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Neritidae (Mollusca, Gastropoda) from the Miocene of western Amazonia (Peru, Colombia and Brazil)

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Six neritid species are recorded from the Miocene (Pebas Formation) of western Amazonia (Peru, Colombia and Brazil), two of which, *Neritina* (?) *patricknuttalli* and *N.* (?) *elephantina*, are described as new. The subgeneric status of Pebasian neritids remains unresolved. Palaeoecological and palaeobiogeographical implications are briefly discussed.

KEY WORDS: South America, Amazonia, Miocene, Neritidae, *Neritina*, new species.

Introduction

In the well-preserved Miocene molluscan faunas of the Pebas Formation in western Amazonia, specimens of *Neritina* are common. In his seminal review of South American non-marine molluscan faunas, Nuttall (1990) considered all Miocene species of *Neritina* from the western Amazonia to be conspecific and he used the name ?*N. ortoni* Conrad, 1871 for them. With the exception of a single neritid from the Cantaure Formation (Miocene) of northern Venezuela, Nuttall was unable to link the Pebasian neritids to any other fossil or extant taxa. The Pebasian neritids are characterised by their commonly velatiform outline (*i.e.*, expanded inner lip callus, basal portion of body whorl in a plane strongly inclined to the shell's axis, and flaring outer lip) and by the absence of an opercular peg. The latter feature is shared with extant *N. (Fluvinerita) tenebricosa* (Adams, 1851) from Jamaica, but Nuttall (1990) found that species to differ from the Pebasian neritids by its thick, spirally striated, non-velatiform shell, and dismissed it as a possible close relative of Pebasian *Neritina*. A study of newly collected material from the Pebas Formation, and a re-examination of museum specimens from Neogene deposits of northwest South America have now shown Pebasian *Neritina* to comprise several species. These species are most easily, but not exclusively, distinguished by their colour patterns, although this feature is notorious for its intraspecific variation (see *e.g.*, Willmann, 1981 for *Theodoxus*; Costa *et al.*, 2001 for *Neritina*).

The aim of the present paper is to provide diagnoses for differentiation of Miocene western Amazonian neritids, to examine relationships with other Recent and fossil neotropical neritids, and to discuss palaeoecological and palaeobiogeographic implications. Because of the uncertain subgeneric status of the six species of *Neritina* known to date from the Pebas Formation and of its close relatives (see below), the informal name 'Pebasian *Neritina*' is used here to characterise this group.

Systematic palaeontology

Abbreviations — To denote the repositories of material referred to in the text, the following abbreviations are used:

- BMNH The Natural History Museum, London (formerly British Museum [Natural History]);
- CAS California Academy of Sciences, San Francisco;
- GG collections of the Department of Palaeontology (BMNH; see Nuttall, 1990);
- INGEMMET Geological Survey, San Borja, Lima;
- NYSM New York State Museum, Syracuse;
- PIMUZ Paläontologisches Institut und Museum der Universität Zürich;
- RGM Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Geologie en Mineralogie), Department of Palaeontology, Division of Cainozoic Mollusca
- RMNH Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum voor Natuurlijke Historie), Department of Evertebrates, Malacology Division.

Stratigraphic age estimates are adapted from Hoorn (1993); locality data are listed in Appendix 1, while the material studied, with the exception of type specimens, is listed in Appendix 2.

Superfamily Neritoidea Lamarck, 1809
Family Neritidae Lamarck, 1809
Genus *Neritina* Lamarck, 1816

The Pebasian neritids are characterised by a velatiform shell form and the absence of an opercular peg. Using these features, the following neotropical species are attributed to the 'Pebasian *Neritina* group':

* Miocene, western Amazonia:
Neritina (?) *ortoni* Conrad, 1871, *N.* (?) *puncta* Etheridge, 1879, *N.* (?) *etheridgei* Roxo, 1924, *N.* (?) *roxoi* de Greve, 1938, *N.* (?) *patricknuttalli* n. sp., and *N.* (?) *elephantina* n. sp.

* Miocene, northern Venezuela:
N. aff. *woodwardi* Guppy, 1866

* Miocene, Ecuador:
N. pacchiana Palmer *in* Liddle & Palmer, 1941

Three other species, *Neritina dominicana* Costa *et al.*, 2001 and *N. jungi* Costa *et al.*, 2001 (Miocene, Dominican Republic) and *N.* sp. Woodring, 1973 (Eocene, Panama) are assigned to the 'Pebasian *Neritina* group' with some hesitation (see Discussion).

Diagnosis — Small to large (shell width 4-22 mm), low-spired, ovate to globose, commonly shouldered neritid; low-spired (velatiform) species commonly involute, with a hooked suture viewed from above; ovate species with prominent erect nucleus and a suture describing a spiral when viewed from above; subsutural ramp convex to (more commonly) concave; growth lines strongly prosocline; shells with a wide range of colour patterns, including efface white to zigzag and punctate; colour patterns superficial; diffuse spiral striae visible on abraded (portions of) specimens; subdued spiral and/or axial ribs rare, but characteristic of a single species; very fine, minute, slightly irregular spiral cords on very well-preserved specimens of most species; a flaring outer lip on most larger species; inner lip callus well developed to prominent, often thickened; callus expanding in some species over the entire basal shell; operculum lacking peg.

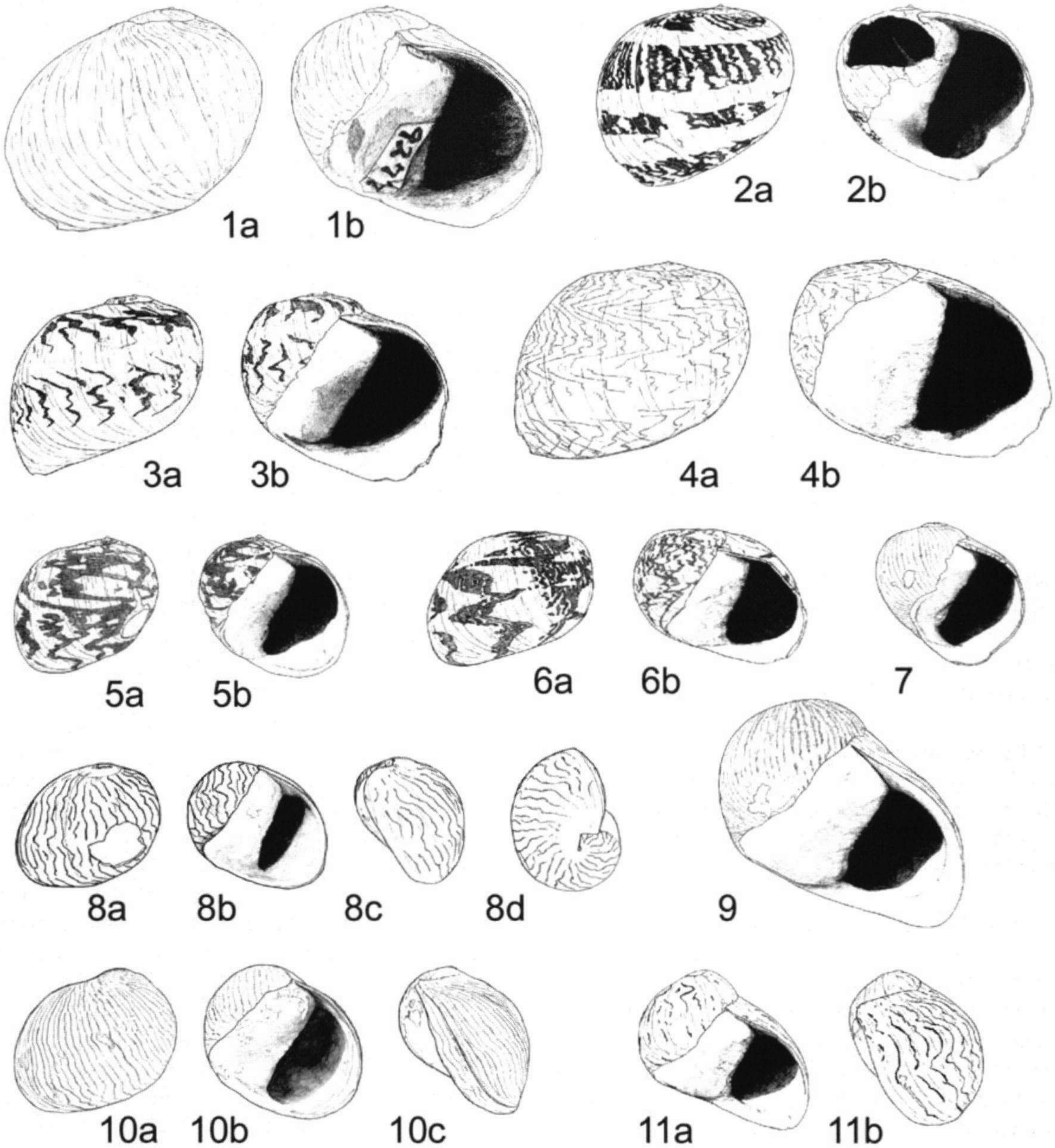
Differentiation — Species of the genus *Puperita* have obscure spiral ribs (Costa *et al.*, 2001), but are comparatively high-spired and lack the prominent columellar area typical of the species of *Neritina* (?) discussed herein. The group of *Neritina fulgopicta* Maury, 1917 (Miocene, Dominican Republic) and *N. virginea* (Linné, 1758) (extant, Caribbean) differs from the Pebasian neritids in having smaller, higher-spired shells, with more whorls, a non-flaring outer lip, in dental architecture and presence of a dark colour band subsuturally on most specimens. Nuttall (1990) discussed and rejected a close relationship between Pebasian *Neritina* and extant *Neritina zebra* (Bruguière, 1792). *Neritilia succinea* (Récluz, 1841 (extant, Greater Antilles and central America) has a 'subpatelliform' outline (Russell, 1941, p. 398) in common with the Pebasian species of *Neritina*. However, it is very small (shell width < 6 mm) and the colour is deeply impregnated into the shell, while in the Pebasian species colours form part of the outer shell layers only, and easily come off. The Pebasian neritids differ from other extant neotropical neritids in having a low spire (see *e.g.*, Russell, 1941). The range of morphological variation resembles that of the Eurasian genus *Theodoxus* de Montfort, 1810. It is only by virtue of the disjunct temporal and geographic distribution, as well as the tropical distribution of the Pebasian species of *Neritina*, *vs* a temperate-subtropical distribution of *Theodoxus*, that these two taxa are treated as distinct for the time being. There is no living species of the 'Pebasian *Neritina* group' to test this. The shell outline of several of the Pebasian neritids superficially resembles that of the Caribbean *Neritina punctulata* Lamarck, 1816 (Figure 21). However, the presence of an opercular peg argues against a close relationship between these two.

Isolated opercula (see Nuttall, 1990, fig. 26a, b) are common in the Pebas Formation, but they cannot be attributed to any particular species with certainty. All of these opercula, however, lack a peg, and it is therefore safe to assume that they do indeed belong to the Pebasian species documented below.

Initially, I placed Pebasian species of *Neritina* in the subgenus *Fluvinerita* Pilsbry, 1932 (extant, freshwater, Jamaica), on the basis of the absence of an opercular peg. However, a recent discussion with H.K. Mienis (Hebrew University, Tel Aviv) has convinced me that several other characters displayed by the Jamaican taxon (*e.g.*, absence of denticles on columellar lip, a comparatively poorly developed inner lip callus, a higher spire and a rather convex whorl profile) are incompatible with the Pebasian neritids, and the previous subgeneric assignment was abandoned.

Neritina* (?) *ortoni Conrad, 1871
Figures 1-7

1869 *Neritina pupa* (Linné) – Gabb, p. 197, pl. 16, fig. 2.
*1871 *Neritina ortoni* Conrad, p. 195, pl. 10, figs 5, 11.
1871 *Neritina ortoni* Conrad – Woodward, p. 103, pl. 5, fig. 2a, b.
1878 *Neritina ortoni* Conrad – Boettger, p. 428.
1938 *Neritina (Vitta) amazonensis* de Greve, p. 62, pl. 5, figs 4-6, 8.
1938 *Neritina (Vitta) etheridgei* Roxo – de Greve, p. 66, pl. 5, figs 1-3, 7, 9.
1966 *?Neritina amazonensis* de Greve – Willard, p. 66, pl. 62, fig. 3.



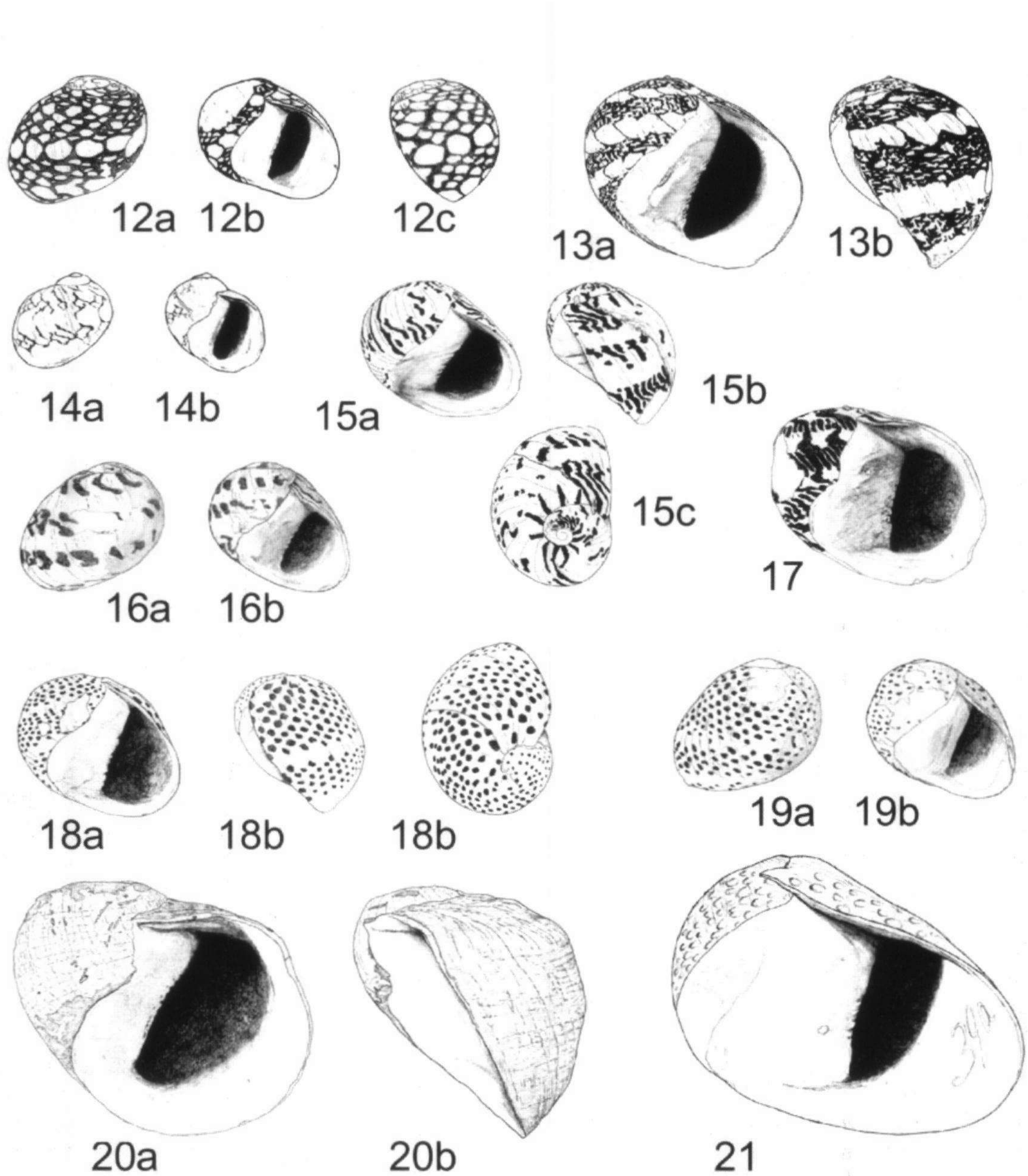
All specimens illustrated, with the exception of Figure 21, are from the Miocene Pebas Formation; for locality data see Appendix 1.

Neritina (?) ortoni Conrad, 1871

1 – lectotype, NYSM 9277 (J. Hauxwell Colln), 'Pichua' (probably Santa Rosa de Pichana), Loreto department, Peru;
2 – paralectotype, NYSM 9276, same locality;
3 – RGM 456 092, Santa Rosa de Pichana, Loreto department, Peru;
4 – RGM 456 100, Santa Elena III, Loreto department, Peru (collected from surface);
5 – RGM 456 134, C14 Hoorn Colln, Santa Julia, Loreto department, Peru;
6 – RGM 456 102, sample F502, Santa Elena III, Loreto department, Peru;
7 – RGM 456 099, sample F86, Santa Teresa, Loreto department, Peru.

Neritina (?) etheridgei Roxo, 1924

8 – RGM 456 131, sample F15, Los Chorros I, Amazonas department, Colombia;
9 – RGM 456 119, sample F70, Nuevo Horizonte, Loreto department, Peru;
10 – RGM 456 132, Los Chorros (no additional locality data), Amazonas department, Colombia, Hoorn Colln;
11 – RGM 456 130, Puerto Caiman, Caqueta department, Colombia, Hoorn Colln.



Neritina (?) roxoi de Greve, 1938
12 – RGM 456 125, sample F37, Villareal, Amazonas department, Colombia;
13 – RGM 456 107, sample F488, Santa Elena II, Loreto department, Peru;
14 – RGM 456 133, sample F51, Salado del Pamaté, Amazonas department, Colombia.

Neritina (?) patricknuttalli n. sp.
15 – RGM 456 113, **holotype**, sample F703, Porvenir IV, Loreto department, Peru;
16 – GG 21786, Pichana, Peru, J. Hauxwell Colln;
17 – RGM 456 118, **paratype**, sample F70, Nuevo Horizonte, Loreto department, Peru.

Neritina (?) puncta Etheridge, 1879
18 – RGM 456 115, Porvenir, Loreto department, Peru;
19 – GG 19993 **lectotype**, Canamá, Peru (Barrington Brown Colln).

Neritina (?) elephantina n. sp.
20 – INGEMMET 4241, **holotype**, sample F502, Santa Elena III, Loreto department, Peru.

Neritina punctulata (Lamarck, 1816)
21 – NNM unregistered, Jamaica, H. Cuming & C. van Dalen Colln

1966 *Neritina etheridgei* Roxo – Willard, p. 66, pl. 62, figs 1, 2.
1990 *?Neritina ortoni* Conrad – Nuttall, p. 178 *(partim)*, figs 9-15, 17-18, 22 (*non* figs 7, 8, 16, 20, 21, 23, 24).

Types — Lectotype, designated herein, is NYSM 9277 (leg. J. Hauxwell), from 'Pichua' (presumably Santa Rosa de Pichana), Loreto department, Peru; Pebas Formation, Middle Miocene. Illustrated by Conrad (1871, pl. 10, fig. 5). NYSM 9276 from the same locality, illustrated by Conrad (1871, pl. 10, fig. 11), is designated paralectotype.

Material studied — See Appendix 2.

Diagnosis — Shell medium to large-sized (shell width 15-24 mm), shouldered, with a well-developed subsutural ridge and marked convex perimeter of the body whorl; colour pattern characterised by thin bifurcating (cf. reticulate) lines on early teleoconch, and irregular, thick, not sharply delimited, zigzag lines on later teleoconch whorls with common dark areas, composed of fine lines, usually arranged in spiral bands; nucleus upright; suture when viewed from above describes a spiral; 3.0-3.4 (rarely 4.2) adnate whorls; growth lines numerous, very fine, prosocline; spiral micro-ornament occasionally visible on well-preserved specimens; body whorl perimeter below rounded shoulder broadly rounded; abraded shells with a spirally arranged, fuzzy telescoping pattern or with broad poorly defined axial zones; outer lip broadly rounded; plain of aperture strongly inclined; inner lip callus the least expanded of all Pebasian *Neritina*; inner lip margin strongly to moderately inclined (10-25 degrees), upper 5-30% smooth, central part with 7-15 denticles of highly variable strength, lower 5-25% smooth; junction between inner and basal lip occasionally sharp, as in *N.* (?) *etheridgei.*

Differentiation — This species is larger than *N.* (?) *roxoi*, *N.* (?) *puncta* and *N.* (?) *patricknuttalli* n. sp., and its colour patterns bear no resemblance to that of those species. It is smooth, unlike *N.* (?) *elephantina* n. sp. *Neritina* (?) *ortoni* closely resembles *N.* (?) *etheridgei*, but the subsutural ridge is better developed in *N.* (?) *ortoni*, being absent or subdued in *N.* (?) *etheridgei*. Furthermore, the outline is more naticiform, less flaring/shouldered, the inner lip callus less prominent and the apertural plain less inclined than in *N. etherridgei*. Also the colour patterns differ: that of *N.* (?) *etheridgei* is almost invariably composed of rather simple, thin, yet clearly defined, axially arranged, slightly zigzagging lines, where lines in *N.* (?) *ortoni* are usually thicker, may be diffuse and often bifurcating. However, some of the studied populations yield specimens of *N.* (?) *ortoni* that cannot be distinguished from *N.* (?) *etheridgei* on colour pattern alone; other shell features (*e.g.*, subsutural ridge, less domed outline etc.) are needed to make the distinction. Dark coloured fields (often composed of densely packed, fine coloured lines) also occur, and such are absent in *N.* (?) *etheridgei*.

Distribution — This species is limited to the Pebas Formation, where it is found in intervals dated as late Early to Middle Miocene.

Remarks — Bandel (2002) referred to occurrences of this species in the Miocene of the Cuenca Basin (Ecuador), but failed to indicate the whereabouts of his material. I have not seen any specimens that could be attributed to *N.* (?) *ortoni* from this basin, although its presence there cannot be ruled out (see Discussion below). *Neritina* (?) *ortoni* is commonest in the small *Dyris* and tall *Dyris* assemblages (Wesselingh *et al.*, 2002), characteristic of lacustrine ramp and shoreface depositional environments. The species is absent from the fluvio-lacustrine Thiaridae-Pulmonata assemblage.

Neritina* (?) *etheridgei Roxo, 1924
Figures 8-11

1879 *Neritina ziczac* Etheridge, p. 85, pl. 7, fig. 10, 10a.
*1924 *Neritina etheridgei* Roxo, p. 47.
1938 *Neritina (Vitta) ortoni* Conrad – de Greve, p. 61, pl. 5, figs 12-15.
1990 *?Neritina ortoni* Conrad – Nuttall, p.178 *(partim)*, figs 19-21 (*non* figs 7-18, 23, 24).

Types — Lectotype, designated by Nuttall (1990, p. 179), is BMNH GG19994 (Barrington Brown Colln), from Canamá, Peru; Miocene, Pebas Formation, illustrated by Etheridge, 1879, pl. 7, fig. 10; the specimen in pl. 7, fig. 10a is a paralectotype.

Material studied — See Appendix 2.

Diagnosis — Large-sized (shell width 17-22 mm), velatiform *Neritina* with strongly inclined apertural plain and flaring outer lip; about half of the specimens evolute, the other half involute; evolute shells with upstanding nucleus and suture describing a spiral when viewed from above and adnate whorls; involute specimens with submerged nucleus, and suture describing a hooked spiral when viewed from above; adult shell with 3.3-3.7 whorls; subsutural ridge usually absent or very indistinct; perimeter body whorl regularly convex, only very rarely slightly concave subsuturally; colour pattern of slightly zigzagged, thin and sharp lines, rarely interrupted by spiral zones devoid of lines; on high-spired specimens (see *e.g.* Figure 11), the lines can be very slightly thickened; lines rarely bifurcate; some specimens are colourless; abraded shells show a spiral pattern of diffuse broad axial lines, and/or a fine, diffuse, spirally arranged telescoped pattern; well-preserved shells with very fine irregular spiral cords; upper part outer lip usually high, in some specimens (*e.g.*, Figure 11) more rapidly descending; outer lip broadly convex; junction of basal and inner lip commonly very sharp, often delimited by a sharp ridge (when viewed from below, see Nuttall, 1990, fig. 13); inner lip callus greatly expanding, well left of the shell's axis; in large specimens the callus is corrugate; thickenings may be present at its base and/or the top; inner lip margin strongly inclined (typically *c.* 10-15 degrees, rarely up to 25 degrees); upper 10-30% of the inner lip margin smooth, median portion with 5-17 denticles that are very variable in strength; pronounced denticles may occur randomly distributed, lower 10-20% (sometimes up to 35%) smooth; lower part of inner lip margin in high-spired specimens often sinistrally deflected.

Distribution — Pebas Formation (late Early-early Late Miocene) of western Amazonia (Peru, Colombia, Brazil); especially common in lacustrine assemblages, and absent from fluvio-lacustrine ones (Wesselingh *et al.*, 2002).

Differentiation — The generally velatiform outline with a strongly expanded inner lip callus typical of *N.* (?) *etheridgei*, is not that pronounced in other Pebasian species. *Neritina* (?) *etheridgei* resembles some specimens of *N.* (?) *ortoni* (see above), especially in colour patterns, but these species differ in development of subsutural ridge and ramp. The velatiform outline and the hooked suture, typical of *N.* (?) *etheridgei*, are also seen in *N. punctulata* (see Figure 21); this differs from *N.* (?) *etheridgei* in having an even more expanded inner lip callus, an inner lip that runs almost parallel to the shell's axis, a more widely expanding outer lip and an apertural peg.

Remarks — H.K. Mienis (pers. comm.) pointed out to me that Sowerby (1836, 1849) used the name *Neritina ziczac* in referring to *N. zigzag* Lamarck, 1822 (p. 185). However, Sowerby's material should be assigned to *N. coromandeliana* Sowerby, 1836 (eastern Indian Ocean, Pacific Ocean), whereas Lamarck's specimen are best referred to as *N. gagates* (Lamarck, 1822) (western Indian Ocean). Von Martens (1879) and Tryon (1888) listed the specific name *ziczac*; *N. etheridgei* is a replacement name (for *N. ziczac* Etheridge, *non N. zigzag* Lamarck).

Neritina* (?) *puncta Etheridge, 1879
Figures 18, 19

*1879 *Neritina puncta* Etheridge, p. 85, pl. 7, fig. 9.
1924 *Neritina puncta* Etheridge – Roxo, p. 47.
1990 ?*Neritina ortoni* Conrad – Nuttall, p. 178 (*partim*), figs 7,8 (*non* figs 9-28).

Types — Lectotype, designated by Nuttall (1990, p. 179), is BMNH GG19992 (Barrington Brown Colln), Canamá, Peru; Miocene, Pebas Formation. This probably is the specimen illustrated by Etheridge (1879, pl. 7, fig. 9). Note that in the caption, Nuttall erroneously indicated his fig. 7 (GG19993) to be the lectotype.

Material studied — See Appendix 2.
Diagnosis — Small (shell width 7, rarely up to 10 mm), ovate but slightly shouldered, characterised by a punctate colour pattern; nucleus just visible in most specimens, occasionally covered by subsequent whorls; suture when viewed from above commonly hooked at the nucleus, but otherwise describing a spiral; shell with 1.2-1.7 whorls; subsutural ridge absent; subsutural zone under an angle of 70-80 degrees to the shell's axis, but with a rounded shoulder effacing into comparatively steep sides; the punctations may be absent in two or three spirally arranged zones; shell smooth; outer lip broadly rounded; inner lip callus well developed, thick especially in its basal portion where it is most expanded; upper 25-30% of inner lip margin smooth, central part with 6-7 thin, but generally well-defined denticles (notably poorly defined in the lectotype), lower 20-25% smooth; inner lip margin strongly inclined (*c.* 10 degrees).

Distribution — Known only from the Middle to lower Upper Miocene of western Amazonia (Peru and Brazil).

Differentiation — The punctate colour pattern is highly typical and precludes confusion of this species with other Pebasian taxa of *Neritina*.

Remarks — This species occurs at a few levels only within the Pebas Formation, but when present it is common; mainly found in association with an admixture of endemic Pebasian cochliopine snails and pachydontine bivalves, as well as common cerithioideans (*e.g.*, *Aylacostoma browni* (Etheridge, 1879), *Hemisinus kochi* Bernardi, 1856, *Charadreon* sp. and *Sheppardiconcha* spp.). These associations are indicative of marginal lacustrine habitats, possibly from near rivers (Wesselingh *et al.*, 2002).

Neritina* (?) *roxoi de Greve, 1938
Figures 12-14

1924 *Neritina*, unnamed species – Roxo, p. 47, fig. B, B'.
*1938 *Neritina roxoi* de Greve, p 64, pl. 5, figs 10, 11, 16.
1990 ?*Neritina ortoni* Conrad – Nuttall, p. 178 (*partim*), figs 23, 24 (*non* figs 7-22, 25-28).

Type — Holotype is PIMUZ 216B (Peyer Colln), Iquitos, Peru; Miocene, Pebas Formation.

Material studied — See Appendix 2.

Diagnosis — Small to medium-sized (shell width 8, rarely up to 11 mm), ovate *Neritina* characterised by a dark, net-like colour pattern with two or three spirally arranged zones of larger open blotches; nucleus erect, but often abraded; suture when viewed from above describing a spiral; shell with up to 3.2 whorls; subsutural ridge absent; perimeter body whorl convex; two-three spiral zones of larger open blotches located at different heights in different specimens; outer lip broadly rounded; inner lip callus expanded, especially at the base; inclination of inner lip margin strong (*c.* 10 degrees); upper 15-20% of inner lip margin smooth, central part with 4-14 poorly developed denticles; lower 15-20 % smooth.

Distribution — Upper Lower to lower Upper Miocene of western Amazonia (Colombia, Peru, Brazil) and lower Middle Miocene of ?Cuenca Basin (Ecuador); see discussion below.

Differentiation — The colour pattern is highly typical and precludes confusion with any of the other Pebasian species of *Neritina*, with the exception of *N.* (?) *elephantina* n. sp. (see below), which has a very distinct rugose ornament.

Remarks — *Neritina* (?) *roxoi* occurs in marginal lacustrine and fluvio-lacustrine assemblages of the Pebas Formation (Wesselingh *et al.*, 2002), being rare in the lacustrine assemblages dominated by endemic Pachydontinae and Cochliopinae. It is the only Pebasian species of *Neritina* that is found in non-endemic associations with pearly freshwater mussels, ampullariids and planorbids. Poorly preserved specimens of *Neritina* from the Loyola Formation of the Cuenca Basin (CAS, Hungerbühler Colln) possibly belong here, but identification is with a query on account of poor preservation of the material.

Neritina* (?) *patricknuttalli n. sp.
Figures 15-17

1990 ?*Neritina ortoni* Conrad – Nuttall, p. 178 (*partim*), fig. 16 (*non* figs 7-15, 17-28).

Types — Holotype is RGM 456 113, Porvenir IV (Loreto, Peru), outcrop in left (west) bank of Amazon River, 200 m north of southern edge of village (*c.* 73°23'W, 4°14'S), level 703 (5 September 1996); paratypes (locality data Appendix 1) are RGM 456 104, Santa Elena III, F502 (2); RGM 456 112, Porvenir, surface find (2); INGEMMET 4240, Porvenir, surface find (1); RGM 456 114, Porvenir IV (1) and RGM 456 118, Nuevo Horizonte, F70 (1).

Diagnosis — Small to medium-sized (shell height 13 mm), ovate to slightly shouldered *Neritina* characterised by thick, often bifurcating, zigzag lines with rounded edges that are absent in two or three spirally oriented zones; subsutural region straight to slightly concave.

Derivatio nominis — Named after C.P. Nuttall (formerly BMNH), in recognition of his outstanding work on the Pebas fauna.

Description — The nucleus is erect, but damaged in most of the specimens studied. The suture, when viewed from above, describes an occasionally slightly distorted spiral. A subsutural ridge is rare. The shell has *c.* 2.5 whorls. The body whorl perimeter is broadly convex and the subsutural region commonly straight to slightly concave. Growth lines are usually well visible. Fine spiral ornament exists on well-preserved specimens, similar to micro-sculpture seen on well-preserved specimens of *N.* (?) *etheridgei.* In a single, strongly abraded specimen (RGM 456 104, paratype), a telescoped pattern emerges which somewhat resembles the colour pattern in *N. tenebricosa* Adams, 1851, type species of *Fluvinerita.* The inner lip callus is strongly expanded, especially in the lower part. The inner lip margin is usually very strongly inclined (0-10 degrees, rarely up to 35 degrees). The upper 20-30% is smooth, the central part shows 6-7 denticles and the lower 20% is smooth.

Dimensions —

	H	HAP	W	n
RGM 456 113 (**holotype**)	9	6	10	2.6
RGM 456 103	12	7	11	n.a.
RGM 456 103	13	9	13	n.a.
RGM 456 118	9	7	11	2.6

Differentiation — This species differs from the other Pebasian neritids by its colour pattern. When viewed from above, some specimens display colour patterns in the form of sticks, also rarely seen in *N.* (?) *puncta*, to which it might be closely related. The inner lip denticles in the latter species, however, are much better defined than in *N.* (?) *patricknuttalli* n. sp.

Distribution — This rare species was found in mixed assemblages; it is known exclusively from Middle–lower Upper Miocene intervals of the Pebas Formation.

Neritina* (?) *elephantina n. sp.
Figure 20

Types — Holotype is INGEMMET 4241, Santa Elena III (Loreto, Peru), outcrop located 300 m west of woodmill (71°24'W, 3°53'S), sample 502 (28 August 1996). Paratypes are RGM 456 104, same locality and level (6), and RGM 456 105, same locality, collected from surface (1).

Diagnosis — Large (shell width 15-20 mm), strongly shouldered and irregularly reticulately ornamented *Neritina* (?).

Derivatio nominis — Shell ornament and colour resemble an elephant's skin.

Description — The nucleus is abraded in all specimens, with the exception of the holotype. Here, the protoconch/teleoconch boundary is located at 0.6 whorl, and marked by an axial depression. When viewed from above, the suture describes a (occasionally slightly irregular) spiral. The shell comprises 2.3-2.7 whorls. A distinct subsutural ridge bounds a concave subsutural ramp. At least one, but often two, rounded ridges develop on the upper part of the whorls, the upper of which forms a distinct shoulder. The body whorl perimeter below the shoulder is rounded, and shows one or two, very poorly defined angles. Shells are commonly abraded on the frontal side. The ornament consists of axial ribs (regular in early teleoconch whorls, irregular on body whorl) and well-defined, irregular spiral incisions which sometimes bifurcate. The latter bound small lunate areas in a general reticulate pattern on early teleoconch whorls, irregular on last part of the body whorl, resembling elephant's skin. The shell is dark coloured, varying from efface dark, to net-like patterns sometimes with 1-3 irregularly arranged spiral zones of small, irregular elongate open blotches. The upper part of the outer lip may be deflected upwards, but is usually more or less perpendicular to the shell's axis. Sometimes the area below the shoulder is slightly concave. The lower part of the outer lip and basal lip are broadly rounded. The apertural plane is comparatively little inclined. Inner lip callus is expanded, but less than in *e.g. N.* (?) *ortoni* and *N.* (?) *patricknuttalli* n. sp. The inner lip margin is sharply to intermediately inclined (10-20 degrees). The upper 10-20% (rarely 30%) is smooth, the central part shows 8-12 not very pronounced denticles and the lower 20-40% is smooth.

Differentiation — The ornament of this species sets it apart from any of the other Pebasian neritids.

Dimensions —

	H	HAP	W	n
INGEMMET 4241 (**holotype**)	18	16	20	2.4
RGM 456 104	18	15	19	2.4
RGM 456 104	15	12	17	n.a.
RGM 456 104	16	13	18	2.7
RGM 456 104	16	13	17	2.2
RGM 456 105	19	14	21	2.6

Distribution — This species was found at a single horizon, in a species-poor fauna dominated by *Tryonia* cf. *scalarioides* (Etheridge, 1879), *Dyris lintea* (Conrad, 1874), *Dyris ortoni* (Gabb, 1869) and *Mytilopsis sallei* (Récluz, 1854). Sample F502 is located in the upper part of the *Crassoretitriletes* Zone (late Middle Miocene; see Hoorn, 1993).

Species closely related to Pebasian *Neritina*

Shell outline of *Neritina* aff. *woodwardi* Guppy, 1866, recorded by Jung (1965) from the Miocene Cantaure Formation of northern Venezuela and discussed and re-illustrated by Nuttall (1990, fig. 25), resembles that of *N.* (?) *ortoni*. The former species is more domed, and the colour pattern of thick ophistocline axial zones spanning the entire whorl is unlike that of *N.* (?) *ortoni*. A single specimen was reported by Jung (1965) from a fauna with marine and some mangrove-type molluscs, but lacking freshwater indicators.

Four species of *Neritina* have been recorded from Miocene deposits of the Cuenca Basin in Ecuador. The general outline of *Neritina pacchiana* Palmer *in* Liddle & Palmer, 1941 from the Loyola Formation is similar to some of the Pebasian neritids. The colour pattern described by Palmer bears a slight resemblance to that of *N.* (?) *roxoi*, but apparently lacks the two or three spirally oriented, open zones with blotches. Neritids from the Loyola Formation collected by D. Hungerbühler and housed in the CAS collections appear to be attributable to *N.* (?) *roxoi*. Parodiz (*in* Bristow & Parodiz, 1982) described another species from the Loyola Formation, *Neritina loyolaensis*, and in addition recorded an unidentifiable neritid. *Neritina loyolaensis* Parodiz, 1982 is much higher spired than any of the Pebasian species. According to Parodiz (1982), the species should be included in the subgenus *Vitta*. *Neritina* sp. of Parodiz (1982) might possibly be conspecific with *N. ortoni*, but the poor preservation of the material precludes any certain identification.

A single, unidentified *Neritina* recorded by Woodring (1973, p. 467) from the Late Eocene Gatuncillo Formation of Panama might be included in the Pebasian *Neritina* group as well, based on its slightly shouldered outline. However, the poor preservation of the specimen also precludes a certain attribution in this case.

In outline and ornament, *Neritina jungi* Costa *et al.*, 2001 from the middle-late Late Miocene upper Cercado Formation and lower Gurabo Formation of the northern Dominican Republic resembles *N.* (?) *ortoni*. However, the shell is much smaller (height 8 mm, *vs* 18-22 mm in *N.* (?) *ortoni*) and the inner lip denticles are much more strongly developed. The rare, co-occurring *N. dominicana* Costa *et al.*, 2001 is very small (height 3 mm) and ovate. Its colour pattern of densely packed, very fine spirals and irregular blotches is unlike that of any other species of the Pebasian *Neritina* group. These two species have been recorded from brackish to shallow-marine associations (Costa *et al.*, 2001). No opercula are known for these species, thus their attribution to the Pebasian *Neritina* group remains uncertain.

Discussion

Five of the six species listed above are endemic to the Pebas Formation. The sixth species, *Neritina* (?) *roxoi*, may have occurred in the Miocene Cuenca Basin of Ecuador. Its possible occurrence, together with species of *Neritina* assigned to subgenus *Vitta*, could be an indication of faunal exchange between western Amazonia and the Pacific coastal region during the Middle Miocene. Such a connec-

tion was already suggested by *e.g.* Steinmann *et al.* (1999). Apart from a possible biogeographic connection between the Pacific and western Amazonia, other data hint at connections between western Amazonia and the Llanos/Caribbean (Vonhof *et al.*, 1998; Wesselingh *et al.*, 2002). The Pebasian endemics were merely confined to lacustrine habitats and were absent from surrounding rivers and streams (Wesselingh *et al.*, 2002). Lake Pebas was an evolutionary long-lived lake, where extensive radiations of pachydontine bivalves and cochliopine snails occurred (Wesselingh *et al.*, 2002). The five endemic species of *Neritina* form only a minor part of this endemic fauna.
Missing from the Pebas Formation are common coastal neotropical species of *Neritina*. These species, such as *N. pupa* (Linné, 1767), *N. zebra* (Bruguière, 1792) and *N. virginea* (Linné, 1758), also have a considerable Neogene record (Russell, 1941; Rodriguez, 1963; von Cosel, 1986; Costa *et al.*, 2001). Given the extensive indications of freshwater settings in the Pebas Formation (Vonhof *et al.*, 1998; Wesselingh *et al.*, 2002), it seems likely that the absence of these common species (or close relatives) from the Pebas is a salinity-related phenomenon.

Conclusions

Six species of *Neritina* (?) are recognised in the Miocene Pebas Formation of western Amazonia, five of which are endemic, and two of which (*N.* (?) *patricknuttalli* and *N.* (?) *elephantina*) are described as new. The Pebasian species are grouped with one certain and three doubtful fossil species with a neotropical/Caribbean distribution, whose subgeneric status remains unclear. The relationship between this group and the Eurasian genus *Theodoxus* needs further study. The absence of widely distributed coastal species of *Neritina* from the Pebas Formation is attributed to the predominantly freshwater nature of that system.

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Appendix 1 – Localities (ranked alphabetically); leg. F.P. Wesselingh, unless stated otherwise.

Barrio Florido (Loreto, Peru): outcrop on west bank of confluence Nanay and Amazon rivers, below refinery, 200 m north of village (*c.* 73°12'W, 3°37'S), sample F78 (October 1991)
Indiana IV (Loreto, Peru), outcrop in left bank (west bank) of Amazon River, 1.4 km south of port (*c.* 73°04'W, 3°30'S), sample F340 (8 August 1996)
Indiana VI (Loreto, Peru), outcrop in left bank (west bank) of Amazon River, 1.9 km south of port (*c.* 73°04'W, 3°30'S), sample F83 (October 1991)
Los Chorros I (Amazonas, Colombia), outcrop left bank (north bank) Loreto-Yacu, at confluence with Amazon (*c.* 70°22'W, 3°46'S), sample F42 (September 1991)
Los Chorros III (Amazonas, Colombia), outcrop left bank (north bank) of Amazon River, 1,300 m east of confluence with Loreto-Yacu (*c.* 70°22'W, 3°46'S), sample F23 (September 1991)
Los Chorros (no additional locality data) (Amazonas, Colombia), outcrop left bank (north bank) of Amazon River, between confluences with Loreto-Yacu and Amacayacu (*c.* 70°22'W, 3°46'S) (leg. M.C. Hoorn, 1989)
Macedonia (Amazonas, Colombia), outcrop in left bank (north bank) of Amazon River, 500 m west of port (*c.* 70°15'W, 3°48'S), sample C5 (leg. M.C. Hoorn, 1989)
Mishana (Loreto, Peru), outcrop in right bank (south bank) of Nanay River at western end of village (*c.* 73°29'W, 3°52'S), sample F72 (October 1991)
Nuevo Horizonte I (Loreto, Peru), road cutting (eastern side) along Iquitos-Nauta road, km 40, north of bridge in village (*c.* 73°25'W, 4°05'S), sample F70 (September 1991)
Palo Seco (Loreto, Peru), left bank (west bank) of Itaya River (*c.* 73°22'W, 4°00'S), collected from surface of outcrop (13 September 1996)
Porvenir (Loreto, Peru), left bank (west bank) of Amazon River below village, exact location unknown (*c.* 73°23'W, 4°14'S), collected from surface of outcrop (September 1996)
Porvenir IV (Loreto, Peru), outcrop in left bank (west bank) of Amazon River, 200 m north of southern tip of village (*c.* 73°23'W, 4°14'S), sample F703 (5 September 1996)
Porvenir XI (Loreto, Peru), outcrop in left bank (west bank) of Amazon River, 100 m north of northern tip of village (at sugar mill, *c.* 73°23'W, 4°14'S), sample F727 (6 September 1996)
Puerto Caiman (Caqueta, Colombia), right bank (south bank) of Caqueta River, at port (*c.* 70°12'W, 1°25'S) (leg. M.C. Hoorn, 1989)
Salado del Pamaté (Amazonas, Colombia), outcrop in spring northeast of village of Buenos Aires (*c.* 70°22'W, 3°16'S), sample F51 (October 1991)
San Martin (Amazonas, Colombia), outcrop in left bank (east bank) of Amacayacu River, at landing stage (*c.* 70°20'W, 3°44'S), sample F39 (September 1991)
San Miguel Cochiquinas (Loreto, Peru), outcrop at right bank (south bank) of Amazon River, *c.* 1.5 km downstream (east) of confluence with Cochiquinas River (*c.* 71°36'W, 3°47'S), collected from surface (28 August 1996)
Santa Elena I (Loreto, Peru), right bank (south bank) of Amazon River, 1 km west of Santo Tomas Amazonas (*c.* 71°23'W, 3°52'S) (27 Augsut 1996)
Santa Elena II (Loreto, Peru), right bank (south bank) of Amazon River, 500 m west of Santa Elena I (*c.* 71°23'W, 3°52'S), samples F488, 489 (28 August 1996) and unnumbered sample collected from surface
Santa Elena III (Loreto, Peru), 150 m long outcrop; located 300 m west of woodmill, and 600 m west of outcrop Santa Elena II (*c.* 71°24'W, 3°53'S), sample F502 and shells collected from surface without further indication (28 August 1996)
Santa Julia (Loreto, Peru), left bank (north bank) of Amazon River, 2,650 m east of naval base Pijoyal, published in Hoorn, 1993 (*c.* 71°47'W, 3°11'S), collected from surface (September 1991)
Santa Rosa de Pichana (Loreto, Peru), outcrop right bank (west bank) of Amazon River, *c.* 200 m south of confluence with Pichana River (71°46'W, 3°40'S), collected from surface (30 August 1996)
Santa Sofia (Amazonas, Colombia), outcrop in left bank (north bank) of Amazon River, *c.* 4 km northwest of village, below finca, at northwestern tip of Isla Santa Sofia (*c.* 70°09'W, 3°57'S), sample F61 (September 1991)
Santa Teresa I (Loreto, Peru), outcrop left bank (west bank) of Amazon River below village (*c.* 73°00'W, 3°29'S), sample F86 (September 1991)
Santo Tomas/ Amazonas (Loreto, Peru), outcrop at right bank (south bank) of Amazon River, at western tip of Isla San Isidro (*c.* 71°22'W, 3°52'S) (27 August 1996)
Tamshiyacu (Loreto, Peru), right bank (east bank) of Amazon River, 500 m east of port (*c.* 73°09'W, 4°01'S), collected from surface (8 September 1996)
Villareal (Amazonas, Colombia), outcrop in left bank (north bank) of Amazon River, at port (*c.* 70°13'W, 3°55'S), sample F37 (September 1991).

Appendix 2 – Material studied (other than types)

Neritina puncta
RGM 456 115, Porvenir (13)
RGM 456 106, Santa Elena II, F488 (13)
RGM 456 109, Santa Elena II, F489 (3)
RGM 456 110, Santa Elena II, collected from surface (1)

Neritina roxoi
RGM 456 120, Barrio Florido, F78 (8)
RGM 456 113, Porvenir, collected from surface (4)
RGM 456 123, Mishana, F72 (4, 2 fr.)
RGM 456 124, Santa Sofia, F61 (1, 5 fr.)
RGM 456 125, Villareal, F37 (1)
RGM 456 126, Los Chorros III, F23 (1)
RGM 456 107, Santa Elena II, F488 (2)
RGM 456 121, Indiana VI, F 83 (23, partially juv.)
RGM 456 122, Indiana IV, F340 (1)

Neritina ortoni
RGM 456 092, Santa Rosa de Pichana, collected from surface (5)
RGM 456 094, Tamshiyacu, collected from surface (3)
RGM 456 095, Palo Seco, collected from surface (2)
RGM 456 097, Santo Tomas/Amazonas (4)
RGM 456 099, Santa Teresa, F86 (1)
RGM 456 100, Santa Elena III, collected from surface (7)
RGM 456 102, Santa Elena III, F502 (1)
RGM 456 099, Santa Elena II, F488 (4)

Neritina etheridgei
RGM 456 108, Santa Elena II, F488 (4)
RGM 456 101, Santa Elena III, collected from surface (4)
RGM 456 096, Palo Seco, collected from surface (4)
RGM 456 093, Santa Rosa de Pichana, collected from surface (7)
RGM 456 111, Porvenir, collected from surface (4)
RGM 456 116, Porvenir XI, F727 (1)
RGM 456 098, SantoTomas/ mazonas, collected from surface (2)
RGM 456 117, San Miguel de Cochiquinas, collected from surface (2)
RGM 456 129, Macedonia, C1 (1)
RGM 456 128, San Martin, F39 (3)
RGM 456 119, Nuevo Horizonte, F70 (15)
RGM 456 127, Los Chorros I, F42 (19)
RGM 456 130 Puerto Caiman, collected from surface (9).