



## **NORTHERN GONDWANAN SILURO-DEVONIAN PALAEOGEOGRAPHY ASSESSED BY CEPHALOPODS**

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### **ABSTRACT**

Worldwide distribution of cephalopod limestone biofacies distribution is used herein to assess the reconstruction of the North Gondwana margin, with implications for southern hemisphere palaeobiogeography during the Silurian-Early Devonian. Three areas are of concern: the Tinduf Basin (Northwest Sahara, Morocco), the Uppony Mountains (Northeast Hungary), and perhaps the Ukrainian continental platform, which may have been part of northern Gondwana.

Key words – Palaeobiogeography, cephalopod biofacies, faunal similarity Gondwana.

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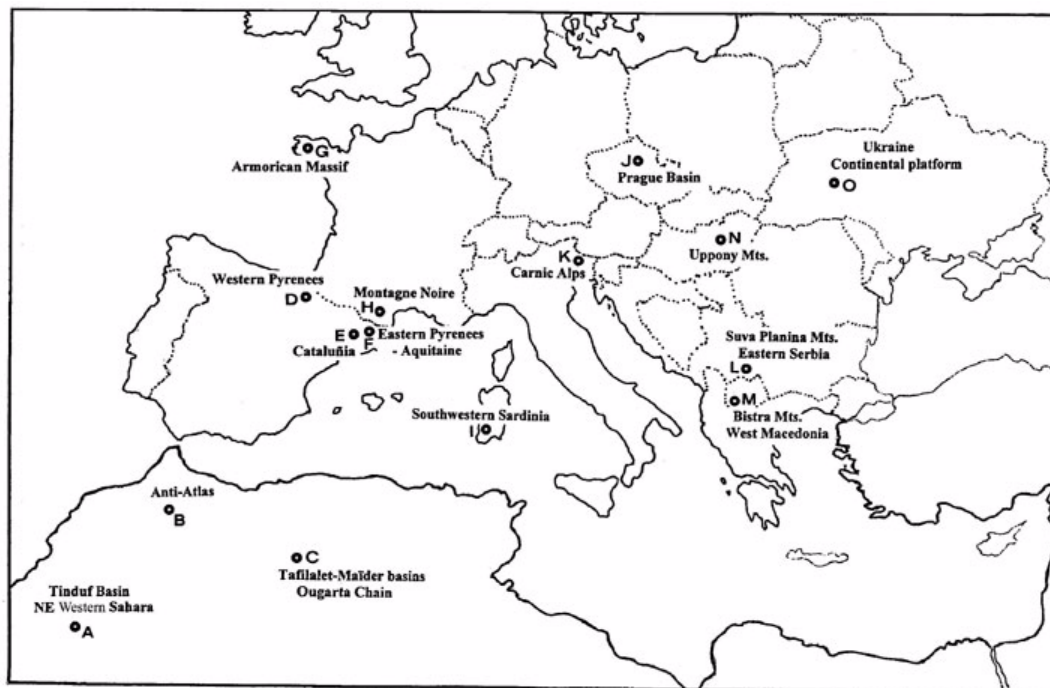
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### **INTRODUCTION**

During the Silurian-Early Devonian, cephalopod limestone biofacies represent one of the best documented sedimentary deposits in the stratigraphic column. Reconstruction of the northern margin of Gondwana by means of cephalopod limestone biofacies also represents one of the most interesting topics of Early Palaeozoic palaeobiogeography.

Several authors have investigated the geographical position of various fossil groups during the Silurian-Early Devonian, including: nautiloid cephalopods (Crick 1990), bryozoans (Tuckey 1990), brachiopods (Cocks and McKerrow 1973; Boucot and Blodgett 2001), phytoplankton (Colbath 1990), ostracodes (Berdan 1990), higher land plants (Edwards 1990), palynology and plant dis-

persal patterns in the Ludford-Prídolí interval and Silurian-Devonian boundary (Richardson et al. 2001), Silurian stromatoporoids (Nestor 1990), Devonian stromatoporoids (Stock 1990), rugose corals (Pedder and Oliver 1990), algae (Poncet 1990), and Early-Middle Devonian gastropods (Blodgett et al. 1990). Nevertheless, in his discussion of Silurian biogeography Boucot (1990, pp. 191-196) noted that, "A number of potentially useful groups such as the nautiloids and stony bryozoans remain largely unstudied." As reported previously by Holland (1971, p. 70) "...The predominant impression is of cosmopolitan faunas, but this may be because outcrops of effectively observable Silurian rocks broadly follow the supposed Silurian equator. Platforms were apparently exceptionally large and geosynclines limited in the Silurian; the platforms comprise two "magnafa-



**Figure 1.** Map showing modern locations of the localities in which nautiloid cephalopod biofacies during the Silurian-Early Devonian (see text for detailed locality descriptions).

cies," characterised by (a) shelly faunas and (b) graptolite-bivalve-orthocone faunas." (see also Cocks 2001). This latter represents the subject of this investigation.

### THE CEPHALOPOD LIMESTONE BIOFACIES IN THE GONDWANA NORTHERN BORDERLAND

Boucot et al. (1968) report the first citation of a micritic orthoceratid limestone in the entire circum-Mediterranean Silurian, later followed by Vai (1978). According to Kríz (1984), Ferretti and Kríz (1995) and Kríz and Serpagli (1993) the cephalopod limestone biofacies in the Prague Basin, southwestern Sardinia, Carnic Alps, and Montagne Noire represents a useful hard substratum for the settlement of the **Cardiola** Community Group. This faunal assemblage is mostly composed of epibysate forms. Kríz (1984, pp. 191-192) writes, "The accumulation of empty cephalopod shells on the sea floor created good conditions for the attachment of organisms in this environment, with constant water flow providing a sufficient food supply. The origin and distribution of this biofacies was closely related to surface currents carrying empty floating shells of cephalopods before they were deposited on the relatively shallow sea floor." Many bivalve community groups are linked to nautiloid cephalopod tapho-communities that represent the remnant of living cephalopods inhabiting relatively

shallow shelves or platforms (see Crick 1990 and Kríz 1999).

Another important environmental factor is that "The persistence in space and recurrence in time of the "**Orthoceras**" limestone facies are probably linked to both eustatic-climatic sea-level changes affecting the CCD, and periodic reactivation of the rifting system." (Vai 1991, pp. 234-237). According to the same author, the effect of a very shallow carbonate compensation depth (CCD), reinforced by high non-calcareous productivity (e.g., graptolites, acritarchs, and chitinozoans), constituted a crucial event in the Palaeozoic. "Eustatic sea-level falls may explain synchronous recurrence of widespread "**Orthoceras**"-limestone horizons, which can be traced as key beds for more than 1200 kilometers from Mali to Algeria, as observed by the Silurian-Devonian Boundary Subcommittee during their 1971 field-trip" (see Kríz 1984). According to Vai (1991) this is attributable to differing regimes of oceanic and atmospheric circulation due to a warmer, more uniform climate than at present. Frakes (1979, p. 107), who provides an exhaustive study of climates throughout geologic time, writes: "A widespread marine transgression in Early Silurian reflects the melting of polar ice in Africa and South America, and several features combine to indicate generally warm and possibly dry climates during the Silurian and Devonian periods. Carbonates in general and reefs in particular seem to be more abundant than in the earlier Palaeozoic."

Frakes continues (p. 106) "In summary, the paleolatitudinal distributions of several climatic indicators fall generally within the latitudinal ranges for their modern counterparts. This, while establishing the credibility of the paleomagnetic reconstruction for the Silurian and Devonian, also suggests that early Paleozoic temperature gradients and humidity patterns did not differ greatly from those of today. There is some faunal indication of warming in the early Silurian and gentle cooling until the middle Devonian, followed by a warm late Devonian. Overall, aridity seems to have typified Silurian and Devonian climates, except for the late Silurian and early late Devonian."

Before entering into any palaeobiogeographic and palaeoecological speculations based on nautiloid cephalopod assemblages, Crick's (1990, p. 147) comment on nautiloid paleoecology is worth noting; "The distribution of fossil nautiloids illustrated here (Late Cambrian to end of Devonian), and those of Flower (1976) and Crick (1980), indicates that these nautiloids were not truly part of the nekton capable of oceanic dispersal, but were members of the shallow-shelf vagrant benthos and were thus capable of dispersal only along continuous shelves or over shallow stretches of open ocean. For these reasons, simple distance and the depth of water separating shallow shelf seas were capable of restricting the dispersal of nautiloid cephalopods until such time as the physical environment removed these barriers." According to Crick, taking into account various magnitude events controlling in general the biogeography of nautiloid cephalopods and in particular those of the first magnitude such as geotectonic, it is possible to separate nautiloid biogeography into four episodes: (1) Late Cambrian; (2) Ordovician; (3) Silurian through Early Devonian; and (4) Middle through Late Devonian. The third episode is the concern of this article.

Holland et al. (1994) documented the commonly high concentration of specimens, characterizing the cephalopod limestone biofacies, describing Ordovician to Devonian examples from widely separated parts of the world. According to these authors different environmental causes could explain the high concentration of fossils. They also consider Doyle and MacDonald's (1993, p. 67) suggestions regarding so-called 'belemnite battlefields' as most likely caused by post-spawning mortality. In conclusion, however, they write: "Thus we are left with catastrophic mass-mortality as the most likely explanation of the Palaeozoic concentrations. It must be said that this is adequate but that its precise nature may be difficult or impossible to discover." (Holland et al. 1994, p. 96).

## TAXONOMIC NOMENCLATURE

Because the nautiloid taxa reported here from various localities have been referred to in publications by authors from the nineteenth century onwards, a revised taxonomic nomenclature was employed whenever possible. For example, according to Serpagli and Gnoli (1977) **Orthoceras bohemicum** Barrande, 1866 is considered the senior synonym of **Orthoceras fluminense** Meneghini, 1857. Likewise, Serpagli and Gnoli (1977) referred to Meneghini's species as **Orthocycloceras? fluminense** (Meneghini 1857). Thus, any occurrence of **Orthoceras bohemicum** Barrande, 1866 is here reported as **Orthocycloceras? fluminense** (Meneghini 1857). Similarly, in its original binomen **Orthoceratites subannularis** Münster, 1840 was first changed to **Orthoceras subannulare** by Barrande (1866) and remained so for the following 112 years, before being assigned to **Metaspyroceras** Foerste by Zhuravleva (1978). Accordingly, all occurrences of this species are herein reported as **Metaspyroceras subannulare** (Münster 1840).

## NEW DATA ON CEPHALOPOD LIMESTONE BIOFACIES FROM NORTHEAST HUNGARY

Kovács (1989) reported olistoliths from the Strázsahegyi Formation in the Uppony Mountains (northeastern Hungary) bearing nautiloid orthocones in profusion («orthoceratid lumachella») within the Ludlow Series (Gorstian) belonging to the **Ozarkodina s. sagitta - Ancoradella ploekensis** conodont biozones. Gnoli (in Gnoli and Kovács, 1992) described and illustrated this faunule and, despite the poor preservation of the inner features in the available material due to slight metamorphism, recognized **Michelinoceras michelini** (Barrande 1866), **Mimogeisonoceras? cf. liberum** (Barrande 1870), **Kopaninoceras** sp. sensu Gnoli in Gnoli and Kovács, 1992, **Kionoceras? cf. adactum** (Zhuravleva 1978), **Leurocycloceras** or **Dawsonoceras** cf. **dulce** (Barrande 1868) and **Columenoceras? cf. grande** (Meneghini 1857). In addition to the following distinctive areas I would tentatively add a new Silurian region corresponding to the northeastern Hungarian Uppony Mountains because of its orthocone nautiloid content (Gnoli and Kovács 1992). These strata—cropping out on the western ridge of the Strázsa Hill and locally called "Harka-tető"—can be closely compared to the Plöcken facies of the Carnic Alps (Schönlaub 1979, 1980).

A manuscript entitled "Correlation of the Szendrő - Uppony Palaeozoic (Northeast Hungary) with the Carnic Alps - South Karavanken Alps and Graz

Palaeozoic: some paleogeographic implications” by Ebner, Kovács and Schönlaub (Kovacs, personal commun., 1995) exists which advanced one interpretation of these occurrence patterns: “The close similarities between these Variscan sequences suggest their original proximity on the southern (Apulian) carbonate shelf of the Alpine-Dinaric arm of Prototethys”. These authors stated in the summary that: “The Silurian pelagic olistoliths of olistostrome derive, however, unambiguously from the coeval reddish pelagic carbonate formations of the Carnic Alps-South Karavanken Alps (Kok Limestone, **Alticola** Limestone).” According to these authors “The overlapping of the Carnic Alps, respectively Graz Palaeozoic characteristics in the Szendrő-Uppony Palaeozoic, indicate that the Periadriatic Lineament was not a paleogeographic boundary.” Unfortunately, this manuscript was never published (Schonlaub, personal commun., 2002). Another possibility (Boucot, personal commun., 2002) is that the Carnic Alps and adjacent Karavanken might have been located near the southern end of the western Urals in the earlier Paleozoic. This assumes that their present position in the Early Carboniferous was linked to the exceptional coeval crustal shortening (Neugebauer 1988) which would explain some of the lithostratigraphy and also the ‘Uralian’ nature of the Early Devonian faunas.

Looking at the paleogeographic reconstruction of Paris and Robardet (1990), Robardet et al. (1994) and Vai (1991), there are several circum-Mediterranean microplates besides the Variscan Terranes on the northern margin of Gondwana. These areas (Fig. 1) represent Silurian continental platforms (shelves) covered by relatively shallow water. From West to East they are: Tinduf Basin, Anti-Atlas, Ougarta Chains (Aulacogen), Cantabrian Mountains, Central Iberian Domain, French Massif Central, Mid-North Armorican Domain, Eastern Pyrenees-Aquitaine, Montagne Noire, Southwest Sardinia, Carnic Alps (may be equivalent to the Southern Urals), Prague Basin, Eastern Serbia - Suva Planina Mountains, Zebrina locality (Kriz and Veselinovic 1974), Uppony Mts. (northeastern Hungary), Western Macedonia (Bouček et al. 1968), and beyond the Armorican sea tongue and ?Rheic Ocean (Carls 2001) towards the East, the Podolia continental platform. The latter must, however, be considered as belonging to Baltica (Bullard et al. 1965). The nautiloid cephalopod fauna of the Ukraine (Podolia) is tentatively compared to those reported above to check with possi-

ble links on biogeography during Silurian-Early Devonian time. A Variscan crustal shortening of about a thousand kilometres is indicated. This shortening, plus the strong westward rotation of Gondwana, probably constitute exceptional events, particularly during the Carboniferous (Neugebauer 1988), necessitating revisions in previous paleogeographic reconstructions. The hypothetical Palaeozoic Hercynian Ocean separating Europe from Africa, somewhere south of the Tornquist Line, has been discovered by Vai (1991) because of the distribution of the circum-Mediterranean “**Orthoceras**” limestone (see also Berry and Boucot 1967; Kriz 1998).

### FAUNAL CONTENT OF THE CEPHALOPOD LIMESTONE BIOFACIES IN THE VARISCAN TERRANES

#### Tinduf Basin (Northwestern Sahara) [A].

Ratschiller (1970-71) in the northeastern part of Western Sahara (former Spanish Sahara) described two formations: the Dammia and Afreiyat Formations. He writes (pp. 44-46), “The boundary between the two formations is lithologically very distinct. The Dammia shale contains interbedded thin siltstone layers that are dark red on exposed surfaces at the contact between greyish green and red shale of the Dammia Fm and massive, predominant greyish-blue calcarenite beds of the Afreiyat Fm and surfaces. The Afreiyat calcarenite contains abundantly ‘**Orthoceras**’. These beds exhibit a characteristic shimmer and are observable for long distances along the Afreiyat Fm of the southern flank of the Tinduf Basin. An angular unconformity of a few degrees (2°-3°) seems to be present between the two formations along the area of the Tifariti basement. It is not well observable because of extensive fluvial deposit.” Ratschiller continues (p. 45), “Based on its fossil content the Afreiyat Fm. belong to the Silurian. In the graptolitic limestone of Rag Bularsag the following graptolites were collected: **Pristiograptus (Saetograptus) chimaera** (Barrande), **Monograptus? unguiferous** (Perner), **Pristiograptus dubius** (Suess), **Monograptus flemingi** (Salter).” These index graptolites correspond approximately to the following conodont zones or time intervals [Storch, personal commun., 1995 (Geol. Inst. AS CR, Prague, Czech Republic)]:

**Pristiograptus (Saetograptus) chimaera** (Barrande) to **Ancoradella ploekensis**



**Figure 2.** Picture of 6-8 cm thick nautiloid-bearing calcarenite slab from the Dammia/Afreiyyat Formation boundary bed, Western Sahara; slab has been naturally polished by wind.

Upper Gorstian such as the **scanicus zone** (Middle Ludlow);

**Monograptus? unguiferous** (Perner) to the Lower Gorstian;

**Pristiograptus dubius** (Suess) to **Ozarkodina boh. bohémica** (Wenlock-Ludlow);

**Monograptus flemingi** (Salter) to **O. sagitta sagitta** (Middle Wenlock).

Inasmuch as the cephalopod limestone biofacies in this area are of special importance, the following is reported from Ratschiller (1970-71, pp. 45-56, fig. 2 and enclosures 1-4) *ad litteram*.

#### **Afreiyyat Formation**

Lithology: "In the type section area the top of the formation is a key horizon (thickness 5 m) of calcarenite, with abundant "**Orthoceras**" compact of finely crystalline, and grayish-red. Below the calcarenite greenish-red shale predominates. It is thin bedded to laminate, with some interstratified, thin, gray limestone beds (thickness 73 m). Below the shale is another red, calcarenite horizon, with abundant orthocones (maximum length 40 cm, diameter 7-8 cm). This calcarenite overlies 57 m of green or variegated shale, laminated, with crystals of limonitized pyrite and thin, interbedded, graptolitic, sandstone beds at the bottom." In the lithostratigraphic description of section "Rio 21" at the base of the "upper section" of the Southern flank of Tinduf Basin near Tifariti, Ratschiller reported the presence in silty lime-

stone of **Dawsonoceras annulatum** (Sow-erby 1818).

The writer was kindly invited by Dr. Ratschiller visit his personal fossil collection in the late spring of 1995, and had an opportunity to study a cephalopod slab, naturally polished by wind abrasion (Fig. 2) from the boundary of the Dammia and Afreiyyat formations. This slab contained very abundant **Arionoceras submoniliforme** (Meneghini 1857), a few specimens of **A. affine** (Meneghini 1857), and scattered **Michelinoceras (M.) michelini** (Barrande 1866). [Note: **A. affine** could represent the sexual dimorph (female) of **A. submoniliforme** (Meneghini 1857) (see Gnoli 1998)].

This slab is from 26°32'30" North and 9°16'26" West along the road that cuts toward the northeast boundary of the Afreiyyat and Dammia formations. Biostratigraphically, its age belongs to the **Anco-radella ploeckensis** conodont Biozone. The cephalopod and conodont fauna it contains represents typical, monospecific populations probably due to the particularly high-energy depositional environment of this nautiloid-bearing calcarenite. Wave motion dominated this microfacies as evidenced by the presence of a normally packed oolite consisting of single-coated, rounded grains in which the nuclei are minute fragments of cephalopod shells. This is a good example of the "Standard Microfacies 15" that today is very common in tidal bars (see Wilson 1965).

#### **Anti-Atlas (Morocco) [B]**

Knowledge of the cephalopod limestone biofacies developed here is reported several times



**Figure 3.** Picture of a portion of a polished cephalopod limestone slab from Tazzarine, Anti-Atlas, Morocco, exhibiting arionoceratid nautiloids.

and can be summarized by the existing literature on this topic. The Tafilalet structural platform can be traced over an area approximately 80 kilometers in a north-south direction and 30-40 kilometers in an east-west direction. It is characterized by a thin succession (5-50 m in the center) of Upper Frasnian/Lower Famennian, cephalopod-bearing, limestone strata, showing distinct lateral facies variation and frequent hiatuses. To the north and south, Devonian rocks are overlain by Upper Cretaceous strata. A possible continuation of the platform towards the north, however, may be inferred from the reappearance of Upper Devonian rocks of similar facies in the eastern Meseta, about 200 kilometers to the northwest (Hollard 1967; Bensaid, 1974). An extremely reduced (3 m), isolated, Upper Devonian limb of a platform is found in the north Jebel Rheris area. Because Devonian rocks are eroded towards the north and east, the extent of this platform remains uncertain (Wendt et al. 1984). These authors speak of slow, shallow pelagic deposition of the Upper Devonian cephalopod limestone biofacies on the structural Tafilalet-platform. The same type of depositional pattern of this biofacies occurs in southwestern Sardinia, also during the Lower Devonian (Gnoli 1983, 1985).

The author also had the opportunity to see a polished slab of Silurian nautiloid cephalopod dark limestone from Tazzarine in which several orthoceratid species were recognized, including: **Michelinoceras (M.) michelini** (Barrande 1866), **Kopaninoceras jucundum** (Barrande 1870), among Geisonoceratidae **Arionoceras affine** (Meneghini 1857), **Arionoceras aff. capillosum** (Barrande, 1868), **Ar. submoniliforme** (Meneghini 1857), and **Harrisoceras cf. vibrayei** (Barrande

1859). This fauna is similar to those of southwestern Sardinia and Central Bohemia (Perunica). The age assignment—cross-checked by conodonts—is lowermost Ludfordian, Ludlow [**P. siluricus** Biozone (Serpagli, personal commun., 1995)]. A comparable slab is also stored in the Museum at Modena (Fig. 3). In addition, **Dawsonoceras dulce** (Barrande 1868) was recovered by Termier and Termier (1952) from the Silurian at Amdekhelni.

#### **Ougarta Chains Aulacogen (sensu Wendt 1995) Southern Algeria [C]**

These are approximately north of the Ahnet Basin and south of Beni Abbes locality, South Algeria, "Due to excellent outcrops in all this area, the number of available data is virtually unlimited" (Wendt (1995, p. 163). The exposed shallow and marginal basin limestones extend from the northwest to southeast for more than 200 kilometers, the central part of which is at 31° 30' north and 1° 6' west (Wendt 1995, fig. 1).

Nautiloid cephalopod assemblages from this area remain poorly known. Massa (1965, p. 48) reports a Silurian-Lochkovian sequence cropping out in some formations (e.g., Qien Ali, Zemlet, Saheb el Djir) described by Alimen et al. (1952), Poueyto (1950, 1952), and Menchikoff (1933). In the Tafilalet-Maïder Basin and associated platform, Massa (1965) reports: **Calorthoceras? pseudocalamiteum** fide Engeser "Data Retrieval System Nautiloidea", 1997-2002 in CD-ROM, after courtesy of the Author. (Barrande in Quenstedt 1851)—already regarded as **Anaspyroceras** by various authors, Chen in Chen et al. (1981, p. 98) systematically revised the above reported Barrande taxon

as type species of the newly proposed genus **Calorthoceras**—**Lamellorthoceras coralliforme** Le Maitre, 1952 (revised as belonging to **Coralloceras** by Zhuravleva 1962), **L. vermiculare** Termier and Termier, 1955, various Orthoceratidae spp. ind., and **Gomphoceras** sp. sensu Massa, 1965. The remnant reported cephalopod fauna mainly contains various genera of ammonoids (e.g., **Agoniatites**, **Foordites**, **Blacheoceras**, **Cabrioceras**, **Cymaclymenia**, **Cyrtoclymenia**, **Curvites**, **Dimeroceras**, **Discoclymenia**, **Goniclymenia**, **Kosmoclymenia**, **Koenetites**, **Lobotornoceras**, **Maenioceras**, **Manticoceras**, **Mimosphinctes**, **Pharciceras**, **Pinacites**, **Prionoceras**, **Platiclymenia**, **Sobolewia**, **Sellanarcestes**, **Sporadoceras**, **Sphenoclymenia**, **Subanarcestes**, **Sympharciceras**, **Timanites**, **Tornoceras**, **Trochoclymenia**, **Wedekindella**, and **Wocklumeria**) linked to 'Kellwasser facies'. Consequently, it is not possible to compare these ammonoid assemblages with those of the so-called 'Clymenia Limestone' of Sardinia which is pelagic.

Additional data on the Silurian Ougarta Chains (Aulacogen) is provided by Legrand (1981). Orthocone nautiloids occur in South Algeria in profusion and their sedimentology and taphonomy have been investigated by Wendt et al. (1993) and Wendt (1995).

#### Western Pyrenees [D]

According to Depéret and Loutrel (1908-9, p. 111) the best outcrops of fossiliferous dark limestone included nodules of various dimensions in which **Orthocycloceras? fluminense** (Meneghini 1857) (a senior synonym for **O. bohemicum** Barrande 1866, see Serpagli and Gnoli 1977), **Arionoceras? severum** (Barrande 1868), **Parakionoceras originale** (Barrande 1868), **Protobactrites styloideum** (Barrande 1866), **Columenoceras cf. agassizi** (Barrande 1866), **Metaspyroceras subannulare** (Münster 1840) (may belong to **Metaspyroceras**, see Zhuravleva 1978), and **Plagiostomoceras pleurotomum** (Barrande 1866) occur. These represent a Silurian nautiloid cephalopod faunule that occurs near the village of Castelnau together with the bivalves **Maminka** sp. ind., **Panenka** cf. **subaegualis**, a pygidium of the trilobite **Arethusina**, the graptolite **Monograptus priodon**, and the brachiopod **Atrypa** cf. **philomela**.

#### Spain - Catalunya [E].

Vidal (1875) reports **Orthoceras regularis** (Schlotheim 1820) and **Orthoceras bohemicum** Barrande, 1868 [senior synonym of **Orthocycloceras? fluminense** (Meneghini 1857)] from the cen-

tral region of Lérida Province and characterizing the Prídolí (see also Serpagli and Gnoli 1977). The presence of the latter was confirmed by Barrois (1901). Faura Hy Sans (1913) notes "**Orthoceras**" limestone with the bivalve **Cardiola interrupta** (?Wenlock-Ludlow). Gómez-Alba (1988) reports from Catalunya: **Columenoceras grande** (Meneghini, 1857) and **Parakionoceras originale** (Barrande 1868), and **Vericeras? barroisi** (Vidal 1914). Note that **Orthoceras barroisi** Vidal 1914 is here regarded as dubiously belonging to **Vericeras** Kolebaba because Vidal in the description of his newly proposed species writes: "y se distinguen por las finas y rectas costillas longitudinales que con mucha regularidad cubren la concha. Esta, en vez de aparecer todas iguales, como en el **O. originale**, presentan diferente relieve, aunque no mucho, distinguiéndose costillas principales y otras secundarias". These features are peculiar to the Kolebaba genus **Vericeras**. It is suspected that the correct identification is **Vericeras cf. ambigena** (Barrande 1867).

#### Eastern Pyrenees - Aquitaine [F]

These areas are geologically linked by the collision that allowed subduction of the southern Iberian Plate (Ebro pro-foreland basin) below the northern European Plate (Aquitaine retro-foreland basin) beyond the eastern Pyrenean axial zone (Morris, in press) in which Silurian sedimentary terranes were mixed.

Vidal (1886) in the Gerona Province and 1914 in the Upper Silurian (? Prídolí of the Catalan Pyrenees) records **Orthocycloceras? fluminense** (Meneghini 1857), **?Orthoceras distans** Barrande (probably **?Orthoceras distans** Barrande, see Sowerby in Murchison 1839), **?Rayonoceras giganteum** (Sowerby, 1819), **Cycloceras striatum** (Sowerby 1840), **O. laterale** Phillips, 1836, **O. tenuis** Wahlenberg, 1821, **Mimogeisonoceras timidum** (Barrande 1866), **O. placidum** Barrande, 1868, **Parakionoceras originale** (Barrande 1868), **Armenoceras nummularium** (Sowerby 1839).

#### Armorican Massif [G]

From this area Babin (1966) described and figured the following Silurian and Early Devonian nautiloid cephalopods: **Endoceras? sp.**, **Ormoceras puzosi** (Barrande 1866), **Ormoceras multicamerata** Babin, **Kopaninoceras jucundum** (Barrande 1870), **Arionoceras repetitum** (Barrande), **Arionoceras cf. repetitum** (Barrande, 1866), **Orthocycloceras? cf. fluminense** (Meneghini), **Temperoceras temperans** (Barrande 1867), **Harrisoceras vibrayei** (Barrande 1859), **Murchinsoniceras murchisoni** (Barrande

1867), **Dolorthoceras occidentale** Babin, **Dolorthoceras** n. sp., **Mimogeisonoceras** cf. **barbarum** (Barrande 1870), **Geisonoceratoides? bicingulatum** (Sandberger and Sandberger 1852), **Geisonoceroides? sp. 1, 2**, **Spyroceras pulchrum** (Barrande 1866), **Spyroceras calamiteum** (Münster 1840), **Calorthoceras pseudocalamiteum** (Barrande in Quenstedt 1851), **Spyroceratinae** gen. indet. **reluctans** Barrande, 1868, **Arthrophyllum vermiculare** (Termier and Termier 1955), **Arthrophyllum gracile** (Termier and Termier 1955), **Jovellania buchi** (de Verneuil 1850), **Jovellania** cf. **kochi** (Kayser, 1878, revised by Zhuravleva 1974 as belonging to **Tripleuroceras**), **Cyrthoceratites? zeileri** (Bayle 1878), and **Cyrthoceratites? sp. 1-3**.

In the Pridoli of 'la Meignanne' Kriz and Paris (1982) reported the **Cheiopteria bridgei** and **Snoopya insolita** assemblages, including **Orthocycloceras? fluminese** (Meneghini 1857), **Parakionoceras** sp. and **Orthoceratida** indet. div. spp. Babin et al. (1979) also described the nautiloid cephalopods **Arionoceras arion** (Barrande 1868) [= **A. affine** (Meneghini 1857)] and **Parakionoceras** sp. from the Pridoli of the 'Vouned Section'.

#### Montagne Noire [H]

In the southern part of the Montagne Noire M.-C. Chaubet (1937, pp. 84, 175) reports that at "Col de l'Orte" and "Combe d'Yzarne" the following nautiloids occur: **Sphooceras truncatum** (Barrande 1860), "**Orthoceras**" **pyrenaicum** Leymerie, **Vericeras barroisi** (Vidal 1914), **Michelinoceras? perstrictum** (Barrande 1867), **M. amoenum** (Barrande 1867), **Orthocycloceras? fluminese** (Meneghini 1857), **Parakionoceras originale** (Barrande 1866), the **Dawsonoceras** group of **annulatum** (Sowerby 1816), the **Kopaninoceras?** group of **cavum** (Barrande 1867), **Protobactrites** aff. **styloideum** (Barrande 1866), **Geisonoceras** aff. **gryphus** (Barrande 1868), **Chryzoceras?** or **Mimogeisonoceras** aff. **timidum** (Barrande 1866), **Metaspyroceras** aff. **subannulare** (Münster 1840), **Geisonoceras** aff. **inchoatum** (Barrande 1868), and **Arionoceras chaubete** (Ristedt 1968). Kriz (1996) also reported from this area and the nearby Mouthoumet Massif the bivalve-dominated **Cardiola agna figusi** Community, **Cardiola donigala** Community, **Cardiola docens** Community and the **Snoopya insolita** Community. Following Chaubet (1937) the ostracodes **Bolbozoe? bohémica** (Barrande), **Bolbozoe? lanceolata** Canavari, **Kloedenia** sp., several **Entomis (Richteria) migrans** (Barrande) and some telsonal parts of the phyllocarid **Ceratiocaris bohémica** (Barrande) are also present.

#### Southwestern Sardinia [I]

Upper Silurian nautiloid cephalopods of the Fluminimaggiore Formation (Gnoli et al. 1990) have been studied by Serpagli and Gnoli (1977), and Gnoli (1987, 1990, 1992c) who recognised the following nautiloids, most already described by Barrande in Central Bohemia. The following species are all described by Barrande unless otherwise noted. **Akrosphaerorthoceras gregale** Ristedt, 1968, **Hemicosmorthoceras laterculum** Ristedt, 1968, **H. aff. serratum**, **H. semiannulatum**, **Hem. sp. ind. sensu Ristedt**, 1968, **Kopaninoceras jucundum**, **Kopaninoceras? thyrus**, **Michelinoceras currens**, **M. (Shaerorthoceras) beatum** (Ristedt 1968, see also see Kiselev and Gnoli 1992), **Michelinoceras (Shaerorthoceras) teichert** (Ristedt 1968), **Michelinoceras (S.) curvum** (Ristedt 1968), **Plagiostomoceras gruenewaldti**, **Plagiostomoceras** cf. **pleurotomum**, **Calorthoceras? pseudocalamiteum**, **Orthocycloceras? cf. lynx**, **Kionoceras doricum**, **Parakionoceras originale**, **Harrisoceras vibrayei**, **Orthocycloceras? fluminese** (Meneghini, 1857), **Metarmenoceras meneghinii** Serpagli and Gnoli, 1977, **Oocerina abdita**, **Oonoceras plebeium**, **Arionoceras affine** (Meneghini 1857), **A. submoniliforme** (Meneghini 1857), **A.? repetitum**, **Merocycloceras declive** Ristedt, 1968, **Kosovoceras? sandbergeri**, **Ormoceras richteri**, **Pseudocycloceras transiens**, **Hemicosmorthoceras aff. serratum**, **Merioceras? cf. simois**, **M.? cf. sericatum**, **Plagiostomoceras culter**, "**Parasphaerorthoceras**" sp. ind. B sensu Ristedt 1968, "**P.**" sp. ind. H sensu Ristedt, 1968, "**P.**" sp. ind. J sensu Ristedt, 1968, "**P.**" sp. ind. K sensu Ristedt, 1968, **Cryptocycloceras? cf. deludens**, **Vericeras ambigena**, **Columenoceras grande** (Meneghini 1857), **C. agassizi**, **C? degener**, **C.? intermixtum**, **Geisonoceras? cf. socium**, **Murchisoniceras? calamoides**, **Sphooceras truncatum**, **Temperoceras temperans**, **Phragmoceras broderipi subleve**, **Ph. cf. labiosum**, and **Protophragmoceras minus**. In addition, according to Teichmüller (1931) some other Barrande species (e.g., **Kionoceras bronni**, **Dawsonoceras dulce** and **Oonoceras potens**) represent the southwestern Sardinian Silurian nautiloid fauna.

From these data it is evident that there is an intimate cephalopod faunal relationship with Bohemia. This link was pointed out by Serpagli and Gnoli (1977), and Gnoli (1990, 1993) also describes other faunal components (e.g., phyllocarids [**Ceratiocaris bohémica** (Barrande 1872), **C. cornwallisensis damesi** Chlupáč 1963, **C.**



**grata**\_Chlupáč 1984, **Echinocaris** sp.], eurypterids [**Pterygotus divers-Eurypterus pugio** (Barrande 1872)] and the problematic organism **Kolihaia sardiniensis** Gnoli (Gnoli and Serpagli 1984; Gnoli 1992a; 1992b). To sum up, during the Silurian, as already remarked by Kríz (1996, pp. 36-39) “good faunal affinities permit to state intimate relationships between Bohemia, Carnic Alps, southwestern Sardinia and Montagne Noire.” These affinities aid reconstruction of the Northern Margin of Gondwana during the Silurian.

From the Early Devonian of southwestern Sardinia, Gnoli (1983) described the following from various outcrops belonging to the Mason Porcus Formation (Gnoli et al. 1990): **Hemicosmorthoceras semimbricatum** Gnoli, 1983, **Kopaninoceras floweri**, Gnoli, 1983, **K.** sp. ind. A and B sensu Gnoli, 1983, **Merioceras karagandense** Zhuravleva, 1978, **Michelinoceras currens** (Barrande, 1870), **M. (M.) michelini** (Barrande 1866), **M. (S.) effrenatum** (Ristedt 1968), **M. (S.)** sp. ind. A and B sensu Gnoli, 1983, **Mimogeisonoceras** cf. **liberum** (Barrande 1870), **Mimogeisonoceras** cf. **timidum** (Barrande, 1870), **Arkonoceras?** cf. **adjectum** Zhuravleva, **Plagiostomoceras?** **squamatum** (Barrande), **P.** sp. ind. sensu Gnoli, 1983, **Akrosphaerorthoceras** cf. **gregale** Ristedt 1968, **Orthocycloceras pseudoextensum** Gnoli, 1983, **Murchisonoceras?** **subnotatum** (Barrande 1868), **Disjunctoceras** sp. ind. sensu Gnoli and Kiselev, 1994, and **Jovellania buchi** (de Verneuil 1850).

The lack of modern taxonomic revision and unsolved problems of synonymy prevent direct comparison of the Sardinian fauna with coeval assemblages from central and southern Europe (Gnoli 1983, p. 75). However, the beginning of the Devonian seems to signal a break in the close Silurian relationship between the Sardinian and Bohemian faunas.

#### Prague Basin (Czech Republic) [J]

Quite recently Kríz (1998) recognized eight recurrent events in account seven areas (ibid. figs. 1, 5) from the Middle Wenlock to the Lower Devonian. Cephalopod limestones occur in the **Testograptus testis**, **Colonograptus colonus**, upper **Saetograptus\_\_chimaera**, lower **S. linearis**, **Monograptus fragmentalis** and **M. ultimus**, upper **M. transgrediens**, and lower **M. uniformis uniformis** biozones, plus another level recovered by S. Manda (Kríz, personal commun., 2002) at the base of the **Saetograptus chimaera** Biozone.

Kríz (1998, pp. 184, 197) wrote that cephalopod limestone biofacies “usually mark a significant

change in sedimentation in a generally low-energy environment in sequences dominated by shale with micritic limestone intercalations. Deposition of the cephalopod limestone facies took place in the upper photic zone below wave base, where surface currents reached the bottom and aligned the shells of nekto-benthic cephalopods... indicating eustatic lowstands, of which most are in agreement with the standard Silurian sea-level curve (Johnson 1996). Other occurrences may be interpreted as lowstands caused by synsedimentary tectonics.” This area remains in a northern position if geographically compared to already reported localities and, furthermore belongs to the ‘Perunica’ micro paleocontinent (Havlíček et al. 1994; Havlíček 1999).

The Prague Basin has benefited from the extensive work of Barrande (1860, 1865-1874), who first described and figured more than a thousand Silurian-Lower Devonian nautiloid cephalopods. Many scientists, from the nineteenth century to now—including the author in 1999—have tried to carry out systematic revision of this giant work. However, lack of topotype Barrandian material has, thus far, prevented the development of a truly phyletic classification. The original material represents only comparable type-material useful to “routine” taxonomical work. Without judging the taxonomic validity of a number of Barrande’s taxa, the summary of Barrandian revised taxa are presented as follows.

For details see Gnoli (1999). In addition, there are a further dozen species revised by Marek (1998) and Manda (1999, 2001). A more complete report of valid genera is beyond the scope of this investigation. For example, **Cyrtoceras** Goldfuss 1832 is now divided into more than 30 cyrtochaonic-type genera. Moreover, with few exceptions, in the Barrandian literature it is very difficult to find a nautiloid cephalopod taxon not already reported in any of the Gondwanan Europe and North Africa Terranes.

#### PALEOAPULIAN CARBONATE SHELF

In this region four main Silurian-Early Devonian by cephalopod limestone biofacies can be recognized and linked to one another, including: (1) Carnic Alps, (2) Bistra Mts. in Western Macedonia (Bouček et al. 1968), (3) Suva Planina Mountains, Zebrina locality in Eastern Serbia (Kríz and Veselinovic 1974), and (4) Uppony Mt. in northeastern Hungary (Ebner et al. 1991; Gnoli and Kovács 1992).

Table 1. Summary of Barrandian to date revised taxa.

Barrande' s time genera	Total original described species	To date revised species	Dzik revised	Others revised
<b>Bactrites</b>	1	0	0	0
<b>Goniatites</b>	18	18	0	18
<b>Nothoceras</b>	1	1	1	0
<b>Bathmoceras</b>	2	2	0	2
<b>Adelphoceras</b>	2	2	1	1
<b>Cyrtoceras</b>	332	54	5	49
<b>Gomphoceras</b>	77	45	5	40
<b>Gyroceras</b>	10	4	0	4
<b>Hercoceras</b>	2	1	1	0
<b>Lituites</b>	1	0	0	0
<b>Ophioceras</b>	6	1	0	1
<b>Nautilus</b>	8	6	3	3
<b>Orthoceras</b>	563	123	9	114
<b>Endoceras</b>	3	0	0	0
<b>Phragmoceras</b>	49	14	1	13
<b>Tretoceras</b>	1	0	0	0
<b>Trochoceras</b>	49	35	7	28
<b>Ascoceras</b>	11	3	2	1
<b>Aphragmites</b>	2	1	0	1
<b>Glossoceras</b>	2	1	0	1
Totals	1140	311	35	276

### Carnic Alps [K]

Here the 'Cellon Profil,' 'Rauchkofels,' and 'Plöckengebiet' represent the best-studied Silurian sections from a stratigraphical or paleontological point of view; as well as the Kok Limestone Section on the Italian side of the Carnic Alps. Ristedt (1968) reported the nautiloid species **Merocycloceras declive**, **Michelinoceras (Sphaerorthoceras) carnicum**, **M. (S.)** spp. ind. D and F sensu Ristedt, 1968, "**Parasphaerorthoceras**" **accuratum**, "**P.**" spp. ind. A, C, D, F, and L, sensu Ristedt, 1968, **Hemicosmorthoceras laterculum**, and **H. celloni** Ristedt, 1968. At present, the author (in close cooperation with Dr. K. Histon, Geological Survey of Austria) has recognized the following Bohemian-type nautiloids (all Barrande's species unless otherwise specified) on the Italian side of the Carnic Alps (mainly from Mt. Cocco): **Michelinoceras (M.) michelini**, **Michelinoceras? (M.)** cf. **nobile**, **M.?** sp., **Kopaninoceras? cf. jucundum**, **Plagiostomoceras gruenewaldti**, **P.** sp., **Arionoceras affine** (Meneghini), **A. submoniliforme** (Meneghini), **Columenoceras** aff. **grande** (Meneghini), **Geisonoceras** sp., **Akrosphaerorthoceras gregale** Ristedt, **Calorthoceras? cf. pseudocalamiteum**, **Orthocycloceras? cf. lynx**, **Kionoceras** cf. **carminatum**, **Parakionoceras**

**originale**, **Rutoceras? mulus**, and **Oocerina** cf. **nuntius**.

Gortani and Vinassa (1909) reported other Bohemian-type nautiloids from the Carnic Alps (Italian side), among which **Michelinoceras amoenum**, "**O.**" **alticola**, **Metaspyrocera subannulare** (Münster 1840), **Oonoceras potens**, "**O.**" **pelagium**, "**O.**" **firmum**, **Michelinoceras (M.) michelini**, **Plagiostomoceras** cf. **pleurotomum**, **Dawsonoceras dulce**, "**O.**" **littorale**, and **Spyrocera pulchrum** await systematic revision. Recently, in an unpublished PhD thesis, Dr. P. Serventi reported **Hemicosmorthoceras** cf. **celloni** Ristedt 1968, **H. semimbricatum** Gnoli 1983, **H.** aff. **serratulum** Ristedt 1968, **Kopaninoceras jucundum**, **K. thyrsus**, and **Michelinoceras (Mich.)** cf. **currens**, **M. (Mich.) michelini** from the Italian side of the Carnic Alps.

Many of the above reported **Sphaerorthoceras** and **Parasphaerorthoceras**—Ristedt's species occur on the Austrian side of the Carnic Alps—plus **Kionoceras** cf. **carminatum**, **K.** cf. **electum**, **Akrosphaerorthoceras gregale** Ristedt 1968, **Sphooceras truncatum**, **Andigenoceras andigense** Kiselev, **Columenoceras? cf. duponti**, **Geisonoceras** cf. **nobile**, **G. rivale**, **Vericeras? cf. dorulites**, and some indeterminable specimens of **Armenoceras** and **Ormoceras**. These last taxa

were first described and figured by Serventi and Gnoli (2000). Serventi and Gnoli (2000) also pointed out the Silurian faunal affinities between the Carnic Alps and Central Bohemia (Perunica), with 18 of the 21 species in common. Histon (1999) revised the Silurian nautiloid cephalopods of the Heritsch (1929) collection previously collected by Stache mainly at “Kokberg” (Mt. Cocco) and stored in the Austrian Geological Survey, among which **Oocerina?** sp., **Barrandoceras** sp., **Uranoceras** sp., and **Lechritrochoceras** cf. **hoernesii** (Barrande 1865) must be added to the Carnic Alps nautiloid assemblage.

#### **Suva Planina Mountains, Eastern Serbia (Kriz and Veselinovic 1975) [L]**

“Upper Silurian (Pridolí) and Lower Devonian (Lochkovian) carbonate rocks represent the core of the Suva Planina Mountains in eastern Serbia and are exposed in the upper part of Zli Do, east of Tuponica village and the Rebrina locality near the town of Ni.” (Kriz and Veselinovic 1975, text-figs. 1, 2). In the latter area, in a little quarry, a black bituminous limestone crops out from which Bohemian-type bivalves were recovered, among with the nautiloids **Orthocycloceras?** **fluminense** (Meneghini 1857), and **Parakionoceras** sp. The detailed stratigraphic distribution of the cephalopod-bearing horizons in this locality is shown in Figure 4 after Kiselev (Kiselev, personal commun., 2002).

#### **Bistra Mountains - Western Macedonia [M]**

Bouček et al. (1968) wrote “In the mountain Bistra (2163) in Western Macedonia (the internal zone of Dinarides) near the locality named “Tonivoda.” on the right side of the road Mavrovogalicnik, the clayey slates the age of which is not yet up to now determined with certitude were developed. Over this series the fine-grained gray limestones with Devonian Crinoids are lying. In the summer of 1963 a rather rich fauna containing relics especially of nautiloid shells followed by tentaculites, badly preserved ostracodes and rarely brachiopods was developed in the layers situated over the clayey slates, the lenses or intercalations of dark gray sometimes almost black limestones”. In addition, the nautiloids **Geisonoceras** sp., **Dawsonocera** sp. and **Plagiostomoceras** aff. **pleurotomum** (Barrande) also occur. According to Bouček et al. (1968, p. 8) these Lochkovian to Pragian rocks exhibit a close relationship with the typical Bohemian fauna.

#### **Uppony(I) Mts. (Northeastern Hungary) (Gnoli and Kovács 1992) [N]**

Gnoli in Gnoli and Kovács (1992) described and illustrated the following nautiloid orthocone taxa: **Michelinoceras** (M.) **micelini** Barrande, 1866, **Mimogeisonoceras?** cf. **liberum** Barrande, 1870, **Kopaninoceras** sp. sensu Gnoli in Gnoli and Kovács, 1992, **Kionoceras?** cf. **adactum** (Zhuravleva 1978), **Leurocycloceras?** or **Dawsonoceras** cf. **dulce** (Barrande 1868) and **Columnoceras?** cf. **grande** (Meneghini 1857), all of which are Lower to Middle Ludlow in age.

#### **Ukraine - (former Podolia) continental platform [O]**

This area was investigated by Kiselev, 1982, 1995, with summaries of Balashov and Kiselev, 1968; Kiselev, Mironova and Sinitsyna, 1987, who reported the Silurian-Devonian nautiloids: **Kionoceras?** **canaliculatum** (Eichwald 1839), **K. decoratum** (Eichwald 1861), **K. loxias** (Hall 1868), **K.?** **ludense** (Sowerby), **K. neptunicum** Barrande, 1868, **K. scammoni** (McChensney 1861), **Harrisoceras** **abdium** Kiselev, 1968, **M. migrans** (Barrande 1868), **M. amoenum** (Barrande 1867), **Harrisoceras** **volkovense** Kiselev, 1968, **Mimogeisonoceras** **timidum** (Barrande 1868), **Eushantungoceras** **pseudoimbricatum** (Barrande 1870), **Brodekoceras** **dnestrovense** Balashov, 1975, **Mandaloceras** **ellipticum** (M'Coy 1854), “**Orthoceras**” **seps** Eichwald 1860, “**Cyrtoceras**” sp. ind. sensu Eichwald 1860, **Dawsonoceras** **americanum** (Foord 1888), **D. annulatum** (Sowerby 1816), **D. dulce** (Barrande 1868), **Dawsonocera** **barrandei** Horný, 1956, **D. althi** (Venjukov 1899), **D. hisingeri** (Billings), **D. kendalense** (Blake), “**Orthoceras**” **bacillus** Eichwald, 1830, **Polygrammoceras** **bullatum** (Sowerby 1839), “**Orthoceras**” **excentricum** Sowerby 1839, **Phragmoceras?** **arcuatum** Sowerby, 1839, **Gomphoceras** **pyriforme** (Sowerby 1839), **Anthoceras** **vaginatum** (Schlotheim 1813), **Protokionoceras** **multilineatum** (Venjukov 1899), **Peismoceras** cf. **asperum** (Barrande 1865), **Phragmoceras** **longum** (Barrande 1865), **Metarizoceras** **sinkovense** Balashov, 1968, **Uroniella** **cochleata** (Schlotheim 1813), **Parakionoceras?** **annulatocostatum** (Billings)—suspected to have been authored actually by Boll 1857—**Protokionoceras** **anticostiense** Foerste in Twenhofel, 1928, **P.?** cf. **virgatum** (Sowerby 1839), **Jovellania** **podolica** (Siemiradzki), **J. elliptica** (Siemiradzki), **Oocerina** **gorodokia** (Balashov 1968), **Mandaloceras?** **ellipticum** (M'Coy 1854), **Gomphoceras** **pyriforme** (Sowerby), **Bickmorites?** **rapax** (Barrande 1865), **Ormoceras?** cf.

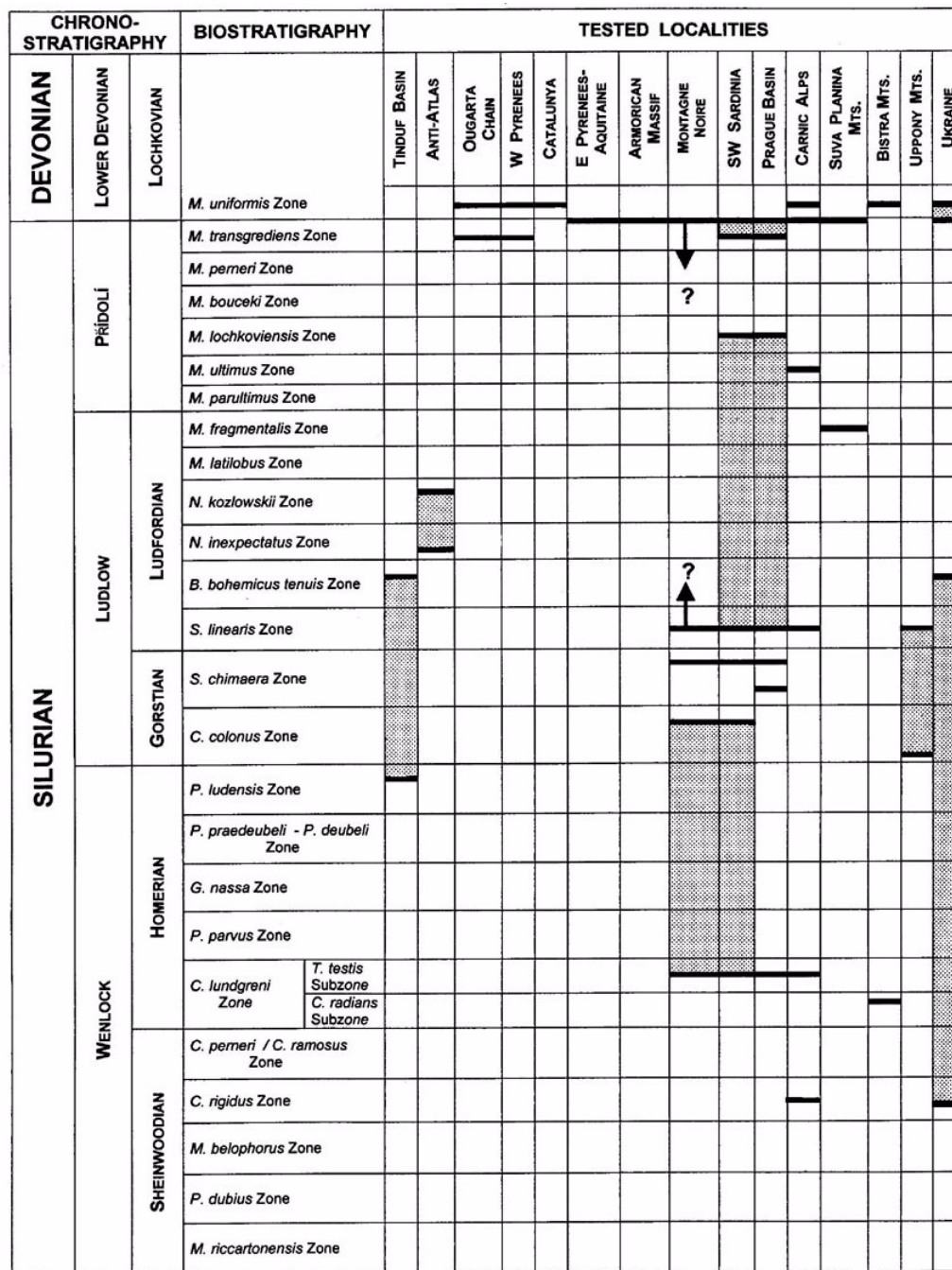
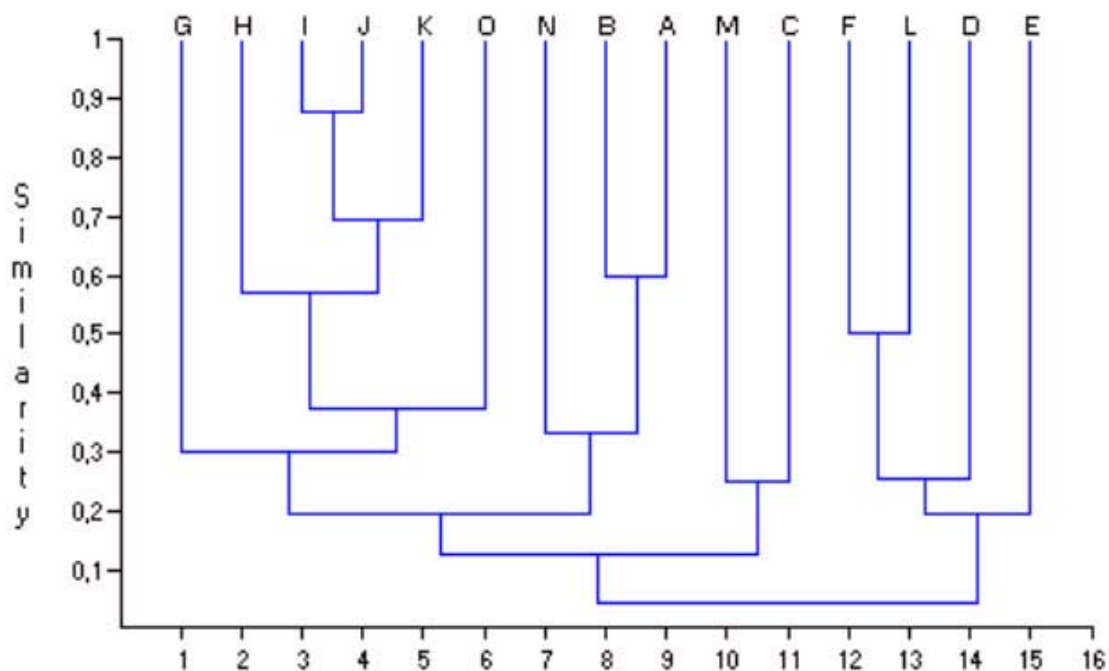


Figure 4. Stratigraphic horizons in which cephalopod Limestone biofacies are distributed, indicated by locality (after Kriz 1998 with adjustments).

*picteti* (Barrande 1868), *O. explanans* (Barrande 1867), *Metarizoceras? grave* (Barrande 1867), "Orthoceras" *roemeri* Alth, 1874, *Oonoceras? cf. nuntius* (Barrande 1866), *Oocerina? formidandum* (Barrande 1867), *Elrodoceras smotritchenense* Balashov, 1959, *Eridites astrovae* Zhuravleva, 1961, *Harrisoceras volkovense* (Balashov 1960), *Pseudorthoceras amplum* Kiselev, *Rizoceras podolicum* Balashov, 1968, *Ormoceras rashkovense* Balashov, 1968, *O.*

*seretense* Balashov 1968, *O. skalaense* Balashov, 1968, *O. dobroljanense* (Balashov 1968), *Podolicoceras giganteum* (Balashov 1968), *Umbeloceras tumescens* (Barrande 1865), *Armenoceras jupiterense* Foerste, 1928, *Bickmorites falcigerum* (Eichwald 1857), *Bickmorites podolicum* Balashov, 1975, *Gasconoceras planiventrum* Foerste, 1936, *Gordonoceras podolicum* Balashov, 1975, *Leurocyloceras bucheri* Flower, 1941, *L. brucense*



**Figure 5.** Results of a Q-mode cluster analysis based on the estimated faunal similarities between nautiloid assemblages at the 16 localities (A to O, see text for detailed locality descriptions). Binary similarities estimated using the Jaccard coefficient.

(Williams 1919), *Metaspyroceras* cf. *ruedemanni* (Foerste 1928), *Polygrammoceras restevense* Balashov, 1972, *Protokionoceras anticoste* Foerste, 1928, *P. dnestrovense* Balashov 1972, *P. multilineatum* (Venjukov 1839), and *Sphooceras truncatum* (Barrande 1860).

As outlined by Kiselev (1982, pp. 57-59) nautiloid faunas occur in the Ukraine with different assemblages in at least four stratigraphic stages: early Wenlock, mid-late Ludlow, Pridolí, and Lochkovian with a hiatus corresponding to the interval between the late Wenlock and early Ludlow. Detailed stratigraphic distribution of the cephalopod-bearing horizons in Ukraine Continental Platform are shown in Figure 4.

#### Faunal Similarity

The Raup and Crick (1979) statistical procedure was used to obtain a quantitative estimate of similarities between the different taxonomic content of these various nautiloid cephalopod faunas (Appendix I). This index ranges from 0 (no similarity) to 1 (identity). A matrix is presented with the comparisons between all pairs of associations. The Raup-Crick index (Raup and Crick 1979) uses a 'Monte-Carlo' randomization procedure, comparing the observed number of taxa occurring in both associations with the distribution of co-occurrences from 1000 random replicates.

In some localities (i.e., African and Eastern Europe) this index is very low despite the fact that the few taxa checked show identity at the species level and are also important from a stratigraphic point of view. Taking into account the value of this index for the Ukraine nautiloid assemblage, results indicate a certain similarity that can provide an idea of a possible assembling of the northern Gondwana margin belt. The median faunal similarity index (FSI) probability value of the Ukrainian Continental Platform nautiloid assemblage (shown in Appendix I in red) compared with 12 other localities corresponds to 0.482. This result appears to support the present paleogeographic reconstruction of northern Gondwana.

To further probe faunal similarity between various tested localities, a Q-mode cluster analysis was also undertaken on a matrix of faunal similarities estimated by means of the Jacard coefficient. Results are shown in Figure 5. According to this approach, the greatest faunal similarity is recorded from southwestern Sardinia and the Prague Basin (0.89) followed by Carnic Alps and the last two (0.70). These are then followed by similarity between the Tinduf Basin and Anti-Atlas (0.60), between Carnic Alps and Montagne Noire (0.58), and between Eastern Pyrenees-Aquitaine and Suva Planina Mts. (0.50) followed by all others. Without more up-to-date and homogeneous sys-

tematics, it is only possible to make further conclusions if the same scientist checks the various nautiloid assemblages from the localities in which the so-called "Orthoceras Limestone" biofacies occurs.

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