Ann. Naturhist. Mus. Wien	86	A	13–40	Wien, September 1984

Middle Miocene (Badenian) free-living bryozoans from the Vienna Basin

By W. BALUK [1]) and A. RADWANSKI [1])

(With 12 plates)

Manuscript submitted on November, 20th, 1982

Abstract

The assemblage of free-living bryozoans from the Middle Miocene (Badenian) deposits of the Vienna Basin, kept at the Naturhistorisches Museum in Vienna, comprises six species, the revised taxonomy of which reveals the genus *Cupuladria* CANU & BASSLER being represented by the two species, *Cupuladria canariensis* (BUSK) and *C. vindobonensis* sp. n., the latter of which, *C. vindobonensis* sp. n., is established for a stock formerly kept in *C. canariensis* (BUSK). The new genus *Reussirella* gen. n. comprises the species first recognized by REUSS in the Vienna Miocene deposits, *R. haidingeri* (REUSS), and the rare species *R. reussiana* (MANZONI) which is new for the Vienna Miocene. New for the region is also *Discoporella umbellata* (DEFRANCE). The species *Lunulites androsaces* MANZONI completes the list of the revised taxa. Anatomical studies show that the genera *Reussirella* gen. n. and *Discoporella* d'ORBIGNY are to be joined into a separate family, the Discoporellidae fam. n. Moreover, recognized is regeneration of colonies in *Cupuladria vindobonensis* sp. n., *Reussirella haidingeri* (REUSS), *Discoporella umbellata* (DEFRANCE), and *Lunulites androsaces* MANZONI. Ecological requirements of the investigated free-living bryozoans and their paleoclimatical (tropical and/or subtropical) significance are shortly discussed. Finally, some problems of the Miocene bioprovinces, and Indo-Pacific affinities of the European Miocene floral and faunal communities are indicated.

Zusammenfassung

Die am Naturhistorischen Museum in Wien aufbewahrten frei-lebenden Bryozoen der mittelmiozänen (Badenien) Ablagerungen des Wiener Beckens umfassen nach einer Revision sechs Arten: die Gattung *Cupuladria* CANU & BASSLER mit zwei Arten: *C. canariensis* (BUSK) und *C. vindobonensis* nov. spec. Diese neue Art wurde von den unter *C. canariensis* aufbewahrten Formen abgetrennt. Die neue Gattung *Reussirella* nov. gen. mit der erstmals von REUSS aus den Ablagerungen des Wiener Raumes beschriebenen *R. haidingeri* (REUSS) und der seltenen Art *R. reussiana* (MANZONI), die erstmals aus dem Wiener Raum nachgewiesen wird, ebenso wie *Discoporella umbellata* (DEFR.). *Lunulites androsaces* MANZONI komplettiert die Artenliste.

Anatomische Studien zeigen, daß die Gattungen *Reussirella* nov. gen. und *Discoporella* d'ORB. zu einer eigenen Familie zusammenzufassen sind: Discoporellidae nov. fam. Ferner konnte die Regeneration von Kolonien bei *Cupuladria vindobonensis* nov. spec., *Reussirella haidingeri* (REUSS), *Discoporella umbellata* (DEFR.) und *Lunulites androsaces* MANZONI nachgewiesen werden.

Die ökologischen Ansprüche von rezenten frei-lebenden Bryozoen werden kurz in Hinblick auf ihre paläoklimatologischen Aussagen (tropisch und/oder subtropisch) diskutiert. Letztlich wird auf die

[1]) Address of the Authors: Doz. Dr. Waclaw BALUK and Prof. Dr. Andrzej RADWANSKI, Institute of Geology, University of Warsaw, Al. Zwirki-i-Wigury 93, PL 02-089 Warsaw. – Poland.

Problematik der Miozänen Bioprovinzen, besonders auf die Indo-Pazifischen Beziehungen der Europäischen Miozänen Floren- und Faunen-Gemeinschaften hingewiesen.

Introduction

The free-living bryozoans, the most commonly known and representative species of which is *Cupuladria canariensis* (BUSK, 1859), have long been comprehensively studied due to the striking features of their life habit, and of ability to regenerate their colonies even from small fragments. These two features distinguish pronouncedly the genus *Cupuladria* CANU & BASSLER, 1919, and its allies from all other members of the cheilostome bryozoans.

The species *Cupuladria canariensis* (BUSK) is the only one which was the subject of an extensive monograph written by LAGAAIJ (1963), and emphatically entitled "*Cupuladria canariensis* (BUSK) – portrait of a bryozoan". This monograph which contains both discussion on the nature of the species, as well as on its biology and ecology, has become an outstanding example to summarize the knowledge on a definite bryozoan species. Nevertheless, in a couple of years it was indicated by COOK (1965*a, b*) that a part of the material described by LAGAAIJ offered really a portrait of another species, which COOK classified as "*Cupuladria biporosa* CANU & BASSLER, 1923".

A decade later, CADÉE (1975) showed that the species *Cupuladria monotrema* (BUSK, 1884), previously regarded (see HASTINGS 1930, COOK 1965*b*) as possibly conspecific with either *C. canariensis* (BUSK) or *C. biporosa* CANU & BASSLER, is also a separate species. On the other hand, within the material referred to as *C. canariensis* (BUSK) by some authors, CADÉE (1975) distinguished another separate species, *C. surinamensis* CADÉE, 1975. In result, the "*Cupuladria canariensis* group", as named by COOK (1965*a*) and supplemented by CADÉE (1975), comprised the four species (*C. canariensis, C. biporosa, C. monotrema, C. surinamensis*), the taxonomic separateness of which has, to some extent, been subsequently doubted by CADÉE himself (1979, 1981). Of these four species, only the first two are known from ancient epochs, and these will be discussed hereafter.

The populations of *Cupuladria canariensis* (BUSK) recognized from the Miocene and/or Pliocene deposits of Europe are often associated (see LAGAAIJ 1952, 1953, 1963; COOK 1965*b*, p. 210; BUGE & DEBOURLE 1971; BUGE 1972, 1973; CADÉE 1977*a*; BALUK & RADWANSKI 1977*b*) with the species *Cupuladria haidingeri* (REUSS, 1847) which has never been reported from present-day environments, and whose relation to the *C. canariensis* group remained unclear (see BALUK & RADWANSKI 1977*b*). This species, established by REUSS (1847) for the Middle Miocene (Badenian) specimens from the Vienna Basin (Leithakalk of Steinebrunn and Nußdorf, Tegel of Baden), was subsequently treated by MANZONI (1877) who supplemented the original description by quoting the REUSS' posthumous manuscript. The illustrations presented both by REUSS (1847, Pl. 7, Figs 26–27) and by MANZONI (1877, Pl. 16, Fig. 54) showed specimens with some opesia wholly covered by a calcareous lamina, and thus with the anatomical features more close to those of the genus *Discoporella* d'ORBIGNY, 1852, than to any species of the *Cupuladria canariensis* group.

Of the genus *Discoporella*, those features concern the extant species *D. umbellata* (DEFRANCE, 1823) which is often associated with *Cupuladria canariensis* (BUSK) and/or *C. haidingeri* (REUSS) in the Miocene deposits of the Atlantic gulfs in France (BUGE 1972, Table 3), and of the North Sea Basin (LAGAAIJ 1953; BUGE 1973, Table 1). Taking into account that in the Vienna Basin the species *Discoporella umbellata* (DEFRANCE) had never been reported (see VÁVRA 1977, 1979), and this very species was sometimes confused with some *Cupuladria* species (COOK 1965*a*, p. 179, and 1965*b*, p. 200), it seemed that *C. haidingeri* from the Vienna Basin may represent a preservation case (damaged colonies) of *Discoporella umbellata* DEFRANCE). The cupuladriid bryozoans recognized (BALUK & RADWANSKI 1977*b*) in the Middle Miocene (Badenian) Korytnica Basin on the southern slopes of the Holy Cross Mts, Central Poland, were also represented only by *C. canariensis* (BUSK) and *C. haidingeri* (REUSS), the latter being however different from the Vienna Basin specimens by the absence of any structures covering the opesia. The above circumstances were the reason of necessity to study the original collection of REUSS, and the other specimens of the cupuladriid bryozoans reported from the Miocene deposits of the Vienna Basin.

The first insight into the REUSS' collection and other topotypic materials, kept at the Naturhistorisches Museum in Vienna, enabled to find them much deviated from the statements on the labels, and from the actual state of knowledge on the ancient free-living bryozoans. Further studies revealed also that the taxonomy of some of the investigated species appears much more perplexed that anybody could expect and, consequently, a thorough revision of the whole *canariensis – haidingeri* swarm became requested.

The revision of all the free-living bryozoans collected from the Middle Miocene (Badenian) deposits of the Vienna Basin has resulted in the following statements:

1. Established is a new species, *Cupuladria vindobonensis* sp. n., which covers a stock formerly included into *Cupuladria canariensis* (BUSK, 1859), and under that latter name reported from the Vienna Basin (MANZONI 1877, CANU & BASSLER 1925, LAGAAIJ 1963, DAVID & POUYET 1974, VÁVRA 1977, CADÉE 1979);
2. Indicated is the presence of true *Cupuladria canariensis* (BUSK, 1859), the representatives of which have neither been reported from the Vienna Basin nor from any Miocene deposits of Europe;
3. The anatomical structure of the species *haidingeri* of REUSS (1847) indicates that it is neither of the genus *Cupuladria* nor *Discoporella*; consequently, a new genus is established, *Reussirella* gen. n., with *Reussirella haidingeri* (REUSS, 1847) as its type species;
4. Following discussion on the systematic position of the newly established genus *Reussirella* gen. n. which is related to *Discoporella* more closely than to *Cupuladria,* the new family is founded, Discoporellidae fam. n., that comprises the genera *Discoporella* d'ORBIGNY, 1852, and *Reussirella* gen. n.;

5. Recognized is the presence of *Reussirella reussiana* (MANZONI, 1869) and *Discoporella umbellata* (DEFRANCE, 1823), the both being hitherto unknown from the Vienna Basin;

6. Confirmed is the presence of *Lunulites androsaces,* and MANZONI (1869) is recognized as its creator; this species cannot be ascribed to ALLIONI (1757) or MICHELOTTI (1838), as given in former references.

The hereafter presented discussion on particular species will be preceded by a general account of taxonomy of the free-living bryozoans, both at their higher-leveled ranks, and at the infraspecific level within the most confused genus *Cupuladria.*

Taxonomy at the Family and Generic Rank

The taxonomy of the free-living bryozoans is commonly identified with that of the lunulitiform bryozoans, the group of which contains the cupuladriid bryozoans (genera *Cupuladria* CANU & BASSLER, and *Discoporella* d'ORBIGNY; as understood by COOK 1965*a*) and a morphologically similar, but certainly not closely related (see COOK 1965*a*; HÅKANSSON 1973, 1976) extinct genus *Lunulites* LAMARCK. The range of these genera, primarily of the first two has, however, been long interpreted variously, and some of the events in the former taxonomic procedure still have an important bearing upon the present-day status of a few taxa.

When studying the specimens from the Vienna Basin, it has become evident that some of the taxonomical errors result, partly at least, from misinterpretation of systematic position of the species *haidingeri* of REUSS (1847), and of a group of the genus *Cupuladria*, namely of the "*C. owenii* group" distinguished by COOK (1965*a*) who included the species *haidingeri* into that very group.

To understand this problem, the systematic status of the three above indicated genera will firstly be presented. In the last decades, since the Treatise on Invertebrate Paleontology Volume prepared by BASSLER (1953) has appeared, it was kept as follows:

The genus *Cupuladria* CANU & BASSLER, 1919, belongs to the family Membraniporidae BUSK, 1854, to which the family Cupuladriidae established by LAGAAIJ (1952) was included (BASSLER 1953, pp. G 155–G 156);

The genus *Lunulites* LAMARCK, 1816, plus a poorly known genus *Volviflustrellaria* BRYDONE, 1936, make up a separate family, the Lunulitidae of LAGAAIJ (1952), much distant in the systematics to the former one (BASSLER 1953, p. G 171);

The genus *Discoporella* d'ORBIGNY, 1852, belongs to the family neighboring the former one (Lunulitidae), namely the Calpensiidae CANU & BASSLER, 1923; of this family, BASSLER (1953, p. G 171) excluded the genus which formerly was regarded as a calpensiid by CANU & BASSLER (1923, 1925, 1928), namely *Cupularia* BLAINVILLE, 1830, the name of which was put by BASSLER (1953, p. G 234) into the "unrecognized generic names".

As a further step, it is to state that the species *haidingeri* of REUSS (1847) has long been kept in the genus *Cupularia*, and thus regarded as a calpensiid (CANU &

BASSLER 1923, 1925). When creating the genus *Cupuladria*, CANU & BASSLER (1919) included into this genus only the species *canariensis* and, afterwards, the species *biporosa* established in 1923. Another then established species, *multispinata*, CANU & BASSLER (1923) put into the genus *Cupularia* in which they also kept such species as *doma* of d'ORBIGNY, 1853, and *haidingeri*, i. e. the species of the "*Cupuladria owenii* group" of COOK (1965*a*).

All the species of the "*Cupuladria owenii* group" of COOK (1965*a*) have always been regarded by CANU & BASSLER (1923, 1925, 1928) as far distant from the species bunched into the "*Cupuladria canariensis* group" by COOK (1965*a*). As evidenced below, this statement was right. To the truth, it has never been formally objected by anybody. The misunderstanding in the cupuladriid bryozoans has originated when LAGAAIJ (1952, 1953), bewildered presumably by a joint-occurrence of the species *canariensis* and *haidingeri* in the Dutch Mio-Pliocene samples, assigned the both species to the genus *Cupuladria*. This attribution was followed by COOK (1965*a, b*) and by all the subsequent authors. However, when rejecting the generic name *Cupularia*, there was no reason to include the *oweni-haidingeri-doma* group of species automatically into the genus differing of one character in its name, but of many features in its anatomy. The common occurrence of the species *canariensis* and *haidingeri* in the same samples, in which they often dominate over the other bryozoans, does not excuse for such treatment, the more so that the both may also be associated with *Discoporella umbellata* (DEFRANCE). It is to note that some of the American authors did not follow the above treatment (e. g. CHEETHAM & SANDBERG 1964, p. 1022) and attributed the species *doma* to the genus *Discoporella*, the statement having not been accepted by COOK (1965*b*, p. 216). The same species was also designated as "*Cupuladria*" *doma* by HÅKANSSON (1976).

In the Author's opinion, the four groups of species recognized by COOK (1965*a*, p. 167) really exist, viz. (1) "*Cupuladria canariensis* group", (2) "*Cupuladria guineensis* group", (3) "*Cupuladria owenii* group", and (4) "*Discoporella umbellata* group", but a marked difference appears not only between the groups 1–3 (= *Cupuladria*) and 4 (= *Discoporella*), but also between (1) and the remainder. The *oweni-haidingeri-doma* group bears the features distinct both from the *C. canariensis* group and from the *D. umbellata* group, and it is here distinguished as a separate genus, *Reussirella* gen. n., to which the species *reussiana* of the *D. umbellata* group of COOK (1965*a*) is also included.

The "*Cupuladria guineensis* group" of COOK (1965*a*), which is not represented in the material investigated, is excluded from further discussion as the features of its few species are not evidently diagnostic. Its "type species" either belongs to *Cupuladria* or to *Reussirella* to which it approaches by the absence of kenozoidal chambers, by its underside tuberculated, and by having closures of the central zooecia (see HASTINGS 1930, p. 714; CHEETHAM & SANDBERG 1964, p. 1021). The latter feature is also revealed by the species *indica* of COOK (1965*a*), the underside of which is typical of *Reussirella*.

The Authors accept the statement of LAGAAIJ (1952, 1963) that the genus *Cupuladria* makes up a separate family, the Cupuladriidae LAGAAIJ, 1952. Because the *oweni-haidingeri-doma* group of species in its anatomy is more distant from all the *Cupuladria* species than from the *Discoporella* species, the genus *Reussirella* gen. n. is not included into the Cupuladriidae, but joined with *Discoporella* into a separate family, the Discoporellidae fam. n. It markedly differs from the rest of the family Calpensiidae, and the mutual relation of these two families is not decided. Possibly, the Discoporellidae are near to the Cupuladriidae, but neither their phylogenic relationship evidenced by common ancestors nor convergent evolution due to the same free-living habit are documented. Anyway, the so-understood Discoporellidae remain distant to the Lunulitidae. The handy term of the lunulitiform bryozoans is however kept when necessary to speak about all the three discussed families, i. e. the Cupuladriidae, the Discoporellidae, and the Lunulitidae.

The systematic position of the other free-living bryozoans, called sometimes also the lunulitiform bryozoans (see LAGAAIJ 1953; GREELEY 1967, 1970; CADÉE 1975; COOK & CHIMONIDES 1978), is not to be discussed in the present paper.

The accepted taxonomy which concerns the free-living bryozoans recognized in the Middle Miocene (Badenian) deposits of the Vienna Basin is given in the forthcoming chapters, where diagnoses of the taxa higher than species are also

Table 1

Diagnostic features of the investigated families and genera of the free-living cheilostome bryozoans

Cupuladriidae LAGAAIJ, 1952	Discoporellidae, fam. n.	
Cupuladria CANU & BASSLER, 1919	*Reussirella*, gen. n.	*Discoporella* d'ORBIGNY, 1852
Zoaria free in adult stages Zooecia with asymmetrical vibracula, distal to each zooecium		
Vicarious vibracula sometimes present in some species	Vicarious vibracula not stated	
Central zooecia open	Central zooecia closed by a calcareous lamina	
Vestibular arch absent	Vestibular arch present	
Cryptocyst simple, without spinules	Cryptocyst incomplete, with spinules, sometimes joined	Cryptocyst complete, with two rows of opesiules
Kenozoidal chambers arranged in series oblique to the sole of the basal pad	Kenozoidal chambers absent	
Underside sectored, with pores	Underside with alternating grooves and ridges, tuberculate	

included. The basic features of, and the differences between the investigated genera and families are summarized in a tabular form (Table 1). Omitted will be a discussion on the well established genus *Lunulites*, the representative of which, *L. androsaces* MANZONI, 1869, is reported by the end of systematic descriptions.

Taxonomy of the Genus *Cupuladria*

The taxonomic jungle within the genus *Cupuladria* CANU & BASSLER, 1919, became apparent to the Authors when the original descriptions of the investigated species had been taken into account. At first, it became evident that a part of the *Cupuladria canariensis* stock which had been excluded from that nominative species by COOK (1965*a, b*), was erronously classified by her as "*Cupuladria biporosa* CANU & BASSLER, 1923". This error has been repeated by the subsequent authors (HÅKANSSON 1973; CADÉE 1975, 1979, 1981). The diagnosis of the species *Cupuladria biporosa* CANU & BASSLER, 1923, has been largely and such arbitrarily extended by COOK (1965*b*, pp. 204–205), and thus it became much deviated from the original description by CANU & BASSLER (1923, pp. 29–30), as already noted by CADÉE (1979, p. 457; and 1981, p. 7). The holotype specimen (CANU & BASSLER 1923, Pl. 47, Figs 1–2) bears in each sector 2 pores only, which show the one-by-one array along the colony radius. What is more dramatic, the modified diagnosis offered by COOK (1965*b*) appears identical with that presented by BUSK (1859*a*, p. 66) for his *Cupuladria canariensis*! It is clear that COOK (1965*b*) was speaking about two different species, and this is accepted by the present Authors; but, she used a wrong name to the species which had its well established name. It also means that "*Cupuladria biporosa*" of COOK (1965*b*, pp. 203–209) is the typical *Cupuladria canariensis* of BUSK (1859*a*), and what was regarded as "*Cupuladria canariensis*" by COOK (1965*a, b*) becomes devoid of any name! The source of this fault is recognizable in another paper by BUSK, published in the same year of 1859.

It really happened that BUSK in this second paper (BUSK 1859*b*) illustrated in Pl. 13 (nomen omen), Fig. 2d, under the name of *canariensis*, the two different species ("*biporosa*" and "*canariensis*" as understood by COOK 1965*b*). Evidently, the diagnosis provided with a very adequate illustration and designation as a new species ("*Cupularia Canariensis*, n. sp."), given in his earlier paper (BUSK 1859*a*, p. 66; referenced already by BUSK 1859*b*) has priority. The content of this earlier paper (BUSK 1859*a*) concerns the species which was erronously called "*biporosa*" by COOK (1965*b*) and by the subsequent authors.

Consequently, the remaining stock of "*canariensis*" of BUSK (1859*b*), and the whole species "*canariensis*", as understood by COOK (1965*a, b*), would be provided with a new name. The herein introduced new name, *Cupuladria vindobonensis* sp. n., will cover all the discussed name-lacking specimens, and the one illustrated by BUSK (1859*b*, Pl. 13, right picture of Fig. 2d) is regarded as the holotype.

The species *Cupuladria biporosa* CANU & BASSLER, 1923, which caused so extreme confusion to COOK (1965*b*) is treated by the Authors as a separate species, documented however only by its original report of CANU & BASSLER (1923) from the Miocene of Santo Domingo, and possibly supplemented by a Miocene material from Trinidad (CADÉE 1979, p. 457).

Taxonomy at the Infraspecific Rank in *Cupuladria*

The problems of the taxonomy at the infraspecific level in some of the *Cupuladria* species appeared quite recently, when CADÉE (1979) distinguished two subspecies in his "*Cupuladria canariensis* (BUSK)" [recte: *Cupuladria vindobonensis* sp. n.]. The distinction was based by CADÉE (1979) on the number of kenozoidal chambers, the feature of which was postulated as taxonomically important. The beneath presented arguments do not allow, however, to accept that statement.

The kenozoidal chambers are formed during the colony growth by an accretion of the basal pad. The latter is deposited obliquely to the basal margin, and thus the number of kenozoidal chambers beneath a zooecium/vibraculum couple remains more of less constant and evidently lesser than the number of zooecium/vibraculum couples within a given file (radius) on the upper side of the colony (see TAVENER-SMITH 1973, Fig. 1a and 1b). The number of kenozoidal chambers is therefore a function of the thickness of the basal pad. It is to note that the series of kenozoidal chambers are not the "layers", as named by COOK (1965*a, b*) and CADÉE (1979), because they are situated along the growth lamellae that run obliquely to the colony base.

In present-day specimens of *Cupuladria canariensis* (BUSK), the number of kenozoidal chambers usually varies between 2 and 6 or even 8, being one at the colony margin (see WATERS 1921, Pl. 29, Fig. 1; TAVENER-SMITH 1973, Fig. 1; HÅKANSSON 1973, Fig. 1). This number has always been stated as more than one (CADÉE 1975, 1979), or as "many" (COOK 1965*b*, p. 205).

In present-day *Cupuladria monotrema* BUSK), the number of kenozoidal chambers varies, being stated as either one (HASTINGS 1930, p. 715; COOK 1965*b*, p. 209), the feature regarded to be distinctive from the preceding species (COOK 1965*b*, p. 210), or as more than one (CADÉE 1975).

Within the forms attributed to the new species *Cupuladria vindobonensis* sp. n., the number of kenozoidal chambers also varies, as stated by CADÉE (1979) who distinguished the present-day forms with one "layer" of kenozoidal chambers as the nominative subspecies of his "*Cupuladria canariensis canariensis* (BUSK)", and the ancient forms with the number of "layers" more than one as a separate subspecies, "*Cupuladria canariensis cavernosa* CADÉE". Such a separation does not seem however to be justified, as all the ancient specimens from the European Neogene are known from sediments, the depositional environment of which differs from the present-day ones in type of the substrate and other ecological factors (see BALUK & RADWANSKI 1977*b*, HOFFMAN 1979*a*). Generally, it concerns much lesser depths at which the ancient cupuladriids have lived, as evidenced in the Korytnica Basin (BALUK & RADWANSKI 1977*b*). Under such environmental conditions featured by an extremely high ecological heterogeneity, the thickness of the basal pads (thus, the number of kenozoidal chambers) is assumed to have resulted from adaptation to the prevailing biotope conditions. The specimens with a different number of kenozoidal chambers would therefore be regarded only as the ecotypes, and no "kenozoidally differing" subspecies of any of the *Cupuladria* species are to be distinguished.

Systematic Descriptions

Family Cupuladriidae Lagaaij, 1952

The family Cupuladriidae is understood the same as definied by Lagaaij (1952), to include only the genus *Cupuladria* Canu & Bassler, being therefore the type genus. Rejected are statements of Bassler (1953) who included the Cupuladriidae to the Membraniporidae, and of Cheetham & Sandberg (1964) and Cook (1965*a*) who extended the range of the family to contain also the genus *Discoporella*.

Diagnosis: Zoaria free in adult stages; zooecia with asymmetrical vibracula, distal to each zooecium. Vicarious vibracula sometimes present in some species. Central zooecia open, without closures by a calcareous lamina. Zooecia rounded, and vestibular arch not developed. Cryptocyst simple, in the form of a narrow ledge, without spinules. Kenozoidal chambers arranged in series running obliquely to the sole of the basal pad; number of kenozoidal chambers variable. Underside sectored, with pores.

Genus *Cupuladria* Canu & Bassler, 1919

Type species: *Cupuladria canariensis* (Busk, 1859)

Diagnosis: The same as for the family.

Species included: *Cupuladria canariensis* (Busk, 1859); *C. monotrema* (Busk, 1884); *C. biporosa* Canu & Bassler, 1923; *C. surinamensis* Cadée, 1975; *C. vindobonensis* sp. n.

Cupuladria canariensis (Busk, 1859)
(Plates 1 and 8)

1859a *Cupularia Canariensis* n. sp., Busk, pp. 66–67, Pl. 23, Figs 7–8.
1859b *Cupularia canariensis* Busk – Busk, p. 87, Pl. 13, Fig. 2d (left picture only).
1918 *Cupularia canariensis* Busk – Canu & Bassler, pp. 119–120, Pl. 53, Figs 6–7.
1919 *Cupuladria canariensis* Busk – Canu & Bassler, p. 78, Pl. 1, Figs 9–10 (the same as Canu & Bassler 1918, Pl. 53, Figs 6–7).
1920 *Cupuladria canariensis* Busk – Canu & Bassler, p. 103, Text-fig. 24D (the same as Canu & Bassler 1918, Pl. 53, Fig. 6).
1921 *Cupularia canariensis* Busk – Waters, pp. 410–412, Pl. 29, Figs 1–5.
1923 *Cupuladria canariensis* Busk – Canu & Bassler, pp. 28–29, Pl. 1, Figs 8–9 (the same as Canu & Bassler 1918, Pl. 53, Figs 6–7).
1953 *Cupuladria canariensis* (Busk) – Bassler, Text-fig. 118/2a–2b (the same as Canu & Bassler 1918, Pl. 53, Figs 6–7).
1962 *Cupuladria canariensis* – Marcus & Marcus, p. 285, Pl. 1, Fig. 3.
1963 *Cupuladria canariensis* (Busk) – Lagaaij, Pl. 26, Figs 4–5.
1965b *Cupuladria biporosa* Canu & Bassler – Cook, pp. 203–209, Text-fig. 1g–1j, Pl. 1, Figs 2–6.

1973 *Cupuladria biporosa* CANU & BASSLER – HÅKANSSON, Pl. 1, Figs 1–5.
1975 *Cupuladria biporosa* CANU & BASSLER – CADÉE, pp. 324–325, Pl. 3b.
1979 *Cupuladria biporosa* CANU & BASSLER – CADÉE, Text-fig. 1A.
1981 *Cupuladria canariensis cavernosa* CADÉE – CADÉE, Text-figs 1–3.
1981 *Cupuladria biporosa* CANU & BASSLER – CADÉE, Text-figs 4–6.

Material:
One complete, young zoarium (Pl. 1, Fig. 1a–1b; Catalogue Number 1859. L. 999/3), three fragments of larger zoaria (Pl. 1, Figs 2a–2b, 3a–3b and 4a–4b; Catalogue Numbers 1859. L. 993/4 through 1859. L. 993/6 respectively), one fragment with vicarious vibracula (Pl. 8, Fig. 3; Catalogue Number 1859. L. 993/7), five other fragments (Catalogue Number 1859. L. 993/8), all from Baden; Labelled as "*Lunulites Haidingeri* Rss".

Remarks: The investigated specimens coincide with those included into the synonymy which does not contain the forms which escape from the specific recognition (e. g., presented by HASTINGS 1930, Pl. 8, Figs 38 and 40; SILÉN 1942, Text-figs 7–9 and Pl. 4, Figs 15–16).

Some of the investigated specimens bear the vicarious vibracula which are either singly distributed throughout the zoarium (Pl. 1, Fig. 2a; magnified in Pl. 8, Fig. 4) or they gather in pairs (Pl. 8, Fig. 3), regardless the distance to the colony center. The presence of vicarious vibracula, sometimes frequent in some zoaria, although occurring usually in the ancestrular area, is typical of this species (see COOK 1965*a*, p. 155, and 1965*b*, p. 209). The basal pad contains several kenozoidal chambers arranged in series, similarly as in the present-day specimens (see WATERS 1921; COOK 1965*b*, p. 209; TAVENER-SMITH 1973; HÅKANSSON 1973). The number of pores within a sector of the underside attains for a colony or a given fragment an average value of 3.48 to 3.59, with a range of 1 to 6, what coincides with the reference data (COOK 1965*b*, p. 205; CADÉE 1975, 1979, 1981).

The only juvenile specimen (Pl. 1, Fig. 1a–1b) agrees well with those reported from the present-day environments (see COOK 1965*b*, Pl. 1, Figs 3–4 and 6; HÅKANSSON 1973, Pl. 1, Fig. 5).

Occurrence: The species, as taxonomically understood in the present paper, was formerly unknown from the Vienna Basin and from any Miocene deposits of Europe. Within the ancient deposits in Europe, it has previously been reported only from the Pliocene, primarily from the Coralline Crag of England (see BUSK 1859*a*, BUGE & DEBOURLE 1971, CADÉE 1981).

In the West Atlantic province the species ranges from the Miocene to the present-day (see CANU & BASSLER 1923, COOK 1965*b*). At present it lives also in the tropical and subtropical zones of the Eastern Atlantic and the Eastern Pacific (COOK 1965*b*).

Cupularia vindobonensis sp. n.
(Plates 2–3 and Pl. 9, Figs 1–2)

Holotype: The specimen illustrated by BUSK (1859*b*, Pl. 13, right picture of Fig. 2d).

Derivation of the name: After Vindobona, the Roman name of Vienna.

Diagnosis: Cupuladriid species distinguished by their basal sectors, the majority of which are long, with pores ranging usually between 6 and 12, and their maximum range observed 2 to 20 in a sector; the number of kenozoidal chambers variable, usually from one to three or four; vicarious vibracula not definitely stated.

1859b *Cupularia canariensis* Busk – Busk, p. 87, Pl. 13, Fig. 2d (right picture only).
1869 *Cupularia Canariensis* Bk. – Manzoni, pp. 26–27, Pl. 2, Figs 17 and 17'.
1877 *Cupularia canariensis* Busk – Manzoni, pp. 72–73, Pl. 17, Fig. 56a–56c.
1921 *Cupularia canariensis* Busk – Waters, pp. 410–412, Pl. 30, Figs 11–12 (non Pl. 29, Figs 1–5 = really *Cupuladria canariensis*).
1928 *Cupuladria canariensis* (Busk) – Canu & Bassler, p. 15, Pl. 1, Figs 7–9.
1935 *Cupuladria canariensis* (Busk) – Dartevelle, p. 560, Pl. 19, Figs 1–2.
1949 *Cupuladria canariensis* Busk – Vigneaux, p. 38, Pl. 2, Figs 8–9.
1952 *Cupuladria canariensis* Busk) – Lagaaij, pp. 33–34, Pl. 2, Fig. 1a–1b.
1953 *Cupuladria canariensis* (Busk) – Lagaaij, pp. 15–16, Pl. 1, Fig. 1a–1b.
1963 *Cupuladria canariensis* (Busk) – Lagaaij, Pl. 25, Figs 1a–1b and 3–5.
1963 *Cupuladria canariensis* (Busk) – Annoscia, p. 225, Pl. 9, Fig. 1, Pl. 10, Fig. 1, Pl.11, Fig. 1a–1b, Pl. 12, Fig. 1a–1b.
1964 *Cupuladria canariensis* (Busk) – Cheetham & Sandberg, p. 1021, Text-figs 11 and 13.
1965b *Cupuladria canariensis* (Busk) – Cook, pp. 197–203, Text-fig. 1a–1f, Pl. 3, Fig. 4 (non Pl. 1, Fig. 1A–1B = *Cupuladria surinamensis* Cadée, as indicated by Cadée 1979, p. 446).
1966 *Cupuladria canariensis* (Busk) – Camacho, pp. 42–43, Pl. 6, Fig. 4a–4b.
non 1971 *Cupuladria canariensis* (Busk) – Barbosa, Text-figs 1–4 (= *Reussirella* sp.).
non 1972 *Cupuladria canariensis* (Busk) – Buge, Pl. 2, Figs 1–2 (= ?*Cupuladria surinamensis* Cadée).
1973 *Cupuladria canariensis* (Busk) – Buge, p. 36, Pl. 6, Figs 1–2.
1975 *Cupuladria canariensis* (Busk) – Cadée, Pl. 3d.
1977b *Cupuladria canariensis* (Busk) – Baluk & Radwanski, Pl. 1, Figs 1–6, Pl. 2, Figs 1–5, Pl. 3, Figs 1–2.
1977a *Cupuladria canariensis* (Busk) – Cadée, p. 45, Pl. 1, Fig. 3.
1979 *Cupuladria canariensis canariensis* (Busk) plus *Cupuladria canariensis cavernosa* n. subsp. – Cadée, Text-figs 1C–1F and 4.

Material:

One complete zoarium from Eisenstadt (Pl. 2, Fig. 1a–1b; Catalogue Number 1867. XL. 318/1); Labelled as: "*Cupularia* sp.", and by Vávra (1976) *) as "*Cupuladria haidingeri* (Reuss 1848)".

One complete zoarium from Steinebrunn (Pl. 3, Fig. 1a–1b; Catalogue Number 1867. XL. 315/5); Labelled as: "*Lunulites Haidingeri*", by David & Pouyet (1974) *) as "*Cupuladria haidingeri* Rss.; paratype", and by Vávra (1976) as "*Cupuladria haidingeri*".

One complete zoarium (Pl. 2, Fig. 2a–2b; Catalogue Number 1983/74/1) and one fragment (Catalogue Number 1983/74/2) from Baden; Labelled as "*Lunulites Haidingeri* Reuss".

Fragmented zoaria from Grinzing: Two specimens illustrated in Pl. 3, Fig. 3a–3b (Catalogue Number Acqu. 1904, Karrer/1) and Pl. 3, Fig. 4a–4b (Catalogue Number Acqu. 1904, Karrer/2), and 15 other specimens (Catalogue Number Acqu. 1904, Karrer/3).

Fragmented zoaria from Baden: One specimen illustrated (Pl. 3, Fig. 2a–2b; Catalogue Number 1859. L. 993/1) and 5 other specimens (Catalogue Number 1859. L. 993/2); Labelled as "*Lunulites Haidingeri* Rss".

*) "Vávra (1976)" and "David & Pouyet (1974)" are the dates of labelling of the specimens referred to the papers by Vávra (1977) and by David & Pouyet (1974).

14 fragmented zoaria from Baden-Soos; Catalogue Number 1977/1946/1; Labelled as "*Cupuladria* spp.".

4 fragmented zoaria from Rodaun; Catalogue Number 1977/1945/2; Labelled as "*Cupuladria canariensis* (BUSK)".

Remarks: The investigated specimens coincide with those included into the synonymy which covers a part of the formerly understood species *Cupuladria canariensis* (BUSK).

Within the investigated specimens, the number of kenozoidal chambers varies from one (usually vertically elongated) to three or four; the section of a zoarium presented by MANZONI (1877, Pl. 17, Fig. 56c) runs along a sectorline, and thus the chambers are not exposed. The number of pores within a sector of the underside varies usually between 6 and 12, with the observed range 2 to 18 that agrees with the reference data recording the maximum number of 20 (COOK 1965*b*, p. 199; CADÉE 1975, p. 325 and 1979, p. 446).

Occurrence: The species formerly reported, under the name of *C. canariensis*, from the Vienna Basin by:

MANZONI (1877, pp. 72–73, Pl. 17, Fig. 56): Grinzing, Perchtoldsdorf; and Kostel (= Podivin) in Czechoslovak part of the Basin;

CANU & BASSLER (1925, p. 673): Eisenstadt, Steinebrunn; and Porzteich (= Sedleč) in Czechoslovak part of the Basin;

LAGAAIJ (1963, Text-fig. 15a);

DAVID & POUYET (1974, p.102);

VÁVRA (1977, p. 77): Burgenland (Eisenstadt), Niederösterreich (Perchtoldsdorf, Steinebrunn), Wien (Grinzing); and Porzteich (= Sedleč), Kostel (= Podivin) in Czechoslovak part of the Basin;

CADÉE (1979, pp. 452–453; as *C. c. cavernosa* CADÉE): Eisenstadt, Steinebrunn (collection USNM Washington).

Outside the Vienna Basin, all the occurrences were also reported under the name of *C. canariensis*, as follows.

Other Central Paratethys basins: Transylvanian Basin at Bujtur-Lapugy (MANZONI 1877, COOK 1965*b*), Korytnica Basin (COOK 1965*b*, p. 199, at Karsy; BALUK & RADWANSKI 1977*b*), Carpathian Foredeep at Benczyn (MALECKI 1951; LAGAAIJ 1963, Text-fig. 15*a*).

Other European occurrences reviewed by: LAGAAIJ (1952, 1953, 1963), COOK 1965*b*), BUGE (1972, 1973), VÁVRA (1977), and CADÉE (1979).

Occurrences outside Europe reviewed by: LAGAAIJ (1963) and COOK (1965*b*).

Family Discoporellidae fam. n.

The family Discoporellidae fam. n. is herein established to comprise the genus *Discoporella* d'ORBIGNY and a related genus which is described as a new one, *Reussirella* gen. n. The genus *Discoporella* has been formerly placed either (BASSLER 1953) within the family Calpensiidae CANU & BASSLER, or (COOK 1965*a*) within the Cupuladriidae LAGAAIJ. The species gathered herein within the genus

Reussirella gen. n. have hitherto been included either into the genus *Cupuladria*, or partly to *Discoporella* (see synonymies, and the preceding discussion).

Diagnosis: Zoaria free in adult stages; zooecia with asymmetrical vibracula, distal to each zooecium. Vicarious vibracula not stated. Central zooecia closed by a calcareous lamina. All zooecia with vestibular arch well developed. Cryptocyst with spinules or completely covering the opesium. Kenozoidal chambers absent within the basal pad. Underside with alternating grooves and ridges, tuberculate.

Genus *Reussirella* gen. n.

Type species: *Reussirella haidingeri* (Reuss, 1847)

Derivation of the name: In honour of August Emanuel von Reuss (1811–1873), a prominent Austrian paleontologist, whose monograph of the Miocene bryozoans from the Vienna Basin (Reuss 1847) offered the original description of the species which is now the best recognized of the whole group, and designated herein as the type species of the genus.

Diagnosis: Discoporellid genus bearing the incomplete cryptocyst provided with spinules, sometimes joined over the opesium.

Species included: *Reussirella haidingeri* (Reuss, 1847); *R. reussiana* (Manzoni, 1869); *R. multispinata* (Canu & Bassler, 1923); *R. doma* (d'Orbigny, 1853); *R. oweni* (Gray, 1828).

Reussirella haidingeri (Reuss, 1847)

(Plates 4–6 and 10)

1847 *Lunulites Haidingeri*, m. – Reuss, p. 58, Pl. 7, Figs 26–27.
1859b *Cupularia denticulata* Conrad – Busk, pp. 85–86, Pl. 13, Figs 1a–1e and 3a–3e.
1877 *Cupularia Haidingeri* Rss. – Manzoni, pp. 71–72, Pl. 16, Fig. 54.
1952 *Cupuladria haidingeri* (Reuss) – Lagaaij, pp. 35–37, Pl. 2, Fig. 2a–2b.
1953 *Cupuladria haidingeri* (Reuss) – Lagaaij, p. 16, Pl. 1, Fig. 2a–2b.
1972 *Cupuladria haidingeri* (Reuss) – Buge, Pl. 2, Figs 5–6.
1973 *Cupuladria haidingeri* (Reuss) – Buge, p. 36, Pl. 6, Figs 3–4.
1977b *Cupuladria haidingeri* (Reuss) – Baluk & Radwanski, Pl. 4, Figs 1–7.
1977a *Cupuladria haidingeri* (Reuss) – Cadée, p. 45, Pl. 1, Fig. 2a–2b.

Material: *)

Five complete zoaria from Steinebrunn: the lectotype (Pl. 4, Fig. 1a–1b; Catalogue Number 1867. XL. 315/1) designated by David & Pouyet (1974, p. 101) and four paralectotypes, the two of which are illustrated in Pl. 4, Fig. 2a–2b (Catalogue Number 1867. XL. 315/2) and Pl. 5, Fig. 3a–3b (Catalogue Number 1867. XL. 315/3), and the remaining two being not illustrated (Catalogue Number 1867. XL.

*) The material item listed by David & Pouyet (1974, p. 101) as the Catalogue Number "1859. 50. 990" bears a topographic error (repeated bona fide by Vávra 1977, p. 78): this is evidently the Catalogue Number 1859. L. 993, as given in the present paper.

The material kept under the Catalogue Number 1860. L. 286, labelled as "*Cupularia Haidingeri* Rss", and listed by Vávra (1977, p. 78), comes from the Lower Miocene (Eggenburgian) deposits of Eggenburg; it contains two counterparting pieces of sandy gravelstone with an external cast of a free-living zoarium which cannot be however recognized as to its generic and specific rank.

315/4); Labelled as "*Lunulites Haidingeri* RSS.", by DAVID & POUYET (1974) as "*Cupuladria haidingeri* R.", and by VÁVRA (1976) as "*Cupuladria haidingeri*".

One complete zoarium from Eisenstadt (Pl. 5, Fig. 1a–1b; Catalogue Number 1867. XL. 318/2); Labelled as "*Cupularia* sp.", and by VÁVRA (1976) as "*Cupuladria haidingeri* (REUSS 1848)".

Four complete zoaria from Baden: one specimen illustrated (Pl. 6, Fig. 1a–1b; Catalogue Number 1983/75/1) and 3 other specimens (Catalogue Number 1983/75/2–4); Labelled as "*Lunulites haidingeri*".

Nine complete zoaria and many fragments from Baden; illustrated are four complete zoaria (Pl. 4, Fig. 3a–3b – Catalogue Number 1859. L. 993/8; Pl. 4, Fig. 4a–4b.– Catalogue Number 1859. L. 993/9; Pl. 6, Fig. 2a–2c – Catalogue Number 1859. L. 993/11; Pl. 6, Fig. 3a–3b – Catalogue Number 1859. L. 993/12) and one fragment (Pl. 5, Fig. 2a–2b – Catalogue Number 1859. L. 993/10); the remaining material being not illustrated (5 complete zoaria and about 80 fragments – Catalogue Number 1859. L. 993/13); Labelled as "*Lunulites haidingeri* RSS".

One complete zoarium from Gainfarn; Catalogue Number 1846. 37. 981; Labelled as "*Lunulites Haidingeri* REUSS", and by VÁVRA (1976) as "*Cupuladria haidingeri*".

One fragmented zoarium from Pötzleinsdorf; Catalogue Number 1861. XXVIII. 102; Labelled as "*Cupuladria Haidingeri* REUSS".

7 fragmented zoaria from Rodaun; Catalogue Number 1977/1945/1; Labelled as "*Cupuladria haidingeri* (REUSS)".

3 fragmented zoaria from Baden-Soos; Catalogue Number 1977/1946/2; Labelled as "*Cupuladria* spp.".

Remarks: The investigated specimens represent the species well established by REUSS (1847) from the Vienna Basin. The specimens from the other European countries bear the features typical of the lectotype and paralectotype designated by DAVID & POUYET (1974) within the material from Steinebrunn. The closures of central zooecia by a calcareous lamina, pictured both by REUSS (1847, Pl. 7, Fig. 26*c*) and by MANZONI (1877, Pl. 16, Fig. 54), are also of the same type as in the other European specimens (see BUGE 1973, Pl. 6, Fig. 3; CADÉE 1977*a*, Pl. 1, Fig. 2a). The zooids covered by a lamina are interpreted to have functioned as a passive excurrent chimney, in the same way as in the present-day free-living bryozoans (see COOK 1979; CHIMONIDES & COOK 1981, p. 212). The section through the colony, picturing the extent and shape of autozooids and the absence of kenozoidal chambers, always agrees with that presented by MANZONI (1877, Pl. 16, Fig. 54).

The species "*Lunulites vandenheckei*", introduced by MICHELIN (1840–1847, pp. 279–280, Pl. 63, Fig. 12a–12c), and sometimes regarded (BUSK 1859*b*, p. 82; VIGNEAUX 1949; MALECKI 1951) as a valid species and separate to *Reussirella haidingeri* (REUSS), or possibly valid and having priority to the REUSS' species (LAGAAIJ 1952, p. 36) represents large forms (up to 20 mm in diameter) with the zooecial pattern much deviated from that in *Reussirella*. The cryptocysts in the species "*vandenheckei*" are devoid of spinules, and vibracula are either of circular shape or elongated transversally to the colony radius, although the central zooecia are closed by a calcareous lamina. Regardless its true specific nature, neither the description nor illustration presented by MICHELIN (1840–1847) are to be accepted as a picture of the species established by REUSS (1847), viz. of *Reussirella haidingeri* (REUSS).

The species "*Lunulites denticulata*", introduced enigmatically by CONRAD (1841), was first described and ilustrated by BUSK (1859*b*, pp. 85–86, Pl. 13, Figs 1a–1e and 3a–3e); the latter evidently offers a good picture of *Reussirella haidingeri*

(REUSS), as already indicated by CANU & BASSLER (1923, p. 77), VIGNEAUX (1949, p. 52) and by LAGAAIJ (1952, p. 35). The note written by CONRAD (1841, p. 348) cannot be accepted as depicting the species established by REUSS (1847). The name "*denticulata*", sometimes used in the present times (see COOK 1965*b*), is therefore to be rejected from the list of valid species.

Occurrence: The species formerly reported from the Vienna Basin by:

REUSS (1847, p. 58, Pl. 7, Figs 26–27): Steinebrunn, Nußdorf, Baden;

MANZONI 1877, pp. 71–72, Pl. 16, Fig. 54): Grinzing, Niederleis, Steinebrunn, Nußdorf, Baden, Forchtenau; and Grußbach (= Hrusovany), Raussnitz (= Rousinov), Kostel (= Podivin), and Porzteich (= Sedleč) in Czechoslovak part of the Basin;

CANU & BASSLER (1925, p. 676): Eisenstadt, Steinebrunn; and Porzteich (= Sedleč) in Czechoslovak part of the Basin;

DAVID & POUYET (1974, pp. 100–101): Gainfarn, Baden, Pötzleinsdorf, Steinebrunn, Eisenstadt;

VÁVRA (1977, p. 78): Eggenburgian (several localities), and Badenian: Burgenland (Eisenstadt, Forchtenstein), Niederösterreich (Baden, Gainfarn, Niederleis, Steinebrunn), Wien (Grinzing?, Nußdorf, Pötzleinsdorf); and Grußbach (= Hrusovany), Raussnitz (= Rousinov), Kostel (= Podivin), Porzteich (= Sedleč) in Czechoslovak part of the Basin.

Other Central Paratethys basins: Pannonian Basin at Szob (MANZONI 1877), Transylvanian Basin at Bujtur-Lapugy (MANZONI 1877), Korytnica Basin (BALUK & RADWANSKI 1977*b*), Carpathian Foredeep at Benczyn (MALECKI 1951).

Other European occurrences are reported by LAGAAIJ (1952, 1953), BUGE (1972, 1973), and VÁVRA (1977).

Reussirella reussiana (MANZONI, 1869)
(Plate 11)

1869 *Cupularia Reussiana*, mihi – MANZONI, pp. 27–28, Pl. 2, Figs 19 and 19'.
1923 *Cupuladria reussiana* MANZONI, 1869 – CANU & BASSLER, pp. 78–79, Pl. 1, Figs 19–22.
1953 *Cupuladria reussiana* (MANZONI, 1869) – ANNOSCIA, pp. 226–227, Pl. 9, Fig. 2; Pl. 10, Fig. 2; Pl. 13, Fig. 1; Pl. 14, Fig. 1a–1b.
1965b *Discoporella reussiana* (MANZONI) – COOK, pp. 219–220, Text-fig. 2f and Pl. 3, Fig. 1.

Material:

One complete zoarium (Pl. 11, Fig. 1) from Eisenstadt; Catalogue Number 1867. XL. 318/3; Labelled as "*Cupularia* sp.", and by VÁVRA (1976) as "*Cupuladria haidingeri* (REUSS, 1848)".

Remarks: The investigated specimen is poorly preserved, being partly worn, and partly crushed. No other fragments attributable to this species have been found in any collection material studied.

Occurrence: The species formerly unknown from the Vienna Basin. It is primarily known from the Neogene (Tortonian until Astian) and Pleistocene (Sicilian) deposits of Italy, and from some Pliocene localities in France and Spain (see MANZONI 1869; and references in CANU & BASSLER 1923, ANNOSCIA 1963). In present-day environments it was first stated by COOK (1965*b*) from the Bay of Biafra, West Africa.

Genus *Discoporella* d'ORBIGNY, 1852

Type species: *Discoporella umbellata* (DEFRANCE, 1823)

Diagnosis: Discoporellid genus bearing the cryptocyst complete, with two rows of opesiules, and a few central pores.

Species included: *Discoporella umbellata* (DEFRANCE, 1823) and all its subspecies and the so-called "types" of zoarium ("*Discoporella umbellata* group" of COOK 1965*a*, p. 167); *D. robertsoniae* (CANU & BASSLER, 1923); *D. ocellata* (COOK, 1965*b*).

Discoporella umbellata (DEFRANCE, 1823)
(Plate 7 and Pl. 9, Figs 3–4)

1869 *Cupularia umbellata* DEFR. – MANZONI, p. 26, Pl. 2, Figs 16 and 16'.
1918 *Cupularia umbellata* DEFRANCE – CANU & BASSLER, pp. 118–119, Pl. 53, Figs 2–4.
1919 *Cupularia umbellata* DEFRANCE – CANU & BASSLER, pp. 85–86, Pl. 1, Figs 5–7 and Pl. 2, Figs 17–21.
1923 *Cupularia umbellata* DEFRANCE – CANU & BASSLER, pp. 80–82, Text-fig. 13A–13F, Pl. 2, Figs 15–19.
1928 *Cupularia umbellata* DEFRANCE – CANU & BASSLER, p. 64, Pl. 2, Figs 1–3.
1930 *Discoporella umbellata* (DEFRANCE) – HASTINGS, pp. 718–719, Pl. 11, Fig. 54.
1949 *Cupularia umbellata* DEFRANCE – VIGNEAUX, p. 51, Pl. 4, Figs 14–15.
1953 *Discoporella umbellata* (DEFRANCE) – LAGAAIJ, pp. 16–17, Pl. 1, Fig. 3a–3b.
1964 *Discoporella umbellata* (DEFRANCE) – CHEETHAM & SANDBERG, p. 1022, Text-fig. 14.
1965a,b *Discoporella umbellata* (DEFRANCE) – COOK.
1972 *Discoporella umbellata* (DEFRANCE) – BUGE, Pl. 2, Figs 3–4.
1973 *Discoporella umbellata* (DEFRANCE) – BUGE, pp. 36–37, Pl. 6, Figs 5–6.

Material: Six fragmented zoaria illustrated in Pl. 7, Figs 1–6 (Catalogue Numbers 1859. L. 993/14 through 1859. L. 993/19 respectively), and 11 other specimens (Catalogue Number 1859. L. 993/20), all from Baden; Labelled as "*Lunulites haidingeri* RSS".

Remarks: The investigated specimens coincide with those included into the synonymy.

Occurrence: The species formerly unknown from the Vienna Basin. It is common in the Neogene deposits of Italy (MANZONI 1869), France and the Netherlands (see LAGAAIJ 1953; BUGE 1972, 1973), and ranges until the present days from the southern Mediterranean to the tropical and subtropical zones of the Atlantic, eastern coasts of Africa, Caribbean, and the eastern Pacific (see COOK 1965*b*, Text-fig. 4).

Family Lunulitidae LAGAAIJ, 1952
Genus *Lunulites* LAMARCK, 1816

Type species: *Lunulites radiata* LAMARCK, 1816

Lunulites androsaces MANZONI, 1869
(Plate 12)

1869 *Lunulites androsaces* ALL. – MANZONI, p. 28, Pl. 2, Figs 18 and 18'.
1877 *Lunulites androsaces* ALL. – MANZONI, p. 73, Pl. 17, Figs 57a–57c.
1910 *Lunulites androsaces* MICHELOTTI – CANU, p. 843, Pl. 16, Figs 11–13.
1949 *Lunulites androsaces* MICHELOTTI – VIGNEAUX, p. 44, Pl. 3, Figs 7–8.

Material:

The material from Baden, described by MANZONI (1877; see also DAVID & POUYET 1974, p. 120; VÁVRA 1977, p. 92) consists of 18 (13 according to DAVID & POUYET) small and very badly preserved pieces of broken zoaria (Catalogue Number 1859. L. 994); Labelled as "*Lunulites* n. sp.". One of the largest pieces is shown herein by photos (Pl. 12, Fig. 2a–2b; Catalogue Number 1859. L. 994/1), and the others remain not illustrated (Catalogue Number 1859. L. 994/2).

The newly recognized material represents a small, regenerated zoarium from Immendorf near Grund (Pl. 12, Fig. 1a–1b; Catalogue Number 1861. XXXV. 103); Labelled as "*Lunulites* nov. spec.".

Remarks: The species *Lunulites androsaces* has long been commonly regarded (MICHELIN 1840–1847; BUSK 1859*b*, p. 82; CANU 1910; VIGNEAUX 1949; LAGAAIJ 1963, p. 198; DAVID & POUYET 1974; VÁVRA 1977) as established by MICHELOTTI (1838). A documentation offered by MICHELOTTI (1838, p. 191, Pl. 7, Fig. 2) [not p. 53 and Pl. 2, Fig. 2, as given by VIGNEAUX (1949), DAVID & POUYET (1974), and VÁVRA (1977)], the same as that by MICHELIN (1840–1847, p. 75, Pl. 15, Fig. 6a–6b) can hardly be however accepted as picturing any *Lunulites*. MICHELOTTI himself (1838), followed by MANZONI (1869, 1877), attributed this species to ALLIONI, whose designation (ALLIONI 1757, pp. 16–17) of "*Madrepora Androsaces*" is still more nebulous. It is apparent that the first adequate documentation was given just lately by MANZONI (1869, p. 28, Pl. 2, Figs 18 and 18'), and this very author is recognized herein as the creator of the species, and the specimen illustrated by him designated as the holotype.

The regeneration has neither been recorded in *Lunulites androsaces* MANZONI nor in any other *Lunulites* species known from the younger Tertiary (Miocene and Pliocene) strata.

Occurrence: The species reported formerly from Baden in the Vienna Basin (MANZONI 1877, DAVID & POUYET 1974, VÁVRA 1977). In the other countries it is primarily known from the Miocene and Pliocene deposits of Italy (see MANZONI 1869, 1877), and Miocene of France (see VIGNEAUX 1949, DAVID & POUYET 1974). Its whole stratigraphic range and geographic distribution seem to be confined to the Miocene and Pliocene of Europe (see LAGAAIJ 1963, Text-fig. 18).

Regeneration of the Colonies

The regeneration in the investigated free-living bryozoans is well displayed by the colonies of *Cupuladria vindobonensis* sp. n., *Reussirella haidingeri* (REUSS), *Discoporella umbellata* (DEFRANCE), and *Lunulites androsaces* MANZONI.

The fragments of primary colonies, which usually display their zooecia larger and arranged differently than those of the newly-grown, regenerated parts, are well detectable on the frontal (upper) side of the investigated specimens from Baden and Steinebrunn. The zooecia of the first regenerated rim are usually smaller, and they embrace the primary fragment tightly what sometimes causes a slight deformation in their shape. The basal (lower) side of the investigated colonies bears a well pronounced regeneration seam (arrowed in Pl. 2, Fig. 2b; Pl. 3, Fig. 1b; Pl. 4, Fig. 4b; Pl. 6, Fig. 1b; Pl. 7, Fig. 3b). The successive rims of regenerated zooecia yield a tendency to obtain more or less circular outlines, typical of the undamaged colonies. Nevertheless, as the fragment of primary colonies in *Cupuladria vindobo-*

nensis sp. n. are usually triangular, and ledge-shaped in *Reussirella haidingeri* (REUSS), the final shape of the regenerated colonies is much deviated from an isometric, circular outline. In *Cupuladria vindobonensis* sp. n. it is more or less obtuse-triangular (Pl. 2, Fig. 2 and Pl. 3, Fig. 1), and in *Reussirella haidingeri* (REUSS) it becomes elongated, more or less rectangular (Pl. 4, Fig. 4 and Pl. 6, Fig. 1). In *Discoporella umbellata* (DEFRANCE), the investigated material is too scant to recognize comparable relations, and the best specimen represents the regeneration of a larger fragment of unknown shape and size (Pl. 7, Fig. 3).

The regeneration in lunulitiform bryozoans was first recognized by DARTEVELLE (1935) in the present-day material of *Cupuladria vindobonensis* [called as *C. canariensis* (BUSK)] from Madeira, and from the Algerian coast, western Mediterranean (DARTEVELLE 1935, Pl. 19, Figs 1–2; reillustration in: LAGAAIJ 1963, Pl. 25, Fig. 5); similar regeneration was displayed by "*Cupuladria lowei* BUSK" [correctly: *Discoporella umbellata* (DEFRANCE) – vide MARCUS & MARCUS (1962, p. 294), and COOK (1965*a*, pp. 158 and 177–178)], also from Madeira. In *Cupuladria canariensis* (BUSK), the regeneration was reported by MARCUS & MARCUS (1962, Pl. 1, Fig. 3) in a specimen from the coasts of Brasil. In the other species of the present-day *Cupuladria*, the regeneration was also stated by SILÉN (1942, Pl. 3, Figs 10–12) in *C. guineensis* (BUSK) from the west coast of Sumatra, and by COOK (1965*a*) in *C. indica* COOK.

In the ancient forms, the regeneration was first stated in the genus *Lunulites* LAMARCK, and it was also DARTEVELLE (1933, 1935), who recognized this phenomenon in *Lunulites quadrilatera* CANU & BASSLER from the Eocene of Belgium. In this very genus the regeneration has subsequently been reported in: *Lunulites jacksonensis* (CANU & BASSLER) and *L. bouei* LEA from the Eocene of the Gulf Coastal Plain, United States (GREELEY 1970), *L. barbosae* BUGE & MUNIZ from the Paleocene of Brasil (BUGE & MUNIZ 1974), and in *L. hagenowi* v. HAGENOW from the Upper Cretaceous (Maastrichtian) of the Netherlands (VOIGT 1979).

The cases of regeneration in the ancient forms of cupuladriid and discoporellid bryozoans may supposedly be detected in some older illustrations, but their interpretation and recognition of the species remain uncertain (see a review by BALUK & RADWANSKI 1977*b*, footnote in p. 150). The evident examples, both in *Cupuladria vindobonensis* sp. n. and *Reussirella haidingeri* (REUSS), have hitherto been reported by the Authors (BALUK & RADWANSKI 1977*b*) from the Korytnica Basin, the material of which contains a wide range of regenerated colonies, and some specimens of *Cupuladria vindobonensis* sp. n. display a fragment of the primary colony which belonged to the only zooid that survived the breakage and remained alive to be regenerated (BALUK & RADWANSKI 1977*b*, Pl. 1, Figs 2–3). Subsequently, CADÉE (1979) mentioned a common occurrence of regenerated colonies in *Cupuladria vindobonensis* sp. n. from the Miocene and Pliocene deposits of various European countries.

Although the fragmentation of the lunulitiform bryozoans during their life, apparent from the structure of regenerated colonies, both present-day and ancient, is so common that it is regarded (MARCUS & MARCUS 1962; BOARDMAN & CHEE-

THAM 1973, p. 173) as providing an important means of colony reproduction, the causes of such a destruction remain not definitely clarified. Usually, the predatory activity of various benthic animals either upon the colonies themselves (LAGAAIJ 1963, CADÉE 1975) or upon their commensals (GREELEY 1967) is suggested. In the Korytnica Basin, both the holothurians and hermit crabs have been discussed as the most responsible for the damage of the colonies (BALUK & RADWAŃSKI 1977*a*, *b*).

To a review, the fragmentation of zoaria of *Cupuladria* [called as *C. canariensis* (BUSK)] by predatory animals has been first recognized by LAGAAIJ (1963) who noted the presence of fragments, and even of entire colonies, in the stomach of a holothurian. Formerly, SILÉN (1942, p. 13) reported on the colonies found in the stomach of the sea-urchin *Meoma ventricosa* from the Caribbean. In consequence, LAGAAIJ (1963) postulated that the fragmentation of the *Cupuladria* colonies results mostly from the destructive activity of the animals, and it is not due to mechanical breakage in a highly agitated environment which has earlier been commonly suggested (DARTEVELLE 1933, 1935; STACH 1936). A slight damage of *Cupuladria* [supposedly *C. canariensis* (BUSK)] and *Discoporella umbellata* (DEFRANCE) by small hermit crabs which search for the commensal coelenterates growing on the basal side of the bryozoan colonies was observed by GREELEY (1967) in a natural life spot in the Gulf of Mexico.

Consequently, either predacious or accidental activity of various benthic animals is thought to be the reason of damage of the investigated cupuladriid and discoporellid colonies from Baden and Steinebrunn.

Mode of Life of the Colonies and their Life Habitat

The opinions on the mode of life of the cupuladriid bryozoans have long been much controversial. Various schools of interpretations were kept, ranging from their resting or "straddling" by hypothetical rootlets on the seafloor, to almost free swimming (even planktic, as reported by SILÉN 1942, p. 13; cf. also COOK 1965*b*, p. 194; GREELEY 1967) or attaching to algal fronds (see LAGAAIJ 1963, pp. 184–187). Discussing all these former views, LAGAAIJ (1963) first concluded on a truly benthic mode of life of *Cupuladria*, the present-day forms of which live on a stable, small-particle bottom at depths sufficient not to be washed up and stranded ashore, i. e. below the wave base (see also STACH 1936, SILÉN 1942).

The larvae of the *Cupuladria* and *Discoporella* species settle upon and attach to small objects on the seafloor, such as sandgrains or shell debris. The growing colonies gradually stretch out of the margins of these objects, and become free living, the sedimentary particle having been incorporated into the enlarging colony (see SILÉN 1942; LAGAAIJ 1963; GREELEY 1967; DRISCOLL & al. 1971; HÅKANSSON 1973; TAVENER-SMITH 1973).

In the investigated material, the objects to which the larva has attached are well recognizable in the two specimens of *Reussirella haidingeri* (REUSS) from Steinebrunn. In the both cases it is a sandgrain which either remains adhered and partly incorporated into the colony (Pl. 4, Fig. 2b), or becomes strongly embedded into the growing zoarium (Pl. 5, Fig. 3b). In the latter colony, the parts of the zoarium overlapped the sandgrain from its sides, and they had not covered it wholly. All the remaining colonies do not display any detectable objects, either adhered or deeply incorporated within the apical parts of the zoaria, or any attachment scars which should be left if such objects have ever been present.

As observed in living specimens of *Discoporella umbellata* (DEFRANCE) by MARCUS & MARCUS (1962), *Reussirella doma* (d'ORBIGNY) and *Discoporella umbellata* by COOK (1963) who reared these species in seawater aquaria, as well as in the case of the latter species and of *Cupuladria* [supposedly *C. canariensis* (BUSK)] examined by GREELEY (1967) in a natural environment in the Gulf of Mexico, the adult colonies rest on the bottom in an apex-up position. They are supported by the stiff, marginal vibracular setae which, being in constant motion, sweep the surface of the colonies (see also LAGAAIJ 1963, COOK 1979).

The same mode of life is postulated for all the investigated cupuladriid and discoporellid species from the Vienna Basin. Formerly, it was also inferred to those inhabiting the Korytnica Basin (BALUK & RADWANSKI 1977*b*). In both these basins, the cupuladriids and discoporellids are thought to have lived completely free, being semi-vagile on the seafloor, in a way comparable to that observed in aquaria by GREELEY (1967, Pls 1–2).

A similar mode of life has also been postulated by HÅKANSSON (1976) for some Upper Cretaceous *Lunulites*, and by GREELEY (1970) for Eocene representatives of this genus. The discussed mode of life may therefore be regarded as typical of all the lunulitiform bryozoans (see also RIDER & COWEN 1977, BALUK & RADWANSKI 1977*b*).

Concerning the nature of the seafloor on which the cupuladriid and discoporellid bryozoans can not only settle down but also live further on, the present-day representatives of *Cupuladria canariensis* (BUSK) and *C. vindobonensis* sp. n. preferentially choose small-particle bottom (quartz or carbonate sand), and they never occur on a bottom consisting entirely of clay (LAGAAIJ 1963). A small-particle bottom, with greater amount of calcareous skeletal grains, was noted as the life habitat of various cupuladriids, as well as of *Discoporella umbellata* (DEFRANCE), on the Guyana shelf (CADÉE 1975), and in a life spot of *Cupuladria* [supposedly *C. canariensis* (BUSK)] and *Discoporella umbellata* (DEFRANCE) in the Gulf of Mexico (GREELEY 1967).

The bottom conditions of the Steinebrunn sedimentary environment match well to those above discussed modern situations. Within in the areas of the Baden Clay deposition, such very conditions were established temporarily, when a greater supply of fine-grained skeletal material appeared and made up the seafloor scenery comparable to that required by the present-day cupuladriids and discoporellids.

Within the Korytnica Basin, the clay sequence of which has commonly been referred to the Baden Clay type, the environmental conditions were controlled by the topography of an inundated valley which became a shallow bay during the Middle Miocene (Badenian) transgression; the clay material from the nearby shores was transported primarily by currents, whilst sedimentation from suspension was subordinate (RADWANSKI 1969; BALUK & RADWANSKI 1977*a, b*). The gradual filling of the bay with clays resulted in a successive shallowing of the basin, the original depth of which was about 60 to 40 meters. All the cupuladriid and discoporellid material comes from the uppermost part of the clay sequence that originated on the bottom densely overgrown by seagrasses, at the depth of a few meters, and thus much smaller than reported for the present-day biotopes of the cupuladriids (see SILÉN 1942, LAGAAIJ 1963, CHEETHAM & SANDBERG 1964, CADÉE 1975). It is therefore reasonable to conclude that in ancient protected areas, such ones as for instance the Korytnica Basin, the cupuladriids and discoporellids were more tolerant to the bathymetry than they are in the hitherto recognized present-day conditions (see also discussion on the ecological evolution by HOFFMAN 1979*a*).

Finally, it is to note that in the present-day environments the cupuladriids often make up extremely frequented populations forming highly specialized communities, and yielding even up to 15,500 specimens per sq meter, e. g. on the Guyana shelf (CADÉE 1975; here other references on the density value). Neither the Vienna Basin nor any other occurrence area in the European Miocene which bear the cupuladriid and discoporellid material (northern France, see BUGE 1972; North Sea Basin, see BUGE 1973; Korytnica Basin, see BALUK & RADWANSKI 1977*b*) attains so high values.

Climatic Requirements

The present-day distribution of *Cupuladria canariensis* (BUSK), the stock of *C. vindobonensis* sp. n. including, is limited by the 14° C isocrymes (LAGAAIJ 1963). In Europe, the cupuladriids occur only in southern Portugal, just of the Strait of Gibraltar, through which they enter the African coast of the western Mediterranean, but their further eastward expansion is hampered by the increasing salinity of sea water (LAGAAIJ 1963). As evident from other reports (CANU & BASSLER 1919; CHEETHAM & SANDBERG 1964; COOK 1965*b*; BUGE 1972; 1973; CADÉE 1975), both *Cupuladria canariensis* (BUSK) and *C. vindobonensis* sp. n. should be regarded as tropical and/or subtropical species, and the same concerns *Discoporella umbellata* (DEFRANCE) which lives under similar conditions (LAGAAIJ 1953; COOK 1965*a,b*; CADÉE 1975). The rarely occurring species *Reussirella reussiana* (MANZONI) is known in present-day environments only from the Bay of Biafra, West Africa (COOK 1965*b*).

The four of the investigated cupuladriid and discoporellid bryozoans which are extant, viz. *Cupuladria canariensis* (BUSK), *C. vindobonensis* sp. n., *Reussirella reussiana* (MANZONI), and *Discoporella umbellata* (DEFRANCE), are therefore the tropical and/or subtropical elements in the Miocene of the Vienna Basin. The two extinct species, *Reussirella haidingeri* (REUSS) and *Lunulites androsaces* MANZONI, always associated with one or more of the former, should certainly be also of the same significance (see CADÉE 1977*a*, BALUK & RADWANSKI 1977*b*).

It is to mention that not a long time ago *Cupuladria vindobonensis* sp. n. and *Discoporella umbellata* (DEFRANCE) were the only two bryozoan species from the

Miocene of Europe, the climatic requirements of which have been known (see LAGAAIJ 1952, 1953; BUGE 1972, 1973; BALUK & RADWANSKI 1977*b*) as higher than those of the present-day southernmost European species. The list of the tropical and/or subtropical elements in the Miocene bryozoan faunas of Europe has recently been much enlarged by VÁVRA (1980) who recognized such significance in the eight species from the Vienna Basin and other basins of the Central Paratethys, and belonging to the genera *Reteporidea, Tremopora, Steginoporella, Canda,* and *Metrarabdotos.* An account on the tropical requirements of the genus *Metrarabdotos* was presented earlier by CHEETHAM (1967, 1968), and on *Steginoporella* by POUYET & DAVID (1979*a, b*).

Biogeographic Affinities

The present-day distribution of the species *Cupuladria canariensis* (BUSK) plus *C. vindobonensis* sp. n., the same as of *Discoporella umbellata* (DEFRANCE) is confined to the Atlantic province, ranging from Africa (south-western Mediterranean including) to the Caribbean and Gulf of Mexico (SILÉN 1942, LAGAAIJ 1963, CHEETHAM & SANDBERG 1964, COOK 1965*a, b,* CADÉE 1975). The range of *Cupuladria vindobonensis* sp. n. is supposedly extended to the Eastern Pacific, from Gulf of California to Ecuador and Galapagos as stated by CHEETHAM & SANDBERG (1964) who, however, described a material mixed with *C. surinamensis* CADÉE, as indicated by CADÉE (1975, p. 326). The same extent is also displayed by a variety of *Discoporella umbellata* (DEFRANCE), another variety of which enters East African waters (see COOK 1965*b*).

When analysing the diverse faunal communities of the Miocene of Central and Southern Europe, it was stated (RADWANSKI 1974, 1975; BALUK & RADWANSKI 1977*a, b*) that they contain many elements typical of the present-day Indo-Pacific bioprovince. It consequently appears that the Miocene basins of Europe were highly influenced by, or they directly belonged to the north-western outskirts of the Miocene Indo-Pacific province. At the Miocene decline, the damming of the routes of oceanic connections through Turkey and the Persian Gulf resulted from the coeval crustal upheavals, and they became responsible both for a cessation of warm water inputs, and of faunal spreads (RADWANSKI 1975, p. 399). This conclusion has recently been confirmed by the results of a faunal analysis of the Qum Formation in Iran (CHAHIDA, PAPP & STEININGER 1977), comparisons of the seagrass-associated macrobenthic communities (HOFFMAN 1979*b*), composition of the Maltese faunal assemblages (ZAMMIT-MAEMPEL 1979), and by the above mentioned bryozoans of the Vienna Basin (VÁVRA 1980).

The problems which however remain open for discussion and further research are in: (i) Connections between the Indo-Pacific and Atlantic bioprovinces throughout the European continent during the Miocene, and mutual migration of some faunas, e. g. of the investigated cupuladriid and discoporellid bryozoans (see BALUK & RADWANSKI 1977*b*); (ii) Possible persistence of the Indo-Pacific Miocene elements in the present-day Mediterranean Sea, as suggested for some seagrass communities (see HOFFMAN 1979*b*); (iii) Possible migrations of the European Miocene faunas to the Indo-Pacific province and their persistence there until the present-day, as it happens for instance with the bryozoan genus *Steginoporella* and presumably also with *Reteporidea* (see POUYET & DAVID 1979*a*, *b*; VÁVRA 1980).

Acknowledgements. The most cordial thanks are offered to Dr. F. RÖGL and Dr. O. SCHULTZ, Naturhistorisches Museum in Vienna, for their hospitality and help when studying the Museum collections, and for making all the needed materials easily accessible. Many valuable informations and copies of hardly available old papers have kindly been supplied by Miss P. L. COOK, British Museum (Natural History); Dr. J.-C. PLAZIAT, Laboratoire de Géologie Structurale et Appliquée, Université Paris-Sud; Dr. G. C. CADÉE, Nederlands Instituut voor Onderzoek der Zee at Texel; Dr. E. HÅKANSSON, Institut for Historisk Geologi og Palaeontologi, Københavns Universitet. The Authors are also much indebted to Prof. Dr. F. STEININGER and Dr. N. VÁVRA, Institut für Paläontologie, University of Vienna, for discussion on the bryozoan distribution in the Vienna Basin and on the stratigraphic setting of the bryozoan-bearing strata.

References

ALLIONI, C. (1757): Oryctographiae pedemontanae specimen, exhibens corpora fossilia terrae adventitia. – Paris.

ANNOSCIA, E. (1963): Antozoi e briozoi nelle argille calabriane di Venosa (Potenza). – Geol. Romana, **2**: 215–237. – Roma.

BALUK, W. & RADWANSKI, A. (1977*a*): Organic communities and facies development of the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). – Acta Geol. Polonica, **27** (2): 85–123. – Warszawa.

— & — (1977*b*): The colony regeneration and life habitat of free-living bryozoans, *Cupuladria canariensis* (BUSK) and *C. haidingeri* (REUSS), from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Poland). – Acta Geol. Polonica, **27** (2): 143–156. – Warszawa.

BARBOSA, M. M. (1971): *Cupuladria canariensis* (BUSK) no Brasil (Bryozoa: Cheilostomata, Anasca). – Bol. Museu Nacional, Nov. Sér. (Geologia), **35**: 1–6. – Rio de Janeiro.

BASSLER, R. G. (1953): Bryozoa. – In: R. C. MOORE (Ed.): Treatise on Invertebrate Paleontology, Part G: G1–G253. – Lawrence, Kansas.

BOARDMAN, R. S. & CHEETHAM, A. H. (1973): Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. – In: R. S. BOARDMAN, A. H. CHEETHAM & W. A. OLIVER Jr. (Eds.): Animal colonies development and function through time, pp. 121–220. – Stroudsburg, Pennsylvania (Dowden, Hutchinson & Ross).

BUGE, E. (1972): Bryozoaires. – In: P. BASSOMPIERRE & al.: Le gisement redonien de Fécamp (Seine-Maritime). – Bull. Bur. Rech. Géol. Min. (Sér. 2), No. **1**: 29–47. – Orléans.

— (1973): Les Bryozoaires Miocènes du Nord-Ouest de l'Allemagne. – Paläont. Z., **47** (1–2): 32–53. – Stuttgart.

— & DEBOURLE, A. (1971): Présence dans le Bartonien d'Aquitaine occidentale de *Cupuladria boulangeri* n. sp. (Bryozoaire Cheilostome). – Bull. Centre Rech. Pau-SNPA, **5** (1): 35–47. – Pau.

— & MUNIZ, G. (1974): *Lunulites (Heteractis) barbosae*, nouvelle espèce de Bryozoaire lunulitiforme (Bryozoa, Cheilostomata) du Paléocène du nord-est du Brésil. – Ann. Paléont. (Invertébrés), **60** (2): 191–202. – Paris.

BUSK, G. (1859*a*): Zoophytology. On some Madeiran Polyzoa. – Quart. J. Microsc. Sci., **7**: 65–67. – London.

— (1859*b*): A monograph of the fossil Polyzoa of the Crag. – Mon. Palaeontograph. Soc., **11** (5): 1–136. – London.

CADÉE, G. C. (1975): Lunulitiform Bryozoa from the Guyana shelf. – Netherlands J. Sea Research, **9** (3–4): 320–343. – Leiden.

— (1977*a*): Bryozoa from the Late Miocene mica clay of Morsum Kliff, Sylt, Western Germany. – Meded. Werkgr. Tert. Kwart. Geol., **14** (2): 43–50. – Leiden.
— (1977*b*): The *Cupuladria canariensis* complex. – Fourth Intern. Confer. Intern. Bryozool. Assoc., p. 16. – Woods Hole, Massachusetts.
— (1979): The *Cupuladria canariensis* complex. – In: G. P. LARWOOD & M. B. ABBOTT (Eds.): Advances in Bryozoology. – Systematics Assoc. Spec. Volumes, **13**: 443–449. – London, New York, San Francisco (Academic Press).
— (1981): Notes on Bryozoa, 1. *Cupuladria canariensis* from the British Pliocene Coralline Crag. – Meded. Werkgr. Tert. Kwart. Geol., **18** (1): 3–9. – Rotterdam.
CAMACHO, H. H. (1966): Invertebrados. – In: A. V. BORRELLO (Ed.): Paleontografia bonaerense, Fasc. **3**. – Com. Invest. Cient. Prov. de Buenos Aires Gobern. – La Plata.
CANU, F. (1910): Les Bryozoaires fossiles des terrains du sud-ouest de la France. – Bull. Soc. Géol. France, (Sér. 4), **10**: 840–855. – Paris.
CANU, F. & BASSLER, R. S. (1918): Bryozoa of the Canal Zone and related areas. – Smithsonian Inst. U. S. Natl. Mus. Bull., **103**: 117–122. – Washington.
— & — (1919): Fossil Bryozoa from the West Indies. – Publ. Carneg. Institution, **291**: 73–102. – Washington.
— & — (1920): North American Early Tertiary Bryozoa. – Smithsonian Inst. U. S. Natl. Mus. Bull., **106**: 1–879. – Washington.
— & — (1923): North American Later Tertiary and Quaternary Bryozoa. – Smithsonian Inst. U. S. Natl. Mus. Bull., **125**: 1–302. – Washington.
— & — (1925): Contribution à l'étude des Bryozoaires d'Autriche et de Hongrie. – Bull. Soc. Géol. France, (Sér. 4), **24**: 672–690. – Paris.
— & — (1928): Fossil and Recent Bryozoa of the Gulf of Mexico region. – Proc. U. S. Natl. Mus., **72** (14): 1–199. – Washington.
CHAHIDA, M. R., PAPP, A. & STEININGER, F. (1977): Fossilführung der Oligo/Miozänen Qum-Formation in Profilen bei Abegarm-Zefreh bei Isfahan (Zentraliran). – Beitr. Paläont. Österreich, **2**: 79–93. – Wien.
CHEETHAM, A. H. (1967): Paleoclimatic significance of the bryozoan *Metrarabdotos*. – Trans. Gulf Coast Assoc. Geol. Soc., **17**: 400–407.
— (1968): Morphology and systematics of the bryozoan genus *Metrarabdotos*. – Smithsonian Misc. Coll., **153** (1): 1–121. – Washington.
— & SANDBERG, P. A. (1964): Quaternary Bryozoa from Louisiana mudlumps. – J. Paleont., **38** (6): 1013–1046. – Menasha, Wisconsin.
CHIMONIDES, P. J. & COOK, P. L. (1981): Observations on living colonies of *Selenaria* (Bryozoa, Cheilostomata), II. – Cahiers Biol. Mar., **22**: 207–219. – Roscoff.
CONRAD, T. A. (1841): Appendix to Mr. Hodge's paper, describing the new shells, etc. – In: J. T. HODGE: Observations on the Secondary and Tertiary formations of the southern Atlantic States. – Amer. J. Sci. and Arts (referenced also as "Sillimans' Journal"), **41**: 332–348. – New Haven, Connecticut.
COOK, P. L. (1963): Observations on live lunulitiform zoaria of Polyzoa. – Cahiers Biol. Mar., **4** (4): 407–413. – Roscoff.
— (1965*a*): Notes on the Cupuladriidae (Polyzoa, Anasca). – Bull. Brit. Mus. (Nat. Hist.), Zoology, **13** (5): 153–187. – London.
— (1965*b*): Polyzoa from West Africa. The Cupuladriidae (Cheilostomata, Anasca). – Bull. Brit. Mus. (Nat. Hist.), Zoology, **13** (6): 191–227. – London.
— (1979): Some problems in interpretation of heteromorphy and colony integration in Bryozoa. – In: G. LARWOOD & B. R. ROSEN (Eds.): Biology and systematics of colonial organisms. – Systematics Assoc. Spec. Volumes, **11**: 193–210. – London, New York, San Francisco (Academic Press).
— & CHIMONIDES, P. J. (1978): Observations on living colonies of *Selenaria* (Bryozoa, Cheilostomata), I. – Cahiers Biol. Mar., **19**: 147–158. – Roscoff.

DARTEVELLE, E. (1933): Contribution à l'étude des Bryozoaires fossiles de l'Eocène de la Belgique. – Ann. Soc. Royale Zool. Belg., **63**: 55–116. – Bruxelles.

— (1935): Zoarial regeneration of free Polyzoa. – Ann. Mag. Nat. Hist., (Ser. 10), **15** (89): 559–561. – London.

DAVID, L. & POUYET, S. (1974): Revision des Bryozoaires cheilostomes miocènes du Bassin de Vienne – Autriche. – Docum. Lab. Géol. Fac. Sci. Lyon, **60**: 83–257. – Lyon.

DRISCOLL, E. G., GIBSON, J. W. & MITCHELL, S. W. (1971): Larval selection of substrate by the Bryozoa *Discoporella* and *Cupuladria*. – Hydrobiologia, **37** (2): 347–359. – The Hague.

GREELEY, R. (1967): Natural orientation of lunulitiform bryozoans. – Geol. Soc. Amer. Bull., **78** (9): 1179–1182. – Boulder, Colorado.

— (1970): Life-orientation relationships of some Eocene bryozoan-coral associations. – J. Paleont., **44** (2): 343–345. – Menasha, Wisconsin.

HÅKANSSON, E. (1973): Mode of growth of the Cupuladriidae (Bryozoa, Cheilostomata). – In: G. P. LARWOOD (Ed.): Living and Fossil Bryozoa, pp. 287–298. – London, New York (Academic Press).

— (1976): Population structure of colonial organisms. A palaeo-ecological study of some free-living Cretaceous bryozoans. – Docum. Lab. Géol. Fac. Sci. Lyon, (H. S.) **3** (2): 385–399. – Lyon.

HASTINGS, A. B. (1930): Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. CROSSLAND on the cruise of the S. Y. 'St. George'. – Proc. Zool. Soc., **1929** (4): 697–740. – London.

HOFFMAN, A. (1979*a*): The applicability of marine macrobenthos for paleoenvironmental analysis in Neogene settings. – Ann. Géol. Pays Hellén., (Hors Sér.) fasc. **2** (7th Intern. Congr. Mediterr. Neogene): 529–535. – Athens.

— (1979*b*): Indian Ocean affinities of a Badenian (Middle Miocene) seagrass-associated macrobenthic community of Poland. – Ann. Géol. Pays Hellén., (Hors Sér.) fasc. **2** (7th Intern. Congr. Mediterr. Neogene): 537–541. – Athens.

LAGAAIJ, R. (1952): The Pliocene Bryozoa of the Low Countries and their bearing on the marine stratigraphy of the North Sea region. – Mededel. Geol. Stichting, (Ser. C) **5**: 1–233. – Maastricht.

— (1953): The vertical distribution of the lunulitiform Bryozoa in the Tertiary of the Netherlands. – Mededel. Geol. Stichting, (n. ser.) **7**: 13–19. – Maastricht.

— (1963): *Cupuladria canariensis* (BUSK) – portrait of a bryozoan. – Palaeontology, **6** (1): 172–217. – London.

MALECKI, J. (1951): Contribution a la connaissance des Bryozoaires du Miocène de Benczyn. – Roczn. PTG (Ann. Soc. Géol. Pologne), **19** (4): 487–491. – Kraków.

MANZONI, A. (1869): Bryozoi pliocenici italiani. – Sitzungsber. Kais. Akad. Wiss., Math.-Naturwiss. Cl., Abt. I, **59**: 17–28. – Wien.

— (1877): I Briozoi fossili del Miocene d'Austria ed Ungheria. – Denkschr. Kais. Akad. Wiss., Math.-Naturwiss. Cl., **37** (2): 49–78. – Wien.

MARCUS, E. & MARCUS, E. (1962): On some lunulitiform Bryozoa. – Bol. Fac. Fil. Cien. Letr. Univ. Sao Paulo, Zoologia, **24**: 281–324. – Sao Paulo.

MICHELIN, H. (1840–1847): Iconographie zoophytologique, description par localités et terrains des Polypiers fossiles de France et pays environnants. – pp. 1–348. – Paris.

MICHELOTTI, I. (1838): Specimen zoophytologiae diluvianae. – pp. 1–227.

POUYET, S. & DAVID, L. (1979*a*): Révision systématique du genre *Steginoporella* SMITT, 1873 (Bryozoa Cheilostomata). – Géobios, **12** (6): 763–817. – Lyon.

— & — (1979*b*): Revision of the genus *Steginoporella* (Bryozoa Cheilostomata). – In: G. P. LARWOOD & M. B. ABBOTT (Eds.): Advances in Bryozoology. – Systematics Assoc. Spec. Volumes, **13**: 565–584. – London, New York, San Francisco (Academic Press).

RADWANSKI, A. (1969): Lower Tortonian transgression onto the southern slopes of the Holy Cross Mts. – Acta Geol. Polon., **19** (1): 1–164. – Warszawa.

— (1974): Palaeoecological observations on Miocene communities of Poland. – Bull. Geol. Soc. Denmark, **23** (3–4): 336–340. – København.

— (1975): Climatic changes recorded by marine macrofauna. – Proc. 6th Congr. Mediterran. Neogene Stratigr., **1**: 397–400. – Bratislava.

REUSS, A. E. (1847): Die fossilen Polyparien des Wiener Tertiärbeckens. – Naturwiss. Abh., **2**: 1–109. – Wien.

RIDER, J. & COWEN, R. (1977): Adaptive architectural trends in encrusting ectoprocts. – Lethaia, **10** (1): 29–41. – Oslo.

SILÉN, L. (1942): On spiral growth of the zoaria of certain Bryozoa. – Arkiv Zool., **34**A (2): 1–22. – Stockholm.

STACH, L. W. (1936): Correlation of zoarial form with habitat. – J. Geol., **44** (1): 60–65. – Chicago.

TAVENER-SMITH, R. (1973): Some aspects of skeletal organization in Bryozoa. – In: G. P. LARWOOD (Ed.): Living and Fossil Bryozoa. – pp. 349–359. – London, New York (Academic Press).

VÁVRA, N. (1977): Bryozoa tertiaria. – In: H. ZAPFE (Ed.): Catalogus fossilium Austriae, Heft Vb/3. – Wien, New York (Springer).

— (1979): Die Bryozoenfaunen des österreichischen Tertiärs. – N. Jb. Geol. Paläont., Abh. **157** (3): 366–392. – Stuttgart.

— (1980): Tropische Faunenelemente in den Bryozoenfaunen des Badenien (Mittelmiozän) der Zentralen Paratethys. – Sitzungsber. Österr. Akad. Wiss., Math.-naturw. Kl., Abt. I, **189** (1–3): 49–63. – Wien.

VIGNEAUX, M. (1949): Révision des Bryozoaires néogènes du Bassin d'Aquitaine et essai de classification. – Mém. Soc. Géol. France, (Nouv. Sér.) **60**: 1–155. – Paris.

VOIGT, E. (1979): Bryozoen der Kunrader Schichten in Süd-Limburg (Oberkreide, Ob. Maastrichtium); I. Cheilostomata. – Grondboor en Hamer, **2**: 33–88. – Oldenzaal.

WATERS, A. W. (1921): Observations upon the relationships of the (Bryozoa) Selenariadae, Conescharellinidae, etc., Fossil and Recent. – J. Linn. Soc. (Zool.), **34**: 399–427. – London.

ZAMMIT-MAEMPEL, G. (1979): The Indo-Pacific affinity of some Maltese Tertiary fossils. – Centr. Mediterr. Naturalist, **1** (1): 1–12. – La Valetta.

Explanation of plates

Plate 1

Cupuladria canariensis (BUSK, 1859)

Fig. 1. Juvenile colony from Baden: 1a – frontal view, 1b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/3).

Fig. 2. Colony fragment from Baden: 2a – frontal view, 2b – basal view, both × 15; In *2a* arrowed is the vicarious vibraculum magnified in Pl. 8, Fig. 4. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/4).

Fig. 3. Colony fragment from Baden: 3a – frontal view, 3b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/5).

Fig. 4. Colony fragment from Baden: 4a – frontal view, 4b – basal view, both × 15; In *4a* arrowed is the zooecium magnified in Pl. 8, Fig. 2. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/6).

Plate 2

Cupuladria vindobonensis sp. n.

Fig. 1. Large colony from Eisenstadt: 1a – frontal view, 1b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 318/1).

Fig. 2. Large, regenerated colony from Baden: 2a – frontal view, 2b – basal view (arrowed is the regeneration seam), both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1983/74/1).

Plate 3
Cupuladria vindobonensis sp. n.

Fig. 1. Large, regenerated colony from Steinebrunn: 1a – frontal view, 1b – basal view (arrowed is the regeneration seam), both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 315/5).

Fig. 2. Colony fragment from Baden: 2a – frontal view, 2b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/1).

Fig. 3. Fragment of large colony from Grinzing: 3a – frontal view, 3b – basal view, both × 15; In *3a* arrowed is the zooecium magnified in Pl. 9, Fig. 1. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number Acqu. 1904. Karrer/1).

Fig. 4. Fragment of another large colony from Grinzing: 4a – frontal view, 4b – basal view, both × 15; In *4a* arrowed is the zooecium magnified in Pl. 9, Fig. 2. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number Acqu. 1904. Karrer/2).

Plate 4
Reussirella haidingeri (Reuss, 1847)

Fig. 1. Large colony from Steinebrunn, the lectotype designated by David & Pouyet (1974, p. 101): 1a – frontal view, 1b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 315/1).

Fig. 2. Small colony (paralectotype) from Steinebrunn: 2a – frontal view, 2b – basal view, both × 15; In *2b* visible is a sandgrain to which the larva has attached, and which has partly been incorporated into the colony during its growth. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 315/2).

Fig. 3. Small colony from Baden: 3a – frontal view, 3b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/8).

Fig. 4. Small, regenerated colony from Baden: 4a – frontal view, 4b – basal view (arrowed is the regeneration seam), both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/9).

Plate 5
Reussirella haidingeri (Reuss, 1847)

Fig. 1. Small colony from Eisenstadt: 1a – frontal view, 1b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 318/2).

Fig. 2. Fragment of large colony from Baden: 2a – frontal view, 2b – basal view, both × 15; In *2a* arrowed is the zooecium magnified in Pl. 10, Fig. 2. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/10).

Fig. 3. Small colony (paralectotype) from Steinebrunn: 3a – frontal view, 3b – basal view, both × 15; In *3b* visible is a sandgrain strongly embraced by the growing colony. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 315/3).

Plate 6
Reussirella haidingeri (Reuss, 1874)

Fig. 1. Small, regenerated colony from Baden: 1a – frontal view, 1b – basal view, both × 15; In *1b* arrowed is the regeneration seam outlining a piece around which the colony has regenerated; this very primary piece is well visible in *1a* due to its stronger convexity and different orientation of the zooids. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1983/75/1).

Fig. 2. Small colony from Baden, with well preserved calcareous laminae in the ancestrular part of the colony: 2a – frontal view, 2b – basal view, both × 15; 2c – ancestrular region of the colony, × 75. (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/11).

Fig. 3. Another small colony from Baden: 3a – frontal view, 3b – basal view, both × 15. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/12).

Plate 7

Discoporella umbellata (DEFRANCE, 1823)

Figs 1–6. Diverse colony fragments from Baden; all presented in frontal (*a*) and basal (*b*) views, taken × 15; In *2a* arrowed is the zooecium magnified in Pl. 9, Fig. 4; In *3b* arrowed is the regeneration seam. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Numbers from 1859. L. 993/14 to 1859. L. 993/19, respectively for the specimens presented in Figs 1 through 6).

Plate 8

Cupuladria canariensis (BUSK, 1859)

Fig. 1. Magnified (× 40) part of colony presented in Pl. 1, Fig. 4a.

Fig. 2. Magnified part (× 80) of the same colony, to show the zooecium arrowed in Pl. 1, Fig. 4a.

Fig. 3. Small fragment of a colony from Baden, to show two vicarious vibracula (marked as "*v*") contacting each other; taken × 70. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 993/7).

Fig. 4. Vicarious vibraculum from the colony fragment presented in Pl. 1, Fig. 2a (*arrowed*); taken × 100.

Plate 9

Cupuladria vindobonensis sp. n.

Fig. 1. Magnified (× 80) part of colony presented in Pl. 3, Fig. 3a (*arrowed*).

Fig. 2. Magnified (× 80) part of colony presented in Pl. 3, Fig. 4a (*arrowed*).

Discoporella umbellata (DEFRANCE, 1823)

Fig. 3. Zooecium with the cryptocyst bearing two rows of opesiules and several central pores; magnified (× 80) part of colony presented in Pl. 7, Fig. 2a.

Fig. 4. Zooecium neighboring the former one, with its cryptocyst broken away; the same part of colony presented in Pl. 7, Fig. 2a (*arrowed*).

Plate 10

Reussirella haidingeri (REUSS, 1847)

Fig. 1. Magnified (× 40) part of colony presented in Pl. 5, Fig. 2a; numbered *2, 3, 4* are the zooecia shown in Figs 2–4 of this plate.

Fig. 2. Zooecium (arrowed in Pl. 5, Fig. 2*a*), to show its general outline; taken × 80.

Fig. 3. Another zooecium, to show the spinules; taken × 80.

Fig. 4. Zooecium covered by a calcareous lamina; taken × 80.

Plate 11

Reussirella reussiana (MANZONI, 1869)

Fig. 1. Poorly preserved colony from Eisenstadt; side view, taken × 35; arrowed is the part magnified in Fig. 2 of this plate. – (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1867. XL. 318/3).

Fig. 2. Magnified (× 150) part of the same colony, to show the structure of zooecia.

Plate 12

Lunulites androsaces MANZONI, 1869

Fig. 1. Small, regenerated colony from Immendorf: 1a – frontal view, 1b – basal view, both × 25. (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1861. XXXV. 103).

Fig. 2. Fragment of large colony from Baden: 2a – frontal view, 2b – basal view, both × 25. (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1859. L. 994/1).

Plate 1

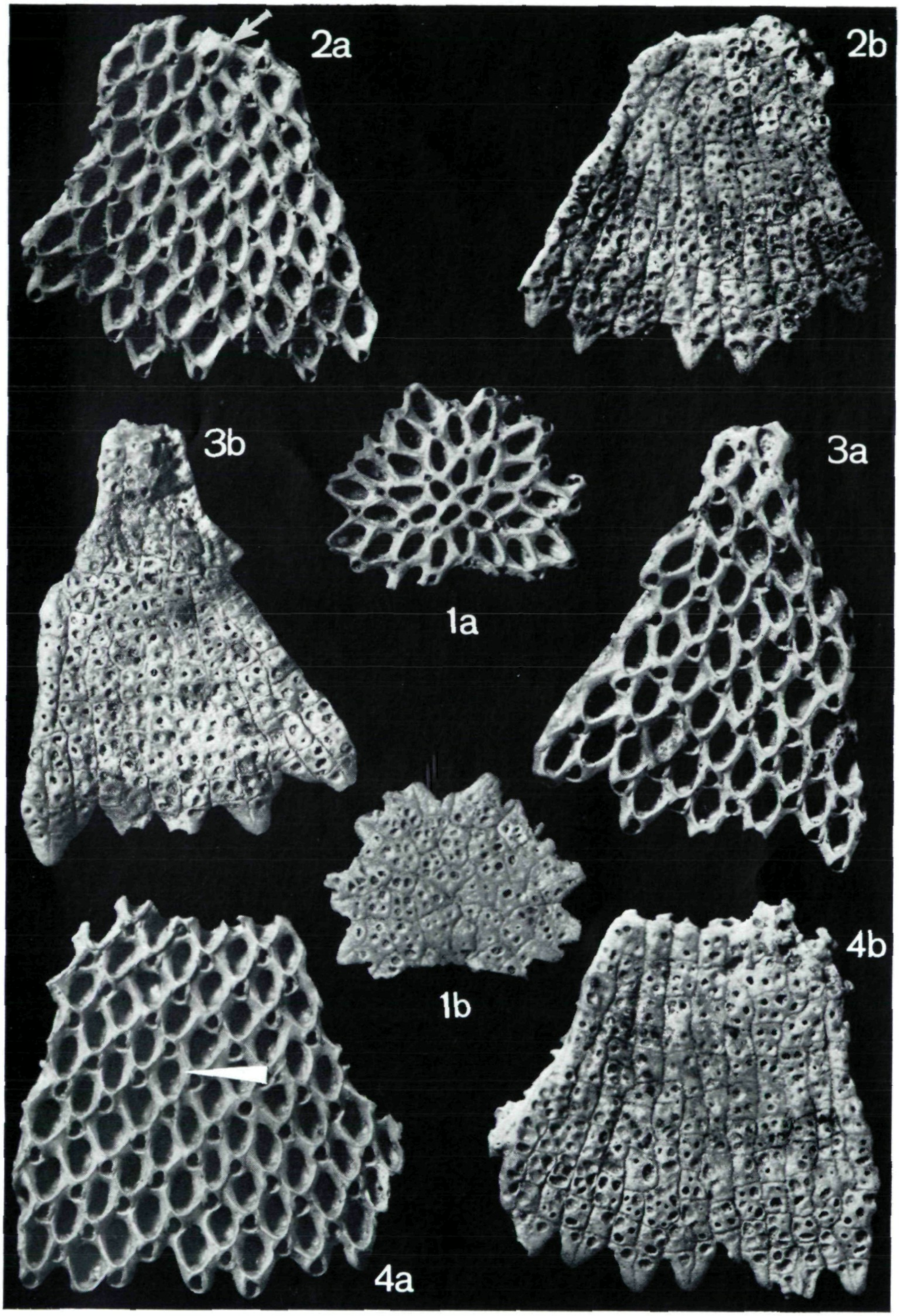
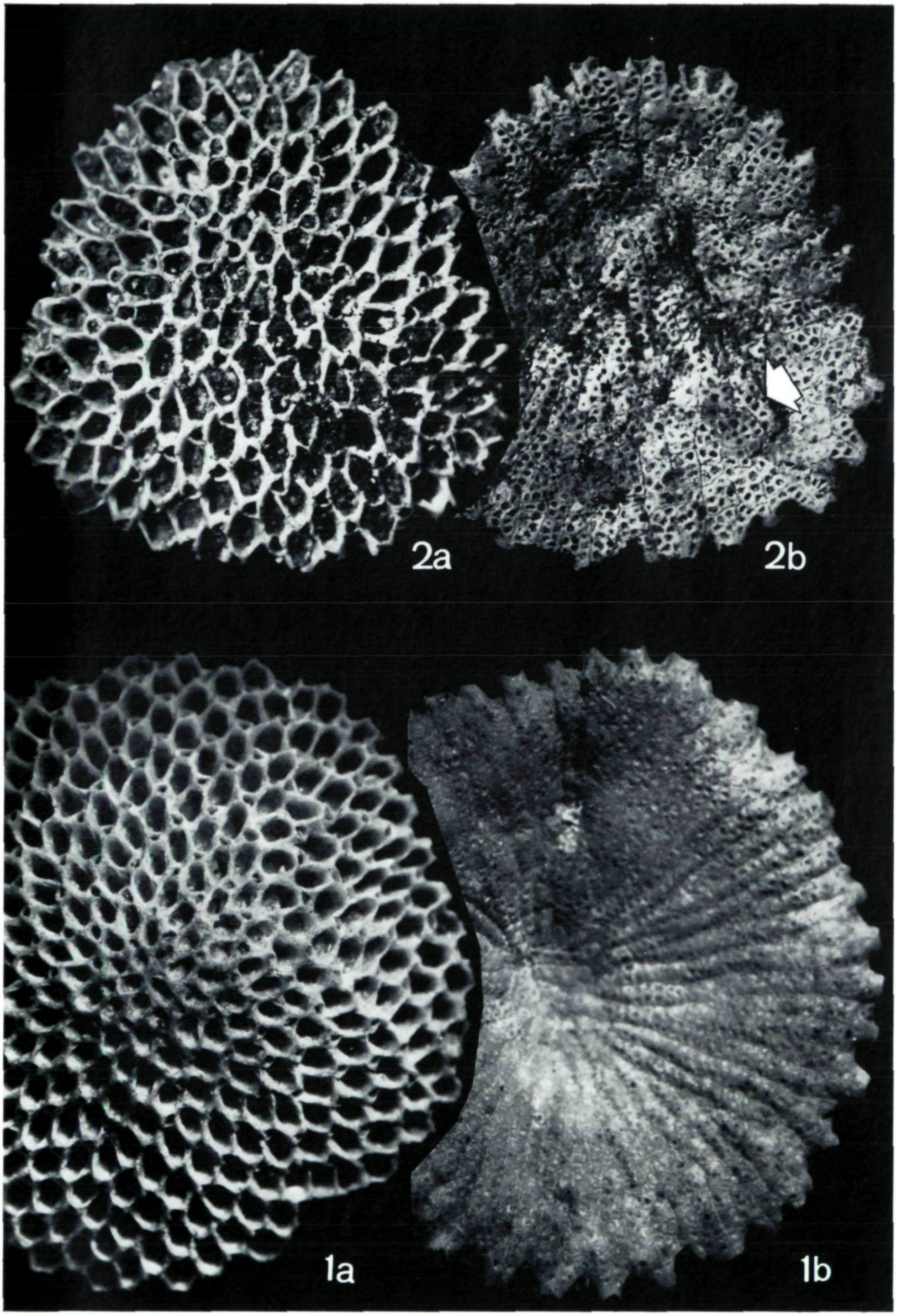
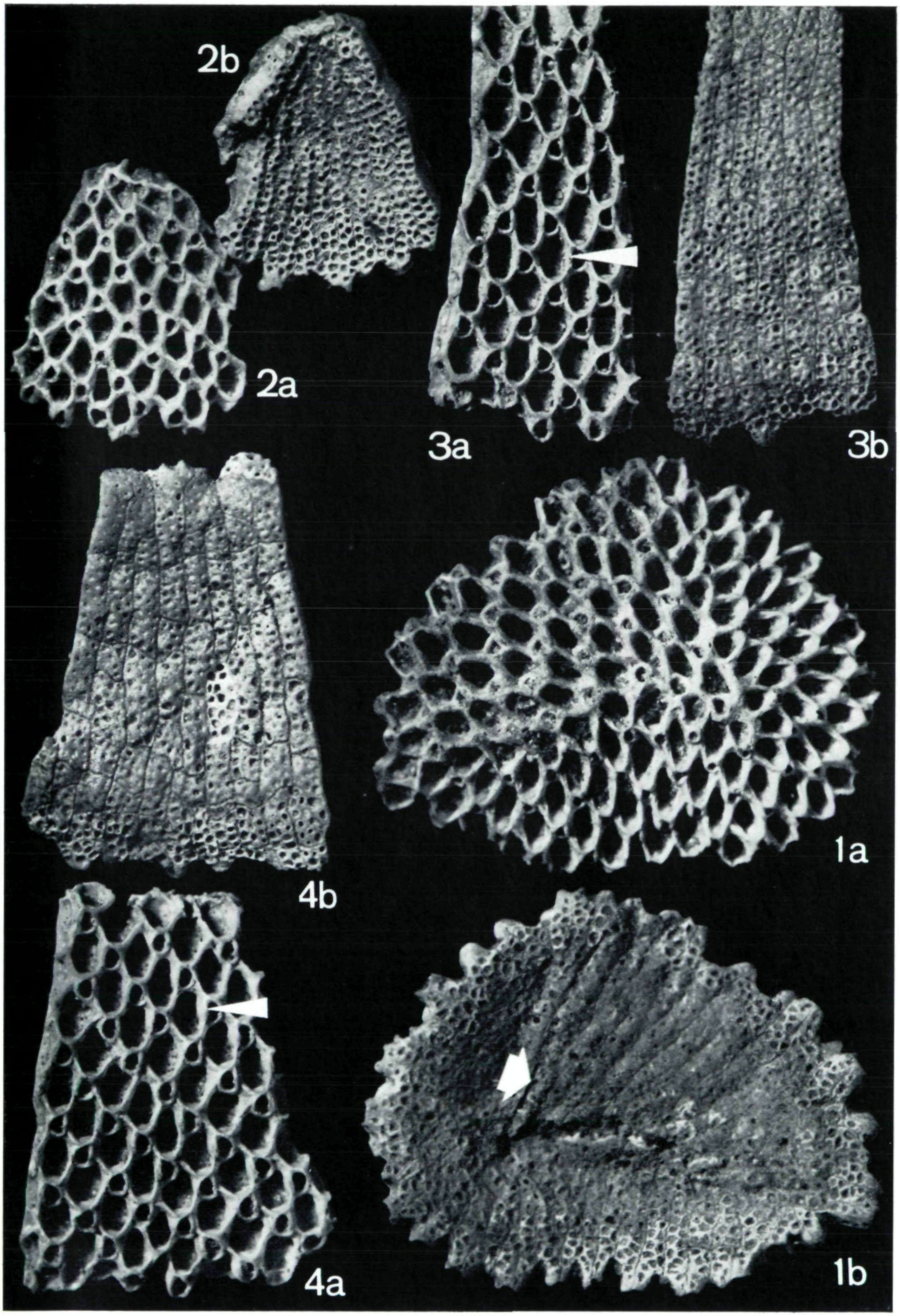
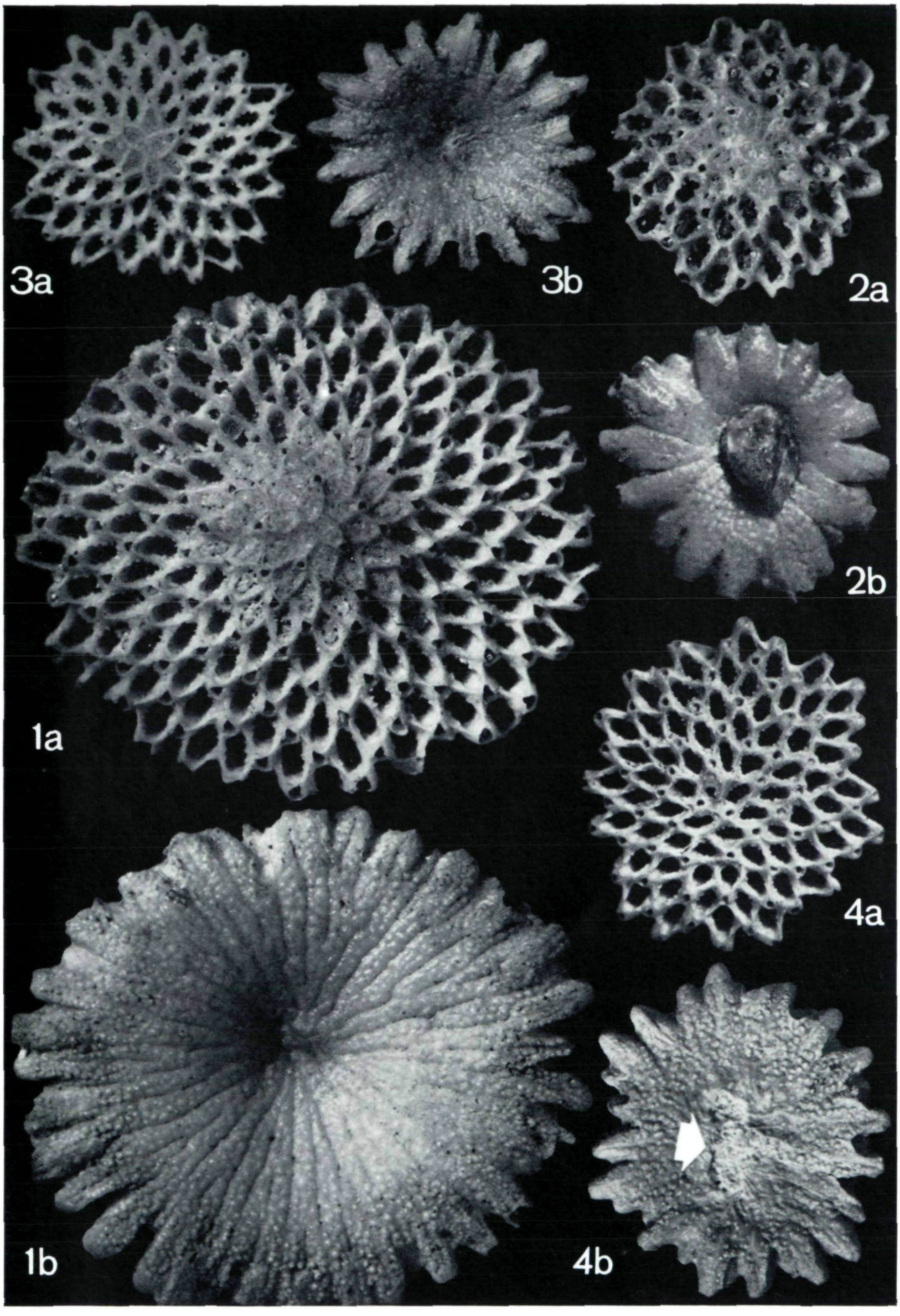
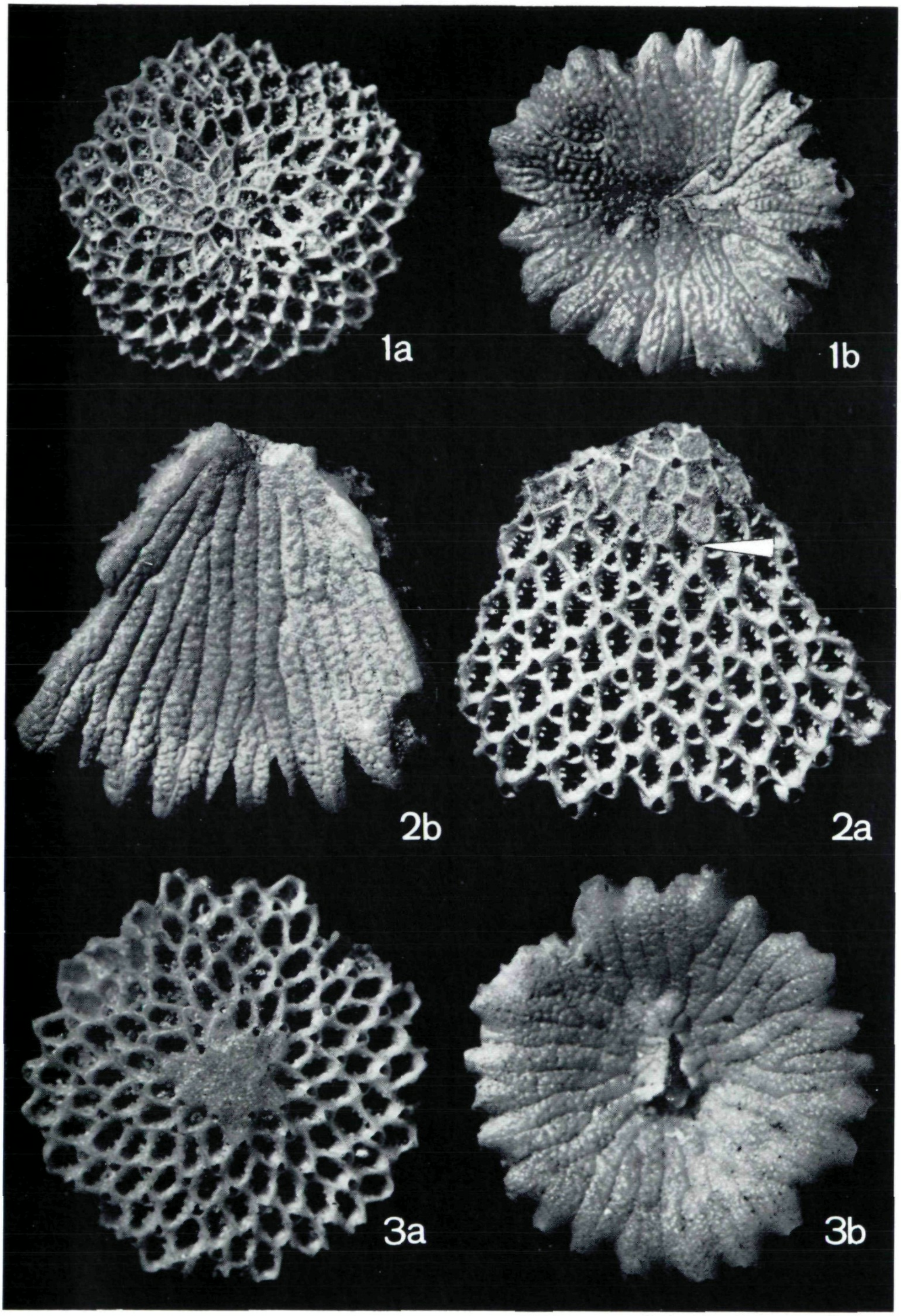


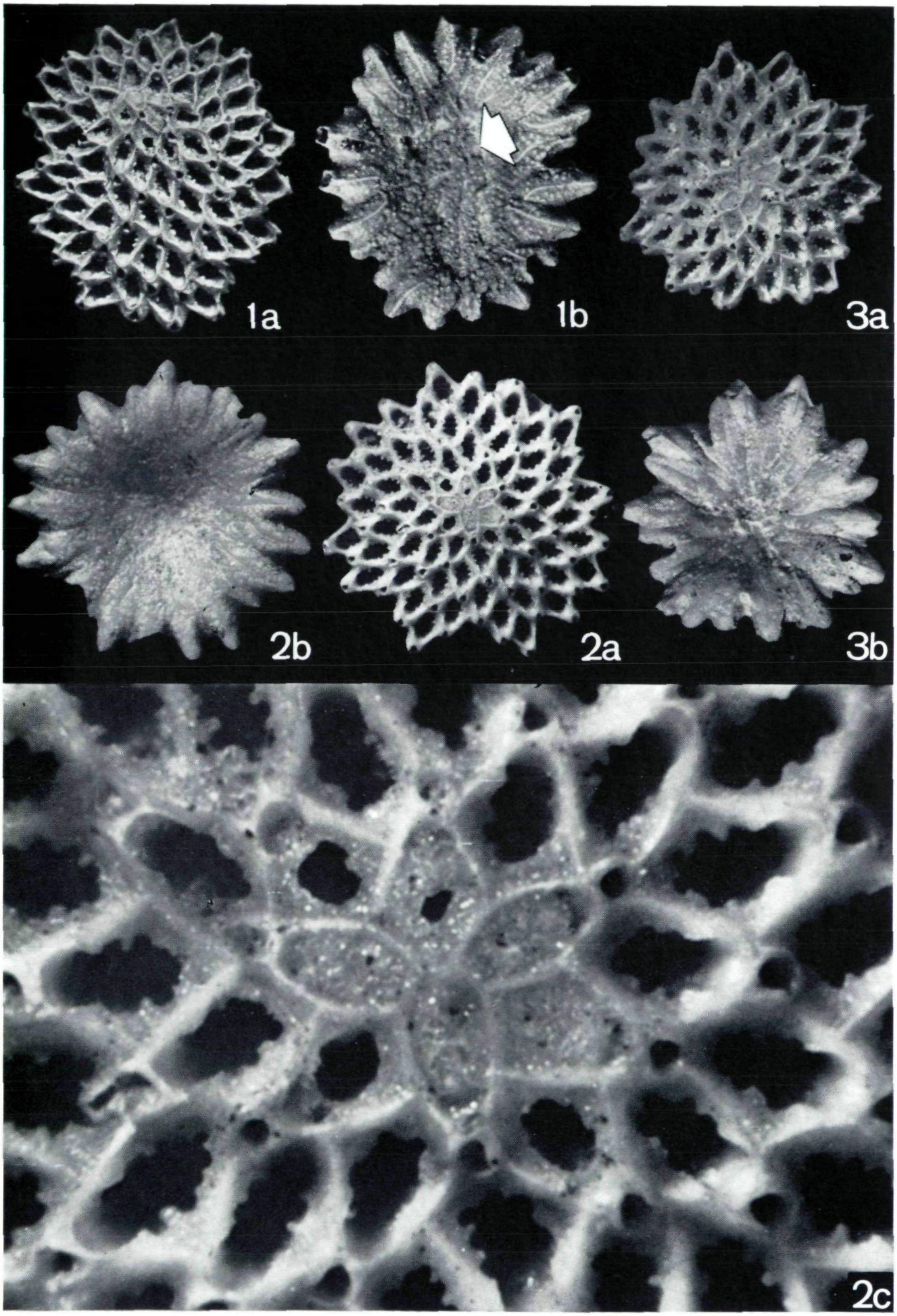
Plate 2

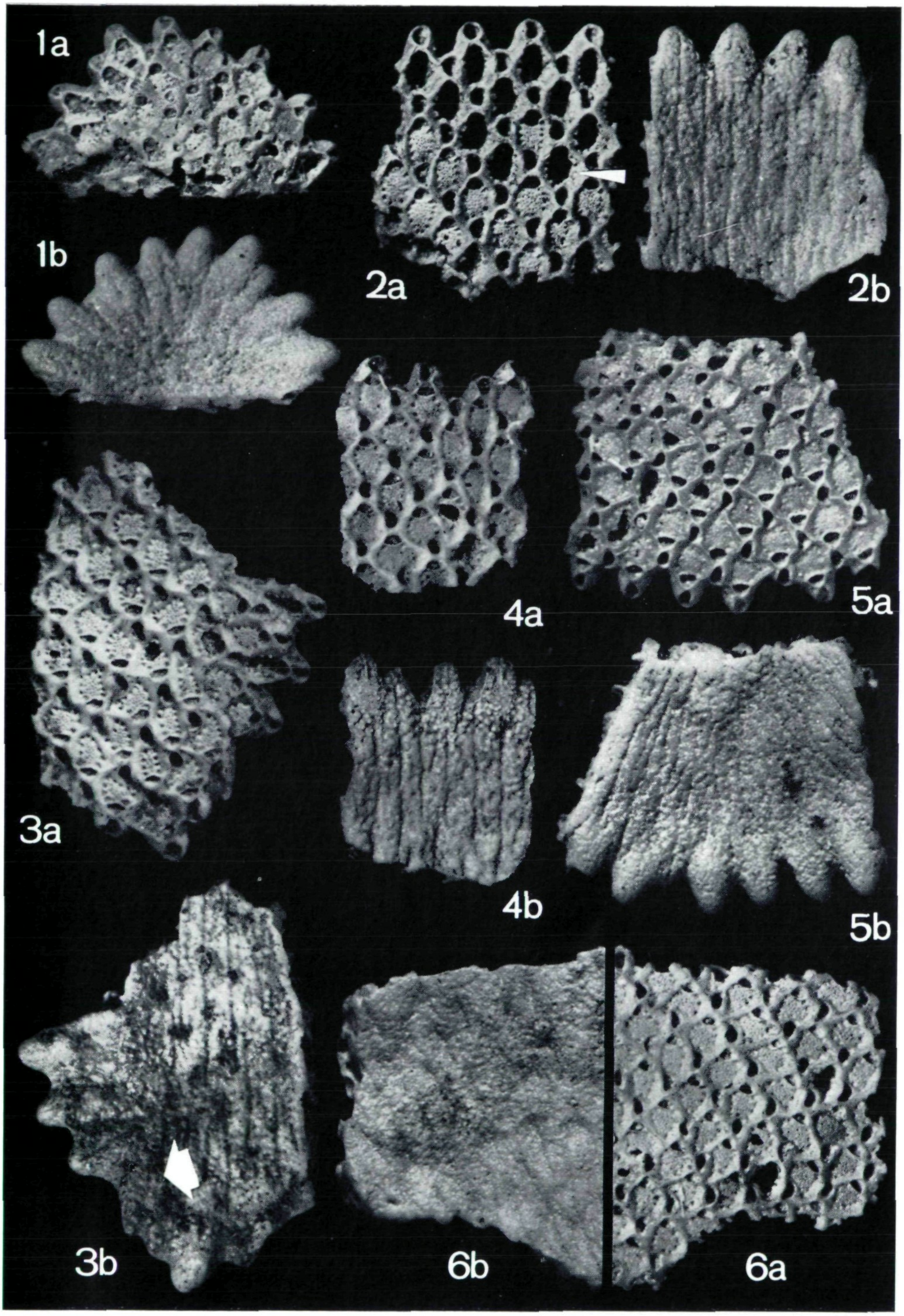


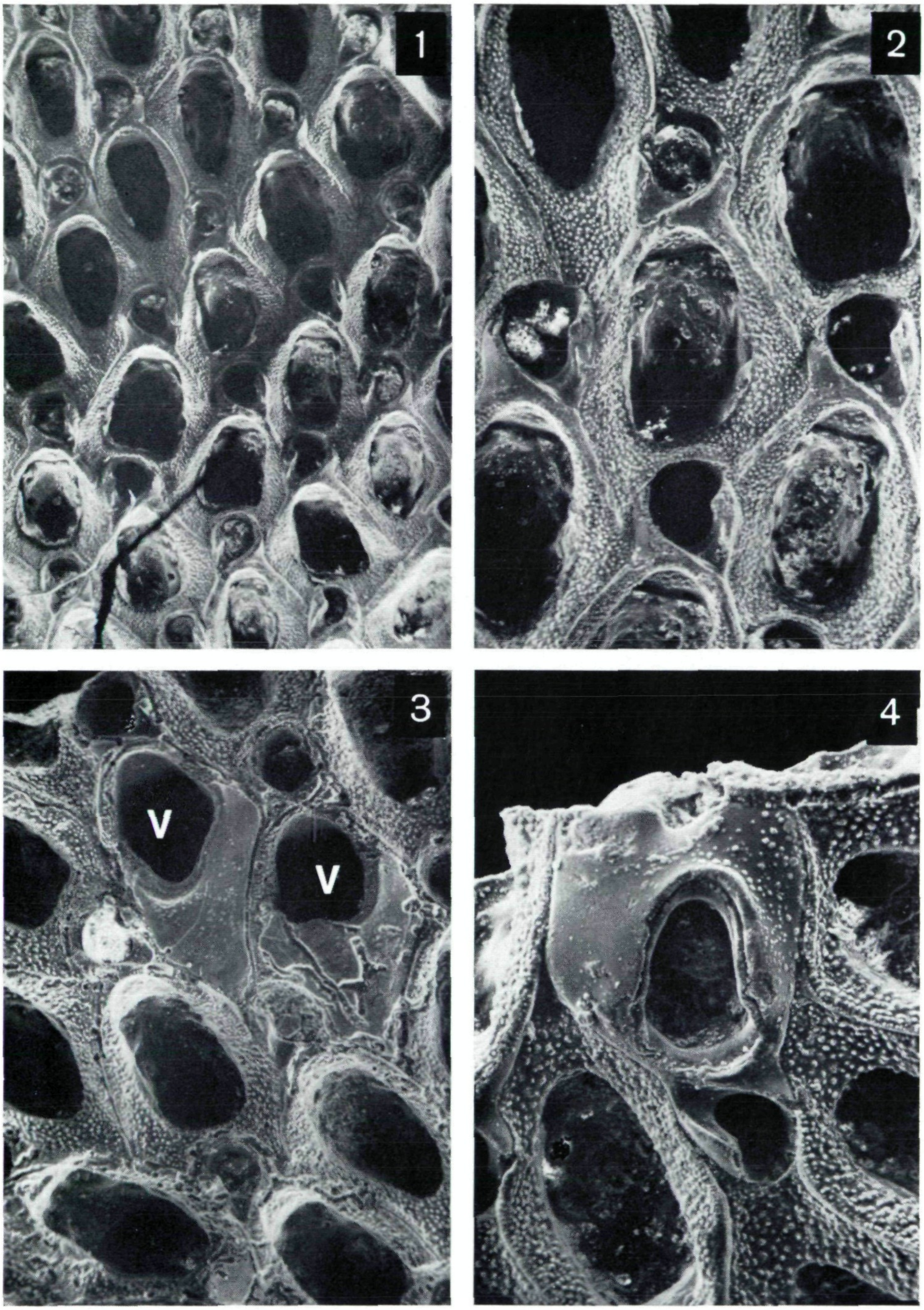

2b
2a
3a
3b
4b
1a
4a
1b

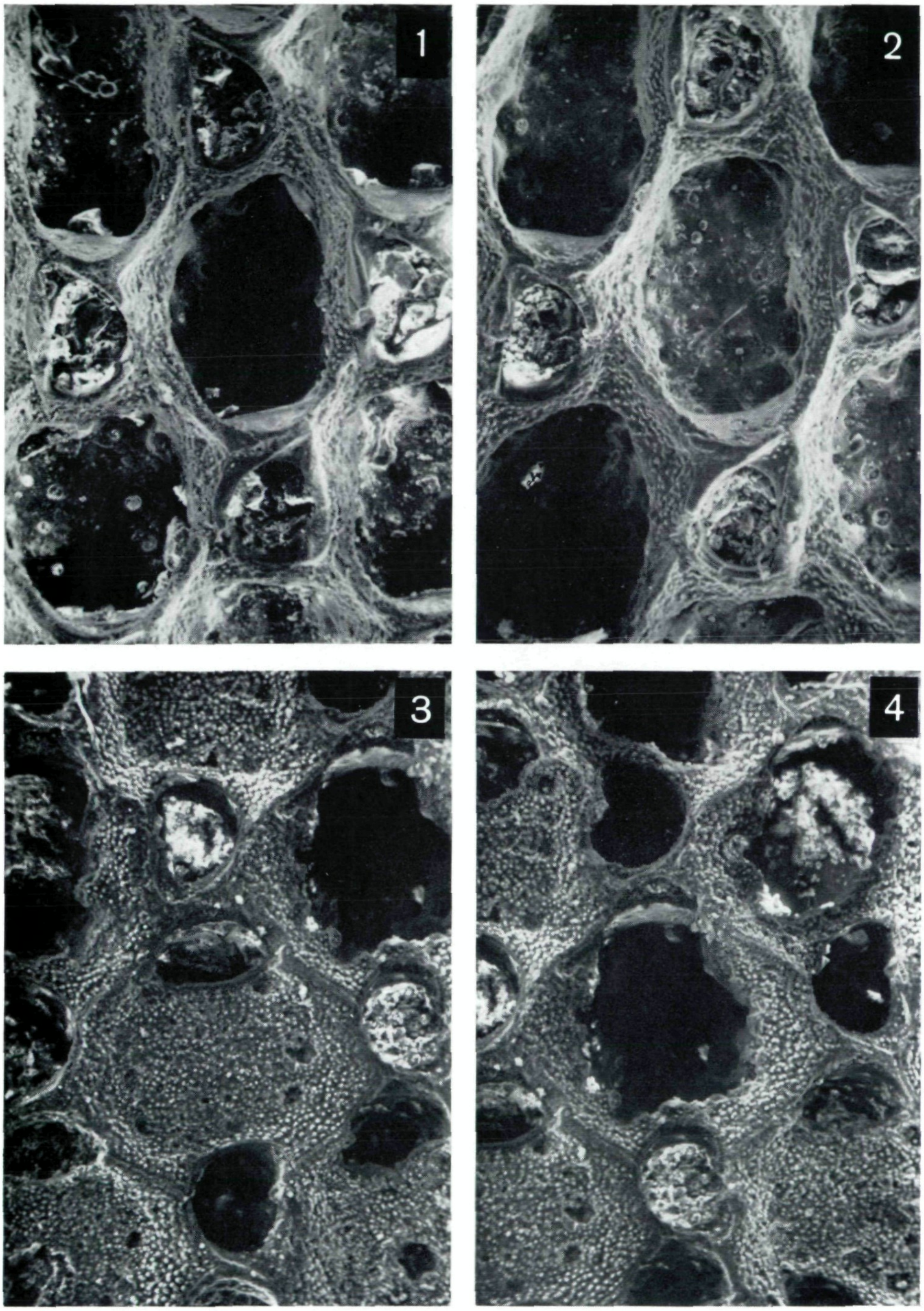

3a
3b
2a
1a
2b
4a
1b
4b

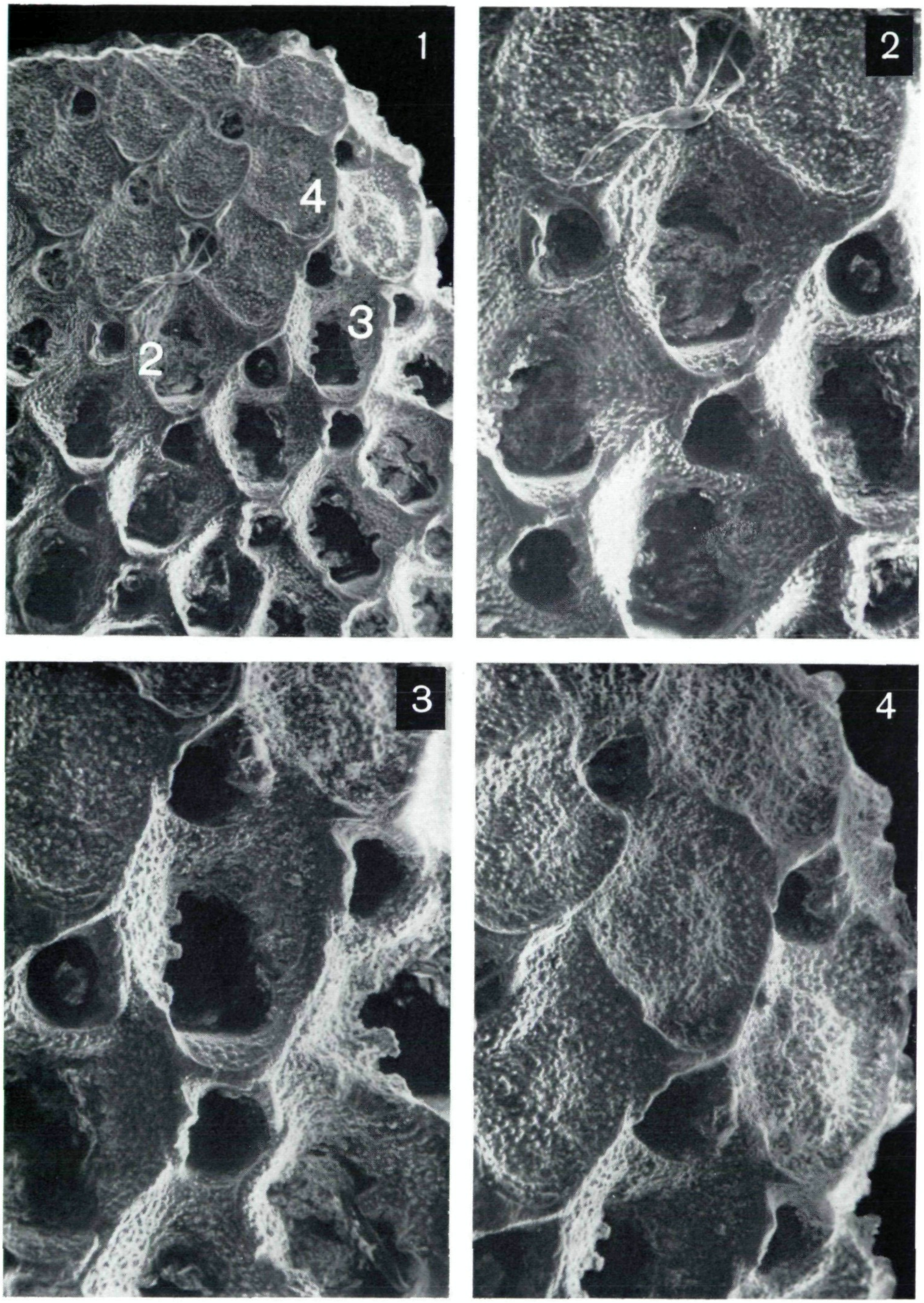

1a
1b
2b
2a
3a
3b

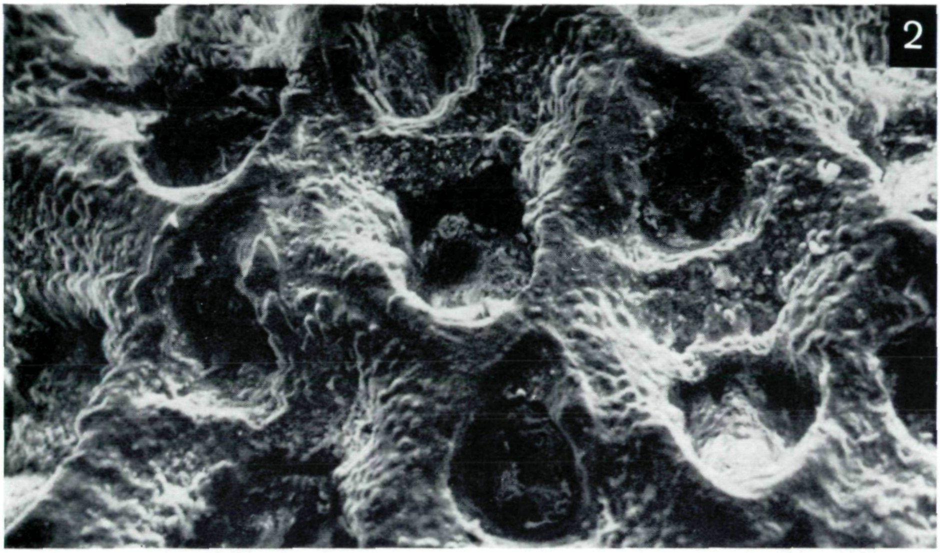

1a
1b
3a
2b
2a
3b
2c

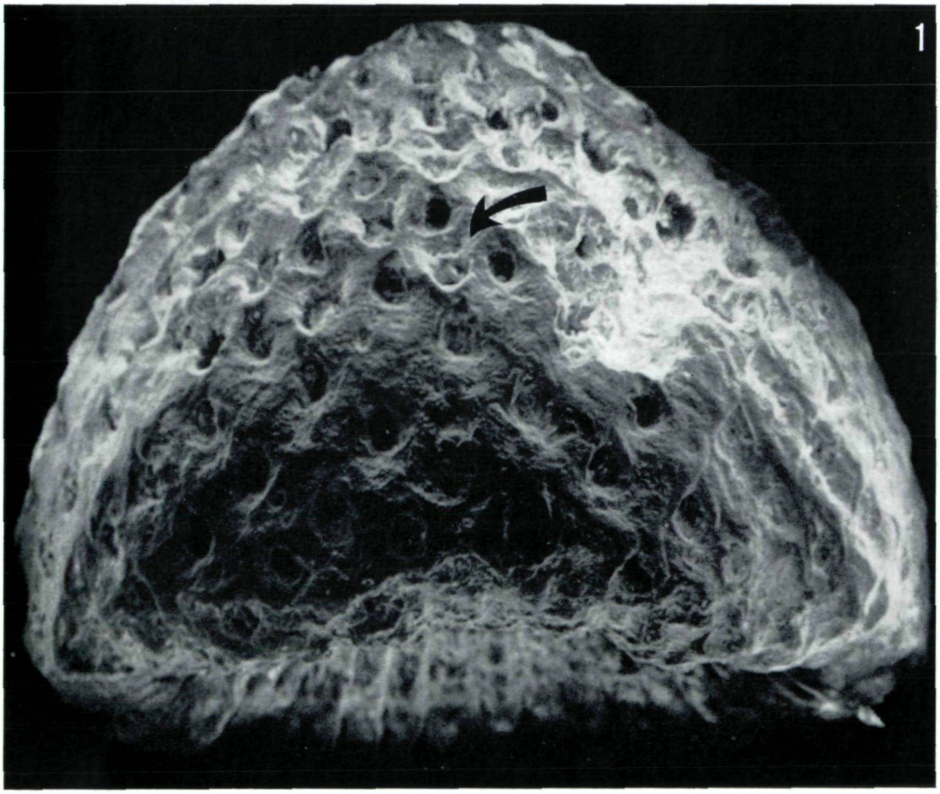

1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b

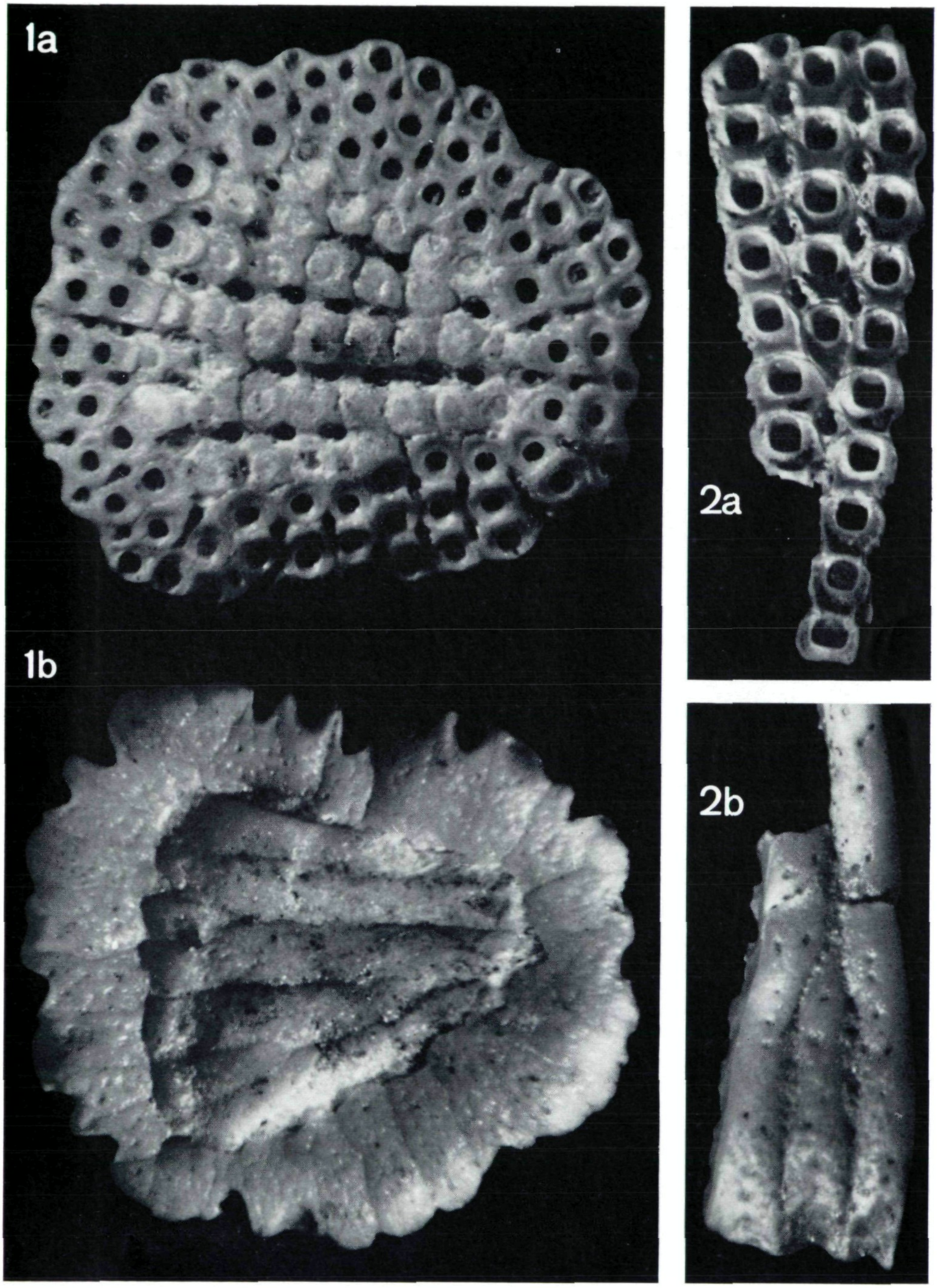

1
2
3
V
V
4


1
2
3
4


1
4
3
2
2
3
4


2


1


1a
1b
2a
2b