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Resolution of taxonomic issues in the Horneridae (Bryozoa: Cyclostomata)

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1. Introduction

Marine bryozoans in the family Horneridae are large and robust, growing as erect arborescent or fenestrate colonies (Figure 1). Autozooidal apertures generally open only on the frontal side of the colony; the dorsal (or reverse) side, except in the genus *Calvetia*, has no autozooidal openings but may contain inflated brood chambers (gonozooids) roofed by interior wall calcification. Openings of small kenozooidal polymorphs, termed cancelli, occur on both the frontal and dorsal sides of the branches. Longitudinal ridges, sometimes referred to as nervi, may develop between the apertures. There are no calcified exterior walls apart from the small basal lamina.

Representatives of Horneridae occur throughout the world, mainly in cool to cold marine waters and usually at shelf water depths¹ or deeper.² Over 150 species in nine

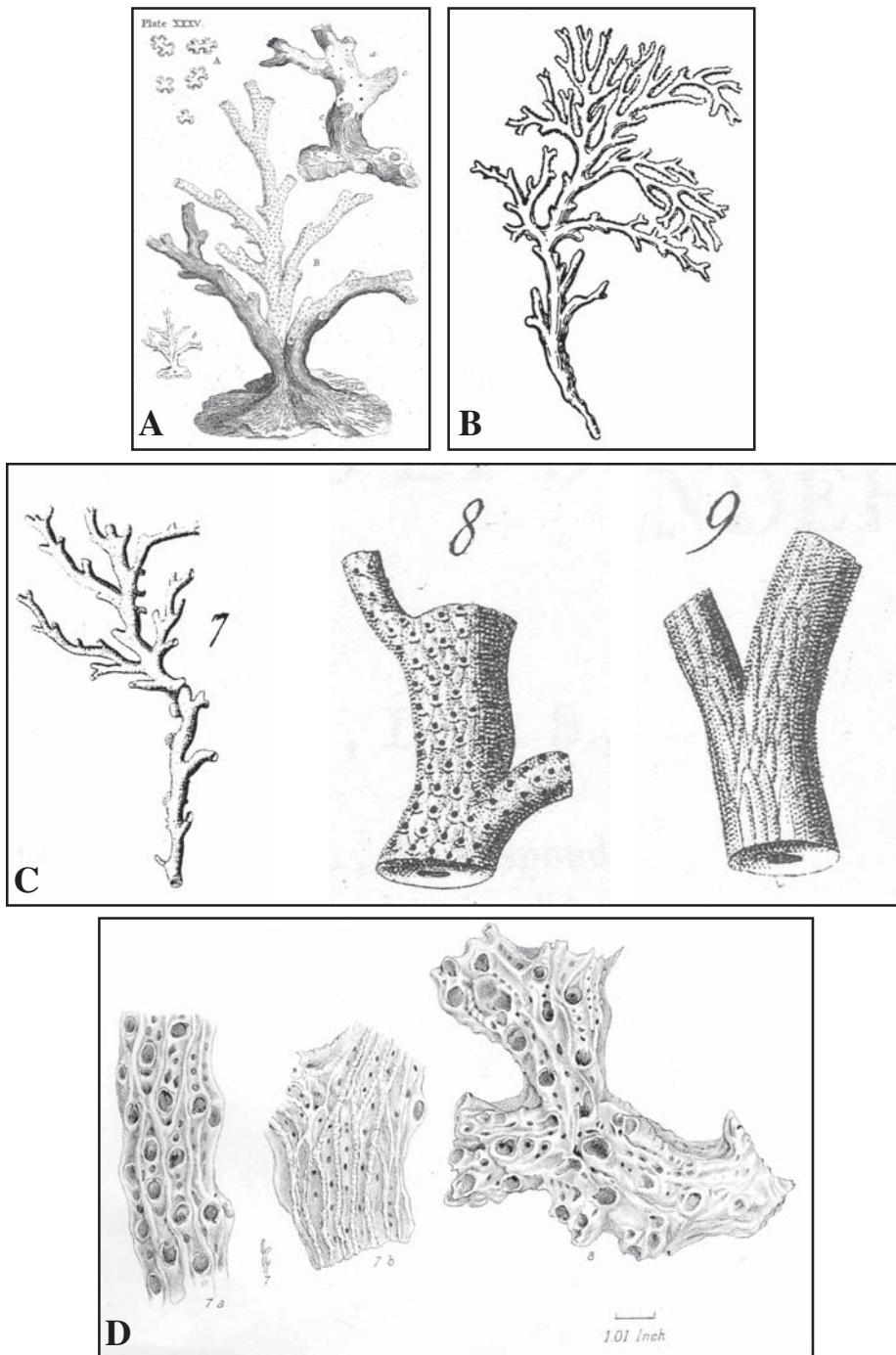


Figure 1. Illustrations of the genus *Hornera*. A. *Millepora lichenoides* (Ellis, 1755, plate 35); B. *Hornera frondiculata* (Bassler 1953, plate 25, fig 1a, p. G59); C. *Hornera frondiculata* (Lamouroux 1821, tab. 74, figs 7-9); D. *Hornera frondiculata* (MacGillivray 1895, Figs 7-8).

genera have been ascribed to the Horneridae, spanning Cretaceous to Recent. Despite having widespread geographical and geological distributions and a fairly extensive literature (for a modern cyclostome), the Horneridae is taxonomically and nomenclatorally vexed. The intent of this paper is to outline and resolve some of these problems.

2. Order Cyclostomata and Suborder Cancellata

The classification of the cyclostomes has long posed problems, chiefly because of a dearth of diagnostic characters. Early systems based mainly on colony shape and zooid geometry³ depended too heavily on characters that are variable and plastic. Indeed, Arthur Waters tellingly remarked⁴ "...I have known that the Cyclostomata must shortly be dealt with, and have looked forward to this with feeling almost of dismay, because the Cyclostomata possess so few characters that can be used for the purposes of determination". Although he went on to add to the small arsenal of characters, arguing that the terminal diaphragm (which he called an opercular plate) which closes off some cyclostome tubes is an important character, Waters later observed⁵ "We do not seem to make much progress with the discouraging Cyclostomata". He was the first to comment that the morphology of the brood chambers (when present) could be a useful aid to species identification in the cyclostomes,⁶ and he also noted discrepancies between classifications of living and fossil cyclostomes.⁷

In 1896 Gregory remarked on the artificiality of genera in the Cyclostomata and reflected sadly that⁸ "there is no hope in this order of ever establishing divisions with the same absolute diagnoses as in most other groups of Invertebrates". Two years later, Harmer⁹ argued for the utility of brood chambers as diagnostic features, and explicitly mentioned *Hornera* as a genus in which they had diagnostic value. Canu and Bassler¹⁰ went on to classify the Cyclostomata based on brood chamber size, form and position. But, as Borg noted¹¹, "it is probably impossible to establish a satisfactory classification of any group of animals by using only one distinguishing character". He also remarked that brood chamber size and form are likely to be too variable to be helpful, calling all the classifications used hitherto¹² "more or less artificial", and commenting that¹³ "the actual position as regards the classification of the Cyclostomata is, with regard to the recent forms, not very encouraging".

Borg's classification¹⁴ of the Cyclostomata was based chiefly on Recent species using three principal groups of characters: colony development, body-wall structure, and brood-chamber structure. In his division Pachystega, comprising only the family Horneridae, colony development is different from most of the rest of the cyclostomes in that the first zooid grows upright from the protoecium (primary disk), as in the Crisiidae but without the joints or rhizoids seen in this unrelated family. The double body-wall structure recognized by Borg is now called free-walled and is found in hornerids, other cancellates, rectangulate and cerioporine cyclostomes.¹⁵ Hornerid brood-chambers are free-walled gonozooids; their dorsal location is unusual, although shared with the tubuliporine family Terviidae.

Brood¹⁶ remarked on the scarcity of cyclostome type material, compounded by poor-quality illustrations and inadequate descriptions. He used the structure of the zooecial walls to delineate suborders but applied a far broader species concept than that of most other bryozoologists.¹⁷

Gregory¹⁸ had already in 1896 erected the suborder Cancellata (equivalent to Borg's Pachystega of 1926¹⁹), named for the cancellate wall structure typical of the Horneridae and Petaloporidae. This suborder contains such families as the Horneridae, Stigmatoechidae, Crisinidae, Cytididae, Petaloporidae, Dipetaloporidae, Canaliporidae, Pseudidmoneidae, Calvetiidae, and Stegohorneridae according to later authors.²⁰ Gregory's taxon Cancellata remains in general use despite suggestions that Borg's Pachystega is preferable²¹ or that it should properly be named suborder Cancellatina.²²

Hayward and Ryland²³ avoided any superfamilial classification within the order Cyclostomata, restricting their list to families. Boardman too used informal groupings, and commented that²⁴ "any sort of natural classification for much of the post-Triassic and Recent species seems unlikely." He noted a great deal of diversity in polypide anatomy and insisted that, where possible, soft-part anatomy should be used in conjunction with skeletal characteristics (internal and external) in species descriptions and identification. Taylor and Weedon²⁵ used a suite of 46 mainly skeletal characters in their cladistic analysis of the Cyclostomata, finding the Cancellata to be monophyletic, nesting within the paraphyletic Tubuliporina and being most closely related to the genus *Fenestulipora* Taylor and Gordon, 1997²⁶ of those analysed.

Despite 250 years of research, the higher classification of cyclostome bryozoans is still problematic. Which characters are truly significant, which are synapomorphies, which plesiomorphous and which homoplasous or ecophenotypic? Are Northern Hemisphere species really found in the Southern Hemisphere? A combined analysis of morphospecies and molecular genetics of living specimens is desperately needed to elucidate cyclostome taxonomy. In the meantime it appears that the suborder Cancellata is fairly robust, based on a suite of skeletal characters,²⁷ and that the family Horneridae properly belongs in this suborder.

3. Family Horneridae

Hornerid bryozoans were first illustrated in 1755 by both Ellis²⁸ (1755, plate 25) and Pontoppidan²⁹ (1755, p. 158) both of whom figured these "corals" under the name *Millepora* (Figure 1A). Still identified as corals, hornerids appear to have been illustrated in other early catalogues³⁰ under various names including *Millepora* and *Retepora*.

The bryozoan genus *Hornera* was formally erected in 1821³¹ by Lamouroux (Figure 1C) who described his new genus as being of an escharid type. In 1834 de Blainville³² moved hornerid bryozoans to the Milleporidae Fleming, 1828, a family of hydrozoan cnidarians, receiving disapproval from Milne Edwards³³ who placed *Hornera* in the cyclostome family Tubuliporidae Johnston, 1838. The family Horneridae was erected for the type genus in 1866 by Smitt,³⁴ who listed two Scandinavian species: *H. violacea* Sars,

1862 (moved to *Stegohornera* in the Stegohorneridae by Borg³⁵), and *H. lichenoides* (Linnaeus, 1758). Busk³⁶ included 6 species of *Hornera* in his British Museum catalogue of 1875, though he did not recognise the family Horneridae, instead placing the genus in the family Idmoneidae Busk, 1859, as did MacGillivray.³⁷ Smitt later³⁸ included the genus *Filisparsa* d'Orbigny, 1853 (subsequently moved to the Oncousoeciidae Canu, 1918 by Canu³⁹) alongside *Hornera* in the family Horneridae. Hincks,⁴⁰ too, listed the family Horneridae in his compendium of British Marine Polyzoa from 1880, and has been wrongly credited as the author of the family in some later publications.⁴¹ Neviani⁴² and Bassler⁴³ placed *Hornera* in the Tubuliporidae, but most authors had adopted the Horneridae by the 20th century.

Authorship of the Horneridae is also sometimes erroneously credited to Gregory, 1899.⁴⁴ Gregory⁴⁵ did place the Horneridae in his suborder Cancellata within the Cyclostomata, but the family was erected by Smitt in 1866.⁴⁶ Smitt's description is minimal: *Gemmificatio lateralis in apice stirpis erectae perficitur; zooecia igitur a latere postico gemmae communis ad frontem coloniae surgunt*. "Lateral budding occurs on the tips of erect stems: therefore the zooids arise on the side of the shared bud at or near the front of the colony." (translated from Smitt⁴⁷).

Bassler contributed more: "Zoaria ramose, erect, attached by expanded base. Zooecia with lamellose or squamose walls traversed by vacuoles which open on all sides of zoarium; zooecial apertures confined to front. Ovicell large, sac-shaped, symmetrically placed on back of zoarium, with lateral oeciostome."⁴⁸ (see also Figure 1). Brood,⁴⁹ too, provided a description of the family.

More than 150 living and fossil species have been described in the Horneridae; of these 115 species in six genera remain there (see Appendix). The 31 or so living species make up about 4% of the estimated 850 species of Recent cyclostomes.⁵⁰ The monospecific genera *Siphodictyum*, *Eohornera* and *Spiniornera*, along with the three species of *Calvetia* (two Recent, one fossil) and four Tertiary species of *Crassohornera* are greatly outnumbered by more than 100 nominal species of *Hornera* (Appendix).

4. Fossil Genera in the Horneridae

Various fossil genera were originally placed in the Horneridae but have since been moved to other families. The Cretaceous genera *Hemicellaria* d'Orbigny, 1850 (type species *H. ramosa*, d'Orbigny, 1850)⁵¹ and *Phormopora* Marsson, 1887 (type species *P. irregularis* Marsson, 1887)⁵² were synonymised with *Filicrisina* d'Orbigny, 1853 (type species *F. retiformis* d'Orbigny, 1853)⁵³ by Canu and Bassler⁵⁴ and later placed in the Petaloporidae.⁵⁵ Brood⁵⁶ reinstated the name *Phormopora* on the basis of its cancellate wall structure but the type species seems to be a fixed-walled tubuliporine on the basis of his figures 5 and 6.

Brien⁵⁷ listed two additional Cretaceous genera in the Horneridae: *Osculipora* d'Orbigny, 1849⁵⁸ and "*Trinicolula* Hogenow, 1851". *Trinicolula* appears to be a misspelling (as well as Hogenow). We have been unable to find any other reference to this genus (in, for

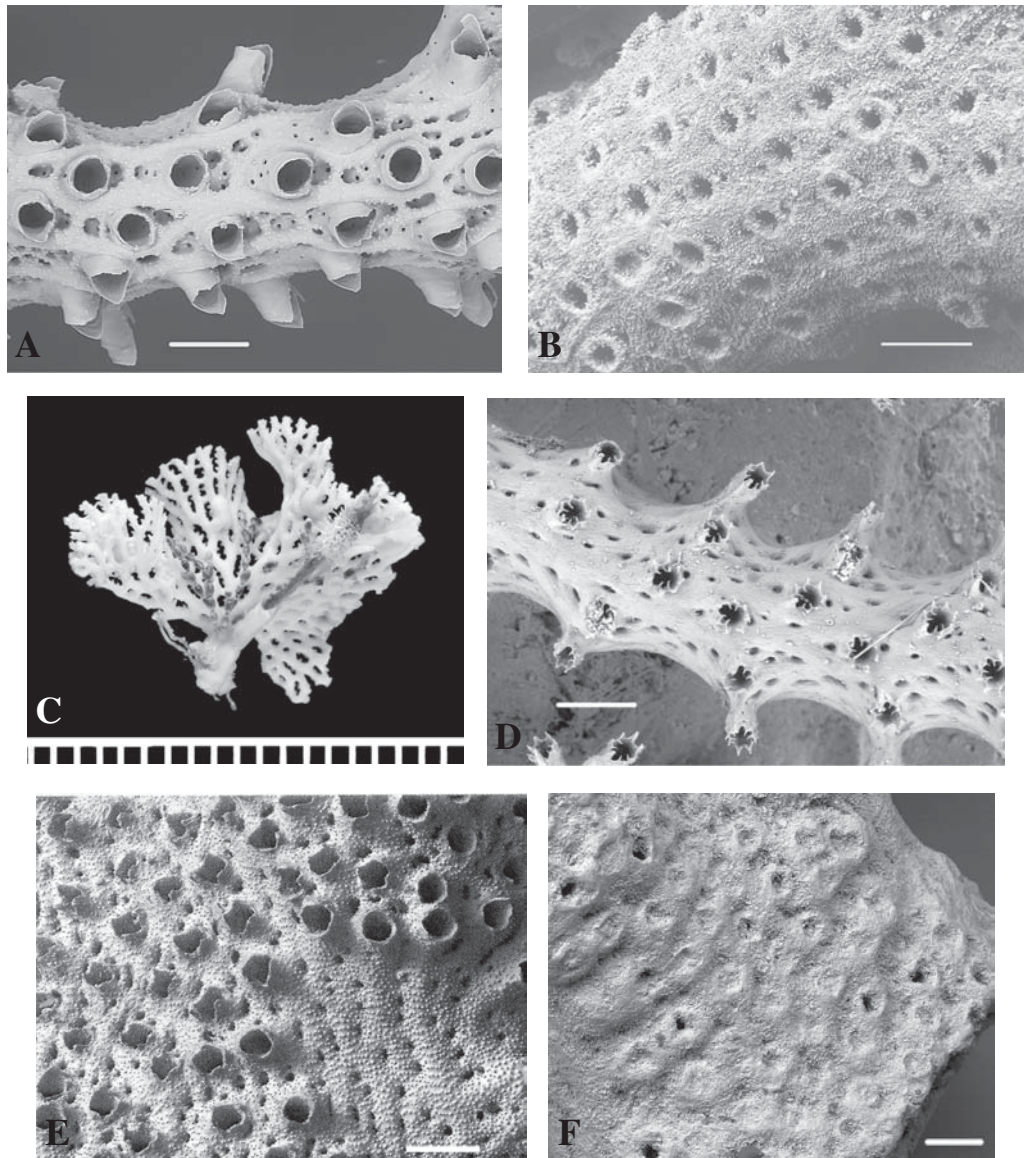


Figure 2. Genera in the Horneridae (scale bars = 200 μm , except C where scale is in mm). A. *Hornera frondiculata* from the Mediterranean (Natural History Museum London reg. no. 2002.6.19.25); B. *Hornera striata* from the Pliocene of Suffolk, England (Natural History Museum London reg. no. D6897); C. *Retihernera corbicula* (Natural History Museum London reg. no. 69.12.3.6); D. *Spinihernera spinigera* from the Indian Ocean (type, Natural History Museum London reg. no. 88.1.25.87); E. *Calvetia osheai* from New Zealand (National Institute of Water and Atmosphere Wellington reg. no. P-1343); F. *Crassohornera waipukerensis* from New Zealand (type, Manchester Museum Manchester reg. no. H.1186).

example: *Zoological Record*, Google Scholar, ITIS Catalogue of Life, or *Nomenclator Zoologicus*). Von Hagenow did, however, describe a fossil called *Truncatula* in 1851,⁵⁹ apparently unaware that the name had earlier been used by Leach in 1847⁶⁰ for a gastropod, so that later Bassler⁶¹ proposed the new name *Truncatulipora* for this genus. The type species is *Truncatula filix* von Hagenow, 1851, a Maastrichtian fossil from The Netherlands. Both *Osculipora* and *Truncatulipora* appear to belong in the Cytididae d'Orbigny, 1853.⁶²

A Cretaceous-Paleocene genus, *Retecava* d'Orbigny, 1853,⁶³ type species *Retecava clathrata* Goldfuss, 1827,⁶⁴ was placed in the Horneridae by Canu,⁶⁵ moved to the Tubuliporidae by Bassler⁶⁶ and then transferred back to the Horneridae by Brood⁶⁷ because of its cancellate wall structure. *Retecava* differs from *Hornera* in that the apertures are always arranged in lateral series, the branches are flattened and bifoliate, and the gonozooid is frontally placed.⁶⁸ These features, plus the exterior-walled gonozooid (PDT unpublished), exclude *Retecava* from the Horneridae.

The genera *Stegohornera* Borg, 1944⁶⁹ and *Horneroides* Kluge, 1946⁷⁰ were placed in the Stigmatoechidae Borg, 1944 by Brood.⁷¹ The Ordovician-Silurian genus *Pseudohornera* Roemer, 1876⁷² was placed by Ulrich in 1890⁷³ into his new family Phylloporinidae, and the cryptostome affinities of this genus are clear from the detailed morphological study of Brood.⁷⁴

Three post-Palaeozoic fossil genera may, however, remain in the Horneridae: *Crassohornera*, *Eohornera* and *Siphodictyum*. The type species of *Crassohornera* Waters, 1887, *C. waipukurensis* Waters, 1887⁷⁵ (Figure 2F), comes from the Pliocene of New Zealand. Julien⁷⁶ incorrectly equated this genus with *Ceriopora* Goldfuss, 1827⁷⁷ but for some reason retained the junior synonym. Another species assigned to *Crassohornera* by Canu and Bassler⁷⁸ is *Ceriopora arbusculum* Reuss, 1848⁷⁹ from the European Cenozoic. Bobies⁸⁰ in 1958 described *Crassohornera densipunctata*, which Mongereau⁸¹ subsequently regarded as a species of *Hornera* with fewer than usual nervi, although Vávra⁸² retained the species in *Crassohornera*. Mongereau⁸³ claimed that the genus *Crassohornera* was of doubtful validity, but it is still occasionally used. Hara,⁸⁴ for example, referred an unnamed species from the Antarctic Eocene to *Crassohornera*.

Eohornera Brood, 1972,⁸⁵ with the type and only species *Retepora langethalii* von Hagenow, 1839, is an Upper Cretaceous genus from Germany, Sweden and Denmark that differs from *Hornera* in having a frontal gonozooid and nanozoocia. Although von Hagenow's material is lost, some of Brood's specimens reside at the Geological Institute at the University of Stockholm. Scanning electron microscopy of material from the E. Voigt Collection (PDT unpublished) raises doubts over the placement of this genus in the Horneridae: not only is the gonozooid frontal, but it is roofed by pseudoporous exterior wall calcification contrasting with the interior wall calcification of other hornerid gonozooids. Further research is needed to resolve the issue of its taxonomic position.

The Barremian-Aptian genus *Siphodictyum* Lonsdale, 1849, type species *S. gracile* Lonsdale, 1849,⁸⁶ closely resembles *Hornera*. Colony branches have a distinct dorsal side covered by kenozooids and housing the interior-walled gonozooid. Beneath each autozooidal aperture on the branch frontal surface, however, is a tiny pore, a feature not

present in *Hornera*. Placed in the Horneridae by Gregory⁸⁷ and the Ascosoeciidae by Canu and Bassler,⁸⁸ this genus was subsequently moved by Bassler⁸⁹ to the Petaloporidae Gregory, 1899 but returned to the Horneridae by Pitt and Taylor.⁹⁰ Viskova⁹¹ recently described a new Middle Jurassic (Callovian) bryozoan from the Moscow region of Russia as *Siphodictyum primarium*. However, it is clear from her description and illustrations that this bryozoan does not belong to *Siphodictyum* but is a tubuliporine. The vacuoles (cancelli) described by Viskova are actually overgrowths, autozooids are fixed-walled, and the diagnostic free-walled cancellate brood chamber is lacking.

5. Genus *Hornera*

The genus *Hornera* was erected in 1821 by Lamouroux⁹² for the Recent species *Hornera frondiculata* Lamouroux, 1821, which is thus the type species of the genus by monotypy. The genus was named for Johann Kaspar Horner (1774–1834) of Zurich. He was a mathematician and astronomer who accompanied naturalist Dr. Wilhelm Gottlieb Tilesius, also known as Vilgelm Gotlob von Tilenau (1769–1857), on an early Russian circumnavigation of the world's oceans, commanded by Estonian Captain Adam Johann von Krusenstern (1770–1846). The dedication by Lamouroux reads: "This polyzoan is dedicated to Mr. Horner, astronomer with the expedition around the world commanded by Captain Krusenstern, in the name of his friend Mr. Tilesius" (translated).⁹³ *Hornera* has been occasionally misspelled *Horneria*.⁹⁴

Jean Vincent Félix Lamouroux (1776–1825) was, by all accounts, an enthusiastic and successful professor of natural history who founded the Muséum d'Histoire Naturelle de Caen. He concentrated his research on algae, polyps and zoophytes (as they were then called), describing well over 500 species in the course of his career, and was honoured in his lifetime by awards from many scientific academies.⁹⁵ His collection was lodged in Caen; those specimens that survived World War 2 are now lodged in Paris at the Muséum National d'Histoire Naturelle. As far as can be determined, his specimens of *Hornera* were destroyed.

Lamouroux's description of *Hornera* focused on characteristics of the whole colony: *Polypier pierreux, dendroïde, fragile, comprimé et contourne irrégulièrement; tige et rameaux garnis de cellules sur la face extérieure; cellules petites, éloignées les unes des autres, situées presque en quinconce sur des lignes diagonales; face opposée, légèrement sillonnée*.⁹⁶ = "Colony is stony, tree-like, fragile, twisted and turning irregularly; stalk and branches covered with pores on the external surface; little pores quite well spaced, arranged in staggered rows on diagonal lines; the opposite face is lightly fluted."

Busk⁹⁷ added that the branches can be free or "united by short transverse ramules so as to constitute a retiform expansion." He also commented that branches of "the true *Hornerae*" have a particularly fibrous or striated texture.

Mongereau described the genus more precisely: *Le zoarium est fixé par un disque basal forme par des tubes accessoires. Les premiers tubes sont érigés, il n'y a pas de stade encroûtant. Les branches du zoarium peuvent rester libres ou s'anastomoser. Les*

*ramifications sont dichotomiques. La section des branches est semi-circulaire, circulaire, ou elliptique. Le zoarium présente une face frontale dite supérieure et un face dorsale dite inférieure. La face frontale montre les peristomes bordés par les nervi qui limitent les sulci garnis de vacuoles. L'ovicelle est dorsale et correspond à la partie terminale dilatée d'un gonozoïde. L'oeciostome est en position variable.*⁹⁸ = "The zoarium is mounted on a basal disk formed by secondary tubes. Primary tubes are erect; there is no encrusting stage. The branches of the zoarium can stand free or anastomose. Branching is dichotomous, and the cross-section of branches is round, semicircular, or elliptical. The zoarium has a frontal, or superior, face and a dorsal, inferior face. The frontal face shows peristomes bordered by nervi which limit the sulci, perforated by vacuoles. The brood chamber is dorsal and corresponds to the terminal dilated part of a gonozooid. The ooeciostome is variable in position."

Even in 1859, when only a few species of *Hornera* had been described, George Busk in his monograph of fossil bryozoans from the Plio-Pleistocene Crags of eastern England reflected on the difficulty of working with the genus: "No genus in the whole of this Memoir has required more time or closer examination, and it is only after the most mature consideration that I have arrived at the not very certain conclusions here stated".⁹⁹ He blamed the extreme degree of variation in morphology within a single colony for the difficulty; they "could not fail, from their extreme diversity, to lead to the conclusion that they belonged to distinct species or even genera." Canu and Bassler went so far as to say that: "The variations in this genus are extraordinary and it is often useless to attempt to determine an isolated specimen".¹⁰⁰

Four species of putative *Hornera* (*Hornera verrucosa* Jullien and Calvet, 1903; *H. eburnea* Jullien and Calvet, 1903; *H. galatea* Smitt, 1872 and *H. gravieri* Calvet, 1911) described from the Azores and Florida¹⁰¹ subsequently proved to be stylasterine hydrocorals¹⁰². These and other species originally in the Horneridae that have subsequently been moved to other taxa (e.g., Petaloporidae) are listed in the Appendix for completeness, but given in bold typeface.

Of the 105 species listed in the genus *Hornera* (Appendix), some 38 (36%) have type specimens known still to be in existence (Figure 3A). A further 18 (17%) have at least partial type information available, but 49 species (47%) have type material that is missing, destroyed, or has not been identified.

Only 18 (16%) *Hornera* species have been reported solely from the Recent, with a further five from the Cenozoic and Recent (Figure 3B). Twelve species were reported from the Cretaceous or Cretaceous and Cenozoic. The majority, 58 species (52%), have been reported from the Cenozoic. For 11% of species, the geological age is unknown or unreported).

The genus is dominantly temperate, with only 5% of species found in tropical or subtropical areas (Figure 3C). The dominance of northern temperate (50%) over southern temperate (19%) species may, however, reflect the distribution of researchers as much as that of the bryozoans.

Knowledge of the taxonomy of *Hornera* languished for almost a century until

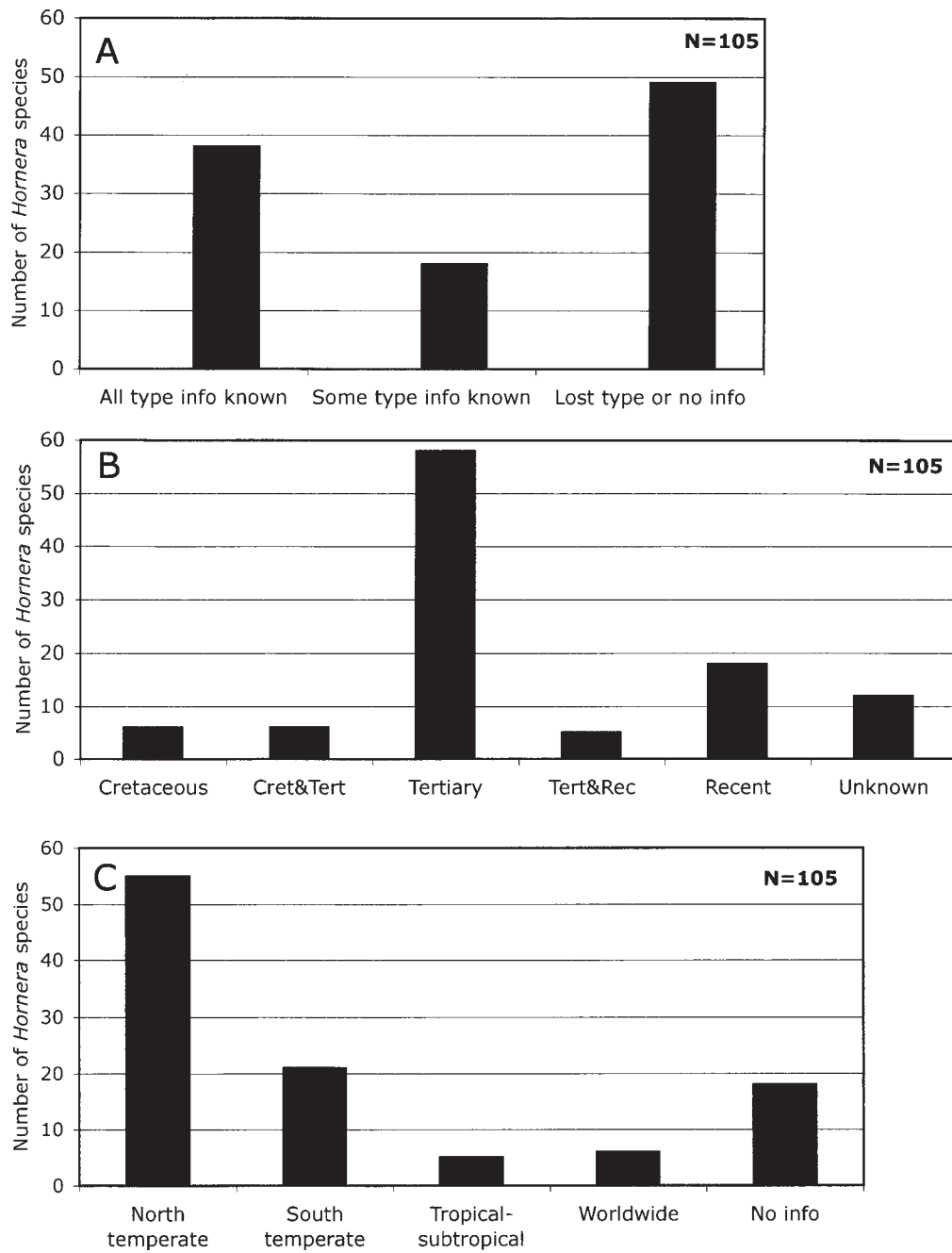


Figure 3. Characteristics of species in the genus *Hornera*. A – availability of type material; B – Distribution through time; C – Geographical distribution. Data from Appendix.

Mongereau¹⁰³ substantially revised it, retaining 26 of 54 European species ranging from the Eocene to Recent.

6. Genus *Retihornera*

The genus *Retihornera* was erected by Kirchenpauer in 1869¹⁰⁴ for six species of Australian and South Sea bryozoans with fenestrate colony forms: *R. graeffei*, *R. affinis*, *R. plicata*, *R. parasitica*, *R. dentata*, and *R. corbicula*. Of these *R. graeffei* appears to have been already described as *Kirchenpaueria elegans* Graeffe in an unpublished MS (according to Harmer's notebooks¹⁰⁵). *Kirchenpaueria* Jickeli, 1883 is, however, currently in use as a genus of Northern Hemisphere hydroids.

Kirchenpauer himself did not assign his new genus to a particular family, though he did note its similarity to *Hornera* (which he placed in the Idmoneadae [sic]). In 1875 Busk¹⁰⁶ added MacGillivray's¹⁰⁷ Australian *H. foliacea* to the genus and suggested it could be synonymous with *R. dentata* and *R. plicata* (expressing, however, some doubt in his notes). He commented that Kirchenpauer's new genus appeared to contain some *Retepora*-like cheilostomes, but recommended that *Retihornera* be retained as a cyclostome genus for fenestrate relatives of *Hornera*.

A type species for *Retihornera* was not designated by Kirchenpauer and, to our knowledge, none has ever been selected subsequently. Kirchenpauer listed *R. graeffei* first in his descriptions (p.30), but *R. corbicula* headed his master list (on p. 119). Unfortunately, none of the six species listed by Kirchenpauer in his new genus has a recognised type specimen (but see below). *R. graeffei* has been placed in *Reteporella*,¹⁰⁸ *R. affinis* has been synonymised with *H. frondiculata*,¹⁰⁹ and *R. parasitica*, *R. plicata*, and *R. dentata* were each described by Kirchenpauer as unusual or atypical in some way. Two Kirchenpauer specimens of *R. plicata* exist in the collections of the Zoologisches Museum der Universität Hamburg; these are numbers B 424 and B 538, both from the Gulf of St Vincent.¹¹⁰ *R. corbicula* is apparently more typical of the genus as it was used, was listed by Kirchenpauer as "common", and furthermore there is an extant specimen of this species in London. As first revisers we therefore designate *Retihornera corbicula* Kirchenpauer, 1869 to be the type species of the genus. Only one Kirchenpauer specimen of this species is known to be in existence and it is deemed to be the type (holotype if no other specimens are found, lectotype should additional syntypes be forthcoming). The details of this fertile colony (Figure 2C) are: Natural History Museum (London), spirit collection specimen no. 69.12.3.6, no locality details, purchased from W. J. D. E. Schmelz (who wrote the forward to Kirchenpauer's 1869 work).

From 1869 to 1884 *Retihornera* was used, as suggested by Busk,¹¹¹ for fenestrate hornerids from the Southern Hemisphere. Hutton,¹¹² for example, listed *R. foliacea* MacGillivray and *R. gouldiana* Busk in his *Manual of the New Zealand Mollusca* of 1880. Waters¹¹³ returned in 1884 to the use of *Hornera foliacea* MacGillivray, as did MacGillivray¹¹⁴ himself two years later. Busk in 1886 agreed, stating that he no longer regarded *Retihornera*: "as forming more than a subgenus, as in all essential characters it

perfectly agrees with such forms as *Hornera lichenoides*...”¹¹⁵

The Rev. Julian Tenison-Woods described a fossil bryozoan from New Zealand which he called “provisionally” *Retehornera* [sic] *haastiana*, despite the single specimen being¹¹⁶ “imperfect... imbedded in stone, face downwards, and the cells are not visible.” He referred to Kirchenpauer as the author of this genus and noted that there was a living representative in New Zealand waters (probably *Retihornera foliacea*, now usually known as *Hornera foliacea*); clearly Tenison-Woods (and later Whitten¹¹⁷) misspelled *Retihornera* and did not intend to erect a new genus. “*Retehornera*” did not appear in any contemporaneous or subsequent listings¹¹⁸ or New Zealand works,¹¹⁹ though the species *Hornera haastiana* (Tenison-Woods, 1880) reappeared much later.¹²⁰

By 1889, all described *Retihornera* species had been assigned to different genera.¹²¹ *R. foliacea* (MacGillivray, 1868) and *R. parasitica* Kirchenpauer, 1869 were moved into *Hornera*. *R. dentata* Kirchenpauer, 1869, *R. plicata* Kirchenpauer, 1869, *R. corbicula* Kirchenpauer, 1869, *R. squamosa* Hutton, 1873, and *R. gouldiana* Busk, 1875 were all synonymised with *H. foliacea* MacGillivray, 1868. *R. affinis* Kirchenpauer, 1869 was subsumed within *H. frondiculata* Lamouroux, 1821. *R. graeffei* Kirchenpauer, 1869 was synonymised with the cheilostome species *Retepora producta* Busk, 1886 by Jelly who, inexplicably, retained the younger name.¹²² It has since been interpreted¹²³ as a distinct species of cheilostome, *Reteporella graeffei* (Kirchenpauer, 1869).

Future research, particularly using molecular methods, may possibly show that Southern Hemisphere fenestrate hornerids are sufficiently distinct to warrant a separate genus. If this proves to be the case, the genus *Retihornera* is available to be re-instated once the type species has been carefully described. Fossil fenestrate hornerids from the Northern Hemisphere should then be re-evaluated as they may or may not also belong within *Retihornera*.

7. Genus *Spiniornera*

The genus *Spiniornera* Brood, 1979 was proposed¹²⁴ for *Hornera spinigera* Kirkpatrick, 1888¹²⁵ from the Recent of the Indian Ocean (Figure 2D), which had previously been described and figured by several others.¹²⁶ It has characteristic pinnate branches and zooids arranged in lateral lines with numerous apertural spines. The holotype is held at the Natural History Museum in London.

8. Genus *Calvetia*

The Calvetiidae (sole genus *Calvetia* Borg, 1944¹²⁷) was considered to be a related family but has recently been subsumed within the Horneridae.¹²⁸ The type species of *Calvetia* is *C. dissimilis* Borg, 1944 from the Recent of Patagonia, and *C. osheai* (Figure 2E) is a new addition to the contemporary New Zealand fauna.¹²⁹ An unnamed Eocene species of *Calvetia* has also been described from Antarctica.¹³⁰

9. The type species of *Hornera*

Hornera frondiculata Lamouroux, 1821 was listed by Lamouroux¹³¹ (see Figure 2A) as the only species of his new genus, which makes it the type species by monotypy. Although this erect frondose bryozoan is commonly reported from Europe, ranging from the Miocene to Recent, the type material evidently came from the Kamchatka Peninsula in the North Pacific.

Lamouroux listed three tentative synonyms for his new species: *Millepora tubipora* Ellis & Solander, 1786,¹³² *M. lichenoides* Linnaeus, 1758,¹³³ and *Retepora frondiculata* Lamarck, 1816.¹³⁴ He was apparently not at all sure how well these previously-described “corals” fitted into his new genus; all his presumed synonyms are annotated with question marks. It is clear from examining other parts of Lamouroux’s article that where he was more certain he listed synonyms unadorned.

One of these tentative synonyms, *Millepora lichenoides* Linnaeus, 1758, has generally since been regarded as the distinct boreal species *Hornera lichenoides* (Linnaeus, 1758). It is possible, albeit unlikely given their respective distributions, that these two names refer to the same biological species.

The identity of a second synonym, *M. tubipora* Ellis & Solander, 1786, is not clear, but this name has not been used for a hornerid species for over 100 years. Most workers have considered it to be a synonym of *M. lichenoides*; indeed Ellis and Solander listed *M. lichenoides* Linnaeus as a synonym in their description.¹³⁵ Almost certainly, this name can be formally synonymised with *Millepora lichenoides*.

The third tentative synonym, *Retepora frondiculata* Lamarck, 1816, is potentially a senior homonym of *H. frondiculata* Lamouroux, 1821 if the two nominal species are considered congeneric. Lamarck’s material came from the Mediterranean and it is quite likely that his and Lamouroux’s species of the same name are different biological species (i.e., they are not synonyms).

Prevailing usage clearly favours the name *H. frondiculata* Lamouroux. Lonsdale (1849), de Blainville (1834) and Milne Edwards (1838) registered unqualified acceptance of Lamouroux’s authorship,¹³⁶ as did subsequent authors, although sometimes reluctantly.¹³⁷ Busk explicitly approved of “taking the common Mediterranean *Hornera frondiculata*, Lamx, as the type of the genus...”¹³⁸ calling it “the well-known Mediterranean form, originally figured by Ellis, subsequently named *Hornera frondiculata* by Lamouroux, and which has since been figured and described by Milne Edwards”. After 1899, only Neviani in 1900¹³⁹ has used *H. frondiculata* Lamarck, but this sole example, by a single year, means that ICZN Article 23.9.1 cannot be invoked to preserve Lamouroux’s name. Assuming that both species are members of *Hornera*, the only way for this usage to be preserved is to apply to the ICZN for a ruling under Article 23.9.3. It is our intention to do so and, in the interim, use of the junior homonym *Hornera frondiculata* Lamouroux, 1821 is to be maintained.

One potential problem with this approach is that “prevailing usage” refers mostly to Mediterranean Recent specimens and fossil specimens from the European Tertiary.

Suppression of Lamarck's name by the Commission would mean that this usage would not be preserved if Kamchatka specimens proved to be separable. Nevertheless, the only alternative (i.e., using Lamarck's name) would not preserve existing usage either.

What we do not know (because Lamouroux's material is lost) is whether this Mediterranean species is indeed the same as the Kamchatkan species described by Lamouroux. The geographical distance between the Mediterranean and the Pacific suggests that the two occurrences may be different species.

Lamouroux's description of *H. frondiculata* from Kamchatka was short and not particularly diagnostic: *Ramifications presque flabelliformes, irrégulièrement countournées: grandeur, environ un decimetre: coulour blanche un peu rosée.*¹⁴⁰ = "Structure almost fan-shaped, irregularly twisted; size about 10 cm; colour white or slightly pink." Such a description could fit many species of *Hornera* known today. Examination of topotypic material (in the absence of the type material) is clearly necessary to determine whether Lamouroux's *H. frondiculata* is really the same as the common Mediterranean species that also bears that name.

Buge¹⁴¹ noted that Canu and Lecointre¹⁴² and Lagaaij¹⁴³ had added greatly to Lamouroux's description with good illustrations. In both cases, however, they were examining European material. Waters¹⁴⁴ described the brood chambers of supposed *H. frondiculata*, and though he did not specify the locality, it appears to have been Busk's material and is therefore most probably European.

Hornera frondiculata is the most frequently cited species name in the genus *Hornera*. Our appendix gives 58 citations for the species (19 in the last 50 years), well ahead of the next most cited species (*H. striata* with 40 citations). Recent specimens identified as *H. frondiculata* have been described from the Mediterranean Sea, eastern Atlantic, Red Sea, and Kamchatka, in water depths ranging from 40 to 200 m. Cenozoic fossil examples have been described from all over Europe, Morocco and Australasia.

Citations from 1821 to 1972 appeared to have developed a coherent, though probably incorrect, view of what was meant by *H. frondiculata* Lamouroux, 1821 – a common and typical hornerid from the European Cenozoic and Recent of the Mediterranean and elsewhere (Figure 2A). However, Noël Mongereau's revision of *Hornera*¹⁴⁵ complicated matters. This work was based on extensive (mainly fossil) collections from across Europe. Mongereau's material of putative *H. frondiculata* included a few Recent specimens from the Mediterranean Sea and fossils from the Cenozoic of Britain, France, Austria, Italy, Poland and Belgium. Unfortunately, he had no material from the type locality in Kamchatka. He described in detail the difficulty of distinguishing between *H. frondiculata* and *H. striata* Milne Edwards, 1838 (Figures 2A,B), claiming that he had seen characteristics of both (as well as a third undescribed morphology) on branches in a single colony.¹⁴⁶ He argued that there are three distinct morphologies (possibly ontogenetic stages) visible within this single species. As a consequence, he synonymized *H. striata* with *H. frondiculata* and delineated the morphological differences by the creation of three "formes" – a term analogous to "variant" – that is, infrasubspecies.

In the absence of Lamouroux's original type material of *H. frondiculata*, Mongereau

designated a neotype from the Mediterranean (Muséum National d'Histoire Naturelle, Paris d'Orbigny Collection, 13773) and named it "*Hornera frondiculata* AUCT. forme *frondiculata* nov." For *Hornera striata* Milne Edwards, 1838, he designated a neotype from the Pliocene Coralline Crag (Natural History Museum, London, D6897, S.V. Wood collection – note its number is not B-6897 as listed by Mongereau; Figure 2B) and called it "*Hornera frondiculata* AUCT. forme *striata* Busk, 1859". Presumably he gave Busk the credit for this forme because the neotype came from the Coralline Crag material described by Busk.¹⁴⁷ D'Hondt¹⁴⁸ has recently identified a specimen (MNHN Paris, Milne Edwards Collection, No. 4417) which appears to be Milne Edwards' original type specimen or perhaps a syntype of *H. striata*. Mongereau further separated out a new forme which he called "*Hornera frondiculata* AUCT. forme *lagaaiji* nov", designating a type from the S.V. Wood Collection at the Natural History Museum, London (D38451).

Mongereau attempted to establish time ranges for these "formes" – *frondiculata* ranging from the Eocene to the present, *striata* from the Eocene to Pliocene, and *lagaaiji* from the Miocene to perhaps the Pleistocene. After all this, he noted (translated) that "It is beyond doubt that *H. frondiculata* does not correspond to a biological species, but is a 'paleontological ensemble'".¹⁴⁹ This statement is remarkable given that *H. frondiculata* was originally described from the Recent.

Finally, Mongereau moved nine *Hornera* species (*affinis*, *bipunctata*, *fibrosa*, *loevis*, *pertusa*, *porosa*, *radians*, *rhomboidalis*, *trabecularis*; see Appendix for authorships) into one or more of these formes. In each case he described the distribution of all three formes within Europe but not elsewhere, despite listing worldwide distributions of other species in the same publication.

Mongereau did not appear to have understood that the type specimen of *H. frondiculata* came from the northern Pacific, near Kamchatka. He did not even list Kamchatka in its distribution, and made no attempt to acquire topotypic material with which to compare his extensive European material. This omission means that his observations about *H. frondiculata* apply to the Mediterranean species known by that name and not necessarily to *H. frondiculata* sensu-stricto. His neotype for *H. frondiculata* forme *frondiculata* in particular, being from Europe, is not from the type locality and is therefore invalid according to Rule 75.3.6 of the ICZN. The neotype of forme *striata* is at least from the Coralline Crag, which was the type locality for *Hornera striata* (Milne Edwards, 1838). However, as noted above, d'Hondt¹⁵⁰ has reported the rediscovery of Milne Edwards' type of *H. striata*. Under Rule 75.8 of the ICZN, the neotype is set aside.

If Mongereau was correct and he did observe "*striata*-like" branches co-existing with "*frondiculata*-like" branches on the same colony, then some taxonomic changes were certainly necessary. Because the three forms appeared to occur on the same colony, never mind in the same population, they cannot be distinct subspecies. The correct action would have been to synonymize the three forms under *Hornera frondiculata* Lamouroux, 1821, acknowledging that this species is highly variable.

Mongereau's use of the authorship *auctorum* for *Hornera frondiculata* seems unusual to say the least. He justified it by saying that "this choice might be considered as

incorporating a synthesis of diverse studies that have been dedicated to this species”¹⁵¹ (translated). If, as seems likely, European so-called *H. frondiculata* is different from the true *H. frondiculata*, as defined by topotypic Kamchatkan material, then a new name (perhaps *H. striata* Milne Edwards, 1838) will be required for the European species, but merely designating it *auctorum* is not a satisfactory solution.

If Mongereau had erected subspecies then the proper designation for the type subspecies should have been *H. frondiculata frondiculata* Lamouroux, 1821. Similarly, the credit for *H. frondiculata* forme *striata* properly belongs to Milne Edwards, who described *H. striata*, not to Busk (even though Busk described and illustrated what was to become Mongereau’s neotype). Braga and Barbin,¹⁵² for example, referred to this taxon as “*Hornera frondiculata* AUCT forma *frondiculata* Mongereau, 1972”, adding further complexity to the attribution of authorship.

The taxonomic status of Mongereau’s three “formes” is apparently infrasubspecific, and thus not covered by the ICZN.¹⁵³ As the “formes” are flawed both taxonomically and nomenclatorally, we recommend that they be discarded. Indeed, subsequent authors working with European hornerid fossils appear to have dispensed with Mongereau’s modifications. Vávra¹⁵⁴ (1979), for example, listed *H. frondiculata* Lamouroux, 1821 and *H. striata* Milne Edwards, 1838 from the Miocene of Styria, Austria. While he mentioned Mongereau’s “formes” in his synonymy, he retained the more traditional species. So too did Zágorský and Hukáková¹⁵⁵ working on fossils from the Vienna Basin. Moissette et al.¹⁵⁶ and Moissette and Saint Martin¹⁵⁷ retained the synonymy of *H. frondiculata* and *H. striata*, uniting them under the older name *Hornera frondiculata* Lamouroux, 1821. The only palaeontological study in Europe using Mongereau’s terminology is apparently that of Braga and Barandin¹⁵⁸ who listed fossils from Italy. Identification guides for living species¹⁵⁹ state only that the type species for the genus is *Hornera frondiculata* Lamouroux, 1821. There appear to have been no further references to *H. frondiculata* forme *lagaaiji*.

The consensus view from the literature is that *Hornera frondiculata* Lamouroux, 1821 is a common but highly variable species. There is less agreement on whether the fossil *H. striata* Milne Edwards, 1838 is a variant or a separate species. The neotypes erected by Mongereau for these two species are either invalid (*H. frondiculata*) or no longer have type status (*H. striata*).

While we have managed here to elucidate some of the problems associated with the type species of *Hornera*, more remains to be done. Topotypic material of *H. frondiculata* must be acquired and compared with Mediterranean Recent material as well as European fossil material that is commonly identified as this species. A morphological study comparing differences and similarities with *H. striata*, as well as the nine species synonymised by Mongereau, should also be undertaken.

10. Summary and Conclusions

Much taxonomic confusion has arisen over the years in relation to the hornerid bryozoans. Ranging from minor errors of attribution to wholesale taxonomic carnage,

here we summarise the points raised.

- The higher taxonomy of the Horneridae is currently: Phylum Bryozoa Ehrenberg, 1831; Class Stenolaemata Borg, 1926; Order Cyclostomata Busk, 1852; Suborder Cancellata Gregory, 1896.

- The family Horneridae was erected in 1866 by Smitt,¹⁶⁰ and not in 1880 by Hincks¹⁶¹ or in 1899 by Gregory¹⁶² as is sometimes stated.

- The family Horneridae contains the Recent genera *Hornera* Lamouroux, 1821, *Calvetia* Borg, 1944 and *Spiniornera* Brood, 1979. Both *Retiornera* Kirchenpauer, 1869 and its misspelling *Retehornera* have been synonymised with *Hornera*, despite the fact that the fenestrate colonial form appears to be a potentially useful diagnostic character. *Retiornera* is, however, available for future delineation of fenestrate hornerid bryozoans. We designate *Retiornera corbicula* Kirchenpauer, 1869 the type species of the genus, and we erect a neotype from the collections of the Natural History Museum, London.

- The family Horneridae provisionally contains three additional extinct genera: *Siphodictyum* Lonsdale, 1849, *Crassohornera* Waters, 1887, and *Eohornera* Brood, 1972, although the exterior-walled brood chamber of the latter places a major question mark over its assignment to this family. There is little reason for placing a fourth genus, *Retecava* d'Orbigny, 1853, into the Horneridae. Some other genera once placed in the Horneridae are now assigned elsewhere, including: *Hemicellaria* d'Orbigny, 1850, *Phormopora* Marsson, 1887, *Osculipora* d'Orbigny, 1849, *Truncatula* (sometimes misspelled *Trinicolula*) von Hagenow, 1851, *Stegohornera* Borg, 1944, *Horneroides* Kluge, 1946 and *Pseudohornera* Roemer, 1876.

- The genus *Hornera* Lamouroux, 1821 (sometimes misspelled *Horneria*) currently contains 105 nominal species. Half of these species are from the northern temperate and 19% from southern temperate regions, the remainder from elsewhere or unknown locations.

- Geologically, the earliest records of *Hornera* are from the Eocene, as it is doubtful if any of the 12 species recorded from the Cretaceous truly belong in this genus. The majority of species of *Hornera* (52%) are Cenozoic fossils; only 18 species have been described from the Recent. The stratigraphical range of the Horneridae currently extends back to the Barremian stage of the Early Cretaceous.

- The type species of *Hornera*, *H. frondiculata*, was originally described by Lamouroux (1821), with a rather unclear synonymy. While the argument can be made that Lamarck (1816) is properly the author of this species, almost every paper over the last 200 years, credits the species to Lamouroux (1821), and we will apply to the ICZN for a ruling under Article 23.9.3 that this usage continue. Whether the European material identified as *H. frondiculata* is really this species is doubtful given that the type material of *H. frondiculata* came from Kamchatka in the North Pacific. At least some of the European material may be *H. striata* Milne Edwards, 1838.

- Mongereau's¹⁶³ classification of *H. frondiculata* into three "formes" is without utility, is not covered by the International Rules of Zoological Nomenclature and should be

discarded.

• Lamouroux's type specimen (now destroyed) of *H. frondiculata* was from Kamchatka. The neotype erected by Mongereau for *H. frondiculata* forme *frondiculata*, from the Mediterranean, is therefore invalid as it is not topotypical. A detailed study of *Hornera frondiculata*, both living and fossil from a wide range of localities, looking carefully at similarities with *H. striata*, should be undertaken.

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Appendix

Genera and species reported as occurring in the family Horneridae (Bryozoa: Cyclostomata: Cancellata). Distribution, type location, references and comments are given where available. Species given in plain bold type are no longer in the Horneridae.

Genus *Calvetia* Borg, 1944

- Calvetia dissimilis* Borg, 1944
Tierra del Fuego, Antarctica; Recent
Borg 1944, Taylor & Gordon 2003
Type species
- Calvetia osheai* Taylor & Gordon, 2003
New Zealand; Recent
Type: NIWA Wellington, NZ; H-816
Taylor & Gordon 2003
- Calvetia* sp.
Seymour Island, Antarctica; Eocene
Hara 2001, Taylor & Gordon 2003

Genus *Crassohornera* Waters, 1887

- Crassohornera arbuscula* (Reuss, 1848)
Italy, France; Eocene
Reuss 1848, Canu & Bassler 1920, Julien 1940, Bassler 1953
Originally described as *Ceriopora arbuscula*
- Crassohornera densipunctata* Bobies, 1958
Austria; Miocene
Type: Naturhistorisches Museum in Wien; no. 254/1957
Bobies 1958, Mongereau 1972
Mongereau 1972 believed this species to be a member of *Hornera*
- Crassohornera* sp.
Seymour Island, Antarctica; Eocene
Hara 2001

Crassohornera waipukurensis Waters, 1887

New Zealand; Tertiary

Type: Manchester Museum, UK, Waters Collection; H.1186.7585

Waters 1887, Canu & Bassler 1920, Bassler 1953

Type species of the genus. Misspelled *waipukerauensis* on type specimen label**Genus *Eohornera* Brood, 1972***Eohornera langethalii* (von Hagenow, 1839)

Sweden; U Cretaceous

Types: Geological Institute, University of Stockholm, Sweden; GI.D293, 314, 289a & b von Hagenow 1839, Marsson 1887, Gregory 1899, Levinsen 1925, Voigt 1959, Maryanska 1969, Brood 1972

Originally described as *Retepora langethalii*, later placed in *Hornera* by Marsson 1887 and then *Hemicellaria* by Maryanska 1969. Brood 1972 erected new genus. May belong to a different family.**Genus *Hornera* Lamouroux, 1821*****Hornera affinis* Milne Edwards, 1838**

Sicily; Cretaceous - Tertiary

Type: Mus Nat Hist Naturelle, Paris France, Milne Edwards Collection; 4416

Milne Edwards 1838, Bronn 1848, d'Orbigny 1852, Busk 1859, Jelly 1889, d'Hondt 2006
Busk 1859 synonymised with *H. frondiculata*, also see Jelly 1889. If not synonymous, then secondary synonymy with *Retihornera affinis* Kirchenpauer, 1869 may occur. Regarded by d'Hondt (2006) as a compound specimen formed from *Tubulipora liliacea* overgrowing *Fron dipora verrucosa*.*Hornera airensis* Maplestone, 1903

Australia; Tertiary

Type: perhaps in National Museum, Australia

Maplestone 1903

Hornera americana d'Orbigny, 1839

South Africa, Antarctica

d'Orbigny 1839, d'Orbigny 1852, Jelly 1889, O'Donoghue 1924, Borg 1944

Hornera andegavensis Michelin, 1847

England, France, Poland; Cretaceous, Miocene

Type: Muséum national d'Histoire naturelle, Paris, Michelin collection; 201

Michelin 1847, d'Orbigny 1852, Busk 1859, Julien 1940, Buge 1957, Mongereau 1972

Busk 1859 synonymised with *H. frondiculata*, see also Jelly 1889*Hornera antarctica* Waters, 1904

Cape Horn, Antarctica, Seymour Island; Eocene, Recent

Waters 1904b, Canu & Bassler 1920, Thornely 1924, Borg 1926, 1944, Livingstone 1928, Hara 2001

Hornera aotearoa Whitten, 1979 MS

New Zealand; Pleistocene, Recent

Auckland University?, New Zealand; no. J21, Station AA, AU6747

Whitten 1979

Unpublished PhD thesis, thus **not a valid name**. Resembles *H. frondiculata*.*Hornera asperula* Reuss, 1869

France, Italy, Czechoslovakia; mid-late Eocene to lower Oligocene

Type: Naturhistorisches Museum in Wien

Reuss 1869, Gottardi 1886, Waters 1892, Hejjas 1894, Canu 1908b, Mongereau 1972, Braga & Barbin 1988, Braga & Finotti 1980, Zagorsek 1992, Braga 2007

Mongereau declared the holotype lost and erected a neotype

Hornera australis Kirchenpauer, 1869

Australia; Recent

Kirchenpauer 1869, Jelly 1889

Hornera biloba Reuss, 1848

Austria, Germany, Italy; Eocene - Miocene

Reuss 1848, 1851, Manzoni 1877, Bobies 1958, Udin 1964, Mongereau 1972

Manzoni placed this species in *Filisparsa*; Udin moved it into *Oncousoecia*

Hornera bipunctata Roemer, 1863

Germany; Oligocene

Type: Inst. Palaeontologie, Clausthal-Zellerfeld, Germany, Roemer collection; 540

Roemer 1863, Busk 1859, Mongereau 1972

Mongereau 1972 declared this to be synonymous with *H. frondiculata* forme striata

Hornera biseriata Philippi, 1844

Germany; Oligocene

Philippi 1844, Bronn 1848, David et al. 1968, Mongereau 1972

Type lost. Mongereau moved this species to *Reteporidae* in the Petaloporidae

Hornera borealis Busk, MS

Norway, Finland, Denmark, Kamchatka, Shetland, Coralline Crag; Recent

Busk 1859, Sars 1862, Alder 1864, Waters 1904

Busk 1859 referred to "in MS". Incorporated into *H. lichenoides* by Smitt 1866, see also Jelly 1889, but Waters 1904 kept separate.

Hornera brancoensis Calvet, 1907

Chile; Recent

Calvet 1907, 1931

Some *H. frondiculata* specimens in the NHM (London) collections were re-identified as *H. brancoensis* by P. L. Cook (according to their labels) but this has not been published

Hornera caespitosa Busk, 1875

Chile, Argentina, South Africa, Magellanic, Netherland East Indies, Antarctica; Recent

Busk 1875, Jelly 1889, Calvet 1907, Harmer 1915, Thornley 1924, O'Donoghue 1924, Livingstone 1928

Misspelled *coespitosa* by Calvet 1907

Hornera canaliculata Busk, 1859

England, Netherlands; Pliocene

Type: NHM London, Wood Collection; D37806

Busk 1859, Lagaij 1952, Mongereau 1972

Hornera canui Calvet, 1911

Azores; Recent

Calvet 1911, 1931

Hornera carinata Reuss, 1845

Europe; Cretaceous

Reuss 1845, Bronn 1848, Hagenow 1850, Gregory 1909, Mongereau 1972

Type lost; Gregory 1909 placed in *Homoeosolen* in the Cytididae

Hornera cervicornis Ortmann, 1889

Japan; Recent

Ortmann 1889

Hornera circumporosa Beutler, 1908

Germany; upper Eocene

Beutler 1908, Mongereau 1972

Hornera circumsulcata Hijjas, 1894

Europe; Eocene

Hijjas 1894

Hornera compressa von Hagenow, 1851

Sweden; Late Cretaceous

Von Hagenow 1851, Gregory 1899

Hornera concatenata Reuss, 1869

Italy, Slovakia, Hungary, Germany, Austria, Poland, France, Belgium, Romania, Libya; Paleocene, Eocene, Oligocene to Miocene

Type: Naturhistorisches Museum in Wien, Vicenza Italy, Reuss collection; 46

Reuss 1869, Seguenza 1879, De Stefani 1884, Waters 1884a, Pergens & Meunier 1886, Gottardi 1886, Pergens 1889b, Hijjas 1894, Gregory 1899, Neviani 1900, Beutler 1908, Canu & Bassler 1920, MaLecki 1963, David et al 1968, Mongereau 1972, Braga & Finotti 1980, Braga & Barbin 1988, Zagorsek 1992, Zagorsek 2003, Braga 2007, El Safori & Muftah 2007

Hornera contortilis (Lonsdale, 1845)

New Jersey; Cretaceous

Lonsdale 1845, Busk 1859, Canu & Bassler 1933

Described as *Idmonea contortilis*, moved to *Oncousoecia* in the family Oncousoeciidae by Canu & Bassler 1933***Hornera crassa*** Lonsdale, 1845

Silurian

Lonsdale 1845, Bronn 1848

Bronn 1848 refers it to *Idmonea* in the family Idmoneidae*Hornera crispa* Defrance, 1821

France; mid-Eocene

Neotype: Canu collection, Muséum national d'Histoire naturelle, Paris

Defrance 1821, de Blainville 1834, Bronn 1848, Mongereau 1972

Mongereau erected a neotype, but states it could be synonymous with *H. hippolithus**Hornera curva* MacGillivray, 1895

Australia; Tertiary

Type possibly in Museum Victoria, Melbourne

MacGillivray 1895

Hornera curvirostra Hijjas, 1894

Europe; Eocene

Hijjas 1894

Hornera cylindracea Seguenza, 1879

Italy; Pliocene

Seguenza 1879, Neviani 1900

Hornera d'achiardii Reuss, 1869

Italy, Germany; upper Eocene

Type: Naturhistorisches Museum in Wien

Reuss 1869, Gottardi 1886, Beutler 1908, Mongereau 1972

Hornera decipiens Eichwald, 1830

Europe; "Fossil"

Eichwald 1930, Bronn 1848

Hornera depressa (d'Orbigny, 1853-4)

France; Cretaceous

d'Orbigny 1850, Pergens 1890, Gregory 1899

Placed in *Hemicellaria* in the family Petaloporidae by Gregory 1899*Hornera diffusa* MacGillivray, 1895

Australia; Tertiary

- Type possibly at Museum Victoria, Melbourne
MacGillivray 1895
- Hornera dorsocavata* Bobies, 1958
Austria, France; Miocene
Type: Naturhistorisches Museum in Wien; 256/1957
Bobies 1958, Udin 1964, Mongereau 1970, Mongereau 1972
Mongereau synonymised with *H. frondiculata*
- Hornera eburnea** Jullien & Calvet, 1903
Azores; Recent
Jullien & Calvet 1903, Hickson 1916, Zibrowius 1981
Re-identified as hydrocoral *Errina (Lepidopora) hicksoni* Boschma, 1963
- Hornera edwardsii* d'Archiac, 1848
France; Eocene
Type: D'Archiac collections, Ecole des Mines, Paris
d'Archiac 1848, Canu 1912, Mongereau 1972
- Hornera elegans** DeFrance, 1821
France; Cretaceous
Type lost
DeFrance 1821, de Blainville 1834, Bronn 1848, d'Orbigny 1852
Mongereau claimed this was a *nomen oblitum*
- Hornera elevata* MacGillivray, 1895
Australia; Tertiary
Type possibly at Museum Victoria, Melbourne
MacGillivray 1895
- Hornera erugata* Hayward & Cook, 1979
Cape of Good Hope, S Africa; Recent
Holotype: NHM, London; 1842.11.30.45
Paratypes: S African Museum; A-26456
Hayward & Cook 1979
- Hornera falklandica* Borg, 1944
Antarctic/subantarctic
Borg 1944, Androsova 1968
- Hornera farehamensis* Gregory, 1893
England; Palaeogene
Type: NHM, London B3831
Gregory 1893, Mongereau 1972
- Hornera ferussaci* (Michelin, 1845)
France; Tertiary
Type: Muséum national d'Histoire naturelle, Paris, Michelin Collection
Michelin 1845, Mongereau 1972
Described as *Retepora ferussaci*
- Hornera fibrosa* Reuss, 1866
Germany; Tertiary
Type: Söllingen, Reuss Collection; 1866-III-78
Reuss 1866, Mongereau 1972
Mongereau placed in synonymy with *H. frondiculata*
- Hornera fissurata* (Busk, 1884)
Busk 1886, Waters 1888, Jelly 1889, Canu & Bassler 1920
Described as *Idmonea fissurata*

Hornera flabelliformis (de Blainville, 1834)

Eocene-Miocene

de Blainville 1834, Busk 1859

Hornera foliacea MacGillivray, 1868

Antarctica, Australia, New Zealand, Auckland Islands; Neogene

Syntypes: Museum Victoria, Melbourne, Australia; F45480

MacGillivray 1868, 1886, 1895, Busk 1886, Hutton 1873, 1891, 1904, Waters 1884b, Jelly 1889,

Hamilton 1898, Thornley 1924, Livingstone 1928, Stach 1936

MacGillivray noted could include Busk's *H. gouldiana*. Hutton placed it in *Retehornera foliacea*; later Busk returned it to *Hornera*, and Jelly synonymised all the *Retihornera* species with this species*Hornera frondiculata* Lamouroux, 1821

Italy, France, Spain, Poland, Russia, Red Sea, Porto Praya, St. Iago, Cape de Verde, Italy, Sicily, England, Austria, Slovakia, Germany, Netherlands, Morocco, Crete, Rhodes, Australia, New Zealand; Eocene to Recent

Neotype (invalid): Muséum national d'Histoire naturelle, Paris, d'Orbigny collection; 13773

Lamouroux 1821, de Blainville 1834, Milne Edwards 1838, Lonsdale 1849, Sars 1851, Busk 1859,

1875, 1886, Heller 1867, Waters 1877, 1878, 1884b, 1887, Manzoni 1876, 1877, Seguenza 1879,

De Stefani 1884, Lovisato 1885, Pergens 1887, 1889a,b, Hejjas 1894, MacGillivray 1895, Neviani

1896a, b, 1900, Jelly 1889, Hamilton 1898, Hutton 1904, Beutler 1908, Canu 1909, 1912, Gillard

1938, Roger & Buge 1946, Vigneaux 1949, Lagaij 1952, MaLecki 1952, Bassler 1953, Buge

1957, Bobies 1958, Udin 1964, David 1965, Mongereau 1970, Mongereau 1972, Wass & Yoo

1975, Harmelin 1976, Tillier 1977, Vavra 1979, Zabala 1986, Rosso 1987, Zabala & Maluquer

1988, Braga & Barbin 1988, Carriol 1993, Moissette et al 1993, Moissette & Spjeldnaes 1995,

Moissette & Saint Martin 1995, Zagorsek & Hudackova 2000, Braga 2007

Type species. Originally figured as *Millepora* spp., or perhaps as Lamarck's 1816 *Retepora frondiculata*. Bassler claims only Recent. Mongereau suggested three "forms" now re-united (according to Moissette & Spjeldnaes). Holotype destroyed in WWII, Mongereau proposed a neotype from d'Orbigny collection, a procedure rejected in this paper***Hornera galatea*** Smitt, 1872

USA (Florida)

Smitt 1872, Waters 1888, Jelly 1889, Zibrowius 1981

Re-identified as hydrocoral *Errina (Lepidopora) cochleata* Pourtalès, 1867*Hornera gambierensis* Busk, 1860

South Australia; Tertiary

Busk 1860

Hornera gouldiana Busk, 1859

New Zealand (Chatham Is), Australia

Busk 1859, Hutton 1873, Jelly 1889

Hutton 1873 placed it in *Retihornera gouldiana*; synonymised with *H. foliacea* by Jelly 1889*Hornera gracilis* Philippi, 1844

Germany; Oligocene, L. Cretaceous

Type lost

Philippi 1844, Bronn 1848, von Hagenow 1850, d'Orbigny 1852, Reuss 1854, 1855, 1866,

Stoliczka 1862, Roemer 1863, Gregory 1899, Mongereau 1972

Hornera "gracilis" Whitten, 1979 MS non Philippi, 1844

New Zealand (Mokohinau Islands); Pleistocene, Recent

Material: Auckland University? New Zealand; J22, Station 71, AU3088

Whitten 1979

Unpublished PhD thesis, thus **not a valid name**

Hornera gravieri Calvet, 1911

Azores; Recent

Calvet 1911, Zibrowius 1981

Re-identified as hydrocoral *Pliobothyrus symmetricus* Pourtalès, 1868**Hornera haastiana** (Tenison-Woods, 1880)

New Zealand; Tertiary

Tenison-Woods 1880, Fleming 1971

Described as *Retehornera haastiana***Hornera haueri** d'Orbigny, 1852

Austria; Cretaceous

d'Orbigny 1852

D'Orbigny proposed this name to replace *H. hippolithus* Reuss, 1848 which is not the same as *H. hippolithus* DeFrance, 1820. Nobody seems to have picked up on the suggestion.**Hornera hippolithus** DeFrance, 1820

England, Belgium, France, Austria, Italy, Germany, Russia, Poland; Eocene to Pliocene

Type lost

DeFrance 1820, de Blainville 1834, Milne Edwards 1838, d'Archiac 1848, Bronn 1848, Busk 1859, Stoliczka 1862, Manzoni 1877, Seguenza 1879, De Stefani 1884, Hejjas, 1894, Canu 1908b, 1909, 1912, 1918b, Harmer 1915, Canu & Bassler 1929, Pazdro 1929, Darteville 1933, MaLecki 1952, 1963 Bobies 1958, Mongereau 1972

This species has been variously spelled and dated: "*H. hippolyta* DeFrance 1859" (Pazdro 1929, MaLecki 1952, 1963); "*H. hippolitha* DeFr." (Seguenza 1879); "*H. hyppolyta* DeFrance" (Stoliczka 1862); and "*H. hippolytus* DeFrance 1930" (Neviani 1900). Manzoni 1877 noted that the *H. hippolitha* figured by Milne Edwards & Busk is not the same as *H. hippolithus* DeFrance. Bobies 1958 erected a subspecies, *H. h. echinate*, and Mongereau 1972 synonymised *H. hippolithus* with *H. crispa*.**Hornera hippolithus** Reuss, 1848

Germany; Tertiary

Reuss 1848, 1851, Seguenza 1879

This species is not the same as *H. hippolithus* DeFrance, 1820. Seguenza 1879 erected *H. reussi* to cover the Reuss material, despite d'Orbigny's earlier suggestion of *H. haueri* for the same purpose.**Hornera humilis** Busk, 1859

England, Netherlands, Russia; Pliocene

Lectotype: NHM, London, SV Wood Collection; D6896

Busk 1859, Lagaaij 1952, Malecki 1952, Mongereau 1972

Hornera hybrida (d'Archiac, 1848)

France, Poland; Eocene

Syntypes: Ecole des Mines, Paris, d'Archiac coll.

d'Archiac 1848, Canu 1912, Pazdro 1929, MaLecki 1963, Mongereau 1972

d'Archiac described as *Idmonea hybrida*, moved to *Hornera* by Canu 1912**Hornera infundibulata** Busk, 1859

England, Netherlands; Pliocene

Lectotype: NHM, London, Wood Collection; D6894

Busk 1859, Lagaaij 1952

Hornera involuta MacGillivray, 1895

Australia; Tertiary

Type possibly in Museum Victoria, Melbourne

MacGillivray 1895

Hornera jacksonica Canu & Bassler, 1920

USA (Florida to N Carolina); Eocene

Type: USNM; 65242, 65312

Canu & Bassler 1920

Hornera laevis Milne Edwards, 1838

France; Miocene

Type: Muséum national d'Histoire naturelle, Paris, Milne Edwards collection; 4418

Milne Edwards 1838, Bronn 1848, Canu 1909, d'Hondt 2006

Canu 1909 suggested it could be *Filisparsa*. Transferred to *Adeonellopsis* by d'Hondt (2006)*Hornera lamellosa* Roemer, 1863

Germany; Oligocene

Type: Inst. Paleontol. Clausthal-Zellerfeld, Germany, Roemer collection; 543

Roemer 1863, Mongereau 1972

Hornera langethali (von Hagenow, 1839)

Germany; Late Cretaceous

Type lost

von Hagenow 1839, 1850, Roemer 1841, Bronn 1848, Marsson 1887, Gregory 1899

von Hagenow 1839 described in *Retepora*. Bronn notes has been misspelled *langethalii**Hornera lasarevi* Androsova, 1968

Antarctic/subantarctic; Recent

Androsova 1968

Hornera latiramae Canu and Bassler, 1929

Belgium; Eocene

Type: Inst Roy Sci Nat, Brussels; 3497

Canu & Bassler 1929, Darteville 1933, Mongereau 1972

Mongereau synonymised with *H. hippolithus* Defrance*Hornera lichenoides* (Linnaeus, 1758)

Arctic, Norway, Svetland, Denmark, Greenland, Rockall Bank, Shetlands, Faroes, Hebrides, Barents Sea, Spitsbergen, North Sea, Mediterranean, Italy, Naples, Gulf of St Lawrence, St George's Bank, Argentina, Australia; Cretaceous, Pliocene to Recent

Pontoppidan 1752, Ellis 1755, Linnaeus 1758, d'Orbigny 1852, Smitt 1866, Busk 1875, 1886,

Kirchenpauer 1874, 1875, Hincks 1880, MacGillivray 1895, Neviani 1896b, 1900, Kirkpatrick

1888b Jelly 1889, Waters 1904, Borg 1926, Calvet 1931, Marcus 1940, Kluge 1962, Hayward &

Ryland 1985, Zabala & Maluquer 1988, Ryland & Hayward 1991, Gontar 1996

Originally described as *Millepora lichenoides*. Kluge 1962 noted it is an arctic boreal species,which suggests the Australian record is doubtful. Calvet 1913 commented that *H. mediterranea*Waters, 1905 is *H. lichenoides*.*Hornera lunata* Busk, 1859

England, Netherlands; Pliocene

Type lost

Busk 1859, Lagaaij 1952

Hornera lunularis Stoliczka, 1865

New Zealand; Miocene

Syntype: Naturhistorisches Museum in Wien, Stoliczka coll; zb-18650XLIX-6

Stoliczka 1865, Mongereau 1972

Mongereau states the Stoliczka material is now missing

Hornera mediterranea Waters, 1904

Naples; Recent

Waters 1904, Calvet 1931

Waters noted this specimen could be *H. serrata* of Meneghini but since *serrata* had been used byReuss already, he created this new name. Calvet 1931 synonymised with *H. lichenoides**Hornera nitens* Roemer, 1863

Germany; Oligocene

Type lost

Roemer 1863, Mongereau 1972

- Mongereau states the material is now missing
Hornera nummulitorum d'Orbigny, 1852
 France; Cretaceous
 d'Orbigny 1852
- Hornera oculata* von Hagenow, 1850
 Germany; L Cretaceous
 von Hagenow 1850, Gregory 1899
- Hornera opuntia** Defrance, 1821
 France; "fossil"
 Type lost
 Defrance 1821, de Blainville 1834, Bronn 1848, Mongereau 1972
 Mongereau proposed *nomen oblitum*
- Hornera pacifica* Stoliczka, 1865
 New Zealand, Miocene
 Type: Naturhistorisches Museum in Wien, Stoliczka coll.; ZB-1865-XLIX-7
 Stoliczka 1865, Mongereau 1972
- Hornera parasitica* (Kirchenpauer, 1869)
 Kirchenpauer 1869, Jelly 1889
 Described as *Retihornera parasitica*
- Hornera pectinata* Busk, 1861
 Madeira, Canary Islands; Recent
 Type: NHM, London, Busk Collection; 75.5.29.26
 Busk 1861, 1875, Jelly 1889, Johnson 1897, Norman 1909, Calvet 1931, Osburn 1953.
 Also reported from California, Borneo and New Zealand but A.M. Smith (unpublished) re-identified these specimens as different species.
- Hornera perrieri** Pergens, 1890
 France; Cretaceous
 Pergens 1890, Gregory 1899, Mongereau 1972
 Gregory 1899 synonymised with *Hemicellaria* in the family Petaloporidae
- Hornera pertusa* Busk, 1959
 England, Austria; Miocene, Pliocene
 Lectotype: NHM, London, Wood Collection; D 37807
 Busk 1859, Lagaij 1952, Bobies 1958, Mongereau 1972
- Hornera pinnata* Canu & Bassler, 1929
 China Sea, Borneo, Philippines S California, Baja California; Recent
 Canu & Bassler 1929, Osburn 1953
- Hornera polyporoides* Canu & Bassler, 1920
 USA (Mississippi, N. Carolina), Poland; Eocene
 Type: USNM 65329
 Canu & Bassler 1920, Malecki 1963
- Hornera porosa* Stoliczka, 1862
 Germany, Poland, SE USA; Oligocene, Eocene
 Types: USNM 65332, 65478, 65479; also Naturhistorisches Museum in Wien, Stoliczka coll.; zb-XXII-48
 Stoliczka 1862, Pergens 1889b, Canu 1912, Canu & Bassler 1920, Pazdro 1929, MaLecki 1963, Mongereau 1972
 now *H frondiculata* (see Jelly 1889, Canu 1912, Mongereau 1972)
- Hornera prominens* MacGillivray, 1895
 Australia; Late Miocene - Pleistocene
 Type possibly at Museum Victoria, Melbourne
 MacGillivray 1895, Wass & Yoo 1975

Hornera pseudolichenoides Gontar, 1996

Spitsbergen, Barents Sea; Recent

Type: Zoological Institute, St Petersburg, nos. 48571-4
Gontar 1996*Hornera quadrata* MacGillivray, 1895

Australia; Tertiary

Type possibly at Museum Victoria, Melbourne
MacGillivray 1895*Hornera radians* Defrance, 1821

France; Miocene

Defrance 1821, de Blainville 1834, Bronn 1848, Canu 1909, Canu & Lecointre 1934, Roger & Buge 1946, Vigneaux 1949, Buge 1957, Mongereau 1972
Mongereau 1972 placed in synonymy with *H. frondiculata**Hornera radiata* (Lamarck, 1816)

Australia

Lamarck 1816, de Blainville 1834

Lamarck described as *Retepora radiata****Hornera ramosa*** MacGillivray, 1886

Australia

Syntypes: Museum Victoria, Melbourne; 45481

MacGillivray 1886, Waters 1888, Pergens 1890, Gregory 1899, Waters 1904

synonymised with *H. lichenoides* by Jelly 1889. Waters 1904 notes: "Miss Jelly gives *H. ramosa* MacG. as a synonym... however, as *Reteporidae ramosa*, d'Orb. is *Hornera*, MacGillivray's species cannot stand."***Hornera ramosa*** (King, 1846?)

Bronn 1848

Bronn 1848 lists this species as being described by King as *Fenestella ramosa*. We can find no further reference to a species with this authorship.***Hornera ramosa*** (d'Orbigny, 1850)

d'Orbigny 1850, Bassler 1953

Described as *Reteporidae ramosa*, moved to *Hemicellaria* in the Petaloporidae (Bassler 1953).*Hornera reteporacea* Canu, 1909 non Milne Edwards, 1838

France; Miocene

Type: Muséum national d'Histoire naturelle, Paris, Canu collection

Canu 1909, Vigneaux 1949, Buge 1957, Mongereau 1972

Canu erected variety *australis* for an Argentinian specimen from the lower Eocene. Mongereau regarded Canu's specimens as *H. frondiculata* var *striata*, but noted that *reteporacea* is in common use in the Miocene, and suggested it still has some worth.*Hornera reteporacea* Milne Edwards, 1838

England, France, Austria, Slovakia, Germany; Cretaceous, Oligocene, Miocene, Pliocene

Types: Muséum national d'Histoire naturelle, Paris, Milne Edwards Collection; 4419 (also see 4420, 4421)

Milne Edwards 1838, Wood 1844, Bronn 1848, d'Orbigny 1852, Busk 1859, Stoliczka 1862, Canu 1909, Canu & Lecointre 1934, Roger & Buge 1946, Vigneaux 1949, Buge 1957, Mongereau 1972, Zagorsek & Hudackova 2000. d'Hondt 2006

Misspelled *retiporacea* by Bronn. Mongereau's neotype (no. B1610, Wood coll., NHM London) superceded by d'Hondt's (2006) discovery of original material in the MNHN Paris Milne Edwards collection.*Hornera reteramae* Canu & Bassler, 1920

USA (N. Carolina), Poland; Eocene

Type: USNM; 65328

Canu & Bassler 1920, Pazdro 1929, Drexler 1976, Cuffey & Drexler 1979, McKinney et al 1993

Hornera reticulata (Busk, 1859)

England, Netherlands; Pliocene

Lectotype: NHM, London, Wood Collection; D37760

Busk 1859, Lagaaij 1952, Mongereau 1972, Taylor & Gordon 2003

Busk described it as *Heteropora reticulata*; Lagaaij 1952 placed it in *Hornera*; Mongereau 1972 returned it to *Heteropora*; and Taylor & Gordon 2003 suggested it could belong to the genus *Calvetia* (pending study of gonozooids)

Hornera reussi Seguenza, 1879

Italy; Miocene to Pleistocene

Types lost. Specimens in Canu collection, Muséum national d'Histoire naturelle, Paris; 38-668-1 Seguenza 1879, Neviani 1896b, 1900, Mongereau 1972

New species erected to replace *H. hippolithus* Reuss non DeFrance

Hornera rhipis Busk, 1859

England, Netherlands; Pliocene

Lectotype: NHM, London, Wood Collection; 1612

Busk 1859, Lagaaij 1952, Mongereau 1972

Hornera rhomboidalis Busk, 1859

England, Poland; Pliocene

Type lost, specimens in SV Wood Coll. NHM London

Busk 1859, MaLecki 1963, Mongereau 1972

Mongereau 1972 placed in synonymy with *H. frondiculata*

Hornera robusta MacGillivray, 1882

Australia, New Zealand; Recent to "Fossil"

Syntypes: Museum Victoria, Melbourne, 1895 collection; F45482

MacGillivray 1883, 1886, Jelly 1889, Stach 1936, Probert et al. 1979, Hall et al 2002

Stach 1936 was first record of fossil occurrence

Hornera royana (d'Orbigny, 1850)

France; Cretaceous

d'Orbigny 1850, Pergens 1890, Gregory 1899

Described in genus *Hornera* by Pergens 1890, moved to *Hemicellaria* by Gregory 1899, later moved to Petaloporidae (Bassler 1953)

Hornera rubeschii (Reuss, 1848)

Austria; Miocene

d'Orbigny 1852, Vavra 1977, p. 146

Hornera rugosula Jullien, 1883

NE Atlantic, Chile; Recent

Jullien 1883, Jelly 1889, Calvet 1907

Hornera rugulosa Busk, 1860

Australia; Tertiary

Busk 1860

Busk only listed the name (with a question mark), with no figures or description

Hornera scobionosa (Michelin, 1841-1848)

Miocene

Michelin 1841-1848, Busk 1859

Hornera seriatopora Reuss, 1848

Roumania, Austria, Germany: Eocene, Miocene

Type lost

Reuss 1848, 1851, Stoliczka 1862, Manzoni 1877, Bobies 1958, Zagorsek 1992

not *Hornera* according to Bobies 1958, Mongereau 1972 synonymised with *Tervia irregularis* Meneghini, 1845 in the family Terviidae

Hornera serrata Meneghini, 1844

Adriatic; Recent

Meneghini 1847, Neviani 1900

Hornera serrata d'Orbigny, 1852

France; Cretaceous

Type lost

d'Orbigny 1852, Mongereau 1972

Jelly 1889 synonymised with *H. frondiculata*; Mongereau 1972 claimed *nomen oblitum*.**Hornera serrata** Reuss, 1869

Italy, Poland; upper Eocene, Pliocene

Type: Naturhistorisches Museum in Wien, Reuss coll.; ZB-1870-XIII-45

Reuss 1869, Seguenza 1879, de Stefani 1884, Gottardi 1886, Waters 1892, Hejjas 1894, Beutler

1908, Canu 1908b, Mongereau 1972

Mongereau 1972 moved it to *Tervia* in the Terviidae*Hornera simplex* Seguenza, 1879

Italy; Miocene, Pliocene

Seguenza 1879, Neviani 1900

Hornera simplicissima Braga, 1988

Italy; upper Eocene to lower Oligocene

Type: Museo Istituto di Geologia, Università di Padova, 26618-26619

Paratype: Muséum d'Histoire naturelle de Genève GEPI, 88-01

Braga & Barbin 1988, Braga 2007

Hornera smitti Borg, 1944

Antarctic/subantarctic

Borg 1944, Androsova 1968, 1972, Moyano 1979

Hornera sparsa Reuss, 1865

Poland; Eocene

Type: Naturhistorisches Museum in Wien, Reuss coll., zb-1865-VII-29

Reuss 1865, Hejjas 1894, Beutler 1908, Pazdro 1929, Malecki 1963, Mongereau 1972

Mongereau 1972 moved it to *Reteporidea* in the family Petaloporidae**Hornera sparsipora** Hennig, 1894

Sweden; Cretaceous

Type lost

Hennig 1894, Gregory 1909, Mongereau 1972, Brood 1972

Mongereau 1972 eliminated this species from *Hornera* based on original figures*Hornera spinigera* Kirkpatrick, 1888

Mauritius, Netherlands East Indies, Lifu

Type: NHM, London; 88.1.25.37, also known as 97.5.1.1112

Kirkpatrick 1888a, Jelly 1889, Philipps 1899, Harmer 1915, Canu & Bassler 1929, Osburn 1953,

Brood 1976, 1979

Brood (1979) erected new genus *Spinihornera* for this species*Hornera squamosa* Hutton, 1873

New Zealand; Recent

NHM, London, Hutton Collection; no. 75.1.5.39

Hutton 1873

Hornera steenstrupi Pergens & Meunier, 1886

Belgium, Denmark; Cretaceous

Pergens & Meunier 1886, Levinsen 1925

Moved to *Meliceritella* by Levinsen*Hornera striata* Milne Edwards, 1838

England, France, Austria, Slovakia, Belgium, Netherlands, Poland, Italy, Rhodes, Argentina, New

Zealand; Cretaceous, Eocene - Pliocene, Recent

Type: Muséum national d'Histoire naturelle, Paris, Milne Edwards coll. 4417
 Milne Edwards 1838, Michelin 1841-1848, Wood 1844, Bronn 1848, d'Orbigny 1852, Busk 1859, Roemer 1863, Stoliczka 1865, Gottardi 1886, Waters 1877, Manzoni 1877, 1878, Hutton 1873, 1880, 1891, 1904, De Stefani 1884, Pergens 1887, Seguenza 1879, Neviani 1896a, b, 1900, Hamilton 1898, Canu 1908, Canu 1912, Cipolla 1921, Canu & Bassler 1924, Scotti 1936, Gillard 1938, Julien 1940, Roger & Buge 1946, Lagaiij 1952, Buge 1957, Bobies 1958, Malecki 1963, Udin 1964, David 1965, Mongereau 1972, Vavra 1979, Carriol 1993, Zagorsek & Hudackova 2000, d'Hondt 2006

Jelly gave author as Stoliczka but Stoliczka gave Milne Edwards. Mongereau 1972 placed in *H frondiculata* var. *striata*. Mongereau could not find any types and thus proposed a neotype (NHM B6897, Wood coll), however, d'Hondt (2006) reported discovery of Milne Edwards' type specimen in Paris.

Hornera subannulata Philippi, 1844

Austria, Czechoslovakia, Germany, Poland; Eocene - Oligocene

Type: Naturhistorisches Museum in Wien, Bobies coll.; 258/1957

Philippi 1844, Bronn 1848, Stoliczka 1862, Reuss 1866, Pergens 1889b, Hejjas 1894, Beutler 1908, Bobies 1958, Malecki 1963, Mongereau 1972, Vavra 1979, Zagorsek 1992

Stoliczka 1862 and Reuss 1866 synonymised *H. biseriata* with this species but Mongereau moved *H. biseriata* out of the Horneridae.

Hornera subcancellata (d'Archiac, 1847)

France; Eocene

Type: Ecole des Mines, Paris, D'Archiac collection
 d'Archiac 1848, Canu 1912

Originally described as *Retepora subcancellata*

Hornera subdubia Goldstein, 1882

Marion Islands

Type possibly in Museum Victoria, Melbourne
 Goldstein 1882, Waters 1888, Jelly 1889

A hydrocoral (according to Waters)

Hornera sulcata MacGillivray, 1895

Australia; Tertiary

Type possibly at Museum Victoria, Melbourne
 MacGillivray 1895

Hornera sulcato-punctata Roemer, 1863

Germany; Oligocene

Type: Inst. Paleontol. Clausthal-Zellerfeld, Germany, Roemer coll.; 544
 Roemer 1863, Mongereau 1972

Mongereau synonymised with *H. frondiculata*

Hornera sulcosa Reuss, 1866

Germany, Poland, France, Italy; mid-Tertiary

Type lost

Reuss 1866, Canu 1909, Pazdro 1929, Gillard 1938, MaLecki 1963, Mongereau 1972, Braga & Finotti 1980, Braga 2007

Mongereau synonymised with *H. gracilis*. Canu 1909 suggested it is synonymous with *H. porosa*.

Hornera tenuirama Canu & Bassler, 1920

USA (N. Carolina); Eocene

Type USNM; 65330

Canu & Bassler 1920, Drexler 1976, Cuffey & Drexler 1979

Hornera tenuis MacGillivray, 1895

Australia; Late Miocene - Pleistocene

Type possibly at Museum Victoria, Melbourne
 MacGillivray 1895, Wass & Yoo 1975

Hornera tortuosa Roemer, 1863

Germany; Oligocene

Type: Inst. Paleontol. Clausthal-Zellerfeld, Germany, Roemer Coll.; 541

Roemer 1863, David et al. 1968, Mongereau 1972

Hornera trabecularis Reuss, 1869

Italy; upper Eocene

Type: Naturhistorisches Museum in Wien, Reuss coll.; ZB 1870-XIII-42

Reuss 1869, Gottardi 1886, Canu 1912, Mongereau 1972

Mongereau synonymised with *H. frondiculata***Hornera tridactylites** Busk, MS

Patagonia, Tierra del Fuego, Australia; Recent

Busk 1859

Busk 1859 referred to "in MS" but not, as far as we know, ever published.

Hornera trigonopora von Hagenow, 1851

Sweden; Cretaceous

von Hagenow 1851, Gregory 1899

Hornera truncatulinoidea Mokrinskij, 1916

Russia; Tertiary

Mokrinskij 1916

Hornera tuberculata MacGillivray, 1895

Australia; Late Miocene - Pleistocene

Type possibly at Museum Victoria, Melbourne

MacGillivray 1895, Wass & Yoo 1975

Hornera tuberosa Canu & Bassler, 1920

USA (Florida); Eocene

Type: USNM; 65331

Canu & Bassler 1920

Hornera tubulifera von Hagenow, 1850

Belgium; Cretaceous - Paleocene

Type lost

von Hagenow 1850, 1851, Pergens & Meunier 1886, Hennig 1894, Mongereau 1972

von Hagenow named this species in 1850 but deferred description to his 1851 paper

Hornera tubulosa Meneghini, 1844

Arctic seas, Naples, Marseille; Recent

Syntype: NHM, London; 99.7.1.4274

Meneghini 1844, Heller 1867, Busk 1875, Jelly 1889

Author sometimes erroneously given as Busk 1875, who used this name for part of *H. violacea*.Later synonymised with *H. frondiculata* by Jelly 1889**Hornera verrucosa** Jullien & Calvet, 1903

Azores; Recent

Jullien & Calvet 1903, Hickson 1916, Zibrowius 1981

re-identified as hydrocoral *Errina (Errina) dabneyi* (Pourtalès, 1871)*Hornera verrucosa* Reuss, 1848

Austria, France, Italy, Germany; Eocene to Miocene

Neotype: Naturhistorisches Museum in Wien, Bobies coll.; 255/1957, 257/1957

Reuss 1848, 1851, 1866, Stoliczka 1862, Reuss 1866, Manzoni 1877, Gottardi 1886, Canu &

Bassler 1924, Bobies 1958, Udin 1964, Mongereau 1972, Vavra 1979, Braga & Barbin 1988,

sometimes erroneously cited as Reuss, 1851 or 1866.

Hornera versipalma (Lamarck, 1816)

Lamarck 1816, Lamouroux 1821, de Blainville 1834, d'Orbigny 1852

Lamarck described in *Retepora*

Hornera violacea Sars, 1863

Arctic Atlantic, North Sea, Denmark, Rockall Bank, Shetlands, Norway; Recent
 Sars 1863, Smitt 1866, Busk 1875, 1861, 1886, Kirchenpauer 1875, Hincks 1880, Jelly 1889,
 Jullien & Calvet 1903, Borg 1926, 1944, Marcus 1940, Kluge 1962, Ryland & Hayward 1991
 Moved to *Stegohornera* by Borg 1944, Kluge 1962

Genus Retecava Marsson, 1887**Retecava areolata** Marsson, 1887

Germany
 Marsson 1887, Brood 1972
 Brood synonymised with *R. clathrata*

Retacava clathrata (Goldfuss, 1827)

Denmark, Sweden, France, Germany; Cretaceous to Paleocene
 Goldfuss 1827, von Hagenow 1851, d'Orbigny 1850, 1854, Hamm 1881, Pergens 1889, Gregory
 1899, Canu 1918, Marsson & Levinsen 1925, Voigt 1951, Bassler 1953, Brood 1972, Voigt 1983
 Type species of genus. Bassler 1953 moved to Tubuliporidae, Brood 1972 moved back to
 Horneridae. Not a hornerid (P.D. Taylor, unpublished).

Genus Retihornera Kirchenpauer, 1869*Retihornera affinis* Kirchenpauer, 1869

Fiji; Recent
 Kirchenpauer 1869, Jelly 1889
 Synonym of *H frondiculata* (see Jelly 1889)

Retihornera corbicula (Kirchenpauer, 1869)

Australia (Bass Strait); Recent
 Kirchenpauer 1869, Jelly 1889
 Described as *H corbicula*, later synonymised with *H foliacea* (Jelly 1889). Designated type
 species of *Retihornera* in this paper.

Retihornera dentata Kirchenpauer, 1869

Australia (Bass Strait); Recent
 Kirchenpauer 1869, Jelly 1889
 Synonymised with *H foliacea* (see Jelly 1889)

Retihornera foliacea McGillivray, 1869

New Zealand (Chatham Is), Australia; Miocene - Recent
 Hutton 1873, 1880, Busk 1875, Jelly 1889
 Synonym of *H foliacea* (see Jelly 1889)

Retihornera gouldiana Busk, 1859

New Zealand (Chatham Is), Australia
 Busk 1859, Hutton 1873, 1880, Jelly 1889
 Synonym of *H foliacea* (see Jelly 1889)

Retihornera graeffei Kirchenpauer, 1869

Fiji; Recent
 Kirchenpauer 1869, Hayward 2004
 Was *Kirchenpaueria elegans* Graeffe, then re-identified as cheilostome *Reteporella graeffei* by
 Hayward 2004

Retihornera haastiana Tenison-Woods, 1880

New Zealand; Tertiary
 Tenison-Woods 1880
 Described as "*Retehornera*", later considered a *Hornera* species

Retiornera parasitica Kirchenpauer, 1869

Kirchenpauer 1869, Jelly 1889

Moved to *Hornera* by Jelly 1889

Retiornera plicata Kirchenpauer, 1869

Australia; Recent

Kirchenpauer 1869, Jelly 1889

Synonym of *H. foliacea* (see Jelly 1889)

Retiornera squamosa Hutton, 1873

New Zealand; Recent

One specimen in Hutton collection at Otago Museum

Hutton 1873, Jelly 1889

Synonym of *H. foliacea* (see Jelly 1889)

Genus *Siphodictyum* Lonsdale, 1849

Siphodictyum gracile Lonsdale, 1849

England, France; Lower Cretaceous

Type: NHM, London; 46804

Lonsdale 1849, Pitt & Taylor 1990 (and references therein)

Genus *Spiniornera* Brood, 1979

Spiniornera spinigera (Kirkpatrick, 1888)

Mauritius, Netherlands East Indies

Kirkpatrick 1888a, Jelly 1889, Harmer 1915, Canu & Bassler 1929, Osburn 1953, Brood 1976,

Brood 1979

Genus *Stegohornera* Borg, 1944

Ryland & Hayward 1991 placed in Stegohorneridae

Stegohornera arctica (Kluge, 1946)

Barents Sea, Kara Sea, E Siberian Sea

Kluge 1946, 1962

Described as *Horneroides arctica* Kluge

Stegohornera violacea (Sars, 1863)

Barents Sea, Norway, Steland Is, North Sea, Bay of Biscay, Mediterranean, Gulf of St Lawrence;

Recent

Sars 1863, Smitt 1866, Borg 1944, Kluge 1962, Ryland & Hayward 1991

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