Handbook of Zoology
Phylum Bryozoa

Handbook of Zoology

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Edited by Thomas Schwaha

DE GRUYTER

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Preface

Despite almost 200 years of research on bryozoans, bryozoology, these animals remain comparatively little studied and many different aspects of their biology are still poorly understood. The mere numbers of several thousand Recent species and even more fossil ones just indicate how diverse bryozoans are, but only still little how these evolved in time and space. Most researchers are easily intrigued by this phylum of colonial animals and easily realize how little we still know about this fascinating group.

In 2017 I was asked to edit the volume ‘Bryozoa’ for the *Handbook of Zoology* series, which I gladly accepted as the series is of high quality and can be used as good reference work for several phyla already. Such an undertaking is, of course, always a challenge. Based on my own background, it focuses on Recent bryozoans and only has one chapter dedicated to fossils. Recently, Bryozoan Paleobiology by Paul Taylor was just published this year and offers an excellent summary on this particular topic.

This book tries to provide an overview of several general aspects of bryozoan biology and a more detailed insight into the various diverse groups. It brings together several authors of various disciplines. I hope my efforts in the compilation of this book will yield students, more experienced researchers and specialists a useful summary.

I’m deeply grateful to Andreas Schmidt-Rhaesa for offering me to edit this volume and also all the authors involved in this long and intense project. Numerous colleagues also provided images or samples used for some of the chapters: Sebastian Decker (Vienna), Paul Taylor (London), Priska Schäfer (Kiel), Piotr Kuklinski (Sopot), Peter Batson (Dunedin), Joachim Scholz (Frankfurt), Matthew Dick (Sapporo), Phil Bock (Melbourne). I’m also indebted to Mary Spencer Jones for letting me dig through the Natural History Museum London collection, which provided several specimens used for some of the chapters.

Thomas Schwaha
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Contents

Appendix

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Thomas Schwaha

1 General introduction

1.1 A brief introduction to bryozoans

Bryozoa is a phylum of colonial aquatic suspension feeders. To date, bryozoans comprise over 6,500 Recent and over 15,000 fossil species (Bock & Gordon 2013, see also http://bryozoa.net/diversity.html). Almost all species live in marine habitats, with comparatively few species living in fresh or brackish waters. Colonies are predominantly sessile, with a few exceptions, which are either creeping or unattached and capable of moving on the substrate as solitary or colonial forms. The bathymetric distribution of bryozoans ranges from the intertidal to the shallow continental shelf and further to the abyssal zone (Ryland 1970). Some of the deepest recordings of bryozoans exceed over 5,000 m depth (d'Hondt & Hayward 1981).

Bryozoans can be found on any kind of substrate and habitats. Most obvious to any common observer, snorkeler, or diver are the large and prominent cheilostome colonies that can be easily observed (Fig. 1.1). For example, these can form large encrusting sheets on stones or other hard substrates or erect branching colonies that form large bushy to tuft-like or frondose to foliate colonies. Bryozoans often show conspicuous bright colorations, e.g. orange, yellow, purple, or many others (Fig. 1.1). Several species are specialized to live in soft to muddy bottoms (e.g. Hirose 2011), in interstitial habitats (Winston & Hakansson 1986, Cook 1988) or are epizooic, living on other animals. Epizooic species are frequently encountered on various parts of crustaceans, pycnogonids, mollusc shells, echinoderms, ascidians, or even vertebrates such as sea turtles or sea snakes (e.g. Ryland 1970, Key *et al.* 1995, 1996a,b).

Coloniality is not a unique feature and shared with some other benthic organisms such as certain cnidarians or ascidians, but unique for bryozoans is that essentially all members of the phylum are colonial. Colonies are modular formations, and each single module or individual is termed zooid in bryozoans. Zooids carry a ciliated tentacle crown or lophophore that is protruded in the open water column and used for suspension feeding (Mukai *et al.* 1997; Fig. 1.2). Besides coloniality, a distinct and unique feature of all bryozoans is a defensive mechanism: the retraction of the lophophore and associated structures (the polypide) into the body wall (or cystid). Body walls are calcified/mineralized in two clades of bryozoans, which evolved independently from uncalcified ancestors (Todd 2000, Ernst & Schäfer 2006). Calcified skeletons also account for the large amount of fossil species, which date back to the Ordovician (see chapter 2).

Colonies are formed by asexually produced reproductive stages or by sexually produced larvae. In the latter case, the founding zooid of a colony is termed ancestrula, which forms after settling and metamorphosis of the larva (Reed 1991). Owing to its smaller size, the ancestrula is often distinguishable in colonies (Fig. 1.3). The ancestrula forms several asexually produced buds that increase the size and spreading of the colony. Naturally, the number and growth direction of these buds depend on the species-specific structure and arrangement of the zooids in the colony. Colony development is referred to as astogeny in bryozoans (Ryland 1970).

Polypides of bryozoans originate by the formation of a bud; even during metamorphosis of larvae, the formation of the polypide is essentially a budding process (cf. Nielsen 1971). The first indications of polypide buds are discernible as thickening of the epidermis of the body wall and a second adjacent peritoneal (mesodermal) layer. Early buds thus consist of an inner (epidermal) budding layer and an outer (peritoneal) budding layer, which subsequently will form a two-layered vesicle protruding into the zooidal cavity (cf. Schwaha & Wood 2011). This vesicle gradually develops into the polypide in ontogeny.

Polypide longevity is rather short and lasts from a week to a month, sometimes also two months (Gordon 1977). After that, it degenerates and the soft tissues are resorbed to form a so-called brown body, a characteristic feature of all bryozoans. With the exception of the Phylactolaemata, polypide recycling is possible in all bryozoans (Taylor & Waeschenbach 2015). In this case, a new polypide can form in the vacant zooid.

Knowledge on bryozoan food is not extensive and most data are empirically provided by food given to artificial cultures (cf. Ryland 1976, see also chapter 6). Ingested food predominantly seems to be phytoplankton or bacteria, which are then digested. Some of the large phylactolaemate species often contain entire rotifers in their stomach.

In contrast, bryozoans are preyed upon by several organisms, most notably by nudibranch mollusks that rasp of colony pieces or pycnogonids that suck out zooids.

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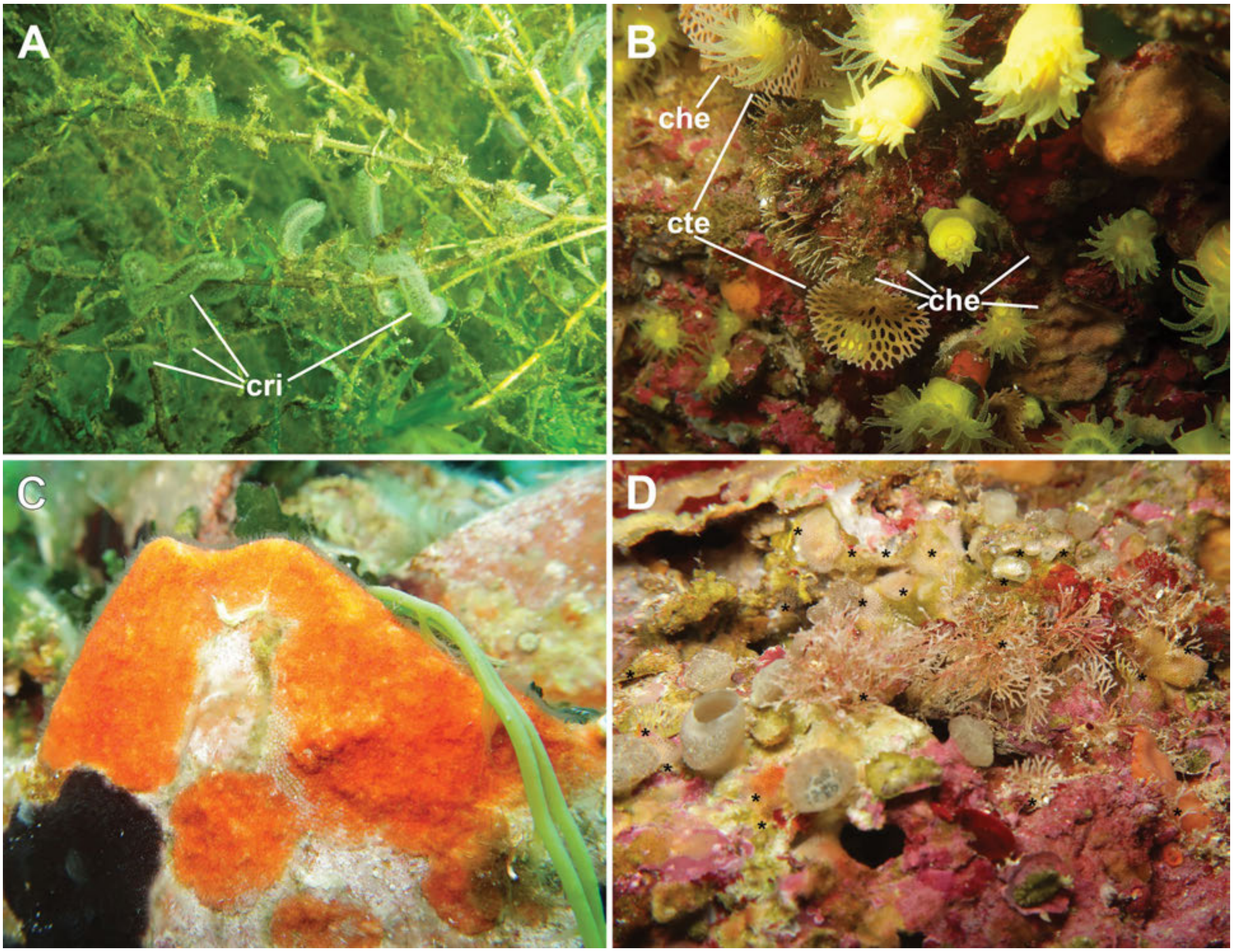

Fig. 1.1: General overview of bryozoans photographed in their natural habitat. (A) Over 25 colonies of the worm-shaped colonies of the phylactolaemate *Cristatella mucedo* in the Neue Donau, Vienna, Austria. Photo provided by Andrew N. Ostrovsky. (B–D) Macrophotographies provided by Sebastian Decker (Vienna) showing some growth forms and amount of bryozoans in benthic communities. Ctenostome and cheilostomes are visible in B, whereas C has two large cheilostome encrusters forming orange to black sheets. Abundant, single colonies in D are displayed by asterisks.

Abbreviations: che – cheilostome, cri – *Cristatella*, cte – ctenostome.

Other predators include fish that chip off colony pieces or echinoderms such as sea urchins that graze the sea floor (McKinney & Jackson 1989).

1.2 Past summaries on bryozoans

Several previous summaries, reviews, and compendia are available on bryozoans that are still a valuable source today: Cori (1941) wrote the original chapter on bryozoans in *Handbuch der Zoologie*. Brien (1960) compiled a similar summary in the French series *Traité de Zoologie* in 1960. Almost at the same time Libbie Hyman's summarizing chapter on bryozoans was published (Hyman 1959). Later, two excellent summaries on bryozoans were provided by Ryland in 1970 and 1976. *Biology of Bryozoans*, a book summarizing several aspects of bryozoan biology in 16 chapters was published in 1977 (Woollacott & Zimmer 1977). Some specific aspects included in this book, such as interzooidal communication (Bobin 1977) or ageing in bryozoans (Gordon 1977), have not advanced since that time and are thus still up to date. A bryozoan volume of the series *Treatise on Invertebrate Paleontology* was released in 1983 (Robinson 1983), which gives a good summary on general features of the main clades. Some years later, McKinney and Jackson (1989) wrote a book on bryozoan evolution, which has some very good information on growth forms and ecological aspects of calcified marine bryozoans.

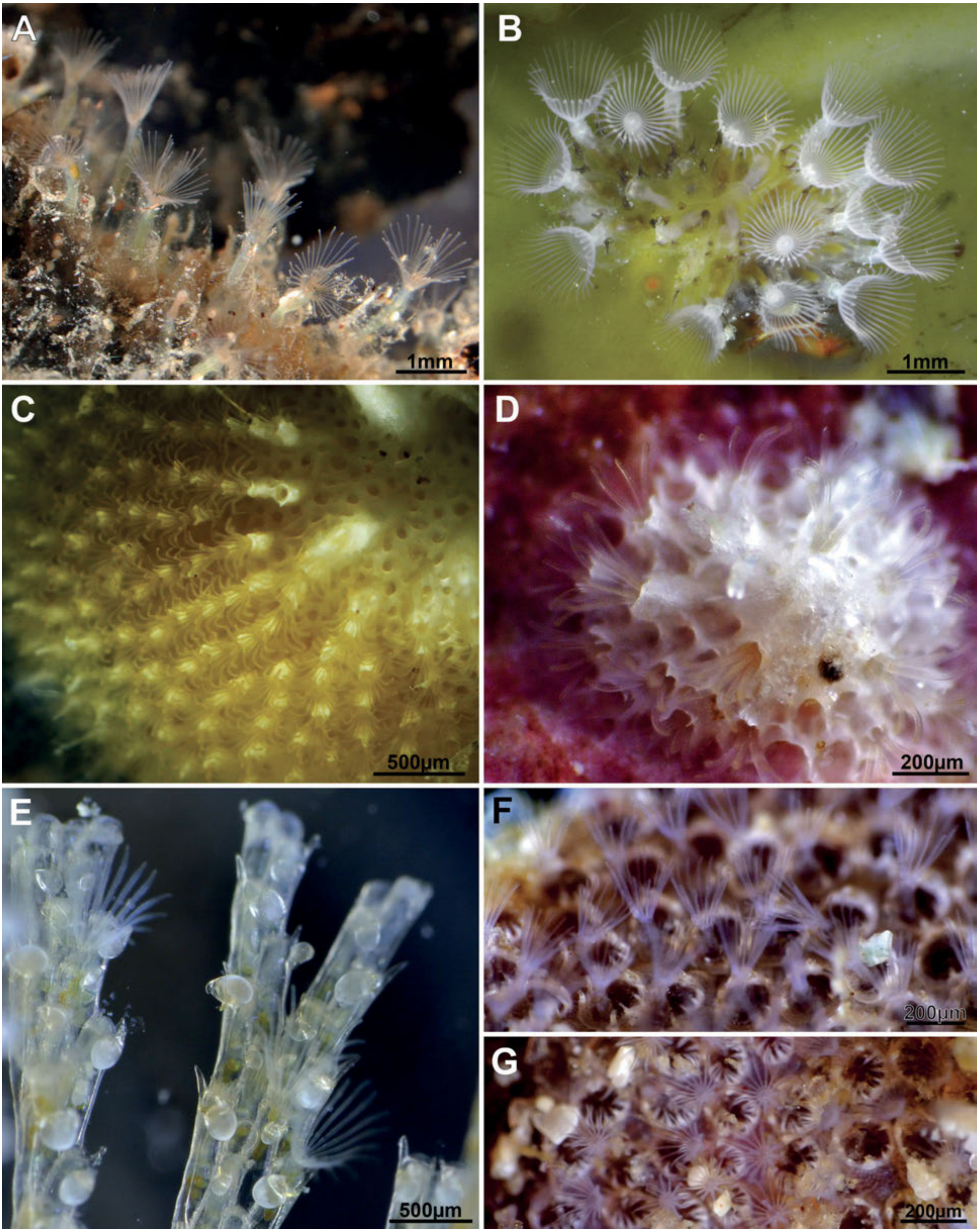

Fig. 1.2: Live bryozoans showing protruded lophophores. (A) Phylactolaemata, *Stephanella hina*. (B) Ctenostomata, *Flustrellidra hispida*. (C) Cyclostomata, *Patinella radiata*. (D) Disporellid cyclostome. (E) Cheilostomata, *Bugula* sp. (F&G) Cheilostomata, *Electra pilosa*.

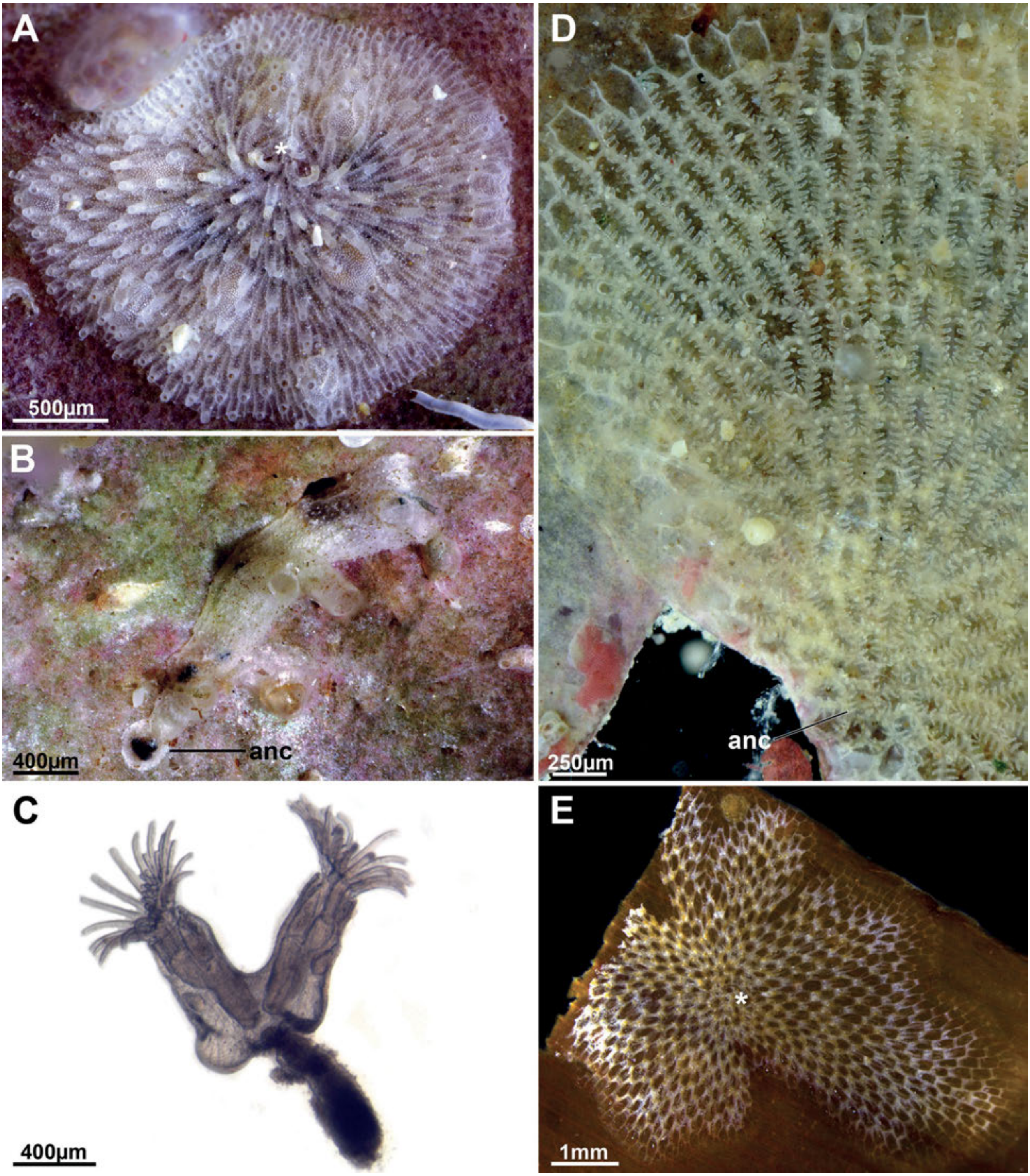

Fig. 1.3: Bryozoan ancestrulae and colonial growth. (A) Tubuliporid cyclostome showing ancestrular area (asterisk) where asexual buds initially formed to build an extensive colony. Note the direction of the tubular skeletal extensions of individual zooids. (B) Tubulipord ancestrula with few zooidal buds formed. (C) Ancestrula of the phylactolaemate *Plumatella fungosa*. (D) Calloporid cheilostome colony showing the small ancestrula in bottom of the image and growing edge on top. (E) Malacostegine cheilostome with ancestrular area (asterisk). Abbreviation: anc – ancestrula.

The first best summary on bryozoan reproduction was provided by Reed (1991) in the book series *Reproduction of marine Invertebrates*. Mukai *et al.* (1997) summarized morphological data of bryozoans in the series *Microscopic Anatomy of Invertebrates*. Reproduction, especially of Gymnolaemata, was recently summarized by Ostrovsky

(2013). Two volumes on Australian Bryozoa, one covering general aspects of bryozoans and the second a systematic overview of Australian taxa, were released in 2018 (Cook *et al.* 2018a).

1.3 Topics in bryozoan research

During over 160 years of bryozoology, one of the main research areas was taxonomy and systematics – naturally with a focus on the diverse skeletal forms. Likewise, paleontology has a long tradition in bryozoan research, and these two disciplines are still the strongest in current times. Scanning electron microscopy, used since the 70s of the last century, opened an entire new perspective and world in bryozoology. It remains the most frequently used tool for imaging specimens and analyzing the skeletal morphology of colonies and zooids. Studies on soft tissues are, in comparison, only few (see chapter 3), and currently, very few research groups work on this topic. Another particular strong emphasis lies in ecological studies that analyze settlement parameters, biotic and abiotic factors affecting bryozoans, growth, substrate preference, inter- and intraspecific competition, interactions with other organisms, etc. The behavior of bryozoans, including feeding, has been studied most diligently by Winston (see chapter 6), reproduction has been studied quite extensively in the past decades by Ostrovsky (2013, see also chapter 4). Embryology was studied only by few researchers (see chapter 5), but an important new study on cleavage pattern and blastomere fates was recently published (Vellutini *et al.* 2017). Mineralogy of bryozoans has been an important field in bryozoan research (recently summarized by Taylor *et al.* 2015) and still remains a very important one today (see below).

Molecular phylogenetic studies have been applied for less than two decades, with some early works appearing in the beginning of the century (e.g. Dick *et al.* 2000, 2003). The first molecular studies on phylactolaemates appeared in 2005 and onwards (e.g. Wood & Lore 2005, Hirose *et al.* 2006, 2008), whereas the most important contributions to the other clades were provided by Waeschenbach *et al.* (2006, 2009, 2012, 2015).

Bryozoans have little to no economic significance. Neither do they deliver any potential food source nor are they a threat to humans. They are an important part of benthic ecosystems, sometimes forming the most abundant group in certain areas. They are generally easily overlooked or not recognized as animals or mistaken, e.g. as corals. The most important human-related topics were recently summarized in volume 1 of Australian bryozoans (Cook *et al.* 2018a): 1) Bryozoans as biofoulers (Gordon 2018). Many species frequently settle on many anthropogenic substrates such as ship hulls, which can increase drag and thus fuel consumption and economic costs. In addition, biofouled objects are vectors for bryozoan dispersal, which results in increasing number of invasive species and subsequent changes in natural species distributions and compositions. 2) Bryozoans as source of pharmacologically important substances (Prinsep 2018). Several natural compounds isolated from bryozoans have the potential for pharmacological applications. The earliest and best studied compounds of bryozoans are bryostatins, first isolated in the 80s of the 20th century (Pettit *et al.* 1982). Clinical trials have shown anticancer effects of bryostatins, but they are also being explored for treating HIV/AIDS or Alzheimer's disease. 3) Bryozoans and ocean acidification (Smith 2018). Ocean acidification and climate change is a fact, which results in lowered pH and less available carbonate ions. This poses a serious threat on organisms with calcified skeletons such as bryozoans or corals. Experimental approaches on bryozoans aid in monitoring the impact and effects of ocean acidification.

Severe gaps are still present in numerous fields of bryozoology: Sensory systems, communication, and colonial integration is a field that is almost not studied at all. Based on descriptive morphological studies, few sensory organs were detected in the tentacles. Modern techniques and functional approaches have not been conducted, however. Likewise, the colonial nervous system and metabolic exchange within a colony remain an open field. A third totally unexplored topic is physiology of bryozoans, with only few experimental observations (Ryland 1970).

1.4 Terminological issues

Bryozoans were first regarded as Zoophytes by early naturalists, which grouped several "plant-like" animals such cnidarians or ascidians together with bryozoans. The first specific taxonomic name bestowed upon bryozoans was "Polyzoa" and dates back to Thompson (1830), who first recognized the distinctiveness of bryozoans from other groups of zoophytes. Almost simultaneously, the German naturalist Christian Gottfried Ehrenberg created the name Bryozoa for the same group of animals in 1831. Several decades later, Nitsche divided this clade into "Entoprocta" (Kamptozoa) and "Ectoprocta" (Bryozoa) based on the position of the anus in respect to the tentacle crown of these phyla (Nitsche 1869).

Polyzoa was the most common used name for bryozoans in Britain until the 60s of the 20th century (e.g.

Ryland 1962). Bryozoa is the most commonly used name nowadays and the valid name accepted by the International Bryozoology Association, which was founded in 1965 (Cheetham 2002, see also Cook *et al.* 2018b). Other names should thus be disregarded and not be used in the future. Polyzoa has also been used for uniting Kamptozoa, Cycliophora, and Bryozoa as a related clade (Hejnol *et al.* 2009), but confuses as it is an old synonym for bryozoans. The term Ectoprocta is particularly meaningless as a condition, with the anus being located outside the food collecting organ is the more usual situation found in tentaculated suspension feeders; i.e. a phoronid or a cycliophoran is also ectoproct. In contrast, the entoproct condition of kamptozoans is a characteristic feature of this phylum.

1.5 Phylogeny and systematics of bryozoans

1.5.1 Relationship of bryozoans to other phyla

1.5.1.1 The morphological perspective

The phylogenetic placement of bryozoans remains quite uncertain. Traditional scenarios unite bryozoans with phoronids and brachiopods into a clade called Lophophorata (Hyman 1959). The latter clade or concept is based on similarities in the morphology of the tentacle crown or lophophore. Lophophorates are coelomate and the lophophore and each tentacle is supplied with a peritoneal lining, either as a separate coelomic compartment as found in phoronids and some brachiopods or is continuous with the lining of the remaining body cavity as in most bryozoans. Tentacle amount varies in the different phyla: in phoronids, it varies from 28 to several hundred with a maximum of about 1,500 (Emig 1982); brachiopods usually start with few tentacles in ontogeny that multiply in later stages and also can reach several hundred. Phylactolaemate bryozoans vary from 20 to 100 tentacles, whereas the predominantly marine ones range from 8 to 30.

Lophophorates use upstream-feeding or so-called ciliary sieving (see Riisgard *et al.* 2010) for particle capture. The basic feeding mechanism is very similar, and also tentacle ciliation for creating feeding currents is identical. All lophophorates show lateral, latero-frontal, and frontal cilia used for suspension feeding (Riisgard *et al.* 2010). It has been previously emphasized that tentacle ciliation is monociliated in phoronids and brachiopods versus multiciliated in bryozoans and that this difference might be of phylogenetic significance. In fact, this condition does not seem to be of phylogenetic value as multiciliation of bryozoans is a mere adaptation to smaller size and fewer cells in tentacle cross-section compared to phoronids or brachiopods. The latter two phyla show 40–80 monociliated cells in cross-sectioned tentacles, whereas bryozoans have 9–12 multiciliary ones (cf. Schwaha *et al.* 2020). Consequently, multiciliation is a necessity for creating proper feeding currents and thus a functional adaptation. In addition to an identical ciliation pattern, tentacle muscles consist of two longitudinal muscle bands in each tentacle in all three phyla (cf. Schwaha & Wanninger 2012).

The general body organization of bryozoans is very similar to phoronids; brachiopods are characterized by two mineralized shells that superficially resemble those of bivalve molluscs. A trimeric body organization as previously suggested (e.g. Hyman 1959) is particularly not present in bryozoans and should conceptually be abandoned in these phyla. The digestive system is u-shaped in all lophophorates (when complete in brachiopods). In contrast to bryozoans, brachiopods and phoronids share a blood vascular system and metanephridial system. As coelomate organisms, the latter two are strongly interconnected systems with excretory processes occurring via ultrafiltration at podocytes lining the blood vessels, although metanephridial systems are also capable of removing excretory coelomocytes/phagocytes. Because of their small zooidal size, these two organ systems apparently became redundant and bryozoans lack a distinct blood vascular and nephridial system.

Recently, new data of the nervous system of bryozoans and other lophophorates identified significant similarities in the general organization and tentacle innervation in the three lophophorate phyla, which was subsequently used as argument for lophophorate monophyly (cf. Temereva 2017). Bryozoans show a significant difference, however, in regard to the location of the nervous system, which is subepithelial in contrast to a basi-/intraepithelial organization in phoronids and brachiopods. But again – maybe a consequence of miniaturization?

An alternative, old hypothesis was that bryozoans could be related to Kamptozoa (e.g. Nitsche 1869, Nielsen 1971). However, there is not any morphological support for such a relationship since they differ e.g. in their general body organization (acoelomate vs. coelomate), feeding mechanism (downstream vs. upstream, incl. different tentacle ciliation and muscles) and solitary vs. colonial (colonial kamptozoans are later-branching and the solitary loxosomatids are ancestral). In fact, there are merely some similarities in larval morphology and metamorphosis of some species (e.g. Nielsen 2012). Metamorphosis in bryozoans is generally regarded as "catastrophic"; i.e. most organ systems of the larva degenerate and polypides are actually formed de novo by a budding process in the settled ancestrula (Mukai *et al.* 1997). Kamptozoan metamorphosis in the early branching loxosomatids involves mostly elongation of the anterior-posterior axis to form the stalk, reduction of the apical organ and foot and reorganization of the oral side of the larva to form the tentacle crown (cf. Nielsen 1971, 2012).

Several molecular phylogenies reconstruct a closer relationship of phoronids and brachiopods with other phyla, such as nemerteans (e.g. Nesnidal *et al.* 2010) or annelids (Kocot *et al.* 2017). Irrespective of the monophyletic state of the Lophophorata, it remains difficult to link the three phyla to other lophotrochozoans, especially in regard to body plan evolution. Back in the 20th century, a close association of lophophorates to deuterostomes, particularly to the morphologically similar pterobranchs, was taken into account (e.g. Salvini-Plawen 1982). However, since the emergence of molecular phylogenetic analyses, it became clear that these phyla are lophotrochozoans and not related to any deuterostomes.

1.5.1.2 The molecular perspective

Whereas morphologically the lophophorates are currently the most feasible concept, molecular phylogenetic analyses were hardly able to reconstruct lophophorates. A close relationship of the phoronids and brachiopods is supported in most phylogenies (cf. Kocot 2016), but bryozoans generally drop out. Molecular analyses placed bryozoans at various positions clustering with different lophotrochozoan phyla (e.g. Hausdorf *et al.* 2007, 2010, Helmkampf *et al.* 2008, Hejnol *et al.* 2009, Mallatt *et al.* 2012), but none of the placements seemed to repeatedly persist. Only recent molecular phylogenetic studies were able to reconstruct lophophorates (Nesnidal *et al.* 2013, 2014, Marlétaz *et al.* 2019).

Most molecular phylogenies were based on fast-evolving mitochondrial genes or nuclear ribosomal genes. More robust phylogenetic reconstructions involving phylogenomic data are just starting to emerge (Kocot *et al.* 2017). Currently, however, phylogenomic data on bryozoans is only available for a few cheilostomes, a group of late branching bryozoans. In the near future, new phylogenomic data from other, more early-branching groups will probably yield new trees that will shed new light on the phylogenetic position of bryozoans.

1.5.2 Internal systematics and phylogeny of bryozoans

Bryozoans are divided into three distinct clades: Phylactolaemata, Stenolaemata, and Gymnolaemata. Phylactolaemata is a small group of sole freshwater inhabitants characterized by a horseshoe-shaped lophophore and dormant buds called statoblasts. Less than 100 species have been described in this clade. Stenolaemata is one of the taxa that evolved calcified cystid walls and comprises over 11,000 species, including Recent and fossil ones. With the exception of the Cyclostomata, all the other taxa of stenolaemates were almost exclusively present in the Paleozoic and are now extinct (see chapter 2). Approximately 700 Recent species of Cyclostomata are described. Gymnolaemata is the dominant group that contains the paraphyletic "Ctenostomata" and the monophyletic Cheilostomata. Fossil and Recent species included, over 11,000 species have been described, but in contrast to stenolaemates, over 5,800 Recent species of gymnolaemates are currently described. Ctenostomes are a small group of ~350 species, whereas the bulk of gymnolaemates are cheilostomes (http://bryozoa.net/diversity.html). The latter is the second clade that evolved calcified cystid walls, hence their large fossil record.

Originally the term Gymnolaemata created by Allman (1856) included stenolaemates and gymnolaemates, but it became accustomed that Gymnolaemata is restricted to the clade of Cteno- and Cheilostomata. An outdated name for the current Gymnolaemata was Eurystomata (Marcus 1938), which, however, was only used by very few authors and has not been applied to any larger work on bryozoans. Likewise, new descriptions of cteno- and cheilostomes in the past decades almost exclusively used the name Gymnolaemata (see also Schwaha *et al.* 2020).

Addressing some of the subgroups of the large clades often has two distinct spellings that can be found dispersed in publications: cyclostome vs. cyclostomate, ctenostome vs. ctenostomate, cheilostome vs. cheilostomate.

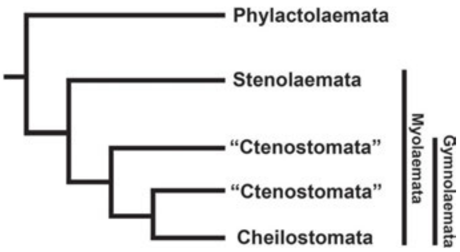

Fig. 1.4: Phylogeny of the major bryozoan clades, after Schwaha *et al.* (2020), general topology redrawn from Taylor & Waeschenbach (2015).

The former version of these spellings is the more common and nowadays used term.

The interrelationship of the three large clades is well supported, with Phylactolaemata being the sister-group of a clade of Stenolaemata and Gymnolaemata. The latter two are sister-groups (Waeschenbach *et al.* 2012, Taylor & Waeschenbach 2015; Fig. 1.4). Recently, the name "Myolaemata" was proposed for the clade comprising Stenolaemata and Gymnolaemata. Distinct characters of this taxon are: 1) myoepithelial pharynx with triradiate lumen used for suction feeding, 2) circular lophophore (even though this could also be a plesiomorphic character), 3) pylorus with cilia and specific mode of digestion (see chapter 3), 4) lophophoral coelomic cavity in the form of a simple ring canal (see chapter 3), 5) anal growth direction (opposed to the oral one of Phylactolaemata, cf. Jebram 1973), 6) zooidal polymorphism, and 7) polypide recycling (Schwaha *et al.* 2020).

1.6 Outline of this book

The main aim of this book is to give a thorough insight in the phylum Bryozoa. Chapters 2–6 are general, comparative chapters on bryozoan biology that have not been recently summarized. Several topics such a phylogeny or biomineralization have thus not been included into this volume as they are subject to change in the near future in case of phylogeny or have been recently summarized (Taylor *et al.* 2015).

Chapter 2 is a short introduction into bryozoan paleontology, because understanding bryozoan evolution requires a necessary background into this old phylum. The remaining book is focused on Recent Bryozoa and chapters 3–5 deal with morphology (predominantly of soft-tissues), reproduction and development. Chapter 6 deals with the behavior of bryozoans, whereas the remaining chapters 7–11 introduce the systematic groups.

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Andrej Ernst

2 Fossil record and evolution of Bryozoa

2.1 Introduction

The Phylum Bryozoa has a long and extensive fossil record (Fig. 2.1) counting ca 15,000 fossil species (Horowitz & Pachut 2000, Gordon *et al.* 2009). Their remnants are found in the majority of marine sediments of the Phanerozoic. They played important roles in various communities and were significant contributors to carbonate sedimentation and reefs. Bryozoans belong to the few phyla of which no fossilized representatives are known during the Cambrian explosion. They were repeatedly reported from the strata prior to the Ordovician, but which appeared to be findings of non-bryozoan nature (see reviews in Ross 1964, 1985, Taylor & Ernst 2004). Most recently, Landing *et al.* (2010, 2015) described fossils from the lower Tiñu Formation of the Upper Cambrian of Mexico, which they claimed were bryozoans. However, their assignment to bryozoans appears doubtful (Taylor *et al.* 2013). Confirmed records of earliest bryozoans are known from the Early Ordovician (Tremadoc) of China (Ma *et al.* 2015). Calcified bryozoans appeared in the Early Ordovician of China and diversified very fast (Hu & Spjeldnaes 1991, Xia *et al.* 2007, Ma *et al.* 2015). The majority of Palaeozoic bryozoan faunas were distributed in tropics, whereas the post-Palaeozoic bryozoans tend to occur in temperate or even cool-water environments (Taylor & Alison 1998, Taylor & Sendino 2010).

The majority of Palaeozoic bryozoans belong to the Class Stenolaemata, although gymnolaemates (burrowing Ctenostomata) are also known throughout the Palaeozoic. Ma *et al.* (2014) introduced the suborder Palaeostomata for the free-walled (i.e. without calcified frontal walls, in contrast to those with calcified frontal walls and therefore called fixed-walled; see chapter 8) “Palaeozoic” stenolaemates including the orders Cystoporata, Esthonioporata, Trepostomata, Cryptostomata, Fenestrata, and the group of Timanodictyina, whose position is still under discussion. The authors also erected the Order Esthonioporata, elevating its status from suborder to order level.

All the Palaeostomata except Timanodictyina appeared and diversified during the Great Ordovician Biodiversification Event (Taylor & Ernst 2004, Ernst 2018). The majority of palaeostomates (as well as cyclostomes) possessed a calcitic skeleton with a stable low-Mg content, allowing excellent preservation of fossil bryozoans. The representatives of the Order Esthonioporata Ma *et al.*, 2014 may have possessed high-Mg calcite in their skeleton (Taylor & Wilson 1999).

The sister group of Palaeostomata, the Order Cyclostomata, appeared in the Early Ordovician, too. They are also calcified bryozoans, but in contrast to Palaeostomata, cyclostomes survived the end-Palaeozoic and Triassic crises and radiated during the Mesozoic (Schäfer & Fois-Erikson 1987, Taylor & Ernst 2008). This group includes some few hundreds of species in the modern seas and gives clues for understanding the morphology of the Palaeostomata, which are not represented in modern faunas (Boardman 1971, Boardman *et al.* 1992, Ernst & Schäfer 2006).

The gymnolaemate Order Ctenostomata appeared in the Ordovician, too. Borings belonging to endolithic ctenostomes were discovered in the Early Ordovician of Spain and Russia (Mayoral 1991, Mayoral *et al.* 1994, Taylor & Rozhnov 1996). Boring ctenostomes are known from Ordovician to present (e.g. Pohowsky 1974, 1978, Viskova & Pakhnevich 2010). Otherwise, the fossil record of ctenostomes is rather scarce. Normally, uncalcified ctenostome bryozoans (as other soft-bodied invertebrates) have little chance for preservation. Due to organic overgrowth of unmineralized organisms, their natural molds may be formed. This process is called bioimmuration (Vialov 1961). Such fossils usually appear as negative relief and often show exceptional details of the surface of the bioimmured organism (Taylor 1990b). Bioimmured ctenostomes are mainly known from the Jurassic and Cretaceous (Voigt 1977, Taylor 1978, 1990a,b, Todd 1994, Todd *et al.* 1997).

Cheilostome bryozoans derived most certainly from ctenostome-grade gymnolaemates during the Jurassic (Pohowsky 1973, Taylor 1981a, 1986, 1994). This group diversified during the Cretaceous and especially in the post-Cretaceous time until the present (Taylor & Larwood 1990, Lidgard *et al.* 1993, Jablonski *et al.* 1997, Sepkoski *et al.* 2000).

Phylactolaemata are the group of entirely freshwater bryozoans, which are regarded as earliest branch of all bryozoans (e.g. Fuchs *et al.* 2009, Waeschenbach *et al.* 2012, Taylor & Waeschenbach 2015). Phylactolaemates are not calcified; their bodies are covered by gelatinous or chitinous material (e.g. Ryland 1970, Wöss 2005, see also chapter 7); therefore their preservation potential is very low. However, phylactolaemates produce dormant stages called statoblasts that possess chitinous shells. Fossil

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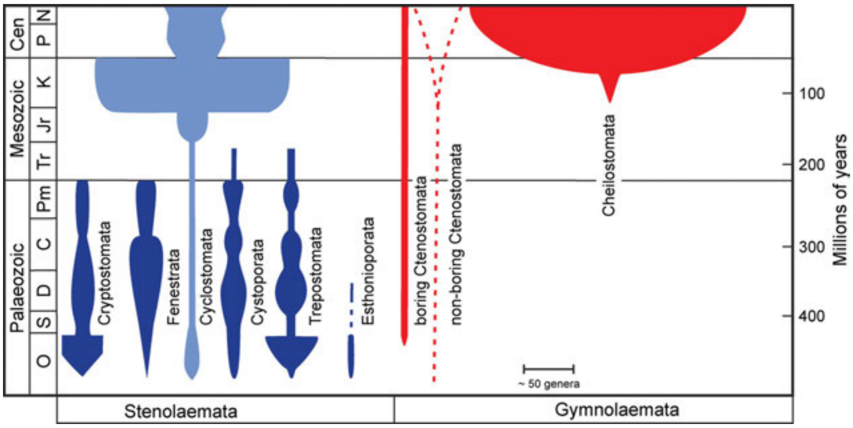


Fig. 2.1: Ranges and approximate generic diversity of higher taxa of stenolaemates (left, blue) and gymnolaemates (right, red). Dark blue: Palaeostomata (modified after McKinney & Jackson 1989).

statoblasts are known from few records, with the oldest from the Permian (Vinogradov 1996) of Russia and Triassic of South Africa (Kohring & Hörnig 2002). The reason for the missing earlier records might be that statoblasts represent an adaptation of living in freshwater, whereas the earliest phylactolaemate ancestors were supposedly marine and therefore did not produce statoblasts (Taylor & Waeschenbach 2015).

The present chapter gives an outline of the evolutionary history of bryozoans and their fossil record, as well as some detailed insights in the morphology and general taxonomy of Palaeostomata.

2.2 Methods for studying fossil bryozoans

In contrast to cyclostomes and cheilostomes, the Palaeostomata display a great variety of internal characters that cannot be studied externally. Therefore, the most important method of their study is the use of oriented thin sections. Three orientations are generally needed: tangential (showing the character of autozooecial apertures, heteromorphs, and skeletal structures such as styles), longitudinal, and transversal, which reveal the shape of autozooecia and their internal structures (Figs. 2.2 and 2.5 A–C). Alternatively, the methods of acetate peels can be used for studying the internal morphology of palaeostomates (Boardman & Utgaard 1964). This method works on well preserved carbonate material and is not appropriate for silicified or dolomitized rocks. The idea of this method is based on the solution of carbonate by a weak acid with creation of a relief, which can be replicated by plastic softened by acetone.

For the preparation of peels, the specimen is cut and polished as for the preparation of thin sections. Then its surface is put in weak acid (hydrochloric or formic in 1%–5% solution) for 20–40 seconds. After washing and drying, the etched surface is doused by acetone and covered by a piece of acetone-soluble plastic. After evaporation of the acetone, the plastic is peeled (the name!) from the sample, with the relief replicated on its surface. There are advantages and disadvantages of both methods. Thin sections deliver highest quality, but they are fragile and their preparation destroys the sample or at least a large portion of it. Acetate peels are worse in quality, they often curve, and the high relief prevents production of high-magnification photographs. However, the samples are less affected by the preparation of peels (important in case of museum material), and it is possible to produce new peels from them. In fact, this method can be used to produce serial peels in distances of few microns and to arrange these images to a three-dimensional model using visualization software.

External characters such as micro- and ultrastructure of autozooecial walls can be studied using scanning electron microscopy (SEM) (e.g. Taylor & Jones 1996). Useful are also analytic methods such as Raman spectroscopy (Taylor *et al.* 2008, Di Martino *et al.* 2016) or x-ray diffraction analysis (Fortunato *et al.* 2012). Post-Palaeozoic bryozoans (cyclostomes and cheilostomes) are studied almost exclusively by use of the SEM.

2.3 Development and evolution of bryozoans in the Palaeozoic

Bryozoans of the Palaeozoic age are represented by the classes Gymnolaemata and Stenolaemata. The records of Palaeozoic Gymnolaemata are exclusively boring ctenostomes known since the Early Ordovician. Several genera were described from the Palaeozoic: *Ropalonaria* Ulrich, 1879 (Fig. 2.10 D), *Vinella* Ulrich, 1890, *Condranema* Bassler, 1952, *Eliasopora* Bassler, 1952, *Casteropora* Pohowsky, 1978, *Bascomella* Morningstar, 1922, and *Orbignyopora* Pohowsky, 1978. The genera *Allonema*

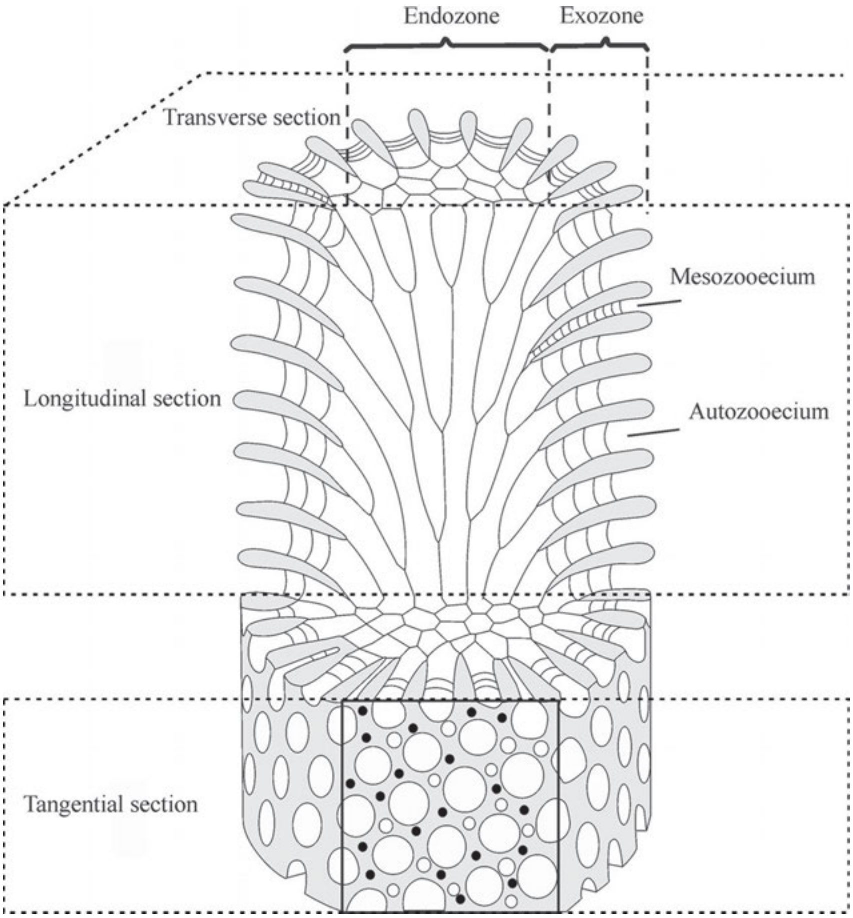


Fig. 2.2: Cutaway diagram of a segment of a branched colony of the Palaeostomata showing orientations of standard sections used for study (modified after Boardman 1984).

Ulrich & Bassler, 1904 and *Ascodictyon* Nicholson & Etheridge, 1877 were originally described as ctenostome bryozoans. However, their closer study showed that they have no apertures for lophophore protrusion and apparently represent encrusting bases of unknown articulated organisms (Wilson & Taylor 2014). Jarochowska and Munnecke (2014) suggested that *Allonema* Ulrich & Bassler, 1904 is a senior synonym for *Wetheredella* Wood, 1948, an encrusting problematicum widely distributed in the Palaeozoic.

The Class Stenolaemata Borg, 1926 comprises bryozoans with complete interior vertical walls producing tubular, conical, or sac-shaped zooecia (Boardman 1983). The modern classification favors the division of Stenolaemata in two superorders: Palaeostomata and Tubuliporata. The latter comprises the Order Cyclostomata, which ranges from the Early Ordovician to the Recent. This clade is regarded as monophyletic (e.g. Brood 1973, Viskova 1992, Taylor & Waeschenbach 2015). Alternative hypotheses suggest the polyphyletic origin of cyclostomes (Boardman 1984, Ernst & Schäfer 2006).

The Palaeostomata derived apparently from tubuliporate cyclostomes (= Palaeotubuliporina Brood, 1973). In contrast to cyclostomes, the Palaeostomata are exclusively free-walled, lacking calcified exterior walls (e.g. Boardman 1971, 1998, Boardman & Cheetham 1973). In contrast, cyclostomes may also possess a so-called fixed-walled skeletal organization having a calcified exterior wall (see chapter 8, this volume). Curiously, some Early Palaeozoic ceramoporids (Order Cystoporata) possess communication pores in their internal walls, a structure known from cyclostomes with calcified exterior walls (Fig. 2.9 E). The communication pores are necessary because exterior walls prevent fluid exchange and communication between autozooecia. In free-walled stenolaemates communication between zooecia occurs above the interior walls. Communication pores in cystoporates apparently evolved independently from those of the post-Palaeozoic cyclostomes (e.g. Boardman 1998).

The Superorder Palaeostomata Ma *et al.*, 2014 comprises fewer than 600 genera distributed from the Early Ordovician to the Late Triassic and includes the orders Cystoporata, Esthonioporata, Trepostomata, Cryptostomata, Fenestrata, and the group of Timanodictyina. The latter is recognized as a separate order by Gorjunova (1992, 1994), who postulated their origin from cystoporate bryozoans. Alternatively, timanodictyines are regarded being related to cryptostomes (Blake 1983a). The Palaeostomata are indeed the dominant bryozoan group in the Palaeozoic, representing more than 95% of total generic composition at that time.

2.3.1 Morphology of the Palaeostomata

2.3.1.1 Definition of Palaeostomata

Ma *et al.* (2014) separated the Palaeozoic orders of free-walled stenolaemates into the Superorder Palaeostomata. They proposed the following definition:

> Hemispherical, massive, ramose, frondose, reticulate or encrusting, occasionally articulated colonies. Maculae evenly spaced, present on colony surfaces of broadly multiserial taxa, monticulate, flat or depressed. All skeletal walls above basal exterior colony wall interior in origin, calcified frontal exterior walls lacking. Autozooecia short to long, polygonal to rounded in cross-section, apertures sometimes with lunaria. Walls usually with a lamellar microstructure, occasionally granular, typically non-porous; pseudopores wanting. Basal diaphragms common to absent; hemiphragms, ring septa and cystiphragms present or absent. Styles often present. Mesozooecia and exilazooecia commonly present. Apparent brooding structures in some groups present. (Ordovician – Triassic)

Palaeostomates differ from cyclostomes in some important morphological characters. The key feature of the Superorder Palaeostomata is the absence of calcified exterior walls above the basal lamina (Borg 1926, Boardman 1983). Furthermore, palaeostomates possess various kinds of intrazooecial partitions (basal diaphragms, cystiphragms, hemiphragms, etc.), which are rare or absent in cyclostomes (Boardman 2001).

2.3.1.2 Morphology of Palaeostomata

Palaeostomata are often known as “stony bryozoans” because of their heavy calcification. The majority of palaeostomates possess a well-developed external calcitic skeleton. In contrast to other Palaeozoic colonial animals such as tabulate and rugose corals or stromatoporoids, bryozoan colonies did not reach large sizes. The largest colonies of Palaeostomata are known from the Trepostomata and are mostly restricted to the Ordovician or Permian (e.g. Ross & Ross 1962, Håkansson & Madsen 1991, Key *et al.* 2005). Massive trepostome bryozoans from the Ordovician of Estonia reach sizes of 30 cm in diameter and 10 cm in height. Branched trepostomes from the Ordovician of the USA reached heights of up to 66 cm (Cuffey & Fine 2005). Late Palaeozoic fenestrates are known up to 30 cm in height (Wood *et al.* 1996). However, the majority of Palaeozoic bryozoans are smaller, having sizes of few centimeters or even smaller.

As colonial (modular) organisms, bryozoans produce colonies by proliferation of new zooids and extrazooidal tissue (e.g. Ryland 1981, McKinney & Jackson 1989). The form of the colony (or growth form, growth habit) is determined by the position of new zooids in respect to those formed earlier including their shape, orientation, and rate of addition in each portion of the colony. Bryozoans are able to develop colonies of various forms that are of immense adaptive importance. Therefore, a significant number of attempts to use colony forms for palaeoecological studies, especially as indicators for depth and water energy, were undertaken (e.g. Stach 1936, Nelson *et al.* 1988, Hageman *et al.* 1997, 1998, Amini *et al.* 2004). In fact, observations on Mediterranean bryozoans from different habitats revealed distinct plasticity in colony forms according to the habitat (Harmelin 1973, 1976).

Simplest colony forms are encrusting and represented by runners (Fig. 2.9 D) and sheets (Figs. 2.9 E and 2.14 D). The latter may be a single layer (Fig. 2.13 K) or multilayered (Figs. 2.4 B and 2.12 F). Massive colonies are especially common among early taxa of Esthonioporata, Cystoporata, and Trepostomata (Figs. 2.4 A, 2.9 G, and 2.10 I). Erect branched colonies occur among these three groups (especially Trepostomata) but are also typical for rhabdomesine cryptostomes (Figs. 2.5 A–C, N, O, 2.6 D–M, 2.10 B–C, 2.11 G–K, 2.12 G–J, 2.13 C–E, and 2.14 A–C). Many cyclostomes and cheilostomes develop erect branched colonies, too, which can be rigid or flexibly connected (Fig. 2.14 F, G). Among erect (arborescent) colonies, unilaminate and bilaminate (Figs. 2.4 F–H, 2.6 A–C, 2.9 J, 2.10 J, 2.11 D–F, and 2.13 B, M), or even trilaminate (Fig. 2.4 E), forms can be distinguished. Unilaminate erect colonies can be of various shape and are especially diverse in Palaeozoic fenestrates (Figs. 2.7 A–I, 2.9 I, 2.10 J, 2.11 B, 2.12 A, K–M, and 2.13 A, G–I).

A special character of the colony surface are so-called maculae, areas of the colony surface with different morphology. They usually consist of larger zooecia (e.g. macrozooecia in trepostomes) or smaller polymorphs like mesozooecia and exilazooecia, as well as vesicular skeleton or extrazooidal skeleton. Many maculae are elevated above the colony surface and in that case are called monticulae (Fig. 2.4 I). Others are rather depressed or positioned at the level of the colony surface. Maculae are usually rounded or oval in shape, but also stellate ones are common, as for example in the cystoporate genus *Constellaria* or in the Devonian genus *Stellatoides* (Ernst *et al.* 2014), or in large trepostomes from the Permian of

Greenland (Key *et al.* 2002, 2011). The major interpretation of maculae is their function in the regulation of feeding currents (see section 2.6.1.2). Maculae are common in the Palaeostomata as well as in branched post-Palaeozoic Cyclostomata.

Palaeostomata mainly had low-Mg calcitic skeletons (Smith *et al.* 2006), whereas esthoniporines seem to have had high-Mg calcite (Taylor & Wilson 1999, Ma *et al.* 2014). The skeleton in Palaeostomates is usually laminated, normally in the exozone, or rather hyaline, amorphic in the endozone or in the cores of styles (Tavener-Smith 1969a,b, Armstrong 1970, Blake 1973). In their appearance, the laminated internal walls may be merged, without visible zooecial boundary, or serrated, with distinct boundary between adjacent zooecia (Boardman & Buttler 2005). Fenestrate and cryptostome bryozoans had extensive sheets of external laminated skeletal material, whereas the majority of cystoporates developed a special vesicular skeleton, which filled the space between autozooecia (Utgaard 1983). Such a vesicular skeleton is in less extent also present in other groups such as in trepostomes (Boardman & Buttler 2005), in ptilodictyines (Karklins 1983, Gorjunova & Lavrentjeva 1993), and in fenestrates (Morozova 2001). A vesicular skeleton is not known from rhabdomesines (Blake 1983b, Gorjunova 1985, 1996). Kenozooids and rootlets are known in fenestrates (Morozova 2001).

Different types of styles are known in various groups of Palaeostomata. Their function is mainly regarded as protective or structural (Tavener-Smith 1969a, Armstrong 1970, Blake 1973, 1983b, Boardman & Cheetham 1973, Boardman & Buttler 2005). It is supposed that the function of acanthostyles might be to raise exterior membranous walls above zooecial apertures and skeletal surfaces in order to improve communication between zooids (Boardman 1983). Acanthostyles are the principal type of styles consisting of hyaline cores surrounded by laminated sheaths (e.g. Figs. 2.5 H, I and 2.6 M). In the Permian genus *Dyscritellina*, acanthostyles are as large as zooecia (Fig. 2.5 I). They usually protrude above the colony surface, whereas the others such as paurostyles, heterostyles, or aktinotostyles are partly or completely embedded in the skeleton (Blake 1983b). Different kinds of inhomogeneities such as tubules and spherules are known in the skeleton of mainly trepostomes, but also some cryptostomes (Boardman & Buttler 2005). Especially erydotrypellid and ulrichotrypellid trepostomes are characterized by the presence of such structures (Fig. 2.5 L–O). Mural (or zooecial) spines are spine-like structures developed inside of autozooecia and occur mainly in trepostomes, being rare in cryptostomes (Fig. 2.3 G, H). They are usually interpreted as ligament attachment points (Boardman 1960b, 1971, Farmer 1979).

Structures related to brooding are known in some Palaeostomata, especially in fenestrates (Tavener-Smith 1966, Stratton 1981, Southwood 1985, Bancroft 1986a, 1988, Morozova 2001). They are mostly represented by different kinds of rounded chambers attached to autozooecia (Fig. 2.7 E, G). Some few apparent brooding structures are known in cystoporates (Utgaard 1973, Buttler 1991, Pachut & Horowitz 2013). Distinct reproductive structures are still unrevealed in trepostomes, rhabdomesines and ptilodictyines, although large autozooecia (macrozooecia) of Trepostomata may have served for brooding of larvae (Ulrich 1890, Astrova 1965).

In contrast to the Cyclostomata, representatives of Palaeostomata reveal various internal morphological characters in form of lateral projections or chamber partitions. Functional morphology of these structures is often difficult to interpret as they are largely unknown among Recent stenolaemates.

Autozooecial chambers in Palaeostomata are often portioned by horizontal structures called basal diaphragms (Boardman 2001). These structures seal off interiors of colonies from nutrition and further growth (Figs. 2.4 C and 2.5 B, D, F). Such structures are not known in modern cyclostomes and their interpretation remains difficult. However, they supposedly served as a “floor” of the living chambers of feeding zooids (Boardman 2001). Furthermore, some diaphragms in trepostome bryozoans are regarded as terminal, which capped living chambers. Some structures like the cap-like apparatus sensu Conti and Serpagli (1987), known from halloporine bryozoans, may also be a kind of terminal diaphragm (Fig. 2.3 I). In fenestrate bryozoans, centrally perforated terminal diaphragms are considered to represent secondary nanozooecia, polymorphic structures comparable to vibracula of cheilostomes (Bancroft 1986b).

Various kinds of partitions of autozooecial chambers are mainly known in trepostome and cystoporate bryozoans, such as hemiphragms, ring-septa, cystiphragms (Fig. 2.5 K), funnel-shaped cystiphragms, and flask-shaped chambers (Fig. 2.12 C, D). The function of hemiphragms, ring-septa, and cystiphragms may be considered as portioning of the autozooecial chambers or possible attachment structure of retractor muscles (Boardman 1971), whereas the funnel-shaped cystiphragms and flask-shaped chambers are rather seen as polymorphs (Utgaard 1973, 1983, Boardman & McKinney 1976).

Cryptostome, fenestrate, and some cystoporate bryozoans also have a kind of lateral structures, which are called hemisepta. These are shelflike, straight, or curved

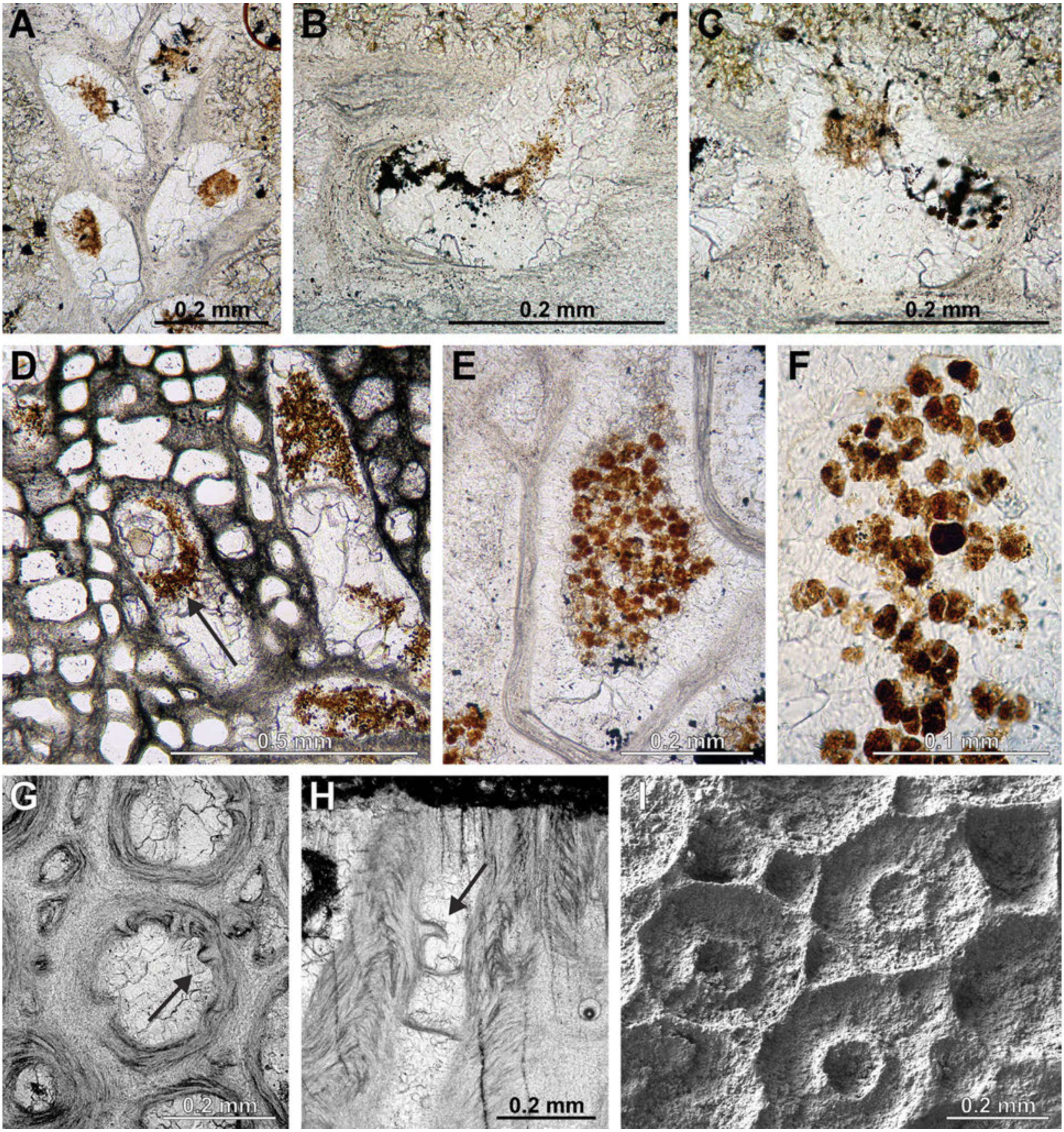


Fig. 2.3: (A–F) Indications of soft parts and fossilized brown deposits in autozooecial chambers of Palaeostomata (thin sections): A–C, *Hemitrypa* sp. (Fenestrata), Eifelian, Middle Devonian, Germany (A – tangential section, B, C – longitudinal sections); D, *Cyclophaenopora robusta* Spjeldnaes, 1984 (Cryptostomata, Rhabdomesina), oblique section showing encapsulated brow deposits (arrow). Vasalemma Formation, lower Katian, Upper Ordovician; Vasalemma Quarry, Estonia; E, F, Unidentified trepostome bryozoan, Pirgu Stage, Katian, Upper Ordovician; Vormsi island, Estonia. (G, H) Trepostome *Leptotrypella provecta* Boardman, 1960a, Emsian, Lower Devonian; Cantabrian Mountains, northwestern Spain. Tangential (G) and longitudinal (H) sections showing mural spines in autozooecial walls (arrows). (I) Cap-like apparatus, covering autozooecial apertures, *Hallopora* sp. (Trepostomata), Rakvere Stage, Katian, Upper Ordovician; Pechurki Quarry, Russia.

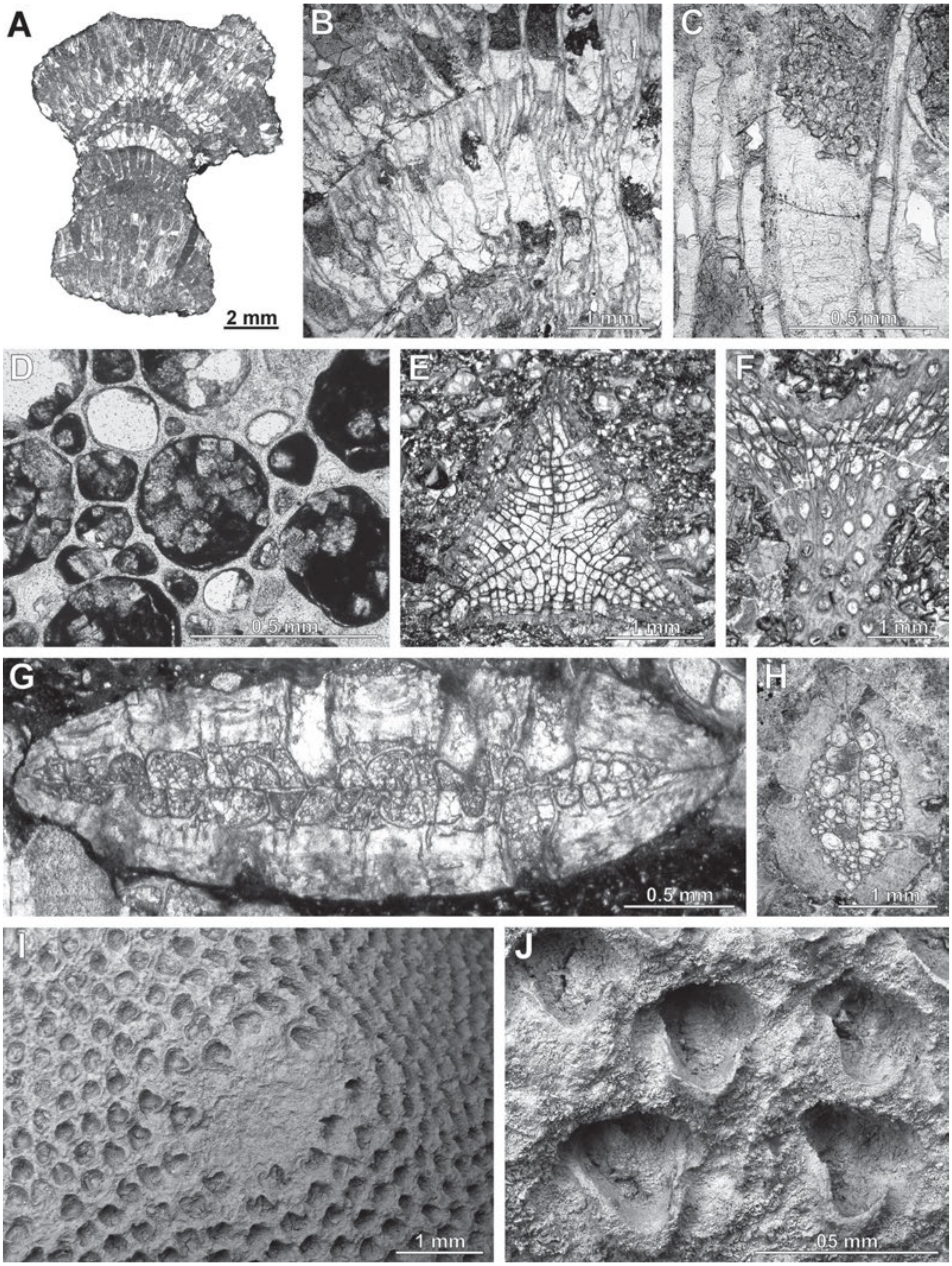
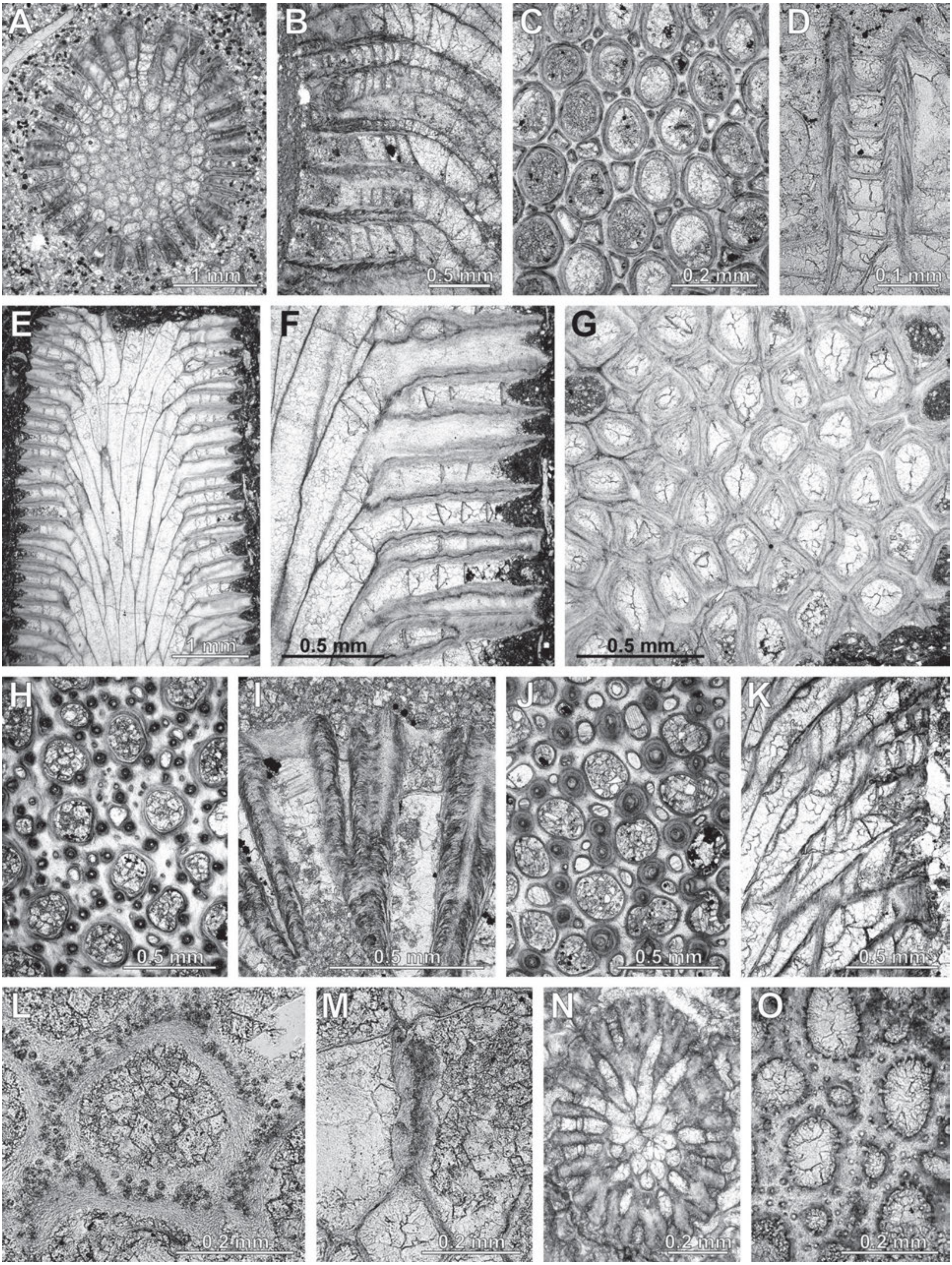


Fig. 2.4: Morphology of the Palaeostomata (Esthonioporata and Cystoporata). (A–D) Esthonioporate *Revalotrypa gibbosa* Bassler, 1911b. A, Longitudinal section of a fungi-shaped colony; B, C, longitudinal section showing autozooecial chambers and neozooecia; D, tangential section. Lower Ordovician, B III β, Kunda Stage; Putilovo Quarry at Volkhov, NW Russia. (E) Cystoporate *Prismopora triangulata* (White, 1878), branch transverse section. Horquilla Formation, Desmoinesian (late Moscovian), Pennsylvanian, Carboniferous; Cerros de Tule, Sonora, Mexico. (F) Cystoporate *Sulcoretepora nitida* (Ulrich, 1890). Oblique section of the branch. Tierra Blanca Member, Lake Valley Formation, Mississippian (Osagean); Sierra County, New Mexico, USA. (G) Cystoporate *Cystodictya lineata* Ulrich, 1884. Branch transverse section. Tierra Blanca Member, Lake Valley Formation, Mississippian (Osagean); Sierra County, New Mexico, USA. (H) Cystoporate *Ramiporalia robusta* Delvolve & McKinney, 1983, branch transverse section. Upper Viséan, Mississippian, Carboniferous; Roque Redonde, Montagne Noire, southern France. (I, J) Cystoporate *Fistuliphragma eifelensis* Ernst, 2008: I, Colony surface with a monticula; J, Autozooecial apertures with lunaria. Junkerberg Formation, Eifelian, Middle Devonian; Gondelsheim, Prüm Syncline, western Rhenish Massif, Germany.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projections that extend from the wall partway into autozooecial chambers (Karklins 1983). According to their position, hemisepta may be superior if they project from the proximal wall into the autozooecial chamber (Figs. 2.7 B and 2.12 I, J) or inferior if they originate from the mesotheca or distal wall (Figs. 2.6 K, L and 2.11 I).

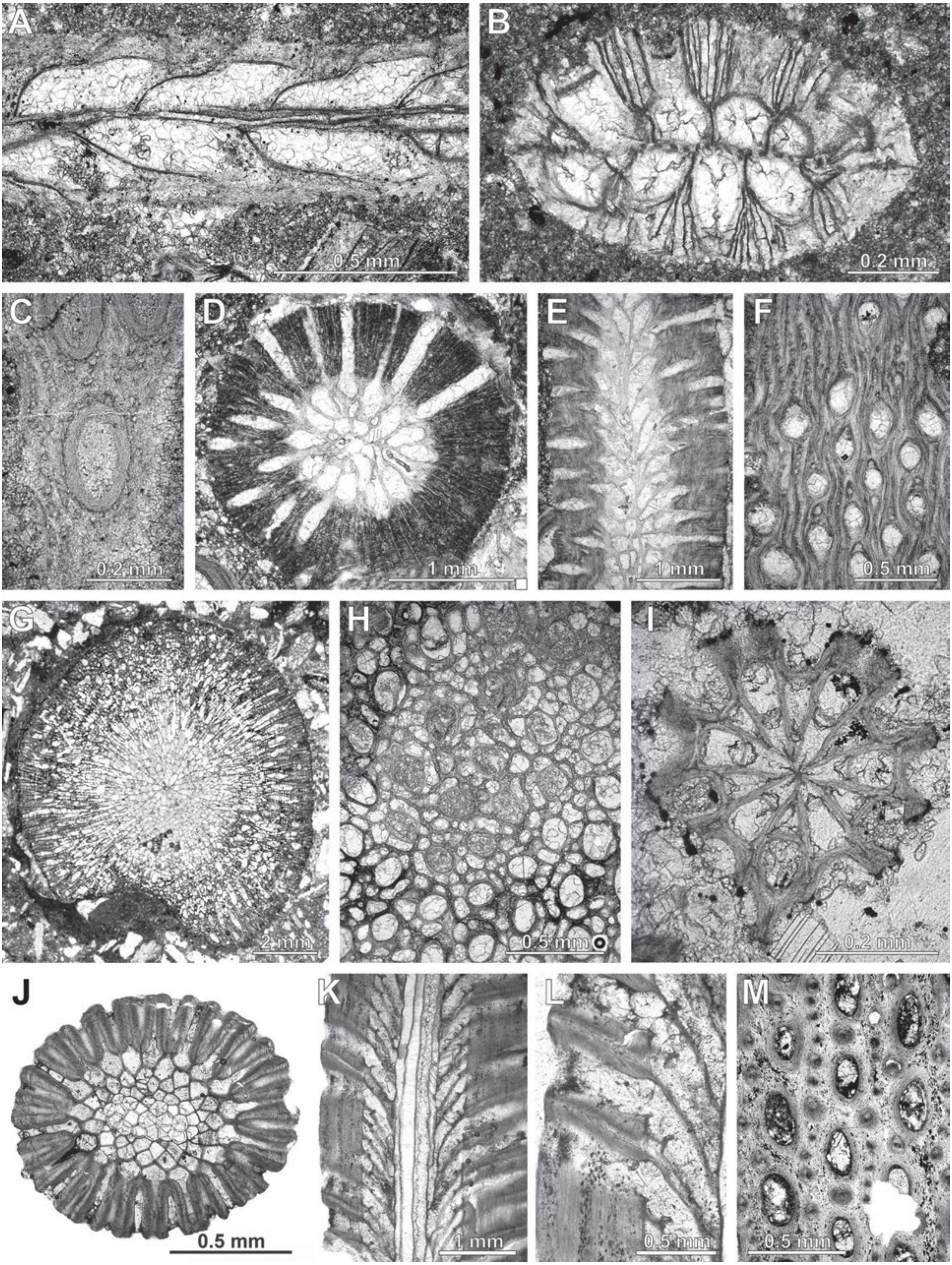
Lunaria are structures of a semicircular shape representing projections in form of hoods on the colony surface (Fig. 2.4 I, J). Lunaria originate at early ontogenetic stages of autozooecial development and are located at the proximal part of autozooecial chambers (Utgaard 1973, 1983). In tangential sections, lunaria are microstructurally different from autozooecial walls and commonly have a shorter radius of curvature (Fig. 2.13 L). In the majority of genera, lunaria are oriented toward the nearest macula (Fig. 2.4 I). Lunaria are an exceptional character of the Order Cystoporata. However, structures similar to lunaria were found in the Devonian rhabdomesine cryptostome *Lunostoma* Ernst *et al.*, 2012c, which are apparently homeomorphic in origin. In post-Palaeozoic stenolaemates, similar structures are known in Jurassic and Recent lichenoporid bryozoans (Borg 1944, Utgaard 1968, Boardman 1984, Voigt 1993). Their origin is also most probably due to homeomorphy.

Fenestrate and cryptostome bryozoans reveal a significant number of structures called allozooecia, amplozooecia, cavernozooecia, cyclozooecia, fossazooecia, leptozooecia, macrozooecia, metaxizooecia, minutozooecia, parazooecia, tectitozooecia, and aviculomorphs (Morozova 1973, 1974, 1987, 2001). In their majority, these are chamber- or tube-like structures (Fig. 2.7 F), which are often regarded as equivalents of avicularia and vibracularia of cheilostome bryozoans, or special kenozooids for improving stability (Morozova 2001). Some of them, like microzooecia, are thought to be of reproductive importance (Morozova 1973, 1974). Aviculomorphs are rounded chambers with triangular projections (Fig. 2.7 D) and occur in the Devonian genus *Fenestrapora*. They are regarded as analogous development to true avicularia of Cheilostomata (McKinney 1998, Morozova 2001). Notable is the genus *Aviculofenestella* Xia, 2002 with two species from the Bajocian (Middle Jurassic) of northern Tibet, which is characterized by the presence of aviculomorphs. The Jurassic age of this record appears to be doubtful; the age of the block from where this material was extracted may be most probably Middle Palaeozoic.

Trepostome bryozoans are relatively poor in polymorphs. They have generally two types of tube- or prismatic-shaped heteromorphs called mesozooecia and exilazooecia (which are sometimes regarded being extrazooidal structures, see Boardman & Buttler 2005). These structures were called “unmature zooecia” by early authors, because of their smaller size compared to the autozooecia. The main difference is the presence of closely spaced diaphragms in mesozooecia (Fig. 2.5 B, D) and their absence in exilazooecia (Fig. 2.5 I). The presence of mesozooecia generally constitutes the Suborder Halloporina, while the Amplexoporina possess exilazooecia (Astrova 1965, 1978). The importance of both of these zooecia seems to be of structural character. It was shown that exilazooecia played a space-filling role in order to maintain regular spacing of autozooecia (Key *et al.* 2001; Fig. 2.12 E, F). Mesozooecia apparently had the same function (Astrova 1965, 1978, Boardman & Buttler 2005). Both mesozooecia and exilazooecia can give rise to new autozooecia during ontogenetic development. Esthonioporate bryozoans possess similar structures called “neozooecia” (Fig. 2.4 A–C).

Autozooecial chambers in fossil bryozoans are known to bear so-called brown deposits, which are regarded as fossilized brown bodies remaining after degeneration-regeneration cycles (e.g. Borg 1926, Gordon 1977, Boardman 1999, Ernst & Voigt 2002). Especially Early Palaeozoic trepostomes and cryptostomes are rich in brown deposits, which can indicate the position of soft-bodied structures (Fig. 2.3 A–F).

◄ **Fig. 2.5**: Morphology of the Palaeostomata (Trepostomata). (A–D) *Parvohallopora ramosa* (d’Orbigny, 1850): A, Branch transverse section; B, longitudinal section; C, tangential section; D, longitudinal section of a mesozooecium with closely spaced diaphragms. Furuberget Formation, Sandbian, Upper Ordovician; Mjøsa District, Norway. (E–G) *Amplexopora crassiparietum* Ernst & Nakrem, 2015: E, F, longitudinal section; G, tangential section. Steinsfjorden Formation, Brattstad Member, Sheinwoodian–Homerian, Wenlock, lower Silurian; Ødegårdsviken, Ringerike, Norway. (H, I) *Dyscritella angularis* (Trizna, 1948): H, tangential section showing autozooecial apertures, exilazooecia and acanthostyles; I, longitudinal section showing an autozooecial chamber with diaphragm and exilazooecium (arrow). Zechstein, Upper Permian; Gera, Germany. (J) *Dyscritellina* cf. *aculeata* Morozova in Morozova & Krutchinina, 1986, tangential section. Upper Permian; Canada. (K) *Homotrypa niagarensis* Ernst *et al.*, 2019, longitudinal section showing cystiphragms. Reynales Formation, Hickory Corners Member, Aeronian, Llandovery, Lower Silurian; Hickory Corners, New York, USA. (L, M) *Ulrichotrypa incrustata* Ernst, 2001: L, tangential section; M, longitudinal section showing autozooecial wall with tubules. Zechstein, Upper Permian; Gera, Germany. (N, O) *Microcampylus regularis* Ernst, 2008: N, oblique section of the branch; O, tangential section showing tubules in autozooecial walls. Upper Nims Member, Junkerberg Formation, Eifelian, Middle Devonian; Brühlborn, Prüm Syncline, western Rhenish Massif, Germany.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2.3.1.3 Overview of the orders of the Palaeostomata

Subdivision of Palaeostomata and phylogenetic relations within the clade is not consistently accepted at the current stage of research. There are two main views on the taxonomic division of Palaeozoic bryozoans, represented by Western and Soviet (now Russian) schools of bryozoology. A detailed history of the subdivision of the Palaeostomata is beyond the scope of the present review. The main differences concern the rank of some taxonomic units, for example the order rank of Rhabdomesina supported by Russian colleagues (suborder of the Cryptostomata according to Utgaard 1983) or the relation of Fenestellida (Fenestrata) to the Gymnolaemata (e.g. Ulrich 1890, Viskova & Morozova 1988, Gorjunova 1996, Morozova 2001, Xia 2002). At present, the following orders within the Superorder Palaeostomata are accepted: Esthonioporata, Cystoporata, Trepostomata, Fenestrata, and Cryptostomata (e.g. Ma *et al.* 2014, Taylor & Waeschenbach 2015). The group of Timanodictyida is regarded as suborder of the Order Cryptostomata (Blake 1983a). However, the position of the latter clade is controversial, Russian specialists consider both Cryptostomida and Timanodictyida as separate orders (e.g. Gorjunova & Lavrentjeva 1993, Gorjunova 1994, 1996).

Esthonioporate bryozoans were usually considered to belong to Trepostomata or Cystoporata (e.g. Astrova 1978, Gorjunova 1996). Ma *et al.* (2014) erected the Order Esthonioporata, which they defined as follows:

> Hemispherical, massive and rarely encrusting colonies. Maculae common on colony surface. All mineralized walls above basal exterior colony walls are interior in origin. No differentiation recognized between endozone and exozone. Autozooecia long with polygonal cross-sections. Walls granular or with indistinct laminae. Diaphragms common or absent, thin, ring septa may develop. Styles often present, mesozooecia and exilazooecia absent, neozooecia present (Ordovician – Devonian).

The Order Cystoporata was erected by Astrova (1964), who extracted them from Cyclostomata. The following definition is modified after Utgaard (1983) and Gorjunova (1996):

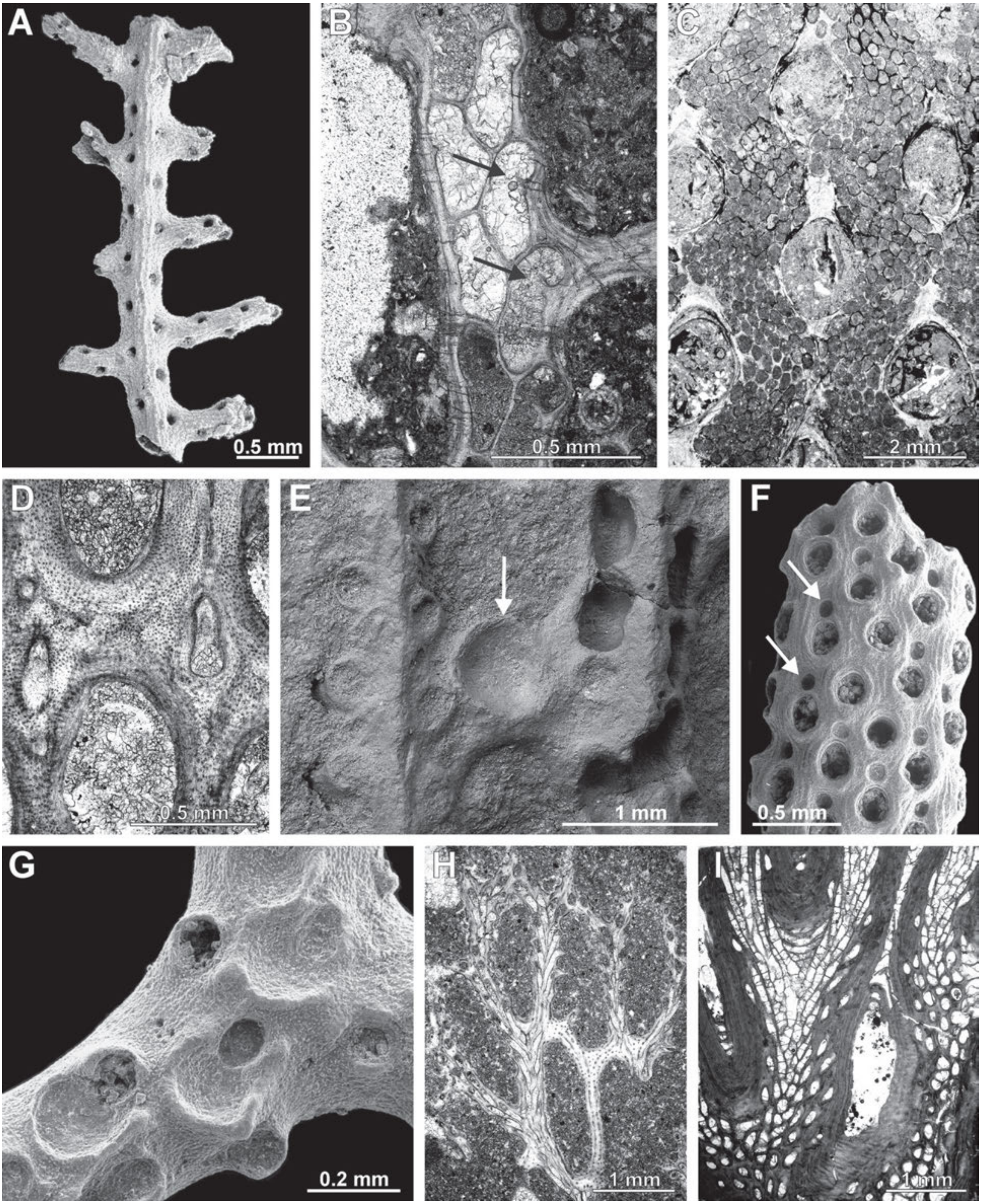
> Hemispherical, massive, encrusting, branched, lenticulate (bifoliate), or reticulate colonies. Maculae common on colony surface. All mineralized walls above basal exterior colony walls are interior in origin. Differentiation between endozone and exozone distinct or absent. Autozooecia cylindrical or prismatic, often with polygonal cross-sections in endozones and circular apertures in exozones. Apertures often with lunaria. Walls granular or laminated. Diaphragms common or absent, thin, cystiphragms and hemiphragms may develop. Vesicular skeleton between autozooecia often developed. Styles often present, but mainly restricted to the vesicular skeleton. Communication pores present in some genera (ceramoporines). Apparent brooding structures known in few genera (Ordovician – Triassic).

The Order Trepostomata was erected by Ulrich (1882). The content of the order changed through time, and currently, the division in the suborders Amplexoporina and Halloporina is widely accepted (Astrova 1965). The current diagnosis is modified after Gorjunova (1996):

> Lamellar encrusting (mono- and multilamellar), hemispherical, massive, discoidal, branched ramose, and rarely lenticular (bifoliate). Maculae common on colony surface. All mineralized walls above basal exterior colony walls are interior in origin. Differentiation between endozone and exozone usually distinct. Autozooecia long or short, prismatic with polygonal cross-sections. Walls distinctly laminated, often irregularly thickened, in some genera containing spherules and tubules. Communication pores absent. Diaphragms common or absent, thin or thick; cystiphragms, ring septa, hemiphragms may develop. Styles often present, mesozooecia or exilazooecia often present. Apparent brooding structures unknown (Ordovician – Triassic).

The following orders were formerly summarized within the Order Cryptostomata Vine, 1884, which apparently had the most complex history of research. The earliest attempt of a division was made by McNair (1937), who suggested principal differentiation by colony form. Astrova and Morozova (1956) accordingly defined the Order Cryptostomata and established three suborders: Fenestelloidea, Ptilodictyoidea, and Rhabdomesoidea.

◄ **Fig. 2.6**: Morphology of the Palaeostomata (Cryptostomata). (A–C) *Trigonodictya parvula* Ernst & Carrera, 2012 (Ptilodictyina): A, longitudinal section; B, transverse section; C, tangential section of an aperture. Las Plantas Formation, Sandbian, Upper Ordovician; San Juan Province, Precordillera of Western Argentina. (D–F) *Timanodictya* sp. (Timanodictyina): D, transverse section; E, longitudinal section; F, tangential section. Toroweap Formation, Artinskian, Lower Permian; Nevada, USA. (G, H) *Cyclophaenopora robusta* Spjeldnaes, 1984: G, transverse section; H, tangential section. Vasalemma Formation, lower Katian, Upper Ordovician; Vasalemma Quarry, Estonia. (I) *Moyerella parva* Ernst *et al.*, 2019 (Rhabdomesina), branch transverse section. Reynales Formation, Hickory Corners Member, Aeronian, Llandovery, lower Silurian; Hickory Corners, New York, USA. (J–M) *Ascopora triseriata* Schulga-Nesterenko, 1955 (Rhabdomesina): J, branch transverse section; K, L, longitudinal section showing axial zooecia and autozooecial chambers with hemisepta; M, tangential section showing autozooecial apertures, acanthostyles and paurostyles. Rod El Hamal Formation, upper Viséan-Westphalian, Pennsylvanian, Carboniferous; Wadi Araba area, Egypt.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Elias and Condra (1957) constituted the Order Fenestrata (=Suborder Fenestelloidea Astrova & Morozova, 1956). Later, Viskova and Morozova (1988) raised this suborder to the rank of the Order Fenestellida. The Order Fenestrata is currently divided in two suborders: Phylloporinina and Fenestellina, following Lavrentjeva (1985). In contrast, Gorjunova (1996) and Morozova (2001) raised both suborders to orders Phylloporinida and Fenestellida within the Infraorder Fenestelloidea. The following diagnosis of the Order Fenestrata is modified, combining the diagnoses for Phylloporinida (Suborder Phylloporinina) and Fenestellida (Suborder Fenestellina) from Gorjunova (1996) and Morozova (2001):

> Arborescent unilaminate colonies of various shape: pinnate, freely dichotomizing (without connection), reticulate funnel- or fan-formed, reticulate screw-shaped, and rarely complex encrusting (Fig. 11G). Autozooecia usually short, box-shaped, with vestibules at proximal ends, in Phylloporinina long, tubular, often containing diaphragms (Fig. 7I). Hemisepta often present (Fig. 7B). Autozooecial apertures rounded to circular. Protective superstructures develop in some genera. Walls divided in internal granular and external laminated skeleton. Autozooecial apertures are usually arranged in rows and may be divided by longitudinal keels which can carry nodes. Heterozooecia include microzooecia, parazooecia, cavernozooecia, cyclozooecia, aviculomorphs, and metaxizooecia. Apparent brooding structures in form of spherical chambers attached to vestibules of autozooecial chambers common (Ordovician – Permian).

Shishova (1968) raised Rhabdomesoidea to the order rank (Order Rhabdomesida), and this opinion is still followed by Russian specialists (e.g. Gorjunova 1985, 1996). Later, Gorjunova (1987) raised Ptilodictyoidea to the rank of order (Order Cryptostomata). The main difference between ptilodictyines and rhabdomesines is their budding pattern. In ptilodictyines, zooecia bud from a mesotheca (or median wall), producing bifoliate branches (Figs. 2.6 A, B and 2.11 D, F), whereas in rhabdomesines, they originate from the more or less distinct median axis (e.g. Blake 1983a, Gorjunova 1985, Gorjunova & Lavrentjeva 1993; Figs. 2.6 G, I and 2.11 H, K). In some genera, the median part of the colony is composed of one or many heterozooids, like an axial tube (Fig. 2.12 H–J), or bundle of axial zooecia (Figs. 2.6 J, K, and 2.13 D, E).

The Order Cryptostomata is currently divided into two suborders, Ptilodictyina and Rhabdomesina, whereas Blake (1983a) accepted the fenestrates and timanodictyines as the third and the fourth suborders of Cryptostomata.

The modified diagnosis of the Order Cryptostomata Vine, 1884 in its currently accepted composition (Ptilodictyina and Rhabdomesina; consider Boardman 1983) is compiled after Blake (1983a), Gorjunova and Lavrentjeva (1993) and Gorjunova (1996):

> Arborescent colonies of various shape: bush-like, or reticulate (usually anastomosed). Branch transverse section circular or lens-shaped; secondary overgrowths rare. Clear distinction between endozone and exozone. Apertures common on all branch surfaces, arranged in regular longitudinal or spiral rows; apertures elliptical, subcircular, rhombic or rectangular. Autozooecia generally short, rarely elongate, usually with zooecial bend at endozonal-exozonal boundary. Hemisepta and mural spines present in some taxa; interzooecial pores absent. Vesicular skeleton may be developed (Ptilodictyina). Polymorphs represented by metazooecia, mesozooecia, tectitozooecia, allozooecia and axial zooecia; distinct brooding structures unknown. Striae, ridges, styles and stylets commonly well-developed on colony surface (Ordovician – Permian; an apparent rhabdomesine cryptostome *Tebitopora* reported from the Middle Triassic).

2.4 Evolutionary history of Bryozoa

2.4.1 Ordovician

Although Ordovician bryozoan faunas are widely known and intensively studied worldwide, the earliest events in

◄ **Fig. 2.7**: Morphology of the Palaeostomata (Fenestrata). (A) *Penniretepora* sp. (Fenestellina). Las Llacerias Formation, Kasimovian, Pennsylvanian; Asturias, Cantabrian Mountains, northwestern Spain. (B) *Laxifenestella kondrovensis* (Schulga-Nesterenko, 1955) (Fenestellina), mid-tangential section of autozooecial chambers with hemisepta (arrows). Upper Viséan, Mississippian, Carboniferous; Roque Redonde, Montagne Noire, southern France. (C) *Protoretepora* sp. Bruten Yard, Western Australia; Noonkanbah Formation, Kungurian, Lower Permian. (D) *Fenestrapora transcaucasica* Morozova & Lavrentjeva, 1998 (Fenestellina). Thin section of the reverse surface showing aviculomorphs (arrows). Upper Nims Member of the Junkerberg Formation, middle Eifelian, Middle Devonian; Brühlborn near Rommersheim, Germany; (E) Colony obverse surface showing autozooecial apertures and a reproductive heterozooecium (arrow). Müllert Subformation of the Ahbach Formation, lowermost Givetian, Middle Devonian; Üxheim-Ahütte, Germany. (F) *Thamniscus perplexus* Ernst in Lisitsyn & Ernst, 2004 (Fenestellina), obverse colony surface with cyclozooecia (arrows). Zechstein, Upper Permian; Beeckerwerth near Duisberg, Germany. (G) *Acanthocladia anceps* (Schlotheim, 1820) (Fenestellina), branch with reproductive heterozooecia (arrows). Zechstein, Upper Permian; Beeckerwerth near Duisberg, Germany. (H) *Chasmatopora rossae* Ernst & Carrera, 2012 (Phylloporinina). Las Plantas Formation, Sandbian, Upper Ordovician; San Juan Province, Precordillera of Western Argentina. (I) *Pseudohornera surculosa* Lavrentjeva, 1985 (Phylloporinina). Sandbian, Kukruse stage (Kivioli Member), Upper Ordovician; Kiviõli, Estonia.

bryozoan evolution are still unclear (e.g. Ross 1985, Taylor & Larwood 1990, Taylor & Ernst 2004, Ernst 2018). The earliest calcified bryozoans were apparently morphologically simple corynotrypids (Fig. 2.9 D), which originated from an unmineralized bryozoan (apparently ctenostome-like ancestor) with a simple, uniserial, encrusting colony form (Taylor & Larwood 1990, Gorjunova 1992, Taylor & Ernst 2004, Ma *et al.* 2015, Taylor & Waeschenbach 2015). Cyclostome bryozoans are considered as basal stenolaemates that mainly form uniserial encrusting colonies during the Ordovician, with the earliest record from the Dapingian of Russia (*Gorjunovia* Taylor & Rozhnov, 1996). Some more complex forms possessing pseudopores are known from the Ordovician and Silurian (Fig. 2.9 C, E). However, the oldest known bryozoans belong to the Palaeostomata, and they already show relatively advanced skeletal morphology (e.g. Taylor & Curry 1985, Hu & Spjeldnaes 1991, Cuffey *et al.* 2012). The oldest known bryozoan is the cryptostome *Prophyllodictya simplex* Ma *et al.*, 2015 from the lower Nantzinkuan Formation, lower Tremadoc, which developed ramose (branching) colonies. Slightly younger faunas of the Fenxian Formation of South China contain additionally encrusting to dome-shaped *Nekhorosheviella* (Esthonioporata) and branched *Orbiramus* (Trepostomata) (Xia *et al.* 2007, Adachi *et al.* 2012). Early bryozoan faunas represented mainly by esthonioporines and trepostomes are known from the Floian of Baltoskandia (e.g. Koromyslova 2011, Fedorov *et al.* 2017). Apparently, bryozoans had a long period of earlier evolution that left no fossil evidence (e.g. Taylor & Waeschenbach 2015).

Boring ctenostomes (Gymnolaemata) are known from the Early Ordovician, too (Mayoral 1991, Mayoral *et al.* 1994, Taylor & Rozhnov 1996). The genera *Ropalonaria* Ulrich, 1879 and *Vinella* Ulrich, 1890 were reported from the Late Ordovician of USA.

A single example of a soft-bodied ctenostome preserved by bioimmuration is known from the Early Ordovician of Great Britain and Czech Republic (Fig. 2.9 A, B). The species *Bolopora undosa* Lewis, 1926 has been described from the basal Arenig (Early Ordovician) of the Ffestiniog district, North Wales. Initially, this fossil has been regarded as a cyclostome bryozoan. The same fossil was described by Prantl (1939) as the cyclostome bryozoan *Berenicea vetera* Prantl, 1939 from the Skiddavian (=Arenigian) Stage of Bohemia. Ross (1964) and then Hofmann (1975) claimed this fossil (*Bolopora undosa*) to be an alga. Study of the type material of *Bolopora undosa*, deposited at the Sedwick Museum in Cambridge, as well as material on *Berenicea vetera* Prantl, 1939 from the Klabava Formation (Early Ordovician, Floian), from Ejpovice in Czech Republic (provided by Michal Mergl, Prague), showed that this fossil is rather a soft-bodied ctenostome bryozoan preserved by bioimmuration in phosphatic oncoids (Taylor & Ernst 2006).

The genus *Schallreuterella* Hillmer, 1987 from the Late Ordovician (Hirnantian) of Sweden bears some superficial similarities to cheilostome bryozoans, especially in the shape of the aperture with proposed hinge line for an operculum and the shape of the autozooecia. These morphological features lead to the assumption of a huge gap in the fossil record between the Ordovician and Jurassic, the time of confirmed origination of cheilostomes (Hillmer 1991). In fact, *Schallreuterella* appears rather related to the Suborder Fenestellina (Order Fenestrata), a group that has often been regarded being ancestral to Cheilostomata because of their box-like zooecia and avicularia-like heteromorphs, as well as occasional findings of opercular structures (e.g. Morozova 1973, 1974, 1987, Wyse Jackson & Bancroft 1994). The alleged similarities between fenestrates and cheilostomes are due to evolutionary convergence.

The majority of bryozoan faunas of the Ordovician occurred in tropical or subtropical climatic zones, whereas some others existed in temperate environments such as shelves of Gondwana. The sea level was high during most of the Ordovician, with extensive epicontinental seas, especially in the tropics (e.g. Haq & Schutter 2008, Pratt & Holmden 2008), and the climate was predominantly warm with high levels of CO_2 (“green-house”), followed by a rapid cooling at the end of this period (Hirnantian glaciation).

Bryozoans diversified rapidly during the Ordovician (Fig. 2.8). Within a short time interval, all orders except the group of Timanodictyina were established. Bryozoan diversity increased in several waves from the Tremadoc to the early Katian, with the peak in the late Sandbian (Taylor & Ernst 2004, Ernst 2018). This diversification event coincided with the beginning of the global flooding (e.g. Ross & Ross 1992, 1996). The reasons for the biodiversification of benthic suspension feeders, such as bryozoans, brachiopods, or echinoderms, are often explained by increasing phytoplankton availability (e.g. Servais *et al.* 2008, 2010, 2016).

The level of bryozoan generic endemism was high during the Early and Middle Ordovician, whereas the bryozoan faunas in the Late Ordovician (Katian) became more cosmopolitan (Tuckey 1990a, Taylor & Ernst 2004). This loss of endemism is explained by the global warming in the late Katian (Boda Event), which enabled intermixing of temperate and tropical faunas (Jiménez-Sánchez & Villas 2010). The Late Ordovician was signed by a series of extinctions among bryozoans, the first and the strongest

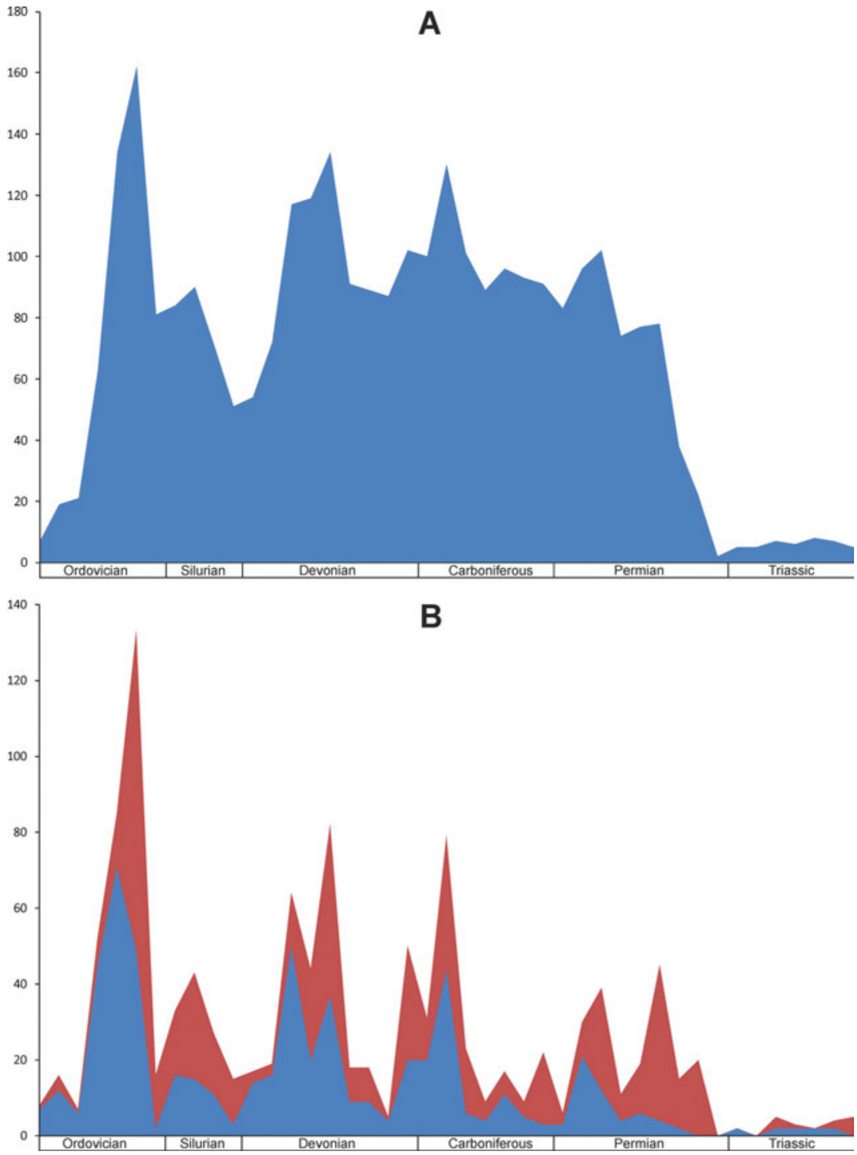
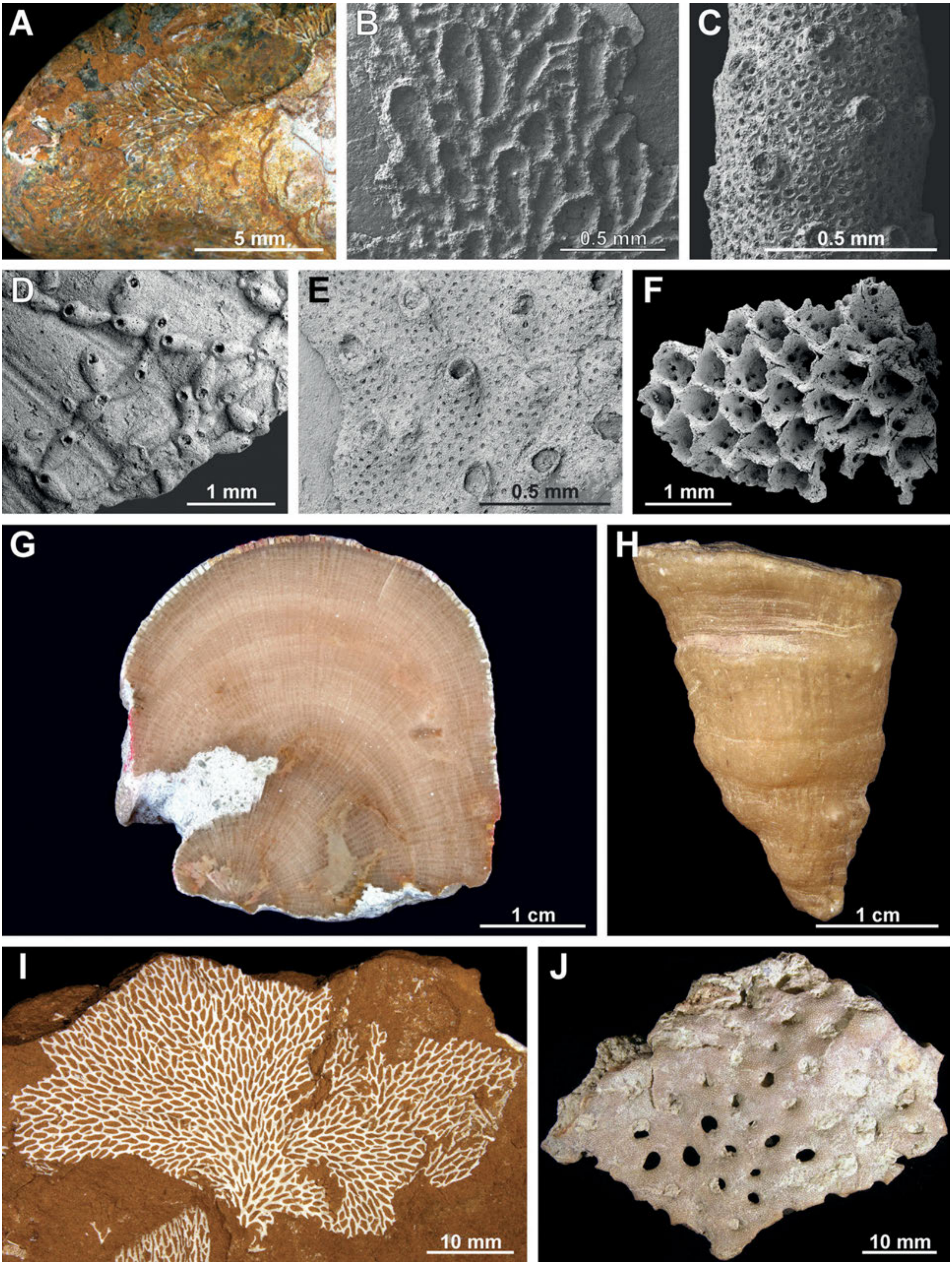


Fig. 2.8: Diversity dynamics of the Palaeostomata. (A) Generic diversity (raw data including Lazarus genera and singletons). (B) Generic originations (blue) and extinctions (red). Data set was compiled in January 2019 on the temporal distribution of 581 genera of Palaeostomata.

of them happened in the early Katian (Tuckey & Anstey 1992, Ernst 2018). The second extinction occurred in the late Katian, apparently caused by the Boda Event. Both first extinctions were interrupted by a slight recovery in bryozoan diversity. The third and the weakest extinction coincided with the global cooling in the Hirnantian. The diversity dynamic shows not only high extinctions rates, but also low rates of originations of new genera (Ernst 2018).

Ordovician bryozoan faunas are dominated by trepostomes, cystoporates and ptilodictyine cryptostomes, whereas fenestrates and rhabdomesine cryptostomes are less diverse. Esthonioporine and trepostome bryozoans produced a variety of growth forms from which massive hemispherical, or dome-shaped, ones (Figs. 2.4 A, 2.9 G, and 2.10 I) are unmistakably characteristic for the Early Palaeozoic (e.g. Taylor & James 2013). Dome-shaped trepostomes from Baltica reached significant sizes (Fig. 2.9 G). Some species of the esthonioporine genus *Dianulites* developed horn-shaped colonies (Fig. 2.9 H). Ptilodictyine cryptostomes developed exclusively ramose bilaminate colonies, which were lancet-shaped, bifurcating, or reticulate (Figs. 2.6 A–C and 2.9 J). In these colonies, autozooecia budded from a median lamina called mesotheca. This group of bryozoans declined significantly during the Silurian and much more during the Devonian (Fig. 2.11 D–F). In the Carboniferous, some few holdovers of ptilodictyines are known, and the last species of the suborder is known from the Early Permian of Canada (Ernst & Nakrem 2007).

Fenestrate bryozoans of the Ordovician are mainly represented by the Suborder Phylloporinina, with only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few species of the Suborder Fenestellina known from the Late Ordovician. Phylloporines developed typical fenestrate growth forms: branched dichotomous, pinnate, and reticulate (Fig. 2.7 H, I). A well-known example for the diverse phylloporine fauna is the so-called kukersite (e.g. Bekker 1921), a light-bright marine oil shale of the Sandbian age, which occurs mainly in Estonia and North West Russia (Fig. 2.9 I). The majority of the esthonioporates disappeared at the end of the period.

2.4.2 Silurian

The Silurian has been characterized as a period of low provinciality for marine invertebrates, with little biogeographic differentiation being observed in faunas from major continents. This situation was caused by the closing of the Iapetus Ocean, which ceased to be a barrier to larvae of marine animals (Cocks & Fortey 1982, Cocks 2001). This had consequences for animal diversity. Tuckey (1990b) studied the global bryozoan palaeobiogeography in the Silurian. He stated a low level of endemism for bryozoans during this period and postulated a correlation between provinciality and bryozoan diversity. Controversially, McCoy and Anstey (2010) came to the result that bryozoans are characterized by a high level of endemism in the Silurian, much higher than other groups of organisms. Buttler *et al.* (2013) showed that the provinciality was heterogeneous during the Silurian. During the Llandovery, bryozoans exhibited distinct provincialism, but this declined during the Wenlock, only to reemerge during the Ludlow. Late Silurian (Přidoli) faunas show a possible division into two provinces.

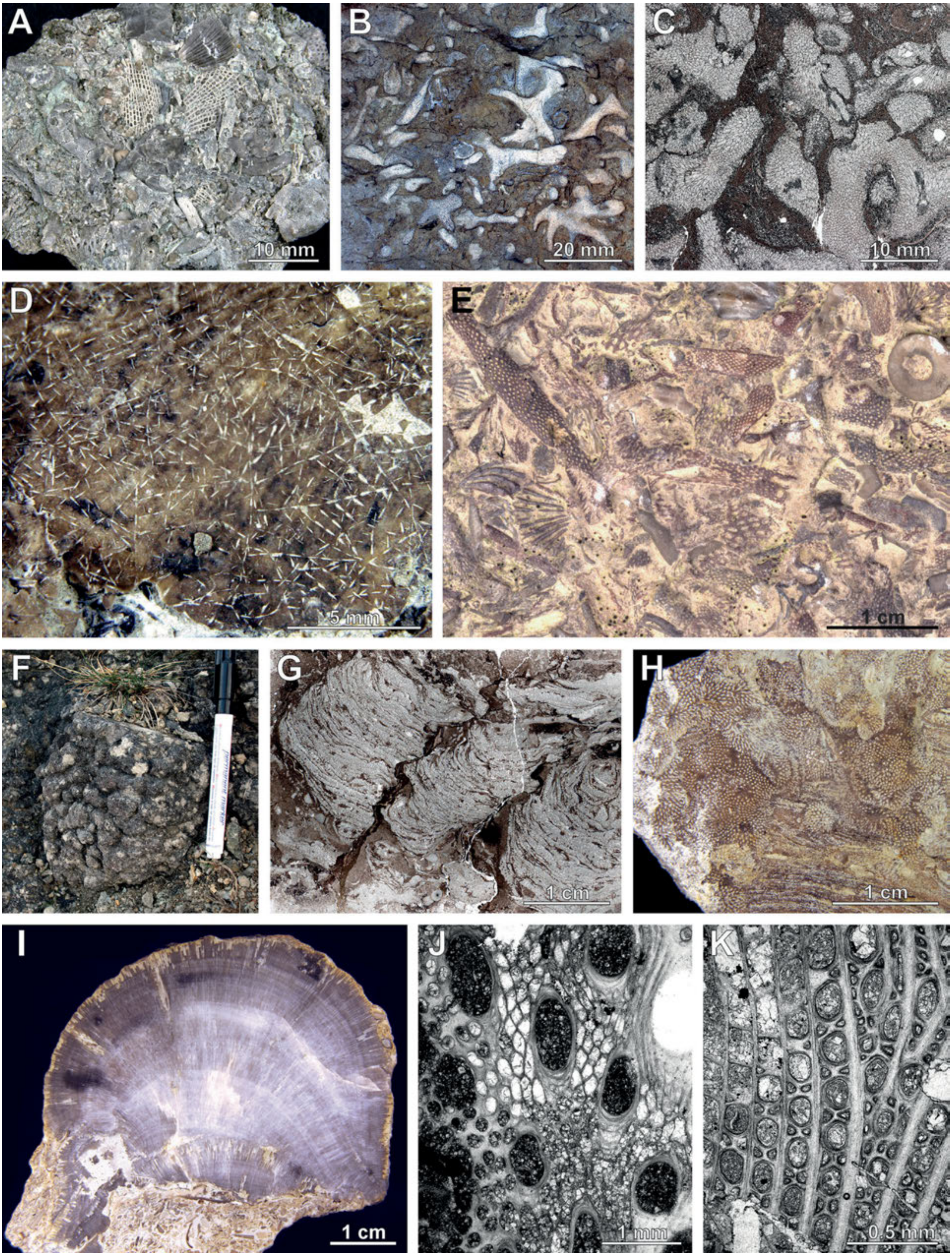
Bryozoan diversity was relatively low during the Silurian, showing little recovery during the Wenlockian. The extinction of bryozoans at the end of the Silurian is evident and corresponds to the Mid-Přidolian bioevent. The causes of this event are supposed to be a change of the sedimentation regime and diminishment of suitable habitats (e.g. Kaljo *et al.* 1996, Calner 2008). Among the bryozoan groups, ptilodictyine cryptostomes experienced the highest decline. The phylloporines were largely replaced by fenestellines, which became much more diverse and abundant during the Silurian. Trepostome bryozoans suffered also significant losses during the Early Silurian, with slight recovery in the Wenlockian. The majority of Ordovician dome-shaped taxa disappeared (Fig. 2.10 I); the trepostomes in the Silurian are represented by branched ramose and encrusting species (Fig. 2.10 B–C, H). In contrast, the cystoporate diversity increased in the Silurian compared to the Ordovician. They produced mainly encrusting, globular, or branched ramose colony forms.

Although not as abundant and diverse as in the Ordovician, bryozoans were important elements of the benthic communities during the Silurian and were locally rock-forming (Fig. 2.10 A–C, E, H). Well-studied Silurian bryozoan faunas are known from North America and Eurasia.

2.4.3 Devonian

During the Devonian, several bioevents of smaller scale occurred (e.g. Walliser 1996). Bryozoans showed a slightly different sensitivity to these events than other fossil groups (Cuffey & McKinney 1979, Bigey 1988, Morozova *et al.* 2002). The Choteč Event at the Emsian–Eifelian boundary strongly affected brachiopods and trilobites, whereas corals and bryozoans did not show any noticeable changes in their diversity (Chlupáč & Kukal 1986, 1988, Ernst *et al.* 2012b, Ernst 2013). The bryozoan diversity increased steadily during the Early Devonian and reached its maximum in the Givetian (Fig. 2.8). In the subsequent Frasnian stage, the drop in bryozoan diversity is dramatic (Horowitz *et al.* 1996, Taylor & Larwood 1988). The Givetian/Frasnian bryozoan extinction most probably corresponds to the late Givetian Taghanic bioevents (e.g. House 2002, Boucot 1990). This crisis represents a series of faunal changes, with the impact on different groups shifted in time (e.g.

◂ **Fig. 2.9**: Ordovician bryozoans. (A) Apparent ctenostome *Bolopora undosa* Lewis, 1926 (=*Berenicea vetera* Prantl, 1939). Arenig, Lower Ordovician; Ejpovice, Czech Republic (photo by Paul D. Taylor, London). (B) Same as in A, SEM photograph showing shallow zooids. (C) Cyclostome *Kukersella borealis* (Bassler, 1911b). Rakviere Stage, Upper Ordovician; Rakvere, Estonia. (D) Cyclostome *Corynotrypa* sp. Bromide Formation, Sandbian; Arbuckle Mountains, Oklahoma, USA (photo by Paul D. Taylor, London). (E) Cystoporate *Ceramopora* sp. Pin Formation, Upper Ordovician; Spity Valley, India (large communication pores inside of autozooecia). (F) Cyclostome *Cuffeyella* sp., Lorraine Group, Ordovician; Cincinnati, Ohio (photo courtesy Paul D. Taylor). (G) Trepostome *Diplotrypa* sp. Rakvere Stage, Upper Ordovician; Pechurki Quarry, NW Russia (polished slab). (H) Esthonioporate *Dianulites detritus* Eichwald, 1829. Kunda Stage, Darriwilian, Lower Ordovician; west side of Volkhov River, NW Russia. (I) *Chasmatopora papillosa* (Bekker, 1921) (Fenestrata, Phylloporinina). Sandbian, Kukruse stage (Kivioli Member), Upper Ordovician; Kohtla quarry, Estonia. (J) *Stictoporellina* sp. (Cryptostomata, Ptilodictyina). Oandu Stage, Upper Ordovician; quarry Slantsy, NW Russia.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Baird & Brett 2008). The Taghanic event was considerable not only for bryozoans but also for other groups such as ammonoids (House 1996), trilobites (Chlupáč 1994) and corals (Oliver & Pedder 1994). It was apparently caused by transgression and marked the end of faunal provincialism, which had persisted since the Early Devonian (Johnson 1970). This may also explain its heavy impact on bryozoans because they seem to be sensitive to changes in provincialism, as shown for the Ordovician (Taylor & Ernst 2002, Tuckey 1990a). The increase of cosmopolitanism and reduction of available habitats as a result of the Taghanic transgression (with subsequent deepening of carbonate platforms) seem to bias bryozoan generic diversity.

In contrast to the Taghanic event, the Frasnian/Famennian bioevent did not greatly affect bryozoans (e.g. Bigey 1988, Morozova *et al.* 2002). Indeed, there are even signs of a slight recovery of bryozoan faunas during the early Famennian (Ernst 2013). Different causes for the Frasnian/Famennian bioevent (the so-called Kellwasser event) have been discussed, ranging from a worldwide anoxia (e.g. McGhee 1996, Schindler 1990, Walliser 1996) to an asteroid shower (Sandberg *et al.* 2002).

The Hangenberg bioevent at the Devonian/Carboniferous boundary was apparently caused by glaciation resulting in a strong drop in sea level (e.g. Caplan & Bustin 1999, Kaiser *et al.* 2006, 2008). This resulted in a significant shift in the composition of many animal groups including bryozoans (Horowitz & Pachut 1993, Gutak *et al.* 2008, Tolokonnikova & Ernst 2010, Ernst 2013). An important factor affecting bryozoan diversity in the Late Devonian was strong endemism of some faunas (Tolokonnikova & Ernst 2010). Remarkably, many Devonian bryozoans, especially fenestrates, developed structures of obvious defensive character (e.g. McKinney *et al.* 2003). This morphological trend may reflect increasing pressure of predators during the mid-Palaeozoic predator revolution (e.g. Signor & Brett 1984, Sallan *et al.* 2011).

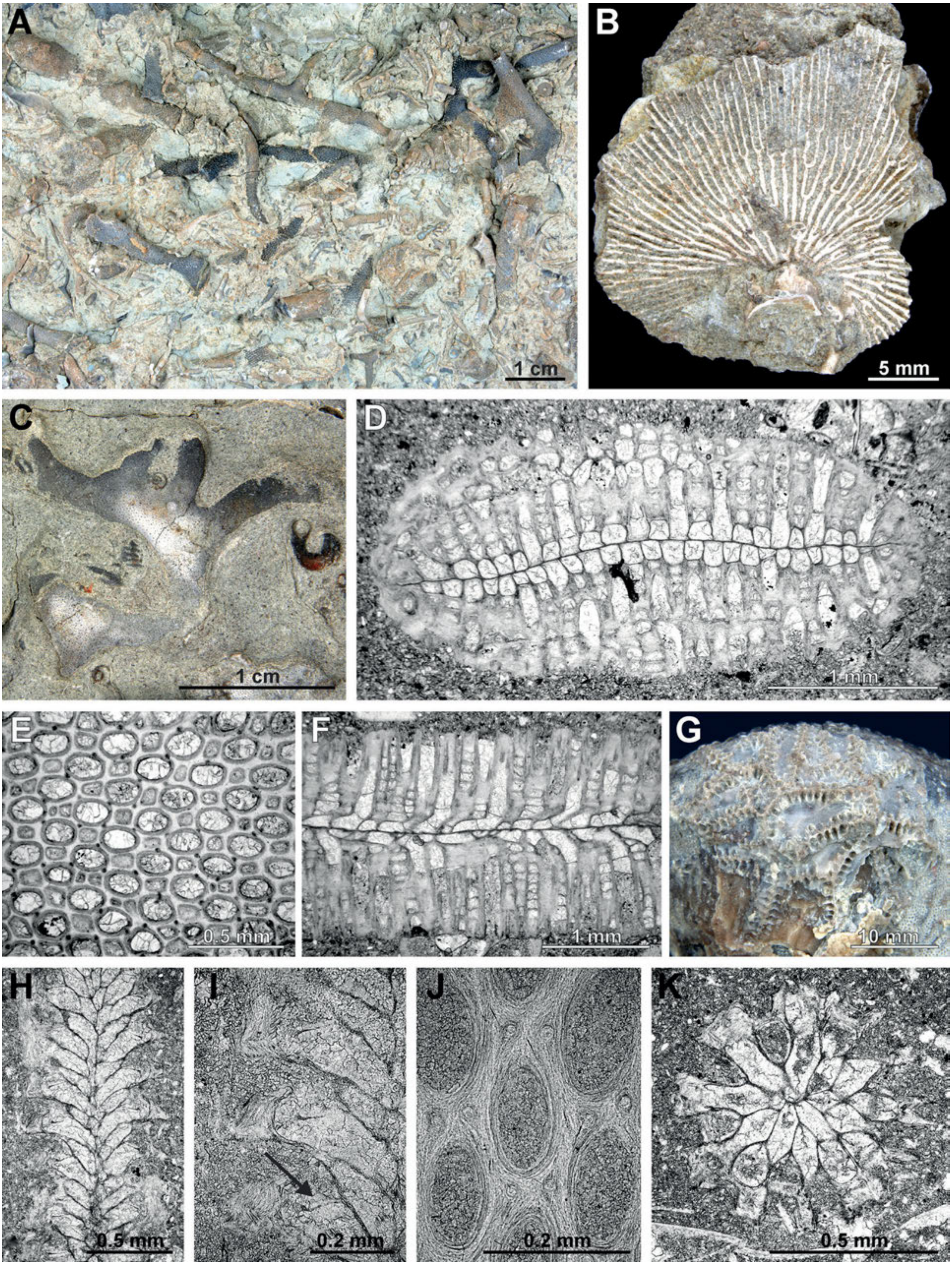
Devonian bryozoan-bearing sediments are widely distributed worldwide and contain amazing fossils (Fig. 2.11 A–C, G). This was a time for restructuring of the bryozoan fauna. During this interval, trepostomes and cystoporates lost their dominance, whereas fenestrates (Figs. 2.7 D, E and 2.11 B, G) and rhabdomesine cryptostomes (Fig. 2.11 H–K) became a dominant group (Cuffey & McKinney 1979, Bigey 1988, Ernst 2013). This constellation largely influenced the composition of bryozoan faunas in the Late Palaeozoic.

2.4.4 Carboniferous

In the Mississippian, the phylum Bryozoa underwent rapid diversification and phylogenetic differentiation but showed a gradual decline in the Pennsylvanian (Ross 1981, Bancroft 1987). The Tournaisian-Viséan rise in bryozoan diversity was the last significant diversification event among the Palaeostomata (Tolokonnikova *et al.* 2014; Fig. 2.8). Brachiopods (e.g. Shen *et al.* 2006) and corals (Wang *et al.* 2006) show similar diversity patterns usually explained by fluctuations of sea level (Ross & Ross 1996), which was high in the Mississippian and low in the Pennsylvanian. The rapid diversification of bryozoans during the Viséan can be explained by filling of niches emptied by the Hangenberg extinction and the lowering of predator stress (Brett & Walker 2002, Sallan *et al.* 2011). The influence of the reduced predation on bryozoan diversification is suggested by a strong decrease of protective morphologies in Carboniferous bryozoans.

Two major extinction events were identified during the Carboniferous: Mid-Tournaisian Event and Mid-Carboniferous Event (Walliser 1996). The Mid-Tournaisian Event has been connected with the worldwide occurrence of anoxic facies as a consequence of a rapid transgression (e.g. Becker 1993). On the contrary, the Mid-Carboniferous Event coincides with a strong regression documented by unconformities (Ramsbottom 1977). It is not known in detail how bryozoans reacted to these events, but generally a drop in diversity during Serpukhovian and Bashkirian is postulated (Ross & Ross 1996). The decline of bryozoan diversity

◄ **Fig. 2.10**: Silurian bryozoans. (A) Surface of bryozoan-rich limestone. Reynales Formation, Hickory Corners Member, Aeronian, Llandovery, Lower Silurian; Hickory Corners, New York, USA. (B, C) Trepostome bryozoans (*Amplexopora crassiparietum* Ernst & Nakrem, 2015) in the Steinsfjorden Formation, Brattstad Member, Silurian, Wenlock, Sheinwoodian-Homerian Ødegårdsviken, Ringerike, Norway (B, rock surface; C, thin section). (D) Boring ctenostome *Rhopalonaria attenuata* Ulrich & Bassler, 1904. Klinteberg beds, Wenlock, lower Silurian. Gothem Hammer 3, Gotland, Sweden. (E) Surface of bryozoan-rich limestone. Rochester Shale, Wenlock, lower Silurian; Niagara Street, New York, USA. (F) Bryoliths (pen 145 mm long). Wenlock, lower Silurian; Nors stenbrott (Blå Lagunan), Gotland, Sweden. (G) Thin section of the bryolith showing bryozoan-microbial crusts. (H) Underside of a stromatoporoid encrusted by cystoporate and trepostome bryozoans. Wenlock, lower Silurian; Ireviken, Gotland, Sweden. (I) Trepostome bryozoan *Monotrypa* sp. Polished slab of a hemispheric colony. Ninase Formation, Jaani Stage, Wenlock, lower Silurian; Kuriku, island Saarema, Estonia. (J) *Phylloporina asperatostriata* Hall, 1852 (Fenestrata, Phylloporinina). Rochester Shale, Wenlock, lower Silurian; Niagara River, New York, USA. (K) *Phaenopora multifida* (Hall, 1883) (Cryptostomata, Ptilodictyina). Reynales Formation, Hickory Corners Member, Aeronian, Llandovery, lower Silurian; Hickory Corners, New York, USA.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