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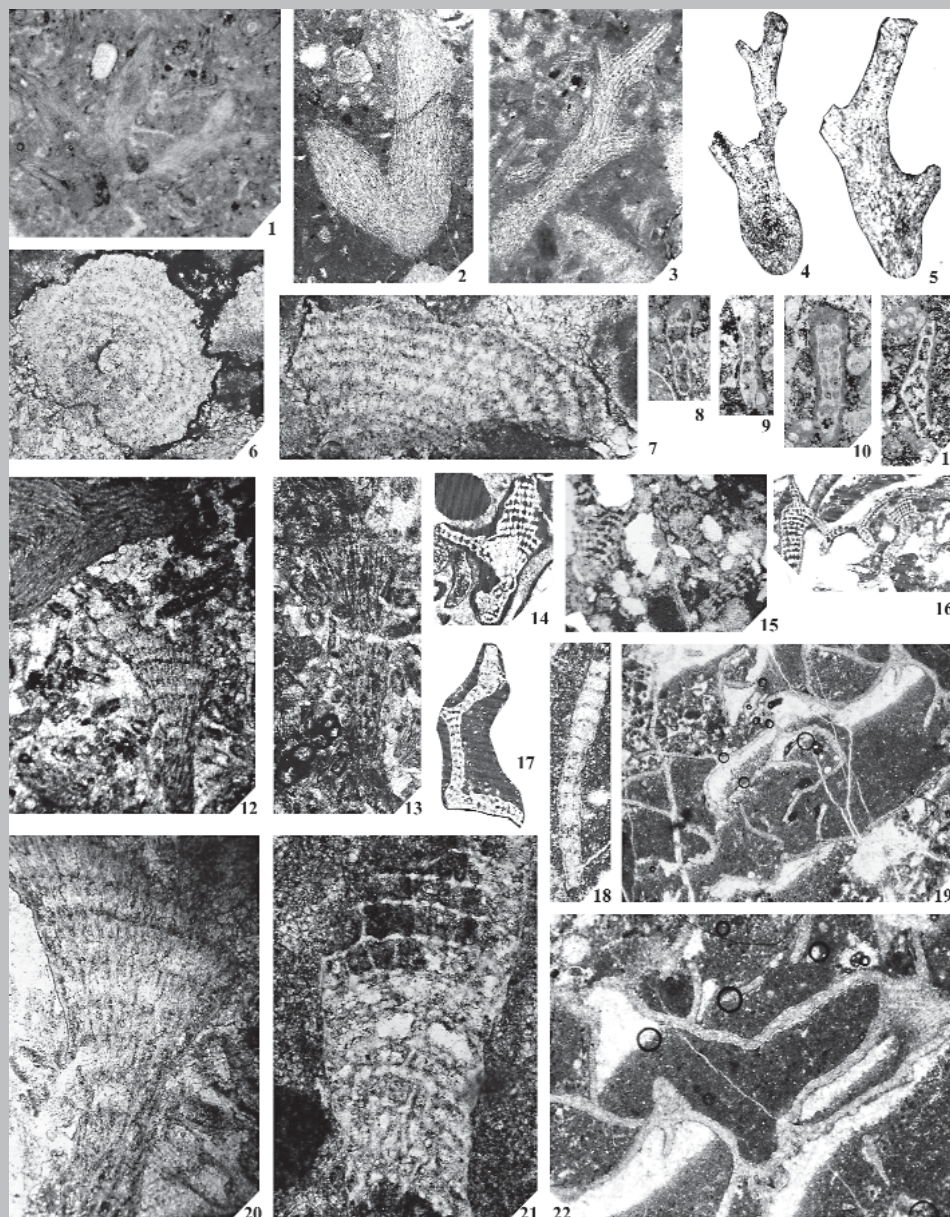
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Portada: Portada: Diferentes especies carboníferas y pérmicas de *Algospongia*. Microfotografías de Daniel Vachard y Pedro Cózar (para explicación, ver lámina 12 en Vachard y Cózar, presente volumen).

Cover: Cover: Some Carboniferous and Permian species of *Algospongia*. Microphotographies by Daniel Vachard and Pedro Cózar (for explanation, see plate 12 of Vachard and Cózar, this volume).

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An attempt of classification of the Palaeozoic *incertae sedis* Algospongia

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Resumen

El presente trabajo presenta una profunda revisión de la clase Algospongia, que es emendada y definida de nuevo de manera exhaustiva. Un mejor conocimiento de la macroevolución y una serie de formas de transición permiten agregar al grupo formas tan diferentes tales como los wetheredélidos, issinélidos, moravammínidos (= Palaeosiphocladales = Palaeoberesellaceae), beresélidos, donezélidos, aoujgálidos y calcifólidos. Dichos conjuntos son generalmente considerados como unidades independientes, con un consenso sobre su naturaleza de algas *incertae sedis*. Cada uno, analizado por separado, tendría más relaciones con las algas rojas, algas verdes, foraminíferos protozoos xenophyophoros o incluso con microesponjas. Se discuten las afinidades biológicas, al menos botánica o zoológica, para establecer una nomenclatura coherente como base de la sistemática precisa de estos microfósiles, en ocasiones tan frecuentes en rocas del Carbonífero y del Pérmico. Sin embargo, ninguno de estos grupos a los que han sido atribuidos los Algospongia permite encontrar auténticos equivalentes actuales. Los diversos miembros de los Algospongia, aunque sean a veces morfológicamente muy diferentes, tienen claras semejanzas entre ellos, especialmente al estudiar el tipo de pared calcárea, similitudes que no comparten con ningún otro grupo a los que fueron propuestos para su clasificación supragenérica. Las algospongas viven en ambientes fóticos (hecho por el que en ocasiones se atribuyeron a las algas verdes), pero en muchas ocasiones, los ambientes en los que se encuentran se han interpretado sin lugar a dudas como disfóticos, en incluso, afóticos. Como resultado del trabajo, se prefieren afinidades a los protozoarios, a su vez con próximas relaciones con los foraminíferos (esqueleto, sistema de fijación, apertura central funcional, cámaras, gran profundidad de algunos biotopos), pero estos últimos, como cualquier otro de los grupos previamente mencionados, no tienen una relación directa con los Algospongia. Los Algospongia tienen una macroevolución que se desarrolla independientemente de la de los foraminíferos de la clase Fusulinata (además muy poco numerosos en el Palaeozoico inferior y el Devónico inferior-medio). Aparentemente los Algospongia, con su primera aparición en el registro fósil en el Ordovícico, co-existen durante mucho tiempo en competencia directa con los foraminíferos sesiles contemporáneos. El acmé de los Algospongia se extiende desde el Devónico inferior hasta el Tournaisiense superior, aunque el Viseense es el periodo en el cual están mejor estudiados. La clase Algospongia está constituida por dos ordenes y seis subordenes, ya descritos al menos al rango de familias: Moravaminida (incluyendo cuatro subordenes: Wetheredellina, Moravaminina, Beresellina y Donezellina), y Aoujgaliida (con los subordenes Aoujgaliina y Calcifoliina), los cuales son brevemente descritos y discutidos. Se revisan todos los géneros ya descritos, enumerando todas aquellas especies que se han considerado incluidas dentro de cada uno de ellos. La revisión y descripción de todas estas categorías taxonómicas, además de emendar alguna de ellas, pero también se describen dos nuevas familias (Asphaltinidae y Cuneiphycidae), cuatro generos nuevos (*Denisella*, *Costacheoides*, *Multiporidium*, y *Fasciolium*) y ocho nuevas especies (*Wetheredella? munnecke*, *Asphaltinoides falgairasensis*, *Tubeus avesnellensis*, *Multiporidium dilectum*, *Aoujgalia woodlandensis*, *Fasciella desquamata*, *Fasciolium pantherinum* y *Calcifolium castelsequense*).

Palabras clave: Incertae sedis, Protozoarios, Algas, Taxonomía, Devónico, Carbonífero, Pérmico.

Abstract

The Algospongia have in common morphological and palaeoecological affinities with different extant groups but no real modern equivalents among the foraminifers, protists, red algae, green algae or calcisponges. The class is based on the following shared characters: 1) similar wall (yellowish, apparently granular); 2) functional apertures (especially a lateral or terminal aperture) which permits the communication between successive chambers or cells; 3) frequent wall perforations; 4) apical growth; and 5) sessile or attached mode of life. Their description is controversial because of the uncertain assignment. The small size of perforations excludes them as calcisponges or microstromatoporoids. They have many characters in common with the foraminifers: e.g., external calcification, potential uniseriate chambers, and terminal aperture. Nevertheless, they differ by the absence of a proloculus, type of calcite unknown, and general evolution. The attribution to other protists remains difficult because of the absence of modern equivalents and the often huge productivity, a character more generally attributed to the algae. However, some similarities with the Xenophyophora are noteworthy. If assigned to the algae, the Algospongia cannot correspond to green algae because of their abundance in dysphotic or aphotic marine environments. They can appear as a group closely linked to red algae because of living depths, some morphological similarities ("cellular" network of *Ungdarella*), and the great variety of groups assigned to the fossil red algae (solenoporaceans, moniliporellaceans, katavellaceans). Following this assignment to red algae, the apertures of the Aoujgaliida are generally considered as synapses; the wall as an equivalent of the cell calcification in the corallinales; attachment bracelets as conceptacles. Moreover, it becomes possible to explain by comparison with the modern corallinales: 1) the abundance of the aoujgaliids, 2) their commonly associated shelter porosities, 3) endosymbiotic filaments, 4) their habituses (often attached or dwelling in soft substrates). Nevertheless, these supposed similarities are only subjective, and counter-arguments can be always presented. The class Algospongia includes two orders and six suborders, previously described at least as families: Moravamminida [with four suborders, Wetheredellina, Moravamminina (= Palaeosiphonocladales), Beresellina, and Donezellina], and Aoujgaliida (with two suborders, Aoujgaliina and Calcifoliina). These orders and suborders are briefly described, discussed, and in some cases emended. The families Asphaltinidae and Cuneiphycidae are created. Four new genera and eight new species are described. They are (in alphabetical order), *Costacheoides*, *Denisella*, *Fasciolium*, *Multiporidium*, *Aoujgaliia woodlandensis*, *Asphaltinoides falgairasensis*, *Calcifolium castelsequense*, *Fasciella desquamata*, *Fasciolium pantherinum*, *Multiporidium dilectum*, *Tabus avesnellensis*, and *Wetheredella? munneckeii*.

Key words: Incertae sedis, Protozoa, Algae, Systematics, Devonian, Carboniferous, Permian.

1. INTRODUCTION

Carbonate microproblematica, informally referred to pseudo-algae, algae *incertae sedis* or palaeosiphonales, are commonly recorded in Palaeozoic carbonates. They are generally assigned to red algae, green algae or not classified (Mamet, 1991). No modern algal equivalents are identified. Owing to similarities exhibited by several genera with Foraminifera or Pharetronidea, the name of pseudo-algae was selected by H. Termier *et al.* (1977), following the ancient informal category of Pia (1937). Nevertheless, this denomination will be abandoned herein because this name also includes other meanings or distinct taxa (e.g., Cavalier-Smith, 2002, p. 314).

Three phylogenetical interpretations have been suggested previously for the representatives of this group: 1) They are atypical members of several orders or classes of red algae, green algae or *incertae sedis* algae, and thus, phylogenetically not linked (Maslov, 1956a; Mamet & Roux, 1975a, 1977; Roux, 1985; Mamet, 1991); 2) they constitute a

phylogenetic group, the class Algospongia, related to the superclass Calcispongia (G. Termier *et al.*, 1977; H. Termier *et al.*, 1977); and 3) they are a complex *incertae sedis* lineage, apparently linked to the animal kingdom, with possible foraminiferal affinities (Vachard *et al.*, 1994).

The class Algospongia is deemed valid here, and it encompasses several *incertae sedis* groups which are phylogenetically linked, due to numerous transitional forms. Its questionable validity has been discussed by previous authors (e.g., Mamet & Roux, 1977, 1978a; Roux, 1985; Skompski, 1980, 1981, 1986, 1996; Mamet, 1991). According to the evolutionary trends and the successive appearances, this class is considered to be composed of the following orders: Moravamminida Pokorný, 1951, *nomen transl.* and *emend.* G. Termier *et al.*, 1975 (with four suborders: Wetheredellina Vachard *in Dil et al.*, 1977, *nomen transl.* and *emend.* herein; Moravamminina = Palaeosiphonocladales Shuysky; Beresellina Vachard, 1994b, *nomen transl.* herein; and Donezellina G. Termier *et al.*, 1975, *nomen transl.* herein); and Aoujgaliida

G. Termier *et al.*, 1975 (with two suborders: Aoujgaliina G. Termier *et al.*, 1975 *nomen transl.* herein, and Calcifoliina G. Termier *et al.*, 1977), all re-described below. Nevertheless, identification and characterization of several genera are difficult because they are endemic to particular areas, rare, in some cases with poor original descriptions and/or illustrations, and indeed, affected by various stages of diagenesis, and thus, their definite attribution to any suprageneric level might remain as questionable.

The Algospongia are recorded from the Ordovician to the Late Permian. The Ordovician-Silurian is characterized by *Wetheredella* reefs. The Issinellidae and Moravamminidae appear in the Late Silurian and are diversified in the Early Devonian. Nevertheless, Gotland Island and the Urals must be studied more for their algosponges. The Givetian (Middle Devonian) is characterized by the presence of *Labyrinthoconus* and the acme of *Moravammina*. The Frasnian (Late Devonian) is poor in Algospongia; *Kleinbergella*, *Pokorninella* and *Evlania* might be used in local biozonations.

From the Early Devonian to lowermost Late Devonian (Frasnian), three areas must be accurately re-described: 1) the outcrops of the Moniello Formation in northwestern Spain (Méndez-Bedia, 1978) are probably the most interesting; 2) the Franco-Belgian Basin (although investigated in detail by Mamet, Prétat and Boulvain in famous monographs); and 3) the Urals, where associated Dasycladales and Caulerpales are well known.

The late Famennian to earliest Tournaisian time interval is characterized by *Serrisnella* and *Uralites*; the Tournaisian by the acme of *Kamaena*. New investigations seem to be necessary in the Baelen limestone in Belgium (Lombard, 1957), and in the Strunian limestones of the type locality, the “tranchée d’Avesnelles”, and the “carrière Bocahut” (all outcrops located in northern France). Apparently, the equivalent beds of the Donbass are favourable for the foraminifers (quasiendothyrids and laxoendothyrids, essentially), but are relatively poor in Algospongia, and poorly described. The outcrops of Sains and Rainsart (northern France) (Mamet & Roux, 1975a) and the Velbert Anticline (Rheinisches Schiefergebirge, Germany) (Herbig, 2006; Herbig & Mamet, 2006) are also interesting to re-investigate.

The FAD (= first appearance datum = oldest appearance) of *Stacheoides* is late Tournaisian in age. *Luteotubulus* is characteristic of the Cf4δ Foraminiferal Subzone in Belgium and more or less coeval in Russia and Morocco, although it first occurs from the Cf4β in Ireland (Jones & Somerville, 1996).

Zidella is characteristic of the latest Asbian in Montagne Noire (southern France), but very poorly known in other regions, Urals excepted. The FAD of *Pokorninella gracilis* and *Epistacheoides* can also characterize the Cf5 (Holkerian) biozone of foraminifers, but further work is necessary to confirm these facts, because the latter is documented in the Arundian in Ireland. The genera *Fasciella* and *Kamaenella* have their acme in the Asbian. The FAD of *Ungdarella* is the principal marker of the base of the latest Asbian. The Calcifoliida are probably the most important guides for the Brigantian-Serpukhovian time with the lineage *Frustulata-Falsocalcifolium-Calcifolium* in some basins. The Beresellina and Donezellina have an acme in the Moscovian. *Fourstonella* emend. (= *Efluegelia* auct.) is abundant in Late Pennsylvanian-Early Permian and a secondary marker in the late Middle Permian and Late Permian, as well as a Lazarus effect of *Donezella* (alias *Alanyana*) and the LAD (= Last Appearance Datum = complete disappearance) of *Stacheoides* and *Ungdarella*. It is interesting to notice that the longevity of *Stacheoides* is closely similar to that of the foraminifer *Tetrataxis*, whereas the FAD and LAD of *Ungdarella* in turn are more or less synchronous with those of the foraminifer *Climacammina*. Nevertheless, these puzzling longevities cannot be actually explained.

Palaeobiogeographically, the Algospongia are mostly concentrated into the northern border of the Palaeo-Tethys (at least since the latest Devonian) and its oceanic and shelf dependencies of the Urals, Canadian Arctic and northern Alaska. Subprovinces can exist but are subordinate to further discoveries.

2. PREVIOUS WORK AND ASSIGNMENTS

Poorly described in the 19th and first half of 20th centuries (Brady, 1876; Maslov, 1929, 1956a; Termier & Termier, 1950; Pokorný, 1951; Kordé, 1951), the knowledge of the Algospongia group began actively with the pioneer work

of Petryk & Mamet (1972) and Mamet & Rudloff (1972) and the successive publications of Mamet & Roux (from 1974 to 1994) and Mamet *et al.*, 1992 and authors using their classification (e.g., Brenckle, 1977, 1985; Groves, 1983; Ivanova, 1988; Bogush *et al.*, 1990). Nevertheless, H. Termier *et al.* (1975, 1977), G. Termier *et al.* (1977), and Vachard *et al.* (1994) proposed alternative hypotheses for this group. In Europe, different works (e.g., Berchenko, 1981; Adams, 1983; Skompski, 1986, 1996; Gallagher, 1996) provided contradictory results. The definitive counterargument was given by the publications on a preserved palaeo-slope in northern Spain (e.g., Della Porta *et al.*, 2002, 2003, 2004, 2005; Bahamonde *et al.*, 2004; Kenter *et al.*, 2005), which described buildups of the so-called dasycladales *Donezella* at 300 m depth. In such a bathymetry, no Recent algae exist (the maximal depth for isolated specimens of living red algae seems to be 250 m; e.g., Adey & MacIntyre, 1973), and only cyanobacteria or animals can survive. Devuyt & Lees (2001) confirmed the relative water depth for some Algospongia (namely, the moravamminids), between 50 and 100 m, in the basal beds of Waulsortian "banks". In fact, all the Moravamminida are not photozoan elements, but can be also heterozoans and support cooler and/or deeper water environments (see definitions and complementary discussions in Reid *et al.*, 2007).

Generally, these microfossils are considered as members of separate groups (i.e., phyla, classes, orders). However, they might be considered, as here, as a monophyletic class, although this hypothesis is not apparently in agreement with the affiliation of extremely varied morphologies to a single group. Nevertheless, bearing in mind a nummulite or a bath sponge, it becomes very difficult to conclude that *Disyringa* or *Discoramulina* (Figs 1.1-1.3) are a sponge and a foraminifer respectively, and not two representatives of the same group.

The unity of the Algospongia is suggested by the occurrence of many transitional forms (see below). Nevertheless, if the group is evidently homogeneous, this latter is globally difficult to assign to an animal or botanical phylum.

The assignment of the Algospongia to the algae by Petryk & Mamet (1972), Mamet & Roux (1974) and Mamet (2006) is usually based on morphological similarities,

without consideration on the microstructure of the wall, the taphonomical behaviour, or the comparative palaeoecology suggested by the entire assemblage.

The genus *Donezella* summarizes the problem because, due to its abundance (60-90%) in diverse microfacies, it can easily be interpreted as the remains of algal meadows. Furthermore, its morphology resembles that of dasyclads but that is impossible because of the palaeobathymetry in which it was recorded in living position (Della Porta *et al.*, 2002). The so-called algal morphology of *Donezella* has been discussed for a long time [e.g., by Pia (1937) criticizing Maslov (1929)]. Although an exact palaeobathymetry is always a controversial debate in palaeontology, it is clear that the modern dasycladales are abundantly living between 1 to 5 m, and are rarely massively transported by storms below 40-70 m (Valet, 1979). Maximal depths for living isolated dasycladales are 50 to 70 or 90 m (De Castro, 1997; Bucur & Sasaran, 2005), whereas *Donezella* is still abundant, *in situ*, at 300 m depth (Della Porta *et al.*, 2002). As a result of this opposite interpretation, the numerous palaeobathymetric models (subdivided into aphotic, dysphotic and photic zones), based on the interpretation of the Algospongia as green and red algae (e.g., Madi *et al.*, 1996), must be revised and independent and coeval Palaeozoic bathymetric markers should be proposed.

2.1. Arguments against their assignment to the Spongia

H. Termier *et al.* (1977) and G. Termier *et al.* (1977) assigned the Algospongia group to the Ischyrospongia (hypercalcified sponges), based on: 1) the genus *Komia* was compared with the microstromatoporoids (Wilson *et al.*, 1963), and the stromatoporoids with calcisponges (Hartman & Goreau, 1970; Termier & Termier, 1973); and 2) similarities with a uniseriate organism, 2.3 mm long, with quadratic chambers which was assigned to "a small calcisponge", *Calymenospongia* Elliott, 1963. However, their conclusion is only valid for some genera, such as *Stacheia* (Fig. 1.5), morphologically similar to a trabecular Sphinctozoa (Senowbari-Daryan, 1991, text fig. 4, p. 230), for example *Stylophthalmia* sp. (Vacelet, 1977, 1979; Gautret, 1985) or the modern Sphinctozoa-like, hypercalcified sponge *Vaceletia* (Vacelet, 1977, pl. 1, figs 6-7;

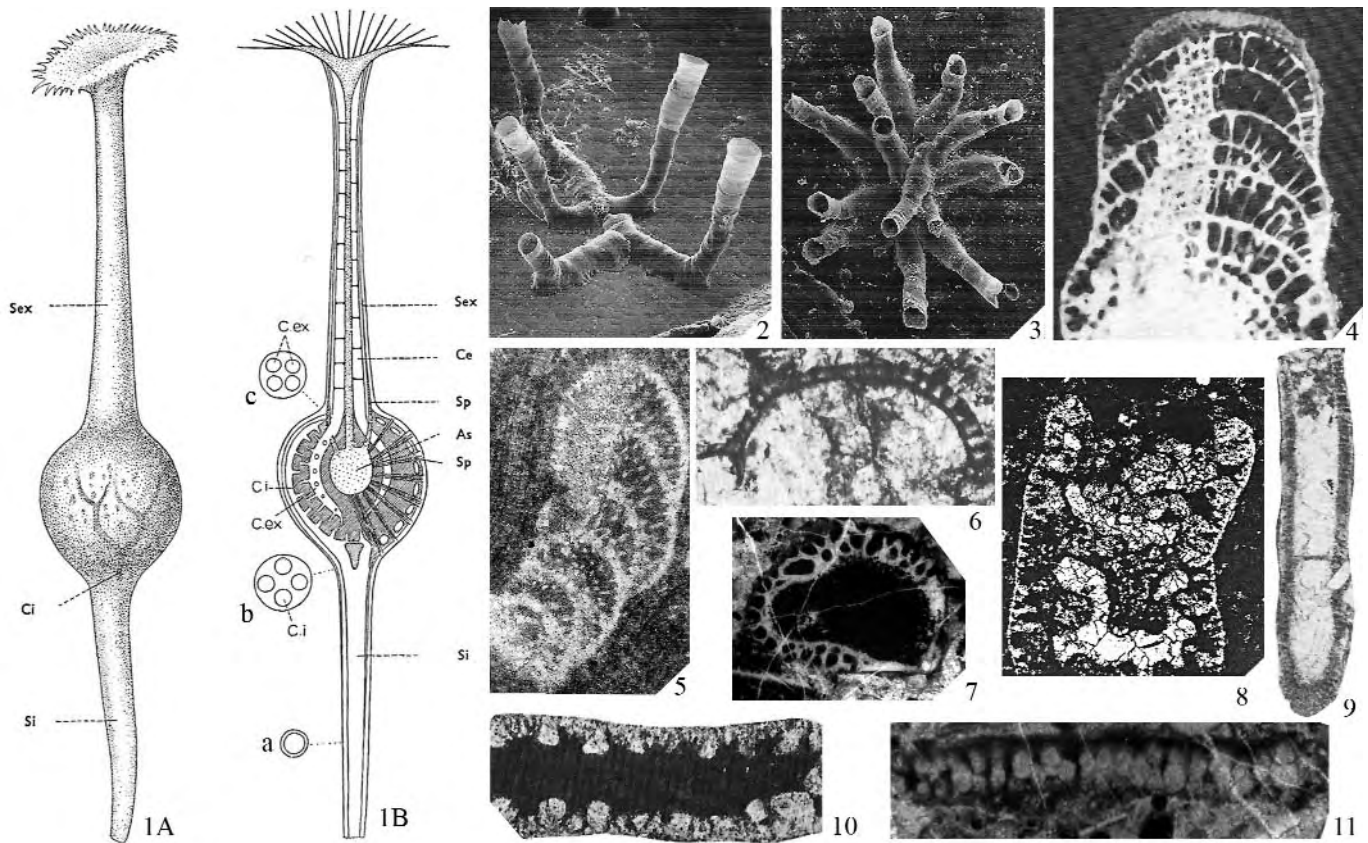


Figure 1. Morphological similarities of the Algospongia with invertebrates. **1**, *Disyrynga dissimilis* Sollas (after Brien, 1973, text-fig. 106, Recent, Torres Strait, Park Darwin, Australia); 1A. Entire sponge (left); x 0.75. 1B. Longitudinal section (right); x 0.75; a-c. Successive transverse sections [a = at the base of the body; b = at level of exhaling tube; c = at level of inhaling siphon (Si)]; Ci = inhaling channels of sponge body, Ce = exhaling channels of body and exhaling siphon, Sp = radial spicules, As = spiculated axis, Sex = exhaling siphon; C = exhaling channels (C.i = inner C, C.ex = external C). This model was initially used by G. Termier *et al.* (1975) to explain the genera similar to *Kettneramma*, *Vasiceckia*, *Uralites* and *Cribrakmaena*. **2-3**, *Discoramulina bollii* Seiglie. A Holocene model for the Moravamminina and Donezellina; according to Harmelin & Venec-Peyré, 1992 (2 = pl. 1, fig. 5; 3 = pl. 1, fig. 6); 2, x 47; 3, x 46. **4**, *Vaceletia crypta* (Vacelet) (after Vacelet, 1977, pl. 1, fig. C), Recent, Iles Glorieuses (France, Indian Ocean); x 11; compare the network of pillars and the perforated wall with that of *Stacheia* (Fig. 1.5). **5**, *Stacheia marginulinooides* Brady (after Vachard & Berkli, 1992, pl. 4, fig. 17). x 55. **6-7, 11**. Misinterpretations between ostracods and algae. **6**, *Hypocaustella cartimanduae* Elliott, 1980 described as an alga (after the text-fig. 2 of Elliott, 1980); Great Scar Limestone (North Yorkshire, England); x 90; see also the “alga” *Vermiporella* of Zupalova (1981a, pl. 40, fig. 1. 9). **7**, A kirkbyid sometimes confused with *Nostocites* (sample 3976, latest Brigantian, South China, location in Vachard *et al.*, 1991); x 55. **8**, *Coscinophragma cribrorum* (Reuss) according to Maync, 1957, text-fig. 2 (Urigo-Aptian, Regenbolshorn, Adelboden, Switzerland, x 21.5), compare the perforations with Fig. 1.10 (see also Fig. 11). **9**, *Uraloporella* sp. showing a diaphragm and the typical finely canalliculate wall (after Roux, 1985, pl. 3, fig. 11); x 35. **10**, *Exvotarissella* (*sensu* Roux, 1985, pl. 3, fig. 7) (Middle Viséan of Great-Britain, x 40); in this case, the wall perforations of *Exvotarissella* are more similar to those of the Textulariata foraminifer *Coscinophragma* of the Fig. 1.8 than a dasycladale (see also Fig. 14). **11**, A true alga *Nostocites* sp. Compare with Fig. 1.7 (sample 3976, latest Brigantian, South China, location in Vachard *et al.*, 1991); x 55.

Gautret, 1985, pl. 1, figs 1-2, 5-6) (Fig. 1.4), which is in fact a keratose demosponge (Wörheide, 2008). Nevertheless, these apparent similarities are only morphological because: 1) the possible spongocoel corresponds actually to the emplacement of the bacillar substrate, and 2) the porosity of the Algospongia is weak and apparently non-functional for a sponge.

Algae and calcisponges can be confused, e.g., a) the probable misinterpretation of *Guadalupia* and *Mizzia* (Mamet

& Roux, 1978a); and b) the calcisponges *Hikorocodium* often considered as dasycladales or problematica (e.g., Kochansky-Devidé & Herak, 1960).

Vachard *et al.* (1994) previously documented arguments against the Spongia-like hypothesis: 1) absence of spongocoel, 2) perforations too thin to be functional, 3) type of calcification, 4) absence of spicules, and 5) differences with the macroevolution of true Calcispongia.

2.2. Arguments against their assignment to the green algae

Many Algospongia have been generally attributed to the Chlorophyta, particularly within the concept of Palaeosiphonocladales, often adopted for designating the Moravamminida. The arguments were: 1) the comparison between *Anthracoporellopsis* and *Anthracoporella* proposed by Maslov (1956a), 2) the *Dvinella* was called *Eomizzia*, and 3) Skompski (1987) advocated for an assignment of *Exvotarisella* to the metaspondyl dasyclads. Many observations are contrary to this hypothesis: pluri-

cellularity, "conceptacles" (*sensu* Saltovskaya, 1984b) (see below), nature of calcification, strong partitions impossible to interpret as intusannulations, and the tufts of *Exvotarisella* are aspondyl (i.e., randomly arranged) and not really metaspondyl (i.e., regularly spaced) as the dasycladales. In order to understand the differences, we provide comparative illustrations of the false metaspondylity of *Exvotarisella* (*sensu* Skompski, 1987); reillustrated here as Figs 2.1, 2.4, 2.7) with a true metaspondylity such as in *Palaeodasycladus* (Figs 2.2-2.3; from Barattolo *et al.*, 1994).

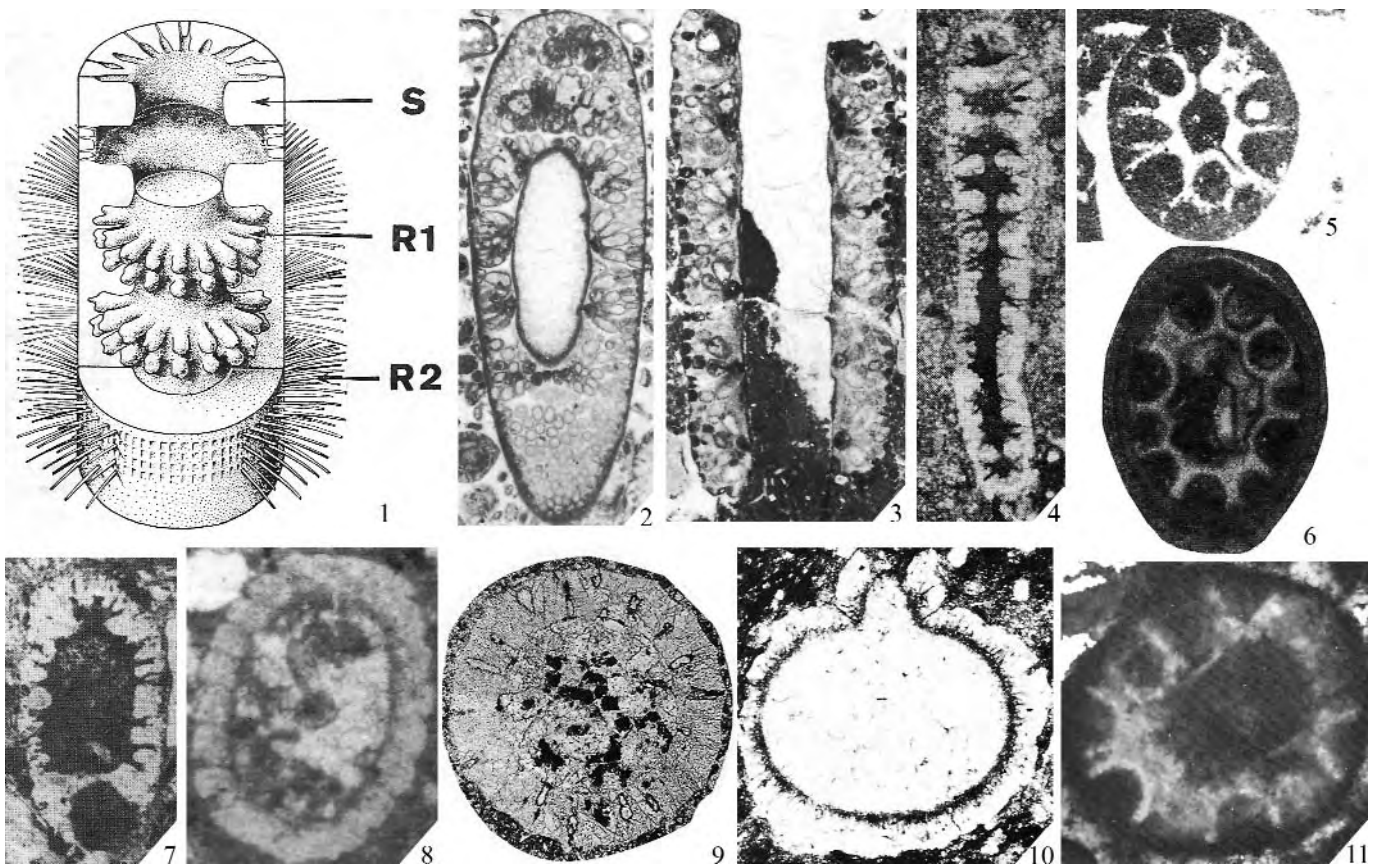


Figure 2. Comparison with the algae Dasycladales. **1-5**, Comparison of the pseudo-tufts of *Exvotarisella* (1, 4, 7) and true tufts of *Eodasycladus barrabei* (Lebouché and Lemoine) (2-3). **1**, Reconstruction after Skompski, 1987, text-fig. 2 p. 26; S = wall, R1 = irregular superficie of the chamber, R2 = perforations through the wall, allowing the passage of cytoplasmic branchlets from chamber to external environment (to compare with Fig. 1.10 and Figs 2. 2-3). **2-3**, True metaspondyl tufts of the dasycladale *Eodasycladus barrabei* (Lebouché and Lemoine) according to Barattolo *et al.*, 1994, pl. 2, figs 1-2; both from Middle Lias of Saint-Chinian, southern France; x 25. **4-5**, *Exvotarisella* in Skompski, 1986, pl. 8, figs 8 (x 100) and 1 (x 90), respectively, Lublin basin, Poland, late Viséan. **6**, *Cyliodroporella sudgeni* Elliott (after Bassoullet *et al.*, 1978, pl. 8, fig. 3 after type material of Elliott); Early Cretaceous, Fahud (Oman), x 54. **7**, *Atractyliopsis* sp. (*sensu* Sebbar & Mamet, 1999) (pl. 2, fig. 10) (Early Bashkirian and early Moscovian respectively; Bechar Basin, Algeria; x 40) (compare with Figs 2.5, 2.11). **8-10**, Different Charophytes. **8**, Cenozoic or Mesozoic Characeae of Sebbar *et al.* (2000, pl. 9, fig. 1), Aouinet-Legraa section, Tindouf Basin, Algeria, x 50; misinterpreted as late Viséan "Scydiales". **9**, True *Sycidium* illustrated by Langer (1976, pl. 25, fig. 12; the wall and organization differ absolutely from Fig. 2.8), Devonian of Eifel (Germany), x 90. **10**, *Chovanella burgessi* Peck & Eyer after Eyer (1971, pl. 5, fig. 5), also different from Fig. 2.9; Cedared Formation, Devonian of British Columbia (Canada), x 75. **11**, *Cyliodroporella* cf. *arabica* Elliott (after Elliott, 1975, pl. 50, fig. 5); oblique-transverse section, Great Oolite (Bathonian) of Gloucestershire (England), x 100. This alga, which belongs in fact to *Holosporella siamensis* (= *Sarfatiella dubari*) (Granier, pers. comm., October, 2010) represents another assignment for the false *Atractyliopsis* Sebbar & Mamet, 1999 (see above Pl. 2, fig. 7).

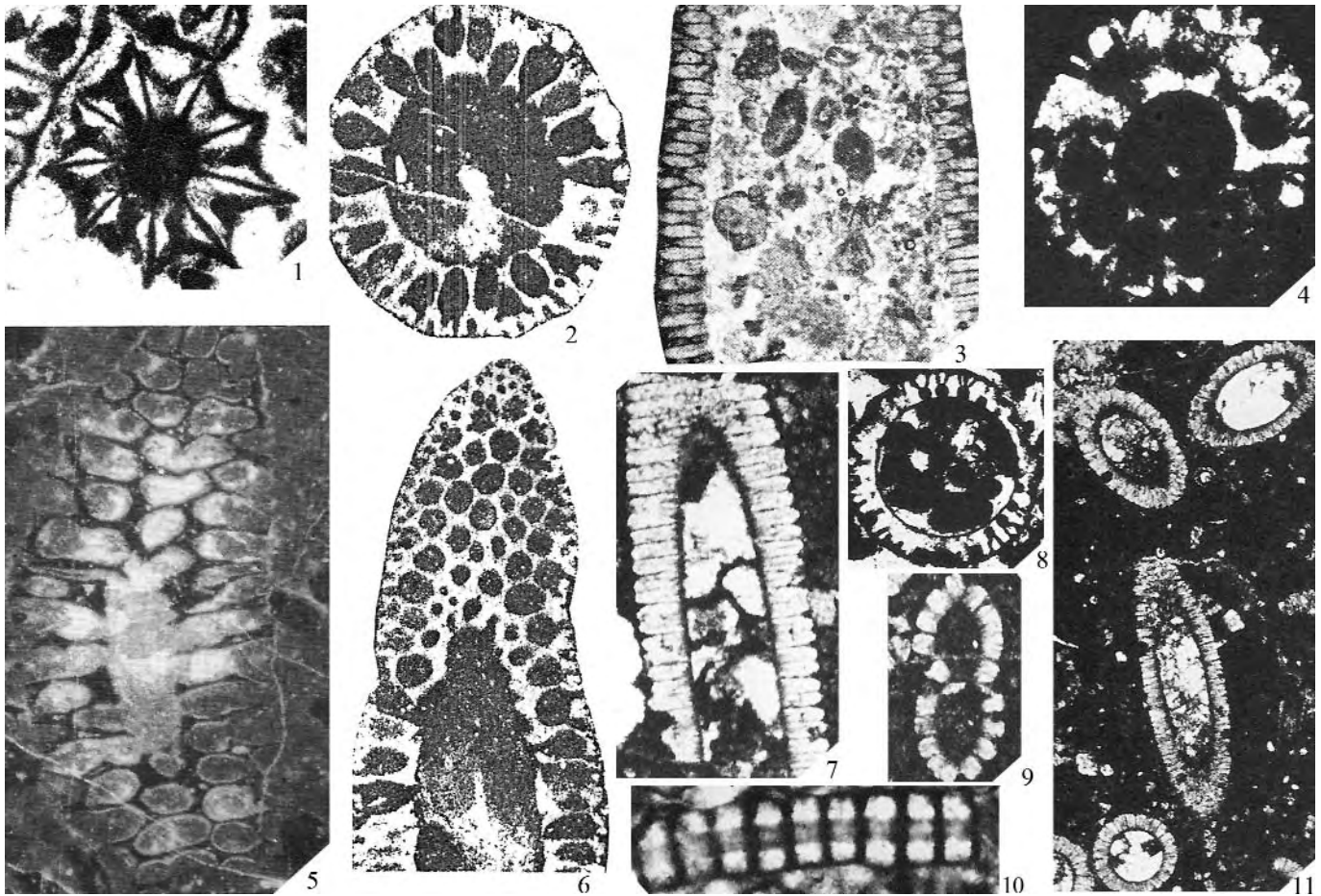


Figure 3. Atypical “dasycladales”, Lazarus issinellids and possible misinterpretations of *Zergabriella* and *Koninckopora*. **1**, *Clypeina jurassica* Favre (this specimen should be quoted as *C. sulcata*, according to Granier, pers. comm., October, 2010); bilayered atypical “dasycladale”, after Bassoullet et al., 1978, pl. 4, fig. 5; Berriasian, Val de Fier, France, x 107. **2**, *Zergabriella embergeri* Bouroulllec & Deloffre; oblique section of another bilayered atypical “dasycladale”, after Granier (1989, pl. 1, fig. 6), Berriasian, Provence (France), x 60. **3**, *Koninckopora pruvosti* Güvenç (*sensu* Mamet & Roux, 1975a, pl. 3, fig. 1; *part.*) third bilayered atypical “dasycladale”. Early Asbian, Great Britain, x 18.75. **4**, **6**, *Hoegenites kringla* Nitecki & Spjelnaes; after Nitecki & Spjelnaes, 1989 (figs 2. 2 and 2. 10 respectively); this “Ordovician tubular microporellid” (sic) is evidently something similar to *Cymopolia*, the paragon of Cenozoic-Recent dasycladales (compare with Fig. 3.4); Helgøya (9 km north of Oslo, Norway); indicated as Caradocian (Ordovician) in age. x 32.5. **5**, *Cymopolia barberae* Elliott, 1968, pl. 8, fig. 2; transverse section, Palaeocene/ Early Eocene, Iraq, x 50. **7**, **8**, **11**, *Hensonella cylindrica* Elliott questioned here as an issinellid Lazarus effect, after Elliott, 1968, pl. 22, figs 3, 5, 1 respectively; Early Cretaceous, Qamchuqa Formation, Iraq, 7, x 45, 9, x 45, 11, x 27. **9**, *Dissocladella savitriae* Pia, after Elliott, 1968, pl. 11, fig. 1, Palaeocene, Sinjar Formation, Iraq, x 25; another dasycladale similar to *Hoegenites*. **10**, *Salpingoporella apenninica* Sartoni and Crescenti, after Elliott, 1968, pl. 20, fig. 5, Late Jurassic, Najmah Formation, Kirkuk well, Iraq, x 45 (*S. apenninica* is a junior synonym of *S. annulata*, according to Granier, pers. comm., October, 2010); true euspondyl dasycladale confused with *Hensonella*. The shape is similar, but the wall is different.

Within the published arguments by Mamet & Roux (1978a) for an assignment to algae, there are the great concentrations of Palaeoberesellidae and Donezellidae which corresponds more to algal accumulations. Nevertheless, the assignment to the green algae especially to dasycladales seems not to be plausible in such aphotic and disphotic environments. Morphologically also, *Exvotarissella* differs from the dasycladale because: a) the perforations (often interpreted as dasyclad laterals) are not really verticillated [compare e.g., Dil et al. (1977) and

Skompski (1987) with De Castro, (1997)], and the groups of canalicules are in fact aspondyl and not metaspondyl tufts (Dil et al., 1977, fig. 14); b) the regular septation is not equivalent with a dasyclad intusannulation (see definition in De Castro, 1997, p. 187); and finally c) *Exvotarissella* can exhibit a monocristalline extinction (in cross-polarised light), that is absolutely unknown among the dasycladales.

The most important counterargument was always the original aragonitic nature of the calcification in dasyclads,

demonstrated in dasycladale specimens from the Ordovician, *versus* the originally calcitic nature of the tests of the Algospongia (see below in the discussion of *Hensonella*).

Furthermore, many Algospongia seem to be well adapted to dysphotic environments (as well as the modern red algae), more than to photic environments, in which the green algae, especially dasycladales, are predominant. The evolution of the dasycladales differs entirely from that of Algospongia. Moreover, this evolution of the dasycladales appears markedly homogeneous since the Ordovician because there are Ordovician dasyclad algae *Hoeegenites* Nitecki & Spjeldnaes, 1989 [see revisions in Mamet & Pr at (2005) and Mamet (2006)] remarkably similar to the Mesozoic, Cenozoic or Recent *Cymopolia* (compare with Elliott, 1968; Bassoullet *et al.*, 1978; Mu, 1982; Deloffre & G enot, 1982) (Figs 3.2, 3.4, 3.6, 3.8). As other cases of morphological repetitions in the evolution of dasycladales, we can quote 1) the "bauplan" of some Devonian and Carboniferous seletonellaceans and diploporaceans is repetitive (see, for discussion, Vachard *et al.*, 2001, and Pille & Vachard, in press); 2) the Vis ean dasyclad of Sebbar & Mamet (1999, pl. 2, fig. 10) is not very different from an Early Cretaceous *Cylindroporella* (compare with Elliott, 1968, 1975, pl. 40, fig. 4; Bassoullet *et al.*, 1978) (Figs 2.5-2.6, 2.11).

Finally, in this section on biostratigraphically ambiguous Palaeozoic taxa, we can add: 1) the gyrogonites of Mesozoic or Cenozoic Charophytes interpreted also as Vis ean Sycidiales (Sebbar *et al.*, 2000, pl. 9, figs 1-3; compare with Langer, 1976, and herein Figs 2.8-2.10), and 2) some Carboniferous ornamented ostracodes occasionally interpreted as algae, especially *Nostocites*: e.g., *Hypocaustella* Elliott, 1980, and the false *Nostocites* of Mamet & Roux (e.g., 1978b, pl. 7, figs 1, 3; 1983, pl. 10, figs 12-13), Mamet *et al.* (1987, pl. 30, fig. 1), Sebbar & Mamet (1996, pl. 3, fig. 3) or Toomey & Windland, 1973 (text-fig. 7F p. 1062) (see also the *Hedraites* of Toomey *et al.*, 1977, fig. 8L; and Krainer *et al.*, 2003, pl. 6, fig. 8) (Figs 1.6-1.7, 1.11). Misinterpreted Chlorophyta are re-interpreted here (Table 1).

2.3. Arguments against their assignment to the Foraminifera

Several Algospongia were interpreted as Foraminifera because they exhibit some of the following characters: a comparable geometry and size of chambers, a relatively large central aperture, complete mineralization in calcium carbonate of the often perforated wall, and especially a uniseriate development of chambers. For instance, Poko-

Groups attributed to Chlorophyta in the literature		Assignments proposed herein	
1	Codiaceae	Codiaceae	
2	Codiaceae	Cyanobacteria Garwoodiaceae	
3	euspondyl and metaspondyl Dasycladaceae	True Dasycladaceae	
4	aspondyl Dasycladaceae	Vermiporellaceae Analiporaceae Seletonellaceae	not necessarily Dasycladales
5	Dasycladaceae (<i>Koninckopora</i>)	Not necessarily dasycladales (but distinct of 4)	
6	Moravamminida	Algospongia	
7	Issinellideae	Algospongia	
8	Beresellideae	Algospongia	
9	Calcifoliina	Algospongia	
10	Wetheredellida	Algospongia	
11	Phylloid algae	Rhodophyta + microsparitization + endolite bacteria	
12	Gymnocodiaceae	Rhodophyta	

Table 1. New assignments of 12 groups occasionally considered as green algae in the micropalaeontological literature.

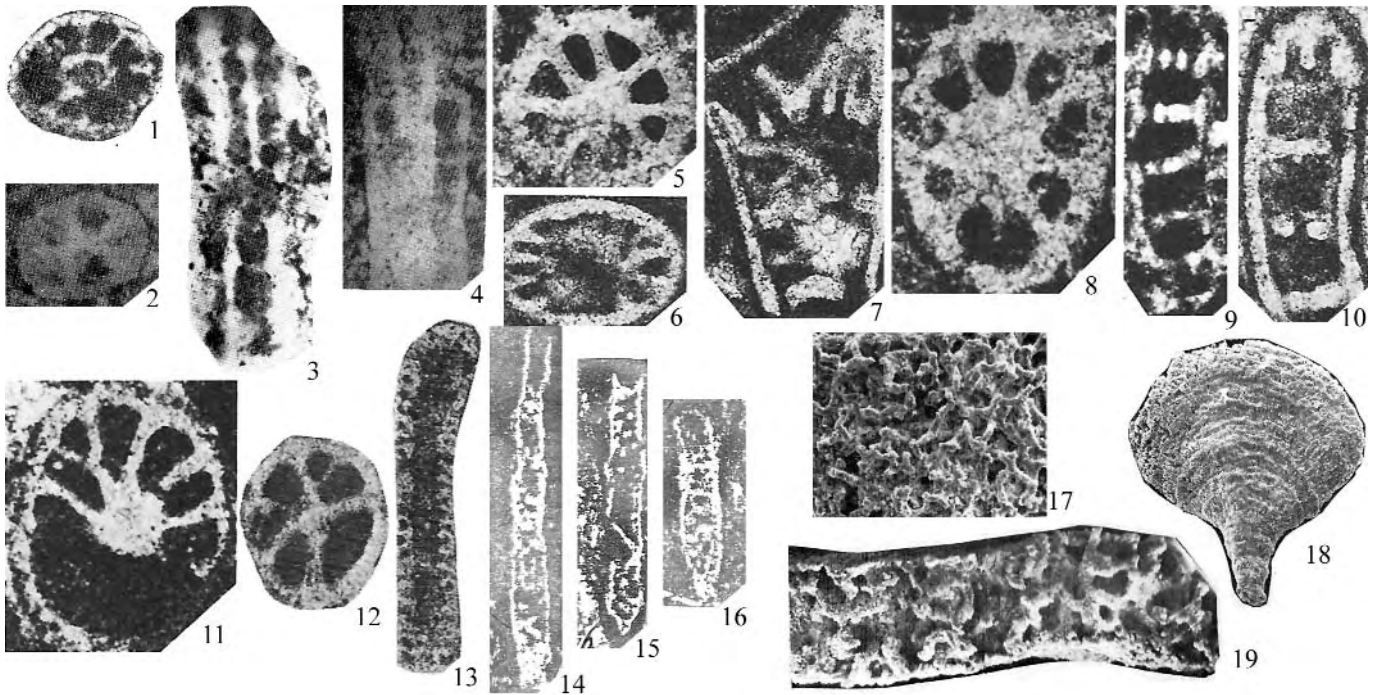


Figure 4. Algospongia with complex internal structure and geometric tests, Uralitidae *nom. transl.* (1-13). Comparison of *Proninella* and *Eifeliflabelum* (14-19). **1-4**, *Uralites regularis* Chuvashov after Chuvashov, 1973, pl. 2, figs 1, 4-5, 3; (Late?) Famennian, eastern slope of southern Urals; 1, Holotype, x 108. 2, 3, Paratypes, x 95. 4, Paratype, x 82. **5-11** *Cribrokamaena citrosa* Brenckle after Brenckle, 1985 (pl. 1, figs 6, 2-3, 8-11, 45 respectively, all x 75 except Fig. 4.7, x 65 (note the possible cribrate aperture in Figs 4.7, 4.9, 4.10)). **12-13**, *Issinella devonica* Reitlinger (*sensu* Roux, 1985, pl. 3, figs 1-2) (= Mamet & Roux, 1981, pl. 1, fig. 1, 15). Late Tournaisian of British Columbia (Canada) and late Viséan of Utah (U.S.A.), respectively; 12, x 55, 13, with questionable conceptacles; x 67; (compare with the *Cribrokamaena* of Figs 4.5, 4.8, 4.11). **14-16**, *Proninella tamarae* Menner & Reitlinger, 1971, three types illustrated by Menner & Reitlinger, 1971, pl. 1, figs 11, 12, 10; Tunguska Syncline, Siberia, Russia, Frasnian. x 60; note the large size, the sarmentoid assemblages and the irregularity in width in the growth of the enveloping tubular part (compare to *Pokorninella* and conclude that they have nothing common). **17-19**, *Proninella opuntia* (Langer), three paratypes after Langer (1979, text-figs 12, 14, 16 respectively), Givetian of Eifel (Germany); 17, x 58; 18, x 29; 19, x 115.

rny (1951) considered *Moravammina* as a foraminifer, and Brady (1876), *Stacheia marginuloides* as comparable to a nodosarioid. Universally accepted, the Algospongia are not Foraminifera, because of the absence of a proloculus, absence of a cribrate aperture [although a cribrate-like “aperture” was illustrated in *Cribrokamaena* by Brenckle (1985) (Figs 4.7, 4.9-4.10), and *Anthracoporellopsis* by Skompski (1996)], and a type of mineralization and an evolution which differ totally from those of coeval foraminifers.

Numerous groups of Recent foraminifers exhibit homeomorphies with algae: e.g., *Rhizammina algaeformis* Brady (see Cartwright *et al.*, 1989; Heinz & Hemleben, 2003), the “morphogroup A” of Jones & Charnock (1985), *Discoramulina bollii* Seiglie (see Harmelin & Venec-Peyré, 1992) (Fig. 1.2-1.3), *Gypsina* and *Acervulina* (e.g., Perrin, 1992, p. 726), *Miniacina* and *Homotrema* (Krautwig *et al.*,

1998), Arboramminidae Shires, Gooday & Jones (1994), and consequently, they resemble Algospongia. Fossil examples exist also.

2.4. Arguments against their assignment to the red algae

The ungdarellaceans (*sensu lato*) are generally assigned to the red algae (Figs 5-6). The fossil Rhodophyta can be characterized by some of the criteria of the Recent Corallinales (e.g., Woelkerling, 1988; Braga, 2003), 1) presence or absence of genicula; 2) number of pores of the conceptacles (uniporate or multiporate); 3) presence or absence of connections between cellular rows (by secondary pits or cell fusions); and 4) presence or absence of sporangial plugs. No Algospongia, even *Ungdarella*, possess these criteria. Many Algospongia have a perforated wall, with

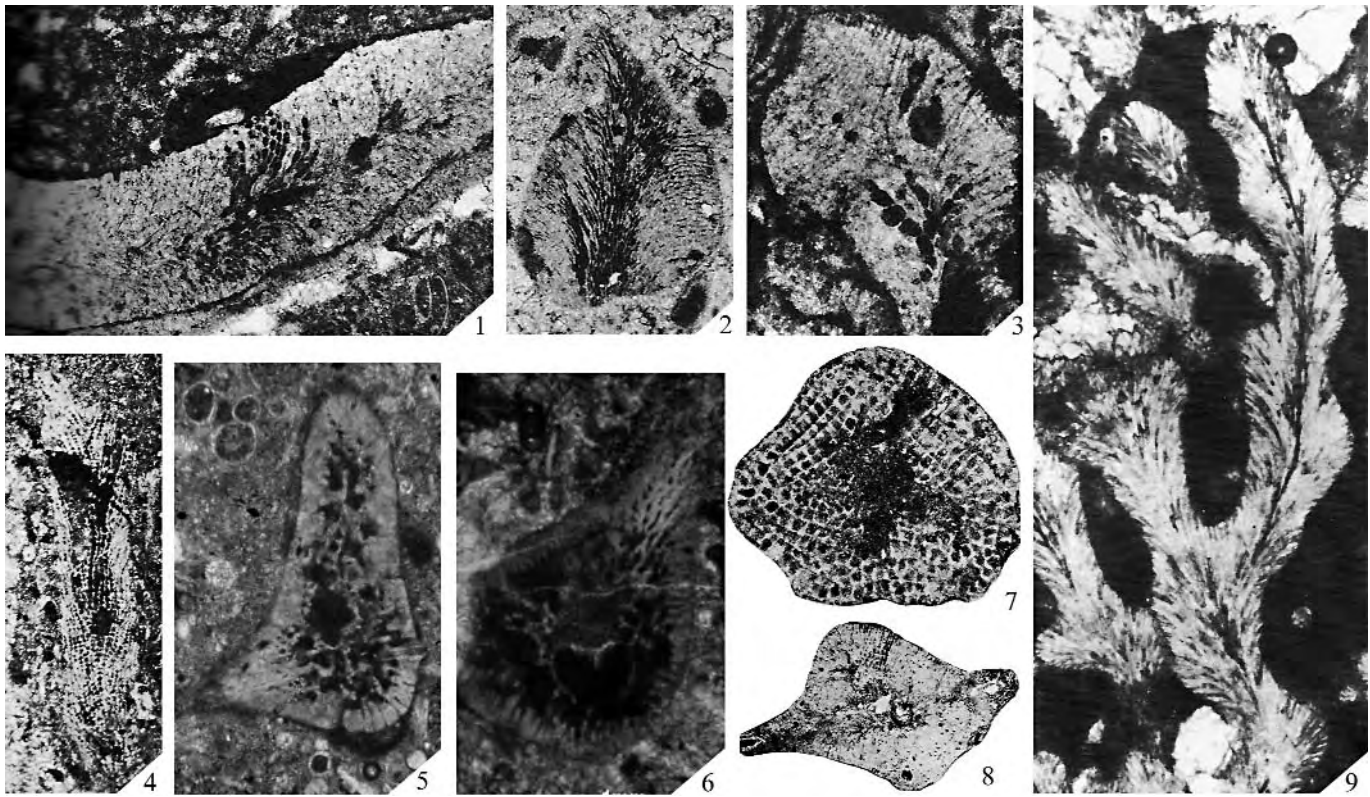


Figure 5. Comparison with the red algae. **1-3**, *Ethelia alba* (Pfender), after Massieux & Denizot (1964, pl. 1, figs 1-3, respectively), as an example of a true red alga. 1. Longitudinal section, Vigny (France), Palaeocene. x 32. 2. Fragment showing the mesothallus. Les Garniers (Switzerland). Cenozoic. x 25. 3. Fragment showing three mesothallic cells and perithallic cells (top center). Stutz-s/Pillon (Switzerland), Eocene, x 61. **4**, Well preserved *Ungdarella* (after Bensaïd *et al.*, 1979, pl. 16, fig. 6), late Serpukhovian of Central Morocco, x30. **5-6**, False hypothallus (confused with an internal sarmentoid series of chambers in 5, and a tangential section of the external series of chambers in 6) and perithallus in *Roquesselsia* G. Termier *et al.*, 1977; Tizra Formation, type locality (Central Morocco), Early Brigantian, after Karim, 2007, figs 1.9. **7-8**, *Mametella skimoensis* (Mamet and Rudloff, 1972), two diametrically opposite stages of preservation illustrated by Mamet & Roux (1977, pl. 1, figs 9, 12 respectively); both Brigantian of Yorkshire, Great Britain. 7. x 42; 8. x 17. **9**, *Dendronella articulata* Moussavian & Senowbari-Daryan, 1988, pl. 41, fig. 4, longitudinal section relatively homeomorph of *Ungdarella* but exhibiting true rows of cells; Cassian Formation, Carnian, southern Alps, Italy, x 50.

functional perforations, communicating with the exterior. With functional apertures, although small and/or obliterated by entire secondary calcification, and not the closed cells of the corallinales, it is easier to explain the micrite present within the most minute chambers; that demonstrates a calcification different from the corallinales-type, and the functionality of the aperture from the exterior to the most internal parts of the skeleton. This is not the cases with the red algae where the secondary pits, cell fusions, and even the synapses (Fig. 5.3) are small (e.g., Braga, 2003) and early diagenesis obturated them. *Ungdarella* itself is not constant in its “polystromatic” (i.e., with several tissues) appearance and does not contain any conceptacle (Figs 6.1, 6.3-6.4, 6.8-6.9). Some rare, rounded structures cannot be interpreted as conceptacles because they are not perforate [either semi-circular (Fig. 6.8) or completely

closed, such as the bracelets of the Moravamminida, or loops of the Beresellina, as well as examples in *Claracrusta*, *Komia*, and *Fasciella* cited in the literature]. The calcification differs also fundamentally from the theoretical scheme of the intra- and extracellular carbonate precipitation among the plantae quoted, for example, by Roux (1985, text-fig. 2, p. 492).

The Aoujgaliida differ from the red algae Melobesioidea by the irregularities of chambers; apertures between the chambers (the cells of Melobesioidea are completely closed), and absence of conceptacles (Vachard *et al.*, 2001). We interpret *Ungdarella* such as in Vachard & Montenat (1981, fig. 19), and this reconstructed organization differs from that of a true red alga which is similar externally; for instance, the Triassic *Dendronella* Moussavian & Senowbari-Daryan, 1988 (Fig. 5.9). The Aoujgali-

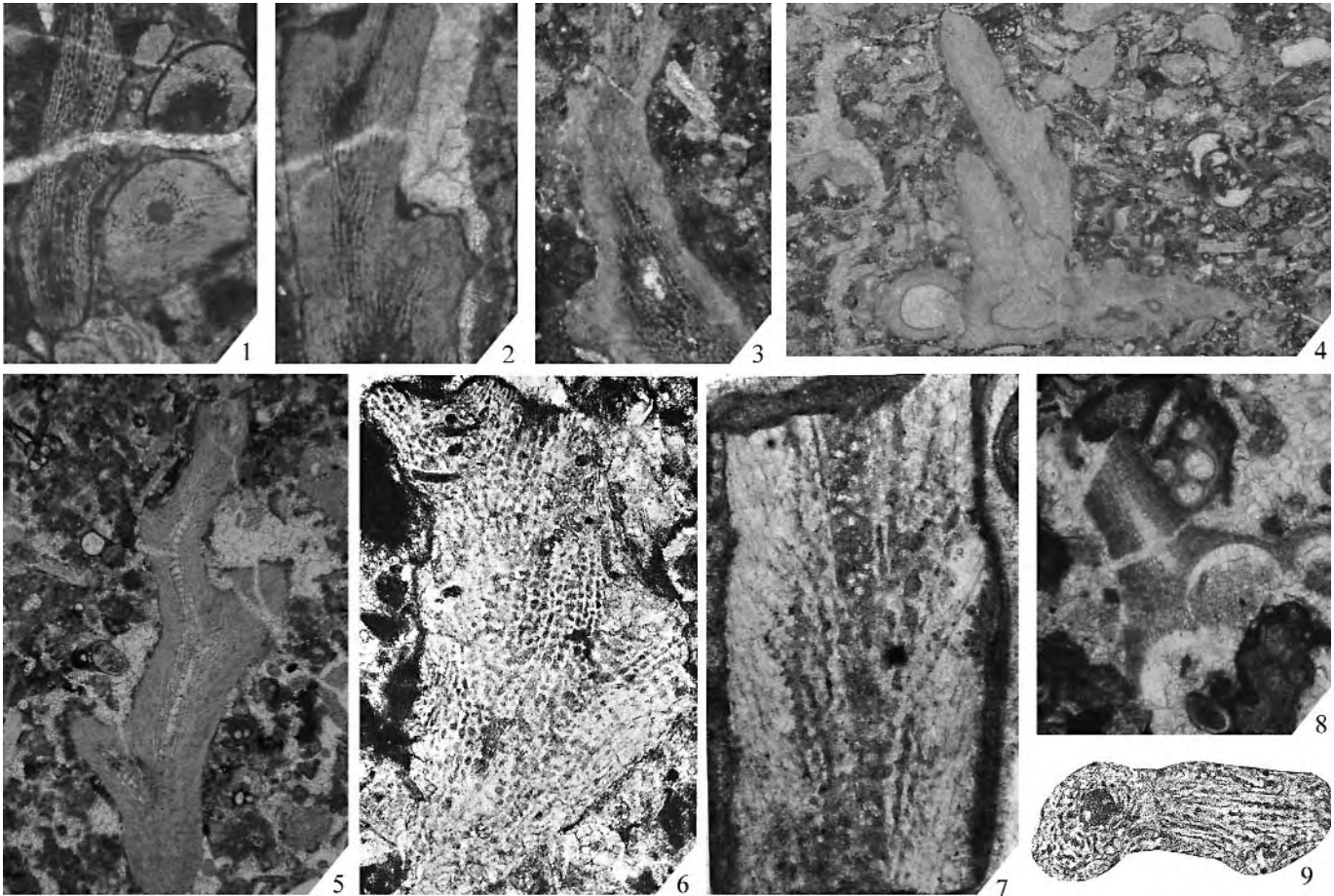


Figure 6. Stages of preservation of the Aoujgaliina *Ungdarella*. **1-5, 8**, *Ungdarella uralica* Maslov, 1956; different stages of preservation in the Tizra Formation (central Morocco), late Asbian-Brigantian, as illustrated in the unpublished PhD Karim, 2007, fig. 1.9. 3, 1-2, 4, 9, 5, fig. 1.8. 5); 1, x 27.5; 2, x 25.5; 3, x 43.5; 4, x 12.5; 5, x 10.5; 8, x 12.5. **6-7, 9**, *Ungdarella uralica* from other references. 7. After Chanton-Güvenç, 1972 pl. 13, fig. 4; Tabain-out, central Morocco, late Viséan, x67. 8. After Vachard and Fadli, 1991, pl. 1, fig. 15, Mellila Formation, Late Asbian, Mdakra, central Morocco, x80. 5. 9. After Sebbar & Mamet, 1996, pl. 3, fig. 9, Djenien Formation, Djebel Arbal, Béchar Basin, Algeria. Serpukhovian, x 62. Specimen showing the initial encrusting “basket” of irregular rows of chamberlets resembling *Stacheoides tenuis* Petryk & Mamet, 1972. Compare with the other types of attachment of Figs 6.4, 6.8.

ida differ from the Calcispongia by the too weak communication between the skeletal elements and the absence of spongocoel. The Aoujgaliida differ from the stromatoporooids by a less regular skeletal structure and much smaller size. Rather common homeomorphoses between red algae and microstromatoporoids can be also documented, e.g., 1) *Keega* Wray and *Stachyodes* Bargatzky (see Lachkhem & Mistiaen, 1994); 2) see also the controversies between solenoporaceans and chaetetids (Brooke & Riding, 1987, 1998; Aguirre & Barattolo, 2001; Riding, 2004; Cózar & Vachard, 2005). The fundamental difference in size with chaetetids and especially a different type of wall dark microgranular versus yellowish granular.

Whether some solenoporaceans are really red algae (as demonstrated for instance for *Maimonachaetetes* – see

Cózar & Vachard, 2006), this family is present since the Early Cambrian with *Bija* Vologdin, 1932 and evolves up to the Miocene (Elliott, 1973). Many other groups assigned to red algae by Chuvashov *et al.* (1987); namely, Moniliporellaceae Gnilovskaya, 1972, and Katavellaceae, *Kordé* ex Chuvashov *et al.*, 1987 as summarized by Shuysky (1999; Table 2) are very questionable. *Hortonella* and *Lysvaella* can be other red algae related to the Solenoporaceae by the intermediary of the Moniliporellaceae, or they are fragments of primitive terrestrial plants (compare the structures illustrated by Banks *et al.*, 1975) or root structures (see Cózar & Vachard, 2005). True corallinales (polystromatic; i.e., with differentiated tissues) appear with *Neoprincipia* (may be preceded by *Hortonella* and *Principia*), but they remain poorly known. Only one witness is

CLASSIFICATION OF SHUYSKY (1999)		This work
Moniliporellaceae	RED ALGAE	incertae sedis algal groups
Demidellaceae		
Katavellaceae		
Lysvaellaceae		
Ungdarellaceae		
Stacheiaceae		Algospongia Aoujgaliina
Fasciellaceae		Algospongia Calcifoliina
Archaeolithophyllaceae		Red algae Corallinales
Solenoporaceae		Red algae Solenoporales
Gymnocodiaceae	GREEN ALGAE	Red algae Nemalionales

Table 2. Proposed assignments of 10 groups of so-called red algae.

the Artinskian *Aseelahella*, but no transition is known up to the Triassic genera *Dendronella* Moussavian & Senowbari-Daryan, 1988 and *Norithamnium* Senowbari-Daryan *et al.*, 2002, and especially till to the profusion of the Early Cretaceous corallinales. According to Bucur *et al.* (2009, p. 965), “other reports of coralline algae in pre-Cretaceous sediments (...) are also doubtful”.

In fact, there is no evidence that true primitive corallinales, solenoporaceans, Permian Gymnocodiaceae, Algospongia and other subordinate Palaeozoic groups, have something in common (total absence of transitions). Conversely, some calcified Recent algae have no accurate fossil antecedents [e.g., *Pedobesia* (= *Derbesia*); see Loreau, 1982].

Misinterpreted Rhodophyta are re-interpreted here (Table 2). The *bona fide* Palaeozoic red algae are consequently scarce, because many of the so-called ancestral corallines of Wray (1971, 1972, 1977) and several other authors are included in the Aoujgaliida, as re-defined here. Finally, the evolution of Algospongia and Rhodophyta seem to be distinct. Nevertheless, the hypothesis that the Rhodophyta are not Plantae but Protista or Protoctista (Copeland, 1938; Ragan & Gutell, 1995) can provide new phylogenetic links between these two groups.

2.5. Discussion of a Protista assignment

The Algospongia might belong to a group of Protista distinct from the Foraminifera. The Xenophyophores might be proposed [based on the work of Tendal (1990); Gooday

(1996); Richardson (2001); Pawlowski *et al.*, (2003); and Lecroq *et al.* (2009)], but despite some morphological similarities between *Aschemonella* Brady (Xenophyophorida; Fig. 7) and *Palaschemonella* Beckmann (Moravamminina), the wall microstructures differ (Xenophyophores are agglutinating and secrete barytine crystals; see Hopwood *et al.*, 1997).

The Xenophyophores, such as the Algospongia, were successively assigned to sponges or a related group, a rhizopod-like group, *incertae sedis* and plants (Schröder *et al.*, 1989, p. 15). The group is currently placed in the class Rhizopodea (subclass Xenophyophoria).

Moreover, as a completely opposite view to the alga sponge interpretation, Xenophyophorida were proposed as explanations for the phylloid algae and the ichnites *Palaeodictyon*. Nevertheless, these assignments are not free of controversy (Levin, 1994; Maybury & Evans, 1994; Torres, 1997; Rona *et al.*, 2009).

Atypical foraminifers, the Komokiidae permit easily reconstructions in 3D for the Algospongia (e.g., Schröder *et al.*, 1989; Gooday *et al.*, 2007) (Fig. 7), although their ecology and taxonomy (see e.g., Nozawa *et al.*, 2006) are distinct. They can also provide a contribution to the nomenclature of the Algospongia (Figs 7-8). According to the Protista hypothesis, a) Wetheredellina and Moravamminina are relatively easy to explain morphofunctionally, b) Aoujgaliida could correspond to some hyperspecializations of attached foraminifers (e.g., *Acervulina*, *Homotrema*, *Carpenteria*, *Miniacina*, or *Gypsina*; see Krautwick *et al.*, 1998), c) but *Ungdarella* and the Calcifoliina, in turn,


Protists Xenophyorida and Kokomiidae					Comparison with Algospongia
Group 1	Group 2	Group 3	Group 4	Sketches	
MULTIRAMOSA	Tumultuose	Chaotic	<i>Lana</i>		Morphotypes of <i>Falsocalcifolium</i> and Claracrustidae
		Reticulate	<i>Reticulum</i>		
		Longiramosae	<i>Septuma</i>		
	Radiate	Bulbose	<i>Normanina</i>		
		Multiramose	<i>Komokia</i>		
		Robustiramose	<i>Ipoa</i>		
RAMOSA	Vertebral	Spinose	<i>Arbor</i>		Moravamminina
		Obtuse	<i>Baculella</i>		
	Catenulate	Nodose	<i>Calos</i>		
		Compressed	<i>Catena</i>		
	Ramose	Constricted	<i>Aschemonella</i>		
		Unconstricted	<i>Clados</i>		
		Lobose	<i>Cactos</i>		
COMPACTA	Coralline	Cerebral	<i>Cerebrum</i>		Aoujgaliina
		Argillose	<i>Edgertonia</i>		
		Spherular	<i>Staphylion</i>		
	Tuberose	Multiconstricted	<i>Crambis</i>		Palaeoberesellidae
		Pauciconstricted	<i>Tuber</i>		Anthracoporellopsidae

Figure 7. Protists Kokomiidae and Xenophyophorida and their morphological similarities with Algospongia (after Schröder *et al.*, 1989, text-fig. 2).

are morphofunctionally difficult to understand. For example, among the *Fasciella*, some details are impossible to reconcile with this interpretation because “interstratified” attached *Eotuberitina* can be observed (e.g., Ivanova, 1975, pl. 1, fig. 1; Vachard *et al.*, 2004, pl. 1, fig. 4). These latter indicate that the *Fasciella* were early and strongly calcified, and the wall exposed during the life of the organism. Moravamminina, Aoujgaliina, and Calcifoliina share predominant attached modes of life (with all the surface, coiled part or bracelets; Figs 8.11-8.14). Some forms only implanted in muddy substrates can exist (e.g., *Devonoscala*, Labyrinthoconidae, “*Subkamaena*”).

Actually, it seems plausible that the Algospongia were Protista, but it seems to be impossible to select between the groups of this kingdom (in the sense of Cavalier-Smith, 1993, 2002). The principal question is the exact interpretation of the perforations (Fig. 9). Due to the known or supposed distributions of the groups, the root of the alga-spongal tree is inferred at the divergence with foraminifers, amoeba and thecamoebians. As *Wetheredella* and true Foraminifera are known since the Cambrian (Mamet, 1991; Culver, 1994, respectively), this divergence can occur in the Late Proterozoic.

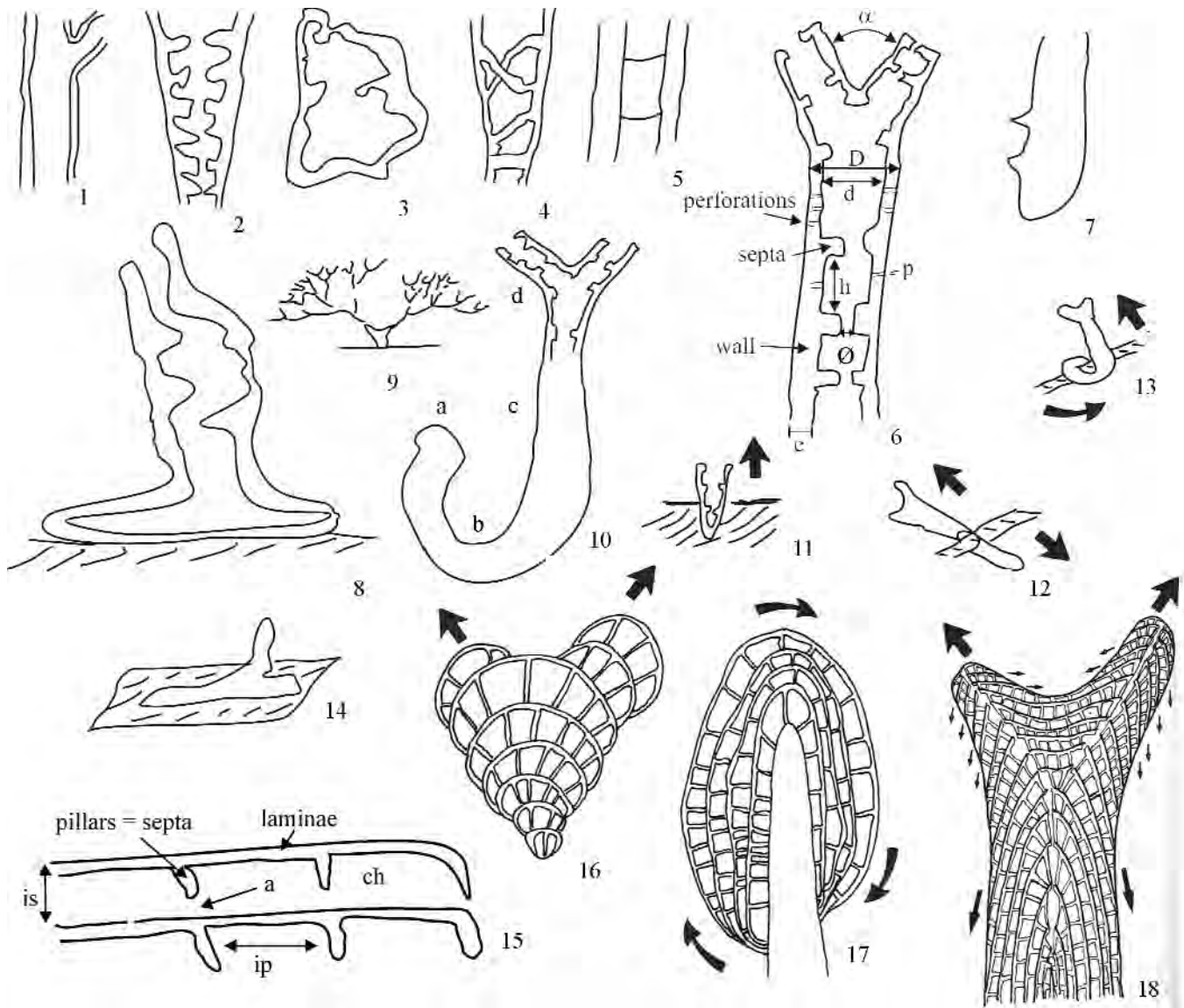


Figure 8. Nomenclature of the alcosponges (not to scale). Black arrows = sense of growth. 1-5. Endoskeleton of Moravamminida. 1, Undivided, bifurcated tube of *Kettnerammina*. 2, True septa of *Devonoscala*. 3 Pseudo-septa of *Evlania* and *Anthraporellopsidae*. 4, Sarmentoid assemblage of *Proninella* and *Labyrinthoconidae*. 5, Diaphragms of *Beresellina*. 6, Nomenclature of *Palaeoberesellidae*. D = outer diameter, d = inner diameter, e = wall thickness, h = height of chamber, Ø = diameter of aperture, p = diameter of pores, α = angle of bifurcation. 7-10. Stages of growth of Moravamminida. 7. With bracelet, which is not located exactly at the end. 8. Relatively elongate attached initial part. 9. Bushy growth: *Kamaenella* or *Donezella*. 10. Coiled and uncoiled growth; a = "first chamber" just inflated not a proloculus, b = attached part around a cylindrical substrate, c = erect part, d = bifurcated terminal part; a-b corresponds to *Litya*, a-d = *Moravammina*, c-d = *Kamaena*. 11-14, Types of attachment (black arrows indicate the directions of the growth). 11. On a soft substrate. 12. With bracelet. 13. Coiled. 14. Crust upon a hard substrate. 15, Nomenclature of *Aoujgaliina*; a = aperture, ch = chamber or chamberlet, is = interlaminae space (= "cell height" of the authors), ip = interpillar (= interseptal) space (= "cell width" of the authors) (depending of the association with septa or pillars). 16-18, Stages of growth of *Aoujgaliina* (see G. Termier *et al.*, 1975, text-fig. 2, p. 218). 16. *Stacheiidae* (= *Ptychocladidae* (*sensu* G. Termier *et al.*, 1975) = *Cuneiphycidae* herein); 17. *Aoujgaliidae*; 18. *Ungdarellidae*. Black arrows indicate the directions of the growth: uniseriate, incrusting or bilaterally directed (backward, as here, in the case of *Ungdarella* or downward in the case of *Komia*).

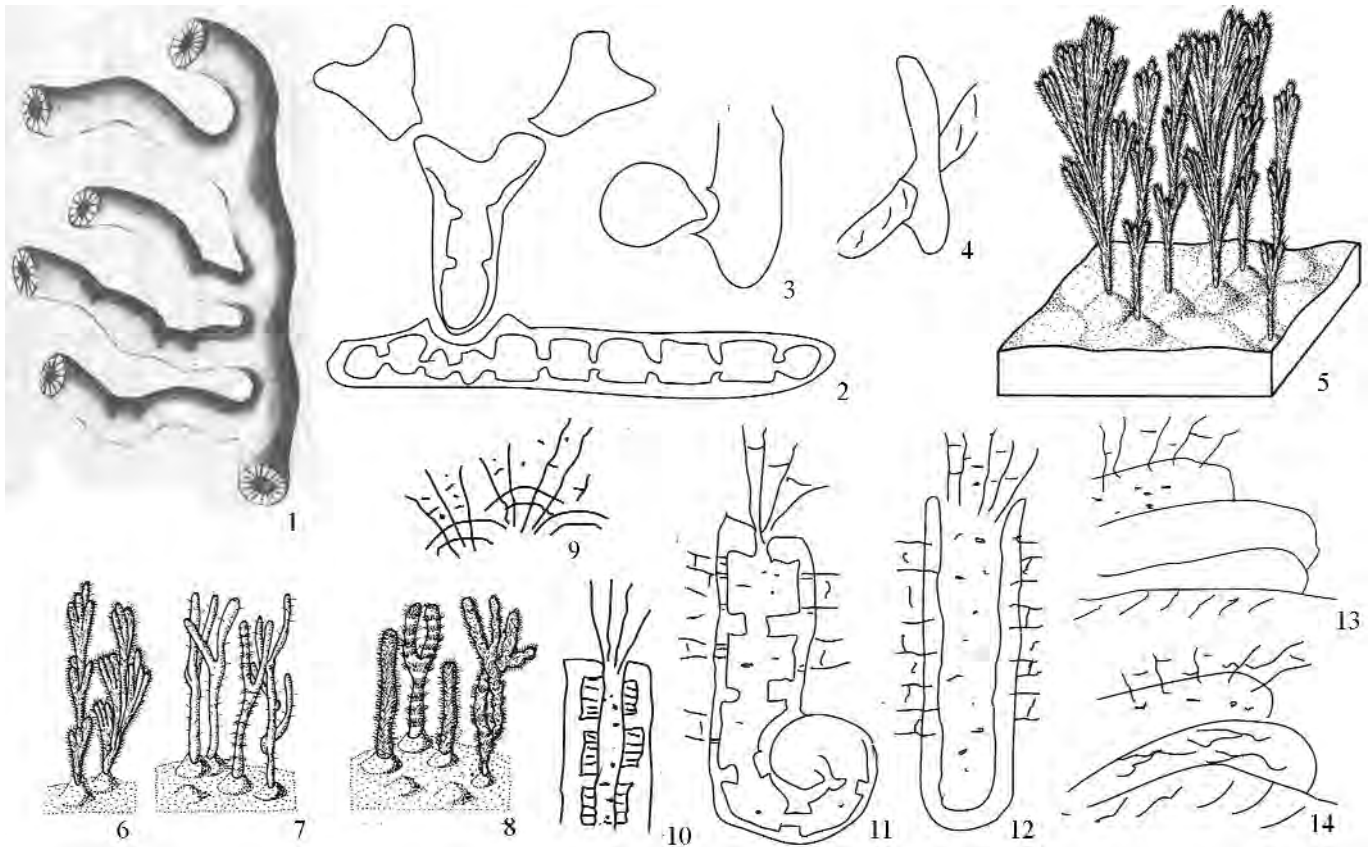


Figure 9. Palaeobiological sketches (attempts to reconstruct the algospongia in life position). 1, *Tubus* according to Chuvashov *et al.*, 1985 (text-fig. 5 p. 95). 2-4, Interpretations of the bracelets. 2. As a ramification and articulation. 3. As a conceptacle emplacement. 4. As a system of attachment (see Fig. 8.12). 5-8, Algospongia reconstructed as algae. 5, 6. *Issinella*; 7. *Palaeoberesella*; 8. *Donezella*. 5. After Roux, 1985 (text-fig. 14 p. 570); 6-8. After Roux, 1985 (text-fig. 43 p. 675). 9-14, Alternative reconstructions as protists. 9. *Wetheredella* and wetheredellids, 10. *Beresellina* and *Donezellina*, 11. *Moravaminidae* and *Paleoberesellidae*, 12. *Issinellidae*, 13. *Fasciella*, 14. *Falsocalcifolium*.

3. ONTOGENESIS AND EARLY DIAGENESIS

Ontogenic characters of the Algospongia are summarized in Figure 8. Some characteristics of the Algospongia, often compared with algal organs, are summarized here in four figures compared with homologous structures among the foraminifers (Figs 10-13). Some details can be highlighted concerning some onto- and diagenetic characters.

3.1. Wetheredellina

Some hemispherical chambers pass from vesicular to sub-tubular in the periphery of the colonies. Few recrystallizations occur; nevertheless some walls are affected (*Wetheredella*) with a tripartite microsparitic filling of the chamber; some wetheredellids are sparitized (see Vachard, 1993, pl. 3, figs 10-11, "groupes de sphères

sparitisées"). Because the homeomorphy and presence of the Aphralysiaceae in the Cambrian is prior to the Wetheredellina, the former are possibly ancestors of the latter. The aphralysiaceans have a true carbonate skeleton. Hence, the mechanism of an indirect calcification postulated for *Wetheredella* by Kázmierczak & Kempe (1992, text-fig. 7, p. 302) can be only possible for the Precambrian ancestor of *Aphralysia*.

3.2. Moravaminida, twins and monocrystalline extinction

According to the descriptions of Pokorný (1951), it is evident that *Moravamina* presents an initial coiled part. In consequence, during the growth it seems to be evident that four stages of growth can be individualized in *Moravamina* and moravaminids in general (Fig. 8.10), first chamber, coiled part, erect part, bifurcation. It seems

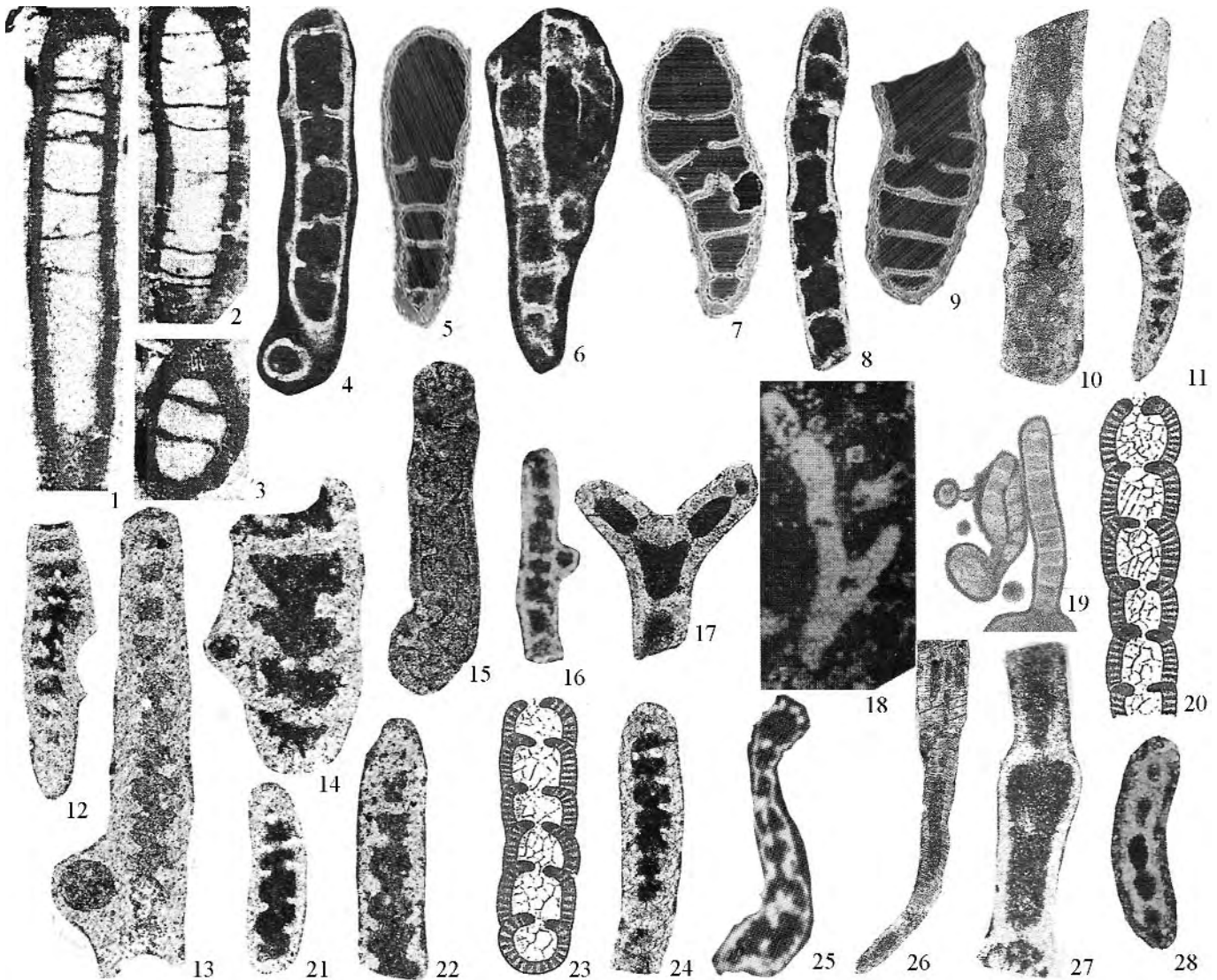


Figure 10. Septated tubes, diaphragms, necks and bracelets of Moravamminida. **1-3**, Diaphragms of *Uraloporella*. After Saltovskaya, 1984b. 1 (= pl. 12, fig. 9) x 36; 2 = (pl. 12, fig. 8) x 47; 3 (= pl. 12, fig. 5) x 46. **4-9**, Small necks of *Kamaenella denbighi* Mamet and Roux compared with the apertures of the foraminifer *Discoramulina bolii* Seiglie. 4, 6, 8. *Kamaenella denbighi* Mamet & Roux; after Mamet & Roux, 1974; pl. 7, figs 15, 11, 9; all from Denbigh (Great Britain). Early Asbian, x 68. 5, 7, 9. *Discoramulina bolii* Seiglie, after Harmelin & Venec-Peyré, 1992, pl. 2, fig. 7; Recent, Mediterranean Sea. x 150. **10-14**, Bracelets of different Palaeoberesellidae. 10. *Exvotarissella?* sp. (*sensu* Mamet & Pr at, 1992, pl. 1, fig. 15), early Givetian, Belgium, x 58. 11-13. *Palaeoberesella lahuseni* (von M oller), after Mamet & Roux, 1974, pl. 2, fig. 19, pl. 3, fig. 10, pl. 4, fig. 14.; all from Great-Britain and Ireland, and all x 68. 14. *Exvotarissella index* (Ehrenberg *emend.* von M oller) Mamet and Roux, after Mamet and Roux, 1974, pl. 6, fig. 2, Djebel Tekzim, Morocco, early Asbian, x 106. **15-28**, Different Palaeoberesellidae and similar genera. 15. *Kamaena delicata* Antropov; after Mamet and Roux, 1974, pl. 1 fig. 31; Azzel Matti Formation, Algeria, early Serpukhovian, x 68. 16. *Kamaenella tenuis* (von M oller, 1879), after Sebbar and Mamet, 1996, pl. 2, fig. 8; Notice that the perpendicular bifurcation is not a bracelet, Harrez-Igli Formation, Algeria, late Vis ean, x 21. 17, 28. *Pseudokamaena armstrongi* Petryk & Mamet, 1972, after Sebbar & Mamet 1996, pl. 2, figs 17, 16 respectively, Djenien Formation, Algeria, early Serpukhovian; 17, x 54; 28, x 28. 18. *Kulikaella unistratosa* Berchenko, after Berchenko in Aizenverg *et al.* 1983, pl. 9, fig. 4. Holotype, Strunian, C₁^a₂ of Donbass (Ukraine), x 52.5. 19-24, *Septamina* as discussed as a synonym of *Palaeoberesella*. 19. After Meunier, 1888, pl. 7, fig. 6. Arundian of Cussy-en-Morvan (France), x 37.5. 20-21. "*Nodosinella lahuseni*" after von M oller, 1879, 20 = pl. 5, fig. 6a, x 75; 23 = pl. 5, fig. 7, x 75; Vis ean of Russia. 21-22, 24. *Palaeoberesella lahuseni* (von M oller); after Mamet & Roux, 1974, pl. 3, figs 1, 17, 24 respectively, Middle-late Vis ean, western Europe, all x 55. 25. *Donezella delicata* Berchenko (probably an ancestral stage of *Multiporidium* gen. nov. = *Masloviporidium*, *auct.*; *nomen imperfectum*), after Berchenko, 1982, pl. 11, fig. 2, Holotype, D₇⁴ limestone, earliest Bashkirian, Voznessensky, Kalmius river, Donbass Basin, Ukraine. x 70. 26. *Kettnerammina* sp. (= *Issinella devonica* Reitlinger *sensu* Mamet & Pr at, 1992, pl. 1, fig. 17), early Givetian, Belgium. Notice the strong twins in the wall. x 44. 27. *Vasicekia?* sp. (*sensu* Mamet *et al.*, 1999, pl. 4, fig. 2), Mechraa Ben Abbou (central Morocco), Eifelian, x 63.75.

that the two first stages can be replaced by a bracelet (Figs 8.7, 9.2-9.4, 10.13-10.14) which has been confused with a proloculus or conceptacles, according to its location along the tubes. As these bracelets exist in *Exvotarisella*, *Palaeoberesella* and *Ardengostella*, they seem to be an advanced character in the Palaeoberesellidae and a primitive character in the Beresellidae. The donezellin *Kamaenella* seems to present small necks around the apertures as in some foraminifers (compare Mamet & Roux, 1974, pl. 7, figs 9, 11, 15 and Harmelin & Venec-Peyré, 1992, pl. 2, fig. 7 with three sections; here Figs 10.4-10.9). The bereselloid wall occurs repetitively in the Moravaminida (*Zidella*, *Pseudonanopora*, *Evlaniopsis* and *Einorella*) before becoming established in the Beresellidae and the Donezellidae *Donezella*. The ontogenesis, phylogeny, morpho-functional interpretation and advantages of a bereselloid wall are entirely unclear for us. Another unusual character is the monocrystalline extinction in *Exvotarisella*, *Palaeoberesella* and *Devonoscala* (see Vachard, 1991, pl. 3, figs 13-14, 21), rarely observed in other genera of Palaeoberesellidae.

During the ontogenesis of the Issinellidae, Anthracoporellopsidae and Beresellidae, some diaphragms appear (Figs 1.9, 8.5, 10.1-10.3, 11.1, 11.3, 11.5). Apparently, this criterion is evolutive because the maximal frequency is obvious in the advanced genera of the lineages (for example, in *Dvinella* and *Uraloporella*). These diaphragms are meniscus-shaped with apparently the convexity upward contrary to Saltovskaya (1984b) (re-illustrated here Fig. 11.1). They are rather similar to the endoskeleton elements of problematica as such as *Tebagatubus* or "caunopores", occasionally assigned to annelids (Senowbari-Daryan, 2005) but this also permits to discard any algal assignment. Other differences with algae are: 1) no bifurcations are truly obvious, but twin individuals are observed in one case (quoted in Lys & Leboulanger, 1977, pl. 52, fig. 1, re-illustrated in Vachard, 1991, pl. 5, fig. 6); 2) conceptacles appear in fact as loops of the diaphragms [see especially Saltovskaya (1984b, pl. 12, fig. 1)] (Figs 11.1, 11.3, 11.5). Recrystallizations are rare, except in some microsparitizations of diaphragms.

We have discussed above the character of false metaspondyl of *Exvotarisella* (Figs 2.1, 2.4, 2.7); more comparisons seem possible with some walls of foraminifers (see also Figs 1.8, 1.10, 12.7, 13.4).

3.3. Aoujgaliida

The three types of growth (H. Termier *et al.*, 1977) are confirmed by this study (Figs 8.16-8.18). The skeletal diagenesis can be strong in some Aoujgaliidae and Ungdarellidae: especially, "*Mametella*", *Epistacheoides* and *Ungdarella* (Figs 5.8, 6.4) as in the Cuneiphycidae fam. nov. (Figs 14.1-14.9), and many taphotaxons (*sensu* Lucas, 2001) can exist.

Rare false conceptacles exist in some Algospongia as well as some false-algae, as *Solenomeris*, where the "conceptacles" are foraminiferal juvenaria (Figs 11.11-11.12) and bibliographic references in Perrin (1992, 2009).

3.4. Calcifoliina

They show an evolutive strategy entirely different to the rest of the Aoujgaliida. Their strong homeomorphy with algae can correspond in fact to an absolute victory of a cyanobacteria farming *in situ* and *per se*. The living part, yet very narrow at the beginning (*Fasciella*, *Fascifolium* gen. nov.) seems to be absent in the advanced forms (*Falsocalcifolium*, *Calcifolium*), or is entirely replaced by the organic matter of endosymbiotic bacteria forming a ramified inner network of filaments, whose length, diameter and ramifications are similar to those of the ortonellacean cyanobacteria. Except for these filaments, the microfossil is only constituted by the "wall" (i.e., in form of leaf, petal or cup), the colour of which can be clear-yellow or dark, contrasting strongly with the filaments filled by microsparite (the filaments do not have a calcified wall). Rarely, the filaments are (secondary?) filled by iron oxides. The genera are rather well defined after recent revisions, but in contrast, *Frustulata* is poorly established because it is difficult to characterize its apparent absence of filaments: primitive stage of evolution, ontogenetic absence or diagenetic disappearance.

4. SYSTEMATICS

For pragmatic purposes, nomenclature related to the foraminifers is generally used for the taxonomic descriptions. Hence, the genera are erected following the general shape, type of calcification, shape of chambers, types

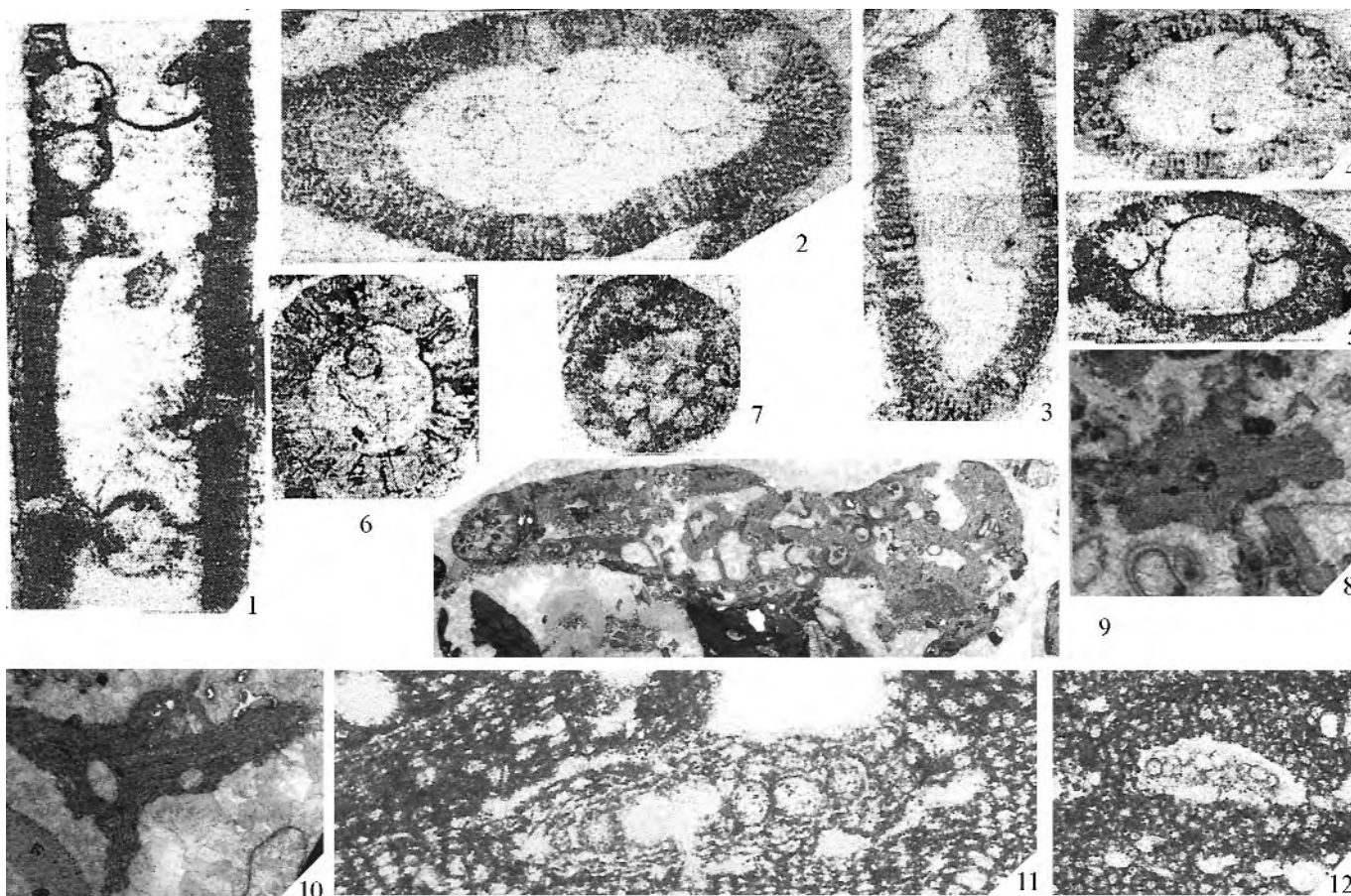


Figure 11. Several false conceptacles (see comments in the text). **1-7**, In the *Uraloporella* of Saltovskaya, 1984b (pl. 12-13); 1 (= pl. 12, fig. 1) x 80; 2 (= pl. 13, fig. 1) x 55; 3 (= pl. 13, fig. 2) x 52; 4 (pl. 13, fig. 4) x 50; 5 (= pl. 13, fig. 7) x 51; 6 (pl. 13, fig. 5) x 62; 7 (= pl. 13, fig. 6) x 42.5. **8-10**, In *Claracrusta ungdarellloidea* Vachard in Vachard *et al.*, 2001 (they might correspond in this case to commensal microfossils); 8 (= fig. 18.2 of Vachard *et al.*, 2001) x 21; 9 (= fig. 18.4) x 7.5; 10 (fig. 18.5) x 12.5. **11-12**, Case of *Solenomeris* (*sensu* Elliott, 1964, pl. 107; Palaeocene, Iraq), where the so-called conceptacles correspond to initial stages of the foraminifer *Acervulina* (see also Perrin, 1992, p. 727). 11 (= pl. 107, fig. 2); x 66. 12 (pl. 107, fig. 1); x 40.

of apertures, characteristics of the wall perforations (number, diameter, arrangement, possible ramifications), eventual presence of bracelets, and the possible differentiation in laminae. The species depend principally on the dimensions of the generic parameters, especially the outer diameter (D), inner diameter (d) of test and/or rows of chambers, thickness of test wall (t), thickness of septa (s), width of aperture (s), and the dimensions of wall perforations (p). This nomenclature, summarized in Figure 8, as well as the possible “biological sketches” (Fig. 9), corresponds generally to the definitions of Loeblich & Tappan (1987), with some additional terms from Galloway & Saint Jean (1957) and G. Termier *et al.* (1977), such as “maculate” and “sarmentoid” respectively.

The wall is supposed to be originally calcite according to the criteria emphasized in different treatises (e.g., Flügel,

2004). On the other hand, two types of early recrystallizations must be highlighted: (a) the pseudo-monocrystalline extinction of some Moravamminida (especially, *Devonoscala*); (b) the complete occlusion by micro-radial sparite of some Aoujgaliida (e.g., *Aoujgalia* at the “*Mamebella*” stage or *Ungdarella*).

The growths of the Algospongia are roughly concentric in many Wetheredellina and Aoujgaliidae, and apical (maybe directional in the Beresellina, Moravamminina, Stacheiidae and Ungdarellidae).

Kingdom and phylum indeterminate
Class ALGOSPONGIA G. Termier *et al.*, 1977, *orth.*
mut., emend. herein

Emended diagnosis.— Small carbonate tests with a yellow,

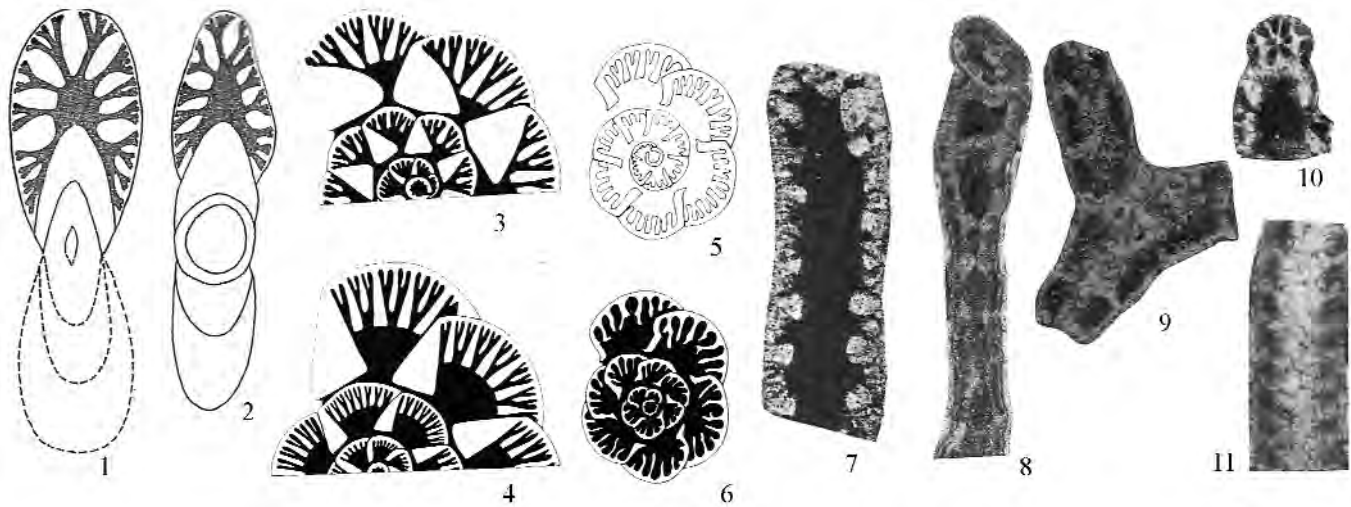


Figure 12. Wall perforations of algospongia and foraminifera. 1-6. Some reconstructions of the network of wall perforation in foraminifera Cyclammininae, considered here as more similar to the network of *Exvotarisella* than this one of metaspondyl dasycladales (exemplified here by *Windsoporella* Fig. 12.10). 1-2. *Cyclammina cyclops* McNeil; after McNeil, 1988, text-fig. 3A-B (respectively), Eocene, Arctic Canada, x 10. 3-6. *Alveolophragmium* (*Reticulophragmium*) spp. after Banner, 1970, pl. 3, figs 8, 7, 5, 6 respectively. No magnification indicated. 7-11. *Exvotarisella*, other algospongia and a metaspondyl dasycladale. 7. *Exvotarisella index*, reproduced again (see Fig. 1.10) for another comparison (after Roux, 1985, x 40.5). 8. *Anthracoporellopsis machaevii* Maslov (sic; very probably another species and/or another genus) after Sebbar & Mamet, 1999, pl. 2, fig. 6; Mezarif Formation, Algeria, Early Moscovian, x 30. 9-11. After Sebbar & Mamet, 1996, pl. 3, figs 1-2, 6 respectively. 9. *Donezella lutugini* Maslov, Oued el Hamar Formation, Algeria, late Bashkirian, x 52.5. 10. *Windsoporella* (misinterpreted as *Pseudoveleitella*) *pareyni* (Mamet & Roux), El Guelmouna Formation, Early Serpukhovian, x 21. 11. *Beresella* sp., upper Tagnana Formation, Algeria, Bashkirian, x 52.5.

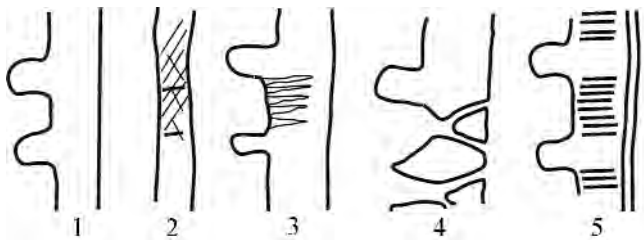


Figure 13. Cartoons of the wall of the Algospongia. 1. Imperforate. 2. Rarely perforated with twins. 3. Abundantly perforated. 4. The pseudo-metaspondyl network of *Exvotarisella* and the Palaeoberesellidae. 5. The annulated and blind rings of *Donezella* and *Beresella* (compare with Figs 12.9, 12.11 for the true aspect).

calcitic, perforated or finely canaliculate wall, microspartitized in the ancestral forms. Growth habit attached (sometimes encrusting) to erect. Skeleton characterized by vesiculiform, tubular and/or laminar, roughly to well-organized rows of chambers whose wall calcification is variable. Chambers in contact by cylindrical apertures.

Composition.— Two orders (Tables 3-4): Moravamminida Pokorny, 1951, *nomen transl.* Vachard in G. Termier *et al.*, 1975, *emend.* herein; and Aoujgaliida G. Termier *et al.*, 1975, *emend.* herein.

Remarks.— The Algospongia constitute a group of problematical fossils with the following characteristics: 1) small dimensions; 2) the dominance during the Palaeozoic; 3) flexuous and undetermined morphologies to rectilinear and more regular skeleton; 4) multilocular structure unknown in all the Recent groups of algae; 5) an existence mainly in photic or dysphotic zones but also possibly in aphotic zones; 6) the wall yellowish, granular (sometimes monocristalline), often perforated (*Issinellidae*, *Beresellidae*, *Exvotarisella*) with aspondyl groups of laterals, often blind (i.e., without communication with the outer environment); and 7) phylogenies differing from those of the Palaeozoic foraminifers or calcisponges, especially because of a shared type of wall: calcitic, mostly low magnesian, yellowish, rarely prismatic-fibrous, generally granular, and occasionally showing a monocristalline “echinodermic” extinction.

The assignment of this group to the sponges, by G. Termier *et al.* (1977) is irrelevant (see Vachard, 1991, p. 272-273; Vachard *et al.*, 1994, p. 9-10). Most Algospongia are rather similar to the Foraminifera because of the morphological similarities noticed by previous authors (from

ORDER	SUBORDER	FAMILY	GENUS
Moravamminida	Wetheredellina	Wetheredellidae	<i>Wetheredella</i> Wood, 1948 (= <i>Cateniphycus</i> sensu Maslov 1956a)
			<i>Disonella</i> Conil & Lys, 1964 (= ? <i>Triplosphaerina</i> Edgell, 2004)
			<i>Sphaeroporella</i> Antropov, 1967
		Asphaltinidae	<i>Asphaltina</i> Mamet in Petryk & Mamet, 1972
	<i>Asphaltinoides</i> Devera, 1987 (= ? <i>Cuzbassia</i> Ivanova in Bogush et al., 1990)		
	<i>Permocatena</i> Vachard & Miconnet, 1990		
	Moravamminina	Issinellidae	<i>Issinella</i> Reitlinger, 1954 (= ? "Nanopora" auctorum)
			<i>Amarellina</i> Mamet, 1995
			<i>Baculella</i> Conil & Dreesen in Dreesen et al., 1985 (= <i>Dreesenullella</i> Vachard, 1991)
			<i>Eouraloporella</i> Berchenko, 1981
			<i>Issinellina</i> Shuysky in Shuysky & Shirshova, 1988
			<i>Jansaella</i> Mamet & Roux, 1975c
			<i>Lemosquetella</i> Mamet & Sebbar, 1998
			<i>Luteotubulus</i> Vachard in Vachard et al., 1977
			' <i>Pseudonanopora</i> ' Mamet & Roux, 1975a (partim)
			<i>Serrisnella</i> Vachard, 1981
			<i>Tubus</i> Chuvashov in Chuvashov et al., 1985
			<i>Zidella</i> Saltovskaya, 1984a
			? <i>Calcicaulis</i> Shuysky & Shirshova in Chuvashov et al., 1987
			Anthracoporellopsidae
		<i>Crassikamaena</i> Brenckle, 1985	
		<i>Dokutchaevskella</i> Berchenko, 1981	
		<i>Evlania</i> Bykova, 1952	
		<i>Evlaniopsis</i> Vachard in Vachard & Montenat, 1981	
		<i>Pseudonanopora</i> Mamet & Roux, 1975a (holotype)	
		? <i>Brazhnikovia</i> Berchenko, 1981	
		? <i>Catenaenella</i> Shuysky in Chuvashov et al., 1987	
		? <i>Culmiella</i> Shuysky in Shuysky & Shirshova, 1988	
		? <i>Einorella</i> Saltovskaya, 1984a	
		? <i>Groenlandella</i> Mamet & Stemmerik, 2000	
		Uralitidae	<i>Uralites</i> Chuvashov, 1973
			<i>Cribrókamaena</i> Brenckle, 1985
		Labyrinthoconidae	<i>Labyrinthoconus</i> Langer, 1979
			<i>Proninella</i> Reitlinger in Menner & Reitlinger, 1971 (= <i>Eifeliflabellum</i> Langer, 1979)
		Moravamminidae	<i>Moravammina</i> Pokorny, 1951 (= <i>Litya</i> Bykova in Bykova & Polenova, 1955)
			<i>Kettnerammina</i> Pokorny, 1951 (= ? <i>Saccorhina</i> Bykova in Bykova & Polenova, 1955 = ? <i>Pseudoissinella</i> Mamet & Rudloff, 1972)
			<i>Palaschemonella</i> Beckmann, 1953
			<i>Triangulinella</i> Mamet & Pr�eat, 1985
		Palaeoberesellidae	<i>Vasiceckia</i> Berchenko, 1981 (= <i>Parmacaulis</i> Shuysky & Shirshova in Chuvashov et al., 1987)
			<i>Palaeoberesella</i> Mamet & Roux, 1974 (= ? <i>Septamina</i> Meunier, 1888)
			<i>Devonoscala</i> Langer, 1979 (= <i>Stylaella</i> Berchenko, 1981)
			<i>Exvotarissella</i> Elliott, 1970 emend. Mamet & Roux, 1974
			<i>Kamaena</i> Antropov, 1967 (= <i>Subkamaena</i> Berchenko, 1981)
			<i>Kulikaella</i> Berchenko, 1981
			<i>Parakamaena</i> Mamet & Roux, 1974
			<i>Pseudokamaena</i> Mamet in Petryk & Mamet, 1972
			<i>Turgajella</i> Ivanova in Bogush et al., 1990
? <i>Metakamaena</i> Endo, 1969			
Beresellina		Beresellidae	<i>Beresella</i> Makhaev, 1937
			<i>Ardengostella</i> Vachard in Perret & Vachard, 1977
			<i>Dvinella</i> Khvorova, 1949 (= <i>Eomizzia</i> Endo & Horiguchi, 1957)
			<i>Trinodella</i> Maslov & Kulik, 1956
			<i>Uraloporella</i> Kord�e, 1950 (= <i>Samarella</i> Maslov & Kulik, 1956)

Table 3. Systematics of Moravamminida.

ORDER	SUBORDER	FAMILY	GENUS		
Moravaminida	Donezelliina	Claracrustidae	<i>Claracrusta</i> Vachard in Vachard & Montenat, 1981 (= <i>Berestovia</i> Berchenko, 1981)		
			<i>Asphaltinella</i> Mamet & Roux, 1978b		
			<i>Denisella</i> gen. nov.		
			<i>Kleinbergella</i> Mamet & Boulvain, 1992		
			<i>Peristacheia</i> Mamet & Roux, 1983		
			<i>Pokorminella</i> Vachard in Perret & Vachard, 1977 (= <i>Proninella</i> sensu Mamet & Roux, 1978b)		
			<i>Precorninella</i> Vachard, 1991		
		<i>Ungdarellina</i> Mamet, 2002			
		Donezellidae	<i>Donezella</i> Maslov, 1929 (= ? <i>Coksuella</i> Güvenç, 1965; = ? <i>Alanyana</i> Güvenç, 1967)		
			<i>Kamaenella</i> Mamet & Roux, 1974		
<i>Praedonezella</i> Kulik, 1973					
Aoujgaliida	Aoujgaliina	Aoujgaliidae	<i>Aoujgalia</i> Termier & Termier, 1950 (= <i>Mametella</i> Brenckle, 1977 = <i>Valuzieria</i> G. Termier, Termier & Vachard, 1977)		
			<i>Asteroaoujgalia</i> Brenckle, 2004		
			<i>Costacheoides</i> gen. nov.		
			<i>Epistacheoides</i> Petryk & Mamet, 1972 (= <i>Dromastacheoides</i> Vachard in Perret & Vachard, 1977, part.)		
			<i>Pseudostacheoides</i> Petryk & Mamet, 1972		
			<i>Roquesselsia</i> G. Termier, Termier & Vachard, 1977		
			<i>Sinustacheoides</i> G. Termier, Termier & Vachard, 1977		
			<i>Stacheoides</i> Cummings, 1955b (= <i>Chantonia</i> G. Termier, Termier & Vachard, 1977 = <i>Stacheoidella</i> Mamet & Roux in Mamet et al., 1987)		
			Ungdarellidae	<i>Ungdarella</i> Maslov, 1950 (= <i>Pseudoungdarella</i> Ivanova, 1999 = <i>Ungdarellodes</i> Chuvashov & Anfimov, 2007 = <i>Urtasimella</i> Chuvashov & Anfimov, 2007 = <i>Suundukella</i> Chuvashov & Anfimov, 2007)	
				<i>Cheggatella</i> Poncet, 1989	
				<i>Foliophycus</i> Johnson, 1960 (= <i>Dromastacheoides</i> Vachard in Perret & Vachard, 1977, part.)	
				<i>Komia</i> Kordé, 1951 (= ? <i>Turkomia</i> Gaillot, 2006 (nom.nud.) = <i>Pseudokomia</i> Racz, 1964)	
				<i>Petschoria</i> Kordé, 1951	
				<i>Ungdarellita</i> Mamet & Villa, 2004	
				Cuneiphycidae	<i>Cuneiphycus</i> Johnson, 1960
					<i>Masloviporidium</i> Groves & Mamet, 1985 emend. Vachard & Maslo, 1996
			<i>Multiporidium</i> gen. nov.		
			? <i>Iberiaella</i> Racz, 1984		
	Stacheiidae	<i>Stacheia</i> Brady, 1876 (= <i>Conilalia</i> Vachard in Massa & Vachard, 1979)			
		<i>Fourstonella</i> Cummings, 1955a (= ? <i>Amorfia</i> Racz, 1964 = <i>Chuvashovia</i> Vachard in Vachard and Montenat, 1981 = <i>Efluegelia</i> Vachard in Massa & Vachard, 1979 = <i>Foliophycopsis</i> Gaillot, 2006 (nom. nud.) = <i>Parastacheia</i> Mamet & Roux, 1977)			
	Fasciellidae	<i>Fasciella</i> Ivanova, 1973 (= <i>Shartymophycus</i> Kulik, 1973)			
		<i>Fascifolium</i> n. gen.			
	Calcifoliina	Calcifoliidae	<i>Calcifolium</i> Shvetsov & Birina, 1935		
			<i>Falsocalcifolium</i> Vachard & Cózar, 2005		
			<i>Frustulata</i> Saltovskaya, 1984a emend. Vachard & Cózar, 2005 (= <i>Pseudodonezella</i> Mamet & Herbig, 1990)		

Table 4. Systematics of the Donezelliina (Moravaminida) and Aoujgaliida.

Brady, 1876 to Loeblich & Tappan, 1964), but Algospongia are not consistent with the evolutionary trends of this group, which evolves from agglutinated to microgranular, porcelaneous or hyaline test walls (e.g., Loeblich & Tappan, 1987; Ross & Ross, 1991). Additionally, they are devoid of a proloculus or juvenarium. Nevertheless, some elements of the skeleton are more comparable with apertures, chambers, and walls of foraminifers than cells,

synapses and calcified membranes of algae. The interpretation of Algospongia as a group of fossil Protista independent from the Foraminifera (see Vachard et al., 1994, p. 10) can be reconciled with a strong biosedimentological production (e.g., issinellids, donezellids and beresellids) and not necessarily to an enormous productivity of algal bloom type.

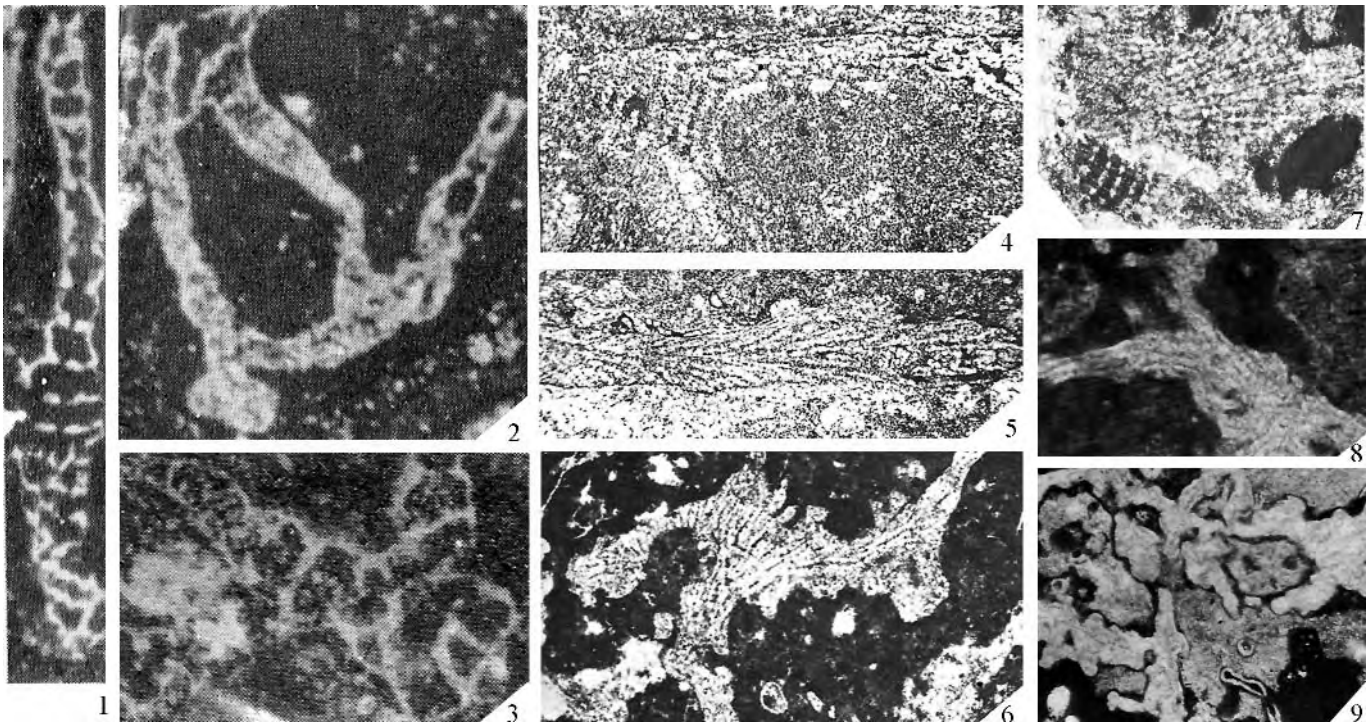


Figure 14. Poorly known Algospongia whose nomenclature is strongly affected by recrystallization. **1, 3**, *Donezella delicata* Berchenko, after Berchenko, 1982, pl. 11, fig. 3 and 4, respectively; two paratypes (see also the holotype reproduced here Fig. 10.25), Earliest Bashkirian, D₇⁴ limestone, Kalmius river, Donbass, Ukraine, x 70. **2**, *Praedonezella tenuissima* Berchenko, after Berchenko, 1982, pl. 11, fig. 1 (holotype); Earliest Bashkirian, D₇⁴ limestone, Kalmius river, Donbass, Ukraine, x 70. **4-5**, *Foliophycus llanoensis* Johnson, two figures after Johnson, 1963 showing the ambiguity of the type material of genus: 4 resembles *Multiporidium* gen. nov. and 5 is similar to *Ungdarella* or *Iberiaella*; hence, *Foliophycus* is a misinterpretation or truly another genus. Atokan, Marble Falls Limestone (Texas, U.S.A.), x 30. **6-7**, *Iberiaella carbonica* Racz designated as *Foliophycus llanoensis* Johnson by Lemosquet and Poncet, 1977, pl. 8, figs 7 (x 20.25)-8 (x 40.5), respectively. Compare Fig. 14. 6 with the *Masloviporidium* of the literature renamed here *Multiporidium* gen. nov. **8-9**, *Iberiaella carbonica*, type material, after Racz 1984 (figs 3B and 3A respectively, both x 34). Compare with Figs 14.6-14.7.

According to the genera, there are strong morphological similarities between different groups: red algae (*Ungdarella*); foraminifers (e.g., *Moravammina* and *Triangulinella*); microstromatoporids (*Komia*); labyrinthic ("sarmentoid") microsponges (*Labyrinthoconus* and *Sinustacheoides*); hypercalcified microsponges (*Stacheia* and *Anthracoporellopsis*); or green algae (*Exvotarisella*, *Beresellina*). Organizations in "tissues" described in some genera (e.g., *Epistacheoides*) related to a perithallus and a hypothallus, actually correspond to two orientations of the skeletal elements. Morphologies within this group are varied, and in general, the Aoujgaliina and the Calcifoliina adopted algal-like morphologies, but their ancestors show protistan-like morphologies. Apparently, the skeleton of the Beresellina resembles that in the dasycladales but some anatomical characters (diaphragms and blind pores) are not consistent with this comparison. The *Moravammina* are the most closely linked to foraminiferal mor-

phologies but no true proloculus were found. The Wetheredellina have morphological similarities with several primitive groups (Aphralysiaceae), as well as certain Foraminifera (e.g., *Tscherdyncevella* Antropov, 1950). Because of the type of wall (externally with a dark layer, microgranular), the size and the growth, the Wetheredellina group was initially placed in the Cyanobacteria (e.g., Vachard *et al.*, 2001) but due to the presence of microsparitized wall (e.g., *Sparaphralysia* Vachard in Vachard & Beckary, 1991), this assignment must be re-examined. It is also the case for the Reitlingerellida Vologdin, 1958 assigned either to the Cyanobacteria or the Foraminifera.

Occurrence.— Ordovician-Permian. Ordovician with the Wetheredellidae and some *Moravammina*? (see below); Late Silurian?-Early Devonian-Late Permian for the other families (Fig. 15).

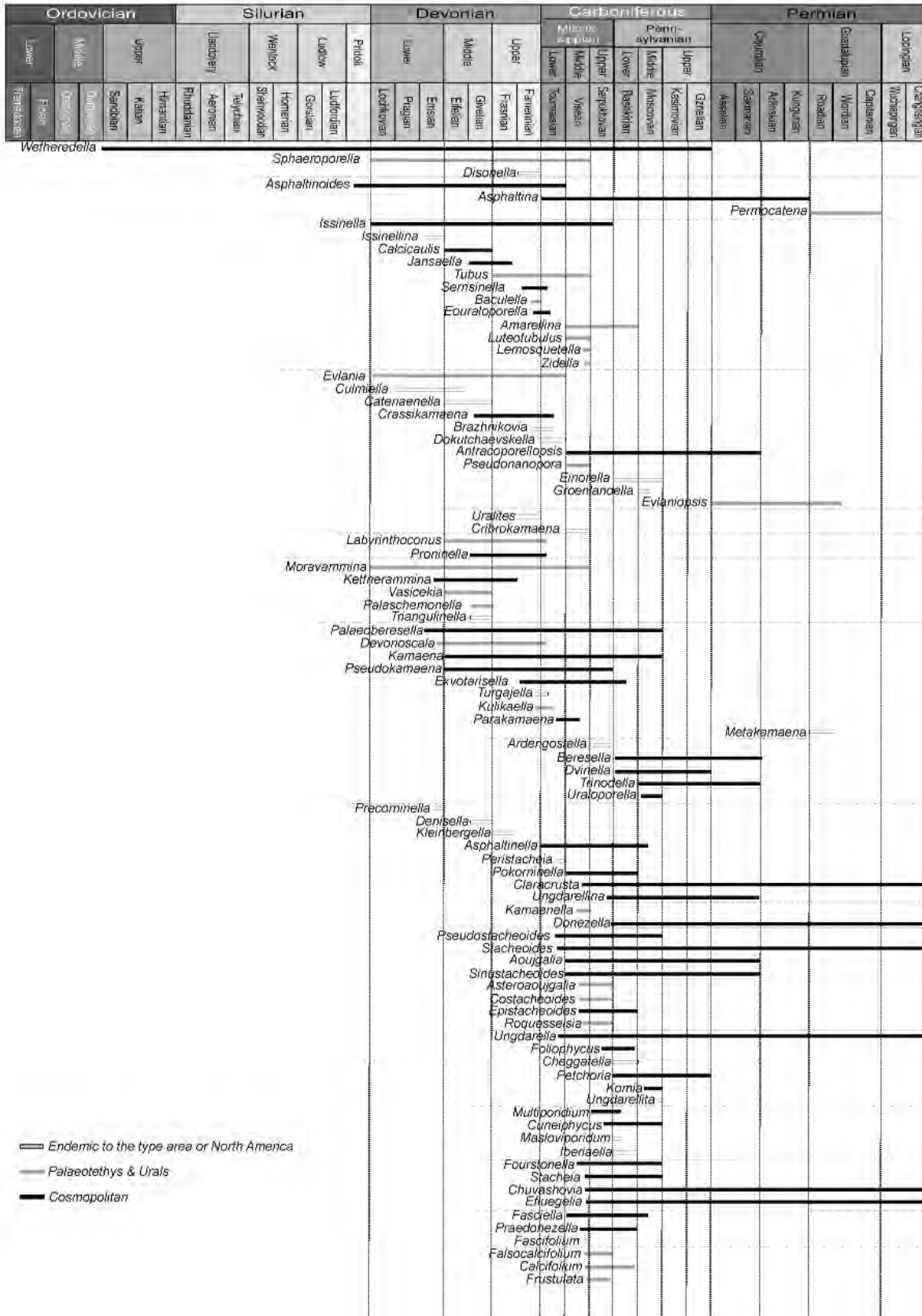


Figure 15. Biostratigraphic range of the genera of the class Algospongia.

Order MORAVAMMINIDA Pokorny, 1951, *nomen transl.* G. Termier *et al.*, 1975, *emend.* herein

Synonymy.— Palaeoberesellinae Mamet & Roux, 1974; *Kamaena-Donzellina* group (*sensu* Chuvashov & Riding, 1984); and Palaeosiphonocladales Shuysky, 1985.

Emended diagnosis.— Tests generally tubular, sometimes bifurcated, rarely laminar, divided by foraminifer-like septa or pseudosepta. The system of attachment, generally unknown or constituted by a whorl of chambers around the substrate (e.g., *Kettnerammina*, *Moravamina*); by “bracelets” (Dil *et al.*, 1977) (*Exvotarisella*, *Ardengostella*); or rarely, it is encrusting (*Evlania*). Wall calcareous, hyaline (granular to prismatic), generally perforated, with relatively common visible polysynthetic twinning of calcite, and exceptionally monocrystalline extinction. Perforations are generally simple, aspondyl pores, in some taxa with up to third order of subdivisions. Pores vary from rare and sporadic to abundant and concentrated in specialized sectors. Generally functional and communicating with the exterior (Moravaminina), they become blind (Beresellina).

Composition.— Four suborders: Wetheredellina Vachard *in* Dil *et al.*, 1977, *nomen transl.* herein; Moravaminina Pokorny, 1951, *emend.* G. Termier *et al.*, 1975; Beresellina Vachard, 1994b, *nomen transl.* herein; Donzellina G. Termier *et al.*, 1975, *nomen transl.* herein.

Remarks.— The lateral walls of chambers/pseudo-septa are absent or almost absent in Kettneraminidae, moderate to strong in Moravaminidae, strong but asymmetrical in Anthracoporellopsidae, and irregular in Labyrinthonidae. The wall occurs exceptionally as monocrystalline (e.g., *Devonoscala*). Additional characteristic structures are the bracelets (in particular, in *Exvotarisella*: Vachard *in* Dil *et al.*, 1977, fig. 13, pl. 6, fig. 1; Vachard, 1991, pl. 5, fig. 2; Madi *et al.*, 1996, pl. 24, fig. 7), the diaphragms and false-conceptacles of Beresellina (observed also in issinellids and *Evlania*), and the bereselloid-wall which occurs in all the Beresellina, as well as the genera *Evlaniopsis* and *Donzellina*.

Many representatives of the suborder Moravaminina are the most inconsistent with the algal interpretations of the Algospongia, and remain assigned to the foraminifers by

several authors (Loeblich & Tappan, 1964, 1984 and 1987; Vdovenko *et al.*, 1993).

Phylogeny.— Because of the calcitic, yellowish type of wall, and despite the difference in the canallicule textures, all the Moravaminida have been assigned to a single order (G. Termier *et al.*, 1975; H. Termier *et al.*, 1977; Vachard, 1991). The first representatives of Moravaminida are considered to be the Wetheredellina and the Issinellidae (Fig. 16), which are the earliest in presenting the tubular test, the Moravaminidae derive by a progressive development of septation (pseudo-septa to well-developed septa). The Anthracoporellopsidae although very “deformed” in shape are included here in the Moravaminina because their evolution (convergence with the foraminifers, complex perforation of the wall, attached mode of life, pseudo-septation) follows the same major lines. It is not the case for the Beresellina and Donzellina (hence, they were separated from a long time ago by the Russian authors); consequently, they are considered here as two different suborders, which were derived from the Moravaminina (see below). Although more advanced than the Moravaminina, the Beresellidae resemble Issinellinidae but due to a convergence and a disappearance or complete modification of the septation (perhaps, the imperforate diaphragms replacing the perforate septa).

Occurrence.— Late Silurian-latest Pennsylvanian, ?earliest Permian. Generally cosmopolitan.

Suborder WETHEREDELINA Vachard *in* Dil *et al.*, 1977, *nomen transl.* (from family)

Diagnosis.— Encrusting, globular to prostrate colonies composed of closely packed, vesicular to tubular chambers, communicated by perforations throughout the wall. Wall hyaline, yellowish, fibrous, tiny perforated, in some cases, two-layered with a thin internal micritic layer.

Composition.— Two families, Wetheredellidae Vachard *in* Dil *et al.*, 1977 (= Wetheredellaceae Berchenko *in* Chuvashov *et al.*, 1987); and Asphaltinidae fam. nov.

Remarks.— The skeletons assigned here to this family were also attributed to foraminifers, dasyclads, cyanobacteria, annelids or *incertae sedis* (e.g., Chuvashov & Riding,

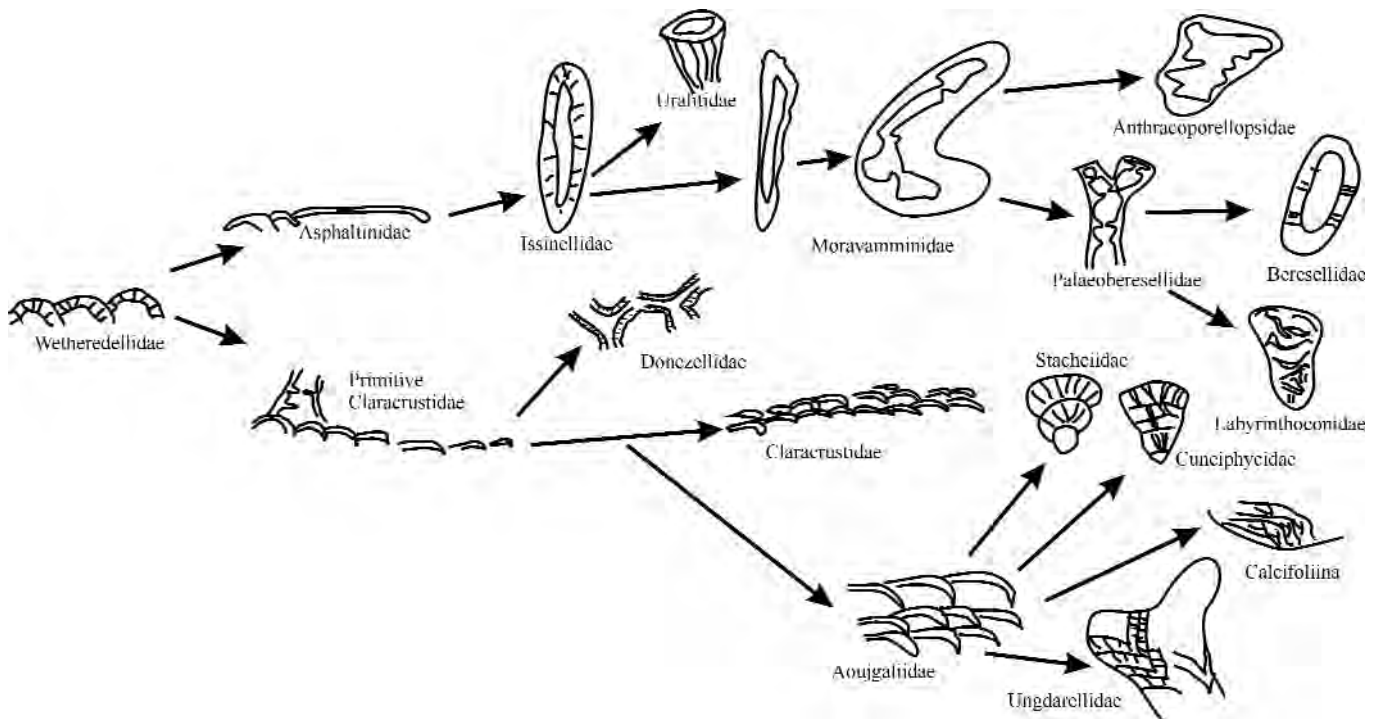


Figure 16. Morphological evolution of the class Algospongia.

1984; Mamet, 1991), or to microbial structures (Kazmierczak & Kempe, 1992).

The Wetheredellina, generally photic, differ from the foraminifers because of their simple morphology (Vachard, 1991) and resemble cyanobacteria Aphralysiaceae Vachard *et al.*, 2001. Nevertheless, their wall differs from these two latter groups. Some specimens of *Aphralysia* in Belka (1981, fig. 4 A-B) are probably misidentified *Wetheredella*. Similarly, the interpretations proposed by Kazmierczak & Kempe (1992) for *Wetheredella* concern more exactly the aphralysiacean *incertae sedis* (or eventually their Precambrian ancestors). The Wetheredellina are considered here as the group linking the Aphralysiaceae and Algospongia, and constitute eventually the boundary between the cyanobacteria and protista. *Sparaphralysia* Vachard in Vachard & Beckary, 1991 share many morphological similarities with genera of this order, but the wall nature is distinct, sparitized surely, entirely recrystallized and of a high magnesium calcite composition in origin.

Occurrence.— They are rare in the Cambrian-Ordovician, common in the Silurian-Devonian and relatively rare in the Mississippian (Great-Britain, Morocco, Spain, Turkey).

Occasionally, some specimens have been documented in the Bashkirian (Early Pennsylvanian) in Donbass, Japan and Pyrenees but they might be poorly preserved *Sparaphralysia*.

Only *Wetheredella* is cosmopolitan; the other genera are geographically more restricted.

Family WETHEREDELLIDAE Vachard in Dil *et al.*, 1977

Synonymy.— Wetheredellaceae Berchenko in Chuvashov *et al.*, 1987.

Diagnosis.— Encrusting tests. Closely packed, vesicular to tubular chambers. Wall hyaline, yellowish, fibrous, tiny perforated, with an external microgranular layer.

Composition.— Three genera (see Vachard, 1991, p. 264), *Wetheredella* Wood, 1948 (= *Cateniphycus* Maslov, 1956a); *Disonella* Conil & Lys, 1964; and *Sphaeroporella* Antropov, 1967.

Occurrence.— ?Cambrian, Late Ordovician-Bashkirian; geographical distribution different according to the genera.

Wetheredella is cosmopolitan; the other genera are palaeogeographically more restricted.

Genus *Wetheredella* Wood, 1948

(Fig. 9.9, Pl. 1, Figs 1-3, 5, 7)

Type species: *Wetheredella silurica* Wood, 1948.

Synonymy.— *Cateniphycus* Maslov, 1956a; Salebrids (*sensu* Jeffery & Stanton, 1996, p. 118, fig. 6d-e); Salebridae Dreesen *et al.*, 1985, pl. 7, figs 9, 11.

Diagnosis.— Hemispherical to irregular, attached aggregates of small, vesicular, undivided, single chambers. Numerous tiny wall perforations. Wall yellowish microgranular, eventually bilayered with a faint outer dark layer.

Composition.— *Wetheredella silurica* Wood, 1948; *W. cucinuli* Vachard in Dil *et al.*, 1977 (= ?*Amarellina hirotaniae* Mamet, 2002); *Cateniphycus friatus* Maslov, 1956a; *W. gigantea* Bao, 1992; *W. minuta* Bao, 1992; *W. multiformis* Ischenko in Ischenko & Radionova, 1981; *Wetheredella? munnecke* sp. nov.; *W. pachythea* Mamet & Roux in Héroux *et al.*, 1977 (= ?*Rhabdoporella flexuosa* Ischenko in Ischenko & Radionova, 1981); *W. pusilla* Shuysky in Shuysky & Patrunov, 1991; *W. starobeshevense* (*sensu* Vachard *et al.*, 1989 non Berchenko in Aisenverg *et al.*, 1983); *Cateniphycus tchussovensis* Malakhova & Chuvashov in Chuvashov, 1965; *W. tenuis* (*orth. mut.* herein for *tenuis*, neutral not feminine) Radionova in Ischenko & Radionova, 1981; and *W. tumulus* Copper, 1976.

Excluded species.— *W. starobeshevense* Berchenko in Aisenverg *et al.*, 1983 (= *Sparaphralysia*).

Remarks.— The relationship suggested by Ischenko & Radionova (1981) between *Wetheredella* and dasycladaceans was established on the basis of the connection between the *Wetheredellidae* and the *Issinellidae* (the latter being considered as dasycladaceans by these authors). However, this relationship is basically the transition between the most primitive vesicular Algospongia passing into the primitive tubular undivided moravamminids. Rothpletzellacean cyanobacteria exhibit frequent associations with *Wetheredella* (Wood, 1948; Mamet *et al.*, 1992, pl. 1, fig. 4, pl. 10, fig. 1; Nose *et al.*, 2006, p. 250) which is interpreted here as a probable ancestral micro-

ecosystem of the macroids *Ottonosia* with *Clara crusta* and cyanobacteria (see below) and then, those of the corallinale red algae with hyaline foraminifers *Acervulina* and/or *Gypsina* (see above).

The bioconstructions of *Wetheredella* seem to be similar to the “*Solenomeris*” build-ups of the foraminifers *Acervulina*, currently well-known (Perrin, 1992). According to the latter author, the bioconstructions of *Acervulinidae* occur in the modern reefs where the concurrence of red algae decreases (i.e., in 60-70 m deep fore-reef, or in cryptic habits).

Vachard (1980) and Vachard *et al.* (1993) interpreted the salebrids as excroissances around a spine of reticularioid brachiopod, maybe also related to *Draffania* Cummings, 1957. Homeomorphs of Salebridae are constituted by the *Ovommuridae* Munnecke *et al.*, 2000, but reticularian spines are absent in this group.

The *Wetheredellidae* differ from the *Salebridae* by the type of wall, absence of reticularioid spine, and attachment on a relatively broad and large substrate. The clusters of vesicles are rather similar to those in *Spumisalebra*. If they are not interpreted as elements of brachiopods, the *Salebridae* might be assigned to bryozoans (Jeffery & Stanton, 1996).

Occurrence.— ?Cambrian (rare). Late Ordovician-Silurian, cosmopolitan bioconstructors). Devonian (bioconstructors in South China and Australia; Shen & Webb, 2004; Adachi & Ezaki, 2007; Adachi *et al.*, 2007; Shen *et al.*, 2008), Viséan (rare but cosmopolite) (see details in Roux, 1985, p. 596). Rare in the Bashkirian (Donbass, Pyrenees, Japan).

***Wetheredella? munnecke* sp. nov.**

(Pl. 1, Figs 1-3, 5, 7)

- ? 1985 cf. *Salebra* sp. – Dreesen *et al.*, pl. 5, fig. 9.
- ? 1985 *Salebridae* – Dreesen *et al.*, pl. 7, figs 9, 11.
- ? 1985 *Incertae sedis* – Dreesen *et al.*, pl. 7, fig. 12.
- 1996 *Salebrids* – Jeffery & Stanton, p. 118, fig. 6d-e.

Etymology.— Dedicated to Dr. Axel Munnecke, who sampled the type material, and for his contributions on the Palaeozoic carbonates.

Type locality.– Feltrim Hill Quarry (circa 10 km N of Dublin, Ireland).

Type level.– Late Tournaisian.

Holotype.– Pl. 1, Fig. 1 (microphotograph number 14.06.07.5).

Diagnosis.– Test attached on shells or tubular substrates. Clusters of bananoid, thin-walled tubes (yellowish and dark). Some columnar elements occur, without central reticulariacean elements.

Description.– Substrates are constituted by sparitized undetermined tubes and fenestellid bryozoans. Gregarious sets of tubes are elongate and low, generally constituted by 4-6 rows of chambers. Chambers are semicircular, to bananoid, to rarely subtubular in longitudinal sections. Chambers are closely packed. The bottom of a chamber is constituted by the top of the preceding row. The wall is composed of a dark outer layer and an inner ochreous layer, apparently microgranular. The filling of the chamber compose a “trilete mark” (i.e., a tripartite contact of the filling microcrystallites). Wall perforations are apparently scarce. Maximal dimensions of sets of chambers = 0.050 mm. Dimensions of chambers = 0.040-0.070 mm.

Remarks.– Some specimens (20%) in the population have an aphralysiacean-like chamber shape (Pl. 1, fig. 5).

Type material.– 28 specimens (collection of Axel Munnecke).

Repository of the types.– Erlangen University (Germany).

Comparison.– *Wetheredella?* *munnecke* sp. nov. differs from the typical *Wetheredella* (especially from *W. cuniculi*) by the more elongate tubes; from *Spumisalebra* (particularly *S. spumosa* Bogush & Brenckle, 1982) by the absence of reticulariacean central elements; and from *Aphralysia* by the type of wall.

Occurrence.– Questionable in the Famennian of Belgium. Waulsortian (late Tournaisian) of New Mexico (U.S.A.) and Ireland.

Genus *Disonella* Conil & Lys, 1964

Type species: *Disonella lucens* Conil & Lys, 1964.

Synonymy.– ?*Triplosphaerina* Edgell, 2004.

Diagnosis.– More or less coiled Wetherellidae.

Composition.– Monospecific.

Remarks.– Although *Disonella* is controversial and originally assigned to the tournayellid foraminifers (Conil & Lys, 1964; Poyarkov, 1979), revision by one of the authors (D.V. in 1975) of the type material suggests that it is a wetheredellid. This revision of the type material of Conil & Lys, 1964 (which unfortunately remains unpublished) was based on the thin sections RC3363, RC3364, RC3365, RC3366. In thin section RC3363, some specimens are relatively similar to *Sphaeroporella aksubaica* Antropov, 1967. Specimens illustrated by Bouckaert *et al.* (1967) and Dreesen *et al.* (1985) are more representative of the genus than those others illustrated in Conil & Lys (1964), with not enough contrast.

The unique specimen of *Triplosphaerina medaensis* illustrated by Edgell (2004) seems to be a subaxial section of *Disonella* (this proposal is also consistent with its size and stratigraphic range of this specimen).

Occurrence.– Famennian of Belgium (biozone DFZ5 of Poty *et al.*, 2006); ?late Famennian of Canning Basin (Western Australia).

Genus *Sphaeroporella* Antropov, 1967

Type species: *Sphaeroporella aksubaica* Antropov, 1967.

Diagnosis.– Small, vesicular, undivided, single chambers. Numerous wall perforations. Wall bilayered with an external dark tectum and internal yellowish pseudofibrous layer.

Composition.– *S. aksubaica* Antropov, 1967; *S. asturiana* Vachard, 1991; *Tikhinella bulbosa* Reitlinger, 1954; and *Cateniphycus? conchatiformis* Malakhova & Chuvashov in Chuvashov, 1965.

Excluded species.– See Vachard (1991, p. 265), and to add *Sphaeroporella* sp. [*sensu* Mamet, 2002, p. 503, pl. 4, fig. 1 (= *Sparaphralysia*)].

Remarks.— *Sphaeroporella* differs from *Wetheredella* by the relatively thick dark outer layer always present, and less chambers in the tests (for example the *Wetheredella* of Mamet & Pr eat, 2009, pl. 5, fig. 6 should be considered as a *Sphaeroporella*). Many *Sphaeroporella* of the literature (e.g., Mamet, 2002; Mamet & Roux, 1975a, pl. 14, fig. 1) might be assigned to *Sparaphralsia* or to the *incertae sedis* Salebriidae. *Sparaphralsia* does not belong to the Wetheredellidae, because of its microsparitic type of wall calcification, but more probably to the apherlasiaceans.

Occurrence.— Devonian (Vachard, 1991); latest Devonian (Ivanova & Bogush, 1992); or Devonian-Vis ean (Mamet, 1991). Western Palaeo-Tethys and Urals.

Family ASPHALTINIDAE fam. nov.

Diagnosis.— Encrusting to erect tests. Closely to loosely packed, sphaerical to tubular chambers. Wall hyaline, yellowish, fibrous, tiny perforated by pores simple, fine and aspondyl.

Composition.— Three genera, *Asphaltina* Mamet in Petryk & Mamet, 1972; *Asphaltinoides* Devera, 1987 (= ?“foraminif eres” *sensu* Poncet, 1965 =? *Cuzbassia* Ivanova in Bogush *et al.*, 1990); *Permocatena* Vachard & Miconnet, 1990.

Comparison.— The Asphaltinidae differ from the Wetheredellidae by the elongate chambers, and from the Issinellidae by gregarious chambers and absence of terminal apertures.

Occurrence.— Early Devonian-Middle Permian. *Asphaltina* is Tournaisian-Early Permian, principally North-American, but scarce in the Palaeo-Tethys older than the Early Permian. *Permocatena* is restricted to a few middle Permian Neo-Tethyan basins.

Genus *Asphaltina* Mamet in Petryk & Mamet, 1972

(Pl. 1, Fig. 13)

Type species: *Asphaltina cordillerensis* Mamet in Petryk & Mamet, 1972.

Diagnosis.— Encrusting tests constituted by tubular undivided tubes, closely packed. Wall yellowish, pseudofibrous, with thin, dark outer layer.

Composition.— Monospecific. Other species attributed to this genus, such as *A.?* *macadami* Brenckle & Groves, 1987 was later attributed to *Asphaltinoides* by Hoare & Skipp (1995); both generic identifications remain questionable.

Remarks.— *Asphaltina* Mamet in Petryk & Mamet, 1972, occasionally assigned to the Wetheredellida (Mamet, 1991, p. 383), was interpreted as a globular coiled animal with erect terminal parts (maybe an annelid according to Vachard, 1991). For example, the *Asphaltina* sp. of Mamet & Boulvain (1992, pl. 4, fig. 4) seems to be a glomus of *Spirorbis* sp. The genus *Asphaltinoides* Devera, 1987 might be also included in the same animal group. This latter genus might correspond with the micro-organisms interpreted as foraminifers by Poncet (1965, fig. 1-6; 1970, fig. 23). Usually, *Asphaltina* seems to be in photic environments; although in Afghanistan and Iran, *Asphaltina* tolerated relatively cool and turbid waters, due to the proximity of Gondwanan tilloid sediments, and the input of clay, silt and quartz sand in the *Asphaltina*-bearing limestones.

Occurrence.— Mississippian-Middle Pennsylvanian in North America, from Idaho to Alaska and Canada (see Mamet, 1991). Tournaisian of Western Siberia (Ivanova & Bogush, 1992, tab. 1 p. 41). Latest Vis ean of Algeria (Sebbar & Mamet, 1996). Serpukhovian of Siberia (Ivanova & Bogush, 1988; 1992, tab. 1, p. 241). Early Permian of Afghanistan, Carnic Alps and Urals (Vachard & Montenat, 1981; Chuvashov & Anfimov, 1988; Forke, 1995). Early Permian of eastern Iran (D. V., unpublished data).

Genus *Asphaltinoides* Devera, 1987

(Pl. 1, Figs 4, 8-10)

Type species: *Asphaltinoides grandtowerensis* Devera, 1987.

Synonymy.— ?*Cuzbassia* Ivanova in Bogush *et al.*, 1990.

Diagnosis.— Asphaltinidae with single-layered wall, coarsely prismatic and bifurcated tests.

Composition.— *Asphaltinoides grandtowerensis* Devera, 1987; *A. falgairasensis* sp. nov.; ?*Cuzbassia botryosa* Ivanova in Bogush *et al.*, 1990 (the glomus possesses eventually more evolute whorls). *Asphaltinoides*

macadami (sensu Hoare & Skipp, 1995 and Harris *et al.*, 1997) is questionable. The “Foraminifères” of Poncet (1965, figs 1-6) differ from *Asphaltinoides* by more elongate chambers and less perforated walls, this character might suggest a new species, the best specimen of which was illustrated by Poncet (1970, fig. 23).

Occurrence.— Uppermost Silurian (probably Prídolí or Lochkov) of southern France-Early Devonian (“Siegenian” of western France)-early Middle Devonian U.S.A. ?Early Tournaisian of Kuzbass (Russia) for *Cuzsbassia*. ?Early Mississippian of Iowa.

***Asphaltinoides falgairasensis* sp. nov.**

(Pl. 1, Figs 4, 8-10)

Etymology.— From the Falgairas, a hill in Montagne Noire, southern France.

Type locality.— Falgairas, between the outcrops F and O of Feist & Schönlaub (1974, text-fig. 3, p. 203).

Type level.— Late Prídolí (more or less equivalent of the levels F2 and O4 of Feist & Schönlaub, 1974, text-fig. 6, p. 206).

Holotype.— Pl. 1, Fig. 4 (sample DV214a).

Diagnosis.— *Asphaltinoides* with scarcely perforated wall and irregular external surface.

Description.— Test gregarious, incrusting, composed of few packed tubes, the first ones form a crown around the substrate. The other ones are elongate along the substrate, and/or the preceding tubes. Substrates are constituted by crinoids or bryozoans. Lumen of the undivided tube rather large. Regular inner surface of the tube and externally rugose. Aperture not observed. Wall thickness finely perforated in the crown, pale yellow, prismatic, rarely or not perforated and maculed in the last part. Dimensions of crown = 0.800 x 0.400 mm, dimensions of elongate tubes: length = 1.500-9.000 mm, height = 0.200-0.300 mm, wall thickness = 0.070-0.100 mm.

Type material.— 11 sections in 3 thin sections.

Repository of the types.— Collection of Palaeontology in the Lille University.

Comparison.— *Asphaltinoides falgairasensis* sp. nov. differs from *A. grandtowerensis* by the less intensively perforated wall and the irregular external surface of the tube.

Occurrence.— Same as type level and type locality.

Genus *Permocatena* Vachard & Miconnet, 1990

(Pl. 1, Figs 17-19)

Type species: *Permocatena jennyae* Vachard & Miconnet, 1990.

Diagnosis.— Elongate test, moniliform, composed of an uniseriate row of subspherical chambers. Wall yellowish, hyaline, fibrous, crossed by many simple and thin perforations.

Composition.— Monospecific.

Occurrence.— Middle Permian of Italy. Middle Permian of Turkey (Lycian nappes), ?Afghanistan and ?Oman (D.V. unpublished data).

Suborder MORAVAMMININA Pokorny, 1951, *nomen transl.* herein (from order)

Synonymy.— Palaeoberesellinae Mamet & Roux, 1974; *Kamaena-Donzella* group (sensu Chuvashov & Riding, 1984, *part.*); Palaeosiphonocladales Shuysky, 1985.

Diagnosis.— Tubular Moravaminida divided by generally strong septa or pseudosepta. System of attachment often constituted by a whorl of chambers around the substrate, “bracelets” or a surface of attachment. Monocrystalline extinction or visible twins of calcite relatively common. Isolated or common wall perforations, rarely arranged in groups (pseudo-tufts), generally single but occasionally ramified until the third order. Aperture terminal, central; always simple, except in two cases of cribrate apertures (*Anthraco-porellopsis* and *Cribrókamaena*).

Composition.— Six families: Issinellidae Deloffre, 1987, *emend.* herein; Anthracoporellopsidae Shuysky, 1985, *emend.* Vachard, 1994a, *nomen transl.* herein; Uralitidae Vachard, 1991, *nomen transl.* and *emend.* herein; Labyrinthoconidae Langer, 1979; Moravaminidae Pokorny, 1951, *emend.* G. Termier *et al.*, 1975; and Palaeoberesellidae Mamet & Roux, 1974, *nomen transl.* herein.

Occurrence.— Late Silurian-Middle Pennsylvanian (latest Moscovian). Acme from Early Devonian to Pennsylvanian. Cosmopolitan or limited to the shelves of Western Palaeo-Tethys and Urals.

Family ISSINELLIDAE Deloffre, 1987, *emend.* herein

Synonymy.— Issinelleae Deloffre, 1988; and Issinelleae Saltovskaya, 1990.

Emended diagnosis.— Cylindrical tests, undivided, eventually with very rare diaphragms. Wall hyaline yellowish, clear to maculate, with diverse groups of thin, single and open canalicules (see Vachard, 1991, text-figs 5-6).

Composition.— *Issinella* Reitlinger, 1954, *emend.* Vachard, 1991; *Amarellina* Mamet, 1995; *Baculella* Conil & Dreesen in Dreesen *et al.*, 1985 (= *Dreesenullella* Vachard, 1991); *Eouraloporella* Berchenko, 1981; *Issinellina* Shuysky in Shuysky & Shirshova, 1988; *Jansaella* Mamet & Roux, 1975b; *Lemosquetella* Mamet & Sebbar, 1998; *Luteotubulus* Vachard in Vachard *et al.*, 1977; “*Pseudonanopora*” Mamet & Roux, 1975 (*part.*); *Serrisinella* Vachard, 1991; *Tubus* Chuvashov in Chuvashov *et al.*, 1985; *Zidella* Saltovskaya, 1984a; ?*Calcicaulis* Shuysky & Shirshova in Chuvashov *et al.*, 1987.

Remarks.— The Issinellidae are the Moravamminida composed of single tubular tests, occasionally bifurcated, and with outer surface smooth (*Issinella*), irregular (*Zidella*) or costulate (*Lemosquetella*), and generally finely canaliculate. The wall is single-layered; clear yellow (*Issinella*) to maculate (*Luteotubulus*). In many genera, several diaphragms (Vachard, 1991, fig. 4.4) can occupy the entire central cavity (mainly in *Jansaella*, *Issinella*? and *Luteotubulus*). Owing to these diaphragms and yellowish hyaline wall, the similarity with Dasycladales must be abandoned (see also discussion on true and false *Nanopora* in Vachard & Aretz, 2004). The morphological similarity between the dasyclad *Nanopora* and *Issinella* is only superficial, while their wall mineralogies are completely different. The issinellids and especially *Serrisinella*, differ by the aspondylity and the calcitic, yellowish wall. Moreover, *Nanopora fragilissima* (Maslov) described by Bogush *et al.* (1990, p. 112-113, pl. 13, fig. 5-8) belongs to *Serrisinella*. Other Devonian *Nanopora* such as *N. uralica* Shirshova in Shuysky & Shirshova, 1988, are also in-

terpreted as issinellids. Both genera, *Nanopora* and *Serrisinella*, exemplify the differences between the dasyclad algae and the tubular Algospongia. Nevertheless, the diaphragms have no equivalents among the Protista, just perhaps the phrenothecae of the Fusulinida Schwagerinoidea (e.g., Thompson, 1964) or the lamellae of the possible Serpulidae *Barbafera* (see Senowbari-Daryan, 1997).

The absence of a proloculus prevents their attribution to the foraminifers, and the small diameter of the canalicules is not consistent to those in the Spongia, particularly in *Disyringia* Ridley (see Brien, 1973, fig. 106; Fry & Fry, 1979, fig. 1), although the atypical sponge *Disyringia* (Fig. 1.1) is morphologically rather similar to *Dreesenullella*, *Uralites* or *Cribrókamaena*.

Plate 1

1-3, 5, 7, Wetheredella? munnecke sp. nov. Collection Axel Munnecke (Erlangen, Germany). Late Tournaisian (Waulsortian mud-mound) of Feltrim Hill Quarry (E. Ireland). 1. Holotype. Photo 14.6.07.62; x 17. 2. Paratype. Photo 14.6.07.54; x 17. 3. Detail of 4. Photo 14.6.07.59; x 80. 5. Paratype. Photo 14.6.07.58 (left); x 17. 7. Paratype. Photo 14.6.07.58 (right); x 17.

4, 8-10, Asphaltinoides falgairaisensis sp. nov. 4. Holotype. Sample DV241a. Photo 14.6.07.75. Falgairas (between the outcrops F and O), Montagne Noire, southern France. Late Pridoli (equivalent to F2 and O4). See Feist and Schönlaub (1974, text-figs 3, 6), x 14. 8. Paratype, with a crown (bottom, right) and elongate tubes (top). Sample DV241a. Falgairas (between the outcrops F and O), Montagne Noire, southern France. Late Pridoli (equivalent to F2 and O4). See Feist and Schönlaub (1974, text-figs 3, 6), x 42. 9. Detail of holotype showing the rugosities of the wall. Sample DV241a. Falgairas (between the outcrops F and O), Montagne Noire, southern France. Late Pridoli (equivalent to F2 and O4). See Feist and Schönlaub (1974, text-figs 3, 6), x 27. 10. Paratype with elongate tubes (top). Sample DV241b. Photo 14.6.07.75. Falgairas (between the outcrops F and O), Montagne Noire, southern France. Late Pridoli (equivalent to F2 and O4). See Feist & Schönlaub (1974, text-figs 3, 6), x 40.

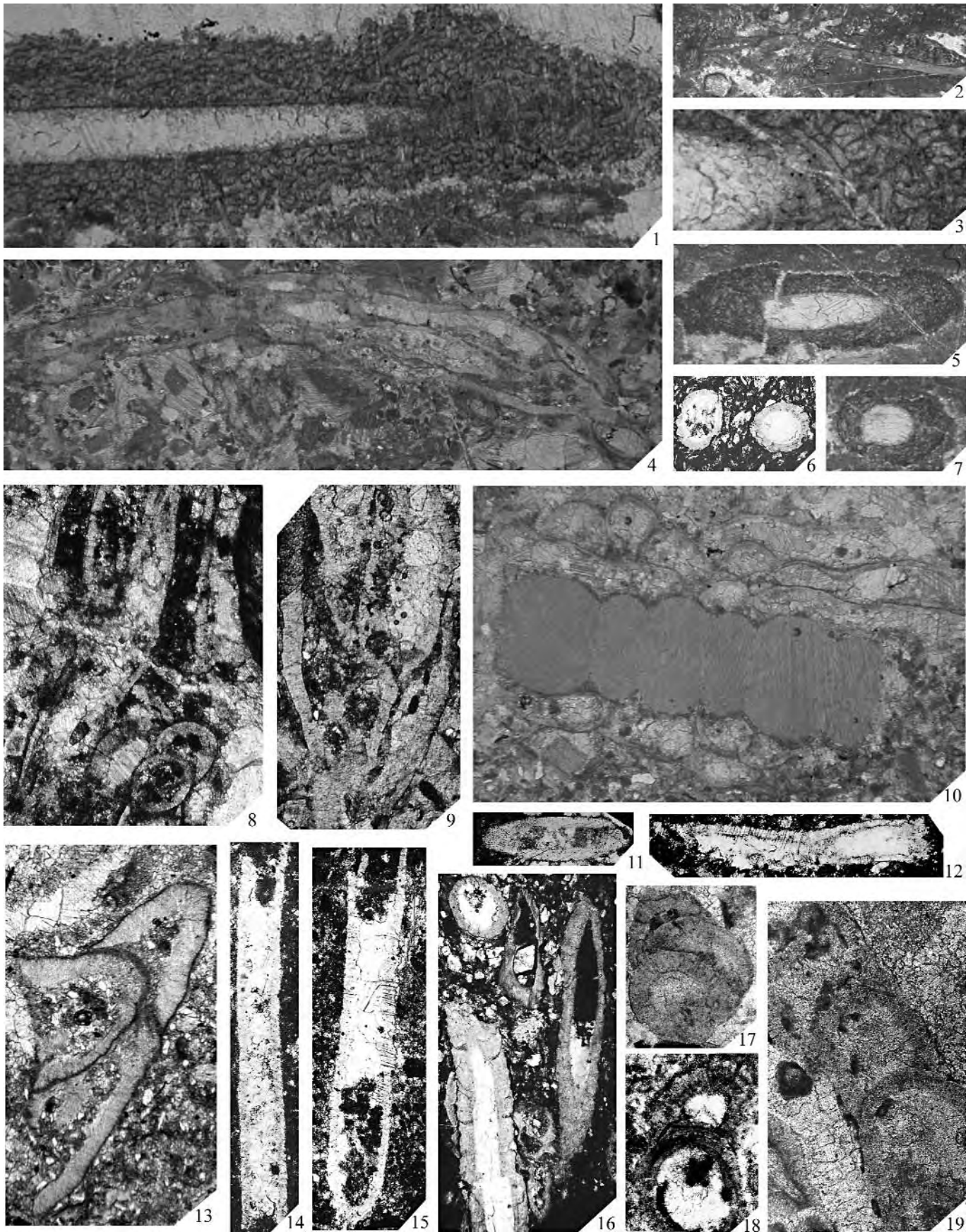
6, 16, Issinella aff. grandis Chuvashov, 1965. Late Tournaisian. 6. Saint-Ghislain Borehole (Belgium). Photo RC 15113; x 50. 16. Saint-Ghislain Borehole (Belgium). 3943.50 m. Photo RC 15116; x 33.

11, Issinella sp. transitional to *Serrisinella* sp. Frasnian of Belgium. Sample Tailfer 2513 (VW 122bis A2), Photo RC 13936; x 50.

12, 14-15, Issinella devonica Reitlinger, 1954. Longitudinal section. Frasnian of Belgium. 12. Subaxial section. Sample Tailfer 2518 (VW 131) Photo RC 13950; x 50. 14. Sample Tailfer 1246 (VW58). Photo RC13953; x 50. 15. Oblique section. Sample Tailfer 83 III. Photo RC 14001; x 50.

13, Asphaltina cordillerensis Mamet in Petryk & Mamet, 1972. Longitudinal section. Collection Sasan Bagheri. Early Permian; Central Iran; x 80.

17-19, Permocatena jennyae Vachard in Vachard & Miconnet, 1990. 17. Subtransverse section. Sample MF 2-1. Midian? (late Middle Permian) reworked in the Triassic. Monte Facito, Italy; x 33. 18. Oblique section. Sample P5 (ML7872). Murgabian or Midian (Middle Permian). Bulola High (northern Afghanistan); x 33. 19. Longitudinal section. Sample MF 1-3. Midian? (late Middle Permian) reworked in the Triassic. Monte Facito, Italy; x 48.



Dreesenulella Vachard, 1991 replaced *Baculella* Conil & Dreesen in Dreesen *et al.*, 1985 which would have been preoccupied in the animal kingdom (see Loeblich & Tappan, 1987). However, this latter genus was only described as a “microproblematicum”, and its assignment to the animal realm is not clearly established, thus, *Baculella* is re-used here. New material provided by E. Poty (Liège; July 2009) confirms the narrow relationship of the wall with *Serrissinella* (= “*Issinella*” *auct.*). Contrary to the assignment of Vachard (1991), *Magnitella* Malakhova, 1975 belongs more probably to the Foraminifera Earlandioidea, as indicated by Vdovenko *et al.* (1983, p. 41); and *Beresella praecursor* Vachard, 1977, was re-interpreted to be a *Magnitella* by Pille (2008).

Diaphragms in a taxon illustrated as “*Issinella*” by Bogush *et al.* (1990, pl. 12, fig. 9 top), in *Luteotubulus* were illustrated by Vachard (1994b, pl. 1, figs 1, 3-4, 6-8); and in *Uraloporella* by Saltovskaya (1984b, pl. 12, figs 1-10, pl. 13, figs 2, 7, 9) and Mamet & Villa (1995, pl. 1, fig. 5, with 4 or 5 diaphragms).

Phylogeny.– The Issinellidae might derive from the Wetheredellida by an elongation of the vesicular chamber passing to a tube, and multiplication of the canalicules. This evolution was previously suggested between the Wetheredellida and the seletonellacean tubular genus *Rhabdoporella* by Ishchenko & Radionova (1981), but this latter taxon is interpreted to be a true Chlorophyta Seletonellaceae (Bassoullet *et al.*, 1979).

Occurrence.– Early Devonian to late Serpukhovian, and they remain rare up to the Bashkirian (*Amarellina*). In Belgium, *Luteotubulus* is a good marker of late Moliniacian (= Arundian). In Ireland, *Luteotubulus* is regarded as a marker for the early Viséan (Chadian-Arundian) (Jones & Somerville, 1996). In the Montagne Noire (southern France), *Zidella* seems to be limited to the latest Asbian, updated by Pille (2008). Geographic distribution poorly known, but probably cosmopolitan.

Genus *Issinella* Reitlinger, 1954

(Figs 4.12-4.13, 9.5, 9.8; Pl. 1, Figs 6, 11?-12, 14-16)

Type species: *Issinella devonica* Reitlinger, 1954, *emend.* Vachard, 1991.

Synonymy.– ?*Nanopora* (*sensu* Berchenko, 1981).

Diagnosis.– Small, cylindrical, undivided, single tests, rarely bifurcated. No diaphragms. Wall yellowish, without visible twins, no dark inner layer, perforated by numerous aspondyl canalicules.

Composition.– *Issinella devonica* Reitlinger, 1954, *emend.* Vachard, 1991 (*non sensu* Mamet & Roux, 1981 = several genera; *nec sensu* Saltovskaya, 1990 = *Serrissinella*); *I. grandis* Chuvashov, 1965; *Zidella minor* Ivanova, 1988; *I. simplex* Shuysky in Shuysky & Patrunov, 1991; *I. sp.* (*sensu* Zupalova, 1981a, pl. 46, fig. 5); ?*I.* (?) *sp.* (*sensu* Pille, 2008, p. 63, pl. 21, figs 1-8); ?*Nanopora woodi* Berchenko, 1981; ?*Nanopora undata* Ivanova in Bogush *et al.*, 1990.

Excluded species.– *Issinella?* *ilychensis* Ivanova, 1988 (= *Luteotubulus*); *I. sp.* [*sensu* Zupalova, 1981b, pl. 11, fig. 3 (= *Kettnerammina*)]; and all the species assigned below to *Serrissinella*.

Remarks.– *Issinella* differs from *Luteotubulus* and *Zidella* by the absence of diaphragms. This genus differs from *Kettnerammina* by the absence of twins in the wall.

The reconstruction of Mamet & Roux (1981, text fig. 1, p. 153), Cnudde & Mamet (1983, pp. 186, 188) or Roux (1985, text-fig. 14, p. 570; reproduced here Figs 9.5-9.8) is questionable and it can be related to that of *Serrissinella*, due to the numerous bifurcations and too numerous perforations. A habitus similar to that reconstructed for *Tubus* by Chuvashov in Chuvashov *et al.* (1985, text-fig. 5 p. 94; here Fig. 9.1) is more consistent with the sections observed by us. The *Issinella* with diaphragms illustrated by Bogush *et al.* (1990, pl. 12, fig. 9) could be considered as a distinct taxon, probably transitional to *Jansaella* Mamet & Roux, 1975b.

Occurrence.– Early Devonian-Viséan, cosmopolitan. The FAD of the genus [Emsian as indicated by Vachard (1991) or older] is poorly established; as well as the LAD [the species of the Urals disappear at the end of the middle Viséan (Bogush *et al.*, 1990, tab. 1, p. 10)]. Questionable specimens are present in the late Serpukhovian of the Pyrenees (Pille, 2008).

Genus *Amarellina* Mamet, 1995

(Pl. 2, Figs 1-9)

Type species: *Amarellina huvelinii* Mamet, 1995.

Diagnosis.— Test erect, cylindrical, bifurcated. Wall perforated by euspondyl, acrophore, ramified laterals. Long primary branches to the perforations and short secondary, ramified branches.

Composition.— Monospecific.

Excluded species.— *Amarellina hirotaniae* Mamet, 2002 (= probably *Wetheredella cuniculi* Vachard in Dil *et al.*, 1977).

Remarks.— *A. hirotaniae* Mamet, 2002 resembles the transitional forms between *Wetheredella* and *Issinella*; it is not congeneric with *A. huvelinii* and can be attributed to *Wetheredella* (*sensu lato*), most probably *W. cuniculi*.

Occurrence.— Viséan-Bashkirian. Central Morocco, Ireland, England, and western Algeria (Béchar Basin).

Genus *Baculella* Conil & Dreesen in Dreesen *et al.*, 1985

Type species: *Baculella gemina* Conil & Dreesen in Dreesen *et al.*, 1985.

Synonymy.— *Dreesenulella* Vachard, 1991 (only valid if the taxon belongs unquestionably to the botanical realm; that is at the moment impossible to prove).

Diagnosis.— Test similar to *Serrisinella*, but frequently very inflated, and possibly linked together by a pair of sub-spherical chambers (see Vachard, 1991, text-fig. 6D).

Composition.— Monospecific. See also some Silurian “*Saccomminopsis*” and *Nodosaria* (?) *mediana* Bykova, 1956.

Remarks.— This poorly known form might represent a life stage of *Serrisinella*.

Occurrence.— Early late Famennian of Belgium and Urals.

Genus *Eouraloporella* Berchenko, 1981

Type species: *Eouraloporella kordeae* Berchenko, 1981.

Diagnosis.— Test similar to *Issinellina* (i.e., with a smooth internal periphery and a rugose external one; see Vachard, 1991, text-fig. 5P). Wall perforations very numerous. Diaphragms present.

Composition.— *Eouraloporella kordeae* Berchenko, 1981; *Rhabdoporella?* sp. Brazhnikova & Rostovceva, 1966, pl. 23, figs 1-6.

Occurrence.— Devonian-Carboniferous boundary, Donets Basin and Alaska (Mamet, 1986, 1991).

Genus *Issinellina* Shuysky in Shuysky & Shirshova, 1988

Type species: *Issinella primitiva* Shuysky, 1973.

Diagnosis.— Issinellidae characterized by the large size and the rugose periphery.

Composition.— *Issinella primitiva* Shuysky, 1973; *Issinellina calva* Shuysky in Shuysky & Shirshova, 1988; *I. irregulare* Shuysky in Shuysky & Patrunov, 1991.

Excluded species.— The other species of the genus, *Issinellina calva* Shuysky in Shuysky & Shirshova, 1988 and *I. irregularis* Shuysky in Shuysky & Patrunov, 1991 (correct spelling for *irregulare*) are considered here as Dasycladales Seletonellaceae.

Occurrence.— Late Early Devonian of Central Urals.

Genus *Jansaella* Mamet & Roux, 1975b

Type species: *Jansaella ridingi* Mamet & Roux, 1975b.

Diagnosis.— Small, cylindrical, single tests, rarely bifurcated, divided by numerous septa. Wall yellowish, perforated by very numerous canalicules.

Composition.— Monospecific.

Occurrence.— Givetian-Frasnian of Alberta (Canada), Poland (Racki & Sobón-Podgórska, 1992) and Germany (May, 1994, pl. 39, fig. 8). Questionable in the Frasnian of Urals and Strunian of Donbass.

Genus *Lemosquetella* Mamet & Sebbar, 1998

(Pl. 2, Fig. 10)

Type species: *Lemosquetella annulata* Mamet & Sebbar, 1998.

Diagnosis.— Small, cylindrical, undivided, single test. Numerous single, aspondyl perforations, no diaphragms. A transverse external costulation regularly developed and imperforate. Wall yellowish, without visible polysynthetic twinning.

Remarks.— This genus is very rare, and just a single specimen was recognised by one of us (P.C.) in Ireland.

Occurrence.— Brigantian of Algeria (Oubeur Formation, Béchar Basin) and late Asbian in the Bricklieve Mountains (NW Ireland) (Cózar et al. 2005a).

Genus *Luteotubulus* Vachard in Vachard et al., 1977

(Pl. 2, Figs 11-14)

Type species: *Uraloporella licis* Malakhova, 1975.

Synonymy.— *Uraloporella* (part.); *Issinella* (part.); ?*Kamaena* sp. (sensu Petryk & Mamet, 1972, pl. 3, fig. 10); *Goksuella* (sensu Pelhâte & Poncet, 1975, pl. 2, fig. D).

Diagnosis.— Large tubular tests, cylindrical, undivided, perhaps bifurcated, with perforations and diaphragms. Wall yellowish, finely canaliculated, and often maculate.

Composition.— *Uraloporella licis* Malakhova, 1975; *Issinella? ilychensis* Ivanova, 1988.

Remarks.— Diaphragms of *Luteotubulus* were illustrated by Vachard et al. (1977, pl. 3, figs 1, 4), Vachard (1991, pl. 5, fig. 3; 1994b, pl. 1, figs 1, 3-4, 6-8) and Jones & Somerville (1996, fig. 4g). *Luteotubulus* sp. (sensu Cózar & Somerville, 2005c, fig. 5.8) with its complete septa is atypical, and it is closer to *Evlania?* sp., as well as *Issinella devonica* (sensu Brenckle & Milkina, 2003, pl. 2, fig. 25).

Occurrence.— Late Early Viséan (Cf4γ)-latest Viséan (upper Cf6δ); Palaeo-Tethys and Ural platforms. In Belgium, *Luteotubulus* is a good marker of late Moliniacian (= Arundian), as well as the Bobrykovsky horizon, its equivalent in Russia. In Ireland, *Luteotubulus* is regarded as a marker

for the early Viséan (Chadian-Arundian) (Jones & Somerville, 1996).

Genus *Serrisinella* Vachard, 1991

(Pl. 2, Figs 15-17)

Type species: "*Issinella*" *serrensis* Vachard, 1988b.

Synonymy.— *Issinella* (part.); "*Issinella*"; *Anthracoporella* (part.); *Rhabdoporella* (part.); *Pseudoissinella* (part.).

Plate 2

1-9, *Amarellina huvelinii* Mamet, 1995. 1. Note that one of the ramifications presents a diaphragm and the other, present well communicated chambers. Pc1473, Kesh Corann Hill, Bricklieve Mts., late Asbian, NW Ireland, x 75. 2. Oblique section of the bifurcation, inconnected. Pc1596, Doonaveeragh, Bricklieve Mts., late Asbian, NW Ireland, x 77. 3. Oblique section with three chambers, inconnected. Pc1612, Doonaveeragh, Bricklieve Mts., late Asbian, NW Ireland, x 102. 4. High-angled bifurcation. Pc2917, Rockdale Lst. Fm, late Asbian, Northern Ireland, x 40. 5. Two consecutive bifurcations. Pc2917, Rockdale Lst. Fm, late Asbian, Northern Ireland, x 40. 6. Detail of Pl. 2, Fig. 5, showing a well developed wall in between the chambers. Pc2917, Rockdale Lst. Fm, late Asbian, Northern Ireland, x 102. 7. Detail of the second bifurcation in Pl. 2, Fig. 5. Pc2917, Rockdale Lst. Fm, late Asbian, Northern Ireland, x 102. 8. Oblique section, showing the outer ornamentation. Pc933, Clogrenan Quarry, late Brigantian, SE Ireland, x 34.5. 9. Detail of Pl. 2, Fig. 4, Rockdale Lst. Fm, late Asbian, Northern Ireland, x 102.

10, *Lemosquetella annulata* Mamet & Sebbar, 1998. Pc1494, Carnaweelen Hill, Bricklieve Mts., late Asbian, NW Ireland, x 38.

11, *Luteotubulus* sp., Large crushed specimen below the *Koninckopora* Pc2135, Sierra del Castillo Quarry, late Asbian, SW Spain, x 77.

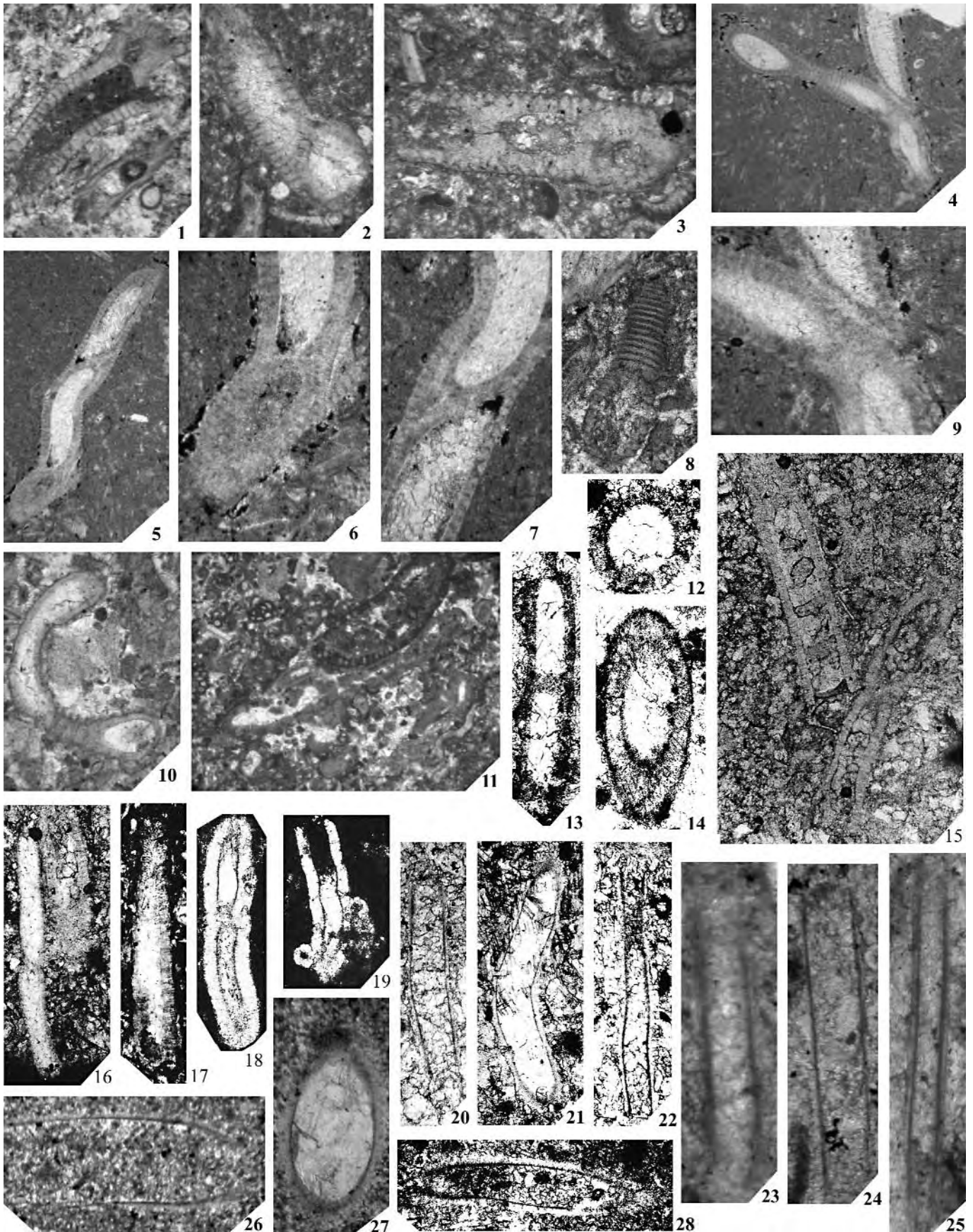
12-14, *Luteotubulus licis* (Malakhova, 1975). Early Viséan. 12. Corphalie K (Belgium). Sample RC 2124. Photo RC14359; x 50. 13. Specimen with very maculate wall and diaphragms, Velbert 4 (Germany), "16, 8 m ht". Sample RC2019. Photo RC 14770; x 33 (see Vachard, 1994b, pl. 1, fig. 8). 14. Corphalie K (Belgium). Sample RC 2124. Photo RC14360; x 50.

15, 16, Rectilinear *Serrisinella serrensis* Vachard, 1988b and articulated *S. melekessensis* (Kulik, 1957). 15. Sample RC 529. Photo RC13879. Rainsart 50; x 50. 16. Sample RC 529. Rainsart. Northern France. Famennian; x 33.

17, *Serrisinella melekessensis* (Kulik, 1957). Sample RC 547. Photo RC13884. Rainsart 49 (northern France), late Famennian, x 50.

18-19, *Tubus ajensis* Chuvashov in Chuvashov et al., 1985. Sample Tailfer 2192. Frasnian of Belgium. 18. Isolated tube. Photo RC14011; x 50. 19. Three connected tubes. Photo RC14010; x 50.

20-28, *Tubus? avesnellensis* sp. nov. 20. Paratype. Longitudinal section with slightly incurved axis. Sample HGT 117 (collection Termier). Strunian. Avesnelles (northern France); x 67. 21. Paratype. Longitudinal section with incurved axis. Collection Conil. Photo RC14975. Strunian. Avesnes 3/106 (northern France); x 50. 22. Paratype. Longitudinal section with slightly undulating axis. Collection Conil. Photo RC14980. Strunian. Avesnes 3/106 (northern France); x 50. 23. Paratype. Longitudinal section with straight axis. Sample DV698X. Photo 14.6.07.78; x 80. 24. Paratype. Longitudinal section with straight axis. Sample DV701A. Photo 14.6.07.80; x 80. 25. Holotype. Typical longitudinal section. Sample DV698. Photo 14.6.07.79; x 80. 26. Paratype. Irregular specimen. Sample DV704A. Photo 14.6.07.82; x 80. 27. Paratype. Oblique section. Sample DV704A. Photo 14.6.07.81; x 80. 28. Paratype. Oblique section with the two-layered wall well visible. Collection Conil. Sample RC6216. Photo RC14082. Strunian. Avesnes 3/106 (northern France); x 50.



Diagnosis.— Small, cylindrical, segmented tests, rarely bifurcated. Wall yellowish perforated.

Composition.— “*Issinella*” *serrensis* Vachard, 1988b; *Issinella antis* Saltovskaya, 1990; *I. cereiformis* Saltovskaya, 1990; *Anthracoporella kasachiensis* Maslov, 1939; *Rhabdoporella melekesensis* Kulik, 1957 (= *I. ? sainsii* Mamet & Roux, 1975a); *Pseudoissinella* sp. (*sensu* Dreesen *et al.*, 1985, pl. 5, fig. 10, pl. 7, fig. 8); *I. moniliformis* Saltovskaya, 1990; and *I. ramulosa* Saltovskaya, 1990.

Remarks.— The wall perforations of *Serrisinella* are more similar to the dasycladale seletonellacean *Rhabdoporella* than those in *Luteotubulus*, due to their relatively wider diameter.

Occurrence.— Famennian-earliest Tournaisian of Tadzhikistan, Russian Platform, Urals (Ivanova & Bogush, 1992, tab. 1, p. 241), northern and southern France, Belgium, Poland, Galice Bank, Donets Basin (Ukraine), Morocco, Afghanistan, Turkey, Urals, Kazakhstan, Siberia, Utah.

Genus *Tubus* Chuvashov in Chuvashov *et al.*, 1985

(Fig. 9.1, 9.12, Pl. 2, Figs 18-19, 20-28)

Type species: *Umbella? vermis* Bogush & Juferev, 1962.

Synonymy.— *Umbella* (*part.*; only *sensu* Bogush & Juferev, 1962).

Diagnosis.— Small, cylindrical, undivided, single tests, perhaps bifurcated. Rare perforations.

Composition.— *Umbella? vermis* Bogush & Juferev, 1962; *Tubus agapovensis* Ivanova, 1988; *T. ajensis* Chuvashov in Chuvashov *et al.*, 1985; and *Tubus avesnellensis* sp. nov.

Remarks.— It differs from *Issinella* (*sensu stricto*) by the bilayered wall and the rare perforations.

The reconstruction of Chuvashov in Chuvashov *et al.* (1985, text-fig. 5, p. 94) is interpreted to be more consistent with our observations upon the issinellids than those of Mamet & Roux (1981, text fig. 1 p. 153) or Roux (1985, text-fig. 14 p. 570), especially for the rarity of the perforations. The specimens with numerous perforations are included in *Issinella* (not articulated) and *Serrisinella* (articulated).

Occurrence.— Late Devonian-Late Viséan Urals. Frasnian-Strunian northern France, Moravia (D.V., unpublished data).

***Tubus avesnellensis* sp. nov.**

(Pl. 2, Figs 20-28)

? 1981a ?*Issinella* types – Zupalova, pl. 56, fig. 4?, 5.

Etymology.— From Avesnelles, a locality in northern France.

Type locality.— Tranchée d’Avesnelles (northern France).

Type level.— Strunian (latest Devonian).

Holotype.— Pl. 2, Fig. 25 (Sample DV698).

Diagnosis.— Rather perforated wall, regular inner surface and irregular external surface, apparently not bifurcated.

Description.— Test free, tubular, composed of straight fragments, rarely incurved or slightly undulating. Lumen of the undivided tube rather large. Inner surface of tube regular, but external one occasionally irregular, maybe slightly annulated. Aperture terminal simple. Wall two-layered, with a very thin inner dark layer and a thicker outer layer intensively perforated, yellow, and granular. Dimensions of elongate tubes: length = (rarely 0.470) 0.600-0.960 mm, outer diameter = (rarely 0.170) 0.200-0.233 mm, inner diameter = (rarely 0.090) 0.120-0.160 mm, wall thickness = 0.010-0.020 mm (inner layer = 0.003-0.005 mm).

Type material.— 12 sections in 8 small thin sections.

Repository of the types.— Collection of Palaeontology of Lille University.

Remarks.— The new species differs from *Issinella* by the type of wall, and from the other *Tubus* by the wall less intensively perforated and the irregular external surface of tube.

Occurrence.— Type level and locality and possibly in the Frasnian/Famennian of Moravia.

Genus *Zidella* Saltovskaya, 1984a

(Pl. 3, Figs 1-6)

Type species: *Zidella maxima* Saltovskaya, 1984a.

Synonymy.—*Einoriella* (sensu Bogush et al., 1990, p. 107); *Issinella* (sensu Mamet; part.).

Diagnosis.—Cylindrical test, with external and internal surface irregularities, and groups of blind, thin laterals linked in irregular rings within the skeleton. No diaphragms were observed (see Vachard, 1991, fig. 2).

Composition.—*Zidella maxima* Saltovskaya, 1984a; *Uraloporella aurivella* Vachard, 1977.

Remarks.—*Zidella* was questionably assigned to Uraloporelleae by Shuysky (1985, p. 94). Herbig & Mamet (1994, text-fig. 4, p. 101) considered “*Luteotubus* (sic), *Zidella*, etc.” as synonyms of *Issinella grandis* Chuvashov, 1965. Those three genera are different (see remarks in Vachard, 1993); in contrast, *Zidella minor* Ivanova, 1988 is considered here as an *Issinella*.

Occurrence.—Late Viséan of Tien-Shan (Saltovskaya, 1984a), central and southern Urals (e.g., Ivanova, 1988; Bogush et al., 1990; Ivanova & Bogush, 1992) and Sumatra (Vachard, 1989a). Latest Asbian (rather common) to latest Brigantian (rare) in the Montagne Noire (Pille, 2008). Ladeninsky (= Mikhailovsky = late Brigantian) of Urals. Asbian of central Morocco (Berkhli, 1999, p. 108; from this data, we suggest that the FAD is probably lower MFZ13 = Cf6 α = Cf4 = V3b α). Late Viséan in Spain and Ireland.

Genus ?*Calcicaulis* Shuysky & Shirshova in Chuvashov et al., 1987

Type species: *Calcicaulis vesiculosum* Shuysky & Shirshova in Chuvashov et al., 1987.

Diagnosis.—Questionable Issinellidae with a central row of cavities in the wall.

Composition.—Monospecific.

Remarks.—The illustrations rather evoke a tabulate auloporein affected by thallophytic perforations.

Occurrence.—Middle Devonian of Urals.

Family ANTHRACOPORELLOPSIDAE Shuysky, 1985, *nomen transl.* Vachard in Vachard et al., 1989 (from tribe Anthracoporellopsiae (sic) = Anthracoporellopsieae orth. mut.), emend. herein

Emended diagnosis.—Tubular tests with irregular development of a strong septation. Initial stage attached, occasionally coiled. Adult stage erect, tubular with rather strong and irregular chambers and septa.

Composition.—*Anthracoporellopsis* Maslov, 1956a; *Crasikamaena* Brenckle, 1985; *Dokutchaevskella* Berchenko, 1981; *Evlania* Bykova, 1952; *Evlaniopsis* Vachard in Vachard & Montenat, 1981; *Pseudonanopora* Mamet & Roux, 1975a (only the holotype); ?*Brazhnikovia* Berchenko, 1981; ?*Catenaella* Shuysky in Chuvashov et al., 1987; ?*Culmiella* Shuysky in Shuysky & Shirshova, 1988; ?*Einorella* Saltovskaya, 1984a; and ?*Groenlandella* Mamet & Stemmerik, 2000.

Remarks.—The limits of the genera are poorly defined, as several “genera” might correspond to different sections of only a single genus.

The apparently primitive character of this family must be secondary, as in all the attached groups. Consequently, the supposed lineage is: Issinellidae-Moravamminidae-Anthracoporellopsidae.

Occurrence.—Late Silurian-Middle Permian. Palaeo-Tethys, Neo-Tethys and Ural Ocean platforms.

Genus *Anthracoporellopsis* Maslov, 1956a

(Fig. 12.8, Pl. 3, Figs 7, 9)

Type species: *Anthracoporellopsis machaevii* Maslov, 1956a.

Diagnosis.—Test cylindrical, erect, bifurcated. Chamber and septa strongly calcified with a central or excentric aperture. Chambers undivided. Septa incomplete and irregularly distributed. Wall yellowish, granular, perforated by aspondyl, acrophore, ramified laterals.

Composition.—*Anthracoporellopsis machaevii* Maslov, 1956a; *Anthracoporella girtyi* Mamet & Roux in Mamet et al., 1987; ?*Anthracoporellopsis ramosus* Ivanova in Bogush et al., 1990; ?*Donezella askynica* Ivanova, 1999.

Remarks.— Despite its name, the genus is totally lacking in similarity with the dasycladale *Anthracoporella*, and any seletonellecean algae in general; this genus is comparable with attached foraminifers, and especially *Coscinophragma cribrosum* (Reuss), as illustrated by Maync (1957, text-fig. 2, p. 184) (Fig. 1.8). Furthermore, it resembles *Evlania* Bykova, 1952, described as a foraminifer; and this genus is probably its ancestor in the Devonian and the Mississippian (see Vachard, 1993). The Viséan-Serpukhovian *Anthracoporellopsis* of Mamet & Roux are generally *Evlania*. A good reconstruction of *Anthracoporellopsis* was published by Skompski (1996, text-fig. 9, p. 226); unfortunately, the cribrate apertures are not observed in the material studied by the authors (although it should be a strong argument for foraminiferal affinities).

The presence of the genus in the Urals remains doubtful [compare Chuvashov (1974, pl. 20, figs 1-2) and Mamet & Villa (2004, p. 161)]. *Donezella askynica* Ivanova, 1999 might be an atypical form of the Urals.

Occurrence.— ?Early Tournaisian of Kuzbass (Russia). ?Viséan-?Serpukhovian of Western Europe. Bashkirian-Sakmarian (acme in Bashkirian-Moscovian), Donets Basin (Ukraine), ?Urals, northern Spain, Lublin Basin (Poland), Canadian Arctic, Tien Shan, Moscow Syncline. Doubtful in the Changhsingian of Hazro (Turkey) (Gaillot, 2006).

Genus *Crassikamaena* Brenckle, 1985

Type species: *Crassikamaena foraminosa* Brenckle, 1985.

Diagnosis.— Test cylindrical, incurved, with rectangular chambers, wide apertures and imperforate septa thicker than the intensely perforated wall. Wall perforations acrophore, single and aspondyl.

Composition.— *Crassikamaena foraminosa* Brenckle, 1985; *C. aculeata* Ivanova in Bogush et al., 1990; *C. inceptoris* Ivanova in Bogush et al., 1990; *C. kurganensis* Ivanova in Bogush et al., 1990.

Remarks.— The North-American type species of *Crassikamaena* is well characterized. Nevertheless, Russian taxa in general, and the material of Mamet (2006), are atypical and they might be assigned to *Evlania* or *Pseudonanopora*. Inversely, according to Brenckle (1985, p. 62), *Evlania?* *camerata* Chuvashov, 1965 can belong to *Crassikamaena*.

This assignment is not admitted here and this latter species is considered as a true *Evlania* (see below).

Occurrence.— Late Middle-Late? Devonian of Iowa and Colorado. Late Famennian-early Tournaisian of Western Siberia [Ivanova & Bogush, 1992; tab. 1, p. 241; the indication of *Crassikamaena kurganensis* in the same table as characteristic of the Serpukhovian is probably a *lapsus calami* because it is indicated as Strunian in age (*Quasiendothyra kobeitusana* Zone) by Ivanova in Bogush et al. (1990)]. Viséan *Crassikamaena* from the Viséan of Alberta (Canada) (Mamet, 2006) belongs questionably to this genus.

Genus *Dokutchaevskella* Berchenko, 1981

Type species: *Dokutchaevskella inaequalis* Berchenko, 1981.

Diagnosis.— Irregular in shape, with a variable septation, wall yellowish, prismatic, with polysynthetic twinning. Initial stage coiled to erect but no attached forms are known.

Composition.— Monospecific.

Remarks.— The genus is similar to *Evlania*, from which it differs by the absence of a initial attached stage. The type species might be a junior synonym of *Evlania prava* Chuvashov, 1965.

Occurrence.— Earliest Mississippian (early Hastarian) of Donbass, Ukraine (C₁^a₂-C₁^b₁).

Genus *Evlania* Bykova, 1952

(Fig. 8.3, 8.8, 8.14; Pl. 3, Figs 8, 10?-11?, 12-15)

Type species: *Evlania transversa* Bykova, 1952.

Diagnosis.— Moravaminida irregular in shape and with an incomplete to complete septation, but never as regular as in the Moravaminidae. Attached initial stage, occasionally coiled, followed by an uncoiled stage, erect or prostrate. Wall yellowish, with visible twins in some cases, with rare perforations.

Composition.— *Evlania transversa* Bykova, 1952; *E.?* *camerata* Chuvashov, 1965; *Evlania devonica* Bykova, 1952; *E.*

hispanica Vachard, 1991; *E. mistiani* Vachard, 1988a; *E. prava* Chuvashov, 1965; *E.? scabrosa* Vachard, 1980; and *E. villedae* Vachard, 1994a (see also Vachard, 1991, p. 276-277; 1994a, p. 58-59).

Remarks.— See Vachard (1980, 1991 and 1994a) for discussions on more questionable taxa, such as: “Eine Foraminifere” (*sensu* Rothpletz, 1913), ?*Pseudonanopora* sp. (*sensu* Mamet & Roux, 1975a), ?*Anthracoporellopsis machaevii* (*sensu* Mamet & Roux, 1975a and *sensu* Mamet & Pinard, 1985), ?*Exvotarissella?* cf. *E.? simplex* (Möller) (*sensu* Mamet, 1976), ?*Anthracoporella girtyi* Mamet, Roux & Nassichuk, 1987, ?*Psammonyx vitreus* Langer, 1969, ?*Anthracoporellopsis?* sp. Mamet, Mortelmans & Roux, 1978, and ?*Anthracoporellopsis* aff. *machaevii* Mamet, Mortelmans & Roux, 1978.

Occurrence.— Devonian-Viséan, ?Moscovian, Palaeo-Tethys. The first occurrence of *Evlania*, even *Moravammina*, in the late Silurian is possible, and three old studies (Rothpletz, 1913; Milon, 1928; and Miller, 1956) recorded specimens rather similar to the moravamminids, although those records could not be contrasted in recent studies. If those records are contrasted, the diversification of the families is clearly during the Devonian, but some of the taxa could arise in earlier times, during the Late Silurian (Vachard, 1991).

Genus *Evlaniopsis* Vachard in Vachard & Montenat, 1981

(Pl. 3, Fig. 16)

Type species: *Evlaniopsis montana* Vachard in Vachard & Montenat, 1981.

Diagnosis.— Test tubular, wavy, irregular, maybe partially attached at the beginning. Chambers ovoid, irregular, pseudo-septa very short. Hyaline wall with numerous, thin, aspondyl canalicules evocating those of *Donezella* or other beresellids.

Composition.— Monospecific.

Remarks.— It differs from *Evlania* by the numerous perforations in the wall organized as those of the *Uraloporella* or primitive *Beresella*.

Occurrence.— Early Permian of central Thailand (Fontaine

et al., 1999). Roadian-Wordian of Afghanistan (Vachard & Montenat, 1981). Midian of Italy (Vachard & Miconnet, 1990). Midian of Thailand (Caridroit *et al.*, 1990; Fontaine *et al.*, 1998). Midian of Oman (Vachard *et al.*, 2001). Middle Permian of Lycian nappes, Turkey (Vachard & Moix, unpublished data). Late Midian and doubtful in the Changhsingian of Hazro, Turkey (Gaillot, 2006).

Genus *Pseudonanopora* Mamet & Roux, 1975c (part.)

(Pl. 3, Fig. 19)

Type species: *Pseudonanopora stockmansii* Mamet & Roux, 1975c.

Diagnosis.— Small, cylindrical, undivided, single tests, perhaps bifurcated. Numerous euspondyl thin wall perforations, no diaphragms but some prominent re-entrants of the wall. Broad apertures. Wall yellowish, hyaline, granular, finely perforated.

Composition.— Monospecific.

Comparison.— It differs from *Evlania* by the absence of attached initial stage and less developed pseudosepta, but the erect parts of both genera may become identical. The type material corresponds probably to four organisms: 1) a part, including the holotype is *Evlania*-like (Mamet & Roux, 1975c, plate II, figs 1-2), 2) a second part resembles *Crassikamaena* (Mamet & Roux, 1975c, plate II, figs 3-4); 3) the third one evocates *Anthracoporellopsis* (Mamet & Roux, 1975c, plate II, figs 5-6); 4) the last part is indeterminate (Mamet & Roux, 1975c, plate II, figs 7-8).

Occurrence.— ?Early Tournaisian of Siberia, Viséan of Belgium, ?Serpukhovian of Morocco and Donbass.

Genus ?*Brazhnikovia* Berchenko, 1981

Type species: *Brazhnikovia undata* Berchenko, 1981.

Diagnosis.— Questionable Anthracoporellopsidae with large apertures, wall thinner than the septa, septa inclined upward, and sutured contact between chambers.

Composition.— Monospecific.

Remarks.— This genus is well defined but it seems to be endemic. Nevertheless, *Kamaena tobolensis* Ivanova in

Bogush *et al.*, 1990, of the *Quasiendothyra kobeitusana* Zone of southern Urals, might be similar. The *Brazhnikovia undata* illustrated by Mamet & Pr eat (2009, pl. 5, fig. 1) seems to be a *Labyrinthoconus*, the internal network of which was destroyed.

Occurrence.– Devonian/Carboniferous boundary of Donbass (Ukraine). ?Middle Devonian of Belgium (Mamet & Pr eat, 2009).

Genus ?*Catenaenella* Shuysky in Chuvashov *et al.*, 1987

Type species: *Catenaenella curvata* Shuysky in Chuvashov *et al.*, 1987.

Diagnosis.– Cylindrical tests, straight or incurved, with semi-ellipsoidal, thin-walled, chambers. Interocular wall curved downward in direction of growth. Rare broad perforations.

Composition.– Monospecific.

Remarks.– The exact microstructure of the wall is poorly known; that explains the question mark. *Catenaenella* might be assigned to the Anthracoporellopsidae if it possesses a hyaline granular wall. If the wall is recrystallized in microsparite, this remains could be also attributed to a microbored gastropod.

Occurrence.– Middle Devonian (Eifelian) of Urals.

Genus ?*Culmiella* Shuysky in Shuysky & Shirshova, 1988

Type species: *Culmiella ovalis* Shuysky in Shuysky & Shirshova, 1988 (*orth. mut.* for *ovale*).

Diagnosis.– Anthracoporellopsidae (?) with moniliform tubes.

Composition.– *Culmiella ovalis* Shuysky in Shuysky & Shirshova, 1988; *C. silicula* Shuysky in Shuysky & Shirshova, 1988; and *C. sphaerica* Shuysky in Shuysky & Shirshova, 1988.

Remarks.– The genus was initially assigned to the Beresellidae. Morphologically, the fragments resemble some dasycladales Epimastoporaceae. Consequently, due to a bereselloid wall and moniliform chambers, an affinity

with the wall of *Evlania-Evlianopsis* is suggested and a hypothetical emplacement in the Anthracoporellopsidae.

Occurrence.– Endemic to the Pragian-Eifelian in the Urals.

Genus ?*Einorella* Saltovskaya, 1984a

(Pl. 3, Figs. 17-18)

Type species: *Einorella globosa* Saltovskaya, 1984a.

Diagnosis.– Similar to *Evlaniopsis* but longer, more compressed and with more elongate chambers.

Plate 3

1-3, *Zidella maxima* Saltovskaya, 1984a. 1. Longitudinal section. Pc1698, Tankardstown Borehole, early Asbian, SE Ireland, x 40. 2. Tangential section. Pc2133, Sierra del Castillo Quarry, late Asbian, SW Spain, x 125. 3. Detail of Fig. 1 showing the wall. Pc1698, Tankardstown Borehole, early Asbian, SE Ireland, x 320.

4-6, *Zidella aurivella* Vachard, 1977. Late Asbian (late Vis ean). Lentilles de la route (Montagne Noire, southern France). 4. Longitudinal section showing the external ornamentation and the numerous wall perforations. Sample DV293E, x 27. 5. Transverse section showing the external ornamentation and the numerous wall perforations. Sample DV600B; x 67. 6, *Zidella aurivella* Vachard, 1977. Transverse section showing the external ornamentation and the numerous wall perforations. Sample DV332D. Late Asbian (late Vis ean). Lentilles de la route (Montagne Noire, southern France), x 67.

7, *Anthracoporellopsis machaevii* Maslov, 1956a. Encrusting test with few developed pseudo-septa; Northern Spain. Sample E1213; x 27.

8, 13-15, *Evlania hispanica* Vachard, 1991. Three longitudinal sections. Moniellos Formation (northern Spain). Early Devonian. 8. Longitudinal section with *Praecorninella hieroglyphica* Vachard, 1991 (top left and right). Sample M342-10(bis); x 47. 13. Longitudinal section with pseudosepta and diaphragm. Sample M370-6; x 47. 14. Longitudinal section with rare pseudosepta and two diaphragms. Sample M370-5; x 29. 15. Transverse section to compare with Pl. 7, fig. 2. Moniellos Formation (northern Spain). Early Devonian. Sample M370-4; x 47.

9, *Anthracoporellopsis* sp., Pc714, El Collado section, early Brigantian, SW Spain, x 59.

10-11, *Evlania?* sp., 10. Pc1738, Tankardstown Borehole, early Asbian, SE Ireland, x 125. 11. Pc1738, Tankardstown Borehole, early Asbian, SE Ireland, x 125.

12, *Evlania* sp., Pc720, El Collado section, early Brigantian, SW Spain, x 35.

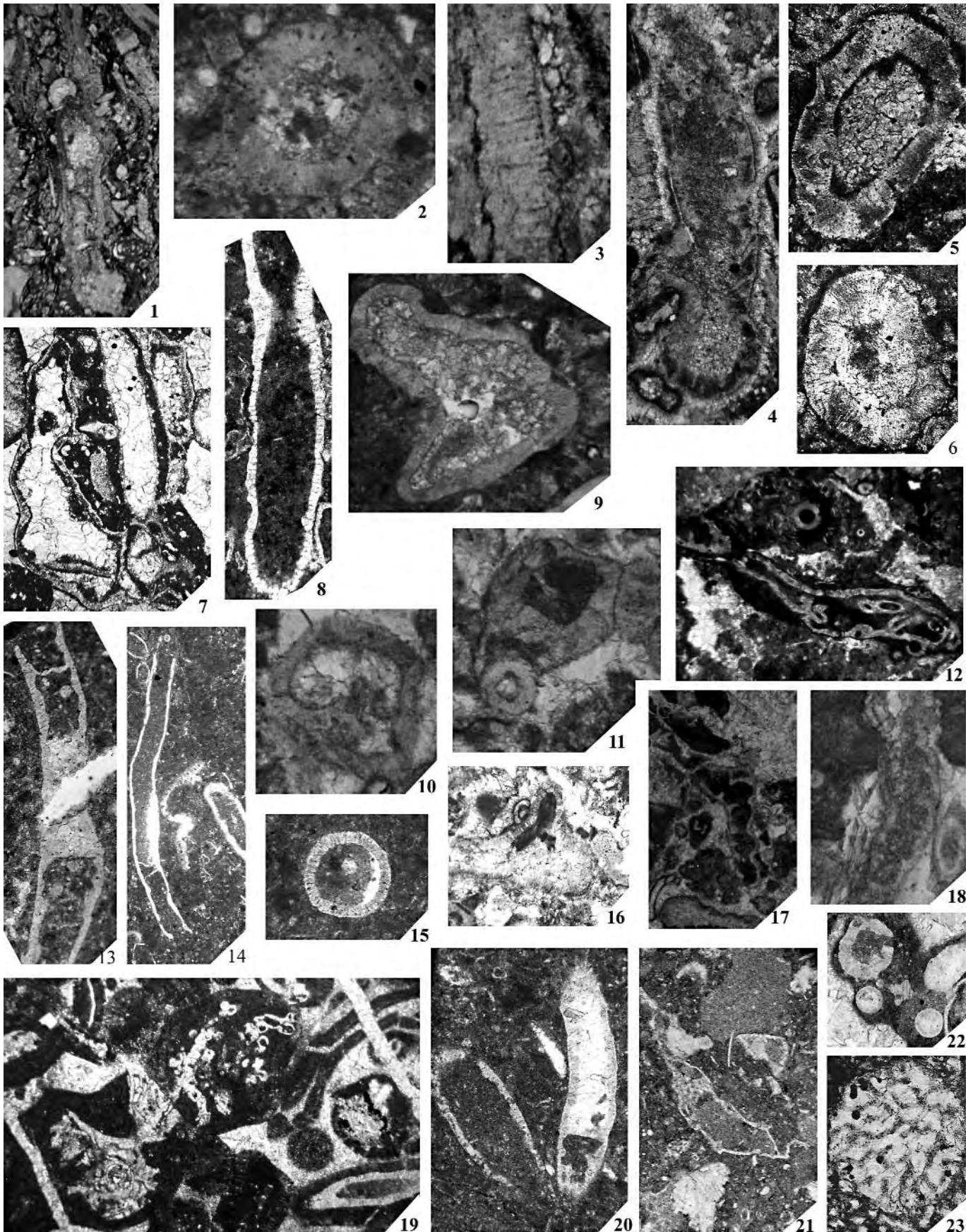
16, *Evlaniopsis montana* Vachard, 1980. 16. Bifurcated test. Sample DV464, Tezak (central Mountains of Afghanistan). Middle Permian (Early Murgabian) (see Vachard & Montenat, 1981, pl. 15, fig. 5), x 40.

17-18, *Einorella?* sp. 17. Pc-LL9034, Las Llaceras section, Kasimovian, NW Spain, x 125. 18. Pc1738, Tankardstown Borehole, early Asbian, SE Ireland, x 125.

19, Oolitic grainstone microfacies with *Kamaenella* sp. (top, centre), *Fasciella kizilia* (bottom left) and *Pseudonanopora* (bottom right). Central Morocco, late Vis ean, Sample HGT.M.3.17; x 27.

20-22, *Uralites?* sp. Three specimens. Moniellos Formation (northern Spain). Early Devonian. 20. Longitudinal section (right) with *Evlania hispanica* Vachard, 1991 (left). Sample M370-7; x 47. 21. Oblique to tangential section. Sample M150-9(bis); x 47. 22. Transverse section. Sample M150-16; x 47.

23, *Labyrinthoconus clausmuelleri* Langer, 1979. Transverse section. Blacourt Formation. Griset Member. Givetian of Boulonnais (northern France). Sample B.Gr.54, x 66.



Composition.— *Einorella globosa* Saltovskaya, 1984a; *E. elongata* Saltovskaya, 1984a; ?*Donezella callosa* Ivanova, 1999.

Remarks.— The differences with *Groenlandella*, *Evlaniopsis*, *Zidella* and *Anthracoporellopsis* are not clear.

Occurrence.— ?Late Viséan of Urals (more probably *Zidella*), and ?Ireland (Pl. 3, fig. 18). Early or Middle Pennsylvanian of Tadzhikistan. ?Late Bashkirian of Urals. ?Early Moscovian of Libya (see Massa & Vachard, 1979, pl. 5, fig. 7), Kasimovian of NW Spain (Pl. 3, fig. 17).

Genus ?*Groenlandella* Mamet & Stemmerik, 2000

Type species: *Groenlandella enigmatica* Mamet & Stemmerik, 2000.

Diagnosis.— Similar to *Einorella* but with a bifurcated test, with barrel-shaped cells.

Composition.— Monospecific.

Remarks.— The differences with *Einorella* might be only specific.

Occurrence.— Early Moscovian of Greenland.

Family URALITIDAE Vachard, 1991, *nomen transl.*
herein from subfamily

Diagnosis.— Small to large cylindrical, single tests, bifurcated, composed of two concentric tubes linked by radial septa, and also subdivided by transverse partitions. Wall of partitions are cribrate. Outer wall yellowish, granular, finely perforated.

Composition.— *Uralites* Chuvashov, 1973; *Cribrókamaena* Brenckle, 1985.

Remarks.— This family described originally as a subfamily of Issinellidae is considered here as a family of Moravamminina because of its complete septation.

Occurrence.— ?Early Devonian of Spain; ?Middle Devonian of Belgium; Late Devonian-Viséan, Urals, U.S.A., South China (unpublished data, Hance *et al.*).

Genus *Uralites* Chuvashov, 1973

(Fig. 4.1-4.4; Pl. 3, Figs 20-22)

Type species: *Uralites regularis* Chuvashov, 1973.

Diagnosis.— Small, cylindrical, single tests composed of two concentric tubes linked by radial septa, and also subdivided by transverse septula.

Composition.— Monospecific. However, *Cribrókamaena? vesiculifera* Vachard, 1991, *Nanopora fragilissima* (*sensu* Berchenko, 1981, pl. 5, figs 8-12), and perhaps *Issinella devonica* (*sensu* Mamet & Prétat, 1992, pl. 1, fig. 17 only, *non* figs 10, 12 = *Issinella* or *Kamaena*) might be included in *Uralites* [another partial synonymy was originally indicated by Brenckle, 1985, between *Cribrókamaena* and another material of Mamet & Roux (1978b, pl. 1, fig. 16 and 1981, pl. 1, figs 9-15)].

Occurrence.— Famennian of Urals. ?Emsian of Spain, ?earliest Givetian of Belgium.

Genus *Cribrókamaena* Brenckle, 1985

(Figs 4.5-4.11)

Type species: *Cribrókamaena citrosa* Brenckle, 1985.

Diagnosis.— Small, cylindrical, single tests, bifurcated, composed of a columella and a concentric tube, linked by radial longitudinal septa, and divided by cribrate transverse septula.

Composition.— *Cribrókamaena citrosa* Brenckle, 1985; *C. furcillata* Brenckle, 1985; and *C. ferniensis* Mamet, 2006.

Occurrence.— Viséan of the U.S.A. and Canada.

Family LABYRINTHOCONIDAE Langer, 1979

Diagnosis.— Tubular, tapering, mass-shaped, fan-shaped or irregular tests with erratic, meandriform (or labyrinthic or sarmentoid) endoskeleton and enveloping wall. Wall calcareous, hyaline, yellowish and granular.

Composition.— *Labyrinthoconus* Langer, 1979; and *Proninella* Reitlinger in Menner & Reitlinger, 1971 (*non auct.*) (= ?*Eifeliflabellum* Langer, 1979).

Remarks.– The interpretation of *Proninella* Reitlinger in Menner & Reitlinger, 1971 by Mamet & Roux (1978b), Roux (1985), or Mamet (1991) does not seem to correspond to the original diagnosis by Reitlinger. On the other hand, the definition of “*Proninella*” (*sensu* Mamet & Roux, 1978b) is considered to be included in the family Claracrustidae.

Actually, this group is poorly studied (Langer, 1979; Mamet *et al.*, 1982; Vachard, 1994) although relatively characteristic of the Givetian and Frasnian, and probably very important for the knowledge of the convergences between Moravamminida and Aoujgaliida.

Occurrence.– Uppermost Early-lowermost Late Devonian, probably cosmopolitan but poorly known.

Genus *Labyrinthoconus* Langer, 1979

(Pl. 3, Fig 23; Pl. 4, Figs 1-3)

Type species: *Labyrinthoconus clausmuelleri* Langer, 1979.

Synonymy.– ?*Brazhnikovia* (*sensu* Mamet & Pr at, 2009; see above).

Diagnosis.– Tapering to club-shaped, irregular test, with a meandriform inner skeleton with a continuous outer wall.

Composition.– Monospecific, although subdivided into two subspecies: the eponym one, and *L. c. hyperconicus* Langer, 1979. *Proninella* sp. (*sensu* Zupalova, 1981b, pl. 11, figs 1-2) might be another species of the genus.

Occurrence.– Givetian, geographical distribution poorly known: Belgium, northern, northeastern and western France, Germany, Moravia, Poland, ?Morocco, ?Alberta. Questionable in Eifelian, Frasnian and Famennian and earliest Tournaisian (Vachard, 1988b).

Genus *Proninella* Reitlinger in Menner & Reitlinger, 1971

(Figs 4.14-4.19; Pl. 4, Figs 4-7)

Type species: *Proninella tamarae* Reitlinger in Menner & Reitlinger, 1971.

Synonymy.– *Eifeliflabellum* Langer, 1979 (type species: *Eifeliflabellum opuntia* Langer, 1979).

Diagnosis.– Test flabelliform or tapering with sarmentoid inner endoskeleton and outer continuous wall.

Composition.– *Proninella tamarae* Reitlinger in Menner & Reitlinger, 1971; *Proninella* (?) *labyrinthica* Reitlinger in Menner & Reitlinger, 1971; *Kamaena* sp. (*sensu* Brunner, 1975); *Eifeliflabellum opuntia* Langer, 1979; and ?*Semitextularia* cf. *thomasi* (*sensu* Kettenbrink & Toomey, 1975, pl. 2, fig. 1).

Excluded species.– *Proninella enigmatica* Mamet & Roux, 1978a (= *Pokorninella*); *Proninella* sp. [*sensu* Zupalova, 1981b pl. 11, figs 1-2 (= *Labyrinthoconus*)]; and *P.* sp. [*sensu* May, 1994, pl. 39, fig. 1 (= *Caligella*)].

Remarks.– There are two distinct concepts for the genus *Proninella*, (a) the strict sense by Reitlinger in Menner & Reitlinger (1971) and (b) the interpretation of this taxon since early studies by Mamet & Roux (1978b) and subsequent publications (e.g., Mamet, 1991; 2006). For this paper, a sarmentoid shape of the internal structures in the specimens have been considered valid, and for us, closer to the original diagnosis and illustrations of the Siberian types than to the subsequent re-interpretations by other authors. *Eifeliflabellum* is only more flabelliform than *Proninella*. These taxa are considered as congeneric. *Proninella* can also represent a high transverse section or a frontal axial section in the adult stage, or a subtransverse section in a juvenile stage of “*Eifeliflabellum*”.

Occurrence.– Givetian-Strunian of Siberia, northern France, Belgium, Poland, Mexico, Alberta. Givetian of Germany. Givetian-Frasnian of Poland (Racki & Sob n-Podg rska, 1992). ?Frasnian of Iowa.

Family MORAVAMMINIDAE Pokorny, 1951, *nomen transl.* Loeblich & Tappan, 1961 (from subfamily), *emend.* G. Termier *et al.*, 1975

Synonymy.– Kettneramminidae G. Termier *et al.*, 1975.

Diagnosis.– Test tubular, pseudo-septate to regularly septate, bifurcated, isolated tubes, occasionally coiled in the initial stage. Wall hyaline, yellowish, granular, with perforations not numerous.

Composition.– Five genera: *Moravamina* Pokorny, 1951, *emend.* Vachard, 1991 (= *Litya* Bykova in Bykova & Polen-

ova, 1955); *Kettnerammina* Pokorny, 1951 (= ?*Saccorhina* Bykova in Bykova & Polenova, 1955 = ?*Pseudoissinella* Mamet & Rudloff, 1972); *Palaschemonella* Beckmann, 1953; *Triangulinella* Mamet & Prétat, 1985; and *Vasiceckia* Pokorny, 1951 (= *Parmacaulis* Shuysky & Shirshova in Chuvashov *et al.*, 1987).

Remarks.—The coiling of the initial part and progressively developed septa are the common characters of the Moravamminidae.

Occurrence.—Devonian-Mississippian.

**Genus *Moravammina* Pokorny, 1951, emend.
Vachard, 1991**

(Figs 8.10, 8.13; Pl. 4, Figs 13-17, ?18-21)

Type species: *Moravammina segmentata* Pokorny, 1951.

Synonymy.—? *Triangulinella* Mamet & Prétat, 1985 (*part.*); ? *Kamaena* Antropov, 1967 (*part.*); ? “*Kamaena-Palaeoberesella*” (*sensu* Prétat & Mamet, 1989, pl. 7, fig. 1); ? *Nodosinella* (*sensu* Malakhova, 1975; *part.*); ? *Halysis* Høeg, 1932 (*sensu* Mamet *et al.*, 1992; *part.*) (see also Vachard, 1991); ? *Nodosinella* (*sensu* Edgell, 2004).

Diagnosis.—Test tubular, septate, bifurcated, firstly coiled later erect. Tube rounded to triangular in cross-section. Chambers regular, quadrate. Septa perpendicular to the wall, of the same thickness, pierced in its centre by a round terminal aperture. Wall hyaline, yellowish, granular, with sporadic perforations.

Composition.—*Moravammina segmentata* Pokorny, 1951; *M. carbonica* Fomina, 1960; *M.(?) constricta* Eichkoff, 1970; *Kamaena delicata* Antropov, 1967 (*sensu* Mamet & Prétat, 1992, pl. 1, fig. 16); *Moravammina fragilis* Bykova in Bykova & Polenova, 1955; *M. koktjubensis* Vdovenko, 1962; *Litya(?) novonikolaevensis* Vdovenko in Brazhnikova & Vdovenko, 1973; *Moravammina recta* Eickhoff, 1973; *Moravammina* sp. (*sensu* Bless *et al.*, 1976); *Moravammina?* sp. (*sensu* Zupalova, 1981a, pl. 29, fig. 2, pl. 30, fig. 1; 1981b, pl. 12, figs 1-3); *Litya syzranensis* Bykova in Bykova & Polenova, 1955; ? *Nodosinella crassithea* Malakhova, 1975; ? *Nodosinella canningensis* Edgell, 2004; ? “*Nodosinella*” Brazhnikova & Rostovceva, 1966 (or other moravamminids); ? *Palaeoberesella burlensis* Ivanova, 1988; ? *P. aff. lahuseni* (*sensu* Mamet *et al.*, 1999);

? *Triangulinella tricarinata* Mamet & Prétat, 1985; ? Foraminifer sp. A Ebner, 1973; and ? *Lituotuba dubia* Miller & Carmer, 1933 (see Poyarkov, 1979).

Excluded species.—*Moravammina simplex* Eickhoff, 1968; *M.(?) plena* Reitlinger in Menner & Reitlinger, 1971; *M.* sp. (*sensu* Conil *et al.*, 1980; see Vachard, 1991); and *M.* sp. (*sensu* May, 1994, pl. 38, figs 3-4 = *Caligella*).

Remarks.—The best section of a Visean *Moravammina* was published by Bless *et al.* (1976) (see herein Pl. 4, Fig. 14). In several cases, the differences in the identifications can be only semantic. Indeed *Moravammina* was abundantly cited up to the 1970s (e.g., Güvenç, 1966a, p. 158; Mouravieff & Bultynck, 1967, p. 154-155; Menner & Reitlinger, 1971; Pel, 1975, pl. 1, fig. 5, pl. 2, figs 5-6; Mamet & Roux, 1974, pl. 7, fig. 19; Bless *et al.*, 1976); then, *Moravammina* disappeared almost completely from the literature and was replaced by *Kamaena*. Similarly, *Kettnerammina* disappeared on behalf of *Issinella*.

Occurrence.—Early Devonian-Serpukhovian, Palaeo-Tethyan (including Thailand in this epoch) and Ural Ocean platforms.

Genus *Kettnerammina* Pokorny, 1951

(Figs 8.1, 10.26; Pl. 4, Figs 22-28, 34-35, Pl. 5, Fig. 1)

Type species: *Kettnerammina givetiana* Pokorny, 1951.

Synonymy.—*Saccorhina* Bykova in Bykova & Polenova, 1955; *Kamaena* (*part.*) (e.g., Petryk & Mamet, 1972, pl. 3, fig. 10 only; the polysynthetic twinning are visible and distinguish this form from *Issinella*, *Luteotobulus* or *Jansaella*); ? *Pseudoissinella* Mamet & Rudloff, 1972; *Serrissinella* (*sensu* Mamet & Pohler, 2002); ? *Parakamaena* (*sensu* Mamet & Prétat, 2009, pl. 4, fig. 16).

Diagnosis.—Test tubular, undivided, bifurcated. Wall hyaline, yellowish, granular to monocrystalline, poorly perforated, with well visible polysynthetic twins.

Composition.—*Kettnerammina givetiana* Pokorny, 1951; *K.(?) mesodevonica* Pokorny, 1951; *K.(?) pauciseptata* Vachard, 1991; *Issinella devonica* (*sensu* Chuvashov, 1965, pl. 20, figs 4-5); *I.* sp. (*sensu* Zupalova, 1981b, pl. 11, fig. 3); *Saccorhina trivirgulina* Bykova, 1952; “?svetlaya trubchataya” (clear tube; *sensu* Ivanova, 1973, pl. 10,

fig. 1); ?*Pseudoissinella alaskaensis* Mamet & Rudloff, 1972; ?*Parakamaena exilis* (sensu Mamet & Prétat, 2009, pl. 4, fig. 16).

Remarks.— Because of its polysynthetic twinning and absence of septa, *Pseudoissinella* might be a synonym of *Ketneramma*, but the initial part and age are different.

Occurrence.— Late Emsian of northern Spain. Eifelian of New South Wales (Australia). Givetian-Frasnian of Belgium, northern and western France, Morocco, Germany, ?Poland, Moravia, Donbass, northern Turkey, Russian Platform, Urals. ?Viséan of Alaska, Alberta and British Columbia (as *Pseudoissinella*).

Genus *Palaschemonella* Beckmann, 1953

Type species: *Palaschemonella torleyi* Beckmann, 1953.

Diagnosis.— Test tubular, undivided, with a large polygonal chamber and several apertures at the ends of long necks. Wall hyaline, yellowish, prismatic, rarely maculate.

Composition.— *Palaschemonella torleyi* Beckmann, 1953; *P. maroccana* Vachard, 1994a; and *P. beckmanni* Flügel & Hötzl, 1971.

Remarks.— *Palaschemonella* can also be interpreted as a *Vasicekia* with a large bulbous part, and short tubular part.

Occurrence.— Givetian of Morocco and Germany.

Genus *Triangulinella* Mamet & Prétat, 1985

Type species: *Triangulinella tricarinata* Mamet & Prétat, 1985.

Diagnosis.— Moravamminidae with large apertures, wall thinner than the septa, septa inclined upward, and no sutured contact between chambers. Triangular cross-section, and curved surface of attachment.

Composition.— Monospecific.

Remarks.— Vachard (1991, 1994a) regarded this genus as a synonym of *Moravammina*. However, Mamet (2006, p. 346) justified both genera as independent.

Occurrence.— Givetian of Belgium.

Genus *Vasicekia* Pokorny, 1951

(Fig. ?10.27)

Type species: *Vasicekia moravica* Pokorny, 1951.

Synonymy.— *Parmacaulis* Shuysky & Shirshova in Chuvashov *et al.*, 1987 (type species: *Parmacaulis hulgensis* Shuysky & Shirshova in Chuvashov *et al.*, 1987).

Diagnosis.— Test consisting in elongate segments, tubular, with a bulbous part near one of the extreme and the aperture in the other extreme.

Composition.— *Vasicekia moravica* Pokorny, 1951; *Vasicekia?* sp. of Mamet *et al.* (1999, pl. 4, figs 1-2); and *Parmacaulis hulgensis* Shuysky & Shirshova in Chuvashov *et al.*, 1987.

Excluded species.— *Vasicekia obscura* K. Miklukho-Maklay, from the Middle Permian of Russia that belongs more probably to *Syzrania* or *Earlandia*.

Occurrence.— Eifelian of Morocco. Givetian of Moravia. Early-early Middle Devonian of Northern and Prepolur Urals.

Family PALAEOBERESELLIDAE Mamet & Roux, 1974,
nomen transl. herein

Diagnosis.— Test tubular, strongly septate, bifurcated. Attached by bracelets, or directly implanted in muddy substrate. Wall hyaline, yellowish, with up to three orders of ramifications in the perforations.

Composition.— Nine genera: *Palaeoberesella* Mamet & Roux, 1974 (= ?*Septamina* Meunier, 1888); *Devonoscala* Langer, 1979 (= *Stylaella* Berchenko, 1981); *Exvotarisella* Elliott, 1970; *Kamaena* Antropov, 1967 (= *Subkamaena* Berchenko, 1981); *Kulikaella* Berchenko, 1981; *Parakamaena* Mamet & Roux, 1974; *Pseudokamaena* Mamet in Petryk & Mamet, 1972; *Turgajella* Ivanova in Bogush *et al.*, 1990; ?*Metakamaena* Endo, 1969.

Remarks.— Mamet & Roux (1978a) considered that the “paleoberesellaceans” have nothing in common with *Moravammina* although *Kamaena index* Antropov, 1967 was synonymized with *Moravammina simplex* Eickhoff,

1968 by Mamet & Roux (1974, p. 138) and Mamet (1991, p. 407). In fact, we interpret the Palaeoberesellidae as being derived from Moravamminidae by the loss of the coiled initial stage.

The Moravamminina are frequent in disphotic (Waulsortian reefs) and even aphotic zone. After a correct interpretation of the accumulations of moravamminins (Lees *et al.*, 1985; Lees & Miller, 1985), Lees modified his interpretation and considered the moravamminins as photic algae, at least in the majority (due to the misinterpretations of Mamet & Roux, 1974, and especially Skompski, 1987, with his dasycladale). Consequently, the subsequent interpretations of Lees were less precise (Lees & Miller, 1995; Lees, 1997). The initial location of the bioaccumulations of kamaenids between 250 and 300 m in the deepest Waulsortian reefs (Lees *et al.*, 1985) was probably the more accurate data. Furthermore, Devuyt & Lees (2001, p. 1145, text-fig. 16 p. 1146) more or less confirmed, for the “plurilocular foraminifera and moravamminids”, a maximum depth “of the order of 200 m”. Nevertheless, it is clear that *Exvotarissella* and the “palaeoberesellids” of the authors (see Gallagher, 1998, p. 197) dominate in the photic zone. Similarly, in some groups of foraminifers the bathymetry can be very different from a genus to each other. The phenomenon is also known in the same genus of foraminifer, for example *Amphistegina* or *Operculina*, with eventual correlative variation of the test shape.

Occurrence.— Middle Devonian-Middle Pennsylvanian.

Genus *Palaeoberesella* Mamet & Roux, 1974

(Figs 8.6, 9.2-9.4, 9.6, 10.11-10.13, ?10.19, 10.20-10.24; Pl. 4, Figs 29-33)

Type species: *Nodosinella lahuseni* Möller, 1879.

Synonymy.— ?*Septammina* Meunier, 1888 *non auct.* (see literature in Mamet, 1967); *Kamaena* (*part.*) (e.g., Petryk & Mamet, 1972, pl. 3, fig. 14).

Diagnosis.— Similar to *Kamaena* but larger, more undulating, more rarely bifurcated, with less regular chambers, more incomplete septa, wider aperture and more numerous simple laterals in the wall. Presence of bracelets.

Composition.— *Nodosinella lahuseni* Möller, 1879; *Nodosinella? scalaris* Malakhova, 1975; *Palaeoberesella*

scalaris Ivanova, 1988; ?*Septammina renaulti* Meunier, 1888; ?*S. dichotoma* Meunier, 1888; and *Palaeoberesella* sp. nov. (Pl. 4, Figs 32-33).

Plate 4

- 1-3**, *Labyrinthococcus clausmuelleri* Langer, 1979. 1. Longitudinal section. Early Givetian. Belgium. Collection Pel. Sample GV59. Photo RC15009; x 50. 2. Longitudinal section. Early Givetian. Belgium. Collection Pel. Sample GV60. Photo RC15025; x 50. 3. Longitudinal section. Blacourt Formation. Griset Member. Givetian of Boulonnais (northern France). Sample B.Gr.55, x 66.
- 4-7**, *Proninella tamarae* Reitlinger in Menner & Reitlinger, 1971. 4. Regular test. Sample Tailfer 2215 (VW109), Frasnian of Belgium. Photo 13958; x 50. 5. Typical specimen. Sample Tailfer 2513 (VW122 bis A2), Frasnian of Belgium. Photo 13942; x 50. 6. Longitudinal section. Frasnian of Boulonnais (northern France). Sample 50e; x 47. 7. Longitudinal section. Frasnian of Boulonnais (northern France). Sample 507.34. 1; x 66.
- 8-12**, *Devonoscala tatarstanica* (Antropov, 1959). 8. Large specimen, Lublin (Poland), Frasnian; x 53. 9. Sample Tailfer 2534 (VW147). Photo 13948; x 50. 10. Sample Tailfer 2513 (VW122bisA2). Photo 13939; x 50. 11. Sample Tailfer 2217 (VW83.IX). Photo 13896; x 50. 12. Sample Tailfer 2513 (VW122bisA2). Photo 13931; x 50.
- 13**, *Moravammina* cf. *fragilis* Bykova in Bykova & Polenova, 1955, according to Zukalova, 1981b, pl. 12, fig. 3. Moravia, Nemcicky 2-Borehole, Frasnian; x 53.
- 14-15**, *Moravammina carbonica* Fomina, 1960. 14. Complete specimen. Houthem (the Netherlands) borehole, 284a-285.38. Photo RC 12879; x 50. 15. Longitudinal erect section similar to *Kamaena* except for the curved initial part and the absence of bifurcation. Sample DV123C-18, Cabrières, Saint-Rome, (southern France), late Brigantian; x 33
- 16**, *Moravammina segmentata* Pokorný, 1951. Frasnian. Tizra Formation (pebble in the Viséan conglomerates). Sample TZ180. Late Asbian. Central Morocco; x 33.
- 17**, *Moravammina* sp. 3. Moniellos Formation (northern Spain). Early Devonian. Sample M342-6; x 47.
- 18-21**, Transition between *Kettnerammina* and *Moravammina*. Blacourt Formation. Griset Member. Givetian. Boulonnais (northern France). 18. Sample B.GR103; x 29. 19. Sample B.GR131.2; x 29. 20. Sample B.GR103; x 43. 21. Sample B.GR131-2; x 43.
- 22**, *Kettnerammina* sp. 1. Sample DV237B. Pridolí. Falgairas (Montagne Noire, southern France), coeval with *Asphaltinooides falgairasensis* sp. nov. x 29.
- 23-25**, *Kettnerammina* sp. 2 (cf. *K. mesodevonica* Pokorný, 1951). Moniellos Formation (northern Spain). Early Devonian. 23. Sample M150-12; x 47. 24. Sample M1000-1; x 47. 25. Sample M150-3; x 47.
- 26-27**, *Kettnerammina* sp. 3. Transition to *Issinella devonica* (see Pl. 3, figs 3-5). Moniellos Formation (northern Spain). Early Devonian. 26. Sample M249-3(bis); x 47. 27. Sample M103-2; x 47.
- 28**, *Kettnerammina* sp. 4. Long, slender and incurved. Moniellos Formation (northern Spain). Early Devonian. Sample M1000-9; x 47.
- 29-31**, *Palaeoberesella lahuseni* (von Möller, 1879) Mamet and Roux, 1974. 29. Belgium, Tramaka, late Viséan, sample DV 634; x 50. 12. South China. Sample DV3971. Photo 3.11; x 47. 30. Pc962, Bannagogle Quarry, early Brigantian, SE Ireland, x 29. 31. Moniellos Formation (northern Spain). Early Devonian. Sample M1018-2; x 47.
- 32-33**, *Palaeoberesella* sp. nov., 32. Pc4058, Souk el Had, Central Morocco, Brigantian, x 38. 33. Pc4058 Souk el Had, Central Morocco, Brigantian, x 50.
- 34**, *Kettnerammina givetiana* Pokorný, 1951. Longitudinal section. Blacourt Formation. Griset Member. Boulonnais (northern France). Sample B.GR100; x 29.
- 35**, *Kettnerammina* sp. 2 (cf. *K. mesodevonica* Pokorný, 1951). Blacourt Formation. Griset Member. Givetian of Boulonnais (northern France). Sample B.GR131.2; x 47.



Excluded species.— *Palaeoberesella burlensis* Ivanova, 1988 (probably a *Moravammina*).

Remarks.— This genus is transitional between *Kamaena* and *Exvotarisella*. It has no morphological or phylogenetical relation with the Beresellina, and thus, its name is inappropriate. Moreover, it probably corresponds to *Septamina* Meunier, 1888 *non* Mamet, 1967 (and compiled literature in this publication). The type material of *Septamina* (examined by D.V. in 1975 in Muséum d'Aulun collection) is clearly an aggregate with an endothyroid foraminifer, indeterminate grains, and a relatively well preserved tube, identical to a *Palaeoberesella* (Fig. 10.19). Nevertheless, this genus was frequently misinterpreted and *Palaeoberesella* can be preserved to designate the taxon. Furthermore, it seems to be monospecific because the differences between *P. lahuseni* and *N? scalaris* are scarce. The bracelets of this genus were rarely illustrated (see Mamet & Roux, 1974, pl. 2, fig. 19, pl. 3, fig. 10, pl. 4, figs 10?, 14; re-illustrated here Figs 10.11-10.13).

Occurrence.— Emsian of New South Wales (Mamet & Pohler, 2002). Middle Devonian-late Moscovian (Mamet & Villa, 2004); cosmopolitan (except Japan) (Mamet, 1991). Acme in the Middle Viséan; for example in Urals (Ivanova & Bogush, 1992, tab. 1, p. 241).

Genus *Devonoscala* Langer, 1979

(Figs 8.2, 8.11; Pl. 4, Figs 8-12)

Type species: *Nodosinella tatarstanica* Antropov, 1959.

Synonymy.— *Kamaena* (*part.*) (e.g., Petryk & Mamet, 1972, pl. 3, fig. 9 only; Mamet & Préat, 2009, pl. 4, figs 11-13, 14-15, respectively as *K. tatarstanica* and *K. delicata*); and *Stylaella* Berchenko, 1981.

Diagnosis.— Test small, short, tapering, with only one row of quadratic chambers. Chambers rectangular. Aperture, terminal, proportionally broad, simple, central. Wall yellowish, finely prismatic, imperforate, often with a monocrystalline extinction.

Composition.— *Nodosinella tatarstanica* Antropov, 1959; *Multiseptida akkusica* Bogush & Juferev, 1962; *Moravammina tatarstanica* forma *magna* Menner & Reitlinger, 1971; *Moravammina tatarstanica* forma *parva* Menner & Reitlinger, 1971; and *Stylaella rhomboidea* Berchenko, 1981.

Remarks.— The similarities with *Kamaena* led Mamet and Préat (2009) to consider both genera as synonyms; the tapering, finely externally costulated and not ramified tubular chamber in *Devonoscala* justify the existence of both genera.

Occurrence.— Late Emsian of Spain; late Eifelian-early Tournaisian, probably cosmopolitan; ?late Tournaisian (Kosvinsky) of southern Urals.

Genus *Exvotarisella* Elliott, 1970

(Figs 1.10, 2.1, 2.4, 2.5, 8.7, 8.12, ?10.10, 10.14, 12.7, 13.4; Pl. 5, Figs 2-12)

Type species: *Nodosinella index* (Ehrenberg, 1854 *sensu* Möller, 1879) (= *Exvotarisella maponi* Elliott, 1970 *fide* Mamet & Roux, 1974).

Diagnosis.— Large and cylindrical *Palaeoberesellidae*. Curved septa, thick, perpendicular to truncated ellipsoidal chambers. Laterals aspondyl, numerous, with three or rarely four orders of ramification. The bracelets are rarely preserved.

Composition.— *Nodosinella index* (Ehrenberg, 1854 *sensu* Möller, 1879) (= *Exvotarisella maponi* Elliott, 1970 *sensu* Mamet & Roux, 1974); *Exvotarisella dili* Vachard *in* Dil *et al.*, 1977; ?*E.?* sp. (*sensu* Mamet, 2006, pl. 4, fig. 10); and *Exvotarisella* sp. nov. (Pl. 5, Fig. 12).

Remarks.— Owing to its ramified perforations, this genus might be attributed to the dasycladales. However, two arguments allow to rule out this assignments: 1) although arranged in tufts, the wall perforations of *Exvotarisella* are aspondyl, and their base is not euspondyl nor metaspondyl; 2) similar ramified perforations can exist among the Foraminifera Cyclammininae (compare with Banner, 1970, pl. 3, figs 1-12; McNeil, 1988, text-fig. 3, p. 120) (Fig. 12).

The rare bracelets are observed in Mamet & Roux (1974, pl. 6, fig. 2), Vachard *in* Dil *et al.* (1977, fig. 13), Vachard (1991, pl. 5, fig. 2), Madi *et al.* (1996, pl. 24, fig. 7) and Flügel (2004, pl. 108, fig. 3) (see also the examples in the similar genus *Palaeoberesella* Mamet & Roux, 1974, pl. 2, fig. 19, pl. 4, figs 10, 14).

Occurrence.— ?Givetian of Belgium (Mamet & Préat, 1992, pl. 1, fig. 15). Famennian-Serpukhovian. England,

Ireland, Belgium, France, Spain, Poland, Greece, Donbass, Russian Platform, southern and middle Urals, Kuzbass, Siberian Platform, Omolon Massif; Algeria, Tarim, Newfoundland, Morocco, Montagne Noire, Turkey, Australia (Dil *et al.*, 1977; Mamet & Roux, 1983; Roux, 1985; Ivanova & Bogush, 1988; Bogush *et al.*, 1990; Cózar, 2004). Acme in the Middle Viséan in Morocco (our data) and Urals (Ivanova & Bogush, 1992, tab. 1 p. 241). Early Bashkirian of Algeria (Sebbar & Mamet, 1996; Sebbar, 2000).

Genus *Kamaena* Antropov, 1967

(Figs 8.10c-d, 10.15; Pl. 5, Fig. 13)

Type species: *Kamaena delicata* Antropov, 1967.

Synonymy.– *Subkamaena* Berchenko, 1981 (type species: *Subkamaena razdolnica* Berchenko, 1981).

Diagnosis.– Test small, short, cylindrical, cylindrical to tapering, bifurcated, uniseriate, with quadratic chambers. No sutures. Aperture terminal, broad, simple, central. Wall yellowish, finely perforated by rare aspondyl primary canalicules.

Composition.– *Kamaena delicata* Antropov, 1967; *K. awirsi* Mamet & Roux, 1974; *K. itkillikensis* Mamet & Rudloff, 1972; *K. magna* Ivanova, 1988; *K. minuta* Ivanova in Bogush *et al.*, 1990; *K. omolonica* Ivanova in Bogush *et al.*, 1990; *K. pirleti* Mamet & Roux, 1974; *Subkamaena razdolnica* Berchenko, 1981; *S. concaviuscula* (*sic*) Berchenko, 1981; ?*S. sibirica* Ivanova, 1988; ?*S. torosa* Ivanova, 1988; ?*Kamaena* sp. (*sensu* Dreesen *et al.*, 1985, pl. 7, figs 1-2; relatively atypical because of the very conspicuous polysynthetic twinning).

Excluded species.– *Kamaena maclareni* Mamet & Rudloff, 1972; ?*K. lata* Ivanova, 1988 (= ?*Parakamaena*); ?*K. tobolensis* Ivanova in Bogush *et al.*, 1990 (= another genus).

Occurrence.– Middle Devonian to Moscovian, cosmopolitan: Palaeo-Tethyan, Siberia, North America, Bolivia, Australia (Mamet & Roux, 1974; Zadorozhnyi & Juferev, 1980; Roux, 1985; Mamet, 1991, 1994; Vachard *et al.*, 1991; Ivanova & Bogush, 1992; and Cózar *et al.*, 2008b). Acme in the Tournaisian of Belgium, South China (unpublished data), and Urals (Ivanova & Bogush, 1992, tab. 1, p. 241).

Genus *Kulikaella* Berchenko, 1981

(Fig. 10.18; Pl. 5, Figs 14-16)

Type species: *Kulikaella unistratosa* Berchenko, 1981.

Diagnosis.– Similar to *Kamaena* but smaller and curved, with pseudosepta, and oblique bifurcations.

Composition.– *Kulikaella unistratosa* Berchenko, 1981; *K. minima* Berchenko, 1981; “a branching *Palaeoberesella* in the centre” (*sensu* Herbig & Mamet, 2006, pl. 3, fig. 1).

Excluded species.– *Kulikaella partita* Ivanova (*sensu* Ivanova & Bogush, 1992, pl. 49, figs 10-11). Considered as characteristic of the Serpukhovian in the Urals (Ivanova & Bogush, 1992, tab. 1, p. 241), this species perhaps belongs to *Praedonezella*.

Remarks.– Many *Kamaena*, “*Eodonezella*”, and *Palaeoberesella* of the literature can correspond to this palaeoberesellid which seems to be characteristic of the Strunian substage.

Occurrence.– Strunian of Donbass, northern France, Germany and Afghanistan. Early Tournaisian of Donbass. ?Late Tournaisian of Siberia.

Genus *Parakamaena* Mamet & Roux, 1974

Type species: *Kamaena?* *tenuisepta* Mamet & Rudloff, 1972.

Synonymy.– *Kamaena* (*part.*) (e.g., Petryk & Mamet, 1972, pl. 3, fig. 11 only).

Diagnosis.– Palaeoberesellidae with septa markedly thinner than the wall, and devoid of sutures.

Composition.– *Kamaena?* *tenuisepta* Mamet & Rudloff, 1972; *Parakamaena exilis* Ivanova in Ivanova & Bogush, 1988; *P. irregularis* Berchenko, 1981; ?*Kamaena lata* Ivanova in Bogush *et al.*, 1990.

Remarks.– Except for the thin septa, this genus can be confused with *Moravammina*.

Occurrence.– ?Middle Devonian of Belgium (Mamet & Prétat, 2009, pl. 4, fig. 16). Late Tournaisian of North America, ?Urals, ?Siberian Platform, and Donbass (Ukraine). Middle Viséan of England.

Genus *Pseudokamaena* Mamet in Petryk & Mamet, 1972

(Figs 10.17, 10.28)

Type species: *Pseudokamaena armstrongi* Mamet in Petryk & Mamet, 1972.

Synonymy.—? *Dasyoporella* (sensu Berchenko, 1981).

Diagnosis.— Cylindrical test, bifurcated. Curved septa. Chambers spherical, ovoid or pear-shaped. Apertures relatively long and arcuate. Wall yellowish, hyaline, granular, scarcely perforated.

Composition.— *Pseudokamaena armstrongi* Mamet in Petryk & Mamet, 1972; *P. atypica* Berchenko, 1981; *P. boulderensis* Mamet in Petryk & Mamet, 1972; and *P. dentifera* Ivanova in Bogush et al., 1990.

Remarks.— Although included in the original diagnosis of the genus *Pseudokamaena*, pores are not always observed in each species assigned to this taxon.

True *Moravamina* of Menner & Reitlinger (1971) were included in *Pseudokamaena* by Mamet & Roux (1974).

Occurrence.— Middle Devonian-Serpukhovian Palaeo-Tethys, Urals, Siberia, and North-America.

Genus *Turgajella* Ivanova in Bogush et al., 1990

Type species: *Turgajella peculiaris* Ivanova in Bogush et al., 1990.

Diagnosis.— Similar to *Kamaena* but with diaphragms and septa of different thicknesses.

Composition.— Monospecific.

Occurrence.— Strunian (= late Zavolzhsky) of southern Urals.

Genus ?*Metakamaena* Endo, 1969

Type species: *Metakamaena gracilis* Endô, 1969.

Diagnosis.— A revision is necessary because the original diagnosis apparently does not correspond to the illustration of the holotype.

Composition.— Monotypic.

Remarks.— Very poorly known, never seen in our collections. The type material looks like perforated brachiopods or bivalves.

Occurrence.— Early Middle Permian of Thailand.

Suborder BERESSELLINA Vachard, 1994b, *nomen transl.* herein (from family)

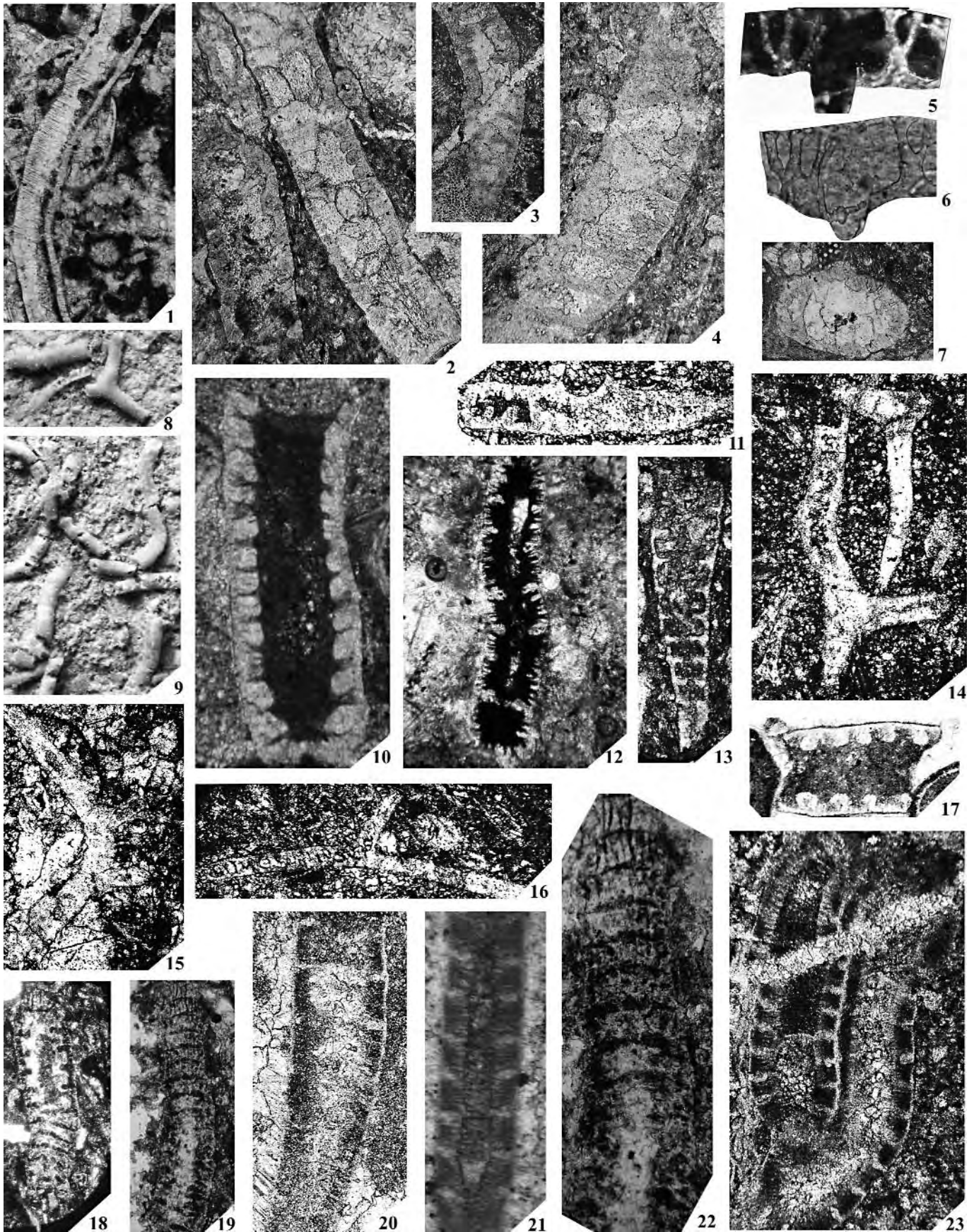
Diagnosis.— Cylindrical tests, undivided but with diaphragms according to the genera. Wall hyaline yellowish, with diverse groups of thin, single- to bi- and tri-furcate blind canalicules (see Vachard, 1991, fig. 5).

Composition.— One family, Beresellidae Maslov & Kulik, 1956.

Remarks.— Many authors assigned Beresellina to Dasycladales (Elliott, 1970; Herak et al., 1977; Deloffre, 1987,

Plate 5

- 1, *Kettneramina* sp. 4. Long, slender and incurved. Moniellos Formation (northern Spain). Early Devonian. 1. Sample M151-7 (bis); x 47.
 2-7, *Exvotarissella dili* Vachard in Dil et al., 1977. 2. Longitudinal section. Late Viséan. Sample Dil 2; x 66. 3. Oblique section. Sample Dil 2; x 66. 4. Oblique section. Sample Dil 2; x 66. 5. Wall and perforations with transmitted light. Sample Dil 2; x 255. 6. Ibidem, with polarized light. Sample Dil 2; x 225. 7. Oblique section. Sample Dil 2; x 66.
 8-11, *Exvotarissella index* Ehrenberg, 1854 (von Möller, 1879) Mamet and Roux, 1974. 8. Bifurcated test in the surface of a sample. Jebel Aoujgal (central Morocco). Middle Viséan. Sample HGT.M.1.1, x 20. 9. Numerous tests on the surface of a limestone. Jebel Aoujgal (central Morocco). Middle Viséan. Sample HGT.M.1.1; x 13. 10. Longitudinal section, Les Pascales (Montagne Noire, southern France). Late Brigantian. Sample DV601A; x 66. 11. Longitudinal section with bracelet. Strunian. Sémeries Y 41 (northern France). Sample RC 6417. Photo 14021; x 50.
 12, *Exvotarissella* sp. nov., Archerbeck Borehole, BGS-E-1860', Archerbeck Beds, late Asbian, S Scotland, x 75.
 13, *Kamaena* cf. *razdolnica* (Berchenko, 1981) comb. nov. Strunian (Tn1α). Avesnelles (northern France); x 66.
 14-16, *Kulikaella* cf. *unistratosa* Berchenko, 1981. 14. Strunian. Sémeries Y 41 (northern France). Sample RC 6417. Photo 14024; x 50. 15. Strunian. Avesnes 3/59 (northern France). Sample RC 6186. Photo 14045; x 50. 16. Strunian. Avesnes 3/125 (northern France). Sample RC 6291. Photo 14085; x 50.
 17, Transition to *Dvinella*. Bashkirian of Northern Thailand. Sample T291(2); x 50.
 18-19, 22, "*Beresella*" *machaevii* Kulik, 1964. 18. Sample DV783A. Mikhailovsky, Oka river (Russia), 1/12B; x 27. 19. Sample DV783B. Mikhailovsky (Upper Viséan), Oka river (Russia), 1/12B; x 27. 22. Sample DV783B. Mikhailovsky, Oka river (Russia), 1/12B; x 27.
 20, 23, *Beresella* sp. 1. 20. Moscovian of Rhodes (Greece). Sample PL532-1; x 100. 23. Northern Spain; x 66.
 21, *Beresella* sp. 2. Moscovian of Alborz (northern Iran). Sample JJ268(4); x 60.



1988; Granier & Grgasovic, 2000), but the type of wall is irrelevant of this order of algae. This wall is two-layered with an outer yellow layer forming re-entrants until the internal cavity. In between, the re-entrants, darker rings, are finely canaliculate (see Vachard, 1991, fig. 5). The canalicules are blind, because they are overlain by a continuous external yellow layer. This type of wall has been defined as “bereselloid wall” (Vachard, 2009, p. 201). In many genera, several diaphragms (Vachard, 1991, fig. 4.4) can occur in the entire central cavity (*Beresella* and *Uraloporella*; see especially Saltovskaya, 1984b, pl. 12). Because of these diaphragms, Berger & Kaefer (1992, p. 31) admitted that some genera of this family “may not even be algae”. Because of the diaphragms, blind canalicules and yellowish hyaline wall, the similarity with dasyclads must be abandoned.

Family BERESSELLIDAE Maslov & Kulik, 1956, *nomen transl.* H. Termier *et al.*, 1977; see also G. Termier *et al.*, 1977, p. 141 (from tribe) (*non* Deloffre, 1987, *nec* Shuysky, 1987, *nec* Deloffre, 1988)

Synonymy.— *Beresella* group (*sensu* Chuvashov & Riding, 1984); *Uraloporellae* Shuysky, 1985.

Diagnosis.— As for the order.

Composition.— Five genera: *Beresella* Makhaev, 1937 *ex* Maslov & Kulik, 1956; *Ardengostella* Vachard *in* Perret & Vachard, 1977; *Dvinella* Khvorova, 1949; *Trinodella* Maslov & Kulik, 1956; and *Uraloporella* Kordé, 1950 (= *Samarella* Maslov & Kulik, 1956).

Remarks.— Because of their extraordinary abundance, their small sizes and simple morphologies, Beresellidae can easily be confused with chlorophyte algae. The representative of this family were even included within the phylogeny of the Dasycladales by several authors (e.g., Kochansky-Devidé & Gusic, 1971; Herak *et al.*, 1977; Deloffre, 1987, 1988; Deloffre & Granier, 1991). In older studies by Deloffre (e.g., in Bassoullet *et al.*, 1979), the Beresellina were excluded from the Dasycladales.

The “central cavities” are interrupted by diaphragms (see especially Saltovskaya, 1984b, pl. 12, figs 1-10, pl. 13, figs 2, 7, 9; Roux, 1985, pl. 3, fig. 11; Chuvashov *et al.*, 1987, pl. 16, fig. 13, with 9 diaphragms; Mamet *et al.*,

1987, pl. 13, fig. 19, with 5 diaphragms, pl. 14, fig. 8; Vachard, 1991, pl. 5, fig. 7 with 5 diaphragms; Mamet & Villa, 1995, pl. 1, fig. 5, with 4 or 5 diaphragms; Khodjanyazova & Mamet, 2003, pl. 2, fig. 18, with approximately 10 diaphragms). The “conceptacles” have no pores, and they are systematically associated with diaphragms as illustrated by Saltovskaya (1984b, pl. 12, figs 1, 1A, pl. 13, figs 5-8) and Chuvashov *et al.* (1987, pl. 16, fig. 14) (Fig. 9). This type of conceptacle is entirely unknown among the Chlorophyta as well as Rhodophyta. Moreover, due to the morphological transition with moravamminids (see “*Beresella*” *machaevii* Kulik, 1964), beresellids are considered here as algosponges.

Occurrence.— Latest Viséan, Late Serpukhovian-earliest Permian; cosmopolitan. Rare in the Brigantian-Arnsbergian in the Urals, with *Beresella machaevi* Kulik, 1964 and in the Arnsbergian of southern France with *Ardengostella*, they are common in the Bashkirian-Moscovian, and survive up to the earliest Permian (Asselian) with *Beresella* and *Dvinella*. Acme during the Moscovian (e.g., Choh & Kirkland, 2008). The Beresellidae are rare during the Late Pennsylvanian (see Vachard & Krainer, 2001). The last populations seem to be constituted of *Trinodella*, in the Asselian of Urals and in the earliest Permian of New Mexico (D.V., unpublished data). Cosmopolitan in the Pennsylvanian.

Genus *Beresella* Makhaev, 1937 *ex* Maslov & Kulik, 1956

(Figs 9.10, 12.11, 13.5; Pl. 5, Figs 20-21, 23)

Type species: *Beresella erecta* Maslov & Kulik, 1956.

Diagnosis.— Test cylindrical, straight, never ramified but occasionally twin. Wall of the family with simple, straight and acrophore laterals. Rare diaphragms, generally curved (according to Vachard, 2009, p. 203).

Composition.— *Beresella erecta* Maslov & Kulik, 1956; *B. bilguetayae* Güvenç, 1966b *orth. mut.*; *B. erecta turkiana* Güvenç, 1966b; *B. gissarica* Saltovskaya, 1970; *B. herminae* Racz, 1964; *B. ishimica* Kulik, 1964; *B. polyramosa* Kulik, 1964; and *B. translucens* Kulik, 1964 (*orth. mut.* herein for *translucea*).

Excluded species.— *B. machaevii* Kulik, 1964 (as seen in our material, Pl. 5, Figs 18-19, 22, some sections of the lit-

erature look like recrystallized *Issinella* or *Kamaenella*, other ones seem to be comparable with *Ardengostella* or *Exvotarissella*). As noticed by Vachard & Maslo (1996), true *Beresella* are unknown up to the Bashkirian.

Remarks.— We agree with the analysis of the genus by Mamet (1991), completed by the twin tests (Lys & Le Boulenger, 1977, pl. 52, fig. 1), bifurcated or pseudo-ramified tubes (Chuvashov *et al.*, 1987, pl. 16, fig. 11; Mamet *et al.*, 1987, pl. 13, fig. 12) and the presence of diaphragms (Vachard, 1993); because of the abundance of the illustrations, these diaphragms are constitutive of the Beresellinae, and cannot be interpreted as interruptions of the growth.

Beresella described by Groves (1986, figs 6.6-6.10) might be a *Dvinella* or even a *Trinodella* (Vachard, 2009).

The taxon was denominated *Beresella* Makhaev *ex* Kulik, 1964 by Granier & Grgasovic (2000), but no details were given for this modification.

Occurrence.— Bashkirian to Orenburgian (acme in Moscovian); cosmopolitan (see Groves, 1986). ?Up to Sakmarian according to Granier & Deloffre (1995, p. 61).

Genus *Ardengostella* Vachard *in* Perret & Vachard, 1977

Type species: *Ardengostella perretae* Vachard *in* Perret & Vachard 1977.

Diagnosis.— Cylindrical tests, with regular central cavity, and groups of blind, thin laterals linked in relatively regular rings crossing through the wall. Two orders of ramifications in the laterals. External layer, yellow, costulate. Presence of bracelets, but absence of diaphragms.

Composition.— Monospecific.

Remarks.— *Ardengostella* is the first true Beresellinae. It is different from the Bashkirian-Moscovian genus *Dvinella* Khvorova, 1949, by the costulate periphery and the faint differentiation of the rims with and without canalicules (Vachard, 1991, fig. 5).

Occurrence.— Apparently endemic of the type locality (late Serpukhovian of Pyrenees), but some *Beresella*

machaevii Kulik, 1964, *Dvinella secunda* Kulik, 1964 and *D. distorta* Kulik, 1964 (*sensu* Bogush *et al.*, 1990) might correspond to *Ardengostella*, because 1) they are coeval and 2) true *Beresella* and *Dvinella* are only known since the late Bashkirian. Unfortunately, these forms of the Urals were poorly or never illustrated. The Namurian "*Dvinella*" documented in Mamet (1991) might be attributed to *Ardengostella*.

Genus *Dvinella* Khvorova, 1949

(Pl. 5, Fig. 17, Pl. 6, Figs 1, 6)

Type species: *Dvinella comata* Khvorova, 1949.

Synonymy.— *Eomizzia* Endo & Horiguchi, 1957.

Diagnosis.— Beresellidae with ramified perforations.

Composition.— *Dvinella comata* Khvorova, 1949; *Dvinella crassithea* Kulik, 1964; *D. cuvillieri* Güvenç, 1966b; *D. distorta* Kulik, 1964; *D. gracilis* Kulik, 1964; *D. secunda* Kulik, 1964; and *D. unifurcata* Kulik, 1964.

Remarks.— The validity of both genera, *Dvinella* and *Beresella*, was questioned by Groves (1986, p. 481), however, the occurrence of ramified perforations is considered here as enough to justify both genera as independent.

Occurrence.— Bashkirian-Orenburgian, cosmopolitan. The Early Permian forms mentioned by Mamet (1991) were never observed by us; nevertheless, *Trinodella* has been recognized in the latest Carboniferous (Bursumian = Orenburgian) in Newell Peak section (New Mexico, U.S.A.) (D.V., unpublished data).

Genus *Trinodella* Maslov & Kulik, 1956

Type species: *Dvinella (Trinodella) bifurcata* Maslov & Kulik, 1956.

Diagnosis.— Beresellidae with triple order of perforations.

Composition.— *Dvinella (Trinodella) bifurcata* Maslov & Kulik, 1956; *Dvinella (Trinodella) variolonga* Kulik, 1964; ?*Uraloporella* (*sensu* Choh & Kirkland, 2008; fig. 2B).

Remarks.— The different order of perforations is considered here of generic level.

Occurrence.— Late Pennsylvanian (Moscovian-Orenburgian) in the Russian Platform, Carnic Alps, Croatia Serbia, Arctic Canada and New Mexico, Tunisia, northern Spain and Uzbekistan. Early Permian (early Wolfcampian) of New Mexico (D.V., unpublished data).

Genus *Uraloporella* Kordé, 1950

(Figs 1.9, 8.5, 10.1-10.3, 11.1-11.7; Pl. 6, Fig. 13)

Type species: *Uraloporella variabilis* Kordé, 1950.

Synonymy.— *Samarella* Maslov & Kulik, 1956.

Diagnosis.— Beresellinae with randomly arranged aspondyl fine canalicules within the walls. Diaphragms often numerous.

Composition.— *Uraloporella variabilis* Kordé, 1950; *Samarella massieuxae* Güvenç, 1966b; *Uraloporella rara* Saltovskaya, 1984b; *Samarella setosa* Kulik, 1964; and *Uraloporella sieswerdai* Racz, 1964.

Remarks.— Diaphragms of *Uraloporella* have been illustrated by Saltovskaya, 1984b, pl. 12, figs 1-10, pl. 13, figs 2, 7, 9, and Mamet & Villa, 1995, pl. 1, fig. 5, with 4 or 5 diaphragms. False conceptacles more or less closely associated with diaphragms have been illustrated by Saltovskaya (1984b, pl. 12, figs 1, 1A, pl. 13, figs 5-8) and Chuvashov *et al.* (1987, pl. 16, fig. 14). See here Figs 10.1-10.3 and Figs 11.1-11.7.

Occurrence.— Moscovian in the Urals, Canadian Arctic, northern Spain, Greenland, Tunisia, Turkey, Russian Platform, Iran (Alborz), Uzbekistan, Tadjikistan. The genus is absent from the North-American craton (*Uraloporella* recently reported from New Mexico, U.S.A., by Choh & Kirkland (2008), is another beresellid, probably *Trinodella*, see above).

Suborder DONEZELLINA G. Termier *et al.*, 1975, *nomen transl.* herein (pro family)

Diagnosis.— Algospongia with laminar, prostrate, attached initial part and/or erect and septate tubes. Wall yellowish, sometimes bereselloid (e.g., *Donezella*).

Composition.— Two families: Claracrustidae Vachard in Vachard *et al.*, 2001 *nomen transl.* herein; and Donezel-

lidae G. Termier *et al.*, 1975 emend herein (=Goksuellinae H. Termier *et al.*, 1977).

Remarks.— Initially, Moravamminida encompassed the Moravamminina and the Donezellina derived from them. The Donezellina are morphologically and phylogenetically transitional to the Moravamminina and Aoujgaliina because they possess the scalariform, septate tubes of the former and the laminar, roughly concentric growth of the latter [see the first tentative signs of this hypothesis in Vachard & Montenat (1981) and Vachard (1993)].

The Donezellina present diverse evolutive trends; 1) concerning the microstructure of wall: 1a) compact wall (Claracrustidae, *Kamaenella*); 1b) bereselloid wall (*Donezella* = *Goksuella*); 2) concerning the mutual arrangement of initial laminae and terminal tubes: 2a) no tubes were observed (*Claracrusta*, *Asphaltinella*); 2b) the septate tubular elements are relatively equal in number to the initial concentric laminae (*Pokorninella*); 2c) they are only present (*Kamaenella*, *Donezella*). It is possible, due to the biostratigraphical record, to describe two families encompassing these different criteria: Claracrustidae (with 1a, 2a, 2b) and Donezellidae (with 1a, 1b, 2c).

Occurrence.— Early Devonian-Late Permian, cosmopolitan (*Donezella*) or limited to the Palaeo-Tethys (*Kamaenella*). Middle Permian of Turkey and latest Permian of South China (Gaillot, 2006; Vachard & Moix, in press).

Family CLARACRUSTIDAE Vachard in Vachard *et al.*, 2001, *nomen transl.* herein

Diagnosis.— Donezellina encrusting, prostrate, crustose, laminar with concentric to uniseriate growth, in cases initial laminar chamber rows followed by tubes, with differentiated development of both parts depending on the genera, with rare erect rows of chambers. Wall calcitic, yellowish, hyaline, granular.

Composition.— Eight genera: *Claracrusta* Vachard in Vachard & Montenat, 1981 [= *Berestovia* = *Ottonosia* (part.) = *Girvanella* (part.) = *Donezella* (part.)]; *Asphaltinella* Mamet & Roux, 1978b; *Denisella* gen. nov.; *Kleinbergella* Mamet & Boulvain, 1992; *Peristacheia* Mamet & Roux, 1983; *Pokorninella* Vachard in Perret & Vachard, 1977 [= *Proninella* (*sensu* Mamet & Roux, 1978b or 1983 *non* Reitlinger in Menner & Reitlinger, 1971) em-

placed herein among the Labyrinthoconidae]; *Pre-corninella* Vachard, 1991; and *Ungdarellina* Mamet, 2002.

Remarks.— This family is considered as transitional between the Moravamminida and Aoujgaliida because of the co-occurrence of the tubes and the laminae which characterize each order respectively.

Particularly, morphological similarities exist between the ungdarellids and claracrustids (see the species *Claracrusta ungdarelloidea* Vachard *et al.*, 2001; see also *Ungdarellina* Mamet, 2002 more similar to *Claracrusta* than *Ungdarella* in the laminar type of growth).

Occurrence.— Early Devonian to Late Permian. Palaeo-Tethyan to cosmopolitan, depending on the genera.

Genus *Claracrusta* Vachard in Vachard & Montenat, 1981

(Figs 11.8-11.10; Pl. 6, Figs 2-5, 7)

Type species: *Girvanella catenoides* Homann, 1972.

Synonymy.— *Girvanella* (*part.*); *Berestovia* Berchenko, 1982; *Donezella* (*sensu* Chuvashov, 1974; *part.*).

Diagnosis.— Test crustose composed of continuous rows of highly calcified hemispherical to ellipsoidal chambers, flattened at the base, well-defined by impersistent pseudosepta. Wall hyaline, yellowish, granular.

Composition.— *Girvanella catenoides* Homann, 1972; *Claracrusta calamistrata* Vachard, 1980; *Donezella delicata* Berchenko, 1982; *Berestovia filaris* Berchenko, 1982; *Claracrusta hirtipes* Vachard in Vachard & Montenat, 1981; *Donezella intertexta* Chuvashov, 1974; and *Claracrusta ungdarelloidea* Vachard *et al.*, 2001.

Remarks.— The single apparent difference between *Berestovia* and *Claracrusta* is the size and shape of the chambers. The former contains minute chambers with only slight wavy tops whereas the chambers of the latter are better defined, larger, with more hemispherical to ovoid shape. This difference is considered here as insufficient to retain both genera as independent, and only valid for distinguishing species.

The *Ottonosia* biopisoids, composed of cyanobacteria and *Claracrusta*, in the Late Pennsylvanian and Early Permian

(e.g., Homann, 1972; Vachard, 1980) are probably palaeoecologically comparable with the modern macroids with *Acervulina* (i.e., biopisoids growing in relatively deep, 60-70 m deep fore-reef, or cryptic habits).

Occurrence.— Late Viséan (late Asbian)-Late Permian, cosmopolitan (Vachard & Montenat, 1981; Ivanova, 1988; Bogush *et al.*, 1990; Mamet, 1994; Sebbar *et al.*, 2000; Cózar & Somerville, 2004, 2005a-c; Said, 2005; Mamet & Zhu, 2005; Cózar *et al.*, 2008a-b). The FAD occurs at the base of the Brigantian, as in Central Morocco (Cózar *et al.*, 2008b, text-fig. 4). The LAD is latest Permian (Gaillot, 2006). The acme is Asselian-Sakmarian in age with the *Ottonosia* biopisoids. Palaeo-Tethyan in the Viséan-Serpukhovian times, *Claracrusta* becomes cosmopolitan probably by the Bashkirian.

Genus *Asphaltinella* Mamet & Roux, 1978b

(Pl. 6, Figs 8-9, 10-12)

Type species: *Asphaltinella horowitzi* Mamet & Roux, 1978b.

Diagnosis.— Test encrusting, constituted of interwoven layers of cylindrical small tubes. Wall hyaline yellowish, granular.

Composition.— *Asphaltinella horowitzi* Mamet & Roux, 1978b; *A. (?) bangorensis* Mamet & Roux, 1978b; *?A. peratrovichensis* Mamet & Pinard, 1985 (maybe a Labyrinthoconidae).

Remarks.— This genus is rather similar to *Pokorninella*; however, the latter exhibits erect or projected tubes, never described in *Asphaltinella*, which usually occurs in more encrusting forms. Thus, *Pokorninella* might be interpreted morphologically as an intermediary form between *Asphaltinella* and *Claracrusta*, as well as biostratigraphically.

Occurrence.— Tournaisian of Montana (U.S.A.; Sando & Mamet, 1981); Viséan-early Moscovian, probably cosmopolitan (see Mamet, 1991, p. 384, and add: Algeria (Sebbar & Mamet, 1999; Sebbar *et al.*, 2000), ?Iran (Vachard, 1996), Spain (Cózar, 2005).

Genus *Denisella* gen. nov.

(Pl. 6, Figs 21-23)

Type species: *Pokorninella bricae* Vachard, 1988a.

Diagnosis.— Test encrusting, constituted of interwoven prostrate, layers of chambers followed by cylindrical with one to four erect and septate tubes. Wall hyaline yellowish, granular.

Composition.— Monospecific.

Remarks.— This genus seems to be endemic to northern France where it is occasionally common (Vachard, 1988a; Darras *et al.*, 2008).

Occurrence.— Givetian of northern France (Boulonnais).

Genus *Kleinbergella* Mamet & Boulvain, 1992

Type species: *Kleinbergella filosa* Mamet & Boulvain, 1992.

Diagnosis.— Test encrusting with several laminae, more or less concentric to excentric, constituting projections, with dichotomous ramifications developing interlaminar chamber-like spaces, elongated and irregular.

Composition.— Monospecific.

Remarks.— This genus represents one of the transition between Moravamminina and Aoujgaliina. The other possibilities are *Pokorninella* or *Precorninella* or *Pseudostacheoides*.

Occurrence.— Frasnian of Belgium.

Genus *Peristacheia* Mamet & Roux, 1983

Type species: *Peristacheia jonesi* Mamet & Roux, 1983.

Diagnosis.— Test encrusting, constituted of interwoven layers of cylindrical large tubes, with marked quadrate chambers, no projections or erect tubes are known. Wall hyaline yellowish, granular.

Composition.— Monospecific.

Remarks.— This genus is poorly known and probably endemic.

Occurrence.— Latest Tournaisian of New South Wales (Australia).

Genus *Pokorninella* Vachard in Perret & Vachard, 1977

(Pl. 6, Figs 14, 16, 20, Pl. 7, Fig. 4)

Type species: *Pokorninella strigosa* Vachard in Perret & Vachard, 1977.

Diagnosis.— Test encrusting, constituted of interwoven prostrate layers of chambers followed by cylindrical, small, divided, erect tubes. Chambers pear-shaped to barrel-shaped. Wall hyaline yellowish, granular.

Synonymy.— *Proninella* (*sensu* Mamet & Roux, 1978b or 1983 *non* Reitlinger in Menner & Reitlinger, 1971).

Composition.— *Pokorninella strigosa* Vachard in Perret & Vachard, 1977; *P. gracilis* Vachard in Meissami *et al.*, 1978; *Proninella enigmatica* Mamet & Roux, 1978b; *Proninella* sp. (*sensu* Mamet, 1976, pl. 9, figs 1-3, pl. 11, fig. 2?, pl. 40, fig. 4, pl. 41, figs 1-4, pl. 59, figs 2?, 3?, 4?); *Palaeobereselle* (*sensu* Vieslet, 1983, pl. 5, fig. 9); *Proninella* (*sensu* Mamet *et al.*, 1986, pl. 13, figs 1-2, pl. 15, figs 1-2, 3?, 4); *Proninella* spp. (*sensu* Brenckle *et al.*, 2009, pl. 12, figs 5, 7-10); ?*Pokorninella graeca* Vachard & Clément, 1994; ?*P. minuscula* Ivanova in Bogush *et al.*, 1990 (or a moravamminid).

Remarks.— The genus *Pokorninella* is commonly confused in the literature with *Proninella* (e.g., Mamet, 2002, 2006; Brenckle *et al.*, 2009) (see *Proninella* remarks). This problem would be probably solved with a more accurate subdivision of the genus. Firstly, the Givetian ancestral forms are described here as *Denisella* gen. nov., because of its transitional characters with some moravamminids, *Moravamina* or *Triangulinella* for example. The species *Pokorninella graeca* might be also a distinct genus but the species remains poorly known because the type material is recrystallized, and the reconstruction of Vachard & Clément (1994) is idealized. *P. gracilis*, *P. strigosa* and *P. enigmatica* are distinct forms due to the dimensions, number of tubes, and unequal development of the initial laminar part.

Occurrence.— Viséan-Bashkirian. Palaeo-Tethys and North America (Alaska, Tennessee, Sonora).

Genus *Precorninella* Vachard, 1991

(Pl. 6, Figs 15, 17-19, Pl. 7, Fig. 3)

Type species: *Precorninella hieroglyphica* Vachard, 1991.

Diagnosis.— Test encrusting, constituted of interwoven layers of quadratic to irregular large tubes, with erect-like projections poorly defined. Wall with aspondyl, acrophore perforations relatively numerous.

Composition.— Monospecific.

Remarks.— This primitive form is probably poorly represented in the world.

Occurrence.— Late Emsian of Spain. ?Middle Devonian of Siberia.

Genus *Ungdarellina* Mamet, 2002

Type species: *Ungdarella peratrovichensis* Mamet & Rudloff, 1972.

Diagnosis.— Similar to *Claracrusta* but with an apparently more complex endoskeleton, the rows seem to be formed of transverse oblique and not longitudinal tubular chambers.

Composition.— *Ungdarella peratrovichensis*; ?*Claracrusta catenoides* (*sensu* Forke, 1995, p. 241, fig. 15/7).

Occurrence.— ?Late Serpukhovian-Pennsylvanian-Early Permian. The geographical distribution given by Mamet (2002, p. 500) is North America, Japan, and Spain. The questionable illustration of Forke (1995) comes from the Early Permian of the Carnic Alps.

Family DONEZELLIDAE G. Termier *et al.*, 1975

Synonymy.— Goksuellinae H. Termier *et al.*, 1977.

Diagnosis.— Donezellina only composed of erect septate tubes, gregarious, often adjacent or multiple, with quadratic to barrel-shaped (dolioliform) chambers. Wall simple yellowish to differentiated bereselloid (see above; i.e., with annular segments repetitively perforated and not perforated). Aperture small, terminal and areal.

Composition.— Three genera: *Donezella* Maslov, 1929 *ex* Vachard *in* Meissami *et al.*, 1978 (= *Goksuella* Güvenç, 1966b; =? *Alanyana*, Güvenç, 1967), *Kamaenella* Mamet & Roux, 1974, and *Praedonezella* Kulik, 1973 *emend.*

Occurrence.— Middle-late Viséan. Serpukhovian. Bashkirian-Moscovian. Rare survivors in the Late Pennsylvanian and all the Permian.

Genus *Donezella* Maslov, 1929 *ex* Vachard *in* Meissami *et al.*, 1978

(Figs 8.9, 9.8, 12.9, 13.5; Pl. 6, Figs 25-27, Pl. 7, Figs 1-2, 6-7, ?8, 9, ?10)

Type species: *Donezella lutugini* Maslov, 1929 *ex* Vachard *in* Meissami *et al.*, 1978.

Synonymy.— *Goksuella* Güvenç, 1966b; *Ptychocladia?* (*sensu* Glinzboeckel & Rabaté, 1964); and ?*Alanyana*, Güvenç, 1967.

Diagnosis.— Test composed of numerous, frequently bifurcated, tubular, slightly tapering to the bifurcation, generally constricted. Wall bereselloid.

Composition.— *Donezella lutugini*; *D. lunaensis* Racz, 1964 [although it is synonymized by some authors, this species seems to be distinct; see Vachard *in* Proust *et al.* (1996)]; *Goksuella maslovi* Güvenç, 1966b; *G. oblica* Güvenç, 1966b; ?*Alanyana reicheli* Güvenç, 1967.

Remarks.— The microstructure of the wall was not fixed in the diagnosis of *Donezella*; and microgranular walls (e.g., the foraminiferal test *Insolentitheca* as indicated by Meissami *et al.*, 1978; Vachard *in* Bensaid *et al.*, 1979; Groves, 1987; Vachard & Cózar, 2004); yellow claracrustiid and/or aoujgaliiid walls, and bereselloid walls (firstly described in the diagnosis of *Goksuella*) were mixed in the type material. Nevertheless, in our collection of Donbass as well as the other Palaeotethyan outcrops from Spain to Thailand the bereselloid wall dominates. Consequently, *Donezella* (*sensu stricto*) must be defined with 1) the morphology of Maslov (1929, 1956a, 1962, 1973), 2) the type species of Meissami *et al.* (1978), and 3) the bereselloid wall (synonymy with *Goksuella*). Theoretically, it seems that *Goksuella* is a priority name, but to maintain the stability of nomenclature, we prefer *Donezella* because it is universally adopted.

Alanyana, morphologically very similar could differ by its “microgranular, radious and porous” wall (after the original diagnosis of Güvenç, 1967).

Excluded species.— *Donezella delicata* Berchenko in Aizenverg *et al.*, 1983 (= *Masloviporidium*); *Donezella intertexta* Chuvashov, 1974 (= *Claracrusta*); *Goksuella kuchtikovi* Saltovskaya [*sensu* Chuvashov *et al.*, 1987, pl. 16, fig. 11 (= a dichotomous *Beresella*)]; *Donezella callosa* Ivanova, 1999 (= ?*Einorella*); *D. askynica* Ivanova, 1999 (= ?*Anthracoporellopsis*).

Occurrence.— The “*Donezella*” of the latest Viséan-early “Namurian” are probably misidentified *Kamaenella* and/or *Praedonezella*. A FAD in the Zapaltiubinsky (latest Serpukhovian) of Urals is possible. Acme during the Bashkirian-Moscovian, cosmopolitan (Donets Basin, Russian Platform, Urals, Tien Shan, Tarim, northern Spain, Serbia, Poland, Algeria, Libya, Tunisia, Turkey, Iran, Afghanistan, Sarawak (Malaysia), Canadian Arctic, Alaska, Oklahoma, Arkansas, Idaho, Nevada, Utah; according to Groves, 1986, completed; as far as Bolivia; Mamet, 1994). Rarely mentioned in the Late Pennsylvanian and Early Permian, Artinskian-Kubergandian of Afghanistan and Midian? of Thailand (as *Alanyana* sp.). Very rare in Middle-Late Permian (Midian of Hazro, Turkey, and Changhsingian of South China) (Gaillot, 2006). The occurrence of *Alyana* is Middle-Late Permian, Turkey, Afghanistan and Thailand (Güvenç, 1967; Vachard & Montenat, 1981; Fontaine *et al.*, 1988).

Genus *Kamaenella* Mamet & Roux, 1974

(Figs 8.9, 10.4, 10.6, 10.8, 10.16; Pl. 6, Fig. 24, Pl. 7, Fig. 5)

Type species: *Kamaenella denbighi* Mamet & Roux, 1974.

Diagnosis.— Groups of small, intensively obliquely bifurcated and septate tests. Chambers higher than wide. No laterals. No sutures. Base of colonies unknown. Wall yellow.

Composition.— *Kamaenella denbighi* Mamet & Roux, 1974; *Nodosinella tenuis* Möller, 1879; and ?*Kamaena delicata* (*sensu* Saltovskaya, 1974).

Remarks.— Contrary to the earlier view of Vachard *et al.* (2004), *Kamaenella* and *Praedonezella* are considered here as the ancestors of *Donezella*, due to the similarity of shape and the frequent bifurcations of the skeletal tubules. The great productivity of this taxon (constituting up to 50-

60% of the rock volume, according to Cózar, 2004, p. 373) announces that of *Praedonezella* and *Donezella*.

Occurrence.— Middle-late Viséan, Palaeo-Tethyan as far as Newfoundland and North China and Sumatra. Serpukhovian in SW Spain (Cózar, 2005) and Algeria (Sebbar & Mamet, 1996, 1999).

Genus *Praedonezella* Kulik, 1973 emend.

(Pl. 7, Fig. 2, Pl. 16, Figs 1-14)

Type species: *Praedonezella cespeformis* Kulik, 1973.

Plate 6

1, *Dvinella comata* Khvorova, 1949. Moscovian of Rhodes (Greece). Sample PL183-1; x 66.

2-5, *Claracrusta catenoides* (Homann, 1972) Vachard, 1980. 2. Detail of fig. 3, x 140. 3. Biopisolate complex. Early Permian. Djambi (Sumatra). Sample IN456 (LM2); x 18. 4. “*Berestovia filiaris* Berchenko, 1982” (pl. 12, fig. 3). Bashkirian of Donbass, D₇ limestone, showing the synonymy with *Claracrusta*. x 43. 5. Crust with intercalated *Efluegelia*. Sample DV249a. Tezak section (central Mountains of Afghanistan); x 43.

6, *Dvinella* sp., Bashkirian, Northern Spain. Sample E1141; x 47.

7, *Claracrusta hirtipes* Vachard in Vachard & Montenat, 1981. Sample DV/ML4203(2). Central Mountains of Afghanistan; Middle Permian. x 29.

8-9, *Pokorninella* (= *Asphaltinella?*) *bangorensis* Mamet & Roux, 1978b. 8. Type material of Mamet & Roux, 1978b, pl. 4, fig. 13; paratype; early Serpukhovian; Bangor Limestone (U.S.A.); x 42. 9. Type material of Mamet & Roux, 1978b, pl. 4, fig. 11; holotype; middle Viséan; St. Louis Limestone (U.S.A.), x 42.

10, *Asphaltinella horowitzi* Mamet & Roux, 1978b. Type material of Mamet and Roux, 1978, pl. 4, fig. 6; paratype; early Serpukhovian; Bangor Limestone (U.S.A.); x 42.

11-12, *Asphaltinella* aff. *horowitzi* Mamet & Roux, 1978b. 11. Late Tournaisian. Saint Ghislain borehole (Belgium). 3943.50m (150E/387) Photo RC 15117; x 50. 12. Late Tournaisian. Saint Ghislain borehole (Belgium). 3943.50 m. Photo RC 15111; x 50

13, *Uraloporella variabilis* Kordé, 1950 with diaphragms. Moscovian of Alborz (northern Iran). Sample JJ247; x 60.

14, 16, *Pokorninella strigosa* Vachard in Perret & Vachard, 1977. Late Viséan of Dchar Ait Abdallah (central Morocco). 14. Longitudinal tubular part. Sample 13.9.69(1); x 66. 16. Initial part. Sample 13.9.69(2); x 66.

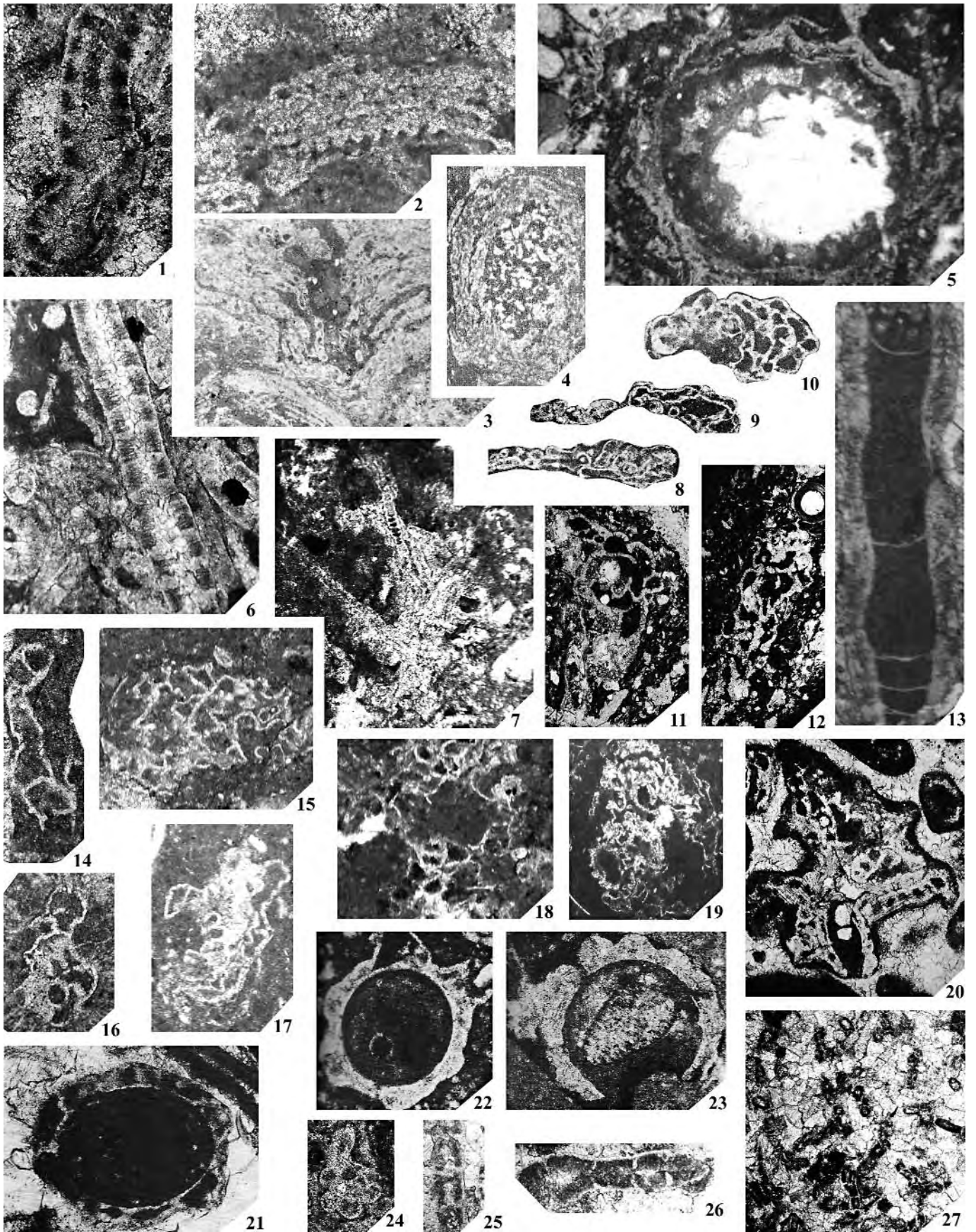
15, 17-19, *Precorninella hieroglyphica* Vachard, 1991. Moniellos Formation (northern Spain). Early Devonian. 15. Sample M342. 17. Sample M342-15; x 27. Sample M342-4 bis; x 20. 18; x 27. 13. M342.9; x 27. 19. M118.

20, *Pokorninella gracilis* Vachard in Meissami *et al.*, 1978. Middle Viséan. Sample Iran 80 (Alborz, Iran). Sample RC7469. Photo 15017; x 50.

21-23, *Denisella bricae* (Vachard, 1988). Blacourt Formation. Griset Member. Givetian of Boulonnais (northern France). 21. Sample B.GR41; x 66. 22. Sample B.GR67; x 66. 23. Sample B.GR67; x 66.

24, *Kamaenella* a basal part to compare with *Pokorninella* of Pl. 6, Fig. 16. Sample DV332B-7. Late Viséan (late Asbian). Lentilles de la route (Montagne Noire, southern France) ; x 50.

25-27, *Donezella lutugini* Maslov, 1929. 25-26. Urals, collection Lys, Moscovian, Sample 6/35; x 66. 27. Urals, collection Lys, Sample 6/55; x 27.



Synonymy.– *Donezella* Maslov, 1929 (*part.*).

Diagnosis.– Groups of tubules often bifurcated and connected to each other. Bases of the groups of tubules as short plates. Chamber subquadratic to ovoid with an areal aperture. Wall yellowish, simple without perforation.

Composition.– *Praedonezella cespeformis* Kulik, 1973; *P. primitiva* Vachard *et al.*, 2004; *P. cespeformis* (*sensu* Bogush *et al.*, 1990; probably *sp. nov.*); *P. catenuliformis* Ivanova *in* Bogush *et al.*, 1990; *P. sp. sensu* Sanz-López *et al.*, 2006 (fig. 7.4); *?Asphaltinella? bangorensis sensu* Mamet, 2002 (pl. 7, figs 5-6), *?Undetermined genus (sensu* Mamet, 2002, pl. 7, fig. 10).

Excluded species.– *Praedonezella carbonica* (Racz) *sensu* Vachard *et al.*, 1989 (pl. 1, fig. 10, pl. 4, figs 5, 7-8) rather corresponds to *Frustulata*. *Praedonezella tenuissima* Berchenko, 1982 is considered as a species of *Maslovioporidium* Groves & Mamet *emend.* Vachard & Maslo, 1996.

Remarks.– *Praedonezella* was created as a Rhodophycean Gigartinales (Kulik, 1973), and successively transferred to the Pharetronida Calcifoliida (Perret & Vachard, 1977), to the Paleosiphonocladales Beresellaceae (Chuvashov *et al.*, 1987), to the Siphonocladales Palaeoberesellaceae (Bogush *et al.*, 1990), to the algae *sensu lato* (Vachard *et al.*, 1991), or to the Fasciellia, due to the encrusting initial part (Vachard *et al.*, 2004). It is probably one of the most discussed assignments in the literature. The material assigned to this genus is probably multi-generic; particularly the material of Perret & Vachard (1977). For example, it is possible that the basal fasciellid layer described by Perret & Vachard (1977) is a character of another genus.

True *Donezella* appear in the early Bashkirian, at the base of Krasnopolyansky (Vachard & Maslo, 1996, text-fig. 1 p. 359); hence, the Serpukhovian can be characterized by the acme of *Praedonezella* and *Calcifolium okense*, the rarity (and/or LAD) of *Fasciella* and the absence of true *Donezella* (= *Goksuella*) (Perret & Vachard, 1977 re-interpreted; see a relatively similar conclusion in Ivanova & Bogush, 1992, tab. 1 p. 241).

Occurrence.– Asbian-late Bashkirian: southern Urals, southern France (Montagne Noire, Pyrénées), northern,

eastern and southwestern Spain, ?Algeria, Austria, Greece, Donbass, Turkey, southern Urals, Kazakhstan, Afghanistan (Hindu Kush), Malaysia, Thailand, Japan (see Vachard *et al.*, 2004, p. 271). Doubtful in the late Midian of Hazro (Turkey) (Gaillot, 2006).

Order AOIJGALIIDA G. Termier *et al.*, 1975, *emend.*
herein

Synonymy.– *Ungdarella-Stacheia* group (*sensu* Chuvashov & Riding, 1984).

Emended diagnosis.– Attached, laminar to cylindrical or conical, bifurcated tests, composed of rows of chambers forming laminae, with a concentric or uniseriate growth. Encrusting or erect test. Irregular shape, generally subconical, occasionally cylindrical, ramified. Endoskeleton constituted by rows of chambers connected with a central or basal communication. Chambers quadratic to hemispherical, generally irregular in shape. The system of attachment is generally undifferentiated but can be preserved as “baskets” (e.g., *Ungdarella*). Wall calcitic, yellowish, hyaline and granular, generally compact or finely perforate (*Pseudostacheoides*, *Costacheoides* gen. nov.). Some interruptions of the chamber wall can exist (*Ungdarella*). In the Calcifoliina, the interlaminar space is firstly thinner and then absent because the laminae evolve to petaloid forms, which finally contain filaments.

Composition.– Two suborders: Aoujgaliina G. Termier *et al.*, 1975, *nomen transl.* herein and Calcifoliina G. Termier *et al.*, 1977.

Remarks.– The Aoujgaliina differ from the red algae Melobesioidea by the irregularities of chambers; apertures between the chambers; and absence of conceptacles; whereas the Calcifoliina differ from the green algae Udoteaceae by an absence of true siphons. Nevertheless, Calcifoliina share the same bathymetrical spectrum as the modern Udoteaceae. They can be shallow (10 m) with the maximum diversity of foraminifers, but also attain the limit of the euphotic zone with the deepest green algae (Pille *et al.*, unpublished data).

Phylogeny.– The ancestor genus of the Aoujgaliida is probably among the Donezellina Claracrustidae, *Denisella* or *Kleinbergella*. The most primitive Aoujgaliina are proba-

bly *Pseudostacheoides*, *Costacheoides* gen. nov. or *Stacheoides*. A second lineage corresponds to an irregular organisation of the entire test and a sarmentoid skeleton (*Sinustacheoides*). Two lineages develop specialized terminal chambers: 1) more radial (*Epistacheoides*); 2) more quadratic (namely, the group *Aoujgalia*). The latter genus generates probably *Fourstonella* and the *Stacheiidae*. *Stacheoides tenuis* Petryk & Mamet, 1972 is probably the ancestor of *Ungdarella* (Vachard & Tahiri, 1991). Contrary to the hypothesis of Vachard & Maslo (1996), we suggest that the ancestor of the *Cuneiphycidae* n. fam. is more probably another species of *Stacheoides*. The *Calcifoliina* could be derived from *Pseudostacheoides* or *Stacheoides*.

Occurrence.— Late Tournaisian-Late Permian (acme during the middle-late Viséan), principally Palaeo-Tethyan.

Suborder AOIJGALIINA G. Termier *et al.*, 1975, *nomen transl.* herein (from family)

Diagnosis.— Attached tests with roughly concentric rows of chambers, with quadratic, hemispherical or labyrinthic shape of cells. Wall yellowish granular sometimes entirely recrystallized.

Composition.— Four families: *Aoujgaliidae* G. Termier *et al.*, 1975 (= *Pseudostacheoididae* Chuvashov *in Chuvashov et al.*, 1987); *Ungdarellidae* Maslov, 1956b, *emend.* herein; *Cuneiphycidae* n. fam.; and *Stacheiidae* Loeblich & Tappan, 1961, *nomen transl.* and *emend.* herein.

Remarks.— The *Aoujgaliina* are photic, especially *Roqueselsia*, *Ungdarella* and *Aoujgalia* due to their frequent assemblages with green algae: *Koninckopora*, *Eovelebitella* and *Murvielipora* (Pille, 2008). We agree with Gallagher (1998, p. 208), who emplaced *Ungdarella* “at or above 10 m” water depth. Some *Aoujgalia*, of the morphotype *Mametella*, are relatively deeper and can be found in Mississippian microbialite mounds (Jeffery & Stanton, 1996, figs 6f-h).

Occurrence.— Late Tournaisian-Late Permian, probably cosmopolitan.

Family AOIJGALIIDAE G. Termier *et al.*, 1975, *nomen transl.* herein

Synonymy.— Tribe Mametelleae Chuvashov *in Chuvashov et al.*, 1987; tribe *Pseudostacheoideae* Chuvashov *in Chuvashov et al.*, 1987.

Diagnosis.— *Aoujgaliina* with low to broad chambers growing subconcentrically, with variable shapes: hemispherical, labyrinthic; ellipsoidal to subquadratic chambers; in some cases, presenting two groups of chambers: in centre, irregular ones limited by labyrinthic walls or absent, in the periphery radial chambers limited by radiate walls sometimes T-shaped. Wall yellowish, granular.

Composition.— Eight genera: *Aoujgalia* Termier & Termier, 1950 (= *Valuzieria* G. Termier *et al.*, 1977 = *Mametella* Brenckle, 1977); *Asteroaoujgalia* Brenckle, 2004; *Costacheoides* gen. nov.; *Epistacheoides* Petryk & Mamet, 1972; *Pseudostacheoides* Petryk & Mamet, 1972; *Roqueselsia* G. Termier *et al.*, 1977; *Sinustacheoides* G. Termier *et al.*, 1977; and *Stacheoides* Cummings, 1955b (= ?*Chantonion* G. Termier *et al.*, 1977; = ?*Stacheoidella* Mamet & Roux *in Mamet et al.*, 1987).

Comparison.— The *Aoujgaliidae* differ from the *Ungdarellidae* by quadratic chamberlets (and consequently perpendicular pillars) by the attached growth, less cylindrical tests and less bifurcations.

Occurrence.— Late Tournaisian-Late Permian, probably cosmopolitan (biogeographic distribution varying according to the genera).

Genus *Aoujgalia* Termier & Termier, 1950

(Figs 5.7-5.8, 8.17; Pl. 7, Figs 11-21, Pl. 8, Figs 1-15, Pl. 9, Figs 1-5)

Type species: *Aoujgalia variabilis* Termier & Termier, 1950.

Synonymy.— *Aoujgalia?* (*sensu* Bozorgnia, 1973); *Asphaltinella* (*sensu* Mamet & Pinard, 1985, pl. 1, fig. 20); *Dromastacheoides* (*part.*; e.g., Vachard, 1980); *Fourstonella* (*part.*; e.g., Brazhnikova *et al.*, 1967, pl. 15, fig. 11); *Mametella* Brenckle, 1977; ?*Pseudostacheoides* sp. (*part.*; e.g., Mamet, 1994, pl. 1, figs 23-24, or *Epistacheoides*); *Stacheia* (*part.*; e.g., Petryk & Mamet, 1972, pl. 7, fig. 8); *Stacheia?* (*part.*; e.g., Sando *et al.*, 1981, p. 470); *Stacheoides* (*part.*; e.g., Malakhova, 1975, pl. 8, figs 1-4 or Vieslet, 1983, pl. 5, fig. 4); *Turoholia* Mamet *in Mamet et al.*, 1986 (*nomen nudum*; ?*lapsus calami* for

Aoujgalia); *Ungdarella* (part.; e.g., Chuvashov, 1974); *Valuzieria* G. Termier et al., 1977.

Diagnosis.– Test encrusting, conical to fusiform. Chambers irregularly quadratic grouped in grossly concentric series around the supports generally central. Wall hyaline yellowish. Inner part of the chambers often recrystallized in the same calcite than the wall.

Composition.– *Aoujgalia variabilis* Termier & Termier, 1950; *A. regularis* G. Termier et al., 1977; *A. elliotti* Mamet & Roux, 1977; *A. richi* Mamet & Roux, 1978b; *A. woodlandensis* sp. nov.; *Mametella chautauquae* Brenckle, 1977; *Stacheia? skimoensis* Mamet & Rudloff, 1972; *Valuzieria sescenti* G. Termier et al., 1977; *Dromastacheoides topi* Vachard, 1980; *Stacheoides* sp. (sensu Vieslet, 1983, pl. 5, fig. 4); *Turoholia* sp. (sensu Mamet in Mamet et al., 1986, pl. 12, fig. 14); ?*Ungdarella* sp. 1 (sensu Chuvashov, 1974, p. 31, pl. 19, figs 1-2); and ?*Epistacheoides? richi* G. Termier et al., 1977.

Remarks.– *Valuzieria* is similar to *Aoujgalia*, but with turri-form expansions, and some alignments of the lateral walls (pillars) of the chamberlets. It could appear as transitional between *Aoujgalia* and *Asteroaoujgalia*; nevertheless, after a revision of the type locality, in Montagne Noire (Pille, 2008), this character appears very discrete and cannot characterize a different genus.

Mametella is only more regularly-chambered than *Aoujgalia*. The species are valid, but both genera are supposed synonyms (with *A. regularis* G. Termier et al., 1977 as a transitional form; see Pl. 11, Figs 6, 8-9).

Occurrence.– ?Late Tournaisian-Early Viséan of Siberia (Ivanova & Bogush, 1992, tab. 1 p. 241; not illustrated). ?Late Tournaisian of British Columbia (Mamet et al., 1986). Middle Viséan-early Bashkirian. Palaeo-Tethys (Ireland, Morocco, Algeria, Libya, Spain, France, England, Belgium, Germany, Czech Republic, Donbass, Kazakhstan, western Siberia, Taimyr, Verkhoysansk area, Japan). Scarce in North America (Canadian Arctic, Alaska, American Cordillera, Tennessee, Idaho, Utah, Mississippi, New Mexico) and Australia. ?Late Carboniferous and Early Permian of Middle Urals (Chuvashov, 1974, as *Ungdarella* sp. 1, p. 31, pl. 19, figs 1-2). ?Permian of Canadian Arctic (Mamet, 1991, p. 379).

***Aoujgalia woodlandensis* sp. nov.**

(Pl. 8, Figs 1-15)

Etymology.– From Woodland Borehole, the type locality.

Type locality.– Woodland Borehole (Pennines, northern England).

Type level.– Early Serpukhovian (Crag Limestone).

Holotype.– Pl. 8, Fig. 13 (sample BGS-K-BU9437).

Diagnosis.– *Aoujgalia* with the external chambers well-calcified, irregularly quadratic, rarely fused due to the poor calcification of some pillars, grouped in grossly concentric series around the central part, in general weakly

Plate 7

1-2, *Donezella lutugini* Maslov, 1929. 1. Sample E1146 (northern Spain); collection Institut Français du Pétrole; x 29. 2. with *Praedonezella* cf. *cepsiformis* Kulik, 1973. Bashkirian of Taurus (Turkey), collection J. Sigal (sample 19579); x 47.

3, *Precorninella hieroglyphica* Vachard, 1991. Moniellos Formation (northern Spain). Early Devonian. Sample M342-4 bis; x 30.

4, *Pokorninella gracilis* Vachard in Meissami et al., 1978. Middle Viséan. Sample Iran 80 (Alborz, Iran). Sample RC7469. Photo 15110, x 75.

5, *Kamaenella* sp. Bifurcated test. Blue limestone. Late Viséan, Dchar Ait Abdallah Central Morocco. HGT. 4174; x 100.

6-7, 9, *Donezella lutugini* Maslov, 1929. 6. Sample E1221. Herrerruela de Castillera (northern Spain), Moscovian, maybe with a basal structure; x 27. 7. Northern Spain, sample PL 183-5, x 100. 9. Bashkirian of Taurus (Turkey), collection J. Sigal (sample 19579; see also here Pl. 18, fig. 6); x 47.

8, 10, *Alanyana* sp. Middle Permian of Himmetli (Taurus, Turkey), collection Sigal (sample 97380). 8; x 66, 10; x 47.

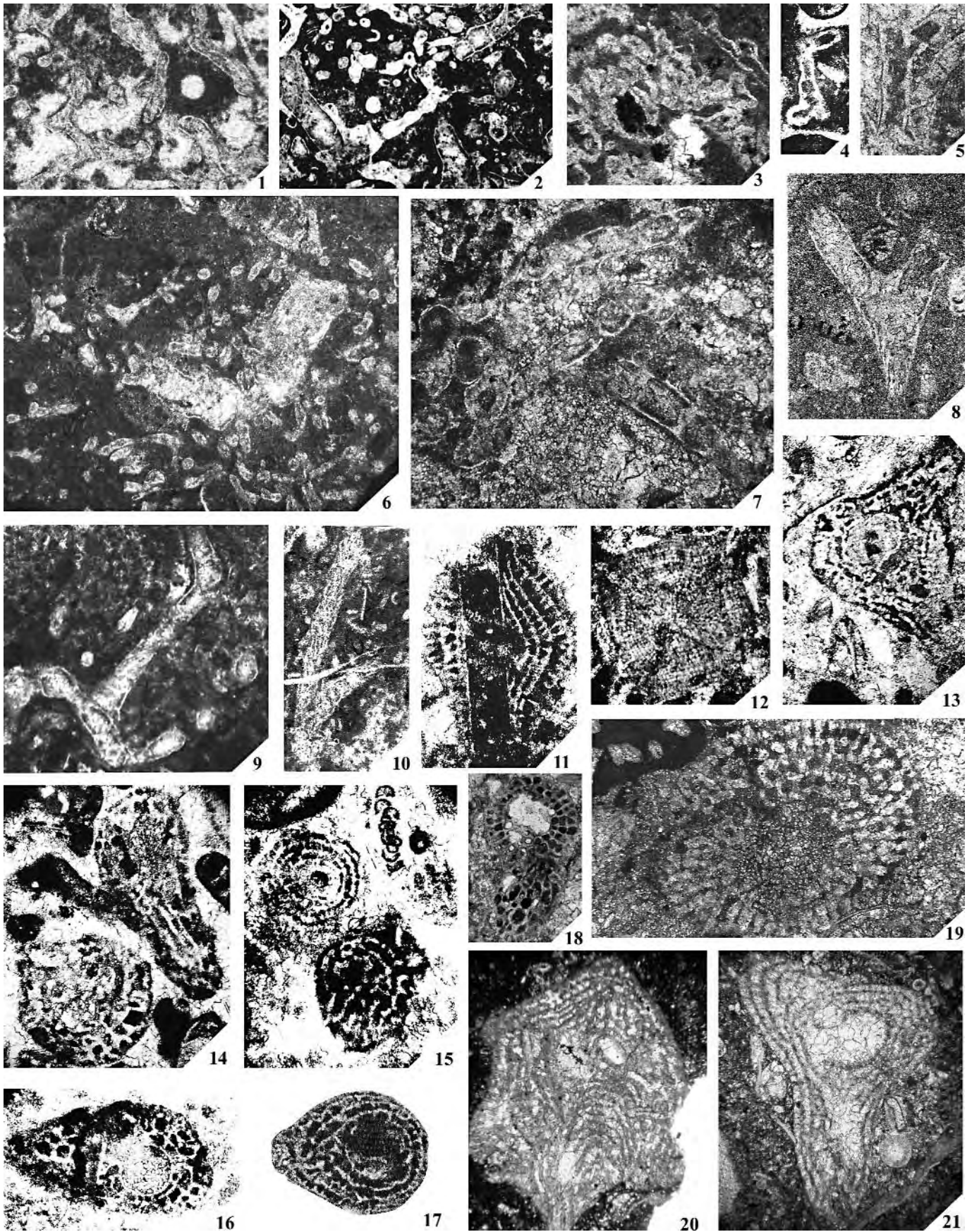
11-13, Transition between *Aoujgalia* and *Mametella* (evolutionary order: Fig. 13-Fig. 11-Fig. 12). 11. *Aoujgalia regularis* G. Termier et al., 1977. Visé 65 (Belgium). Late Viséan; Sample RC 14009, Photo 16420; x 50 [compare with *Fourstonella* sp. (sensu Brazhnikova et al., 1967, pl. 15, fig. 11)]. 12. *Aoujgalia* (= *Mametella*) *skimoensis* (Mamet & Rudloff, 1972). Anglesey (N. Wales, UK), late Viséan; Sample RC 11919, Photo 15083, Angl. 131; x 33. 13. *Aoujgalia variabilis* Termier & Termier, 1950. Anglesey (N. Wales, UK), Sample RC 11919, Photo 15106, Angl. 131; x 33.

14-18, *Aoujgalia richi* Mamet & Roux, 1978b. Mid-late Viséan. 14. Alborz (Iran; "Iran 80"), sample RC7469, Photo 15109; x 50. 15. Anglesey (N. Wales, UK), Late Viséan; sample RC11920, Photo not numbered; x 50. 16. Anglesey (N. Wales, UK), sample RC11920, Photo 15169; x 50. 17. According to Mamet & Roux, 1978b, paratype, pl. 5, fig. 2, St. Louis Limestone (U.S.A.); x 21. 18. Pc998, Bannagogle Quarry, late Brigantian, SE Ireland, x 40.

19, *Aoujgalia* cf. *variabilis* Termier & Termier 1950, Bashkirian, northern Spain, x 66.

20, *Aoujgalia variabilis* Termier & Termier 1950, Archerbeck Borehole, 1923'1", Archerbeck Beds, late Asbian, S Scotland, x 30.

21, *Aoujgalia regularis* G. Termier et al., 1977. Archerbeck Borehole, 2027'3", Archerbeck Beds, late Asbian, S Scotland, x 27.



calcified pillars and base of the pseudoconcentric rows, showing entirely irregular to digitated chambers.

Description.— Large *Aoujgalia* with length of mature specimens = 0.700-1.700 mm. Numbers of pseudo-concentric rows in mature specimens of 7 up to 20, around large central pivots, brachiopods spines, fenestellid bryozoans, crinoids, intraclasts, other *Aoujgalia*, recrystallized molluscs. Thin wall, 0.010-0.015 mm in thickness. Fused chambers reach up to 0.300 mm in length and 0.200 mm in height.

Type material.— more than 50 specimens (in varied sections).

Repository of the types.— British Geological Survey at Keyworth.

Remarks.— Differs from other species of *Aoujgalia* by the weak calcification of the central part and more irregular chambers, in some cases, with concentric rows almost absent.

Occurrence.— Early Serpukhovian of northern England, and early Brigantian in Southwest Spain (Pl. 8, Figs 14-15; see location of the sections in Cózar, 2004 and Stephenson *et al.*, 2010).

Genus *Asteroaoujgalia* Brenckle, 2004, emend. herein

Type species: *Asteroaoujgalia gibshmanae* Brenckle, 2004.

Emended diagnosis.— Aoujgaliidae with concentric rows of quadratic chamberlets and relatively common turriform expansions.

Composition.— Monospecific.

Remarks.— This genus questionably assigned to the “Aoujgaliaceae” by Brenckle (2004) is similar to *Aoujgalia* stage *Valuzieria* and differs only by the more numerous expansions, and the pillars less vertically aligned (nevertheless, intermediate cases exist: see e.g., Brenckle 2004, pl. 8, fig. 5, left, bottom). It is relatively a homeomorph of *Iberiaella* Racz, 1984 as emended here, it differs by the roughly arranged rows of chamberlets.

Occurrence.— Late Viséan of Tarim (China) and “Ser-

pukhovian” (but most probably late Viséan also) of Precaspian basin (Kazakhstan) (Brenckle, 2004). Late Brigantian of Boulonnais northern France (D.V. unpublished data).

Genus *Costacheoides* gen. nov.

(Pl. 9, Figs 6-15, ?16)

Type species: *Stacheoides cannindahensis* Mamet & Roux, 1983.

Etymology.— From *Stacheoides*, and *costa*, chop in Latin. Masculine.

Synonymy.— *Stacheoides* (part.); “*Stacheoides*” (*sensu* Cózar, 2005, fig. 6.9).

Diagnosis.— Test attached. More or less concentric rows of chambers, locally arranged in parallel, erect series (= towers). Chambers semi-ovoid to circular in section. Wall hyaline yellowish calcitic, fibrous. Wall sporadically perforated. Apertures of the chambers slightly excentric.

Composition.— Monospecific. However some other specimens show more elongated chambers (*Costacheoides* sp. 1, Pl. 9, Figs 10-15), and could represent a different species.

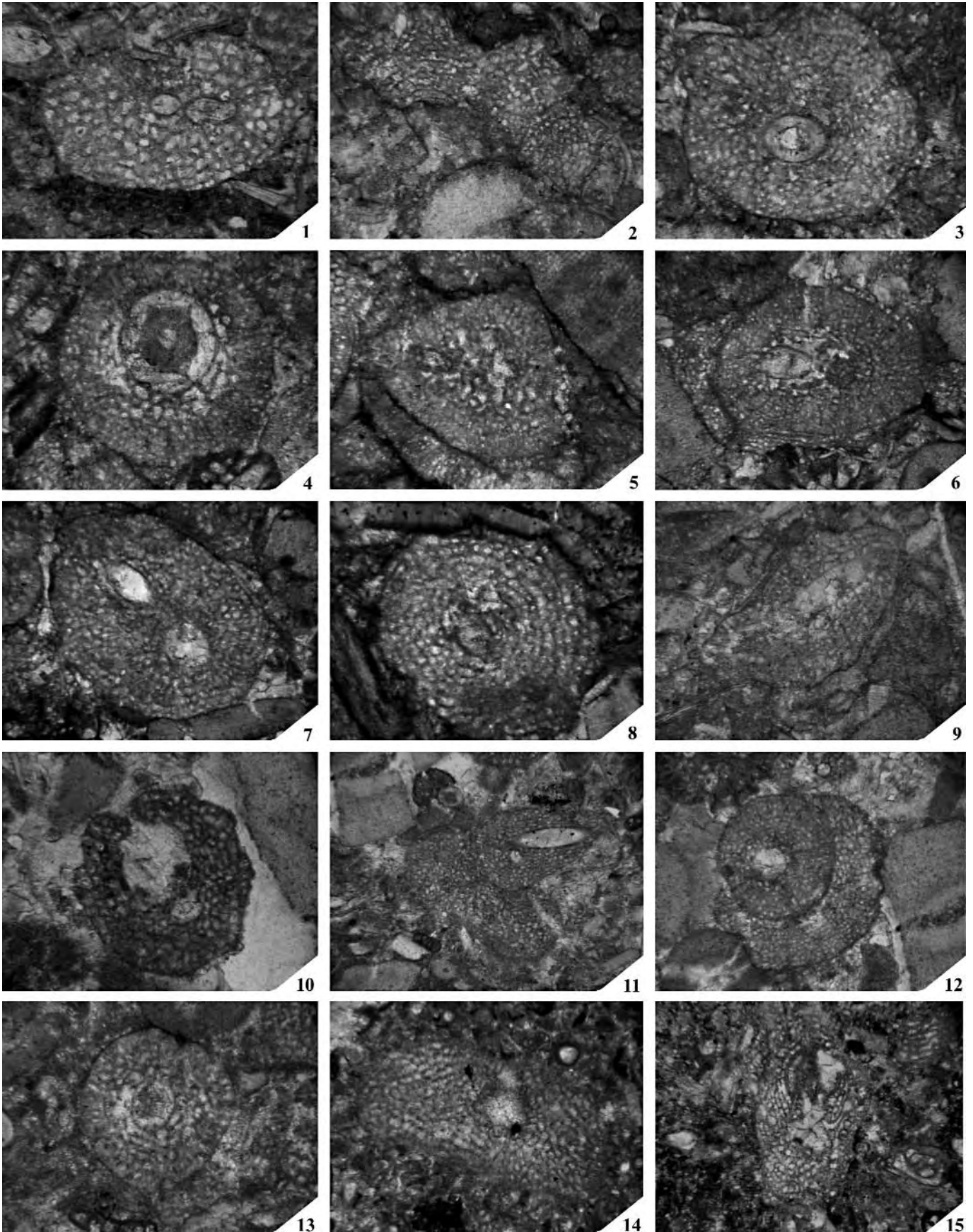
Comparison.— Differs from *Stacheoides* by the towers, location of apertures and the irregular shape of the chambers, larger size of chambers, from *Pseudostacheoides* by the chambers better individualized; from *Asphaltinella* by the more complex (plurilaminar) towers and the more concentrically arranged prostrate series of chambers, and *Pokorninella* by tower and no erect tubes.

Remarks.— As *Pseudostacheoides*, *Costacheoides* gen. nov. appears as a very primitive Aoujgaliida because of the mode of formation of the chamberlets.

Occurrence.— Livian-early Asbian of Queensland (Australia). Brigantian-Early Serpukhovian from southern Spain

Plate 8

1-15, *Aoujgalia woodlandensis* sp. nov. 1-8. BGS-K-BU9446, Shelly Lst. Above Great Lst., 9-13. BGS-K-BU9437, Crag Lst., Woodland Borehole, Early Serpukhovian, N. England. 1. x 64. 2. x 40. 3. x 50. 4. x 50. 5. x 40. 6. x 30. 7. x 30. 8. x 64. 9. x 30. 10. x 50. 11. x 25. 12. x 30. 13. x 35. 14. Pc1829, Fuenteobejuna, early Brigantian, SW Spain. x 30. 15. Pc722, El Collado, early Brigantian, SW Spain. x 35.



(Guadiato area), England, Scotland and Algeria (Béchar basin). Brigantian of eastern Morocco (Vachard & Berkli, 1992) and South China (Vachard *et al.*, 1991).

Genus *Epistacheoides* Petryk & Mamet, 1972

(Pl. 9, Figs 17-23)

Type species: *Epistacheoides nephroformis* Petryk & Mamet, 1972.

Synonymy.— *Ungdarella* (*part.*), *Petschoria* (*part.*; *sensu* Chanton, 1965), *Stacheoides* (*part.*), *Pseudokomia* (*part.*; *sensu* Bless *et al.*, 1976, pl. 12, fig. 20); *Dromastacheoides* (*part.* the type species *D. wilsoni* Perret & Vachard, 1977); ?*Pseudostacheoides* (*part.*; *sensu* Mamet, 1994, pl. 1, figs 23-24 or *Peristacheia*).

Diagnosis.— Encrusting Aoujgaliina, irregular in shape, with two types of laminae, irregular and sarmentoid in the centre, radial and closely arranged at the periphery and forming a more compact wall. Labyrinthic chamberlets in the centre, tubular chamberlets at the outer part, each one with an aperture on the periphery. Wall yellowish, hyaline, granular.

Composition.— *Epistacheoides nephroformis* Petryk & Mamet, 1972; *E. connorensis* Mamet & Rudloff, 1972; *E. taimyricus* Ivanova *in* Bogush *et al.*, 1990; and *Dromastacheoides wilsoni* Perret & Vachard, 1977.

Excluded species.— *Epistacheoides* (?) *richi* G. Termier *et al.*, 1977 (= ?*Aoujgalia*); *E. chantoni* (*sic*; *chantonae* is the correct spelling) Mamet & Roux, 1977 (= *Roquesselsia*); *E. nephroformis* (*sensu* Skompski, 1996, p. 216, pl. 3, figs 1-3) (= *Roquesselsia*); *E. sp.* 1 (*sensu* Brenckle *et al.*, 1982, p. 61, pl. 7, figs 11-12, 14 = *Aoujgalia* *ex gr. topi*); *Epistacheoides? peratrovichensis* (Mamet & Pinard, 1985) *sensu* Mamet, 2006.

Remarks.— Some ecotypic stages of *Roquesselsia* displays convergences with typical *Epistacheoides*, but it differs by less calcified central labyrinthic chamberlets, and less regularly arranged external radial chamberlets.

Occurrence.— Middle Viséan to Bashkirian; cosmopolitan (Mamet, 2006).

Genus *Pseudostacheoides* Petryk & Mamet, 1972

(Pl. 10, Figs 1-4, 6-7)

Type species: *Pseudostacheoides loomisi* Petryk & Mamet, 1972.

Diagnosis.— Test attached, irregular, with roughly concentric rows of laminae, divided by pseudosepta poorly defined, low and hemispherical chambers. Wall calcitic, yellowish, granular.

Composition.— *Pseudostacheoides loomisi* Petryk & Mamet, 1972; *P. loomisi* (*sensu* Skompski, 1986, p. 269, pl. 13, figs 1-4); *P. loomisi* (*sensu* Sebbar & Mamet, 1996, pl. 3, fig. 8); *P. sp.* (*sensu* Vieslet, 1983, pl. 5, fig. 5); *P. sp.* (*sensu* Vieslet, 1983, pl. 5, fig. 7).

Remarks.— *Pseudostacheoides* *sp.* (*sensu* Mamet, 1994, pl. 1, figs 23-24) rather corresponds to *Epistacheoides* or a primitive *Aoujgalia*. These transitional specimens remain rare and no relationship might be accurately proposed.

Plate 9

1-5. *Aoujgalia* (= *Valuzieria*) *sescenti* G. Termier *et al.*, 1977. 1. Pc2393, Tizra 2, early Brigantian, Central Morocco, x 60. 2. Pc3290, Mouarhaz, late Brigantian, Central Morocco, x 69. 3. Pc3290, Mouarhaz, late Brigantian, Central Morocco, x 34.5. 4. Pc2392, Tizra 2, early Brigantian, Central Morocco, x 30. 5. Pc3290, Mouarhaz, late Brigantian, Central Morocco, x 34.5.

6-9. *Costacheoides cannindahensis* (Mamet & Roux, 1983). 6. Goulub (central Morocco), Early/middle Viséan, Sample HGT. M53; x 66. 7. Dinant 42/38 (Belgium), Early Viséan, Sample RC5566, Photo RC6818; x 50. 8. BGS-E-PS4224, Spilmersford Borehole, Middle Longcraig, early Brigantian?, Midland Valley, Scotland, x 60. 9. Pc722, El Collado, early Brigantian, SW Spain, x 125.

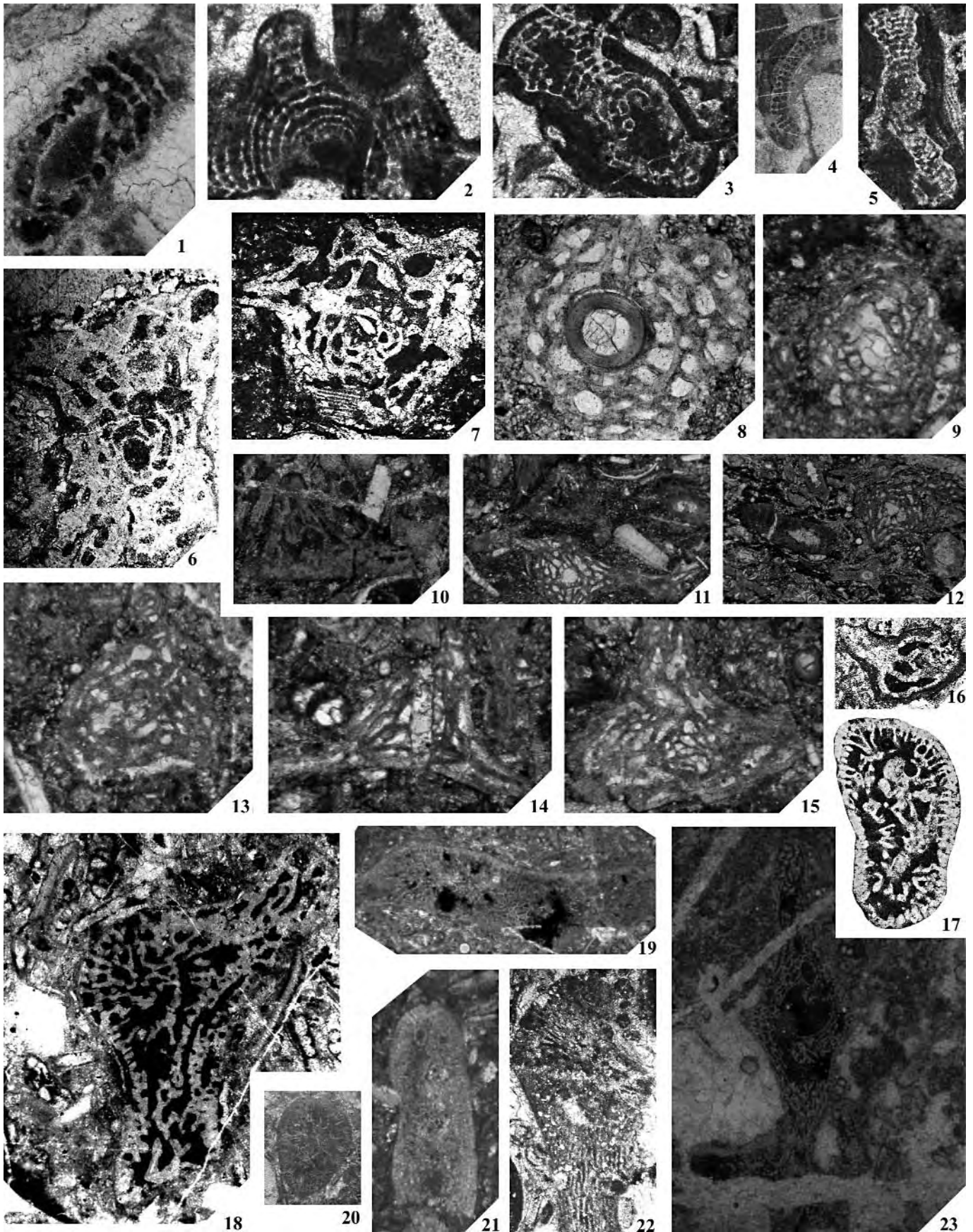
10-15. *Costacheoides* *sp.* 1. 10. Pc323, Urquilla Baja, Serpukhovian, SW Spain, x 34.5. 11. BGS-K-Rookhope Borehole, 361', Five Yard Limestone, late Brigantian, x 17.25. 12. BGS-K-AH53, Allenheads Borehole, Smiddy Lst., early Brigantian, N England, x 17.25. 13. Pc722, El Collado, early Brigantian, SW Spain, x 77. 14. Pc722, El Collado, early Brigantian, SW Spain, x 77. 15. Pc722, El Collado, early Brigantian, SW Spain, x 59.

16. Transition between Claracrustinae and *Costacheoides* n. gen. Latest Tournaian. Martinrive 6 (Belgium). Sample Noël 836. Photo RC 14455; x 50.

17-18. *Epistacheoides connorensis* Mamet & Rudloff, 1972. 17. Transverse section (*sensu* Mamet and Roux, 1978, pl. 6, fig. 9). Bangor Limestone (U.S.A.), Early Serpukhovian; x 42. 18. Longitudinal section. Sample 3976. Viséan/Serpukhovian boundary, South China; x 29.

19-22. *Epistacheoides nephroformis* Petryk & Mamet, 1972. 19. Pc1829, Fuenteobjuna, early Brigantian, SW Spain, x 40. 20. Pc888, Clogrenan Quarry, early Brigantian, SE Ireland, x 17.25. 21. Pc714, El Collado section, early Brigantian, SW Spain, x 48. 22. Dchar Ait Abdallah (central Morocco), sample 13.9.69 (collection Termier), late Viséan; x 33.

23. *Epistacheoides* aff. *nephroformis* Petryk & Mamet, 1972. Pc525. Peñarroya 2, early Brigantian, SW Spain, x 9.



Occurrence.— Late Tournaisian-late Serpukhovian, probably cosmopolitan. Rare in Bashkirian and early Moscovian? The misinterpreted Permian forms are more probably *Komia?* and/or *Claracrusta*.

Genus *Roquesselsia* G. Termier et al., 1977

(Figs 5.5-5.6; Pl. 10, Figs 5, 8-9, ?19-21)

Type species: *Roquesselsia radians* G. Termier, Termier & Vachard, 1977.

Synonymy.— *Epistacheoides* Petryk & Mamet, 1972 (*part.*); *Anthraco-porellopsis* Maslov, 1956a (*part.*); *Anthraco-porella* Pia, 1920 (*part.*).

Diagnosis.— Test attached. External shape relatively regular varying from foot-shaped to cross-shaped. Inner cavity narrow and generally not calcified surrounded by radial skeletal elements regular in shape and organized in one to three rows. In tangential longitudinal section, these elements appear parallel and can be confused with a medullar zone (“hypothallus” *auct.*). The lateral chamberlets between these radial elements are narrow, and eventually might be confused with laterals of green algae (e.g., *Anthraco-porella*). Wall yellowish, hyaline, granular.

Composition.— *Roquesselsia radians* G. Termier, Termier & Vachard, 1977 (= *E. chantoni* (*sic*) Mamet & Roux, 1977); *Anthraco-porella baschirica* Kulik, 1973; *Anthraco-porella insolita* Ivanova, 1988; *E. nephroformis sensu* Skompski, 1996 (p. 216, pl. 3, figs 1-3).

Remarks.— *Roquesselsia* exhibits four morphotypes: 1) the typical foot-shaped elongate sections (e.g., Pille, 2008, pl. 27, fig. 16); 2) a form more or less similar to *Epistacheoides*; 3) the “*Anthraco-porella*” of Kulik, 1973 and Ivanova, 1988; 4) the false *Anthraco-porellopsis machaevii* of Skompski (1996), which differs from *Anthraco-porellopsis machaevii* by a weaker to absent internal septation, and from *Anthraco-porella insolita* Ivanova, 1988 by a shorter length (1.300-2.000 mm versus 3.000-3.600 mm) for a similar outer diameter (see also Sánchez-Chico et al., 1995, pl. 3, fig. 9).

Occurrence.— Asbian of Tarim, Spain, Poland, Morocco and Algeria. Ladeininsky-Kurmakovsky of Urals. Rare in the Serpukhovian of Algeria. Late Asbian-Brigantian of Ireland. Brigantian-early Serpukhovian of southwestern

Spain. Late Viséan and Serpukhovian of southern Urals. Latest Asbian-early Brigantian of northern England. Latest Asbian-Brigantian of Montagne Noire.

Genus *Sinustacheoides* G. Termier et al., 1977

(Pl. 10, Figs 10-14, ?15)

Type species: *Stacheoides meandriiformis* Mamet & Rudloff, 1972.

Synonymy.— *Stacheoides* (*part.*; e.g. Groves, 1986; Mamet, 1991; Brenckle & Milkina, 2003; Brenckle et al., 2009).

Diagnosis.— Test attached, digitate to irregular. Sarmentoid (labyrinthic) network of incompletely calcified chamberlets, with total absence of radial arrangement. Wall hyaline yellowish, granular.

Composition.— *Stacheoides meandriiformis*; *Sinustacheoides* sp. (*sensu* Vachard & Montenat, 1981, p. 62-

Plate 10

1-4, *Pseudostacheoides loomisi* Petryk & Mamet, 1972. 1. Pc722, El Collado section, early Brigantian, SW Spain, x 77. 2. Pc722, El Collado section, early Brigantian, SW Spain, x 48. 3. Pc1173, Ballyadams Quarry, late Asbian, SE Ireland, x 17.5. 4. Pc-COR/8d, Cornuda Section, late Serpukhovian, x 14.5.

5, 8-9, *Roquesselsia radians* G. Termier et al., 1977. 5. Pc1671, Durrow 2 Borehole, early Asbian, SE Ireland, x 48. 9. Pc521, Peñarroya 2, early Brigantian, SW Spain, x 40. 8. Pc1698, Tankardstown Borehole, early Asbian, SE Ireland, x 59.

6-7, *Pseudostacheoides* cf. *loomisi* Petryk & Mamet, 1972. 6. Oulmès area (Central Morocco). Sample 293.1. Late Viséan; x 66. 7. Libya, Serpukhovian, Sample SM 894; x 29.

10-11, *Sinustacheoides* sp. 1. 10. Pc720, El Collado section, early Brigantian, SW Spain, x 16.5. 11. Pc1829, Fuenteobejuna, early Brigantian, SW Spain, x 59.

12-13, *Sinustacheoides meandriiformis* (Mamet & Rudloff, 1972). 12. Pc-COR/8c, Cornuda Section, late Serpukhovian, x 40. 13. Pc1300, Dunamase Quarry, late Brigantian, SE Ireland, x 34.5.

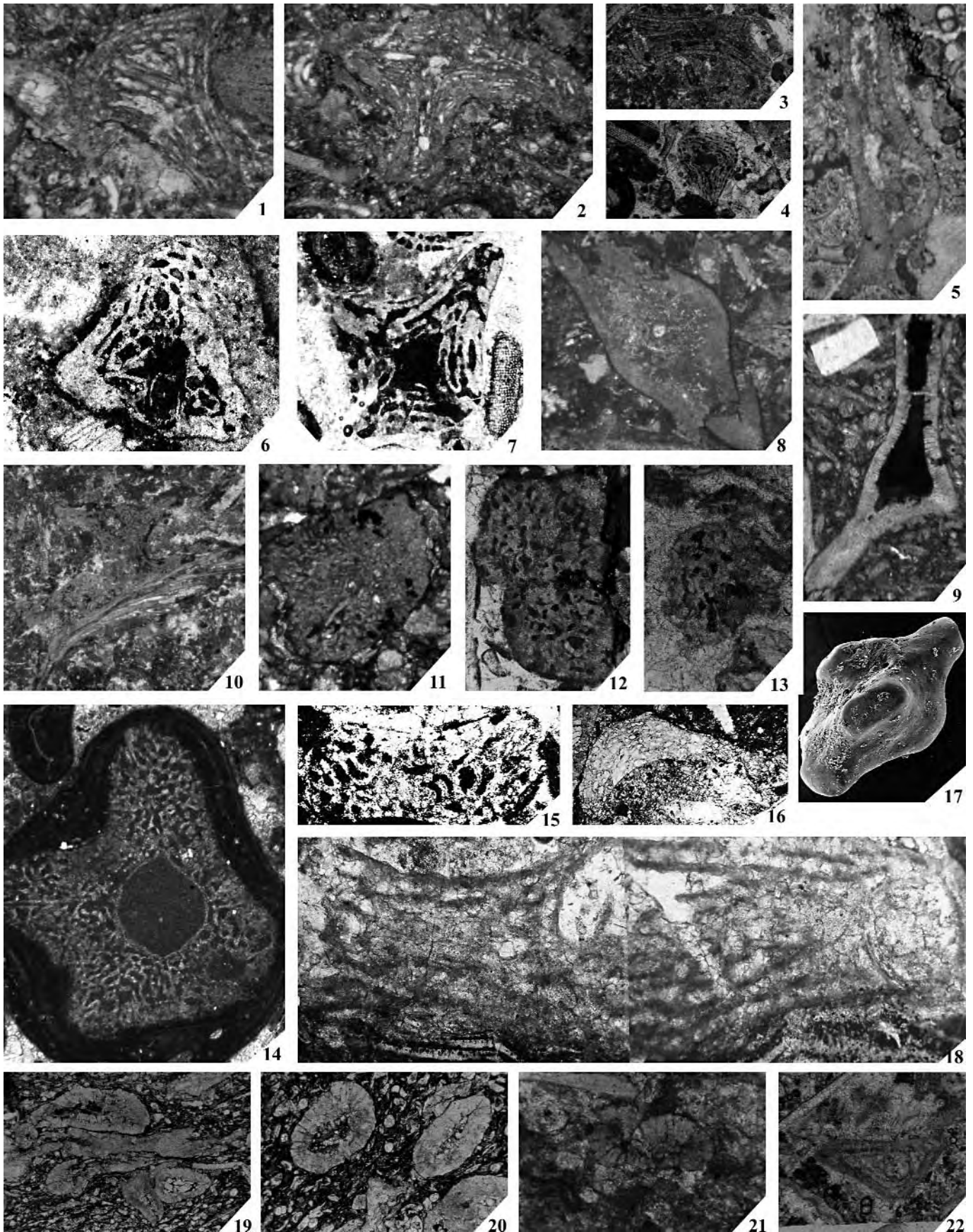
14, *Sinustacheoides* sp. Late Asbian, central Morocco. Sample Huvelin 9.1290/1; x 33.

15. Transition between *Sinustacheoides* and a primitive *Aoujgalia* (e.g., *A. cf. topi* Vachard, 1980), because the outer row of subquadratic chamberlets; see also *Aoujgalia richi* (*sensu* Sebbar, 1998, pl. 2, fig. 7). Mid Viséan, Belgium, Photo 10756 (collection Conil); x 50.

16-17, *Stacheoides* spp. 16. Angl 9513/10 (Anglesey, N. Wales, UK, late Viséan). Sample RC 13968 (see Conil et al., 1980). Photo 15121; x 50. 17. Early Brigantian. Japhet (Montagne Noire, southern France), Sample DV164-0; x 30.

18, 22, *Stacheoides* (= *Chantonia*) *maslovi* (Chanton, 1965). 18. Topotype of “*Ungdarella*” *maslovi*, Sample PAR 399-347. Central Morocco; late Viséan; x 66. 22. Pc1201, Ballyadams Quarry, late Asbian, SE Ireland, x 17.25.

19-21, *Roquesselsia?* sp. 19. Pc1115, Ballyadams Quarry, late Asbian, SE Ireland x 17.25. 20. Pc115, Ballyadams Quarry, late Asbian, SE Ireland, x 34.5. 21. BGS-K-BS91, Back Scar Borehole, Great Scar, late Asbian, N England, x 34.5.



63, pl. 10, fig. 14); *Stacheoides meandriformis* (sensu Ivanova & Bogush, 1988, pl. 17, figs 11-12); *S. meandriformis* (sensu Bogush et al., 1990, pl. 28, figs 7-8); and *Sinustacheoides* sp. 1 herein (Pl. 10, Figs 10-11).

Occurrence.– Viséan of Morocco, Spain and Northern America (Groves, 1986). Tulskey of Kazakhstan. Latest Chesterian-Morrowan-Atokan of Idaho (Groves, 1984, text-figs 6-7; 1986, text-figs 3-4). Latest Viséan of Urals (Bogush et al., 1990) and Alaska (Armstrong & Mamet, 1974). Middle Pennsylvanian of Yukon and Canadian Arctic. Early Permian of Canadian Arctic (Mamet et al., 1987). Bashkirian-Sakmarian of Bolivia (Mamet, 1994). Moscovian of Brasil (D.V. unpublished data).

Genus *Stacheoides* Cummings, 1955b

(Pl. 10, Figs 16-18, 22, Pl. 11, Figs 1-11, ?13)

Type species: *Stacheia polytrematoides* Brady, 1876.

Synonymy.– *Chantonia* G. Termier et al., 1977; ?*Stacheoidella* Mamet & Roux in Mamet et al., 1987; and ?*Ungdarella* (part.).

Diagnosis.– Tests attached, with roughly concentric rows of irregular laminae whose curvatures limit chambers, and external protuberances. Chambers irregular more or less ellipsoidal in shape. Wall calcitic, yellowish.

Composition.– *Stacheia polytrematoides* Brady, 1876; *Stacheia congesta* Brady, 1876; *S. papillata* Cummings, 1955b; *S. tenuis* Petryk & Mamet, 1972; *Ungdarella maslovi* Chanton, 1965 (type species of *Chantonia*); *Stacheoides? spissa* Petryk & Mamet, 1972 (type species of *Stacheoidella*); *Stacheia cicatrix* Conkin, 1961; *S. neopropoides* Conkin, 1961; and *S. trepeilopsiformis* Conkin, 1961.

Excluded species.– *Stacheoides meandriformis* Mamet & Rudloff, 1972 (= *Sinustacheoides*); *S. cannindahensis* Mamet & Roux, 1983 (= *Costacheoides*).

Remarks.– *Chantonia* is considered here as a species of *Stacheoides* with more quadratic chamberlets. *Stacheoidella* is re-interpreted as a taphotaxon of *Stacheoides*. Indeed, a skeletal organization similar to *Stacheoides* is observable but it is followed by an undifferentiated crust of yellow calcite supposed diagenetically constituted.

Occurrence.– ?Famennian of Verkhoyansk area (Ivanova & Bogush, 1992, tab. 1, p. 241; not illustrated). Late Tournaisian-Late Permian; probably cosmopolitan (Perret & Vachard, 1977) during the Carboniferous, rarely documented in the Permian: Afghanistan, Sumatra, Zagros (Iran) and Hazro (Turkey) (Gaillet, 2006).

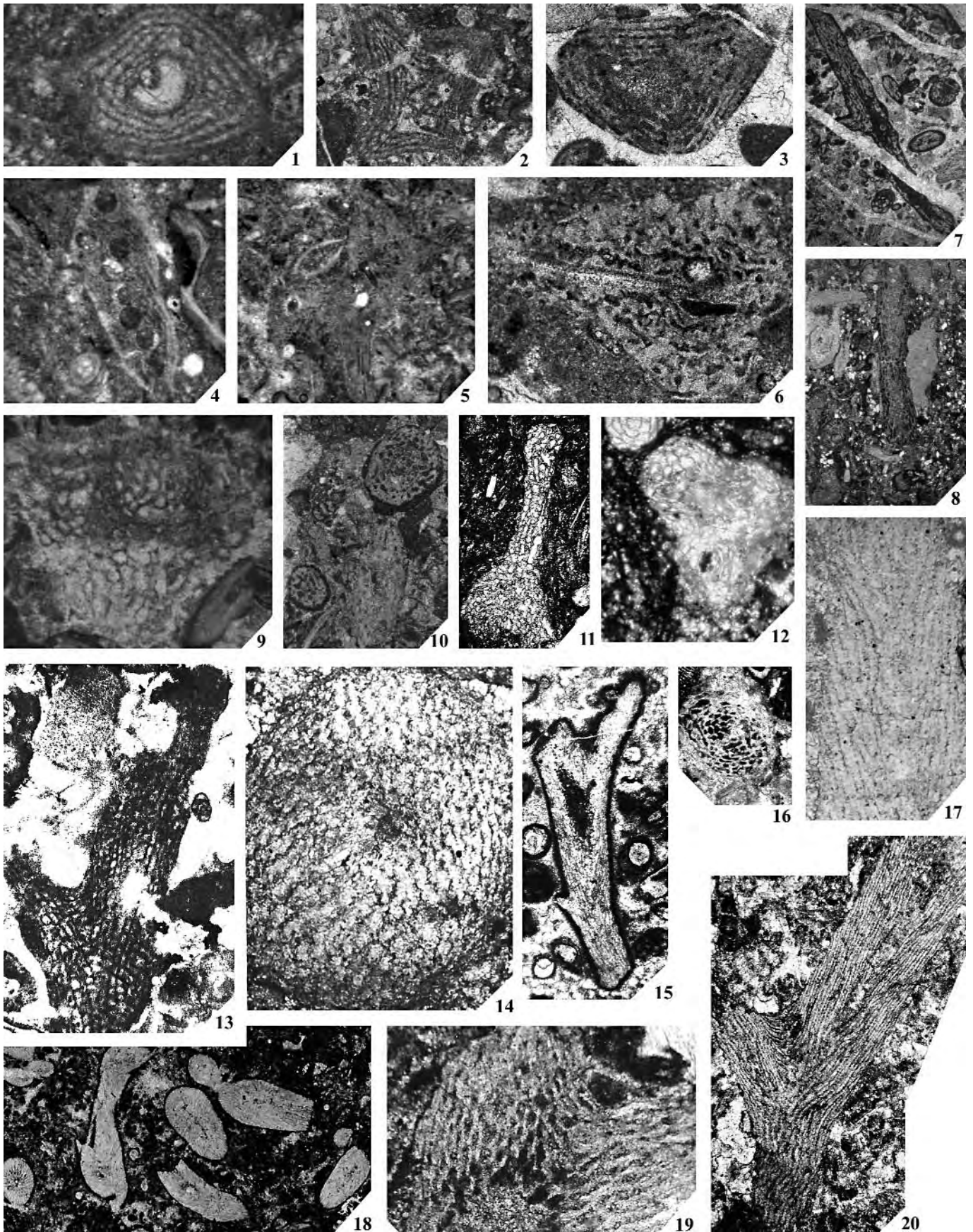
Family UNGDARELLIDAE Maslov, 1956b

Diagnosis.– Aoujgaliida showing an attached to arborescent shape, cylindrical and branched, and embracing growth of the chamber rows. Sometimes, there is an initial stage, attached, similar to *Stacheoides*, followed by an erect stage (see Madi et al., 1996, pl. 22, fig. 5). The endoskeleton is composed of conical to paraboloid concentric laminae growing upward continuous rows of chambers, and perforated pillars, transverse, perpendicular to each lamina, acting as communications between the chambers (see Vachard, 1980, fig. 74). Wall calcitic, yellowish, and hyaline.

Composition.– Six genera: *Ungdarella* Maslov, 1956a (= *Pseudoungdarella* Ivanova, 1999 = *Ungdarelloides* Chuvashov & Anfimov, 2007 = *Urtasimella* Chuvashov & Anfimov, 2007 = *Suundukella* Chuvashov & Anfimov, 2007);

Plate 11

- 1-3**, *Stacheoides* (= *Chantonia*) *maslovi* (Chanton, 1965). 1. Pc1597, Doonaveeragh, Bricklieve Mts., late Asbian, NE Ireland, x 59. 2. BGS-K-Rookhope Borehole, 1152' depth, Melmerby Scar 2 Lst., late Asbian x 17.25. 3. Pc-COR/3a, Cornuda Section, early Serpukhovian, 40.
4-5, 11, *Stacheoides tenuis* Petryk & Mamet, 1972. 4. Note the 8 holes of the bacillar substrate. Pc1560, Carrane Hill I, late Asbian, NW Ireland, x 102. 5. Pc1474, Kesh Corann, Bricklieve Mts., late Asbian, NW Ireland, x 38. 11. Anglesey (N. Wales, UK), sample RC13968, photo 15120, late Viséan; x 50.
6, *Stacheoides spissa* Petryk and Mamet, 1972. Pc2324, Idmarrach 2, Adarouch, early Serpukhovian, Central Morocco, x 60.
7-10, *Stacheoides polytrematoides* (Brady, 1876). 7. Pc819, Peñarroya 2, late Asbian, SW Spain. x 9. 10. Pc823, Peñarroya 2, late Asbian, SW Spain, x 18. 9. Pc1812, Fuenteobejuna, early Asbian, SW Spain, x 102. 8. Pc821, Peñarroya 2, late Asbian, SW Spain, x 9.
12, *Ungdarella* sp., Archerbeck Borehole, 1921'2", Archerbeck Beds, late Asbian, S Scotland, x 69.
13, Transition between *Stacheoides tenuis* and *Ungdarella uralica*, late Viséan of Anglesey (N. Wales, UK), sample 13268, photo 15160; x 29.
14-20, *Ungdarella uralica* Maslov, 1956a. 14. Recrystallized transverse section. Khwahan (North Afghanistan), sample 5Kh; Late Pennsylvanian; 97. 15. Lentilles de la route (Montagne Noire, southern France), sample DV293E, late Asbian; x 27. 16. Transverse section, sample 3972, Viséan/Serpukhovian boundary, South China; x 33. 17. Recrystallized longitudinal section. Khwahan (North Afghanistan), sample 5Kh; Late Pennsylvanian; x 66. 18. Numerous tests in a late Viséan lagoon, Vailhan (Montagne Noire, southern France), Early Brigantian, sample DV246F-0; x 13. 20. Typical specimen, sample 6/28 (collection Lys), x 40.



Cheggatella Poncet, 1989; *Foliophycus* Johnson, 1960; *Komia* Kordé, 1951 (= *Pseudokomia* Racz, 1964; = *Turkokia* Gaillot & Vachard *nom. invalid.*); *Ungdarellita* Mamet & Villa, 2004; and ?*Petschoria* Kordé, 1951 (*part.*).

Occurrence.– Late Asbian-Late Permian. The FAD is located at the base of the late Asbian (biozones Cfm6, Cf6γ or Cf6γ2, Vachard, 1989b; Gallagher, 1996; Gallagher & Somerville, 1997; Cózar & Somerville, 2004, text-fig. 12). Cosmopolitan up to the Early Permian; after that, Palaeo- and Neotethyan.

Genus *Ungdarella* Maslov, (1950) 1956a

(Figs 5.4, 6.1-6.9; Pl. 11, Figs 12, 13?, 14-20, Pl. 12, Figs 1-5)

Type species: *Ungdarella uralica* Maslov (1950) 1956a.

Synonymy.– *Pseudoungdarella* Ivanova, 1999; *Ungdarelloides* Chuvashov & Anfimov, 2007; *Urtasimella* Chuvashov & Anfimov, 2007; and *Suundukella* Chuvashov & Anfimov, 2007.

Diagnosis.– Test cylindrical and branched. Sometimes there is an initial stage, attached, similar to *Stacheoides*, followed by an erect stage (see Maslov, 1962; Madi *et al.*, 1996, pl. 22, fig. 5). The endoskeleton is composed by conical to paraboloid concentric laminae growing upward and perforated pillars perpendicular to each lamina (see Vachard, 1980, fig. 74). A medium perforation within the pillar acts as communication between the chamberlets (“cells” of the authors). Wall calcitic, yellowish, granular.

Composition.– *Ungdarella uralica* Maslov, 1956a [= ?*Ungdarelloides squalidus* Chuvashov & Anfimov, 2007 = ?*Urtasimella concentrica* Chuvashov & Anfimov, 2007 = *Suundukella mirabilis* Chuvashov & Anfimov, 2007 = *Pseudoungdarella linearis* Ivanova, 1999 (see also Ivanova, 2008, pl. 26, fig. 6, pl. 7, fig. 10)]; ?*Ungdarella conservata* Kordé, 1951; ? *U. deceanglorum* Elliott, 1970; ?*U. gracilissima* Kulik, 1973; ?*U. kagozi* Güvenç, 1966c; ?*U. michaelsensis* Chuvashov & Anfimov, 2007; ?*U. parallela* Kulik, 1973; ?*U. stellata* Kordé, 1965.

Excluded species.– *Ungdarella americana* Toomey & Johnson, 1968 (= *Komia*); *U. peratrovichensis* Mamet & Rudloff, 1972 (= *Ungdarellina*).

Remarks.– See discussion on the year of description of this genus in Mamet & Rudloff, 1972 (p. 90-91), Mamet & Roux (1983, p. 86) or Mamet (2002, p. 500). *Ungdarella* is generally interpreted as a red alga, with a hypothallus and a perithallus (Mamet, 1991), but this interpretation does not correspond with our observations (see also Cózar & Somerville, 2005b, p. 74). The skeletal network of *Ungdarella* is generally sharply recrystallized, but when it is well preserved, it appears as perforated and sometimes filled by micrite (see Bensaid *et al.*, 1979, pl. 16, figs 4, 6; Vachard & Fadli, 1991, pl. 1, fig. 15; Sebbar & Mamet, 1996, pl. 3, fig. 9; Madi *et al.*, 1996, pl. 22, fig. 5), and differs from the completely closed cells of red algae. Systems of attachment were illustrated by Nguyen Duc Tien (1979, pl. 28, fig. 6; 1989, pl. 34, fig. 5); Madi *et al.* (1996, pl. 22, fig. 5); Proust *et al.* (1996, pl. 1, fig. 2, pl. 2, figs 10-11); Vachard & Krainer (2001, pl. 5, fig. 7); Flügel (2004, pl. 108, fig. 8); and Karim *et al.* (2005, fig. 3L). A specimen of *Ungdarella* directly attached to a coral was illustrated by Said (2005, fig. X. 1. 11). According to Vachard & Tahiri (1991), *Stacheoides tenuis* might be the ancestor of *Ungdarella* (and see here Pl. 11, fig. 13).

Due to the strong recrystallization, the representatives of *Ungdarella* can be interpreted as generically different (see *Ungdarelloides*, *Urtasimella* and *Suundukella*, recently created by Chuvashov & Anfimov, 2007). However, all these forms are considered by us as different diagenetic stages of *Ungdarella*, and all probably of *U. uralica*.

Occurrence.– Late Viséan (late Asbian) to latest Permian (Changhsingian). The FAD is located at the base of the late Asbian (biozones Cfm6, Cf6γ or Cf6γ1, Vachard, 1989b; Gallagher, 1996; Gallagher & Somerville, 1997; Cózar & Somerville, 2004, text-fig. 12; 2005b, text-fig. 3; 2005c, text-fig. 3). The references in the Middle Viséan of Urals (Bogush *et al.*, 1990) are probably due to misinterpreted *Stacheoides*. Cosmopolitan up to the Early Permian; after that, Palaeo- and Neo-Tethyan.

Genus *Cheggatella* Poncet, 1989

Type species: *Cheggatella denticula* Poncet, 1989.

Diagnosis.– Ungdarellidae with the central row (“medullar zone” of Poncet) composed of irregularly aligned chamberlets.

Composition.— Monospecific.

Remarks.— This taxon need revision, because its unique illustrated material is difficult to distinguish from *Ungdarella* or some paratypes of *Foliophycus*.

Occurrence.— Apparently endemic of the late Bashkirian of Béchar Basin (Algeria).

Genus *Foliophycus* Johnson, 1960

(Figs 14.4-14.5, Pl. 13, Fig. 10)

Type species: *Foliophycus llanoensis* Johnson, 1960.

Synonymy.— ?*Dromastacheoides* Vachard in Perret & Vachard, 1977 *sensu* Vachard, 1980 (*part.*).

Diagnosis.— Test erect, cylindrical, often bifurcated. Wall yellowish. Internal chamber rows typical of the ungdarellids, clinogonally arranged from each side of the symmetry plane. External chamber rows as in *Komia* with concentric laminae and subquadratic chambers. Wall calcitic, yellowish, and hyaline.

Composition.— Monospecific (see also *Iberiella* emend., below).

Remarks.— The type material of Johnson is affected by numerous truncation facets, but the specimen figured by Mamet & Pinard (1985, pl. 3, fig. 1, under the name *Ungdarella uralica*) or the “*Komia abundans*” misinterpreted by Fontaine & Vachard (1979, text-fig. 8, p. 22) show the complete structure. It differs from *Ungdarella* or *Komia* by the composition of the skeletal elements, from *Pseudokomia* Racz, 1964 or *Cheggatella* Poncet, 1989, by frequent bifurcations and more regular cortical and medullar zone, and from *Fourstonella* Cummings, 1955a emend., by the protuberances and the type of skeleton. *Dromastacheoides sensu stricto*, assigned herein to *Epistacheoides*, might be also the ancestor of *Foliophycus* due to its elongate and bifurcated test.

Occurrence.— Late Atokan (= Podolskian) of west Texas. ?Late Serpukhovian of southern France. Late Bashkirian of northern Thailand. ?Late Bashkirian-early Moscovian of Yunnan under the name of *Komia* (see below) (Nakazawa *et al.*, 2009).

Genus *Komia* Kordé, 1951

(Fig. 8.18; Pl. 13, Fig. 9)

Type species: *Komia abundans* Kordé, 1951.

Synonymy.— *Ungdarella* (*part.*); ?*Pseudokomia* Racz, 1964; ?*Turkomia* Gaillot, 2006 (*nom. nud.*).

Diagnosis.— Test cylindrical and bifurcated. The endoskeleton is composed of continuous, concentric rows of subquadratic cells, more or less arranged in concentric laminae growing downward or laterally. Wall calcitic, yellowish, granular.

Composition.— *Komia abundans* Kordé, 1951; *Ungdarella americana* Toomey & Johnson, 1968 emend. Wilson, 1969; *Komia eganensis* Wilson, Waines & Coogan, 1963; *Pseudokomia cansecoensis* Racz, 1964; and ?*Komia erki* Güvenç, 1966c.

Remarks.— *Pseudokomia* seems to be poorly established, since pseudokomia-like individuals are frequent in our populations of Spain, Mexico and New Mexico.

According to Mamet & Pinard (1985), only one *Pseudokomia* was found in Arctic Canada, and the illustration of Zagorodnyuk (1979, pl. 3, fig. 4) shows an upper section typically *Komia* in shape, and a lower one more displays an aspect of *Pseudokomia*. Moreover, the relations of *Pseudokomia sensu stricto*, with *Petschoria* and *Foliophycus*, are difficult to establish. *Turkomia*, created with *Komia erki* as type species, is a *nomen nudum* introduced in a Ph.D.; moreover, if the species is clearly established, the Permian *Komia* are very similar to the Moscovian ones and can constitute some floatstones (Kolodka *et al.*, unpublished data), and a new genus might only be justified by the great difference of age between Middle Pennsylvanian (true *Komia*) and Middle Permian (*Komia?* *erki*).

Occurrence.— Apparently limited to the Moscovian and possibly only late Moscovian according to our observations. The long-ranging distribution proposed by Mamet (1991) is apparently due to the inclusion of other aoujgaliid genera. Palaeo-Tethyan (from Spain to ?Yunnan and Vietnam; see Nakazawa *et al.*, 2009 and D.V. unpublished data), Urals and North America (as far as northern Mexico). Upper beds of Atokan of Idaho (Groves, 1984). Possible Lazarus effect in the Early Permian of Alanya area,

Turkey (Güvenç, 1966c) and Late Midian to Changhsingian of Hazro (Turkey) and Kuh-e Gakhum (Zagros, Iran), and Lopingian of Kuh-e Surmeh (Zagros, Iran) (Gaillot, 2006; Kolodka *et al.*, unpublished data).

Genus *Ungdarellita* Mamet & Villa, 2004

Type species: *Ungdarellita articulata* Mamet & Villa, 2004

Diagnosis.– Segmented *Ungdarella*.

Remarks.– This taxon is endemic to its type level and its type locality, because although we have seen millions of ungdarellids, we have never seen an equivalent in other parts of the world. A local diagenetic phenomenon (boudinage?) is possible. In particular, we felt in the revision of the stratotype (see Cózar *et al.*, 2007), where no other specimen of this genus was found, and thus, this problem could not be solved.

Occurrence.– Latest Moscovian of northern Spain.

Genus ?*Petschoria* Kordé, 1951

Type species: *Petschoria elegans* Kordé, 1951.

Diagnosis.– Test cylindrical, rarely ramified, with braided inner part and *Komia*-like, radially and transversely arranged, external part.

Composition.– Monospecific.

Remarks.– Our definition comes from the interpretation of the illustrations of Mamet & Zhu (2005, figs 5F, K, O) which are not necessarily consistent with the unclear holotype of Kordé (1951), the text-fig. 19a-b of Maslov & Kordé (1963), and the illustrations of Chuvashov *et al.* (1987, pl. 21, figs 2-3).

Occurrence.– ?Middle-Late Carboniferous of northern Urals (Russia), Tarim (China), Yukon (Canada), New Mexico (according to Mamet & Zhu, 2005, p. 8).

Family CUNEIPHYCIDAE fam. nov.

Diagnosis.– Erect Aoujgaliina with uniseriate chambers and/or rows of chambers. Wall calcitic, yellowish, hyaline, often maculate.

Composition.– Four genera: *Cuneiphyucus* Johnson, 1960 non Groves & Mamet, 1985; *Masloviporidium* Groves & Mamet *emend.* Vachard & Maslo, 1996; *Multiporidium* gen. nov.; and ?*Iberiaella* Racz, 1984 *emend.* here.

Remarks.– Many morphological convergences can be found between cuneiphyceans and stacheiaceans. Nevertheless, two fundamental differences exist: 1) Stacheiidae are attached and Cuneiphycidae erect; 2) The possible ancestors are different: *Aoujgalia* at the stage *Mametella* for the Stacheiidae; *Asteroaoujgalia* for the Cuneiphycidae.

Occurrence.– Latest Viséan-Bashkirian, cosmopolitan.

Genus *Cuneiphyucus* Johnson, 1960

Type species: *Cuneiphyucus texana* Johnson, 1960.

Diagnosis.– Test fan-shaped (flabelliform) composed of curved to semicircular laminae with pillars limiting quadrate chamberlets, with additional branches composed of short laminae with chamberlets but never donezellan (erect, septate, uniseriate tubes; inversely to *Multiporidium*). The wall often maculate is imperforate. The tests are generally fragmentary conical or cylindrical fragments.

Composition.– *Cuneiphyucus texana* Johnson, 1960; and *C. aliquantula* Johnson, 1960.

Excluded species.– *Cuneiphyucus johnsoni* Flügel, 1966 (= *Fourstonella*).

Occurrence.– Protvinsky (Serpukhovian) of Kazakhstan (Brenckle & Milkina, 2003, pl. 5, fig. 5), Moscovian of Spain. Pennsylvanian Texas, New Mexico, Missouri.

Genus *Masloviporidium* Groves & Mamet, 1985, *emend.* Vachard & Maslo, 1996

(Figs 10.25, 14.1-14.3; Pl. 12, Figs 8-11)

Type species: *Donezella delicata* Berchenko, 1982.

Synonymy.– *Pseudodonezella* Mamet & Herbig, 1990 (*sensu stricto*) because we assign the type species of this genus *Praedonezella tenuissima* in the same genus as *Donezella delicata* designated as type species of *Masloviporidium*.

Diagnosis.– Test cylindrical, tapering, bifurcated. Attached, uniseriate in initial part. Uniseriate with large chambers in the second part and then, subdivided in chamberlets by rare additional pillars. Wall yellowish, hyaline, granular.

Composition.– *Donezella delicata* Berchenko, 1982; *Praedonezella tenuissima* Berchenko, 1982.

Remarks.– *Masloviporidium* as emended here and really defined by its type-species *Donezella delicata* seems to be a transitional form between a stacheiid and *Multiporidium* gen. nov.

Donezella delicata was assigned to *Praedonezella* by Bogush *et al.* (1990, p. 83-84); hence it is clear that *delicata* and *tenuissima* belong to the same genus. Vachard & Maslo, 1996 considered that *Praedonezella tenuissima* Berchenko, 1982 is synonym of *Donezella delicata*. Nevertheless, both species could be distinct, and at least *tenuissima* could be denominated *Masloviporidium tenuissimum*. Moreover, both species *Donezella delicata* and *Praedonezella tenuissima* were designated as type species of *Masloviporidium* and *Pseudodonezella*, respectively.

Cózar (2005, fig. 5.9) indicated the presence of the emended genus as early as the early Serpukhovian in southwestern Spain.

Occurrence.– Earliest Bashkirian of Donbass Basin (Ukraine) (D³₇-D⁷₇ in our collections; D¹⁰₅-D⁸₇ for the distribution indicated for “*D.*” *delicata* in Aizenverg *et al.*, 1983, p. 126; and D²₇-D⁴₇ for “*P.*” *tenuissima* in Aizenverg *et al.*, 1983, p. 126).

Genus *Multiporidium* gen. nov.

(Pl. 12, Figs 6-7, 12-18, 20-21)

Type species: *Multiporidium dilectum* sp. nov. (= *Masloviporidium delicata sensu* Groves & Mamet, 1985, *nomen invalidum*).

Synonymy.– *Criporidium* Maslov, 1973 *nomen nudum*; Genus A *sensu* Groves, 1983; *Masloviporidium* (*non sensu auct.* because the genus concept is not consistent with the designated type species).

Composition.– Monospecific.

Etymology.– Latin multi = several and ending poridium; because this taxon has numerous pores and was called *Masloviporidium*.

Diagnosis.– Similar to *Cuneiphycus* (*sensu stricto*) but the wall between the pillars can be perforated by stolons (= “intercellular pores” of Groves, 1983, text-fig. 4). The pillars are tapering from bottom to top. Some towers are donezellid (i.e., with one row of uniseriate barrel-shaped chamberlets).

Description.– Test conical to pyramidal consisting of laminar walls shared in chamberlets by perpendicular pillars, trapezoidal more than cylindrical in three dimensions. Chamberlets are subquadrate in both complementary planes of sections. Stolons are open in the top of the preceding chambers and also open on the roof of the next lamina. The stolon are diagonally arranged through the wall. Only one stolon per chamberlet. Turriform, uniseriate protuberances expand from the planar to slightly curved laminae. Turriform expansions are composed of dolioliform chambers, with a central aperture. Wall yellowish, granular. The entire specimens are generally recrystallized in radiaxial to granular yellowish sparite; hence, the inner skeleton becomes poorly visible in many cases.

Remarks.– *Multiporidium* (= *Masloviporidium sensu* Groves & Mamet, 1985); *invalidum* because of the chosen type species differs from *Cuneiphycus* (*sensu stricto*), by the shape of the chamberlets and pillars, and the presence of stolons.

Occurrence.– ?Latest Viséan; Serpukhovian-early Bashkirian of northern and southern Urals (Bogush *et al.*, 1990). Protvinsky (Serpukhovian) of Kazakhstan (Brenckle & Milkina, 2003, pl. 5, fig. 5); Deblin Formation of Lublin Basin (Poland; Skompski, 1996). Early Bashkirian of western Palaeotethys (Spain, southern France, Algeria), Donbass, Kazakhstan, U.S.A. (Alaska, Texas, Oklahoma, Kansas, Idaho, Utah).

***Multiporidium dilectum* gen. nov. sp. nov.**

(Pl. 12, Figs 6-7, 12-18, 20-21)

1979 *Cuneiphycus* sp. – Massa & Vachard, pl. 9, figs 7-8.

1983 Genus A species A – Groves, p. 26, pl. 10, figs 1-9.

- 1985 *Masloviporidium delicata* (Berchenko) – Groves & Mamet, p. 485-486, figs 1-2a-l (with 14 references in synonymy).
- 1986 *Masloviporidium delicata* (Berchenko) – Groves, p. 87-89, figs 7.3-7.5 (with 6 references in synonymy).
- 1986 *Masloviporidium delicata* (Berchenko) – Poncet, p. 190-191, pl. 3, figs 1-3 (with 3 references in synonymy).
- 1989 *Masloviporidium delicata* (Berchenko) – Skompski, pl. 3, figs 1-3.
- 1989 *Cuneiphyucus aliquantulus* Johnson – Vachard *et al.*, p. 709, pl. 1, fig. 5, pl. 4, figs 4, 6.
- 1990 *Masloviporidium delicata* (Berchenko) – Bogush *et al.*, p. 133-134, pl. 30, figs 8-10, pl. 31, figs 1-4.
- 1991 *Masloviporidium delicata* (Berchenko) – Mamet, fig. i.
- 1991 *Cuneiphyucus aliquantulus* Johnson – Vachard & Beckary, p. 324, pl. 2, fig. 1.
- 1995 *Cuneiphyucus texanus* Johnson – Pajic & Filipovic, pl. 48, figs 1-2.
- 1996 *Masloviporidium delicata* (Berchenko) – Skompski, p. 223-224, pl. 15, figs 5-6 (with 14 references in synonymy).
- 2003 *Cuneiphyucus* sp. – Brenckle & Miklina, pl. 5, fig. 15.

Etymology.– Latin *dilectus*, appreciated because this species was often quoted under an erroneous name during the last ninety years. Neutral.

Type locality.– Arkansas (U.S.A.).

Type level.– Bashkirian.

Diagnosis.– As for the genus.

Description.– Maximal dimensions = less than 10,000 mm; height of chamberlets = 0.020-0.060, width of chamberlets = 0.015-0.030 mm. Diameter of stolons = 0.005-0.010 mm; laminae thickness = 0.010-0.025; average width of pillars = 0.005-0.010 mm

Holotype.– Pl. 15, fig. 3 (= Groves 1983, pl. 10, Fig. 3)

Repository of the plates.– University of Oklahoma (U.S.A.).

Occurrence.– As for the genus.

Genus ?*Iberiaella* Racz, 1984, emend. herein

(Figs 14.8-14.9 14.6-14.7?; Pl. 12, Figs 19, 22)

Type species: *Iberiaella carbonica* Racz, 1984.

Synonymy.– *Ptychocladia* (*sensu* Massa & Vachard, 1979); *Foliophycus* (*sensu* Lemosquet & Poncet, 1977; Poncet, 1986 and Pajic & Filipovic, 1995); *Contortiporidium* Maslov, 1973 (*nomen nudum*: no description).

Diagnosis.– Test ramose composed of small initial parts similar to *Multiporidium* linked in an elongate colony (?) by long terminal part uniseriate with an unique row of chambers. Preserved and/or diagenetic wall similar to *Multiporidium*.

Composition.– Monotypic.

Remarks.– *Iberiaella* differs from *Cuneiphyucus* and *Multiporidium* by large uniseriate parts linking the small conical parts. Some *Multiporidium* are transitional (Pl. 12, Fig. 16).

A part of the type-material of *Iberiaella* (holotype, Racz, 1984, fig. 3a and fig. 3c) resembles the calcifoliin *Frustulata* but the multilayered tubes (fig. 3d) differentiate it, and correspond more to a donezellid. The other specimens (fig. 3b, e-f) are similar to *Claracrusta* (= *Berestovia*). That

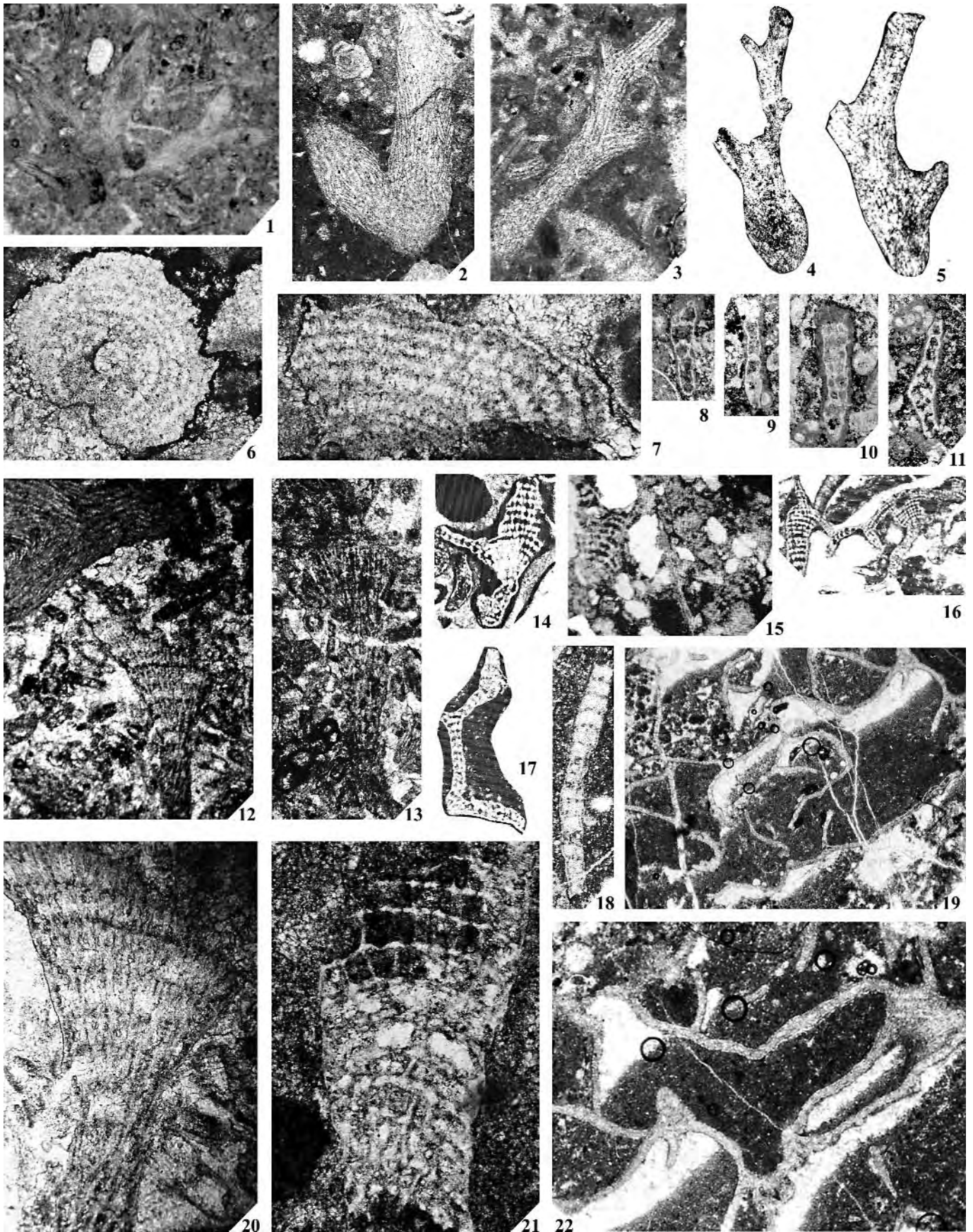
Plate 12

1-5, *Ungdarella uralica* Maslov, 1956a. 1. Pc4064, Souk el Had, Central Morocco, Brigantian, x 32. 2. Late Permian of Himmetli (Taurus, Turkey), sample 97337, x 70. 3. Late Permian of Himmetli (Taurus, Turkey), sample 97337, x 70. 4. Asbian/Brigantian boundary, Roquemaillère, sample DV137G.19, x 35. 5. late Asbian, Roquemaillère, sample DV137B.19, x 50.

6-7, 12-18, 20-21, *Multiporidium dilectum* gen. nov. sp. nov. 6. Paratype. Transverse section. Bashkirian of northern Spain; x 66. 7. Paratype. Longitudinal section. Bashkirian of northern Spain; x 66. 12. Longitudinal section showing the stolons and the form of pillars and laminae, associated with *Ungdarella uralica* (top), sample 6/28, collection Lys; x 66. 13. Tangential section, sample 6/28, collection Lys; x 66. 14. Holotype, according to Groves, 1983; x 21. 15. Paratype, according to Vachard *et al.*, 1989 (pl. 4, fig. 4). Sample Esca 1bas. Bashkirian of Spanish Pyrenees; x 27. 16. Paratype, according to Groves, 1983, transitional to *Iberiaella* emend. herein; x 21. 17. Paratype according to Groves, 1983; x 21. 18. Tangential and axial sections, Bashkirian of Libya, sample 17/1, photo 8-29, x 43. 20. Detail of Pl. 29, fig. 8, sample 6/28, collection Lys, x 143. 21. Longitudinal section showing the stolon and the form of pillars and laminae, Bashkirian of Libya, sample 17/1, photo 8-28, x 170.

8-11, *Masloviporidium delicatum* (Berchenko, 1982) emend. herein. Donbass Basin (Ukraine), Voznessensky stage (Bashkirian); x 50.

19, 22, *Iberiaella carbonica* Racz emend. herein. 19. Sample E1146 (northern Spain), photo 8-23, Bashkirian; x 11. 22. Sample E1146 (northern Spain), photo 8-25, Bashkirian; x 15.5.



explains probably why Sebban & Mamet (1999, fig. 3. 99) and Sebban (2000, fig. 22) denominated a taxon: “*Berestovia?* or *Iberiaella?* sp.”.

Occurrence.— Bashkirian of northwestern Spain (San Emiliano Formation) and Algeria.

Family STACHEIIDAE Loeblich & Tappan, 1961, *nomen transl.* from subfamily, *emend.* herein

Synonymy.— Ptychocladidae Elias, 1950 *emend.* H. Termier *et al.*, 1977 (*part.*).

Diagnosis.— Aoujgaliida attached, showing many rows of quadratic chambers with uniseriate growth, partly overlapping. Chambers quadrate or higher than wide with distal and proximal, curved borders, and lateral borders rectilinear.

Composition.— Two genera: *Stacheia* Brady, 1876 (= *Conilalia* Vachard in Massa & Vachard, 1979); and *Fourstonella* Cummings 1955a *emend.* (= *Amorfia* Racz, 1964 = *Parastacheia* Mamet & Roux, 1977 = *Efluegelia* Vachard in Massa & Vachard, 1979 = *Chuvashovia* Vachard, 1980).

Remarks.— No subsequent revision has confirmed the interpretation of *Ptychocladia* Ulrich & Bassler, 1904 as an aoujgaliid. We re-consider now *Ptychocladia* as the bryozoa and/or foraminifer described by the authors. Hence, we exclude, at least temporarily, the ptychocladids from the aoujgaliids. Many genera of this group and *Stacheia* itself are morphologically similar to a nodosarioid foraminifer or to a pharetronid sponge (Fig.1.4-1.5).

Occurrence.— Late Viséan-Late Permian, probably cosmopolitan (especially *Efluegelia*).

Genus *Stacheia* Brady, 1876

(Figs 1.5, 8.16; Pl. 13, Figs 1-7, 13, 15, 19, Pl. 14, ?16-?17)

Type species: *Stacheia marginulinoides* Brady, 1876.

Synonymy.— *Conilalia* Vachard in Massa & Vachard, 1979.

Diagnosis.— Test attached, with uniseriate growth of chamber rows. Chambers higher than wide with distal and proximal, curved borders, and lateral borders rectilinear.

Composition.— *Stacheia marginulinoides* Brady, 1876; *S. pupoides* Brady, 1876; *Conilalia africana* Vachard in Massa & Vachard, 1979.

Excluded species.— *Stacheia acervalis* (Brady, 1876) (probably an attached Miliolata: *Calcivertella* or *Ammovertella*); *S. cicatrix* Conkin, 1961 (probably *Stacheoides*); *S. moriformis* Howchin, 1888 (*Salebridae?*); *S. neopupoides*

Plate 13

1-2, *Stacheia marginulinoides* Brady, 1876. 1. Pc3294, Mouarhaz, late Brigantian, Central Morocco, x 69. 2. Pc-COR/4b, Cornuda Section, early Serpukhovian, SW Spain, x 40.

3-4, *Stacheia pupoides* Brady, 1876. 3. Pc993, Bannagogle Quarry, late Brigantian, SE Ireland, x 34.5. 4. BGS-K-IB1455, Roebank Glen, North Ayrshire, late Brigantian, Midland Valley, Scotland, x 60.

5-6, 19, *Stacheia* (= *Conilalia*) *africana* (Vachard in Massa and Vachard, 1979) *n. comb.* 5. Pc1397, Guilleen Quarry, late Brigantian, SE Ireland, x 34.5. 6. UCD-CKQ/33, Rockdale Limestone Formation, Cookstown Quarry, late Brigantian, NE Ireland, x 34.5. 19. Bashkirian of Libya, sample OB874. Holotype; x 29.

7, *Stacheia* aff. *africana* (Vachard in Massa & Vachard, 1979) *n. comb.* Pc 1358, Clogrenan B Borehole, early Brigantian, SW Ireland, x 34.5.

8, 25, *Fourstonella* (= *Chuvashovia*) *densifolia* (Vachard in Vachard & Montenat, 1981). 8. BGS-E, Archerbeck Borehole, 1923'1" depth, Archerbeck Beds, late Asbian, S Scotland, x 34.5. 25. Pc-COR/2b, Cornuda Section, early Serpukhovian, SW Spain, x 40.

9, *Komia abundans* Kordé, 1951. Late Moscovian. Sample Panda 11 (collection Termier), northern Spain; x 47.

10, *Foliophycus* sp. with false conceptacle. Moscovian. Sample P2 (collection Termier), northern Spain; x 47.

11, 24, *Fourstonella fusiformis* (Brady, 1876). 11. Japhet (Montagne Noire, southern France), sample DV164-0, early Brigantian; x 40. 24. Ardengost (Pyrénées, southern France), late Serpukhovian, sample MFP/AH20; x 27.

12, 16-17, 20, 23, 27, *Fourstonella* (= *Efluegelia*) *johnsoni* (Flügel, 1966). 12. Early Permian, Djambi (Sumatra), sample IN456; x 30. 14. Middle Permian, Tezak, sample DV374, x 75. 16. Pc-SA/2-3, San Antonio Section, early Serpukhovian, SW Spain, x 40. 17. Pc-COR/5a, Cornuda Section, late Serpukhovian, SW Spain, x 40. 20. Middle Permian, Middle Permian, Tezak, sample DV484, x 40. 23. Early Permian, Central Mountains of Afghanistan; x 27. 27. BGS-E-IB1347, Blackhall Lst., River Avon, Lanarkshire, Late Brigantian, Midland Valley, Scotland, x 90.

13, *Stacheia* cf. *marginulinoides* Brady, 1876. Libya, A1-49 borehole, sample 1095-96 (2), early Serpukhovian, x 100.

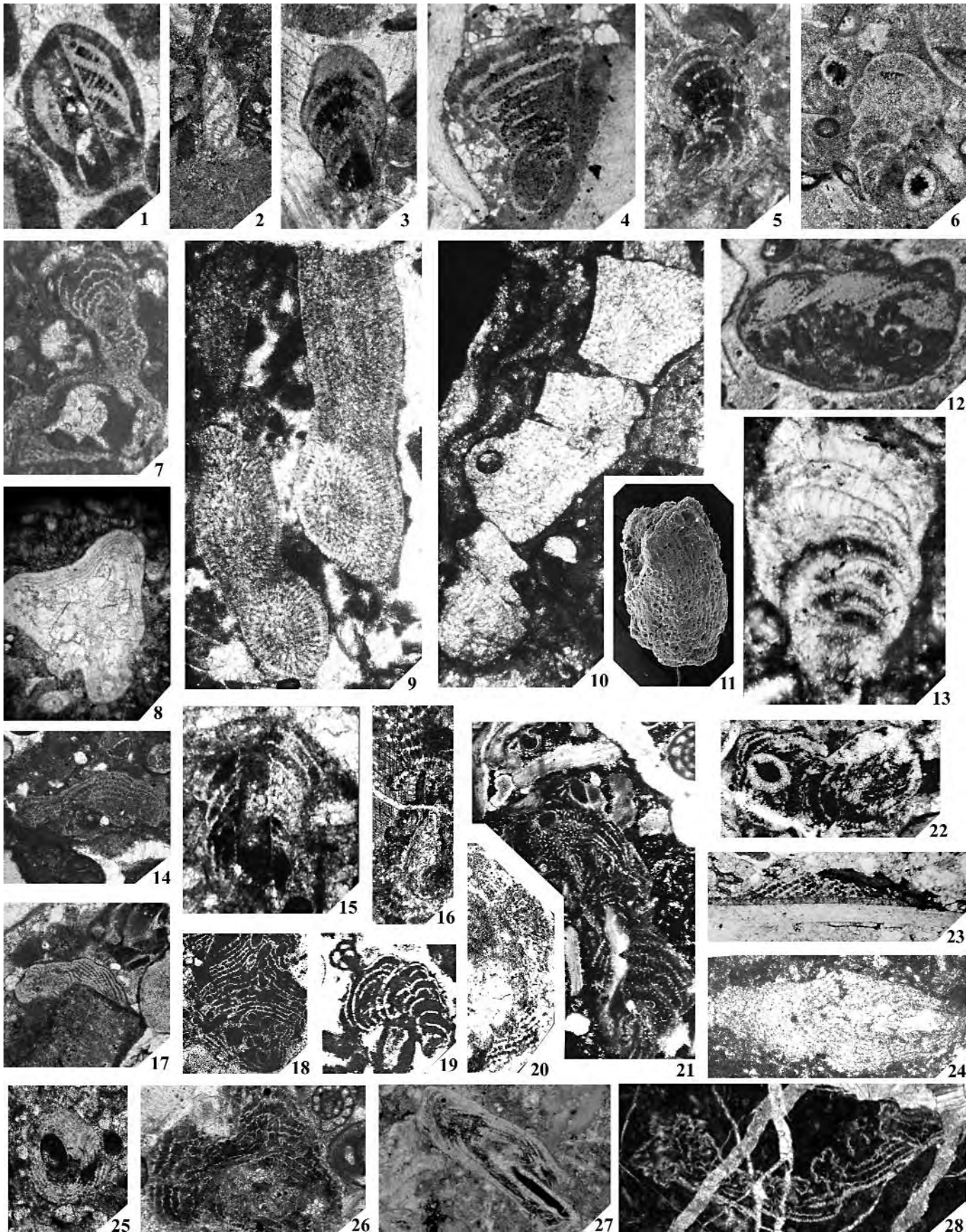
14, 28, *Fourstonella* (= *Efluegelia* sp. 2) sp., Pc-COR/7, Cornuda section, late Serpukhovian, SW Spain, x 40. 28. Longitudinal section showing the perforated wall and the circular transverse sections of some pillars. Kubergandian (Early Middle Permian), Lycian Taurus, Turkey. Sample 464/072508. x 21.

15, *Stacheia* cf. *pupoides* Brady, 1876. Late Viséan, Royseux (Belgium); x 66.

18, *Fourstonella* (= *Chuvashovia* sp. 1) sp., misinterpreted as *Cuneiphycus johnsoni* by Lys, Stampfli and Jenny, 1978, pl. 5, fig. 1, Bashkirian of Alborz (Iran); x 29.

21-22, *Fourstonella* (= *Chuvashovia* sp. 2) sp. 21. Moscovian of eastern Alborz, sample JJ251-6(1), collection Jenny, x 30. 22. surrounding a dasycladale *Nanopora anglica*. South China, sample 3972; latest Viséan, x 50.

26, *Fourstonella* (= *Efluegelia*) sp. nov., Pc1401, Guilleen Borehole, SE Ireland, Late Brigantian, x 34.5.



Conkin, 1961 (probably *Stacheoides*); *S. simulans* Chapman & Howchin, 1905 (indeterminate microfossil); *S. stomatifera* Chapman, 1901 (indeterminate microfossil); *S. subglobosa* Waters, 1927 (indeterminate microfossil); *S. trepeilopsiformis* Conkin, 1961; *S. verbeeki* Lange, 1925 (= ?*Calcivertella*).

Remarks.— *Conilalia* is similar to *Stacheia* but larger and with a more enveloping last laminae. Because of the rarity of this material, it is considered here as another species of *Stacheia*.

Occurrence.— ?Early Viséan of Siberian Platform (Ivanova & Bogush, 1992, tab. 1 p. 241; not illustrated). Late Viséan-Serpukhovian Palaeo-Tethyan as far as the Maritime Provinces of Canada [with rare localities in Arkansas and perhaps Idaho (U.S.A.), and Australia]. Latest Viséan of South China (Vachard *et al.*, 1991). Serpukhovian-early Bashkirian, Great-Britain, Algeria, U.S.A., Libya. Early Bashkirian of Algeria (Sebbar, 2000) and Donets Basin (Vachard & Maslo, 1996). ?Moscovian of Libya, the Canadian Arctic Islands and Spain (Massa & Vachard, 1979; Mamet, 2002; and D.V., unpublished data, respectively)

Genus *Fourstonella* Cummings, 1955a emend.

(Pl. 13, Figs 8, 11-12, 14, 16- 18, 20-28, Pl. 14, Fig. 1-14, ?15)

Type species: *Stacheia fusiformis* Brady, 1876.

Synonymy.— *Amorfia* Racz, 1964; *Parastacheia* Mamet & Roux, 1977; *Efluegelia* Vachard in Massa & Vachard, 1979; *Chuvashovia* Vachard, 1980; *Foliophycopsis* Gaillot, 2006 (*nomen nudum*).

Diagnosis.— Test attached, fusiform to lemon-shaped, or elongate, occasionally with irregular protuberances. Test attached, elongate, with large uniseriate growth of chamber rows with symmetrical or asymmetrical growth. The test can surround the substrate as in the case of *Fourstonella* (which differs by another type of chamber wall, see Vachard *et al.*, 1989) or be partially ("*Efluegelia*") or completely covered ("*Chuvashovia*"). Chambers quadratic with curved roofs and triangular pillars. Chambers disposed in superimposed uniseriate, elongate rows. Wall calcitic yellowish. The test is often completely recrystallized and yellowish with a ghost of the rows of chambers.

The number of chamber rows is elevated, forming large laminae, but the shape of the test is rather irregular.

Composition.— *Stacheia fusiformis*; *Parastacheia iglii* Mamet & Roux, 1977; *Fourstonella irregularis* Mamet & Roux, 1977; *Amorfia jalinki* Racz, 1964; *Cuneiphycus johnsoni* Flügel, 1966; *Komia abundans* (*sensu* Lys *et al.*, 1978, pl. 3, figs 17, 18?); *Cuneiphycus johnsoni* (*sensu* Lys *et al.*, 1978, pl. 5, fig. 1); *Eflugelia johnsoni* (*sensu* Cózar & Rodríguez, 2004, fig. 9. 16); *Chuvashovia densifolia* Vachard, 1980; *C. densifolia* (*sensu* Cózar & Rodríguez, 2004, fig. 9.17); *Foliophycopsis guevenci* Gaillot, 2006 (*nom. nud.*); and *Stacheia* sp. (*sensu* Malakhova, 1980, pl. 20, fig. 5).

Remarks.— Morphologically different from algae, the genera *Fourstonella*, *Efluegelia* and *Chuvashovia* are more similar to microstromatoporoids. We consider that *Amorfia* and *Parastacheia* are two recrystallized taphotaxa of *Fourstonella sensu stricto*. The spelling "*Efluegelia*", and not *Eflugelia* as originally written, is justified by Krainer *et al.* (2003). As previously indicated by several authors (e.g., Groves, 1986; Mamet & Villa, 2004), "*Efluegelia*" Vachard in Massa & Vachard 1979 and "*Chuvashovia*" Vachard, 1980 are synonyms of *Fourstonella* (see Vachard *et al.*, 1989, text-fig. 3). Differences advocated between *Fourstonella* and "*Eflugelia*" (see Vachard *et al.*, 1989, text-fig. 3) are only differences between well preserved and recrystallized specimens. Nevertheless, the habituses differ: *Fourstonella* envelops symmetrically the substrate, *Efluegelia* covers asymmetrically the support; "*Chuvashovia*" is laterally more expanded. The wall of *Fourstonella* appears continuous; the wall of "*Efluegelia*" is perforated as in calcisponges (for example *Stylothalamia sensu* Schroeder, 1984, fig. 2. 1-5); the pillars of *Fourstonella* are broad and rectangular, those of "*Efluegelia*" are cylindrical; hence, all the sections of pillars of *Fourstonella* appear identical; those of "*Efluegelia*" appear small and round in transverse section. It is evident, for example, that the specimen illustrated by Flügel (1980, pl. 7, fig. 6) cannot be a *Fourstonella* nor a *Cuneiphycus*. It is also evident that the specimens of *Fourstonella johnsoni* in the literature are often *Fourstonella fusiformis* or *F. irregularis*; especially, *Eflugelia johnsoni* (*sensu* Skompski, 1986, pl. 10, figs 1-2) is a *Fourstonella irregularis*.

After revision, *Foliophycopsis* is generically a synonym of *Fourstonella* ("*Chuvashovia*") and corresponds only to a

taphotaxon with strong calcitic recrystallization.

Occurrence.—Typical *Fourstonella* occur apparently from ?Late Tournaisian of Verkhojansk area (Ivanova & Bogush, 1992, tab. 1 p. 241; not illustrated). Middle Viséan to Kasi-movian, western Palaeo-Tethys (Newfoundland Shelf, England, Ireland, Germany, Poland, Austria, Ukraine, southern France, southwestern Spain, Morocco, Algeria, Libya, Iran, ?Siberia, rare in Canadian Arctic), questionable in Tarim Basin (North-West China), ?Bolivia, Mor-rowan-Atokan of Idaho (Groves, 1986). It is also well-known in the Moscovian-Early Permian of Urals; Middle Permian of Turkey, Afghanistan, Greece, Oman, and NW Thailand. Late Permian of Zagros (Iran) and Hazro (Turkey) (Gaillot, 2006, modified in this study). Consequently, this genus can be interpreted as Neo-Tethyan for the Middle-Late Permian.

Suborder CALCIFOLIINA G. Termier *et al.*, 1977 nom.
translat. herein (for order)

Diagnosis.—Colonies encrusting, laminar to erect ramose, petaloid, pseudophylloid, or phylloid. Skeleton strongly calcified. Central part reserved to the organic component, narrow and hardly fossilized. The calcified part is composed of a yellowish to dark calcite; diverse types of filaments can occur, filled with microsparite, micrite or iron oxides. Skeleton calcitic yellowish or dark, lamellar to petaloid. The space occupied by the organic living matter was probably very narrow. Internal, thin, tubular structures poorly understand (pivots or filaments).

Composition.—Two families: (1) Fasciellidae Shuysky, 1999 nomen translat. Vachard, Somerville & Cózar, 2004 (pro family); (2) Calcifoliidae Shuysky in Chuvashov *et al.*, 1987 emend. Vachard & Cózar, 2005.

Phylogeny.—Two hypotheses can be advanced for the origin of this order: (a) it could be derived from Tournaisian *Kulikaella* or Frasnian *Kleinbergella*, i.e., from Moravamminida; (b) the genera *Pseudostacheoides* Petryk & Mamet, 1972 or *Stacheoidella* Mamet & Roux *in* Mamet *et al.*, 1987 can be ancestors of Fasciellidae, which, in this case, evolved from Aoujgaliida.

Remarks.—The petaloids are isolated, although often deposited together in packstones; some macroids are built

by *Fasciella crustosa* and *Falsocalcifolium* morphotype E (see below). The Calcifoliida are often located between the two limits of Burchette & Wright (1992), Fair-Weather Wave-Base and Storm- Weather Wave-Base; i.e. in the mid ramp. *Fasciella* is located at a shallower depth, from 25-50 m (Gallagher, 1998; Cózar *et al.*, 2003, 2006a; Pille, 2008), then occurs *Frustulata* which can coexist with *Saccaminopsis* between 50 and 100 m depths approximately.

Calcifolium and *Falsocalcifolium* can occur in shallow water depths (10 m) with the maximum diversity of foraminifera, but they can also attain the limit of the euphotic zone with the deepest water green algae (Pille & Vachard, in press).

Many observations cannot be sufficiently explained in terms of palaeobiology: the possible assemblages with cyanobacteria (“filaments”, spicules), although, with *Fascifolium*, the evolving character seems to be well established. The attached *Eotuberitina* upon the *Fasciella* are important but not well understood. The reophily (affinity for strong currents) of the Calcifoliids is evident, with the examples of the resistant *Fasciella*; parallel oriented, plane *Frustulata*; the morphotypes of *Falsocalcifolium*; and cups of *Calcifolium*. Similarly to the attached *Eotuberitina*, the relatively frequent shelter porosities of *Calcifolium* indicate the early strong calcification of the Calcifoliida. The type of reproduction is unknown; perhaps by release of embryos by the central apertures. The dispersion of the embryos is probably in the vicinity. Hence, the dispersion of the algosponges is relatively very faint, and their distribution indicate necessarily connections between carbonate platforms, microplates, blocks and plates, and location in the tropical belt of the World (consequently the palaeobiogeographic value is important).

The internal filaments of Calcifoliina have an ontogenetic growth; they are not the microperforations of some authors.

Occurrence.—Occasionally in the early-mid Viséan (*Fasciella*), common in the interval from the late Viséan (Asbian) to late Serpukhovian (Arnsbergian), and rare in the Bashkirian and early Moscovian. Palaeo-Tethyan (*Fasciella* is cosmopolitan; the Calcifoliidae are limited to the western and central Palaeo-Tethys).

Family FASCIELLIDAE Shuysky, 1999

Diagnosis.—Laminar Calcifoliina. Skeleton calcitic yellowish. The space occupied by the organic living matter was probably very narrow. Internal, thin, tubular structures poorly understood (pivots). Elongate, cylindrical to pear-shaped or cone-shaped, sometimes ramose, incrusting set of concentric carbonate laminae surrounding a cylindrical axis or pivot. Laminae separated by very narrow micritic intervals. The pivot is generally monaxone spicule-shaped but occasionally bifurcated. It can correspond to a bacillar substrate, spicule, central siphon, or a broad filament. In the advanced? taxa, some filaments (rarely bifurcated) can appear within the laminae (*Fascifolium* gen. nov.), whereas, on the other hand, the pivot can be septate (*F. scalaeformis*), or absent (*F. crustosa*). The carbonate laminae of the skeleton are hyaline and yellowish; while the pivot and the filaments are microsparitized and whitish, the intervals between the laminae (i.e., corresponding to the living parts) are only visible as sutures, sometimes micritized or ferruginized. Some interruptions of the growth can be demonstrated by the attachment of eotuberitines on the external surface of the laminae.

Composition.—Two genera: *Fasciella* (= *Shartymophycus*); and *Fascifolium* gen. nov.

Remarks.—Due to the joint growth of the pivot and laminae, a consortium is inferred similar to that reconstructed in the stage *Rigidicaulis* Senowbari-Daryan & Flügel, 1993 of *Tubiphytes* Maslov, 1956a, as confirmed by Gaillot & Vachard in Gaillot (2006) (see here Pl. 32, figs 1-2).

Occurrence.—Middle Viséan to Moscovian, cosmopolitan.

Genus *Fasciella* Ivanova, 1973

(Fig. 9.13; Pl. 14, Figs 18-31, Pl. 15, Figs 1-8)

Type species: *Fasciella kizilia* Ivanova, 1973.

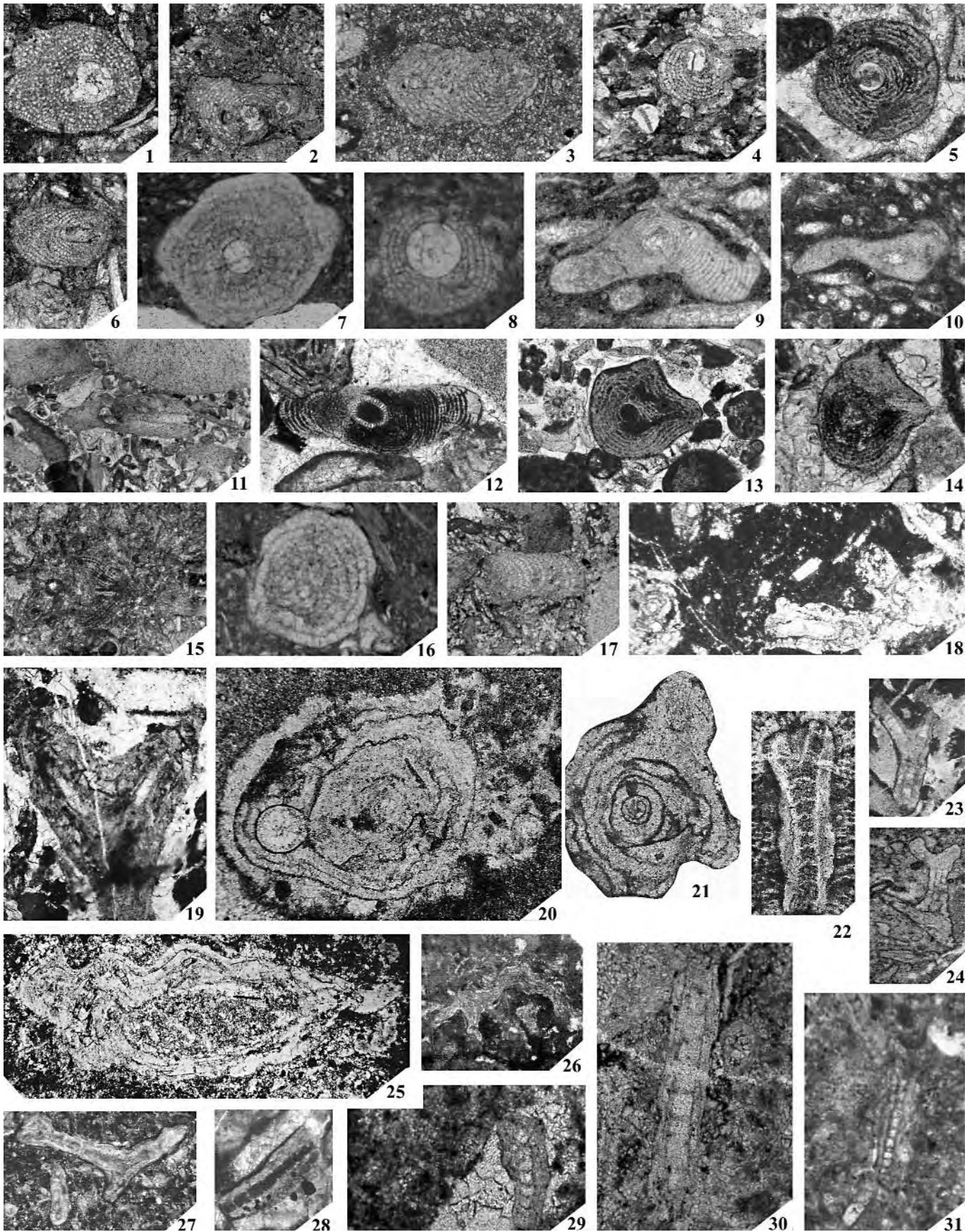
Synonymy.—*Shartymophycus* Kulik, 1973 *sensu* Mamet & Roux, 1975a.

Diagnosis.—Elongate, cylindrical to pear-shaped or cone-shaped, sometimes ramose, incrusting set of concentric carbonate laminae surrounding a cylindrical axis or pivot. Laminae separated by very narrow micritic intervals. The

pivot is generally monaxone spicule-shaped but occasionally bifurcated. The carbonate laminae of skeleton are hyaline and yellowish; the intervals between the laminae are very narrow and low. Some interruptions of the growth can be materialized by the attachment of eotuberitines

Plate 14

- 1-5, 7-8**, *Fourstonella irregularis* Mamet & Roux, 1977. 1. Pc-COR/4b, Cornuda Section, late Serpukhovian, SW Spain, x 40. 2. Pc-SA/4, San Antonio Section, late Serpukhovian, SW Spain, x 40. 3. Pc1371, Clogrenan Quarry, late Asbian, SE Ireland, x 34.5. 4. Pc988, Bannagogle Quarry, late Brigantian, SE Ireland, x 34.5. 5. Pc1134, Ballyadams Quarry, late Asbian, SE Ireland, x 34.5. 7. BGS-E-PS4218, Spilmersford Borehole, Middle Longcraig Lst., early Brigantian?, Midland Valley, Scotland, x 60. 8. BGS-E-PS4218, Spilmersford Borehole, Middle Longcraig Lst., early Brigantian?, Midland Valley, Scotland, x 60. **6, 9**, *Fourstonella* ex gr. *fusiformis* (Brady, 1876). 6. BGS-K-AH31, Five Yard Lst., Brigantian, Allenheads Borehole, N England, x 34.5. 9. Pc322, Urquilla Baja, Serpukhovian, SW Spain, x 34.5. **10-11**, *Fourstonella fusiformis* (Brady, 1876). 10. Pc322, Urquilla Baja, Serpukhovian, SW Spain, x 18. 11. Pc1002, Bannagogle Quarry, late Brigantian, SE Ireland, x 29. **12**, *Fourstonella* (= *Chuvashovia* sp. 2). Pc-MIN/8a, Lavadero de la Mina section, late Serpukhovian, SW Spain, x 40. **13-14**, *Fourstonella* sp. 13. Pc-COR/8c, Cornuda Section, late Serpukhovian, SW Spain, x 40. 14. Pc1115, Ballyadams Quarry, late Asbian, SE Ireland, x 34.5. **15**, Transitional form between *Aoujgalia* and *Fourstonella*. Pc957, Bannagogle Quarry, early Brigantian, SE Ireland, x 29. **16**, Transitional form between *Stacheia* and *Fourstonella*. BGS-E-PS4218, Spilmersford Borehole, Middle Longcraig Lst., early Brigantian?, Midland Valley, Scotland, x 60. **17**, *Stacheia?* sp. nov. Pc-SA/4, San Antonio Section, Late Serpukhovian, SW Spain, x 40. **18-21, 24-25, 27**, *Fasciella kizilia* Ivanova, 1973. 18. Large colonies constituting a build-up. Japhet, early Brigantian (Montagne Noire, southern France). Sample DV127A. Photo LP8/5; x 4. 19. Longitudinal section with false conceptacles. Sample RR2.2/98. Photo 9.9.9.3/115. Early Brigantian. Roque Redonde (southern France, Montagne Noire); x 33. 20. (= pl. 1, fig. 4 of Vachard *et al.*, 2004), sample DV 130A, late Brigantian. Saint-Rome (Montagne Noire, southern France); x 66. 21. (= pl. 1, fig. 2 of Vachard *et al.*, 2004), sample DV 293C, late Asbian. Lentilles de la route (Montagne Noire, southern France); x 27. 24. Bifurcated tests with relatively broad pivot. Roquemaillère, Early Brigantian (Montagne Noire, southern France). Sample ML.UM.ROQ. Photo LP9.7/136; x 19. 25. Typical longitudinal and transverse sections. Sample DV128B. Photo 8/01. Early Brigantian. Japhet (Montagne Noire, southern France); x 33. 27. Bifurcated test and bifurcated pivot showing the similarity of growth of both elements. Lentilles de la route, latest Asbian (Montagne Noire, southern France). Sample DV332'A(2). Photo LP 7/150; x 19. **22-23, 28-31**, *Fasciella scalaeformis* Vachard *et al.*, 2004. 23. Japhet; earliest Brigantian (Montagne Noire, southern France). Sample DV126F. Photo LP9/13; x 27. 22. Paratype (pl. 2, fig. 9), Sample DV431E, Mounio (Montagne Noire, southern France), late Brigantian; x 66. 28. Mounio, latest Brigantian (Montagne Noire, southern France). Sample DV431A. Photo LP9.9/8; x 27. 29. Pc2768, Tizra 4, Adarouch, late Asbian, Central Morocco, x 60. 30. Pc2387, Tizra 2, Adarouch, early Brigantian, Central Morocco, x 60. 31. Pc524, Peñarroya 2, early Brigantian, SW Spain, x 102. **26**, *Fasciella crustosa* Vachard *et al.*, 2004. La Boutinelle, Brigantian (Montagne Noire, southern France). Sample MA25.16B. Photo LP9.7/16; x 7.



and unpreserved organic microfossils on the external surface of the laminae (Pl. 16, fig. 2).

Composition.— *Fasciella kizilia* (= *Shartymophycus fusus* Kulik, 1973 = *Fasciella ivanovae* Saltovskaya, 1984a = *F. ramosa* Saltovskaya, 1984a; according to Mamet, 1991, 2002 = ?*Shartymophycus multiplex* Kulik, 1973); *F. crustosa* Vachard et al., 2004; *F. scalaeformis* Vachard et al., 2004; and *Fasciella desquamata* sp. nov.

Remarks.— The typical specimens seem to encrust a short cylindrical microsparitic axis (bacillar substrate, spicule, central siphon?). The most ramose species is *Fasciella ramosa* Saltovskaya, 1984, but its generic assignment might be questionable. Some specimens show a large uncalcified axis (Mamet & Roux, 1977, pl. 14, fig. 7; Mamet & Pinard, 1985, pl. 2, fig. 13, 17; Vachard et al., 1991, pl. 1, fig. 1, 2004, pl. 1, figs 3, 5, 7) in correlation with an absence of pivot. Conversely, rare specimens show a scalariform axis (Vachard & Aretz, 2004; Vachard et al., 2004). Paradoxically, this scalariform axis has a size and proportions very similar to the “hypothallus” of *Ungdarella “conservata”* Kordé, 1951 (Pl. 14, fig. 5).

The “interstratified” *Eotuberitina* (e.g., Ivanova, 1975, pl. 1, fig. 1; Vachard et al., 2004, pl. 1, fig. 4; here Pl. 14, fig. 20) evocated in the diagnosis prove that the calcification of the *Fasciella* was early and strong, and their wall exposed during the life or very quickly after the death. It is more a character of a protist, rather similar to a foraminifer (this group is excluded due to the absence of a proloculus and perforation).

Occurrence.— Middle Moliniacian, formerly early Viséan “V1b” (Vachard et al., 1991). Rather common since the late Moliniacian (“V2a”) (Vachard, 1977, tabl. 1) to Bashkirian (Ivanova, 1973; Vachard et al., 1991). Acme in the Asbian-Brigantian (e.g., Cózar et al., 2008b, text-figs 3-4). ?Early Moscovian (Sebbar & Mamet, 1999). ?Late Atokan (Groves, 1984). Cosmopolitan (see Mamet, 1991).

***Fasciella desquamata* sp. nov.**

(Pl. 15, Figs 1-8)

- 2007 Some microfacies – Karim, figs I.5.7-8.
- 2007 *Praedonezella* aff. *cespeformis* Kulik – Karim, figs I.12.1.

- 2007 *Claracrusta catenoides* (Homann) Vachard – Karim, figs I.12.5.

- 2007 *Fasciella crustosa* Vachard, Somerville & Cózar – Karim, figs I.12.8, I.13.7.

- 2007 Oncoid – Karim, fig. I.21.4.

Etymology.— Latin *desquamatus*, loosing its skin, because of the detached last laminae.

Type locality.— Tizra (central Morocco).

Type level.— Late Brigantian.

Holotype.— Pl. 15, Fig.1 = sample AK.N3.

Diagnosis.— The fasciellid part is followed by erect parts, with some cavities as in *Frustulata asiatica* and maybe some filaments.

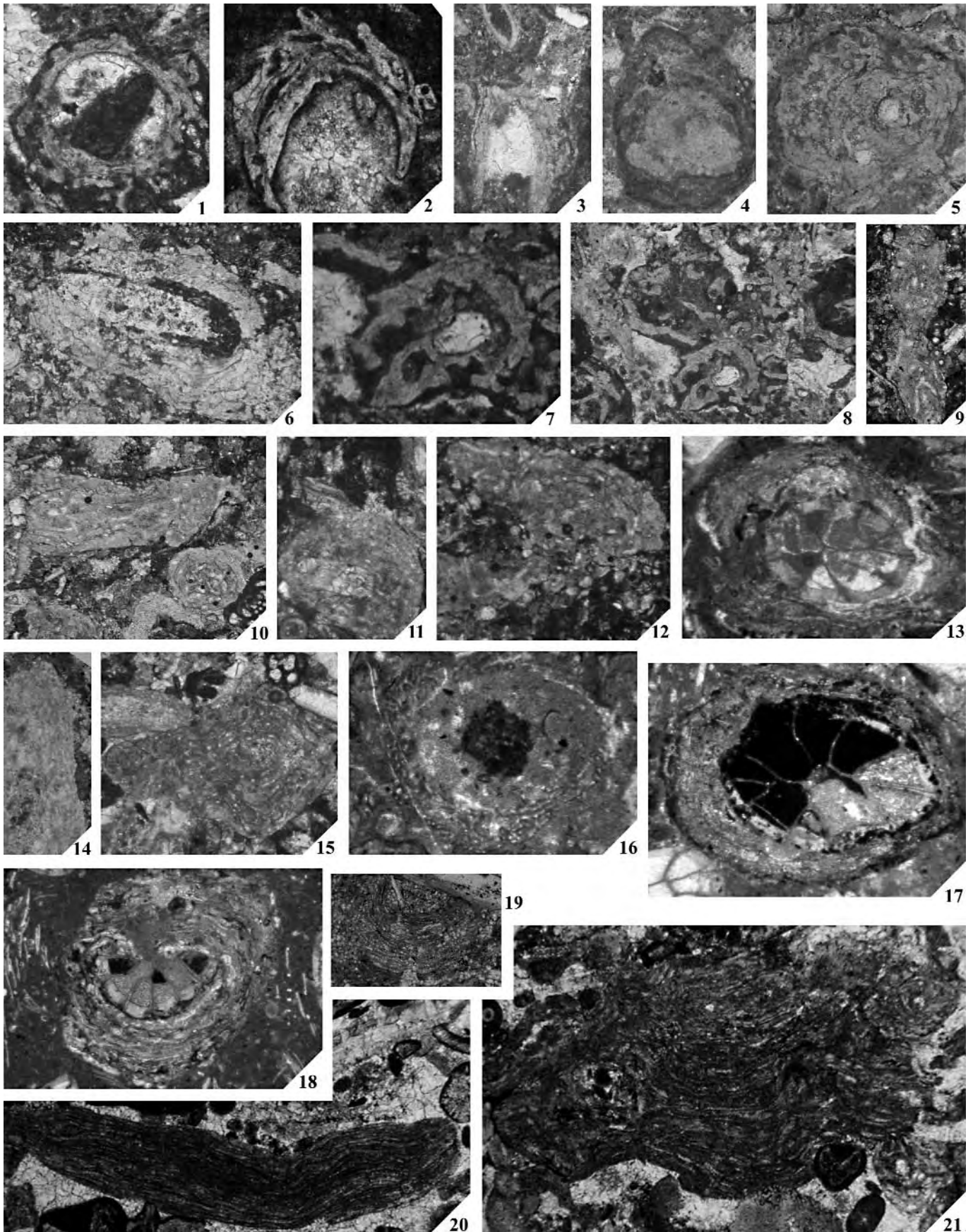
Description.— Laminae are numerous as in *F. crustosa*, they are closely arranged. They are relatively regular in thickness, and almost concentric. The intervals between them are relatively distinct, occasionally broad. The fila-

Plate 15

1-8, *Fasciella? desquamata* sp. nov. 1. Holotype. Transverse section of the basal attached part. Tizra hill (central Morocco), sample N3, latest Brigantian; x 33. 2. Paratype. Transverse section of a basal part semi-attached on the substrate. Les Pascales (Montagne Noire, southern France, sample DV601D, late Brigantian; x 66. 3. Paratype. Tizra hill (central Morocco), sample N3, latest Brigantian; x 66. 4. Paratype. Tizra hill (central Morocco), sample TZ30, early Brigantian; x 13. 5. Paratype. Tizra hill (central Morocco), sample TZ35, early Brigantian; x 13. 6. Paratype. Tizra hill (central Morocco), sample TZLen, latest Brigantian; x 13. 7. Paratype. Tizra hill (central Morocco), sample N3, latest Brigantian; x 23. 8. Paratype. Tizra hill (central Morocco), sample N3, latest Brigantian; x 29.

9-18, *Fascifolium pantherinum* Vachard, Karim and Cózar gen. nov. sp. nov. 9. Paratype. Sample AK.VII.TZ175, Tizra Formation. Early Brigantian, photo AK.PC075, notice the bifurcated filament at bottom of specimen; x 33. 10. Paratype. Sample AK.VII.TZ175, Tizra Formation. Early Brigantian, photo AK.PC074; x 33. 11. Paratype. Sample AK.VII.TZ139, Tizra Formation. Early Brigantian, photo AK.PC038; x 33. 12. Paratype. Sample AK.VII.TZ175, Tizra Formation. Early Brigantian, photo AK.PC031; x 33. 13. Pc2315, Idmarrach 1, Adarouch, late Serpukhovian, Central Morocco, x 38. 14. Paratype. Sample AK.VII.TZ184, Tizra Formation. Early Brigantian, photo AK.PC07; x 33. 15. Holotype. Sample AK.VII.TZ175, Tizra Formation. Early Brigantian, photo AK.PC037; x 33. 16. Pc4058, Souk el Had, Central Morocco, Brigantian, x 50. 17. Pc2315, Idmarrach 1, Adarouch, late Serpukhovian, Central Morocco, x 38. 18. Pc2315, Idmarrach 1, Adarouch, late Serpukhovian, Central Morocco, x 25. [N.B. in 13, 17 and 18 specimens are encrusting heterocorals]

19-21, *Fascifolium* sp. nov., 19. BGS-K-IB364, MacDonald Lst., River Ayr, South Ayrshire, early Serpukhovian, Midland Valley, Scotland, x 60. 20. Pc-MIN/8a, Lavadero de la Mina Section, late Serpukhovian, SW Spain, x 14.5. 21. Pc-MIN/8d, Lavadero de la Mina Section, late Serpukhovian, SW Spain, x 14.5.



ments are absent (Morocco) to very rare (Montagne Noire). The laminae are rapidly uncoiled, obliquely erect. Length = 1.000-5.000 mm, breadth = 1.000-4.500 mm, laminae thickness = 0.010-0.030 mm, distance between filaments = 0.025-0.050 mm, pivot ? diameter = 0.120 mm.

Type material.– 20 specimens.

Repository of the types.– University of Lille

Remarks.– *Fasciella desquamata* differs from all the other species of *Fasciella*, and especially from the morphotype “*F. ramosa*” by less ramified erect laminae. “*F. ramosa*” can also correspond to a *Falsocalcifolium* encrusted by a *Fasciella crustosa*,

Occurrence.– Latest Asbian-Brigantian of central Morocco and Montagne Noire (southern France)

Genus *Fascifolium* gen. nov.

(Pl. 15, Figs 9-21)

Type species: *Fascifolium pantherinum* gen. nov., sp. nov.

Etymology.– *Fasciella* with the filaments of *Falsocalcifolium* or *Calcifolium*.

Synonymy.– *Chantonia* (*part.*).

Diagnosis.– Test similar to *Fasciella* but with single to bifurcated filaments sporadically dispersed within the laminae.

Composition.– *Fascifolium pantherinum* sp. nov.; *Chantonia maslovi* (*sensu* Brenckle & Milkina, 2003).

Occurrence.– Early Brigantian to late Serpukhovian, Central Morocco. “Serpukhovian” of Kazakhstan (Brenckle & Milkina, 2003).

***Fascifolium pantherinum* Vachard, Karim &**

***Cózar* sp. nov.**

(Pl. 15, Figs 9-18)

? 1983 *Kulikaella multiplex* Kulik – Berchenko in Aizenverg *et al.*, pl. 83, figs 6-7.

? 2003 *Chantonia maslovi* (Chanton) – Brenckle & Milkina, pl. 5, fig. 8.

? 2007 *Fasciella pantherina* sp. nov. – Karim, p. 81, figs 1.7. 8-9, 1.13. 1, 5-8 (invalid. name in a PhD).

Etymology.– Latin *pantherinus*, speckled as a panther skin.

Type locality.– Tizra Hill (central Morocco).

Type level.– Early Brigantian.

Holotype.– Pl. 15, Fig. 15 (= Karim, 2007, pl. 1.13, fig. 4), sample AK.VII-TZ175.

Diagnosis.– As for the genus.

Description.– Apparently, the specimens are never bifurcated, generally cylindrical, sometimes biconical (as the holotype). Laminae are numerous as in *F. crustosa*, they are closely arranged. They are relatively regular in thickness, and almost concentric. The intervals between them are apparently absent (indicating very narrow space for the cytoplasm). The filaments are numerous, randomly disposed, but regular in shape and size. Very rare bifurcation of filaments were observed. The intervals between the filaments is two or three times broader than the filament diameter. Length = 1.000-4.000 mm, breadth = 0.310-2.500 mm, filament diameter = 0.010-0.020 mm, distance between filaments = 0.025-0.050 mm, pivot ? diameter = 0.200-0.500 mm.

Type material.– 80 specimens (60 of which occur in the sample AK.VII-TZ175).

Repository of the types.– Palaeontological collection of the University of Lille.

Remarks.– *Chantonia maslovi* (*sensu* Brenckle & Milkina, 2003) has a darker endoskeleton, and apparently, another network of filaments.

Occurrence.– As for the genus.

Family CALCIFOLIIDAE Shuysky *in* Chuvashov *et al.*, 1987, *orth. mut.* pro Calcifoliae; emend. Vachard & Cózar, 2005

Diagnosis.– Pseudophylloid, or phylloid Calcifoliina. Skeleton calcitic yellowish or dark, lamellar to petaloid. Internal, thin, tubular structures poorly understood (filaments).

Composition.— Three genera: *Calcifolium* Shvetsov & Birina, 1935; *Falsocalcifolium* Vachard & Cózar, 2005; *Frustulata* Saltovskaya, 1984a (*sensu* Vachard & Cózar, 2005; = *Pseudodonezella* Mamet & Herbig, 1990).

Remarks.— Pseudophylloid was introduced by Vachard & Cózar (2005) for a short laminar test structure in which horizontal development of the petaloid tests is well developed, more than the vertical growth of the test. Filament is adopted from Mamet (1991) for the indeterminate endoskeletal internal structures, to those diverse interpretations have been suggested in the literature: laterals (siphons), spicules, microperforations (Maslov, 1956a; Perret & Vachard, 1977; Sebbar & Mamet, 1996). See possible interpretations in Vachard & Cózar (2005).

Occurrence.— Late Viséan-Earliest Bashkirian. Shelves of Palaeo-Tethys and Ural Oceans.

Genus *Calcifolium* Shvetsov & Birina, 1935

(Pl. 16, Figs 15-22, Pl. 17, Figs 1-13)

Type species: *Calcifolium okense* Shvetsov & Birina, 1935.

Diagnosis.— Petals or cups of yellowish calcite, often dark, composed of tiny fibres. Apical extremity acute, and generally in the plane of symmetry. Anastomosed petals of calcite, with their bases slightly widened (“embase”). Petals sometimes conical or parallel growth (confused with sections of a wide siphon). The filaments are dichotomous, and are arranged in a single layer near one face of the petal. In transverse section most of these filaments are round, but some are quadrate. In longitudinal section, they exhibit a series of dichotomous ramifications, and that have the form of a tuning fork or an ortonellacean structure. They are generally white, and clearly visible in the darker petal.

Composition.— *Calcifolium okense* Shvetsov & Birina, 1935 (= *C. bruntonense* Johnson, 1958); and *Calcifolium castelsequense* Pille, Vachard & Cózar sp. nov.

Remarks.— See the summary of the discussions to the attribution of *Calcifolium* in Cózar & Somerville (2005b), and Vachard & Cózar (2005).

In our material from Ardengost (Pyrenees), many petals of

C. okense appear devoid of filaments, and correspond to *Frustulata (sensu stricto)*. *Frustulata* is composed of elongate, irregular calcareous plates (phylloids to petaloids), regularly ramified or anastomosed and acute apical extremity. The holotype of *Frustulata asiatica* exhibits embases.

Palaeobiogeographically, *Calcifolium* was considered absent from China and Japan up to its discovery in Tarim (NW China) (Mamet & Zhu, 2005). It is also present in South China (Hance *et al.*, unpublished data). Hence, this genus can now testify to sporadic connections between Kazakhstan and Tarim, and between Tarim, North-West China, and South China.

Occurrence.— Late Viséan to early Bashkirian. Western and central Palaeo-Tethys. The FAD is controversial: e.g., Aleksinsky (Late Viséan) in Russia (Maslov, 1956a, pl. 9, figs 2-3, 5), Mikhailovsky (Late Viséan) (see Maslov, 1956a, pl. 9, fig. 4; Bertrand, 1972, pl. 3, fig. 10), Aleksinsky/Venevsky (*sic*) Late Viséan) of Kazakhstan (Brenckle & Milkina, 2003), Gubashkinsky-Kurmakovsky (Late Viséan) of Urals (Ivanova, 1988), Protvinsky-Bogdanovsky (late Serpukhovian- early Bashkirian) of Urals (Kulagina, 1988, p. 26; Kulagina & Pazukhin, 1988, p. 41); latest Brigantian of England and Ireland (Cózar & Somerville, 2004, text-figs 5, 12; 2005b, text-fig. 3; Somerville, 2008, p. 220); late Brigantian-Serpukhovian of southwestern Spain (Cózar *et al.*, 2003; Cózar *et al.*, 2006b, p. 276); early Serpukhovian of Illizi Basin (Algeria). *Calcifolium okense* is absent in our material from Montagne Noire and very abundant in the late Serpukhovian of the Pyrenees.

***Calcifolium castelsequense* Pille, Vachard & Cózar sp. nov.**

(Pl. 16, Figs 15-19, 21)

2008 *Falsocalcifolium? castelsequensis* sp. nov. – Pille, p. 104, pl. 33, figs 6-13 (*nomen nudum*)

Etymology.— From Castelsec, the type locality.

Type locality.— Castelsec (Montagne Noire, southern France).

Type level.— Early Brigantian.

Holotype.— Pl. 16, Figs. 15-16 (Sample Markus Aretz 10-9).

Diagnosis.—Elongate fragments of possible cups. Filaments parallel, “monaxons” rarely bifurcated from the base (and not in diapason as in true *Falsocalcifolium* or *Calcifolium*).

Description.—Length = 3.055-3.090 mm; width = 0.705-0.720 mm (up to 1.075 in holotype); filament diameter = 0.010-0.020 mm (average = 0.015 mm).

Type material.—5 specimens (fragments in longitudinal section).

Repository of the types.—University of Cologne (Germany).

Remarks.—Differs from *Falsocalcifolium punctatum* by the parallel filaments, differs from *Calcifolium okense* by incomplete cups and another network of filaments, apparently morphologically transitional between *Falsocalcifolium* (several layers) and *Calcifolium* (apparently often “monaxons”).

Occurrence.—Early Brigantian of Montagne Noire.

Genus *Falsocalcifolium* Vachard & Cózar, 2005

(Fig. 9.14; Pl. 17, Figs 14-22)

Type species: *Calcifolium punctatum* Maslov, 1956a.

Synonymy.—*Calcifolium* (part.).

Diagnosis.—Irregular ramified petaloid fan-shaped skeletal elements consisting of cups ranging in form from platose to erect and exhibiting a plane of symmetry. In an encrusting mode bushes form that include irregular dichotomous tuning-fork shaped internal structures, more or less subdivided, and occupying the total thickness of the skeletal element. Filaments are randomly arranged throughout the wall, except in the encrusting specimens, where they are more or less sub-parallel to the encrustation. The filaments are filled by microspar or diagenetic iron oxides. Wall fibrose hyaline, yellowish, sometimes dark-coloured.

Composition.—*Calcifolium punctatum* Maslov, 1956a (morphotypes A-N); ?*Falsocalcifolium* cf. *punctatum* (morphotypes 1-2) described herein.

Remarks.—In this genus, some specimens appear almost

black (e.g., Burgess, 1965; Mamet & Roux, 1975), whereas others (e.g., Vachard, 1996; Sebbar, 1998; Sebbar & Mamet, 1999) are a light yellow.

The study of Cózar & Vachard (2005) about *Falsocalcifolium* was a pionner document about the morphotypes of algaespongia. Ecotypes are morphologically changing according to the bathymetry and/or other limiting factors. Two additional morphotypes are mentioned here.

Occurrence.—Earliest Brigantian of Ireland (Cózar, 2004, p. 382) and Central Morocco (Cózar *et al.*, 2008b, text-fig. 4). Late early Brigantian (from the Smiddy and Gayle limestones)-Pendleian (Great Limestone) of northern England (Cózar & Somerville, 2004). Brigantian of Ireland (Cózar & Somerville, 2004, 2005a, 2005c). Brigantian-Serpukhovian boundary in Scotland and Poland (Burgess,

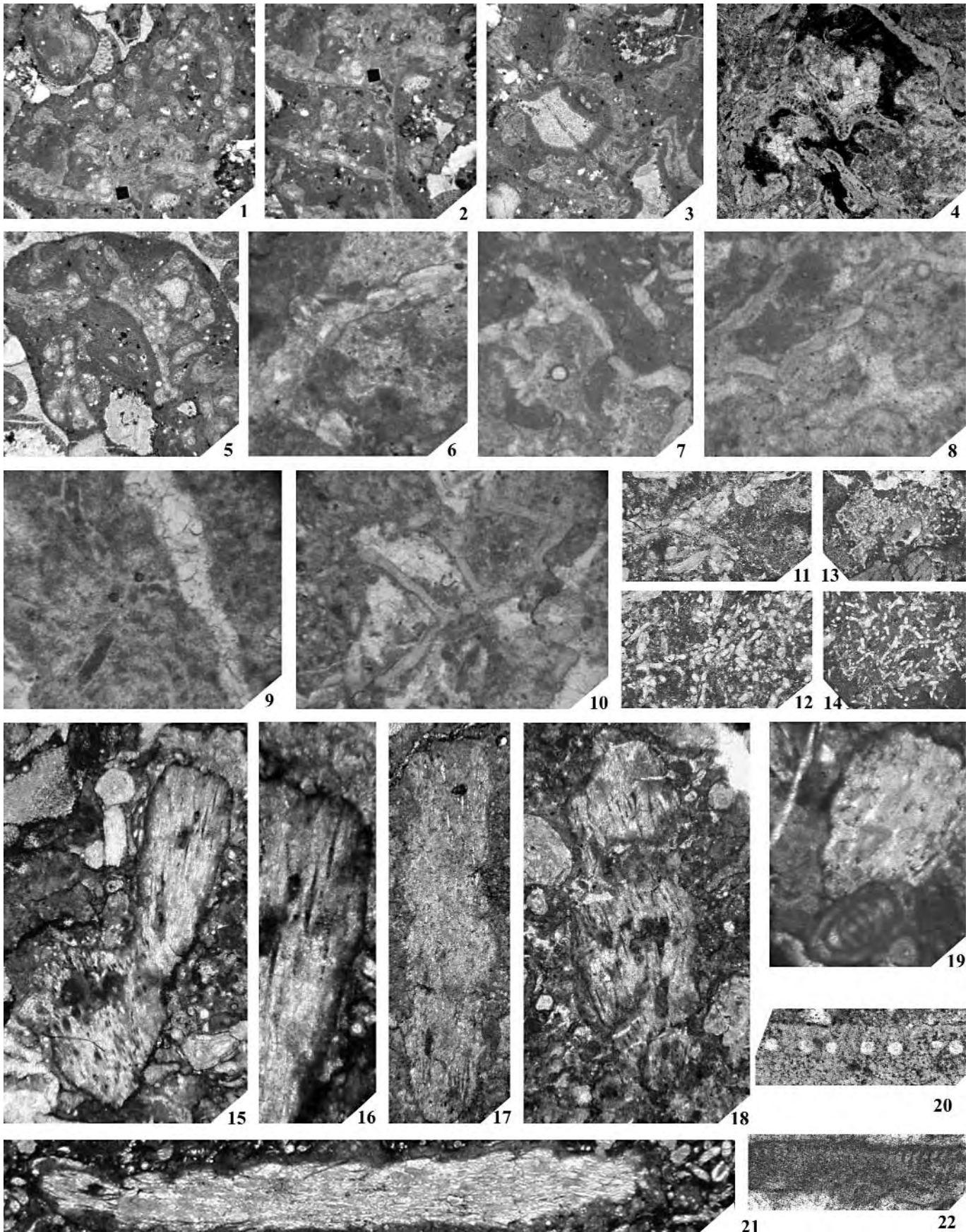
Plate 16

1-12, *Praedonezella cespeformis* Kulik, 1973. 1. Pc3272, Mouarhaz, Adarouch, late Brigantian, Central Morocco, x 34.5. 2. Pc3272, Mouarhaz, Adarouch, late Brigantian, Central Morocco, x 34.5. 3. Pc3272, Mouarhaz, Adarouch, late Brigantian, Central Morocco, x 34.5. 4. BGS-K-IB335, Netherfield Limestone, Calder River, Calderwood Castle, Brigantian, Midland Valley, Scotland, x 19. 5. Pc3272, Mouarhaz, Adarouch, late Brigantian, Central Morocco, x 34.5. 6. Pc848, Casa de la Nava, latest Brigantian-Serpukhovian, SW Morocco, x 59. 7. Pc848, Casa de la Nava, latest Brigantian-Serpukhovian, SW Morocco, x 35. 8. Pc848, Casa de la Nava, latest Brigantian-Serpukhovian, SW Morocco, x 59. 9. Pc2120, Sierra del Castillo Quarry, late Asbian, SW Spain, x 102. 10. Pc2117, Sierra del Castillo Quarry, late Asbian, SW Spain, x 48. 11. Ardengost, late Serpukhovian (Pyrenees, southern France). Sample MFP.AH18c. Photo LP9.9.4/61; x 27. 12. Ardengost, late Serpukhovian (Pyrenees, southern France). Sample MFP.AH18h. Photo LP 9.9.4/63; x 19.

13, 14, *Praedonezella primitiva* Vachard *et al.*, 2004. 13. Re-illustration of the holotype; Les Pascales, late Brigantian (Montagne Noire, southern France). Sample DV601A. Photo LP9.9/12; x 12. 14. La Serre de Péret, Brigantian (Montagne Noire, southern France). Sample MA.SP24. Photo LP9.2/25; x 10.

15-19, 21, *Calcifolium castelsequense* sp. nov, Form rare in the Early Brigantian from Castelsec (Montagne Noire). 15. Holotype. Partial longitudinal section in a cup with the filaments. Sample MA.10.9. Photo LP355; x 6. 16. Holotype. Detail of the holotype showing the filaments. Sample MA.10.9. Photo LP356; x 12. 17. Paratype. Fragment of longitudinal section. Sample MA.10.81. Photo LP377; x 18. 18. Paratype. Tangential section. Sample MA.10.12, Photo 2-P1010124; x 9. 19. Paratype. Oblique section with the base of the white filaments, associated with *Eostaffella mosquensis*. Sample MA.10.9. Photo 3-P1010102; x 20. 21. Paratype. Another fragment of longitudinal section. Sample MA.10.12. Photo 3.123; x 12.

20, 22, *Calcifolium okense* Shvetsov & Birina, 1935. 20. Longitudinal section, clear colour of the skeleton. Thin-section AH18 [E] (collection Perret). Late Serpukhovian (Arnsbergian). Ardengost (Pyrénées) (location in Perret and Vachard, 1977); x 165. 22. Longitudinal section. Thin-section PC-1792, Section I in Mamet and Martínez (1981), 32 m above the base, SW Spain, latest Asbian/earliest Brigantian?; x 35.



1965; Hallett, 1970; Skompski, 1981, 1996; Skompski *et al.*, 1989; Cózar *et al.*, 2008a, 2010 and southwestern Spain (Guadiato area, Cózar & Rodríguez, 2004; Cózar, 2004; Cózar *et al.*, 2006b: as early as the late Brigantian in Guadalquivir Valley). In the Moscow Basin, it ranges from the Aleksinsky to the Venevsky (Maslov, 1956a; Bertrand, 1972; Ivanova, 1973; but Hecker (2002) assigned all of these Russian stages to the Brigantian). Serpukhovian of Donbass (limestones C₄ to D₅) (Aizenverg *et al.*, 1983, tabl. p. 36-37); early Serpukhovian in Libya, ?Algerian Sahara (re-interpretation of Wendt *et al.*, 2009), Iran, and southern France (Massa & Vachard, 1979; Vachard & Massa, 1984; Vachard *et al.*, 1991; Vachard, 1996); Brigantian-late Serpukhovian in Algeria: Béchar, Reggane and Illizi, near the Libyan border (Mamet, 1972; Massa & Vachard, 1979; Sebbar & Mamet, 1996, 1999; Sebbar, 1998). Pendleian in eastern Turkey (Altiner, 1981) and Brigantian in western Turkey (this study). Another evidence of this provincialism is the absence of *F. punctatum* in the southern Urals (Ivanova, 1973).

***Falsocalcifolium punctatum* (Maslov, 1956a)**

(Pl. 17, Figs 20-22)

- 1956a *Calcifolium punctatum* sp. nov. – Maslov, p. 64-65, text-fig. 8, pl. 8, fig. 2, pl. 9, fig. 1, pl. 10, fig. 2.
- 2005 *Falsocalcifolium punctatum* (Maslov) – Vachard & Cózar, p. 809-811, figs 4.1-4.10, fig. 5.1-5.3 (with 37 references in synonymy).
- 2005 *Falsocalcifolium punctatum* (Maslov) – Cózar, text-fig. 3, p. 408, text fig. 4 p. 409, fig. 7.1.
- 2006b *Falsocalcifolium punctatum* (Maslov) – Cózar *et al.*, p. 276 (no illustration).
- 2006 *Falsocalcifolium punctatum* (Maslov) – Vachard & Cózar, pl. 1, figs 5.1-5.3, figs 10-14, pl. 2, figs 1-4.
- 2008 *Falsocalcifolium punctatum* (Maslov) – Pille, p. 103-104, pl. 33, figs 4-5 (with 19 references in synonymy).
- 2009 reworked skeletal remains penetrated by numerous limonitic fissures and borings – Wendt *et al.*, 2009, text-fig. 14A, p. 464.

Description.– Dimensions are not constant, except those of the filaments: diameter = 0.010 mm; angle = 30°. Other measurements are less significant due to the great mor-

phological variation of the species (Cózar & Vachard, 2004). These typical remains correspond to the morphotypes F to L of Cózar & Vachard (2004, text-fig. 3).

Occurrence.– As for the genus.

***Falsocalcifolium cf. punctatum* (Maslov, 1956a)**

morphotype 1

(Pl. 17, Figs 18-19)

Description.– In the late Viséan of Montagne Noire (southern France), *F. punctatum* are rare. Commonly, the filaments are very slightly marked. Because of populations of true *F. punctatum* and *F. cf. punctatum* are mixed together in Montagne Noire as well in Balya-Maden, Turkey (Pille *et al.*, unpublished data for a revision of the material of Argyriadis *et al.*, 1976), no different species are separated. Nevertheless, as *F. punctatum* and *F. cf. punctatum* display convergent morphotypes, two species might be also admitted.

Occurrence.– Brigantian of Montagne Noire (southern France) and Balya-Maden (Turkey).

***Falsocalcifolium cf. punctatum* morphotype 2**

(Pl. 17, Figs 16-17)

- 2004 *Praedonezella* ex gr. *cespeformis* Kulik – Vachard & Aretz, p. 659, figs 12.1-12.6.
- 2004 *Praedonezella?* sp. – Vachard *et al.*, p. 274, pl. 3, figs 11-12.
- 2006 *Falsocalcifolium cf. punctatum* (Maslov) Vachard & Cózar – Sanz-López *et al.*, figs 7.9-10.
- 2008 *Frustulata* sp. 5 – Pille, p. 102-103, pl. 32, figs 5-8, pl. 33, figs 1-3.

Description.– Petaloid to cup shaped fragments. Very faint filaments radiating from the base and apparently superficial. The parallel petaloids, are connected by transverse elements, the petaloids are also enlarged and form probably the premises of cups. Hence, many sections are V-shaped. The surfaces show radiate elements which are only grooves or the first elements similar to the filaments of *Falsocalcifolium* or *Calcifolium*. Length = 2.500-4.000 mm; width = 1.600-2.000 mm; filament diameter = 0.005 mm; distance between filaments = 0.040 mm. This morphology corresponds to the morphotypes C or N of Cózar & Vachard (2004, text-fig. 3).

Comparison.—The morphotype 1 is morphologically transitional between several species of *Frustulata*, *Praedonezella*, *Falsocalcifolium* und *Calcifolium*. It differs from the faint filaments of the other morphotypes, and from morphotype 1 by not having anastomosed cups,

Occurrence.—Viséan/Serpukhovian (La Serre) boundary beds of Montagne Noire (France) and eastern Catalan Pyrenees (Spain).

Genus *Frustulata* Saltovskaya 1984a emend. Vachard & Cózar, 2005

(Pl. 17, Figs 23-32)

Type species: *Frustulata asiatica* Saltovskaya emend. Vachard & Cózar, 2005

Synonymy.—*Pseudodonezella* Mamet & Herbig, 1990 (see Vachard & Maslo, 1996 and Vachard & Cózar, 2006); *Pseudodonezella tenuissima* Berchenko [sensu Mamet & Herbig, 1990 (see Vachard & Maslo, 1996)] (= *Frustulata hispanica* Pille, 2008 *nomen nudum*); *Donezella* (*pars*, for example sensu Buchroithner *et al.*, 1980); *Praedonezella* (*pars*).

Diagnosis.—Elongate, irregular calcareous plates (phylloids to petaloids), regularly ramified or anastomosed and acute apical extremity. Internal part of the wall uncalcified, dissolved and/or labyrinthic with pseudosepta. Ampuliform cavities exist in some cases (fertile specimens?). The “pores” described by several authors might correspond to the filaments of the other Calcifoliidae. Wall hyaline yellowish calcitic, cavities filled by micrite.

Remarks.—A part of the type-material of *Iberiaella* (holotype, Racz, 1984, fig. 3a and fig. 3c) looks like *Frustulata*, but the multilayered tubes differentiate it, and correspond more to *Donezella* Maslov, 1929 ex Vachard in Meissami *et al.*, 1978 (see above). The other specimens (Racz, 1984, fig. 3b, e-f) are similar to *Claracrusta* (= *Berestovia*) (fig. 3b, e-f). That explains probably why Sebbar & Mamet (1999, fig. 3. 99) and Sebbar (2000, fig. 22) denominated a taxon: “*Berestovia?* or *Iberiaella?* sp.”.

As indicated by Vachard & Maslo, 1996, *Praedonezella tenuissima* Berchenko, 1982 must be denominated *Masloviporidium tenuissimum*, because (a) it is not a *Praedonezella*, (b) it was designated as type species of

Masloviporidium, and (c) “*Pseudodonezella*”, illustrated by its type material, is not present in the Donets Basin.

Composition.—*Frustulata asiatica*; *F. cf. asiatica* morphotype 1; *F. cf. asiatica* morphotype 2; “*Frustulata cf. asiatica*” sensu Krainer & Vachard, 2002 (p. 15, pl. 3, figs 1, 5), “*Frustulata?* sp.” sensu Said, 2005 (p. 181); *F. ex gr. asiatica sensu* Vachard & Cózar (2005, fig. 3. 1-3).

Remarks.—*Frustulata* differs from *Falsocalcifolium* and *Calcifolium* by the total absence of filaments, from *Fasciella* in being not encrusting and from *Praedonezella* by the poorly individualized chambers.

This genus is too poorly known. Either it is a primitive stage of the calcifoliid lineage (as interpreted here) or it corresponds to those *Calcifolium* without filaments (disappearance ontogenic or diagenetic), but can also correspond to *Pseudonezella* (but to the type species designed of the genus which is a *Masloviporidium* emend. Vachard & Maslo, 1996), *Falsocalcifolium* or *Iberiaella*. It can also correspond to the deepest water morphotype of *Falsocalcifolium*, due to its location in the palaeobathymetric profiles of Montagne Noire (Pille, 2008), and in this case is a priority-synonym of this genus *Falsocalcifolium*, and a new genus than *Frustulata* to be named.

Praedonezella carbonica (sensu Vachard *et al.*, 1989, pl. 1, fig. 10, pl. 4, figs 5, 7-8) corresponds in fact to *Frustulata* (see below).

Occurrence.—Undifferentiated Viséan from Tadjikistan, Yakarchin suite, Zeravshano-Gissar area (Saltovskaya, 1984a). Late Viséan (Ladeinsky-Kurmakovsky; updated as early Serpukhovian Pendleian by Hecker, 2002, tabl. 3)-late Serpukhovian (Zapaltiubinsky) from the southern Urals (Bogush *et al.*, 1990; Ivanova & Bogush, 1992). Late Serpukhovian from Pyrenees (Delvolvé *et al.*, 1994, 1998). Brigantian-early Serpukhovian from Montagne Noire (southern France) (Roquemaillère ML 764, Castelsec, MA10 et MA10-23, and La Serre GIK 1807, GIK 1858; collections M. Legrand-Blain & M. Aretz). Brigantian/Pendleian-late Serpukhovian from Austria (Krainer & Vachard, 2002, Nötsch area, and unpublished data: collection Amler, samples PR 116-1, 4, 5, 7, PR 120 a1, PR 125-1, K 7-1). Late Viséan-late Serpukhovian from southern Spain (Betic Cordillera, Balearic Islands) and northern Morocco (Rif Mountains)

(Buchroithner *et al.*, 1980; Herbig & Mamet, 1985; Flügel & Herbig, 1988; Mamet & Herbig, 1990). Late Brigantian in Ireland (Cózar *et al.* 2005b; Vachard & Cózar 2005). Late Serpukhovian-earliest Bashkirian (zone 19) from Algeria (Sebbar & Mamet, 1999; Sebbar, 2000). Brigantian of Turkey (this study). Late Serpukhovian of NW China (Vachard *et al.*, 2003). Bashkirian *Pseudodonezella* are documented in Algeria by Sebbar & Mamet (1999, fig. 3) and Sebbar (2000, fig. 21). In the Baskhirian of northern Spain, the taxon is possibly represented by *Iberiaella*. The youngest forms are probably the early Moscovian “indeterminate donezellids” from Libya (Massa & Vachard, 1979), but only poorly preserved sections are available. *Pseudodonezella* appears similar to *Frustulata*, but its type species belong in fact to *Masloviporidium* emend. Vachard & Maslo, 1996). Bashkirian.

Pseudodonezella are documented in Algeria by Sebbar & Mamet (1999, fig. 3) and Sebbar (2000, fig. 21). In the Baskhirian of northern Spain, the taxon is possibly represented by *Iberiaella*. The youngest forms are probably the early Moscovian “indeterminate donezellids” from Libya (Massa & Vachard, 1979), but only poorly preserved sections are available.

***Frustulata* cf. *asiatica* morphotype 2**

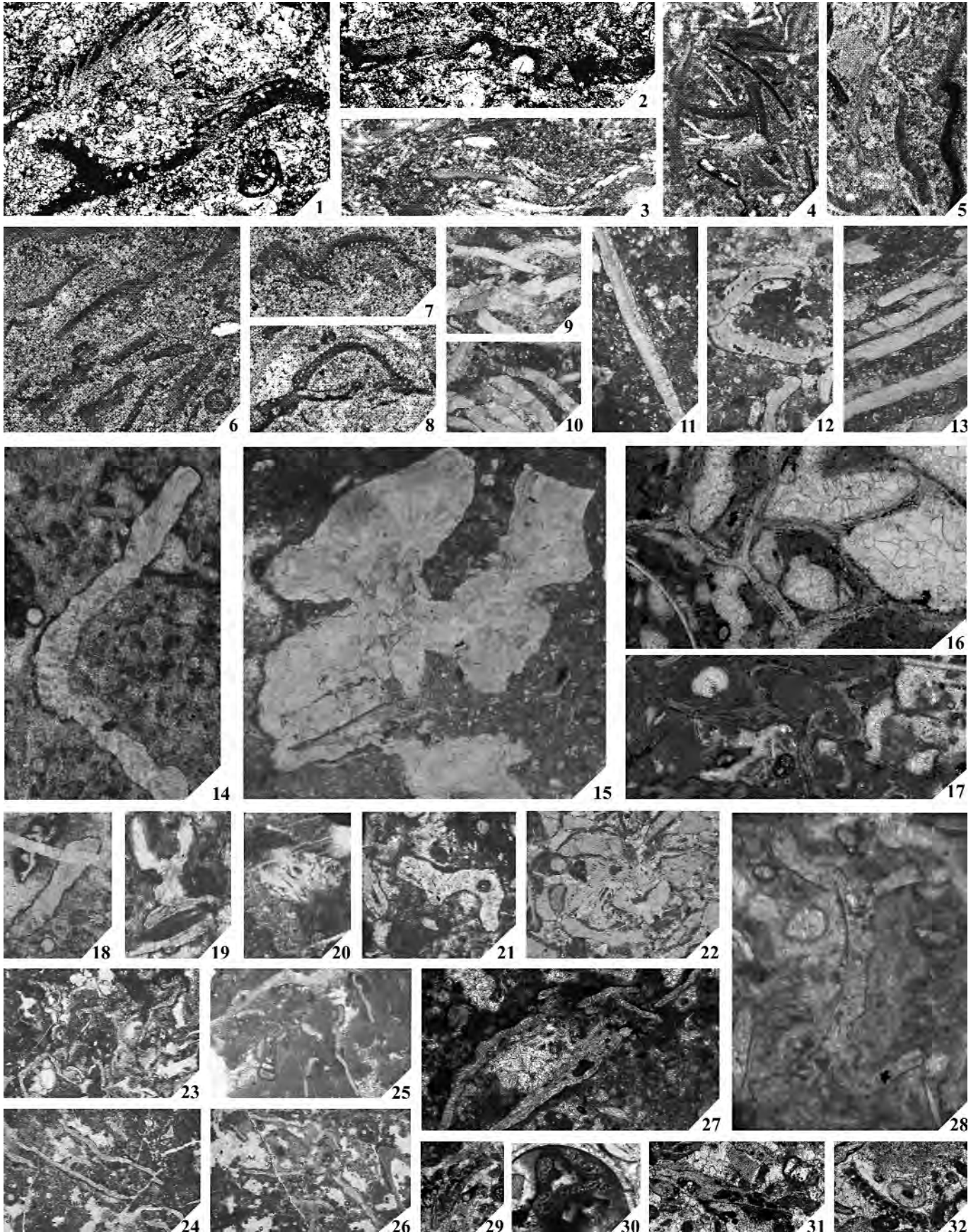
(Pl. 17, Figs. 23-27)

- 1989 *Praedonezella carbonica* (Racz) – Vachard, Perret & Delvolvé, p. 706-707, pl. 1, fig. 10, pl. 4, figs 5, 7-8.
- 2008 *Frustulata hispanica* nom. nov. pro *Pseudodonezella tenuissima* Mamet & Herbig, 1990 – Pille, p. 101-102 (no illustration).

Plate 17

1-13, *Calcifolium okense* Shvetsov & Birina, 1935. The filaments are all located in one side of the petal. 1. Tangential section. Thin-section RC 13963. Photomicrograph 15178 (collection Conil). Great Britain (Angl. 14) (location in Conil *et al.*, 1980). Late Viséan; x 30. 2. Longitudinal section of an prolate cup beginning by an “embase”. Thin-section RC 13963. Photomicrograph 15182 (collection Conil). Great Britain (Angl. 9513/4) (location in Conil *et al.*, 1980). Late Viséan; x 33. 3. Cup and petal, dark wall and white filaments in one side. Thin-section R 3 (collection Izart). Pikalova quarry. Venevsky (Upper Viséan). Moscow Basin. x 3. 4. Longitudinal section (= Cózar & Somerville, 2004, fig. 13.19), dark colour of the skeleton. Thin-section BGS-AH11, Allenheads No. 2 Borehole, Great Limestone, northern England, early Serpukhovian; x18. 5. Longitudinal section, clear colour of the skeleton. Thin-section AH18 [E] (collection Perret). Late Serpukhovian (Arnsbergian). Ardengost (Pyrenées) (location in Perret and Vachard, 1977); x 165. 6. In a porous wackestone. Thin-section R 41 (collection Izart). Okladnienskoe quarry. Aleksinsky (Upper Viséan). Moscow Basin; x 6. 7. Folded petal. Thin-section R 41 (collection Izart). Okladnienskoe quarry. Aleksinsky (Upper Viséan). Moscow Basin; x 6. 8. Several connections. Thin-section R 3 (collection Izart). Pikalova quarry. Venevsky (Upper Viséan). Moscow Basin; x 6. 9. Two petals with an embase (top, center) and other longitudinal sections. Sample MFP.AH18H. Photo LP9.9.9.4/66. Late Serpukhovian (Zapaltiubinsky). Ardengost Formation. Montagne d’Arenge (Pyrenees, southern France); x 27. 10. Numerous oblique and longitudinal sections of petals showing the transverse sections of the filaments. Sample MFP.AH28E. Photo LP9.9.9.4/29. Late Serpukhovian (Zapaltiubinsky). Ardengost Formation. Montagne d’Arenge (Pyrenees, southern France); x 27. 11. Typical specimen of the Pyrenean population (already illustrated by Perret and Vachard, 1977, pl. 10, fig. 4). Sample MFP.AH28E. Photo LP9.9.9.4/31. Late Serpukhovian (Zapaltiubinsky). Ardengost Formation. Montagne d’Arenge (Pyrenees, southern France); x 27. 12. Longitudinal section with ferruginized filaments. Sample MFP.AH20E. Photo LP9.9.9.4/135. Late Serpukhovian (Zapaltiubinsky). Ardengost Formation. Montagne d’Arenge (Pyrenees, southern France); x 27. 13. Numerous parallel longitudinal sections; notice the complete absence of encrustations or biofilms covering the petals indicating a rapid death and burying. Sample MFP.AH18F. Photo LP9.9.9.4/8. Late Serpukhovian (Zapaltiubinsky). Ardengost Formation. Montagne d’Arenge (Pyrenees, southern France); x 27. **14-15**, *Falsocalcifolium* cf. *punctatum* (Maslov, 1956a) Vachard & Cózar, 2005 morphotype 1. 14. Axial sagittal section encrusted by *Scalebrina* sp.

(s). Sample DV/MLUM.ROQ. Photo LP97.139. Early Brigantian. Roque-maillère hill (Montagne Noire, southern France); x 23. 15. Sample DV601A. Photo LP99.57. Late Brigantian. Les Pascales hill (Montagne Noire, southern France); x 18. **16-17**, *Falsocalcifolium* cf. *punctatum* morphotype 2. 16. BGS-K-IB971, Broadstone Lst., Nettlehurst Quarries, early Brigantian, Midland Valley, Scotland, x 19. 17. BGS-K-IB965, Broadstone Lst., Nettlehurst Quarries, early Brigantian, Midland Valley, Scotland, x 11. **18-19**, *Falsocalcifolium* cf. *punctatum* morphotype 1. 18. Subtransverse section in a petaloid; notice the very faint internal filaments and the associated *Archaediscus chernousovensis* (bottom, centre) and *Scalebrina* sp. (top, left). Sample ML.UM.ROQ. Photo LP 9.7/124. Early Brigantian, Roque-maillère (Montagne Noire, southern France); x 27. 19. Flabellate section announcing the cups of the typical morphotype (see Cózar & Vachard, 2004). Sample DV 601B. Photo 9.9/36. Late Brigantian, Les Pascales (Montagne Noire, southern France); x 19. **20-22**, *Falsocalcifolium punctatum* (Maslov, 1956a). 20. Bifurcated filaments. Sample DV327B. Photo LP9.8/115. Brigantian, Vailhan-Roque de Loup (Montagne Noire, southern France); x 27. 21. Overview of the typical punctations. Sample DV 601C. Photo 9.9/47. Late Brigantian, Les Pascales (Montagne Noire, southern France); x 27. 22. Same aspect. Sample IA.B35. Photo 9.9.9.6/39. Brigantian. Balia-Maden (Turkey); x 19. **23-27**, *Frustulata* cf. *asiatica* morphotype 2. 23. Longitudinal sections of clustered petaloids. Sample DV248B. Photo LP9.8/68. Brigantian, Vailhan-Castelas (Montagne Noire, southern France); x 9. 24. Longitudinal sections of subparallel petaloids showing a bifurcation. Sample DV248. Photo LP9.8/77. Brigantian, Vailhan-Castelas (Montagne Noire, southern France); x 9. 25. Tangential (top, left) and longitudinal sections (right). Sample MA44. Photo LP9.9.1/51. Brigantian, Roc de Murviel (Montagne Noire, southern France); x 9. 26. Longitudinal sections of subparallel and bifurcated petaloids. Sample DV133D. Photo LP9.9.5/.5. Early Brigantian, Roque-maillère (Montagne Noire, southern France); x 6. 27. *Frustulata* cf. *asiatica* morphotype 2. Sample MA10-23. Photo 3-P1010026. early Brigantian; Castelsec (Montagne Noire) (collection Aretz); x 9. **28-32**, *Frustulata* ex gr. *asiatica* Saltovskaya, 1984a. 28. Pc1782, Fuenteobejuna Quarry, late Asbian-early Brigantian, SW Spain, x 59. 29. Pc1188, Ballyadams Quarry, late Asbian, SE Ireland, x 29. 30. Pc-VCR/0, Via Crucis Section, early Serpukhovian, SW Spain, x 14.5. 31. Pc-SA/2-3, San Antonio Section, early Serpukhovian, SW Spain, x 40. 32. Pc-SA/2-3, San Antonio Section, early Serpukhovian, SW Spain, x 40.



Description.— *Frustulata asiatica* characterized by the large, thin and undulating tetrahedrons forming a loose network with relatively large cavities. Maximum dimensions (although deposited as an intraclastic remain) = 4.150x0.500 mm, length of petaloids = 0.200-0.715 mm, diameter of petaloids = 0.025- 0.070 mm, inner cavities width = 0.010 mm.

Comparison.— See above, the previously discussed morphotypes of *Falsocalcifolium*. This morphology does not correspond to any morphotypes of Cózar & Vachard (2004, text-fig. 3), but it is relatively similar to the morphotype D, although less complicated.

Occurrence.— Viséan/Serpukhovian (La Serre) boundary beds of Montagne Noire (France).

***Frustulata ex gr. asiatica* Saltovskaya 1984a**

(Pl. 17, Figs 28-32)

- v. 2003 *Frustulata cf. asiatica* Saltovskaya – Vachard *et al.*, p. 656 (no illustration).
- v. 2005 *Frustulata ex gr. asiatica* Saltovskaya – Cózar, text-fig. 3 p. 408, text-fig. 4 p. 409, figs 7.3-7.4.
- v. 2005 *Frustulata ex gr. asiatica* Saltovskaya – Vachard & Cózar, fig. 3.1-3
- v. 2008 *Frustulata meridionalis* sp. nov. – Pille, p. 102, pl. 32, figs 1-4 (*nomen nudum*).

Description.— Large phylloid to petaloid *Falsocalcifolium punctatum* with parallel rectilinear skeletal elements, no embase and no inner filaments. Total dimensions of specimens = 3.000-10.000 mm. Petaloid length = 1.000-3.0000 mm. Width = 0.100-0.300 mm. This aspect corresponds to the morphotypes A and B of Cózar & Vachard, 2004, text-fig. 3.

Occurrence.— Late Viséan-early Serpukhovian in southern France, SW Spain and Ireland.

5. ALGOSPONGIA EVOLUTION

To understand the Algospongia evolution (Figs 16-17), three characters must be considered: a) the modification of tubular chambers in a series of chambers and chamberlets (i.e., the passage from tubes to laminae); b) the

wall perforations; and c) the nature of the septation. On the other hand, the microstructure of the calcite wall and apertures do not present many modifications. As argued previously by Vachard (1993) and Vachard *et al.* (1994), seven steps in the evolution of Algospongia can be proposed: 1) vesicular; 2) tubular; 3) laminar with tubes; 4) essentially laminar; 5) uniseriate laminar; 6) uniseriate ramified; and 7) petaloid with filaments, although exceptions exist. The appearance of those characters is in part, randomly recorded, with rapid evolution stages and periods in which, the characters did not evolve. The most evolved characters are already observed in the Mississippian, and new characters are not recognised during the Pennsylvanian and Permian. The earliest diversification of the Class is observed during the Devonian, in particular in the Early Devonian, where the Issinellidae, Moravamminidae, Anthracoporellopsidae and Claracrustidae arose.

Despite this diversification from the base of the Early Devonian, the flourishing of the Algospongia can be recognized between the Middle Devonian and the Moscovian (Figs 15, 18), with a marked increase during the Viséan. In fact, the Algospongia increased its diversity progressively during the Devonian and at the end of this stage, 27 genera could co-exist. These numbers are similar during the Tournaisian, with 28 genera which potentially might co-exist. Despite the disappearance of numerous taxa at the top of the Tournaisian (12 genera), but the new 24 genera generated in the Viséan increased notably its diversity up to a total of 41 co-existing genera. The subsequent disappearance of 11 and 8 genera in the top of the Viséan and Serpukhovian, reduced slightly the diversity in the Serpukhovian (36 genera) and Bashkirian (35 genera), also reduced slightly more for the Moscovian (with 29 co-existing genera). The top of the Moscovian is clearly the upper boundary of the flourishing episode in the Algospongia and the beginning of the progressive impoverishment up to their final extinction at the top of the Permian (Fig. 15). These general tendencies in diversity is similar if the endemic taxa are not considered (Fig. 18). Regarding those numbers, the latest Devonian, and the Serpukhovian/Bashkirian mass extinctions did not exert an strong influence on the Algospongia, only that at the Permo-Triassic boundary, although, certainly, the Class exhibits a progressive impoverishment from the Moscovian upward.

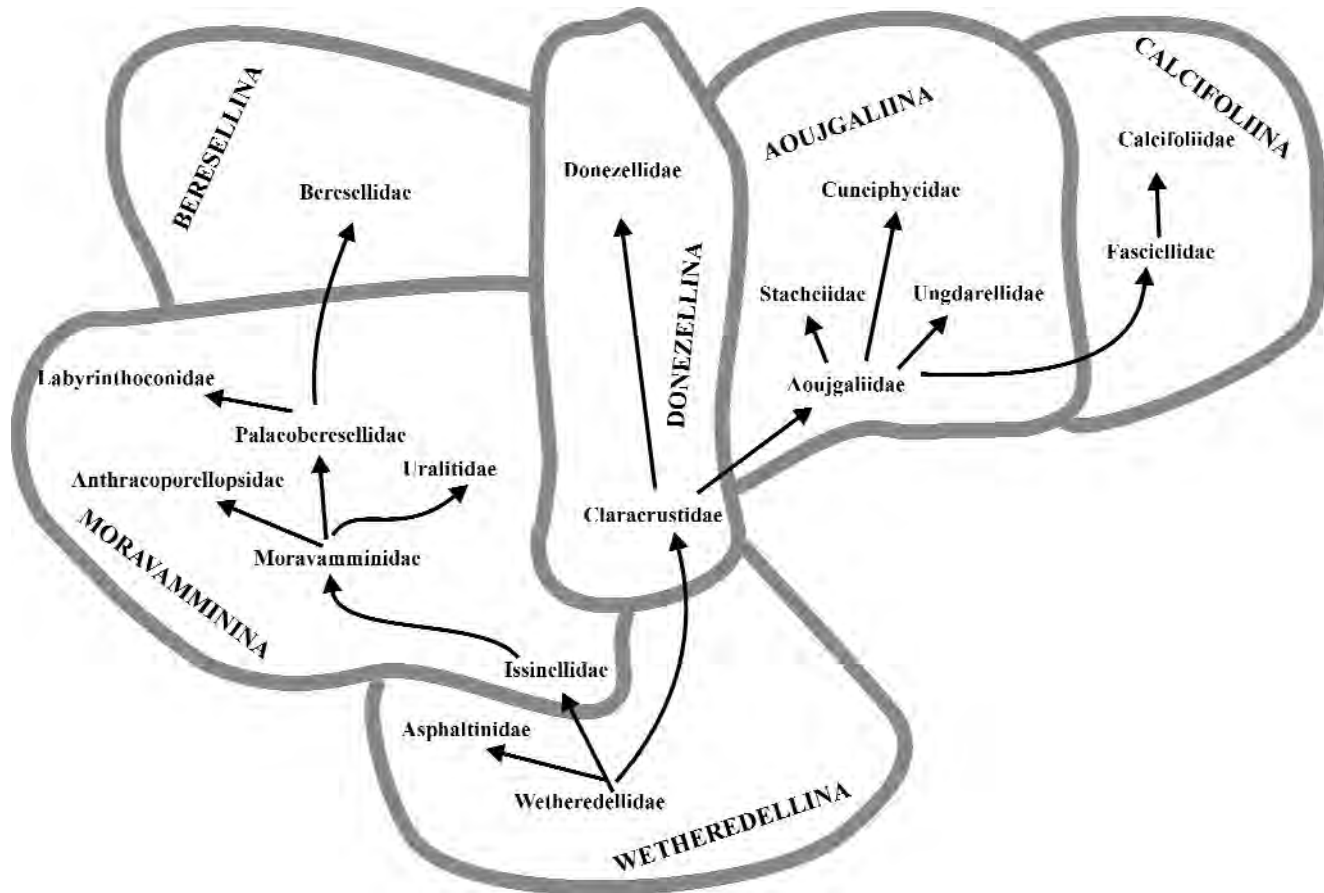


Figure 17. Macroevolution of the class Algospongia showing suborders and families.

It might be concluded that the Class is restricted to the Palaeozoic and became extinct at the end of the era. However, three unusual cases, at least, are published in the literature, and could be denominated as potential Lazarus taxa: *Koskinobullina socialis* Cherchi & Schroeder, 1979, *Kamaena khuraiensis* Adams & Al-Zahrani, 2000, and maybe *Hensonella cylindrica* Elliott, 1960.

Koskinobullina is similar to *Wetheredella* with smaller chambers and a Cretaceous Mesozoic age. The revisions of the genus by Cherchi & Schroeder (1985) and Dupraz & Strasser (1999) do not highlight sufficiently the extraordinary similarity between *Koskinobullina* and *Wetheredella*. In fact, without the enormous gap between the latter representatives of the genus *Wetheredella* in the Pennsylvanian and the Mid Jurassic first occurrences of *Koskinobullina*, this latter might be considered as a species of the former, and in consequence, it could be included within the Wetheredellidae.

Hensonella cylindrica Elliott, 1960 (Figs 3.7, 3.9, 3.11) shows a medium-sized cylindrical and undivided test, with numerous perforations, and no diaphragms. The wall is yellowish, bilayered, with a very thin dark inner layer. Elliott (1960) did not admit the assignment of his genus to the algae, nevertheless, many authors consider *Hensonella* as a senior synonym of the dasyclad *Salpingoporella* (see Bassoullet *et al.*, 1978, p. 238; De Castro, 1997, pl. 6, figs 2-4, pl. 9, figs 1-3; pl. 10, figs 1-2; Carras *et al.*, 2006, pp. 40-472; Hosseini & Conrad, 2008). On the basis of this aspect, some genera might be similarly excluded from the dasyclads, despite their morphological similarities: e.g., *Koninckopora*, *Zergabriella*, and even *Clypeina jurassica* (Figs 3.1, 3.3, 3.5). Moreover, despite the adaptation of most modern dasycladales to normal marine salinity, *Zergabriella* is associated with charophytes in hypersaline environments (Bucur & Sasaran, 2005). The synonymy of *Hensonella* with *Salpingoporella* is ques-

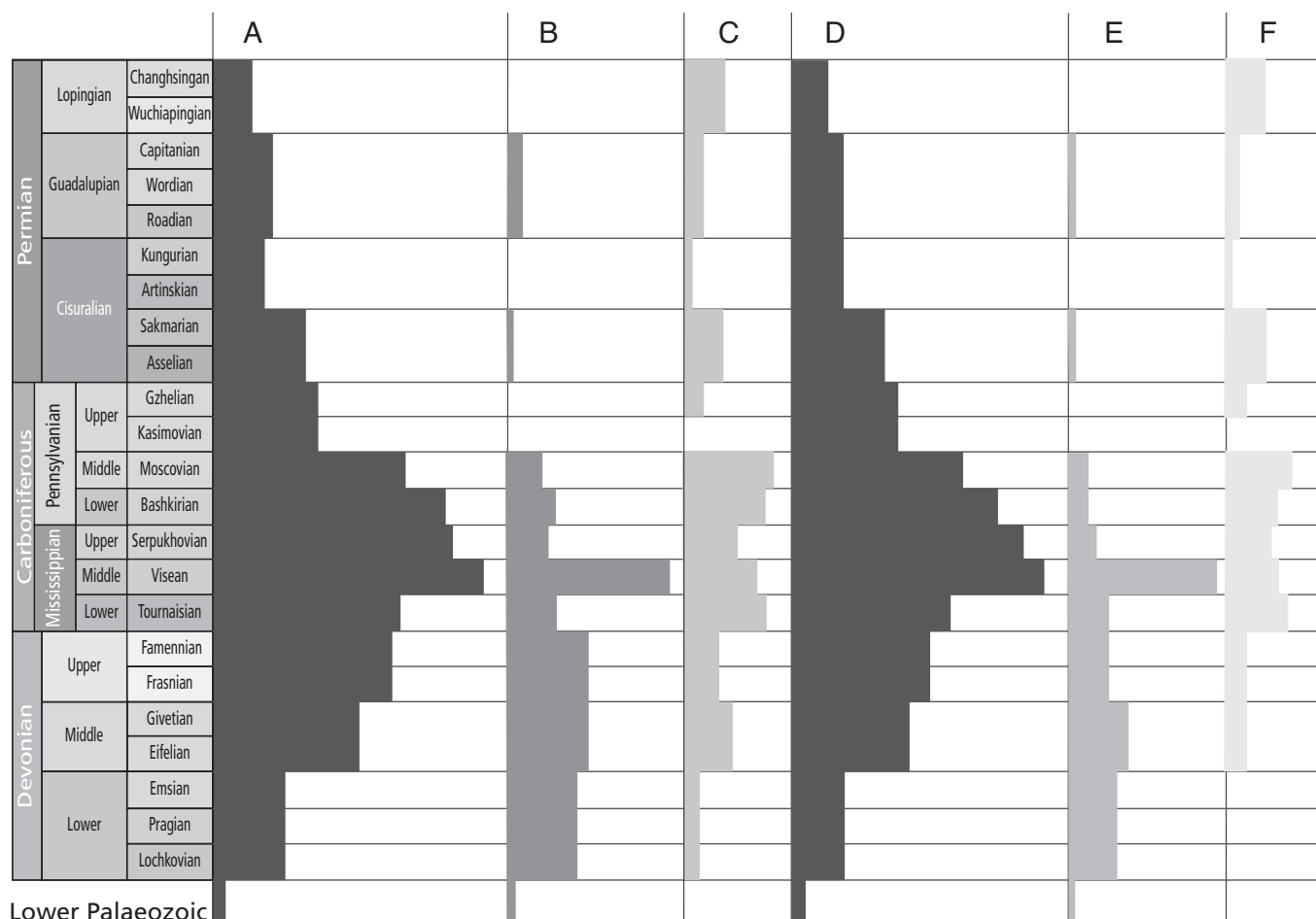


Figure 18. Histograms of Algospongia diversity in each interval. A. co-existing genera; B. number of first appearances; C. number of last occurrences; D. co-existing genera (excluding endemic taxa); E. number of first appearances (excluding endemic taxa); F. number of last occurrences (excluding endemic taxa).

tioned here; the fundamental difference in their calcification was confirmed by Simmons *et al.* (1991) and Masse & Isintek (2000, p. 369-370), *Hensonella* is originally calcitic, whereas *Salpingoporella* was evidently aragonitic, as all the dasycladales during all their history [old dasycladales preserved in aragonite are known from the Permian (Wendt, 1997), but the same type of recrystallization exists from the Ordovician]. Thus, it can be proposed an hypothetical assignment of *Hensonella* to the issinellids. Its stratigraphic range is exclusively Mesozoic, in the Early Cretaceous, Europe, North Africa, Middle East and Kalimantan (Häntzschel, 1975).

Kamaena khuraisensis Adams & Al-Zahrani, 2000, although described within the genus, but it can belong to another genus because of the maculate wall and the Jurassic age.

Despite the morphological similarities, it is difficult to admit those taxa as Lazarus effects due to the significant gap of appearances in respect to their Palaeozoic homeomorphs.

6. CONCLUSIONS

1. Algospongia, often informally referred to as “pseudalgae”, “palaeosiphonales”, “algae *incertae sedis*” or “microproblematica”, are a group of test-forming microfossils that have been mostly documented in various marine environments of Devonian, Carboniferous and Permian times. Contrary to what is widely assumed, these micro-organisms cannot be directly algal, due to their repeated occurrences in the aphotic

- zone along preserved palaeoslopes or reconstructed palaeoenvironments.
2. Currently, the group is still poorly known, and further investigations are necessary. The assignment to protozoans is the most justified, although not the extent of the problems. *Algospongia* can constitute a key group for testing the hypotheses of previous authors in zoology and protistology due to its abundance in the Early Palaeozoic, and its possible divergence since the Late Proterozoic.
 3. The systematics of the protozoan class of the *Algospongia* is emended herein, and two orders and six suborders recognised: order 1, *Moravamminida* (with the suborders *Wetheredellina*, *Moravamminina*, *Beresellina* and *Donezellina*); and order 2, *Aoujgaliida* (*Aoujgaliina* and *Calcifoliina*). They are emended here, and their families and genera are accurately discussed.
 4. Biostratigraphically, the *algospongia* can become the most important group in the Tournaisian biostratigraphy with the conodonts, due to the rarity of foraminifera and true dasycladales at least in Europe (western Palaeo-Tethys) and Gondwana.
 5. Although some genera appear as stenobaths of the euphotic zone, the group in total is relatively eurybathic, because of its possible occurrences and abundance in the aphotic zone of preserved or reconstructed palaeoslopes.
 6. *Wetheredellida* are the most primitive group, probably derived from the aphralysiacean microorganisms, interpretable as cyanobacteria or primitive protista (their aphralysiacean wall seems to be girvanellacean in microstructure, but the unilocular files of calcified chamberlets/vesicles is also foraminiferal in shape).
 7. *Issinellidae* are small perforated tubes without a proloculus; consequently they can be confused with sellitonellacean dasycladales but many other characters, especially the diaphragms, permits to reject this assignment.
 8. *Moravamminida* resemble foraminifera because they occupy probably the same biotopes (compare the donezellan *Pokorninella* with the hyaline *Polymorphinidae Discoramulina*), but although the polymorphinids are generally less productive now, the *Moravamminida* (especially the *Issinellidae*) are very productive (probably due to the weak bioconcurrency) and in this way are comparable more to modern algae than modern protista.
 9. *Aoujgaliidae* present concentric to uniseriate growths, but show more similarity to foraminifera such as *Acervulina* and *Gypsina* than to algae or microstromatopores.
 10. *Calcifoliina* are the most puzzling case, as well as the most evolved forms in the order, from a palaeobiological point of view, the cytoplasm disappears progressively (*Fasciella* to *Calcifolium*) and is replaced by endosymbiont cyanobacteria more or less similar to ortonellacean cyanobacteria. No modern equivalent of this type of evolution is known.

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Ostracods from the Strait of Hormuz and Gulf of Oman, Northern Arabian Sea

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Resumen

Se realizó un estudio taxonómico de la fauna de ostrácodos basado en 12 muestras de sedimentos del fondo, obtenidas en el Estrecho de Ormuz y el Golfo de Omán a profundidades que van desde 30 a 103 m. La fauna es moderadamente diversa cuando se la compara con otras similares de regiones indo-pacíficas. No obstante, la mayor parte de las especies están representadas solamente por unos pocos ejemplares (a veces sólo una o dos valvas). Se han identificado 83 especies pertenecientes a 53 géneros, de las que se discute su distribución biogeográfica. Se describen nueve nuevas especies (*Neonesidea paiki*, *Costa afrorientalis*, *Bosella hormuzensis*, *Quasibradleya pseudoandamanae*, *Microcythere crescentiformis*, *Paradoxostoma butticulum*, *P. curvirostrum*, *P. ensiformis*, *P. procerum*) y otras once especies se describen en nomenclatura abierta. La fauna muestra estrechas afinidades con otras del Mar Rojo y el Indo-Pacífico. Sólo una especie "cosmopolita" (*Falsocythere terryi*) es compartida con el Mediterráneo.

Palabras clave: Ostrácodos, sistemática, biogeografía, Estrecho de Ormuz, Golfo de Omán, Mar de Arabia.

Abstract

A taxonomical study of ostracod fauna was performed on 12 bottom sediment samples collected from the Strait of Hormuz and the Gulf of Oman at depths ranging from 30 to 103 m. In relation to faunas from other Indo-Pacific regions, the ostracod fauna in the studied area was moderately diverse. However, majority of the species were represented only by a few specimens (some times by one or two single valves). A total of 83 species belonging to 54 genera were identified and their biogeographic distributions has been discussed. Nine species (*Neonesidea paiki*, *Costa afrorientalis*, *Bosella hormuzensis*, *Quasibradleya pseudoandamanae*, *Microcythere crescentiformis*, *Paradoxostoma butticulum*, *P. curvirostrum*, *P. ensiformis*, *P. procerum*) are described as new and eleven species left in open nomenclature. The fauna shows close affinities to those of the Red Sea and the Indo-Pacific region. Only one "cosmopolitan" species (*Falsocythere terryi*) is common to the Hormuz/Oman region and the Mediterranean.

Key words: Ostracod, systematics, biogeography, Strait of Hormuz, Gulf of Oman, Arabian Sea.

1. INTRODUCCIÓN

Ostracod faunas of the Gulf of Oman are poorly studied. There are only a few references which have dealt with this subject from the Indian coasts of the Arabian Sea (e. g. Jain, 1978, 1981; Bhatia & Kumar, 1979; Hussain & Ra-

jeshwara Rao, 1996). Hence, the objective of the present study is to provide a detailed account on taxonomy, distribution and zoogeography of ostracod species collected from the northern coast of the Gulf of Oman at depths ranging from 30 to 103 m.

The Gulf of Oman is the northwestern part of the Arabian Sea (Fig. 1) connected to the Persian Gulf by the Strait of Hormuz. Shallow areas comprise narrow belts both along the Iranian and Omani coasts; they increase in width surrounding the Strait of Hormuz (Hartmann *et al.*, 1971; Reynolds, 1993; Sheppard, 1993; Pous *et al.* 2004a). Along the Omani coast, the continental slope falls sharply to depths exceeding 3000 m (Roe *et al.*, 1997; Prasad *et al.*, 2001). The highly saline and warm water masses formed by evaporation over the Persian Gulf sink to the bottom and flow into the Gulf of Oman via the Strait of Hormuz as the Persian Gulf Water (PGW). The region is marked by salinity levels higher than 37‰ and by temperatures more than 20°C, thus allowing identify the PGW masses from the Persian Gulf to the Arabian Sea (Pous *et al.*, 20004b). The outflow of PGW water masses is compensated by inflow of the Indian Ocean Surface Water (IOSW) from the northern Gulf of Oman (Bower *et al.*, 2000; Swift & Bower, 2003; Johns *et al.*, 2003). At the top of the Gulf of Oman, the salinity of the outflow PGW decreases due to mixing with IOSW (Matsumaya *et al.* 1998; Bower *et al.* 2000). High rates of mixing are ascribed to topographic impacts and to internal waves with amplitudes ranging up to 2 m (Pous *et al.*, 2004b).

Circulation in the Gulf of Oman is characterized by a cyclonic rotation in the west and by an anticyclonic rotation in the east which generated cold water, upwelling feature along the Iranian coast (Reynolds, 1993; Bower, *et al.*, 2000). The circulation pattern seems to exist in summer and winter, but its strength is contingent on winds (Reynolds, 1993; Bower *et al.* 2000; Pous *et al.* 2004b). The seasonal cycle of winds over the Gulf of Oman is dominated by monsoon reversals. During the summer monsoon, the prevailing winds blow from SW, while during the winter monsoon the wind direction reverses and wind speed decreases.

Pous *et al.* (2004a, b) described five distinct water masses in the Gulf of Oman which differ in their depths, temperatures and salinities: 1) the seasonal thermocline waters which are restricted to the upper 25 m and are produced during summer months with a temperature range of ~ 30 °C and a salinity of ~ 37‰. 2) the Indian Ocean Surface Water which is confined to depths ranging from 50 to 100 m, have a temperature range of ~ 20-22 °C and a salinity range of ~ 36-36.5‰. 3) the Persian Gulf Water which oc-

curs at depths between 150 and 300 m, has a temperature range of ~ 20-22 °C and a salinity range of 37.25-37.5‰. 4) the Red Sea Water which lies at 800 m depths only along the Oman coast, with a temperature range of ~ 10-12 °C and a salinity range of ~35.55‰. 5) the North Indian Deep Water exists at depths between 2000 and 4000 m, has a temperature range of ~ 2 °C and salinity range of ~ 34.8‰. This latter was observed only along the south coast of Oman. A considerable mixing is found in the upper 300 m which may be resulted either by wind and tidal activities in the Strait of Hormuz or by turbulence within the Persian Gulf Water masses.

The last decade of the warming of the Eurasian land masses and reduced spring and winter snow cover is a key driver of the stronger monsoon winds in the Arabian Sea and therefore also of stronger upwelling which immensely enhances the biological productivity during summer months of up to than 350% more along the coasts and 300% offshore waters (Goes *et al.*, 2005).

2. MATERIAL AND METHODS

Sediment samples were collected utilizing the facilities on the research ship *Ghods* during the winter of 2006 from 12 stations in the northern Gulf of Oman and the Strait of Hormuz (Figure 1 and Table 1). Samples ranged in water depth from 30 to 103 m. Bottom sediments were collected using a 0.1 m² Van Veen grab sampler. Three samples were gathered of each station by a 6.15 cm² area slender sampler. All the sediment samples were treated with formalin (4% concentrated solution) in plastic boxes. The benthic environmental factors including water depth, temperature, dissolved oxygen, salinity and pH were measured by a CTD system at the same stations.

Grain size analysis was undertaken on each sample. For this grain size analyses, 25 grams of each dried sediment sample were mixed with tap water to a total volume of 250 ml. 10 ml of Sodium hexametaphosphate (6.2 g/l) was added to disperse the sediment particles. The sediments were then stirred mechanically (15 min), allowed to soak (overnight), stirred mechanically again (15 min), washed in a 0.063 mm sieve with tap water and dried again (70 °C – overnight). The remaining dried material on the sieve

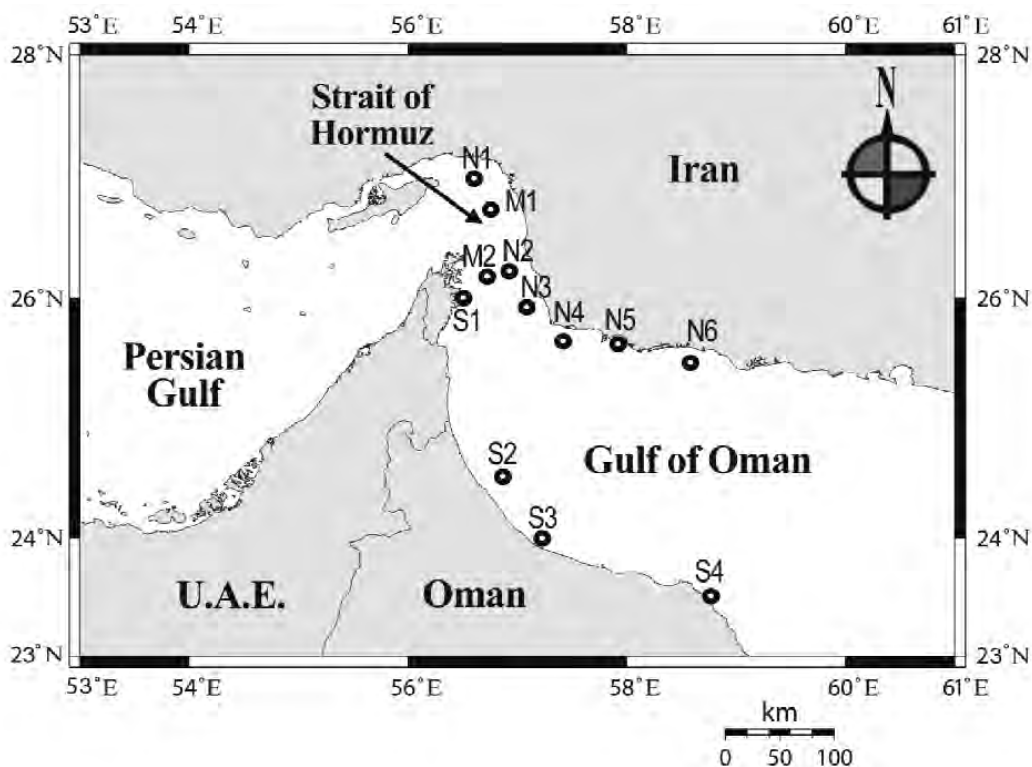


Figure 1. Geographical location of the studied area showing position of stations referred to in the text.

was transferred into the uppermost of a stacked series of graded sand sieves (4, 2, 1, 0.5, 0.25, 0.125 and 0.063 mm.). The remaining material on each sieve was then carefully removed and weighed. At the end, the percentage of each particle fraction was calculated.

The total organic matter (TOM) in each sample was measured by calculating the loss of weight during combustion. The sediment samples crucible was weighed © and half filled with wet sediment and dried in an oven (70°C) to constant weight (about 24 hrs.). After removal from the oven, it was allowed to cool and was reweighed (A). It was then placed in a Muffle furnace (550°C – overnight), removed, cooled and reweighed again (B). The total content of organic matter (TOM) was determined by the loss of weight on ignition at this temperature. [%TOM = 100 (A-B) / (A-C)].

Calcium carbonate concentration was measured based on the reaction with HCl. Twenty-five grams (W_1) of dried sediment (7 – 8 hrs.) was mixed with HCl (0.1.N) and stirred until no CO_2 bubbles were discernable, and al-

lowed to soak (24 hrs.). The upper liquid phase was discharged and the remaining sediments were filtered (with filter paper), dried (7 – 8 hrs.) and reweighed again (W_2). Calcium carbonate percentage was measured by the following formula [% $CaCO_3$ = 100 ($W_1 - W_2$) / W_1].

Latitude E	Longitude N	Station
56° 39. 30	27° 01. 40	N1
56° 54. 00	26° 15. 00	N2
57° 11. 30	25° 53. 40	N3
57° 24. 05	25° 40. 04	N4
57° 54. 00	25° 38. 20	N5
58° 36. 91	25° 26. 80	N6
56° 43. 20	26° 43. 20	M1
56° 46. 00	26° 13. 00	M2
56° 31. 77	26° 08. 76	S1
56° 50. 74	24° 33. 15	S2
57° 13. 81	24° 05. 51	S3
58° 46. 10	23° 31. 00	S4

Table 1. Position of stations referred in the text.

Station	Depth (m)	Temperature (°C)	DO (mg/l)	Salinity (ppt)	pH	TOM (%)	CaCO ₃ (%)
N1	30.39	22.76	6.17	36.74	7.96	14.93	-
N2	70.60	23.72	3.97	38.00	7.90	14.63	20.26
N3	54.94	22.28	5.39	36.47	7.93	13.79	9.49
N4	63.37	22.13	5.44	36.46	7.95	13.97	16.07
N5	54.08	22.55	5.64	36.54	7.95	12.11	-
N6	48.80	22.54	5.16	36.51	7.94	11.83	16.31
M1	63.01	22.57	5.59	36.91	7.94	24.53	11.56
M2	103.11	22.65	4.93	39.59	7.93	11.75	9.12
S1	95.12	22.73	5.44	39.90	8.23	9.82	9.92
S2	66.59	22.63	4.83	36.56	7.93	8.08	8.04
S3	56.02	21.69	2.65	36.33	7.76	17.35	8.78
S4	53.62	22.66	5.11	36.51	7.88	8.29	-

Table 2. Water depth (m), temperature (°C), dissolved oxygen (DO), salinity (pp), pH and total organic matter (TOM) at the sampling stations.

3. OSTRACOD DISTRIBUTION

In comparison with the other regions in the Indo-Pacific, the ostracod fauna of the study area was moderately diverse. However, the majority of the species identified were represented only by a few specimens (often by one or two single valves). In contrast, foraminifers, both benthic and planktonic species, are very diverse and abundant in all stations, followed by bivalves and gastropods. However, at stations M 1 and N 2 the diversity of the planktonic foraminifers decreased. Of a total of 83 ostracod species identified in the studied area, 17 (*Argilloecia* sp., *Alocopocythere reticulata*, *Callistocythere arcana* Costa *afriorientalis*, *Cytheroma dimorpha*, *Cytheropteron alabarda*, *Cytheropteron pulcinella*, *Falsocythere terryi*, *Hemicytherura aegyptica*, *Loxoconcha amygdalanux*, *Loxoconcha ornatovalvae*, *Moosella striata*, *Neonesidea* sp., *Propontocypris bengalensis*, *Propontocypris* sp., *Puricythereis exquisita*, *Tanella gracilis*) are common with the Red Sea. *Cytheropteron pulcinella* is also reported from the South Africa (Mostafawi, 2003), *Hemicytherura aegyptica* from the West Africa (Witte, 1993) and *Falsocythere terryi* from the Mediterranean and West Africa (Ruggieri, 1973; Witte, 1993). The following 4 species, *Hemicytherura aegyptica*, *Tanella gracilis*, *Venericythere darwinii* and *Venericythere papuensis*, are shared with the fauna of NW Australia (Yassini *et al.* 1993; Yassini & Jones, 1995). However, the majority of the ostracod species are

reported from the Indo-Malaysian regions and from the Persian Gulf. Only one species, *Falsocythere terryi*, is widely distributed in tropical shallow waters ranging from Indo-Pacific, East Pacific to West Africa and the Mediterranean (Witte, 1993; Jellinek, 1993).

4. SYSTEMATIC DESCRIPTIONS

The majority of the species are well known from the Persian Gulf. Mostafawi (2003) gave a comprehensive account of ostracod fauna from this area. Therefore, we treat here only the taxonomy of the taxa which were not recorded in the study mentioned above. However, the total species found in the present study are listed in appendix 1. Soft parts were not preserved. All specimens figured are deposited at the Micropalaeontological Section of Senckenberg Museum (Frankfurt am Main) under catalogue numbers SMF Xe 22250 - 22556.

Genus *Cytherella* Jones, 1850

Cytherella adenensis, Malz & Jellinek, 1989

Pl. 1, Fig. 1

- 1989 *Cytherella adenensis* Malz & Jellinek, 205, Pl. 7, Figs. 56-60; Pl. 8, Fig. 61.
 1993 *Cytherella adenensis* Malz & Jellinek. Jellinek, 107, Pl. 1, Fig. 17.

Remarks.— Whatley & Zhao (1987) assigned their specimens from the Malacca Straits to *C. hemipunctata* (Swanson, 1969) originally described from the Miocene of New Zealand, which are identical in all morphological features and seem to be conspecific with *Cytherella adenensis*. The present species also displays a close affinity to *Cytherella semitalis* Brady, 1868 illustrated by Whatley & Zhao (1987), likewise from the Malacca Straits. However, the latter species can be easily distinguished by its coarsely developed ornamentation. At its type locality (Gulf of Aden), *Cytherella adenensis* was found at 76 m depths (Malz & Jellinek, 1989). The species occurs also in mediolittoral to circalittoral zones (13 - 22 m) of the Kenyan barrier reef (Jellinek, 1993), as well as in the Malacca Straits. In the study area, the species is represented only by three specimens at the Station S 3 in 56 m water depth.

***Cytherella interpunctata* Malz & Jellinek, 1989**

Pl. 1, Fig. 2

- 1989 *Cytherella interpunctata* Malz & Jellinek, 204, Pl. 6, Figs. 50-51; Pl. 7, Figs. 52-55.
1989 *Cytherelloidea* sp.B Whatley & Keeler, 82, Pl. 5, Fig. 19.
1993 *Cytherella interpunctata* Malz & Jellinek. Jellinek, 107, Pl. 1, Figs. 11-12.

Remarks.— The species was originally described by Malz & Jellinek (1989) from E African coasts at a water depth of 20 m. It is also reported from mediolittoral to circalittoral zones (2 - 26 m) of the Kenyan barrier reef (Jellinek, 1993), Réunion, Java Sea and from Solomon Islands as *Cytherelloidea* sp. B (Whatley & Keeler, 1989). In the present study area, the species was encountered (two valves) only at station S 3 at 95 m water depth.

Genus *Neonesidea* Maddocks, 1969

***Neonesidea paiki* sp. nov.**

Pl.1, Fig. 3-5

- 1977 *Bairdoppilata* sp. A. Paik, Pl. 1, Figs. 12-13.

Derivatio nominis.— In honour of. K. W. Paik., who originally introduced the species from the Persian Gulf.

Holotype.— LV, Pl. 1, Fig. 3; Station S 1, SMF X 2251.

Paratypes.— Pl. 1, Figs.4-5, Station S 1; SMF X 22512.

Dimensions.— 1.06-1.09 mm length, 0.69-0.75 mm height.

Diagnosis.— A large species of the genus *Neonesidea* with smooth surface. Left valve highly arched in dorsal margin, subtriangular in lateral view, with rounded dorsocentral angle, very short pointed caudal process below mid-height.

Description.— A large and moderately thick-shelled species. Left valve subtriangular in lateral view; greatest height mid-length marked by a rounded, but prominent centrodorsal angle. Dorsal margin sloping straight anteriorly, slightly convex posteriorly. Anterior margin asymmetrically rounded, extremity just above mid-height. Posterior margin pointed below mid-height. Ventral margin straight; anteroventral and posteroventral slopes slightly convex. The dorsal margin of right valve, between cardinal angles, is short and straight to weakly convex, inclined slightly to the posterior margin. Anterior and posterior slopes are straight, becoming slightly concave near extremities. Posterior caudal process well developed, gently upturned. Ventral margin sinuate, posteroventral slope broadly convex. Surface of the valves smooth, normal pore canals are simple and numerous, densely distributed at anterior margin, with simple setae varying in size. In well preserved specimens the valves are fringed with minute spines, about 10 at anteroventral margin and 14 at posteroventral margin.

Remarks.— *Neonesidea vscripta* Titterton & Whatley, 1988 reported also from the Solomon Islands is greatly similar to the new species, but has asymmetrically arched dorsal margin, its dorsal angle is located anterior of mid-length in LV and its dorsal margin in RV is strongly slopes to the posterior end, which is sharply acuminate, posterodorsal and anterodorsal regions are less concave. Surface is densely covered by minute punctae. The dorsal angle of *Paranesidea? confusa* Titterton & Whatley also reported from the Solomon Islands is distinctly positioned before the mid-length in LV. Consequently, the dorsal is unequally arched. The dorsal margin (between the cardinal angles) in right valve slopes backward and is longer, in comparison to the new species. *Paranesidea* sp. 2, *sensu* Maddocks, 1969 from Nosy Be is characterized by a rounded posterior cardinal angle and is comparatively less high in proportion to length, possessing a less angular dorsal margin and has a prominent caudal process in LV.

***Neonesidea* sp.**

Pl. 1, Fig. 6

Remarks.— The only one complete carapace from the Station S 4 is similar to *N. schulzi* from the Red Sea, but clearly differs in outlines and ornamentation. Dorsal and ventral margins are convex in left valve, converging posteriorly. Posterior margin is acutely pointed just below mid-height, dorsal margin marked by a small corner. Surface is ornamented by circular punctae, which increase in diameter and space towards the central region the valve. The species is perhaps apparently conspecific with the specimen from the Gulf of Aqaba reported by Bonaduce *et al.* (1978) as *Neonesidea schulzi*, but insufficient material is available in this study to make a definitive identification.

Genus *Paranesidea* Maddocks, 1969

***Paranesidea* sp. cf. *P. fracticorallicola* Maddocks, 1969**

Pl. 1, Fig. 7

- 1969 *Paranesidea fracticorallicola* n. sp. Maddocks, 43, Figs. 16A-I, 17 A-D, 18 A-F; Pl. 1, Figs, 5-6.
 1995 *Paranesidea fracticorallicola* Maddocks. Maddocks, 207, Pl.3, Figs. 7-10; Pl. 11, Figs. 5-8 (q. v. for long synonymy list).

Remarks.— Shape of left valve elongate, suboval in lateral view. Dorsal margin broadly arched, without distinct cardinal angles. Surface ornament consists of circular punctae which are evenly distributed, decreasing in diameter peripherally. The single carapace from the Station S 1 is smaller and its dorsal margin is not as highly convex as in *P. fracticorallicola* from Nosy Be, Madagascar.

***Paranesidea* sp. cf. *P. spongicola* Maddocks, 1969**

Pl. 1, Fig. 8

- 1969 *Paranesidea spongicola* n. sp. Maddocks, 51, Figs 25 A-F, 26 A-F; Pl. 1, Figs. 9-10.
 1995 *Paranesidea spongicola* Maddocks. Maddocks, 212, Pl.5, Figs.5-8; Pl. 13, Figs. 5-7.

Remarks.— Left valve of the three single valves from the Stations S 2 and S 4 is oval in lateral view, dorsal margin evenly arched, without distinct angles. Anterior margin broadly rounded, posterior margin marked by a very short, weakly tapering caudal process below mid-height. Valve

surface is densely covered by circular punctae that increase slightly in size and spacing toward the centre of the carapace. *Paranesidea algicola* from Nosy Be is distinctly larger, thickened at anterior and posterior, producing a prominent rim. *Paranesidea spongicola* Maddocks from the same area is also distinctly larger and highly convex. The dorsal margin is symmetrically arched.

Genus *Triebelina* Van den Bold, 1946

***Triebelina bradyi* Triebel, 1948**

Pl. 1, Fig. 9

- 1890 *Bairdia truncata* Brady, 494, Pl. 2, Figs. 1-2.
 1948 *Triebelina bradyi* n. sp. Triebel, 18.
 1995 *Triebelina bradyi* Triebel. Maddocks, 214, Pl. 10, Figs. 9-10; Pl. 14, Figs. 1-2.
 2000 *Triebelina bradyi* Triebel. Whatley, Jones & Wouters, 84, Pl. 2, Figs. 11-12 (q. v. for long synonymy).

Remarks.— Brady (1890) described this species from Samoa and New Caledonia under the name of *Bairdia truncata*. However, Triebel (1948) replaced the name with *T. bradyi*, because the species name was already occupied by *Bairdia truncata* Kirkby, 1858. The species is widely distributed in the littoral zone of Indo-Pacific (Titterton & Whatley, 1988; Jellinek, 1993; Maddocks, 1995). Easter Island, southeastern Pacific is so far its most easterly occurrence (Whatley *et al.*, 2000). Fossil records range from the Upper Miocene of Fiji to the Holocene of Batu Islands, Sumatra (Keij, 1974). In their remarks concerning *T. sertata*, Mostafawi *et al.* (2005), state that "It is appropriate to note that *Triebelina truncata* (Brady, 1890) from Samoa, as can be seen from the SEM illustration provided by McKenzie (1986), displays conspicuous similarity to *T. sertata*. It may be that these two forms are conspecific". However, they preferred to keep *T. bradyi* Triebel, 1948 (herein) and *T. sertata* are very similar, but can be distinguished by a short median ridge parallel to dorsal margin in the left valve of *T. sertata* and its ventrolateral carina is marked by a prominent U-shaped tubercle in the middle in both valves. In the study area, the species was represented by two single valves at the Station S 1.

Genus *Copytus* Skogsberg, 1939

***Copytus posterosulcus* Wang, 1985**

Pl. 2, Fig. 9

- 1985 *Copytus posterosulcus* Wang (in Zhao *et al.*), 211, Pl. 21, Figs. 9-13.
1988 *Copytus posterosulcus* Wang. Wang *et al.* 243, Pl. XLI, Fig. 19.
1993 *Copytus cf. posterosulcus* Wang. Jellinek, 122, Pl. 8, Figs. 184-185
1995 *Copytus posterosulcus* Wang. Yassini & Jones, 365, Figs. 615-617.
2006 *Copytus posterosulcus* Wang. Titterton & Whatley, 181, Pl. 1, Figs. 1-6; Fig. 4, Nos. 1-2, 4-5 (q. v. for detailed synonymy).

Remarks.— The species shows certain variability in outlines and also in internal features, as illustrated by Titterton & Whatley (2006). The anterior margin of the specimens from the Gulf of Oman is rather bluntly rounded and is not angular truncate. For this reason, Jellinek (1993) attributed the specimens from Kenyan coast with hesitation to *Copytus posterosulcus*. However, Titterton & Whatley (2006) considered the east African occurrence as being conspecific. The species is widely distributed in the Indo-Pacific area reaching from E Africa to Solomon Islands. In the present study it very rarely occurs at Stations S 1 and S 2, mostly in immature stages.

Genus *Bishopina* Bonaduce, Masoli & Pugliese, 1978

***Bishopina* sp.**

Pl. 2, Fig. 7

Remarks.— The outline of the single valve from the Station S 3 is very similar to *B. guhai* Jain 1978 which is also present in the same sample, but differs in ornamentation. The entire surface of the latter species is evenly covered with foveae.

Genus *Costa* Neviani, 1928

***Costa afriorientalis* sp. nov.**

Pl. 1, Figs. 13-16

- 1978 *Costa* cf. *C. punctatissima* Ruggieri. Bonaduce, Masoli & Pugliese, 384, Pl. 5, Fig. 2.

Derivatio nominis.— L. With reference to the occurrences of the species.

Holotype.— Right valve, Pl. 1, Fig. 13, Station S 4; SMF X 22518.

Paratypes.— Pl. 1, Figs. 14-16, + 3 valves, Station S 4; SMF X 22519.

Dimensions.— 0.73-0.79 mm length, 0.35-0.40 mm height.

Diagnosis.— A species of *Costa* with coarse reticulation, fossae tegminate in central area; anteroventral costa bifurcate, ventral margin concealed by overhanging rib.

Description.— Carapace subrectangular, somewhat inclined toward the posterior in lateral view.

Anterior margin broadly rounded, extremity below mid-height, furnished by about 17 spines.

Posterior margin bluntly pointed, apex below mid-height; posterodorsal slope slightly concave, posteroventral slope straight, fringed with about 10 spines that are arranged in 5 double rows. Dorsal margin straight to slightly convex, inclined towards the posterior. Ventral margin concealed by overhanging ventral rib. Greatest length just below mid-height, greatest height at the anterior cardinal angle. Valve surface covered by prominent reticulum with emphasis on three solid longitudinal costae. Intercostal fossae are polygonal in dorsocentral area, distinctly tegminate in centroventral region. Fine riblets, formed from enhanced muri of the reticulae, extend toward the anteromarginal and dorsomarginal ribs. A prominent rib starts from the eye tubercle parallels to the anterior margin then extends to form the bifurcate ventrolateral rib. The median rib is connected with the dorsal rib by a short transverse riblet in the posterodorsal area. Ventral rib is sinuate and bifurcate. The space between costae is covered by oval to rectangular fossae.

Remarks.— *Costa punctatissima* Ruggieri, 1962 from the Plio-Pleistocene of Mediterranean is the closest species, but differs in many respects. Its dorsal margin is straight, anterior margin evenly arched. The ornament consists of rounded or polygonal fossae varying in size, some of which often form small clusters and frequently coalesce. The surface of *Costa edwardsii* (Roemer, 1838), an extant Mediterranean species, is evenly covered by relative small and polygonal fossae. The longitudinal costae are relatively weakly developed. The median and ventrolateral costae are not linked with the anterior margin. Bonaduce

et al. (1978) referred the single specimen, found in Gulf of Aqaba (Red Sea) at a depth of 370 m, with reservation to *C. punctatissima*, and noted that it may have “drifted” down to the recorded depth.

Genus *Moosella* Hartmann, 1964

***Moosella striata* Hartmann, 1964**

Pl. 1, Fig. 18

1964 *Moosella striata* Hartmann, 111, Pl. 46, Figs. 270-273; Pl. 50, Figs. 289-292; Pl. 51, Figs. 93-97.

1978 *Moosella striata* Hartmann. Bonaduce, Masoli & Pugliese, Pl. 5, Fig. 7.

1980 *Moosella striata* Hartmann. Bonaduce, Masoli, Minichelli & Pugliese, Pl. 4, Figs. 1-4.

Remarks.— The three single valves from Stations S 1 and S 3 agree well in ornament and size with the left valves illustrated by Bonaduce *et al.* (1980) from the Gulf of Aqaba, but in the present specimens interstitial foveae are coarser, circular in shape and evenly placed. In addition, the longitudinal striae are less prominent in centroventral region in the present species.

Genus *Hiltermannicythere* Bassiouni, 1970

***Hiltermannicythere* sp.**

Pl. 1, Fig. 19

Remarks.— The single valve from the Station S 4 is strongly ornamented. The dorsolateral rib is interrupted by an oval pit; central and ventrolateral ribs and joined at both ends to form a tube-shaped sculpture which is connected to the dorsal margin by a hook-shaped riblet. The posterior is furnished by three prominent spines.

Genus *Kingmacythere* Zhao & Whatley, 1989

***Kingmacythere seddighii* (Mohan, Ravi, Hussain & Rajeshwara Rao 2001)**

Pl. 1, Fig. 17

1977 *Hemitracyleberis* sp. A. Paik, Pl. 3, Figs. 56-58; Pl. 9, Fig. 157.

1981 *Hemitracyleberis* sp. Jain, Pl. 2, Fig. 8.

2001 *Hemitracyleberis seddighii* n.sp. Mohan, Ravi, Hussain & Rajeshwara Rao, 9. Pl. 2, Figs. 7-12.

Remarks.— *Kingmacythere cruysi* (Kingma, 1948), type species of the genus, described from the Pliocene of Java

and restudied by Zhao & Whatley (1989a) is superficially similar in shape and outline, but differs in details of ornamentation and in being clearly smaller. *K. seddighii* is reported from the Persian Gulf (Paik, 1977), west coast of India (Jain, 1981) and from the inner shelf of the Bay of Bengal off Karikkattukuppam (Mohan *et al.*, 2001). In the study area, the species is represented by a single valve at the Station M 1.

Genus *Lankacythere* Bhatia & Kumar, 1979

***Lankacythere coralloides* (Brady 1886)**

Pl. 1, Figs. 10-11

1886 *Cythere coralloides* n. sp. Brady 307, Pl. 39, Figs. 19-22.

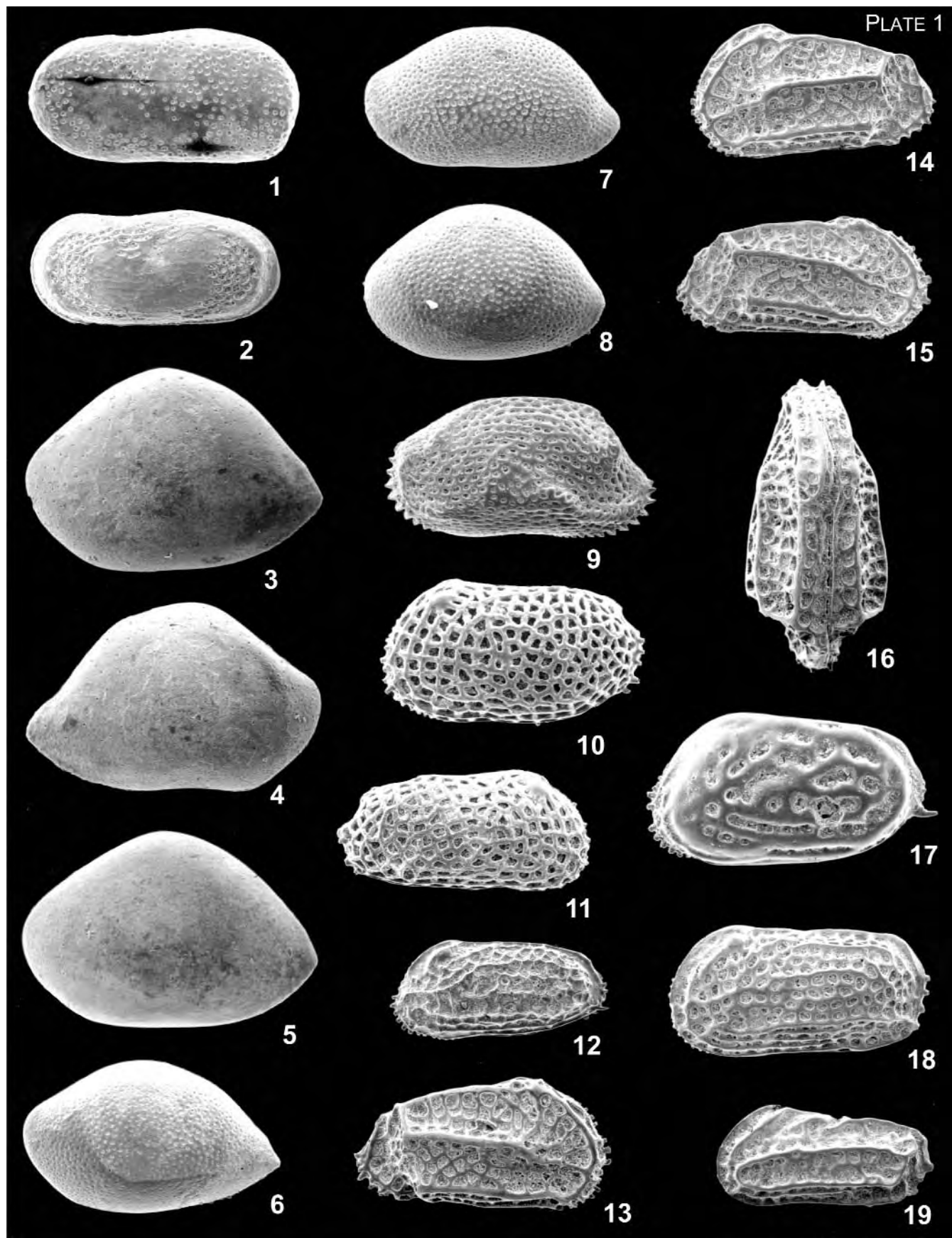
1971 Genus B sp. Bate, Pls. 1-3, Figs. p.

1979 *Lankacythere coralloides* Brady. Bhatia & Kumar, 176, Pl. 1, Figs. 1-5.

2002 *Lankacythere coralloides* Brady. Sridhar *et al.*, 27, Pl.2, Fig. 19 (q. v. for detailed synonymy).

Remarks.— When Zhao & Whatley (1989a) restudied Kingma’s collection, they considered that *Cythereis reticulinea* Kingma, 1948 from the Pliocene of N Sumatra and E Java was conspecific with *Cythere coralloides* Brady, 1886 from off Sri Lanka, and noted that specimens from the west coast of India selected by Bhatia & Kumar (1979) as the type species of *Lankacythere* were identical with Brady’s types, which they examined in the Hancock Mu-

Plate 1. 1, *Cytherella adenensis* Malz & Jellinek, 1989; LV, external lateral view, S 3, SMF Xe, 22509, x 70. 2, *Cytherella interpunctata* Malz & Jellinek, 1989; LV, external lateral view, S 1, SMF Xe 22510, x 70. 3-5, *Neonesidea paiki* sp. nov.; 3, Holotype, LV, external lateral view, S 1, SMF Xe 22511 x 50; 4, Paratype, RV, external lateral view, S 1, SMF Xe 22512, x 50; 5, Paratype, LV, external lateral view, S 2, SMF Xe 22512, x 50. 6, *Neonesidea* sp.; LV, external lateral view, S 1, SMF Xe 22513, x 60. 7, *Paranesidea* cf. *P. fracticorallia* Maddocks, 1969; LV, external lateral view, S 4, SMF Xe 22514, x 60. 8, *Paranesidea* cf. *spongicola*, Maddocks, 1969; LV, external lateral view, S 2, SMF Xe 22515, x 60. 9, *Triebelina bradyi* Triebel, 1948; LV external lateral view, S 1, SMF Xe 22516, x 80. 10-11, *Lankacythere coralloides* (Brady, 1886); 10, female, LV, external lateral view, S 1, SMF Xe 22523, x 60; 11, male, RV, external lateral view, S 1, SMF Xe 22523, x 60; 12, *Chrysocythere keiji* Jain, 1978; male, LV, external lateral view, N 1, SMF Xe 22524 x 60. 13-16, *Costa afriorientalis* sp. nov.; 13, Holotype female, RV, external lateral view, S 2, SMF Xe 22518, x 60; 14, Paratype, female, LV, external lateral view, S 2, SMF Xe 22519 x 60; 15, Paratype, male, RV, external lateral view, S 4, SMF. Xe 22519, x 60; 16, Paratype, carapace, dorsalview, S 2, SMF Xe 22519 x 60 17, *Kingmacythere seddighii* (Mohan, Ravi, Hussain & Rajeshwara Rao 2001); LV, external lateral view, M 1, SMF Xe 22522, x 60. 18, *Moosella striata* Hartmann, 1964; LV, external lateral view, S 4, SMF Xe 22520, x 60. 19, *Hiltermannicythere* sp., LV, external lateral view S 1, SMF Xe 22521, x 60.



seum. Apparently, the slide (Slide 1.56.30) checked by Mostafawi (1992) does not contain the original contents. Nevertheless, is here considered that the specimens from the Malacca Straits reported by Zhao & Whatley (1989a) and those from the Pliocene of Java illustrated by Zhao & Whatley (1989b) display differences to specimens attributed to this species from the Persian Gulf (Bate, 1971) or from the Arabian Sea (Bhatia & Kumar, 1979; Jain, 1981) and from southeast coasts of India (Hussain 1998; Mohan *et al.*, 2001; Sridhar *et al.*, 2002; Hussain *et al.* 2004; Hussain, *et al.*, 2006). The specimens from the Pliocene of E Java and the Recent material from the Malacca Straits have a fine but distinct dorsolateral rib which extends from just behind the eye spot to the posterior and overhangs the dorsal margin posteriorly.

Genus *Chrysocythere*, Ruggieri, 1962

***Chrysocythere keiji* Jain, 1978**

Pl. 1, Fig. 12

- 1977 *Chrysocythere* sp. Paik, 40, Pl.4, Figs65-67; Pl. 9, Fig.167.
 1978 *Chrysocythere keiji* n. sp. Jain, 113, Figs.3L1-2; 6K.
 2002 *Chrysocythere keiji* Jain. Sridhar, Hussain, Kumar, Periakali, 26, Pl. 2, Fig. 12.
 2003 *Chrysocythere coralloides* Brady. Mostafawi, 62, Figs. 22 A-C.

Remarks.— Mostafawi (1992, 2003) considered this species as a junior synonym of *Cythere coralloides*. However, this species is here regarded as distinct from *C. coralloides* as deferred by Bhatia & Kumar (1979 and Zhao & Whatley (1989). The species is widely distributed from the Persia Gulf to southeast coast of India. In the studied area, the species was rarely represented at Stations N 1, M 2 and S 4.

Genus *Falsocythere* Ruggieri, 1972

***Falsocythere terryi* (Holden, 1967)**

Pl. 2, Fig. 11

- 1967 *Neocaudites terryi* n. sp. Holden 43, Figs. 33a–33d.
 1988. *Falsocythere maccagnoi* (Ciampo). Szczechura & Abd-Elshafy, 307, Pl. 11, Figs. 8a-b.
 1989 *Falsocythere indica* n. sp. Khosla & Nagori, 25, Pl. 3, Figs. 4-6.

1993 *Falsocythere terryi* (Holden). Witte, 47, Pls., Fig. 22-26 (q. v. for detailed synonymy).

1993 *Falsocythere terryi* (Holden). Jellinek, 140, Pl. 11, Figs. 218-231.

Remarks.— *F. terryi*, an extant Miocene (possibly Oligocene) species of Tethyan origin, is one of the most widely distributed ostracod species have been reported from all tropical to subtropical littoral seas across the globe - extending from Caribbean, Gulf of Mexico, East Pacific Ocean, East Atlantic, Mediterranean including Red Sea and Persian Gulf and from the Indo-Pacific Ocean (Jellinek, 1993; Witte, 1993). It has however been reported under different names, mostly as *F. maccagnoi* Ciampo, 1971. Cronin (1988) recognised that *Neocaudites pacifica pacifica*, *N. pacifica mnima* Alison & Holden, 1971 from Clipperton Island and *N. scottae* Teeter, 1975 from Belize are junior synonymous of *N. subimpressus* (Edwards, 1944) from the Upper Miocene of North Carolina which is also regarded as being a possible senior synonym (Witte, 1993). The comprehensive study of *F. terryi* by Witte (1993) revealed that *Occultocythereis maccagnoi* Ciampo, 1971 from the Pleistocene of Taranto (Italy) and *Neocaudites purii* from Western Niger Delta are junior synonyms of *F. terryi*. Further specimens from the Lower Miocene of Kerala (SW India), described as *Falsocythere indica* by Khosla & Nagori (1989), are identical with *F. terryi* in all external morphological features and here considered junior synonymous. The specimen reported by Mohan *et al.* (2001) from the Bay of Bengal differs in some respects from *F. terryi*. In the studied area, the species was present (two single valves) only in Station M 2.

Genus *Occultocythereis* Howe, 1951

***Occultocythereis* sp.**

Pl. 2, Fig. 10

Remarks.— The surface of two specimens found in sample S 3 is very delicately reticulated and densely covered by very fine punctae. The normal pore canals are relatively large, increasing in number anteriorly. Some of them are developed as conical protrusions. *O. angusta* (Bold, 1963) from the Upper Miocene and Pleistocene of Trinidad is very similar in outline, but differs in having an alate ventrolateral rib.

Genus *Patrizia* Bonaduce & Russo, 1990

***Patrizia indopacifica* Whatley & Zhao, 1988**

Pl. 2, Fig. 1

- 1977 *Brachycythere* (B.) sp. A. Paik, Pl. 4, Figs. 74-75; Pl. 9, 163.
1988 *Ruggieria indopacifica* n. sp. Whatley & Zhao, 16, Pl. 8, Figs. 14-18.

Remarks.— The species is characterized by a tegminate reticulum and by a row of oblique spines in posteroventral region. Specimens from the Java Sea reported by Dewi (1997) have a strongly arched dorsal margin and the row of oblique posteroventral spines is absent. *P. bonaducei* Jellinek, 1993 from the Kenyan barrier reef is the closest species, but can easily be distinguished by lacking the ventral inflation and by the ornamentation, which consists of circular to rectangular foveae and concentrically arranged costae. Dorsal margin of *P. mascellaroi* Bonaduce & Russo, 1990 from the Gulf of Aden is arched in left valve, with greatest height before mid-length. Its posterior margin is produced as a caudal process in lower half, bearing a small spine. The reticulum consists of deep foveae which decrease in size, and the anteromarginal rib is lacking. The species is reported from the Persian Gulf (Paik, 1977) and Malacca Straits (Whatley & Zhao, 1988). The species was very rare in the present study occurring at Stations N 2, M 2 and S 1.

Genus *Neohenryhowella* Bhatia & Kumar, 1979

***Neohenryhowella hartmanni* Jain, 1978**

Pl. 2, Fig. 2

- 1977 *Echinocythereis* sp. A. Paik, Pl. 4, Figs. 77-78.
1975 *Actinocythereis tumefacensis* Lubimova & Guha. Honappa, Pl.1-3 (non *Actinocythereis tumefacensis* Lubimova and Guha, 1961).
1978 *Neohenryhowella hartmanni* n. sp., Jain, 106, Figs 3 F 1-4; 6 G.
1979 *Neohenryhowella* (*Neohenryhowella*) *hartmanni* Jain. Bahtia & Kumar, 174, Pl. 3, Figs. 1-3.

Remarks.— We consider *Neohenryhowella* an independent genus from *Henryhowella* because of differences in ornamentation and in the nature of the frontal scar. *Neohenryhowella* is characterized by two faint longitudinal ribs and by two distinctive furrows: one is the longitudinal

median furrow; another is an oblique furrow present below the eye spot. Bhatia & Kumar (1979) recognized that the specimens identified by Honnappa (1975) as *Actinocythereis tumefacensis* are conspecific with *Neohenryhowella hartmanni*, we support this view. The species is reported from the Persian Gulf (Paik, 1977) and from the west coast of India (Jain, 1978, 1981; Bhatia & Kumar, 1979; Hussain & Rajeshwara Rao 1996). In the study area, it has been encountered at Stations M 2, N2, N4, S 1 and S 3.

Genus *Bosella* Bonaduce, 1985

***Bosella hormuzensis* sp. nov.**

Pl. 2, Figs. 3-4, 8

Derivatio nominis.— Reference to the Strait of Hormuz.

Holotype.— Left valve, Pl. 2, Fig. 3, Station S 1; SMF Xe 22529.

Paratypes.— 2 right valves, Pl. 2, Figs. 4, 8 + 2 valves, Station S 1; SMF Xe 22530.

Dimensions.— 0.84-0.89 mm length; 0.47-0.54 mm height.

Diagnosis.— A medium sized species of the genus *Bosella* with a tubercle-like complex of muri over the muscle scar region having a central Y-shaped mural structure; coarse reticulum with muri of equal strength. Ventral rib ala-like, overhanging margin, furnished with a spine at the top.

Description.— Carapace medium in size, thick-shelled, subrectangular in lateral view. Dorsal margin undulate, slightly sloping posteriorly, with a distinct ear at the posterior cardinal angle in left valve. Anterior margin broadly rounded, bearing 13-15 denticules. Posterior margin of the left valve obliquely rounded, of the right valve blunt, subtriangular, without noticeable caudal process, in upper part concave, in lower part convex, with 8-10 small spines. Ventral margin concealed by overhanging ventrolateral ala. Greatest height at anterior cardinal angle, greatest length about mid-height. Valve surface covered by a robust and well developed reticulum. A thin rib initiated from the eye spot runs parallel to anterior margin for some distance to reach the ala-like ventral rib, which possesses a terminal spine. A fine, zig-zag dorsolateral rib originating a little below the eye spot, turns posteriorly downward, runs parallel to the posterior margin to reach

the ala posteroventrally. Three costae formed by enhanced longitudinal muri of the reticulum extend posteriorly to join a tubercle-like complex of muri over the muscle scar region, which is characterized by a prominent central Y-shaped member. Fossae are larger and triangular in shape near anterior and posterior margins. Four to five fossae coalesce to a large pit in the postero-central region. Inner lamella moderately wide, line of concrescence coincides throughout with inner margin. Marginal pore canals fairly numerous, straight, simple.

Remarks.— *Hemicythere? borchersi* Hartmann, 1964 from the Red Sea possesses three longitudinal ribs of which the dorsal one overhangs the dorsal margin posteriorly, and the median rib is interrupted in the central muscle scar region by a sulcus.

Genus *Quasibradleya* Benson, 1972
***Quasibradleya pseudoandamanae* sp. nov.**

Pl. 2, Figs. 5-6

1977 *Bradleya* (*B.*) *andamanae* Benson. Paik, Pl. 6, Figs. 99-100.

Derivatio nominis.— Pseudo (gr.) meaning sham + andamanae.

Holotype.— Left valve, Pl. 2, Fig. 6, Station S1; SMF Xe 22531.

Paratypes.— Right valve, Pl. 2, Fig. 6 + 2 valves, Station S 1; SMF Xe 22532.

Dimensions.— 0.84-0.86 mm length (without spines), 0.45-0.49 mm height.

Diagnosis.— A species of *Quasibradleya* which is coarsely reticulate, ventral margin obscured by projecting mural costae posteriorly, median rib join with ventral rib, forming a posteroventral loop.

Description.— Median to large, thick-shelled, subrectangular in lateral view. Anterior margin broadly rounded, fringed with about 17 small spines; posterior margin straight to slightly concave in upper part, produced and convex in lower part, wearing 4 spines. Dorsal margin concealed by overhanging dorsal rib, otherwise straight; ventral margin sinuate, obscured by projecting mural

costae posteriorly. Greatest length below the mid-height; greatest height at the anterior cardinal angle. Valve surface coarsely reticulate, mural elements enhanced and bound deeply excavated fossae; dorsolateral rib curved, overhangs the dorsal margin and extends to the posterior margin; it unites anteriorly with the bold ocular riblet and continues to reach the median rib, which joined with ventral rib forming a posteroventral loop.

Remarks.— *Bradleya andamanae* Benson, 1972 from the Andaman Sea is much smaller (0.70 mm compared to size of present specimens: 0.84-0.86 mm) and shows typical *Bradleya* features. The posterior margin of *Q. plicocarinata* Benson, 1972 from the Great Australian Bight is obliquely enlarged toward the posteroventer. Its dorsal rib joined with the median rib in the posterior to form a loop. The species is rarely present at Stations M 1, M 2, S I and S 3.

Genus *Caudites* Coryell & Fields, 1937

***Caudites javana* Kingma, 1948**

Pl. 2, Fig. 12

1948 *Caudites medialis* Coryell & Fields var. *javana* Kingma, 85, Pl. 10, Figs. 5a-b.

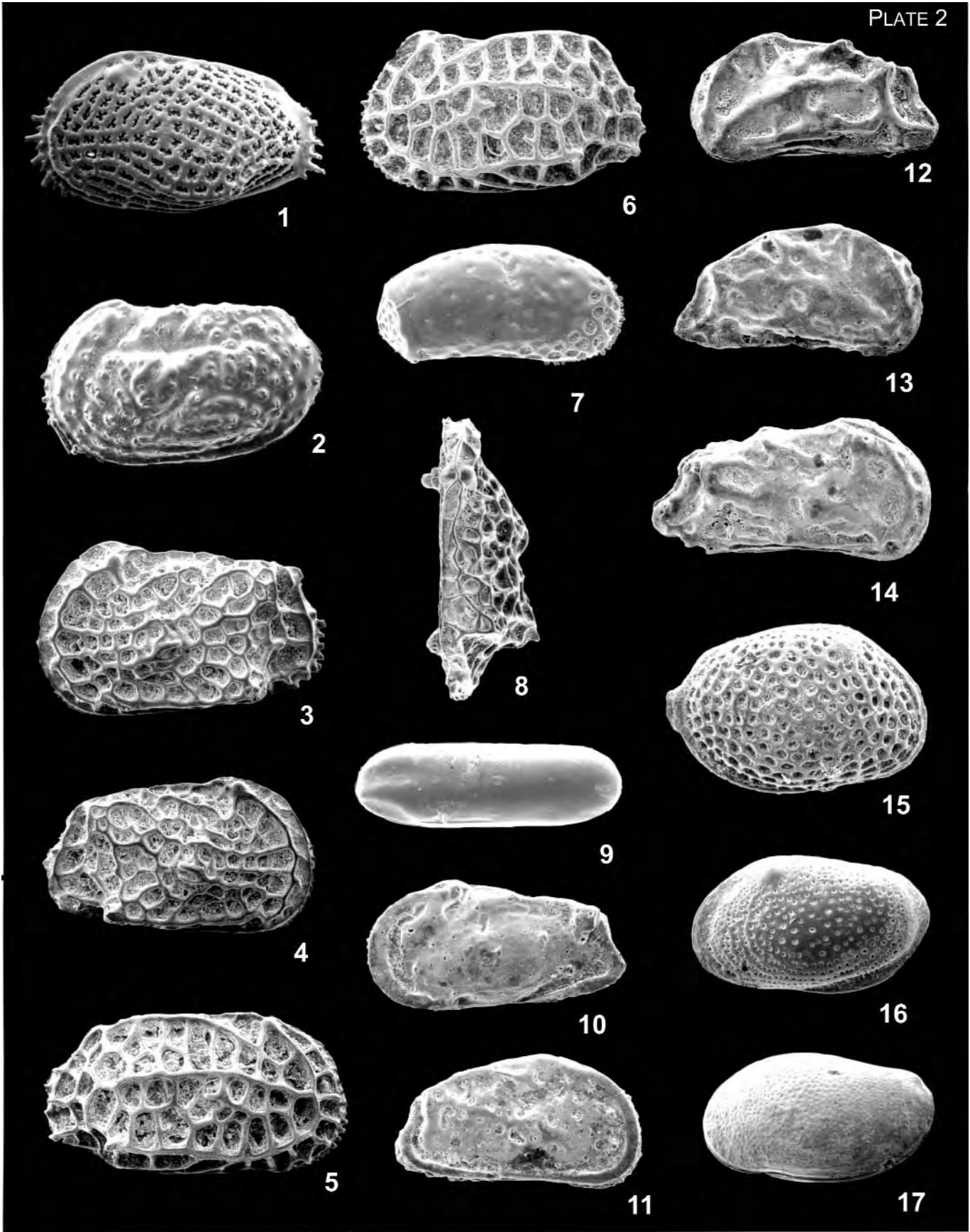
1978 *Caudites javana* Kingma. Jain, 122, Fig. F1-3.

1989a *Caudites javana* Kingma. Zhao & Whatley, 244, Pl. 4, Figs. 13-14.

1998 *Caudites javana* Kingma. Hussain, 11, Pl. 2, Fig. 15 (q. v. for more synonymy).

Plate 2. 1, *Patrizia indopacifica* Whatley & Zhao 1988; female, LV, external lateral view, M 2, SMF Xe 22627, x 60. 2, *Neohenryhowella hartmanni* Jain, 1981; female, LV, external lateral view, N 2, SMF Xe 22528, x 60. 3-4, *Bosella hormuzensis* sp. nov.; 3, Holotype LV, external lateral view, S 1, SMF Xe 22529, x 60; 4, Paratype, RV, external lateral view, S 1, SMF 22530, x 60. 8, Paratype, RV, dorsal view, S 1, SMF Xe 22530, x 60. 5-6 *Quasibradleya pseudoandamanae* sp. nov.; 5, Holotype, RV, external lateral view, M 2, SMF Xe 22532, x 60; 6, Paratype, LV, external lateral view, M 2, SMF Xe 22533, x 60. 7, *Bishopina* sp.; RV, external lateral view, S 3, SMF Xe 22517, x 80. 9, *Copytus posterosulcus* Wang, 1985; LV, external lateral view, (lost), x 110. 10, *Occultocythereis* sp.; RV, external lateral view, M 2, SMF Xe 22526, x 90. 11, *Falsocythere terryi* (Hoden, 1969); RV, external lateral view, M 2, SMF Xe 22525, x 90. 12, *Caudites* sp.; LV, external lateral view, S 3, SMF Xe 22535, x 90. 13, *Caudites javana* Kingma, 1948; RV, external lateral view, S 1, SMF Xe 22533, x 90. 14, *Caudites munita* Bonaduce, Masoli, Minechelli & Pugliese, 1080; carapace RV, external lateral view, S 3, SMF Xe 22534, x 90. 15, *Loxoconchagruendeli* Jain, 1977; RV, external lateral view, S 1, SMF 22536, x 100. 16, *Loxoconcha* sp. 1; LV external lateral view, S 4, SMF Xe 22537, x 90. 17, *Loxoconcha* sp. 2; carapace, external lateral view of LV, S 2 (lost) x 100.

PLATE 2



Remarks.— The species was originally described from the Upper Pliocene of E Java, it has also been found in the Miocene of Andaman Islands (Guha, 1968). Recent findings are from Banda and Celebes Seas of Indonesia (Keij, 1953, 1954) as well as from Mandvi Beach, west coast of India (Jain, 1978). However, some of occurrences reported from Indian coasts are questionable (Mohan *et al.*, 2001). Specimens reported from the Gulf of Mannar, southwest coast of India (Hussain, 1998) may represent *Orionina territoriae* Howe & McKenzie, 1989 from north-western Australia. We found two single valves of the species at the station S 1.

***Caudites munita* Bonaduce, Masoli, Minichelli & Pugliese, 1980**
Pl. 2, Fig. 13

1980 *Caudite munita* n. sp. Bonaduce, Masoli, Minichelli & Pugliese, 154, Pl. 6, Figs. 6-9.

Remarks.— Hitherto, the species was known only from the Gulf of Aqaba (Red Sea) where it has been found at a water depth of 25 m. In the present study, it is represented by two closed carapaces at Stations S 1 and S3.

***Caudites* sp.**
Pl. 2, Fig. 14

Remarks.— The present single left valve from the Station S 3 is characterized by two distinct longitudinal ribs connected to the oblique posterior rib, which extends from the dorsal margin a short distance to the posterior cardinal angle posteroventrally and branches just before termination. Intercostal regions are smooth, with an elliptical subcentral pit. *Caudites exmouthensis* Hartmann, 1978 from west coast of Australia lacks the ventral rib and the intercosal areas are reticulated. The centrolateral rib of *C. anterocatenularis* Whatley & Keeler, 1989 from Reunion Island is divided into two halves; the rear part is loop-shaped.

Genus *Loxoconcha* Sars, 1866
***Loxoconcha gruendeli* Jain, 1978**
Pl. 2, Fig. 15

1978 *Loxoconcha gruendeli* n. sp. Jain, 124, Fig. 4 J 1-4.
1981 *Loxoconcha gruendeli* Jain. Jain, Pl.3, Figs. 4, 8.

Remarks.— The species is represented in our material by a single right valve (Station S 1) and is identical with the specimens from Mandvi Beach and Kerala coast, W India, illustrated by Jain (1978, 1981).

***Loxoconcha* sp. 1**
Pl. 2, Fig. 16

Remarks.— The present two adult valves from the Station S 3, are identical with specimens which have been considered by Bate & Gurney (1981, Fig. 8 A, B) as being juveniles of *Loxoconcha amygdalanux* Bate & Gurney, 1981 from the Persian Gulf.

***Loxoconcha* sp. 2**
Pl. 2, Fig. 17

Remarks.— The only one closed carapace obtained (Station S 1) is identical with the specimens from the Persian Gulf identified by Bate & Gurney (1981) as *Loxoconcha indica*, Jain, 1978, but differs in some respects from specimens reported from Mandvi Beach (type locality).

Genus *Phlyctocythere* Keij, 1958
***Phlyctocythere* sp.**
Pl. 3, Fig. 1

Remarks.— Mostafawi (2003) ascribed the specimens from the Persian Gulf to *Phlyctocythere retifera* Bonaduce, Masoli & Pugliese, 1978 from the Red Sea. The latter species is similar in its ornamentation, but differs in outlines and in having a prolonged and upturned caudal process. The species was represented by two single valves (one adult and one juvenile) at the Station M 3.

Genus *Cytheropteron* Sars, 1866
***Cytheropteron alabarda* Bonaduce, Masoli & Pugliese, 1978**
Pl. 3, Fig. 5

1978 *Cytheropteron alabarda* n. sp. Bonaduce, Masoli & Pugliese, 392, Pl. 9, Figs. 7-8.
1987 *Cytheropteron alabarda* Bonaduce, Masoli & Pugliese. Whatley & Zhao, 347, Pl.4, Figs. 15-17.
2006 *Cytheropteron alabarda* Bonaduce, Masoli & Pugliese. Warne, Whatley & Bladgen, 112, Pl. 2, Fig. 25.

Remarks.— This species was originally reported from the Gulf of Aqaba, Red Sea, at a water depth of 150 m. Subsequently, it was recovered in the Malacca Straits at a water depth of 75-100 m (Whatley & Zhao, 1988) and from N Australia (Warne *et al.*, 2006). The species resembles *C. malaccaensis* Whatley & Zhao, 1987 from the Malacca Strait, but differs in having a straight dorsal margin in right valve and in having a convex dorsal margin in left valve. Its surface is covered by circular punctae decreasing in size peripherally. *Cytheropteron* sp. 2 *sensu* Yassini *et al.*, 1993 reported from the Gulf of Carpentaria may be conspecific with *C. alabarda*.

***Cytheropteron* sp. cf. *C. quadratocostatum* Whatley & Zhao, 1987**

Pl. 3, Fig. 4

1987 *Cytheropteron quadratocostatum* n. sp. Whatley & Zhao, 348, Pl. 4, Figs. 23-25.

1992 *Cytheropteron quadratocostatum* Whatley & Zhao. Mostafawi, 154, Pl. 6, Fig. 125.

Remarks.— The present few specimens from Stations M 1, S 1 and S 2 have the appearance of *C. quadratocostatum* from the Malacca Straits in regard to outline and their smooth surface, but differ in having a somewhat shorter ala and in lacking anterior and posterior transverse striae, which in *C. quadratocostatum* connect the dorsal rib with the ala anteriorly and posteriorly respectively. The species display also great affinity to *C. excisum* Bonaduce, Masoli & Pugliese, 1978 from the Red Sea. However, the left valve of the latter shows in the central part of the surface fine circular punctae varying in size, and has a furcate posterior transverse stria.

Genus *Hemicytherura* Elofson, 1941

***Hemicytherura aegyptica* Hartmann, 1964**

Pl. 3, Fig. 3

1964 *Hemicytherura videns aegyptica* n. ssb. Hartmann 50, Pl. 13, Fig. 61; Pl. 14, Figs. 62-66.

1975 *Hemicytherura videns aegyptica* Hartmann, Hoskin, Text-Fig. 1, 5.

1981 *Hemicytherura aegyptica* Hartmann, Gurney, Stereo-Atlas of Ostracoda, 8 (2) 7-12.

1983 *Hemicytherura* sp. Bonaduce, *et al.* Pl. 7, Fig. 8.

1998 *Hemicytherura subulata* Ahmad, Neale & Sid-

diqui. Hussain, 12, Pl. 3, Fig. 3 (non *Hemicytherura subulata* Ahmad, Neale & Siddiqui, 1991).

2002 *Hemicytherura* sp. Sridhar *et al.*, 31, Pl. 3. Fig. 16.

Remarks.— Hartmann (1964) described specimens from the Red Sea as *Hemicytherura videns aegyptica*. When Gurney (1981) reexamined Hartmann's type material, she raised it to independent specific range, due to sufficient differences in the arrangement of central lateral group of fossae as well as in the detailed structure of the male copulatory appendages, and noted that the specimens from the Persian Gulf, as well as those from the Arabian Sea, are conspecific with *H. aegyptica*. However, the holotype (right valve of female) of *H. aegyptica* reillustrated by Gurney (1981) displays a thinner caudal process than the present material and also than specimens from the Indian Ocean, cited above. The specimens from the West Africa that were attributed to *H. cellulosa* (Norman, 1865) by Witte (1993) are identical with *H. aegyptica*. The only difference may be that all five central fossae are separated from surrounding fossae by a thick murus. *H. cellulosa* differs in having a produced anterior and distinct central cluster of seven circular/subcircular fossae, whereas West African specimens exhibit only five fossae. Another notable differential feature between *H. aegyptica* and *H. cellulosa* is that the latter shows a transverse row of seven fossae extending from the anterodorsal region to the postroventral area. *Hemicytherura cellulosa* is an inhabitant of temperate to cool waters, widely distributed in high latitudinal regions ranging from the Atlantic coast of France to the Baltic Sea (Athersuch, 1981; Athersuch *et al.*, 1989). One of the holotypes *H. hartmanni* Yassini & Jones, 1995 (Fig. 575) from Windang Island, southeastern Australia appears to be conspecific with *H. aegyptica*.

Genus *Eucytherura* G. W. Mueller, 1894

***Eucytherura poroleberis* Zhao, 1988**

Pl. 3, Fig. 7

1988 *Eucytherura poroleberis* n. sp., Zhao, 261, Pl. 50, Figs. 15-18.

Remarks.— The species is characterized by a dorsal costa that extends from the eye spot and turns posteriorly to form a precaudal riblet, and by a short median costa which branches anteriorly to form a triangle with anterior

oblique costa. So far, this species is reported only from the East China Sea, and is rarely present in the Stations M 1, M 2.

Genus *Xestoleberis* Sars, 18866

***Xestoleberis* cf. *ghardaqa* Hartmann, 1964**

Pl. 3, Fig. 6

1964 *Xestoleberis ghardaqa* n. sp. Hartmann, 71, Pl. 27, Figs. 142-148; Pl. 28, Figs. 149-153.

Remarks.— The rare specimens from the Stations M 2, S 1 and S 2 display some differences to the specimens from the Red Sea in having a straight ventral margin, a somewhat produced posterior in the right valve and a somewhat larger size.

Genus *Saida* Hornibrook, 1952

***Saida herrigi* Keij 1975**

Pl. 3, Fig. 2

1975 *Saida herrigi* n. sp. Keij, 238, Pl. 2, Figs. 5-8.
1988 *Saida herrigi* Keij, Zhao, 279, Pl. 58, Fig. 10-12.
2006 *Saida herrigi* Keij, Warne, Whatley & Blagden, 110, Pl. 1, Fig. 1.

Remarks.— The species was originally described from the Holocene of Indo-Malaysia, subsequently has been found in East China Sea (Zhao, 1988), and northern Australia (Warne *et al.*, 2006). External morphological differences between the species of *Saida* are small (Wouters, 2007). *S. herrigi* differs from *S. torresi* (Brady, 1880) from the Torres Strait in having a more triangular-shaped ala in each valve and usually a more arched and thickened posterodorsal rib (Warne *et al.*, 2006). *S. truncala* Hornibrook, 1952 from New Zealand has a less prominent posterodorsal rib, a straight and flat dorsal margin. According to Whatley & Downing (1983) *S. truncala* is a junior synonym of *S. torresi*, but Warne *et al.* (2006) consider them as separate species. The species is very rare in the studied area, only 2 specimens have been found at the Station S 2.

Genus *Microcythere* G. W. Mueller, 1894

***Microcythere crescentiformis* sp. nov.**

Pl. 3, Figs. 8-9

1971 *Cytherois* sp. Bate, Pl. 1, Figs. 1gg, 2gg.

1978 *Microcythere* sp. Bonaduce, Masoli & Pugliese, 386, Pl. 5, Fig. 10 (non Fig. 9).

Derivatio nominis.— Latin, meaning crescent-shaped.

Holotype.— Left t valve, Pl. 3, Fig. 8, Station S2; SMF Xe 22545.

Paratypes.— Pl.3, Fig. 9, Station S2; SMF Xe 22546.

Dimensions.— 0.30-0.33 mm length, 0.12-0.14 mm height.

Diagnosis.— A crescent-shaped species of *Microcythere* with narrowly rounded anterior margin and a posterior margin that is arched strongly and continuously downwards to form almost a right angle with the ventral margin.

Description.— Small, moderately thin-shelled, crescent-shaped in lateral view. Anterior margin narrowly rounded, extremity below mid-height. Posterior margin arched strongly and continuously downwards to make almost a right angle with the ventral margin, extremity just above the ventral margin. Dorsal margin widely arched, sloping continuously to anterior and posterior margins. Ventral margin concave in oral region. Maximum length ventrally, maximum height in posterior third. Inner lamella wide at anterior and posterior, narrower in the oral region where inner margin and line of concrescence coincide over short distance. Vestibulum is large at anterior, only slightly smaller at posterior. Marginal pore canals short, simple moderate in number.

Remarks.— This species shows a certain similarity to *P. obliqua* G.W. Mueller, 1894 from the Bay of Naples, but differs in having a more acuminate posterior margin. *Microcythere* sp. *sensu* Whatley & Zhao, 1988 from the Malacca Strait is also similar, but has a weakly convex dorsal margin, a concave posterodorsal slope and a smaller size. The new species was rare at Stations M 1, M 2, S 1, S 2, and S 4.

Genus *Paradoxostma* Fischer, 1855

***Paradoxostoma butticulum* sp. nov.**

Pl. 3, Figs. 10-12, 13

Derivatio nominis.— Latin, meaning small bottle.

Holotype.— Right valve, Pl. 3, Fig. 10, Station M 2; SMF Xe 22527.

Paratypes.— Pl. 3, Figs. 11-13, Station M 2; SMF Xe 22528.

Dimensions.— 0.46-0.50 mm length, 0.17-0.19 mm height.

Diagnosis.— A small species of *Paradoxostoma* marked by its bottle-shaped outline in lateral view with a prominent caudal process and bluntly rounded anterior margin.

Description.— Small. Thin-shelled, subcylindrical in lateral view. Anterior margin bluntly rounded; posterior margin distinctly caudate with pointed apex at about mid-height. Dorsal margin convex; ventral margin sinuate. Posterodorsal slope concave; posteroventral slope straight to slightly concave. Maximum length mid-height; maximum height behind mid-length. Inner lamella wide anteriorly, narrow at ventral and posterior regions. Line of concrescence and inner margin rather widely separated anteriorly, but coinciding elsewhere, except for slight deviation in the posteroventral region where they form a narrow vestibule. Marginal pore canals short, simple, straight, not numerous. Sexual dimorphism is pronounced; the male carapace is more elongate than the female one, and also less wide.

Remarks.— The new species is most similar to *P. acuminata* G. W. Müller, 1894 from the Mediterranean. The former is elongate, has a narrowly rounded anterior margin and narrowly arched dorsal margin. *Paradoxostoma* sp. *sensu* Warne, Whatley & Blagden, 2006 from northern Australia differs in being larger and in having subparallel dorsal and ventral margins converging to the more narrowly rounded anterior margin. *P. stipulatum* Zhao, 1988 from the East China Sea, which is represented by one single valve at the Station M 2 (herein Pl. 3, Fig. 23), is larger, has a more convex dorsal margin and a straight posterodorsal slope. The new species was very rare at Stations M 2 and S 1.

***Paradoxostoma curvirostrum* sp. nov.**

Pl. 3, Figs. 16-18, 22

Derivatio nominis.— Latin, meaning beak

Holotype.— Right valve, Pl. 3, Fig. 16, Station M 2; SMF Xe 22549.

Paratypes.— Pl. 3, Figs. 17-18, 22, Station M 2; SMF Xe 22550.

Dimensions.— 0.56-0.61 mm length, 0.17-0.19 mm height.

Diagnosis.— Small, thin-shelled species of *Paradoxostoma*, subcylindrical in lateral view. Anterior margin rather narrowly rounded; posterior prominently caudate with pointed apex just above ventral margin.

Description.— Small. Thin-shelled, subcylindrical in lateral view. Anterior margin narrow and rounded with apex below mid-height. Posterior margin sharply caudate with apex just above ventral margin. Dorsal margin widely arched posterodorsal slope concave. Ventral margin straight, posteroventral slope concave. Maximal length mid-height, maximal height about mid-length. Inner lamella moderately wide anteriorly, narrow in posterior and ventral areas. Line of concrescence and inner margin separated only at anterior and posterior margins. Vestibule, cup-shape anteriorly, narrow crescent-shape posteriorly. Marginal pore canals moderate in number, bifurcate at anterior margin, elsewhere simple.

Remarks.— This species resembles *P. butticulum* sp. nov., but differs in being larger, in having a more acuminate anterior margin and in a stronger caudal process situated just above the ventral margin. *P. hallistica* Whatley, Jones & Wouters, 2000 from Easter Island is elongate and larger, its dorsal and ventral margins are subparallel, diverging to the maximum height at the posterior caudal process. The new species was rarely found at the Station M 2.

***Paradoxostoma procerum* sp. nov.**

Pl. 3, Figs. 14-15

2003 *Paradoxostoma* sp. 1 Mostafawi, 71, Fig. 46.

Derivatio nominis.— Latin, meaning slender.

Holotype.— Left valve, Pl.3, Fig. 14, Station M 2; SMF Xe 22551.

Paratypes.— Pl. 3, Figs. 15, Station S1; SMF Xe 22552.

Dimensions.— 0.82 -0.86 mm length, 0.23 -0.25 mm height.

Diagnosis.— A large, elongate and thin-shelled species of *Paradoxostoma* with subcylindrical shape in lateral outline. Posterior margin attenuated with long caudal process.

Description.— Large. Elongate, thin-shelled, subcylindrical in lateral view. Anterior margin narrow and asymmetrically rounded with extremity at about mid-height. Posterior margin produced to a strong caudal process with pointed apex at about mid-height. Dorsal margin gently convex, anterodorsal and posterodorsal slopes straight in left valve, slightly concave in right valve. Ventral margin sinuate, posteroventral slope straight. Inner lamella narrow at margins. Large, fist-shaped vestibule anteriorly and small sub-triangular posteriorly. Marginal pore canals relatively numerous, short, straight and simple.

Remarks.— The present species is closely resembles to *Paradoxostoma* sp. 2 sensu Whatley & Zhao, 1988 from the Malacca Straits concerning the outline but the latter has a short caudal process. *P. elegans* Bonaduce, Masoli, Minichelli & Pugliese, 1980 from the Red Sea is distinctly smaller (0.43-0.44 mm length), has short and rather upturned caudal process. *P. subtile* Bonaduce, Masoli, Minichelli & Pugliese, 1980 from the Red Sea has an oblique and somewhat upturned anterior margin and a straight ventral margin. The new species was recovered at Stations M 2, S 1 and S 2.

***Paradoxostoma ensiformis* sp. nov.**

Pl. 3, Figs. 19-20

Derivatio nominis.— Latin, meaning sword-like.

Holotype.— Left valve, Pl. 3, Fig. 19, Station S1; SMF Xe 22553.

Paratypes.— Pl. 3, Fig. 21, Station S 1; SMF Xe 22554.

Dimensions.— 0.66 -0.68 mm length, 0.20 -0.22 mm height.

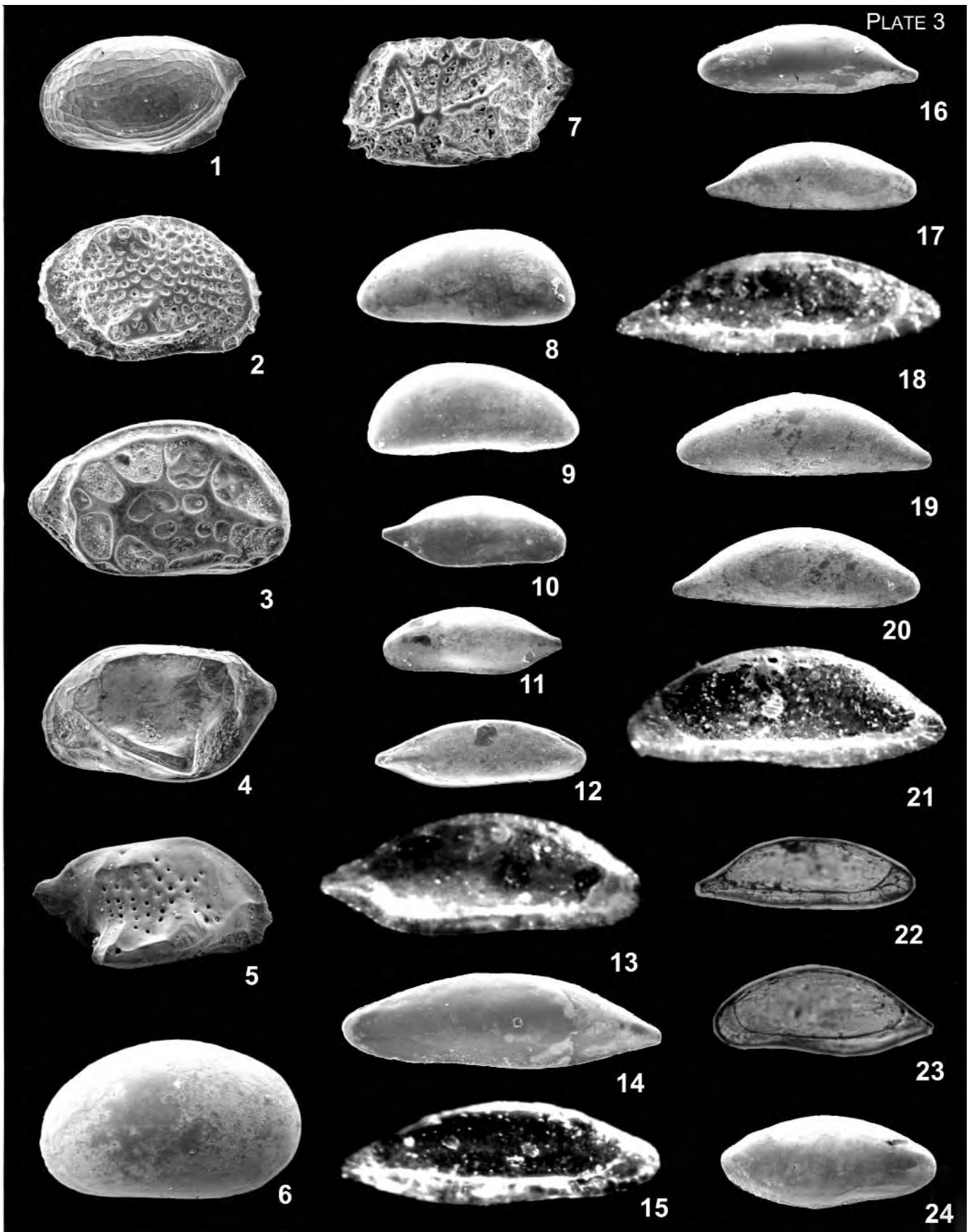
Diagnosis.— Medium-sized to large, moderately thin-shelled species of *Paradoxostoma* with an almost symmetrical anterior, evenly arched dorsal margin, distinctly acuminate posterior and a straight ventral margin.

Description.— A medium-sized to large species with bow-

shaped outlines in lateral view. Anterior margin narrow and rounded with straight anterodorsal and anteroventral slopes in left valve, but with slightly convex anterodorsal slope in right valve. Posterior clearly acuminate, extremity just above ventral margin. Dorsal margin arched; ventral margin straight; maximum length below mid-height; maximum height at about mid-length. Inner lamella wide anteriorly, narrower ventrally and posteriorly. Vestibule large and cup-like anteriorly small and subtriangular in shape posteriorly. A total of about 21-22 marginal pore canals are more or less evenly spaced throughout the anterior, ventral and posterior marginal zone. All pore canals are straight and simple. They are short at anterior, but relatively long in ventral and posterior regions.

Remarks.— The species is similar to *P. curvirostrum* sp. nov., but the latter is smaller and has concave anterodorsal and posteroventral slopes, its maximum height is behind the mid-length and its ventral margin is sinuate. The species is very rare, only 3 single valves were found at the Station S 1.

Plate 3. 1, *Phlyctocythere* sp.; LV, external view, S 1, SMF Xe 22538, x 100. 2, *Saida herrigi* Zhao, 1988; LV, external view, M 3, SMF, Xe 22544, x 120. 3, *Hemicytherura aegyptica* Hartmann, 1964; carapace, external lateral view of RV, S 1, SMF Xe 22541, x 150. 4, *Cytheropteron* cf. *C. quadratocostatum* Whatley & Zhao, 1987; LV, external lateral view, M 2, SMF Xe 22540, x 120. 5, *Cytheropteron alabarda* Bonaduce, Masoli & Pugliese, 1978; RV, external view, S 2, SMF Xe 22539, x 120. 6, *Xestoleberis* cf. *ghardaqa* Hartmann, 1964; LV, external lateral view, S 2, SMF Xe 22543, x 120. 7, *Eucytherura poroleberis* Zhao, 1988; RV, external lateral view, S 2, SMF Xe 22542, x 100. 8-9, *Microcythere crescentiformis* sp. nov.; 8, Holotype, LV, external lateral view, S 2, SMF. Xe 22545, x 130; 9, Paratype, RV, external lateral view, M 2, SMF Xe 22546, x 120. 10-13, *Paradoxostoma butticulum* sp. nov.; 10, Holotype, carapace external lateral view of RV, S 1, SMF, Xe, 22547, x 70; 11, Paratype, LV, external lateral view, S 1, SMF, Xe, 22548, x 70; 12, Paratype, male, carapace external lateral view of RV, S 1, SMF, Xe, 22548, x 70; 13, Paratype, RV, female, under transmitted light, external lateral view, S 1, SMF, Xe, 22548, x 130. 14-15, *Paradoxostoma procerum* sp. nov.; 14, Holotype, LV, external lateral view, S 1, SMF, Xe, 22551, x 70; 15, Paratype, RV, under transmitted light, external lateral view, S 1, SMF, Xe, 22552, x 70. 16-18, 22. *Paradoxostoma curvirostrum* sp. nov.; 16, Holotype, LV, external lateral view, M 2, SMF, Xe, 22549, x 70; 17, Paratype, RV, external lateral view, M 2, SMF, Xe, 22549, x 70; 17, LV, external lateral view, M 2, SMF, Xe, 22550, x 70 18, Paratype, RV, under transmitted light, external lateral view, M 2, SMF, Xe, 22550, x 110; 22, Paratype, RV, under transmitted light, external lateral view, M 2, SMF, Xe, 22550, x 90. 19-20, *Paradoxostoma ensiformis* sp. nov.; 19, Holotype, LV, external lateral view, S1, SMF Xe 22553, x 70; 20, Paratype, RV, external lateral view, SMF Xe 22554, x 70. 21, *Paradoxostoma* sp.1, LV, under transmitted light, external lateral view, S 2, SMF Xe 22555, x 70. 23, *Paradoxostoma stipulatum* Zhao, 1988; LV, under transmitted light, external lateral view, M 2 (lost), x 70. 24, *Paradoxostoma* sp. 2; RV, external lateral view, M 2, SMF Xe 22556, x 70.



Paradoxostoma sp. 1

Pl. 3, Fig. 21

Remarks.— A relatively large species with evenly arched dorsal margin and sinuate ventral margin. Anterior margin narrowly rounded, posterior margin acuminate. Maximum length below mid-height; maximum height at about mid-length. Inner lamella wide anteriorly, narrower in posterior and ventral margins. The line of concrescence does not coincide with the inner margin. Vestibule is large anteriorly, narrower elsewhere. The species is represented by only 2 specimens at the Station S2.

Paradoxostoma sp. 2

Pl. 3, Fig. 24

Remarks.— Bate (1971) attributed the specimens from Abu Dhabi (Persian Gulf) to *P. longum* Hartmann, 1964 from the Red Sea. However, the latter species has a straight dorsal margin and a weakly sinuous ventral margin. Jain (1978) introduced the species as *Paradoxostoma* sp. from Mandvi Beach, west coast of India. This species was also very rare in the studied area, only one single specimen encountered at the Station M 2.

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APPENDIX 1

List of species present in the studied samples that have not been treated in the taxonomic part.

Station	N1	N2	N3	N4	N5	N6	M1	M2	S1	S2	S3	S4
Species												
<i>Polycope regina</i> Hasan, 1983	1	1	2	2				2		1	3	
<i>Cytherella sericea</i> Mostafawi, 2003		2		2		3		1		2		
<i>Cytherella retroflexa</i> Mostafawi, 2003	2		3				1		1	3	2	
<i>Cytherella bigemina</i> Mostafawi, 2003	1		1			2	2		3	1		
<i>Neomonoceratina iniqua</i> (Brady, 1868)	1		1		4			1		1		2
<i>Spinoceratina spinosa</i> (Zhao & Whatley, 1988)			2						2		1	2
<i>Paijenborchella calcarina</i> Mostafawi, 2003		2	2			2		3		1	3	
<i>Paijenborchellina venosa</i> Gurney, 1979	1					1		1		1		
<i>Hemicytheridea paiki</i> Jain, 1978	2	1			2			1		1	3	
<i>Callistocythere arcana</i> B., M. & P., 1978*	1	2		4			2		1	3	2	
<i>Tanella gracilis</i> Kingma, 1948			1					3		2	1	
<i>Bishopina guhai</i> (Jain, 1978)				1		2	1		2	1	1	
<i>Krithe kroemmelbeini</i> Jain, 1978		1		3	1	1		3	2	4		2
<i>Acantocythereis scutigera</i> (Brady, 1868)	1	1	1		4			2	3	4	2	
<i>Keijella nealei</i> Jain, 1978	1	1	2					1	2		1	
<i>Kaijella karwarensis</i> (Bhatia & Kumar, 1979)		1						1	4	2	1	
<i>Asymmetricythere whatleyi</i> (Jain, 1978)		1					1		1	2	1	
<i>Lankacythere elaborata</i> Whatley & Zhao, 1988			1		3			3	2	6	5	3
<i>Alocopocythere reticulata</i> (Hartmann, 1964)	1	2	1			3	5	2	3	1	5	
<i>Venericythere darwinii</i> (Brady, 1868)	2				1	2		3		4	2	1
<i>Venericythere papuensis</i> (Brady, 1880)		1	2		2		1	2	3	2	1	1
<i>Tandonella batei</i> (Jain, 1978)		1	1			1			2		2	1
<i>Puricythereis exquisita</i> (Bate & Sheppard, 1980)		2		1	1	2		3	3	2	4	
<i>Atjella jacobi</i> Malz, 1981	1			1	1				2		2	1
<i>Hemicythere peterseni</i> Jain, 1978	1		1			2	2		1	1	3	
<i>Loxoconcha amygdalanux</i> Bate & Sheppard, 1980	2		3	1	1		4		3	4	7	1
<i>Loxoconcha ornatovalvae</i> Hartmann, 1964	2		1	1	1			1	2	1	1	
<i>Heinzmalzina ocellata</i> Mostafawi, 2003		2			1				2	3	5	1
<i>Sagmatocythere nupta</i> Mostafawi, 2003	2		1		2			1	5	3	2	1
<i>Cytheropteron pulcinella</i> B., M. & P., 1978*	1		1		2	1		3	3	4	2	1
<i>Bythoceratina malaysiana</i> Whatley & Zhao, 1987			2		1			1	1	2	5	
<i>Bythoceratina paiki</i> Whatley & Zhao, 1987					1			5	2		1	
<i>Bythoceratina mandviensis</i> Jain, 1978	1			1		1			1		2	
<i>Cytheroma dimorpha</i> Hartmann, 1964			2	1		1	3		2	4	3	1
<i>Paradoxostoma</i> sp.2 sensu Mostafawi, 2003		1					1		1		2	
<i>Propontocypris bengalensis</i> Maddocks, 1969	1		2	1		1		2	1	4	3	
<i>Propontocypris</i> sp. sensu Mostafawi, 2003		1							1		3	2
<i>Aglaiocypris pellucida</i> Mostafawi, 2003		1		2			2		1	2	5	3
<i>Argilloecia</i> sp. sensu Mostafawi, 2003			1				1			1	2	

*= Bonaduce, Masoli & Pugliese

Evidencias de depredación en ostrácodos holocenos del Parque Nacional de Doñana (SO de España)

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Resumen

Este trabajo analiza las evidencias de depredación observadas en la revisión de más de 5.000 valvas y caparazones de ostrácodos extraídos en sedimentos holocenos del Parque Nacional de Doñana (SO de España). Estas evidencias son muy escasas (0,15%), debido en parte a la alta proporción de mudas juveniles. Se pueden distinguir dos tipos de perforaciones (*Oichnus paraboloides* Bromley y *Oichnus simplex* Bromley), localizadas preferentemente en las áreas central y anterior de las valvas y atribuidas principalmente al ataque de gasterópodos. Estas perforaciones afectan a los adultos y a las últimas mudas juveniles de especies con ornamentación externa lisa. No se existe correlación estadística entre la abundancia de ostrácodos y el número o porcentaje de valvas depredadas, así como entre el diámetro de las perforaciones y el tamaño de las valvas que las presentan.

Palabras clave: Ostrácodos, depredación, Holoceno, SO España.

Abstract

[*Predation on Holocene ostracods of the Doñana National Park (SW Spain)*] This paper examines the evidences of predation observed in the study of more than 5,000 ostracod shells extracted from Holocene sediments of the Doñana National Park (SW Spain). These evidences are very rare, partly due to the high proportions of juvenile instars. Two types of evidences are distinguished (*Oichnus paraboloides* Bromley and *Oichnus simplex* Bromley), preferentially located in the central and anterior areas of the valves and attributed mainly to gastropods. These holes were found in adults and the last juvenile instars of species with smooth shells. There is not statistical correlation between: a) the abundance of ostracods and the number or percentage of predated shells; and b) the hole diameter and the size of the valves that contain them.

Key words: Ostracods, predation, Holocene, SW Spain.

1. INTRODUCCIÓN

Los ostrácodos constituyen una de las posibles presas de distintos grupos acuáticos, tales como gasterópodos, bi-

valvos carnívoros, escafópodos, equínidos, peces o incluso otros ostrácodos (p.e., Leal, 2008). El análisis del contenido estomacal ha revelado que estos microcrustáceos no suelen suponer más del 5 % de la dieta de estos

organismos, si bien los caparazones de algunas especies pueden ser muy abundantes en las heces de determinadas aves (Green *et al.*, 2008).

En el registro fósil, las evidencias de depredación en sus valvas y caparazones se han detectado desde el Cámbrico. Los distintos tipos de perforaciones observadas se han atribuido a la acción post-mortem de hongos (Reyment y Elewa, 2002) o a las estrategias de depredación de diversos invertebrados (Maddocks, 1988; Vannier *et al.*, 2003). La mayoría de estos estudios se han centrado en poblaciones fósiles o actuales de ostrácodos marinos (p.e., Reyment, 1963, 1966; Reyment *et al.*, 1987).

Este trabajo analiza las evidencias de depredación en poblaciones holocenas de ostrácodos del Parque Nacional de Doñana (SO de España). Estas evidencias son medidas, dibujadas y comparadas con las dimensiones de las valvas que las contienen, así como con los estadios ontogénicos en los que se presentan.

2. EL ÁREA DE ESTUDIO: REGISTRO HOLOCENO DEL PARQUE NACIONAL DE DOÑANA

2.1. El Parque Nacional de Doñana

El río Guadalquivir conforma un amplio estuario (~1.800 km²) en su desembocadura en el océano Atlántico. Este estuario incluye el Parque Nacional de Doñana, uno de los humedales más amplios de Europa, con más de 50.000 ha. Esta Reserva de la Biosfera está constituida básicamente por un sistema de canales fluviales delimitados por *levees*, entre los que se disponen marismas fluviomarales y un conjunto de depresiones ocupadas por lagunas dulceacuícolas, denominadas localmente "lucios". La topografía general de esta Reserva es esencialmente plana, sólo interrumpida por un conjunto de pequeños promontorios ocupados por *cheniers*, crestas bioclásticas y crestas arenosas. Estas formaciones geomorfológicas se alcanzan unos 2-2,5 m sobre el nivel medio de las marismas adyacentes y suelen presentar una morfología en cresta de playa (Ruiz *et al.*, 2008). Todo este sistema está parcialmente protegido por dos flechas arenosas (Fig. 1a: Doñana y La Algaida), constituidas por sistemas cuaternarios de dunas activas.

El análisis pluridisciplinar del relleno holoceno mediante testigos continuos ha revelado la evolución del Parque Nacional de Doñana desde el máximo de la transgresión Fladriense en este sector (~6.500 años BP; Zazo *et al.*, 1994). Básicamente, el sector meridional del Parque estaba constituido por un amplio lagoon con conexión marina, que fue progresivamente colmatándose. Su relleno también incluye depósitos tsunamigénicos y tempestícos con edades comprendidas entre los 5.000 y 1.500 años BP (Ruiz *et al.*, 2004, 2005, 2008; Pozo *et al.*, 2010). Dos de estos testigos han sido seleccionados para este trabajo (Fig. 1b).

2.2. Los testigos continuos

El testigo A está constituido por limos arcillosos verde-grisáceos, entre los que se intercalan niveles tsunamigénicos y tempestícos caracterizados por un importante contenido bioclástico. Estos sedimentos finos se depositaron en un lagoon abierto, con una colmatación progresiva y una disminución de los aportes mareales entre los 4.300 y 3.500 años BP (Fig. 1b). La asociación de ostrácodos está dominada por *Cyprideis torosa* (Jones 1850), *Loxoconcha elliptica* Brady 1868 y *Leptocythere castanea* (Sars 1866), parcialmente reemplazados por especies de afinidad marina como *Carinocythereis whitei* (Baird, 1850) o *Urocythereis oblonga* (Brady 1868) en los niveles tsunamigénicos (Ruiz *et al.*, 2005).

El testigo B está formado por limos arcillosos grisáceos, masivos, cuyas asociaciones de ostrácodos marcan una transición desde un lagoon abierto (*C. torosa*, *L. elliptica*, *L. castanea*) a una laguna de aguas dulces o "lucio", con dominio de *Heterocypris salina* (Brady 1868), entre los 2.500 y 2.000 años BP, aproximadamente (Ruiz *et al.*, 2004).

3. METODOLOGÍA

Se obtuvieron 22 muestras de 15 g cada una para el análisis de las evidencias de depredación en las poblaciones de ostrácodos, que fueron seleccionadas en función de los cambios litológicos observados en los testigos. La litología, textura, mineralogía, paleontología, dataciones y reconstrucciones paleoambientales de estos testigos pueden ser consultadas en Ruiz *et al.* (2004, 2005).

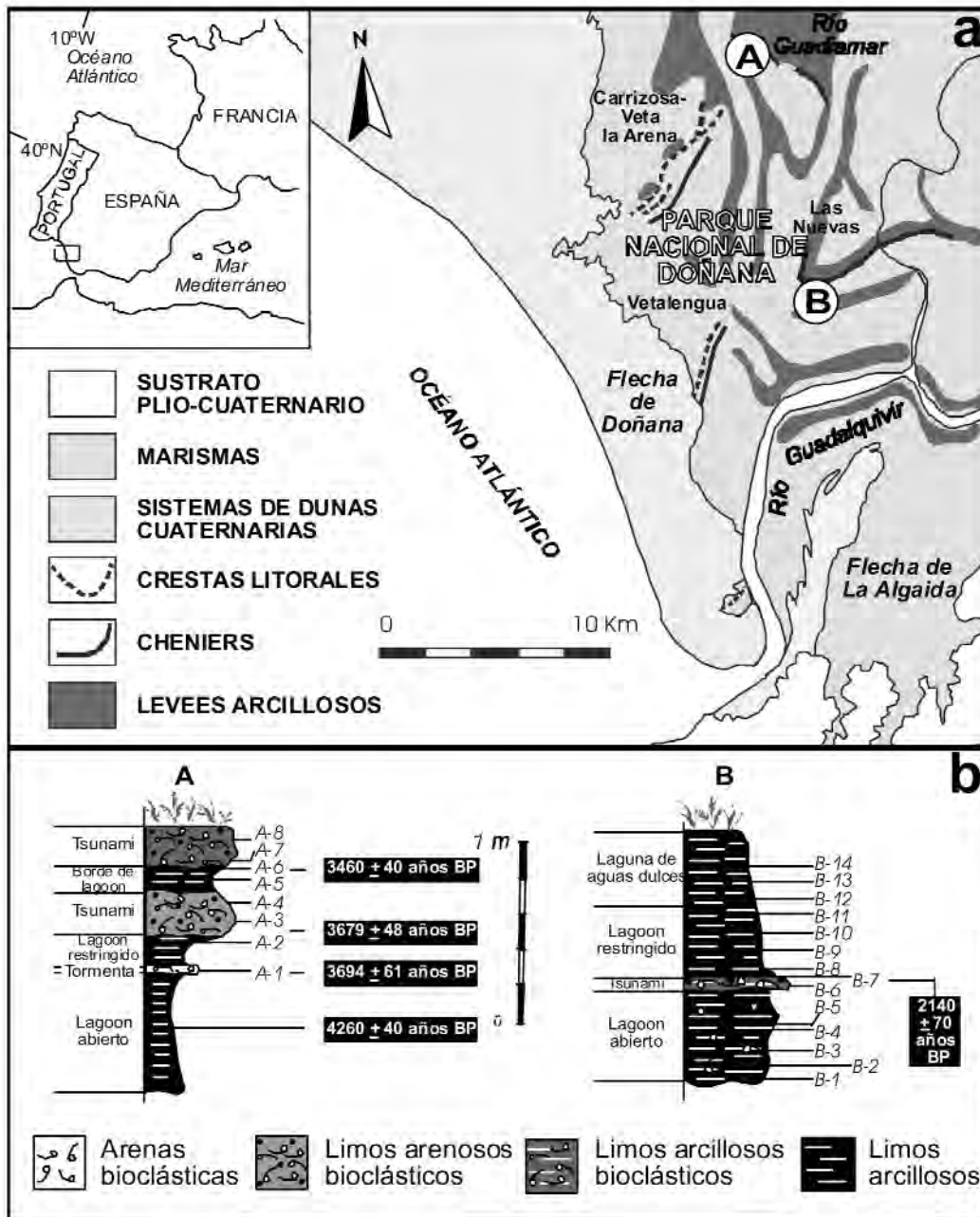


Figura 1. a, Localización y principales rasgos geomorfológicos del Parque Nacional de Doñana. b, Testigos: litología, dataciones (no calibradas) y muestreo realizado (modificado de Ruiz et al., 2004, 2005).

Figure 1. a, Location and main geomorphic features of the Doñana National Park. b, Cores: lithology, datings (un-calibrated) and sampling (modified from Ruiz et al., 2004, 2005).

Las muestras fueron levigadas a través de un tamiz de 63 μ m y secadas en estufa a 70°C. Si fue posible, se separaron un mínimo de 150 individuos de cada muestra, con una extrapolación posterior para calcular el número total de ostrácodos en la muestra total y el número de individuos presentes en 10 g de sedimento seco. Si el número

de especímenes fue inferior a 150, se separaron todos los caparazones y valvas presentes.

En un segundo paso, se separaron y dibujaron aquellos ejemplares con evidencias de depredación, si bien fueron rechazadas las formas rotas o con señales de abrasión. La localización de las perforaciones fue clasificada

como anterior, central, posterior, dorsal y ventral. Además, el diámetro externo (para perforaciones circulares) o el eje mayor (para perforaciones elípticas) de las perforaciones fue medido y comparado con la longitud y la altura de las valvas que las contienen.

Finalmente, el estadio ontogénico de cada valva perforada fue determinado a partir de datos obtenidos de diversas notas cortas del Stereo Atlas of Ostracod Shells (Kilenyi y Whittaker, 1974; Athersuch y Whittaker, 1976).

4. RESULTADOS Y DISCUSIÓN

4.1. Porcentajes de depredación, especies y medios

Las evidencias de depredación son muy escasas en las muestras analizadas, con solo 8 valvas perforadas de un total de 5.446 valvas y caparazones separados (0,15%).

Este promedio es claramente inferior al obtenido en diversas investigaciones de medios marinos, donde suelen situarse entre el 1-5% e incluso alcanzar más del 37% en determinadas especies (Honappa y Venkachalapathy, 1978; Reymont *et al.*, 1987; Bhatia *et al.*, 1989). Los porcentajes pueden superar el 10% en muestras aisladas con escasas poblaciones de ostrácodos (1 individuo/10 g). No obstante, debe indicarse que, en este estudio, no existe correlación alguna entre la abundancia de ostrácodos y el número o porcentaje de valvas depredadas, ya que no se han encontrado perforaciones en las valvas extraídas de muestras con más de 100 individuos por gramo (Tabla 1).

La depredación afecta a las 4 especies más abundantes en estos testigos (*C. torosa*, *L. elliptica*, *L. castanea*, *H. salina*). Se ha detectado principalmente en sedimentos inicialmente depositados en lagoons restringidos, lagunas de aguas dulces o debido a la acción de eventos de alta energía (tsunamis, tormentas).

INTERPRETACIÓN PALEOAMBIENTAL	Especies Muestras	<i>Cyprideis torosa</i>	<i>Heterocypris salina</i>	<i>Leptocythere castanea</i>	<i>Loxiconcha elliptica</i>	Individuos extraídos	Individuos/10 g	% Valvas perforadas
	A-8					2	< 1	
	A-7	2				19	1	10.52
Borde de lagoon	A-6					29	2	
	A-5					10	1	
Tsunami	A-4					68	5	
	A-3					63	4	
Lagoon restringido	A-2			1		51	3	1.96
Tormenta	A-1				1	286	98	0.35
Laguna de aguas dulces	B-14		1			163	110	0.61
	B-13					341	97	
	B-12	1				233	39	0.43
Lagoon restringido	B-11					341	86	
	B-10					284	323	
	B-9					504	845	
	B-8	1				308	1340	0.59
Tsunami	B-7	1				382	3220	0.26
	B-6					357	3190	
Lagoon abierto	B-5					401	2270	
	B-4					369	4670	
	B-3					447	10120	
	B-2					376	8530	
	B-1					412	6440	

Tabla 1. Evidencias de depredación observadas en las poblaciones holocenas de ostrácodos del Parque Nacional de Doñana, con indicación del número de individuos extraídos, abundancia relativa de ostrácodos y porcentajes de valvas perforadas.

Table 1. Predation evidences on Holocene ostracod populations of the Doñana National Park, with indication of the number of individuals picked, relative abundance of ostracods and percentages of bored valves.

4.2. Número, localización y tipo de perforaciones

Cada valva perforada presenta una única perforación. El análisis de los diagramas de Pope (*sensu* Carriker, 1955) indica una concentración preferencial de estas perforaciones en las zonas central y anterior de las valvas. Una localización preferente posterodorsal o central ha sido hallada en otros estudios de poblaciones actuales (Ruiz, 1997) y fósiles (Bhatia *et al.*, 1989).

Se pueden diferenciar dos tipos de perforaciones:

a) *Oichnus paraboloides* Bromley (Fig. 2a: *L. castanea*, *L. elliptica*). Son perforaciones elípticas o subparabólicas en vista externa, con un diámetro externo mayor que el interno. Es frecuente la presencia de un área periférica adyacente a la perforación con arañazos o incisiones superficiales. Estas perforaciones se atribuyen usualmente a la acción de gasterópodos natícidos (Reyment, 1966; Jonkers, 2000), aunque también deben considerarse a otros grupos de gasterópodos como posibles depredadores (p.e., familias Cassidae y Tonnidae; Mayoral, 1986).

b) *Oichnus simplex* Bromley (Fig. 2a: *C. torosa*). Incluye perforaciones cilíndricas, con abertura interna y externa de diámetro similar. Parecen responder a la estrategia depredadora de gasterópodos murícidos o eulimínidos (Carriker, 1955; Reyment, 1963; Donovan y Pickerill, 2004) y pequeños turbelarios (Maddocks, 1988).

4.3. Diámetro de las perforaciones vs tamaño de las valvas perforadas

El diámetro de las perforaciones está comprendido entre las 25 μm y las 85 μm (Fig. 2b). Este diámetro se sitúa en el intervalo inferior del rango de diámetros de perforación (35-500 μm) observado en medios litorales del suroeste de España (Ruiz, 1997).

La comparación entre este diámetro y las dimensiones de las valvas perforadas refleja una ausencia de correlación entre el tamaño de la perforación y de las valvas que las incluyen (Fig. 2b). Otros estudios indican una relación positiva, a veces con significación estadística, entre ambos parámetros, tanto en ostrácodos (Reyment, 1966; Aranki, 1987) como en braquiópodos (Hoffmeister, 2002).

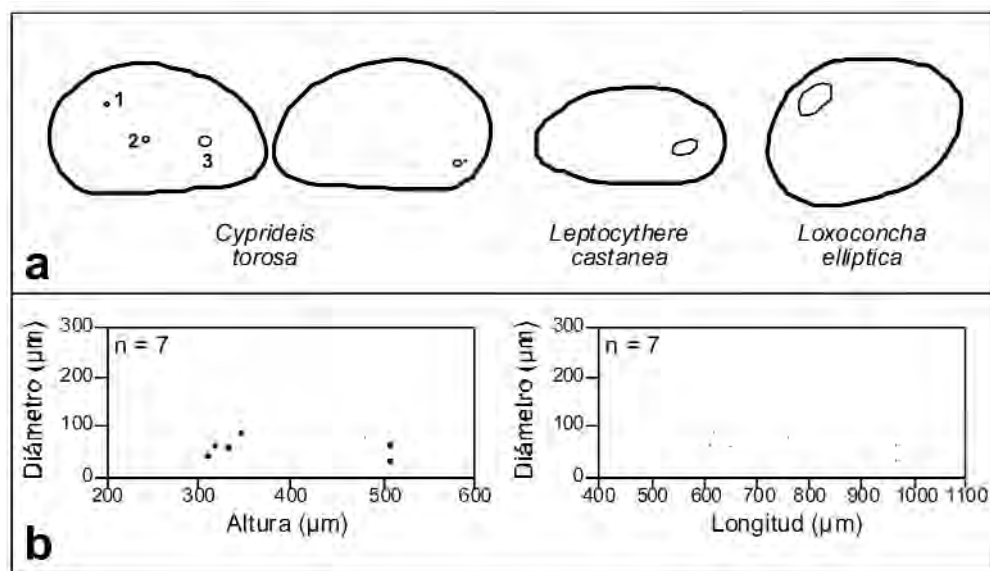


Figura 2. a, Diagramas de Pope (*sensu* Carriker, 1955), con la situación de algunas de las evidencias de depredación observadas. Escala no respetada. b, Diagramas: diámetro de las perforaciones vs altura de las valvas perforadas y diámetro de las perforaciones vs longitud de las valvas perforadas.

Figure 2. a, Pope's diagrams (*sensu* Carriker, 1955), with location of some predation evidences. Scale not respected. b, Diagrams: hole diameter vs height of the predated valves and hole diameter vs length of the predated valves.

4.4. Depredación y ontogenia

El análisis ontogénico realizado ha permitido delimitar la presencia de adultos y mudas (A-1 a A-6) en las especies más abundantes, bien preservadas y sin evidencias de transporte. Sin embargo, sólo las últimas mudas juveniles (A-1 y A-2) y los adultos presentan evidencias de depredación. La abundancia de las mudas juveniles intermedias en los testigos analizados podría explicar el bajo porcentaje total de valvas depredadas en relación con otros estudios, que indican proporciones de hasta el 8 % de depredación en muestras constituidas casi exclusivamente por adultos (Reyment *et al.*, 1987).

4.5. Depredación y ornamentación

Las cuatro especies perforadas presentan una ornamentación externa lisa o levemente punteada. Reyment *et al.* (1987) observan una depredación selectiva de valvas lisas en ostrácodos del Cretácico Superior y Paleoceno Inferior de Israel y Nigeria. Sin embargo, otros estudios realizados en medios marinos someros indican que la depredación afecta a las especies más abundantes, independientemente del patrón ornamental externo (Reyment, 1966; Ruiz, 1997).

5. CONCLUSIONES

Las evidencias de depredación son muy escasas en las poblaciones holocenas de ostrácodos del Parque Nacional de Doñana, observándose una ausencia de relación entre su número y la abundancia de estos microcrustáceos. Los dos tipos de perforaciones distinguidos parecen corresponder al ataque de distintas familias de gasterópodos sobre los ejemplares adultos y las últimas mudas juveniles de especies lisas o poco ornamentadas. En este estudio, las dimensiones de estas perforaciones no se correlacionan con el tamaño de las valvas perforadas.

6. AGRADECIMIENTOS

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A short nomenclature note: New names for the Recent Ostracod species *Paradoxostoma dorsostriata* Titterton & Whatley, 2009a and *Loxoconcha athersuchi* Titterton & Whatley, 2009b

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A new species of *Paradoxostoma* was described from the recent Solomon Island fauna from Shortland Island by Titterton & Whatley, 2009a and assigned the name *Paradoxostoma dorsostriata*. Since its publication we have been kindly informed by Prof. E. Kempf that the name is a primary junior homonym of *Paradoxostoma dorsostriata* Howe & McKenzie, 1989 and requires a new name. We, therefore, propose the name *P. hyperknestum*. Similarly a new species of *Loxoconcha* was described from Honiara Bay by Titterton & Whatley, 2009b. This is a primary junior homonym of *Loxoconcha athersuchi* Whatley & Maybury, 1988. We propose the new name *Loxoconcha guadalcanalensis*.

***Paradoxostoma hyperknestum* nom. nov.**

2009a *Paradoxostoma dorsostriata* Titterton & Whatley p. 42, Fig. 4, Nos 6, 7; Pl. 1, Figs 31-33.

Derivatio nominis.— Gr. ὕπερκνεστὺς hyper = dorsal and knestos = scratched or scraped referring to the striations parallel to the dorsal margin.

Remarks.— The present species differs primarily in shape from *P. dorsostriata* from Australia, being more acuminate both anteriorly and posteriorly and the striations are over a slightly more distinctive cardinal angle.

***Loxoconcha guadalcanalensis* nom. nov.**

2009b *Loxoconcha athersuchi* Titterton & Whatley p. 301, Fig. 4, Nos 3, 6; Pl. 1, Figs 12-19.

Derivatio nominis.— L. named for the type locality, the island of Guadalcanal.

ACKNOWLEDGEMENTS

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Müller, A. H. 1979. Fossilization (Taphonomy). In: *Treatise on Invertebrate Paleontology* (Eds. R. A. Robison and C. Teichert). The University of Kansas Press & The Geological Society of America, Boulder, 2-78.

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SUMARIO

- DANIEL VACHARD AND PEDRO CÓZAR
An attempt of classification of the Palaeozoic *incertae sedis* Algospongia 129-242
- NASSER MOSTAFAWI, SAYED MOHAMMAD B. NABAVI AND BABAK MOGHADDASI
Ostracods from the Strait of Hormuz and Gulf of Oman, Northern Arabian Sea 243-265
- FRANCISCO RUIZ, MANUEL ABAD, MARÍA LUZ GONZÁLEZ-REGALADO, ANTONIO TOSCANO,
JOAQUÍN RODRÍGUEZ VIDAL, LUIS MIGUEL CÁCERES, MANUEL POZO, MARÍA ISABEL
CARRETERO Y EDITH XIOMARA GARCÍA
Evidencias de depredación en ostrácodos holocenos del Parque Nacional de
Doñana (SO de España) /Predation on Holocene ostracods of the Doñana National
Park (SW Spain) 267-273
- ROSEMARY TITTERTON AND ROBIN C. WHATLEY
A short nomenclature note: New names for the Recent Ostracod species
Paradoxostoma dorsostriata Titterton & Whatley, 2009a and *Loxoconcha*
athersuchi Titterton & Whatley, 2009b..... 275



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