Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia

F.P. Wesselingh,
with contributions by L.C. Anderson & D. Kadolsky

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Frank P. Wesselingh, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands and Biology Department, University of Turku, Turku SF20014, Finland (wesselingh@naturalis.nnm.nl); Lauri C. Anderson, Department of Geology and Geophysics, Louisiana State University, Baton Rouge, LA 70803, U.S.A. (landerson@geol.lsu.edu); D. Kadolsky, 66, Heathhurst Road, Sanderstead, South Croydon, Surrey CR2 OBA, England (kadolsky@zoo.co.uk).

Key words – Mollusca, systematics, Pebas Formation, Miocene, western Amazonia.
The mollusc fauna of the Miocene Pebas Formation of Peruvian and Colombian Amazonia contains at least 158 mollusc species, 73 of which are introduced as new; 13 are described in open nomenclature. Four genera are introduced (the cochliopid genera *Feliconcha* and *Glabertryonia*, and the corbulid genera *Pachyrotunda* and *Concentricavalva*) and a *nomen novum* is introduced for one genus (*Longosoma*). A neotype is designated for *Liosoma glabra* Conrad, 1874a. The Pebas fauna is taxonomically dominated by two families, *viz*. the Cochliopidae (86 species; 54%) and Corbulidae (23 species; 15%). The fauna can be characterised as aquatic (155 species; 98%), endemic (114 species; 72%) and extinct (only four species are extant). Many of the families represented by a few species in the Pebas fauna include important ecological groups, such as indicators of marine influence (e.g., Nassariidae, one species), terrestrial settings (e.g., Acavidae, one species) and stagnant to marginally agitated freshwaters (e.g., Planorbidae, four species). Only seven species (4%) representing undisputedly elevated salinities were found, whereas 31 species (20%) are undisputed restricted to freshwater biotopes. Only three (2%) terrestrial gastropod species are known. The Pebas system experienced profuse radiations of molluscs that led to an overwhelmingly endemic fauna, typical of a long-lived lake environment. Several extant genera, which nowadays live outside Amazonia, may have originated within the Pebas system. The stratigraphic continuity of species and lineages, at least for the late Early-early Late Miocene interval (*c.* 18-9 Ma), indicates that lakes continuously occupied the system and never were entirely replaced by rivers or the sea. The rare occurrence of marine taxa indicates that the system was at sealevel and occasionally experienced marine incursions.

Contents

Introduction

Nuttall (1990) reviewed the mollusc faunas of the Pebas Formation and other non-marine Neogene inland strata of northwestern South America. For the Miocene Pebas

Formation of Peru and Colombia, and associated deposits in adjacent areas (including the 'La Tagua Beds' of southern Colombia, here considered part of the Pebas Formation), Nuttall presented a fauna of slightly over 50 species. Extensive collecting during 1991 and 1996 by the present author added much material and many new species. Many of the species proved important for ecologic (Vonhof *et al*., 1998, 2003; Wesselingh *et al*., 2002, 2006c; Kaandorp *et al*., 2006), stratigraphic (Wesselingh *et al*., 2006a, b) and biogeographic studies (Wesselingh & Macsotay, 2006a; Wesselingh & Salo, 2006). The aim of the present monograph is to document the mollusc species of the Pebas fauna. The Pebas fauna is defined here as the Miocene mollusc faunas from Amazonian and sub-Andean basins, dominated in abundance and species numbers by corbulid bivalves and cochliopid gastropods. Some of the taxa from the Early Miocene 'La Cira' fauna (MZ1) of the Colombian Magdalena and Llanos Basins are assessed here as well in order to elucidate their relationship with the Pebas fauna.

Material

Institutional abbreviations –

ANSP	Department of Mollusca, Academy of Natural Sciences, Philadelphia, U.S.A.
CAS	Department of Palaeontology, California Academy of Sciences, San Francisco, U.S.A.
BMNH	Department of Palaeontology, The Natural History Museum, London, England.
INGEMMET	Laboratorio de Paleontologia, Servicio Geologico, San Borja, Lima, Peru.
LSU	Department of Geology and Geophysics, Louisiana State University, Baton Rouge, U.S.A.
NMB	Naturhistorisches Museum Basel, Switzerland.
RGM	Division of Fossil Mollusca, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (formerly Rijksmuseum voor Geologie en Mineralogie).
RMNH	Division of Mollusca, same institution, formerly Rijksmuseum voor Natuurlijke Historie.
UNC	Departamento de la Geologia, Universidad Nacional, Bogota, Colombia.

Abbreviations –

DL	datum level of exposure (river level at date of collection in case of river exposures, surface of road in case of road exposure).
fr.	fragment.
H	height.
Hap	height of aperture, parallel to axis of the shell.
L	length.
LV	left valve.
MZ	mollusc zone (Wesselingh *et al*., 2006a).
RV	right valve.
SA	mean spiral angle (for adult specimens).
SD	semi-diameter (height of shell when viewed laterally).

All measurements are in mm. Scale bars are in mm unless stated otherwise. The scales of illustrations of details should be inferred from the overall size of the shells. The mollusc biozonation scheme is that of Wesselingh *et al*. (2006a), which explains their stratigraphic distribution.

Most of the shells were collected by F.P.W. in the Amazonas department, Colombia (1991) and the Peruvian department of Loreto (1991 and 1996; for localities see Fig. 1). The exposures are located in erosive bends of the Amazon River and its tributaries. No independent reference level or datum level can be assigned for such exposures, other than the relative position of a horizon with respect to the river level at the given date (which is given as DL). The section Santa Rosa de Pichana is a composite section, whose DL has been established by H. Vonhof and R. Kaandorp in 1998 (see Wesselingh *et al*., 2006c). The coordinates of the exposures are estimates from satellite imagery; those of a few localities (including Santa Rosa de Pichana) were checked later by colleagues using GPS and the original estimates were found to be only marginally incorrect. The newly collected material consists of over 3000 lots (Wesselingh *et al*., 2006a). Only material specifically used in the descriptions is listed. Apart from the collected material, fossils were studied in several museums, including the BMNH and the ANSP.

Genera of the Cochliopidae, Cerithioidea and Corbulidae are diagnosed and discussed extensively. Diagnoses are more extensive for available species in these groups than for newly described taxa in order to allow for useful comparison. The species in species-rich genera are ordered by morphological similarity, in order to facilitate comparison. The genera of other families are not treated in detail. Descriptions are based on material referred to as 'material studied' or 'type material'. For available species, material published by Nuttall (1990), much of which was studied by the author during a visit to the BMNH in 1993, where at the time material also was available on loan published by de Greve (1938), has been used to add to the descriptions. Type specimen data of almost all existing species has been given in Nuttall (1990). Some 80 cochliopid specimens were subjected to a SEM study of apical details. The general discussion on Cochliopidae and the section on *Longosoma* (three species) are by F.P.W. and D. Kadolsky, whereas L. Anderson and F.P.W. described *Corbula cotuhensis*.

Systematic palaeontology

Class Gastropoda
Family Neritidae Lamarck, 1809
Genus *Neritina* Lamarck, 1816

Type species – *Nerita pulligera* Linné, 1766, Recent, Indo-Pacific.

Remarks – Wesselingh (2003) discussed the (sub)generic attribution of the Pebasian neritines, but could not resolve this matter. One of the possible candidates, *Neritina* (*Fluvinerita*), is amongst others characterised by the lack of an opercular peg (Nuttall, 1990). Pebasian neritine opercula studied by Nuttall (1990) and Wesselingh (2003) were lacking the peg, a feature until now thought to be characteristic of all Pebasian neritine opercula. In the newly collected material from older stratigraphic intervals (MZ4-MZ5), opercula were recovered with a well-developed apophysis and peg (Fig.

Fig. 1a. Sampling localities. Overview of fieldwork areas in northwestern South America with localities outside the core working area indicated. The black line depicts the approximate maximum limits of the Pebas system. Background modified from www.photojournal.jpl.nasa.gov.

2) or reduced peg (Fig. 3). The recognition of such opercula makes a reconsideration of the subgeneric affinity of Pebasian neritines desirable, but as long as opercula cannot be matched unequivocally to species, discussion remains speculative. Furthermore, specimens in the new material attributed to *Neritina ortoni* were found to resemble in shell shape *Neritilia succinea* (extant in streams of Central America and the Greater Antilles). It is at the moment impossible to attribute the Pebasian neritines to subgenera and additional systematic work is needed. For description, extensive synonymy and differentiation of Pebasian neritine species, the reader is referred to Wesselingh (2003).

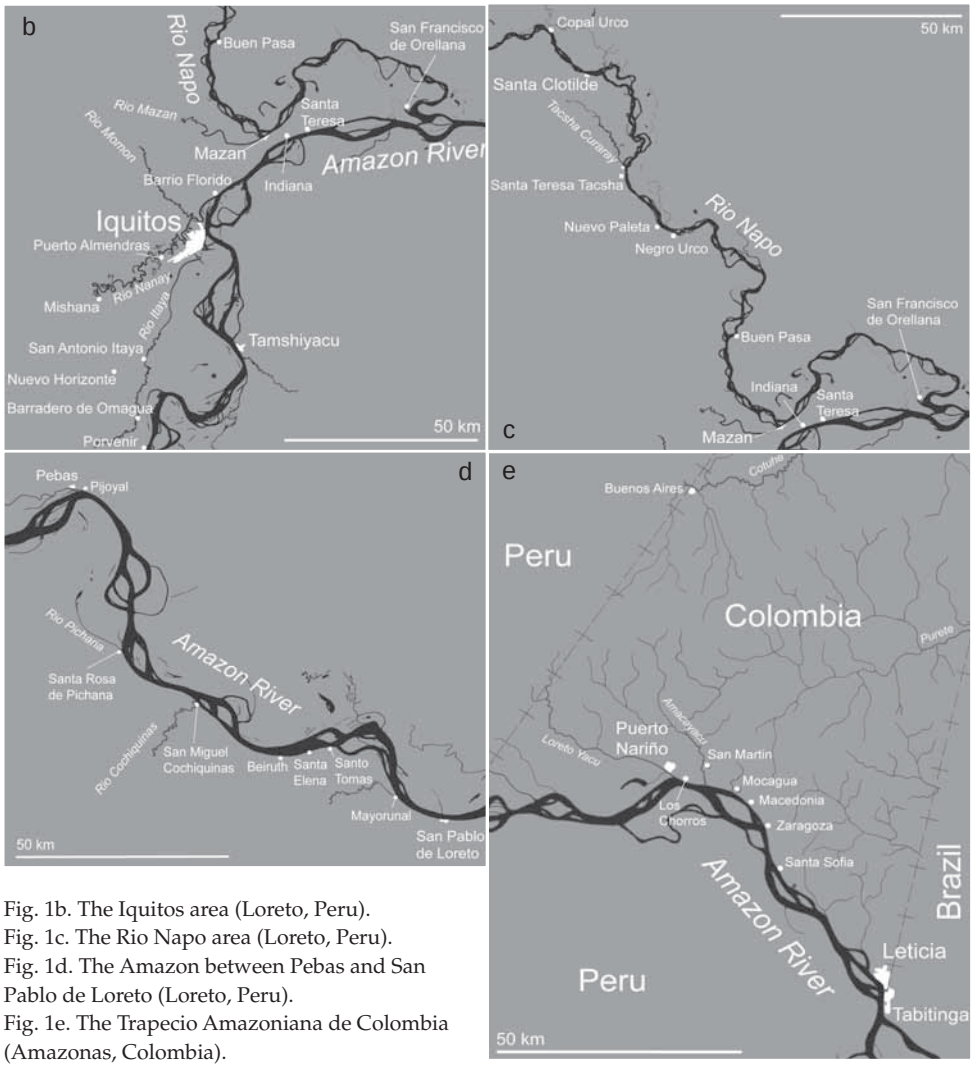


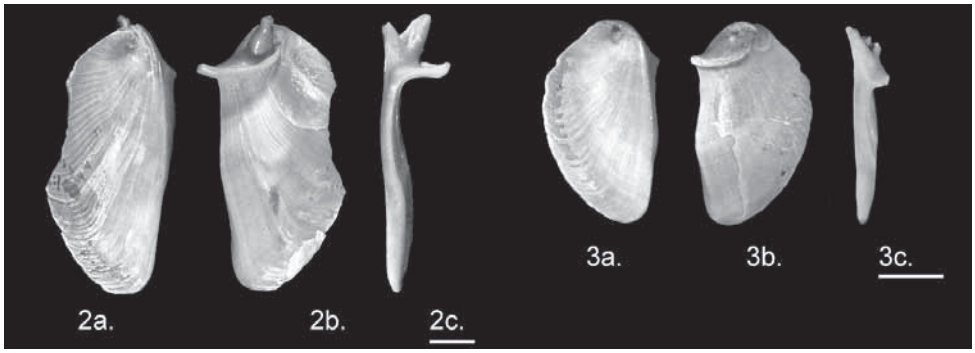
Fig. 1b. The Iquitos area (Loreto, Peru).
Fig. 1c. The Rio Napo area (Loreto, Peru).
Fig. 1d. The Amazon between Pebas and San Pablo de Loreto (Loreto, Peru).
Fig. 1e. The Trapecio Amazoniana de Colombia (Amazonas, Colombia).

Neritina ortoni Conrad, 1871

Figs. 4-7.

1871 *Neritina ortoni* Conrad, p. 195, pl. 10, figs. 5, 11.
2003 *Neritina* (?) *ortoni* Conrad; Wesselingh, p. 118, figs. 1-7.

Material studied – RGM 456 102, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 300 m west of wood mill (3°53'S 71°24'W), level F502 (0.2 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.



Figs. 2-3. *Neritina* sp. (unidentified opercula).

Fig. 2. RGM 456 352, Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S, 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. a, external surface. b, internal surface. c, lateral view.
Fig. 3. RGM 456 353, Socosani (Loreto, Peru), easternmost exposure in north bank Rio Napo, *c.* 2 km downstream confluence Rio Socosani (3°17'S 72°53'W), level F387 (1 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 19-8-1996. a, external surface. b, internal surface. c, lateral view.

Scale bars represent 1 mm.

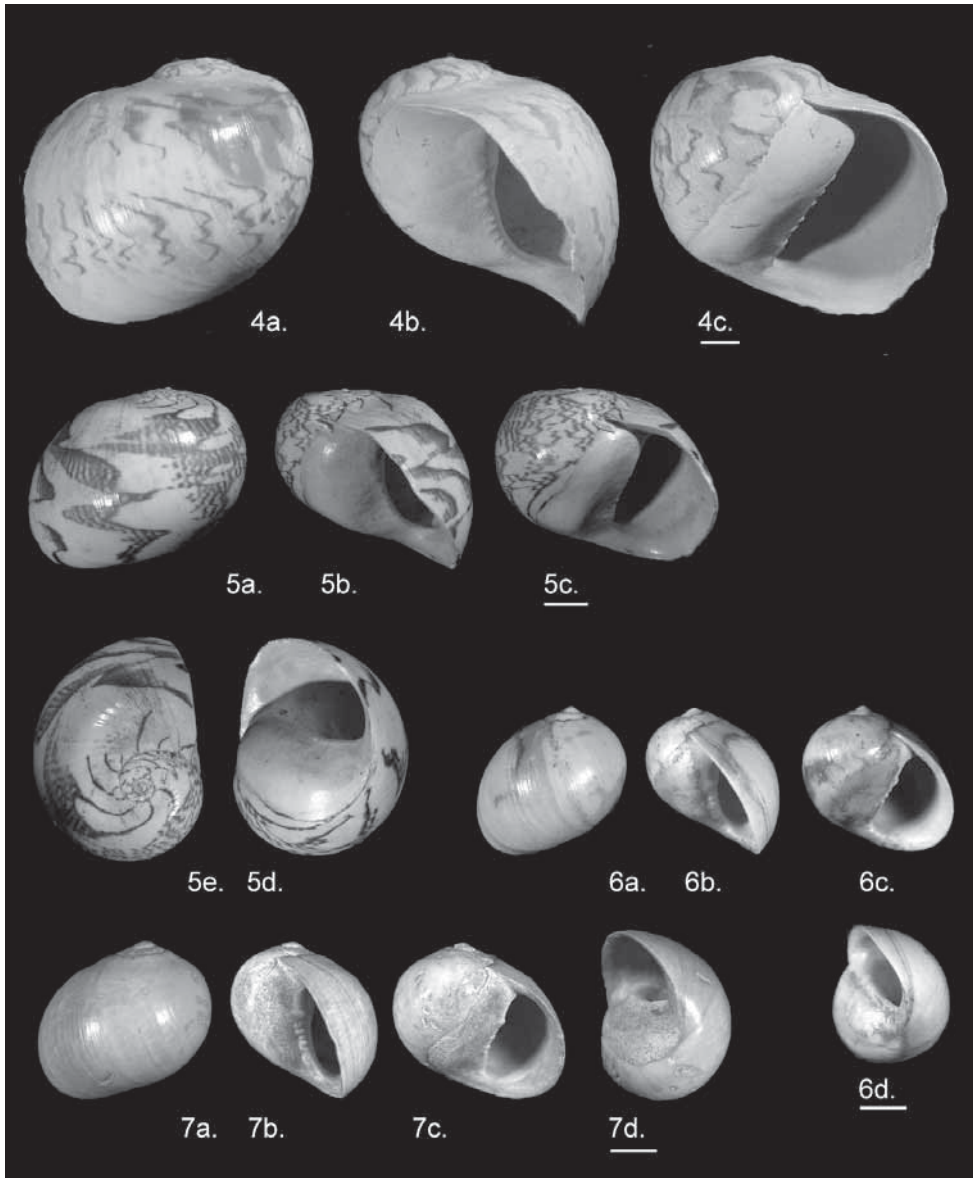
RGM 456 092, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN12, Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, below village school (3°29'S 73°00'W), level F648 (0.3 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); Leg. F.P. Wesselingh, 1-9-1996. RGM 456 354, same locality. For additional studied material, see Wesselingh (2003, p. 128).

Diagnosis – Small to large-sized, shouldered *Neritina*; shell with well-developed subsutural ridge and a marked convex body whorl perimeter; suture when viewed from above describing perfect spiral; colour patterns from efface to axial ornamented zigzag lines, often concentrated or pronounced in spiral bands; the lines bifurcate.

Dimensions – RGM 456 102: H 9.6; W 10.1; Hap 8.6; *c.* 3.2 whorls. RGM 456 092: H 15.2; W 15.5; Hap 13.6; 3.2 whorls. INGEMMET TN12: H 3.6; W 3.9; Hap 3.2; *c.* 2.8 whorls. RGM 456 354: H 3.4; W 3.2; Hap 3.0; 2.2 whorls.

Range – Pebas Formation, MZ4 - MZ9 (late Early - early Late Miocene), Peruvian Amazonia.

Remarks – Since Wesselingh (2003), new material has become available, especially from lower stratigraphic intervals (MZ4 - MZ5), within which the species is much smaller (H *c.* 3-4 mm) and exhibits a wide array of colour patterns, ranging from entirely ef-



Figs. 4-7. *Neritina ortoni* Conrad, 1871.

Fig. 4. RGM 456 092, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view. Scale bar represents 2 mm.
Fig. 5. RGM 456 102, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view. e, apical view. Scale bar represents 2 mm.
Fig. 6. INGEMMET TN12, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view. Scale bar represents 1 mm.
Fig. 7. RGM 456 354, same locality as Fig. 6. a, rear view. b, lateral view. c, front view. d, basal view. Scale bar represents 1 mm.

face to complete zigzagging patterns. Figures 6-7 illustrate typical, presumably mature specimens from these older intervals. The specimens are in general more thick-shelled and more robust than specimens treated in Wesselingh (2003). The uppermost parietal denticle in these specimens is slightly pronounced. The stratigraphically older specimens are connected through morphologically intermediate specimens to the larger forms of MZ6 - MZ8. In size and outline the older small specimens resemble extant *Neritilia succinea* (Récluz, 1841), a freshwater species from the Greater Antilles and Central America (Russel, 1941). The latter, however, lacks apertural denticulations entirely.

Neritina etheridgei Roxo, 1924

Figs. 8, 9.

1924 *Neritina etheridgei* Roxo, p. 47.
2003 *Neritina* (?) *etheridgei* Roxo; Wesselingh, p. 121, figs. 8-11.

Material studied – RGM 456 357, Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2 in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991. RGM 456 119, same locality. For additional studied material, see Wesselingh (2003, p. 128).

Diagnosis – Large-sized, almost velatiform *Neritina* with strongly inclined apertural plane and flaring outer lip; subsutural ridge indistinct; colour pattern of thin and sharp zigzagging lines that only very rarely bifurcate; when viewed from above, the suture describes a spiral, but more often it has marked angles; junction of basal and inner lip usually very sharp; inner lip callus greatly expanding (well visible from above) and irregularly thickened.

Dimensions – RGM 456 357: H 13.3; W 12.1; Hap 11.4; >1.6 whorls. RGM 456 119: H 20.6; W 21.5; Hap 18.3; >2.3 whorls.

Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.

Neritina puncta Etheridge, 1879

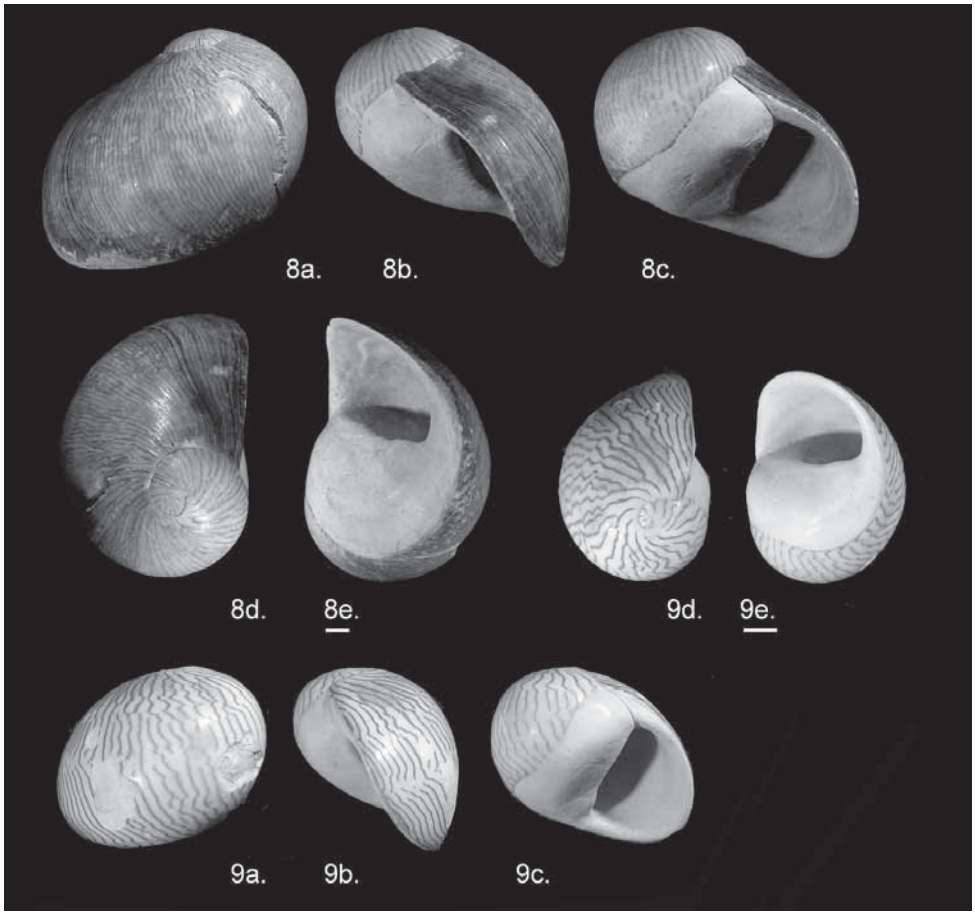
Fig. 10.

1879 *Neritina puncta* Etheridge, p. 85, pl. 7, fig. 9.
2003 *Neritina* (?) *puncta* Etheridge; Wesselingh, p. 122, figs. 18, 19.

Material studied – RGM 456 355, Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996. For additional studied material, see Wesselingh (2003, p. 128).

Diagnosis – Small, ovate, but slightly shouldered *Neritina* with a characteristic punctate colour pattern; suture, when viewed from above, describes a hooked spiral.

Dimensions – RGM 456 355: H 5.3; W 6.0; Hap 5.0; >1.1 whorls.



Figs. 8, 9. *Neritina etheridgei* Roxo, 1924.

Fig. 8. RGM 456 119, Nuevo Horizonte (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.
Fig. 9. RGM 456 357, same locality as Fig. 8. a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Scale bars represent 2 mm.

Range – Pebas Formation, MZ8 - MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Neritina roxoi de Greve, 1938

Figs. 11, 12.

1938 *Neritina roxoi* de Greve, p. 64, pl. 5. figs. 10, 11, 16.
? 1941 *Neritina pacchiana* Palmer *in* Liddle & Palmer, p. 40, pl. 9, figs. 3, 4.
2003 *Neritina* (?) *roxoi* de Greve; Wesselingh, p. 122, figs. 12, 13.

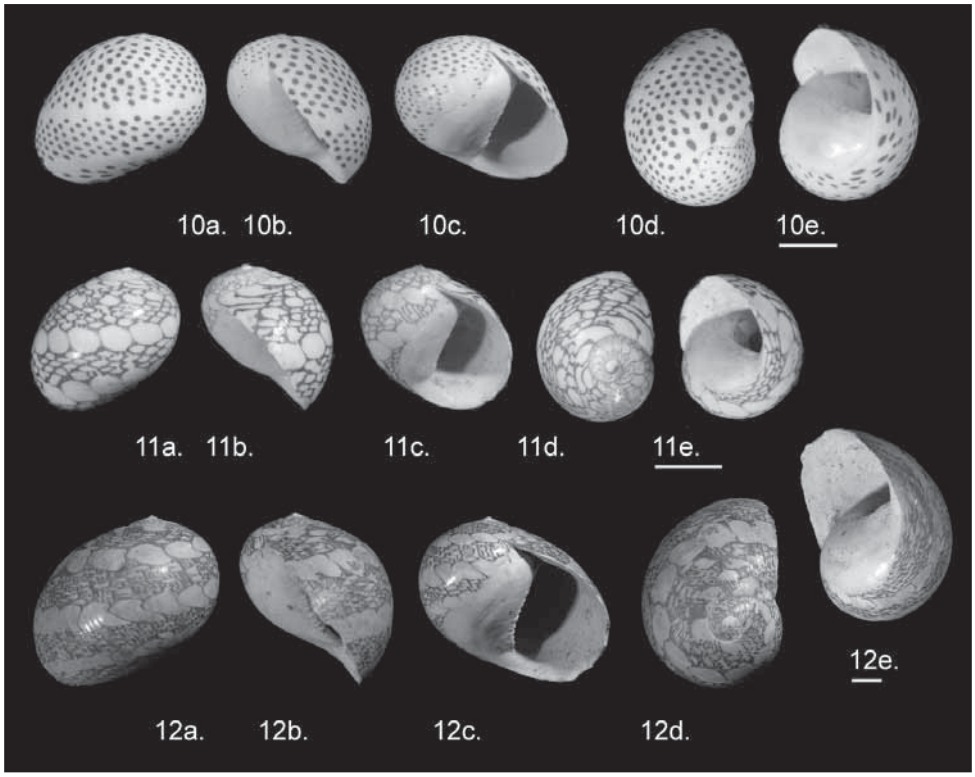


Fig. 10. *Neritina puncta* Etheridge, 1879. RGM 456 355, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Figs. 11-12. *Neritina roxoi* de Greve, 1938.

Fig. 11. RGM 456 356, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.
Fig. 12. RGM 456 107, same locality as Fig. 11. a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Scale bars represent 2 mm.

Material studied – RGM 456 356, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 107, same locality. For additional studied material, see Wesselingh (2003, p. 128).

Diagnosis – Small, ovate *Neritina* with a characteristic dark, net-like colour pattern with two or three spirally arranged zones of larger open blotches; nucleus prominent; suture when viewed from above describing a perfect spiral.

Dimensions – RGM 456 356: H 4.2 W 4.5; Hap 3.7; 2.2 whorls. RGM 456 107: H 11.3; W 12.3; Hap 10.6; 3.2 whorls.

Range – Pebas Formation, MZ5 - MZ12 (late Early - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia; Loyola (?) and Mangan formations (Middle - Late Miocene), Cuenca Basin, Ecuador.

Remarks – Neritines described as *Neritina pacchiana* Palmer, *in* Liddle & Palmer, 1941, of the Miocene Loyola and Mangan formations of the Cuenca Basin (Ecuador) have a very similar colour pattern to *Neritina roxoi*. *Neritina pacchiana* has a higher spire than the Pebasian species, although the H/W ratio of the latter may be variable. *Neritina pacchiana* is assigned, uncertainly, to *N. roxoi*.

Neritina patricknuttalli Wesselingh, 2003

Fig. 14.

2003 *Neritina* (?) *patricknuttalli* Wesselingh, p. 123, figs. 15-17.

Material studied – RGM 456 118 (paratype), Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991. For additional studied material, see Wesselingh (2003, p. 123).

Diagnosis – Small to medium-sized, ovate to slightly shouldered *Neritina*, characterised by commonly bifurcating, markedly thick zigzag lines with rounded edges that are absent or reduced in number in two or three spirally oriented zones; subsutural region straight to slightly concave; nucleus erect.

Dimensions – RGM 456 118: H 9.1; W 10.4; Hap 8.9; 2.6 whorls.

Range – Pebas Formation, MZ7 - MZ9 (Middle - early Late Miocene), Peruvian Amazonia.

Neritina elephantina Wesselingh, 2003

Fig. 13.

2003 *Neritina* (?) *elephantina* Wesselingh, p. 123, fig. 20.

Material studied – INGEMMET 4241 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 300 m west of wood mill (3°53'S 71°24'W), level F502 (0.2 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996. For additional studied material, see Wesselingh (2003, p. 123).

Diagnosis – Large, strongly shouldered *Neritina* with a markedly flaring, but rounded, outer lip; subsutural ridge well-developed, bordering a concave subsutural ramp; shell irregularly ornamented, with a surface resembling the skin of an elephant.

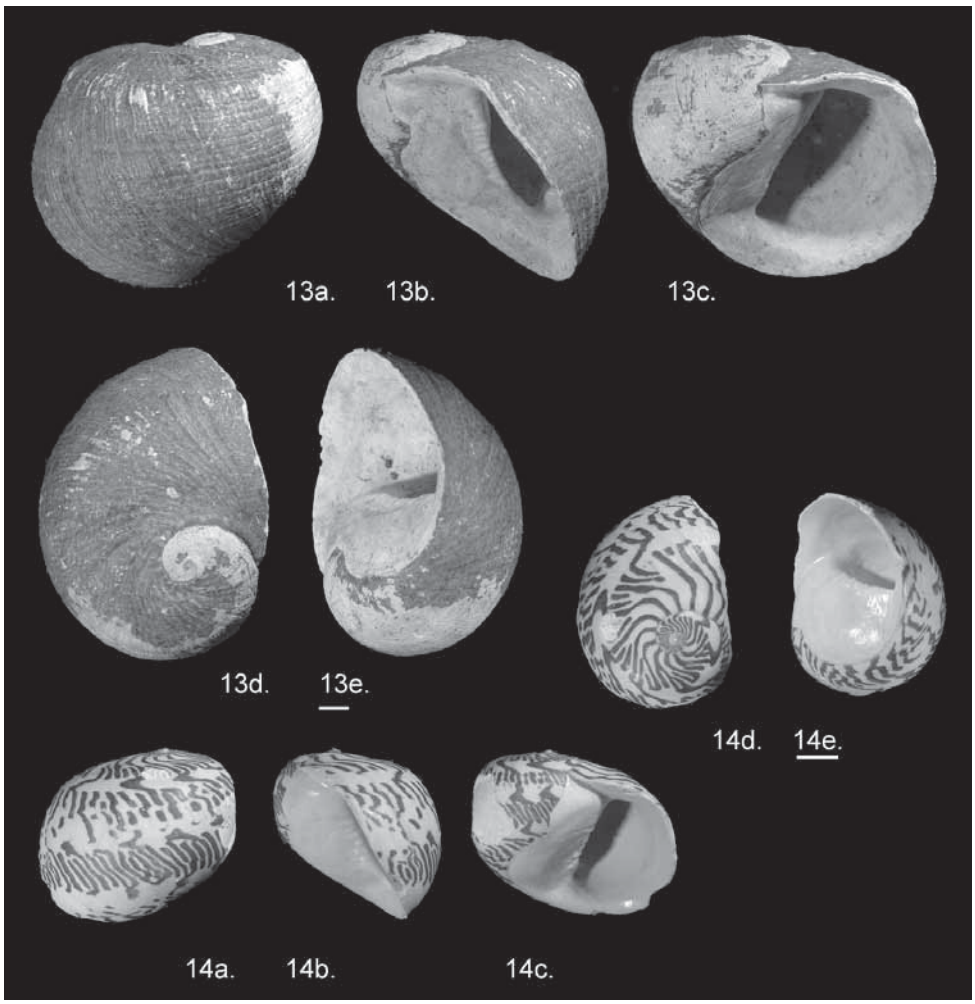
Dimensions – INGEMMET 4241: H 17.6; W 19.6; Hap 17.0; 2.7 whorls.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Family Ampullariidae Gray, 1824
Ampullariidae indet.

Material studied – RGM 456 543 (one upper part of specimen broken in three fragments, one fragment), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 300 m west of wood mill (3°53'S 71°24'W), level F502 (0.2 m above DL). Pebas Formation, *Grimsdalea* zone, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.

Description – The apex is corroded. An axial line is present at *c.* 2.2 whorls. The teleoconch is ornamented with numerous fine, wrinkled, slightly prosocline growth lines.



Just below suture, one continuous spiral groove develops, accompanied by 3-4 discontinuous grooves on a slightly depressed shoulder. The interaction with growth lines produces an irregular wrinkled reticulate to mammilate ornament on the shoulder. Below the shoulder, very shallow, barely visible spiral grooves develop. Width of broken upper part *c.* 20 mm.

Remarks – The material is too fragmentary to be properly described or attributed to a genus. Ampullariid fragments are rare in the Pebas fauna, but they are common in the Upper Miocene Solimões Formation of Brazilian Amazonia and in present-day Amazonia (Santos & Castro, 1967; Wesselingh *et al*., 2006d). Ampullariid fragments may be present in a number of samples, but are indistinguishable from pulmonate shell fragments.

Family Cochliopidae Tryon, 1866

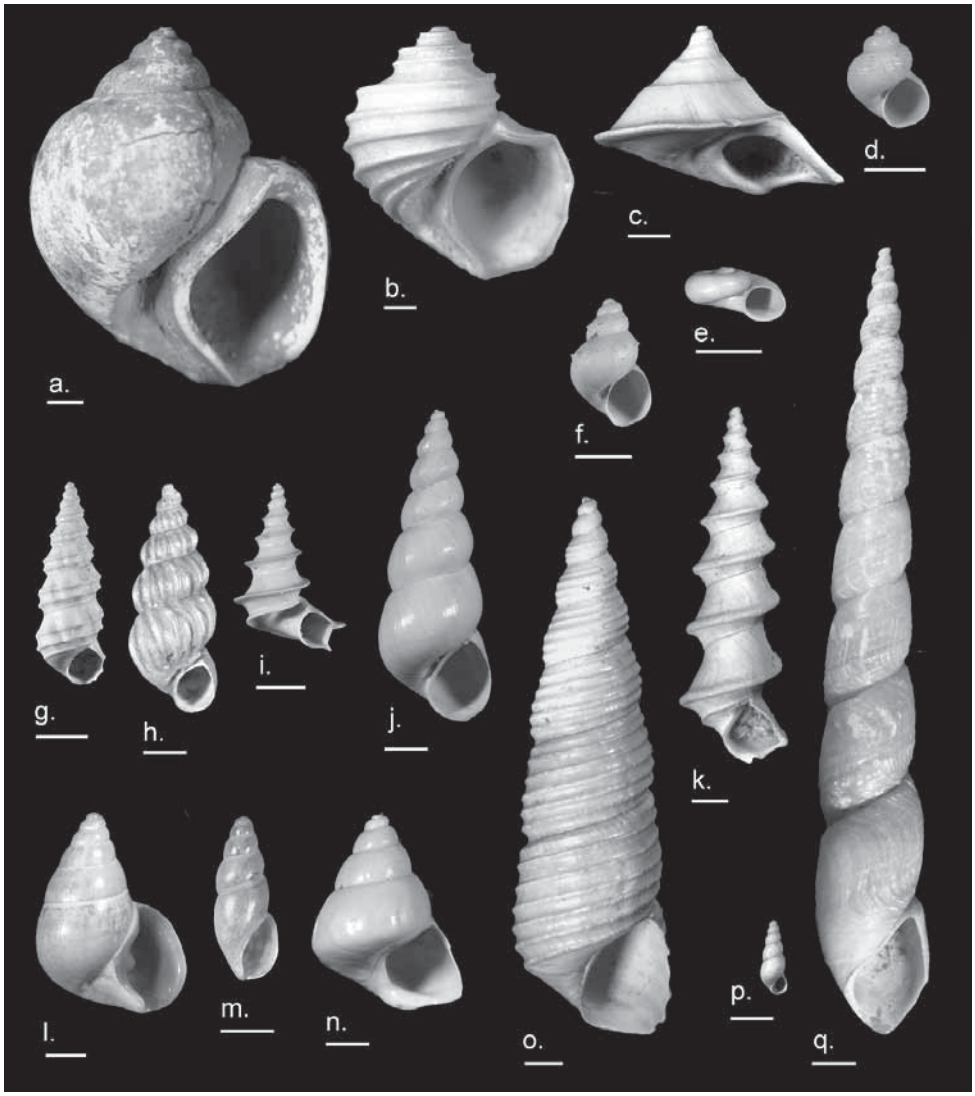
Remarks – All Pebasian rissooid snails are placed in the Cochliopidae which only recently has been elevated to the rank of family (Wilke *et al*., 2001). The Cochliopidae in the Pebas Formation contain at least 14 genera and 85 species, making it the most diverse family in the studied material; the number of species is expected to increase with further systematic treatment. The attribution of Pebasian species to cochliopid genera is fraught with difficulty. For a number of Pebasian genera, the possibility of an attribution to the Lithoglyphidae (Thiele, 1929; see discussion in Nuttall, 1990; Kadolsky, 1980) has been considered specifically (see below). The definition of the extant cochliopid genera is largely based on soft-part anatomy and shell morphological characters are often ambiguous (Hershler & Thompson, 1992; Hershler, 2001; Hershler *et al*., 1999). Furthermore, the Pebasian snails include a number of morphological characters that are unusual for non-marine Rissooidea, including Cochliopidae, and need consideration. Herein, the diagnostic aspects of the Pebasian cochliopids are discussed, the attribution of Pebasian species to genera is treated and arguments for their attribution to the Cochliopidae are provided. The reader is referred to Hershler & Thompson (1992) for authorship and type specimen data of the extant genera. Data and diagnoses on Pebasian genera are treated below.

Pebasian cochliopids include minute (H 1.5 mm) to very large (H 19.5 mm) species (compare Fig. 15p, q). The variation in shell-shapes is exuberant, including discoid, narrowly elongate, ovate conical, globose and truly conical species (Fig. 15). The suture may be adnate to deeply impressed. In some *Dyris* species, the suture on adult whorls is fissure-like (Fig. 15u). The teleoconch ornament includes a broad variety of axial and spiral ornament types (occasionally producing reticulate ornament), knobs, rarely

◀ Figs. 13. *Neritina elephantina* Wesselingh, 2003. INGEMMET 4241, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

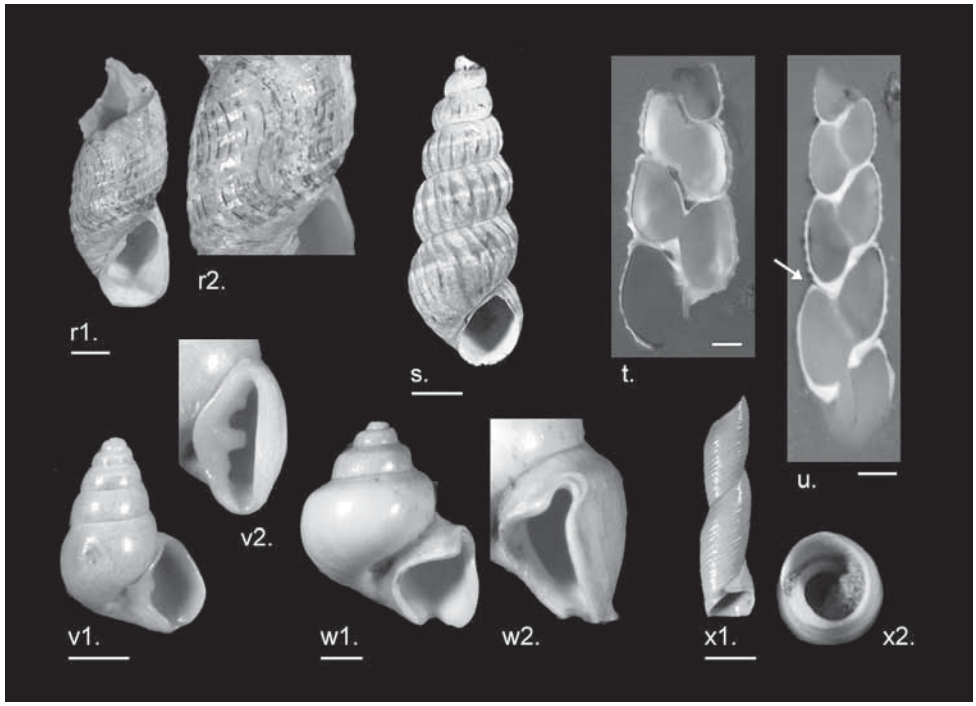
Figs. 14. *Neritina patricknuttalli* Wesselingh, 2003. RGM 456 118, paratype, Nuevo Horizonte (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Scale bars represent 2 mm.



Figs. 15a-x. Examples of the variety of shell-shape and ornamentation as well as unusual morphological characters in Pebasian cochliopid snails.

a, *Sioliella ovata* Wesselingh, 2000. RGM 445 336, holotype, Mocagua (Amazonas, Colombia). Large naticiform shell with pronounced basal apertural siphonal retraction. b, *Sioliella bella* (Conrad *in* Woodward, 1871). RGM 456 326, Santa Rosa de Pichana (Loreto, Peru). Strongly ribbed naticiform shell with flaring outerlip and a well-developed deep umbilicus. c, *Tropidebora tertiana* (Conrad, 1874a). INGEMMET TN07, San Miguel de Cochiquinas (Loreto, Peru). Depressed conical shell resembling that of the unrelated marine genus *Calliostoma*. d, *Onobops microconvexus* sp. nov. INGEMMET TN62, holotype, Santa Elena (Loreto, Peru). Very small globose, spirally ribbed shell. e, *Cochliopina*? *hauxwelli* (Nuttall, 1990). RGM 456 523, Copal Urco, (Loreto, Peru). Planorbiform shell. f, *Pyrgophorus* sp. INGEMMET TN43, Santa Elena (Loreto, Peru). Shell with small spines. g, *Tryonia scalarioides tuberculata* (de Greve, 1938). RGM 456 440, Tamshiyacu (Loreto, Peru). Tuberculate shell. h, *Tryonia nuttalli* sp. nov. INGEMMET TN71, paratype, Mishana (Loreto,



Peru). Turbonilliform shell with pronounced axial ribs. i, *Feliconcha feliconcha* sp. nov. INGEMMET TN63, holotype, Santo Tomas Amazon (Loreto, Peru). Shell with pronounced median carina. Note the detachment of the last part of the body whorl. j, *Dyris ortoni* (Gabb, 1869). RGM 456 418, Tamshiyacu (Loreto, Peru). Large, smooth, hydrobiiform shell. k, *Dyris carinatus* sp. nov. RGM 456 397, paratype, Porvenir (Loreto, Peru). Shell with strong median keel. l, *Toxosoma denticulatum* sp. nov. RGM 456 348, holotype, Porvenir (Loreto, Peru). Robust hydrobiiform shell with strong apertural denticles. Note the slight torsion of the apertural plane upward. m, *Longosoma curtum* (Conrad, 1874a). RGM 456 590, neotype, Santa Rosa de Pichana (Loreto, Peru). Elongate, smooth, almost spindle-shaped shell. n, *Littoridina conica* sp. nov. INGEMMET TN19, holotype, Santa Elena (Loreto, Peru). Smooth, conical shell. o, *Dyris bicarinatus sofiaensis* subsp. nov. RGM 456 632, holotype, Santa Sofia (Amazonas, Colombia). Large, rather straight-sided turritelliform shell. p, *Onobops minissimus* sp. nov. RGM 456 578, paratype, Santo Tomas Amazon (Loreto, Peru), one of the smallest Pebasian cochliopids. q, *Dyris elongatus* sp. nov. RGM 456 402, holotype, Santa Sofia (Amazonas, Colombia). The tallest Pebasian cochliopid. r, *Dyris elongatus* sp. nov. RGM 456 404, paratype, Santa Sofia (Amazonas, Colombia). Note the black collabral periostracal bands overlying light olive-brown periostracum. s, *Tryonia nuttalli* sp. nov. RGM 456 542, paratype, Mishana (Loreto, Peru). Note the spiral colour bands on the shell. t, *Dyris bicarinatus sofiaensis* subsp. nov. RGM 456 634, paratype, Santa Sofia (Amazonas, Colombia). Cross-section that shows the open coiling of the columella that itself is an open tube. u, *Dyris elongatus* sp. nov. RGM 456 635, paratype, Santa Sofia (Amazonas, Colombia). Cross-section that shows the open coiling of the columella. The suture is a fissure that extends from the exterior of the shell way into the columella (marginally visible at arrow). v, *Toxosoma eboreum* Conrad, 1874a. INGEMMET TN11, San Francisco (Loreto, Peru). Detail of the columellar folding resulting in apertural denticles. w, *Sioliella bisiphonata* sp. nov. INGEMMET TN02, paratype, Indiana (Loreto, Peru). Detail of siphonal structures at apertural base and the junction between the outerlip and parietal margin. x, *Dyris acicularis* sp. nov. RGM 456 569, paratype, Santo Tomas (Loreto, Peru). Specimen that has a widely openly coiled columella effectively leading to a tube-like shell.

Scale bars represent 1 mm.

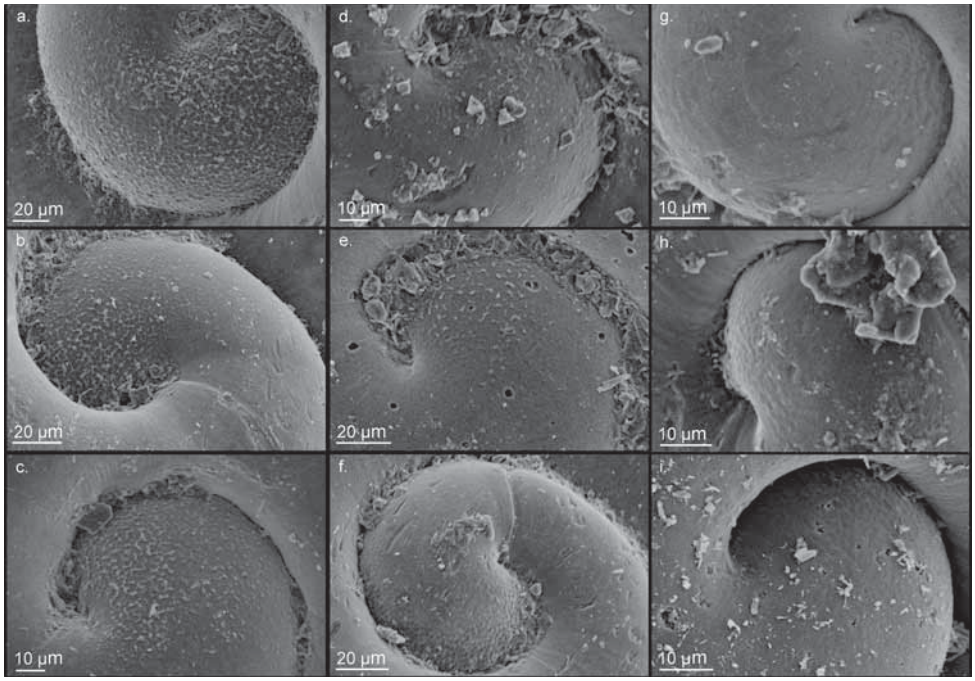
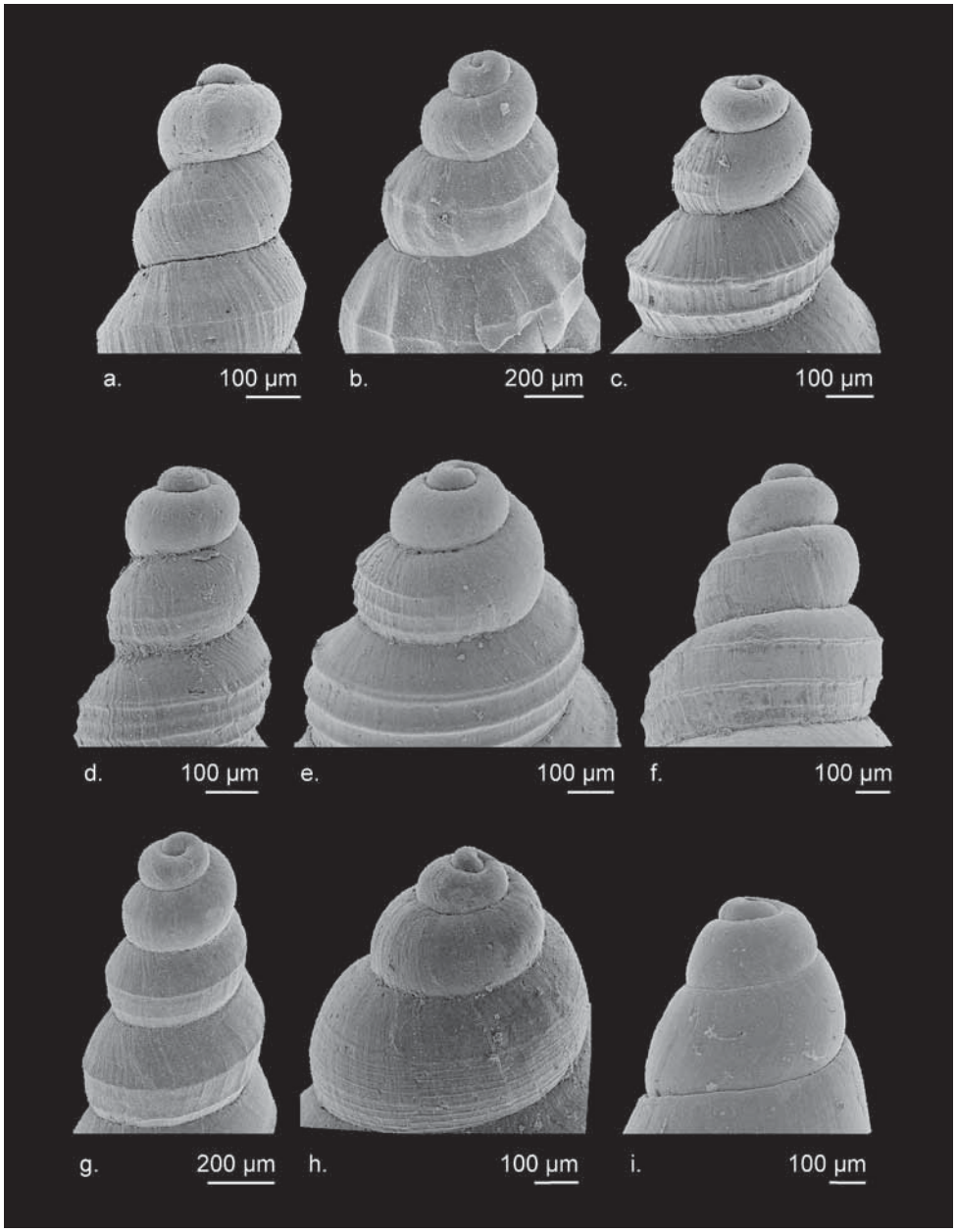


Fig. 16. Embryonic shell ornamentation types on Pebasian cochliopid taxa.

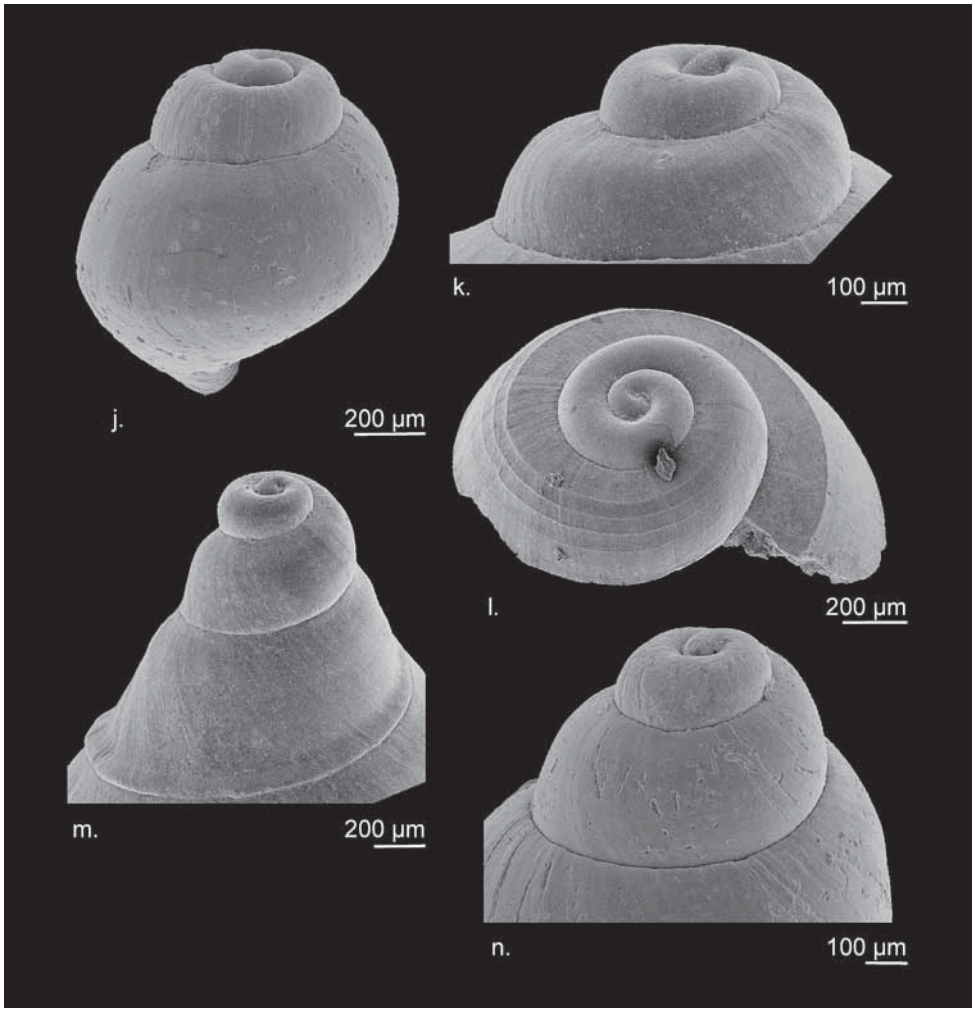
a, *Sioliella kadolskyi* sp. nov. RGM 456 615, paratype, Copal Urco (Loreto, Peru). Broadly honeycomb ornament, breaking apart into pustules away from the tip of the nucleus. b, *Sioliella fusiformis* sp. nov. RGM 456 614, paratype, Santa Elena (Loreto, Peru). Honeycomb ornament at tip, breaking apart into pustules away from the tip before fading. c, *Sioliella kadolskyi* sp. nov. RGM 456 616, paratype, Boca Momon (Loreto, Peru). Discontinuous honeycomb ornament at tip, breaking apart into pustules away from the tip before fading. d, *Toxosoma contortum* sp. nov. RGM 456 611, paratype, Porvenir (Loreto, Peru). Fine, sharp pustules at tip. e, *Littoridina pebasana* (Conrad, 1874a). RGM 456 613, Santa Elena (Loreto, Peru). Discontinuous honeycomb ornament at tip, breaking apart into pustules away from the tip before fading. f, *Cochliopina*? *bourguyi* (Roxo, 1924). RGM 456 610, Porvenir (Loreto, Peru). Low honeycomb ornament at tip. g, *Onobops elongoides* sp. nov. RGM 456 617, paratype, Iquitos (Loreto, Peru). Low malleate ornament at tip. h, *Dyris microturritella* sp. nov. RGM 456 609, paratype, Porvenir (Loreto, Peru). Low mammilate ornament at tip. i, *Dyris hauxwelli* Nuttall, 1990. RGM 456 612, Nueva Paleta (Loreto, Peru). Low malleate ornament at tip.

Fig. 17. Protoconch types of Pebasian cochliopid taxa. ▶

a, *Feliconcha feliconcha* sp. nov. RGM 456 618, paratype, Porvenir (Loreto, Peru). Gradual onset of median keel after protoconch - teleoconch (p-t) boundary demarcated by a very fine axial line at the right side of the second whorl. b, *Tryonia nuttalli* sp. nov. RGM 456 619, paratype, Nuevo Paleta (Loreto, Peru). Nucleus strongly inclined, p-t boundary demarcated by fine axial line with gradual onset of median keel afterwards. c, *Dyris carinatus* sp. nov. RGM 456 620, paratype, Porvenir (Loreto, Peru). The p-t boundary is clearly demarcated by an axial riblet; onset of two spiral ribs with pronounced subsutural ramp above almost immediately afterwards. d, *Dyris microturritella* sp. nov. RGM 456 621, paratype, Porvenir (Loreto, Peru). The p-t boundary is formed by fine axial line at the very right side of the second whorl with onset of two spiral ribs soon afterwards, followed by the gradual onset of a third upper rib bounding the



subsutural ramp. e, *Dyris romeroi* sp. nov. RGM 456 623, paratype, Porvenir (Loreto, Peru). Thin axial lineament demarcating the p-t boundary with almost instantaneous onset of three spiral ribs and pronounced subsutural ramp afterwards. f, *Onobops elongoides* sp. nov. RGM 456 622, paratype, Iquitos (Loreto, Peru). Barely visible, slightly prosocline axial lineament (right part second whorl) demarcates the p-t boundary; gradual onset of upper spiral rib, followed within 0.2 whorls by lower rib. g, *Onobops? bisulcatus* sp. nov. RGM 456 624, Buen Pasa (Loreto, Peru). Thin lineament at the extreme right margin of second whorl demarcates the p-t boundary, with very gradual onset of low median keel 0.2 whorls



afterwards. h, *Onobops communis* sp. nov. RGM 456 625, paratype, Porvenir (Loreto, Peru). Bulbous shell with strongly inclined nucleus. The p-t boundary is barely visible at the rightmost side of the second whorl. Note that on the lower half of the lower whorl thin spirals appear to be draped over the shell. i, *Longosoma curtum (*Conrad, 1874a). RGM 456 626, Santa Elena (Loreto, Peru). Smooth conical apex with a flat top. Protoconch-teleoconch boundary not visible. j, *Toxosoma contortum* sp. nov. RGM 456 627, paratype, Porvenir (Loreto, Peru). Wide, smooth apex, with flat top. The embryonic shell is separated from protoconch-2 by axial depression. A very poorly visible line at one quarter from the left margin of the second whorl presumably marks the protoconch-teleoconch boundary. k, *Sioliella kadolskyi* sp. nov. RGM 456 615, paratype, Copal Urco (Loreto, Peru). Strongly intorted embryonic shell separated by clear axial lineament from protoconch-2. l, *Tropidebora*? *conica* sp. nov. RGM 456 628, paratype, Santa Elena (Loreto, Peru). Flat, planispiral apex; a thin axial lineament at 1.7 whorls marks the p-t boundary; instantaneous onset of five thin, regularly spaced spirals, the upper one of which bounds the broad and flat subsutural ramp. m, *Littoridina pebasana* (Conrad, 1874a). RGM 456 618, Santa Elena (Loreto, Peru). A very thin line at the rightmost part of the second whorl marks the p-t boundary. n, *Littoridina crassa* (Etheridge, 1879). RGM 456 630, Porvenir (Loreto, Peru). Broadly conical apex with slightly inclined nucleus; a p-t boundary is not visibly developed.

spines (in *Pyrgophorus*) and commonly smooth shells (Fig. 15). Spiral rib types include thin, slightly irregular spiral threads that appear to be draped over the shell (common in *Onobops*; Fig. 17h), to broad and massive ribs that 'make' and 'shape' the shells in various other genera (e.g., Figs. 15b, g-i, k, 17a-g). In many genera, a subsutural ramp is prominently developed. Growth lines are most commonly prosocline, but can be orthocline and are rarely opisthocline. A thick, olive-brown periostracum has been found on a number of *Dyris*, *Tryonia* and *Onobops* samples. In *Dyris elongatus*, black collabral alignments overlay the brownish periostracum in specimens of one sample (Fig. 15r). In one sample of *Tryonia nuttalli*, spirally arranged colour bands were found in the shell that are presumably the result of diagenetic imprint of (formerly overlying) pigmented periostracum (Fig. 15s). This colour patterning resembles that of the Mexican cochliopid genus *Mexipyrgus* Taylor, 1966.

A well-expressed protoconch-1 - protoconch-2 - teleoconch succession is present in almost all Pebasian species, but can be hard to recognise in the smooth species. The protoconch-1 (= embryonic shell) is usually inclined, often tilted. The nucleus has a diameter typically between 30 and 80 µm. Ornamentation on the embryonic shell is usually restricted to the margins and the tip of the nucleus, and includes very fine wrinkles, mammillae, malleations, and sharp, low and small triangular nodules, as well as honeycomb patterns (Fig. 16). Although some variation exists, the protoconch-2 is usually smooth (apart for few extremely thin growth lines) and has a convex to bulbous whorl profile with a (deeply) impressed suture (Fig. 17). The protoconch-teleoconch boundary is variably developed, from clearly demarcated by an axial lineament in *Dyris* to poorly recognizable in *Tryonia,* and in smooth-shelled *Sioliella* and *Toxosoma* species.

The presence of a short protoconch-1 in Pebasian cochliopids, with a variety of thin and low, marginally located irregular wrinkles suggests a lecitotrophic development. The length of the protoconch-2 in, for example, some of the *Dyris* and *Onobops*? species over 1.5 whorls suggests that these may have had a planktotrophic phase after hatching. A planktotrophic stage would explain the geographically widespread occurrence of identical shells of cochliopid species within single biozones in the Pebas Formation (Wesselingh *et al*., 2006a).

The onset of teleoconch ornament (in sculptured species) starts with densely spaced, fine growth lines or low axial folds and is followed by the development of spiral elements within 0.5 whorls after the protoconch-teleoconch boundary. In *Dyris* (Fig. 17c-e), two to three spirals set in typically almost near-simultaneously. In many of the *Onobops* species, spirals are added apparently randomly throughout the shell (Fig. 17h; see also Nuttall, 1990, fig. 54b, c). In *Tropidebora*? *conica*, five delicate, regularly spaced spirals develop immediately at the protoconch-teleoconch boundary (Fig. 17l) that disappear within a whorl.

The parietal apertural margin of Pebasian cochliopids is usually adnate, but the aperture in various groups is commonly detached (especially in *Tryonia* and *Feliconcha*). The largest detachment concerns the last 0.3 whorls in some *Feliconcha feliconcha* specimens (Fig. 15i). Other species have broadly adnate apertures. The apertural plane is most commonly straight to slightly inclined. In some taxa, such as in *Tropidebora tertiana*, the apertural plane is tilted downward. In some *Toxosoma* and *Longosoma* species, on the other hand, the apertural plane is somewhat curved upward. The apertural margins are commonly thin or slightly thickened only; no varices are found in the Pebasian cochliopids.

Apertural modifications exist in the form of a basal siphonal retraction in *Sioliella, Tropidebora, Lithococcus, Longosoma* and *Toxosoma,* upper apertural retractions are found in *Toxosoma* and especially well pronounced in some *Sioliella* species (e.g., Fig. 15w).

Open, corkscrew-like coiling of the columella is found in various *Dyris* species, and is also seen in *Longosoma* and some *Toxosoma*. A columellar fold is known from *Toxosoma, Longosoma, Littoridina* and at least one *Dyris* species. In *Toxosoma* up to three denticle-like modifications can be present on the inner lip and up to two additional ones inside the outer lip (Fig. 15v). The columellar fold develops on the columella of juvenile shells and remains present throughout growth. Pebasian cochliopids include imperforate, rimately umbilicate and broadly umbilicate shells.

Wesselingh (2000) transferred Pebasian naticiform to conical gastropods classified by Kadolsky (1980) and Nuttall (1990) as *Eubora* Kadolsky, 1980, to the extant Amazonian *Sioliella*, based on the general shell-shape, as well as the spiral micro-ornament. However, extant *Sioliella effusa* has a basal apertural projection instead of a siphonal notch, which has led D.K. to question the attribution of the Pebasian gastropods to *Sioliella*. A single species, *S. saloi*, tends to develop a sort of basal projection, similar to that of *S. effusa*. However, the former has a clear siphonal retraction developed at the junction of the basal and outer lip, lacking in *S. effusa*. The combination of the globose shell shape and the fine, slightly divergent spiral microsculpture in *S. effusa* (the latter also seen in subadult specimens of *S. ovata*) favours attribution of these Pebasian taxa, considered by Kadolsky as *Eubora*, to *Sioliella*, but the argument is circumstantial and further research into this matter is needed.

The record of *Lithococcus* in the Pebas fauna is new, but also open to further scrutiny. The attribution is based on resemblance between the Pebasian and extant species in the general shell habitus, including the depressed conical nature, relatively thick shell and spiral ornament that tends to be undulating. However, the broad basal apertural retraction of Pebasian *Lithococcus* (and *Sioliella*) is unknown from living cochliopids (including extant *Lithococcus*). In Pebasian *Lithococcus*, this retraction becomes more pronounced in successive stratigraphic intervals, suggesting that it may derive from an ancestor with an entire apertural base, similar to modern *Lithococcus*. Pebasian *Lithococcus* resembles Pebasian *Sioliella* in shell shape, ornamentation and apertural characteristics, suggesting a close relationship.

The apertural modifications ('siphons') are best developed in *Sioliella*, where the lower siphon may be deep and well entrenched into slightly thickened margins. A similarly pronounced upper siphon may also be present. Functionally, such retractions are attributed to modification of inhalant and exhalant water currents of larger snails living in/on soft bottoms. By channelling water circulation through siphons, snails are able to process large amounts of water without stirring sediments into the inhalant water currents (Gorthner, 1992). Shell modifications for siphons are common in a range of marine gastropod families and independently developed in some freshwater cerithioideans (Gorthner, 1992), but almost entirely unknown in rissooid snails.

The assignment of four Pebasian species to *Littoridina* is with some hesitation and open to further scrutiny. Various cochliopids with smooth conical shells exist, including *Heleobia*, *Heleobops* and *Littoridinops*. However, the Pebasian snails have rather strong shells and in general a depressed conical outline comparable to those of a number of extant *Littoridina* species. The three aforementioned genera have generally thinner shells that are ovate conical rather than conical.

The distinction between Pebasian *Dyris* and Pebasian *Tryonia* is straightforward in most of the Pebas Formation, but not so in older stratigraphic intervals. Pebasian *Tryonia* species are characterised by the gradual development of one or two low and rounded keels or thin spiral ribs that are draped over the shell, far after the protoconch-teleoconch boundary. In subsequent whorls, axial ribs replace these as the predominant type of ornament. Spirals usually disappear and the subsutural ramp is in general less developed than in *Dyris*. However, in older (MZ2-MZ4) *Tryonia* species such as *T. semituberculata*, the onset of the spiral ornament is identical to that of *Dyris* (with almost simultaneous development of two robust spirals after the protoconch-teleoconch boundary). This implies that either the generic differentiation should be reconsidered or that *Tryonia* in the Pebas Formation diverges from a *Dyris*-like ancestor. Miocene records for *Tryonia* exist from North America (R. Hershler, pers. comm.) and northern Venezuela (Wesselingh & Macsotay, 2006b). The Early Miocene Venezuelan species, *T. vivasi* Wesselingh & Macsotay, 2006b, yields specimens with a typical Pebasian *Tryonia* protoconch, others with a typical *Dyris* protoconch and some that appear intermediate. If the North American records would predate the Pebasian *Tryonia* records (which is currently unclear), the Pebasian axially ornamented gastropods are convergent with *Tryonia* and should be attributed either to *Dyris* or a new genus. With all these uncertainties, I have maintained the name *Tryonia* for the axially ribbed species for the moment.

The distinction between *Onobops* and *Dyris* in most of the Pebas Formation similarly seems pretty straightforward. The rapid development of two to three robust spirals after the protoconch-teleoconch boundary is typical for *Dyris* species. Spiral ribs in Pebasian *Onobops* may occur almost instantaneously at the boundary, but usually develop long after the boundary, are thin and appear in random order. In *O. elongoides*, the oldest putative Pebasian *Onobops* species, a change of a *Dyris*-type of ornamentation towards the *Onobops* type is seen in successive stratigraphic intervals (MZ4-MZ6), suggesting a derivation from *Dyris*. Extensive documentation of intermediate series, as well as improved insights into the generic identity of equally old *Onobops*? *bisulcatus* will be necessary in order to confirm such a relationship. The Pebasian records of *Onobops* are the first outside the coastal marshes of the North American Atlantic and Gulf regions. The generic attribution of the Pebasian shells is based on the almost identical habitus of Pebasian *Onobops communis* (especially from the younger stratigraphic intervals) and extant *Onobops* species, such as *O. jacksoni* (Bartsch, 1953; see Hershler & Thompson, 1992, fig. 53a). The species have very similar ovate conic shells with fine spiral threads that occur at random and are draped over the shell. The shape of the aperture is almost identical, with the basal part of the columellar lip being at or even slightly to the left of the shells axis. The embryonic shell of extant *O. jacksoni* develops a remarkable spirally ornamented surface (Davis & McKee, 1989, fig. 5e, g) that becomes lost from the apex in later stages. The resulting embryonic shell (Davis & McKee, 1989, fig. 5h) has a broadly malleate ornament, very similar as those seen in Pebasian *Onobops* specimens.

The clear columellar fold, typical of *Toxosoma* and *Longosoma*, is documented herein for *Dyris denticulatus*, but otherwise unknown in the Cochliopidae (in Pebasian *Littoridina crassa* and *L. pebasana* it is very low and broad). *Dyris denticulatus* shows a distinct change of a ribbed morphology on the early teleoconch towards a smooth, thick-shelled body whorl with relatively rounded whorls, similar to the general whorl architecture of various *Toxosoma* species. *Dyris denticulatus* occurs in lower part (MZ2, late Early - early

Middle Miocene) of the Pebas Formation and stratigraphically precedes any known *Toxosoma* species. It might, therefore, be a transitional form between both genera. In that scenario, *Toxosoma* (and the possibly closely related *Longosoma*) must have developed more elaborate denticulations and a siphonal notch during the successive MZ3 interval, as both genera are well represented and fully developed in MZ4 interval samples in the Pebas Formation. Additional study of material from the intervening MZ3 is required to confirm the suggested derivation of *Toxosoma* from *Dyris*.

A number of *Dyris* species contain an openly coiled (corkscrew-like) columella. In one species, *Dyris acicularis*, this has led to a nearly tube-like shell (Fig. 15x). Tube-like shells occur in the cochliopid subterranean genus *Phreatoceras* Hershler & Longley, 1987b. The tube-like appearance of the latter snails is, however, the result of uncoiling instead of twisting of the columella. Uncoiling of the later part of the body whorl has been seen in a number of *Dyris*, *Tryonia* and *Feliconcha* species, but is usually limited to the very last part of the body whorl. The most extreme uncoiling has been found in *Feliconcha feliconcha*, where up to the last 0.3 whorls are detached and produced.

The attribution of four Pebasian cochliopid species to *Cochliopina*? follows a suggestion made by Fukuda & Ponder (2003). Originally, these species were all attributed to *Nanivitrea* Thiele, 1927, based on general shell shape. Fukuda & Ponder (2003) classified *Nanivitrea* questionably in the Assimineidae, as did Thiele (1927). The shell Thiele (1927) identified as *Nanivitrea helicoides* Gundlach *in* Poey, 1865 (*op. cit*. Nuttall, 1990, p. 212) and designated as type species is, according to Fukuda & Ponder (2003), not identical with Poey's species. As anatomical and molecular genetic data are not known for either Poey's or Thiele's species, their relation is at present uncertain. The original habitat of Poey's material is similar to that of assimineid snails, "on moist ground near the seashore, accompanied by ellobiids; not submerged but deeply hidden under fallen leaves in moist places" (Poey, 1865, p. 70, as *Paludinella helicoides* from near Cárdenas, Cuba).

Extant *Cochliopina* has generally spirally ribbed shells. No traces are seen of spirals in the Pebasian shells (apart for internal spiral structures that became exposed in an abraded part of a protoconch of Nuttall's *Nanivitrea colombiana* Nuttall, 1990, fig. 158b, c therein). The attribution of the Pebasian species to *Cochliopina* is thus open to further scrutiny.

In the recent fauna of South American hydrobioids, three families are recognized:

a. Lithoglyphidae with the only genus *Potamolithus* Pilsbry, 1896, in the Parana drainage (Davis & Pons da Silva, 1984);
b. Pomatiopsidae with the genus *Idiopyrgus* Pilsbry, 1911 (synonyms *Hyalacme* Haas, 1938, and *Aquidauania* Davis, 1979) in Brazil; and
c. Cochliopidae with the genera *Aroapyrgus* Baker, 1931, *Cochliopina* Morrison, 1946, *Heleobia* Stimpson, 1865, *Lithococcus* Pilsbry, 1911, *Littoridina* Souleyet, 1852 and *Pyrgophorus* Ancey, 1888.

Similarities in habitus between *Potamolithus* and the Pebasian *Sioliella* have led Kadolsky (1980) and Nuttall (1990) to consider placing the latter (referred by them to as *Eubora*) in the Lithoglyphidae, which was then treated as a subfamily of Hydrobiidae. Within some of the *Potamolithus* species from southern South America, as illustrated in Pilsbry (1911), Pons da Silva & Davis (1983), Davis & Pons da Silva (1984) and Nuttall (1990), shallow, siphon-like basal apertural notches exist that resemble those of Pebasian *Sioliella*, *Tropidebora*, *Lithococcus*, *Toxosoma* and *Longosoma*, but are usually weaker

developed and hardly perceptible in some species. In one species (*Potamolithus filiponei* von Ihering, 1910), rather well defined incisions exist both at the apertural base and at the top of the outer lip. If the occurrence of a siphonal notch in the Pebasian genera is an apomorphy, all of these genera could be placed in the Lithoglyphidae. Many lithoglyphid genera, including South American *Potamolithus,* contain species with irregularly thickened shells, a feature that is lacking in extant cochliopids as well as in the Pebasian snails. The protoconch microsculpture is distinctly spiral in several North American genera of the Lithoglyphidae (Thompson, 1984; Hershler, 1989; Hershler & Frest, 1996). The only exception is the genus *Phreatodrobia* in which it is malleate (Hershler & Longley 1987a; attribution to Lithoglyphidae by Hershler *et al.,* 2003). Unfortunately, the protoconch microsculpture of South American *Potamolithus* is unknown. As the protoconch microsculpture of the Pebasian taxa is markedly different from the microsculpture of Lithoglyphidae as known to date, there is no reason to assume any Pebasian taxa belong to this family.

The shells of the only pomatiopsid genus in South America, *Idiopyrgus*, are elongate, smooth and have a strongly curved, inverted 'S'-shaped outer lip when viewed from the side. The microsculpture of the protoconch is unknown and is also very incompletely known of the other (non South American) genera in this family. None of the Pebasian taxa shows an obvious similarity with *Idiopyrgus*. For the moment there are no pervasive arguments to attribute any of the Pebasian genera to the Pomatiopsidae. In order to be able to reject such an attribution completely, the protoconch characters of the South American pomatiopsids should be investigated.

The Cochliopidae is a very diverse family that at present is mostly restricted to the Americas (Hershler & Thompson, 1992). The range of shell characters overlaps completely with that in the families Hydrobiidae (northern hemisphere and Australia) and Pomatiopsidae (mainly southeastern Asia, with few separate genera in Australia, Africa, and North and South America). The protoconch microsculpture of the Cochliopidae is very variable and includes the features recorded in the family Hydrobiidae. It cannot be compared with that of the Pomatiopsidae due to lack of data on the latter. In the Cochliopidae, great variety exists in the shell and soft part morphology, and in the degree of genetic differentiation as interpreted in molecular genetics. This degree of divergence and diversity is strongly indicative of a long evolutionary history in the tropical and subtropical regions of the Americas. It follows that this family is the obvious candidate for attribution of the Pebasian hydrobioid taxa.

The shell morphology of Pebasian hydrobioids is compatible with the range of forms known in recent Cochliopidae. In Recent genera, planispiral, globose, elongately conical and tube-like shells occur (Hershler & Thompson, 1992). Strong axial and/or spiral ornament is developed in several of the genera, indicating the potential of the Cochliopidae to develop ornamentation similar as those of the Pebasian snails.

Pebasian hydrobioids have a well-developed protoconch-1 and protoconch-2, with the boundary between them often clearly marked. The protoconch-1 is of less than 0.6 whorls and has a variety of ornament, including honeycomb patterns, isolated sharp pustules, low mammillae and malleations. The ornament tends to fade away from the nucleus and protoconch-2 is either smooth or with very few growth lines. Comparable protoconchs are known from several cochliopid genera (*Littoridinops, Pyrgophorus*, *Texadina* and *Zetekina,* and possibly *Onobops* and *Cochliopina*). In other cochliopid genera the

protoconch-teleoconch boundary is less distinct, but still clearly recognizable by a change in ornamentation, usually the onset of growth lines (see illustrations of protoconchs of extant cochliopids in Hershler, 1985; Hershler & Thompson, 1992; Davis & McKee, 1989). Differentiation of the protoconchs-1 and -2 is indistinct or absent in Hydrobiidae, but widespread in Cochliopidae and is here interpreted as a plesiomorphy in this family.

A second type of protoconch organisation also exists in extant cochliopids. This type, present in many extant genera, including *Tryonia*, consists of a strongly inclined protoconch with pronounced wrinkles that may extend more than a whorl and give the early shell an irregular paper-like texture. The protoconch is not visibly delimited from the teleoconch. The presence of the second type of protoconch organisation in extant *Tryonia* and the first type in Pebasian *Tryonia* sheds doubts about the classification of the latter.

The protoconch-2 is often well defined and up to 2.5 whorls long in some specimens of *Onobops elongoides* and *Dyris lanceolatus,* suggesting the presence of planktotrophy during development of the protoconch-2 in Pebasian cochliopids. Several of the extant brackish cochliopid genera have a known planktotrophic development phase (Hershler & Thompson, 1992).

Three main groups within the Cochliopidae, at first based on soft part anatomy and later broadly confirmed by phylogenetic analyses and molecular genetics (Hershler & Thompson, 1992; Wilke *et al.,* 2001; Liu *et al.,* 2001; Hershler *et al*., 2003) have been given the rank of formal subfamilies by Bouchet *et al.* (2005). The Pebasian genera group in these subfamilies as follows:

Subfamily Cochliopinae Tryon, 1866: *Lithococcus* and *Cochliopina*;

Subfamily Littoridininae Thiele, 1928: *Littoridina*, *Littoridinops*, *Pyrgophorus* and *Tryonia*; and

Subfamily Semisalsinae Giusti & Pezzoli, 1980: *Onobops*.

The attribution of *Sioliella* is uncertain as no material collected alive has been available for study of anatomical characters.

The plesiomorphic status and occurrence in almost all clades of the Cochliopidae of the Pebasian protoconch type precludes definitive assumptions on the genus-level relationships of the Pebasian hydrobioids within recent cochliopids. Nonetheless, several species are assigned to extant genera on the basis of overall shell habitus and microsculpture, viz. to *Tryonia*, *Dyris*, *Onobops*, *Pyrgophorus*, *Littoridinops*?, *Lithococcus*, *Sioliella*, *Littoridina* and *Cochliopina*? If these assignments are correct, all three subfamilies as defined to date within the Cochliopidae, were present in the Pebas fauna.

Two groups of Pebasian hydrobioids show shell characteristics not developed in recent cochliopids: several high-spired *Dyris* species, in which the columella is so strongly twisted that no solid central axis (columella *sensu stricto*) exists any more; and five genera (*Sioliella, Toxosoma, Longosoma, Tropidebora, Lithococcus*) with a siphonal notch and commonly an accompanying umbilical ridge, and less commonly a second, adapical notch in the aperture. Two genera, *Toxosoma* and *Longosoma*, also have a columellar fold and sometimes additional denticles. Columellar folds are also seen in one *Dyris* species and in *Littoridina*. As these features are exceptional in freshwater rissooideans, they provide no clue as to the relationships of the genera. As their protoconch microsculpture is similar to that of Pebasian cochliopids without these characters, and to many extant cochliopids, it is here proposed to attribute these genera also to the Cochliopidae. Most of the morphological features seen in the Pebasian snails are known

from extant cochliopid taxa and the unusual shell features (twisting of the columella, siphonal retractions and columellar plicae) should be considered as evolutionary innovations facilitated by the long-lived nature of the Pebas system.

It is concluded that there are a range of arguments for the attribution of the Pebasian hydrobioid snails to the Cochliopidae. However, the attribution of several of the Pebasian species to extant genera is by no means well established and deserves further study. Major uncertainties remain over the generic status of Pebasian *Tryonia, Sioliella, Lithococcus*, *Littoridina* and *Cochliopina*?

Genus *Tryonia* Stimpson, 1865

Type species – *Tryonia clathrata* Stimpson, 1865. Recent, springs in southern Nevada, U.S.A.

Diagnosis (for Pebasian *Tryonia*) – Small, elongate snails with usually a well-developed axial ornament on the teleoconch whorls; some species develop reticulate or nearly smooth shells; embryonic shell inclined to strongly inclined with very marginal, poorly developed, low malleate or mammilate ornament; separated from protoconch-2 at 0.5-0.65 whorls by a low depression or a fine axial line; protoconch-2 smooth, bulbous, with very deep suture; onset of densely spaced growth lines after protoconch-teleoconch boundary at 1.3-2.1 whorls, often with a gradually developing single (or two) spiral rib(s) much later (typically 0.2-1 whorls after the protoconch-teleoconch boundary) that usually disappear(s) on later teleonch whorls; ovate aperture adnate along the parietal margin or detached.

Range – Miocene-Pliocene, northwest South America; Pliocene-extant Central America; Miocene-extant, southwest U.S.A.

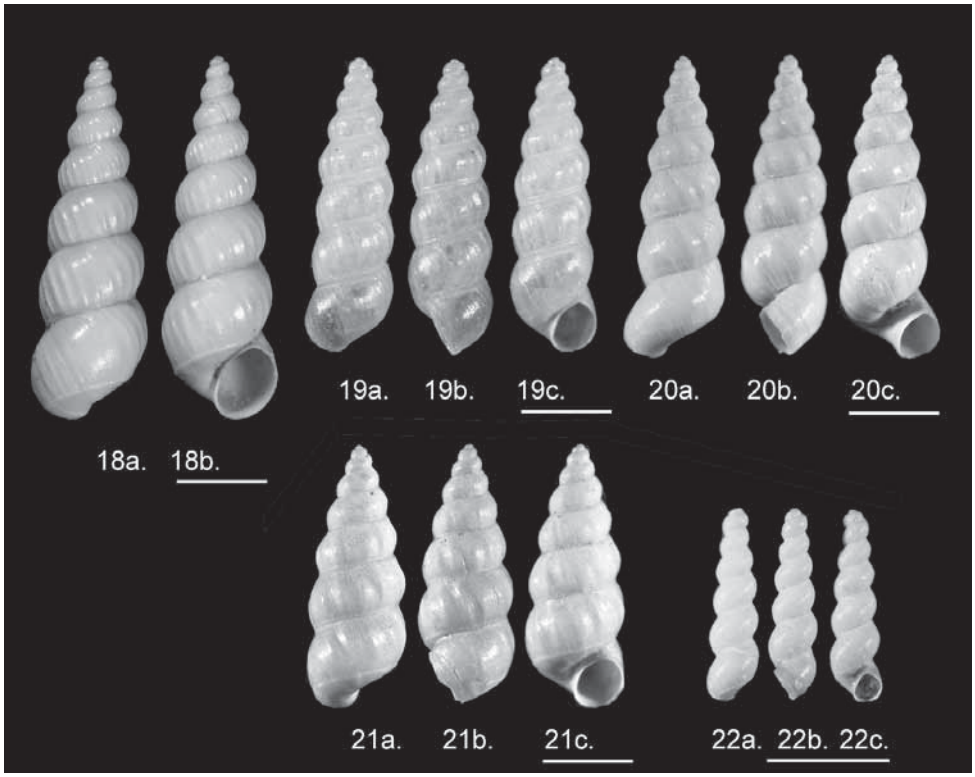
Remarks – In the Pebas Formation, axially ornamented snails formerly attributed to *Liris* Conrad, 1871 (Nuttall, 1990), are transferred here to *Tryonia*. The taxonomy of Pebasian *Tryonia* is in need of further study which is expected to increase the number of species. Uncertainties of the generic status of Pebasian *Tryonia* are dealt with in the discussion under Cochliopidae, above.

Tryonia minuscula (Gabb, 1869)

Figs. 18-21.

1869 *Turbonilla minuscula* Gabb, p. 197, pl. 16, fig. 1.
1871 *Liris laqueata* Conrad, p. 194, pl. 10, fig. 3, pl. 11, fig. 8.
1878 *Turbonilla minuscula* Gabb; Boettger, p. 496, pl. 13, fig. 13.
1938 *Liris laqueata* Conrad; de Greve, p. 89, pl. 2, figs. 10, 14-31, text-figs. 6-11.
? 1980 *Liris minuscula* (Gabb); Costa, p. 881 (*pars*), pl. 2, figs. 3, 4(?), *non* figs. 1, 2.
1990 *Liris minuscula* (Gabb); Nuttall, p. 204, figs. 124-138.

Material studied – RGM 456 535, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.



Figs. 18-21. *Tryonia minuscula* (Gabb, 1869).

Fig. 18. RGM 456 483, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, front view.
Fig. 19. RGM 456 538, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 20. RGM 456 539, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 21. RGM 456 537, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Fig. 22. *Tryonia acicularis* (Nuttall, 1990). RGM 456 441, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

RGM 456 536, Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. INGEMMET TN70, same locality. RGM 456 537, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F536 (6.6 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN71 and RGM 456 538, same locality. RGM 456 539, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996.

Extended diagnosis – Small, thin-shelled, high-spired *Tryonia*; SA 22-29°; nucleus strongly inclined, separated at 0.5-0.6 whorls by a well-defined spiral lineament from remainder protoconch that is smooth and bulbous; protoconch-teleoconch boundary at 1.6-2.1 whorls very poorly defined, occassionally through low, poorly defined axial depression, otherwise only by onset of very fine, densely spaced, prosocline growth lines; *c.* 0.5 whorls after, development of slightly prosocline low axials ribs and gradual development of one or two very fine spiral cords; axials die out towards upper and lower suture, 14-28 axials per whorl; spirals usually disappear in the first two teleoconch whorls; a small spiral rib can develop at the lower suture from the second teleoconch whorl onwards that becomes visible as a fine thread at the base of the rounded body whorl; irregular, microscopic spiral groovelets common on later whorls; whorl profile rounded to subrounded, suture shallow; aperture adnate to detached and produced, semicircular; apertural margins thin; parietal margin may be attached through narrow parietal platform; shell imperforate.

Dimensions – RGM 456 535: H 3.5; W 1.05; Hap 0.8; 8.2 whorls. RGM 456 536: H 3.1; W 1.1; Hap 0.75; 7.3 whorls. INGEMMET TN70: H 4.2; W 1.3; Hap 0.9; 8.2 whorls. RGM 456 537: H 3.0; W 1.1; Hap 0.65; 7.3 whorls. INGEMMET TN71: H 2.5; W 0.9; Hap 0.6; 7.4 whorls. RGM 456 538: H 2.65; W 0.8; Hap 0.5; 8.1 whorls. RGM 456 539: H 3.5; W 1.2; Hap 0.55; 8.3 whorls.

Range – Pebas Formation, MZ7 - MZ9 (Middle - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.

Tryonia acicularis (Nuttall, 1990)

Fig. 22.

1990 *Liris acicularis* Nuttall, p. 207, figs. 147, 148.

Material studied – RGM 456 441, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F532 (5.7 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN94, same locality.

Extended diagnosis – Minute, high spired (SA *c.* 17°), thin-shelled *Tryonia*; nucleus (diameter *c.* 50 µm) slightly inclined; protoconch-teleoconch boundary at 2.2 whorls marked by an almost indistinguishable fine axial thread; whorl profile of first 1.5 whorls markedly bulbous, later whorls subrounded; shell surface with numerous, very fine, prosocline growth lines; very fine spiral thread may develop at two thirds of the whorl height on early teleoconch whorls, but is absent on later whorls; microscopic axial threads are present throughout the shell; rounded and poorly defined basal keel bounding base of body whorl present in some specimens, otherwise the base of the body whorl is evenly rounded; aperture semicircular, margins thin; aperture detached.

Dimensions – RGM 456 441: H 1.6; W 0.45; Hap 0.3; 6.7 whorls.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Tryonia scalarioides scalarioides (Etheridge, 1879)

Figs. 23-25.

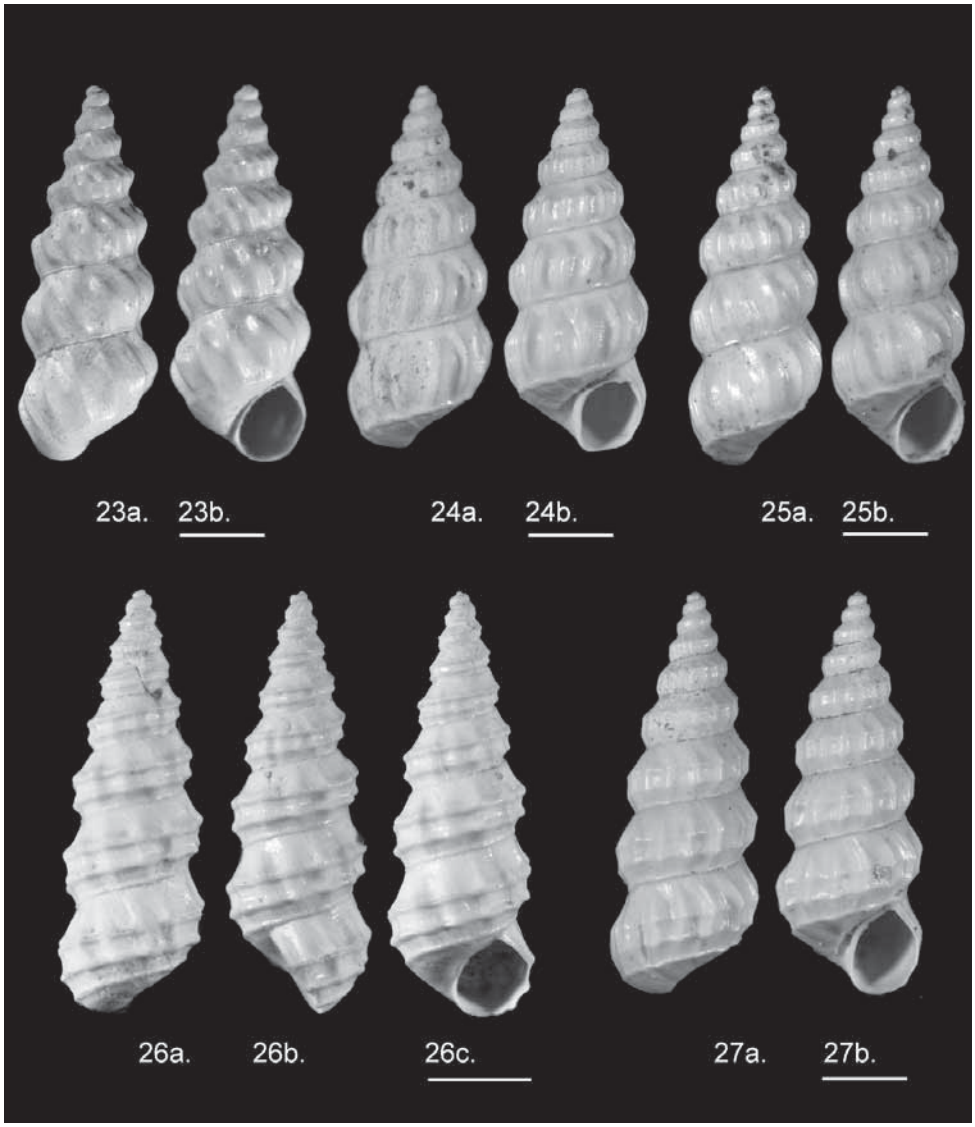
1879 *Melania scalarioides* Etheridge, p. 88, pl. 7, fig. 8.
? 1980 *Liris minuscula* (Gabb); Costa, p. 881 (*pars*), pl. 2, figs. 1, 2(?) (*non* figs. 3, 4).
1990 *Liris scalarioides* (Etheridge); Nuttall, p. 206 (*pars*), figs. 139(?), 456 (*non* figs. 139-146).

Material studied – INGEMMET TN66, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F489 (9.4 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 518, same locality. RGM 456 520, Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Extended diagnosis – Robust, tuberculate *Tryonia* (SA 22-27°) with a characteristic spiral keel delimiting the base of the body whorl; robust, broad (sometimes elongate knob-like), slightly prosocline axial ribs that lower towards the sutures, reaching the largest height about medially giving the shell a shouldered appearance; median spiral rib well developed on early teleoconch whorls, becoming very thin and low on later teleoconch whorls; embryonic shell (nucleus diameter 40-70 µm) inclined with very fine low marginal wrinkles; boundary with teleoconch-2 at *c.* 0.6 whorls marked by a broad and low axial depression; remainder protoconch markedly bulbous and erect; protoconch-teleoconch boundary at 1.3-1.8 whorls poorly delimited by sudden increase of densely spaced growth lines; gradual development of spiral keel at two thirds to three fifths of the whorl height, with increasingly well-developed subsutural ramp; both fade after the third teleoconch whorl; 9-14 microscopic, regularly spaced spiral riblets may develop on the first two teleoconch whorls; at the second teleoconch whorl broad, slightly prosocline, axial undulations develop that later become clear ribs (13-17 per whorl); at the third teleoconch whorl a very fine secondary spiral may be present at two fifths of the whorl height and uncommonly a spiral rib may be visible at the lower suture; the latter becomes visible before the aperture as a marked, robust spiral that bounds the rather flat base of the body whorl; growth lines very fine and prosocline, on early teleoconch whorls crossing axial ribs; on later whorls becoming less prosocline; axials with broad, concave interspaces; aperture adnate or very rimately detached, subovate; margins thin; columellar lip can be slightly erect; shell imperforate or with rimate umbilicus.

Dimensions – INGEMMET TN66: H 4.45; W 1.55; Hap 1.05; 8.4 whorls. RGM 456 518: H 4.3; W 1.65; Hap 0.9; >7.7 whorls. RGM 456 520: H 4.25; W 1.6; Hap 0.85; 8.2 whorls.

Range – Pebas Formation, MZ8 - MZ12 (late Middle - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.



Figs. 23-25. *Tryonia scalarioides scalarioides* (Etheridge, 1879).

Fig. 23. RGM 456 520, Macedonia (Amazonas, Colombia). a, rear view. b, front view.
Fig. 24. RGM 456 518, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 25. INGEMMET TN66, same locality as Fig. 24. a, rear view. b, front view.

Figs. 26, 27. *Tryonia scalarioides tuberculata* (de Greve, 1938).

Fig. 26. RGM 456 440, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 27. INGEMMET TN65, Santa Elena (Loreto, Peru). a, rear view. b, front view.

Scale bars represent 1 mm.

Remarks – This species has a prominent basal spiral keel bounding the base of the body whorl, lacking in other coarse-ribbed *Tryonia* species, such as *Tryonia nuttalli*. Sample F489 is in many respects remarkable. In stratigraphic older samples, the bicarinate *T. s. tuberculata* occurs, in younger samples only the monocarinate *T. s. scalarioides*, but in sample F489 both co-occur with morphs that can be considered as intermediate. For example, specimens exist where the secondary spiral keel, typical of *T. s. tuberculata*, is prominently developed, but in other specimens it occurs as a very thin spiral to become reduced in succeeding whorls and disappears on later teleoconch whorls. I interpret both forms as stratigraphic successive forms in a single lineage, hence the subspecies status of both.

Tryonia scalarioides tuberculata (de Greve, 1938)

Figs. 15g, 26, 27.

1938 *Liris tuberculata* de Greve, p. 96, pl. 2, figs. 32-35, pl. 3, figs. 1-20, text-figs. 19-22.
1966 *Liris tuberculata* de Greve; Willard, pp. 69, 93.
1990 *Dyris tuberculata* (de Greve); Nuttall, p. 196, fig. 103a-c.
2002 *Tryonia tuberculata* (de Greve); Wesselingh *et al.,* fig. 3n.

Material studied – RGM 456 440, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996. INGEMMET TN65, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F489 (9.4 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Extended diagnosis – Robust, bicarinate, tuberculate *Tryonia*; SA 24-27°; embryonic shell (diameter 50-60 µm) flat or slightly inclined, with very thin marginal wrinkles; separated at 0.5-0.65 whorls by a very low axial depression from protoconch-2; second whorl markedly bulbous; protoconch/teleoconch boundary at 1.4-1.7 whorls marked by an axial constriction or very fine lineament; at first fine numerous, densely spaced growth lines develop after the boundary, followed by gradual onset of one spiral rib at three fifths of the whorl height or of two spiral ribs at one quarter and two thirds of whorl height; upper spiral developing within a whorl to well-defined rib that bounds a well developed straight to concave subsutural ramp; growth lines numerous, fine, prosocline; spirals well-defined throughout the shell, but increasingly broader; secondary spirals may develop between the primary spirals; broad, slightly prosocline axial undulations or ribs develop at the second teleoconch whorl onwards that on early teleoconch whorls are obliquely cut by growth lines; interspaces concave; axials fade upward on subsutural ramp and are lacking below lower spiral; at intersections of axials and spirals, broad, slightly elongate, low knobs (tubercles) may develop; upper spiral hanging concave-down between axials; a third spiral is present at or just below the suture and becomes visible at the body whorl, where it can form a prominent rib that bounds the smooth base of the body whorl; microscopic irregular spiral grooves present throughout the shell; aperture semicircular, adnate, but occasionally detached; margins thin; shell imperforate.

Dimensions – RGM 456 440: H 4.2; W 1.45; Hap 0.95; 8.5 whorls. INGEMMET TN65: H 4.8; W 1.7; Hap 1.1; 8.8 whorls. RGM 456 517: H 4.1; W 1.8; Hap 1.05; 7.6 whorls. RGM 456 519: H 4.8; W 1.8; Hap 1.15; 8.4 whorls.

Range – Pebas Formation, MZ4 - MZ8 (late Early - early Late Miocene), Peruvian Amazonia.

Remarks – The species has two spiral keels (three on the body whorl) instead of one, such as in *T. s. scalarioides* (see remarks above).

***Tryonia semituberculata* (Nuttall, 1990)**
Figs. 28-32.

1990 *Dyris semituberculata* Nuttall, p. 196, figs. 87-91, 93-98, 92?, 99-102?

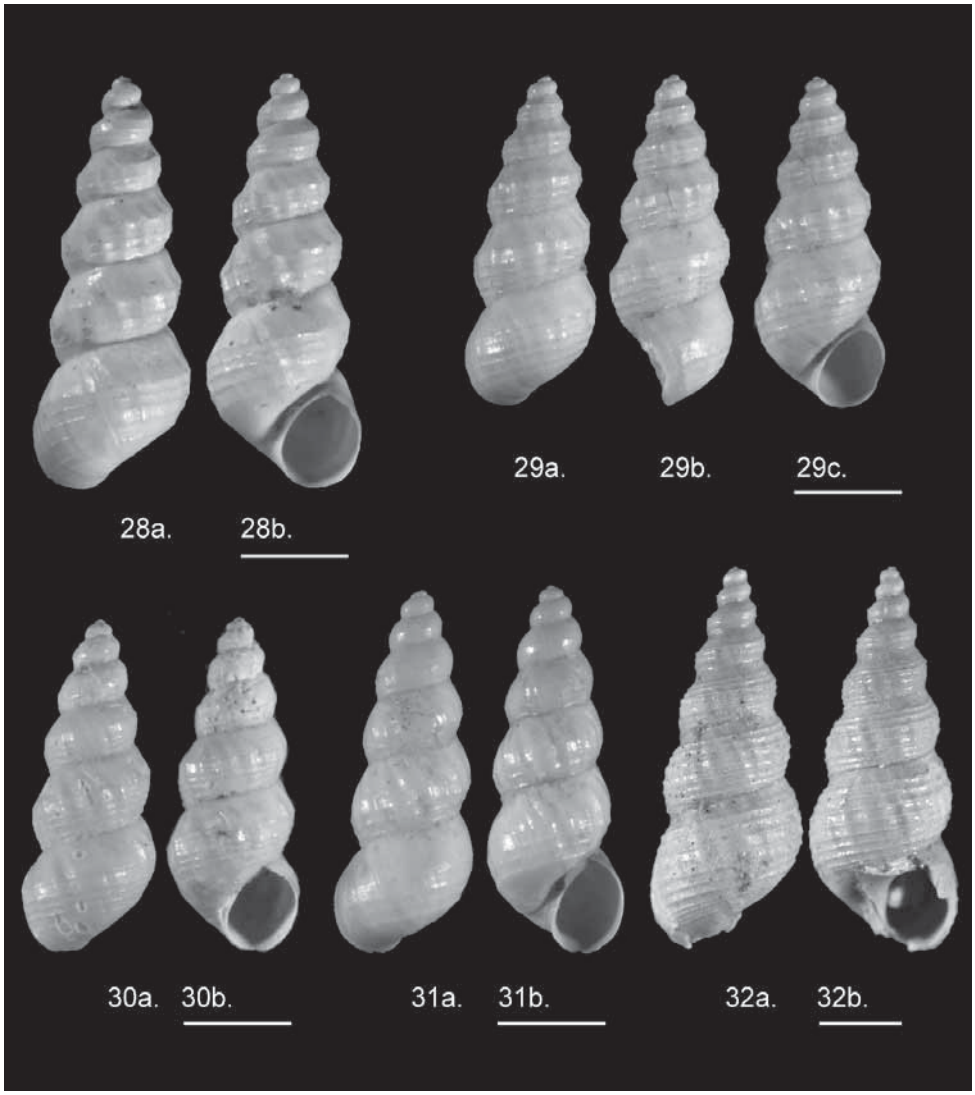
Material studied – RGM 456 549, La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 9-11'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. INGEMMET TN74, Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S 73°00'W), level F318 (1.35 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996. RGM 456 550, RGM 456 551, INGEMMET TN75, same locality.

Extended diagnosis – *Tryonia* with numerous low spiral ribs and wavy, low axial ribs; SA 28-31°; first 0.7 whorls of protoconch tilted; diameter nucleus 70-80 µm; protoconch-2 smooth, with convex whorls; protoconch-teleoconch boundary at 1.6-1.7 whorls marked by very fine axial lineament; afterwards two or three primary spirals develop with a marked subsutural ramp above; at second teleoconch whorl very low, undulating, slightly prosocline axial folds or ribs, *c.* 20-25 per whorl, develop; spiral ribs (up to nine) unevenly spaced; growth lines fine, prosocline; teleoconch whorl profile developing from bicarinate to subrounded; base of body whorl smooth; semicircular aperture can be detached, attached through the parietal wall or completely adnate; shell imperforate or narrowly rimate.

Dimensions – RGM 456 449: H 4.45; W 1.8; Hap 1.2; 7.6 whorls. INGEMMET TN74: H 4.0; W 1.5; Hap 0.9; 7.0 whorls. RGM 456 550: H 3.3; W 1.3; Hap 0.8; 6.6 whorls. RGM 456 551: H 3.6; W 1.3; Hap 0.9; 6.7 whorls. INGEMMET TN75: H 3.2; W 1.25; Hap 0.8; 6.6 whorls.

Range – Pebas Formation, MZ2 - MZ5 (late Early - early Middle Miocene), Peruvian and Colombian Amazonia.

Remarks – *Tryonia semituberculata* has at least three primary spirals, unlike the two in *T. tuberculata*. The axial ribs in the latter are much more robust and finer spiral ribs are lacking.



Figs. 28-32. *Tryonia semituberculata* (Nuttall, 1990).

Fig. 28. INGEMMET TN74, Santa Teresa (Loreto, Peru). a, rear view. b, front view.
Fig. 29. RGM 456 550, same locality as Fig. 28. a, rear view. b, lateral view. c, front view.
Fig. 30. INGEMMET TN75, same locality as Fig. 28. a, rear view. b, front view.
Fig. 31. RGM 456 551, same locality as Fig. 28. a, rear view. b, front view.
Fig. 32. RGM 456 549, La Tagua (Putumayo, Colombia). a, rear view. b, front view.

Scale bars represent 1 mm.

***Tryonia nuttalli* sp. nov.**
Figs. 15h, s, 17b, 33-37.

1938 *Liris minuscula* (Gabb); de Greve, p. 92, pl. 1, figs. 31-35, pl. 2, figs. 1-9, 11-13, text-figs. 12-18.
1981 *Liris minuscula* (Gabb); Costa, p. 643, pl. 1, figs. 9, 10.
1990 *Liris scalarioides* (Etheridge); Nuttall, p. 206 (*pars*), figs. 140-146 (*non* figs. 139, 456).

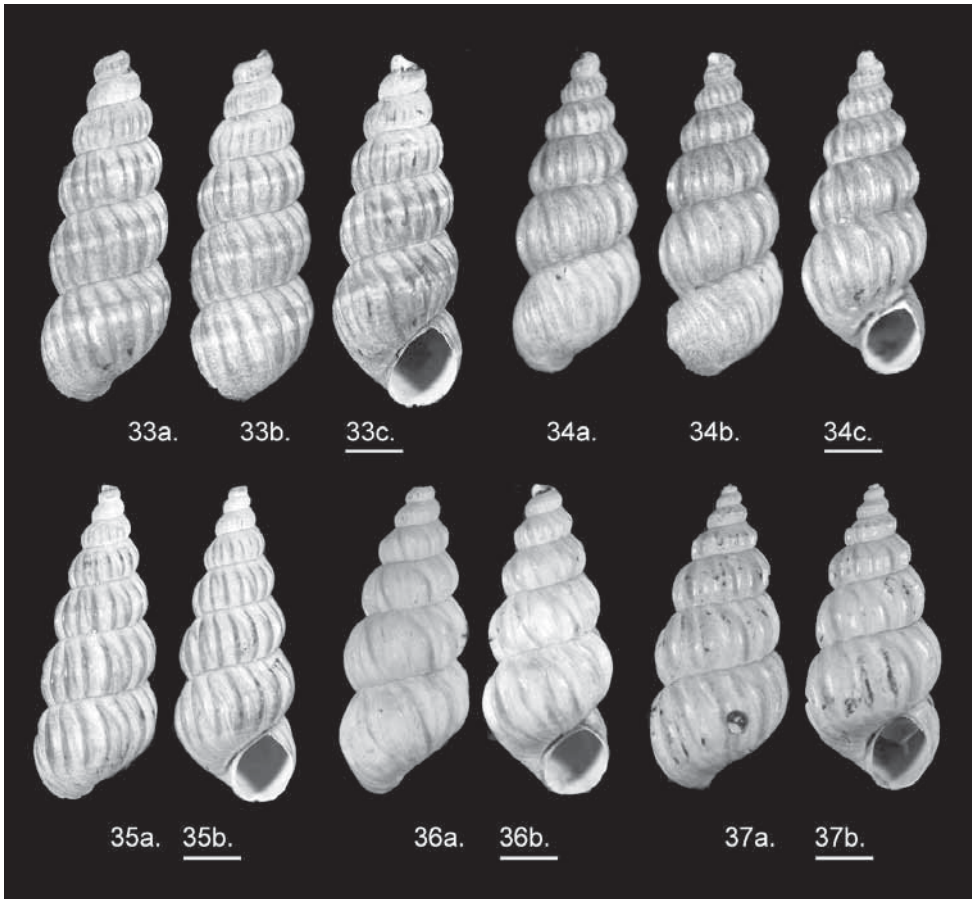
Type material – RGM 456 540 (holotype), Mishana (Loreto, Peru), exposure in south bank Rio Nanay, 100 m west of landing stage (3°52'S 73°29'W), level F72 (at DL). Pebas Formation, *Grimsdalea* zone, MZ8 (late Middle - early Middle Miocene); leg. F.P. Wesselingh, 10-1991. INGEMMET TN72, TN73, RGM 456 541, 456 542 (paratypes), same locality. RGM 456 619 (paratype), Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ 5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996.

Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Peruvian, Brazilian and Colombian Amazonia.

Derivatio nominis – Named after Patrick Nuttall, retired curator at the BMNH, in honour of his meticulous work on the Neogene inland molluscs of northwestern South America.

Diagnosis – Relative wide *Tryonia* (SA 28-34°) with convex whorl profile and impressed sutures ornamented by 14-25 robust slightly prosocline axials that on later teleoconch whorls run from suture to suture.

Description – The nucleus (diameter *c.* 60 µm) is inclined. There is a slight axial constriction at *c.* 0.6 whorls, separating the embryonic shell from the protoconch-2 that is smooth and somewhat rounded. The protoconch-teleoconch boundary is located at 1.3 whorls in the holotype and 1.7 whorls in one of the paratypes, and marked by a fine axial lineament. Soon after, the low and broad axial ribs develop, as well as two spirals at one fifth and two thirds of the whorl height. The upper rib defines a well-developed subsutural ramp on early teleoconch whorls. Within a whorl a fine secondary spiral rib may develop in between the primaries. The spirals disappear on later teleoconch whorls. The axial ribs dominate the shell. They are broad and rounded, but prominent. The shells contain 15-22 axial ribs per whorl; Nuttall (1990, p. 206 as *L. scalarioides*) counted 14-25 ribs. Initially, the axial ribs lower towards the sutures, but on later teleoconch whorls they extend from upper to lower suture. Growth lines are more inclined and obliquely run over the axials. The periphery is subrounded and the suture impressed. Most specimens increase their width regularly, but on some specimens, including the holotype, the largest width is reached on the penultimate whorl. The aperture is semicircular; the apertural margins are thin. The aperture is commonly adnate at the parietal margin, where a thin callus is present that is not expanding. The columellar margin is usually slightly erect and thin. However, specimens with completely detached apertures also occur. The shell is imperforate or has a rimate, very shallow umbilical depression. In some specimens (including RGM 456 542, Fig. 33), clear colour



Figs. 33-37. *Tryonia nuttalli* sp. nov.

Fig. 33. RGM 456 542, paratype, Mishana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 34. RGM 456 541, paratype, same locality as Fig. 33. a, rear view. b, lateral view. c, front view.
Fig. 35. INGEMMET TN73, paratype, same locality as Fig. 33. a, rear view. b, front view.
Fig. 36. INGEMMET TN72, paratype, same locality as Fig. 33. a, rear view. b, front view.
Fig. 37. RGM 456 540, holotype, same locality as Fig. 33. a, rear view. b, front view.

Scale bars represent 1 mm.

bands are seen. Most of the shell of RGM 456 542 is grey-bluish coloured, but there are two spirally arranged cream-coloured zones at about half the whorl height and occupying the upper one fifth.

Dimensions – RGM 456 540: H 6.1; W 2.4; Hap 1.4; 6.7 whorls. INGEMMET TN72: H 5.6; W 2.3; Hap 1.2; >6.5 whorls. INGEMMET TN73: H 5.5; W 2.15; Hap 1.2; >7.7 whorls. RGM 456 541: H 5.4; W 2.2; Hap 1.15; >6.7 whorls. RGM 456 542: H 5.3; W 2.3; Hap 1.2; >6.5 whorls.

Remarks – This species is wider and had more convex whorls than *T. minuscula*. The axial ribs occupy the entire height of the teleoconch whorls, unlike in *T. minuscula* and *T. scalarioides scalarioides*.

Genus *Feliconcha* gen. nov.

Type species – *Feliconcha feliconcha* sp. nov., Miocene, Pebas Formation, western Amazonia.

Other species – *Feliconcha reticulata* sp. nov., Miocene, Pebas Formation, western Amazonia.

Derivatio nominis – *Concha,* Latin for shell; *feli* from *Felis* (Latin for cat), because the aperture of the type species resembles, when turned 90°, the outline of a cat's head; gender feminine.

Diagnosis – Small (H typically 2-3 mm), high spired shell with one median spiral keel and an additional basal spiral keel that bounds the imperforate base of the shell; nucleus strongly inclined, first half whorl tilted; boundary embryonic shell-protoconch-2 often poorly developed, but uncommonly marked by axial lineament at 0.3-0.6 whorls; protoconch-2 smooth, bulbous, with deeply impressed suture; protoconch-teloconch boundary very poorly defined, occasionally marked by a fine line axial lineament at *c.* 1.7 whorls; median keel gradually developing, typically 0.5 whorls after protoconch-teleoconch boundary; growth lines prosocline; aperture semicircular, parietal adnate to entirely detached.

Range – Pebas Formation, MZ7 - MZ10 (Middle - early Late Miocene), western Amazonia (Peru, Colombia, Brazil).

Remarks – *Feliconcha* has a similar onset of teleoconch spiral ribs as Pebasian *Tryonia*, but the adult ornamentation is completely dominated by spiral instead of axial elements. In the spirally ribbed *Dyris*, two (or rarely three) spiral ribs develop after the protoconch-teleoconch boundary.

Feliconcha feliconcha sp. nov.

Figs. 15i, 17a, 38-40.

1990 *Dyris gracilis* Conrad; Nuttall, p. 186 (*pars*), fig. 43a-c (*non* figs. 41, 42, 44-48, 454-455).
2002 genus and species indet; Wesselingh *et al.*, fig. 3h.

Type material – INGEMMET TN63 (holotype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 498 (paratype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F489 (9.4 m above DL). Pebas Formation, MZ8 (late Middle - early Late

Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 499 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 618 (paratype), same locality, level F703 (0.6 m above DL).

Range – Pebas Formation, MZ8 - MZ10 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – As for the genus.

Diagnosis – High-spired carinate shell commonly with a markedly detached body whorl (increasing SA from *c.* 35° on penultimate whorl to 43-46° on body whorl); prominent erect keel bounding base of shell; umbilicus deep.

Description – The nucleus (diameter 40-60 µm) is strongly inclined. At 0.3 whorls, an axial depression marks the boundary between the embryonic shell and the remainder protoconch. The first whorl is extremely bulbous and prominently erect above the rest of the shell. The protoconch-teleoconch boundary, located at 1.7 whorls, is barely visible. About half a whorl after the boundary a spiral keel develops gradually at *c.* three fifths of the whorl height. At first the keel is broad and subrounded, but within a whorl it is a marked blade-like extension. Above and below a long straight to slightly concave sub- and suprasutural ramp are present. In subsequent whorls, a low and rounded spiral ridge becomes visible at the lower suture, above which a depression develops. The suture itself is either adnate or overlain by the ridge. The lower rib becomes fully visible at the base of the body whorl. It is also very prominent, blade-like and pronounced by a spiral depression running parallel to it, located below. The base of the body whorl grades into the deep umbilicus. The slightly prosocline growth lines are in general very thin and difficult to distinguish. The ultimate 0.1-0.3 whorls are detached and produced. The aperture is entirely ovate-circular (as in paratype RGM 456 499) or has a broadly rounded inner lip and a straight outer lip with two abaxial extensions corresponding to the (partially open) keels at the base and the middle of the outer lip. The apertural margins are not or only barely thickened. Growth lines are more pronounced on the last detached part of the shell.

Dimensions – INGEMMET TN63: H 3.3; W 2.2; Hap 0.85; 7.8 whorls. RGM 456 498: H 3.0; W 2.0; Hap 0.9; 7.1 whorls. RGM 456 399: H 3.4; W 1.9; Hap 0.7; 7.9 whorls.

***Feliconcha reticulata* sp. nov.**

Figs. 41, 42.

Type material – RGM 456 500 (holotype), Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996. INGEMMET TN64 (paratype), same locality, level F 756.

Range – Pebas Formation, MZ7 (Middle Miocene), Peruvian Amazonia. In samples from MZ4 and MZ5 intervals, some as of yet unsatisfactorily identified *Tryonia*-like gastropod populations were found that show similarities with *F. reticulata*. Further investigation may extend the stratigraphic range of this species downward.

Derivatio nominis – Named after the reticulate appearance.

Diagnosis – High-spired *Feliconcha* (SA 24-26°) with prominent median keel, crossed by regularly spaced, low axial riblets producing a (semi-)reticulate ornament; aperture only slightly detached.

Description – The nucleus (diameter *c.* 50 µm) is inclined, the embryonic shell is strongly tilted. The embryonic shell is bounded from the remainder protoconch at 0.5 whorls by an axial depression. The protoconch-2 is smooth and has convex whorls, separated from the teleoconch at *c.* 1.7 whorls by a very poorly visible axial thread. Shortly after, a median spiral rib develops that is low and rounded. Within a whorl it becomes a prominent median keel that is blade-like and erect. The overlying subsutural ramp is slightly concave and slightly higher than the suprasutural ramp. The shell has more or less regularly spaced, low prosocline ribs (14-22 per whorl) that, together with the spiral, give the shell a reticulate appearance. Growth lines are very fine and numerous; on the subsutural ramp they are strongly prosocline (and obliquely overlay the axial ribs), becoming less strongly prosocline below the median keel. From the third teleoconch whorl onwards a basal spiral keel develops just above the suture. It becomes fully visible at the base of the body whorl, where it is as prominent as the median keel. A microsculpture of poorly delimited, very low and irregular spiral grooves is seen on later teleoconch whorls. The lower keel bounds the flat base of the body whorl that grades into the rimate umbilicus. Apparently, the aperture is subovate to semicircular. The outer margin of the aperture is damaged in the studied material. The apertural margins are thin. The inner lip is broadly rounded and slightly erect. The apertural plane is strongly inclined.

Dimensions – RGM 456 500: H 3.3; W 1.2; Hap 0.65; 7.8 whorls. INGEMMET TN64: H 3.1; W 1.1; Hap 0.7; 7.6 whorls.

Remarks – This species differs from *F. feliconcha* by the occurrence of regularly spaced axial riblets that, together with the median keel, produce a reticulate appearance. Furthermore, the apertural detachment is only very short.

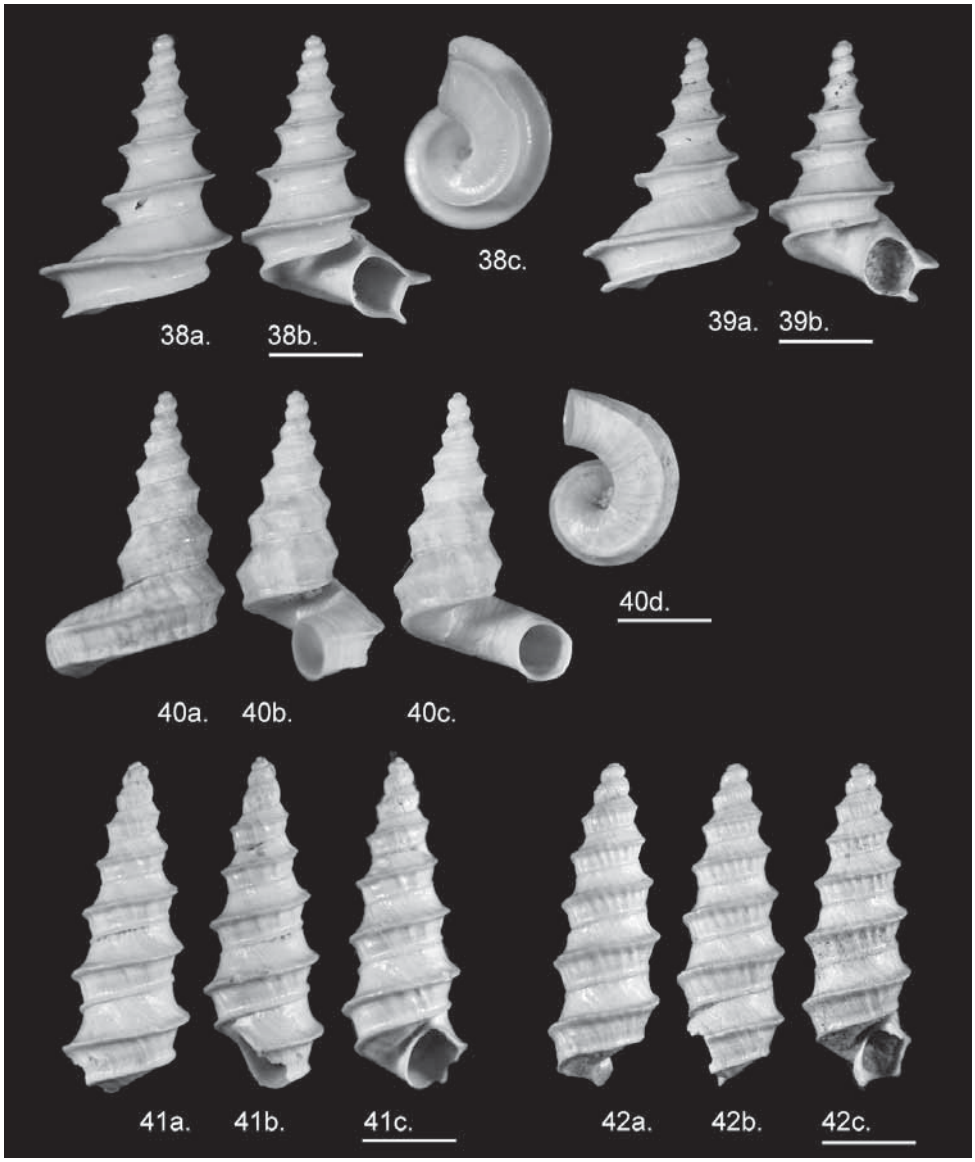
Genus *Glabertryonia* gen. nov.

Type species – *Glabertryonia glabra* sp. nov., Miocene, Pebas Formation, western Amazonia.

Other species – *Glabertryonia* sp. 1., Pliocene, Las Piedras Formation, eastern Venezuela; *Glabertryonia* sp. 2., Holocene, coastal zone, Surinam (see below).

Derivatio nominis – *Glaber* from *glabra* (Latin for smooth); *Tryonia* after the cochliopid genus *Tryonia*; gender feminine.

Diagnosis – Small, smooth hydrobiiform cochliopid; inclined nucleus small (*c.* 40 µm) with marked honeycomb micro-ornamentation; embryonic shell separated from remainder of shell by an axial constriction at 0.3-0.5 whorls; no boundary between protoconch-2 and teleoconch observed; perimeter barely rounded; very narrow, rounded, subsutural ridge may produce a spiral line at the uppermost part of the whorl; growth



lines fine, prosocline; adnate aperture semicircular to drop-shaped, pointed above, slightly constricted below preceding whorl; apertural margins thin; parietal callus very narrow; the parietal callus reduces about halfway the inner lip; below, the slightly erect columellar lip develops; leftmost part of inner lip at or to the left of the axis of the shell; upper one third of body whorl in mature specimens tends to be slightly concave.

Range – Pebas Formation, MZ6 - MZ11 (Middle - early Late Miocene), western Amazonia (Peru, Colombia); Pliocene, Eastern Venezuela Basin; Holocene (and probably extant), coastal lowlands of Surinam.

Remarks – Within the Pebas fauna, there is only one other smooth elongate cochliopid taxon, described as *Littoridinops*? *amazonicus* below. That species is ovate-conical. In the extant Neotropical cochliopid fauna there are a number of genera of smooth, hydrobiiform snails. These include several *Tryonia* species, several *Heleobia* species, *Littoridinops* and *Mesobia*. However, these taxa lack the depression at the upper part of the body whorl and the honeycomb ornament on the nucleus characteristic of *Glabertryonia*. *Glabertryonia* resembles most *Texadina* (brackish marshes, Gulf of Mexico south to Jamaica) that can develop a slight concavity on the upper part of the later teleoconch whorls. However, the aperture of that genus is evenly subovate-semicircular and detached, and not narrowly adnate as in *Glabertryonia*. Given the common presence of *Glabertryonia* in Holocene deposits of Surinam, it is likely an extant genus.

***Glabertryonia glabra* sp. nov.**
Figs. 43-45.

1998 *Tryonia* sp.; Vonhof *et al.,* p. 88 (table).
1998 Hydrobiid sp.; Vonhof *et al.,* fig. 2.3.

Type material – RGM 456 571 (holotype), Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42 (4°04'S 73°25'W), level F367a (1.0 m above DL). Pebas Formation, *Grimsdalea* zone, MZ9 (late Middle - early Late Miocene); leg. F.P.

◀ Figs. 38-40. *Feliconcha feliconcha* sp. nov.

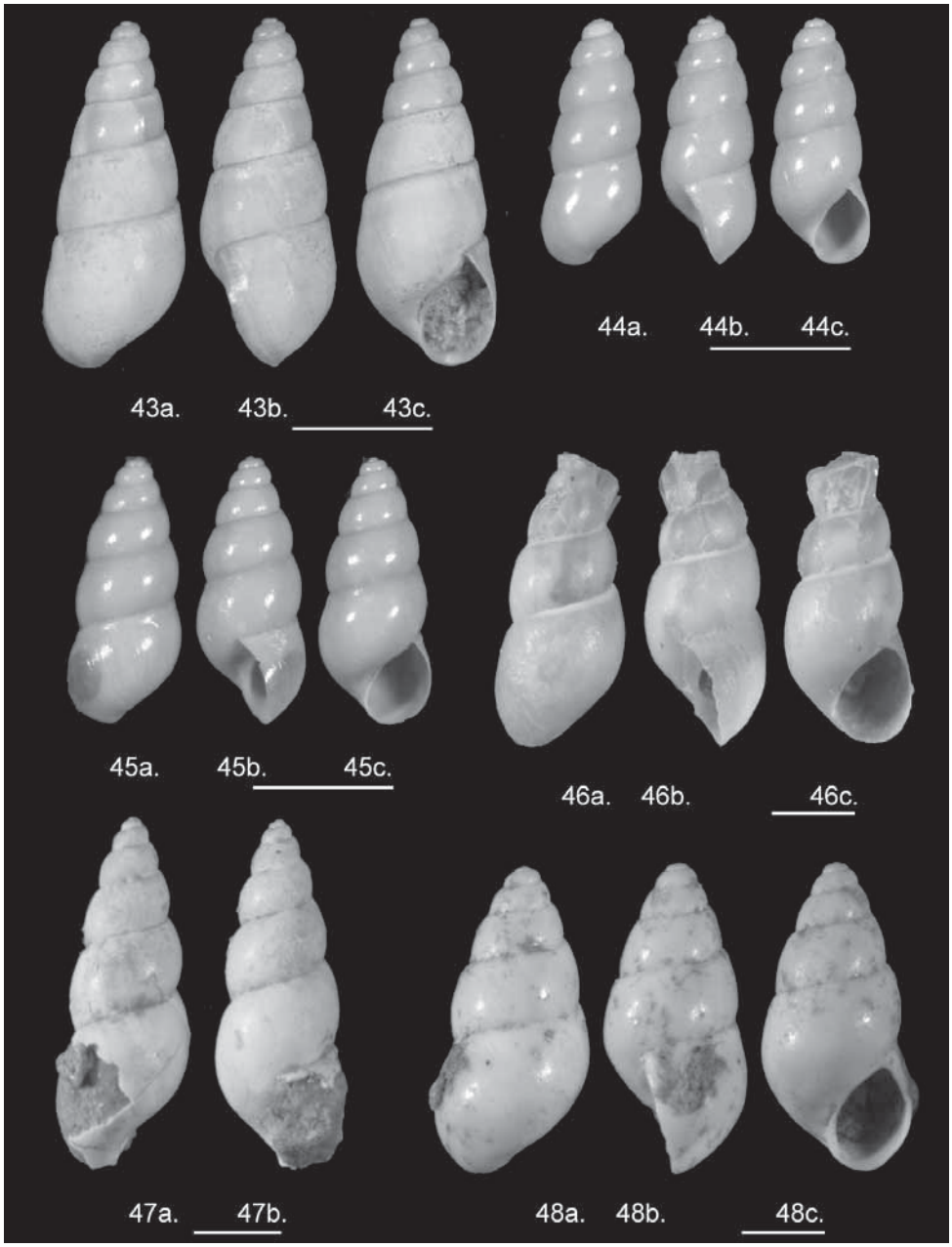
Fig. 38. INGEMMET TN63, holotype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, front view. c, basal view.
Fig. 39. RGM 456 498, paratype, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 40. RGM 456 499, paratype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d. basal view.

Figs. 41, 42. *Feliconcha reticulata* sp. nov.

Fig. 41. RGM 456 500, holotype, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 42. INGEMMET TN64, paratype, same locality as Fig. 41. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

Wesselingh, 11-8-1996. INGEMMET TN81 (paratype), same locality. RGM 456 572 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, *Grimsdalea* zone, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.



Range – Pebas Formation, MZ7 - MZ10 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – *Glabra* (Latin) refers to the smooth exterior of this species.

Diagnosis – Small, relatively high-spired *Glabertryonia* (SA 31-32°) with a well-developed subsutural concave zone on later teleoconch whorls.

Description – The nucleus (diameter 40-50 µm) is slightly inclined and has a well-developed honeycomb ornament that covers the margins as well as some of the central part. At 0.3-0.5 whorls the embryonic shell is separated from the remainder of the shell by a delicate, but well-defined, axial lineament. No traces of a protoconch-teleoconch boundary could be found. The early whorls are slightly subrounded with a somewhat impressed suture. The perimeter of subsequent whorls becomes lower and the suture shallower. Growth lines are fine, numerous and slightly prosocline. The shell has a glossy, smooth surface. A very narrow, almost indistinct, rounded subsutural ridge develops during growth. This ridge can be expressed as a spiral line just below the suture. On later teleoconch whorls a very subtle depression develops below, covering the upper one fifth of the body whorl. The periphery of the penultimate whorl in most specimens is located just above the suture. The base of the body whorl is evenly rounded. On the body whorl, traces of microscopic spiral groovelets are visible. The aperture is adnate and drop-shaped. The parietal callus is very thin and very narrow. At about half the height of the inner lip it retracts, leaving a very short zone devoid of any extensions, before the slightly erect and out-folding columellar lip sets in. The latter is about as narrow as the parietal callus. The basal and outer margins are very thin and broadly rounded. The upper part of the outer lip is slightly produced. The shell is imperforate or extremely narrowly rimate with a shallow umbilicus.

◀ Figs. 43-45. *Glabertryonia glabra* sp. nov.

Fig. 43. RGM 456 574, paratype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 44. INGEMMET TN81, paratype, Nuevo Horizonte (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 45. RGM 456 561, holotype, same locality as Fig. 44. a, rear view. b, lateral view. c, front view.

Figs. 46, 47. *Glabertryonia* sp. 1.

Fig. 46. RGM 456 573, La Llanera (Monagas, Venezuela), eastern valley wall, *c.* 0.6 km east of village. Las Piedras Formation (Pliocene). Leg. F.P. Wesselingh, 1996. a, rear view. b, lateral view. c, front view.
Fig. 47. RGM 456 574, same locality as Fig. 46. a, rear view. b, front view.

Fig. 48. *Glabertryonia* sp. 2. RMNH n.n., Groningen (Surinam), collected from Holocene shell ridge. Leg. B.G. Geyskes, 1955. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

Dimensions – RGM 456 571: H 1.95; W 0.85; Hap 0.65; 6.0 whorls. INGEMMET TN81: H 1.85; W 0.75; Hap 0.6; 5.6 whorls. RGM 456 572: H 2.5; W 1.0; Hap 0.7; 6.6 whorls.

Remarks – Two undescribed *Glabertryonia* species resemble *G. glabra* from the Pebas Formation. *Glabertryonia* sp. 1 from the Pliocene Las Piedras Formation of the eastern Venezuela Basin (Figs. 46, 47) is larger; it has the periphery at the lower suture, a slightly more rounded perimeter and lacks the subsutural depression on teleoconch whorls. *Glabertryonia* sp. 2 from the Holocene of the coastal region of Surinam (described and illustrated by van Regteren Altena, 1975, p. 16, fig. 2a, b, as Hydrobiidae species 1; Fig. 48 herein) has a wider shell (SA 40-42°), only develops the subsutural depression on the last part of the body whorl on larger specimens, has a more expanded parietal callus and the subsutural line is clearly developed in most specimens.

Genus *Dyris* Conrad, 1871

Type species – *Dyris gracilis* Conrad, 1871. Pebas, Pichana (probably Santa Rosa de Pichana; Loreto, Peru). Pebas Formation (Middle Miocene).

Diagnosis – Turritelliform to hydrobiiform snails, usually with a well developed spiral ornamentation; nucleus inclined with low malleate ornamentation in the margins; protoconch-2 bulbous, smooth, often clearly demarcated from the teleoconch by an axial line or riblet; two (rarely three) spiral ribs develop simultaneously slightly after the protoconch-teleoconch boundary; the upper spiral bounds a well defined subsutural ramp on early teleoconch whorls; further development of ornament on later teleoconch whorls includes increase or reduction of spiral bands and, in some species, the development of more profound axial elements; growth lines prosocline; columellar folding occurs in one species and is hinted at in at least two other; corkscrew-like coiling of the columella occurs in various species; shell usually imperforate, but occasionally with a well-developed umbilicus.

Range – Miocene, northwest South America; extant Tapajos River, Brazil (Wesselingh, 2000).

Remarks – *Dyris* is distinguishable from *Feliconcha* by the development of two, sometimes three spiral ribs after the often well demarcated protoconch-teleoconch boundary at 1.6-2.3 whorls. *Dyris* species are generally dominated by spiral ornamentation and *Tryonia* species by axial ribs. The onset of teleoconch ornamentation in *Dyris* species consists of two or three well-defined spiral keels with a well-developed subsutural ramp above. Pebasian *Tryonia* species are characterised by the gradual development of one or two low and rounded keels after protoconch-teleoconch boundary, that in subsequent whorls become replaced by axial ribs as the predominant type of ornament. Spirals usually disappear and the subsutural ramp is in general less developed than in *Dyris*. For additional comments on the distinction between both genera, the reader is referred to the introductory remarks on the Cochliopidae above. *Dyris* is by far the most specious genus in the Pebas fauna, with 26 species accepted, but the number is bound to rise somewhat with further work.

Dyris ortoni (Gabb, 1869)

Figs. 15j, 49, 50.

1869 *Mesalia ortoni* Gabb, p. 195, pl. 16, fig. 3.
1871 *Odostomia*? Woodward, p. 103, pl. 5. fig. 4a, b.
1871 *Isaea (Mesalia) ortoni* (Gabb); Woodward, p. 108.
1871 *Isaea ortoni* (Gabb); Conrad, p. 193, pl. 10, figs. 10, 13.
1878 *Hydrobia (Isaea) ortoni* (Gabb); Boettger, p. 490, pl. 13, figs. 8, 9.
1878 *Hydrobia (Isaea) confusa* Boettger, p. 491, pl. 13, figs. 4-7.
1924 *Isaea (Mesalia) ortoni* Gabb; Roxo, p. 49.
1938 *Hydrobia (Conradia) ortoni* (Gabb); de Greve, p. 79, pl. 1. figs. 5, 6.
1938 *Hydrobia (Conradia) confusa* Boettger; de Greve, p. 80, pl. 1. figs. 1-4.
1966 *Hydrobia confusa* Boettger; Willard, p. 65, pl. 63, figs. 3, 4.
1966 *Isaea ortoni* (Gabb); Willard, p. 66, pl. 63, figs. 1, 2.
1990 *Dyris ortoni* (Gabb); Nuttall, p. 200, figs. 104-112.
2002 *Dyris ortoni* (Gabb); Wesselingh *et al.*, fig. 3e.

Material studied – INGEMMET TN33, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996. RGM 456 418, same locality.

Extended diagnosis – Mainly smooth, hydrobiiform shell; SA 26-28°; nucleus smooth, inclined and separated from the remainder shell at *c.* 0.5 whorls by a fine spiral thread; protoconch-teleoconch boundary at *c.* 1.7-2.1 whorls marked by a similar fine axial thread; two weak, well-defined spirals developed at a quarter and a half of the whorl-height; upper spiral may bound a steeply dipping sutural ramp; in the subsequent whorl up to four spirals are present, but these disappear on later whorls; growth lines prosocline; whorl profile at first convex, progressively becoming flatter; aperture drop-shaped, margins not thickened; parietal adnate; columellar lip bounds a rimate umbilicus.

Dimensions – INGEMMET TN33: H 11.6; W 4.4; Hap 3.3; *c.* 8.5 whorls. RGM 456 418: H 7.3; W 2.6; Hap 2.0; 7.6 whorls.

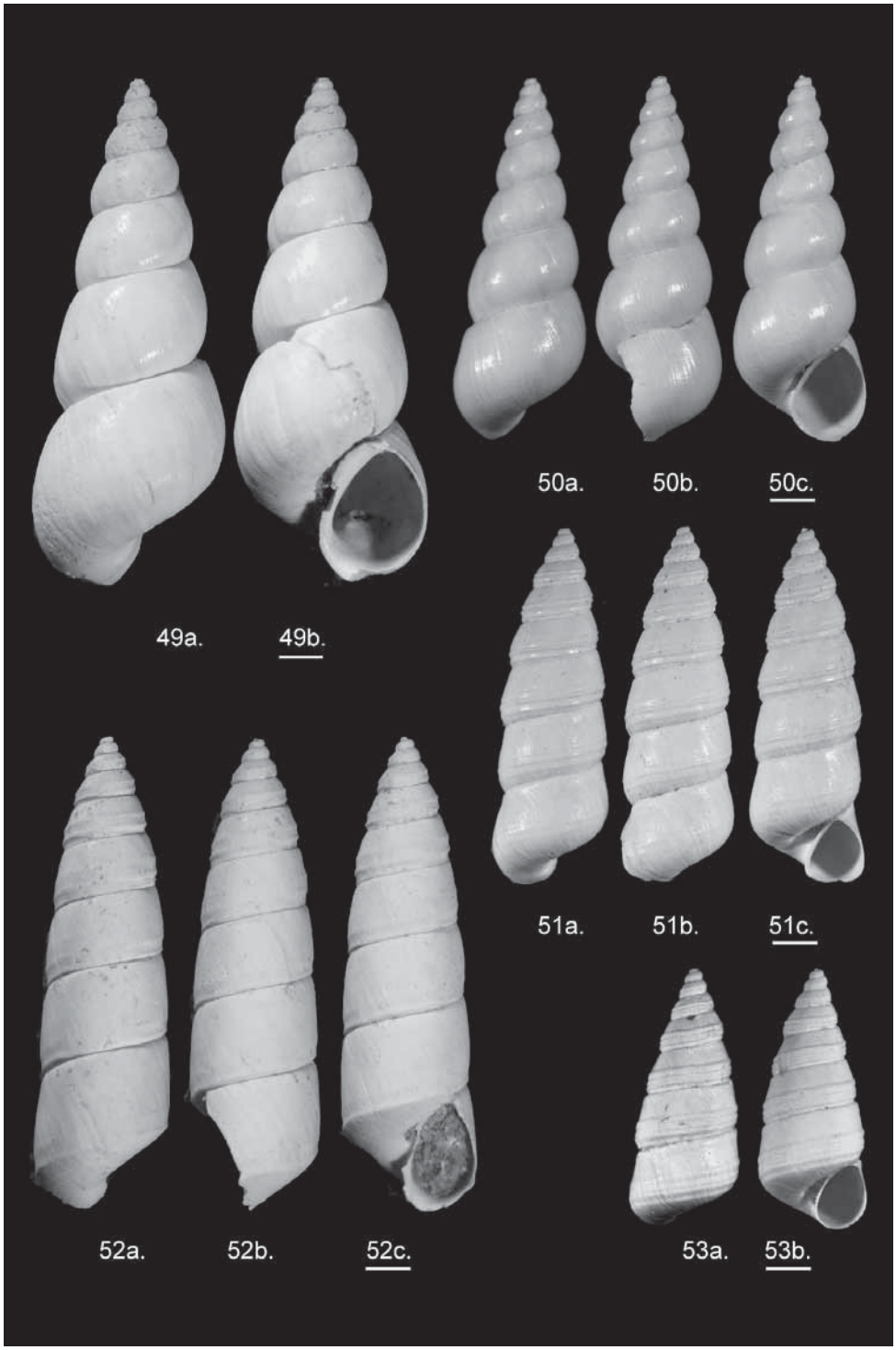
Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.

Remarks – This common species is found almost in the entire (stratigraphic) range of the Pebas Formation (Wesselingh *et al*., 2006a). Differences exist in the morphological variation of outliers in successive intervals and some forms appear to be characteristic for particular stratigraphic intervals. However, the few diagnostic morphological features of this species have precluded recognition of potential additional species.

Dyris pebasensis sp. nov.

Figs. 51-53.

1980 *Hydrobia tricarinata* Boettger; Costa, p. 878, pl. 1, figs. 5, 6.


50a.
50b.
50c.
49a.
49b.
51a.
51b.
51c.
52a.
52b.
52c.
53a.
53b.

Type material – INGEMMET TN34 (holotype), Pebas/Ave Maria (Loreto, Peru), exposure in north bank Amazon River, 1350 m east of naval base Pijoyal (base at 3°20'S 71°50'W), level F400 (0.3 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 21-8-1996. RGM 456 419 (paratype), same locality. RGM 456 420 (paratype), Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996.

Range – Pebas Formation, MZ7 (Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the village of Pebas (Loreto, Peru), in the vicinity of which this species has been found.

Diagnosis – Large, tightly coiled *Dyris*; SA 18-22°; two to three spiral ribs on the basal half of early teleoconch whorls that disappear on later whorls; increase in whorl width progressively less; maximum width attained near base of whorls; base of body whorl delimited by a rounded basal keel; shell imperforate to rimate.

Description – The apex is damaged in all material available, precluding observation of the nucleus and the protoconch. The onset of spiral ribs on the teleoconch is gradual. At first two spirals (at one quarter and half the height of the whorl) are formed, often followed by a third and occasionally a fourth spiral within a whorl. The spirals are located on the lower half of the whorl; the upper spiral bounds a poorly defined, steeply dipping, smooth subsutural ramp. The interspaces are slightly concave. Spirals can be at a regular distance or the upper or lower spiral may be located about twice as far apart from the adjoining rib as the distance between the other ribs. However, these distances, as well as the strength of the ribs, remain constant throughout the shell, although the ribs become progressively more confined to the basal part of the whorls. On the later teleoconch whorls, the spiral ribs become lower and less distinct, and may even disappear. The prosocline growth lines are numerous and fine. Very fine, microscopic, irregular grooves occur on the entire surface. The whorl profile on early teleoconch whorls is somewhat rounded, with an impressed suture, becoming progressively flatter with a

◀ Figs. 49, 50. *Dyris ortoni* (Gabb, 1869).

Fig. 49. INGEMMET TN33, Tamshiyacu (Loreto, Peru). a, rear view. b, front view.
Fig. 50. RGM 456 418, same locality as Fig. 49. a, rear view. b, lateral view. c, front view.

Figs. 51-53. *Dyris pebasensis* sp. nov.

Fig. 51. INGEMMET TN34, holotype, Pebas/ Ave Maria (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 52. RGM 456 420, paratype, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 53. RGM 456 419, paratype, Pebas/ Ave Maria (Loreto, Peru). a, rear view. b, front view.

Scale bars represent 1 mm.

shallower suture. The maximum width shifts from about midwhorl on the early teleoconch to about a quarter of the whorl height later on the shell. The base of the body whorl can be broadly rounded (as in the holotype), but can also be formed by a rounded angle corresponding to the lower spiral. The base is flat, but becomes entrenched into a deep umbilicus. The aperture is subrounded to drop-shaped with a wide base. The apertural margins are thin. Only the upper part of the aperture is adnate. The top of the aperture may be slightly bulbous, thus giving the body whorl a somewhat shouldered appearance.

Dimensions – INGEMMET TN34: H 7.5; W 3.4; Hap 1.6; >8.7 whorls. RGM 456 419: H 5.4; W 2.3; Hap 1.4; >7.6 whorls. RGM 456 420: H 10.0; W 2.8; Hap 2.5; >9.2 whorls.

Remarks – The large, smooth outline of *Dyris pebasensis* resembles that of *D. ortoni.* The latter has a more convex whorl profile and lacks the basal keel bounding the base of the body whorl.

Dyris tricarinatus (Boettger, 1878)

Fig. 54.

1871 *Isaea tricarinata* Conrad; Woodward, p. 108 (*nomen nudum*).
1878 *Hydrobia (Isaea) confusa* Boettger, p. 491, pl. 13, figs. 4-7.
1878 *Hydrobia (Isaea) tricarinata* Boettger, p. 492, pl. 13, figs. 10, 11.
1938 *Hydrobia (Conradia) tricarinata* Boettger; de Greve, p. 81, pl. 1, figs. 7-9.
1966 *Hydrobia tricarinata* Boettger; Willard, p. 65, pl. 62, figs. 4-6.
1990 *Dyris tricarinata* (Boettger); Nuttall, p. 190 (*pars*), figs. 63, 66, 67 (*non* figs. 59-62, 64, 65, 68-78).

Material studied – RGM 456 417, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F535 (6.3 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN95, same locality.

Extended diagnosis – Small to intermediate in size (H 6), spirally ornamented hydrobiiform hydrobiid, with a distinct sutural ramp; SA *c.* 28°; nucleus (diameter *c.* 40 µm) smooth and inclined, separated from the remainder of the shell at *c.* 0.5-0.55 whorls by a fine spiral thread and a very low axial depression; protoconch-teleoconch boundary at *c.* 1.6-1.8 whorls marked by a very poorly visible, fine axial thread; two to three well-defined, regularly spaced spirals develop well after the boundary; upper spiral bounds characteristic, smooth, steeply dipping straight to slightly concave sutural ramp; a fourth spiral develops at the base of the whorl, forming a suprasutural ridge; growth lines prosocline; whorl profile at first convex, but progressively flatter; aperture semicircular, margins not thickened; parietal adnate; columellar lip bounds a rimate umbilicus.

Dimensions – RGM 456 417: H 4.8; W 2.0; Hap 1.4; 7.0 whorls.

Range – Pebas Formation, MZ4 - MZ9 (late Early - early Late Miocene), Peruvian and Colombian Amazonia.

***Dyris lataguensis* sp. nov.**
Figs. 55-59.

1990 *Dyris tricarinata* (Boettger); Nuttall, p. 190 (*pars*), figs. 72, 73 (*non* figs. 59-71, 74-78).

Type material – RGM 456 544 (holotype), La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 9-11'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. RGM 456 545 - 456 548 and UNC nn. (all paratypes), same locality.

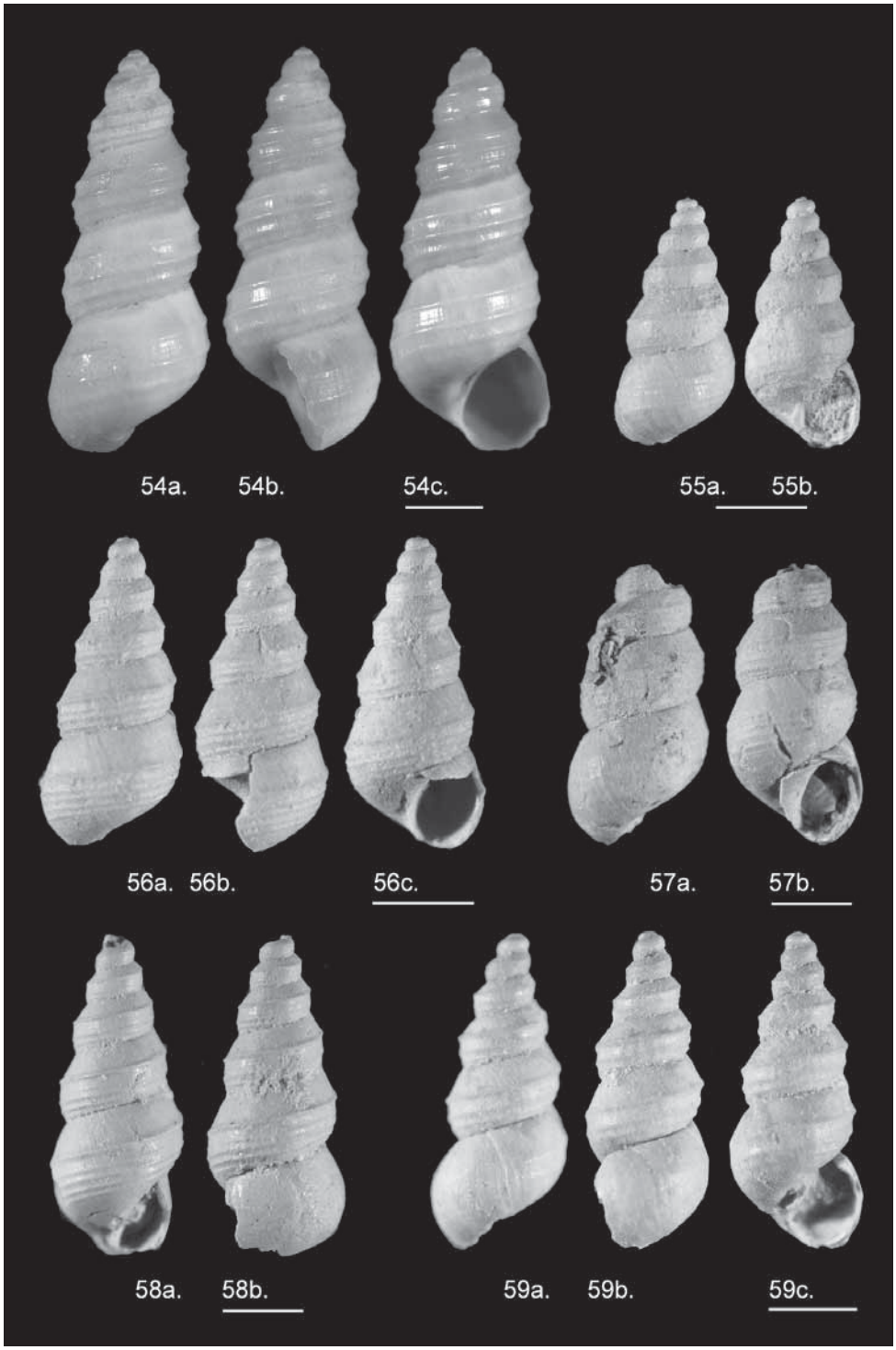
Range – Pebas Formation, MZ2 - MZ4 (late Early - early Middle Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Named after the village of La Tagua (Putumayo, Colombia), in the vicinity of which this species has been found.

Diagnosis – Small (H 3), spirally ornamented hydrobiiform shell, with a distinct sutural ramp covering the upper half of the whorls, giving the shell a slightly carinate to shouldered outline; SA 35-38°; spiral ornament of two to three primary spirals, the upper of which is slightly pronounced and rather sharp; up to five secondary spiral ribs may develop.

Description – The nucleus (diameter 50-60 µm) is slightly inclined. The embryonic shell is separated from the remainder of the protoconch by a very fine axial thread at *c.* 0.3 whorls. The remainder protoconch has rather convex whorls and a somewhat impressed suture. At *c.* 1.9 whorls, a very poorly visible lineament marks the protoconch-teleoconch boundary. Two spiral ribs develop gradually on the first 0.5 teleoconch whorls located at about one fifth and three fifths of the whorl height. The upper spiral becomes slightly pronounced and is sharp, that is, it has well-defined walls. It bounds a straight subsutural ramp above. The position of the spirals lowers on subsequent whorls, the upper rib becoming positioned about half the height of the whorl. Up to six secondary spiral ribs can develop between and below the primary spirals. Some of these may reach a similar strength as the primaries. Distances between ribs are uneven. The spiral ornamentation fades on the body whorl. Growth lines are numerous, very fine and slightly prosocline. The rounded base of the body whorl usually is smooth, but some fine spirals may also be present. The whorl profile is depressed shouldered to carinate on early teleoconch whorls and rounded on the body whorl. The suture is shallow. The aperture is damaged in all material available; it appears to be semicircular. The parietal margin is adnate; the columellar lip may be slightly expanding. The basal and outer lip are invariably broken. The shell is imperforate.

Dimensions – RGM 456 544: H 3.1; W 1.35; Hap 0.8; 6.6 whorls. RGM 456 545: H 2.6; W 1.25; Hap 0.85; 6.1 whorls. RGM 456 547: H 3.9; W 1.65. RGM 456 546: H 3.5; W 1.4; Hap 0.9; 6.7 whorls. RGM 456 548: H 3.3; W 1.6; Hap 1.0.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56c.
57a.
57b.
58a.
58b.
59a.
59b.
59c.

Remarks – This species resembles *Dyris tricarinatus* in the general outline and the well-defined straight subsutural ramp. In *Dyris lataguensis*, however, the subsutural ramp is larger, the upper spiral is often slightly pronounced and sharp (it is rounded in *D. tricarinatus*), and there is a large variation of secondary spiral ribbing lacking in the latter.

Dyris lintea (Conrad, 1871)

Figs. 62, 63.

1871 *Isaea lintea* Conrad, p. 193, pl. 10, fig. 6.
? 1878 *Hydrobia (Isaea) lintea* (Conrad); Boettger, p. 492.
? 1924 *Isaea lintea* Conrad; Roxo, p. 49.
1938 *Hydrobia (Conradia) lintea* (Conrad); de Greve, p. 83, pl. 1, figs. 10-30.
1990 *Dyris lintea* (Conrad); Nuttall, p. 190 *(pars),* figs. 49-53 (*non* figs. 54-58).

Material studied – INGEMMET TN55, Mishana (Loreto, Peru), exposure in south bank Rio Nanay, 100 m west of landing stage (3°52'S 73°29'W), level F72 (at DL). Pebas Formation, MZ8 (late Middle - early Middle Miocene); leg. F.P. Wesselingh, 10-1991. RGM 456 477, same locality.

Extended diagnosis – Large, rather plump and thick-shelled *Dyris*; SA 25-29°; 6-9 irregularly spaced, robust, often flat spiral ribs with irregularly sized interspaces (sometimes grooves) in between; upper spiral forms rounded, very narrow shoulder; adult whorls straight-sided to slightly concave; base of body whorl subrounded to flat with fine, irregularly spaced spirals; growth lines slightly prosocline and somewhat sigmoid; aperture adnate, ovate, usually damaged; inner lip callus slightly thickened, hardly expanding; shell imperforate.

Dimensions – INGEMMET TN55: H 9.1; W 3.3; Hap 3.6; >7.2 whorls. RGM 456 477: H 6.2; W 2.5; Hap 2.0; >7.0 whorls.

Range – Pebas Formation, MZ5 - MZ8 (late Early - early Late Miocene), Peruvian Amazonia.

◀ Fig. 54. *Dyris tricarinatus* (Boettger, 1878). RGM 456 417, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Figs. 55-59. *Dyris lataguensis* sp. nov.

Fig. 55. RGM 456 545, paratype, La Tagua (Putumayo, Colombia). a, rear view. b, front view.
Fig. 56. RGM 456 544, holotype, same locality as Fig. 55. a, rear view. b, lateral view. c, front view.
Fig. 57. RGM 456 548, paratype, same locality as Fig. 55. a, rear view. b, front view.
Fig. 58. RGM 456 547, paratype, same locality as Fig. 55. a, rear view. b, front view.
Fig. 59. RGM 456 546, paratype, same locality as Fig. 55. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

***Dyris hershleri* sp. nov.**
Figs. 60, 61.

Type material – RGM 456 426 (holotype); Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996. INGEMMET TN36 (paratype) and RGM 456 427 (two damaged sub-adult paratypes), same locality.

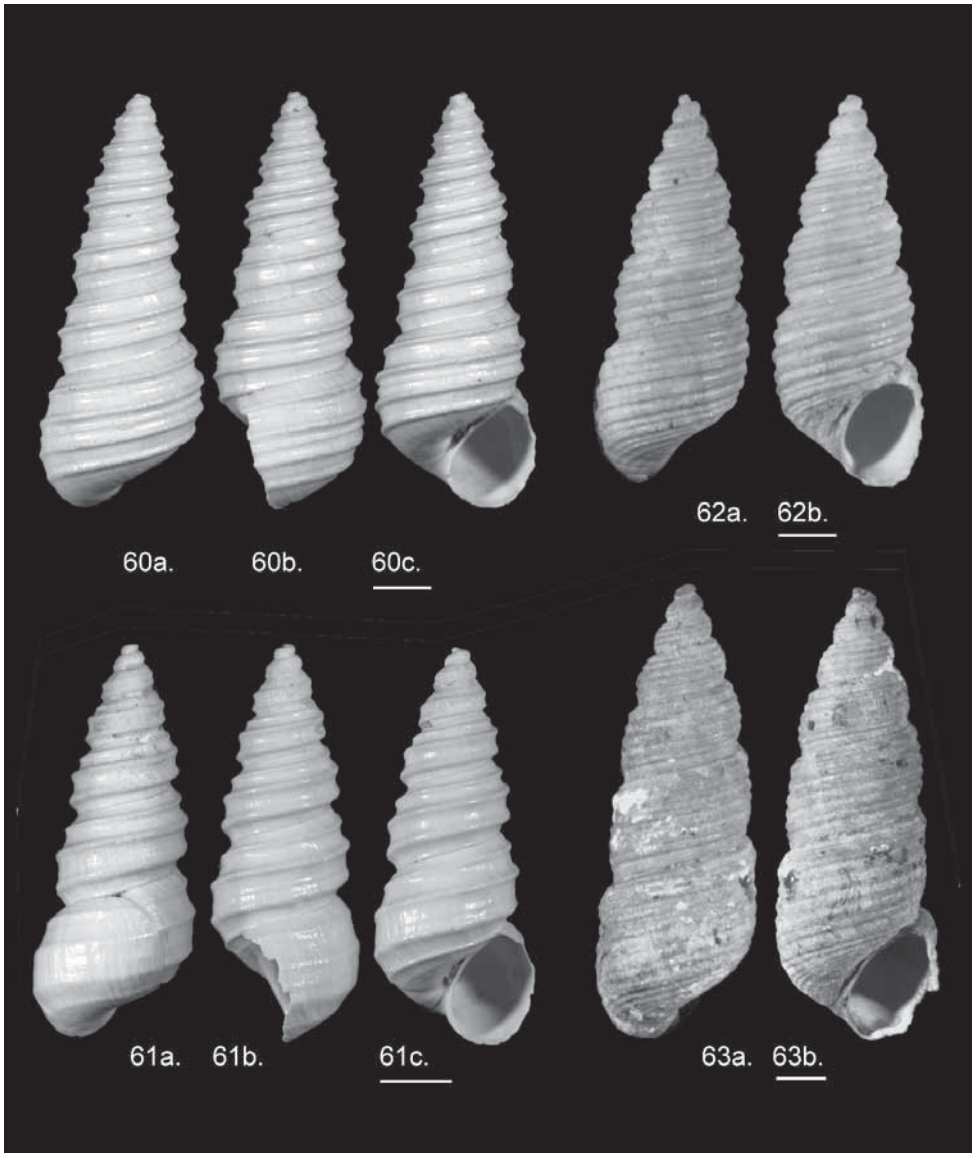
Range – Pebas Formation, MZ6 - MZ7 (Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after Robert Hershler (USNM, Washington, D.C.) in honour of his extensive work on cochliopid snails.

Diagnosis – Thin, hydrobiiform shell (SA 27-29°) with two well defined spiral keels on early teleoconch whorls, increasing to four primary and several secondary keels on later teleoconch whorls; suture in a progressively well-defined sutural depression; primary keels remain strong throughout; aperture subrounded with thin margins; shell narrowly rimate to imperforate.

Description – The nucleus is flat to very slightly inclined and has a diameter of approximately 60 µm. The protoconch is separated from the teleoconch by a very fine axial constriction at 1.7-2.1 whorls. At the protoconch-2, the whorl profile is convex with a deep suture. Soon after the protoconch-teleoconch boundary, two spiral ribs develop at one third and two thirds of the whorl height, the upper of which bounds a well-developed subsutural ramp. Within a whorl a third spiral may become visible on the base of the whorl that subsequently migrates slightly upward. On most specimens this basal keel only becomes apparent at the penultimate whorl or body whorl. At the second teleoconch whorl a spiral rib develops gradually (first as a broad, rounded zone, later more erect and well-defined), located just below the upper suture. This rib fills the subsutural ramp. The ribs are separated by concave interspaces, about three times as wide as the ribs, although distances between ribs may be uneven. Ribs remain for most of the shell at the same, occasionally uneven distances. The suture is adnate and located in a well-defined sutural depression bounded by spiral ribs on later teleoconch whorls. Thin secondary ribs may develop on the penultimate whorl and the body whorl, usually first between the second and third primary spiral, later between the other ribs. The primary ribs broaden and lower slightly on the last two whorls. Growth lines are numerous and slightly prosocline. At intersections with the spirals in the last whorls they may develop very low, irregular and hardly visible tubercles. The aperture is semicircular, broadly rounded below and subrounded in the top. The apertural margins are thin. The upper one fifth of the inner lip is adnate, the remainder forms a sharp, thin, erect inner wall that covers most of the umbilical area, where a rimate umbilicus may still be visible in some of the specimens.

Dimensions – RGM 456 426: H 7.2; W 3.8; Hap 2.0; >7.6 whorls. INGEMMET TN36: H 5.5; W 2.2; Hap 1.6; >7.1 whorls.



Figs. 60, 61. *Dyris hershleri* sp. nov.

Fig. 60. RGM 456 426, holotype, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 61. INGEMMET TN36, paratype, same locality as Fig. 60. a, rear view. b, lateral view. c, front view.

Figs. 62, 63. *Dyris lintea* (Conrad, 1871).

Fig. 62. RGM 456 477, Mishana (Loreto, Peru). a, rear view. b, front view.
Fig. 63. INGEMMET TN55, same locality as Fig. 62. a, rear view. b, front view.

Scale bars represent 1 mm.

Remarks – This species shares similarities with *Dyris tricarinatus* and *D. lintea*. The more convex whorl-profile, infill of the subsutural ramp by a spiral rib and continuous strength of the spiral ribs make *D. hershleri* different from *D. tricarinatus*. *Dyris lintea* has flatter sides, more ribs that also develop more irregularly, even flattening and produce grooves in some specimens, and has the largest width of the whorls at about a quarter of the whorl height (approximately half the height in *D. hershleri*). It also lacks the characteristic sutural depression of the latter species.

Dyris gracilis Conrad, 1874a

Figs. 64-66.

1874a *Dyris gracilis* Conrad, p. 195, pl. 10, fig. 8, pl. 11, fig. 7.
1990 *Dyris gracilis* Conrad; Nuttall, p. 186 (*pars*), figs. 41, 42 (*non* figs. 43-48, 545-555).

Material studied – RGM 456 482, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F686 (5.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996. RGM 456 483, same locality, level F685 (3.0 m above DL). INGEMMET TN56, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F533 (5.9 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996.

Dyris cf. *gracilis*: RGM 456 484, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F685 (3.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996.

Extended diagnosis – High-spired (SA *c.* 14°), thin-shelled, turritelliform gastropod; shell ornamented with typically four thin, sharp spiral ribs at regular distances, separated by concave interspaces that are two to three times as wide; nucleus smooth (diameter 40-50 µm), slightly inclined; axial thread at 0.5 whorls separates the embryonic shell from the remainder protoconch; protoconch-teleoconch boundary at 2.0-2.1 whorls marked by another fine axial thread, soon followed by the gradual development of two spirals at two fifths and four fifths of the whorl height, followed within a whorl by a third basal spiral and on later whorls by a fourth; subsutural ramp well developed; spirals become located at equal distances and grow equally strong giving the shell a regular ornament; fifth basal spiral bounds smooth and flat base of body whorl; suture located in a marked sutural depression bounded by ribs above and below; growth lines very delicate, slightly prosocline; aperture adnate, semilunate-subovate; parietal callus thin, but robust and slightly expanding; columellar lip slightly thickened; columella tightly corkscrew coiled; shell imperforate.

Dimensions – RGM 456 482: H 5.3; W 1.2; Hap >0.8; 10.0 whorls. RGM 456 483: H 4.2; W 1.15; Hap 0.9; 9.1 whorls. INGEMMET TN56: H 5.4; W 1.35; Hap 1.15; 9.1 whorls.

Range – Pebas Formation, MZ6 - MZ7 (Middle Miocene), Peruvian Amazonia. In samples from MZ4 and MZ5 intervals, some as of yet unsatisfactorily identified *Dyris* specimens were found that show similarities with *D. gracilis*. Further investigation may extend the stratigraphic range of this species.

Remarks – *Dyris gracilis* appears to be a morphologically very constant species. However, forms co-occur that closely resemble *D. gracilis*, but seem not to be connected through intermediate forms to the typical form (Fig. 66; *D.* cf. *gracilis*). Such specimens tend to have slightly broader, rounded spiral ribs, typically five instead of four (six or seven on body whorl) that are located at slightly irregular distances. Pending further study, these forms are attributed with a query to *D. gracilis*.

***Dyris microbispiralis* sp. nov.**

Figs. 67-69.

1990 *Dyris gracilis* Conrad; Nuttall, p. 186 (*pars*), fig. 47a, b (*non* figs. 41-46, 48, 545-555).

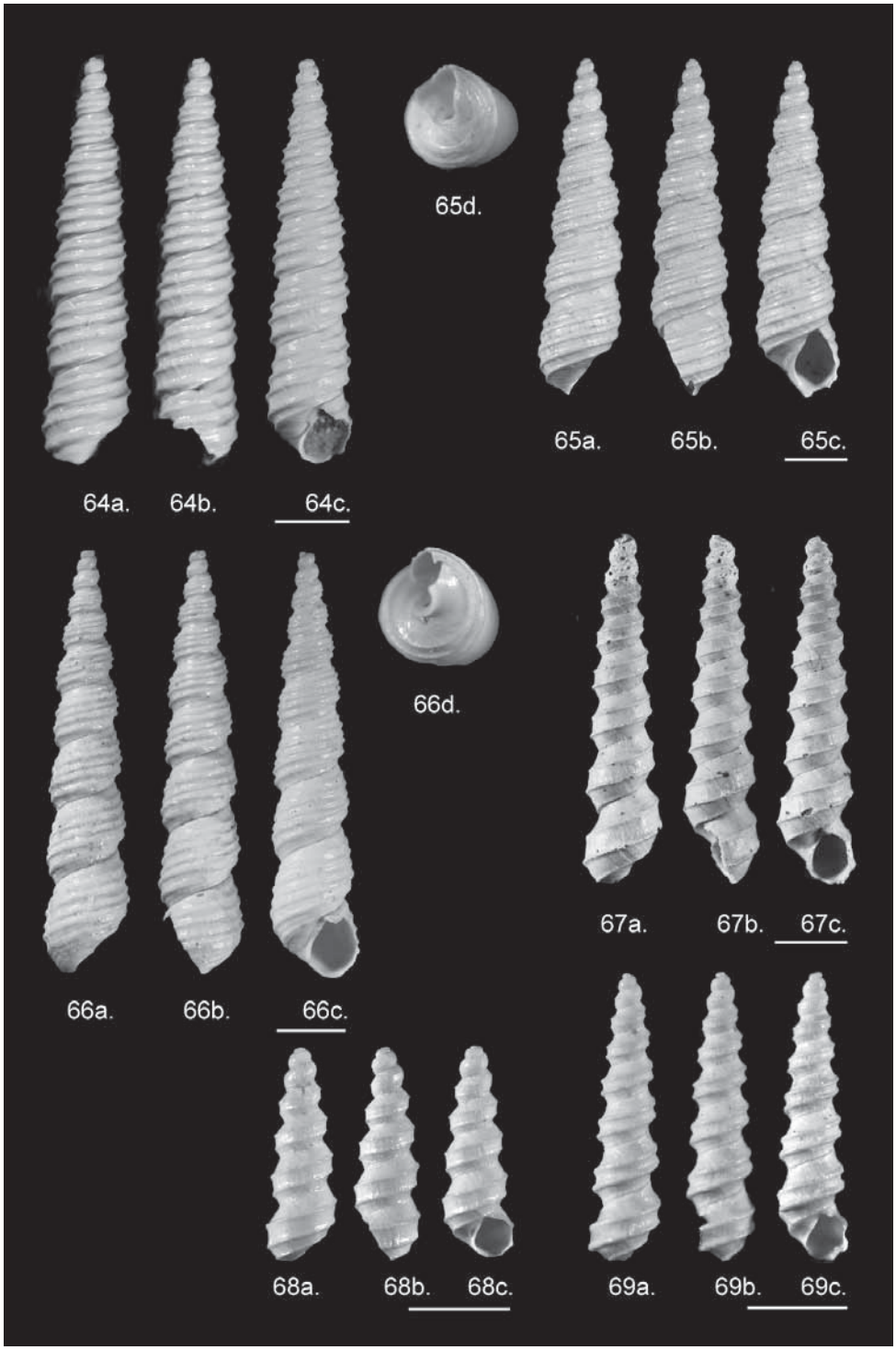
Type material – INGEMMET TN57 (holotype), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F532 (5.7 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. RGM 456 486 (paratype), same locality, level F533 (5.9 m above DL). RGM 456 485 (paratype), Puerto Almendras (Loreto, Peru), exposure in east bank Rio Nanay, at landing stage (3°49'S 73°22'W), level F835 (1.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 15-9-1996.

Range – Pebas Formation, MZ7 (Middle Miocene), Peruvian Amazonia.

Derivatio nominis – *Micro* for its small size; *bispiralis* for the two robust and prominent spiral ribs that dominate the outline of this species.

Diagnosis – High-spired (SA 14-16°), small, thin-shelled *Dyris* with two prominent spiral ribs; subsutural and suprasutural ramp about as large, producing a distinct sutural depression; columella tightly coiled.

Description – The nucleus (diameter *c.* 40 µm) is slightly inclined. The embryonic shell is separated from the remainder of the protoconch by a fine axial constriction at *c.* 0.5-0.7 whorls. The protoconch is smooth and has a convex perimeter with a rather deep suture. At *c.* 2.4 whorls, the teleoconch ornament gradually starts to develop. It consists of two spiral ribs, first at about a quarter and then two thirds of the whorl height. The ribs gain in strength and become located at one third and two thirds of the whorl height. The ribs are delicate, yet robust. In between, the perimeter of the shell is straight to slightly concave. The slightly concave subsutural ramp is about as high as the suprasutural ramp and together form a prominent sutural depression. The shell has a distinct bicarinate outline. A low spiral rib becomes visible at the lower suture in later teleoconch whorls. This spiral bounds the base of the body whorl. Growth lines are fine and slightly prosocline as well as slightly sigmoid. The semilunate aperture is adnate and the apertural margins are thin. The outer lip is invariably broken in adult specimens. The basal lip is broadly and shallowly retracted. The parietal lip is short, located within the aperture and contains a very narrow, thin, non-expanding parietal callus. It flushes into the larger columellar lip that is formed by the non-thickened columella. The base of the columellar lip can be located to the left of the axis of the shell. The columella is tightly coiled corkscrew-wise. The shell is imperforate.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68a.
68b.
68c.
69a.
69b.
69c.

Dimensions – INGEMMET TN57: H 4.9; W 1.1; Hap 0.9. RGM 456 485: H 2.8; W 0.75; Hap 0.5; 8.4 whorls. RGM 456 486: H 2.0; W 0.7; Hap 0.5; 6.8 whorls.

Remarks – The species is easily distinguished from other small and high-spired *Dyris* species by the characteristic two robust and regularly developed spiral ribs.

***Dyris renemai* sp. nov.**

Figs. 70-72.

Type material – RGM 456 487 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 488 (paratype, fragment), same locality. INGEMMET TN58 (paratype), Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42 (4°04'S 73°25'W), level F367a (1.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 11-8-1996.

Range – Pebas Formation, MZ8 - MZ12 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – Named after Dr W. Renema (Naturalis, Leiden, the Netherlands), who has supported me throughout this work in a variety of ways.

Diagnosis – Small, high-spired *Dyris* (SA *c.* 19°) with two primary spirals on early teleoconch whorls and a distinct bicarinate outline; on later teleoconch whorls up to five primary spirals present, added with secondary spirals and a distinctly rounded whorl profile with deep suture; spiral cords may contain poorly defined elongate, low tubercles; columella coiled, corkscrew-like.

◀ Figs. 64-66. *Dyris gracilis* Conrad, 1871.

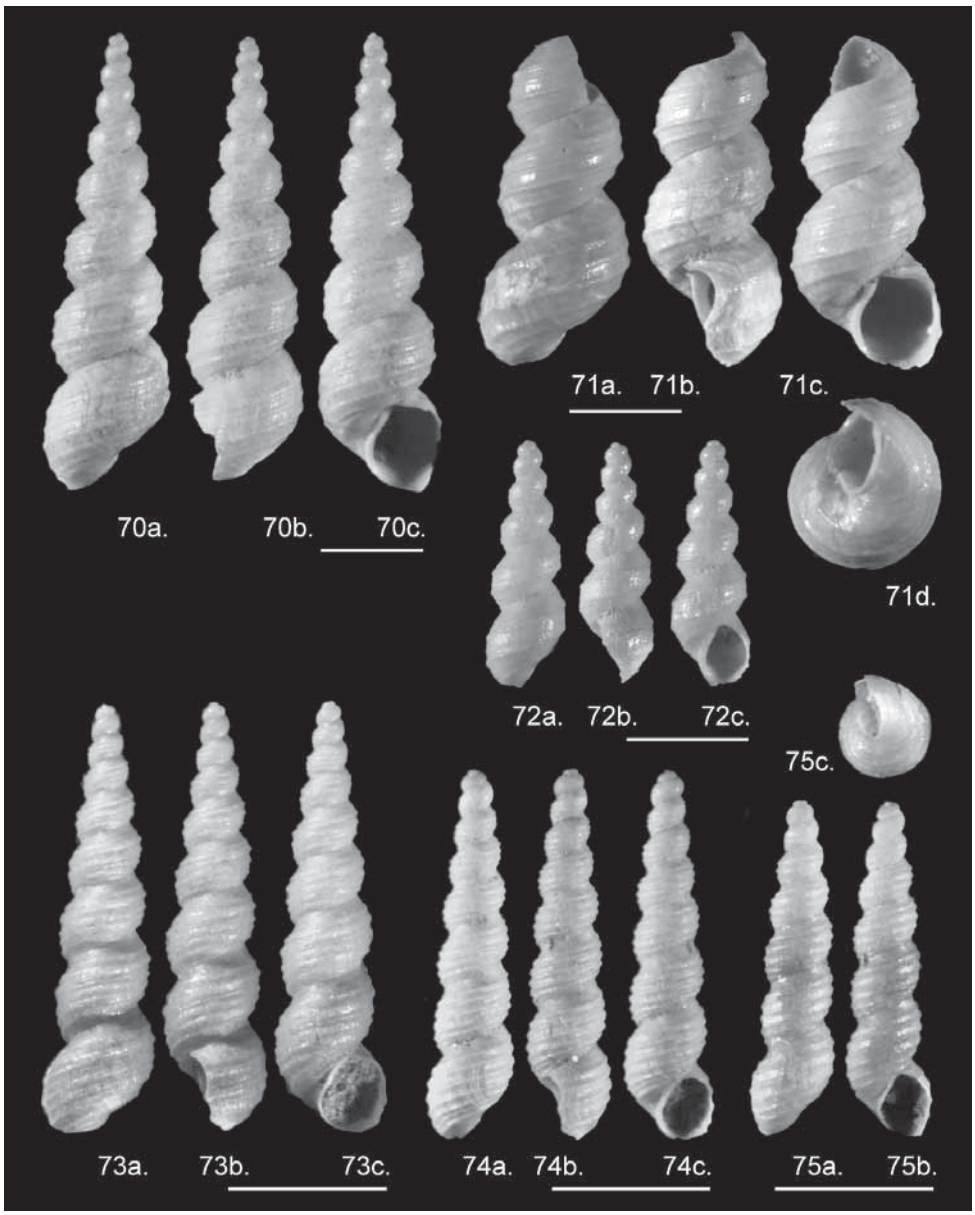
Fig. 64. RGM 456 482, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 65. INGEMMET TN56, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 66. *Dyris* cf. *gracilis* Conrad, 1871, RGM 456 484, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Figs. 67-69. *Dyris microbispiralis* sp. nov.

Fig. 67. INGEMMET TN57, holotype, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 68. RGM 456 486, paratype, same locality as Fig. 67. a, rear view. b, lateral view. c, front view.
Fig. 69. RGM 456 485, paratype, Puerto Almendras (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

Description – The nucleus (diameter *c.* 30 µm) is inclined and contains very poorly defined, low marginal malleate wrinkles. The boundary between the embryonic shell and the protoconch-2 is very poorly delimited. The first 0.7 whorls are coiled in plane, but the remainder of the protoconch is markedly bulbous with a deep suture. The protoconch-teleoconch boundary is marked by a very fine axial constriction at 1.7-2.3 whorls. Densely packed growth lines occur at first. Within 0.1-0.4 whorls after the boundary, two spiral ribs develop at one third and two thirds of the whorl height. The



upper one bounds a straight subsutural ramp, the lower an equally sized suprasutural ramp. These ramps together form a prominent sutural depression that give the early teleoconch a distinctly bicarinate outline. At the third or fourth teleoconch whorl the profile becomes more rounded, and a third and a fourth spiral develop between and below the earlier spirals. The spiral ribs are rounded, and may contain low, very poorly defined, elongate tubercles, especially on the upper and the lower ones. Thin, often poorly defined and low secondary spirals may develop on later teleoconch whorls as well. A spiral rib may be present at the lower suture. Growth lines are fine, prosocline and sigmoid. The whorl profile becomes progressively rounded with a deep suture. The base of the body whorl is poorly defined and rounded. The aperture is subquadrate. The parietal wall is lacking and the top of the columellar lip disappears below the upper part of the outer lip. The outer and basal lips are thin. The outer lip, when viewed from aside, describes an inverted 'S'. The basal lip is broadly retracted (Fig. 71d). The inner lip is formed by the slightly reinforced columella that is coiled like a corkscrew. The inner lip margin may be slightly thickened and elevated, but is otherwise adnate. The shell is imperforate.

Dimensions – RGM 456 487: H 4.9; W >1.3; Hap 1.3; *c.* 9.2 whorls. RGM 456 488: H 2.8; W 1.3; Hap 0.9. INGEMMET TN58: H 2.0; W 0.65; Hap 0.4; 6.0 whorls.

Remarks – The protoconch and early teleoconch whorls of *D. renemai* are almost identical to those of *D. microbispiralis*. However, after the second teleoconch whorl the two spirals as well as the bicarinate whorl profile are maintained in the latter, whereas the former develops at least two other primary spirals (sometimes three), as well as secondary spirals. The whorl profile of *D. renemai* becomes distinctly rounded.

***Dyris microturritella* sp. nov.**
Figs. 16h, 17d, 73-75.

Type material – INGEMMET TN59 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W),

◀ Figs. 70-72. *Dyris renemai* sp. nov.

Fig. 70. RGM 456 487, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 71. RGM 456 488, paratype, same locality as Fig. 70. a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 72. INGEMMET TN58, paratype, Nuevo Horizonte (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Figs. 73-75. *Dyris microturritella* sp. nov.

Fig. 73. INGEMMET TN59, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 74. RGM 456 489, paratype, same locality as Fig. 73. a, rear view. b, lateral view. c, front view.
Fig. 75. RGM 456 490, paratype, same locality as Fig. 73. a, rear view. b, lateral view. c, basal view.

Scale bars represent 1 mm.

level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 489 and 456 490 (paratypes), same locality. RGM 456 609 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 621 and 456 609 (paratypes), same locality.

Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – *Micro* refers to the size; *turritella* refers to the resemblance of this species to *Turritella* species in general.

Diagnosis – Small, high-spired *Dyris* (SA 16-17°); whorl profile rounded; shell ornamented with up to six primary spirals; the median spirals lay furthest apart, ribs above and below progressively closer spaced; aperture subquadrate.

Description – The nucleus is strongly inclined and has a low mammilate ornament. At 0.45-0.55 whorls a fine opisthocline axial lineament marks the boundary between the embryonic shell and the protoconch-2. Thereafter, the protoconch becomes markedly bulbous with a deep suture. A fine axial thread marks the protoconch-teleoconch boundary at 1.8-2.3 whorls. Densely-spaced growth lines occur after this thread. Three spirals develop within 0.2 whorls after the boundary. Some variation exists as to the location and order of onset of the spiral ribs after the protoconch-teleoconch boundary. The spirals are rounded and the interspaces are about twice as wide. A subsutural ramp develops, but is less pronounced than in other small-sized, elongate *Dyris* species. A fourth and a fifth spiral develop on later teleoconch whorls, and sometimes a sixth and even a seventh at the base of the whorl. The median spirals are at equal distances. Distances between ribs above and below progressively decrease. Growth lines are almost obsolete. They are prosocline, sigmoid. The base of the body whorl is rounded. The adnate aperture is subquadrate. The columellar lip can be slightly erect and very slightly thickened. A thin inner lip callus is present that can be very slightly expanded in the parietal region. The leftmost margin of the inner lip (near the base) can be located slightly left of the shell's axis. When viewed from below, the base is broadly and shallowly retracted (Fig. 75c), and is thin, as is the outer lip. The top of the outer lip is produced. The shell is imperforate.

Dimensions – INGEMMET TN59: H 3.6; W 0.95; Hap 0.7; 9.1 whorls. RGM 456 489: H 2.45; W 0.65; Hap 0.45; 7.8 whorls. RGM 456 490: H 2.25; W 0.65; Hap 0.45; 7.7 whorls.

Remarks – The high spire, in general rounded whorl profile with up to seven, slightly unevenly spaced spiral ribs and comparatively poorly expressed sutural depression distinguish this taxon from other small, high-spired species, such as *D. gracilis*. *Dyris renemai* is slightly wider and has a characteristic bicarinate outline on early teleoconch whorls, lacking in *D. microturritella*, and may develop low tubercles on the spirals lacking in the latter as well.

***Dyris regularis* sp. nov.**
Figs. 76, 77.

Type material – INGEMMET TN30 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 401 (paratype), same locality.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

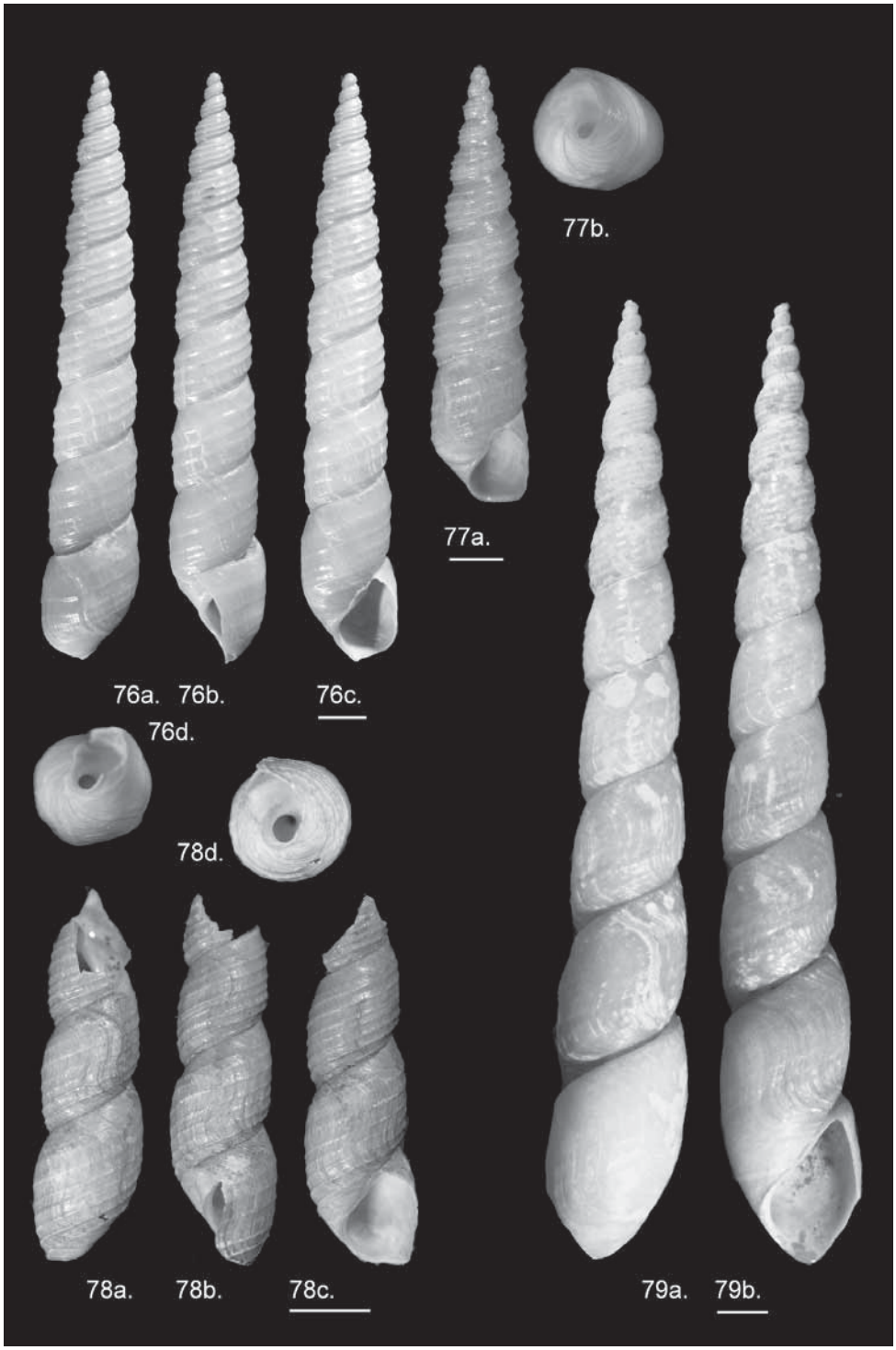
Derivatio nominis – Named after the regularly interspaced spiral ribs.

Diagnosis – High-spired (SA *c.* 11°), intermediate-sized, turritelliform, increasingly straight-sided *Dyris* with 3-4 very regular spiral ribs; columella openly coiled; base of columellar margin situated left of the axis of the shell.

Description – The nucleus is flat. At 0.5 whorls, an axial constriction marks the boundary between the embryonic shell and the protoconch-2, that is smooth and has a convex whorl profile. The protoconch-teleoconch boundary cannot be distinguished on the studied specimens. An ornament of three spiral ribs at one fifth, two fifths and three fifths of the whorl height develop gradually from 2.2 whorls onwards. The upper rib bounds a steep subsutural ramp. The ribs are equally strong and separated by slightly concave to flat interspaces at equal distances. The suture is located in a sutural depression formed by the sub- and suprasutural ramps. From the second teleoconch whorl onwards a fourth spiral rib develops at four fifths of the whorl height. Also, a poorly visible spiral develops at the base of the whorl at the suture, that may cover the latter rib. The growth lines are fine, prosocline and sigmoid. The subsutural ramp broadens on later teleoconch whorls and the regularly spaced spiral ribs are shifted slightly downward on the whorls. On the last 1.5 whorls, the ribs become lower and low, poorly defined secondary ribs may develop. The adnate aperture is inverted comma-shaped to lunate. The outer lip is thin and runs almost vertically, apart for the upper quarter that is broadly rounded. The basal lip is horizontal when viewed from the front and is broadly concave when viewed from below. The parietal wall is retracted below the upper part of the outer lip and has a very thin parietal callus. The columellar lip is prominent, its basal part expands well to the left of the axis of the shell. The columella is reinforced and describes a spiral. As a result, the shell is openly coiled when viewed from below. The shell is imperforate.

Dimensions – INGEMMET TN30: H 12.9; W 2.2; Hap 1.9; 12.5 whorls. RGM 456 401: H 8.1; W 2.0; Hap 1.8; 10.7 whorls.

Remarks – The relative flat sides, larger size, lowering and broadening of the spiral ribs, that are more numerous, and the more widely openly coiled columella distinguish this species from *Dyris gracilis*.


77b.
77a.
76a.
76b.
76c.
76d.
78d.
78a.
78b.
78c.
79a.
79b.

***Dyris elongatus* sp. nov.**
Figs. 15q, r, u, 78, 79.

Type material – RGM 456 402 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below Finca opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F60 (17.1 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 403 (fragment), RGM 456 404 (fragment), RGM 456 635 (sectioned shell) and UNC nn. (all paratypes), same locality.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – Named after the elongate outline (Latin: *elongatus* for prolonged).

Diagnosis – Very tall, high-spired (SA *c.* 12°), turritelliform to lanceolate, increasingly straight-sided *Dyris* with increasingly irregular spiral ribs, five on early teleoconch whorls, up to eight on body whorl; suture of later teleoconch whorls fissure-like; columella openly coiled; base of columellar margin distinctly left of the axis of the shell.

Description – The apical area of the studied specimens is damaged. Five spiral ribs on the holotype are seen on early teleoconch whorls that are situated at regular distances with a well-developed, steep subsutural ramp above and a narrow suprasutural ramp below. From the fifth teleoconch whorl onwards, the ribs broaden and become lower, and the distances between them start to vary slightly. Additionally, two poorly defined spiral ribs are added, and on the last few teleoconch whorls the ribs are so low and broad that the ornament has changed into very low, irregular grooves. Spiral ribs remain well defined on the body whorl only rarely. The body whorl may even have a smooth appearance. Growth lines are numerous, prosocline and sigmoid. Remains of a light-brown periostracum are seen on several of the specimens. Black collabral lines overlay the brown periostracum on RGM 456 404 (Fig. 15r). The sutural

◀ Figs. 76, 77. *Dyris regularis* sp. nov.

Fig. 76. INGEMMET TN30, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 77. RGM 456 401, paratype, same locality as Fig. 76. a, front view. b, basal view.

Figs. 78, 79. *Dyris elongatus* sp. nov.

Fig. 78. RGM 456 403, paratype, Santa Sofia (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 79. RGM 456 402, holotype, same locality as Fig. 78. a, rear view. b, front view.

Scale bars represent 1 mm.

depression is well defined on early teleoconch whorls, but becomes shallower and indistinct later on the shell, where the suture becomes a fissure. The base of the body whorl is very narrow and bounded by the reinforced, openly coiled, columellar margin of the aperture. The aperture is thin. The base is horizontal when viewed from the front, but when viewed from below it is broadly retracted. The outer lip is retracted furthest about halfway when viewed from the side, and is strongly expanding forward on the adapical side, where it overlays the small parietal wall that has a very thin callus and is located well within the aperture. The columellar lip is very prominent and formed by the reinforced columella. The basal part is well to the left of the axis of the shell. The openly coiled columella shows as a tube when the shell is viewed from below.

Dimensions – RGM 456 402: H 18.5; W 2.8; Hap 2.7; >12.6 whorls. RGM 456 403: H 9.4. RGM 456 404: H 6.4; UNC nn.: H 14.5; W 2.8; Hap 2.3.

Remarks – The shell closely resembles *Dyris regularis*, but is larger and has a more irregular ornament of five to eight spiral ribs at irregular distances, instead of a very regular ornament of three to four spiral ribs that are and remain at the same distance on the teleoconch, only to fade on the body whorl.

***Dyris romeroi* sp. nov.**
Figs. 17e, 80-83.

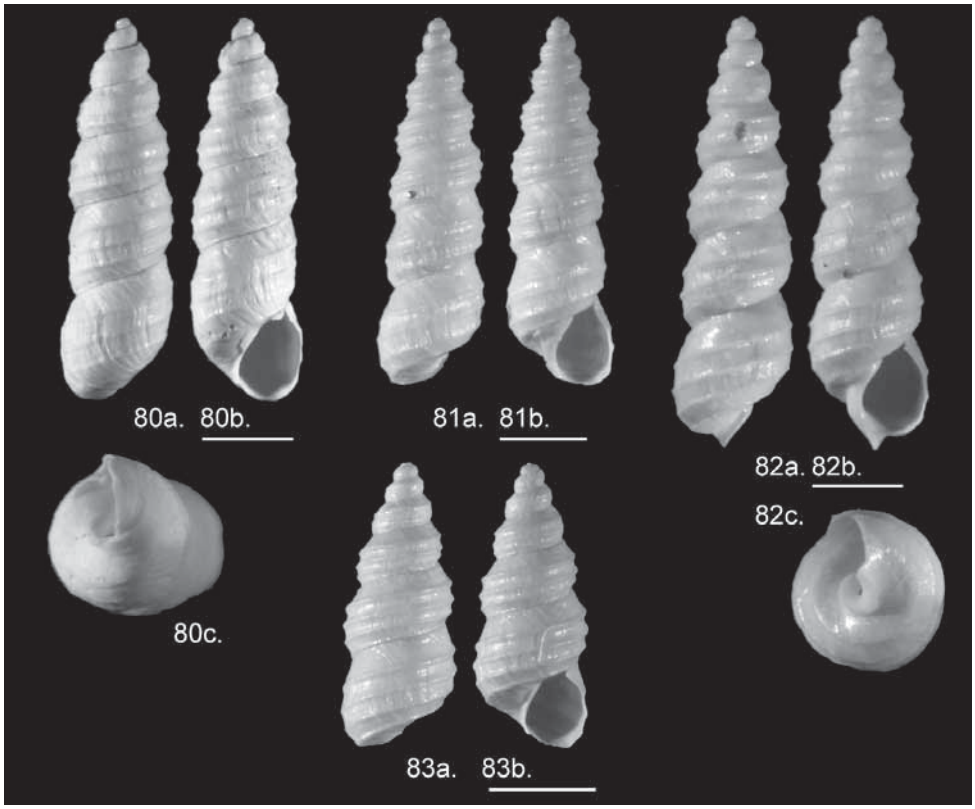
1980 *Dyris gracilis*? Conrad; Costa, p. 883, pl. 2, figs. 5, 6.

Type material – INGEMMET TN54 (holotype), Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42 (4°04'S 73°25'W), level F367a (1.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 11-8-1996. RGM 456 475 and 456 476 (paratypes), same locality. RGM 456 474 (paratype), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence Loreto Yacu (3°46'S 70°22'W), level F31 (7.8 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. UNC nn., same locality. RGM 456 623 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, MZ 9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.

Range – Pebas Formation, MZ8 - MZ11 (late Middle - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.

Derivatio nominis – Named after Prof. Dr Lidia Romero Pittmann (INGEMMET and Universidad San Marcos, Lima, Peru), in honour of her work on the palaeontology of Peru.

Diagnosis – Intermediate-sized, very thin-shelled *Dyris* with three spiral ribs separated by relative broad, flat to slightly concave interspaces; SA 20-21°; middle part adult



Figs. 80-83. *Dyris romeroi* sp. nov.

Fig. 80. RGM 456 474, paratype, Los Chorros (Amazonas, Colombia). a, rear view. b, front view. c, basal view.
Fig. 81. RGM 456 475, paratype, Nuevo Horizonte (Loreto, Peru). a, rear view. b, front view.
Fig. 82. INGEMMET TN54, holotype, same locality as Fig. 81. a, rear view. b, front view. c, lateral view. d, basal view.
Fig. 83. RGM 456 476, paratype, same locality as Fig. 81. a, rear view. b, front view.

Scale bars represent 1 mm.

whorls occasionally straight-sided; exterior of shell has a paper-like appearance; apertural margins thin and damaged; columella tightly corkscrew coiled.

Description – The nucleus (diameter 40-50 µm) is slightly inclined and contains very low wrinkles or abraded pustules in the margins. The embryonic shell is separated from the protoconch-2 at 0.45 whorls by a barely visible lineament or very low depression. The protoconch is smooth, apart for fine sigmoid growth lines, and has a convex perimeter with a comparatively deep suture. The protoconch-teleoconch boundary at 2.0-2.2 whorls is marked by a fine to clear axial riblet. Almost immediately after, sometimes two or, usually, three spiral ribs develop. The upper spiral bounds a well-defined

subsutural ramp that is flat to slightly concave. Growth lines are numerous and densely spaced. They are orthocline to progressively prosocline and sigmoid. A basal spiral develops above the lower suture on the first teleoconch whorl, and within one whorl the three spirals are equally strong and spaced at equal distances (at one fifth, two fifths and three fifths of the whorl height, respectively), with broad, slightly concave interspaces in between. A fourth spiral may surface from below the lower suture on later whorls and becomes visible at the body whorl, where it bounds the poorly delimited, rounded base. The suture is located in a shallow depression. The teleoconch whorl perimeter is at first subrounded. During growth, the part between the upper and third rib becomes almost straight-sided. The adnate aperture is subovate with a flat base. The outer and basal margins are usually damaged. The parietal lip is short and located in the top of the aperture. The columellar margin is long, evenly rounded, and the basal part is reinforced and can be slightly expanded. The columella is coiled as a tight corkscrew. The species is imperforate.

Dimensions – INGEMMET TN54: H 3.9; W 1.1; Hap >1.1; 8.0 whorls. RGM 456 474: H 4.5; W 1.4; Hap 1.1; >6.2 whorls. RGM 456 475: H 4.5; W 1.3; Hap >1.0; 8.0 whorls. RGM 456 476: H 2.9; W 1.2; Hap 0.8; 5.8 whorls; UNC nn.: H 4.2; W 1.3; Hap 1.0.

Remarks – The combination of a thin shell, papery texture of the surface and the corkscrew coiled nature of the columella distinguish this species from previously treated *Dyris* species.

***Dyris lanceolatus* sp. nov.**

Figs. 84-86.

Type material – RGM 456 566 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 567 (paratype), same locality. INGEMMET TN79: Santa Elena (Loreto, Peru), exposure in south bank Amazon River, *c.* 300 m east of wood mill and *c.* 1.5 km east of Santo Tomas (3°52'S 71°23'W), level F498 (5.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the lanceolate outline (Latin: *lanceolatus* for spear-like).

Diagnosis – High-spired (SA 12-14°), intermediate sized *Dyris* with almost straight sides; spiral ornamentation of very low, very fine, but well visible spiral lineaments or ribs; growth lines sigmoid; inclined aperture rectangular; columella coiled tightly, corkscrew-like.

Description – The nucleus (diameter 50-60 µm) is flat. The embryonic shell is separated from the remainder of the protoconch at 0.3 whorls by a strong axial depression (holotype) or a very fine axial lineament (paratype INGEMMET TN79). The protoconch has rounded whorls and an impressed suture, and is separated by a fine axial lineament at 2.2-2.9 whorls from the teleoconch. After the protoconch-teleoconch boundary, at first two spirals at one third and two thirds of the whorl height develop. A third, slightly finer spiral is added within a whorl at one sixth of the whorl height. The upper spiral can be slightly pronounced and bounds the straight, steeply dipping, smooth subsutural ramp. Growth lines are orthocline, sigmoid and numerous, and become slightly prosocline with a distinct basal retraction on later whorls. A very fine spiral rib develops halfway on the subsutural ramp at the fourth teleoconch whorl and a basal rib appears at the lower suture. All ribs are extremely thin and low, and hardly make a mark at the periphery. The suture is slightly retracted below the lower rib in some specimens, producing slightly imbricate whorls. Otherwise, the whorl profile is entirely flat on later teleoconch whorls. On the last few teleoconch whorls very broad and shallow, straight spiral depressions and elevations may develop between ribs. The basal spiral bounds the rather flat base of the body whorl acutely. The aperture is subovate or, when fully grown such as in RGM 456 567, rectangular, with the long axis inclining towards the base of the axis of the shell. The junction of the outer and parietal lips is pointed; the basal lip is slightly rounded and somewhat retracted. The outer lip is usually in line with the preceding whorl, but on RGM 456 567 it is slightly flaring. No boundary can be defined between the parietal and columellar lip. A thin parietal callus may be slightly expanding. The columellar lip is formed by the slightly reinforced columella that is tightly coiled. The base of the columellar lip is located left of the axis of the shell. The shell is imperforate.

Dimensions – RGM 456 566: H 8.8; W 1.55; Hap 1.3; 11.6 whorls. RGM 456 567: H 7.4; W 1.5; Hap 1.4; >7.0 whorls. INGEMMET TN79: H 5.35; W 1.15; Hap 1.0; 9.8 whorls.

Remarks – The species has almost straight sides and very low spiral ornamentation, distinguishing it from all other elongate *Dyris* species.

***Dyris acicularis* sp. nov.**

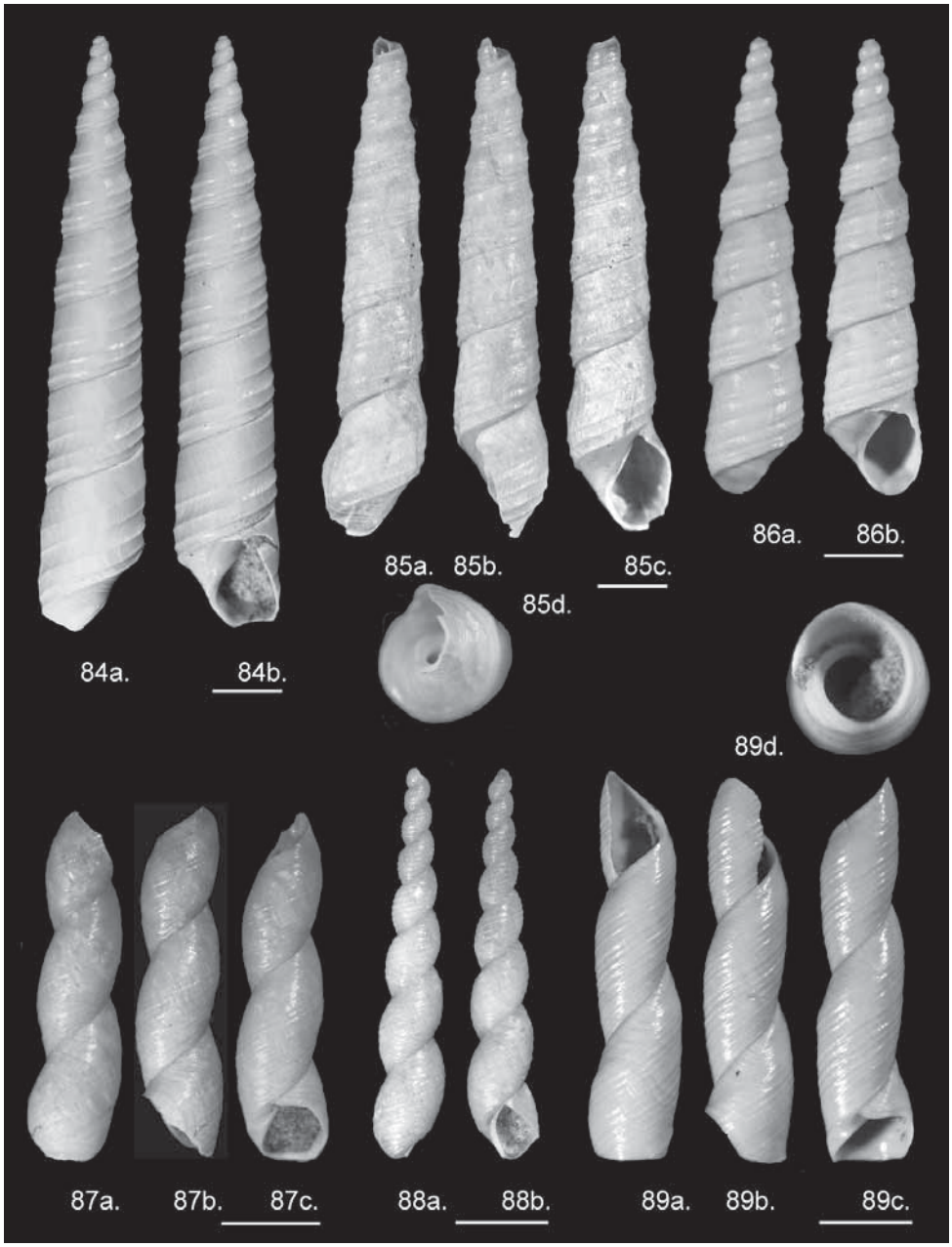
Figs. 15x, 87-89.

2002 *Dyris* sp. Wesselingh *et al.*, fig. 3f.

Type material – INGEMMET TN80 (holotype, damaged juvenile): Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 568 (paratype, fragment), same locality. RGM 456 569 (paratype, fragment), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Range – Pebas Formation, MZ7 - MZ11 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – Named after the needle-like outline (Latin; *acicula* for small pin).



Diagnosis – Small, thin-shelled, high-spired *Dyris* (SA *c.* 12°) with depressed whorls ornamented with up to 17 spiral ribs; columella very broadly coiled, producing a tubiform shell.

Description – The nucleus (diameter 40-50 µm) is only slightly inclined. The embryonic shell is separated from the protoconch-2 at 0.4 whorls by a fine axial lineament. The protoconch-2 is smooth, has convex whorls and a rather deep suture. At 2.2 whorls the boundary with the teleoconch is marked by a fine axial thread. Directly afterwards, densely spaced growth lines occur. Almost immediately two spiral ribs develop at two fifths and four fifths of the whorl height, followed within half a whorl by five more spirals. Interspaces are about twice as wide as the spirals. Early teleoconch whorls are broadly rounded. At later whorls the spirals become lower and rounded, and additional spiral ribs are added resulting in up to 17, unevenly spaced low spirals on the last whorls. The lower spiral may slightly overhang the suture, resulting in a slightly imbricate whorl profile for some of the specimens. The lower spiral bounds rather acutely the short base of the body whorl that lacks spiral ornamentation. Growth lines are prosocline and sigmoid. At later whorls both the upper and the lower limb of the growth lines become subhorizontal. The suture angle increases, resulting in increasingly high whorls. The aperture is adnate. It is subovate in subadult specimens and becomes subquadrate on adult specimens. The margins are thin. The inner lip is entirely formed by the reinforced columella. The upper part disappears below the top of the outer lip. The basal lip is broadly retracted, but straight in frontal view. The outer lip has subhorizontal upper and lower parts when viewed from the side; the upper limb may even be slightly curved upward in side view behind the foremost point. The upper, overhanging part is fused with the columella through a thin, folded parietal callus. The columella is widely coiled like a corkscrew. When viewed from below it is possible to look up into the shell as if it were a tube. The base of the body whorl only forms about one fourth of the radius of the circular outline when the shell is viewed from below. The apertural plane is directed abapically.

Dimensions – INGEMMET TN80: H 4.35; W 0.8; Hap >0.6; >7.5 whorls. RGM 456 568: H >3.7; W 1.0; Hap 0.65. RGM 456 569: H >3.8; W 1.0; Hap 0.45.

◀ Figs. 84-86. *Dyris lanceolatus* sp. nov.

Fig. 84. RGM 456 566, holotype, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 85. RGM 456 567, paratype, same locality as Fig. 84. a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 86. INGEMMET TN79, paratype, same locality as Fig. 84. a, rear view. b, front view.

Figs. 87-89. *Dyris acicularis* sp. nov.

Fig. 87. RGM 456 568, paratype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 88. INGEMMET TN80, holotype, same locality as Fig. 87. a, rear view. b, front view.
Fig. 89. RGM 456 569, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Remarks – The very broadly, open coiled nature of the columella, making this species in effect a tube, distinguishes *D. acicularis* from all other high-spired *Dyris* species.

***Dyris hauxwelli* Nuttall, 1990**

Figs. 16i, 90-93.

1871 *Isaea ortoni* (Gabb); Conrad, p. 193 (*pars*).
1938 *Dyris* (?) *gracilis* Conrad; de Greve, p. 186 (*pars*), pl. 5, figs. 30, 37 (*non* pl. 3, figs. 21-28).
1990 *Dyris hauxwelli* Nuttall, p. 192, figs. 79-85.

Material studied – RGM 456 428; Tamshiyacu (Loreto, Peru), exposure in east bank of Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F756. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 1996. INGEMMET TN37, same locality. RGM 456 429, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F542 (12.7 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. RGM 456 430, same locality.

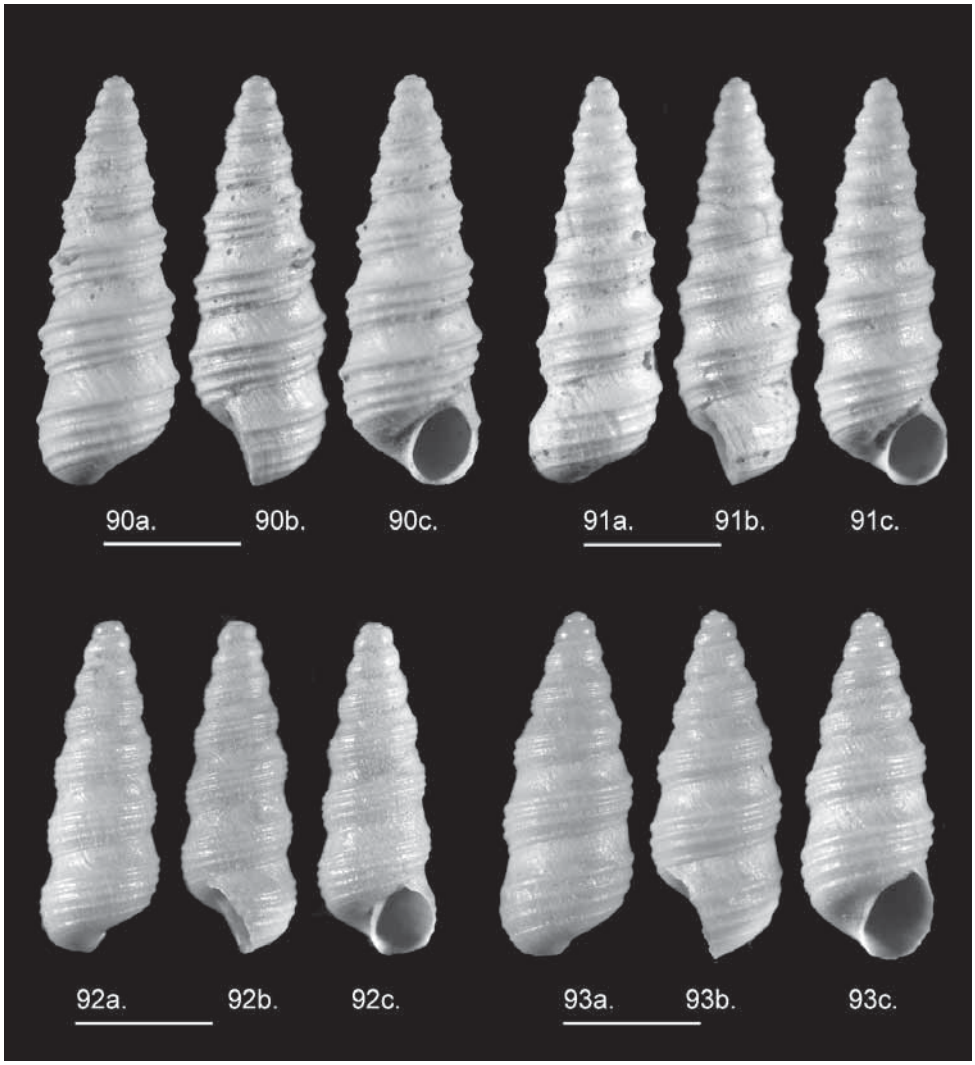
Dyris cf. *hauxwelli*: RGM 456 612, Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996.

Extended diagnosis – Small *Dyris*; SA 22-26°; nucleus inclined to strongly inclined, diameter 30-60 µm; low malleate ornament in margins; boundary of embryonic shell and protoconch-2 at 0.45-0.55 whorls defined by very poorly (often in-)visible axial lineament; protoconch-2 smooth, with convex whorls and deep suture; protoconch-teleoconch boundary at 1.7-1.9 whorls marked by fine axial lineament; onset of two, sometimes three spiral ribs on the lower two thirds of the whorl shortly after; upper rib bounding a very distinct, steeply dipping, straight to slightly concave subsutural ramp; fourth primary spiral visible at body whorl; growth lines prosocline, numerous, regularly spaced; growth lines and spirals may produce a reticulate ornament (see Nuttall, 1990, figs. 84, 85), in most specimens the spiral ornament dominates; aperture semicircular, margins thin; top part parietal margin usually adnate, sometimes detached; top outer lip often attached; shell imperforate.

Dimensions – RGM 456 428: H 3.0; W 1.0; Hap 0.6; 8.1 whorls. INGEMMET TN37: H 3.1; W 1.1; Hap 0.6; 8.8 whorls. RGM 456 429: H 2.6; W 0.9; Hap 0.5; 8.0 whorls. RGM 456 428: H 2.7; W 1.05; Hap 0.6; 7.2 whorls.

Range – Pebas Formation, MZ4 - MZ7 (late Early - Middle Miocene), Peruvian Amazonia.

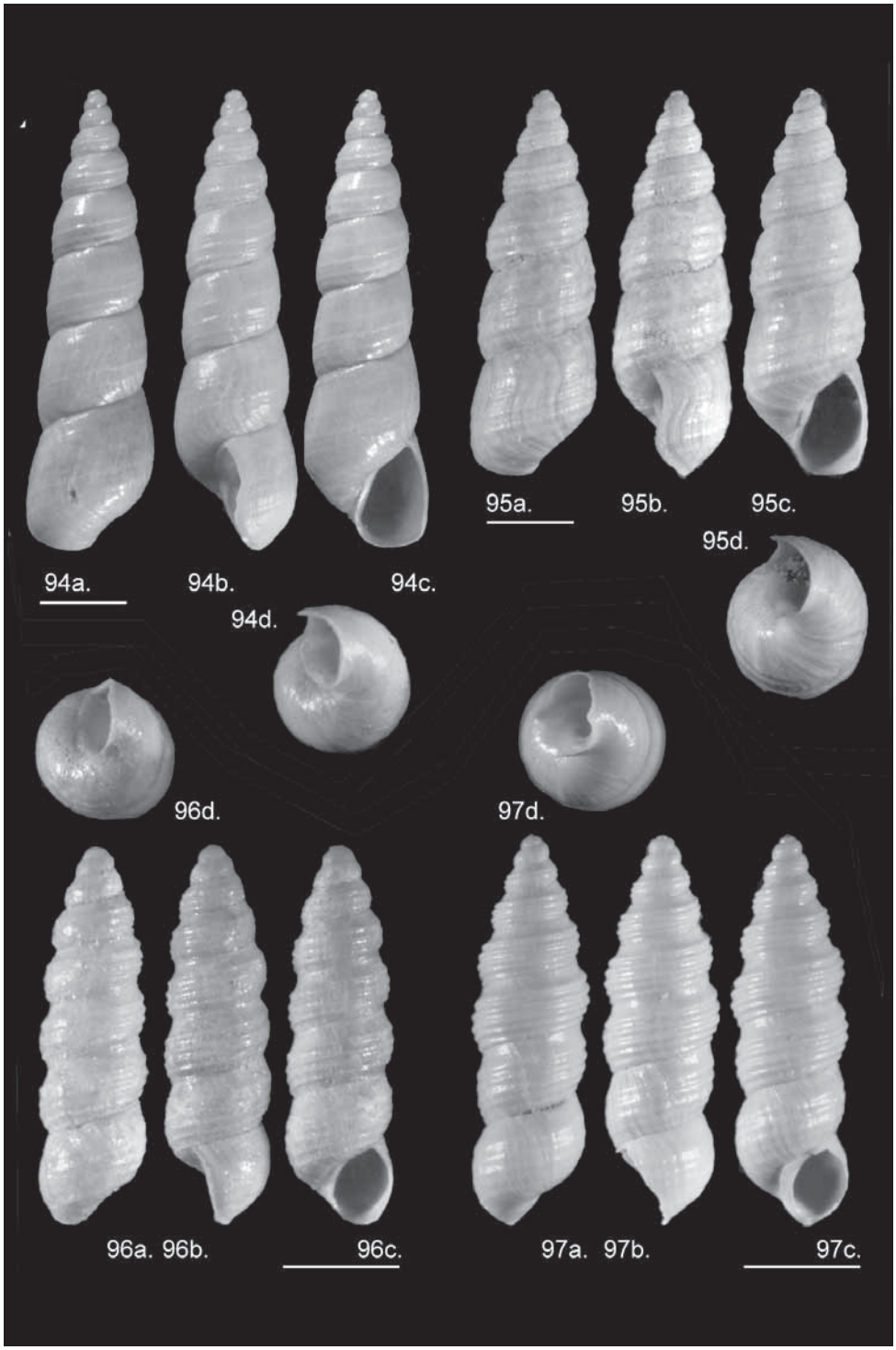
Remarks – In samples, two morphs may co-occur that are attributed to this species (compare Figs. 90 and 93 with Figs. 91 and 92). One of the morphs is slightly more elongate, has in general a slightly thinner shell and a higher translation rate. The general architecture of the morphs (type and location of ornamentation) is similar, suggesting that they may represent sexual dimorphism.



Figs. 90-93. *Dyris hauxwelli* Nuttall, 1990.

Fig. 90. RGM 456 428, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 91. INGEMMET TN37, same locality as Fig. 90. a, rear view. b, lateral view. c, front view.
Fig. 92. RGM 456 429, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 93. RGM 456 430, same locality as Fig. 92. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.


94a.
94b.
94c.
94d.
95a.
95b.
95c.
95d.
96a.
96b.
96c.
96d.
97a.
97b.
97c.
97d.

Dyris mattii sp. nov.
Figs. 94, 95.

Type material – RGM 456 472 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. INGEMMET TN52 (paratype), same locality.

Range – Pebas Formation, MZ7 - MZ10 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – The species is named after Professor Dr Matti Räsänen (Geology faculty, University of Turku, Finland), in honour of his work on sedimentology and depositional regimes in Neogene deposits of western Amazonia, and our long-standing cooperation.

Diagnosis – Small-intermediate, rather straight-sided *Dyris* with shallow suture; SA 19-24°; 3-4 regularly spaced, low spiral ribs covering the lower three fifths of whorls with a very steep and smooth subsutural ramp above; aperture adnate, margins thin; basal lip when viewed from below with broad, shallow retraction; columella slightly twisted.

Description – The nucleus (diameter 40-50 µm) is slightly inclined. The first 2.0 whorls are smooth and rather convex-sided with a relatively deeply impressed suture. No obvious protoconch-teleoconch boundary seen in the studied specimens. After 2.0 whorls, two spiral ribs develop at one third and two fifths of the whorl height, shortly after followed by a basal third rib. The ribs become located slightly upward on the whorl in successive whorls. The three primary ribs are regularly spaced, have interspaces twice as wide and occupy the lower three fifths of the whorl of the remainder shell, sometimes later accompanied by a fourth spiral rib. The spiral ribs become lower and less well defined on the ultimate whorls. The upper spiral bounds a very steeply dipping, smooth subsutural ramp that on early teleoconch whorls is only marginally subrounded, but on

◀ Figs. 94, 95. *Dyris mattii* sp. nov.

Fig. 94. RGM 456 472, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 95. INGEMMET TN52, paratype, same locality as Fig. 94. a, rear view. b, lateral view. c, front view. d, basal view.

Figs. 96, 97. *Dyris huberti* sp. nov.

Fig. 96. INGEMMET TN53, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 97. RGM 456 473, paratype, same locality as Fig. 96. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

the remainder of the shell is straight. Irregularly developed, microscopic spiral groovelets and very thin spiral riblets are present on later whorls. The sigmoid growth lines are orthocline to marginally prosocline. The base of the body whorl is smooth, apart for the growth lines. The perimeter becomes straighter and the suture shallower during growth. The maximum width lies near the base of the whorls. In frontal view the aperture has a long, nearly straight outer lip and a straight basal lip. The apertural margins are thin. The columellar lip is also straight and somewhat longer than the parietal lip. The inner lip callus is very thin and not expanding. The aperture is adnate. A very low twist is developed on the upper part of the columellar lip. The basal lip, when viewed from below, is regularly and broadly retracted. The shell is imperforate.

Dimensions – RGM 456 472: H 5.3; W 1.5; Hap 1.2; 9.1 whorls. INGEMMET TN52: H 4.4; W 15.5; Hap 13; 7.5 whorls.

Remarks – The combination of the tightly packed, comparatively straight-sided whorls, the presence of a very subtle columellar twist, the absence of a columella coiled like a corkscrew and the regularly organised spiral ornament with three or four primary spirals on the basal three fifths of whorls distinguishes this taxon from other *Dyris* species.

***Dyris huberti* sp. nov.**
Figs. 96, 97.

Type material – INGEMMET TN53 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 473 (paratype), same locality.

Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – The species is named after Dr Hubert Vonhof (Vrije Universiteit, Amsterdam), as an acknowledgement for our close cooperation on geochemical and palaeoecological issues of the Pebas system.

Diagnosis – Small, thin-shelled *Dyris* with four regularly-spaced spiral ribs on the lower four fifths of the whorl and a slightly concave subsutural ramp above; SA *c.* 21°; perimeter convex; aperture semicircular; largest width may be reached two to three whorls before aperture.

Description – The nucleus (diameter 40-50 µm) is inclined and ornamented by poorly defined, very slightly spirally arranged, irregular, low elongate wrinkles. The boundary between the embryonic shell and the protoconch-2 at 0.45 whorls is marked by a very fine axial depression. The protoconch-2 is smooth and has a convex perimeter with a comparatively deep suture. An axial lineament marks the protoconch-teleoconch

boundary at 1.7-2.0 whorls. Almost immediately after the boundary, densely spaced growth lines and two spiral ribs develop (at one quarter and two thirds of the whorl height), soon followed by a third at half the whorl height and a fourth rib at the base of the whorl. The spirals have interspaces that are somewhat wider than the spirals themselves and remain at the same spacing throughout the shell. The upper spiral bounds a short subsutural platform that is straight, but more often slightly concave. The lower spiral bounds a very narrow suprasutural depression. A fifth spiral may be seen at the suture or is located slightly below, and becomes visible at the body whorl where it bounds the base of the shell. Growth lines are numerous, very fine and slightly prosocline. The whorls are convex to subrounded. At the apex, the shell is rapidly expanding. At around the fifth whorl the maximum width is reached, which thereafter remains constant or decreases slightly. The spiral ribs may become lower on the body whorl. The semicircular aperture is adnate. The margins are thin. The inner lip callus is very thin and not expanded. The leftmost part of the columellar lip is located at the axis of the shell. The basal lip is broadly and shallowly retracted when viewed from below. The columella has an obsolete chink behind the aperture, visible in the paratype where the outer lip is broken. The shell is imperforate.

Dimensions – INGEMMET TN53: H 3.2; W 0.9; Hap 0.7; 8.2 whorls. RGM 456 473: H 3.7; W 1.1; Hap 0.8; 8.4 whorls.

Remarks – The rounded perimeter, four more pronounced spiral ribs and circular aperture differentiate this species from *D. mattii*. *Dyris huberti* resembles *D. hauxwelli*, but the latter increases regularly in width, has more variation in the number and location of the spiral ribs, and has a more shouldered appearance.

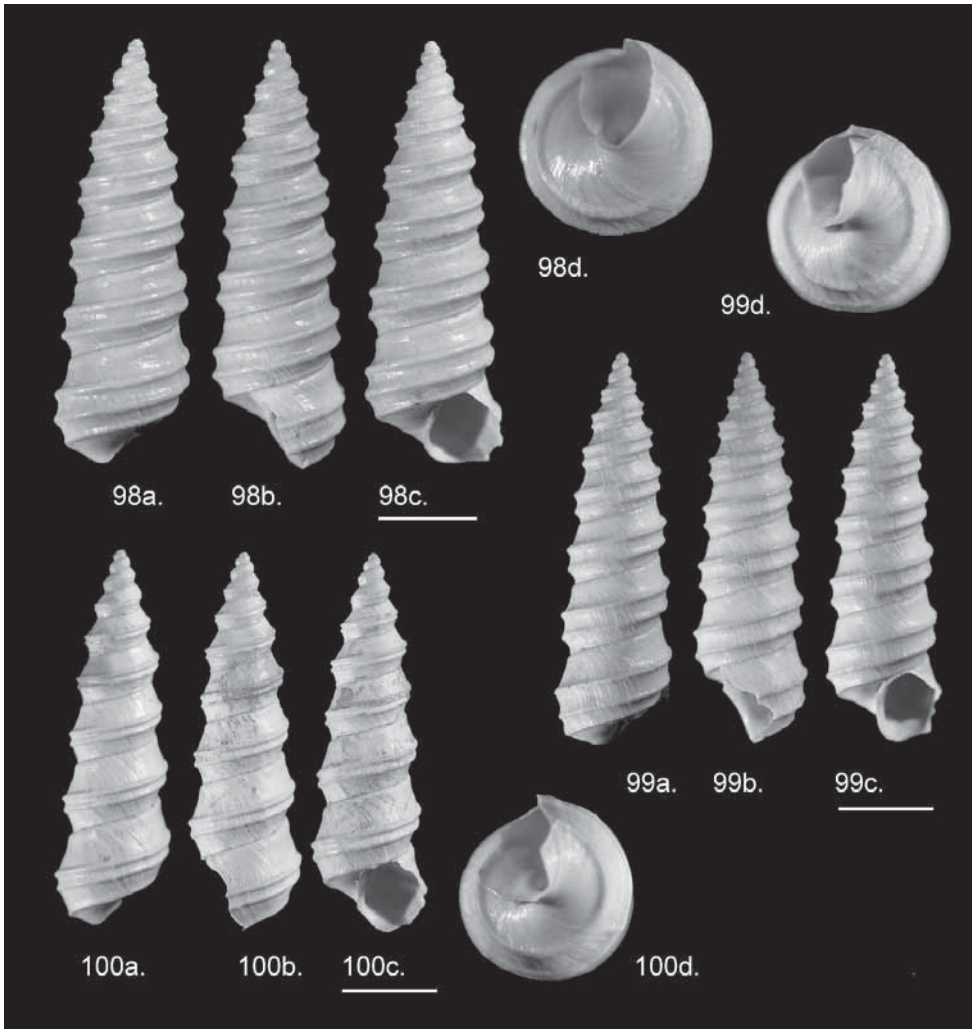
In samples of this species, very often two morphologies are discernable, a higher form (e.g., Fig. 96), and a form whose width increases faster, has its largest width before the body whorl and in general is somewhat wider (Fig. 97). Since all other morphological characters, including the very regular architecture of the spiral ornamentation, are the same and both morphs usually co-occur, I consider them as sexual dimorphs of a single species.

Dyris guerreroi sp. nov.

Figs. 98-100.

Type material – INGEMMET TN68 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River located 300 m west of wood mill, westernmost exposure (3°53'S 71°24'W), level F508 (3.6 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996. RGM 456 531 (paratype), same locality. RGM 456 532 (paratype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.



Figs. 98-100. *Dyris guerreroi* sp. nov.

Fig. 98. RGM 456 531, paratype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 99. INGEMMET TN68, holotype, same locality as Fig. 98. a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 100. RGM 456 532, paratype, same locality as Fig. 98. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Derivatio nominis – Named after Professor Dr Javier Guerrero (Universidad Nacional, Bogota, Colombia), an eminent Cainozoic stratigrapher of inland basins of northwestern South America.

Diagnosis – Intermediate to large sized, bicarinate *Dyris* with a very regular ornament of two well-defined and robust spiral keels; third basal spiral forms a keel delimiting the rather flat base of the body whorl; SA 19-22°; apertural margins thin; parietal callus slightly expanding over upper part columellar margin; shell imperforate.

Description – The nucleus is inclined. The embryonic shell is separated from the remainder of the protoconch at 0.5-0.6 whorls by an axial constriction that is particularly well developed on the paratypes. The protoconch-2 is smooth and bulbous, with a deep suture. A barely visible axial thread at 1.8-2.3 whorls marks the protoconch-teleoconch boundary. Subsequently, two spirals gradually develop at *c.* one quarter and three-quarters of the whorl height. Within a whorl, these spirals are well defined and robust, and located at *c.* one quarter and two thirds of the whorl height, where they remain throughout the shell. The two spirals are more tightly located at *c.* two fifths and three fifths of the whorl height on RGM 456 532, but this is exceptional. The subsutural ramp and the interspace between the ribs are straight at first, but become slightly concave after the second teleoconch whorl. The whorl profile of the shell is regularly bicarinate. A spiral becomes visible at the lower suture at the second or third teleoconch whorl. This spiral is fully visible at the base of the body whorl, where it is acute. Irregular, microscopic spiral grooves occur on later teleoconch whorls. The numerous fine growth lines are prosocline and reversed J-shaped with a strong retraction just above the lower suture. The base of the body whorl is rather flat and imperforate. The aperture is subrounded to subquadrate. The margins are thin. The outer lip has two or three folds corresponding to the spiral ribs. The parietal lip is adnate and a thin parietal callus slightly expands also covering the upper part of the columellar lip to form a low angulation on the columella. The columellar lip is adnate or slightly erect. The columella is tightly coiled like a corkscrew.

Dimensions – INGEMMET TN68: H 8.6; W 2.5; Hap 1.9; 10.0 whorls. RGM 456 531: H 8.4; W 2.6; Hap 1.75; 9.8 whorls. RGM 456 532: H 8.5; W 2.6; Hap 1.7; 10.2 whorls.

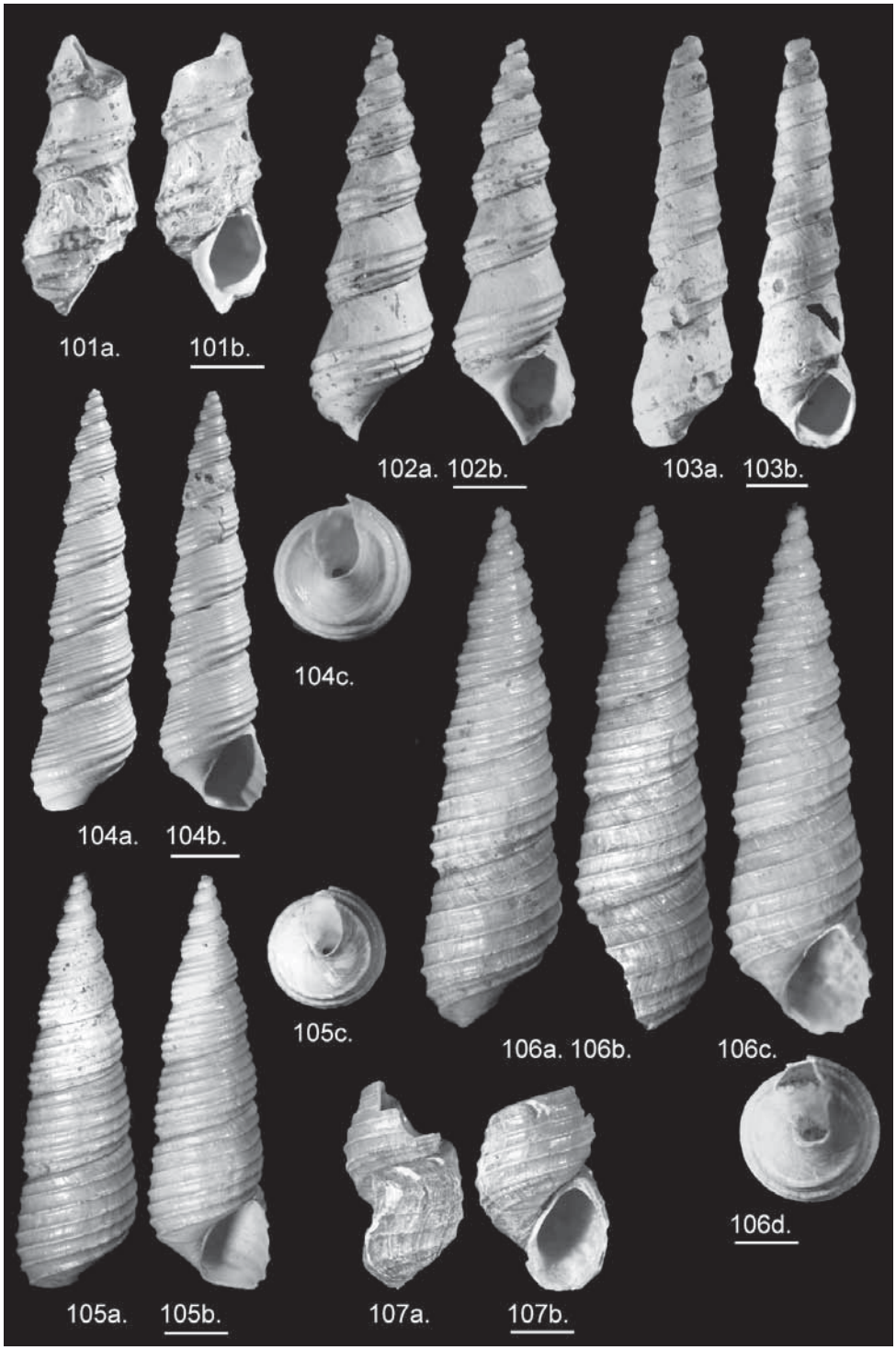
Remarks – Differentiation from other tall and high-spired *Dyris* species, such as *Dyris bicarinatus bicarinatus*, is given below.

***Dyris bicarinatus bicarinatus* (Etheridge, 1879)**

Figs. 101-104.

1879 *Melania bicarinata* Etheridge, p. 88, pl. 7, fig. 7.
1990 *Dyris gracilis* Conrad; Nuttall, p. 186 (*pars*), fig. 454 (*non* figs. 41-48, 455).

Material studied – RGM 456 527 (fragment); Puerto Nariño (Amazonas, Colombia), exposure in north bank of Loreto Yacu, *c.* 1 km east of village (3°46'S 70°22'W), level F29 (24.9 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 528 (damaged specimen), and UNC nn., same locality. RGM 456 529 (damaged specimen), same locality: level F28b (25.3 m above DL). RGM 456 000; Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.


101a.
101b.
102a.
102b.
103a.
103b.
104c.
104a.
104b.
105c.
106a.
106b.
106c.
106d.
105a.
105b.
107a.
107b.

Extended diagnosis – Rather large, turritelliform *Dyris* ornamented with 3-4 primary spirals on the lower three fifths of the whorl that increase in strength downward on the whorl; a variety of secondary spirals can develop on later teleoconch whorls; SA 18-22°; upper part of whorl distinctly concave, basal primary spiral or the one above forming the largest width and bounding a short, but distinct, suprasutural depression, giving the shell a slightly imbricate whorl profile; growth lines slightly prosocline, reversed J-shaped, strongly retracting slightly above lower suture; adnate aperture irregularly quadrate with more or less straight parietal, columellar and basal lips; parietal callus thin, slightly expanding over the upper part of columellar lip producing a pseudo-fold on columella; columella coiled like a corkscrew.

Dimensions – RGM 456 527: H 7.1. RGM 456 528: H 11.0; W 3.2; Hap 2.8; >8.1 whorls. RGM 456 529: H 14.1; W 3.3; Hap 2.8; >8.1 whorls. RGM 456 530: H 12.1; W 3.0; Hap 2.7; >11.1 whorls.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Remarks – This species is larger than other high-spired *Dyris* species described above, with the exception of *D. guerreroi*. The latter has a regular ornamentation of two primary spirals only, with a short subsutural ramp.

Almost all specimens studied, including those of of Etheridge (1879), contain dissolution holes and marks. The species is found in samples that would typically be assigned to the tall *Dyris* assemblage of Wesselingh *et al.* (2002), but may also occur in samples assigned to the *Tryonia* and Thiaridae-Pulmonata assemblages of these authors, that represent marginal lacustrine to fluviolacustrine settings. Given the morphological resemblance and the stratigraphic successive position of *Dyris guerreroi* and *D. b. bicarinatus*, it is well possible that both are members of a single lineage. In the available samples no intermediate forms have been found.

◀ Figs. 101-104. *Dyris bicarinatus bicarinatus* (Etheridge, 1879).

Fig. 101. RGM 456 527, Puerto Nariño (Amazonas, Colombia). a, rear view. b, front view.
Fig. 102. RGM 456 528, same locality as Fig. 101. a, rear view. b, front view.
Fig. 103. RGM 456 529, same locality as Fig. 101. a, rear view. b, front view.
Fig. 104. RGM 456 000, Macedonia (Amazonas, Colombia). a, rear view. b, front view. c, basal view.

Figs. 105-107. *Dyris bicarinatus sofiaensis* subsp. nov.

Fig. 105. RGM 456 633, paratype, Santa Sofia (Amazonas, Colombia). a, rear view. b, front view. c, basal view.
Fig. 106. RGM 456 632, holotype, same locality as Fig. 105. a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 107. RGM 456 634, paratype, same locality as Fig. 105. a, lateral view. b, front view.

Scale bars represent 2 mm.

***Dyris bicarinatus sofiaensis* subsp. nov.**
Figs. 15o, t, 105-107.

Type material – RGM 456 632 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F59 (10.0 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991; UNC nn., RGM 456 633 and RGM 456 636 (sectioned specimen), all paratypes from same locality.

Range – Pebas Formation, MZ12 (late Middle - early Late Miocene), Colombian Amazonia.

Derivatio nominis – The name refers to the type locality (Santa Sofia).

Diagnosis – Large, rather thin-shelled and flat-sided *Dyris*, regularly increasing in size; SA 18-21°; five primary spirals that become progressively adapically; secondary spirals may develop on later whorls; well-defined, smooth, inclined base of body whorl; base of columellar lip left of the shells axis; columella coiled like a corkscrew.

Description – The apex is lacking in the material. Three spiral ribs are visible at the onset of the shell somewhere on the early teleoconch on the holotype. A fourth rib develops within a whorl at the base that becomes located at *c.* one sixth of the whorl height afterwards. On early teleoconch whorls the upper third is smooth, but a fifth spiral develops there at the third whorl. The five spiral ribs are prominent, becoming broader and better defined the lower that they are situated on the whorl. Interspaces are flat to concave and typically 5-6 times as wide as the ribs. A suprasutural ridge may be visible, but can also be covered and become visible as the basal (sixth) rib bounding the well-defined base of the body whorl. Distances between the spiral ribs can vary somewhat; for example, the interspace between the second and third rib from above almost doubles and a secondary rib develops in between on the last three whorls of the holotype. Very thin secondary ribs may develop between the basal primary ribs on the body whorl. Low, elongate, barely distinguishable nodes may develop on the primary ribs on the last two whorls. The suture may be bounded by a low suprasutural ridge above or by a distinct suprasutural depression formed by the lower primary spiral. The suture may become fissure-like on the body whorl (for example, RGM 456 316) and a very narrow, rounded shoulder may develop. Growth lines are numerous, fine, slightly prosocline and slightly sigmoid. The adnate aperture is drop-shaped to ovate. The outer and basal lips are thin. The parietal lip is short, retracted within the aperture and has a narrow, thin parietal callus. The columellar lip is also rather thin and has a very narrow callus slightly expanding over the columella that is coiled like a corkscrew. The lower half of the columellar lip expands to the left of the axis of the shell. Remains of light-brown periostracum are common on the type specimens. The shell is imperforate.

Dimensions – RGM 456 632: H 16.2; W 4.6; Hap 3.9; >9.1 whorls. RGM 456 663: H 12.7; W 3.7; Hap 3.6; >9.4 whorls. UNC nn.: H 12.3; W 4.2; Hap >2.8. RGM 456 664: H 6.0.

Remarks – The shell is thinner than that of *D. b. bicarinatus*. *Dyris b. sofiaensis* has almost straight-sided whorls, whereas in *D. b. bicarinatus* the shells have a concave upper part and a tendency to become slightly imbricate in outline. Specimens of *D. b. bicarinatus* in sample F32 (Macedonia, Colombia; Fig. 104) occur that have almost identical ribbing as *D. b. sofiaensis*, with four primary spirals increasing in strength downward with additional secondary spirals throughout the shell on later teleoconch whorls. However, the whorl profile of these Macedonia specimens shows a distinct concave upper part and a short dipping lower part, giving the shells the characteristic imbricate outline. Further, specimens lacking the secondary spirals and the generally abapical increase in robustness of spirals, as well as intermediate specimens, occur in that sample. Given the geographic locality of Macedonia and Santa Sofia (the type locality of *D. b. sofiaensis)*, and the regional dip, it is almost certain that the latter strata overlay the former. It is very likely that the two forms are stratigraphic successive forms and hence are considered subspecies.

***Dyris hoornae* sp. nov.**
Figs. 108, 109.

Type material – INGEMMET TN78 (holotype, base damaged): Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 395 (paratype, juvenile), same locality. RGM 456 565 (six damaged juveniles, paratypes): Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42, *c.* 150 m north of exposure with level F367a (4°04'S 73°25'W), level F368 (1.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 11-8-1996.

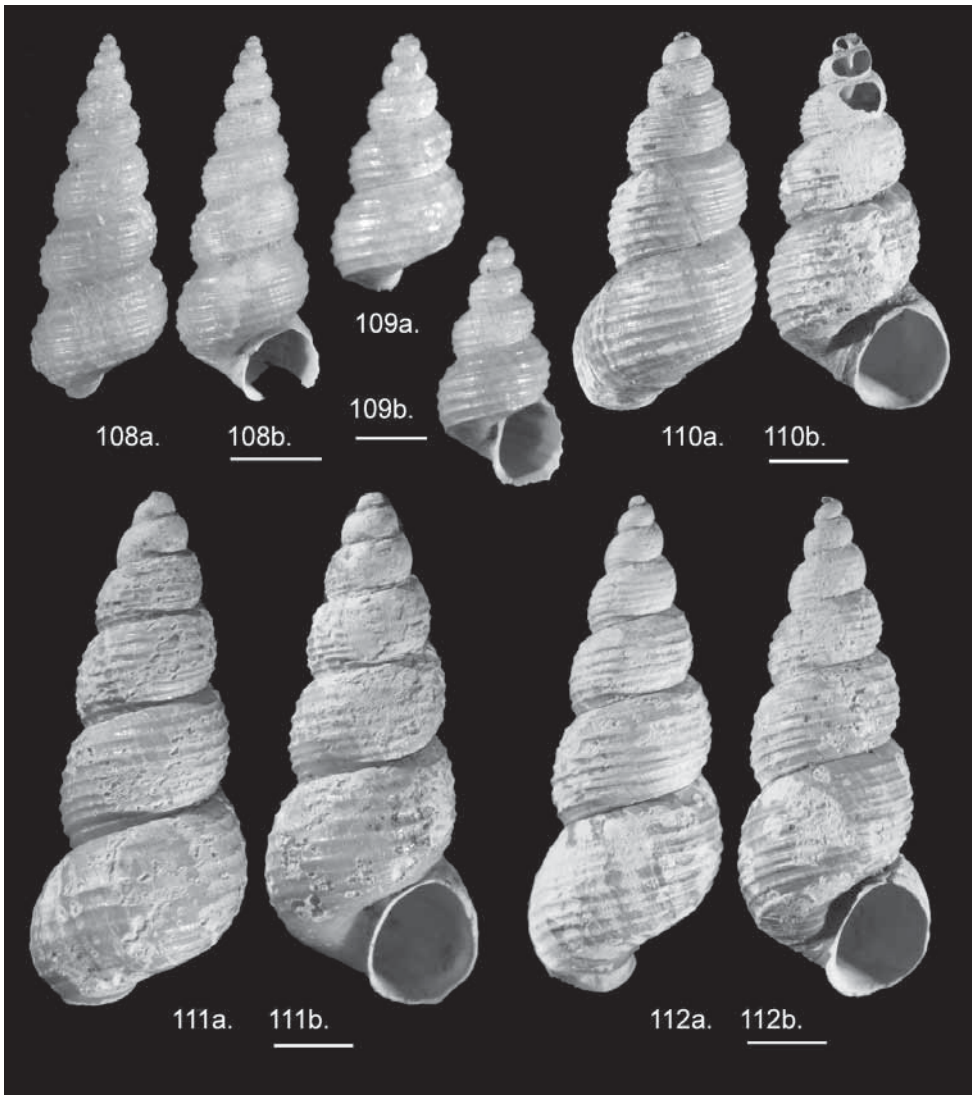
Range – Pebas Formation, MZ7 - MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after Dr Carina Hoorn (Universiteit van Amsterdam), a palynologist and stratigrapher of Amazonian deposits who introduced me to this subject and has been a great support over the years in my research.

Diagnosis – Intermediate-sized, thin-shelled *Dyris* with convex whorl profile and four narrow, but well defined, spiral ribs; SA *c.* 26°; base of body whorl slightly flattened; aperture detached; shell narrowly umbilicate.

Description – The nucleus (diameter 50-60 µm) is slightly inclined. The apex of the first whorl is flat. The protoconch is smooth apart for very fine, slightly prosocline growth lines. It has rather convex whorls and a deep suture. The protoconch-teleoconch boundary is located at 1.8-1.9 whorls and indicated by a very fine axial thread. Thereafter, two spiral ribs develop gradually at *c.* one third and two thirds of the whorl height. Four spiral ribs are present at the second teleoconch whorl, covering the lower two thirds of the whorl at even distances. A smooth, slightly convex, poorly expressed subsutural ramp is located above. The whorl profile remains more or less rounded. Growth lines are numer-

ous, closely spaced and prosocline. The spiral ribs are thin, but well defined, and separated by interspaces about four times as wide. Up to two low secondary spirals may develop between lower spirals on later whorls. At the fourth teleoconch whorl a spiral becomes visible at the lower suture. This lower spiral bounds the somewhat flattened and (apart for the growth lines) smooth base of the body whorl. The aperture is semilunate and detached. The margins are thin and damaged in all available specimens. The shell is narrowly umbilicate; the umbilicus is partially hidden obliquely behind the slightly expanding and erect inner lip margin.



Dimensions – INGEMMET TN78: H 8.2; W 3.1; Hap *c.* 1.8; 9.2 whorls. RGM 456 564: H 3.3; W 1.6; Hap 11.5; 6.1 whorls.

Remarks – *Dyris hoornae* has some resemblance to *D. lintea*. The latter has a thicker shell, more straight-sided whorl profile, lower and broader ribs with more variation in their number and position, and a less impressed suture.

***Dyris ariei* sp. nov.**

Figs. 110-112.

1990 *Dyris lintea* (Conrad); Nuttall, p. 190 (*pars*), fig. 58 (*non* figs. 49-57).
1990 *Dyris tricarinata* (Boettger); Nuttall, p. 190 (*pars*), figs. 74, 75 (*non* figs. 59-73, 76-78).

Type material – RGM 456 561 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F60 (17.1 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 562, RGM 456 563 and UNC nn. (paratypes), same locality.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Colombian Amazonia.

Derivatio nominis – Named after Arie W. Janssen, retired curator of the Cainozoic Molluscs of the Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands, who has facilitated and supported my research throughout the years.

Diagnosis – Very large and plump (SA 29-34°), but nevertheless relatively thin-shelled *Dyris* with subrounded whorl profile; base of body whorl bounded by rounded secondary keel; columella slightly coiled; shell imperforate.

Description – The apex is damaged in all available material. The first whorls are in general very much worn and show dissolution holes. On the early teleoconch whorls the profile is rounded, with an impressed suture and seven, narrow, well-defined,

◀ Figs. 108, 109. *Dyris hoornae* sp. nov.

Fig. 108. INGEMMET TN78, holotype, Porvenir (Loreto, Peru). a, rear view. b, front view.
Fig. 109. RGM 456 564, paratype, same locality as Fig. 108. a, rear view. b, front view. Scale bar represents 1 mm.

Figs. 110-112. *Dyris ariei* sp. nov.

Fig. 110. RGM 456 563, paratype, Santa Sofia (Amazonas, Colombia). a, rear view. b, front view.
Fig. 111. RGM 456 561, holotype, same locality as Fig. 110. a, rear view. b, front view.
Fig. 112. RGM 456 562, paratype, same locality as Fig. 110. a, rear view. b, front view.

Scale bars represent 2 mm, unless stated otherwise.

slightly unevenly spaced spiral ribs. These are separated by interspaces about three times as wide. The upper rib is located rather close to the upper suture. Growth lines are fine and prosocline. Secondary spirals develop between primary ribs; up to nine ribs are present on the body whorl. The basal spiral rib is low and rounded, and bounds the subrounded base of the body whorl. The aperture is subovate to semicircular and detached. The apertural margins are thin and the columellar lip is slightly erect. The shell has a narrow, deep umbilicus.

Dimensions – RGM 456 561: H 13.1; W 5.5; Hap 3.3; >6.2 whorls. RGM 456 562: H 12.7; W 4.9; Hap 2.8; >6.7 whorls. RGM 456 563: H 9.8; W 4.6; Hap 2.7; >5.5 whorls. UNC nn.: H 10.9; W 4.5; Hap 2.8.

Remarks – *Dyris ariei* shares the general convex whorl profile, rather thin-shelled nature and type of spiral ornamentation, with *D. hoornae*. However, *D. ariei* is larger, wider, has more and lower ribs on the later teleoconch whorls, and has more variation in secondary ribs. *Dyris lintea* has a thicker shell, lower and broader ribs with more variation in their number and position. *Dyris ariei* increases regularly in width throughout growth, in contrast to *D. lintea*. *Dyris hoornae* and *D. ariei* may form two stratigraphic successive forms of a single lineage. No intermediate forms were found.

***Dyris carinatus* sp. nov.**

Figs. 15k, 17c, 113, 114.

2002 *Dyris* sp. Wesselingh *et al.*, fig. 3l.

Type material – INGEMMET TN29 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9, (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 620 (paratype), same locality, level F703 (0.6 m above DL). RGM 456 397 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation MZ9, (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996.

Range – Pebas Formation, MZ8 - MZ10 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – Named after the prominent median keel (Latin, *carina* for keel).

Diagnosis – Strongly carinate, elongate *Dyris* (SA 19-23°); base of body whorl bounded by secondary keel; columella slightly coiled; shell imperforate.

Description – The nucleus is slightly inclined and small (diameter *c.* 30 µm), with some broad, low, poorly defined mammillae near the sutures. The first 1.6 whorls are convex with a deeply impressed suture. A fine, axial constriction or lineament marks the protoconch-teleoconch boundary at 1.6-1.8 whorls. Thereafter, two keels soon develop at one quarter and a half to two thirds of the whorl height, with straight ramps above, below and in between. The fine, numerous growth lines are located at regular

distances on the first teleoconch whorls, giving this part of the shell a slightly reticulate appearance. The lower keel fades after three teleoconch whorls and the upper keel migrates to the middle of the whorl, resulting in a distinctly carinate outline of this species. Also, a third, basal keel becomes visible at the lower suture. Growth lines become progressively more prosocline and sigmoid. The basal keel becomes prominently visible at the body whorl, bounding the rather narrow base. The aperture is subquadrate with two hollow angulations corresponding to the two remaining keels, but is damaged in all specimens. The aperture is adnate with a very thin outer lip. The columellar lip is formed by the coiled columella and dips away at the top below the slightly produced upper margin of the outer lip. The shell is imperforate.

Dimensions – INGEMMET TN29: H 6.4; W 2.3; Hap 1.5; 9.6 whorls. RGM 456 397: H 8.9; W 2.7; Hap 1.8; >9.6 whorls.

Remarks – This species resembles *Dyris* sp. (*Dyris tricarinata* (Boettger) of Nuttall, 1990, figs. 76-78) from the Miocene San Cayetano Formation, Loja Basin, Ecuador. The latter is broader, has well-developed spiral ribs below the median keel and lacks a pronounced basal keel. *Dyris carinatus* also superficially resembles *Feliconcha feliconcha*, but the latter lacks the the two well-defined spiral ribs after the protoconch-teleoconch boundary that are well expressed in the former.

***Dyris megacarinatus* sp. nov.**
Figs. 115, 116.

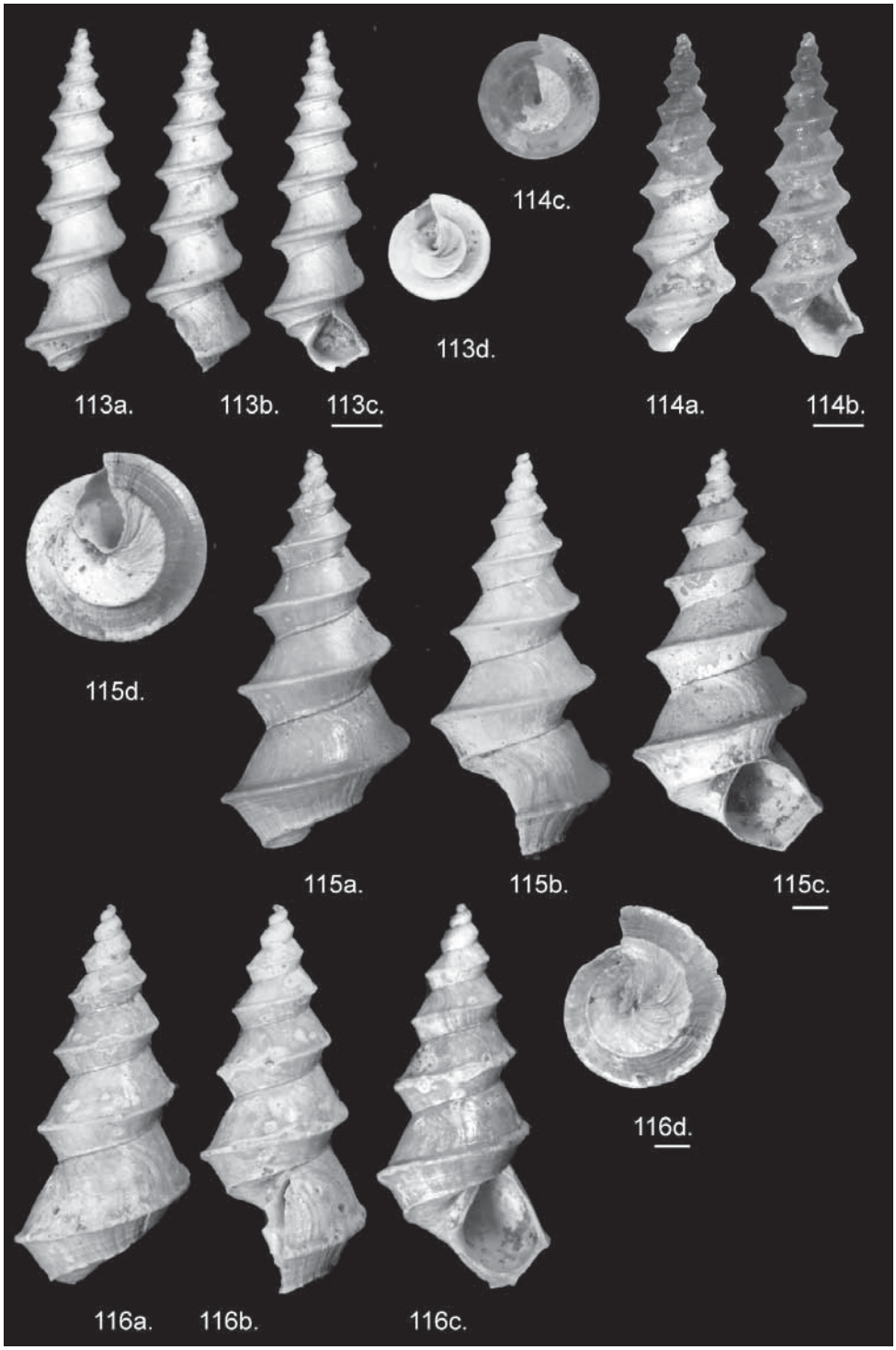
Type material – RGM 456 394 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F60 (17.1 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 395, 456 396 (apical fragment), UNC nn. (two fragments), all paratypes from the same locality.

Range – Pebas Formation, MZ11 - MZ12 (late Middle - early Late Miocene), Colombian Amazonia.

Derivatio nominis – The name reflects the size (Greek, *megas* meaning large) and the prominent carina (Latin, *carina* for keel).

Diagnosis – Large, relatively wide *Dyris* (SA 33°) with a prominent median keel, base of body whorl bounded by secondary keel; shell narrowly rimate.

Description – The nucleus is slightly inclined and has a diameter of approximately 40 µm. No protoconch-teleoconch boundary was observed in the slightly abraded material. The top of the first 1.3 whorls are planar, but descend rapidly thereafter. The second whorl is convex with a deep suture. From 1.7 whorls onward, a prominent median spiral keel gradually develops. Traces of secondary spirals can be seen at *c.* one third of the whorl height, but disappear early on the teleoconch. The median keel bounds a


114c.
113d.
113a.
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113c.
114a.
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116d.
116a.
116b.
116c.

steeply dipping, straight subsutural ramp. The perimeter is carinate. Growth lines are at first very slightly prosocline and faintly sigmoid, but become more pronounced prosocline and sigmoid on later whorls. A second keel is seen at the lower suture. On the body whorl it becomes entirely visible as a marginally elevated keel that bounds the base of the body whorl. Fine spiral lirae develop between the two keels at the last two teleoconch whorls and uncommonly just above the median keel. The aperture is entire, only the boundary area between the parietal and outer lip margins appears to be attached, but is damaged. The apertural margins are thin. The columellar lip is slightly bent outward. The outer lip contains two angulations corresponding to the two primary spiral keels. The umbilicus is narrow, but deep.

Dimensions – RGM 456 394: H 11.2; W 5.1; Hap 3.0; >7.8 whorls. RGM 456 395: H 10.9; W 4.3; Hap >3.6; >7.2 whorls. RGM 456 396: H 2.6; W 1.6; 4.8 whorls.

Remarks – This species closely resembles and is likely the descendant of *Dyris carinatus* sp. nov. It differs from that species by the larger size and higher W/L ratio.

***Dyris denticulatus* sp. nov.**

Figs. 117-119.

1990 *Dyris* sp. Nuttall, p. 201, figs. 113-120.

Type material – RGM 456 554 (holotype), La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 13'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. RGM 456 555, 456 556 (both paratypes) and UNC nn., same locality.

Range – Pebas Formation, MZ2 (late Early - early Middle Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – The umbilical chink in mature specimens gives the shell a somewhat toothed appearance (Latin, *denticulum* means tooth).

◀ Figs. 113, 114. *Dyris carinatus* sp. nov.

Fig. 113. RGM 456 397, paratype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 114. INGEMMET TN29, holotype, same locality as Fig. 113. a, rear view. b, front view. c, basal view.

Figs. 115, 116. *Dyris megacarinatus* sp. nov.

Fig. 115. RGM 456 394, holotype, Santa Sofia (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view. Scale bar represents 1 mm.
Fig. 116. RGM 456 395, paratype, same locality. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Diagnosis – Rather straight-sided *Dyris*; SA 23-25°; early teleoconch whorls with a spiral ornamentation of 4-5 very fine spiral ribs that cover the lower three fifths of the whorl and a very steeply dipping (almost vertical), smooth subsutural ramp above; whorl profile flat, but increasingly convex at the last teleoconch whorls, where the shell becomes thick; columella with a broad chink.

Description – The nucleus (diameter 60 µm) is inclined. The embryonic shell is tilted, and separated from the remainder protoconch by a slight and broad axial depression at *c.* 0.3 whorls. The remainder of the protoconch has rather convex whorls and a somewhat impressed suture. At 1.7 whorls a very poorly visible axial lineament marks the protoconch-teleoconch boundary. Two spiral ribs develop gradually on the first 0.5 teleoconch whorls located at *c.* one quarter and three fifths of the whorl height. The upper spiral bounds a straight, very steeply dipping, smooth subsutural ramp above. Two or three additional spirals develop within one whorl on the lower part. The lower spiral may border a narrow suprasutural depression for about two whorls. From the second to the fourth teleoconch whorl, the spirals become lower, broaden and disappear, and the whorls become smooth, apart for the fine, slightly prosocline growth lines. The base of the body whorl is rounded and the body whorl of larger specimens is convex; preceding whorls are almost straight-sided. The shell at the body whorl is markedly thickened. The aperture is damaged in all available material. The basal and outer lip are invariably broken. The aperture appears to be semicircular. The inner lip callus expands over the columella. The columella itself bears a broad and well visible chink, located about half the height of the columellar lip. Apparently, the extension of the umbilical lip covers the umbilical area, but when broken a rimate umbilicus appears. The lack of specimens with a well-preserved shell base precludes assessment of the umbilical region.

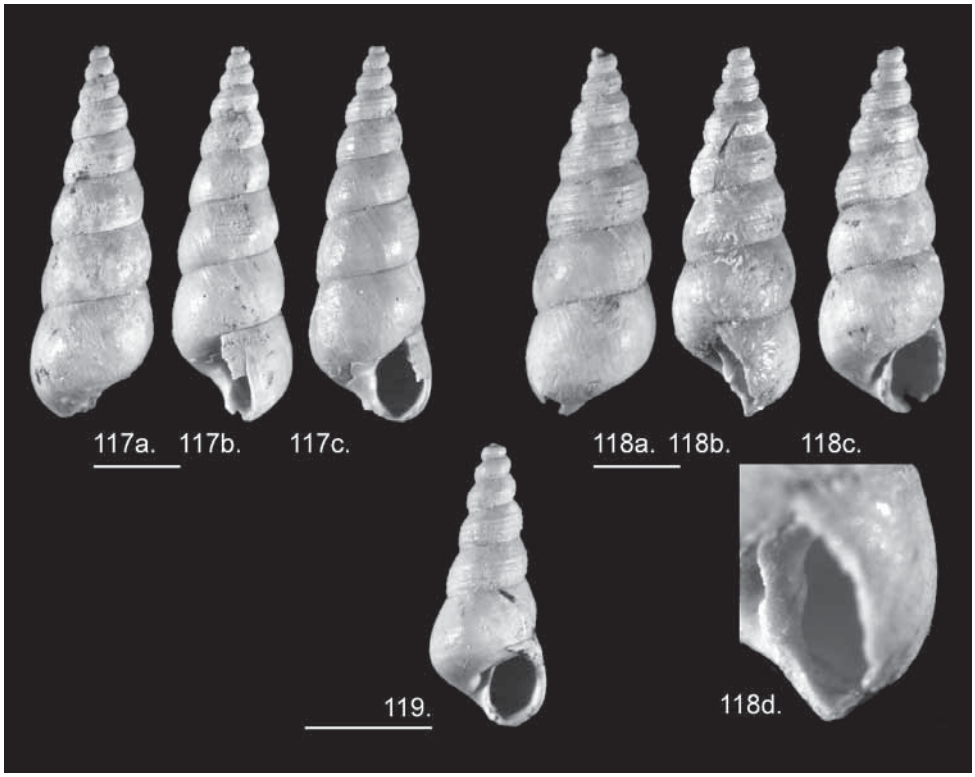
Dimensions – RGM 456 554: H 4.5; W 1.45; Hap 1.1; *c.* 9.1 whorls. RGM 456 555: H 4.45; W 1.55; Hap *c.* 1.1; >8.2 whorls. RGM 456 556: H 2.5; W 1.0; Hap 0.75; 7.1 whorls. UNC nn.: H 5.7; W 1.8; Hap 1.2.

Remarks – The whorl profile and spiral ornament on early teleoconch whorls resemble the general architecture of *D. mattii*. However, the combination of an umbilical chink and the slightly rounded, very thick and smooth later teleoconch whorls make *D. denticulatus* different from all other *Dyris* species.

Genus *Onobops* Thompson, 1968

Type species – *Onobops crassus* Thompson, 1968, coastal marshes, Florida.

Diagnosis – Small to intermediate (L 1.5-5 mm), ovate conical to elongate cochliopids; shell ornamented with fine spiral ribs; some variation in the onset of teleoconch ornament exists, but often quick onset of >3 spiral ribs at the protoconch-teleoconch boundary at 1.5-2.7 whorls; spiral ribs mostly low and narrow, draped over the surface of the shell; some of the ribs may come to dominate, otherwise additional small ribs may develop or the spiral ornament may disappear on later teleoconch whorls; subsutural



Figs. 117-119. *Dyris denticulatus* sp. nov.

Fig. 117. RGM 456 554, holotype, La Tagua (Putumayo, Colombia). a, rear view. b, lateral view. c, front view.
Fig. 118. RGM 456 555, paratype, same locality as Fig. 117. a, rear view. b, lateral view. c, front view. d, detail aperture showing low columellar chink.
Fig. 119. RGM 456 556, paratype, same locality as Fig. 117, front view.

Scale bars represent 1 mm.

ramp usually not well pronounced; ovate-semicircular aperture usually adnate; leftmost margin of the columellar lip at or to the left of the axis of the shell.

Range – Miocene, western Amazonia; Quaternary and Recent, coastal marshes Atlantic and Gulf coasts, U.S.A. and Mexico.

***Onobops communis* sp. nov.**

Figs. 17h, 120-123.

1990 *Dyris lintea* (Conrad); Nuttall, p. 190 (*pars*), figs. 54, 55 (*non* figs. 49-53, 56-58).
2002 *Onobops*? sp. Wesselingh *et al.*, fig. 3i.

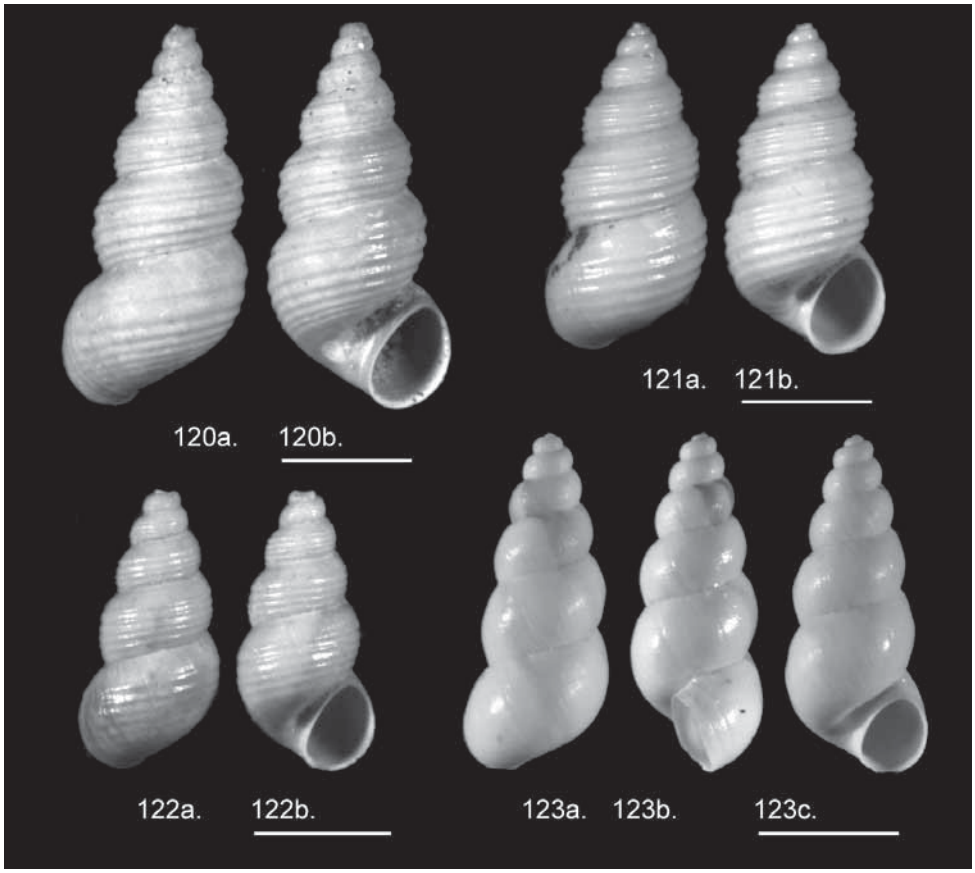
Type material – INGEMMET TN60 (holotype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 491 (paratype), same locality. RGM 456 492: Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 493: Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence Loreto Yacu (3°46'S 70°22'W), level F31 (7.8 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 625 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, MZ 9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.

Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – This species is among the most common (Latin, *communis*) species in the MZ7-MZ12 of the Pebas Formation.

Diagnosis – Small, ovate-conical *Onobops*; SA 32-37°; ornament of 3-8 spiral ribs of variable strength develop almost instantaneously after the protoconch-teleoconch boundary at 1.5-1.7 whorls, leaving the upper one third of the whorl smooth; ribs may remain strong throughout the shell or disappear within a whorl to produce a smooth shell; aperture semicircular-subovate, commonly detached.

Description – The nucleus (diameter *c.* 40-50 µm) is inclined to strongly inclined and contains very low, poorly defined wrinkles in the margins. The embryonic shell may be separated from the remainder of the protoconch by a barely visible axial lineament or depression at 0.4-0.55 whorls. The first whorl is flat; the second whorl rapidly descends and is rather convex with a deep suture. The protoconch-teleoconch boundary is located at 1.5 to 1.7 whorls and marked by a fine, often barely visible axial thread. Closely spaced growth lines appear immediately after the boundary. Almost directly after the boundary spiral ribs may develop. They occur apparently at random, but within half a whorl 3-8 very fine spiral ribs are present that appear to be draped over the shells surface. The upper rib is located at *c.* two thirds of the whorl height, leaving the upper third of the whorl as a smooth, slightly convex, poorly defined subsutural ramp. Additional ribs on later teleoconch whorls occasionally occupy the ramp. The interspaces are on average 1.5 to 2.0 times as wide as the spirals. Ribs become wider and thicker during growth, but also can become lower or even disappear. In the type material, apart from RGM 456 493, 7-9 spirals are present on the body whorl, but specimens illustrated in Nuttall (1990, figs. 54, 55) there are up to 22. Spirals are usually located at equal distances on early teleoconch whorls, but especially later, some variation is possible. The upper rib is strongest and comparatively far from the adjoining rib on the holotype. The growth lines are common, irregularly spaced, fine and prosocline. The profile of the teleoconch whorls is evenly rounded. The aperture is semicircular to subovate. The upper part of the parietal lip may



Figs. 120-123. *Onobops communis* sp. nov.

Fig. 120. INGEMMET TN60, holotype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, front view.
Fig. 121. RGM 456 491, paratype, same locality as Fig. 120. a, rear view. b, front view.
Fig. 122. RGM 456 492, paratype, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 123. RGM 456 493, paratype, Los Chorros (Amazonas, Colombia). a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

be adnate, but the aperture can also be completely detached. The inner lip is long, only very marginally bent, and typically 20-30° inclined in respect with the shells axis. The basal and outer lips are thin and rounded. In specimens where the aperture is detached, the apertural margins are slightly thickened, especially on the inner lip side. The shell has a very shallow, partially or wholly covered, umbilicus.

Dimensions – INGEMMET TN60: H 3.0; W 1.4; Hap 0.9; *c.* 6.7 whorls. RGM 456 491: H 2.5; W 1.2; Hap 0.8; 6.2 whorls. RGM 456 492: H 2.0; W 1.0; Hap 0.65; *c.* 5.6 whorls. RGM 456 493: H 2.5; W 1.05; Hap 0.6; 6.5 whorls.

Remarks – The variation of ribbing is very large in this species. The MZ7 populations are almost entirely made up of specimens with very thin spirals only and these have a smooth appearance. Specimens of MZ8 intervals have in general well developed spiral ribs, but finely ornamented and intermediate specimens occur. In the MZ9-MZ12 populations, specimens are again very finely ribbed and have a smooth appearance. The presence of intermediate forms indicates that these populations represent a single species.

***Onobops minissimus* sp. nov.**
Figs. 124-128.

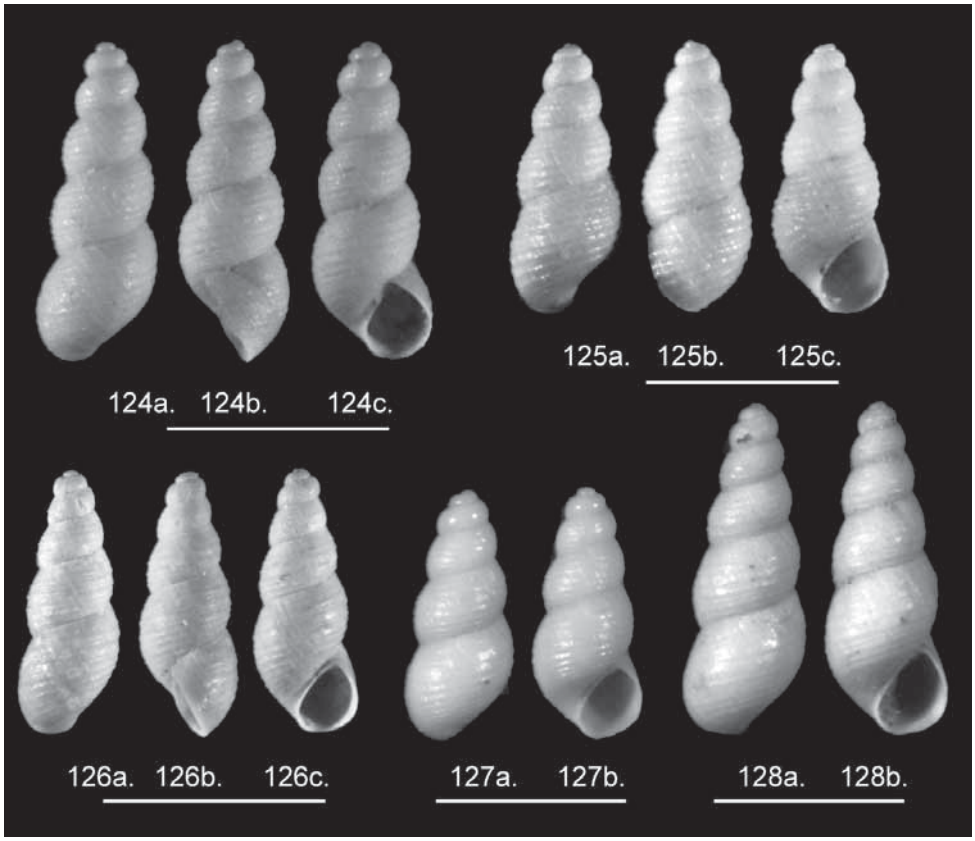
Type material – INGEMMET TN82 (holotype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 576-456 579, all paratypes from the same locality.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – *Minissimus* is the superlative of *minimus* (Latin for least), and refers to the small size of this species.

Diagnosis – Minute, ovate-conical *Onobops* ornamented with 9-16 thin, well defined spirals of slightly variable strength; SA 26-30°; whorl profile somewhat depressed; aperture drop-shaped to subovate; left part of the columellar lip left of the axis of the shell.

Description – The nucleus (diameter 40-50 µm) is inclined. The embryonic shell is tilted. It is separated at 0.4-0.6 whorls by a fine, obvious axial thread from the protoconch-2, that is smooth, has convex whorls and an impressed suture. A well visible axial thread marks the boundary with the teleoconch at 1.8-2.0 whorls. Directly after the protoconch-teleoconch boundary, six spirals develop, leaving an indistinct, smooth, subsutural zone above. The spirals are well developed and increasing in number during growth up to about ten on the penultimate whorl, and 11-16 on the body whorl. Their strength, as well as the width of the interspaces, is somewhat variable; the interspaces are typically about twice as wide as the ribs. The spiral ribs disappear a short distance before the outer lip on larger specimens. The growth lines are numerous, fine, well visible and prosocline. On the later whorls the upper one sixth becomes smoother, although some irregular spiral elements may still be present. The perimeter is depressed convex and the suture slightly impressed. The aperture is subovate to drop-shaped. It may be almost entirely adnate as well as completely detached. The outer- and basal lips are broadly rounded and thin. The inner lip is usually rather long. A thin parietal callus is present. The columellar lip is slightly thickened when attached, but otherwise thin and slightly erect. The leftmost part of the columellar lip is well left of the axis of the shell. The shell is imperforate.



Figs. 124-128. *Onobops minissimus* sp. nov.

Fig. 124. INGEMMET TN82, holotype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 125. RGM 456 576, paratype, same locality as Fig. 124. a, rear view. b, lateral view. c, front view.
Fig. 126. RGM 456 577, paratype, same locality as Fig. 124. a, rear view. b, lateral view. c, front view.
Fig. 127. RGM 456 578, paratype, same locality as Fig. 124. a, rear view. b, front view.
Fig. 128. RGM 456 579, paratype, same locality as Fig. 124. a, rear view. b, front view.

Scale bars represent 1 mm.

Dimensions – INGEMMET TN82: H 1.5; W 0.55; Hap 0.4; 5.6 whorls. RGM 456 576: H 1.6; W 0.6; Hap 0.4; 5.2 whorls. RGM 456 577: H 1.35; W 0.6; Hap 0.4; 5.6 whorls. RGM 456 578: H 1.2; W 0.55; Hap 0.35; 5.1 whorls. RGM 456 579: H 1.7; W 0.6; Hap 0.4; 5.9 whorls.

Remarks – *Onobops minissimus* is smaller and more slender than *O. communis*. It has a less convex whorl profile, caused by the commonly broadly adnate nature of the inner lip, and more spiral ribs.

***Onobops ventricosus* sp. nov.**
Figs. 129-131.

Type material – RGM 456 494 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 493 (paratype), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence Loreto Yacu (3°46'S 70°22'W), level F31 (7.8 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. INGEMMET TN61 (paratype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

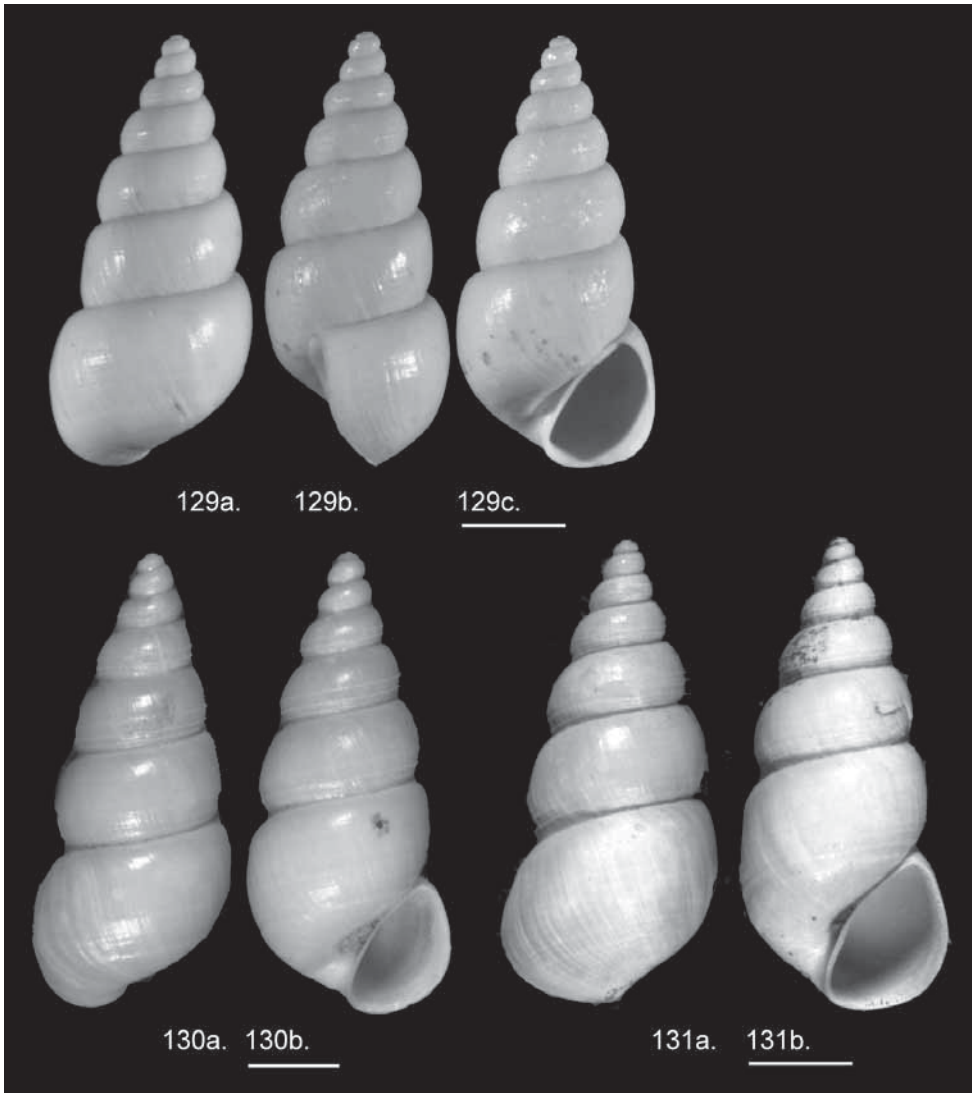
Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – *Ventricosus* named after the belly shaped (bulbous) whorl profile of this species (Latin, *venter* for belly).

Diagnosis – Intermediate to large *Onobops* with markedly bulbous whorls; SA 33-35°; three to four delicate spiral ribs on the lower half of the whorls that usually fade on later teleoconch whorls.

Description – The nucleus is flat or slightly inclined, has a diameter of *c.* 40-60 µm and has very low wrinkled ornament at the tip. The embryonic shell is separated from protoconch-2 at 0.5 whorls by a broad, poorly defined axial depression. The protoconch-2 is smooth, apart for very fine orthocline growth lines. The first whorl is flat; from the second whorl on the shell rapidly descends and the perimeter becomes markedly convex. Fine, densely spaced growth lines occur at the protoconch-teleoconch boundary (1.7-2.1 whorls). Three to four very thin and delicate spiral ribs develop after *c.* 0.3 whorls after the boundary at the lower half, leaving the upper half smooth. The distances between the spiral ribs are slightly unequal, the upper usually being separated slightly further than the others. The ribs gradually lower and usually disappear on later teleoconch whorls. Growth lines are numerous, very fine and prosocline to slightly sigmoid. Very low and poorly defined irregular microscopic ribs or grooves are found throughout the surface of the shell on later teleoconch whorls. The aperture is subovate to semicircular with a broadly rounded, and very shallowly and broadly retracted base. The inner lip is long, almost straight and inclined at about 30° with respect to the axis of the shell. The margins are thin or only very slightly thickened. The parietal margin is adnate; the basal part of the inner lip is slightly erect and can even be slightly folding. The shell has a shallow, rimate umbilicus.

Dimensions – RGM 456 494: H 4.6; W 2.1; Hap 1.45; 7.8 whorls. RGM 456 495: H 4.6; W 2.0; Hap 1.5; 7.9 whorls. INGEMMET TN61: H 4.7; W 2.1; Hap 1.6; 7.7 whorls.



Figs. 129-131. *Onobops ventricosus* sp. nov.

Fig. 129. RGM 456 495, paratype, Los Chorros (Amazonas, Colombia). a, rear view. b, lateral view. c, front view.
Fig. 130. RGM 456 494, holotype, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 131. INGEMMET TN61, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, front view.

Scale bars represent 1 mm.

Remarks – This species is wider and has more bulbous whorls than *O. communis*, and has a characteristic ornament of three to four spirals restricted to the lower half of the whorls.

***Onobops bispiralis* sp. nov.**
Figs. 132, 133.

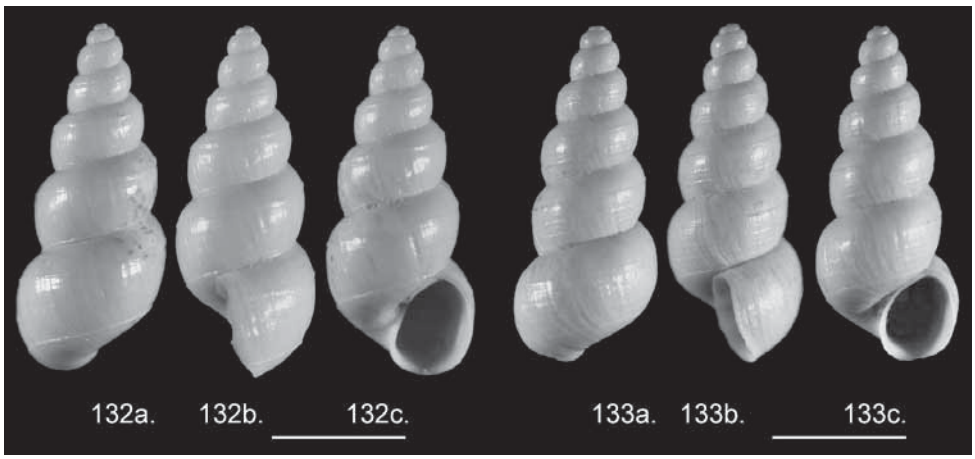
Type material – INGEMMET TN83 (holotype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 580 and RGM 456 581 (paratypes), same locality.

Range – Pebas Formation, MZ6 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – *Bispiralis* named after the common pronouncement of the upper and lower spiral in this species.

Diagnosis – Intermediate-sized *Onobops* with convex whorl profile; SA 31-32°; shell with smooth appearance, but with 1-4 very fine thin, well-defined spirals; two spirals (upper one bounding subsutural ramp, lower one bounding base of body whorl) may be pronounced.

Description – The nucleus (diameter 40 µm) is flat. The embryonic shell is separated from the remainder of the protoconch at 0.3 whorls by a fine axial lineament. The protoconch has rounded whorls and a somewhat impressed suture. At 2.4-2.6 whorls it is



Figs. 132, 133. *Onobops bispiralis* sp. nov.

Fig. 132. RGM 456 580, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 133. INGEMMET TN83, holotype, same locality as Fig. 132. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

separated from the teleoconch. The protoconch-teleoconch boundary is very poorly defined and can often only be identified by the onset of densely spaced, thin, slightly prosocline growth lines. After the boundary, two to four, slightly irregular spiral cords gradually develop, the upper one of which becomes slightly pronounced within a whorl. The whorl profile remains rounded and the suture moderately impressed. The upper spiral bounds a convex, smooth subsutural zone on the upper one third of the whorl. Interspaces between the spirals are very wide. Another spiral may become visible at the lower suture on the teleoconch and is well visible on the body whorl. The base of the body whorl is rounded. The aperture is circular. The upper part of the inner lip is adnate. The columellar lip is slightly erect and thin. The basal and outer lip are broadly rounded and thin, but in the holotype and RGM 456 580 a low and poorly defined thickening occurs just behind the aperture that is only barely visible at the exterior of the shell. The shell is imperforate or narrowly rimate.

Dimensions – INGEMMET TN83: H 2.6; W 1.05; Hap 0.7; 6.7 whorls. RGM 456 580: H 2.65; W 1.1; Hap 0.8; 6.7 whorls. RGM 456 581: H 2.85; W 1.15; Hap 0.8; 7.0 whorls.

Remarks – The convex whorl profile of *Onobops bispiralis* resembles that of *O. ventricosus*. The whorls of the latter are more bulbous, especially with the base more produced, and lack the thin spirals typical of *O. bispiralis*.

***Onobops elongoides* sp. nov.**
Figs. 16g, 17f, 134-139.

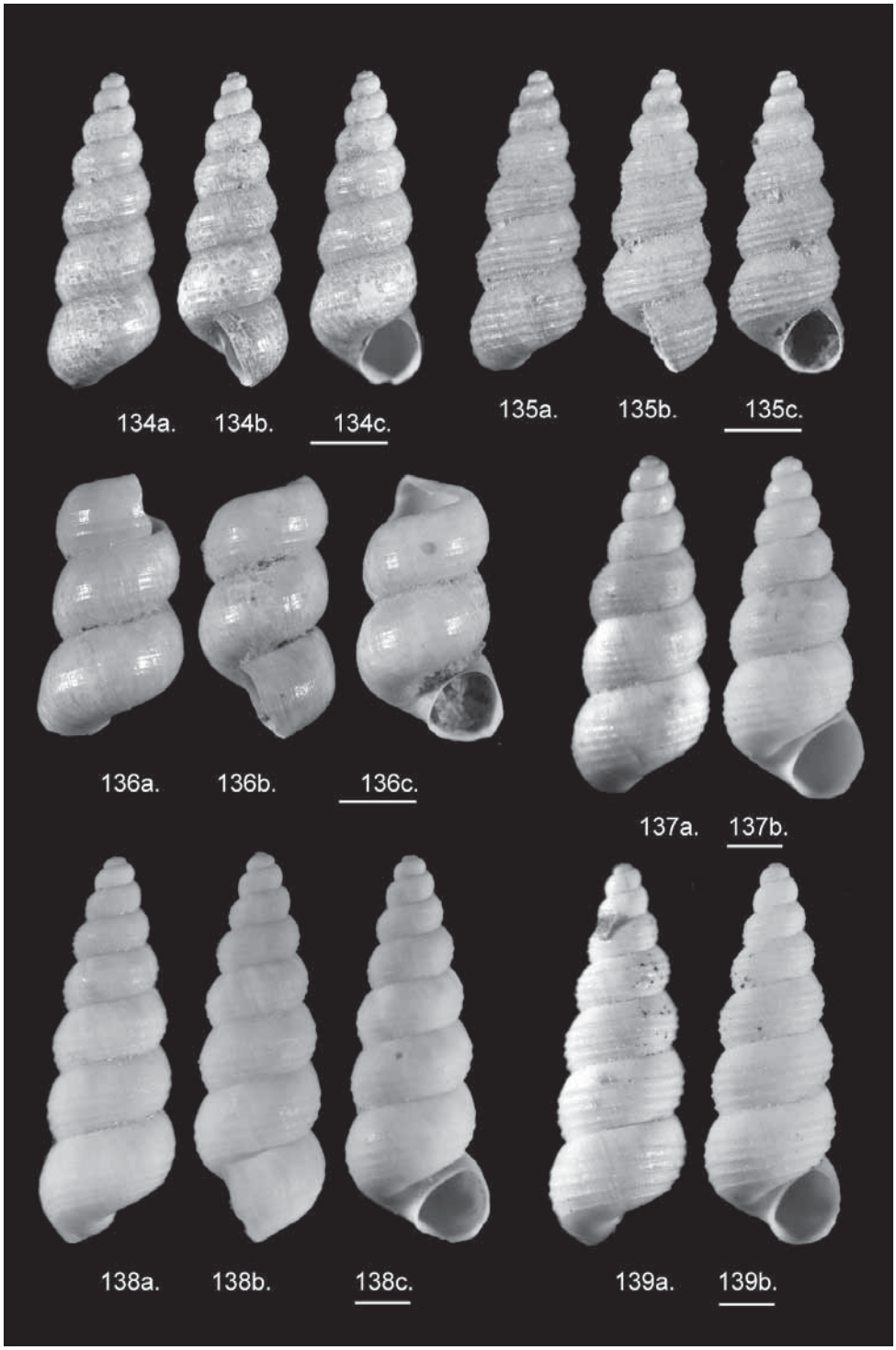
Type material – INGEMMET TN77 (holotype), Iquitos (Loreto, Peru), cliff exposure in west bank Amazon River at Puerto Ganso-Azul (3°45'S 73°11'W), level F75 (4.9 m above DL). Pebas Formation, MZ6 (Middle Miocene); leg. F.P. Wesselingh, 10-1991. RGM 456 559, 456 560, 456 617 and RGM 456 622, all paratypes from the same locality. INGEMMET TN76 (paratype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S 73°00'W), level F318 (1.35 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996. RGM 456 557 (paratype) and RGM 456 558 (paratype), same locality.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – *Elongoides* refers to the elongate nature of this species.

Diagnosis – Shell rather large and elongate for *Onobops* (L up to *c.* 5; SA 25-29°), with three to four spiral ribs at the lower half of the rounded whorls that usually fade on later teleoconch whorls; subsutural ramp may be well developed on the later teleoconch; base of body whorl rounded to slightly depressed; umbilicus narrowly rimate.

Description – The nucleus (diameter 30-40 µm) is slightly inclined and contains very low wrinkles or low mammillae in the margins. At 0.4-0.5 whorls a fine axial line or


134a.
134b.
134c.
135a.
135b.
135c.
136a.
136b.
136c.
137a.
137b.
138a.
138b.
138c.
139a.
139b.

axial depression marks the boundary between the embryonic shell and the protoconch-2. The latter has convex whorls, an impressed suture and, apart for an occasional orthocline axial lineament, is smooth. The protoconch-teleoconch boundary is extremely poorly visible; uncommonly a very fine axial lineament is present. Densely spaced growth lines occur at about 1.8-2.3 (possibly up to 2.7) whorls, followed by three spiral ribs within 0.3 whorls. The whorl perimeter is rounded and may later become somewhat shouldered. On later whorls a fourth spiral rib develops and the ribs gradually shift to occupy the lower three fifths of the whorl, marking a well defined, slightly convex, but more often straight subsutural ramp above. Additionally, one or two secondary ribs may develop between the primaries on later whorls. The spiral ribs become progressively lower and wider on later whorls of larger specimens. Growth lines are prosocline. The base of the body whorl is rounded and can be slightly flattened. The aperture is semilunate to subrounded with thin apertural margins. The parietal lip may be adnate, but equally commonly the entire aperture is detached. The inner lip is strongly inclined and there is no (sample F75) or only a slight (sample F318) separation between the parietal and columellar margin. The basal and outer lip form a broad rounding. The umbilicus is very narrowly rimate.

Dimensions – INGEMMET TN76: H 3.6; W 1.25; Hap 0.7; 8.5 whorls. RGM 456 557: H 3.25; W 1.3; Hap 0.75; 7.8 whorls. RGM 456 558: H 3.5; W 1.25; Hap 0.8; 8.2 whorls. INGEMMET TN77: H 4.3; W 1.45; Hap 1.0; 7.7 whorls. RGM 456 559: H 4.2; W 1.6; Hap 0.9; *c.* 7.8 whorls. RGM 456 560: H >3.5; W 1.95; Hap 1.1.

Remarks – The rounded nature of later teleoconch whorls of *O. elongoides* somewhat resembles that of *O. ventricosus*. The latter has more bulbous whorls and lacks the slightly flattened base seen in most of the larger specimens of *O. elongoides*. Further, *O. elongoides* is more slender and has more pronounced spiral ribbing on early teleoconch whorls. The elongate outline distinguishes the species from *O. communis*.

***Onobops microconvexus* sp. nov.**

Figs. 15d, 140-142.

Type material – INGEMMET TN62 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3

◀ Figs. 134-139. *Onobops elongoides* sp. nov.

Fig. 134. INGEMMET TN76, paratype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 135. RGM 456 557, paratype, same locality as Fig. 134. a, rear view. b, lateral view. c, front view.
Fig. 136. RGM 456 558, paratype, same locality as Fig. 134. a, rear view. b, lateral view. c, front view.
Fig. 137. RGM 456 559, paratype, Iquitos (Loreto, Peru). a, rear view. b, front view.
Fig. 138. INGEMMET TN77, holotype, same locality as Fig. 137. a, rear view. b, lateral view. c, front view.
Fig. 139. RGM 456 560, paratype, same locality as Fig. 137. a, rear view. b, front view.

Scale bars represent 1 mm.

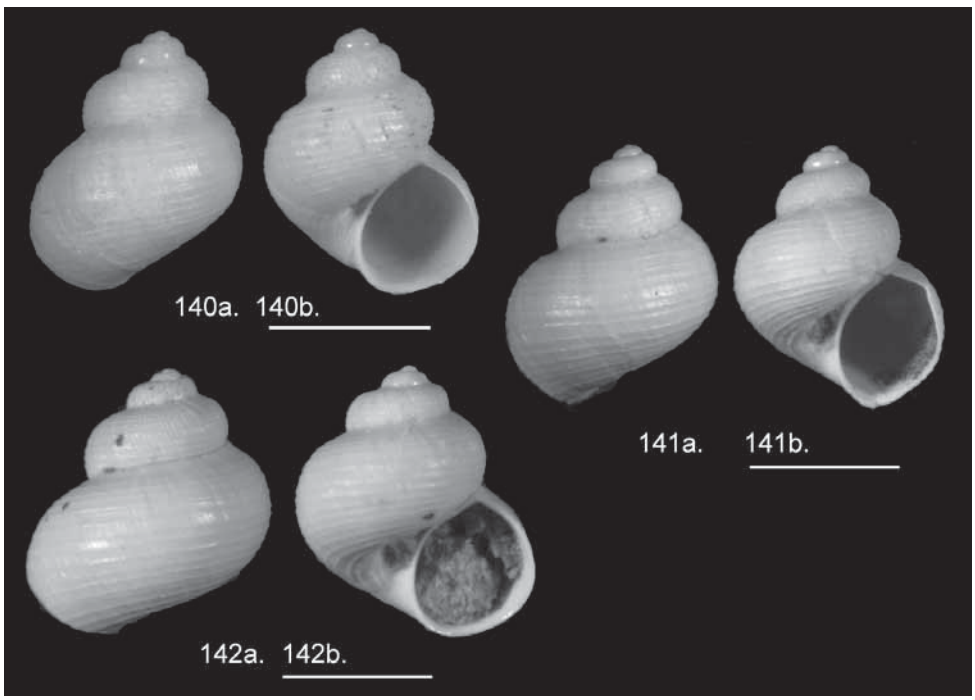
m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 496 and RGM 456 497 (paratypes): Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – *Micro* (Greek, *mikros* for small) refers to the minute size; *convexus* (Latin for arched) refers to the convex whorl profile.

Diagnosis – Minute, broadly convex (SA 74-76°), umbilicate pomatiasiform *Onobops* with 9-10 thin spiral ribs on the penultimate whorl.

Description – The nucleus is inclined (diameter *c.* 60-80 µm) and the embryonic shell is prominently tilted. It is separated from the remainder protoconch at 0.5 whorls



Figs. 140-142. *Onobops microconvexus* sp. nov.

Fig. 140. INGEMMET TN62, holotype, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 141. RGM 456 497, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, front view.
Fig. 142. RGM 456 496, paratype, same locality as Fig. 141. a, rear view. b, front view.

Scale bars represent 1 mm.

by an axial constriction. The protoconch-2 itself is smooth and has a convex whorl profile. The boundary with the teleoconch at 1.7-1.8 whorls is marked by a fine axial thread, after which the spiral ornament consisting of 6-7 very fine spirals immediately develops. The upper one seventh of the early teleoconch whorls has either reduced spirals or lacks them altogether, giving it the impression of the presence of a poorly defined subsutural ramp. The number of spirals increases to 9-10 on the penultimate whorl and 18-19 on the body whorl. The thin, well-defined spirals are slightly irregularly spaced, with interspaces being about two to three times as wide. Ribs can be slightly displaced at the common interruptions of growth. The prosocline growth lines are numerous, very fine and regularly spaced. The base of the body whorl curves into the wide and deep umbilicus. The aperture is nearly circular, with a slightly rounded angle at the junction of the parietal and outer lips. The upper part of the parietal lip is adnate. The margins are only very slightly thickened, if at all. The apertural plane is slightly inclined.

Dimensions – INGEMMET TN62: H 1.65; W 1.35; Hap 0.95; 3.9 whorls. RGM 456 496: H 1.9; W 1.6; Hap 1.05; 3.9 whorls. RGM 456 497: H 1.8; W 1.45; Hap 1.05; 4.1 whorls.

Remarks – The small size and depressed conical to convex outline distinguish *O. microconvexus* from all other *Onobops* species.

***Onobops*? *iquitensis* sp. nov.**
Figs. 143-145.

Type material – INGEMMET TN69 (holotype), Iquitos (Loreto, Peru), cliff exposure in west bank Amazon River at Puerto Ganso-Azul (3°45'S 73°11'W), level F75 (4.9 m above DL). Pebas Formation, MZ6 (Middle Miocene); leg. F.P. Wesselingh, 10-1991. RGM 456 533 and 456 534 (paratypes), same locality.

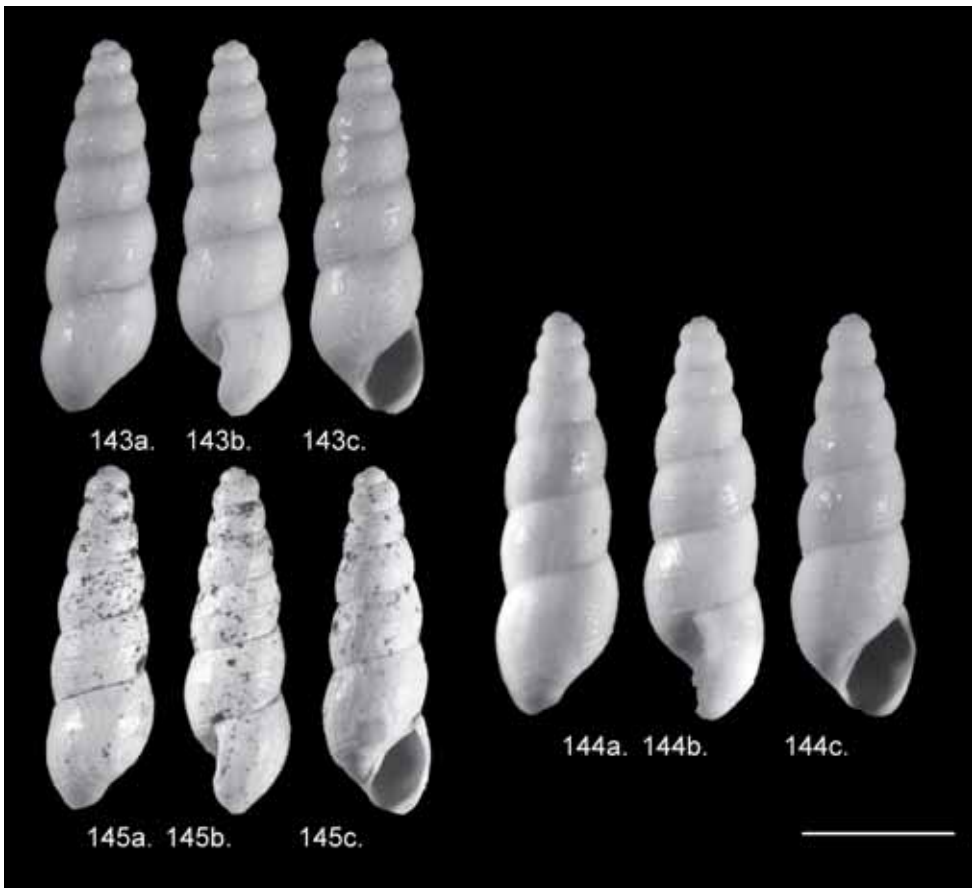
Range – Pebas Formation, MZ6 - MZ7 (Middle Miocene), Peruvian Amazonia.

Derivatio nominis – *Iquit* is derived from the first part of the name of the city of Iquitos (Loreto, Peru), where this species was commonly found in samples collected from exposures at the harbour.

Diagnosis – Small, relatively high-spired shell (22-24°); up to *c.* eight spirals, one or two of which, located at the middle of the whorl, may be slightly pronounced; growth lines sigmoid, orthocline to slightly opisthocline; aperture adnate, outer lip produced; slight umbilical chink may be present behind the ovate aperture; shell imperforate.

Description – The nucleus (diameter *c.* 40-60 µm) is slightly inclined to flat. At 0.4-0.5 whorls the embryonic shell is separated from the remainder protoconch by a wide axial constriction. The protoconch is low dome-shaped, with a slightly impressed suture. A barely visible axial thread marks the protoconch-teleoconch boundary that is located at 2.0-2.2 whorls. Thereafter, 6-8 very fine spiral ribs develop almost immediately, two of which (at approximately one third and three fifths of the whorl height)

may be slightly more pronounced. The upper one fifth of the whorl is more or less straight and smooth. Growth lines are very fine and numerous. They are orthocline to slightly opisthocline and sigmoid. In general, the spiral ribs and growth lines are so fine and low that the shell may appear smooth. The whorl profile is depressed. The base of the body whorl is not clearly separated. The apertural axis is inclined. The columellar and lower two thirds of the outer lip run parallel. The basal lip is flat in frontal view. The parietal lip and upper part of the outer lip converge into the bluntly pointed top of the aperture. In side view, the outer lip is sigmoid. When viewed from below, the basal lip has a shallow and wide retraction. The aperture is adnate. The parietal callus is narrow. The columellar lip is very slightly thickened. A low umbilical chink is



Figs. 143-145. *Onobops*? *iquitensis* sp. nov.

Fig. 143. RGM 456 534, paratype, Iquitos (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 144. INGEMMET TN69, holotype, same locality as Fig. 143. a, rear view. b, lateral view. c, front view.
Fig. 145. RGM 456 533, paratype, same locality as Fig. 143. a, rear view. b, lateral view. c, front view.

Scale bar represents 1 mm.

present on the columella, behind the aperture on RGM 456 534, but is not seen in the other specimens. The shell is imperforate.

Dimensions – INGEMMET TN69: H 2.8; W 0.9; Hap 0.75; 7.2 whorls. RGM 456 533: H 2.45; W 0.75; Hap 0.65; 6.9 whorls. RGM 456 534: H 2.65; W 0.8; Hap 0.65; 7.1 whorls.

Remarks – *Onobops*? *iquitensis* is high-spired compared to previously described *Onobops* species and has a very low spiral ornament, as well as orthocline to opisthocline sigmoid growth lines. This species, as well as the possibly closely related *O.*? *erectus* and *O.*? *bisulcatus*, are attributed hesitantly to *Onobops* based on the generally sudden onset of teleoconch spiral sculpture at the protoconch-teleoconch boundary. However, the orthocline to opisthocline growth lines, the generally very thin spiral ribbing and the depressed whorl profile are not characteristic for the genus. Further investigation is needed for establishing the generic identity of these three species.

***Onobops*? *bisulcatus* sp. nov.**
Figs. 17g, 146-148.

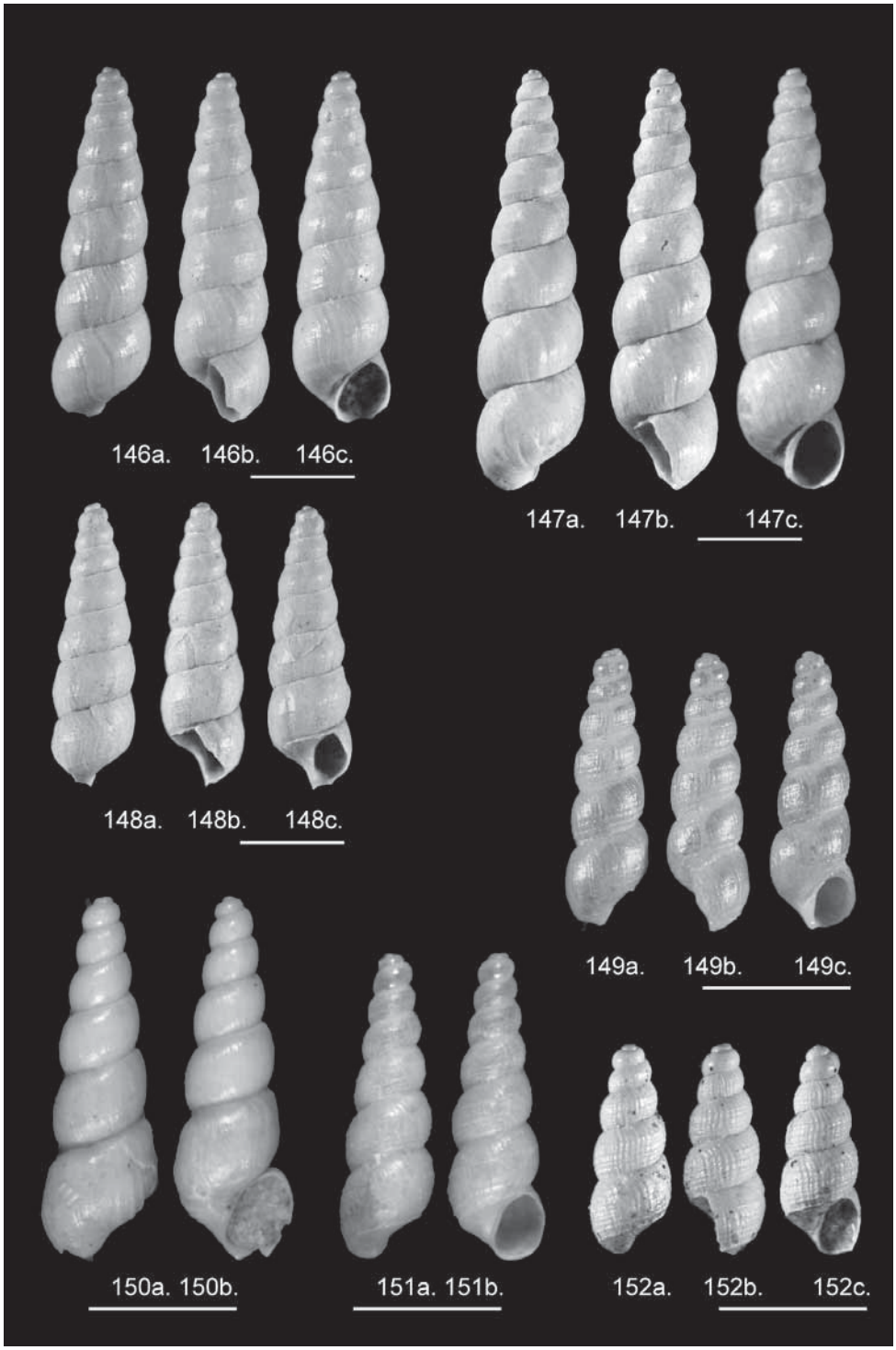
Type material – RGM 456 585 (holotype), Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996. INGEMMET TN85, RGM 456 586 and RGM 456 587 (paratypes), same locality. RGM 456 624 (paratype), Buen Pasa (Loreto, Peru), exposure in east bank Rio Napo, 800 m east of village (3°15'S 73°11'W), level F899 (*c.* 8 m above DL). Pebas Formation, MZ 4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after poorly developed, low, but commonly occurring, subtle, pronounced double median spiral keels.

Diagnosis – High-spired shell (SA 18-22°) with slightly convex, very weakly carinate or bicarinate whorls containing one or two very low and rounded, subtle (poorly defined) spiral keels; growth lines numerous, slightly prosocline to slightly opisthocyrth; later teleoconch whorls on larger specimens become more rounded with a slightly more impressed suture; umbilicus narrowly rimate.

Description – The nucleus (diameter 50-60 µm) is inclined and contains some fine, marginal wrinkles. The embryonic shell is somewhat tilted and separated from the remainder protoconch at 0.45-0.6 whorls by a fine axial lineament. The protoconch-2 has rather convex whorls with an impressed suture. At 1.7 whorls a poorly visible, very fine axial lineament marks the boundary with the teleoconch. Gradually afterwards a single, low, wide and rounded spiral keel develops at *c.* three fifths of the whorl height. This keel bounds a straight, steeply dipping subsutural ramp above. A second, very low and rounded keel may develop within a whorl at about one fifth of the whorl height. The slightly prosocline growth lines are numerous and may coincide with very poorly de-


146a. 146b. 146c.
147a. 147b. 147c.
148a. 148b. 148c.
149a. 149b. 149c.
150a. 150b.
151a. 151b.
152a. 152b. 152c.

fined, low axial undulations. Poorly expressed spiral striae may occur on the basal half of the shell on later teleoconch whorls. Spiral ornamentation becomes less pronounced and disappears on the last teleoconch whorls. The shell has an extremely low carinate or bicarinate whorl profile with broad and rounded keels. On the ultimate whorls of larger specimens, such as INGEMMET TN85, the whorl profile becomes rounded and the suture increasingly impressed. The base of the body whorl is rounded in larger specimens and grades into the very narrowly rimate umbilicus, that may be obscured by the inner lip. On smaller specimens the base of the body whorl may be formed by a rounded angulation. The aperture is semicircular. The parietal margin is adnate. The columellar margin is slightly erect. The basal lip and outer lip are thin and rounded.

Dimensions – RGM 456 585: H 3.3; W 0.95; Hap 0.6; 8.3 whorls. INGEMMET TN85: H 3.95; W 1.0; Hap 0.75; 9.5 whorls. RGM 456 586: H 2.7; W 0.8; Hap 0.6; 7.7 whorls. RGM 456 587: H 3.2; W 0.9; Hap 0.65; 8.5 whorls.

Remarks – *Onobops*? *bisulcatus* has less elongate and slightly more convex whorls than *O.*? *iquitensis*. The latter has a slightly elongate aperture, whereas *O.*? *bisulcatus* has a semicircular aperture.

***Onobops*? *erectus* sp. nov.**
Figs. 149-152.

Type material – INGEMMET TN84 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 582, 456 583 and 456 584, all paratypes from the same locality.

◀ Figs. 146-148. *Onobops*? *bisulcatus* sp. nov.

Fig. 146. RGM 456 585, holotype, Nuevo Paleta (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 147. INGEMMET TN85, paratype, same locality as Fig. 146. a, rear view. b, lateral view. c, front view.
Fig. 148. RGM 456 586, paratype, same locality as Fig. 146. a, rear view. b, lateral view. c, front view.

Figs. 149-152. *Onobops*? *erectus* sp. nov.

Fig. 149. RGM 456 583, paratype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 150. INGEMMET TN84, holotype, same locality as Fig. 149. a, rear view. b, front view.
Fig. 151. RGM 456 582, paratype, same locality as Fig. 149. a, rear view. b, front view.
Fig. 152. RGM 456 584, paratype, same locality as Fig. 149. a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Derivatio nominis – The name refers to the erect (Latin, *erectus* for upright) outline of the shell.

Diagnosis – Minute, high-spired (SA 22-23°), thin-shelled gastropod with low whorl profile, but somewhat impressed sutures; orthocline sigmoid growth lines may form riblets on early teleoconch whorls contributing to a marked reticulate ornament; very narrow, rounded shoulder on body whorl of larger specimens.

Description – The nucleus (diameter 40-60 µm) is inclined. At 0.3-0.5 whorls a very fine axial lineament, sometimes located in a broad axial depression, bounds the smooth embryonic shell. The protoconch-2 is smooth, rather convex, with a somewhat impressed suture. Some slightly sigmoid growth lines may be present on the later part of the protoconch. The protoconch-teleoconch boundary is located at 1.3-2.2 whorls and is marked by an axial lineament. Directly after, densely packed sigmoid growth lines are present. About four very thin and low spirals develop on the holotype; on paratypes, five spirals are present that are more distinct. The growth lines on the holotype and RGM 456 582 remain rather low, whereas in the other paratypes the growth lines form riblets, producing a distinct reticulate ornament on the first four or so teleoconch whorls. Spiral ribs are of different strengths, located at variable distances, and may yield very low and rounded, elongate tubercles. Usually, they are more densely packed on the basal third of the whorls. The upper one quarter usually remains devoid of spiral riblets. Growth lines and spirals become progressively thinner and lower on later whorls, apart for the basal spiral that bounds the rather flat base of the body whorl and remains relatively strong (but rounded). The whorl profile becomes progressively flatter, with narrowly rounded upper and lower margins on later teleoconch whorls dipping into a rather impressed suture. The upper part of the whorl forms a very narrow, rounded shoulder on larger specimens, such as the holotype. The adnate aperture is subovate with a slightly flattened base. The margins are thin. The outer lip is subrounded. The parietal margin has a very thin and very narrow callus. The columellar lip may be very slightly erect. The base of the columellar lip is at or slightly to the left of the axis of the shell. The shell is imperforate.

Dimensions – INGEMMET TN84: H 2.3; W 0.8; Hap 0.55; 7.0 whorls. RGM 456 582: H 1.9; W 0.65; Hap 0.4; 7.1 whorls. RGM 456 583: H 1.8; W 0.55; Hap 0.35; 7.0 whorls. RGM 456 584: H 1.3; W 0.5; Hap 0.3; 5.6 whorls.

Remarks – *Onobops*? *erectus* resembles *O.*? *iquitensis* and *O.*? *bisulcatus*. *Onobops*? *bisulcatus* has a slightly more regular increase in width and a less convex whorl profile. It also lacks the dense spiral as well as the axial riblets of *O.*? *erectus*. Instead, it has very thin and low median spirals, giving it a very low bisulcate or sulcate whorl profile on early teleoconch whorls lacking in *O.*? *erectus*. *Onobops*? *iquitensis* is narrower and has a smoother shell with often a faint sulcate whorl profile, lacking in ?*O. erectus*; the aperture of the former is more elongate.

Genus *Pyrgophorus* Ancey, 1888

Type species – *Pyrgulopsis spinosus* Call & Pilsbry, 1866, Comal Creek, Texas, U.S.A.

Diagnosis – Small, ovate to ovate conical shell; spiral ribs at lower three quarters of the whorl; upper spiral may develop into a keel bounding a smooth subsutural ramp above; regularly spaced low spines may develop on the keel; aperture ovate to semicircular.

Range – Miocene, western Amazonia; Quaternary and Recent, lowland Neotropics and circum-Caribbean.

Pyrgophorus sp.

Figs. 15f, 153-155.

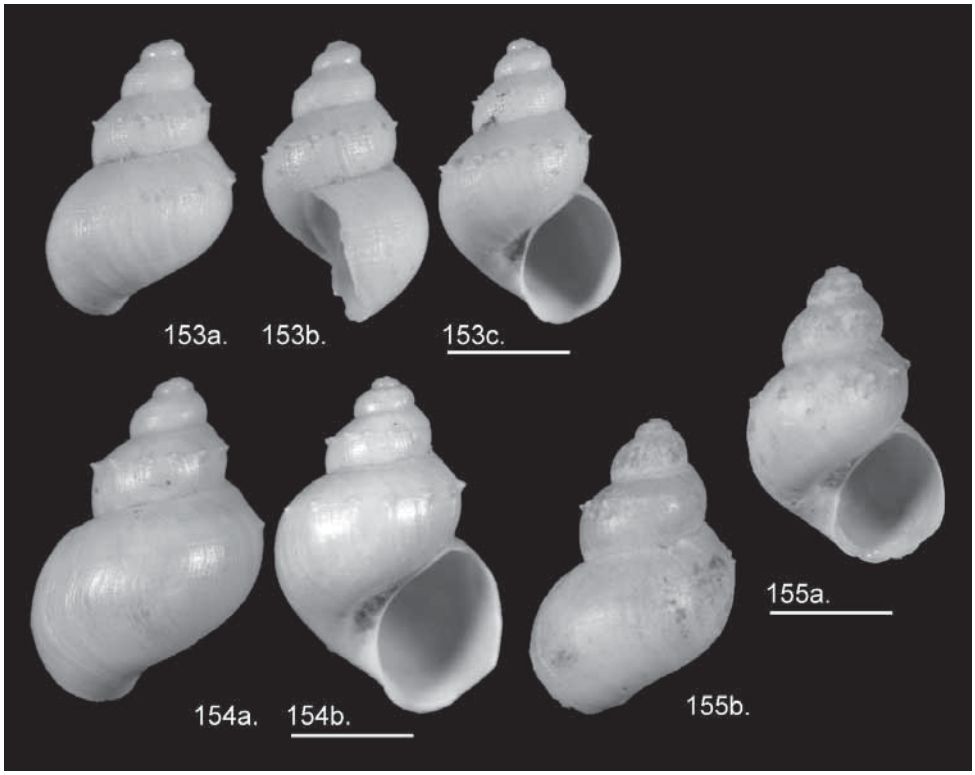
Material studied – INGEMMET TN43, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 445, same locality. RGM 456 446, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 1996.

Description – Small *Pyrgophorus* with a spiral angle of 53-56°. The inclined nucleus has an approximate diameter of 50 µm. The first (apical) whorl is flat; later whorls become convex with somewhat impressed suture. The protoconch-teleoconch boundary is located at *c.* 1.6-1.8 whorls and characterised by the sudden onset of *c.* 7-8 microscopic spiral riblets at the lower two thirds of the whorl. The upper spiral may be pronounced, forming a keel bounding a slightly convex subsutural ramp. Between 2.8 and 3.3 whorls, regularly spaced short spines occur on the keel (15-16 per whorl) that disappear about half a whorl before the aperture. Growth lines are prosocline and become progressively sigmoid. The base of the body whorl is evenly rounded. The aperture is ovate to subcircular and has thin margins. The upper part of parietal margin is adnate. The shell is umbilicate.

Dimensions – INGEMMET TN43: H 2.5; W 1.6; Hap 1.3; 4.6 whorls. RGM 456 445: H 2.8; W 1.8; Hap 1.5; 4.9 whorls. RGM 456 446: H 2.2; W 1.4; Hap 1.1; 4.6 whorls.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Remarks – *Pyrgophorus* sp. has a general outline typical for many modern *Pyrgophorus* species of which Hershler & Thompson (1992, p. 94) stated that "the species level systematics ... is chaotic, which is complicated by the morphological variation within populations." The few diagnostic characters of the Pebasian species have refrained me from formally naming this species.



Figs. 153-155. *Pyrgophorus* sp.

Fig. 153. RGM 456 446, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 154. RGM 456 445, Santa Elena (Loreto, Peru). a, rear view. b, front view.
Fig. 155. INGEMMET TN43, same locality as Fig. 153. a, rear view. b, front view.

Scale bars represent 1 mm.

Pyrgophorus thompsoni sp. nov.

Figs. 156-159.

2002 *Pyrgophorus* sp. Wesselingh *et al.*, fig. 3k.

Type material – INGEMMET TN89 (holotype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. RGM 456 594 and 456 596 (paratypes): Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996. RGM 456 595 (paratype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S

73°00'W), level F318 (1.35 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after Dr F.G. Thompson (Florida Museum of Natural History, Gainesville) in honour of his long-standing research on Cochliopidae.

Diagnosis – Thin-shelled, bulbous *Pyrgophorus* with 2-3 poorly defined, slightly wavy spiral ribs at the base of the whorl; SA 45-56°; some specimens with long, hollow spines.

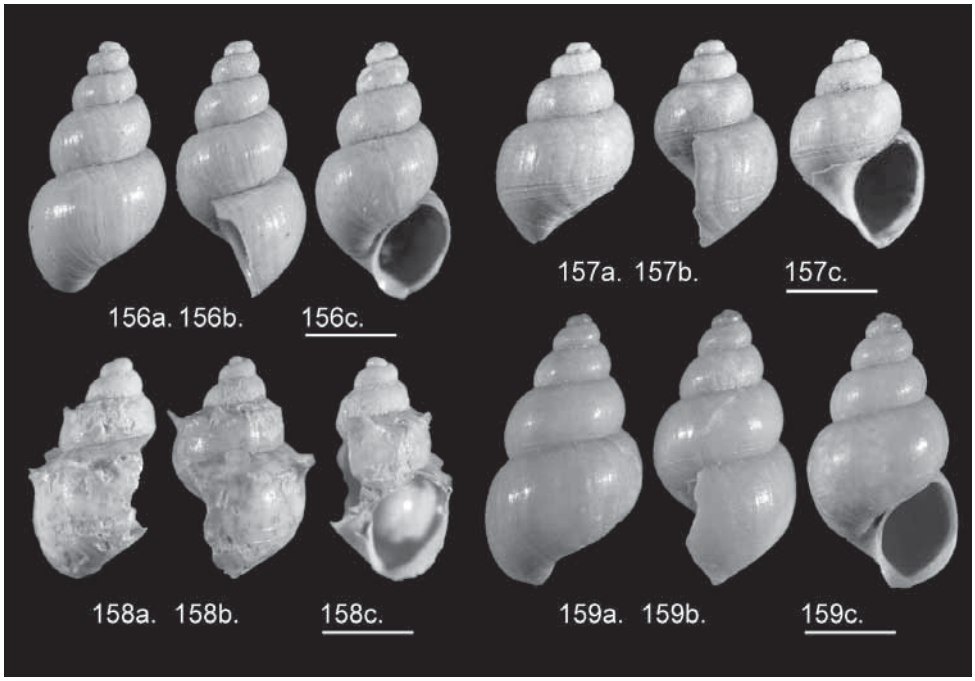
Description – The corrugate nucleus (diameter 80-100 µm) is broad, flat and slightly inclined. The embryonic shell is separated at 0.2-0.4 whorls from the remainder protoconch by a very fine axial lineament. The protoconch-teleoconch boundary at 0.6-0.9 whorls is also marked by a very fine axial lineament; slightly prosocline growth lines may be present just before this boundary. Directly after the boundary, four very fine and low spirals are seen that disappear soon after. The teleoconch whorls are rounded with an impressed suture. The shell is mainly smooth, apart from poorly developed spiral ribs and numerous growth lines producing a slightly wrinkled appearance. Growth lines are at first slightly prosocline, and become progressively more prosocline and sigmoid. Traces of irregular microscopic spiral grooves are seen on later teleoconch whorls. Two or three irregularly developed spiral ribs are also developed just above the suture on the last two or three whorls. Rarely, a shoulder develops on early teleoconch whorls, occupied by large and hollow spines (eight per whorl). The base of the body whorl is evenly rounded. The aperture is semicircular. The parietal wall is adnate; the columellar margin is slightly erect and folded outwards. The basal and outer lip are rounded and thin. The upper part of the outer lip may be narrowly and roundly shouldered in larger and wider specimens. The shell is narrowly rimate.

Dimensions – INGEMMET TN89: H 3.0; W 1.7; Hap 1.2; 4.7 whorls. RGM 456 594: H 2.7; W 1.6; Hap 1.15; 4.6 whorls. RGM 456 595: H 2.2; W *c.* 1.5; Hap 1.25; 3.9 whorls. RGM 456 596: H 2.3; W 1.55; Hap 1.2; 3.7 whorls.

Remarks – The whorl profile of *Pyrgophorus thompsoni,* with its distinctive basal spirals, is more convex than *Pyrgophorus* sp. The basal spirals are another unique feature to the former species. Spines on *Pyrgophorus* sp., where present, are robust and lower than those of *P. thompsoni* that are hollow.

Genus *Littoridinops* Pilsbry, 1952

Type species – *Amnicola tenuipes* Couper *in* Haldeman, 1844, Atlantic coast, North America.



Figs. 156-159. *Pyrgophorus thompsoni* sp. nov.

Fig. 156. RGM 456 594, paratype, Nuevo Paleta (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 157. RGM 456 596, paratype, same locality as Fig. 156. a, rear view. b, lateral view. c, front view.
Fig. 158. RGM 456 595, paratype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 159. INGEMMET TN85, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view.

Scale bars represent 1 mm.

Diagnosis for Pebasian Littoridinops? – Ovate conical, smooth shell; SA 36-42°; (traces of) spiral ornamentation on early teleoconch whorls absent; clear lineament at 1.8 whorls marks the protoconch-teleoconch boundary; suture comparatively deep; growth lines orthocline to slightly prosocline and faintly sigmoid on later teleoconch whorls; aperture ovate; apertural margins thin; parietal lip adnate; umbilicus rimate.

Range – Miocene?, Pebas Formation, western Amazonia (Colombia); Recent rivers and coastal zones of northern Caribbean up to the Atlantic coast of the United States.

Remarks – A single species is found in the upper parts of the Pebas Formation that is attributed with a query to *Littoridinops*. It resembles smooth-shelled hydrobiiform Pebasian *Dyris* species, such as *Dyris ortoni*, but lacks the characteristic onset of spiral ornament on the early teleoconch. The attribution to *Littoridinops* is uncertain, given the

few diagnostic shell characters available. The apical area of *Littoridinops tenuipes* (Couper *in* Haldeman, 1844), as illustrated in Hershler & Thompson (1992, fig. 41c), appears to have a very clear lineament separating the protoconch from the teleoconch at *c.* 1.0 whorls, very reminiscent to a similar lineament seen in the species described below, where it is located at *c.* 1.8 whorls.

***Littoridinops*? *amazonicus* sp. nov.**
Figs. 160, 161.

Type material – RGM 456 442 (holotype), Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991; UNC nn., RGM 456 443, 456 444 and 456 631, all paratypes from the same locality.

Range – Pebas Formation, MZ11 - MZ12 (late Middle - early Late Miocene), Colombian Amazonia.

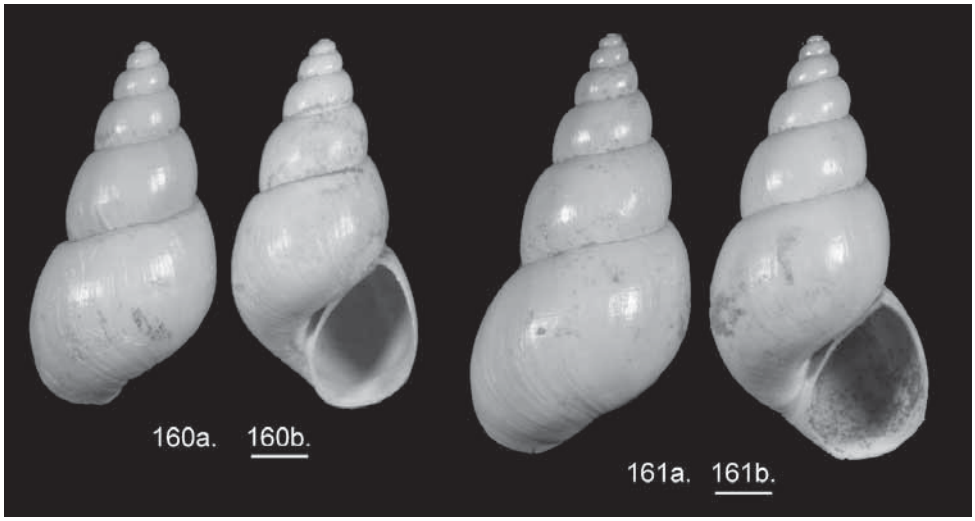
Derivatio nominis – Named after the Amazon River.

Diagnosis – See under genus above.

Description – The nucleus (diameter 40-60 µm) is smooth and only marginally inclined. At 0.3 whorls, a slight axial depression marks the boundary with the protoconch-2. The first 0.8 whorls are flat with an almost adnate suture. The protoconch-2 is smooth and convex with a deeply impressed suture. A clear lineament marks the protoconch-teleoconch boundary at 1.8 whorls. On later teleoconch whorls the whorl profile is subrounded with a slightly impressed suture. The shell is smooth apart for fine and numerous growth lines and microscopic irregular spiral grooves on later teleoconch whorls. Growth lines are orthocline at first, but they become slightly prosocline and slightly sigmoid. The growth lines and spiral grooves give the surface of the shell on later teleoconch whorls a slightly irregular appearance when viewed at magnification of 10 x and more. The base of the body whorl is rounded and grades into a rimate umbilicus. The aperture is ovate and the margins are thin. A thin parietal callus expands onto the columella. The sharp columellar lip is slightly erect or folding out towards the umbilical area. The aperture, when viewed from the side, reaches its most forward point adapically as well as at about one third of the outer lip height, and is broadly sinuate between and below.

Dimensions – RGM 456 442: H 6.1; W 3.1; Hap 2.7; 6.6 whorls. RGM 456 443: H 7.4; W 3.6; Hap 3.0; 7.2 whorls. RGM 456 442: H 7.2; W 3.7; Hap 2.9; 7.1 whorls.

Remarks – Within the Pebas fauna this species only resembles *Dyris ortoni*. At the onset of the teleoconch, *D. ortoni* develops two or three spiral ribs that disappear on later teleoconch whorls; these are lacking in *L.*? *amazonicus*.



Figs. 160, 161. *Littoridinops*? *amazonicus* sp. nov.

Fig. 160. RGM 456 442, holotype, Macedonia (Amazonas, Colombia). a, rear view. b, front view.
Fig. 161. RGM 456 444, paratype, same locality as Fig. 160. a, rear view. b, front view.

Scale bars represent 1 mm.

Genus *Toxosoma* Conrad, 1874a

Type species – *Toxosoma eboreum* Conrad, 1874a. Miocene, Pebas Formation, Pebas, Old Pebas or Santa Rosa de Pichana (see Nuttall, 1990, p. 220), Peru.

Diagnosis – Smooth to carinate, rather small (2-6 mm) conical-ovate to globose shells; nucleus with fine marginal pustules; protoconch-teleoconch boundary often not visible, but in some specimens found as a very fine axial lineament at 1.5-1.7 whorls; columella with plicae of variable strength; in some species in the inner side of the outer lip grooves or denticles present; basal aperture with a notch; outer lip flaring markedly in some species.

Range – Miocene, Pebas Formation, western Amazonia

Remarks – The name *Toxosoma* is derived from *toxon* (Greek, arrow) and *soma* (Greek, body). The grammatical gender is neuter (see International Commission on Zoological Nomenclature, 1999, article 30.1.2).

Toxosoma eboreum Conrad, 1874a

Figs. 15v, 162, 163.

1874a *Toxosoma eborea* [*sic*] Conrad, p. 31, pl. 1, fig. 7.
1878 *Pseudolacuna macroptera* Boettger, p. 416, pl. 13, figs. 14, 15.

1938 *Pseudolacuna macroptera* Boettger; de Greve, p. 74, pl. 5, figs. 17, 18, 24-29, 31-36.
1944 *Toxosoma eboreum* Conrad; Pilsbry, p. 151, fig. 3a, b.
1980 *Toxosoma eboreum* Conrad; Kadolsky, p. 373 (*pars*), figs. 15, 17 (*non* fig. 16).
1990 *Toxosoma eborea* Conrad; Nuttall, p. 219 (*pars*), figs. 179, 180 (*non* figs. 181-184).

Material studied – INGEMMET TN11, San Francisco (Loreto, Peru), exposure in south bank Amazon River opposite to southern tip Isla de Pichana (3°43'S 71°43'W), level F530 (2.1 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 29-8-1996. RGM 456 350, same locality. RGM 456 351, Tamshiyacu (Loreto, Peru), exposure in east bank Amazon River, *c.* 500 m east of port (4°01'S 73°09'W), level F685 (3.0 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 2-9-1996.

Extended diagnosis – Ovate-conical *Toxosoma* (SA 55-64°) with comparatively convex whorl profile, resulting in an evenly rounded, often slightly bulbous base of the body whorl; shell smooth apart for growth lines that are opisthocline on early teleoconch whorls and become prosocline on the body whorl with a deflection at the top; aperture irregularly fusiform; top of aperture retracted; long apertural axis inclines towards the apex; columellar plicae irregular, but most often consisting of a prominent central elevation and similar prominent overlying depression, that is bounded by a secondary overlying projection and a secondary depression and elevation below; umbilicus closed; 'denticulation' as well as H/W ratios variable.

Dimensions – INGEMMET TN11: H 3.7; W 3.0; Hap 2.2; 5.4 whorls. RGM 456 350: H 3.6; W 2.4; Hap 1.9; 6.1 whorls. RGM 456 351: H 4.3; W 3.2; Hap 2.0; *c.* 5.8 whorls.

Range – Pebas Formation, MZ6 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Remarks – *Toxosoma eboreum* is a variable species. Higher and lower spired specimens are found associated with intermediate specimens within samples. *Toxosoma eboreum* may be the predecessor of both *T. denticulatum* and *T. contortum*.

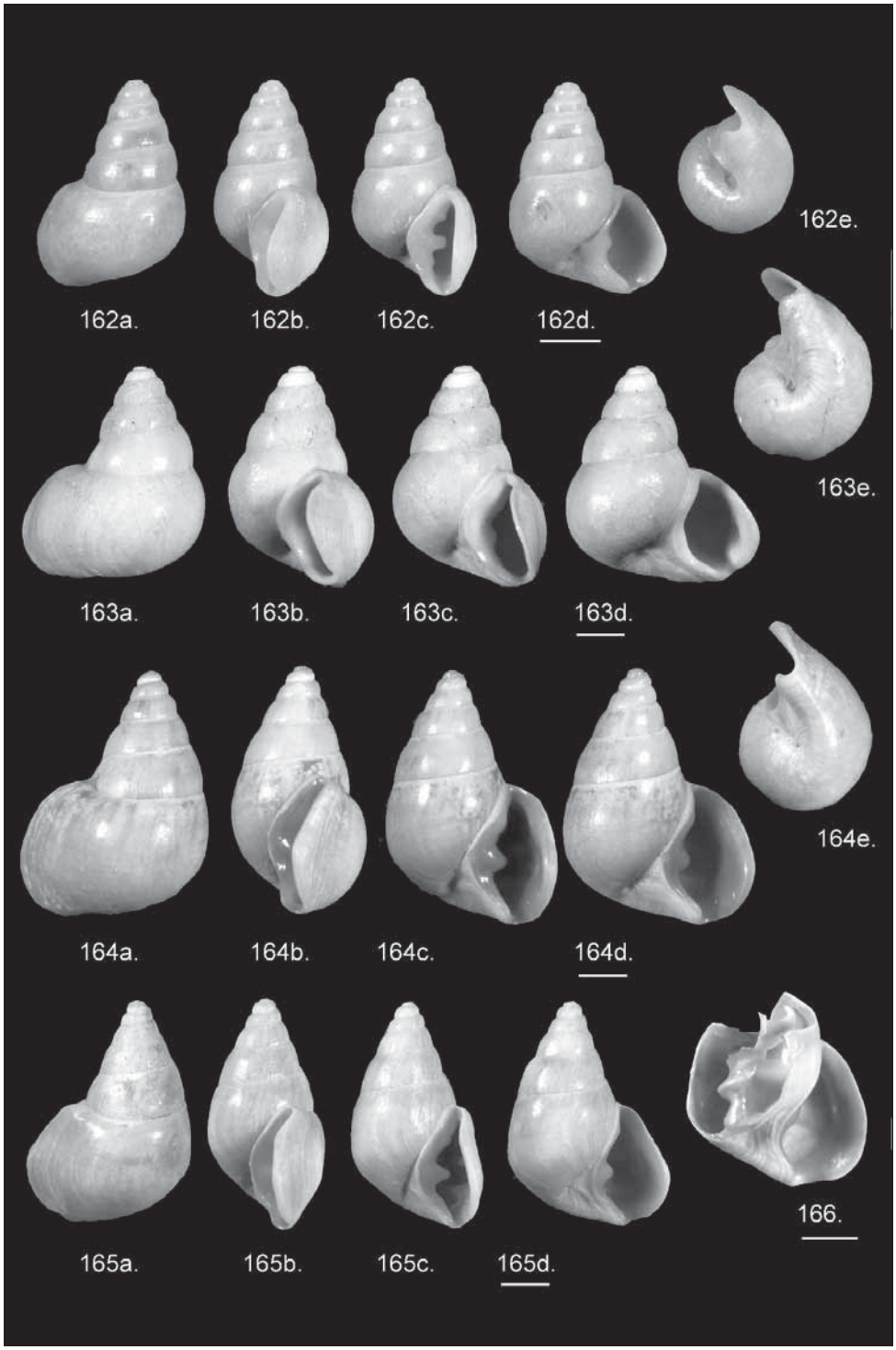
***Toxosoma denticulatum* sp. nov.**

Figs. 15l, 164-166.

1879 *Pseudolacuna macroptera* Boettger; Etheridge, p. 85, pl. 7, fig. 12.
1980 *Toxosoma eboreum* Conrad; Kadolsky, p. 372 (*pars*), fig. 16 (*non* figs. 15, 17).
1981 *Toxosoma eboreum* Conrad; Costa, p. 642, pl. 1, figs. 7, 8.
1990 *Toxosoma eborea* Conrad; Nuttall, p. 219 (*pars*), fig. 181a, b (*non* figs. 179, 180, 182-184).

Type material – INGEMMET TN10 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 348 and 456 349 (paratypes), same locality.

Range – Pebas Formation, MZ8 - MZ11 (late Middle - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.


162a.
162b.
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162e.
163a.
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164e.
165a.
165b.
165c.
165d.
166.

Derivatio nominis – Named after the pronounced spiral plicae on the columellar lip and within the outer lip, that produce denticle-like features (Latin, *denticulus* for tooth).

Diagnosis – Robust, ovate to ovate-conical (SA 57-58°), thick-shelled *Toxosoma* with thick apertural margins, a very prominent central columellar fold, flanked by two weaker folds; two spiral ribs (denticles) at the inner side of the outer lip behind the aperture; apertural plane slightly curved upward.

Description – The nucleus (diameter *c.* 50 µm) is inclined and contains fine elongate wrinkles on the margins. The embryonic shell is delimited from the protoconch-2 at 0.3 whorls by a very fine axial lineament or constriction. The protoconch-teleoconch boundary has not been recognised. The shell is smooth, apart from growth lines and a few, widely spaced, discontinuous, microscopic spiral grooves. The perimeter is rather flat, only very slightly convex. The suture is barely impressed. The base of the body whorl is evenly rounded. The aperture is prominent and the margins are reinforced. The adapical end is retracted. The plane of the aperture is bent upward, *c.* 5° with respect to the columellar axis. The parietal lip is attached through a very narrow parietal platform to the preceding whorl. The columellar lip has a very strongly developed elevation about midway that shows as a tooth. Strong depressions are present above and below; secondary slight elevations are visible above and below these depressions. The central elevation is prominent on the columella throughout the body whorl and becomes lower about one whorl before the aperture. Two spiral ribs are developed rather deep behind the outer lip margin at the shells interior. The basal apertural notch is deep and narrow. The outer lip is strongly produced. The shell is slightly flattened when viewed from below. The umbilicus is closed. Between the umbilical area and the base of the inner lip, a triangular platform is present formed by the exterior wall of the inner lip. The columella is coiled.

◀ Figs. 162, 163. *Toxosoma eboreum* Conrad, 1874a.

Fig. 162. RGM 456 350, San Francisco (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar plicae. d, front view. e, basal view.
Fig. 163. RGM 456 351, Tamshiyacu (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar plicae. d, front view. e, basal view.

Figs. 164-166. *Toxosoma denticulatum* sp. nov.

Fig. 164. INGEMMET TN10, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar plicae. d, front view. e, basal view.
Fig. 165. RGM 456 348, paratype, same locality as Fig. 164. a, rear view. b, lateral view. c, oblique lateral view showing columellar plicae. d, front view.
Fig. 166. RGM 456 349, paratype, same locality as Fig. 164. d, front view of fragment showing columellar plicae *c.* 0.6 whorls before aperture.

Scale bars represent 1 mm.

Dimensions – INGEMMET TN10: H 5.3; W 3.6; Hap 2.6; 6.7 whorls. RGM 456 348: H 4.6; W 3.2; Hap 2.4; 6.1 whorls.

Remarks – The robust nature, ovate outline, strongly thickened apertural margins and strongly developed apertural 'denticles' make this species different from most other *Toxosoma* species. *Toxosoma denticulatum* most resembles *T. eboreum*, which has a more convex whorl profile, especially well visible on the body whorl, and more strongly developed secondary spiral elevations at the inner lip. The outer lip is less produced than in *T. denticulatum* and the apertural plane less curved upward.

***Toxosoma contortum* sp. nov.**
Figs. 16d, 17j, 167-169.

1990 *Toxosoma eborea* Conrad; Nuttall, p. 219 (*pars*), fig. 182a, b (*non* figs. 179-181, 183, 184).
2002 *Toxosoma* sp. Wesselingh *et al.*, fig. 3j.

Type material – INGEMMET TN20 (holotype); Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, *Grimsdalea* zone, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 376 (paratype), same locality. RGM 456 611 (paratype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, *Grimsdalea* zone, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 611 and 456 627 (paratypes), same locality. RGM 456 375 (paratype); Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River, 1.3 km east of confluence with Loreto Yacu (3°46'S 70°21'W), level F22 (1.7 m above DL). Pebas Formation, *Grimsdalea* zone, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Range – Pebas Formation, MZ8 - MZ11 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Named after the contorted nature of the aperture (Latin, *contortus* for twisted).

Diagnosis – Elongate to ovate-conical, relatively high-spired *Toxosoma* with a remarkable flaring outer lip; SA increasing from *c.* 45° on penultimate whorl to 57-68° on body whorl; plane of aperture bent upward; columellar plicae and plicae at the inner wall of the outer lip well defined and robust.

Description – The nucleus is inclined (diameter *c.* 60 µm). Low, somewhat sharp pustules or low wrinkles occur on the sutural margins on the embryonic shell. The boundary with the protoconch-2 is located at 0.3-0.5 whorls and defined by a low axial depression or constriction. At 1.5-1.7 whorls, a poorly defined (often invisible) axial lineament marks the protoconch-teleoconch boundary. The whorls are at first

somewhat convex with relatively deeply incised sutures, but become progressively flatter. Very fine orthocline to slightly prosocline sigmoid growth lines are numerous. Growth lines become opisthocline in the last half whorl before the aperture. The base of the body whorl is rounded. The long axis of the ovate-spindle shaped aperture is inclined towards the shells apex. At the top and base the aperture is retracted. The plane of aperture is bent upward. The parietal lip is attached through a thin callus to the preceding whorl. The columellar lip is strongly thickened and located on a base that is formed by the flattened exterior margin of the innerlip. The columella has a very strong median production in frontal view. Strong, spirally arranged depressions are present above and below, and a second strong production is present above the upper depression, behind the inner lip. The base of the inner lip is strongly expanded towards the right and merges into the entrenched basal apertural retraction. The latter is inequilateral, when viewed from below, with the sharp outer lip strongly expanding. When viewed from the side, the most produced part of the outer lip is located at about the middle of the height of the aperture. Two well defined and robust, but short, elongate elevations are present inside the outer lip, *c.* 0.2 whorls behind the margin. When viewed from above, the upper apertural retraction is rather acute. The columella is coiled in a spiral.

Dimensions – INGEMMET TN20: H 3.0; W 2.7; Hap 1.6; 5.5 whorls. RGM 456 375: H 3.3; W 2.9; Hap 1.5; 5.8 whorls.

Remarks – The upward curvature of the plane of aperture, the flaring outer lip, and the columellar and interior plicae of the outer lip distinguish *Toxosoma contortum* from all other *Toxosoma* species, with the exception of *T. denticulatum*. The latter is wider.

***Toxosoma grande* sp. nov.**

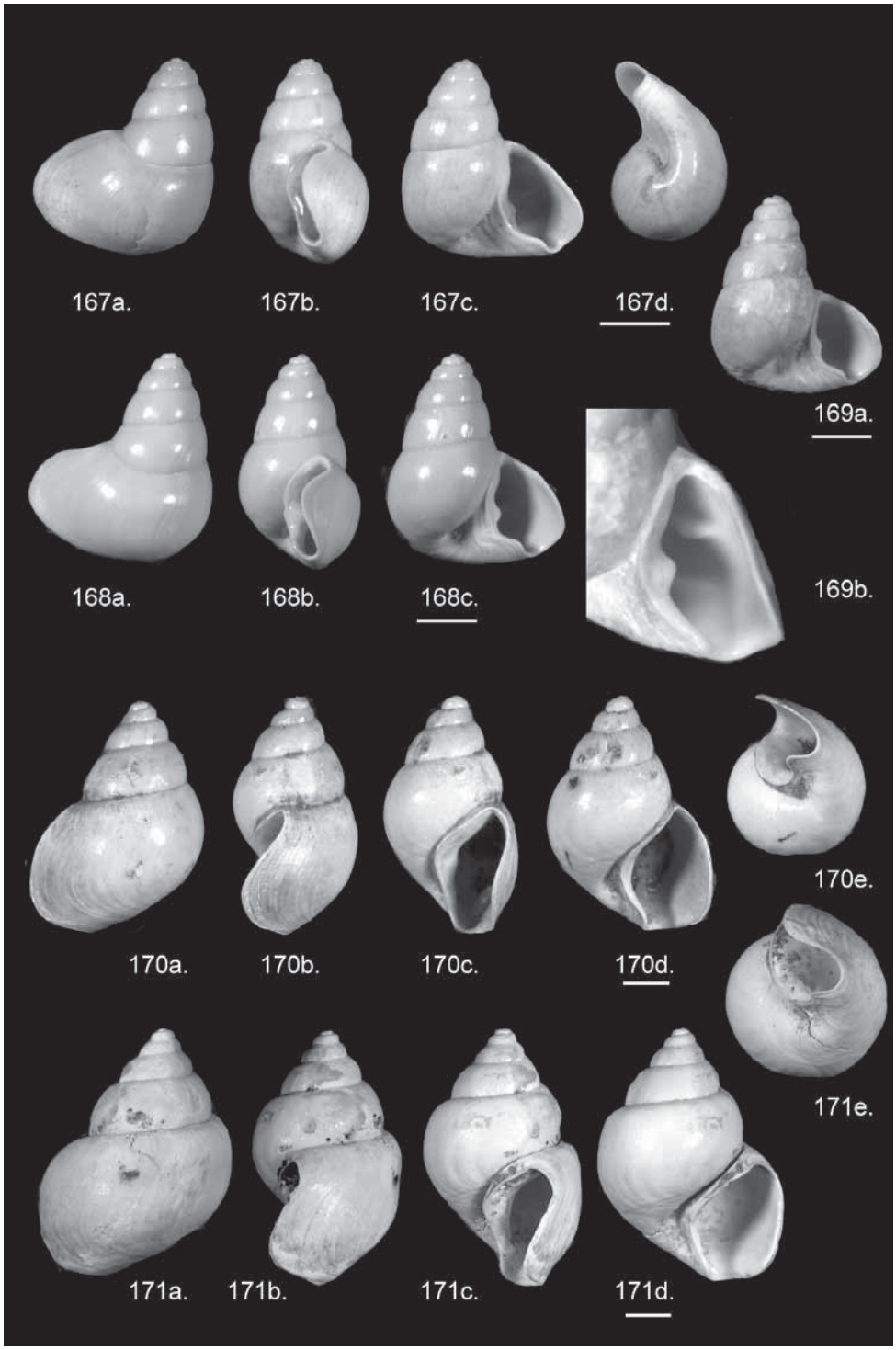
Figs. 170, 171.

1980 *Pseudolacuna macroptera* Boettger; Costa, p. 886, pl. 3, figs. 1-6.
1990 *Toxosoma eborea* Conrad; Nuttall, p. 219 (*pars*), figs. 183, 184 (*non* figs. 179-182).

Type material – RGM 456 346 (holotype), Puerto Nariño (Amazonas, Colombia), exposure in north bank of Loreto Yacu, *c.* 1 km east of village (3°46'S 70°22'W), level F29 (24.9 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 347 (paratype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F61 (18.2 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991; UNC nn. (paratype), same locality.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.

Derivatio nominis – Named after the size, which is large for *Toxosoma*.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167b.
167c.
167d.
169a.
168a.
168b.
168c.
169b.
170e.
170a.
170b.
170c.
170d.
171e.
171a.
171b.
171c.
171d.

Diagnosis – Comparatively large (H 6), thin-shelled and globose *Toxosoma*; SA 55-60°; outer lip when viewed from aside sigmoid, opisthocline; columellar elevations variable, but usually low.

Description – The nucleus is flat. The embryonic shell has a rugose surface and is delimited from the remainder shell at 0.2 whorls. Thereafter, the shell increases regularly in size. No protoconch-teleoconch boundary has been recognised on the studied material. The surface is smooth, apart for growth lines and common irregular scars, presumably the marks of predation. The growth lines are at first slightly prosocline and straight to inverse opisthocyrt. During growth they become orthocline, and at the body whorl even opisthocline and sigmoid. A fine, irregular and widely spaced ornament of microscopic spiral grooves is present on the shell. The whorl profile is rather convex and the suture deep. The suture is a very narrow fissure in RGM 456 347. The large aperture has a slightly retracted upper part. The outer lip is non-thickened and flaring. It is most strongly projected about one third of the height of the aperture. The inner lip is thickened. The parietal margin is attached to the preceding whorl. The basal apertural notch is broad, deep and rounded, and has reinforced margins. The umbilical area consists of a poorly defined, very shallow depression. A slight columellar chink is present behind the aperture.

Dimensions – RGM 456 346: H 5.5; W 3.6; Hap 3.1; 5.2 whorls. RGM 456 347: H 5.6; W 3.7; Hap 3.2; 5.4 whorls. UNC nn.: H 5.9; W 4.1; Hap 3.2; 5.1 whorls.

Remarks – The large size, thin shell, globose outline and the common reduction of columellar plicae makes this species different from other *Toxosoma* species.

***Toxosoma ovatum* sp. nov.**
Figs. 172, 173.

Type material – RGM 456 383 (holotype), Socosani (Loreto, Peru), easternmost exposure in north bank Rio Napo, *c.* 2 km downstream confluence Rio Socosani (3°17'S

◀ Figs. 167-169. *Toxosoma contortum* sp. nov.

Fig. 167. INGEMMET TN20, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 168. RGM 456 375, paratype, Los Chorros (Amazonas, Colombia). a, rear view. b, lateral view. c, front view.
Fig. 169. RGM 456 377, same locality as Fig. 168. a, front view. b, detail aperture showing columellar plicae and grooves/denticles in the outerlip

Figs. 170, 171. *Toxosoma grande* sp. nov.

Fig. 170. RGM 456 346, holotype, Puerto Nariño (Amazonas, Colombia). a, rear view. b, lateral view. c, oblique lateral view showing low columellar folding. d, front view. e, basal view.
Fig. 171. RGM 456 347, paratype, Santa Sofia (Amazonas, Colombia). a, rear view. b, lateral view. c, oblique lateral view showing low columellar folding. d, front view. e, basal view.

Scale bars represent 1 mm.

72°53'W), level F387 (1 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 19-8-1996. INGEMMET TN24 (paratype), same locality.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after its ovate (Latin, *ovatus* for egg-shaped) outline.

Diagnosis – Regularly ovate-conical *Toxosoma* (SA 50-53°) with a single median columellar modification, located behind the inner lip.

Description – The nucleus is slightly inclined (diameter 40-60 µm). The first whorl is planar coiled. The whorls are smooth, apart for traces of irregular, microscopic, spirally-arranged impressed grooves. Growth lines are orthocline. The whorl profile is slightly convex with a somewhat impressed suture. The base of the body whorl is broadly rounded. A very thin, spiral rib is present halfway around the body whorl on the holotype. The aperture is broadly adnate. The basal part of the aperture contains a broad retraction, whose deepest point is located somewhat towards the columellar margin. The outer lip is subrounded, thickened, and very slightly and broadly retracted at the top. The plane of the aperture tends to be very slightly bent upward. A strong columellar fold is visible behind the inner lip at about half the height of the aperture. The shell is imperforate.

Dimensions – RGM 456 383: H 3.5; W 2.3; Hap 1.6; 5.4 whorls. INGEMMET TN24: H 3.6; W 2.3; Hap 1.6; 5.7 whorls.

Remarks – This species resembles other smooth-shelled *Toxosoma* species, such as *T. eboreum, T. denticulatum* and *T. contortum*. The latter two species have plicae within the outer lip, lacking in *T. ovatum*. *Toxosoma eboreum* has sometimes two and often three plicae on the inner lip (*T. ovatum* only one), and has a more bulbous body whorl.

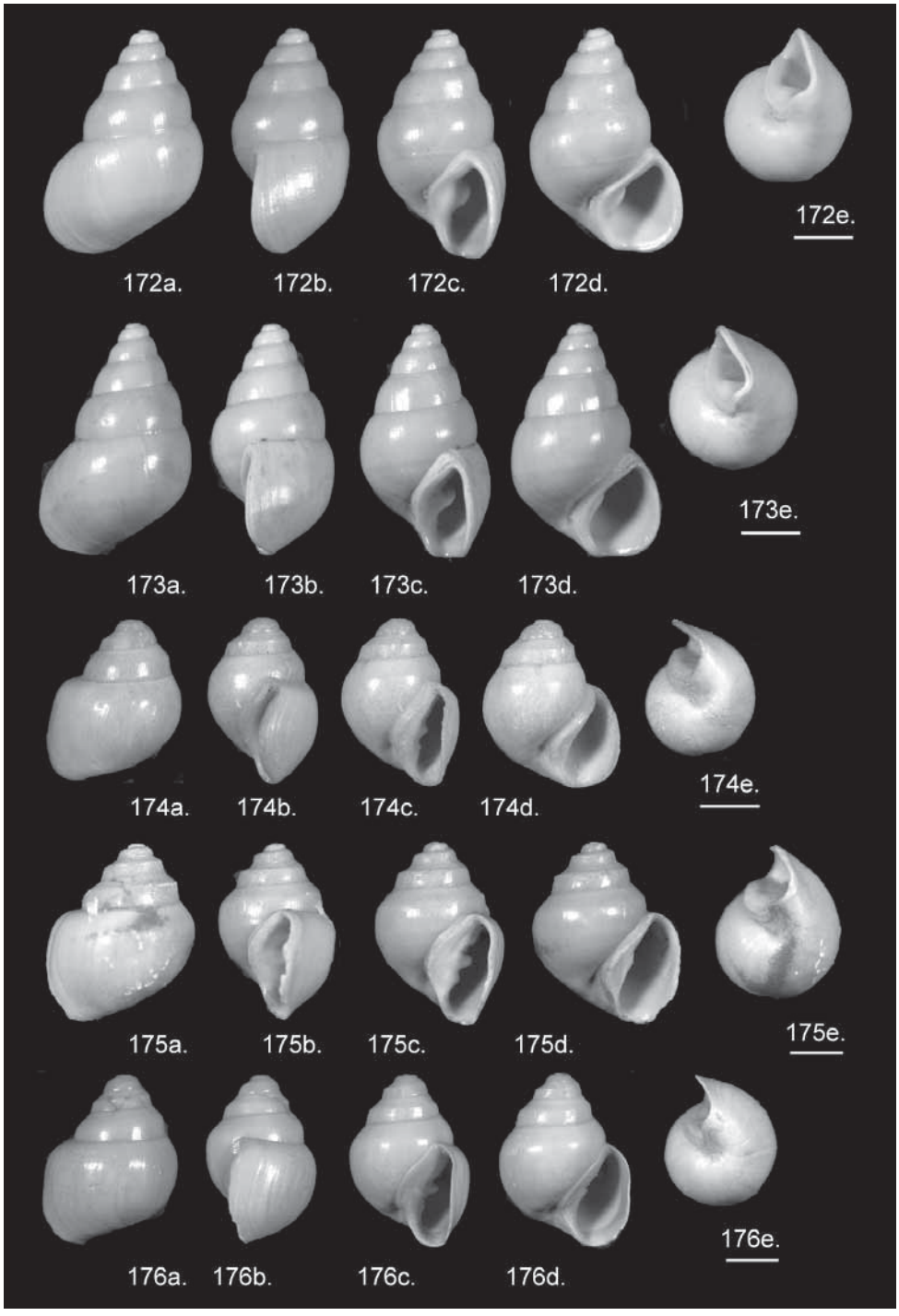
Figs. 172, 173. *Toxosoma ovatum* sp. nov. ►

Fig. 172. RGM 456 383, holotype, Socosani (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.
Fig. 173. INGEMMET TN24, paratype, same locality as Fig. 172. a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.

Figs. 174-176. *Toxosoma globosum* sp. nov.

Fig. 174. RGM 456 382, paratype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.
Fig. 175. RGM 456 381, paratype, same locality as Fig. 174. a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.
Fig. 176. INGEMMET TN23, holotype, same locality as Fig. 174. a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.

Scale bars represent 1 mm.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***Toxosoma globosum* sp. nov.**
Figs. 174-176.

Type material – INGEMMET TN23 (holotype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, below village school (3°29'S 73°00'W), level F648 (0.3 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 1-9-1996. RGM 456 381 (paratype), same locality. RGM 456 382 (paratype), same locality, level F326 (0.2 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after its globose outline (Latin, *globosus* for spherical).

Diagnosis – Small, globose *Toxosoma* (SA 59-69°) with shouldered whorl profile on early teleoconch whorls; shell thin; upper part aperture distinctly retracted.

Description – The nucleus (diameter 40-50 µm) is slightly inclined. The first whorl is planispiral. At the second whorl, an angulation gradually develops at two thirds of the whorl height bounding a subsutural ramp that is *c.* 45° inclined at first, but becomes increasingly steeper. The second and third whorls have a shouldered outline. The angulation fades completely on the body whorl, where the whorl profile is markedly convex. The shell is smooth with traces of microscopic spiral grooves. Growth lines are orthocline, but become sigmoid on the body whorl. The aperture is semilunate and adnate. The parietal callus is thin and the columellar lip is thickened. The basal retraction is broad. The outer lip is thin and almost straight, apart for the upper part that is evenly rounded and distinctly retracted. Inside the aperture, a massive knob is present on the columella behind the parietal lip. A second, lower knob is found below and in some specimens above the primary knob; a third low knob is present. The inner side of the outer lip lacks modifications. The shell is imperforate.

Dimensions – INGEMMET TN23: H 3.1; W 2.5; Hap 1.8; 5.0 whorls. RGM 456 381: H 3.4; W 2.7; Hap 2.0; 5.1 whorls. RGM 456 382: H 2.9; W 2.2; Hap 1.8; 4.4 whorls.

Remarks – The globose outline distinguishes this species from other *Toxosoma* species.

***Toxosoma carinatum* sp. nov.**
Figs. 177, 178.

Type material – INGEMMET TN22 (holotype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, below village school (3°29'S 73°00'W), level F648 (0.3 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 1-9-1996. RGM 456 380 (paratype), same locality.

Range – Pebas Formation, MZ4 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the prominent keel (Latin, *carina* for keel).

Diagnosis – Thick-shelled, ovate *Toxosoma* (SA 53-59°) with a very prominent median keel, and low, massive knobs and thickenings within the aperture; shell ornamented with densely packed, microscopic spiral furrows.

Description – The nucleus (approximate diameter 50-60 µm) is inclined, but the apical parts are worn in the studied material, precluding the observation of a potential protoconch-teleoconch boundary. The first whorl is planispiral; the second whorl has a convex outline with an impressed suture. At 2.1-2.3 whorls a median keel gradually develops, bounding a straight subsutural ramp above that inclines *c.* 45° in respect to the axis of the shell, subsequently becoming steeper. A ramp develops below the keel that at first is slightly concave, but becomes straight on later whorls. The keel is well-defined, erect and robust. The suture becomes adnate, and located halfway in a depression formed by the supra- and subsutural ramps. Growth lines are prosocline. Numerous, densely packed, microscopic, impressed spiral furrows cover the shell. On the body-whorl, a second, rounded keel becomes apparent, that is faded on larger specimens. The aperture is ovate and adnate. The parietal and, especially, columellar lip have a strong callus and are attached to the preceding whorl by a platform. The outer lip is thick and slightly folded outward. The upper part of the outer lip is slightly and broadly retracting. The basal apertural retraction is robust, and has a shape between a 'U-' and a 'V'-shape when viewed from below. A massive thickening occurs on the columella slightly behind the base of the parietal lip. A secondary, somewhat lower thickening is found below. Two broad and rounded knobs are present behind the outer lip, in the basal two thirds. The shell is imperforate.

Dimensions – INGEMMET TN22: H 4.1; W 2.8; Hap 2.0; 5.7 whorls. RGM 456 380: H 4.6; W 3.1; Hap 2.3; 6.3 whorls.

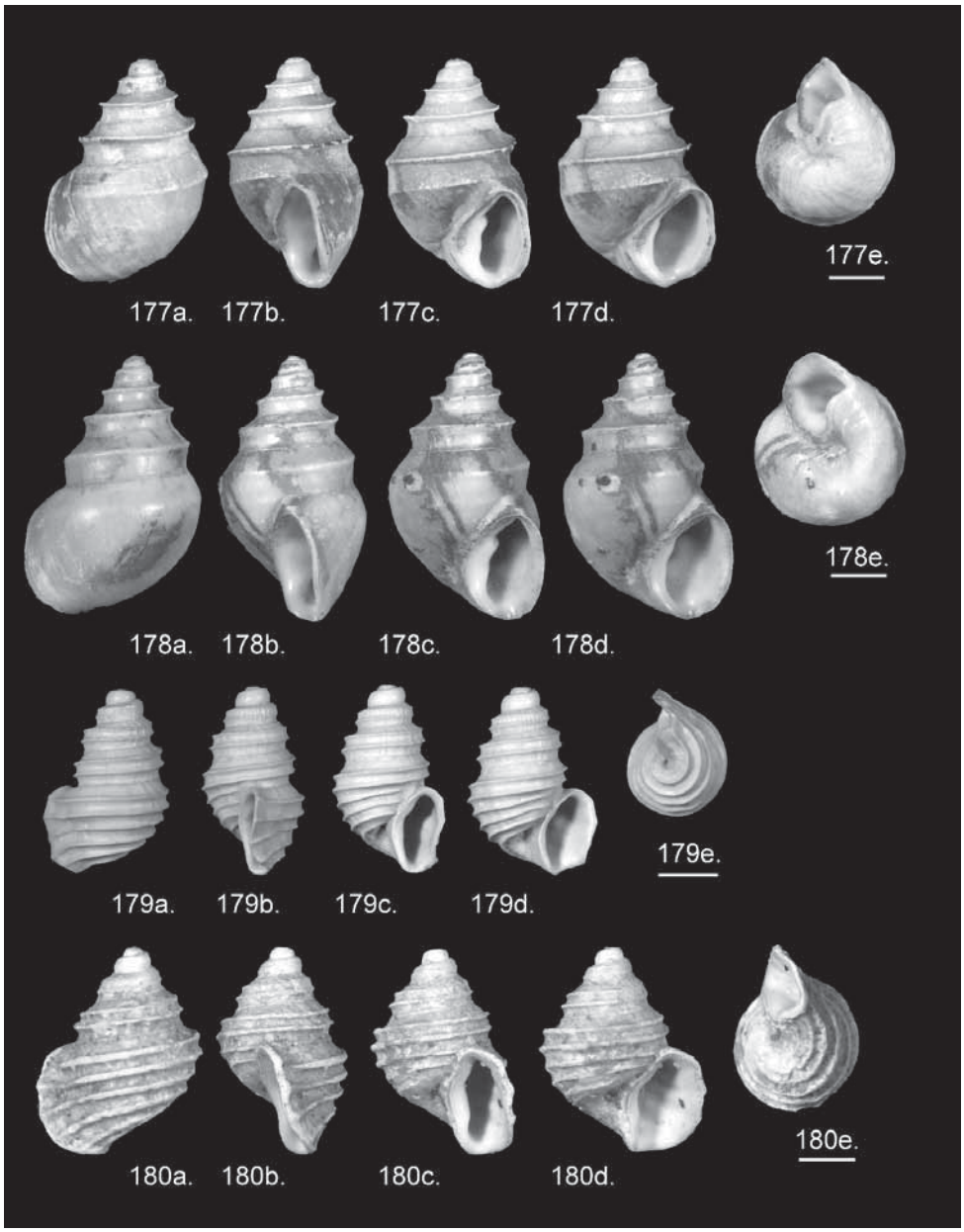
Remarks – *Toxosoma carinatum* resembles *T. multicarinatum*, but the latter has a thinner shell, with two spirals on earlier teleoconch whorls and up to six spirals on the body whorl.

***Toxosoma multicarinatum* sp. nov.**
Figs. 179, 180.

Type material – RGM 456 378 (holotype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 3.1 km south of Indiana and 150 m north of the landing stage of Barradero de Mazan (3°31'S 73°05'W), level F353#1 (0.0-0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. INGEMMET TN21 (paratype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S 73°00'W), level F318 (1.35 m above

DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996. RGM 456 379 (paratype), same locality.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.



Derivatio nominis – Named after multiple keels that ornament the shell (Latin, *carina* for keel).

Diagnosis – Thin-shelled, elongate to broadly ovate conical *Toxosoma* (SA 55-65°) with two sharply defined spiral keels on early teleoconch whorls and up to six keels on the body whorl; outer lip bent outward; umbilicus rimate.

Description – The nucleus (diameter 50-60 µm) is slightly inclined. The first protoconch whorl has a convex whorl profile and a deep suture. The protoconch-teleoconch boundary could not be distinguished. At *c.* 2.2 whorls, a barely distinguishable lineament may represent the boundary, after which a regularly thin axial ornament develops. However, the two spiral keels of the early teleoconch whorls are already present before that lineament, albeit as rounded and low angulations. The keels are located at one third and four fifths of the whorl height. The upper keel bounds an almost horizontal subsutural ramp. At the second teleoconch whorl, the two keels are intersected by regularly spaced fine and thin orthocline axial riblets, resulting in a reticulate ornament. On later teleoconch whorls these axials fade away. The suture is located in a broad depression bounded by a subsutural and suprasutural ramp, and becomes progressively adnate. Six well-defined, sharp spiral ribs are present at the body whorl, with broad concave interspaces. In the holotype and one paratype, the ribs are at the same distance; in another paratype, the distance between the ribs diminishes downward. The aperture is ovate, and has vaguely to strongly outward folding outer and basal margins. The parietal lip is adnate through a narrow parietal platform. The columellar lip is slightly thickened. The basal apertural retraction is broad and shallow, and located slightly on the left side of the apertural base. Very slight, poorly delimited thickenings are present inside the parietal and the columellar margins. A poorly defined, broad and low thickening is present inside the outer lip in the holotype. Five grooves are present in one of the paratypes, corresponding to the spiral keels that ornament the shell. The umbilicus is rimate.

◀ Figs. 177, 178. *Toxosoma carinatum* sp. nov.

Fig. 177. INGEMMET TN22, holotype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.
Fig. 178. RGM 456 380, paratype, same locality as Fig. 177. a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.

Figs. 179, 180. *Toxosoma multicarinatum* sp. nov.

Fig. 179. RGM 456 378, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.
Fig. 180. INGEMMET TN21, paratype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view showing columellar folding. d, front view. e, basal view.

Scale bars represent 1 mm.

Dimensions – RGM 456 378: H 3.2; W 2.2; Hap 1.5; 5.5 whorls. INGEMMET TN21: H 3.5; W 2.8; Hap 1.9; 5.2 whorls. RGM 456 379: H 3.1; W 2.3; Hap 1.6; 5.1 whorls.

Remarks – This species has more spirals and is thinner shelled than *Toxosoma carinatum* sp. nov. Some of the broader specimens resemble *Sioliella carinata* sp. nov., but the latter lacks denticles in the aperture.

Genus *Longosoma* Wesselingh & Kadolsky (*nomen novum pro Liosoma* Conrad, 1874a, *non* Brandt, 1835 (Holothuria), *nec* Fitzinger, 1843 (Reptilia)).

Type species – *Liosoma curtum* Conrad, 1874a, by monotypy of *Liosoma* Conrad. Santa Rosa de Pichana, Loreto, Peru; Pebas Formation, MZ7 (Middle Miocene).

Derivatio nominis – The name *Longosoma* is derived from *longus* (Latin), long, and *soma* (Greek), body. The grammatical gender is neuter (see International Comission on Zoological Nomenclature, 1999, Article 30.1.2).

Diagnosis – Small, smooth, ovate conical to elongate ovate gastropods; nucleus slightly inclined; embryonic shell with fine wrinkles to sharp pustules, especially well developed at the sutural edges; separated from protoconch-2 at 0.35-0.60 whorls by a very fine axial lineament; the protoconch-teleoconch boundary is in general invisible; aperture elongately triangular with rounded top and flat base; long axis of aperture inclined towards the base of the axis of the shell; left-most part of columellar margin at or left of the axis of the shell; upper part of outer lip retracted, basal part of outer lip projecting; plane of aperture orthocline-opisthocline; junction columellar lip and basal lip, forming a short, siphon-like retraction; columella tightly open coiled, with a single, broad, chink; shell imperforate.

Range – Miocene, Pebas Formation, western Amazonia (Peru).

Remarks – *Longosoma* resembles *Toxosoma* (Conrad, 1874a; Miocene, Pebas Formation), to which it almost certainly is closely related. However, *Longosoma* species have a more elongate shell, a single broad columellar chink and lack an umbilicus or umbilical depression distinguishing them from *Toxosoma*. Furthermore, the position of the leftmost part of the columellar margin, at or to the left of the axis of the shell in *Longosoma,* differs from that of *Toxosoma*, where it is located well to the right of the axis of the shell.

We believe that the three species described below form a single lineage endemic to the Pebas system. No intermediates have been found between the three species.

Longosoma curtum (Conrad, 1874a)

Figs. 15m, 17i, 181, 182.

1874a *Liosoma curta* [*sic*] Conrad, p. 31, pl. 1, fig. 8.
1980 *Toxosoma eboreum* Conrad; Kadolsky, p. 372 (*pars*, *non* figs. 15-17).
1990 *Toxosoma eborea* Conrad; Nuttall, p. 219 (*pars*, *non* figs. 179-184).

Type material – RGM 456 590 (neotype), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F535 (6.3 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996.

Remarks – Nuttall (1990) was unable to retrace the original specimens on which Conrad (1874a) based the description of *Liosoma curta* and presumed it lost. Because Nuttall (1990) considered *L. curta* a junior synonym of *Toxosoma eborea*, he did not assign a neotype for the former. The new material shows that both taxa are distinct and, therefore, we designate a neotype for *Liosoma curta (= Longosoma curtum)*.

Other material studied – INGEMMET TN87, Pebas/Santa Julia (Loreto, Peru), exposure in north bank Amazon River, 2250 m east of naval base Pijoyal (base at 3°20'S 71°50'W), level F415 (3.3 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 23-8-1996. RGM 456 626, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, *c.* 300 m E of wood mill and *c.* 1.5 km east of Santo Tomas (3°52'S 71°23'W), level F498 (5.1 m above DL). Pebas Formation, MZ 8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.

Extended diagnosis – Elongate (SA 29-30°), conical to fusiform *Longosoma*, with comparatively many and low whorls; nucleus (diameter 50-70 µm) slightly inclined with fine wrinkles especially near the margins; boundary embryonic shell/protoconch-2 at 0.3 whorls; protoconch-teleoconch boundary not visible; apex domed; shell smooth apart for numerous fine growth lines that appear rather suddenly at *c.* 2.3 whorls in one specimen, orthocline sigmoid with very short limbs on early teleoconch whorls to prosocline with retracted upper and lower parts on later whorls; whorl profile depressed, suture shallow; adnate aperture small for genus (height approximately 0.4 of H shell); long axis of aperture inclined; apertural plane coiled upward; narrow siphonal retraction in basal lip at junction with columellar lip; apertural margins slightly thickened; columellar chink elongate; shell imperforate.

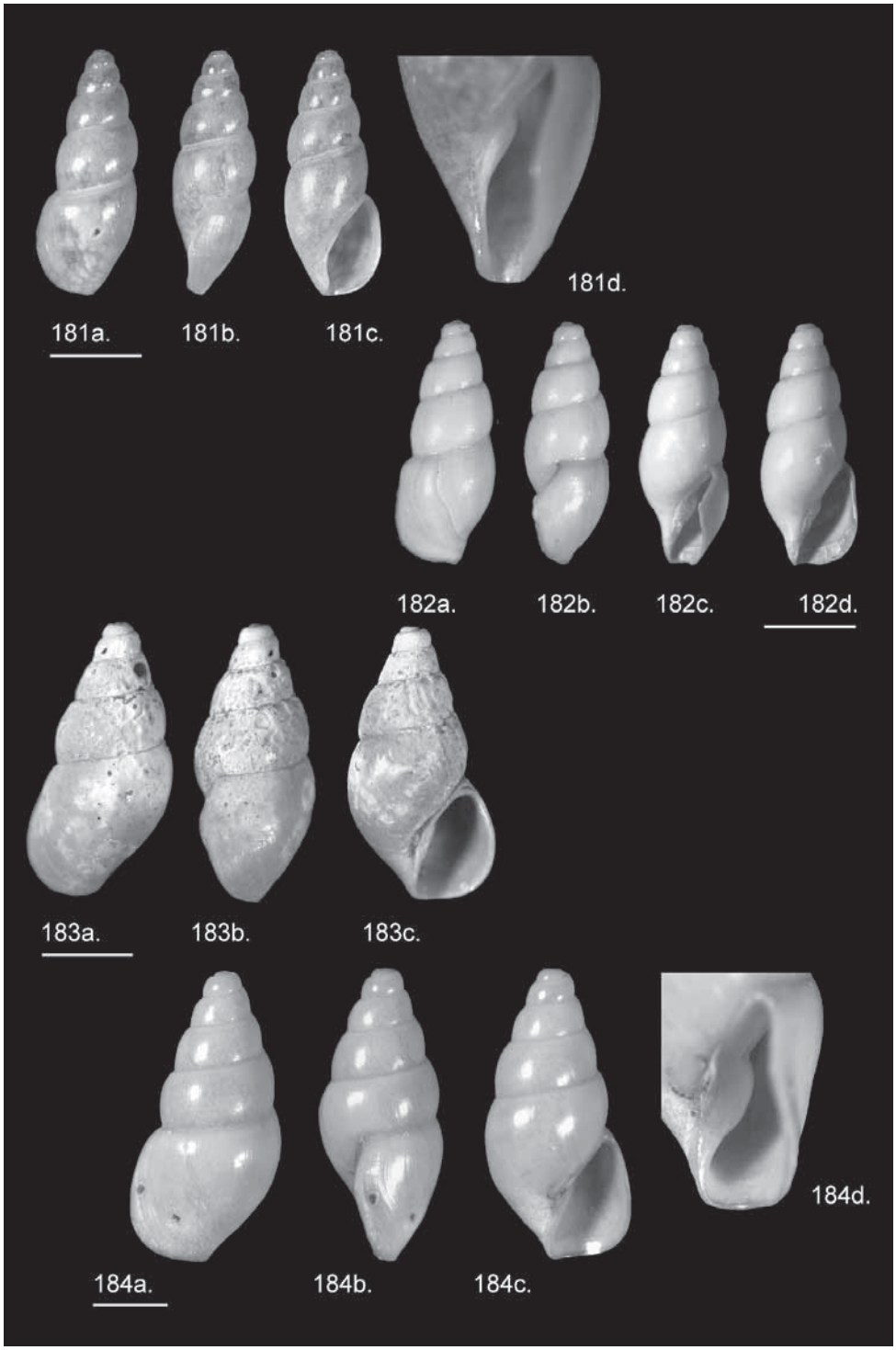
Dimensions – RGM 456 590: H 3.1; W 1.2; Hap 1.2; 5.6 whorls. INGEMMET TN87: H 2.7; W 1.1; Hap 1.1; 5.4 whorls.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Longosoma glabrum Wesselingh & Kadolsky sp. nov.

Figs. 183, 184.

Type material – RGM 456 588 (holotype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, below village school (3°29'S 73°00'W), level F669 (0.1 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 1-9-1996. RGM 456 589 (paratype), same locality. INGEMMET TN86 (paratype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at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184c.
184d.

3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the smooth exterior of the shell (Latin, *glabra* for smooth).

Diagnosis – Rather large, elongate-conical, smooth *Longosoma* with relatively convex whorls; SA 40-41°; apertural base broad; plane of aperture orthocline; leftmost part of columellar margin at axis of the shell.

Description – The nucleus (diameter 60 µm) is slightly inclined. The embryonic whorl is separated at 0.3 whorls from the remainder of the shell. No additional protoconch-teleoconch boundary has been found in the studied material. The top of the first 1.3 whorls is planar coiled, rapidly descending thereafter. The shell is smooth apart for the numerous, very fine, slightly prosocline growth lines. The whorl profile is subrounded and the sutures are slightly impressed. The aperture has a more or less straight inner lip, a flat basal lip (in frontal view) that grades into the rounded base of the outer lip. The apertural margins are slightly thickened. The basal lip is slightly retracted at the columellar side when viewed from below. In side view the outer lip is retracted at the base as well as at the upper margin. It is most produced at *c.* three fifths of the apertural height. The parietal callus is robust, but narrow. It grades into the median columellar fold that forms a platform directed towards the outer lip. The columella is openly coiled. The shell is imperforate.

Dimensions – RGM 456 588: H 3.6; W 1.8; Hap 1.65; 5.7 whorls. INGEMMET TN86: H 3.0; W 1.5; Hap 1.3; 5.2 whorls.

◀ Figs. 181, 182. *Longosoma curtum* (Conrad, 1874a).

Fig. 181. RGM 456 590, neotype, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, detail of aperture showing coiled columella.
Fig. 182. INGEMMET TN87, Pebas/ Santa Julia (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view. d, front view.

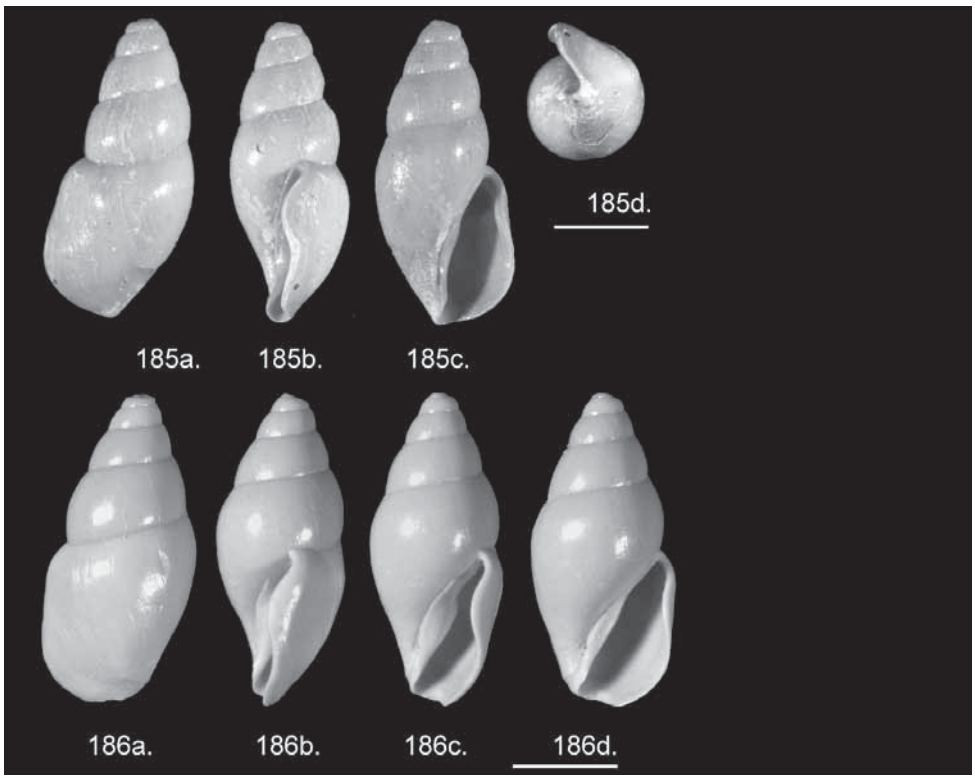
Figs. 183, 184. *Longosoma glabrum* Wesselingh & Kadolsky sp. nov.

Fig. 183. INGEMMET TN86, paratype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view.
Fig. 184. RGM 456 588, holotype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, detail of aperture showing coiled columella.

Remarks – *Longosoma glabrum* has a wider, more conical shell than *L. curtum*. Its columellar chink is also broader and more robust. The species has also fewer and higher whorls.

***Longosoma fusiforme* Wesselingh & Kadolsky sp. nov.**
Figs. 185, 186.

Type material – RGM 456 608 (holotype), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. INGEMMET TN94: Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42 (4°04'S 73°25'W), level F367a (1.0 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 11-8-1996.



Figs. 185, 186. *Longosoma fusiforme* Wesselingh & Kadolsky sp. nov.

Fig. 185. RGM 456 608, holotype, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 186. INGEMMET TN94, paratype, Nuevo Horizonte (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view. d, front view.

Scale bars represent 1 mm.

Range – Pebas Formation, MZ9 (early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the spindle-shaped (fusiform) outline (Latin, *fusus* for spindle).

Diagnosis – Fusiform *Longosoma*, with a large aperture (approximately half the height of the shell) that is turned upward; SA 37-38°; whorls relatively high; growth lines orthocline to slightly opisthocline, sigmoid.

Description – The nucleus (diameter 50-70 µm) is slightly inclined. The embryonic whorl is separated at 0.3 whorls from the remainder of the shell and is covered with short, sharp wrinkles that are especially common near the sutures. The first whorls thereafter are smooth and have a very depressed rounded outline with shallow sutures. A very fine axial lineament is visible on the paratype at 2.1 whorls, after which densely packed, very fine orthocline growth lines develop. This is also accompanied by a slight change in colour from whitish before to yellowish after the lineament. The lineament is almost certainly the protoconch-teleoconch boundary. The shell is smooth, but at large magnifications a very fine microscopic ornament of numerous spiral groovelets is seen. The aperture is very large for the genus (about half the height of the shell). It is broadly adnate and fusiform. A short, but pronounced, retraction is present at the columellar side of the basal lip. The outer lip is very pronounced and thickened. Viewed from the side it has a strong retraction at the top, a short expansion at *c.* two thirds of the height, a median broad retraction and a lower expansion that is slightly more produced than the upper expansion, before plunging into the basal siphonal retraction. The apertural plane is slightly bent upward. The inner lip is long and almost straight. The inner lip callus is thin, but well developed, not expanding. About half the height a broad and low, but well developed, umbilical chink occurs. The columella is openly coiled. A very shallow groove may be present to the left of the inner lip, but the shell should be considered imperforate.

Dimensions – RGM 456 608: H 3.1; W 1.4; Hap 1.6; 5.3 whorls. INGEMMET TN94: H 3.3; W 1.55; Hap 1.6; 5.4 whorls.

Remarks – *Longosoma fusiforme* most resembles *L. glabrum*. It differs from the latter by a fusiform instead of a conical outline, the comparatively larger aperture and ortho-opisthocline sigmoid, instead of prosocline, growth lines. *Longosoma fusiforme* differs from *L. curtum* by its larger size, wider outline, higher whorls, the comparatively larger aperture and a more convex whorl profile.

Genus *Sioliella* Haas, 1949
(= *Eubora* Kadolsky, 1980 = *nomen novum pro Ebora* Conrad *in* Woodward, 1871 (*non Ebora* Walker, 1867) = *Nesis* Conrad *in* Woodward, 1871 (*non Nesis* Mulsant, 1850 *nec* Stål, 1860))

Type species – *Sioliella effusa* Haas, 1949, Rio Tapajos, Brazil, Recent (Wesselingh, 2000).

Diagnosis – Naticiform to conical, robust, intermediate-large cochliopid (H 5-10 mm); embryonic shell inclined with well-developed honeycomb ornament; rarely visible lineament at *c.* 1.7-1.9 whorls defines protoconch-teleoconch, although teleoconch ornament may occur in other species as early as 1.2 whorls; shell smooth (frequently with microscopic, irregular impressed spiral lineaments) to carinate, with a basal apertural retraction (siphon); most of the ovate species are umbilicate; conical species lack an umbilicus.

Range – Miocene, Pebas Formation, western Amazonia; extant, Tapajos River, central Amazonia, Brazil.

Sioliella crassilabra (Conrad, 1871)

Fig. 187.

1871 *Ebora crassilabra* Conrad; Woodward, p. 102 (*pars*, *non* pl. 5, fig. 1a, b).
1871 *Ebora (Ebora) crassilabra* Conrad, p. 194, pl. 10, fig. 14.
1874a *Ebora crassilabra* Conrad; Conrad, p. 32, pl. 1, fig. 9.
1878 *Lacuna (Ebora) crassilabris* (Conrad); Boettger, p. 494, pl. 13, fig. 12a-d.
1980 *Eubora crassilabra* (Conrad); Kadolsky, p. 367, figs. 3, 4 (fig. 5?).
1990 *Eubora crassilabra* (Conrad); Nuttall, p. 216 (*pars*), figs. 171, 172.

Material studied – RGM 456 324, San Miguel de Cochiquinas (Loreto, Peru), exposure in south bank Amazon River, *c.* 1.5 km downstream from confluence with Rio Cochiquinas (3°47'S 71°36'W), material collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 28-8-1996. INGEMMET TN96, same locality.

Extended diagnosis – Relatively high-spired (SA *c.* 65°), almost turreted, relatively thin-shelled *Sioliella* with rounded whorls and comparatively deep suture; shell with prosocline growth lines and microscopic, irregularly impressed spiral lineaments; basal apertural inflection (siphon) well developed and bordered by slightly thickened margins; umbilicus well-developed and bordered by an umbilical ridge.

Dimensions – RGM 456 324: H 8.5; W 6.4; Hap 4.6; 5.8 whorls. INGEMMET TN96: H 8.0; W 5.9; Hap 4.7; *c.* 5.6 whorls.

Range – Pebas Formation, MZ7 (Middle Miocene), Peruvian Amazonia.

Remarks – Woodward (1871) was published before Conrad (1871) by a few months. Woodward quotes Conrad's diagnosis of *Ebora* almost literally, and this is deemed to be a combined diagnosis of both genus and species group name according to Article 12.2.6 (International Commission on Zoological Nomenclature, 1999), with Conrad as author (article 50.1.1). Kadolsky (1980, p. 367, fig. 3) designated Conrad's only specimen of *Ebora crassilabra* as the holotype under the assumption that the name was made available by him (Conrad, 1871). It is debatable whether the earlier publication of Woodward is exclusively based on Conrad's material or whether some of Woodward's own mate-

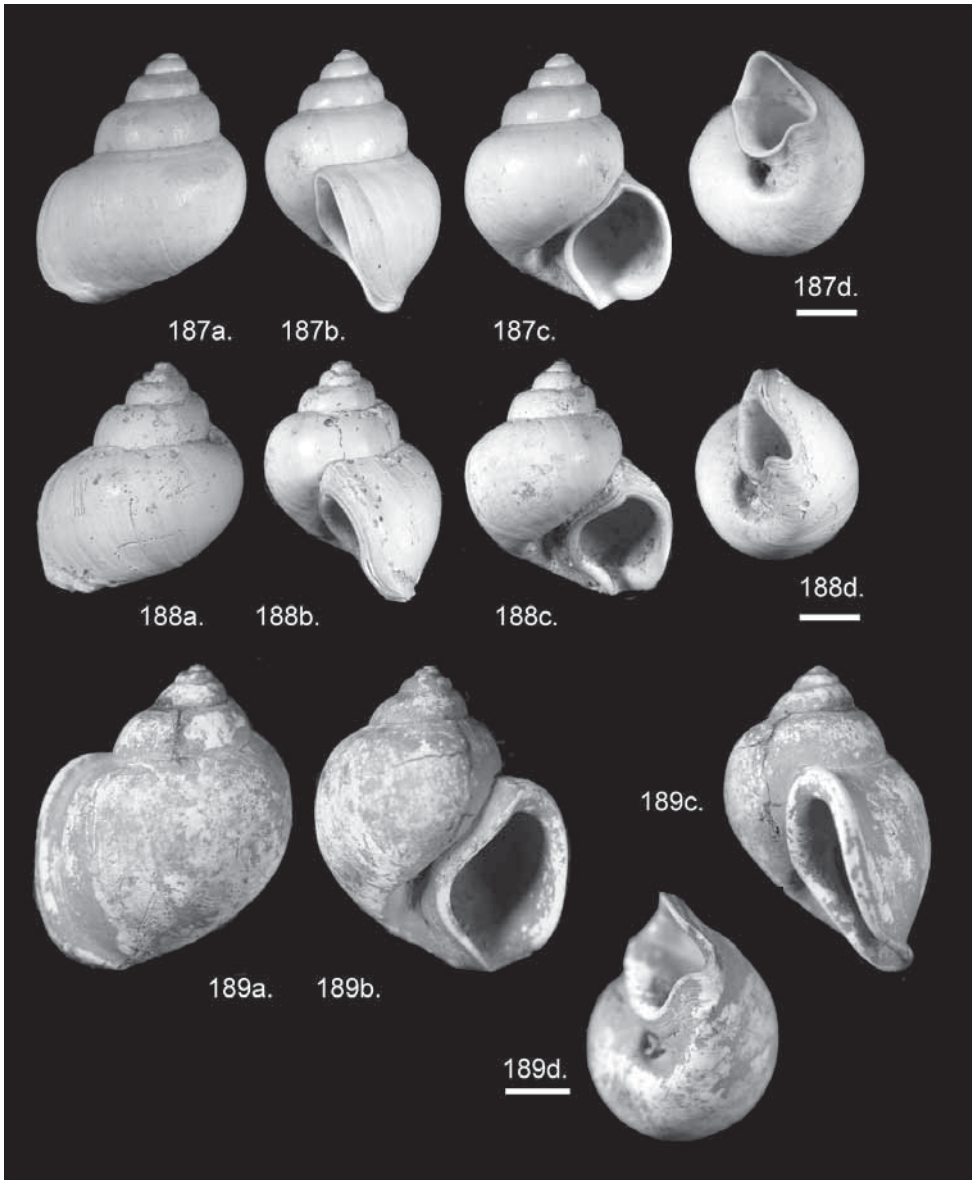


Fig. 187. *Sioliella crassilabra* (Conrad, 1871). RGM 456 324, San Miguel de Cochiquinas (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 188. *Sioliella woodwardi* (Kadolsky, 1980). RGM 456 325, San Miguel de Cochiquinas (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 189. *Sioliella ovata* Wesselingh, 2000. RGM 445336 (holotype), Mocagua (Amazonas, Colombia). a, rear view. b, front view. c, lateral view. d, basal view.

Scale bars represent 2 mm.

rial (Kadolsky, 1980, fig. 4; Nuttall, 1990, figs. 171, 172), not mentioned by that author, forms also part of the type series. In that case the status of the 'holotype' would have to be changed to lectotype (Article 74.6). Woodward illustrated a shell from his material as *Ebora crassilabra*, but as he expressed doubt about the identification ("We venture to refer the specimen figured on our plate (figs. 1a, b) to this species; but Mr. Conrad's figure is very obscure"; Woodward, 1871, p. 102), this specimen does not form part of the type series; Kadolsky (1980) separated it as *Eubora woodwardi*.

Sioliella woodwardi (Kadolsky, 1980)

Fig. 188.

1871 *Ebora crassilabra* Conrad; Woodward, p. 102 (*pars*), pl. 5, fig. 1a, b.
1980 *Eubora woodwardi* Kadolsky, p. 368, figs. 6, 7.
1990 *Eubora woodwardi* Kadolsky; Nuttall, p. 216, fig. 173.

Material studied – RGM 456 325, San Miguel de Cochiquinas (Loreto, Peru), exposure in south bank Amazon River, *c.* 1.5 km downstream from confluence with Rio Cochiquinas (3°47'S 71°36'W), material collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 28-8-1996. INGEMMET TN97, same locality.

Extended diagnosis – Thick-shelled, slightly depressed, but naticiform, robust *Sioliella*; SA *c.* 75°; shell smooth, apart for strongly prosocline, on the body whorl slightly sigmoid growth lines; whorl profile convex; aperture thickened; top of the aperture located well below a parietal platform that connects the aperture to the preceding whorl; base of columellar lip in adult specimens strongly expanding to the right; outer lip almost vertical; maximum width of body whorl located at *c.* half the height of the shell.

Dimensions – RGM 456 325: H 7.4; W 6.5; Hap 4.6; 5.6 whorls. INGEMMET TN97: H 7.5; W 6.3; Hap 4.6; *c.* 4.8 whorls.

Range – Pebas Formation, MZ6 - MZ7 (Middle Miocene), Peruvian Amazonia.

Remarks – The depressed outline, thicker shell and the base of the columellar lip that is strongly deflected to the right, as well as the maximum width of whorls, that is located higher up the whorl than in *S. crassilabra*, all serve to differentiate *S. woodwardi* from the former species.

Sioliella ovata Wesselingh, 2000

Figs. 15a, 189.

1981 *Eubora woodwardi* Kadolsky; Costa, p. 641, pl. 1, figs. 5, 6.
1990 *Eubora crassilabra* (Conrad); Nuttall, p. 216 (*pars*, *non* figs. 171, 172).
2000 *Sioliella ovata* Wesselingh, p. 133, figs. 6, 7.

Material studied – RGM 445 336 (holotype), Mocagua (Amazonas, Colombia), exposure in north bank Amazon River below Finca, 1.3 km east of village school (3°48'S 70°17'W), level F9 (6.8 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 445 340 (paratype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F60 (17.1 m above DL). Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Extended diagnosis – Large naticiform *Sioliella*, with fine prosocline to slightly sigmoid growth lines and microscopic irregular impressed spiral cords; shell of well-preserved juveniles contains a structure of slightly divergent spiral lines; SA *c.* 78°; suture slightly impressed, successive whorls not fused at the suture, resulting in a very narrow (<0.1 mm) fissure; aperture large (between 0.5 and 0.65 H) and more or less spindle-shaped; base of aperture deflected, pointing into a well-developed, U-shaped siphonal reflection that points backward; apertural margins thickened; a well-developed umbilical ridge bounds the narrow and deep umbilicus.

Dimensions – RGM 445 336: H 10.0; W 8.2; Hap 7.5; 5.2 whorls. RGM 445 340: H 7.9; W 5.9; Hap 5.9; 5.1 whorls.

Range – Pebas Formation, MZ8 - MZ12 (late Middle - early Late Miocene), Peruvian, Colombian and Brazilian Amazonia.

Remarks – The more regular naticiform (ovate) outline and the very large aperture distinguish this species from other smooth *Sioliella* species, namely *S. crassilabra* and *S. woodwardi*.

***Sioliella grevei* (Kadolsky, 1980)**

Fig. 190.

1938 *Lacuna (Ebora) crassilabris* (Conrad); de Greve, p. 70 (*pars*), pl. 5. figs. 19-21, 23 (*non* fig. 22).
1980 *Eubora grevei* Kadolsky, p. 369, fig. 12.
1990 *Eubora grevei* Kadolsky; Nuttall, p. 218.

Material studied – RGM 445 637, Pebas-Pijoyal (Loreto, Peru), exposure in north bank Amazon River, 350 m east of naval base Pijoyal (the latter at 3°20'S 71°50'W), level F427 (0.5 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 24-8-1996. INGEMMET TN99, same locality.

Extended diagnosis – Intermediately sized (H. 6.4), ovate, slightly shouldered *Sioliella* with two low and poorly defined spiral ribs; upper rib strongest, defining at first flat and later slightly convex subsutural ramp above; perimeter between upper and lower rib markedly straight; a low, poorly defined third rib may develop below second rib at body whorl; all ribs fade on penultimate whorl and disappear on body whorl shortly before the aperture; aperture adnate through broad, slightly retracted parietal platform;

inner lip robust; siphonal retraction in the middle of the apertural base; outer lip flaring, thin; umbilicus closed or narrowly rimate and very shallow.

Dimensions – RGM 445 637: H 6.4; W *c.* 5.5; Hap 4.9; >5.1 whorls. INGEMMET TN99: H >5.4; W 4.9; Hap 3.2; 5.1 whorls.

Range – Pebas Formation, MZ6 - MZ7 (Middle Miocene), Peruvian Amazonia.

Remarks – *Sioliella grevei* most closely resembles *S. bella*, but has fewer keels that are low (and not very prominent as in *S. bella*) and a plugged umbilicus.

***Sioliella bella* (Conrad *in* Woodward, 1871)**

Figs. 15b, 191.

1871 *Ebora (Nesis) bella* Conrad; Woodward, p. 102, pl. 5, fig. 3.
1871 *Ebora (Nesis) bella* Conrad, p. 194, pl. 10, fig. 17.
1878 *Lacuna (Ebora) bella* (Conrad); Boettger, p. 494, pl. 13, fig. 3.
1878 *Lacuna (Ebora) bella* (Conrad) var. *semisculpta* Boettger, p. 495, pl. 13, fig. 2.
1938 *Lacuna (Ebora) bella* (Conrad); de Greve, p. 72.
1980 *Eubora bella* (Conrad); Kadolsky, p. 369, figs. 9, 10.
1990 *Eubora bella* (Conrad); Nuttall, p. 217, figs. 174, 175.
2002 *Sioliella bella* (Conrad); Wesselingh *et al.*, fig. 3m.

Material studied – RGM 456 326, Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN98, same locality

Extended diagnosis – Robust, spirally ribbed and shouldered *Sioliella*; SA *c.* 80°; onset of well-defined keels at *c.* one third and two thirds of whorl height soon after the protoconch/teleoconch boundary; upper spiral bounds a well-defined, slightly concave subsutural ramp; lower spiral bounds a similarly well-defined suprasutural depression; at the lower suture a ridge corresponding to a third spiral on the body whorl may be visible; body whorl covered with up to seven regularly spaced keels; growth lines slightly prosocline, opisthocyrt to faintly sigmoid; lower keel serves as an umbilical ridge for a well-defined umbilicus; aperture large, subquadrate; apertural margins thickened; outer lip slightly flaring; well-defined siphonal-like incursion located towards the outer lip at the base of the aperture.

Dimensions – RGM 456 326: H 7.1; W 6.4; Hap 4.9; 5.0 whorls. INGEMMET TN98: H 6.9; W 5.8; Hap 4.4; 4.5 whorls.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Remarks – *Sioliella bella* differs from *S. grevei* principally by the very strongly developed spiral ornament and the well-defined umbilicus. See remarks concerning authorship under *S. crassilabra*, above.

***Sioliella* sp.**
Fig. 192.

Material studied – RGM 456 343, Beiruth (Loreto, Peru), exposure in south bank Amazon River, below village (3°53'S 71°28'W), level F492 (3.9 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 27-8-1996.

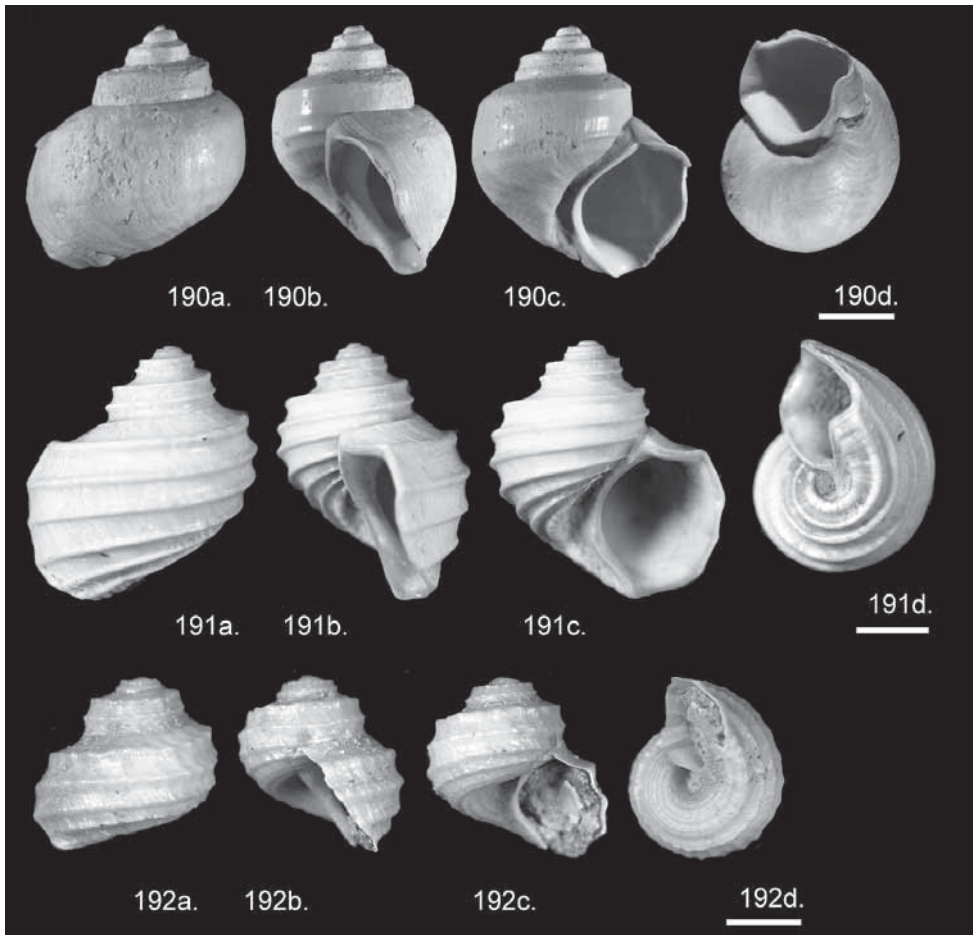


Fig. 190. *Sioliella grevei* (Kadolsky, 1980). RGM 456 637, Pebas-Pijoyal (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 191. *Sioliella bella* (Conrad *in* Woodward, 1871). RGM 456 326, Santa Rosa de Pichana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 192. *Sioliella* sp. RGM 456 343, Beiruth (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 2 mm.

Description – The nucleus is only slightly inclined. The top of the first 1.5 whorls is planar coiled and the whorl descends only afterwards. No boundary between protoconch and teleoconch has been observed. The onset of a thin, well-defined spiral at four fifths of the whorl height is at 1.2 whorls, almost immediately followed by the onset of a second spiral rib at *c.* two fifths of the whorl height. A third spiral rib becomes visible at the lower suture from *c.* 2.3 whorls onwards. The upper rib delimits a wide and flat subsutural platform, resulting in a distinctly shouldered outline. The ribs are crossed by numerous prosocline growth lines. Regularly recurring, broad axial undulations occur from 2.1 whorls onwards. At intersections with the spiral ribs they produce elongated knobs. A fourth strong rib becomes visible before the aperture. Interspaces between the ribs are progressively narrower downward. Another four, closely spaced, spiral ribs of the same strength as the overlying four, form an ornament to the base of the body whorl, that grades into the very deep umbilicus. The aperture is damaged and possibly not full grown. The apparently undamaged parts of the apertural margins are thin. The aperture is only attached at the parietal margin. From growth lines at the base of the body whorl, the presence of a shallow basal apertural retraction can be deduced. The apertural base is broken.

Dimensions – RGM 456 343: H 4.9; W 5.0; Hap 3.0; 4.2 whorls.

Range – Pebas Formation, MZ 9 (late Middle- early Late Miocene), Peruvian Amazonia.

Sioliella kadolskyi Wesselingh sp. nov.

Figs. 16a, c, 17k, 193, 194.

Type material – INGEMMET TN01 (holotype), Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. RGM 456 327, RGM 456 615, RGM 456 615 (all paratypes) and

Figs. 193, 194. *Sioliella kadolskyi* sp. nov. ▶

Fig. 193. INGEMMET TN01, holotype, Copal Urco (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 194. RGM 456 327, paratype, same locality as Fig. 193. a, rear view. b, lateral view. c, front view. d, basal view.

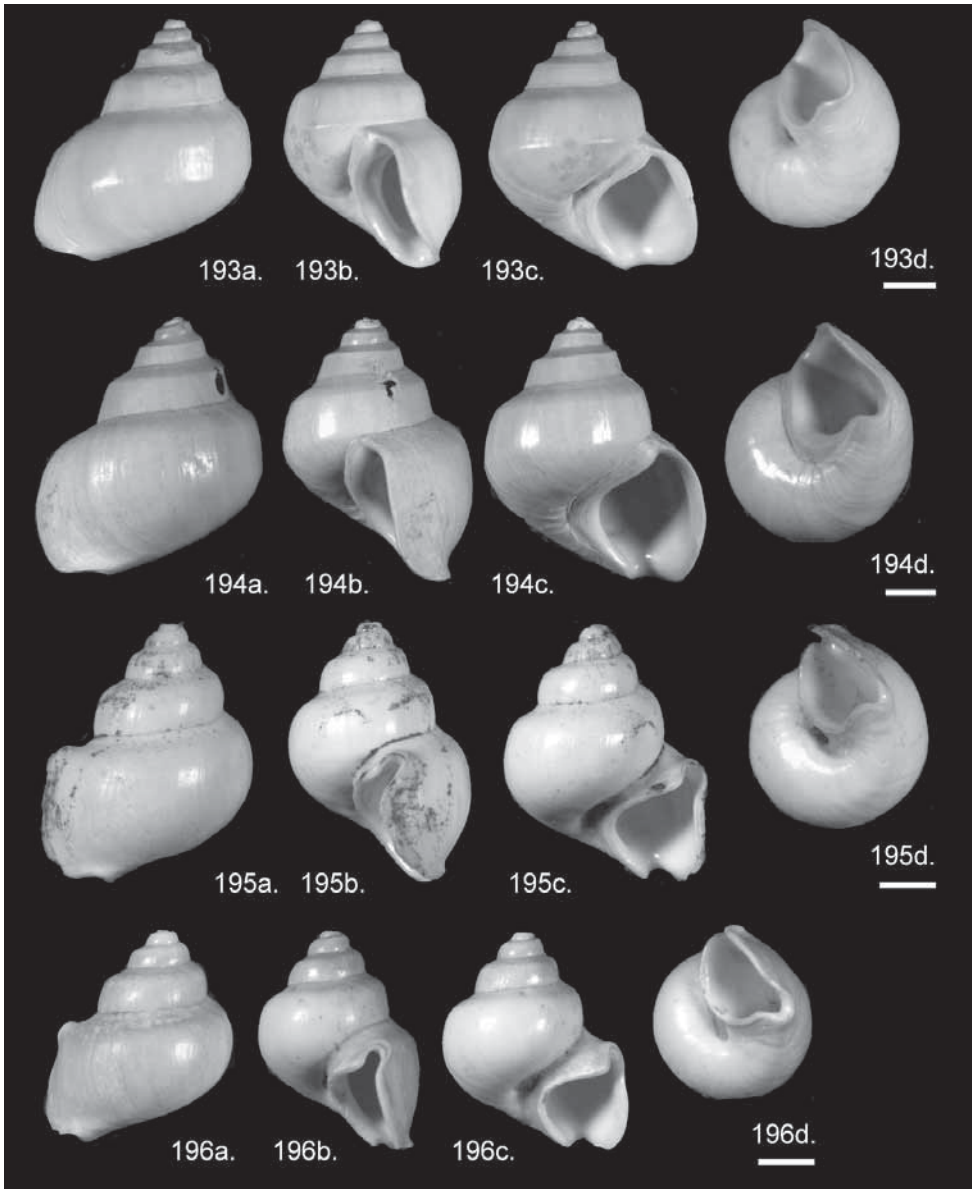
Figs. 195, 196. *Sioliella bisiphonata* sp. nov.

Fig. 195. RGM 456 329, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 196. INGEMMET TN02, paratype, same locality as Fig. 195. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

RGM 456 328 (64 paratypes), same locality. RGM 456 616 (paratype), Boca Momon (Loreto, Peru), exposure in north bank Rio Momon, *c.* 300 m upstream of confluence with Rio Nanay (3°41'S 73°15'W), level F357 (location in respect to DL unknown). Pebas Formation, MZ 6 (Middle Miocene); leg. F.P. Wesselingh, 12-8-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.



Derivatio nominis – Named after Dietrich Kadolsky (Croydon, England), who has investigated many problematic fossil hydrobioid and lacuniform gastropods, including those of the Pebas Formation, and who has been a great help in shaping the general discussion on Cochliopidae above.

Diagnosis – Ovate conical *Sioliella* with a subrounded keel at two thirds of the whorl height that bounds a well-defined subsutural ramp resulting in a shouldered outline, particularly on the third and fourth whorl; second keel at or below suture; low keel usually becoming obsolete on later whorls; aperture broadly adnate, thickened; upper part parietal margin thickened; umbilicus closed or very shallow; SA 68°.

Description – The nucleus is inclined. The embryonic shell is covered for *c.* three quarters by a broad honeycomb ornament. At 0.5 whorls an axial line in a low depression marks the boundary with the protoconch-2. The first one and a half whorls are coiled almost in plane, thereafter the whorls rapidly descend. In one of the specimens a sharp, non-reinforced angulation develops at *c.* two thirds of the height of the whorl at *c.* 1.5 whorls; in another it develops at *c.* 1.9 whorls. The keel is prominent at the second and third whorl, and becomes more rounded and obsolete on later whorls. The subsutural ramp above the keel is at first almost flat, but becomes later steeper. A secondary keel develops at the lower suture from *c.* 1.5 whorls onward. This keel can be covered by successive whorls, but usually is seen at the lower suture. At the body whorl this keel is rounded and delimits a poorly defined, rounded basis of the body whorl. Whorls are adpressed. The surface of the shell is smooth apart from numerous, fine orthocline to slightly prosocline growth lines. Traces of microscopic irregularly impressed spiral grooves are seen on some well-preserved specimens. The aperture is subquadrate, pointed in the top. The inner lip margin is deeply curved. The aperture has a reinforced basal siphon that is located in the centre of the apertural basis. Slightly within the aperture, a thickening occurs on the top of the parietal lip. The umbilicus is covered by the expanded inner lip. In some specimens the coverage is not entire, exposing a shallow and narrow umbilicus.

Dimensions – INGEMMET TN01: H 4.8; W 3.8; Hap 2.6; 5.1 whorls. RGM 456 327: H 5.5; W 3.9; Hap 3.2; >5.1 whorls.

Remarks – This species is distinguished from all other *Sioliella* species by its smooth, but shouldered, morphology, with only two, non-reinforced keels present.

***Sioliella bisiphonata* sp. nov.**
Figs. 15w, 195, 196.

2002 *Sioliella* sp.; Wesselingh *et al.*, fig. 3c.

Type material – RGM 456 329 (holotype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 3.1 km south of Indiana and 150 m north of the landing stage of Barradero de Mazan (3°31'S 73°05'W), level F383 (0.0-0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. INGEMMET TN02 (paratype) and RGM 456 330 (six paratypes), same locality.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the siphonal-notches at the top and the base of the aperture (Latin, *bis* for two, *siphon* for pipe).

Diagnosis – *Sioliella* with a prominent second siphon at the junction of the upper and outer lip; parietal lip almost horizontal; whorl profile rounded; SA 67-70°.

Description – The nucleus is flat, slightly inclined. The embryonic shell is separated from the protoconch at *c.* 0.4 whorls by a barely visible axial constriction. The first 1.5 whorls form a flat top of the shell, thereafter the shell rapidly descends. No protoconch-teleoconch boundary has been observed. The whorl profile becomes convex, with deeply impressed sutures. The shell is smooth, apart for poorly developed, fine orthocline growth lines. The growth lines become clearer on later whorls. On the body whorl they are both slightly prosocline and slightly sigmoid. The aperture is small (Hap less than 0.5 H). The columellar margin is deeply curved, the parietal margin is almost horizontal and the outer lip margin almost vertical. The long axis of the aperture inclines some 30° towards the columella. A well-defined, slightly backward pointing siphon with reinforced margins forms the lower end of the axis. The top of the apertural axis coincides with the second siphon that is even more restricted, by amongst others a produced parietal margin, and has reinforced margins. The parietal lip is located on a broad platform that is attached to the preceding whorl. This platform covers most of the umbilicus that is very shallow only.

Dimensions – RGM 456 329: H 5.2; W 3.7; Hap 2.2; 5.1 whorls. INGEMMET TN02: H 4.5; W 4.0; Hap 2.4; 4.6 whorls.

Remarks – This species resembles *S. crassilabra* in general outline, but is smaller, has a somewhat thicker shell and an upper apertural sinus. The upper sinus is only poorly developed or lacking in subadult specimens of *S. bisiphonata,* that is higher-spired than *S. woodwardi*.

***Sioliella umbilicata* sp. nov.**
Figs. 197, 198.

Type material – RGM 456 331 (holotype), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River, 1.3 km east of confluence with Loreto Yacu (3°46'S 70°21'W), level F22 (1.7 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. INGEMMET TN03 (paratype), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Range – Pebas Formation, MZ8 - MZ11 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Named after the prominent umbilicus (Latin for navel) of this species .

Diagnosis – Ovate-conical, robust, smooth *Sioliella*; SA 71-77°; shell shouldered; basal apertural siphon prominent, strongly deflected; umbilicus very prominent, broad and deep, bordered by a strongly developed umbilical ridge.

Description – The nucleus is slightly inclined. The protoconch-teleoconch boundary is poorly defined. It is likely represented by a minute axial lineament at 2.1-2.2 whorls, after which densely spaced growth lines as well as traces of microscopic spiral groovelets occur. The shell contains increasingly inclined prosocline growth lines, as well as common microscopic spiral linear impressions. A very fine spiral line may develop below the upper suture that marks a slightly concave depression located halfway on the poorly defined shoulder. This depression is slightly more pronounced on the penultimate whorl. The suture tends to be adpressed. A prominent umbilical ridge becomes visible at the base of the body whorl. It is bounded and accentuated adapically by a depression. Growth lines retract at the umbilical ridge. The aperture is (sub)rounded. The interior margins of inner and outer lips are broadly curved. The outer lip is barely thickened; the inner lip and basal margins are thickened. The upper one-third to one-fifth of the inner lip is attached through a flat or even retracted parietal platform to the preceding whorl. The lower part of the columellar lip is strongly expanded to the right, where it borders the very prominent basal apertural siphon. The siphon is located at the centre or towards the right of the aperture and corresponds to the prominent umbilical ridge. The umbilicus is wide and deep.

Dimensions – RGM 456 331: H 6.9; W 5.2; Hap 4.6; >4.6 whorls. INGEMMET TN03: H 6.9; W 5.8; Hap 4.8; 5.0 whorls.

Remarks – No other species of *Sioliella* has a similarly broad umbilicus bordered by such a prominent umbilical ridge.

Figs. 197, 198. *Sioliella umbilicata* sp. nov. ▶

Fig. 197. RGM 456 331, holotype, Los Chorros (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 198. INGEMMET TN03, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

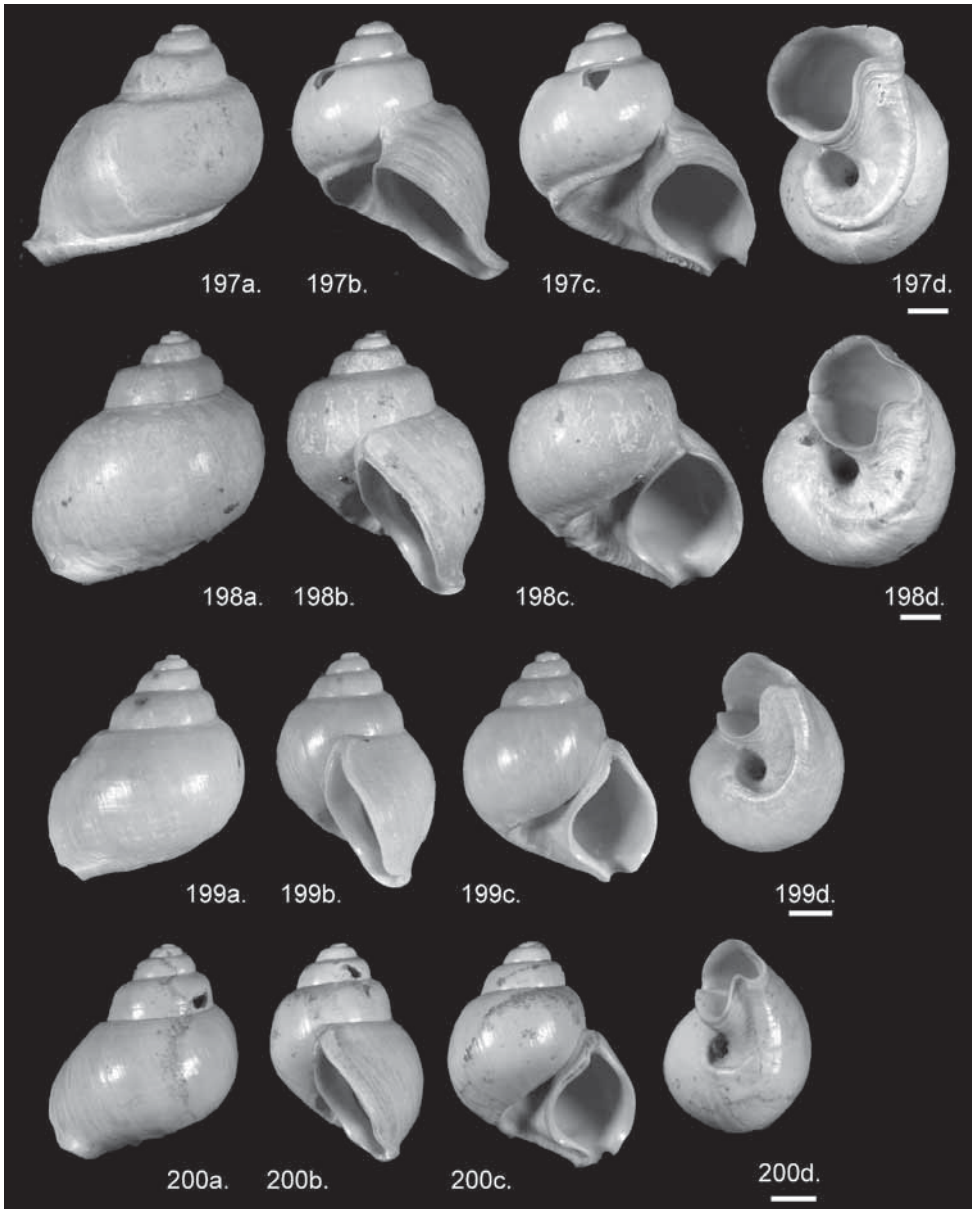
Figs. 199, 200. *Sioliella fusiformis* sp. nov.

Fig. 199. INGEMMET TN04, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 200. RGM 456 332, paratype, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

***Sioliella fusiformis* sp. nov.**
Figs. 16b, 199, 200.

Type material – INGEMMET TN04 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 614 (paratype), same locality. RGM 456 332 (paratype),



Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Range – Pebas Formation, MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the more or less spindle-shaped outline of the shell as well as the aperture (Latin, *fusus* for spindle).

Diagnosis – Robust, spindle-shaped, smooth *Sioliella* with a spindle-shaped aperture; SA 69-70°; basal siphon well-developed; a second siphonal retraction visible at the top of the aperture; umbilicus prominent, bordered by an umbilical ridge; shell with well-developed, microscopic, irregular spiral linear impressions.

Description – The nucleus is slightly inclined. The margins contain very fine, short and discontinuous wrinkles or yield a honeycomb pattern that breaks apart into small, sharp triangular pustules. At 0.45 whorls a thin line or very shallow depression marks the boundary between the embryonic shell and the protoconch-2. The first *c.* 1.3 whorls of the shell are coiled in plane, thereafter the whorls rapidly descend. Possibly a very fine lineament, observed in two specimens at 1.9 whorls, represents the protoconch-teleoconch boundary. The whorls are rounded and the suture is slightly impressed. The shell appears smooth, apart for growth lines and microscopic spiral ornamentation. The fine growth lines are numerous. They are orthocline on early teleoconch whorls and become slightly prosocline on later whorls. Commonly microscopic spirally arranged linear impressions occur on the last two whorls. An umbilical ridge occurs at the base of the body whorl, separated from the remainder of the body whorl by a shallow spiral depression. The aperture is fusiform. The apertural margins are thickened. The upper two fifths of the inner lip is attached through a straight or retracting parietal platform with the preceding whorl. The long apertural axis is almost parallel to the vertical axis of the shell. The basal apertural siphon is retracted and well developed. The upper siphonal retraction is also prominent and deflected backward, and can be more pronounced due to a thickening at the upper part of the parietal lip. The umbilicus is prominent and deep. The umbilical ridge corresponds to the basal apertural siphon. When viewed from the front, the spirally arranged linear impressions are well visible inside the umbilicus. A shallow spiral depression may be present at the inner side of the umbilical ridge, emphasizing both the umbilical ridge and basal siphon.

Dimensions – INGEMMET TN04: H 5.5; W 4.4; Hap 3.7; 5.1 whorls. RGM 456 332: H 5.5; W 4.3; Hap 3.4; 5.2 whorls.

Remarks – This species has the upper siphonal retraction in common with *Sioliella bisiphonata*. However, it is spindle-shaped and has a prominent umbilicus, lacking in the latter. The prominent umbilicus and umbilical ridge are reminiscent to those of *Sioliella umbilicata*, with which it co-occurs. The latter species is larger, broader and lacks the siphonal retraction at the top of the aperture.

***Sioliella carinata* sp. nov.**
Figs. 201, 202.

Type material – RGM 456 337 (holotype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, below village school (3°29'S 73°00'W), level F89 (sample at DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 10-1991. INGEMMET TN06 (paratype), Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. RGM 456 338 (paratype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S 73°00'W), level F318 (1.35 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996.

Range – Pebas Formation, late Early- early Middle Miocene, Peruvian Amazonia.

Derivatio nominis – Named after the keeled ornament of this species (Latin, *carina* for keel).

Diagnosis – Conical *Sioliella* with a well-developed spiral ornament consisting of two (subadult whorls) to four (sometimes five) spirals on body whorl; SA 64-65°; aperture subquadrate.

Description – The nucleus is inclined. At 0.4-0.55 whorls an irregular spiral constriction separates the embryonic shell from the teleoconch-2. The first 1.1 whorls are planispiral, thereafter the shell descends rapidly. In two specimens an irregular axial lineament is observed that may represent the protoconch-teleoconch boundary at 1.7 whorls. Directly after the lineament numerous, closely spaced growth lines develop, and very soon after two spiral ribs at one quarter and two thirds of the whorl height appear. The upper spiral bounds a slightly concave subsutural platform. Growth lines are at first orthocline, but become progressively slightly prosocline. Some specimens develop barely distinguishable, broad axial undulations. At the body whorl usually four, but sometimes five spiral ribs are visible. The upper two are the strongest, and the lower ones are usually progressively thinner and lower, but some variations exists as to the strength and number of ribs. The aperture is subquadrate. It is slightly elevated from innerlip platform. The parietal part of the platform is thin. The apertural margins are barely thickened. The basal siphon is broad, but well developed. The umbilicus is usually closed or rimate and shallow.

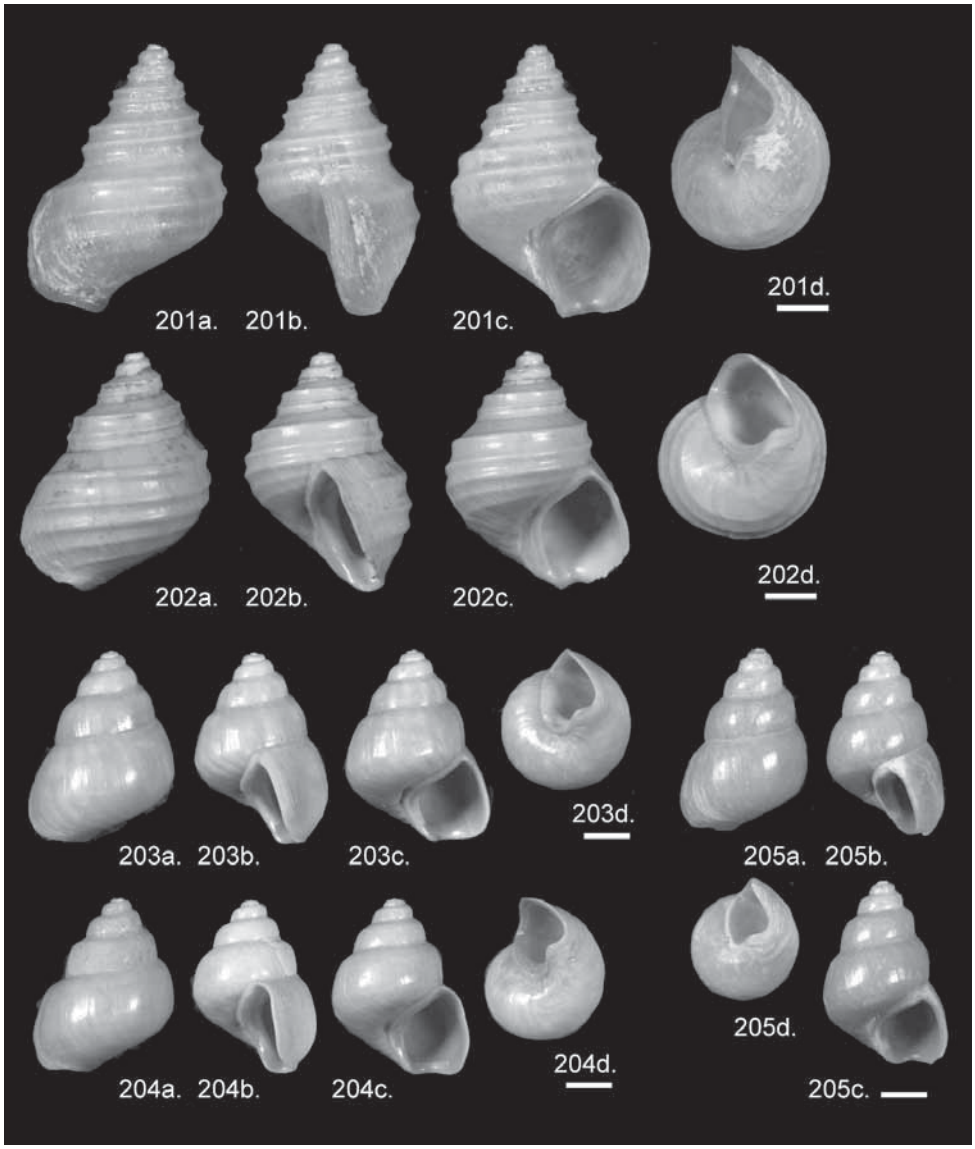
Dimensions – RGM 456 337: H 5.3; W 3.6; Hap 2.4; 5.8 whorls. INGEMMET TN06: H 3.9; W 2.8; Hap 1.8; 5.0 whorls. RGM 456 338: H 4.4; W 2.8; Hap 1.8; 5.0 whorls.

Remarks – The outline of this species shows some resemblance to that of *S. littoridinaeformis*, but the latter is smaller and smooth. Other spirally ornamented species, such as *S. bella* and *S. grevei*, are larger, more globose and lack the typical conical shape of *S.*

carinata. *Toxosoma multicarinata* has a similar ornament, but is easily distinguishable from *S. carinata* by the presence of columellar modifications.

***Sioliella littoridinaeformis* sp. nov.**
Figs. 203-205.

Type material – INGEMMET TN05 (holotype): Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 1.4 km south of port (port at 3°30'S 73°03'W), level F681 (1.1 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P.



Wesselingh, 1-9-1996. RGM 456 333, RGM 456 334, RGM 456 335 (all paratypes) and RGM 456 336 (33 paratypes), same locality.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – This species resembles *Littoridina* in outline.

Diagnosis – Small, conical, smooth-shelled *Sioliella*; SA 55-60°; aperture subquadrate; umbilicus closed.

Description – The nucleus is inclined is broadly covered by a honeycomb-like ornament. The embryonic shell is bounded from the protoconch by an axial constriction at 0.5 whorls. The first 1.3 whorls are planar, thereafter the shell rapidly descends. The whorl profile can be described as slightly convex. Numerous fine growth lines occur abruptly at 1.6 whorls in one specimen. In another, a very poorly defined axial lineament at 1.7 whorls preceeds similar dense growth lines, suggesting that the protoconch-teleoconch boundary might be located at 1.6-1.7 whorls. The upper part is dipping less steeply at the second and third whorls giving them a very vaguely shouldered appearance. Slightly prosocline growth lines are numerous and a very fine microscopic ornament of irregularly impressed spiral lineaments is visible. The base of the body whorl is vaguely delimited from the remainder body whorl, but is nevertheless rather broad. The aperture is subquadrate; the columellar and parietal margins are about as long. The inner lip margins are reinforced and attached to the preceding whorl. The umbilicus is covered by the expanding inner lip. A broad, but well-defined, siphonal retraction is located at the base of the aperture.

Dimensions – INGEMMET TN05: H 3.9; W 2.9; Hap 1.9; 5.0 whorls. RGM 456 333: H 3.7; W 3.0; Hap 2.1; 4.7 whorls. RGM 456 334: H 3.8; W 2.6; Hap 1.7; 5.1 whorls. RGM 456 335: H 3.7; W 3.0; Hap 1.9; 4.8 whorls.

◀ Figs. 201, 202. *Sioliella carinata* sp. nov.

Fig. 201. RGM 456 337, holotype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 202. RGM 456 338, paratype, same locality as Fig. 201. a, rear view. b, lateral view. c, front view. d, basal view.

Figs. 203-205. *Sioliella littoridinaeformis* sp. nov.

Fig. 203. INGEMMET TN05, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 204. RGM 456 333, paratype, same locality as Fig. 203. a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 205. RGM 456 334, paratype, same locality as Fig. 203. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Remarks – The small size, smooth surface and conical outline make *Sioliella littoridinaeformis* different from all other *Sioliella* species. The basal apertural notch distinguishes *S. littoridinaeformis* from *Littoridina*. *Sioliella littoridinaeformis* resembles *Eubora pygmaea* Kadolsky, 1980, from the Itaya River cliff near Iquitos in general outline and size. That species differs from *S. littoridinaeformis* by more rounded whorls, the presence of a weak umbilical ridge, and by the columellar margin that is erect and distinctly curved abaxially. The single specimen of this taxon found to date is also slightly larger than *S. littoridinaeformis*, viz. 4.4 mm high (not 4.8 mm as stated erroneously by Kadolsky, 1980, p. 371).

***Sioliella saloi* sp. nov.**
Figs. 206, 207.

Type material – INGEMMET TN14 (holotype), Mayoruna (Loreto, Peru), exposure in south bank Amazon River, *c.* 200 m south of confluence with Rio Nuevo Octubre (3°58'S 71°12'W), level F482 (3.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 369 (paratype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 300 m west of wood mill (3°53'S 71°24'W), material collected from surface scree. Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

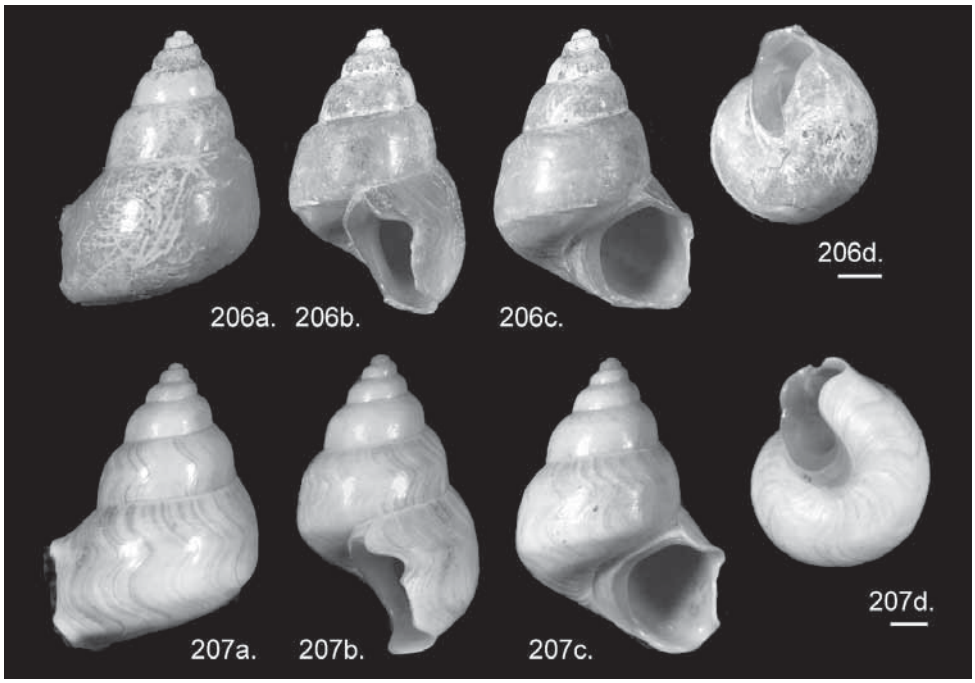
Derivatio nominis – Named after Professor Dr Jukka Salo (University of Turku, Finland), who made this research possible and also in honour of his work on biodiversity in lowland Amazonia.

Diagnosis – Conical, *Littoridina*-shaped *Sioliella*; SA 55-56°; growth lines with a median retraction corresponding to an upper apertural notch; lower apertural retraction located abaxially.

Description – The rather bulbous embryonic shell is visible on some specimens. It is separated from the protoconch-2 at 0.3 whorls by an axial constriction. A protoconch-teleoconch boundary could not be located. The whorl profile of the early teleoconch whorls is subrounded, but becomes progressively flatter. The suture is not impressed. Shells are often smooth and shiny, but the numerous growth lines are prominent. They are orthocline, but have a pronounced median retraction. Spiral zones of discoloration are seen in the shells. The aperture is subquadrangular; the outer lip is thin. The inner lip margins are thickened and located on a platform that attaches the aperture to the remainder shell. The basal apertural retraction is located abaxially. A second apertural notch is located at *c.* four fifths of the apertural height. Both notches have slightly reinforced margins. The upper gives the shell a vaguely shouldered appearance and the aperture its squarish shape. The outer lip is invariably damaged between the two retractions. The inner lip callus covers the entire umbilical area.

Dimensions – INGEMMET TN14: H 8.8; W 5.6; Hap 3.8; 5.7 whorls. RGM 456 369: H 7.9; W 5.6; Hap 3.8; 5.7 whorls.

Remarks – The smooth conical outline makes this species different from other *Sioliella* species, apart from *S. littoridinaeformis*. *Sioliella saloi* differs from the latter by the larger size, the more subquadrate outline of the body whorl and the median retraction of the growth lines that corresponds to the upper apertural retraction (lacking in *S. littoridinaeformis*). This outline of *S. saloi* more closely resembles the Pebasian *Littoridina* than *Sioliella* species, with the exception of *S. littoridinaeformis* . What makes *S. saloi* rather different from the other Pebasian species is the very abaxial location of the basal apertural retraction. A similar abaxial location of the basal apertural retraction (that is very shallow) is seen in the extant type species of *Sioliella*, *S. effusa* Haas, 1949.



Figs. 206, 207. *Sioliella saloi* sp. nov.

Fig. 206. INGEMMET TN14, holotype, Mayoruna (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 207. RGM 456 369, paratype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Genus *Tropidebora* Pilsbry, 1944

Type species – *Pachytoma tertiana* Conrad, 1874a. Pebas, 'Old Pebas' or Pichua (probably Santa Rosa de Pichana; Loreto, Peru; see Nuttall, 1990, p. 324). Pebas Formation, Middle Miocene.

Diagnosis – Ovate conical to widely conical shell; ornament usually made up by two primary keels; nucleus ornamented with small, sharp triangular pustules; protoconch-teleoconch boundary may be defined by axial thread, located at 1.0-1.7 whorls; base of body whorl subrounded to broad and flat, and bounded by a distinct keel; growth lines prosocline to strongly prosocline; aperture subquadrate; apertural margins reinforced; base of aperture with broad siphonal retraction; umbilicus closed.

Range – Miocene, Pebas Formation, western Amazonia (Peru).

Tropidebora tertiana (Conrad, 1874a)

Figs. 15c, 208, 209.

1874a *Pachytoma tertiana* Conrad, p. 31, pl. 1, fig. 11.
1938 *Helicina? tertiana* (Conrad); de Greve, p. 68, pl. 4, figs. 26-28, 31.
1944 *Tropidebora tertiana* (Conrad); Pilsbry, p. 150, fig. 2.
1990 *Tropidobora* [sic] *tertiana* (Conrad); Nuttall, p. 218, figs. 176-178.
2002 *Tropidebora tertiana* (Conrad); Wesselingh *et al.*, fig. 3o.

Material studied – RGM 456 014, Iquitos (Loreto, Peru), cliff exposure in west bank Amazon River at Puerto Ganso-Azul (3°45'S 73°11'W), level F75 (4.9 m above DL). Pebas Formation, MZ6 (Middle Miocene); leg. F.P. Wesselingh, 10-1991. INGEMMET TN07, San Miguel de Cochiquinas (Loreto, Peru), exposure in south bank Amazon River, *c.* 1.5 km downstream from confluence with Rio Cochiquinas (3°47'S 71°36'W), material collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P.

Figs. 208, 209. *Tropidebora tertiana* Conrad, 1874a. ►

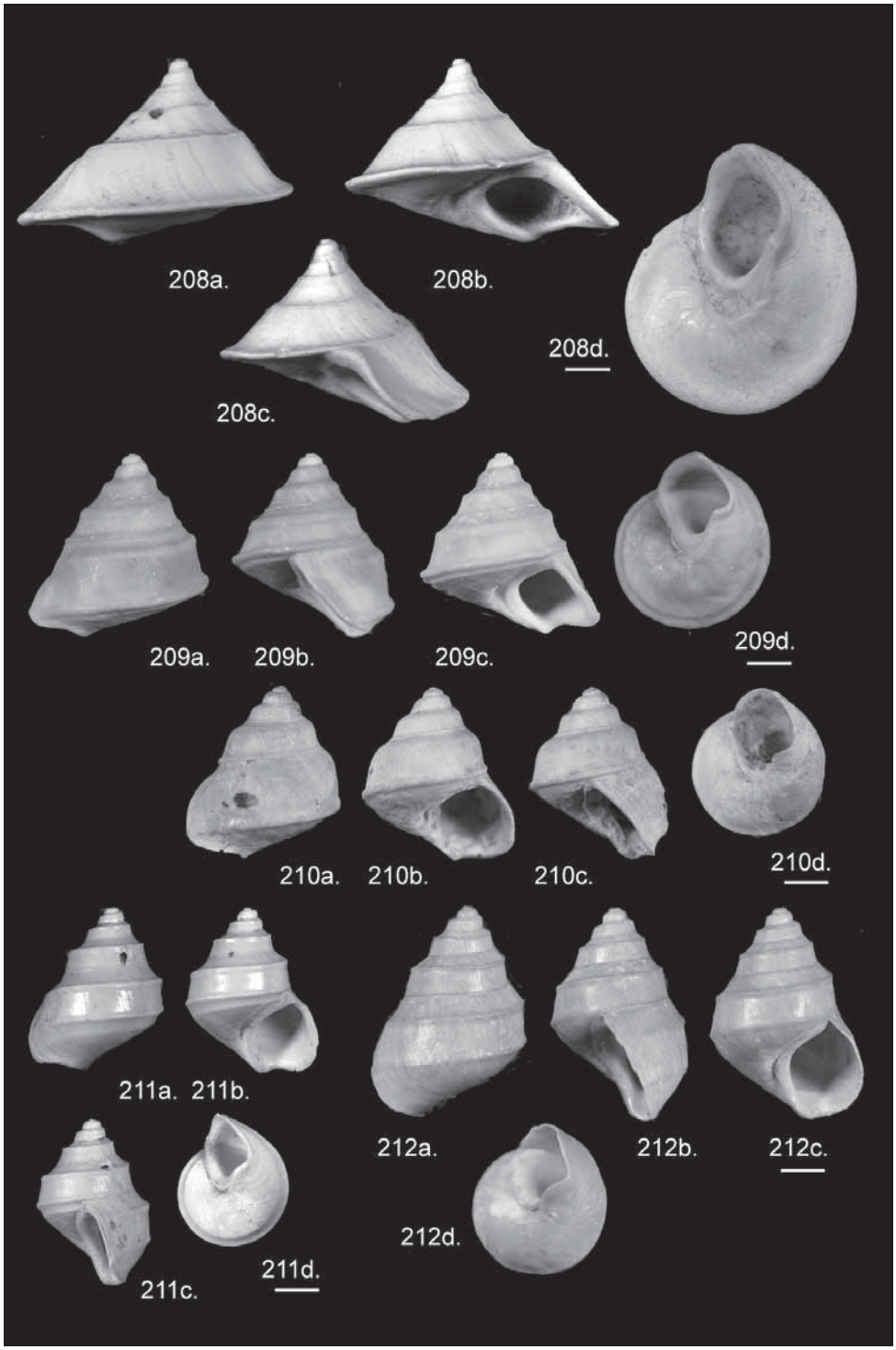
Fig. 208. INGEMMET TN07, San Miguel de Cochiquinas (Loreto, Peru). a, rear view. b, front view. c, lateral view. d, basal view.
Fig. 209. RGM 456 014, Iquitos (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 210. *Tropidebora* sp. RGM 456 341, Barrio Florido (Loreto, Peru). a, rear view. b, front view. c, lateral view. d, basal view.

Figs. 211, 212. *Tropidebora simplex* sp. nov.

Fig. 211. RGM 456 340, holotype, Copal Urco (Loreto, Peru). a, rear view. b, front view. c, lateral view. d, basal view.
Fig, 212. INGEMMET TN08, paratype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.


208a.
208b.
208c.
208d.
209a.
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211a.
211b.
211c.
211d.
212a.
212b.
212c.
212d.

Wesselingh, 28-8-1996. RGM 456 616 (top fragment), Boca Momon (Loreto, Peru), exposure in north bank Rio Momon, *c.* 300 m upstream of confluence with Rio Nanay (3°41'S 73°15'W), level F357 (location in respect to DL unknown). Pebas Formation, MZ6 (Middle Miocene); leg. F.P. Wesselingh, 12-8-1996.

Extended diagnosis – *Calliostoma*-shaped shells ornamented with two keels; SA 65-85°; nucleus inclined; embryonic shell ornamented with honeycomb patterns on the tip, breaking apart into small, sharp pustules; boundary with protoconch-2 at 0.45 whorls marked by an axial line in a depression; a thin line at 1.5-1.6 whorls may represent the protoconch-teleoconch boundary; an upper keel at *c.* three quarters of the whorl height develops almost directly after and bounds a subsutural ramp; two ribs develop below; upper keel may become obsolete on later whorls; whorl profile straight-concave or slightly shouldered with a concave ramp below; lower keel at or just below the lower suture, but very prominent at the body whorl where it bounds the broad base; a spiral depression below the lower keel at the base of the body whorl accentuates it; growth lines prosocline to very steeply inclined prosocline; aperture lozenge-shaped; apertural plane strongly inclined; apertural margins reinforced; columellar lip strongly expanding to the right; basal and outer lip meet abaxially with a blunt angulation; basal apertural retraction ('siphon') broad; inner lip callus covering the umbilical area.

Dimensions – INGEMMET TN07: H 4.4; W 6.1; Hap 1.9; 5.3 whorls. RGM 456 339: H 4.3; W 4.1; Hap 2.3; 5.2 whorls.

Range – Pebas Formation, MZ6 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Remarks – Very wide specimens (e.g., Fig. 208) are restricted to MZ7 and MZ8. In the underlying MZ6 only smaller, higher-spired specimens occur (Fig. 209). However, these specimens occur with intermediate forms to the broad specimens in MZ7 (see, e.g., Nuttall, 1990, fig. 178a-d), indicating that the material must be considered a single species.

***Tropidebora* sp.**

Fig. 210.

Material studied – RGM 456 341, Barrio Florido (Loreto, Peru), exposure in west bank Rio Amazon, at former confluence with Rio Nanay (3°37'S 73°12'W), level F78 (6.4 m above DL). Pebas Formation, MZ5 or MZ6 (late Early - Middle Miocene); leg. F.P. Wesselingh, 10-1991.

Dimensions – RGM 456 341: H 4.4; W 3.6; Hap 2.1; 4.7 whorls.

Range – Pebas Formation, MZ5 or MZ6 (early Late to Middle Miocene), Peruvian Amazonia.

Remarks – Fragmentary material has been found of a form with a rounded shoulder that appears intermediate between *T. tertiana* and *T. simplex.* This form most closely resembles *T. tertiana*, but differs from it by the upper spiral (that is rounded in *Tropidebora* sp. and acute in *T. tertiana*), the subsutural ramp and suprasutural margin (that are subrounded in *Tropidebora* sp. and straight-concave in *T. tertiana*), and the height and size of the aperture (larger and higher in *Tropidebora* sp.). The studied sample is from a stratigraphic intermediate interval between those yielding *T. simplex* (below) and *T. tertiana* (above). The presence of only fragmentary material, and one damaged and poorly preserved specimen (with abraded shell surface, and a damaged inner and basal lip area), precludes formal naming and description for now.

***Tropidebora simplex* sp. nov.**
Figs. 211, 212.

Type material – RGM 456 340 (holotype), Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. INGEMMET TN08 (paratype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – The name refers to the 'simple' outline of this species compared to that of *T. tertiana*.

Diagnosis – High-spired (SA 58-62°), ovate-conical *Tropidebora* ornamented with two primary keels; a third keel may develop on the base of the body whorl; shell shouldered; whorl profile below shoulder straight to slightly convex.

Description – The nucleus is inclined. The protoconch is separated from the teleoconch by a very fine axial line at 1.0-1.3 whorls. The first 1.3 whorls are planispiral. After the protoconch-teleoconch boundary, an upper spiral develops swiftly at *c.* two thirds of the whorl height. It bounds a slightly concave to straight subsutural ramp above that gives the shell a distinctly shouldered appearance. The perimeter below the shoulder is straight to slightly convex. A second keel becomes visible at the lower suture at around the second whorl. Growth lines are numerous and fine. They are at first orthocline, becoming slightly prosocline on later whorls. A low third spiral rib may develop below the second keel at the body whorl. The aperture is subquadrate. The inner lip is thickened (barely so in the paratype), and attached through a parietal platform and callus to the remainder shell. The basal apertural margin is wide and contains a median retraction. The junction of the basal and outer lip is rounded. The umbilicus is covered.

Dimensions – RGM 456 340: H 3.6; W 3.4; Hap 2.3; 4.8 whorls. INGEMMET TN08: H 5.3; W 3.6; Hap 2.7; 5.6 whorls.

Remarks – This species is higher spired than *Tropidebora* sp. and *T. tertiana*. The upper keel is more pronounced in *T. simplex* than in *Tropidebora* sp.

***Tropidebora*? *conica* sp. nov.**
Figs. 17l, 213, 214.

Type material – RGM 456 370 (holotype), Mayoruna (Loreto, Peru), exposure in south bank Amazon River, *c.* 200 m south of confluence with Rio Nuevo Octubre (3°58'S 71°12'W), level F482 (3.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. INGEMMET TN15 (paratype), same locality. RGM 456 628 (paratype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7,3 m above DL). Pebas Formation, MZ 8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

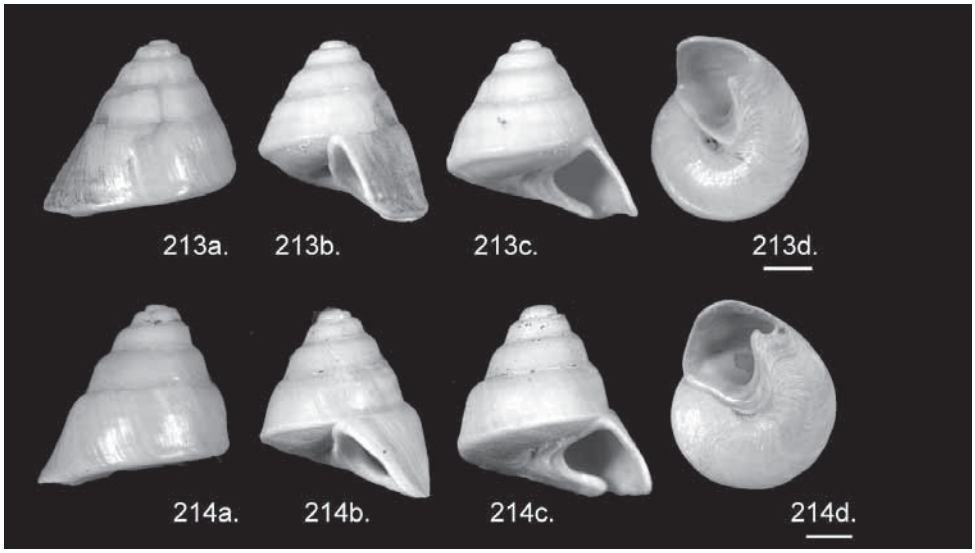
Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the conical outline (Latin, *conus* for cone).

Diagnosis – Conical shell with a flat base; 4-5 fine regularly spaced spiral ribs on first teleoconch whorl; SA 62-65°; basal apertural retraction located abaxially, deeply incised.

Description – The embryonic shell is flat to slightly inclined and delimited from the protoconch-2 at 0.3-0.4 whorls by a low axial depression; thin, sharp, triangular pustules broadly occupy the margins of the nucleus. The protoconch-2 is semiconvex and the suture is not very much impressed. A fine sharp axial lineament at 1.7 whorls marks the protoconch-teleoconch boundary. Five thin, regularly spaced spirals occur almost directly after, the upper one of which bounds a flat wide subsutural ramp. The lower four disappear within about one whorl; the upper can also disappear, but may develop as a rounded shoulder. A basal spiral rib may develop at the lower suture. Microscopical irregular spiral grooves occur on later teleoconch whorls. The lower spiral appears before the aperture as a low, rather robust, rounded rib that bounds the prominent and almost flat base of the body whorl. The aperture has reinforced margins. The columellar lip is deeply incised; the parietal and outer lips are straight. The basal apertural retraction is located abaxially, and is very deeply incised and pronounced by a promontory at the columellar side. The aperture is broadly adnate and covers the umbilicus partially or wholly. In the former case, a rimate and shallow umbilicus is present.

Dimensions – RGM 456 370: H 4.2; W 4.2; Hap 2.0; 5.2 whorls. INGEMMET TN15: H 4.5; W 4.2; Hap 1.9; 5.3 whorls.



Figs. 213, 214. *Tropidebora*? *conica* sp. nov.

Fig. 213. RGM 456 370, holotype, Mayoruna (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 214. INGEMMET TN15, paratype, same locality as Fig. 213. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Remarks – This species is more regularly conical than the other *Tropidebora* species; its basal apertural incision is more deeply retracted and it bears fine spiral ribs on the first teleoconch whorl, a feature unknown from the other species. The location of this species in *Tropidebora* is with some hesitation, because it can develop a rimmed umbilicus, a feature otherwise unknown for the genus. Furthermore, the fine spirals that are visible on the first teleoconch whorl and disappear soon after are another uncharacteristic feature for *Tropidebora*. The species resembles the extant Uruguayan *Potamolithus filiponei* Ihering, 1910 (see Nuttall, 1990, fig. 166a, b), in general outline. The latter appears to lack the very strong retraction at the abaxial side of the apertural basis.

Genus *Lithococcus* Pilsbry, 1911

Type species – *Lithoglyphus multicarinatus* Miller, 1879, Rio Cayapas (Esmeraldas, Ecuador).

Diagnosis – Globose, depressed-conical, thick, trochoiform shell with moderately rounded whorls in some species; ornament of spiral ribs, bearing knob-like nodes on later whorls in some species; aperture with wide base, slightly retracted in Pebasian species; parietal part of the aperture adnate and in most species expanding to the umbilical area; umbilicus closed or rimate.

Range – Recent, rivers draining into the Pacific Ocean (Ecuador, Colombia, Costa Rica); Miocene, Pebas Formation, western Amazonia (Peru, Colombia).

***Lithococcus carinatus* sp. nov.**
Figs. 215, 216.

Type material – RGM 456 342 (holotype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 1.4 km south of port (port at 3°30'S 73°03'W), level F371 (1.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 15-8-1996. INGEMMET TN09 (paratype), Santa Teresa (Loreto, Peru), exposure in west bank Amazon River, 200 m north of village at inlet of stream (3°29'S 73°00'W), level F318 (1.35 m above DL). Pebas Formation, MZ4 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 7-8-1996.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the ornament, particularly well developed on the holotype (Latin, *carina* for keel).

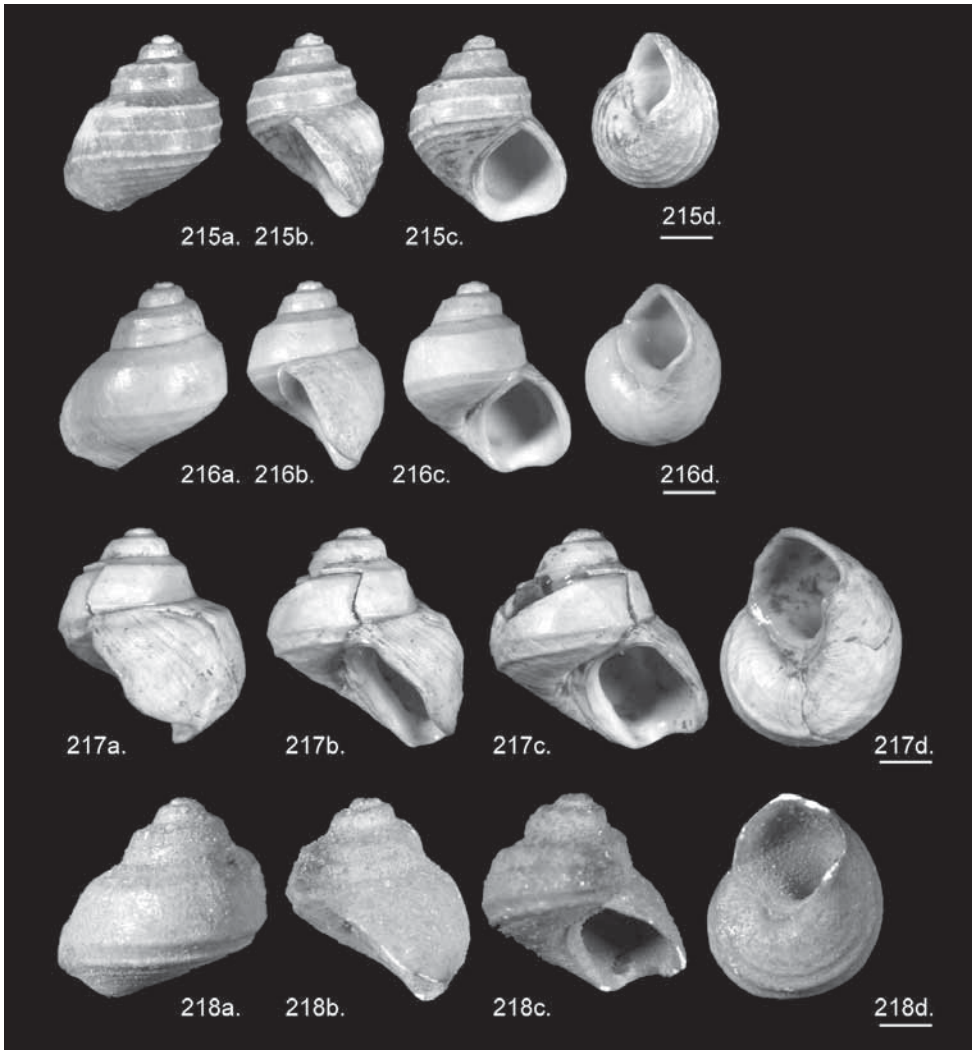
Diagnosis – High-spired and shouldered, rather small *Lithococcus* with a subquadrate aperture; SA 66-70°; shell with 2-3 primary spirals (and 5-6 thinner spirals on the base of the body whorl); basal apertural retraction broad and very shallow.

Description – The nucleus is inclined. The apical area is worn on the holotype. On the paratype an axial constriction at 0.7 whorls may represent the protoconch-teleoconch boundary. After this boundary, the onset of the upper spiral is gradual, but soon followed by the second lower spiral. The spirals are located at two thirds and one third of the whorl height, respectively. On the holotype both spirals remain robust, but the lower of the two disappears within one whorl after onset on the paratype. A third thick spiral is visible at the body whorl. This bounds the base that is ornamented with 5 to 6 additional thin, low and less distinct spirals. The interspaces between the thicker and basal spirals are typically about three times as wide as the spirals themselves. All spirals become less distinct shortly before reaching the outer lip. The aperture is subquadrate, tending to subovate. The apertural margins are reinforced. The basal apertural inflection is broad and shallow. An umbilicus is lacking.

Dimensions – RGM 456 342: H 3.5; W 2.9; Hap 2.3; 3.9 whorls. INGEMMET TN09: H 4.0; W 3.3; Hap 2.3; 4.1 whorls.

***Lithococcus amazonicus* sp. nov.**
Figs. 217, 218.

Type material – RGM 456 344 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F61 (18.2 m above DL).



Figs. 215, 216. *Lithococcus carinatus* sp. nov.

Fig. 215. RGM 456 342, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 216. INGEMMET TN09, paratype, Santa Teresa (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Figs. 217, 218. *Lithococcus amazonicus* sp. nov.

Fig. 217. RGM 456 344, holotype, Santa Sofia (Amazonas, Colombia). a, lateral view. b, oblique lateral view. c, front view. d, basal view.
Fig. 218. RGM 456 345, paratype, Los Chorros (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Pebas Formation, MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 345 (paratype), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River, 1.3 km east of confluence with Loreto Yacu (3°46'S 70°21'W), level F21 (0.4 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – The name refers to the Amazon River, along which localities are situated from which this species is described.

Diagnosis – Somewhat depressed-conical, shouldered *Lithococcus* with comparatively poorly developed spiral ribs; SA 70-72°.

Description – The nucleus is slightly inclined. The first 1.2 whorls are planispiral. At 0.7 whorls a very thin, barely distinguishable axial line may represent the protoconch-teleoconch boundary. The onset of teleoconch ornament is not visible in the studied material due to wear. An upper spiral at two thirds of the whorl height develops at 1.5 whorls. This spiral bounds a well-defined subsutural platform that gives the shell a shouldered outline. Slightly later, a much weaker second spiral develops at one third of the whorl height. On the paratype, a third spiral is present in between at about half the height of the whorl. The perimeter below the upper spiral is straight. Growth lines are prosocline. At the last half whorl, barely visible, low axial undulations can be developed, making the shoulder also slightly wavy in appearance. Another strong spiral appears at the body whorl, delimiting its base; another three spirals are seen there. All spiral ribs fade towards the outer lip. Growth lines on the base of the body whorl are broadly sinuate. The aperture is subquadrate and adnate. The interior of the inner and outer lip run almost parallel. A small parietal platform is present between the parietal lip and the preceding whorl. The basal apertural deflection is broad, but deeper than in *L. carinatus*.

Dimensions – RGM 456 344: H 4.4; W 4.2; Hap 2.9; 4.0 whorls. RGM 456 345: H 4.2; W 3.9; Hap 3.1; *c.* 4.1 whorls.

Remarks – This species is larger and wider than *L. carinatus*. The deflection at the base of the aperture is deeper.

Genus *Littoridina* Souleyet, 1852

Type species – *Littoridina gaudichaudi* Souleyet, 1852, Recent, Rio Guayas, Ecuador.

Diagnosis – Ovate or elongate conical to conical shell, smooth or with very weakly developed spiral striae; protoconch-teleoconch boundary poorly developed or not observable; growth lines prosocline; narrowly umbilicate to imperforate; columella in some species very slightly twisted; base of aperture straight or with a broad and shallow retraction.

Range – Miocene, Pebas Formation, western Amazonia (Peru, Colombia, Brazil); extant in rivers, streams, estuaries (brackish marshes) along the Pacific coast from Ecuador to Mexico, rivers in the coastal zone of the Gulf, northern Mexico-Texas.

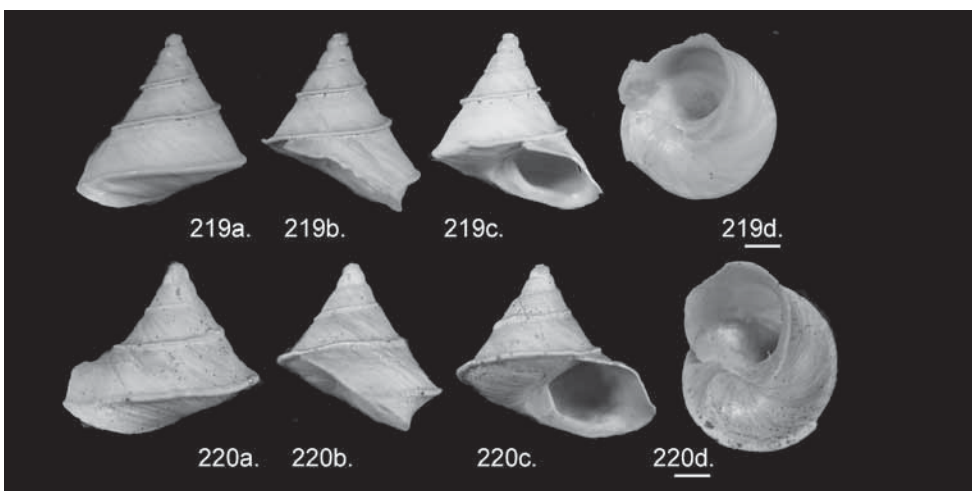
***Littoridina pebasana* (Conrad, 1874a)**
Figs. 16e, 17m, 219, 220.

1874a *Cyclocheila pebasana* Conrad, p. 82, pl. 1, fig. 17.

Material studied – RGM 456 371, Beiruth (Loreto, Peru), exposure in south bank Amazon River, below village (3°53'S 71°28'W), level F492 (3.9 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 613, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. INGEMMET TN16, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 613, same locality.

Range – Pebas Formation, MZ6 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Extended diagnosis – *Calliostoma*-shaped *Littoridina* with a distinct, well defined, spiral rib at the lower suture; base of shell wide; SA 61-73°; embryonic shell tilted; nucleus



Figs. 219, 220. *Littoridina pebasana* (Conrad, 1874a).

Fig. 219. RGM 456 613, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 220. RGM 456 371, Beiruth (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

has a honeycomb ornament fringe that gives away to thin, sharp pustules that cover larger parts; a shallow axial depression at 0.3 whorls marks the boundary with the smooth and convex protoconch-2; protoconch-teleoconch boundary possibly as a thin axial line at 1.5 whorls; a suprasutural keel appears suddenly at the supposed boundary; perimeter becoming straight at that point and from there on progressively more inclined with respect to the columellar axis; growth lines numerous, fine; basal keel well defined, slightly imbricate, clearly delimiting the very wide, almost flat shell-base; apertural plane is strongly inclined; parietal margin located below the upper part of the outer lip; columellar and outer margins almost run parallel; base of aperture flat and, when viewed from below, forming a broad and very shallow sinus; outer lip can be markedly expanded (flaring); shell imperforate.

Dimensions – RGM 456 371 H 4.5; W 4.9; Hap 3.0; 5.2 whorls. INGEMMET TN16: H 4.6; W 4.7; Hap 2.3; 5.4 whorls.

Remarks – This species can be distinguished from the conical *Tropidebora tertiana* by the absence of a basal apertural retraction. The resemblance is a nice example of convergence.

***Littoridina crassa* (Etheridge, 1879)**

Figs. 17n, 221.

1879 *Assiminea crassa* Etheridge, p. 86.
1879 *Hydrobia dubia* Etheridge, p. 86, pl. 7, fig. 11.
1980 *Littoridina crassa* (Etheridge); Kadolsky, p. 371, figs. 13, 14.
1990 *Littoridina*? *crassa* (Etheridge); Nuttall, p. 202, figs. 121-123.

Material studied – Lectotypes and paralectotypes (see Nuttall, 1990, p. 202). INGEMMET TN17, Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996. RGM 456 372, Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Extended diagnosis – Ovate conical, smooth *Littoridina*; SA 52-58°; nucleus inclined with very low mammillae in the very sutural margins. A thin lineament seen on specimen at 0.3 whorls possibly marks the boundary between the embryonic shell and the protoconch-2. A protoconch-teleoconch boundary has not been observed. The shell is smooth apart for numerous, fine, slightly prosocline, faintly sigmoid growth lines; whorl profile straight to very slightly convex, with a rounded and poorly expressed shoulder; sutures incised; aperture large; outer and basal lip thin, invariably damaged; columellar lip with well-developed callus and slight median chink; judging from growth lines, the apertural base must have been a broad and very shallowly retracted; shell imperforate.

Dimensions – INGEMMET TN17: H 6.5; W 4.2; Hap 3.4; 5.4 whorls. RGM 456 372: H 5.3; W 3.4; Hap 2.7; 5.0 whorls.

Range – Pebas Formation, MZ7 - MZ11 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

***Littoridina elongata* sp. nov.**
Figs. 222, 223.

Type material – INGEMMET TN18 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F489 (9.4 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 373 (paratype), same locality.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the elongate appearance (Latin, *elongatus* for prolonged).

Diagnosis – High-spired smooth *Littoridina* (SA 45°) with a flat whorl profile apart from the suture that is impressed; upper part of the outer lip slightly retracted.

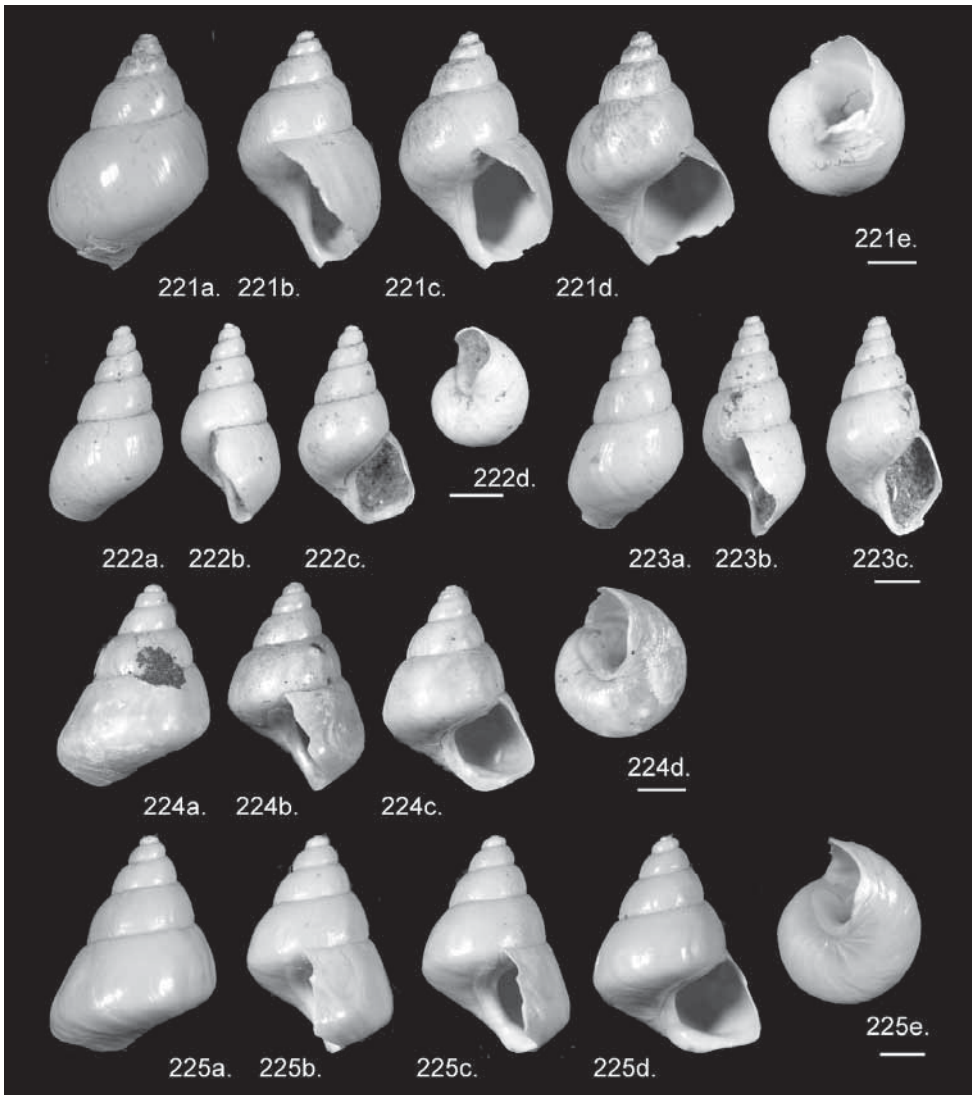
Description – The nucleus is inclined. On the holotype a well-defined constriction at 0.6 whorls may mark the boundary between the embryonic shell and the protoconch-2 or teleoconch. The shell is smooth, apart for the numerous, very fine, slightly prosocline growth lines. These can become very slightly sigmoid on later teleoconch whorls. On the paratype, some microscopic, irregular and discontinuous spiral grooves are seen. The whorl profile is mostly flat, apart for the most ab- and adapical parts that dip into the suture. The columellar, basal and outer lip are located at about right angles. The basal and outer lips are thin, and damaged in most material. The outer and columellar lips are almost parallel. A well-developed callus marks the parietal and columellar lip. The columellar lip in the holotype has a barely observable median chink; in the paratype, sediment covers the area directly behind the aperture, precluding its investigation. The basal lip describes a broad retraction when viewed from below. When viewed from the side, the outer lip is slightly prosocline and somewhat retracted at the upper and basal ends. The most forward part of the outer lip is located at *c.* three-quarters of the apertural height. An umbilicus is lacking.

Dimensions – INGEMMET TN18: H 3.8; W 2.5; Hap 1.8; 5.2 whorls. RGM 456 373: H 4.9; W >2.4; Hap 2.3; 5.7 whorls.

Remarks – The shell resembles that of *L. crassa* with which it can co-occur. It is distinctly slimmer and has a slight retraction at the top of the outer lip.

***Littoridina conica* sp. nov.**
Figs. 15n, 224, 225.

Type material – INGEMMET TN19 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 374 (paratype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, *c.* 300 m east of wood mill and *c.* 1.5 km east of Santo Tomas (3°52'S 71°23'W), level F498 (5.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.



Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the conical shape (Latin, *conus* for cone).

Diagnosis – Distinctly conical, smooth-shelled *Littoridina* with a subquadrangular aperture; SA 52-53°; inner side basal aperture dipping smoothly, but straight towards the junction with the outer lip; growth lines slightly sigmoid.

Description – The nucleus is inclined. A very low and broad axial depression may mark the otherwise poorly defined boundary between the embryonic shell and the protoconch-2. No apparent protoconch-teleoconch boundary was observed. The shell is smooth, apart for the numerous orthocline to slightly prosocline sigmoid growth lines. The whorls are only very slightly convex and also marginally shouldered. Superficially, the whorl profile seems to be straight sided. On early teleoconch whorls the suture is slightly impressed, on later whorls it becomes adnate. The base of the body whorl is separated from the remainder of the shell by a regularly rounded angulation. The parietal, columellar and basal lips are callous. The callus is strongest at the junction of the columellar and basal lip. From there on the inner side of the basal lip continues in a straight line towards the junction with the outer lip. The exterior of the basal lip is almost parallel with the inner side of the parietal lip; the columellar and outer lips are also almost parallel, giving the aperture its nearly quadrate outline. No chink is present on the columella. The outer lip is somewhat damaged in all specimens, but from the growth lines it is shown that it is furthest produced at *c.* one third of the height of the aperture. A distinct, broad retraction is developed above. The apertural base is, when viewed from below, broadly retracted. An umbilicus is lacking.

Dimensions – INGEMMET TN19: H 4.6; W 3.5; Hap 2.2; 5.2 whorls. RGM 456 374: H 4.8; W 3.5; Hap 2.2; 5.2 whorls.

◀ Fig. 221. *Littoridina crassa* (Etheridge, 1879). RGM 456 372, Santo Tomas Amazon (Loreto, Peru). a, rear view. b, lateral view. c, oblique lateral view. d, front view. e, basal view. Scale bar represents 2 mm.

Figs. 222, 223. *Littoridina elongata* sp. nov.

Fig. 222. INGEMMET TN18, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 223. RGM 456 373, paratype, same locality as Fig. 222. a, rear view. b, lateral view. c, front view.

Figs. 224, 225. *Littoridina conica* sp. nov.

Fig. 224. INGEMMET TN19, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 225. RGM 456 374, paratype, same locality as Fig. 224. a, rear view. b, lateral view. c, oblique lateral view. d, front view. e, basal view.

Scale bars represent 1 mm except where stated otherwise.

Remarks – *Littoridina conica* is more conical than the other *Littoridina* species. Its subquadrangular apertural outline and sigmoid growth lines are characters that are not (well) expressed in the other species.

Genus *Cochliopina* Morrison, 1946

Type species – *Cochliopa riograndensis* Pilsbry & Ferriss, 1906, extant, Texas-northern Mexico.

Diagnosis for Pebasian Cochliopina? – Small, smooth helicoid to planispiral shell; growth lines prosocline; parietal adnate; umbilicus deep and prominent.

Range – Miocene?, Pebas Formation, western Amazonia (Peru, Colombia, Brazil); extant, freshwater habitats in Central America, and along the Pacific coast of Colombia and Ecuador.

Remarks – Considerations on the attribution to *Cochliopina*? are given in the discussion under the family Cochliopidae above. Nuttall (1990, p. 222-226) discussed at great length the attribution of the Pebasian *Cochliopina*? *hauxwelli* and *C.*? *degrevei* (= *C.*? *bourguyi*) to the Vitrinellidae. Nuttall did not consider a close relationship of these two species with *Nanivitrea* that he also treated in the same volume (describing his *Nanivitrea colombiana*). Pebasian *C.*? *hauxwelli* and *C.*? *bourguyi* have very similar shells as some Neotropical marine vitrinellids, but the general architecture of the protoconch of the Pebasian specimens is perfectly in line with that of other Pebasian cochliopids. The description of a new species below with intermediate morphological characteristics between the two species and *C.*? *colombiana* indicate that they should be united under one genus.

Cochliopina? colombiana (Nuttall, 1990)
Fig. 226.

1990 *Nanivitrea colombiana* Nuttall, p. 213, figs. 158-163.

Material studied – RGM 456 521, La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 9-11'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. UNC nn., same locality.

Extended diagnosis – Shell depressed helicoid, slightly wider than high; diameter nucleus 90-110 µm; apex flat, very slightly sunken; top of first 1.5 whorls almost coiled in plane, later whorls rapidly descending, with a well-expressed rounded shoulder; largest width at base of whorl; base of body whorl broadly rounded; suture impressed; growth lines prosocline; shell smooth; aperture semicircular with blunt angulation on upper side; margins slightly thickened; parietal adnate; umbilicus prominent.

Dimensions – RGM 456 432: H 2.6; W 2.8; Hap 1.45; 3.7 whorls. UNC nn.: H 2.3; W 2.4; Hap 1.7; 3.7 whorls.

Range – Pebas Formation, MZ2 (late Early - early Middle Miocene), Peruvian and Colombian Amazonia.

Cochliopina? *bourguyi* (Roxo, 1924)

Figs. 16f, 227.

1924 *Planorbis bourguyi* Roxo, p. 50, fig. E.
1990 *Planorbis* sp. de Greve, p. 107, pl. 4, figs. 29, 30.
1990 *Vitrinella (Vitrinellops) degrevei* Nuttall, p. 226, fig. 198a-d.
2002 *Nanivitrea degrevei* (Nuttall); Wesselingh *et al*., fig. 3g.

Material studied – RGM 456 522, Zaragoza (Amazonas, Colombia), exposure in north bank Amazon River, 300 m east of landing stage (3°52'S 70°11'W), level F34 (0.5 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 610, Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F703 (0.6 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.

Extended diagnosis – Relatively large, smooth, disc-like *Cochliopina*? with rounded margins; nucleus slightly inclined, ornamented with a honeycomb pattern covering about half the embryonic shell; axial lineament and constriction at 0.4 whorls mark the boundary with protoconch-2; protoconch-teleoconch boundary uncertain, possibly at a very fine lineament at 1.8 whorls; teleoconch whorls markedly adnate when viewed from above; suture very shallow; growth lines very fine, prosocline; aperture subovate to broadly inverted comma-shaped; parietal lip adnate; parietal callus thin, not expanded; columellar and outer lip margins marginally thickened; columellar lip broadly rounded; basal lip relatively flat; umbilicus wide and deep.

Dimensions – RGM 456 432: H 2.6; W 2.8; Hap 1.45; 3.7 whorls.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Peruvian, Brazilian and Colombian Amazonia.

Remarks – The depressed disc-shape distinguishes *C.*? *bourguyi* from *C.*? *colombiana*. The overall outline resembles marine vitrinellid species (Nuttall, 1990), but these are unknown from fresh water settings.

Cochliopina? hauxwelli (Nuttall, 1990)

Figs. 15e, 228.

1990 *Vitrinella (Vitrinellops) hauxwelli* Nuttall, p. 226, figs. 195-197.
? 1990 *Vitrinella (Vitrinellops)* sp. Nuttall, p. 228, fig. 199a-d.
2002 *Nanivitrea hauxwelli* (Nuttall); Wesselingh *et al*., fig. 3b.

Material studied – RGM 456 523, Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S, 23°47'W), level F871 (2.5

m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996.

Extended diagnosis – Small, flat to slightly elevated *Cochliopina*? with adjoining rounded whorls separated by deep suture; nucleus flat (diameter 40 µm); thin axial re-

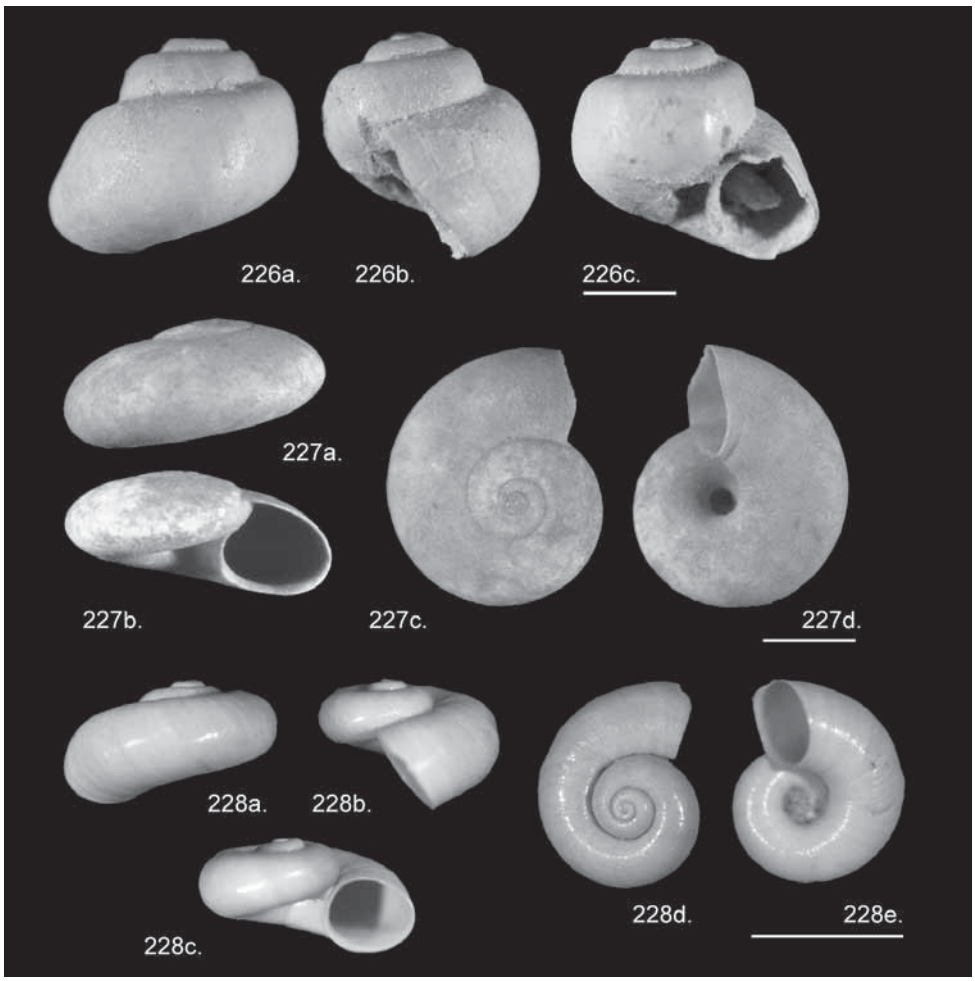


Fig. 226. *Cochliopina*? *colombiana* (Nuttall, 1990). RGM 456 521, La Tagua (Putumayo, Colombia). a, rear view. b, lateral view. c, front view.

Fig. 227. *Cochliopina*? *bourguyi* (Roxo, 1924). RGM 456 522, Zaragoza (Amazonas, Colombia). a, rear view. b, front view. c, apical view. d, basal view.

Fig. 228. *Cochliopina*? *hauxwelli* (Nuttall, 1990). RGM 456 523, Copal Urco (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Scale bars represent 1 mm.

striction at 0.5 whorls terminating embryonic shell; cross-section of the whorls as well as aperture circular; growth lines fine, numerous, prosocline; aperture narrowly attached at the parietal wall or detached; umbilicus wide and deep.

Dimensions – RGM 456 523: H 0.8; W 1.5; Hap 0.6; 3.2 whorls.

Range – Pebas Formation, MZ4 - MZ11 (late Early - early Late Miocene), Peruvian and Colombian Amazonia.

Remarks – The flat nature of *C.*? *hauxwelli*, as well as the deep suture and small size make it very different from *C.*? *bourguyi* and *C.*? *colombiana*.

***Cochliopina? convexa* sp. nov.**
Figs. 229, 230.

Type material – INGEMMET TN67 (holotype), Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. RGM 456 524 (paratype), same locality.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the convex whorl profile (Latin, *convexus* for arched outward).

Diagnosis – Helicoid *Cochliopina*? with rather pointed apex and relatively small nucleus; whorls rounded; suture deep; aperture circular; apertural margins thin.

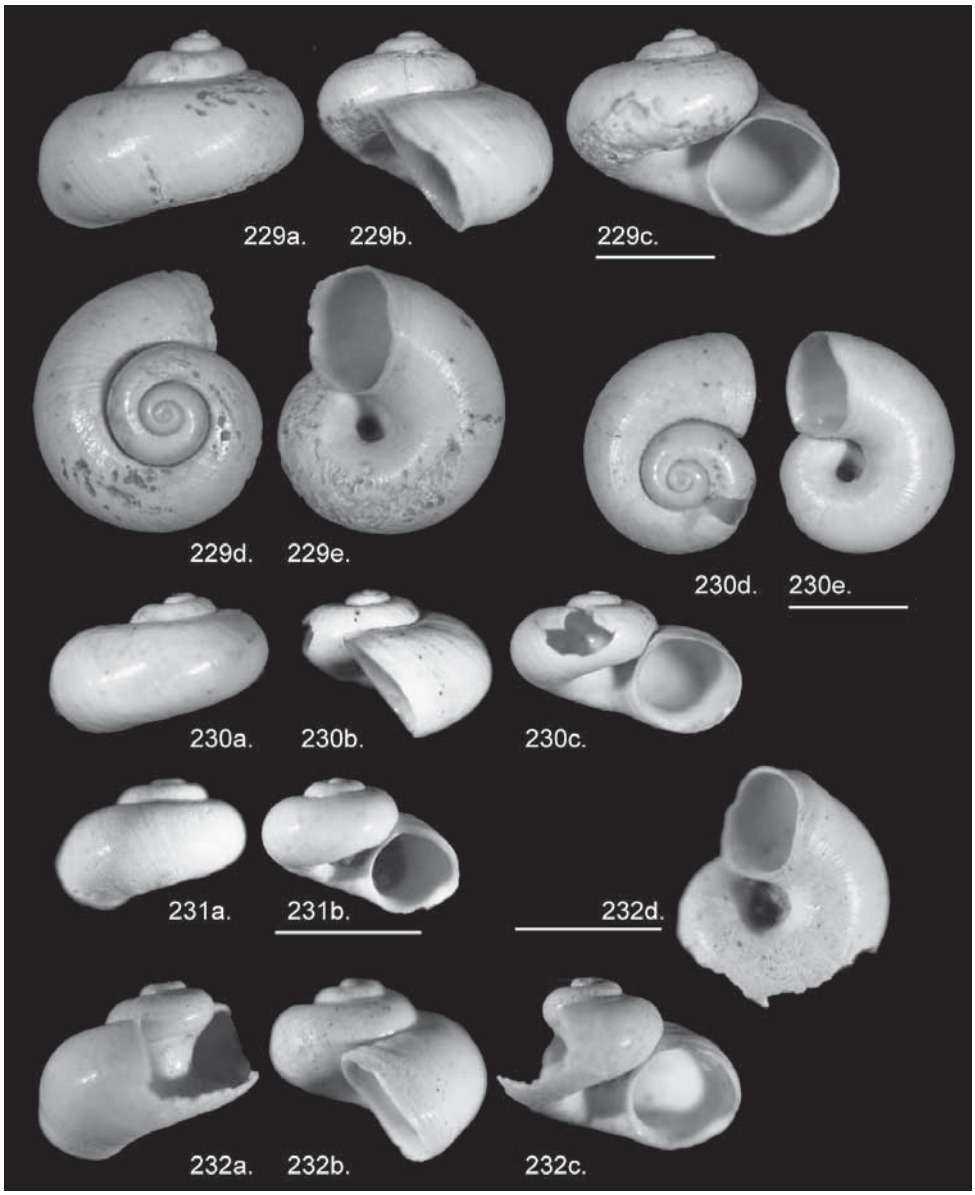
Description – The embryonic shell (diameter 50 µm) is flat and separated from the remainder of the shell at 0.5-0.6 whorls by a very fine axial constriction. The whorls are rounded-subrounded and the suture is deep. The widest point of the periphery is at or very slightly above the lower suture. The base of the body whorl is broadly rounded, and grades into the wide and very deep umbilicus. The aperture is circular. Over a short distance the parietal wall is adnate, apart from the topmost part. The apertural margins are thin or only very slightly reinforced. The apertural plane is inclined.

Dimensions – INGEMMET TN67: H 1.75; W 2.3; Hap 1.0; 4.1 whorls. RGM 456 524: H 1.35; W 1.95; Hap 0.8; 3.5 whorls.

Remarks – *Cochliopina*? *convexa* lacks the shouldering characteristic of *C.*? *colombiana*, and has a higher spire than *C.*? *bourguyi* and *C.*? *hauxwelli*. Also, the whorl diameter of *C.*? *hauxwelli* increases less during growth.

***Cochliopina?* sp.**
Figs. 231, 232.

Material studied – RGM 456 525 and RGM 456 526, Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.



Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Description – Helicoid *Cochliopina*? with a large nucleus (diameter 90-100 µ). The whorl profile is convex and the suture deep. The aperture circular; the margins are slightly reinforced.

Dimensions – RGM 456 525: H 1.35; W >1.7; Hap 0.95; 2.6 whorls. RGM 456 526: H 1.1; W 1.4; Hap 0.75; 2.8 whorls.

Remarks – The general outline of *Cochliopina*? sp. is almost identical to that of *C.*? *convexa*. However, consistent differences exist in the relative height of the aperture (Hap/H ratio slightly below 0.6 in *C.*? *convexa* and around 0.7 in *Cochliopina*? sp.), the width of the nucleus (50 µm vs 90-100 µm), the number of whorls (comparatively lower in *Cochliopina*? sp.), the lack of a visible embryonic shell and the slightly thicker apertural margins in the latter.

Superfamily Cerithioidea Fleming, 1822

Remarks – Supraspecific classification of South American freshwater cerithioideans is far from settled. Nuttall (1990, p. 228) provided a thoughtful discussion on the genus and family assignment of the various fossil and Recent species. However, subsequent studies have shown that the definition of genera and the attribution of them to families are open to further scrutiny (Wesselingh, 1996; Wesselingh *et al*., 1996). Here, two families are used to subdivide the genera and species, that is, the Thiaridae (characterised by a basal columellar truncation) and the Pachychilidae (lacking such a truncation). Only two fossil genera are confirmed for the Thiaridae, *Hemisinus* and *Aylacostoma*. *Hemisinus (Longiverena) eucosmius* (Pilsbry & Olsson, 1935), assigned by Nuttall (1990) to the genus *Longiverena*, is here attributed to the pachychilid *Charadreon*. *Longiverena colombiana* Nuttall, 1990, is transferred to *Sheppardiconcha* that also is transferred to the Pachychilidae. The status of *Sheppardiconcha* is also open to further scrutiny given the presence of closely resembling extant species assigned to *Pachychilus* (Central America; Fischer & Crosse, 1902) and a specimen of *Doryssa transversa* from Guyana (Haltenorth & Jaekel, 1940, pl. 6, fig. 15a).

◀ Figs. 229, 230. *Cochliopina*? *convexa* sp. nov.

Fig. 229. INGEMMET TN67, holotype, Copal Urco (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.
Fig. 230. RGM 456 524, paratype, same locality as Fig. 229. a, rear view. b, lateral view. c, front view. d, apical view. e, basal view.

Figs. 231, 232. *Cochliopina*? sp.

Fig. 231. RGM 456 526, Barradero de Omagua (Loreto, Peru). a, rear view. b, front view.
Fig. 232. RGM 456 525, same locality as Fig. 231. a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 1 mm.

Family Thiaridae Gill, 1871
Genus *Hemisinus* Swainson, 1840

Type species – *Melania lineolata* Wood, 1828, Recent, Jamaica.

Diagnosis – Intermediate sized (H 20-30), spirally ornamented, spindle-shaped shells with a truncate columellar base, separating the basal lip from the inner lip; ornament usually consisting of wide flat spiral ribs that are separated by grooves rather than interspaces; body whorl often bulbous, but rarely shouldered.

Range – Miocene, northwest South America; Neogene-Recent, Caribbean; extant, eastern South America.

Hemisinus kochi (Bernardi, 1856)
Figs. 233, 234.

1856 *Melania kochi* Bernardi, p. 83, pl. 3, fig. 6.
1871 *Hemisinus sulcatus* Conrad, p. 194, pl. 10, fig. 2.
1938 *Semisinus sulcatus* de Greve, p. 99, text-fig. 23, pl. 4. figs. 17-19, 21-25.
1990 *Hemisinus kochi* (Bernardi); Nuttall, p. 240, figs. 227-242.
1990 *Hemisinus brasiliensis* (Moricand); Nuttall, p. 244 (*pars*), figs. 243, 247 (*non* figs. 244-246).

Material studied – RGM 456 358, Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 359, Mishana (Loreto, Peru), exposure in south bank Rio Nanay, 100 m west of landing stage (3°52'S 73°29'W), level F72 (at DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 10-1991.

Extended diagnosis – Large (H 30), spindle-shaped, spirally grooved cerithioid with a truncate columellar base; first three teleoconch whorls dominated by opisthocline sigmoid growth lines and numerous irregular, very fine spiral striae; spiral grooves develop after the third whorl, bounding flat and low ribs; 7-10 ribs on early teleoconch whorls, *c.* 20 on body whorl; spirals may be absent on the central part of the whorls; axial sigmoid colourations or broadened growth line accumulations may be present; body whorl rather bulbous, subadult specimens high-spired; apertural margins not thickened; inner lip slightly expanded over the columellar region; basal apertural margin and the base of the columella are truncated by a short siphonal like fasciole.

Dimensions – RGM 456 358: H 21.5; W 9.0; Hap 10.8; >7.6 whorls. RGM 456 359: H 30.1; W 13.0; Hap 15.0; >7.3 whorls.

Range – Pebas Formation, MZ8 (late Middle - early Late Miocene), Peruvian Amazonia; extant, rivers in East Brazil.

Remarks – See Nuttall (1990, p. 244) for an extended synonymy. Subadult specimens of *Hemisinus kochi* lack the bulbous body whorl and resemble the straight-sided

H. brasiliensis (Moricand, 1838; Nuttall, 1990, p. 244). Ontogenetic series of this species could be arranged in the newly collected material facilitating the attribution of juvenile straight-sided specimens to *H. kochi* (see, e.g., Fig. 233). The occurrence of this species is remarkably limited in time. It occurs in fluviolacustrine assemblages of MZ8 only, and is not found in older or younger parts of the Pebas Formation.

Genus *Aylacostoma* Spix *in* Spix & von Wagner, 1827

Type species – *Aylacostoma glabrum* Spix *in* Spix & von Wagner, 1827, Recent, eastern Brazil.

Diagnosis – Spirally ribbed gastropod with a strong ornamentation; truncations at the base of the columella, separating the basal lip from the inner lip; later teleoconch whorls usually shouldered; embryonic shells bulbous.

Range – Oligocene-Miocene, northwestern South America; extant, eastern South America.

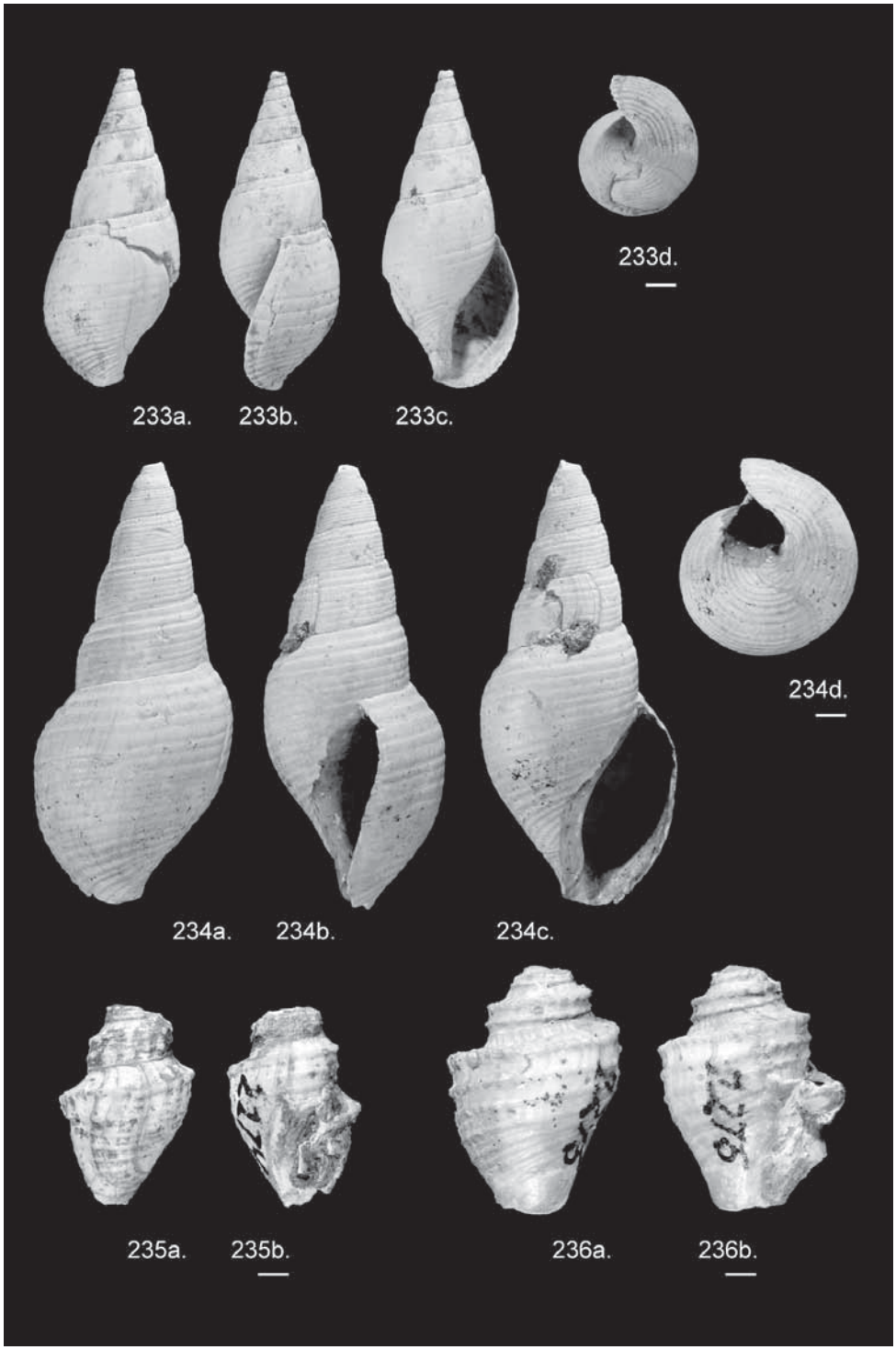
Remarks – Species referred to by Nuttall as *Verena* (Adams & Adams, 1854) are included here in *Aylacostoma*. The genus differs from *Hemisinus* by the shouldered, non-spindle shaped outline.

Aylacostoma ava (Pilsbry & Olsson, 1935)
Figs. 235, 236.

1935 *Hemisinus (Verena) avus* Pilsbry & Olsson, p. 15, pl. 3, figs. 6, 7.
1935 *Hemisinus (Verena) laevicarina* Pilsbry & Olsson, p. 15, pl. 3, figs. 10-12.
1990 *Verena crenocarina ava* (Pilsbry & Olsson); Nuttall, p. 255, figs. 273-276.

Material studied – ANSP n.n., locality unknown, but judging from the collections, preservation and co-occurring molluscs probably from the La Cira-Oponcitos area (Santander dept., Colombia). 'La Cira Formation', zone MZ1 (Early Miocene); leg. unknown, presumably A.A. Olsson, early 20th century. RGM 550 006. San Juan RioSeco (Cundinamarca, Colombia), exposure in bed of RioSeco, 1 km upstream of bridge, *c.* 1.5 km northeast of San Juan RioSeco. Santa Teresa Formation ('La Cira Beds'), MZ1 (Early Miocene); leg. F.P. Wesselingh, 28-11-1996.

Extended diagnosis – Intermediate (H *c.* 20), robust, shouldered shell; all studied material damaged and lacking apex; two spiral ribs on early teleoconch whorls, the upper of which can possess robust knobs on regularly spaced intersections with the slightly opisthocline sigmoid growth lines; up to eleven spirals on body whorl; upper spirals usually bear well-developed knobs, which disappear towards the base of the whorl; upper spiral bounds a prominent, straight to concave subsutural ramp; aperture severely damaged in all studied specimens. In a specimen illlustrated by Pilsbry & Olsson (1935, pl. 3, fig. 12), the basal columellar retraction separating the basal and inner lip is well visible.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Dimensions – ANSP n.n. (Fig. 235a, b): H >16.9; W *c.* 14.4. ANSP n.n. (Fig. 236a, b): H >13.0.

Range – 'La Cira Beds' and 'Santa Teresa Formation' (Early Miocene), MZ1; Magdalena Basin and Llanos Basin (Colombia).

Remarks – The La Cira material has undergone various states of diagenesis and tectonic deformation. Altered specimens tend to loose the knobs on the spiral ribs before loosing the ribs themselves, producing shells with an almost perfect spiral ornament. Nuttall (1990, p. 253) noted the resemblance of this species to the extant *Aylacostoma crenocarina* (Moricand, 1841). He classified *A. ava* as a subspecies of *A. crenocarina* (that he assigned to the genus *Verena* Adams & Adams, 1854). Although both species are superficially similar in outline, there are several differences. *Aylacostoma crenocarina* has low and wide opisthocline ribs that cover almost the entire whorl. These do produce undulations, which are well seen in the keel that borders the subsutural ramp, but also on other ribs. Such broad axial ribs are lacking on shells of *A. ava*. The knobs are pronounced instead. Further, spiral ribs on the subsutural ramp, as seen in *A. crenocarina*, do not occur on *A. ava*. Finally, the number of spiral ribs on the body whorl of *A. crenocarina* (*c.* 15) exceeds that of *A. ava* (*c.* 10-11). Given the lack of similar forms between the Early Miocene *A. ava* from northwestern South America and the extant *A. crenocarina* from eastern Brazil, these taxa should be treated as independent species. In material without locality data in the collections of the ANSP, presumably from the La Cira-Infantas region, fragments and damaged specimens of a variety of *Aylacostoma* might represent additional species for the La Cira Formation; however, the lack of locality data precludes a worthwhile taxonomical treatment.

Aylacostoma lataguensis (Nuttall, 1990)

Fig. 239.

1990 *Verena lataguensis* Nuttall, p. 258, figs. 284, 285.

◀ Figs. 233, 234. *Hemisinus kochi* (Bernardi, 1856).

Fig. 233. RGM 456 358, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 234. RGM 456 359, Mishana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.

Figs. 235, 236. *Aylacostoma ava* (Pilsbry & Olsson, 1935).

Fig. 235. ANSP n.n., locality unknown, but judging from the collections, preservation and co-occurring molluscs probably from the La Cira-Oponcitos area (Santander dept., Colombia). 'La Cira Formation'. Photograph by A. 't. Hooft (Leiden, the Netherlands). a, rear view. b, front view.
Fig. 236. ANSP n.n., same locality as Fig. 235. Photograph by A. 't. Hooft (Leiden, the Netherlands). a, rear view. b, front view.

Scale bars represent 2 mm.

Material studied – BMNH 19920 (holotype), La Tagua (Caqueta, Colombia), locality CAE 33/480-560 cm, 'La Tagua Beds' (now assigned to the Pebas Formation), MZ2 (late Early Miocene); leg. M.J. Eden, 1978 (Nuttall, 1990, p. 258). BMNH 19921-2 and BMNH 19923 (paratypes), same locality. RGM 456 360 (one damaged specimen, three fragments), La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 9-11'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. RGM 456 361 (one damaged specimen and a fragment), same locality, level LT14.

Extended diagnosis – Small (H presumably < 15), thin-shelled, rather bulbous *Aylacostoma*; apical region is lacking in all material studied; shell ornamented with *c.* 6-8 thin spirals on early teleoconch whorls and 18-21 spirals on the body whorl; upper spiral shortly below the upper suture, bounding a very thin and poorly pronounced subsutural ramp (pronounced in other species of *Aylacostoma*); apertural margins not reinforced; base of columella truncate.

Dimensions – BMNH 19920: H 9.0; W 5.3; Hap 4.6. BMNH 19921: H 9.1; W 6.0; Hap 5.8 (Nuttall, 1990, p. 258).

Range – Pebas Formation, MZ2 (late Early - early Middle Miocene), Colombian Amazonia.

Aylacostoma browni (Etheridge, 1879)

Figs. 237, 238.

1879 *Melanopsis? browni* Etheridge, p. 87, pl. 7, fig. 4.
1924 *Melanopsis? browni* Etheridge, Roxo, p. 46.
1981 *Aylacostoma (Aylacostoma) browni* (Etheridge); Costa, p. 644, pl. 1, figs. 11, 12.
1982 *Aylacostoma browni* (Etheridge); Bristow & Parodiz, p. 48, fig. 22.
? 1982 *Aylacostoma* sp. Bristow & Parodiz, p. 49.
1990 *Verena browni* (Etheridge); Nuttall, p. 256, figs. 278-282.
1990 *Verena* aff. *browni* (Etheridge); Nuttall, p. 258, fig. 283.
1990 *Aylacostoma* sp. Nuttall, p. 261, figs. 292, 293.

Material studied – RGM 456 362, Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 350 m north of southern tip of village (4°15'S 73°23'W), level F715 (1.6 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996. RGM 456 363, Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996.

Extended diagnosis – Spirally ornamented, tightly shouldered cerithoid with sigmoid growth lines and a retracted apertural base; no apical whorls on adult specimens, but bulbous embryonic shells are often found in samples containing adults; first four whorls dominated by opisthocline growth lines and fine spiral striae; after the fourth whorl strong spirals gradually develop; upper spiral or the second spiral below the suture becomes somewhat pronounced, bounding a small, concave subsutural

ramp (in the latter case, the upper spiral is located on the sutural ramp); uncommonly, ribs broaden and the interspaces become groove-like; rarely median ribs disappear; aperture spindle-shaped; outer lip slightly thickened, inner lip thickened; in the inner side of outer lip a thickened zone with spiral grooves occurs just behind apertural margin; columellar lip straight to sigmoid; base of aperture distinctly truncate.

Dimensions – RGM 456 362: H 20.5; W 10.9; Hap 12.3; >6.7 whorls. RGM 456 363: H 18.1; W 8.0; Hap 9.1; >7.3 whorls.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Peruvian, Brazilian and Colombian Amazonia; Mangan Formation (Late Miocene), Cuenca Basin, Ecuador.

Remarks – In the Pebas Formation, this species shows considerable variation in the H/W ratio, and the strength and number of the spiral ribs. Cerithioids (cited in the synonymy above) from the Late Miocene Mangan Formation (Cuenca Basin, Ecuador) fall within the range of morphological variation of *A. browni*, although the material is poorly preserved and has apparently suffered from compaction.

Family Pachychilidae Fischer & Crosse, 1892
Genus *Charadreon* Woodring, 1973

Type species – *Charadreon leptus* Woodring, 1973, Eocene, Canal Zone, Panama.

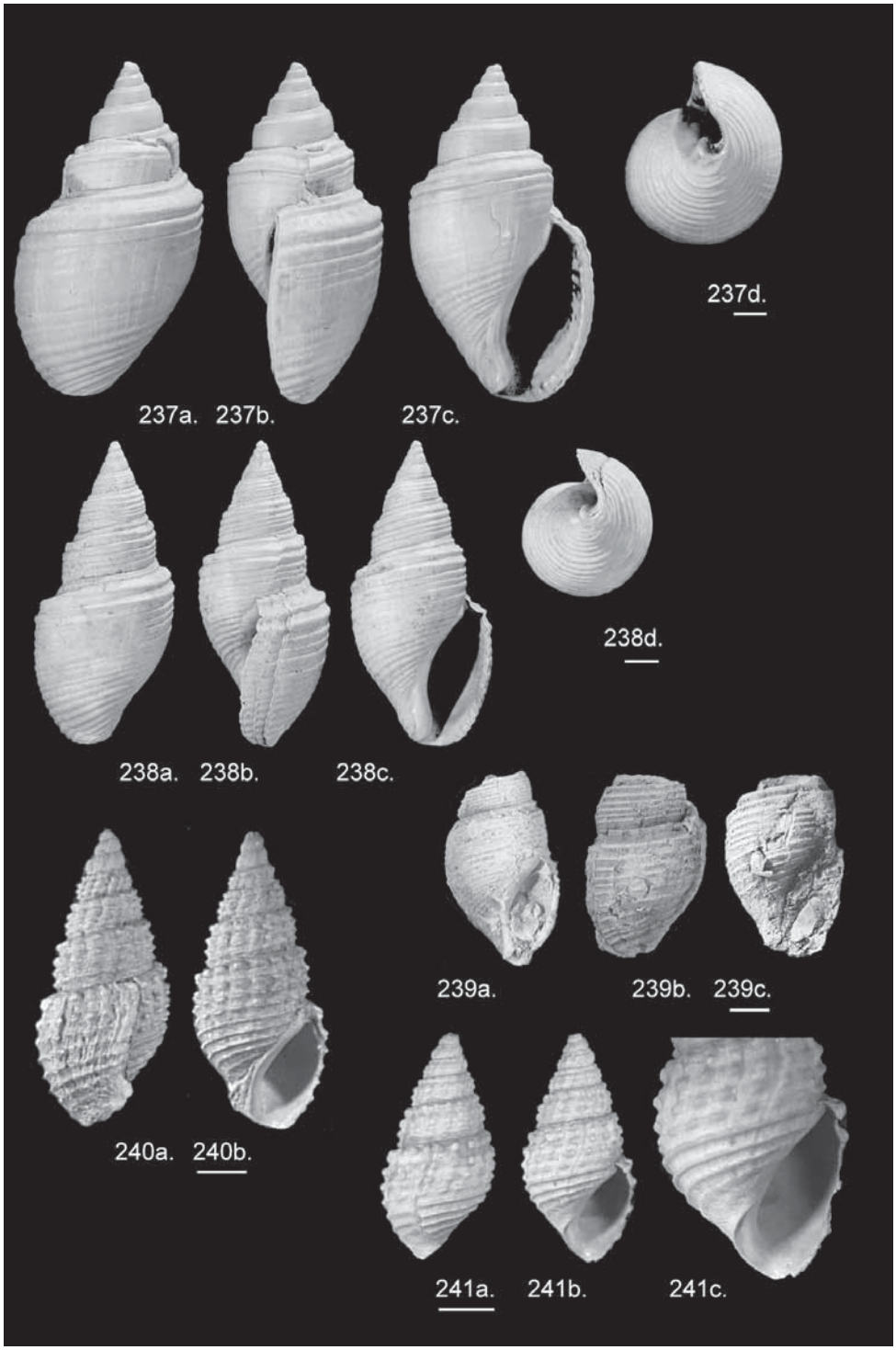
Diagnosis – Intermediate-sized, melanopsiform often decollate shells; ornamentation ranging from reticulate and tuberculate to smooth; base of columella forming spatulous pseudumbilical platform that is mostly or entirely covered by expanding inner lip; basal apertural sinus lacking.

Range – Eocene-Pliocene, Central America; Eocene-Oligocene, Lesser Antilles; latest Oligocene-Late Miocene, northwest South America (Wesselingh, 1996).

Remarks – *Charadreon* is a cerithioidean snail whose family assignment is open to further scrutiny. The shells are less elongate than other South American Pachychilidae, such as *Sheppardiconcha* and *Pachychilus*. *Charadreon* resembles both old-world Melanopsidae as well as native South American Thiaridae in gross morphology. The lack of a basal columellar truncation separates *Charadreon* from the latter, a large geographic gap from the former.

***Charadreon eucosmius* (Pilsbry & Olsson, 1935)**
Figs. 240, 241.

1935 *Hemisinus (Longiverena) eucosmius* Pilsbry & Olsson, p. 13, pl. 3, fig. 2.
1935 *Hemisinus (Longiverena) lapazanus* Pilsbry & Olsson, p. 13, pl. 3, figs. 3, 4.
1935 *Hemisinus (Longiverena) hopkinsi* Pilsbry & Olsson, p. 14, pl. 3, fig. 8.
1935 *Hemisinus (Longiverena) laciranus* Pilsbry & Olsson, p. 14, pl. 3, fig. 5.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1935 *Hemisinus (Longiverena) waringi* Pilsbry & Olsson, p. 14, pl. 3, fig. 9.
1938 *Semisinus peyeri* de Greve, p. 104, pl. 4, figs. 7-11.
1982 *Aylacostoma dickersoni* (Palmer); Bristow & Parodiz, p. 48.
1990 *Longiverena eucosmia* (Pilsbry & Olsson); Nuttall, p. 250 (*pars*), figs. 263, 265-267 (*non* fig. 264).

Material studied – RGM 456 364, Santa Teresa Tacsha (Loreto, Peru), exposure in west bank Rio Napo, *c.* 2 km below confluence with Rio Tacsha Curaray (2°50'S 73°33'W), level F890 (sample at DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 29-9-1996. RGM 456 365, Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Extended diagnosis – Shell thin-walled for *Charadreon*, elongate-fusiform and ornamented with 3-5 spiral ribs (up to eleven on body whorl) that are dotted by increasingly prominent tubercles on crossings with slightly opisthocyrt (or on body whorl S-shaped) collabral folds; tubercles restricted to the upper 4-5 spiral ribs on body whorl, fading downward; base of body whorl ornamented with spiral ribs; aperture elongate fusiform; base of columellar lip slightly broadened into a low spatulous depression, lacking a basal incision; inner lip callus slightly expanded.

Dimensions – RGM 456 364: H 12.6; W 5.4; Hap 5.5; >7.2 whorls. RGM 456 365: H 8.3; W 4.0; Hap 4.9; >6.8 whorls.

Range – This species is common in Early - early Middle Miocene deposits of inland basins in northwestern South America.

Remarks – In some geological units, such as in the La Cira 'Beds' (Magdalena Basin, Colombia), the morphological range encompassed by this taxon is large, prompting earlier authors to describe a variety of species that were all properly synonymized by Nuttall (1990, p. 250). *Charadreon mugrosanus* (Pilsbry & Olsson, 1935; Oligocene, Mug-

◀ Figs. 237, 238. *Aylacostoma browni* (Etheridge, 1879).

Fig. 237. RGM 456 362, Porvenir (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 238. RGM 456 363, same locality as Fig. 237. a, rear view. b, lateral view. c, front view. d, basal view.

Fig. 239. *Aylacostoma lataguaensis* (Nuttall, 1990). a, BMNH 19920, holotype, La Tagua (Caqueta, Colombia). Front view. b-c, BMNH 19921, paratype, same locality as (a). b, rear view. c, front view. Images courtesy C.P. Nuttall (BMNH).

Figs. 240, 241. *Charadreon eucosmius* (Pilsbry & Olsson, 1935).

Fig. 240. RGM 456 364, Santa Teresa Tacsha (Loreto, Peru). a, rear view. b, front view.
Fig. 241. RGM 456 365, Indiana (Loreto, Peru). a, rear view. b, front view. c, detail of aperture showing spatulous base of columella.

Scale bars represent 2 mm.

rosa Formation, Magdalena Basin, Colombia) is a more straight-sided species with a more subdued ornament and is possibly the predessor of *C. eucosmius*. It is very likely that *C. eucosmius* is the predessor of *C. intermedius* and ultimately *C. glabrum* (see below). The three species occur in marginal lacustrine assemblages in successive stratigraphic intervals in the Pebas Formation. The morphology shows a progressive reduction of the ornament, although intermediate specimens between these three subspecies have not been encountered.

***Charadreon intermedius* sp. nov.**
Figs. 242, 243.

Type material – INGEMMET TN13 (holotype), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 366 (paratype), same locality.

Range – Pebas Formation, MZ7 - MZ8 (Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – *Intermedius* refers to the interpreted intermediate evolutionary position between *C. eucosmius* and *C. glabrum* as well as its intermediately developed ornament.

Diagnosis – Small to intermediate sized *Charadreon* with wide, opisthocyrth ribs and very fine spiral grooves on early teleoconch whorls that fade later on shell.

Description – The apex is missing in all material; the shell appears decollate. Early teleoconch whorls are worn. A well-developed ornament of blunt axial ribs and fine spiral grooves is present on the first whorls. The axial ribs are opisthocline, reversed C-shaped. They disappear well below the upper suture and only shortly above the lower suture. These ribs are separated by concave interspaces about twice as wide and fade on later teleoconch whorls that are smooth. There are four fine spiral grooves

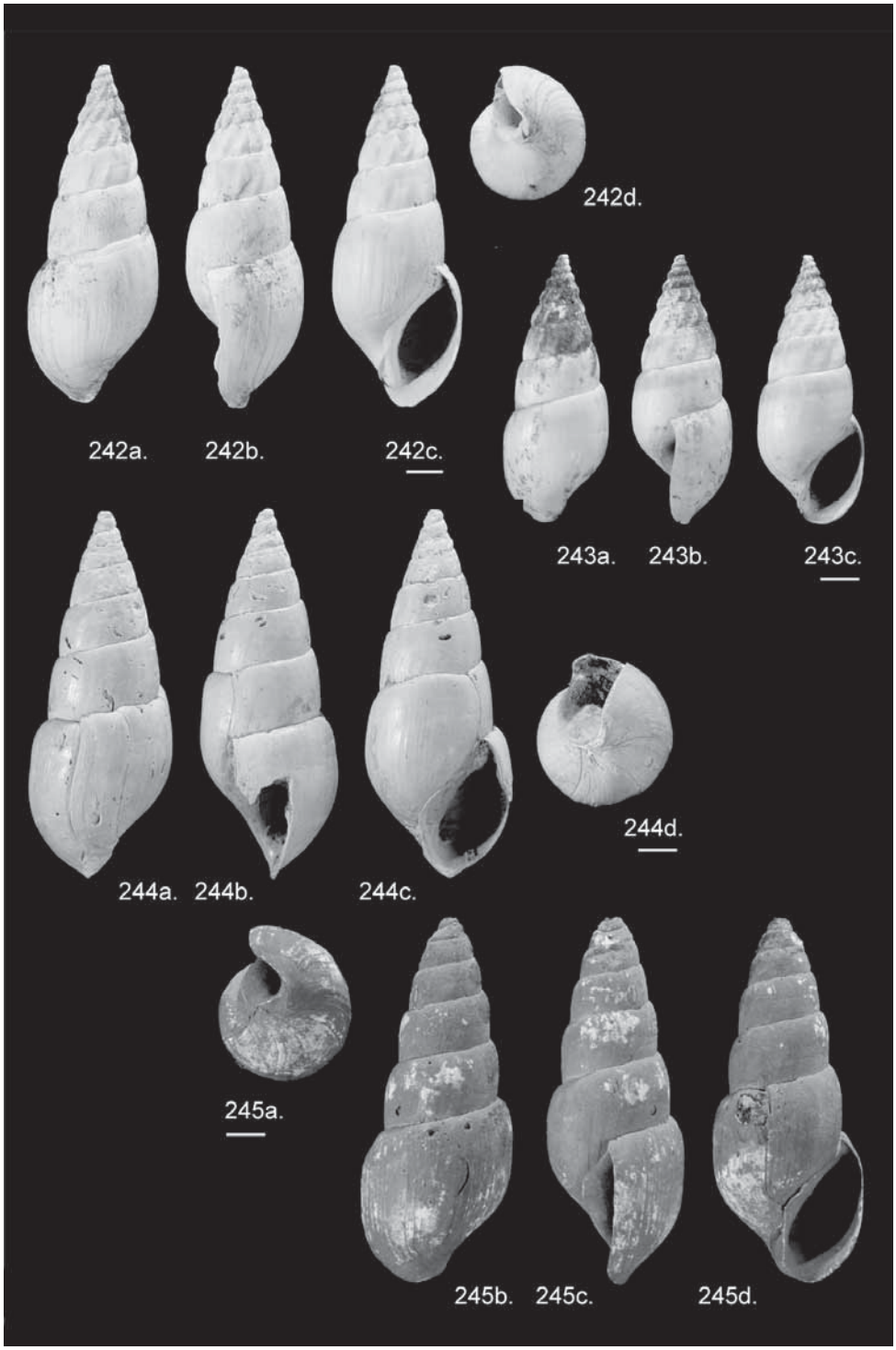
Figs. 242, 243. *Charadreon intermedius* sp. nov. ►

Fig. 242. INGEMMET TN13, holotype, Santa Elena (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 243. RGM 456 366, paratype, same locality as Fig. 242. a, rear view. b, lateral view. c, front view.

Figs. 244, 245. *Charadreon glabrum* sp. nov.

Fig. 244. RGM 456 368, paratype, Macedonia (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 245. RGM 456 367, holotype, Los Chorros (Amazonas, Colombia). a, basal view. b, rear view. c, lateral view. d, front view.

Scale bars represent 2 mm.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on the upper three-quarters of the whorls. At intersections with very fine opisthocline growth lines, that may also be developed as grooves, small hook-shaped impressions are present, reminiscent of ornamentation on *Sheppardiconcha* species treated below. The spiral grooves also peter out abaxially. The body whorl is smooth apart for numerous slightly opisthocline, slightly sigmoid growth lines. A single spiral groove may be present at the base of the body whorl. The aperture is adnate and spindle-shaped. Apertural margins are not thickened, apart for the parietal margin and then only slightly. A pseudumbilical platform is present at the base of the columella. This platform is almost entirely covered by the expanding inner lip, producing a spatulous depression.

Dimensions – INGEMMET TN13: H 18.8; W 7.0; Hap 7.3; >8.5 whorls. RGM 456 366: H 14.1; W 6.0; Hap 6.0; >7.2 whorls.

Remarks – Differs from *C. eucosmius* by the restriction of spiral ornament to the early teleoconch whorls, and the lack of collabral folds and tubercles on later whorls.

***Charadreon glabrum* sp. nov.**
Figs. 244, 245.

Type material – RGM 456 367 (holotype), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River, 1.3 km east of confluence with Loreto Yacu (3°46'S 70°21'W), level F21 (0.4 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 368 (paratype), Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Range – Pebas Formation, MZ10 - MZ11 (late Middle - early Late Miocene), Colombian Amazonia.

Derivatio nominis – Latin, *glabra* for smooth.

Diagnosis – Intermediate to large sized *Charadreon* with a smooth and thick shell; aperture fusiform, but with slightly broadened base; body whorl tends to become shouldered in larger specimens.

Description – The shell is thick-walled and robust. The apex is missing in all material; the early teleoconch whorls are plugged from within (decollate). The shells have no macrosculpture. They have numerous, very fine opisthocline growth lines that are reversed C-shaped or even inverted J-shaped. Up to three very fine, irregular and poorly developed spiral grooves are present on some of the specimens. The whorl profile is flat; in some specimens a very narrow, rounded shoulder is seen. The aperture is fusiform and adnate. The inner lip is thickened. The base of the columella forms a spatulous pseudumbilical platform that is partially or wholly covered by the expanding inner lip.

Dimensions – RGM 456 367: H 19.2; W 7.5; Hap 8.1; >7.2 whorls. RGM 456 368: H 19.2; W *c.* 8.0; Hap *c.* 8.9; >8.1 whorls.

Remarks – *Charadreon glabrum* differs from *C. intermedius* and *C. eucosmius* by the entire lack of macro ornamentation, and a larger and thicker shell.

Genus *Sheppardiconcha* Marshall & Bowles, 1932

Type species – *Sheppardiconcha bibliana* Marshall & Bowles, 1932, Miocene, Cuenca Basin, Ecuador.

Diagnosis – Elongate, intermediate-sized pachychilid; early teleoconch whorls markedly straight-sided; ornamentation ranging from spiral to irregularly ribing containing both spiral and axial ribs; microsculpture of semilunate grooves between two spiral grooves present at *c.* three-quarters of the whorl height which may be repeated below on early teleoconch whorls and, in some species, more extensively developed on later teleoconch whorls; growth lines reversed sigmoid, opisthocline; base of aperture broadly retracted, but lacking siphonal notch.

Range – Oligocene-Late Miocene, northwest South America, Neogene?-Recent, Central America (see remarks under Cerithioidea, above).

Remarks – Almost all *Sheppardiconcha* shells in the Pebas Formation have severely damaged outer lip margins. The type of damage, with acute, broadly serrate edges, suggests heavy incidence by crustacean-type peeling predation. Similar repair scars are also common on the shells. Very often, the damage aperture looks as if it contains a retracted base, resembling the thiarid siphonal notch. However, study of growth lines slightly before the aperture shows that a notch was never present.

Sheppardiconcha tuberculifera (Conrad, 1874b)

Figs. 246, 247.

1874b *Hemisinus tuberculiferus* Conrad, p. 83, pl. 12, fig. 4.
1938 *Semisinus tuberculiferus* (Conrad); de Greve, p. 104, pl. 4, figs. 1-6, 12.
1966 *Hemisinus (Sheppardiconcha) tuberculiferus* (Conrad); Willard, p. 466, pl. 63, figs. 6-8.
1990 *Sheppardiconcha tuberculifera* (Conrad); Nuttall, p. 234, figs. 215, 216.
1990 *Longiverena colombiana* Nuttall, p. 249 (*pars*), fig. 259 (*non* figs. 256-258, 260-262).
1990 *Sheppardiconcha bibliana* Marshall & Bowles; Nuttall, p. 234 (*pars*), fig. 213 (*non* figs. 210-212, 214).

Material studied – INGEMMET TN49, Copal Urco (Loreto, Peru), exposure in east bank Rio Napo, 500 m south of confluence with Rio Urco (2°20'S 23°47'W), level F869 (1.9 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 26-9-1996. RGM 456 459, Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Extended diagnosis – Shell high-spired; apex damaged in studied specimens; at first the shell is smooth with a slightly convex whorl profile containing numerous opisthocline, curved growth lines; at *c.* third whorl a slight keel develops just above the lower suture, giving the juvenile shell a pagodiform appearance, followed 1-4 whorls later by an additional spiral keel at *c.* two thirds of whorl height; elongate tubercles (7-12 per whorl) develop on spirals; third spiral develops some whorls later just below the upper suture; secondary spirals, uncommonly with tubercles, may develop on later teleoconch whorls; upper spiral may develop enlarged tubercles on later teleoconch whorls; tubercles become progressively rounded; fine spiral grooves with fine, irregular reversed C-shaped axial groovelets may be found between the primary spirals; basal spiral rib may be visible just above lower suture, corresponding to basal rib bounding base of body whorl with additionally 7-8 thin, low spiral ribs; aperture invariably damaged, semicircular-subquadrate; margins not thickened; basal margin entire; parietal callus thin; shell imperforate.

Dimensions – INGEMMET TN49: H 31.2; W 12.3; Hap >9.0; >11.6 whorls. RGM 456 459: H 14.6; W 11.3; Hap 4.1; >9.2 whorls.

Range – Pebas Formation, MZ2 - MZ7 (late Early - Middle Miocene), Colombian and Peruvian Amazonia; Loyola Formation (Middle Miocene), Cuenca Basin (Ecuador).

Remarks – In some specimens, the upper of the two primary spirals may develop heavy tubercles early on the teleoconch that remain dominant. These specimens resemble *Sheppardiconcha coronota* (for differentiation see below).

***Sheppardiconcha coronata* (Etheridge, 1879)**

Figs. 248, 249.

1879 *Cerithium coronatum* Etheridge, p. 87, pl. 7, fig. 5.
1924 *Cerithium coronatum* Etheridge; Roxo, p. 46.
1938 *Cerithium*(?) *coronatum* Etheridge; de Greve, p. 106, pl. 3, figs. 13-16, 20.
1967 *Aylacostoma* (*Longiverena*) *coronatum* (Etheridge); Santos & Castro, p. 413, figs. 4-6.
1981 *Aylacostoma* (*Longiverena*) *coronatum* (Etheridge); Costa, p. 645, pl. 1, figs. 13, 14.
1990 *Sheppardiconcha coronata* (Etheridge); Nuttall, p. 236, figs. 217, 218.

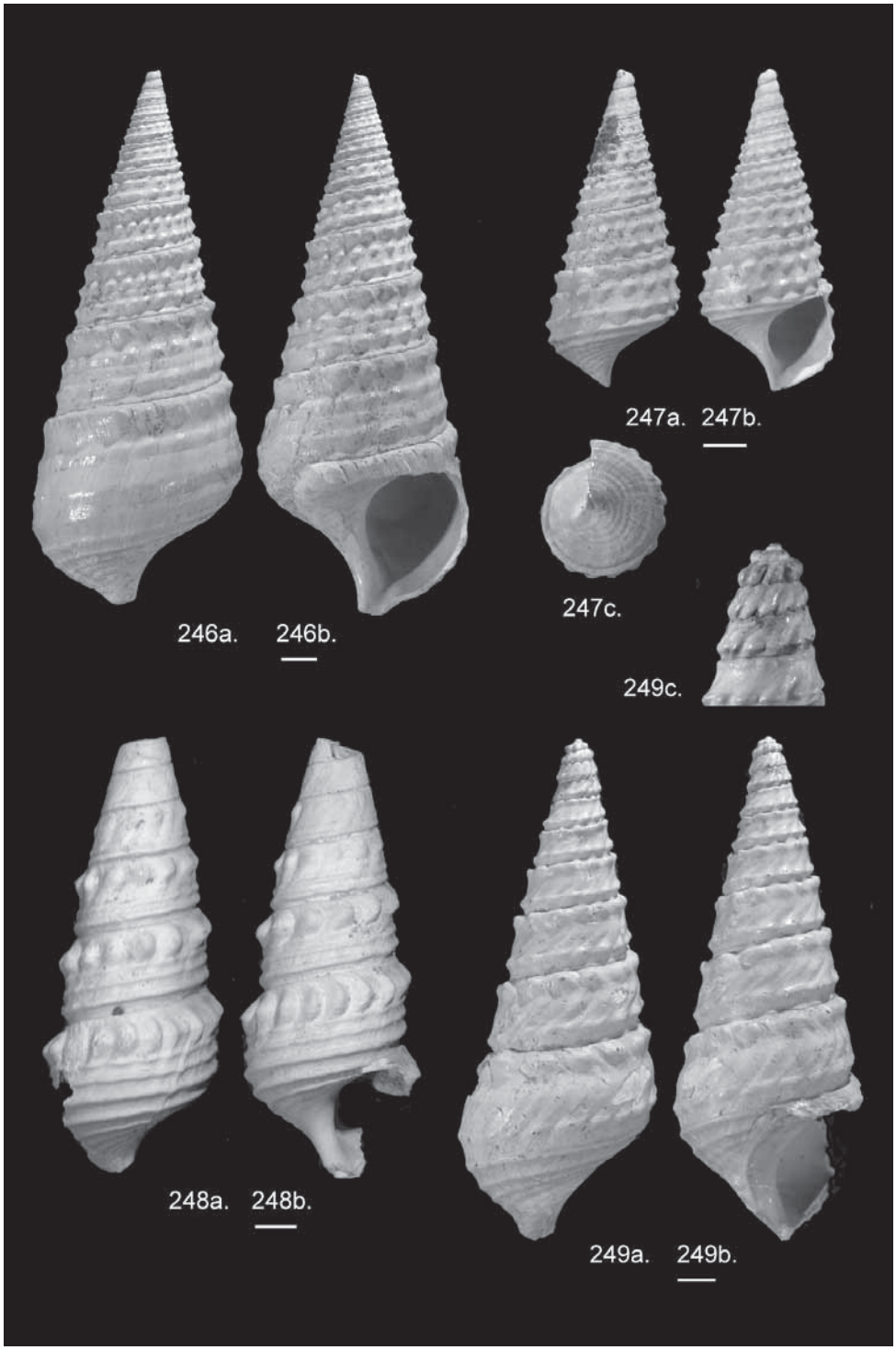
Figs. 246, 247. *Sheppardiconcha tuberculifera* (Conrad, 1874b). ►

Fig. 246. INGEMMET TN49, Copal Urco (Loreto, Peru). a, rear view. b, front view.
Fig. 247. RGM 456 459, Indiana (Loreto, Peru). a, rear view. b, front view. c, basal view.

Fig. 248. *Sheppardiconcha coronata* (Etheridge, 1879). INGEMMET TN50, Porvenir (loreto, Peru). a, rear view. b, front view.

Fig. 249. *Sheppardiconcha* cf. *coronata* (Etheridge, 1879). RGM 456 460, Mishana (Loreto, Peru). a, rear view. b, front view. c, detail of apex.

Scale bars represent 2 mm.


246a. 246b.
247a. 247b.
247c.
249c.
248a. 248b.
249a. 249b.

Material studied – INGEMMET TN50, Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996. RGM 456 460, Mishana (Loreto, Peru), exposure in south bank Rio Nanay, 100 m west of landing stage (3°52'S 73°29'W), level F72 (at DL). Pebas Formation, MZ8 (late Middle - early Middle Miocene); leg. F.P. Wesselingh, 10-1991.

Extended diagnosis – Shell high-spired; apex damaged in most studied material (see remarks below); early teleoconch whorls smooth and markedly straight-sided with adnate suture; first onset of opisthocline, inverted J-shaped growth lines, followed by two pairs of fine spiral grooves at the base and about half the whorl height; fine axial, slightly inverted C-shaped grooves between the spiral grooves; the basal groove pair develops into a basal keel; at four fifths of the whorl height a broad keel develops that contains prominent, robust, rounded tubercles at regular distances (*c.* 12-20 per whorl) and bounds a steep subsutural ramp above; additional pairs of fine spiral grooves are seen on later teleoconch whorls; the median pair of grooves develops into a well-defined spiral rib and a third spiral rib may also develop, leaving the shell with an upper row of knobs and two to three spiral ribs below; suture located into progressively developing sutural depression; base of body whorl bounded by spiral rib and ornamented with five low spiral ribs; aperture damaged, semicircular; shell imperforate.

Dimensions – INGEMMET TN50: H >21.8; W >8.7; Hap >6.3; >6.4 whorls. RGM 456 460: H 27.4; W >8.6; Hap >11.3; >12.0 whorls.

Range – Pebas Formation, MZ7 - MZ11 (Middle - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia. The typical form (see remarks below) is restricted to MZ9 - MZ11.

Remarks – The typical form (Fig. 248) of this species is not uncommon in MZ9 - MZ11 deposits. However, different forms were found in samples attributed to MZ7 and MZ8 (Fig. 249). In these specimens, the lower spiral contains tubercles. An additional two lower median spiral ribs may develop. Furthermore, the apical area of shells in one of the samples is intact (Fig. 249c). The shells have a slightly inclined nucleus (diameter *c.* 50 µm). At *c.* 1.5 whorls an irregular axial constriction separates the protoconch from the teleoconch, after which massive rounded knob-shaped axial ribs develop (*c.* 12-13 per whorl). In subsequent teleoconch whorls these ribs flatten and become more elongate. The upper and lower parts of these ribs become more pronounced, resulting in the change of an axially- to spirally-dominated ornament. The shells have characteristics in common with both *S. tuberculifera* and *S. coronata*. The lack of elongate tubercles on the upper spiral rib (typical for *S. tuberculifera*), as well as the presence of only five spirals at the base of the body whorl has led to the provisional assignment of these specimens to *S. coronata*. Actually, such shells may form stratigraphic intermediate populations between the otherwise distinct *S. tuberculifera* and *S. coronata*. Additional investigation is needed in order to elucidate the relationship between both species and the identity of these intermediate populations.

Sheppardiconcha septencincta (Roxo, 1937)

Fig. 250.

1937 ?*Hemisinus* sp. Roxo, p. 8, figs. 4, 5, 7.
1937 *Hemisinus septencinctus* Roxo, p. 9, fig. 6.
2002 *Sheppardiconcha* sp. Wesselingh *et al*., fig. 8.
2006d *Sheppardiconcha septencincta* (Roxo); Wesselingh *et al*., pp. 424, 426, figs. 6-10.

Material studied – RGM 456 461, Los Chorros (Amazonas, Colombia), exposure in north bank of Amazon River, *c.* 1.5 km downstream from concluence with Loreto-Yacu (3°47'S 70°20'W), collected from surface scree. Pebas Formation, *Grimsdalea* zone, MZ11 (late Middle - early Late Miocene); leg. M.C. Hoorn, 1989.

Extended diagnosis – Straight-sided *Sheppardiconcha* with 6-8 spiral ribs of regular strength and a slightly rounded body whorl; apex invariably damaged; early teleoconch whorls straight-sided with six broad, spiral ribs separated by narrow grooves; interspaces broaden and eventually become about twice as wide as the ribs; eight spiral ribs on penultimate whorl, 13 on body whorl; growth lines opisthocline, inverted J-shaped, numerous, fine; damaged aperture circular; parietal callus thin, but expanding; base part entire; shell imperforate.

Dimensions – RGM 456 461: H >27.3; W 10.0; Hap >7.2; >9.2 whorls.

Range – Pebas Formation, MZ9 - MZ10 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia; Solimões Formation, late Miocene, Brazilian Amazonia (see Wesselingh *et al*., 2006d).

Remarks – The regular spiral ornamentation is unique for Neogene South American *Sheppardiconcha* species.

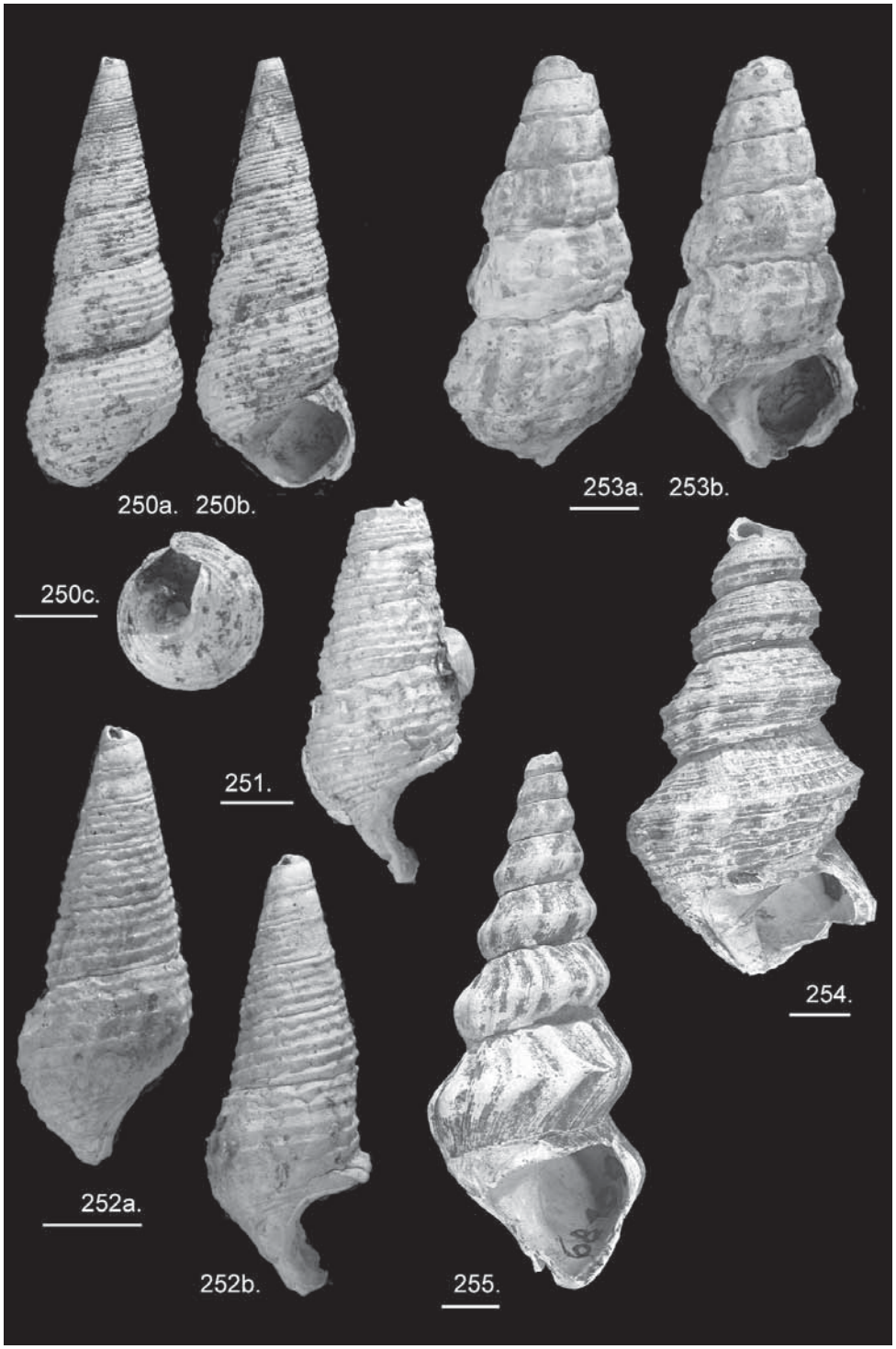
Sheppardiconcha lataguensis Nuttall, 1990

Figs. 251, 252.

1990 *Sheppardiconcha lataguensis* Nuttall, p. 237, figs. 219-222.

Material studied – RGM 456 462, La Tagua (Putumayo, Colombia), exposure in south bank Rio Caqueta, in the vicinity of the village (0°03'S 74°40'W), level 'La Tagua 13'; Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. RGM 456 462, same locality.

Extended diagnosis – Markedly straight-sided species with a bulbous body whorl; five spiral ribs at regular distances separated by interspaces about twice as wide; inverted J-shaped growth lines, fine, numerous; low collabral folding may develop (up to *c.* 15 folds on body whorl); at intersections with spirals, irregular, very low, elongate knobs may develop; 11-12 spirals on body whorl; upper spiral may develop slightly more pronounced tubercles and delimit a narrow shoulder on the body whorl; paired spiral grooves with axial groovelets seen on some of Nuttall's (1990) specimens at vari-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253a. 253b.
250c.
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252a.
252b.
255.

ous parts of the shell; suture adnate or in very low and narrow sutural depression; left part of body whorl expanded abaxially; aperture apparently circular; inner lip callus thickened and expanding; shell imperforate.

Dimensions – RGM 456 462: H >26.9; W >10.1; Hap >8.3; >7.5 whorls. RGM 456 463; H >22.8.

Range – Pebas Formation, MZ2 (late Early - early Middle Miocene), Colombian and Peruvian Amazonia.

Remarks – *Sheppardiconcha lataguensis* resembles mostly *S. septencincta.* It differs from the latter by the bulbous body whorl, the presence of five instead of 6-8 spiral ribs and the possibility to develop collabral folding. The species also resembles *S. bibliana* Marshall & Bowles, 1932 (Miocene, Cuenca Basin, Ecuador and Marañon Basin, Peru). The latter has a marked subsutural depression on early teleoconch whorls, as well as thinner, more irregularly spaced spiral ribs (up to 12 on penultimate whorl) and more numerous, irregularly spaced, growth lines.

Sheppardiconcha colombiana **(Nuttall, 1990)**

Figs. 253-255.

1990 *Longiverena colombiana* Nuttall, p. 249 (*pars*), figs. 256-258, 260-262 (*non* fig. 259).

Material studied – RGM 456 464, La Tagua (Putumayo, Colombia), exposure in south bank of Caqueta River, near the village (0°03'S 74°40'W), level 'La Tagua 9-11'. Pebas Formation ('La Tagua Beds'), MZ2 (late Early - early Middle Miocene); leg. M.C. Hoorn, 1989. CAS 68409, Curaray River (Pastaza, Ecuador), exposure 47 km in straight line west of junction Curaray and Conoco rivers at longitude 76°W, level D361. Curaray Formation (= Pebas Formation), MZ2-3 (late Early - early Middle Miocene); leg. J.J.

◀ Fig. 250. *Sheppardiconcha septencincta* (Roxo, 1937). RGM 456 461, Los Chorros (Amazonas, Colombia). a, rear view. b, front view. c, basal view.

Figs. 251, 252. *Sheppardiconcha lataguensis* Nuttall, 1990.

Fig. 251. RGM 456 462, La Tagua (Putumayo, Colombia). Front view.
Fig. 252. RGM 456 463, same locality as Fig. 251. a, rear view. b, front view.

Figs. 253-255. *Sheppardiconcha colombiana* (Nuttall, 1990).

Fig. 253. RGM 456 464, La Tagua (Putumayo, Colombia). a, rear view. b, front view.
Fig. 254. CAS 68409, Curaray River (Pastaza, Ecuador). Photograph by A. 't. Hooft (Leiden, the Netherlands). Front view.
Fig. 255. CAS 68409, Curaray River (Pastaza, Ecuador). Photograph by A. 't. Hooft (Leiden, the Netherlands). Front view.

Scale bars represent 5 mm.

Dozy, 1942 (more than 40 specimens); CAS 68410 (10 specimens) and CAS 68409 (25 specimens) from the same locality.

Extended diagnosis – Large (H up to *c.* 50), robust *Sheppardiconcha* with a variety of forms of ornamentation, commonly dominated by blunt, very prominent opisthocyrth collabral folds; early teleoconch whorls straight-sided to marginally rounded, smooth, apart from opisthocyrth growth lines that can be numerous, very fine, and densely and regularly spaced; primary strong spiral keel at base (one sixth to one quarter of whorl height) progressively located upward (up to half the height of the penultimate whorl); sometimes development of two rounded primary spirals; secondary spirals thin, often regularly spaced on earlier, but irregularly spaced on later teleoconch whorls; usually 6-12 on body whorl, but up to 25 on some specimens; broad, massive, opisthocyrth ribs usually present, 12-13 in later teleoconch whorls, not extending to the base of the whorl; aperture circular; parietal callus expanding; shell imperforate.

Dimensions – RGM 456 464: H >29.1; W *c.* 13.4; Hap >11.3. CAS 68409 (Fig. 254); H >39.1; W >20.2; Hap n.a. CAS 68409 (Fig. 255); H >46.1; W >17.1; Hap >15.3.

Range – Pebas Formation, MZ2, possibly MZ3 (late Early - early Middle Miocene), Colombian, Ecuadorean and Peruvian Amazonia.

Remarks – The large size, carinate to pagodiform shape and commonly very prominent opisthocyrth collabral folds separate this species from other Pebasian *Sheppardiconcha* species. However, *Sheppardiconcha colombiana* resembles *Potamides mcgilli* Pilsbry & Olsson, 1935, from the Eocene Los Corros Formation of the Magdalena Basin (Colombia), but the poorly preserved specimen of the latter illustrated by Pilsbry & Olsson apperently contains more bulbous early teleoconch whorls. The large temporal gap, with stratigraphically intermittent faunas in the Magdalena Basin lacking similar *Sheppardiconcha* species (the Mugrosa and La Cira faunas), indicates that the resemblance is most likely a matter of convergence.

***Sheppardiconcha solida* sp. nov.**

Figs. 256, 257.

Type material – INGEMMET TN51 (holotype), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. RGM 456 465 (paratype) and RGM 456 466 (5 damaged juvenile specimens and 5 fragments, paratypes), same locality. RGM 456 467 (4 damaged paratypes): Santa Teresa Tacsha (Loreto, Peru), exposure in west bank Rio Napo, *c.* 2 km below confluence with Rio Tacsha Curaray (2°50'S 73°33'W), level F890 (sample at DL). Pebas Formation, MZ 5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 29-9-1996.

Range – Pebas Formation, MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the somewhat solid appearance of this species (Latin, *solidus* for firm).

Diagnosis – Elongate to conical, relatively wide *Sheppardiconcha*; spiral and collabral ornament well developed on early, but almost lacking on later teleoconch whorls, apart for fine spiral grooves with opisthocyrth axial groovelets in between spirals on the base of the body whorl.

Description – The apex is missing in all studied material. The early teleoconch whorls are straight-sided and the suture is adnate. Two or three very low and broad spiral ribs or poorly defined elevations are present on the early teleoconch whorls. These spirals may bear low to very low, flat tubercles arranged in an inverse J-shaped order, as are the numerous fine growth lines. The spirals and tubercles disappear to give the last three or four teleoconch whorls a smooth appearance. However, a fine microsculpture of paired spiral grooves, with numerous, densely and regularly spaced reversed C-shaped axial groovelets in between, is found just below the upper suture in almost all specimens, but can also be developed on the entire surface of later teleoconch whorls. The last teleoconch whorls develop a very narrow, almost flat shoulder that in some specimens tends to be very vaguely tuberculate. The base of the body whorl is rounded and bears 7-9 thin, low spiral ribs. The aperture is severely damaged in all specimens. The parietal callus is very thin. When viewed from below, the growth lines indicate that the base of the aperture has a broad and shallow retraction. The surface of most studied shells is strongly corroded.

Dimensions – INGEMMET TN51: H >35.3; W *c.* 12.9; Hap >12.9; >10.6 whorls. RGM 456 465: H 31.0; W *c.* 13.1; Hap *c.* 12. RGM 456 467: H>37.9; W >17.1; Hap *c.* 15.

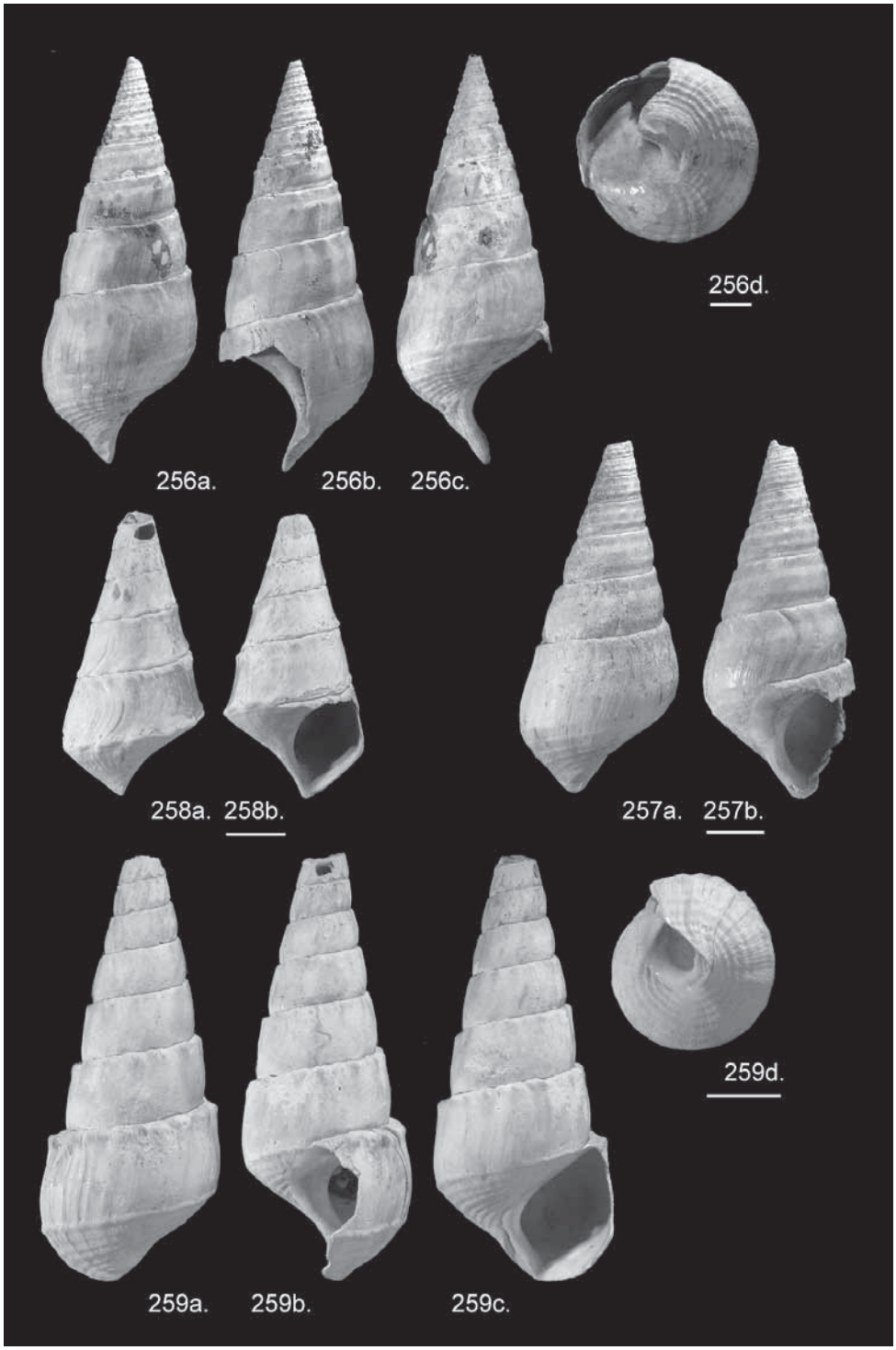
Remarks – The broad nature and smooth appearance make this species different from earlier described Pebasian *Sheppardiconcha* species.

***Sheppardiconcha*? *clavata* sp. nov.**
Figs. 258, 259.

Type material – RGM 456 368 (holotype), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F58 (3.1 m above DL). Pebas Formation, MZ11 or MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 369 (paratype), 456 470 (4 damaged paratypes), same locality. RGM 456 471 (paratype), Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Range – Pebas Formation, MZ11, possibly also MZ12 (late Middle - early Late Miocene), Colombian Amazonia.

Derivatio nominis – *Clavata* after the club-shape (Latin, *clava* for club).


256d.
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259d.
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Diagnosis – Large, thin-shelled, club-shaped cerithioid; shell concave to straight-sided on early teleoconch whorls; narrowly shouldered with low tubercles on shoulder of later teleoconch whorls; slightly opisthocline, wide and low, inversed J-shaped axial ribs on early teleoconch whorls, that fade on later whorls apart for the upper (and sometimes lower) end; later teleoconch whorls predominantly smooth, apart for base of body whorl that contains regular, low spiral ribs; distinct spiral separates base of body whorl from remainder shell; shell imperforate.

Description – The apex is missing in all available material. The early teleoconch whorls have concave to straight sides that in the holotype run almost parallel. They contain 14-15 very low and broad, slightly opisthocline axial ribs that fade on later teleoconch whorls, apart for their upper end that become expressed as tubercles on the rimate shoulder that develops on later whorls; in some specimens it also develops on the lower end of the whorl. Growth lines are fine, numerous, and, like the axial ribs, slightly opisthocline and inverted J-shaped. The base of the body whorl is bounded by a well-defined spiral rib and ornamented with another seven, thin, regularly spaced ribs. The aperture is semicircular-subquadrate. The margins are thin; the parietal callus is very thin and not expanding beyond the aperture. The outer lip is sigmoid when viewed from the side and furthest produced just above the base. The inner junction of the columella and basal lip is subangular. A very shallow and narrow spatulous pseudumbilical depression is developed on the holotype.

Dimensions – RGM 456 368: H >29.5; W 12.2; Hap 9.9; >7.3 whorls. RGM 456 369: H> 23.3.

Remarks – This species shares a number of similarities with *Sheppardiconcha convexa*, such as general shape and the smooth appearance of later teleoconch whorls with the exception of the spiral ribs on the base of the body whorl, as well as the very narrow shoulder that is bounded by a somewhat tuberculate subsutural ridge. However, *S.? clavata* is less pointed, has a predominance of low axial elements instead of spiral elements on early teleoconch whorls and has the left side of the columellar margin to the left of the axis of the shell. Some morphological features, such as the almost parallel

◀ Figs. 256, 257. *Sheppardiconcha solida* sp. nov.

Fig. 256. INGEMMET TN51, holotype, Indiana (Loreto, Peru). a, rear view. b, lateral view. c, front view. d, basal view.
Fig. 257. RGM 456 465, paratype, same locality as Fig. 256. a, rear view. b, front view.

Figs. 258, 259. *Sheppardiconcha*? *clavata* sp. nov.

Fig. 258. RGM 456 471, paratype, Macedonia (Amazonas, Colombia). a, rear view. b, front view.
Fig. 259. RGM 456 368, holotype, Santa Sofia (Amazonas, Colombia). a, rear view. b, lateral view. c, front view. d, basal view.

Scale bars represent 5 mm.

sides on early teleoconch whorls, predominance of axial ornamentation and the leftward extension of the columellar lip, are also found on shells of extant *Doryssa* species of the streams and rivers of the Guyana Shield. The progressive reduction of ornament in *S.*? *clavata* is unknown from *Doryssa*.

Family Melongenidae Gill, 1871
Genus *Melongena* Schumacher, 1817

Type species – *Melongena fasciata* Schumacher, 1817 (= *Murex melongena* Linné, 1758), Recent, Gulf of Mexico, Carribbean, northern South America.

Melongena woodwardi (Roxo, 1924)
Figs. 260, 261.

1924 *Purpura woodwardi* Roxo, p. 49 (*pars*), fig. C, C' (*non* fig. D).
1959 ?*Thais (Stramonita)* aff. *T. haemastoma* (Linné); Woodring, p. 222, pl. 28, figs. 13, 14.
1967 *Aylacostoma woodwardi* (Roxo); Santos & Castro, p. 413 (*pars*), figs. 4, 5 (*non* fig. 6).
1990 *Verena crenocarina* (Moricand); Nuttall, p. 253 (*pars*) (*non* figs. 269-272).
1998 *Thais woodwardi* (Roxo); Vonhof *et al*., p. 88 (table), fig. 2.
2002 *Melongena woodwardi* (Roxo); Vermeij & Wesselingh, p. 265, figs. 1, 2.

Material studied and dimensions – See Vermeij & Wesselingh (2002, p. 265).

Diagnosis – Small (H 32) relatively thin-shelled *Melongena*, ornamented with distinct spiral cords on which two rows of tubercles are developed on the body whorl; aperture lacking strongly armoured structures; inner lip only very slightly thickened; columellar lip smooth; abapical siphonal notch short, but well developed, as is the fasciole.

Range – Pebas Formation, MZ9 - MZ10 (late Middle - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia; Gatun Formation (Late Miocene), Canal Zone, Panama.

Family Nassariidae Iredale, 1916
Genus *Nassarius* Duméril, 1806

Type species – *Buccinum arcularius* Linné, 1758, Recent, tropical Indo-Pacific.

Nassarius? *reductus* Vermeij & Wesselingh, 2002
Figs. 262-263.

1924 *Purpura woodwardi* Roxo, p. 49 (*pars*), fig. D (*non* fig. C, C').
1967 *Aylacostoma woodwardi* (Roxo); Santos & Castro, p. 413 (*pars*), fig. 6 (*non* figs. 4, 5).
1998 *Phos* spec.; Vonhof *et al*., p. 88 (table), fig. 1.
2002 ?*Nassarius reductus* Vermeij & Wesselingh, p. 267, figs. 3, 4.

Material studied and dimensions – See Vermeij & Wesselingh (2002, p. 267).

Diagnosis – Small (H 12), relatively thin-shelled *Nassarius* with 8-15 rounded axial ribs that do not extend to the upper and lower suture, and numerous fine spiral striae

between and sometimes on the ribs; shell slightly shouldered; outer lip with smooth adaxial side; base of aperture with a siphonal notch; columella yielding a weak fold.

Range – Pebas Formation, MZ9 - MZ10 (late Middle - early Late Miocene), Colombia, Peruvian and Brazilian Amazonia.

Family Pyramidellidae Gray, 1840
Genus *Odostomia* Fleming, 1813

Type species – *Turbo plicatus* Montagu, 1803.

***Odostomia nuttalli* van Aartsen & Wesselingh, 2000**
Fig. 264.

2000 *Odostomia nuttalli* van Aartsen & Wesselingh, p. 167, figs. 1, 2.

Material studied and dimensions – See van Aartsen & Wesselingh (2000, p. 167).

Diagnosis – Relatively large (H 3), ovate *Odostomia*; well-developed subsutural ridge with small depression below; growth lines conspicuously sinuate; suture markedly incised; aperture relatively large with rather flat base; adapical part of the aperture retracted; columella openly coiled; umbilical chink present.

Range – Pebas Formation, MZ9 - MZ11 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

***Odostomia cotuhensis* van Aartsen & Wesselingh, 2000**
Fig. 265.

2000 *Odostomia cotuhensis* van Aartsen & Wesselingh, p. 168, fig. 5.

Material studied and dimensions – See van Aartsen & Wesselingh (2000, p. 168).

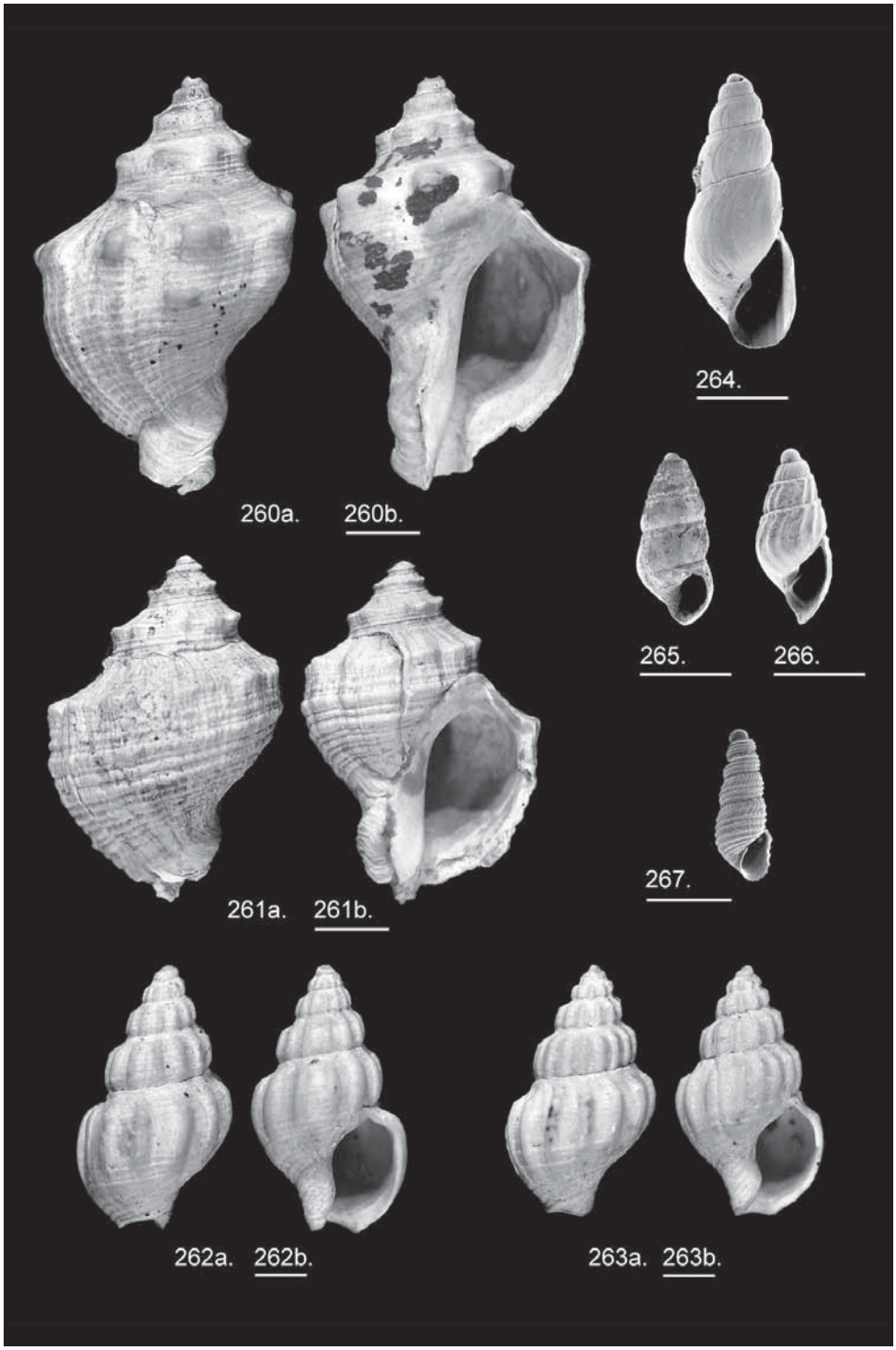
Diagnosis – Shell small (H 2), thick-walled; apex obtuse, giving the shell a cylindroconical appearance; suture well-defined, pronounced by robust subsutural ridge; shell smooth except for subsutural rib and straight to slightly opisthocline growth lines; aperture is relatively small; a barely perceptible columellar thickening.

Range – Pebas Formation, MZ9 - MZ10 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Odostomia *sensu lato* sp. indet. van Aartsen & Wesselingh, 2000
Fig. 266.

2000 *Odostomiidae* sp. indet; van Aartsen & Wesselingh, p. 169, figs. 6. 7.

Material studied and dimensions – See van Aartsen & Wesselingh (2000, p. 169).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263b.

Description – Shell small (H 2) and conical. The teleoconch whorls are slightly convex and separated by a well-incised suture. A subsutural angulation marks narrow, well-defined shoulder that dips *c.* 45° with respect with columellar axis. The shell is ornamented with sinuous-sigmoid, opisthocline axial ribs, fifteen on last whorl. Weak spiral striae occur between axial ribs. The aperture is comparatively large. The columella has robust fold that shows as a tooth on the inner lip.

Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Genus *Iolaea* Adams, 1867

Type species – *Iolaea scitula* (Adams, 1860), extant, Japan.

Iolaea amazonica van Aartsen & Wesselingh, 2005
Fig. 267.

2005 *Iolaea amazonica* van Aartsen & Wesselingh, p. 22, figs. 1-3.

Material studied and dimensions – See van Aartsen & Wesselingh (2005, p. 22).

◀ Figs. 260, 261. *Melongena woodwardi* (Roxo, 1924).

Fig. 260. RGM 394 332, Buenos Aires (Amazonas, Colombia). a, rear view. b, front view. Scale bar represents 5 mm.
Fig. 261. RGM 445 333, Nuevo Horizonte (Loreto, Peru). a, rear view. b, front view. Scale bar represents 5 mm.

Figs. 262, 263. *Nassarius*? *reductus* Vermeij & Wesselingh, 2002.

Fig. 262. RGM 445 334, paratype, Buenos Aires (Amazonas, Colombia). a, rear view. b, front view. Scale bar represents 2 mm.
Fig. 263. RGM 394 331, holotype, same locality as Fig. 262. a, rear view. b, front view. Scale bar represents 2 mm.

Fig. 264. *Odostomia nuttalli* van Aartsen & Wesselingh, 2000. RGM 445 342, holotype, Nuevo Horizonte (Loreto, Peru). Front view.

Fig. 265. *Odostomia cotuhensis* van Aartsen & Wesselingh, 2000. RGM 445 345, holotype, Nuevo Horizonte (Loreto, Peru). Front view.

Fig. 266. *Odostomia s.l.* sp. indet. van Aartsen & Wesselingh, 2000. RGM 445 347, Porvenir (Loreto, Peru). Front view.

Fig. 267. *Iolaea amazonica* van Aartsen & Wesselingh, 2005. RGM 456 800, holotype, Porvenir (Loreto, Peru). Front view.

Scale bars represent 1 mm unless stated otherwise. Images by A. 't. Hooft (Figs. 260-263). and J. Goud (Figs. 264-267), both of Leiden.

Diagnosis – Small (H 1.8), almost cylindrical, obtuse species with four pronounced spiral ribs (seven on the body whorl) crossed by conspicuously thickened, inverted S-shaped growth lines resulting into almost reticulate ornament; suture markedly incised; aperture rather small, about one third of the height of the shell; sinus located at the adapical side of the outer lip corresponding with the upper spiral rib, which may be slightly weaker than the other three; columella with a pronounced tooth.

Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Family Planorbidae Gray, 1840

Remarks – At least four different planorbid species have been found in samples from the Pebas Formation. Most of the material is so fragmentary that the species cannot be attributed to genera with certainty, nor can the presence of additional species be ruled out. The state of the material also precludes formal naming. In general, planorbid snails are very rare in the Pebas fauna. The systematic account follows that of Baker (1945).

Genus *Helisoma* Swainson, 1840

Type species – *Planorbis bicarinatus* Sowerby, 1821, extant, North America.

Helisoma? sp. 1
Fig. 268.

Material studied – RGM 456 501(damaged subadult specimen) and 456 402 (ten fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Description – The shell is comparatively high and has broadly rounded whorls. The umbilicus is deep. The aperture is regularly kidney-shaped with almost parallel bent inner and outer margins. The upper and lower margins are evenly rounded, somewhat elevated above/sunken below the upper/lower shell margin on subadult shells. Growth lines are numerous, regularly spaced and prosocline. The surface of the shell is dull.

Dimensions – RGM 456 501: H 1.3; W 1.8. A minimum width of 4 mm is estimated from the fragments.

Range – Pebas Formation, MZ5 - MZ9 (late Early - early Late Miocene), Peruvian Amazonia.

Helisoma? sp. 2
Fig. 269.

Material studied – RGM 456 503 (severely damaged subadult specimen) and 456

404 (eleven fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996. RGM 456 509 (ten fragments), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 1.4 km south of port (port at 3°30'S 73°03'W), level F371 (1.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 15-8-1996.

Description – The shell is high and has a glossy surface lacking traces of growth lines. The upper part of the outer lip on subadult specimens is sloping. The aperture is very broadly kidney-shaped with rounded upper and lower margins; the lower margin is wider than the upper margin. Both are produced with respect to upper and lower shell surface; the lower margin tends to be stronger produced. The upper margin tends to become shouldered. The shell is deeply umbilicate.

Dimensions – RGM 456 503: H 1.7; W 1.8. A minimum width of 3 mm is estimated from the fragments.

Range – Pebas Formation, MZ5 - MZ12 (late Early - early Late Miocene), Peruvian and Colombian Amazonia.

Genus *Tropicorbis* Brown & Pilsbry, 1914

Type species – *Planorbis liebmanni* Dunker *in* Küster *et al*., 1886, extant, Central America

***Tropicorbis*? sp. 1**
Fig. 270.

Material studied – RGM 456 505 (damaged subadult specimen) and 456 406 (six fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, *Grimsdalea* zone, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Description – Shell gyrauliform and depressed. The upper and lower margins run parallel. The shell has a dull surface with closely spaced, prosocline growth lines and on first 2.1 whorls up to *c.* 24 regularly spaced, very fine spiral riblets. At 2.1 whorls, these disappear abruptly. The aperture is broadly semilunate with rounded upper and outer margins, and a slightly depressed lower margin. The upper margin is slightly extending above coiling plane. The inner lip callus is thin.

Dimensions – RGM 456 505: H 0.45; W 1.4; 2.4 whorls. A minimum width of 4 mm is estimated from the fragments.

Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

***Tropicorbis*? sp. 2**
Fig. 271.

Material studied – RGM 456 507 (slightly damaged specimen) and 456 508 (*c.* 100 fragments), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 1.4 km south of port (port at 3°30'S 73°03'W), level F371 (1.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 15-8-1996.

Description – The robust shell is straight-sided and rather high. The perimeter of early whorls is markedly bulbous. The base of the aperture is slightly elevated, possibly as the result of damage by predation. The shell is deeply umbilicate. The surface contains numerous, densely and regularly spaced, slightly prosocline to orthocline growth lines. Up to 30 fine, slightly irregular, densely packed spiral riblets occur that fade on the body whorl. The aperture is semilunate with approximately parallel inner and outer margins. The inner lip callus is thin.

Dimensions – RGM 456 507: H 1.9; W 3.6; Hap 1.65; 4.0 whorls.

Range – Pebas Formation, MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Fig. 268. *Helisoma*? sp. 1. RGM 456 501, Barradero de Omagua (Loreto, Peru). a, basal view. b, apical view. c, front view. ▶

Fig. 269. *Helisoma*? sp. 2. RGM 456 503, Barradero de Omagua (Loreto, Peru). a, front view. b, rear view.

Fig. 270. *Tropicorbis*? sp. 1. RGM 456 505, Barradero de Omagua (Loreto, Peru). a, basal view. b, apical view. c, front view.

Fig. 271. *Tropicorbis*? sp. 2. RGM 456 507, Indiana (Loreto, Peru). a, basal view. b, apical view. c, front view.

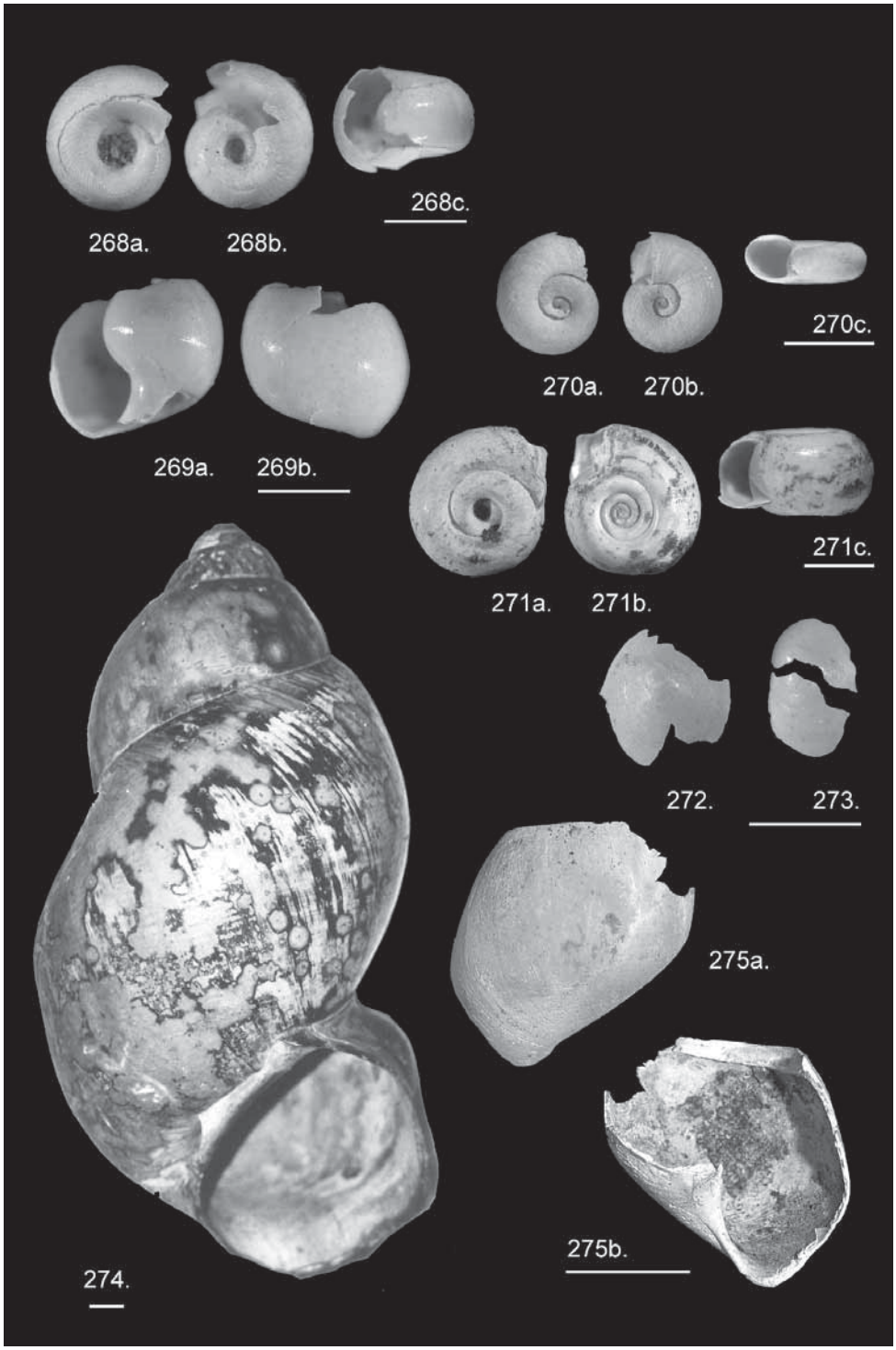
Fig. 272. *Gundlachia* sp. 1. RGM 456 512, Barradero de Omagua (Loreto, Peru). Apical view.

Fig. 273. *Gundlachia radiata*? (Guilding, 1828). RGM 456 510, Barradero de Omagua (Loreto, Peru). Apical view.

Fig. 274. *Pebasiconcha immanis* Wesselingh & Gittenberger, 1999. Unnumbered paratype, "vicinity of Pebas" (Loreto, Peru). M. Callegari coll. (Iquitos, Peru). Front view. Scale bar represents 10 mm.

Fig. 275. *Orthalicus* sp. RGM 456 553, Zaragoza (Amazonas, Colombia). a, rear view. b, front view. Scale bar represents 5 mm.

Scale bars represent 1 mm unless stated otherwise.


268a.
268b.
268c.
269a.
269b.
270a.
270b.
270c.
271a.
271b.
271c.
272.
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274.
275a.
275b.

Family Ancylidae Rafinesque, 1815
Genus *Gundlachia* Pfeiffer, 1849

Type species – *Gundlachia ancyliformis* Pfeiffer, 1849, Recent, Cuba.

Remarks – The use of the genus name *Gundlachia* is based on that of C. Ituarte (Museo de la Plata, Buenos Aires, Argentina) in his assessment of modern molluscs of the Pacaya-Samiria area (Loreto, Peru: www.flmnh.ufl.edu/ucamara/mollusks.htm). The generic status of this extremely rare taxon has not been fully investigated.

Gundlachia radiata? (Guilding, 1828)
Fig. 273.

1990 *Hebetancylus*? sp. Nuttall, p. 262, fig. 294a-d.

Material studied – RGM 456 510 (broken specimen) and 456 511 (six fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Diagnosis – Shell extremely thin and fragile; ovate when viewed from above; relatively highly cap-formed when viewed from the side; nucleus strongly eccentric, located *c.* one quarter from top and one third from posterior margin; broad and shallow concentric depression around nucleus; growth lines very fine; shell margins with very densely spaced, very fine, slightly irregular radial riblets (possibly *c.* 70 on the lower half of the shell).

Dimensions – RGM 456 510: H 1.2; W 1.7.

Range – Pebas Formation, MZ5 - MZ9 (late Early - early Late Miocene), Peruvian Amazonia.

Gundlachia sp.
Fig. 272.

Material studied – RGM 456 512 (damaged specimen) and 456 513 (two fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Description – The shell is broadly ovate to semicircular, when viewed from above. It is depressed cap-formed when viewed from the side. The nucleus is strongly eccentric, located *c.* one third from top and one quarter from posterior margin. Growth lines are fine; they are expressed as low concentric wrinkles. Halfway between nucleus and shell margin, widely spaced, discontinuous radial riblets occur (*c.* 20 on lower half of the shell). Near the margins densely spaced radial riblets instantaneously appear, *c.* 50 at lower half of the shell.

Dimensions – RGM 456 512: H 1.9; W 2.0 (W for undamaged specimen estimated at *c.* 2.5).

Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Family Orthalicidae Albers & von Martens, 1860
Genus *Orthalicus* Beck, 1837

Type species – *Buccinum zebra* Müller, 1774, extant, probably South America (see Nuttall, 1990, p. 262).

***Orthalicus* sp.**
Fig. 275.

Material studied – RGM 456 552 (*c.* 20 fragments), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996. RGM 456 553 (fragment of body whorl), Zaragoza (Amazonas, Colombia), exposure in north bank Amazon River, 300 m east of landing stage (3°52'S 70°11'W), level F34 (0.5 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Description – Conical *Orthalicus* with a slightly irregularly arranged microsculpture of very low and poorly defined knobs that are arranged in spiral bands, often completely worn. The periphery is acutely rounded and located low on the whorl.

Dimensions – RGM 456 552: (H largest fragment) 11 mm. RGM 456 553: H 32, W 33.

Range – Pebas Formation, MZ9-MZ11 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Remarks – Only fragments are available of the terrestrial *Orthalicus* sp. precluding further description. This species differs from *Orthalicus linteus* (Conrad, 1871, Miocene, Pebas Formation, Santa Rosa de Pichana, Peru; see Nuttall, 1990, p. 262, for extensive description) by the very subdued nature of the micro-ornamentation, the location of the periphery lower on the whorl and the more acutely rounded nature of that periphery in *Orthalicus* sp.

Family Acavidae Pilsbry, 1895
Genus *Pebasiconcha* Wesselingh & Gittenberger, 1999

Type species – *Pebasiconcha immanis* Wesselingh & Gittenberger, 1999, Miocene, Pebas Formation, Colombian and Peruvian Amazonia.

Pebasiconcha immanis Wesselingh & Gittenberger, 1999
Fig. 274.

1999 *Pebasiconcha immanis* Wesselingh & Gittenberger, p. 67, figs. 1, 2.

Material studied and dimensions – See Wesselingh & Gittenberger (1999, p. 67).

Diagnosis – Shell very large (H >250); body whorl very large, but adnate aperture markedly constricted; slightly behind the upper part of the outer lip, a massive knob occurs on the exterior of the shell.

Range – Pebas Formation, MZ7 - MZ10 (Middle - early Late Miocene), Colombian and Peruvian Amazonia. Fragments of this species have also been observed in lignites in Peruvian localities assigned to MZ4 and MZ5, extending its range down to the late Early - early Middle Miocene.

Class Bivalvia
Family Tellinidae de Blainville, 1814
Genus *Macoma* Leach, 1819

Type species – *Macoma tenera* Leach, 1819 (= *Tellina calcarea* Gmelin, 1791), Recent, northern Atlantic Ocean.

Macoma sp.
Figs. 276-279.

1998 *Psammotreta* sp. Vonhof *et al.*, p. 88 (table).

Material studied – RGM 456 384 (damaged pair), Buenos Aires (Amazonas, Colombia), exposure in cliff at south bank Rio Cotuhé, below village (3°23'S 70°25'W), collect-

Figs. 276-279. *Macoma* sp. ►

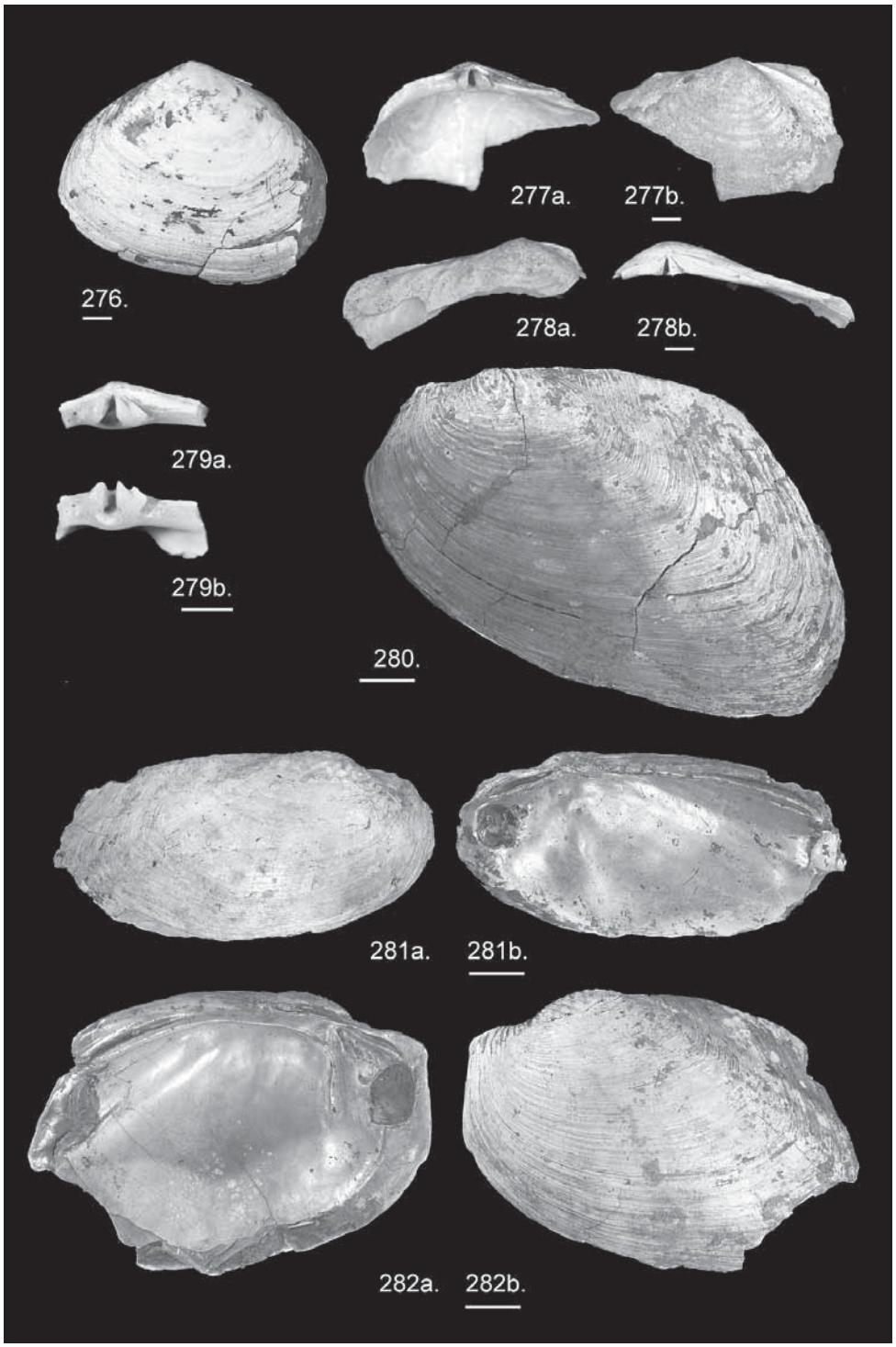
Fig. 276. RGM 456 384, Buenos Aires (Amazonas, Colombia). LV view of paired specimen.
Fig. 277. RGM 456 398, same locality as Fig. 276. a, RV fragment interior. b, exterior.
Fig. 278. RGM 456 400, same locality as Fig. 276. a, RV fragment exterior. b, interior.
Fig. 279. RGM 456 399, same locality as Fig. 276. a, RV fragment interior. b, oblique interior view showing bifid nature of posterior cardinal tooth.

Scale bars represent 1 mm.

Figs. 280-282. *Diplodon longulus* (Conrad, 1874a).

Fig. 280. RGM 456 386, Santa Rosa de Pichana (Loreto, Peru). LV view of paired specimen.
Fig. 281. INGEMMET TN25, same locality as Fig. 280. a, RV exterior. b, RV interior.
Fig. 282. RGM 456 387, Pebas/Santa Julia (Loreto, Peru). a, LV interior. b, LV exterior.

Scale bars represent 10 mm.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281a.
281b.
282a.
282b.

ed from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F. P. Wesselingh, 9-1991. RGM 456 398 - RGM 456 400 (RV fragments) and UNC nn., same locality, level F49c (2.7 m above DL).

Description – Intermediate (L 22), slightly triangular and flat *Macoma*. The surface, if well-preserved, contains numerous fine commarginal low riblets. Wear may produce a coarse concentric pseudo-ribbing. The posterior end and plane of commissure are slightly twisted. Two well-defined cardinal teeth in the RV are separated by a deep, elongate-triangular depression. The anterior cardinal is erect with a triangular cross-section of the base. The RV posterior cardinal tooth is uncommonly bifurcate, but in one specimens it is entire. A prominent flaser-like ligament area is located near posterodorsal margin.

Dimensions – RGM 456 384: H 19.7; L 22.3. RGM 456 398: L 8.9. RGM 456 399: L 8.2. RGM 456 400: L 2.7.

Range – Pebas Formation, MZ8 - MZ9 (late Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Family Hyriidae Swainson, 1840
Genus *Diplodon* Spix *in* Spix & von Wagner, 1827

Type species – *Diplodon ellypticum* Spix *in* Spix & von Wagner, 1827, Recent, Sao Francisco River, eastern Brazil (Nuttall, 1990, p. 265).

Diplodon longulus (Conrad, 1874a)
Figs. 280-282.

1874a *Triqueta longula* Conrad, p. 29 (*pars*), pl. 1, fig. 10 (*non* fig. 13).
1928 *Prodiplodon singewaldi* Marshall, p. 2. pl. 1, figs. 3, 6.
1928 *Prodiplodon bassleri* Marshall, p. 3. pl. 1, fig. 1.
1928 *Eodiplodon gardnerae* Marshall, p. 4. pl. 1, figs. 2, 8.
1928 *Prodiplodon paucarpatensis* Marshall, p. 4, pl. 1. fig. 4.
1928 *Eodiplodon pebasensis* Marshall, p. 5. pl. 1, figs. 5, 7.
1938 *Hyria* sp. de Greve, p. 20, pl. 7, figs. 24, 25.
1966 *Triplodon latouri* Pilsbry [*sic*]; Willard, p. 90, pl. 56, fig. 1.
1990 *Diplodon (Diplodon) longulus* (Conrad); Nuttall, p. 270, fig. 302.
1990 *Diplodon* sp. Nuttall, p. 271, figs. 303-305.

Material studied – INGEMMET TN25 (RV) andd RGM 456 386 (pair), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. RGM 456 387 (LV), Pebas/Santa Julia (Loreto, Peru), exposure in north bank Amazon River, 2550 m east of naval base Pijoyal (base at 3°20'S 71°50'W), shell collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 10-1991.

Diagnosis – Shell large (L *c.* 80), equivalve, inaequilateral; umbo located at *c.* one-fifth from the anterior side; shape varies from nearly straight-sided, wedge-formed to (usually more convex) elliptical; posterior margin extended, straight to slightly curved; postero-ventral margin more or less rounded to angular; the short posterodorsal margin tends to be bluntly alate in well-preserved specimens; on the umbonal area an irregular chevron sculpture is developed around a single median 'V'; ribs fade shortly from the umbo; isolated rib fragments on anterior-ventral area rare; area below the postero-dorsal margin slightly depressed; hinge robust; posterior lateral area slightly higher than anterior lateral; adductors deeply impressed.

Dimensions – INGEMMET TN25: H 365; L 726; SD 136. RGM 456 386: H 637; L 902; SD 145. RGM 456 387: H 564; L 753; SD 184.

Range – Pebas Formation, MZ5 - MZ11 (late Early - early Late Miocene), Peruvian and Colombian Amazonia; possibly (as *D*. cf. *longulus*) also Solimões Formation (Late Miocene), Brazilian Amazonia (Wesselingh *et al*., 2006d).

Remarks – This species exhibits a wide variety of outlines that, for example, led Marshall (1928) to attribute material to five species (in two genera). However, intermediate forms between the ovate-elliptical, convex (in cross-section) shells and comparatively higher flatter specimens have been found, indicating that we are dealing with a single species. *Diplodon longulus* is found in low numbers in almost all mollusc assemblages in the Pebas Formation (Wesselingh *et al*., 2002), bar from the profundal lacustrine *Pachydon obliquus* assemblage. Lacustrine specimens (from the small *Dyris* assemblage) are relatively flat and high, whereas shells from marginal lacustrine and fluviolacustrine assemblages are usually thicker, more convex and more elliptical.

***Diplodon amygdalaeformis* sp. nov.**
Figs. 283, 284.

Type material – RGM 456 390 (holotype, LV) and INGEMMET TN27 (paratype, LV), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 50 m north of southern tip of village (4°15'S 73°23'W), level F702 (0.3 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.

Range – Pebas Formation, MZ8 - MZ9 (late Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the almond-shape (Greek, *amygdale* for almond).

Diagnosis – Small (L *c.* 40), thin-shelled, almond-shaped mussel covered with *c.* 15-20 rather coarse radial ribs that cover about four fifths of the shell; a single V shaped chevron zone present in the centre.

Description – The shell is almond-shaped. The umbo is located at two fifths distance from the anterior end. The postero-dorsal margin is rounded, with a poorly defined,

very slight and rounded angle halfway. The posterodorsal and ventral margins meet at a more distinct rounded angle that corresponds to a low, irregular posterior ridge. The posterior part of the ventral margin is slightly concave. The lower margin is evenly rounded. At the anterior end it grades into the dorsal margin through a sharp rounding. The antero-dorsal margin is almost straight. The shell has 15-18 well-developed radial ribs that centre on a tightly angled median 'V'. Interspaces are about twice as wide as the ribs and contain numerous fine growth lines. The ribs cover about four fifths of the shell and break apart into irregular, elongate pustules on the lower part. The posterodorsal margin has several, variably developed, but low, diverging riblets. Remains of olive-grey-green periostracum are present on many of the specimens. The interior of the shells is made up of brilliant, slightly greyish nacre. The adductor scars are relatively small, equidimensional and connected by a fine, well-defined pallial line that is located at some distance from the shell margin. the cardinal area in the holotype is somewhat abraded and covered with matrix. The two postero-lateral teeth are elongate, sharply erect (almost lamellar) blades separated by a narrow and deep depression. The lower of the two is the most prominent. The ligament area is prominent and becomes slightly wider posteriorly. A small, but robust, triangular erect cardinal is present in the paratype. The posterior laterals are again elongate, blade-like, with a deep spatulous depression between. The dorsal side of the lower lateral is distinctly grooved radially.

Dimensions – RGM 456 390: H 400; L 282; SD 104. INGEMMET TN27: H >349; L >275, SD 99.

Remarks – This species is differs from any other Pebasian hyriid in its shorter and higher outline, the almond shape and the far extension of the radial ribs on the shell. The almond-shape distinguishes it from *Diplodon biblianus* (Marshall & Bowles, 1932) from the Miocene Loyola Formation of the Cuenca basin in Ecuador, that furthermore contains several chevrons instead of a single median 'V' ornament on the shells exterior. The poorly preserved *Diplodon* aff. *bristowi* Parodiz, 1982 (*in* Bristow & Parodiz, 1982; see Nuttall, 1990, p. 273, fig. 311) from the La Tagua beds has a cuneate outline and appears to have more irregular ribbing on the exterior of the shell, as well as a straight lower margin.

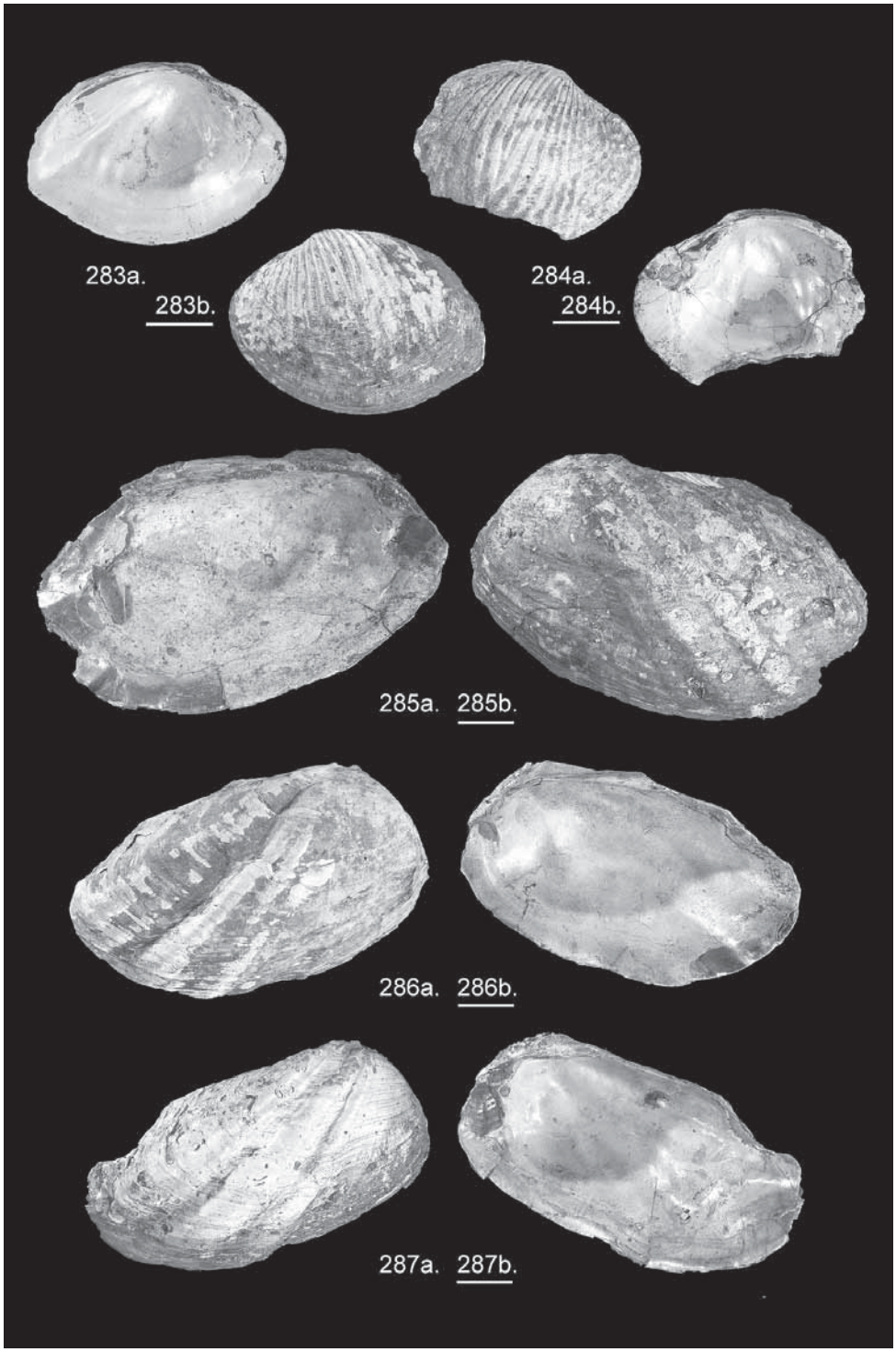
Figs. 283, 284. *Diplodon amygdalaeformis* sp. nov. ▶

Fig. 283. RGM 456 390, holotype, Porvenir (Loreto, Peru). a, LV interior. b, LV exterior.
Fig. 284. INGEMMET TN27, paratype, same locality as Fig. 283. a, RV exterior. b, RV interior.

Figs. 285-287. *Diplodon indianensis* sp. nov.

Fig. 285. INGEMMET TN28, holotype, Mazan (Loreto, Peru). a, LV interior. b, LV exterior.
Fig. 286. RGM 456 391, paratype, same locality as Fig. 285. a, RV exterior. b, RV interior.
Fig. 287. RGM 456 392, paratype, same locality as Fig. 285. a, RV exterior. b, RV interior.

Scale bars represent 10 mm.


283a.
283b.
284a.
284b.
285a. 285b.
286a. 286b.
287a. 287b.

Despite the huge progress made by Nuttall (1990) in clarifying the supraspecific arrangement of fossil unionoids of South American, the definition of genera and subgenera within the material awaits a further revision. The current species would easily fall within the subgenus *Diplodon (Ecuadorea*) Marshall & Bowles, 1932, as used by Nuttall (1990, p. 271), but the unresolved supraspecific nature of the entire family precludes me from using subgenera for the moment.

***Diplodon indianensis* sp. nov.**
Figs. 285-287.

Type material – INGEMMET TN28 (holotype, LV), Mazan (Loreto, Peru), exposure at east bank Rio Napo, *c.* 900 m south of port (3°30'S 73°06 'W), level F902 (1.0 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 1-10-1996. RGM 456 391 and 456 392 (both RV, paratypes), and 456 393 (paratypes, three damaged valves), all same locality.

Range – Pebas Formation, MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the village of Indiana (Loreto, Peru), where this species was found commonly in exposures nearby.

Diagnosis – Strongly inequilateral, elongate ovate to kidney-shaped, convex *Diplodon* with three to five characteristic wide ribs that run from the umbo to the posteroventral margin.

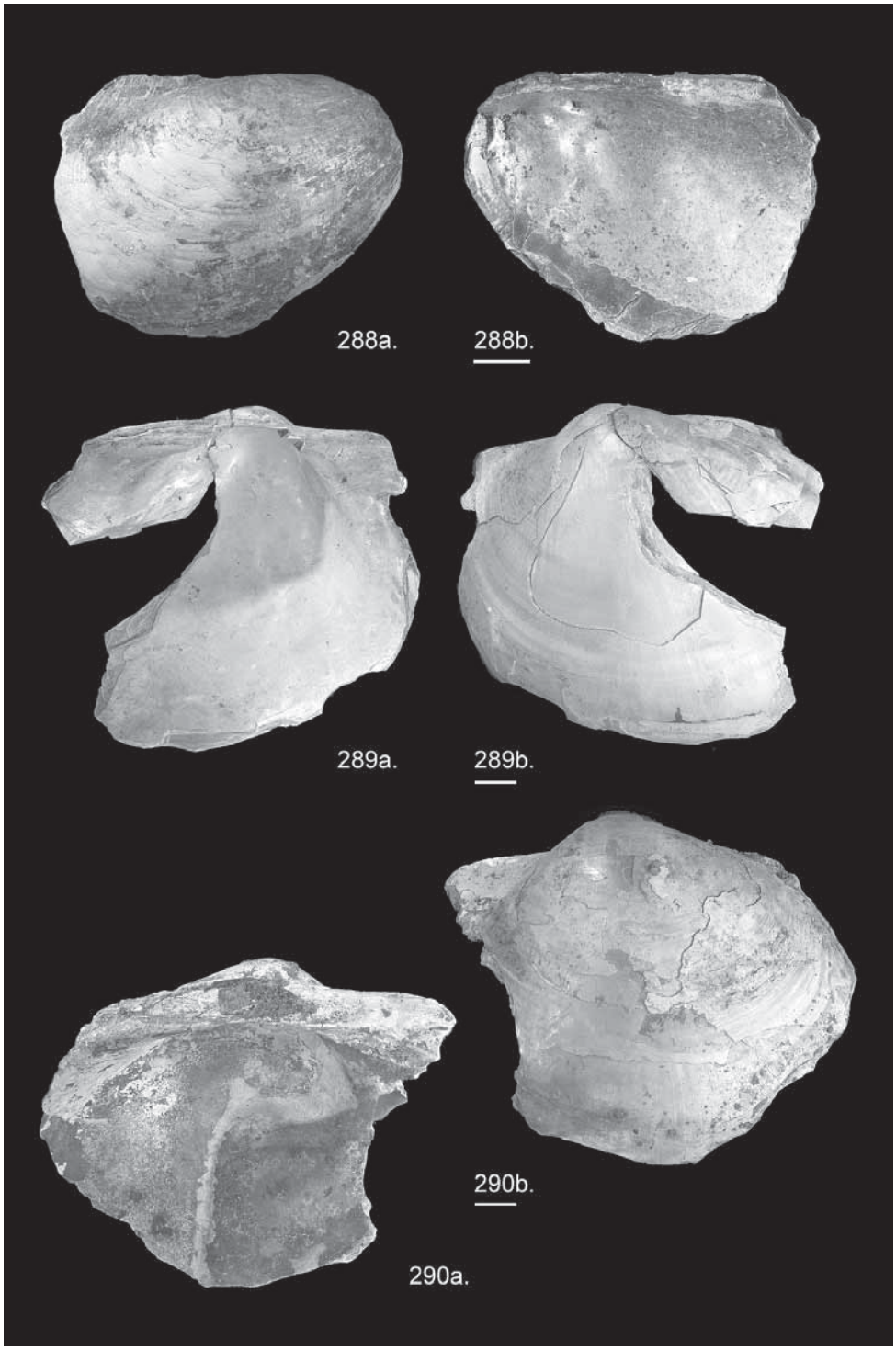
Description – The umbo is located at *c.* one sixth from the anterior margin. The posterodorsal margin is at first horizontal, but dips after a rounded angle about halfway. The posterior end is rounded. The ventral margin is broadly rounded, but curving more upward at the anterior than at the posterior side. The anterior tip is rounded in adults, but is higher and distinctly alate in juveniles. The anterodorsal margin is short, straight and horizontal in subadults, dipping and subrounded in adults. The shell outlines and convexity show considerable variation. A chevron ornament of irregular, knobby radial ribs around a single, irregular median 'V' is present in the umbonal region, but disappears soon after. At the anterodorsal side these ribs may extend to anterior margin, but they become very thin, almost thread-like. Some isolated, thread-like radial rib fragments are also present on the adjacent part of the antero-ventral margin. At least three,

Figs. 288. *Anodontites batesi* (Woodward, 1871). RGM 456 388, Los Chorros (Amazonas, Colombia). a, RV exterior. b, RV interior. ▶

Figs. 289, 290. *Anodontites capax* (Conrad, 1874b).

Fig. 289. RGM 456 389, Los Chorros (Amazonas, Colombia). a, LV interior. b, LV exterior.
Fig. 290. INGEMMET TN26, San Antonio Itaya (Loreto, Peru). a, LV interior. b, LV exterior.

Scale bars represent 10 mm.


288a.
288b.
289a.
289b.
290b.
290a.

but up to five wide and low radial ribs run from the umbonal area to the posteroventral margin. The posterior rib is actually a posterior ridge and is the strongest, bounding a posterior slope. Anteriorly, ribs become progressively lower and less distinct. Fine growth lines are numerous and often very well preserved between the radial ribs. The hinge is severely damaged in all studied specimens. The posterior lateral teeth are long, blade-like and separated by a narrow, elongate depression that is ornamented by horizontal grooves on the dorsal side. The posterior adductor is deeply embedded and slightly behind/above lays a small, deeply impressed, semicircular retractor scar. A poorly defined, often almost invisible, pallial line connects the adductors.

Dimensions – All material has damaged edges. INGEMMET TN28: H *c.* 570; L *c.* 760; SD *c.* 225. RGM 456 391: H *c.* 460; L *c.* 670; SD *c.* 220. RGM 456 392: H *c.* 455; L *c.* 650; SD *c.* 210.

Remarks – The three or more wide ribs that run from the umbo the posteroventral area make this species distinct from all other *Diplodon* species.

Family Mycetopodidiae Gray, 1840
Genus *Anodontites* Bruguière, 1792

Type species – *Anodontites crispata* Bruguière, 1792, Recent, French Guyana (see Nuttall, 1990, p. 274).

***Anodontites batesi* (Woodward, 1871)**
Fig. 288.

1871 *Anodon batesi* Woodward, p. 103, pl. 5, fig. 10.
1874a *Anodonta pebasana* Conrad, p. 29, pl. 1, fig. 5.
1878 *Anodonta batesi* (Woodward); Boettger, p. 498.
1990 *Anodontites (Anodontites) batesi* (Woodward); Nuttall, p. 275, fig. 315.

Material studied – RGM 456 388 (RV), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence Loreto Yacu (3°46'S 70°22'W), presumably level F16 of Wesselingh (1991; 14.5 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. M.C. Hoorn, 1989.

Diagnosis – Intermediate-large (L *c.* 70), elongate, flat, extremely inaequilateral *Anodontites*, with minute beaks located at *c.* one fifth from the anterior margin; posterior hingeline long and straight; anterior part of shell tapering; hinge edentulous.

Dimensions – RGM 456 388: H 543; L 583; SD >150.

Range – Pebas Formation, MZ7 - MZ11 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

***Anodontites capax* (Conrad, 1874b)**
Figs. 289, 290.

1874b *Haplothaerus capax* Conrad, p. 83, pl. 12, figs. 1-3.

1938 Nayadidae de Greve, p. 19, text-fig. 1.
1966 *Anodontites lacivansis* [*sic*] Pilsbry & Olsson; Willard, pl. 56, fig. 1.
1990 *Anodontites capax* (Conrad); Nuttall, p. 274, fig. 314.

Material studied – INGEMMET TN26 (LV), San Antonio Itaya (Loreto, Peru), exposure in west bank Rio Itaya at southern side of the village (4°02'S 73°23'W), level F810 (6.9 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996. RGM 456 389 (LV), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence Loreto Yacu (3°46'S 70°22'W), presumably level F16 of Wesselingh (1991: 14.5 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. M.C. Hoorn, 1989.

Diagnosis – Shell large (estimated L 150), thick, slightly alate, comparatively round; umbo slightly in front of middle of shell; surface smooth apart from vague, low, concentric ribs and growth lines; hinge area well-developed, wide, slightly curved; hinge edentulous, with wide ligament area.

Dimensions – INGEMMET TN26: H 855; L 1050; SD 308. RGM 456 389: H 864; L 925; SD *c.* 290.

Range – Pebas Formation, MZ7 - MZ10 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

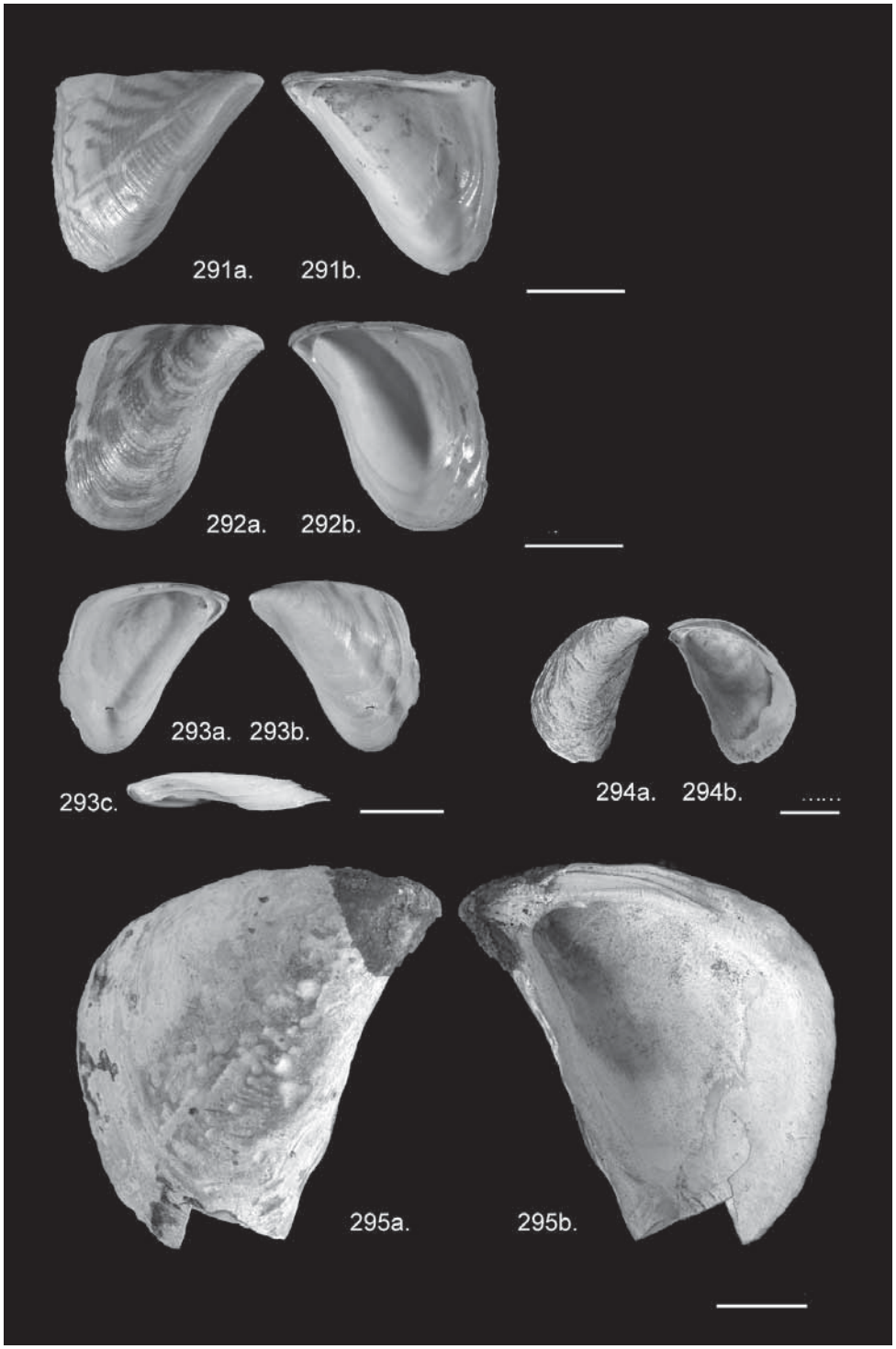
Remarks – This large species easily disintegrates. As a result, it is difficult to collect and has few references in the literature despite being common in fluviolacustrine assemblages of the Pebas Formation.

Family Dreissenidae Gray, 1840
Genus *Mytilopsis* Conrad, 1858

Type species – *Mytilus leucophaetus* Conrad, 1831, Recent, coastal rivers, eastern United States, secondarily introduced elsewhere (Nuttall, 1990).

Mytilopsis scripta (Conrad, 1874a)
Fig. 291.

1874a *Dreissena (Mytiloides) scripta* Conrad, p. 29, pl. 1, figs. 12, 16.
? 1878 *Dreissena fragilis* Boettger, p. 496 (*pars*), pl. 13, figs. 16, 18 (*non* fig. 17a-c).
1879 *Dreissena acuta* Etheridge, p. 82, pl. 7, fig. 1.
1924 *Dreissena acuta* Etheridge; Roxo, p. 44 (*pars*), figs. A3, A4, A'3, A'4 (*non* figs. A1, A2, A'1, A'2).
1935 *Mytilopsis cira* Pilsbry & Olsson, p. 19, pl. 5, fig. 2.
1938 *Congeria scripta* (Conrad); de Greve, p. 56, pl. 9, figs. 4, 5, 10, 12; text-figs. 4, 5.
1938 *Congeria fragilis* (Boettger); de Greve, p. 49 (*pars*), pl. 9, figs. 8, 9, 14 (*non* fig. 15).
1938 *Congeria* cf. *fragilis* (Boettger); de Greve, p. 51, pl. 9, figs. 19, 20.
1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. I de Greve, p. 53, pl. 9, figs. 13, 16, 17.
1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. IV de Greve, p. 55, pl. 9, figs. 18, 21, 22.
1990 *Mytilopsis scripta* (Conrad); Nuttall, p. 285, figs. 345-351.


291a.
291b.
292a.
292b.
293a.
293b.
293c.
294a.
294b.
295a.
295b.

Material studied – RGM 456 600 and INGEMMET TN92, Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

Diagnosis – Thin-shelled *Mytilopsis* with straight or nearly straight dorsal margin and acute ventral ridge; shell outline triangular; ventral side commonly straight or slightly concave; irregular, fuzzy, zigzag colour pattern common; apophysis elongate, located adjacent to dorsal margin, partially under the septum.

Dimensions – RGM 456 600: H 9.7; L 11.1; SD 3.5. INGEMMET TN92: H 10.3; L 10.1; SD 2.7.

Range – Miocene Subandean basins (part of which are today intramontane) from the Magdalena Basin (Colombia) in the north to the Marañon Basin (Peru) in the south, Early to early Middle Miocene (MZ1-MZ4), and Pebas Formation, Peruvian, Brazilian and Colombia Amazonia, MZ5-MZ12 (late Early to early Late Miocene). The species appears to be absent during MZ4 in the Pebas Formation.

Mytilopsis sallei (Récluz, 1849)

Figs. 292-295.

1849 *Dreissena sallei* Récluz, p. 69.
1878 *Dreissena fragilis* Boettger, p. 496 (*pars*), pl. 13, fig. 17 (*non* figs. 16, 18).
1924 *Dreissena acuta* Etheridge; Roxo, p. 44 (*pars*), figs. A1, A2, A'1, A'2 (*non* figs. A3, A4, A'3, A'4).
1938 *Congeria fragilis* (Boettger); de Greve, p. 49 (*pars*), pl. 9, fig. 15 (*non* figs. 8, 14).
1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. II de Greve, p. 54, pl. 9, figs. 23-25, 27.
1938 *Congeria* n. sp. aff. *fragilis* (Boettger) var. III de Greve, p. 54, pl. 9, fig. 26.
1966 *Anisothyris obliqua* (Gabb); Willard, p. 65, pl. 57, figs. 2, 3.
1989 *Mytilopsis lopesi* Alvarenga & Ricci, p. 27, figs. 1-9.
1990 *Mytilopsis sallei* (Récluz); Nuttall, p. 280, figs. 327-344.

Material studied – INGEMMET TN93 (RV), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S

◀ Figs. 291. *Mytilopsis scripta* (Conrad, 1874a). RGM 456 600, Santo Tomas Amazon (Loreto, Peru). a, RV exterior. b, RV interior.

Figs. 292-295. *Mytilopsis sallei* (Recluz, 1849).

Fig. 292. INGEMMET TN93, Santo Tomas Amazon (Loreto, Peru). a, RV exterior. b, RV interior.
Fig. 293. RGM 456 603, Santa Elena (Loreto, Peru). a, LV interior. b, LV exterior. c, LV lateral view of dorsal margin showing concavity. Scale bar represents 2 mm.
Fig. 294. RGM 456 602, Barradero de Omagua (Loreto, Peru). a, RV exterior. b, RV interior. Scale bar represents 2 mm.
Fig. 295. RGM 456 601, same locality as Fig. 294. a, RV exterior. b, RV interior.

Scale bars represent 5 mm unless stated otherwise.

71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 601 (RV) and 456 602 (juvenile RV), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996. RGM 456 603 (LV), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, *c.* 300 m east of wood mill and *c.* 1.5 km east of Santo Tomas (3°52'S 71°23'W), level F498 (5.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996.

Diagnosis – *Mytilopsis* with gently curved, faintly convex dorsal margin and ventral ridge; ventral side commonly slightly concave; shell of variable strength, but the exterior commonly bears irregular concentric elevations; apophysis elongate and located adjacent to the dorsal margin, partially under the septum; byssal depression on shell exterior just below umbo common.

Dimensions – INGEMMET TN93: H 10.6; L 10.1; SD 3.1. RGM 456 601: H 21.9; L 22.4; SD 5.3. RGM 456 602: H 4.5; L 5.0; SD 1.3. RGM 456 603: H 4.0; L 4.1; SD 0.8.

Range – Oligocene-Recent, Caribbean, extending up to Tocantins River (northern Brazil) in the east and the coastal areas of Ecuador in the west; Miocene, northwestern South America; presumably introduced in India, West Africa and Fiji (see Nuttall, 1990, p. 283).

Remarks – The generally curved dorsal margin, as well as the wide and rounded posterior ridge, distinguish *Mytilopsis sallei* from *M. scripta*. The range of morphological variation in *M. sallei* in the Pebas fauna is very large. Most specimens conform to the general form illustrated by Nuttall (1990, figs. 327-344; see Fig. 292a-b herein). However, in some populations very flat specimens occur with a concave ventral margin, possibly for byssus attachment, in side view (Fig. 293a-c). Intermediates with regular forms occur indicating this to be an ecophenotype, presumably adapted to fluid bottoms (this form is found in lacustrine assemblages of Wesselingh *et al.*, 2002). In several samples with typical fluvial faunas, a large, low, robust form with a marked rounded dorsal margin is found (Figs. 294, 295). This form has a very broad dorsal ligament groove, but is otherwise connected with intermediate forms to the typical forms of *M. sallei*. The broad form resembles *M. sallei* described from the Tocantins River in eastern Brazil (Alvarenga & Ricci, 1989, as *Mytilopsis lopesi*).

Family Corbiculidae Gray, 1847
Genus *Corbicula* Gray, 1847 [1]

Type species – *Corbicula fluminalis* (Müller, 1774), indigenous in southern and eastern Asia, but expanded in the last century into Africa, Europe and the United States.

[1] *Note added in proof.* I was pointed by Cristián Ituarte (Museo de La Plata, Buenos Aires, Argentina) to the fact that the Pebasian corbiculids possess a short pallial sinus, which is indicative for the exclusively neotropical freshwater genus *Corneocyclas*. The Pebasian corbiculids should therefore be placed in that genus. I thank Cristián Ituarte for this addition.

Corbicula cf. *cojitamboensis* Palmer *in* Liddle & Palmer, 1941

Figs. 296-299.

1941 *Corbicula (Cyanocylas) cojitamboënsis* Palmer *in* Liddle & Palmer, p. 408, pl. 9, fig. 6.
? 1941 *Corbicula (Cyanocylas) pacchiana* Palmer *in* Liddle & Palmer, p. 407, pl. 9, fig. 5.
? 1945 *Corbicula (Cyanocylas) desolai* Palmer, p. 19, pl. 2, figs. 8, 12, 13, 16.
? 1945 *Corbicula (Cyanocylas) monagasensis* Palmer, p. 20, pl. 2, figs. 9-11, 14, 15.
1982 *Neocorbicula cojitamboensis* (Palmer); Bristow & Parodiz, p. 29, figs. 6, 7.

Material studied – INGEMMET TN41 (LV) and TN42 (juv. RV), and RGM 456 438 (juv. LV) and 456 439 (subadult RV), Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991.

Diagnosis – Subtriangular to semicircular flat (juvenile) to inflated and high (adult) *Corbicula*; umbo at two fifths distance from anterior; anterior margin relatively high and short, posterior margin long, regularly sloping and merging into slightly tapering posterior end; dorsal margin rounded; growth lines numerous, fine; regular concentric ribbing on adult shells; cardinals bifid; lateral teeth long, finely serrate; posterior adductor located slightly higher in shell than anterior adductor; pallial line with small sinus.

Dimensions – INGEMMET TN41: H 13.4; L 15.5; SD 5.2. INGEMMET TN42: H 3.8; L 4.3; SD 1.1. RGM 456 438: H 3.9; L 4.6; SD 1.1. RGM 456 439: H 6.1; L 6.4; SD 2.1.

Range – Pebas Formation, MZ8 - MZ10 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia; Loyola and Mangan Formations (Middle-Late Miocene), Cuenca basin, Ecuador, Las Piedras Formation? (Pliocene), eastern Venezuela basin (see remarks below).

Remarks – The status and distribution of this species is in need of further study. *Corbicula* species are common in Neogene Andean fluvial deposits, but the Andean fossil shells often have suffered compaction and deformation. As a result it is currently almost impossible to assess the taxonomic status of these corbiculids. Within the Pebas fauna, *C.* cf. *cojitamboensis* occurs infrequently in samples. Usually populations are made up entirely of juveniles.

Family Sphaeriidae Deshayes, 1854
Genus *Eupera* Bourguignat, 1854

Type species – *Pisidium (Eupera) moquinianum* (Bourguignat, 1854), Recent, Congo, Africa.

Eupera sp.

Figs. 300, 301.

Material studied – INGEMMET TN39 (LV) and RGM 456 436 (RV), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S 72°23'W),

level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Description – Large, rather flat *Eupera*. The umbo is located at *c.* one third of the shell length. The posterior margin is widely rounded. The anterior margin is also rounded, but very slightly tapering as well. The shell contains broad growth lines. The lateral teeth are well-defined, but rather short. The posterior lateral tooth is located about halfway from the postero-dorsal margin. The anterior lateral tooth lays about halfway from the antero-dorsal margin. The adductor scars and pallial line are well visible in the slightly thickened shell. The surface within the pallial line is rugose, with a number of horizontally arranged ovate scars just above the pallial line in some of the specimens.

Dimensions – INGEMMET TN39: H 4.3; L 5.2; SD 1.3. RGM 456 436: H 4.7; L 6.1; SD 1.4.

Range – Pebas Formation, MZ9 - MZ11 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia; Solimões Formation, Late Miocene, Brazilian Amazonia (Wesselingh *et al*., 2006d).

Genus *Pisidium* Pfeiffer, 1821

Type species – *Pisidium amnicum* (Müller, 1774), Recent, Europe.

Pisidium sp.

Figs. 302, 303.

Material studied – INGEMMET TN40 (RV) and RGM 456 437 (damaged LV), Barradero de Omagua (Loreto, Peru), exposure in east bank Rio Itaya, below village (4°10'S

Figs. 296-299. *Corbicula* cf. *cojitamboensis* Palmer, 1941. ►

Fig. 296. INGEMMET TN41, Nuevo Horizonte (Loreto, Peru). a, LV interior. b, LV exterior. Scale bar represents 5 mm.
Fig. 297. RGM 456 439, same locality as Fig. 296. a, RV exterior. b, RV interior.
Fig. 298. INGEMMET TN42, same locality as Fig. 296. a, RV exterior. b, RV interior.
Fig. 299. RGM 456 438, same locality as Fig. 296. a, LV interior. b, LV exterior.

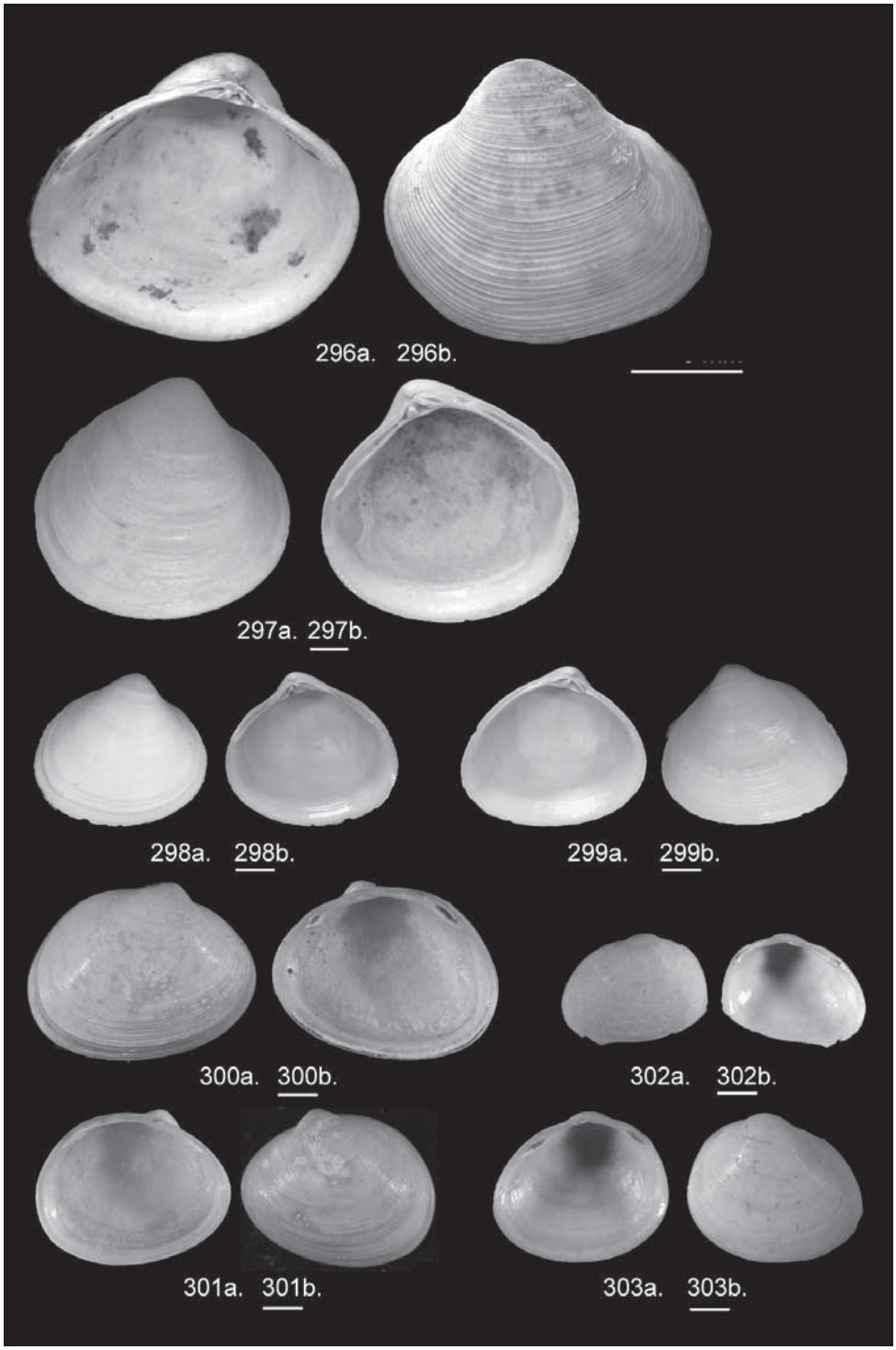
Figs. 300, 301. *Eupera* sp.

Fig. 300. RGM 456 436, Barradero de Omagua (Loreto, Peru). a, RV exterior. b, RV interior.
Fig. 301. INGEMMET TN39, same locality as Fig. 300. a, LV interior. b, LV exterior.

Figs. 302, 303. *Pisidum* sp.

Fig. 302. RGM 456 437, Barradero de Omagua (Loreto, Peru). a, LV exterior. b, LV interior.
Fig. 303. INGEMMET TN40, same locality as Fig. 302. a, RV interior. b, RV exterior.

Scale bars represent 1 mm unless stated otherwise.


296a. 296b.
297a. 297b.
298a. 298b.
299a. 299b.
300a. 300b.
302a. 302b.
301a. 301b.
303a. 303b.

72°23'W), level F800 (3.1 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 13-9-1996.

Description – Thin-shelled, rather high, subquadrangular to ovate *Pisidium*. The umbo is located at *c.* 45% from the nearly straight posterior margin. The postero-dorsal margin is elevated. The ventral margin is broadly rounded. LV laterals are short, but erect. The shell contains fine, regularly spaced growth lines.

Dimensions – INGEMMET TN40: H 2.2; L 2.55; SD 0.65. RGM 456 437: H >1.8; L 2.2; SD 0.55.

Range – Pebas Formation, MZ9 (late Middle - early Late Miocene), Peruvian and Colombian Amazonia.

Remarks – The outline of *Pisidium* sp. closely resembles that of *Pisidium iquito* Ituarte, 2004 (Recent, Peruvian Amazonia). The antero-lateral hinge in the former appears to be slightly more robust, but additional study is needed in order to establish a possible synonymy between these two species.

Family Corbulidae Lamarck, 1818
Genus *Corbula* Bruguière, 1797

Type species – *Corbula sulcata* Lamarck, 1801, Recent, West Africa (subsequent designation).

***Corbula cotuhensis* Wesselingh & Anderson sp. nov.**
Figs. 304-307.

1937 *Corbula* sp. Hedberg, p. 2012, pl. 8, fig. 4.
1998 *Pachydon* cf. *ovalis* Nuttall; Vonhof *et al.*, fig. 5.
1998 *Pachydon cebada* (Anderson); Vonhof *et al.*, p. 88 (table).

Type material – RGM 456 604 (holotype, LV): Buenos Aires (Amazonas, Colombia), exposure in cliff at south bank Rio Cotuhé, below village (3°23'S 70°25'W), level F49c (2.7 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. Paratypes: RGM 456 605 (RV) and 456 606 (pair), LSA nn. (RV), LSU nn. (LV), UNC nn. (RV) and UNC nn. (RV), same locality. RGM 456 607 (pair), same locality, collected from surface scree.

Range – Pebas Formation, MZ6-MZ9 (Middle - early Late Miocene), Peruvian and Colombian Amazonia.

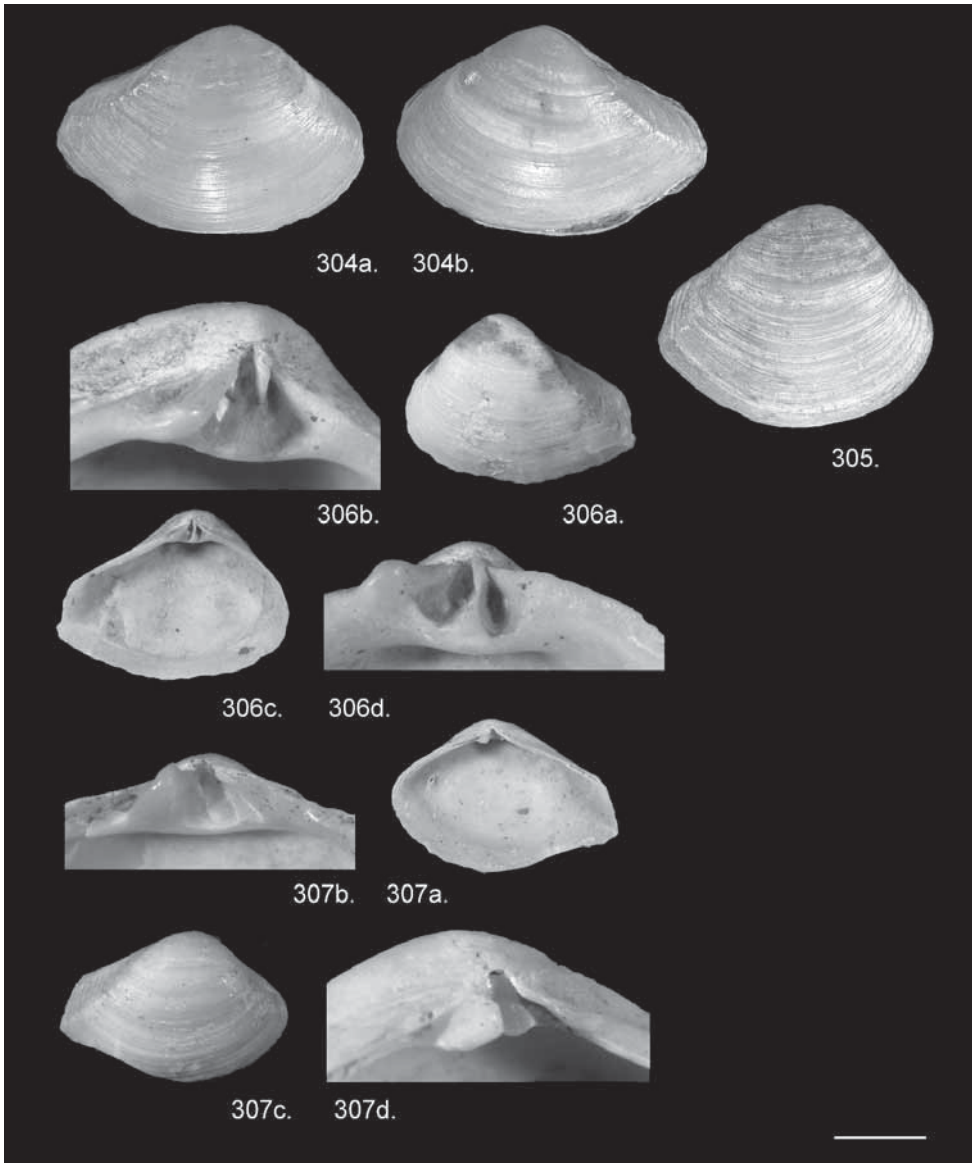
Derivatio nominis – Named after the Cotuhé River in Colombian Amazonia, along which the exposure of Buenos Aires yields the oligohaline faunas where this species is commonly present.

Diagnosis – Medium- to large-sized subovate to subtriangular, slightly inequivalve, more or less smooth corbulid with a markedly bifid LV hinge.

Description – The shell outline is somewhat variable, ranging from elongate subovate to subtriangular. The RV slightly overlaps the LV, which is witnessed by a receiving furrow in the RV on the posterior half near the ventral margin. The commissural plane is slightly undulating. The broad, orthogyrate umbo is located about mid-shell, sometimes slightly to the front. The beaks are indistinct, located slightly below the umbo and orthogyrate. They are in contact. They are bounded below by an erosion hole. The posterior ridge is variably developed, often rounded, but can also be subrounded. The posterior slope is not well delimited, but nevertheless well visible. The posterior end is slightly obliquely truncate. Growth lines are numerous and oblique lineaments may occur on the posterior margin, but are not common. Short radial ribs may develop on the LV at the ventral margin, about mid shell. Traces of radial ribs also may occur at the ventral margin just before the posterior ridge. The RV cardinal is a massive, erect, slightly tapering knob. The RV resilifer is elongate drop-shaped. It is somewhat prosogyrate and the plane is tilted slightly forward. The rear margin of the RV resilifer is elevated, producing a sort of low septum giving the RV hinge a slightly bifid appearance. The LV hinge is distinctly bifid. The socket is deeply conical with massive, robust erect walls. It is separated from an equally deep conical resilifer in front by a massive median septum. The nymph is pronounced, massive, short and erect. Lateral grooves ('teeth') are present on the anterior margin and the rear end of the posterior margin in the RV. The posterior adductor is semicircular, irregular and slightly embedded. The anterior adductor is semilunate, low, and radially and concentrically striate. The broad pallial line is well visible and contains a blunt retraction below the posterior adductor. The anterior retractor is a small, embedded ovate depression lying in front of the anterior adductor. The posterior retractor is an irregular small ovate extension of the posterior adductor.

Dimensions – RGM 456 604: H 9.3; L 12.6; SD 3.7. RGM 456 605: H 8.2; L 12.3; SD 3.5. RGM 456 606: H 10.7; L 13.7; diameter 8.6. RGM 456 607: H 15.5; L 15.0; diameter 7.5. LSU nn.: H 8.2; L 11.1; SD 2.7.

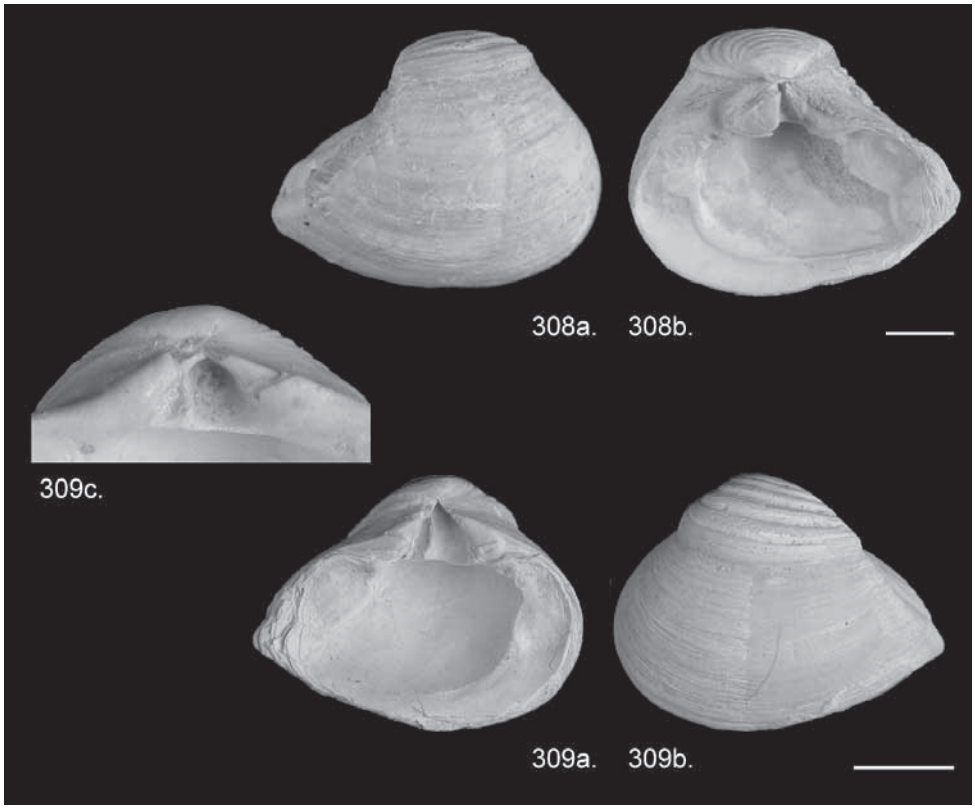
Remarks – Juvenile outlines of some of the higher specimens of *Corbula cotuhensis* resemble *Pachydon trigonalis* Nuttall, 1990. However, the bifid nature of the LV chondrophore in the former separates it from all Pebasian *Pachydon* species. Furthermore, *P. trigonalis* has well developed lateral ridges ('teeth') lacking in *C. cotuhensis*. The bifid LV hinge is a character that *C. cotuhensis* has in common with *C. gatunensis* (Toula, 1909; Miocene, Panama-Venezuela, Figs. 308, 309 herein). The latter species has a very thick shell and coarse commarginal ribs on juvenile and subadult parts of the shell that are lacking in *C. cotuhensis* (Anderson & Roopnarine, 2003). *Corbula gatunensis* is a large (>25 mm maximum length), thick-valved species with a pronounced change in commarginal sculpture during ontogeny, from highly rounded to low irregular. Ornament is highly variable in the genus, however, and the common hinge features clearly unite *C. cotuhensis* and *C. gatunensis*. The cardinal tooth and chondrophore are less robust in *C. cotuhensis* than in *C. gatunensis* and the type species of *Corbula*, *C. sulcata*.



Figs. 304-307. *Corbula cotuhensis* Wesselingh & Anderson, sp. nov.

Fig. 304. RGM 456 607, paratype, Buenos Aires (Amazonas, Colombia). a, RV view of paired specimen. b, LV view.
Fig. 305. RGM 456 606, paratype, same locality as Fig. 304. RV view of paired specimen.
Fig. 306. RGM 456 604, holotype, same locality as Fig. 304. a, LV exterior. b, LV, detail of hinge. c, LV interior. d, LV detail of hinge, oblique view.
Fig. 307. RGM 456 605, paratype, same locality as Fig. 304. a, RV interior. b, RV, detail of hinge. c, RV exteror. d, RV detail of hinge, oblique view.

Scale bar represents 5 mm.



Figs. 308, 309. *Corbula gatunensis* Tula, 1909.

Fig. 308. NMB 13665, Paraguana Peninsula (Falcón, Venezuela), Cantaure Formation, late Early Miocene. a, RV exterior. b, RV interior.
Fig. 309. NMB 13666, same locality as Fig. 308. a, LV interior. b, LV etxerior. c, LV, detail of hinge.

Scale bars represent 5 mm.

However, the nature of the hinges are identical, especially the chondrophore on which a resilifer-like pit develops on the anteroventral surface and a posterior knob on the upper surface of the chondrophore becomes greatly enlarged. This knob represents the left valve 'tooth' in Lamarck's (1801) original description of *Corbula*. In addition, *C. gatunensis* is found in roughly coeval Miocene deposits of Panama and Venezuela as *C. cotuhensis*. The presence of *C. cotuhensis* in Miocene deposits of northeastern Venezuela, and the Caribbean-Panamanian distribution of its close ally *C. gatunensis,* are both indicative for the Neotropical nature of the marine incursion faunas of the Pebas Formation. Other Neotropical marine components in the incursions faunas are *Melongena woodwardi* (Roxo, 1924; Vermeij & Wesselingh, 2002) and *Iolaea amazonica* van Aartsen & Wesselingh, 2005. Various paired specimens of *C. cotuhensis* were found in the Buenos Aires exposure, indicating that the species actually lived there. The co-occurring fauna (including mollusc species, barnacles and bryozoans) and mangrove flora have been interpreted to reflect

oligohaline settings (Vermeij & Wesselingh, 2002), which agrees with strontium isotope geochemical evidence (Vonhof *et al.*, 1998, 2003). Earlier, this species has erroneously been attributed to *Panamicorbula* (Vermeij & Wesselingh, 2002; Wesselingh *et al.*, 2002). This species is almost entirely represented by juveniles in the Pebas fauna; only in the Buenos Aires sample from Colombia were adult specimens found.

Genus *Pachydon* Gabb, 1869

Type species – *Pachydon obliquus* Gabb, 1869, Miocene, Pebas Formation, western Amazonia.

Diagnosis – Extremely variable corbulids, with shells ranging from extremely inequivalve to equivalve, from extremely inaequilateral to equilateral, from convex to flat, with or without rostrum; surface with weak growth lines and commonly with a posterior ridge; umbones and beaks usually prosogyrous, but rarely orthogyrous/ophistogyrous; commissural plane often twisted; RV cardinal usually very prominent; RV resilifer lanceolate; pallial line located well within the edge, entire or acutely truncate posteriorly; shell often markedly thickened anteriorly, anterior adductor embedded; RV margin often grooved for reception LV.

Range – Late Cretaceous? - Paleocene, United States; Miocene, northwestern South America (Venezuela, Colombia, Ecuador, Peru and Brazil).

Remarks – The monophyly of this genus is uncertain (Anderson *et al.*, 2006) and subject of further study. *Pachydon acreanum* Maury, 1937, has been transferred to the unionoid genus *Callonaia* (Wesselingh *et al.*, 2006d).

Pachydon obliquus Gabb, 1869

Figs. 310-312.

1869 *Pachydon obliquus* Gabb, p. 99, pl. 16, fig. 5a-e.
1871 *Pachydon obliquis* [*sic*] Gabb; Conrad, p. 196, pl. 10, fig. 15.
1871 *Anisothyris (Pachydon) obliqua* (Gabb); Woodward, p. 106, pl. 5, fig. 5a-b.
1878 *Anisothyris obliqua* (Gabb); Boettger, p. 501, pl. 14, figs. 18-22.
1878 *Anisothyris obliqua* (Gabb) – *A. carinata* (Conrad), transitional form; Boettger, p. 501, pl. 14, figs. 16, 17.
1938 *Anisothyris obliqua* (Gabb); de Greve, p. 40, pl. 7, figs. 5, 9, 12, 14, 23.
1966 *Anisothyris obliqua* (Gabb); Willard, p. 65, pl. 57, figs. 2, 3.
1990 *Pachydon obliquus* Gabb; Nuttall, p. 292, figs. 358-361.
2006 *Pachydon obliquus* Gabb; Anderson *et al.*, figs. 3-1, 3-2, 3-4, 3-5, 3-8.

Material studied – RGM 456 192 (paired specimen), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ8 (Middle Miocene); leg. F.P. Wesselingh, 1996. RGM 456 193 (paired specimen), Puerto Almendras (Loreto, Peru), exposure in east bank of Nanay River, at landing stage (3°46'S

73°15'W), level F73 (at DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 19-10-1991.

Extended diagnosis – Medium-sized, ovate-circular, strongly convex, thick-shelled and inequivalve corbulid; RV strongly inflated, much larger and more convex than LV; umbones incurved (shells may make up to 1.5 volution; Fig. 312), located at anterior margin; commissure undulating; shell strongly thickened at posterior margin; posterior end rounded to marginally tapering; irregular, poorly defined, low commarginal ridges on exterior; traces of short radial ribs at anterior margin just below apex; hinge extremely robust with very massive, blunt cardinal tooth that is folding upward and has a rugose surface; resilifer deeply behind, tilted downward; extremely deep and prominent socket; adductors well expressed; pallial line impressed deeply within shell and located far from the shells margin, with blunt, slightly irregular short siphonal retraction.

Dimensions – RGM 456 192: RV: H 15.6; L 16.4; SD 8.9; LV: H 12.0; L 15.0; SD 6.6.

Range – Pebas Formation, MZ4 - MZ11 (late Early - early Late Miocene), Peruvian, Brazilian and Colombian Amazonia.

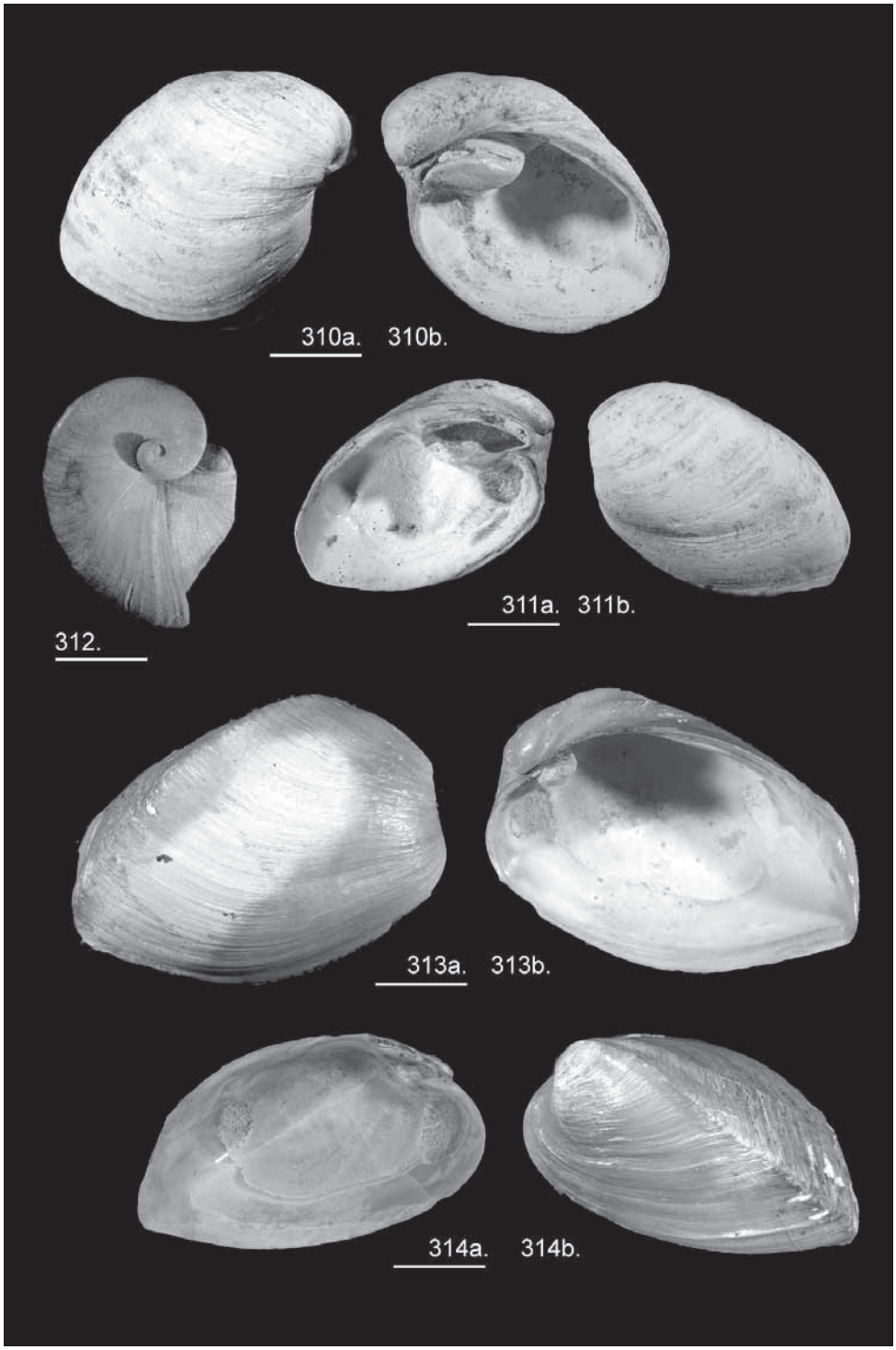
***Pachydon carinatus* Conrad, 1871**

Figs. 313, 314.

1871 *Pachydon carinatus* Conrad, p. 196, pl. 10, fig. 7.
1871 *Anisothyris carinata* (Conrad); Woodward, p. 106, pl. 5, fig. 6.
1872 *Anisothyris carinata* (Conrad); Dall, p. 89.
1878 *Anisothyris carinata* (Conrad); Boettger, p. 501, pl. 14, figs. 23-27.
1879 *Anisothyris carinata* (Conrad); Etheridge, p. 83.
1924 *Anisothyris carinata* (Conrad); Roxo, p. 44.
1938 *Anisothyris carinata* (Conrad); de Greve, p. 43, pl. 9, figs. 1-3, 6, 7.
1990 *Pachydon carinatus* Conrad; Nuttall, p. 296, figs. 368-373.

Material studied – RGM 456 412 (RV) and 456 413 (LV), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F536 (6.6 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996.

Extended diagnosis – Large, ovate-rectangular, robust corbulid with prominent, rather acute dorsal keel; RV strongly inflated, and much larger and more convex than LV; commissure undulating; umbo located near anterior margin; shell thickened at antero-dorsal margins; umbo broadly incurved, prosogyrate; secondary ridges on posterior slope common; irregular, poorly defined, low commarginal ridges on exterior; well-developed oblique riblets around posterior ridge and slope; furrow within RV for corresponding LV well-developed; massive hinge with strong, knob-like, upward curved cardinal tooth that has an irregular rugose surface; RV resilifer almost perpendicular to commissural plane; LV socket deep, massive, subquadrate; elongate LV resilifer located in slight depression on posterior platform; large adductor scars


310a. 310b.
311a. 311b.
312.
313a. 313b.
314a. 314b.

dominated by prominent cauliflower ornamentation; irregular radially modified pallial line that runs slightly towards ventral margin posteriorly, slightly retracted below posterior adductor; anterior retractor scars formed by several small, deeply embedded pits.

Dimensions – RGM 456 412: H 14.7; L 20.9; SD 7.0. RGM 456 413: H 13.4; L 18.8; SD 5.2.

Range – Pebas Formation, MZ4 - MZ11 (late Early - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.

Pachydon tenuis Gabb, 1869

Fig. 315.

1869 *Pachydon tenua* Gabb, p. 199, pl. 16, fig. 6, 6a.
1871 *Anisothyris hauxwelli* Woodward, p. 105, pl. 5. fig. 7a-d.
1871 *Anisothyris hauxwelli* var. α *distorta* Woodward, p. 105.
1871 *Anisothyris hauxwelli* var. β *crassa* Woodward, p. 105.
1871 *Anisothyris hauxwelli* var. α *distorta* Woodward, p. 105.
1871 *Pachydon tenuis* Gabb; Conrad, p. 196, pl. 10, fig. 1, 1a.
1871 *Pachydon ovatus* Conrad, p. 197, pl. 10, fig. 4.
1872 *Corbula (Anisothyris) tenuis* (Gabb); Dall, p. 91.
1874b *Pachydon tenuis* Gabb; Conrad, p. 83, pl. 12, fig. 5.
1878 *Anisothyris tenuis* (Gabb); Boettger, p. 499, pl. 13, fig. 22.
1879 *Anisothyris tenuis* (Gabb); Etheridge, p. 83.
1879 *Anisothyris hauxwelli* Woodward; Etheridge, p. 83.
1924 *Anisothyris hauxwelli* Woodward; Roxo, p. 44.
1938 *Anisothyris tenuis* (Gabb); de Greve, p. 32, pl. 6, figs. 1-3, 5, 9-15.
1966 *Anisothyris hauxwelli* Woodward; Willard, p. 66.
1966 *Anisothyris* cf. *hauxwelli* Woodward; Willard, p. 57, fig. 4.
1966 *Anisothyris tenuis* (Gabb); Willard, p. 68.
1966 *Anisothyris* cf. *tenuis* (Gabb); Willard, p. 58, fig. 1.
1990 *Pachydon tenuis* Gabb; Nuttall, p. 294, figs. 362-367.
2006 *Pachydon tenuis* Gabb; Anderson *et al*., figs. 3-9, 3-12.

◀ Figs. 310-312. *Pachydon obliquus* Gabb, 1869.

Fig. 310. RGM 456 192a, Santa Rosa de Pichana (Loreto, Peru). a, RV exterior. b, RV interior.
Fig. 311. RGM 456 192b, same locality as Fig. 310. a, LV interior. b, LV exterior.
Fig. 312. RGM 456 193, Puerto Almendras (Loreto, Peru). Lateral view of paired specimen showing the coiled umbones.

Figs. 313, 314. *Pachydon carinatus* Conrad, 1871.

Fig. 313. RGM 456 412, Santa Rosa de Pichana (Loreto, Peru). a, RV exterior. b, RV interior.
Fig. 314. RGM 456 413, same locality as Fig. 313. a, LV interior. b, LV exterior.

Scale bars represent 5 mm.

Material studied – RGM 456 435 (paired specimen), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 1996.

Extended diagnosis – Large, ovate, usually inequivalve robust corbulid; RV slightly larger and more convex than LV; umbo one fifth from anterior margin; commissure slightly undulating; well developed prosogyrate umbo; posterior wall of RV cardinal tooth part of exterior of shell; posterior ridge and slope poorly defined; shell with growth lines and traces of short, thin, radial riblets at posteroventral margin on RV; oblique riblets common on posterior margin; low comarginal furrow slightly within edge of RV for reception of LV; RV cardinal large, broadly triangular, curved upward, with

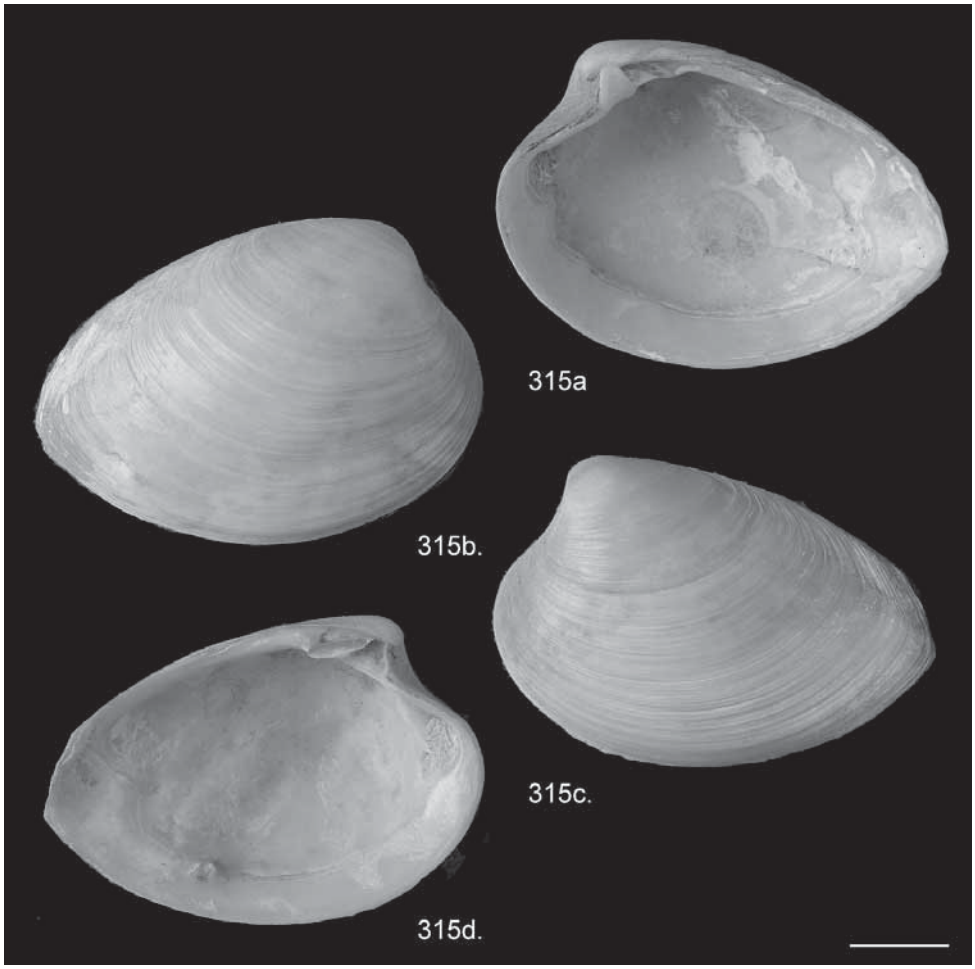


Fig. 315. *Pachydon tenuis* Gabb, 1869. RGM 456 435, Santa Rosa de Pichana (Loreto, Peru). a, RV interior. b, RV exterior. c, LV exterior. d, LV interior. Scale bar represents 10 mm.

uncommonly a central depression; RV resilifer deeply behind cardinal, inclined; LV socket robust, triangular; LV nymph subhorizontal, located on elevated posterior platform; lateral grooves ('teeth') slightly expressed on RV; anterior adductor scar especially prominently embedded, semilunate, with strong cauliflower ornament; comarginal pallial line well defined, broad, with slight radial distortions and lineaments; pallial retraction very subdued; anterior retractor scar formed by a deep, irregular depression between adductor and base of hinge platform.

Dimensions – RGM 456 435: RV: H 35.6; L 46.6; SD 13.1; LV: H 32.1; L 46.0; SD 11.3.

Range – Pebas Formation, MZ5 - MZ11 (late Early - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.

***Pachydon amazonensis* (Gabb, 1869)**

Figs. 316, 317.

1869 *Tellina amazonensis* Gabb, p. 198, pl. 16, fig. 4.
1924 *Tellina amazonensis* Gabb; Roxo, p. 44.
1938 *Anisothyris amazonensis* (Gabb); de Greve, p. 30, pl. 6, figs. 18, 19, pl. 7. figs. 2-4, 7, 8, 10, 11.
1990 *Pachydon amazonensis* (Gabb); Nuttall, p. 308, figs. 409-411 (fig. 412?).

Material studied – INGEMMET TN90 (LV), Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 597 (RV), Pebas/Pijoyal (Loreto, Peru), exposure in north bank Amazon River, 350 m east of naval base Pijoyal (base at 3°20'S 71°50'W), level F427 (0.5 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 24-8-1996.

Extended diagnosis – Medium-sized, nearly equivalve, elongate oval corbulid with slightly tapering posterior end; largest H behind mid shell; RV slightly higher at central and posteroventral margins than LV; umbo *c.* one fifth length from anterior margin; commissure planar to slightly undulating; small ridge may bound a very narrow lunule on RV; umbo broad; beak small, pointed and prosogyrate; posterior ridge and slope indistinct; short radial riblets may develop near ventral margin about mid shell; a thin furrow just within the margin of the shell for reception of LV present in posterior half of RV; hinge platform narrow with a small, somewhat pointed, folded cardinal tooth; elongate-spatulous resilifer is subhorizontal and slightly inclined with respect to commissure; LV socket low, broadly triangular, with elongate subhorizontal resilifer on the base of posterior margin; lateral grooves ('teeth') thin, on entire anterior margin and in the middle part of the posterior margin; pallial line almost invisible, possibly somewhat truncate; adductors irregular semilunate, shallow.

Dimensions – INGEMMET TN90: H 3.5; L 6.8; SD 1.8. RGM 456 597: H 2.9; L 5.2; SD 1.0.

Range – Pebas Formation, MZ5 - MZ12 (late Early - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.

Remarks – Shell smaller, more elongate and more equivalved than *P. tenuis*.

***Pachydon ellipticus* sp. nov.**
Figs. 318, 319.

? 1878 *Anisothyris amazonensis* (Gabb) Boettger, p. 499 (*pars*), pl. 13, figs. 20, 21 (*non* fig. 19).

Type material – INGEMMET TN91 (holotype, RV): Santo Tomas Amazon (Loreto, Peru), exposure in south bank Amazon River, opposite of western tip of Isla San Isidro (3°52'S 71°22'W), level F483 (2.7 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 598 (paratype, LV), same locality.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Named after the elliptical outline.

Diagnosis – Regularly elliptical, small to medium-sized equivalve *Pachydon* with markedly developed lateral ridge and furrows ('lateral teeth').

Description – The shell is often almost perfectly elliptical, with rounded anterior and posterior margins, and almost parallel, elongate dorsal and ventral margins. The broad, slightly prosogyrate umbo, located at *c.* one quarter length from the anterior margin, hardly protrudes from the dorsal margin. The beaks are very small and prosogyrate. Neither posterior ridge nor slope is developed. The left valve is marginally higher at the postero-ventral margin than the RV. The shells are rather flat and moderately thickened:

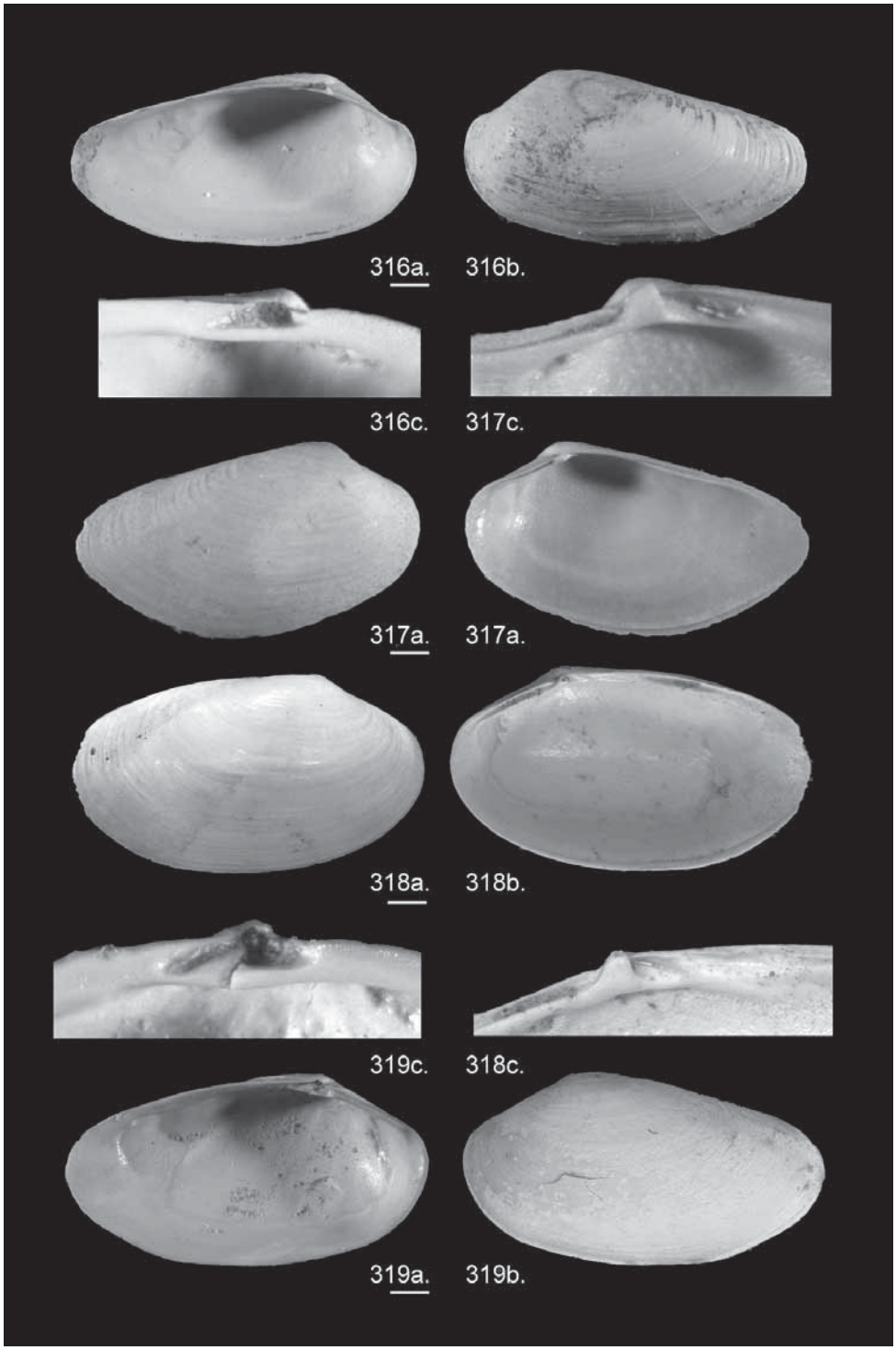
Figs. 316, 317. *Pachydon amazonensis* (Gabb, 1869). ▶

Fig. 316. INGEMMET TN90, Santo Tomas Amazon (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 317. RGM 456 597, Pebas/ Pijoyal (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Figs. 318, 319. *Pachydon ellipticus* sp. nov.

Fig. 318. INGEMMET TN91, holotype, Santo Tomas Amazon (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.
Fig. 319. RGM 456 598, paratype, same locality as Fig. 318. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.

Scale bars represent 1 mm.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319b.

they can be slightly more thickened on the posterior part. The commissure is planar. A very low ridge bounding a very narrow lunule may be present on the RV. The exterior of the shell is smooth, apart from generally fine growth lines and some low, irregularly developed, oblique riblets near the posterior margin that represent modifications of former periostracum. The hinge plate is small, and overlays a small and shallow umbonal cavity. The cardinal tooth is small and folded upward. Behind lies the elongate spatulous subhorizontal resilifer that is slightly inclined in respect with the commissure plane. The LV socket is formed by a shallow, broadly triangular depression. The resilifer is rather large, spatulous and almost horizontal. The LV nymph is indistinct. The lateral grooves ('teeth') are very regularly developed, and run along both the antero- and posterodorsal margins of the RV. The adductors are well defined and have a semilunate shape. A pronounced cauliflower ornament is located on the interior half of the anterior adductor. The posterior retractor scars consist of two or three very small, embedded elongate pits below the dorsal wall. The anterior retractor scar is a small, elongate, deeply embedded depression also located in the dorsal wall. The pallial line is impressed, located well within the shell margin and slightly irregularly oriented. The interior surface within the pallial line is granular, but otherwise smooth. The pallial line is truncate in the holotype and has a small sinus just below the posterior adductor in the paratype.

Dimensions – INGEMMET TN91: H 4.0; L 6.9; SD 1.5. RGM 456 598: H 4.9; L 9.4; SD 2.0.

Remarks – *Pachydon ellipticus* broadly resembles *P. tenuis*, *P. amazonensis* and *P. cuneatus*. It differs from *P. tenuis* by the smaller size, more regular elliptical outline and the planar commissure. It is more elongate and lacks the cuneiform posterior margin of *P. cuneatus*. Also, the base of the hinge platform of *P. ellipticus* lacks the arch-like architecture seen in *P. cuneatus*. *Pachydon ellipticus* most closely resembles *P. amazonensis*, but it differs by its shorter, more regular elliptical outline, lacking the tapering posterior typical of the latter. The largest H of *P. ellipticus* is located at *c.* one half the L, whereas in *P. amazonensis* it is located near two-thirds of the shell L.

***Pachydon andersonae* sp. nov.**

Figs. 320-322.

Type material – INGEMMET TN45 (holotype, RV): Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. RGM 456 448 (paratype, LV) and 456 449 (paratypes, three valves), same locality. RGM 456 450 (paratype, LV): Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996.

Range – Pebas Formation, MZ4 - MZ6 (late Early - Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after Professor Dr Laurie Anderson (Louisiana State University, Baton Rouge), in honour of her extensive work on the Corbulidae.

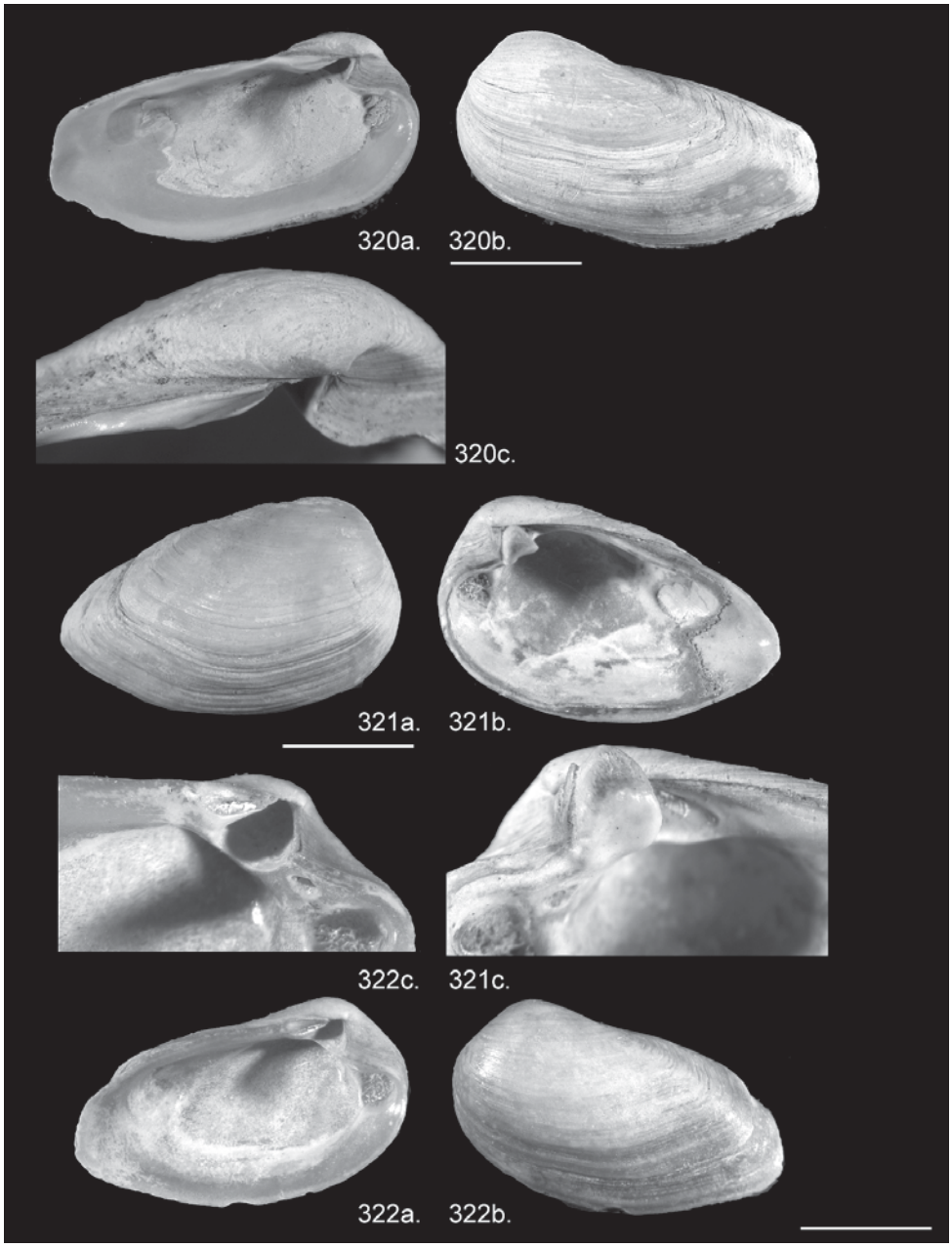
Diagnosis – Medium-sized to large, thick-shelled, elongate, strongly inaequilateral posteriorly tapering corbulid; lateral walls of LV hinge prominent, pronouncing the deep socket; posterior margin rounded and robust; commissure undulating.

Description – The shell has a distinctly rounded anterior margin and a slightly tapering posterior end. It is very slightly twisted. The RV is slightly larger and slightly more convex than the LV. Both valves are intermediately inflated. The blunt and slightly prosogyrate umbo is located at *c.* one sixth to one eighth the length from the anterior margin. Slightly below lies the small, somewhat incurved and prosogyrate beak. The shell is strong, and is thickened in the umbonal regions and posteriorly. The posterior wall of the cardinal tooth forms part of the exterior of shell. The posterior ridge is rounded. A poorly defined posterior slope is present. The posterior end is subrounded to tapering. The dorsal architecture, together with a low central elevation running from the umbo to the ventral margin slightly behind mid shell, gives the shell a slightly overall flexured appearance. The surface of the shell is lined with growth lines and irregular commarginal low ridges. Traces of radial ribs are seen near the ventral margin on the LV. Oblique lineaments attesting of former periostracum occur in the posterior slope region. Within the central portion of the RV ventral inner margin, a furrow is present for the reception of the LV. The RV hinge platform is robust, and overlies a deep and pronounced umbonal cavity. The RV cardinal is broad and massive, triangular in frontal view with a median furrow at the base. The frontal surface is rugose and it is hooked upward from side view. The RV resilifer is lanceolate, prosogyrate and only marginally pointing downward. The LV socket is characteristically prominent, slightly oblique, triangular, deep with pronounced, robust, erect walls. The resilifer is elongate and located high on the posterior wall that bears an elongate, low, but robust nymph. The socket walls are massive and infringe upon the socket. Lateral grooves ('teeth') are seen halfway along the RV posterodorsal margin. The deeply embedded anterior adductor scar is semicircular. It is mainly ornamented with a sharp cauliflower-like structure, but has a radially striate outer fringe. The posterior adductor is semilunate to irregularly ovate and is mainly radially striate, with only an inner fringe of cauliflower ornament. The poorly defined pallial line is located far within the shells margin. It runs slightly oblique towards the posterior end and is slightly retracted below the posterior adductor. A small deep pit below the cardinal in the RV forms a pedal retractor scar. An anterior retractor scar pit is found on the anterior side of the lower hinge plate wall.

Dimensions – INGEMMET TN45: H 9.9; L 12.8; SD 4.7. RGM 456 448: H 6.4; L 10.4; SD 3.0. RGM 456 449 (LV): H 9.9; L 12.8; SD 4.7. RGM 456 449 (RV): H >11.5; L >14.6; SD 5.5. RGM 456 449 (LV): H 12.4; L >15.7; SD 4.9. RGM 456 450: H 8.5; L 13.9; SD 3.5.

Remarks – *Pachydon andersonae* combines morphological characters of *P. tenuis* and *P. amazonensis*, and may have been the predecessor of both. It has a more elongate, ec-

centric, thicker shell with a more regularly rounded anterior margin than *P. tenuis*. The species is inequivalve, and generally higher and much thicker than *P. amazonensis*, the latter being almost equivalve.



Pachydon cuneatus Conrad, 1871
Figs. 323, 324.

1871 *Pachydon cuneatus* Conrad, p. 197, pl. 10, fig. 12.
1871 *Anisothyris cuneata* (Conrad); Woodward, p. 107, pl. 5, fig. 8a-b.
1874a *Pachydon cuneata* Conrad; Conrad, 2 p. 8, pl. 1, fig. 3.
1878 *Anisothyris cuneata* (Conrad); Boettger, p. 500 (*pars*), pl. 14, figs. 1-11.
1879 *Anisothyris (Pachydon) tumida* Etheridge, p. 83, pl. 7, fig. 2.
1924 *Anisothyris cuneatus* (Conrad); Roxo, p. 44.
1938 *Anisothyris cuneata* (Conrad); de Greve, p. 34, pl. 6, figs. 4, 6-8, 16, 17, pl. 8, figs. 18, 19.
1966 *Anisothyris cuneata* (Conrad); Willard, p. 66 (*pars*), pl. 59, figs. 2, 3 (*non* fig. 1).
1990 *Pachydon cuneatus* Conrad; Nuttall, p. 301, figs. 389-393.
2006 *Pachydon cuneatus* Conrad; Anderson *et al*., figs. 3-3, 3-6.

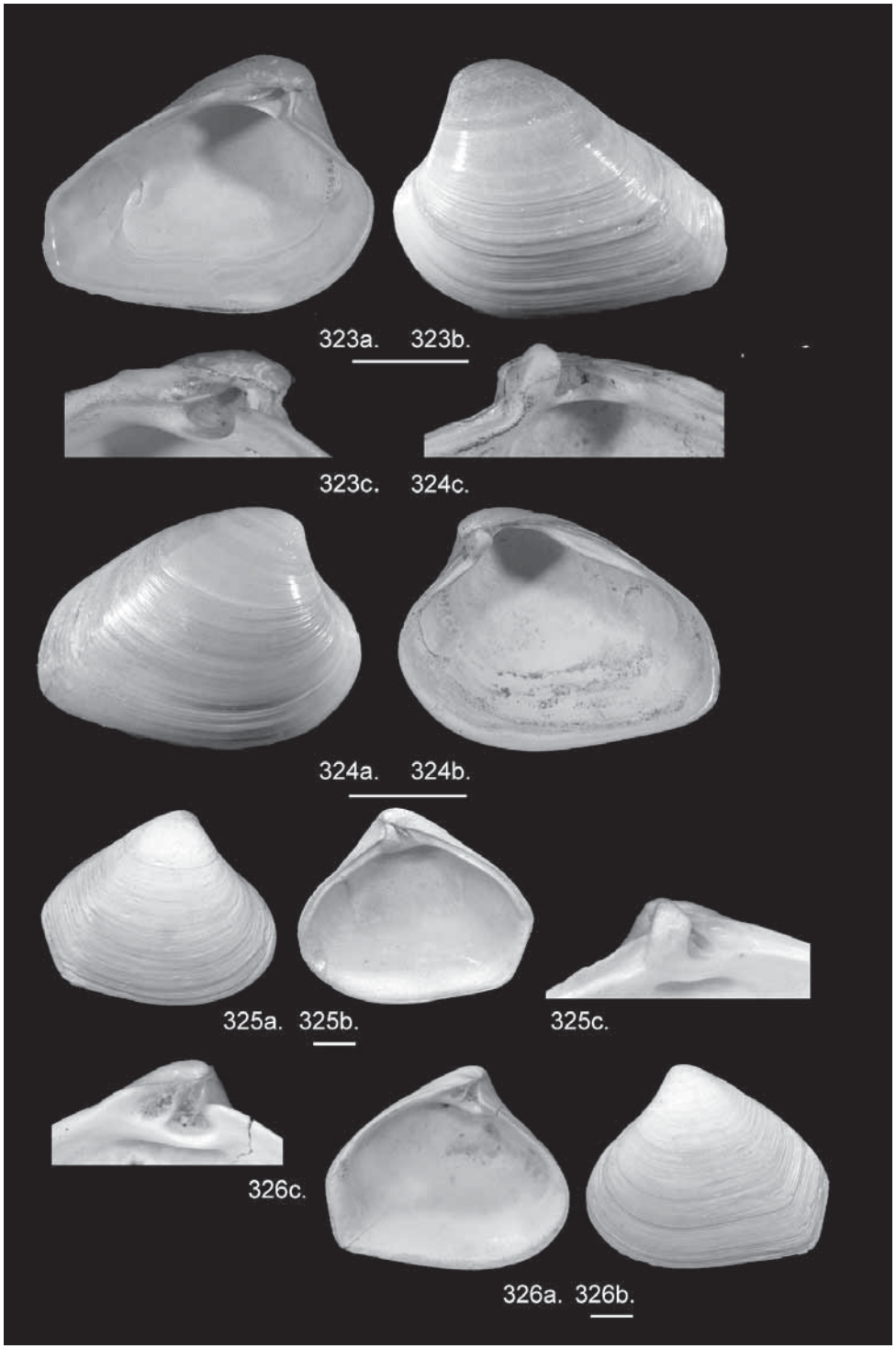
Material studied – RGM 456 431 (paired specimen), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996. RGM 456 432 (pair), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996.

Extended diagnosis – Medium-large sized, rounded triangular, wedge-formed, equivalve to slightly inequivalve *Pachydon*; LV occasionally slightly larger with straighter postero-dorsal margin giving it a more triangular outline than the RV; broad, pronounced prosogyrate umbo at one fifth to one seventh length from posterior margin; commissure planar; species with intermediate to thick shell that can be strongly thickened on upper posterior part; posterior wall of RV cardinal tooth part of exterior of the shell; posterior ridge low, rounded; traces of radial riblets at ventral margin; oblique ridges may develop near posterior margin; hinge plate characteristically curved upward behind large, massive RV cardinal tooth which is curved towards posterodorsal margin and contains a rugose frontal surface; LV socket triangular, deep, well delimited by erect walls; spatulous LV resilifer located on posterior socket wall; lateral grooves ('teeth') short on anterior margin, but pronounced on the middle part of the posterior margin; anterior adductor semilunate, deeply embedded with distinct cauliflower ornament; pallial line sharp, with a short siphonal retraction; anterior, posterior and pedal retractor scars small and deeply embedded.

◀ Figs. 320-322. *Pachydon andersonae* sp. nov.

Fig. 320. RGM 456 450, paratype, Nuevo Paleta (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, dorsal view.
Fig. 321. INGEMMET TN45, holotype, Indiana (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.
Fig. 322. RGM 456 448, paratype, same locality as Fig. 321. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.

Scale bars represent 5 mm.


323a. 323b.
323c. 324c.
324a. 324b.
325a. 325b.
325c.
326c.
326a. 326b.

Dimensions – RGM 456 431: LV: H 11.4; L 14.9; SD 5.1; RV: H 10.5; L 14.0; SD 4.4. RGM 456 432: LV: H 24.6; L 27.8; SD 12.0; RV: H 25.8; L 28.4; SD 12.6.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Colombian, Peruvian and Brazilian Amazonia.

Pachydon trigonalis Nuttall, 1990

Figs. 325, 326.

1990 *Pachydon trigonalis* Nuttall, p. 309, figs. 413-419.
1998 *Pachydon trigonalis* Nuttall; Vonhof *et al*., fig. 4.

Material studied – RGM 456 405 (RV), San Martin (Amazonas, Colombia), exposure at landing stage, east bank Amacayacu River (3°44'S 70°20'W), level F39 (0.7 m above DL). Pebas Formation, MZ10 (late Middle- early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 406 (LV), same locality.

Extended diagnosis – Small-medium sized, equivalve triangular corbulid; pointed and slightly prosogyrate umbo slightly before mid-shell; shell moderately thick; very narrow escutcheon may be developed; anterior wall cardinal tooth part of exterior of the shell; posterior ridge low, but well developed; posterior end broadly truncate; the RV cardinal is massive and hooked upward; the spatulous RV resilifer is prosogyrate and relatively short; socket triangular, deep and well defined by erect walls; drop shaped LV resilifer located on slightly elevated posterior platform; LV nymph robust, elongate, somewhat erect; posterior and anterior lateral grooves ('teeth') well developed in RV, robust; posterior adductor large, shallow, subquadrate; anterior adductor almost invisible; pallial line almost invisible, separating a rugose inner part of the shells interior from smooth outer part, located very far from the shell margins.

Dimensions – RGM 456 405: H 5.0; L 5.8; SD 1.6. RGM 456 406: H 5.2; L 6.0; SD 1.4.

◀ Figs. 323, 324. *Pachydon cuneatus* Conrad, 1871.

Fig. 323. RGM 456 431a, Santa Elena (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 324. RGM 456 431b, same locality as Fig. 323. a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Scale bars represent 5 mm.

Figs. 325, 326. *Pachydon trigonalis* Nuttall, 1990.

Fig. 325. RGM 456 405, San Martin (Amazonas, Colombia). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.
Fig. 326. RGM 456 406, same locality as Fig. 325. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.

Scale bars represent 1 mm.

Range – Pebas Formation, MZ9 - MZ12 (late Middle - early Late Miocene), Colombian, Peruvian and Brazilian Amazonia.

Pachydon hettneri Anderson, 1928

1928 *Corbula hettneri* Anderson, p. 24, pl. 1, figs. 11-14.
1928 *Corbula scheibi* Anderson, p. 25, pl. 1, figs. 16-18.
1944 *?Ostomya terminalis* Pilsbry, p. 149, pl. 11, fig. 33.
1944 *Corbicula* sp. Pilsbry, p. 147, pl. 11, fig. 37.
1944 ?'undetermined pelecypod' Pilsbry, pl. 11, fig. 40.
1990 *Pachydon hettneri* Anderson; Nuttall, p. 302, figs. 394-402.
1990 *Pachydon cebada* Anderson; Nuttall, p. 311 (*pars*), figs. 424, 425 (*non* figs. 420-423).
2006a *Pachydon hettneri* Anderson; Wesselingh & Macsotay, p. 3, figs. 4-6.

Material studied – RGM 456 599 (*c.* 100 damaged (compacted and diagenetically altered) pairs, valves and fragments), San Juan RioSeco (Cundinamarca, Colombia), exposure in bed of RioSeco, 1 km upstream of bridge, *c.* 1.5 km northeast of San Juan RioSeco. Santa Teresa Formation ('La Cira Beds'), MZ1 (Early Miocene); leg. F.P. Wesselingh, 28-11-1996.

Extended diagnosis – Very robust and thick shelled, high-triangular, equivalved *Pachydon*; umbo at mid shell, subdued; shells commonly contain a median depression/flexure running from umbo to the middle of the ventral margin; both the anterior and posterior lobe may be slightly produced; commissure slightly wavy; posterior ridge variable, but usually prominent and robust, rounded to acute; RV cardinal drop-shaped, massive; resilium tightly triangular, very deep behind cardinal; lateral grooves ('lateral teeth') very strong, covering the upper half of the steeply dipping, straight anterodorsal and posterodorsal margins.

Dimensions – The largest H of the studied specimens (that have suffered compaction) is *c.* 13 mm, the largest L *c.* 12 mm and the diameter *c.* 8 mm. Material studied by Nuttall reached a height of 14.6 mm.

Range – Early to early Middle Miocene (MZ1- MZ2), Subandean basins (nowadays partially intramontane basins) from the eastern Venezuela basin in the north to the Ucayali basin (Peru) in the south (see Wesselingh & Macsotay, 2006a).

Remarks – The only *Pachydon* that resembles *P. hettneri* is *P. trigonalis*. The latter has a thinner shell that is not bilobed. For *Pachydon hettneri* and *P. cebada*, I have only fragmentary and mostly compacted material available. For illustrations of these species, the reader is referred to Nuttall (1990).

Pachydon cebada (Anderson, 1928)

1928 *Corbula cebada* Anderson, p. 24, pl. 1, fig. 15.
1935 *Corbula abundans* Pilsbry & Olsson, p. 19, pl. 2, figs. 13, 14.
1944 *Corbula arcana* Pilsbry, p. 149, pl. 11, fig. 38.
1944 'undetermined pelecypod' Pilsbry, pl. 11, fig. 34.

1990 *Pachydon ovalis* Nuttall: p. 305, figs. 403-406 (figs. 407?, 408?).
1990 *Pachydon cebada* Anderson; Nuttall, p. 311 (*pars*), figs. 420-423 (*non* figs. 424, 425).
1990 *Pachydon erectus* Conrad; Nuttall, p. 297 (*pars*), figs. 380-384 (*non* figs. 374-379).

Material studied – Only poorly preserved fragments from the La Tagua locality (Putumayo Basin, Colombia) were available for study, so the diagnosis below is based on material described in Nuttall (1990) as well as specimens from unspecified localities from the Magdalena Basin in the ANSP collections.

Extended diagnosis – Intermediate, thick-shelled, ovate to elongate-triangular, slightly inequivalve *Pachydon*; the umbo is indistinct, prosogyrous; the shell outline is variable, and includes slightly and broadly shouldered forms; posterodorsal margin straight, posterior margin rounded, lower margin evenly rounded, anterior margin tapering; RV occasionally slightly bilobed along a faintly developed depression running from umbo to the ventral margin at *c.* one third of the length from the posterior margin; posterior ridge rounded and low; RV cardinal small, erect; LV hinge thin and narrow; pallial sinus deeply and broadly truncate.

Dimensions – Specimens are typically up to 10 mm long, but the type of Nuttall's *Pachydon ovalis* is *c.* 16 mm in length.

Range – Early to early Middle Miocene (MZ1- MZ2), Subandean basins (nowadays partially intramontane basins) from the Magdalena basin (Colombia) in the north to the Ucayali basin (Peru) in the south.

Remarks – In most of the strata where this species occurs, the only co-occurring species is *P. hettneri*, which is much higher-shelled, and has a very prominent and acute dorsal ridge.

***Pachydon maaikeae* sp. nov.**
Figs. 327, 328.

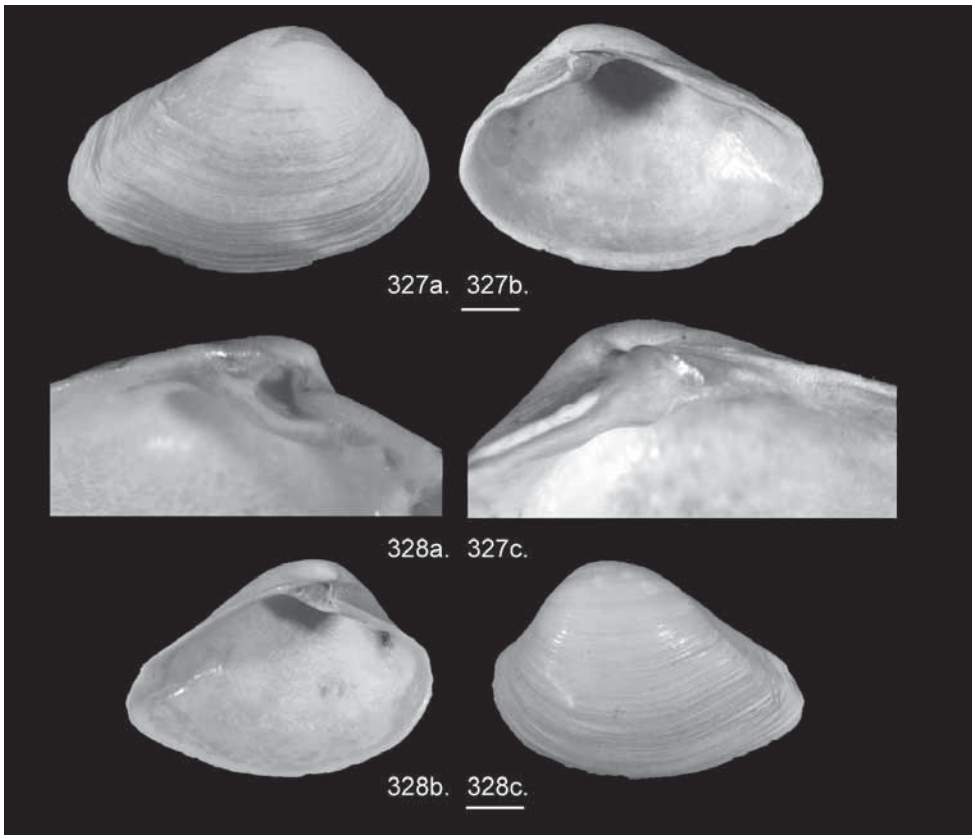
Type material – INGEMMET TN38 (holotype, RV): Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996. RGM 456 433 (paratype, LV), same locality.

Range – Pebas Formation, MZ4 - MZ5 (late Early - early Middle Miocene), Peruvian Amazonia.

Derivatio nominis – Named after my wife Maaike Wickardt, for her continuing support of my work.

Diagnosis – Small, subovate to subtriangular corbulid with broadly erect umbo; posterior ridge subrounded, well developed; base of hinge plate curved upward behind cardinal tooth in RV; pallial line truncate.

Description – The shell varies from thin to rather robust. The species is slightly inequivalve, the RV being slightly larger and more convex. The broad, slightly prosogyrate umbo is located at *c.* one third of the shell length from the posterior margin. The commissure is slightly undulating. The shell is not or only marginally thickened at the posterior margin. The anterior margin of the RV cardinal tooth forms part of the exterior of the shell. The posterior ridge and slope can be well developed, although the former is rounded; the posterior end is obliquely truncate to subrounded. The surface contains fine growth lines and regular, low commarginal ridges as well as common oblique lineaments attesting of the former presence of thick periostracum. A furrow for the reception of the LV is developed on the central part of the ventral RV interior margin. The base of the RV hinge platform is curved upward behind the cardinal tooth. The latter is variable, from



Figs. 327, 328. *Pachydon maaikeae* sp. nov.

Fig. 327. INGEMMET TN38, holotype, Indiana (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.
Fig. 328. RGM 456 433, paratype, same locality as Fig. 327. a, LV hinge, detail, oblique view. b, LV interior. c, LV exterior.

Scale bars represent 1 mm.

erect and slightly pointed to bluntly curved and broadly knob-like. The lanceolate subhorizontal RV resilifer is rather short. The LV socket is broadly triangular and clearly delimited by the erect anterior wall. The subhorizontal LV resilifer is located on an elevated posterior platform. The LV nymph is broad, elongate, massive and low, not erect. Lateral grooves ('teeth') are prominent on the anterior margin, and the middle and posterior part of the posterior margin on the RV. The adductors are comparatively large, semilunate to irregularly semicircular. The anterior adductor has an internal zone with a cauliflower ornament and an outer smoothly striate fringe. The latter dominates the posterior adductor. The pallial line is sharp and located well within the shell. It is commarginal and truncate posteriorly. Small embedded elongate pits between the anterior adductor and the base of the hinge plate mark the anterior retractor scars. The posterior retractor scar is formed by a very small semicircular extension of the posterior adductor.

Dimensions – INGEMMET TN38: H 4.5; L 6.4; SD 2.3. RGM 456 433: H 4.0; L 5.4; SD 1.9.

Remarks – This species most closely resembles *P. cuneatus*. *Pachydon maaikeae* is smaller and more convex, and has a straight to slightly concave posterodorsal margin (that is convex in *P. cuneatus*). The umbones of *P. maaikeae* are very subdued compared to those of *P. cuneatus*. *Pachydon trigonalis* is more triangular and flatter.

It is possible that *P. maaikeae* is the predecessor of *P. cuneatus*. They share a number of morphological traits (such as the characteristic curvature of the base of the hinge plate in the RV) and occur in successive stratigraphic intervals. No intermediates have been found between these two species.

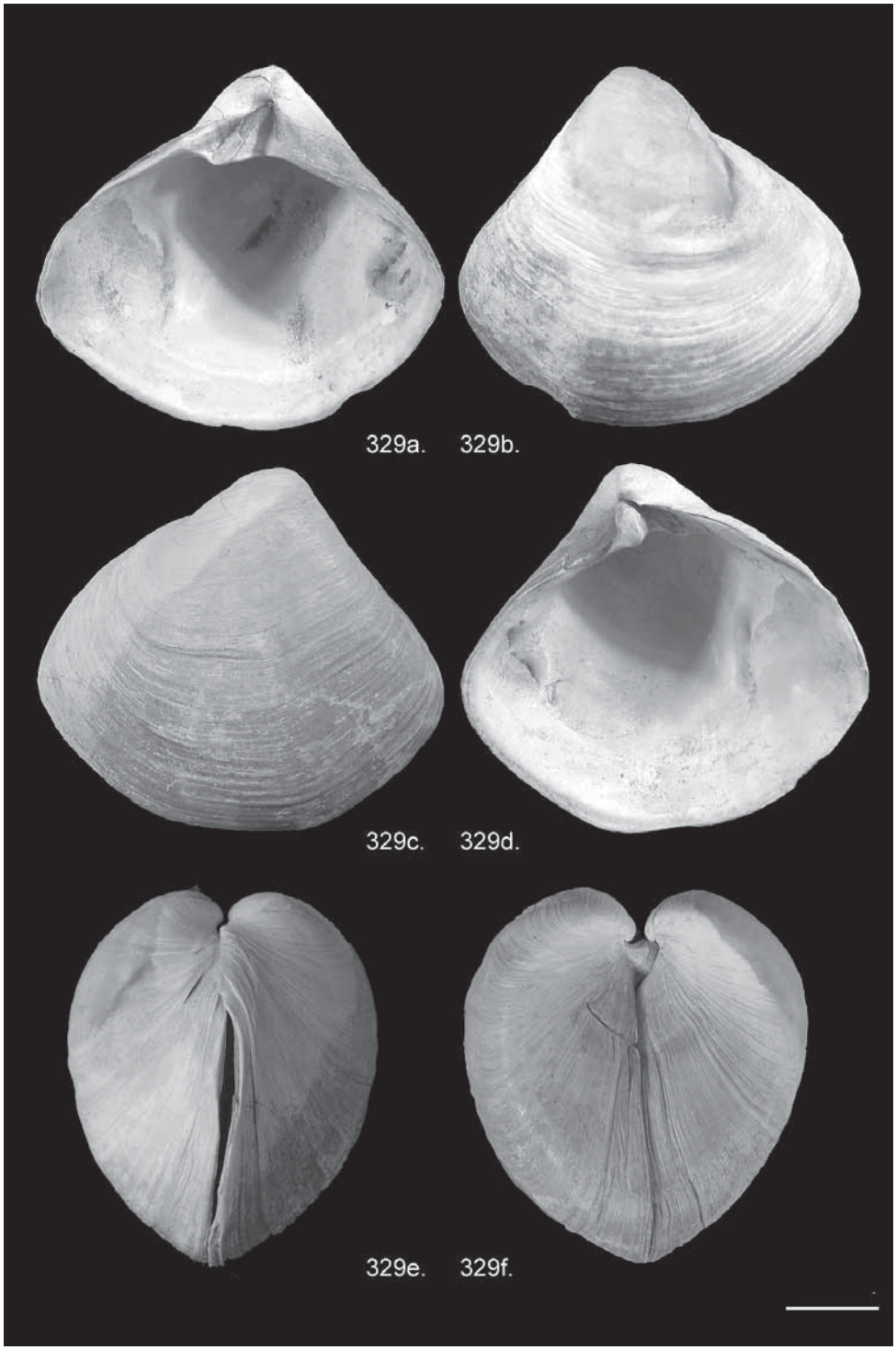
***Pachydon erectus* Conrad, 1871**

Figs. 329, 333.

1871 *Anisothyris erecta* (Conrad); Woodward, p. 107, pl. 5, fig. 9a-b.
1878 *Anisothyris erecta* Conrad; Boettger, p. 500 (*pars*), pl. 14, fig. 12 (*non* fig. 13).
1871 *Pachydon erectum* Conrad, p. 197, pl. 10, fig. 16.
1871 *Pachydon altum* Conrad, p. 197, pl. 11, fig. 1.
1879 *Corbula canamaensis* Etheridge, p. 84, pl. 7, fig. 3, 3a.
1938 *Anisothyris erecta* (Conrad); de Greve, p. 36 (*pars*), pl. 8, figs. 1-3, 8 (*non* figs. 4, 5).
1938 *Anisothyris erecta* (Conrad) – *Anisothyris tenuis* (Gabb); de Greve, pl. 7, figs. 1-6.
1966 *Anisothyris erecta* (Conrad); Willard, p. 65 (*pars*), pl. 58, fig. 2 (*non* fig. 3).
1990 *Pachydon erectus* Conrad; Nuttall, p. 297 (*pars*), figs. 374-376, 377?, 378-379 (*non* figs. 380-384).
? 1990 *Pachydon erectus elongatus* (Boettger); Nuttall, p. 300 (*pars*) (*non* figs. 385-388).
2006 *Pachydon erectus* (Conrad); Anderson *et al*., fig. 2-3, 2-6.

Material studied – RGM 456 199 (pair) and RGM 456 591 (LV), Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), collected from surface scree. Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 1996.

Extended diagnosis – Large to very large, erect triangular equivalve inflate *Pachydon*; the erect orthogyrate umbo located slightly before middle of shell; anterodorsal margin


329a.
329b.
329c.
329d.
329e.
329f.

may be concave, making the umbo more pronounced; commissure straight to very slightly undulating; lunule well expressed, broad and concave; shell slightly thickened anteriorly; anterior margin cardinal tooth part of the exterior surface of the shell; posterior ridge and slope absent; exterior of the shell with growth lines, low irregular commarginal ridges and broad low radial ribs as well as poorly expressed traces of thinner radial riblets; oblique lineaments on lateral margins, some also on central portion; umbonal cavity RV large; RV cardinal massive, knob-like, erect (hardly curved) with a subquadrangular frontal surface; LV socket triangular, rather shallow; LV resilifer prosogyrate, well expressed, slightly elevated from socket; nymph short and robust; semi-lunate anterior adductor deeply embedded, striate; posterior adductor irregular ovate, shallow; pallial line shallow, broad, well within margin of shell, commarginal with a blunt comparatively deep retraction; a distinct, but narrow posterior gape is present (Fig. 329e).

Dimensions – RGM 456 199 (RV): H 43.7; L 48.6; SD 20.0. RGM 456 199 (LV): H 43.4; L 48.6; SD 19.0. RGM 456 591: H 24.9; L 30.8; SD 10.5.

Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Colombian, Peruvian and Brazilian Amazonia.

Pachydon iquitensis (de Greve, 1938)

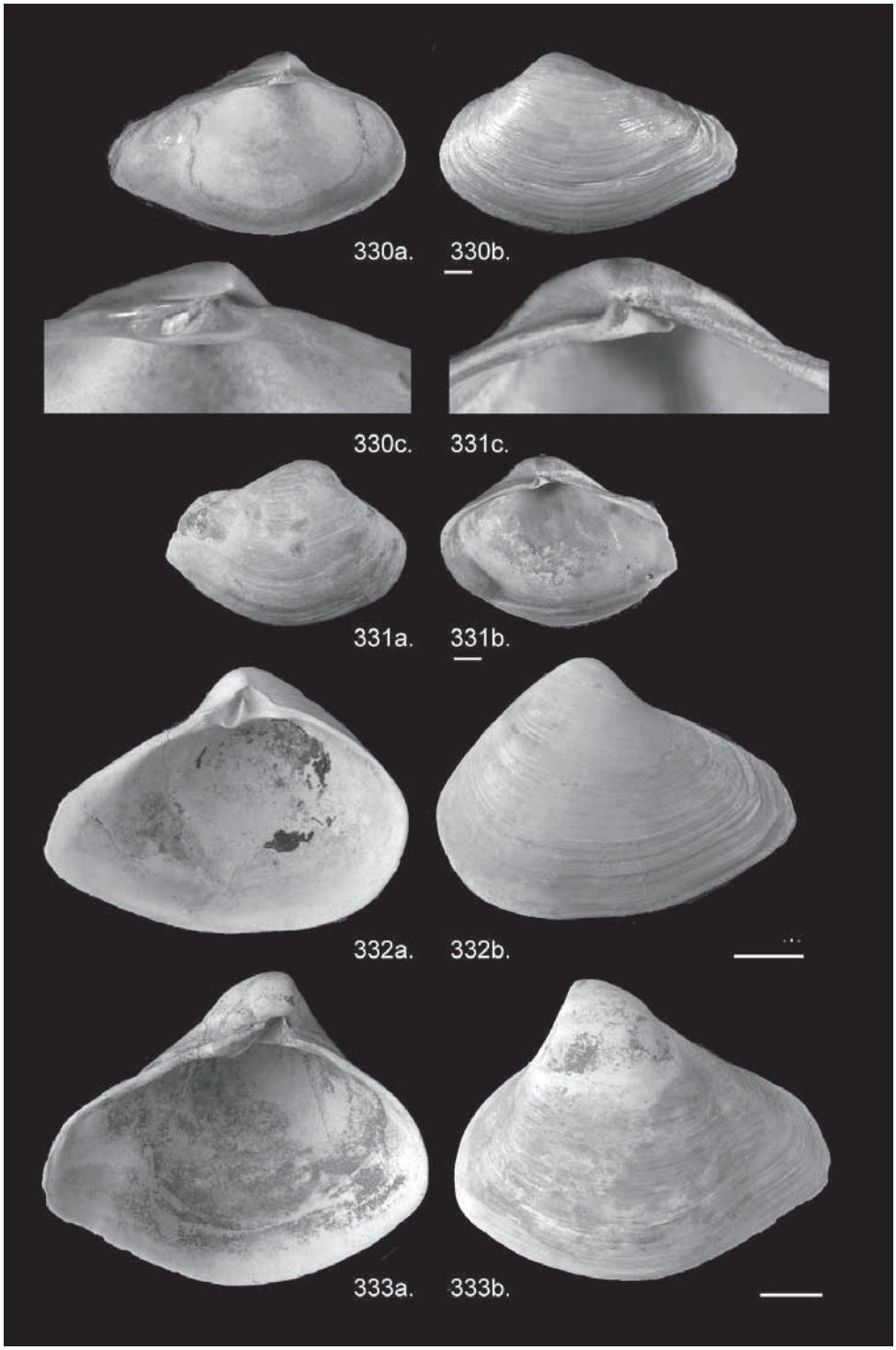
Figs. 330-332.

1878 *Anisothyris erecta* Conrad; Boettger, p. 500 (*pars*), pl. 14, fig. 13 (*non* fig. 12).
1938 *Anisothyris iquitensis* de Greve, p. 46, pl. 5, figs. 38-41.
1938 *Anisothyris erecta* (Conrad); de Greve, p. 36 (*pars*), pl. 8, figs. 4, 5 (*non* figs. 1-3, 8).
1966 *Corbula abundans* (Pilsbry); Willard, p. 216, pl. 56, fig. 3.
1966 *Anisothyris erecta* (Conrad); Willard, p. 220 (*pars*), pl. 58, fig. 3 (*non* fig. 2).
1990 *Pachydon iquitensis* (de Greve); Nuttall, p. 315, fig. 430a-d.
? 1990 *Pachydon erectus elongatus* (Boettger); Nuttall, p. 300 (*pars*), fig. 388a-c? (*non* figs. 385-387).

Material studied – RGM 456 592 (LV), Porvenir (Loreto, Peru), exposure in west bank Amazon River along village (4°15'S 73°23'W), material collected from surface scree. Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1996. INGEMMET TN88 (LV) and RGM 456 593 (RV), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Extended diagnosis – Small to large, variable subovate to subtriangular, slightly inequivalve *Pachydon*; RV slightly larger and more convex than LV, well inflated; slightly pointed umbo located just before mid shell; umbo orthogyrate to slightly opisthogyrate; commissure slightly undulating; posterior wall cardinal tooth part of exterior of

◀ Fig. 329. *Pachydon erectus* Conrad, 1871. RGM 456 199, Santa Rosa de Pichana (Loreto, Peru). Paired specimen. a, LV interior. b, LV exterior. c, RV exterior. d, RV interior. e, posterior view, note slit-like gape. F, anterior view, note broad concave anterior plane. Scale bar represents 10 mm.


330a.
330b.
330c.
331c.
331a.
331b.
332a.
332b.
333a.
333b.

the shell; posterior ridge rounded, often pronounced by low radial depression in front; posterior slope variable, but generally well visible; posterior end subrounded to obliquely truncate; shell with few low, irregular concentric ridges, some ventral radial ribs and rib fragments as well as oblique lineaments, especially common on posterior margin; receiving furrow in RV on central part near ventral edge; cardinal tooth relatively small, pointed, curved upwards; LV socket broadly triangular, more pronounced in larger specimens; nymph becomes robust in larger specimens, widest posteriorly; thin lateral grooves ('teeth') on anterodorsal margin; adductors large, semilunate, mostly with concentric lineaments; pallial line clear, well within shells margin, truncate.

Dimensions – RGM 456 592: H 18.2; L 25.3; SD 8.2. INGEMMET TN88: H 6.4; L 10.7; SD 2.7. RGM 456 593: H 5.9; L >8.8; SD 2.5.

Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Colombian and Peruvian Amazonia.

Remarks – Specimens from the older intervals (MZ4-MZ6) of the stratigraphic distribution range are more elongate, the LV is slightly flatter and the postero-dorsal flank is not very well developed. Additional study of this taxon is needed in order to establish whether it comprises a single species. *Pachydon iquitensis* closely resembles *P. erectus*. The latter is always more erect (compare Figs. 333 and 332), more triangular, and has a concave margin before the umbo and a more pronounced rostrum-like posterior.

***Pachydon ledaeformis* (Dall, 1872)**

Figs. 334, 335.

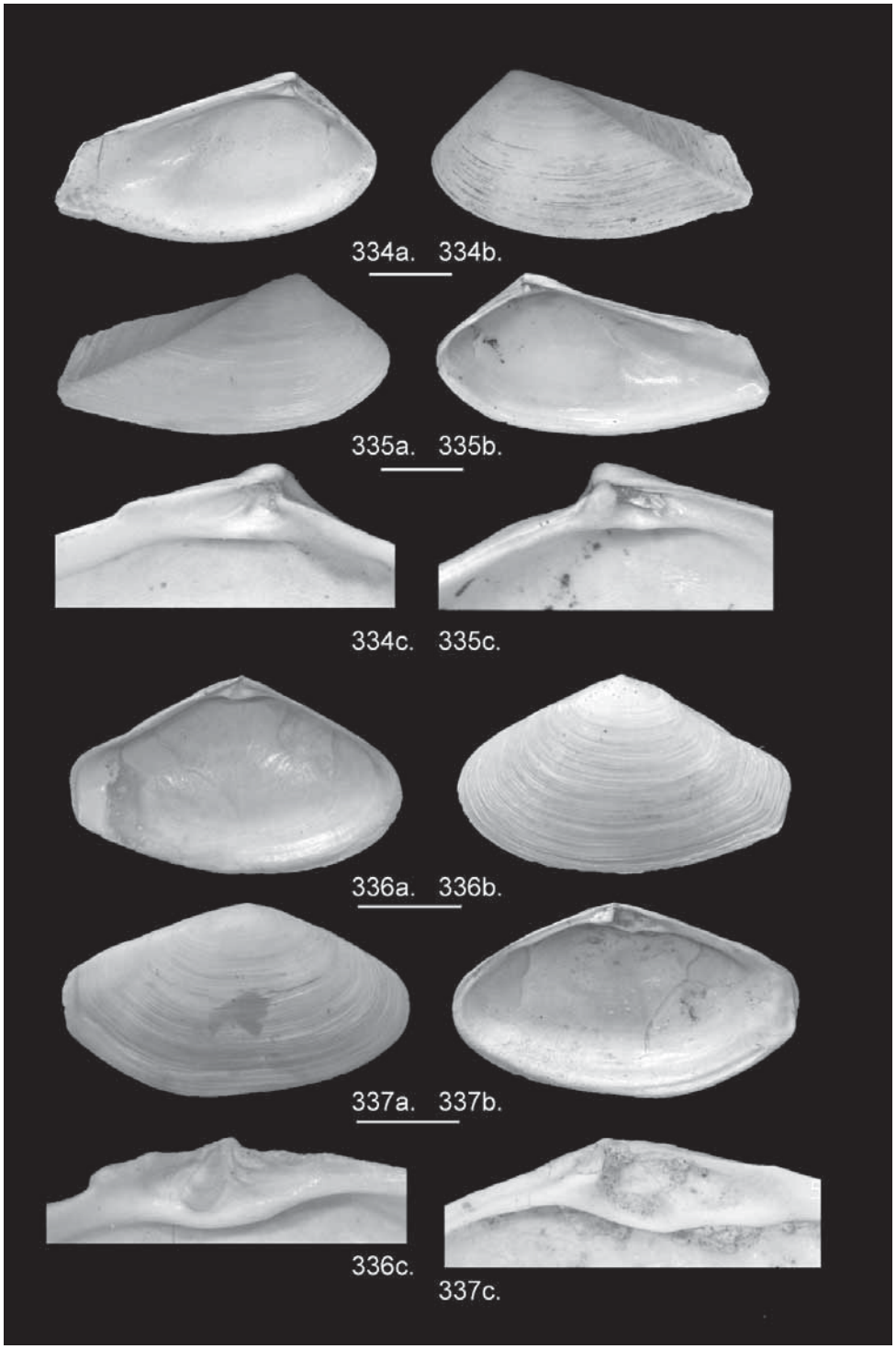
1872 *Corbula ledaeformis* Dall, p. 92, pl. 16, figs. 14, 15.
1878 *Anisothyris erecta* var. *elongata* Boettger, p. 500 (*pars*), pl. 14, fig. 14 (*non* fig. 15).
1990 *Pachydon ledaeformis* (Dall); Nuttall, p. 314, figs. 426-429.
1990 *Pachydon erectus elongatus* (Boettger); Nuttall, p. 300 (*pars*), figs. 385-387 (*non* fig. 388a-b).

Material studied – INGEMMET TN31 (RV) and RGM 456 407 (LV), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, 1 km west of Santo Tomas (3°52'S 71°23'W), level F488 (7.3 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 27-8-1996.

◀ Figs. 330-332. *Pachydon iquitensis* de Greve, 1938.

Fig. 330. INGEMMET TN88, Indiana (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view. Scale bar represents 1 mm.
Fig. 331. RGM 456 593, same locality as Fig. 330. a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view. Scale bar represents 1 mm.
Fig. 332. RGM 456 592, Porvenir (Loreto, Peru). a, LV interior. b, LV exterior. Scale bar represents 5 mm.

Fig. 333. *Pachydon erectus* Conrad, 1871, RGM 456 591, Santa Rosa de Pichana (Loreto, Peru). a, LV interior. b, LV exterior. Scale bar represents 5 mm.


334a. 334b.
335a. 335b.
334c. 335c.
336a. 336b.
337a. 337b.
336c.
337c.

Extended diagnosis – Small to intermediate, flat, elongate to rostrate, equivalved *Pachydon*; umbo *c.* one fifth of the shell length from posterior margin; commissure planar; bluntly acute, very marginal ridge defining very narrow escutcheon; umbo slightly pointed, orthogyrate; beak small, pointed prosogyrate; sharp posterior ridge defining clear, slightly concave posterior slope; posterior end truncate; shell smooth apart for growth lines; hinge plate narrow with small massive cardinal that is slightly hooked upward; LV socket poorly defined, broadly triangular; LV resilifer in posterior socket wall; nymph elongate, bluntly erect; lateral grooves ('teeth') developed about halfway anterodorsal margin; smooth adductors, with poorly expressed radial striae and concentric lineaments; pallial line poorly visible, deeply within shell, broadly truncate.

Dimensions – INGEMMET TN31: H 4.0; L 7.7; SD 1.2. RGM 456 407: H 4.1; L 8.1; SD 1.1.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Remarks – In MZ11 and MZ12 intervals, *P. ledaeformis* is comparatirely high. Additional study is needed in order to investigate the potential presence of subspecies.

***Pachydon telliniformis* sp. nov.**

Figs. 336, 337.

Type material – RGM 456 200 (holotype, RV): Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991. INGEMMET TN32 (paratype, LV) and RGM 456 409 (paratypes, 83 damaged valves and fragments), same locality.

Range – Pebas Formation, MZ7 - MZ12 (Middle - early Late Miocene), Colombian and Peruvian Amazonia.

◀ Figs. 334, 335. *Pachydon ledaeformis* (Dall, 1872).

Fig. 334. RGM 456 407, Santa Elena (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 335. INGEMMET TN31, same locality as Fig. 334. a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Figs. 336, 337. *Pachydon telliniformis* sp. nov.

Fig. 336. INGEMMET TN32, paratype, Nuevo Horizonte (Loreto, Peru). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 337. RGM 456 200, holotype, same locality as Fig. 336. a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Scale bars represent 2 mm.

Derivatio nominis – Named after the telliniform outline of the shell.

Diagnosis – Medium-sized, flat, trapezoid to telliniform *Pachydon* with a broad posterior rostrum; umbo slightly erect, orthogyrate; commissure at posterior end slightly bent; pallial line massively truncate.

Description – The RV is slightly larger and more convex than the LV. The umbo is located about mid-shell. A robust, acutely rounded ridge bounds a very narrow escutcheon. A low, poorly defined posterior ridge defines the low, but obvious, posterior slope. The posterior margin is truncate and rather wide. The exterior of the shell has growth lines, some very low concentric ridges, and common oblique lineaments along ventral margin and on the posterior part of the shell. A furrow for the reception of the LV is present just within the posteroventral margin of the RV. The hinge plate is flat, and bounds a broad and low umbonal cavity. The RV cardinal is a small, slightly folded, bluntly triangular lamella. The RV resilifer is poorly defined, very broad and inverse heart-shaped. Its posterior wall is slightly elevated, forming a very low septum. The LV socket is broadly triangular and well delimited by the low, erect walls. The resilifer is broad, drop-shaped and prosogyrate. The nymph is elongate and well expressed. Lateral grooves ('teeth') are omnipresent anteriorly, but poorly expressed posteriorly on the RV. The posterior adductor is irregularly semicircular. The anterior adductor is irregularly subquadrate. Both are shallow and smooth. The pallial line is thin in the LV and poorly expressed in the RV, and has a massive truncation. It runs from the posterior adductor to about the middle of the shell. The anterior retractor scar is developed as a slight ovate depression that lies behind the anterior adductor.

Dimensions – RGM 456 200: H 7.6; L 13.3; SD 2.1. INGEMMET TN32: H 6.0; L 10.2; SD 1.3.

Remarks – The flat and rostrate nature of this species only resembles that of *Pachydon ledaeformis*. The latter is distinctly inaequilateral and has a more tapering posterior.

Genus *Exallocorbula* Nemésio, Aronowsky & Anderson, 2006

Type species – *Pachydon (Anisorhyncus) dispar* Conrad, 1874a, Miocene, Pebas Formation, western Amazonia.

Diagnosis – Strongly bilobed, inequivalve corbulid with a large convex RV and smaller concave LV; RV carinal very prominent, hanging down from strongly incurved umbo; LV hinge plate turned 90°.

Range – Miocene, Pebas Formation, western Amazonia (Peru, Colombia, Brazil).

Exallocorbula dispar (Conrad, 1874a)

Figs. 338-341.

1874a *Pachydon (Anisorhynchus?) dispar* Conrad, p. 27, pl. 1. fig. 1.
1938 *Anisorhynchus* (?) *jaenneti* de Greve, p. 24, pl. 8, figs. 6, 7, 9-17, 20, text-figs. 2, 3.

1990 *Pebasia dispar* (Conrad); Nuttall, p. 315, figs. 432-436.
2006 *Pebasia dispar* (Conrad); Anderson *et al*., fig. 2-1, 2-2, 2-4, 2-5.

Material studied – RGM 456 203 (RV) and RGM 456 414 (LV), Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991. RGM 456 415 (RV), Nuevo Paleta (Loreto, Peru), exposure in south bank Rio Napo, 2 km west of Negro Urco (3°00'S 73°25'W), level F895 (0.5 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 30-9-1996. RGM 456 416 (LV), Indiana (Loreto, Peru), exposure in west bank Amazon River, *c.* 2.3 km south of port (port at 3°30'S 73°03'W), level F382 (1.3 m above DL). Pebas Formation, MZ5 (late Early - early Middle Miocene); leg. F.P. Wesselingh, 8-8-1996.

Extended diagnosis – Medium-sized, strongly inequivalve bilobed, *Pandora*-shaped corbulid; RV extremely inflated; LV concave, markedly smaller than RV; umbo located at one sixth to two fifths length of the shell from anterior; strongly sinuous commissure; acute ridge bounding a very narrow escutcheon on RV; umbo prominent, incurved, orthogyrate; low, obvious posterior ridge and depression on RV; acute, but low, on LV; posterior slope slightly concave, well expressed on LV; posterior end truncate; median depression separating frontal and rear lobe prominently developed; rear lobe produced; distinct receiving furrow in rear lobe of RV; RV umbonal cavity pronounced; RV hinge platform folded inward, LV hinge platform flat and massive; cardinal tooth massive, hanging down from dorsal margin with plicate frontal surface; LV socket broad, low, with overhanging low upper and posterior walls; anterior adductor large, irregularly triangular with radial striae; posterior adductor subquadrate, poorly defined; pallial line very deep within shell, poorly expressed, commarginal with LV margins undergoing blunt, slightly irregular retraction; retraction scars small; anterodorsal margin tilted with acute ridge bounding small, well expressed escutcheon in LV.

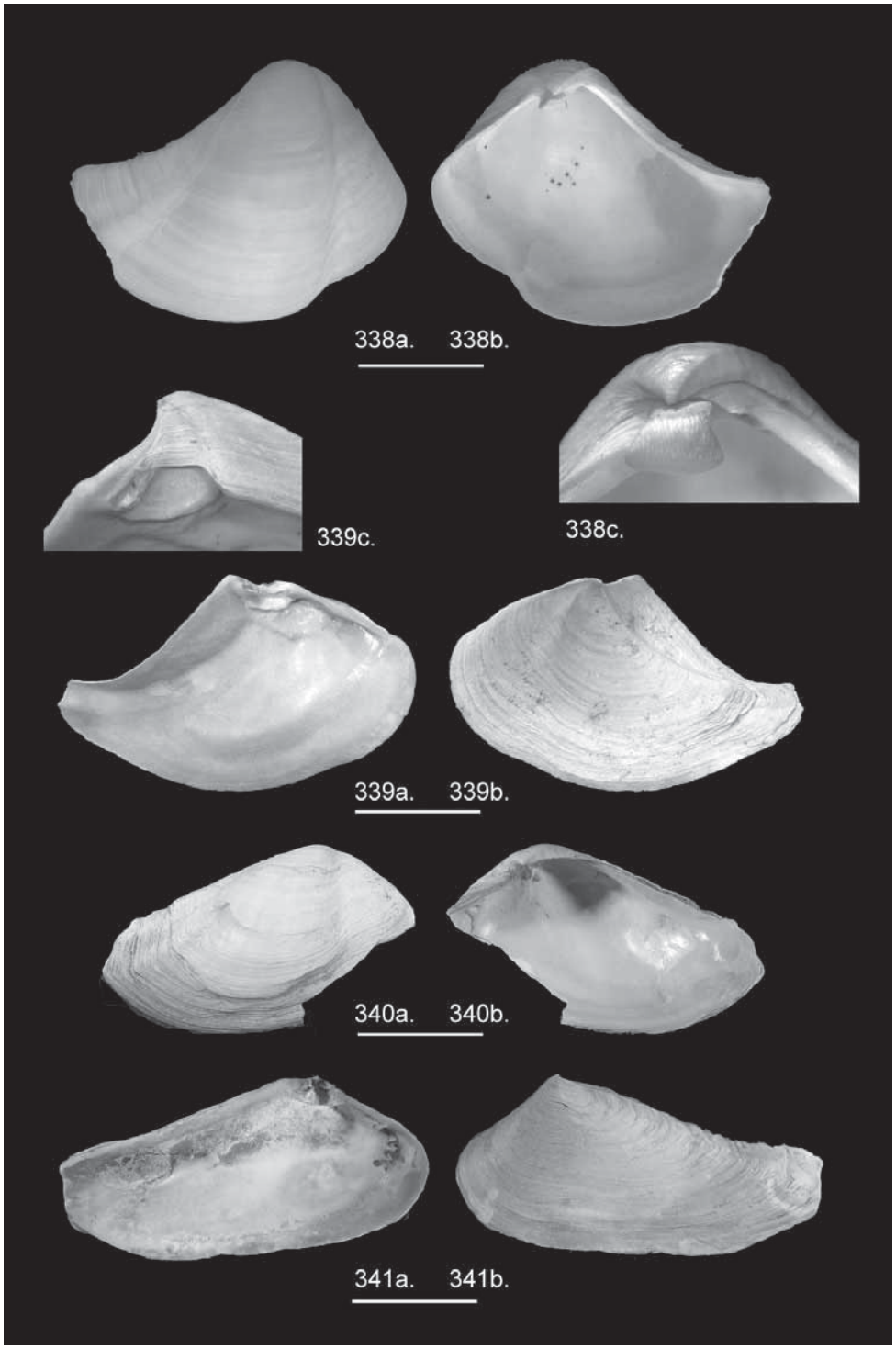
Dimensions – RGM 456 203: H 11.1; L 13.7; SD 5.0. RGM 456 414: H 9.1; L 15.4; SD 2.8. RGM 456 415: H 12.1; L >20.2; SD 6.4. RGM 456 416: H 13.7; L >24.8; SD 4.1.

Range – Pebas Formation, MZ2 - MZ12 (late Early - early Late Miocene), Colombian, Brazilian and Peruvian Amazonia.

Remarks – Specimens from the older intervals of the stratigraphic range are more elongate, the RV is flatter and the postero-dorsal flank is not very well developed. The presence of additional scarring on the exterior of the shell in some samples, possibly an indication of a chemosymbiontic living mode, was explored by Wesselingh (2006).

Genus *Ostomya* Conrad, 1874a

Type species – *Ostomya papyria* Conrad, 1874a, Miocene, Pebas Formation, western Amazonia.


338a. 338b.
339c.
338c.
339a. 339b.
340a. 340b.
341a. 341b.

Diagnosis – Thin, trapezoid shell; exterior with commarginal growth lines and wrinkles, as well as oblique lineaments giving the shell a wrinkled outline; umbo subdued, prosogyrate; RV may be slightly bilobed, LV not; RV with rather small pointed cardinal; large resilifers dominate the hinge; pallial line truncate to sinuate.

Range – Early Paleocene, United States; Miocene, western Amazonia (Colombia, Peru and Brazil).

Remarks – *Ostomya* is thinner-shelled, has a reduced RV cardinal and a slightly bilobed RV that are generally lacking in *Pachdyon* species. Until recently, *Ostomya* was considered an endemic Neogene northwestern South American genus, but new finds from the Early Paleocene of North America (Anderson *et al*., 2006) considerably extended the stratigraphic and geographic range of this genus.

Ostomya papyria Conrad, 1874a

Figs. 342, 343.

1874a *Ostomya papyria* Conrad, p. 30, pl. 1, fig. 6.
1990 *Ostomya papyria* Conrad; Nuttall, p. 318 (*pars*), figs. 438, 439 (*non* fig. 437a-e).
2006 *Ostomya papyria* Conrad; Anderson *et al*., fig. 4-4, 4-5, 4-7, 4-8, 4-9, 4-12.

Material studied – RGM 456 421 (RV) and 456 422 (LV), Macedonia (Amazonas, Colombia), exposure in north bank Amazon River, *c.* 500 m west of landing stage (3°48'S 70°15'W), level F32 (*c.* 7 m above DL). Pebas Formation, MZ11 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Extended diagnosis – Medium-sized, trapezoid, nearly equivalve, thin *Ostomya* with wrinkled surface; RV slightly bilobed, slightly larger and more convex than LV; umbo broad, orthogyrate, located about mid shell; beak ending in eroded hole at top LV socket; posterior slope well visible, slightly more pronounced in LV; oblique lineaments throughout shells exterior; hinge platform narrow and flat; cardinal small; resilifers broad and prominent, slightly turned forward; LV socket broadly triangular, well defined by low erect sharp walls; LV nymph erect, produced posteriorly; pallial line well within shells margin, somewhat truncate.

Dimensions – RGM 456 421: H > 7.9; L >12.0; SD 2.7. RGM 456 422: H 7.1; L 12.0; SD 2.0.

◀ Figs. 338-341. *Exallocorbula dispar* (Conrad, 1874a).

Fig. 338. RGM 456 203, Nuevo Horizonte (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail.
Fig. 339. RGM 456 414, same locality as Fig. 338. a, LV interior. b, LV exterior. c, LV hinge, detail.
Fig. 340. RGM 456 415, Nuevo Paleta (Loreto, Peru). a, RV exterior. b, RV interior.
Fig. 341. RGM 456 416, Indiana (Loreto, Peru). a, LV interior. b, LV exterior.

Scale bars represent 5 mm.

Range – Pebas Formation, MZ4 - MZ12 (late Early - early Late Miocene), Colombian and Peruvian Amazonia.

Remarks – Specimens from MZ4-MZ5 intervals have their umbones located more eccentrically. Additional study as to the systematic status of these specimens is needed.

***Ostomya carinata* sp. nov.**
Figs. 344-346.

1990 *Ostomya papyria* Conrad; Nuttall, p. 318 (*pars*), fig. 437a-e (*non* figs. 438, 439).

Type material – RGM 456 423 (holotype, RV): Santa Rosa de Pichana (Loreto, Peru), exposure in west bank of Amazon River, *c.* 200 m south of confluence with Rio Pichana (3°40'S 71°46'W), level F532 (5.7 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 30-8-1996. INGEMMET TN35 (RV), and RGM 456 424 (LV fragment) and 456 425 (20 fragments), all paratypes, same locality, level F535 (6.3 m above DL).

Range – Pebas Formation, MZ6 - MZ9 (Middle - early Late Miocene), Peruvian Amazonia.

Derivatio nominis – Named after the posterodorsal keel (Latin, *carina* for keel).

Diagnosis – Small to medium sized, thin, triangular-subtriangular equivalve *Ostomya*.

Description – The shell is equivalve. The pointed, orthogyrate umbo is located slightly before the shell's central axis. The beak is also orthogyrate and may be trimmed by an erosion hole at the top of the hinge. The commissure is planar or very marginally undulating. The posterior ridge is usually low and sharp, but can be rounded. It defines a commonly well-defined posterior slope. A very marginal, low depression runs from the umbo to the ventral margin on the RV, but it is so weak that it does not give the shell

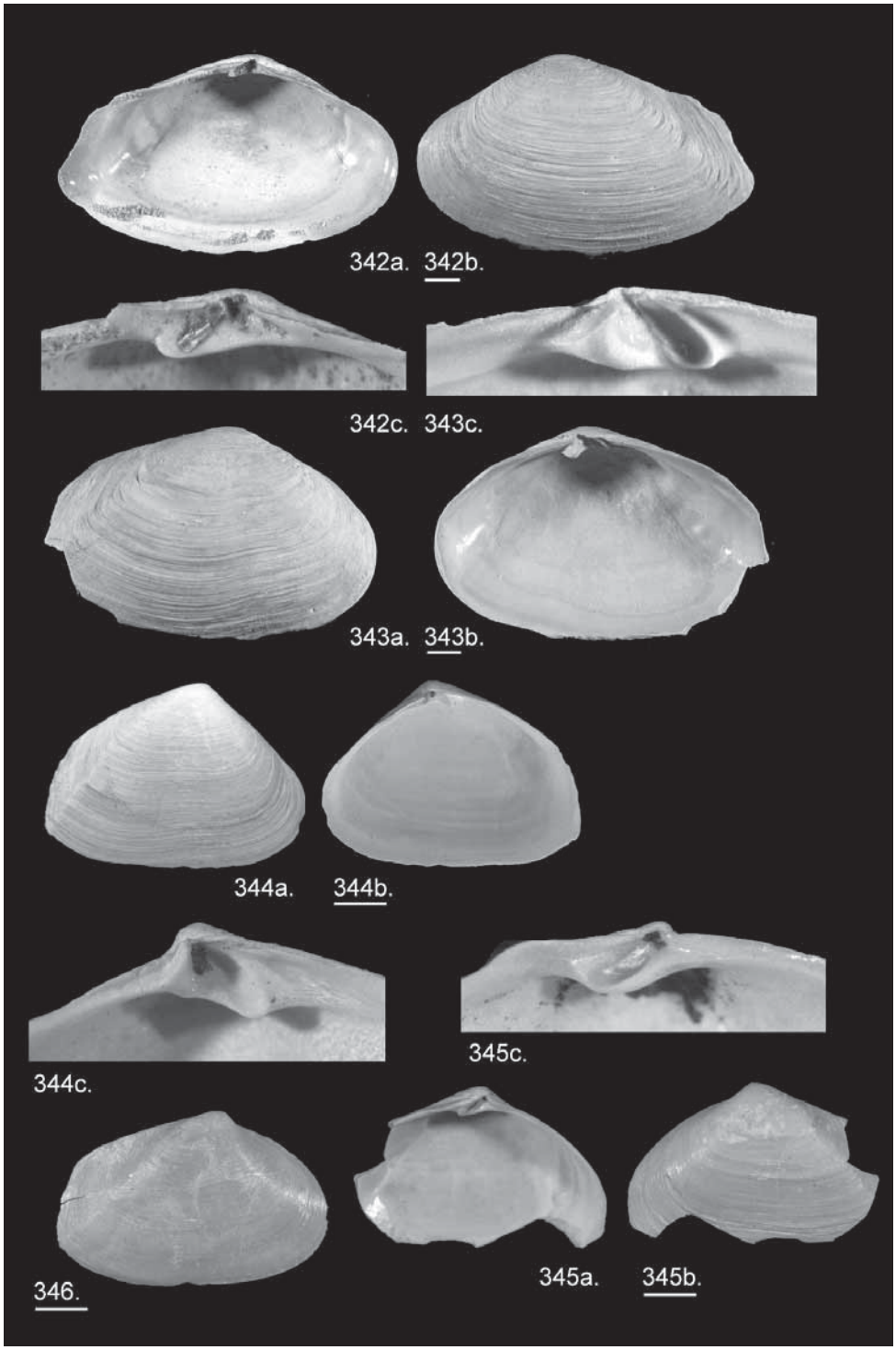
Figs. 342, 343. *Ostomya papyria* Conrad, 1874a. ►

Fig. 342. RGM 456 422, Macedonia (Amazonas, Colombia). a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 343. RGM 456 421, same locality as Fig. 342. a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Figs. 344-346. *Ostomya carinata* sp. nov.

Fig. 344. RGM 456 423, holotype, Santa Rosa de Pichana (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail.
Fig. 345. RGM 456 424, paratype, same locality as Fig. 344. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 346. INGEMMET TN35, paratype, same locality as Fig. 344. RV exterior.

Scale bars represent 1 mm.


342a. 342b.
342c. 343c.
343a. 343b.
344a. 344b.
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345c.
346.
345a. 345b.

a bilobed appearance. Growth lines, and some co-occurring oblique lineaments on the ventral portion of the shell, may give the surface a slightly papery texture. The hinge plate is narrow. It is dominated by the strongly developed resilifers. The large RV resilifer is drop-shaped, prosogyrate and extends below the base of the hinge platform. The cardinal is a small fold protruding from the lateral wall. The LV socket is broad and retracted. It contains a well-expressed spatulous resilifer whose plane is slightly turned anteriorly and located in a massively walled cup. The LV nymph is elongate, somewhat erect, mostly so on the posterior side. A short lateral groove ('tooth') exists in front of the RV cardinal tooth. The posterior adductor is large and broadly semilunate, but shallow. The anterior adductor is invisible. The pallial line is very poorly expressed, apparently truncate or even slightly sinuate.

Dimensions – RGM 456 423: H 3.5; L 5.0; SD 0.9. INGEMMET TN35: H 3.3; L 5.1; SD 0.8. RGM 456 424: L 3.8.

Remarks – The species is smaller, higher and more triangular-shaped than the trapezoid *O. papyria.*

***Ostomya myiformis* sp. nov.**
Figs. 347-350.

Type material – RGM 456 206 (holotype, LV), Beiruth (Loreto, Peru), exposure in south bank Amazon River, below village (3°53'S 71°28'W), level F492 (3.9 m above DL). Pebas Formation, MZ7 (Middle Miocene); leg. F.P. Wesselingh, 27-8-1996. INGEMMET TN48 (paratype, LV fragment), same locality. RGM 456 458 (paratype, RV fragment), Santa Elena (Loreto, Peru), exposure in south bank Amazon River, *c.* 300 m east of wood mill and *c.* 1.5 km east of Santo Tomas (3°52'S 71°23'W), level F498 (5.1 m above DL). Pebas Formation, MZ8 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 28-8-1996. RGM 456 207 (paratype, damaged RV in matrix), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence with Loreto Yacu, (3°46'S, 70°22'W), level F42 (1.4 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991.

Range – Pebas Formation, MZ6 - MZ10 (Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – This species resembles *Mya* in gross outline, particularly the northern Atlantic *Mya truncata*.

Diagnosis – Large *Ostomya* with a produced anterior and a short, truncate posterior side; shell with posterior gape.

Description – The juvenile stage of the shell is trapezoid, very much like *Ostomya papyria*, but slightly higher. From a height of *c.* 4 mm, the posterior margin becomes truncate while the anterior margins expands, resulting in an inequilateral shell with an

anterior portion up to twice as long as the posterior part. The shell is rather flat. The broad orthogyrate to very slightly prosogyrate umbo lies behind the middle of the shell. The beak is small and indistinct. It is slightly prosogyrate and often completely eroded by a hole at the top of the hinge platform. The commissure is undulating. The anterior side appears to be gaping. The shell is very slightly thickened around the posterodorsal margin. A very low and poorly defined depression that runs from the umbo to the ventral margin is found in the RV, but it hardly compromises the shells shape; no lobes are developed. The shell is ornamented with growth lines, low concentric folds as well as numerous very pronounced oblique lineaments (attesting of former periostracum), giving it a papery appearance. The hinge plate is narrow, and yields an extremely pronounced and produced chondrophore. It overlies a narrow and shallow umbonal cavity. The RV cardinal is a robust and thinly folded lamella. The RV resilifer is large, spatulous and slightly bent, and is located in a massive cup. The hinge is slightly turned forward. The LV socket is broad and retracted. The resilifer there is well expressed, prosogyrate, spatulous and has robust walls. It extends below the lower margin of the hinge plate. The nymph is short, massive and erect. The hinge plate slightly dips away below the dorsal margin. A low and broad platform develops at the anterior side of the hinge on the RV. The posterior adductor is large, irregularly drop-shaped and embedded. It has pronounced radial striae or even fine ridgelets on its inner part. The anterior adductor is also large, semilunate and shallow. It has a shiny surface with concentric lines and very faint radial streaks. It is located slightly higher in the shell than the posterior adductor. The pallial line is wide and irregular. It has radial constrictions and lineaments, and is located well within the shells margins. It runs obliquely towards the margin posteriorly and undergoes a massive truncation below the posterior adductor. The retractor scars are low, irregular, small elongate depressions that occur apparently at random between the base of the hinge plate and the adductors.

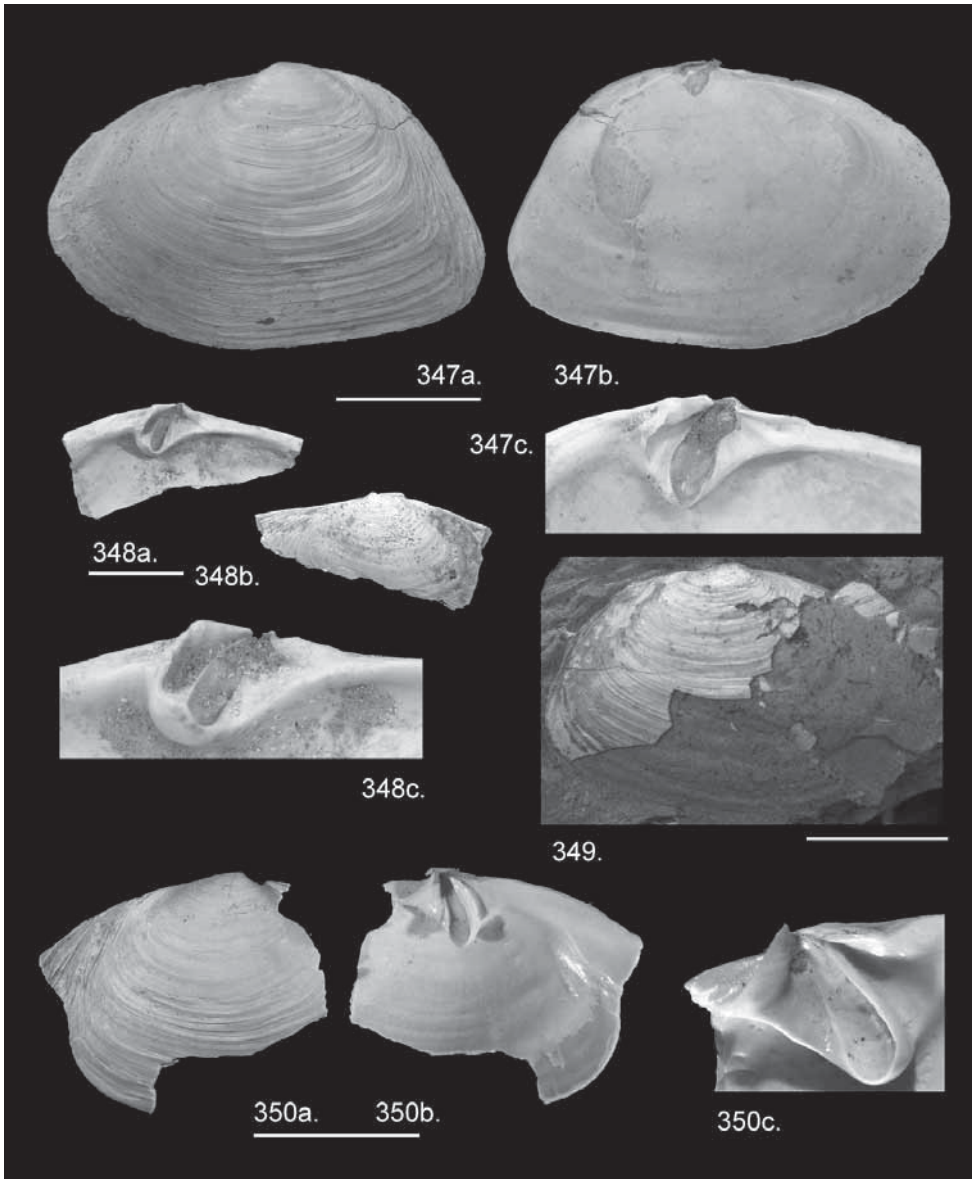
Dimensions – RGM 456 206: H 15.3; L 23.2; SD 4.2. INGEMMET TN48: L 12.3. RGM 456 458: L 8.9. RGM 456 207: H 13.2; L 19.9.

Remarks – The species is larger and higher than the other *Ostomya* species, and it has a strongly reduced posterior part.

Genus *Anticorbula* Dall, 1898

Type species – *Himella fluviatilis* Adams, 1860, Marañon River, Peru.

Diagnosis – Strongly inaequilateral, quadrangular to elongate kidney-shaped to hiatelliform, distinctly bilobed corbulid; umbones at or near posterior margin, prosogyrate; growth lines numerous, irregular, as are thin oblique ridges attesting of thick periostracum; cardinal tooth RV ranging from a folded upwards and pointed end of anterior margin to completely reduced; RV socket and resilifer narrowly elongate, almost horizontal; broad depression running from umbo to about the middle of the ventral margin; posterior lobe enlarged.



Figs. 347-350. *Ostomya myiformis* sp. nov.

Fig. 347. RGM 456 206, holotype, Beiruth (Loreto, Peru). a, LV exterior. b, LV interior. c, LV hinge, detail.
Fig. 348. INGEMMET TN48, paratype (fragment), same locality as Fig. 347. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.
Fig. 349. RGM 456 207, paratype, Los Chorros (Amazonas, Colombia). RV in matrix, exterior.
Fig. 350. RGM 456 458, paratype (fragment), Santa Elena (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.

Scale bars represent 5 mm.

Range – Early Paleocene, U.S.A.; Miocene, Pebas Formation, Peruvian and Colombian Amazonia; Pliocene-Quaternary, eastern Venezuela and Trinidad; Recent, Amazon drainage (Peru, Brazil), rivers and estuaries of Guyana and Surinam.

Remarks – The status of this genus and the suprageneric classification has been in doubt until recently. Nuttall (1990) placed species here attributed to *Anticorbula* in *Guianadesma* Morrison, 1943, which I consider to be a junior synonym of *Anticorbula*. Extant *Anticorbula sinuosum* (Morrison, 1943) was reported by Nuttall from the coastal rivers of Guyana and Surinam, and has since been reported from the Amazon and associated rivers in Brazil (Leistikow & Janssen, 1997; Simone, 1999). The new Amazonian observations indicate that the very old records of the type species from the Marañon River in Peru by Adams (1860) and Pilsbry (1944) might be correct. Simone (1999) favoured an attribution of this species in the Lyonsidae, based on anatomical arguments, but the shell characteristics are clearly those of corbulids (Nuttall, 1990; Anderson *et al*., 2006). Some elongate corbulids from the Early Miocene La Cira fauna of the Magdalena valley (*Corbula magdalensis* Pilsbry & Olsson, 1935, and *Ostomya colombiana* Pilsbry & Olsson, 1935) may, in fact, belong to a single *Anticorbula* species. However, the material on which Pilsbry & Olsson based their descriptions lacks important details of exterior surface of the shells and the hinges, precluding any further assignment than Corbulidae indet. The recent range extension of this genus into the Early Paleocene of North America (Anderson *et al*., 2006) indicates that the fossil record of this freshwater corbulid is extremely incomplete.

Anticorbula mencheri (Palmer, 1945)

Fig. 351.

1945 *Ostomya mencheri* Palmer, p. 21, pl, 2. figs. 1-7.
1990 *Guianadesma sinuosum* Morrison; Nuttall, p. 319 (*pars*) (*non* figs. 440-442).
2006 *Anticorbula* spec.; Anderson *et al*., figs. 4-13, 4-14, 4-15, 4-17, 4-18.

Material studied – RGM 456 435 (damaged RV), Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991.

Extended diagnosis – Medium-sized, rectangular, rather thick-shelled, slightly bilobed *Anticorbula*; umbo broad, located at *c.* one sixth of the shell length from anterior margin; commissure undulating; posterior ridge bluntly acute, delimiting a well defined posterior slope; posterior end truncate; a dorso-ventral depression separating two lobes is well defined; exterior of the shell ornamented with growth lines and numerous low concentric ridgelets, as well as very common oblique lineaments; hinge platform narrow apart for blunt, low and hooked knob-like cardinal extension of the anterior lateral wall, with rugose frontal surface; RV resilifer short, subhorizontal; plane of resilifer turned downward; anterior adductor embedded, semilunate, striate; posterior adductor large, shallow, broadly semilunate; the latter lies higher than the former; pallial line well defined, bluntly truncate to sinuate; area within the pallial line distinctly pitted; retractor scars well developed.

Dimensions – RGM 456 435: H 5.5; L 8.7; SD 2.0.

Range – Pebas Formation, MZ10 (late Middle - early Late Miocene), Peruvian Amazonia; Las Piedras Formation (Pliocene), eastern Venezuela.

Remarks – Usually, *Anticorbula* has a completely reduced RV cardinal tooth. However, in material studied from the Pliocene Las Piedras Formation, La Llanera, Monagas, Venezuela, specimens with cardinals like those of the Pebas specimen were found, as well as specimens with completely reduced cardinals and intermediates.

***Anticorbula miocaenica* sp. nov.**
Figs. 352, 353.

Type material – INGEMMET TN44 (holotype, LV) and RGM 456 447 (paratype, damaged RV), Porvenir (Loreto, Peru), exposure in west bank Amazon River, *c.* 300 m north of southern tip of village (4°15'S 73°23'W), level F707 (sample at DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 5-9-1996.

Range – Pebas Formation, MZ2 - MZ12 (late Early - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Named after the Miocene epoch.

Diagnosis – Thin-shelled, elongate *Anticorbula* with larger bilobed RV and smaller rectangular RV; posterior slope usually acute, with additional radial ridgelet on posterior slope.

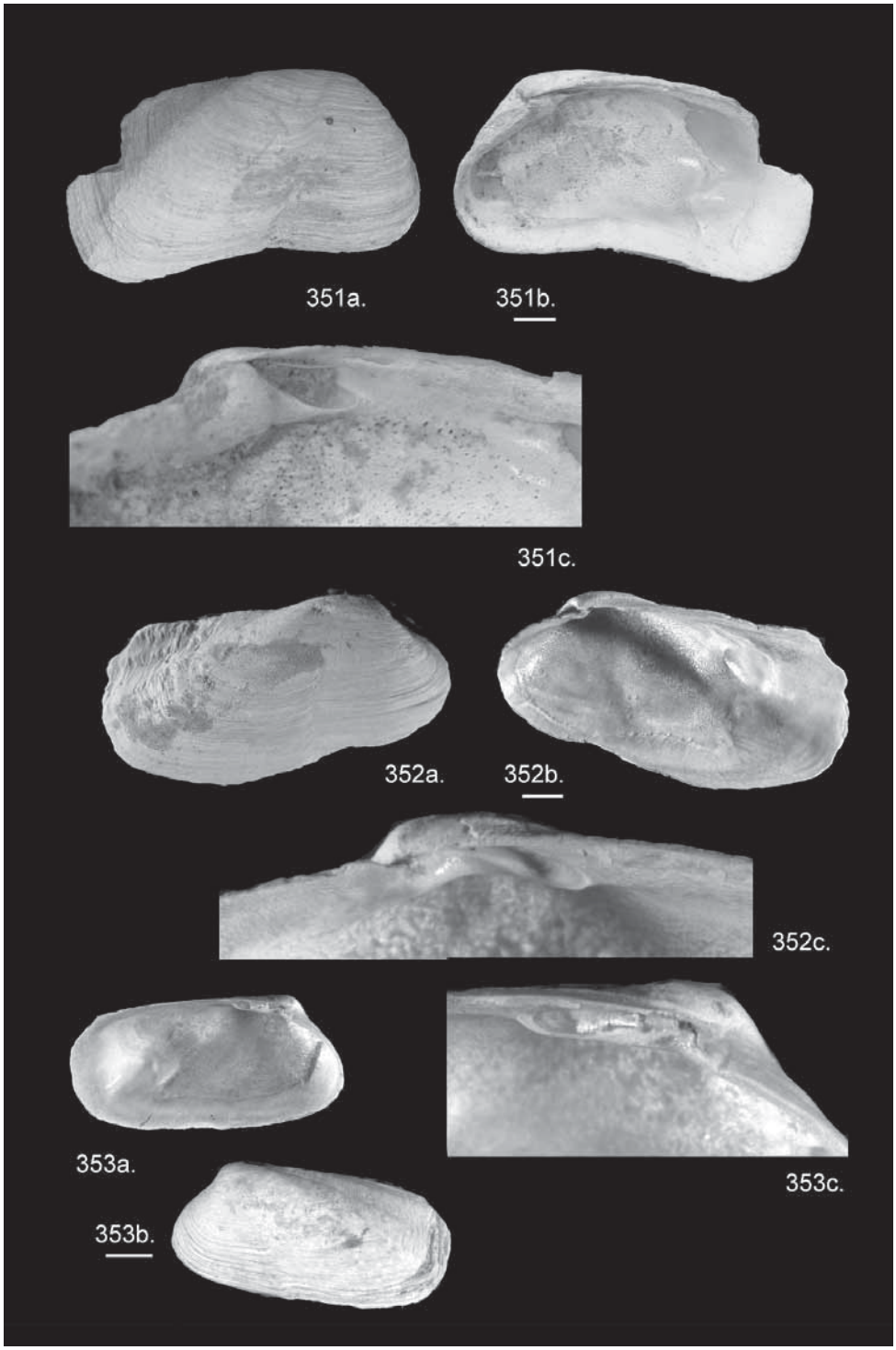
Description – The shell is small to medium sized. The right valve has an irregular elongate kidney-shape, the left valve is almost perfectly rectangular. The RV is much larger and distinctly bilobed. The median depression that separates both lobes on the RV is developed as a narrowly defined lineament on the LV, where the growth lines make a very short step only. The commissure is undulate. The umbo, located at about one sixth to one seventh of the shell length from the anterior margin, is broad, incurved and orthogyrate to marginally prosogyrate. The beak is small, prosogyrate and located just below

Figs. 351. *Anticorbula mencheri* (Palmer, 1945), RGM 456 435, Nuevo Horizonte (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view. ►

Figs. 352, 353. *Anticorbula miocaenica* sp. nov.

Fig. 352. RGM 456 447, paratype, Porvenir (Loreto, Peru). a, RV exterior. b, RV interior. c, RV hinge, detail, oblique view.
Fig. 353. INGEMMET TN44, holotype, same locality as Fig. 352. a, LV interior. b, LV exterior. c, LV hinge, detail, oblique view.

Scale bars represent 1 mm.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the umbo. The posterior ridge is variably developed. It is low, irregular, but broadly acute; on the RV it may be more rounded. The posterior slope is well defined, especially on the LV, and ornamented with further fine radial ridgelets. The posterior end is rounded truncate. A concentric ornament of low, irregular, ridgelets, and common, thin, oblique lineaments throughout the shell, give the surface a wrinkled papery appearance. The RV has a low furrow for reception of the LV in the rear lobe. The hinge plate is narrow in the LV and folded away in the RV. The RV cardinal is formed by a slight fold in the posterior end of the anterior lateral wall. Deeply behind lies the elongate-lanceolate, slightly bent subhorizontal resilifer, whose plane is almost perpendicular to the commissure. The LV socket is indistinct. A spatulous, horizontal resilifer is present. A lateral groove ('tooth') may be somewhat developed on the anterodorsal margin of the RV. The anterior margin of the RV is markedly rounded. The adductors are large, semilunate and smoothish. The posterior adductor is located high in the shell, just below the dorsal wall. The pallial line is wide and has irregular margins, radial impressions and striae. It has a distinct pallial sinus. The posterior retractor is a low extension of the posterior adductor. The anterior retractor is a small elongate pit that lies just behind the anterior retractor.

Dimensions – INGEMMET TN44: H 2.2; L 6.1; SD *c.* 1.2. RGM 456 447: H 5.0; L >9.0; SD *c.* 2.0.

Remarks – *Anticorbula miocaenica* is thinner, more elongate and more inequivalve than *A. mencheri.* It resembles the extant *A. fluviatilis*. The latter is much more irregularly shaped and lacks the posterior ridge.

Genus *Pachyrotunda* gen. nov.

Type species – *Pachyrotunda rotundata* sp. nov., Miocene, Pebas Formation, western Amazonia.

Derivatio nominis – The name is a merger of *Pachydon* and *rotundata*, the latter referring to the rotund outline (Latin *rotundus,* spherical). Gender feminine.

Diagnosis – Rotund, thin-shelled corbulid with a concave posterior slope and large, broad resilifers.

Range – Miocene, Pebas Formation, western Amazonia (Peru, Colombia)

Remarks – The thin-shelled *Diplodonta*-like outline of this genus makes it different from other pachydontine bivalves. In outline it resembles some Neotropical tellinid genera such as *Florimetes*, but the tellinid hinge architecture of the latter is very different from the simple corbulid bauplan of *Pachyrotunda*.

***Pachyrotunda rotundata* sp. nov.**
Figs. 354-357.

Type material – RGM 456 453 (holotype, damaged RV), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence with Loreto Yacu (3°46'S

70°22'W), level F42 (1.4 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 454 (paratype, damaged LV), same locality. RGM 456 455 (paratype, damaged pair partially covered with sandstone), Santa Sofia (Amazonas, Colombia), exposure in north bank Amazon River, 3 km upstream of Santa Sofia below land house opposite northwestern tip Isla Santa Sofia (3°57'S 70°09'W), level F58 (3.1 m above DL). Pebas Formation, MZ11 or MZ12 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. INGEMMET TN47 (apical fragment LV), and RGM 456 456 (apical fragment RV) and 456 457 (apical fragment LV), all paratypes from Nuevo Horizonte (Loreto, Peru), exposure in western wall of road Iquitos-Nauta at km 42 (4°04'S 73°25'W), level F367a (1.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 11-8-1996.

Range – Pebas Formation, MZ5 - MZ12 (late Early - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Refers to the rotund outline of the shell.

Diagnosis – See diagnosis of genus.

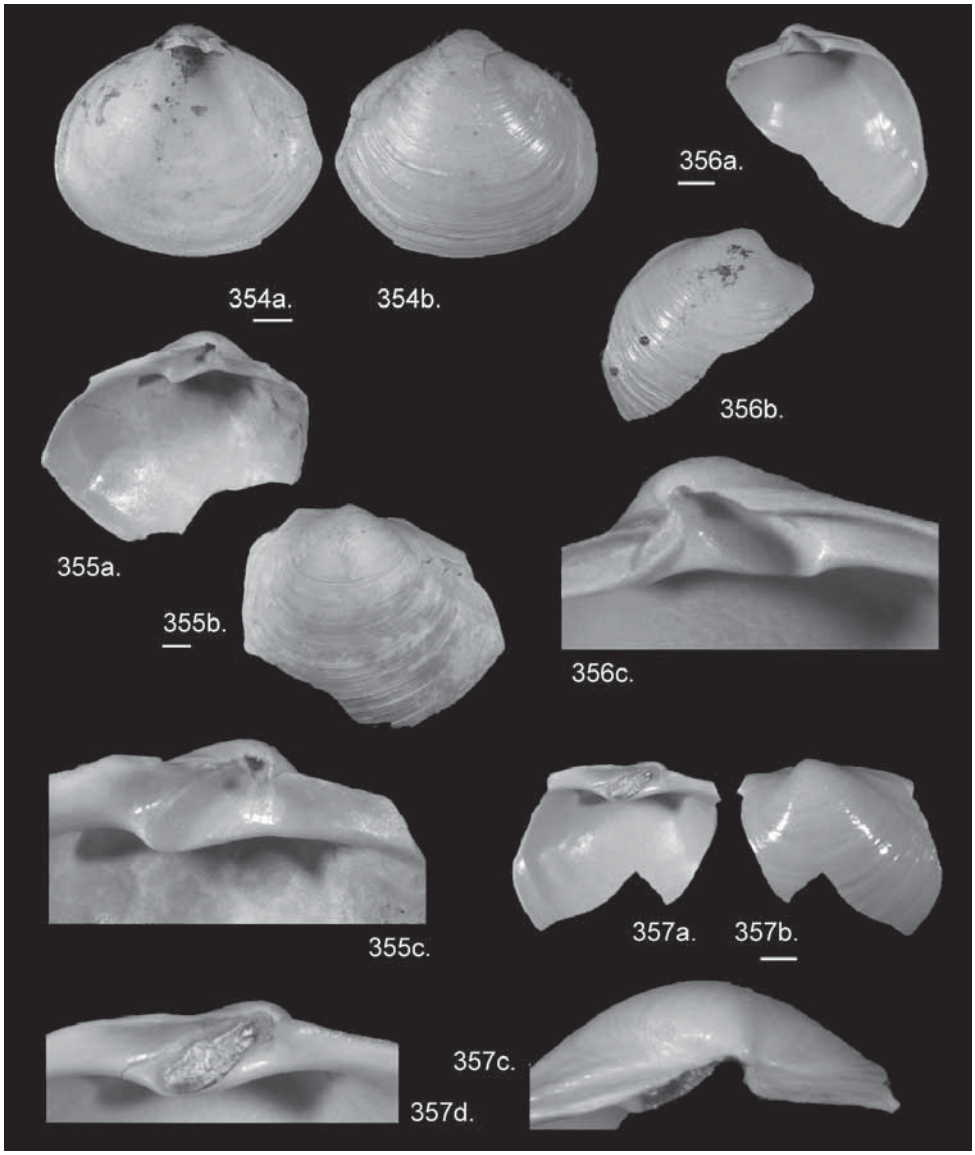
Description – The species has small to medium sized, semicircular equivalve shells. The umbo is located in the middle of the shell. The commissure is straight to very slightly undulating. The shell is rather thin. A very narrow ridge on the LV bounds a rimate escutcheon. The umbo is broad and orthogyrate to slightly prosogyrate. The small beaks are often bounded by an erosion hole below. The posterior ridge is rounded, but well visible. It bounds a distinct, concave posterior slope. The posterior margin is slightly obliquely truncate. The surface of the shell contains growth lines, and oblique lineaments may occur around the posterior ridge and near the ventral margin. The RV cardinal is a robust, elegant, reversed comma-shaped, erect triangular feature. The resilifer is elongate ovate, prosogyrate. The resilifer plane is slightly inclined. The LV socket is ovate and rather deeply embedded within erect, but rounded, lateral walls. The broadly ovate resilifer occupies most of the socket. The nymph is short, rounded, slightly erect and robust. Lateral grooves occur along both dorsolateral margins. The adductors are large, semilunate to subquadrate, shallow and poorly defined. The poorly defined pallial line appears to be broad, and lacks a retraction. No traces of possible retractor scars were found.

Dimensions – RGM 456 453: H 12.1; L 13.7; SD 3.7. RGM 456 454: L 16.4. RGM456455: H 9.0; L 10.8; diameter 5.5. INGEMMET TN47: L 5.4. RGM 456 456: L 6.1. RGM 456 457: L 9.9.

Genus *Concentricavalva* gen. nov.

Type species – *Concentricavalva concentrica* sp. nov., Miocene, Pebas Formation, western Amazonia

Derivatio nominis – *Concentrica* refers to the concentric ornament; *valva* for valve; gender feminine.



Figs. 354-357. *Pachyrotunda rotundata* sp. nov.

Fig. 354. RGM 456 453, holotype, Los Chorros (Amazonas, Colombia). a, RV interior. b, RV exterior.
Fig, 355. RGM 456 454, paratype, same locality as Fig. 354. a, LV interior. b, LV exterior. c, detail of hinge, oblique view.
Fig. 356. RGM 456 456, paratype, Nuevo Horizonte (Loreto, Peru). a, RV interior. b, RV exterior. c, detail of hinge.
Fig. 357. INGEMMET TN47, paratype, same locality as Fig. 356. a, LV interior. b, LV exterior. c, LV hinge, dorsal view. d, LV hinge, detail, oblique view.

Scale bars represent 1 mm.

Diagnosis – Intermediate, markedly flat and thin-shelled subquadrate corbulid with concentric folds; hinge plate low, massive with very pronounced resilifers; LV nymph auriculate.

Range – Pebas Formation, Middle - early Late Miocene, western Amazonia (Peru, Colombia, Brazil)

Remarks – This genus cannot be confused with any other corbulid. The thin, concentrically ribbed shell resembles that of the mactraid *Raeta plicatella* (extant, Caribbean, northern and northeastern South America), but the hinge of the latter is entirely different.

***Concentricavalva concentrica* sp. nov.**
Figs. 358-363.

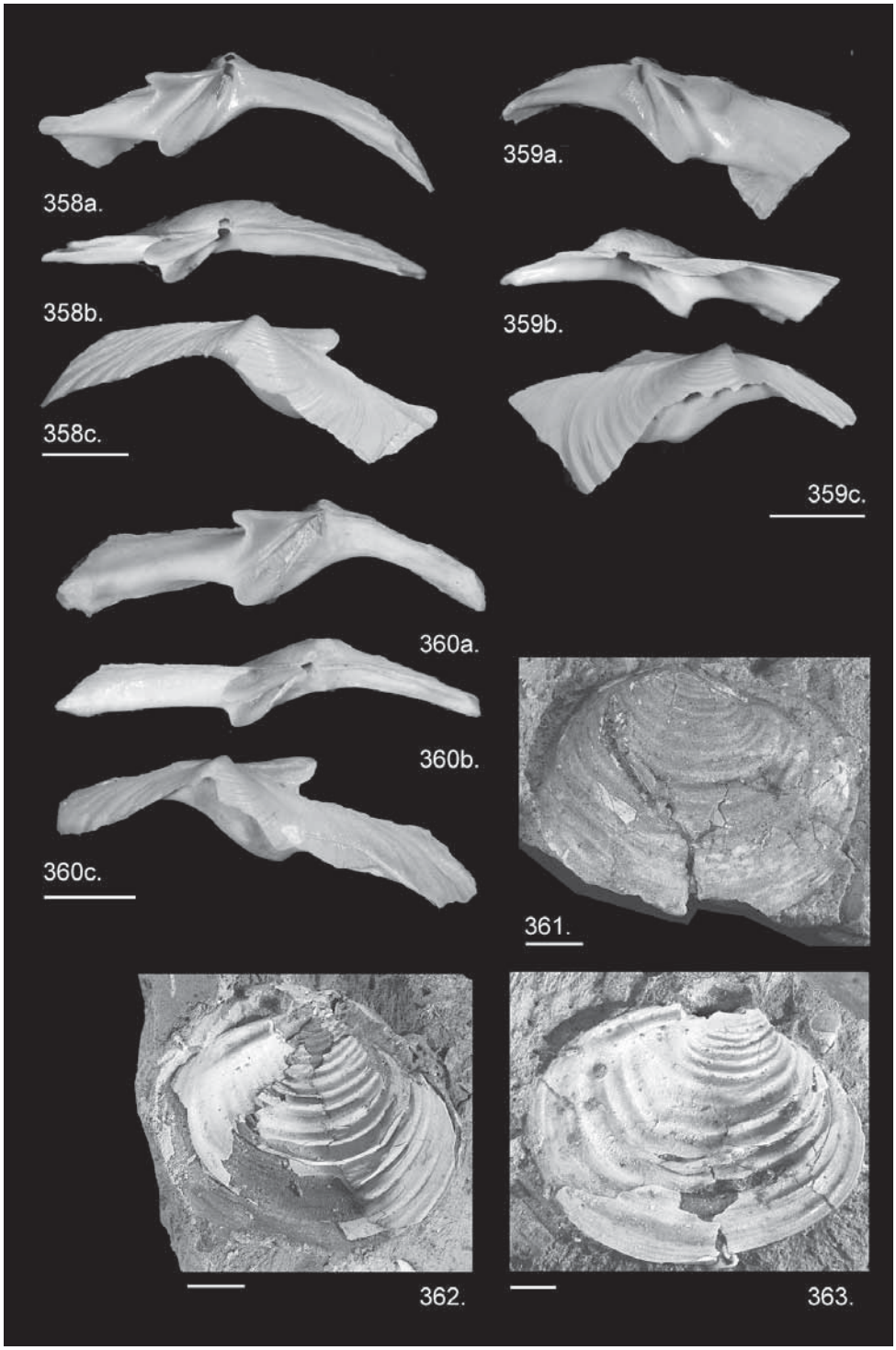
Type material – RGM 456 210 (holotype, damaged LV in matrix), 456 451 (paratype, damaged LV in matrix) and 456 452 (paratype, damaged RV in matrix), Los Chorros (Amazonas, Colombia), exposure in north bank Amazon River at confluence with Loreto Yacu, (3°46'S 70°22'W), level F42 (1.4 m above DL). Pebas Formation, MZ10 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 9-1991. RGM 456 208 (RV top fragment) and 456 209 (LV top fragment), and INGEMMET TN46 (LV top fragment), all paratypes from Nuevo Horizonte (Loreto, Peru), exposure at the road Iquitos-Nauta at km 45.2, in village (4°05'S 73°25'W), level F70 (2.0 m above DL). Pebas Formation, MZ9 (late Middle - early Late Miocene); leg. F.P. Wesselingh, 18-10-1991.

Range – Pebas Formation, MZ6 - MZ12 (Middle - early Late Miocene), Colombian and Peruvian Amazonia.

Derivatio nominis – Concentric refers to the concentric folds on this species.

Diagnosis – As for the genus.

Description – The shell is so fragile that not a single complete valve has been recovered. Several damaged valves in matrix, as well as a number of fragments, form the basis for this description. The flat shell is subquadrate with rounded margins and presumably equivalve. The very slightly erect, orthogyrate umbo is located slightly before the middle of the shell. The beak is often bounded by an erosion hole below. The commissure was likely either straight or only very marginally undulating. The shell is very thin. Neither posterior ridge nor posterior slope are present. The ornament consists of broad, more or less regularly spaced, low concentric folds that are also expressed on the shell's interior. The exterior has also common oblique lineaments, attesting of former periostracum, and can even be corrugate in part. The outer margins of the valves may have been almost totally flat. The hinge platform is markedly broad, flat and robust, and overlays a thin, deep umbonal cavity. The cardinal tooth is entirely reduced. Instead, a prominent spatulous chondrophore is present in the RV. The chondrophore is slightly prosogyrate and its plane is turned slightly forward. No socket is developed on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the LV platform. The chondrophore is a reversed copy of the RV chondrophore; both are projecting well below the base of the hinge platform. The LV nymph is produced, robust, auriculate and has a spatulous outline. A marked nymph-like extension exists behind the umbo on the RV. It is a thin lamella that is almost perpendicular to the commissure. Viewed from above it is a broad triangular area, with almost regular grooves developing on the rear end. A very broad and low lateral groove is present on the posterodorsal side of the RV. No traces of adductors or a pallial line were found in the available material.

Dimensions – RGM 456 210: H >12.8; L 15.0; SD estimated at *c.* 2.0. RGM 456 451: H 15.3; L ≥20.0; SD estimated at *c.* 2.5. RGM 456 452: H *c.* 11.6; L 14.2; SD estimated at *c.* 1.5. RGM 456 208: L 7.6. RGM 456 209: L 9.3. INGEMMET TN46: L 8.8.

Discussion

In this paper, species are defined primarily on the occurrence of morphological discontinuities with other species, both in time and space. In a number of cases, closely similar endemic species occurring in successive stratigraphic intervals can be interpreted as members of a lineage. Stratigraphically intermediate samples were found with intermediate populations between two such successive morphs in some instances. In such cases, the successive morphs within that lineage were defined as stratigraphic subspecies (e.g., *Tryonia scalarioides tuberculata* and *T. s. scalarioides*; *Dyris b. bicarinatus* and *D. b. sofiaensis*).

Another source of morphological variation that had to be dealt with was the possibility of ecophenotypy. An ecological framework, presented by Wesselingh *et al.* (2002) for the Pebas fauna (and elaborated in more detail by Wesselingh *et al.*, 2006c), allowed for the investigation of transitional morphs in adjacent biotopes within single biozones. Examples of ecophenotypy encountered appear to be restricted to variation in size and thickness (see, e.g., *Pachydon trigonalis*; Wesselingh, 2006).

The possibility of sexual dimorphism was also considered. In the Cochliopidae, examples exist of large size differences between males and females in some of the extant

◀ Figs. 358-363. *Concentricavalva concentrica* sp. nov.

Fig. 358. INGEMMET TN46, paratype (apical fragment), Nuevo Horizonte (Loreto, Peru). a, RV interior. b, dorsal view. c, exterior.
Fig. 359. RGM 456 208, paratype (apical fragment), same locality as Fig. 358. a, LV interior. b, dorsal view. c, exterior.
Fig. 360. RGM 456 209, paratype (apical fragment), same locality as Fig. 358. a, RV interior. b, dorsal view. c, exterior.
Fig. 361. RGM 456 452, paratype (damaged RV in matrix), Los Chorros (Amazonas, Colombia). Exterior view.
Fig. 362. RGM 456 451, paratype (damaged LV in matrix), same locality as Fig. 361. Interior view.
Fig. 363. RGM 456 210, holotype (damaged LV in matrix), same locality as Fig. 361. Interior view.

Scale bars represent 2 mm.

species (Hershler, 2001). Possible sexual dimorphs have been encountered in the Pebasian *Dyris huberti* and *D. hauxwelli*. Samples of these species contain a high-spired and a broad morph that conform the same bauplan; the two morphs co-occur. The apical characteristics of such morphs are similar (in early ontogeny one would not expect the expression of well established sexual differences). Although not absolute proof, these indications together are used to interpret morphs as sexual dimorphs and group them under one species.

Criteria for the establishment of genera are more problematic. Commonly used criteria in neontology, such as genetic distance and monophyly, are difficult or impossible to apply to the fossil material that lacks DNA, and contains rather few and commonly convergent morphological characters. Again, the morphological distinctness is the only available leading criterion, although admittedly subjective. For example, it is possible that the genus *Toxosoma* originates from *Dyris denticulatus* during MZ2 or MZ3. At the time, distinct *Dyris* species existed, that had diverged by the time of origin of *Toxosoma*. As a consequence, *Dyris* might be a paraphyletic genus. More study is needed to the faunas of the older Pebas intervals (MZ2-MZ4) to address the order of origination, to document the context and timing of diversifications, and to assess the status of several of the genera (for example, *Tropidebora, Sioliella* and *Longosoma*). These older intervals are largely exposed in areas where the security situation has made fieldwork impossible (e.g., Colombian Putumayo Basin).

The fauna could not entirely be studied in the time available. Emphasis has been on species of importance for biostratigraphic, ecologic, evolutionary or biogeographic studies. All non-endemics encountered were treated systematically. Several endemic species with a broad range of morphologies and a broad stratigraphic range (such as *Dyris ortoni* and *Pachydon iquitensis*) might be subdivided in further species after additional study. Furthermore, several rare endemic species in species-rich genera have remained untreated for the moment. As a result, I would expect the current material to hold an additional twenty species or so, most of them belonging to the endemic Pebasian Cochliopidae.

Mollusc faunas that are contemporaneous to those of the Pebas Formation have been very unevenly preserved in tropical South America. For example, Miocene marine faunas are abundant and well preserved in the Caribbean region, less well known from the Pacific coasts, poorly preserved in the present-day Amazon-mouth region, and lacking altogether in the coastal plains of the Guyanas and most of Brazil. Comparatively well-preserved Miocene freshwater mollusc faunas occur in the Andean and Subandean regions, but are entirely absent from the regions to the east of the Pebas Formation. The assessment of the potential endemicity of Pebasian taxa is therefore not straightforward. Species are considered non-endemic when they are extant or are known from fossil occurrences outside the Pebas Formation or are found in fluvial or marginal marine associations or represent terrestrial settings within the Pebas system. By this definition, the overwhelming majority of species of the Pebas Formation (114 species: 72%) is considered as endemic. I would not expect that many of the 'endemics' would have lived beyond the Pebas system. The general character of tropical marginally marine faunas, and fluvial and lacustrine faunas (other than those of long-lived lakes), is totally incompatible with the Pebas fauna. Within modern and Miocene

Neotropical coastal mollusc faunas, widely distributed mangrove-associated taxa such as the snail genera *Littoraria* and *Cerithidea*, oysters and arcids occur, all of which are lacking in the Pebas fauna. Miocene and modern Neotropical fluvial and lacustrine faunas are dominated by species of pearly freshwater mussels, sphaeriid and corbiculid clams, and ampullariid, planorbiid and ancylid snails. Very low numbers of co-occurring cochliopid and cerithioidean snails may also occur in these environments. Instead, the Pebas fauna is characterised by high numbers of co-occurring species (up to 95 species in a single biozone). The dominant groups in the Pebas fauna (cochliopid snails and corbulid bivalves) have developed an unusual range of morphologies and high numbers of species (see, e.g., Wesselingh, 2006 for the pachydontine corbulids). Therefore, the character of the Pebas fauna is very different from Miocene and modern fluvial and lacustrine faunas, as well as marginal marine faunas. The endemic status of the vast majority of these Pebasian species is thus likely, as comparable environments are not proven outside the western Amazonia. However, it is possible that the Llanos Basin (Colombia-Venezuela) to the north may have served as an episodic extension of the Pebas system, although fossil evidence is scarce. But future studies might extend the range of Pebasian endemics into the Llanos region. The percentage endemics (72%) in the Pebas fauna is high in species numbers, but it is even higher in abundances. Wesselingh *et al.* (2002) estimated that endemics formed over 90% of the shells present in the Pebas fauna, based on faunal estimates from 285 samples. An endemicity ratio of 95% of shell numbers is found for 16 completely elaborated samples in Wesselingh *et al*. (2006c).

The high endemicity rates complicate the autecological assessment of the Pebas fauna. Species (and genera) endemic to the Pebas system have no living representatives from which feeding habits, habitat characteristics and reproductive ecology can be assessed using actualistic comparisons. However, isotope geochemical studies on the Pebas molluscs (Vonhof *et al*., 1998, 2003; Wesselingh *et al*., 2002; Kaandorp *et al*., 2006) clearly indicate that the endemic Pebasian mollusc taxa must have been freshwater inhabitants (see further discussion in Wesselingh *et al*., 2006c).

The nature of the Pebas fauna conforms to the nature of long-lived lake faunas (reviews in Michel, 1994, for long-lived lake gastropods and in Wesselingh, in press, for long-lived lake bivalves). Long-lived lakes themselves are a poorly defined concept, but are generally characterised by their geological longevity and endemic faunas (see review in Martens, 1997). Most species in such lakes evolved *in situ* from freshwater or (marginal) marine ancestors by either anagenesis or cladogenesis, giving rise to species flocks, evolution beyond usual ecological tolerances (behavioural, feeding and reproductive and physical) and excessive morphological variation. The European Neogene-Quaternary Paratethyan Lake Pannon, the Euxinian lakes, Lake Aktchagyll and the Caspian Sea faunas share a number of characters with the Pebas fauna. All are dominated by bivalves of marine ancestry or with euryhaline capacities (Lymnocardiidae and Dreissenidae versus Corbulidae). The gastropod species composition is dominated by endemic rissooid snails of a number of families in the Paratethyan faunas and the Cochliopidae in the Pebas fauna. Additionally, cerithioideans and neritids underwent some radiations in both systems (the former radiated profusely in Lake Pannon only). The Pebas fauna therefore can be considered a typical long-lived lake fauna.

Table 1. Ecological grouping of the Pebasian molluscs; note that (fluvio-)lacustrine mollusc taxa mentioned below as a rule inhabit adjacent biotopes as well.

A.	Marginal marine group. *Corbula cotuhensis, Macoma* sp., *Melongena woodwardi, Nassarius*? *reductus*, Pyramidellidae (4 spp.).
B.	Coastal plain freshwater mollusc taxa. *Glabertryonia glabra, Anticorbula mencheri, A. miocaenica.*
C.	Molluscs from stagnant - slightly agitated fresh water. *Pisidium* sp., *Eupera* sp., *Gundlachia* (2 spp.), Planorbidae (4 spp.), Ampullariidae indet.
D.	Molluscs from running or agitated fluvial and fluviolacustrine environments. Most Thiaridae, Pachychilidae, Mycetopodidae and Hyriidae, *Neritina roxoi*, *Mytilopsis sallei, Corbicula* cf. *cojitamboensis.*
E.	Terrestrial group. *Pebasiconcha immanis, Orthalicus* sp., Ampullariidae indet.
F.	Marginal lacustrine group (foreshore, prodelta, interdistributary bay). High diverse fauna dominated by Corbulidae and Cochliopidae, but also with representatives of Dreissenidae, Pachychilidae and Thiaridae. Some common species include *Neritina roxoi, Tryonia nuttalli*, large *Dyris* spp. such as *Dyris ortoni, D. lintea, D. pebasensis* and *D. b. bicarinatus, Toxosoma grande, Mytilopsis sallei, Pachydon carinatus.*
G.	Lacustrine ramp/shelf group (between fair weather and storm wave base). Very high diverse fauna dominated by Corbulidae and Cochliopidae. Characteristic species include *Tryonia minuscula,* small elongate *Dyris* species such as *Dyris gracilis, D. microturritella* and *D. acicularis, Onobops* spp., *Toxosoma* spp., *Cochliopina*? *hauxwelli*, *Pachydon* spp., *Ostomya* spp., *Exallocorbula dispar, Concentricavalva concentrica.*
H.	Lacustrine bottom group (at or below storm wave-base). Diverse fauna dominated by *Pachydon obliquus*. Other common species include smaller and thin-shelled corbulids, such as *Ostomya* spp. and *Concentricavalva concentrica*, small and thin-shelled cochliopids such as *Cochliopina*? *hauxwelli*, *Onobops communis*, *Dyris microbispiralis* and *D. hauxwelli*.

Wesselingh *et al.* (2002) presented an ecological framework with pooled species groups. A slight expansion of this ecological grouping is given herein, with some of the characteristic species (Table 1). By far the highest species diversities are found in lacustrine ramp/shelf associations and only slightly lower numbers occur in the marginal lacustrine group.

Conclusions

At least 158 mollusc species are recognised in the Miocene Pebas Formation of western Amazonia, up from slightly over 50 species in the last review of the fauna (Nuttall, 1990). The Pebas fauna is aquatic, and dominated by endemic species of cochliopid snails and corbulid bivalves. Undisputed freshwater taxa are not common. Taxa representing elevated salinities are rare. Terrestrial snail species numbers are very low. The Pebas fauna harbours various species-rich genera with a prolific morphological variation and unusual morphological characters, especially in the dominant Cochliopidae and Corbulidae. Together with high endemicity rates (even higher in terms of abundance), the Pebas fauna represents a typical long-lived lake fauna. Through this work the vast majority of Pebasian mollusc species has been named and made available for further investigations.

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