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Climatic changes and development of benthic communities through the Mediterranean Ordovician

Klimatické změny a rozvoj bentických společenstev během ordoviku v mediteránní provincii

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Abstract: North Africa and South Europe are assigned as a rule to the Mediterranean zoogeographic province which in the whole is a cold-water province of the circumpolar zone; marginal parts of this province may reach the temperature zone. Extensive shelves and intracratonic basins in North Africa were a domain of *Tigillites* and inarticulate brachiopod communities, as a rule controlled by a very cold climate and lower salinity of the Sea. The communities of the Moroccan-Bohemian type are confined to the Anti-Atlas Mts. and South Europe and colonize also the mobile Variscan belt. Significant *Aegiromena-Drabovia* fauna originated as late as in the Middle Ordovician; in the uppermost Ordovician, it was substituted by the *Hirnantia* fauna. The upper Beroun and lower Kralodvor are characterized by a marked increase of temperature resulting in colonization of extensive areas in South Europe by warmer-water fauna of the Anglo-Baltic type. Two phases of glaciation have been recognized: the earlier one is assigned to the Beroun (central Libya only); the main glacial event is of Kosovian age and affected the whole Mediterranean province. The Mid-European Sea, separating the Gondwanaland from the North European platform, was no significant barrier prohibiting interchange of the fauna during the whole Ordovician.

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Introduction

Spjeldnaes (1961) assigned to the Mediterranean province an extensive area of the former Gondwanaland ranging from Syria in the east to Florida and Alabama in the west. The Mediterranean province in his concept covered South and Central Europe, the Balkans, and much of North Africa. From the zoogeographic point of view, it was considered as a cold-water province affected by the Pole position at about centre of the Gondwanaland, thus being easily distinguishable from the American-Arctic, Appalachian, and Anglo-Scandic provinces bearing warmer-water marine fauna.

The Mediterranean province contains a set of benthic communities inhabiting various environments and depths of the Ordovician basins between the Mid-European Sea in concept of Whittington and Hughes (1972) (later called the Rheic Ocean, e.g. Cocks - Fortey 1982) and the emergent Precambrian shields in North Africa. When using the trilobites for zoogeographic treating, it roughly corresponds to the *Selenopeltis* province as suggested by Whittington and Hughes (1972). Havlíček (1974) pointed to the fact that the benthic fauna is far from being uniform over the whole Mediterranean province; this depends on latitudinal-climate control, geographic distribution, and various modes and rates of migrations of individual animal groups. Whereas the trilobites form richly diversified assemblages throughout the Ordovician, the brachiopod assemblages are poor in the lower Ordovician and usually lack elements common to two or more areas within the Mediterranean province. A distinctive *Aegiromena-Drabovia* fauna originated as late as in the Middle and Upper Ordovician and spread out also beyond the Mediterranean province into the Andean region of the Gondwanaland (Havlíček - Branisa 1980). The *Aegiromena-Drabovia* fauna is distinct from the warmer-water shelly faunas with abundant brachiopods of the *Orthida* and *Clitambonitacea* of the Anglo-Baltic provenience, although some features common to both types of fauna do exist. Although a cold-water character of the Mediterranean province was generally accepted, we must bear in mind that the whole province is not located in the circumpolar sphere, because the marginal parts of the Gondwanaland, inhabited by the Mediterranean brachiopod faunas, extend far from the Pole as far as the temperate zone. For example, the Ordivician sequence of the Prague basin (central Bohemia) occurred in the temperate zone as evidenced by intensive weathering of detritus and presence of red beds in the lower part of the sequence (Kukal *in* Suk et al. 1984). Moreover, the palaeomagnetic data indicate the position of the Prague basin at a low latitude (around 28 °S; Krs - Krsová - Pruner - Havlíček 1986). In spite of its geographic position, the benthic fauna of the mobile Variscan belt, including the Prague basin, is assigned here to the cold-water Mediterranean fauna which, when migrating around the Gondwanaland, extended from the circumpolar zone to the temperate zone.

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Origin of the benthic fauna

Due to regression in the upper Cambrian, a substantial part of the Mediterranean province became dry land except for small areas in the Iberian Peninsula, southern France, and probably in North Africa. This regression was fatal for many animal groups; when investigating the brachiopods, we can state that only a few genera have taken its origin in the indigenous Upper Cambrian stocks; for example, *Protambonites (Clitambonitacea)* was most probably derived from the Upper Cambrian genus *Billingsella* inhabiting the shelves in Spain (Havlíček - Josopait 1972).

By far greater part the Tremadocian and Arenigian shelly faunas involve the immigrants from the Anglo-Baltic province, thus indicating that the Rheic Sea of that time was no significant barrier for fauna to cruise it from shelves surrounding the North European platform to those surrounding the Gondwanaland. Among the brachiopods of Tremadoc age, the genera *Orbithele, Thysanotos, Palaeoglossa, Lacunites, Eosiphonotreta* a.o. are common to both the zoogeographic provinces. The same immigration route was used by *Rowellella, Leptembolon,* and *Ranorthis* in the Arenig. The immigration of brachiopods into Bohemia was accompanied by an influx of trilobites from Scandinavia over the supposed Rheic Sea, thus accentuating that no important barrier separated the two provinces in the lower Ordovician. According to Mergl (1984), a close relation of the Mediterranean province to Scandinavia is apparent from the fact that over 50 % of the trilobite genera found in the Tremadoc in Bohemia are common to both the regions.

The same picture may be observed in the Middle and Upper Ordovician, when the Sea between the Gondwanaland and the North European platform never reached such an extent to prohibit interchange of the fauna. For this reason, the rise of a distinctive *Aegiromena-Drabovia* fauna was much more controlled by latitudinal and climatic conditions than by a barrier in the form of an extensive Sea.

Tigillites and Cruziana Communities

The benthic assemblages inhabiting the North African stable shelves and intracontinental basins greatly differ from those of mobile belts around the Gondwanaland. The sandstones surrounding or covering the Precambrian Reguibat, Leo, Touareg, and Nubian-Arabian shields, are of shallow-water marine, fluviomarine, or even fluviatile origin, as a rule lacking shelly fauna and trilobites. They often take up the whole sequence of the Ordovician with the exception of the uppermost Ordovician (Kosov) which is formed as sediments of glacial origin. Owing to lack of fossils, the exact correlation with the British and Bohemian scales has usually been done approximately; moreover, gaps in sedimentation are not excluded.

In the Murzúq basin (Libya), the sandstones were assigned to the Ash Shabíyat Formation (probably Tremadoc) and the Hawáz Formation (probably Arenig to Llandeilo), both bearing extremely shallow-water *Tigillites* Community. Collomb (1962) discerned two members with abundant *Tigillites;* the lower one with *Tigillites, Cruziana,* and *Harlania* occupying the lower part of the Ash Shabíyat Formation, the upper one (= *Tigillites* supérieurs) restricted to the Hawáz Formation. Pařízek, Klen and Röhlich (1984) suggested a shore-related, probably subtidal environment for the Ash Shabíyat Formation with a possible shallowing during the deposition of its upper part. Voss (1981) supposed presence of a subaquatic fan delta system with distributary channels and swash bars in the Hawáz Formation.

Tigillites Community is further widespread over the Central Sahara where it has been found in the Ajjers Formation of supposed Tremadoc and Arenig age, and in the In Tahouite Formation of Llandeilo to Caradoc age. A mixed facies, persisting through almost the whole Ordovician sequence, is supposed for both the formations, with fluviatile, usually obliquely bedded sandstones alternating with marine sandstones rich in ichnofossils of the *Tigillites* and *Cruziana* Communities, but with extremely rare valves of inarticulate brachiopods confined to intercalations of lowermost Ordovician age (Beuf et al. 1971).

In the eastern part of the Mediterranean province, the marine sandstones with a significant proportion of terrestric rocks are restricted mainly to the lower Ordovician. Based on trace fossils *(Cruziana furcifera),* Wolfart (1967) supposed an Arenig age for sandstones in North Jordan. In South Jordan and the Arabian Peninsula, a marine environment of the middle and upper Ordovician is documented by rather frequent graptolites and trilobites indicating a *Selenopeltis* (= Mediterranean) province.

Tigillites and *Cruziana* Communities are widespread in the Iberian-Armorican region, where the Armorican Quartzite Formation (lower —middle Arenig) bears characteristic trace fossils *Skolithos, Cruziana, Phycodes, Daedalus, Rusophycus,* rarely accompanied by infaunal inarticulate brachiopod *Ectenoglossa lesueuri* (Rouault) and "*Dinobolus*" *brimonti* (Rouault). In the Armorican Massif, several bivalves, trilobites, chitinozoans, and acritarchs were found in the Armorican Quartzite Formation (Hammann et al. 1982).

The lower Ordovician quartzites, often intercalated by slates, extend eastwards to Central Europe, where they have yielded the index ichnofossil *Phycodes circinatum* Richter but no shelly fauna of the Bohemian-Moroccan type (Taunus: *henningsmoeni* and *grandior* Quartzites of Arenig age; Struve 1975; Thuringia: Frauenbach and Phycodes Formations, Tremadoc and Arenig age; Pietzsch 1956).

In Bohemia, the *Tigillites* Community represents the *Skolithos* ichnofacies in the Skalka and Řevnice Quartzites (Dobrotiv and lower Beroun), which are confined to the marginal parts of the Prague and "metamorphic islets" basins as deposits of near-shore, shallow-water plains, sandy barriers, and in some areas of wide deltas (Kukal 1957). In Bohemia, the *Tigillites* Community contains exceptionally fragments of trilobites and brachiopods.

Rocky bottom communities

Rocky bottom communities have so far been found only in Bohemia, where they are confined to the Prague basin. The pre-Ordovician chert cliff and boulders below it are coated with one-layered or bulb-shaped bryozoan *Berenicea* and with stromatolitic crusts (Klabava Formation, Arenig; Mergl 1983).

Communities dominated by inarticulate brachiopods

In North Africa, the areas farther from the former coast were dominated by inarticulate brachiopods. According to Massa, Havlíček, and Bonnefous (1977), the Ghadamis basin (Tunisia, Libya) was a "lingulid domain" keeping its low rate of sedimentation and an extremely shallow-water environment during almost the whole Ordovician. The Sanrhar Formation (Tremadoc) has yielded the *Tunisiglossa* Community with dominant infaunal "lingulids" *Tunisiglossa* and *Palaeoglossa,* accompanied by ichnofossils (burrowings perpendicular to bedding planes) and extremely rare epifaunal elements *(Siphonotretidae)*.

In the middle and upper Ordovician, the *Tunisiglossa* Community was replaced by the "*Lingulella*" Community in the Bin-Ben-Tartar and Djeffara Formations (Llanvirn—Beroun) characterized by common infaunal elements *"Lingulella"* and *Palaeoglossa* accompanied by sedentary inarticulate brachiopods *Orbiculothyris* and *Trematis*, and minute specimens of *"Torynelasma"*. Articulate brachiopods, although very rare, also occur in the *"Lingulella"* Community *(Aegiromena, Onnizetina)*. According to Massa, Havlíček, and Bonnefous (1977), the striking prevalence of inarticulates over other animal groups was controlled by very cold climate, lower salinity of the Sea, and a restricted marine environment; these living conditions were not much suitable for the development of articulate brachiopods and trilobites.

Another upper Ordovician community with rather diversified inarticulates was recorded by Havlíček and Massa (1973) in the Melaz Shuqrán Formation (Beroun Series) in the western flank of the Murzúq basin (Libya), where *Fezzanoglossa, Libyaeglossa, Orbiculoidea, Orbiculothyris*, and *Drabodiscina* occur in phosphatic and ferrugineous nodules; other fossils enclosed in the nodules are fragments of conulariids and an articulate brachiopod *Rafinesquina* cf. *pseudoloricata* (Barrande). At localities, where the nodules are absent, the most common brachiopod is *"Aratanea"* (= *Rhynchotrema* cf. *clariondi* in Havlíček - Massa) accompanied by *Drabovinella*, fragments of trilobites and cystoids (Havlíček - Massa 1973; Pařízek, Klen, Röhlich 1984).

In the central and western Sahara, the poorly diversified assemblages of inarticulate brachiopods penetrate deep into the domain of *Tigillites* ichnofacies. In the Hoggar Mts., Legrand, Poueyto, and Rouaix (1959) recorded *"Lingula" hawkei* (Rouault), *"Lingula" crumena* (Phillips), and *Dinobolus? amguidensis* sp. n. together with a bivalve *Modiolopsis?* in greywackes of Tremadoc or Arenig age.

In the western Sahara (Adrar, Mauritania), Legrand (1969) and Trompette (1973) recorded *Westonia chudeaui* Legrand and *"Lingulella" pseudocrumena* in the uppermost Cambrian or in the lowermost Ordovician (exact age not yet proved).

A community consisting only of inarticulate brachiopods was recorded by Poulsen (1960) in a sequence of green clayey and ferrugineous shales and siltstones (over 100 m thick) interbedded between the sandstones with abundant *Tigillites* (= grès à *Skolithos* inférieurs and grès à *Skolithos* supérieurs). The most common inarticulates are the lingulellids and *Orbithele spinulosa* (Poulsen) and *O. sougyi* (Poulsen); according to Mergl (1981), the latter two species indicate a lower Ordovician (Tremadoc) age.

Inarticulate brachiopods are also common in the upper Ordovician of South Jordan, where Wolfart (1967) found *Orbiculothyris costellata* Wolfart, *Trematis* sp., *Dalmanella* a.o. brachiopods.

In Europe, the communities dominated by large inarticulate brachiopods are mostly confined to the lower part of the Ordovician sequence, deposited after a break in sedimentation on a pre-Ordovician basement. In the Tremadoc of Bohemia (Třenice Formation), the fairly large inarticulates are confined to sandstones deposited in an environment of fanglomerates, alluvial fans, or in a fluviomarine environment (Kukal 1963) to form the poorly diversified *Hyperobolus* Community. This consists of large specimens of *Hyperobolus feistmanteli* (Barrande) and *Expellobolus expulsus* (Barrande), rarely accompanied by *Thysanotos primus* (Koliha). Another shallow-water benthic community in the Třenice Formation, restricted to a small area in the northern flank of the Prague basin, is formed by numerous specimens of *Westonisca lamellosa* (Barrande) and *W. arachne* (Barrande). In the upper Tremadoc of Bohemia (Mílina Formation), the *Hyperobolus* Community was replaced by the *Thysanobolus* Community, consisting of *Thysanobolus lingulides* Havlíček, *Thysanotos siluricus* (Eichwald), and an clitambonitaceid *Protambonites kolihai* (Havlíček). Beyond the Prague basin, the benthic fauna dominated by large inarticulates (*Thysanotos* a.o.) was discovered by Prantl and Růžička (1941) in eastern Bohemia (Lipoltice Beds in the Železné hory Mts.).

In eastern Serbia (Yugoslavia), the *Hyperobolus* Community occupies the lowermost part of the Ordovician sequence just above the pre-Ordovician metamorphosed basement, thus recalling position of this community in Bohemia. For this reason, we may assume the same living conditions in both the areas. Krstić (1984) recorded in the metamorphosed sandstones of the Kučaj Belt (Serbia) the index genera *Hyperobolus, Thysanotos, Orbithele,* and *Leptembolon,* originally published under the names *Lingulobolus feistmanteli, Obolus barrandei, Thysanotos siluricus, Obolus complexus, Orbiculoidea,* and *Lingulella* cf. *insons.* A closely similar age and living conditions may be postulated for the assemblage consisting of fairly large inarticulates found at Bosiljgrad (south-eastern Serbia) in the sericite slates and sericite quartzites by Pavlović (1962), who figured *"Lingulobolus" hawkei* (Rouault) and *Pseudobolus salteri* (Davidson). As in Bohemia, the assemblage of large inarticulates in Serbia is overlain by slates with abundant (but deformed) lingulellids and conical inarticulate brachiopods (*Acrotretacea?*).

Another type of shore-related, shallow-water communities is that dominated by inarticulate brachiopods of small to medium size; in Bohemia, the *Leptembolon insons* Community consists of small obolids of lingulellid outline (*Leptembolon, Rowellella*), minute conical acrotretaceans, and circular shells of *Orbithele,* all often accompanied by spicules of sponges and fragments of other animal groups (but never occur together with trilobites!).

In the Montagne Noire, the small inarticulate brachiopods, although fairly common in the lower Ordovician, never participate as dominant elements in the benthic communities. The fauna of Tremadoc and Arenig age is richly diversified with numerous trilobites, gastropods, and bivalves together with articulate and inarticulate brachiopods (*Spondyglossella, Conotreta, Lingulepis, Rafanoglossa;* Babin et al. 1982).

Deeper water communities dominated by inarticulate brachiopods

The black shale lithofacies, occupying the deeper, nonaerated central parts of the basins, is usually poor in benthic organisms. In the Prague basin, the fairly common small inarticulate brachiopods *Anx, Paterula,* and less common acrotretaceans, are often accompanied by minute articulate brachiopods *Brandysia benigna* Havlíček, *Benignites primulus* (Barrande) (Dobrotiv), *Aegiromena descendens* (Havlíček), *Karlicium patens* Havlíček (upper Beroun), *Chonetoidea tenerrima* Havlíček (Kralodvor), which are not typical bottom dwelling organisms as they may have lived attached to seaweed not uncommonly floating. The taxic diversity of the Ordovician black shale lithofacies is usually low; some parts of the Ordovician sequence are unfossiliferous (e.g. often in the Libeň Formation, Prague basin), some have yielded scarcely disseminated exoskeletons of trilobites and shells of bivalves, gastropods, hyoliths a.o., exceptionally accumulated to cover the bedding planes. This deeper-water *Paterula* Community was dealt with in a greater detail by Havlíček (1982).

The *Didymograptus-Lingulella* assemblage recorded by Iordan (1981) in the Llanvirn (Moesian platform, Romania) may also reflect the deeper-water, anoxic basin-floor regime.

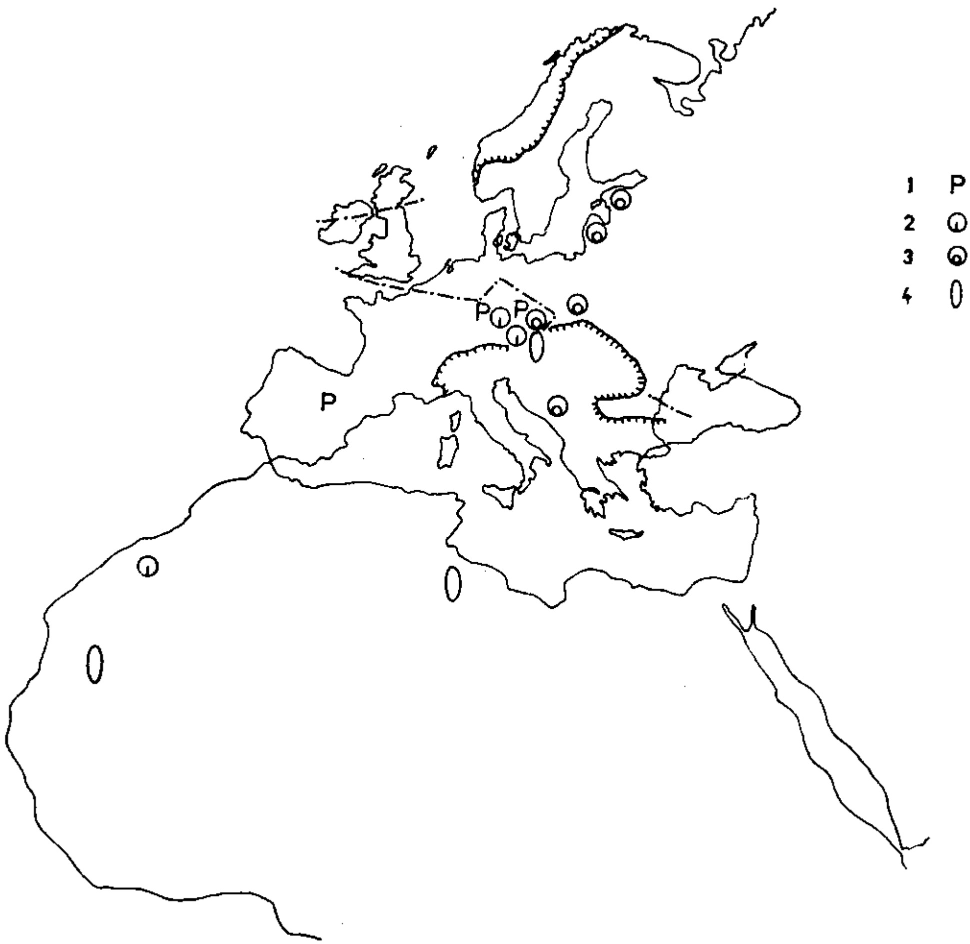
Communities of the Moroccan-Bohemian type

The Ordovician sequences in Morocco, South and Central Europe bear characteristic, usually richly diversified assemblages of trilobites assigned to the *Selenopeltis* zoogeographic province by Whittington and Hughes (1972). As follows from the material summarized by Whittington and Hughes and completed by recent papers, the most common families of trilobites are the *Trinucleidae, Cyclopygidae, Calymenidae,* and *Dalmanitidae* which, in association with members of other families, represent a distinctive trilobite fauna in all series of the Ordovician in the Mediterranean province (Dean 1966, 1971; Hammann 1974, 1976, 1977; Hammann - Henry 1978; Henry 1980; Henry - Nion - Paris - Thadeu 1974; Courtessole - Pillet - Vizcaino 1981, 1983; Mergl 1984; Rábano 1984; Šnajdr 1984 and many others). On the other hand, the brachiopods are rare and not uniform in the lower Ordovician to characterize a separate zoogeographic province. This is due to various origins of the brachiopods inhabiting the shelves and intracontinental basins of the Gondwanaland at that time. A distinctive Mediterranean brachiopod fauna was gradually formed during the middle and upper Ordovician to give rise to a significant *Aegiromena-Drabovia* fauna, clearly differring from the brachiopods of the Anglo-Baltic and Scottish assemblages. In the upper Ordovician, the *Aegiromena-Drabovia* fauna consists of numerous brachiopods of the families *Draboviidae* and *Heterorthidae*, and the subfamilies *Aegiromeninae* and *Orthostrophiinae*, together with much less frequent membres of other families. A "pure" *Aegiromena-Drabovia* fauna is best developed in Morocco and Central Europe (Bohemia), whereas in South Europe it often acquires many Anglo-Baltic warmer-water elements due to immigration in the upper Beroun and lower Kralodvor ages.

Tremadoc

As mentioned above, the communities dominated by *Tigillites* and large inarticulates were widespread over the Mediterranean province, whereas the articulate brachiopods formed a subordinate part of the benthic communities in the lowermost Ordovician. The *Orthida* were found at a few localities in South and Central Europe, usually together with small to medium-sized inarticulates (e.g. Leimitz Slates; Sdzuy 1955). Of genera, confined exclusively to the Mediterranean province, the most important are *Protambonites* and *Poramborthis. Protambonites* was found in the lower Tremadoc of the Iberian Chains (Spain; Havlíček - Josopait 1972) and Bohemia; *Poramborthis* occurs in Bohemia, the Iberian Chains, and Bavaria (Sdzuy 1955). Occurrence of *Jivinella* beyond Bohemia is not sure (Bavaria?, the Iberian Chains?).

A unique assemblage of benthic fauna is confined to a small lens of haematite at Holoubkov (lower Tremadoc, Bohemia), where the fairly richly diversified brachiopods lived in a rough-water, near-shore environment. At Holoubkov, the genera *Ferrobolus, Conotreta, Orbithele, Rosobolus, Siphonobolus, Eosiphonotreta, Lacunites, Kolihium, Jivinella, Apheoorthina, Robertorthis, Poramborthis,* and *Protambonites* were



1. Distribution of index brachiopod genera in the Tremadoc
1 — Poramborthis; 2 — Orbithele; 3 — Thysanotos; 4 — Palaeoglossa

accompanied by cystoids *Palaeosphaeronites* and Glyptosphaerites, both attached with their wide bases to the substrate (Havlíček 1977, 1982; Prokop 1964). It is difficult to consider this benthic fauna as representing the Mediterranean province, because most of the genera listed above are not known beyond Bohemia.

In the Tremadoc of the Anti-Atlas Mts. (Morocco), the only articulate brachiopod is *Plectorthis simplex* Havlíček not yet found in Europe (Havlíček 1977). Moreover, the upper Tremadoc of the Anti-Atlas Mts. has yielded *Ranorthis* which became fairly common in the Arenig of the Mediterranean province.

A r e n i g

In the Arenig, the brachiopods are more abundant than in the previous Tremadoc Series, but the composition of the benthic communities is not uniform over the whole province. The fairly common *Orthida Ranorthis* and *Paurorthis* cannot indicate a well-defined zoogeographic province as they both are cosmopolitan genera described from North Africa (Morocco), South and Central Europe, and also from the Baltic regions (i.e. beyond the Mediterranean province in the strict sense).

The most diversified *Orthida* of Arenigian age are confined to the Montagne Noire, where M é l o u (1982) recognized the genera *Hesperonomia, Ranorthis, Ocorthis, Orthambonites, Pleurorthis, Sinorthis, Prantlina, Paurorthis, Gonambonites, Progonambonites,* and *Aportophylla,* often accompanied by small inarticulates *Spondyglossella, Conotreta, Rafanoglossa, Westonia,* and *Lingulepis.* In the Montagne Noire, the brachiopods, bivalves, gastropods, and trilobites are much more diversified than in Bohemia.

In Central Europe, the most fossiliferous sequence of the Arenig is that of Bohemia. Whereas the inarticulate brachiopods occur throughout the whole sequence (although in some parts very rare), the *Orthida* are confined only to the top of the Klabava Formation. *Nocturnellia* Community is widespread along the north-western limb of the Prague basin where it occupied an extensive, shallow-water plain, and partly extended even beyond this area. The valves of *Nocturnellia* were sorted by waves and sometimes accumulated in bodies analogous with tidal bars. *Nocturnellia* is rarely accompanied by *Prantlina, Ranorthis, Nereidella* and minute inarticulate brachiopods.

Another type of a shallow-water community is that inhabiting the top of a submarine pyroclastic accumulation near Komárov (Prague basin, Bohemia) dominated by *Nereidella pribyli* (H a v l í č e k) in association with *Prantlina desiderata* (B a r r a n d e) and *Ferrax oolithicus* (H a v l í č e k); trilobites and gastropods *(Mimospira)* are rare at that locality.

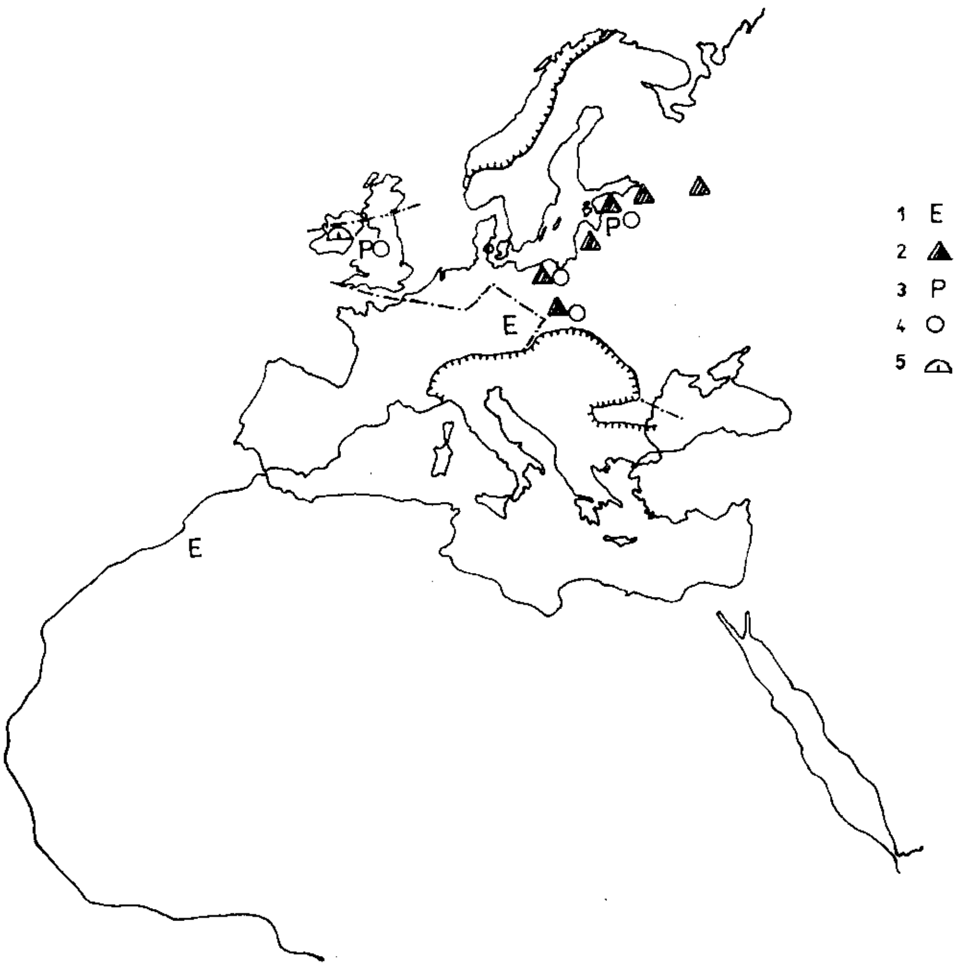
The genus *Prantlina* was also found in Bavaria (S d z u y 1971).

Interesting is an interchange of the fauna between the Mediterranean province and southwestern China; the genera *Tarfaya* and *Paurorthis* occur in the lower Arenig both in the Anti-Atlas Mts. (Morocco) and southwestern China (X u H a n - k u i - L i u D i - y o n g 1984). Some genera, frequent in the lower Arenig in southwestern China, appear in Bohemia for the first time in the upper Arenig *(Nocturnellia)* or even in the lower Llanvirn *(Euorthisina).*

The south American affinity is indicated by *Incorthis*, an index genus in the Arenig of Bolivia (H a v l í č e k - B r a n i s a 1980), which was recently discovered in the Anti-Atlas (Morocco) (P. Huvellin).

L l a n v i r n

The Llanvirn of the Mediterranean province is marked by prevalence of black shales and siltstones of anoxic facies over sandy deposits;



2. Distribution of index brachiopod genera in the Llanvirn
1 — Euorthisina; 2 — Clitambonitacea; 3 — Porambonites; 4 — Orthis, Orthambonites; 5 — Aegiromena

this environment was not suitable for sedentary animals, whereas other benthic groups underwent an explosive development (trilobites, bivalves, gastropods, hyoliths). In several areas, the Llanvirn is documented by trilobites and graptolites without any data concerning sessile benthos (Bulgaria: Haberfelner - Bončev 1934; South Jordan, Syria, Arabian Peninsula: Wolfart 1967). In North Africa and Arabia, the inshore, epicratonic deposits often bear poorly diversified trilobite assemblage with the index genus *Neseurethus* indicating environment of high latitudes (Fortey - Morris 1982; El-Khaydal - Romano 1985). Index brachiopod is *Euorthisina* which is abundant in Bohemia (Šárka Formation) and in the Anti-Atlas, Morocco (Havlíček 1971). *Euorthisina,* however, is not an indigenous stock in the Mediterranean province as it immigrated from England where it was recovered by Williams (1974) in the upper Arenigian Mytton Flags (Shropshire). Also in the Andean region of the Gondwanaland (Bolivia), *Euorthisina* was of Arenigian age being derived from the Tremadocian genus *Notorthisina* (Havlíček - Branisa 1980). Another significant Llanvirnian genus is *Eodalmanella* which is a probable descendant of the Arenigian *Ranorthis.* Beyond Bohemia, *Eodalmanella* has so far been recorded in the Shin Brook Formation of the Magog belt (New Brunswick, Newfoundland; Neuman 1968). In North Africa (Anti-Atlas, Ougarta region), the Llanvirn Series has yielded *Euorthisina* and the cosmopolitan gens *Orthambonites.*

By contrast to Central Europe and North Africa, the significant *Orthida* in the Iberian Peninsula are *Cacemia ribeiroi* (Sharpe) and the species of *Tissintia, Apollonorthis,* and *Palaeoglossa* (lower unit of the Cacemes Formation, Central Portugal; Mitchell 1974). Beyond the Iberian Peninsula, *Cacemia* also occurs in the lower member of the Postolonnec Formation in the Armorican Massif (Hammann et al. 1982).

Dobrotiv

The Dobrotiv, approximately corresponding to the lower and middle parts of the Llandeilo, is the earliest series of the Ordovician Period when the sedentary organisms tended to form a more or less homogeneous benthic assemblage in the Mediterranean province. The *Heterorthidae* became a stock widespread over Europe and North Africa. In the Anti-Atlas Mts., *Tissintia* and *Tafilaltia* are the index genera in sandstones of the First Bani Formation; both the genera have been recorded also in Central Europe (Skalka Quartzite, Bohemia). Moreover, *Tissintia* was discovered beyond the Mediterranean province in England (lower

3. Distribution of index brachiopod genera in the Dobrotiv (Llandeilo)
1 — Clitambonitacea; 2 — Sowerbyella; 3 — Aegiromena; 4 — Tissintia; 5 — Svobodaina; 6 — Heterorthina; 7 — Cacemia, Apollonorthis; 8 — Orthidae

Llanvirn—Llandeilo, Shropshire; Williams 1974) and in Bolivia (Llanvirn and Llandeilo; Havlíček - Branisa 1980). In the Iberian Peninsula, *Tissintia* cf. *convergens* Havlíček is a common brachiopod in the upper unit of the Cacemes Formation (Central Portugal), where it is accompanied by *Cacemia, Apollonorthis, Dalmanella, Fascifera, Tazzarinia, Palaeoglossa,* and rare *Eorphipidomella* (= *Crozonorthis*) (Mitchell 1974; Mélou 1976). A similar assemblage, consisting of the genera *Apollonorthis, Cacemia, Eorhipidomella,* and

Heterorthina, was studied by M é l o u (1975, 1976) in the upper member of the Postolennec Formation in the Armorican Massif.

Further, the genera *Eorhipidomella* and *Heterorthina* occur in the Dobrotiv of Spain (Castillejo Formation; V i l l a s 1985). *Aegiromena,* which became an index genus in the Beroun, appeared in the Mediterranean province for the first time in the Dobrotiv of the Iberian Peninsula and Armorican Massif (M é l o u 1973, V i l l a s 1985), but did not reach at that time Central Europe and North Africa. Origin of *Aegiromena* is to be sought beyond the Mediterranean province as the earliest species of *Aegiromena* were recorded in the Llanvirn of Bolivia (H a v l í č e k - B r a n i s a 1980) and Ireland (H a r p e r - R a s t 1965). Another index brachiopod in the Beroun Series is *Drabovia,* which appeared in Central Spain in the same way as *Aegiromena,* i.e. in the pre-Berounian strata (Dobrotiv) before immigrating into Central Europe (G u t i é r r e z - M a r c o et al. 1984).

The benthic fauna of the High Atlas and Anti-Atlas Mts. (Morocco) includes plectorthid genera either not seen in Europe *(Atlantida)* or discovered in the Carnic Alps in rocks of Dobrotiv to lower Beroun age *(Paterorthis:* H a v l í č e k - K ř í ž - S e r p a g l i 1987).

B e r o u n

In the Beroun, the benthic assemblages of the Moroccan-Bohemian type are characterized by the widely distributed *Aegiromena-Drabovia* fauna preferring the sandy or silty bottom in a shallow-water, subtidal environment to moderately deep environment passing laterally into the deeper-water *Paterula* Community confined to the black shale lithofacies, not uncommonly with graptolites.

The most significant families and subfamilies in the Mediterranean province are the *Heterorthidae, Draboviidae,* and *Aegiromeninae,* less abundant are the genera of the *Dalmanellidae, Orthostrophiinae, Triplesiidae,* and inarticulate brachiopods. Rare are the strophomenaceans and rhynchonellaceans. By contrast to the Anglo-Baltic province, no clitambonitaceids participate in the *Aegiromena-Drabovia* fauna. The complete sequences of richly diversified brachiopod assemblages have been studied in the Prague basin (Bohemia; H a v l í č e k - V a n ě k 1966, H a v l í č e k 1977, 1982) and in the Anti-Atlas Mts. (Morocco; H a v l í č e k 1971); in other areas of Europe, the Moroccan-Bohemian *Aegiromena-Drabovia* fauna either acquired several warmer-water elements due to immigration from the Anglo-Baltic province (e.g. in the Iberian Chains, Montagne Noire, Sardinia, Carnic Alps), or it was poorly diversified and not developed through the whole sequence of the Beroun. Sporadic data on the *Aegiromena-Drabovia* fauna have been obtained in the Balkans [*Aegiromena* cf. *aquila* (Barrande); Kučaj belt in Serbia; Krstić 1984) and Turkey (*Svobodaina* cf. *ellipsoides* (Barrande); Amanos Mts.; El Ishmawi 1972], where the lower Palaeozoic sequences are metamorphosed and strongly faulted and folded. A few elements of the *Aegiromena-Drabovia* fauna penetrated deep into the domain of inarticulates in the Ghadamis basin in Libya (*Aegiromena* cf. *descendens* Havlíček and *Onnizetina* sp.) (Massa - Havlíček - Bonnefous 1977).

The *Aegiromena-Drabovia* fauna was also recovered in the Andean part of the Gondwanaland (Bolivia) where Havlíček and Branisa (1980) determined the genera *Heterorthis, Destombesium, Drabovinella, Rostricellula,* and *Eorhipidomella,* mostly collected from the clasts in a diamictite rock of the Zapla tillite.

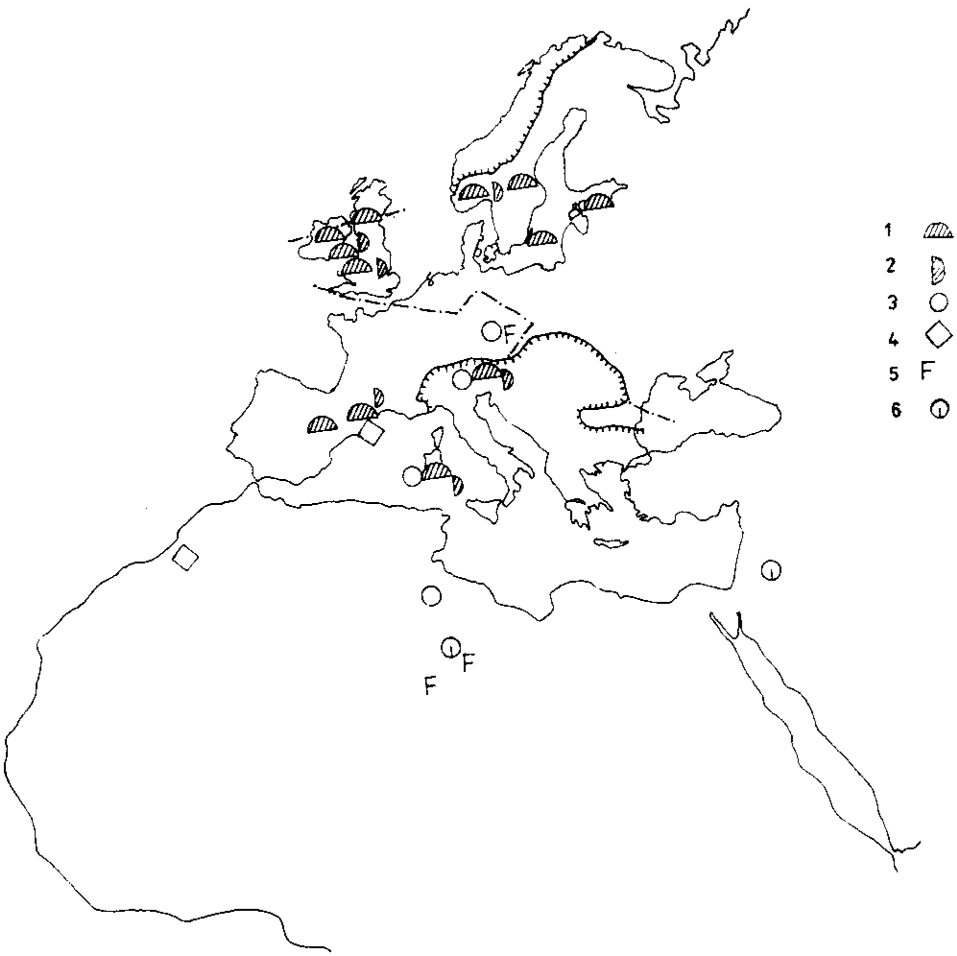
In Bohemia, the significant genera of the Beroun are *Tazzarinia, Gelidorthis, Jezercia, Cilinella, Heterorthina, Marionites, Heterorthis, Svobodaina, Onniella, Howellites, Onnizetina, Saukrodictya, Mirorthis, Drabovia, Drabovinella, Hirnantia, Chrustenopora, Bicuspina, Aegiromena, Blyskavomena,* accompanied by cosmopolitan genera *Triplesia, Rafinesquina,* and *Rostricellula.* The Bohemian type fauna extends westward to Taunus (Hessen, FRG), where the Andreasteich Quartzite has yielded *Rostricellula ambigena* (Barrande), *Rafinesquina* aff. *pseudoloricata* (Barrande), and species of *Hirnantia, Drabovia, Howellites,* and *Onniella* associated with rare trilobites and other fauna (Struve 1975).

The Moroccan benthic fauna comprises *Tazzarinia, Gelidorthis, Dalmanella, Onniella, Howellites, Mirorthis, Tafilaltia, Heterorthis, Drabovia, Drabovinella, Protomendacella, Triplesia, Bicuspina, Cliftonia, Aegiromena, Kiaeromena, Rafinesquina,* and *Rostricellula.* The genera *Irhirea* and *Destombesium* were never found in Europe; the latter genus, however, was recorded in sandstone of Berounian age in Bolivia.

In Central Portugal, the Beroun Series is not complete, because the Louredo and Porto do Santa Anna Ash Formations correspond to the Libeň and Letná Formations of the Bohemian scale (Mitchell 1974); among brachiopods, the following Moroccan-Bohemian elements prevail: *Drabovia* cf. *redux* (Barrande), *Aegiromena* cf. *aquila praecursor* (Havlíček), *Gelidorthis* cf. *partita* (Barrande), *Howellites* sp., *Onniella* sp., *Tazzarinia* cf. *drotae* Havlíček, *Triplesia* cf. *simplex* Havlíček, *Chrustenopora* sp., *Dalmanella* cf. *agadirensis* Havlíček, *Saukrodictya porosa* (Havlíček), further species of *Svobodaina, Petrocrania, Rafinesquina,* a.o. A weak influx of warmer-water elements may be documented by the presence of *Glyptorthis* and *Porambonites*.

Although poorly diversified, the sessile benthos in the Armorican Massif has yielded the index genera of the *Aegiromena-Drabovia* fauna, namely *Drabovia* (Sangsurière Shale: **Pillet - Robardet** 1968), *Svobodaina* (Raguenez Shale: **Babin - Mélou** 1972), and *Aegiromena* (group of *A. descendens;* Caradoc at Coëvrons: **Mélou** 1973).

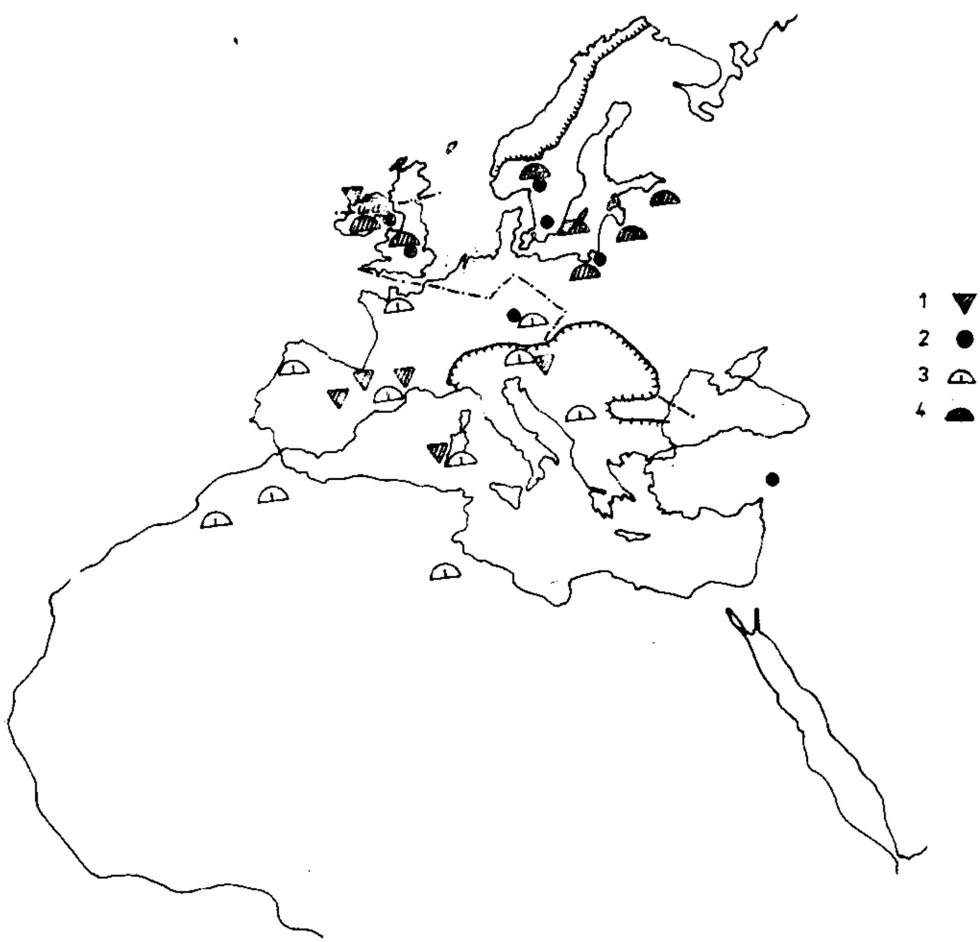
Presence of the *Aegiromena-Drabovia* fauna has also been proved in the Iberian Chains, Montagne Noire, Sardinia, and Carnic Alps, i.e., in



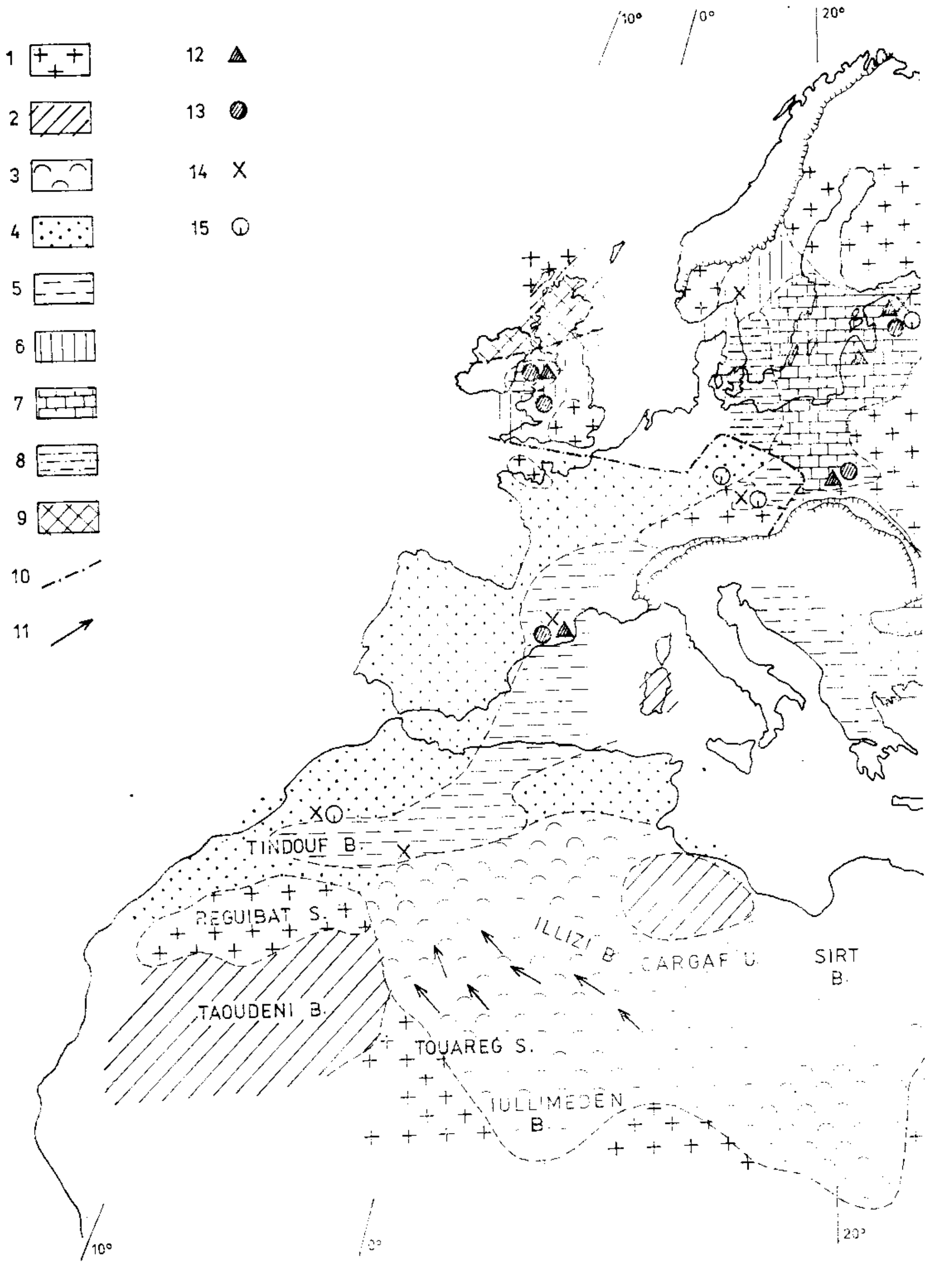
4. Distribution of index brachiopod genera in the Beroun (Caradoc)
*1 — Nicolella; 2 — Dolerorthis: 3 — Onnizetina; 4 — **Protomendacella**; 5 — **Fezzanoglossa**; 6 — Orbiculothyris*

areas where the warmer-water brachiopods are frequent. In Spain (Cadenas Ibericas Orientales), V i l l a s (1985) assigned to the middle and upper Beroun the Fombuena Formation which has yielded the following "Mediterranean" genera: *Gelidorthis, Aegiromena, Svobodaina, Drabovia, Drabovinella, Hirnantia,* in association with the cosmopolitan genera *Triplesia, Rafinesquina,* and *Rostricellula* [the latter two indicate a close Bohemian affinity as they contain the Bohemian species *R. pseudoloricata* (B a r r a n d e) and *R. ambigena* (B a r r a n d e)].

The Mediterranean genera in the Beroun of the Montagne Noire are *Aegiromena, Drabovia, Tafilaltia, Tissintia, Heterorthis, Svobodaina,* and



5. Distribution of index brachiopod genera in the Beroun (Caradoc)
1 — Leangella; 2 — Sericoidea; 3 — Aegiromena; 4 — Sowerbyella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TAOUDENI B.
TOUAREG S.
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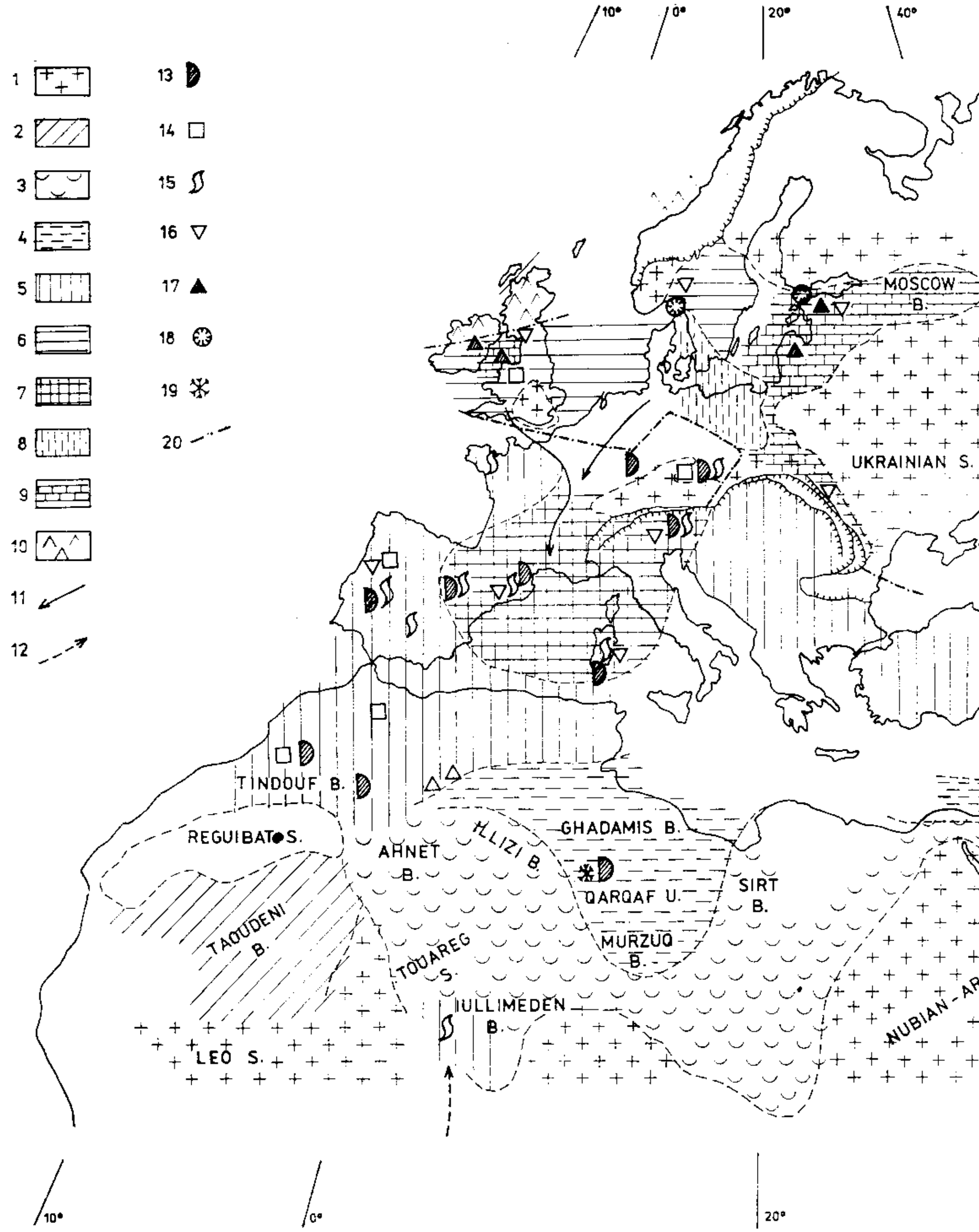
DISTRIBUTION OF BENTHIC COMMUNITIES AND OCCURRENCES OF INDEX BRACHIOPOD GENERA IN THE ARENIG

1 — pre-Palaeozoic shields; *2* — post-Tremadocian regression of the Sea; *3* — fluvial and fluviomarine deposits (mixed facies), ***Tigillites*** and ***Cruziana*** Communities; *4* — mainly marine sandy deposits with trace fossils and inarticulates, ***Tigillites*** and ***"Lingula"*** Communities; *5* — basinal deposits dominated by trilobites and orthids of Mediterranean type; *6* — Anglo-Welsh associations dominated by inarticulates and orthids; *7* — Baltic type communities; *8* — mostly graptolitic shale pelagic community; *9* — Scottish type communities; *10* — boundaries of zoogeographic provinces; *11* — fluviatile transport, direction of currents (after Beuf et al. 1971); *12* — *Clitambonitacea; 13* — ***Orthis, Orthambonites; 14*** — ***Ranorthis, Paurorthis; 15*** — ***Orbithele***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SIRT B.
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DISTRIBUTION OF BENTHIC COMMUNITIES AND OCCURRENCE OF INDEX BRACHIOPOD GENERA IN THE BEROUN (CARADOC)

1 — pre-Palaeozoic shields; *2* — regression of the Sea in the Beroun; *3* — marine and fluviomarine sandstones, mostly *Tigillites* Community; *4* — communities dominated by inarticulate brachiopods; *5* — Moroccan-Bohemian communities (*Aegiromena-Drabovia* fauna); *6* — communities of Anglo-Welsh type; *7* — mixed Moroccan-Bohemian and Anglo-Welsh faunas; *8* — graptolitic shale pelagic community with small inarticulates; *9* — communities of Baltic type; *10* — Scottish communities; *11* — probable way of invasion of warm-water elements into the Mediterranean province; *12* — probable way of invasion of Mediterranean type benthic fauna into the Iullimeden basin; *13* — *Drabovia, Drabovinella; 14* — *Heterorthis; 15* — *Svobodaina, Cilinella; 16* — *Porambonites (Porambonites); 17* — *Clitambonitacea; 18* — reef bodies; *19* — evidence of glaciation; *20* — boundaries of zoogeographic provinces

Protomendacella, associated with *Paucicrura, Triplesia, Leptestiina, Leangella,* and *Rafinesquina,* all accompanied by a suite of warmer-water brachiopods (mostly *Orthida* and *Porambonites:* Havlíček 1981).

Aegiromena-Drabovia fauna is represented in the upper Beroun of Sardinia by *Svobodaina, Onniella, Onnizetina, Saukrodictya, Aegiromena,* and *Aegironetes* in association with *Paucicrura, Leptestiina, Leangella, Iberomena, Leptaena, Nicolella, Eridorthis, Glyptorthis, Dolerorthis, Ptychopleurella, Reuschella, Eoanastrophia, Porambonites,* and *Bicuspina,* some of them indicating an influx of Anglo-Baltic elements (Havlíček - Kříž - Serpagli 1986).

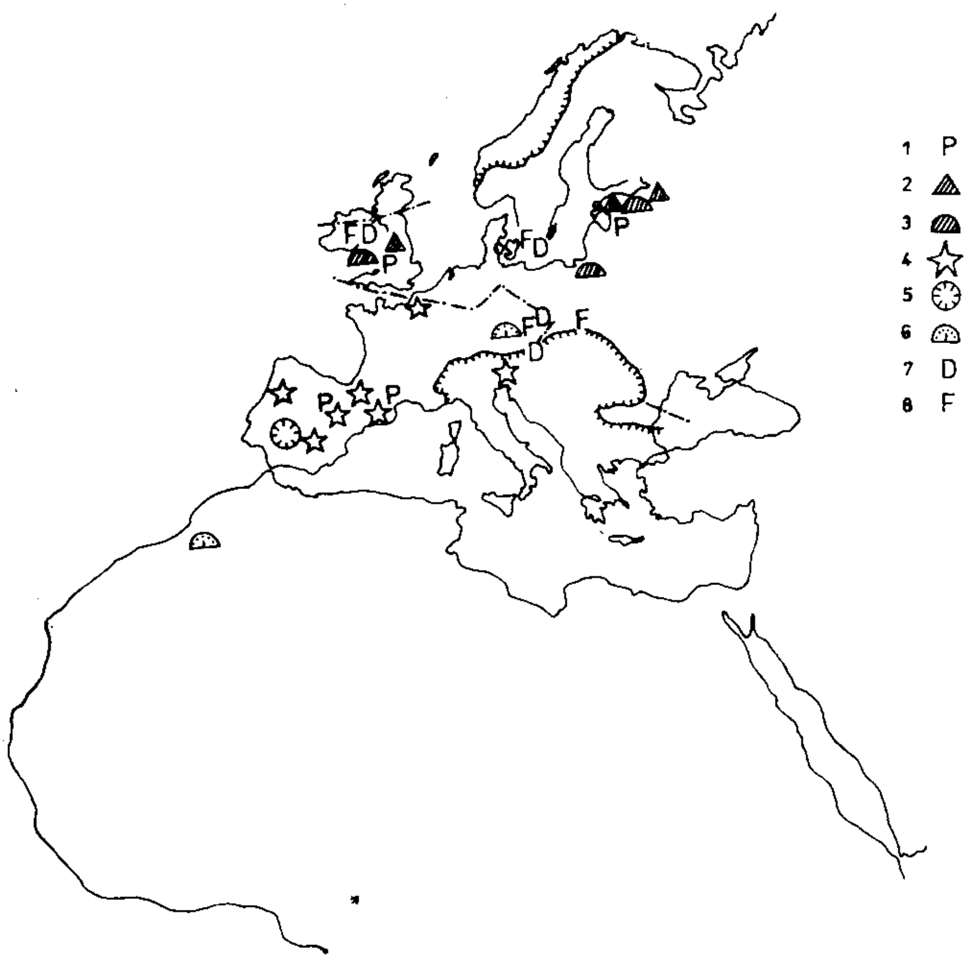
In the Carnic Alps (mainly Hoher Trieb and Uqua Mts.), the siltstones and greywackes of middle—upper Beroun contain many genera widespread over the Mediterranean province, including the index brachiopods *Aegiromena, Gelidorthis, Saukrodictya, Svobodaina, Drabovia,* and *Drabovinella,* accompanied by *Nicolella, Multicostella, Dolerorthis, Triplesia, Leangella, Longvillia, Porambonites, Eoanastrophia, Iberomena,* and *Leptaena,* some of which may be regarded as immigrants from the Anglo-Baltic provice (Havlíček - Kříž - Serpagli 1986).

An unexpected discovery of the Berounian fauna was done in the Adrar Iforas (south of the Hoggar Mts., Central Sahara) at the north-western margin of the Iullimeden basin, where Gatinskij, Kločko, Rozman, and Trofimov (1966) have listed the following brachiopods: *Orbiculoidea, Mesodalmanella* ex gr. *flava* Havlíček (= *Onniella*), *Dalmanella* aff. *bouceki* Havlíček (= *Mirorthis*), *Heterorthina notata* (Barrande), *Rostricellula* ex gr. *ambigena* (Barrande), and *Svobodaina* ex gr. *inclyta* (Barrande), further the trilobites *Calymenella, Dalmanitina,* and several graptolites. The present author had the opportunity to examine a slab with "*Svobodaina*" coming from this locality, and came to the conclusion that the valves accumulated on the bedding plane are rather to be assigned to *Cilinella,* as the well-developed plates supporting their brachiophores converge to the valve floor as in the Bohemian *C. svobodai* (Havlíček). The marine fauna probably invaded into the Iullimeden basin along the mobile belt of Mauritanides surrounding the Precambrian shields. It is not probable that the fauna used the direct route between the Tindouf and Iullimeden basins through the extensive areas dominated by *Tigillites* and *Cruziana* Communities (see pl. 2).

• Kralodvor

In the Kralodvor, the claystones, marlstones, and limestones prevail over the sandy and silty sediments, thus differring from the previous

Beroun Series. For this reason, the composition of the sessile benthos is different. Brachiopods of the *Draboviidae* and *Heterorthidae* became a subordinate part of the assemblage, whereas the *Aegiromeninae* and small inarticulate brachiopods were locally frequent. It is worth to comment that the "typical" Bohemian fauna extended beyond the limits of the Meditarranean province and reached South Sweden, where the Bohemian type brachiopods were discovered in the Jerrestad Mudstone. Sheehan (1973) assigned this fauna to the relatively deep-water *Fo-*



6. Distribution of index benthic fossils in the Kralodvor (lower Ashgill)·
1 — Porambonites; 2 — Clitambonitacea; 3 — Sowerbyella; 4 — Heliocrinites and other cystoids; *5* — reef body with tetracorals; *6 — Chonetoidea; 7 — Dedzetina; 8 — Foliomena*

liomena Community dominated by ostracods and trilobites; among shelly fauna, he found several brachiopods closely related to the Bohemian ones: *Foliomena folium* (Barrande), *Anoptambonites* sp., *Leptestiina prantli* Havlíček, *Kozlowskites ragnari* Sheehan, *Sericoidea* sp., and *Dedzetina* sp. Moreover, a significant interchange of the trilobite fauna between Bohemia and Poland has been discussed thoroughly by Kielan (1959).

In Bohemia, a deeper-water *Rafanoglossa* Community takes most of the Kralodvor sequence; in claystones, the sedentary organisms are much less abundant than the vagile benthos. The dominant brachiopod is the infaunal obolid *Rafanoglossa leiskowiensis* (Barrande), not uncommonly found in living position in vertical burrows; other inarticulates, although fairly frequent, have not yet been revised. The minute articulate brachiopods *Ravozetina honorata* (Barrande), *Cyclospira barrandei* Cooper, *Chonetoidea tenerrima* Havlíček and *C. radiatula* (Barrande) are scarcely disseminated through the whole Kralodvor sequence. The latter two species most probably lived attached to seaweed above the bottom of the Sea. *Comatopoma, Hirnantia, Aegiromena,* and *Anisopleurella* rarely occur in the lower part of the claystone sequence in association with abundant trilobites.

Another community, called *Dedzetina* Community by Havlíček (1982), occurs in the layer of shale with a considerable amount of silty admixture and muscovite in the *Tretaspis seticornis* Horizon. The common brachiopods are *Dedzetina, Karlicium, Leptestiina, Foliomena,* and locally *Kozlowskites.*

A distinctive, richly diversified deeper-water *Proboscisambon* Community is confined to a silty shale with rather high proportion of carbonate; it contains rather frequent cystoids and trilobites together with brachiopods *"Lingula", Orbiculoidea, Conotreta, Acanthambonia, Jezercia, Ravozetina, Epitomyonia, Salopina, Boticium, Cliftonia, Aegironetes, Kozlowskites, Anoptambonites, Proboscisambon, Leptaena, Eoanastrophia,* and *Cryptothyrella* (Havlíček - Mergl 1982).

In the Anti-Atlas Mts. (Morocco), the Upper Ktaoua Formation has yielded a poorly diversified shelly fauna containing the Bohemian type brachiopods, namely *Chonetoidea, Comatopoma, Hirnantia* together with *Eochonetes* and *Aphanomena.*

In South Europe, the marlstones and limestones are rather frequent in the Kralodvor, usually with abundant cystoids. In the Carnic Alps, the brachiopods are rare in the limestone; Havlíček (1977) mentioned *Dedzetina microstoma* Havlíček in association with other not determinable shells.

In the Iberian Chains (Spain), the Calizas de Cistideos Formation (limestones, dolomites) of lower Kralodvor age has yielded many species of crinoids and cystoids, accompanied by trilobites and conodonts (list of species: V i l l a s 1985). In this formation, the brachiopods form a mixed assemblage containing both the Mediterranean and Anglo-Baltic elements; the latter are more frequent as follows from the list of the genera: *Eridorthis, Fertranella?, Oxoplecia, Iberomena, Doleorthis, Nicolella, Saukrodictya, Eoanastrophia, Plaesiomya, Epitomyonia, Leptestiina,* and *Hedstroemina* (V i l l a s 1985).

The Urbana Limestone (lower Kralodvor, Central Spain), containing debris of cystoids, crinoids, trilobites, and brachiopods, is in the Almaden region of reefal or perireefal origin with numerous tetracorals (T a m a i n 1971).

K o s o v

Variably thick sequence of siltstones, sandstones, and diamictites in the uppermost Ordovician often rests on the Berounian or even earlier rocks with an erosional unconformity, which in the vicinity of Mauritanides (West Africa) passes into a marked angular unconformity (D e y n o u x - T r o m p e t t e 1981). In North Africa, this unconformity reflects the epeirogenic movements leading into uplift and emergence of the whole Saharan platform, and to reactivating of the old Pan-African faults (B i j u - D u v a l - D e y n o u x - R o g n o n 1981). In Central Europe (Bohemia, Carnic Alps), the clayey sedimentation of the upper Kralodvor was interrupted by deposition of sandstones (often with pebbles) at the beginning of the Kosov, thus reflecting deformation of the sedimentary basin (H a v l í č e k 1982). The fault movements were also established in Scandinavia (Oslo-Asker District; B r e n c h l e y - C o c k s 1982). Moreover, the beginning of the Kosov coincides with a drastic cooling of the climate as documented by deposits of glacial origin; the glaciation of that time caused glacio-eustatic regression. Both the glacio-eustatic and tectono-eustatic events resulted in considerable changes of the benthic communities. Several brachiopods of the earlier *Aegiromena-Drabovia* fauna survived till the uppermost Ordovician, namely, the genera *Aegiromena* and *Hirnantia* which, together with other stocks, formed a distinctive *Hirnantia fauna.* By contrast to the Berounian *Aegiromena-Drabovia* fauna, the ecological distribution of the *Hirnantia* fauna is strikingly broad; in the Tindouf basin (Morocco), it occurred below and above the tillite in a pronouncedly cold-water environment, whereas in South Sweden, Oslo-Asker District in Norway, and in Ireland, it has been discovered in proximity of the contemporaneous reefs; for this reason Rong (1984) supposed that the *Hirnantia* fauna extended from the circumpolar sphere into the temperate to tropical zones.

Excellently preserved and richly diversified *Hirnantia* fauna was discovered in a shallow-water, subtidal environment in the upper part of the Kosov Formation in Bohemia. In addition to the index species *Hirnantia sagittifera* (M'Coy), the following brachiopod genera have been found: *Trematis, Orbiculoidea, Philhedra, Sanxiaella, Aegiromena, Paromalomena, Aphanomena, Eostropheodonta, Leptaena, Leptaenopoma, Fardenia, Giraldibella, Comatopoma, Cliftonia, Kinnella, Draborthis, Dalmanella, Ravozetina, Trucizetina, Zygospira, Plectothyrella,* and *Cryptothyrella;* the brachiopods are accompanied by bivalves, blastoids *(Mespilocystites)*, gastropods, trilobites a.o. groups (Marek - Havlíček 1967; Havlíček 1982).

In Central Europe, the *Hirnantia* fauna has also been recovered in the uppermost Ordovician of the Carnic Alps where it yielded the genera *Hirnantia, Kinnella, Dalmanella,* and *Clarkeia* (Jaeger - Havlíček - Schönlaub 1975).

Richly diversified *Hirnantia* fauna, confined to the Second Bani Formation in the Anti-Atlas Mts. and the Ougarta region, contains the index brachiopod *Hirnantia sagittifera* (M'Coy) and the species of *Mirorthis, Arenorthis, Destombesium, Eostropheodonta, Plectothyrella,* and *Undithyrella;* distribution of the species below and above the tillite indicates a cold-water environment (Destombes 1981).

In Libya, the uppermost Ordovician Mamúniyát Formation is mainly developed as subglacial and periglacial deposits intercalated with marine sandstone layers bearing *Tigillites* (Massa in Havlíček - Massa 1973). The poor benthic fauna is confined to a single layer in the middle part of the Mamúniyát Formation which yielded *Hirnantia* aff. *sagittifera* (M'Coy) and *Plectothyrella libyca* Havlíček.

Beyond the Mediterranean province, the *Hirnantia* fauna was thoroughly studied in the Holy Cross Mts., Poland (Temple 1965), South Sweden (Bergström 1968, Sheehan 1979), Oslo-Asker District, Norway (Cocks 1982, Brenchley - Cocks 1982), English Lake District (Temple 1965), Wales (Cocks - Price 1975, Hiller 1980), Ireland (Wright 1968), Yangtze and Western Yunnan-Tibet Regions, China (Wang Xao-feng et al. 1983; Rong Jia-yu 1984), and other regions.

It is worth to note that the brachiopods of the uppermost Ordovician may be grouped in the Oslo-Asker District into a few associations (i.e. *Hirnantia, Hindella-Cliftonia,* and *Dalmanella* Associations), all located on a palaeoslope (Brenchley - Cocks 1982). By contrast to Norway, all Bohemian species lived together in a subtidal, shallow, quiet-water environment, not differentiated into separate associations.

Interesting is the extension of the *Hirnantia* fauna to China; in spite of enormous distance, the shelly fauna of the Bohemian and Chinese basins is closely similar and contains not only the genera, but also many species common to both the regions.

Climatic changes: phase of a marked increase of temperature

The Ordovician is characterized by a much cooler climate than the later Silurian and Devonian Periods as shown by glaciation in the lower Tremadoc of the Andean region of the Gondwanaland (Keidel 1944), further in the Beroun (Libya) and in the Kosov when the ice-cap covered most of the Gondwanaland. The fluctuations of the Earth climate may be explained by processes in the solar system both by the secular change in obliquity of the spin axis of the Earth, which is attributed to secular rotation of the plane of the solar system and is responsible for long-period (1000—2000 m.y.) changes of temperature, or by the rotation of the solar system around the galactic center (moderate-period climatic changes, 100—200 m.y.) (G. Williams 1972).

Climatic fluctuations may also be explained by galactic processes supposing that the solar system moves on an elliptic path around the center of the galaxy. Steiner and Grillmair (1973) called a complete revolution a cosmic year; its duration decreases from 400 m.y. in the Precambrian to the present duration of 274 m.y. The causal relationship between the periods of glaciations and the galactic model of Steiner and Grillmair is evident but cannot be explained yet.

The Ordovician benthic faunas are differentiated into several zoogeographic provinces reflecting various climatic zones from circumpolar region to the tropical zone. The cool climate, however, was interrupted by a short phase of a marked increase of temperature in the upper Beroun and lower Kralodvor. At that time, the first reefs originated in the Mediterranean province (reefs in Urbana Limestone, lower Kralodvor; central Spain — Tamain 1971), and warm-water Anglo-Baltic fauna colonized extensive, rather stable, shallow-water plains to give rise to typically mixed assemblages. In South Europe, these assemblages consist of original stocks of the *Aegiromena-Drabovia* fauna supplemented by many Anglo-Baltic (less commonly North American) elements. The mixed assemblages, called Anglo-French province by Williams (1973), never reached North Africa which remained a circumpolar sphere till the end of the Ordovician. The mixed assemblages are absent in Central Europe where the linear sedimentary basins of rift origin were not surrounded by extensive, shallow-water shelves convenient as habitats of warm-water benthic fauna. The mixed assemblages were studied in Belgium (upper Beroun?—lower Kralodvor; Sheehan 1975), the Iberian Chains (upper Beroun—lower Kralodvor; Villas 1985), Sardinia (upper Beroun; Havlíček - Kříž - Serpagli 1987), the Carnic Alps, Austria and Italy (upper Beroun; Vai 1971, Havlíček - Kříž - Serpagli 1987) and Brittany (Caradoc, tuff and limestone of Rosan; Mélou 1971). In addition to the indigenous Mediterranean genera, the benthic assemblages acquired many warmer-water elements, namely the thick-shelled brachiopod *Porambonites*, further orthids *Nicolella, Glyptorthis, Eridorthis, Dolerorthis,* and a strophomenid *Longvillia; Reuschella* sp. and *Bicuspina spiriferoides* (M'Coy), both found in Sardinia, indicate a close relation to faunas of the upper Caradoc of Great Britain. An index genus of the "mixed fauna" is *Iberomena,* which may be derived from the cosmopolitan genus *Strophomena.* On the other hand, *Eoanastrophia,* occurring in all areas of South Europe, indicates an Kazakhstanian origin. The South European "mixed fauna", dominated by *Nicolella actoniae* (Sowerby), roughly corresponds to the *Nicolella* Community described by Pickeril and Brenchley (1979) from the middle Caradoc of North Wales.

Climatic changes: glacial events

Two glacial periods have been recorded in the Ordovician of the Mediterranean province. The earlier one is confined to the Beroun Series (Melaz Shuqrán Formation) of central Libya where Collomb (1962) discovered a typical diamictite rich in pebbles and boulders of rocks of various origin. Massa (*in* Havlíček - Massa 1973) supposed a glacial origin of this diamictite and ranged it to the glacial event of Berounian age.

In Arabian Peninsula, a pre-Kosovian age may be postulated for the tillite occurring at the top of the Ra'an Shale which has yielded trilobites and graptolites of probable upper Caradocian age (Young 1981).

Much more important is the second glacial period in the Kosov (uppermost Ordovician), when the continental ice-cap covered most of the Sahara. In North Africa, the glacial sediments were studied in northern Ethiopia (Endaga Abri Tillite; Hambrey 1981, Saxena - Assefa 1983), Sirt and Murzúq basins, Libya (Hofra Formation, upper part: Massa - Delort 1984; Mamúniyát Formation: Massa *in* Havlíček - Massa 1973), central Sahara (Tamadjert Formation: Beuf et al. 1971, Biju-Duval - Deynoux - Rognon 1981, Legrand 1974), Taoudeni basin in West Africa (Tichit Group: Deynoux 1971, Deynoux - Trompette 1981), Sierra Leone (Waterfall Formation; Tucker - Reid 1981), and in the Tindouf basin (Second Bani Formation; Destombes 1968, 1971, 1981). Zonation of the glacial sediments is best recognized in the central Sahara; the terrestrial tillites of the Tamadjert Formation (Unit IV) prevail in the southern Hoggar; in the northern Hoggar, the terrestrial tillites together with reworked fluviatile, lacustrine, and marine deposits fill a rather irregular topography with many glacial palaeovalleys which characterize the ice-sheet margins. The ice-flow and meltwater discharge below the continental glacier trended mostly towards north to north-west. Judging from the presence of several superimposed glacial pavements, several glacial phases existed which can amount three to four in the Sahara (Biju-Duval - Deynoux - Rognon 1981). Farther from the centre of the glaciation (i.e. in the north Saharan basins), the Tamadjert Formation became much thicker (up to several hundred meters) to involve more marine deposits than sediments of a glacial origin.

In the Iberian Peninsula, Normandy, and Thuringia, the uppermost Ordovician (Kosov) is characterized by a glaciomarine sedimentation as it is evident from the poorly sorted and pebbly greywackes and shales with numerous ice-rafted stones (Arbey - Tamain 1971; Dangeard - Doré 1971; Robardet 1981; Doré - Le Galle 1973; Doré 1981; Katzung 1961; Franke 1978 a.o.); some drop-stones are striated. All tillites in the European part of the Gondwanaland were deposited on shallow marine shelves surrounding emerged areas subjected to temporary glacierization.

In South Europe, there are extensive areas lacking periglacial deposits (see pl. 3); this is easy to explain by a lack of the uppermost Ordovician sediments in this region due to a break in sedimentation and/or an erosion of the post-Berounian deposits.

Beyond the Mediterranean province, the glacial activity was recorded by Williams (1981) in the Middle to Upper Ordovician in western Ireland where the Dalradian Cordillera was supposed to support a highland glaciation.

Mid-European Sea

Shallow-marine and fluvio-marine deposits are confined to extensive shelves and intracratonic basins, usually with a low rate of sedimentation; they cover most of the North African and South European stable fundament. On the other hand, the region between the Gondwanaland and North European platform was formed as a highly mobile belt of variable width in separate areas. By contrast to the craton of the Gondwanaland, the rate of sedimentation, although different in separate time-spans, was usually high as documented by considerable thicknesses of the Cambrian and Ordovician sequences. The mobile Variscan belt was differentiated into several troughs and highs, often with volcanic activity and slight to strong metamorphism. The Ordovician rocks of these troughs, if fossiliferous, have yielded rare trilobites and shelly fauna of the Mediterranean type, for instance Thuringia (Gräfenthal Formation: Sdzuy 1971), Taunus in Hessen (Andreasteich Quartzite: Struve 1975), Belgium (Sart-Bernard Formation — mainly bivalves in association with *Dalmanitina proeva* and *Cyclopyge rediviva:* Maillieux 1939), a.o.

When dealing with the zoogeographic provinces, the Mid-European Sea (= Rheic Ocean or Tornquists Sea, e.g. Cocks - Fortey 1982, Neuman 1984 a.o.) was usually supposed to be wide enough to function as a considerable barrier prohibiting interchange of the fauna. From this point of view, its inferred extent should have been comparable to that of the Proto-Atlantic (= Iapetus Ocean), separating the Laurentian continental margin from the Baltic continental margin. The present study, however, has shown that the Sea between the Gondwanaland and the North European platform was not an important barrier against interchange of the fauna. This is apparent from the fact that each significant increase and decrease of temperature was followed by migration of the fauna across the Mid-European Sea. For this reason, it is likely that the dimension of the Mid-European Sea was overestimated in almost all studies. The Sea, though less large than so far estimated, did exist before its closing; this can be demonstrated by the post-Ordovician distance between the tillites in Normandy and the reef bodies in northern England (Keisley Limestone) and Ireland (Kildare Limestone); this distance does not surely correspond to the original situation in the uppermost Ordovician when these facies had to be much farther from each other. It is also very probable that the Swedish Boda reef was more distant from the periglacial deposits in Thuringia than the distance indicated on the present-day geological maps. The maps compiled by the present author have not been palinspastically restored, because the palaeomagnetic data concerning the Ordovician of Central Europe, are not yet fully satisfying.

The limit of the Mediterranean province has been drawn approximately along the inferred margin of the North European platform; in Moravia, this boundary is bent abruptly towards the SW, because the Brno unit

(Brunovistulicum) is to be excluded from the Gondwanaland; it is likely a part of the Fenno-Sarmatian platform and continues eastwards in the basement of the West Carpatians to link directly the Ukrainian shield (Suk et al. 1984). In Romania, the margin of the Mediterranean province may coincide with the boundary between the Moesian and Moldavian platforms (see Iordan 1981).

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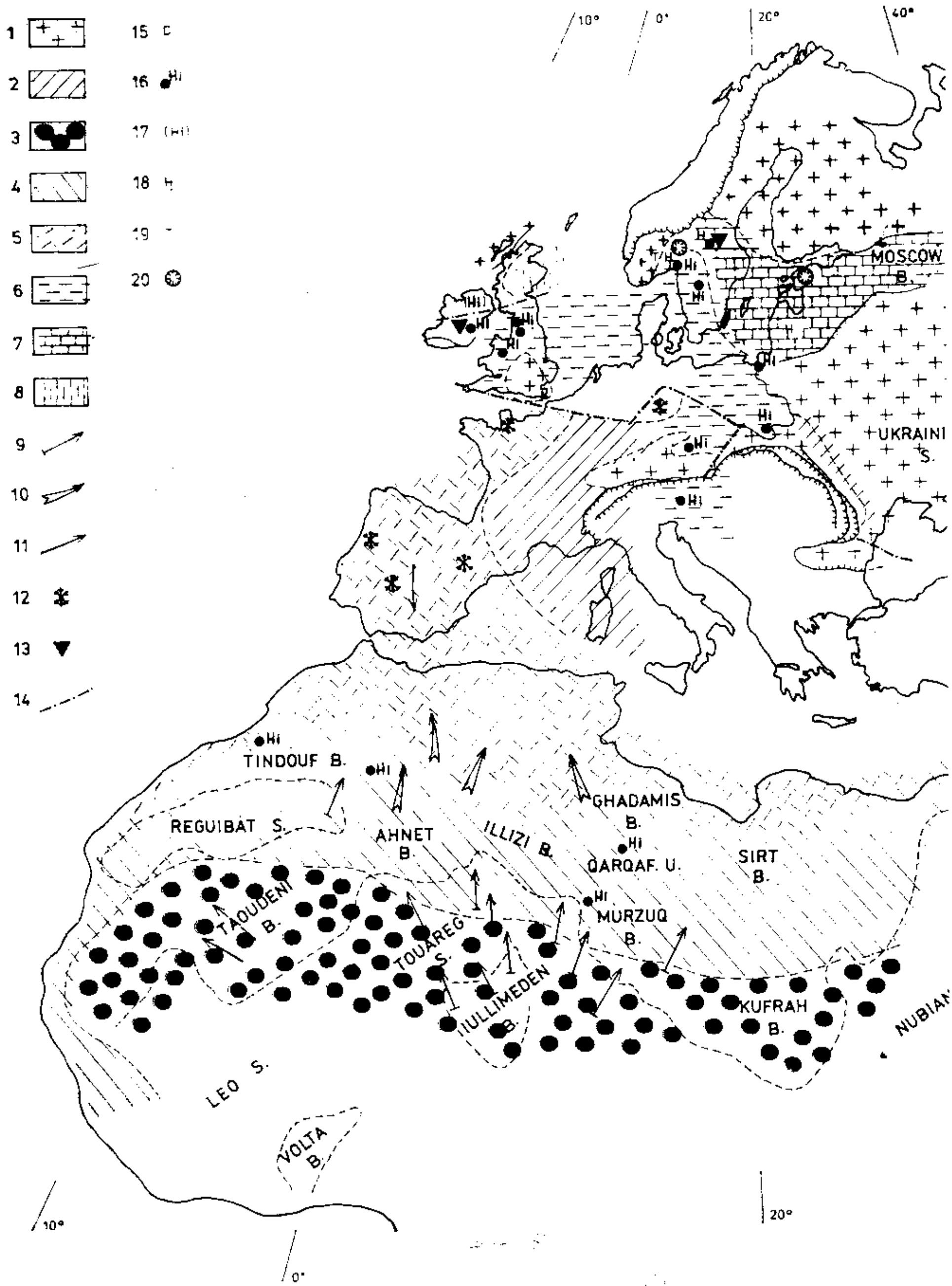
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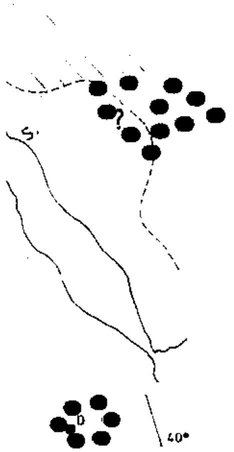
DISTRIBUTION OF GLACIAL DEPOSITS AND BENTHIC COMMUNITIES, TOGETHER WITH OCCURRENCES OF INDEX BRACHIOPOD GENERA IN THE KOSOV



1 — pre-Palaeozoic shields; *2* — regression of the Sea in the Kosov; *3* — mainly terrestrial tillites (after Beuf et al. 1971); *4* — mainly fluviatile, lacustrine, or marine periglacial deposits; *5* — shallow-water, glacio-marine sediments with common ice-rafted stones; *6* — communities of the *Hirnantia* fauna; *7* — mainly marls with Baltic type communities; *8* — graptolitic shale pelagic community; *9* — meltwater discharge below continental glacier (after Beuf et al. 1971); *10* — transport direction of icebergs calving from glaciers; *11* — ice-flow direction; *12* — evidence of glaciation in Europe (tillites, bedrock-surface striations); *13* — reefs; *14* — boundaries of zoogeographic provinces; *15* — *Discophyllum (Hydrozoa)*; *16* — *Hirnantia* fauna; *17* — restricted shelly fauna containing a few elements of the *Hirnantia* fauna; *18* — *Holorhynchus*; *19* — *Thebesia* and *Brevilamnulella* Associations; *20* — *Palaeofavosites, Palaeohalysites*

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Klimatické změny a rozvoj bentických společenstev během ordoviku v mediteránní provincii

(Résumé anglického textu)

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Předloženo 29. ledna 1986

Autor této práce měl možnost studovat velkou část brachiopodů ordoviku Gondwany, a to jak z ordoviku střední a západní Evropy, tak i ze severní Afriky a Jižní Ameriky (Bolívie). Bližší poznání této brachiopodové fauny bylo pak základem pro stanovení zvláštností a vývoje brachiopodových společenstev během ordoviku.

Severní Afrika a jižní Evropa (včetně Českého masívu) jsou považovány za součást mediteránní zoogeografické provincie, která je provincií chladnovodní, vázanou na cirkumpolární zónu; vzhledem ke značné rozhlehlosti mediteránní provincie zasahovaly její okrajové části až do mírného pásma.

Rozsáhlé šelfy a intrakratonické pánve byly během ordoviku doménou tigillitových společenstev, místy přecházejících až do společenstev s převahou inartikulátních brachiopodů, a to převážně pod silným vlivem velmi chladného klimatu a nižší salinity moře. Společenstva marocko-českého typu, dobře známá z Antiatlasu a jižní Evropy, obsadila rovněž mobilní oblast variscid vroubící gondwanský kontinent. Význačná aegiromenová a draboviová fauna vznikla až ve středním a svrchním ordoviku; je považována za chladnovodní a je rozšířena od severní Afriky až do střední a západní Evropy a zčásti i do Jižní Ameriky (Bolívie). Zajímavé je období svrchního berounu a králodvoru, v němž došlo k výraznému otepletí klimatu a s ním spojené kolonizaci rozlehlých šelfů v západní Evropě faunou anglo-baltského typu, která je považována za teplovodní. V ordoviku Gondwany byla zjištěna dvě období s velmi chladným klimatem; starší z nich spadá do berounu, kdy projevy zalednění byly doloženy v Libyi; hlavní glaciální období spadá do nejvyššího ordoviku (kosovu), kdy kontinentální ledovec kryl převážnou část Gondwany; hirnantiová fauna, současná s tímto zaledněním, značně překročila rámec mediteránní provincie a rozšířila se do Skandinávie, Velké Británie, Číny aj.

Jak ukázala studie ordovických společenstev, nepředstavovalo tzv. Středoevropské moře mezi Gondwanou a severoevropskou platformou významnou bariéru, bránící migraci fauny. Naopak, vzájemná výměna fauny mezi šelfy a intrakratonickými pánvemi vázanými jak na Gondwanu, tak i severoevropskou platformu se opakovala několikrát během ordoviku.

Vysvětlivky k obrázkům

1. Rozšíření vůdčích brachiopodových rodů v tremadoku.
2. Rozšíření vůdčích brachiopodových rodů v llanvirnu.
3. Rozšíření vůdčích brachiopodových rodů v dobrotivu (llandeilu).
4. Rozšíření vůdčích brachiopodových rodů v berounu (caradoku).
5. Rozšíření vůdčích brachiopodových rodů v berounu (caradoku).
6. Rozšíření vůdčí bentické fauny v králodvoru (spodním ashgilu).

Vysvětlivky k přílohám

Příl. 1

Rozšíření bentických společenstev a výskyty vůdčích brachiopodových rodů v arenigu. *1* — předkambrické masívy; *2* — potremadocká mořská regrese; *3* — fluviální a fluviomarinní uloženiny (smíšené facie), společenstva s *Tigillites* a *Cruziana; 4* — převážně mořské uloženiny se stopovými fosiliemi a inartikulátními brachiopody, tigillitová a „lingulová" společenstva; *5* — pánevní uloženiny s převahou trilobitů a orthidních brachiopodů mediteránního typu; *6* — asociace s převahou inartikulátů a orthid anglo-waleského typu; *7* — společenstva baltického typu; *8* — převážně pelagická společenstva graptolitových břidlic; *9* — společenstva skotského typu; *10* — hranice zoogeografických provincií; *11* — směry fluviatilního transportu (podle S. Beufa et al. 1971); *12 — Clitambonitacea; 13 — Orthis, Orthambonites; 14 — Ranorthis, Paurorthis; 15 — Orbithele.*

Příl. 2

Rozšíření bentických společenstev a výskyty vůdčích brachiopodových rodů v berounu (caradoku).
1 — předkambrické masívy; *2* — regrese moře v berounu; *3* — marinní a fluviomarinní pískovce, převážně tigillitové společenstvo; *4* — společenstva s převahou inartikulátních brachiopodů; *5* — společenstva marocko-českého typu (aegiromenová a drabovivá fauna); *6* — společenstva anglo-waleského typu; *7* — smíšené fauny marocko-českého a anglo-waleského typu; *8* — pelagické společenstvo graptolitových břidlic s drobnými inartikuláty; *9* — společenstva baltického typu; *10* — společenstva skotského typu; *11* — pravděpodobný směr imigrace teplovodních elementů do mediteránní provincie; *12* — pravděpodobný směr imigrace bentické fauny mediteránního typu do iullimedenské pánve; *13 — Drabovia, Drabovinella; 14 — Heterorthis; 15 — Svobodaina, Cilinella; 16 — Porambonites (Porambonites); 17 — Clitambonitacea; 18* — útesy; *19* — doklady berounského zalednění; *20* — hranice zoogeografických provincií.

Rozšíření ledovcových uloženin a bentických společenstev a výskyty vůdčích brachiopodových rodů v kosovu.

1 — předkambrické masívy; *2* — regrese moře v kosovu; *3* — převážně terestrické tillity (podle S. Beufa et al. 1971); *4* — převážně fluviatilní, lakustrinní nebo mořské periglaciální uloženiny; *5* — mělkovodní glaciomarinní uloženiny s driftovanými balvany; *6* — společenstva s hirnantiovou faunou; *7* — převážně jílovité vápence se společenstvy baltického typu; *8* — pelagické společenstvo graptolitových břidlic; *9* — směr odtoku tavných vod pod kontinentálním ledovcem (podle Beufa a kol. 1971); *10* — směr transportu ledovcových ker, oddělujících se od čela kontinentálního ledovce; *11* — směr pohybu kontinentálního ledovce; *12* — doklady pro zalednění v Evropě (tillity, rýhování skalního podkladu); *13* — útesy; *14* — hranice zoogeografických provincií; *15* — *Discophyllum (Hydrozoa)*; *16* — hirnantiová fauna; *17* — bentická fauna s ojedinělými prvky hirnantiové fauny; *18* — *Holorhynchus*; *19* — asociace s *Thebesia* a *Brevilamnulella*; *20* — *Palaeofavosites*; *Palaeohalysites*.

Изменения климата и развитие сообществ бентонных организмов в средиземноморской провинции в ордовикский период

Северная Африка и южная Европа являются частью средиземноморской зоогеографической провинции, считаемой холодноводной, связанной с циркумполярной зоной; краевые части этой провинции могут переходить даже в умеренный пояс. Обширные шельфы и внутрикратонные бассейны в ордовикский период являлись областью обитания сообществ червей рода Tigillites, переходящих местами в сообщества с преобладанием беззамковых плеченогих, именно вследствие преимущественно холодного климата и пониженной солености моря. Руководящая фауна с родами Aegiromena и Drabovia появилась лишь только в среднем и верхнем ордовике, а в наиболее верхней его части была она замещена фауной с родом Hirnantia. В верхнебероунском и краподворском веках значительно повысилась температура, обусловившая заселение большей части шельфов сообществами англо-балтийского типа. В ордовике установлены две фазы оледенения. Более древняя из них доказана в бероунском ярусе на территории Ливии. Главное оледенение относится к наиболее верхнему одровику, когда материковым ледником покрылась большая часть Гондваны и холодноводная фауна с родом Hirnantia переселилась вне пространства первичной средиземноморской провинции, именно в Скандинавию, Великобританию, Китай и другие области. Как вытекает из изучения ордовикских сообществ, т. наз. Среднеевропейское море, простирающееся между Гондваной и Североевропейской платформой, не являлось барьером, препятствующим взаимному обмену фауны.

Přeložil A. Kříž