

Taxonomic revision of *Polymesoda solida* (Philippi, 1846) (Bivalvia: Corbiculidae), a new name for *Polymesoda arctata*, the estuarine clam of Lake Maracaibo and other estuaries of the tropical Atlantic coasts of America

Héctor José Severeyn*^{1,2}, Yajaira García de Severeyn^{1,2} and Joseph Jay Ewald¹

¹Laboratorio de Sistemática de Invertebrados Acuáticos (LASIA)

Facultad Experimental de Ciencias, Departamento de Biología, La Universidad del Zulia.

²Division of Mollusks, Department of Invertebrates, National Museum of Natural History
Washington D.C., U.S.A.

Recibido: 24-03-94 Aceptado: 23-08-94

Abstract

This paper presents a summary of recent taxonomic findings concerning the estuarine clam *Polymesoda solida* (Philippi, 1846), part of a more extensive revision that covers 147 species of the genus *Polymesoda* (Rafinesque, 1820) described between 1750 and 1950 (2).

Research was done on collections of the Division of Mollusks of the United States National Museum of Natural History, Washington D.C. (USNM). Additional specimens, especially Types, from the British Museum (BMNH) and the Museum of Comparative Zoology, Harvard, USA (MCZ) were also reviewed. Non-type specimens were also reviewed from other museums.

Based on an analysis of 21 shell characters and eight anatomical soft body features it is recognized that at least six formally described species fall within the taxonomic description of *Polymesoda solida* (Philippi, 1846), the species name that prevails because of the Priority Rule of the International Code of Zoological Nomenclature. A detailed description of the diagnostic features of the Genus and Subgenus to which this species belongs, as well as synonyms, geographic and ecological ranges, fossil data and a distribution map are presented.

Key words: Bivalvia; Corbiculidae; estuarine; *Polymesoda*; taxonomic review.

Revisión taxonómica de *Polymesoda solida* (Philippi, 1846) (Bivalvia: Corbiculidae), nuevo nombre de *P. arctata*, la almeja estuarina del Lago de Maracaibo y otros estuarios de las costas atlánticas tropicales de América

Resumen

Este trabajo es un resumen de los hallazgos taxonómicos acerca de la almeja estuarina *Polymesoda solida* (Philippi, 1846) el cual forma parte de una más extensa revisión que cubrió 147 especies del Género *Polymesoda* (Rafinesque, 1820) descritas entre 1750 and 1950 (2).

* Corresponding author. P.O. Box 1198, Maracaibo 4001-A, Venezuela.

Aquí, sólo es presentada la información taxonómica concerniente a esta especie para aclarar la confusión existente acerca de ella.

La investigación fue realizada en la División de Moluscos del Museo Nacional de Historia Natural de USA, en Washington, D.C. (USNM), sin embargo, ejemplares adicionales, especialmente Tipos, fueron obtenidos en el Museo Británico (BMNH), Inglaterra, y en el Museo de Zoología Comparada de la Universidad de Harvard (MCZ), USA. Ejemplares no-tipo fueron también revisados en otros museos.

Basado en el análisis de 21 caracteres definidos en las conchas y ocho características anatómicas blandas se reconocieron que seis especies, descritas posteriormente a *Polymesoda solida* coinciden con la definición taxonómica de ésta. Por ello, *Polymesoda solida* (Philippi, 1846), el nombre de la especie más antigua descrita, prevalece como el nombre válido siguiendo el Criterio de Prioridad establecido por el Código Internacional de Nomenclatura Zoológica. Son dados aquí redescriptiones, con características diagnósticas, del Género y Subgénero a los cuales pertenece *P. solida* así como una lista de sinónimos, distribución geográfica y ecológica, datos paleontológicos y un mapa de distribución.

Palabras claves: Bivalvia; Corbiculidae; estuarino; *Polymesoda*; revisión taxonómica.

Introduction

The taxonomy of the species of the estuarine Genus *Polymesoda*, bivalve mollusks of economical importance in several countries of the world, was recently reviewed by one of us (1,2). Because one of the species that was reviewed, *Polymesoda arctata*, is the traditionally known "Lake Maracaibo clam" and, the only *Polymesoda* species living in Venezuelan estuaries, it was decided to write this article to make available the information gathered about this species hoping to correct the misinformation that exists about this estuarine mollusk. A taxonomic explanation of why *Polymesoda solida*, and not *Polymesoda arctata*, is the acceptable name for our local clam is given.

Methods

This study was mainly done at the Mollusk Division of the National Museum of Natural History in Washington D.C., USA. However, additional specimens were obtained from different museum collections. The Type material was obtained from the British Museum and the Museum of Comparative Zoology of Harvard. Non-type

specimens came from another five museums. Appendix 1 lists all material examined and their respective locations.

The study was performed using, for most part, dry material (shells). The characterization of *Polymesoda solida*, and the analysis of types of the species which were determined to be synonyms, was based on new qualitative taxonomic characters of the shells (Figure 1). Traditionally used characters in this group, such as shell form, coloration (inner and outer shell surface) and the general position of teeth were determined unsuitable for taxonomic identification because of their excessive ambiguity and variation at the intraspecific level. Preserved specimens with soft parts were used too. However, characters obtained from soft parts were only employed to support the shell morphology analysis.

Results

When we initiated this research the taxonomy of the Genus *Polymesoda* was in a disarray. There were more than 150 names, with at least 90 of them described as new species. After two years of reviewing type material and large museum collec-

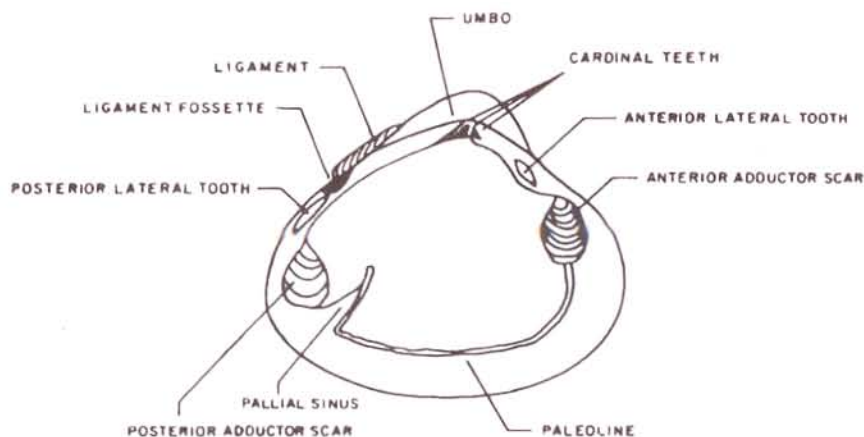


Figure 1. Internal morphological features of the right valve of *Polymesoda solida*.

tions, we found that only 14 species were valid. Not only the species were confused, but also their respective Generic and Sub-generic categories. Thus, a former revision of one us (2) also covered these supraspecific levels. Here, we only present the information that concerns *Polymesoda solida* (Philippi, 1846)(3), the correct name for the previously known *Polymesoda arctata* (Deshayes, 1854)(4), the small clam that lives on the shores of Lake Maracaibo.

The following is a description of the Genus and Subgenus to which *Polymesoda solida* belongs followed by a discussion of all information gathered about this species, including a list of synonyms and fossil data.

Redescription of Taxonomic Categories

Genus *Polymesoda* Rafinesque, 1820 (5)

Type species:

- Polymesoda (Polymesoda)*
- caroliniana* (Bosc, 1801)(6)
- Cyclas* Bruguière, 1792 (7)**
- Cyrena*, Lamarck 1818 (8)**
- Isodoma*, Deshayes 1857* (9)
- Cyprinella* Gabb, 1864* (10)
- Diodus* Gabb, 1868* (11)
- Americana* Clessin, 1879 (12)

* = Fossil species. See comment below.

** = The generic names *Cyclas* Bruguière, and, *Cyrena* Lamarck are considered taxonomically "emptied" today. Thus, many recent authors do not use then any more (Eg. 40). *Egetaria* Mörch, and, *Leptosiphon* Fischer, has been considered synonyms of the Genus *Polymesoda* (40) but in strict taxonomic sense they really are Subgenera. *Isodoma* Deshayes, is a generic name for fossils that really are *Polymesoda*. A complete discussion of this synonymy is given by one of us (2).

Polymesoda lives exclusively in estuarine habitats. Sporadically it is found in freshwater areas but is not able to reproduce under such as conditions. Never, it has been found living in true marine conditions. A species of the Subgenus *Pseudocyrena*, *Polymesoda (Pseudocyrena) salmacida* can be found living in secondary saline lakes in some Caribbean islands (2).

Shells vary in form from rounded, trigonal to ovate, inflated, with a prosogyrate beak. Each valve has three cardinal teeth, lightly joined at their tops, but clearly separated in a radiating or fan pattern. Anterior and posterior lateral teeth are present, both short (1 to 3 times the length of the middle cardinal teeth), the posterior one larger, elevated and, of smooth aspect. No

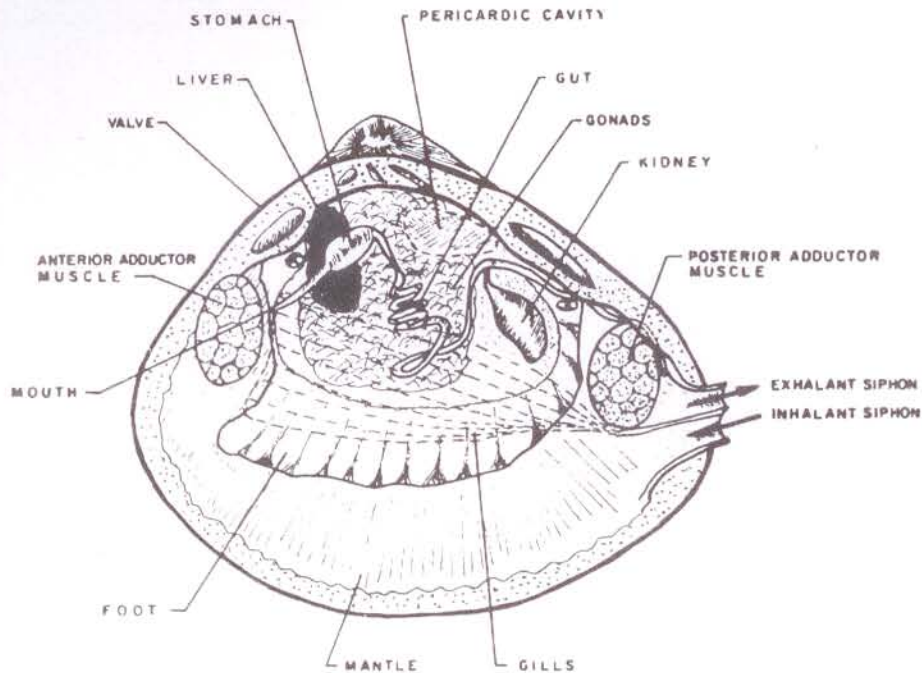


Figure 2. Anatomical soft parts of *Polymesoda solida*.

distinct crenulation or ridges are present on the surface of lateral teeth. The pallial line displays a pallial sinus that can vary from very small, with its posterior side confluent with the posterior adductor scar, to very large (sinus length up to 3 times its width), and totally independent of the posterior muscle scar. The pallial sinus sides can be straight, curved or undulated, with the tip highly variable in shape. The inner shell surfaces are not iridescent or pearly but usually display white, violet, pink or orange color. Most shells are a combination of white and violet, with an infinite grade of mixtures. Pink and orange tones are absent in some species and generally rare in most. Totally white shells also occur. The outer shell is covered by a thick periostracum, also very variable in color (black, dark green, green brown, olive green, yellow green, light yellow), normally eroded at the beak but abundant on ventral sides. This

kind of periostracum gives the non-marine shell aspect typical of estuarine bivalves. The ligament is opisthodontic and paravincular.

Polymesoda has a worldwide distribution in estuaries of tropical and subtropical zones, and absent only on both sides of the African continent. Adult shells vary in size, normally ranging from 30 to 150 millimeters. The animal itself is oval, transverse, with the mantle lobes unfused on the ventral and front edges but fused behind into two large siphons that are well separated. The foot is variable in form, mostly elongate, ovate and trigonal. The gills are unequal, the inner demibranch subquadrangular, the outer one smaller and subtrigonal (Figure 2).

Subgenus **Neocyrena** Crosse & Fischer
(1893)(13)

Type species: *Polymesoda (Neocyrena)*
solida (Philippi, 1846)(3)

New World *Polymesoda* species have shells with a glossy, polished periostracum with strongly projecting commarginal growth lines separated by broad valleys. The species of this Subgenus have an overall aspect that converges with the Indian Ocean Genus *Villorita* and with the worldwide *Corbicula fluminea*. *Neocyrena*, however, differs in having lateral teeth with smooth surfaces. The periostracum is thick, normally dark or olive green, with radiating black bands that run from the beak toward the ventral edge of the shell, sometimes only evident at the ventral edges. The pallial sinus is well developed, with a muscle insertion area variable in size and position (2). The sinus is always an open "V" (Figure 1) that can be shallow or very deep. Inner shell surfaces are mostly violet, either in patches or totally colored. Some specimens can have the inner shell surface totally white or pink, and display a totally yellow external periostracum. Violet morphs can also have pink or peach tones. The shells are small but heavy, strong and inflated. The posterior adductor scar is not divided. The ligament fossette is near or almost reaching the anterior end of the posterior lateral tooth (Pii). This Subgenus is broadly distributed along Central America and northern South America on both eastern Pacific and West Atlantic coasts where three species live (2).

The Subgenus *Neocyrena* was established without type species (14). It was divided into two sections: *Leptosiphon* (15), that included four species, only two of which correspond to *Polymesoda solida* (3). The second section was *Cyrenocapsa* (15) that included one species, *Polymesoda salmacidia* (16), a species that we verified is not a *Neocyrena* but a species that belongs to another Subgenus, *Pseudocyrena*. Later, *Cyrena nicaraguana* (17) was settled on as the type species of the Subgenus *Neocyrena*

(18), however, *Cyrena nicaraguana* is a name that was introduced (19) as a synonym of *Cyrena solida* (3), because this name, *Cyrena solida*, was in use for another species (20). Hence, *Cyrena solida* (3) becomes, by tautonomy, the type species of the Subgenus *Neocyrena*.

Polymesoda (Neocyrena) solida
(Philippi, 1846)(3)

Type locality: Nicaragua, Central America.

Cyrena solida Philippi, 1846:78 (3),
non Dunker 1846 (20);
non *solida* Sowerby in
Reeve 1878:20 (21)

Cyrena arctata Deshayes, 1854:20 (4)

Cyrena acuta Prime, 1861:355 (22)

Cyrena regalis Prime, 1865:18 (18)

Cyrena ordinaria Prime, 1865:19 (18)

Cyrena nicaraguana Prime, 1869:146 (19)

Cyrena germana Prime, 1870:417 (23)

Cyrena boliviana Clessin, 1879:124 (12)

Polymesoda acuta Prime, von Martens
1890:547 (24)

Polymesoda germana Prime, von Martens
1890:547 (24)

Polymesoda placens Philippi, von Martens
1890:545 (24)

Polymesoda solida Philippi, von Martens
1890:544 (24)

Cyrena (Polymesoda) panamensis Adams,
Fluck 1906:3 (25)

Polymesoda arctata Deshayes, Baker
1923:60 (26)

Polymesoda aequilatera Deshayes, Cosel
1973:50 (27)

Corbicula arctata Deshayes, Counts
1980:71 (28)

Diagnosis and morphological variation

Pallial sinus triangular, v-shaped, with a long curved muscle insertion area, departing from its anterior side, completely separate from the anterior adductor scar (Figure 1). Its base is wide, with the length/width ratio very variable (mean =

2.3, range: 1.4 to 3.8). The muscle insertion area of the sinus is usually deflected strongly toward the posterior side of the shell. The valves of *Polymesoda solida* are trigonal, extended posteriorly, asymmetrical, and the beak placed near the middle. The posterior end may be round in juveniles or worn in old specimens but always with a small sharp projection in the posteroventral end. The posterior end is never truncate. The shell surface is marked by wide protruding commarginal growth lines separated by spaces and covered by a glossy, olive to dark-green periostracum. The shells are strong, inflates, with dense walls. The surface of the shells is usually marked with radiating black stripes that run from the beak toward the ventral edge. These stripes were very common in Nicaraguan and Venezuelan specimens. A weak protrusion along the posterior-dorsal slope forms a narrow fold in some animals. The interior of the shells is mostly violet mixed with white, non-glossy, with irregularly distributed shades of pink or peach spots. Quantitative analysis of the color frequency distribution on the inner shell surface (29) has shown that the violet morph accounts for 71%, whereas the pink\white morph makes up a mere 1.5% of the populations. All white morphs were present in 4% of the samples and violet/pink morphs in 23.5% of the animals studied. *P. solida* is the smallest species within the Subgenus. Adults normally reach no more than 40 mm (the largest animal measured was 46 mm in length).

Comparison

Polymesoda (Neocyrena) solida is endemic to the Western Atlantic coast of Central and South American and constitutes the sister species of another two *Neocyrena* species living along the tropical East Pacific of America: *P. radiata* and *P. fontainei* (2). The general shell aspect of *Neocyrena* is distinct and its commarginal projecting growth lines do not allow confusion with other non *Neocyrena* species. However, separating *P. solida* from its two East Pacific

sister species is not easy. Adult, unworn specimens are necessary to clearly identify them. The most reliable character is the pallial sinus that tends to be relatively stable within each *Neocyrena* species (2).

Biogeographic Range

Western Atlantic coast of Central and South America from eastern Venezuela to Belize. The present report expands the geographic range of this species because of new synonymy. For example, *Cyrena solida* was listed as living in Central America, between Honduras and Nicaragua (24). The same authors (24) listed *C. germana* as a different species found only in northeastern Mexico. Later *Polymesoda solida* was reported as *P. arctata* (32) from northwestern Venezuela and northeastern Colombia. The same author in another publications (36) extended this range to Costa Rica. Despite the fact that we found *C. germana* to be *P. solida*, the record from Tampico, Mexico (24) must be treated with caution. The locality may be a mistake, because there is no place known as "Panaco River", a name that was also misspelled as "Panuco" (24), near or around Tampico, Mexico (30). Of this, the following was written by J. P. Morrison on a label we found with the type specimen (MCZ 176944): "never seen again, is this the correct locality?, Oct. 1958". Thus, considering the whole set of specimens reviewed in this investigation, the confirmed range of *Polymesoda solida* extends along the North coast of South America and East coast of Central America, from the Orinoco River in Venezuela to Gales Point, Belize (Figure 3). This range also includes a record for the Caribbean Sea at St. Thomas, Barbados. The record from Tampico needs corroboration to extend the actual range beyond Belize (Gales Point, USNM 802403).

This range (without Mexico), is comparable to that of *P. radiata* on the eastern Pacific coast. This distribution agrees well with the marine current pattern of the Western Atlantic ocean where the combination

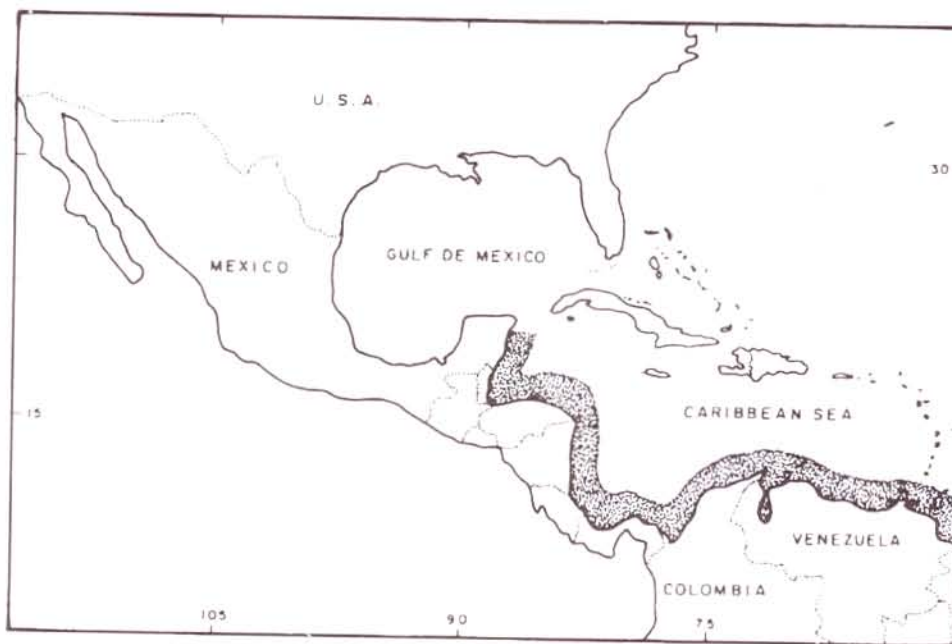


Figure 3. Biogeographic distribution of *Polymesoda solida*.

of the Guiana and Caribbean currents may give significant support to the idea that all *P. solida* populations surveyed in this investigation belong to the same taxonomic unit (2).

Habitat

The habitat where *Polymesoda solida* lives (reported as *P. arctata*) and several ecological features have been described (31, 32). This species prefers fine, sandy sediments of the low to medium salinity estuarine zone, sometimes close to a river mouth. These habitats are characterized by having sediments of a high organic content and salinities ranging from 3 to 20 ppt.

Sporadically, the species is found in almost freshwater conditions. It also is able to support strong desiccating situations. These conditions are very common due to the fact that *P. solida* is frequently found in the intertidal zone where it is daily exposed to the air and rising temperatures. It is also found associated with coastal mangroves,

where it can live within their roots in muddy anoxic sediments.

Stratigraphic range

The Subgenus *Neocyrena* has been reported from Eocene sediments of England and France (33) [as *Polymesoda (Pseudocyrena) convexa*]. Another fossil from Pliocene estuarine sediments of Trinidad, East Caribbean Sea, recorded as *Cyrena semistriata* (9), seems to be very close to living *P. solida*. Guppy (34) states: "It is akin to *C. solida* Philippi, of Central American Rivers". We have not seen the type specimens of the later fossil but we did see other specimens identified as *C. convexa* and *C. semistriata*, and in addition of being the same fossil species, they are remarkably similar to living *Neocyrena*. The fossil from Trinidad is from an area very close to the Venezuela east coast where abundant populations of *Polymesoda solida* presently live, suggesting that *Cyrena craigiana*, the name given by Guppy (34) to *Cyrena semistriata*, may be the same *Polymesoda solida*. Because of the

above facts, we are suggesting provisionally, until new evidence be gathered, that the stratigraphic range of *P. solida* is from Pliocene to recent and that of the Subgenus *Neocyrena* from Miocene to recent.

Discussion

Six species, whose types and/or figures coincide with the description of *Polymesoda solida*, were studied in this investigation. These are being synonymized here. They are: (I) *Cyrena arctata* (4), described from Lake Maracaibo, Venezuela; (II) *C. acuta* (18) described from "Central America". Its morph exactly matches specimens collected in Panama (Chepo River, ANSP 155424); (III) *C. ordinaria* (18) reported from "South America" with a morph that coincides with *C. germana* (23); (IV) *C. regalis* (18), described from the Gulf of Uraba, Colombia; (V) *C. germana* (23) from Panaco River, Veracruz, Mexico; and (VI) *C. boliviana* (12), based on a specimen from "Centralamerika, Neugranada".

The type of *C. boliviana* was not available, but the figures in its original description are from a juvenile that agrees with *Polymesoda solida*. Hence, considering that "Neugranada" is a synonym from Colombia, the agreement between locality and figures gives no option other than to assign *Cyrena boliviana* as a synonym of *P. solida*.

The review of the types of these six species revealed no taxonomic differences. Variation in shell form and coloration fall within the variation found by several authors (29,31,35) for *P. solida* (as *P. arctata*) from Lake Maracaibo, Venezuela. Additionally, the exceptional similarity of the pallial sinus of these types clearly establishes their synonymy.

Cyrena nicaraguana (19), has no type and, as explained before, it was just a new name introduced by Prime to substitute *C. solida* (3).

Polymesoda placens (24) referred to

specimens collected in Honduras (no locality given) and Guatemala (Livingston) on the Atlantic coast, so it is deduced that he collected specimens of *P. solida*. The true *P. placens* is a synonym of another *Neocyrena* species, *Polymesoda (Neocyrena) radiata* (2).

Specimens collected on the Atlantic coast of Nicaragua and, identified as *C. panamensis* (25), a synonym of another species, *P. inflata* (2) are really *P. solida*. We reviewed this material at the U.S. National Museum in Washington, D.C. and confirmed its identity as such.

The report of *Polymesoda solida* as *P. aequilatera*, from specimens collected on the Atlantic coast of Colombia (27) is a mistake later corrected by the same author (36) (as *P. arctata*).

Finally, *Corbicula arctata* (28) is just a name mentioned in a list of likely species that may belong to the Genus *Corbicula*. We spoke with this author and confirmed that he was making reference to *Polymesoda arctata* of Lake Maracaibo.

We must note that the types of *Polymesoda solida* (MCZ 152935) and *P. radiata* (MCZ 176946) were found combined when we inspected them. Apparently this mixing of specimens was done by J. P. Morrison when he examined these specimens around 1958. We deduced this based on labels and hand written comments found inside the shells. The inscriptions were identical to those on other hand-written documents that Morrison made. We left the specimens, the labels and the writings on the shell as we found them, but we are conforming here that both types correspond to two different species. This was also shown by another author (37), who likely saw the specimens before Morrison. He (37) probably did not find the specimens mixed and selected MCZ 152935 as cotypes of *P. solida* (3) and MCZ 176946 as paratypes of *P. radiata* (38). One of the labels left by Morrison, inside the box of *P. solida* (MCZ

152935) says: "holotype of *solida* Phil., he figured (from 'California') . Von Martens figured the only two paratypes [from L. Izabal]. In other words the paratypes were *radiata*". An analysis of the statements of Morrison leads to the following: **(a)** the paratypes of *P. solida* figured (24) are in the Zoologisches Museum (Humboldt Universität, Berlin, Germany) and could not be examined, however von Martens' figures (24) (Table 42, figs. 8 and 9) are so good that the pallial sinus of each specimen is suitable for detailed analysis. The sinus of both specimens is identical to that of Central American specimens of *P. solida*. **(b)** "L. Izabal" is a lake on the Atlantic side of Guatemala, within the range of *Polymesoda solida*. Biogeographically speaking, the location also agrees with this species. **(c)** As stated by Morrison, the specimens in the Museum of Comparative Zoology (MCZ 152935) (one of them, that we marked with number 11, which we chose as lectotype) may be recognized as Syntypes because it agrees well with Philippi's figures and measurements (3). **(d)** the specimens used by this author (3) to describe *C. solida* were not collected by himself, so the localities given by him, especially "California" may be a mistake. The other location mentioned by him "Central America" and the types agree well with the specimens we reviewed from different locations between Costa Rica and Panama.

In brief, all evidence seems to indicate that *P. solida* (3) is the oldest available name supported by a written description and types that coincide with contemporary collections (see Appendix 1). We have no doubt that this name is, based on the Principle of Priority of the International Code of Zoological Nomenclature (39), the valid and correct name to the six species described posteriorly within the Gulf of Mexico and the Orinoco River, in Venezuela.

Acknowledgements

Ours special thanks to Eric van den Berghe for all his support and encouragement throughout all phases of this research. We also thank to Thomas Waller from the U.S. National Museum for facilitating access to the Smithsonian collections, support the loans through which we got the Types, and especially for his personal advice in scientific issues of this investigation. Thanks to all those who helped us in many ways in the completion of this work: Clement Counts, Kenneth McKaye, Raymond Morgan, Gustav Paulay, Alan Kabat, Richard Houbriek. In addition, the staff members of the Division of Mollusks of the National Museum of Natural History, Washington D.C. and library personnel are gratefully acknowledged. To the following persons and institution, A. López of the Universidad Centro Americana of Nicaragua, Arthur Bogan and Gary Rosenberg of The Academy of Natural Sciences of Philadelphia, Kenneth Boss and Silvard Kool of the Museum of Comparative Zoology of Harvard, Paul Scott of the Santa Barbara Museum of Natural History, John Taylor and Kathie Way of the British Museum, José Parodiz of the Carnegie Museum of Natural History, Pittsburgh, and Kurt Auffenberg and Fred Thompson, and E. Raiser of Florida Museum of Natural History, Gainesville, ours endless thanks for making available specimens on their collections. Also thanks to Brian Morton of University of Hong Kong, Antonieto Tan Tiu of Indiana University of Pennsylvania, Pieter Kat of the National Museum of Kenia and Rudo von Cosel of the Paris Museum of Natural History for advice on collections of *Polymesoda* in their institutions.

Support was provided by the Appalachian Environmental Laboratory and the MEES program at the UMES Campus of the University of Maryland. Thanks to the Universidad del Zulia, Maracaibo, Venezuela.

The Smithsonian Institution and the University of Maryland which provided institutional support.

Bibliographic References

1. MOSQUERA A.: Personal communications.
2. SEVEREYN H.: Taxonomic Revision and Phylogeny of the Genus *Polymesoda* (Bivalvia: Corbiculidae). (Ph.D. Thesis). pp. 427. University of Maryland, Princess Anne (USA), 1993.
3. PHILIPPI R.A.: Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien unter mithilfe mehrerer deutscher. *Conchyliologen* 2:75-79, 1846
4. DESHAYES G.: Description of new species of shells from the collection of H. Cumming. *Proceedings of the Zoological Society of London* 22:13-23, 1854
5. RAFINESQUE M.C.: Monographie des coquilles Bivalves fluviatiles de la rivièrè Ohio, contenant douze genres et soixante-huit espèces. *Annales générales des sciences physiques* 5:21-56, plates 80-82, 1820.
6. BOSCH L.A.: *Histoire Naturelle des coquilles*. Tome III. Chez Verdière Libraire, Quai des Augustinus 25:55-56, 1801.
7. BRUGUIÈRE R.: *Encyclopédie Méthodique*. Vol. 1, plates 301-302, 1792.
8. LAMARCK M.: *Cyrena*. In: *Histoire Naturelle des Animaux sans vertèbres*. Tome 5. Paris (France), 1818, pp. 551-555.
9. DESHAYES G.: *Description des animaux sans vertèbres découverts dans le bassin de Paris pour servir de supplément à la description de coquilles fossiles des environs de Paris comprenant une revue générale de toutes les espèces actuellement connues*. Vol. 1-2, Atlas, J. Baillière et fils, Paris (France), 1857.
10. GABB W.M.: Description of the Cretaceous Fossils. *Paleontology of California* 1:55-236, 1864
11. GABB W.M.: Description of the Cretaceous Fossils. *Paleontology of California* 2:1-254, 1868.
12. CLÉSSIN G.: Cycladea. In: Martini und Chemnitz (Eds.), *Systématique Conchiologie Cabinet* 9(3):103-228, 1879.
13. CROSSE H., FISCHER P.: 1893. See Fischer & Crosse.: 1894, pp. 634.
14. FISCHER C. H., CROSSE H.: Etudes sur les Mollusques terrestres et fluviatiles du Mexique et du Guatemala. *Mission scientifique au Mexique et dans l'Amérique Centrale Recherches Zoologiques* 1:1-19, 1894.
15. FISCHER P.: Note sur l'Anatomie des Cyrenes. *Annals of the Lyceum of Natural History of New York* 10:191-197, 1872
16. MORELET A.: *Testacea Novissima Insulae Cubanae et America Centralis*. J.B. Baillière. Paris (France), 1851, pp. 1-30.
17. PRIME T.: *Monograph of American Corbiculidae*. Smithsonian Institution, Washington (USA), 1865, pp. 96.
18. KEEN M., CASEY R.: Superfamily Corbiculacea. In: *Treatise on Invertebrate Paleontology*. Moore R. Mollusca 6, Vol. 2, part N. 1969, pp. 664-669.
19. PRIME T.: Catalogue and synonymy of the Genera, Species and Varieties of the recent Mollusca, described prior to January 1st. 1867.-Part 3.- Corbiculadae. *American Journal of Conchology*. Appendix to volumen 5: 1869, pp. 141-150.
20. DUNKER W.: *Monographie der Norddeutschen Wealdenbildung*, 1846, pp. 434.
21. REEVE L. A.: *Conchologia Iconica: or illustration of the shells of molluscous animals* 20 (Volumen finished by G. Sowerby). Paris (France), 1878.
22. PRIME T.: Description of new species of *Cyrena*, *Corbicula* and *Sphaerium*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1861, pp. 125-128.
23. PRIME T.: Notes on Species of the family Corbiculidae, with figures. *Annals of the*

- Lyceum of Natural History of New York* 1864-1870 [8:57-92, 213-237 (1866), 414-418 (1867), 9:298-301 (1869)].
24. MARTENS E. von.: *Biologia Centrali-Americana, Land and freshwater Mollusca*. Taylor & Francis. London (England), 1890-1901, pp. 540-550.
 25. FLUCK W. H.: Shell-collecting on the Mosquito coast of Nicaragua. *The Nautilus* 20:1-5, 1906.
 26. BAKER H.: Mollusca collected by the University of Michigan Williamson Expedition in Venezuela. *Occasional paper of the Museum of Zoology, University of Michigan* 137:61-63, 1923.
 27. COSEL R. von.: Lista preliminar de los moluscos de la Ciénaga Grande de Santa Marta. *Memorias del Instituto Colombo-Alemán de Investigaciones Científicas* 7:47-56, 1973
 28. COUNTS C.: The genus *Corbicula* Muhlfield (Bivalvia: Corbiculidae) in Africa and South America: Zoogeographic and Taxonomic problems. *Bulletin of the American Malacological Union* 1980:71-72, 1980.
 29. SEVEREYN H., GARCÍA DE SEVEREYN Y., RODRÍGUEZ G.: Análisis cuantitativo de los patrones de coloración valvar interna de *Polymesoda arctata* (Bivalvia-Corbiculidae) en el Lago de Maracaibo. *Acta Científica Venezolana* XXXVII, Supl. 1:38, 1986.
 30. NIS Gazetteer.: *Mexico*. Office of Geography, Dept. of Interior, CIA, Washington D.C., 1956.
 31. GARCÍA Y.: Biología y ecología de *Polymesoda arctata* (Deshayes) almeja presente en el Lago de Maracaibo. (Trabajo Especial de Grado). pp. 125. La Universidad del Zulia. Maracaibo (Venezuela), 1984.
 32. COSEL R. von.: The genus *Polymesoda* on the North coast of South America (Bivalvia: Corbiculidae). *Archives Molluskenkunde* 108 (4-6):202-214, 1977
 33. NEUFFER O.: Die bivalven des Unteren Meeressandes (Rupellum) im Mianzer Becken. *Abdelhund hessarace Loste-Amerium Bodenforsch* 68 (113):76-77, 1973.
 34. GUPPY R. L.: On some fossil shells from Comparo Road, Trinidad. *Bulletin of Miscellaneous Information of the Botanical Department*, July:114-115, 1908.
 35. SEVEREYN H., EWALD J., GARCÍA DE SEVEREYN Y., RODRÍGUEZ A., MORALES F.: Estudio de las estrategias reproductivas y adaptativas de la almeja *Polymesoda arctata* en el Lago de Maracaibo. (Reporte Final-CONDES). pp. 21. La Universidad del Zulia. Maracaibo (Venezuela), 1986.
 36. COSEL R. von.: Moluscos de la región de la Ciénaga Grande de Santa Marta (Costa del Caribe de Colombia). *Anales del Instituto de Investigaciones Marinas Punta de Betín* 15-16:1-370, 1986.
 37. JOHNSON R. I.: The types of Corbiculidae and Sphaeriidae (Mollusca: Pelecypoda) in the Museum of Comparative Zoology, and a bio-bibliographic sketch of Temple Prime, an early specialist of the group. *Bulletin of the Museum of Comparative Zoology* 120 (4):430-479, 1959.
 38. HANLEY S.: Description of new species of *Cyrena*, *Venus* and *Amphidesma*. *Proceedings of the Zoological Society of London*: 159-161, 1844.
 39. International Trust for Zoological Nomenclature.: *International Code of Zoological Nomenclature*. University of California Press. Berkeley (USA), 1985, pp. 338.
 40. ABBOTT T.: *American Seashells*. Van Nostrand Co., New York (USA), 1974, pp. 521.

Appendix 1

This is a list of all specimens reviewed. Museums are abbreviated as follow:

- BMNH= British Museum of Natural History, London, England
 MCZ= Museum of Comparative Zoology, Harvard, USA
 USNM= National Museum of Natural History, Washington, USA
 ANSP= Academy of Natural Science, Philadelphia, USA
 FMNH= Florida Museum of Natural History, Gainesville, USA
 CMNH= Carnegie Museum of Natural History, Pittsburghs, USA
 MBLUZ= Museo de Biología de la Universidad del Zulia, Maracaibo, Venezuela.

Type Material

Cyrena solida Philippi 1846 (3), two cotypes (MCZ 152935), Central America. No locality appears on the label, but Philippi (1846)(3) gave Nicaragua and California. The last locality must be a mistake as it was not collected by Philippi. We selected specimen MCZ 152935 as lectotype that we marked with the number 11. The other specimen becomes a paratype.

Cyrena arctata Deshayes 1854 (4), three syntypes (BMNH 1956-12-3-28/29/30), Lago de Maracaibo, Venezuela. Specimen 1956-12-3-28 was selected by Johnson (1959)(37) as the lectotype. Cosel (1978)(32) confirmed this and defined syntypes 1956-12-3-29 and 1956-12-3-30 as paratypes.

Cyrena acuta Prime, 1865 (18), holotype (MCZ 176951), Central America (no locality).

Cyrena ordinaria Prime, 1865(18), holotype (MCZ 176880), South America (no locality).

Cyrena regalis Prime, 1865 (18), holotype (MCZ 176894), Isla de Muertos, Golfo de Uraba, Colombia.

Cyrena germana Prime, 1867 (19), holotype (MCZ 176944), Rio Panaco, Tampico, México.

Non-type material

- USNM - 011591, 1 specimen, Lago de Maracaibo, Venezuela.
 - 011618, 1 specimen, Nicaragua (no locality).
 - 017410, 1 specimen, Honduras (no locality).
 - 024928, 2 specimens, Lago de Maracaibo, Venezuela.
 - 023993, 4 specimens, Greytown, Nicaragua.
 - 053605, 1 valve, Lago de Maracaibo, Venezuela.
 - 063316, 2 specimens + 1 valve, Greytown, Nicaragua.
 - 086810, 1 specimen, Nicaragua (no locality).
 - 098551, 1 specimen + 1 valve, Greytown, Nicaragua.
 - 101475, 2 specimens, Lago de Maracaibo, Venezuela.
 - 122449, 1 specimen, Isla de Muertos, Uraba, Colombia.
 - 122450, 1 specimen + 1 valve, Lago de Maracaibo, Venezuela.
 - 122454, 1 specimen, St. Thomas, Barbados.
 - 125447, 3 specimens + 1 valve, Bluefields, Nicaragua.
 - 126079, 1 specimen, Costa Rica (no locality).
 - 150333, 1 valve, Belize (no locality).
 - 181837, 6 specimens, Wounta Haulover, Nicaragua.
 - 181838, 6 valves, Kukra Point, Nicaragua.
 - 217775, 3 specimens, Bahía El Tabiazo, Zulia, Venezuela.

- 252597, 4 valves, Bahía El Tablazo, Zulia, Venezuela.
 - 253491, 2 specimens, Wounta Haulover, Nicaragua.
 - 253495, 2 specimens, Wounta Haulover, Nicaragua.
 - 364262, 6 valves, Río Sinu, Bolívar, Colombia.
 - 364298, 1 valve, Caveñas, Colombia.
 - 421638, 3 specimens, Bluefields, Nicaragua.
 - 426060, 2 specimens, Wounta Haulover, Nicaragua.
 - 505930, 3 specimens, Bluefields, Nicaragua.
 - 536114, 17 specimens, Playa Yacht Club, Zulia, Venezuela.
 - 599520, 1 specimen + 2 valves, Turbo, Antioquia, Colombia.
 - 612249, 3 valves, Puerto Limón, Costa Rica.
 - 612250, 1 specimen + 9 valves, Coco Plum, Panamá.
 - 612251, 1 valve, Old Best Point, Boca del Toro, Panamá.
 - 612252, 2 valves, Mt. Hopes, Canal Zone, Panamá.
 - 612253, 1 valve, Convenas, Colombia.
 - 612254, 13 valves, Cispata, Río Sinu, Colombia.
 - 622090, 2 specimens, Lago de Maracaibo, Venezuela.
 - 672999, 7 valves, Titumate, Colombia.
 - 706720, 3 specimens, Lago de Maracaibo, Venezuela.
 - 706736, 1 specimen + 2 valves, Livingston, Guatemala.
 - 706737, 2 specimens, Puerto Barrios, Guatemala.
 - 706738, 9 specimens, Puerto Cortez, Honduras.
 - 706739, 2 specimens, Livingston, Guatemala.
 - 802403, 8 specimens, Gales Point, Stann Creek, Belize.
- ANSP - 120530, 1 specimen, Golfo de Maracaibo, Venezuela.
 - 308872, 3 specimens + 3 valves, Ciénaga Grande, Colombia.
- FMNH - 015569, 24 specimens, Belfate, Honduras.
 - 017629, 14 specimens, Belfate, Honduras.
 - 021212, 1 specimen, Tortuguero, Costa Rica.
 - 087891, 1 specimen, Maracaibo, Venezuela.
 - 087892, 2 specimens, Isla Izabal, Livingston, Guatemala.
 - 128404, 1 specimen, El Roble, Costa Rica.
 - 150363, 2 specimens + 2 valves, Coco Plum, Panamá.
 - Uncatalogued, 1 specimen, Puerto Limón, Costa Rica.
- MCZ - 152930, 1 specimen, Belize (no locality).
- MBLUZ - Uncatalogued, 12 specimens, Bahía El Tablazo, Zulia, Venezuela.
 - Uncatalogued, 2 specimens, Güiria, Sucre, Venezuela.
 - Uncatalogued, 1 specimen, Curriapo, Delta Amazonas, Venezuela.
- CMNH - 613954, 3 specimens, Wanta Haulover, Nicaragua.
 - 613955, 3 specimens, Kukra Point, Nicaragua.
 - 616495, 7 specimens, Guatemala (no locality).
 - 617071, 6 specimens, Río Dulce, Livingston, Guatemala.
 - 18958, 2 specimens, Lago de Maracaibo, Venezuela.