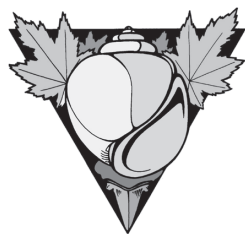


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New species of Neritidae (Gastropoda, Neritimorpha) from the Solent Group (late Eocene and early Oligocene) of the Hampshire Basin

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Three previously undescribed species in the family Neritidae are introduced from the Solent Group of the Isle of Wight, Hampshire Basin, southern England. New species: *Clithon (Pictoneritina) pococki* sp. nov., *Clithon (Pictoneritina) mortoni* sp. nov. and *Clithon (Pictoneritina) hillae* sp. nov. The palaeoenvironments of the Solent Group *Pictoneritina* are compared with the habitats of Recent members of the subgenus.

KEY WORDS: Neritimorpha, Neritidae, *Clithon*, *Pictoneritina*, new species, late Eocene, early Oligocene, Isle of Wight, palaeoecology

Introduction

The taxonomy of the Neritidae of the Solent Group was reviewed by Symonds (2006), a new genus erected and two new species described. Since then more material from the Solent Group has been discovered, mostly as a result of continuing fieldwork on the Isle of Wight, and the primary purpose of this paper is to describe three new species of *Clithon* which have been found there. The palaeoecology of *Clithon (Pictoneritina)* is compared with the ecology of extant species of the subgenus and of *Clithon (Clithon)*. All specimens referred to are held in the Department of Earth Sciences at the Natural History Museum, London (Institution code: NHMUK).

Systematic palaeontology

Superorder Neritimorpha Golikov and Starobogatov (1975, p. 200)

Order Cycloneritimorpha Bandel and Frýda (1999, p. 220)

Family Neritidae Rafinesque (1815, p. 144, as Neritina)

Genus *Clithon* de Montfort (1810, p. 327)

Type species – *Nerita corona* Linnaeus (1758, p. 777, nr. 629), by original designation. Recent, fresh to brackish water, Eastern Indian Ocean to the Southwestern Pacific.

Diagnosis (emended from Symonds and Pacaud, 2010, p. 59) – Neritid with small spire and large body whorl, some species with a subsutural row of spines; labial area smooth with one or more teeth on the margin; operculum smooth or bearing minute granules on the exterior

surface, inner side with two apophyses connected by a calcareous callus.

Discussion – De Montfort did not specify the gender of *Clithon* and it has been treated by most authors as a masculine noun. However, in accordance with Article 30.2.4 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999), it should be regarded as neuter (Steve Tracey, ICZN Secretariat, pers. comm.).

Subgenus *Pictoneritina* Iredale (1936, p. 288)

Type species – *Neritina oualaniensis* Lesson (1831, p. 379), by original designation. Recent, in estuaries and brackish lagoons, Indo-Pacific.

Diagnosis (emended from Symonds and Pacaud, 2010, p. 59) – *Clithon* with small smooth shell; septum weakly arched with one large and several small teeth.

Discussion – Although Holthuis (1995, pp. 196-197) synonymised *Pictoneritina* under the nomenclaturally senior genus *Clithon* on anatomical grounds, Symonds (2006, p. 31) following Wenz (1938, p. 423) retained *Pictoneritina* as a subgenus of *Clithon* in view of the substantial morphological differences between the shells of the two type species. *Clithon (Clithon) corona* is considerably larger than *C. (P.) oualaniense* with a thick periostracum and usually a row of prominent spines around the shoulder whereas *C. (P.) oualaniense* is smooth and glossy without spines or periostracum and with elaborate colour patterns. There are in excess of fifty generally recognised

species of extant *Clithon* (Eichhorst, in prep.) of which only about ten are *Pictoneritina*. All extant species of *Clithon* (*Pictoneritina*) are small, smooth, glossy, without spines, lacking a discernable periostracum or with only a very thin transparent one, with distinctive colour patterns and with one large and several small teeth on the septum edge. Extant species of *Clithon* (*Clithon*) are generally larger, usually with a more or less rough textured shell, often with spines, the colour pattern wholly or partially obscured by a periostracum and the teeth on the septum edge similar to *Clithon* (*Pictoneritina*) but more variable. There is no single characteristic which can be used to differentiate the two subgenera but when all these morphological features are taken into account *Clithon* (*Pictoneritina*) can be readily separated from *Clithon* (*Clithon*).

The new taxa herein described have been compared with the other species of Cenozoic *Pictoneritina* from north-west Europe.

***Clithon* (*Pictoneritina*) *pococki* nov. sp.**

Pl. 1, figs 1-6

2006 *Clithon* (*Pictoneritina*) *concaucus* (J. de C. Sowerby, 1823) – Symonds, p. 33, figs 9-12 [not *Clithon* (*Pictoneritina*) *concaucus* (J. de C. Sowerby, 1823)].

Type material – Holotype NHMUK PI TG 26755 (Pl. 1, figs 1a-c), height 6.6 mm, width 6.4 mm. Paratype 1 operculum (broken) NHMUK PI TG 26756 (Pl. 1, figs 2a-b), width 2.8 mm. Paratype 2 NHMUK PI TG 26757 (Pl. 1, figs 3a-c), height 7.0 mm, width 7.0 mm. Paratype 3 NHMUK PI TG 26758 (Pl. 1, figs 4a-c), height 6.0 mm, width 5.8 mm. Paratype 4 NHMUK PI TG 26759 (Pl. 1, figs 5a-c), height 4.8 mm, width 5.2 mm. Paratype 5 NHMUK PI TG 26760 (Pl. 1, figs 6a-c), height 5.2 mm, width 5.2 mm. All from the type locality, (all Malcolm Symonds leg.). Paratypes 1-4 from type stratum, paratype 5 from Totland Bay Member of the Headon Hill Formation, ‘*Cyrena pulchra* Bed’.

Type locality – Headon Hill, Isle of Wight, England, 50°40′16″N 1°34′09″W (estimated from Google Earth).

Type stratum – Late Eocene (Priabonian), Headon Hill Formation, Totland Bay Member, green clay between two limestone bands, the upper of which is immediately below the ‘*Cyrena pulchra* Bed’.

Etymology – Named after my colleague William Pocock, a molluscan palaeontologist who has accompanied me on many field trips to the Isle of Wight.

Diagnosis – A medium size *Pictoneritina* with an exerted spire, two and a quarter teleoconch whorls, which are somewhat shouldered, an almost edentate septum edge and a very variable colour pattern.

Description – A medium-sized shell consisting of about

two and a quarter whorls, semiglobular with an exerted spire. The protoconch is smooth, obovate and approximately 0.3 mm wide. The exterior of the teleoconch is glossy and covered by numerous fine, closely spaced col-labral ridges. The suture is impressed and the whorls are convex and rather shouldered.

The colour pattern is very variable consisting of dark brown lines on a pale background. Some specimens are almost entirely white with only a narrow band of markings above and below the suture (paratype 3); in others the brown lines coalesce leaving between them a series of pale dots of irregular size and shape (paratype 2) and in a few examples the dots are hardly noticeable and the whole teleoconch appears brown (paratype 5).

The aperture is oblique, semicircular and broad. The septum is flat and almost smooth; the edge concave. The dentition on the septum edge is indistinct, many specimens appearing edentate, where present it consists of one broad, shallow tooth, at about a third of the distance from the apical end, with up to six small, irregular and scarcely defined teeth abapical to it. The outer lip is thin and smooth within. The apertural tooth is in the form of a narrow oblique ridge below the abapical end of the septum which does not project beyond the septum edge.

The outer surface of the operculum is slightly concave and smooth apart from faint growth lines. On the inner surface a shallow groove runs in an arc from the nucleus to the middle of the columellar edge. The ventral apophysis consists of a prominent curved ridge projecting beyond the edge of the operculum with the well-developed dorsal apophysis at right angles to it and joined to it for approximately half its length by a thin calcareous callus. There is a pit at the base of the dorsal apophysis.

Distribution – Apart from the type horizon, *Clithon* (*Pictoneritina*) *pococki* also occurs slightly higher in the Totland Bay Member in the ‘*Cyrena pulchra* Bed’ at Headon Hill: paratype 5; and lower in the member in greenish marl underlying the ‘Brockenhurst Bed’ at Whitecliff Bay, Isle of Wight, 50°40′18″N 1°05′41″W (estimated from Google Earth) (Bed F of Stinton, 1971, p. 405): NHMUK PI TG 26761 (Malcolm Symonds leg.) and in the Colwell Bay Member of the Headon Hill Formation in the ‘Milford Marine Bed’ at Milford, Hampshire, England, 50°43′35″N 1°36′51″W (estimated from Google Earth): NHMUK PI TG 12267-9 (D. Curry leg.).

Other material studied – Approximately six hundred and sixty specimens were examined from the type horizon, a further six hundred from the ‘*Cyrena pulchra* Bed’, eighty-five from the marl below the ‘Brockenhurst Bed’ at Whitecliff Bay and twenty from the ‘Milford Marine Bed’ (all Malcolm Symonds private coll.)

Discussion – In the type stratum there is considerable lateral variation in distribution with *Clithon* (*Pictoneritina*) *pococki* common in some parts of the bed and absent in others (pers. obs.). Opercula were obtained by soaking a large number of shells of *C. (P.) pococki* in hot water to loosen the matrix, agitating them to clean out

the apertures and passing the resulting residue through a fine sieve; a method suggested by Alan Morton (pers. comm.). Of the four opercula recovered all were broken, paratype 1 being the most complete with the apophyses perfectly preserved.

This species is closest in appearance to *Clithon (Pictoneritina) planulatum* (Edwards in Lowry, 1866). It differs most obviously from it in its smaller protoconch and teleoconch, variable colour pattern and poorly defined dentition on the septum edge. The operculum is different with the dorsal peg much reduced in *C. (P.) planulatum* and connected to the ventral apophysis by a distinct arcuate ridge (Symonds, 2006, fig. 25). In *C. (P.) concavum* the colour pattern is far less variable, the protoconch is larger, the spire more prominent and the whorls less shouldered giving the teleoconch a more elongate appearance. The operculum is also different with the dorsal apophysis much reduced compared to that of *C. (P.) pococki* (Symonds, 2006, fig. 24). *Theodoxus (Vittoclithon) hoeseleensis* (Marquet, Lenaerts, Karnekamp & Smith, 2008) from the Borgloon Formation (early Oligocene, Rupelian) of Belgium also has a variable colour pattern but it is a smaller shell, maximum height 6 mm. (Marquet *et al.*, 2008, p. 32), and the dentition on its septum edge is distinct, unlike that of *C. (P.) pococki* which is almost edentate.

***Clithon (Pictoneritina) mortoni* nov. sp.**

Pl. 1, fig. 7

Type material – Holotype NHMUK PI TG 26762 (Pl. 1, fig. 7a-c), height 5.6 mm, width 5.4 mm. Paratype 1 NHMUK PI TG 26763, height 9.4 mm, width (broken) 8.8 mm. Paratype 2 NHMUK PI TG 26764, height 4.8 mm, width 4.8 mm, all from type locality and type stratum (all Alan Morton leg.).

Type locality – Burnt Wood near Porchfield, Isle of Wight, England, 50°43'55"N 1°23'08"W (estimated from Google Earth).

Type stratum – Late Eocene (Priabonian) [taking the top of the Bembridge Marls Member as the Eocene/Oligocene boundary, after Hooker *et al.*, 2009], Bouldnor Formation, Bembridge Marls Member, the 'Corbicula Bed' at the base of the Bembridge Marls Member which rests unconformably on the Bembridge Limestone Formation.

Etymology – Named after my colleague Alan Morton, a palaeontologist who first found this species whilst carrying out field work on the Isle of Wight.

Diagnosis – A medium size *Pictoneritina*, smooth and glossy; spire not exerted, protoconch covered by the first whorl of the teleoconch; colour pattern of collabral, dark brown lines on a white background.

Description – A medium-sized shell, most specimens being similar in size to the holotype and substantially small-

er than paratype 1. The protoconch is covered by the first whorl of the teleoconch. The spire is not exerted, and is mainly covered by the following whorl. The surface of the teleoconch is smooth and glossy. The last whorl is convex, but slightly flattened below the suture which is well defined. The colour pattern consists of narrow, dark brown, collabral lines on a white background.

The aperture is oblique, semicircular and broad. The septum is convex, smooth apart from microscopic pustules, the edge slightly concave with one tooth about a third of the distance from the apical end and up to five smaller teeth abapical to it; the teeth are poorly defined in some specimens. The apertural tooth consists of a long, narrow slightly curved ridge below the abapical end of the septum.

Distribution – Apart from the type locality, *C. (P.) mortoni* is known only from Howgate Bay near Bembridge, Isle of Wight, 50°40'37"N 1°05'07"W (estimated from Google Earth), where it occurs in the Bembridge Marls Member in green clay below the 'Insect Limestone': NHMUK PI TG 26765 (Alan Morton leg.). It has not been found above the 'Insect Limestone' at either locality.

Other material studied – Twelve additional specimens from the type horizon were examined (eleven from Alan Morton private coll., one from William Pocock private coll.) and furthermore one from Howgate Bay (Alan Morton private coll.).

Discussion – This species is distinctive among Solent Group *Clithon* species in that the spire is not exerted and the protoconch is obscured by the teleoconch. In *Clithon (Vittoclithon) headonense* Symonds, 2006 the protoconch is sometimes partly obscured in this way but it is readily distinguished from *C. (P.) mortoni* by the teeth on the septum edge which are four to seven in number, small but well defined with the adapical tooth not or only slightly larger than the others. The colour pattern is also very different consisting of a regular network of white dots on a dark background (Symonds, 2006, figs 20-22). Rare specimens of *C. (P.) pisiforme* (Férussac, 1823) from the early Eocene, Blackheath Formation of England and the early Eocene, Sparnacian, 'Sables de Pourcy' of France have a very similar colour pattern to *C. (P.) mortoni* (Rundle, 1971, pl. 44, figs 1-4). However the shape of the shell is different; the spire of *C. (P.) pisiforme* is exerted and the protoconch is not obscured by the teleoconch in contrast to *C. (P.) mortoni*.

***Clithon (Pictoneritina) hillae* nov. sp.**

Pl. 1, figs 8, 9

Type material – Holotype NHMUK PI TG 26766 (Rosemary Hill leg.) (Pl.1, fig. 8a-c), height 9.0 mm, width 9.4 mm. Paratype 1 operculum NHMUK PI TG 26767 (William Pocock leg.) (Pl.1, fig. 9a-b), width 3.4 mm, from the 'Polymesoda beds' above the 'Insect Limestone' at the type locality. Paratype 2 NHMUK PI TG 26768 (Alan

Morton leg.), height 5.0 mm, width 5.0 mm, from Burnt Wood, Isle of Wight, Bouldnor Formation, Bembridge Marls Member, 'Corbicula Bed' at the base of the Member.

Type locality – Howgate Bay near Bembridge, Isle of Wight, England, 50°40'40"N 1°05'03"W (estimated from Google Earth).

Type stratum – Late Eocene (Priabonian), Bouldnor Formation, lower Bembridge Marls Member, above the 'Insect Limestone'.

Etymology – Named after my colleague Rosemary Hill, a conchologist, who found the holotype.

Diagnosis – A medium size *Pictoneritina* with a depressed spire; dentition on the septum edge well defined; colour pattern of irregular pale spots on a brown background.

Description – A medium size shell, the holotype being the largest specimen known. The protoconch, though rather worn in all available specimens, appears to be smooth, obovate and approximately 0.4 mm wide. The exterior of the teleoconch is smooth apart from growth lines which form prominent, regular ridges on the holotype. The whorls are evenly rounded, except for a prominent indentation immediately below the suture, and the spire is depressed. The suture is sharp and well defined. The colour pattern consists of irregular pale spots of varying size on a brown background. The aperture is oblique, semicircular and rather broad. The septum is smooth and slightly convex; the edge concave in the centre. The labial dentition, which is distinct, consists of one large tooth, at about one-third of the distance from the adapical end, with up to nine small teeth abapical to it. The outer lip is thin and smooth within. The apertural tooth starts as a narrow ridge below the abapical end of the septum edge, curving back to end in a knob behind the septum edge. The operculum is semicircular; the outer surface is slightly concave with a low median ridge and a series of conspicuous chevron-shaped grooves along the labial third and a distinct depression around the nucleus. On the inner surface a low ridge runs from the nucleus in an arc to the middle of the columellar edge. The double apophysis consists of a sharp ventral arcuate ridge, which projects well beyond the operculum edge, with the second apophysis in the form of a shorter ridge at an acute angle to and joined, throughout its length, to the ventral apophysis by a calcareous callus. There is a deep pit at the base of the apophyses.

Distribution – *Clithon (Pictoneritina) hillae* also occurs (paratype 2) at the base of the Bembridge Marls Member in the 'Corbicula Bed' at Burnt Wood, Isle of Wight, the type locality of *C. (P.) mortoni*. Three specimens of *Clithon* from the 'Oyster Bed' near the base of the Bembridge Marls Member, Whitecliff Bay, Isle of Wight: NMHUK GG 22783-5 (F. Stinton leg.) may well be this species but their worn condition makes it impossible to be sure.

Other material studied – Two additional specimens were examined from the type horizon (William Pocock private coll.) and two from the 'Corbicula Bed' at Burnt Wood (Alan Morton private coll.).

Discussion – Three opercula were found by William Pocock in the 'Polymesoda beds' of the Bembridge Marls at the type locality, one of which is designated paratype 2 (the other two being in William Pocock private coll.). All three are conspecific and as *C. (P.) hillae* is the only species known from there it is reasonable to assume that they belong to that species.

The spire of *Clithon (Pictoneritina) hillae* is depressed in contrast to the exerted spires of *C. (P.) pococki*, *C. (P.) planulatum* and *C. (P.) cranmoreense* Symonds, 2006 and the whorls lack the slight shouldering of *C. (P.) pococki* and *C. (P.) planulatum*. The shell is closest in shape to *C. (P.) bristowi* Wenz (1929, p. 117) from which it differs in its larger size, more depressed spire, prominent and more numerous teeth on the septum edge and the distinctive apertural tooth which is absent in *C. (P.) bristowi*. The operculum differs from that of *C. (P.) bristowi* (see Symonds, 2006, fig. 26 and Curry, 1960, p. 267, fig. 2) which lacks the chevron-shaped grooves on the outer surface and has the dorsal apophysis approximately at right angles to the ventral one and only joined to it at the base.

Palaeoecology of *Pictoneritina*

Various authors have regarded the species of *Clithon* from the Solent Group as belonging to the genus *Theodoxus* de Montfort, 1810 (e.g. Curry, 1960; Paul 1988; Daley, 1999). However, *Theodoxus* is an essentially freshwater genus with a lecithotrophic larval stage (Fretter & Graham, 1962, pp. 398-399) enabling it to occupy freshwater habitats far removed from the sea. *Clithon*, on the other hand, has a planktotrophic larval stage, the veliger larvae usually being transported by river currents to the sea where they remain for a period, the length of which varies between species, during which the larval shell develops (Bandel, 2001, pp. 73-74). They then settle in river estuaries and some species make their way upstream eventually reaching freshwater. The difference in ontogeny is clearly reflected in the shape of the protoconch (Bandel, 2001, p. 132) with that of *Clithon*, when well preserved, showing the division between the embryonic and larval shells. The protoconchs of the fossil species from the Solent Group are consistent with a planktotrophic larval stage and accordingly they should be placed in *Clithon* rather than *Theodoxus*. With the sole exception of *C. (V.) headonense*, the *Clithon* species from the Solent Group all belong to *Pictoneritina*.

Clithon (Clithon) corona, in common with many other *Clithon* species, migrates upstream to reach freshwater (Bandel, 2001, pp. 97, 108). Adult *Clithon (Pictoneritina) oualaniense*, on the other hand, are to be found on stones and gravel in brackish lagoons and river mouths close to the sea, not in freshwater (Symonds, 2014). The same ap-

plies to other Recent *Clithon* (*Pictoneritina*) such as *C. (P.) pauluccianum* (Gassies, 1870) (placed in *Pictoneritina* by Komatsu, 1986) and *C. (P.) luctuosum* (Récluz, 1841) all of which favour brackish rather than freshwater conditions (Symonds, 2014). It is significant that fossil *Clithon* from the Solent Group also appear to have lived mainly in brackish rather than freshwater habitats. They commonly occur in the same deposits as *Corbicula*, *Potamides* and *Melanoides* which together, within the context of the Solent Group, are indicators of brackish conditions (Armenteros *et al.*, 1997, p. 112) whilst the purely freshwater beds contain few molluscs apart from lymnaeids, planorbids, *Viviparus*, *Unio* and terrestrial species (Bristow *et al.*, 1889, p. 147). Freshwater limestones such as the Howledge Limestone (Headon Hill Formation) and the Bembridge Limestone (Bembridge Limestone Formation) contain numerous freshwater molluscs but neritids are absent (pers. obs.). Within the Hatherwood Limestone (Hatherwood Limestone Member of the Headon Hill Formation) *C. (P.) planulatum* occurs in two relatively narrow horizons both of which coincide with brackish periods separated by a substantial freshwater interval (Paul, 1988, p. 151, fig. 3). This division between freshwater and brackish beds based on the molluscan fauna is supported by examination of the ostracod assemblages (Keen, 1977). *Clithon* (*Pictoneritina*) *bristowi* is common in, and apparently confined to, the 'Nematura Bed' in the Hamstead Member of the Bouldnor Formation, early Oligocene (Rupelian). *Polymesoda convexa* (Brongniart, 1810) are abundant in this bed with common *Stenothyra parvula* (Morris, 1856) (formerly *Nematura*) which is also a brackish water indicator (Chatwin, 1960, p. 69). *Clithon* (*Pictoneritina*) *concaum* is abundant in the 'Neritina Bed' near the base of the Colwell Bay Member of the Headon Hill Formation (Symonds, 2009, p. 33) with other brackish water indicators including *Corbicula* and *Ptychopotamides* (Daley, 1999, p. 48). The 'Cerithium beds' in the Cranmore Member of the Bouldnor Formation, early Oligocene (Rupelian), the type stratum of *C. (P.) cranmorensis*, contain brackish water genera, in particular large numbers of *Polymesoda* and *Granulolabium*. The type stratum of *C. (P.) mortoni* is packed with *Corbicula obovata* (J. Sowerby, 1817) and *C. (P.) hillae* is found in beds full of *Polymesoda convexa*. The only exception is *C. (P.) pococki*. Where it occurs in the 'Cyrena pulchra Bed' (Totland Bay Member), *Potomomya plana* (J. Sowerby, 1814), *Geloina pulchra* (J. de C. Sowerby, 1826) and other brackish water molluscs are common (Daley, 1999, p. 41). In the type stratum, however, it is accompanied mainly by freshwater pulmonate gastropods: lymnaeids and planorbids. It is possible that this is an example of different molluscan assemblages being mixed post mortem but the gastropods are quite common and in good condition showing no sign of wear from transportation (Steve Tracey, pers. comm.) and it may well be that *C. (P.) pococki* was tolerant of both brackish and freshwater conditions. All the other species of *Pictoneritina* evidently favoured brackish water habitats, a characteristic shared with the extant species.

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Plate 1

- 1-6. *Clithon (Pictoneritina) pococki* nov. sp. 1a-c: **holotype** NHMUK PI TG 26755 height 6.6 mm, width 6.4 mm; 2a-b: **paratype 1** NHMUK PI TG 26756 width (broken) 2.8 mm; 3a-c: **paratype 2** NHMUK PI TG 26757 height 7.0 mm, width 7.0 mm; 4a-c: **paratype 3** NHMUK PI TG 26758 height 6.0 mm, width 5.8 mm; 5a-c: **paratype 4** NHMUK PI TG 26759 height 4.8 mm, width 5.2 mm; 6a-c: **paratype 5** NHMUK PI TG 26760 height 5.2 mm, width 5.2 mm. All from Headon Hill, Isle of Wight, England (Malcolm Symonds leg.); paratypes 1-4 from type stratum, paratype 5 from Headon Hill Formation, Totland Bay Member, 'Cyrena pulchra Bed'.
7. *Clithon (Pictoneritina) mortoni* nov. sp., 7a-c: **holotype** NHMUK PI TG 26762 (Alan Morton leg.), height 5.6 mm, width 5.4 mm.
- 8-9. *Clithon (Pictoneritina) hillae* nov. sp. 8a-c: **holotype** NHMUK PI TG 26766 (Rosemary Hill leg.) height 9.0 mm, width 9.4 mm. 9a-b: **paratype 1** NHMUK PI TG 26767 (William Pocock leg.), width 3.4 mm. From type locality and type stratum.

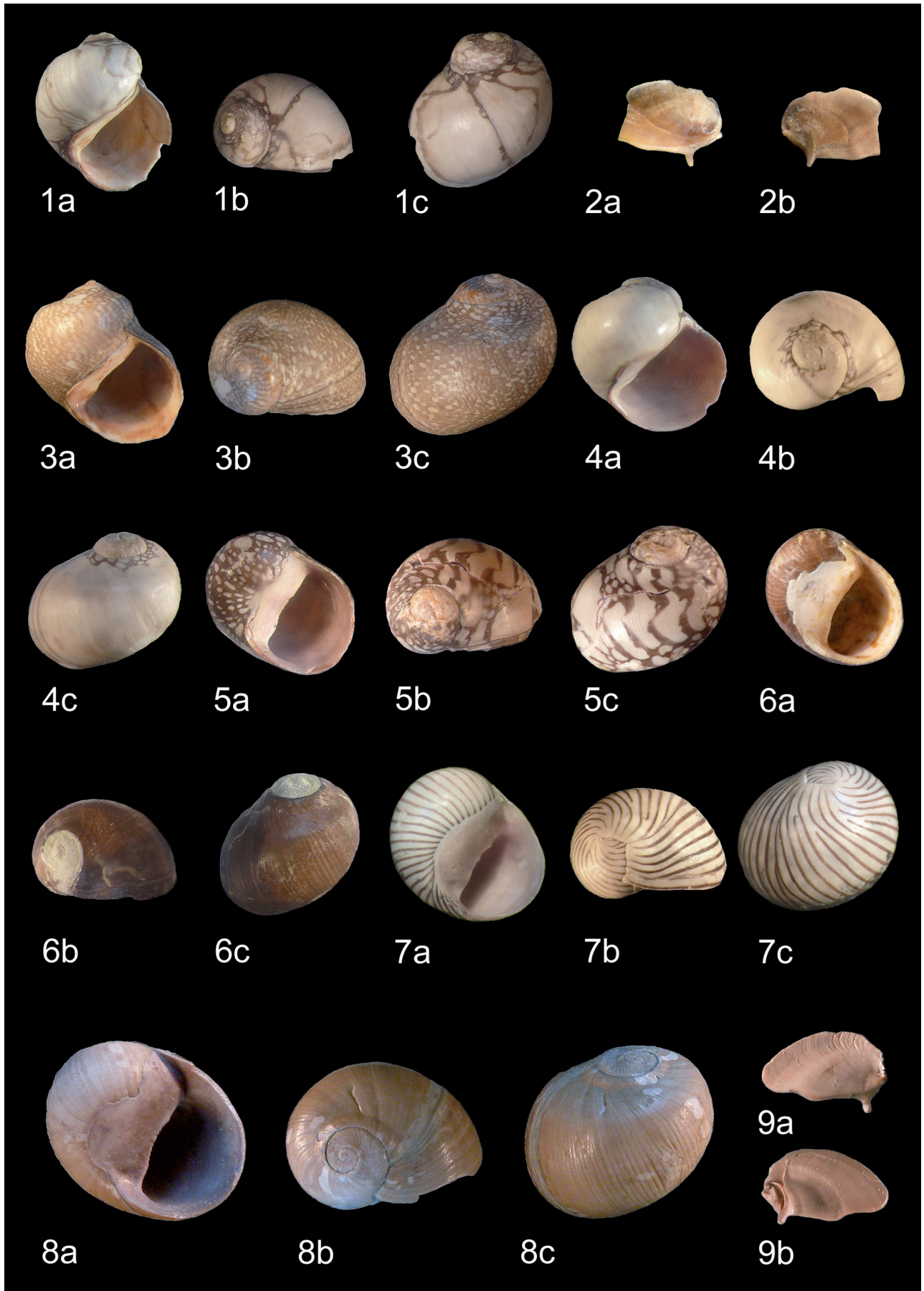


Plate 1