Three new species of *Clithon* (Mollusca, Gastropoda, Neritimorpha, Neritidae) are described from the Solent Group (late Eocene and early Oligocene) of the Hampshire Basin, England

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Gastropods of the family Neritidae in the Solent Group of the Hampshire Basin, southern England are briefly reviewed and three previously undescribed taxa are introduced. New species: *Clithon* (*Pictoneritina*) *greteliae*, *Clithon* (*Pictoneritina*) *pacaudi* and *Clithon* (*Pictoneritina*) *cliffendense.* New combination: *Clithon* (*Pictoneritina*) *headonense* (Symonds, 2006).

KEY WORDS: Solent Group, Hampshire Basin, Neritidae, *Clithon*, *Pictoneritina*, new species.

Introduction

Continuing research into the fauna of the Solent Group, in particular by Alan Morton and Bill Pocock, has resulted in the discovery of new species. The Solent Group, which spans the late Eocene and the early Oligocene (Priabonian and Rupelian), (Insole *et al.,* 1998, p. 19), consists 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, p. 3). *Clithon* Montfort, 1810 are common in some brackish water deposits and they form an important part of the molluscan fauna. The opportunity is taken here to describe three new *Clithon* species which have recently been discovered and to comment briefly on the larval development of the Solent Group Neritidae, as indicated by their protoconchs.

Taxonomy

Superorder Neritimorpha Golikov & Starobogatov, 1975
Order Cycloneritimorpha Bandel & Frýda, 1999
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritinae Rafinesque, 1815
Genus *Clithon* Montfort, 1810

Type species – by original designation: *Nerita corona* Linnaeus, 1758. Present-day fresh to brackish water, eastern Indian Ocean to the southwestern Pacific.

Diagnosis – 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 (Symonds, 2015, p. 147).

Remarks – *Clithon* was proposed as a genus by Montfort (1810, p. 327) but Baker (1923, pp. 154-156) considered *Clithon* to be a subgenus of *Theodoxus* Montfort, 1810, based mainly on features of the radula. This classification was followed by Wenz (1929, pp. 2899-2900), Keen (1960, 1 p. 285) and Vaught (1989, p. 13). However, Wenz (1938, pp. 422-423) reinstated *Clithon* to generic level and Holthuis (1995, p. 184) confirmed this status, based on anatomical data. She has since been followed by Eichhorst (2016, p. 154) and *Clithon* is now generally accepted as a valid genus as originally proposed.

Subgenus *Pictoneritina* Iredale, 1936

Type species – by original designation, *Neritina oualaniensis* Lesson, 1831. Present-day, in estuaries and brackish lagoons and intertidally on sheltered, sandy beaches with freshwater seeps. Indo-Pacific.

Diagnosis – Small *Clithon* with smooth, rounded whorls without spines; septum weakly arched with one large and several small teeth (emended from Keen, 1960, 1 p. 285).

Remarks – Wenz (1938, p. 423) considered *Pictoneritina* to be a valid subgenus of *Clithon* and he was followed by a number of authors (Symonds, 2006; Symonds *et al*., 2018 and Vrinat, 2019) all of whom placed *Clithon* species from the Tertiary of Europe in the subgenus *Pictoneritina* despite Holthuis (1995, pp. 196-197) having concluded, following dissection of *Clithon*, that the type species of *Clithon* and *Pictoneritina* were too similar anatomically to justify retaining *Pictoneritina* as a subgenus of *Clithon.* Eichhorst (2016, p. 154) also thought that *Pictoneritina* should not be used for extant species but he did concede that the subgenus might have more relevance for extinct species. The shells of *C.* (*C.*) *corona* and *C.* (*P.*) *oualaniense*, the type species of *Clithon* and *Pictoneritina* respectively, are very different. *Clithon* (*Clithon*) *corona* (Linnaeus, 1758) is substantially larger than *C.* (*P.*) *oualaniense*, it has a rough, thick periostracum and usually a row of prominent spines around the shoulder (Eichhorst, 2016, p. 171, pls 9-11). *Clithon* (*Pictoneritina*) *oualaniense* is small, smooth and glossy with elaborate colour patterns and no discernible periostracum; it never has a shoulder or spines (Eichhorst, 2016, pp. 208-209, pls 34-38). In consideration of these substantial differences, *Pictoneritina* is retained as a subgenus of *Clithon*.

Clithon (*Pictoneritina*) *headonense* (Symonds, 2006)

Plate 1, figs 1a-c.

1823 *Nerita aperta* J. de C. Sowerby 5: pl. 424, fig. 4. (non *Nerita aperta* J. de C. Sowerby, 1823 5: 30, pl. 424, figs 2, 3)

2006 *Clithon* (*Vittoclithon*) *headonensis* Symonds, pp. 37-38, figs 20-22.

Type material – Holotype: NHMUK GG 22782 (M.F. Symonds coll.). (Pl. 1, figs 1a-c). Paratypes (three): NHMUK GG 22781 (M.F. Symonds coll.); NHMUK PL TG 7963 (D. Curry coll.), NHMUK PL TG 7964 (D. Curry coll.).

Diagnosis – Small *Pictoneritina* with spire not or hardly exserted; centre of septum edge slightly concave with one broad, often obscure tooth, up to nine very small, well-defined teeth abapical to it. Colour pattern: network of pale dots on dark brown background (emended from Symonds, 2006, p. 38).

Description – Small *Pictoneritina*, largest in NHMUK collection slightly under 8 mm in width, 4.5 mm to 7 mm more common. Protoconch approximately 0.3 mm wide, smooth, spherical, multispiral, frequently well preserved and prominent, sometimes partly obscured by first whorl of teleoconch. Spire not or hardly exserted, in juveniles often wholly or partially covered by following whorl; teleoconch about two whorls, surface smooth but not glossy, due to numerous fine, collabral threads which intersect microscopic spiral ridges; last whorl convex, becoming flat or slightly concave below suture which is impressed, well-defined. Aperture oblique, semi-circular, wide; septum broad, flat or slightly convex, smooth; edge with long, shallow central concavity with four to nine very small, well-defined teeth, main adapical tooth substantially broader than the others, often hardly projecting, occasionally with two or three very small teeth adapical to it; apertural tooth short, curved projection below abapical end of septum; outer lip slightly flared, smooth within, forming narrow gutter at adapical junction with septum. Colour pattern: network of pale dots on dark brown background; dots round, oval or elongate but generally consistent in size, shape and arrangement on any individual. Operculum semi-circular; outer surface glossy, numerous, faint, sinuous growth lines becoming more pronounced towards dorsal margin which is bordered by shallow groove, conspicuous depression around nucleus, otherwise flat; inner side with double apophysis consisting of long, thin, ventral arcuate ridge terminating in narrow, cylindrical knob projecting beyond opercular edge; at right angles to it, short, rounded dorsal knob.

Remarks – As noted by Symonds (2006, p. 38), 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 the original specimen has been lost and it is impossible to be sure. The original description of *C.* (*V.*) *headonensis* (Symonds, 2006, pp. 37-38) has been emended to include features apparent from the greater range of material now available and a description of the operculum, which has since been found (Plate 1, figs 5a, b). Wenz (1929, pp. 2899-2900) considered *Clithon* and *Vittoclithon* Baker, 1923 to be subgenera of *Theodoxus* Montfort, 1810 and he was followed by Keen (1960, p. 285). Subsequently, when Wenz (1938, pp. 422-423) promoted *Clithon* to generic rank he made *Vittoclithon* a subgenus of *Clithon*. Eichhorst (2016, p. 1037) placed the type species (by original designation) of *Vittoclithon*, *Neritina meleagris* Lamarck, 1822, in *Vitta* Mörch, 1852. Eichhorst (2016, p. 1016) elevated *Vitta*, formerly regarded as a subgenus of *Neritina* Lamarck, 1816, to generic level, making *Vittoclithon* a junior subjective synonym of *Vitta*. However, *C.* (*P.*) *headonense* does not belong in *Vitta*; it lacks a definite spire, which is an important feature of *Vitta,* and the septum edge of *C.* (*P.*) *headonense* has a central concavity and a broad, adapical tooth unlike that of *V. meleagris* which is fairly straight with narrow, well-defined teeth but without the broad, adapical tooth (Eichhorst 2016, p. 1036, pl. 319). The shell morphology of *C.* (*P.*) *headonense* is consistent with *Pictoneritina* and the features of the operculum, not available at the time of the original description, also accord with *Pictoneritina*. Accordingly, *C.* (*P.*) *headonense* should be placed in *Clithon* (*Pictoneritina*) rather than in *Vitta*.

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

Plate 1, figs 2a-c; Plate 2, fig. 9.

Zoobank registration – urn:lsid:zoobank.org:act:12C85400-2CA1-450F-BBB9-5ED7FFA44BB2

Type material – Holotype NHMUK PI TG 27345 (*leg.*

Alan Morton, M.F. Symonds coll.) height 5.2 mm, width 6 mm (Pl. 1, figs 2a-c). Paratype NHMUK PI TG 27352 (Alan Morton coll.), height 1.7 mm, width 1.6 mm (Pl. 2, fig. 9), both from type locality and type stratum.

Type Locality – Base of Bouldnor Cliff, Cranmore, Isle of Wight, England, 50°43'14"N 1°26'37"W (estimated from Google Earth).

Type Stratum – Bouldnor Formation, Hamstead Member, base of the "White Band", a series of muds interbedded with bands of shell debris, which occurs about 20 m above the base of the member (Insole & Daley, 1985, p. 96).

Etymology – In honour of my friend Greteli Morton who has participated in many joint expeditions to the Isle of Wight.

Diagnosis – Small, semiglobose *Pictoneritina*; protoconch large, not or hardly exserted; fine dentition on the septum edge; colour pattern: brown, zigzag lines on pale background.

Description – Small *Pictoneritina*; protoconch not or hardly exserted, obovate, smooth apart from minute radial wrinkles on last part of whorl, paucispiral, approximately 0.5 mm wide. Teleoconch smooth, glossy with very fine collabral growth lines, about two and a quarter whorls, semiglobular, spire low; whorls evenly rounded with slight concavity below suture on body whorl; suture sharp, well defined. Aperture oblique, semi-circular; septum flat or slightly concave, smooth; septum edge slightly concave, one broad tooth about one third of distance from adapical end, abapical to it up to five very small, rounded, occasionally poorly defined, denticles; outer lip thin, evenly rounded, smooth within. Apertural tooth low, narrow, slightly curved ridge below abapical end of septum, becoming higher internally, terminating in small knob. Colour pattern: narrow, brown lines on pale background forming regular zigzags. Operculum semi-circular, outer surface glossy, smooth apart from faint growth lines, shallow groove from nucleus to ventral margin, otherwise flat; inner surface smooth, concave area in centre of ventral side; apophysis thin curved ridge joined by callus to base of dorsal knob, knob itself missing in only known specimen.

Remarks – The above description of the operculum is not comprehensive, based as it is on the only known example which, unfortunately, is broken and incomplete. *Clithon* (*Pictoneritina*) *greteliae* is similar to *C.* (*P.*) *cranmorense* Symonds, 2006 and could be ancestral to that species. However, the protoconch of *C.* (*P.*) *cranmorense* (Pl. 2, fig. 11) is smaller (maximum width 0.4 mm), exserted and prominent (Symonds 2006, p. 37) while that of *C.* (*P.*) *greteliae* (Pl. 2, fig. 9) is larger (approximately 0.5 mm wide) and does not protrude above the first whorl of the teleoconch. Also, the colour pattern of *C.* (*P.*) *cranmorense* is variable, consisting of pale, round or elongate spots on a brown background, brown zigzag lines on a pale background or, sometimes, a combination of both. Symonds (2006, p. 37) described the colour pattern of *C.* (*P.*) *cranmorense* as generally consisting 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". Since then, however, several hundred more specimens have been examined from which it appears that specimens with pale spots on a brown background are by far the more common form. With *C.* (*P.*) *greteliae*, on the other hand, the colour pattern is remarkably uniform, always consisting of narrow, brown zigzag lines on a pale background. For a comparison with *C.* (*P.*) *pacaudi* n. sp. see below.

Distribution – *Clithon* (*Pictoneritina*) *greteliae* is known only from the type locality.

Other material studied – 158 additional specimens were examined from the type stratum (35 from Alan Morton coll., 13 from William Pocock coll. and 110 from M.F. Symonds coll.).

***Clithon* (*Pictoneritina*) *pacaudi* nov. sp.**
Plate 1, figs 3a-c; Plate 2, fig. 10.

Zoobank registration – urn:lsid:zoobank.org:act:BE58B7BA-A9AA-446D-96F9-A7CC05CF19EC

Type material – Holotype NHMUK PI TG 27346 (M.F. Symonds coll.) height 6.6 mm, width 6.4 mm (Pl.1, figs 3a-c). Paratype NHMUK PI TG 27353 (Alan Morton coll.), height 1.6 mm, width 1.8 mm (Pl. 2, fig. 10), both from type locality and type stratum.

Type locality – Foreshore, Hamstead, Isle of Wight, England, 50°43'32"N 1°25'47"W (estimated from Google Earth).

Type stratum – Bouldnor Formation, Gurnard Member, Bed 6 of Daley (1999, p. 54, text-fig. 26).

Etymology – In honour of my colleague Jean-Michel Pacaud, a palaeontology researcher at the Muséum national d'Histoire naturelle, Paris.

Diagnosis – Small to medium, semiglobose *Pictoneritina*; protoconch not or hardly exserted, one broad tooth on the septum edge, up to six small denticles abapical to it; colour pattern: pale, triangular blotches on brown background.

Description – Small to medium *Pictoneritina*; protoconch not or hardly exserted, obovate, smooth, paucispiral, approximately 0.35 mm in width. Teleoconch smooth, glossy with very fine, closely packed, collabral growth lines, about two and a quarter whorls, semiglobular, spire not or hardly exserted; whorls evenly rounded usually with concavity below suture which is impressed. Aperture wide, oblique, semi-circular; septum flat or slightly

concave, smooth, callus swollen, particularly towards posterior, on mature specimens; septum edge slightly concave, one broad tooth about one third of distance from adapical end, abapical to it three to six small, sometimes clearly defined, often obscure, squarish denticles; outer lip evenly rounded, smooth within. Apertural tooth narrow, curved, rather insignificant ridge below abapical end of septum. Colour pattern: numerous, small, often closely spaced, regular or irregular pale blotches on brown background, usually triangular in shape with the apex always pointing towards aperture, often with narrow, dark brown margin on leading edges; rarely white specimens occur without colour pattern. Operculum semi-circular, outer surface distinctly concave, smooth apart from faint growth lines, shallow groove in an arc from nucleus to ventral margin, depression around nucleus; inner surface smooth, slight ridge in an arc from nucleus to ventral margin corresponding to groove on outer surface; double apophysis, ventral thin curved ridge projecting beyond operculum margin; dorsal apophysis at about 90° to it, joined at base, ending in prominent knob.

Distribution – A *Clithon* which occurs in a narrow band approximately 3 m above the top of the White Band in Bouldnor Cliff and just below a red paleosol marker (Andy Gale in prep.) appears to be this species. Although common, almost all specimens are crushed or otherwise distorted and have lost the outer, calcitic layer containing the colour pattern. Rare specimens, however, retain sufficient of the calcitic layer to show a colour pattern which is identical to that of *C.* (*P.*) *pacaudi* and unlike any other fossil Solent Group *Clithon*. Apart from this, *C.* (*P.*) *pacaudi* is known only from the type locality.

Other material studied – Approximately 675 additional specimens were examined from the type locality, many of them distorted or incomplete, (approximately: 350 from Alan Morton coll., 45 from William Pocock coll. and 280 from M.F. Symonds coll.).

Remarks – The colour pattern of *C.* (*P.*) *pacaudi* is distinctive with its pale, triangular blotches, often with a dark band on the leading edges producing a three-dimensional effect which is particularly noticeable on freshly exposed material. This is the only *Clithon* in the Solent Group with this feature but it does occur in some extant species, such as *C. ruginosum* (Récluz, 1841), see Eichhorst (2016, p. 226, pl. 48). *Clithon* (*Pictoneritina*) *hillae* Symonds, 2015 has a colour pattern of pale spots on a brown background but, unlike those on *C.* (*P.*) *pacaudi*, they are irregular in size and shape, seldom triangular and never with a dark band around them. *Clithon* (*Pictoneritina*) *hillae* is a rather larger *Clithon* with more pronounced growth lines, more numerous and finer labial teeth and an apertural tooth which curves back into the aperture ending in a knob (Symonds, 2015, p. 150) unlike the apertural tooth in *C.* (*P.*) *pacaudi* which lacks a terminal knob. There are also various differences in the opercula: in particular the chevron shaped grooves along the labral margin of the outer surface of *C.* (*P.*) *hillae* are not apparent on the operculum of *C.* (*P.*) *pacaudi* and the second apophysis on *C.* (*P.*) *hillae* takes the form of a ridge at an acute angle to the ventral apophysis and is joined to it by callus throughout its length (Symonds, 2015, p. 150, pl. 1, fig. 9) whereas that of *C.* (*P.*) *pacaudi* is at an angle of at least 90° to the ventral apophysis, is joined only at the base and ends in a prominent knob (Pl. 1, fig. 6a, b). *Clithon* (*Pictoneritina*) *cranmorense* exhibits various forms of colour pattern one of which consists of pale spots on a brown background but the spots are rounded rather than triangular and are never edged in dark brown. The protoconch of *C.* (*P.*) *cranmorense* is smaller, the spire more prominent and the teeth on the septum edge smaller and less clearly defined than those of *C.* (*P.*) *pacaudi*. *Clithon* (*Pictoneritina*) *pococki* Symonds, 2015 exhibits a wide range of colour patterns including pale spots on a brown background, occasionally even triangular spots but always lacking a dark edging (Symonds, 2015, p. 148, pl. 1, figs 1-6). Like *C.* (*P.*) *cranmorense*, *C.* (*P.*) *pococki* has a smaller protoconch than *C.* (*P.*) *pacaudi* and a more prominent spire. In *C.* (*P.*) *pococki* the teeth on the septum edge are small and poorly developed, with some specimens appearing to be edentate, in contrast to the teeth on *C.* (*P.*) *pacaudi* which are larger and can be well-developed. *Clithon* (*Pictoneritina*) *pacaudi* is similar in terms of shell morphology to *C.* (*P.*) *greteliae* although the colour pattern is completely different with *C.* (*P.*) *pacaudi* having small, pale, triangular spots on a brown background and *C.* (*P.*) *greteliae* showing a distinctive pattern of narrow, brown, zigzag lines on a whitish background. *Clithon* (*Pictoneritina*) *pacaudi* is rather larger than *C.* (*P.*) *greteliae* but with a smaller protoconch; the spire of *C.* (*P.*) *greteliae* is low while that of *C.* (*P.*) *pacaudi* is not or hardly exserted; the aperture of *C.* (*P.*) *pacaudi* is wider and the callus on the septum more extensive than that of *C.* (*P.*) *greteliae* and *C.* (*P.*) *greteliae* lacks the swollen callus that develops on older specimens of *C.* (*P.*) *pacaudi*. Rare white specimens lacking colour pattern could be confused with *C.* (*P.*) *bristowi* Wenz, 1929 but *C.* (*P.*) *bristowi* is a rather larger, more globose species with a low but definite spire unlike the depressed spire of *C.* (*P.*) *pacaudi*.

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

Plate 1, figs 4a-c.

Zoobank registration – urn:lsid:zoobank.org:act:981814D4-E1DC-41E1-B07D-3E7092651282

Type material – Holotype NHMUK PI TG 27347 (Alan Morton coll.) height 7 mm, width 7.6 mm (Pl. 1, figs 4a-c). Paratype NHMUK PI TG 27359 (M.F. Symonds coll.), height 4.8 mm, width 5 mm. both from type locality and type stratum.

Type locality – Between Colwell Bay and Cliff End, Isle of Wight, England, 50°41’38”N 1°32’01”W (estimated from Google Earth).

Type stratum – Headon Hill Formation, Cliff End Member, "Trizonatum Bed" of Keeping & Tawney (1881, p. 103, 104, fig. 3).

Etymology – Named after the Cliff End Member in which this species occurs and Cliff End, close to which the holotype was found.

Diagnosis – Medium size *Pictoneritina*, smooth and glossy; spire not exserted, protoconch covered by the first whorl of the teleoconch; variable colour pattern of wavy, dark brown lines, which may interlace to form irregular network, on white background.

Description – Medium size *Pictoneritina*. Protoconch completely covered by first whorl of teleoconch. Spire not exserted, covered by following whorl; surface of teleoconch smooth, glossy; last whorl convex, but slightly flattened below impressed suture. Aperture oblique, semicircular, broad; septum flat or slightly convex, smooth apart from microscopic pustules, septum callus wide; centre of septum edge concave, one broad but not prominent tooth about a quarter of distance from apical end; up to eight small, usually prominent, well-spaced teeth abapical to it, poorly defined in some specimens; outer lip smooth within, slightly flared, forming narrow gutter at junction with adapical end of septum, end of gutter curving towards apex; apertural tooth short, narrow ridge, increasing in height towards the interior, below abapical end of septum. Colour pattern variable, consisting of narrow, dark brown, wavy lines, sometimes interlacing to form irregular network on white background, some specimens with two broad, white, spiral bands.

Distribution – Apart from the type stratum, *C.* (*P.*) *cliffendense* is known from a sandy bed of variable thickness with shell lenticles containing numerous specimens of *Melanopsis* spp. approximately 1 m above the Trizonatum Bed, described in a section taken by E. Forbes and H.W. Bristow in or about 1852 (Reid & Strahan, 1889, p. 131) as: "White, yellowish and dark sand, with clayey streaks. *Melanopsis fusiformis, M. subcarinata*? *Cyrena pulchra*. Lenticular patches of dead *Melanopsis* and *Cyrena obovata* in the lower part." ("Melanopsis Bed"). Also, from a bed intermediate between the two containing poorly preserved material. Recently, Alan Morton has found a single specimen of this species in the "Venus Bed" (Headon Hill Formation, Colwell Bay Member) in Colwell Bay below the Brambles Chine slipway, where it must be extremely rare as it has never previously been recorded from this bed.

Other material studied – 45 additional specimens were examined from the type stratum (13 from Alan Morton coll., 9 from William Pocock coll. and 23 from M.F. Symonds coll.) and a further 27 specimens from the "Melanopsis Bed" (10 from Alan Morton coll., 6 from William Pocock coll. and 11 from M.F. Symonds coll.).

Discussion – The only other *Clithon* in the Solent Group with the spire wholly concealed by the body whorl is *C.* (*P.*) *mortoni* Symonds, 2015 to which *C.* (*P.*) *cliffendense* is very similar and may well be ancestral. The most obvious difference is in the colour pattern: that of *C.* (*P.*) *mortoni* consisting of narrow, dark, collabral lines on a light background, with little intraspecific variation, while *C.* (*P.*) *cliffendense* has a variable colour pattern with dark, wavy lines on a light background, often interlacing to form an irregular network interrupted, on some individuals, by broad, pale spiral bands. In addition, *C.* (*P.*) *mortoni* has a more globular shell than *C.* (*P.*) *cliffendense* with a distinctly convex septum unlike the septum of *C.* (*P.*) *cliffendense* which is flat or only slightly convex. The aperture of *C.* (*P.*) *cliffendense* is broader and the septum callus more extensive than that of *C.* (*P.*) *mortoni*. The gutter at the adapical end of the septum is shorter on *C.* (*P.*) *mortoni* and it lacks the curve towards the apex which is a feature of *C.* (*P.*) *cliffendense.* The teeth on the septum edge are also different with *C.* (*P.*) *mortoni* having one prominent tooth and up to five fine, closely spaced teeth abapical to it. On *C.* (*P.*) *cliffendense* the main tooth is broad but not prominent and the small teeth, up to eight in number, are usually larger, more prominent and more widely spaced than those on *C.* (*P.*) *mortoni.* On both species the small teeth may be much reduced on some specimens.

Discussion

Only two genera of Neritidae are known to be present in the Solent Group: *Clithon* and *Monsneritina* Kowalke, 2002. The type species of *Monsneritina* (by original designation) is *Neritina montensis* Briart & Cornet, 1887 which has a multispiral protoconch indicative of a planktonic veliger stage (Kowalke, 2002, p. 113, pl. 1, figs 6, 7). The type species of *Pseudodostia* Symonds, 2006, *Nerita aperta* J. de C. Sowerby, 1823 (by original designation) in contrast, has a protoconch which consists of one whorl (Plate 2, fig. 7) which is consistent with a lecithotrophic larval stage (Bandel, 2001, p. 70). However, the teleoconch morphology of the two species is similar and they belong in the same genus despite the difference in early ontology as shown by their protoconchs. Accordingly, *Pseudodostia* is a junior, subjective synonym of *Monsneritina*. In the Solent Group, *Monsneritina* is represented by a single species: *M. aperta*. Of the other Eocene genera, *Nerita* Linnaeus, 1758, although represented in the Eocene of France, has not been found in the Solent Group, probably because the palaeoenvironment was unsuitable. Most extant species of *Nerita* are marine, intertidal and live mainly on rocky shores (Eichhorst, 2016, p. 426) whereas the Solent Group was deposited in fresh to brackish water environments with a few brief marine incursions (Gale, 2019, p. 20). There is no evidence of fully marine conditions and even in the "Venus Bed", which represents the most significant incursion in the Solent Group and which has the richest molluscan assemblage in the Colwell Bay Member, the fauna is "indicative of inshore, muddy, river influenced, somewhat hyposaline conditions" (Daley, 1999, p. 49). *Tomostoma* Deshayes, 1824 is present in the Lutetian of the Hampshire Basin and the Lutetian and Bartonian of France (Symonds,

2009, p. 42) but may have become extinct before the Solent Group was laid down. *Otostoma* d'Archiac, 1859, a genus which reached peak diversity in the Cretaceous and which is particularly well represented in Late Cretaceous marine sediments which are indicative of shallow, subtropical, warm water conditions (Saul & Squires, 1997, p. 138) may also have become extinct before the deposition of the Solent Group or its absence may be due to the conditions which were generally unsuitable for a marine genus. *Velates* Montfort, 1810, common in the Ypresian of France, survived into the late Eocene (Priabonian) and possibly the Oligocene (Plaziat, 2012, pp. 36-39) but has not been found in England. (Bandel (2008, p. 20) has placed *Otostoma* and *Velates* in the Otostomidae Bandel, 2008 and the Velatininae Bandel, 2001 respectively).

Of the *Clithon* species present: *C.* (*P.*) *headonense, C.* (*P.*) *cliffendense* and *C.* (*P.*) *mortoni* are distinct in having a spire which is depressed and wholly or partially obscured by subsequent whorls and they may represent a separate line of evolution. The remaining species, ranging from *C.* (*P.*) *concavum* (J. de C. Sowerby, 1823) in the Headon Hill Formation at the base of the Colwell Bay Member to *C.* (*P.*) *cranmorense* in the Cranmore Member at the top of the Bouldnor Formation, all have a spire which is distinct, even if low in some species, that is never obscured. Almost all the species can be readily separated by their colour pattern, the only exception being *C.* (*P.*) *bristowi* which normally lacks any trace of colour but rare examples do have a colour pattern which, in some cases, can resemble that of *C.* (*P.*) *hillae.* It is possible that some described species are actually ecophenotypes whose colour pattern is a response to environmental factors. However, colour pattern is regarded as a key factor in identifying extant *Clithon* (Eichhorst, 2016, pp. 154-310) and it is more likely to be a case of new species evolving during the deposition of the Solent Group which lasted for approximately 4 million years (Gale, 2019, p. 18, fig. 10).

As adults, many extant *Clithon*, including *C.* (*C.*) *corona*, the type species of *Clithon*, live in freshwater streams and rivers above tidal influence. In contrast, *C.* (*P.*) *oualaniense*, the type species of *Pictoneritina*, is found in brackish water in mangroves, lagoons, tidal sections of streams and rivers and on beaches with freshwater seeps but never in purely freshwater conditions (Eichhorst, 2016, p. 209). *Clithon* in the Solent Group are also found in brackish horizons and not in freshwater deposits; even in the Hatherwood Limestone Member of the Headon Hill Formation, a predominately freshwater deposit, *C.* (*P.*) *planulatum* (Edwards, 1866) only occurs in two narrow horizons which correspond with brackish water intervals (Paul, 1989, p. 151, fig. 3). The only possible exception being *C.* (*P.*) *pococki* Symonds, 2015 which is found in the "Cyrena Pulchra Bed" of Bristow *et al*. (1889), Totland Bay Member, Headon Hill Formation, accompanied by brackish water species such as *Potamomya plana* (J. Sowerby, 1814) and *Geloina pulchra* (J. de C. Sowerby, 1826) (Daley, 1999, pp. 41 & 45) but the type stratum of the species appears, from the presence of well-preserved lymnaeids and planorbids, to be a freshwater deposit possibly indicating that *C.* (*P.*) *pococki* was euryhaline (Symonds, 2015, p. 151). Alternatively, it could be an example of the "post-mortem mixing of different salinity assemblages" within a "paralic aqueous complex in which salinities differed laterally" postulated by Daley in his palaeoenvironmental interpretation of the Headon Hill Formation (Daley, 1999, p. 45).

In suitable habitats, extant *Clithon* can be found in considerable numbers, often with a variety of species present. Eichhorst, for instance, identified seven species of *Clithon* from a single locality (Eichhorst, 2016, p. 154). In the Solent Group, in contrast, even where *Clithon* are abundant there is not usually more than one or at the most two species present at any horizon. Where two species are present, there can be considerable lateral variation not just in the overall number of individuals but also in the relative proportions of the numbers of each species. For instance, a bulk sample of the "Neritina Bed" near the base of the Colwell Bay Member exposed on the foreshore near Brambles Chine, Colwell Bay, contained about 1,700 specimens of *C.* (*P.*) *concavum* but no other *Clithon* species. Proceeding in a southerly direction from there, a sample of the "Neritina Bed" at Warden Point produced: 172 *C.* (*P.*) *concavum* and 20 *C.* (*P.*) *headonense*; at Widdick Chine the same bed yielded: 17 *C.* (*P.*) *concavum* and 54 *C.* (*P.*) *headonense* and at Headon Hill the results were: 68 *C.* (*P.*) *concavum* and 146 *C.* (*P.*) *headonense.*

Present-day Neritidae deposit their eggs on hard surfaces within egg capsules, strengthened with agglutinated material, each capsule containing many eggs, the actual number depending on the species (Bandel, 2001, p. 73). After hatching the larvae of most genera emerge from the egg capsules as free-swimming veligers which feed on phytoplankton, during which time the larval shell is secreted ("planktonic development"). The exact duration of this stage is unknown and is likely to vary between species (Bandel, 2001, pp. 73-76). In the case of freshwater species, the veligers are swept downstream into the sea where they live in the plankton (Bandel, 2001, p. 67). After completing the larval stage, they settle in stream and river mouths and crawl upstream, eventually reaching freshwater (Bandel, 2001, p. 97). In the genus *Theodoxus* Montfort, 1810, the young develop within the egg capsule, usually with nurse egg feeding (Bandel, 2001, p. 67), and emerge as crawling miniature adults ("benthonic development"). Holthuis (1995, pp. 232-233) regarded planktonic development as the ancestral means of development from which she considered benthonic development had evolved four times represented by: *Nerita signata* Lamarck, 1822, *Vitta usnea* (Röding, 1798), *Theodoxus* and *Fluvinerita* Pilsbry, 1932. According to Eichhorst (2016, p. 142), at least one species of *Clithon* also features benthonic development. A study of the Australian intertidal species *Nerita melanotragus* E. A. Smith, 1884 has shown that it exhibits both planktonic and benthonic development (Prezlawski, 2011, 2012). Since the two forms of development can occur within a genus and even within a single species, they should not be regarded as significant diagnostic features for the purpose of separating genera or species.

The protoconchs of all Neritidae with planktotrophic larvae are almost spherical, smooth and multispiral with up to 2.5 whorls. In contrast, benthonic larvae have paucispiral protoconchs of not more than one whorl which tend to be larger than the protoconchs of planktonic species and often have prominent growth lines or radial wrinkles (Bandel, 2001, pp. 69-77). Among the extant *Clithon* of which the larval stage is known, benthonic development is clearly the exception but that is not the case with the Solent Group *Clithon* where only *C.* (*P.*) *headonense* (Pl. 2, fig. 8) is known to have a protoconch which is typical of planktonic development being small, almost spherical, smooth and multispiral. Apart from *C.* (*P.*) *mortoni* and *C.* (*P.*) *cliffendense,* the protoconchs of which are obscured by the first whorl of the teleoconch, and *C.* (*P.*) *hillae*, a reasonably preserved protoconch of which has yet to be found, all the other species have paucispiral protoconchs of one whorl or slightly less, indicating benthonic development. *Clithon* (*Pictoneritina*) *greteliae* (Pl. 2, fig. 9) has a larger protoconch than *C.* (*P.*) *headonense*, the final part of which exhibits the radial wrinkles referred to by Bandel (2001, pp. 70, 77) as being a feature of benthonic development. The protoconch of *C.* (*P.*) *pacaudi* (Pl. 2, fig. 10) is slightly smaller and smooth while *C.* (*P.*) *cranmorense* (Pl. 2, fig. 11) has a relatively small protoconch the surface of which is covered with radial wrinkles. *Clithon* (*Pictoneritina*) *pococki* (Pl. 2, fig. 12) has a larger protoconch which is entirely smooth. That of *C.* (*P.*) *bristowi* (Pl. 2, fig. 13) is large and smooth apart from very fine radial ridges at the end of the whorl. *Clithon* (*Pictoneritina*) *concavum* (Pl. 2, fig. 14) and *C.* (*P.*) *planulatum* (Pl. 2, fig. 15) both have protoconchs which are somewhat smaller than *C.* (*P.*) *bristowi* and are smooth, apart from faint growth lines towards the junction with the teleoconch in the case of *C.* (*P.*) *planulatum*.

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Plate 1

1. *Clithon* (*Pictoneritina*) *headonense* (Symonds, 2006). Holotype, a. apertural, b. apical, c. abapertural views. Height 4.3 mm, width 4.9 mm. Headon Hill Formation, Colwell Bay Member. Headon Hill, Isle of Wight. NHMUK GG 22782 (M.F. Symonds coll.).
2. *Clithon* (*Pictoneritina*) *greteliae* n. sp. Holotype, a. apertural, b. apical, c. abapertural views. Height 5.2 mm, width 6 mm. Bouldnor Formation, Hamstead Member. Cranmore, Isle of Wight. NHMUK PI TG 27345 (*leg.* Alan Morton, M.F. Symonds coll.).
3. *Clithon* (*Pictoneritina*) *pacaudi* n. sp. Holotype, a. apertural, b. apical, c. abapertural views. Height 6.6 mm, width 6.4 mm. Bouldnor Formation, Gurnard Member. Hamstead, Isle of Wight. NHMUK PI TG 27346 (M.F. Symonds coll.).
4. *Clithon* (*Pictoneritina*) *cliffendense* n. sp. Holotype, a. apertural, b. apical, c. abapertural views. Height 7 mm, width 7.6 mm. Headon Hill Formation, Cliff End Member. Colwell Bay, Isle of Wight. NHMUK PI TG 27347 (Alan. Morton coll.).
5. *Clithon* (*Pictoneritina*) *headonense* Symonds, 2006. Operculum, a. outer surface, b. internal surface. Width 3.6 mm. Headon Hill Formation, Colwell Bay Member. Headon Hill, Isle of Wight. NHMUK PI TG 27348 (M.F. Symonds coll.).
6. *Clithon* (*Pictoneritina*) *pacaudi* n. sp. Operculum, a. outer surface, b. internal surface. Width 3.2 mm. Bouldnor Formation, Gurnard Member. Hamstead, Isle of Wight. NHMUK PI TG 27349 (M.F. Symonds coll.).

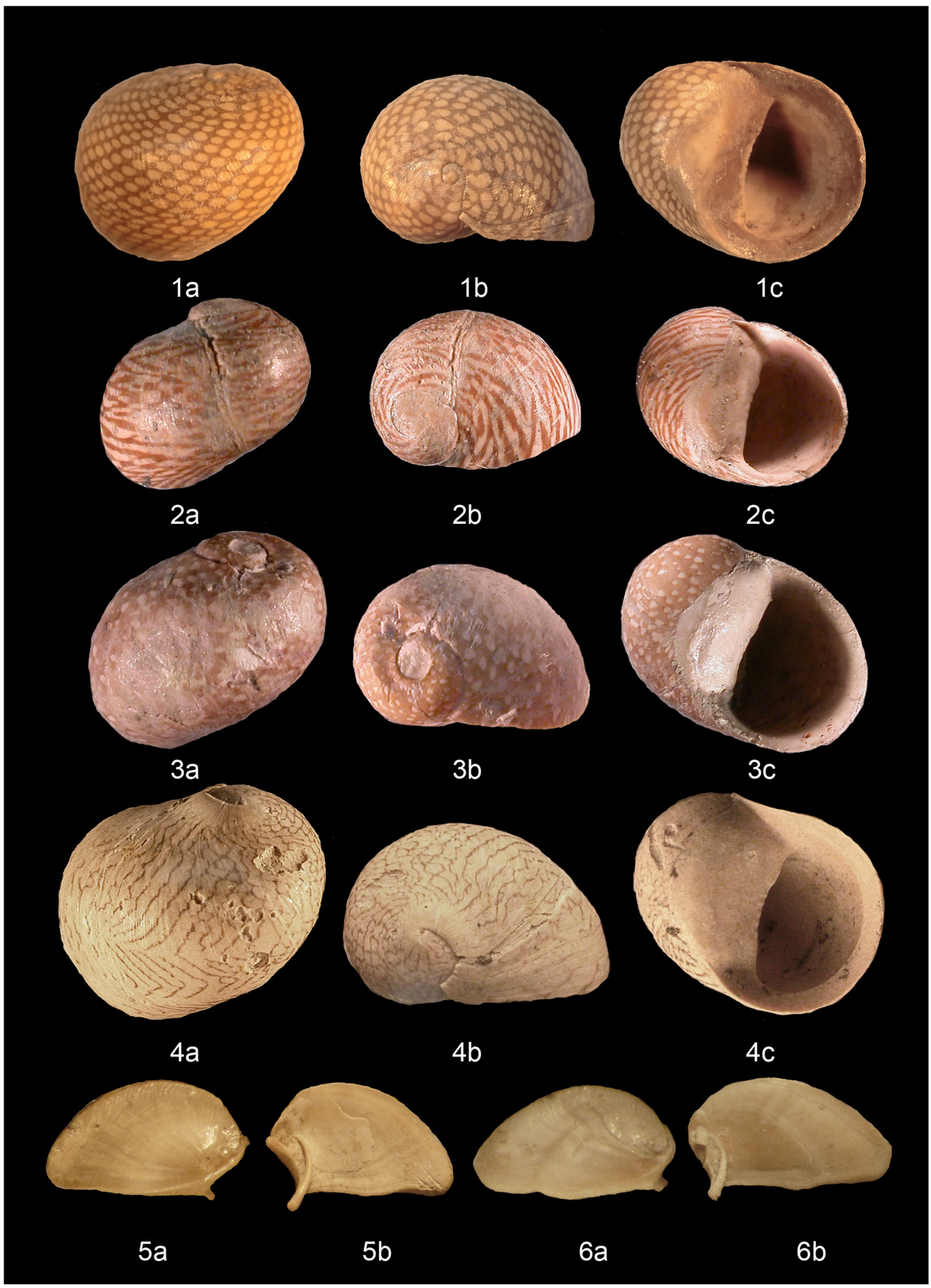

Plate 1

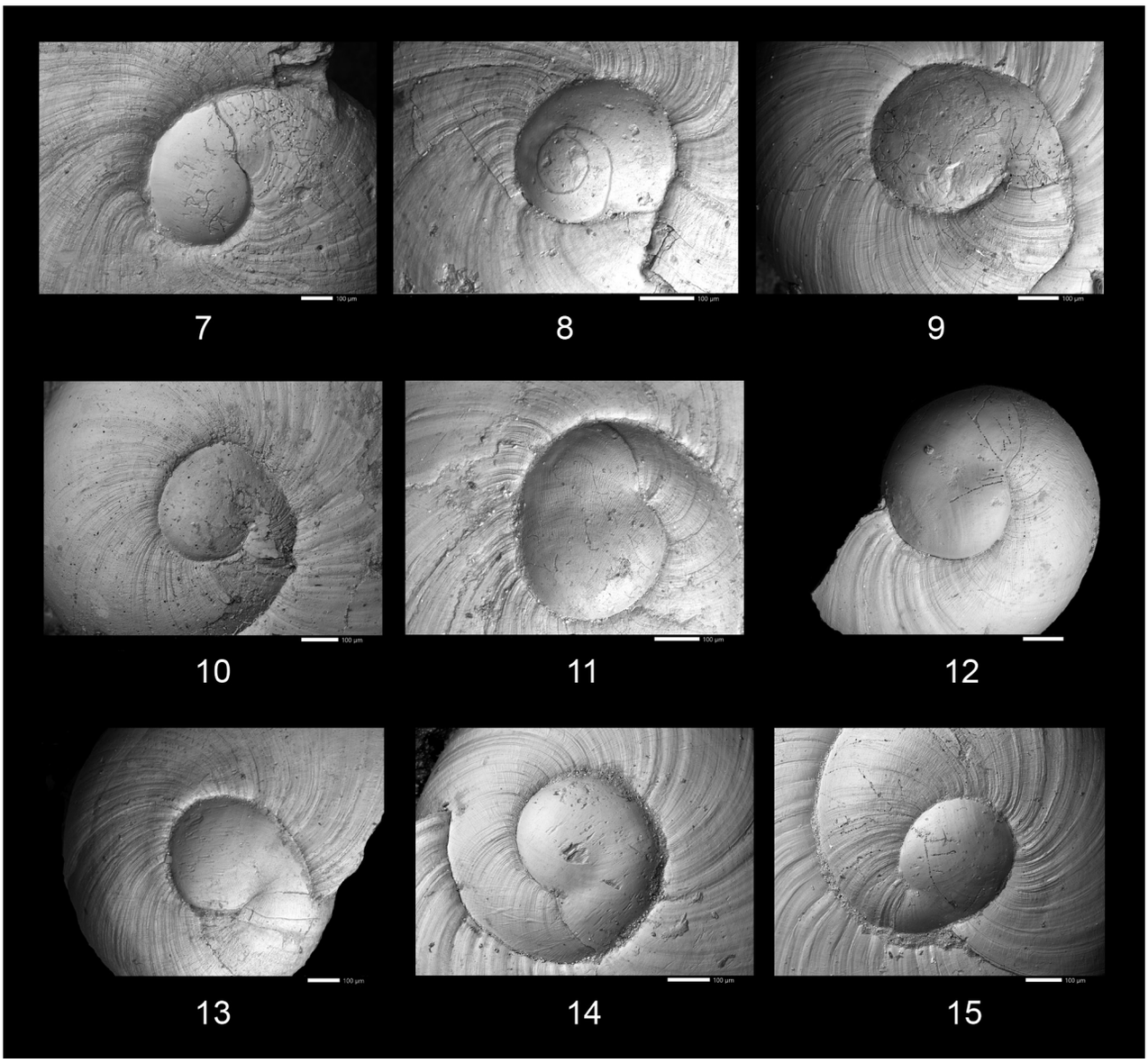

Plate 2

7. *Monsneritina aperta* (J. de C. Sowerby, 1823) Headon Hill Formation, Colwell Bay Member, "Oyster Bed". Colwell Bay, Isle of Wight. NHMUK PI TG 27350 (M.F. Symonds coll.).
8. *Clithon* (*Pictoneritina*) *headonense* Symonds, 2006. Headon Hill Formation, Colwell Bay Member, "Chocolate Clay" of Forbes. Headon Hill, Isle of Wight NHMUK PI TG 27351 (M.F. Symonds coll.).
9. *Clithon* (*Pictoneritina*) *greteliae* n. sp. Paratype. Bouldnor Formation, Hamstead Member, base of "White Band". Base of Bouldnor Cliff, Cranmore, Isle of Wight. NHMUK PI TG 27352 (Alan Morton coll.).
10. *Clithon* (*Pictoneritina*) *pacaudi* n. sp**.** Paratype. Bouldnor Formation. Gurnard Member, Bed 6 of Daley 1999. Hamstead, Isle of Wight. NHMUK PI TG 27353 (Alan Morton coll.).
11. *Clithon* (*Pictoneritina*) *cranmorense* Symonds, 2006 Bouldnor Formation, Cranmore Member, Cerithium Beds. Bouldnor Cliff, Isle of Wight. NHMUK PI TG 27354 (M.F. Symonds coll.).
12. *Clithon* (*Pictoneritina*) *pococki* Symonds, 2015 Headon Hill Formation, Totland Bay Member, green clay below Brockenhurst Bed (Bed F of Stinton, 1971). Whitecliff Bay, Isle of Wight. NHMUK PI TG 27355 (M.F. Symonds coll.).
13. *Clithon* (*Pictoneritina*) *bristowi* Wenz, 1929 Bouldnor Formation, Hamstead Member, Nematura Bed. Western exposure, foreshore, Bouldnor, Isle of Wight. NHMUK PI TG 27356 (M.F. Symonds coll.).
14. *Clithon* (*Pictoneritina*) *concavum* (J. de C. Sowerby, 1823) Headon Hill Formation, Colwell Bay Member, Neritina Bed. Totland, Isle of Wight. Warden Point. NHMUK PI TG 27357 (M.F. Symonds coll.).
15. *Clithon* (*Pictoneritina*) *planulatum* (Edwards, 1866) Headon Hill Formation, Hatherwood Limestone Member, base of Hatherwood Limestone, fallen block. North of North Buttress, Headon Hill, Isle of Wight. NHMUK PI TG 27358 (M.F. Symonds coll.).

For figures 7-15 scale bar = 100µm.