

Alcide d'Orbigny's work on Recent and fossil bryozoans

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Abstract – Alcide d'Orbigny was a prolific taxonomist and bryozoans were one of the phyla for which he described an enormous number of new species and supraspecific taxa. He was introduced to these colonial invertebrates by his father as early as 1819 when observing living colonies at La Rochelle, and collected further examples of Recent bryozoans during his explorations of South America (1826–1834). This South American collection, comprising 44 new and two existing species, was described between 1841 and 1847. However, d'Orbigny's main work on bryozoans concerned fossil species and was published between 1850 and 1854 in the *Prodrome* and, more particularly, in the Volume 5 of the *Terrains crétacés*. The latter contains descriptions of approximately 900 species, and 170 new genera. Although most of these taxa are illustrated, the stylised nature of the figures has frequently hampered their recognition, despite the valuable revisionary work published by Pergens, Canu and Voigt. D'Orbigny developed a logical system of classification and nomenclature, parts of which survive in contemporary bryozoan taxonomy. A new study focusing on the type specimens of type species of bryozoan genera erected by d'Orbigny is in progress, primarily for the revised cheilostome and cyclostome volumes of the *Treatise on Invertebrate Palaeontology*. This research, using SEM imaging of uncoated specimens to reveal small-scale details of taxonomic significance, is permitting a re-evaluation of d'Orbigny's genera some of which have been unjustifiably neglected. **To cite this article:** P.D. Taylor, D.P. Gordon, C. R. Palevol 1 (2002) 533–547. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bryozoa / taxonomy / history of science

Résumé – Les travaux d'Alcide d'Orbigny sur les Bryozoaires fossiles et actuels. Alcide d'Orbigny fut un taxonomiste extrêmement prolifique. Les Bryozoaires représentent un des embranchements pour lesquels il décrit un grand nombre des nouveaux taxons du niveau espèce et supérieur. Son père lui fit découvrir ces invertébrés coloniaux dès 1819, par l'observation de colonies vivantes, à La Rochelle. D'Orbigny recueillit d'autres exemples de Bryozoaires actuels pendant ses explorations en Amérique du Sud (1826–1834). La collection sud-Américaine comprend 44 espèces nouvelles et deux déjà nommées, qu'il décrivit entre 1841 et 1847. Néanmoins, les premières œuvres de d'Orbigny concernèrent les Bryozoaires fossiles, lesquels furent décrits entre 1850 et 1854 dans le *Prodrome* et, en particulier dans le tome 5 des *Terrains crétacés*. Ce dernier volume contient les descriptions d'environ 900 espèces nouvelles et de 170 nouveaux genres. Bien que la plupart de ces taxons soient illustrés, les figures et schémas sont généralement stylisés, ce qui a fréquemment gêné leur identification, en dépit des révisions valables publiées par Pergens, Canu et Voigt. D'Orbigny développa un système logique de classification et nomenclature, dont certains éléments persistent dans la taxonomie contemporaine des Bryozoaires. Nos récentes études ont porté sur les spécimens des espèces types des genres caractérisés par d'Orbigny, principalement pour les tomes révisés portant sur les Cheilostomes et les Cyclostomes dans le *Treatise on Invertebrate Paleontology*. Nos recherches, utilisant des images de microscopie électronique à balayage (SEM) d'échantillons non métallisés, ont révélé des détails à petite échelle, taxonomiquement significatifs. En conséquence, plusieurs des genres de d'Orbigny, qui furent négligés sans justification, ont pu être ré-évalués. **Pour citer cet article :** P.D. Taylor, D.P. Gordon, C. R. Palevol 1 (2002) 533–547. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bryozoaires / taxonomie / histoire des sciences

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1. Introduction

Alcide d'Orbigny (1802–1857) was a remarkable naturalist [4, 7, 10, 27]. The breadth of his scientific work was astonishing, ranging across geology, palaeontology, zoology, anthropology, archaeology and geography. Furthermore, within several of these individual disciplines he published prolifically. Nowhere is this more apparent than in his taxonomic work. D'Orbigny described a huge number of species and higher taxa, both fossil and Recent. Taxonomic publications differ from most other scientific works in that their relevance does not diminish with time – when ascertaining the correct name of any organism the principles of priority are applied, thereby ensuring that early publications remain of importance to the contemporary taxonomist. Thus, whereas many of d'Orbigny's theories may now be considered obsolete and of historical interest only, his taxonomic work is as relevant today as it was when first published 150 years ago.

One of d'Orbigny's enormous projects was to describe the entire fauna of fossil invertebrates of France and adjoining countries. To this end, he described thousands of species in the *Paléontologie française*, leaving a legacy that remains apparent in lists of fossil species published since that time by the numerous species names bearing his name as author. Among the fossil invertebrate groups he dealt with were the Bryozoa, an extant phylum of colonial marine invertebrates with a rich fossil record. Descriptions of some 900 species of bryozoans, mainly of Cretaceous age, are given in the fifth volume (1851–1854) of the *Terrains crétacés* of the *Paléontologie française* [17]. This is undoubtedly d'Orbigny's single most important contribution to bryozoology. The enormous effort made by d'Orbigny in completing this monumental work has not been matched by subsequent research on Cretaceous bryozoans, and his 1192-page publication is still the only comprehensive monograph of the Cretaceous bryozoan fauna of France and, for that matter, of any other country in the world having a significant Cretaceous bryozoan fauna. As late as 1953, Bassler in the original bryozoan *Treatise on Invertebrate Palaeontology* [1] had no option but to use coarsely executed copies of figures from the *Terrains crétacés* to accompany his brief descriptions of d'Orbigny's genera – d'Orbigny's figures were then, and often still are, the only illustrations available in the literature of these genera. In addition to the *Terrains crétacés*, d'Orbigny published a few other works, either wholly concerned with bryozoans or having an appreciable bryozoan content, in the eleven-year period between 1841 and 1852. His impact on the taxonomy of fossil and Recent Bryozoa has been

considerable and lasting. It is unfortunate, however, that d'Orbigny's work is beset with various sorts of problems (see below) that have caused much consternation among bryozoologists trying to interpret his taxa.

Our interest in d'Orbigny began in connection with the revision of the bryozoan part of the *Treatise on Invertebrate Palaeontology*. It was clear that a restudy of d'Orbigny's type material, which is housed in the 'Laboratoire de paléontologie', 'Muséum national d'histoire naturelle', Paris (abbreviated MNHN), was essential before much progress could be made diagnosing a significant number of cyclostome and cheilostome bryozoans included in this generic synopsis. This *Treatise*-related work and the associated website under development <www.nhm.ac.uk/palaeontology/i&p/pdt/dorbigny.html> has led to the genera review of d'Orbigny's contributions to bryozoology which is presented here. After a very brief introduction to the Bryozoa, we summarise the content of d'Orbigny's successive publications dealing with bryozoans. Examples are reproduced of his figures and compared with newly prepared scanning electron micrographs of the type specimens. His bryozoan classification is also discussed.

2. Bryozoa

Bryozoans are colony-forming aquatic invertebrates. Ryland [23] and McKinney and Jackson [11] provide good general accounts of the Bryozoa. Recent molecular studies have shown the phylum to be allied to brachiopods, molluscs and annelids within the Lophotrochozoa [6]. Some 6000 species of bryozoans are alive at the present-day, predominantly marine and ranging from the intertidal to the abyss in bathymetric distribution although most inhabit the continental shelf. The secretion of a calcareous skeleton in the overwhelming majority of marine species explains the rich fossil record of the Bryozoa that commences in the Ordovician. Bryozoans are the dominant skeletal epifauna over some parts of the continental shelf where they can be important in structuring benthic communities; for example, the branching colonies of arborescent bryozoans provide habitats for diverse sessile and mobile animals. Similarly dense communities of bryozoans in the geological past are responsible for the bryozoan limestones that are common in the geological record. They include some reef limestones with bryozoans as the principal reef builders.

The individual modules forming a bryozoan colony are known as zooids. Although within a colony the zooids are all genetically identical, they are not neces-

sarily identical in morphology. This is because partitioning of biological functions between zooids often results in zooidal polymorphism. Feeding zooids (autozooids), larval brooding zooids (gonozooids) and defensive zooids (avicularia) are among the variety of polymorphs that occur in bryozoans. Each autozooid has a lophophore consisting of a ring of tentacles surrounding a mouth. Bryozoans are suspension feeders, using cilia on the tentacles to create a current of water that drives food particles (mainly phytoplankton) towards the mouth. The lophophore emerges through an opening, the orifice or aperture, in the frontal surface of the zooidal skeleton. When danger threatens the lophophore can be retracted rapidly into the safety afforded by the tubular or box-shaped zooid. Colonies grow principally by budding new zooids, an asexual process. Sexual reproduction, and also dispersal, is usually accomplished via a short-lived larval stage. After settling on a hard or firm substratum, the larva metamorphoses into the founder zooid (ancestrula) of the colony that then begins budding new zooids. The pattern of zooidal budding is important in determining colony-form, which varies considerably between species and sometimes within a single species. Some bryozoan colonies take the form of thin encrusting sheets or runners or large multilamellar mounds, whereas others grow upright into bushy or mesh-like shapes, and yet others develop cap-shaped, free-living colonies.

There is little overlap taxonomically between the orders of bryozoans that dominated Palaeozoic faunas and those of the post-Palaeozoic. D'Orbigny was mostly concerned with the latter. The great majority of taxa he described belonged to two orders now known as the Cyclostomata and Cheilostomata but termed 'Centrifuginés' and 'Cellulinés' respectively by d'Orbigny (note that d'Orbigny included some genera belonging to extinct stenolaemate bryozoan orders within the 'Centrifuginés'). Zooids in the first order are usually tubular zooids whereas those in the second are typically box-shaped. Cyclostomes have an Ordovician to Recent range, cheilostomes Jurassic to Recent although none older than Cretaceous were known until the 1970s. Some of the richest post-Palaeozoic bryozoan localities in the world are to be found in France, and both the Jurassic and Cretaceous of France contain a diversity of bryozoans unrivalled elsewhere for rocks of these ages. D'Orbigny had access to and described fossil bryozoans from such classic French Jurassic localities as Ranville and Luc-sur-Mer (Calvados), and Cretaceous localities, including Le Havre and Fécamp (Seine-Maritime), Le Mans (Sarthe), Rouen and Saintes

(Charente Maritime), Villedieu and Tours (Loire), and Meudon (Hauts-de-Seine).

Contemporary bryozoan systematics relies overwhelmingly on skeletal characters. Hence there is no conflict between the taxonomies employed by neontologists and palaeontologists. Both colonial and zooidal characters are utilised, the former tending to be given more emphasis in cyclostomes, the latter in cheilostomes with their greater levels of zooidal complexity and polymorphism. In spite of his grounding in micropalaeontology and observation and description of zooid-level characters in bryozoans, d'Orbigny emphasised colony-level characters when classifying bryozoans. Therefore, his classification of cheilostomes differs from modern schemes more than does his classification of cyclostomes.

3. D'Orbigny's publications on bryozoans

The earliest evidence of Alcide d'Orbigny's contact with bryozoans comes from a letter written by his father Charles d'Orbigny in 1819 which is translated in Heron-Allen [7, p. 7] as follows: "One day he [Alcide] brought me some Polyzoa [Bryozoa] which he had just gathered on the rocks at Marsilly at very low tide; we placed them in water with the idea of seeing one of the Polyyps develop". The discovery of foraminifera associated with these bryozoans led father and son to the false conclusion that they were predators of bryozoans.

D'Orbigny's research on bryozoans began in earnest when describing Recent species collected during his exploration of South America. During the last decade of his life, as his interests became focused on systematic palaeontology and stratigraphy, d'Orbigny's interests in bryozoans turned towards the rich Cretaceous faunas of France. Bryozoans form an appreciable component of the huge collection of Mesozoic and Cainozoic invertebrates that he assembled.

All of d'Orbigny's research on bryozoans was published in the 13-year period between 1841 and 1854. However, the exact date of publication of individual works, however, is often difficult to establish. This is particularly unfortunate in view of the issues of taxonomic priority raised by his publications. Sometimes the date given on the title page is incorrect. D'Orbigny's custom of appending the year in which he wrote a taxonomic description to the taxonomic name adds further to the confusion as these dates invariably antedate the year of publication which is when the taxon becomes 'available' in a nomenclatural sense.

3.1. *Voyage dans l'Amérique méridionale (1841–1847)*

Much has been written about d'Orbigny's exploration of South America between 1826 and 1834 [10]. The publication detailing the results of the *Voyage* comprises a seven-volume folio plus two atlases. Part 4 of Volume 5 concerns zoophytes [12], within which d'Orbigny recognised two divisions, 'Bryozoaires' and 'Anthozoaires', both attributed to Ehrenberg. The bryozoan section of this work lacks an introduction and comprises systematic descriptions of 46 Recent species from both the Atlantic and Pacific coasts of South America. A great many of these were collected from the Falkland Islands ('Îles Malouines'). Other bryozoan localities included Rio de Janeiro (Brazil), Rio Negro (Argentina), Valparaiso (Chile) and the Peruvian coast. Forty-four of the bryozoan species were considered to be new. The names of the new species are suffixed by 'd'Orb., 1839', with two exceptions (*Criserpia dichotoma* and *Idmonea milneana*) where no date is given. As is usual with d'Orbigny's publications, this date signifies the year in which he wrote down the description, not the year of publication. The actual date of publication of the text may be as late as 1847 [25], although the plates, which are sufficient to validate the species, appeared considerably earlier, in 1841 (pls 1, 3 and 5) and 1842 (pls 2, 4, and 6-13).

D'Orbigny classified the 46 bryozoan species into four families: Cellaridae, Escharidae, Tubuliporidae and Terebriporidae. He used the cheilostome family Cellaridae for species with articulated colonies belonging to both cheilostomes and cyclostomes; Escharidae for non-articulated, lamellar cheilostomes; the cyclostome family Tubuliporidae for non-articulated cyclostomes plus two cheilostomes assigned to *Vincularia*; and Terebriporidae, a new family, for boring ctenostomes. Two new genera are described by d'Orbigny in this work, *Fasciculipora* and *Terebripora*. The first of these, a cyclostome, was revised by Borg [2], and the second, a boring ctenostome, was by Pohowsky [21]. Three of d'Orbigny's *Voyage* species were designated as type species of genera named by later authors: *Idmonea milneana* d'Orbigny, 1842 is the type species of *Nevianipora* Borg, 1944, *Vincularia elegans* d'Orbigny, 1842 the type species of *Ogivalia* Jullien, 1881, and *Escharina bougainvillei* d'Orbigny, 1842 the type species of *Celleporella* (*Antarctothoa*) Moyano, 1986.

A species described by d'Orbigny from Rio de Janeiro as *Escharina torquata* (Lamouroux, 1825) and now known as *Watersipora subtorquata* (d'Orbigny, 1852) is represented by specimen No. 13637, encrusting a bivalve shell, in the d'Orbigny Collection at the

MNHN, Paris (Fig. 1). This ascophoran cheilostome has particular significance as an important fouling species in today's seas [5]. It is found on man-made structures in harbours around the world, having been dispersed widely by shipping movements.

3.2. *Description de quelques genres nouveaux de Mollusques bryozoaires (1849)*

This short unillustrated paper in the *Revue et Magasin de zoologie pure et appliquée* [13] describes 27 new genera of fossil bryozoans: *Trochopora*, *Sulcopora*, *Pyripora*, *Cellulipora*, *Omniretepora*, *Uniretepora*, *Subretepora*, *Reteporidae*, *Reticulipora*, *Reteporina*, *Fenestrellina*, *Penniretepora*, *Sulcoretepora*, *Biretepora*, *Ennalopora*, *Archimedipora*, *Bidiastopora*, *Domopora*, *Radiopora*, *Zonopora*, *Osculipora*, *Echinopora*, *Acanthopora* [now regarded as a sponge], *Monticulipora*, *Meandropora*, *Leptopora*, and *Rhyzopora*. Twenty-four of these genera were dated 1847 by d'Orbigny, the remainder 1848, and represent descriptions originally intended for first publication in the *Prodrome*, but delayed by political circumstances. D'Orbigny divided his new genera between five families – Escharidae, Celleporidae, Reteporidae, Crisidae, Myrizooumidae. Unusually for the time, type species are very clearly designated for these genera. Most of these are species described by previous authors but for three monospecific genera (*Cellulipora*, *Omniretepora* and *Leptopora*) are represented by species introduced for the first time by d'Orbigny in this publication.

Several of the new genera are from the Palaeozoic, including such well-known bryozoans as *Penniretepora*, *Sulcoretepora* and *Ennalopora*. Another genus first introduced in this paper is *Monticulipora*, a trepostome common in the Ordovician, especially of the Concinnati region of the USA, but ranging from Palaeozoic to Cainozoic in d'Orbigny's original concept. Subsequently, *Monticulipora* was the subject of an opinion of the ICZN [9] in which *Monticulipora* d'Orbigny, 1850 as later described in the *Prodrome*, type species *M. mammulata*, a trepostome from the Ordovician of the USA, was conserved in preference to *Monticulipora* d'Orbigny, 1849, type species *Ceripora pustolosa* (Michelin, 1845), a cyclostome from the Jurassic of France.

3.3. *Prodrome de paléontologie stratigraphique universelle des Animaux mollusques et rayonnés faisant suite au Cours élémentaire de paléontologie (1850–1852)*

The *Prodrome* [14] was published in three volumes and is a listing of species in stratigraphical order according to the 27 stages of geological time

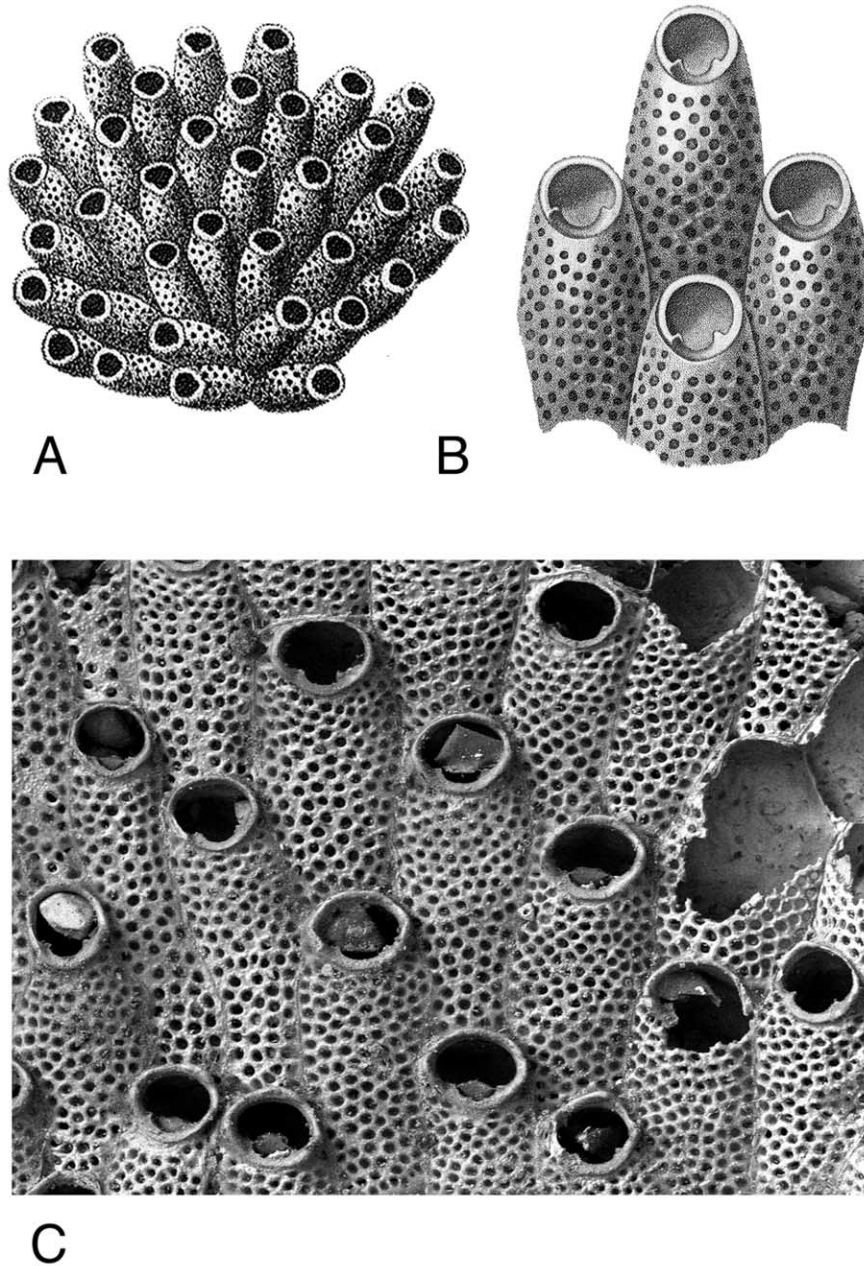


Fig. 1. The common fouling cheilostome bryozoan *Watersipora subtorquata* (d'Orbigny, 1852), as depicted by d'Orbigny in the Zoophyte section of the *Voyage dans l'Amérique méridionale* [10 (pl. 4, figs 2 and 3)] under the name *Escharina torquata* (A, B). Scanning electron micrograph of d'Orbigny's type specimen (MNHN, d'Orbigny Collection 13637; Recent; Rio de Janeiro) showing a group of autozooids, $\times 28$ (C).

Fig. 1. *Watersipora subtorquata* (d'Orbigny, 1852), Cheilostomata, Bryozoaire commun encroûtant. tel qu'il est représenté par d'Orbigny dans la section de Zoophytes du *Voyage dans l'Amérique méridionale* [10 (pl. 4, figs 2 et 3)] sous le nom d'*Escharina torquata* (A, B). Photographie au MEB du spécimen type de d'Orbigny (MNHN, collection d'Orbigny 13637 ; Actuel ; Rio de Janeiro), montrant un groupe d'autozoïdes, $\times 28$ (C).

recognised by d'Orbigny. There are no illustrations and species descriptions are sparse or non-existent, but are accompanied by brief synonymies and locality information. Most of the bryozoans are listed under 'Mollusques bryozoaires' apart from some taxa we now recognise as bryozoans which d'Orbigny included with

corals as 'Zoophytes'. No family-level classification is given. Volume 1 of the *Prodrome*, published in 1850, lists species of 'Silurien supérieur' (= Ordovician in modern usage) to 'Oxfordien' (basal Upper Jurassic) age. Among these, 50 new bryozoan species and one new genus, *Monticulipora* (discussed above) are intro-

duced. Fossils of ‘Corallien’ (Upper Jurassic) to ‘Parisien’ (Eocene) age are dealt with in Volume 2, also published in 1850, with 130 species and four genera (*Hemicellaria*, *Crisisina*, *Crisina* and *Peripora*) of bryozoans introduced for the first time. Published in 1852, Part 3 of the *Prodrome* listed species from two stages only, ‘Falunien’ and ‘Subapennin’, with four species of bryozoans introduced from the younger substage of the Falunien. In total, therefore, 184 new species and five new genera of bryozoans are introduced in the *Prodrome*: *Monticulipora*, *Hemicellaria*, *Crisisina*, *Crisina* and *Peripora*.

The *Prodrome* species have created considerable problems for taxonomists for two reasons. Firstly, the brevity of the descriptions and lack of figures has hampered recognition of the species, many of which have been treated as *nomina nuda* by subsequent generations of palaeontologists. Indeed, Cox and Arkell submitted a case to the International Commission of Zoological Nomenclature to have all of the names in the *Prodrome* discarded as *nomina nuda*. This application, however, was unsuccessful [8] and the names therefore remain available provided they fulfil Articles 11 and 12 of the current Code. In fact, a significant proportion of the species and genera introduced do not meet the requirements of the Code, being without illustration, description or reference to a previously published work. Forty-eight bryozoan species (e.g., *Escharina micropora*, the type species of *Reptoporina* d’Orbigny, 1852, see Fig. 2B and D), mainly from the Senonian, can be interpreted as *nomina nuda* for this reason, even though most do cite references to plates in the *Terrains crétacés* whose exact publication date is unclear but is unlikely to have antedated the first two volumes of the *Prodrome* (see below). Two genera – *Crisina* and *Peripora* – appear also to be *nomina nuda*. D’Orbigny gave new names to 28 bryozoan species he considered to have been misidentified by later authors; for example, *Ceripora michelini* was proposed for *C. corymbosa* sensu Michelin non Lamouroux.

The second problem is that many of d’Orbigny’s bryozoan species names intended for publication in the *Terrains crétacés* actually appeared first in the *Prodrome*. Thus, for example, the name *Vincularia normaniana* was introduced, without description but with locality information, in volume 2 of the *Prodrome* published in 1850. The full description of the species was published the following year (1851) in the *Terrains crétacés* (p. 63). However, the *Prodrome* does cite a plate reference from the *Terrains crétacés* (pl. 600, figs 14–16) making it clear that this plate had been prepared, if not published, by 1850.

3.4. *Note sur quelques espèces nouvelles de Bryozoaires fossiles des terrains crétacés de la France (1850)*

This small and neglected paper [15] from the *Revue et Magasin de zoologie pure et appliquée* for February 1850 contains two lists of bryozoan species, accompanied by brief descriptions; no new genera are introduced. The first list is of species from the ‘Cénomaniens ou de la craie chloritée’ and repeats the species descriptions given in the *Prodrome*. However, the second list, covering species from the ‘Sénonien ou craie blanche’, differs from the equivalent listing in the *Prodrome* in that it includes brief descriptions of the species but lacks any reference to *Terrains crétacés* plate numbers. Unlike the undescribed *Prodrome* species, the names of these species are therefore available taxonomically. For example, *Reticulipora obliqua*, which subsequently became the type species of *Reticrisina* Gregory, 1899, was listed though not described in the *Prodrome*, but here has a two line description sufficient to satisfy criteria of availability.

3.5. *Catalogue des espèces fossiles de Mollusques bryozoaires, de Polypiers et d’Amorphozoaires de l’étage néocomien (1850)*

Similar to the previous paper in style, this paper [16] lists species from the Neocomian and essentially repeats the content of the equivalent section in the *Prodrome* (Volume 2, pp. 86–87). Interestingly, however, some additional genera (*Polytrema*, *Ceripora* and *Monticulipora*) not classified as bryozoans in the *Prodrome* are here reassigned to this phylum. Fifteen putative bryozoan species, including three belonging to genera now regarded as sponges, are introduced in this paper.

3.6. *Paléontologie française. Terrains crétacés. Bryozoaires (1851–1854)*

This monumental work [17] contains 1191 pages of text plus 201 plates. Although the emphasis is very much on Cretaceous species, as implied by the title, a smaller number of descriptions, some with figures, are given of Jurassic, Cainozoic and Recent taxa. All in all, about 900 species are described, of which about 700 are from the ‘Sénonien’ (Coniacian, Santonian, Campanian and Maastrichtian). A total of 170 new genera are introduced, comprising 97 cyclostomes and 73 cheilos-tomes. Without doubt this is d’Orbigny’s most important publication on bryozoans. Figs. 2–5 give examples of some type species of bryozoan genera, comparing original figures with photomicrographs and scanning electron micrographs of specimens from the d’Orbigny Collection.

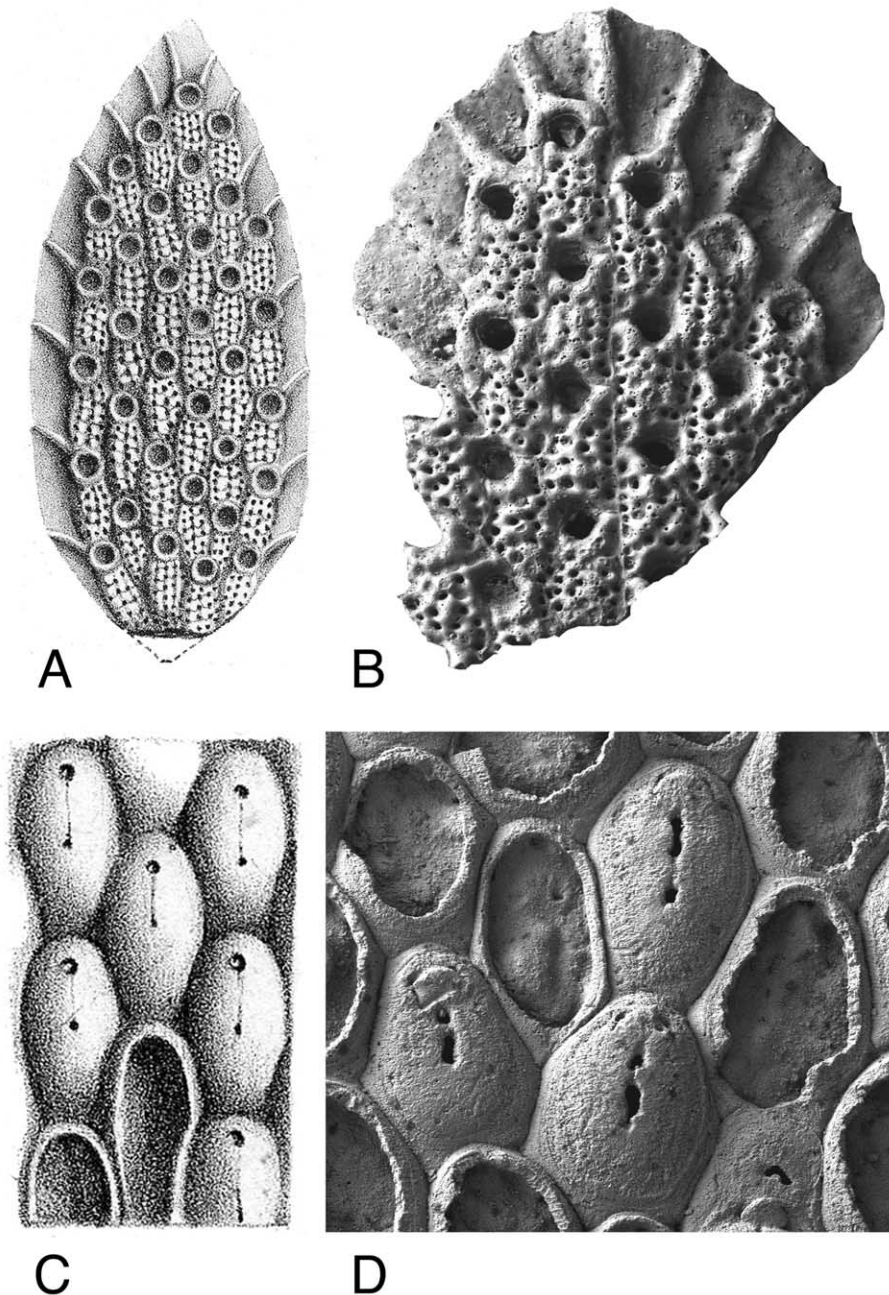


Fig. 2. Comparisons between d'Orbigny's illustrations (A, B) from the *Terrains crétacés* of the type species of two of his cheilostome bryozoan genera, and scanning electron micrographs (C, D) of the putative type specimens. A, C, *Lanceopora elegans* d'Orbigny, 1851; A, pl. 680, fig. 8 [17]; C, MNHN, d'Orbigny Collection 13615(a), Recent, Malacca, only the distal end of the bifoliate frond figured by d'Orbigny remains, $\times 28$. B, D, *Reptoporina micropora* d'Orbigny, 1852; B, pl. 605, fig. 5 [17] (as *Escharina micropora*); D, MNHN R61707, d'Orbigny Collection, Senonian, Fécamp, showing some zooids with calcareous closure plates perforated by two elongate, medial holes and bearing an impression of the operculum, $\times 34$.

Fig. 2. Comparaisons entre les illustrations de d'Orbigny (A, B), extraites des *Terrains crétacés*, représentant les espèces types de deux de ses genres de Bryozoaires cheilostomes, et les micrographies MEB (C, D) des spécimens types putatifs. A, C, *Lanceopora elegans* d'Orbigny, 1851; A, pl. 680, fig. 8 [17]; C, MNHN, collection d'Orbigny 13615(a), Actuel, Malacca, seule la pointe distale de la fronde bifoliée a été préservée, $\times 28$. B, D, *Reptoporina micropora* d'Orbigny, 1852; B, pl. 605, fig. 5 [17] (comme *Escharina micropora*); D, MNHN R61707, collection d'Orbigny, Sénonien, Fécamp, montrant quelques zooïdes, avec des diaphragmes calcaires perforés de deux cavités médianes allongées, conservant une impression d'opercule, $\times 34$.

D'Orbigny summarised the stratigraphical distribution of bryozoan genera and species at the end of the

Terrains crétacés. Data from his table on p.1082, showing the number of species through time, have been

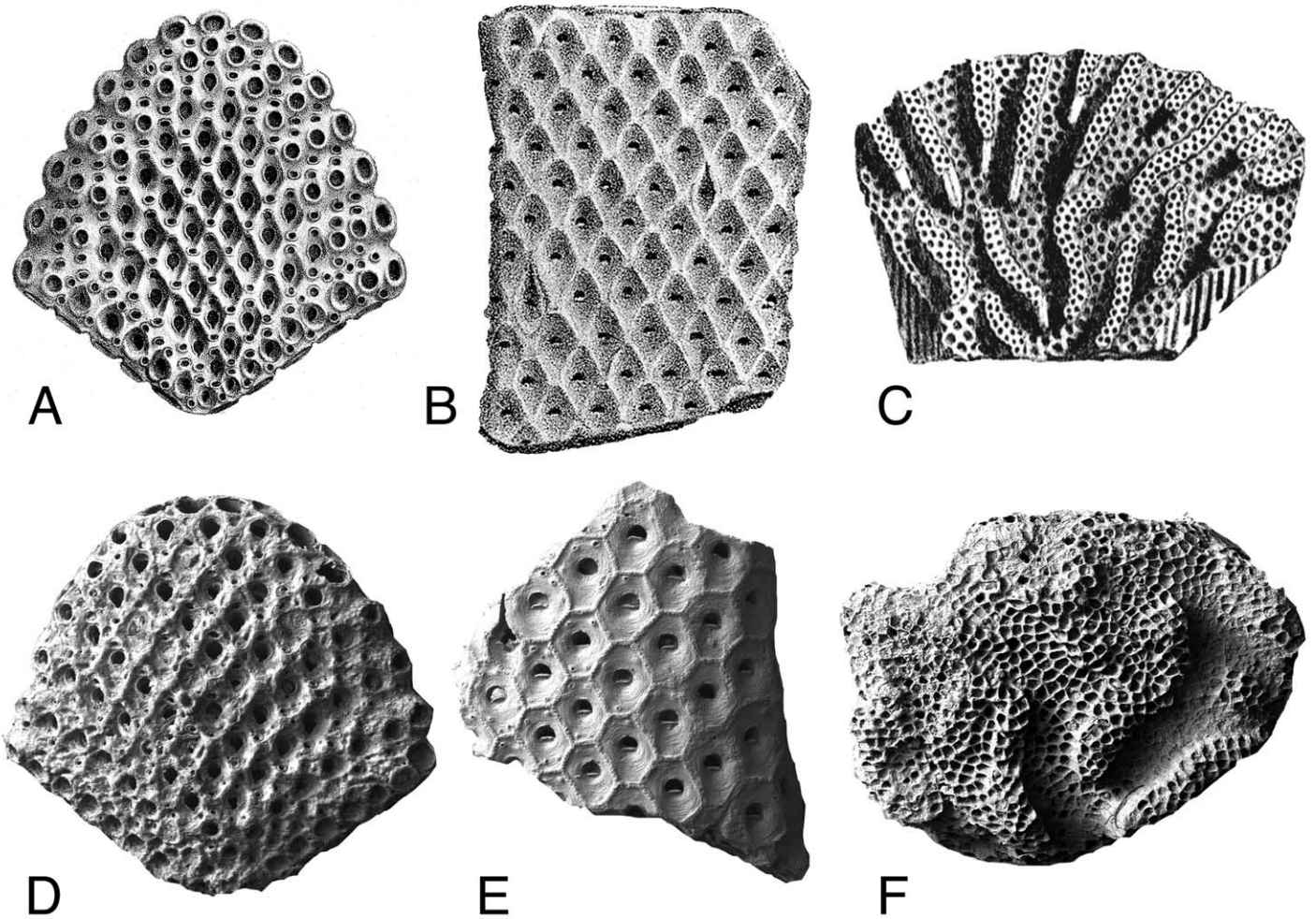


Fig. 3. Comparisons between d'Orbigny's illustrations (A–C) from the *Terrains crétacés* of the type species of three of his bryozoan genera, and scanning electron micrographs (D–F) of the putative type specimens. **A, D**, *Flabellopora elegans* d'Orbigny, 1851, a rooted cheilostome; **A**, pl. 661, fig. 2 [17]; **D**, MNHN, d'Orbigny Collection 13669, Recent, Malacca, $\times 17$. **B, E**, *Escharifora argus* d'Orbigny, 1852, a bifoliate cheilostome; **B**, pl. 666, fig. 14 [17] (as *Escharella argus*); **E**, MNHN, d'Orbigny Collection 7962, Senonian, Néhou, $\times 17$. **C, F**, *Meandrocavea elevata* d'Orbigny, 1853, a lamellar cyclostome; **C**, pl. 780, fig. 2 [17]; **F**, MNHN R61821, d'Orbigny Collection, Senonian, Vendôme, $\times 6$.

Fig. 3. Comparaisons entre les illustrations de d'Orbigny (A–C), extraites des *Terrains crétacés*, représentant les espèces types de trois de ses genres bryozoaires, et les micrographies MEB (D–F) des spécimens types putatifs. **A, D**, *Flabellopora elegans* d'Orbigny, 1851, un cheilostome fixé ; **A**, pl. 661, fig. 2 [17]; **D**, MNHN, collection d'Orbigny 13669, Actuel, Malacca, $\times 17$. **B, E**, *Escharifora argus* d'Orbigny, 1852, cheilostome bifolié ; **B**, pl. 666, fig. 14 [17] (comme *Escharella argus*) ; **E**, MNHN, collection d'Orbigny 7962, Sénonien, Néhou, $\times 17$. **C, F**, *Meandrocavea elevata* d'Orbigny, 1853, un cyclostome lamellaire ; **C**, pl. 780, fig. 2 [16] ; **F**, MNHN R61821, collection d'Orbigny, Sénonien, Vendôme, $\times 6$.

used to construct Fig. 6. Peaks in diversity are apparent in d'Orbigny's 'Carboniférien', 'Bathonien', 'Cénomanién', 'Sénonien' and 'Falunien' stages. In a modern context, d'Orbigny's Bathonien peak reflects the mid-Mesozoic radiation of the cyclostomes, and the 'Cénomanién' and 'Sénonien' peaks correspond with the Late Mesozoic diversification of bryozoans, especially the explosive radiation of cheilostomes [28].

Like the *Prodrome*, the *Terrains crétacés* poses many taxonomic problems. As Voigt [29] has commented, the

quality of the figures is uneven and they do not correspond wholly with the original specimens: they are restored by adding missing parts, particular features are exaggerated and embellished, and many are composites constructed from several different specimens. This makes the recognition of figured type specimens very difficult, especially in cases where d'Orbigny's material is voluminous and comes from more than one locality, details of which are not specified in the figure captions.

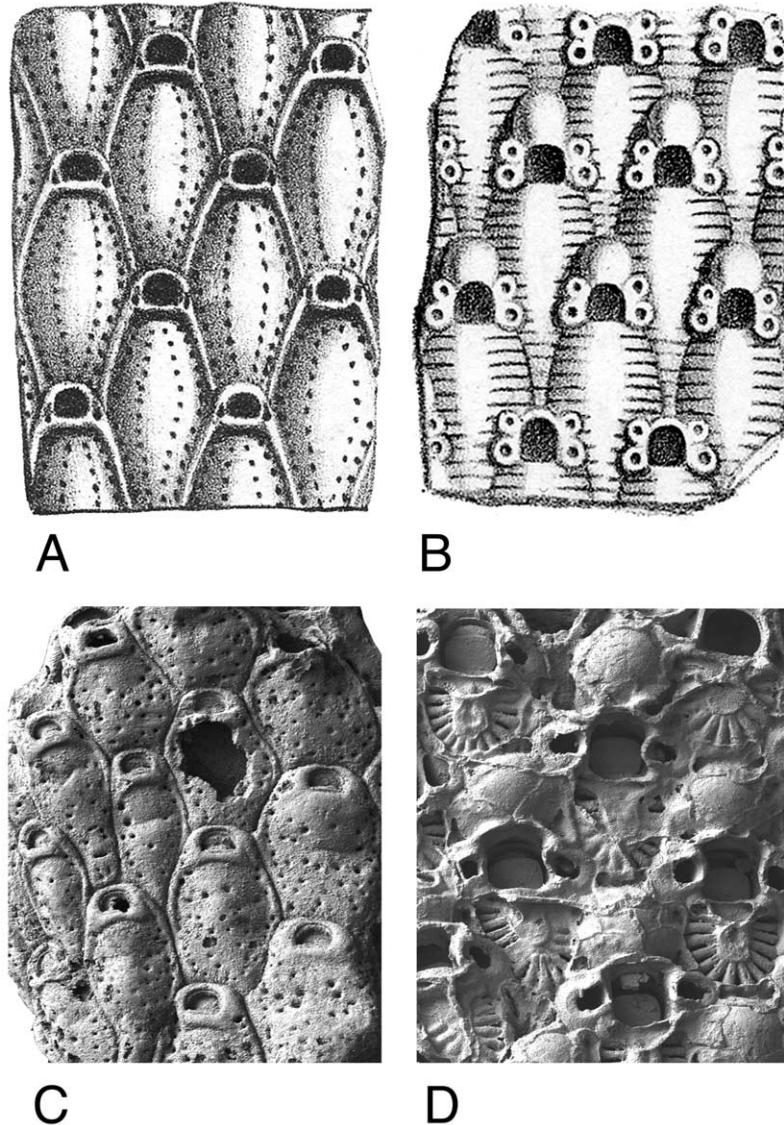


Fig. 4. Comparisons between d'Orbigny's illustrations (A, B) from the *Terrains crétacés* of the type species of two of his Cretaceous cheilostome bryozoan genera, and scanning electron micrographs (C, D) of the putative type specimens. A, C, *Escharipora inornata* d'Orbigny, 1852; A, pl. 686, fig. 18 [17]; C, MNHN R61719, d'Orbigny Collection, Senonian, Saintes-Colombe, $\times 19$. B, D, *Multescharipora insignis* d'Orbigny, 1853; B, pl. 720, fig. 13 [17]; D, MNHN R61732, d'Orbigny Collection, Senonian, Meudon, $\times 30$.

Fig. 4. Comparisons entre les illustrations de d'Orbigny (A, B), extraites des *Terrains crétacés*, représentant les espèces types de deux de ses genres de Bryozoaires cheilostomes du Crétacé, et les micrographies MEB (C, D) des spécimens types putatifs. A, C, *Escharipora inornata* d'Orbigny, 1852; A, pl. 686, fig. 18 [17]; C, MNHN R61719, collection d'Orbigny, Sénonien, Sainte-Colombe, $\times 19$. B, D, *Multescharipora insignis* d'Orbigny, 1853; B, pl. 720, fig. 13 [17]; D, MNHN R61732, collection d'Orbigny, Sénonien, Meudon, $\times 30$.

Another difficulty is raised by uncertainties regarding the dates of publication of the livraisons of text and sets of plates. Sherborn [24] deduced the likely dates of publication of the text livraisons, mainly based on evidence from the *Neues Jahrbuch*. Publication dates for the plates have not, however, been documented (J.-C. Fischer, personal communication to PDT April 2001). Internal evidence implies that the plates were published to a large extent independently of the text. Whereas the text of the *Terrains crétacés* deals with

cheilostomes first (pp. 23–584) followed by cyclostomes (pp. 585–1080), this sequence is not repeated in the plates: pls 600–607 mostly depict mixtures of cyclostome and cheilostome species, pls 608–650 show cyclostomes, pls 651–734 cheilostomes, and pls 735–800 cyclostomes again. It seems likely that the plates were published, at least initially, in advance of the text. For example, pls 651–653 were cited as early as the third livraison of text (pp. 29–44) published in 1851. In many cases, generic attributions of species

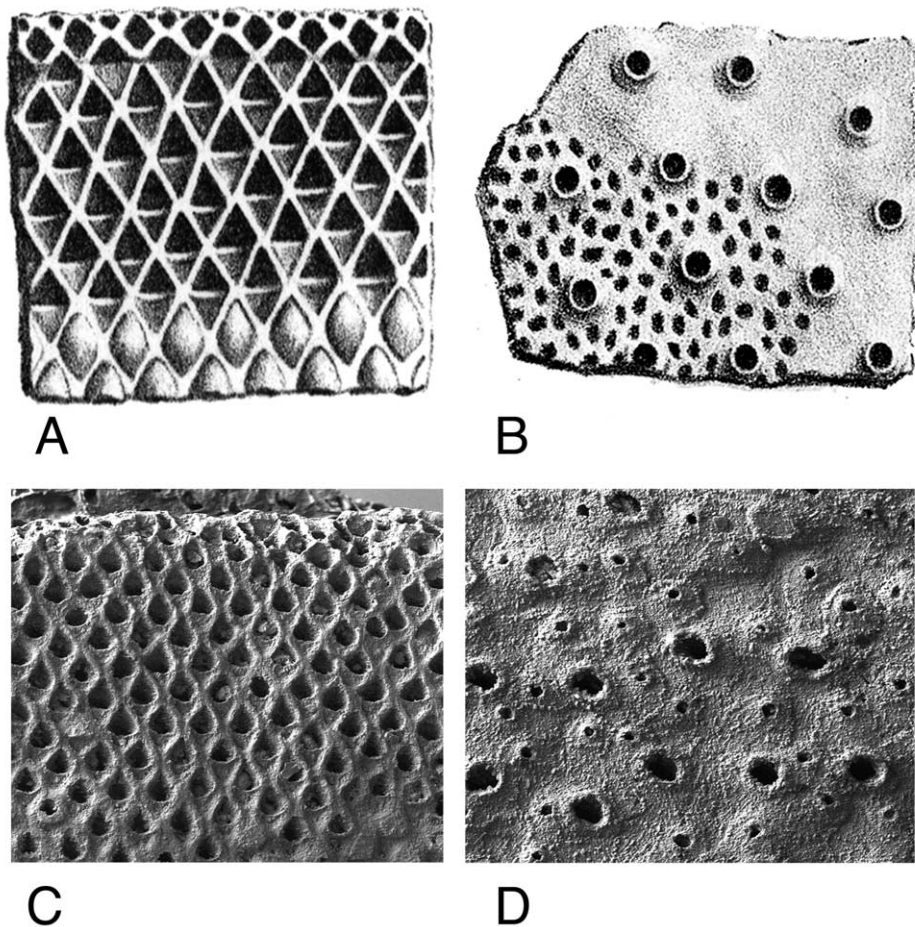


Fig. 5. Comparisons between d'Orbigny's illustrations (A, B) from the *Terrains crétacés* of the type species of two of his Cretaceous cyclostome bryozoan genera, and scanning electron micrographs (C, D) of the putative type specimens. A, C, *Retetelea pulchella* d'Orbigny, 1853; A, pl. 762, fig. 14 [17]; C, MNHN, d'Orbigny Collection 8193(a), ?Turonian, ?Senonian, Troot, distal edge of bifoliate colony showing ontogenetic zonation from open apertures to apertures closed by terminal diaphragms (lower right), $\times 18$. B, D, *SemimultiCLAUSA variabilis* d'Orbigny, 1853; B, pl. 767, fig. 8 [17]; D, MNHN, d'Orbigny Collection 8324(a), Senonian, Villedieu, showing small apertures of secondary nanozooids, which are not evident in d'Orbigny's figure, $\times 35$.

Fig. 5. Comparisons entre les illustrations de d'Orbigny (A, B), extraites des *Terrains crétacés*, représentant les espèces types de deux de ses genres bryozoaires cyclostomes du Crétacé, et les micrographies MEB (C, D) des spécimens types putatifs. A, C, *Retetelea pulchella* d'Orbigny, 1853; A, pl. 762, fig. 14 [17]; C, MNHN, collection d'Orbigny 8193(a), ?Turonien, ?Sénonien, Troot, bord distal d'une colonie bifoliée montrant une zonation ontogénétique, depuis des opercules ouverts jusqu'à des opercules fermés par des diaphragmes terminaux (en bas, à droite), $\times 18$. B, D, *SemimultiCLAUSA variabilis* d'Orbigny, 1853; B, pl. 767, fig. 8 [17]; D, MNHN, collection d'Orbigny 8324(a), Sénonien, Villedieu, montrant de petites ouvertures de nanozoïdes secondaires, qui ne sont pas évidents sur la figure de d'Orbigny, $\times 35$.

depicted in plates had been updated by the time the text was published. For instance, a species labelled as *Idmonea virgula* in pl. 631, figures 15–17, was described as *Reptotubigera virgula* in the text (p. 753). This uncertainty about the dates of appearance of the plates has implications for the dates of publication of the taxa concerned given that d'Orbigny's illustrations alone are sufficient to make the names available under Article 12.2.7 of the Code. Pending firm evidence of plate publication dates, however, the only pragmatic option is to assume that the taxa were validated when the

relevant page of text was published using the dates given by Sherborn.

Early revisions of the *Terrains crétacés* bryozoans were published by Pergens [20] for cyclostomes and by Canu [3] for cheilostomes. Both of these works, published in 1890 and 1900 respectively, synonymise many of d'Orbigny's species. Unfortunately, neither revision comes even close to being adequately illustrated. They also fail to give full descriptions of all species, list specimens by their registered numbers or select type

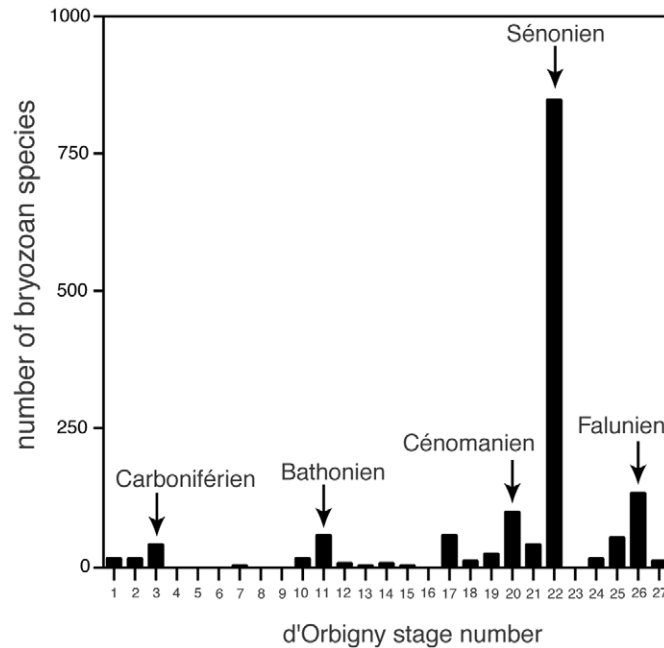


Fig. 6. Bryozoan species diversity through time as understood by d'Orbigny [17 (p. 1082)]. Five of his 27 stages containing especially large numbers of species are labelled.

Fig. 6. Diversité stratigraphique des espèces de Bryozoaires telle qu'elle a été comprise par d'Orbigny [17 (p. 1082)]. Cinq de ses 27 étages, contenant un particulièrement grand nombre d'espèces, sont répertoriés.

specimens from the syntype series left by d'Orbigny. At about the same time, A.W. Waters briefly examined the Recent species published in the *Terrains crétacés* and elsewhere by d'Orbigny and published some taxonomic notes [31]. Subsequent studies providing better revisions of parts of the collections were published by Prud'homme [22], Walter [30], and Voigt [29], but there is still great need for a more comprehensive treatment.

3.7. Recherches zoologiques sur la classe des Mollusques bryozoaires (1851–1852)

This two-part, unillustrated publication [18] deals mainly with the classification of the Order 'Cellulinés' (i.e., Cheilostomata). Families and genera are diagnosed and keys are given to their identification. Much of the text replicates that of the *Terrains crétacés* and there are frequent references to page and figure numbers in the *Terrains crétacés*, implying that these had already been produced even if not yet published. Seventeen families of 'Cellulinés' are here recognised, containing 98 genera, of which 71 were authored by d'Orbigny himself in previous publications.

3.8. Cours élémentaire de paléontologie et de géologie stratigraphiques (1852)

The second volume [19] of d'Orbigny's textbook of palaeontology and stratigraphy contains a section on

bryozoans (pp. 97–113). A selection of families and genera are described, a few of the generic descriptions being accompanied by figures (some taken from the *Terrains crétacés*, others seemingly original). Brief comments are made on classification and stratigraphical distribution etc. Out of 69 genera described in this paper, d'Orbigny considered 2 to be present in all of his 27 stratigraphical stages, and 67 to have more restricted distributions allowing them to be used as stratigraphical indicators.

4. D'Orbigny's classification of bryozoans

D'Orbigny's schemes of bryozoan classification evolved during the course of his research. The first livraison of the *Terrains crétacés* [17] tabulates (p. 22) a tripartite division of bryozoans into three orders: 'Cellulinés', 'Tubulinés' and 'Foraminés'. These orders were based on the form of the zooecia, respectively cell-like, tubular and with holes. Colony-form was then used to distinguish 13 families, five belonging to each of the 'Cellulinés' and 'Tubulinés' and three to the 'Foraminés' (Table 1). That this early scheme was soon abandoned is evident from d'Orbigny's *Recherches...* paper [18], where the 'Classe Mollusques bryozoaires' is reduced to two orders, 'Cellulinés' and 'Centrifuginés', the 'Tubulinés' and the 'Foraminés' becoming

Table 1. Classification tabulated by d’Orbigny in the first livraison of the bryozoan volume of the *Terrains crétacés* [17 (p. 22)].

Tableau 1. Tableau de classification de d’Orbigny dans la première livraison du volume sur les Bryozoaires des *Terrains crétacés* [17 (p. 22)].

			Order Cellulinés	Order Tubulinés	Order Foraminés
Colony articulated		zoecia on two sides zoecia on on side	Cellaridae Catenaridae	Pericrisidae Crisidae	
Colony non-articulated	free	zoecia on two sides zoecia on one side	Escharidae Candidae Celleporidae	Periporidae Reteporidae Tubuliporidae	Myriozoumidae Osculiporidae Polytremidae
	fixed				

divisions of the ‘Centrifuginés’. ‘Cellulinés’ and ‘Centrifuginés’ respectively correspond very closely with Busk’s orders Cheilostomata and Cyclostomata, which are used today in bryozoan classification. Among the slight differences are d’Orbigny’s inclusion of the cheilostome family Myriozoumidae (= Myriaporidae) in the Centrifuginés and the boring ctenostome *Terebripora* in the Cellulinés.

D’Orbigny [17, 18] distinguished two orders of Cellulinés – ‘Radicellés’ and ‘Empâtés’. The former included erect bushy colonies that were basally rooted, as well as some encrusting runner-like forms that may be stoloniform (e.g., *Aetea*). The assigned families, though often including a heterogeneous mix of genera by today’s standards, nevertheless generally correspond to modern families except where the name of the type genus has been synonymised. Hence the Acamarchisidae corresponds to the Bugulidae (*Acamarchis* is a junior objective synonym of *Bugula*), and the Catenaridae to the Catenicellidae (*Catenaria* is junior homonym of a cestode genus and the name was modified to *Catenicella* by de Blainville). D’Orbigny included in the families Flustridae and Cellaridées (i.e. Cellariidae) several unrelated genera that today comprise the types of other families; otherwise these family names are still in use. The Electriniidae (now Electridae) included a mix of lightly-calcified encrusting and erect rooted taxa, the latter now ironically included in his family Candidae. D’Orbigny [17] named the Candidae in the first livraison (1851) of the *Terrains crétacés* (Table 1), giving a brief diagnosis, but he did not subsequently use it, submerging it in the Electriniidae (Table 2).

Of the twelve families included in the ‘Empâtés’ – encrusting, free-living and fixed-erect forms – only one, the ‘Porinidae’, is in current use. The others are based on genera that were subsequently abandoned or are now *nomina oblita*. There is one potential exception, however, viz. the Steginoporidae. This was based on a cribrimorph (acanthostegan) genus whose type species, *Steginopora ornata*, was exceptionally well illustrated by d’Orbigny. Unfortunately, there appear to

be no known specimens of *S. ornata*, but pending revision of the many cribrimorph taxa that now exist, and with the assurance that topotypic material would be easily recognisable, the family name Steginoporidae could yet have validity.

The classification of Centrifuginés used by d’Orbigny in the *Terrains crétacés* similarly distinguished two suborders (Table 3). The more minor of these, the Radicellés, with colonies attached by ‘roots’, contained only two families, Crisidae and Serialaridae, distinguished respectively by the presence and absence of articulations. Whereas d’Orbigny’s understanding of Crisidae was essentially identical to the modern concept of this cyclostome family, his Serialaridae contained genera now placed in the bryozoan order Ctenostomata, including *Amathia*. D’Orbigny divided his larger suborder – ‘Empâtés’ – into four divisions: ‘Operculés’, ‘Fasciculinés’, ‘Tubulinés’ and ‘Foraminés’. The ‘Operculés’ were, as the name implies, character-

Table 2. Classification of the Order ‘Cellulinés’ (mainly cheilostomes) adopted by d’Orbigny [17, 18].

Tableau 2. Classification de l’ordre des Cellulinés (principalement les cheilostomes) adoptée par d’Orbigny [17, 18].

Order ‘Bryozoaires Cellulinés’	
Suborder ‘Cellulinés Radicellés’	Family Acamarchisidae Family Flustridae Family Electriniidae Family Catenaridae Family Cellaridées (Cellaridae)
Suborder ‘Cellulinés Empâtés’	Family Escharidae Family Escharinellidae Family Porinidae Family Escharellinidae Family Escharellidae Family Porellidae Family Porellinidae Family Eschariporidae Family Steginoporidae Family Flustrellaridae Family Flustrellidae Family Flustrinidae

Table 3. Classification used by d'Orbigny for the Order 'Centrifuginés' (mainly cyclostomes) in the bryozoan volume of the *Terrains crétaçés* [17].

Tableau 3. Classification utilisée par d'Orbigny pour l'ordre Centrifuginés (principalement les cyclostomes) dans le volume sur les Bryozoaires des *Terrains crétaçés* [17].

Suborder 'Radicellés'	
	Family Serialaridae
	Family Crisidae
Suborder 'Empâtés'	
Division 'Operculés'	Family Eleidae
	Family Myriozoumidae
Division 'Fasciculínés'	Family Fascigeridae
	Family Fasciporidae
Division 'Tubulinés'	Family Tubigeridae
	Family Sparsidae
	Family Clausidae
	Family Crisnidae
	Family Caveidae
Division 'Foraminés'	Family Ceidae
	Family Cavidae
	Family Cytisidae
	Family Crescisidae

ised by having zooids with an operculum, a hinged flap closing the orifice. D'Orbigny mixed families we now regard as cyclostomes (Eleidae) and cheilostomes (Myriozoumidae = Myriaporidae) in this division, but he deserves credit for recognising that the Eleidae, despite their substantial convergence with cheilostomes, are in fact cyclostomes. His three other divisions – 'Fasciculínés', 'Tubulinés' and 'Foraminés' – are all non-operculate cyclostomes differing in the arrangement and structure of the zooids. The zooids are bundled into fascicles in the 'Fasciculínés', have projecting peristomes in the 'Tubulinés', and are non-projecting in the 'Foraminés'. These divisions correspond respectively to skeletal organisations termed mixed-walled, fixed-walled and free-walled [26]. The phylogenetic significance of these organisational types, and hence their value as taxonomic subdivisions, has yet to be established.

There is one important respect in which d'Orbigny's classification of cyclostomes differs from schemes used nowadays. The skeletal structures and shapes of brooding zooids (gonozooids) are today regarded as crucial in the definition of higher taxa of cyclostomes [26]. Gonozooids, however, played no part in d'Orbigny's classification and very few gonozooids were even figured by d'Orbigny: two examples [17, pl. 761, figs 3' and 7] are referred to in his text as 'cellules accessoires'. D'Orbigny's apparent failure to notice gonozooids

is less surprising when the rarity of these polymorphs in most cyclostome species is taken into consideration: it is not unusual to require several hundred branch fragments of erect colonies before a gonozooid is discovered.

D'Orbigny's generic classification of cyclostomes emphasised colony-form. Sometimes this philosophy was applied to such an extent that encrusting colonies with different shapes as a result of growing on different substrates were placed in different genera. Colonies of *Actinopora* and *Reptoclausa*, which grew around perished cylindrical substrates were, for instance, the basis of d'Orbigny's genera *Conotubigera* and *Semiclausa* respectively. Genera within his families tended to be recognised and named according to their colony-form, leading to a very logical system of nomenclature. For example, genera with multilayered colonies had 'multi' within their names, those with clavate colonies 'clavi', reptant colonies 'repto' etc. The root of the family was also incorporated in the generic name, apart from those genera named before he had developed the full classification expounded in the *Terrains crétaçés*. Thus, genera within the Family Cavidae have names ending with '-cava', those within the Clausidae end with '-clausa', Sparsidae with '-sparsa' etc. Both the family affiliation of any given genus and some aspect of its colony-form are consequently evident from its name. For example, *Multisparsa* is a multilayered genus belonging to the Sparsidae, and *Clavicleusa* is a clavate genus within the Clausidae. An unfortunate consequence of this system is that genera with comparable colony-forms placed within the similarly spelt families Caveidae and Cavidae have names that are very easily confused, e.g., *Semimulticavea* vs *Semimulticava*, *Clavicleavea* vs *Clavicleava*.

5. Discussion

The legacy left by d'Orbigny to bryozoology is almost entirely taxonomic – he erected a plethora of species, genera and families of bryozoans, many of which remain in use today. With regard to cyclostome bryozoans (Centrifuginés), a total of about 370 nominal genera can be found in the literature. Of these, Alcide d'Orbigny is the author of approximately 30% (113; omitting an objective junior synonym and a genus now known to be a cheilostome), by a considerable margin the greatest number named by any single taxonomist. A further 13 d'Orbigny species have since been designated as the type species of genera by later authors. While some of d'Orbigny's cyclostome genera are little known or seldom used (e.g., *Pyricavea*), others are employed routinely (e.g., *Fasciculipora*) in contemporary bryozoan taxonomy.

D'Orbigny introduced 75 new cheilostome genera. Following our study, and discarding those for which type species are lost and which may never be properly understood, we regard 40 of these as having current availability. This number represents only 4% of the 1013 genera and subgenera currently compiled for the *Treatise* revision of cheilostomes. We shall reinstate many that were previously overlooked or ignored by Bassler [1]. These comprise *Filiflustrina*, *Latereschara*, *Lateroflustrina*, *Multescharella*, *Multescharipora*, *Pyriflustrina*, *Reptescharella*, *Reptoflustrina*, *Reptolunulites*, *Reptoporella*, *Reptoporina*, *Reptescharinella*, *Semiescharipora*, *Semiflustrina*, *Semiflustrina*, and *Reptescharipora*. On the other hand, a number of d'Orbigny's genera have long been in use, including *Conescharella*, *Discoporella*, *Flabellopora*, *Fusicellaria*, *Poricellaria*, *Porina*, and *Pyripora*, among others.

While it is reasonable to portray d'Orbigny as a taxonomic splitter who over-emphasised colony-form and paid too much regard to stratigraphical differences, Heron-Allen's contention [7, p. 60] that for these reasons his work "was to all intents and purposes ignored by MacCoy, Hagenow and Haime in their later and more authoritative works on the group" surely exaggerates the truth.

D'Orbigny's taxonomic descriptions were often of a comparable standard to those published by other authors at the time. Furthermore, he developed thoughtful and logical systems of classification that, in some cases, have stood the test of time. His work has, however, caused a great many difficulties for subsequent students

of the Bryozoa. Problems arise from: (1) dates of publication which do not coincide with those given on the title pages of the works and in some instances (*Terrains crétacés* plates) are unknown (publication delays were not d'Orbigny's fault but were associated with political unrest at the time of the abdication of King Louis-Philippe and declaration of the Second Republic); (2) d'Orbigny's habit of using the same species name (e.g., *cenomana*) over and over again within different genera; (3) his tendency to create confusingly similar generic and familial names (e.g., *Escharipora* (Fig. 4A and C) and *Escharifora* (Fig. 3B and E); Escharinellidae and Escharellinidae); (4) the use of stylised and/or composite figures, as in the *Terrains crétacés*; (5) taxonomic oversplitting, owing, for example, to slight differences in colony form or stratigraphical differences (no species were 'allowed' to occur in more than one stratigraphical stage because of d'Orbigny's belief that total extinction of all life occurred at the end of each stage, followed by a fresh creation at the beginning of the next); (6) his confusing habit of attributing generically reassigned species to himself (e.g., *Pustulopora pseudospiralis* Michelin was renamed '*Peripora pseudospiralis* d'Orbigny' when he transferred the species to the genus *Peripora*); (7) appending his new taxa with the date that he penned the taxonomic description rather than the actual date of publication and hence availability of the taxon (e.g., '*Trochopora* d'Orbigny, 1847' was actually published in 1849 [13]); (8) in many instances, listing new taxa without figures or adequate descriptions.

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