



Paleogeographic Implications of a Devonian (Givetian, Lower Varcus Subzone) Rugose Coral Fauna from the Ma'der Basin (Morocco)*

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4 Text-Figures and 11 Plates



*Morocco
Devonian
Rugose Corals
Paleogeography
Biostratigraphy*

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Paläogeographische Schlussfolgerungen aus einer devonischen Korallenfauna (Givet, untere varcus-subzone) aus dem Ma'der-Becken (Marokko)

Zusammenfassung

Eine wahrscheinlich aus der tieferen photischen Zone stammende Korallenfauna frühgivetischen Alters vom Jbel Ou Driss wird untersucht. Die Gattungen *Zonophyllum*, *Lekanophyllum*, *Siphonophrentis*, *Heliophyllum* und *Spinophyllum* werden revidiert und die neuen Arten *Zonophyllum maderense*, *Z. pegoconus*, *Lekanophyllum hollardi* und *Stringophyllum coenaubertae* aufgestellt.

Die Otsuka Koeffizienten wurden berechnet, um den Ähnlichkeitsgrad in der gattungsmässigen Zusammensetzung der Rugosa des Ma'der-Beckens im Vergleich zu derjenigen in 15 anderen Gebieten zu bestimmen. Sehr hohe Werte werden erreicht beim Vergleich mit den Gebieten Nordspanien – Pyrenäen – Vendée und Nordvogesen – Saar – Mähren. All diese Gebiete lagen wahrscheinlich auf der Gondwana-Seite des Rheischen Paläoozeans. Ein geringerer, aber immerhin hoher OK Wert zwischen dem Ma'der-Becken und der rhenohercynischen Zone deutet auf die geringe Breite des Rheischen Ozeans hin. Der Vergleich mit dem Appalachengürtel ergibt einen wesentlich geringeren OK Wert und nicht mehr als 17 % der Rugosa des Ma'der-Beckens haben ihre Vorläufer in der ostamerikanischen Faunenprovinz.

*) Geological Survey of Canada Contribution 1998256.

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Im Givet hatte die Migration der Korallen aus der ostamerikanischen Faunenprovinz aufgehört oder weitgehend nachgelassen und der Transport von Korallenlarven erfolgte wahrscheinlich in südwestlicher Richtung durch den schmalen Rheischen Ozean. Der Ähnlichkeitsgrad nimmt gegen Osten vom Ma'der-Becken entlang Nordgondwana nach Ostaustralien ab. Die Baoshan-Luxi-Mikroplatte war im Givet wahrscheinlich mit Gondwana in Verbindung oder in seiner Nähe, in einem Längenabschnitt zwischen dem nordpakistanischen Teil des indischen Schildes und Westaustralien. Der Otsuka-Koeffizient zwischen dem Ma'der-Becken und der Altay-Sayan-Einheit weist darauf hin, dass die allochthonen Gebiete mit givetischen Rugosa im Givet nicht an den Angaraschild angeschweißt waren und wahrscheinlich in einer Breite niedriger als 40° lagen.

Abstract

A probable deep, or moderately deep, photic zone coral fauna of early Givetian age is examined from Jbel Ou Driss. The genera *Zonophyllum*, *Lekanophyllum*, *Siphonophrentis*, *Heliophyllum* and *Spinophyllum* are reviewed, and the new species *Zonophyllum maderense*, *Z. pegoconus*, *Lekanophyllum hollardi* and *Stringophyllum coenaubertae* are erected. Otsuka coefficients have been calculated to determine similarities between the genus composition of the Rugosa of the Ma'der basin and those of 15 other regions.

Very high OC values are obtained from comparisons with the northern Spain-Pyrénées-Vendée and northern Vosges-Saar-Moravia regions. All these regions were likely situated on the Gondwana side of the Rheic paleo-ocean. A lesser, but nevertheless high OC value between the Ma'der basin and the Rhenohercynian zone indicates that the Rheic paleo-ocean was narrow. Comparison with the Appalachian belt gives a considerably lower OC value, and no more than 17 % of the Ma'der basin Rugosa had an Eastern Americas Realm ancestry. In Givetian time, coral migration from the EAR had ceased or was greatly reduced, and transport of coral larvae was likely in a southwest direction through the narrow Rheic paleo-ocean. Similarities decrease eastwards from the Ma'der basin along northern Gondwana to eastern Australia. The Baoshan-Luxi microplate was likely attached, or close to Gondwana in Givetian time, at a longitude between the northern Pakistan part of the Indian shield and western Australia.

The OC value between the Ma'der basin and the Altay-Sayan collage suggests that the allochthons carrying Givetian Rugosa were not accreted to the Angaran shield in Givetian time, and were likely situated at <40° latitude.

1. Introduction

From early days of the study of North African faunas, Devonian corals have played an important rôle in establishing the migration of Eastern Americas Realm genera to the Old World Realm by way of Africa (LE MAÏTRE, 1947, 1951; OLIVER, 1973, 1977; JOSEPH & TSIEN, 1977; OLIVER & PEDDER, 1989).

Identifications and figures of Middle Devonian Rugosa from northwest Africa have been published in several works (COTTREAU, 1941; LE MAÏTRE, 1947; SAMPELAYO, 1948; TERMIER & TERMIER, 1950; SOUGY, 1964; COEN-AUBERT, 1987). However, most of the illustrations are uninformative, except those of LE MAÏTRE and COEN-AUBERT, and only one of the faunas providing the illustrated material is precisely dated. This is the coral biostrome at Ouahlane (= Ouhlane), northern Ma'der basin, which was thought to be Givetian by HOLLARD (1962), but is now believed to be of Eifelian *kockelianus* Zone age (BULTYNCK, 1985, Text-Fig. 10).

In 1991, during a Subcommittee on Devonian Stratigraphy meeting, the author had the opportunity to collect a well dated Givetian, Lower *varcus* Subzone fauna (BULTYNCK, 1989) from the Jbel Ou Driss east section in southwestern Ma'der basin. A preliminary investigation of the Rugosa of the fauna revealed the presence of several new species. It also showed that before the Rugosa could provide meaningful paleogeographic data, a rigorous review of some of the genera and at least one previously described species would be necessary.

The purpose of this paper is to suggest refinements to existing knowledge of Givetian paleogeography on the basis of new coral systematics, and quantitative comparisons of the Jbel Ou Driss Rugosa with those of Givetian faunas from other regions.

2. Jbel Ou Driss Locality and Fauna

Jbel Ou Driss is situated in the Zagora graben on the southwest extremity of the Ma'der basin (Text-Fig. 1). The section known as Jbel Ou Driss est, or east, was described first in detail by Hollard (1974, p. 31, Text-Fig. 4)

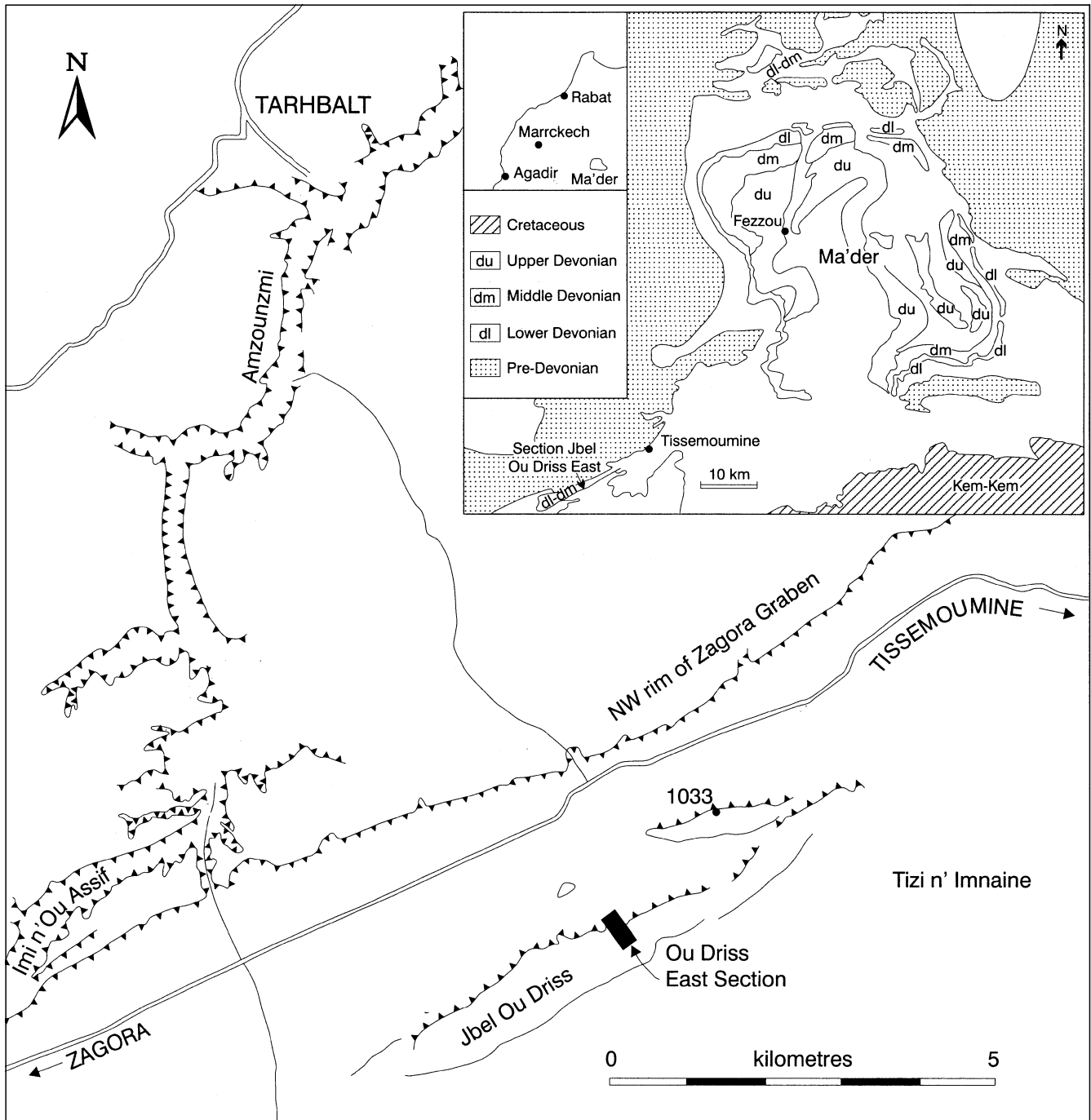
and secondly by BULTYNCK (1989), who provided conodont evidence of a Lower *varcus* Subzone age for the corals forming the basis of the present work.

Rugosa dominate the megafauna; other elements include a few brachiopods, rare tabulate corals and a phacopid trilobite. A small epifauna comprises hederelloid and other bryozoa and serpulid worms. One unoriented and unidentifiable metriophyllid coral has been seen in thin section. This, combined with the presence of a trilobite with large eyes and absence of stromatoporoids, suggest a deep, or moderately deep, photic zone environment with an unstable substrate. The presence of *Agoniatites obliquus* (WHIDBORNE, 1889) below, and *Stringocephalus* cf. *burtini* (DEFRANCE, 1824, above the coral fauna, suggests a shallowing upward sequence, and also confirms the Givetian age of the corals. In the absence of evidence from other faunal groups, the corals alone would be judged to be early Givetian age.

COEN-AUBERT (in BULTYNCK, 1989, p. 97) has published a list of determinations of the coral fauna and will describe some of its elements (pers. com., 1998). As a result of the present investigation, the fauna consists of *Zonophyllum maderense* sp. nov., *Z. pegoconus* sp. nov., *Z.* sp. indet., *Lekanophyllum hollardi* sp. nov., *Stringophyllum coenaubertae* sp. nov., *Siphonophrentis belgebaschica* (IVANIYA, 1955), *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME, 1851), *Spinophyllum* sp. nov. A, *Heliophyllum halli* subsp. undet., *Mcgeea* sp. undet. (Pl. 11, Figs. 6, 7), *Thamnophyllum* sp. indet. (Pl. 8, Figs. 1, 4) and two new corals, each represented by a single specimen, referred to as incertae sedis 1 and 2 (Pl. 8, Figs. 2, 3, 5; Pl. 9, Figs. 5, 7, 8).

For analysis of the pre Middle *varcus* Subzone age fauna of the whole Ma'der basin, *Acanthophyllum vermiculare* (GOLDFUSS, 1826) and *Calceola sandalina* (LINNÉ, 1771) should be added to the list. The first of these additions was identified in the Jbel Ou Driss east section by COEN-AUBERT; the other occurs in the well known Ouahlane section above the Eifelian coral fauna described by LE MAÏTRE (1947), and is about the same age as the Jbel Ou Driss coral fauna (BULTYNCK, 1985, Text-Fig. 10).

The only rugose corals known from the Givetian of the Ma'der basin, that are likely or could have had an Eastern



Text-Fig. 1. Location of the Jbel Ou Driss east section, redrawn from BULTYNCK (1989, Text-Fig. 1).

North Americas Realm lineage, are *Siphonophrentis belgebschica* and the subspecies of *Heliophyllum halli*. All of the others identified to species, or in the case of *Mcgeea* and *Thamnophyllum* to genus level, are of unequivocal Old World Faunal Realm origin. This also reflects in the Otsuka coefficients given in Text-Figure 2.

Three conclusions arise from this analysis:

- 1) The Eastern North Americas Realm influx into Africa, which began in Early Devonian time, had either stopped, or had considerably waned by early Givetian time.
- 2) The inferred movement of Givetian coral larvae was predominantly southwestwards in the Rheic paleo-ocean, at least as far as the present Anti Atlas of Morocco. The transporting current would be much like

Oczlon's (1990, Text-Fig. 1) south equatorial current, rather than the reverse current shown by Joseph & Tsien (1977, Text-Fig. 1).

- 3) The wide separation between northern Gondwana and Givetian Europe, including northern Spain and the Rhenohercynian zone, inferred by Van Der Voo (1988), is unlikely.

3. Comparisons with Other Regions

The methodology used for comparing the Jbel Ou Driss fauna with other Givetian faunas is the same as that outlined in a more general paper (Pegger & Oliver, 1990, p. 268). To achieve a uniform taxonomy in widely scattered regions, all genus identifications have been made with

Text-Fig. 2. Occurrences of rugose coral genera in the Jbel Ou Driss Lower *varcus* Sub-zone fauna, and Givetian occurrences of the same genera in regions compared with Jbel Ou Driss. Otsuka coefficients based on total Rugosa genera in the compared regions, except for rare small corals of the pelagic facies, which are omitted.

GENERA	REGIONS															
	APPALACHIAN BELT, E.A.R.	MA'DER BASIN, MOROCCO	N. SPAIN, PYRÉNÉES, VENDÉE	N. VOSGES, SAAR, MORAVIA	RHENOHERCYNIAN ZONE	N.W. IRANIAN PLATE	HELMAND BLOCK, AFGHANISTAN	BAOSHAN-LUXI MICROPLATE	YANGXI BLOCK, CHINA	HUANAN BLOCK, CHINA	NORTHWESTERN AUSTRALIA	EASTERN AUSTRALIA	W. URALS, NOVAYA ZEMLYA	ALTAY-SAYAN	WESTERN CANADA	GREAT BASIN, U.S.A.
<i>Zonophyllum</i>	●	●	●	●		●	●		●	●		●	●	●	●	●
<i>Lekanophyllum</i>		●		●	●				●	●		●	●	●	●	
<i>Calceola</i>		●	●	●	●	●			●			●	●	●		
<i>Stringophyllum</i>		●	●	●	●	●			●	●	●	●	●	●	●	
<i>Siphonophrentis</i>	●	●			●	●	●	●						●	●	
<i>Acanthophyllum</i>		●	●	●	●			●				●		●		
<i>Spinophyllum</i>		●	●	●	●	●	●	●	●	●		●	●	●		●
<i>Heliophyllum</i>	●	●	●		●	●	●							●	●	●
<i>Macgeea</i>		●	●	●	●	●	●	●	●	●						
<i>Thamnophyllum</i>		●	●	●	●	●	●		●	●			●	●		
<i>Incertae sedis 1</i>		●														
<i>Incertae sedis 2</i>		●														
OTSUKA COEFFICIENTS MOROCCO TO OTHER AREAS	20		51	47	44	53	46	33	35	24	12	29	30	49	24	25

standard generic diagnoses formulated or accepted by either OLIVER or PEDDER. Rugosa flourished in a limited variety of shelf habitats, so that the danger of comparing faunas of similar age and faunal province, but dissimilar facies, is less with them than with some other benthic groups. The problem can be reduced in rugosan work by removing predominantly basin dwelling genera from the faunal lists. This practice has been maintained in the current work. The binary similarity index used for the comparisons is the Otsuka coefficient (CHEETHAM & HAZEL, 1969), and is applied to genera.

3.1. Appalachian Belt, Eastern Americas Realm

Rugosa of this region have a long history of study, but much of the older descriptive work of faunas from basins west of the Appalachian belt requires revision. Nevertheless, following many modern works by W.A. OLIVER, Jr., composition of the coral faunas of the Eastern Americas Realm is well known at the genus level.

Results tabulated in Text-Figure 2 show only three genera common to both the Appalachian belt and the Jbel Ou Driss Givetian fauna, and an Otsuka coefficient value of only 20 between the regions. These are lower figures than would be expected from comparisons of Eifelian faunas of the regions. The lack of any evidence of reverse faunal migration from North Africa to the Eastern Americas Realm, in Devonian time, before opening of the Atlantic Ocean, is worth reiterating.

Easily recognised Middle Devonian coral genera such as *Heliolites*, *Mesophyllum*, *Calceola*, and whole families and sub-families such as the Stringophyllidae, Phillipsastraeiidae and the Ptenophyllinae are absent from Givetian faunas of the Appalachian belt.

3.2. Northern Spain, Pyrénées and the Vendée

Tectonics associated with the Cretaceous opening of the Bay of Biscay and consequent rotation of the Iberian Peninsula have generated considerable discussion, much of it summarised in MATHEWS (1985) and SIBUET & COLLETTE (1991). Data now favour a scissors-like movement around a pole of rotation near Bordeaux (44.6° N; 0.3° W), with sinistral motion along the North Pyrenean fault of about 80 km (SIBUET & COLLETTE, 1991). This hypothesis places the original locations of the Devonian faunas of the Cantabrian Mountains and the Pyrénées close to a small Givetian fauna from Villdé d'Ardin (LE MAITRE, 1937), which is situated south of the Massif Central suture, in the South Brittany nappes of the Vendée, (MATTE, 1991, Text-Fig. 5).

The Givetian corals from the Pyrénées are poorly preserved (JOSEPH & TSIEN, 1975), and only a few of the Givetian Rugosa from northern Spain are adequately described (BIRENHEIDE & SOTO, 1992). As these faunas are presently described, the Otsuka Coefficient between this region and the Ma'der basin is 51. However, two of the genera involved in the calculation are known from the re-

gion only in the Vendée fauna, which is a stromatoporid assemblage, and is shallower than any of the Givetian faunas from the Ma'der basin used in the calculations. If the two genera (*Dendrostella* and *Grypophyllum* s.s.) are removed from the total fauna of the region, the Otsuka Coefficient between the northern Spain-Pyrénées-Vendée region and the Ma'der basin increases to 53.

3.3. Northern Vosges, Saar, Moravia

The Vosges massif north of the Lalaye-Lubine Baden-Baden shear zone and west of the southern Rhine graben (ROUSSET et al., 1993) has provided a few small coral faunas described by FIRTION (1957). These and a meagre sub-surface fauna described by BIRENHEIDE (1976) from the Saar 1 borehole come from the Saxothuringian zone of Europe (FRANKE, 1989). In Text-Figure 2 they are combined with faunas from the Moravian sedimentary basin, which is presently situated east of the Bohemian massif, and separated from it by the Moldanubian thrust. The south-east border of the Moravian sedimentary basin at surface is the Carpathian segment of the Alpine front, and its northeastern margin is the Elbe-Dobrogea fracture. Since the possible eastern extension of the Saxothuringian zone is on the other side of the Elbe-Dobrogea fracture, in the West Sudetes of Poland (FRANKE et al., 1993), the combining of these various coral faunas is not entirely satisfactory. However, they could not have been separated by any great distance in Givetian time, since all were situated between north Gondwana and the Rheic paleo-ocean.

The best known Devonian rugose coral fauna from the Moravian sedimentary basin is the Celochovice fauna described by KETTNEROVÁ (1932). Its age has been debated for some time, but on the evidence of tentaculites is Givetian (LUKES, 1993). Other Rugosa from the basin have been described by GALLE (1981, 1984, 1993). The high Otsuka coefficient of 47 obtained from a comparison of these faunas with those of the Ma'der basin is consistent with their geographical positions indicated by the SCOTESE Givetian map (GOLONKA et al., 1994).

3.4. Rhenohercynian Zone

The Southern border of this zone is the line of nappes of the mid-German crystalline rise. In Givetian time, the effective northern border of the seaway occupying the zone was the Old Red Continent. HOLDER & LEVERIDGE (1986) emphasised the tectonic continuity of the zone prior to disruption along the major late Carboniferous dextral shear known to them as the Bristol Channel-Bray fault (also known as the Severn-Wight lineament). In light of LE GALL'S 1991 publication, HOLDER & LEVERIDGE'S synthesis is oversimplified. Nevertheless, if the probable 150 km dextral movement along the Elbe-Dobrogea fracture is reversed to restore the eastern part of the zone and the Holy Cross Mountains to their original Givetian positions relative to each other, the fossiliferous marine Givetian rocks of the Rhenohercynian zone extend almost 2000 km from the eastern coast of the present day Celtic Sea to south central Poland.

Historically this is the most important area for the study of Middle Devonian corals, as it includes the faunas of the Ardennes massif and Rheinisches Schiefergebirge. BIRENHEIDE (1978) constitutes a useful résumé of the coral literature covering it, which is too big to be mentioned in detail. Many of the subsequent works of note are referred to in the systematic section of this work.

The Otsuka value of 44 shown in Text-Figure 2 is, as expected from the SCOTESE (in GOLONKA et al. 1994) maps, less than that between the Ma'der basin and northern Spain. Also as expected, it is less than the Otsuka coefficients between the Ma'der basin and the Northwestern Iranian plate and the Helmand block, which were both attached to Gondwana in Givetian time.

3.5. Northwest Iranian Plate

In the Devonian, the Northwest Iranian plate was part of northern Gondwana. It separated from Gondwana as part of the Cimmerian continent in late Permian to early Triassic time, and by late Triassic had become accreted to Laurasia. During the Jurassic, it was pulled away from Laurasia by tectonics associated with rotation of the Lut block and movement along the Sanandaj-Sirjan zone, approximately along the line of the Zagros suture, which currently separates the Northwest Iranian plate from the Arabian shield (ŞENGÖR et al., 1988). Mesozoic separation of the Northwest Iranian plate from Laurasia led to the opening of the small Sevan-Akera-Qaradagh ocean (ŞENGÖR et al., 1988), but by the end of Cretaceous time, this ocean had closed (LOMIZE, 1987). The resulting suture now forms part of the northeastern margin of the Northwest Iranian plate. Other boundaries of the plate are shown in ŞENGÖR et al. (1991, Text-Fig. 9) and ZONENSHAIN et al. (1991, Text-Fig. 149).

Although a few Givetian Rugosa have been described from the east Elburz part of the plate (GHODS, 1982), most of the described Devonian corals from the plate are from Armenia, near the extreme northwestern edge of the plate (SOSHKINA, 1952; ULITINA, 1968; SYTOVA & ULITINA, 1974). SPASSKIY'S (1983) analysis of Devonian corals from the area shows that many of the non-cystimorph corals have yet to be described. Coral workers sometimes refer to these Armenian faunas as the Trans-Caucasus faunas, but it may be important to note that they are not on the Trans-Caucasus plate of LOMIZE (1987) and others.

The Otsuka coefficient between the Givetian rugose faunas of the Northwest Iranian plate and the Ma'der basin is 53, and is equalled only by the coefficient obtained by the comparison of Spain and the Pyrénées with the Ma'der basin.

3.6. Helmand Block, Afghanistan

This small block is almost triangular in shape, reflecting squeezing against the Pamir syntaxis. On the northwest and east it is bordered by the Panjao (Waser) and Charman (Waziristan) sutures. To the south it is separated from the Makran accretionary complex by an ophiolitic belt (TAPONNIER et al., 1981); to the west, a flysch trough and strike-slip faults separate it from the rotated Lut block of central Iran (SBORSHCHIKOV, 1980).

The Helmand block is part of ŞENGÖR'S (1984) Cimmerian continent, and as late as early Triassic, likely remained attached to Gondwana between Arabia and India (ŞENGÖR et al., 1988; SCOTESE in GOLONKA et al. 1994). Thus, the paleogeography of its Devonian faunas is unequivocal.

Givetian corals of the Helmand block come from sections west and northwest of Ghazni. Some have been described by BRICE (1970); others are under study by J.-C. ROHART, who provided preliminary identifications for MISTIAEN (1985). The author is privileged to have been shown some of these collections in Lille. The Givetian faunas are

notable for having no *Calceola* and few cystimorphs, and may be younger than the Jbel Ou Driss fauna. Despite any discrepancy of age, the Otsuka coefficient of 46 between the two regions is high. Another interesting feature of the Helmand corals is a late occurrence in the Samersang section of *Siphonophrentis* associated with early Frasnian brachiopods of BRICE's biozone 6.

3.7. Baoshan-Luxi Microplate

Tectonic history of the narrow Baoshan-Luxi microplate is not well known, although it is now probable that the microplate is not part of the Shan Thai or Sibumasu terrane of older work. The Eifelian rugose coral faunas of the Paddukpin biostrome of Myanmar (AUNG, 1995) are believed to be on the Baoshan-Luxi microplate, but plate boundaries in Myanmar are only vaguely known. In western Yunnan, the Baoshan-Luxi microplate is bounded on the west by the Nu Jiang suture and on the east by the Kejie suture. CHEN & AI (1984, Text-Fig. 1) show the Kejie suture merging with the Changning-Shuanjing suture, and show the Changming-Shuanjiang suture terminating against the Nu Jiang suture. This interpretation places the Givetian coral fauna of the Baoshan-Shidian area of western Yunnan near the present northern edge of the microplate. GUO (1985) and JAHNKE & SHI (1989, Text-Fig. 1c), on the other hand, show the plate to extend several hundred km northwards, towards the East Qiangtang block.

Upper Devonian conodonts have been reported from the topmost Heyuanzhai Formation in the Baoshan area (TAN et al., 1982, p. 204). The same authors reported the presence of *Polygnathus varcus* and *Nowakia# otomari* lower in the upper part of the formation, and there is no reason to doubt that the rugose corals described by WANG (1994) from the Upper Heyuanzhai Formation are Givetian. However, the absence of cystimorph corals and *Stringocephalus* from the fauna and the presence of *Phillipsastrea hennahi*, suggest that it is younger than the Jbel Ou Driss fauna.

FANG & FAN (1993) concluded from paleomagnetic investigations that Baoshan was at 38° S during the Middle Devonian. This suggests that it may have been attached to northern Gondwana, but WANG HONGZHEN et al. (1989, Text-Fig. 27) show it (labelled Bb in their figure) separated from Gondwana in Lower Devonian time, as one of a group of plates comprising their Southeast subprovince. This subprovince seems to include fragments of the Cimmerian continent of ŞENGÖR (1984, 1987) and others. The most satisfactory conclusion to be drawn from the available data is that the Baoshan-Luxi microplate was situated close to northern Gondwana in Givetian time, at a longitude between the northern Pakistan part of the Indian shield and western Australia. The Otsuka coefficient of 33 obtained from a comparison of the Baoshan and Jbel Ou Driss rugose faunas, and the data presented by WANG XUNLIAN et al. (1996) are entirely compatible with this conclusion.

3.8. Yangzi Block

HSÜ et al. (1988), HSÜ et al. (1990) and ŞENGÖR et al. (1988) contend that the old concept of a South China platform is false and that the region is a collage of three continental blocks, named Yangzi, Huanan and Dongnanya, separated by the Banxi-Nanpanjiang and Gunanhai sutures. They believe the Yangzi and Huanan blocks to have been separated by ocean from late Proterozoic to at least Permian time. DOBSON & HELLER (1992) cited works

supporting this postulate, and speculated that a Jurassic remagnetisation of Carboniferous sediments on the Huanan block may have been associated with the collision and suturing of the Yangzi and Huanan or North China blocks. Although, at present, there is little evidence from coral studies to support or deny these views, the author's data base keeps the Yangzi and Huanan coral records separate. No Devonian coral is known from the Dongnanya block.

Givetian Rugosa faunas from the Yangzi block compiled for Text-Figure 2 come mostly from near the edges of the present block boundaries in the Longmenshan area of Sichuan, the Poshi area of Yunnan and the Dushan area of Guizhou. Many authors have been involved in the description of these faunas. No fauna of the Qinling fold belt is included in Text-Figure 2. The Givetian Otsuka coefficient between the Yangzi block and Morocco is 35, and is noticeably higher than the value of 24 between the Huanan block and Morocco.

3.9. Huanan Block

The present approximate margins of the Huanan block in China are shown in HSÜ et al. (1990, Text-Fig. 4). The block extends into northern Vietnam as far as the Red River (Song Hong) fault, which currently has a sinistral dislocation of about 400 km. Earlier suggestions that the block may extend south as far as the Song Da fault, have been refuted (REN & JIN 1995).

Givetian coral faunas of the Huanan block occur at many localities in Guangxi, and at least two occurrences are known in northern Vietnam. Principal authors of the descriptions of these faunas are YOH (1937), JIA in JIA et al. (1977), YU et al. (1974) and YU & KUANG (1983). The reason, or reasons why the value of the Otsuka coefficients for the Huanan and Yangzi blocks differ so much in Text-Figure 2 are not known. Perhaps it is related to the suspected separation of the two blocks in Givetian time; a direct comparison of the Chinese faunas is warranted to test this.

3.10. Northwestern Australia

The author is familiar with a total of only six platform dwelling rugosan genera from the Canning and Carnarvon basins of western Australia. Since these genera were undoubtedly autochthonous on the Australian part of Gondwana, it is assumed that the low Otsuka coefficient of 12 between the region and the Ma' der basin, is a distortion due to the low number of genera involved.

3.11. Eastern Australia

Two of three principal sources for Givetian Rugosa in eastern Australia are the Broken River embayment and Burdekin basin in the Townsville hinterland of northern Queensland. Faunas of these areas occur in intracratonic basins and were autochthonous on Gondwana. The other important source of Givetian corals in eastern Australia is in limestones exposed around the Timor anticline of New South Wales. These limestones were laid down on the exotic Gamilaroi terrane, which likely was not accreted to the Australian craton until Late Devonian time (FLOOD & AITCHISON, 1992). The New South Wales and Queensland Givetian Rugosa are currently 1500 km apart, and may have been separated by greater distances in Givetian time. Nevertheless, they are remarkably similar, sharing the

same endemic genera, such as *Amaraphyllum*, *Blysmatophyllum* and *Sanidophyllum*, and many of the same absentees, including the entire Phillipsastraedidae and Siphonophrentidae.

The Burdekin basin Givetian Rugosa are well known from the works of HILL (1942), ZHEN (1994) and ZHEN & JELL (1996). Coral faunas from Broken River have not been published, and those of the Timor Limestone have been studied only in a preliminary fashion (PEDDER et al., 1970). As expected from Australia's Givetian position at the eastern end of Gondwana, the Otsuka coefficient of 29 between the region and the Ma'der basin, is less than the coefficients between the Ma'der basin and any other northern Gondwana region with large Givetian faunas.

3.12. Western Urals and Novaya Zemlya

In Givetian time, marine faunas now exposed on the western slopes of the Uralian fold belt were allochthonous on the margin of the East European craton, facing the Uralian paleo-ocean. Presently, the Devonian faunas of southern Novaya Zemlya are almost 2000 km north of the southernmost Devonian faunas of the Urals. But in the Givetian, when the present east-west direction on the East European craton was closer to a north-south direction, not only would connected marine platforms have existed between Novaya Zemlya and the western slopes of the Urals, but Novaya Zemlya would have been at only a slightly higher latitude than the western Urals (GOLONKA et al., 1994, Text-Figs. 23, 24).

Most of the description of Givetian Rugosa from the region has been accomplished by SOSHKINA (1949, 1952), SPASSKIY (1955) and TSYGANKO (1981), although it should be noted that these authors included Eifelian corals from the Afonino Horizon and correlatives in the Givetian (KHALYMBADZHA & CHERNYSHEVA, 1990). The present author is very fortunate to have been shown important collections from Novaya Zemlya by G.K. LAKHOV in St. Petersburg.

For Givetian Rugosa, the Otsuka coefficient between the western Uralian fold belt, combined with Novaya Zemlya, and the Ma'der basin is 30, very similar to that between eastern Australia and the Ma'der basin. Nevertheless, in Givetian time, the western Urals and Novaya Zemlya, and eastern Australia were sufficiently separated in opposite hemispheres to have had a mutual Otsuka coefficient of no more than 44.

3.13. Altay-Sayan

Altay-Sayan is a large (approx. 1000 km²) Altaid collage (ŞENGÖR, 1987), bordered on the northeast by the Angaran shield, on the southeast by the Tuva-Mongolian microcontinent, and on the southwest by the Irtysh suture. To the northwest it is overlain by post Paleozoic cover. Most of the collage lies in south central Russia, but parts extend into northeastern Kazakhstan, the Altai Shan of China, and western Mongolia. A large Russian literature, authored mainly by IVANIYA (1955–1988) and BULVANKER (1958), is devoted to Devonian corals of the collage occurring in the Tom-Kolyvan fold zone, Kuznetsk basin (Kuzbass), Salair, the Minusa and Uymen depressions and the Gorny, Rudny and Mongolian Altay zones.

The paleogeography of these coral faunas is disputed. On the early maps of SCOTSE (Q in PEDDER & OLIVER, 1990, Text-Fig. 1) they were located at about 45°–50° N latitude, on the edge of the Angaran shield. However, it is not likely that large rugosan faunas would have flourished at such a

high latitude (PEDDER & OLIVER, 1990, p. 270), especially as no Devonian rugosan fauna existed at comparable southern latitudes. According to subsequent SCOTSE maps (SCOTSE & MCKERROW, 1990; GOLONKA et al., 1994), the Altay-Sayan Givetian Rugosa would still be autochthonous on the Angaran shield, but would be situated at about 40°–45° N.

More recently, ZONENSHAIN et al. (1991) have provided a tectonic synthesis and palinspastic reconstructions for Altay-Sayan. Their review suggests that, with the exception of a single described species from the Minusa depression, none of the Devonian Altay-Sayan corals was autochthonous on the Angaran shield. ZONENSHAIN et al. also note that the consumption of the Paleosianic ocean floor between the Angaran shield and Kazakhstania began in the Middle Devonian, and was not completed before Late Carboniferous. In their reconstructions, the part of Angaran shield to which the allochthons bearing most of the Devonian Altay-Sayan coral faunas became attached, was at less than 40° N latitude at the time of accretion. If this and other aspects of the synthesis are correct, the original latitudes of the large Givetian faunas of the Altay-Sayan would have been less than 40° N.

The Otsuka coefficient value of 49 between Altay-Sayan and Ma'der basin Givetian rugosan faunas is high, and obviously favours the lower Devonian latitudes suggested by ZONENSHAIN et al. for Altay-Sayan. The Givetian occurrences of *Siphonophrentis belgebasschica* in both the Altay-Sayan and along northern Gondwana resemble the disjunct distributions of some modern Indo-Pacific scleractinian species (VERON, 1995, Text-Fig. 65).

3.14. Northwestern Canada

Many surface and subsurface Givetian faunas are known from the northwestern part of the North American craton. Lists assembled for the construction of Text-Figure 2 include faunas from northern Saskatchewan and the Manitoba Devonian outcrop belt, in addition to numerous faunas from areas shown by MCLEAN (1997, Text-Fig. 1). Rare Givetian corals from the Canadian Arctic Archipelago are not included. Most of the western Canadian Givetian Rugosa are undescribed; a summary of those that have been described has been given by MCLEAN (1997).

The absence of *Calceola*, *Acanthophyllum* and any phillipsastraedids from the Middle Devonian of the North American craton, and the presence of several unusual cystimorphs and cyathophyllids in western Canada, are partly responsible for the low Otsuka coefficient of 24 shown for western Canada in Text-Figure 2.

3.15. Great Basin, U.S.A.

Most of the Givetian Rugosa of this region come from the Lower *varcus* and Upper *disparilis* Subzones in the Denay Limestone of Nevada. Others are from less precisely dated levels in the Woodpecker Limestone of the same state, and the Oñate Formation of New Mexico. A few of these corals have been described by MERRIAM (1974a) and SORAUF (1987); larger faunas are under study by the present writer.

4. Conclusions

In early Givetian time, only three rugose coral genera were common to the Appalachian belt of the Eastern Americas Realm and the Jbel Ou Driss rugosan fauna; and

Otsuka coefficient between the two regions for the same time is only 20. Of 12 early Givetian species of platform dwelling Rugosa present in the Ma'der basin, four have definite, and four have probable Old World Realm ancestry, and only two have possible Eastern Americas Realm ancestry; the ancestry of two is equivocal. This indicates that the migration of Devonian corals from the Appalachian belt to Morocco, which began in Early Devonian time, had ceased, or was dramatically reduced by early Givetian time. There was no detectible reverse migration of corals from North Africa to the Appalachian belt. Although it must have been possible for coral larvae to travel southwestwards through the narrow Rheic paleo-ocean, to at least as far as the present Anti Atlas, on currents similar to OCZLON's (1990) south equatorial current.

Wide separation of northern Gondwana from Givetian Laurasia, suggested by an earlier paleomagnetic study, is unlikely in view of the high Otsuka coefficients between the Ma'der basin and northern Spain, Pyrénées and the Vendée (51), the northern Vosges, Saar and Moravia (47) and the Rhenohercynian zone (44).

There was faunal continuity along the northern margin of Gondwana in Givetian time. The similarity between regions and the Ma'der basin declined eastwards from Morocco. Otsuka coefficients between the Ma'der basin and the Northwestern Iranian plate, the Helmand block of Afghanistan and eastern Australia are 53, 46 and 29 respectively.

Compared with the Ma'der basin, the Baoshan-Luxi microplate has an Otsuka coefficient value of 33, suggesting that if it is of Gondwana origin as Chinese workers suppose it to be, it was likely positioned close to the present northern Pakistan part of the Indian shield, between the Helmand block and Australia.

Contrary to early paleogeographic maps, parts of the Altay-Sayan Altaid collage carrying abundant Givetian rugose coral faunas were not attached to the Angaran shield in Givetian time. A more recent interpretation of the tectonic history of the collage presented by ZONENSHAIN et al. (1991) places the latitude of the Givetian coral faunas of the Altay-Sayan at less than 40° N, which is compatible with the degree of similarity between the Altay-Sayan and Ma'der basin faunas.

5. Systematic Paleontology

Specimens with catalogue numbers prefixed with the letters GSC are deposited in the Geological Survey of Canada type collection, located in Ottawa.

Order: Cystiphyllida NICHOLSON, 1889
(in NICHOLSON & LYDEKKER, 1889)
Suborder: Cystiphyllina NICHOLSON, 1889
(in NICHOLSON & LYDEKKER, 1889)
Family: Cystiphyllidae
MILNE EDWARDS & HAIME, 1850

Remarks: An excellent review of efforts to classify Lower and Middle Devonian cystimorph corals has been given by ULITINA (1968, p. 10–16). From the 1920s to 1960s several attempts to establish lineages led to various concepts of cystimorph families and subfamilies. Since the early 1970s, BIRENHEIDE's 1964 and 1968 works, together with WEYER's 1971 contribution, which removed the genus *Plasmophyllum* from the Cystiphylli-

dae, have provided new foundations for cystimorph taxonomy. Although BIRENHEIDE's publications have strongly influenced modern taxonomic studies in western Europe, to workers outside western Europe his two principal cystimorph subgenera evidently appear excessively lumped (ULITINA, 1968; MCLEAN, 1976; SPASSKIY, 1977; HILL, 1981; OLIVER & SORAUF, 1981; TSYGANKO, 1981; PEDDER, 1985; SCRUTTON, 1985; LIN et al., 1995). And there is suspicion that the quadrinomial taxa employed by BIRENHEIDE are more cumbersome than phylogenetically precise.

Since there has been so little agreement on phylogenies within the Cystiphyllidae, subfamilies are not recognized in the present work. Genera used are refined "operational" genera, which may be polyphyletic.

Genus: *Zonophyllum* WEDEKIND, 1924

- e.p. 1924 *Zonophyllum* – WEDEKIND, p. 12.
1924 *Zonophyllum* (*Legnophyllum*) – WEDEKIND, p. 19.
1963 *Patridophyllum* – ULITINA, p. 5, 11, 12, 15 (nomen nudum).
e.p.? 1966 *Patridophyllum* – ULITINA in SYTOVA & ULITINA, p. 207 (nomen nudum).
1968 *Patridophyllum* – ULITINA, p. 86.
1977 *Dansikophyllum* ULITINA – SPASSKIY, p. 134, non ULITINA, 1963.

Type species (LANG et al., 1940, p. 142): *Zonophyllum duplicatum* WEDEKIND, 1924, p. 14, Text-Figs. 6–8. Nohn-er Horizon, now the lower Nohn Formation, lower Eifelian; Nohn, Hillesheim syncline, Eifel region of Germany. Species revised by BIRENHEIDE (1978, p. 176, Text-Fig. 111a-e).

Diagnosis: Genus of solitary cystiphyllid corals. Septal cones thin in type species, thick in others, more centred than excentric, typically not fully fused in early stages. Septal crust non septate or septate adaxially. Marginal septal skeleton weak, comprising short spines, and in some species, very minor septal crests.

Remarks: *Zonophyllum* is difficult to interpret, principally because WEDEKIND's meagre material of the type species forced BIRENHEIDE (1968, p. 12) to choose a single transverse section of an immature stage to serve as a lectotype. BIRENHEIDE's 1978 interpretation of the type species united *Z. primum* WEDEKIND, 1924, *Z. cylindricum* WEDEKIND, 1924, *Z. caducum* WEDEKIND, 1924, and much of BIRENHEIDE's less strict 1964 interpretation of *Cyathophyllum antilimbatum* QUENSTEDT, 1879, with *Z. duplicatum*, and is completely plausible.

By designation of LANG et al. (1940, p. 76), *Z. cylindricum* is the type species of *Legnophyllum*. The holotype of *Z. cylindricum* is likely to be a topotype of *Z. duplicatum*.

Previously, PEDDER (1985, p. 291) and PEDDER & MURPHY (1997, p. 346) used *Lythophyllum* WEDEKIND (1925, p. 32) in a broad sense for solitary species that had commonly been placed in *Cystiphyllodes* CHAPMAN, 1893, p. 46, non YOH, 1937, p. 53. The reason for this was that the neotype (designated and figured by MCLEAN, 1976, p. 7, Pl. 1, Fig. 1; Pl. 2, Figs. 2, 3; Pl. 3, Fig. 2) and all other specimens of *C. aggregatum* BILLINGS, 1859 (p. 137, Text-Fig. 28), which is the type species of *Cystiphyllodes*, are phaceloid. Now, the present author believes his previous interpretation of *Lythophyllum* to be too broad. And in any case, *Nardophyllum* WEDEKIND (1925, p. 36), which was regarded by HILL (1981, p. F120) and PEDDER (1985) as the junior synonym of *Lythophyllum*, was, in fact, the correct genus to have used. BUL'VANKER (1958, p. 30),

SPASSKIY (1960b, p. 33), and ULITINA (1968, p. 55) all, as earlier revisers, had removed *L. marginatum* WEDEKIND, 1924, the type species of *Lythophyllum*, to *Nardophyllum*, thus making *Nardophyllum* the senior synonym (I.C.Z.N., 3rd edit., 1985, Art. 24). Current data concerning the type species of *Lythophyllum*, its objective synonyms, and *Nardophyllum* and *Plagiophyllum* WEDEKIND & VOLLBRECHT (1931, 1932) have been given previously (PEDDER, 1985, p. 293). All these genera should be placed under *Nardophyllum*, and distinguished from *Zonophyllum* by their distinctly excentric and asymmetric septal cones, which are commonly only semicones, open to the concave side of the corallum.

Patridophyllum has *P. paternum* ULITINA, 1968, p. 86, Pls. 18, 19, for type species. The species is rare and apparently confined to outcrops on Arpa River, near Danzik village, on the Armenian part of the Northwest Iranian plate. ULITINA considered it to be an upper Eifelian species, but MAMEDOV (1983, Fig. 5), SPASSKIY (1983, Table 1) and MAMEDOV & RZHONSNIYSKAYA (1985, Text-Fig. 1) indicate that it is restricted to the uppermost beds of the Lower Sharur Suite. Conodonts date this part of the Sharur Suite as lower Eifelian *partitus* Zone (EIKHGORN et al., 1983, Table 2; MAMEDOV & RZHONSNIYSKAYA, 1985, Table 1). ULITINA believed *Patridophyllum* to be a primitive digonophyllid genus linking the Digonophyllidae to *Nardophyllum*, which was put in the Lythophyllidae in 1968 (Dansikophyllidae in 1963). It seems that regardless of whether this proposed lineage is correct, the type species of *Patridophyllum* is much closer to *Zonophyllum* than to *Digonophyllum*, or any closely related genera.

On page 15 of the printed abbreviated version of ULITINA's (1963) dissertation, it is clearly indicated that *Dansikophyllum* is a nomen novum for *Lythophyllum* WEDEKIND, 1925, non MÜLLER, 1859. As such, *Dansikophyllum* is an objective synonym of *Wedekindophyllum* STUMM, 1949, and a subjective synonym of *Nardophyllum* WEDEKIND, 1925. However, ULITINA also indicated that the genus was being used for species that differed from the colonial genus *Cystiphyllodes* CHAPMAN, 1893, by being solitary, which conceptually makes it a subjective synonym of *Zonophyllum* not *Nardophyllum*. Subsequently, ULITINA abandoned *Dansikophyllum* in favour of *Cystiphyllodes*. SPASSKIY (1977) attempted to re-establish *Dansikophyllum*. His intent was to use it for solitary species that other workers had assigned to *Cystiphyllodes*, and to this end, claimed *Lythophyllum corneolum* WEDEKIND & VOLLBRECHT, 1932, for its type species. But he attributed the genus to ULITINA, 1963. The same taxonomic procedure was adopted by IVANIYA & CHEREPNINA (1986, p. 70), although they romanised the name to *Dansicophyllum*. However, as noted, *Dansicophyllum* ULITINA, 1963, must have the same type species as *Lythophyllum* WEDEKIND, 1925, which is *L. marginatum* WEDEKIND, 1925, p. 32, 33, Pl. 6, Figs. 32, 33. *L. marginatum* is a species of *Nardophyllum*, whereas WEDEKIND & VOLLBRECHT's many excellent illustrations of *L. corneolum* show it to be a typical example of *Zonophyllum*.

MCLEAN (1976, p. 12) stressed the presence of generally long and usually fused marginal spines in his diagnosis of *Zonophyllum*. This led to the opinion that *Cystiphyllodes* YOH, 1937, non CHAPMAN, 1893, and *Zonophyllum* (*Neozonophyllum*) ULITINA, 1968, p. 52, are synonymous with *Zonophyllum*. However, BIRENHEIDE'S (1978, p. 177) description of *Z. duplicatum* includes the statement "short septal spines on the dissepiments (with or without stereome)

almost absent to rare". For the moment, it seems preferable to refer *Zonophyllum*-like species having little septal crust but well developed marginal spines to *Neozonophyllum*.

Zonophyllum maderense sp. nov.

(Pl. 1, Figs. 1–16, 19, 20)

Type series: Holotype, GSC 116623. Seven paratypes, GSC 116624–GSC 116630.

Diagnosis: Small species of *Zonophyllum* with maximum adult diameter <14.0 mm. Septal cones up to 3.0 mm thick, generally well centred, but progressively thinned toward one side of the corallum. Septal spines very weak, rare, absent from most specimens.

Description: Corallum small, solitary, ceratoid, with relatively prominent growth rings and abundant, very minor rejuvenescences. Rejuvenescences commonly result in slight changes of growth axis, giving the corallum an irregular appearance. Calice preserved in only one available specimen (GSC 116628); calicular rim narrow, rounded; calicular pit irregularly funnel-shaped, depth suggested by the cones in longitudinal sections about 8–15 mm. Where not adhered to a septal cone, thickness of outer wall 0.1–0.8 mm. No radiform process in type series. Largest mean diameter 13.8 mm; length of largest corallum, measured along the convex side before sectioning, estimated to be in the order of 35 mm. Septal cones abundant, well centred, up to 3.0 mm thick, but generally progressively thinned toward one side of the corallum; some occupy the full width of the corallum. Most cones, including all those of the holotype, appear as non trabeculate, continuous, structureless stereome that does not degenerate abaxially into either crests or spines. Upper surfaces of cones in two specimens, (GSC 116626, GSC 116628) denticulate, apparently caused by projecting tips of spines, or bases of short, blunt spines.

Horizontal skeletal elements supporting septal cones poorly differentiated. Presepiments, including some that are elongate, greatly outnumber flatter plates locally present in the periaxial region. Number of presepiments counted over a vertical distance of 10.0 mm, close to the periphery of the corallum, 4–16, commonly 6–10.

Remarks: The new coral is unlikely to be confused with any previously established species. Its septal cones are not excentric as they are in species of *Nardophyllum*. Nor are its changes in growth axes as great as in the species for which the genera *Skoliophyllum* and *Praenardophyllum* were intended.

The almost uniform small size of the corallum and the prominent, weakly or non spinose septal cones are distinctive features of *Zonophyllum maderense*. Somewhat similar cones have been figured in *Cayugaea hispanica* BIRENHEIDE & SOTO, 1981 (p. 263, Pl. 3, Figs. 17, 18) from the upper Emsian and possibly lower Eifelian of the Cantabrian Mountains, and in a paratype of *C.(?) transitoria* STUMM, 1968 (p. 69, Pl. 2, Figs. 5, 6) from the Givetian of Ohio. However, the Spanish and American species are larger with maximum diameters of 25 and 27 mm, and their cones are excentric and relatively thinner than those of *Z. maderense*. Furthermore, *Cayugaea hispanica* has a deeper calice (>17 mm deep) with steeper sides and a narrower less rounded rim, while "*C.*" *transitoria* is much more clystose than the new species.

Three transverse sections of corals identified by FENTON & FENTON (1938, p. 232, Pl. 24, Figs. 4, 5, 7) as "*Cystiphyllum*" *conifollis* (HALL, 1877), from the Givetian Moscow Formation of New York, resemble *Zonophyllum maderense*. *Cyathophyllum conifollis* HALL, 1877, Pl. 30, Figs. 3–9, from Bosanquet, Ontario, as well as Moscow, New York, has been listed often in the literature, recently as a species of *Cystiphyllodes* (e.g. OLIVER & SORAUF, 1981, p. 103; BAIRD & BRETT, 1983, p. 444), but was never described by HALL. Nor has the species received modern taxonomic treatment other than that accorded it by FENTON & FENTON (1938). HALL's most informative illustration (1877, Pl. 30, Fig. 7) together with FENTON & FENTON's other illustrations (1938, Text-Fig. 20, Pl. 24, Fig. 6) and MA's (1956, Pl. 29, Fig. 1; Pl. 30, Fig. 1; Pl. 31, Fig. 3a, b; Pl. 59, Figs. 1–11) numerous figures, all apparently of corals from the Moscow Formation of New York, show "*Cystiphyllodes*" *conifollis* to be a much larger species than *Z. maderense*, and to have many presepiments and septal spines.

BIRENHEIDE's (1964, p. 21) revision of *Cyathophyllum antilimbatum* QUENSTEDT (1879, p. 467; 1881, Pl. 158, Fig. 40), which incorporated what BIRENHEIDE originally thought was eight certain and five questionable synonyms of the species, has been largely superseded by his later reassessment of *Zonophyllum duplicatum* (BIRENHEIDE, 1978, p. 176).

Microplasma fractum SCHLÜTER (1882, p. 209; 1889, p. 84, Pl. 6, Figs. 4–8), which is the type species of *Pseudomicroplasma* SOSHKINA (1949, p. 53), is from the Middle Devonian of the Sötenich syncline, northern Eifel region. The lectotype and paralectotypes (CHENG, 1971, Pl. 1, Figs. 12–16) and new material from the Givetian of the type area (LÜTTE & OEKENTORP, 1988, Text-Fig. 2c-d) lack septal cones, and their septal spines are either confined to the outer wall (CHENG, 1971) or concentrated around the peripheral region of the corallum (LÜTTE & OEKENTORP, 1988).

As noted by IVANOVSKIY & SHURYGINA (1980, p. 17) and PEDDER (1985, p. 293), four very similar species described by SOSHKINA (1936, p. 27–33, 71, 72, Text-Figs. 7–20; 1949, p. 52, Pl. 13, Fig. 1a-f) under the names *Lythophyllum minimum*, *L. aconicum*, *L. platycalix* and *Nardophyllum vermiforme* are almost certainly synonymous. They come from a single, probable Eifelian bed, exposed on Malý Patok River on the western slope of the northern Urals. BIRENHEIDE (1964, p. 21) believed *L. platycalix* to be a possible synonym of "*Plasmophyllum*" *antilimbatum* (QUENSTEDT, 1879), but the species which was given the four names by SOSHKINA resembles *Zonophyllum maderense* more than "*P.*" *antilimbatum*. The multi-named species is about the same size, or only slightly larger than *Zonophyllum maderense*, but is differentiated from it by its more numerous, finer presepiments, thinner, trabeculate cones and abundant septal spines. CAO & OUYANG (1987, p. 182, Pl. 24, Fig. 3a, b) identified an upper Emsian coral from the Lower Dangdou Formation in the western Xinling fold belt as *Lythophyllum platycalix* SOSHKINA. Further study of the population represented by this coral is required before any relationship can be firmly established between it and either "*L.*" *platycalix* or *Z. maderense*. It appears to differ from the new species by having thinner septal cones and a few coarse spines emanating from them.

Etymology: Mader from Ma'der Basin, and suffix -ensis, -ensis, -ense.

Zonophyllum pegoconus sp. nov.

(Pl. 1, Figs. 17, 18, 21–23; Pls. 2, 3; Pl. 4, Fig. 11)

Type series: Holotype, GSC 116631. Seven paratypes, GSC 116632–GSC 116638.

Diagnosis: Species of *Zonophyllum* with adult diameter 19.0–43.0 mm. Adult calice with broad exsert rim underlain by large subhemispherical presepiments. Marginal septal spines moderately abundant, mostly projecting 0.1–0.3 mm above the surface of the sclerenchyme in which they are bedded. Septal crusts very thick, may be completely fused in early stages; in adult stages, their thickness in the periaxial region normally equals, or exceeds, the height of the spaces separating them.

Description: Corallum solitary, trochoid to ceratoid, becoming subcylindrical in adult stages; lacks major rejuvenescences. Calice typically 8–12 mm deep, with a crudely funnel-shaped lower part, and an exsert rim, best developed in adult stages. Where not reinforced with sclerenchyme, thickness of outer wall 0.1–0.4 mm. Radiciform processes absent from the type series and other topotypes. No complete specimen available; estimated length of large specimens, measured over the side of greatest curvature, is in the order of 140 mm. Diameters of adult coralla 19.0–43.0 mm; adult diameter of holotype 31.0 mm.

Peripheral septal apparatus comprises randomly distributed, short, broad-based, holacanthate spines. Most of these project 0.1–0.3 mm above the surface of the sclerenchyme in which they are bedded; the longest seen projects 0.7 mm above the upper surface of a sclerenchymal layer. Adaxially, septal spines tend to increase in length and abundance and incorporate themselves into the outer parts of dense cone-shaped crusts. As preserved, the crusts appear structureless, with smooth upper surfaces; except in one paratype (GSC 116637), in which some upper surfaces of the crusts are weakly spinose. Up to the stage where the corallum attains a diameter of 15 mm, septal crust commonly occupies most, if not all of the corallum. Centrally situated septal crust remains well developed in adult stages, so that the intercrustal spaces in the periaxial region are commonly less voluminous than the crusts. Marginal dissepiments subhemispherical and large. In transverse section many of the dissepiments around the summit of the exsert rim appear subcircular. In longitudinal section, 12–16 dissepiments occur over a vertical distance of 10.0 mm in the region below the exsert rim of the calice.

Remarks: The type series has been chosen to express as fully as possible the variation observed in the type population. GSC 116638 and GSC 116634 have the least and greatest adult diameters. GSC 116633 and GSC 116636 have the least septal crust; GSC 116634 and GSC 116635 have the most. Parts of GSC 116634 have the best developed peripheral spines, in contrast to GSC 116632, which has the least developed spines in the peripheral region.

The new species needs to be distinguished from three previously described Middle Devonian species.

Comanaphyllum tumidum (FLÜGEL), from Feke on the Geyik Dagı tectono-stratigraphic unit, Turkey, was originally established as two subspecies, *C. tumidum tumidum* and *C. tumidum falcatum* by H. FLÜGEL (in FLÜGEL & FLÜGEL, 1961, p. 389–391, Pl. 2, Fig. 6a, b; Pl. 3, Fig. 7a, b), and was discussed later by BIRENHEIDE (1964, p. 25) as *Plasmo-*

phyllum (P.) secundum tumidum. It is very similar to the new species in size (length >120 mm; adult diam, 19–40 mm) and shape (cylindrical with broad exsert calicular rim in adult stages), and has similar subhemispherical outer dissepiments (11–14 occurring over a vertical distance of 10.0 mm). It differs from the new species by having no demonstrable septal spine or septal crust.

Lythophyllum schluteri (WEDEKIND), from the Eifel region of Germany, was originally named *Microplasma schlüteri* by WEDEKIND (1922b, p. 61, Pl. 1, Fig. 5a, b). It was included in *Comanophyllum* by H. FLÜGEL (in FLÜGEL & FLÜGEL, 1961, p. 388) and was revised by BIRENHEIDE (1964, p. 29) as *Plasmophyllum (P.) secundum schlueteri*. It resembles *Zonophyllum pegoconus* in having an exsert calicular rim. However, on average, it is larger (adult diam. 31–80 mm), its calicular rim is narrower and usually less exsert, it has only a few layers of thin septal crust, and its peripheral septal apparatus is said by BIRENHEIDE to consist of only rare to moderately frequent rows of isolated trabecular grains. In *Z. pegoconus*, the peripheral septal spines are randomly distributed and not aligned in rows.

Zonophyllum paternum (ULITINA, 1968), the type species of *Patridophyllum*, was thought to be a species of *Plasmophyllum auctores* non DYBOWSKI, 1873, by IVANOVSKIY (1976, p. 126), but was assigned to *Cystiphyllodes* by MCLEAN (1976, p. 6). The species resembles *Zonophyllum pegoconus* in having numerous thick, well centred septal cones that are poorly split abaxially into septal crests. It differs from the new species by being larger (length >160 mm; adult diam. 50 mm) and by having a deep cone-shaped calice with sharp upper edges. It also differs in that its septal cones are clearly composed of coarse monacanth, although this difference is likely due more to preservation than original microstructure.

Etymology: Greek, pegos, meaning strong or solid, and konos a cone, in Latin form.

***Zonophyllum* sp. indet.**

(Pl. 4, Figs. 3, 7, 9)

Material: One incomplete specimen, GSC 116639.

Remarks: Despite the much eroded condition of the specimen, its marginal subhemispherical presepiments clearly form a well rounded, exsert calicular rim, similar to that of *Z. pegoconus* sp. nov. And like *Z. pegoconus*, this coral also has only a few weak marginal spines. It differs from *Z. pegoconus* in having thinner, more widely spaced septal cones and smaller, more crowded presepiments.

Zonophyllum schluteri (WEDEKIND, 1922b) and *Z.(?) tumidum* (FLÜGEL, 1961), which were demoted to subspecies of *Z. secundum* (GOLDFUSS, 1826) by BIRENHEIDE (1964, 1978), have similar calicular rims, but they have very much weaker septal cones. Furthermore, *Z. schluteri* is considerably larger with minimum and maximum adult diameters of 31 and 80 mm.

Genus: *Lekanophyllum* WEDEKIND, 1924

- e.p. 1924 *Lekanophyllum* – WEDEKIND, p. 29 (pars = *Mesophyllum*).
1925 *Hemicystiphyllum* – WEDEKIND, p. 28.
1925 *Atelophyllum* – WEDEKIND, p. 37.
1925 *Dialytophyllum* – WEDEKIND, p. 40.
1978 *Dialithophyllum (Protodialithophyllum)* – KONG in KONG & HUANG, p. 158.

Type species (LANG et al., 1940, p. 75): *Lekanophyllum punctatum* WEDEKIND, 1924, p. 30–34, Text-Figs. 36–38. Dohmophyllenstufe, lower Middle Devonian; Auberg near Gerolstein, Eifel region, Germany. The type stratum is in the middle Eifelian Junkerberg Formation.

Diagnosis: Solitary Cystiphyllidae, with variably, but mostly well developed, radially arranged, septal crests in ephebic stages. Septa may be weakly dilated in neanic stages, but not so as to form fused crests that entirely fill the corallum. Periaxial dilation of septa insignificant in ephebic stages. Discrete peripheral carinae either very rare or absent.

Remarks: The present treatment of *Lekanophyllum* assumes the following: *L. punctatum* and *L. kayseri* WEDEKIND, 1924 (p. 34, Text-Figs. 39–42) have virtually identical type occurrences in the Junkerberg Formation of the Gerolstein syncline, and are conspecific. *L. punctatum* is chosen as the name-bearer for the species.

An Eifel coral figured by MA in 1937 (p. 21, Fig. 1a, b) as *Cystiphyllum vesiculosum* (GOLDFUSS, 1826) and in 1956 as *C. pseudoseptatum* (SCHULZ, 1883), and corals from the Junkerberg Formation of the Hillesheim syncline figured by BIRENHEIDE in 1964 (Pl. 4, Figs. 12–14; Pl. 5, Fig. 15; Pl. 17, Fig. 79) as *Plasmophyllum (P.) auburgense* and in 1978 (Text-Fig. 109a-e) as *Mesophyllum (M.) auburgense*, are conspecific with the species described first from the Junkerberg Formation of the Gerolstein syncline by WEDEKIND, 1922b (p. 53, Pl. 1, Fig. 3a, b) as *Mesophylloides auburgensis* and later (1924, p. 35, Text-Fig. 43) as *Lekanophyllum auburgense*. This species has very weak septal crests and could be referred to either *Zonophyllum* or *Lekanophyllum*. Here, it is called *Lekanophyllum auburgense* (WEDEKIND, 1922b).

The development of marginal septal crests in species derived from *Zonophyllum* occurred more than once, possibly many times. The new Moroccan species assigned to *Lekanophyllum* is unlikely to have shared the later part of its phyletic lineage with any of the type species of the genera assigned to *Lekanophyllum* in the above synonymy of the genus.

***Lekanophyllum hollardi* sp. nov.**

(Pl. 4, Figs. 1, 2, 4–6, 8, 10, 12–14)

Type series: Holotype, GSC 116640. Paratype, GSC 116641.

Diagnosis: Species of *Lekanophyllum* with weak, carinate septal crests. Exsert marginarium includes many relatively large subhemispherical dissepiments. Rounded marginarial surfaces well differentiated from much flatter tabularial surfaces. About 34 major septal crests at corallum diameter of 22 mm.

Description: Corallum solitary, ceratoid to trochoid in early stages, becoming subcylindrical at maturity. Rejuvenescences modest; growth rings delicate. Calice with rounded everted rim, steep sides and an undulating, flat to moderately concave base; depth of calice measured from summit of rim to base of calice 9–11 mm. Outer wall, where not reinforced with sclerenchyme, 0.1–0.5 mm thick. A prominent cystose radiform process present in both types; one transverse section of holotype shows mean diameters of both the corallum and the radiform process to be 6.0 mm. Mean adult diameters of holotype and paratype, 21.5 mm (estimated from eroded specimen) and 29.0 mm. Length estimated from incomplete specimens, before sectioning

and measured along the convex side of the corallum, >50 mm and 60 mm.

Transverse sections of early stages (diam. <12 mm) show cysts overlain by partly structureless, but mostly septate stereocones; spaces between cones and cysts vary. As the coral approaches maturity (diam. approx. 15 mm), short strands of lamellar septal crest appear in the marginarium. At full maturity, stereocones overlie many of the tabularial surfaces, but because most are <1.0 mm thick (max. thickness 3.0 mm), horizontal skeletal elements remain well separated. Septal skeleton at maturity consists of many spines embedded in stereocones in both the tabularium and marginarium and on the corallum wall, as well as fragmentary lamellar septal crests, radially arranged and mostly situated around the region corresponding to the summit of the calicular rim. Most septal spines project only about 0.1 mm above the surface of the stereome that embeds them. Septal crests poorly differentiated into orders; too irregular to count in the paratype; about 34 major septal crests present in adult stage of holotype. Diameter of trabeculae in septal crests about 0.1 mm. Trabeculae comprising septal crests mostly contiguous, but not well aligned, causing carination of the crests. Marginarium and tabularium much better differentiated than in many cystimorph corals. Five or six rows of large, well inflated dissepiments and presepiments usually present in marginarium. Nine to 13 plates counted over a vertical distance of 10.0 mm in the tabularium.

Remarks: The combination of features given in the diagnosis makes this such an unusual species that few comparisons with other species of the genus are required.

Lekanophyllum punctatum WEDEKIND, 1924, has some scattered marginal trabeculae outside of the septal crests, but the septal crests are much longer as viewed in transverse section. They are also more numerous, more closely spaced, and are differentiated into major and minor orders of crests.

L. pustulosum PEDDER & MCLEAN, 1982 (p. 76, Text-Fig. 11, Pl. 12, Figs. 1–9) from the upper Emsian of Ellesmere Island, is comparable in size to *L. hollardi* and has large inflated dissepiments, but its relatively wide marginarium is not exsert, its septal crests are longer and more sinuous, as seen in transverse sections.

L. qiannanense (KONG, in KONG & HUANG, 1978, p. 159, Pl. 54, Fig. 7a, b), from the Eifelian Longdongshui Formation on the Guizhou part of the Yangzi block, is the type species of *Protodialithophyllum* KONG, 1978. There is some resemblance between it and *L. hollardi* in longitudinal section, but its dissepiments are smaller and include many that are lateral on the marginal septal crests. The septal crests themselves are as many as 45 in number and are more uniform in appearance.

A transverse section of a Middle Devonian coral from Feke on the Geyik Dagı tectono-stratigraphic unit, Turkey, was illustrated by H. FLÜGEL (in FLÜGEL & FLÜGEL, 1961, Pl. 2, Fig. 5) as *Dialytophyllum auburgense* (WEDEKIND, 1922b). The coral has very irregular septal crests like those of *L. hollardi*. However, it has so many lateral dissepiments that it cannot be either *Lekanophyllum auburgense* (WEDEKIND, 1922b) or *L. hollardi*, although it is certainly a species of *Lekanophyllum*.

Etymology: Patronym for Henri HOLLARD, pioneer of Moroccan geology, who introduced the author to the Devonian Rugosa of Morocco in 1971.

Suborder: Pholidophyllina WEDEKIND, 1927

Family: Stringophyllidae WEDEKIND, 1922

Remarks: Numerous additional Devonian species of the Stauromatidiidae have been found in the Carnic Alps, Yukon Territory (both by PEDDER, unpublished) and Asia (ULITINA, 1992; JIA in LIN et al., 1995) since the family was first erected by PEDDER & OLIVER (1982), and it is virtually certain now that the Stringophyllidae were derived from the Stauromatidiidae, principally by loss of a septothecal marginarium. Since the Stauromatidiidae were themselves derived from the Tryplasmataidae, it is appropriate to assign the Stringophyllidae to a suborder within the Order Cystiphyllida NICHOLSON, 1889, and not to the Ptenophyllina WEDEKIND, 1927, where they were questionably placed by HILL (1981, p. F72). The oldest name available for this suborder is Pholidophyllina, herein transferred from Section Pholidophyllia of WEDEKIND (1927, p. 9).

Genus: *Stringophyllum* WEDEKIND, 1922

1922a *Stringophyllum* – WEDEKIND, p. 8.

1922a *Neospongophyllum* – WEDEKIND, p. 10.

1925 *Neospongophyllum* (Loipophyllum) – WEDEKIND, p. 54, 55.

1925 *Schizophyllum* – WEDEKIND, p. 59 (non VERHOEFF, 1895, p. 243).

1951 *Vollbrechtophyllum* – TAYLOR, p. 182 (nomen substitutum pro *Schizophyllum* WEDEKIND, 1925, non VERHOEFF, 1895, p. 243).

1981 *Schizophyllia* – IVANIYA, p. 34 (nomen substitutum pro *Schizophyllum* WEDEKIND, 1925, non VERHOEFF, 1895, p. 243).

1995 *Stauroneospongophyllum* – JIA in LIN et al., p. 298, 751.

Type species (WEDEKIND, 1925, p. 64): *Stringophyllum normale* WEDEKIND, 1922a, p. 9, Text-Figs. 5, 6. *Stringocephalus* Limestone, base of upper Middle Devonian; Sundwig near Iserlohn, western Sauerland, Germany. See ENGEL & SCHOUPE (1958, p. 89) and BIRENHEIDE (1962, p. 119; 1978, p. 152, Pl. 19, Fig. 1b, c = holotype). The type stratum is Givetian, apparently in either the Upper Honsel Formation or overlying Massen Limestone.

Remarks: The synonymies established by BIRENHEIDE (1962, 1978) for *Stringophyllum normale* WEDEKIND, 1922a and *Neospongophyllum variabile* WEDEKIND, 1925, the type species of *Neospongophyllum*, are generally considered orthodox and are accepted here. Both genera have been retained, either at full genus or subgenus rank, by some authors, including ENGEL & SCHOUPE (1958), HILL (1981) and LIN et al. (1995). However, the degree of development of presepiments, which is the criterion for separating the genera, has been found to be too unstable in the Stringophyllidae to be workable. For the same reason, *Loipophyllum* and *Schizophyllum* WEDEKIND non VERHOEFF are both believed to be synonymous with *Stringophyllum*.

Stauroneospongophyllum is based on *Stringophyllum obnuptum* KONG in KONG & HUANG (1978, p. 107, Pl. 36, Fig. 5a, b) from probable Eifelian beds, near Puan, on the southern part of the Yangzi block of China. JIA (in LIN et al., 1995, p. 298) evidently considered it to be a stauromatidiid coral resembling *Neospongophyllum* (= *Stringophyllum* of most modern work) but differing from it by having scattered trabeculae in the periaxial region. KONG's illustrations of the type species are poor, but his description of it includes nothing that would lead one to remove it from *Stringophyllum*, and certainly there is no indication in either the figures or description of a septotheca that would suggest a stauromatidiid coral.

The genera *Solipetra* FONTAINE (1961, p. 159) and *Stringophylloides* (JIA in JIA et al., 1977, p. 157) are both based on solitary Givetan species from the Huanan block of China and Vietnam. At one time, BIRENHEIDE (1978, p. 152) considered *Solipetra* to be synonymous with *Stringophyllum*; HILL (1981, p. F248, F250), on the other hand, accepted *Solipetra*, but questioned whether *Stringophylloides* could be separated from *Stringophyllum*. In the author's view, *Solipetra* is distinguished by its well aligned, mostly contiguous trabeculae that form continuous, beeded septa of both orders. *Stringophylloides* has lamellar major septa, and although all appear to be complete, the interseptal plates are so elongate and so little inflated that JIA called them tabulae rather than dissepiments.

***Stringophyllum coenaubertae* sp. nov.**

(Pl. 5)

e.p. 1947 "*Schizophyllum*" *acanthicum* FRECH - LE MAÎTRE, p. 50, Pl. 5, Figs. 3, 10 only.

Type series: Holotype, GSC 116642. Six paratypes, GSC 116643-GSC 116648.

Diagnosis: Species of *Stringophyllum* with adult diameter 13.5-27.5 mm. Outer wall mostly 0.15-0.3 mm thick, but locally reinforced by sclerenchyme, which increases the wall's total thickness to 0.6-1.5 mm. Number of major septa in adult corallites 34-54. Trabeculae forming major septa coarse, elliptical in cross section, diameter measured across long axis commonly 0.5-1.2 mm, maximum 1.5 mm. Trabeculae forming major septa usually discrete in the outer marginarium and innermost tabularium, contiguous elsewhere. Trabeculae representing minor septa, more slender than those forming the major septa, mostly discrete, confined to the inner marginarium and outer tabularium, rare or absent in small specimens. Dissepiments outnumber presepiments,

commonly arranged in four to six rows. Dt:Dc 0.41-0.60 in adult stages.

Description: Corallum solitary, trochoid to ceratoid in early stages; straight to slightly curved subcylindrical in adult stages. Presently known only from incomplete specimens, <65 mm long, that lack proximal tips and distal ends. Mean adult diameter 13.5-23.5 mm, except for one exceptionally large specimen (GSC 116645) with corallite diameter of 27.5 mm.

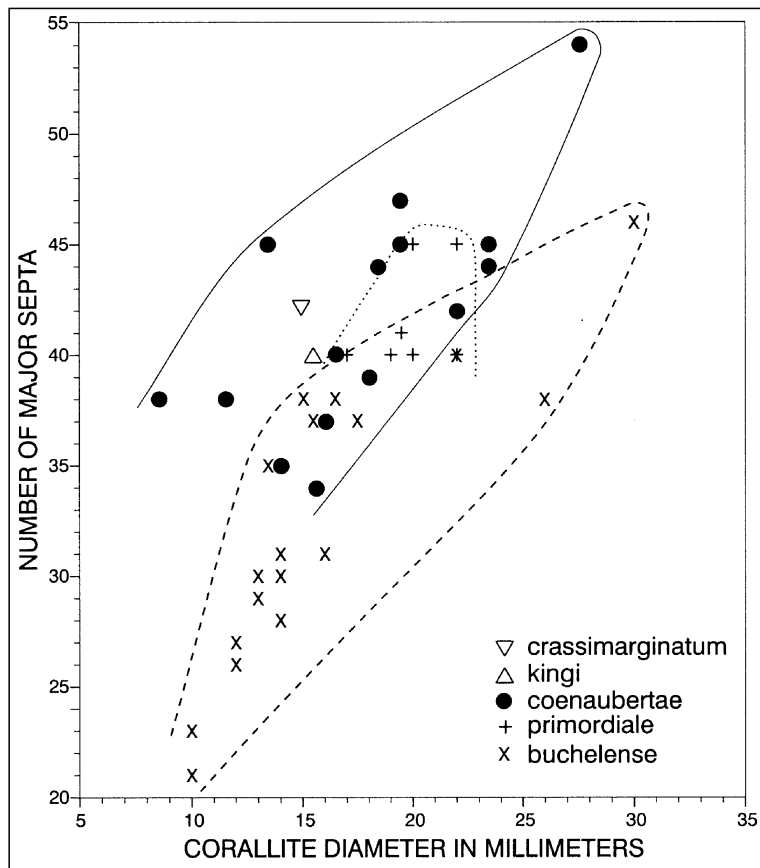
Rejuvenescences minor, affecting outer dissepimentarium more than tabularium. Longitudinal sections suggest calice would have a very narrow rim, and a callicular pit with steep lower sides and a variable, broad, funnel-shaped base. Outer wall mostly eroded from the available material, where present usually 0.15-0.3 mm thick. Locally, sclerenchyme, continuous with sclerenchyme on the upper surfaces of some dissepimentarium surfaces, envelops the most peripheral trabeculae of minor septa and increases the wall's thickness to as much as 1.6 mm.

Septa entirely trabeculate, highly differentiated into two orders. Major septa unequally long, bilaterally arranged about a plane which normally does not quite coincide with the cardinal-counter plane, determined on the basis of the position of the infra-lateral minor septa (term from HUDSON, 1935, p. 71). Lengths of cardinal and counter septa variable; cardinal septum commonly shorter, counter septum commonly longer than adjacent major septa. In the marginarium, some major septa are continuous and generally have a beeded appearance in transverse section. Others are discontinuous due to separation of the trabeculae; a few are well withdrawn from the periphery and separated from it by a presepiment. Counts of major septa given in Text-Figure 3. Minor septa poorly developed and, apart from ridges on

the interior of the outer wall and two weak infra-laterals, may remain suppressed in small specimens. The most fully developed minor septa almost equal the major septa in number, but comprise only discrete trabeculae in the marginarium and a few closely spaced or contiguous trabeculae around the outer tabularium.

Trabeculae monacanthine, long, elliptical in section perpendicular to the axis of the trabecula. Individual trabeculae directed upwards and inwards with very little curvature. Curvature caused by bifurcation and rarely trifurcation of the trabeculae close to the boundary between tabularium and marginarium. Thickness of trabeculae variable, but apparently greater than in other described species. Typical and maximum diameters measured across the long axis of the elliptical cross sections of trabeculae 0.5-1.2 mm and 1.5 mm. Diameter of discrete trabeculae in marginarium and the periaxial region of the corallite typically 0.18-0.4 mm.

Adult marginarium consists of four to six, rarely seven, rows of dissepiments and some presepiments. Individual dissepiments elongate, only moderately inflated, increasing in inclination



Text-Fig. 3. Scatter diagram of number of major septa x corallite diameter in five species of *Stringophyllum*.

adaxially. Thickness of sclerenchyme on dissepimental surfaces 0.1–0.3 mm. Boundary between marginarium and tabularium sharp. Tabulae broad, normally disrupted by adaxial septal ends. Tabularial surfaces sinuous, as viewed in longitudinal section, and despite the sinuosity are mostly gently to deeply concave. Ten to 19, most commonly 13–18 tabulae occur over a vertical distance of 10 mm. Orientation of the longitudinal sections was determined by the curvature of the corallites and is random relative to the cardinal-counter plane. Ratios of the diameter of the tabularium to that of the corallum (dt:dc) 0.41–0.60 in adult stages. It is expected that ratios obtained from longitudinal sections cut precisely along the cardinal-counter plane would give higher dt:dc values, whereas any cut precisely perpendicular to the cardinal-counter plane should give a lower dt:dc value.

Remarks: Four previously named Givetian species from Europe resemble the new species and are likely to be closely related to it phylogenetically. These are *Stringophyllum buchense* (SCHLÜTER, 1889, p. 63, Pl. 7, Fig. 8), *S. primordiale* WEDEKIND (1922a, p. 10, Text-Fig. 7), *S. kingi* TAYLOR (1951, p. 179, Pl. 2, Fig. 8) and *S. crassimarginatum* BIRENHEIDE & SOTO (1992, p. 115, Pl. 2, Fig. 9a, b).

Stringophyllum buchense (SCHLÜTER), known principally from the Bergisches Land and Sauerland of Germany, has been reassessed by several authors, including ENGEL & SCHOUPE (1958, p. 96), BIRENHEIDE (1962, p. 118, 119, 121; 1978, p. 153) and MAY (1993, p. 49). On average, it is smaller, has fewer septa (see Text-Fig. 3), finer trabeculae with diameter <0.5 mm (MAY, 1993, p. 49), and has many more presepiments, than *S. coenabertae*.

According to the synonymies of BIRENHEIDE (1962, p. 118–120; 1978, p. 153), *Stringophyllum primordiale* WEDEKIND, which comes from the Bergisches Land and Eifel regions of Germany, is also, on average, smaller with fewer septa, and has finer trabeculae than *S. coenabertae*. Although the trabeculae forming the major septa in *S. primordiale* are fine, most of them are contiguous, even in the marginarium, and thus form mostly uninterrupted major septa. Another distinction between the two species is that *S. primordiale* apparently has consistently less sclerenchyme.

The unique specimen of *Stringophyllum kingi* TAYLOR comes from Plymouth, England. It is unavailable for study, and is too poorly illustrated and described to be identified with certainty. It appears to have 40 major septa at a diameter of 15.5 mm. and was diagnosed in part by TAYLOR as "*Stringophyllum* with major septa that are thick near the periphery and there invested in much lamellar tissue, forming a thick wall". TAYLOR's single silhouette figure of a transverse section suggests that the minor septa are longer than those of *S. coenabertae*, and that there is significantly more peripheral sclerenchyme in *S. kingi* than in *S. coenabertae*. Furthermore, in *S. kingi*, "the major septa show a tendency for their monacanth to separate in the peripheral wall, but never actually separate" (TAYLOR, 1951, p. 180).

Stringophyllum crassimarginatum BIRENHEIDE & SOTO is based on a single small trochoid specimen from the Cantabrian Mountains of Spain. It much resembles what is known of *S. kingi* TAYLOR. The trochoid form suggests that it may be an immature individual, since mature specimens of *Stringophyllum* are normally subcylindrical. It differs from *S. coenabertae* by having considerably more peripheral sclerenchyme, and its septa are more bilaterally ar-

ranged than those of *S. coenabertae* having a comparable diameter.

LE MAÎTRE's specimens assigned to *Stringophyllum coenabertae* come from Middle Devonian beds with *Calceola*, at Mechra ben Abbou on the Moroccan Meseta.

Etymology: Patronym for MARIE COEN-AUBERT, who provided the first identifications of Givetian Rugosa from Jbel Ou Driss.

Order: Stauriida VERRILL, 1865

Suborder: Stauriina VERRILL, 1865
(sensu HILL, 1981)

Family: Siphonophrentidae
MERRIAM, 1974

Remarks: For the most recent and authoritative review of the family see OLIVER (1993, 1998).

Genus: *Siphonophrentis* O'CONNELL, 1914

1914 *Siphonophrentis* – O'CONNELL, p. 187, 190, 191.

1955 *Altaiophyllum* – IVANIYA, p. 85.

1960a *Zmeinogorskia* – SPASSKIY, p. 120 (nomen nudum).

1960b *Zmeinogorskia* – SPASSKIY, p. 31.

1960 *Zmeinogorskia* – SPASSKIY in BUL'VANKER et al., p. 238.

Type species: *Caryophyllia gigantea* LE SUEUR, 1821, p. 296. Species revised on the basis of a neotype by OLIVER (1993, p. B25–B28), who synonymised it with *Siphonophrentis elongata* (RAFINESQUE & CLIFFORD, 1820). The neotype is from the Onondaga Limestone, probably the lower Eifelian Edgecliff Member, near Leroy, New York.

Diagnosis: See OLIVER (1993, p. B26).

Remarks: Russian studies on what are considered now to be siphonophrentid corals have been led by IVANIYA and co-authors (1955–1988). IVANIYA's conclusions differ substantially from those reached by OLIVER (1993, 1998) from investigations of the same family. Two genera, now placed in the Siphonophrentidae, were recognized by IVANIYA. These were *Heterophrentis* sensu IVANIYA non BILLINGS and her own genus *Altaiophyllum*. In IVANIYA's view, *Heterophrentis* is a zaphrentid coral distinguished from other members of the family by lacking carinae. *Altaiophyllum*, on the other hand, was attached to the Halliidae because of its peculiar septal dilation, and was separated from other halliids on the basis of its different tabularial morphology and lack of dissepiments. IVANIYA never compared or contrasted *Heterophrentis* with *Siphonophrentis*, but distinguished *Altaiophyllum* from *Siphonophrentis* by an alleged absence of a siphonofossula from *Altaiophyllum*.

In practice, IVANIYA and co-authors assigned siphonophrentids having appreciable amounts of marginal sclerenchymal thickening to *Altaiophyllum* and those lacking such deposits to *Heterophrentis*. However, one of the important results presented in OLIVER's 1993 work is that *Heterophrentis spatiosa* BILLINGS (1858, p. 178), which is the type species of *Heterophrentis* BILLINGS (1874, p. 235), resembles the genus *Kionelasma* and is neither a siphonophrentid, zaphrentid, nor a halliid coral.

Illustrated transverse sections of IVANIYA's "*Heterophrentis*" are of advanced stages, and, as with *Zaphrentis subgigantea* CHAMPERNOWNE, 1884, and *Siphonophrentis cantabrica* BIRENHEIDE, 1978, it is not known whether any peripheral sclerenchymal thickening is present in earlier stages.

SPASSKIY erected the genus *Zmeinogorskia* three times and its type species twice. Although he was aware of the

close similarity between *Zmeinogorskia* and *Altaiophyllum*, he distinguished *Zmeinogorskia* from *Altaiophyllum* by its thinner septa and shorter minor septa. He also noted that minor and major septa in *Zmeinogorskia* are not drawn close enough together to become attached and form what he called paired septa. However, this last distinction is an inevitable consequence of the brevity of the minor septa. SPASSKIY's other points are refuted by his own material and actions. Two topotypic paratypes of *Zmeinogorskia bublichenkoi*, the type species of the genus, have thick septa (SPASSKIY, 1960b, Pl. 11, Fig. 3; Pl. 13, Fig. 1) and *Z. sagsayica*, which was erected by SPASSKIY (1960a) just before the type species was, has strong asymmetric thickening of the septa, which leaves some minor septa attached to major septa. SPASSKIY retained *Z. sagsayica* in *Zmeinogorskia* throughout his subsequent career (SPASSKIY, 1977, p. 117). SPASSKIY assigned *Zmeinogorskia* to the Kodonophyllidae, but this is not supported by numerous studies of the family summarised by HE & CHEN (1996, p. 37). In *Zmeinogorskia*, trabeculae, if present at all, are fine, major septa are not rotated and fused periaxially, and tabulae are not arched. These features remove *Zmeinogorskia* from the Kodonophyllidae. One must agree with all Russian authors, other than SPASSKIY, that *Zmeinogorskia* is synonymous with *Altaiophyllum*. It is also likely to be synonymous with *Siphonophrentis*.

Siphonophrentis has been studied at length recently in a beautifully illustrated paper by WANG XUNLIAN (1994, p. 365–379). OLIVER's main siphonophrentid work was published in June, 1993, and could not have been seen by WANG much before his own work was sent to print, which may explain why OLIVER's work appears to have influenced WANG so little. WANG synonymised the genera *Amplexiphyllum* STUMM (1949, p. 9), *Breviphrentis* STUMM (1949, p. 13), *Breviphyllum* STUMM (1949, p. 25), *Baoshanophyllum* SONG (1974, p. 112; 1982, p. 21) and *Puanophyllum* WANG ZHIPING (1983, p. 66) with *Siphonophrentis*. But a more serious error was his failure to take note of valid choices of neotypes for *Siphonophrentis gigantea* (LE SUEUR, 1821) by OLIVER (1993, p. B25–B28), and for *S. elongata* (RAFINESQUE & CLIFFORD, 1820) by STUMM (1965, p. 23–24). Both neotypes (OLIVER, 1993, Pl. 20, Figs. 3, 4; Pl. 21, Fig. 3) reveal asymmetric peripheral thickening of septa in their cardinal quadrants, such as occurs in *Altaiophyllum*. Thus, the assertion that *Altaiophyllum* differs from *Siphonophrentis* by having dilated septa in its cardinal quadrants (WANG, 1994, p. 370) is unsustainable. *Amplexus hamiltoniae* HALL (1877, Pl. 19, Figs. 20–23), from the Hamilton Group of western New York, is the type species of *Amplexiphyllum*. It was never described by HALL and despite work by BUSCH (1941, p. 397, Text-Figs. 17–27) and STUMM & WATKINS (1961, p. 446, Pl. 58, Figs. 29–32, 40–50), the species has remained poorly founded by modern standards. As currently interpreted, it is a small, commonly irregularly contorted coral, differing from *Siphonophrentis* by having major septa, which in early stages are fused at the axis, but elsewhere are separated by broad interseptal loculae.

Amplexus invaginatus STUMM (1937, p. 427, Pl. 53, Fig. 2; Pl. 54, Fig. 2a–c) is the type species of *Breviphrentis*. Its holotype evidently comes from the Emsian inversus Zone in the Coils Creek Limestone, on Fish Creek Range, Nevada. It differs from species of *Siphonophrentis* by having thick monacanth and periodic calicinal expansions (PEDDER & MURPHY, 1997, p. 353, Text-Figs. 5.1, 2, 4–6).

Amplexus lonensis STUMM (1937, p. 428, Pl. 53, Fig. 4; Pl. 54, Fig. 4a, b) is the type species of *Breviphyllum*. The holotype was probably collected loose from some part of the Emsian McColey Canyon Formation on Lone Mountain, Nevada. It resembles *Breviphrentis*, but the longitudinal section shows dissepiments and possibly presepiments (HILL, 1981, Text-Fig. 95, 3a), making it even more distinct from *Siphonophrentis* than *Breviphrentis* is.

Baoshanophyllum is based on *B. cyli(n)dricum* SONG (1974, p. 112, Pl. 76, Fig. 5a–e; 1982, p. 21, Pl. 1, Fig. 4a–d). The type specimen probably came from the late Givetian part of the Heyuanzhai Formation at Malutang, on the Baoshan-Luxi microplate in western Yunnan. WANG (1994, p. 377, Text-Fig. 8, Pls. 14–16) revised the species under the name *Siphonophrentis minor* (SUNG, 1982). These and other species from the Huanan, Yangxi and Shaluli Shan blocks of southern China resemble *Siphonophrentis* and could be regarded as a subgenus of it, but they are consistently smaller, have relatively wider septothecae and only rarely are their fossulae and infra-lateral minor septa clearly distinguishable.

Puanophyllum has *P. gigantum* WANG ZHIPING (1983, p. 67, Text-Fig. 1a, b, Pl. 1, Fig. 1a, b) for type species. It is from the upper Emsian or lower Eifelian Lijiawan or Guanziyao Formation, on the western Guizhou part of the Huanan block, and is likely to be synonymous with *Baoshanophyllum*.

Among the many species attributed to *Siphonophrentis* by WANG (1994) is a coral identified as "*Tabularia*" *tareica* KRAVTSOV by LATYPOV in VOLKOVA & LATYPOV (1976, p. 14, Pl. 7, Fig. 3a, b). It comes from the Emsian Nelichen Formation of the Selennyakh terrane, in the Kolymian structural loop of northeastern Russia. This coral superficially resembles *Siphonophrentis*, but apparently completely lacks second order septa; it was recorded as new genus 26 by OLIVER & PEDDER (1979, p. 236, 237).

IVANOVSKY'S (1976, p. 15) remark that PICKETT believed *Altaiophyllum* to be synonymous with *Temnophyllum* was due to a lapsus calami; it was *Alaiophyllum* that was synonymised with *Temnophyllum* by PICKETT (1967 p. 28).

Several problems concerning the Old World Realm Siphonophrentidae cannot be resolved with currently available data. For this work, all IVANIYA'S species of *Altaiophyllum* and *Heterophrentis* are tentatively included in *Siphonophrentis*, together with *Zaphrentis subgigantea* CHAMPERNOWNE, 1884, and *Siphonophrentis cantabrica* BIRENHEIDE, 1978. OLIVER (1993), IVANIYA and co-authors (1955–1988) and HILL (1981, p. 150) all excluded *Altaiophyllum* from *Siphonophrentis*, presumably because described species of *Altaiophyllum* from Altay-Sayan generally have weak siphonofossulae. However, some transverse sections of *Altaiophyllum belgebaschicum*, the type species of the genus, clearly show a well developed siphonofossula (IVANIYA, 1965, Pl. 64, Fig. 278), and SPASSKIY reported the presence of a fossula in some specimens of *Zmeinogorskia*.

Species assigned: Probable Old World Realm species of *Siphonophrentis* excluded from *S. belgebaschica* are as follows: *Zaphrentis subgigantea* CHAMPERNOWNE, 1884, p. 499, Pl. 22, Figs. 2–5. Neotype and other topotypes apparently from the Lummaton Shell Bed, Givetian *varcus* Zone (MATHEWS, 1970), at Lummaton Quarry, Torquay, England. Species revised by SMITH & THOMAS (1963, p. 167, Pl. 8, Figs. 3–5). Enlargement of part of a likely topotype illustrated in Figure 6, Plate 8.

Zmeinogorskia *publichenkoi* SPASSKIY, 1960b, p. 32, Pl. 11, Figs. 3–5; Pl. 12, Figs. 1, 2; Pl. 13, Fig. 1 (also erected in BULVANKER et al., 1960, p. 239, Pl. 53, Fig. 1a, b). Holotype from the Strizhkovo Beds, on Matveevsky Stream near Zmeinogorsk, Rudny Altay part of Altay-Sayan, southern central Russia. The associated fauna at the type locality is undiagnostic, but the Strizhkovo Beds at a nearby outcrop and in subsurface are Eifelian age (ZHELTONOGOVA et al., 1994).

Heterophrentis bifurcata IVANIYA in ZHELTONOGOVA & IVANIYA, 1961, p. 370, Pl. D-28, Fig. 2a, b (also erected in IVANIYA, 1965, p. 14, Pl. 16, Fig. 79a-g). "*Euryspirifer cheehiel*" fauna, Lebedyanskoe Beds (of Siberia, not Russian Platform), Givetian, in limestone quarry on the right bank of Alchedat Creek, Lebedyanskoe Village, northern Kuzbass, Gorny Altay region of Altay-Sayan, southern central Russia.

Heterophrentis interrupta IVANIYA, 1965, p. 15, Pl. 23, Figs. 102, 103. Occurrence as for *H. bifurcata* IVANIYA, 1965.

Heterophrentis sibirica IVANIYA, 1965, p. 262, 264, 265, 304; Pl. 16, Fig. 78a-v, 78v(bis). Occurrence as for *H. bifurcata* IVANIYA, 1961. Although this species was illustrated, and was used as a zone fossil in the Kuzbass region of Altay-Sayan (IVANIYA, 1965, p. 304), as far as the present author is aware, it has remained a nomen nudum.

Heterophrentis brevisseptata IVANIYA & TSCHERNYSHOVA in IVANIYA, 1965, p. 264, 265, 374, Pl. 31, Figs. 148, 149 (nomen nudum, validated under IVANIYA's authorship in 1988).

Siphonophrentis cantabrica BIRENHEIDE, 1978, p. 69, Pl. 9, Fig. 2a, b. Lower Portilla Formation, Middle *varcus* Subzone, Esla Valley, Cantabrian Mountains, Province of León, Spain.

Heterophrentis brevisseptata IVANIYA in IVANIYA & GUMEROVA, 1988, p. 22, Pl. 1, Figs. 4, 5. Occurrence as for *H. bifurcata* IVANIYA, 1965.

Heterophrentis brevisseptata pyjinica GUMEROVA in IVANIYA & GUMEROVA, 1988, p. 23, Pl. 1, Figs. 6, 7; Pl. 2, Fig. 1. "*Euryspirifer cheehiel*" Horizon, Givetian, left side of the middle reaches of Pyzha Stream, a left tributary of Biya River, Gorny Altay region of Altay-Sayan, southern central Russia.

Altiophyllum yunnanense WANG, 1994, p. 382, Pl. 23, Fig. 2a, b. Upper Heyunzhai Formation, upper Givetian part of formation; Malutang, near Shidian on the Bao-shan-Luxi microplate, western Yunnan, China.

Distribution: The following occurrences and possible occurrences of *Siphonophrentis* are in addition to those given for the types of the non EAR species assigned to the genus, and for the species included in *S. belgebashchica*.

Emsian or Eifelian: Wunur Formation; Toudaoqiao, Sino-Cimmerides between the central Mongolian-Argun massif and the Great Hinggan suture, northern Nei Mongol, China (Guo, 1990, p. 28, Pl. 2, Fig. 1a, b). Lower Naquan Suite – considered Eifelian by KHOA & THOM (1980, p. 278), but is reported to yield *Nowakia barrandei* BOUČEK & PRANTL, and therefore may be Emsian; Cao Bang region, northeast of the Red River (Song Hong) fault on the Vietnam part of the Huanan block (KHOA & THOM, 1980, p. 91, Pl. 25, Fig. 3a, b). This specimen was identified as *Tabulophyllum* cf. *curtoseptatum* BULVANKER. However, it apparently lacks presepiments, and appears to have a siphonofossula and well developed infra-lateral minor septa.

Eifelian: Edgecliff Member of Onondaga Formation, *partitus* Zone; New York (OLIVER, 1993, Pl. 20, Figs. 1–4). Anderdon Member of Lucas Formation, *costatus* Zone; Ingersoll-Woodstock area, Ontario (LAMBE, 1901, Pl. 9, Fig. 3, 3a? and new material, see Pl. 8, Fig. 6). Famine Formation, *costatus* Zone (UYENO & LESPÉRANCE, 1997); Saint-Georges area, mid-Appalachians, Québec (OLIVER, 1971, Pl. 3, Figs. 5, 6). Columbus Formation, *costatus-australis* Zones, north central Ohio (OLIVER, 1993; WANG & CHEN, 1989, Pl. 2, Fig. 8a, b). Jeffersonville Formation, "coral zone", *patulus-partitus* Zones (KLUG, 1983); Falls of the Ohio and areas around Louisville, Kentucky, and Jeffersonville, Indiana (STUMM, 1965, Pl. 13, Figs. 1–4; OLIVER, 1993, Pl. 21, Figs. 1–6; Pl. 22, Figs. 1–7).

Givetian: Subsurface Lingle Formation, Lower *varcus* Subzone; Coles County, Illinois Basin (OLIVER, 1987, Pl. 1, Figs. 5–7). Lower Candás Formation, Middle *varcus* Subzone; near Gijón, Asturias, Spain (ALTEVOGT, 1968, Pl. 1, Fig. 8a-c). Unnamed limestone, west of Bishopsteignton, Devon, England (SMITH & THOMAS, 1963, Pl. 8, Fig. 4). Massen Limestone, Middle *varcus* Subzone; Iserlohn area, western Sauerland, Germany (MAY, 1991, Fig. 13; 1994, Fig. 6.1a, b). Unnamed beds probably now referred to the Sadarak Suite; Arpa River, near Danzik Village, Armenian part of the Northwest Iranian plate (SYTOVA & ULITINA, 1974, Pl. 5, Fig. 1a, b). Ramparts Limestone, conodont zone undeterminable, Mackenzie Mountains near Gayna River, western District of Mackenzie (undescribed material – not related to the Ramparts coral *Siphonophrentis* cf. *gigantea* sensu WARREN & STELCK, 1956, Pl. 4, Fig. 8, which is not a siphonophrentid). Horn Plateau Reef, Middle *varcus* Subzone; near Fawn Lake, Horn Plateau, southern District of Mackenzie (MCLAREN & NORRIS, 1964, Pl. 2, Fig. 3a, b; and new material). ? "Nevada Limestone", Denay Formation of current nomenclature, Givetian (or Eifelian) part, "Bobcat Peak", Roberts Mountains, Nevada (MERRIAM, 1974a, Pl. 1, Figs. 16, 17).

Rejected species: *Siphonophrentis variabilis* OLIVER, 1960, p. 87, Pl. 13, Figs. 1–17. Reef facies of the Coeymans Limestone, Lochkovian; Madison and Onondaga Counties, New York. Removed to *Contophrentis* by OLIVER (1993, 1998).

Zmeinogorskia zaisanica SPASSKIY, 1960a, p. 121, Pl. 4, Fig. 1a-g. Lower Zaisanskoy Suite, Givetian?; Saur Range, Irtysh-Zaysan terrane, eastern Kazakhstan. Has long, periaxially rotated major septa, a uniformly broad septotheca and strongly arched tabularial surfaces.

Siphonophrentis variabilis europa IVANOVSKIY in IVANOVSKIY et al., 1971, p. 34, Pl. 1, Fig. 1a-g. Subsurface bed, Lochkovian?; Veklino Village, northeastern Bulgaria. Unidentifiable; has dissepiments and uniformly thickened septa, but these do not form a broad septotheca such as occurs in *Contophrentis variabilis* (OLIVER, 1960).

Siphonophrentis (Breviphrentis) kobehensis MERRIAM, 1974b, p. 43, Pl. 14, Figs. 1–15; Pl. 16, Fig. 14. Lower Nevada Limestone; Lone Mountain (type occurrence) and other localities in central Nevada. In current terminology, all known occurrences are in the Pragian part of the Kobeh Limestone. Has calycinal expansions like *Breviphrentis*, but probably (known material silicified) lacks coarse monacanthos.

Siphonophrentis dongujumqinensis Guo, 1976, p. 78, Pl. 31, Fig. 5a, b. Wendu'er'aobaote Formation, Eifelian?; Dongfang Hong Commune, East Wuzhumuqin Banner,

in the Barimobinskiy-Khegenshan suture zone, which separates the northern and southern parts of the eastern extension of the Southern Gobi microcontinent (RUZHENTSEV et al., 1992), Nei Mongol, China. Has coarse trabeculae; possibly related to *Breviphrentis*, but no calycinal expansion has been revealed.

in the Barimobinskiy-Khegenshan suture zone, which separates the northern and southern parts of the eastern extension of the Southern Gobi microcontinent (RUZHENTSEV et al., 1992), Nei Mongol, China. Has coarse trabeculae; possibly related to *Breviphrentis*, but no calycinal expansion has been revealed.

Siphonophrentis(?) multitabulata GUO, 1976, p. 78, Pl. 31, Fig. 4a, b. Occurrence as for *S. dongujumqinensis* GUO, 1976, and like that species, has coarse trabeculae and apparently no calycinal expansion.

Siphonophrentis(?) variabilis OLIVER sensu LATYPOV in VOLKOVA & LATYPOV, 1976, p. 12, Pl. 4, Fig. 2a, b. Nelichen Formation, Emsian; Krivoy Creek, Selennyakh terrane, Kolymanian structural loop of northeastern Russia. This small coral (diam. 11.5 mm) with short, axially expanded septa and a row of dissepiments was recorded as new genus 28 by OLIVER & PEDDER (1979, p. 244, 245).

Altaiophyllum flexuosum KAPLAN, 1977, p. 29, Pl. 9, Fig. 3a, b. Holotype from Aydarla Formation, Givetian; Akkozu Mountains, Bayanaul' region, Tarbagatay-Chingiz terrane (FENG et al., 1989, Text-Fig. 2)?, northeastern Kazakhstan; other unfigured material from Aydarla Formation on the northern slope of the Tarbagatay Range. Unidentifiable; is small with only a few wedge-like septa and widely spaced subplanar tabulae.

Siphonophrentis alengchuensis YU & LIAO, 1978, p. 250, Pl. 1, Figs. 1a-2b. Banmandaodi Formation, Emsian (upper Zlichovian); Jinsha River at Alengchu, Lijiang County, northwestern Yunnan part of the Shaluli Shan block, China. Longitudinal figures were reproduced upside down. The two figured specimens, especially the holotype, appear to be typical examples of *Baoshanophyllum*.

Siphonophrentis asperatus YU & KUANG, 1982, p. 55, Pl. 2, Figs. 4-6; Pl. 7, Figs. 8, 9, and its possible synonym *Zelophyllia longiseptata* YU & LIAO in WANG et al., 1974, p. 34, Pl. 9, Figs. 1, 2, which was removed to *Siphonophrentis* by YU & KUANG, 1982, p. 54, Pl. 2, Figs. 1-3. Both from the Lower Beiliu Formation, Upper Emsian, 2 km north of Beiliu County, Guangxi part of the Huanan block, China. These species resemble *Siphonophrentis*, but have irregularly bent septa that tend to be distinctly rotated. In extreme cases, the bending is zigzag, producing carinate protuberances. No etymology was given; the Latin adjective *asperatus* was probably intended, which would be *asperata* in combination with *Siphonophrentis*. OLIVER & PEDDER (1979, p. 244, 245) made these species new genus 29.

Altaiophyllum tenue YU & KUANG, 1983, p. 252, Pl. 1, Fig. 8a, b. Lower Mintang Formation, Givetian; Liujing, Guangxi part of the Huanan block, China. Unidentifiable; the fragmentary holotype was prepared as an oblique cross section and a short incomplete longitudinal section. Neither section shows the typical morphology of either *Siphonophrentis* or *Altaiophyllum*.

Siphonophrentis(?) xinjiangensis CAI, 1983, p. 136, Pl. 32, Fig. 4a-c. Kulumudi Formation, Middle Devonian; Ba'erleike Mountain, Toli (= Tuoli) County, West (Northwest of some authors) Junggar, or Alakol block (location of Ba'erleike Mountain not known to present author). Xinjiang Uygur, northwestern China. Unidentifiable; septa are strongly zigzagly carinate locally.

Siphonophrentis cuneata CAO in CAO & OUYANG, 1987, p. 144, Pl. 23, Figs. 2a-3. Lower Gala Formation, Pragian or lower Emsian; Tewo, southern Gansu Province, western Qinling fold belt, China. Is small (diam. 15 mm) and has curved, cuneate major septa in all quadrants and concave tabulae.

Siphonophrentis sp. CAO et al., 1982, p. 62, Pl. 59, Fig. 6. Lower Xiaputonggon Formation, Lochkovian? (CAO & OUYANG, 1987, p. 192); Tewo, southern Gansu Province, western Qinling fold belt, China. Unidentifiable; a single transverse section of a small coral (diam. 13.5 mm) with very short septa and a relatively broad septotheca is all that is available. The coral resembles "*S. dongujumqinensis* Guo and "*S. yandelli* sensu Guo, 1976, but it is not known whether it has coarse trabeculae as Guo's specimens do.

Siphonophrentis sp. 1 and *S. sp. 2* YU & KUANG, 1983, p. 251, Pl. 1, Fig. 6a-7b. Occurrences as for *Altaiophyllum tenue* YU & KUANG, 1983. Both specimens are small (diam. 22.8 and 13.7 mm), and have adaxially protruding trabeculae and subplanar to concave tabulae.

Siphonophrentis belgebaschica (IVANIYA, 1955)

(Pls. 6, 7)

- ? 1882 *Zaphrentis gigantea* LE SUEUR – BARROIS, p. 199, Pl. 7, Fig. 6a-c. Not *Caryophyllia gigantea* LE SUEUR, 1821, p. 296 (species revised by OLIVER, 1993, p. B26-B28).
- ? 1947 *Siphonophrentis (Zaphrentis) gigantea* LE SUEUR – LE MAITRE, p. 28, Pl. 5, Figs. 11-13; Pl. 6, Figs. 6, 7.
- 1955 *Altaiophyllum belgebaschicum* – IVANIYA, p. 85, Text-Figs. 1-4.
- 1958 *Altaiophyllum belgebaschicum* IVANIYA – IVANIYA, p. 101, Text-Figs. 1-4, Pl. 1, Figs. 1, 2.
- 1958 *Altaiophyllum altaicum* LEVASCHOV (in litt.) – IVANIYA, p. 103, Pl. 1, Fig. 3; Pl. 2, Fig. 4.
- 1958 *Altaiophyllum corgonicum* POLYANSKI (in litt.) – IVANIYA, p. 105, Pl. 3, Figs. 5, 6.
- 1960a *Zmeinogorskia sagsayica* – SPASSKIY, p. 120, Pl. 3, Fig. 1a-v.
- 1961 *Altaiophyllum belgebaschicum* IVANIYA – ZHELTONOGOVA & IVANIYA, p. 369, Pl. D-27, Figs. 2a-3.
- 1961 *Altaiophyllum altaicum* LEVASCHOV – ZHELTONOGOVA & IVANIYA, p. 369, Pl. D-27, Fig. 4a, b; Pl. D-28, Fig. 1.
- 1964 *Altaiophyllum belgebaschicum* IVANIYA – BESPROZVANNYKH, p. 59, Pl. 1, Figs. 2-3b.
- 1965 *Altaiophyllum belgebaschicum* IVANIYA – IVANIYA, p. 11, Pl. 28, Figs. 136, 137; Pl. 29, Figs. 138, 139; Pl. 30, Figs. 142-144; Pl. 64, Figs. 275-279; Pl. 65, Figs. 280-284; Pl. 66, Figs. 285, 286.
- 1965 *Altaiophyllum altaicum* LEVASCHOV – IVANIYA, p. 12, Pl. 66, Figs. 287, 288; Pl. 67, Fig. 289.
- 1965 *Altaiophyllum corgonicum* POLYANSKI – IVANIYA, p. 12, Pl. 29, Figs. 140, 141; Pl. 30, Fig. 145.
- e.p.? 1966 *Altaiophyllum belgebaschicum* IVANIYA – IVANIYA, p. 66, Pl. 1, Figs. 1-3; non? Pl. 2, Figs. 6, 7.
- 1966 *Altaiophyllum altaicum* LEVASCHOV – IVANIYA, p. 67, Pl. 2, Figs. 4, 5; Pl. 7, Fig. 20.
- ? 1968 *Altaiophyllum belgebaschicum* IVANIYA – KAPLAN, p. 899.
- e.p.? 1970 *Siphonophrentis gigantea* LE SUEUR – BRICE, p. 259, Pl. 15, Figs. 3?, 7, 8.
- ? 1975 *Siphonophrentis elongata* (RAFINESQUE & CLIFFORD) – JOSEPH & TSIEN, p. 196, Pl. 3, Fig. 4.
- 1977 *Zmeinogorskia sagsayica* SPASSKIY – SPASSKIY, p. 117, Pl. 24, Fig. 2a, b.
- 1978 *Breviphrentis kullmanni* – BIRENHEIDE, p. 69, Pl. 9, Fig. 3a, b.
- 1986 *Altaiophyllum corgonicum* POLYANSKI – IVANIYA & CHEREPNINA, p. 43.
- 1986 *Altaiophyllum belgebaschicum* IVANIYA – IVANIYA & CHEREPNINA, p. 43, Pl. 87, Figs. 183a-184b; Pl. 88, Figs. 183v-184g.

- e.p. 1986 *Altaiophyllum altaicum* LEVASCHOV – IVANIYA & CHEREPNINA, p. 43, Pl. 86, Fig. 181a-v, top left Fig. 181b only (lower right Fig. 181b = "*Heterophrentis bifurcatum* IVANIYA).
- 1988 *Altaiophyllum belgebaschicum* IVANIYA – IVANIYA & GUMEROVA, p. 21, Pl. 1, Figs. 1–3.
- 1994 *Altaiophyllum sagsayicum* (SPASSKIY) – WANG, p. 381, Pl. 23, Fig. 1a, b.
- ? 1994 *Altaiophyllum shidianense* – WANG, p. 383, Pl. 23, Fig. 3a, b.

Material: Six figured specimens, GSC 116649–GSC 116654.

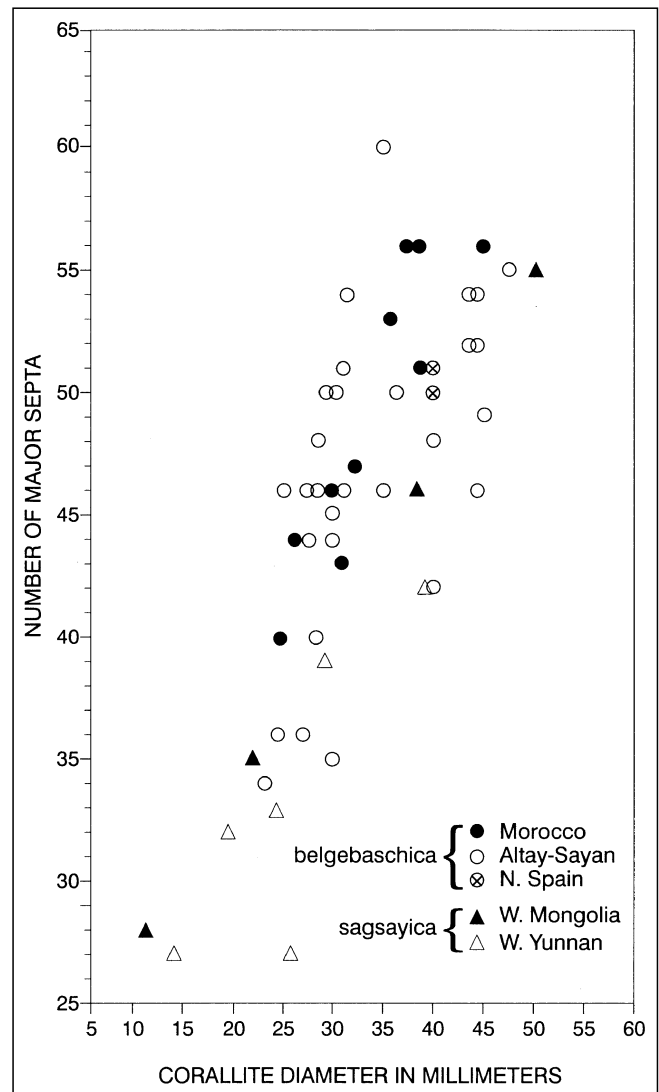
Description: Corallum large and solitary. Neither the calice nor the proximal part of any corallum is preserved in the available material; preserved parts of coralla cylindrical and straight, or, more commonly, slightly curved. Length of largest incomplete specimen about 90 mm measured over the side of greatest curvature. Maximum mean diameter 38.0 mm. Exteriors extensively eroded, but fine growth rings and shallow, narrow septal furrows, separated by much broader, flat-topped interseptal ridges are visible on some specimens. Rejuvenescences rare and mostly insignificant.

Primary fine structure of the partly silicified wall not adequately preserved to be assessed. In places, septal bases appear embedded in lamellar sclerenchyme, which extends on to the faces of the septa. However, the lamellar appearance of the wall is almost certainly secondary. Thickness of wall mostly 0.6–1.5 mm midway between adjacent septa. Septa in two orders. Septal arrangement radial except for some local curving of the two major septa on either side of the shortened cardinal septum toward the cardinal-counter plane. Major septa irregularly amplexoid with longest parts extending more than half way to the axis. Counter septum may be slightly longer or shorter than adjacent major septa. Minor septa not amplexoid, in transverse section typically appear one third to one fifth as long as the major septa. Infra-lateral minor septa (term from HUDSON, 1935, p. 71) on each side of the counter septum longer than other minor septa. Maximum number of septa 56×2 (see Text-Fig. 4 for septal counts).

Sclerenchymal thickening of the septa extremely variable. Commonly, it continues onto the outer distal tabularial surfaces, and it is normally asymmetric relative to the cardinal-counter plane, although its greatest development is usually closer to the cardinal septum than it is to the counter septum. In extreme cases it is virtually absent, even in young stages, or it may be sufficiently thick to engulf minor septa and close interseptal loculae exterior of the outer, downturned part of the tabularium.

Dissepiments absent. Siphonofussula present, randomly positioned relative to the curvature of the corallum. Tabulae broad, but only very rarely complete. Tabularial surfaces generally subplanar to weakly concave in the periaxial region, downturned and concave in loculae between adjacent major septa. A narrow outermost part of some tabulae is upturned towards the wall. Very rarely a peripheral tabella mimics a dissepiment. One such tabella is visible in the centre of the left hand side of the thin section illustrated in Plate 7, Figure 7. Six to 13 tabulae occur over a vertical distance of 10.0 mm.

Remarks: The above description is based solely on material from Jbel Ou Driss. The present author follows IVANIYA's own decision (in IVANIYA & GUMEROVA, 1988) to synonymise her three 1958 species under the trival



Text-Fig. 4. Scatter diagram of number of major septa x corallite diameter in *Siphonophrentis belgebaschica* and *S. sagsayica* in five regions indicated. Note that *S. belgebaschica* from Morocco are separable from *S. sagsayica* from western Mongolia and western Yunnan, but all three populations fall within the variation of *S. belgebaschica* in its type region of Altay-Sayan. Principal source of data for *S. belgebaschica* in type region is IVANIYA (1958).

name *belgebaschica*. The main difference between the Jbel Ou Driss and Altay-Sayan populations of *Siphonophrentis belgebaschica* is that the position of the siphonofossula is random relative to the curvature of the corallum in the Jbel Ou Driss material, whereas it has been described as being on the convex side of the corallum in the Altay-Sayan populations. None of the descriptions of Altay-Sayan material mentions that the sclerenchymal thickening of the septa in the cardinal quadrants may be asymmetric about the cardinal-counter plane. Nevertheless, this kind of asymmetry is shown in several illustrations (ZHELTONOGOVA & IVANIYA, 1961, Pl. D-27, Fig. 4a; IVANIYA, 1965, Pl. 66, Figs. 287, 288; 1966, Pl. 1, Fig. 2).

Specimens of *Altaiophyllum* identified as *Zmeiogorskia sagsayica* (SPASSKIY, 1960a, 1977) from western Mongolia and others from western Yunnan identified as *Altaiophyllum sagsayicum* (WANG, 1994), and the probably synonymous species *A. shidianense* WANG, 1994, have asymmetric sclerenchymal thickening and are very similar to *A. belge-*

baschicum. Compared with specimens from Jbel Ou Driss they have more septa at comparable corallum diameters, but are not distinguished in this respect from populations in the Russian part of the Altay-Sayan (see Text-Fig. 4).

In spite of SMITH & THOMAS' 1963 contribution, *Siphonophrentis(?) subgigantea* (CHAMPERNOWNE, 1984) remains difficult to identify. No significant sclerenchymal thickening of its septa has been demonstrated, although one of CHAMPERNOWNE'S now lost specimens (1884, p. 501, Pl. 22, Fig. 3) was said to have "an illusory aspect of great stoutness of the septa", which CHAMPERNOWNE thought was due to secondary crystallization. Compared to *S. belgebaschica*, *S. (?) subgigantea* apparently has a larger adult diameter, and in at least one probable topology, some major septa have forked adaxial ends (See Pl. 8, Fig. 6).

OLIVER (1993, p. B8) presumed the Siphonophrentidae to have had originally a septal structure that included fine trabeculae. The material from Jbel Ou Driss is not well enough preserved to reveal fine trabeculae, but BIRENHEIDE'S (1978) description of *Siphonophrentis kullmanni* states that the fine septal structure includes small trabeculae. In all other respects, *S. kullmanni* fits well into the morphological variation displayed by the Jbel Ou Driss population of *S. belgebaschica*.

Distribution: *Euryspirifer pseudocheehiel* Beds, Givetian, near the mouth of Bel'gebash River in the Bel'gebash graben, Gorny Altay, southern central Russia (type occurrence). From IVANIYA and co-author's works (1958–1988), the species also occurs in similar *E. pseudocheehiel* bearing beds at numerous localities in the Gorny Altay, including localities on Korgon and Korgonchik Rivers and Korgonskiy Ridge, as well as on the Tyute River of Southeast Altay, the Korkodom River of West Altay, and on the Uchal-Uykaratsh divide in the Uyem depression, Northeast Altay.

Other Givetian occurrences in Altay-Sayan are in the Lebedyanskoe Horizon (= Borodavka Limestone) on Borodavka River in the northwestern Kuzbass (BESPROZVANNYCH, 1964), and in unnamed beds near Ulan Ula in western Mongolia (SPASSKIY, 1960a; WANG, 1994, and L.M. ULITINA collections, Moscow). SPASSKIY thought the Mongolian occurrences to be Eifelian, but they are known now to be Givetian (pers. com. L.M. ULITINA, 1994).

In China, the species occurs in the upper Givetian part of the Upper Heyunzhai Formation near Shidian on the Baoshan-Luxi microplate, western Yunnan (WANG, 1994).

In Spain, the species occurs in the Portilla Limestone, Lower or Middle *varcus* Subzone, of Elsa Valley in León Province (BIRENHEIDE, 1978).

In Morocco, it is probably present in the Eifelian *cockeliani* Zone coral biostrome at Ouahlane, northern Ma'der basin (LE MAITRE, 1947), as well as in the Lower *varcus* Subzone, at Jbel Ou Driss in the southwest part of the Ma'der basin.

Other possible Givetian occurrences of *S. belgebaschica* requiring verification are in the Ossau Valley, western Pyrénées of France (JOSEPH & TSIEN, 1975); Dacht-e-Nawar on the Helmand block of Afghanistan (BRICE, 1970); and a listing from the Akkozu Mountains in the Bayanaul' region of northeastern Kazakhstan (KAPLAN, 1968). This is apparently on the Tarbagatay-Chingiz terrane of FENG et al. (1989, Text-Fig. 2).

Suborder: Ptenophyllina WEDEKIND, 1927

Family: Spongophyllidae
DYBOWSKI, 1873

Subfamily: Ptenophyllinae WEDEKIND, 1923

Genus: *Acanthophyllum* DYBOWSKI, 1873

- e.p. 1873 *Acanthophyllum* – DYBOWSKI, p. 339 (pars = Silurian Rugosa).
- e.p. 1874 *Acanthophyllum* – DYBOWSKI, p. 493 (pars = Silurian Rugosa).
- e.p. 1922b *Mesophylloides* – WEDEKIND, p. 51 (pars = *Mesophyllum* & *Lekanophyllum*).
- e.p. 1923 *Ptenophyllum* – WEDEKIND, p. 26–34 (pars = *Grypophyllum*).
- 1924 *Ptenophyllum* (*Astrophyllum*) – WEDEKIND, p. 46.
- 1924 *Ptenophyllum* (*Rhopalophyllum*) – WEDEKIND, p. 52.
- 1925 *Leptoinophyllum* – WEDEKIND, p. 4.
- e.p. 1925 *Stenophyllum* – WEDEKIND, p. 9, non VERHOEFF, 1897, p. 122 (pars = *Grypophyllum*).

Type species (SCHLÜTER, 1889, p. 296): *Cyathophyllum heterophyllum* MILNE EDWARDS & HAIME, 1851, p. 367, Pl. 10, Fig. 1–1b. Devonian; Eifel, Germany. Thin sections of holotype described and illustrated by COEN-AUBERT, 1997, p. 11, 12, Pl. 1, Figs. 1, 2.

Diagnosis: See COEN-AUBERT (1997, p. 10).

Acanthophyllum heterophyllum
(MILNE EDWARDS & HAIME, 1851)

(Pl. 9, Figs. 1–4, 6, 9)

- 1851 *Cyathophyllum heterophyllum* – MILNE EDWARDS & HAIME, p. 367, Pl. 10, Fig. 1–1b.
- 1937 *Ptenophyllum heterophyllum* (EDWARDS & HAIME) – MA, p. 30, Pl. 7, Fig. 3; Pl. 8, Figs. 1a-2b; Pl. 9, Figs. 1a-2d; Pl. 10, Figs. 1a-2f; Pl. 11, Fig. 2a-e.
- 1947 *Acanthophyllum heterophyllum* MILNE EDWARDS & HAIME – LE MAITRE, p. 41, Pl. 4, Fig. 1.
- 1954 *Rhopalophyllum heterophyllum* (EDWARDS & HAIME) – RÓZKOWSKA, p. 230, Text-Figs. 23–26.
- e.p. 1956 *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME) – MA, p. 58, Pl. 8, Fig. 2; Pl. 20, Figs. 1a-2e; Pl. 21, Figs. 1a-2b; Pl. 22, Figs. 1a-2d; Pl. 23, Figs. 1a-2d; Pl. 24, Figs. 1a-2b; Pl. 25, Fig. 3; Pl. 37, Fig. 5; Pl. 38, Fig. 4?; Pl. 60, Figs. 1, 3, 4; Pl. 61, Figs. 1–5?; Pl. 63, Figs. 6, 7?; non Pl. 35, Figs. 1a-2d.
- 1961 *Acanthophyllum* (*Acanthophyllum*) *heterophyllum* (EDWARDS & HAIME) – BIRENHEIDE, p. 89, Text-Fig. 2, Pl. 1, Figs. 3–6; Pl. 2, Figs. 8a-9; Pl. 3, Figs. 10a-11; Pl. 4, Figs. 12–13 (cum syn.).
- 1969 *Acanthophyllum heterophyllum* (EDWARDS & HAIME) – TSIEN, p. 111, Pl. 43, Figs. 1–5; Pl. 51, Fig. 20.
- 1973 *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME) – BIRENHEIDE, Text-Fig. 2.
- 1978 *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME) – BIRENHEIDE, p. 146, Text-Fig. 90a-d.
- 1981 *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME) – HILL, p. F233, Fig. 146, 3a, b.
- 1997 *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME, 1851) – COEN-AUBERT, p. 11, Pl. 1, Figs. 1–4; Pl. 2, Figs. 5–7 (cum syn.).
- 1997a *Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME) – SCHRÖDER, p. 16, Pl. 3, Figs. 30a-31b.

Material: Two figured specimens, GSC 116655, GSC 116656.

Diagnosis: See COEN-AUBERT (1997, p. 11).

Remarks: The above synonymy list has been assembled primarily to support the distribution given for the species. Most of the identifications excluded from the list were published by COEN-AUBERT (1997, p. 11).

Distribution: In the Eifel, the minimum range of the species is from near the base of the Eifelian Stage, in the Lower Nohn Formation, to the lower Givetian Ahbach

Formation, above the incoming of *Polygnathus hemiansatus*. The species may range higher in the Givetian to the overlying Loogh and Cürten Formations (BIRENHEIDE, 1978). However, unless some of the illustrated "Middle Devonian" specimens from the Eifel are from the Loogh or Cürten Formation, there is no illustration of an *Acanthophyllum heterophyllum* from beds as young as these formations anywhere in Germany.

In the southern Dinant Basin of Belgium and extreme north central France, the species has a similar range, from near the base of the Eifelian (Co2b) to poorly dated Eifelian-Givetian boundary beds (TSIEN, 1969; COEN-AUBERT, 1997). In Poland, *Acanthophyllum heterophyllum* has been figured only from the lower Eifelian Grzegorzowice Formation of the Dobruchna Valley in the Holy Cross Mountains (RÓZKOWSKA, 1954). In Morocco, besides Jbel Ou Driss, a transverse section of the species has been illustrated from the Eifelian *kockelianus* Zone coral biostrome at Ouahlane (LE MAÎTRE, 1947).

Suborder: Columnariina SOSHKINA, 1941

Family: Characterophyllidae PEDDER, 1972

Genus: *Spinophyllum* WEDEKIND, 1922

1922a *Spinophyllum* – WEDEKIND, p. 5.

1978 *Temnophyllum* (*Temnocarina*) YU & LIAO (ms.) – KONG & HUANG, p. 98 (nomen nudum).

1983 *Temnophyllum* (*Truncicarinulum*) – YU & KUANG, p. 253, 275.

1989 *Charisphyllum* – OLIVER & SORAUF, p. 9.

Type species: *Campophyllum spongiosum* SCHLÜTER, 1889, p. 46. Upper Middle Devonian; abandoned Büchel quarry near Herrenstrunden, Bergisch-Gladbach-Paffrath syncline, Bergisches Land, Germany. Species revised by BIRENHEIDE & LÜTTE, 1990, p. 4, Pls. 1–3, and WRZOLEK & WACH, 1994, p. 53, Pl. 2, Fig. 11a, b. The type horizon is referred now to the Büchel Formation.

Diagnosis: See BIRENHEIDE & LÜTTE (1990, p. 3), MCLEAN (1993, p. 110) and WRZOLEK & WACH (1994, p. 52).

Remarks: The genus has been discussed extensively by BIRENHEIDE & LÜTTE (1990, p. 3), MCLEAN (1993, p. 110) and ZHEN & JELL (1996, p. 72). Many of the corals now referred to *Spinophyllum* were previously placed in either *Heliophyllum* HALL, 1846, or *Characterophyllum* SIMPSON, 1900.

Although the types of these three genera are well known, serious taxonomic problems concerning similar carinate species have yet to be resolved. The type and closely related species of *Heliophyllum* have comparatively thin monacanth, which may be simple, branched or bundled, to form three different types of carinae (SORAUF & OLIVER, 1976). Species having thin septa with these kinds of carinae were referred to morphology one by OLIVER & SORAUF (1989). Species referred to morphology two of *Heliophyllum* by OLIVER & SORAUF (1989) have thicker septa in the inner marginarium, but also included forms only doubtfully assigned to the genus with thick, simple but locally branched monacanth, which typically separate or become poorly aligned in the outer marginarium, forming coarse yardarm and zigzag carinae.

A third septal morphology discussed by OLIVER & SORAUF (1989) is displayed by *Charisphyllum altevogti* OLIVER & SORAUF, the type species of the genus from the Givetian Middle *varcus* Subzone of the Cantabrian coast. The most important feature of the *Charisphyllum* morphology is that the monacanth are not only separated peripherally to form yardarm carinae, but adaxially they are

flexed in the characterophylloid manner (PEDDER, 1972, p. 698). OLIVER & SORAUF (1989) questionably assigned *Charisphyllum* to the Characterophyllidae PEDDER, 1972. Subsequent to the erection of *Charisphyllum*, BIRENHEIDE & LÜTTE (1990, p. 2) revived the genus *Spinophyllum* WEDEKIND, 1922, based on a thorough revision of its type species, and placed it in the Zaphrentidae MILNE EDWARDS & HAIME, 1850, of the Cyathophyllidae DANA, 1846a, b. This was followed by a paper by MCLEAN (1993), in which *Spinophyllum* was synonymised with *Charisphyllum* and *Truncicarinulum*, YU & KUANG, 1983, and placed in the Characterophyllidae. WRZOLEK & WACH (1994) also synonymised these three genera, but placed *Spinophyllum* in the Disphyllidae HILL, 1939 (= Columnariidae NICHOLSON, 1879).

SORAUF (1998, p. 53–57, Pl. 2, Figs. 1–4; Pls. 24, 25, Pl. 26, Figs. 1, 2) has recently reassessed the genus *Characterophyllum*, the type genus of the Characterophyllidae, based on an excellently illustrated study of the Upper Devonian type species from the type area in Iowa. SORAUF stressed the non-carinate nature of the septa in *Characterophyllum* and also noted that the axial ends of the septa are periodically dilated. These features separate *Characterophyllum* from *Heliophyllum*, *Spinophyllum* and *Charisphyllum*.

Considerably more data than are currently available are required to elucidate the relationships between carinate and non-carinate Columnariina corals, and those between the Eastern Americas Realm zaphrentids and Old World Realm cyathophyllids. In the absence of these data, and in the interests of taxonomic stability, *Spinophyllum* is here referred to the Characterophyllidae and *Heliophyllum* to the Zaphrentidae. Also, atypical species of *Heliophyllum* questionably included in *Heliophyllum* group two by OLIVER & SORAUF (1989) are transferred to *Spinophyllum*, even though many of them do not show characterophylloid flexing of the trabeculae.

Distribution: *Spinophyllum incompositum* SCHRÖDER (1997a, p. 9, Pl. 1, Figs. 6a–13b), from the Upper Eifelian Freilingen Formation in the Dollendorf syncline of the Eifel, is the earliest well described member of the genus. Other illustrations of the genus are virtually all of Givetian corals from the Devonian Old World faunal realm. Known Givetian occurrences of *Spinophyllum* are as follows: Cantabrian coast of Spain (OLIVER & SORAUF, 1989, Text-Figs. 5A–7G); ? Devonshire, England (MIDDLETON, 1959, Text-Fig. 5b, c); northern Eifel and Inde syncline near Aachen, Germany (LÜTTE, 1984, Pl. 1, Figs. 5, 6; Pl. 2, Figs. 1–4; BIRENHEIDE & LÜTTE, 1990, Pl. 1, Figs. 1, 2, 7–9; Pl. 2, Figs. 10, 12–14); Bergisches Land, Germany (WEDEKIND, 1922a, Text-Fig. 2; HILL, 1981, Text-Fig. 172.3a, b; BIRENHEIDE & LÜTTE, 1990, Pl. 1, Fig. 3; Pl. 3, Figs. 15, 16); northern Sauerland, Germany (BIRENHEIDE & LÜTTE, 1990, Pl. 1, Figs. 4–6; Pl. 2, Fig. 11; Pl. 3, Figs. 17–20); Moravian sedimentary basin, Czech Republic (KETTNEROVA, 1932, Text-Fig. 41; GALLE, 1981, Pl. 34, Figs. 1–4; Pl. 35, Figs. 1–4); Holy Cross Mountains, Poland (SOBOLEV, 1904, Pl. 5, Fig. 4, 4a; WRZOLEK & WACH, 1994, Pl. 1, Figs. 1a–6b; Pl. 2, Figs. 1a–6); Dewal, Helmand block, Afghanistan (MISTIAEN, 1985, p. 196 & collections in Lille) western slope of the southern and central Urals (SOSHKINA, 1941, Text-Fig. 24; 1949, Pl. 36, Figs. 1a–5; 1951, Pl. 12, Figs. 1a–3b; 1952, Pl. 27, Fig. 95; Pl. 28, Fig. 97); eastern slope of the central and northern Urals (SHURYGINA, 1972, Pl. 37, Figs. 2a–3); Sair, Altay-Sayan (ZHELTONOGOVA & IVANIYA, 1961,

Pl. D-52, Fig. 3; Pl. D-53, Fig. 1); western Mongolian part of Altay-Sayan (L.M. ULITINA's collections, Moscow); Chinese (Xinjiang Uygur) part of Altay-Sayan (CAI, 1983, Pl. 34, Figs. 4a-5b); Tarbagatay-Chingiz terrane, Russia (SMELOVSKAYA, 1963, Pl. 43, Figs. 5-7); Guangxi part of the Huanan block, China (YU & KUANG, 1983, Text-Fig. 1, Pl. 1, Figs. 1a-3); Guizhou part of the Yangzi block, China (KONG & HUANG, 1978, Pl. 33, Figs. 4a-5b, 10a, b; BIRENHEIDE & LIAO, 1985, Pl. 2, Figs. 8a-9d; Pl. 3, Fig. 10a, b); Sichuan (Longmenshan) part of Yangzi block, China (HE, 1978, Pl. 63, Figs. 6a-9b; Pl. 64, Figs. 4a-5d; HE & FAN, 1988, Pl. 29, Figs. 2a, b, 4a-5b, 9a, b); Qinling fold belt, China (CAO et al., 1982, Pl. 24, Fig. 1a, b; CAO & OUYANG, 1987, Pl. 31, Fig. 6a-c); Burdekin basin, northern Queensland, Australia (HILL, 1942, Pl. 8, Figs. 5-10b; ZHEN & JELL, 1996, Pl. 11, Figs. 6a-8; Pl. 12, Figs. 1a-3).

***Spinophyllum* sp. nov. A**

(Pl. 10, Figs. 1-5, 7)

Material: Two specimens, GSC 116657, GSC 116658.

Remarks: This new species is characterised by its large size (adult diam. 25 mm; length >60 mm), numerous septa (in order of 40×2 at maturity) and fine monacanthids (diam. mostly 0.1-0.3 mm), which form well spaced carinae in the outer marginarium; the carinae are only rarely of the yardarm type. The species is to be described by M. COEN-AUBERT.

Suborder: Cyathophyllina NICHOLSON, 1889
(in NICHOLSON & LYDEKKER, 1889)

Family: Zaphrentidae
MILNE EDWARDS & HAIME, 1850

Genus: *Heliophyllum* HALL in DANA 1846

1846a *Cyathophyllum* (*Heliophyllum*) – HALL in DANA, p. 356.

1846b *Cyathophyllum* (*Heliophyllum*) – HALL in DANA, p. 183.

1893 *Heliogonium* – CHAPMAN, p. 45.

?1949 *Heliophylloides* – STUMM, p. 18.

Type species: *Strombodes helianthoides* (GOLDFUSS)? HALL, 1843, p. 209, Text-Fig. 87.3, repeated as Fig. 3 on Table of organic remains 48. Renamed *Heliophyllum halli* by MILNE EDWARDS & HAIME (1850, p. lxix). Hamilton Group; figured specimen now mislaid, was from York, Livingston county, New York. The specimen illustrated by MILNE EDWARDS & HAIME (1851, Pl. 7, Fig. 6-6b) has been sectioned and made the neotype of *H. halli* by COEN-AUBERT (1987, p. 152, 153). It is probably from the Givetian Lower to Middle *varcus* Subzone in the Moscow Formation at Leicester (previously called Moscow), Livingston County, New York.

Diagnosis: See OLIVER & SORAUF (1989, p. 5).

Remarks: Some Old World Realm species referred to *Heliophyllum* may have had a cyathophyllid ancestry and not be phylogenetically related to the Eastern Americas Realm Zaphrentidae (COEN-AUBERT, 1996). W.A. OLIVER and J.E. SORAUF are currently studying the *Heliophyllum* species of New York State and adjacent areas. Until this study is completed, the author has little to add to his earlier discussion of the genus (PEDDER, 1990, p. 91).

Typical species of *Heliophyllum* are larger than typical species of *Spinophyllum*, and generally have relatively finer monacanthids which form yardarm and other compound carinae. Their monacanthids are not flexed in the

characterophylloid manner as they are in some species currently referred to *Spinophyllum*. Except in a few species from Spain and the Longmen Mountains of China, true yardarm carinae are rare or absent in *Spinophyllum*.

Distribution: The genus is abundant in Emsian to Givetian faunas of the Eastern Americas Realm, from Québec to Venezuela, and westward, from New York State to Iowa and Missouri. West of the Transcontinental Arch, which separated the Old World and Eastern Americas Realm faunas in Middle Devonian time, *Heliophyllum* is extremely rare. Only three specimens have been seen by the writer. One is a fragmentary Givetian coral from northwestern District of Mackenzie (67° 59' N; 130° 10' W), illustrated in Figures 3, 4 of Plate 11; the others are from the Lower *varcus* Subzone of the Roberts Mountains, Nevada.

The oldest Old World Realm coral currently assigned to *Heliophyllum* is *H. beiliuense* YU & KUANG, 1982 (Pl. 6, Fig. 1a-c) from near the base of the Eifelian in the top-most part of the Beiliu Formation on the Guangxi part of the Huanan block. Other well dated Eifelian species of the genus are from the Eifel and Belgium. These are *H. dahlemense* HALLER, 1936 (Pl. 33; Pl. 34, Fig. 1a-c), from the lower Eifelian Nohn Formation of the Blankenheim (BIRENHEIDE, 1963, Pl. 62, Figs. 63-65; 1978, Text-Fig. 43; COEN-AUBERT, 1996, Pl. 4, Figs. 1-5) and Rohr synclines (BIRENHEIDE & GABRIELLI, 1993, Text-Fig. 3a-c), *H. yakowlevi* HALLER, 1936 (Pl. 36, Fig. 1a, b), from the middle Eifelian Ardorf Formation of the Hillesheim syncline (COEN-AUBERT, 1996, Pl. 4, Figs. 6, 7), and *H. halleri* SCHRÖDER, 1995, from the upper Eifelian, Freilingen Formation in the Dollendorf (SCHRÖDER, 1995, Text-Figs. 4-5b; Pl. 2; Pl. 3, Figs. 11a-12b; 1997b, Pl. 1, Figs. 4a-5b) and Blankenheim synclines (SCHRÖDER, 1997a, Pl. 2, Fig. 14). In Belgium, *Heliophyllum*, referred to *H. dahlemense*, occurs in the uppermost Eifelian, near the base of the Hanonet Formation in southern Dinant basin (COEN-AUBERT, 1996, Pl. 1, Fig. 8; Pl. 3, Figs. 1-5).

An Eifelian or Givetian species of *Heliophyllum*, named *H. qingheense*, has been described from the Beitashan Formation of the Chinese (Xinjiang Uygur) part of Altay-Sayan (CAI, 1983, Pl. 34, Fig. 1a, b). Other imprecisely dated Middle Devonian examples of the genus have been illustrated from subsurface beds of the Moravian sedimentary basin (GALLE, 1993, Pl. 3, Figs. 1, 2).

In addition to northwestern African occurrences, the following Givetian Old World Realm occurrences of *Heliophyllum* are known: Cantabrian coast of Spain (ALTEVOGT, 1968, Pl. 2, Fig. 5a-c; OLIVER & SORAUF, 1989, Text-Figs. 1A-2E, 4A-F); Somerset, England (WEBBY, 1964, p. 3; OLIVER & SORAUF, 1989, p. 5); Holy Cross Mountains, Poland (OLIVER & SORAUF, 1989, p. 5); Armenian part of the Northwest Iranian plate (SOSHKINA, 1952, Pl. 27, Fig. 94); Helmand block, Afghanistan (BRICE, 1970, Pl. 18, Fig. 6); southeastern Altay-Sayan (ZHELTONOGOVA & IVANIYA, 1961, Pl. D-52, 2a-v; IVANIYA, 1965, Pl. 101, Figs. 433-436); Tarbagatay-Chingiz terrane (SMELOVSKAYA, 1963, Pl. 51, Figs. 1, 2); and in the Barimobinsky-Khegenshan suture zone, Nei Mongol, China (GUO, 1976, Pl. 32, Fig. 2a-d; Pl. 33, Fig. 1a, b).

Heliophyllum halli

MILNE EDWARDS & HAIME, 1850

1850 *Heliophyllum halli* – MILNE EDWARDS & HAIME, p. lxix.

1851 *Heliophyllum halli* – MILNE EDWARDS & HAIME, p. 408, Pl. 7, Figs. 6-6b.

- 1987 *Heliophyllum halli halli* MILNE EDWARDS & HAIME – COEN-AUBERT, p. 155, Pls. 1–5 (cum syn.).
 1990 *Heliophyllum halli halli* MILNE EDWARDS & HAIME – PEDDER, Pl. 4.1.
 1997 *Heliophyllum halli halli* MILNE EDWARDS & HAIME – OLIVER, Pl. 1, Figs. 1–4, 7.

Remarks: *Heliophyllum halli* ranges from Emsian to almost the top of the Givetian in New York State (OLIVER, 1997, p. 53, Text-Fig. 1).

***Heliophyllum halli moghrabiense* LE MAÏTRE, 1947**

- e.p. 1947 *Heliophyllum halli* MILNE EDWARDS & HAIME – LE MAÏTRE, p. 31, Pls. 1, 2, Pl. 3, Fig. 1 (syn. includes *H. halli halli*).
 1947 *Heliophyllum moghrabiense* – LE MAÏTRE, p. 35, Pl. 3, Figs. 2, 3.
 e.p. 1970 *Heliophyllum halli* MILNE EDWARDS & HAIME -BRICE, p. 263, Pl. 18, Fig. 6 (non syn.).
 e.p.?1987 *Heliophyllum halli moghrabiense* LE MAÏTRE – COEN-AUBERT, p. 162, Pl. 6.

Lectotype (COEN-AUBERT, 1987, p. 162): Specimen illustrated by LE MAÏTRE (1947, Pl. 3, Figs. 2, 3). The type occurrence is in a Middle Devonian limestone with *Calceola* sp. at Mechra ben Abbou on the Moroccan Meseta.

Diagnosis: Subspecies of *Heliophyllum halli* invariably having (40–43)×2 septa at diameters of 35–50 mm (COEN-AUBERT, 1987, p. 162).

Remarks: The figured specimen and most of the other material definitely assigned to the subspecies by COEN-AUBERT (1987) came from the Eifelian *kockelianus* Zone biostrome at Ouahlane in the northern Ma’der basin. One specimen included in the subspecies by COEN-AUBERT, came from the Lower *varcus* Subzone at Jbel Ou Driss and may not be consubspecific with *H. halli moghrabiense*. The specimen figured by BRICE (1970) is from a Givetian bed at Dacht-e-Nawar on the Helmand block of Afghanistan. A specimen of *Heliophyllum* figured by COTTREAU (1941, Pl. 7, Fig. 6, 6a) comes from the Middle Devonian in either western Algeria, northern

Mauritania or northern Mali, and is known from exterior views only. It is a complete turbinate specimen with about 45×2 septa and a maximum diameter of 77 mm. The number of septa and diameter are greater than allowed by COEN-AUBERT’s diagnosis. However one specimen of *Heliophyllum* from Ouahlane was said by LE MAÏTRE (1947, p. 32) to have 46×2 septa.

***Heliophyllum halli* subsp. undet.**

(Pl. 10, Figs. 6, 8, 9; Pl. 11, Figs. 1, 2, 5, 8)

Material: Three figured specimens, GSC 116659–GSC 116661.

Remarks: These specimens conform to the diagnosis given by COEN-AUBERT (1987) for the slightly older subspecies *H. halli moghrabiense* LE MAÏTRE, 1947, but differ from the illustrated specimens assigned to that subspecies by COEN-AUBERT, by having a narrower tabularium, and extremely thin and very strongly flexed adaxial ends to the major septa. The taxonomic importance of these differences cannot be assessed at the present time. COEN-AUBERT (1987, p. 163) referred her single specimen from Jbel Ou Driss to *H. halli moghrabiense*, but noted that its calice is “excavé” and surrounded by a narrow horizontal platform.

Acknowledgments

The paper draws on knowledge acquired while studying collections from Novaya Zemlya with G.V. LACKOV in St. Petersburg. B. MISTIAEN & J.-C. ROHART provided the opportunity to study collections from Afghanistan in Lille, and L.M. ULITINA kindly allowed the author to study her Mongolian collections in Moscow. W.A. OLIVER, Jr., provided data on Givetian genera of the Eastern Americas Realm. M. COEN-AUBERT shared her knowledge of the Jbel Ou Driss species of *Stringophyllum* and sent photographs of her specimens. A. MAY provided information concerning *Siphonophrentis* in the Sauerland. The generosity of these geologists is much appreciated. Careful reviews by B. HUBMANN and W.A. OLIVER, Jr., led to improvements to the original version of the paper.

B.C. RUTLEY prepared the photographs used in the paper, and D.R. THEN drew the Text-Figures.

Plate 1

***Zonophyllum maderense* sp. nov.**

Lower *varcus* Subzone, Jbel Ou Driss.

- Figs. 1,6,12: Holotype, GSC 116623.
 Two transverse and a longitudinal section, × 2.5.
 Figs. 2,7: Paratype, GSC 116627.
 Transverse and longitudinal sections, × 2.5.
 Figs. 3,8: Paratype, GSC 116630.
 Transverse and longitudinal sections, × 2.5.
 Figs. 4,9: Paratype, GSC 116629.
 Transverse and longitudinal sections, × 2.5.
 Figs. 5,10,11: Paratype, GSC 116625.
 Three transverse sections, × 2.5.
 Fig. 13: Paratype, GSC 116628.
 Longitudinal section, × 2.5.
 Figs. 14,15: Paratype, GSC 116624.
 Transverse and longitudinal sections, × 2.5.
 Figs. 16,19,20: Paratype, GSC 116626.
 Two transverse and a longitudinal section, × 2.5.

***Zonophyllum pegoconus* sp. nov.**

Lower *varcus* Subzone, Jbel Ou Driss.

- Figs. 17,18,22: Paratype, GSC 116638.
 Two transverse and a longitudinal section, × 2.5.
 Figs. 21,23: Paratype, GSC 116635.
 Longitudinal and transverse sections, × 2.5.
 See also Pl. 2, Fig. 9.

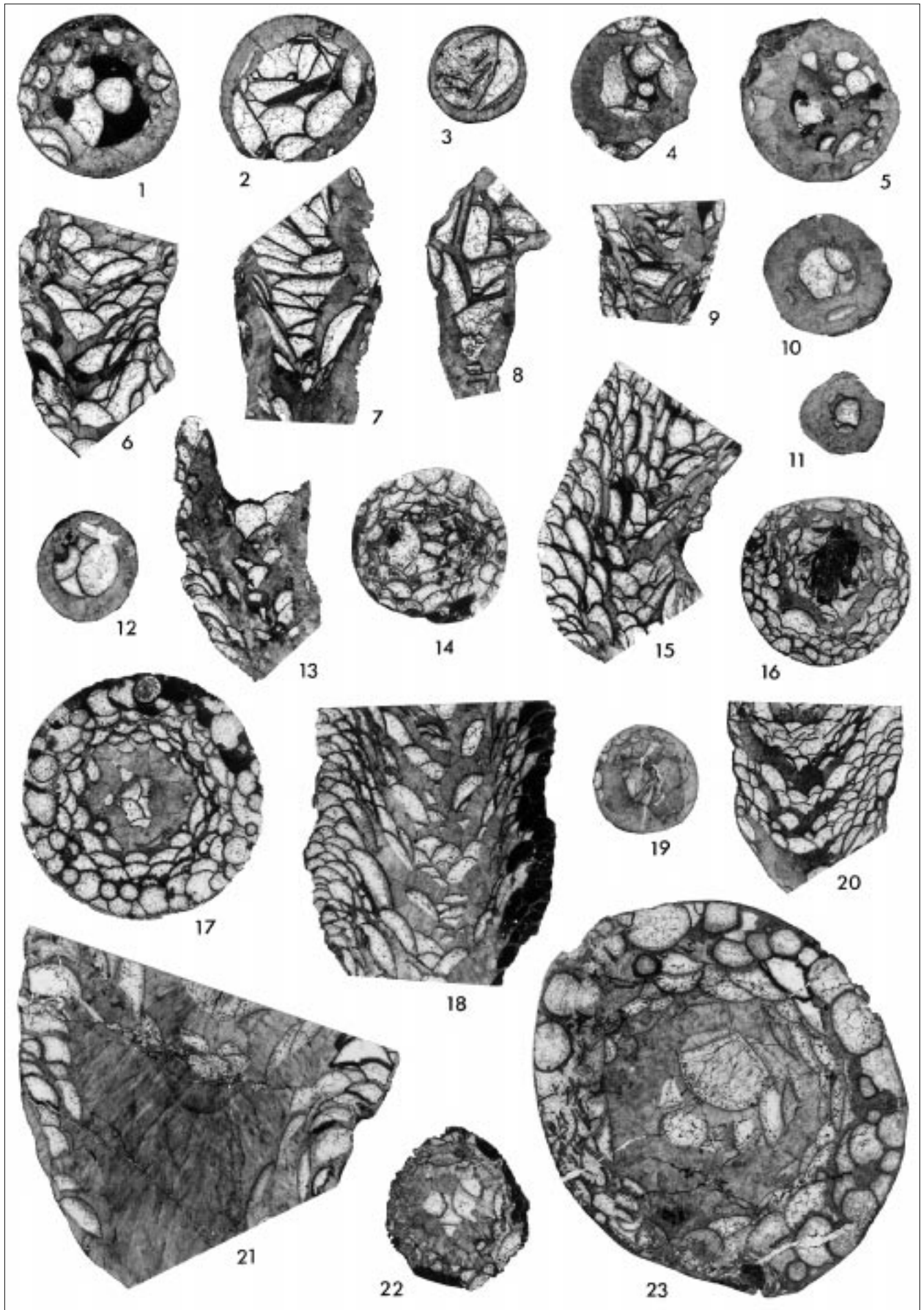


Plate 2

***Zonophyllum pegoconus* sp. nov.**
Lower *varcus* Subzone, Jbel Ou Driss.

- Figs. 1,5,8: Holotype, GSC 116631.
Two transverse and a longitudinal section, × 2.5.
- Figs. 2–4: Paratype, GSC 116636.
Three transverse sections, × 2.5.
See also Pl. 3, Fig. 5.
- Figs. 6–7: Paratype, GSC 116634.
Longitudinal and transverse sections, × 2.5.
See also Pl. 3, Fig. 7.
- Fig. 9: Paratype, GSC 116635.
Transverse section, × 2.5.
See also, Pl. 1, Figs. 21, 23; Pl. 3, Fig. 8.
- Fig. 10: Paratype, GSC 116637.
Longitudinal section, × 2.5.
-

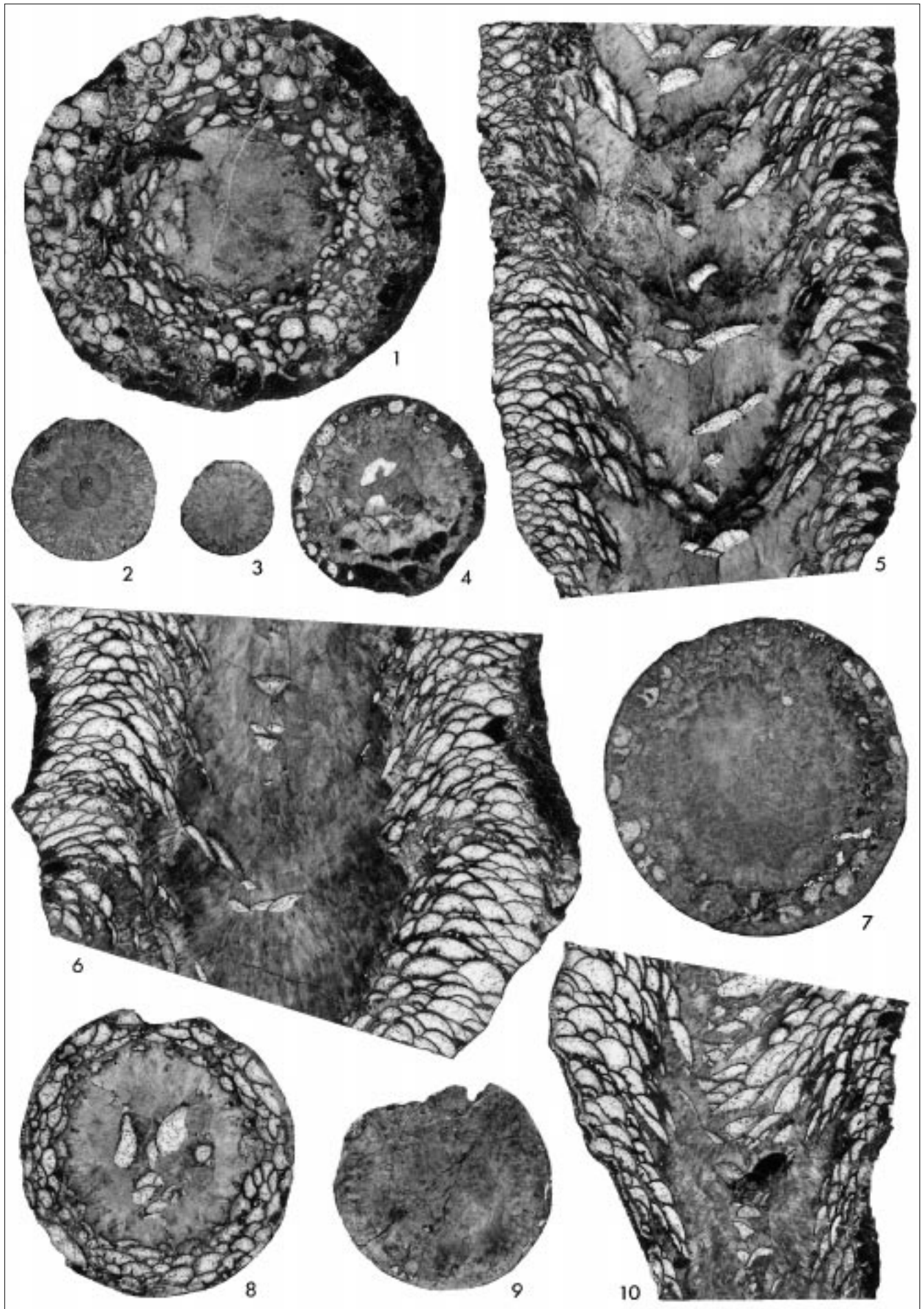


Plate 3

***Zonophyllum pegoconus* sp. nov.**
Lower varcus Subzone, Jbel Ou Driss.

- Figs. 1–3: Paratype, GSC 116632.
Longitudinal and transverse sections, × 2.5
And part of a transverse section, × 7.5.
See also Pl. 4, Fig. 11.
- Figs. 4,6: Paratype, GSC 116633.
Longitudinal and transverse sections, × 2.5.
- Fig. 5: Paratype, GSC 116636.
Longitudinal section, × 2.5.
See also Pl. 2, Figs. 2–4.
- Fig. 7: Paratype, GSC 116634.
Part of a longitudinal section, × 7.5.
See also Pl. 2, Figs. 6, 7.
- Fig. 8: Paratype, GSC 116635.
Part of a longitudinal section, × 7.5.
See also Pl. 1, Figs. 21, 23; Pl. 2, Fig. 9.
-

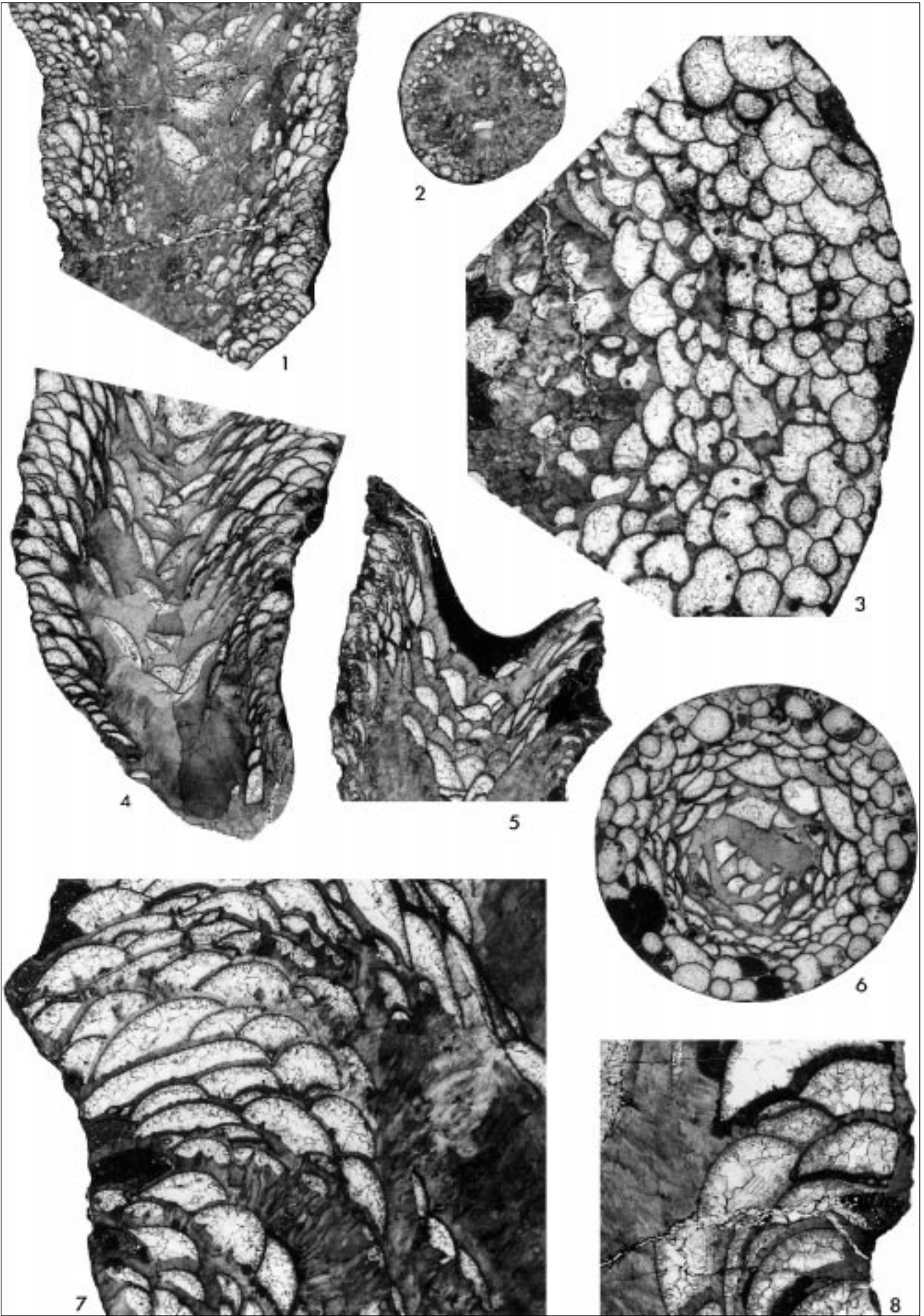


Plate 4

***Lekanophyllum hollardi* sp. nov.**

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 1,2,4-6,8: Holotype, GSC 116640.
Longitudinal and four transverse sections, × 2.5.

Figs. 10,12-14: Paratype, GSC 116641.
Three transverse and a longitudinal section, × 2.5.

***Zonophyllum* sp. indet.**

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 3,7,9: GSC 116639.
Two transverse and a longitudinal section, × 2.5.

***Zonophyllum pegoconus* sp. nov.**

Lower *varcus* Subzone, Jbel Ou Driss.

Fig. 11: GSC 116632.
Transverse section, × 2.5.
See also Pl. 3, Figs. 1-3.

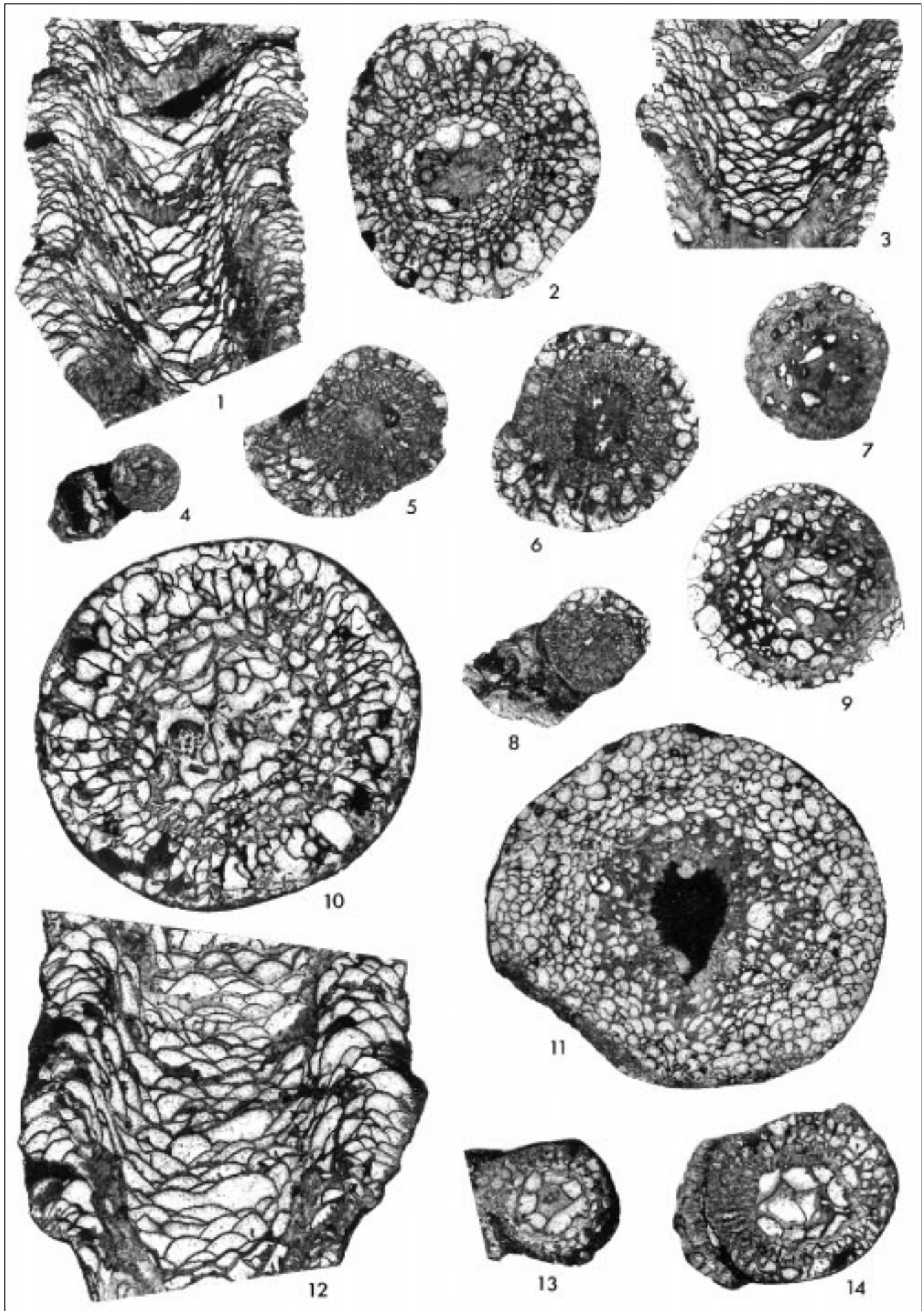


Plate 5

Stringophyllum coenaubertae sp. nov.

Lower *varcus* Subzone, Jbel Ou Driss.

- Figs. 1,2,5: Paratype, GSC 116643.
Two transverse and a longitudinal section, × 2.5.
And part of a longitudinal section, × 7.5.
- Figs. 3,4: Paratype, GSC 116646.
Transverse and longitudinal sections, × 2.5.
- Figs. 6–9: Holotype, GSC 116642.
Transverse and longitudinal sections, × 2.5.
And part of a transverse section, × 7.5.
- Figs. 10,11: Paratype, GSC 116647.
Transverse and longitudinal sections, × 2.5.
-

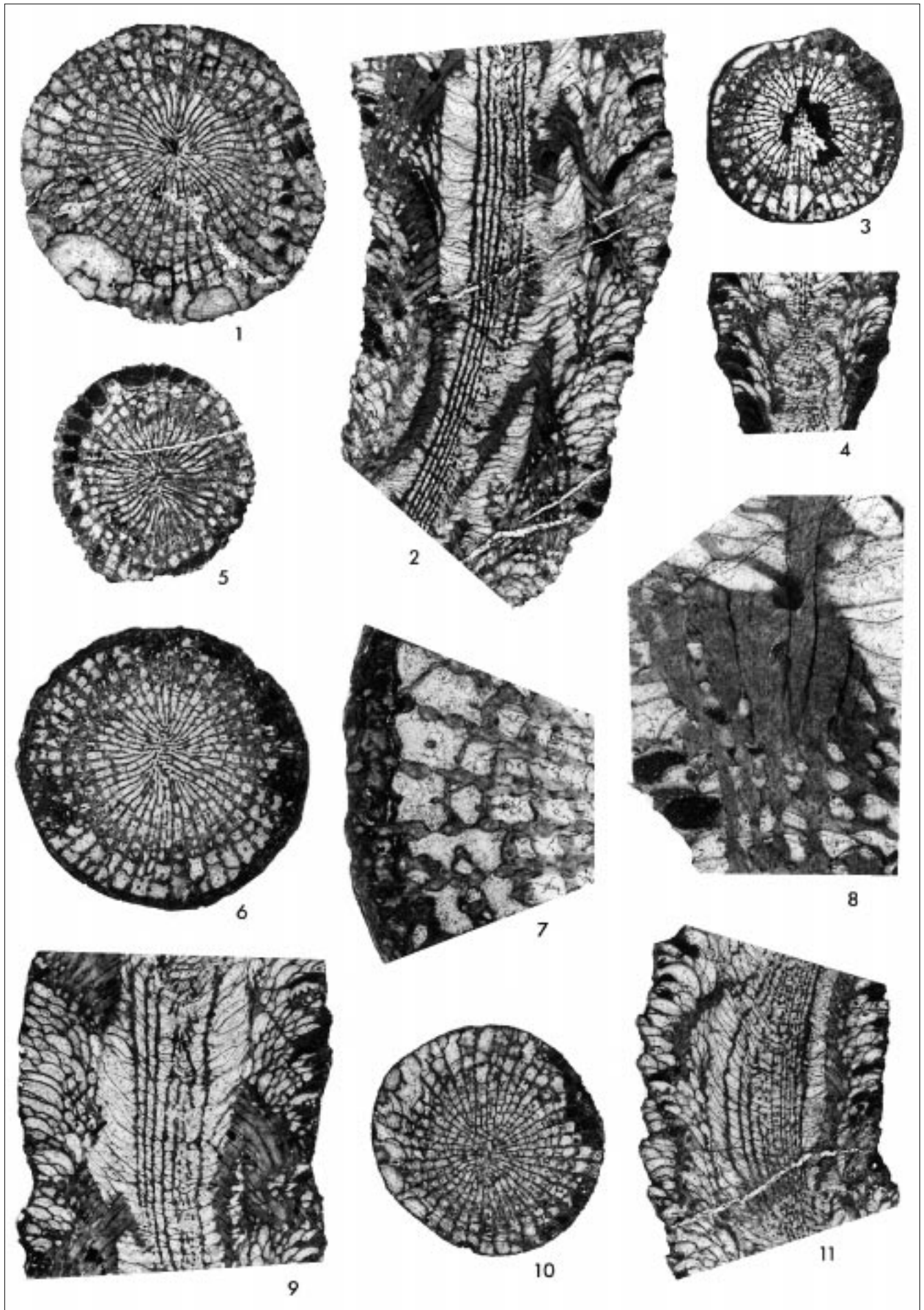


Plate 6

Siphonophrentis belgebaschica (IVANIYA, 1955).

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 1,5: GSC 116650.
Longitudinal and transverse sections, × 2.5.

Figs. 2-4,6: GSC 116651.
Two transverse and a longitudinal section, × 2.5 and part of a transverse section, × 7.5.
Cardinal fossula is on right side of Figure 4.

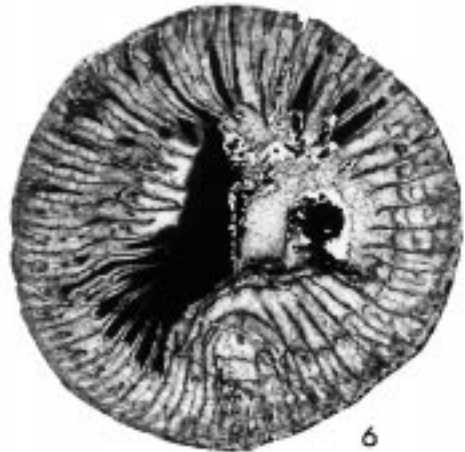
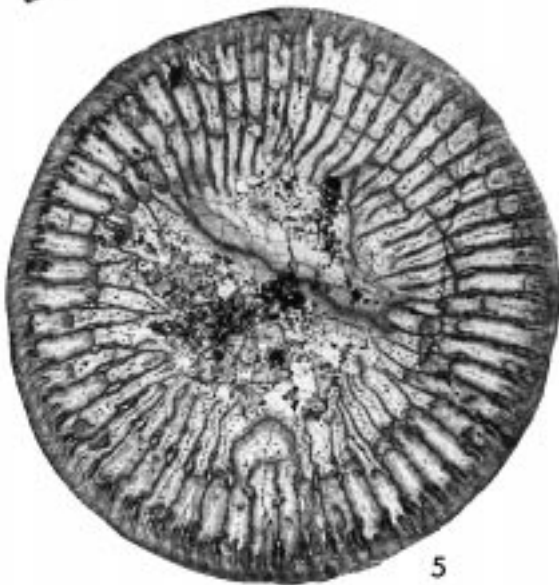
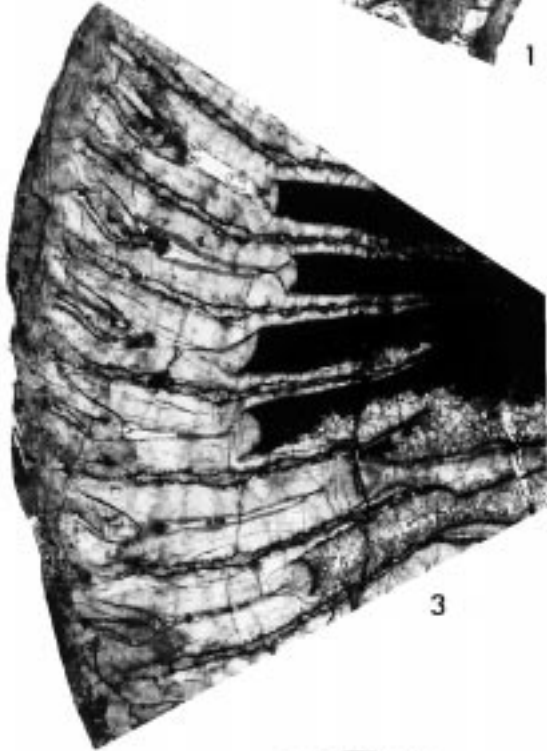
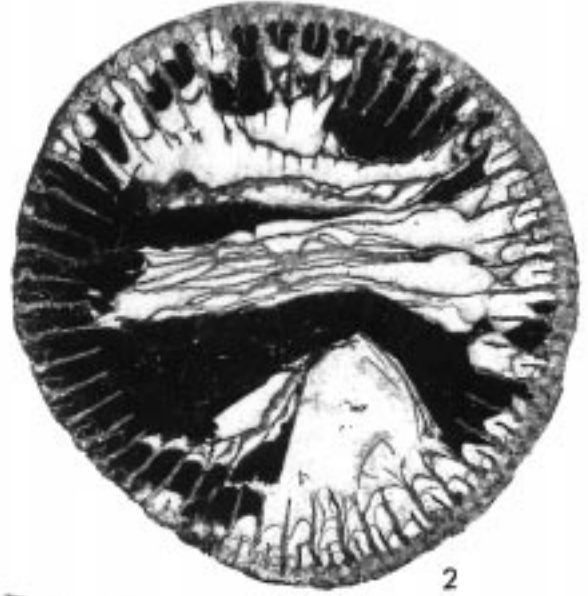


Plate 7

***Siphonophrentis belgebaschica* (IVANIYA, 1955).**

Lower varcus Subzone, Jbel Ou Driss.

- Fig. 1: GSC 116654.
Part of a transverse section with cardinal fossula and septum, × 7.5.
- Figs. 2,4: GSC 116652.
Longitudinal and transverse sections, × 2.5.
- Figs. 3,6: GSC 116653.
Transverse and longitudinal sections, × 2.5.
- Figs. 5,7,8: GSC 116649.
Transverse and longitudinal sections, × 2.5 and part of longitudinal section, × 7.5.
-

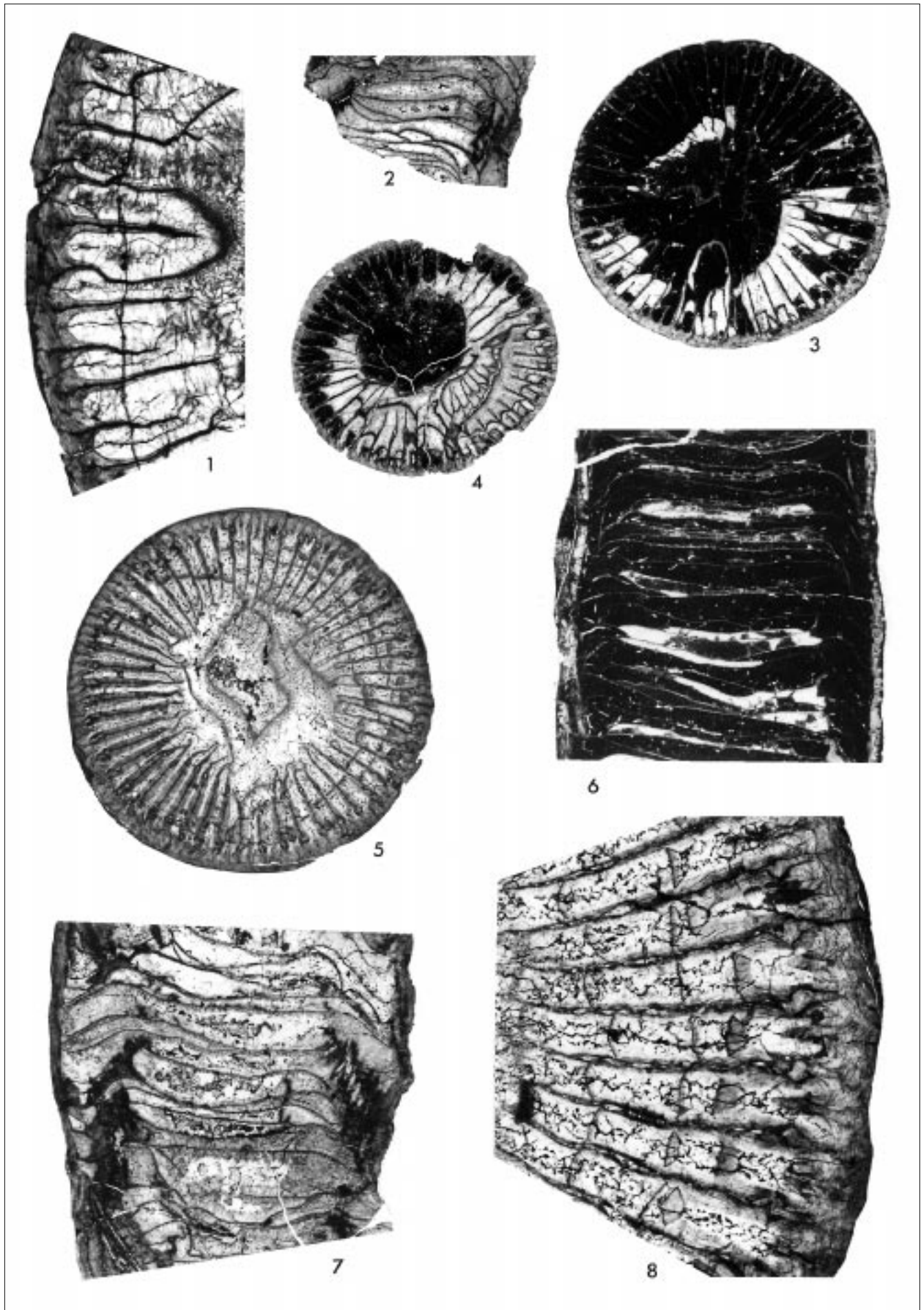


Plate 8

***Thamnophyllum* sp. indet.**

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 1–4: GSC 116662.
Transverse and longitudinal sections, × 4.

***Incertae sedis* 1.**

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 2,3,5: GSC 116664.
Two transverse and a longitudinal section, × 4.

***Siphonophrentis(?) subgigantea* (CHAMPERNOWNE, 1884).**

Lummaton shell bed, *varcus* Zone, Lummaton Quarry, Devonshire.

Fig. 6: Unregistered specimen collected by the author, 1960.
Part of a transverse section, × 7.5.
The forked adaxial ends of some of the major septa make this an atypical example of the genus.

***Siphonophrentis elongata* (RAFINESQUE & CLIFFORD, 1820).**

Anderdon Member of the Lucas Formation, *costatus* Zone, Ingersoll-Woodstock area, Ontario.

Fig. 7: GSC 116666, collected by the author, 1957;.
Part of a transverse section, × 7.5.

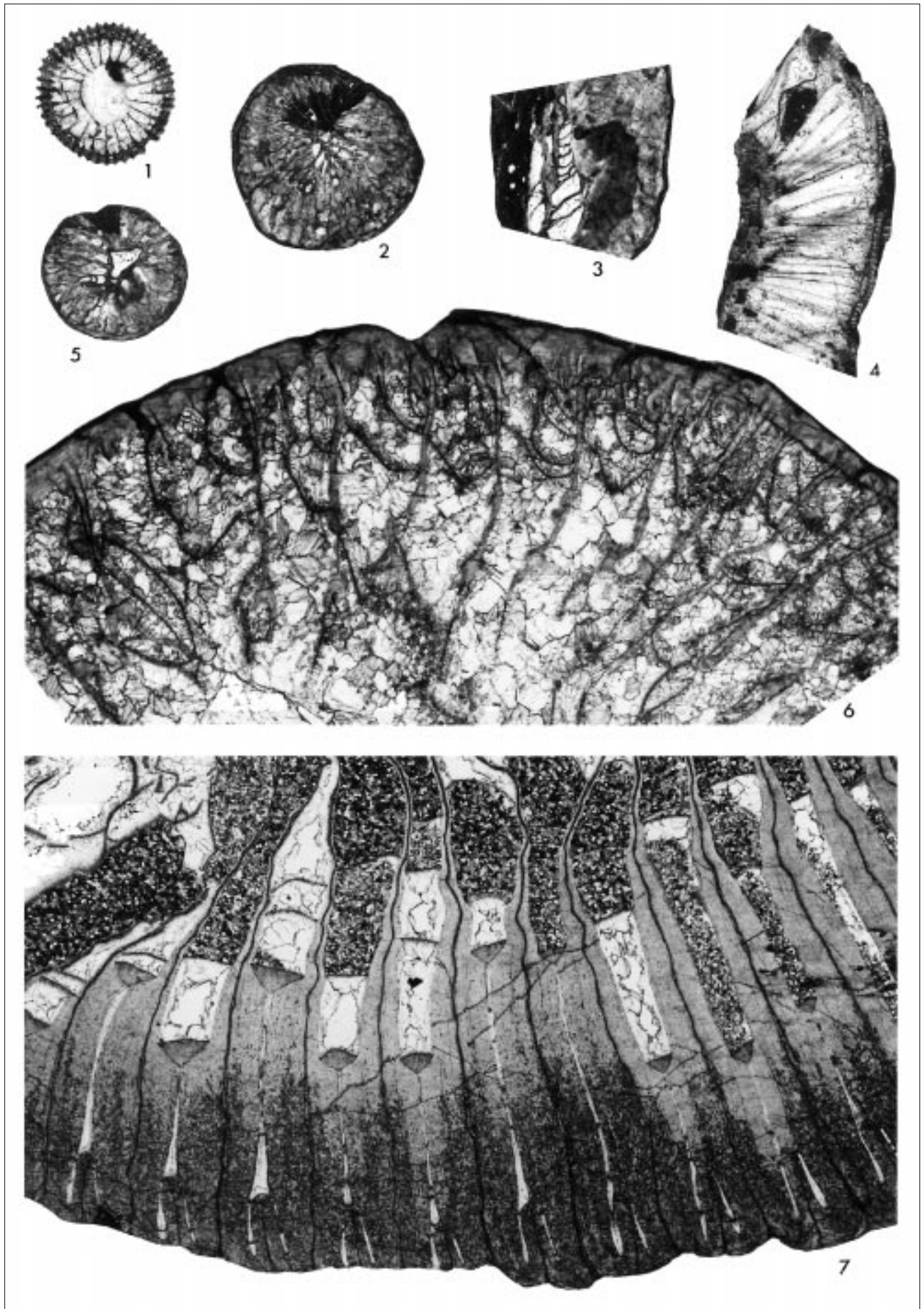


Plate 9

***Acanthophyllum heterophyllum* (MILNE EDWARDS & HAIME, 1851).**
Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 1,3,4,9: GSC 116655.
Two transverse and two longitudinal sections, × 2.5.

Figs. 2,6: GSC 116656.
Transverse and longitudinal sections, × 2.5.

Incertae sedis 2.
Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 5,7,8: GSC 116665.
Two transverse and a longitudinal section, × 4.

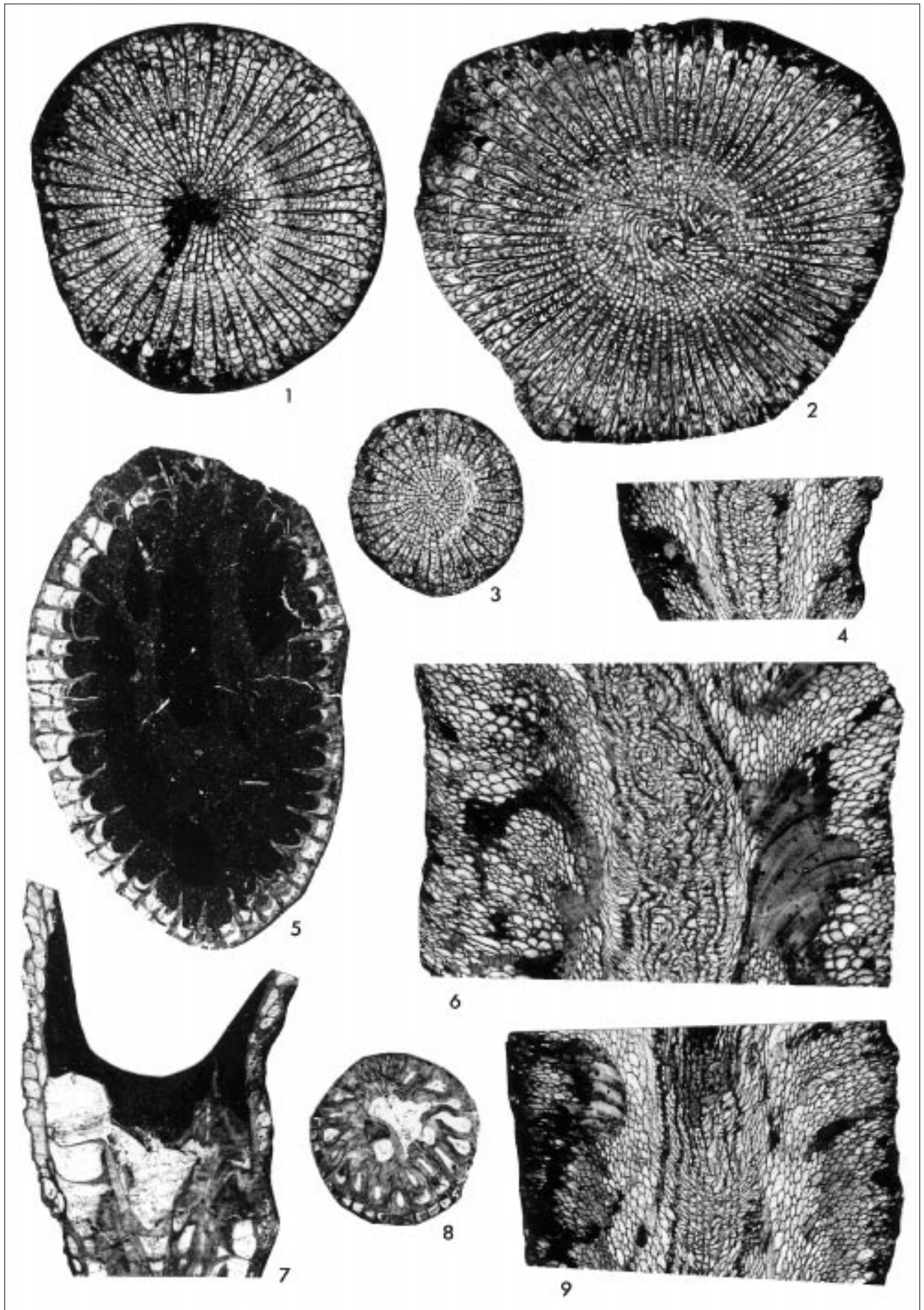


Plate 10

Spinophyllum sp. nov. A.

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 1-5,7: GSC 116657.
Three transverse and a longitudinal section, × 2.5.

Figs. 3,4: GSC 116658.
longitudinal and transverse sections, × 2.5.

Heliophyllum halli MILNE EDWARDS & HAIME, 1850, subsp. undet.

Lower *varcus* Subzone, Jbel Ou Driss.

Figs. 6,8: GSC, 116660.
Longitudinal and transverse sections, × 2.

Fig. 9: GSC 116661.
Part of a transverse section, × 7.5.
See also Pl. 11, Figs. 2, 5.

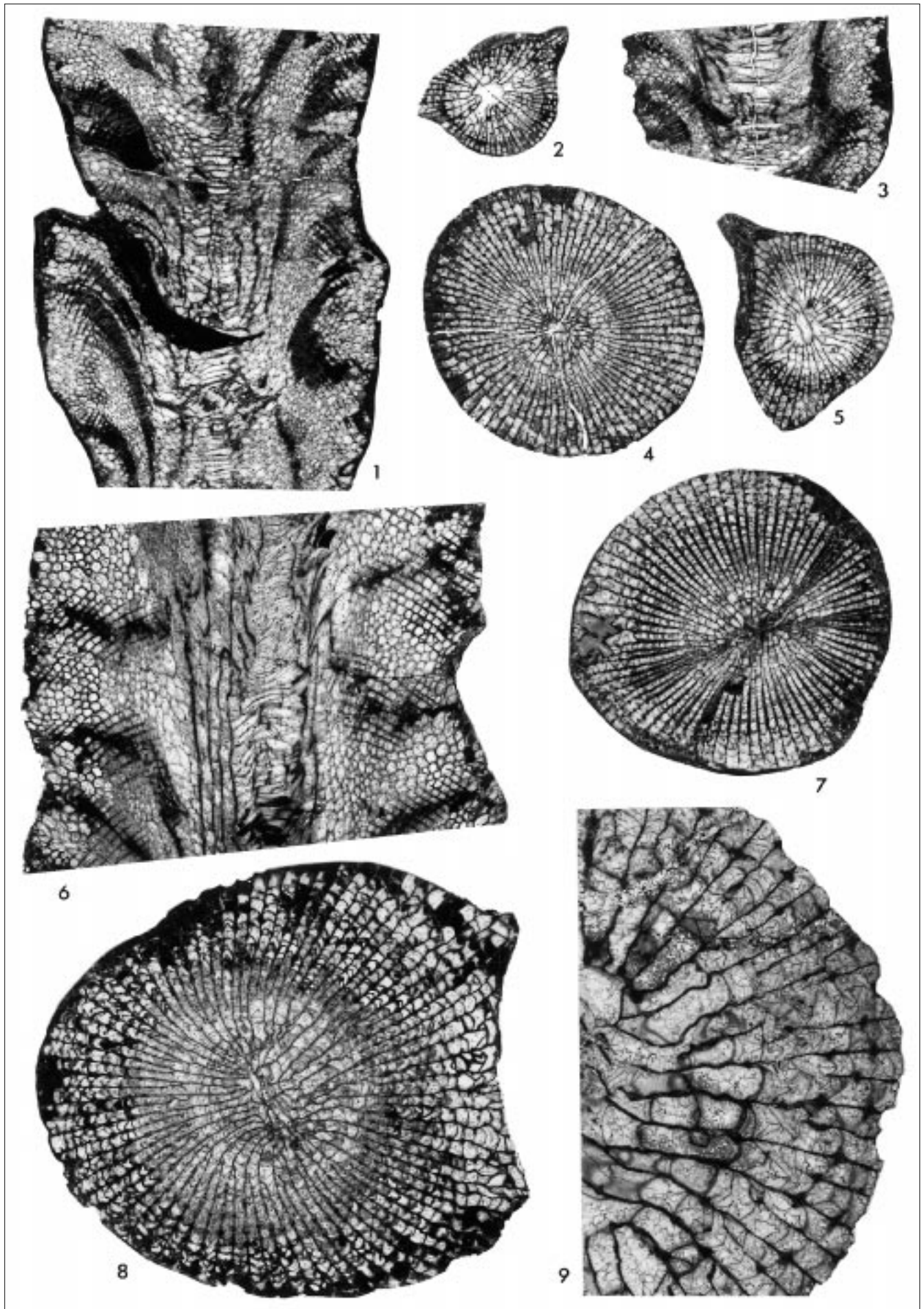


Plate 11

***Heliophyllum halli* MILNE EDWARDS & HAIME, 1850, subsp. undet.**
Lower varcus Subzone, Jbel Ou Driss.

Figs. 1,8: GSC 116659.
Transverse and longitudinal sections, × 2.

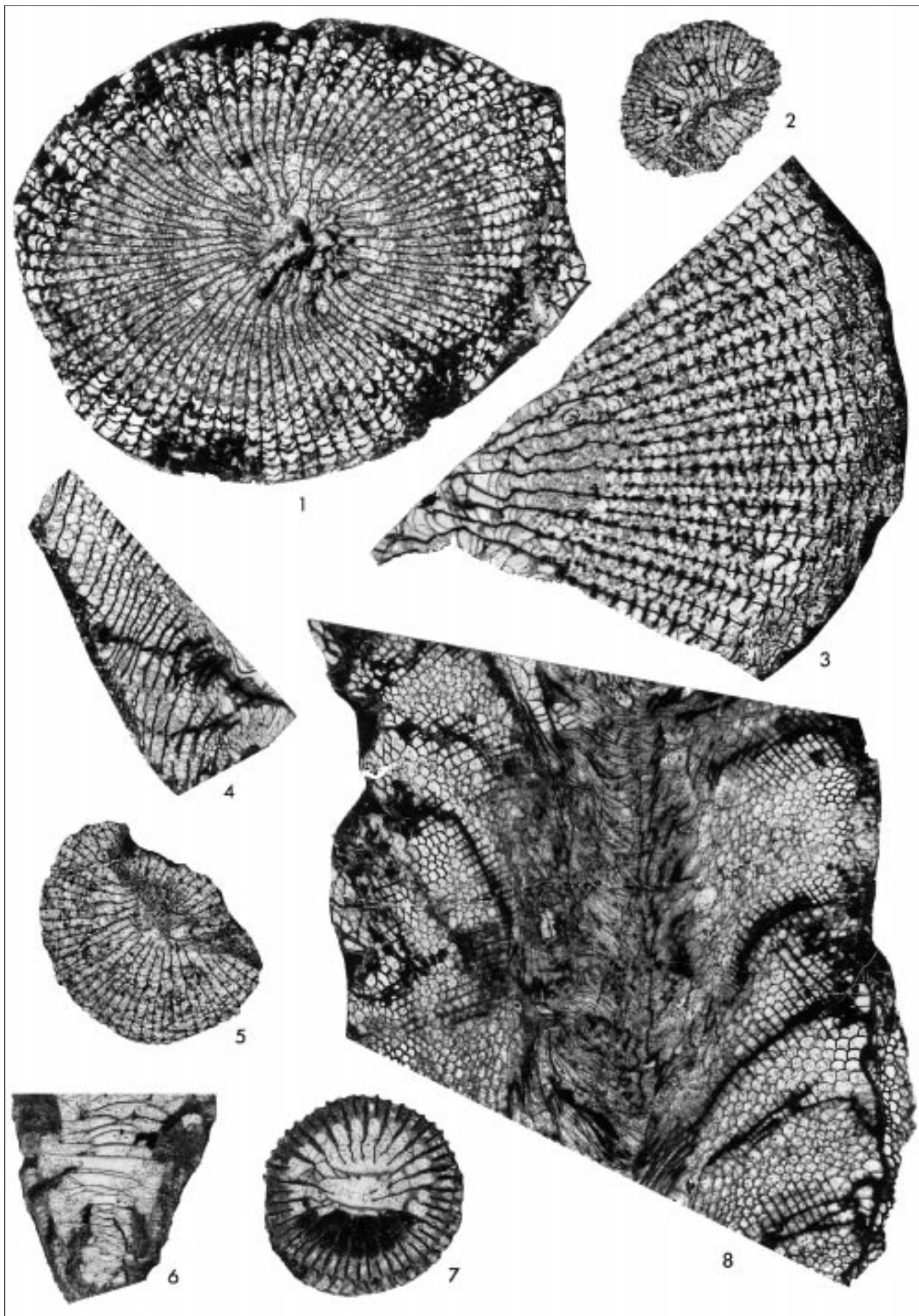
Figs. 2,5: GSC 116661.
Two transverse sections, × 2.
See also Pl. 10, Fig. 9.

***Heliophyllum* sp. indet.**
Givetian, northwestern District of Mackenzie (67° 59' N; 130° 10' W).

Figs. 3,4: Unregistered fragmentary specimen in collections of Shell Canada Limited, Calgary.
Fragments oriented as transverse and longitudinal sections, × 2.5.
Specimen mentioned in section concerning the distribution of *Heliophyllum*.

***Mcgeea* sp. undet.**
Lower varcus Subzone, Jbel Ou Driss.

Figs. 6,7: GSC 116663.
Longitudinal and transverse sections, × 4.



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Manuskript bei der Schriftleitung eingelangt am 2. Oktober 1998