Enigmatic microfossils from Belgian Oligocene sediments are serpuloidean, not gastropod opercula

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Small calcareous opercula occurring in early Rupelian euryhaline deposits in Limburg (Belgium) have been described by Bosquet (1859, 1861), Sandberger (1861) and Karnekamp (1983). They were interpreted as opercula of the gastropods *Stenothyroides pupa* (Nyst, 1836) (Truncatelloidea: Stenothyridae) or *Sandbergeria cancellata* (Nyst, 1836) (Cerithioidea: Diastomatidae), disregarding the fact that neither shape nor morphological details of opercula of living relatives fit either of the two gastropods, which, moreover, are expected to have had non-calcareous opercula which would not be preserved as fossils. These microfossils fit well into the range of opercular morphologies described from living species of the genus *Spirobranchus* Blainville, 1818 (family Serpulidae, phylum Annelida). They are redescribed as *Spirobranchus limburgicus* n. sp.

KEY WORDS: *Spirobranchus*, Serpulidae, Stenothyridae, Diastomatidae, *Sandbergeria*.

Introduction

The lower Oligocene sediments known from outcrops in Belgium and adjacent areas of the Netherlands contain a diverse fauna. Amongst the macrofossils, molluscs are prominent and documented in several monographic publications (Nyst, 1836, 1845a,b; Albrecht & Valk, 1943; Glibert & Heinzelin, 1954; A.W. Janssen, 1963; Marquet *et al*., 2008). The lithostratigraphic nomenclature has undergone significant transformation over time. In the scheme of Marquet *et al.,* (2008), followed herein, the lower Oligocene (Rupelian) sediments are divided into 5 formations, reflecting facies variability, including salinity and water depth changes, in near-coastal to subtidal marine settings at the SW margin of the North Sea Basin.

The Borgloon Formation lies in the lower part of the Rupelian, which was traditionally treated as a separate local stage and referred to as "Tongrien", and the Borgloon Formation as "Tongrien supérieur" (Table 1). Its mollusc fauna indicates a near-coastal environment, with freshwater and land molluscs mixed into polyhaline fauna (Marquet *et al*., 2008). Amongst the fossils of the Borgloon Formation are small operculum-like structures which have hitherto either been interpreted as gastropod opercula or have been ignored (see 'taxonomic history' below). We reject the interpretation as gastropod opercula, redescribe and name these structures, and interpret them as the calcareous endplates of opercula of a member of the Serpuloidea, class Polychaeta, phylum Annelida.

Material and methods

Of 9 available specimens, four were drawn using a Wild M5 binocular microscope with a drawing tube. Afterwards these specimens were imaged by SEM.

The material is now housed at: **BSPG** = Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; and **SMF** = Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Taxonomy

Phylum Annelida
Class Polychaeta
Subclass Sedentaria
Order Sabellida
Family Serpulidae Rafinesque, 1815
Genus *Spirobranchus* Blainville, 1818

Type species – Serpula gigantea Pallas, 1776 (present-day, tropical West Atlantic).

Note – The genera *Pomatoceros* Philippi, 1844 and *Pomatoleios* Pixell, 1913 were synonymised with *Spirobranchus* by Pillai (2009), Rzhavsky *et al.* (2014), Ippolitov *et al.* (2014), Kuprianova *et al.* (2019) and Brandão & Brasil (2020).

***Spirobranchus limburgicus* n. sp. (Figs 1-6)**

1859 *Nematura pupa* – Bosquet: 7 [sub *N. bidens*], pl. 1 figs 7a-b [*partim*, non *Paludina pupa* Nyst, 1836].

Age (m.a.)	Chrono-stratigraphy	Group	Formation	Member	
				Vlaams Brabant, Antwerp, Limburg	Limburg
23.03	Chattian		Voort	Voort Veldhoven	
28.1	Rupelian	Rupel	Eigenbilzen		
			Boom	Putte	
				Terhagen	
				Belsele-Waas	
			Bilzen	Kerniel	
				Kleine Spouwen	
				Berg	
		Tongeren	Borgloon	Kerkom	Alden Biesen
				Boutersem	Henis
			Zelzate / Sint-Huibrechts-Hern	Ruisbroek	
				Watervliet	
				Bassevelde	
33.9					Grimmertingen

Table 1. Lithostratigraphy of the Oligocene in Belgium; after Marquet *et al.* (2008).

1860 *Sandbergeria pupa* – Weinkauff: 184, 185 [*partim*, non *Paludina pupa* Nyst, 1836]

1861 *Sandbergeria cancellata* – Sandberger (livr. 5): 167-168, pl. 21 figs 7, 7a (copy Bosquet 1859) [partim, non *Pyramidella cancellata* Nyst, 1836]

1861 *Sandbergeria cancellata* – Bosquet: 54-55, 57, pl. 1 figs 2a-b [*partim*, non pl.1 fig.1; non *Pyramidella cancellata* Nyst, 1836]

1983a Operculum van *Stenothyra pupa* – Karnekamp: 27, pl. 1 figs 1a-1b [*tantum*, non *Paludina pupa* Nyst, 1836) (Kleine Spouwen, Zanden van Oude Biezen)

2008 *Sandbergeria cancellata* – Marquet *et al*.: 35-36 [*partim*, non pl. 7 fig. 6] (literature list includes citations of opercula: Sandberger, 1861 pl. 21 fig. 7, Bosquet 1861 fig. 2; but opercula not mentioned in text)

2008 *Stenothyroides pupa* – Marquet *et al*.: 50 [*partim*, non pl. 12 fig. 3] (literature list includes citation of operculum Bosquet 1859: fig. 7; opercula not mentioned in text)

Holotype – SNSB-BSPG 2021 I 1 (Fig. 1)

Paratypes – No. 1-3 SNSB-BSPG 2021 I 8-10 (Figs 2-6), No. 4-8 SMF XVI 1031-1035.

Type locality – Belgium, Limburg, Kleine Spouwen, Nachtegaalstraat (50° 50’ 9”N, 5°33’0” E; now part of the city of Bilzen; locality description see Marquet *et al*. (2008: 9-10, textfig. 8).

Type stratum – Sands, Alden Biesen Member (= Zanden van Oude Biezen, Sables de Vieux-Joncs), Borgloon Formation, lower Rupelian (after Marquet *et al*., 2008).

Historical material – Bosquet (1859, 1861) reported the opercula from the locality Vliek in Belgian Limburg (50°46’22”N, 5°46’22”E), where formations he informally named ‘Argile de *Nucula*’ [*Nucula* clay] and ‘Sables à Pétoncles’ [*Glycymeris* sands] were outcropping. He gave no information from which formation the opercula originated. Probably it was the “*Glycymeris* sand”, now Berg Sand, which contains a stenohaline fauna, but also reworked Alden Biesen fossils (Marquet *et al.,* 2008). Sandberger (1861) referred only to material received from Bosquet.

Derivatio nominis – after the occurrence in Belgian Limburg.

Description – Small operculum-like calcareous structures, outline irregularly rounded. One side is more or less convex, carrying one large or three smaller tubercles, its margin falling off more steeply than the main part of the surface. The other side is gently concave, with the centre of the depression located beneath the single

large tubercle, or, if three peripheral tubercles are developed, unrelated to the position of the tubercles; margin of the concave side often raised for ¼ to ½ of the entire circumference, typically on the side of the single large tubercle; a zone around the entire margin bevelled. Margin of the fossil usually in a wavy plane. Tubercles broad, rounded, their tops flat or with a depression. Sculpture on the concave side none, the convex side with growth lamellae. Paratype 2 (Fig. 6) shows also a faint radial undulation. The centre of the concentric lamellae is the top of the single tubercle, or, in the case of three tubercles being present, there are two centres located at the tops of the two larger tubercle (paratype 3, Fig. 4).

Variability – The specimens show strong variability. The holotype (Fig. 1) bears a single large eccentric tubercle with a large apical depression; the tubercle almost reaches the periphery of the structure. Paratype 1 bears a smaller tubercle with an apical depression; the tubercle is less eccentric and sits in a well developed depression. Paratypes 2 and 4 have a large eccentric tubercle with a flat top, and well developed growth lamellae. Paratype 7 has a central tubercle without an apical depression. Paratypes 3, 6 and 8 have two peripheral tubercles of unequal shape and without apical depressions; a much lower tubercle is visible on the opposite side in paratype 3, but not in paratypes 6 and 8.
The specimen illustrated by Bosquet (1859, 1861) and copied by Sandberger (1861) has three tubercles whose positions differ from those of paratype 3: two small ones are peripheral, and the larger one is slightly eccentric; on the concave side there is a corresponding depression, just as in the specimens with one tubercle. In Sandberger's figure, the middle and one peripheral tubercle have an apical depression, but in Bosquet's figure all three have.

Additional observations – All surfaces bear small pits (Figs 5a-b), whose number varies greatly between specimens. As neither the arrangement nor the size and shape of these pits show any regularity, the pits are regarded as secondary features, caused by microorganisms. Most pits are on the convex, tubercle-bearing side.

Measurements – (Table 2). D1 and D2 are measurements of width at right angles to each other. D1 is measured at right angle to the less strongly curved edge.

Palaeoecology – The Alden Biesen Member consists of alternations of clay, argillaceous sands and clean sands. The moderately diverse mollusc fauna indicates a nearshore euryhaline environment: all groups known to be stenohaline are absent, and sporadically freshwater and terrestrial molluscs are swept into this environment.

Taxonomic history – Bosquet (1859) was the first to describe and figure opercula from the locality Vliek in Belgium. He interpreted them as opercula of the gastropod *Stenothyroides pupa* (Nyst, 1836) (Truncatelloidea: Stenothyridae) (Fig. 7). In the following year he thought it appropriate to create a new genus *Sandbergeria* because of the peculiar form of the supposed operculum. He communicated the name in a letter to Sandberger (Bosquet, 1861: 54) who in turn communicated it to Weinkauff, an amateur collector of Mainz Basin fossils (Weinkauff, 1860: 179, 187 footnote, 193). Weinkauff (1860) published the name *Sandbergeria* in a list of fossils from the Mainz Basin, attributing the name *Sandbergeria* to Bosquet and assigning *Stenothyroides pupa* to it as the only species.
Still in 1860, Bosquet changed his mind about the opercula and reinterpreted them as opercula of the gastropod *Sandbergeria cancellata* (Nyst, 1836) (Cerithioidea: Diastomatidae) (Fig. 9). This he also communicated to Sandberger, who became the first author to publish the name *Sandbergeria* in association with the gastropod that had originally been described *Pyramidella cancellata* Nyst, 1836 (Sandberger, 1860: legend to pl. 20 figs 8-8a). Bosquet, apparently unaware of Weinkauff's and Sandberger's earlier introductions of the name *Sandbergeria*, again proposed this name as new (1861); he included the characters of the operculum in the genus diagnosis and refigured one.
The name *Sandbergeria* has since been applied solely to a group of gastropods typified by *S. cancellata*. Honouring the earlier publication by Weinkauff or Bosquet's reason for creating the genus *Sandbergeria*, *viz.* the characters of the supposed gastropod opercula, would have completely unwanted consequences for nomenclatural stability and cause major confusion. An application was submitted by D. Kadolsky & R. Janssen in 2021 as Case 3855 to the

	D1	D2	Figures	Institution	Inventory number
Holotype	0.70	0.68	Fig. 1	BSPG	2021 I 7
Paratype 1	0.84	0.85	Figs 2, 5	BSPG	2021 I 8
Paratype 2	0.68	0.67	Figs 3, 6	BSPG	2021 I 9
Paratype 3	0.54	0.56	Fig. 4	BSPG	2021 I 10
Paratype 4	0.72	0.72		SMF	XVI 1031
Paratype 5	0.56	0.58		SMF	XVI 1032
Paratype 6	0.62	0.62		SMF	XVI 1033
Paratype 7	0.70	0.70		SMF	XVI 1034
Paratype 8	0.58	0.52		SMF	XVI 1035

Table 2. Measurements of the opercula of *Spirobranchus limburgicus* n. sp.

International Commission on Zoological Nomenclature to preserve *Sandbergeria* in its accustomed sense, *i.e.* with *Pyramidella cancellata* Nyst, 1836 as type species. This application was rejected by the ICZN editor(s) in an incomprehensive decision, contrary to the principal goal of the Commission to promote nomenclatural stability. To preserve nomenclatural stability, existing usage of the name *Sandbergeria*, *i.e.* with the gastropod *Pyramidella cancellata* Nyst, 1836 as type species, should be maintained until a more satisfactory nomenclatural solution can be found.
The opercula remain unnamed to date, as they had only been considered as opercula of named gastropod species.

Familial and generic taxonomy – The characters of the opercula fit well with the calcareous endplate of the operculum present in the genus *Spirobranchus* Blainville, 1818 (Ten Hove & Kuprianova, 2009; Ippolitov *et al*., 2014). In modern *Spirobranchus* species these plates show a strong intraspecific and interspecific variability. Endplates of many species have calcareous spines, which can even develop antler-like branches, but species without spinose endplates are also common. Many species are far larger than the species here described, but species with endplates in similar sizes do also exist, *e.g. S. minutus* (Rioja, 1941). Endplates similar to those of *S. limburgicus* n. sp., *i.e.* without spines and with one more or less central tubercle have been described for *S. polycerus augeneri* Ten Hove, 1970 (p. 38, figs 119-121), *S. eitzeni* Augener, 1918 (Zibrowius, 1973: 66-67, figs 6a-h), *S. lima* (Grube, 1862) (Zibrowius, 1968: 154-157, pl. 6 figs 29-32, pl. 7 fig. 1), *S. lirianeae* Brandão & Brasil, 2020 (p. 3-7, figs 2A-C, 2F-G, 3A, 3D, 4A-C), *S. minutus* (Rioja, 1941) (p. 734-738, pl. 9 figs 17-21 (as *Pomatoceros*); Zibrowius, 1968: pl. 7 figs 26-29; Brandão & Brasil, 2020: 9-11, figs 6C, D, E), *S. polytrema* (Philippi, 1844) (Rioja, 1917: 87-88, figs 25a-b (as *Pomatostegus*); Dew, 1959: 42-43, figs 15A-C (as *Pomatostegus*); Zibrowius, 1968: 157-160, pl. 7 figs 10-13; Bianchi & Morri, 2000: 262, figs 4A-C), *S. terraenovae* (Benham, 1927) (Dew, 1959: 39, fig. 13B (as *Pomatoceros*)).
The record of *Pomatoceros* sp. from middle Palaeocene strata of the Emperor Seamounts in the NW Pacific by Lommerzheim (1981) is cited by Ippolitov *et al.* (2014) as the oldest certain fossil record of a *Spirobranchus*-type operculum. These authors regard a much older specimen as a questionable *Spirobranchus*: an unnamed operculum reported by Lommerzheim (1979: 153, fig. 5) from Cenomanian formations of W Germany as being of the "*Pomatoceros*-*Spirobranchus*-Typ". The Oligocene *S. limburgicus* n. sp. thus complements the fossil record within the accepted age range of the genus.

Conclusions

The hypothesis that the objects are gastropod opercula, is rejected for three reasons:

1. Their shape does not agree with the shape of the aperture of the candidate species, *Stenothyroides pupa* and *Sandbergeria cancellata*. Figs 7 and 9 illustrate these two species with the outline of the largest specimen of *Spirobranchus limburgicus* overlain in the apertures. It is obvious that the shapes do not fit, and that the opercula are too small for *Sandbergeria cancellata*.
2. The present-day relatives of these two species do not have calcified opercula. Opercula made of organic material are hardly ever fossilised. Figs 8a-c illustrate a specimen of *Stenothyra deltae* (Benson, 1836), believed to be confamiliar with *Stenothyroides* (in Stenothyridae) with its operculum. Figs 10a-c show a specimen of *Diastoma melanioides* (Reeve, 1849) believed to be confamilar with *Sandbergeria cancellata* (Fig. 9) (in Diastomatidae, Superfamily Cerithioidea)[1] with its operculum. Both species have oval opercula with a pointed adapical end, fitting the shape of the aperture; the outside shows a spiral structure, with growth occurring at the edge of the whorl's end; in *Spirobranchus limburgicus* growth occurs concentrically outward all round (Figs 3d, 6). The operculum of *Stenothyra* Benson, 1856 has elaborate structures on the inside (Fig. 8c), whereas that of *Diastoma melanioides* is simple inside.
3. The candidate gastropod species and their congeners are known from other localities in none of which these opercula occur.

Bosquet (1859, 1861) and Sandberger (1861) may not have been familiar with the opercular shape of the nearest living relatives of *Stenothyroides* and *Sandbergeria*, but they could have become suspicious because of their outline not fitting the shape of the gastropod apertures. The case presented in this study is a classical example of 'thinking inside the box': Specialists have been too much focussed on their own taxonomic group(s) and forced an improbable interpretation on the objects instead of thinking of alternatives.

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[1] *Sandbergeria* is often placed into the family Scaliolidae (Superfamily Cerithioidea), but scaliolids lack the siphonal notch present in *Sandbergeria* and in *Diastoma* species. Further, *Diastoma melanioides* (Reeve, 1849), the only living species in the family Diastomatidae, has an indistinct columellar fold, as has *Sandbergeria cancellata* (W. Ponder in litt., March 2022; Houbrick, 1981).

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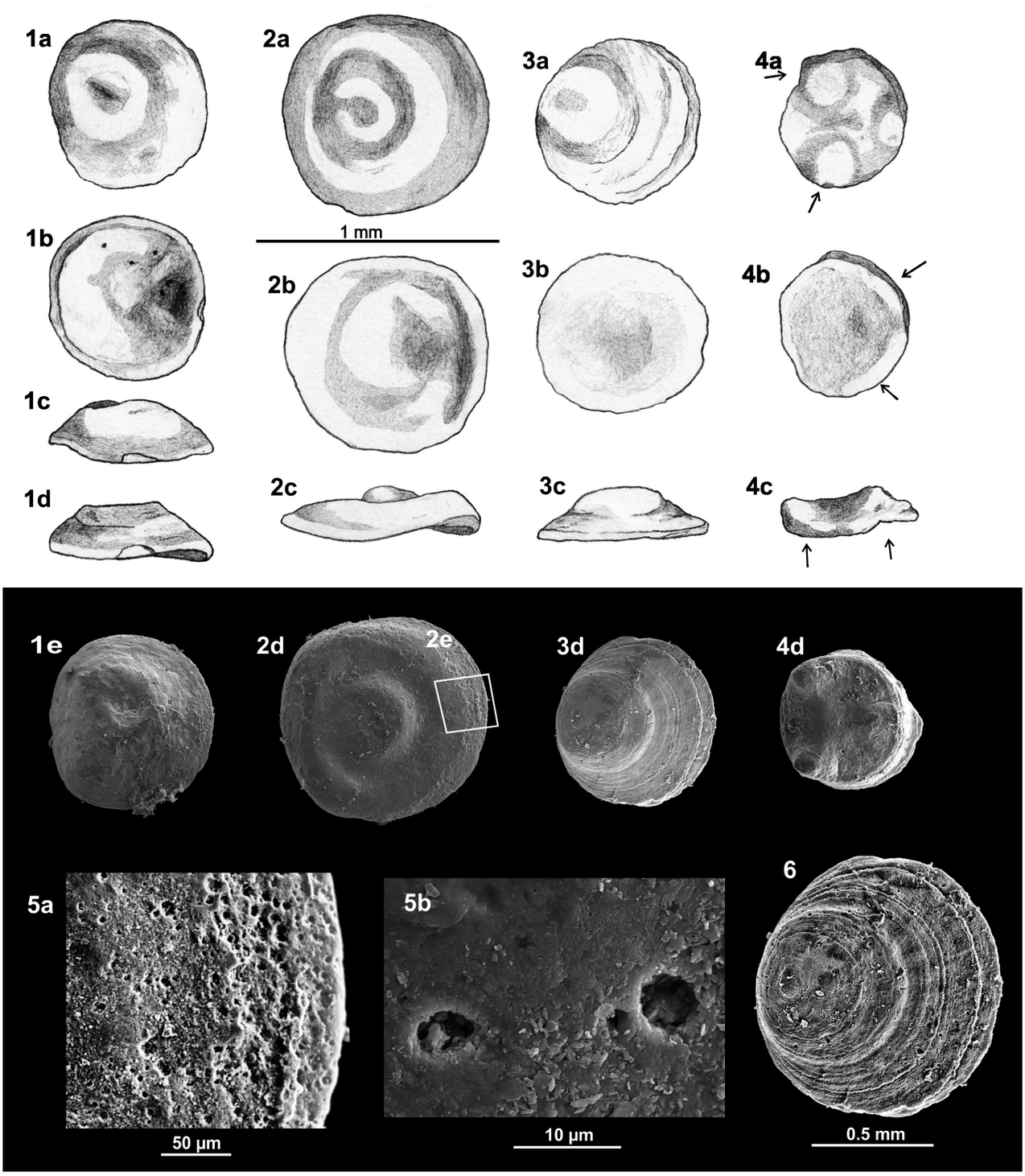
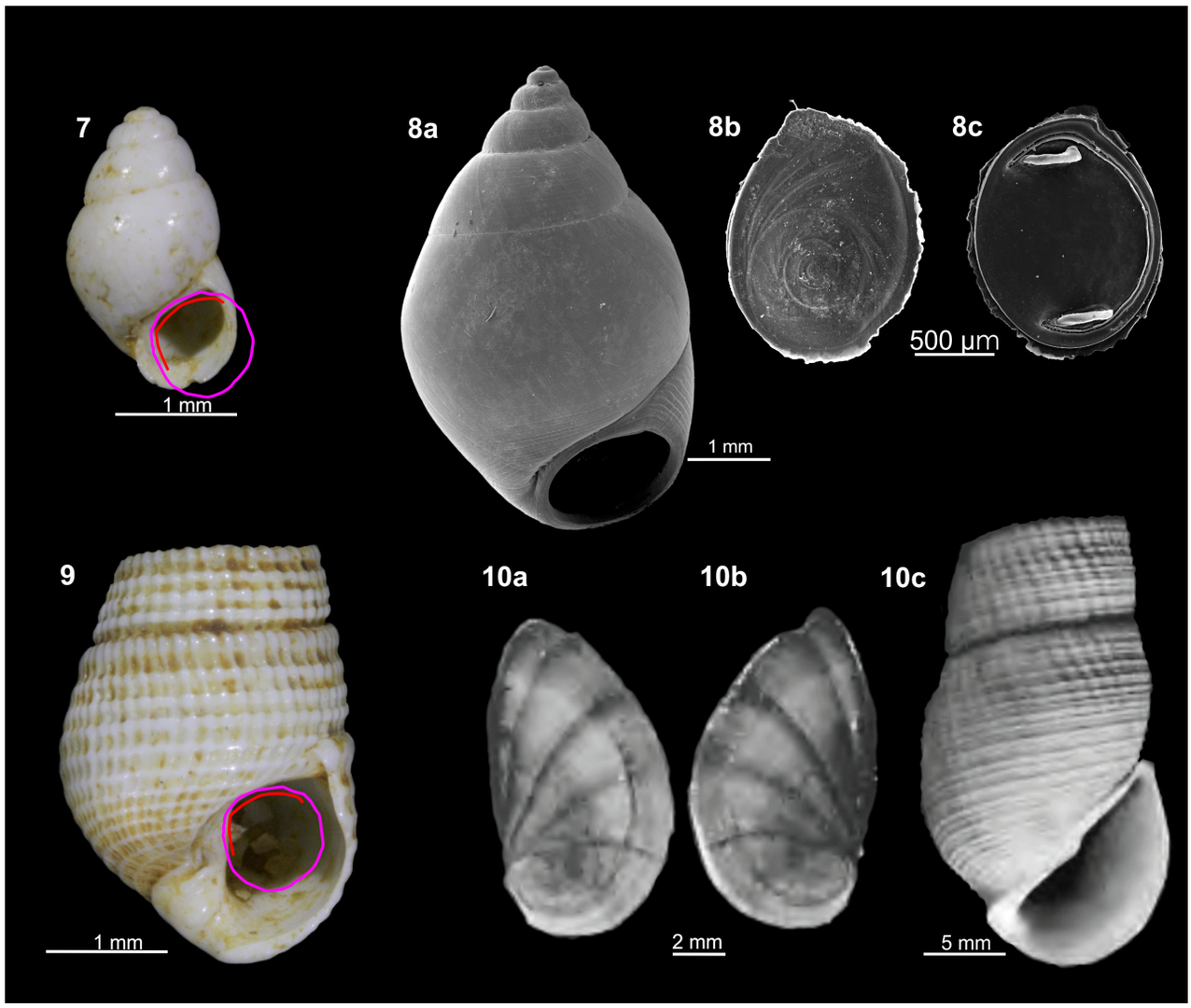


Figs 1-6. *Spirobranchus limburgicus* n. sp. All from Nachtegaalstraat, Kleine Spauwen, Limburg, Belgium. Alden Biesen Member, Borgloon Formation, Rupelian.

1a-e. Holotype, apical, proximal, 2 side views and SEM of apical view. SNSB-BSPG 2021 I 7.
2a-d. Paratype 1. The square in Fig. 2d is shown magnified in Fig. 5a. SNSB-BSPG 2021 I 8.
3a-d. Paratype 2. SNSB-BSPG 2021 I 9.
4a-d. Paratype 3. SNSB-BSPG 2021 I 10.
5a-b. Detail of perforations in Paratype 1.
6. Paratype 3 magnified to show radial undulations.

Drawings by D. Kadolsky. SEM micrographs by B. Reichenbacher. Figs 5a and 6 processed by "local equalisation" in Coreldraw X8.



Figs 7-10. Shells of the gastropods which had incorrectly been interpreted to be bearers of the serpulid opercula, and examples of present-day relatives with their opercula.

7. *Stenothyroides pupa* (Nyst, 1836). Castle park Alden Biesen, Limburg, Belgium. Alden Biesen Member, Borgloon Formation. Coll. Kadolsky. The outline of paratype 1 of *Spirobranchus limburgicus* is shown in the aperture. Height of shell 2.33 mm.
8. *Stenothyra deltae* (Benson, 1836). India, present-day. Trechmann coll., NHMUK. a) shell; b) outside of operculum, c) inside of operculum. Note these opercula are not calcified and hence are not preserved as fossils. Length of operculum 1.59 mm, height of shell 5.60 mm.
9. *Sandbergeria cancellata* (Nyst, 1836). Last two whorls of a fully grown specimen. Castle park, Alden Biesen, Limburg, Belgium. Alden Biesen Member, Borgloon Formation. Coll. Kadolsky. The outline of paratype 1 of *Spirobranchus limburgicus* is shown in the aperture. Width of shell 2.46 mm.
10. *Diastoma melanioides* (Reeve, 1849). Present-day, southern Australia. a) operculum outside, b) operculum inside, c) last two whorls of a fully grown shell. Length of operculum *ca* 12 mm; width of shell 15.3 mm. From Houbrick (1981: figs 1J, K, H).

Photographs Figs 7, 9 by D. Kadolsky, SEM micrographs Figs 8a-c by A. Kaim (Warsaw), Figs 10a-c from Houbrick (1981) with permission by The Biological Society of Washington (Email by S. Gardiner 30.3.2022).