

The Neritidae of the Solent Group (Late Eocene and Early Oligocene) of the Hampshire Basin

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Gastropods of the family Neritidae in the Solent Group of the Hampshire Basin, southern England are reviewed and two previously undescribed taxa are described. New genus: *Pseudodostia*. New species: *Clithon* (*Pictoneritina*) *cranmorensis* and *Clithon* (*Vittoclithon*) *headonensis*. Neotypes designated for *Neritina planulata* Edwards, 1866 and *Neritina tristis* Forbes, 1856. Amended diagnosis: subgenus *Vittoclithon*. New combinations: *Pseudodostia aperta* (J. de C. Sowerby, 1823), *Clithon* (*Pictoneritina*) *concavus* (J. de C. Sowerby, 1823), *Clithon* (*Pictoneritina*) *planulatus* (Edwards, 1866) and *Clithon* (*Pictoneritina*) *bristowi* Wenz, 1929.

KEY WORDS: Mollusca, Gastropoda, Neritidae, Palaeogene, Hampshire Basin.

Introduction

Although the number of species of Neritidae in the Solent Group is rather limited, specimens are common at certain horizons and they have received the attention of numerous authors in the past. In particular Curry (1960, 265-270) dealt in detail with the taxonomy of *Theodoxus concavus* (J. de C. Sowerby, 1823), *Theodoxus planulatus* (Edwards, 1866) and *Theodoxus bristowi* Wenz, 1929. The purpose of this paper is to update Curry's work and to cover additional species.

The Solent Group spans the Late Eocene and the Early Oligocene (Priabonian and Rupelian), (Insole *et al.*, 1998: 19). It is composed mainly of non-marine deposits interrupted by a few, short-lived marine transgressions, the most extensive being that represented by the Colwell Bay Member of the Headon Hill Formation (Daley, 1999: 3). The Neritidae are common only in a few brackish or freshwater deposits, in particular: the "Neritina Bed" in the Colwell Bay Member with other brackish water species such as *Ptychopotamides* and *Corbicula* (Daley, 1999: 48), the "Theodoxus planulatus Bed" containing brackish water elements within the Hatherwood Limestone Member of the Headon Hill Formation, which is otherwise a freshwater limestone with *Lymnaea* and planorbids (Daley, 1999: 44) and the "Nematura Bed" in the Hamstead Member of the Bouldnor Formation with a brackish water fauna which includes *Stenothyra* (*Nematura*) *pupa* and *Bithinella* sp. (Daley, 1999: 52).

Systematic Palaeontology

Family Neritidae Rafinesque, 1815

Genus *Pseudodostia* gen. nov.

Type species — *Nerita aperta* J. de C. Sowerby, 1825. Eocene, Headon Hill Formation.

Derivatio nominis — The name reflects the close resemblance between the shell of the type species of this genus and that of *Nerita crepidularia* Lamarck, 1822, the type species of *Dostia* Gray, 1847.

Diagnosis — Spire depressed. Outer surface of teleoconch almost smooth or with spiral ridges. Septum edge with a prominent tooth at about one quarter of the distance from the apical end and smaller denticles abapical, and in some cases, adapical to it. Outer lip somewhat thickened, usually with fine lirae within. Operculum semicircular with a ridge on the inner surface running from the nucleus to a prominent medial tooth on the columellar side. A double apophysis, the ventral being a thickened, arcuate ridge, the dorsal an elongate peg.

Discussion — *Pseudodostia* resembles subgenus *Theliostyla* Mörch, 1852 of genus *Nerita* Linné, 1758 in the shape of the shell but differs from it and indeed from *Nerita sensu stricto* and all other generally recognised subgenera (Vermeij, 1984: 688-692), in the characteristics of the teeth on the septum edge and of the operculum. These characteris-

tics also distinguish *Pseudodostia* from *Neritina* Lamarck, 1816 *sensu lato* (including subgenus *Dostia*) and from *Theodoxus* Montfort, 1810. The lirae within the outer lip are not apparent in *Theodoxus* or *Clithon* Montfort, 1810. *Nerita tricarinata* Lamarck, 1804 from the Bracklesham Group of the Hampshire Basin and from the Eocene of France and *Nerita baylei* Vasseur, 1881, also from the Eocene of France, both have shells and opercula the morphology of which fits within the above diagnosis and they belong in this genus. *Nerita bartonensis* Symonds, 2002 from the Barton Group may also belong in *Pseudodostia*; its shell closely resembles that of *N. baylei* but differs from it in having less well defined teeth on the septum edge and in lacking the lirae within the outer lip. However, without the operculum of *N. bartonensis*, which has not yet been seen, its taxonomic position cannot be definitely established. The fossil species within this genus may be the ancestors of three recent Indo-Pacific species namely: *Neritina bensoni* Récluz, 1850, *Neritina guerini* Récluz, 1841 and *Neritina siquijorensis* Récluz, 1844 (Henk Mienis, pers. comm.). These species form a small, discrete group, characterised by the lirae within the outer lip, which merits recognition at the generic level (Dekker, 2000: 56). They have shells with morphological characters which fit *Pseudodostia* although the operculum, in each case, differs slightly from the fossil species; in particular the medial tooth is not so well developed.

***Pseudodostia aperta* J. de C. Sowerby, 1823**
Figures 1-5, 23

- Nerita aperta* J. de C. Sowerby, 1823: 5: 30, pl. 424, figs 2 & 3 but probably not fig. 4.
Nerita aperta Lowry *et al.*, 1866: pl. 3.
Neritina (*Mitrula*) *aperta* Sowerby; Sandberger, 1872: 269, pl. 15, figs 15, 15a & 15c.
Neritina aperta J. Sowerby; Wood, 1877: 347, pl. 34, fig. 20, a, b.
Neritina Forbesii Wood, 1877: 348, pl. 34, fig. 16, a-c.

- Neritina zonula* Wood, 1877: 348, pl. 34, fig. 19.
Theodoxus apertus (J. de C. Sowerby); Wrigley in Jackson, 1925: 365.
Theodoxus apertus British Museum (Natural History), 1959: 62, pl. 17, figs 2 & 3.

Type material — Holotype: Location unknown. A search of the collection in the Department of Palaeontology, The Natural History Museum, London (hereinafter called: "BMNH") has failed to locate the specimens used for Sowerby's illustrations.

Stratum typicum — Headon Hill Formation, Colwell Bay Member.

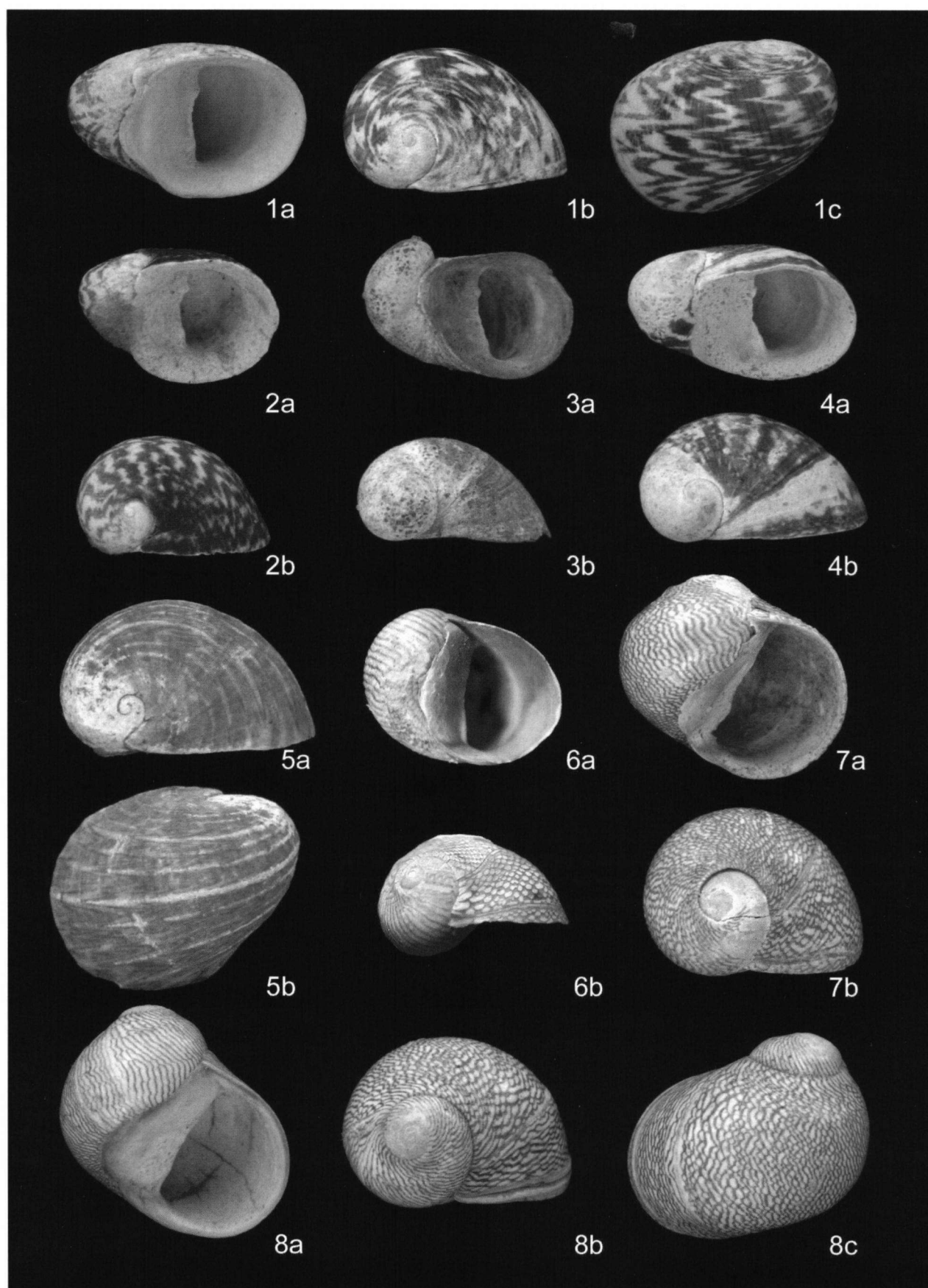
Locus typicus — Not precisely specified; Sowerby's figure 3 is from Colwell Bay, Isle of Wight, "while fig. 2 is from a Barton example". Since this species is not known to occur in the Barton Group, it is likely that the specimen illustrated in figure 2 is from an exposure of the Headon Hill Formation in the cliffs to the east of Barton at Hordle or Milford.

Diagnosis — A rather small *Pseudodostia* with a depressed spire and a smooth or spirally ridged teleoconch. One large labial tooth with small denticles abapical to it. The colour pattern usually consists of dark brown zigzag lines on a light background.

Original description — Sub-hemispherical, smooth; spire visible, depressed; aperture orbicular, expanded; inner lip obscurely crenated, bearing one large tooth. In most specimens the surface is marked with acutely zigzag brown lines of width equal with the white between them.

Description — Shell rather small for the genus, consisting of about two and a half whorls, semiglobular, elongate ovate to broadly ovate in adapertural view and almost symmetrical.

- Figure 1.** *Pseudodostia aperta* (J. de C. Sowerby, 1823), a. apertural, b. apical, c. abapertural views. Height 6.7 mm, width 7.5 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH GG22775 (D. Curry coll.).
Figure 2. *Pseudodostia aperta* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 5.7 mm, width 6.3 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH 73202 (F. E. Edwards coll.).
Figure 3. *Pseudodostia aperta* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 5.8 mm, width 6.1 mm. Aberrant specimen with exerted spire. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH TG 11165 (D. Curry coll.).
Figure 4. *Pseudodostia aperta* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 6.7 mm, width 7.1 mm. Elongate form corresponding to *Neritina forbesii* Wood, 1877. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH TG 11166 (D. Curry coll.).
Figure 5. *Pseudodostia aperta* (J. de C. Sowerby, 1823), a. apical, b. abapertural views. Height 6.9 mm, width 7.8 mm. Ribbed form corresponding to *Neritina zonula* Wood, 1877. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH 72304 (F. E. Edwards coll.).
Figure 6. *Clithon* (*Pictoneritina*) *concavus* (J. de C. Sowerby, 1823), Lectotype, a. apertural, b. apical, views. Height 7.1 mm, width 6.8 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH G78285 (Sowerby coll.).
Figure 7. *Clithon* (*Pictoneritina*) *concavus* (J. de C. Sowerby, 1823), a. apertural, b. apical, views. Height 8.2 mm, width 7.9 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH GG22777 (D. Curry coll.).
Figure 8. *Clithon* (*Pictoneritina*) *concavus* (J. de C. Sowerby, 1823), a. apertural, b. apical views, c. abapertural. Height 8.6 mm, width 7.9 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH GG22778 (D. Curry coll.).



The protoconch is approximately 0.5 mm wide, smooth and obovate, consistent with a planktotrophic larval stage

(Bandel, 2001: 74). The spire is depressed. The external surface is generally smooth, except for numerous, trans-

verse growth lines but some specimens have spiral ridges, normally from two to six in number and usually rather indistinct but occasionally quite prominent. The colour pattern usually consists of prominent, dark brown, zigzag lines on a pale background (Figure 1). Some specimens from the “Milford Marine Bed” in the cliffs at Milford on Sea, Hampshire are wholly or partially black (Figure 4). The aperture is large and semicircular, the septum is broad, smooth or with small pustules and ridges; the edge is straight or slightly concave in the centre. The dentition consists of a large, prominent tooth at approximately one quarter of the distance from the apical end and a series of small, irregular denticles, up to 6 in number, abapical to it. The apertural tooth, below the abapical end of the septum, consists only of a slight ridge. The outer lip is slightly thickened within, usually smooth but occasionally with about 12 fine lirae.

The operculum (Figure 23) is semicircular, the outer side is smooth with two shallow grooves running from the nucleus in an arc to the columellar side. The inner surface is marked with growth lines; a prominent ridge runs from the nucleus in an arc culminating in a prominent medial tooth on the columellar edge. There is a distinctive, double apophysis, the ventral being the culmination of a thickened, arcuate, ridge; the dorsal consisting of an elongate, rounded peg.

Dimensions — The specimen illustrated in figure 1 is of average size and measures approximately 6.7 mm in height and 7.5 mm in width.

Discussion — Sandberger placed *Pseudodostia aperta* in the genus *Neritina* Lamarck, 1816 subgenus *Mitrula* Récluz, 1850 = *Dostia* Gray, 1847 (Keen in Joint Committee on Invertebrate Paleontology, 1960: 1284). According to Sherborne (1926, 2014), 1840 is the date of publication for *Dostia* but in this earlier work *Dostia* is a nomen nudum being simply listed by Gray without a description or type species (1840: 147) and accordingly 1847, when Gray first designated the type species (1847: 148), is the correct date. Whilst in general the morphology of the shell resembles that of *Dostia*, the teeth on the septum edge are different. As described above, *P. aperta* has one large tooth and several smaller teeth whereas the type species of *Dostia* has a series of small, regular denticles occupying the concave central section of the septum edge. The operculum of *Dostia* differs from that of *P. aperta* in several respects, in particular it lacks the arcuate grooves on the outer surface. *Pseudodostia aperta* resembles *P. tricarinata* (Lamarck, 1804) from the Bracklesham Group and although the latter has strong, spiral ribbing this characteristic is present, to a lesser extent, in occasional specimens of *P. aperta* (Figure 5). The overall shell shape of *P. tricarinata* is similar to that of *P. aperta* as is the labial dentition but in *P. aperta* the lirae, which are present on the inside of the outer lip of *P. tricarinata*, are either missing or less conspicuous. The operculum of *P. tricarinata* (Figure 27) is very similar to that of *P. aperta* indicating a close relationship between the two taxa.

Neritina forbesii was separated by Wood from *P. aperta* because of its narrower form; “that is to say, it has a more extended outer lip, the aperture being wider or more expanded from the inner lip to the outer than in the preceding species. The apex is also much depressed, and the upper part of the shell is nearly flat, with spire indicated by a narrow depressed suture. The colour markings are various.” (Wood in Edwards, 1877: 348). However, the relative width of the aperture is quite variable, particularly in specimens from the “Milford Marine Bed” and there is a range of forms between the broad apertures of typical specimens of *P. aperta* (Figure 1) and the elongate apertures of *N. forbesii* (Figure 4). All other features of *N. forbesii* match those of *P. aperta* including the operculum, Wood’s illustration of which clearly shows the strong internal ridge and medial tooth which are characteristic of *P. aperta* (Wood in Edwards, 1877: Pl. 34, Fig. 16c, wrongly captioned 15c). I consider *N. forbesii* to be well within the range of variation of *P. aperta* and to be at most a form of it.

Wood also described a ribbed form as *Neritina zonula* which, according to him, “resembles *N. aperta* in outward form, its most material difference consisting in having six or seven very distinct ridges or carinulae not quite equidistant, and somewhat rounded,” (Wood in Edwards, 1877: 348). Whilst clearly ribbed specimens (Figure 5) are uncommon, faint spiral ribbing is by no means unusual in *P. aperta* and the strongly ribbed specimens appear to be no more than an extreme development of this characteristic within the species. In all other respects the shell morphology is the same as that of *P. aperta* and I do not consider *Neritina zonula* to be a separate species. I have not, however, seen an operculum from a strongly ribbed specimen.

Range and distribution — Within the Solent Group this species appears to be confined to the Colwell Bay Member of the Headon Hill Formation. At Colwell Bay in the Isle of Wight it is conspicuous in “grey sandy mud” above the “Venus Bed” (Daley, 1999: 48) and it is common in the “Milford Marine Bed” at Milford on Sea, Hampshire. Also there are two specimens, in the Gosport Museum collection (HMCMS: G2000.30.10), from the “Venus Bed” at Roydon, Hampshire.

According to Sowerby (1823: 30), his figures 3 and 4 are of specimens from Colwell Bay but figure 2 “is from a Barton example that we have just received from our kind friend Miss Salisbury”. I think it likely that this came from an exposure of the Headon Hill Formation in Hordle Cliff, near Barton, rather than from the Barton Group at Barton itself. There is a single specimen of this species in a tube of *Clithon passyanus* (Deshayes, 1864) (BMNH 72306, F. E. Edwards coll.) labelled “Lower Barton, Highcliff” (Symonds, 2002: 8). Although it is slightly worn, the preservation of this specimen is similar to those from the Colwell Bay Member of the Headon Hill Formation in the Isle of Wight where this species is common. I think it probable that this single specimen came from the Colwell Bay Member and was inadvertently mixed with material from the Barton Group. However, there are two specimens of *P.*

aperta labelled: "Lower Barton 3. Highcliff" (BMNH PITG23582-3, A.G. Davis coll.) which are, presumably, from the Barton Group. They are distinct from typical specimens in the Colwell Bay Member in that the small denticles abapical to the main tooth are better developed than usual and there are well defined lirae within the outer lip, which, as mentioned above, only occurs occasionally in this species. These two specimens bear some resemblance to small specimens of *Pseudodostia baylei* but lack the denticle adapical to the main tooth which is a feature of that species and also the colour pattern differs from that of *P. baylei*. They differ from *Nerita bartonensis* in the presence of lirae, the outer lip of *N. bartonensis* being smooth within, in the dentition on the septum edge, and in the colour pattern.

There are also two specimens of this species in the BMNH collection labelled "*Theodoxus subornatus*, Blackheath Beds, Charlton, history unknown". I assume these specimens have been wrongly labelled as there is no other evidence of *P. aperta* occurring in the Palaeocene.

Genus *Clithon* Montfort, 1810

Type species — by original designation: *Nerita corona* Linné, 1758. Recent, fresh to brackish water, Eastern Indian Ocean to the Southwestern Pacific.

Diagnosis — 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.

Remarks — Although proposed as a genus by Montfort (1810: 327), Baker (1923: 154-156), working mainly on the characteristics of the radula, considered *Clithon* to be a subgenus of *Theodoxus* Montfort, 1810. This classification was followed by Keen in Joint Committee on Invertebrate Palaeontology (1960: 1285) and, more recently, by Vaught (1989: 13). However, Wenz (1938: 422-423) recognised *Clithon* as a distinct genus and this was confirmed by Holthuis (1995: 184) on the basis of anatomical data. In his classification based on ontogeny, Bandel (2001: 65-164) split his new family Neritinae into two subfamilies: Theodoxinae and Neritinae. The former includes the genus *Theodoxus*, which Bandel restricts to those freshwater species which do not have a planktotrophic larval stage but instead develop within the egg capsule, feeding on nurse eggs (2001: 70-71). The subfamily Neritinae is based on the genus *Neritina*, which Bandel interprets to include the genus *Clithon*. Species within this subfamily all have a veliger larval stage. According to Bandel (2001: 67-68) it is possible to establish whether a fossil species had a planktotrophic larval stage and accordingly to determine to which subfamily it belongs by a detailed examination of the protoconch, where this is sufficiently well preserved. The species described below all have obovate protoconchs which fit Bandel's description of species with veliger lar-

vae and accordingly could not belong in the genus *Theodoxus*, as interpreted by him.

Subgenus *Pictonerita* Iredale, 1936

Type species — by original designation, *Neritina oualaniensis* Lesson, 1831. Recent, in estuaries and brackish lagoons, Indo-Pacific.

Diagnosis — The shell is small and smooth. The septum is weakly arched with one large and several small teeth.

Remarks — The only description given by Iredale is that "the columellar dentition is very irregular and obscure and the painting consists of streaks" (Iredale, 1936: 288). Iredale mentioned Baker's inclusion of *Neritina oualaniensis* in his section *Vittocliton* but observed that Baker himself had remarked upon the notable differences between the radula of *N. oualaniensis* and that of other species in this section (Baker 1923: 156). In the absence of a more detailed description by Iredale the above diagnosis has been taken from that given by Keen in Joint Committee on Invertebrate Palaeontology (1960: 1285). In the type species the large tooth is about a third of the distance from the apical end of the septum with up to 5 small teeth abapical to it. The shell is glossy and the colour patterns are very variable.

Wenz (1938: 423) regarded *Pictoneritina* and *Vittocliton* as subgenera of *Clithon*. Holthuis (1995: 196-197) synonymised *Pictoneritina* under the superior *Clithon* because she found the two to be anatomically almost identical. However the shells of the two type species are morphologically quite distinct; *Clithon corona* is substantially larger than *Pictoneritina oualaniensis*, with a rough, thick periostracum and usually a row of prominent spines around the shoulder. *P. oualaniensis* is smaller, smooth and glossy with elaborate colour patterns: it never has spines. In view of these substantial differences, I prefer to retain *Pictoneritina* as a subgenus of *Clithon*.

Clithon (Pictoneritina) concavus (J. de C. Sowerby, 1823) Figures 6-12, 24

Neritina concava J. de C. Sowerby, 1823: (in part) 4: 118, pl. 385, figs 3, 4, 6, 7 & 8 only.

Nerita concava Nyst, 1843: 436, pl. 47, fig. 30.

Neritina concava Lowry et al., 1866: pl. 3.

Theodoxus concavus (J. de C. Sowerby); Curry, 1960: 265 - 266, fig. 3.

Type material — (Designated by Curry, 1960: 265) Lectotype: BMNH G78285 (Sowerby coll.), (Figure 6), Paralectotypes: BMNH G78284, G78286, G78287 & G78288 (Sowerby coll.).

Stratum typicum — Not specified. The lectotype, according to Curry (1960: 265), is almost certainly from the "Neritina Bed" in the Colwell Bay Member.

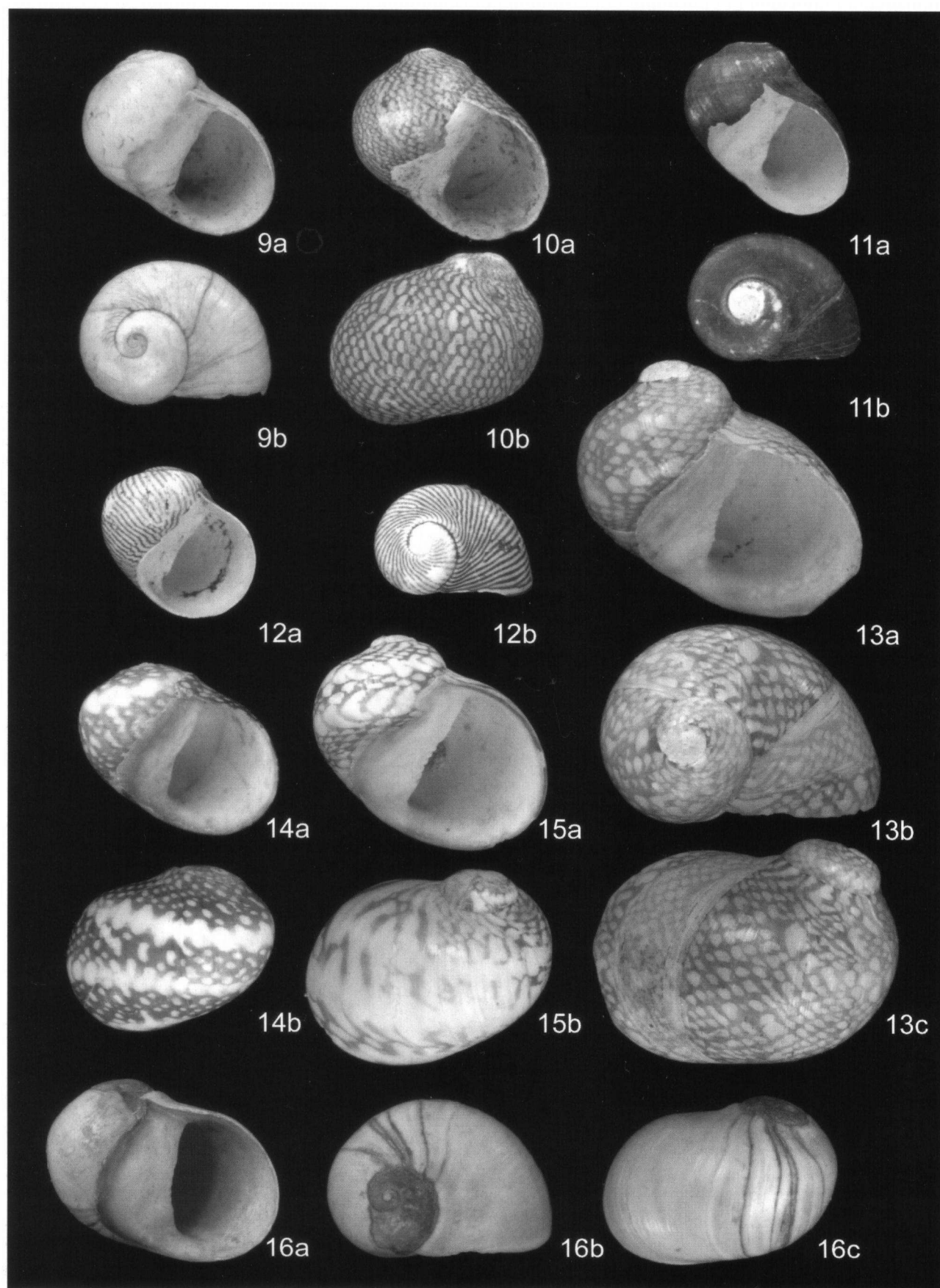


Figure 9. *Clithon (Pictoneritina) concavus* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 6.4 mm, width 6.3 mm. White morph. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH 72320 (F. E. Edwards coll.).

Figure 10. *Clithon (Pictoneritina) concavus* (J. de C. Sowerby, 1823), a. apertural, b. abapertural views. Height 6.3 mm, width 6.2 mm. Spotted colour morph. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH TG 12267 (D. Curry coll.).

Figure 11. *Clithon (Pictoneritina) concavus* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 5.5 mm, width 5.1 mm. Black morph. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH TG 12268 (D. Curry coll.).

Figure 12. *Clithon (Pictoneritina) concavus* (J. de C. Sowerby, 1823), a. apertural, b. apical views. Height 4.5 mm, width 4.4 mm. Striped colour morph. Colwell Bay Member, "Milford Marine Bed", Milford on Sea, Hampshire. BMNH TG 12269 (D. Curry coll.).

Figure 13. *Clithon (Pictoneritina) planulatus* (Edwards, 1866), neotype, a. apertural, b. apical, c. abapertural views. Height 10.2 mm, width 9.5 mm. Hatherwood Limestone Member, Headon Hill, Isle of Wight. BMNH G88658 (D. Curry coll.).

Figure 14. *Clithon (Pictoneritina) planulatus* (Edwards, 1866), a. apertural, b. abapertural views. Height 6.9 mm, width 6.7 mm. Spirally banded colour morph. Hatherwood Limestone Member, Headon Hill, Isle of Wight. BMNH PITG 8128 (D. Curry coll.).

Figure 15. *Clithon (Pictoneritina) planulatus* (Edwards, 1866), a. apertural, b. abapertural views. Pale colour morph. Height 8.3 mm, width 8.1 mm. Hatherwood Limestone Member, Headon Hill, Isle of Wight. BMNH PITG 8129 (D. Curry coll.).

Figure 16. *Clithon (Pictoneritina) bristowi* (Wenz, 1929), neotype, a. apertural, b. apical, c. abapertural views. Height 7.5 mm, width 7.8 mm. Hamstead Member, "Nematura Bed", Bouldnor Cliff, Isle of Wight. BMNH GG22774 (D. Curry coll.).

Locus typicus — Not specified, probably Colwell Bay or Headon Hill, Isle of Wight.

Diagnosis — A medium-sized *Pictoneritina* with a prominent spire; whorls concave below the suture. The feeble dentition on the septum edge consists of one broad tooth with smaller dentitions abapical to it. Colour pattern is variable but usually incorporates a network of fine, wavy brown lines, which may anastomose, on a whitish background.

Original description — Obovate, with a prominent obtuse spire; upper part of each whorl concave, aperture semicircular; lip entire.

Description — Shell medium-sized for the subgenus, consisting of about two and a half whorls, semiglobular with a prominent spire. The protoconch is smooth and obovate, approximately 0.4 mm wide. The teleoconch is glossy and smooth apart from numerous fine, closely spaced, transverse lines which cover the surface. The whorls are evenly convex becoming noticeably concave below the suture. The suture is sharp and well defined.

The colour pattern generally consists of fine, wavy, transverse, dark brown lines, on a white background, which usually interlace to form a network with uneven dots and lines between them. Some specimens, including the lectotype, show a transition from stripes to a netted pattern. The pale spiral bands, which are common in *Clithon planulatus* (Edwards, 1866), do not occur in *Clithon concavus*. White specimens are common (Figure 9), although most show some traces of colour pattern immediately below the suture, and black shells occur occasionally (Figure 11) particularly in the "Milford Marine Bed" where there are also individual specimens striped with broad, transverse lines (Figure 12).

The aperture is oblique, semicircular and rather elongate. The septum is convex and smooth. The septum edge is slightly concave; there is one broad tooth on the septum edge, which is never prominent and is usually indistinct, and up to 7 denticulations abapical to it which are also usually indistinct and may be completely absent. The outer lip is evenly rounded, thin and smooth within. The apertural

tooth consists of a low, slightly curved ridge below the abapical end of the septum.

The operculum is semicircular; the outer side smooth, rather depressed around the nucleus, otherwise flat. On the inner surface a slight ridge runs from the nucleus in an arc to the middle of the columellar edge. The double apophysis consists of a ventral arcuate ridge and, at right angles to it, a short, pointed dorsal peg (Figure 24).

Dimensions — Lectotype: height 6.6 mm, width 6.5 mm. Larger specimens measure up to 8.5 mm in height.

Remarks — As pointed out by Curry (1960: 265), of the 8 specimens illustrated by Sowerby the original of figure 1 is *Clithon planulatus* (Edwards, 1866) from the Hatherwood Limestone Member, Headon Hill. Figure 2, stated by Sowerby to be from Muddiford, is *Clithon passyanus* (Deshayes, 1864) from the Barton Group, in Curry's view probably from Bed A3 of Burton (1933). Curry was unable to trace the original of figure 5 in the BMNH collection. However, according to Sowerby, it was "a mutilated specimen found at Highgate" and presumably is of a different species as *C. concavus* is not known to occur there. Specimens from the Milford Marine Bed which are striped with broad, transverse lines (Figure 12), also differ slightly in shape in that the concave area below the suture is rather more pronounced than in typical *T. concavus*. It is possible that this is a separate species but I consider it more likely that it is, at most, a form adapted to a different level of salinity or some other environmental factor.

Range and distribution — In the Totland Bay Member: the "Cyrena Pulchra Bed" at Headon Hill (Daley, 1999: 45) and in "greenish beds comprising the uppermost 1m of the Member" at Whitecliff Bay in the Isle of Wight (Daley, 1999: 24). In the Colwell Bay Member where it is common in the "Venus Bed" and abundant in the "Neritina Bed" both at Colwell Bay and at Headon Hill; it is again common near the top of the Member at Headon Hill in the "Batillaria Bed", formerly the "Cerithium Ventricosum Bed", (Keeping & Tawney, 1881: 91 fig. 1). It is also common in the "Milford Marine Bed" at Milford on Sea. A few specimens of this species in the BMNH collection have

labels which indicate that they are from the Barton Group (Symonds 2002: 8). However, the state of preservation and the matrix are more like that in the Colwell Bay Member and I think it unlikely that this species occurs in the Barton Group.

***Clithon (Pictoneritina) planulatus* (Edwards, 1866)**

Figures 13-15, 25

Neritina concava J. de C. Sowerby, 1823: (in part) 4: 118, pl. 385, fig. 1 only.

Neritina planulata Edwards in Lowry, 1866: pl. 3.

Neritina planulata (Edwards MS); Sandberger, 1873: 268, pl. 15, figs 14-14c.

Neritina planulata (Edwards MS); Wood, 1877: 349, pl. 34, figs 21a, 21b.

Theodoxus planulatus (Edwards); Curry, 1960: 266 - 268, figs 1a, 1b.

Type material and locus typicus— The holotype is not known. The specimen illustrated in Lowry is not identifiable in the Edwards collection at the BMNH. Other than the figure itself no description is given in Lowry and the stratum typicum and locus typicus are not specified. However the illustration in Lowry of the holotype shows a specimen typical of the Hatherwood Limestone Member of the Headon Hill Formation at Headon Hill, Isle of Wight, where this species is common. I consider it important to designate a neotype to support the description of the species and to fix the type locality.

Neotype (herein designated): BMNH G88658 (D. Curry coll.), (Figures 13, 25) from the Hatherwood Limestone Member of the Headon Hill Formation, Headon Hill, Isle of Wight.

Diagnosis — A medium size *Pictoneritina* with a prominent spire and somewhat shouldered whorls. The dentition on the septum edge is well defined and consists of a single broad tooth with smaller denticulations abapical to it. The colour pattern consists of a net-like pattern with pale dots on a dark brown background, some specimens having, in addition, two pale, spiral bands.

Description — A medium sized shell consisting of about two and a half whorls, semiglobular with an exerted spire. The protoconch is smooth, obovate and approximately 0.4 mm wide. The exterior of the teleoconch is glossy and covered by numerous minute, closely spaced collabral ridges. The whorls are convex with a short concavity immediately below the suture and are slightly shouldered.

The colour pattern consists of white dots, of irregular size and shape, on a brown background. Many specimens, about 50% according to Curry (1960: 268), have two or more whitish spiral bands within which the dots are larger or coalesce to form a continuous white stripe (Figure 14). Occasional specimens are completely white, lacking any pattern.

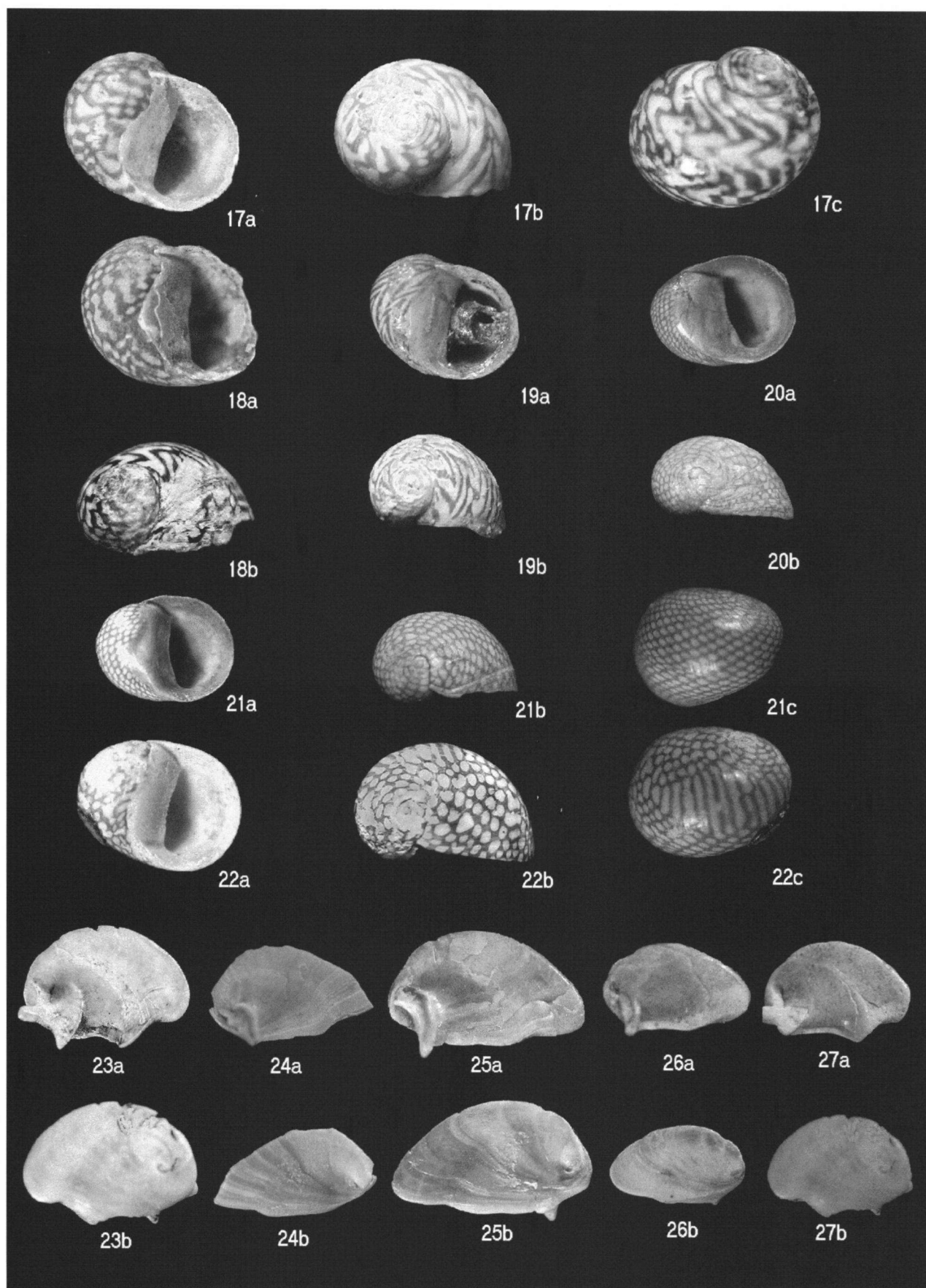
The aperture is oblique, semicircular and rather broad especially at its base. The septum is flat or only slightly convex; the edge concave. The dentition on the septum edge is distinct and consists of one broad tooth, at about a third of the distance from the apical end, with up to 7 small, irregular but well-defined teeth abapical to it. Some specimens also have 2 or 3 indistinct teeth on the adapical side of the principal tooth. The outer lip is thin and smooth within. The apertural tooth is in the form of a short, low, slightly curved and often indistinct ridge below the abapical end of the septum.

The operculum is semicircular; the outer side smooth, somewhat depressed around the nucleus, otherwise flat. 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 ventral arcuate ridge and, at right angles to it, a short, pointed dorsal peg (Figure 25).

Dimensions — The neotype is approximately 10.2 mm in height and 9.5 mm in width. The specimen illustrated in Sowerby's figure 1 (1823: pl. 385) is about 10.3 mm in height and 9.3 mm in width. Some specimens are larger, up to 12.5 mm in height and 12 mm in width (BMNH 72318, F. E. Edwards coll.).

Remarks — This species is rather similar to *Clithon concavus*. It differs most obviously from it in its larger size, colour pattern and well-defined dentition. Less obvious differences include the shape of the whorls and the broader aperture of *C. planulatus*. Curry (1960: 268) referred to the great variability in colour pattern within some living species of *Neritina* and its relatives and doubted whether these two species should be separated. However he concluded that: "in view of the fact that they characterize slightly different geological horizons and that a valid name is available for each it seems best to treat them as separate species at least until further evidence on their status becomes available". Paul (1989: 159) also compared the colour patterns and questioned whether *C. planulatus* "is really a distinct species or merely a very low salinity variant".

Certainly, colour pattern in some Neritidae can vary with the salinity. Gunderson and Minton (1997: 22-23) carried out experiments with *Puperita pupa* (Linné, 1758), which were living in pools of high salinity, and *Puperita tristis* (d'Orbigny, 1842) which were in low salinity pools. Specimens of *P. pupa* moved to low salinity pools developed the typical spotted pattern of *P. tristis* and similarly examples of *P. tristis* moved to a high salinity environment developed stripes typical of *P. pupa*. It seems likely that, although described as separate species, they are actually the same species with the variation in colour pattern being attributable to environmental differences. In the case of *C. concavus* and *C. planulatus*, however, quite apart from the differences in colour pattern, there are also the differences in shell morphology as described above. Although the two taxa appear to be closely related I consider that, as they are readily separable on the basis of shell morphology and as they represent different horizons, it is better to continue to treat them as separate species.



- Figure 17.** *Clithon (Pictoneritina) cranmorensis* sp. nov., holotype, a. apertural, b. apical, c. abapertural views. Height 6.6 mm, width 6.9 mm. Cranmore Member, Bouldnor Cliff, Isle of Wight. Conchological Society 366 (J. W. Taylor coll.) on permanent loan to BMNH.
- Figure 18.** *Clithon (Pictoneritina) cranmorensis* sp. nov., paratype, a. apertural, b. apical views. Height 6.6 mm, width 7 mm. Cranmore Member, Bouldnor Cliff, Isle of Wight. Conchological Society 367 (J. W. Taylor coll.) on permanent loan to BMNH.
- Figure 19.** *Clithon (Pictoneritina) cranmorensis* sp. nov., paratype, a. apertural, b. apical views. Height 3.7 mm, width 4.2 mm. Cranmore Member, Bouldnor Cliff, Isle of Wight. BMNH GG22776 (F. Stinton coll.).
- Figure 20.** *Clithon (Vittocliton) headonensis* sp. nov., paratype, a. apertural, b. apical views. Height 4.4 mm, width 4.7 mm. Colwell Bay Member, Headon Hill, Isle of Wight. BMNH GG22781 (M. F. Symonds coll.).
- Figure 21.** *Clithon (Vittocliton) headonensis* sp. nov., holotype, a. apertural, b. apical, c. abapertural views. Height 4.3 mm, width 4.9 mm. Colwell Bay Member, Headon Hill, Isle of Wight. BMNH GG22782 (M. F. Symonds coll.).
- Figure 22.** *Clithon (Vittocliton) headonensis* sp. nov., a. apertural, b. apical, c. abapertural views. Height 5.2 mm, width 6.3 mm. Bouldnor Formation, Hamstead, Isle of Wight. BMNH 72317 (F. E. Edwards coll.).
- Figure 23.** *Pseudodostia aperta* (J. de C. Sowerby, 1823), operculum a. inner face, b. outer face. Approximate width 4.1 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH GG6860 (F. E. Edwards coll.).
- Figure 24.** *Clithon (Pictoneritina) concavus* (J. de C. Sowerby, 1823), operculum, a. inner face, b. outer face. Approximate width 3.4 mm. Colwell Bay Member, Colwell Bay, Isle of Wight. BMNH GG22779 (M. F. Symonds coll.).
- Figure 25.** *Clithon (Pictoneritina) planulatus* (Edwards, 1866), neotype, operculum. a. inner face, b. outer face. Approximate width 5.3 mm. Hatherwood Limestone Member, Headon Hill, Isle of Wight. BMNH G688658 (D. Curry coll.).
- Figure 26.** *Clithon (Pictoneritina) bristowi* (Wenz, 1929), operculum. a. inner face, b. outer face. Approximate width 3.4 mm. Hamstead Member, "Nematura Bed", Bouldnor Cliff, Isle of Wight. BMNH G88659 (D. Curry coll.).
- Figure 27.** *Pseudodostia tricarinata* (Lamarck, 1804), operculum. a. inner face, b. outer face. Approximate width 2.9 mm. Cuisian, Sables de Cuise, Cuise-la-Motte, France. BMNH GG22780 (S. Tracey coll.).

Range and distribution — Within the Headon Hill Formation this species is apparently confined to the Hatherwood Limestone Member. Specimens from the Bembridge Marls Member of the Bouldnor Formation, Whitecliff Bay, Isle of Wight, although rather worn, appear to be this species (BMNH GG 22783-5 F. Stinton coll.). Two specimens of this species in a tube of *Clithon passyanus* (BMNH 72306 F. E. Edwards coll.), from the Barton Group, show the exceptionally good state of preservation typical of material from the Hatherwood Limestone (Symonds, 2002: 8) and I believe they were probably included in error with the material from the Barton Group.

***Clithon (Pictoneritina) bristowi* Wenz, 1929**
Figures 16, 26

Neritina tristis Forbes, 1856: 46 (non d'Orbigny, 1841).
Theodoxus bristowi Wenz, 1929: 11, 117.
Theodoxus bristowi Wenz; Curry, 1960: 269-270, fig. 2.

Type material and locus typicus— No holotype was specified or illustrated. The stratum was given as: "The Hempstead Series" of Forbes (1856: 45-46). This species is common in and apparently confined to the "Nematura Bed" in the Hamstead Member of the Bouldnor Formation at Bouldnor, Isle of Wight and it is considered important to designate a neotype to more precisely define the stratum typicum and to establish a type locality.
 Neotype (herein designated): BMNH GG22774 (D. Curry coll.), (Figure 16) from the "Nematura Bed", Hamstead Member, Bouldnor Formation, Bouldnor Cliff, Isle of Wight.

Diagnosis — A rather small *Pictoneritina* with an excerted spire. Dentition on the septum edge is poorly defined. Colour pattern almost always lacking.

Original description — A small, globose shell, with the volutions rather angulated; aperture semilunate, inner lip obscurely denticulated, surface smooth without ornamentation (Forbes, 1856: 46).

Description — A rather small, wide shell, the teleoconch comprising about two and a half whorls, semiglobular with an excerted spire which is seldom prominent. The protoconch is smooth, obovate and approximately 0.4 mm wide. The exterior of the teleoconch is smooth and glossy with numerous microscopic collabral lines. The whorls are evenly rounded and slightly concave immediately below the suture. The suture is sharp and well defined. The shell almost always lacks any trace of colour pattern but rarely there is a pattern of pale spots of varying size on a light brown background (BMNH 72313 F. E. Edwards coll.). The aperture is oblique, semicircular and rather broad. The septum is slightly convex; the edge is concave. The labial dentition, which is distinct in some specimens, indistinct in others, consists of one large tooth, at about one third of the distance from the adapical end, with up to 7 small teeth abapical to it. The outer lip is thin and smooth within. The apertural tooth is not apparent.

The operculum is semicircular; the outer surface with irregular growth lines and a slight depression below the nucleus. The inner surface is slightly convex with a conspicuous pit at the base of the apophyses. The ventral apophysis is in the form of a broad, rounded arcuate ridge the tip of which is missing in the only known specimen. The dorsal apophysis, approximately at right angles to the ventral, is broad, ovate in cross section and rounded at the tip (Figure 26). This description of the operculum is, of necessity, based on a single specimen and accordingly takes no account of any variation which may exist within the species.

Dimensions — The neotype (Figure 16) is 7.5mm in height, 7.8 mm in width. Some specimens are slightly lar-

ger, such as BMNH 72316 (F. E. Edwards coll.): 8.3 mm in height, 8.3 mm in width.

Remarks — This species is superficially similar to white colour morphs of *C. concavus* but, in general, in *C. bristowi* the aperture is broader, the spire lower and the labial dentition better defined. However, the most important distinction is in the operculum which, as Curry pointed out (1960: 268), differs considerably from the operculum of *C. concavus*.

Range and distribution — The Hamstead Member of the Bouldnor Formation where it is apparently restricted to the “Nematura Bed”.

***Clithon (Pictoneritina) cranmorensis* sp. nov.**
Figures 17-19

Derivatio nominis — Named after the Cranmore Member at Cranmore, Isle of Wight where this species occurs.

Type material — Holotype: Conchological Society 366 (J. W. Taylor coll.) on permanent loan to BMNH, (Figure 17). Paratypes (two): Conchological Society 367 (J. W. Taylor coll.) on permanent loan to BMNH, (Figure 18). BMNH GG22776 (F. Stinton coll.), (Figure 19).

Stratum typicum — Bouldnor Formation, Cranmore Member, “Cerithium Beds”.

Locus typicus — Bouldnor Cliff, Cranmore, Isle of Wight.

Diagnosis — A small, semiglobose *Pictoneritina* with an exerted spire and poorly defined dentition on the septum edge. The colour pattern is usually of dark brown, zigzag lines on a light background.

Description — Shell small for the subgenus, the teleoconch consisting of about two and a quarter whorls, semiglobose with an exerted spire. The protoconch is conspicuous, smooth, obovate and approximately 0.3 mm wide. The exterior of the teleoconch is smooth and glossy with fine col-labral growth lines. The whorls are strongly convex becoming slightly concave below the suture. The suture is sharp but shallow. The colour pattern generally consists of zigzag, dark brown lines, on a whitish background; the lines in some specimens interlacing to form a network enclosing irregular white dots and splashes (Figure 18a).

The aperture is oblique, semicircular and rather broad. The septum is convex and smooth with a slightly concave edge. There is one main tooth on the septum edge and up to six poorly defined denticulations abapical to it. The outer lip is evenly rounded, thin and smooth within. The apertural tooth consists of a long, low, sharp ridge below the abapical end of the septum, straight or only slightly curved at first and ending in a sharp abapical curve behind the septum edge. The operculum has not yet been found, as far as I am aware.

Dimensions — Holotype: approximate height 6.6 mm, width 6.9 mm. Paratypes: Conchological Society 367 (J. W. Taylor coll.) height 6.6 mm, width 7 mm; BMNH GG22776 (F. Stinton coll.) height 3.7 mm, width 4.2 mm.

Remarks — *Clithon cranmorensis* is similar to both *C. concavus* and *C. planulatus* and is probably closely related to each of them. Apart from its distinctive colour pattern, *C. cranmorensis* is distinguished from both by its small but conspicuous protoconch and from *C. concavus* by its smaller, more globular teleoconch. The overall shape of the teleoconch is closer to that of *C. planulatus* but it lacks the prominent dentition characteristic of that species.

Newton (1891: 252) in his list of the mollusca in the F. E. Edwards collection at the BMNH includes “*Neritina fulminifera* Sandberger, 1853 - the Hempstead Beds, Hempstead.” The single specimen so labelled in the collection (BMNH 72315) is a small shell in a matrix of grey clay, the precise horizon not being specified. It is clearly an example of *C. cranmorensis* but it does not accord with Sandberger’s description or his illustration of *N. fulminifera* (Sandberger, 1863: 153, pl. 7, fig. 13).

Range and distribution — In the Cranmore Member of the Bouldnor Formation it is reasonably common in the “Cerithium Beds” near the top of Bouldnor Cliff, Cranmore, Isle of Wight. It also occurs in the Hamstead Member in the White Band at the base of Bouldnor Cliff (Alan Morton pers. comm.).

Subgenus *Vittoclithon* Baker, 1923

Type species — by original designation, *Neritina meleagris* Lamarck, 1822. Recent, in brackish water, Caribbean.

Amended diagnosis — The shell is small and smooth. The septum is weakly arched with 4 to 10 small teeth.

Remarks — Baker in defining his section *Vittoclithon* of subgenus *Clithon* relied mainly on the radula and did not describe the teeth on the septum (Baker, 1923: 134). Keen in Joint Committee on Invertebrate Palaeontology (1960: 1285) described this subgenus as: “Small, smooth: inner lip weakly arched, with one tooth.” However, Baker designated *Neritina meleagris* Lamarck, 1822 as the type species and this species does not have just one tooth on the septum edge but instead four to ten small, irregular teeth (Russell, 1941: 380), which actually matches the illustration (but not the description) of *Vittoclithon* in Joint Committee on Invertebrate Palaeontology (1960: 1281, fig. 183.12).

***Clithon (Vittoclithon) headonensis* sp. nov.**
Figures 20-22

Nerita aperta J. de C. Sowerby, 1823: 5: pl. 424, fig. 4 appears to be this species.

Derivatio nominis — Named after Headon Hill, Isle of Wight where this species is common.

Type material — Holotype: BMNH GG22782 (M.F. Symonds coll.), (Figure 21). Paratypes (three): BMNH GG22781 (M.F. Symonds coll.), (Figure 20); BMNH PLTG 7963 (D. Curry coll.), BMNH PLTG 7964 (D. Curry coll.).

Stratum typicum — Headon Hill Formation, Colwell Bay Member, “Neritina Bed”.

Locus typicus — Headon Hill, Isle of Wight.

Diagnosis — A small *Vittocliton* with the spire not or hardly exerted. Labial dentition well defined and typical of the subgenus. Colour pattern consists of a network of whitish dots on a dark background.

Description — A rather small shell, the largest in the BMNH collection being a little under 8 mm in width but 4.5 mm to 7 mm is more usual. Spire not or hardly exerted, often in juveniles wholly or partially covered by the following whorl. The protoconch is approximately 0.3 mm wide, smooth, obovate, frequently well preserved and prominent, sometimes partly obscured by the first whorl of the teleoconch. The teleoconch consists of about two whorls, the surface is smooth but not glossy, due to the presence of numerous fine, collabral threads which intersect microscopic spiral ridges. The last whorl is convex, becoming flat or slightly concave below the suture. The suture is sharp and well defined. The colour pattern consists of a network of white dots on a dark brown background; the dots may be round, oval or elongate but are generally consistent in size, shape and arrangement in any individual (but see Figure 22c).

The aperture is oblique, semicircular and broad. The septum is flat or slightly convex, smooth, the edge concave in the middle with 4 to 7 small but well defined teeth, the adapical tooth not or only slightly larger than the others. The apertural tooth consists of a short, curved projection below the abapical end of the septum.

Dimensions — Holotype: height 4.3 mm, width 4.9 mm. Paratypes: BMNH GG22781 (M.F. Symonds coll.) height 4.4 mm, width 4.7 mm; BMNH PLTG 7963 (D. Curry coll.) height 5.6 mm, width 5.8 mm; BMNH PLTG 7964 (D. Curry coll.) height 3.4 mm, width 3.4 mm.

Discussion — This species is common in the “Neritina Bed” in the Colwell Bay Member on Headon Hill, Isle of Wight and it is surprising that it has been overlooked as a separate taxon. This is presumably because the colour pattern resembles that of some specimens of *C. concavus*, although the reticulate pattern in *C. concavus*, when it occurs, is usually less regular than in *C. headonensis*. The morphology is very different: the lack of a prominent spire in most specimens of *C. headonensis*, the almost matt surface, due to more pronounced collabral threads than *C.*

concavus, the different shape of the apertures in the two species and the small, well defined labial teeth of *C. headonensis* contrasting with the large, adapical tooth and several small teeth, all very poorly defined, in *C. concavus*. The specimen illustrated as figure 4 in Sowerby’s plate of *Nerita aperta* (J. de C. Sowerby, 1823: 5: pl. 424, fig. 4) appears to be this species but, as the original specimen cannot now be found, it is impossible to be sure. Certainly the shape of *C. headonensis* closely resembles that of *P. aperta* but they can be readily separated by the thickened outer lip and prominent labial tooth of *P. aperta*.

Range and distribution — Colwell Bay Member. It occurs in the “Venus Bed” in Colwell Bay but I have not found it among several thousand specimens of *C. concavus* from the “Neritina Bed” at that locality. At Headon Hill, on the other hand, it is at least as common as *C. concavus* in the “Neritina Bed” (a bulk sample taken in October 2002 yielded: 77 *C. concavus* and 134 *C. headonensis*). It is also common in the “Milford Marine Bed” in the cliffs at Milford on Sea, Hampshire.

An isolated specimen, BMNH 72317 (F. E. Edwards coll.), is labelled “Hempstead Beds, Hempstead”. This specimen is unusual in that it is the only one I have seen in which the network of white dots is broken by a series of white and brown lines over part of the shell where the dots have apparently coalesced (Figure 22). In all other respects it accords with *C. headonensis* from the Colwell Bay Member and I have no doubt that it is this species. On this basis the range of *C. headonensis* extends to the Bouldnor Formation where it is clearly very rare.

Concluding remarks

Clithon concavus, *C. planulatus*, *C. bristowi* and *C. cranmorensis* are all similar and are probably closely related. It is possible that *C. planulatus*, *C. bristowi* and *C. cranmorensis* are all ecophenotypes of *C. concavus* but as they can be separated on the basis of shell and/or operculum morphology as well as colour pattern and as they each occur in different stratigraphical horizons I prefer to treat them as separate species.

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