Functional analysis of the extraordinary shell of *Sherbornia mirabilis* Iredale, 1917 (Caenogastropoda) and discussion on its current placement within the Pickworthiidae

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In 1917 Iredale described *Sherbornia mirabilis* as a peculiar gastropod from Christmas Island in the Indian Ocean. Its remarkable shell morphology leads to questions on functions and adaptations. The greatly expanded apertural shield, three canals and protoconch morphology suggest relationships to different genera and families, which prompts the question whether morphological adaptations of this species are evolutionary polyphyletic. Based on shell morphology (studied by scanning electron microscope and micro-tomography) we discuss the placement of this species and the closely related extinct species *Faxia macrostoma.* Shell shape, deep sinus in the protoconch, and round aperture support its current allocation within the Cerithioidea. Within this superfamily the canals are unique, as are the expanded peristome/apertural shield, thus supporting placement in a separate family Sherborniidae.

INTRODUCTION

Iredale (1917) described marine gastropods from Christmas Island collected by R. Kirkpatrick, who studied marine sponges. Kirkpatrick brought back material from some dredgings which contained a wealth of micromolluscs. This included *Sherbornia mirabilis* Iredale, 1917, of which he hypothesised a relationship to the Triphoridae J.E. Gray, 1847. Although he only had empty shells at hand, Iredale postulated that the additional canals were used for circulatory purposes and therefore indicated a parasitic relation on living organisms whilst the apertural shield of was used for securing the snail upon its host. He proposed placement of this species in its own family, Sherborniidae Iredale,1917, which would be closely related to the Triphoridae.

Over sixty years passed until this species was discussed again. Marshall (1980) considered the species 'a dwarfed, highly specialised triforid', and therefore closely related with the Triforidae Jousseaume, 1884 (currently known as Newtoniellidae Korobkov 1955; Bakker & Albano, 2022: 5, 13-14) in which he placed Sherborniinae as subfamily. However, Cernohorsky (1981) summarised Iredale's and Marshall's observations and re-allocated the genus to the family Sherborniidae, yet under the so-called Cerithiopsacea (currently the superfamily Triphoroidea, which comprises Triphoridae, Cerithiopsidae and Newtoniellidae), despite observing the deep sinus in the protoconch which he saw as more similar to that of the Cerithiidae. Ponder & Warén (1988: 303) maintained *S. mirabilis* in Triphoroidea, respecting Marshall's view, but cited Cernohorsky (1981) regarding the larval shell. It seems they were the first to mention a possible link between this genus and the Pickworthiidae, based on a personal communication from Le Renard & Bouchet, but they allocated Pickworthiidae to the Truncatelloidea (Ponder & Warén, 1988: 296). They also linked Faxiidae with *Sherbornia* (Ponder & Warén, 1988: 294). Nützel (1998) believed it is outside Triphoroidea and the so-called 'Ptenoglossa', but indeed more similar to Cerithioidea. Based on the apertural shield and tubes, Bouchet & Le Renard (1998) wrote that *"although the genus has long been classified near the Triforidae, the characters of the protoconch allow a con-*

fident allocation in the Pickworthiidae”. Also Le Renard & Bouchet (2003) and Bouchet & Rocroi (2005) listed *Sherbornia* within Pickworthiidae.

There is only one other species in the Sherborniinae, the extinct *Faxia macrostoma* Ravn, 1933 from the Danian (Palaeocene) of Denmark. The shell has a markedly similar shape to *Sherbornia mirabilis*. Clearly not knowing *Sherbornia*, Ravn classified this species in a separate family, Faxiidae Ravn, 1933 (Ravn, 1933: 42), which has later been synonimised with the Sherborniinae (Bouchet & Rocroi, 2005: 250). sem images show that *Faxia macrostoma* has a slightly tilted protoconch with a deep sinusigera notch, as in the Pickworthiidae, indicating a planktotrophic development (Lozouet, 2024: fig. 30E).

Species of Triphoridae have greatly diversified their radula and shells to adapt to the morphological plasticity in Porifera, on which they feed (Marshall, 1983; Wells, 1998; Nützel, 2021). The feeding mode of Newtoniellidae supposedly follows that of the superfamily Triphoroidea in sponges, despite lacking confirmation.

The Pickworthiidae were mostly known from shell grit in shallow to moderately deep (0-200 m) water in the Indo-West Pacific until Kase & Hayami (1992) and Kase (1998, 1999) recorded numerous living specimens and shells from submarine caves and cryptic voids where they may occur in large numbers. Although Kase (1998) stated that "the shells may have accumulated from nearby original biotopes over a long period of time", Kase & Hayami (1992) suggested that most species lived in the caves, and later authors indicated that the Pickworthiidae typically live in submarine caves (e.g. Bouchet & Le Renard, 1998; Le Renard & Bouchet, 2003; Poppe, 2008: 478; Takano & Kano, 2014). However, during scuba diving numerous specimens and species were collected in shallow water (5-35 m) from shell grit between branching corals without submarine caves in sight, thus cryptic voids may be more relevant (personal observation from NW Borneo and Spratly Islands, jgmr). Fossil Pickworthiidae from Europe also indicate a less restricted ecology, with one species strongly suspected to live in deep, muddy environments (Lozouet, 2024: 48).

Apart from *Sherbornia*, the animals have a round aperture without siphons or siphonal canal and therefore can be assumed to feed differently from the Triphoridae. The Pickworthiidae have a sinusigera larval shell in the protoconch, suggesting planktotrophic larval development (Kase, 1998).

In this paper we question the current systematic position of *Sherbornia mirabilis* in Pickworthiidae. There are in general two major hypotheses that can be followed: based on the anal/posterior canal morphology, a closer relationship to Newtoniellidae and Triphoridae, or based upon protoconch morphology (following the current hypotheses) and placement in Pickworthiidae. We investigate the shell morphology with various imaging tools and describe it in

higher detail in order to provide more details about its current systematic position.

MATERIAL AND METHODS

Material & imaging. — Dead collected shells of *Sherbornia mirabilis* from French Polynesia on loan from the Muséum national d'Histoire naturelle (23 specimens, thus far without formal collection numbers) were examined (listed as material studied), based on which a redescription was made (since a detailed description had not previously been made). Besides this, material recorded in the literature is listed (other material). Light photographs were made with a stereomicroscope using stacking software. sem images were made without coating in a jeol jsm-it510 using low vacuum, 10 KV voltage and 30 Pa pressure. A CT scan was made using a NeoScan N80 micro-CT scanner; the output was processed using Avizo software. Based on the CT scan, an enlarged 3D model was printed which facilitated analysis of the shell morphology. The 3D model can be downloaded from www.Basteria.nl (website under construction).

Due to the translucent nature of the shell of *Sherbornia* and the partial coverage of whorls by the large apertural shield, some characteristics are barely discernible. The sem images and the 3D printed model help with this, but the observations made have been rechecked on the specimens.

Abbreviations. — ams = Australian Museum, Sydney, Australia; L = shell length; mguh = Museum Geologicum Universitatis Hafniensis, University of Copenhagen, Denmark; mncn = Museo Nacional de Ciencias Naturales, Madrid, Spain; mnhn = Muséum national d'Histoire naturelle, Paris, France; QM = Queensland Museum, Australia; usnm = Smithsonian National Museum of Natural History, Philadelphia, usa; wam = Western Australian Museum, Australia.

DESCRIPTION

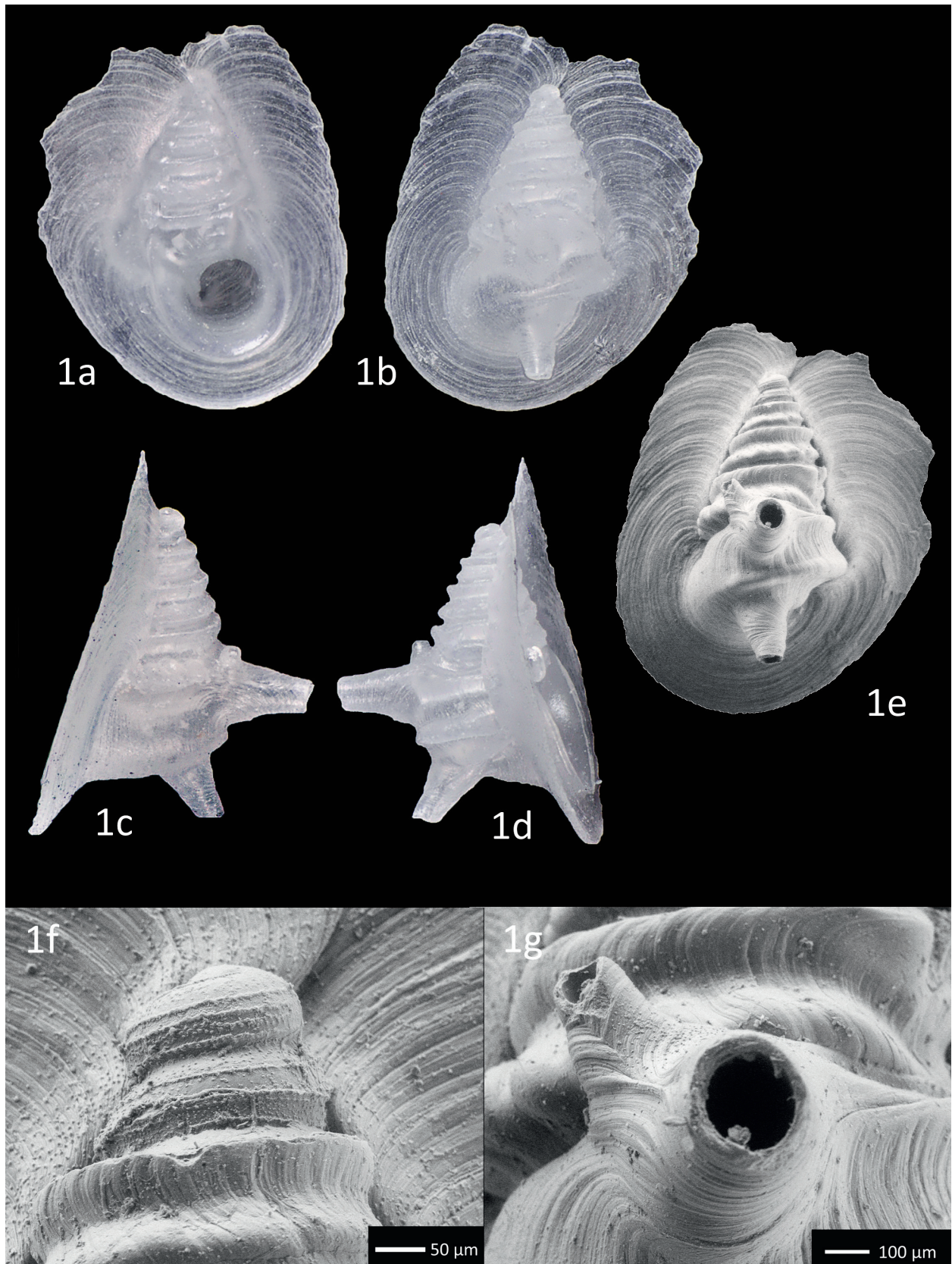### *Sherbornia mirabilis* Iredale, 1917
(Figs 1, 4-9)

Type locality. — Indian Ocean, Christmas Island, North-East point, 183 m [100 fathoms].

Type material. — Holotype, not located (based on literature and online data). Paratype, ams C.49706.

Distribution. — Christmas Island, Australia and French Polynesia.

Material studied (all from mnhn). — french polynesia, Expédition tuam 2011, Tuamotu Archipelago: Stn TAM01, atoll Amanu, 17°54.5'S, 140°52.5'W, 60 m depth (4 sp.); Stn TH02, atoll Hereheretue, 19°52.5'S, 145°00.4'W,

Fig. 1. *Sherbornia mirabilis* Iredale, 1917, French Polynesia, Tuamotu Archipelago. Stn TTE03, atoll Tematangi, 21°42.6'S, 140°34.0'W, 60 m depth, L = 1.8 mm (MNHN). **a-d.** Light microscopy photos. **e-g.** Scanning Electron Microscope images. **a.** Ventral view. **b, e.** Dorsal view. **c, d.** Lateral views. **f.** Detail of fig. 1e showing protoconch. **g.** Detail of fig. 1e showing siphonal and middle canals; note the folding of the growth lines around the canals.

60 m depth (3 sp.); Stn TH02, atoll Hereheretue, 19°52.5'S, 145°00.4'W, 15 m depth (2 sp.); Stn TH03, atoll Hereheretue, 19°52.5'S, 145°00.4'W, 25 m depth (6 sp.); Stn THA01, atoll Hao, 18°03.8'S,140°59.5'W, 55 m depth (2 sp.); Stn TN01, atoll Nukutavake, 19°16.4'S, 138°47.6'W, 65 m depth (2 sp.); Stn TTE01, atoll Tematangi, 21°42.2'S, 140°40.9'W, 65 m depth (1 sp.); Stn TTE03, atoll Tematangi, 21°42.6'S, 140°34.0'W, 60 m depth (4 sp.).

Other material. — australia: Christmas Island, 200 m depth, leg. C. Laseron (wam S77441, 2 sp.; wam S77442, 1 sp.); Christmas Island, Tan & Low, 2014 (QM.Molluscs: MO4938, 1 sp.). french polynesia: drift shells (usnm 720755, 2 sp.); Tahiti (Tröndlé, 2010); Makem (Tröndlé, 2010); Tuamotu Archipelago, Moruroa Atoll (AM C.103039, 1 sp.); Tuamotu Archipelago, Moruroa Island (usnm 819766, 4 sp.); Tuamotu Archipelago, Anaa Island (Cernohorsky 1981); Tuamotu Archipelago, Îles du Vent (mncn D2B0CE86-7C29-1275-E053-5514A8C0FBF9), (mncn B6BB40E7-FCE6-5E23-E053-5014A8C0B867); Tuamotu Archipelago, Raroia, Mataira Island outer beach drift (usnm 698687, 1 sp.).

Depth range. — 5-65 m.

Description. — Shell length 1.8-3.0 mm, width 1.4-2.3 (specimen of Fig. 1 length 1.8 mm, width 1.4 mm, without shield length 1.35 mm, W 0.8 mm). Protoconch (max. width ~0.2 mm) paucispiral, 2.2 globose whorls with a rugose surface and two granular spiral cords (at about 0.4 and 0.6 of whorl height). On the last protoconch whorl a subsutural groove develops. Teleoconch up to 4 whorls, with a horizontal subsutural plateau and marked periphery bending about 110° to form an irregular upper spiral cord, below which there are a deep groove, a broad lower cord with prosocline elongated tubercles and an equally wide, but deeper groove. Halfway the final whorl the upper cord shows a few widely spaced narrow opisthocline radial riblets, below which there is a very wide groove, whereas the lower cord has become completely smooth. One quarter whorl behind the aperture a new structure emerges between the penultimate and the final whorl, expanding apically to form the largest, almost vertical dorsal canal at the level of the lower spiral cord. Slightly further at its apical side an extension forms the narrower and shorter anal canal, which curves slightly until it is about horizontal pointing towards the apex. Below the lower cord a third canal of intermediate size and length (the siphonal canal) is formed, which points abapically at a 45° angle. Final quarter whorl slightly convex with weak orthoclinal growth lines. Eventually the shell expands to an exceedingly large, broad, oval apertural shield, which creates some space underneath. The growth lines of the shield reflect a regular expansion on the abapical side and laterals up to the level of the deep groove on the final whorl, from where the growth lines bend towards the shell allowing rapid accretion towards the apex. The shield touches the upper whorls, but leaves them exposed on the ventral side, also leaving small holes at where the shield meets the spiral grooves. The aperture is round within. Around the aperture a thick U-shaped rim, at the labial edge attached to the shell at the level of the lower spiral cord and ends in an almost axially aligned riblet. On the columellar edge the rim ends lower, with a rib at 45° angle, in some shells continuing over the columella as a narrow riblet, in apertural view visible as a minuscule "tooth". The rim around the aperture and the outer edge of the apertural shield are more or less in the same plane.

FUNCTIONS AND ADAPTATIONS

Faxia macrostoma (Figs 2-3) is markedly similar to *Sherbornia mirabilis*, the aperture having a thick slightly oblique U-shaped reflected edge, in addition to the presence of two canals: a very short siphonal canal and a short dorsal canal that has a marked slit on the apertural side. *Faxia* is also substantially larger, up to 6 mm (Lauridsen & Schnetler, 2014) vs. 3 mm for *Sherbornia*. The dorsal canal of *Sherbor-*
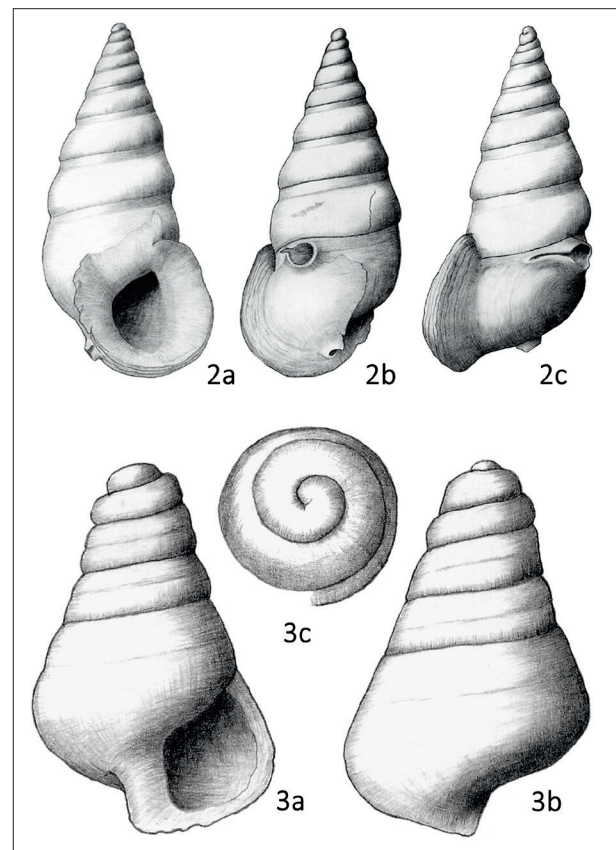
Figures 2-3. *Faxia macrostoma* Ravn, 1933, from the Baunekule facies, Faxe Formation, Fakse, eastern Denmark, Danian, Palaeocene (drawings by Ane Elise Schrøder; from Lauridsen & Schnetler, 2014). **2.** mguh 31003, L = 5.4 mm. **3.** mguh 31004, L = 1.2 mm, diameter of protoconch 0.6 mm.
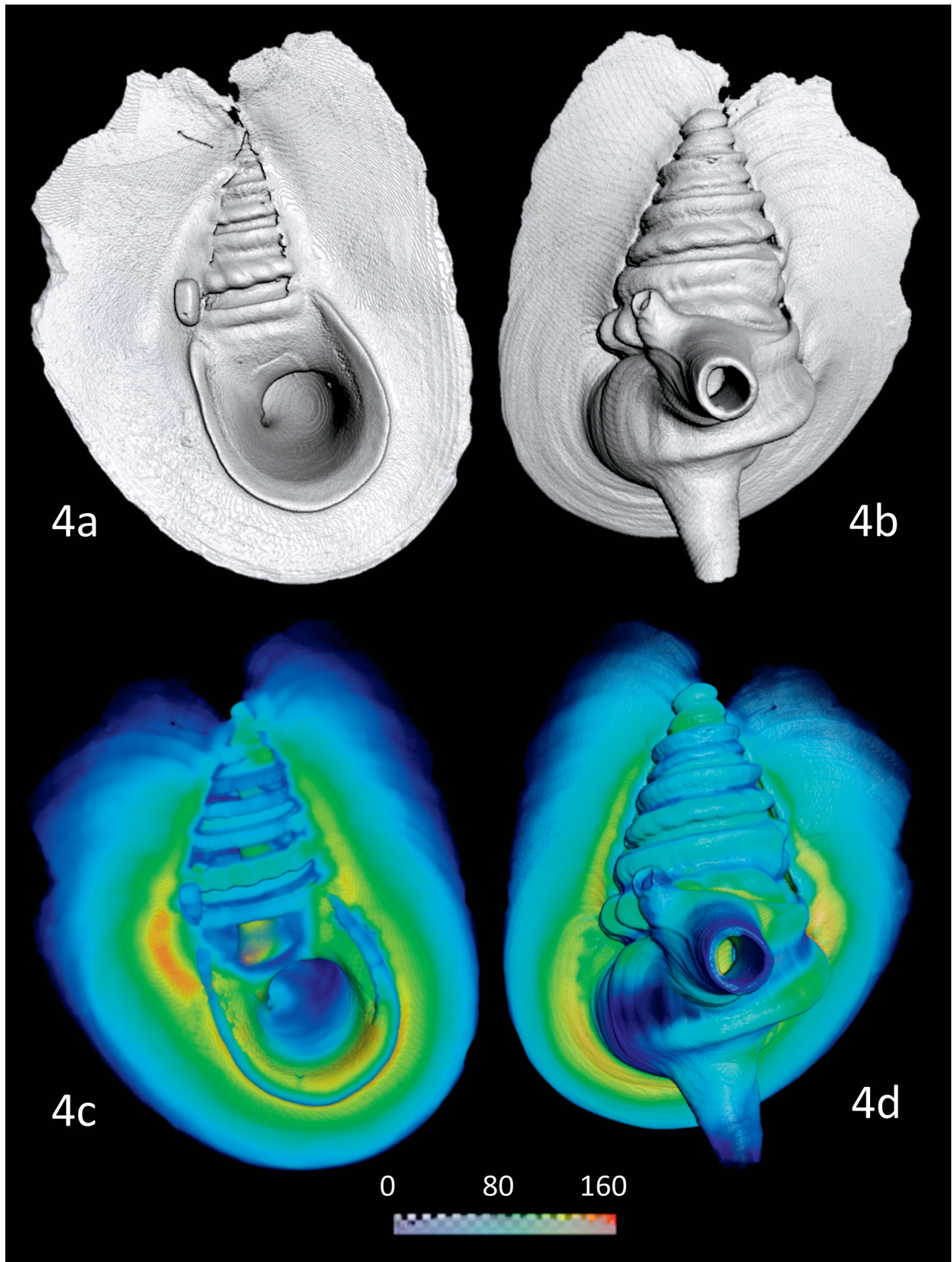
Fig. 4. *Sherbornia mirabilis* Iredale, 1917, same specimen as Fig. 1. **a-b.** 3D model from micro CT scan. **c-d.** 3D model from micro CT scan processed to show shell thickness (scale indicates shell thickness in μm). **a, c.** Ventral view. **b, d.** Dorsal view.
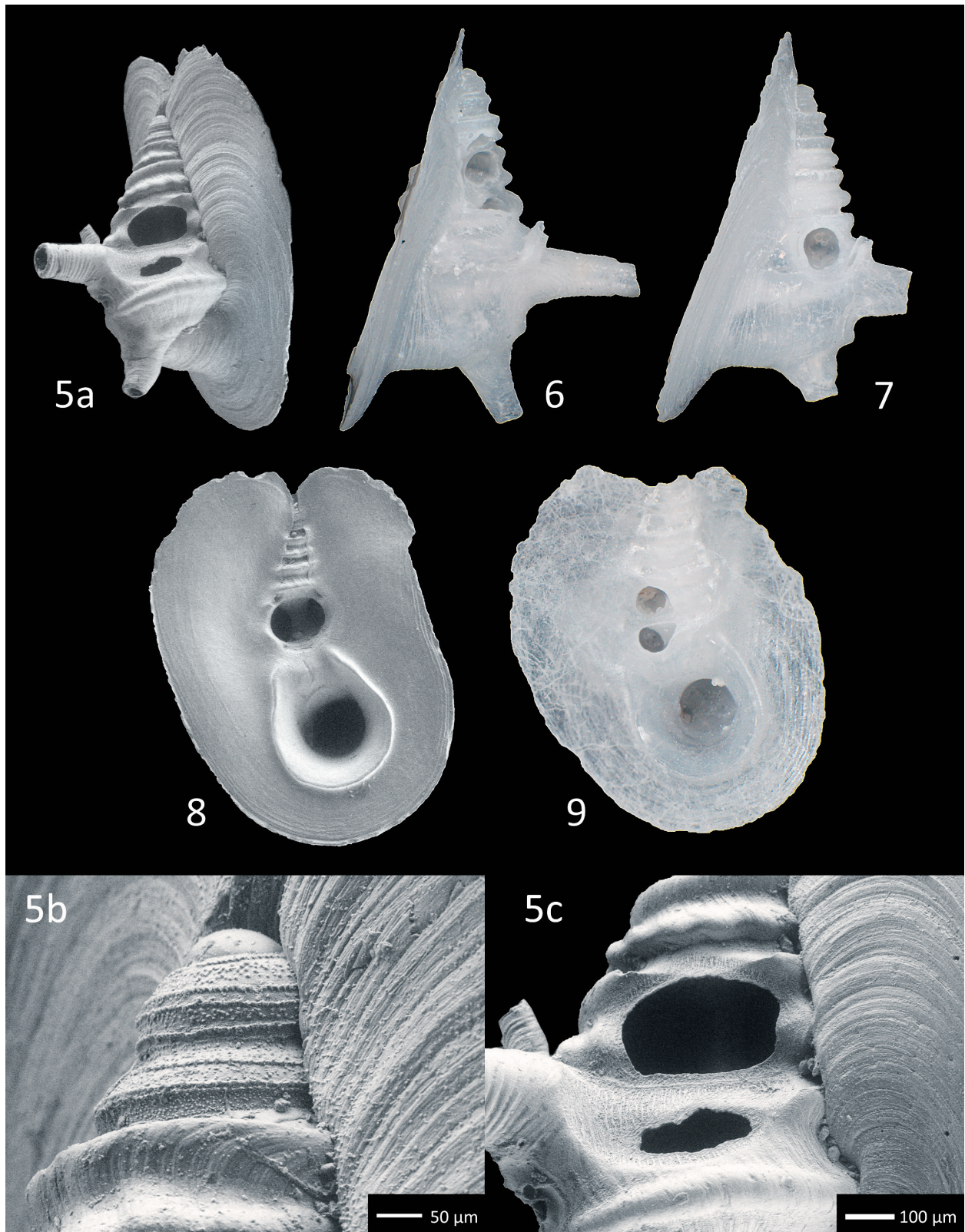
Figs 5-9. *Sherbornia mirabilis* Iredale, 1917, French Polynesia, Tuamotu Archipelago (MNHN), with drill holes. **5.** Stn TTE03, atoll Tematangi, 21°42.6'S, 140°34.0'W, 60 m depth, L = 2.15 mm (MNHN). **5b.** Detail showing protoconch. **5c.** Detail showing drill mark with micro-rasping marks. **6.** Stn TAM01, atoll Amanu, 17°54.5'S, 140°52.5'W, 60 m depth, L = 2.0 mm (MNHN). **7-8.** Stn TH02, atoll Hereheretue, 19°52.5'S, 145°00.4'W. **7.** 60 m depth, L = 2.1 mm (MNHN). **8.** 15 m depth, L = 2.0 mm (MNHN). **9.** Stn THA01, atoll Hao, 18°03.8'S, 140°59.5'W, 55 m depth, L = 1.8 mm (MNHN). **5, 8.** Scanning Electron Microscope images. **6, 7, 9.** Light microscopy photos. **5-7.** Lateral views. **8-9.** Ventral views.

nia is formed in the same position and by a similar process, but it is much broader and longer, the slit is closed with only a seam remaining and there is a separate anal canal. *Faxia* lacks the large apertural shield, but has a strong reflected peristome.

The abapically pointing siphonal canal of *Sherbornia* and *Faxia* is present in many gastropods and it is assumed to serve for the intake of water allowing respiration and chemoreception to locate food (or to enable feeding, in some cases). Such a feature has evolved multiple times in different groups of gastropods (Vermeij, 2007). The canal is much longer in *Sherbornia*. Houbrick (1978) argued that very long or dorsally directed siphonal canals reflect burrowing habits, as such canals would enable buried snails to remain in contact with the water above, but Vermeij (2007) noted many gastropods with dorsally recurved canal that are epifaunal and do not burrow. The large and not entirely flat apertural shield of *Sherbornia* and the wide peristome of *Faxia* allow space for the foot, thus indicating that these species are not burrowers. Note that the siphon itself may be much longer than the canal, allowing feeding all around the shell. For comparison: *Bittium* species from the NE Atlantic have siphons with a length about twice the shell length with which they can feed when not actively moving in winter (personal observation JGMR). In contrast, the small adapically-pointing canal of *Sherbornia* most logically would serve for the disposal of faeces. It is positioned at the base of the larger dorsal canal (Figs 1c, 6-7), in the same position as the base of the slit in *Faxia* (Fig. 2c). The large and wide dorsal canal present both in *Sherbornia* and *Faxia* is here interpreted to serve for the dispersal of larvae, but in *Faxia* it may be combined with the disposal of faeces (through the slit on the side). The larvae are relatively large, but the canal is wide enough for a single larva to pass through (as is evident from the size of the protoconch) and its vertical position releases the larvae into the water stream, away from the zone next to the substrate where water flow is reduced. In *Faxia* the dorsal canal is short and on the apertural side it remains open. In *Sherbornia* it is closed, although it is constructed in a similar way as it is evident from the seam on the apertural side, and it is much longer. Observation of living specimens of *Sherbornia* is required to confirm these hypotheses about the functions of canals.

The growth lines of *Sherbornia* (Figs 1e, 1g) and *Faxia* (Fig. 2) clearly show that the canals (and the apertural shield in *Sherbornia*) are only made once the spire is almost fully grown, i.e. when the animal reaches adulthood. Thus far no juveniles of *Sherbornia* have been identified. Lacking these remarkable structures, they may easily be overlooked. Note that 169 specimens of *Faxia* were available for study, including numerous juveniles and few adults with a complete aperture (Lozouet, 2024; a complete specimen illustrated in Lauridsen & Schnetler, 2014: fig. 54).

This indicates that in samples with *Sherbornia*, juveniles likely have been overlooked as they lack the characteristic canals and shield. The scarcity of adult specimens of *Faxia* specimens with complete aperture may be an indication of intense predation by crustaceans, which eventually led to the development of the apertural shield in *Sherbornia*. Possibly, also damaged adult specimens of *Sherbornia* were not picked from the sediment samples. Such specimens could document successful of failed crustacean attempts to prey upon adult *Sherbornia*.

Very few gastropods make such an apertural extension. Small apertural extensions occur, e.g. in the genus *Distorsio* Röding, 1798 (Personidae), but there the extension is thicker and comparatively smaller, whereas varices are produced at various earlier stages. Similarly nassarids of the subgenus *Plicarcularia* Thiele, 1929 build a thick apertural shield (e.g. Cernohorsky, 1884: figs 104-108, pls 1-6, pl. 7 figs 1-2), but only as adults. is the varices are interrupted by the siphonal canal. It is assumed that these thickenings provide protection against predators, especially crustaceans, which have difficulties to insert their chelae into the aperture with the thickening of the apertural shield (e.g. Vermeij, 1978).

The closest species to *Sherbornia* in relation to the morphology of the apertural shield is the extinct *Umbilia* (*Palliocypraea*) *gastroplax* (McCoy, 1867) (Cypraeidae) from Lower to Middle Miocene deposits of Victoria, Australia (see a.o. Darragh, 2002). This is a large (shell length up to 12 cm) species with a prominent (10-15 mm wide), rather flat lateral flange encircling the body of the shell. Chapman (1929) suggested this is an adaptation to enable the animal to creep over an even-surfaced oozy seabed. It is the only species in the Cypraeidae with such adaptation, so maybe the adaptation was no longer needed when environmental conditions changed.

Many species of Triphoridae and Newtoniellidae are expected to feed on sponges and may be found on and inside sponges. It is unlikely that this is the case in *Sherbornia* as the wide apertural shield would have no logical function and it would hinder the animal from moving around on irregular surfaces. It is thus more likely that the animal is free-living. There is no evidence that *Sherbornia* lives parasitic as postulated by Iredale (1917; repeated by Bouchet & Le Renard, 1998) who supposed the apertural shield was used to hold on to its host and the canals for circulatory purposes. Nützel (2021) discusses characteristics of the shells of parasitic gastropods, to help in recognising extinct species as parasites, which could also help in extant species only found dead, but highlights the difficulties in this. He states that the majority of parasitic gastropods are small and high-spired with a generally low shell morphological disparity. He also mentions that most extant family groups of parasitic gastropods originated during the Late Cretaceous and through adaptive radiation became highly

diverse groups forming a considerable part of marine ecosystems both in species richness and relative abundance. *Sherbornia* is small and has a high spired shell, but the shell morphology does not suit a parasite and the genus clearly is not species rich nor abundant.

The apertural shield of *Sherbornia* may create stability during movement and creates a protected space for feeding. Suspension eating gastropods not only use the siphon for respiration and chemoreception, but also for feeding (as in *Bittium* as discussed above). As in *Sherbornia* the siphonal canal is located outside the shield it can fulfil these functions without having to expose the head. Besides the wide peristome, the aperture is surrounded by a thick rim. The shield is not perfectly flat, so it possibly leaves space for the foot and head. During the preparation of specimens for inspection by sem it was noticed how the apertural shield made it much harder to remove it from the sticky tape compared to other gastropods. As the flange appears to provide sufficient space for the foot, it may enable the animal to adhere strongly to a smooth surface. This would be a similar advantage to that of limpets (strong fixation with the foot fully enclosed within a protective shell), without having to adapt the full shell morphology, whilst maintaining protection against crustacean predators. The wide peristome of *Faxia* may have served a similar purpose. Vermeij (2017) described how at least 54 gastropod families independently evolved a limpet type shell morphology. Many Pickworthiidae have a thick apertural rim, but where in *Sherbornia* the rim is U-shaped (open towards the apex) in Pickworthiidae it is rounded. One of the specimens of *Sherbornia* also had a thick knob on the inner lip (Figs 4a, 4c), but this is a deformation not seen in other specimens, albeit some others also have some irregularities in the rib bordering the aperture.

The CT scan of *Sherbornia* (Figs 4a-b) was processed to measure shell thickness (Figs 4c-d), which shows that the cords, apertural rim and apertural shield are the thickest parts of the shell, whereas the spiral grooves and the canals are thinner. Of the 24 specimens studied, five are perforated by drill holes (Figs 5-9), three on the side and two on the ventral side next to the aperture (further called underneath the shield). The holes are tapering, which often is indicative of predation by naticids (carnivorous gastropods that live in sand; e.g. Vermeij, 1980), but Archuby & Gordillo (2018) found similar shaped boreholes by muricids. Fig. 5c appears to show micro-rasping marks made by the radula as is seen in muricids, whereas naticids use chemical methods. Thus it is possible that the boreholes on the side were made by muricids, whereas those underneath the shield were made by naticids. Although the shield appears to provide good protection against predation by cracking (none of the shields were damaged, whereas in *Faxia* hardly any specimens with undamaged aperture are known), it clearly does not protect against predation through drill-

ing. One illustrated specimen of *Faxia macrostoma* (Fig. 2b) probably survived an attack before the canals and peristome were built. Gofas (2003) described how the complicated aperture of shells in the genus *Trituba* (Newtoniellidae) provides good protection against crab predation, but the coarse sculpture does not protect against drilling by a muricid gastropod. If some of the predators are indeed naticids, *Sherbornia* might live on the sediment rather than on hard substratum, which would explain how the predators could reach the area underneath the shield.

Vermeij (2007) and Webster & Vermeij (2017) described how siphonal canals and varices have developed at different times in various groups of gastropods. Vermeij (2007) specifically described how variations like a dorsally deflected canal, a long canal, and a closed canal originated during the Cretaceous and Cainozoic; the closed siphonal canal, in which the edges join to form a tube, arose 15 times in the evolution of gastropods, all in the adult stages of caenogastropods with determinate growth. Vermeij specifically argued that the acquisitions of energy-intensive, complex innovations that yield greater power have a greater effect on ecosystems, communities, and their resident clades than do reversals, which generally reflect energy savings. This strongly suggests that the energy-intensive construction of three different canals and the huge flange has a great impact on the success of survival and reproduction of *Sherbornia*.

The presence of a single extinct species in the Palaeocene of Denmark and a single extant species in the western tropical Pacific (with a hiatus of ca. 60 million years in time and of 11,000 km in space) demonstrate that the geological record of these animals is very incomplete. *Faxia* was recovered from the Faxe Formation, a calcareous deposit formed by a cold water coral ecosystem, but within this specifically from the Baunekule facies, in which micromolluscs were preserved due to the weak consolidation and early recrystallisation to calcite (Lauridsen & Schnetler, 2014). Calcareous deposits often recrystallise to form hard limestones in which many fossils become unrecognisable. As both *Sherbornia* and *Faxia* appear restricted to coral facies this may explain the low preservation potential of fossils.

SYSTEMATIC POSITION

An overview of key characteristics of the various taxa mentioned above is given in Table 1.

As indicated above, the various canals are also known from Triphoridae and Newtoniellidae, both placed in the Triphoroidea. They are an energy-intensive, complex innovation, completely lacking in the Pickworthiidae. Superficially the greatest similarity is to *Mastoniaeforis lifuana* (Hervier, 1898) (Triphoridae), which has two spectacularly long canals (siphonal and a dorsal one that may be a com-

	Cerithioidea			Triphoroidea	Triphoroidea
	Pickworthiidae*	*Faxia*	*Sherbornia*	**Newtoniellidae**	**Triphoridae**
coiling	dextral	dextral	dextral	dextral	sinistral**
shape	variable	cerithiform	cerithiform	turriculate	turriculate
protoconch	deep sinus	deep sinus	deep sinus	no sinus	sinus
canals	none	2	3	1-2	0-2
aperture	rounded	rounded, U-shaped rim	rounded, U-shaped rim	squarish, often with siphonal canal and anal sinus	squarish, often with siphonal canal and anal sinus
apertural shield	no	no	yes	no	no

Table 1. Key characteristics of the various taxa discussed. * excluding Sherborninae. ** except for *Metaxia* Monterosato, 1884.

bination of anal and spawning) but it is sinistrally coiled (Albano et al., 2023: figs 21a-p). The long dorsal canal suddenly emerges at the level of the upper spiral cord. The siphonal canal is constructed from multiple rings building out. *Tribuba* (Newtoniellidae) is dextrally coiled and has two canals (not three as the name suggests, the third opening being the aperture): a siphonal canal and an anal canal. As in *Sherbornia,* the anal canal originates between the penultimate and last whorl and both canals are formed building out from the side, leaving a seam on the side of both canals (Gofas, 2003: figs 2, 4).

The Pickworthiidae have no canals, but their protoconchs are similar to those of *Sherbornia* and *Faxia*. Thus far few molecular data are available, but based on DNA of the Pickworthiidae *Mareleptopoma iredalei* (Bavay, 1921) and *Microliotia mirabilis* (Kuroda & Habe, 1991) and various Cerithioidea of other families, Takano & Kano (2014: figs 1 & S3) found the family to fit within the Cerithioidea. Shell shape, deep sinus in the protoconch, and rounded aperture support the current allocation of *Faxia* and *Sherbornia* within the Cerithioidea, where it is currently allocated (MolluscaBase, 2024), whereas all Triphoroidea have a turriculate or spindle-like shape. Note that all Cerithioidea are suspension feeders.

Based on the unique combination of characters in *Faxia* and *Sherbornia*, and especially the unique number of three canals and a huge apertural shield in the latter, following the original authors, we recognise these genera in a separate family Sherborniidae Iredale, 1917 (junior synonym Faxidae Ravn, 1933). Vermeij (2007: table 2) also considered Sherborniidae a separate family. Based on the enormous hiatus in the geological record of the family, it is expected to comprise many more taxa. As the group developed multiple canals, it goes well beyond the acquisition and loss of the siphonal canal in various groups of gastropods discussed by Vermeij (2007). However, the discovery of living specimens will certainly contribute to the systematic discussion regarding this group.

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