

2.3. The structure and distribution of the European Cretaceous brachiopod assemblages with emphasis on the Tethyan fauna

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Abstract

The Cretaceous was a time of decline for brachiopods, which tried unsuccessfully to re-occupy lost niches in the neritic communities. The structure of the Cretaceous brachiopod assemblages was much simpler than that of the Paleozoic ones. Nevertheless, the analysis of the quantitative composition of these assemblages provides an instructive view of their development, which is characterized by frequent opportunism and interruptions of the evolution of assemblages. Fluctuations in distribution are also typical for Cretaceous brachiopod paleobiogeography, making the exact delimitation of the mutual boundaries between a Tethyan, a Jura and a Boreal realm problematic, if not speculative in detail.

1. Introduction

Brachiopods are an ancient group of neritic benthic organisms which saw their maximum development during the Paleozoic. At the beginning of the Mesozoic, the brachiopods overcame several crises which diminished their importance in benthic faunas. The history of Mesozoic brachiopod development was an attempt to recolonize the shelves. However, many of the old brachiopod niches had been progressively substituted by other, more adaptable, ecologically more tolerant and flexible groups (MICHALIK, 1987a). Many of the Triassic and Jurassic brachiopod associations were dominated by opportunistic forms (AGER, 1971; VÖRÖS, 1987; MICHALIK, 1989 etc.).

Despite this fact, many specific faunal assemblages developed in various

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regions. Since the basic works of AGER (1967; 1971; etc.) the European brachiopod faunas have been divided into the Mediterranean-, the Jura- and the Boreal types. However, the distribution of individual species changed in space and time, being affected by migration, destruction of populations, by unfavourable environmental conditions, and by geographic specialization. (The differences in individual taxonomic conceptions are not considered here, but they often represent a serious obstacle for the comparison of populations).

These factors make the exact delimitation of the boundaries between the paleobiogeographic zones rather uncertain. On the other hand, despite of the scarcity of reliable, complex and comparable data in the brachiopod literature the quantitative analysis of brachiopod associations could provide a better understanding of their paleobiogeography than some imaginary "index species".

2. Late Jurassic brachiopod development

At the end of the Jurassic, the system of basins with black clay and marl sedimentation originating in the Boreal epicontinental sea belt (London-Paris-, Rhone-, Swabian- and Polish Basins) was bordered by sponge and coral reefs. Here, the brachiopods played only a subordinate role in the benthic communities (FÜRSICH, 1977). The Sub-Mediterranean (Sub-Tethyan) realm, with its characteristic Jura-fauna, formed a belt from SE France through northern Switzerland, southern Poland, Dobrogea, Crimea, northern Caucasus to Kopet-Dagh (cf. MICHALIK, 1989). Brachiopod faunas were infrequent in the Tethyan realm during the Callovian-Oxfordian transgression, but they became more diversified and abundant during the Kimmeridgian and Tithonian. The coral reefs bordering the Mediterranean were inhabited by characteristic brachiopod associations. SMIRNOVA (1975) has described such an association consisting of *Weberithyris moravica*, *Tropeothyris cyclogonia*, *T. immanis*, *Cyclothyris astieriana*, *Lacunosella* sp., etc. from the Inwald locality of the former Stramberk limestone platform belt in the Outer Carpathians (Fig. 1).

Open marine shallow environments on the elevated, faulted block surfaces were inhabited by brachiopod associations dominated by *Camerothyris wahlenbergi*, *Karadagithyris bilimeki*, *Lacunosella hoheneggeri*, *L. zeuschneri* and by *Monticlairella* species. Nucleata and perforated pygopids, although subordinate, were stable components of these associations (BARCZYK, 1971; 1972). This can be shown in the Czorsztyn locality in the outer Carpathian Klippen Belt (Fig. 1).

The pygopids were the most significant (if not the only) elements of the Tethyan basinal brachiopod faunas (AGER, 1967; 1976). However, they also penetrated into northern seas as far as eastern Greenland. This means that the limits of the pygopid distribution (called the "Tethyan index") do not fit in the boundaries of the Tethyan realm. On the other hand, the distribution of the "Tethyan" species was not only controlled by bathymetry and temperature. The simple structure of the South Alpine pygopid associations (DIENI and

MIDDLEMISS, 1981) is rather strange; it provokes some doubts as to whether the sampling methods used have been comprehensive and thorough enough for catching also the scarcely represented species of the brachiopod association (Fig. 1).

AGER (1.a.) suggested that the filtratory system of the pygopids was enormously effective allowing them to live in bathyal depths unfavourable for any other brachiopod groups. The deep-sea environment is poor in fluctuations, supporting the conservation of ancient animals living there. However, the pygopids interpreted as Upper Jurassic-Lower Cretaceous deep sea calm water benthos failed to survive the Lower Barremian and (with the exception of east Greenland) they never extended beyond the Tethyan deep marine basins. The mode of life, the relation to the environment, as well as the parameters governing the distribution of this obscure brachiopod group remain uncertain despite several attempts to elucidate them (AGER, 1978; VOGEL, 1966; etc.).

3. Early Cretaceous brachiopod development

Many brachiopod taxa which arose during the Later Jurassic survived the Tithonian-Berriasian environmental changes and continued to evolve during the Valanginian and Hauterivian until the lowermost Barremian (MIDDLEMISS, 1979; 1981; 1984; Fig. 2). Despite important paleogeographical changes connected with the Neo-Kimmerian orogenetic movements at the end of the Jurassic, the evolution of the principal paleo-biogeographical zones continued with only minor interruptions (MICHALIK et al., 1987). During the Berriasian, Boreal epicontinental seas yielded only few satisfactory conditions for brachiopod life (*Uralorhynchia* etc.). The absence of reefal and other pure limestones in this realm, along with the dominance of terrigenous clastic sedimentation was caused by a cold and relatively humid climate. Fluvial and brackish sedimentation prevailed in many areas. However, during the Valanginian, wide areas from eastern Greenland, Scotland, England to northern Germany were colonized by brachiopods. *Rouillieria*, *Rugitella* and *Rhynchonella*, supposed to be immigrants from the Russian Platform (MIDDLEMISS, 1973; OWEN, 1973) migrated to the west. *Ptilorhynchia* (syn. *Fusirhynchia*, cf. OWEN, l. c.) migrated from western North America through Siberia to eastern Europe. MIDDLEMISS (1973; 1979) reports a Valanginian mass migration of the Jura (or even Tethyan) faunas to the Boreal regions (Paris Basin, Northern Germany: *Oblongarcula*, *Sulciorhynchia*, *Sellithyris carteroniana*, *Musculina sanctaerucis*, *Moutonithyris moutoniana*) and to Spain and Morocco. The Boreal realm was bordered by a dry-land belt to the south, with only shallow and narrow seaways (MIDDLEMISS, 1976; 1979). Valanginian and Hauterivian Boreal cephalopods penetrated into the Mediterranean through the Polish Gate of the Danish-Polish Trough (MICHALIK and KOVAC, 1982). However, no Lower Cretaceous brachiopods have yet been found in the adjacent Polish Basin. This is why the south Germany straits ("Rheinische Senkungszone") are considered as the main path of brachiopod

exchange between the Boreal and the Sub-Tethyan realms. The bottom of the straits between the Paris and London Basins was probably too shallow and too agitated by the high water energy for rendering attachment opportunities for brachiopod larvae. The latter straits gradually lost their function as physiogeographic barriers in the Early Hauterivian (MIDDLEMISS, 1973). In contrast, the Polish Gate closed during the Late Hauterivian (MICHALIK and VASICEK, 1989).

The Sub-Mediterranean (Sub-Tethyan or simply Jura) realm was situated at the southern rim of the north European shelf. Its environment was characterized by well oxygenated water, by warm climate, by many substrates suitable for brachiopods and other benthic life, and by periodic oceanic influences. In this realm, the brachiopods formed a specific bioprovince, characterized by endemic brachiopod genera like *Sellithyris*, *Loriolithyris*, *Boubeithyris*, *Musculina*, *Glosseudesia*, *Lamellaerhynchia*, *Sulcirhynchia*, *Plicatirostrum* and others. Many brachiopods (*Lacunosella*, *Monticlarella*, *Belbekella*, *Plicatirostrum*, *Lamellaerhynchia*, *Belothyris*) came from middle Asia to Kopet Dagh, Caucasus, Crimea and spread into southern France and Morocco. Some even penetrated far north into Boreal basins (Fig. 3). (MIDDLEMISS, 1973; 1979; 1980; 1981; OWEN, 1973; SANDY, 1986; etc.).

No continuous barrier existed between the Subtethyan and the Tethyan realm. The Tethyan forms (*Monticlarella*, *Ismenia*, *Weberithyris*, *Peregrinella*, *Lacunosella*) were dominant in many places along the border of the North European shelf (DIENI et al., 1973). Despite their "conservative" distribution (MIDDLEMISS, 1984) they have spread between northern Caucasus, Crimea (YANIN and SMIRNOVA 1981), the Outer Carpathians (NEKVASILOVA, 1974-1978, cf. Fig. 4), the Pre-Alps of Switzerland and SE France (LE HEGARAT et al., 1973; SANDY, 1986), Sardinia (DIENI et al., 1973) and occurred even in eastern Greenland (AGER, 1963).

4. Mid-Cretaceous brachiopod distribution

All the typical "Jurassic" forms (*Pygope*, *Antinomia*, *Triangope*, *Pygites*, etc.) became extinct during the Lower Barremian. The distribution of the Tethyan and Sub-Tethyan forms diminished considerably. The Paris Basin was affected by a regression. *Moutonithyris* disappeared from Northern Europe, retreating deeply into the Tethyan realm. However, several species which developed during the Early Cretaceous migrated northwards and became dominant elements in the Late Barremian brachiopod assemblages (Fig. 5). This was the beginning of a new pulse of brachiopod migration.

Together with other "southern" forms (*Sulcirhynchia*, *Sellithyris*, etc.), *Moutonithyris* migrates during the Aptian through the German Basin as far as England. On the other hand, *Cyrtothyris* and other Boreal elements (*Platythyris*, *Oblongarcula*, *Rhombothyris*) spread into the Jura domain (Switzerland, SE France, Eastern Spain, SW Morocco) during the Late Albian. Other Tethyan

elements penetrated through the Pyrenees and the opening Gulf of Biscaya into Spain. Sicily and Sardinia were inhabited by true Tethyan assemblages (according to MIDDLEMISS et al., 1973: *Sardope*, *Tropeothyris* etc., cf. Fig. 6). Extensive carbonate platforms of the "Urgonian" facies evolved on the Tethyan shelves, being characterized by rich assemblages of hermatypic corals, rudists, orbitolinids, bryozoans and algae. The lack of terrigenous detritus is correlated with a lower percentage of rhynchonellids in the Tethyan brachiopod assemblages (Fig. 6). These facts indicate a hot and dry climate in the Tethyan Belt, contrasting with the more humid Boreal realm.

A rapid spreading of rhynchonellids during the Albian (*Cyclothyris*, *Orbirhynchia*, *Burmirhynchia*, etc., cf. LOBACHEVA, 1983; POPIEL-BARCZYK, 1977; MIDDLEMISS and Owen, 1980) and increased opportunism by *Ornatothyris*, *Musculina*, *Sellithyris*; (MIDDLEMISS, 1983; etc.) have been connected with a gradual substitution of carbonates by clastic sedimentation in wide areas, caused by important paleogeographical changes during the Austrian Phase of the Alpine Orogeny. This reorganization of environments led to substantial changes in brachiopod faunas. Virtually all the dominant Early Cretaceous types got extinct during the Cenomanian.

5. Early Upper Cretaceous brachiopod evolution

The end of the middle Cretaceous was characterized by a transgression affecting a broad belt of the European Craton. The rapid development of new life habitats led to a new brachiopod migration. However, the evolution and diversification of the brachiopod communities was limited by the predominantly terrigenous character of the sedimentation. The rhynchonellids with a zig-zag commissure (*Burmirhynchia*, *Orbirhynchia*, *Cyclothyris*, *Grasirhynchia*, *Cretirhynchia* etc.), which were well adapted to silty and sandy substrates, became dominant elements of the brachiopod associations. Pelitic environments were inhabited by *Terebratulina*, *Kingena*, *Magas*, etc. (NEKVASIOLOVA, 1964 to 1974; POPIEL-BARCZYK, 1974; MIDDLEMISS and OWEN, 1980; etc.). Other Cenomanian associations consisting of *Concinnithyris*, *Gibbithyris*, *Capillithyris* and *Platythyris* (in marly facies), or of *Grasirhynchia*, *Orbirhynchia*, *Kingena*, etc. (glauconitic limestones) evolved in various environments of NW Europe (OWEN, 1978). Similar associations also inhabited Central and SE Europe. Several specific forms evolving on the Russian epicontinental shelf penetrated into adjacent areas (Don Basin etc., cf. KATZ, 1973) during the Turonian. The latter region was characterized by *Najdinothyris*, *Urbanirhynchia*, *Kaphirnigania*, *Orbignyrrhynchia*, etc.

Subtethyan assemblages consisted mostly of calm-water forms like *Musculina*, *Sellithyris*, *Platythyris* (cf. DIENI et al., 1973; MIDDLEMISS, 1983; LOBACHEVA, 1983; etc.). This fauna is not diverse and shows a strong tendency towards opportunism (Fig. 6). A opportunistic Cenomanian association with *Trigonosemus* occurs in Turkmenia (VANCHUROV, 1966).

As Tethyan brachiopod assemblages of early upper Cretaceous age were extremely rare our knowledge about them is rather poor.

6. Late Cretaceous brachiopod development

The Santonian and Early Campanian was the time of a general retreat of brachiopods. The Cretaceous forms disappeared from all environments without being replaced by any other brachiopod taxa. This extinction event represents the most important crisis in the Mesozoic history of the phylum. The Campanian paleogeography (Fig. 7) differed from the middle Cretaceous one. Large areas were flooded by epicontinental seas and the source areas of clastic sediments diminished. On the other hand, surfaces in the Alpine folded belts which had fallen dry during the Austrian tectonic phase were the source areas for flysch sedimentations. The brachiopods *Neoliothyris* and *Carneiothyris* appeared along the coasts of the European continent in the Late Campanian and persisted until the earliest Palaeocene. They were accompanied by inarticulates (*Danocrania*, *Isocrania*, *Discinisca*, *Lingula*), which occurred frequently on neritic clastic bottoms.

The association of the deeper neritic zone consisted of *Rhynchorina plena*, *Carneiothyris suecica*, *C. uniplicata*, *C. circularis* (in the Don Basin, cf. KATZ, 1973), or of *Trigonosemus elegans*, *Terebratulina striata* and *Carneiothyris carnea* (in Dobrogea; BARBULESCU et al., 1979). Some associations in Poland were dominated by *Terebratulina faujasi* and *Rugia tenuicostata* (BITNER and PISERA, 1979), or by *Carneiothyris circularis*, *C. subpentagonalis*, *Chatwiniothyris subcardinalis*, *Neoliothyris obesa* and *Kingenella kongieli* (POPIEL-BARCZYK, 1968).

Several Maastrichtian associations of Denmark and their temporal variations were described in detail by SURLYK (1972). They were dominated by *Terebratulina chrysalis*, *T. faujasi*, *T. longicollis*, *Dalligas nobilis*, *Argyrotheca hirunda*, *A. bronii* and *Scumululus inopinatus* (Fig. 8). Upper Maastrichtian cancellothyrids (*Terebratulina*, *Gisilina*, *Rugia* and *Meonia*) were substituted by *Argyrotheca* which was dominant at the Maastrichtian-Danian boundary (JOHANSEN, 1987). This last author has described an abrupt extinction event at the Cretaceous/Tertiary boundary, which would be in a good agreement with the impact theory. However, she did not publish any data on the quantitative composition of successive stages of brachiopod assemblages.

Late Cretaceous brachiopods of the Kopet-Dagh in the Sub-Tethyan belt (VANCHUROV, 1967) were represented by craniids. From Danian deposits, VANCHUROV and KALUGIN (1966) have described some brachiopod associations strongly dominated by *Orbirhynchia rionensis* and *Gryphus orientalis*. A strong opportunism was also characteristic for other Sub-Tethyan areas.

Concerning the Tethyan Realm, MAKRIDIN & KATZ (1965) have drawn attention to an occurrence of *Trigonosemus*, *Basiliola* and craniids in the Caucasus area (without any literature citations). Moreover, they mentioned some craniids and rhynchonellids in the Balkan and Pyrenees. On the other hand, AGER

(1973) observed a "surprising lack of information" about brachiopod distribution in many highly fossiliferous Late Cretaceous sequences, especially in the Tethyan region. It seems that the Late Cretaceous crisis (certainly caused not only by the prevalence of fine terrigenous clastics and even flysch deposits in this area) had a more fatal effect on the Tethyan brachiopods.

7. Discussion and summary

The brachiopods represent a group suitable for solving a number of paleogeographical problems: their distribution depends on a narrow substrate tolerance, on small changes in marine currents, on little salinity fluctuations, and on the average water temperature. By studying their paleo-biogeographic distribution several faciological, paleoclimatological and paleoecological problems can be solved. However, such results cannot be achieved by investigating the occurrence of individual specimens. Even the distribution of species merely reflects their special (often irregularly patched) limitations. A more complex view can be obtained by the analysis of changes in assemblages. However, obtaining approximative knowledge of the original composition of fossil communities is not easy. A quantitative analysis of the associations seems to be an appropriate method not only for documenting the study material. Environmental changes are much better reflected by faunal successions than by the traditional "faunal list". Furthermore, these successions allow an estimation of how detailed and complete the knowledge of the individual association is.

In this context, our knowledge of the Cretaceous brachiopods is not adequate enough to give a definitive answer to many questions concerning their migration, the limits of their distribution, and the reasons for their decline. Many of these problems could perhaps be answered by a quantitative analysis of associations, based on sufficiently complete field data.

The mechanisms of the slowly proceeding substitution of "Jurassic forms" in Early Cretaceous brachiopod associations by more progressively evolving groups need to be explained. An interesting but still neglected problem is the relation between the development of the Early Cretaceous carbonate platforms and basins and the development of neritic brachiopod faunas. We also need an interpretation of the gradual retreat of brachiopods from the Tethyan domain during the Late Cretaceous. Tethyan faunas of this age are very inadequately known. Moreover, we know only a few, partly documented examples of brachiopod migrations at that time. Another problem is the insufficient knowledge of the cause, history and meaning of the Santonian crisis in brachiopod development. By recognizing all details of this process in fossiliferous, well sampled sections new light on the problems of animal extinction could emerge.

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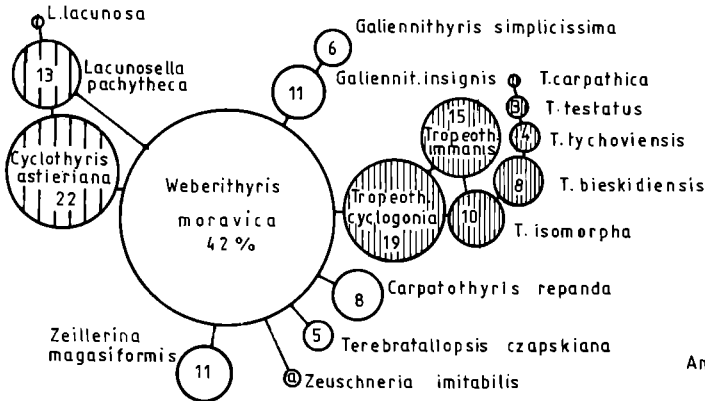
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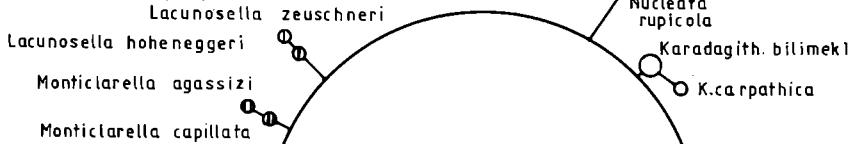
SMIRNOVA 1975 INWALD

Upper Tithonian



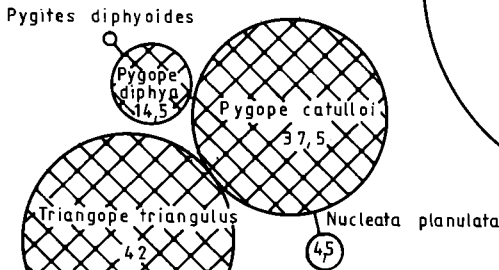
BARCZYK 1971-2 CZORSZTYN

U.Tithonian - Berriasian



DIENI & MIDLEMISS 1981

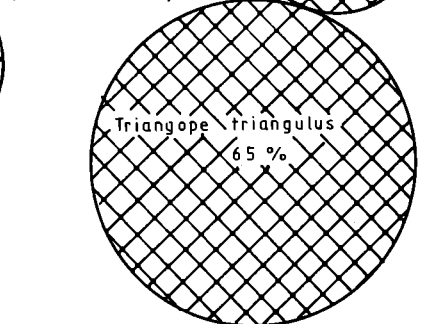
SETTE COMMUNI (U.Tith.-Berrias.)



FONTANA FREDDA

EUGANEI

(U. Tithonian)



ROVERE

(Biancône F.
U.Tith.-Berrias)

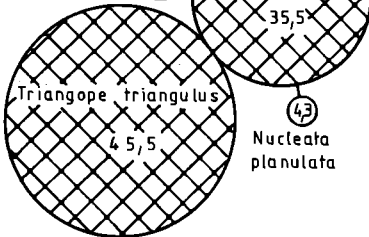


Fig. 1: Quantitative analysis of Late Tithonian and Berriasian brachiopod assemblages. The localities Inwald and Czorsztyn are situated in the western Carpathians, the other three localities are in the Southern (Venetian) Alps. The diameters of the circles represent the percentage of the species in the assemblage. Thin vertical hatching: *Rhynchonellids*; dense hatching: *Tropeothyris*; grating: *Pygopids*.

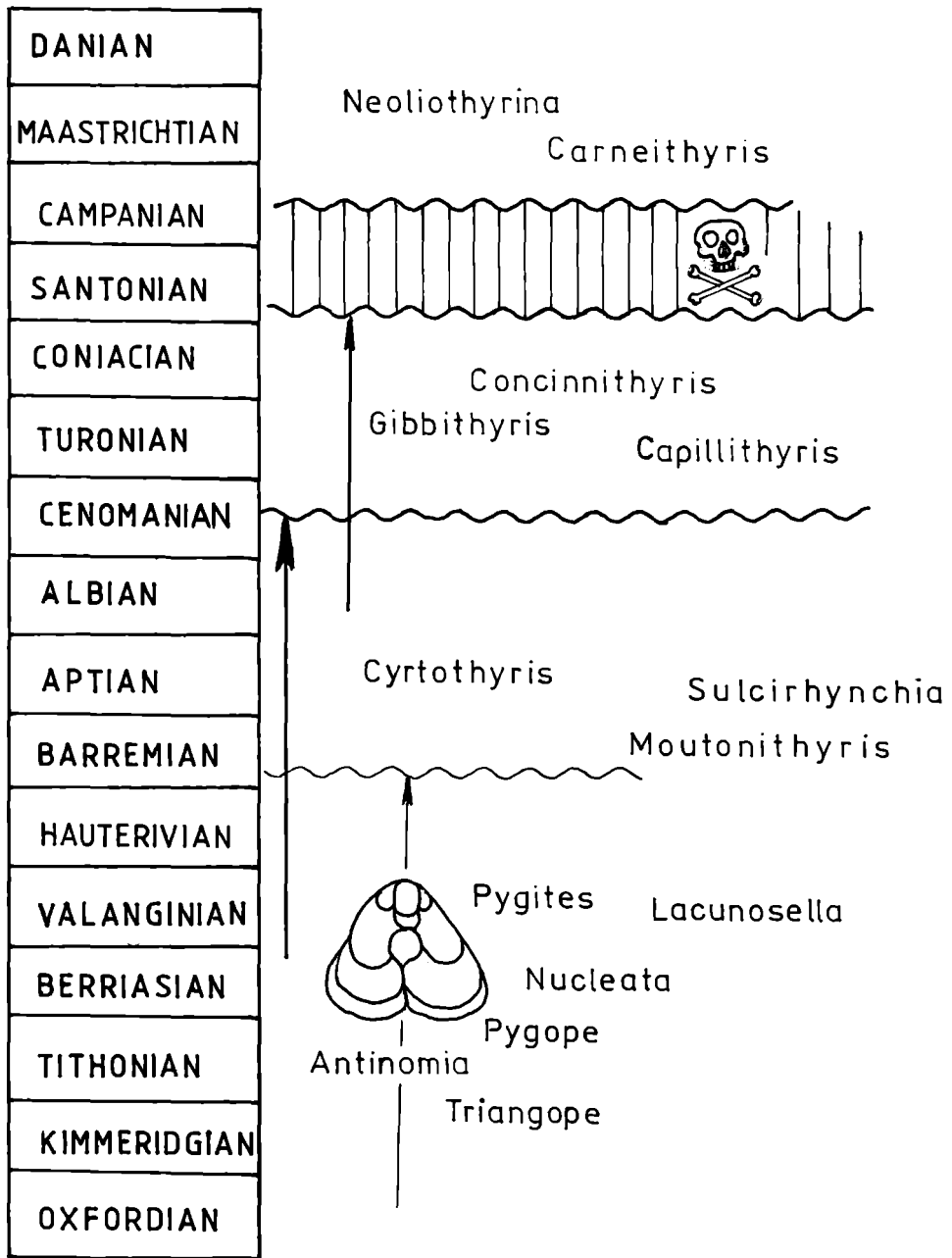


Fig. 2: The phases of Cretaceous brachiopod evolution (sensu MIDDLEMISS, 1984).

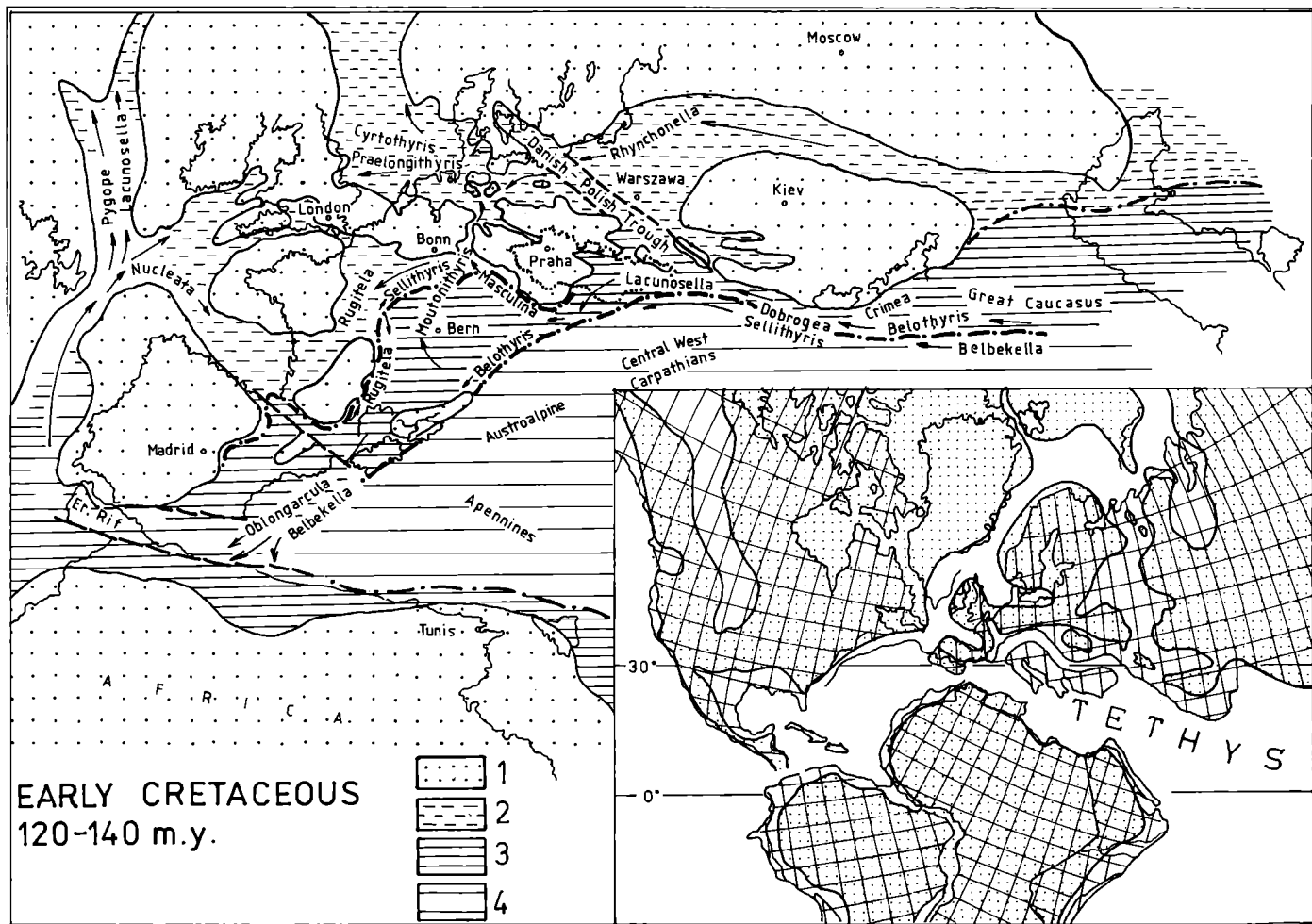


Fig. 3: Lower Cretaceous brachiopod provinces in Europe. Paleogeography after BARRON et al. 1981; OWEN, 1983; MAKRIDIN & KATZ, 1965. 1. Continental areas; 2. Boreal Realm; 3. Jura Subprovince; 4. Tethyan Realm. Arrows indicate supposed migration routes.

NEKVASILOVÁ 1974-8
Valanginian ŠTRAMBERK

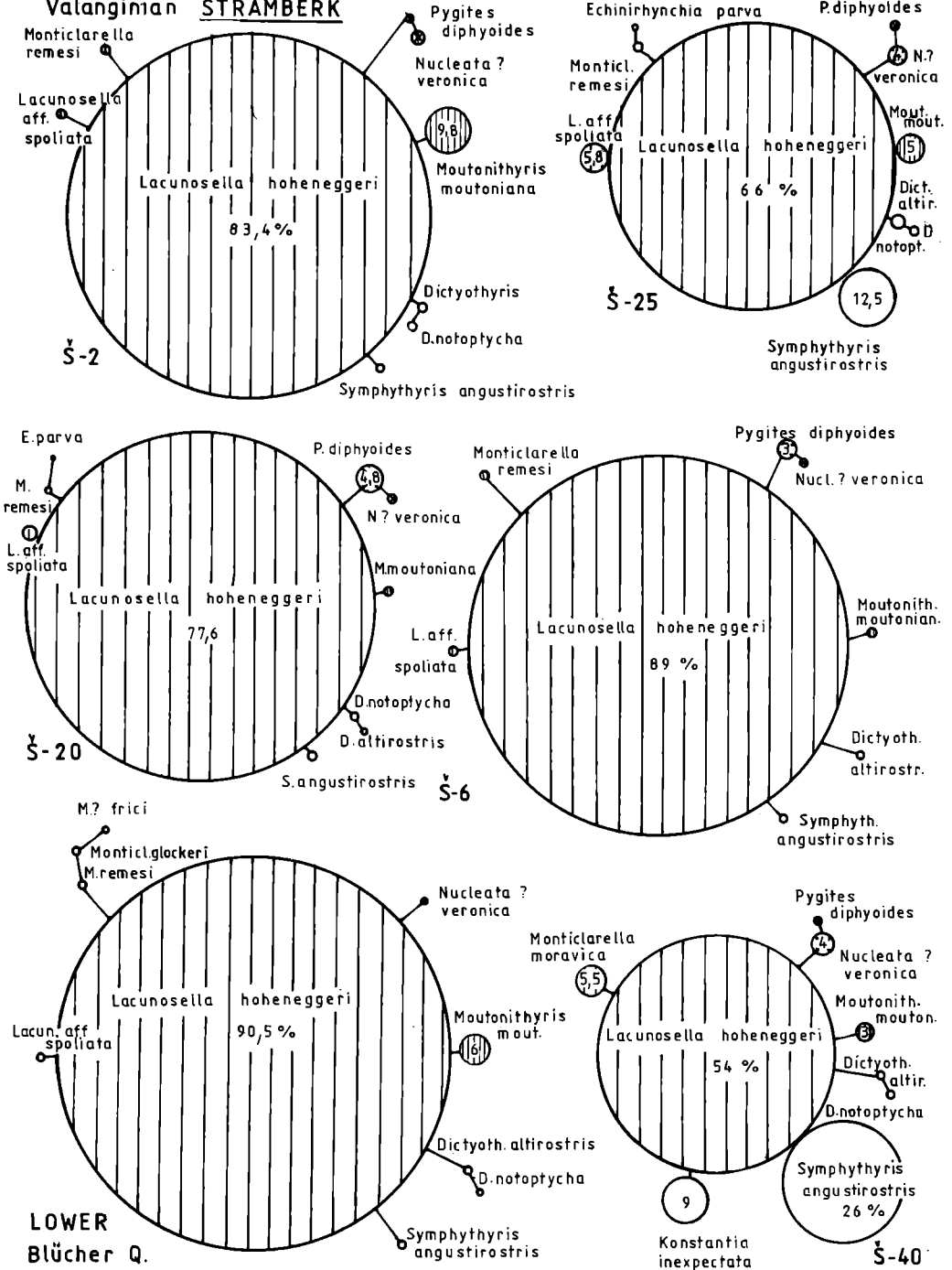


Fig. 4: Quantitative analysis of Valanginian brachiopod associations of the locality Štramberk (Outer Carpathians). Dense hatching: *Moutonithyrus*; other symbols as in figure 1.

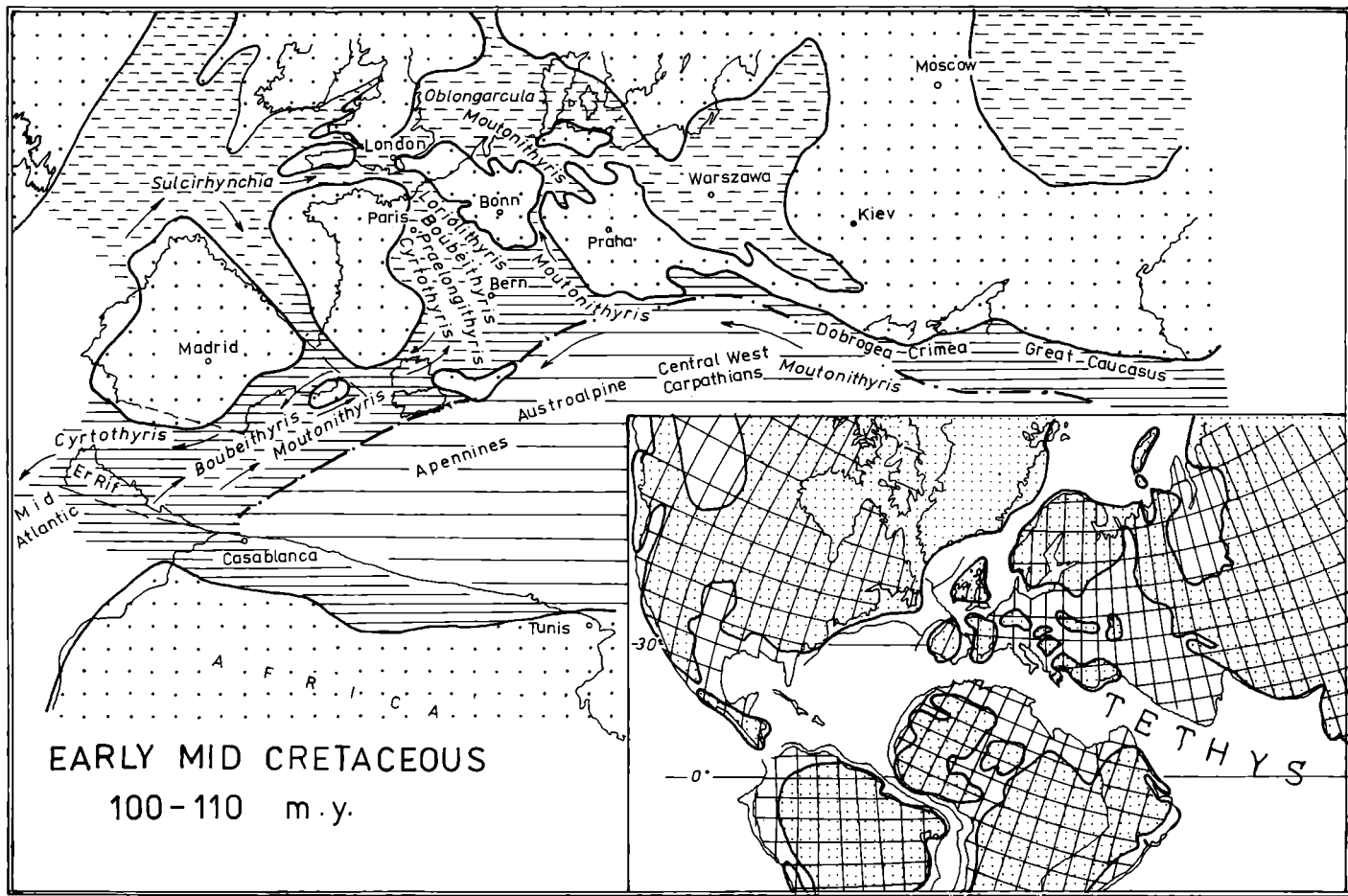
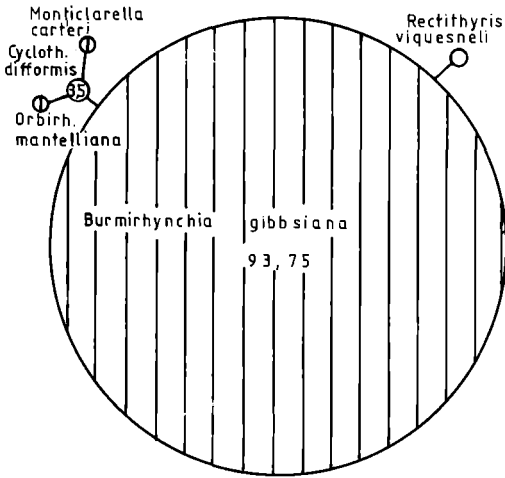
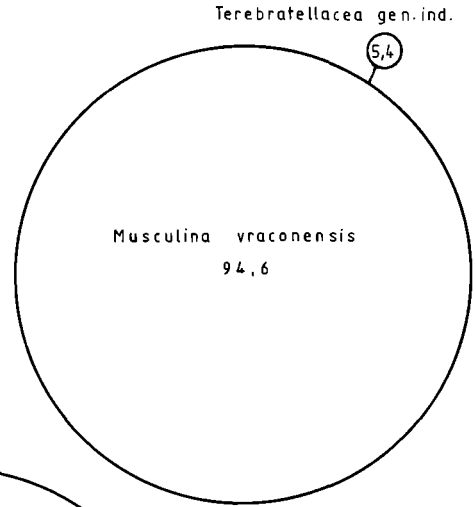


Fig. 5: Distribution of selected middle Cretaceous brachiopod genera in Europe. Paleogeographic base as in figure 3.

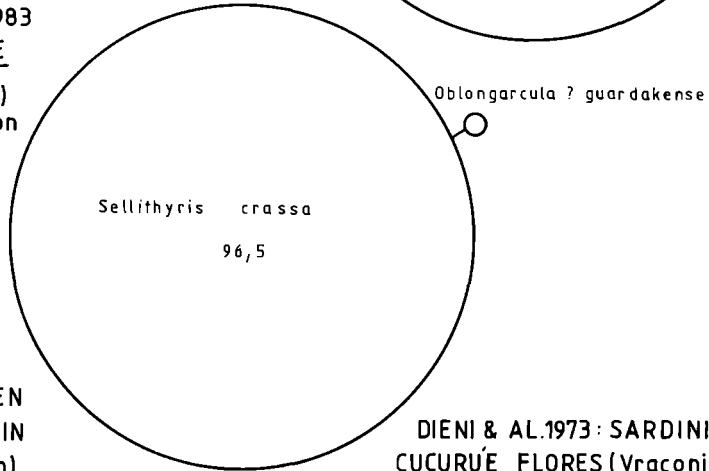
POPIEL BARCZYK 1977
ANNAPOL (Upper Albian)



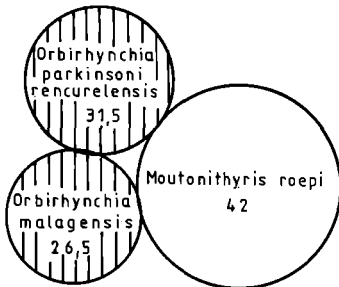
MIDDLEMISS 1983 JURA MTS.
LA VRACONNE (Vraconian)



LOBACHEVA 1983
GISSAR RIDGE
 (Upper Albian)
 composed section



MIDDLEMISS & OWEN
 1980: MALAGA, SPAIN
XIQUENA (U. Albian)



DIENI & AL. 1973: SARDINIA
CUCURUÉ FLORES (Vraconian)
 Nucleata mediterranea

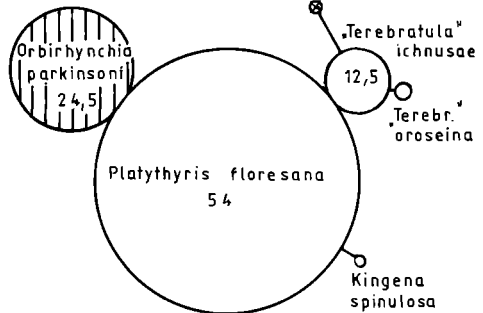


Fig. 6: Quantitative analysis of late Albian brachiopod associations. Annapol and Xiquena belong to the Boreal Realm, the other associations have Sub-Tethyan (Jura-) character.

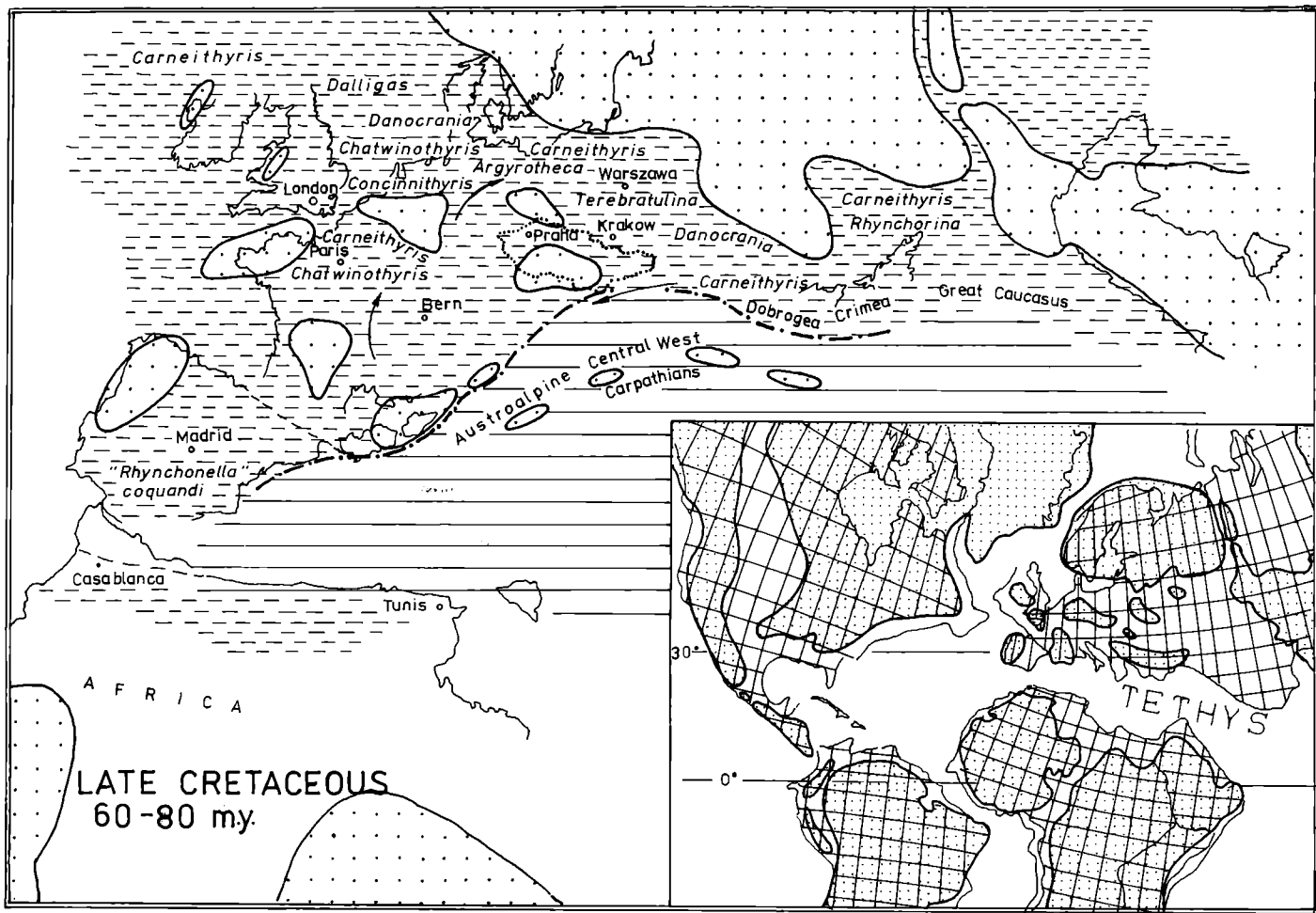


Fig. 7: The distribution of selected Late Cretaceous brachiopod genera in Europe. Paleogeography and symbols as in figure 3.

SURLYK 1972 (Maastrichtian)

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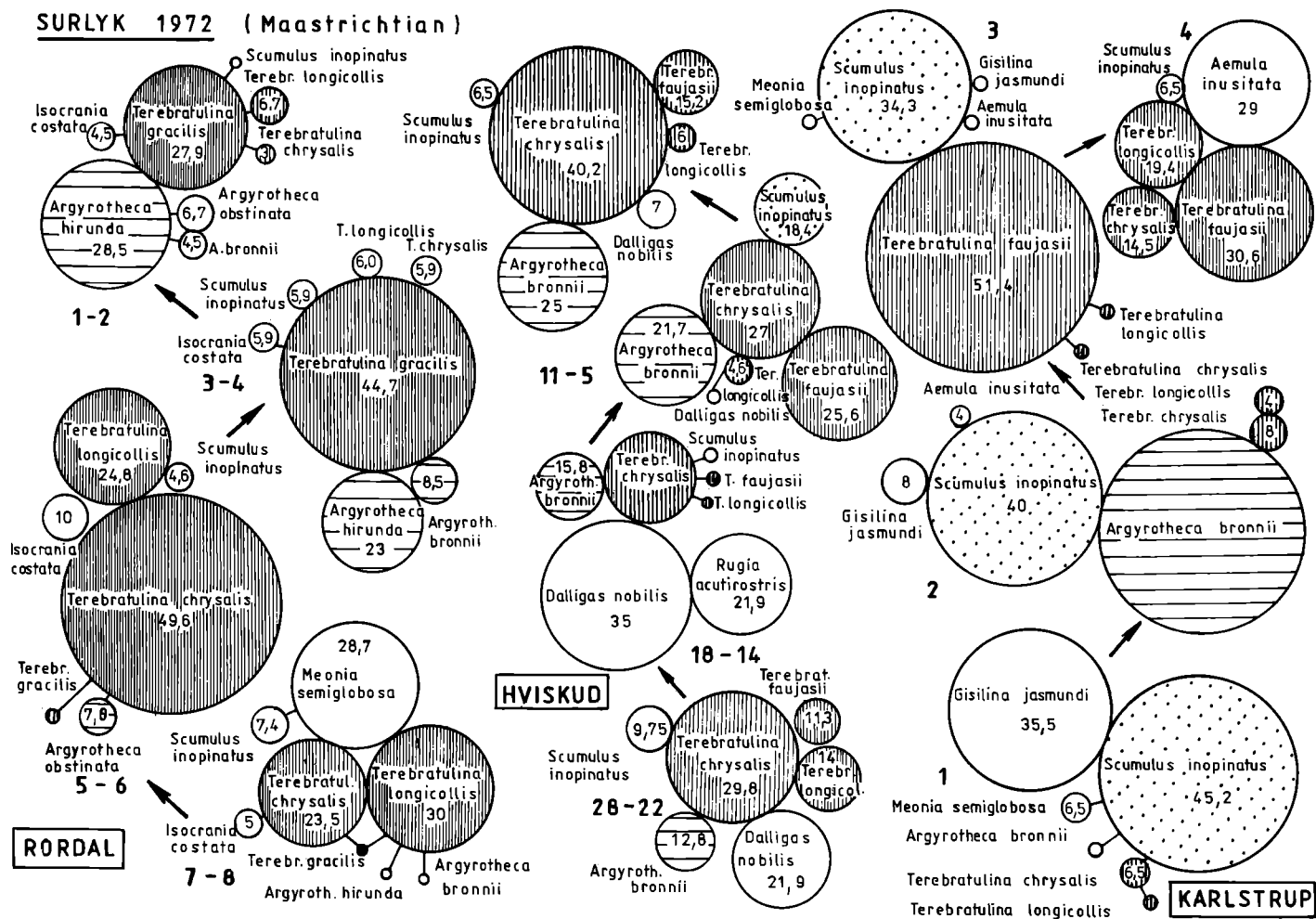


Fig. 8: Quantitative analysis and successive development of Maastrichtian brachiopod associations of three sections in Denmark (after SURLYK, 1972). The numbers refer to the original numbering of the fossiliferous levels by SURLYK. Horizontal hatching: *Argyrotheca*; vertical hatching: *Terebratulina*; dots: *Scumulus*.