Anatomy and Systematics of *Anticorbula fluviatilis* (H. Adams, 1860) (Bivalvia: Lyonsiidae) from the Amazon Basin, Brazil and Peru

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ABSTRACT

Anticorbula fluviatilis (H. Adams, 1860) is an enigmatic freshwater bivalve not closely related to the usual groups of freshwater bivalves. Due to its rarity and consequent lack of specimens, the validity of the genus and species, their occurrence in the freshwater habitat, and even their existence, have been questioned. Other species of closely similar taxa are common in estuarine areas of northern and western South America. The familial allocation of *Anticorbula* has also been problematic. Specimens of *A. fluviatilis* (with soft parts) collected in the Amazon Basin including material from the type locality were examined, and the validity of the genus and species confirmed. A detailed description of the anatomy is provided as the foundation for future systematic comparisons. Diagnostic characters include possibly vestigial lithodesma, small foot with byssus, mantle lobes almost entirely fused (with pedal and pallial apertures only), lack of siphons, very large posterior retractor muscles of foot, stomach with ducts to digestive diverticula only on right side, and style sac separated from intestine. The presence of these characters suggests allocation within the family Lyonsiidae, but this familial allocation should remain provisional until a better definition of the Lyonsiidae is made available.

Key words: Lyonsiidae, *Anticorbula fluviatilis*, Amazon basin, Brazil, Peru, systematics, morphology.

INTRODUCTION

The Amazon Basin is a region of incomparable biodiversity; despite this, its freshwater and terrestrial mollusks are very poorly known. Unusual organisms are often found, including the species re-described herein.

Himella fluviatilis, an unusual freshwater mussel collected in the Marañon River, Peru, was described by H. Adams in 1860. The genus name *Himella* was pre-occupied (Dallas, 1852, Insecta), and a new name was proposed, *Anticorbula* Dall, 1898, as subgenus of the marine genus *Corbula* Bruguière, 1797. Morrison (1943) described the genus *Guianadesma* for an estuarine species, *G. sinuosum*, from Guyana, which is very similar to *Anticorbula fluviatilis*. The genera *Anticorbula* and *Guianadesma* were considered synonyms of *Ostomya* Conrad, 1874 by at least Keen (1969), and Vaught (1989). However, Nuttall (1990) pointed out that *Ostomya* was a distinct taxon and considered *Guianadesma* as valid, an opinion later shared by Leistikow and Janssen (1997). Nuttall (1990) also suggested the possible synonymy between *Guianadesma* and *Anticorbula*. This latter author considered it as *nomen dubium* based on lack of data on types and substantiated locality data (p. 319). On the other hand, Nuttall did not explore further the differences or similarities between these two taxa.

Although the Marañon River, type locality of *A. fluviatilis*, is very distant and far removed inland from the eastern Amazon coastline, most reported occurrences situate this and related species on estuarine and coastal areas (Altena, 1969, 1971; Morrison, 1993; Nuttall, 1990). These reports naturally bring into question whether these organisms actually occur in true freshwater habitats. On the other hand, Adams did not show any doubts about the provenance of *A. fluviatilis*, and Pilsbry (1944) examined additional material from eastern Peru: Essequibo and Cyuni rivers, and even from Marañon River itself. He also figured some specimens of *A. fluviatilis* for the first time. Also addressing this question, Leistikow and Janssen (1997) published their finding of specimens identified as *Guianadesma sinuosum* from Manaus, Brazil, a site located midstream on the Amazon Basin.

The family allocation of the above mentioned genera has also been inconsistent; some authors allocate them to Lyonsiidae (Pandoroidea) (Keen, 1969; Altena, 1971), other authors to Corbulidae (Myoidea) (Pilsbry, 1944; Nuttall, 1990; Leistikow & Janssen, 1997).

Except for the schematic figure and a brief description of the soft parts of *G. sinuosa* (Morrison, 1943), no other anatomical data on South American freshwater and estuarine lyonsiids has been published. The above mentioned references dealt only with conchological and environmental data.

The type specimens of *A. fluviatilis* have not been located (Altena, 1971:82; Nuttall, 1990:290; F. Naggs, pers. comm.), which precludes the resolution of the systematic problems.

A lot with preserved specimens was collected by a team of ichthyologists from the Museu de Zoologia in the Trombetas River, Pará, Brazil (Amazon Basin), a freshwater locality well removed from the coast. The identification of these specimens as *A. fluviatilis* was attained upon examination of the literature and comparison with material from the type locality. The present detailed study of their morphology should help clarify the above mentioned conceptual problems and establish the identity of the species. It should also provide the foundation for further comparative studies of specimens from other (mainly estuarine) areas.

MATERIAL AND METHODS

The specimens were initially preserved in 4% formalin and transferred to 70% ethanol. The dissection was conducted under a stereomicroscope, with the specimens immersed in water. Serial sections were made using standard histological techniques and stained with Mallory. All drawings were made with the aid of a *camera lucida*. The intestinal loops and other visceral structures were examined through dissections and serial sections. The SEM figures were obtained at the "Laboratório de Microscopia Eletrônica do Instituto de Biociências da USP".

The specimen preservation was not good enough to allow for a detailed examination of cilia; these are not shown in detail in the serial section figures (Figures 20–22).

The following abbreviations are used in the figure captions: aa, anterior adductor muscle; an, anus; au, auricle; by, byssus; dd, ducts to digestive diverticula; dh, dorsal hood; es, esophagus; ex, excurrent aperture; fa, foot aperture; ft, foot; ia, intestinal aperture; id, inner demibranch; in, intestine; is, incurrent aperture; lg, ligament; li, lithodesma-like projection of mantle; ll, left mantle lobe; mb, mantle border; mo, mouth; mu, mantle ventral union; od, outer demibranch; pa, posterior adductor muscle; pe, periostracum; pl, pallial line; pp, palps; pr, posterior protractor muscle of foot; ps, pallial sinus; ra, anterior retractor muscle of foot; ri, hinge; rp, posterior retractor muscle of foot; rt, rectum; rv, right valve; sa, sorting area; sp, style sac aperture; ss, style sac; st, stomach; sy, crystalline style; te, testis; um, umbo; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

The following institutional abbreviations are used in the text: ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia; BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

SYSTEMATIC DESCRIPTIONS

Genus *Anticorbula* Dall, 1898

Himella H. Adams, 1860:203 (non Dallas, 1852); type species (by monotypy): *H. fluviatilis* H. Adams, 1860; pre-occupied name (Nuttall, 1990:319).

Corbula (Anticorbula) Dall, 1898:839, *nomen novum*.

Aloidis (Anticorbula).—Morretes, 1949:47 (in part).

Anticorbula.—Keen, 1969:847; Vaught, 1989:140 (in both references as synonym of *Ostomya* Conrad, 1874).

Remarks: *Anticorbula* is the oldest valid name and should be used for this species. The similarity between the type species of the monotypic genera *Anticorbula* and *Guianadesma* is clear; thus these 2 genus names may be synonyms. However, the synonymy will be resolved only after a detailed anatomical analysis of *G. sinuosum* (type of *Guianadesma*).

Anticorbula fluviatilis (H. Adams, 1860) (Figures 1–22)

Himella fluviatilis H. Adams, 1860:203 [Marañon River, Peru].

Corbula (Anticorbula) fluviatilis.—Dall, 1898:839.

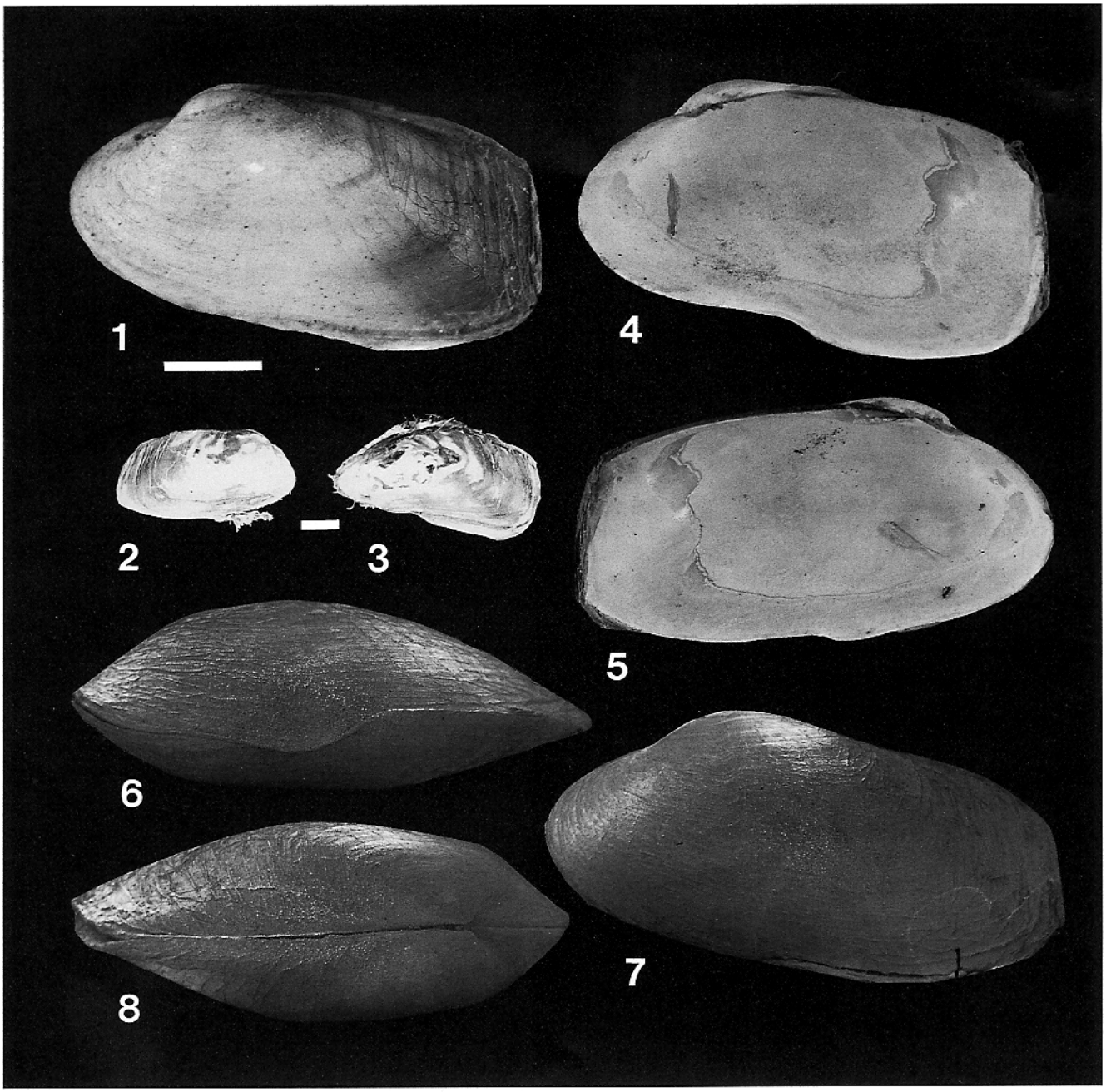
Ostomya fluviatilis.—Pilsbry, 1944:148 (fig. 1 + pl. 11, figs. 42–44)

Aloidis (Anticorbula) fluviatilis.—Morretes, 1949:47.

Anticorbula fluviatilis.—Altena, 1971:82.

Guianadesma sinuosum.—Leistikow and Janssen, 1997:17–20 (figs. 1–3) (*non* Morrison, 1943).

Description: *Shell (Figures 1–9, 19):* Of medium size (up to 25 mm), somewhat elliptical, inequivalve, irregular (Figures 2, 3), ventral edge sigmoid (Figures 6, 19). Umbones inlaid, located on anterior third of hinge, generally eroded. Periostracum semi-transparent, brown, covering ligament (Figure 19). Color light beige, with brown areas on posterior slope (Figure 1). Anterior region rounded, posterior region somewhat straight, oblique. Sculpture lacking except for concentric growth lines and undulations. Hinge edentulous, with a broad tooth in each valve posterior to umbones, each one bearing a longitudinal furrow containing most of ligament (Figures 4, 5, 9, 19). These broad teeth asymmetrical (Figure 19). Left valve tooth somewhat parallel to valve margin and close to median line; right valve tooth oblique, with posterior region relatively distant from median line and separated from the valve border by a smooth area, which gradually approaches from median line to become similar to its analogue. Ligament partly exposed, anterior extremity only a narrow thread. Posteriorly to umbo ligament gradually becomes thick and broad at about ⅓ of its length. Posterior half of this broad region hollow, opened posteriorly, filled by a conic, sharp projection of mantle (Figure 10), which suddenly becomes a narrow thread in its posterior half. Inner surface of each valve smooth, not nacreous (Figures 4, 5). Two anterior scars (Figures 4, 5, 9), a small, circular, dorsal of anterior foot retractor muscle, and other large, reniform, ventral to anterior adductor muscle. Pallial line simple, with a broader anterior region; a shallow sinus is present between this broad region and adductor muscle scar (Figure 9). A large and somewhat triangular posterior scar composed by two roughly equal (in cross-section) muscles, one dorsal to posterior foot retractor muscle, other ventral to posterior adductor muscle. Ven-

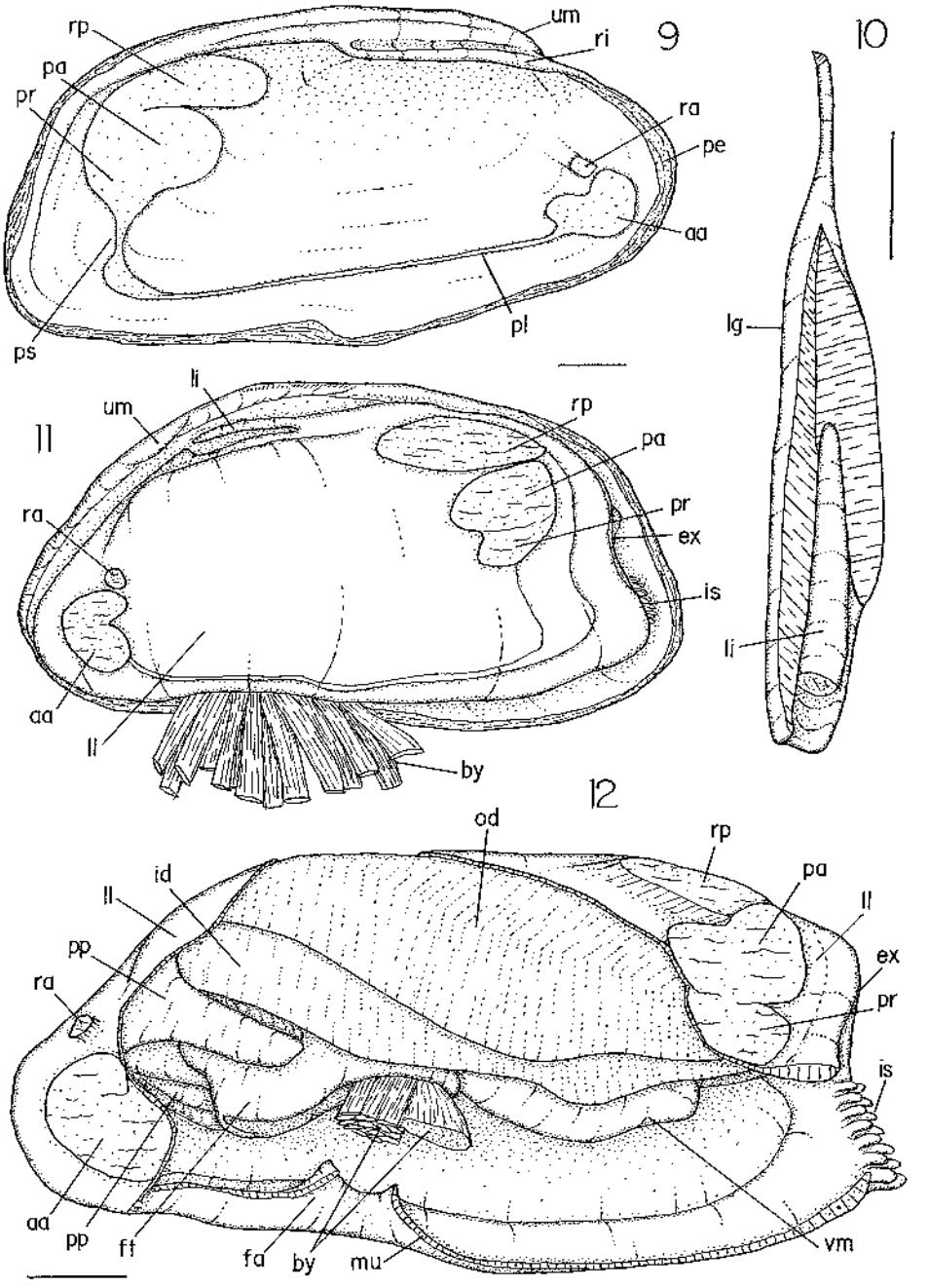


Figures 1–8. Shell of *Anticorbula fluviatilis*. **1.** Left valve showing most frequent color pattern; **2, 3.** Two specimens showing variation in outline; **4.** Right valve, inner view; **5.** Left valve, inner view; **6–8.** SEM micrographs of 1 specimen. **6.** Ventral view; **7.** Left view; **8.** Dorsal view. Scale lines = 2 mm.

tral region of protractor muscle of foot small, triangular. Further details on shell morphology were given by Leistikow and Janssen (1997:17–18, figs. 1–2).

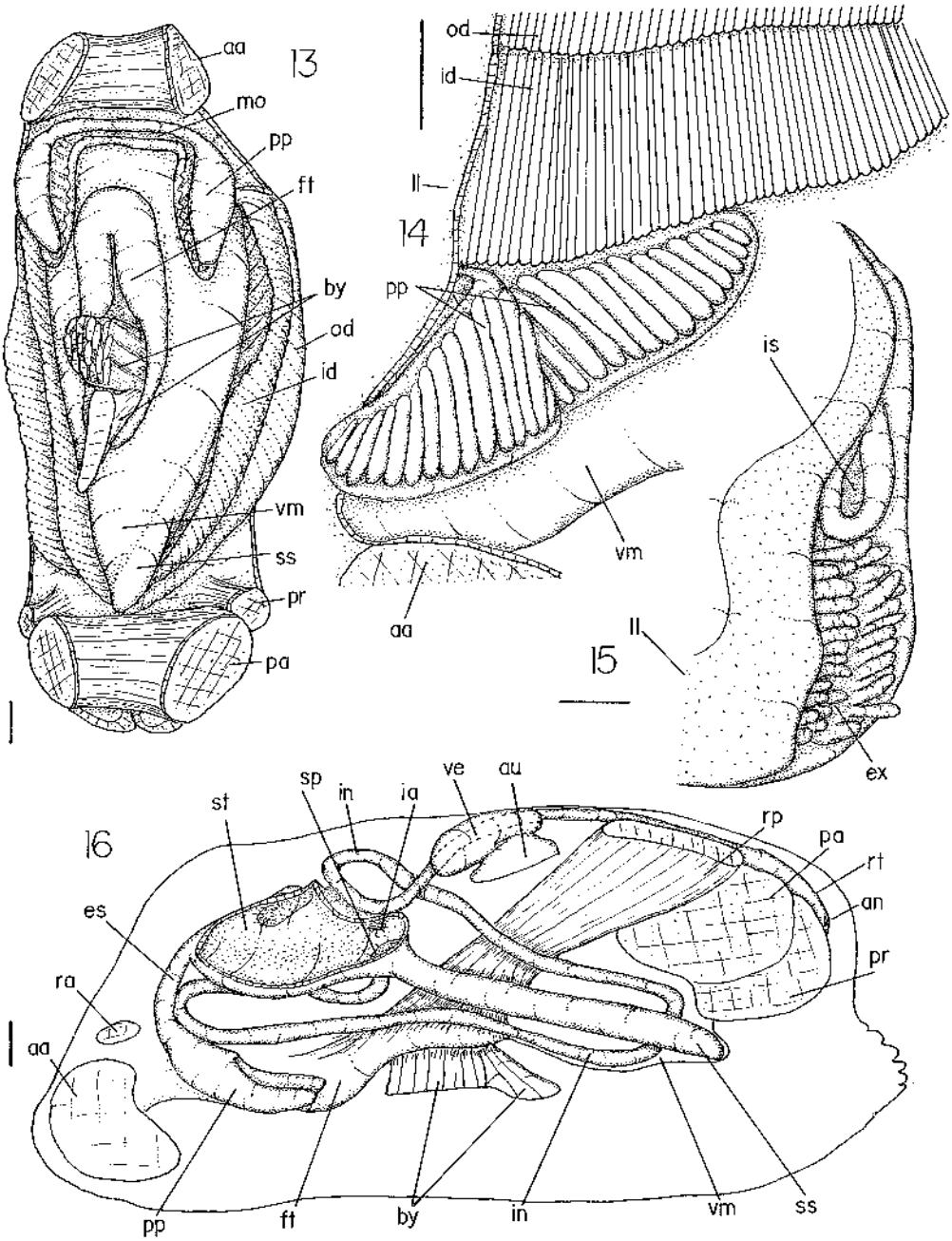
Mantle: Pale cream in color, in some specimens with dark brown spots in umbonal region. Mantle lobe borders almost entire fused (Figures 11, 12, 20), a narrow, funnel-like, conic pedal aperture (Figure 12). Incurrent aperture surrounded by two rows of stubby papillae (Figures 12, 15); each papilla white in color, dark brown minute spots on base, rounded tip. Excurrent aperture narrow, edged by thick borders without papillae (Figure 15). Lobes union evolves inner folds (Figure 20).

Foot and muscles: Foot small, sessile in antero-ventral half of visceral mass (Figures 12, 13). Byssal furrow occupying most of foot ventral region; anterior half a narrow, deep furrow (Figure 13); posterior half broad, opened, bearing two large byssal bundles (Figures 12, 13, 15). Anterior byssal bundle composed by several ribbon-



Figures 9–12. Anatomy of *Anticorbula fluviatilis*. **9.** Shell, left valve, inner view, showing muscle scars and hinge; **10.** Ligament extracted, left view, a quarter was artificially cut to show inner mantle projection, possibly a vestige of lithodesma; **11.** Hole specimen, left view with left valve extracted, outer surface of mantle exposed; **12.** Mantle cavity, left view, infra-branchial portion of mantle extracted by an incision surrounding insertion of ctenidium, visceral mass, adductor muscles and in middle region of ventral mantle fusion. Scale lines = 1 mm.

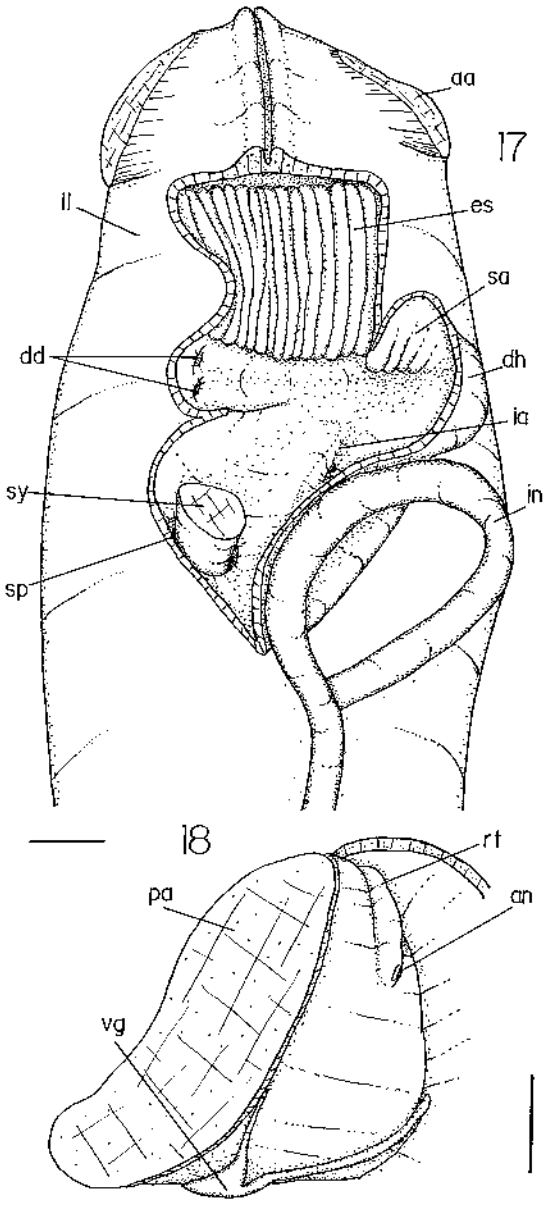
like, flattened fibers; posterior bundle broad and massive. Anterior and posterior adductor muscles somewhat equal in size (Figure 11). Anterior adductor muscle located very anteriorly and ventrally. A pair of large visceral ganglia attached to its ventral surface of posterior adductor muscle (Figure 18). Pair of anterior foot retractor muscles small, slender, inserted in anterior region of foot. Pair of posterior foot retractor muscles large (Figure 16), flattened at origin (longer antero-posteriorly), just dorsal and anterior to posterior adductor muscle, each situated very close to other member of pair, separated only by a narrow space where rectum runs. Posterior retractors gradually become narrow and cylindrical, inserted in foot muscles just dorsally to byssal gland.



Figures 13–16. Anatomy of *Anticorbula fluviatilis*. **13.** Mantle cavity, ventral view, ctenidium part deflected, mantle extracted; **14.** Detail of region of left palp and adjacent structures, left view, outer hemipalp deflected to show its inner folds; **15.** Detail of incurrent and excurrent apertures (incurrent inferior), left, slight posterior view; **16.** Digestive tubes and part of muscular and circulatory systems seen as the animal was transparent, left view, left wall of stomach extracted. Scale lines = 0.5 mm.

Mantle cavity organs: Inner surface of mantle smooth, without additional structures (Figure 11), mantle edge thick. Ctenidium long, about ⅔ of length of mantle cavity and about half of dorso-ventral distance (Figures 12, 13); filaments very narrow, producing a uniform surface. Outer demibranch not covering inner demibranch. Outer demibranch divided into two regions (Figure 12): dorsal ⅓ with oblique filaments, ventral ⅔ with filaments that become perpendicular to free edge of ctenidium. Anterior edge of outer demibranch fused with mantle. Inner demibranch simple, occupying little more than half of volume of outer demibranch, only perpendicular filaments present. Anterior edge fused with mantle and antero-ventral angle partially covered by palps. Food grooves present on free edges of both demibranchs (Figure 20). Profile of ctenidium filaments is shown in Figure 22.

Digestive system: Palps somewhat small, antero-pos-



Figures 17–18. Anatomy of *Anticorbula fluviatilis*. **17.** Stomach and adjacent region, dorsal view, anterior part of gastric dorsal wall extracted, posterior part deflected to right jointed with the intestine loop which crosses this area; **18.** Detail of posterior adductor muscle, left, slight posterior view, left lobe of mantle extracted to show anus and visceral ganglia. Scales = 0.5 mm.

teriorly elongated, free extremity tapering off to a rounded tip (figures 12–14). Outer surface of palps smooth. Inner surface of palps with several broad, oblique folds; profile of folds shown in Figure 21. Each fold with rounded extremities, ending at some distance from palp edge, with smooth inner margin (Figure 14). Inner folds evanesce near mouth (Figure 13). Mouth large, with smooth inner surface. Esophagus wide, short, flattened dorso-ventrally, curved, not attached to, separated from adductor muscle (Figure 16), inner surface with several, uniform, longitudinal, low folds (Figure 17). Stomach (Figures 16, 17) spacious, located just posterior to shell umbones. Esophageal folds end suddenly at same height along esophagus. Two small orifices of digestive diverticula present on left anterior region of stomach. Right anterior region characterized by valve-like, small septum that represent anterior limit of a dorsal hood. Dorsal hood short, broad, with rounded distal extremity, internally with several low, longitudinal folds. A constriction present in stomach region opposite to dorsal hood. Posterior region of stomach with two orifices (Figures 16, 17): aperture of style sac, larger, on left side; intestine origin, smaller, on right side. Style sac long, straight, separated from intestine (Figures 16, 20); posterior extremity rounded, bulging in posterior-ventral extremity of visceral mass (Figures 13, 16). Intestine (Figures 16, 17) narrow, without inner folds; intestine runs anteriorly, surrounding right ventral surface of stomach. After forming a loop near esophagus intestine is directed posteriorly, brodering dorsal surface of foot; near right posterior region of style sac intestine is directed antero-dorsally to postero-dorsal region of stomach; in this region, a loop touches dorsal gastric wall on style sac and intestine apertures. This loop runs dorsally through ventricle, between posterior foot retractor muscle and postero-dorsal surface of posterior adductor muscle. Anus represented by a small orifice without papilla or glands (Figures 16, 18).

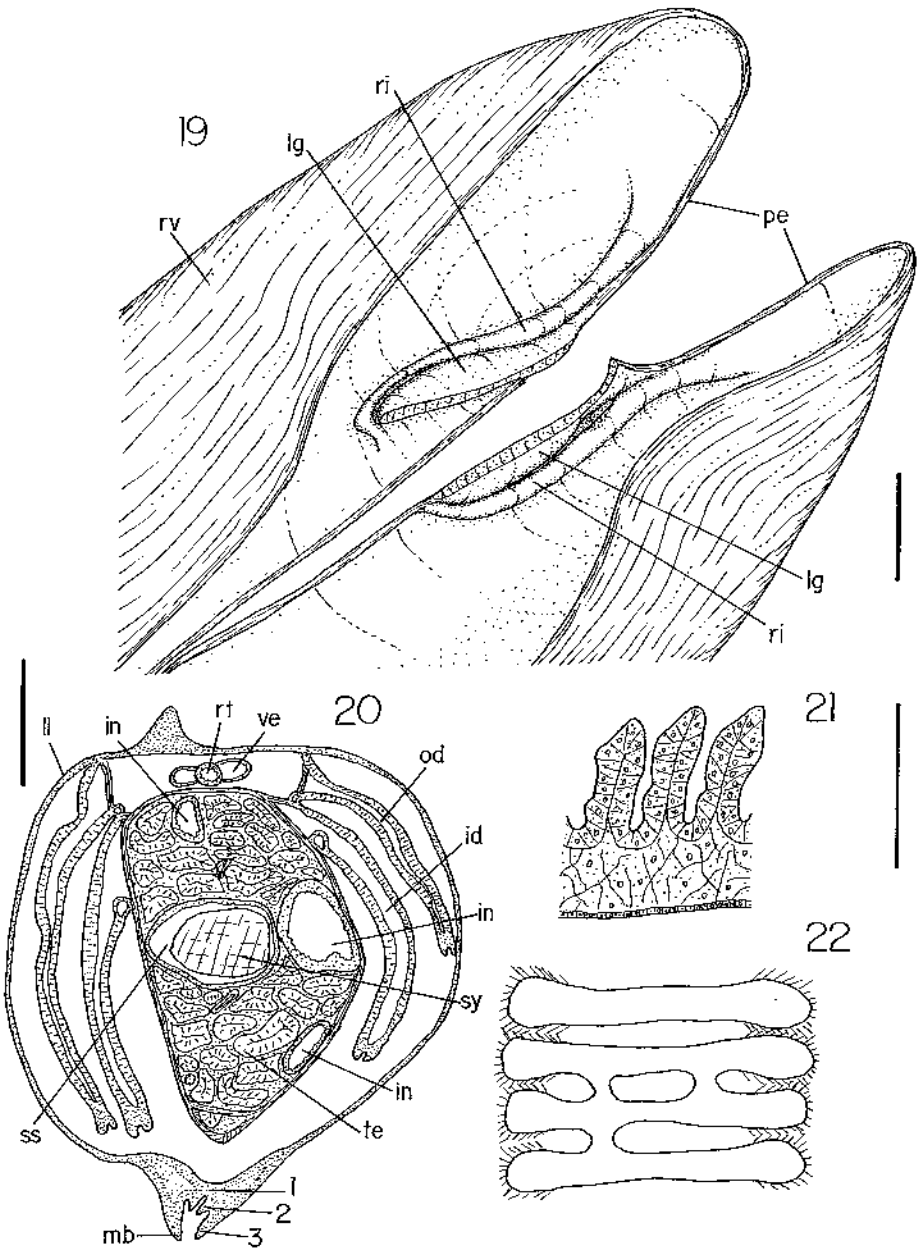
Visceral sac: Digestive diverticula almost completely restricted to space around stomach, in mid-dorsal region of animal. Remainder of visceral sac filled by gonochoristic gonad (Figure 20), which surrounds digestive tubes, and is separated into several elongate, somewhat large acina. Transversal muscles very small, present mainly in ventral, peri-pedal regions.

Habitat: Found in river with mild current, about 5 m in depth, attached by byssus into furrows of dead tree bark.

Material examined: BRAZIL: MZSP 28788, 3 specimens, Pará; Trombetas River, 1°41′51″S 55°51′8″W, Lundberg et al. col., 24 Oct. 1994; MZSP 28787, 5 specimens, Xingu River, Porto de Moz, 5 specimens, 9 Aug. 1968; MZSP 28789, 250 shells, and BMSM 1007, 3 shells, Alenquer River, Ponta de Pedregulho, Lago Grande, 21 Sep. 1969, col. EPA no. 690073–4; PERU: ANSP 125525, 2 shells, Marañon River, Charles M. Wheatley Collection, (material examined by Pilsbry, 1944).

DISCUSSION

The problematic allocation of the genus *Anticorbula* at the family level is mostly due to the poor systematic definitions of the relevant bivalve families; apparently there is no sound information (good diagnoses based on synapomorphies) on each of the following families that



Figures 19–22. Shell and serial sections of *Anticorbula fluviatilis*. **19.** Shell, detail of anterior half, ventral view, valves partially opened to show hinge region. Scale line = 2 mm; **20.** Transversal (frontal) section in approximately middle region of animal. Scale line = 1 mm; **21.** detail of middle region of outer hemipalp, inner folds cut transversally; **22.** Transversal section of ctenidium filaments at midline, outer demibranch. Scale lines (21–22) = 0.1 mm. Histological sections (20–22): Mallory stain, 5 μm.

would allow for the clear cut, indisputable allocation of *Anticorbula* to any of them. As commented in the introduction, various authors have allocated this genus in the families Corbulidae (Myoidea) and Lyonsiidae (Pandoroidea), as well as some affinity with the Myidae (Myoidea), Hiatelloidea and Thraciidae (Pandoroidea) can also be demonstrated.

The familial allocation of *Anticorbula* to is not only a problem of nomenclatural nature. Not belonging to the most common freshwater groups such as Unionoida, Dreissenoidea and Corbiculoidea, *Anticorbula* seems to represent an independent invasion of the freshwater environment.

In present study, *Anticorbula* is provisionally allocated in the family Lyonsiidae. Such allocation is based on conchological characters (outline, thick periostracum covering inclusive the hinge, almost edentulous hinge, a projection of the mantle within ligament which can be a vestige of the lithodesma). On the other hand, anatomical studies on lyonsiids (Yonge, 1952; Thomas, 1993) have described animals with two ducts to the digestive diverticula, fusion of the style sac with the intestine, and

a small pair of posterior foot retractor muscles, all characters that differ from those in *Anticorbula*.

Anticorbula is similar to members of Corbiculidae (Yonge, 1947) in having poor developed siphons and only one duct to digestive diverticula. However, *Anticorbula* differs in hinge characters, in having a reduced foot with byssus, the presence of posterior foot retractor muscles and a style sac separated from intestine.

Similarities with members of Thraciidae are overall shell shape, presence of a lithodesma in ligament and fusion of mantle edge (Morton, 1995). However, *Anticorbula* differs mainly in lacking developed siphons, in having only one duct to digestive diverticula, a separation between style sac and intestine and by the byssus.

Anticorbula is similar to members of Myidae in having fusion of mantle edge and, at least of *Cryptomya californica* (Conrad) (cf. Yonge, 1951) in having not so developed siphons and separation of style sac from intestine. It differs mainly in having a byssus, the reduction of the foot and the absence of hinge teeth.

Based on data from the (Yonge, 1971), *Anticorbula* is similar to members of Hiatellidae in shell shape, in having thick periostracum, reduction of hinge teeth and of foot. In contrast, *Anticorbula* lacks siphons, has only one duct to digestive diverticula and separated style sac and intestine.

The present lyonsiid attribution to *Anticorbula* is, then, provisional. All of the above mentioned families have estuarine representatives and could perfectly include *Anticorbula* and its related genera *Guianadesma* and *Ostomya*.

The shell of *A. fluviatilis* is very similar to that of *Guianadesma sinuosum* (Morrison, 1943; Nuttall, 1990). The morphology of the soft parts of *G. sinuosum* is very superficially known (Morrison, 1943:50–51, fig. 1), and is also similar to inner morphology of *A. fluviatilis*. Both species were not synonymyzed herein mainly due their different habitats (*A. fluviatilis*, true freshwater; *G. sinuosum*, low salinity, estuarine), and also due to the lack of a detailed anatomical study of this latter species.

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