

On the free-living bryozoan fauna from the Miocene Gram Formation (Denmark), with description of two new species, a new genus and a new suborder of Cheilostomata

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The free-living part of the restricted bryozoan fauna in the Late Miocene (Tortonian) Gram Formation, Denmark is described. Four species are recorded: *Cupuladria* sp. aff. *biporosa*, *Lunulites voighti*, *Reussirella germinatio* n. sp. and *Gramipora laxevincta* n. gen., n. sp. The new suborder Cupuladriina nov. is introduced. The concepts of ‘free-living’ vs. ‘free-lying’ colonies are discussed briefly, with three categories of ‘free-living’ colonies considered, all exemplified by the four free-living taxa in the Gram fauna.

Keywords: Bryozoa, functional morphology, taxonomy, new taxa, Cupuladriina.

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Whereas the rich and well-preserved mollusk fauna found in the Gram Clay Pit, Southern Jylland, Denmark (Fig. 1) is the main attraction to the many collectors visiting the pit, the tiny ‘shiny stars’ of the free-living bryozoans are also treasured. This particular group of bryozoans are highly adapted to unattached life on or in unconsolidated sea-floor sediments and, as such, they constitute the overwhelming majority of bryozoans encountered in the silty mica-clay of the Gram Formation. The bryozoan fauna from the Gram Clay Pit is of low diversity, comprising less than ten species, including four free-living species referred to the order Cheilostomata. While three of the free-living species were illustrated by Rasmussen (1966, fig. 7), no formal description of the free-living part of the fauna has been published. Two of these species clearly belong to the cupuladriids. However, Håkansson *et al.* (2023) considered the cupuladriid bryozoans (Cupuladriidae Lagaaij, 1952) the only monophyletic free-living bryozoan clade. In view of

the significant number of advanced traits not shared with other members of the order Cheilostomata, we here propose that the group is raised to the rank of suborder under the name Cupuladriina nov. One further species is assigned to the unsupported family ‘Lunulitidae’, while the latter species has unestablished relations.

The Gram Formation

At the type locality (at Gram, Denmark; Rasmussen 1956) the Upper Miocene part of the Gram Formation (Tortonian) is dominated by mica-rich, silty mud. The mud was deposited in a distal, > 100 m deep pro-delta setting located in the inner part of the Late Miocene North Sea Bight (Rasmussen *et al.* 2010, 2025; Fig. 2). Paralleled by a significant drop in macrofossils, the content of fine to very fine sand increases upwards into the overlying Marbæk Formation, indicating a

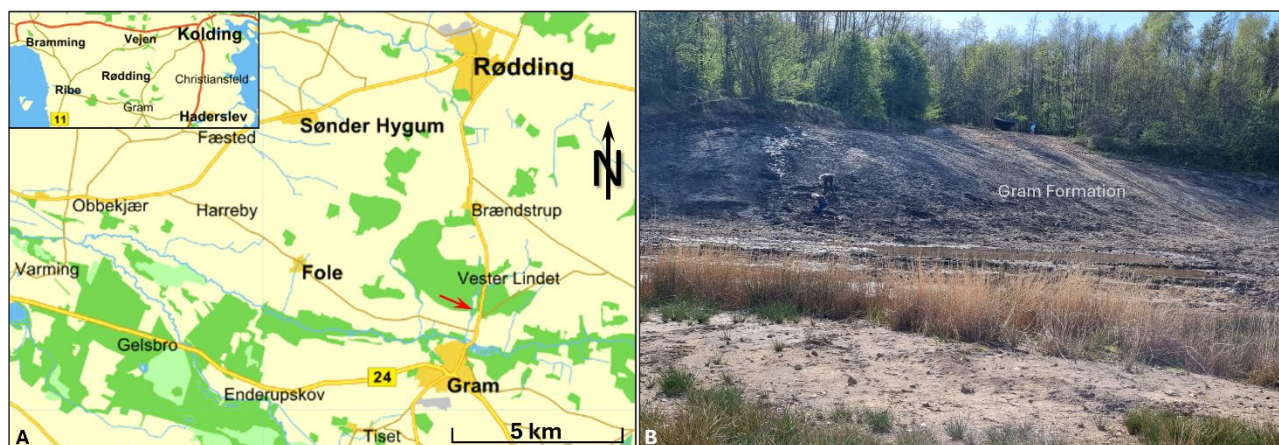


Fig. 1. **A.** Location of the Gram Clay Pit in southern Jylland, Denmark (red arrow on map). **B.** View of the main quarry wall after production was terminated; since 1996, the outcrop has been kept accessible, attracting substantial numbers of collectors (image courtesy Asbjørn Holm, Museum Sønderjylland).

gradual drop in water depth. Finely disseminated pyrite is widespread in the sediment, variously influencing the preservation of the contained fossils. Active quarrying in the pit ceased in 1988, but a section was cleaned and made accessible for collecting in 1996 and has since been continuously maintained by Museum Sønderjylland to enable public access to the fossil rich beds.

The Gram Clay Pit has long been known for its

rich fauna which is dominated by infaunal mollusks (Rasmussen 1968; Schnetler 2005), with occasional decapod crustaceans (Fraaije *et al.* 2005), sharks (Bendix-Almgreen 1983), bony fish (Rasmussen 1963; Schwarzhans & Hocht 2023), seals (Koretsky *et al.* 2014) and whales (Steeman 2009; Ramassamy & Lauridsen 2019). Most of the fauna known from the Gram Formation has been collected from the lower mud-rich part of the Gram Clay Pit (Fig. 1). Bedding

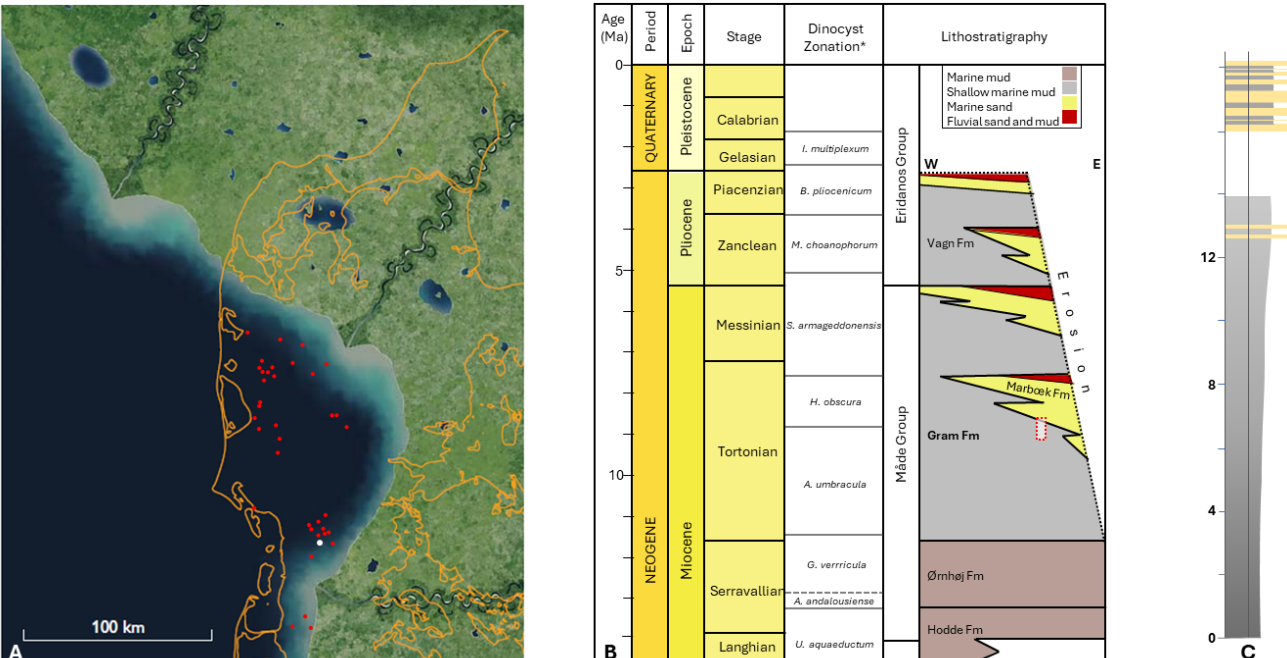


Fig. 2. **A.** The position of the Gram Clay Pit in relation to the paleogeography of the region at the time of deposition of the Gram Formation mudstones (with the Gram Clay Pit indicated with a white dot; present day coastline in light orange). Red dots represent additional coeval occurrences of the free-living fauna from Gram (outcrops or wells no longer accessible; data collated from survey archives, see Rasmussen 1966). **B.** The lithostratigraphic context of the Gram Formation with the approximate position of the Gram Clay Pit succession indicated by the small red-framed box. **C.** Overview log of the succession exposed around Gram, with the approximate position of the Gram-Marbæk boundary in the covered section; the lower part covers the historic clay pit exposure. All figures modified from Rasmussen *et al.* (2010, 2025).

in this part is obscure due to bioturbation and glacially induced disturbance occasionally evident in the pit. The detailed stratigraphic relations between most of the material investigated has therefore not been established. Bryozoans were first mentioned by Ravn (1897) and Rasmussen (1956, 1963), but apart from one free-living species, bryozoans are comparatively rare in the Gram Formation and, from the collections at Gram Museum less than ten cheilostome species have thus far been distinguished; in addition to the four free-living taxa described here, at least one badly preserved cellariid taxon is fairly abundant in washed residues.

With the exception of *Reussirella haidingeri* (Reuss, 1847) included for comparison, all material in this investigation originates from the Gram Formation exposed in the Gram Clay Pit. Unless otherwise indicated, illustrated material is registered at Museum of Southern Jylland, Section of Natural History, Midtsønderjyllands Museum located next to the Gram Clay Pit with registration numbers given through the text.

Free-living bryozoans

While bryozoans typically require a substrate for successful larval metamorphosis, a number of bryozoan clades have evolved towards various modes of unattached life on unconsolidated, particulate shelf sea floors, particularly within the order Cheilostomata, where the earliest free-living species – *Pavolunulites mirabilis* – is of Late Turonian age (Koromyslova & Pervushov 2022). In modern oceans free-living bryozoans are largely restricted to the warmer latitudes.

Because of the fairly narrow environmental conditions under which the development towards free-living life is favored, many of these anascan grade clades share a suite of conspicuous characters, which has led to the assumption that such taxa are closely related. Consequently, most were unified into a single superfamily, ‘Lunulitoidea’ Cook *et al.* (2018, p. 137; but see below: “Superfamily ‘Lunulitoidea’ Gregory, 1893”). Notwithstanding, investigations over many years have led to the understanding that iterative and parallel evolution of analogous char-

acters and character sets have been rampant in the global, near uniform muddy and sandy shelf environments favored by the free-living bryozoans (e.g. Cook *et al.* 2018). We therefore suggest that the evolutionary pathways of the free-living bryozoans to a large extent reflects shared ecology rather than shared ancestry (cf. Håkansson *et al.* 2023).

This general observation applies to a number of features recognizable in most or all of the clades considered free-living. Firstly, a fundamental trend present in all such clades is a general reduction in the size of the substrate required for successful larval metamorphosis – in a restricted number of taxa reaching the ultimate level, where metamorphosis takes place without the support of, or leaving any trace of, a substrate in the colony. Secondly, most clades are readily recognizable by their shared colony architecture, forming more or less flattened, solid or somewhat hollow, domes or cones (Fig. 3) with two types of morphologically and functionally distinct zooids regularly distributed on one side of the colony which, in living populations, typically face upwards. While autozooids, the fundamental element in all bryozoan colonies, have a variety of functions, including feeding and reproduction, the polymorph heterozooids, are variously modified, with highly modified vibracula (see below) present in most free-living taxa.

Thus, all clades considered free-living are characterized by this ecologically essential heteromorph, which is distinguished by a hypertrophied setiform operculum, which is operated by powerful muscles (Fig. 3). In live colonies, the seta has been observed to maintain the colony in a stable position, slightly raised above the sea-floor. Observations of live colonies of free-living species from several unrelated clades suggests that directional movement, as well as the capacity to dig themselves in and out of the soft seafloor sediment could be widespread (e.g., Cook & Chimonides 1978; Håkansson & Winston 1985; O’Dea 2009). From this condition it follows that the term ‘free-living bryozoans’, as applied here, is restricted to the order Cheilostomata.

The third feature to consider is the development of a continuously thickening basal wall which, in most free-living bryozoans, is non-zooidal in origin, thus forming a distinct, colonial part of the skeleton.

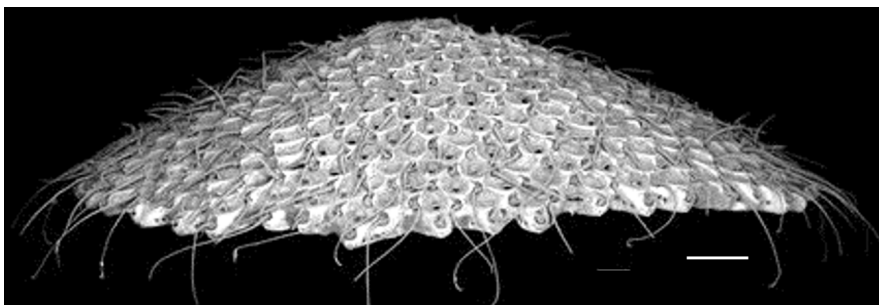


Fig. 3. ‘Dancing’ *Cupuladria biporosa* Canu & Bassler, 1923 (Recent, Panama). Mature colony with the long, bristle-like setae of the marginal vibracula supporting the colony slightly above the sea-floor sediment. Through coordinated activity of the setae the colony achieves directional movement. Scale bar 1 mm (image courtesy Aaron O’Dea).

Finally, it should be mentioned that even though asexual propagation through various means has a wide occurrence across the phylum Bryozoa due to their colonial organization (e.g. Håkansson & Thomsen 2001), it is particularly common and diverse amongst free-living bryozoans (O'Dea *et al.* 2008), to the extent that entire populations of some taxa may be exclusively clonal (see below).

Accordingly, a cheilostome taxon, whether recent or fossil, characterized by the above-mentioned traits can therefore be assumed to be free-living, i.e., finely tuned to life on a sandy to muddy sea floor where colonies rest freely on the soft bottom supported by the stiff, marginal vibracular setae in much the same way as observed for extant Cupuladriina nov. (e.g., Marcus & Marcus 1962; Cook 1963; Håkansson & Winston 1985; Fig. 3), Selenariidae (Cook & Chimonides 1978; Chimonides & Cook 1981) and Otionellidae (Thomas Schwaha, pers. comm.). However, some taxa with colonies possessing only some of these adaptive traits may, nevertheless, be assumed to have a somewhat comparable, unattached mode of life. *Stichopora pentasticha* von Hagenow, 1839 may serve as a typical example. It is one of the most characteristic species in the northern European Maastichtian Chalk, and it has only frontal autozooids, lacks vibracula and a colonial basal wall, and it does not require a substrate but it has, nevertheless, been interpreted to lie free, perhaps somewhat submersed in the soft coccolith ooze bottom (cf. Håkansson 1975). In terms of ecological preferences, this taxon therefore has a mode of life approaching that of the true free-living bryozoans and, for clarity, we therefore find it appropriate to distinguish between 'free-living' and 'free-lying' modes of life based on the presence or absence of vibracular setae (cf. Fig. 4) – 'free-living bryozoans', as per their vibracula setae, have some mobility, whereas 'free-lying bryozoans' have not. In this characterization, the free-living mode of life comprises at least three categories based on the degree of coloniality reflecting changes in the framework of skeletal formation, ranging from all-zooidal to all-colonial (i.e., reflecting which types of coeloms are involved in colony architecture; Fig. 5), with all three categories represented in the Gram fauna. While the total colonial coelom state may be

exclusive to the new suborder Cupuladriina nov., the state with part colonial, part zooidal coelom is shared between multiple, not otherwise related free-living clades, most of which would fall under the obsolete (see below) superfamily 'Lunulitoidea'. The most 'primitive' state, with all coeloms zooidal, is thus far only known from the family Biselenariidae Håkansson & Zágorský, 2020, with the likely unrelated new taxon from Gram, *Gramipora laxevincta* n. gen., n. sp. (see below), now providing an additional example. We have not attempted to subdivide the 'free-lying' category, in which the lack of vibracular seta is the fundamental element, as potential members are not nearly as easily grouped – among the Cheilostomata, characteristic members are e.g. the above-mentioned membraniform *Stichopora pentasticha* (see Håkansson 1975), and the cribrimorph *Stichocados verruculosus* Marsson, 1887, both from the northern European Maastichtian Chalk, where this mode of life seems to be particularly frequent.

In living, undisturbed populations, colonies of free-living bryozoans are usually recorded with their zooidal ('frontal') side facing upwards, and even though a limited number of colonies may be found with their 'basal' side facing upwards, all are typically oriented more or less parallel to the sea floor (Greeley 1967).

It should be added that other bryozoans, with substantially different growth-forms – also outside the order Cheilostomata – might be characterized as 'free-lying'. These include taxa with lyre-shaped colonies (McKinney 1977; McKinney *et al.* 1993), such as, *Lyroporella quincuncialis* (Hall, 1857), *Lyroporella erkosoides* (Etheridge, in Bretnall, 1926) and *Hornera reteramae* Canu & Bassler, 1920, providing good examples from the Ordovician and Palaeogene of North America, as well as the Permian of Western Australia.

The free-living bryozoan fauna from the Gram Formation

A total of four bryozoan species interpreted to be free-living have been collected from the Gram Formation in the Gram Clay Pit, representing all three

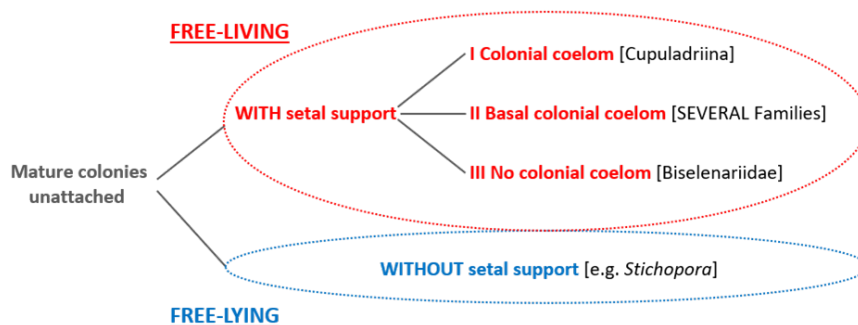


Fig. 4. Schematic illustration outlining the distinction between free-living and free-lying mode of life, with taxonomic examples in brackets. Note that the free-living categories are only realized within the cheilostome body plan, and that similarity in life-style does not *a priori* imply taxonomic relationships.

of the free-living categories distinguished in Fig. 4. They are all interpreted to have had setal support, while only three of them include significant proportions of colonial coelom: *Cupuladria* sp. aff. *biporosa* (Canu & Bassler, 1923) and *Reussirella germinatio* n. sp. both possess a total colonial coelom (Fig. 5), and '*Lunulites*' *voighti* Buge, 1973 is characterized by only possessing a basal colonial coelom (Fig. 5), whereas *Gramipora laxevincta* n. gen., n. sp. includes no colonial coelom (Fig. 5). The free-living species are overwhelmingly dominant amongst the bryozoans encountered from the Gram Formation, with *Reussirella germinatio* n. sp. accounting for more than 80% of the free-living bryozoan fauna and *Cupuladria* sp. aff. *biporosa* and '*Lunulites*' *voighti* being close to even seconds.

The first record of free-living bryozoans from the Gram Clay Pit is the listing of a single species, *Lunulites*

rhomboidalis Goldfuss (Ravn, 1897), a name that is no longer recognized. However, the original illustration by Goldfuss (1826–1844, plate XXXVII, fig. 7) leaves little doubt that this taxon should be referred to the *Cupuladriina* nov. The Gram formation has previously been exposed in multiple, now abandoned clay pits across southern and western Jylland, and although never reported in any detail, free-living bryozoans are known from the entire area. Distribution data collated from Survey archives by Rasmussen (1966) are here brought together in Fig. 2 A.

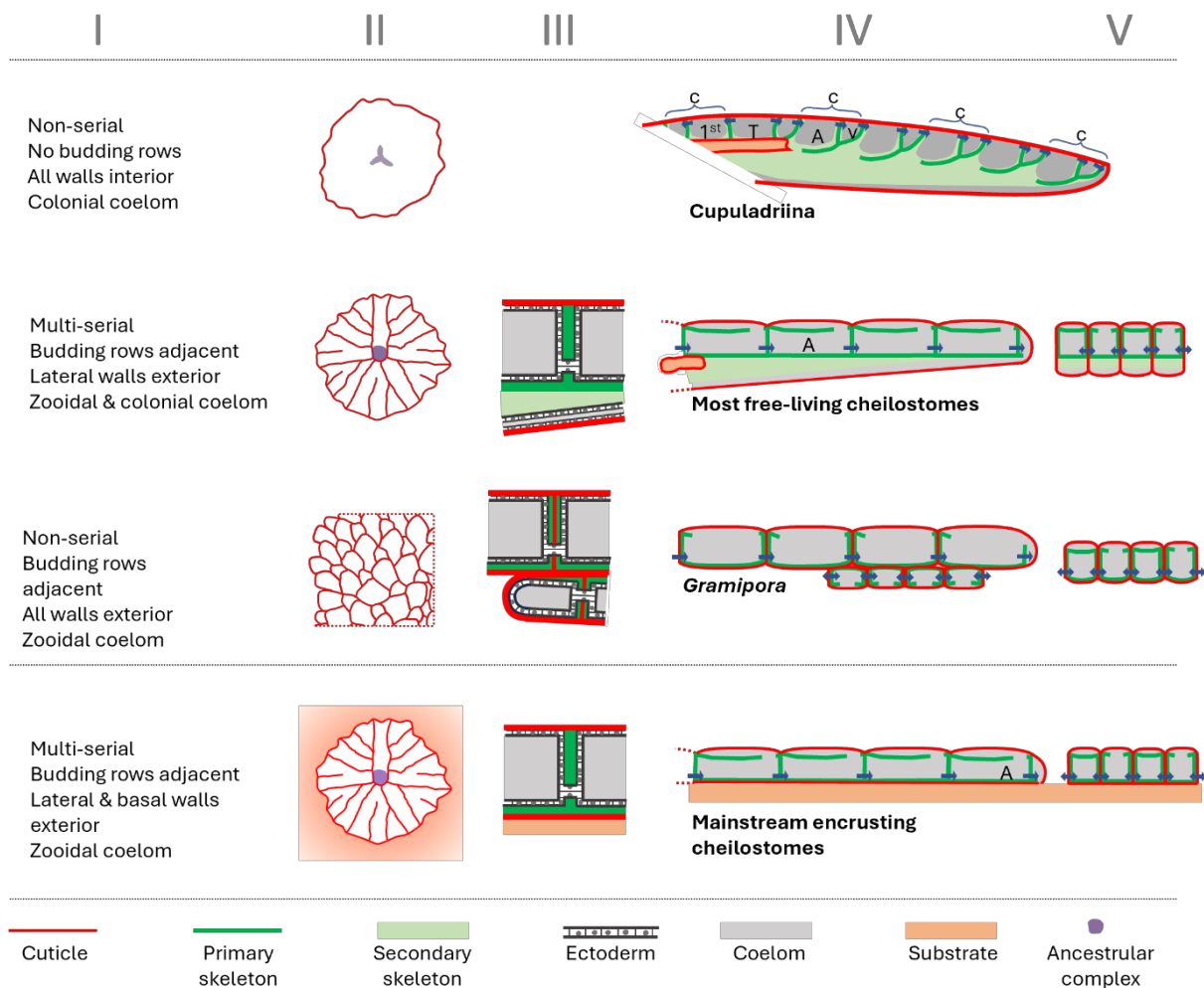


Fig. 5. Diagrammatic presentation of the main types of colony architecture in free-living bryozoans, with the architecture of mainstream encrusting cheilostomes added for comparison. Column I lists the essential differentiating characteristics in budding pattern, skeletal partitioning, and coelomic space; Column II presents the tracing of exterior vertical wall cuticles in a horizontal section; Column III presents details in distal zooidal wall construction including the non-coelomic pore connection (details of column IV); Column IV shows principal longitudinal sections; Column V shows principal cross sections. A few zooids labeled in column IV: A=autozoid; v=vibraculum; T=the longitudinal cormidium in the ancestrular triad characterizing the *Cupuladriina* nov.; 1st=the first budded cormidium in a *Cupuladriina* nov. colony. The c-marked brackets delimit a few *Cupuladriina* nov. cormidia, and the tiny blue arrows indicate communication pores.

Systematic palaeontology

Class Gymnolaemata Allman, 1856

Order Cheilostomata Busk, 1852

Suborder Cupuladriina nov.

(Early Eocene – Recent)

Diagnosis. Disc to cone-shaped free-living cheilostome taxa with zooids restricted to the frontal side; the exterior wall is colonial and non-skeletonized cuticular [except in relation to a substrate] and a colonial, typically aragonitic, skeleton is formed by interior walls partitioning the expanding colonial coelom into cormidia, each comprising one autozooid and one distal vibraculum. The colonial (i.e. non-zooidal) basal wall skeleton increases in thickness through the life of the colony, typically with serial chambers or thin tubes connecting the frontal zooids to the basal coelom. The basal coelom is generally subdivided in segments by more or less regular, radial and tangential cuticular partitions connecting the outer basal wall cuticle to the basal wall skeleton. Coordinated seasonal sex cell production takes place in unmodified autozooids during an interval of degradation-regeneration of all movable soft-parts in the zooid, with the coelomic cavity filled by sperm cells in male zooids and a single, large larva in brooding, female zooids. Fertilization is internal, following release of sperm into the water column. Larval life is brief, followed by rapid metamorphosis and the simultaneous formation of three cormidia into an ancestrular triad (Håkansson 1973;

Fig. 6). Settlement and metamorphosis typically take place on a minute, solid substratum of little or no relevance to the adult colony, but in some taxa, this relation is non-mandatory or non-existing. Across the suborder the vibracular opercula (setae) range from very long, fairly thin bristles (Fig. 3) to shorter, more solid rods, operated by large muscles; the primary role of the vibracular setae is to maintain the colony in a position slightly raised above the sea-floor, including digging the colony in and out of the sea-floor sediment, while a cleaning function has also been suggested. In all species observed alive, slow directional movement occurs, propelled by the vibracular setae. Clonal propagation occurs widely.

Discussion. The suborder Cupuladriina nov. constitutes a well-defined clade deviating significantly from not only all other free-living bryozoan groups, but in many characters also from the fundamentals of the anascan-grade cheilostomes in general. Fundamentally, the standard distinction between a gymnocyst and a cryptocyst in zooidal descriptions of cheilostome taxa is not meaningful, since the entire mineralized skeleton is colonial and interior and therefore a cryptocyst in the sense of Levinsen (1909). Interestingly – and seemingly with little subsequent consequence – this central aspect of this new suborder was noted already by Canu & Lecointre (1925, p. 17) stating “Pas de gymnocyste.” in their brief characterization of the genus *Cupuladria* Canu & Bassler, 1919.

With the growth and function of the colony so highly integrated, the Cupuladriina nov. either parallel or surpass the level of integration of many advanced asporan cheilostomes such as the Lan-

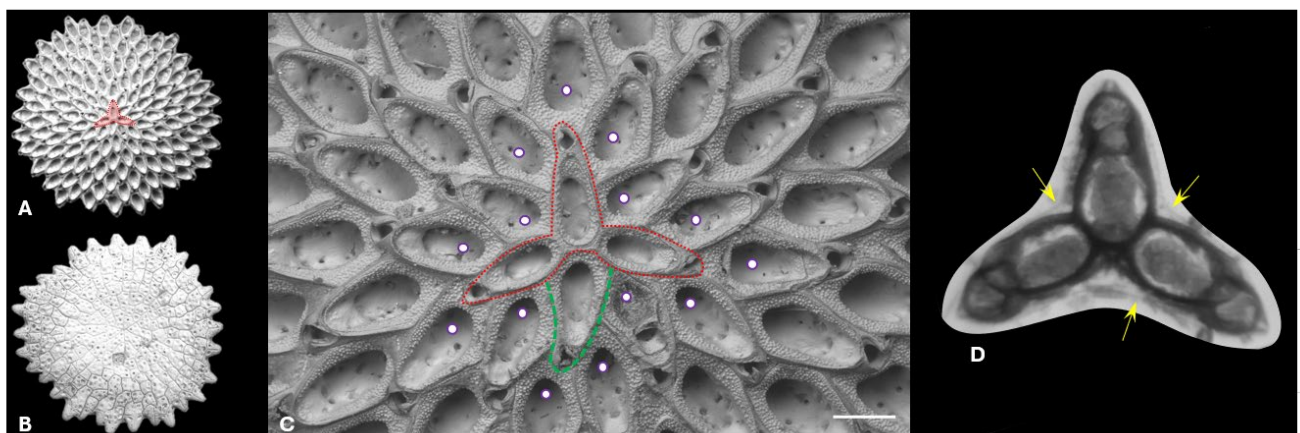


Fig. 6. The diagnostic ancestrular complex in the suborder Cupuladriina nov. **A–C**, aspects of the same colony of *Cupuladria biporosa* (Recent, Panama). **A**. The zooidal or frontal side of the colony, with the ancestrular complex outlined in red. **B**. The basal side showing the prominent pores and blocky sector-lines characterizing this species. **C**. Detail of **A** showing the ancestrular complex (outlined in red) and the early budding pattern, with the first budded cormidium outlined in green, and the autozooids of the subsequent periancestrular cormidia marked with white dots (Scale bar 100 μ m). **D**. Live, newly metamorphosed, not yet fully functional ancestrular triad of *Reussirella doma*, Recent, Capron Shoal, Florida; the yellow arrows point to the very faint outer cuticular body-wall, enclosing the colonial coelom (images courtesy of Aaron O’Dea [A–C] and Judith Winston [D]).

ceoporidae, Euthyrisellidae and Didymosellidae (Cook & Chimonides 1981). So, with only a few of the diagnostic characteristics shared with any other anascan cheilostome taxa, we feel justified in proposing this new suborder. With Cupuladriina nov. dating back to at least the latest Paleocene (Gorodiski & Balavoine 1962), this suborder may be the first cheilostome clade to reach such levels of colony integration in the prolonged recovery phase following the Mesozoic–Cenozoic biotic revolution. Interestingly, the single observation of molting reported from the phylum Bryozoa also falls within the Cupuladriina nov. (*Reussirella doma* (d’Orbigny, 1853); Winston & Håkansson 1989).

With their zooidal morphology evidently in the very simple end of the spectrum within the order Cheilostomata, and their colonial aspects largely misunderstood (see Håkansson 1973), the Cupuladriina nov. has had a somewhat tumultuous past in terms of their systematic position within the Cheilostomata. The suborder Cupuladriina nov. shares a number of highly conspicuous characters with a string of other free-living groups, particularly related to their shared colony architecture, the most notable being the disc-shaped colony with regularly dispersed vibracula and a secondarily thickening basal wall. Because this particular colony architecture directly reflects their shared free-living mode of life, we consider this a very clear case of parallel, convergent evolution (see also Håkansson *et al.* 2023). Furthermore, the fact that the majority of shared characters is *only* with other free-living groups is, in our view, a major reason why the evolutionary isolation of Cupuladriina nov. implied by our suggested elevation to a suborder rank has not been enacted previously. However, complications arriving from this oversight are not restricted to the Cupuladriina nov. Thus, Håkansson *et al.* (2023) considered the cupuladriids to be the only monophyletic major clade of free-living bryozoans within the current state of taxonomy.

Cupuladriina nov. is readily distinguished by the quite distinctive early astogeny of all its species, with larval metamorphosis into sexually recruited colonies resulting in an ancestrular complex comprising three, simultaneously formed zooids (Fig. 6; actually, three cormidia, each integrating a feeding, autozooidal unit and a distal, non-feeding heteromorph vibraculum, cf. Håkansson 1973), which are all fully functional prior to the formation of any subsequent zooidal cormidium. This ancestrular triad is easily recognized at the center of sexually recruited colonies (Figs 6–10), allowing also the identification of asexual, clonal progeny by default (Fig. 11). Accidental fragmentation of colonies followed by regenerative growth is a frequent source of clonal recruitment in most free-living bryozoans (Darteville 1935), in-

cluding the three commonest species recorded from the Gram Formation. However, across the suborder Cupuladriina nov. in particular, a quite extraordinary range of ways to propagate asexually through fragmentation has been described (O’Dea *et al.* 2008), possibly reflecting the colonial, rather than zooidal origin of the skeleton characterizing this family. As discussed elsewhere (Håkansson *et al.* unpublished), this array of shared characters should be expanded to include colony budding, which is identifiable also in fossil populations due to the retained, consistently different budding pattern in the early growth stages of asexually budded colonies (Figs 10–11).

While clonal propagation is found in most free-living cheilostome bryozoan clades, the family Cupuladriidae has been found to rely substantially – albeit highly variable – on clonal propagation, to the extent that entire populations in some species (fossil and living) have been found to contain only clonal, asexually recruited colonies (e.g., Marcus & Marcus 1962; Håkansson & Thomsen 2001). All known members of the suborder are considered category I Free-living (see above).

Stratigraphic distribution. Extant, with a marked diversity hot-spot around Central America and the central Atlantic Ocean established at the beginning of the Miocene (Lagaaij 1963; Håkansson *et al.* 2023). In contrast, the origin and early history of Cupuladriina nov. is only poorly known, with the rare, early occurrences centered in western and northern Africa and southern Europe (Thanetian(?) and Lutetian in Senegal (Gorodiski & Balavoine 1962), as well as Bartonian in Spain (Faura & Canu 1917), France (Buge & Debourle 1971) and Nigeria (Taylor 2012), and Priabonian in Egypt (Ziko 1985); cf. Taylor 2012).

Measurements. In cheilostome taxonomy, description of new taxa is routinely accompanied by the metrics of a few parameters, such as length and width of autozooids and length and width of any heteromorphs, sometimes expanded to include additional diagnostic characters.

However, with the integrated autozooidal-vibracular cormidia constituting the fundamental units in cupuladriid colonies, the traditional measurement protocol applied to other sheet growing cheilostomes is in need of some reconsideration. Firstly, the cormidia are formed individually, around the margin of the colony and, secondly, new cormidia are always initiated in the wedge between existing cormidia, not in budding rows. In other words, as in ordinary colonies the potential length of a developing cormidium is essentially unrestrained by exterior factors while, in contrast, the width is variously restrained by the neighboring cormidia (cf. Figs. 5–6). Hence, in the description of the two members of Cupuladriina

nov. included here, only the measurements of cormidial length are controlled by intrinsic factors. Note also that even the largest sexually recruited colonies of Cupuladriina nov. encountered in this investigation are so small that the traditional 'zone of astogenetic repetition' has not been reached (Fig. 7 A) – in mainstream cheilostome bryozoans this zone begins where the fully 'adult', stable zooid morphology has been reached

Family Cupuladriidae Lagaaij, 1952 [including Discoporellidae Bařuk & Radwanski, 1984; see Cook & Chimonides 1994]

Type genus: *Cupuladria* Canu & Bassler, 1919

Diagnosis, amended. As for the suborder, with the autozooidal frontal wall skeletal features varying from a steep, smooth ledge around the opesia, through simple or branching spines, over coalesced spines, to a horizontal frontal lamina with a varying number of pores, forming the main basis for the separation of the three genera currently recognized in the family, i.e., *Cupuladria*, *Reussirella* Bařuk & Radwanski, 1984 and *Discoporella* d'Orbigny, 1852. Taylor (2012) discussed the genus *Mesosecos* Faura & Canu, 1917, recognizing it as belonging to the family Cupuladriidae; on account of the poor preservation of the single known specimen, we agree with his assessment that their genus should be considered a subjective junior synonym of *Cupuladria* (Taylor 2012, p. 35)

Remarks. According to the Bryozoa homepage (Bock 2021) the family Cupuladriidae comprises four genera – *Cupuladria*, *Reussirella*, *Discoporella* and *Bisele-naria*. However, Håkansson & Zágorřek (2020) erected the new monogeneric family Bisele-nariidae based on a renewed investigation of the rare taxon *Bisele-naria placentula* (Reuss, 1867).

Genus *Cupuladria* Canu & Bassler, 1919

Type species: *Cupularia canariensis* Busk, 1859 [see Cook & Chimonides 1994]

Within Cupuladriina nov. this genus is distinguished by the autozooidal opesia being surrounded by a narrow, steep frontal wall with no spines, and by a basal wall with kenozooidal chambers arranged in vertical series; the basal coelom is subdivided by radial and tangential partitions, leading to a polygonal pattern. In addition to the omnipresent small cormidial vibracula, some species develop large vicarious avicularia in the central part of older colonies (Cook 1965; Herrera-Cubilla *et al.* 2006).

Cupuladria sp. aff. *biporosa* Canu & Bassler, 1923 Fig. 7

- ?1963 *Cupuladria canariensis* (Busk) – Rasmussen, p. 272
- 1966 *Cupuladria canariensis* – Rasmussen, figs 7: 2, 8
- 1966 *Cupuladria haidingeri* – Rasmussen, fig. 7: 7
- non 1966 *Cupuladria canariensis* – Rasmussen, fig. 7: 5

Material. MSJN 5435–5437; plus numerous unregistered specimens in bulk sample Gram 3.

Remarks. This taxon is characterized by a fairly thin basal wall with large more or less spherical kenozooidal chambers connecting the frontal autozooids with the basal coelom. Morphologically, it appears related to both *C. biporosa* Canu & Bassler, 1923 (a mainly American taxon) and *C. canariensis* Busk, 1859. The names *Cupuladria canariensis cavernosa* Cadée, 1979 (and discussed further in Cadée 1981) and *Cupuladria vindobonensis* Bařuk & Radwanski, 1984 (a & b) were proposed with the purpose of clarifying some of the problems in distinguishing between closely similar (and possibly allied) fossil representatives of these two species in the European Neogene. Both of these

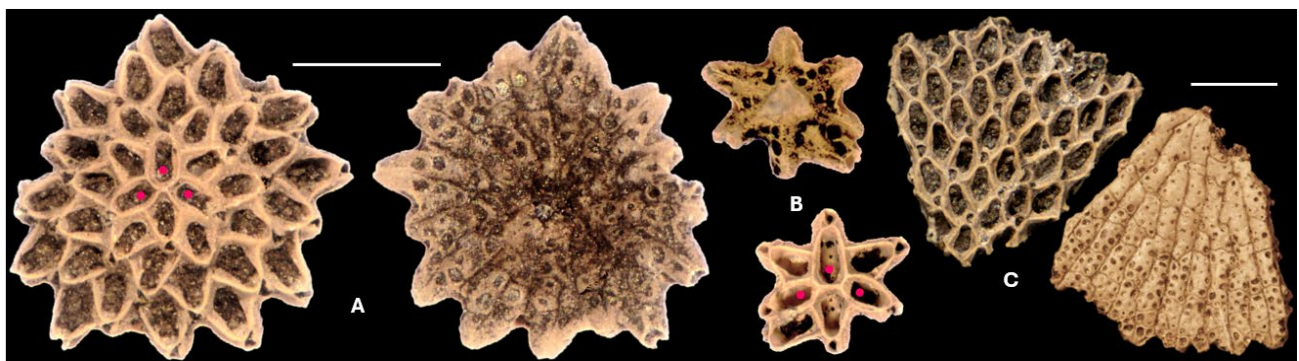


Fig. 7. *Cupuladria* sp. aff. *biporosa* from the Gram Clay Pit. **A.** Young colony (front and back; MSJN 5435) exhibiting the early astogeny of sexual progeny; note the large basal wall pore-chambers and the narrow, spineless zooidal frontal wall surrounding the opesia. **B.** Juvenile colony (front and back; MSJN 5436). Ancestrular triad indicated in both colonies (red dots); note that neither of the two sexually derived colonies contain a substrate. **C.** Fragment of a mature colony, (front and back; MSJN 5437). Scale bars 1 mm.

names might be considered available, but neither the discussions nor the implications put forward by these authors clarified the situation, particularly with respect to *Cupuladria vindobonensis* Bałuk & Radwanski 1984a (see discussion by Cook & Chimonides 1994). Consequently, and in view of the limited material at our disposal from the Gram fauna, we prefer to leave this taxon in open nomenclature.

Cupuladria sp. aff. *biporosa* is infrequent in the Gram Clay Pit and, due to its fragile skeleton, mostly fragmented.

Measurements (listed in the order of min–mean–max values)

Cormidium length: 407–575–741 µm; n=37

Cormidium width: 230–357–474 µm; n=37

Note that the high variability is possibly linked to the ontogenetic position of the measured cormidia.

Genus *Reussirella* Bałuk & Radwanski, 1984a

[amended, Cook & Chimonides 1994]

Type species: *Lunulites haidingeri* Reuss, 1847

The genus *Reussirella* is characterized by a largely incomplete spinous zooidal frontal wall, with the spines ranging from short and simple to larger, commonly branching spines; the basal wall with prominent radiating grooves and variously developed pustules, the basal wall pores varying in frequency, mostly fine, and commonly obscured. This genus essentially overlaps with the concept behind “Genus B” in the theoretical polythetic clustering of the Cupuladriidae

presented by Boardman *et al.* (1970, fig. 10).

Reussirella germinatio n. sp.

Figs 8–11

?1897 *Lunulites rhomboidalis* Goldfuss – Ravn, p. 14

?1956 *Lunulites rhomboidalis* Goldfuss – Rasmussen, p. 20

?1963 *Cupuladria haidingeri* (Reuss) – Rasmussen, p. 272

1966 *Cupuladria haidingeri* (Reuss) – Rasmussen, fig. 7: 1, 4

1966 *Cupuladria canariensis* (Busk) – Rasmussen, fig. 7: 5

?1973 partim *Cupuladria haidingeri* (Reuss) – Buge, fig. 1, non pl. 6, figs 3–4

2001 *Reussirella haidingeri* (Reuss) – Håkansson & Thomsen, fig. 11.8, C-I

Type material.

Holotype: DK 1336, NHMD-2038162 (Fig. 8 A)

Paratypes: MSJN 5438 (Fig. 8 B); MSJN 5439 (Fig. 9 A–B); MSJN 5440 (Fig. 9 C); MSJN 4341 (Fig. 9 D); MSJN 5442 (Fig. 9 E); MSJN 5443 (Fig. 10 A); MSJN 5444 (Fig. 10 B); MSJN 5445 (Fig. 10 C); MSJN 5446 (Fig. 10 D); MSJN 5447 (Fig. 10 E); MSJN 5448 (Fig. 11 A); 5449 (Fig. 11 B); MSJN 5450 (Fig. 11 C);

Additional material. Hundreds of unregistered specimens in bulk sample Gram 3.

Etymology. Named after the prevalence of colony budding in the populations at the type locality (this aspect is developed further by Håkansson *et al.* unpublished).

Type locality. Gram Clay Pit, Gram, Denmark; Late Tortonian (at the *Hystrichosphaeropsis obscura* – Am-

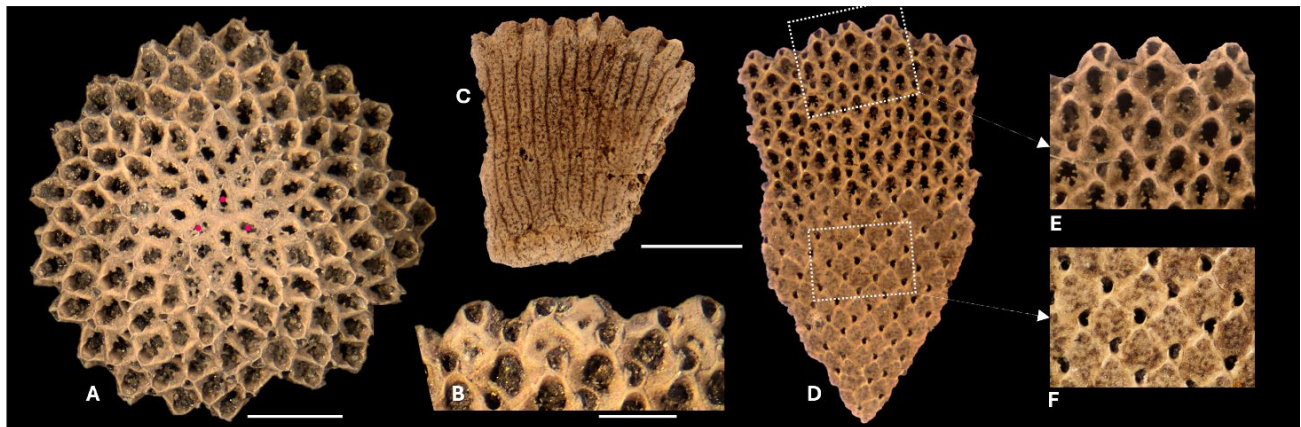


Fig. 8. A–B. *Reussirella germinatio* n. sp. from the Gram Clay Pit. **A.** Frontal view of large, sexually derived colony (Holotype, DK 1336, NHMD-2038162), with the ancestrular triad indicated with red dots. **B.** Terminal margin of mature colony recognized by the prominent zone of reduced autozooids as well as vibracula not associated with autozooids (Paratype, MSJN 5438). **C–F.** *Reussirella haidingeri* (Reuss, 1847) illustrated for comparison (Miocene, Dingden, Germany). **C.** Fragment of large colony (MSJN 5451), basal view displaying the near parallel segmentation as well as the numerous basal wall pores. **D.** Fragment of large colony (MSJN 5452), frontal view displaying a central zone with occluded autozooids but functional vibracula and a marginal zone with fully functional cormidia. **E–F.** Details of D. Scale bars 1 mm (A), 500 µm (B) and 2 mm (C–D).

iculospaera umbracula zonal boundary: Fig. 2).

Diagnosis. *Reussirella* species characterized by smallish (up to 5 mm in diameter), compact colonies, with a thick to massive basal wall, typically with prominent pustules and inconspicuous, or frequently lacking, basal pores. Asexual recruitment from colony budding is dominant at the type locality, whereas asexual recruitment from fragmentation is often low, most likely reflecting the rather massive basal wall skeleton. Maximum colony size indicated by a senescent zone of stunted cormidia around the colony perimeter.

Description. Colony small, not exceeding 5 mm in diameter and mostly near flat, but with larger colonies variously more domal. The populations recovered from the Gram Clay Pit comprise two types of colonies: Sexual progeny resulting from larval settlement and asexual, clonal progeny resulting from either colony budding or regeneration from fragments, with recruitment from colony budding being dominant overall, accounting for about 80% of the population (Håkansson & Thomsen 2001, Håkansson *et al.* unpublished). Sexual recruits (Figs 8 A, 9 C–E and

10 C) are recognized by their ancestrular triad, while clonal recruits resulting from colony budding (Figs 10 B, D–E) are recognized by their fan-shaped initial budding pattern from the single founding zooid initiating the bud. Both sexual and budded progeny are characterized by a primary zone of astogenetic change with gradual but slow increase in zooid dimensions (see Figs 9 C–E and 11 A–C) which, subsequently, seems to increase significantly (Fig. 8 A), raising doubt that a clear zone of astogenetic repetition is actually reached during growth of the comparatively small colonies characterizing this species. A few large colonies or colony fragments have been recorded with a senescent margin composed entirely by vibracula and significantly reduced cormidia (Fig. 8 B), suggesting a genetically constrained maximum size. A comparable development signaling termination of growth has been noted for both fossil (EH unpublished) and Recent (Almeida *et al.* 2021) species of *Discoporella* from South America.

In contrast, in the much larger type species of the genus, *R. haidingeri*, which clearly reaches a stage of astogenetic repetition (cf. Fig. 8 D), a similar terminal stage has not been described.

Autozooids diamond-shaped, approximately as

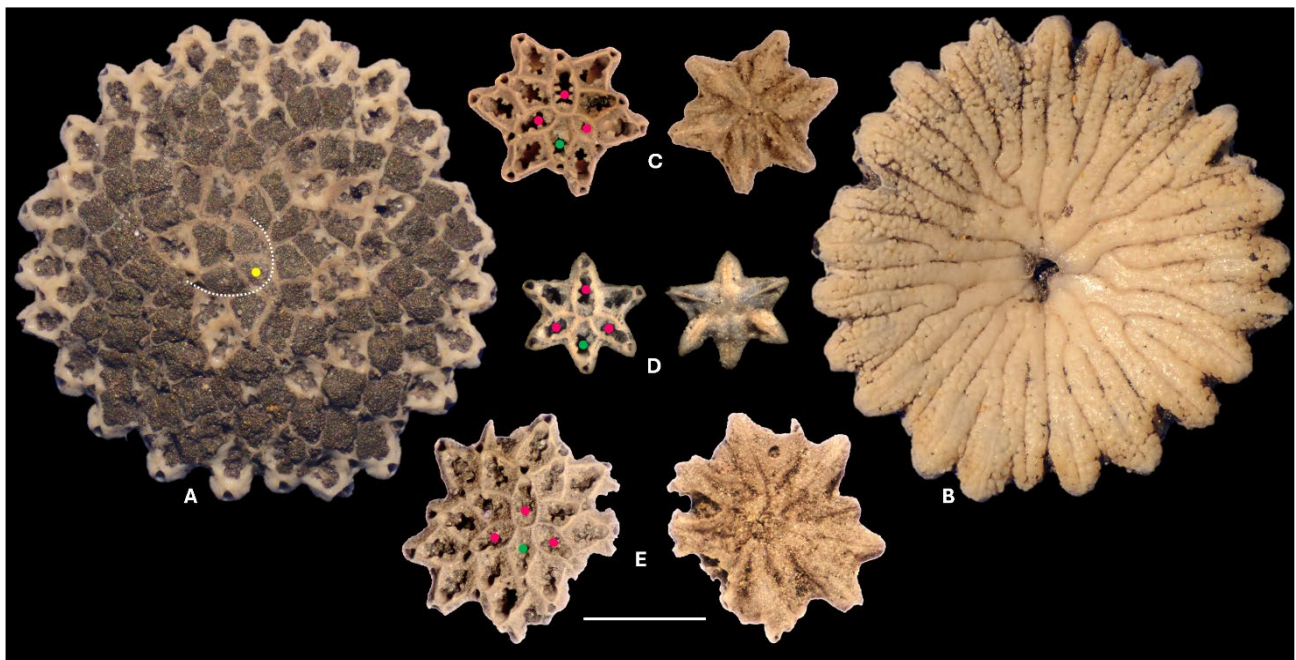


Fig. 9. *Reussirella germinatio* n. sp. from the Gram Clay Pit. A–B. Complete, mature colony (front and back; Paratype, MSJN 5439); partly filled with micro-crystalline pyrite. The contrast in geometry between the frontal (A) and basal (B) sides of the colony – irregular in the central part of the frontal view in contrast to highly regular, radial symmetry of the sector lines in the basal view – reveals the clonal origin of this colony from a colony bud (outline in white stipple, founding zooid indicated with yellow dot). Also, this contrast reveals a decoupling of frontal side budding of zooids and the basal side development of the radial, colonial coelom segments which, in this colony, must have expanded back over the damaged older part of the colony. Note that the pustulose ornamentation on the basal side in this colony is restricted to the younger, more marginal parts. C–E. Early astogenetic stages illustrated by frontal and basal views of three juvenile, sexually recruited colonies, in all cases with the ancestrular triad indicated with red dots and the first budded cormidium indicated with a green dot; note that none of these specimens show any sign of a substrate (C, MSJN 5440; D, MSJN 5441; E, MSJN 5442). Scale bar 1 mm.

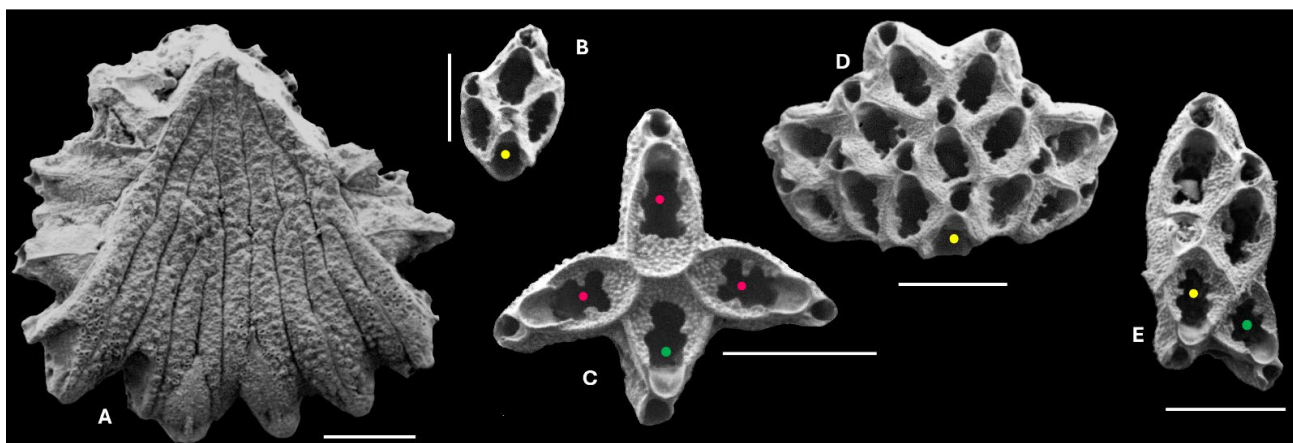


Fig. 10. Selected specimens of *Reussirella germinatio* n. sp. from the Gram Clay Pit, illustrating the morphological characteristics of the three means of propagation recorded in this population: **A**. Clonal propagation by fragmentation; note the thick basal wall of the initial fragment followed by regenerative growth of new thin-walled zooidal cormidia – initiated along the broken faces, to restore the optimal, circular geometry. **B**, **D** and **E**. Clonal propagation by colony budding; in **B** and **D** the founding zooid connecting to the maternal colony (yellow dot) shows no sign of growth after separation, while in **E** the founding zooid (yellow dot) has been reconstructed with the addition of a secondary vibraculum indicating a change in polarity, [rapidly] followed by new growth of a single zooidal cormidium (green dot) accentuating the shift in polarity. **C**. Sexual propagation through larval metamorphosis; note the ancestrular triad (red dots) followed by a single fully grown zooidal cormidium (green dot). Scale bars 500 µm. (MSJN 5443–5447; modified from Håkansson & Thomsen 2001, fig. 11.8).

wide as long, but narrower in the periancestrular area, with the first budded zooid from the ancestrular complex (marked with green dots in Figs 9 C–E and 10 C) being quite variable, largely reflecting the variation in the angle of the two proximal zooids in the ancestrular triad. Zooidal lateral walls granular where exposed, somewhat similar to the variously developed zooidal frontal wall skeleton; separated by the raised, thin mural rim and groove where the frontal exterior wall cuticle connects to the mineralized skeleton of the zooid fronts. Frontal wall spines in this species may be almost rudimentary, simple to trifurcated, developing in a variable number, projecting centrally, and only rarely fusing in the oldest part of the colony (Fig. 8 A), leaving a number of irregularly shaped pores. Secondary closure of central zooids is rare. Opesia elongated.

Vibracular chambers subtriangular, with raised, smooth asymmetrical lateral blunt projections defining an auriform opesia, the rostrum oriented proximally and laterally, typically with alternating orientation.

The basal side of the colony almost flat to slightly concave, displaying radially arranged sectors, each subdividing consistently (maintaining about the same width) with increasing colony diameter; surface typically pustulose to granular, in larger colonies sometimes smooth (Fig. 9 B).

Measurements (listed in the order of min—mean—max values)

Cormidium length: 488–543–603 µm; n=24

Cormidium width: 303–373–475 µm; n=24

Note that the high variability is possibly linked to the

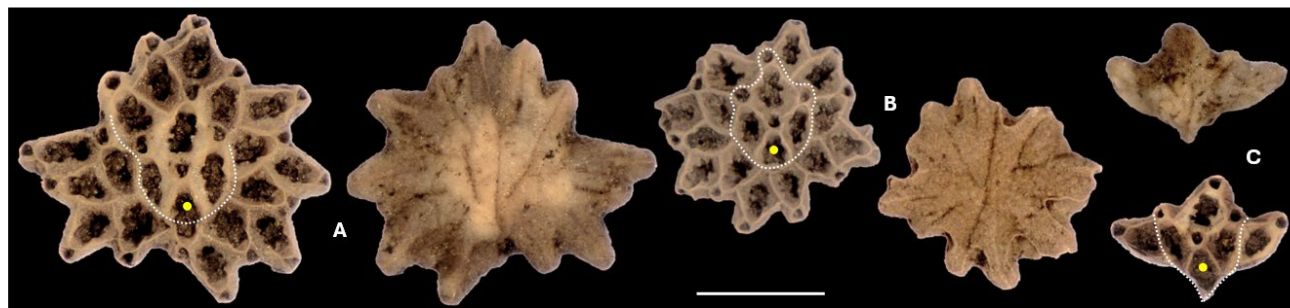


Fig. 11. Examples of young-budded colonies of *Reussirella germinatio* n. sp. from the Gram Clay Pit (front and back), with the founding zooid indicated by a yellow dot. The outline of the original bud indicated in white stipple. Note that the founding zooid in **A** has developed a secondary, proximally directed vibraculum immediately establishing a reverse polarity for the post-separation budding, while this is not the case in **B**. **C**. Newly released budded colony with the proximal part of the founding zooid not fully restored (**A**, MSJN 5448; **B**, MSJN 5449; **C**, MSJN 5450). Scale bar 1 mm.

ontogenetic position of the different cormidia.

Remarks. *Reussirella germinatio* n. sp. resembles *R. haidingeri* (Figs 8 C–F), but differs in both the size and shape of the colony, being considerably smaller and having a proportionally thicker basal wall. Furthermore, autozooidal frontal wall spines in *R. haidingeri* are more prominent and more prone to branching (Fig. 8 D–E), and in larger colonies complete closure of the autozooids may affect the entire central area (Fig. 8 D–F). The vibracula are comparably smaller in the present species, their length being only about 1/3 of an autozooid, whereas it is more than half that length in *R. haidingeri*.

Reussirella germinatio n. sp. is totally dominant in the bryozoan fauna from the Gram Clay Pit. – even constituting more than 80% of the free-living part of the fauna – and with their compact and fairly robust skeleton they are frequently preserved as complete colonies. Colony budding in *R. germinatio* n. sp. was first discussed by Håkansson & Thomsen (2001; as *R. haidingeri*) in relation to data obtained from two bulk populations in combination with a single, pyritized specimen (Håkansson & Thomsen 2001, fig. 11.8 G). New finds reported elsewhere (Håkansson *et al.* unpublished) has now verified the importance of colony budding in the populations of *R. germinatio* n. sp. in the Tortonian Gram Formation around the town of Gram, Denmark. Budded colonies and *post-mortem* separated colony buds of *R. germinatio* n. sp. – both recognizable through their fan-shaped early budding pattern and their single, founding zooid (Figs 10–11) – are dominant in all bulk samples investigated from the Gram Clay Pit, and overall sexual reproduction accounts for less than 20% of the three populations investigated (Håkansson & Thomsen 2001; Håkansson *et al.* unpublished).

Distribution. While the type species of the genus, *R. haidingeri* is frequent in the Miocene across central Europe, from the Carpathian and Alpine foredeeps to western France and the southern parts of the North Sea Basin (e.g. Lagaaij 1952, 1953; Buge 1973; Bałuk & Radwanski 1984 a & b), it appears that *R. germinatio* n. sp. may have a more restricted distribution replacing this larger species in northern Europe, in the northern part of the North Sea Basin (Fig. 2 A). The presence of *R. germinatio* n. sp. outside its Tortonian type locality at Gram has yet to be verified, but we consider it likely that most of the specimens reported (as *Cupuladria haidingeri*) from the Gram Formation by Rasmussen (1966) represent this taxon, as may the northernmost and youngest specimens reported by Buge from northern Germany (1973, fig. 1: Flensburg, less than 75 km from Gram, and Pinneberg).

Suborder Flustrina Smitt, 1868

Superfamily ‘Lunulitoidea’ Gregory, 1893

Notwithstanding their first sentence stating that “The superfamily Lunulitoidea is newly introduced here....” (Cook, Bock, Hayward & Gordon 2018, p. 137; our emphasis), these authors refer the authorship of this taxon to “Lagaaij, 1952 *nom. transl.*”. However, Gregory (1893, p. 224) was the first to introduce a family-group name – Lunulitinae – thus any family-group name subsequent to that should be attributed to Gregory (1893; Dennis Gordon pers. comm.). According to Cook *et al.* (2018) the superfamily ‘Lunulitoidea’ comprises 4 families – other accounts even including the family Cupuladriidae (e.g. Cook & Chimonides 1986) – which, as is the case within the cupuladriids, solely share features directly reflecting their mode of life. The systematic consistency of most of these families is somewhat problematic in themselves (see Håkansson *et al.* 2023) and, until further research becomes available, we therefore suggest disregarding the taxon ‘Lunulitoidea’ in this broad sense.

Family ‘Lunulitidae’ Gregory, 1893

The taxonomic status of the nominal family itself is also unresolved. In 1952 Lagaaij included just the nominal genus in his “Lunulitidae auctt.”, with Bassler (1953) also including *Volviiflustrallaria* Brydone, 1936 in the Bryozoa volume of the Treatise of Invertebrate Paleontology, while Bock (2017) included 6 genera and, currently (July 2025), the World Register of Marine Species includes a total of eight genera. However, in their broad scale assessment of the ‘lunulite bryozoans’, Håkansson *et al.* (2023) questioned the actual relationship between most of these taxa and argued that even the three independent clusters traditionally sharing the name ‘Lunulites’ evolved independently within well-defined stratigraphic and geographic borders – a Late Cretaceous cluster centered in northern Europe; a North American cluster abundant in the Eocene Gulf and Coastal Plains and becoming extinct in the Oligocene and; an ‘Old World’ European cluster recorded somewhat sporadically from the Paleocene into the Pliocene. Notwithstanding, these authors found strong morphological parallels across all three clusters, many shared more broadly with all the free-living bryozoans, simply reflecting their common mode of life.

Most ‘lunulites’ are characterized by a central ancestrula or ancestrular complex and in many species, colony sizes exceed 1 cm. The skeleton is dominantly calcitic in the Cretaceous cluster and typically bimineralic in the Palaeogene and Neogene (Greeley 1969; Rucker & Carver 1969; Smith *et al.* 2006; Taylor *et al.*

2009). All clusters are characterized by a secondarily thickened basal wall, which is mostly pierced by numerous pores or tubes in the post-Cretaceous taxa. The autozooids form distinct budding rows separated by external lateral wall cuticles (cf. Fig. 5) and the vibracula are either distributed fairly evenly across the frontal side of the colonies or forming distinct rows alternating with the autozooidal budding rows. Asexual propagation through fragmentation is significant in many populations, commonly facilitated by the conjoined external walls separating individual budding rows (Darteville 1935; Thomsen & Håkansson 1996; Håkansson & Thomsen 2001; Fig. 5).

son 1996; Håkansson & Thomsen 2001; Fig. 5).

However, despite their shared characters, the actual phylogenetic relationships remain doubtful, with iterative and parallel evolution playing significant roles leading to a remarkable number of free-living clades – again, amongst the free-living bryozoans, shared characters are just as likely to reflect shared ecology rather than shared ancestry.

Measurements. In contrast to *Cupuladriina* nov., budding in most other free-living bryozoans follows the typical cheilostome model, with budding taking



Fig. 12. '*Lunulites*' *voighti* Buge, 1973 from the Gram Clay Pit. **A**. Partial internal mold of a sexually recruited colony showing the internal volume of all zooids, with four outsized marginal female zooids marked (white dots; MSJN 5361). **B–C**. Segment of a large sexually recruited colony (MSJN 5453). **C** is displaying an overview of the highly organized budding pattern characterizing this species, while **B** shows the distribution of the zooid types. Out-sized autozooids (white dots) are interpreted as female zooids; they are concentrated in the marginal zone and irregularly distributed in the normal budding rows; note however, that they may not always be precisely distinguished from an external assessment alone (cf. Fig. **A**). Note that all budding rows are initiated with a vibraculum, commonly followed by a more elongate autozooid with an oval opesia (blue dots). **D** Colony fragment displaying abrupt change in budding direction in association with fragment regeneration (MSJN 5454). **E** The juvenile frontal architecture displayed in a fragment of a younger sexually recruited colony only moderately affected by diagenetic pyrite (MSJN 783). A total of 11 autozooidal budding rows (red stippling) are included in this fragment: row 1 is initiated from the ancestrula (a), row 2 is initiated from a periancestrular autozooid, while all subsequent budding rows are initiated by an avicularium. Note that the conspicuous pattern of alternating rows of autozooids and vibracula (shown in white stipple) has only just been established in this colony (compare to **A** & **C**). **F–G** Complete, sexually recruited colony, front and back, partly filled with micro-crystalline pyrite (MSJN 5455). **F** The slightly worn front displays the very determinate budding pattern characteristic of this species, radiating from the central, enlarged ancestrula (white dot; see also Fig. 14 **D**). **G** The sector lines on the basal side (enhanced by pyrite) are irregularly radiating, only partly reflecting the frontal symmetry; the basal wall pores are large and somewhat irregularly distributed (note that the outermost smaller pores will eventually be located in the distal wall separating the zooidal cavities on the frontal side). Scale bars 1 mm.

place within distinct budding rows, i.e. series of zooids developed within the confinement of a cuticular tube constantly extending distally. However, in contrast to mainstream cheilostomes where both the lateral and basal walls are secreted as a continuation of the outer body wall forming the cuticular tube, other free-living clades – including also ‘*Lunulites*’ *voigti* Buge, 1973 – forms a colonial basal wall secreted from a colonial coelom allowing them to continuously thicken their basal wall skeleton (cf. Fig. 5).

In terms of measurements, therefore, the traditional measurements of zooidal length and width within well-defined budding rows are directly applicable in most free-living clades (other than Cupuladriina), with the same caveats as rule for other cheilostomes.

Genus *Lunulites* Lamarck, 1816

Type species: *Lunulites radiata* Lamarck, 1816

As pointed out above, the genus name *Lunulites* has been applied extensively – and generously – over its long history, and serious revisions are necessary (Cook *et al.* 2018; Håkansson *et al.* 2023), hence we prefer to put the genus name of the sole species in the Gram fauna in inverted commas.

‘*Lunulites*’ *voigti* Buge, 1973

Figs 12–14

- 1953 *Lunulites* sp. – Lagaaij, pl. 2, 6 a–b
- ?1956 *Lunulites radiata* Goldfuss – Rasmussen, p. 20
- 1963 *Lunulites* sp. – Rasmussen, p. 272
- 1966 *Lunulites* sp. – Rasmussen, fig. 7: 3, 6, 9
- 1973 *Lunulites voigti* n. sp. – Buge, 32–39, pls 6–8

Material. MSJN 5361 (Fig. 12 A); MSJN 5453 (Figs 12 B–C); MSJN 5454 (Figs 12 D); MSJN 783 (Fig. 12 E); MSJN 5455 (Figs 12 F–G); MSJN 5456 (Fig. 13); MSJN

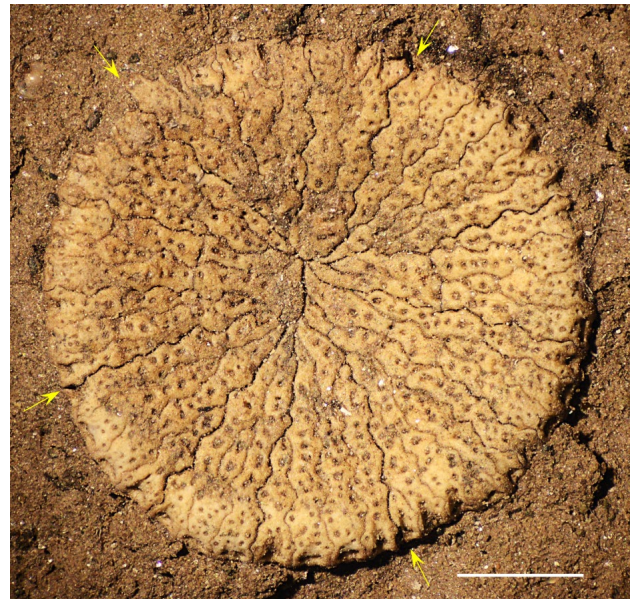


Fig. 13. ‘*Lunulites*’ *voigti* from the Gram Clay Pit. Basal view of mature, sexually recruited colony. Note the thin, radiating cracks (a few indicated by yellow arrows) developed in some of the cuticulated lateral walls as the result of slight diagenetic compaction of the very shallow cone. (MSJN 5456). Scale bar 2 mm.

5457 (Fig. 14 A); MSJN 5458 (Fig. 14 B); MSJN 5459 (Fig. 14 C–D); plus numerous unregistered specimens in bulk sample Gram 3.

Description. A robust ‘*Lunulites*’ with nearly flat colonies, large zooids, and distinctive budding rows with alternating autozooidal rows and discontinuous rows of vibracula (Fig. 12). Budding rows on the basal side are separated by irregular, sometimes distinctly zigzag lines representing the dissolved conjoined lateral cuticles (Fig. 13), in a pattern which does not always correspond to the frontal budding rows (Figs 12 F–G); the basal wall pores are few but prominent and variable in size (Figs 12 G, 13). Ancestr-

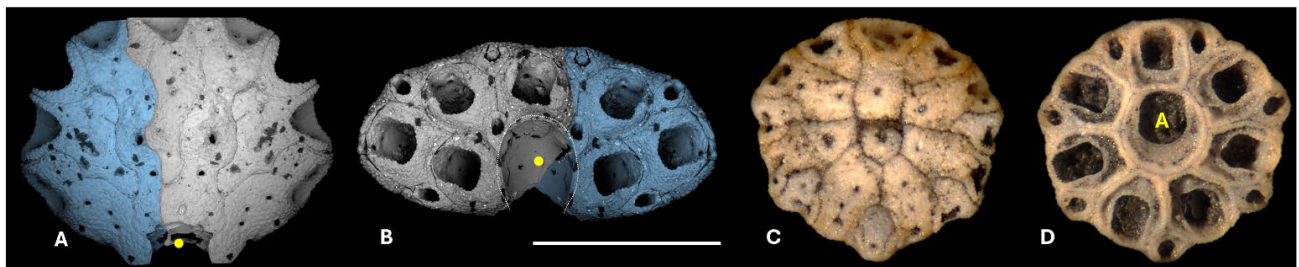


Fig. 14. ‘*Lunulites*’ *voigti*. **A–B** Photographically restored young budded colonies (back and front, respectively), in both cases based on more than a half-seized fragment, with the interpreted part (marked in blue) provided by a mirror image of the preserved fragment. The yellow dot indicates the assumed position of the founding zooid (outlined in white stipple in B). **C–D.** Ancestrular complex (back & front) comprising the ancestrula (A) surrounded by 7 periancestrular autozooids and 7 vibracula, all distinguishable on the basal side at this early stage; note the absence of a substrate. (A, MSJN 4557; B, 5458; C–D, MSJN 5461). Scale bar 1 mm.

trula is larger than the six or seven periancestrular autozooids, and together with an equal number of vibracula they constitute an ancestrular complex (Figs 12 F, 14 D). Autozooids slightly wider than long, with large opesiae surrounded by a pustulose cryptocyst. Vibracula, small and slightly asymmetrical, are scattered in the juvenile part of the colony, where most vibracula initiate budding rows, but with increasing colony diameter they rapidly form distinct rows (e.g., Fig. 12 E). In many budding rows the first autozooid is more elongate, with a proportionally large opesia (blue dots in Fig. 12 G). Brooding, female zooids larger and with a greatly expanded lumen (white dots in Fig. 12 A); they are mostly distinguishable through their over-sized opesiae (large yellow dots in Fig. 12 B), but the frequent presence of intermediate sized opesiae commonly make their identification from the exterior less obvious. Considered category II Free-living (see above).

Measurements (listed in the order of min—mean—max values)

Autozooid length: 417–488–545 µm; n=14

Autozooid width: 409–493–589 µm; n=14

Length of first autozooid in new rows: 662–697–774 µm; n=4

Width of first autozooid in new rows: 394–413–435 µm; n=4

Female zooid length: 465–512–583 µm; n=9

Female zooid width: 541–584–676 µm; n=9

Vibracula length: 345–393–434 µm; n=13

Vibracula width: 212–243–267 µm; n=13

Reproduction. In the Gram Clay Pit population sexual propagation appears to be more widespread than regeneration from fragments; thus, we consider the significant proportion of fragments in bulk samples to result from *in situ* diagenetic compaction (cf. Fig. 13) and/or bulk sample processing. However, interestingly, a few cases of colony budding have also been encountered in this taxon at Gram Clay Pit (Figs 14 A, B).

The significantly expanded internal volume of female zooids is a parallel to the free-living Australian species *Lunularia capulus* (Busk, 1852), which release exceptionally big larva (Cook *et al.* 2018) and reach a fully functional stage only at the completion of 12 autozooids (Håkansson 1981).

Remarks. The skeleton separates easily between the cuticulated lateral walls of the budding rows and – to a lesser extent – along the distal zooidal walls, possibly suggesting the presence of some cuticle also in these walls.

Distribution. This species is known from the Late Tortonian in SW Denmark (around the *Hystriosphæris obscura* – *Amiculosphæra umbracula* zonal

boundary: Fig. 2), as well as from the Miocene of the Netherlands and NW Germany (Lagaaij 1953; Buge 1973).

Incertae sedis

Gramipora n. gen.

Figs 15–16

Type species: *Gramipora laxevincta* n. gen., n. sp.

Etymology. Named after the Gram Formation, combined with *pora*, a suffix frequently applied in bryozoan genus names.

Diagnosis. Colony unattached, bilaminar, flat to slightly arched with two distinctly different layers of zooids arranged back-to-back (cf. Fig. 5), each comprising two different types of zooids, with all four types of zooids displaying a highly variable morphology. The frontal layer (Figs 15 A, D) with evenly distributed autozooids and interspersed vibracula, as well as an occasional space-filling kenozooid, the abfrontal layer (Figs 15 B–C) with near chaotic distribution of irregular kenozooids and vibracula. Frontal autozooids (a in Fig. 15 A) are large and irregular, calloporid-like, each with a variably elliptical opesia surrounded by a narrow gymnocyst and a horse-shoe shaped narrow coarsely pustulose cryptocyst, which is missing distally. Frontal vibracula (v in Fig. 15 A) are asymmetrical, and quite variable, possibly dimorphic with the most consistent type marked with yellow stipples in Fig. 15 A. Abfrontal kenozooids (Figs 15 B–C, 16 A–E) resemble frontal autozooids but are smaller, and with a complete rim of cryptocyst around the smaller central opesia. Abfrontal vibracula (yellow arrows in Figs 16 A, E) tend to be larger, more elongate and more distinctly asymmetrical than their frontal counterparts. No pore connection between the two zooidal layers, and cohesion between individual zooids, and especially the two sides of the colony, is very weak.

Remarks. The zooidal morphologies of this taxon are well within that of the anascan cheilostomes, with the morphology of the frontal vibracula in combination with the lack of any substrate relations clearly suggesting a free-living III mode of life. However, at this point the colony architecture appears to differ markedly from anything else known from the order Cheilostomata, and in view of the limited material available we prefer to leave speculations towards the taxonomic position of *Gramipora* open for now.

Gramipora laxevincta n. gen., n. sp.

Figs 15–16

Type material.

Holotype: MSJN 4045 (Figs 15 A & C–D; Fig. 16 F)

Paratypes: MSJN 5460 (Fig. 15 B; Figs 16 A–E); MSJN 5461 (Figs 16 G–H)

Etymology. A combination of the Latin words *laxe* and *vinctus*, meaning ‘loosely bound’.

Diagnosis. As for the genus.

Type locality. Gram Clay Pit, Gram, Denmark; Tortonian (around the *Hystriosphæropsis obscura* – *Amiculosphæra umbracula* zonal boundary: Fig. 2).

Description. Colonies form bilamellar and seemingly unattached discs; from the few available specimens, possibly quite large, exceeding 1 cm². The two layers of the colony differ significantly, with the assumed frontal layer comprising two types of evenly distributed zooids (ratio almost equaling 1:1). From their morphology they are interpreted to be large autozooids and smaller vibracula, both with a marked variability in both morphology and size (Fig. 15 A). Occasionally this variability leads to the formation of a few tiny, space-filling kenozooids. In contrast, the abfrontal layer consists of a chaotic mosaic of haphazardly shaped kenozooids and less frequent, unevenly distributed vibracula morphologically different from those in the frontal layer (Figs 15 B–C). However, the limited material at hand does not allow any conclusion whether this layer is formed synchronous with the frontal layer. Both layers are characterized by fan-shaped budding patterns (Figs 16 F & G–H) – fairly organized in the frontal layer and less so in the abfrontal layer – and seemingly originating at the colony margin in both layers. Thus, the ancestrula is potentially marginal, but none have thus far been identified with certainty. It is also noteworthy that the fan-shaped budding patterns of the two sides are uncoordinated (Fig. 16 F), and that no pore connection across the basal walls of the two zooidal layers have been seen. Accordingly, it would appear that the connection between the two layers is very limited. Interzooidal cohesion is weak both within layers and between layers, leading to some degree of *in situ* separation of individual zooids in most colonies (Figs 15 A, D). This suggests that all zooidal walls are exterior and therefore that all zooidal walls are cuticulated, with the connective pores in the lateral and distal walls being the only exception.

Autozooids are markedly irregular in shape, with locally undulating boundaries and no discernible budding rows; they are sometimes almost as long as wide, but most often they are irregularly elongate.

The very large opesiae are usually longer than wide, and the narrow frontal margin surrounding them is subdivided, with a smooth outer part and a pustulose inner part separated by a distinct groove. With the variously developed void between all zooids in the frontal layer (cf. Fig. 15 A) interpreted as the position of the conjoined lateral wall cuticles lost through early diagenesis, we suggest that the distinct groove separating the two types of skeletal sculpturing marks the change between a smooth gymnocyst and a pustulose cryptocyst i.e. the transition from a skeletonized outer wall to a non-skeletonized outer, frontal wall. While the gymnocyst completely surrounds the opesia, the gently to steeply sloping cryptocyst is absent at the distal orificial margins. Spines are absent. Few large communication pores sometimes visible at the periphery of the basal wall (white arrows in Fig. 15 A), plausibly leading to the tubular interzooidal connections that can be seen as lateral protuberances of the swollen autozooidal basal surface on the exposed back side of the frontal layer (white arrows in Fig. 15 C). Total regeneration (*sensu* Levinson 1907) has been noted in one autozooid (T in Fig. 15 A).

On the frontal side inter-zooidal vibracula are located disto-laterally to almost each autozooid; they are comparatively small and irregularly quadrangular to rounded polygonal in outline, often with an elongated proximal end wedged in between proximal autozooids, occasionally extending into a rim along the distolateral walls of associated autozooids. The opesia is elliptical to almost figure-eight-shaped due to the mid-length constriction by two inconspicuous, bluntly triangular, condyles facing each other (Fig. 15 A). Rostrum arched and slightly flared, with a narrow palate only developing distally. Abfrontal vibracula comparably larger and more elongate than the frontal ones; ovoidal in shape and markedly asymmetrical, apparently with a single very prominent condyle developing on one side only, at about the midline, leaving an ear-shaped opesia, with a narrow palate developing only at the distal (rostrum) and proximal (talon) ends (Figs 15 A, C).

Frontal kenozooids are rare, small and highly variable, seemingly serving primarily as space-fillers in the overall loosely constrained zooidal mosaic. In the abfrontal layer the kenozooids are somewhat reminiscent of the frontal autozooids; they are equally irregularly shaped and sized, but they do not form a continuous sheet, with a fair number of zooids only partly surrounded by conjoined neighbors. The opesia is ovoidal to drop-shaped, defined by a distinct edge separating the inward sloping pustular cryptocyst and a convexly curved gymnocyst. No ovicell and no ancestrula seen. Tentatively considered category III Free-living (see above).

Measurements. In contrast to ‘L’. *voighti*, *G. laxevincta*

n. gen., n. sp. lacks distinct budding rows, and the zooidal dimensions vary to the point where the traditional approach to measurements fails miserably; accordingly, the range of measured dimensions reported are quite remarkable:

Autozooid length: 373–517–702 μm ; n=25

Autozooid width: 264–379–543 μm ; n=25

Autozooid opesia length: 289–405–523 μm ; n=25

Autozooid opesia width: 172–241–332 μm ; n=25

Vibraculum length (frontal side): 206–269–338 μm ; n=24

Vibraculum width (frontal side): 190–223–258 μm ; n=24

Vibraculum length (abfrontal side): 348–395–472 μm ; n=11

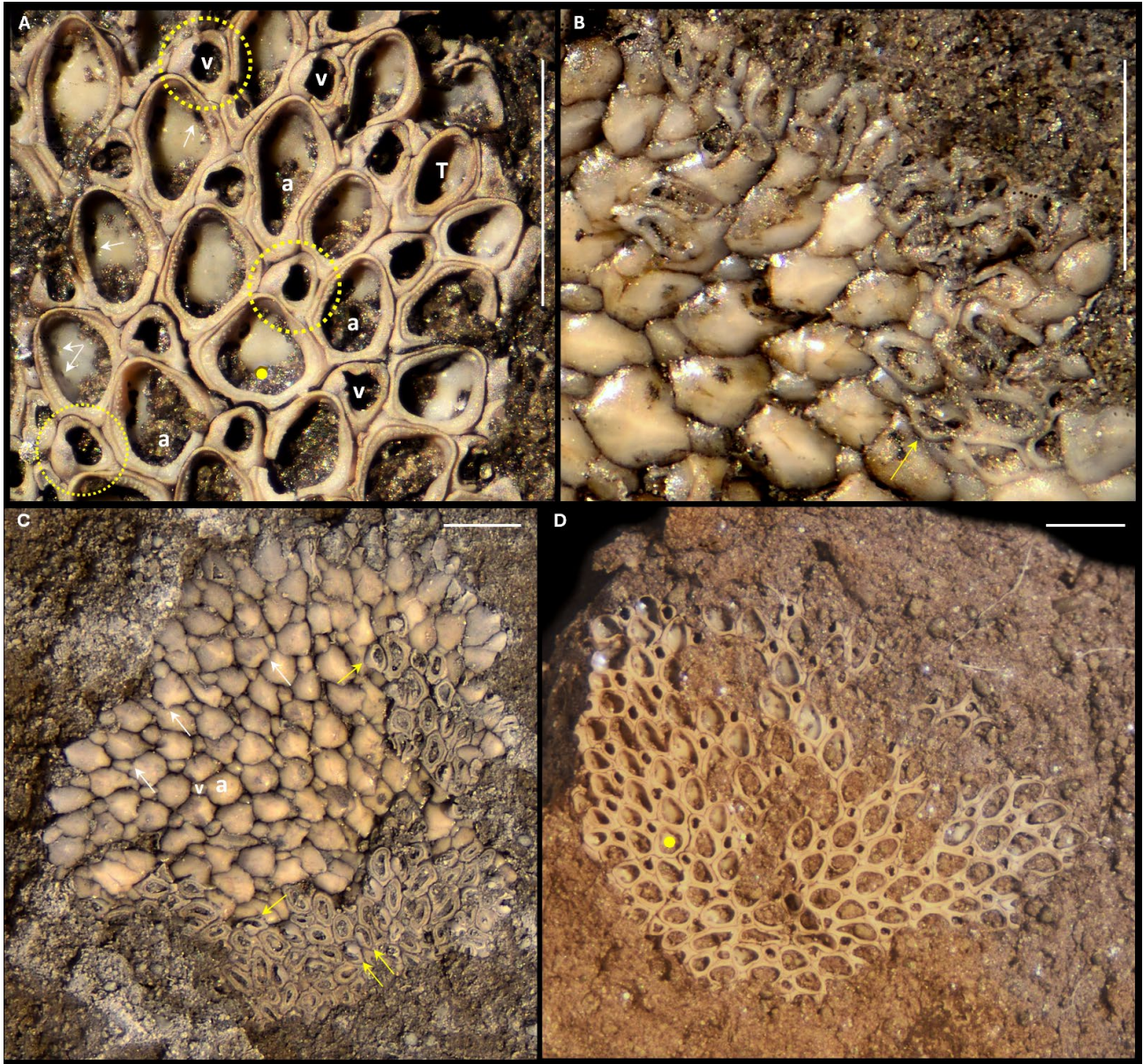


Fig. 15. *Gramipora laxevincta* n. gen., n. sp. from the Gram Clay Pit. **A**, **C–D** Holotype (MSJN 4045); **B** Paratype (MSJN 5460). **A** Frontal zooids (details of **D**) after preparation of the holotype displaying the rather unusual variability in the morphology of both autozooids (a) and vibracula (v); T indicate zooid showing total regeneration. Note the separation cracks variously opening along most zooidal walls. Communication pores visible in some zooids near the base of the lateral walls (indicated by white arrows), with the external aspects of the associated lateral protuberances indicated with white arrows in **C**. **B** Abfrontal view of the paratype displaying the haphazard distribution of the highly irregular kenozooids and variable vibracula (yellow arrow); note the shiny porcelaneous appearance which is typical for this taxon in the Gram Clay Pit. In this specimen only a small part of the abfrontal layer is present along the margin (details of these abfrontal zooids shown in Fig. 16 **A–D**). **C** Abfrontal view of the holotype prior to preparation; only parts of the abfrontal layer of zooids preserved. Note the strong contrast in budding patterns between the two sides of the colony (see Fig. 16). **D** Frontal view of the holotype after preparation; an unusually broad zooid is marked with a yellow dot in both **A** and **D**. Scale bars 1 mm.

Vibraculum width (abfrontal side): 201–237–287 μm ; $n=11$

Remarks. With no modern parallels known to us, the way of life of *Gramipora laxevincta* n. gen., n. sp. does remain open to interpretation; however, with no attachment indicated, and the shape of the colonies combined with the high number of (potentially) powerful vibracula, we suggest that it belongs within the category III Free-living defined above, being somewhat comparable to the two-layer colony architecture in the genus *Biselenaria* as reinterpreted by Håkansson & Zágorský (2020). Like *Biselenaria*, *Gramipora* n. gen. forms bilamellar colonies with significant differences between the (interpreted) frontal and basal sides, and like *Biselenaria* with some delay in the formation of the basal side, with the main function of the basal side suggested to be strengthening the colony. The weak, post-mortem interzooidal cohesion found in *G. laxevincta* n. gen., n. sp. further adds to the similarity in colony architecture with *Biselenaria* but, on current evidence, we consider this just another case of parallel evolution within unre-

lated clades pursuing a free-living mode of life.

With the combination of thin walls and low cohesion between zooids, *G. laxevincta* n. gen., n. sp. has only rarely been noted in washed residue samples, typically as tiny, 'strange' zooidal fragments. Thus, the main reason that any specimens are actually present in the collections is probably the result of the high, silvery reflectance of the basal walls exposed when splitting lumps of sediment along the internal surface separating the two layers in the colony. Note however, that none of the colonies at hand exposes the front of the frontal layer; the images of the frontal features shown in Figs 15 A & D are therefore the result of preparational procedures obliterating the exposed abfrontal side of this colony. Considered category III Free-living (see above).

Distribution. *Gramipora laxevincta* n. gen., n. sp. is only known from the type locality, the Upper Miocene (Tortonian) Gram Formation in the Gram Clay Pit, where it is very rare.

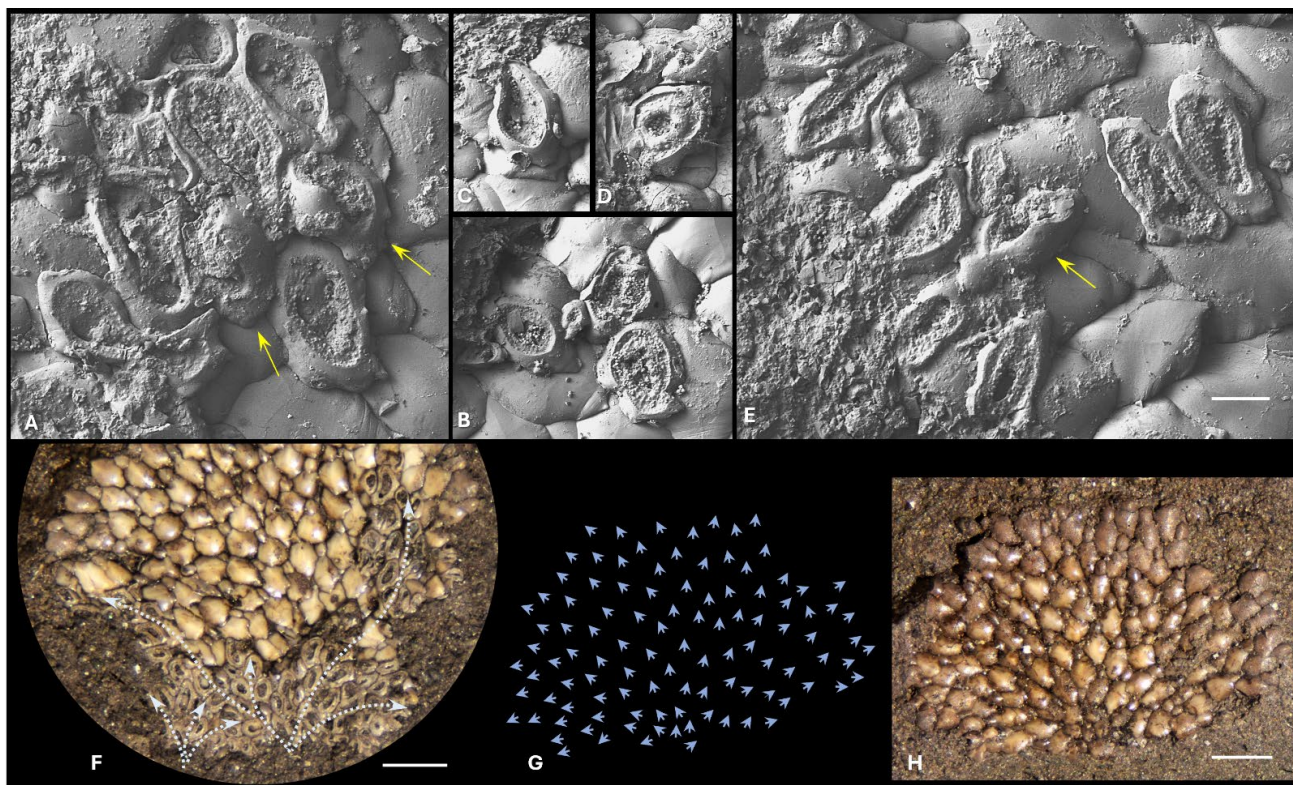


Fig. 16. *Gramipora laxevincta* n. gen., n. sp. **A–E** Details of the abfrontal zooids in the paratype (MSJN 5460, Fig 14 B); some vibracula arrowed. **F** The holotype (MSJN 5461) prior to preparation, showing the difference in budding pattern between the two sides of the colony – the frontal side is characterized by a fairly regular fan shaped budding pattern with a regular distribution between autozooids and vibracula (both seen from their basal side), while the abfrontal side (only partly preserved or developed) is characterized by more irregular fan-shaped budding patterns (blue arrows), with a very uneven proportion between kenozooids and ?vibracula (see also Fig. 15 C). Note that abfrontal budding seems to have originated from two points at the colony margin. **G–H** The basal walls of the frontal zooids in a colony with no abfrontal zooids formed or preserved, clearly displaying the regular fan-shaped budding pattern, accentuated with the blue arrow pattern in G (Paratype; MSN 5461). Scale bars 100 μm (A–E), 1 mm (F–H).

The nomenclatural acts of this paper are registered on ZooBank.

LSID of the new genus *Gramipora*:

Urn:lsid:zoobank.org:act:ECAB34A7-91BA-4758-9DF9-FA861EDDD241

and the LSID of the new species *Gramipora laxevincta*:

Urn:lsid:zoobank.org:act:45407AB4-3D50-47C8-9CD0-13C7B9473448

and the LSID of the new species *Reussirella germinatio*:

Urn:lsid:zoobank.org:act:55101A89-BAC6-4DCC-81A3-269CA940061F

Summary and conclusions

Plasticity and variability in morphology is conspicuous among colonial organisms, particularly when polymorphism is involved. Among bryozoans, the free-living groups provide one of the more spectacular examples, where adaptations towards a distinctive mode of life have led to an amazingly similar colony architecture within multiple clades. Analysis of this kind of convergent morphological evolution within several taxa requires a robust distinction between phylogenetic effects and local selective environmental factors, a distinction that has unfortunately often been blurred. The majority of free-living bryozoans share a suite of strikingly similar characters that have evolved repeatedly over the history of the group. Thus, Håkansson *et al.* (2023) concluded that amongst the free-living bryozoans – a mode of life first appearing in the Late Turonian – only a single clade, the Cupuladriidae [here elevated to subordinal rank as Cupuladriina nov.], may be considered phylogenetically distinct. As a consequence, we are faced with a complex, but largely unfounded, taxonomy based on a series of astonishingly similar adaptations towards the same environmental conditions within several phylogenetically isolated entities.

Similarly, the broad range of variations in mode of life brought together under the broad umbrella ‘free-living’ might be considered to be too loosely constrained, and we have therefore attempted to add a little precision to this part of the overall picture as schematically illustrated in Fig. 4. While the general colony architecture and a negligible substrate size are common to all categories, the presence/absence of vibracula separates the ‘free-lying’ taxa from the ‘free-living’ taxa, with the extent of colonial coelom enabling sub-division of the ‘free-living’ colonies into three groups (I, II and III).

Our main results and conclusions concerning the free-living bryozoan fauna in the Tortonian Gram Formation can be summarized as follows:

- The free-living bryozoan fauna in the Gram

Formation is formally described, comprising four species with an absolute numerical dominance of *Reussirella germinatio* n. sp. (>80%).

- *Cupuladria* sp. aff. *biporosa* and *R. germinatio* n. sp. are classified as ‘Category I free-living’
- ‘*Lunulites*’ *voighti* is classified as ‘Category II free-living’.
- *Gramipora laxevincta* n. gen., n. sp. is considered ‘Category III free-living’.
- Reproduction in *R. germinatio* n. sp. is predominantly clonal, with colony budding most prevalent.
- Reproduction in *C.* sp. aff. *biporosa* is predominantly clonal from regenerated fragments.
- Reproduction in ‘*Lunulites*’ *voighti* is predominantly sexual, with some regeneration from fragments and a few cases of assumed colony budding.
- Reproduction in *G. laxevincta* n. gen., n. sp. is not established – assumed to be sexual through larval metamorphosis, from unknown ovicells or internal brooding?
- The suborder Cupuladriina nov. is described.
- None of the free-living bryozoans encountered from the Gram Clay Pit have been found with a substrate.

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