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On relict hydrobiid species in Brazilian Amazonia (Gastropoda, Prosobranchia, Hydrobiidae)

F.P. WESSELINGH

Nationaal Natuurhistorisch Museum Naturalis, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands; wesselingh@naturalis.nnm.nl

University of Turku Biodiversity Centre, Faculty of Biology, University of Turku, SF 20014 Turku, Finland

Two extant hydrobiid species from the lower Tapajos river of Brazil are redescribed. *Potamopyrgus amazonicus* Haas, 1949, is assigned to the genus *Dyris* Conrad, 1871. At least eleven species from Miocene deposits of Western Amazonia are assigned to *Dyris*, a genus that was previously assumed to be extinct. The apertural features of *Sioliella effusa* Haas, 1949, are considered indicative of a close relationship to Miocene Amazonian taxa formerly assigned to *Eubora* Kadolsky, 1980. *Sioliella ovata* spec. nov., a Miocene species resembling *S. effusa* is described. The two Tapajos species can be regarded as relicts of a speciose, endemic, Miocene Western Amazonian molluscan fauna.

Key words: South America, Amazonia, Miocene, Recent, Hydrobiidae, *Dyris*, *Sioliella*, new species.

INTRODUCTION

Miocene deposits in Western Amazonia (Peru, Colombia and Brazil) referred to as Pebas Formation and/or Solimoes Formation are known for their unusually well-preserved endemic mollusc faunas. Nuttall (1990) listed some 45 species from these deposits. The Pebas fauna is dominated by two groups: cochliopine hydrobiids and pachydontine corbulids. Most of the genera dominating the Pebas fauna are considered extinct (Nuttall, 1990). However, a Recent mollusc fauna described by Haas (1949) from the lower Tapajos river of Central Amazonia (Brazil) contains two species that appear closely related to the Miocene Pebas hydrobiids. The aim of this paper is to redescribe and illustrate the material described by Haas, to compare these taxa with Miocene taxa from the Pebas Formation and to discuss affinities between the two faunas.

Abbreviations for collections: FMNH, Department of Invertebrate Zoology, Field Museum, Chicago, USA; RGM, Division of Cenozoic Mollusca, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands. Abbreviations for shell characters: H, height; HAP, apertural height; W, width.

SYSTEMATICS

Superfamily Rissoidea Gray, 1847
Family Hydrobiidae Troschel, 1857
Subfamily Cochliopinae Tryon, 1866
Genus *Dyris* Conrad, 1871

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

Additional *Dyris* species. — Oligocene-Miocene, Colorado Formation, Magdalena Basin, Colombia: *Potamopyrgus laciranus* Pilsbry & Olsson, 1935. Miocene, Pebas Formation, Amazonas Basin, Colombia, Peru and Brazil: *Mesalia ortoni* Gabb, 1869; *Isaea lintea* Conrad, 1871; *Hydrobia (Isaea) tricarinata* Boettger, 1878; *Melania bicarinata* Etheridge, 1879; *Dyris tuberculata* de Greve, 1938; *Dyris hauxwelli* Nuttall, 1990. Miocene, La Tagua beds, Colombia: *Dyris semituberculata* Nuttall, 1990; *Dyris* spec. (Nuttall, 1990). Miocene, Loyola Formation, Cuenca Basin, Ecuador: ?*Dyris* spec. (Nuttall, 1990). Recent, Tapajos river, Brazil: *Potamopyrgus amazonicus* Haas, 1949.

Diagnosis. — Shell dextral, hydrobiiform to turritelliform. Usually spirally ornamented, occasionally reticulate or nearly smooth; the onset of two to four teleoconch spirals after the protoconch-teleoconch boundary is gradual; primary spirals are well-developed on the second and third teleoconch whorl, as is an adapical sutural ramp; growthlines prosocline; nucleus smooth and inclined; H 4-21 mm.

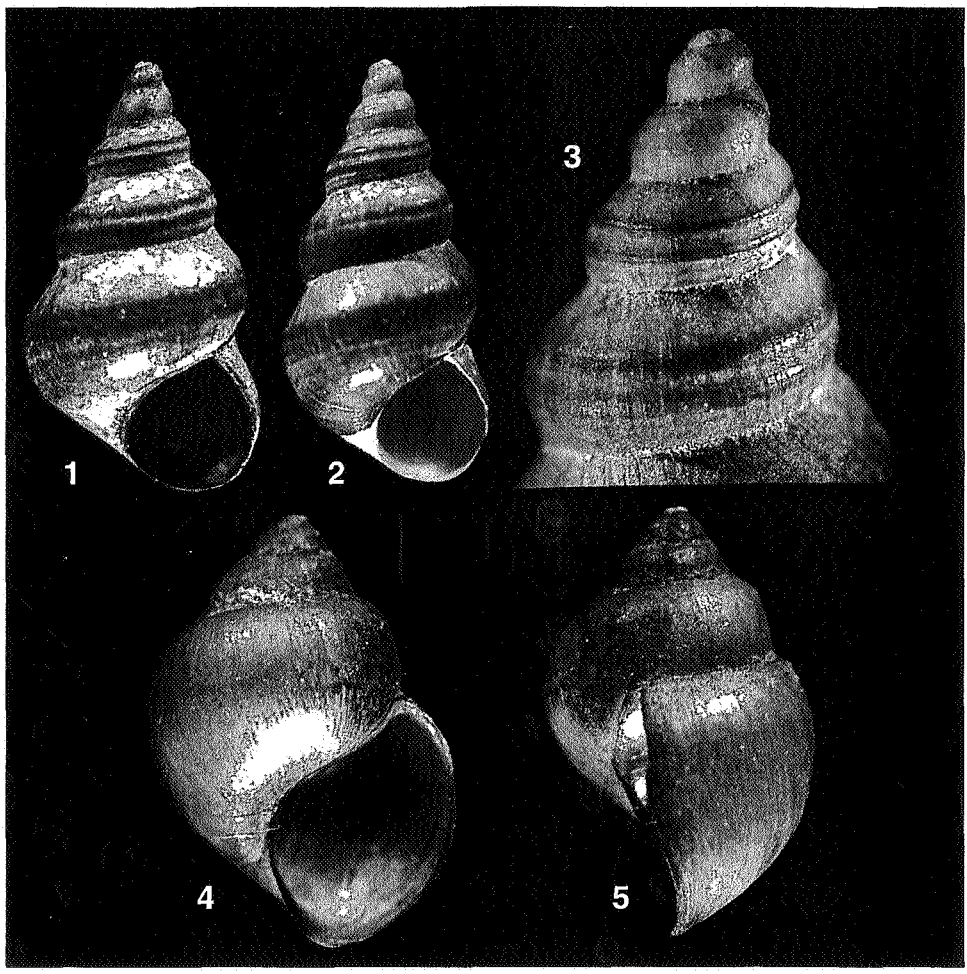
Dyris amazonicus (Haas, 1949) (figs 1-3)

Potamopyrgus (Potamopyrgus) amazonicus Haas, 1949: 313, fig. 6.
Pyrgophorus amazonicus (Haas); Hershler & Thompson, 1992: 91.

Material. — Tapajos river, Belterra, Para, Brazil; at 6 m depth; leg. Dr. H. Sioli, 1946 (FMNH 29197/ holotype, 29198/2 paratypes); unknown locality (Colln Sioli/2 paratypes). Sample FMNH 29198 was studied.

Diagnosis. — Robust, depressed shell with a wide apertural base; covered by a well-developed brown periostracum. Spiral sculpture consisting of two or three prominent ribs on the first two teleoconch whorls; spirals gradually smoothening on lower whorls. Aperture roundish.

Description. — The shell has 6.0–6.5 whorls. Shell width not increasing with the final half of the body whorl. The protoconch of one of the two specimens consists of 0.7 whorls; a fine thread marks the boundary with the teleoconch. Within half a whorl after that boundary three spirals develop, the lower one of which migrates to the suture, and may disappear under the suture in later whorls. At the second and the third teleoconch whorl there are two well-defined ribs, situated at c. one-third and two-thirds of the whorl height, respectively, with a sutural ramp above. These primary ribs become broader and lower on later teleoconch whorls. From the second teleoconch whorl on, up to three secondary ribs develop between the lower primary rib and the suture. Growthlines are slightly prosocline. The suture is impressed and very narrow, with a sutural ridge above. The aperture is discontinuous, semicircular to tear-shaped, with a pointed adapical side



Figs 1-5. Hydrobiid species. 1-3, *Dyris amazonicus* Haas, 1949; paratypes (FMNH 29198); Recent, Tapajos river, Belterra, Para, Brazil (1, H 5.0 mm; 2, H 6.4 mm; 3, detail of 2). 4-5, *Sioliella effusa* Haas, 1949, holotype (FMNH 29209); Recent, Tapajos river, Belterra, Para, Brazil; H 6.4 mm.

and rounded outer, lower and inner margins. The apertural margins are not thickened. Inner margin narrow, covered by a thin parietal callus. The left-most part of the aperture reaches beyond the shell axis. Apertural height between one-third and one-fourth of shell height.

Dimensions: H 5.0-6.4 mm, W 2.6-2.7 mm, HAP 1.3-1.6 mm, spiral angle 38°-43°.

Remarks. — This species is assigned to *Dyris* because of the presence of prosocline growthlines in combination with two well-defined primary spiral ribs on the intial teleoconch whorls, that fade on lower whorls, and a prominent sutural ramp.

Dyris amazonicus is known after only five specimens, all from the Tapajos river near Belterra (Para, Brazil). The central Amazonian area is notoriously under-collected, so its real range may be larger. The lower Tapajos river is actually a lake comprising the drowned lower valley prior to its confluence with the Amazon River. This lake (a so called 'ria-lake') is the result of incision of the valley during glacial sea-level lowstand and the subsequent lack of sediment-fill after sea-level (and river-levels) rose at the end of a glacial period (Irion et al., 1994). The Tapajos river is a clear water river, it drains a hinterland containing a variety of Phanerozoic and Precambrian rocks (Sioli, 1984). The presence of a Paleozoic outcrop belt containing limestone in the drainage area of the Tapajos river is reflected in pH values of 6.5-6.6 (Sioli, 1957). Thorough faunal surveys in the Amazonian floodplains around Manaus (Irmler, 1975), and bottom samples from all over Amazonia studied by Haas (1949), have not yielded *Dyris amazonicus* Haas. Live animals are not known.

Genus *Sioliella* Haas, 1949

Sioliella Haas, 1949: 308. *Eubora* Kadolsky, 1980: 366, nom. nov. for *Ebora* Conrad, 1871: 194 (not Walker, 1867: 415).

Type species. — *Sioliella effusa* Haas, 1949; Recent, Tapajos river, Brazil.

Additional *Sioliella* species. — Miocene, Pebas Formation, Western Amazonia (Peru, Colombia, Brazil): *Eubora grevei* Kadolsky, 1980; *Eubora woodwardi* Kadolsky, 1980; *Ebora crassilabra* Conrad, 1871; *Ebora (Nesis) bella* Conrad, 1871; *Eubora pygmaea* Kadolsky, 1980; *Sioliella ovata* spec. nov.

Diagnosis. — Shell dextral, globose, smooth to carinate, apertural base with a kind of siphonal notch; umbilical ridge prominently developed in most species.

Sioliella effusa Haas, 1949 (figs 4-5)

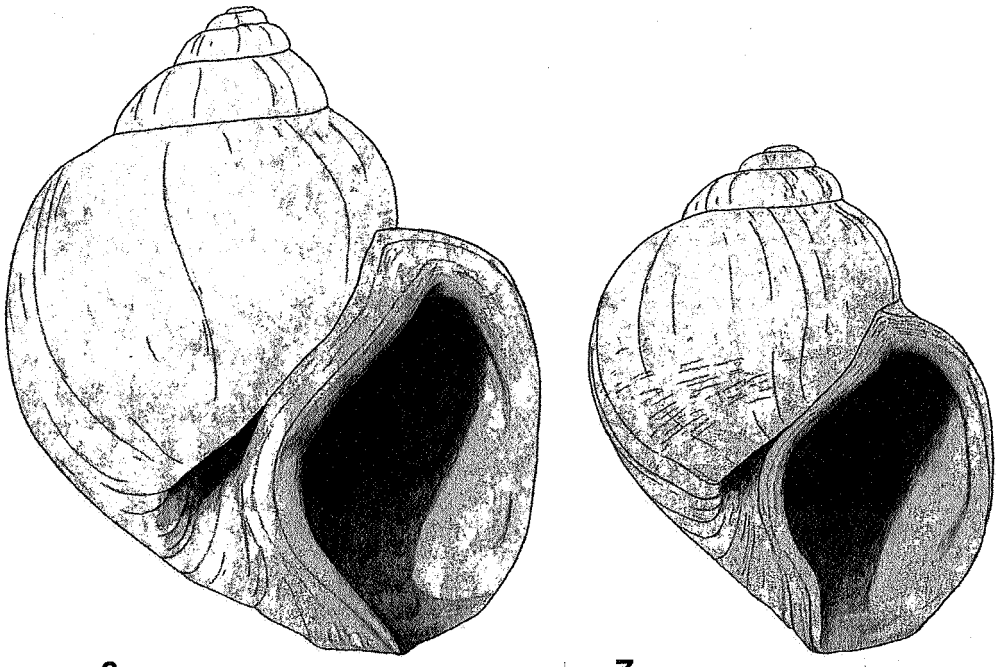
Sioliella effusa Haas, 1949: 309, fig. 2.
Aroapyrgus effusa (Haas); Hershler & Thompson, 1992: 91.

Material. — Tapajos river, Belterra, Para, Brazil at 6 m depth; leg. Dr. H. Sioli, 1946 (FMNH 29209/ holotype). A paratype, a supposed juvenile specimen, from Santarem, Para, Brazil (FMNH 29210), is transferred to *Aroapyrgus latus* (Haas, 1949) (see below). The holotype was studied.

Diagnosis. — Shell thin, with a rather high spire; periostracum cinnamon-brown, well-developed. With fine spiral threads on the body whorl. Umbilicus rimate. Aperture comparatively large, with a siphonal notch.

Description. — The apex of the holotype is damaged and covered with dirt, precluding the observation of the proto-teleoconch boundary. The shell has at least 5.5 whorls. Shell width increases regularly. The upper whorls are smooth, except for numerous, fine, prosocline, slightly sigmoid growthlines. On the body whorl fine spiral threads are observed. The height of the aperture is more than half that of the shell. The apertural border is discontinuous; the margin of the outer lip is rounded, its lower end projecting into a kind of notch. The inner lip is somewhat sigmoid and the left-most part of the aperture is located to the left of the shell axis, therefore. The outer and the inner lip are only slightly thickened. The lower part of the inner lip is dark-brown.

Dimensions: H 6.4 mm, W 4.3 mm, HAP 3.6 mm, spiral angle 77°.



Figs 6-7. *Sioliella ovata* spec. nov., Miocene, Pebas Formation. 6, holotype (RGM 445336); Mocagua, Amazonas, Colombia; H 9.5 mm. 7, paratype (RGM 445340); Santa Sofia, Amazonas, Colombia; H 7.4 mm.

Remarks. — The paratype of this species (FMNH 29210), a shell with four whorls, belongs to *Aroapyrgus latus* (Haas, 1949). It differs considerably from the holotype of *S. effusa*, a.o. in H/W ratio.

Nothing is known about the ecological characteristics of *S. effusa*. Live animals are unknown.

Sioliella ovata spec. nov. (figs 6-7)

Eubora woodwardi Kadolsky; Costa, 1981: 641, pl. 1 figs 5-6.
Eubora crassilabra (Conrad, 1871); Nuttall, 1990: 216 (pars).

Type material. — Amazonas, Colombia; Pebas Formation, *Grimsdalea* interval zone (Hoorn, 1994), late Middle to early Late Miocene; leg. F.P. Wesselingh, ix.1991: Mocagua, level F9 (7 m above river level) (RGM 445336/holotype, 445337/8 paratypes); Los Chorros, level F22 (1.8 m above river level) (RGM 445338/7 paratypes (4 of which fragmentary); Santa Sofia, level F60 (7 m above river level) (RGM 445339/2 paratypes (1 of which fragmentary), 445340/1 paratype).

Diagnosis. — Shell large (H 10 mm), naticiform, smooth, without a shoulder; umbilical ridge well-developed, bordering a deep, rimate umbilicus; siphonal notch at the base

of the aperture well-developed; inner and outer lip thickened.

Description. — The nucleus is smooth and inclined and is bordered by a very fine axial thread at 0.5-0.6 whorls. The shell is smooth, except for fine, prosocline to slightly sigmoid growthlines. On some specimens, especially subadult ones, very fine spiral threads occur on the body whorl. Adult shells have 5.4-6.1 whorls. The suture is slightly impressed. Successive whorls are not fused at the suture, resulting in a very small (<.1 mm) fissure. The aperture is large (nearly 2/3 H) and more or less spindle-shaped. The base of the aperture is deflected, and points into a siphonal notch-like structure. Both outer and inner lip are thickened. A strongly developed, roundish, umbilical ridge borders the prominent umbilicus.

Dimensions: Diameter nucleus 0.06-0.07 mm; H 9.4-10.0 mm; W 7.2-8.2 mm; HAP 5.1-6.3 mm; spiral angle 81°-96°.

Etymology. — Named after the oval outline of the shell.

Discussion. — *Sioliella ovata* spec. nov. differs from *S. woodwardi* (Kadolsky, 1980) by its more convex outline, the presence of a prominent umbilicus (that is narrowly rimate in *S. woodwardi*) and the ratio HAP/H (c. 0.4 in *S. woodwardi* and 0.55 in *S. ovata*). The shell of *S. ovata* differs from that of *S. crassilabra* (Conrad, 1871) by its more regular conical outline. *S. effusa* is more slender than *S. ovata*. It has no strongly thickened lips, and the basal apertural projection is located nearer towards the shell axis than in *S. ovata*. In *S. effusa* the umbilicus is narrowly rimate, but growthlines and spiral micro-sculpture are very similar to that of *S. ovata*.

Sioliella ovata is known only from Pebas Formation deposits assigned to the *Grimsdalea* interval zone (Hoorn, 1994), indicating a late Middle to early Late Miocene age. The species lived in freshwater lacustrine settings (e.g. Vonhof et al., 1998).

Fossil species formerly assigned to *Eubora* are characterised by a generalised naticiform outline, a basal apertural (siphon-like) extension, in combination with the presence of an umbilicus (albeit a very trimmed umbilicus in some species). Some fossil specimens have a spiral microsculpture. These features they share with *Sionella effusa* and, therefore, warrant the assignment of those fossil taxa to the genus *Sioliella*.

DISCUSSION

The supraspecific classification of cochliopine hydrobiids has been addressed in Hershler & Thompson (1992). These authors assigned *Sioliella effusa* Haas, 1949, to *Aroapyrgus* Baker, 1931, a genus predominantly distributed in central and north-western South America. They transferred *Potamopyrgus amazonicus* to the circumcaribbean genus *Pyrgophorus* Ancey, 1888. *Sioliella* is considered here a separate genus in which various Miocene species from Western Amazonia should be classified. The apertural features thought to be characteristic for *Sioliella* (siphonal notch) are missing in the *Aroapyrgus* species. No living animals of *Sioliella* have ever been reported. Shells of *Sioliella* are regular in construction: they lack irregularities in shell-thickness and shape characteristic for South American lithoglyphine shells (see Nuttall, 1990: figs 165-170). The status of the genus *Potamolithoides* Marshall & Bowles, 1932, known from a single Miocene species (*Potamolithoides biblianus* Marshall & Bowles, 1932) from the Cuenca Basin of Ecuador (Bristow & Parodiz, 1982) is unclear. The Cuenca material is so poorly preserved that comparisons with *Sioliella* species are impossible. If new material shows that *Potamolithoides* and *Sioliella* are synonyms, the former name would have priority.

Hershler & Thompson (1992: 129) attributed *Dyris* tentatively to the Cochliopinae. The close morphological similarity between Pebasian *Dyris* and *Tryonia* species supports the classification of *Dyris* in the Cochliopinae.

The appearance of both *Dyris amazonicus* and *Sioliella effusa* in the Tapajos river is not strange compared to the Miocene distribution of their congeners. Either the two species are relicts of taxa that used to be more widespread in fluvial conditions all over Central Amazonia, from which no fossil record is known, or the predecessors of these species invaded this area with the break-through of the Amazon to its present-day easterly course, c. 8 million years ago from Western Amazonia.

The rarity of both extant species is reason for concern. The present distribution ranges of *S. effusa* and *D. amazonicus* are insufficiently known, but it is well possible that they are confined to the Tapajos system, or at most to a few other similar systems nearby (e.g. Xingu river). The fact that no more specimens have been found in either the extensive bottom samples of Sioli in the Central and Eastern Amazon region of Brazil (Haas, 1949), or in the material gathered during extensive surveys in the Amazon/ Solimoes and Rio Negro floodplains of the Manaus region (Irmler, 1975), implies a very restricted range. The species are probably rare, and may be threatened as a result of heavy colonisation pressure along the Tapajos river.

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