Neritilia (Gastropoda, Neritopsina, Neritiliidae): pushing back the timeline

Malcolm Francis Symonds[1] & Steve Tracey[2]

[1] *The Cottage in the Park, Ashtead Park, Ashtead, Surrey KT21 1LE, England; e-mail: symondsmalcolm@hotmail.com*
[2] *ICZN Secretariat, Natural History Museum, Cromwell Road, London SW7 5BD, England; e-mail: s.tracey@nhm.ac.uk*

Received 7 December 2013, revised version accepted 7 February 2014

A new species of the freshwater to brackish neritopsine gastropod genus *Neritilia* is here recognised as the earliest known representative of the Neritiliidae and is described as *Neritilia lawsoni* sp. nov. This discovery is important as it provides fossil evidence of the existence in the early Eocene, some 55 Ma, of a family which has been estimated to have originated in the early Cretaceous but was, until now, unknown as a fossil before the late middle Eocene, approximately 42 Ma. This is also the first record of the family from England.

Key words: Mollusca, Gastropoda, Neritomorpha, Neritopsina, Neritiliidae, *Neritilia*, new species, early Eocene, Ypresian, Blackheath Formation, England.

Introduction

Although the family Neritiliidae was established by Schepman in 1908 it was later classified as a subfamily of Neritidae by Baker (1923, p. 118), followed by various authors including Russel (1941), Keen (1960) and Starmühlner (1976). Based on differences in the protoconch morphology and shell microsculpture, Kano & Kase (2000), following Holthuis (1995), reassigned *Neritilia* to the Neritiliidae. Subsequent anatomical and molecular studies have confirmed the rather distant relationship between *Neritilia* and the Neritidae (Kano *et al*., 2002; Kano & Kase, 2002).

Very few fossil *Neritilia* have been described and only two from Europe: *Neritilia bisinuata* Lozouet, 2004, from the middle Eocene (Lutetian) of northwestern France and *Neritilia neritoides* (Cossmann & Peyrot, 1917) from the Oligocene and early Miocene of southwestern France. A phylogeny of the Neritopsina (= Neritimorpha) proposed by Kano *et al*. (2002), based on molecular clock calibrations from several neritopsine families and on Bandel & Fryda's (1999) hypothesis from the fossil record, suggested that the branch containing the Neritiliidae and Helicinidae diverged from that containing the Neritidae and Phenacolepadidae approximately 135 Ma in the early Cretaceous, while the clade Neritiliidae diverged some 25 Myr later. Until now the earliest neritiliid fossil known was the middle Eocene *Neritilia bisinuata* Lozouet, 2004, which left a gap of approximately 68 Myr from its presumed origin without a fossil record for the family. The present discovery is a significant step towards filling that gap.

Systematic palaeontology

Family Neritiliidae Schepman, 1908

Note – It is difficult to specify characters of the shell morphology that could reliably separate all the genera of the Neritiliidae from those of the Neritidae. Neritiliids are characterised by their minute 'multispiral' larval shell, small overall size, very few whorls, lack of colour pattern, ovoid operculum with a hyaline margin and simple apophysis (where known), and by their occupation of cryptic or extreme habitats ranging from submarine caves to freshwater streams. Most, if not all, of these characters are also found among the neritids. Various authors (Bandel & Riedel, 1998; Kano & Kase, 2000; Lozouet, 2004; Fukumori & Kano, 2014) have considered certain characters of the protoconch to be unique to the Neritiliidae, *e.g.*:

a) a larval shell having spiral microstriae on its last whorl;
b) a globular embryonic shell sometimes wholly obscured by a subsequent, thin larval shell layer of vertical prisms;

c) the axis of the protoconch being significantly tilted relative to the teleoconch axis.
d) all planktotrophic *Neritilia* having a much smaller protoconch than other Recent neritimorph groups.

Character c), a tilted protoconch, is also present in certain fossil and living neritid species assigned to *Nerita* Linnaeus, 1758 or *Pseudodostia* Symonds, 2006 (Tracey & Symonds, in prep.). Characters a) and b) are only present in some neritiliid genera and may or may not be unique to the family. It seems that the most pragmatic diagnosis of shell morphology would be a combination of characters for each genus.

Genus ***Neritilia*** von Martens, 1879

Type species – Neritina rubida Pease, 1865, by original designation. Recent, brackish to freshwater habitats in the Indo-Pacific region.

Diagnosis (emended) – Shell very small, diameter reaching a maximum of about 5.7 mm in the type species, elliptical, or globose-neritiform, unicolorous brown or whitish. Protoconch comprising a sac-like embryonic shell and a tightly coiled, larval shell of few whorls, its axis inclined to the axis of the teleoconch. Larval shell continuous with a thin prismatic shell layer covering the embryonic shell. Last larval whorl with spiral microstriae. Start of teleoconch usually appearing abutted against upper larval lip. Teleoconch of few whorls, rapidly expanding, typically smooth although obscure spiral striae may be present. Shell microstructure of a thin outer layer of vertical calcite prisms, a thick middle crossed-lamellar layer and an inner layer of alternating crossed-lamellar and irregular prismatic structure. Aperture semicircular, outer lip smooth, inner lip straight without teeth, columellar callus with pustular microornament. Small abapical tubercle inside aperture. Operculum oval with a hyaline margin and a single short apophysis.

Remarks – Most Recent *Neritilia* species live in freshwater rivers and streams and their larvae are swept downstream to undergo a planktotrophic stage in a saline environment before returning to estuaries for settlement and metamorphosis, and then migrating upstream as crawling juveniles to spend the rest of their lives in freshwater (Kano *et al*. 2011). The duration of the planktotrophic stage is not known but may be analogous to the larva of *Neritina virginea* (Linnaeus, 1758) which has a larval shell of 2.5 whorls and feeds in the plankton for several weeks according to Bandel (2001, p. 74). Adults of *Neritilia* species have also been found in specialised brackish water environments such as anchialine lakes (*Neritilia mimotoi* Kano *et al*., 2001), anchialine caves (*N. cavernicola* Kano & Kase, 2004) and interstitial habitats (*N. littoralis* Kano *et al*., 2003). Nine genera of Neritiliidae are currently recognised. The larval shell is secreted over the embryonic shell in *Neritilia* and two other genera: *Laddia* Kano & Kase, 2008 (type species *Neritilia traceyi* Ladd, 1965) can be readily separated from *Neritilia* by the convex or slightly sinuous adaxial margin of the inner lip compared to the almost straight or slightly concave inner lip margin of *Neritilia* and the absence, in *Laddia*, of the protuberance within the aperture which is a feature of *Neritilia* (Kano & Kase, 2008); *Platynerita* Kano & Kase, 2003 (type species *P. rufa* Kano & Kase, 2003) is distinguished mainly by anatomical and opercular features and so has not yet been recognised in the fossil record.

Neritilia lawsoni sp. nov.
Figs 1-5

Type material – Holotype PI TG 26754 (ex. S. Tracey & A. Lawson collection), Natural History Museum, London, as yet the only example known.

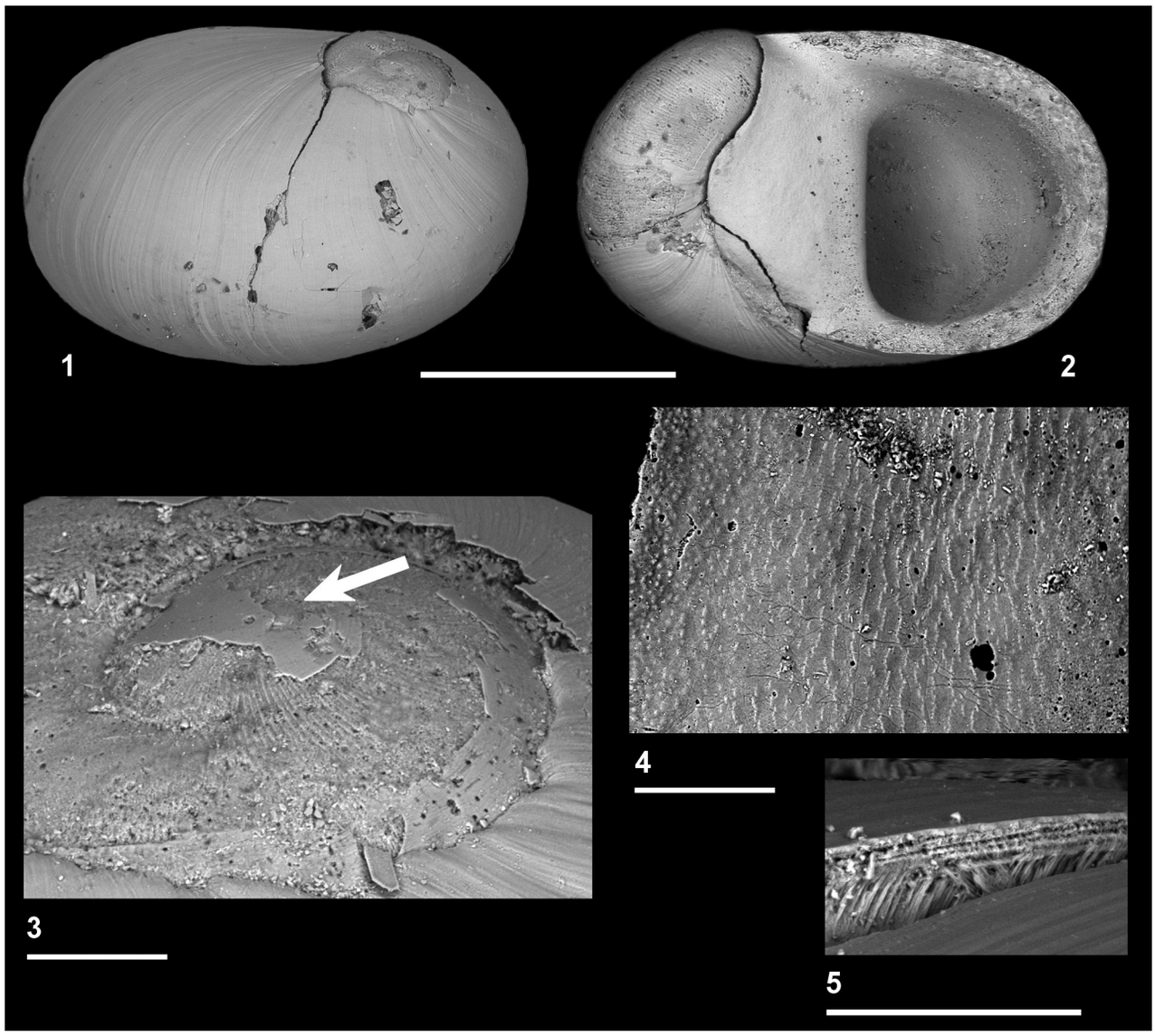
Stratum typicum – Early Eocene (early Ypresian), Blackheath Formation, in a lenticle of shelly sand below the basal pebble bed of the Oldhaven Formation and overlying the upper sands of the Woolwich Formation.

Type locality – Blue Circle Quarry, Swanscombe, Kent, England (51° 25.94′ N 0° 18.35′ E).

Derivatio nominis – Named after our colleague Allan Lawson, a vertebrate palaeontologist who found the unique holotype *c*. 1995.

Diagnosis – A very small, low spired *Neritilia* shell, smooth except for fine growth lines; septum finely pustulate with straight, edentate margin.

Description – Shell minute, height 1.3 mm, maximum diameter 2.1 mm, solid, oval-neritiform with a low spire. Protoconch maximum diameter *c*. 380 μm, somewhat damaged but, as far as can be determined, axis appears slightly inclined relative to teleoconch axis. Larval shell of about 1.5 whorls, apparently smooth without microsculpture, its thin outer shell layer encroaching on and probably covering the embryonic shell when complete. Teleoconch whorls 1.3 in number, increasing rapidly in size, inflated with round periphery, covered with very fine, sinuous growth lines. Suture impressed, shallow, somewhat irregular; microstructure (partly seen in a transverse breakage across the body whorl) shows a thick crossed-lamellar middle layer and a very thin outer layer. Aperture wide, semicircular with a very small, elongate protuberance below the abapical end. Inner lip margin straight, edentate, its septum covered by a callus with micropustules arranged in irregular lateral rows. Outer lip slightly sinuous, smooth within. No trace of colour pattern. Operculum unknown.



Figures 1-5. *Neritilia lawsoni* sp. nov., **holotype** PI TG 26754. Blackheath Formation, Swanscombe, Kent, U.K. 1-2. Shell in dorsal and apertural views (scale bar 1 mm). 3. Protoconch showing remains of damaged larval shell partly overlapping embryonic shell (position indicated by arrow) (scale bar 100 μm). 4. Microornament of columellar callus as orientated in fig. 2 (scale bar 100 μm). 5. Section showing outer and middle parts of shell structure as seen in a natural collabral breakage on the body whorl (scale bar 100 μm).

Remarks

Neritilia bisinuata Lozouet, 2004, from the middle Eocene (Lutetian) of Le Bois-Gouët near Saffré, Loire-Atlantique, France, differs from *N. lawsoni* in having a relatively high spire, obscure spiral ridges on the teleoconch and two notches in the outer lip. The callus on the inner lip of *N. lawsoni* (Fig. 4) is similar to that of *N. neritoides* (Cossmann & Peyrot, 1917) from the Oligocene and early Miocene of southern France but *N. neritoides* is a larger species than *N. lawsoni* and has a more conspicuous elevated spire and a microscopically pitted protoconch (Lozouet, 2004). The shape of the living *N. rubida* (von Martens, 1879), which also has micropustules on the callus of its inner lip in common with the other Recent *Neritilia* species (Y. Kano, pers. comm.), is rather like that of *N. lawsoni* but its thinner shell grows several times larger and it has a more tilted protoconch with spiral striations. Juvenile examples of the neritid *Clithon pisiforme* (Férussac, 1823), which commonly occur in the same strata as *N. lawsoni*, are immediately distinguished by their more globular shape, inner lip with rudimentary teeth and a finely striped colour pattern.

Damage to the protoconch of the unique holotype of *N. lawsoni* makes the presence or absence of microstriae on the larval shell and the degree of tilt of the protoconch axis uncertain, but considering the shell size and shape, the straight smooth inner lip, the thin calcitic layer partly

concealing the embryonic shell and the shell microstructure (Fig. 5), this new species can confidently be referred to *Neritilia*.

Stratigraphy and palaeoecology

The Blackheath Formation (formerly the Blackheath beds and subsequently included as an unnamed unit within the Harwich Formation, but more recently restored to formational status, see Hooker, 2010) is a transgressive channel-filling unit. At Swanscombe the channelled beds are the clays and sands of the basal Eocene (Sparnacian) Woolwich Formation. The lithostratigraphy of the Blackheath Formation elsewhere suggests a palaeoenvironment of nearshore sand and pebble bars while the fauna contains a large proportion of estuarine and perhaps lagoonal molluscs together with a variety of fish, reptile and mammal material. The molluscs found with *Neritilia lawsoni* include abundant *Hydrobia*, *Anamalorbina* and Corbiculidae, together with some *Mytilus*, *Eocantharus*, *Tympanotonos*, *Brotia*, *Clithon* and the myid *Scrobiculabra*, all suggesting a euryhaline fluviatile or estuarine origin. The rarity of *N. lawsoni*, despite large quantities of Blackheath Formation shell beds examined over many years, is perhaps due to its source being in the upper freshwater reaches of a river, in the delta or estuary of which the remainder of the fauna lived.

Acknowledgments

We are grateful to the Natural History Museum, London for use of the Leo 1455VP scanning electron microscope in the preparation of the figures. We are also grateful to Yasunori Kano and Roger Portell for their valuable comments that greatly improved this paper.

References

Baker, H.B. 1923. Notes on the radula of the Neritidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 75: 117–178.

Bandel, K. 2001. The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related Neritimorpha (Gastropoda). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 85: 65-164.

Bandel, K. & Frýda, J. 1999. Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. *Geologica et Palaeontologica* 33: 219-235.

Bandel, K. & Riedel, F. 1998. Ecological zonation of gastropods in the Matutinao River (Cebu, Philippines), with focus on their life cycles. *Annales de Limnologie* 34: 171-191.

Cossmann, M. & Peyrot, A. 1917. Conchologie néogénique de l'Aquitaine. *Actes de la Société Linnéenne de Bordeaux* 3: 1–138.

Férussac, A.E.J.P.J.F. d'A. de, 1823. *Nerites. In*: Deshayes, G.P. & Férussac, A.E.J.P.J.F. d'A. de. *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles, tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles*, livraison 20. *Nérites fossils*. Paris (J.-B. Baillière): pl. 2.

Fukumori, H. & Kano, Y. 2014. Evolutionary ecology of settlement size in planktotrophic neritimorph gastropods. *Marine Biology* 161: 213–227.

Holthuis, B. 1995. *Evolution between marine and freshwater habitats: a case study of the gastropod suborder Neritopsina.* Doctoral dissertation, University of Washington, U.S.A.: 286 pp.

Hooker, J.J. 2010. The mammal fauna of the early Eocene Blackheath Formation of Abbey Wood, London. *Monograph of the Palaeontographical Society, London* 165 (634): 1-162.

Kano, Y., Chiba, S. & Kase, T. 2002. Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. *Proceedings of the Royal Society of London* 269: 2457-2465.

Kano, Y. & Kase, T. 2000. *Pisulinella miocenica,* a new genus and species of Miocene Neritiliidae (Gastropoda: Neritopsina) from Eniwetok Atoll, Marshall Islands. *Paleontological Research* 4: 69-74.

Kano, Y. & Kase, T. 2002. Anatomy and systematics of the submarine-cave gastropod *Pisulina* (Neritopsina: Neritiliidae). *Journal of Molluscan Studies* 68: 365-384.

Kano, Y. & Kase, T. 2003. Systematics of the *Neritilia rubida* complex (Gastropoda: Neritiliidae): three amphidromous species with overlapping distributions in the Indo-Pacific. *Journal of Molluscan Studies* 69: 273-284.

Kano, Y. & Kase, T. 2004. Genetic exchange between anchialine cave populations by means of larval dispersal: the case of a new gastropod species *Neritilia cavernicola*. *Zoologica Scripta* 33: 423-437

Kano, Y. & Kase, T. 2008. Diversity and distributions of the submarine-cave Neritiliidae in the Indo-Pacific (Gastropoda: Neritimorpha). *Organisms Diversity & Evolution* 8: 22-43

Kano, Y., Kase, T. & Kubo, H. 2003. The unique interstitial habitat of a new neritilid gastropod, *Neritilia littoralis*. *Journal of the Marine Biological Association of the United Kingdom* 83: 835-840.

Kano, Y. Sasaki, T. & Ishikawa, H. 2001. *Neritilia mimotoi*, a new neritiliid species from an anchialine lake and estuaries in southwestern Japan. *Venus* 60: 129-140.

Kano, Y., Strong, E.E., Fontaine, B., Gargominy, O., Glaubrecht, M. & Bouchet, P. 2011. Focus on freshwater snails. *In*: Bouchet, P., Le Guyader, H. & Pascal, O. (eds), *The natural history of Santo.* Patrimoines naturels, 69. Paris (Muséum National d'Histoire Naturelle): 257-264.

Keen, M. 1960. Family Neritidae Rafinesque, 1815. *In:* Moore, R. (ed.), *Treatise on invertebrate palaeontology, part N. Mollusca 1.* Boulder Co. (Geological Society of America & University of Kansas Press, U.S.A.): I279-I285.

Ladd, H.S. 1965. Tertiary fresh-water mollusks from Pacific Islands. *Malacologia* 2: 189-197.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum charac-*

teribus, differentiis, synonymis, locis, 1. *Editio decima, reformata*. *Regnum Animale*. Holmiae (Laurentii Salvii): 824 pp.

Lozouet, P. 2004. The European Tertiary Neritiliidae (Mollusca, Gastropoda, Neritopsina): indicators of tropical submarine cave environments and freshwater faunas. *Zoological Journal of the Linnean Society* 140: 447-467.

Martens, E. von. 1879. Die Gattung *Neritina*. *In:* Küster, H.C. & Kobelt, W. (eds), *Systematisches Conchylien-Cabinet von Martini und Chemnitz 2(10)*. Nürnberg (Bauer & Raspe): 1–303.

Pease, W.H. 1865. Descriptions of new genera and species of marine shells from the islands of the Central Pacific. *Proceedings of the Zoological Society of London* 33: 512-517.

Russel, H.D. 1941. The Recent mollusks of the family Neritidae of the Western Atlantic. *Bulletin of the Museum of Comparative Zoology at Harvard College* 88: 347-404.

Schepman, M.M. 1908. The Prosobranchia of the Siboga Expedition 1. Rhipidoglossa and Docoglossa. *Siboga-Expeditie, Monograph* 49: 1–107.

Starmühlner, F. 1976. Ergebnisse der österreichischen Indopazifik-Expedition des 1. Zoologischen Institutes der Universität Wien. Beiträge zur Kenntnis der Süßwasser-Gastropoden pazifischer Inseln. *Annalen des Naturhistorischen Museums in Wien* 80: 473-656.

Symonds, M.F. 2006. The Neritidae of the Solent Group (late Eocene and early Oligocene) of the Hampshire Basin. *Cainozoic Research* 4: 27-39.