *Hypophylloceras*), and *Ammonitina* (*Quenstedtoceras*, *Aconeceras*, *Yokoyamaoceras*, and *Damesites*). The dorsal shell wall of these ammonoids consists of several components deposited sequentially, beginning at the aperture of the living chamber inwards. It attains a full thickness near the last septum. The outermost element of the dorsal wall, visible in the apertural region, is the "wrinkle layer". The wrinkle layer directly covers the ventral wall of the preceding whorl, and consists of acute-angled triangular elements in longitudinal section. The acute apex of the triangle is oriented adapically, and the steep side of the triangle forms its adapertural end. The above elements seen from inside of the living chamber are variable in size and are arranged in parallel to the growth lines, forming different characteristic patterns (Walliser, 1970). The triangle usually has aragonitic infilling. A further stage of dorsal wall development involves filling the space between the apices of triangles, and then adding one or more layers from the inside.

In all genera studied, the above type of the wrinkle layer occurs at least in the early postembryonic stage. In the *Ammonitina* (*Quenstedtoceras*, *Yokoyamaoceras* and *Damesites*), and *Lytoceratina* (*Tetragonites*), no modification was observed. *Phyllopachyceras* (*Phylloceratina*), however, displays rhythmically recurring incurvation of the outer layers of periostracum towards the posterior of the shell. In *Hypophylloceras* (*Phylloceratina*), the periostracum does not bend toward the posterior, but the free, elevated ends of the periostracum are directed adorally.

In *Aconeceras* of the *Ammonitina*, another modification was noted. In the mature stage, this genus shows a marked thickening of the dorsal wall in the apertural area, indicating continuation of calcium carbonate precipitation there during arrested growth. It is concluded that the wrinkle layer develops as a result of carbonate precipitation in the area of supracephalic fold of the mantle. The precipitation preserves the microornamentation of the periostracum originating at the shell edge.

Walliser, O. H., 1970. Über die Runzelschicht bei Ammonoidea. *Göttinger Arb. Geol. Paläont.*, 5: 115-126.

## **AMMONOID EVOLUTION DURING THE CRITICAL INTERVALS BEFORE AND AFTER THE DEVONIAN-CARBONIFEROUS BOUNDARY AND THE MID-CARBONIFEROUS BOUNDARY**

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New calculation of the diversity development of ammonoids during the Carboniferous period have been made possible by using the data stored in the database GONIAT. available in the INTERNET ([www.uni-tuebingen.de](http://www.uni-tuebingen.de), KULLMANN et al. 1998); it is especially designed as a tool for investigations on the systematics of Palaeozoic ammonoids, their palaeogeographic distribution and their biostratigraphic range.

The quantitative and qualitative analysis concentrates on the epochs immediately before and after two fundamental crises in ammonoid evolution: the Devonian-Carboniferous boundary (DCB) and the Mid-Carboniferous boundary (MCB) between the Lower and the Upper Carboniferous subsystems. Both epochs represent critical intervals: several major groups became extinct some time before or at the respective boundary, and some groups were new after the boundary. Only few species crossed the DCB and the MCB.

The changeover at the DCB and MCB are in reality changes in the composition of the faunas. In both cases the morphologic differences concern the configuration of the suture-line and the shell characteristics of their early whorls; significant characters are also the ornamentation and conch shape and size. The general aspect of conch form and suture of the younger faunas (early Tournaisian after the DCB, lower Bashkirian after the MCB) indicates a less advanced degree of the internal characters than the advanced forms of the stratigraphically older faunas (late Famennian before the DCB, Arnsbergian before the MCB).

Both critical intervals had characteristics in common: the older faunas were usually diverse in conch shape and size showing the tendency toward involution of relatively large whorls; many species were strongly ornamented (Clymeniida, partially Tornoceratina before DCB, Girtyoceratidae before MCB). The younger faunas started with smooth and relatively small forms (Prionoceratidae after DCB, Homoceratinae after MCB). The early growth stages were characterised by a wide and low whorl section lacking strong involution of the whorls. The relatively wide conchs gave the young whorls a pachycone or even globular appearance, later growth stages were pachycone or subdiscoidal.

The similarities in ammonoid evolution during the critical intervals under consideration are (1) stepwise decrease in diversity before the boundary from a high diversity phase to a low diversity phase, (2) after the low point the origin of new groups with extremely wide, but small whorls and a low grade of involution, (3) onset of a high diversity phase with complicated conch forms and ornamentation.

The duration of the decrease phase can be estimated at about 3 m.y., but the low diversity phase seems to be very short. The increase phase was apparently shorter than the decrease phase (1 m.y.) with unfavourable life conditions and stressed biota resulting in a graded extinction; possible causes are: sea-level changes due to tectonic activity or glaciation, global cooling caused by decrease of atmospheric CO<sub>2</sub> due to limestone production after uplift and erosion. At present, a fully plausible explanation is not in sight.

## **PALAEOZOIC AMMONOIDEA IN THE DATABASE SYSTEM GONIAT**

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GONIAT is designed as a tool for investigations on the systematics of the Palaeozoic ammonoids, their palaeogeographic distribution and their biostratigraphic range. This database management system provides not only determinations based on morphological characteristics, but also information on occurrence, duration, literature, and phylogenetic relationships of every taxon of family, genus, and species levels. GONIAT is available in the INTERNET (<http://www.uni-tuebingen.de>; KULLMANN et al. 1998).

GONIAT has been established at the University of Tübingen (Germany) as part of a research project (DFG, grant no. Ku164/8: Diversitätsentwicklung und Provinzialismus der Ammonoideen-Faunen im Paläozoikum). The actual GONIAT version 2.8 is using the software package dBASE IV, equipped with a supplementary GONIAT program. It is arranged in the concept of a relational database structure. It consists of six independent databases connected by three link information files: TAX for taxonomy, MORPHA/MORPHB for all distinctive morphological characters in adult or early and middle growth stages, LIT for literature, LOC for localities, BOUND for biostratigraphy. In order to achieve relevant time planes which can be used on a world-wide scale, the radiometric time scale is used as well as biostratigraphic names of global or regional significance. The morphology is described in two MORPH databases (for different growth stages); because of the linkage of these with TAX and BOUND the user does not recognise the separate parts of GONIAT.

The data of each separate database can be looked up on the screen, either one record after another, or as a list.. The linkage of the databases enables the user to switch from one database to another. If viewing TAX, the user can look up the taxonomy and morphology of each taxon, and switch over to a list of the localities and publications connected with that taxon. While examining LOC, the user can immediately produce a list of all species which have been found in a particular layer, and all publications which describe this goniatite locality. In LIT the user can look up the records of the taxa or their localities described in a special publication. The search command enables the user also to search for special characters of the morphology, e.g. characteristics of shell form, ornamentation, suture. Each search condition can be combined with questions concerning the time range.

GONIAT is not yet completed. It includes the complete set of records of the categories Family, Subfamily, Genus, and Subgenus presently recognised. Species and subspecies are covered to at least 95 %. The actual version contains 6219 TAX, 6696 LOC, 1270 LIT, 675 BOUND and 620 PICTURE records. Picture files are incorporated for illustration of ammonoids and localities. System requirements are: IBM compatible PC with DOS, WINDOWS 3.1 or WINDOWS 95/98/NT, 25 MB hard-disk storage; the GONIAT homepage provides the download function for GONIAT database, pictures in PCX format and instruction booklet in WORD6 (including manual of codes, boundaries, classification).

## A GIANT SQUID IN NEW YORK CITY

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On June 10, 1998 a giant squid arrived at the American Museum of Natural History. The squid, a specimen of Architeuthis kirkii Robson, 1887, was caught by commercial fishermen along the Chatham Rise off New Zealand in late December, 1997, while trawling for fish at a depth of 672 m. The fishermen immediately froze the specimen and contacted S. O'Shea who telephoned N. Landman and offered the squid to the American Museum as a gift of the New Zealand National Institute of Water and Atmospheric Research (NIWA). The squid was transported via refrigerated truck from Wellington to Auckland, New Zealand, then by air cargo from Auckland to New York (with a stop over, and unscheduled delay, in Los Angeles), and then by refrigerated truck to the Museum. The squid was injected with and fixed in a bath of 10% saline formalin solution. After two weeks in this solution, the squid was bathed in freshwater and then preserved in 70% ethanol. The two long tentacles are broken off but otherwise the specimen is in an excellent state of preservation with only minor damage to the fin and one of the arms. (A pair of tentacles was procured from another New Zealand specimen of similar size to assemble a complete giant squid for public display.) The specimen is relatively small (dorsal mantle length = 1.24 m), and was originally thought to be a juvenile. However, the presence of a penis and the discovery of a spermatophore indicate that it is a mature male. Mature females of this species from New Zealand tend to be larger with a mantle length of as much as 2 m. Seven other specimens (5 mature males and 2 mature females) were captured at this location during the same time period (December-April). These occurrences suggest that the austral summer may coincide with the time of mating. Further inspection of the historical records of giant squid sightings may reveal insights into the life history patterns of these enigmatic animals.

**MICROBIOLOGICAL AND PHYSIOLOGICAL STUDIES ON BACTERIA POPULATIONS IN THE PERICARDIAL COELOM OF *NAUTILUS POMPILIUS* L.(CEPHALOPODA, TETRABRANCHIATA).**

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Cytological studies on the excretory pericardial appendages of *Nautilus pompilius* L. and *N. macromphalus* G.B. Sowerby revealed abundant bacterial colonies within cavities of the pericardial coelom and the brush border of the coelomic epithelia, an environment with a high ammonia concentration<sup>3)</sup>. First attempts at a microbiological characterization classified them as species belonging to the genus *Pseudomonas*<sup>4)</sup>. More recent microbiological studies on *Nautilus p.*, however, give evidence that there are several genera and species of bacteria. From each of 4 adult animals from Philippine coastal reefs 4, 8, 14 and 12 different types of bacterial colonies were cultivated using different nutrient media. In the standard I nutrient agar and the tryptic soy agar containing 2% NaCl most of the colony types were isolated. By means of several microbiological methods - Gram stain, spores staining, O/F-test and tests on the motility, the carbohydrate utilization, the acid production from different sources of carbohydrates, the pattern of enzymatic activities, the gelatine stab test as well as the numerical analysis of fatty acid patterns<sup>2)</sup> - twelve isolates (three from each animal) were identified:

Animal-No	Colony Type	Genus/Spec. of Bacteria	Animal-No	Colony Type	Genus/Spec. of Bacteria
12/95	orange	<i>Deinococcus</i> sp.	1/97	orange	<i>Nocordia asteroides</i>
	cream-white	<i>Brevibacterium linens</i>		cream-white	<i>Rhodococcus</i> sp.
	light yellow	<i>Micrococcus linens</i>		light yellow	<i>Micrococcus varians</i>
3/96	red-orange	<i>Deinococcus</i> sp.	4/97	orange-red	<i>Micrococcus roseus</i>
	cream-white	<i>Brevibacterium linens</i>		light yellow	<i>Micrococcus varians</i>
	light yellow	<i>Micrococcus luteus</i>		light yellow	<i>Micrococcus varians</i>

All species are Gram-positive, chemoorganotrophic, non-motile coccoid forms without sporulation and showed cyclic morphological changes during their growth. Neither of them had been found in cephalopods up to now but all are typical of marine habitats<sup>1)5)</sup>. With regard to their possible role as symbiotics of *Nautilus* it is of interest, that in ammonia tests (method of Berthelot) at least in mixed cultures - except for *M. roseus* - all species were able to significantly reduce the ammonia concentration in a minimal medium; *M. luteus*, *N. asteroides* and *Rhodococcus* sp. showed this also in pure cultures. The lack of homogeneity in the populations of the pericardial organs of the 4 specimens, however, suggests the need for further studies with bacteria from freshly captured animals.

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## THE TROPHIC CONTROL ON THE FUNCTION OF THE AULACOCERATID AND BELEMNOID GUARD AND PHRAGMOCONE

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The basic shape of the guard and phragmocone of aulacoceratids and belemnoids did not change for nearly 290 million years from the Upper Devonian to the end of the Cretaceous, showing the high efficiency of this combined buoy-ballast structure. It was suggested to balance the body. Calculations showed that the phragmocone balanced the guard (rostrum) in horizontally swimming belemnoids (Monks et al., 1996). However, the advantage of the buoy-ballast structure at the posterior end of the body was not clarified. Whereas the rostrum has a certain weight, the change in liquid content within the phragmocone enables it to change the relative weight of the posterior part of the body. This adjustable posterior ballast must have balanced a change in weight in the frontal part for maintaining a horizontal orientation while swimming.

Calcareous skeletal fragments in the stomach content of ammonoids and extant cephalopods (Jäger and Fraaye, 1997) may hint that the aulacoceratids and belemnoids likewise swallowed the whole prey on its crushed skeletal fragments. It is suggested that the rostrum-phragmocone coupled structure balanced the accumulated weight of the skeletal fragments in the stomach in the anterior part of the body. This enabled it to rapidly swallow great quantities of prey till the accumulated skeletal fragments had to be emitted. It also balanced the horizontally swimming creature while in its arms it was holding a prey which comprised of a heavy exoskeleton. The calcareous and chitinous rostrum of the Upper Paleozoic aulacoceratids became completely calcified (hence heavier) in the Mesozoic belemnoids, suggesting that the latter enriched their diet with prey comprising calcareous skeletons. The evolutionary diversification and increase in abundance of the Boreal belemnoids is associated with the appearance of the calcareous opercular aptychi in Late Liassic ammonoids in the same province. Since ammonoids consumed smaller ones (e.g. Jäger and Fraaye, 1997), belemnoids may have preyed upon ammonoids as well. This kind of food became scarce in latest Cretaceous times and disappeared in the Early Cenozoic. The belemnoids (or ancestral sepiids) had to change their diet to prey with a low (or no) content of calcareous components. The balancing function of the rostrum and phragmocone became useless with this new diet, and their disadvantageous presence in the posterior part of the body had to be eliminated. The Early Tertiary descendants of the belemnoids rapidly reduced the size and weight of the rostrum, and changed the shape of the phragmocone in two trends, as exhibited by the extant *Spirula* and *Sepia*. The bullet-like elongated shape of the rostrum and its pointed end provided secondary means of protection, and enabled the attachment of the muscles of the fins (Monks et al., 1996).

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Monks, N., Hardwick, D., and Gale, A.S., 1996. The function of the belemnite guard. *Paläont. Z.* 70, 425-431.

## TWO AMMONITE MASS-OCCURRENCES OF THE ALPINE LOWER CRETACEOUS (NORTHERN CALCAREOUS ALPS, UPPER AUSTRIA)

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Palaeoecological, sedimentological studies have been carried out in an outcrop in the Ternberg Nappe in Upper Austria. The exact position is about 7 km west of Losenstein, 1 km south of Kienberg and 500 m southwest of the Klausriegler inn (652 m, ÖK 1:50000, sheet 69 Großraming). The assembled stream outcrop (47°55' N and 44°21' E) crosses the western part of the Losenstein Syncline at this point which in this section is in east-west direction between the Kreuzmauer (853 m) in the north and the Pfaffenmauer (1218 m) in the south.

Both mass-occurrences are exposed in stratigraphical order in a single section measuring about 200 meters embracing the complete Lower Cretaceous sequence of upper Steinmühl Formation (U.Berriasian - L.Valanginian), Schrambach Formation (L.Valanginian - U.Barremian) and Tannheim Formation (Aptian). Both mass-occurrences lie in strata of the Schrambach Formation. Of importance is the fact that only in the Losenstein Syncline both mass events are preserved (or at least reported). The two mass-occurrences found in the Ternberg Nappe have different origins, not least because of their different preservation modes and probably also scales.

The first one consists essentially of *Olcostephanus (Olcostephanus) sayni* KILIAN (80%, 126 specimens) in a bed up to 1m thick and is of Upper Valanginian age. Material within the *Olcostephanus* beds is essentially broken and fragmented. Comparable occurrences have previously been reported from western Europe, extending from S.-France, through Switzerland (the Astierian Beds) to northern Germany, but are as yet unreported from the Northern Calcareous Alps and eastern parts of Europe.

The second ammonite mass-occurrence in a bed only 15 cm thick consists essentially of *Karsteniceras cf. pumilum* UHLIG (93%, 535 specimens) and is of Barremian age. The sediment is dark-grey to black with an increasing content of organic matter and pyrite. The high content of 0,89% TOC against 0,22% TOC in the surrounding limestones shows the at least semianoxic condition in the bottom-water column at the time of formation. The material in the *Karsteniceras* mass occurrence is extensively entire. This is unknown elsewhere in the Northern Calcareous Alps or western Europe, but has been described from the Outer Carpathians of the eastern Czech republic. A mass-occurrence of *Leptoceras* from the Berriasian of S.-France is also essentially monospecific and has a similar field appearance as the Austrian Barremian situation.

**SHELL-ACCUMULATION OF THE NAUTILIDAE *ATURIA (ATURIA) ATURI* (BASTEROT, 1825) IN THE RETZ-FORMATION (LOWER AUSTRIA, UPPER EGGENBURGIAN, LOWER MIOCENE)**

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Sediments of the Retz-Formation near Obermarkersdorf occur along a small crystalline crest, which corresponds to one of the numerous small offshore islands, characterising the coastal line along the Bohemian Massive in the area around Retz during the Upper Eggenburgian.

Gastropods predominate the taphocoenosis with abundant *Diloma (Paroxystele) amedei*, *Babylonia eburnoides* and *Ficopsis (Fulguroficus) burdigalensis gauderndorfensis*. Mytilidae prevail among the bivalves, besides *Acanthocardia moeschani* and rare *Glycymeris fichteli*, which were embedded both partly with articulated, gaping shells. The fauna indicates a parautochthonous occurrence of rocky littoral species mixed with subordinate infaunal molluscs from the adjacent sandy littoral to sublittoral.

The most remarkable allochthonous component of the fauna is the Nautilidae *Aturia (Aturia) aturi* (BASTEROT). At least 16 specimens of the cephalopod within one concretion represent an unexpected abundance in this littoral, high energy environment. The shells are mainly broken and fragmented, only two specimens show an intact body chamber. The largest complete specimen has a diameter of 31mm, while single chamber-casts suggest a size about 40mm. Since the shells are dissolved, only steinkerns and moulds are present, but the excellent preservation of sutures and siphonal structures allows a distinct identification.

Another similar mass-occurrence is documented from a sand pit at Unternalb, where *Aturia aturi* is associated with littoral to shallow sublittoral infaunal molluscs.

The necroplanktonic characters of Recent *Nautilus*-shells are well documented, furnishing evidence for postmortal driftings of 3000km distance and floats of more than one year, which are reflected in bioerosion and epifaunal settlement. Open sea surface drift-routes are strongly associated with currents, whereas nearshore drifts are mainly induced by wind directions. Although the actualistic ecological comparison of *Nautilus* with the fossil *Aturia* is complicated by differences in shell outline and suture-line, which may be the result of an adaptation to different habits, the general drift-behaviour is supposed to be identical.

Thus the cephalopod shell-accumulations at Obermarkersdorf and at Unternalb are interpreted as postmortal, allochthonous occurrences. The absence of epifauna or bioerosion points to a short drift-stage, the high percentage of fragmentary shells at Obermarkersdorf corresponds with the high energy environment of the sedimentation area, therefore breakage took place at the shore after the drift-stage.

The high density of nautilid-shells in the coastal sediments of the Retz-Formation is explained by a fairly exposed position of the coastal line, where currents and storms washed the shells ashore from the adjacent deeper molasse-basin. Analogous shell concentrations of *Nautilus pompilius* at the west coast of Thailand suggest rather an accumulation of specimens during a period of several years than by a single storm event.

**EFFECTS OF COMPACTION IN AMMONITE MOULDS AND THEIR TAPHONOMIC IMPLICATIONS. AN EXAMPLE FROM THE ROSSO AMMONITICO OF THE NORTHERN APPENNINES (EARLY-MIDDLE TOARCIAN, UMBRIA-MARCHE, ITALY).**

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Encrustation and/or bioerosion have been observed on both sides of several ammonites sampled from Early-Middle Toarcian Rosso Ammonitico of Umbria-Marche Apennines (Central Italy). The majority of these features are due to the activity of polychaete worms, the simple encrustation is due to serpulids whilst the main simple bioerosion is referable to an unknown ichnogenus similar to *Maeandropolydora* VOIGT. The ornamentation features of the studied samples allowed us to recognise that the recorded upper sides are preserved as composite moulds, while the lower sides as internal moulds. The overprinting of the external shell structures on the internal infillings took place during burial diagenesis.

The presence of boring and/or encrustation in the lower side of an internal mould is classically interpreted as evidence of reworking. Regarding our specimens, if the colonisation phase in their lower sides took place on the internal moulds, it should have occurred after the compaction phase which is characteristic of deep burying. In this case the stratigraphic position of the encrusted and bored moulds should have been sensibly anomalous. Instead, the case-studied specimens are associated with others of the same species which are not encrusted and/or bored, and their stratigraphic position coincide with biostratigraphic data known in literature. Furthermore, none of the studied ammonites display any discontinuity between the body chamber infilling and the surrounding rock and some of them display geopetal structure in agreement with the polarity of the stratigraphic succession.

In our interpretation the phenomena of encrustation and/or boring by polychaete worms occurred before the dissolution of the shells, but it is impossible to ascertain whether the shell was already infilled or not. The encrustation by polychaete worms probably occurred during post-mortem drifting or when the shell was exposed on the sea floor.

The preservation of only half of the boring galleries establish that the shell was in situ when the simple bioerosion phenomena occurred. Similar features have been observed in *Maeandropolydora decipiens* VOIGT, which bores also along the boundary between the calcitic and the aragonitic layers of some bivalve shells and the side of others encrusted to the substrate. In conclusion, there is no need to hypothesise the exhumation of the shell to justify the boring action.

Encrustation and bioerosion cannot be univocally considered as reworking criteria without taking into account other taphonomic evidence, linked to diagenetic processes. It can be seen that the validity of encrustation reworking criterion, is here reinforced: the lower sides of the samples studied (now internal moulds), which are now encrusted, were not originally the surfaces in contact with the substrate at the time of the last sediment burial.

## THE LAST MAASTRICHTIAN AMMONITES IN POLAND

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Latest Maastrichtian ammonites are known from a few regions in Europe (Kennedy 1993). Recent studies of the Late Maastrichtian ammonites from Kazimierz Dolny area, Poland (Marcinowski & Radwanski 1996; Machalski 1996; Machalski & Jagt 1998; Jagt *et al.* 1999), add to the previous data (Błaszkiwicz 1980; Kennedy 1993) on this youngest Polish ammonite fauna. The sections studied comprise a siliceous chalk called Kazimierz Opoka, and an overlying Danian greensand with reworked Maastrichtian fossils.

In total, seven ammonite taxa representing both Ammonitina and Ancyloceratina have been recognised. Of these, *Baculites* sp. and *Hoploscaphites constrictus* (J. Sowerby) occur abundantly throughout the Kazimierz Opoka. Other taxa are extremely rare: *Acanthoscaphites* (*Euroscaphites*) *varians varians* (Łopuski) (see Jagt *et al.* 1999) and *Diplomoceras cylindraceum* (Defrance) occur in the lower part of Kazimierz Opoka, whereas *Menuites terminus* (Ward & Kennedy), *Pachydiscus jacquoti* Seunes, and *Sphenodiscus binckhorsti* (Böhm) are known from its upper part. The greensand has yielded two specimens of *H. constrictus*.

Two parataxa of aptychi have also been recorded (Machalski in prep.). These are "*Aptychus*" *portlocki* Sharpe, which occurs throughout the Kazimierz Opoka and in the greensand, and *Rugaptychus rugosus* (Sharpe) in the lower part of the Kazimierz Opoka.

The presence of *M. terminus* places the upper part of the Kazimierz Opoka in the highest Maastrichtian ammonite zone, the *M. terminus* Zone. However, a biometric study of *H. constrictus* as well as dinoflagellate data suggest a stratigraphic gap at the top of the unit (Machalski 1996).

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## WENLOCK AND LUDLOW CEPHALOPODS IN THE PRAGUE BASIN: COMMUNITIES, PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY (BOHEMIA)

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All known data collected since Barrande's time, together with a new data, have made possible a re-evaluation of the cephalopod distribution in the Prague Basin. The Wenlock and Ludlow deposits in the Prague Basin are developed as three facies: volcanic and shallow-water limestone facies, cephalopod limestone facies, and pelagic facies.

In the volcanic and shallow-water limestone facies occur communities with dominant brachiopods or corals; nekto-benthic nautiloids and orthoceratids are sporadic (*Kionoceras*, *Dawsonoceras*, *Phragmoceras*). The cephalopod limestone facies is developed on several tectonic elevations. The cephalopod evolution was influenced by a total range of the Silurian cephalopod facies which were controlled by eustatic movements and surface currents. Cephalopod facies occur in the Prague Basin as well as in Perigondwana in the *T. testis*, *C. colonus*, and *M. linearis* zones. The Wenlock and Ludlow cephalopod facies was occupied by recurrent communities of the Geisonoceratid Biofacies being characterised by dominant nekto-benthic orthoceratids (*Geisonoceratidae*, *Paraphragmitidae*, *Kionoceratidae*, *Proteoceratidae*), several nekto-benthic nautiloids, and subdominant pelagic orthoceratids (*Michelinoceratidae*, *Arionoceratidae*). The pelagic facies (especially hemipelagites, pelagites and cephalopod wackestones) were deposited close to the submarine volcanic elevations. From the Homeric, and during the Gorstian and Ludfordian the pelagic facies characterised by anoxic and dysaerobic conditions was occupied by a typical cephalopod dominant, pelagic community (with associated graptolites). In this low diversity community occur orthoceratids (*Kopaninoceras*, *Arionoceras*, *Parakionoceras*, *Plagiostomoceras*, *Michelinoceras*, and in the Gorstian to lower Homeric also *Aptychopsis*). The community is formed by free swimming or floating nekton living in the upper part of the water column.

Analysis of cephalopod distribution in the Prague Basin shows that post-mortem drift of the cephalopod shells was insignificant. The Silurian cephalopods belong to a natural associations (communities in Boucot's concept) which were modified only by local taphonomic processes. The significance of cephalopods for bathymetric analysis (in Westermann's concept) seems to be problematic. Cephalopod larvae were transported by surface currents across the north Gondwana and Perunica basins. The Silurian cephalopod fauna of the Prague Basin contains typical Perigondwanan elements and has relationships to the Laurentia, Baltica, and Avalonia.

## DIMORPHISM IN MIDDLE CARBONIFEROUS AMMONOIDS FROM THE SOUTHERN MIDCONTINENT, UNITED STATES

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Approximately 78 species, representing 47 genera and 22 families, comprise the ammonoid assemblage recovered from Chesterian (Upper Mississippian) and Morrowan (Lower Pennsylvanian) strata exposed across northern Arkansas and eastern Oklahoma. For most taxa, large collections numbering hundreds of specimens are available for morphometric analysis from single horizons at single localities. Most individuals are approximately the same size at a particular locality, and these occurrences are interpreted as reflecting semelparous mass mortality of sexually mature individuals. Thus, it seems reasonable to assume that both sexes are represented in these accumulations, since sexes are separate in extant cephalopods.

Middle Carboniferous ammonoid species from the southern midcontinent exhibit predictable changes in both their basic conch parameters (width, height, umbilical diameter) and sutures that clearly reflect ontogeny (expressed as increasing diameter). The bulk of the taxa do not display variation that can be attributed to dimorphism. Only eight genera (17%) exhibit exceptions to this generalization, including the Chesterian girtyoceratid *Tumulites varians* McCaleb, Quinn & Furnish and the cravenoceratid *Emstites fayettevillae* (Gordon), and the Morrowan glaphyritid *Syngastrioceras globosum* (Easton), the reticuloceratids *Retites semiretia* McCaleb, *Arkanites relictus* (Quinn, McCaleb & Webb), *Quinnites henbesti* (Gordon) and *Q. textum* (Gordon), the schistoceratid *Branneroceras branneri* (Smith), and the welleritids *Axinolobus modulus* Gordon and *A. quinni* McCaleb & Furnish. Antidimorphic pairs occur in all assemblages that contain these taxa. The antidimorphs are characterized by a subglobose form with large umbilicus and depressed whorls, and a subdiscoidal form with a comparatively more narrow umbilicus and compressed whorls. For the most part, the antidimorphs occur in equal numbers. In genera with strong external ornament, the subglobose antidimorph is typically more coarsely ornamented when compared with subdiscoidal antidimorphs. There is no significant difference in the sutural configuration between antidimorphs, and early ontogenetic stages appear to exhibit identical patterns of change in conch proportions.

The well known microconch-macroconch dimorphism displayed by most Mesozoic ammonoids has never been described in Paleozoic taxa. It is worth noting that the prolecanitids *Pronorites* and *Pseudopronorites*, presumably within the ancestral lineage, do not exhibit either conch or sutural dimorphism. Antidimorphic pairs have not been recognized as separate species in the Middle Carboniferous of the southern midcontinent with exception of the two species of *Quinnites* and *Axinolobus*, the junior synonyms of which (*Q. textum* and *A. quinni*) should be suppressed.

# EVALUATION OF SEPTAL CROWDING AS AN INDICATION OF SEXUAL MATURITY IN SOME LOWER AND MIDDLE CARBONIFEROUS AMMONOIDS FROM THE NORTH AMERICAN MIDCONTINENT, UNITED STATES

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As most extant *Nautilus* approach sexual maturity, their last few (1-3) septa are thickened and approximated before growth (expressed as lengthening of the living chamber) ceases. However, change in septal spacing does not occur in all mature *Nautilus*, and only about half the individuals from large populations actually exhibit approximation. Septal crowding is also characteristic of many ammonoids and it has been cited commonly as evidence for the attainment of sexual maturity, in spite of the relationship displayed by *Nautilus*.

Many Carboniferous ammonoid assemblages from the North American midcontinent yield large numbers of specimens, presumed to represent both sexes, from single horizons at single localities that are interpreted as reflecting semelparous mass mortality of sexually mature individuals. A small number of the taxa (17%) comprising these assemblages occur as dimorphic pairs. Typically, one antidimorph possesses a subglobose conch with depressed whorls and a wide umbilicus, while the associated antidimorph has a subdiscoidal conch with compressed whorls and a more narrow umbilicus. If the taxon is ornamented, the subglobose form displays coarser ornament. The antidimorphs occur in approximately equal numbers.

In a large population (>100 individuals) of the muensteroceratid *Muensteroceras* from the famous Lower Carboniferous (Osagean-Upper Tournaisian) Rockford Limestone, southern Indiana, septal crowding occurs in only about 5% of the individuals. Phragmocone diameter at the initiation of crowding varies from as small as 14.8 mm to as large as 51.7 mm, and as many as 13 approximated septa have been observed in a single specimen to the termination of its phragmocone. Both antidimorphs exhibit crowding, but it is more common in the subdiscoidal form.

A large population of the Upper Carboniferous (Morrowan-Kinderscoutian-Serpukovian) reticuloceratid *Arkanites* from the basal Prairie Grove Member, Hale Formation, northern Arkansas, exhibits septal crowding in more than 60% of the subdiscoidal antidimorphs with diameters > 30 mm, but it has never been observed in the subglobose antidimorphs even at diameters > 60 mm. As many as 12 approximated septa have been observed in a single specimen extending to the termination of its phragmocone.

It can be observed that ammonoids continued to grow, in some cases for more than a quarter whorl, beyond the initiation of septal crowding. While approximated septa may be associated with the onset of sexual maturity, the two are probably not related directly. Approximation may have more to do with "trimming" the conch than the onset of reproductive capability.

## SEPTAL IMPLOSION IN COILED NAUTILOIDS FROM AN UPPER CARBONIFEROUS UNIT IN OHIO, USA

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More than 200 coiled nautiloids of *Metacoceras mcchesneyi* (Murphy, 1970) from a strip mine in Columbiana County, Ohio were concentrated in a storm deposit shell lag within a silty-shale marine unit (Lower Conemaugh-Upper Pennsylvanian). Apertural and other mature modifications indicate these cephalopods represent a mature or nearly mature population.

The degree of distortion and/or crushing of the nautiloids are variable. Some are diagenetically flattened while others appear to be essentially complete, undistorted three-dimensional specimens. Twenty-seven undistorted specimens were randomly selected and sectioned longitudinally one to three times. Serial sections revealed that the septa in every specimen were collapsed and/or telescoped. Septal fragments were moved and packed towards the conch apex or moved and grouped within the conch with the appearance of having settled out of the carbonate-rich silt that filled the conch. This destruction of internal features without external shell distortion can only be accomplished by limited implosion.

For the nautiloids in this marine unit, a hydrostatic pressure increase could be accomplished by increasing water depth by transgression and/or basin subsidence; however, implosion could not have occurred in the water column or at the water-sediment interface. The specimens had to have been buried to prevent separation of the conch pieces following implosion. Irregularly shaped carbonate concretions are present in the shell lag and fill the conchs of the three-dimensional nautiloid specimens. The concretion lithology is distinct from the silty-shale matrix of the marine unit. Hallam (1962) reported irregularly shaped carbonate concretions to have been emplaced under a thixotropic condition (i.e. in a condition of fine balance between a liquid and solid state). A thixotropic material has the ability to flow when a stress is applied. We have concluded that after burial, the nautiloid cameral spaces were probably filled with both liquid and gas, and the body chamber had to be filled with solid thixotropic material. To prevent conch collapse at the time of septal implosion, thixotropic material filling the three-dimensional nautiloid body chamber acted as a liquid at the time of stress release during septal failure. The stress was produced by combined lithostatic and hydrostatic pressures which fluidized the concretion material that flowed into the phragmocone during septal collapse. The concretion material quickly reformed into a solid state after the septal implosion, thereby preventing the collapse of the conch from lithostatic pressure.

Hallam, A., 1962. A Band of Extraordinary Calcareous Concretions in the Upper Lias of Yorkshire, England. Jour. Sed. Pet. 32, 840-847.

# SIPHUNCULAR MEMBRANES IN UPPER PALEOZOIC PROLECANITID AMMONOIDS FROM NEVADA, USA

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Almost all previous work on intracameral membranes in ammonoids is based on Lower Mesozoic material from Spitsbergen and northeastern Arctic Siberia. This report discusses the formation and function of intracameral membranes in the Upper Paleozoic (Permian) prolecanitid ammonoid *Akmilleria electraensis* (Plummer and Scott).

These prolecanitids are preserved in carbonate concretions exposed near the base of the Arcturus Formation (Lower Permian - Wolfcampian) at Buck Mountain, Nevada. The Buck Mountain concretions are unusual in that they sometimes contain hundreds of carbonized cephalopod mandibles. Detailed *in situ* study of the intracameral membranes utilized complete phragmocones of *Akmilleria* that were prepared as longitudinal and transverse sections etched in weak acetic acid and then observed by SEM.

Intracameral membranes are a relatively new discovery (Weitschat and Bandel, 1991; Checa, 1996 and other reports). In the Triassic material that Weitschat and Bandel (1991) studied, three types were present. In the five Permian prolecanitid specimens we observed, there are only two kinds of intracameral membranes present; there are siphuncular sheets and a modified form of horizontal sheets. Transverse sheets like those in the tips of the sutural lobes of the Triassic ammonoids have not been observed. The prolecanitid intracameral membranes exhibit both regularity in chamber placement and similarity in the branching patterns. Because of this regularity and similarity, it is likely that the membranes were produced at the posterior end of the animal when it was forming a new siphuncle prior to the formation of a new septum. We therefore reject the suggestion that the membranes were formed by chemical changes in the cameral liquid chemistry during fluid removal because changes in cameral liquid chemistry during liquid withdrawal would have created random membrane patterns in each chamber and extensive variation between specimens. We did not observe random membrane patterns; instead there are distinct membrane pattern similarities among the prolecanitid specimens.

Checa, A., 1996. Origin of Intracameral Sheets in Ammonoids. *Lethaia* 29, 61-75.

Weitschat, W. and Bandel, K., 1991. Organic Components in Phragmocones of Boreal Triassic Ammonoids: Implications for Ammonoid Biology. *Palaeont. Zeitschrift* 65, 269-303.

## AMMONITE FAUNAS FROM MARLS WITH PYRITIC AMMONITES (LOWER OXFORDIAN): ORIGINAL FAUNAS AT THE INTERFACE DISTAL PLATFORM AND BASIN

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Some authors had considered the marls with pyritic faunas as deposited in a quite shallow water and containing a reduced size fauna (nanism). But paleogeographical analyses show that this facies appears at the boundary between distal platform and basin. Faunal analyses shows that the faunal spectra are original: 1) two very small sized genera are typical, 2) the quantitative analyses show strong differences on one hand with more proximal platform and on the other hand with basin.

### **Small size adults**

Analyses of numerous populations of Lower Oxfordian age show that two genera have a very small size adult (*closed sutures, opening of umbilicus ridge, ornamental changing on body chamber*). The first one, *Scaphitodites*, has an adult size from 7 mm to 15 mm ; it is characterised by a scaphitoid morphology and a ventral groove at the end of the phragmocone. It is unknown from authors in the ferruginous oolitic facies of more proximal platform and in the SE French basin. The second, *Creniceras*, is always frequent in this facies. It is known in ferruginous oolitic facies (but not frequent); in the SE French basin, except in Ardèche, it is unknown. It can be noticed that adult peristome are almost never preserved in this genus.

Some specimens belonging to the genus *Hecticoceras* have, as soon as a 12 mm diameter, closed sutures. They are interpreted as microconchs because, on the more proximal platform, we found adults with lappets at the same size. The others genera, with greater microconchs (*Cardioceras, Peltoceratoides, Euaspidoceras, Properisphinctes, Prososphinctes, Taramelliceras*), never present adult characters: they are not dwarf .

### **Ammonites spectra**

The Ammonitina change also, from proximal platform to basin, in quantitative characteristics. 1) Cardioceratids, Peltoceratids and Euaspidoceratids, are more frequent towards proximal platform ; 2) Taramelliceratids as Perisphinctids are more frequent towards the basin ; 3) Hecticoceratids are common everywhere but more abundant in marls ; 4) *Scaphitodites* is strictly restricted to marls with pyritic fossils and *Creniceras* frequent.

The Phylloceratina have a more strictly paleogeographical repartition. They abound in the basin where they are always strongly dominated by the genus *Sowerbyceras* ; the other genera (generally 3 to 5) are not frequent. *Sowerbyceras* is always absent in proximal environment at the contrary of other Phylloceratids which are rare but present. When *Scaphitodites* exist, *Sowerbyceras* are rare and more common when *Scaphitodites* disappears. That observation can be explained if we consider that *Sowerbyceras* is a nectobenthic ammonite which claim a minimum of depth ; in this hypothesis, they cannot have a post-mortem drift as other pelagic Phylloceratids.

### **Conclusion**

Analyses of faunas from marls with pyritic fossils shows that this environment is typified by an original assemblage and is colonized by some taxa with steno ecological requirement.

## CHANGE WITHIN AMMONITE ASSEMBLAGES FROM MANGYSHLAK MOUNTAINS (WESTERN KAZAKHSTAN) DURING THE MID-CRETACEOUS TRANSGRESSION

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During the Late Albian through Turonian the territory of Mangyshlak was a part of the European Zoogeographic Realm or North European Province, the limits of which coincided during the Albian and Cenomanian with the Hoplitinid Faunal Province. Along the progress of the mid-Cretaceous transgression the ammonite faunas of the Mangyshlak lose gradually, on the species level, their endemic character.

In the earliest Late Albian (Michalskii Zone) the ammonite assemblage is dominated by representatives of the genus *Semenovicerias* Wright, characteristic for the Central Asia, as well as the less abundant endemic species of the genera *Anahoplites* Hyatt and *Callihoplites* Spath. The species *S. michalskii* (Semenov) and *S. pseudocoleonodus* (Semenov) are known in the identical stratigraphic position in England and northern France, and the species *S. baisunensis* (Luppov) and *S. cf. michalskii* (Semenov) were reported from the Upper Albian of Central Iran. These data indicate clearly the biogeographic contacts of the mentioned regions and the Boreal character of the ammonite fauna within the Hoplitinid Faunal Province.

Following the Late Albian transgression (Inflatum Zone) the west immigrants representing the species *Mortoniceras inflatum* (Sowerby) and *Hysterocheras* sp. of the family Brancoceratidae appear in the record (co-occur with *Semenovicerias*), lowering markedly the endemic character of the ammonite fauna of Central Asia.

In the latest Albian (Dispar Zone = Cantabrigensis Zone) there appears an evolutionary descendant of the genus *Semenovicerias* Wright, namely the genus *Karamaites* Sokolov. It is the typical form for Central Asia and it represents the early evolutionary stages of the placenticeratids (latest Albian - earliest Turonian). In Mangyshlak the representatives of the genus *Karamaites* co-occur with the pandemic hoplitids of the genera *Anahoplites* Hyatt, *Callihoplites* Spath, *P. (Pleurohoplites)* Spath, and *P. (Arrhaphoceras)* Whitehouse.

The Cenomanian through Turonian ammonite fauna is almost identical to that of Central and Western Europe, leaving no doubt that it represents the same province, the North European Province.

# BIOLOGICAL RESPONSE OF AMMONITES TO CHANGING ENVIRONMENTAL CONDITIONS: AN EXAMPLE OF BOREAL *AMOEBOCERAS* INVASIONS INTO SUBMEDITERRANEAN PROVINCE DURING LATE OXFORDIAN

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The territory of Central Poland constituted in the Oxfordian a part of the Submediterranean Province. The ammonites of the Boreal genus *Amoeboceras* are encountered here in larger numbers in the two thin layers only - in so called *Amoeboceras* layers. These layers are known from the Bimammatum Zone of the Upper Oxfordian: the lower one characterized by occurrence of *Amoeboceras ovale* (Quenstedt) is placed in the Hypselum Subzone, the upper one characterized by occurrence of closely related forms: *Amoeboceras bauhini* (Oppel) - *Amoeboceras praebauhini* Salfeld - *Amoeboceras lineatum* (Quenstedt) is recognised in the Hauffianum Subzone. These layers mark short-time invasions of the Boreal forms into the Submediterranean Province.

The ammonites of the genus *Amoeboceras* found in the layers in question do not show any marked differences in size what precludes the recognition of the typical micro-, and macroconchs. All specimens are generally small-sized up to 45 mm in maximum diameter revealing thus in their size and the type of ornamentation some similarity to microconchs. The bulk of the specimens are fully grown, having from 5 1/4 to 5 3/4 whorls. In all specimens studied a distinct development of septa is observed: (1) up to four whorl (*i.e.* up to about 9 mm diameter) the number of septa per each whorl is "normal" and equals 13-14; (2) on the next stage which includes 3/4 to 1 1/4 of whorl the marked septa approximation is observed, and the number of septa equals from 22 to 35, respectively. The observed change in septa density is related with change of ornamentation: from more sharp and more regular ornamentation occurring on inner whorls, to less distinct somewhat irregular ornamentation on the outer whorls.

The observed long-termed approximation of septa is stated in the Boreal ammonites of the genus *Amoeboceras* showing the invasional character of occurrence only. The same feature is not observed in the Submediterranean and Subboreal ammonites found in the same layers as *Amoeboceras*. It may be concluded thus, that the approximation of septa observed in studied *Amoeboceras* faunas is an adaptive reaction of animals to new environmental conditions.

The approximation of septa is treated generally as showing the reduced rate of growth. The reduced rate of growth as shown by approximation of a few last septa is usually related with sexual maturation. In the studied case the gonads maturation has been stimulated through a long time due to untypical for Boreal forms environmental conditions.

# AMMONOID ASSEMBLAGES IN THE SANTONIAN AGE OF HOKKAIDO, JAPAN, WITH SPECIAL REFERENCE TO COVARIANCE OF SHELL SHAPE AND MODE OF OCCURRENCE OF DESMOCERATIDAE

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The Upper Cretaceous sequence of the Yezo Group in Hokkaido, Japan, yields well-preserved and taxonomically diversified ammonoid assemblages at various horizons. The Santonian strata in Haboro-Kotanbetsu-Tappu areas, northwestern Hokkaido consist mainly of bioturbated, fine to coarse siltstone and silty sandstone, with frequent intercalation of sandstone (ca. 5-100mm), in which such bivalves as *Parvamussium* sp. and *Nanonavis* sp. occur commonly. The litho- and biofacies of the strata suggest outer shelf environments. In the study areas, both nearshore facies characterized by frequent intercalation of sandstone and contemporaneous offshore facies characterized by rare intercalation of sandstone are exposed. Thus, we can recognize the lateral change of the various ammonoid assemblages in association with that of lithofacies.

In contrast to the heteromorph ammonites which commonly occur in fragmental condition, almost all normally coiled ammonites except for *Hypophylloceras* retain a complete body chamber in which jaw remains are sometimes preserved *in situ*, suggesting that post-mortem transportation is rare in these ammonites (in the case of *Hypophylloceras*, see Maeda and Seilacher, 1996).

The assemblages, characterized by the abundance of *Baculites*, are recognized occasionally in the bioturbated coarse siltstone or silty sandstone. These assemblages correspond with the *Baculites* facies of Matsumoto and Obata (1962), representing a nearshore, quiet environment. The frequency of occurrence of relatively smooth or weakly ornate ammonites (Phylloceratina, Lytoceratina and Desmocerataceae) increases from the nearshore to the offshore facies. This tendency is especially conspicuous in the Desmocerataceae. In the Tethyan ammonoid Desmocerataceae (Page, 1996), *Damesites sugata* (Forbes), *D. damesi* (Jimbo) and *D. semicostatus* Matsumoto are distributed in the Santonian of the study areas. *D. sugata* and *D. damesi* sometimes co-occur in the same concretions. *D. damesi* exhibits fairly wide individual variation among samples of population. Some specimens of them resemble *D. sugata* in overall shell shape, when the specimens co-occur with *D. sugata*. Some other specimens exhibit the typical shell shape of *D. damesi*, when the specimens occur solitarily. In contrast, *D. semicostatus* occurs locally and never co-occur with other species of *Damesites*. Moreover, this species occurs more abundantly and grows larger than the other two species of *Damesites* listed above. The species composition of *Damesites* of local assemblages is therefore changeable from horizon to horizon and/or from area to area. Covariance of shell shape and mode of occurrence is suggested in each species.

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## MID-CRETACEOUS AMMONITES FROM THE COASTAL CHAIN OF SYRIA

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Occurrences of Cretaceous ammonites from the northern part of the Coastal Chain (As Sahilyeh Mountains) of Syria were described by Dubertret (1937), Schatsky (1966) and Mouty & Saint-Marc (1982). The ammonite faunas indicate Albian, Middle and Upper Cenomanian and Lower Turonian. The Albian is represented by the Engonoceratidae. *Engonoceras gracile* (Douville) was described by Douville occurring from the Moghara Massif (Sinai) towards the east of Suez, associated with Lower Albian *Douvilleiceras mammillatum* (Schlotheim). The Cenomanian is represented by *Eucalycoceras* from the Acanthoceratidae and *Euomphaloceras* from the Euomphaloceratidae both indicating the Upper Cenomanian. *Vascoceras* abundant in the southern part of the Near East is recorded for the first time from Syria indicating the Turonian.

## NAUTILOID SYSTEMATICS BASED ON SIPHUNCULAR STRUCTURE AND POSITION OF MUSCLE SCARS

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Analysis of shell shape and position and size of retractor muscle scars indicates that only a fraction of fossil nautiloids and ammonoids were adapted for active swimming. On the other hand, siphuncular structure indicates that several taxa of nautiloids were probably well adapted for vertical migration.

A hitherto undescribed siphuncular structure was recently discovered in actinoceratids and orthoceratids (Mutvei 1997, 1999, and unpublished). The connecting ring is here composed of two layers: an outer, thin spherulitic-prismatic layer, which is a continuation of that layer from the septal neck; and an inner, thick layer that is calcified and forms a direct continuation of the nacreous layer of the septal neck. The latter layer is traversed by numerous pores through which the exchange of cameral liquid took place. This type of connecting rings also occurs in Lituicidae and Baltoceratidae, both orthocerids. All these taxa have dorsal retractor muscle scars.

The tarphyceratid connecting ring differs from that of orthoceratids-actinoceratids in consisting of a single, thick, spherulitic-prismatic layer. This layer is a continuation of that layer in the septal neck and shows two or more sublayers of different orientation of acicular crystallites (Mutvei, unpublished). There was certainly also an inner glycoprotein (conchiolin) layer that continued from the nacreous layer of the septal neck but was uncalcified and therefore not preserved. Tarphyceratids have ventral and/or lateral retractor muscle scars.

As pointed out by Furnish and Glenister (1964), most ellesmeroceratids are poorly preserved and therefore lack information on muscle scars and siphuncular structures, except that the connecting ring is often said to be thickened. In addition to Baltoceratidae, which are orthoceratids, the families Bathmoceratidae, Cyrtoceratidae and Cyclostomiceratidae also seemingly have no close relationship to the rest of ellesmeroceratids, which still lack a definition and may contain unrelated groups.

Cameral deposits seem to have developed only in orthoceratids and actinoceratids that possessed calcified connecting rings with pores. The formation of these deposits is still poorly understood.

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## **DIVERSITY VERSUS DISPARITY: EXAMPLES FROM PRESENT (COLEOIDS) AND PAST (AMMONITES) CEPHALOPODS**

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The concept of morphological space (considered here to be a complement to the traditional analysis of taxonomic diversity), is especially useful for understanding how the diversity (morphological expression of differences) of a set of organisms is structured and consequently for interpreting shape changes in terms of evolution or adaptation : disparity is the measure of how fundamentally different organisms are. This concept is illustrated here by two examples.

### **1. Ammonoid morphological signal versus sea-level changes : adaptative aspects of form disparity**

Workers investigating ammonites ecology have suggested a correlation between shell morphology and sea-level variations. If such correlations could be generalized, ammonites might then be used as paleo-environmental markers. In practice, establishing correlations runs up against a major difficulty posed by sample selection. In this work we adopt a new approach to test for correlations between morphology and environment in a series of four Upper Callovian (Middle Jurassic) and two Oxfordian (Upper Jurassic) populations from Côte-d'Or (Burgundy, France). This approach is based on minimizing taxonomic constraints when forming samples for analysis. It allows morphodiversity to be read directly without interference from taxonomic subjectivity. The biometric method used is based on mathematical equations (Raup, 1966) whose graphical plots are analogous to the organism's morphology.

### **2. Exploration of morphospace in statoliths and beaks of cuttlefish and squid : evolutionary aspects of form disparity**

This work reports on a study using a Procrustes type analysis (Bookstein, 1991) of shape in exploring the morphospace of cephalopod statoliths and beaks. This method is based on the utilization of anatomically conspicuous points (landmarks). Comparison of their relative positions warrants localization and quantification of morphological differences between ontogenetic stages, individuals or taxa. The aim of this study is (1) to explore morphospace patterns in statoliths and beaks of several decabrachian groups, and (2) to assess biological form disparity between statoliths and beaks in terms of morphological distances that are testable against the phylogenetic trees derived from molecular methods. This approach should allow us to consider two evolutionary aspects complementary to one another, namely adaptive significance versus genetic fixation of statolith and beak morphology.

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## EARLY JURASSIC AMMONOIDS FROM THE PERȘANI MTS. (EAST CARPATHIANS, ROMANIA)

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Early Jurassic ammonoids from the Perșani Mts. (East Carpathians, Romania) have a 120-years-long history of study (e.g. HERBICH, 1878; VADÁSZ, 1908; POPA & PATRULIUS 1996). Well-preserved, loose fossils weathered out from Rosso Ammonitico facies are found abundantly in streambeds (e.g. in Tepei (=Töpe) Valley) and formed the basis of the early studies. Despite the profuse *ex situ* material, little was known about the detailed biostratigraphy until recently. The Rosso Ammonitico beds occur as olistoliths included within the Barremian–Aptian Wildflysch Formation of the Olt Nappe (Transylvanian Nappe System).

An apparently conformable, 12 m thick section was located and sampled for macrofauna along a tributary of the Tepei Creek. Separated from the measured section by a covered interval concealing some 4 m that may be tectonically disrupted, older beds of Rosso Ammonitico marl contain a fauna of the uppermost Hettangian to possibly lowermost Sinemurian Marmoreum Zone (incl. *Schlotheimia* spp., *Charmasseiceras? marmoreum*, *Ectocentrites petersi*). In the measured section, the following biostratigraphic units were recognized based on an abundant ammonoid fauna: Rotiforme Zone, Lower Sinemurian (e.g. *Coroniceras rotiforme*); Jamesoni Zone, Lower Pliensbachian (e.g. *Uptonia* cf. *jamesoni*); and Bifrons Zone, Lower Toarcian (e.g. *Hildoceras semipolatum*). A published compilation of biostratigraphic data from numerous olistoliths in the Perșani Mts. documented a nearly complete composite spanning the Middle Hettangian–Lower Pliensbachian interval (POPA & PATRULIUS 1996). The new results suggest that the deposition of red, nodular marl and limestone continued locally until the Early Toarcian, i.e. longer than previously established. The highly discontinuous nature of the Rosso Ammonitico is either a primary feature, or a result of bedding-parallel, cryptic tectonic omission of less cohesive layers of high clay content after emplacement in the wildflysch.

This study was complemented by a revision of collections made from the area by Vadász and others, and kept in the Hungarian Geological Institute. A significant new finding is the occurrence of middle and late Hettangian *Sunrisites* and *Badouxia*, which provides further evidence for faunal links of the western Tethyan and East Pacific marine basins during the early Liassic. Taxa of Ammonitina and the high proportion of phylloceratids indicate strong paleobiogeographic affinities with the Mediterranean Province, contrary to several other areas in Transylvania and the East Carpathians.

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## AMMONOID BIOSTRATIGRAPHY OF THE TRIASSIC–JURASSIC BOUNDARY NEAR CSÓVÁR, HUNGARY: A PROGRESS REPORT

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A continuous, marine Triassic–Jurassic boundary has recently been recognized near Csóvár, Hungary. Previous findings of *Choristoceras* cf. *marshi*, *C. nobile* and the conodont *Misikella* indicated the topmost Rhaetian Marshi Zone from a quarry in Pokol Valley. Excavation during the 1998 field season connected the intermittent natural outcrops and exposed a nearly 60 m thick section on nearby Várhegy. The succession of well-bedded limestone and calcareous marl with common slump features deposited near the transition of a submarine slope to a restricted basin. Latest Triassic ammonoids found in place include *Choristoceras* spp. and *Cladiscites*. Nearly 20 m of overlying strata have not yielded macrofossils thus far. Higher upsection, earliest Jurassic ammonoids are represented by phylloceratids (including *Phylloceras* "triasicum") and psiloceratids, whereas *Waehneroceras* was collected near the top of the section, indicating the presence of lower and middle Hettangian, respectively. Talus collections yielded *Pleuroacanthites*, *Euphyllites*?, *Caloceras*? and *Fergusonites*, confirming the Early Liassic age assignment.

The Csóvár section is a significant addition to the small number of marine Triassic–Jurassic boundary sections. It provides a rare opportunity for an integrated stratigraphic study using radiolarian and conodont biostratigraphy, magnetostratigraphy and stable isotope and sequence stratigraphy calibrated against the ammonoid biostratigraphy. It is expected that preliminary results from further collecting during the 1999 field season will be available for presentation at the symposium.

# PROBLEM OF SEXUAL DIMORPHISM IN THE VALANGINIAN (LOWER CRETACEOUS) AMMONITES *VALANGINITES NUCLEUS* AND *SAYNOCERAS VERRUCOSUM*

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A rich and well preserved ammonite fauna from the Valanginian clays of the Wawal quarry, Central Poland, enabled the study of the sexual dimorphism in two ammonite species; *Valanginites nucleus* (Roemer, 1840) and *Saynoceras verrucosum* (d'Orbigny, 1841). The analysis was based on samples composed of 200 and 400 specimens, respectively.

In the case of *Saynoceras verrucosum* the dimorphic pair was expected to differ in the adult size. Due to the low number of the completely preserved specimens in the sample, the adult size values were estimated by the size of appearance of the ornament. This character correlates well with the adult size in the species (L.Bulot, M. Company & J.P. Thieuloy, 1990). The measurements show a unimodal distribution indicating the absence of size-related dimorphism in the species *S.verrucosum*.

In contrast to *S.verrucosum*, very clear dimorphism was found in *Valanginites nucleus*, expressed both in different adult size and in the ornament. Early ontogenetic stages are smooth and both morphotypes are identical. They begin to differentiate with the appearance of ornament, which in microconchs appears earlier than in macroconchs. In microconchs the ribs are narrow and sharp, while in macroconchs they are wide and gentle. Moreover, in the latter the ribs are less densely spaced. Both morphotypes differ also in the development of mid-lateral and mid-ventral tubercles. No difference was found in the adult aperture. In regard to all measured characters, the studied sample displays clear bimodal distribution. Based on the analysis of the material, it is inferred that *V.nucleus* is conspecific with the species *Valanginites bachelardi*, and represents its microconch.

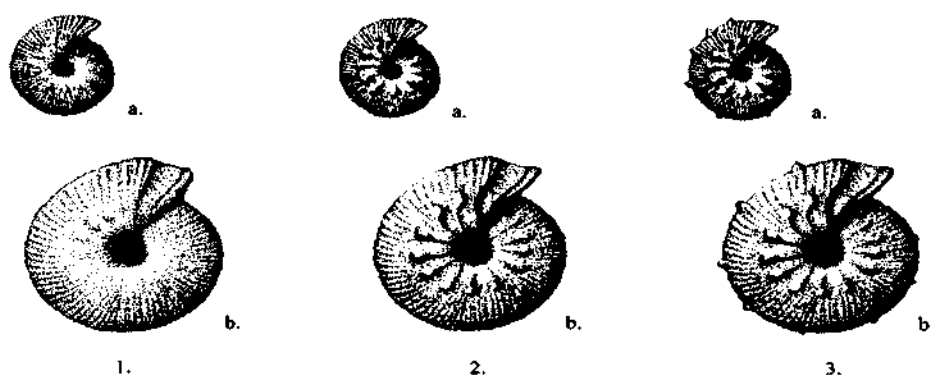


Fig. 1 Variability range of micro - and macroconch in *Valanginites nucleus*; a - microconch, b - macroconch, 1. morphotype nucleus, 2. morphotype wilfridi, 3. morphotype ventrotuberculatum.

2.

3. Reference list:

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## LIMITING FACTORS ON SHELL GROWTH AND SEGREGATION OF AMMONITE POPULATIONS: EVIDENCE FROM ADULT SIZE VARIATIONS WITH TIME AND SPACE.

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The shape and the ornamentation of ammonite shells are often closely related to their habitat but little information is available on ammonite population structure. The purpose of this contribution is to study spatio-temporal variations in adult size of ammonites in order to elucidate the limiting factors acting on shell growth. This work is based on an extensive palaeontological field study of the Valanginian to Lower Hauterivian ammonite fauna from south-east of France. Between the *Campylotoxus* and *Radiatus* zones, more than 23600 ammonites have been found along 9 reference sections of the Vocontian Basin and 2 sections of the Provence Margin with an accurate stratigraphic control. - The evolution of the ammonite fauna was integrated into a sequence stratigraphy framework. The major faunal renewals were correlated to the relative sea-level changes. In the Vocontian Basin, first appearance phases and faunal crisis are contemporary to the third order lowstand (limestone dominant alternation) and transgressive systems tracts (marly dominant alternation) respectively. The diversity and abundance maxima are often closely related to the lower system tract (Reboulet, 1995).

a) The study of the ammonite succession shows also episodic time-size variation. The decrease in adult size is closely correlated with rising sea level. For example, during the transgressive system tract of the *Campylotoxus* zone, the evolution of *Neocomitidae* and *Olcostephanidae* families shows a decrease in size of the mature conch. The increasing in adult size is often correlated with falling sea level (lowstand system tract). - The evolution in adult size variation is not totally controlled by internal factors because such tendencies are obvious in various contemporaneous families. The parallelism between evolution of adult size ammonite and eustatic sea level fluctuations shows that this character is indirectly controlled by bathymetry. In *Nautilus*, as in fossils chambered-shelled Cephalopods, an essential part of the growth process is the emptying of cameral liquid; increasing average habitat depth may cause slower net growth (Ward, 1987). Another limiting factor for shell growth is temperature, which is also closely related to depth.

b) Moreover, the adult size variation of populations is not randomly distributed between basin and platform. At specific or generic levels, larger ammonites are found in shallow platform environments (Provençal Margin) whereas smaller ones occur in much deeper habitats (Vocontian Basin). If the supposed absence of significant geographical barriers is confirmed, this could be related to a behavioural segregation.

This contribution raises some new questions about the structure of ammonite populations, on speciation and on heterochronic processes.

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## SOFT-TISSUE ATTACHMENT STRUCTURES ON PYRITIZED INTERNAL MOULDS OF AMMONOIDS

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Specific dark coloured areas on pyritized internal moulds of ammonoids were described and interpreted as documents of soft tissue and muscle attachment. New material of Upper Devonian, Triassic, Jurassic and Lower Cretaceous ammonoids gave new insight into soft body attachment, its relation to the shell, and their changes in the course of ontogeny and evolution.

Paired and unpaired patterns can be recognized. Paired structures are observed along the umbilicus and on the flanks, and sometimes on the ventral side of the moulds. Unpaired ones appear on the dorsal and ventral sides. Paired double lines on the flanks of the phragmocone and of the body chamber, sometimes additionally connected with crescent shaped tracking bands, were left by lateral muscles. Small round or crescent shaped areas beneath each septum, sometimes connected with a tracking band were left by a ventral muscle. Small dark areas beneath each dorsal lobe were left by a dorsal muscle. Rounded black areas along the umbilicus, often connected with a dark tracking band are remains of a pair of dorsolateral muscles at the posterior end of the soft body. Black tracking bands connected to the incisions of the sutural lobes on the flanks of the phragmocone are interpreted as remains of muscles which fixed the posterior end of the soft body within the body chamber.

Marked differences occur in the attachment structures between Palaeozoic and Mesozoic ammonoids. Devonian ammonoids had only one pair of lateral muscles; the Mesozoic ones, in contrast, had two paired muscle systems, a lateral and dorsolateral. Attachment structures of a small unpaired ventral and dorsal muscle system can be observed especially in Lower Cretaceous heteromorph ammonites. Additionally in some Mesozoic genera a marked change of patterns was developed through ontogenesis (e.g. *Amaltheus*, *Quenstedtoceras*).

In the genus *Cheiloceras* the lateral attachment area appears as a distinct broad black double line running parallel to the ventral side and to the umbilicus on the flanks of the body chamber and phragmocone. In the space between the lines distinct crescent shaped tracking bands are developed. In contrast, the lateral attachment areas of the genus *Tornoceras* is developed as a faint bordering line only on the flanks of the body chamber. There are no tracking bands developed inside the bordering line, but the line is connected with a broad black area beneath the last septum.

The dark lateral and dorsolateral patterns can be interpreted as the attachment of paired retractor muscles. The dark tracking bands behind the incisions of the sutural lobes can be interpreted as remains of lines of tie points keeping the posterior part of the mantle in shape while constructing a new septum. The interpretation of the ventral and dorsal attachment structure is still unclear.

## **HYPOPHYLOCERAS AND THE CLASSIFICATION OF THE PHYLLOCERATIDAE**

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Critical to the history of the study of the Phylloceratidae were misidentifications of the Aptian species, *Hypophylloceras onoense*, by J. P. Smith (1898), whose illustration of the sutural development of "*Phylloceras onoense*" led to misconception of this taxon and introduced confusion in the classification of the family. Smith misidentified *Phylloceras ramosum* and juvenile *Desmophyllites* from the Upper Cretaceous of California as *Phylloceras onoense*, and what he described as the internal lobe of this *Phylloceras* was actually that of a juvenile desmoceratid. On the basis of this supposed aberrancy Salfeld (1924) established *Hypophylloceras*, with *P. onoense* as type species. Wiedmann (1962) discovered that *H. onoense* has a lituid internal lobe as in other phylloceratids, and he reclassified *Hypophylloceras* as a subgenus of *Phylloceras*, assigning most Cretaceous phylloceratids to it.

The Phylloceratidae is a conservative stock that has changed little over its long history. We suggest that heterochronous parallel developments, such as tetraphyllic endings of saddles, are common in the Phylloceratidae, and that the principal branches of the family arose as early as Early Jurassic.. The main early split was between groups without constrictions (Phylloceratinae) and those with constrictions. The latter group includes those with internal constrictions (Calliphylloceratinae), and those with constrictions expressed on the outer shell (Ptychophylloceratinae). *Hypophylloceras* has constrictions in early growth stages and belongs to Calliphylloceratinae, not to Phylloceratinae where it has resided since Wiedmann's work. This produces a more internally consistent classification, but requires re-evaluation of the nomenclature for most Cretaceous Phylloceratinae, which authors, following Weidmann, have assigned to "*Hypophylloceras*". A second major split occurred in the Late Jurassic with the origin of inflated, coarsely-ribbed Phyllopachyceratinae. A close connection between Jurassic and Cretaceous forms assigned to this taxon and the earlier *Partschiceras* is unlikely, as the two taxa differ in most basic characters.

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# INTRASPECIFIC VARIATION OF AMMONOID EMBRYONIC GROWTH STAGES AND ITS BEARING ON POST EMBRYONIC GROWTH

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Ammonoid growth is generally investigated through the quantitative study of variations in shell size and shape. Those few workers who consider the entire course of development report a turning point between embryonic and post embryonic development. This transition is characterised by more or less abrupt changes in shell shape, size and ornamentation. While most studies of ammonoid growth concentrate exclusively on post embryonic stages, comparisons between embryonic growth and the subsequent post embryonic stages could further our understanding of the appearance of many characters during the course of ontogeny. In addition, relations between embryonic and post embryonic modes of growth are still unclear. For example, it is not known whether the size of the embryonic shell influences the size of the mature conch, the number of whorls, the coiling pattern, etc.

Bibliographic quantitative data available about embryonic structures, although still insufficient, do provide a reasonable description of size and shape variability of embryonic shells for Ammonoidea as a whole. In contrast, little is yet known about interspecific variation between closely-related species and virtually nothing is known about intraspecific variation. The result is that there is almost no information about the embryonic shell in species diagnosis.

This work attempts to characterise intraspecific variation of the embryonic shell for *Hecticoceras (Sublunuloceras) discoides* (SPATH, 1928) from the Callovian of Burgundy.

Embryonic structures have been observed on 34 polished sections. Measurements of linear and surface area parameters are used to estimate the intraspecific variability of size and shape of embryonic structures (Fig.1). The results are compared with published data for other Ammonoidea.

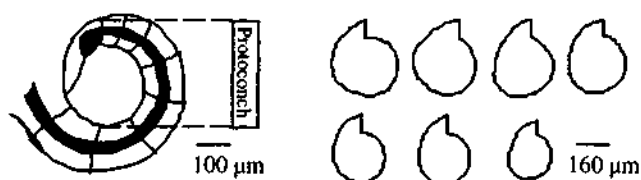


Fig. 1 - Position of the initial chamber (protoconch) and exemples of morphologic variations (for *H. (s) discoides*).

# **CILIATED CELLS ON THE DIGITAL TENTACLES OF *NAUTILUS POMPILIUS* L. INDICATE THEIR FUNCTION AS SENSE ORGANS (CEPHALOPODA, TETRABRANCHIATA)**

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In resting posture the hood of Nautilus is almost closed, only the post- and preocular tentacles, the central part of the eyes, and the tentacular sheathes of the digital tentacles are visible. As Nautilus is neutrally bouyant, only a light attachment with a single tentacle is enough to fasten the animal to the substrate. When food is put into the aquarium the animals start to travel with quick pendulum-like motions which correspond to the respiratory motion of the body. We presume that these motions are useful in building up an olfactory gradient for the localization of the food, which is possibly received by the ocular tentacles<sup>1</sup> or the rhinophores<sup>2</sup>. After the direction of the food is located the digital tentacles form a "cone of search"<sup>3</sup>. The animals swim forward while searching for food. One or two pairs of digital tentacles hang downward with the tips touching the bottom giving the impression of a tactile searching. The digital tentacles discern and grasp the food and they bring it close to the mouth. Following the meal the animals return to the resting posture. Scanning electron microscopical studies on the oral surface possesses closely packed transverse ridges which tend to be more widely spaced towards the distal end. A median groove extends from the distal to the proximal part of the tentacle on the aboral surface. In contrast to the situation in *N. macromphalus*<sup>2,4</sup> sensory ciliated cells extend on the epidermis of digital tentacles of *N. pompilius*. They can be divided into three different cell types according to the number and length of the cilia and their distribution on the tentacle surface. Ciliated cells of Type I are restricted to the anterior surface area of the transverse ridges. They stand close together in "cilia-fields". Cells of Type II spread out frequently all over the epidermis of the lateral surface of the digital tentacle. Type III cells are regularly but less frequently distributed in the aboral groove. Histological studies show that the digital tentacles of Nautilus are substantially different from those of coleoids, although their musculature is organized in a similar manner<sup>5,6</sup>. A distinct network of muscle fibers guarantees their high degree of movability. Transmitted light micrographs of longitudinal sections show that a conspicuous nonmyelinated axial nerve bundle parallels the long axis of the tentacle and terminates directly on a thin and flat epithelium at its tip. Using an indocarbocyanine dye the labeled nerve fibers could be studied under the fluorescence microscope. The tracer stains from the axial nerve bundle over a small nervous plexus to the muscle fibers and to the high columnar epithelium of the transverse ridges, where ciliated cells are located<sup>7</sup>. These findings lead to the conclusion that the digital tentacles of *N. pompilius* are important sense organs for sensitive and tactile reception.

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## SEA LEVEL, AMMONITE TURNOVER AND ISOTOPIC RECORD IN THE EARLY-MIDDLE JURASSIC OF THE BETIC CORDILLERA (SPAIN)

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Several faunal turnover events are analyzed: Pliensbachian-Toarcian boundary. Almost all Domerian inherited taxa disappear only some Arieticeratinae, Grammoceratinae and Dactylioceratinae survive. Such extinction is linked to sea level fall, although it can also be due to an oceanic anoxic event at the beginning of the transgressive phase. In the Falciferum zone a faunal turnover of Dactylioceratidae, Harpoceratinae and Hildoceratinae starts, due to a major transgression. Latest Middle Toarcian-Earliest Late Toarcian. Extinction of Dactylioceratidae and most Hildoceratinae due to sea level fall, a stratigraphic gap ranging from Gradata to Fallaciosum zones is recorded. Radiation of new Grammoceratinae and Hammatoceratinae at the base of the Fallaciosum zone corresponds to a transgression. Late Aalenian-Earliest Bajocian. It is the most important faunal turnover of the Jurassic marked by the extinction of Graphoceratidae, Grammoceratinae, Tmetoceratinae, Hammatoceratidae and Erycitidae, which were replaced by the Haploceratidae, Strigoceratidae, Sonniniidae, Otoitidae and Stephanoceratidae. It corresponds to a regression and the Early Bajocian transgression. Early Bajocian. Sealevel fall and the extinction of Otoitidae, Bradfordiinae and Sonniniidae, followed by a transgression with the origination of Oppeliidae and Sphaeroceratidae; and with maximum diversity of Stephanoceratidae. Latest Early Bajocian. An extinction of the Stephanoceratidae and last representatives of Sonniniidae occurs concomitantly with the radiation of Leptosphinctinae, Parkinsoniidae and Spiroceratidae. The Sphaeroceratidae, Oppeliidae, Haploceratidae and Strigoceratidae, probably living deeper, persisted. Regression in the Humphriesianum zone followed by a transgression of the Late Bajocian explains the evolutionary transition from Stephanoceratidae to Parkinsoniidae and Perisphinctidae. Latest Bajocian. In the Parkinsoni zone extinction of Sphaeroceratidae, Garantianinae and *Spiroceras* occurs, the replacement of Leptosphinctinae by the Zigzagiceratinae and the origination and radiation of Morphoceratidae. It corresponds with a short regression to transgressive phase at the Bajocian-Bathonian boundary. Latest Early Bathonian. A significant turnover at the Early-Middle Bathonian transition is characterised by extinction of Parkinsoniidae, Morphoceratidae and *Nannolytoceras*. They were followed by the Tulitidae, Hecticoceratinae, and diverse Zigzagiceratinae. This event corresponds to a short discontinuity at the beginning of the Middle Bathonian. Latest Middle Bathonian. The Cadomitinae and the *Wagnericeras*, *Procerites* and *Bullatimorphites* become extinct. A discontinuity above the Middle Bathonian ranges in some areas to the Middle Oxfordian. The middle Late Bathonian may be represented (Orbis zone). Latest Bathonian. It is poorly documented corresponding to a large regressive interval recorded worldwide. with the extinction of many Perisphinctidae and Tulitidae. Maximum of ammonite diversity and positive shift in the  $\delta^{13}\text{C}$  are recorded at the Demonense, Bifrons, Propinquans-Humphriesianum, Anceps-Coronatum zones.

## ESTIMATING ACTUAL FECUNDITY OF A LOLIGINID SQUID

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More precise methods for calculating actual fecundity in loliginids are required. True semelparity is now accepted to be the exception rather than the norm, making actual fecundity estimations notoriously difficult. Tagging studies, histological examination of the ovary, and aquarium maintenance have confirmed the chokka squid, *loligo vulgaris reynaudii*, to be a serial spawner. Females were found to move between spawning sites within the general spawning area off the South Coast of South Africa, the ovary was characterized into eight different stages, and chokka squid deposited three batches totalling 8140 eggs over a thirty six hour period in captivity.

This confirmation of serial spawning provides a number of obstacles when estimating actual fecundity. Detailed investigation of the ovary adds even further to our woes. Oocyte atresia, previously unknown in loliginid squid, has now been identified as a regular phenomenon during the reproductive cycle of this species. Atresia takes place in all stages of oocyte development, but is more prevalent in the late yolkless and vitellogenic oocytes. Follicular atresia lowers the number of maturing oocytes in the ovary and true fecundity will certainly be overestimated if follicular atresia is not considered.

Two further results may, however provide some solutions to this complex issue:

Firstly, the atretic oocytes are useful as an index of chokka squid reproductive capability. Spent squid can now be positively identified from the percentage of atretic oocytes in the ovary.

Secondly, post-ovulatory follicles were found in the ovary of actively spawning females, and the rate of breakdown of these follicles may provide us with answers on the number of batches spawned. Analysis of the rate of resorption of post-ovulatory follicles in the ovaries of squid collected at regular intervals over one spawning cycle may provide the number of batches of eggs spawned

## PRESERVATION OF CEPHALOPODS IN THE UPPER JURASSIC NUSPLINGEN LITHOGRAPHIC LIMESTONE (LATE KIMMERIDGIAN, SW GERMANY)

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### Ammonite and nautilid preservation

The laminated Late Kimmeridgian Nusplingen Lithographic Limestone occurs in a small area (less than 1.5 km<sup>2</sup>) on the western part of the Swabian Alb. The limestone accumulated in deep, probably anoxic basins surrounded by sponge-microbial reefs, shallow areas with calcareous oolites and small islands. It is well-known because of its findings of marine vertebrates. Ammonites and isolated aptychi are the most common invertebrate fossils. With few exceptions, ammonites are preserved as extremely compressed casts with the aragonitic shell dissolved during early diagenesis, while the siphuncle is still present. Among the larger ammonites only few are completely preserved. Often the body chamber or the anterior part of the body chamber is missing, probably eaten away from predators. In complete specimens the aptychi, which are assumed to represent the lower jaws, are still found in situ or in the nearest surroundings of the ammonite shell. In several bituminous beds, also isolated wing-like upper jaws are quite abundant. In some specimens of the aspidoceratid *Physodoceras nattheimense* SCHWEIGERT both the aptychi and the corresponding upper jaws have been found still in the body chamber or in near context to the shell. The upper jaws originally consisted of chitin, which is preserved as carbonised organic matter. There is hardly any analogue in shape and assumed function of the jaw apparatus with that of nautilids or coleoids. We could not detect a "rostral tip" at the upper jaws so that a scraping function is more likely than a biting. Within the same beds, also the content of the stomach is sometimes preserved, consisting either of small broken aptychi (*Neochetoceras*), *Saccocoma* skeleton elements (*Physodoceras*), phosphatic material (*Lithacoceras fasciferum*) or foraminiferas (*Lithacoceras ulmense*), thus indicating different diets in different ammonite groups.

Besides ammonites, nautilids are extremely rare. In contrast to ammonites, the siphuncle in the nautilids is not preserved, whereas the embedding and diagenesis of the shell is identical to that in ammonites. One specimen (*Pseudaganides* sp.) has been found with a *Conchorhynchus* and a corresponding *Rhyncholites* in the body chamber. This is the first fossil record of a nautilid with both parts of the jaw apparatus in situ.

### Belemnite and coleoid preservation

Most belemnites of the Nusplingen Lithographic Limestone are preserved by their guard only. While specimens which are bitten at the alveolar end of the guard, mostly lie horizontally on the bedding planes of the laminated limestone, specimens with the phragmocone being stuck obliquely or even vertically in the sediment. This gives evidence for a rapid sedimentation rate and a stiff-plastic consistency of the lime mud. In few cases agglomerates of belemnite tentacle hooks (*Onychites*) and smaller arm hook-lets (*Paraglycerites*) besides fragments of the guard were detected. These rests represent bitten and/or disgorged indigestible parts of belemnites. Coleoids are far less common, like *Trachyteuthis*, *Plesioteuthis*, while the giant *Leptoteuthis* is extremely rare. Also these specimens must be interpreted as bitten by predators.

## RANGE AND DISTRIBUTION OF BELEMNITES IN THE JURASSIC AND CRETACEOUS OF MEXICO - A PROGRESS REPORT

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Since more than one century, belemnites are cited sparsely from the Mexican Jurassic and Cretaceous (e.g. CASTILLO & AGUILERA, 1895) being seldom determined and never investigated. During the last twenty years, Northamerican, Mexican, and German colleagues collected belemnites at Jurassic and Cretaceous sites especially in Northern and Central Mexico and entrusted them to the authors, so that own collections were enlarged to be of biostatistical value. First results were published by SEIBERTZ (1986), SEIBERTZ & BUITRON (1987a, b), SPAETH (1988), and SEIBERTZ & SPAETH (1995, 1998).

From the uppermost Middle Jurassic (Upper Callovian) of central northern Mexico, a single specimen of *Cylindroteuthis puzosiana* (D'ORBIGNY 1842) has been described for the first time. More specimens of this species were found in the Upper Jurassic (Middle Kimmeridgian) together with acroteuthid belemnites. With a gap in the record, belemnites then occur sparsely from the Lower Cretaceous Hauterivian onwards represented by the genus *Hibolites*. In the Upper Aptian, a flood occurrence of typical *Neohibolites wollemanni* STOLLEY 1911 is traceable over the whole Northeast Mexican area, followed by another acme in the Middle Albian with *N. minimus* (MILLER 1826) including the subspecies *N. m. pinguis* STOLLEY 1911, *N. m. obtusus* STOLLEY 1911, and *N. m. clavaformis* SEIBERTZ & BUITRON 1987 (1987 b). This subspecies is considered to be restricted in its distribution to Mexico being the ecologic substitute of the European *N. m. minimus* but ranging higher than the latter. The Upper Albian is represented by the species *N. praeultimus* SPAETH 1971. The last member of the neohibolitids occurs in the basal Upper Cretaceous (Lower Cenomanian) with *N. ultimus* (D'ORBIGNY 1842). With a further gap in belemnite record, *Actinocamax manitobensis* (WHITEAVES 1889) represents the basal Lower Turonian and at the same time the youngest occurrence of belemnites in Mexico known until now. While *Cylindroteuthis* and *Neohibolites* are typical forms of the European boreal regions, *A. manitobensis* indicates faunal immigration from the northerly neighbouring boreal Western Interior seaway. On the other hand, the genus *Hibolites* indicates tethyal influence. In Mexico, belemnites are restricted mainly to shallow water areas in relation to palaeogeographic reconstructions.

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## SOME NEW SILURIAN NAUTILOID CEPHALOPODS FROM THE ITALIAN SIDE OF THE CARNIC ALPS

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A preliminary investigation carried out on scattered blocks of “*Orthoceras*” Limestone from the proximity of the old mines of Mt. Cocco (Ugovizza, Udine, Italian side of the Carnic Alps) allows the taxonomic identification at the generic and specific level of many nautiloid specimens among which I can report: *Hemicosmorthoceras laterculum* Ristedt, 1968, *H. semiannulatum* (Barrande, 1870), *H.?* cf. *semilaeve* (Barrande, 1868), *Sphaerorthoceras carnicum* Ristedt, 1968, *S. curvum* Ristedt, 1968, *S. cf. teichertii* Ristedt, 1968, *Parasphaerorthoceras* sp. H. *sensu* Ristedt, 1968, *P. sp. E sensu* Ristedt, 1968, *P. sp. C sensu* Ristedt, 1968, *Kopaninoceras thyrsus* (Barrande, 1870), *Leurocycloceras subannulare* (Münster, 1840).

Beyond the above reported taxa I can list other taxa of nautiloid cephalopod closely resembling those already studied by Gnoli & Histon (1998) such as *Arionoceras submoniliforme* (Meneghini, 1857) with protoconch, *Kopaninoceras cf. jucundum* (Barrande, 1870), some specimens probably belonging to genera *Kionoceras* Hyatt, 1884 and *Parakionoceras* (Foerste, 1928) and *Plagiostomoceras?* cf. *gruenewaldti* (Barrande, 1866)

All the reported taxa are found for the first time in the Italian side of the Carnic Alps. The reported taxa indicate without doubt a close faunal relationship between Southwestern Sardinia and Central Bohemia.

Further collections will be made from other localities in the Italian Carnic Alps including “Casera Pal Grande”, “Cima Costa Alta”, “Mt. Zermula”.

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## REVISION OF SILURIAN NAUTILOID CEPHALOPODS FROM THE CARNIC ALPS FROM VARIOUS MUSEUM COLLECTIONS

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Various projects are presently in progress on the Silurian Nautiloid fauna of the Carnic Alps the purpose of the investigations being to obtain as much data as possible (taxonomic, biostratigraphic, palaeoecologic and taphonomic) to contribute to a more extensive study of the Silurian Cephalopod biofacies with regard to the paleogeographical setting of the Carnic Alps during the Silurian. This biofacies has been traced along the northern Gondwana margin from the Montagne Noire, Sardinia, Carnic Alps, Bohemia and Siberia.

A detailed taxonomic and biostratigraphical study of the fauna based on newly collected material from this area within good stratigraphic constraints therefore is essential. However, it is also appropriate to redescribe the old collections under the new classification system based both on internal and external features thus avoiding incorrect citations of species distributions. Most of these collections consist of material collected during the original field mapping of the area in the late nineteenth and early twentieth century.

M. Gortani and P. Vinassa de Regny were the main workers who described the Silurian fauna from the Italian Carnic Alps (1908, 1909, 1910, 1913). The nautiloid material contained in the collections of the University of Bologna where M. Gortani was Professor of Geology have been revised (Gnoli *et al.* in press) and additional material from the University of Pisa and Turin is here presented. Among the species and genera represented are *Plagiostomoceras*, *Hemicosmorthoceras*, *Leurocycloceras*, *Kionoceras*, *Murchisoniceras*?, *Michelinoceras*. Unfortunately exact locality and therefore stratigraphic data are sometimes missing.

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## EARLY ONTOGENY OF THREE CALLOVIAN AMMONITE GENERA (*BINATISPHINCTES*, *KOSMOCERAS* AND *HECTICOCERAS*)

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In the past many workers have documented features from the early whorls of different ammonite genera from the Paleozoic and the Mesozoic. Here, the early whorls of three Callovian ammonite genera, *Kosmoceras*, *Binatisphinctes* and *Hecticoceras*, from Ryazan, SE of Moscow, Russia, will be described.

**Shell of ammonitellae:** The protoconch wall consists in the apical and dorsal parts of a single prismatic layer, which is enriched with organic components. In the ventral part, there are three prismatic layers. The wall of the first whorl is composed of two prismatic layers. The first nacre appears with the nepionic swelling and in the first septum after the prosepium, as was elucidated in *Kosmoceras* by Landman & Bandel (1982).

**Internal structures:** The flange consists in *Kosmoceras* and in *Binatisphinctes* only of a narrow ledge, whereas the flange in *Hecticoceras* is broad and extends into the lumen of protoconch. Differences in the structure of the attachment zone of the prosiphon to the protoconch wall exist between *Kosmoceras* and *Binatisphinctes*.

**Size of ammonitellae:** In cross sections the width of the ammonitella, in median sections the ammonitella diameter, protoconch size (minimum and maximum) and the ammonitella angle were measured. *Hecticoceras* has the smallest ammonitellae. This is obvious both in the ammonitella diameter (mean 0,58 mm) and in the ammonitella width (0,49 mm). The other two genera had bigger (mean more than 0,7 mm) and wider (more than 0,55 mm) ammonitellae. The ammonitella diameter is positively correlated with the maximum and minimum protoconch diameter. In all examined genera the ammonitella angle comprises about 280 degrees.

**Microornament of the ammonitellae:** On the ammonitella surface of all three genera a microtubercular ornament is present. Some authors give average values of the tubercle diameter for different genera, so for example in *Sphenodiscus* and *Quenstedtoceras* 2-3  $\mu\text{m}$ , in scaphitids and *Baculites* 4-8  $\mu\text{m}$  (Bandel et al. 1982). The genera examined show a normal distribution of the tubercle diameter. The mean in *Binatisphinctes* is 3,30  $\mu\text{m}$ , in *Kosmoceras* 3,02  $\mu\text{m}$  and in *Hecticoceras* 2,38  $\mu\text{m}$ . The distribution of the circular tubercles shows little variability between the examined forms. In *Hecticoceras*, the inner side of the flank is free from ornamentation. In *Binatisphinctes*, there are elongated tubercle clusters on the inner flank near the protoconch, whereas in *Kosmoceras* they are randomly distributed on the whole outer ammonitella shell.

**Microornament on the juvenile shell:** On the shell of the first post-embryonic whorl there is in *Binatisphinctes* and in *Kosmoceras* a tuberculate microornament in addition to growth lines. These tubercles are oval to longish in outline and they are arranged in rows which are not parallel to the growth lines.

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## IMPACT OF REPRODUCTIVE STRATEGY ON CEPHALOPOD EVOLUTION

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Ammonoid "mean total diversity" is roughly 4 to 5 times greater than for nautiloids. Approximately 212 ammonoid families evolved during ~330 million years, corresponding to an average of 0.64 family-level originations per million years. For "nautiloids" (all non-ammonoids and non-coleoids), there were 83 families during >500 m.y., which is about 0.17 originations/m.y.; using a more contemporary Nautiloidea taxonomic concept, 57 nautiloid families evolved during ~475 m.y., which corresponds to 0.12 family-level originations/m.y. Thus, the ammonoids were by far the most rapidly evolving and species-rich of cephalopod groups in the fossil record, and the cause of that disparity has puzzled paleontologists for years.

One possible solution to the mystery of cephalopod diversity is that taxa in clades characterized by short stratigraphic ranges and high total diversity had a semelparous reproductive strategy (parental mortality follows mass spawning event), whereas taxa in clades with long stratigraphic ranges and low total diversity had an iteroparous reproductive strategy (repeated, isolated breeding events). It has been noted that r-selected species tend to be semelparous, with little parental care provided for the many offspring that are of relatively small size at birth/hatching; conversely, K-selected species tend to be iteroparous and some degree of parental care is commonly provided for the few, relatively large offspring. Although the correlation between reproductive strategy and r versus K population dynamics is not without exception, it has been hypothesized that the size of the cephalopod embryo correlates with reproductive strategy, small embryos indicating semelparity and large embryos indicating iteroparity.

Preliminary results from the Carboniferous of the southern mid-continent, USA, support these hypotheses. The ammonoid taxa studied include 7 reticuloceratid, gastrioceratid, and schistoceratid species; nautiloid taxa include the orthoconic *Reticycloceras croneisi* and the planispiral *Aphelaeceras arkansanum*. Specimens were collected from Upper Mississippian (Chesterian) and Lower Pennsylvanian (Morrowan) units of northern Arkansas. Lithologies are diverse and include concretionary black shales and high energy, calcareous, conglomeratic sandstones. These cephalopod occurrences have been interpreted previously as reflecting mass mortality of populations of sexually mature individuals, possibly as a result of reproduction. Representative specimens were sectioned longitudinally and ground carefully in order to observe the maximum dimension. Mean ammonitella diameter was very similar within families (approximately 0.8 mm), and little variation was seen within species (s.d. <0.05 mm); nautas were typically 3 to 5 times larger than ammonitellas. These results are consistent with data from at least some extant semelparous and iteroparous cephalopods (e.g., *Loligo pealei* and *Nautilus pompilius*, respectively) but are in marked contrast with some recently published accounts of Cretaceous Lytoceratina species (e.g., *Tetragonites glabrus*).

**UPPER JAWS OF PLACENTICERATIDAE FROM THE KARST PLATEAU  
(UPPER CRETACEOUS, SLOVENIA)**

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The black laminated Tomaj Limestone (Campanian, Late Cretaceous) of the Trieste - Komen Plateau represents a short period of reducing conditions within rudistid dominated platform carbonates. Due to extraordinary preservation and careful collecting lower jaws and shells of Placenticeratidae from the villages Dobravlje and Kazlje were described by the authors in 1996, prints of non preserved softparts and a possible crop content in 1999. Two specimens which are interpreted as upper jaws are found separated from lower jaws and from shells. As there are no other ammonites recorded from the Tomaj limestone it is highly likely that also the upper jaws are belonging to Placenticeratidae of the *milleri-bidorsatum* group (1996). The better specimen preserved in a black substance is totally flattened. It shows a bilaterally symmetric beak-like structure with a faintly elongated tip. The flanks are spatulalike with a median ridge, apparently for stabilising and muscular attachment. The total length is about 12 mm, the width at the anterior part about 11 mm. Measurements are fitting to those given by the authors in 1996 for the lower jaws. The attempt to a reconstruction of the jaws of Placenticeratidae leads to a "horny" beak, the lower jaw strengthened by a thin layer of calciumcarbonate, the tips covered by a black shiny substance (? conchioline). Ammonite jaw apparatuses of this type are described from *Scalarites* (TANABE, HIRANO & KANIE 1980) and from *Damesites* (TANABE 1983).

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## HETEROMORPH AMMONITES FROM THE TATA LIMESTONE FORMATION (LOWER CRETACEOUS, APTIAN-ALBIAN), HUNGARY

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The highly condensed basal beds of Tata Limestone Formation (TLF) from four localities include a huge amount of determinable ammonites. According to the latest studies (SZIVES 1996) the rich ammonite fauna belongs to Lower Aptian (Furcata Zone), Middle (Subnodosocostatum Zone), Upper Aptian (Nolani and Jacobi Zones) and Lower Albian (Tardefurcata Zone) also, so the age of the TLF should be determined as Lower Albian. The faunal elements of the TLF came from a highly condensed basal bed, so fossils are preserved as phosphatized and glauconitized internal moulds and therefore the good preservation of sutures is very rare.

The rich ammonite fauna of the basal beds of the Aptian-Albian crinoideal limestone yielded many heteromorphs also. Most of them belong to the genus *Ptychoceras*, to a probably new, "*Hamites*"-like genus and there is only one fragment of *Ancyloceras* sp. Most interesting are the ribbed, nontuberculate, "*Hamites*"-like forms. The lack of ventral spines and the suture lines makes sure that these heteromorphs are not Ancylocerataceae. The nontuberculate, ribbed fragments, according to the ongoing suture line determination, belong to Turrititaceae, they are in close relationship with Hamitidae and Anisoceratidae, but not similar to these groups.

The family Hamitidae includes 5 Albian genera. There is no sure Hamitidae known from the Aptian except JACOB's (JACOB & TOBLER 1906) specimen from the Upper Gargasian of Luitere Zug of Switzerland, however, recent authors (e. g. CASEY 1961) refer JACOB's specimen to genus *Helicancylus*. BREISTROFFER (1933) have recorded *Hamites* from the Tardefurcata Zone associated with *Leymeriella*. CASEY (1961) summarised his opinion about the Hamitidae of the Lower Greensand as follows: "... the gap in the heteromorph succession below the Mammilatum Zone makes it unprofitable to speculate on a possible link between *Hamites* and the *Ancyloceratidae*". Hopefully the nontuberculate, ribbed, probably new forms of the TLF can fill a small part of this gap.

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## MORPHOLOGICAL DIVERSITY OF THE JAWS OF CRETACEOUS AMMONOIDEA

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Jaws (beaks) and radula are occasionally preserved within the body chambers of ammonoids whose exact taxonomic relationships are known. Based on such *in situ* material, ammonoid jaws from 26 Late Paleozoic and Mesozoic genera have been classified into four morphotypes: normal (coleoid), anaptychus, aptychus, and rhynchaptychus types (Lehmann, 1990; Tanabe and Fukuda, 1999). However, a question still remains with respect to these morphotypes, because of the presence of an intermediate form. Furthermore, one must consider the degree of taphonomic loss in actual fossils prior to morphotypic classification.

We have reexamined and compared the jaw morphologies of 18 Cretaceous genera in the suborders Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina, relying upon well-preserved specimens from the Northwestern Pacific Province (Hokkaido and Sakhalin) and the U. S. Western Interior Province, in addition to previously published material. Our results show that the upper jaws of these genera exhibit little morphological variation. They consist of horny reduced outer and large paired inner lamellae, both of which are united in the anterior portion forming a sharp rostral tip. These features are quite different from those of the upper jaws of extant coleoids and *Nautilus*, both of which have a continuous inner lamella. A thin anterior calcitic layer covers the horny lamellae of the upper jaws of *Aconeceras* (Ammonitina, Haplocerataceae) and *Scalarites* (Ancyloceratina, Turrititaceae). The upper jaws of *Gaudryceras* and *Tetragonites* described by Tanabe et al. (1980) and Kanie (1982) are probably deformed lower jaws. Thus, the upper jaws of these genera are still unknown.

In contrast to the morphological conservatism of the upper jaws, the lower jaws of Cretaceous ammonoids exhibit remarkable taxonomic variation in their relative size, overall morphology, and the degree of development of the outer calcitic layer. The lower jaws of Phylloceratina and Lytoceratina are characterized by a well-developed univalved outer chitinous lamella with an anterior calcified rostral tip, which appears to be effective for a scavenging-predatory mode of feeding, as in the jaws of *Nautilus*. Those of the other 15 genera may fall into either aptychus- or anaptychus-types, but this classification has no biological meaning because of the presence of an intermediate form between them. The lower jaws of Acanthocerataceae, Hoplitaceae, Scaphitaceae, and Turrititaceae all possess a widely open, large outer horny lamella with a median depression ("hinge") covered by a thin bivalved calcitic plate. These jaws may have been specialized for feeding on various kinds of microorganisms and could be accommodated within a buccal mass by bending the flexible chitinous outer lamella.

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## COMPARATIVE MICROANATOMY OF THE SIPHUNCULAR CORD IN PERMIAN AMMONOIDS AND RECENT NAUTILUS

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Ammonoids are extinct chambered cephalopods that flourished in the Middle Paleozoic and Mesozoic seas. In spite of their rich fossil records, available data on their soft anatomy have long been restricted to organic hard tissues such as jaws and radula. Certain peculiar calcified or pyritized objects associated with ammonoid conchs have previously been interpreted as remains of soft organs (1-5), but a serious question still remains regarding their biological nature, because of the absence of detailed tissue structure.

We have recently discovered exceptionally well-preserved remains of siphuncular cords in three specimens of a prolecanitid ammonoid *Akmlilleria electraensis*. These specimens were recovered from carbonate concretions, which were collected from the Lower Permian (Wolfcampian) Areturus Formation exposed on the south side of Buck Mountain, Ely County, Nevada. X-ray dispersion microanalysis of one of the specimens reveals that the fossilized siphuncular cord is made of fluorapatite. The siphuncular cord was presumably phosphatized immediately after death and before significant bacterial decay occurred.

Comparative SEM observations of the siphuncular cords of *Akmlilleria* and *Nautilus pompilius* allows us to describe their microanatomy. In cross section, the siphuncular cord of *Akmlilleria* consists of a large central vein, possibly two pairs of arteries, connective tissue, and a thin epithelial layer on the outside. The outer surface of the cord is sculptured by many evenly spaced, longitudinal ridges and grooves; the ridges correspond to the distal ends of individual epithelial cells. These external and internal microanatomical features are also observed in the siphuncular cord of *Nautilus*. However, *Nautilus* possesses relatively smaller and more numerous epithelial cells around the siphuncular cord than *Akmlilleria*. This is the first reported occurrence of soft tissue preservation of the ammonoid siphuncle and reveals anatomical differences between ammonoids and modern *Nautilus*.

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## PREDATION OF EARLY JURASSIC AMMONITES

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Predation of ammonites is widely recognised in Mesozoic findings and has been attributed to decapod crustaceans, reptiles, teleost fish, turtles and other cephalopods. The aim of the present study is to find a correlation between the location of the damaged part of the body chamber and the most likely predators.

Although predated ammonite remains are found through the entire Mesozoic this study concentrate on ammonites from the early Toarcian Posidonia Shale of Southwest Germany. This shale is characterised by a very fine lamination and ammonites occur as periostracal coatings of both flanks collapsed into a common plane subsequent to aragonite dissolution during early diagenesis. This kind of preservation has the advantage that bodychamber and phragmocone are preserved but the disadvantage that only one flank of the ammonite can be examined.

Comparing patterns in shell damage two different types can be distinguished; Type A comprehend shell fractures varying from disappeared bodychambers to crushed phragmocones (fig 1A), and a Type B where the crushed area is restricted to the adapical part of the body chamber (fig 1B).



**Figure 1.** Schematic drawings of specimens *mab a 1518* (A) and specimen *mab a 1528* (B) from Oertijdmuseum De Groene Poort collections representing the two types of predated ammonites.

Type A crushed shell remains are often found clustered in such a way that crushing may be assumed to have taken place at or just above the seafloor and not high in the water column. The most likely predators for type A crushing are generalist moluscivorous predators like fish or decapod crustaceans. Type B shell damage is much more restricted to a small part of the shell indicating a more specialised moluscivorous predator and is more common than the Type A shell damage. The relative position of the damaged part is characteristic for the examined genera (*Hildoceras*, *Harpoceras* and *Dactylioceras*) and implies that the predator was capable of catching, handling and positioning the ammonite prey proceeding the crushing of the shell.

In recent ecosystems *Octopus vulgaris* attacks *Nautilus* sp. in a similar way by positioning the prey prior to perforating the shell making it likely that endocochleate cephalopods were main ammonite predators.

## REMARKS TO POST-MORTEM BEHAVIOUR OF ORTHOCONIC SHELLS

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Post-mortem behaviour of orthoconic shells is the subject of the discussion. Contrary to Reymont (1958) and some other authors (e.g. Ferretti and Kriz 1995) I suppose that after the decay of the soft body, the shells in the majority of orthocones with primarily developed cameral deposits had apex heavier than the apertural part (comp. Turek 1983). After a generally rather short period of post-mortem transport, these orthocones were sinking with the axis of the shell oblique or almost vertical. In a shallow water below wave base, where cephalopod shell accumulated forming so called orthoceras beds, many shells could withstand in contact with the sea bottom in an oblique or almost vertical position (with the aperture oriented up) for rather long time. Water in these depths could penetrate gas chambers very slowly. In such position widely open aperture could 'catch' other cephalopod shells or graptolites sinking to the bottom. So called telescoping one shell into another, rather frequently occurring in some cephalopod concentrations, special cases of occurrence of graptolites within body chamber where the tips of rhabdosomes are in the same orientation as the apex of a cephalopod shell and many examples of complete overgrowth of cephalopod shells by epizoans, can be simply explained by this way. The last case was often interpreted as overgrowth of living cephalopods though there are some serious reasons not to believe to this interpretation. As the examples considered can be mentioned e.g. rather uniformly orientated clusters of cornulitids (*Conchicolithes*) from the Upper Ordovician of Barrandian Area (with the apertures oriented conformable with the aperture of the host shell) heavily encrusting cephalopod shells along the whole outline as well as bryozoans *Monotrypa* completely covering the surface of the shells.

Cases of obliquely or vertically deposited shells discussed e.g. by Holland, Gnoli and Histon 1994 as well as character of the deposition of cephalopod shells in Braník facies type (*sensu* Ferretti and Kriz 1995, Kriz 1998) observed by the author on more than 60 square meters of polished Ludfordian limestone planes (used in past for decorative purposes in one recently restored building in Prague) can support this idea. These samples also indicates that in the environment, in which these deposits were formed, the implosion of the shells (caused by hydrostatics pressure) did not played an important role.

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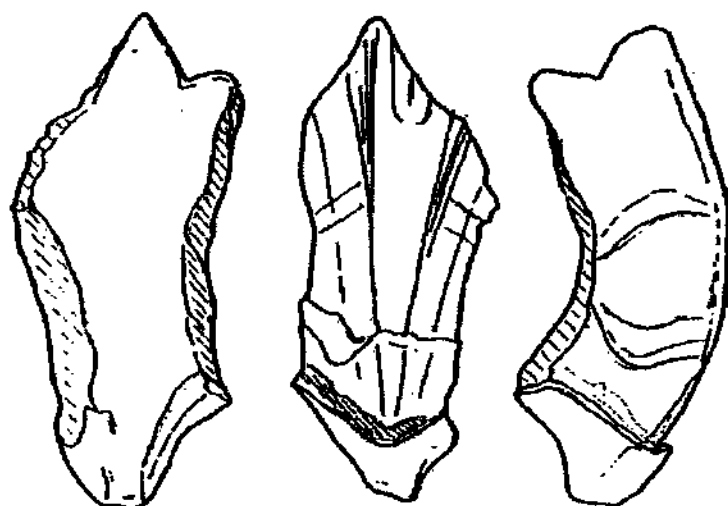
## AN ENIGMATIC CEPHALOPOD JAW ELEMENT FROM THE LATEST MAASTRICHTIAN OF THE NETHERLANDS

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The upper portion of the Meersen Member (Maastricht Formation, subunits Ivf-5/-6) as exposed at the ENCI-Maastricht BV quarry south of Maastricht, has yielded an enigmatic cephalopod jaw (Natuurhistorisch Museum Maastricht collections, no. NHMM JJ 11128) (see Figure).



Structure and size clearly differentiate the present specimen from nautiloid jaw elements (rhyncholites, conchorhynchus) which locally are very common, especially in the basal portions of the various members in the Maastrichtian Formation. In recent years, numerous specimens representing the various ontogenetic stages, have been collected. From the upper Valkenburg and lower Gronsveld members in particular, well-preserved material, partially silicified with dark purple-stained remains of organic material (?) and winglike extensions, is available. These specimens may be assigned to the following taxa: *Rhyncholites minimus* Blinkhorst, 1861, *R. marcellae* Van der Tuuk, 1985 and *Conchorhynchus limburgicus* Van der Tuuk, 1982. There is no doubt that these jaw elements belonged to the two nautiloid taxa known to date from the Maastricht Formation, namely *Cinomia heberti* (Blinkhorst, 1861) and *Eutrephoceras depressus* (Blinkhorst, 1861). However, it should be noted that these are in need of a modern revision. A third species, *Epicymatoceras vaelsense* (Blinkhorst, 1861), appears to be restricted to the Vijlen Member (subunits 0-4, Gulpen Formation).

The present specimen might thus be linked to one of the ammonite taxa known from the Meersen Member, viz. *Menuites terminus*, *Sphenodiscus binckhorsti*, *Baculites vertebralis* and *hoploscaphtes constrictus*. Of these, baculitids and scaphitids have aptychi as lower jaws, and only *M. terminus* appears large enough to have contained such a jaw.

# **PALAEOBIOGEOGRAPHY OF THE EARLY CRETACEOUS (PRE-ALBIAN) CEPHALOPOD-BEARING FORMATIONS OF THE WESTERN CARPATHIANS (CZECH AND SLOVAK REPUBLICS) AND THE NORTHERN CALCAREOUS ALPS (AUSTRIA)**

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During the last ten years I have had an opportunity to participate in field collections in the Lower Cretaceous deposits of the Alpine-Carpathian System, in whose sedimentary basins ammonite facies are developed, and to concern myself with the taxonomic processing of collected cephalopods. If we omit the existing course of the Carpathian Arc formed only in the Tertiary, the following sedimentation units have been studied (in the direction from north to south):

1. Outer (Flysch) Carpathians: a) Silesian Unit (uppermost Berriasian - early Aptian). Dark grey, clayey-marly deposits (mainly the Tešín-Hradiště Formation). b) Pieniny Klippen Belt - PKB (late Valanginian - late Barremian). In the extremely tectonically complicate unit light marly-calcareous deposits prevail. Locally they are interbedded with layers of dark grey claystones.
2. Central Carpathians: a) Maľín Unit (upper part of the early Valanginian - lower part of the late Barremian). b) Krí na Nappe (late Valanginian - late Barremian). In both the units (Vašíček, 1997) light marly-calcareous deposits dominate (Mrázňica Formation).
3. Northern Calcareous Alps (NCA) - Bajuvarian Nappe Complex: a) Ternberg Nappe (late Valanginian - late Barremian; results of Lukeneder, 1998). b) Lunz Nappe (late Berriasian - early Valanginian). In both the units the deposits of the Schrambach Formation with occasional intercalations of distal turbidites occur. c) Reichraming Nappe (late Valanginian - uppermost Hauterivian). In the Ebenforst Syncline the Rossfeld Formation, in the Schneeberg Syncline the Schrambach Formation are developed (Vašíček, 1998).

On the basis of ammonite associations, the following palaeobiogeographic connections can be distinguished:

- a) In the whole system of nappes, the late Berriasian is documented richly by ammonites only in deposits of the Lunz Nappe. It contains merely mediterranean ammonites. b) The occurrence of ammonites of the genus *Platylenticeras* in the lower part of the early Valanginian in the Silesian Unit evidences a temporary communication with the subboreal Lower Saxony Basin (LSB) via the Danish-Polish Furrow. c) In the lower part of the late Valanginian, a repeated communication between the Silesian Unit and the subboreal area is documented by the occurrence of boreal genus *Prodichotomites* and the occurrence of mediterranean elements known both from the Silesian Unit and the LSB (*Saynoceras verrucosum*, *Valanginites wilfridi*). In the PKB *Criohimantoceras gigas*, *Varlheidites peregrinus*, *Bochianites neocomiensis* and *Valanginites cf. nucleus* occur equally to the LSB. By contrast, ammonites from the Central Carpathians as well as the NCA are represented only by mediterranean ammonites. d) The Barremian of the Silesian Unit, the Central Carpathians and the Ternberg Nappe (NCA) is famous, among other matters, for the occurrence of leptoceratoids and other purely mediterranean ammonites. e) In the early Aptian of the Silesian Unit representatives of the genus *Procheloniceras* occur. They indicate the intercommunication between the northern rims of the Tethyan area and the subboreal area by a newly formed way through Northern France and Southern England.

## PALEOENVIRONMENTAL DISTRIBUTION OF MIDDLE TRIASSIC AMMONOIDS IN THE BALATON HIGHLAND (HUNGARY)

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Large ammonoid faunas (several thousand specimens) have been collected from several sections of the Balaton Highland, encompassing the latest Anisian to Early Ladinian interval (Trinodosus and Reitzi Zones). The ammonoid assemblages are dominated by "sphaerocones" (Ptychitidae and Arcestidae); this clearly shows that the whole territory was under moderately deep, pelagic influence. The different topographic elements of the vertically dissected pelagic shelf (pelagic plateaux and basins) are characterized by ammonoid assemblages of different compositions. The environmental distribution of special morphogroups of ammonoids shows that the proportion of "coronates" (strongly ornamented ceratitids) is consistently lower in the basins than in the pelagic plateaux, whereas "sphaerocones" (Ptychitidae + Arcestidae) show inverse relationship. During the studied interval, the proportion of "coronates" decreases, whereas the proportion of "sphaerocones" increases in time in the whole territory (both in the basins and on the pelagic plateaux). This relationship is used to estimate water depth and changes in bathymetry. The results show that both the plateaux and the basins subsided gradually during the time interval in question and the depth difference between them slightly increased. This is in accordance with the general trends of subsidence expected on passive and/or transtensional continental margins and fits well into the paleogeographical picture outlined for the mid-Triassic shelf region including the Southern Alps and the Transdanubian Central Range.

The environmental distribution of ammonoid genera has been studied in the higher part of the Reitzi Zone (Reitzi and Avisianum Subzones). This stratigraphical interval is represented in seven sections and several other localities of the Balaton Highland and provided an extremely rich ammonoid fauna (over 2000 specimens and 40 species, 19 genera). Nine genera have shown definite environmental distribution. *Hungarites*, *Longobardites* and *Latemarites* seem to be connected to the peri-platform areas. The genera *Parakellnerites* and *Aplococeras* show partly similar distribution. *Proarcestes*, *Halilucites* and *Ticinites* are frequent in the basin areas and never occur in the peri-platform areas. Remarkably, in many cases the shell morphology of the ammonoids does not show direct correlation with the paleoenvironment. For example, the involute, compressed and smooth *Hungarites* and *Longobardites* are predominant in the peri-platform areas, though these morphotypes are traditionally believed as deeper-water, pelagic forms. On the other hand, the evolute, strongly ribbed *Ticinites* and *Halilucites* were found mainly in the basinal sequences.

## TRIASSIC AMMONOIDS AND BIOSTRATIGRAPHY OF THE BALATON HIGHLAND: NEW RESULTS FROM THE ANISIAN, LADINIAN AND CARNIAN

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The Triassic formations of the Balaton Highland and their ammonoid fauna are well-known from the famous and voluminous descriptions by J. Böckh and E. Mojsisovics. The multi-authored "Balaton Monograph" from the first decade of this century includes the important contributions of C. Diener, G. Arthaber, F. Frech and L. Lóczy which made the Balaton Highland one of the most important and renowned areas for Triassic stratigraphy. In the last fifteen years we have made significant, detailed collections supported by the Hungarian Geological Institute, the Hungarian Natural History Museum and the National Scientific Research Fund. The collecting and field work, led by the present author, was done mainly by T. Budai, L. Dosztály, and I. Szabó. The study area lies on the northern shore of Lake Balaton, where nine sections were collected in detail and more than 22 other localities yielded ammonoids. The ammonoid fauna consists of more than 12000 specimens and is deposited in the Geological and Paleontological Department of the Hungarian Natural History Museum. The occurrence of ammonoids is chronostratigraphically restricted to the Middle Anisian to Middle Carnian interval. The most important biostratigraphic results have partly been published (e.g.: Vörös 1987, 1993, Tatzreiter & Vörös 1991, Vörös et al. 1996, Márton et al. 1997). The zonal/subzonal scheme worked out or applied for the Middle Anisian to Lower Carnian interval of the Balaton Highland is presented and the most important measured stratigraphic sections with range charts are shown with illustration of the ammonoid fauna.

Perhaps the most important results of our biostratigraphic studies are those concerning the Anisian/Ladinian boundary interval. On the basis of the detailed biostratigraphic data from the Balaton Highland and considering the South Alpine results, a detailed ammonoid zonal/subzonal scheme of this interval was proposed. The correlation of subzones between the Southern Alps and the Balaton area is perfect below and above the proposed Anisian/Ladinian stage boundary (base of the Reitzi Zone).

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**ASSESSMENT OF THE PHYLOGENETIC RELATIONSHIP BETWEEN *OCTOPUS VULGARIS* CUVIER, 1797 AND *O. MIMUS* GOULD 1852, USING MITOCHONDRIAL 16S rRNA**

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The aim of this work was to extend our earlier work about the phylogenetic relationship between *Octopus vulgaris* and *O. mimus* using an additional gene, because the previous results were based on only one single gene, the mitochondrial cytochrome oxidase III (COIII). An additional objective was to elucidate the phylogenetic relationship between *O. vulgaris* s.s. from the Mediterranean and the so-called *O. vulgaris* from the western Atlantic. This question had to be approached since the supposed cosmopolitan distribution of *O. vulgaris* was recently called in question.

For this investigation, the diversity of 16 mitochondrial (mt) DNA sequences belonging to the inferred *Octopus vulgaris/mimus* complex and six additional octopods (*O. bimaculoides*, *O. californicus*, *O. salutii*, *Scaevargus unicirrhus*, *Eledone moschata* and *Bathypolypus* sp.) were measured using the mt ribosomal 16S rRNA-sequences as target. Tissue samples were used from widely separated locations: coastal areas of the Mediterranean (France), Atlantic Ocean (Lanzarote, Senegal, South Africa, Tristan da Cunha, Venezuela and Brazil), the Caribbean Sea (Costa Rica) and the Pacific Ocean (Taiwan, Costa Rica and North Chile). From each sample, up to 500 base pairs of 16S rRNA were amplified by PCR, sequenced and arranged in a multiple sequences alignment. The putative phylogenetic relationships were calculated applying both distance- and character-based analyses of the data, using the PAUP\*-program for the construction of phylogenetic trees.

The results obtained confirm the conclusion drawn from the earlier investigation based on COIII, and from recent morphological studies on the taxonomic position of *O. mimus* as a species distinct from *O. vulgaris*. Additional considerations deal with the distribution of *O. vulgaris* in the eastern and western Atlantic.

## WRINKLE LAYER AND DORSAL MUSCLE SCARS IN AMAUROCERAS FERRUGINEUM FROM THE DOMERIAN OF NW-GERMANY

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Extraordinarily well preserved ammonoids from carbonate-concretions of the Lower Jurassic, Domerian (spinatum Zone, hawskerense Subzone) of NW-Germany are presented. The material comes from glacial erratic boulders and is not known from outcrops. The fauna is composed of ammonoids (*Amauroceras ferrugineum*, *Pleuroceras hawskerense*), belemnoids (*B. elongatus*, *B. milleri*), scaphopods, gastropods, and bivalves.

The original aragonite of the ammonite shell-material is preserved and the phragmocones are usually empty and hollow which allows detailed three-dimensional investigations, especially of the early ontogenetic stages. The siphuncular tube is also present from the very beginning, including the prosiphon which consists of broad sheets attaching the caecum to the inner shell wall of the protoconch. Additional organic sheets are preserved within the first chambers where the siphuncular tube has not reached its ultimate ventral position. These sheets may have functioned not only as an attachment but also for liquid transport from the siphuncular tube to the pellicle. A similar system is also known from Recent *Nautilus*.

The most remarkable features, however, are the preserved wrinkle layer and the presence of an unpaired dorsal muscle scar. The wrinkle layer appears to be present only in early ontogenetic stages. A similar arrangement has been observed in goniatites and ceratites but up to now only very rarely within the Neoammonites of the Jurassic and Cretaceous period. The function of the wrinkle layer is discussed.

The unpaired muscle scars are situated at the dorsal side of the phragmocone just adoral of each septum, have a rounded to ovate outline, and a rugose surface structure. Its structure is usually well visible because the muscle scars penetrate the wrinkle layer. Similar muscle scars have been described from Triassic ammonoids by Weitschat & Bandel (1991). The authors supposed that these unpaired dorsal muscle functioned as the main retractor of ammonoids, but new observations support the reconstructions by Doguzhaeva & Mutvei (1992). Accordingly, as in the Recent *Nautilus*, the main retractor muscles of ammonoids are paired lateral muscles. However, the function of the unpaired dorsal muscle scars still remains an open question.

**CYTOBIOLOGICAL INVESTIGATIONS ON THE DIGESTIVE ORGANS OF *NAUTILUS POMPILIUS* L. (CEPHALOPODA, TETRABRANCHIATA)**

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Physiological studies on the localization of absorption processes in the digestive tract of coleoid cephalopods substantiated that not only in the midgut gland but also in the caecum food absorption takes place (Boucaud-Camou & Péquinant, 1974; Boucaud-Camou et al., 1976). Autoradiographic tracer experiments with leucine suggest that in octopus the crop too is involved in absorption processes (Wells, 1978).

Histological investigations on the digestive organs of *Nautilus pompilius* showed that in the caecum and crop the tunica mucosa, consisting of a lamina epithelialis mucosae and a lamina propria mucosae, is double-folded. The resulting enlargement of the surface is most distinct in the caecum which is a pouch organ lacking the spiral turning seen in dibranchiate cephalopods (Boucaud-Camou, 1968). Cytological studies of the epithelial cells showed a micro-villi border, endocytotic vesicles, acid phosphatase positive „dense bodies“ in the caecum and crop indicating that absorption occurs in these organs (Westermann & Schipp, 1998a,b).

To investigate in which organs of the digestive tract of *Nautilus pompilius* absorption processes take place the animals were fed with <sup>14</sup>C-labelled shrimps (*Crangon crangon*). 6-8 hours after food ingestion the organs (crop, stomach, caecum, midgut and rectum) of the digestive tract were removed. One half of the organs were fixed and embedded for autoradiography. The other half was burned in an incinerator (Oxynizer, Packard) and the radioactivity was measured with a liquid-scintillation analyser.

The results of the liquid-scintillation analyser showed the highest radioactivity in the midgut gland and caecum. These findings were confirmed through the light microscopic and electron microscopic autoradiography. Silver grains as reaction product could be assigned in the terminal alveoli of the midgut gland. The light microscopic autoradiography also showed silver precipitates in the lamina epithelialis mucosae of the caecum and crop. The present results of the liquid-scintillation analyser and the autoradiography as well as the cytological structural analysis indicate that in the caecum digestive and absorption processes occur. But the largest amount of the nutrient is absorbed by the terminal alveoli of the midgut gland which could also be demonstrated by the liquid-scintillation analyser and the autoradiography. <sup>14</sup>C-labelled glycine and/or leucine localized in the lamina epithelialis mucosae of the crop of *Nautilus pompilius* suggest that already the crop epithelium takes up a small amount of the nutrient. The proof of different enzymes in this segment of the digestive tract (Westermann & Schipp, 1998b) showed that in the crop the food is not only stored but also that digestive processes begin in this organ.

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## RECENT HYPOTHESES ON MECHANICAL AND METABOLIC FUNCTIONS OF SEPTAL FLUTING AND SUTURAL COMPLEXITY IN POST-CARBONIFEROUS AMMONOIDS

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Two recent papers suppose that septal fluting and sutural 'complexity' functioned primarily metabolically, not mechanically (see Hewitt & Westermann (1997; *Lethaia* 30:191-204). Higher-order fluting, resulting in increased complexity, was limited to the septum margin and accompanied by thinning, so that the suture acted like a spring or shock absorber. The centre of strong septa was progressively thickened to compensate for stress concentrations. The central/marginal thickness ratio and sutural complexity tended to increase with habitat depth within higher taxa of Mesozoic ammonoids.

Oloriz, Palqvist & Peres-Claros (1997; *Lethaia* 30: 205-212) found no significant differences in fractal-dimension values between epicontinental-platform and epiocenic-swell habitats. They conclude that sutural complexity was unrelated to depth. However: (1) They do not consider whorl diameter, which is positively correlated with fractal-dimension values, nor the scale of the illustrations used. (2) Most of their ammonoid families occur in both megafacies, but strong sutural simplification has been observed in, e.g., epeiric (<100 m) phylloceratids and lytoceratids versus their oceanic (>200 m) relatives (depths based on shell strength). (3) Orders/Suborders were lumped together disregarding strong phylogenetic effects. (4) Shell-strength data should be used for bathymetry. I predict if the authors consider my objections that they will find general trends of increasing sutural complexity and amplitude (approximation) with habitat depth within Suborders.

Daniel, Helmuth, Saunders & Ward (1997; *Paleobiology*: 23: 470-481) use a mathematical model to 'disprove' all strength functions of septal fluting in circular whorl-sections; hence fluting functioned only/mainly metabolically. Indeed, fluted septa are weaker against surface pressure than ancestral semi-hemispherical septa, but not against peripheral load where flutes formed struts supporting the flanks of compressed whorls of the first ammonoids. They stress higher-order fluting to have progressively weakened the septum; hence habitat depth varied inversely with sutural complexity. However, in real septa (1) higher-order fluting did not extend to septum centre; (2) the centre thickened with increasing complexity and margins thinned; (3) basic septal curvature was spherical (not parabolic). (4) Their 'complexity factor', i.e. number of lobes, is strongly correlated with whorl compression and should not be combined with 'sinuosity'. Their conclusion that suture complexity increased mechanical risk and limited depth is therefore valid. Their substitute, metabolic model, i.e. complexity improves cameral liquid transport during re-flooding, if valid provides only a secondary function.

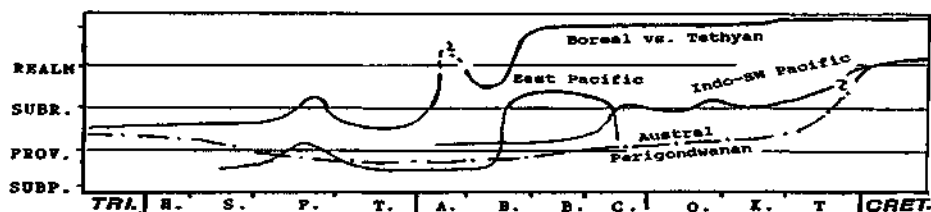
## CEPHALOPODS, VIENNA: BIRTH OF MARINE PALEOBIOGEOGRAPHY

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Roughly a century ago, Melchior Neumayr and Victor Uhlig of Vienna created semi-modern marine paleobiogeography based on ammonites and other molluscs of the Jurassic Period. Neumayr reconstructed climatic belts and distinguished numerous Provinces world-wide; followed by Uhlig who grouped the redefined Provinces into Realms, clearly distinguishing between facies and biogeographic units (biochores). Uhlig, with amazing foresight, distinguished 4 realms, placed in two Climatic Zones: Boreal (Boreal Zone), Mediterranean, Himalayan, and Andean (Tethyan Zone). I will briefly discuss their history, later interpretation and classification.

Realms, like other biochores, are distinguished biotically but defined geographically. They vary through time in area and in rank, according to the degree of endemism of their biota (not single taxa). In fact, most Realms have been either relatively short-lived or reduced to Subrealms or Provinces during much of their duration (figure). Two or three Climatic Belts with "super-realm" rank are presently recognized by some authors, but they were usually asymmetric and are difficult to delineate without biotas.



(A. BOREAL ZONE/BELT [ ? Warm - and Cold- temperate + ? Polar])

1. ? ARTIC REALM - Aal. bivalves, Call. ammonites + bivalves
2. BOREAL REALM - persistent for diverse taxa
- 2a. BOREAL - ATLANTIC REALM/SUBR. --Call. - Cret. cephs. +
- 2b. BOREAL - PACIFIC REALM/SUBR. - ? Aal. bivs., Call.+ cephs.

(B. TETHYAN ZONE/BELT [ Tropics, Subtropics + ? Warm - temperate]).

4. TETHYAN REALM = 4a + 4b - persistent for diverse taxa.
- 4a. MEDITERRANEAN SUBREALM = WEST-TETHYAN SUBREALM --persistent
- 4b. "HIMALAYAN REALM" = INDO-S.W. PACIFIC SUBREALM - persistent
- (5. "PACIFIC REALM" - L. Baj. ammonites; largely tax. error)
- (6. "INDO-PACIFIC REALM" - s.l.= 5+4b, tax. error; s.s. = 4b part)
- (7. "SOUTH ANDEAN REALM" = ANDEAN R. Arkell 1956, non Diener 1916)
- 7a. EAST-PACIFIC SUBREALM - ?Pliensb, U.Baj. - L.Call. ammonites

(C. ? AUSTRAL ZONE/BELT - "mirroring Boreal Z/B. " but lower rank)

8. AUSTRAL REALM/SUBR. - Tith., ?Hett.-Plien. (pectinoids only)
- 8a. PERI-GONDWANIAN REALM/SUBR. = 4b+7 part. - Tithonian

# MIDDLE TURONIAN TO LOWER CONIACIAN AMMONITE ASSEMBLAGES IN NORTHERN GERMANY, WITH REFERENCE TO NOSTOCERATIDS AND DIPLOMOCERATIDS

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Different basin parts are occupied by distinct ammonite assemblages, each of which is characterized by an ensemble of certain morphologies (WESTERMAN 1996). Based on WALTHER's Law of Facies, a lateral shift from proximal to distal ammonite assemblages and back must be also visible in a vertical succession that reflects a transgressive/regressive cycle. This can be observed in the Middle Turonian to Lower Coniacian of northern Germany, where distinct ammonite assemblages can be referred to individual positions in a sea level cycle. As mainly regressive parts of a cycle are documented lithologically, the successions of ammonite assemblages reflect thus shallowing. In the Turonian, i) Scaphitidae, Baculitidae and *Lewesiceras* are ubiquitous. Their presence alone is not significant. It is the absence of other taxa, which is suggestive for distal environments. Smooth forms such as *Mesopuzosia* and *Jimboiceras* co-occur. ii) Collignoniceratinae & Anisoceratidae increase in number in more proximal environments. iii) The shallowest assemblage is mainly characterized by Nostoceratidae (e. g. *Hyphantoceras*, *Neocrioceras*-like forms, *Pseudoxybeloceras*). In the Lower Coniacian, i) the shallowest ammonite fauna is characterized by Peroniceratinae (*Peroniceras*, several species). ii) Nostoceratid/diplomoceratid ammonites (*Neocrioceras*, *Scalarites*) with *Placentoceras* and *Forresteria* (Barroisiceratinae) occupy a more distal position. iii) Like in the Turonian, desmoceratids, Scaphitidae and Baculitidae dominate distal environments. The observed ammonite distribution shows some accordance with other models (comp. WESTERMANN 1996), but the occurrence of *Eubostrioceras*, *Hyphantoceras* and *Neocrioceras*-like forms mostly in near-swell setting deviates from these models that suggest this group occurring in open marine, deeper water environment (e. g. BATT 1989; morphogroup 13: loosely coiled torticones, demersal mode of life; WESTERMAN 1996: water depth 100-200 m). The data contrast KAPLAN (1991), who suggested that the sequence of an allocrioceratid/collignoniceratid fauna, followed by a nostoceratid and a desmoceratid ammonite assemblage in the Upper Turonian of northern Germany reflects transgression. As the nostoceratid/diplomoceratid faunas are comparatively restricted to shallower environment, they should have been sensitive to sea level changes. This may be confirmed by the rapid evolution of this group that shows a clear relation between phylogeny and sea level fluctuation.

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## UPPER CRETACEOUS NAUTILOIDS FROM NORTHERN CANTABRIA, SPAIN

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From 1991 to 1997, the Berlin Cretaceous Working Group studied the Upper Cretaceous succession in northern Cantabria (Spain). During fieldwork, numerous nautiloids were collected, but, due to their limited stratigraphic and palaeoecologic significance, these cephalopods were hitherto almost completely ignored. Now, the stratigraphy and sedimentary dynamics of the Upper Cretaceous sequences in the North Cantabrian Basin (NCB) are well understood (e.g. WIESE & WILMSEN, 1999). Therefore, nearly forty years after the last synoptic work on Cretaceous Nautiloidea from Spain (WIEDMANN 1960), the taxonomy of the nautiloids and their distribution patterns within the depositional environment are currently studied, and some preliminary results are presented here.

For taxonomic analysis, the shape of the suture is considered the most important feature. The form of the shell and location of the siphuncle are also of significance. Based on these criteria, the Cantabrian nautiloids can be referred to the genera *Eutrephoceras* HYATT, 1894 and *Angulithes* MONTFORT, 1808.

During the Late Cretaceous, the NCB was situated at the northern margin of the Iberian microplate forming a narrow, E/W elongated basin in which a variable, ca.

1000 m thick series of marine, predominantly calcareous sediments accumulated. It can be shown that the nautiloids do not occur scattered throughout the succession. Instead, their occurrences are often associated with intervals indicating reduced net-accumulation (condensation and/or transgressive reworking). Nautiloids are especially abundant in the condensed horizons on top of the submerged Altamira carbonate platform (Middle to Late Cenomanian, WILMSEN 1997). Here, adult representatives of the genus *Angulithes* (e.g. fig. 1) predominate and their numbers increase towards the more proximal areas whereas contemporaneous basinal marls are nearly devoid of nautiloids and dominated by ammonite faunas. Another example is presented by a terminal Santonian unconformity which, again, is characterized by abundant nautiloids. Further investigations may provide information on the relationship between nautiloid and ammonite occurrences in the NCB.

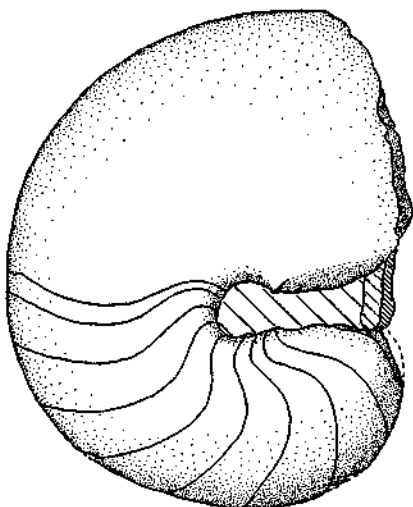


Fig. 1: *Angulithes* cf. *triangularis* (MONTFORT, 1808), Upper Cenomanian of Tagle, lateral view (x 0.5).

## **BUCKMAN'S PARADOX: CONSTRAINTS ON AMMONOID ORNAMENT AND SHELL SHAPE**

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It has repeatedly been observed that the morphology of ammonites follows a particular pattern of covariation. Within a given taxon, there will be gradation between compressed, involute, lightly ornamented forms and depressed, evolute, more heavily ornamented forms. This pattern is so well-established in widespread ammonite groups that Westermann dubbed it the First Buckman Law of Covariation. Several paleontologists have argued that there must be constructional constraints at work here—for example, the process of building a heavy rib might cause the shell to become more rounded.

On the other hand, while rib formation is generally assumed to be controlled by the genetic “growth program” of the individual, shell shape is often assumed to be susceptible to environmental influences, and controlled ecophenotypically. For instance, more compressed, streamlined individuals of a taxon are sometimes associated with higher current energy environments, while the rounder individuals are relegated to deeper, slower water.

This is Buckman's Paradox – are ornamentation and shell shape tightly linked, or is the morphogenesis of one factor controlled genetically, with the other factor controlled environmentally? If the First Buckman Law of Covariation holds, and holds specifically because the growth of a shell's form and ornamentation are tied together, we would expect that a taxon that shows a broad variation in shell shape should also show a broad variation in rib growth and form. Morphometric analyses of acanthoceratid ammonites from the Cenomanian-Turonian Western Interior Seaway of North America do not confirm this claim. Variability of rib characters and of the ontogenetic trajectories for rib width and spacing are not related to variability in shell shape characters. Hence, while some aspects of shell and rib growth may be related (and both constructionally and ecologically constrained), such a link is not reflected in the patterns of variability shown by these features.

These results suggest that controls on ornament and shell shape are different, at least in part. Buckman's covariation certainly exists, and has been well-documented in many ammonite groups. However, the exact nature of this covariation, and what causes it, is unclear. A sufficient and complete explanation for Buckman's covariation requires more, and more detailed, studies of ammonoid morphogenesis.

## CAMPANIAN-MAASTRICHTIAN AMMONITES FROM FAR EASTERN RUSSIA, STRATIGRAPHY AND PALAEOBIOGEOGRAPHY.

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Revision of literature data on Uppermost Cretaceous ammonite faunas of Sakhalin and Shikotan Islands, Korjakia Upland and the north-western coast of Kamchatka Peninsula, supplemented by evaluation of the author's big collection, allow for establishment of biostratigraphic and palaeobiogeographic affinities of the Campanian-Maastrichtian. The detailed biostratigraphic ammonite zonation is proposed for Campanian-Maastrichtian of Far Eastern Russia. Three zones are established in the Campanian and three in the Maastrichtian. According to the literature data the scheme can be employed also in the Upper Cretaceous of Japan. The Santonian-Campanian boundary is defined by the first appearance of endemic *Menuites naumanni*, accompanied by widely cosmopolitan heteromorphs, especially of the genera *Scaphites* and *Diplomoceras*. The Upper Campanian is characterized by typically Pacific ammonites as *Canadoceras multicostatum*, *C. mysticum*, *C. yokoyamai* and *C. kossmati*, accompanied by cosmopolitan *Pachydiscus* (*P.*) *egertoni* and *Desmophyllites diphyloides*. The Campanian-Maastrichtian boundary is defined by the first entry of endemic *Pachydiscus* (*P.*) *subcompressus* and cosmopolitan *P. (P.) neubergicus*. Entry of the latter is the main defining criterion of the Campanian-Maastrichtian boundary in the stratotype section. Although there is more of cosmopolitan genera during the Maastrichtian, the total number of genera diminishes, relatively to the Campanian. The most common Campanian genera belong to Desmoceratidae, Tetragonitidae, Gaudryceratidae, Phylloceratidae, Puzosiidae, Scaphitidae and Diplomoceratidae. The abrupt change of the taxonomic diversity is recorded at the Campanian-Maastrichtian boundary. After that event the representatives of Pachydiscidae became the most important taxa not only in this region but also in whole the Cretaceous world. However the last ammonite species before the final extinction at the Cretaceous/Tertiary boundary belong to Gaudryceratidae, e.g. *Zelandites japonicus* occurs still two meters below the green clay of the Danian. The whole North Pacific region of Russia is divided into two palaeobiogeographic units. The first one is Sakhalin and Shikotan Islands. The second one is Korjakia Upland and the north-western coast of Kamchatka. Although generally these two basins are with similar species during the Upper Cretaceous, on the other hand there are some interesting differences: the typical "Pacific" faunas are recorded in the Upper Campanian of both basins, but the cosmopolitan *Pachydiscus* (*P.*) *egertoni* occurs in Sakhalin only; the Maastrichtian *Patagiosites alaskensis* occurs in Korjak-Kamchatka basin only, but numerous species of Pachydiscidae are common for Maastrichtian of both basins; furthermore, the abundance of heteromorph ammonites is typical for Campanian of Korjak-Kamchatka but neither for Sakhalin nor for Shikotan Islands. Generally, the Campanian-Maastrichtian ammonite assemblages of Sakhalin are of remarkably high taxonomic diversity and good preservation. The Korjak-Kamchatka basin is characterised by more impoverished assemblages, usually of bad preservation. Nevertheless there is biogeographic affinity of these two basins, what is reflected in a single ammonite zonal scheme proposed for whole North Pacific region of Russia.

## BIOGEOGRAPHICAL CHARACTERISTICS OF THE ORDOVICIAN CEPHALOPODS FROM KOREA

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The Cambro-Ordovician Joseon Supergroup is widely distributed in Kangweondo, South Korea. The Ordovician interval of the supergroup is rich in cephalopod fossils. It is divided into the Maggol, Jigunsan, and Duwibong Formations. The Ordovician fauna from Korea shows the strongest affinities with that from North China. Of 34 genera recognized in the Korean Ordovician formations, 24 genera are also known from North China. Broadly speaking, the Korean cephalopod fauna is also closely related to those of Balto-Scandinavia, North America, Manchuria, and Siberian Platform.

The cephalopod fauna of the Maggol Formation shows the strongest affinity with that of South Manchuria in having such common genera and species as *Polydesmia*, *Manchuroceras*, *Wutinoceras robustum*, and *Kogenoceras nanpiaoense*. In addition, three species, *W. robustum*, *M. nakamense*, and *K. nanpiaoense* in the Maggol fauna are known from the Setul Limestone in Thailand and Malaysia (Stait *et al.*, 1987).

The Jigunsan cephalopod fauna characterized by orthoceroids and endoceroids is entirely different from that of Manchuria which comprises many actinoceroids. This fauna shows an affinity with those of North China and the Balto-Scandinavia region. The Hawngho fauna in North China shares 13 common genera with this fauna. Especially, the common occurrence of *Kotoceras*, *Centroonoceras*, *Leptoplathmoceras*, *Stereoplasmoceras*, and *Wenmanoceras* indigous to both regions strongly supports the biological affinities between them. The Middle Ordovician cephalopod faunas of the Oslo region, Norway and the Baltic Sea comprise many lituitids and some *Sactorthoceras* and *Stereoplasmoceras* in which 11 genera are common with the Jigunsan fauna (Sweet, 1958).

The Duwibong cephalopod fauna characterized by actinoceroids has the strongest affinity with that of South Manchuria, based on the common occurrence of *Armenoceras*, *Ormoceras*, *Hoeloceras*, and *Selkirkoceras*. Previous works in the Arcto-America region suggest North America to be the mecca of actinocroid cephalopods. The Arcto-America fauna migrated and extended to East Asia through the Siberian Epicontinental Seaways. The seven genera of actinoceroids and *Tofangoceras* in the Duwibong fauna are also reported in Siberian Platform (Balashov, 1962). In conclusion, the Duwibong cephalopod fauna represents Arcto-American faunal elements.

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## **THE UPPER JURASSIC AMMONITE FAUNA OF ERNSTBRUNN (NE AUSTRIA) AND ITS INTERESTING POSITION BETWEEN THE TETHYDIAN AND SUBBOREAL FAUNAS**

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An overview will be given on the composition of the famous ammonite fauna of the Ernstbrunn Limestone, which has been collected by F. Bachmayer and studied by the author during the last fifteen years. The ammonite fauna is of Middle to lowermost Upper Tithonian age; the main part (ca.50%) of the ammonites belong to the perisphinctids (six genera, three of them are new); the mikroconchs have been found also in other areas of the Tethys, while the macroconchs are known almost only from here or other localities along the northern margin of the Alpine-Carpatho-Basin. Phylloceratids (ca. 12%), Lytoceratids (25%) and Haploceratids (ca. 13%) compose the other half of the fauna; these are mainly Mediterranean forms; but, considering the dimensions of the shells and the ornamentation they can be regarded as forms that lived mostly in shallow seas.

The high percentage of Mediterranean genera is significant for the position of the locality: it is a 'Klippe' situated at the northern margin of the Alpine geosyncline (Flysch Basin), not far from the original deposition area of the shelf sediments covering the Bohemian Massiv.

As the author demonstrated earlier, the ammonite fauna of the underlying Klentnitz Beds is strongly influenced by immigrants from the Easteuropean Subboreal Province; such influences are scarcely to note in the Ernstbrunn Limestone. However, of special interest are some perisphinctids which display an ornamentation of Subboreal character, i.e. the ribbing style is homeomorphic in some parts of the outer shell to those of genera from the eastern European Platform, while the inner whorls don't differ from other Mediterranean forms. A similar tendency has been observed in the Submediterranean Neuburg Formation of Middle Tithonian age. The reasons for these homeomorphic developments are difficult to explain. Most probably, original quite distinct ribbing styles led sometimes accidentally to similar, homeomorphic sculptures.

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