

**Systematics, phylogeny and biogeography of Mesoamerican and Caribbean
freshwater gastropods (Cerithioidea: Thiaridae and Pachychilidae)**

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"It is perhaps a more fortunate destiny to have a taste for collecting shells than to be born a millionaire. Although neither is to be despised, it is always better policy to learn an interest than to make a thousand pounds; for the money will soon be spent, or perhaps you may feel no joy in spending it; but the interest remains imperishable and ever new"
Robert Louis Stevenson

Zusammenfassung

In dieser Arbeit habe ich die Systematik zweier distinkter Taxa von Süßwasserschnecken innerhalb der Superfamilie Cerithioidea untersucht: der Familie Pachychilidae Troschel, 1858 und der Gattung *Hemisinus* Swainson, 1840 aus der Familie Thiaridae Gill, 1871. Durch vergleichende Analysen der morphologischen, anatomischen und molekulargenetischen Daten habe ich den Status der beschriebenen Arten für die gesamten Pachychilidae aus der Karibik und Mittelamerika, sowie für *Hemisinus* aus dem karibischen Raum überprüft. Des weiteren habe ich die Verwandtschaftsbeziehungen dieser Familien zueinander und zu ihren Verwandten aus anderen tropischen Ländern bestimmt. Anhand von Informationen und Material aus Museumssammlungen und von Geländeuntersuchungen habe ich außerdem die Verbreitung der Vertreter beider Familien rekonstruiert.

Innerhalb der neotropischen Thiaridae habe ich alle *Hemisinus*-Arten erneut und erweitert beschrieben. Die Gattung kommt in der Karibik lediglich auf den Großen Antillen vor und wird durch eine endemische Art auf Jamaika (*Hemisinus lineolatus*), welche gleichzeitig der Typus ist, sowie vermutlich zwei endemische Arten auf Kuba (*H. cubanianus* und *Cubaedomus brevis*) vertreten. Morphologisch unterscheidet sich diese Gattung von den anderen Thiaridae durch ein kurzes, anteriores Osphradium, ein Mitteldarm mit einem flach ausgeprägten Blinddarm sowie einen großen „accessory pad“ (zusätzlichem Ballen), der auf dem „glandular pad“ (Drüsenballen) aufsitzt.

Anatomische, molekulare und statistische Untersuchungen zeigen, dass die angenommene Anzahl von ehemals fünf kubanischen Arten innerhalb der Gattung auf zwei, evtl. sogar nur auf eine einzige reduziert werden muss: die stark polymorphe, dennoch monophyletische *Hemisinus cubanianus* und *H. martorelli*, deren Status aufgrund des fehlenden Typmaterials fragwürdig bleibt. Aufgrund der phylogenetischen Analysen ist es weiterhin wahrscheinlich, dass die bislang *Cubaedomus* zugeordnete kubanische Art auch *Hemisinus* angehört.

Diese Analysen zeigen weiterhin, dass die jamaikanische Art *H. lineolatus* eng mit den Thiaridae aus dem nördlichen Südamerika verwandt ist und eine basale Position gegenüber der kubanischen Art *H. cubanianus* einnimmt, was auch durch die anatomischen Untersuchungen bestätigt wird. Aufgrund der Ähnlichkeiten von anatomischen und morphologischen Merkmalen zwischen *Hemisinus* und anderen afrikanischen Familien, die den Thiaridae nahe stehen, lässt sich vermuten, dass diese einen gemeinsamen Vorfahren hatten. Dies wird zusätzlich durch die Topologie der phylogenetischen Analyse unterstützt.

Die biogeografischen Untersuchungen der geologischen Daten und der Verbreitungsmuster der *Hemisinus*-Fauna der Großen Antillen deuten auf einen kontinentalen Ursprung mit einer anschließenden Kolonialisierung und Ausbreitung auf den Inseln hin.

Bei den Pachychilidae Troschel, 1858 ist die Situation komplexer. Trotz der weiten Verbreitung dieser Familie in den Neotropen fehlte bislang eine umfassende taxonomische und systematische Revision dieser Gruppe, die hiermit vorgelegt wird. In Mittelamerika gibt es fünf verschiedene Gattungen und mehr als einhundert beschriebene Arten, die zudem meistens für relativ kleine Gebiete beschrieben worden sind, wie etwa einzelne Flüsse oder Flusssysteme. Obwohl die Pachychilidae von Mittel- bis Südamerika und im karibischen Raum vorkommen, beschränkt sich meine Arbeit allein auf die mittelamerikanischen Vertreter, da die Anzahl der Arten mit unklarem taxonomischen Status in dieser Region besonders hoch ist. Die kubanischen Pachychiliden wurden jedoch in die genetischen und biogeografischen Analysen miteinbezogen.

Aufgrund des systematischen Durcheinanders und des schlechten Verständnisses der Beziehungen innerhalb der mittelamerikanischen und kubanischen Pachychilidae, wurden anatomische Untersuchungen des Gehäuses und der Radula sowie phylogenetische

Analysen von zwei mitochondrialen Genen (COI, 16S) durchgeführt. Dabei wurden feine morphologische Variationen der Schale und der Radula zwischen den meisten Arten gefunden, die jedoch homoplasisch und somit wenig geeignete taxonomische Merkmale sind, um die neotropischen Pachychiliden-Arten unterscheiden zu können. Der Besitz von glatten Gehäusen ist ein konvergentes Merkmal, welches mindestens zweimal in der mittleramerikanischen Region entstanden ist, während die skulptierte Schale eine Synapomorphie ist. Ferner kann ich zeigen, dass die Pachychiliden-Arten aus Zentral-Mexiko sowie die kubanische *Pachychilus* und *P. vallesensis* in andere Gattungen als *Pachychilus* gehören.

Die molekularen Untersuchungen zeigen darüber hinaus, dass die mittelamerikanischen und kubanischen Pachychilidae monophyletisch sind. Außerdem konnte ich die Existenz von verschiedenen, klar abgegrenzten Clades aufdecken, die (wahrscheinlich endemische) Populationen aus einzelnen Flüssen umfassen. Die wahre Diversität in dieser Familie wird aufgrund der großen Ähnlichkeit in der Schalen-Morphologie mit Sicherheit unterschätzt, wobei die meisten der beschriebenen Arten aus Mexiko und Guatemala als gültig betrachtet werden sollten. Zukünftige Revisionen werden höchstwahrscheinlich weitere, bislang noch unbekannte Arten identifizieren.

Geologische, biogeografische und molekulare Daten deuten auf einen vikarianten Ursprung der kubanischen Pachychilidae sowie auf einen dispersiven Ursprung der kontinentalen Mitglieder der Familie hin, der von einem Vorfahren aus Zentral-Guatemala ausging.

Abstract

In this work I reviewed the systematics of two distinct lineages of Mesoamerica and Caribbean freshwater snails within the gastropod superfamily Cerithioidea: Thiariidae Gill, 1871 and Pachychilidae Troschel, 1858. Through comparative analyses of morphological, anatomical and molecular genetic data, I found that the family Thiariidae is represented by the genus *Hemisinus* in the Greater Antilles. Regarding Pachychilidae, the identity of Mesoamerican and Cuban species was reviewed. I also determined relationship patterns between them and their relatives from other tropical countries. Additionally, geographical range reconstructions of the members of both families were made based on the information available in museum collections and from field trips.

Concerning the Neotropical Thiariidae, I redescribed all *Hemisinus* species from the Greater Antilles including the type, which is *Hemisinus lineolatus* from Jamaica. The genus is represented in the region by one endemic species in Jamaica (*Hemisinus lineolatus*), and probably two endemic species in Cuba (*H. cubanianus* and *Cubaedomus brevis*). The diagnostic characters that separate *Hemisinus* from the rest of the thiariid genera are a short and anterior osphradium, and a midgut with shallow caecum and large accessory pad.

Anatomical, molecular and statistical analyses showed that the five former Cuban species assigned to the genus *Hemisinus* are reduced to two: the monophyletic *H. cubanianus*, possessing a highly polymorphic shell, and *H. martorelli*, the specific status of which must remain until its type material has been studied. Phylogenetic analyses showed that the Jamaican *H. lineolatus* has a basal position with respect to the Cuban *H. cubanianus*, which is also confirmed by anatomical studies. In addition, *H. lineolatus* is closely related to the northern South American Thiariidae. Moreover, according to the phylogenetic analyses, it is highly probable that the Cuban *Cubaedomus* is a member of *Hemisinus*. Based on the present findings I suggest that the sharing of anatomical and morphological features of *Hemisinus* with African families other than the Thiariidae could be indicative of common ancestry with an Oriental freshwater lineage. This is also corroborated by the topology of the phylogenetic analysis.

Concerning the biogeography of the group, geological data and geographic distribution of the Greater Antilles *Hemisinus* fauna point to a continental origin with subsequent dispersal to the Islands.

In the Pachychilidae Troschel, 1858, the situation is more complex. The family is widely distributed in the Neotropical region and a comprehensive taxonomic and systematic revision of this group was lacking. In Mesoamerica, five different genera and more than one hundred species have been described, some of which are restricted to rather small areas such as single rivers or river systems. Although there are also representatives of Pachychilidae in the Greater Antilles and South America, I have carried out a critical systematic revision only on the Mesoamerican members of the Pachychilidae. The work was restricted to this specific region because of its large number of described species that do not have a clear taxonomic status. Nevertheless, Cuban representatives of the group were included in the molecular and biogeographical analyses.

Due to the prevailing systematic confusion, and the poor understanding of phylogenetic relationships within the Mesoamerican and Cuban Pachychilidae, anatomical studies of shell and radula characters, as well as phylogenetic analyses based on two mitochondrial genes (COI, 16S), were performed. Subtle morphological variations in shells and radulae were found between most of the species. The molecular analyses showed that the Cuban and Mesoamerican Pachychilidae are monophyletic, and provided evidence for the existence of various well-defined and presumably endemic river clades. Due to the high degree of superficial similarity the true diversity of the group might be underestimated, while I am convinced that most of the described species from Mexico and Guatemala

should be considered as valid. I also expect that future revisions will probably lead to the identification of further, as yet unrecognized species.

I furthermore suggest that shell and radula characteristics are largely homoplastic features that are generally unsuitable for distinguishing Neotropical pachychilids. I present evidence that suggests that the Pachychilidae species from central Mexico, the Cuban *Pachychilus* and *P. vallesensis* belong to genera different than *Pachychilus*. Also, that in the Pachychilidae the possession of a smooth shell is a convergent character which has evolved at least twice in the Mesoamerican region, while a sculptured shell is a synapomorphy.

Geological, biogeographical and molecular data suggest a vicariant origin of the Cuban Pachychilidae, and a dispersal origin of the continental members of the family from a central Guatemalan ancestor.

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1. General Introduction

From the melanians to the PCR

During the 19th Century, the first classificatory attempts on gastropods placed the cerithioideans in the “Melaniidae”, a widespread group without any clear taxonomical limits other than the possession of an operculum and turritiform shells. In this way, affinities between distant or unrelated species were established, based on shell characters only (e.g. in Chapter 5.1).

In the field of classification, since the emergence of simple systems developed in order to “organize” the then known world, several theories were promoted. The first approaches were taxonomical, comprising essentially the description and inventory of the biodiversity of a given place. Thus, the “shell emphasis” made on mollusks’ classification was merely a reflection of the theories of that time. As result, we have numerous catalogs with huge lists of names and localities, as well as thousand of museum samples with confusing names on its labels. As an exception, Férussac (1819) laid the foundations of what is now considered to form the superfamily Cerithioidea, based not only on the shells but also on morphological features of the soft tissues. Following this anatomical tendency, and making reference to the position of the branchia in the snail’s mantle cavity, Thiele (1929) included the Cerithioidea into the subclass Prosobranchia, in which the branchia is lying dorsal at the back of the animal. Moreover, a spiral shell, an operculum, a nervous system with crossed visceral commissure, and separate sexes are considered as diagnostic characteristics of this subclass.

The Cerithioidea, as we known the group today, is one of the largest gastropod groups in terms of family, genera and species numbers, with representatives occurring in marine, estuarine and freshwater habitats around the world (Ponder & Warrén, 1988; Glaubrecht, 1996). It is also a very diverse taxon in terms of reproductive morphology and brooding modes that vary considerably in their complexity and general organization, rendering them as a promising group in evolutionary studies (Glaubrecht, 1996; Köhler *et al.*, 2004; Köhler & Glaubrecht, 2005).

At the middle of the 20th Century the “modern systematics” emerged as one of the major subdivisions of biology, changing the focus of subsequent studies. Systematics was first redefined by Simpson (1961) as “... the scientific study of the kinds and diversity of organisms and of any and all relationships among them...”. Later, Mayr (1997) defined systematics as an analysis which “... includes not only identification and classification of organisms but also the comparative study of all characteristics of species as well as an interpretation of the role of lower and higher taxa in the economy of the nature and in evolutionary history...”. Consequently, systematics experienced a renaissance and moved on to deal with species and populations, drawing together many kinds of knowledge,

theory and methods applied to all aspects of classification. In systematics, major tasks are to determine what the unique properties of each species and higher taxon are by means of comparison, what properties certain taxa have in common, what the biological causes of the differences or shared characters are, and to evaluate the variation within taxa (Mayr & Ashlock, 1991; Mayr, 1997).

Among the diverse classificatory methods, the phylogenetic systematics theory, first proposed by Hennig (1950) initiated a revolution. Hennig's methodology was renamed as cladistics because it essentially takes into account the ancestor–descendant branching pattern (cladogenesis), letting aside the relative amount of subsequent divergence (anagenesis). The cladistic method makes a cautious evaluation of taxonomic characters and tries to reconstruct the branching sequence of phylogeny (or the historical series of divergence events of organismal lineages as they change through time) in order to delimit taxa (Mayr & Ashlock, 1991). As cladistics only deals with cladogenesis, a comprehensive phylogenetic systematics (or phylogenetics) theory, including cladogenesis and anagenesis was defined. As widely understood today, phylogenetics deals with the detection and substantiation of relationships, enabling a testable placement of taxa in a phylogenetic tree depicted as tree graphs (Mayr & Ashlock, 1991; Wägele, 2005). Further conclusions (e.g. on the historical age of a group of organisms, the process of evolutionary adaptation to local ecological conditions, the existence of radiations, the influence of climate changes, as well as plate tectonic events and migrations), can be drawn only when a phylogeny is combined with data on the geographic distribution and the life histories of species (Wägele, 2005).

This phylogenetic theory has also had repercussions on the systematics of the Cerithioidea. However, despite numerous morphological, anatomical and ecological studies that have been conducted on various cerithioidean taxa after Thiele's (1929) work, it is only during the last years that the group has received attention again, mainly owing to its presumed monophyly. Researcher's efforts are now concentrated on molecular works, in particular on the freshwater groups which have been long neglected, since recent phylogenetic analyses have revealed that Cerithioidea members are basal representatives of the major gastropod clade Caenogastropoda, and consequently may play a fundamental role in evaluating higher-order phylogenetic relationships of gastropods (Lydeard *et al.*, 2002). While many phylogenetic and systematic issues remain unresolved or uncertain, some works have done much to clarify phylogenetic relationships within the superfamily (Glaubrecht, 1996; Lydeard *et al.*, 2002), and have shown that at least four independent colonization events of freshwater ecosystems occurred, involving at least one time the Pachychilidae (Glaubrecht, 1999, 2006; Lydeard *et al.*, 2002; Köhler *et al.*, 2004). As well, works on (i) the Pachychilidae in Southeast Asia, including Central

Thailand, the Philippines, Indonesia, and Australia (von Rintelen & Glaubrecht, 1999, 2003, 2005; Köhler & Glaubrecht, 2001, 2002a,b; 2003, 2005, 2006; Glaubrecht & von Rintelen, 2003; Glaubrecht & Köhler, 2004; Köhler *et al.*, 2004), (ii) the Paludomidae in Lake Tanganyika, East Africa (Strong & Glaubrecht, 2002, 2003; Glaubrecht & Strong, 2004), and (iii) the Thiaridae in SE Asia and Australia (Glaubrecht, 1996, 1999; Bandel *et al.*, 1997; Schütt & Glaubrecht, 1999; Facon *et al.*, 2003), have restricted the concept of each family delimiting species and distributional areas.

As previously stated by Wägele (2005), the accurate knowledge of the distributional pattern of a given taxon becomes a key objective in the performance of a systematic conclusion. The geographic distribution of biodiversity over space and time is studied by biogeography, which aims are to reveal where organisms live, their local abundance, and why or why not they are living there (Hedges, 2001). Mesoamerica and the Caribbean are very interesting regions in terms of biogeography because they harbor flora and fauna with high levels of endemism. Also, the geological history and paleogeography of these regions are extremely complex, leading to the suggestion of different scenarios to explain the current distribution of taxa, based on the same evidence. In general, the word Mesoamerica submits to the region from the south of Mexico through Panama, but its borders fluctuated throughout history since the term originally refers more to a cultural region than to a geographical one. Mesoamerica was initially established by Kirchoff (1943) to define a cultural area whose inhabitants share a common cultural heritage. Nevertheless, the definition has been expanding to other areas such as geography, biology and economy (Coe, 2002).

Although some biogeographical studies on continental mollusks have been done in Mesoamerica and the Caribbean region, most of them are outdated, without clearly defined species limits and confusing taxonomy (Bland, 1861, 1866a, 1866b, 1866c; Simpson, 1894; Russell-Hunter, 1955). Not many recent works are available and the new surveys are focusing mainly on land snails (Emberton, 1994; Mavárez *et al.*, 2002; Rosenberg & Muratov, 2005; Cózatl-Manzano & Naranjo-Garcia, 2007; Richling, 2007; Wade *et al.*, 2007; Uit de Weerd, 2008). The only recent studies that have used morphological and molecular evidence to depict the relationships between some of the Central and northern South American species belonging to Pachychilidae and Thiaridae, were done by Lydeard *et al.* (2002) and Köhler *et al.* (2004). Since Simpson's (1894), which was the first to consider the biogeography of *Hemisinus* and *Pachychilus*, there is only one recent study (Goodrich & v.d. Schalie, 1937). Hence, in this work I present the first phylogenetic attempt for Neotropical members of this superfamily as a tool to clarify their as yet enigmatic systematic and biogeographical relationships.

The “Studienobjekt”

Thiaridae and Pachychilidae are two families of freshwater gastropods which belong to the superfamily Cerithioidea Férussac, 1819. Thiaridae Gill, 1871 is a worldwide family primarily circum-tropical in distribution and with many extremely widespread species owing to their “tramp” abilities (Glaubrecht, 1996). The Thiaridae are one of the richest gastropod components of freshwater faunas and at the same time one of the least known because their systematics and taxonomy have been mainly based on shell features. Consequently, there are numerous descriptions of species, the taxonomic status of which remain unresolved (Köhler & Glaubrecht, 2003). This family is also important ecologically as some species have been widely introduced into freshwater habitats around the world. Some of these invasive species have a “positive” effect in the environments they invade, because they can successfully control other freshwater gastropods that are intermediate hosts of parasites affecting man and domestic animals (Faria-Vaz *et al.*, 1986; Ferrer-Lopez *et al.*, 1991; Pointier *et al.*, 1994; Gutierrez *et al.*, 1997). However, a drastically increasing number of invasive species populations lead to enhanced competition for food and space, causing dramatic reduction of the native species (Scholz & Salgado-Maldonado, 2000; Townsend & Newell, 2006; de Kock & Wolmarans, 2008). The Neotropical representatives of this family are *Hemisinus* Swainson, 1840 and *Aylacostoma* Spix, 1827. Approximately 34 species of extant *Hemisinus* have been described from Guatemala to Brazil (including the Greater Antilles) and about ten of *Aylacostoma*, all from South America.

The family Pachychilidae Troschel, 1858 is distributed in the tropical regions of America, Africa, and Asia, as well as in Madagascar. This family was earlier incorporated within the so-called “melanians” and their species have been variously allocated during the last two centuries to other cerithioidean families. Nevertheless, recent cladistic analyses of morphological and molecular data have supported the monophyly of the family and their independence from groups such as Thiaridae, Paludomidae, Melanopsidae and Pleuroceridae (Glaubrecht, 1996; Lydeard *et al.*, 2002; Köhler *et al.*, 2004). In the Neotropics two genera of this family are considered: *Pachychilus*, which seems to be restricted to the central region of America (Mexico, Guatemala, Honduras, Nicaragua, Venezuela and the Antilles), and the much closed related *Doryssa*, which occupies Guianas and Brazil.

1.1 Aim and objectives

In spite of the widely distribution of Cerithioidea and the fact that they have been studied (at least at taxonomical level) during the last two centuries, little is known about the anatomy, ecology and reproductive biology of the Neotropical groups (especially those of

freshwater environments). More than hundred years have passed since the monumental studies of the great malacologists of the nineteenth Century like F.H. Troschel, P. Fischer, H. Crosse, E. von Martens, A. Brot and A. Morelet who attempted to summarize and understand the molluscan fauna of the Neotropical region. Since then, the knowledge e.g. of the land snail fauna from most of the countries of this vast region, rests on comprehensive lists of species or on a couple of works dating from the end of the 19th and the beginning of the 20th Century (Richards, 1938; Thompson, 2003; Rosenberg & Muratov, 2005). The situation is not better with reference to the freshwater mollusks. In general, this fauna is poorly known and compared with other areas of the world the current knowledge is about equivalent to the level of knowledge of the invertebrates a century ago. In addition, taxonomic revisions with the aim of establishing hypotheses on the natural relationships between taxa in freshwater gastropods have only been made for the southeast Asian genus *Brotia*, the North American Pleuroceridae and the Neotropical Ampullariidae (Köhler & Glaubrecht, 2006). Consequently, here I attempted to establish the identity of the species of Thiaridae and Pachychilidae in Mesoamerica and the Caribbean region, as well as to identify relationship patterns between them and their relatives in other tropical countries. Also, by studying the anatomical and morphological characters of these lesser known Neotropical families, in order to analyze their morphological disparity of shells and soft parts, I aim at contributing to the evaluation of the relationships within Cerithioidea. Beyond the revision of the taxonomy and systematics of the Cerithioidea, the goal of this study is therefore to identify regularities in the diversity and geographic distribution and, ultimately, to reveal the causal relationships that underlie these patterns. Based on the currently knowledge of both families, Thiaridae and Pachychilidae in the Neotropical region, I hypothesized that *Hemisinus* in West Indies is product of dispersal colonization from the continent and not of vicariant events. Consequently, if *Hemisinus lineolatus* from Jamaica is the older lineage, it has to be more closely related with the continental forms than the other Antillean species of the same genus. Also, I supposed that there are at least three different species of *Hemisinus* in Cuba, and that the shell diversity of the genus in this island reflects an ongoing ecological speciation. Therefore, *Hemisinus ornatus* is not only one, but two separated entities. Concerning Pachychilidae, I hypothesized that there are less species than the originally described, all belonging to the genus *Pachychilus*. I think that the different shell morphotypes which inhabit one particular microhabitat belong to the same species, and that species can be separate based on their radula and shell features. Additionally, if the Mesoamerican Pachychilidae are species with “poor” dispersal powers, I expected a closely relation between the species of the same basin.

2. Freshwater Cerithioidea in the Neotropics: setting the stage

The Neotropics harbor one of the most diverse biota of the world, the origins of which are not well understood. For some time, the refuge hypothesis was the favorite explanation, assuming that during the Quaternary, glaciations induced the fragmentation of forests promoting allopatric speciation (Rull, 2008). However, this idea has been losing ground because paleoecological evidence now points to a Tertiary origin. Although DNA-based molecular phylogenies, calibrated with radiometrically dated geological evidence, support both Tertiary and Quaternary ages (Rull, 2008), indications from fossil and Recent taxa suggest that the extant Neotropical biota developed in a continual manner since the Late Eocene/Early Oligocene until the Pleistocene. Thus, the present Neotropical biodiversity is more the result of a mixture of species of different ages, having originated through diverse mechanisms, than the product of a single event or age (Rull, 2008).

2.1 The Cerithioidea

Within the order Prosobranchia, the Cerithioidea are differentiated by having more or less turritiform shells, the aperture of which has – or has not – a basal channel or shiponal projection; jaws; usually a short radula characterized by central teeth with serrated edges, middle teeth which migrate to the side, and marginal teeth with dentate edges; as well as males without a copulation organ (Thiele, 1929).

Most cerithioideans, as we now know the superfamily, are tropical in distribution, with herbivore or detritivore diets. In general, they have a thick and well-developed hypobranchial gland (as can be observed in *Pachychilus*), and an epiathroid dialyneurous nervous systems with zygoneury occurring only in some estuarine and freshwater families (which may indicate some kind of selective advantage in this environment). Their reproduction is gonochoristic except in some parthenogenetic thiarids. The pallial gonoducts are open and the males are aphallate, which appears to be truly homologous among its taxa. They have internal fertilization, and all members of the superfamily probably produce spermatophores. One seminal receptacle usually placed in the posterior medial lamina, as well as a spermatophore bursa occurring in the proximal medial lamina, seem to be the norm for most of the members of the group. Ciliated gutters that move sperm into the spermatophore bursa, and seminal receptacles lying along the free edges of the medial laminae of the pallial oviduct, are also diagnostic characters. The presence of euspermatozoa with four elongate midpiece elements that run parallel to the axoneme, distinguishes cerithioideans from all other prosobranch groups. Moreover, the possession of these four elements at the midpiece of the euspermatozoa relates the Cerithioidea with

the Viviparoidea and Cyclophoroidea, the three forming a distinct ancient clade within the Mesogastropoda (Houbrick, 1988; Glaubrecht, 1996).

Despite the monophyly of the whole Cerithioidea, not all the families that compose it are monophyletic as was formerly assumed. In addition, phylogenetic analyses of the Cerithioidea revealed that several independent colonization events of fresh water occurred. Viviparity has also evolved on several independent evolutionary avenues, as well as the detailed viviparous mode (brood pouch or pallial brood sac) (Glaubrecht, 1999; Lydeard *et al.*, 2002; Köhler *et al.*, 2004; Köhler *et al.*, 2008).

2.1.1 The family Thiaridae Gill, 1871

Troschel (1857) established three groups without family status based on their radula features. He erected the Thiarae group for *Thiara holandri*, leaving the species from South America and the Antilles grouped under Melaniae. Later, Gill (1871) established the family Melaniidae with three subfamilies: Melaniinae (Melaniae Troschel, 1857), Tiarinae (Thiarae Troschel, 1857) and Paludominae. Since then, several attempts at delimiting the families into a more “natural” form have been made. More recently, Ponder & Warrén (1988) retained the name Thiaridae according to the ICZN Art. 40B, maintaining Troschel’s concept and synonymizing Melaniidae Lamarck, 1812 and Semisinusinae Fischer & Crosse, 1879 with it. But Ponder & Warrén’s work is considered only as a nominal catalogue without much taxonomical authority. Recently, Bouchet & Rocroi (2005) revived the discussion and established Gill as the author.

As early as 1898, Moore raised the idea about the polyphyly of the Thiaridae based on morphological characters only. Recent results coming from molecular approximations confirmed that the former Thiaridae *sensu lato* are a polyphyletic group comprising at least three independent evolutionary lineages. As result, Thiaridae *sensu stricto* are proposed for animals with a typical brood pouch in the neck region, as well as a midgut with a deep spiral caecum and a large accessory pad (Glaubrecht, 1999; Lydeard *et al.*, 2002; Strong & Glaubrecht, 2002; Glaubrecht & von Rintelen, 2003; Köhler & Glaubrecht, 2003).

Members of the family Thiaridae are mainly defined by the presence of papillae in the mantle edge, which can be quite long; thin and weak hypobranchial gland; large osphradium the length of which may be a little less than the ctenidial length; the presence of a large lateral flange on the outer marginal tooth, which is an unusual feature of some cerithioidean radulae; salivary glands above and anterior to nerve ring; absence of

zygoneury and elongate extensions of the pedal ganglia enervating complex brood pouches in the head-foot. Concerning reproductive strategies, the group shows a spectrum ranging from true parthenogenecity to bisexual reproduction, with parthenogenesis as an autapomorphy of only some thiarid genera. The Thiaridae span environments ranging from rocky, fast moving streams, to broad, slow moving rivers and quiet lakes (Houbrick, 1988). In this work, only the Greater Antilles representatives of the genus *Hemisinus* were taken into account. Nevertheless, affinities between island and continental species are briefly discussed.

2.1.2 The family Pachychilidae Troschel, 1858

The Pachychilidae are a monophyletic clade represented by a diverse group of freshwater snails which are distributed in the tropical regions of the southern continents, with endemics in the Neotropics, Africa, Madagascar, India and south-east Asia (Köhler & Glaubrecht, 2007). It has been suggested that the Pachychilidae are a Gondwanan group, whose distribution was shaped by vicariance in the early to mid Cenozoic rather than by more recent dispersal. Indications of this theory are the distribution pattern of the family, as well as the inability of some of its representatives (e.g. the south-east Asian taxa) to actively pass marine and terrestrial barriers (Köhler & Glaubrecht, 2007).

Since earlier researchers have unsuccessfully attempted to separate the members of the so called “Melanians”, Troschel (1858) proposed the suprageneric “Pachychili”, a natural group among the Melaniids, composed of Neotropical and Asian species, based on morphological and anatomical features. “Pachychili” was established for snails with a paucispiral operculum, and a narrow and very long radula with a square middle tooth less broad than height, an inconspicuous and broad lateral tooth, and strong marginal teeth with small denticles at the edge (Troschel, 1858). Gill (1871) maintained this group separated from the rest of the “Melaniidae”, but changed its name to Melanopidae. Fischer & Crosse (1892), keeping the concept of Troschel and Gill, renamed the group as Pachychilinae. They also established that a smooth mantle edge, short ocular peduncles and numerous otoliths are diagnostic characters of the family. Thiele (1928), neglecting precedent arrangements, treated this clade as a subfamily of Melaniidae. More recently, Ponder & Warrén (1988) used the name Pachychilidae in “... favor of the widely used Pleuroceratidae which it predates...”. Finally, Bouchet and Rocroi (2005) separated Pleuroceridae from Pachychilidae attributing the latter to Fischer & Crosse, 1892. An extended review on the systematic position of the family and its taxonomy can be found in Köhler & Glaubrecht, 2001, 2002, 2003, 2006, 2007; Köhler, 2003; and Köhler *et al.*, 2008.

Only recently have the Pachychilidae been recognized again as a natural group of freshwater gastropods. Cladistic analyses of combined morphological and molecular data support the monophyly of the group and its independence from the other cerithioideans (Glaubrecht, 1996; Lydeard *et al.*, 2002; Köhler *et al.*, 2004). Nevertheless, the family is still one of the most poorly known groups of the superfamily regarding its taxonomy, phylogeny, biology and ecology.

The genus *Pachychilus* was established by I. Lea & H.C. Lea (1850) based on its shell attributes. The first anatomical description was made by Troschel (1858), who stated that all the members of the genus share a radula with seven denticles at the edge of the central tooth, five to six cusps at the lateral tooth, and two to three cusps at the marginal tooth. After this work, Fischer & Crosse (1892) established *Pachychilus* and *Doryssa* as the New World representatives of the family, describing in detail the foregut anatomy as well as the reproductive and nervous system of the former. Martens (1899) described the erosion process of the shell and its causes and made some remarks about the ecology of *Pachychilus*. Thiele (1928) established that the radulae of *Pachychilus* and *Doryssa* are so similar that they can not be separated. Morrison (1954) recorded the egg-laying characters of Mexican *Pachychilus*, and Simone (2001) described the external anatomy as well as the complete circulatory, excretory and digestive systems, with some remarks on the pallial oviduct. In the Neotropics, six genera and more than 140 nominal species or subspecies of Pachychilidae have been described from Mexico to Argentina (including the Caribbean islands), based almost exclusively on the variable adult shell.

2.2 Geographical setting

Freshwater habitats are generally considered as more extreme than marine environments. In a freshwater ecosystem temperature may fluctuate widely, water levels and current speeds are highly unpredictable, and the chemical composition of the medium is very variable, being mainly determined by the type of soil (Dillon, 2000). It is known that the geographical location, catchment, reach and bedform influence some (or all) of these factors. Lateral, longitudinal and vertical components of the landscape that interact with the water bodies also play an important role in the community structure and can account for some of the variation in invertebrate assemblages (Johnson & Gage, 1997; Townsend *et al.*, 2003). At a large scale, spatial patterns in communities' composition are reflections of the superimposition of geography and historical patterns. But at a small scale in freshwater environments, purely geographical patterns in physicochemistry will often be sufficient to explain community assembly (Townsend *et al.*, 2003). Apart from the speciation resulting from adaptive divergence of populations into particular habitats and

modes of life, effective reproductive separation of populations by geographical discontinuity of a habitat may have played a part in species differentiation within the Greater Antilles (Russell-Hunter, 1955). Also, because the distribution of freshwater mollusks seems to be strongly affected by catchment characteristics (see Chapters 4.1 and 5.2) and differences in microclimate due to the geography (see Chapter 4.1), it is important here to delineate the major geographical and hydrographical features of the Caribbean region.

Mesoamerica: Mexico and Central America

Belonging to the North American Plate, Mexico is a country that curves from northwest to southeast, narrowing to the Isthmus of Tehuantepec in the south, and then continuing northeast to the Yucatan Peninsula. Mexico's west and south coast is bordered by the Pacific Ocean and the Sea of Cortes, which lies between the mainland and Baja California (Fig. 1A). The east coast is bordered by the Gulf of Mexico and the Caribbean Sea. The Mexican coastal plains are characterized by swampy lowlands and numerous lagoons. Two north-south trending mountain cordilleras (the western Sierra Madre Occidental and the eastern Sierra Madre Oriental), frame a group of broad central plateaus known as the Altiplano Central. South of this central plateau/cordilleras complex, the Cordillera Neovolcanica runs east-west across the country. The Sierra Madre del Sur stretches across Guerrero and Oaxaca to the Isthmus of Tehuantepec (the narrowest part of Mexico). In the southernmost part of the country, the Pacific lowlands are backed by the Sierra Madre de Chiapas, the Rio de Grijalva basin and the Chiapas highlands (MacPherson, 1990).

Extending from the Isthmus of Tehuantepec to the border between Panama and Colombia, Central America is considered a "land bridge" that communicates the northern and the southern portions of two continents (Fig. 1B-H). To the northeast it is bordered by the Caribbean Sea, while the Pacific Ocean lies to the southwest. Northern Central America is dominated by mountain chains which are an extension of the mountain system of western North America. The central part of the subcontinent exhibits an active zone of volcanism containing also the Nicaragua Depression, which includes the lakes Nicaragua and Managua. To the south, rugged mountains of small cordilleras form a central spine which separates the Pacific and Caribbean watersheds. Only near the Colombian border there are highlands related to the Andean system of South America (MacPherson, 1990).

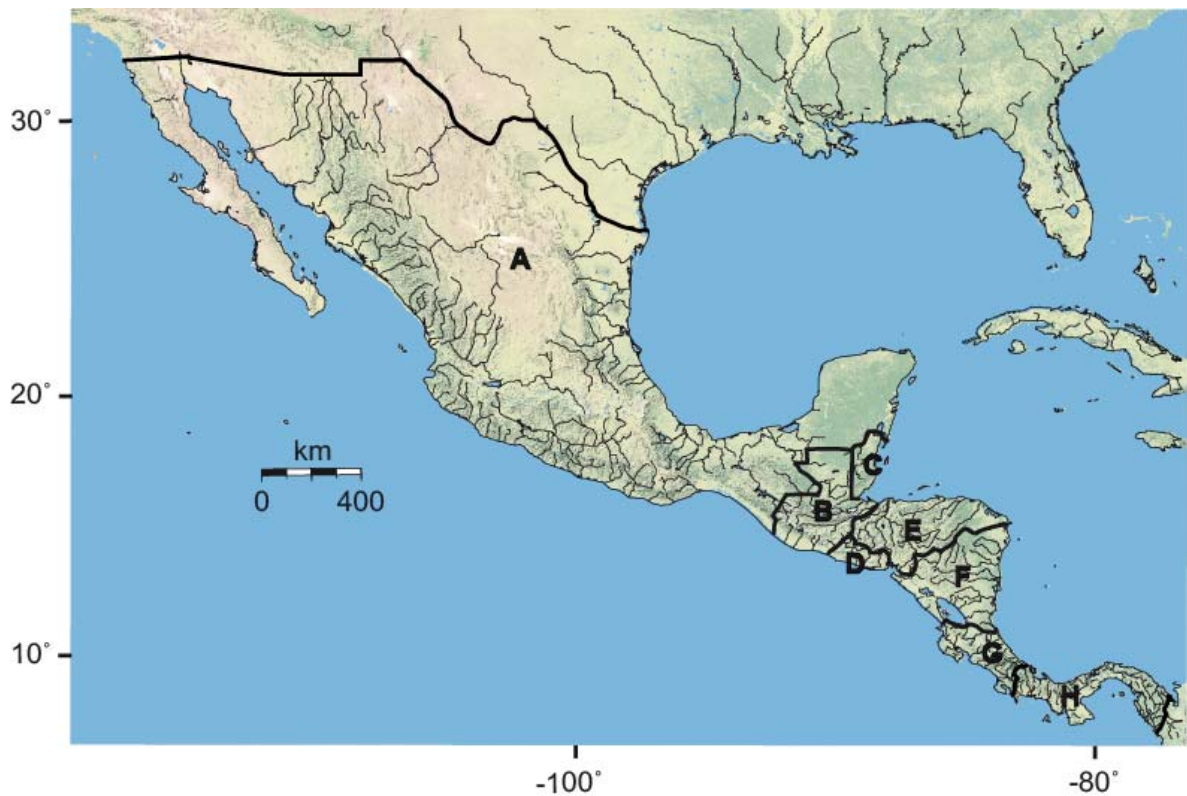


Fig. 1 A. Mexico. B-H. Central America. – B. Guatemala, C. Belize, D. El Salvador, E. Honduras, F. Nicaragua, G. Costa Rica, H. Panama.

The West Indies

The Caribbean region includes the entire area of the Caribbean Sea, the numerous islands of the West Indies, and the adjacent coasts of Central and South America. The West Indies can be considered as a large archipelago composed of the Greater Antilles, the Lesser Antilles and the Bahamas.

The Greater Antilles comprise Cuba, Jamaica, Puerto Rico and Hispaniola, which is divided into Haiti on the west side and the Dominican Republic on the east. In general these islands are old portions of land, which are assumed to have been above sea-level since the Middle Eocene (Ricklefs & Bermingham, 2008). A detailed description of Cuba (Fig. 2A) and Jamaica (Fig. 2B) are found in the Chapters 4.1 and 4.2, respectively.

Hispaniola is the second largest island of the West Indies (Fig. 2C), with five major mountain ranges of which the high and rugged Cordillera Central dominates. The other chains (Cordillera Septentrional, Sierra de Neiba, the Montagnes Noires and the Chaîn des Matheux), run parallel to the Cordillera Central respectively to the north, west and east of the island. The territory of the island belonging to the Dominican Republic is drained by relatively long rivers. The Yaque del Norte River drains to the northwest, the Yuna and Camú rivers drain to the east, the Yaque del Sur River to the southwest. On the

other hand, Haiti's rivers, despite being numerous, are short and swift due to its relief (MacPherson, 1990).

Puerto Rico is the smallest and easternmost island of the Greater Antilles (Fig. 2D). The island is mostly mountainous with large coastal areas in the north and south. The main mountain range is the Cordillera Central. Most of the rivers originating in the Cordillera Central and those in the northern region of the island are longer and of higher water flow rates than those of the south, since the south receives less rain than the central and northern regions (MacPherson, 1990).

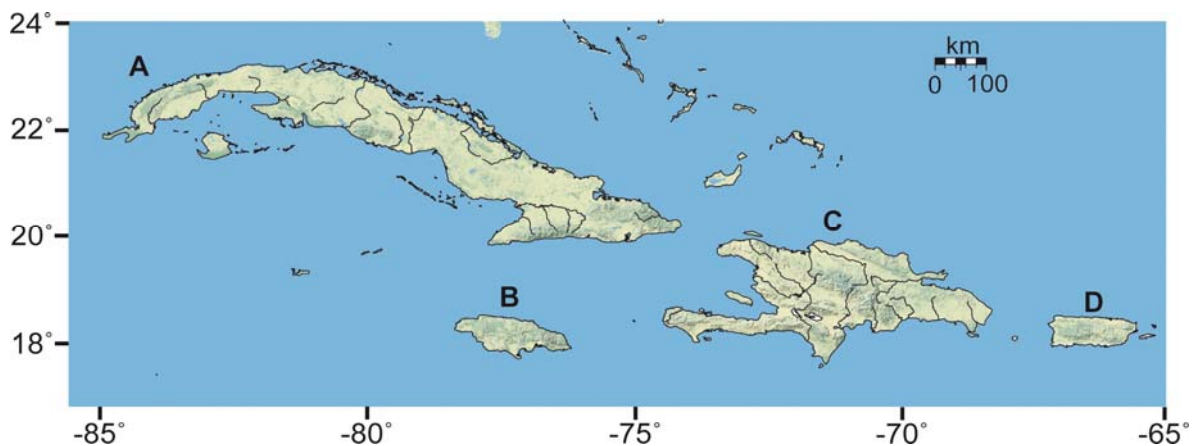


Fig. 2 A-D. Greater Antilles. A. Cuba, B. Jamaica, C. Hispaniola (Haiti and Dominican Republic), D. Puerto Rico.

The Lesser Antilles extend in an arc from Puerto Rico to the northeastern coast of South America, and are of much more recent origin than the Greater Antilles. They include two main chains of islands (the Leeward Islands in the north and the Windward Islands in the south), as well as Barbados, Trinidad and Tobago (Fig. 3). The islands to the north of Guadeloupe (one of the Leeward Islands) form two parallel chains: the western islands are volcanoes of post-Pliocene age while those of the eastern chain were formed during the Cenozoic. In general, the islands are a mixture of rolling hills and flat plains, some with volcanoes of middle elevation and others on which rivers are absent (Simpson, 1894).

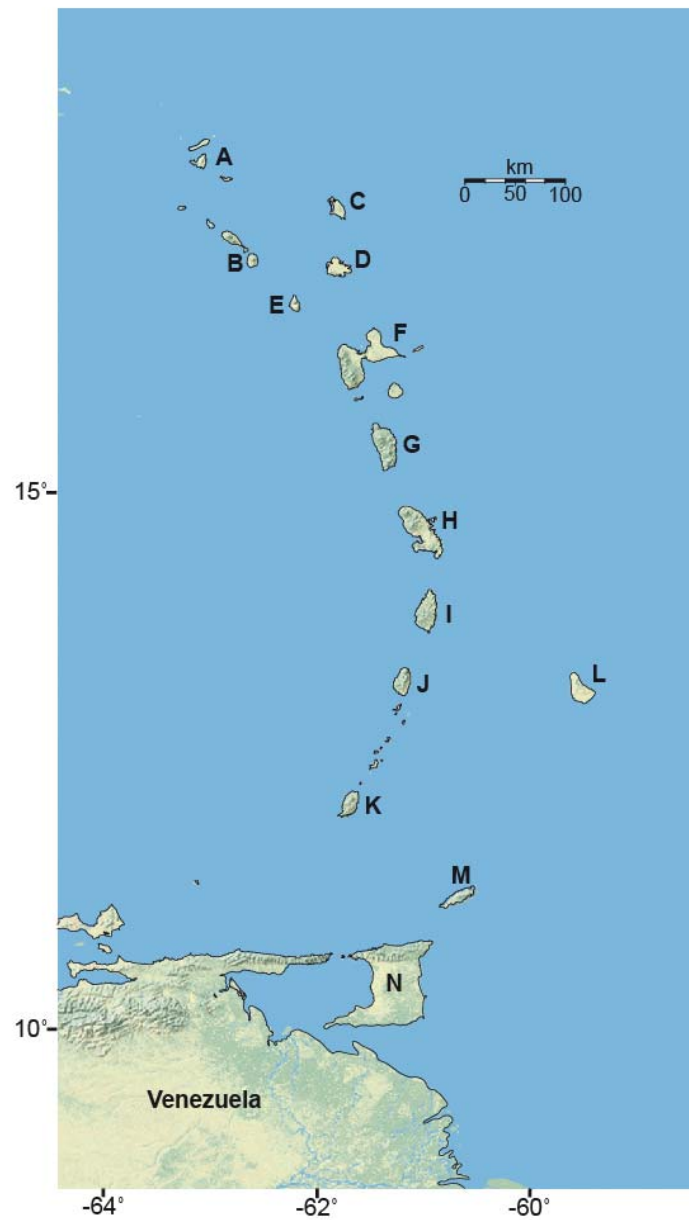


Fig. 3 A-N. The Lesser Antilles. – A-G. Leeward Islands: A. Anguilla, B. St. Kitts & Nevis, C. Antigua, D. Barbuda, E. Montserrat, F. Guadeloupe, G. Dominica. – H-K. Windward Islands: H. Martinique, I. St. Lucia, J. St. Vincent & the Granadines, K. Grenada. – L. Barbados, M. Tobago, N. Trinidad.

2.3 Historical geology of the Caribbean region

*“Even in areas where the stratigraphy, paleontology and areal distribution are thoroughly known, there is usually an element of doubt and uncertainty in interpreting sea and land connections”
(Stanton, 1918)*

Although organisms in freshwater ecosystems occupy locations where physicochemical conditions are favorable, resources are available and enemies do not preclude them, geology and geomorphology also play an important role in the distribution of the biota (Townsend *et al.*, 2003). In several studies, large scale factors such as geology have been found to be strongly related to spatial variation in invertebrate assemblages in freshwater habitats. Some organisms are confined to specific water bodies on a given landmass because it is there where their ancestors evolved, and the descendants have not proven capable of colonizing every “ecologically appropriate” location (Townsend *et al.*, 2003). A detailed geological description of the whole Caribbean region, including continental Mexico and Central America, is beyond the scopes of this work. Thus, only the relevant events concerning the Caribbean tectonics are mentioned.

The Caribbean region (here considered as the West Indies and the continental parts of Central America and northern South America) has a complex geological history which is comparable with those of the Scotia Sea (in the Southern Ocean between Tierra del Fuego and the Antarctic Peninsula) and Banda Sea (surrounding the South Moluccas in Indonesia) (James, 2006). The separation of Gondwana and Laurasia created the “space” for the Caribbean Plate, which formed later in the mid-Cretaceous and then started to move eastwards. Volcanic islands generated along the northern and eastern margin of this plate, formed the proto-Antilles due to subduction of the North American Plate (Hedges, 1996, 2001; James, 2006). For the evolution of the Caribbean region there are two explanatory models: the Pacific and the Inter-American model.

The Pacific model proposed by Wilson (1966) states that the Caribbean Plate formed on the Galapagos hot-spot and then entered the gap between North and South America (Fig. 4). In this model, the Chortis Block originated on the west side of Mexico and moved south-east into its Central America location, while the Maya Block lies along South America coast. Then, the Yucatan Basin opened as an intra-arc or back-arc basin south-west Cuba, colliding with the Bahamas-Florida platform and accreting the North American Plate along with the Yucatan Basin. The defunct northern and southern segments of the Great Arc became extended in an east-west direction, forming the Greater and

Netherlands-Venezuelan Antilles. Remnant north-south trending segments of the arc formed the northern Lesser Antilles and the Aves Ridge (James, 2006; Pindell *et al.*, 2006).

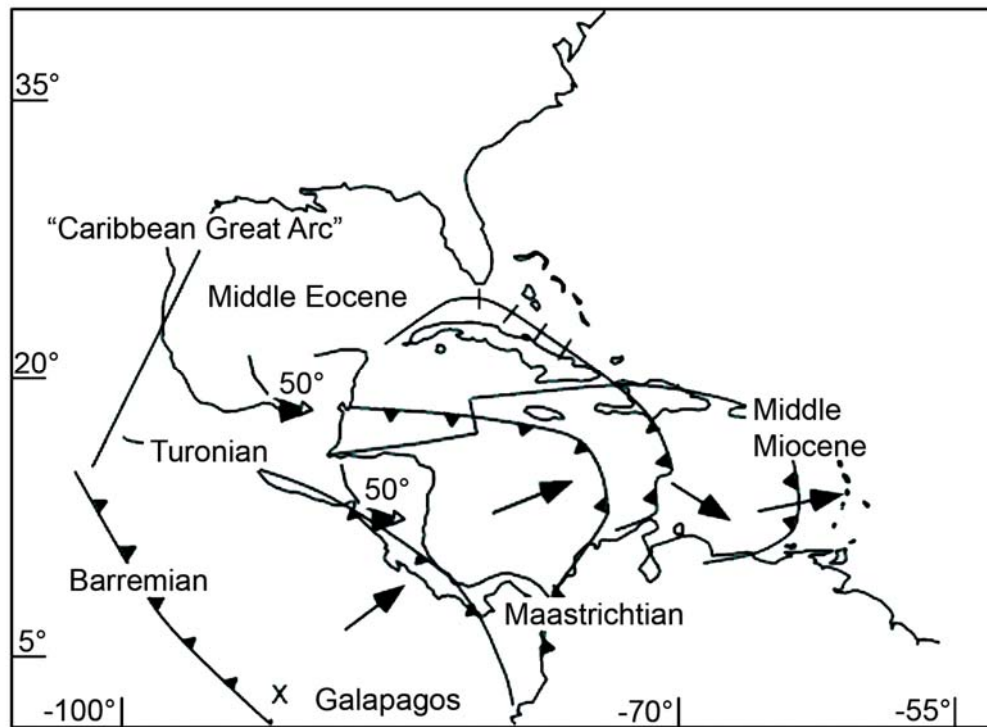


Fig. 4 Pacific model for the origin of the Caribbean Plate, shown against a modern map of the area (after James, 2006).

The Inter-American model proposed by James (2002b), suggests that the Caribbean evolved via sinistral transtension between North and South America (Fig. 5). The early Caribbean formed when North America drifted northwest from Gondwana in the Jurassic-Early Cretaceous. Atlantic and Pacific convergence with the Caribbean area resulted in outward facing island-arcs on the east and west of the Caribbean area, producing isolation of the Caribbean Plate. Continued westward movement of the North American Plate relative to South America and the Caribbean Plate resulted in continued subduction underneath the Lesser Antilles (James, 2006). According to James (2006), the Inter-American model is simple, feasible, and is corroborated by geological data, but the Pacific model is complex, rather improbable, and is not supported. The presence of continental material in the Cayman Ridge, the Nicaragua Ridge and along the walls of the Cayman Trough rules out a Pacific origin (James, 2006). On the other hand, Pindell *et al.* (2006) strongly support the Pacific origin for the Caribbean crust, while refusing a Galapagos origin of the Caribbean Plate. For an extended summary of the arguments in favor and against the Pacific model and the Inter-American model see Iturralde-Vinent & MacPhee (1999) and James (2006).

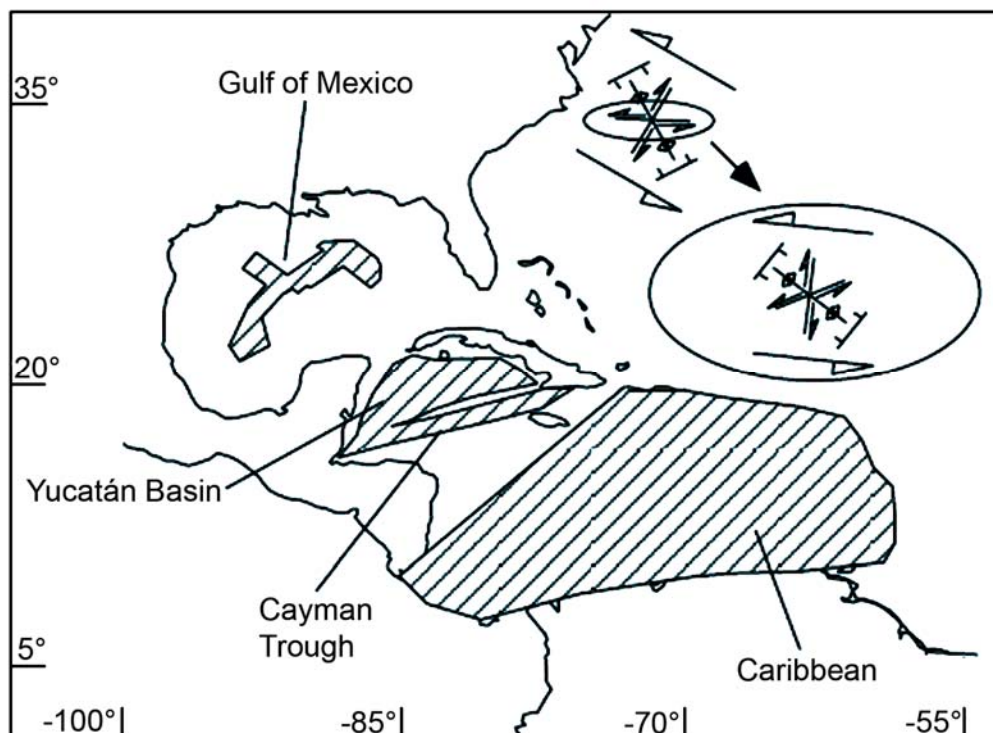


Fig. 5 Inter-American model for the origin of the Caribbean Plate, shown against a modern map of the area (after James, 2006).

2.3.1 The Greater Antilles

Nowadays, there is a general consensus on the assumption that the present Greater Antilles were formed by volcanism resulting from the subduction of the North American Plate beneath the Caribbean Plate during its eastward movement. It is also accepted that Caribbean land masses existed as islands throughout most of the Cenozoic. But there are still some uncertainties about the shape and location of the “islands” through time. Inaccuracies arise because the dimensions of the Caribbean Sea have changed over time and the Greater Antilles are depicted in their current sizes and positions relative to North America, sometimes having been mapped into positions they could never have occupied. The solution to this problem lies on more accurate shoreline reconstructions, which is a difficult task because the evidence needed to make paleogeographical reconstructions is almost inevitably destroyed or substantially modified over geologically long periods of time (Buskirk, 1985; Hedges, 1996, 2006; Iturralde-Vinent & MacPhee, 1999).

Despite some disagreements between different authors, the geological history of the Greater Antilles can be summarized as follows: There is evidence that island arc volcanism and short-lived land environments in the Caribbean Basin occurred during the Cretaceous (Iturralde-Vinent & MacPhee, 1999; Mitchell, 2006). During the Cenozoic, the Greater Antilles in general were subject to periods of elevation alternating with periods

where most of the terranes were submerged (Russell-Hunter, 1955). The early Cenozoic was the time of minimum exposure of the emergent areas. During this time, the island arc comprising southeastern Cuba, northern Hispaniola (which may have been both connected) and Puerto Rico, moved north-eastwards and collided with the Bahamas platform. This may have caused a major fault to develop to the south of Cuba, fixing Cuba and probably northern Hispaniola and Puerto Rico to the American Plate. Subduction along the eastern edge of the Caribbean Plate during the Cenozoic produced an island arc. Initially this arc was the Aves Ridge, which later produced the Lesser Antilles (Buskirk, 1985; Hedges, 1996, 2006; Iturralde-Vinent & MacPhee, 1999; Mitchell, 2006).

In the Eocene-Oligocene, southeastern Cuba and northern Hispaniola were presumably separated. More evidence is required to prove if at this time southwestern Hispaniola and the Blue Mountains Block were closely positioned, and also if western Cuba would be separated by deep-water environments from central and eastern Cuba (Hedges, 1996; Iturralde-Vinent & MacPhee, 1999; Mitchell, 2006).

During the Oligocene a reorientation of plate movements towards the east occurred. Also, in this period Cuba started separating from Jamaica and Hispaniola. This was a time of high sea level although the highlands remained persistently subaerial along the axis of GAARlandia (Greater Antilles + Aves Ridge). Geological evidence suggests that Jamaica was inundated during this epoch, while in Cuba some land areas were emergent throughout this period (but not its westernmost extremity nor the Isla de la Juventud), and the Nicaraguan Ridge was completely uplifted (Aguayo, 1938; Buskirk, 1985; Hedges, 1996; Iturralde-Vinent & MacPhee, 1999).

By the Late Oligocene-Middle Miocene, the Aves Ridge subsided and the communication between Pacific and Atlantic improved. Probably at this time, an incipient circular gulf current started (Iturralde-Vinent & MacPhee, 1999).

During the Miocene, the subduction zone forming the west edge of the Caribbean Plate was well developed and the Lesser Antilles island arc overrode Atlantic crust. In this period, further isolation of land areas took place as a consequence of active tectonic disruption of the northern and southern Caribbean Plate boundaries. Jamaica and southern Hispaniola moved towards their present configurations. Southern Hispaniola collided with northern Hispaniola, and western Cuba achieved dry-land contact with central Cuba after the disappearance of the Havana-Matanzas channel (Buskirk, 1985; Hedges, 1996; Iturralde-Vinent & MacPhee, 1999). Throughout this time and during part

of the Pliocene, large regions of Jamaica and Hispaniola were formed from uplifted ocean floor, a process which continues until today (Buskirk, 1985; Iturralde-Vinent & MacPhee, 1999; Mitchell, 2006).

During the mid- to Late Pliocene, high global sea levels reduced the land masses of the Caribbean islands, increasing the effective distance between them (Buskirk, 1985). During the Pleistocene, sea levels lowered, Cuba was nearly in contact with the exposed Great Bahamas Bank and with the peninsula of Yucatan, and Jamaica was much closer to Central America via the exposed Nicaragua Rise (Russell-Hunter, 1955; Hedges, 1996). The orogenic activity that built the mountain chains in the West Indies is still an ongoing process initialized in the late Cenozoic (Hedges, 1996).

2.3.2 Mexico

Northwestern Mexico is the result of the subduction of the Farallon Plate beneath North America, and to the opening of the Gulf of California (Ferrari *et al.*, 2007). Central Mexico is a region of complex geology and diverse surface configuration. Its major physiographical feature is the uplifted plateau of the Mesa Central. The eastern boundary of the Mesa Central developed during the Eocene the Sierra Madre Oriental (c. 45 Ma). The western boundary (the Sierra Madre Occidental) was formed primarily by volcanic activity in the Oligocene (c. 30 Ma) and Miocene (c. 23 Ma). The southern boundary corresponds with the limit of the geologically active Transmexican Volcanic Belt. Volcanism began during the Late Cretaceous, but the activity that has contributed most to shaping the present land started during mid-Cenozoic (Dominguez-Dominguez *et al.*, 2006). Southern Mexico is characterized by Upper Cretaceous orogenic deformation (Morán-Zenteno *et al.*, 2007).

At least six models for the development of the Yucatan Peninsula (Maya Block) could be found (James, 2006). According to Iturralde-Vinent & MacPhee (1999), the block was uplifted between the Jurassic–Early Cretaceous and during the Late Eocene. Additionally, it was covered intermittently by shallow seas between the late Aptian and the Miocene. It is supposed that some time between the Late Paleocene to Middle Eocene, the terranes of western and central Cuba were detached (Iturralde-Vinent & MacPhee, 1999).

2.3.3 Central America

During the Mesozoic, Central America appeared as several disjunct tectonic units (Fig. 6A), which increasingly merged until the closure of the Isthmus of Panama in the mid-Pliocene (Buskirk, 1985; Beu, 2001; Zeh *et al.*, 2003). According to Kirby *et al.* (2008), the paleogeographic nature of southern Central America before formation of the isthmus is

still disputed, although extensive studies have constrained the timing of this event. The most widespread theory established that Central America arose from bathyal depths during the Neogene as a result of the collision between the Panama microplate and the South American Plate. An alternative view is that the main axis of the volcanic arc had already arisen above the sea level, which would have made Panama a peninsula of Central America by the Neogene (Fig. 6B).

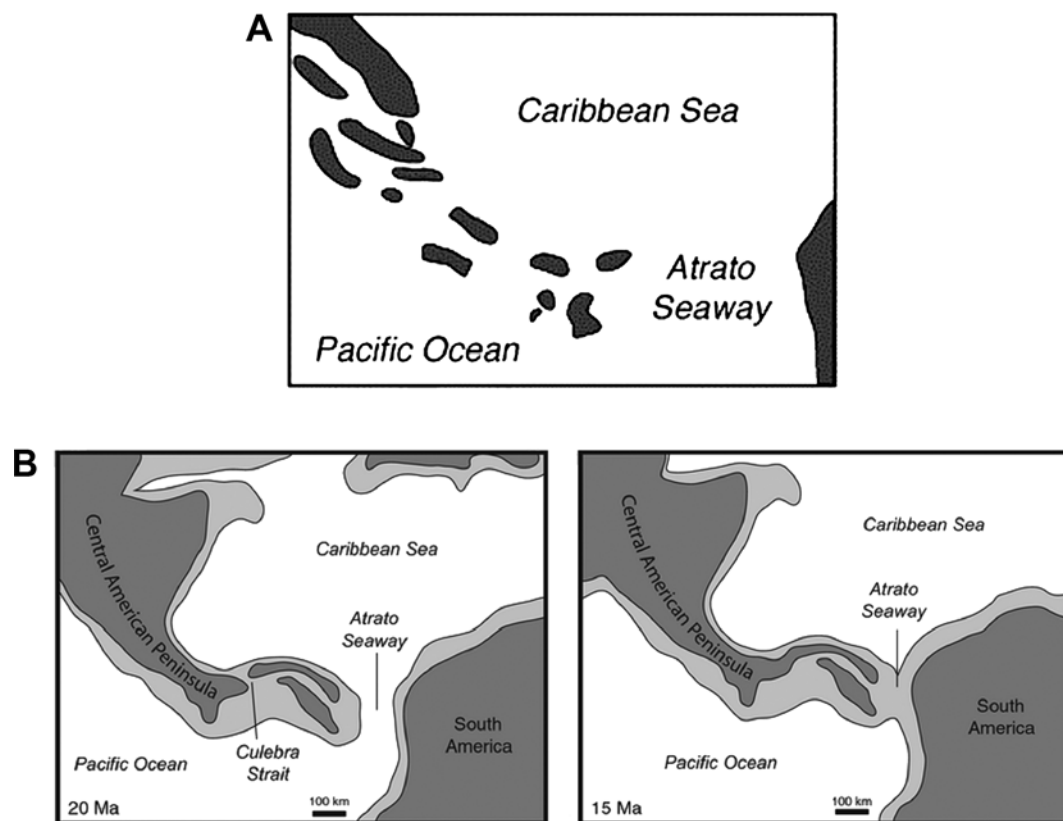


Fig. 6 Paleogeographical models proposed for Central America. A. The Archipelago model (after Kirby & MacFadden, 2005), – B. The Peninsula model, paleogeographic reconstruction of Central America for 20 Ma and 15 Ma (after Kirby *et al.*, 2008).

Although nowadays it is not possible to determine exactly when and how far the Central America Peninsula formed and extended, based on stratigraphical determination of sediments it could be inferred that the Central America Peninsula existed for much of the Miocene. It also suggests that the Atrato seaway (located between Central and South America) remained open until the final formation of the Isthmus of Panama at c. 3 Ma (Kirby *et al.*, 2008).

2.3.4 Land bridges

A land bridge is a connection between landmasses that can be created by marine regression, plate tectonics or post-glacial rebound after an ice age (Newmark, 1987). With respect to the Caribbean there is agreement that (i) no land connections ever linked the Greater Antilles to Florida, and (ii) that a potential land communication between Honduras, Jamaica, Hispaniola and Cuba was not possible because there is no correlation between the fossils of Jamaica and Cuba (Aguayo, 1938; Russell-Hunter, 1955; Iturralde-Vinent & MacPhee, 1999). However, different authors proposed the existence of land-bridges between the Greater Antilles and either Central America or northern South America (Aguayo, 1938; Russell-Hunter, 1955).

Regarding a connection between northern South America and the Antilles, Iturralde-Vinent & MacPhee (1999) proposed the Aves Ridge. This potential land bridge possibly connected the continent with the Greater Antilles Ridge, reaching central and eastern Cuba, north-central Hispaniola and Puerto Rico (which were either in a closed packed array or constituted a single large island). Iturralde-Vinent & MacPhee (1999) considered that the Aves Ridge was exposed during the latest Eocene/Early Oligocene, creating a series of large, closely spaced islands or possibly even a continuous peninsula. However, according to Hedges (1996) and James (2006), the Aves Ridge can be discarded as a land bridge option because there is no geological evidence that this Ridge is a subduction arc, nor that spreading occurred or that ridges existed between Aves Ridge and the Lesser Antilles. Also, the similar origin of the Venezuelan and Colombian crust also provides evidence against an Aves Ridge land bridge.

Parallel to the discussion about where land bridges could have occurred during the evolution of the Caribbean, some other authors entirely preclude the existence of dry land connections, based on evidence coming from sea-level changes and from the fact that deep water is now known to surround many of the islands in the Greater and Lesser Antilles (Buskirk, 1985; Hedges, 1996).

2.4 Biogeography: A review

*"The question is suggested,
Are the faunas of the islands more ancient than those of the continents?"
(Bland 1866a)*

A significant number of the world's terrestrial biota is distributed in the Caribbean region. Many of those species are endemic to the region, to individual islands of the West Indies, and even to isolated areas within the continent or on the islands (Hedges, 2001). The complex geological history of the region has offered many opportunities for vicariance and dispersal to affect biotas (see Chapter 2.3). In addition, evidence from the fossil record suggests that the history of some groups may be more ancient than previously acknowledged (Woods, 2001). Together, these features have made the Caribbean region, and especially the West Indies, an appealing region for the study of historical biogeography (Hedges, 2001). This section provides a brief outline of the definitions, historical explanations and debates in biogeography, as well as of the major hypotheses of Caribbean biogeography and the evidence to support it.

2.4.1 Definition

Biogeography is the science concerned with the study of the complex patterns of spatial interaction among organisms and their environment (Smith, 1989; Morrone & Crisci, 1995; Glaubrecht, 2000). Species populations tend to expand or contract toward areas where conditions are optimal. This range change can be viewed as a function of geographic variation in the availability and level of optimality of certain resources (Smith, 1989). However, this population movement depends on the flexibility of the gene pool of each population.

During the development of the biogeographic theory, different subdivisions, namely ecological, historical, cladistic and phylogenetic biogeography as well as panbiogeography, have been brought up in order to explain organismal diversity and distribution (Morrone & Crisci, 1995; Glaubrecht, 2000). In this work, I am mainly dealing with historical biogeography, which by definition works with evolutionary processes occurring over millions of years on a large scale.

2.4.2 Historical explanations in biogeography

Two traditional approaches, "dispersal" and "vicariance" (which most of the time have remained as separated and irreconcilable events), are the core of biogeographic theory.

In the dispersal approach the range of a given ancestral population, being restricted by a barrier, is suggested to be crossed by some members which may eventually become a new species if they remain isolated for a sufficient period of time. In dispersal the barrier is older than the disjunction and the common ancestor occurred in one of the areas, dispersing later into the other. Therefore, the oldest fossils are expected to be located near the species center of origin (Briggs, 1981; Morrone & Crisci, 1995; Glaubrecht, 2000; Page *et al.*, 2005; Heaney, 2007; Upchurch, 2007).

In contrast, in the vicariance approach the ancestral population was widespread in greater areas that became fragmented, and the descendants survived in the fragments. Here, the barrier is not older than the disjunction and allows the isolated subpopulations to differentiate into distinct taxa with time (Briggs, 1981; Morrone & Crisci, 1995; Glaubrecht, 2000; Page *et al.*, 2005; Heaney, 2007; Upchurch, 2007).

The speciation mechanism acting in both dispersal and vicariance is allopatric speciation. Allopatric speciation results when biological populations, physically isolated by an extrinsic barrier for a sufficient period of time, evolve reproductive isolation. This isolation should prevent interbreeding of the individuals of both populations if the barrier breaks down (Whittaker & Fernández-Palacios, 2007). In contrast, sympatric speciation occurs when a subpopulation of a parental population, despite inhabiting the same geographic region, diverges genetically to become a distinct species. Sympatric speciation events are vastly more common in plants due to their polyploidy. Examples in animals are rare, and generally this type of speciation starts with differences in diets, behavior, and social structures (Whittaker & Fernández-Palacios, 2007). In the West Indies, allopatry is more common in big islands, but in the Lesser Antilles sympatric or parapatric speciation can occur in the form of ecological speciation (Ricklefs & Bermingham, 2008).

2.4.3 Island colonization: the West Indies

The West Indies comprise a mixture of continental fragments and continental islands as well as oceanic islands lying at convergent plate boundaries. They are sufficiently isolated to avoid interaction between the islands and the continent, but at the same time are reasonably close to allow immigration (Whittaker & Fernández-Palacios, 2007; Ricklefs & Bermingham, 2008).

The species we see today on the islands represent the descendants of the colonizing species, but explaining their biotic composition is a difficult task since it is influenced by the type and time of colonization, adaptive radiation and extinction processes that colonizers have to experience (Emerson, 2008).

Colonization of islands could occur through transoceanic dispersal, "jumping" from one island group to the next, or through long distance dispersal from a mainland source (Gillespie *et al.*, 2008). The colonizers have to adapt to their new environment, an event which is modeled by factors like availability of niches, competition and predation. After a successful invasion, speciation processes could arise.

In the West Indies, both dispersal and vicariance could explain the distributional patterns of organisms, which are nowadays much more affected by extinction than by speciation. For this region, vicariance is relatively well supported by the geology, whereas dispersal is still contradictory (for details see Appendix 1).

In his work on freshwater mollusks, Simpson (1894) was the first to raise the idea about dispersal colonization in the Caribbean. He stated that all the diverse faunas could not have arrived on the islands merely through ocean currents and winds. Consequently, he suggested the idea of the existence of a land bridge north or south of Yucatan because the deep ocean floor between the peninsula and the islands ruled out any other option.

On the other hand, for Hedges (1996, 2001) dispersal in the West Indies occurred by means of overwater colonization. He gets support for his idea from present-day ocean currents, which are flowing almost unidirectional from southeast to northwest, allowing the West Indies to get easily colonized from South America. Hedges (2006) claimed that the higher-level taxonomic composition of the West Indian fauna is reduced when compared to that of mainland areas, a pattern which is characteristic of oceanic islands where the fauna has arrived by dispersal. In addition, the fact that many vertebrate groups on Caribbean islands have their closest relatives in South America is strong evidence for his point of view. Hedges' position is dismissed by Iturralde-Vinent & MacPhee (1999) who established that the water current pattern in the Caribbean (initiated around the Miocene-Pliocene boundary) was not always like nowadays. The uplift of the Andes and the closure of the isthmus radically changed the points of discharge of the big South American rivers. Also, experiments made with buoys reveals that deep cyclonic water circulation and storms generally acted towards increasing the trip length, a situation which is physiologically disadvantageous for the surviving of land animals like mammals, but probably not for reptiles (Molinari *et al.*, 1981; Iturralde-Vinent & MacPhee, 1999).

Other arguments against overwater dispersal in the Caribbean are (i) the case of the Cuban Cays, which are not gaining non-endemic populations from the main island despite its proximity, (ii) the depauperate avian fauna on the islands in comparison with that of the continent, and (iii) the fact that the faunas of the larger islands have very high rates of

endemism (indicating that colonization is difficult). All of them suggest that the Caribbean Sea is a substantial barrier even for many groups of flying animals or wind-dispersed plants (Iturralde-Vinent & MacPhee, 1999; Ricklefs & Bermingham, 2008).

Concerning Antillean vicariance, the first model was proposed by del Corral (1939) to explain the mammal fauna in Cuba. This author stated that before the Late Miocene the Greater Antilles were attached to northern South America when receiving their fauna, and then drifted to their current position (Iturralde-Vinent & MacPhee, 1999). Del Corral's vision was retained until Rosen (1975) established that the proto-Antillean archipelago occupied the current location of Central America during the Cretaceous-Eocene. Rosen (1975) proposed that the archipelago interacted at that time with adjacent continental margins on its eastward movement, obtaining the greater part of its biota. Then, during its movement to the current position, the faunas of the islands were further shaped by extinction, local radiation and, in a few cases, overwater dispersal. However, this scenario has been rejected because it advocates the permanent subaerial existence of the islands through time, contradicting the geological history (see Chapter 2.3).

Since geological data strongly support that the West Indies have been islands throughout most of the Cenozoic, the West Indies fauna should derive from overwater colonization and not from fragmentation of original populations of a large land mass. Supporting evidence for this fact comes from immunological distances of reptiles and amphibians, and from lower endemism of the herpetofauna of small islands (Buskirk, 1985; Hedges *et al.*, 1992; Iturralde-Vinent & MacPhee, 1999; Hedges, 2006; Ricklefs & Bermingham, 2008). A historical summary of the colonization events of the West Indies separated by region and animal group is given in the Appendix 1.

The Greater Antilles

It has been claimed that much of the land and fresh water fauna in the Greater Antilles should be relatively homogeneous because they were carried from island to island by currents or storms (Simpson, 1894). But the small number of common species between islands and the restricted distribution of the genera are arguments against this thought. The current distribution of the organisms in the Greater Antilles suggests one colonization pathway from Central America via Cuba or Jamaica to the other islands of the group. The fact that there is more evidence of biotic exchange between Cuba and Jamaica than between the other islands of the archipelago (i.e. from truncatellid land snails) could support this theory (Simpson, 1894; Buskirk, 1985; Hedges, 1996).

Puerto Rico is an exceptional case in the Greater Antilles. There are not many endemic freshwater species, the island shares only few species with Hispaniola, and some of the

widespread genera are absent on the archipelago. It has been suggested that, due to the relatively low topography of the island during the Pliocene subsiding period, only a limited area above sea level persisted which could not harbor many genera (Bland, 1871; Simpson, 1894; Hedges, 1996; Bell, 2001).

The Lesser Antilles

Colonization of the Lesser Antilles has been mostly via continental South America, but there is also evidence of colonization from the Greater Antilles to the southern Lesser Antilles islands (de la Cruz, 2001; Miller & Miller, 2001; Ricklefs & Bermingham, 2008). Migration from the Lesser to the Greater Antilles is not easy because the prevailing north-eastern winds carry the species out to the ocean where they can not survive (Simpson, 1894; Buskirk, 1985; Ricklefs & Bermingham, 2008).

Mesoamerica

Mesoamerica or the Mexican Transition Zone (MTZ) is one of the most complex biogeographical areas in the world due to the confluence of Neotropical and Nearctic biotas. The MTZ includes the south-western USA, Mexico and Central America except Costa Rica and Panama. This region exhibits a long history of geological activity that created barriers and land bridges, which affected the distribution of the biota (Huidobro *et al.*, 2006; Lundberg *et al.*, 2007; Ornelas-Garcia *et al.*, 2008). Despite its geological and biological importance, few studies deal with the biogeography of the taxa of this region. The main emphasis has been on distributional patterns of selected terrestrial taxa like beetles, while only scant information on freshwater organisms exists (Huidobro *et al.*, 2006). It is supposed that in the Late Cretaceous or early Cenozoic, several South American ("Old Southern") groups of reptiles, amphibians and freshwater fishes migrated into Middle America through island arcs developing (and drifting eastward) on the Caribbean plate, which may have functioned as land bridges or stepping-stones between the Americas (Huidobro *et al.*, 2006; Lundberg *et al.*, 2007; Ornelas-Garcia *et al.*, 2008).

Freshwater cerithioidean

Concerning freshwater cerithioideans, the multiple origins and distribution of cerithioidean freshwater taxa, together with fossil evidence (dating back to at least the Cretaceous), suggest that the separation of Pangaea into Laurasia and Gondwana about 200 Ma ago may have played a critical role in their distribution and phylogeny (Lydeard *et al.*, 2002). For the Greater Antilles, Simpson (1894) established that if a land connection had existed between the islands and Central America during a period of elevation, it would have not been difficult for species of *Pachychilus* and *Hemisinus*, which are numerous and diverse

on the continent, to pass from the continent to the islands, or to spread across the islands. Simpson (1894) also noted that some species of Hydrobiidae, Physidae and fresh water bivalves are shared by the islands and the continent, but no species of Pachychilidae and *Hemisinus*.

3. General material and methods

3.1 Material

This study is based on the examination of alcohol material collected between 2005 – 2008 in Mexico, Central America, Great Antilles and northern South America from several sources. All the samples were preserved in 75 – 95% ethanol and constitute the material on which molecular, histological and anatomical studies were performed. Supplementary dry and alcohol material from the Academy of Natural Sciences (Philadelphia), National Museum of Natural History (London), Florida Museum of Natural History (Gainesville), Geowissenschaftliche Sammlung der Universität Bremen, Museum of Comparative Zoology – Harvard University (Cambridge), Muséum d'Histoire Naturelle (Genève), Muséum National d'Histoire Naturelle (Paris), Museu Nacional da Universidade Federal do Rio de Janeiro (Brazil), National Museum of Natural History – Smithsonian Institution (Washington D.C) and Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität zu Berlin were examined as well. For the species revision most of the types were studied.

3.2 Morphology and morphometry

The gross morphology of adult shells and opercula from all the samples were studied under a Leica MZ 95 stereo microscope with *camera lucida*. Features like shell shape, color, aperture form and presence or absence of sculptural elements were described. Pictures of the front and back side of each shell were taken with a digital camera Canon EOS 350D. Drawings and pictures were processed with Adobe Photoshop CS3. Regarding the ovoviviparous/viviparous species, juvenile shells were taken from the female brood pouch, cleaned first on chloride – distillate water baths followed by ultrasound, mounted on adhesive carbon pads and coated with gold-palladium for observation with a LEO 1450VP scanning electron microscope.

As differences in shape between individuals can be produced by a variety of biological processes like disease, injury, adaptation to local geographic factors or long-term evolutionary diversification among others (Zelditch *et al.*, 2004), we used traditional morphometrics in order to compare different populations of the same species, or geometric morphometrics to discriminate one species from other (see details under statistics). In both cases, for each adult shell from our samples and from different museum collections, were measured in millimeters the shell height (h), shell width (w), width of aperture (wa), length of aperture (ha), length of the last whorl (lwl) and length of the last three whorls (ltw), using callipers to 0.1 mm according to Glaubrecht (1996) (Fig. 1a). The

number of whorls (wn) was also registered. For the embryonic shells the diameter of the initial whorl as well as the total height and width were measured also in millimeters by SEM (Fig. 1b-c).

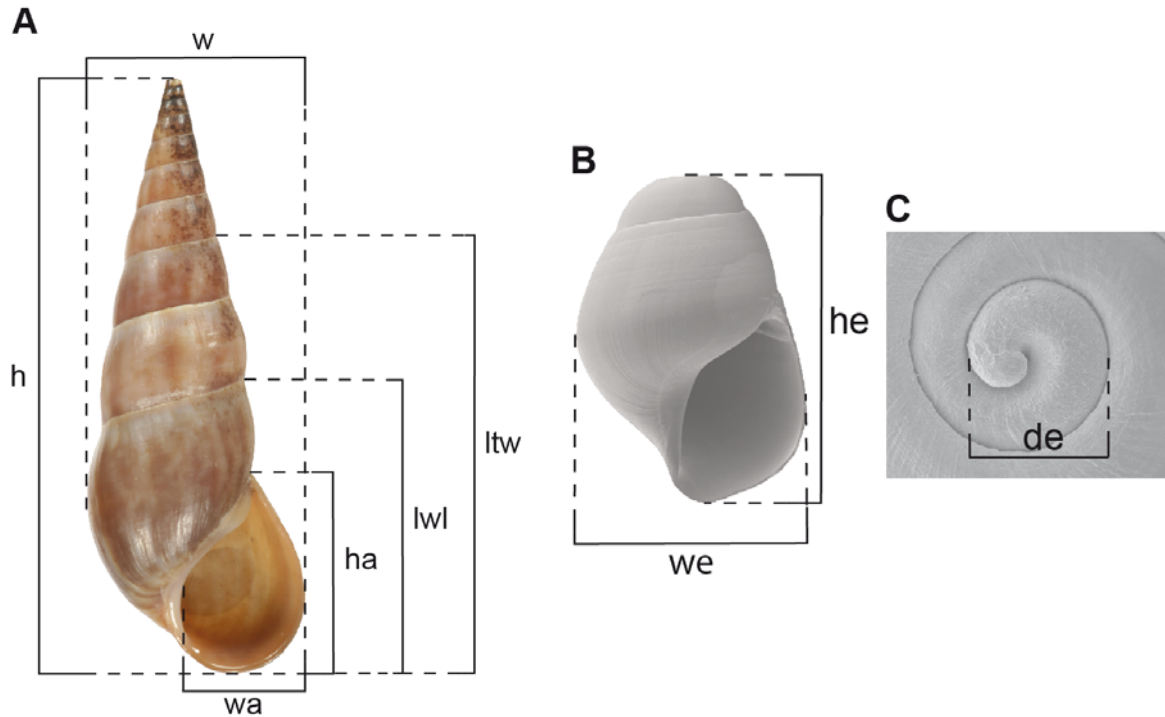


Fig. 1 Adult shell and protoconch measurements.

A. Adult shell; B. Embryonic shell; C. protoconch. Abbreviations: de, diameter of the initial whorl of embryonic shell; h, shell height; he, embryonic shell height; la, length of aperture; ltw, last three whorls; lwl, length of the last whorl; w, shell width; wa, width of aperture; we, embryonic shell width.

3.3 Anatomical and histological methods

Soft bodies preserved in 75% ethanol were used for anatomical and histological analysis, radulae extraction and embryonic shell observations. Anatomy was studied using a stereomicroscope (see above) and drawings were done.

For observations of soft structures using scanning electron microscopy (SEM) we applied the Hexamethyldisilazane (HMDS) method, replacing the ethanol preservation medium with HMDS, which is subsequently evaporated (Nation, 1983; Barré *et al.*, 2006). The preserved snails in 75% ethanol were dissected in order to expose the stomach and the brood pouch and then dehydrated through five minutes baths in increasing ethanol concentrations (80%, 95%, 100%), and 100% HMDS at the end. Finally, the samples were air dried at room temperature over night and mounted on aluminum stubs with adhesive carbon pads. The tissues were immediately coated and observed with SEM (see above).

The complete male and female bodies, as well as the isolate male and female pallial gonoducts, were histologically studied. Females containing embryonic shells in the brood pouch were decalcified in successive solutions of 7% nitric acid (HNO₃, three days), sodium sulphate (Na₂SO₄, one day) and distilled water (one day) before paraffin inclusion (Romeis, 1989). Specimens were dehydrated and paraffin-embedding using an automatic Shandon Hypercenter XP 167506S. Slide sections of 12 µm were cut with a Leica SM 2000R microtome, stained with haematoxylin/eosin and preserved with Canada balsam. Histological cuts were observed with a confocal microscope (Prog/Res 3012) and photographed.

The radula was extracted and enzymatically cleaned using K-proteinase as described by Holznagel (1998), sonicated and then mounted on aluminum specimen stubs with adhesive pads, and then coated for SEM examination. The number of teeth rows was counted and the tooth formula was described as follows: 1) rachidian (number of left side cusps/ median denticle(s)/ number of right side cusps); 2) lateral teeth (inner cusps/ pronounced denticle/ outer cusps); 3) marginal teeth (number of cusps on inner marginal tooth + number of cusps on outer marginal tooth) (Glaubrecht, 1996).

3.4 Molecular methods

The molecular procedure, the sequence alignment and the phylogenetic analysis were carried out by co-workers of the molecular laboratory of the Museum of Natural History – Humboldt University (Berlin) according to the following protocol. Genomic DNA was isolated from about 1-3 mm³ muscle tissue using a CTAB extraction protocol (Winnepeninckx *et al.*, 1993). Muscle tissue was dried, cut into small pieces and macerated in CTAB buffer containing proteinase K. Fragments of the mitochondrial 16S rRNA (~ 862 bp for *Pachychilus* spp. and ~ 890 bp for Thiariadae) and COI (660 bp for *Pachychilus* spp. and 660 bp for Thiariadae) genes were amplified by polymerase chain reaction (PCR) using specific primers (Table 1). Amplifications were conducted in 25 µL volumes containing 50-100 ng DNA, 1x PCR buffer, 200 mM of each dNTP, 0.5 mM of each primer, 2 mM MgCl₂ and 1 U of Taq polymerase. After an initial denaturation step of 3 min at 94°C, 35 cycles of 30 sec at 94°C, 60 sec at 40-45°C (COI) or 50°C (16S rRNA) and 60 (90 for COI) sec at 72°C were performed, followed by a final extension step of 5 min at 72°C. PCR products were purified using NucleoSpin Extract II Kits (Macherey-Nagel). Both strands of the amplified gene fragments were cycle-sequenced using the primers employed in PCR with Big Dye Terminator chemistry version 1.1 (Applied Biosystems Inc.). Sequences were visualized on an Applied Biosystems 3130xl Genetic Analyser.

Table 1. Mitochondrial primers used in this study. M = A or C, Y = C or T and R = A or G.

Primer	Sequence (5'-3')	Source
COI		
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> , 1994
HCO2198var	TAWACTTCTGGGTGKCCAAARAAT	von Rintelen <i>et al.</i> , 2004
16S rRNA		
16S F Thia	CTTYCGCACTGATGATAGCTAG	This study
H3059var	CCGGTYTGAAGTCAGATCATGT	von Rintelen <i>et al.</i> , 2004

3.5 Alignment and phylogenetic analyses

Forward and reverse strands were assembled with CodonCode Aligner v. 2.0.6 (CodonCode Corporation, Dedham, MA, USA). 16S rRNA sequences were aligned using ClustalX v. 2.0.3 (Thompson *et al.*, 1997; default settings) and corrected by eye. Substitution models (Table 2) for Bayesian inference (BI) analyses were estimated with MrModeltest v. 2.3 (Nylander, 2004). Two of four hierarchical likelihood ratio tests implemented in MrModeltest v. 2.3 selected HKY + I + Γ as the best-fit model for both 16S rRNA and COI for all studied taxa. This model was also selected by the Akaike information criterion (AIC). Phylogenetic analyses were performed using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003; BI parameters: 5,000,000 generations, sample frequency = 1.000, no. of chains = 4, burnin value = 2.500).

Table 2. Substitution models selected by MrModeltest v. 2.3.

I = proportion of invariable sites, Γ = gamma distribution shape parameter. I and Γ values refer to the AIC.

Gene	Substitution model	Among-site rate variation		Base frequencies			
		I	Γ	A	C	G	T
<i>Pachychilus</i> spp.							
COI	HKY	0.5423	0.8113	0.2849	0.1570	0.1680	0.3901
16S rRNA	HKY	0.4196	0.9077	0.3670	0.1098	0.1666	0.3566
Thiaridae							
COI	HKY	0.5879	0.7068	0.3139	0.1532	0.1261	0.4068
16S rRNA	HKY	0.3996	0.7762	0.3888	0.1198	0.1339	0.3575

3.6 Statistics

Since differences in shell size and shape have been observed between samples of the same species, I used traditional morphometry for testing if such differences were different than the expected ones due to natural variation within species or not. I performed principal component analysis (PCA) and graphic comparisons employing SPSS (version 11.5) and PAST (PALaeontological STatistics, version 1.67).

Principal component analysis (PCA) is a procedure for finding hypothetical variables (components) which account for as much of the variance as possible in a multidimensional data set. These new variables are linear combinations of the original variables and usually, the first two components accounted most of the variance or the “most important” aspects of the data. The analysis offers the possibility of reduce a data set to only two variables (the principal components) both for plotting and clustering purposes (Hammer *et al.*, 2007). The components can be extracted from either the variance-covariance or the correlation matrix of the measurements, depending on the data type. The PCA routine finds the eigenvalues, or the constant resulting from the linear transformation of the data set matrix for each variable (Davis, 1986; Korn & Korn, 2000). In order to know how many principal components should be considered significant, the Jolliffe cut-off value can be used (Jolliffe, 1986).

To standardize the data matrix for PCA analysis I used the above described shell measurements (h, w, wa, la, lwl and ltw) in millimeters and the whorls number (wn). For standardizing of the data, I made first a linear regression of the raw data and constructed the PCA matrix with the residual values resulting from the regression (Jordaens, *com. per.*). As the variables were standardized, the PCA was performed based on the variance-covariance matrix. After determining the two variables responsible for much of the variance in the data set, scatterplot and biplot graphics were constructed in order to compare intra and interspecific variation.

Geometrical morphometrics methods were applied in order to discriminate species. Morphometrics is a simple quantitative manner of addressing shape comparisons and allows to visualize differences among complex shapes on an easiest way. In the morphometrics context, shape is defined as “... all the geometric information that remains when location, scale and rotational effects are filtered out from an object...” (Zelditch *et al.*, 2004). On geometric morphometrics, the distances of the traditional morphometrics are replaced with landmark coordinates and a centroid size is established. The Landmarks are defined as discrete anatomical loci that can be recognized as the same loci in all specimens in the study, whereas the centroid size is the distance between each landmark and the centroid (location of the centre of the form) (Zelditch *et al.*, 2004).

In order to differentiate shell shapes, a Fourier outline shape (FOS) analysis was performed. FOS is a powerful tool for the morphometric study of two-dimensional form in organisms lacking many biologically homologous landmarks. This analysis takes an outline contour, described it as a polygon of digitized xy-coordinates, and “decomposes” this into a weighted sum of sine and cosine functions (Haines & Crampton, 2000; Allen, 2006). On each shell picture (fronts), the outline was digitalized using the tpsDig2 Program (Rohlf, 2004) and the data saved as coordinates on an x-y plane. This new set of data was analyzed by mean of the programs HANGLE, HMATCH and HCURVE. The first program outputs the Fourier coefficients derived from one or more input files of digitized outline traces. The second program normalizes the Fourier coefficients of each outline for orientation and starting position of the trace, based on properties of the given population of outlines, and the third program performs the inverse Fourier transform and is used to reconstruct outlines from one or more files of Fourier coefficients (Crampton & Haines, 1996). With the results of these three analyses, comparisons with PCA can be performed in order to discriminate species.

3.7 Abbreviations

3.7.1 Museum codens list

The following is the Museum codens list of the supplementary dry and alcohol samples examined:

ANSP – Academy of Natural Sciences, Philadelphia.

BMNH – National Museum (Natural History), London - (formerly British Museum of Natural History).

FLMNH – Florida Museum of Natural History, Gainesville, Fla.

GSUB – Geowissenschaftliche Sammlung der Universität Bremen.

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

MHNG – Muséum d’Histoire Naturelle, Genève.

MNHN – Muséum National d’Histoire Naturelle, Paris.

MNRJ – Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil.

USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.

ZMB – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität zu Berlin.

3.7.2 Anatomy

amf	accessory marginal fold	m	mantle
b	bladder	mep	mantle edge papillae
bd	body wall	mf	marginal fold
bm	buccal mass	mo	mouth
bp	brood pouch	oes	oesophagus
bpp	brood pouch porus	op	operculum
c	caecum	os	osphradium
cg	cerebral ganglia	pe	pedal ganglia
cr1	inner crescentic ridge	Pc.	protoconch diameter
cr2	outer crescentic ridge	pg	pallial gonoduct
ct	ctenidium	pl	pleural ganglia
cu	cuticle lining stomach roof	post.	posterior
dg	digestive gland	sa	sorting area
dgd	digestive gland duct	sb	sub-oesophageal ganglion
f	foot	SD	standard deviation
go	gonad	sg	salivary glands
gp	glandular pad	sn	snout
gs	gastric shield	sp	supra-oesophageal ganglion
h	shell height	ss	style sac
hg	hypobranchial gland	stc	statocyst
ht	heart	sto	stomach
int	intestine	t1	major typhlosole
j	juvenile	t2	minor typhlosole
kd	main kidney chamber	w	shell width
la	aperture height	wa	aperture width
ltw	last three whorls	wn	whorls number
lwl	last whorl length		

3.7.3 Glossary of special terms

Accretion: Process by which material is added to a tectonic plate.

Aptian: Faunal stage of the Early Cretaceous epoch that extends from 125.0 ± 1.0 Ma to 112.0 ± 1.0 Ma approximately.

Aves Ridge: Narrow, northeast trending ridge that crosses the eastern Caribbean northward from the Venezuelan shelf margin, towards the Virgin Islands.

Back-arc basins: Basins associated with tensional forces at some convergent plate boundaries. They develop where island arcs are split longitudinally, roughly along the line of the magmatic axis, forming a rift that matures to the point of seafloor

spreading, thus allowing a new magmatic arc to form on the trenchward side of the basin.

Cayman Ridge: An incomplete finger-like ridge that extends from the southern part of Cuba toward Guatemala, rising above the surface to form the Cayman Islands.

Cayman Trough: Depression area on the seafloor of the Caribbean that extends from the Belize margin to northern Jamaica. The northern boundary of the Caribbean tectonic plate is located along the Cayman Trough.

Chortis Block: A rock mass situated in northern Central America (between Honduras and Nicaragua), which is the only continental part of the present day Caribbean Plate.

Crust: The outermost solid shell of a planet or moon, which is chemically distinct from the underlying mantle.

Farallon Plate: An ancient oceanic plate which began subducting under the west coast of the North American Plate as Pangaea broke apart during the Jurassic.

Galapagos hotspot: A volcanic hot-spot in the East Pacific Ocean responsible for the creation of the Galapagos Islands. The hotspot is located near the Equator on the Nazca Plate not far from the divergent plate boundary with the Cocos Plate.

Havana-Matanzas Channel: Lower-Middle Miocene water channel across western Cuba (Havana-Matanzas) that connected the Atlantic Ocean with the Caribbean Sea.

Maya Block: or Yucatan Block is an independent rock mass which comprises Guatemala north of the Motagua transform fault, Belize, and part of southern Mexico.

Nicaraguan Rise: A wide triangular ridge with a sill depth of about 1.200 m which extends from Honduras and Nicaragua to Hispaniola, bearing the island of Jamaica and separating the Cayman Basin from the Colombian Basin.

Paleogeography: Branch of geography that studies the earth's geography during past geological periods.

Ridge: An elevated area of the sea floor in the center of an ocean basin with rugged topography. Ridges generally stand about 1.000 m to 3.000 m above the adjacent ocean floor and are about 1.500 km in width.

Shelf: Extended perimeter of each continent and associated coastal plain.

Subaerial: "under the air", events or structures located at the Earth's surface.

Transtension: Term used to describe a rock mass or area of the Earth's crust that experiences deformation usually by compressive stress.

4. Thiaridae in the Greater Antilles

4.1 A West Indian enigmatic native: Redescription and anatomy of the ovoviviparous freshwater gastropod *Hemisinus lineolatus* Wood, 1828 (Cerithioidea, Thiaridae) endemic to Jamaica.

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Abstract

The peculiar geological history and geography of the West Indian islands provide the background that makes high biological diversity possible. Invertebrates are not an exception, although the lack of comprehensive studies for most of these groups have hampered many insights into their systematics and biogeography. Given its otherwise high suitability of freshwater gastropods as model organisms in evolutionary biology, the lack of actual data is in particular pronounced in the cosmopolitan Thiaridae that have in this archipelago representatives attributed to *Hemisinus*. Hitherto, this taxon represented by the type species *H. lineolatus* from Jamaica, has only been described on the basis of the shell (as the genus itself was originally founded on shell characteristics alone). Here we present morphological, anatomical and other biological data for the type species, using type and other material from museum collections and field samples. We found that *H. lineolatus* exhibits typical features of the Thiaridae (e.g. operculum, radula, mantle papillae), but also has particular characteristics (such as a short and anterior osphradium and a midgut with a shallow caecum where the crescentic ridge does not enter). In addition, *H. lineolatus* is endemic to Jamaica, with anatomical differences between populations. As morphological and anatomical evidence suggest a basal position of the genus within the family, implications of these results for the systematics and biogeography of Neotropical freshwater Cerithioidea are discussed.

Introduction

Ever since Darwin's (1859) and Wallace's (1876, 1880) epochal insights, the fauna of islands and their affinities to related forms on adjacent continents have figured prominently in the study of evolution, ecology and biogeography, while research on islands has contributed substantially to our understanding of speciation, radiation and extinction (Whittaker, 1998; Whittaker & Fernandez-Palacios, 2007). With classical textbook examples discussed in context, for example, with dispersal (e.g. Darlington, 1938; Hedges *et al.*, 1992; Glor *et al.*, 2005) and vicariance (e.g. Rosen, 1975; Buskirk, 1985), the West Indian archipelago have been considered a laboratory of biogeography and evolution (Ricklefs & Bermingham, 2008), as its islands are inhabited by distinct endemic forms in many groups of organisms, and are sufficiently isolated but also close enough to each other and the mainland to allow a dynamic interaction with the continent.

The peculiar geological history and biogeography of the West Indies provide the background and causation of its rich diversity of organisms and species numbers (Buskirk, 1985; Iturralde-Vinent & MacPhee, 1999). The archipelago is composed of three groups of islands: the Greater Antilles, the Bahamas and the Lesser Antilles. The Greater Antilles are relatively old islands, primarily formed of fragments of continental crust, where many elements of the endemic biota have accumulated over much of the Cenozoic (Hedges, 2001; Ricklefs & Bermingham, 2008).

Jamaica, one of the Greater Antilles, is the third largest island in the Caribbean. It is situated about 145 km south of Cuba and as most of the islands of the region, its platform is remarkably dynamic on an evolutionary time scale. The formation of Jamaica (simultaneous with the southern portion of Hispaniola) was already initiated during the development of the proto-Antilles (Late Cretaceous), but remained isolated throughout its history (Hedges, 2006). The Island was completely submerged during the Late Eocene and reached its maximum uplift in the Blue Mountains during the Late Miocene-Pliocene (Russell-Hunter, 1955; Buskirk, 1985; Mitchell, 2006; Whittaker & Fernández-Palacios, 2007). Jamaica's relief is determined by a mountainous backbone that extends across the island from the west and rises to the Blue Mountains in the east. In the west it exhibits a rugged area deeply dissected by streams and underlain by subterranean rivers. The Rio Grande and the Black River are the country's chief waterways, but neither is navigable for long distances.

Although it is generally agreed that no land connections ever linked the Greater Antilles to Florida, land bridge theories that link either the Honduras peninsula of Central America or

continental South America to the Antillean region, were suggested in an attempt to explain the origin of the island's unique biota (Aguayo, 1938; Russell-Hunter, 1955; Iturralde-Vinent & MacPhee, 1999). For example, Aguayo (1938) speculated on a migratory "wave" from Honduras-Nicaragua to Jamaica at the end of the Cretaceous or beginning of Eocene, when the Antilles were colonized by terrestrial groups as well as freshwater gastropods ("melanids") and bivalves ("unionids"). Buskirk (1985) suggested that Jamaica was colonized mainly by groups of Central American origin, which settled there before invading other Antilles islands, based on evidence from vertebrate fossil assemblages and flowering plants from the Greater Antilles, as well as on the presence of three endemic monotypical genera of Scarabaeinae, Xenodontinae snakes, *Sphaerodactylus* geckos, anguid and *Anolis* lizards on Jamaica, which all have nearest mainland relatives in Central America but not on other Antilles.

It was also suggested that adaptive radiations took place on Jamaica during the Late Miocene and Pliocene, which are well documented for *Anolis* lizards, *Eleutherodactylus* frogs and grapsid crabs. Lizards exhibit several geographic variants, considerable intraspecific variation in chromosome number and a significantly divergence in morphology and ecology to be convergent with species on other islands (Hedges & Burnell, 1990). Most of the frog species are terrestrial in habit and have retained primitive morphological features associated with that lifestyle (Hedges, 1989). Grapsid crabs also show exceptional adaptations to a terrestrial mode of life that include the only active brood-care for larvae and juveniles known in crabs (Schubart, Diesel & Hedges 1998; Schubart, Reimer & Diesel, 1998). In addition, the operculated land shell fauna of Jamaica appears to be the most varied and peculiar among the archipelago (Bland, 1866; Rosenberg & Muratov, 2005).

Accordingly, Jamaica has both geology and faunal composition sufficiently different from those of the other Greater Antilles to the extent that it is considered to be one Caribbean region by itself due to its high proportion of endemic forms (Bland, 1861; Buskirk, 1985; Iturralde-Vinent and MacPhee, 1999).

Traditionally, invertebrates are underrepresented in many biological studies, such as e.g. on phylogeography (cf. Beheregaray, 2008). In particular, molluscs are not an exception, and the lack of comprehensive studies for most of its groups have hampered many insights into their systematics, evolution and biogeography (e.g. Glaubrecht in press). Despite Jamaica being well known due to its natural richness and its central position for Caribbean biogeography, its molluscan fauna has received but little attention. Our

knowledge, mainly based on 19th century's naturalists like Adams, Chitty, Bland and Binney who, among others, published many valuable papers on land- and freshwater-snails from the West Indies, has hardly increased since. These studies, however, omitted to record the localities other than simply "Jamaica" and the special habitats of its species, but suggested a profuse number of species names and descriptions based solely on shells (see e.g. Vendryes, 1899). In contrast to Jamaica's unique land snails fauna, it was assumed that the freshwater molluscs mainly belong to cosmopolitan genera, with exceptions only among species of ampullariid and melaniid freshwater gastropods, for which, however, congeners are found in continental America (Simpson, 1894; Russell-Hunter, 1955; Rosenberg & Muratov, 2005).

Given the otherwise high suitability in particular of freshwater gastropods as model organisms in evolutionary biology and biogeography (see e.g. Glaubrecht, 1996, 1999, 2000, 2006), the lack of data in the cosmopolitan Thiaridae Gill, 1871 is remarkable for West Indian representatives that have been attributed to *Hemisinus*. Hence, in order to shed light on the history of this genus in context with biogeographical studies, we in this paper aim to use an integrative approach of the shell morphology and the body anatomy of a thiarid originally described for Jamaica, viz. *Hemisinus lineolatus* Wood, 1828, which was later erected as type species of the genus.

On Jamaican thiarids

Although cerithioidean freshwater gastropods are one of the richest components of continental freshwater faunas in the tropical areas of the world (Glaubrecht, 1996; 1999, 2006), unfortunately, they are relatively poorly studied in the Neotropics. Some of the characteristics of Thiaridae are the possession of a paucispiral operculum with a small sub-terminal nucleus, a mantle edge with papillae and the presence of a head-foot brood pouch, as well as reproductive biology attributes such as parthenogenesis and various viviparous modes, including intramarsupial nourishment and giving birth to shelled juvenile (Glaubrecht, 1996, 2006). However, the group's monophyletic origin has been questioned since most of the subfamilies previously included in the Thiaridae are no longer placed there (see e.g. Houbrecht, 1988; Glaubrecht, 1996, 1999, 2006; Lydeard *et al.*, 2002).

Several extant genera in the Neotropics comply with the typical thiarid features described above. Among these genera, *Hemisinus* and *Aylacostoma* are traditionally considered as representatives of thiarids in this region. However, apart from nomenclatorial aspects (Cowie *et al.*, 2004), the limit between both genera remains to be clearly established. The same applies to those fossil shells that have been assigned to the Thiaridae due to

superficial resemblance (e.g. Nuttall, 1990). With a plethora of species being described, the taxonomy and systematics even of Recent representatives of Neotropical Thiaridae are based on shell features only. However, due to the lack of sufficient and adequately preserved soft body samples, the phylogenetic systematics remained unknown to date.

Following Swainson's 1840 description of the genus *Hemisinus*, based on "*Strombus*" *lineolatus* Wood, 1828, a variety of subgenera and synonyms have been assigned, comprising generally taxa inhabiting Central or South America. Therefore, subgenera such as *Hemisinus*, *Verena*, *Cubaedomus*, *Longiverena* and *Basistoma* (Chenu, 1859; Fischer, 1880-1887; Thiele, 1928; Pilsbry & Olsson, 1935; Morrison, 1951, 1954; Jaeckel, 1969), as well as species such as *Aylacostoma* (*Longiverena*) *tuberculata* Spix, 1827, *A. glabrum* Spix, 1827, *Verena crenocarina* Moricand, 1841, *Semisinus ruginosus* Morelet, 1849, *Basistoma edwardsii* Lea, 1852, *Hemisinus punctatus* Reeve, 1860 and *Hemisinus planigyris* Vernhout, 1914 are now considered part of the *Hemisinus* "group" (Chenu, 1859; Fischer, 1880-1887; Thiele, 1928; Pilsbry & Olsson, 1935; Morrison, 1951, 1954; Jaeckel, 1969). Consequently, the described distribution range of *Hemisinus*, initially restricted to Caribbean islands like Jamaica and Cuba progressively expanded since the mid 18th century to the inclusion of Central America, Peru, Venezuela, Surinam, Brazil and the Paraguay river (Reeve, 1860; Brot, 1862; Martens, 1873; Fischer, 1880-1887; Ihering, 1901, 1909; Vernhout, 1914). This view was followed even most recently by Simone (2006); see Fig. 1a.

In Jamaica two species of thiarids, viz. *Hemisinus lineolatus* and *H. buccinoides* Reeve, 1860, have been described based on their shell morphologies, and have been regarded as distinct by most subsequent authors (Reeve, 1860; Brot, 1862; Kobelt, 1882). Here we will present the results of comparisons of the adult shell morphology of both taxa and analyse the anatomy of mature individuals from different populations across Jamaica, which is critical for ongoing taxonomical and phylogenetic studies, in order to help clarifying the monophyly and systematic affinity of *Hemisinus* in the Neotropics and of the Thiaridae.

Specific materials and methods

Since Russell-Hunter's work (1955), it was established that the material on which any discussion of snail species in Jamaica can be based is still largely shell collections, which lack information on reproductive isolation, as well as on morphological, physiological and ecological differences. Then, the knowledge of the basic features of *Hemisinus*, will allow the performance of future comparative studies with other species that have been assigned

to the same genus, in order to define the distribution pattern of the group as well as clarify their taxonomical status.

This study is based on the examination of dry and alcohol material from the Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, London (BMNH); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) and Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität zu Berlin (ZMB). These museum collections are mainly composed of dead-shells collected on easily accessible areas like Montego Bay, Fern Gully, Bogwalk and the western and central parishes, while the eastern territories have been poorly sampled. According to Rosenberg & Muratov (2005), the same situation applies for the land snails fauna.

Shell morphometry of the type material from the BMNH and of specimens from other museum collections (see details under the species below) was estimated with callipers with a precision of 0.1 mm (see Glaubrecht, 1996 for details). Measurements include shell height (h) and width (w), aperture length (la) and width (wa), length of the last whorl (lwl), length of the last three whorls (ltw), and the number of whorls (wn).

Since differences in shell size and shape can be observed between the samples, we tested if such differences were different from the expected ranges caused by intraspecific variation. To standardize the data matrix for principal component analysis (PCA), we made a linear regression of each of the shell measurements described above using SPSS (version 15.0) and constructed a new matrix with the standardized residuals. Then, we performed a PCA analysis employing PAleontological Statistics (PAST) version 1.68 (Hammer, Harper & Ryan, 2001) in order to determine the two variables responsible for most of the variance in the data set. Finally, a scatterplot and a boxplot were constructed with the two variables resulting from the PCA, as a graphical way to compare the data.

Soft bodies preserved in 70% ethanol from the ANSP and ZMB collections, were used for anatomical and histological analyses, radulae extraction, and embryonic shell observations. The anatomy was studied using a stereo microscope and drawings were done using a *camera lucida*.

Complete male and female bodies, as well as the isolate male and female pallial gonoducts (ANSP 12087I, n = 4), were histologically studied. Two females (ANSP 12087H) containing embryonic shells in the brood pouch were decalcified in successive solutions of 7% nitric acid (HNO₃, three days), sodium sulphate (Na₂SO₄, one day) and

distilled water (one day), before paraffin inclusion (Romeis, 1989). Specimens were dehydrated and paraffin-embedded using an automatic Shandon Hypercenter XP 167506S. Slide sections of 12 µm were cut with a Leica SM 2000R microtome, stained with haematoxylin/eosin and preserved with Canada balsam. Histological cuts were observed with a confocal microscope (Prog/Res 3012) and photographed.

The radula was extracted and enzymatically cleaned using K-proteinase as described by Holznagel (1998), sonicated, mounted on aluminium specimen stubs with adhesive pads, and then coated for SEM examination as described above. The number of teeth rows was counted and the tooth formula was described as follows: 1) rachidian (number of left side cusps/median denticle(s)/number of right side cusps); 2) lateral teeth (inner cusps/pronounced denticle/outer cusps); 3) marginal teeth (number of cusps on inner marginal tooth + number of cusps on outer marginal tooth) according to Glaubrecht (1996).

Results

Systematics

Hemisinus Swainson, 1840: 199.

Strombus Wood, 1828: pl. 4, fig. 11.

Melania - Griffith & Pidgeon, 1834: pl. 13, fig. 4.

Melanopsis - Poey, 1851-1858: 399.

Melania (*Hemisinus*) Martens, 1873: 51.

Semisinus Fischer, 1880-1887: 701. Cossmann: 1909: 150.

Hemisinus (*Hemisinus*) Thiele, 1931: 201.

Aylacostoma (*Hemisinus*) Morrison, 1951: 9.

Taxonomic remarks.

At the generic level, Wood (1828) illustrated a series of shells from Asia and the Antilles under the genus *Strombus*, with specific names based on their most remarkable shell attribute. After that, the genus was split and some of the species were changed to *Melania* (Wood, 1829). In order to clearly delimit groups inside the family, Swainson (1840) erected the genus *Hemisinus* for shells characterized by the general *Melania* shape but with the base of the aperture contracted and emarginated, and with a crenated outer lip. Then Fischer (1880-1887) placed it into *Semisinus* (*semi* = half, *sinus* = notch), as an *emendation* of *Hemisinus* Swainson, 1840, while Thiele (1931) returned to the use of *Hemisinus* without any further explanations.

The genus *Tania* Gray, 1840 was listed as synonym of *Hemisinus lineolatus* not only by Gray but also by H. Adams & A. Adams (1858). However, as Iredale (1913) stated, Gray's publication of 1840 contained new generic names with scant diagnostic remarks, and concluded that *Tania* could not be treated other than a *nomina nuda*. Another common synonym of *Hemisinus* is *Haemisinus*, which was listed by Rotarides (1933) as synonym of *Fagotia* Bourguignat 1844 in a work on Pleistocene molluscs from Hungary. This corresponds to a geographical and taxonomical misplacing. Thus, we exclude *Tania* and *Haemisinus* from the synonym list of *Hemisinus*.

Diagnosis. Shell ovate-conic or turritiform, smooth or with faint growth spiral lines; colour yellow, green-yellowish or light brown, frequently with continuous or interrupted reddish-brown spiral lines; base of the aperture with a more or less conspicuous channel; the parietal callus is usually thin and in some species the upper part of the aperture is a little thickened. Operculum paucispiral, with a small sub-terminal nucleus. For further details see the respective species below.

Distribution. Jamaica. Similar shells traditionally attributed to *Hemisinus* also occur on Bahamas, Cuba, Guatemala, northern South America and Brazil (Fig. 1A).

Fossils. Fischer (1880-1887) established *Semisinus sulcatus* Conrad from the Cenozoic of South America as a fossil belonging to *Hemisinus*. According to Nuttall (1990), fossil shells from the Paleogene and Neogene of Colombia, Ecuador and Peru were also assigned to this genus.

***Hemisinus lineolatus* (Wood, 1828)**

Strombus lineolatus Wood, 1828: 13, pl. 4, fig. 11.

Melania lineolata – Wood, 1829: 31. Griffith & Pidgeon, 1833: pl. 13, fig. 4 [*non Melania lineolata* Gray in Griffith & Pidgeon, 1833: pl. 14, fig. 4]. Gray, 1847: 153. Philippi, 1848: 33, pl. 5, fig. 10. Reeve, 1860: pl. I. Jousseaume, 1889: 233. Cossmann, 1895-1924: 150. Morrison, 1954: 376. Vega & Perrilliat, 1992: 604.

Hemisinus lineolata – Swainson, 1840: 341.

Melanopsis lineolata – C.B. Adams, 1849a: 45. C. B. Adams, 1851: 187. Hanley, 1854-1858: pl. 4, fig. 29. Bland, 1861: 24. Orcutt, 1928: 12.

Melania (Hemisinus) lineolata – Martens, 1873: 51, 60.

Semisinus lineolata – Vendryes, 1899: 13.

Aylacostoma lineolata – Simone, 2006: 82, pl. 199.

Hemisinus lineolatus – Gray, 1857: 103. H. Adams & A. Adams, 1858: 302, pl.32, fig. 2 a-b. Chenu, 1859: 291, fig. 1995. Reeve, 1860: plate I, fig. 4a-b. Brot, 1862: 61. Brot, 1878: 373, pl. 38, fig. 6, 6a-e. Kobelt, 1882: 131. Johnson & Fox, 1891: 34. Henderson, 1894: 33. Ihering, 1901: 672. Ihering, 1909: 311. Vernhout, 1914: 36. Burrington-Baker, 1930: 30. Thiele, 1931: 201. Pain, 1956: 103. Nuttall, 1990: 239, figs. 224-226. Glaubrecht, 1996: 185.

Melanopsis lineata – Poey, 1851-1858: 399. Poey, 1856: 3.

Hemisinus buccinoides Reeve, 1860: pl. 1, fig. 3a, b.

Hemisinus (Basistoma) buccinoides – Brot, 1862.

Hemisinus lineolatus var. *buccinoides* – Kobelt, 1882: 131.

Semisinus lineolatus – Fischer, 1885: 702.

Melanopsis lineolatus – Vendryes, 1899: 13.

Hemisinus (Hemisinus) lineolatus – Thiele, 1928: 401. Thiele, 1931: 201. Wenz, 1939: 718, fig. 2075. Jaeckel, 1969: 814, pl. 3, fig. 70.

Aylacostoma (Hemisinus) lineolatum – Morrison, 1951: 9. Morrison, 1954: 376.

The authorship of the type species also has been differentially cited since Griffith & Pidgeon (1833-1834). Thus, *Hemisinus lineolatus* was attributed to Gray, to Griffith *in* Cuvier, to Gray *in* Griffith & Pidgeon, to Wood *in* Gray, or to Gray *in* Wood (Swainson, 1840; Poey, 1851-1858, 1856; Gray, 1847; Adams 1849a-b, 1851; Hanley, 1854-1858; Reeve, 1860; Brot, 1860, 1862, 1874-1879; Kobelt, 1882; Fischer, 1885; Fischer & Crosse, 1890-1892; Vendryes, 1899; Ihering, 1901, 1909; Vernhout, 1914; Orcutt, 1928; Thiele, 1928, 1929-1935; Morrison, 1951, 1954; Jaeckel, 1969).

Type locality. Wood (1828) gave no references about the exact locality of his illustrated *Strombus lineolatus*. Later, Phillipi (1842 - 1850) described a *Melania lineolata* (*Strombus*) Wood from Jamaica, that fits Wood and Swainson's description. Subsequent authors restricted the species distribution to Jamaica (Poey, 1851-1858, 1856; Adams, 1849a, 1851; Reeve, 1860; Bland, 1861; Arango y Molina, 1865; Brot, 1874-1879; Johnson & Fox, 1891; Henderson, 1894; Vendryes, 1899; Orcutt, 1928; Nuttall, 1990; Glaubrecht, 1996; Townsend & Newell, 2006). Reeve (1860) described as a new species *Hemisinus buccinoides* from Cuming's samples, but called Jamaica as type locality into question. Pain (1956) cited *H. lineolatus* for British Guiana and Surinam and remarked that the species is known from Jamaica but not from the rest of the West Indies, suggesting that its presence in Guiana might be an introduction by man from Jamaica. Yet Nuttall (1990) remarked that there is no evidence for this.

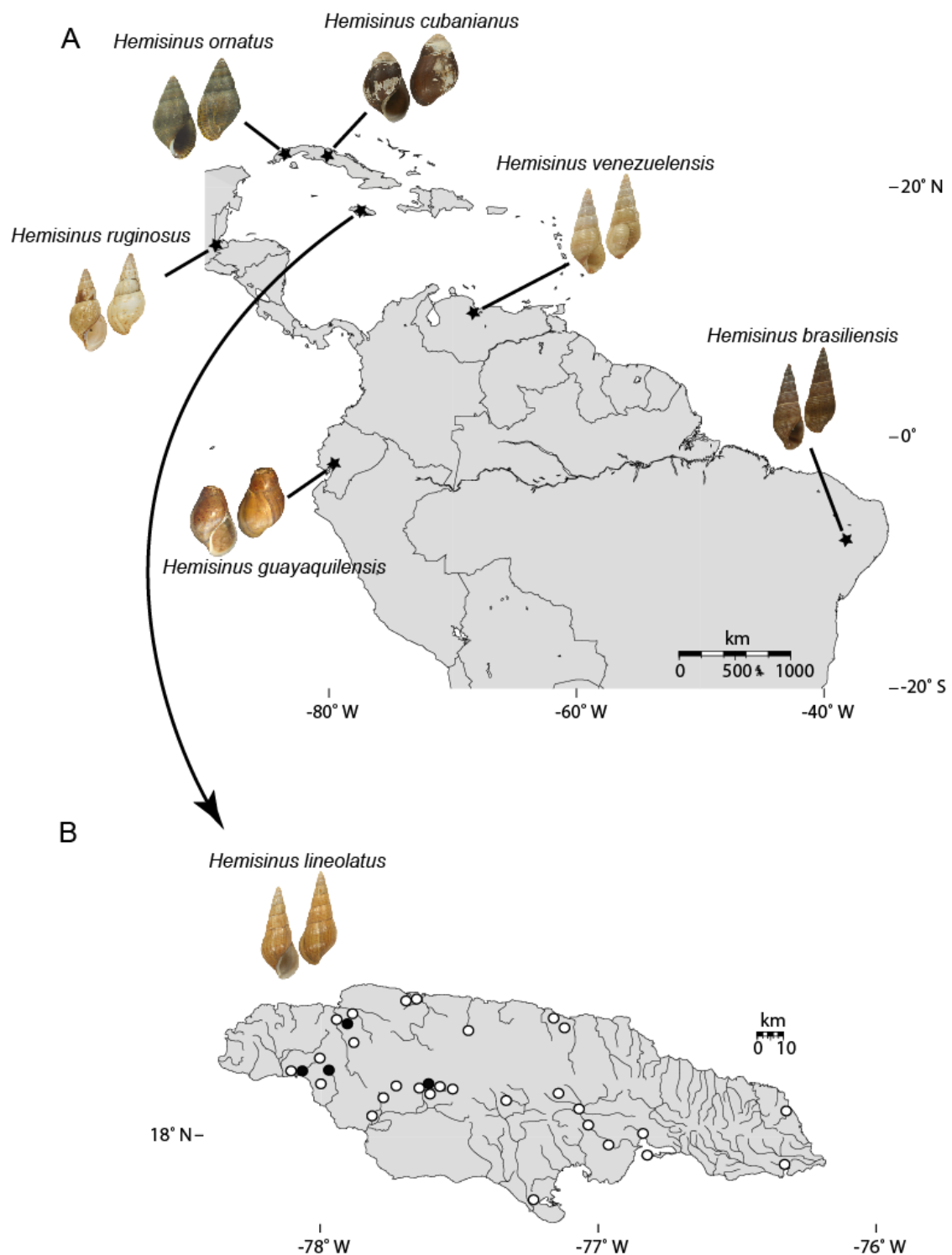


Fig. 1 A. Distribution of *Hemisinus* Swainson, 1840 in the Neotropics. Note that only few representatives are given for South and Central America. – B. Occurrence of the type species *Hemisinus lineolatus* Wood, 1828 on the Caribbean island of Jamaica; for the localities see text.
 o = museum shell material; ● = material preserved in alcohol examined for anatomy and histology.

Type material. Seven specimens are deposited at the BMNH (1984206/1-7) despite Nuttall (1990) referred that the same sample is composed by "... four unlocalized Recent shells...". They were originally labelled as "*Hemisinus lineolatus* Wood Type", from an unknown locality, belong to Gray Collection, but reinterpreted and accordingly re-labelled as "lectotype" and three "paralectotypes" by Nuttall (1990). The discrepancy in reported numbers of specimens herein (7) and in Nuttall (4) can be explained through a label with the specimens which states "Thought to be a lot of 4 shells, 3 smaller shells later found under cotton wool – CP Nuttall May 1995". Then, the number of specimens of the type series is originally seven and not four as Nuttall previously stated.

In Wood's *Index Testaceologicus*, shell dimensions are approximations to round inches. The shell figured by Wood is an inch and a half height (= 3.81 cm) and the biggest specimen of the type series of *H. lineolatus* from the BMNH is 3.97 cm (Fig. 2A). Then, according to its dimensions and appearance (same number of whorls, healed break above aperture), the BMNH specimen is the same illustrated in Wood's *Supplement to the Index Testaceologicus* (1828), and also the one illustrated by Griffith & Pidgeon (1834: pl. 13, fig. 4). According to Article 11.4.3 of the Code, names published before 1931 and included in an index to a work, are acceptable names if they satisfy the principle of binomial nomenclature and the provisions of the Articles 4, 5 and 6. As the name *Hemisinus lineolatus* complies these requirements and those of the Article 12.1, the name is available. In addition, as we can reliably trace the figure of Wood to a single specimen, the figured specimen consequently, is the holotype fixed by monotypy (Article 73.1.2). Since the holotype still exists, the Lectotype designation made by Nuttall is invalid.

One exemplar labelled as *Hemisinus buccinoides* Reeve, Holotype from Jamaica (BMNH 1984208) (Fig. 2B).

Other material examined. **Jamaica:** (ANSP 26797, 26800, 122992, 123029; BMNH 1845.9.16.63, 1857.12.1.1135, 36, 37, 39, 41, 20070080, 20070085; ZMB 113036, 113037, 113038, n = 70). Westmoreland: Savanna-La-Mar (USNM 792463, n = 3); Ditch near Savanna-La-Mar (USNM 127820, n = 2); Sweet River: near Savanna-La-Mar (USNM 127799, n = 8); Water Wheel (ANSP A12088A, A12088B; MCZ 195360, n = 10); Mackfield: Williamsfield Cave (BMNH 29.1.1907, n = 24); Mt. Pleasant (USNM 127821, n = 1). St. James: Anchovy Gully (ANSP A12087H, A12087I, n = 25); Great River (USNM 127827, n = 2); Great River, first falls from the mouth (ANSP 153283, 159740; ZMB 113039, n = 7); Great River, seven miles south of Montego Bay (USNM 792464, n = 3); Montpellier (USNM 168599, 453972, n = 4); Spring Mount: (ANSP 160299, n = 25), Montego Bay: Mt. Horibb (MCZ 88922, n = 4). St. Elizabeth: Route A-2 about 2 mi. NE

Middle Quarters (ANSP 375045, n = 11); Ipswich (USNM 168598, 453973, n = 11); Accompong River, Hole Cockpit (USNM 376369, n = 17); 3 miles north of Balaclava, Opfor Cave (USNM 374547, 396156, n = 9); Wallingford River (USNM 210911, n = 2); Balaclava (ANSP 226265, n = 2); Near Balaclava: Cave at sink of One Eye River (USNM 397352, 397082, 427066, 427096, n = 78); Harbor Shore, Black River (USNM 427037, n = 1); Black River (MCZ 172867, n = 12). Trelawney: Falmouth: Bush Cay (USNM 395818, n = 8); Near Westwood High School (USNM 399377, n = 1); Dornach River (ANSP 157713, n = 19). Manchester: One Eye River (USNM 374377, 375429, 375479, 398576, n = 62); Middlesex, Black River north of Oxford (ZMB 107126, n = 5); Oxford Cave: top of hill over Oxford Cave, 3 mile north (USNM 398577, n = 50). St. Ann: Rio Bueno, near Dornach Power House (USNM 395800, 427097, n = 13); St. Ann's Bay: Roaring River (ANSP 157714; USNM 127826, 453968, n = 46); Fern Gully (ANSP 160259; USNM 511960, 526273, n = 51). Clarendon: Frankfield (USNM 400639, n = 25); Rio Minho (USNM 395751, n = 11); Portland (MCZ 195361, n = 6). St. Catherine: 1 mile from Ewarton to Moneague (USNM 396044, n = 1); Bog Walk (ANSP 61889; BMNH 20070081; USNM 127351, 127822, 453971, 394750, 394861, 395486, 395529, 427094, 427095, n = 111); Bog Walk: Thomas River (USNM 427093, n = 31); Rio Cobre (ANSP 124742, 157271, 26798; USNM 700721, n = 79); Spanish Town: Canal drift (USNM 395743, n = 5). St. Andrew: Port Royal (USNM 442331, n = 1); Hunts Bay (USNM 378057, n = 1). Portland: Priestmans River (USNM 712035, n = 9). St. Thomas: Morant Bay (MCZ 115072, n = 8) (Fig. 1B).

Distribution. Although *H. lineolatus* is present on the entire island of Jamaica, and absent from the rest of the Antilleans, there are also lots of shells from Venezuela, Brazil and Barbados which resemble those of *H. lineolatus*.

Taxonomic remarks. The first name of the species was *Strombus lineolatus* (1828: pl. 4, fig.11), given by William Wood (b 1774 – d 1857) in a work reviewed by J.E. Gray. Later, Griffith & Pidgeon (1833-1834) described a *Melania lineolata* Gray (pl. 13, fig. 4, formerly *Strombus lineolatus*) from the BMNH collection, which presumably is the same specimen of Wood. Griffith & Pidgeon published a work on *Cuvier's Mollusca and Radiata*, where the volume on the molluscs is in part a translation of the second edition of the molluscan volume of Cuvier's *Le Règne Animal* (1830). According to Petit & Coan (2008), the molluscs included by Griffith & Pidgeon in the plates 13 and 14, among others, were supplied by the BMNH under the direction of J.E. Gray, but "... as Wood did not indicate



Fig. 2 A-B. Type material and accompanying original museum labels of taxa of *Hemisinus* Swainson, 1840 from Jamaica; for explanation see text.
 A. Holotype of *Strombus lineolatus* Wood 1828 (BMNH 1984206/1); – B. Holotype of *Hemisinus buccinoides* Reeve, 1860 (BMNH 1984208). Scale bar = 1 cm.

authorship of any species, no credit for any contribution Gray made is to be found among the new specimens name...”, and also “... unlike the Griffith & Pidgeon work, there are no discrete pages or plates in Wood that can be attributed to Gray alone, and so, under the existing Code, Wood is the author...”. This view was early proposed by Adams & Adams (1854-1858) and subsequently supported by Brot (1862), Martens (1873), Johnson & Fox (1891), Burrington-Baker (1930), Nuttall (1990) and Glaubrecht (1996). In agreement with them, and based on the Petit & Coan’s findings, we can consider Wood alone as the author.

Description

Shell. Medium sized; conic, turritiform spire with flattened whorls, thin but solid, usually with five to six whorls, apex not eroded. Body whorl inflated at the middle. Suture narrow and subsutural depression shallow, both forming a light colour band. Hammered surface conformed by faint axial and spiral growth lines. Colour green-brown or yellow-brown or sometimes dark brown to black, with reddish, spiral, interrupted bands in the entire shell. Aperture ovate, angled above, expanded below, inside white (Fig. 3).

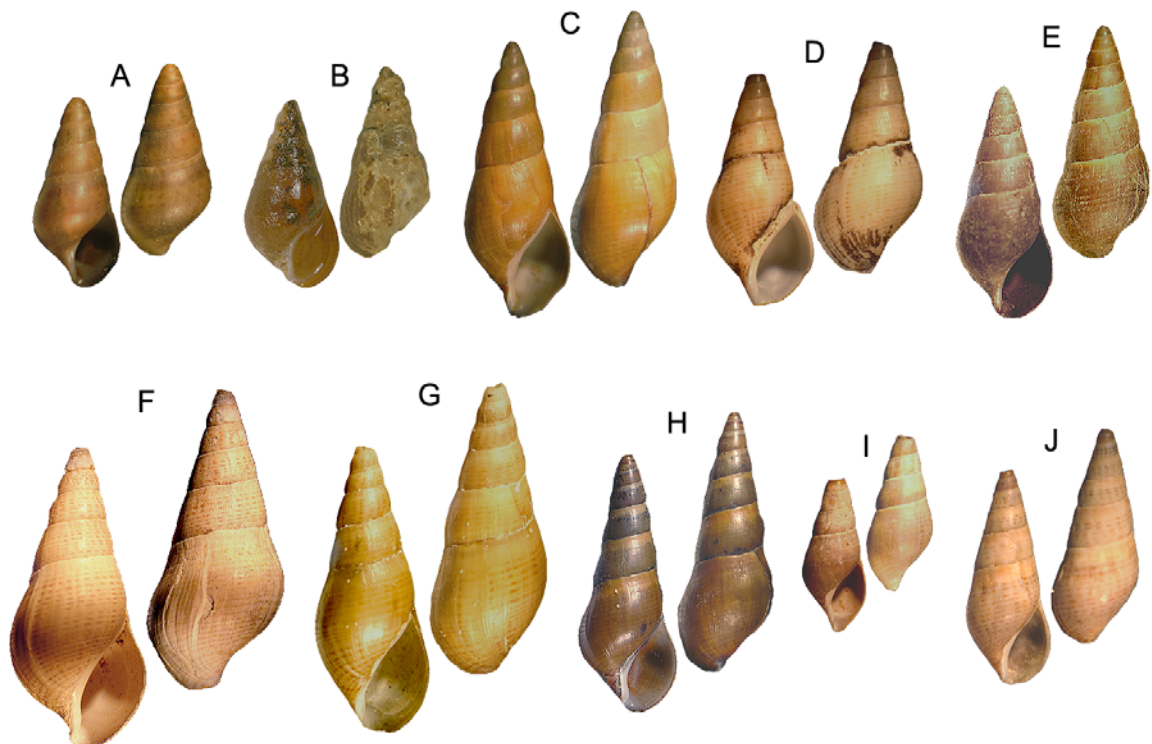


Fig. 3 A-J. Intra-specific variation in shell morphology of *Hemisinus lineolatus* from west to east Jamaica:

A. Westmoreland Parrish (USNM 127820); B. St. James Parrish (ANSP 120871); C. St. Elizabeth Parrish (USNM 397352); D. Trelawney Parrish (USNM 395818); E. Manchester Parrish (USNM 345479); F. St. Ann Parrish (USNM 395800); G. Clarendon Parrish (USNM 395751); H. St. Catherine Parrish (USNM 453971); I. St. Andrew Parrish (USNM 378057); J. Portland Parrish (USNM 712035). Scale bar = 1 cm.

Shell dimensions are given in Table 1. Through PCA analysis we found length of the last whorl (lwl) and shell height (h) as shape explanatory variables for *H. lineolatus*. No significant differences in shell shape were found along Jamaica. We further noticed that *Hemisinus buccinoides* shells correspond to the typical *H. lineolatus* shell shape (Figs. 4A-B).

Table 1. Range in millimetres of the shell measurements of the type specimens of *Hemisinus lineolatus* and *Hemisinus buccinoides*, as well of the Jamaican *H. lineolatus* from different museum collections.

Abbreviations: h, shell height; la, aperture height; ltw, last three whorls; lwl, length of the last whorl; w, shell width; wa, aperture width; wn, whorls number.

Species		h	w	wa	la	lwl	ltw	wn
<i>H. buccinoides</i> type (BMNH 1984208)		37.17	16.78	8.45	17.91	23.43	31.69	6
<i>H. lineolatus</i> type (BMNH 1984206/1)		39.78	16.19	8.20	16.50	23.31	32.30	9
<i>H. lineolatus</i> Jamaica (n = 874)	range	4.35 - 42.77	2.90 - 14.56	1.34 - 7.47	2.75 - 17.02	3.46 - 25.40	4.35 - 36.06	3 - 6
	mean	22.35	9.42	4.20	10.14	14.20	19.20	5.39
	SD	6.10	2.60	1.58	2.82	3.76	5.38	1.31

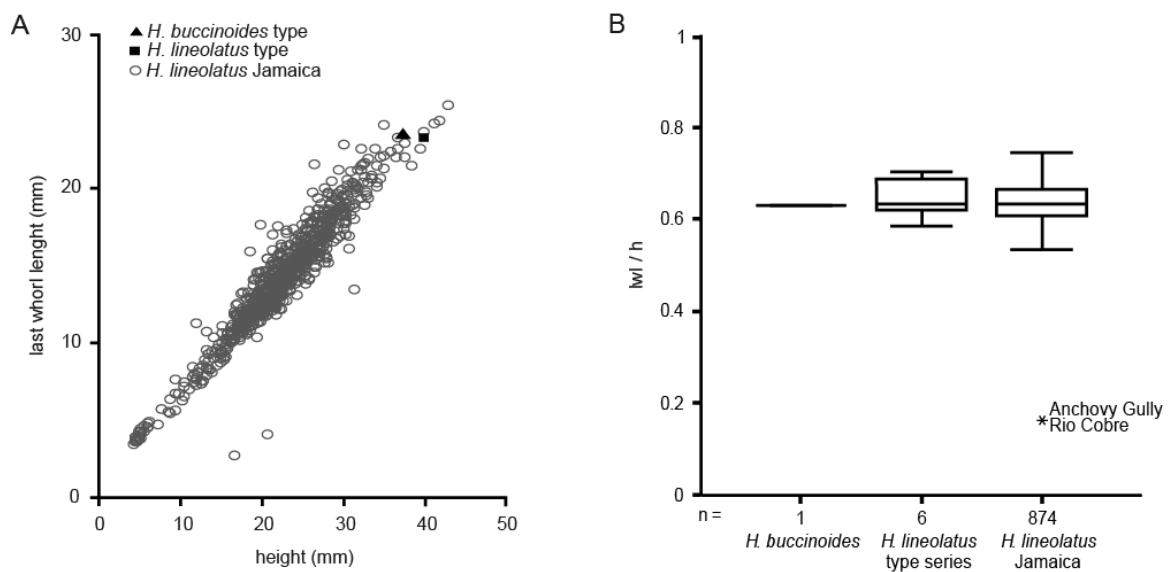


Fig. 4 A. Relation of shell last whorl length vs. total height of *Hemisinus* shells from Jamaica.

▲ = Holotype of *Hemisinus buccinoides* (BMNH 1984208); ■ = Holotype of *Hemisinus lineolatus* (BMNH 1984206/1); ○ = other material examined of *Hemisinus lineolatus* from Jamaica. – B. Boxplot of the relation between last whorl length (lwl) and total height (h) of *Hemisinus buccinoides* and *Hemisinus lineolatus* shells, with two outliers.

Embryonic shell. Juvenile shell (j) globose, smooth, faint growth and spiral lines, shallow suture, 2-3 whorls (Fig. 5A). Colour yellow or light brown. Protoconch with 1.5 narrow, smooth whorls (Fig. 5B-C). Morphometric variation is shown in Table 2. Differences in number of juveniles inside the brood pouch were found between populations of St. James parish (ANSP 12087I, H; n = 10) and from St. Elizabeth parish (ZMB 107126; n = 5).

Table 2. Range in millimetres, mean and standard deviation (SD) of embryonic shells obtained from the brood pouch of *Hemisinus lineolatus* females from Jamaica (n = 7).

Abbreviations: de, protoconch diameter; he, embryonic shell height; we, embryonic shell width.

<i>H. lineolatus</i>				
juveniles	he	we	de	
range	2.42 - 4.88	2.18 - 3.17	0.29 - 0.74	
mean	3.61	2.51	0.46	
SD	0.90	0.40	0.15	

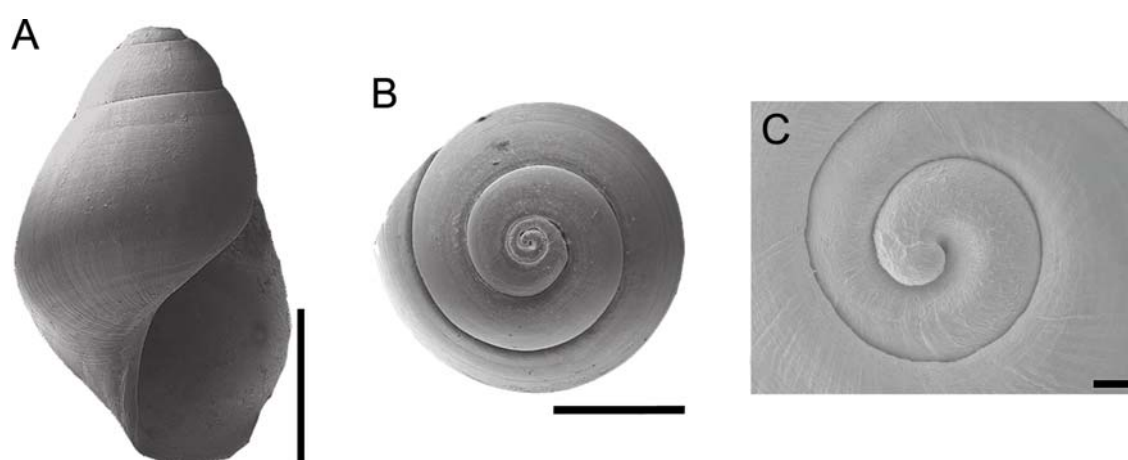


Fig. 5 A-C. Embryonic shell of *Hemisinus lineolatus* obtained from a brood pouch (ANSP 12087H).

A. Embryonic shell, apertural view, scale bar = 300 μm . – B. Embryonic shell, apical view, bar = 200 μm . – C. Initial whorl of embryonic shell, apical view, bar = 50 μm .

External anatomy. Operculum (op) ovate, quitinous, colour reddish-brown; paucispiral, with a small sub terminal nucleus of 2 whorls (Fig. 6A). Animal pale yellow, with brown or dark grey spots in tentacles, snout and anterior part of the foot. Snout (sn) short and broad. Tentacles broad at the base and narrow at the tips. Mantle edge (mep) with 13-21 papillae (n = 17; mean = 17; SD = 2.01) (Fig. 6B).

Mantle cavity. Ctenidium (ct) straight, long, narrow anteriorly and broad posteriorly. Osphradium (os) close to anterior part of ctenidium, curved, short, about one-third of the ctenidial length. In specimens from the Black River population (ZMB 107126, n = 5), the osphradium length is slightly more than twice the average osphradium length of those from the remaining island population. Hypobranchial gland (hg) well developed, thick, with

transverse grooves. Rectum (r) opening into a simple anus (a) close to the mantle edge (Fig. 6B).

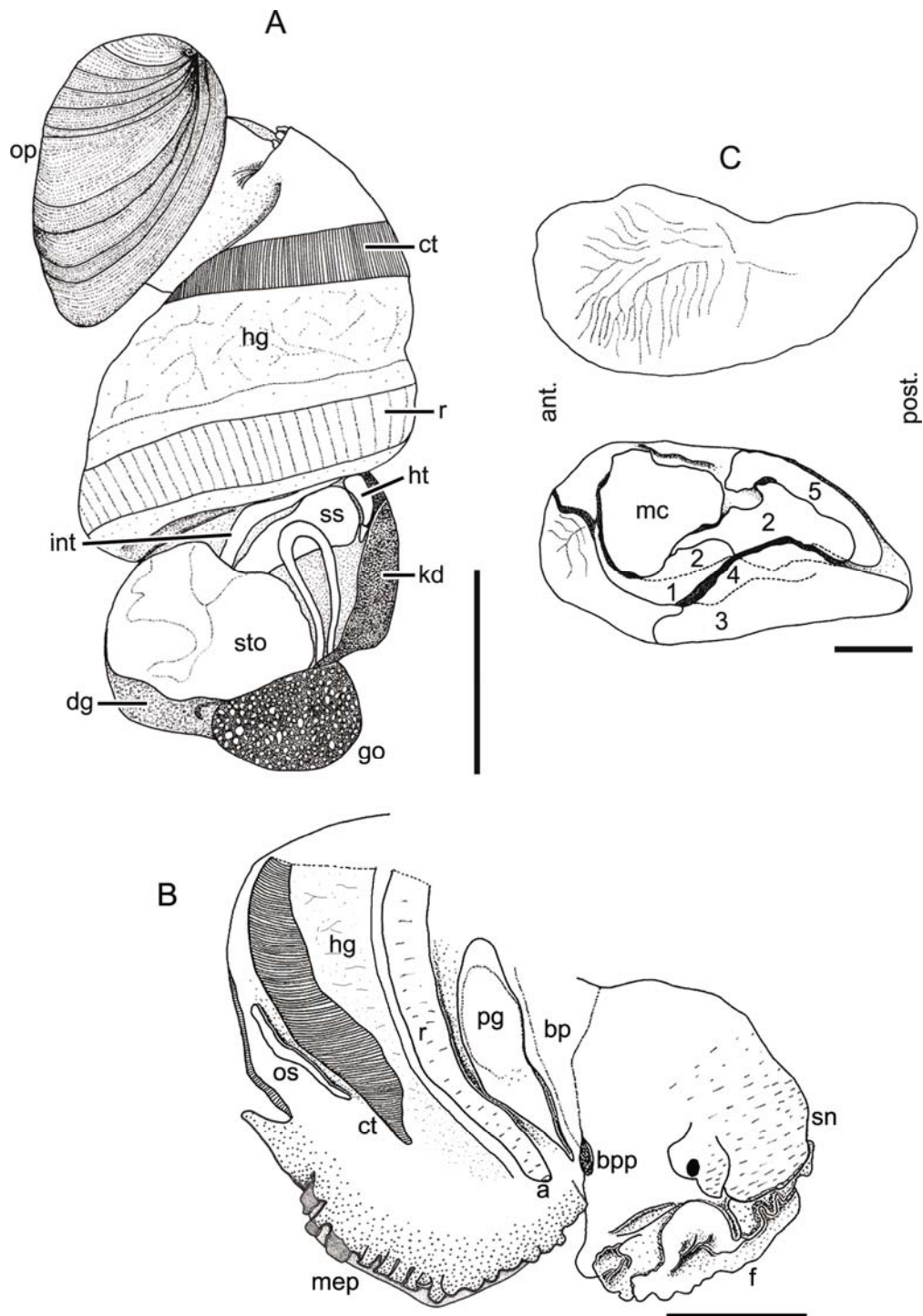


Fig. 6 A-C. Anatomy of *Hemisinus lineolatus* (Westmoreland, Jamaica, ANSP 12088A-B). A. External anatomy, ventral view; bar = 5 mm. – B. Anatomy of the mantle cavity and brood pouch; bar = 2 mm. – C. Kidney morphology, internal view (numbers 1 – 5 indicate lobes); bar = 1 mm. Abbreviations: a, anus; ant., anterior; bp, brood pouch; bpp, brood pouch porus; ct, ctenidium; dg, digestive gland; f, foot; go, gonad; hg, hypobranchial gland; ht, heart; int, intestine; kd, kidney; mc, main kidney chamber; mep, mantle edge papillae; op, operculum; os, osphradium; pg, pallial gonoduct; post., posterior; r, rectum; sn, snout; ss, style sac; sto, stomach.

Radula. For five radulae, an average of 140 rows was found. Rachidian broad, hexagonal, approximately as broad as long, with concave anterior end; cutting edge 2-3/1/2-3 with a central cusp long and rounded and denticles with rounded tip, or central cusp short and square with sharp denticles. Rachidian without basal appendages but with two lateral denticles. Lateral teeth similar in form to the rachidian, bearing also 2-3/1/2-3 with short, broad, squared central cusp flanked by short rounded cusps or long rounded central cusp flanked by sharper cusps. Marginal teeth long and spatulated, both inner and outer similar in cusps number and form; tips with 4-5 + 4-5 thin flanges along their inner and outer edges (Figs. 7A-H).

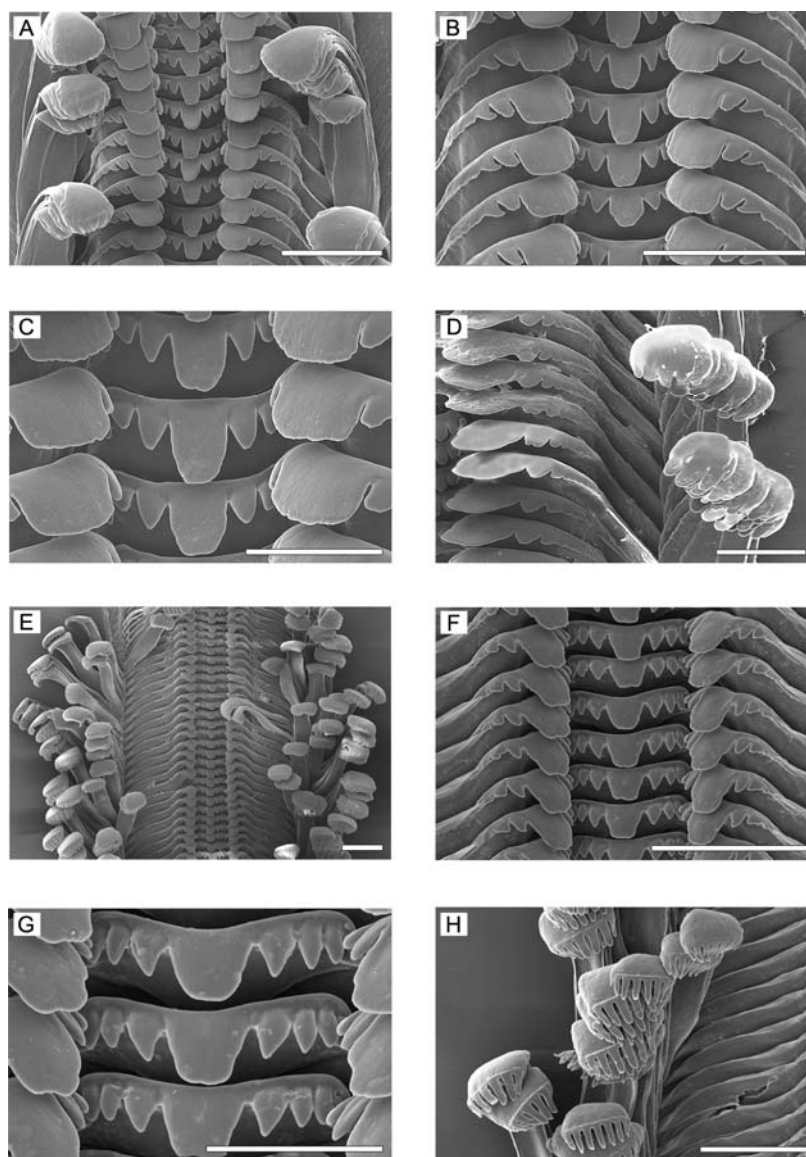


Fig. 7 A-H. Radula of *Hemisinus lineolatus* from Jamaica.

A – D, Anchovy Gully (ANSP A120781). E – H, Black River, Middlesex, Manchester (ZMB 107126). – A. Middle radular ribbon, bar = 100 µm. – B. Rachidian and lateral teeth, bar = 100 µm. – C. Rachidian, bar = 50 µm. – D. Lateral and marginal teeth, bar = 50 µm. – E. Middle radular ribbon, bar = 100 µm. – F. Rachidian and lateral teeth, bar = 100 µm. – G. Rachidian, bar = 50 µm. – H. Lateral and marginal teeth, bar = 100 µm.

Foregut. Buccal mass (bm) robust and pear-shaped. Short radular sac, visible dorsally, slightly posteriorly curved reaching the base of the oesophagus (oes). Strong buccal retractors inserting lateral at the middle of the buccal mass, extending to the lateral walls of the cephalic haemocoel adjacent to cerebral ganglia. Salivary glands (sg) opening dorsal-posterior to buccal cavity, being long and folded over themselves, passing through the nerve ring alongside the oesophagus, reaching it in its first third; left salivary gland passing above the supra-oesophageal ganglion. Oesophagus curving itself over the nerve ring just behind the buccal mass and then continuing as a simple tube. Mid-oesophageal gland absent (Fig. 8A).

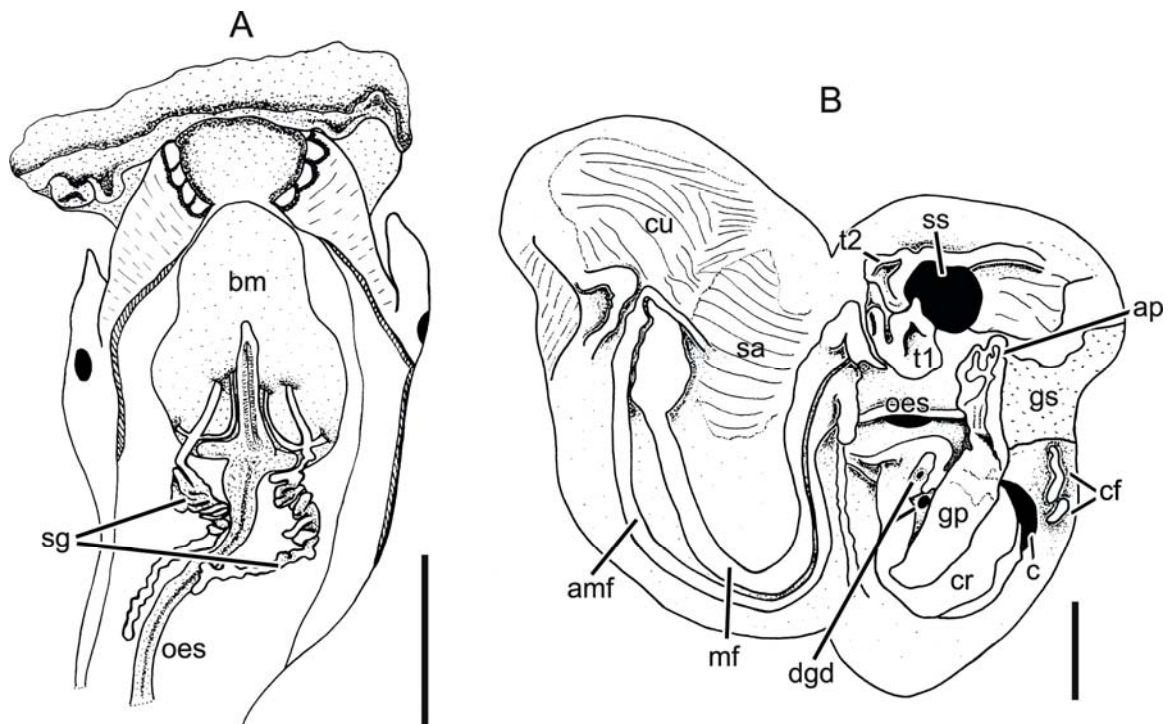


Fig. 8 A-B. Digestive system of *Hemisinus lineolatus*.

A. Foregut morphology, dorsal view (Black River, Jamaica; ZMB 107126), bar = 2 mm. – B. Midgut morphology, dorsal view (Westmoreland, Jamaica; ANSP A12088A). Midgut opened laterally on the right, roof reflected to the left; anterior is uppermost; scale bar = 1 mm. Abbreviations: amf, accessory marginal fold; ap, accessory pad; bm, buccal mass; c, caecum; cf, caecal folds; cr, crescentic ridge; cu, cuticle lining stomach roof; dgd, digestive gland duct; gp, glandular pad; gs, gastric shield; mf, marginal fold; oes, oesophagus; sa, sorting area; sg, salivary glands; ss, style sac; t1, major typhlosole; t2, minor typhlosole.

Midgut. Oesophagus opening at the left on the midgut (oes) floor (Fig. 8B). The roof of the midgut exhibits a big, oval sorting area (sa) with a small cuticularized (cu) anterior portion. Marginal fold (mf) with broad anterior tip, U-shaped bordering the sorting area and passing posteriorly the major typhlosole (t1). Accessory marginal fold (amf) emerging

lateral to the oesophageal aperture, running parallel to the marginal fold and surrounding its posterior tip to reach the sorting area. Crystalline style pocket rounded and small. Gastric shield (gs) narrow, with two caecal folds (cf) right to the glandular pad (gp), the posterior one half the size of the anterior. Glandular pad big, more than twice as long as broad. Large, textured accessory pad (ap) present at anterior end of glandular pad at left. Crescentic ridge (cr) emerging below the oesophageal aperture and running until the posterior tip of the gastric shield folds, without coming into the caecum (c). Paired digestive glands (dgd) opening under folds at the crescentic groove. Shallow caecum extending underneath the glandular pad. Style sac (ss) and intestinal groove separated by fused typhlosoles (Fig. 8B).

Hindgut. Proximal intestine (int) passing along under the entire style sac (ss), extending posteriorly to the anterior end of the gastric chamber, making an U-curve in front of the posterior tip of the gastric chamber and partially above the style sac (Fig. 6A), continuing behind the kidney to enter the pallial roof alongside pallial gonoduct, finishing the rectum (r) into a simple anus (a) close to the mantle edge (Fig. 6B).

Reno-pericardial system. Kidney large, wide, reaching at the front the mantle cavity between intestine and ctenidium, and bounded posteriorly by digestive gland and style sac. Lumen subdivided into chambers (Fig. 6C: 1-5). Voluminous main chamber (mc) partially covered by a fold, but not separated from the chamber that contains the excretory lamellae (Fig. 6C). Pericardial coelom deep, narrow, extending posteriorly underneath the kidney all along the style sac.

Nervous system. Circum-oesophageal nerve ring lying immediately behind the buccal mass. Cerebral ganglia (cg) above the oesophagus, connected by a short commissure, six nerves arising from each ganglion. Pleural ganglia (pl) behind and below cerebral ganglia, forming almost one mass. Two pedal ganglia (pe) closely adjacent, lying ventrally in the foot, with three accessory nerves. Sub-oesophageal ganglion (sb) connected to the left pleural ganglia. Nerve connective to supra-oesophageal ganglion (sp) emerging from the right pleural ganglia and crossing over the left pleural ganglion (Fig. 9C). Statocysts (stc) with up to 50 statoconia, dorsal-posterior to the pedal ganglia, with long connective to the cerebral ganglia (Fig. 9B).

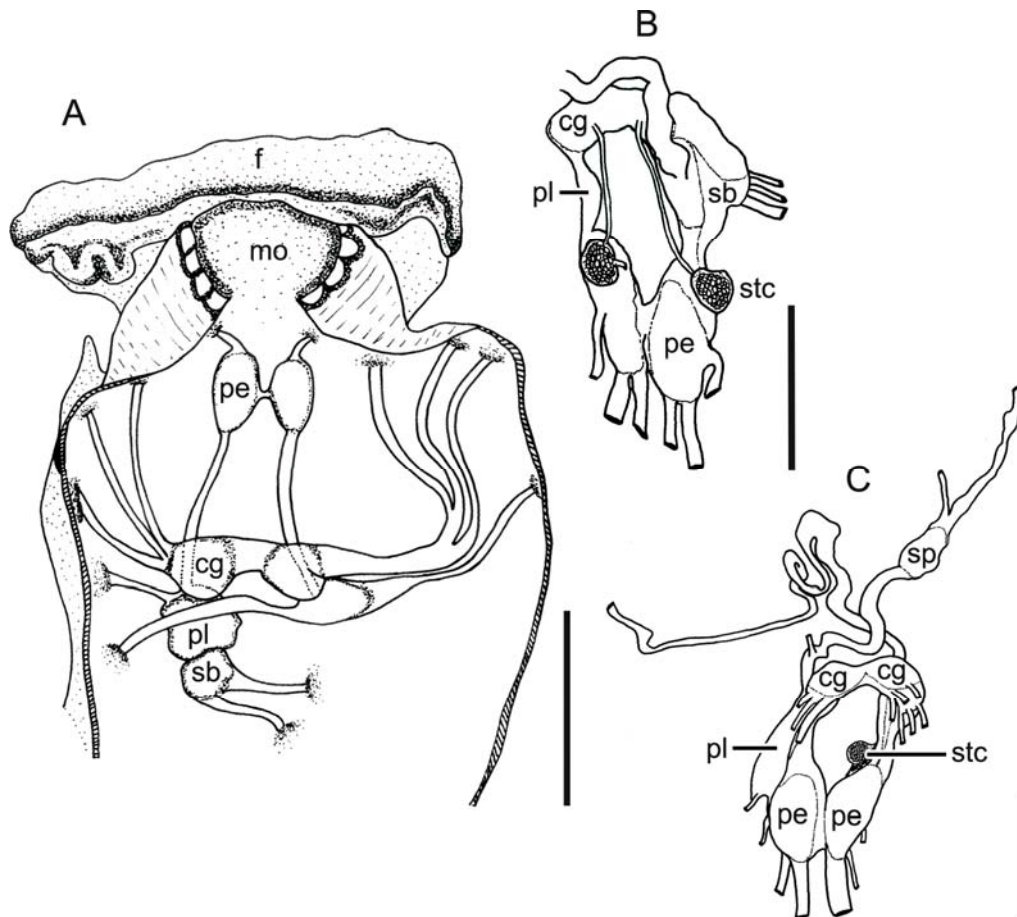


Fig. 9 A-C. Circum-oesophageal nerve ring of *Hemisinus lineolatus*.

A. Circum-oesophageal nerve ring *in situ*, dorsal view (Anchovy Gully, Jamaica; ANSP A120871); scale bar = 2 mm. – B-C. Detail of the nerve ring (Westmoreland, Jamaica; ANSP A12088A), ventral and dorsal view respectively; bars = 1 mm. Abbreviations: cg, cerebral ganglia; f, foot; mo, mouth; pe, pedal ganglia; pl, pleural ganglia; sb, sub-oesophageal ganglion; sp, supra-oesophageal ganglion; stc, statocyst.

Reproductive system. Sexual dimorphism determined by a neck pore (bpp) always present in the right side of the females, while absent in males (Fig. 6B). Sexual proportion of 52% females and 48% males ($n = 21$). Gonad (go) from tip of visceral whorls to posterior end of stomach over the digestive gland, being very similar between males and females (Fig. 6A), gonoduct emerging ventrally from gonad. Females have a dorsal brood pouch (bp) located in the neck's right side, extending from the region behind the right eye in the head-foot, posteriorly to the end of the mantle cavity (Fig. 10A). There are no trabeculae into the lumen of the brood chamber (Fig. 10B-I). The wall of the brood pouch consists of a layer of mantle epithelial cells (mec), followed by a thin layer of smooth muscle (sm) cover of a thin layer of long, square epithelial cells (sec) with big nucleus and lipid droplets (Fig. 10J: arrow). The brood pouch has a pore (bpp) close to the tip of the pallial gonoduct (Figs. 6B, 10F-H). For 15 females of two different populations, the brood

pouch contains either a single large juvenile or up to 3 juveniles of variable size (j) with the shells completely calcified.

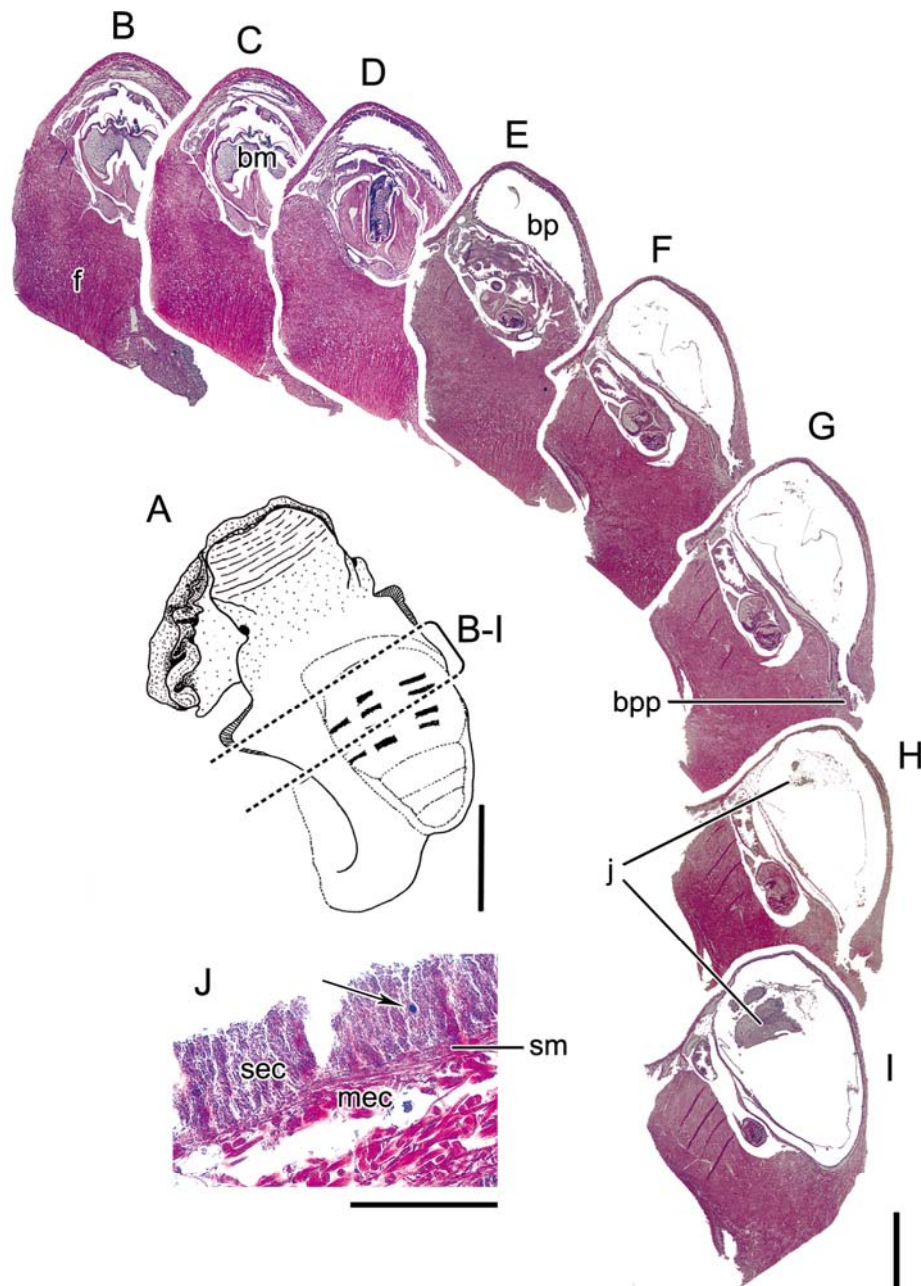


Fig. 10 A-J. Brood pouch anatomy of a mature female of *Hemisinus lineolatus* (Anchovy Gully, Jamaica, ANSP 12087H).

Location of the brood pouch and the histological serial sections, that refer to sections B-I. Bar = 1 mm. – B-I. Cross sections of the brood pouch with a non-compartmented chamber, from anterior (above) to posterior. Bar = 10 μ m. – J. Detail of the brood pouch wall epithelial cells, arrow indicating nucleus of a cell, bar = 1 μ m. Abbreviations: bm, buccal mass; bp, brood pouch; bpp, brood pouch porus; f, foot; j, juvenile; mec, mantle epithelial cells; sec, square epithelial cells; sm, smooth muscle.

For gonoduct descriptions we assume as anterior the tip close to the mantle edge. Female pallial oviduct half open. Dorsal external view shows a posterior, non-glandular, rounded structure that corresponds to the renal oviduct, followed anteriorly by the glandular oviduct (Fig. 12A).

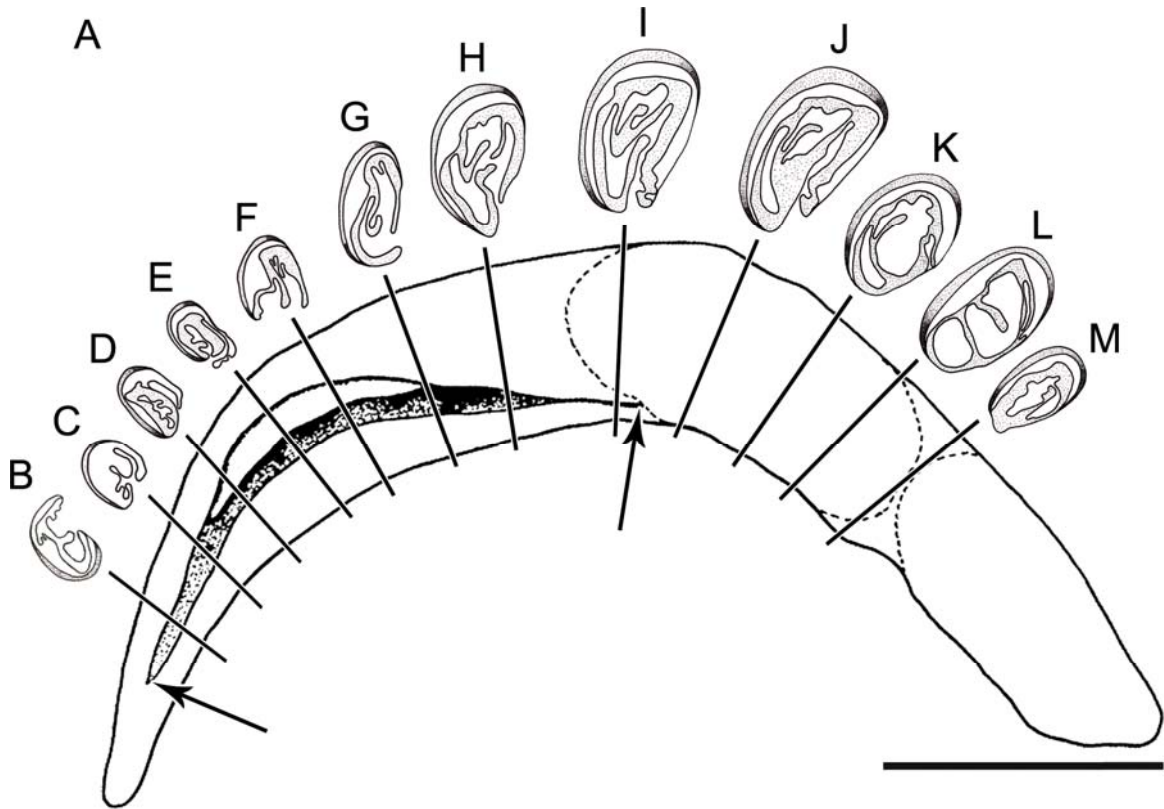


Fig. 11 A-C. Lateral and media lamina from a female pallial oviduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 12087H). A. External, ventral view of the lateral lamina. – B. Internal view of the lateral lamina. – C. Internal view of the medial lamina. Bars = 1 mm. Abbreviations: ag, albumen gland; mo, main oviduct; ovi, renal oviduct; sg, sperm gutter; spb, spermatophore bursa.

Renal oviduct short, curved, bulky (Fig. 11A: ovi), with two branches entering posterior into the main oviduct-spermatophore bursa and albumen gland (Fig. 11A: mo, spb, ag respectively). Albumen gland forming an ovate, straight tube which opens to the sperm gutter at the middle of the gonoduct (Fig. 12I). Anterior deep sperm gutter (sg) restricted by a fold which divides partially the main oviduct and the spermatophore bursa through all its extension (Fig. 11B: double dashed line). Medial lamina with an undulated furrow starting at the level of the spermatophore bursa, transforming anteriorly into a deep groove with conspicuous edge, ending close to the tip of the gonoduct (Fig. 11C). At the

middle of the anterior third, tissue from lateral and medial lamina forms a short, closed, glandular structure which opens both sided to the sperm gutter (Fig. 12C-E).

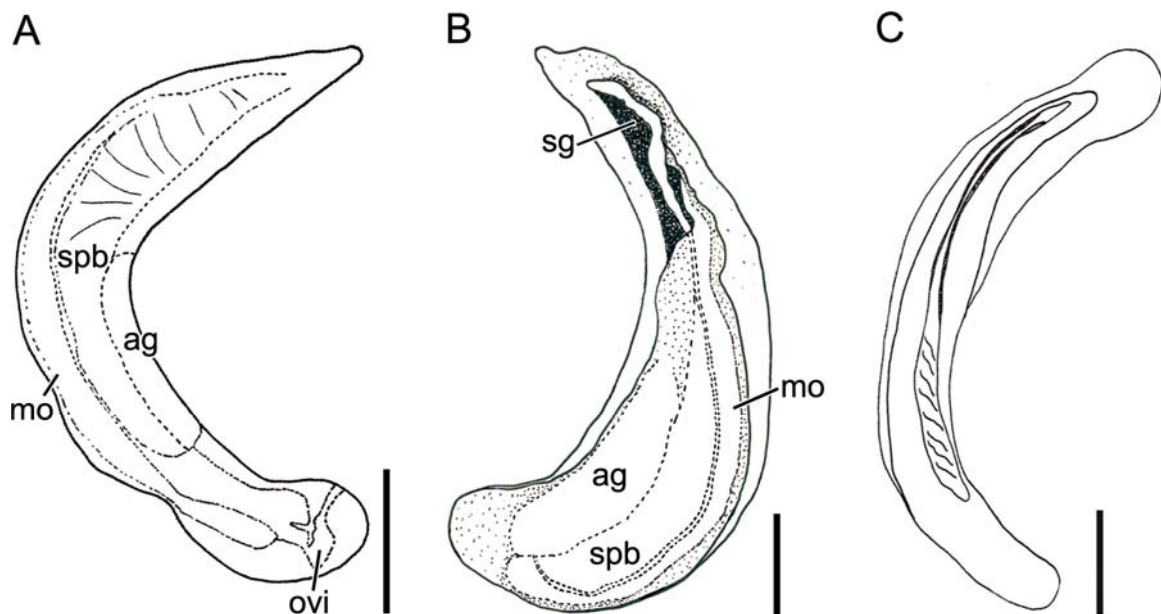


Fig. 12 A-M. External and internal view of the female pallial oviduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 12087H).

A. External, dorsal view of the pallial oviduct. Arrows indicate extent of the gonoduct opening to mantle cavity. – B-M. Reconstruction of the internal anatomy of a female pallial gonoduct (lines represent transversal cross-sections through the pallial oviduct). Anterior is left. – B-C. Opened seminal groove. – D-E. Anterior glandular structure. – F-H. Main oviduct partially divided by a lamina fold. – I. Closure of the main oviduct. – J-L. Formation of the spermatophore bursa and closure of the albumen gland. – M. Renal oviduct entering to the main oviduct. Scale bar = 1 mm.

Histological reconstruction of two pallial oviducts (ANSP 12087I) shows an anterior seminal groove, forming an opened, subdivided chamber line with glandular tissue (Fig. 13A: arrow). This sperm gutter shortly closed at the middle of the anterior third forming a glandular structure which opens again behind (Fig. 13B-C: arrow pointing aperture). Albumen gland with highly convoluted, tall prismatic epithelium (Fig. 13E: arrow). Posteriorly spermatophore bursa (spb) containing dense unorientated sperm (sp) (Fig. 13E-F).

In *Hemisinus lineolatus* the male pallial gonoduct is a simply tube, open along entire length except for a short fused segment at base of mantle cavity (Fig. 14A: arrows). Narrow vas deferens entering straight to the posterior part of the prostate (Fig. 14K). Lateral lamina with a proximal, elongate, glandular prostate and deep grooves running parallel and under the gland toward gonoduct's anterior end. Distal end of the prostate narrowing by a lamina wall fold; anterior portion of lateral lamina with oblique ledge (Fig. 58

14M). Posterior half of the gonoduct with a gland dorsal to the prostate. Gland terminating blindly posteriorly, opening at the middle of the gonoduct to the prostate (Fig. 13F-H). Medial lamina simple, with anterior shallow grooves and posterior glandular tissue.

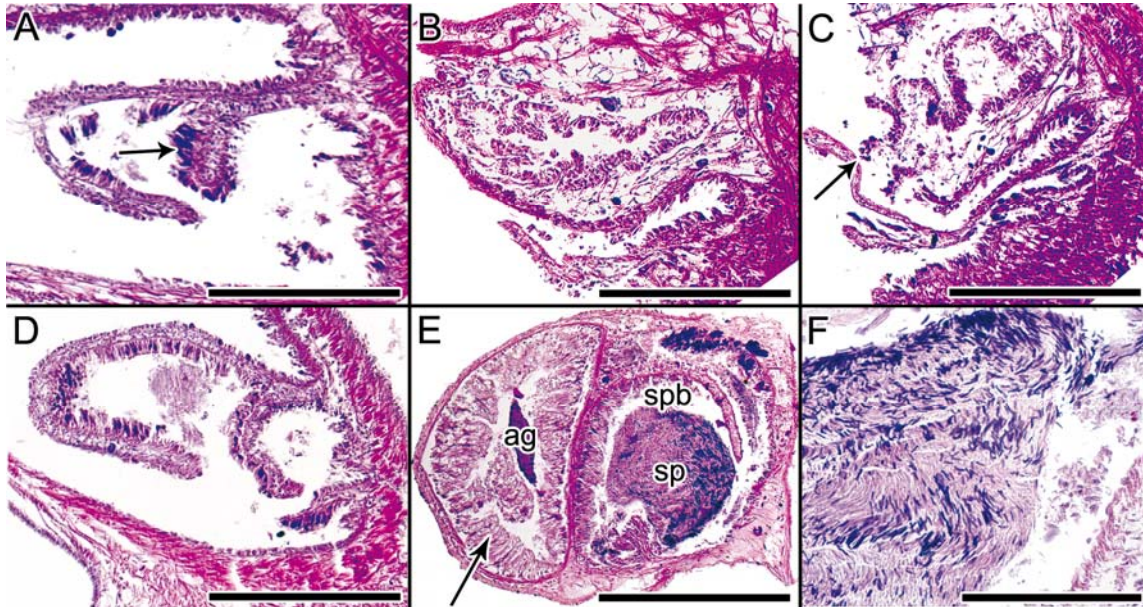


Fig. 13 A-F. Female pallial oviduct histology of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 12087I), from anterior to posterior; compare with figs. 11-12.

A. Cross-section of anterior pallial oviduct, seminal groove line with glandular tissue (arrow). – B. Cross-section showing a close anterior gland with highly convoluted tissue. – C. Anterior gland opening behind to the sperm gutter (arrow pointing place of aperture). – D. Partial division of the main oviduct chamber. – E. Albumen gland line with dense epithelial tissue (arrow) and spermatophore bursa with unoriented sperm. Scale bars = 0.5 μ m. – F. Pack of sperm unoriented in the lumen of the spermatophore bursa. Darkly stained structures are the sperm heads. Bar = 0.125 μ m. Abbreviations: ag, albumen gland; sp, sperm; spb, spermatophore bursa.

A reconstruction of the male gonoduct using histological sections revealed a main chamber with longitudinal folds covered with glandular epithelium (Fig. 15A-B). At the middle of the gonoduct, epithelial tissue projects into the lumen building a backwards gland, line with tall prismatic epithelium, containing unoriented sperm (Fig. 15C-F).

Ecology. Information on the ecology of *H. lineolatus* is scarce, but it can be inferred from the occurrences records in museum collections that they preferably inhabit running water environments. Only literature data are available indicating that *H. lineolatus* was collected by Natives and African Jamaicans as food. Recently, the increasing numbers of introduced *Tarebia granifera* in Jamaican freshwater ecosystems have led to augmented competition for food and space against the native *H. lineolatus* (Orcutt, 1928; Townsend & Newell, 2006).

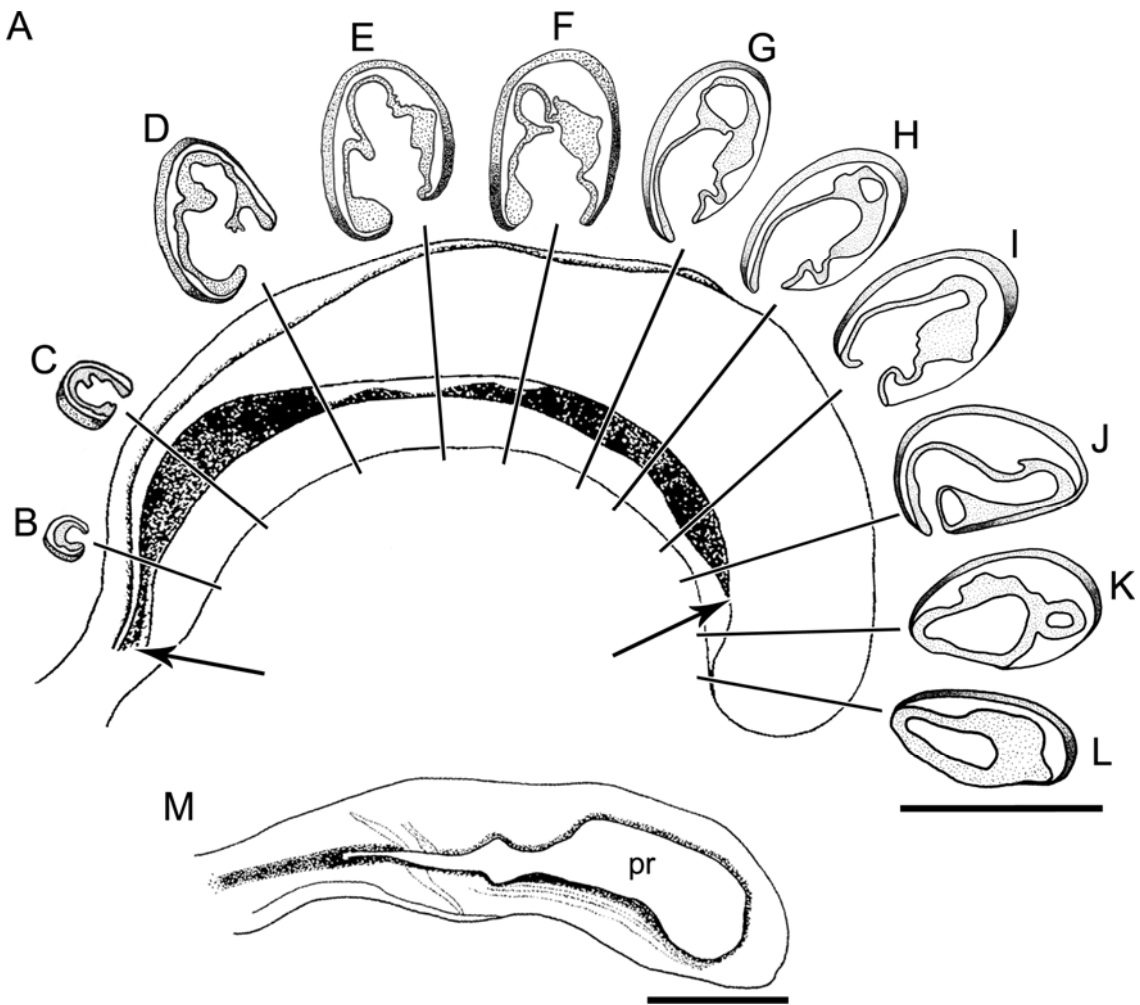


Fig. 14 A-M. Male pallial gonoduct anatomy of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 120871), with sections from anterior (left) to posterior.

A. Prostate, arrows indicate extent of the gonoduct opening to mantle cavity. – B-L. Reconstruction of the internal anatomy through the pallial gonoduct (lines represent transversal cross-sections). – C-E. Main chamber with longitudinal folds building grooves. – F-H. Aspect of the dorsal gland, note that it is blind behind opening to the main gonoduct chamber at the middle of the gonoduct. – K. Vas deferens entrance to the prostate. – M. Internal view of the male lateral lamina. Elongate prostate with parallel grooves and deep anterior sperm groove. Scale bars = 1 mm. Abbreviation: pr, prostate.

Fossils. Some Pleistocene *H. lineolatus* collected from the Coco Ree Cave, St. Catherine parish (Jamaica), are available at the Florida Museum of Natural History (FMNLH 79798, 59360, 79726, 79595). However, these samples were not examined by us.

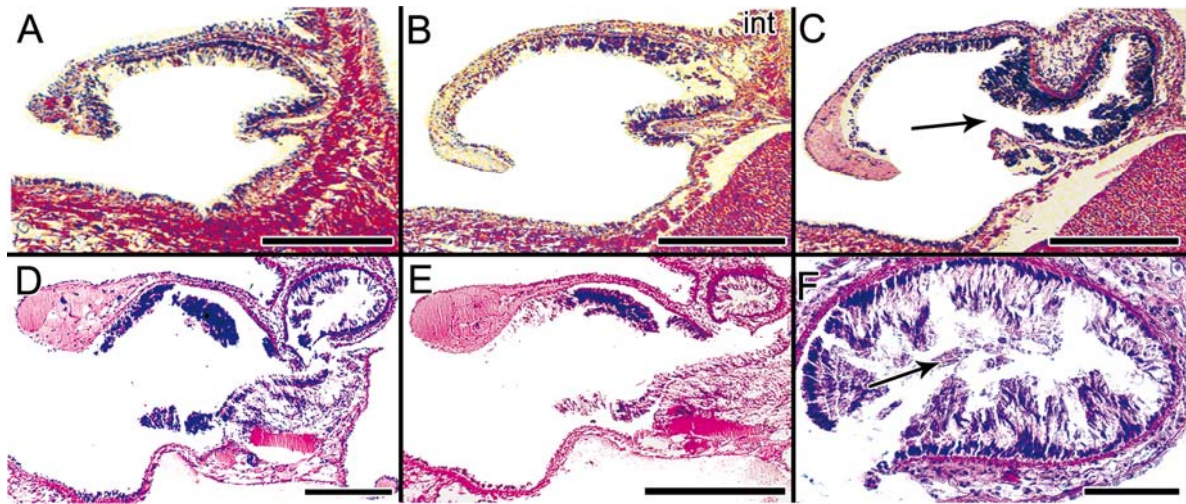


Fig. 15 A-F. Histology of male pallial gonoduct of *Hemisinus lineolatus* (Anchovy Gully, Jamaica; ANSP 120871), cross sections from anterior to posterior. A. Anterior main chamber, line with glandular tissue. – B-E. Cross sections of the middle gonoduct going behind, note the formation of a lateral, dorsal gland (arrow pointing open anterior end of the gland). – F. Detail of the lateral gland (arrow pointing unorientated sperm). Bars = 0.25 μ m. Abbreviation: int, intestine.

Discussion

Taxonomy

Here we established that the genus name *Hemisinus* have priority over the *emendation* *Semisinus*, and reject *Tania* and *Haemisinus* as synonyms of *Hemisinus*. It is now clear that *Hemisinus lineolatus* Wood 1828 is the type species of the genus and that the type specimen is still available in the BMNH collection. We also confirm Wood as the species' author and fixed Jamaica as type locality based on the evidence provided by Philippi and subsequent authors.

On intraspecific variability

Statistical morphometric studies allow us to conclude that there is no significant shell shape variation between the different Jamaican populations, and that the specimens identified as *Hemisinus buccinoides* belong to *H. lineolatus*.

Based on comparisons of shell morphometric parameters we established that *Hemisinus buccinoides* is the same as *H. lineolatus*. The same conclusion was reached by Brot (1878) when he cited *H. buccinoides* Reeve as synonym of *H. lineolatus*, and also by Simpson (1894) when he established that *Hemisinus* is monospecific in Jamaica. Consequently, *H. lineolatus* is the only native Thiaridae in the island.

Anatomical differences in osphradium length, length of the oviductal aperture, and number of juveniles inside the brood pouch were found between one population of the north-west

Jamaican coast (St. James parish, ANSP 120871, *H.*; n = 10) and those from the central part of the island (St. Elizabeth parish, ZMB 107126; n = 5). Specimens from the north-west coast exhibit a short osphradium, an oviductal aperture that extends to the middle of the pallial gonoduct, and only one embryo in each brood pouch examined. Exemplars from central Jamaica have an osphradium twice as long as that of the north-west organisms, as well as an oviductal aperture extending slightly beyond the middle of the gonoduct, and at least three juveniles in different development stages inside the brood pouch. However, adult and embryonic shell features and morphology, as well as the radula, male pallial gonoduct and stomach, exhibit the same variability in both populations. In the case of *H. lineolatus*, morphological disparity could reflect an ongoing ecological speciation without giving rise to a distinct species. In other taxa, such as in Jamaican freshwater crabs, isolation of populations on the northern side of the Blue Mountains from those of the southern side have already led to the evolution of morphologically very closely related yet genetically distinct species (Schubart *et al.*, 1998b; Schubart & Koller, 2005).

It is well known that Jamaica's allopatric diversity suggests informal recognition of at least six biogeographic areas, which are mainly determined by rainfall average and seasonality (Rosenberg & Muratov, 2005). Then, looking for an ecological explanation of the differential reproductive strategies in *H. lineolatus*, which is giving birth to only one juvenile in north-western populations and up to three juveniles in the central Jamaica populations, we found that the organisms from north-western Jamaica were sampled in a dry period (July) while the central Jamaica samples were collected during the peak of the rainy season (October) (Fig. 16). According to Dillon (2000), higher current velocities (as affected by rainfall) could be responsible for a lower survivorship and fecundity in a stream. This may suggest that *H. lineolatus* responds to seasonal change in precipitation by giving birth to a variable number of juveniles. It would be necessary, though, to obtain samples from central Jamaica during the dry period and from the north-western coast of the island during the rainy season in order to state if there are differences between those two populations. Other environmental factors like temperature, wind, insolation and relative humidity are relatively stable during the whole year across the island and can be discarded. Elevation can also be neglected since both populations are found at elevations ranging between 270-290 m. Punctual events like hurricanes, which not always increase the rainfall average, are also not very likely to influence the populations as freshwater snails could not react so fast as to counteract the effects of a particularly rainy year. Only in the long term it is expected that environmental pressures could induce the selection of some changes (Roldán, 1992).

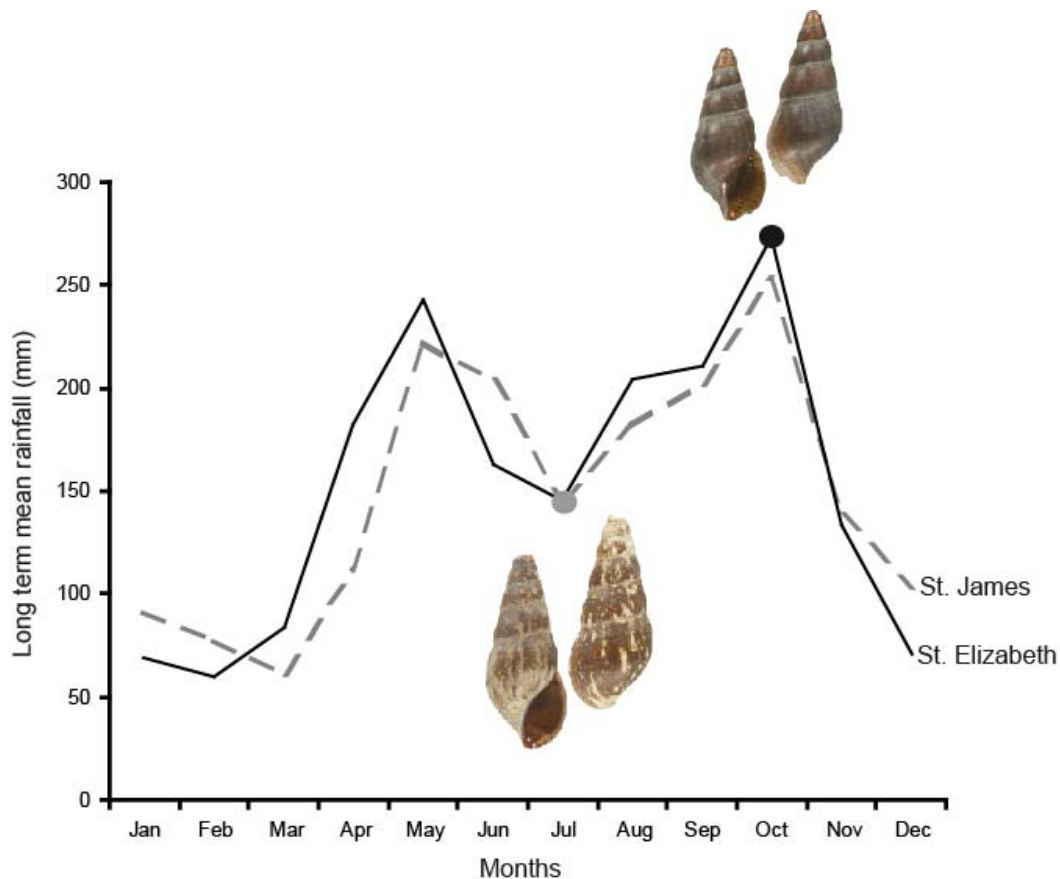


Fig. 16 Monthly precipitation pattern (30 years mean) for the Parishes St. James and St. Elizabeth in Jamaica; data obtained from the Meteorological Service of Jamaica. Note that St. Elizabeth population was sampling during the peak of precipitation.

Reproductive system anatomy

As there are not enough anatomical or histological studies of other members of the genus, we compared *H. lineolatus* with the available information of some Brazilian unidentified *Hemisinus*, *Thiara amarula* (Linné, 1758) the type species of Thiaridae, and with *Melanoides tuberculata* (Müller, 1774) and *Thiara scabra* (Müller, 1774), which are also thiarids. The male pallial gonoduct in *H. lineolatus* is almost completely open, the same as in *Hemisinus* sp. and *T. amarula*. In paludomid gastropods, the male gonoduct exhibits anteriorly a narrow, dorsal tube or spermatophore forming organ, which opens at varying distances along its length to the gonoductal groove (Glaubrecht & Strong, 2004). The posterior dorsal gland found at the male gonoduct of *H. lineolatus* via histological reconstruction, could be a spermatophore forming organ since dense basophilic epithelium lined the walls and spermatozooids in the lumen are present. Nevertheless, no spermatophores or any sign of its presence were found. It will be suitable the analysis of more specimens to drawing a conclusion about the presence or not of spermatophores in the genus.

Concerning the oviduct, the median and lateral lamina are completely fused with a vagina present at the anterior tip in *T. amarula* (Schütt & Glaubrecht, 1999) and in *M. tuberculata* (pers. observ.), whereas in *H. lineolatus* and *Hemisinus* sp. it is half open, presenting a wide opening tip. This configuration could be considered as an intermediate condition between thiarids and other cerithioideans like paludomids. The unique thiarid bursa, which is a modification in the lateral lamina as in *H. lineolatus*, is apparently not homologous to that of marine forms like *Finella* and other cerithiids that also possess a similar structure.

In limnic Cerithioidea the brood pouch used to be a posterior expansion in the dorsal cephalic haemocoel, which extends back from a brood pore in the neck, overlying the oesophagus (Strong & Glaubrecht, 2002). The brood pouch of *H. lineolatus* has this same arrangement but differs in its internal structure and the developmental stage of the embryos from *Hemisinus* sp. from Brazil, *T. amarula*, *M. tuberculata* and *T. scabra*. In the latter there are separate individual compartments that may be occupied by several early embryonic stages (Muley, 1977; Glaubrecht, 1996; Schütt & Glaubrecht, 1999; Ben-Ami & Hodgson, 2005), while in *H. lineolatus* up to three shelled embryos occupy a single compartment and there is no evidence of early stages. From *T. scabra* it is known that the brood pouch compartments are formed by cubical epithelial cells that extend into the brood pouch cavity (Muley, 1977). However, while these kind of cells are also observed in *H. lineolatus*, they do not form compartments and the embryos are scarcely attached to the brood pouch through epithelial tissue. According to Houbick's (1988) classification of cerithioidean brood pouches, *H. lineolatus* therefore exhibits the "intermediate evolutive" morphological array, which is evidenced by the absence of a complex subdividing chamber. Finally, we could not prove that *H. lineolatus* is viviparous since the application of the required chemical and histological analyses was beyond the scope of this work (cf. Ben-Ami & Hodgson, 2005). Also, the presence of a thick albumen gland and a thin layer of epithelial tissue inside the brood pouch, lead us thus we tentatively to conclude that *H. lineolatus* is ovoviviparous.

Although Nuttall (1990) stated that *Hemisinus* is parthenogenetic, and we do not have evidence to reject his hypothesis since there is parthenogenesis reported in the Thiaridae, the finding of similar proportions between males and females within populations indicates that sexual reproduction is most likely the reproductive mechanism in Jamaican *Hemisinus*.

On the systematic position within Thiaridae

At the family level, *Hemisinus* Swainson, 1840 was initially placed in the Melaniidae, which is an invalid name for Thiaridae Gill, 1871 (Glaubrecht, 1996). Subsequently it was transferred to the Melanianae, Melaniinae and Melaniadae (Swainson, 1840; Adams & Adams, 1854-1858; Reeve, 1860), and later brought back to Melaniidae (Vendryes, 1899; Ihering, 1902; Thiele, 1928, 1929-1935; Hylton-Scott, 1954). Later, Morrison (1951, 1954), based on his own observations on the operculum and body features, and following Ihering (1909), refused the family Pleuroceridae as an option and established that *Hemisinus* belongs to the Thiaridae.

Despite the increasing number of studies on cerithioidean and the questioning of the Thiaridae monophyly, important information about the morphology of the different genera of the family is still lacking, and some of the anatomical descriptions already made are still unpublished (Glaubrecht et al., unpubl. data). Due to the lack of sufficient anatomical information on other members of the genus or the related South American genus *Aylacostoma*, we compared the morphology of *Hemisinus* with available data of African and Asian members of the families Thiaridae and Paludomidae (for summary of morphological differences see Table 3). We found that *Hemisinus* exhibits thiarid characteristics regarding to operculum, mantle edge, rachidian, reproductive strategy and midgut anatomy (large, textured accessory pad; two short, prominent caecal folds; fused thyphlosoles). An interesting feature of midgut anatomy in *Hemisinus* is the shallow caecum which it shares with *Melanoides* and the Paludomidae. In all other Thiaridae it is deep and spiral. The difference in morphology and reproductive anatomy (osphradium size, caecum features, extension of the pallial oviduct opening) between *Hemisinus* and the other thiarids could suggest that it does not group with the family Thiaridae, but given the distinctive features of the midgut (see above) and brood pouch, may simply indicate a basal position within the family. Thiele (1928) and Glaubrecht (1996: 188) already compared *Hemisinus* with the west African *Pachymelania*, based on the similarities of radula features, the partial (anterior) open gonoduct in females and the almost all open male gonoduct, but the latter also concludes that the brood pouch strategy clearly point to the thiarids. Consequently, we retain *Hemisinus* within the Thiaridae for the time being.

On ecology and conservation

During this work, we faced difficulties to obtain live material. Most likely, this is because the species has been displaced most recently from its original distribution area by the introduced *Tarebia granifera* as Townsend & Newell (2006) stated. Since populations of *T. granifera* are usually composed only of females carrying between 1-30 shelled embryos in

their brood pouch and records from different countries have shown that this species readily becomes invasive after introduction and competes effectively with the indigenous snails species (Appleton and Nadasan 2002), the increasing numbers of the former species documented from 1996 in Jamaica, agree with the absence of the native *H. lineolatus* from some localities where this species used to be present in Jamaica (Fender, pers. comm.). This could be a strong reason to implement conservation measures in order to evaluate the current status of the species in the island and to take actions directed to its protection.

According to Schubart *et al.* (1998a), Rosenberg & Muratov (2005) and Ricklefs & Bermingham (2008), the diversity in Jamaica is locally confined, showing the need to protect the endangered ecosystems of the island in order to preserve the high level of endemism of West Indian native biota.

Table 3. Summary of morphological differences between *Hemisinus lineolatus* compared to other limnic gastropods classified in the Thiariidae and Paludomidae.

Details from anatomical studies on thiarids and paludomids, respectively, by Glaubrecht, 1996; Glaubrecht & Strong, 2007; Glaubrecht *et al.*, unpubl. data; Strong & Glaubrecht, 2007. Abbreviation: ct, ctenidium.

	Thiariidae			Paludomidae		
	<i>Hemisinus</i>	<i>Thiara</i>	<i>Stenomelania</i>	<i>Laevigieria</i>	<i>Tiphobia</i>	<i>Potadomoides</i>
Juvenile shell	Smooth	Smooth to ribbed	Smooth/Wrinkled	Wrinkled	no information	~Wrinkled
Operculum	Paucispiral	Paucispiral	Paucispiral	Paucispiral	Paucispiral	Paucispiral
Operculum nucleus	Excentric	Excentric	Excentric	Subcentral	Central	Subcentral
Mantle edge	Papillate	Papillate	Papillate	Lobate	Smooth	Smooth
Osphradium length	~One third ct	~Half ct	no information	~Half ct	~One third ct	~Two thirds ct
Rachidian	Hexagonal/broad	Short/broad	Rectangular	Rectangular	Rectangular	Squarish –narrow/ Triangular – broad or narrow
Rachidian denticles	2-3/1/2-3	3-6/1/3-5	2-3/1/2-3	1/1/1	8-15/1/8-15	1-2/1/1-2
Lateral denticles	2-3/1/2-3	2-6/1/2-5	1/1/2-3	1/1/1	3-6/1/5-16	1-2/1/1-3
Marginal denticles	4-5	6-8	6-10	1-5	5-8	1-3/1/8-10
Accessory pad	Large	Large	no information	Large	Small	Small
Caecal folds	2	no information	no information	1	1	1
Caecum	Shallow	Deep and spiral	no information	Shallow	Shallow	Shallow

Conclusions

Given that *Hemisinus lineolatus* is the type species of the genus, the present redescription aims as reference for the application of the genus definition independently of future findings about the relationships and structure within the family Thiariidae. Thus, for the first time, the internal anatomy of *H. lineolatus* is described in detail, contributing significantly

to the establishment of anatomical knowledge about this Neotropical genus in order to compare its characters based on *H. lineolatus* in particular with other congeners and with thiarid species. We here define as diagnostic characters for the species: sexual dimorphism, short osphradium, midgut anatomy (shallow caecum, large and textured accessory pad, two caecal folds), male pallial gonoduct laterally open almost along its length with a simple vas deferens and a glandular structure that resembles a paludomid spermatophore forming organ, and females with conspicuous glands on the pallial oviduct and undivided dorsal brood pouches containing up to three juveniles. We anticipate that *Hemisinus lineolatus* sharing also anatomical and morphological features with the African-Asian Paludomidae might indicate common ancestry with an Oriental freshwater cerithioidean lineage rather than being evidence of the genus belonging to a taxon other than the Thiaridae.

4.2 *Hemisinus* in Cuba: How many species are there?

Introduction

Cuba is the largest and westernmost island of the West Indies, located where the Caribbean Sea meets the Gulf of Mexico and the Bahamas region, its main island is surrounded by groups of small islands (Fig. 1A). The local climate is tropical, though moderated by northeasterly trade winds. In general there is a drier season from November to April and a rainier season from May to October, with frequent hurricanes between September and October (MacPherson, 1990).

Cuba's origin, just like the other Greater Antilles, dates back to the mid-Cretaceous when the proto-Antilles formed along the northern and eastern margin of the Caribbean Plate (Hedges, 1996, 2001; James, 2006). It seems that the southeastern Cuba and northern Hispaniola terranes were conjoined from the Mesozoic until the Eocene-Oligocene, when both separated (Buskirk, 1985; Hedges, 1996, 2006; Iturralde-Vinent & MacPhee, 1999; Mitchell, 2006). There is strong evidence that western Cuba was detached from its original position along the eastern margin of the Maya block (Yucatan platform) during the Jurassic-Cretaceous, achieving contact with central and southern Cuba during the Miocene (Buskirk, 1985; Iturralde-Vinent & MacPhee, 1999; Kerr *et al.*, 1999; Mitchell, 2006).

Cuba possesses three mountainous regions, the rugged Sierra Maestra in the east, the Guaniguanico Cordillera in the west, and the rolling Sierra de Trinidad in the middle. The rest of the island is level or rolling, often with marshy shores fringed by coral reefs and

cays (Aguayo, 1938). The rivers are generally short with the exception of the Cauto, which receives water of the Cuyaguatete, one of the main rivers of the Pinar del Río province (Manso & Bastón, 2006). Pinar del Río is Cuba's westernmost province. This region is characterized by the Guaniguanico Cordillera, which is composed of the Sierra de los Organos and the Sierra del Rosario, reaching its greatest height at El Pan de Guajabon (699 m). This mountain system with big karstic caves hosts also the Sierra del Rosario reservation, known for its high levels of endemic flora (34% of its total species) (Manso & Bastón, 2006). It has been stated that a submersion of the island during a certain period in post-Oligocene time only left the Sierra de los Organos and some other isolated places in central and eastern Cuba as a faunal refuge. Consequently, some genera like *Hemisinus* remained only on west Cuba and Jamaica, while becoming extinct on the rest of the Antilles (Aguayo, 1938).

Because of its geological history and geographical configuration, Cuba has few vertebrate species (Genaro & Tejuca, 2001). According to Arango y Molina (1865) and Aguayo (1938), the molluscan generic groups found on mainland Cuba are widely distributed in the Neotropics, whereas the species are different from those of Jamaica, Puerto Rico, the Lesser Antilles and the close Central American continent. Both authors also stated that, according to their herpetological and malacological faunas, Cuba, Pines Island and the Bahamas once were one vast region.

Regarding Cuba's non-marine molluscan fauna, the main emphasis has been made on its land snails because their attributes render them suitable for biogeographical studies (Pfeiffer, 1839). This fauna is more varied, abundant and conspicuous (i.e. *Polymita*) than the freshwater representatives, and also exhibits shell peculiarities like forams or tubercles not present in other Antillean species (Simpson, 1894).

In Cuban freshwater environments, the Cerithioidea is a well-distributed group with representatives of the families Thiaridae (*Hemisinus*) and Pachychilidae (*Pachychilus*). In Cuba, five species of Thiaridae (*Hemisinus cubanians* d'Orbigny, 1842; *Hemisinus ornatus* Poey, 1854; *Hemisinus pallidus* Gundlach, 1856; *Hemisinus martorelli* Brot, 1878 and *Cubaedomus brevis* d'Orbigny, 1842) and two of Pachychilidae (*Pachychilus nigratus* Poey, 1858 and *Pachychilus conicus* d'Orbigny, 1842) were described. *Pachychilus nigratus* was at times assigned to *Hemisinus* (Poey, 1851-1858; Arango y Molina, 1865), probably due to its small and delicate shell, but its morphological features are clearly those of the Pachychilidae. Aguayo (1938) was the first to record that in Cuba *Hemisinus* is restricted to the western province of Pinar del Río. According to Aguayo (1938),

members of this genus inhabit the headwaters but not the lower part of the Sierra de los Organos' rivers, indicating a high affinity to clean waters. More recently, Pointier *et al.* (2005) suggested that in Cuba the Thiaridae are represented only by two endemic species belonging to the genus *Hemisinus*: *H. cubanianus* and *H. brevis*, assuming that three of the previously described species of *Hemisinus* are synonyms (*H. cubanianus*, *H. ornatus* and *H. pallidus*), and that *Cubaedomus brevis* also belongs to the genus *Hemisinus*. They also stated that in the last decades two exotic thiarids (*Tarebia granifera* and *Melanoides tuberculata*) have been introduced and invaded numerous freshwater habitats. The consequences of this invasion on the endemic thiarids have not been estimated, but recent observations have shown a decline of some local *Hemisinus* populations (Gutierrez *et al.*, 2005). Detailed taxonomical remarks and distributional patterns are presented below under each species.

As confusion about the real number of *Hemisinus* species in Cuba still exists, in this section I concentrate on the four species considered traditionally as *Hemisinus*, leaving aside *Cubaedomus brevis*. Using multivariate morphometrics to describe and compare patterns of shell shape variation as well as morphological and anatomical features, I intend to determine whether or not they are the same species. Also, since the genus *Hemisinus* is only present on Jamaica and Cuba, and *H. lineolatus* from Jamaica and *H. ornatus* from Cuba have been confused (Brot, 1878), a phylogenetic analysis was performed in order to establish relationships between the taxa of both islands.

Specific materials and methods

Dry shells and material preserved in ethanol from the Academy of Natural Sciences, Philadelphia (ANSP); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) and Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität zu Berlin (ZMB) were examined (for the specific localities see the Material-section under the respective species). The distribution map of the samples is shown in Fig. 1B.

Morphometric parameters of the shells were measured as described in Chapter 3.2. As multivariate methods have proven indispensable in providing taxonomic resolution at species level, particularly when coupled with some biological information about the specimens of interest (Marko & Jackson, 2001), a multivariate morphometric approach was performed in order to describe shell shape and size. Prior to analysis, all data were transformed by means of a linear regression of each of the shell variables using SPSS

(version 15.0). A new matrix was constructed with the standardized residuals and a PCA was carried out employing PAleontological Statistics (PAST) version 1.68 (Hammer *et al.*, 2001). Data of the standardized matrix are presented as scatterplots and biplots. Regarding shell shape, I contrasted the shells of the available types of the nominal species (selected as *a priori* group) with the rest of the samples by means of a Fourier outline shape analysis (FOS). For the detailed procedure see Chapter 3.6.

Soft bodies preserved in 70% and 96% ethanol from the ZMB collection were used for anatomical, histological and molecular analyses, as well as for radulae extraction and embryonic shell observations. For methodology see Chapter 3.3.

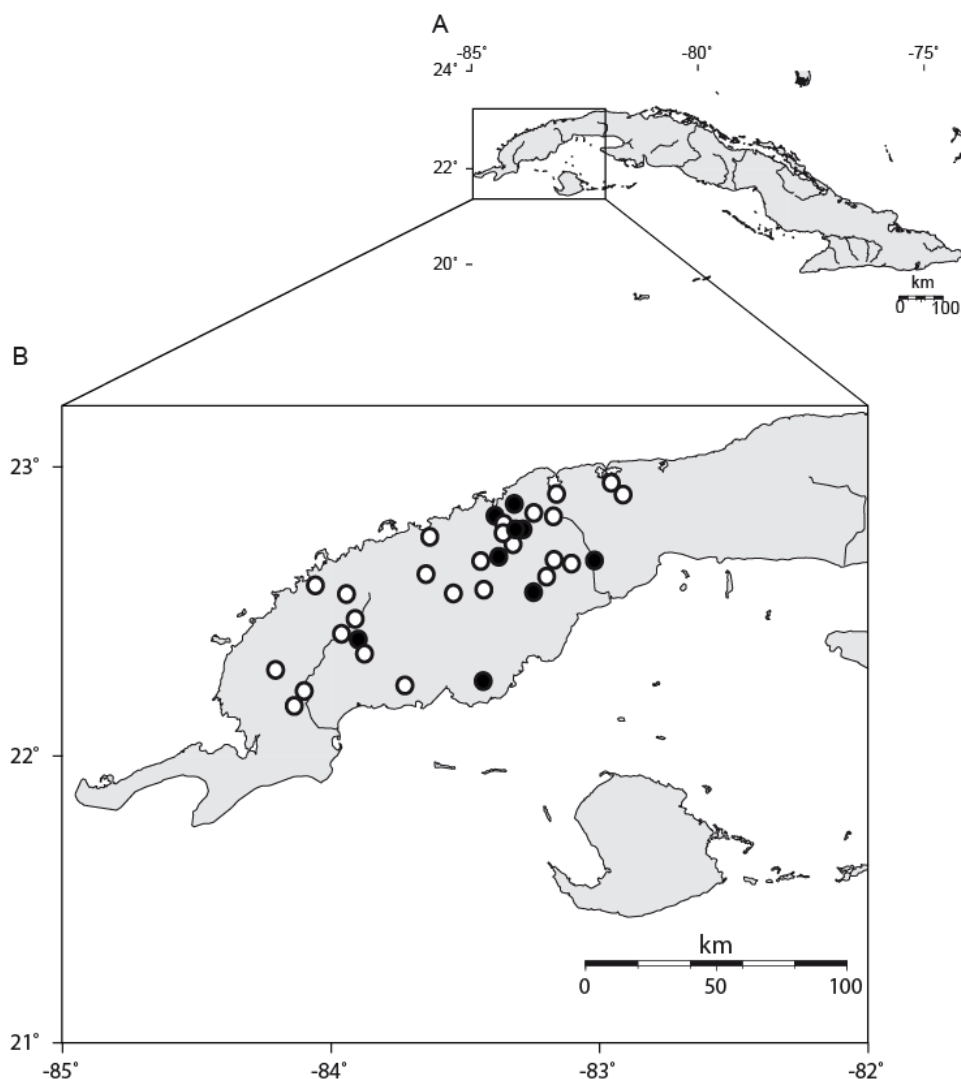


Fig. 1 A. Cuba with the Pinar del Río Province indicated. – B. Distribution of *Hemisinus Swainson, 1840* in Pinar del Río Province, western Cuba; for the localities see text.

O = museum shell material; ● = material in ethanol examined for anatomy and histology.

Results

***Hemisinus* Swainson, 1840**

Diagnosis.

Shell. Medium to small, globose with short spire or ovate-conic to turritiform, smooth or with faint growth spiral lines; color yellow, green-yellowish or from light to dark brown, frequently with continuous or interrupted reddish-brown spiral lines; base of the aperture with a more or less conspicuous channel; parietal callus thin with some species with the upper part of the aperture thickened. Operculum paucispiral, with a small sub-terminal nucleus. Animal with papillated mantle edge; osphradium short, approx. one third of the ctenidial length; radular rachidian broad and hexagonal; stomach with large accessory pad and shallow caecum. For further details see the respective species below.

Systematic account

***Hemisinus cubanianus* (d'Orbigny, 1842)**

Melania cubaniana d'Orbigny, 1842: 11, pl. 10, fig. 16. Poey, 1845: p. 398. Gray *et al*, 1854: 17. Poey, 1856: 10, 67. Reeve, 1860: 358. Arango y Molina, 1865: 141. Arango y Molina, 1867: 88. Arango y Molina, 1880: p. 140.

Hemisinus cubanianus – Brot, 1862: p. 61. Brot, 1870: 311. Brot, 1878: p. 375, pl. 39, fig. 5, 5a-b. Kobelt, 1882: p. 130. Paetel, 1890: 397. Aguayo, 1938: 229. Pointier *et al*, 2005: p. 30, fig. a-d. Gutiérrez *et al*, 2005: 725.

Hemisinus (Hemisinus) cubanianus – Jaume, 1945: 77. Jacobson, 1949: 83.

Melania ornata – Poey, 1854: 422, pl. 33, fig. 5-6. [non *Melania ornata* von dem Busch, 1842: pl. 1, fig. 10 in Philippi 1842-1850]. Pfeiffer, 1855: 89. Poey, 1856: 10. Gundlach, 1856: 18. Arango y Molina, 1865: 140. Arango y Molina, 1867: 88.

Amnicola ornata – Poey, 1854: 398.

Hemisinus ornatus – Reeve, 1860: pl. 5, fig. 20a-b. Brot, 1862: p. 61. Brot, 1870: 312. Brot, 1878: p. 376, pl. 39, fig. 1, 1a. Kobelt, 1882: p. 131. Paetel, 1890: 398. [non *Hemisinus ornatus* Pálffy, 1902: 315-316, pl. 29, fig. 4, 5, Paleocene fossil from Transylvania].

Hemisinus ornatum – Richards, 1933: 172.

Melania pallida – Gundlach, 1856: 16, pl. 1, fig. 5. [non *Melania pallida* Philippi, 1836: 157, pl. 9, fig. 8]. Poey, 1856: 11. Gundlach, 1856: 42. Pfeiffer, 1858: 2. Reeve, 1860: pl. 33, fig. 220. Brot, 1862: 61. Arango y Molina, 1865: 140. Arango y Molina, 1867: 88. Arango y Molina, 1880: 140.

Hemisinus pallidus – Brot, 1878: 378, pl. 39, fig. 4, 4a-b. Kobelt, 1882: 131. Paetel, 1890: 397.

Hemisinus cubanianus var. *pallidus* – Paetel, 1890: 397.

Hemisinus cubanianus pallidus – Aguayo, 1938: 229. Pointier *et al.*, 2005: 30.

Hemisinus (Hemisinus) cubanianus pallidus – Jaume, 1945: 77.

Hemisinus cubanianus torrei – Aguayo, 1938: 229. Pointier *et al.*, 2005: 30.

Type locality. “... dans les rivières de l’île de Cuba” (in the rivers of the island of Cuba).

Type material. Two syntypes from the MNHN collection (Fig. 2A); four syntypes MCZ 94734 (Fig. 2B); three syntypes ZMB 112708 (Fig. 2C). Shell measurements of the type material are given in Tab. 1.

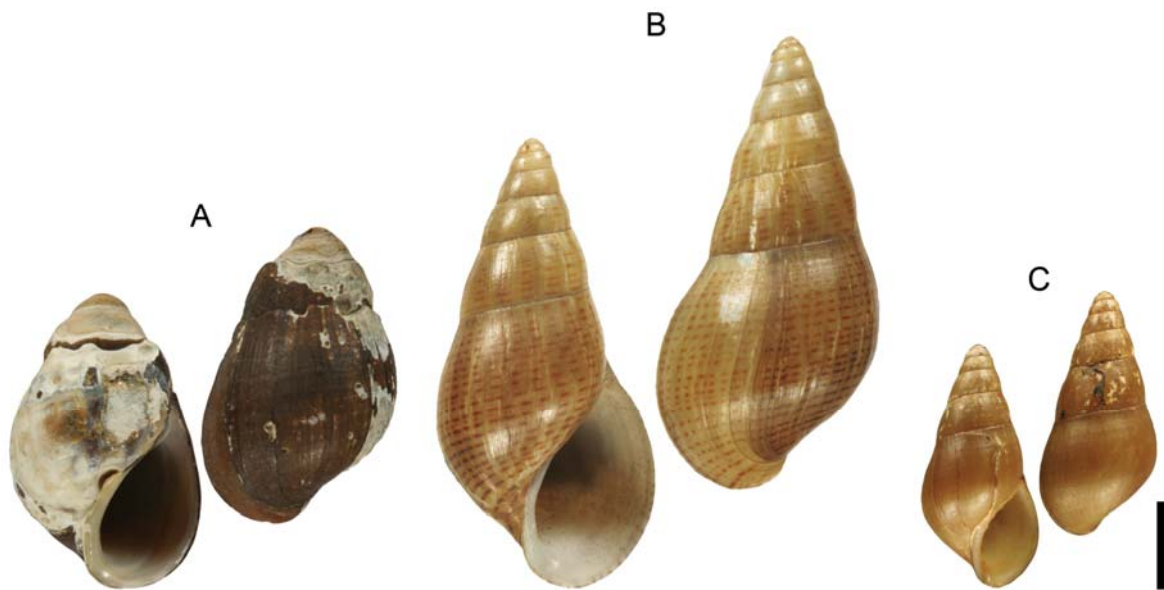


Fig. 2 A–C. Type material of *Hemisinus* Swainson, 1840 from Cuba.

A. Syntype of *Hemisinus cubanianus* d'Orbigny, 1842 (MNHN); – B. Syntype of *Hemisinus ornatus* Poey, 1854 (MCZ 94734); – C. Syntype of *Hemisinus pallidus* Gundlach, 1856 (ZMB 112708). Scale bar = 5 mm.

Other material examined. All samples except the type material are listed following a west-east arrangement. **Cuba:** (ANSP 26802, 26803, 26804, 26806, 26807, 26809, 120734, 120807, 122761, 122776, 122954, 122962, 123737; USNM 118513, 119624, 119712, 119733; ZMB 113048, 113049, 113050, 113051, 113052, 113056, 113058, 113119). Pinar del Río: (ANSP 26801, 192805; MCZ 94734; USNM 169923, 792465; ZMB 113054). Portales de Guane (ANSP 120817, 123030). Sierra Guane (ANSP 139759). La Mina Peak (USNM 203306). Valle de San Carlos: Luis Lazo, Río Cuyaguaje, Resolladero (MCZ 243161). Luis Lazo (USNM 453974). Arroyo del medio (ANSP 122773, 122941, 122967). Cuyaguaje River, Sumidero (USNM 451890, 453976; ZMB 107160). Río San Vicente, Viñales (MCZ 247467). El Guamo (USNM 168914). Sierra de la Guira (ZMB 191151). Cajalbana (ANSP 122769). San Diego River, Finca Caiguanabo (MCZ

247469; USNM 453975). Río La Palma, Consolacion del Norte (MCZ 247466). Río Entronque de Herradura, Consolación del Sur (MCZ 247463). San Marcos River (ZMB 113290); tributary of San Marcos River (ZMB 113271, 113273). Stream tributary of Tortuga River (ZMB 107158). San Diego de los Baños (ANSP 26808; ZMB 113274). Puercos River (ZMB 192001). Río de Guajaibon (MCZ 247460; ZMB 113046, 113060). Arroyo de Jicotea near Guajaibon (ANSP 91502, 122941). Arroyo de Canilla (ANSP 26810). Las Pozas River (USNM 407968); Stream tributary of Las Pozas River (ZMB 192003). San Diego River (ZMB 192002). San Diego de Tapia River (ANSP 26805, 26811; USNM 11187, 11193, 453979; ZMB 113061). Los Palacios, Finca Bacunagua, Río Seco, (ANSP 222628; MCZ 247468; ZMB 113260). Honda River (ANSP 26814 USNM 11184). Santa Cruz River (ANSP 26813, 122955; USNM 11191; ZMB 113055). Rangel, Taco Taco River (ANSP 123035, 151499, 153656; USNM 407992; ZMB 113045, 113047). Rancho Lucas (ZMB 113053, 113057, 113059). Bahia Honda (ANSP 120806). San Cristobal River (ZMB 113257, 192000). La Merced, Loma Cuzco (USNM 453980). Cabañas Harbor (USNM 453978). Río de Jagua (ANSP 26812, 122777; USNM 11192; ZMB 113040, 113044). Arroyo La Sierra (ZMB 200291). Shell measurements are given in Tab. 1.

Distribution. Although *Hemisinus* in Cuba was firstly described for “all the rivers of the island of Cuba”, this genus is restricted to the Province of Pinar del Río (formerly designated as the Vuelta Abajo region) see Fig. 1.

Table 1. Shell measurements in millimeters of the syntypes of *Hemisinus cubanianus*, *H. ornatus* and *H. pallidus*, as well as of the Cuban *Hemisinus* from different museum collections.

Abbreviations: h, shell height; la, aperture height; ltw, last three whorls; lwl, last whorl length; SD, standard deviation; w, shell width; wa, aperture width; wn, whorls number.

Species			h	w	wa	la	lwl	ltw	wn
<i>H. cubanianus</i>			19.3	12.8	6.4	12.4	16.6	19.29	3.5
syntypes MNHN			17.3	11.3	5.7	11.3	14.5	17.14	4
<i>H. ornatus</i>			26.07	11.92	5.26	12.02	17.0	23.06	7
syntypes (MCZ 94734)			25.80	12.94	6.38	13.25	17.22	22.72	8
			23.36	11.66	5.49	1.66	15.71	20.92	5
			23.04	11.64	4.86	11.80	15.75	20.68	7
<i>H. pallidus</i>			10.72	5.92	2.54	5.41	8.21	11.32	7
syntypes (ZMB 112708)			10.34	6.01	2.63	5.08	5.31	11.07	7
			13.06	5.75	2.77	6.27	8.79	11.44	7
<i>Hemisinus</i>	range	9.1-32	5.6-15.5	2.3-4.4	5.4-17.7	6.8-	8.5-	2-8	
other material examined						20.1	26.8		
n = 689	mean	19.48	9.99	4.63	9.91	13.54	17.12	5.29	
	SD	4.03	1.81	0.99	1.91	2.79	3.42	1.50	

Remarks. D'Orbigny (1842) original description was made for an oval-oblong, thick, smooth shell with elongated, eroded spire and slightly convex whorls; color blackish brown with brown lines or an also brown, transversal band around the middle of its height. The shell described is h = 25 mm and w = 15 mm. D'Orbigny (1842) also stated that this species differed from *Melania brevis* in having a more elongated spire and more oval aperture. Poey (1854) described *H. ornatus* for a conic-pyramidal shell with eight convex whorls, transversely striated below; body whorl more than half of the height of the entire shell; tawny-dark in color, decorated with numerous, dark, interrupted spiral stripes; aperture with columellar margin slightly deflected. The shell figured is h = 28 mm; w = 12 mm; la = 13 mm; wa = 6.5 mm. Posteriorly, Gundlach (1856) described *Hemisinus pallidus* for conical-pyramidal shells with seven slightly convex whorls, transversely striated below; pale olive-green in color with dirty appearance; semi-oval aperture with columella slightly deflected. The shell figured is h = 16 mm; w = 7 mm; la = 7 mm; wa = 3.5 mm. Reeve (1860), published a under *H. cubanianus* a shell that resembles those of *H. pallidus*. This author also considered *H. pallidus* as a Pachychilidae. Brot (1860)

described *Melania dimorpha* from Gabon, mentioning that his new species belongs to the *Melania nigrita* group (which is a Pachychilidae). For Brot (1862, 1870, 1878) and Kobelt (1882), *H. pallidus* Gundlach and *M. dimorpha* are a synonym of *H. cubanianus* d'Orbigny. Brot (1878) also mentioned that *H. ornatus* can be confused with *H. lineolatus* due to the colored spots. According to Arango y Molina (1880), *H. ornatus* Poey, *H. pallidus* Gundlach and *Melania attenuata* Anthony are synonyms of *H. cubanianus*. Furthermore, Arango y Molina (1880) pointed out that because *M. attenuata* only differed from *H. ornatus* in the absence of the series of black dots, *M. attenuata* Anthony could not be placed in synonymy with *M. conica* d'Orbigny. Additionally, he stated that *H. pallidus* is a local variety of *cubanianus* but maintain them as separate species since he did not find transitional specimens. Kobelt (1882) also listed *dimorpha* as a synonym of *H. cubanianus*. Paetel (1890) listed *H. pallidus* as a variety of *H. cubanianus*. Aguayo (1935) considered that *H. ornatus* is a subspecies of *H. cubanianus* and established *Hemisus cubanianus torrei* as *nomina nova* for *H. ornatus*. For Aguayo, proof of *H. ornatus* sub-specific character are the facts that *H. ornatus*' shell diagnostic characters are not always present in every lot, and the existence of other forms like *H. cubanianus pallidus* Paetel and *H. cubanianus martorelli* Aguayo, which are also indicative of the irregularity on the color pattern and. Later, Aguayo (1938) listed three subspecies of *H. cubanianus*: *H. cubanianus martorelli*, *H. cubanianus pallidus* and *H. cubanianus torrei* without further descriptions.

Additional localities. De la Sagra (1853) reported that the species inhabits all of Cuba's rivers. Arango y Molina (1865) stated that the locality of this species is unknown, but the same author later (1878-1880) mentioned as localities the rivers and streams of the Vuelta Abajo (Pinar del Río province). The species have also been reported for Pinar del Río: Arroyo Mamey at the base of the Pan de Guajaibon; El Azufre River (San Andres Village, La Palma municipality); Cuyaguaje River; Hondo River and Mamey Creek (Jaume, 1945; Gutierrez *et al.*, 2005). Pointier *et al.* (2005) stated that the type locality of the species is Pan de Guajaibon (Pinar del Río Province). Canillas Stream (Guajaibon); northern slope of the Cordillera de los Organos; 1km from Guane, Sierra Guane; streams tributaries to Maniman River, San Diego de Tapia; Rangel; Bahia Honda; Canilla River; Las Pozas River; Rancho Lucas; Santa Cruz River; Taco-Taco, Platero, Caiguanabo, San Vicente, Viñales, Bacunagua and San Cristobal Rivers (Gundlach, 1856; Reeve, 1860; Arango y Molina, 1865, 1878; Kobelt, 1882; Richards, 1933; Jaume 1945; Pointier *et al.*, 2005).

Description.

Shell. Small to medium size; globose or conical-pyramidal; thin but solid; usually with four up to eight slightly convex whorls, body whorl expanded at the middle, apex not eroded, or with last whorl bigger than the spire and apex eroded. Suture narrow and simple. Sculpture smooth with some faint longitudinal lines. Color from greenish yellow to dark brown, uniform or with reddish continuous or interrupted stripes in all the shell. Aperture long and narrow, angled above and below, callus and columella fused with external lip, external lip simple, inside white (Tab. 1, Fig. 2A-C).

Embryonic shell (es). Globose, color light brown with or without reddish interrupted lines or spots, spire with three to four convex whorls, body whorl inflated and slightly angulated at the middle. Suture simple with sub-sutural line evident at the last two whorls. Sculpture consisting of conspicuous axial growth lines and irregularly spaced spiral lines. Aperture wide, angled above and with a semi channel below, bulky columella (Fig. 3A). Protoconch with two whorls sculptured with axial lines (Fig. 3B-C). Usually three juveniles in different developmental stages inside the brood pouch. Variations of shell measurements are show in Table 2.

External anatomy. Operculum (op) oval, quitinous, brown in color, paucispiral, with small subterminal nucleus of three or four whorls (Fig. 4B). Animal with head-foot black and pale visceral whorls. Snout (sn) moderately long, broad and crossed by minute transversal wrinkles. Short tentacles, broad at the base and narrow at the tips. Mantle edge (mep) with 15 – 23 papillae ($n = 24$; mean = 22.4; SD = 2.43), Fig. 4A.

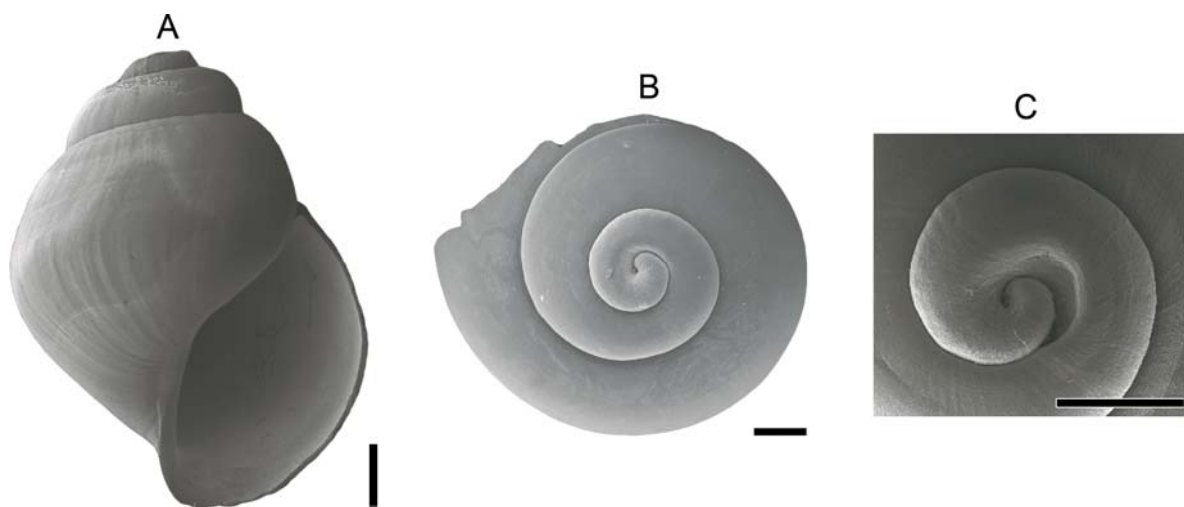


Fig. 3 A–C. Embryonic shell of *Hemisinus cubanianus* (ZMB 192002) obtained from a brood pouch.

A. Embryonic shell, apertural view, scale bar = 300 μm . – B. Embryonic shell, apical view, bar = 300 μm . – C. Initial whorl of embryonic shell, apical view, bar = 200 μm .

Table 2. Range in millimeters, mean and standard deviation of embryonic shells obtained from the brood pouch of *Hemisinus cubanianus* females (ZMB 107158, 192002, 192003, 200291) from Cuba. Abbreviations: de, protoconch diameter; he, embryonic shell height; SD, standard deviation; we, embryonic shell width.

<i>H. ornatus</i> embryonic shell	he	we	de
range	1.55 – 4.79	1.49 – 3.60	0.59 – 0.90
mean	2.94	2.11	0.60
SD	1.01	0.68	0.10

Mantle cavity. Osphradium (os) close to the anterior part of the ctenidium, narrow, rounded tips and slightly curved. Ctenidium (ct) straight, long, narrowing anteriorly and posteriorly, 3–3.5x longer than the osphradium. Hypobranchial gland (hg) narrow, little developed. Rectum (r) opening into a simple anus (a) close to the mantle edge (Fig. 4C).

Radula. For 34 animals an average of 145 teeth rows were found (SD = 18.53). Rachidian twice broad as long, with semi-concave anterior end, and a basal denticle at each outer corner; cutting edge 3-4/1/3-4; central cusp with round tip, scarcely differentiable from the denticles, being sometimes shorter than the latter; denticles may be “subdivided” (Fig. 5C) and have also a round tip. Lateral teeth larger than broader, 2/1/2; with short, broad and rounded central cusp flanked by semi-rounded cusps (Fig. 5B). Marginal teeth long and spatulated with 6 + 15-16 cusps; inner marginal teeth with broad and rounded-tip flanges; outer marginal with narrow and sharp-tip flanges (Fig. 5D).

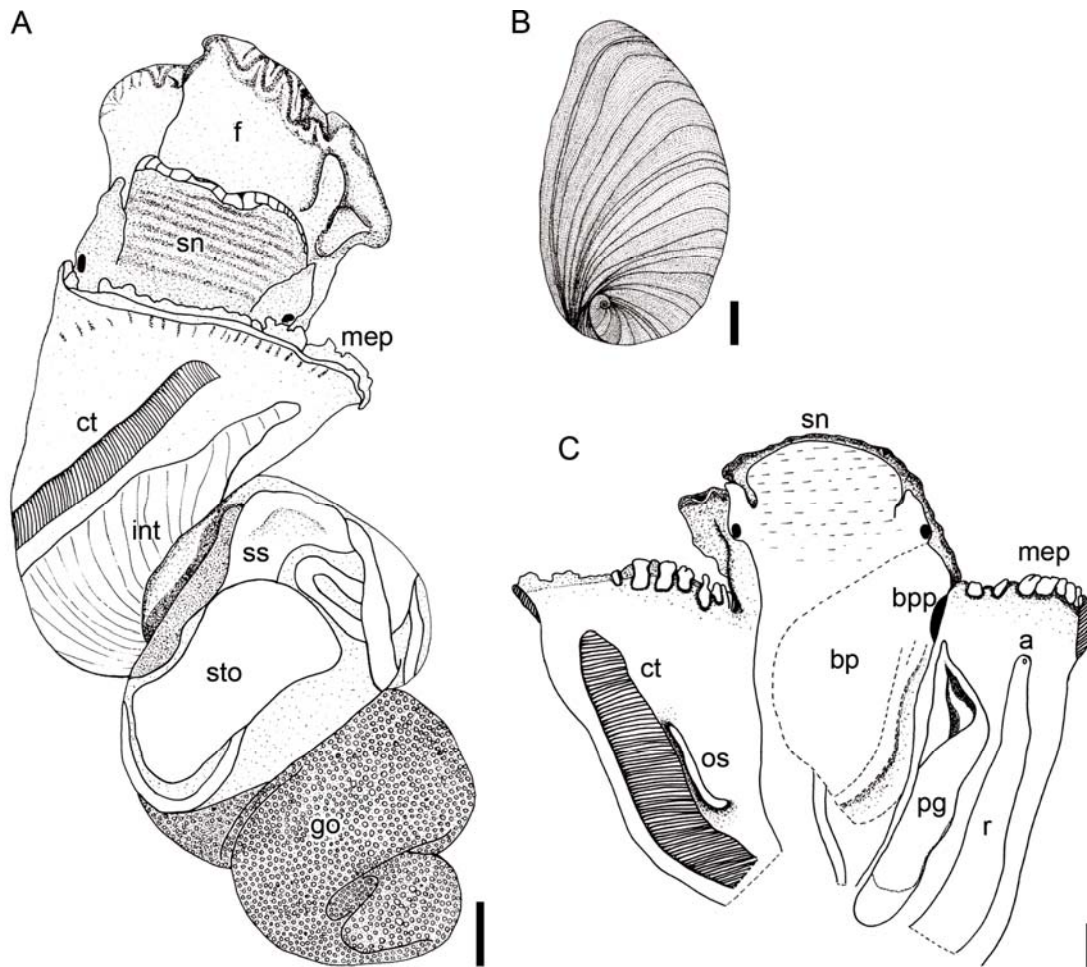


Fig. 4 A–C. Anatomy of *Hemisinus cubanianus* (ZMB 192003, 200291)

A. External anatomy, ventral view. – B. Anatomy of the mantle cavity and brood pouch. – C. Anatomy of the brood pouch. Bar = 1 mm. Abbreviations: a, anus; ant., anterior; bp, brood pouch; bpp, brood pouch porus; ct, ctenidium; f, foot; go, gonad; int, intestine; mep, mantle edge papillae; os, osphradium; pg, pallial gonoduct; post., posterior; r, rectum; sn, snout; ss, style sac; sto, stomach.

Foregut. Buccal mass (bm) short and globose. Radular sac short with the radula dorsally visible, radula posteriorly eight-shaped curved reaching the base of the oesophagus (oes). Strong muscular retractors inserting dorso-laterally at the middle of the buccal mass. Salivary glands (sg) short, opening dorsal-anterior to buccal cavity, both passing through the nerve ring and then folded to the left between the nerve ring, the supra-esophageal ganglion (sp), and the aorta, with the left salivary gland attached by tissue to the pleural ganglion. Then both glands shortly run parallel to the oesophagus finishing below it. Oesophagus as a simple tube, extending posteriorly and then bounding the posterior end of the gastric chamber to enter it at the middle, no presence of mid-esophageal gland (Fig. 6A).

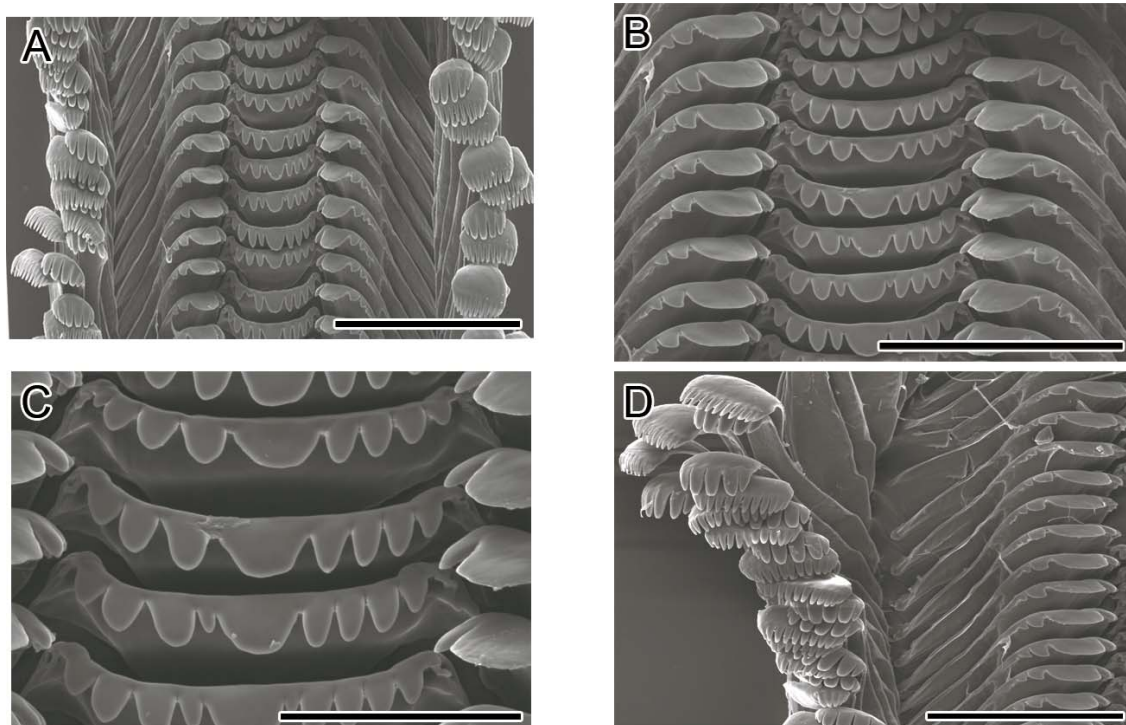


Fig. 5 A–D. Radula of *Hemisinus cubanianus*, view from above (ZMB 192002b). A. Middle radular ribbon, bar = 100 µm. – B. Rachidian and lateral teeth, bar = 100 µm. – C. Rachidian, bar = 50 µm. – D. Lateral and marginal teeth, bar = 50 µm.

Midgut. Oesophagus opening at the mid-left of the midgut's floor (Fig. 6B). Roof of the midgut with a long but narrow sorting area (sa), exhibiting four striated middle “branches” and a big cuticularized (cu) anterior portion also with elevated striae. Barely differentiated tip of the marginal fold (mf) close to the middle of the sorting area, U-shaped, bordering the sorting area and folding itself until reaching posteriorly the major typhlosole (t1). Accessory marginal fold (amf) emerging lateral to the oesophageal aperture, running parallel to the marginal fold until reach posteriorly the big and elaborated sorting area pad (sap). Gastric shield (gs) small, continuous with cuticle of the midgut roof and crystalline style pocket. Two small, rounded and almost parallel caecal folds (cf) at the posterior end of the gastric shield. Glandular pad (gp) big, long and narrow, with an elaborated accessory pad (ap) at the left of its anterior tip. Crescentic ridge (cr) emerging below the oesophageal aperture, bordering the glandular pad and finishing close to the posterior tip of the caecal folds without entering the caecum (c). Paired digestive glands (dgd) opening into a deep groove between the proximal tip of crescentic ridge and left side of the glandular pad, Shallow caecum underneath anterior tip of glandular pad. Style sac (ss) and intestinal groove separated by fused thyphlosoles (Fig. 6B).

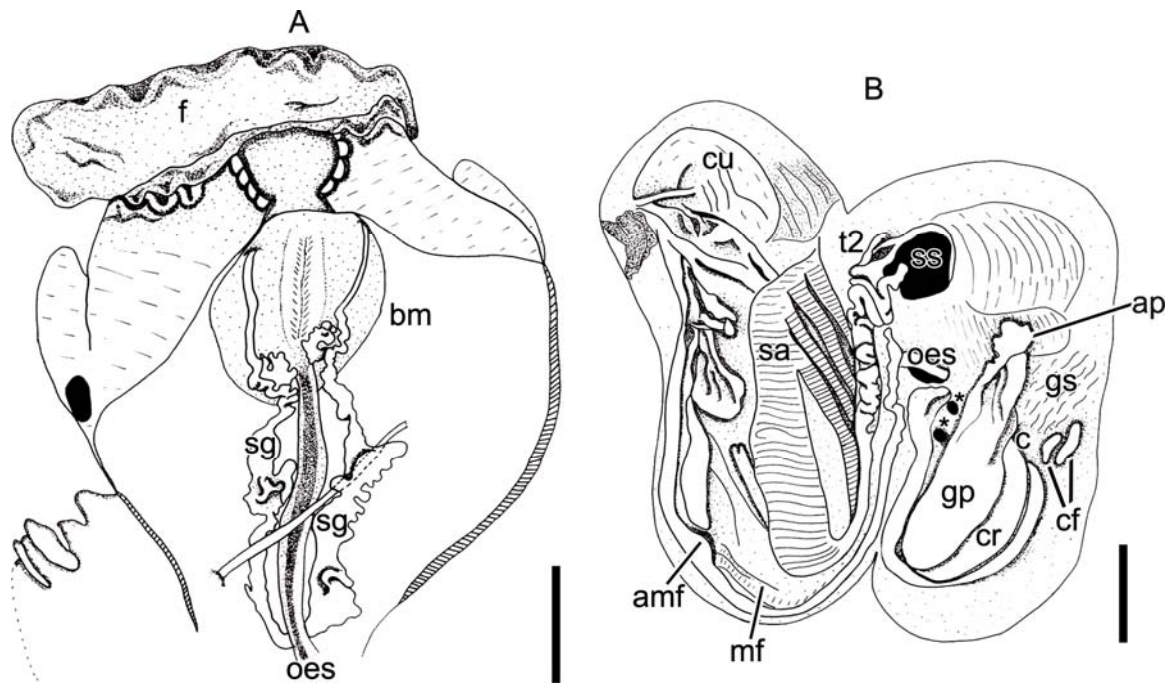


Fig. 6 A–B . Digestive system of *Hemisinus cubanianus*.

A. Foregut morphology, dorsal view (ZMB 192003), bar = 2 mm. – B. Midgut morphology, dorsal view (ZMB 107158). Midgut opening laterally on the right, roof reflected to the left; anterior is uppermost; scale bar = 1 mm. Abbreviations: amf, accessory marginal fold; ap, accessory pad; bm, buccal mass; c, caecum; cf, caecal folds; cr, inner crescentic ridge; cu, cuticle lining stomach roof; gp, glandular pad; gs, gastric shield; mf, marginal fold; oes, oesophagus; sa, sorting area; sg, salivary glands; ss, style sac; t2, minor thyphlosole.

Hindgut. Proximal intestine (int) passing underneath the style sac (ss) to border its anterior tip, extending to form a narrow U-curve between the anterior end of the gastric chamber and the right side of the style sac, continuing behind the kidney, entering pallial roof finishing into a straight rectum with a simple anus close to the mantle edge (Fig. 4A).

Reno-pericardial system. Kidney large, narrow, reaching anteriorly the pallial cavity between intestine and the posterior gonoduct and ctenidium. Posterior end bounded by style sac and partly gastric chamber. Pericardial coelom narrow, extending underneath kidney alongside style sac.

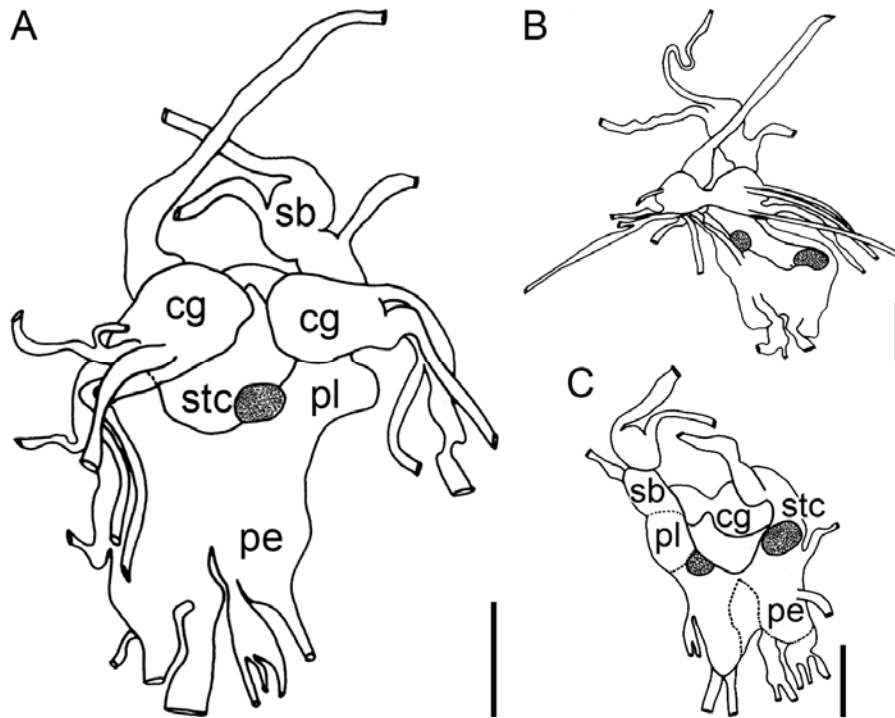


Figure 7 A–C. Circum-oesophageal nerve ring of *Hemisinus cubaniana* (ZMB 192003). A. Dorsal view of the circum-oesophageal nerve ring *in situ*, dorsal view. – B. Circum-oesophageal nerve ring *in situ*, dorsal view. – C. Ventral view detail of the nerve ring, respectively. Scale bars = 0,5 mm. Abbreviations: cg, cerebral ganglia; pe, pedal ganglia; pl, pleural ganglia; sb, sub-oesophageal ganglion; stc, statocyst.

Nervous system. Cerebral ganglia (cg) connected by a short commissure, each ganglion producing five nerves. Pleural ganglia (pg) lying behind and below cerebral ganglia and connected to the latter by short and thick connectives. Sub-oesophageal ganglion (sb) emerging dorsal to the left pleural ganglia, producing two stout nerves and a thin accessory nerve. Supra-oesophageal ganglia (sp) simple, crossing above the salivary glands and the oesophagus. Pedal ganglia widely fused, with two prominent anterior nerves and seven smaller accessory nerves. Statocysts dorsal-posterior to the pedal ganglia, with long and thin connective to the cerebral ganglia; approximately 140 statoconia which can be rounded or elongate and may occur free or in compact masses (Fig. 7).

Reproductive system. Female. Gonad (go) from tip of visceral whorls to posterior end of gastric chamber over the digestive gland (dg), usually of cream or grayish color and sandy appearance, hardly distinguishable from the latter. Pallial gonoduct slightly more than half open. Gonoduct emerging ventral from the gonad, entering folded to the posterior pallial gonoduct. Lateral lamina with main oviduct-spermatophore bursa and albumen gland separated by a narrow, tubular-like portion of tissue which emerges ventrally close to the

end of the glands and runs forward until the end of the anterior third. An accessory fold at the ventral side of the lamina runs parallel to the latter, finishing at the anterior glandular portion closing the gonoduct. Another fold coming from the main oviduct is attached to the medial lamina at the anterior third shaping the sperm gutter. Floor of the lateral lamina and dorsal side of the glandular portion deeply striated (Fig. 8). Medial lamina profusely fluted. Along the dorsal side of the main oviduct and the joining of the two laminae is a deep and narrow longitudinal groove ending at the anterior tip (Fig. 8).

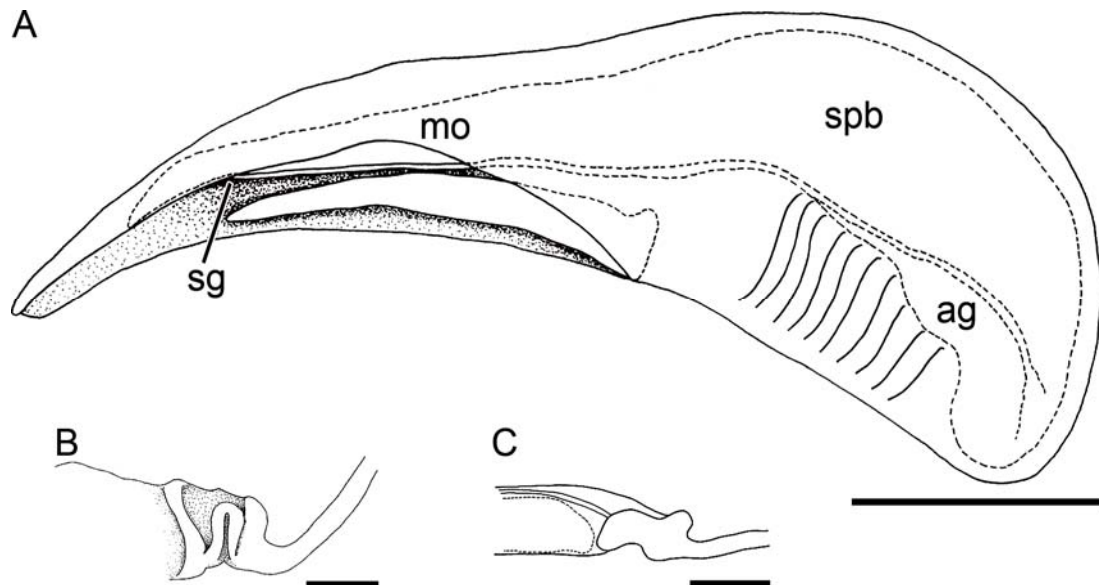


Fig. 8 A. External, dorsal view of a female pallial oviduct of *Hemisinus cubanians* (ZMB 113273). – B. Detail of the pallial oviduct in ventral view. – C. Detail of the pallial oviduct in dorsal view. Scale bars = 1 mm. Abbreviations: ag, albumen gland; mo, main oviduct; sg, sperm gutter; spb, spermatophore bursa.

Females with dorsal brood pouch (bp) at the right side of the neck. Floor of the pouch exhibits a wide groove finely striated longitudinally; the groove runs forward from the posterior part of the pouch to the brood pouch porus (bpp). Roof with a couple of elevated folds above the inferior groove (Fig. 9B). There are no trabeculae into the lumen of the brood chamber. Although the mean number of juveniles is three, between one and five in different developmental stages could be found ($n = 10$). Juveniles (j) firmly attached to the brood pouch wall by means of a tissue (which is different from the wall) wrapping them. Aperture of the juveniles full with fatty tissue. Brood pouch porus at the right side of the foot-head in front of the eye, wide, showing an internal flap below (Fig. 9A). Sexual dimorphism determined by the presence of brood pouch porus in females.

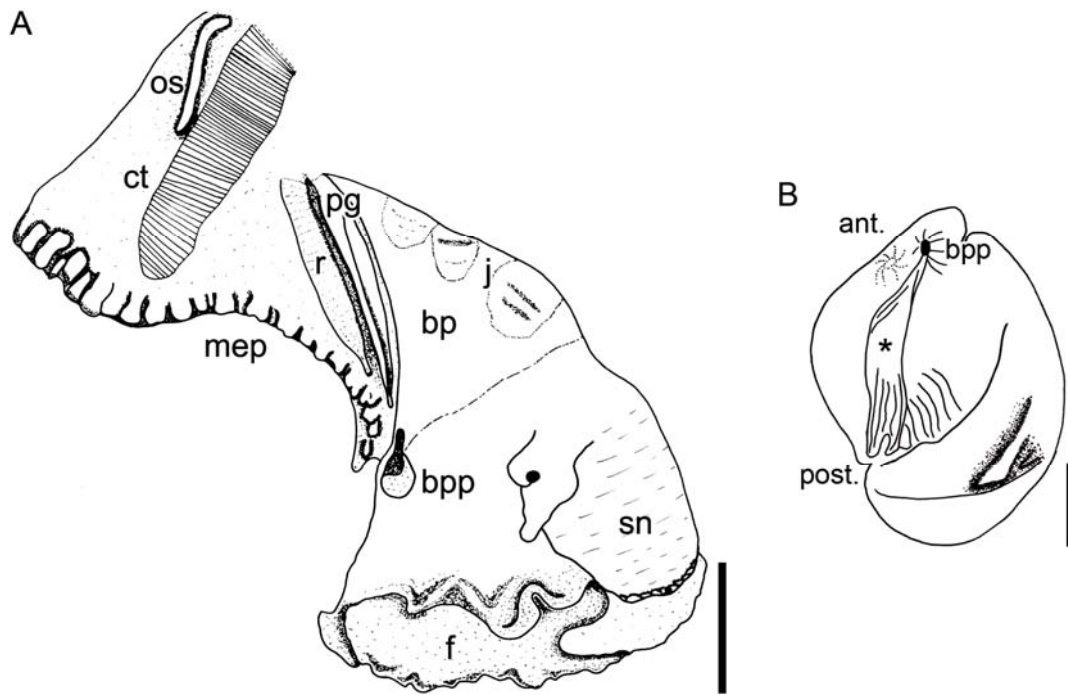


Fig. 9 A–B. Brood pouch anatomy of a mature female of *Hemisinus cubanians* (ZMB 107160A).

A. Location of the brood pouch and of the brood pouch porus. Bar = 1 mm. – B. Internal view of the brood pouch, opened laterally on the left; bar = 1 mm. Abbreviations: ant., anterior; bp, brood pouch; bpp, brood pouch porus; ct, ctenidium; f, foot; j, juveniles; mep, mantle edge papillae; os, osphradium; pg, pallial gonoduct; post., posterior; r, rectum; sn, snout; sm, smooth muscle; * brood pouch floor's groove.

Male. Gonad similar to the female. Vas deferens entering with a double loop towards the posterior part of the pallial gonoduct. Pallial gonoduct open almost along its entire extension except for a fused posterior segment. Lateral lamina exhibits a posterior gland projecting as a closed-tubular anterior tip, which, after a U-curve, opens through a porus into a wide pocket-like structure. This “pocket” structure is formed from a flap of dense tissue. In front of the anterior tip of the pocket, additional tissue forms a thin ventral septum running parallel to a deep dorsal groove (Fig. 10). Medial lamina simple, without remarkable features. Sexual proportion 64% females, 36% males (n = 25).

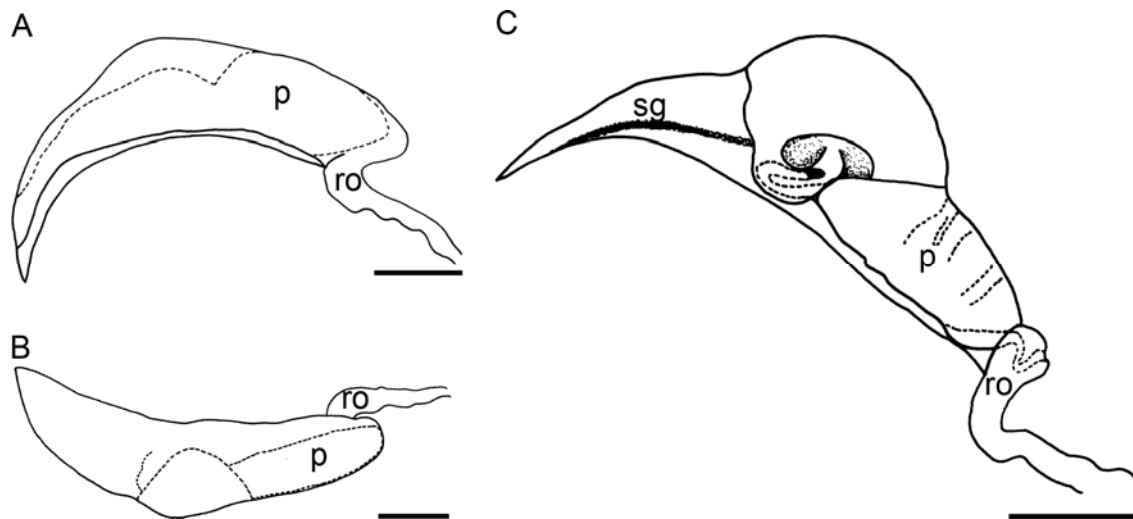


Fig. 10 A–C. *Hemisinus cubanianus* (ZMB 113273) male pallial gonoduct anatomy. Anterior is left.

A. Dorsal external view of the pallial gonoduct. – B. Ventral external view of the pallial gonoduct. – C. Internal view of the lateral lamina. Scale bars = 1 mm. Abbreviations: pr, prostate; ro, renal oviduct; sg, sperm gutter.

Ecology. Poey (1854) reported that these snails are herbivorous, feeding on aquatic plants and cabbage but also on dead crabs. Poey warned that he himself introduced some specimens of *H. ornatus* in Marianao River, “... a quarter of a league above the bridge...”, which are successfully reproducing at the new place. According to Gutiérrez *et al.* (2005), the species was present in high numbers and with a stable population through one year sampling in El Azufre River (which has little signs of human activity), inhabiting the sites together with low densities of *Tarebia granifera*.

***Hemisinus martorelli* Brot, 1878**

Hemisinus martorelli Brot, 1878: 377, pl. 39, fig. 3.

Hemisinus cubanianus martorelli – Aguayo, 1938: 229. Pointier *et al.*, 2005: 30.

Type locality. “Cuba”.

Type material. Not found. Probably deposited in Brot’s collection at the MHNG.

Remarks. Brot (1878) described *H. martorelli* as a turritiform solid shell; color olive green or black; decollate apex; oval aperture, acute above and round below, without basal channel. The shell figured is h = 22 mm; w = 9.5 mm; la = 10 mm; wa = 4.5 mm; wn = 5. According to the author, the shell was previously labeled as *M. attenuata*. Brot (1878) considered that it is a new species since it differs from *M. attenuata* and *H. ornatus* in color and

general shape. Aguayo (1938) mentioned without further explanations that *H. martorelli* Brot is not a different species but a subspecies of *H. cubanianus*. Aguayo & Jaume (1954) considered *H. cubanianus martorelli* as a morph rather than a subspecies. In Brot's (1878) figure, the shell of *H. martorelli* resembles those of *H. ornatus*. However, nothing can be concluded about the identity of the species until examination of the type material.

Statistical analyses.

PCAs were performed for the raw data and for the standardized residuals of the variables after a linear regression. In PCA, if most of the variance is accounted for by the first, or the first and second components, the analysis can be considered as successful. In the analysis of the raw data of the whole sample population (including the type material), the first component accounts for 90.4% of the total variance. Nevertheless, the eigenvalues of the shell height (h), shell width (w) and aperture length (la) are very similar, precluding to draw a firm conclusion. Although in the PCA with standardized residuals the first two components only explain 52.78% of the variance, the eigenvalues permit to select shell height (h) and aperture length (la) as shape explanatory variables for the Cuban *Hemisinus*. Subsequent scatterplot analysis made with the standardized matrix shows that the two variables selected (h and la) are strongly related. The type material was included in the scatter plot together with the other material examined. According to the diagram, the shell size is distributed between the small shells of the types of *H. pallidus* and the large shells of the type of *H. ornatus*, with *H. cubanianus* in the middle (Fig. 11). This first set of analyses indicates that the three species are different.

However, I performed an FOS in order to filtrate the “noise” produced by size, scaling and rotational effects. The result of this analysis shows that the shape of *H. cubanianus* is significantly different from the shell shapes of *H. pallidus* and *H. ornatus*. It can also be observed that the shapes of *H. ornatus* and *H. pallidus* are closely related (Fig. 12A). An additional box-plot analysis also confirmed this result (Fig. 12B).

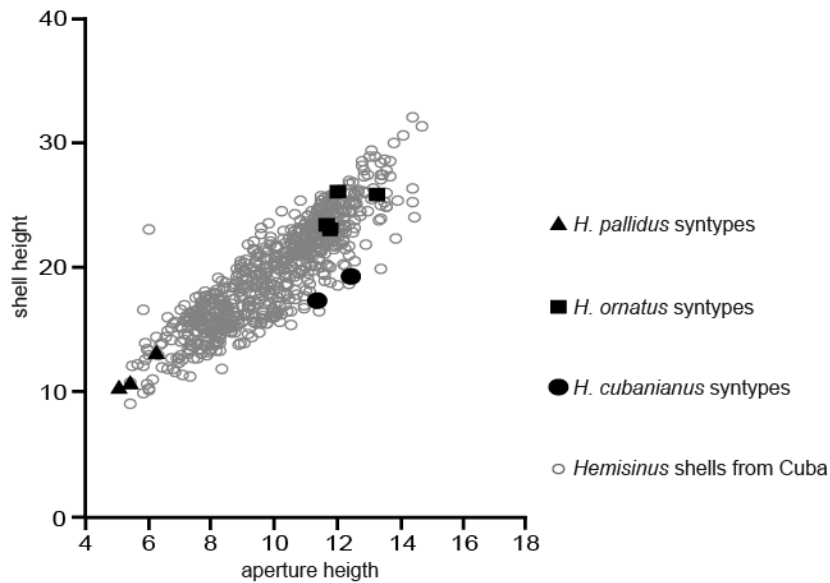


Fig. 11 Scatterplot analysis of the relation shell height vs. aperture height of *Hemisinus* from Cuba.

▲ = *H. pallidus* syntypes (ZMB 112708); ■ = *H. ornatus* syntypes (MCZ 94734); ● = *H. cubanianus* syntypes (MNHN); ○ = other material examined of *Hemisinus* from Cuba.

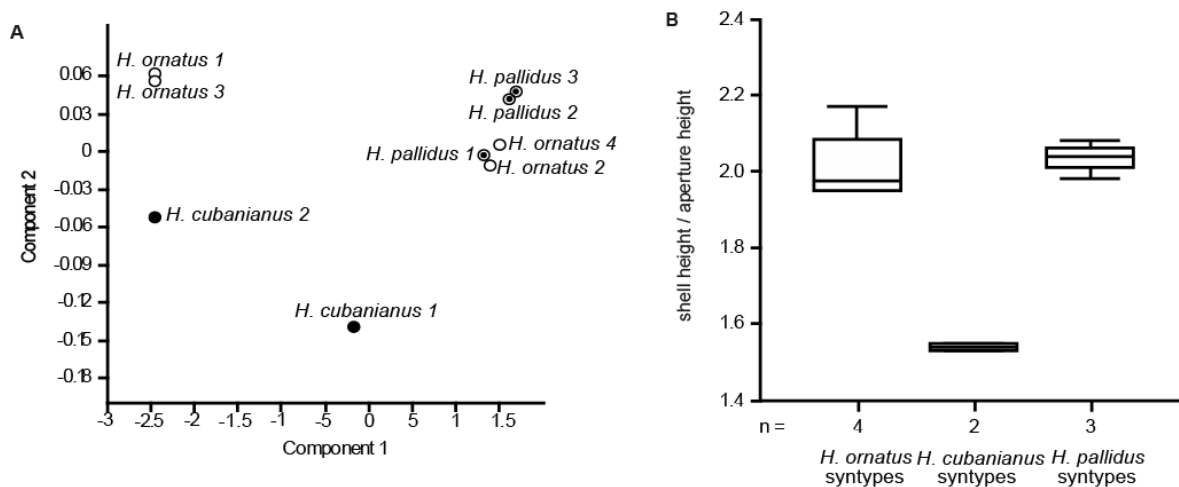


Fig. 3 A. PCA analysis of the type specimens of *Hemisinus* from Cuba based on the FOS matrix. The results are relationships between shell shapes. – B. Box-plot of the relation shell height vs. aperture height of the type material of *Hemisinus* from Cuba.

● = *H. cubanianus* syntypes (MNHN); ○ = *H. ornatus* syntypes (MCZ 94734); ⊙ = *H. pallidus* syntypes (ZMB 112708).

Molecular phylogeny of the Greater Antilles *Hemisinus*

The topologies obtained for the two genes analyzed (16S and COI) are largely identical. Consequently, only the COI tree is shown (Appendix 2). The molecular phylogeny reveals a well-supported monophyletic group comprising the Greater Antilles *Hemisinus*, with *H. lineolatus* from Jamaica basal to the Cuban representatives. On the species level, both *H.*

cubanianus and *Cubaedomus brevis* are separate clades. *H. cubanianus* also forms a monophyletic group. Nevertheless, this clade includes four different haplotypes segregated in two well-defined groups.

Discussion

Taxonomy

It has been stated that the shells of *Hemisinus cubanianus* are very variable in color, ranging from dark brown to light yellow, with the inside of the aperture being much lighter (Pointier *et al.*, 2005). Besides Pointier *et al.* (2005), Brot (1862, 1875), Arango y Molina (1880), Kobelt (1882) and Aguayo (1935) considered *H. cubanianus* as the sole Cuban species of the genus and therefore regarded the other described species as synonyms. Morphometric analyses of the shell shape allow me to conclude that there are significant differences between the shells of *H. cubanianus* and *H. ornatus*, and no significant variation between *H. ornatus* and *H. pallidus*. However, it is also remarkable that shells of *H. cubanianus* were neither found in the different historical museum collections, nor in field excursions made very recently. It can be hypothesized that either the species is already extinct on the island or that the syntypes are only an “aberrant” form. Although *H. cubanianus* shells exhibit a different shape, they are within the size range of the rest of the reviewed samples. Based on the above statements, here I consider the syntypes of *H. cubanianus* as “atypical” shells, and *H. ornatus* and *H. pallidus* as the same species. Consequently, the valid name of the species is *H. cubanianus* since *cubanianus* is the oldest available name and the other species names are junior synonyms. The remaining *H. martorelli* could also be a synonym of *H. cubanianus*, but a decision about the identity of this species can only be made after analysis of the type material.

Intraspecific variation

In Pacific islands like Tahiti and Moorea, geographical barriers are no impediment for the dispersal of land snails. Despite this absence of barriers, marked differences are observed between conspecific populations which appear highly structured in terms of shell shape, shell color, banding patterns and mitochondrial DNA haplotypes (Gillespie *et al.*, 2008). From this statement it could be expected that populations of continental mollusks with relatively low dispersal capabilities may exhibit strong differences among them. Nevertheless, anatomical and morphological comparisons of *H. cubanianus* populations with different shell color patterns show that there are no differences along their distribution area. Although the phylogenetic analysis of the different *H. cubanianus* populations shows the presence of two haplotype groups, when the topology is contrasted with the locality it becomes evident that the catchment area plays a significant role. Populations belonging

to catchments draining to the north-western coast have different haplotypes from those populations living in catchments draining to the south-western coast. However, this haplotype diversity is presumably not a signal of an ongoing ecological speciation process since morphometry, morphology and anatomy are not showing significant differences between populations. Consequently, it can be concluded that *H. cubanianus* is a monophyletic species with wide shell polymorphism.

Anatomy

Regarding anatomical features, *Hemisinus cubanianus* from Cuba and *Hemisinus lineolatus* from Jamaica have the same characteristics in operculum, mantle edge, mantle cavity (e.g. osphradium length and position, ctenidium size, rectum and anus shape) and midgut, as well as a similar sex ratio. Nevertheless, *H. cubanianus* exhibits a higher degree of complexity in some anatomical structures when compared with *H. lineolatus*.

While in *H. lineolatus* the midgut has a flat sorting area and a simple marginal fold, in *H. cubanianus* the sorting area is more structured, forming raised “branches”, and the marginal fold is much elaborated.

In the nervous system, differences in the number of pedal nerves and statoconia are also found between both species. *H. lineolatus* has up to 50 rounded statoconia and three accessory nerves arising from the pedal ganglia, while *H. cubanianus* has more than 100 statoconia, which can be round or spindle-shaped and pedal ganglia with seven accessory nerves.

Although in both *H. lineolatus* and *H. cubanianus* the pallial gonoduct is almost completely open in males and only half open in females, the anatomy of this structure also shows marked differences. The female and male pallial gonoducts of *H. cubanianus* present more septae, better defined glands, and deeper and more numerous grooves than *H. lineolatus*.

Poey (1854) stated that *H. cubanianus* is viviparous, and reported numerous small individuals (the biggest with 3.5 spire whorls) inside the females. I found that *H. cubanianus* has a dorsal brood pouch in the neck, which contains up to five juveniles in different developmental stages, firmly attached to the inner brood pouch wall by additional tissue. Although no chemical or histological studies were conducted on *H. cubanianus* in order to prove its viviparity, the possession of brood pouch walls covered with a thick layer of glandular and fat tissue may be an indication of this mode of reproduction. Concerning the brood pouch, both species *H. cubanianus* and *H. lineolatus* share the position, as well as the absence of trabeculae dividing the internal space of it. However, *H. cubanianus* exhibits a wide flap on the entrance of the brood pouch porus, a feature that is not present in *H. lineolatus*. Additionally, the inner brood pouch shows differences. While *H.*

cubanius has a deep lateral groove with small accessory grooves that lead towards the porus, there are no such structures in *H. lineolatus*.

Biogeography

Although the species attributed to *Hemisinus* are distributed in continental Central and South America as well as in some of the islands of the Greater Antilles, a vicariant origin of *Hemisinus* is less parsimonious since geological data strongly supports the assumption that the West Indies have been islands throughout most of the Cenozoic (Buskirk, 1985; Hedges *et al.*, 1992; Iturralde-Vinent & MacPhee, 1999; Hedges, 2006; Ricklefs & Bermingham, 2008), and that the Greater Antilles were subject to periods of elevation alternating with periods where most of the terranes were submerged (Chapter 2.3.1).

Simpson (1894) stated that continental gastropods have four possibilities of island colonization: by former land connections; through overwater dispersal by means of oceanic currents, winds or storms; by bird transport; by human-mediated dispersal, claiming also that mollusks or their eggs can be attached to plants and to other animals reaching new localities in that way. Simpson (1894) mentioned that Darwin has shown that some land snails will live for considerable periods of time in sea-water, and that many of the freshwater species can remain alive when being exposed to air or to more or less brackish waters for some time and under certain circumstances. Consequently, and based on the facts that (i) there is increasing evidence of biotic exchange between Cuba and Jamaica (i.e. truncatellid land snails, freshwater fishes), (ii) the current distribution of the biota in the Greater Antilles suggests a colonization pathway from Central America via Cuba or Jamaica (Buskirk, 1985; Hedges, 1996), and that (iii) the possession of an operculum may enable *Hemisinus* to survive disadvantageous conditions, a dispersal origin of the group appears more probable than vicariance.

Brown & Pilsbry (1914) suggested that the present *Hemisinus* species of Cuba and Jamaica are descendants of the same South American ancestor because *Hemisinus* fossils from Antigua resemble the “*Hemisinus*-like” shells from mainland South America (sculptured with spiral cords) and from Cuba (without sculpture). However, there is no an approximate estimation of how much time takes to a species to lose or gain its shell ornamentation. Additionally, since the extant species of freshwater gastropods are not well defined in South America, and since the fossil record of freshwater mollusks in the Caribbean region is very fragmentary, it is difficult to say whether the fossils that resemble extant Thiaridae and Pachychilidae are really their ancestors or not.

Conclusions

According to the anatomical, molecular and statistical analyses, the former number of Cuban species assigned to the genus *Hemisinus* is reduced to two: the monophyletic *H. cubanianus* and *H. martorelli*. Although the species status of *H. martorelli* is in doubt until more evidence will be obtained, the name is retained for the time being.

In this work, the internal anatomy of *H. cubanianus* is described for the first time, confirming its affiliation to the genus *Hemisinus* and the possession of a highly polymorphic shell. The fact that *H. cubanianus* midgut and reproductive system anatomies are more complex than in *H. lineolatus* from Jamaica, confirmed Iturralde-Vinent & MacPhee's (1999) and Woods' (2001) proposal. They stated that taking into account the Caribbean geological history, less divergent forms should be found in the western Greater Antilles (Puerto Rico and Hispaniola) or even in Jamaica, and the more derived forms in Cuba (Iturralde-Vinent & MacPhee, 1999; Hedges, 2001). This is also supported by the topology of the phylogenetic analysis, where a well defined monophyletic Cuban clade subsequently diverges to *H. lineolatus*.

Concerning the biogeography of the group, geological and distributive data of the Greater Antilles *Hemisinus* fauna, point out to a continental origin with dispersion to the Islands.

5. Mesoamerican freshwater Cerithioidea

5.1 Annotated catalogue of the nominal taxa of freshwater Pachychilidae from Mesoamerica (Mollusca, Caenogastropoda, Cerithioidea)

*To Isaac Lea
"It was my choice or chance or curse
to adopt the cause for better or worse
and with my worldly goods & wit
and soul & body worship it"
(Edgar Allan Poe, 1829)*

Introduction

The cerithioid family Pachychilidae is widely distributed in the Mesoamerican region. A comprehensive taxonomic and systematic revision of this group, based on modern standards, is lacking to date. The latest complete monographic treatment is that of Fischer & Crosse (1870-1902) whilst among recent systematic literature only Thompson (2008) attempted to summarize the species names.

Mesoamerica comprises a complex combination of ecological systems and topographic zones which have been grouped into two broad categories: the lowlands, with their tropical and subtropical climates, and the *altiplanos* or highlands, which range from dry tropical to cold mountainous climates (Coe, 2002). Except for the northern Maya lowlands (especially the northern portion of the Yucatán peninsula), Mesoamerica is rich in freshwater ecosystems. Additionally, almost all types of ecosystems are present in Mesoamerica, making this a region with one of the richest levels of biodiversity in the world, although the number of species in the red list of the IUCN is growing every year (Popenoe de Hatch *et al.*, 1993-1999).

In Mexico while the largest lakes are found in the central part of the country, the longest rivers originate mainly in Guatemala but flow through the state of Chiapas and then empty into the Gulf of Mexico. In Central America, the larger rivers flow to the Caribbean. The Pacific basin comprises only small streams which are steep and shallow due to the topography (MacPherson, 1990). The longest river in Mesoamerica is the Usumacinta, which forms in Guatemala at the convergence of the Salinas (Chixoy) and La Pasion River, draining north into the Mexican Gulf. Other longer rivers in the region include the Motagua of Guatemala; the Ulúa, Aguán and Hondo of Honduras; the Coco, at the Honduras-Nicaragua boundary; the Río Grande and Escondido of Nicaragua, and the San Juan, which forms a section of the Nicaragua-Costa Rica border. The large lakes of the

region include Lake Nicaragua, Lake Chapala, Lake Peten Itza, Lake Izabal, Lakes Atitlan and Amatitlan, Lake Güija and Lake Managua (MacPherson, 1990).

Since the identification of species in the Mesoamerican Pachychilidae is difficult mostly because their quite variable shells, and also because of the confused older taxonomic literature, there are many uncertainties regarding generic affiliation and validity of many species-group taxa. Although there are also representatives of Pachychilidae in the Greater Antilles and South America, this work is restricted to the Mesoamerican region because its great number of described species does not have a clear generic affiliation. Consequently, a critical systematic revision has been carried out on Mesoamerican members of the Pachychilidae Troschel, 1858. Available type and reference material was reinvestigated and the literature was critically reviewed in order to contribute to a taxonomic fundament for future systematic studies on these freshwater snails. The purposes of this catalogue are (i) to provide a means of identifying the various species, and (ii) to present a synopsis of the literature of these genus- and species-groups.

Specific materials and methods

This inventory is based on the examination of type material from the Academy of Natural Sciences, Philadelphia (ANSP); Florida Museum of Natural History (FLMNH); Geowissenschaftliche Sammlung der Universität Bremen (GSUB); Muséum d'Histoire Naturelle de la Ville de Genève, Geneva (MHNG); Muséum National d'Histoire Naturelle, Paris (MNHN); Natural History Museum, London (BMNH); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) and Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin (ZMB). Shell parameters of type specimens including shell height, width, aperture length, aperture width, last whorl length, and height of last three whorls were measured with a calliper precise to 0.1 mm; whorls were counted. All specimens were compared with the original descriptions and illustrations.

The genus-group taxa are arranged chronologically with the aim of recounting the history of the group in the Neotropics. Species-group taxa are listed in alphabetical order. The type locality is in quotation marks, the information in brackets refers to the translation or the country of the type locality. Under additional localities, places other than the type locality are listed.

Abbreviations used: h, shell height; HT, holotype; la, aperture length; LT, lectotype; ltw, last three whorls height; lwl, last whorl length; PLT, paralectotype; PT, paratype; ST, syntype; w, shell width; wa, aperture width; wn, whorls number.

Results

A – List of genus-group taxa in chronological order

***Pachychilus* I. Lea & H.C. Lea, 1850**

Pachychilus I. Lea & H.C. Lea, 1850: 179. Petit, 1853: 159. Troschel, 1858: 114. Brot, 1870: 273. Martens, 1874: 358. Brot, 1874: 19. Tryon, 1883: 252. Fischer, 1885: 701. Kobelt, 1886: 275. Fischer & Crosse, 1892: 320, 328. Martens, 1899: 437. Thiele, 1928: 381. Thiele, 1929: 189. Wenz, 1938: 685. Morrison, 1951: 8. Morrison, 1954: 364-366. Pilsbry, 1956: 31. Perriliat *et al.*, 2008: 261.

Pachycheilus – H. Adams & A. Adams, 1854: 298. – Gray, 1857: 102. Chenu, 1859: 288. Fischer, 1862: 283. Martens, 1865: 51. Paetel, 1890: 363 [emendation for *Pachychilus*].

Pachychilius – Strebel, 1873: 35 [emendation for *Pachychilus*].

Type species. Pachychilus cumingii I. Lea & H.C. Lea, 1850, by monotypy.

Remarks. *Pachychilus* is composed from two words “Pachys” [Greek: thick] and “cheilos” [Greek: lip], which refers to the allegedly remarkable straight lip and thick columella. I. Lea & H.C. Lea (1850) pointed out that *Pachychilus* differs from species of *Melania* Lamarck, 1799 not only by its thickened lip, but also by absence of a sinus at the base of the aperture and a multispiral operculum with a sub-central nucleus. *Pachychilus* is the first generic name that has been established for Neotropical Pachychilidae and was originally erected to contain only one species, *Pachychilus cumingii* I. Lea & H.C. Lea (1850) from Copan, Honduras. Some authors used the spelling *Pachycheilus* in reference to the allegedly correct version “cheilos”. However, Fischer & Crosse (1892: 320) established that the Greek letters “ε ι” change into “i” when the word is latinized. Irrespectively, the name as originally spelled represents the correct version according to the stipulations of the code (The Code, Art. 11.8, 56.2) and *Pachycheilus* is only an emendation of the original name.

The taxonomy of *Pachychilus* is fraught with difficulties due to the inconsistent usage of names, the inability of previous authors to correctly delimitate natural groups, and misunderstandings especially with regard to the identity of the type species. For example, this Central American genus was treated as a group without taxonomical hierarchy within *Melania* by Martens (1874) or as a subgenus by Fischer (1885) and Kobelt (1886). Fischer & Crosse (1892) referred to *Pachychilus* as a genus of the Melaniidae and without

providing further explanations, established five sections for the species of Mexico and Guatemala: *Pachychilus* s.s., *Cercimelania*, *Glyptomelania*, *Oxymelania* and *species incertae*, each one with its own type species. Fischer & Crosse (1892: 332) stated that the type species would be *Pachychilus graphium* Morelet, 1849, which is incorrect because it ignores the original designation. This statement was followed later by others (i.e., Simone, 2001; Perrilliat et al., 2008) and caused significant taxonomic confusion. Subsequently, Rovereto (1899) argued that the name *Pachychilus* was pre-occupied by the name *Pachychila* Eschscholtz, 1831 (Coleoptera) and suggested the replacement name *Sphaeromelania* in order to avoid homonymy. However, this replacement has been unnecessary as both taxon names are spelled differently (see further discussion below under *Sphaeromelania*). Ihering (1909: 299), Thiele (1929: 189), and Wenz (1938) stated that *Sphaeromelania* is a synonym of *Pachychilus*. Pilsbry (1920: 201) mentioned that the type species *P. cumingii* is identical with *Melania graphium* Morelet, 1849 and assumes *Sphaeromelania* as the new name for the genus. Pilsbry (1920) also stated that the use of *Pachychilus* or *Pachychila* depended upon whether have to be considered as different names or not, and recommend continuing using *Pachychilus*. Nevertheless, in order to avoid confusions, the same author offered the possibility of adopts the name *Cercimelania* instead of *Pachychilus*, with *P. liebmanni* as type species. Thiele (1928) and Pilsbry (1956) faced with the highly variable shell, agreed the suggested subdivision of Fischer & Crosse (1892). Thiele (1928) on his discussion about the history of the group, bring up that an unknown author in 1840 (Penny-Cyclopaedia 17, p. 454, footnote) has been changed the Ampullariidae genus *Pachylabra* into *Pachystoma*, in order to avoid similarities or synonymies with *Pachychilus*. This statement leads probably Burrington-Baker (1930: 27) to conclude that *Cercimelania*, which is the next available name, should be used instead of *Pachychilus*. Later, Pilsbry (1956) discussing about the etymology of the name *Pachychilus*, stated that “cheilus” is a neuter noun which is treated as masculine by all authors, and recommend to follow the names as they usually are written. He also enunciated that the genus includes *P. cumingii* Lea and *M. laevissima* Sowerby (which has erroneously been referred to as the type by Reeve, 1860). Finally, Morrison (1954) treated *Cercimelania* as a junior synonym of *Pachychilus*.

***Pachychilus* Fischer, 1885**

Pachychilus Fischer, 1885: 701. Kobelt, 1886: 275. Fischer & Crosse, 1892: 328. Thiele, 1929: 189. Wenz, 1938: 685. Morrison, 1954: 366.

Pachycheilus – Chenu, 1859: 288. Martens, 1865: 51. Paetel, 1890: 363.

Type species. *Pachychilus graphium* Morelet (Fischer & Crosse, 1892: 332), by original designation.

Remarks. This name was introduced as subgenus of *Pachychilus* in order to establish a *sensu stricto* group. According to Morrison (1954), *Cercimelania* and *Sphaeromelania* are synonyms of *Pachychilus* s.s. Thompson (2008) established 15 species and five subspecies as members of this subgenus.

***Cercimelania* Fischer & Crosse, 1892**

Cercimelania Fischer & Crosse, 1892: 340. Thiele, 1928: 381. Thiele, 1929: 189. Wenz, 1938: 685. Pilsbry, 1956: 31.

Type species. *Pachychilus liebmanni* Philippi, 1848, by original designation.

Remarks. Introduced as a subgenus of *Pachychilus*, comprise species with medium sized and smooth shells from southern Mexico and Guatemala. This taxon was later proposed by Burrington-Baker (1930) as available name instead of *Pachychilus*, but was treated only as synonym by Morrison (1954).

***Glyptomelania* Fischer & Crosse, 1892**

Glyptomelania Fischer & Crosse, 1892: 351. Thiele, 1928: 381. Thiele, 1929: 189. Wenz, 1938: 685. Morrison, 1951: 8. Morrison, 1954: 366. Pilsbry, 1956: 31. Thompson, 2008: 115.

Type species. *Pachychilus glaphyrus* Morelet, 1849, by original designation.

Remarks. Introduced as subgenus of *Pachychilus*, bring together species with large shells and variable sculpture formed by nodules or spines. According to Morrison (1954) this taxon is confined to Central America.

***Oxymelania* Fischer & Crosse, 1892**

Oxymelania Fischer & Crosse, 1892: 366. Martens, 1899: 461. Thiele, 1928: 381. Thiele, 1929: 189. Wenz, 1938: 685. Morrison, 1951: 8; Morrison, 1954: 365; Pilsbry, 1956: 31; Thompson, 2008: 123.

Type species. *Pachychilus schiedeanus* Philippi, 1843, by original designation.

Remarks. It has been introduced as subgenus of *Pachychilus* for small shells with or without sculpture. Later, Morrison (1954) synonymized *Potamanax* and *Lithasiopsis* to *Oxymelania*. According to Morrison (1954) and Thompson (2008), *Oxymelania* ranges from the Panuco River system in Mexico via the Rio Guayalejo system to the headwaters of the Usumacinta River in Guatemala. Thompson (2008) affiliated 18 species and four subspecies within this taxon.

***Potamanax* Pilsbry, 1893**

Potamanax Pilsbry, 1893a: 340, pl. 14, fig. 5, 6. Pilsbry, 1893b: 63. Thiele, 1928: 383. Thiele, 1929: 189. Wenz, 1938: 686. Aguayo, 1944:69. Pilsbry, 1956: 31. Thompson, 2008: 130.

Type species. *Pachychilus rovirosai* Pilsbry, 1893, by original designation.

Remarks. Pilsbry (1893) established this new sub-genus for species that exhibit an operculum very different from that of *Pachychilus* and shells with a sculpture similar to *Hemisinus* but with a distinct shape of the basal lip. Pilsbry (1893) also stated that the description of the operculum is taken from *Melania brevis*, which he consider congeneric. Martens (1899) changed the name of the type species to *Pachychilus pilsbryi* because it is preoccupied by the name *Pachychilus glaphyrus* var. *rovirosai* Pilsbry, 1893a. Martens (1899) additionally established that as the operculum of the Central American species assigned to *Potamanax* “is not yet known”, he preferred to keep them in the genus *Pachychilus*. Aguayo (1944) based on the operculum and a reinterpretation of Pilsbry’s (1893) description, concluded that *Potamanax* belongs to *Hemisinus*. Aguayo (1944) also stated that the sub-genus *Cubaedomus* seems to be a synonym of *Potamanax* and proposed to change the name of the Cuban species for *Hemisinus (Potamanax) brevis*. If *Potamanax* is indeed closely related to or identical with *Hemisinus*, it is not a member of the Pachychilidae but of the Thiaridae.

***Sphaeromelania* Rovereto, 1899**

Sphaeromelania Rovereto, 1899: 109. Ihering, 1901: 656. Cossmann, 1909: 126. Pilsbry, 1956: 31.

Type species. *Sphaeromelania hinkleyi* Marshall, 1920, by original designation.

Remarks. This generic name was introduced by Rovereto (1899) as replacement name for *Pachychilus* I. Lea & H.C. Lea, 1850, which was held to be preoccupied by the older

name *Pachychila* Eschscholtz, 1831 (Coleoptera). However, as stated above, *Pachychilus* is valid and available. Therefore, *Sphaeromelania* is an unnecessary replacement name and permanently invalid (Art. 10.6). Marshall (1920) mentioned that at the U.S. National Museum there is a “rather extensive collection of the genus *Sphaeromelania*”. However, this type designation is invalid given the unavailability of the genus name.

***Lithasiopsis* Pilsbry, 1910**

Lithasiopsis Pilsbry, 1910: 47-50. Wenz, 1938: 700. Goodrich, 1942: 6. Morrison, 1954: 365. Pilsbry, 1956: 31. Thompson, 1959: 2. Thompson, 2008: 104.

Type species. *Lithasiopsis hinkleyi* Pilsbry, 1910, by original designation.

Remarks. *Lithasiopsis* is a name derivation of the Nearctic genus name *Lithasia*, which is a pleurocerid. Pilsbry (1910) described two species from Mexico and introduced the new genus name *Lithasiopsis* for them because he could not relate them to any other known genus within the family Pleuroceridae. This genus was established for shells that resemble those of *Lithasia* but differ by the presence of a rounded-ovate operculum with an almost central nucleus (Pilsbry, 1910). The genus, originally placed under Pleuroceridae, was moved to Thiaridae by Wenz (1938) while retained within the Pleuroceridae by Goodrich (1942). Goodrich (1942) and Morrison (1954: 365) questioned that *Lithasiopsis* should be considered as a distinct genus. Goodrich (1942) stated that the shells and opercula resemble *Pachychilus*. Morrison (1954) mentioned that *Oxymelania* (see details above) would include *Potamanax* Pilsbry, 1893 and *Lithasiopsis*, but this view has been refuted by Pilsbry (1956: 31). Later, Thompson (1959) noticed that *Lithasiopsis* can be distinguished from *Lithasia* in having a thick parietal callus (which is a feature found in many members of the Central American *Pachychilus*). He also stated that the operculum and the radula are typical for the Pleuroceridae. Thompson (1959) described the radula of *Lithasiopsis*, which has so far remained unknown. He mentioned two groups of *Lithasiopsis* species on basis of radular features: One group being confined to the Rio Pánuco system and the other to the Rio Sabinas.

***Pilsbrychilus* Morrison, 1951**

Pilsbrychilus Morrison, 1951: 8. Morrison, 1954: 366; Pilsbry, 1956: 31. Thompson, 1967: 30. Thompson, 2008: 115.

Type species. *Pachychilus dalli* Pilsbry, 1896, by original designation.

Remarks. Morrison (1951) established that the sinuous lip margin of the adult shell of the type species is sufficient distinctive to separated a subgenus. Thompson (1967) included under this group *P. pleurotoma*, *P. corpulentus* and *P. monachus* due to their notched peristome. However, the author also argued that this notch occurs among unrelated species within the genus and that its use as sub-generic criterion is unacceptable. Hence, *Pilsbrychilus* should not be considered as distinct from *Pachychilus*.

***Amnipila* Pilsbry, 1956**

Amnipila Pilsbry, 1956: 38, pl. 4, fig. 7-9.

Type species. *Pachycheilus pila* Pilsbry & Hinkley, 1910, by original designation.

Remarks. This genus was erected based on the globular shape of the shell and on a complete absence of side cusps on all radular teeth. The name fell into oblivion until Thompson (2008) placed it within the Pachychilidae.

B- Species-group taxa in alphabetical order

apheles Thompson, 1967

Pachychilus (Oxymelania) apheles Thompson, 1967: 26, pl. on page 28, upper fig. 1-5. Thompson, 2008: 123.

Type locality. “a spring run 14 miles west-southwest of Ciudad Valles, on the road to Rio Verde, San Luis Potosi” (Mexico).

Type material. Holotype FLMNH 19756 (Tab. 1, Fig. 1A).

Remarks. Thompson (1967) provided dimensions of five representative specimens which were also figured. Types range in size between h = 14.2-20.5 mm; w = 9.0-11.9 mm; la = 7.0-8.9 mm, wn = 2.0-3.3. Thompson (1967) stated that the species resembles forms of *Pachychilus pleurostriatum* Say, 1831 in shape and color, but differs by its small size, more slender shape, smooth sculpture and decollate shell.

Table 1. Shell parameters of the holotype of *Pachychilus apheles* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
HT (FLMNH 19756)	19.26	10.43	8.48	5.41	12.35	19.26	3.2

apis (I. Lea & H. C. Lea, 1850)

Melania apis I. Lea & H.C Lea, 1850: 190. Brot, 1862: 42. Martens, 1865: 71. Brot, 1870: 273. Brot, 1875: 40, pl. 5, fig. 3. Paetel, 1890: 365.

Melania (Pachychilus) apis – Kobelt, 1886: 277.

Pachychilus apis – Fischer & Crosse, 1892: 346.

Pachychilus (Pachychilus) apis – Martens, 1899: 455. Thompson, 2008: 108.

Type locality. “Marshy places, Vera Cruz, Mexico”.

Type material. Syntype USNM 119732 (Tab. 2, Fig 1B).

Remarks. The original description is based on four specimens but dimensions of only one shell were given (h = 20.32 mm, w = 7.62 mm). The present specimen is the only one we could trace and the whereabouts of the other three types are currently unclear. Brot (1875) stated that *P. apis* is probably related with *P. turati*.

Table 2. Shell parameters of the syntype of *Pachychilus apis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (USNM 119732)	18.33	9.60	8.51	5.22	12.92	17.60	4

atratus Pilsbry & Hinkley, 1910

Pachycheilus atratus Pilsbry & Hinkley, 1910: 524, pl. 23, fig. 13-18.

Pachychilus atratus – Thiele, 1928: 382. Pilsbry, 1956: 36, pl. 4, fig. 6, 10, 13-15.

Pachychilus (Oxymelania) atratus – Thompson, 2008: 123.

Type locality. “Tamosopo River near Verastagu, San Luis Potosi, above and below the Natural Bridge” (Tamasopo River, Mexico). The authors mentioned that the types were collected above the bridge.

Type material. Lectotype (Fig. 1C) and three figured paralectotypes ANSP 99570; three paralectotypes ZMB 61703 (Tab. 3).

Table 3. Shell parameters of the type material of *Pachychilus atratus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	30	16	13	9			5-6
	27	15.5	13	11			
	27	14	12.5	10			
LT (ANSP 99570)	29.03	16.67	12.84	8.53	19.14	25.40	7
PLT (ANSP 99570), mean of three shells	25.99	15.88	12.49	8.46	18.22	23.82	5.33
PLT (ZMB 61703), mean of three shells	25.78	16.14	12.10	8.48	17.95	23.06	5.33

Remarks. *Pachychilus atratus* was described based partially on the presence of a very smooth, dense, glossy brownish-black periostracum. The original description gives measures for three shells, but the illustrations probably corresponds to only two of them since one is presumably the back of figure 14. Pilsbry & Hinkley (1910) related this species with *P. humerosus*, from which it differs by having more rounded whorls. Pilsbry (1956: 33) designated one of the figured specimens of the original description as the lectotype. Pilsbry (1956) considered the variety names *ganinus* and *multistriatus* as well as *Pachychilus monachus* as local forms of *P. atratus*, while Thompson (2008) considered only the two varieties as synonyms.

Additional localities. Mexico, San Luis Potosi: Around the Ingenio Agua Buena and also in, above and below the falls at Puente de Dios (Pilsbry, 1956); San Dieguito and Valle River at Mecos Falls (Thompson, 2008).

attenuatus Pilsbry & Hinkley, 1910

Pachycheilus vallesensis attenuatus Pilsbry & Hinkley, 1910: 528.

Pachycheilus (Oxymelania) vallesensis attenuatus – Thompson, 2008: 130.

Type locality. “Chaimai Creek (about halfway between Valles and Pujal) and Casas Viejas River” (Mexico).

Type material. Lectotype and paralectotype ANSP 96592a; four syntypes ZMB 61694 (Tab. 4, Fig. 1D).

Remarks. According to Pilsbry & Hinkley (1910) specimens of this subspecies were previously included into the original description of *P. vallesensis*. They were lately separated as subspecies due to the livid bluish, smaller, much more slender and acute in the spire shell. Pilsbry & Hinkley (1910) also established that this species occurs two

miles far from the type locality of *P. vallesensis*. Pilsbry (1956: 33) selected a lectotype and one paratype.

Table 4. Shell parameters of the type material of *Pachychilus vallesensis attenuatus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	26	11	9				8-9
	28	13.5	12.5				
LT (ANSP 96592a)	26.06	12.41	11.99	6.95	16.12	21.64	8
PLT (ANSP 96592a)	23	11.10	9.39	5.36	14.44	20.01	9
ST (ZMB 61694), mean of four shells	20.28	11.33	9.41	5.56	13.56	17.82	5.25

chrysalis (Brot, 1872)

Melania chrysalis Brot, 1872: 30, pl. 2, fig. 5. Martens, 1872: 134. Brot, 1875: 47, pl. 5, fig. 11.

Melania (Pachychilus) chrysalis – Kobelt, 1886: 280.

Hemisinus chrysalis – Paetel, 1890: 397.

Pachychilus (Cercimelania) chrysalis – Fischer & Crosse, 1892: 342, pl. 51, fig. 8 a-c.

Pachychilus (Pachychilus) chrysalis – Martens, 1899: 457, pl. 27, fig. 6-9, 15-18.

Pachychilus chrysalis – Martens, 1901: 646. Pilsbry, 1893: 340. Bequaert, 1957: 225.

Pachychilus chrysalis chrysalis – Thompson, 2008: 108.

Pachychilus (Pachychilus) chrysalis var. nympa – Martens, 1899: 457, pl. 27, fig. 12-14.

Pachychilus (Pachychilus) chrysalis nympa – Thompson, 2008: 109.

Type locality. “Isthme de Tehuantepec” (Isthmus of Tehuantepec, Mexico).

Type material. Three syntypes MHNG 134; two syntypes ZMB 109581 (Tab. 5, Fig. 1E-F).

Remarks. Brot (1872) noticed the close similarity of *P. chrysalis* with *P. planensis* and *P. mexicanus*, but considered the present taxon as distinct for conchological differences. Brot (1875) stated that *M. panucula* is a close relative of *M. chrysalis*. Fischer & Crosse (1892) proposed synonymy of *P. chrysalis* with *P. planensis*. Pilsbry (1893) suggested the synonymy of *P. larvatus* with *P. chrysalis*. Martens, 1899 described a *variety nympa* from shells with h = 34-36 mm; w = 16-17 mm; la = 15-16.5 mm; wa = 10-11; wn = 4.5-6. Martens (1899), Bequaert (1957: 225) and Thompson (2008) considered *P. larvatus* Brot

and *P. chrysalis* var. *vulnerata* Fischer & Crosse (1892) as synonym of *P. chrysalis*. Thompson (2008) treats the *variety nympha* as a subspecies.

Additional localities. Mexico: Chiapas: Ixtacomitan (Martens, 1899), San Pedro in Cerro la Gineta (Bequaert, 1957); Tabasco: Teapa (Martens, 1901; Thompson, 2008), Puyacatengo River (Thompson, 2008). Nicaragua: Lake of Managua (Thompson, 2008). El Salvador: Rio Sucio (Martens, 1899).

Table 5. Shell parameters of the holotype of *Pachychilus chrysalis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	52	23	23.5	12			4.5
ST (MHNG 134)	51.49	23.78	23.26	11.89	33.48	45.90	5
	46.45	22.72	24.52	11.49	33.12	44.27	5
	46.22	21.05	21.75	10.40	32.27	43.56	5
ST (ZMB 109581)	34.85	18.35	15.98	8.05	23.18	31.78	6
	28.77	15.30	14.70	7.39	20.48	28.41	3.5

cinereus (Morelet, 1849)

Melania cinerea Morelet, 1849: 26, species No. 68. Reeve, 1860: pl.35, fig. 235. Brot, 1862: 42. Brot, 1870: 273. Brot, 1875: 38, pl. 4, fig. 6. Paetel, 1890: 369.

Melania (Pachychilus) cinerea – Kobelt, 1886:281.

Pachychilus (Pachychilus) cinereus – Fischer & Crosse, 1892: 334, pl. 52, fig. 8 a-c. Martens, 1899: 459.

Pachychilus cinereus – Hinkley, 1920: 51.

Type locality. “fluvium civitatis Coban (Vera-Paz)” (River in Coban City, Vera Paz, Guatemala).

Type material. Three syntypes BMNH 1893.2.4.1799-1801 (Tab. 6, Fig. 1G).

Remarks. Morelet (1849) gives measurements for a single shell which is not considered as the designation of a holotype (h = 32 mm; w = 13 mm; wn = 10). Reeve (1860) proposed that *P. cinereus* is allied to *Melania cumingii* I. Lea & H.C. Lea, 1850: 179. Martens (1899), according to personal correspondence with Ihering, considered *P. cinereus* as a local variety of *P. indiorum*. Brot (1870) synonymized *P. graphium* Reeve with *P. cinereus*. The largest type corresponds well with the measurements of Morelet (1849).

Additional localities. Guatemala: Vera Paz (Brot, 1862); Coban (Reeve, 1851-1870). Mexico: (Kobelt, 1886); Chama (Hinkley, 1920).

Table 6. Shell parameters of the types of *Pachychilus cinereus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (BMNH 1893.2.4.1799)	32.60	13.81	13.75	6.99	19.75	26.69	10
ST (BMNH 1893.2.4.1800-1)	31.27	12.68	12.84	6.84	18.48	25.14	11
	32.15	14.22	14.56	7.74	20.28	26.45	10

corpulentus Thompson, 1967

Pachychilus (Oxymelania) corpulentus Thompson, 1967: 28, pl. on page 28, lower fig. 1-5. Thompson, 2008: 124.

Type locality. “Nacimiento de Rio Mante, about 5 miles west of Ciudad Mante, Tamaulipas” (Mexico).

Type material. Holotype FLMNH 19754 (Tab. 7, Fig. 1H).

Remarks. The name of the species is based on its obese shape, short eroded spire and weak sculpture. Thompson (1967) depicted five shells, the selected type and its paratypes. The paratypes range between 19.8–31.7 mm in height; 18.1–19.7 mm in width; 12.2–15.8 mm in aperture height and have 3.3–4.5 whorls. Thompson (1967) established that *P. corpulentus* is similar to *P. monachus* in characteristics of the aperture, and the color, texture and appearance of the lower whorls, but *P. monachus* has nearly flat-sided whorls strongly shouldered below.

Table 7. Shell parameters of the holotype of *Pachychilus corpulentus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
HT (FLMNH 19754)	27.25	17.42	14.17	9.26	21.07	25.58	4

corvinus (Morelet, 1849)

Melania corvina Morelet, 1849: 26, species No. 69. Hanley, 1854-1858: pl. 2, fig. 16; pl. 3, fig. 25. Brot, 1860a: 110. Reeve, 1860: pl.19, fig. 135 a-b. Brot, 1862: 42. Brot, 1870: 273. Brot, 1875: 36, pl. 5, fig. 1, 1a. Paetel, 1890: 370.

Melania (Pachychilus) corvina – Kobelt, 1886: 282.

Melania (Pachycheilus) corvinus – Chenu, 1859: 288.

Pachycheilus corvinus – Adams, H. & Adams, A., 1854: 298, pl. 31, fig. 7a-b. Hinkley, 1914: 1. Hinkley, 1920: 42. Tristram, 1861: 233.

Pachychilus corvinus – Chenu, 1859: 288. Pilsbry, 1893: 340. Hinkley, 1920: 44, 49, 50, 51. Goodrich & v.d. Schalie, 1937: 41. v.d. Schalie, 1940: 7. Morrison, 1954: 365.

Pachychilus (Pachychilus) corvinus – Fischer & Crosse, 1892: 336, pl. 52, fig. 7a-c. Martens, 1899: 460.

Pachychilus (Pachychilus) corvinus corvinus – Thompson, 2008: 109.

Pachychilus (Pachychilus) laevisissimus var. *varicose* – Fischer & Crosse, 1892: 329, pl. 53, fig. 6.

Pachychilus indiorum var. *varicosus* – Martens, 1899: 456.

Type locality. “Rivulos prov. Vera-Paz” (= Streams in the Province of Vera-Paz, Guatemala).

Type material. Four syntypes MNHN (Tab. 8, Fig. 2A).

Remarks. This species was described without illustration for shells ranging between 28–39 mm in height; 9–18 mm in width, with 6–7 whorls. Brot (1875) mentioned an unnamed variety for a shell labeled as *M. laevisissima* in Morelet’s collection. Fischer and Crosse (1892: 336, pl. 53, fig. 7, 7a) named the *variety lutescens* from Coban and Martens (1899) considered *P. indifferens* Fischer & Crosse (1892) as another variety of this species. Hinkley (1920) reported on var. *lutescens* from Livingston (Guatemala). Goodrich & van der Schalie (1937) considered *P. corvinus* as a complex to include *P. schumoi*, *P. lutescens*, *P. cinereus* and *P. panucula* and reported on var. *indifferens* from the shores of the lakes Peten and Eckibix. Van der Schalie (1940: 8) treated *indifferens* as a subspecies (from Rio Seniso near Chamá, headwaters of Rio Panzamala, creek 3 km south of Samac and from a small river near Samanzama in Guatemala). Thompson (2008) treated *P. cinereus* Morelet, *P. panuculus* Morelet, *P. tumidus* Tristram and *P. mexicanus* Reeve as synonyms. The ANSP holds a topotypic specimen.

Additional localities. Mexico: Palenque (Brot, 1875; Fischer & Crosse, 1892; Martens, 1899); Tabasco, Montañas de Poana (Fischer & Crosse, 1892; Pilsbry, 1893; Martens, 1899; Thompson, 2008). Guatemala: Coban; Tactic; Lake of Dueñas; Santa Rosa – tributary of the Rio Negro; Livingston; Mountains of Rio Cavech; Chejel; Chama; Arroyo Xotal; Petenhá; Yalchactilá; Rio Senso; Rio Rubel Cruz; Rio Panzamala; Chiacam, near Lanquin on the Cahabon River and Rio Motagua (Fischer & Crosse, 1892; Pilsbry, 1893; Martens, 1899; Hinkley, 1920; Goodrich & v.d. Schalie, 1937; v.d. Schalie, 1940; Thompson, 2008). Nicaragua: Tugla River (Thompson, 2008).

Table 8. Shell parameters of the syntypes of *Pachychilus corvinus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (MNHN), mean of four shells	24.26	13.89	12.00	7.12	17.23	22.69	5.25

crassa Thompson, 1959

Lithasiopsis crassa Thompson, 1959: 2, fig. 1a, c-f; pl. 1, figs a-f.

Lithasiopsis crassus – Thompson, 2008: 104.

Type locality. “Storm’s Ranch, Río Sabinas, Pano Ayuctle, 5 mi. NE of Gómez Farías, Tamaulipas, México”

Type material. Not examined.

Remarks. Thompson (1959) established the name *crassa* for shells that has been found occupying the same habitat as *P. darnelli*, but exhibiting thicker and heavier shells with an also thicker parietal callus. According to Thompson (1959), the type has wn = 7.5; h = 13.9 mm; wa = 8.6 mm; la = 6.8 mm. Thompson (1959) also remarks that *L. crassa* is highly variable in shell height and width, going from elongate-turreted to squat and globose with short pointed spire. The latter also stated that its position under *Lithasiopsis* is due to the geographical closeness with another two *Lithasiopsis* species previously described.

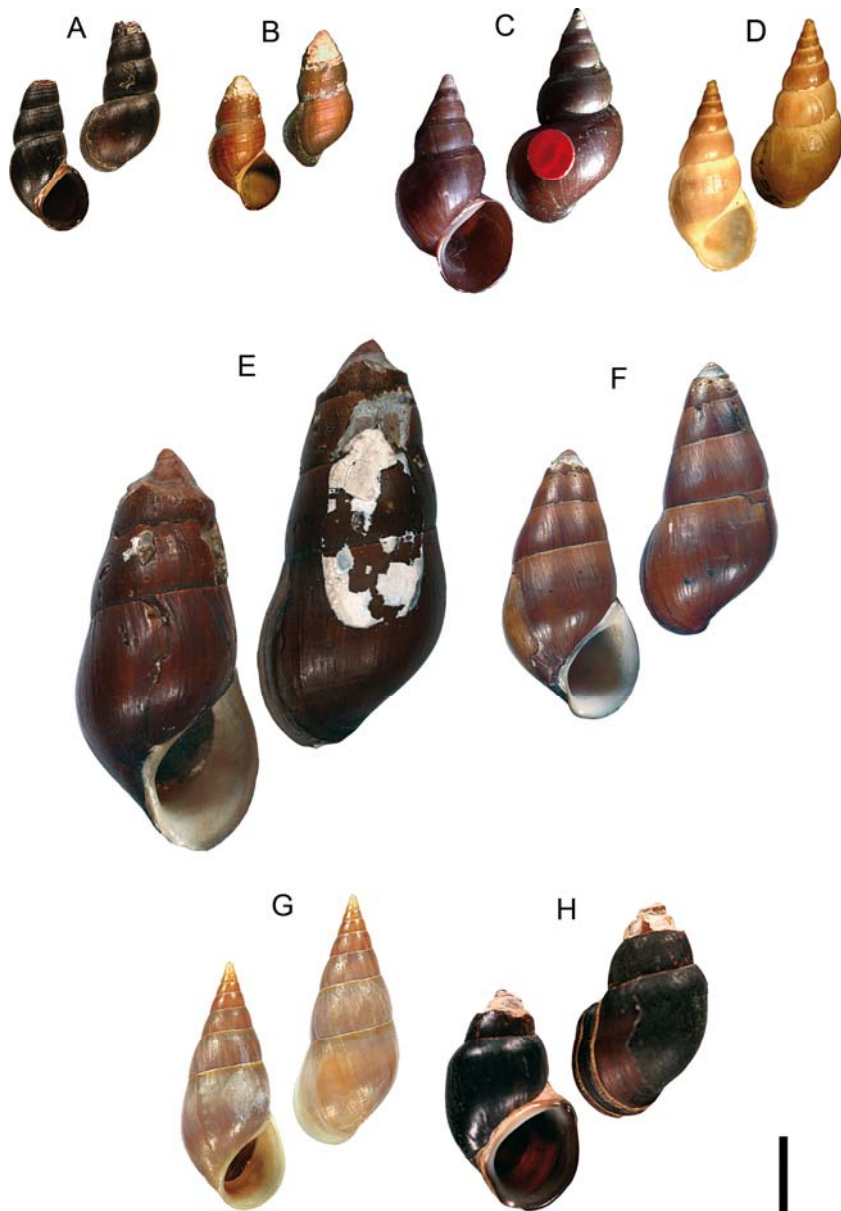


Fig. 1 A-H. Types of Pachychilidae from Mesoamerica (*Pachychilus*).

A- Holotype of *Pachychilus apheles* Thompson, 1967 (FLMNH 19756); – B. Syntype of *Pachychilus apis* I. Lea & H.C. Lea, 1850 (USNM 119732); – C. Lectotype of *Pachychilus atratus* Pilsbry & Hinkley, 1910 (ANSP 99570); – D. Lectotype of *Pachycheilus vallesensis attenuatus* Pilsbry & Hinkley, 1910 (ANSP 96592a); – E. Syntype of *Pachychilus chrysalis* Brot, 1872 (MHNG 134); – F. Syntype of *Pachychilus chrysalis* var. *nympha* Martens, 1899 (ZMB 109581); – G. Syntype of *Pachychilus cinereus* Morelet, 1849 (NHM 1893.2.4.1799); – H. Holotype of *Pachychilus corpulentus* Thompson, 1967 (FLMNH 19754). Bar = 1 cm.

cumingii I. Lea & H.C. Lea, 1850

Pachychilus cumingii I. Lea & H.C. Lea, 1850: 179. Petit de la Saussaye, 1853: 160. Brot, 1862: 43.

Pachycheilus (Aylacostoma) cumingii – Adams, H. & Adams, A., 1854: 299.

Pachychilus (Pachychilus) cumingii – Morrison, 1954: 366.

Melania cumingii – Reeve, 1860: pl. 21, fig. 149.

Pachychilus (Oxymelania) graphium var. *transcendens* – Martens, 1899: 461.

Type locality. “Large rivers, Copan, Central America” (Honduras).

Type material. Three syntypes BMNH 20070009 (Fig. 2B), one syntype USNM 119625 (Tab. 9).

Remarks. *Pachychilus cumingii* I. Lea & H.C. Lea (1850) is the type species of the genus *Pachychilus* by monotypy. In their description, Lea & Lea stated that “... this is a very remarkable shell among the Melanians... It differs very much in form from *Melania laevissima* Sow., which naturally belong to the same genus...”. In the same paper, I. Lea & H. C. Lea (1850: 191) named a new species from the Philippines, *Melania cumingii*. Petit (1853) referred to the original description and mentioned a shell with 32 mm height and 15 mm width. Petit (1853) established that in spite of not have seen the shells described by Lea & Lea, he thought that *P. cumingii* is very similar to Sowerby’s *laevissimus*, and consider that *cumingii* could be a variety of the latter, emphasizing also that Morelet considers his own *P. indiorum* as variety of *P. laevissimus*. Later, Brot (1868: 5) stated that *P. cumingii* (which is the same as his *M. renovata* [see details under the species]), is a synonym of *P. graphium* Morelet. This same view is adopted by Fischer & Crosse (1892), whose proposed that if these taxa are conspecific, the name *M. graphium* Morelet, 1849 as the oldest available name would have priority over *P. cumingii* and *M. renovata*. As the original description of *P. cumingii* was published without depiction of the shell, Reeve (1860) presents an illustration of the shell, referring to *Melania cumingii*. I. Lea & H.C. Lea (1850: 179). Between the reviewed type material, the most similar to the shell described is the largest shell of the BMNH syntypes.

Table 9. Shell parameters of the type material of *Pachychilus cumingii* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	35.6	12.7					11
ST (USNM 119625)	29.63	10.02	10.38	5.89	14.96	21.60	10
ST (BMNH 20070009)	34.70	12.32	11.35	6.80	16.80	25.07	11
ST (BMNH 20070009), mean of two shells	29.39	10.58	10.47	5.36	15.14	21.91	10

dalli Pilsbry, 1896

Pachycheilus dalli Pilsbry, 1896: 269.

Pachycheilus walli – Carus, 1896: 223 [emendation for *P. dalli*].

Pachychilus (Pachychilus) dalli – Martens, 1899: 456, pl. 26, fig. 4.

Type locality. Here fixed to Huilopec, Mexico.

Type material. Five syntypes USNM 133214 (Tab. 10, Fig. 2C).

Remarks. *P. dalli* is the type species of the sub-genus *Pilsbrychilus*. The species was explicitly described for four adult and four young shells housed at the ANSP collection, plus one larger adult belonging to the USNM collection, which is the one figured as can be judged from its lesser erosion. The description was subsequently published in the Zoologischer Anzeiger under the misspelled name *Pachycheilus walli* (Carus, 1896). Martens (1899) established that *P. dalli* is closely related to *P. indiorum*, while Pilsbry (1896) stated that is about equally to *P. laevissimus* var. *indorum* Morelet and *P. chrysalis* Brot. Although the original author only refers to one shell in the USNM, currently there are another four in the same lot, which are herein also considered as types. The type locality was not given in the original description. It is herein fixed to the locality given on the type labels, which is “Huilopec, Mexico”.

Additional localities. Tehuantepec, Mexico (Martens, 1899).

Table 10. Shell parameters of the holotype of *Pachychilus dalli* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	52-54	25-28					6-7
ST (USNMN 133214)	54.04	27.29	25.64	16.18	34.34	46.62	6
ST (USNMN 133214), mean of four shells	50.24	25.79	14.01	24.39	33.45	44.19	6.75

darnelli Thompson, 1959

Lithasiopsis darnelli Thompson, 1959: 4, fig. 1b, g-j; pl. 1, figs g-l. Thompson, 2008: 105.

Type locality. “Río Sabinas, above la Unión, NE of Gómez Farías, Tamaulipas, México”.

Type material. Not examined.

Remarks. The original shell described is h = 12 mm; w = 6 mm; la = 5 mm; wn = 7.25. Thompson (1959) assigned this shells to a new name despite he stated that has been taken together with, and occupying the same habitat as *crassa*, and also without

regarding the fact that *P. darnelli* is very variable in measurements, whorls contour (from flattened to rounded) and form of the parietal callus (from a thin indistinct structure to a thickened shield over the preceding whorl).

ganinus Pilsbry & Hinkley, 1910

Pachycheilus atratus ganinus Pilsbry & Hinkley, 1910: 525, pl. 23, fig. 19-20. Thompson, 2008: 123.

Type locality. “Ganina River three miles southwest of San Dieguito” (Mexico).

Type material. Lectotype (Fig. 2D) and paralectotype ANSP 99577; four paralectotypes ZMB 61700 (Tab. 11).

Remarks. Pilsbry & Hinkley (1910) considered this taxon as a subspecies of *P. atratus* for its dull black shell, the middle and lower whorls being ridged, and the upper whorls being smooth. This taxon has been reported to co-occur with *P. pluristriatus longus* Pilsbry & Hinkley (1910). In the original description two shells have been depicted and measurements of a third, abnormally short shell have been presented. Thompson (2008) suggested synonymy with *Pachychilus (Oxymelania) atratus*.

gassiesii (Reeve, 1860)

Melania gassiesii Reeve, 1860: pl. 35, fig. 236. Brot, 1862: 42. Brot, 1870: 273. Martens, 1874: 358. Brot, 1875: 47, pl. 5, fig. 12. Patel, 1890: 374. [non *M. gassiesi* Gassies, 1893: Faune Conchyl. Terr. et fluv. de la Nouvelle-Calédonie, I: 93, 297].

Melania (Pachychilus) gassiesii – Martens, 1874: 37, pl. 4, fig. 35, 35a-b. Kobelt, 1886: 286.

Pachychilus (Cercimelania) gassiesii – Fischer & Crosse, 1892: 348, pl. 51, fig. 5, 5a.

Pachychilus liebmanni var. *gracilior* – Martens, 1899: 453.

Pachychilus (Pachychilus) liebmanni gracilior – Thompson, 2008: 113.

Pachychilus liebmanni var. *gassiesi* – Martens, 1899: 454.

Pachychilus (Pachychilus) liebmanni gassiesi – Thompson, 2008: 112.

Type locality. “Central America”.

Type material. Not examined.

Remarks. Strebel (1873) considered this taxon as synonym of *P. liebmanni* Philippi, and Brot (1870, 1875) as synonym of *P. sallei*. For Paetel (1890) this species is a variety of *P. sallei*.

Additional localities. Mexico: Veracruz, Atoyac River; Oaxaca (Martens, 1874; Martens, 1899); Oaxaca, Teotalcingo River. Nicaragua (Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008).

Table 11. Shell parameters of the type material of *Pachychilus atratus ganinus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	24	13	11.5				
	17	12	10.5				
LT (ANSP 99577)	23.53	14.08	11.34	7.46	15.95	20.67	6
PLT (ANSP 99577)	15.06	8.25	7.58	3.95	10.39	13.47	5
PLT (ZMB 61700), mean of four shells	17.80	11.84	9.38	5.91	13.09	15.09	5

glaphyrus (Morelet, 1849)

Melania glaphyra Morelet, 1849: 24, species No. 62. Hanley, 1854-1858: pl. 2, fig. 17. Reeve, 1859: pl.2, fig. 8. Brot, 1862: 43. Brot, 1870: 273. Paetel, 1890: 375.

Melanoides glaphyra – H. Adams & A. Adams, 1854: pl. 31, fig. 5a, b. Tristram, 1863: 413.

Pachychilus (Glyptomelania) glaphyrus – Fischer & Crosse, 1892: 351. Martens, 1899: 438. Thiele, 1928: 399. Thiele, 1929: 189. Morrison, 1951: 8. Morrison, 1954: 366.

Pachychilus (Glyptomelania) glaphyrus var. *glaphyra* – Fischer & Crosse, 1892: 352, pl.52,fig.2a-c.

Pachychilus glaphyrus – Pilsbry, 1893a: 339. Pilsbry, 1893b:62. Martens, 1901: 645. Hinkley, 1920: 45. Goodrich & v.d. Schalie, 1937: 39. Morrison, 1954: 365.

Pachychilus glaphyrus var. *glaphyrus* – Martens, 1899: 444.

Pachychilus (Glyptomelania) glaphyrus glaphyrus – Thompson, 2008: 116.

Pachychilus (Glyptomelania) glaphyrus var. *scamnata* – Fischer & Crosse, 1892: 352, pl. 52, fig. 2.

Pachychilus glaphyrus var. *scamnatus* – Martens, 1899: 444

Pachychilus (Glyptomelania) glaphyrus scamnatus – Thompson, 2008: 118.

Melania immanis – Brot, 1874: 21.

Melania immanis var. *glaphyra* – Kobelt, 1886: 290.

Pachychilus (Glyptomelania) glaphyrum – Wenz, 1938: 685, fig. 1966.

Type locality. “ad fontes fluminis Usumasinta” (at the source of the Usumasinta River, Guatemala).

Type material. Three syntypes MNHN from Guatemala (Fig. 2E); three syntypes MNHN from Mexico (Tab. 12).

Remarks. Brot (1870) synonymized *M. lacustris* (Morelet) Reeve to *P. glaphyrus*. Martens (1899) stated that the specimens from the Chajmayu River (Alta Vera Paz, Guatemala) noted by Ihering as *P. opiparis*, probably belong to *semilaevis* variety. Fischer & Crosse (1892) synonymized *P. glaphyrus* with *M. immanis* Brot, Kobelt. Pilsbry (1893b: 62) remarks that *P. glaphyrus* is exceedingly variable, more than any other Mexican melanian. Later, Goodrich & van der Schalie (1937) established that the var. *lacustris* clearly differs from *P. glaphyrus* in the possession of a most strongly developed sculpture.

Additional localities. Central America (Reeve, 1851-1870; Brot, 1862; 1870; Wenz, 1938). Mexico: Tabasco (Fischer & Crosse, 1892; Martens, 1899). Guatemala: Rio de la Pasion (Tristram, 1863; Thompson, 2008); Arroyo Yalchactilá of the Rio de la Pasion (Fischer & Crosse, 1892; Goodrich & v.d. Schalie, 1937; Thompson, 2008); Jocolo (Thompson, 2008); Coban (Martens, 1899; Thompson, 2008); sources of the Usumasinta River (Brot, 1874).

Table 12. Shell parameters of the syntypes of *Pachychilus glaphyrus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	63	20					9
ST (MNHN Guatemala), mean of three shells	61.48	24.50	20.78	11.60	31.77	46.91	9
ST (MNHN Mexico), mean of three shells	73.12	33.63	28.15	14.05	39.87	57.41	7

godmanni (Tristram, 1863)

Melanoides godmanni Tristram, 1863: 413, species 71.

Melania godmani – Brot, 1868: 5.

Melania godmanni – Brot, 1870: 274. Brot, 1874: 25. Paetel, 1890: 375.

Melania (Pachychilus) godmani – Kobelt, 1886: 287.

Pachychilus (Cercimelania) godmani – Fischer & Crosse, 1892: 363.

Type locality. “Another part of Lake Peten, Vera Paz. Not closely to the *M. tumida* locality” (Guatemala).

Type material. Not examined.

Remarks. The shell described is h = 70 mm; w = 26 mm; la = 20 mm; wa = 14 mm; wn = 8-9. According to Brot (1974) and Fischer & Crosse (1892) this species is very close to *M. obeliscus*. Probably the type of *P. godmanni* is lost since at the collections where material from Tristram was deposited it could not be found.

Additional localities. Vera Paz (Kobelt, 1886).

gracilis Tristram, 1863

Pachycheilus gracilis Tristram, 1863: 413, species 74.

Melania gracilis – Brot, 1868: 5. Brot, 1870: 274. Brot, 1875: 42. Paetel, 1890: 375.

Melania (Pachychilus) gracilis – Kobelt, 1886: 287.

Pachychilus tristrami – Fischer & Crosse, 1892: 369.

Type locality. “Lake Peten, Vera Paz” (Guatemala).

Type material. Not examined.

Remarks. Tristram (1863) described a shell h = 26 mm; w = 10 mm; la = 9 mm; wa = 7.5 mm; wn = 5-6. Fischer & Crosse (1892) changed the name of *P. gracilis* into *P. tristrami* due to the existence of another two previously described *Melania gracilis*. However, the species was originally published as *Pachychilus* and not *Melania*. Therefore, *P. tristrami* is an unnecessary replacement name and permanently invalid (Art. 10.6).

Probably the type of *P. gracilis* is lost, since at the collections where material from Tristram was deposited, it could not be found.

Additional localities. Guatemala (Kobelt, 1886).

graphium (Morelet, 1849)

Melania graphium Morelet, 1849: 26, species No. 67. Hanley, 1854-1858: pl. 4, fig. 35. Reeve, 1860: pl.21, fig. 150. Brot, 1862: 42. Brot, 1870: 274. Brot, 1875: 41, pl. 5, fig. 4. Paetel, 1890: 375.

Melania (Pachychilus) graphium – Kobelt, 1886: 288.

Pachycheilus graphium – H. Adams & A. Adams, 1854: 298.

Pachychilus (Pachychilus) graphium – Fischer & Crosse, 1892: 332, pl. 51, fig. 2-2a. Thiele, 1928: 399. Thiele, 1929: 189. Wenz, 1938: 685, fig. 1964.

Pachychilus (Pachychilus) graphium var. *reducta* – Fischer & Crosse, 1892: 333.

Pachychilus (Pachychilus) graphium var. *transcendens* – Fischer & Crosse, 1892: 333, pl. 50, fig. 7-7a.

Pachychilus (Oxymelania) graphium – Martens, 1899: 461. Thompson, 2008: 124.

Pachychilus (Oxymelania) graphium var. *reductus* – Martens, 1899: 461.

Pachychilus graphium – Martens, 1901: 646. Thiele, 1928: 381. Goodrich & van der Schalie, 1937: 21. Wenz, 1938: 685. v.d. Schalie, 1940: 8. Perriliat et al, 2008: 261.

Type locality. “flumina prov. Vera-Paz” (Rivers in Vera-Paz Province, Guatemala).

Type material. Two syntypes MNHN (Tab. 13, Fig. 2F).

Remarks. The shell described is h = 30 mm; w = 10 mm; wn = 10. Brot (1868) established that Reeve’s figure 150 is a variety of *P. cinereus* instead of *P. graphium*. Brot (1870) and Fischer & Crosse (1892) synonymized *P. cumingii* Lea and *P. renovatus* Brot to *P. graphium*. Fischer & Crosse (1892) also stated that due to the existence of two different species both with the same name, *Melania cumingii* from Philippines and “*Melania*” *cumingii* from Honduras, the name of the Honduran species has to be changed. Consequently, Fischer & Crosse (1892) proposed *P. graphium* as the next available name. Since both species were originally described under different genera (*Pachychilus* and *Melania*), according to the Article 59.2. of the code a substitute name is not necessary. Martens (1899) and Thompson (2008) listed also *P. gracilis* Tristram and *P. tristrami* Fischer & Crosse as synonyms. Thompson (2008) synonymized the varieties *reducta* and *transcendens* Fischer & Crosse (1892) to *P. graphium*.

Additional localities. Central America (Paetel, 1890). Yucatan (Martens, 1899). Guatemala: Streams in Vera Paz; Coban; Rio Sinanja; Rio Tactic; Peten; Rio Panzamala; Peten Lake; tributaries of the Usumacinta on road between Coban and Chama; Esmeralda; San Miguel Uspantan (Fischer & Crosse, 1892; Martens, 1899; Goodrich & v.d. Schalie, 1937; Hinkley, 1920; v.d. Schalie, 1940; Thompson, 2008).

Table 13. Shell parameters of the syntypes of *Pachychilus graphium* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (MNHN)	29.27	11.28	10.37	5.24	15.28	21.84	11
	30.95	11.48	11.00	5.70	15.92	23.20	10

hellerii (Brot, 1872)

Melania hellerii Brot, 1872: 29, pl. 4, fig. 1. Brot, 1862: 42. Brot, 1870: 274. Brot, 1875: 33, pl. 4, fig. 4a-b.

Melania helleri – Martens, 1872: 134.

Melania (Pachychilus) hellerii – Kobelt, 1886: 288.

Pachychilus (Pachychilus) helleri – Fischer & Crosse, 1892: 331.

Type locality. “Amerique centrale” (Central America).

Type material. Three syntypes MHNG 154 (Tab. 14, Fig. 2G).

Remarks. Brot (1862) on his Catalogue Sytématique listed a species name “*Hellerii*” Parr. from Central America. Brot (1870; 1875) synonymized *P. laevissimus* (Sow.) to *P. helleri*. But *P. laevissimus* Sowerby, 1824 is a species described from Venezuela. If *hellerii* and *laevissimus* are identical, then *hellerii* is the junior synonym of *laevissimus* and not vice versa because the latter is the older name. Brot (1872: 29) after establishing that he believe that *P. hellerii* Parreyss has been never described or illustrated, make a complete and detailed characterization of the shell, giving measurements and a depiction. Later, Fischer & Crosse (1890) considered *P. hellerii* as a synonym of *P. chrysalis*.

According to the original measurements gave by Brot (1872), the shell width is only two millimeters wider than the aperture width, which is impossible when those values are compared with the shell depicted. Assuming that the value of the shell width was wrong published, there is one of the shells of the MHNG 154 which fits with the remaining measures and also with the drawing in Brot (1872).

Additional localities. In Mexican republic (At the Mexican Republic) (Fischer & Crosse, 1892).

Table 14. Shell parameter of the holotype and paratypes of *Pachychilus hellerii* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	54	14	20	12			9-10
MHNG 154 (HT)	52.90	24.93	19.98	11.34	30.76	43.90	7
MHNG 154 (PT)	52.12	24.21	19.76	12.06	29.90	42.78	8
	63.12	30.70	24.34	14.44	36.78	55.25	6

hinkleyi Pilsbry, 1910

Lithasiopsis hinkleyi Pilsbry, 1910: 48, fig. 1a, 2, 3. Walker, 1920: 57. Thiele, 1931: 193. Wenz, 1938: 700, fig. 2012. Thompson, 2008: 105.

Type locality. “Coy River, a tributary of the Panuco, State of San Luis Potosi, Mexico”.

Type material. One paratype USNM 207473 (Tab. 15, Fig. 3A).

Remarks. According to Pilsbry (1910) this species has in common with the North American Pleuroceridae *Lithasia obovata* Say, the general shape, color and columellar callus. The original publication gave dimensions for four shells but only depicted three (two adults and one young).

Table 15. Shell parameters of the paratype of *Lithasiopsis hinkleyi* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	13.8	7.1					
	13.5	7.9					
	12.3	6.8					
	11.9	7					
PT (USNM 207473)	11.15	6.66	6.59	3.28	8.85	10.17	5

hinkleyi (Marshall, 1920)

Sphaeromelania hinkleyi Marshall, 1920: 301, pl. 17, fig. 4 – 13.

Pachychilus hinkleyi – Hinkley, 1920: 51. v.d. Schalie, 1940: 8.

Pachychilus (Pachychilus) hinkleyi – Thompson, 2008: 111.

Type locality. “Tsalbha River at Chama, Alta Vera Paz, Guatemala”.

Type material. Holotype USNM 336412 (Tab. 16, Fig. 3B).

Remarks. According to Marshall (1920), this new species has to be established for shells that do not agree with any species previously described, and designated the specimen of the figure 6 as holotype (USNM 336412). The name was giving as sign of gratitude to Hinkley, whom collected these exemplars in Guatemala. Marshall (1920) stated that the great intra-specific variation showed by the whole lot is due to mutation. van der Schalie (1940) considered this species as synonym of *P. corvinus*.

Additional localities. Rio Senso near Chama, Guatemala (v.d. Schalie, 1940).

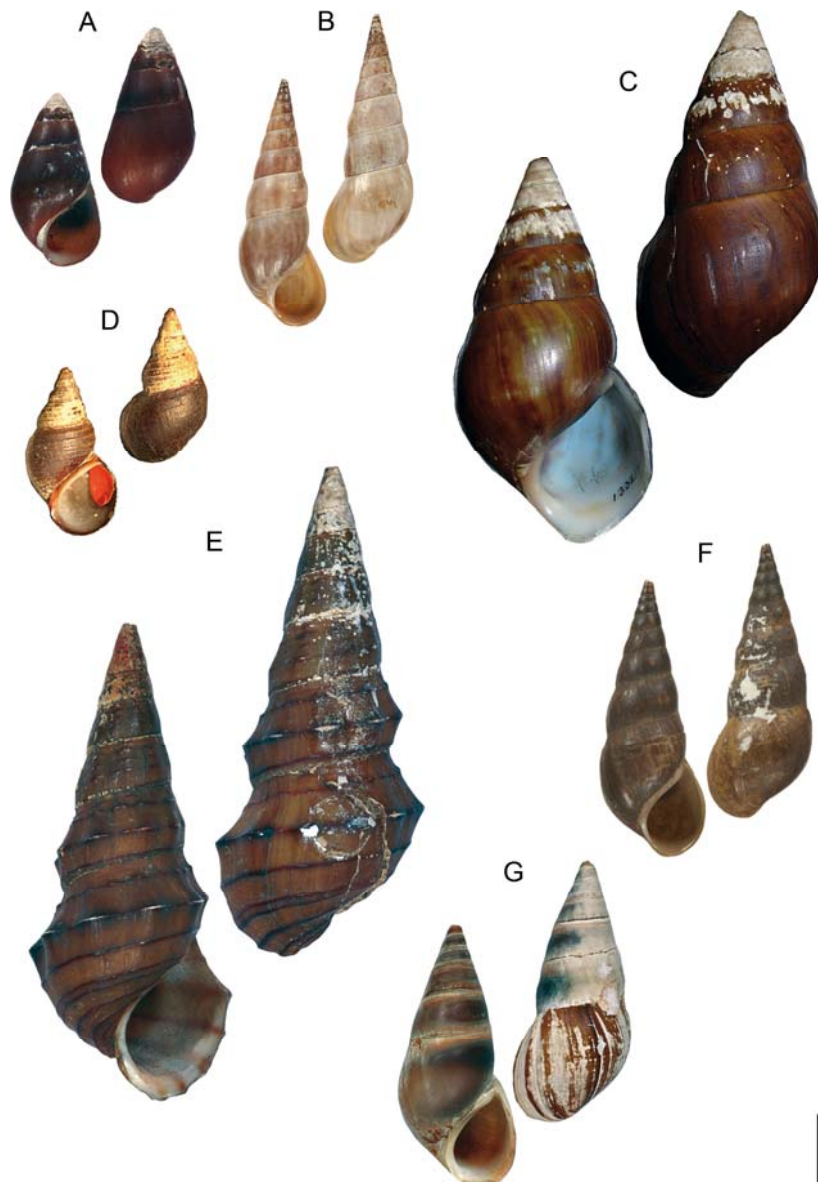


Fig. 2 A-G. Types of Pachychilidae from Mesoamerica (*Pachychilus*).

A. Syntype of *Pachychilus corvinus* Morelet, 1849 (MNHN); – B. Syntype of *Pachychilus cumingii* I. Lea & H.C. Lea, 1850 (NHM 20070009); – C. Syntype of *Pachychilus dalli* Pilsbry, 1896 (USNM 133214); – D. Lectotype of *Pachychilus atratus ganinus* Pilsbry & Hinkley, 1910 (ANSP 99577); – E. Syntype of *Pachychilus glaphyrus* Morelet, 1849 from Guatemala (MNHN); – F. Syntype of *Pachychilus graphium* Morelet, 1849 (MNHN); – G. Syntype of *Pachychilus hellerii* Brot, 1862 (MHNG 154). Bar = 1 cm.

Table 16. Shell parameters of the holotype of *Sphaeromelania hinkleyi* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	37.5	21.5					~ 7
HT (USNM 336412)	38.14	23.74	20.14	13.07	28.12	35.61	6

humerosus Pilsbry & Hinkley, 1910

Pachycheilus humerosus Pilsbry & Hinkley, 1910: 526, pl. 23, fig. 21-25.

Pachychilus (Oxymelania) humerosus – Thompson, 2008: 125.

Type locality. “Tamosopo River, near Verastagu, above and below the Natural Bridge”.

Type material. Lectotype and four paralectotypes ANSP 99579; three paralectotypes ZMB 61701 (Tab. 17, Fig. 3C).

Remarks. Pilsbry & Hinkley (1910) related *P. humerosus* to *P. tristis*. Pilsbry (1956: 33) selected and marked the lectotype and its paralectotypes.

Table 17. Shell parameters of the type material of *Pachychilus humerosus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	28	18	13.5	10			3,5-6
LT (ANSP 99579)	26.52	15.95	11.93	8.17	18.13	23.24	6
PLT (ANSP 99579). mean of four shells	21.90	14.90	12.11	8.04	16.49	20.59	4.75
PLT (ZMB 61701). mean of three shells	23.59	15.23	12.43	7.98	17.95	22.29	4.83

immanis (Morelet, 1851)

Melania immanis Morelet, 1851: 22, species No. 139. Reeve, 1860: pl.35, fig. 238. Brot, 1862: 43. Brot, 1870: 274. Brot, 1874: 19 pl. 2, fig. 1a-g. Paetel, 1890: 377, 378.

Melania (Pachychilus) immanis – Kobelt, 1886: 290.

Pachychilus (Glyptomelania) glaphyrus var. *immanis* – Fischer & Crosse, 1892: 351, pl. 53, fig. 1, 1a.

Pachychilus (Glyptomelania) glaphyrus immanis – Thompson, 2008: 117.

Pachychilus (Glyptomelania) glaphyrus var. *glaphyroides* – Fischer & Crosse, 1892: 352. Martens, 1899: 444.

Pachychilus (Glyptomelania) glaphyrus glaphyroides – Thompson, 2008: 116.

Pachychilus (Glyptomelania) glaphyrus var. *semilaevis* – Fischer & Crosse, 1892: 352, pl. 53, fig. 2, 2a.

Pachychilus glaphyrus var. *semilaevis* – Martens, 1899: 445.

Pachychilus glaphyrus var. *immanis* – Martens, 1899: 438.

Pachychilus glaphyrus immanis – Hinkley, 1914: 1. Hinkley, 1920: 47.

P. glaphyrus var. between *polygonatus* and *immanis* – Pilsbry, 1893a: 339, pl. 14, fig. 5-6; 1893b: 63, pl. 3, fig. 5-6.

Type locality. “rivulos prov. Petenensis” (streams of the Peten province, Guatemala).

Type material. Two syntypes BMNH 1893.2.4.1783+1794 (Tab. 18, Fig. 3D).

Remarks. The shell, originally published without illustration is h = 85 mm; w = 29 mm; wn = 8-9. Brot (1870) synonymized *P. polygonata* Lea to *P. immanis*. Fischer & Crosse (1892) considered *P. immanis* as a variety of *P. glaphyrus*.

Additional localities. Central America (Reeve, 1851-1870; Brot, 1862; Paetel, 1890). Mexico: creeks in Tabasco province (Brot, 1874). Guatemala: Peten; Coban; Dolores and source of the Usumasinta River; Rio Jacinto at Punta Gorda (Brot, 1870; Brot, 1874; Paetel, 1890; Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008); Jocolo (Hinkley, 1914).

Table 18. Shell parameters of the syntypes of *Pachychilus immanis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (BMNH 1893.2.4.1783+1794)	102.01	42.84	34.22	20.48	51.38	75.36	10
	65.23	24.92	20.86	12.66	33.04	48.44	11

indifferens Crosse & Fischer, 1891

Pachychilus indifferens Crosse & Fischer, 1891: 25.

Pachychilus (Pachychilus) indifferens – Fischer & Crosse, 1892: 337, pl. 50, fig. 8, 8a-c.

Pachychilus (Pachychilus) indifferens var. *explicata* – Fischer & Crosse, 1892: 337, pl. 53, fig. 9, 9a, 10, 10a.

Pachychilus (Pachychilus) explicatus – Martens, 1899: 459. – Thompson, 2008: 110.

Pachychilus (Pachychilus) corvinus indifferens – Thompson, 2008: 110.

Type locality. “... in flumine Rio Motagua dicto, Guatemalae (F. Bocourt)” (dictate at the River Motagua, Guatemala by F. Bocourt).

Type material. Two syntypes MNHN 8, 8a-c; one syntype MNHN; ten syntypes MNHN (Tab. 19, Fig. 3E).

Remarks. The illustration of *P. indifferens* was published by Fischer & Crosse (1892), posterior to the original description. Fischer & Crosse (1892) related *P. sargi* and *P. corvinus* to *P. indifferens*. Martens (1899) treated *P. indifferens* as variety of *P. corvinus* and considered the variety *explicata* of Fischer & Crosse, 1892 as a different species.

Additional localities. Guatemala: Rio Machaquila, Department of Peten (Fischer & Crosse, 1892); Lake Peten and Lago de Eckibix (Thompson, 2008).

Table 19. Shell parameters of the type material of *Pachychilus indifferens* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	23	10	10	6.5			6.5
ST (MNHN 8-8a)	22.11	11.58	10.08	5.57	14.15	19.10	7
ST (MNHN 8b-c)	22.50	10.23	9.03	4.80	13.25	18.89	6.5
ST (MNHN), mean of ten shells	20.51	10.29	9.28	4.80	13.37	18.12	5.70

indiorum (Morelet, 1849)

Melania indiorum Morelet, 1849: 25, species No. 66. Morelet, 1851. Hanley, 1854-1858: pl. 3, fig. 24. Brot, 1860a: 110.

Melania indorum – Petit, 1853: 162, pl. 5, fig. 7. Brot, 1862: 42.

Melania (Pachycheilus) indorum – Chenu, 1859: 288, fig. 1963.

Pachycheilus indiorum – Adams, H. & Adams, A., 1854: 298. Hinkley, 1914: 1. Hinkley, 1920a: 79. Hinkley, 1920b: 42.

Pachychilus (Pachychilus) indiorum – Martens, 1899: 455. Thompson, 2008: 111.

Pachychilus indiorum – Hinkley, 1920b: 44, 49. Goodrich & v.d. Schalie, 1937: 42. Bequaert, 1957: 213.

Melania laevissima var. *costato-plicata* – Brot, 1875: 35, pl. 4, fig. 5f.

Pachychilus indiorum var. *costato-plicatus* – Martens, 1899: 456.

Melania laevissima var. *indorum* – Paetel, 1890: 379.

Type locality. “rivulos circa ruinas Palenqueanas” (streams close to the Palenque ruins – Chiapas, Mexico).

Type material. Two syntypes ANSP 63566; one syntype MNHN (Tab. 20, Fig. 3F).

Remarks. Shell originally described is h = 61 mm; w = 23 mm; wn = 8-12. The shell was posteriorly illustrated by Hanley (1854). Morelet (1851) later considered this species the same as *P. laevissimus* var. *major*. Brot (1860a) follows this view and also proposes that *P. hellerii* Parreys and probably *P. cumingii* Lea, are synonyms of *P. indiorum*. But *P. hellerii* Parreys is not a valid name until formally described by Brot (1872). However, Brot cited this manuscript name, which was a *nomen nudum* by then.

Martens (1899) established that after numerous comparisons of material from Venezuela, he can say that *P. laevissimus* is very different to *P. indiorum*. Martens (1899) also

considered *P. sallei* Reeve and *P. radix* Brot as synonyms of *P. indiorum*. Goodrich & v.d. Schalie (1937) stated that the both varieties described by Martens (1899) are synonyms of *P. indiorum*. However, Bequaert (1957) only considered *P. laevissimus* var. *costatoplicata* Brot as synonym. Thompson (2008) keep the synonymy list of Martens (1899), expanding the type locality to all the type localities of the species he synonymized.

Pachychilus indiorum and *Pachychilus laevissimus* have been frequently confused due to their shell similarity. We considered that both species are certainly distinct for the large geographical distance between the two type localities. Regarding to the type material, one syntype MNHN was obtained by Crosse through exchanged with Morelet.

Additional localities. Mexico: San Andres Tuxtla; Isthmus of Tehuantepec, Oaxaca; Censo; Ocosingo; El Real – Selva Lacandona, Chiapas; Monte Libano, Tabasco; Palenque (Brot, 1875; Martens, 1899; Bequaert, 1957). Guatemala: tributaries of the Rio Usumasinta; Livingston; Mountains of Rio Cavech; Panzos; Chejel; Small creek below La Ceiba, Alta Vera Paz; Rio Dulce near Livingston; Jocola (Paetel, 1890; Martens, 1899; Goodrich & v.d. Schalie, 1937; Thompson, 2008).

Table 20. Shell parameters of the syntypes of *Pachychilus indiorum* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (ANSP 63566)	60.50	25.94	26.18	13.92	33.94	48.36	9
	59.22	25.75	24.53	13.45	33.53	47.28	11
ST (MNHN)	45.10	19.52	18.46	9.75	26.36	37.36	7

intermedius (von dem Busch, 1844)

Melania intermedia von dem Busch, 1844 – in R.A. Philippi 1 (7): 160, pl. 3, fig. 4. Reeve, 1860: pl.20, fig. 141. Brot, 1862: 42. Paetel, 1890: 378.

Melania (Pachychilus) largillierti var. *intermedia* – Kobelt, 1886: 292.

Type locality. “Lacus Nicaragua” (Lake of Nicaragua).

Type material. Holotype GSUB 14908 (39/13) (Tab. 21, Fig. 3G).

Remarks. According to Philippi (1844) and Reeve (1860), a close similarity with *P. largillierti* was noticed by von dem Busch. Brot (1868) established that Morelet (unpublished data) considers *P. intermedius* v.d. Busch as synonym of *P. largillierti* Phil. and even both taxa as conspecific.

Additional localities. Nicaragua (Brot, 1862; Paetel, 1890).

Table 21. Shell parameters of the holotype of *Melania intermedia* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	36.92	16.28	13.57	8.68			
GSUB 14908 (39/13)	35.69	15.63	13.45	7.39	20.23	28.96	7

jansoni H. Adams, 1870

Pachycheilus jansoni Adams, H. 1870: 795.

Melania jansoni – Brot 1875: 40. Paetel, 1890: 377.

Melania (Pachychilus) jansoni – Kobelt, 1886: 291.

Type locality. “Province of Chontales, Nicaragua”.

Type material. Not examined.

Remarks. The species was originally published without illustration for a shell with h = 36 mm; w = 15 mm; wn = 6. H. Adams (1870) and Brot (1875) established that *P. jansoni* is related to *P. turati*.

Additional localities. Nicaragua (Kobelt, 1886).

laevissimus (Sowerby, 1824)

Melania laevissima Sowerby, 1824: 60, pl. 5, fig. 5. Deshayes & Edwards, 1838: 441. I. Lea & H.C. Lea, 1850: 179. H. Adams & A. Adams, 1854: 299. Hanley, 1854-1858: pl. 3, fig. 23. Gray, 1857: 102. Troschel, 1858: 115. Chenu, 1859: 288, fig. 1964. Martens, 1865: 71. Brot, 1870: 274. Martens, 1873: 206. Jousseaume, 1889: 257. Burrington-Baker, 1930: 26. Thompson, 1957: 1. Solem, 1960: 416.

Melania laevissima var. *decollata* – Brot, 1875: 35, pl. 4, fig. 5e.

Melania laevissima – Reeve, 1860: pl. 18, fig. 126a-b. Brot, 1862: 42. Brot, 1868: 5. Brot, 1875: 36. Fischer, 1885: 701. Tryon, 1883: 252. Kobelt, 1886: 292. Paetel, 1890: 379. Fischer & Crosse, 1892: 329. Morrison, 1954: 366. Pilbsry, 1956: 31. Thompson, 2008: 107.

Pachychilus (Pachychilus) laevissimus var. *costato-plicata* – Fischer & Crosse, 1892: 329, pl. 53, fig. 5.

Type locality. “Rio de la Guayra” (Venezuela).

Type material. Not examined.

Remarks. We make here reference to this species in spite of not being part of the Mesoamerican Pachychilidae. Since Morelet's emendation (1851), the limit between *Pachychilus indiorum* and *Pachychilus laevisissimus* progressively disappears, to such an extent that is now considered one species with a distributional range from Venezuela to Florida. After Morelet's work, Reeve (1860) described as *P. laevisissimus* shells from Chiapas, south Mexico and established that "... It may be regarded as the type of a good sectional division, forming Mr. Lea's genus *Pachychilus*...". Brot (1860) stated that he is unable to differentiate the *P. laevisissimus* from its wide number of varieties. Brot (1870; 1875) listed *P. indiorum* Morelet and *P. sallei* Reeve as synonyms of *P. laevisissimus*. Fischer & Crosse (1892) established that *P. indiorum* Morelet is synonym of *P. laevisissimus*. Morrison (1951) referenced *P. laevisissimus* as the type species of *Pachychilus*. For Morrison (1954: 366) and Pilsbry (1956), the correct "genotype" is the shell figure by Reeve (1860) suggesting that this is a valid designation. Since then, *P. laevisissimus* is considered the type species of *Pachychilus* s.s. Thompson (2008) listed *P. laevisissimus* and its varieties (*costato-plicata* and *varicosus*) as synonyms of *P. indiorum*. We prefer to keep the name *Pachychilus laevisissimus* for the South American representative and assigned the Mesoamerican *laevisissimus* to another species described for the region.

Additional localities. Venezuela: Puerto Cabello, Caracas, La Mata, Valle del Tuy (Brot, 1875; Fischer & Crosse, 1892). Central America (Brot, 1870; Brot, 1875; Kobelt, 1886). Mexico: Palenque; Isthmus of Tehuantepec, Oaxaca; Chiapas (Reeve, 1860; Brot, 1862; Brot, 1875; Tryon, 1883; Paetel, 1890; Fischer & Crosse, 1892; Martens, 1899). Guatemala: Rio de la Pasion in Peten (Tristram, 1863; Martens, 1865; Paetel, 1890; Fischer & Crosse, 1892; Martens, 1899).

lacustris (Morelet, 1849)

Melania lacustris Morelet, 1849: 25, species No. 64. Hanley, 1854-1858: pl. 3, fig. 26. Reeve, 1859: pl. 2, fig. 5. Brot, 1862: 43. Brot, 1870: 274. Brot, 1874: 25, pl. 3, fig. 2 a-c; 26. Paetel, 1890: 378

Melania (Pachychilus) lacustris – Kobelt, 1886: 292.

Pachychilus (Cercimelania) lacustris – Fischer & Crosse, 1892: 359, pl. 51, fig. 3, 3a, pl. 52, fig. 4, 4a.

Pachychilus (Glyptomelania) lacustris var. *major* – Fischer & Crosse, 1892: 360.

Pachychilus (Glyptomelania) lacustris var. *extenuata* – Fischer & Crosse, 1892: 360.

Pachychilus (Glyptomelania) lacustris var. *pumila* – Fischer & Crosse, 1892: 360, pl. 51, fig. 4, 4a.

Pachychilus (Glyptomelania) lacustris var. *elimata* – Fischer & Crosse, 1892: 360.

Pachychilus (Glyptomelania) lacustris var. *amphibola* – Fischer & Crosse, 1892: 360, pl. 52, fig. 3.

Pachychila (Glyptomelania) lacustris *amphibolus* – Thompson, 2008: 119.

Pachychilus (Glyptomelania) lacustris – Martens, 1899: 447.

Pachychilus (Glyptomelania) lacustris lacustris – Thompson, 2008: 119.

Pachychilus lacustris var. *lacustris* – Martens, 1899: 447.

Pachychilus (Glyptomelania) lacustris var. *conradti* – Martens, 1899: 448, pl. 25, fig. 9-10.

Pachychilus lacustris – Hinkley, 1920: 47.

Pachychilus glaphyrus lacustris – Goodrich & v.d. Schalie, 1937: 40.

Type locality. “*lacustris* circa pagum Izabal, reipublicae Guatemalensis” (lakes close to the Izabal village, Republic of Guatemala).

Type material. Three syntypes BMNH 1893.2.4.1776-78; five syntypes MNHN; three syntypes ZMB 109576, 109577, 109578 (Tab. 22, Fig. 4A–B).

Table 22. Shell parameters of the syntypes of *Pachychilus lacustris* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (BMNH 1893.2.4.1776-78)	62.70	21.12	18.68	10.56	28.53	44.51	8.5
	54.69	19.21	17.74	10.38	27.09	40.81	7
	53.89	18.75	16.80	9.29	25.80	39.77	7
ST (MNHN), mean of five shells	48.62	18.63	16.34	8.50	24.75	37.35	7.2
ST (ZMB 109576)	48.07	18.01	14.67	8.19	23.14	35.51	9
ST (ZMB 109577)	54.05	20.63	17.29	9.68	26.10	41.02	7
ST (ZMB 109578)	49.11	18.84	17.49	9.24	25.83	39.38	7

Remarks. The original description is for a shell with h = 55 mm; w = 18; wn = 7-8. Reeve (1859) was not sure of whether *P. lacustris* should be considered as a distinct species or as conspecific with *P. glaphyra*. Brot (1874) stated that *P. lacustris* is very polymorphic species and remarks that can be easily confused with *P. obeliscus* Reeve. Martens (1899) established that the variety *extenuata* Fischer & Crosse, 1892 is an imperfect much-worn specimen. Martens (1899) also described a variety *conradti* based on two shells with vertical plaits undeveloped. Goodrich & v.d. Schalie (1937) mentioned that sculptured and un-sculptured shells of *P. lacustris* can be found in the same “colonies”. They additionally described the subspecies *glaphyrus lacustris* based on more slender shells with more strongly developed shell sculpture.

Additional localities. Guatemala: Jocolo; Lake Amatitlan; Izabal Lake; Panzos; Arroyo Subin; Rio de la Pasion (Brot, 1862, 1874; Fischer & Crosse, 1892; Martens, 1899; Hinkley, 1920; Goodrich & v.d. Schalie, 1937; Thompson, 2008). Honduras (Brot, 1874; Kobelt, 1886).

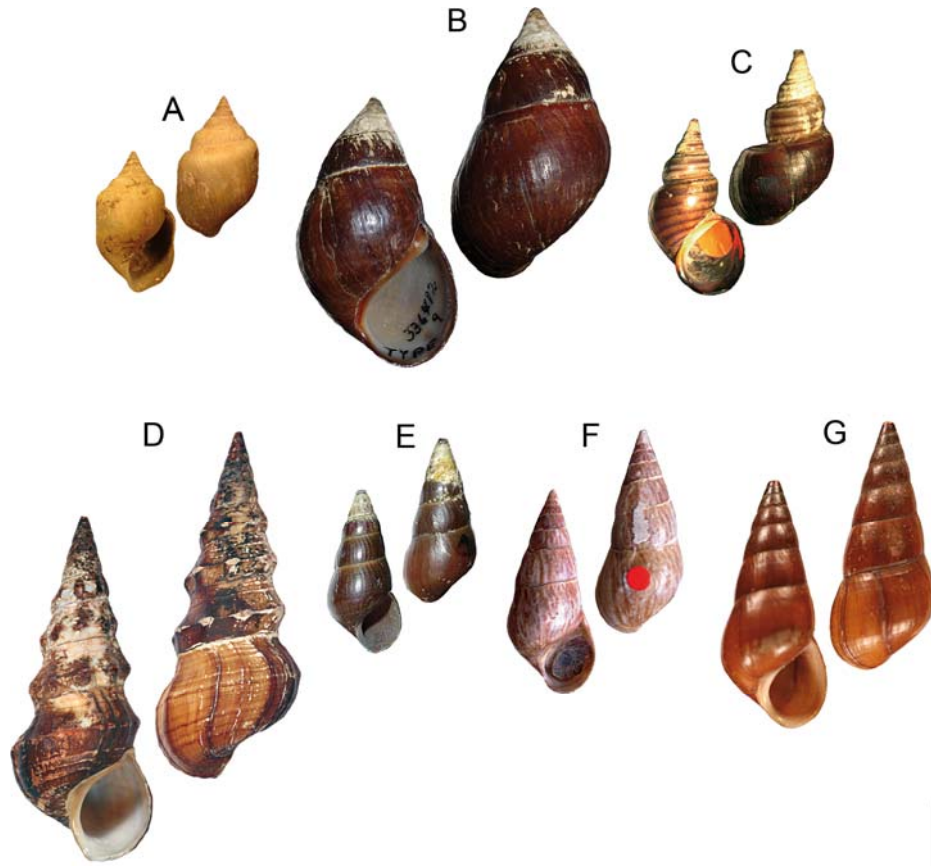


Fig. 3 A-G. Types of Pachychilidae from Mesoamerica (*Lithasiopsis*, *Pachychilus*, *Sphaeromelania*).

A. Paratype of *Lithasiopsis hinkleyi* Pilsbry, 1910 (USNM 207473), bar = 0.5 cm ; – B. Holotype of *Sphaeromelania hinkleyi* Marshall, 1920 (USNM 336412), bar = 1 cm; – C. Lectotype of *Pachychilus humerosus* Pilsbry & Hinkley, 1910 (ANSP 99579), bar = 1 cm. – D. Syntype of *Pachychilus immanis* Morelet, 1851 (NHM 1893.2.4.1783+1794), bar = 2 cm; – E. Syntype of *Pachychilus indifferens* Crosse & Fischer, 1891 (MNHN 8b-c), bar = 1 cm; – F. Syntype of *Pachychilus indiorum* Morelet, 1849 (ANSP 63566), bar = 2 cm; – G. Holotype of *Pachychilus intermedius* von dem Busch, 1844 (GSUB 14908), bar = 1 cm.

largillerti (Philippi, 1843)

Melania largillerti Philippi, 1843: 62, pl. 2, fig. 10. Reeve, 1860: pl. 18, fig. 127. Brot, 1862: 42. Brot, 1870: 275. Brot, 1874: 31, pl. 4, fig. 1a-c. Brot, 1874: 32, pl. 4, fig. 1a. Martens, 1874: 358.

Melania (Pachychilus) largillerti – Strebel, 1874: 38, pl. 4, fig. 36.

Melania (Pachychilus) largillerti – Kobelt, 1886: 292.

Melania L'Argillerti – Paetel, 1890: 379.

Pachychilus (Glyptomelania) largillierti – Fischer & Crosse, 1892: 364, pl. 52, fig. 5, 5a. Martens, 1899: 450, pl. 25, fig. 12. pl. 26, fig. 2.

Pachychilus largillierti – Martens, 1901: 645, pl. 44. fig. 17. Hinkley, 1920: 45. Goodrich & v.d. Schalie, 1937: 40. v.d. Schalie, 1940: 7.

Pachycheilus largillierti – Hinkley, 1920: 38 [emendation for *Pachychilus*].

Pachychilus largillierti – Hinkley, 1920: 44.

Pachychilus (Glyptomelania) largillierti var. *nodulosus* – Martens, 1899: 451, pl. 25, fig. 4.

Pachychilus (Glyptomelania) largillierti var. *stolli* – Martens, 1899: 452, pl. 26, fig. 5-9.

Pachychilus (Glyptomelania) largillierti stolli – Thompson, 2008: 121.

Pachychilus (Glyptomelania) largillierti largillierti – Thompson, 2008: 120.

Sphaeromelania largillierti – Meek, 1908: 205.

Type locality. “America centralis” (Central America).

Type material. One syntype ZMB 112944; three syntypes ZMB 112945; two syntypes ZMB 109580; five syntypes ZMB 109579; 12 syntypes ZMB 70509 (Tab. 23, Fig. 4C-E).

Remarks. The shell originally described is h = 58.6 mm; w = 26 mm; wn = 10-11. Brot (1868: 5) considered that *P. intermedius* and *P. largillierti* are the same. Brot (1870) considered also *P. rusticola* von dem Busch as synonym. Strebel (1873) stated that *P. largillierti* is closely related to *P. mexicanus*. Brot (1874) suggested that besides von dem Busch's species, *P. guatemalensis* Parreyss is also synonym. Martens (1874: 359) concluded that after comparison of the illustrations of the types, *P. mexicanus* is the same *P. largillierti*. Kobelt (1886) synonymized *P. rusticola* von dem Busch and *P. rubicundus* Reeve to *P. largillierti*. For Fischer & Crosse (1892) only *P. intermedius* von dem Busch is synonym of *P. largillierti*. Martens (1899) remarks that is unable to distinguish *P. largillierti* from *P. glaphyrus* Tristram. The latter also stated that *P. indifferens* Fischer & Crosse could be young specimens of *P. largillierti* and includes also *P. intermedius*, *P. rubicundus* and *P. rusticola* as synonyms. Martens (1899: 451, pl. 25, fig. 4) established a variety *nodulosus* which shell presents small knobs that indicates the affinity of *P. largillierti* with the sculptured species of *Pachychilus*. Martens (1899) also described a variety *stolli* for shells ranging h = 26-30 mm; w = 12-13 mm; la = 10-11mm; wa = 7 mm; wn = 4-5, which seems to be nearest to *M. murrea* Reeve (1860: pl. 20, fig. 138a-b). Later, Goodrich & v.d. Schalie (1937) considered that the varieties *salvini* and *stolli* are probably synonyms of *P. largillierti* but not the variety *nodulosus*. Thompson (2008) listed *P. intermedius* v.d. Busch, *P. rusticola* v.d. Busch, *P. rubidus* Reeve, *P. salvini* Tristram, *P. subexaratus* Crosse & Fischer and *P. largillierti* var. *nodulosus* Martens as synonyms of *P. largillierti*,

expanding additionally the type locality to all the localities of the different species synonymized.

Table 23. Shell parameters of the syntypes of *Pachychilus largillierti* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (ZMB 112944)	47.40	18.66	16.77	9.72	24.76	36.35	9
ST (ZMB 112945), mean of three shells	51.47	19.97	17.96	10.05	26.52	38.96	8.67
LT (ZMB 109580), mean of two shells	60.88	22.44	20.59	11.04	30.56	46.23	7.00
ST (ZMB 109579), mean of five shells	34.16	15.30	8.50	11.80	20.41	30.65	5.75
ST (ZMB 70509), mean of 12 shells	24.22	10.98	5.13	9.84	15.17	22.10	4.63

Additional localities. Mexico: Palenque; Yucatan; Chiapas (Strebel, 1874; Fischer & Crosse, 1892). Guatemala: Lagartos near Zacapa; Lake Amatitlan; Rio de las Vacas; Rio de la Pasion; Rio Michatoya; Rio Maria Linda; Paso Antonio near Tortola; Mirandilla near Escuintla; Mountains of Rio Cavech; Plantera; Samac, Cajabón drainage; Izabal: Rio Cavech, Pantera; Retalhuleu (Reeve, 1851-1870; Fischer & Crosse, 1892; Martens, 1899; Hinkley, 1920; Goodrich & v.d. Schalie, 1937; v.d. Schalie, 1940; Thompson, 2008). Nicaragua Lake (Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008). Salvador: Joya (Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008).

larvatus (Brot, 1870)

Melania larvata Brot, 1870: 336, pl. 34, fig. 11 a-b. Brot, 1877: pl. 34, fig. 11, 11a-b. Kobelt, 1878: 31. Paetel, 1890: 379.

Melania (Pachychilus) larvatus – Kobelt, 1886: 292.

Pachychilus (Cercimelania) larvatus – Fischer & Crosse, 1892: 344.

Type locality. “Gineta, Tehuantepec” (Mexico).

Type material. Two syntypes MHNG 190/43a-b; three syntypes MHNG 192; six syntypes MHNG 194 (Tab. 24, Fig. 4F).

Remarks. Brot (1877) established that the young shells of *P. larvatus* looks like *P. liebmanni* Phil. and raise the possibility that *P. larvatus* is the adult form of *P. liebmanni*. Fischer & Crosse (1892) considered *P. larvatus* as a local variation of *P. chrysalis*. Later, Pilsbry (1893) synonymized *P. chrysalis* to *P. larvatus*.

Table 24. Shell parameters of the syntypes of *Pachychilus larvatus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description (Adults)	51-57	25-26	26	20			4-6
Original description (Juvenil)	43	18-20	17.5-20				6
ST (MHNG 192, 194), mean of nine adult shells	48.45	23.24	22.24	11.49	31.67	43.40	5.78
ST (MHNG190, 191), mean of nine juvenile shells	39.84	17.18	17.75	8.95	25.41	35.29	5.38

liebmanni (Philippi, 1848)

Melania liebmanni Philippi, 1848: 58, pl. 5, fig. 8. Reeve, 1860: pl.20, fig. 139. Martens, 1865: 71. Brot, 1870: 275. Brot, 1875: 48, pl. 6, fig. 1. Paetel, 1890: 379.

Melania liebmanni – Brot, 1862: 42. Martens, 1874: 358.

Melania (Pachychilus) liebmanni – Kobelt, 1886: 293.

Pachychilus (Cercimelania) liebmanni – Fischer & Crosse, 1892: 347. Thiele, 1929: 189. Wenz, 1938: 685, fig. 1965.

Pachychilus (Pachychilus) liebmanni – Martens, 1899: 453, pl. 27, fig. 1-2.

Pachychilus (Pachychilus)(sectio Cercimelania) liebmanni – Thiele, 1928: 399.

Pachychilus (Pachychilus) liebmanni liebmanni – Thompson, 2008: 112.

Type locality. “In ditione Reipublicae Mexico” (in the sovereign republic of Mexico).

Type material. Not examined.

Remarks. The shell originally described is h = 36.92 mm and w = 16.28 mm. Strebel (1873) stated that *P. gassiesii* is identical to *P. liebmanni*, while Brot (1875) considered both as distinct although very similar.

Additional localities. Central America (Kobelt, 1886; Wenz, 1938). Mexico: Isthmus of Tehuantepec (Fischer & Crosse, 1892); Playa Vicente, Vera Cruz (Martens, 1899; Thompson, 2008).

maximus (I. Lea & H.C. Lea, 1850)

Melania maxima I. Lea & H.C. Lea, 1850: 187. Brot, 1862: 43. Brot, 1870: 275. Brot, 1874: 23. Paetel, 1890: 380.

Melania (Pachychilus) maxima – Kobelt, 1886: 295.

Pachychilus (Glyptomelania) glaphyrus var. *maxima* – Fischer & Crosse, 1892: 353.

Type locality. “Copan, Central America” (Honduras).

Type material. Not examined.

Remarks. The original publication is from a shell h = 76.20 mm; w = 27.94 mm; wn = 12. Brot (1874) assumed that *P. maximus* is the same *P. immanis* Brot. Bequaert (1957) quoted the existence of a *P. pyramidalis* var. *maximus* (Lea, 1851) from Lake Tzibal, about 50 miles west of Tenosique. The type is probably lost or misplaced since the specimen have not been found on the different collections where Lea's material is housed. *Additional localities.* Central America (Paetel, 1890). Mexico: Tabasco (Bequaert, 1957). Guatemala: Coban (Brot, 1862; Brot, 1870; Kobelt, 1886; Fischer & Crosse, 1892; Bequaert, 1957). Honduras (Bequaert, 1957).

mexicanus (Reeve, 1860)

Melania mexicana Reeve, 1860: pl. 18, fig. 129. Brot, 1862: 42. Martens, 1865: 71. Brot, 1870: 275. Brot, 1875: 45, pl. 5, fig. 9, 9a. Paetel, 1890: 381.

Melania (Pachychilus) mexicana – Kobelt, 1886: 295.

Pachychilus (Cercimelania) mexicanus – Fischer & Crosse, 1892: 340.

Pachychilus panucula var. *mexicanus* – Martens, 1899: 458.

Type locality. "Mexico".

Type material. Not examined.

Remarks. Original description from a short and bold shell, with few whorls, which not possess the characteristic features of the *Pachychilus*. Strebel (1873) considered that Reeve's *P. mexicanus* is only an old, eroded shell of *P. largillierti*. Martens (1874) based on his own observations and quoting Strebel, propose to let only the name *P. largillierti* as valid and to eliminate *mexicanus*. Brot (1870) considered *P. oerstedtii* Mörch as synonym of *P. mexicanus*. For Brot (1875), Reeve's depiction of *P. panuculus* is the same *P. mexicanus*. Kobelt (1886) listed *P. panuculus* Reeve as synonym of *P. mexicanus*.

Additional localities. Guatemala (Fischer & Crosse, 1892).

mexicanus Pilsbry, 1910

Lithasiopsis mexicanus Pilsbry, 1910: 49, fig. 4. Thompson, 2008: 105.

Lithasiopsis mexicana – Thompson, 1959: 6.

Type locality. "Montezuma River, at the ford, a short distance above Tampamolón, State of San Luis Potosí, Mexico".

Type material. Not examined.

Remarks. Pilsbry (1910) established the species for shells with the same appearance of *Goniobasis*, from which differs by its calloused columella and operculum like *L. hinkleyi*. The author gave dimensions of three shells which range between h = 15-17.5 mm; w = 7.3-8.2 mm; la = 6.8-7.8 mm; wn = 9-10.

moctezumensis Pilsbry & Hinkley, 1910

Pachycheilus moctezumensis Pilsbry & Hinkley, 1910: 522, pl. 24, fig. 11-12.

Pachychilus moctezumensis – Thiele, 1928: 382. Pilsbry, 1956: 32.

Pachychilus (Oxymelania) moctezumensis – Thompson, 2008: 125.

Type locality. “Moctezuma River at the ford south of Tampamolón, State of San Luis Potosí” (Mexico).

Type material. Two syntypes ZMB 61697 (Tab. 25, Fig. 4G).

Remarks. The original description is based on shells that have some resemblance to *P. pila*, but from which differ in a more oval shape, with the last whorl less convex and larger, and the aperture less wide. Pilsbry & Hinkley (1910) refers also the presence of “untypical” specimens which in average are h = 23 mm; w = 15 mm; la = 14 mm; wn = 6. Pilsbry (1956: 33) stated that the radula of *P. moctezumensis* approaches to *Amnipila* in the great development of the main cusps of all teeth. Pilsbry (1956: 33) designated a lectotype and three paratypes (ANSP 99568), which were not been found among the type collection of the ANSP. Probably this lot is still mixed with the general collection and further research is in need.

Table 25. Shell parameters of the syntypes of *Pachychilus moctezumensis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	20.5	14.5	13	11			4
	17.5	13	11.5	9			4
ST (ZMB 61697)	16.97	13.68	12.28	7.35	15.12	16.78	5
	16.86	12.67	11.46	6.84	14.53	16.46	6

monachus Pilsbry & Hinkley, 1910

Pachycheilus monachus Pilsbry & Hinkley, 1910: 527, pl. 24, fig. 21-25.

Pachychilus monachus – Thompson, 1967: 30, pl. on page 28, fig. 6-10.

Pachycheilus (Oxymelania) monachus – Thompson, 2008: 126.

Type locality. “Coy River, three miles south of Los Palmas, State of San Luis Potosi, Mexico, in a cave”.

Type material. Lectotype and four paralectotypes ANSP 99581; four paralectotypes ZMB 61693 (Tab. 26, Fig. 5A).

Remarks. The original description figured five shells, but only give measures of three. According to Pilsbry & Hinkley (1910), this species resembles those of *P. atratus suprastratus*, but the spiral striae are coarser and less regular. Pilsbry (1956: 33) selected a lectotype and explained that the companion specimens of the same lot may be considered paratypes.

Table 26. Shell parameters of the type material of *Pachychilus monachus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	32	14.3	13				8
	28	13.3	12				4.5
	25.2	14	12				4.5
LT (ANSP 99581)	29.13	12.91	13.75	7.68	19.78	25.63	7
PLT (ANSP 99581), mean of four shells	26.25	13.32	12.42	7.28	17.88	23.38	5.25
PLT (ZMB 61693), mean of four shells	25.93	13.93	11.68	7.23	17.57	22.78	5.5

murrea (Reeve, 1860)

Melania murrea Reeve, 1860: pl. 20, fig. 138. Brot, 1870: 275. Brot, 1874: 30, pl. 3, fig. 7a-b.

Melania (Pachychilus) murrea – Kobelt, 1886: 296.

Pachychilus (Glyptomelania) lacustris var. *terebralis* – Fischer & Crosse, 1892: 360, pl. 52, fig. 3a-c.

Type locality. Unknown.

Type material. Not examined.

Remarks. Reeve (1860) described a shell pyramidal turreted, with an explanatory note quoted “... a very characteristic species of the Central-American type...”. Then, Brot

(1870) established as type locality “Central America” and from this moment on, the species was considered among the Central American Pachychilidae.

Additional localities. Central America (Brot, 1870). Lake Izabal (Guatemala) and Honduras (Fischer & Crosse, 1892).

obeliscus (Reeve, 1859)

Melania obeliscus Reeve, 1859: pl. 4, fig. 20. Brot, 1862: 43. Brot, 1874: 24, pl.3, fig. 1a-b. Paetel, 1890: 382.

Melanoides obeliscus – Tristram, 1863: 413.

Melania obeliscus unnamed variety – Brot, 1874: 24.

Melania obeliscus unnamed variety – Brot, 1874: 24, pl. 3, fig. 1a.

Melania obeliscus unnamed variety – Brot, 1874: 24, pl. 3, fig. 1b.

Pachychilus (Cercimelania) obeliscus var. *pyrgiscus* – Fischer & Crosse, 1892: 358, pl. 50, fig. 9, 9a. Martens, 1899: 447, pl. 25, fig. 6.

Pachychilus (Glyptomelania) obeliscus pyrgiscus – Thompson, 2008: 122.

Pachychilus (Cercimelania) obeliscus – Fischer & Crosse, 1892: 358.

Pachychilus (Cercimelania) obeliscus var. *exarmata* – Fischer & Crosse, 1892: 358.

Pachychilus obeliscus var. *exarmatus* – Martens, 1899: 447.

Pachychilus (Glyptomelania) obeliscus examartus – Thompson, 2008:121.

Pachychilus (Glyptomelania) obeliscus – Martens, 1899: 446 .

Pachychilus (Glyptomelania) obeliscus obeliscus – Thompson, 2008: 121.

Pachychilus glaphyrus obeliscus – Hinkley, 1920: 47.

Type locality. “Honduras”.

Type material. Not examined.

Remarks. The original description was made for a shell with 8-9 whorls. Reeve (1859) stated that *P. obeliscus* can partakes the typical characteristics of *P. polygonatus*, but is remarkable for the compressed tubercular prominence of the periphery of the last and penultimate whorls. Brot (1874) assured that Hanley's *P. glaphyrus* is synonym of *P. obeliscus*, and established that *P. obeliscus* is probably a local variation of *P. immanis*, due to their close similarities. Brot (1874) also stated that his *P. obeliscus* varieties are analogous but not the same as the *P. immanis* varieties. Fischer & Crosse (1892) synonymized *P. glaphyrus* Hanley to *P. obeliscus*. The latter also considered that *P. obeliscus* is an intermediate species between *P. glaphyrus* and *P. lacustris*. This view is also maintained by Martens (1899).

Additional localities. Guatemala: Jocolo (Hinkley, 1920); Lake Peten (Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008).

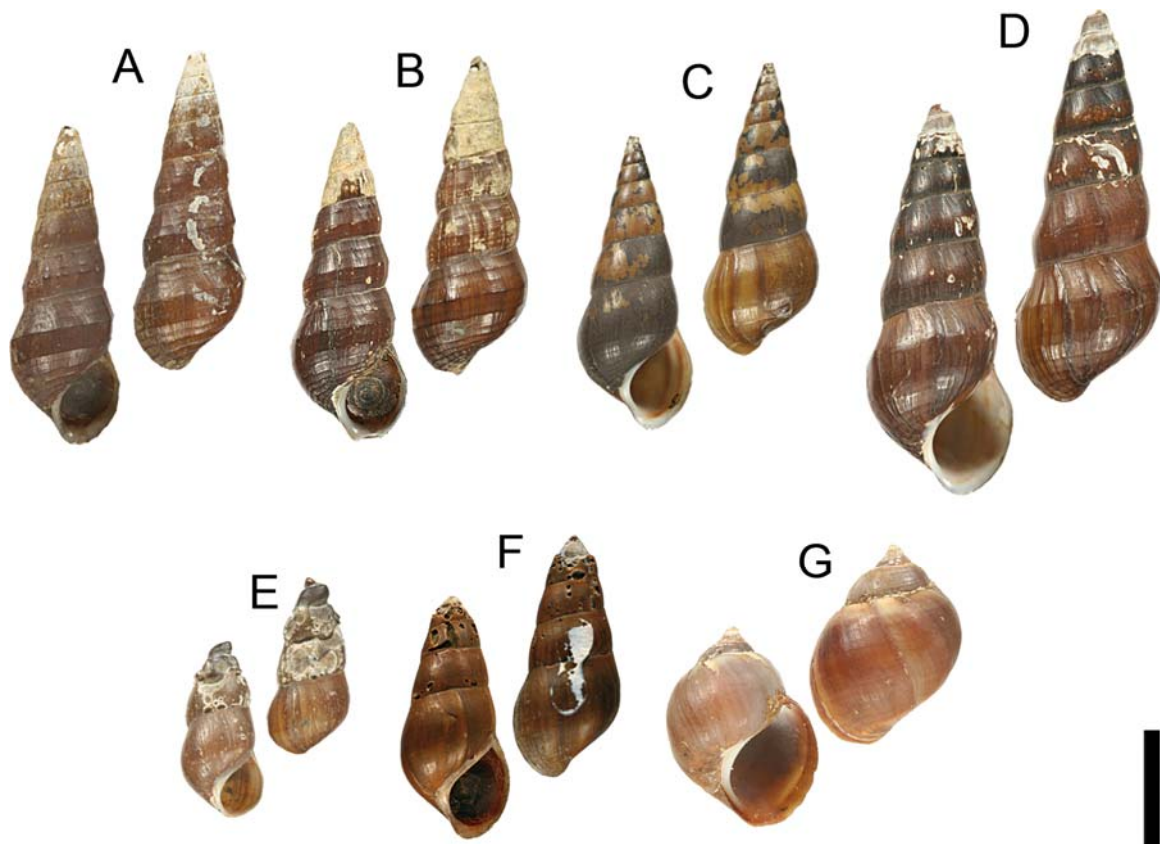


Fig. 4 A-G. Types of Pachychilidae from Mesoamerica (*Pachychilus*).

A. Syntype of *Pachychilus lacustris* Morelet, 1849 (MNHN), bar = 2 cm; – B. Syntype of *Pachychilus* (*Glyptomelania*) *lacustris* var. *conradti* Martens, 1899 (ZMB 109577), bar = 2 cm; – C. Syntype of *Pachychilus largillierti* Philippi, 1843 from Guatemala (ZMB 112944), bar = 2 cm; – D. Syntype of *Pachychilus* (*Glyptomelania*) *largillierti* var. *nodulosus* Martens, 1899 (ZMB 109580a), bar = 2 cm; – E. Syntype of *Pachychilus* (*Glyptomelania*) *largillierti* var. *stolli* Martens, 1899 (ZMB 109579), bar = 1 cm. – F. Syntype of *Pachychilus larvatus* Brot, 1870 (MHNG 190), bar = 2 cm; – G. Syntype of *Pachycheilus moctezumensis* Pilsbry & Hinkley, 1910 (ZMB 61697), bar = 1 cm.

oerstedii Mörch, 1861

Pachychilus oerstedii Mörch, 1861: 79.

Melania oerstedtii – Brot, 1862: 43. Brot, 1875: 46, pl. 5, fig. 10.

Melania (*Pachychilus*) *oerstedti* – Martens, 1872: 134. Kobelt, 1886: 297.

Melania (*Pachychilus*) *oerstedtii* – Brot, 1868: 6. Brot, 1872: 29, pl. 3, fig. 10.

Melania oerstedti – Paetel, 1890: 383.

Pachychilus (*Pachychilus*) *örstedi* – Martens, 1899: 458, pl. 27, fig. 3-5.

Pachychilus (*Pachychilus*) *örstedi örstedi* – Thompson, 2008: 113.

Pachychilus ördstedi – Goodrich & v.d. Schalie, 1937: 42.

Type locality. “Segovia” (Nicaragua).

Type material. Not examined.

Remarks. Mörch (1861) stated that this species is perfectly distinguishable from the other “Melanians” and gave the dimensions of a typical shell (h = 37 mm and w = 17 mm). He also explained that can be also extremely decollated shells with h = 9 mm. Brot (1868) stated that an authentic *P. oerstedii* shell is absolute identical to one *P. mexicanus* from Cuming collection. In following papers, Brot (1872, 1875) raised the idea that *P. oerstedtii*, *P. mexicanus* and *P. chrysalis* are extremely close one to the other. For Brot (1875) *P. oerstedii* looks like a young shell of *P. mexicanus*. Martens (1899) consider that *P. gassiesi* and *P. jansoni* are synonyms of *P. oerstedii*. Thompson (2008) synonymized *P. jansoni* to *P. oerstedii*.

Additional localities. Central America (Brot, 1862). Honduras: Coban, Lancetilla (Thompson, 2008). Nicaragua: Chontales, Chontales; Matagalpa, Arroyo Alasan (Martens, 1899; Thompson, 2008).

olssoni Pilsbry, 1950

Pachycheilus olssoni Pilsbry, 1950: 84, pl. 5, fig. 2, 2a, 2b.

Type locality. “Rio de la Pasion, between P. Sabal and Sayaxche, Peten, northern Guatemala”.

Type material. Three syntypes ANSP 186101; four syntypes USNM 601895 (Tab. 27, Fig. 5B).

Remarks. The species was described based on three shells explicitly deposited at the ANSP (186101), which are the same figured. Nevertheless, Pilsbry (1950) gave dimensions of five shells. Since the type series still exists, the designation as paratypes of the USNM exemplars is unnecessary.

Table 27. Shell parameters of the holotype of *Pachychilus olssoni* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	36.5	15					8-9
	34	15.5					
	34	13					
	32.3	15					
	26	12					
ST (ANSP 186101)	34.07	12.93	10.25	6.64	17.50	26.19	9
	33.52	16.03	12.24	8.55	18.27	26.16	8
	32.23	15.99	12.48	7.81	17.79	24.84	9
ST (USNM 601895), mean of four shells	27.97	13.58	6.78	10.31	16.00	22.59	7.25

opiparis (Morelet, 1851)

Melania opiparis Morelet, 1851: 23, species 140. Reeve, 1860: pl. 35, fig. 241. Brot, 1862: 43. Brot, 1870: 275. Paetel, 1890: 383.

Melania immanis unnamed variety – Brot, 1874: 21.

Melania immanis var. *opiparis* – Kobelt, 1886: 290.

Pachychilus (*Glyptomelania*) *glaphyrus* var. *opiparis* – Fischer & Crosse, 1892: 353, pl. 53, fig. 3-4.

Pachychilus glaphyrus var. *opiparis* – Martens, 1899: 445.

Pachychilus (*Glyptomelania*) *glaphyrus opiparis* – Thompson, 2008: 118 [emendation of *opiparis*].

Type locality. “rivulos prov. Petenensis, haud procul a *Dolorés*, Indiorum pago” (streams of the Peten Province, not far from the Indian village of Dolores, Guatemala).

Type material. One syntype BMNH 1893.2.4.1759 (Tab. 28, Fig. 5C).

Remarks. The shell described by Morelet (1851) is h = 75 mm; w = 25 mm; wn = 7. Thompson (2008) established that the varieties established by Brot and Fischer & Crosse, are synonyms of this species. For a discussion about the identity of the type material see under *polygonatus*.

Additional localities. Mexico: Tabasco (Brot, 1874). Honduras: Copan (Thompson, 2008).

Table 28. Shell parameters of the syntype of *Pachychilus opiparis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (BMNH 1893.2.4.1759)	69.59	32.55	30.48	16.04	41.03	58.89	7

panuculus (Morelet, 1851)

Melania panucula Morelet, 1851: 23, species number 141. Reeve, 1860: pl.18, fig. 131. Brot, 1862: 43. Brot, 1870: 275. Brot, 1874: 27, pl. 3, fig. 3a-b.

Melania (Pachychilus) panucula – Kobelt, 1886: 298.

Melania panuncula – Paetel, 1890: 383.

Pachychilus (Cercimelania) panucula – Fischer & Crosse, 1892: 341, pl. 53, fig. 8, 8a.

Pachychilus (Pachychilus) panucula – Martens, 1899: 458.

Type locality. “flumina prov. Petenensis” (rivers of the Peten province, Guatemala).

Type material. Two syntypes MNHN (Tab. 29, Fig. 5D).

Remarks. The original description is for a shell h = 45 mm; w = 17 mm; wn = 8. Brot (1874) considered that some of the shells labeled as *P. panuculus* at Morelet’s collection could be placed better under *P. indiorum*, *P. laevis* or *P. corvinus*. Brot (1874) also established that Reeve’s depicted *P. panuculus* is a *P. mexicanus*. Fischer & Crosse (1892) stated that *P. panuculus* can be easily confused with *P. mexicanus* Reeve and *P. helleri* Brot.

Additional localities. Guatemala (Reeve, 1851-1870; Brot, 1862; Paetel, 1890). Mexico: Chiapas, Rio Mopan (Fischer & Crosse, 1892; Martens, 1899).

Table 29. Shell parameters of the syntype of *Pachychilus panuculus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (MNHN), mean of two shells	44.91	20.90	19.35	10.24	28.19	39.70	5.50

pasionensis Pilsbry, 1956

Pachychilus passionensis Pilsbry, 1956: 36, pl. 4, fig. 3-5.

Pachychilus (Potamanax) passionensis – Thompson, 2008: 130.

Type locality. “Peten and Alta Vera Paz, Guatemala, in the Río de la Pasión and tributary arroyos. Types from a small arroyo tributary to the Río de la Pasión east of Sebol, in Alta Vera Paz”.

Type material. Holotype UMMZ 65510.

Remarks. The type is h = 34.5 mm; w = 14.2 mm; la = 12.7 mm; wn = 9-10. Pilsbry (1956) stated that the shells are so remarkably similar to those of *P. pluristriatus*, but due to the geographical distance and the radula features, they could be considered different species with probably convergent shell evolution. Pilsbry (1956) also established that "... This snail of the Rio Pasion was formerly identified as *P. pilsbryi*. The two species inhabit eastern and western extremes of the Rio Usumacinta and connecting river systems...". Thompson (2008) synonymized *Pachychilus pilsbryi* to *P. passionensis*. Regarding to the type material, Pilsbry designated some paratypes housed at the ANSP (195981) which I have not been found among the type collection, probably this lot is mixed with the general collection.

petenensis Tristram, 1863

Melania petenensis Tristram, 1863: 414, species 75. Brot, 1868: 5.

Melania petennensis – Paetel, 1890: 384.

Type locality. "Lake Peten, Vera Paz" (Guatemala).

Type material. Three syntypes MHNG 118; three syntypes MHNG 120 (Tab. 30, Fig. 5E).

Remarks. Original description published without illustration. Probably the type of *M. petenensis* is lost since at the collections where material from Tristram was deposited, it could not be found. The only available material are the two lots reviewed from Brot's collection housed at MHNG. It is highly probable that this species is not a Pachychilidae but a Thiariidae, since the shells resembles those of *Hemisinus ruginosus* from Peten, Guatemala. In spite of the lack of anatomical evidence, but based on the shells and the locality, we recommended to separated this species from Pachychilidae.

Table 30. Shell parameters of *Melania petenensis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	29	10	10	5			6-7
ST (MHNG 118), mean of three shells	21.52	8.93	9.10	3.68	13.05	18.72	5.33
ST (MHNG 120), Mean of three shells	25.42	10.56	10.21	4.66	15.10	21.85	5

pila Pilsbry & Hinkley, 1910

Pachycheilus pila Pilsbry & Hinkley, 1910: 521, pl. 24, fig. 1-5.

Pachycheilus pila var. *pilula* – Pilsbry & Hinkley, 1910: 522, pl. 24, fig. 6.

Pachychilus pila – Thiele, 1928: 382, pl. 34.

Type locality. “Tamosopo River above and below the “Natural Bridge”, near Verastagu, State of San Luis Potosi, Mexico”.

Type material. Lectotype and four paralectotypes ANSP 99559; three paralectotypes ANSP 99564; four paralectotypes ZMB 61707; five paralectotypes ZMB 61706 (Tab. 31, Fig. 5F).

Remarks. *Pachychilus pila* was described from short and globose shells of the Tamosopo River and its small tributary streams. Pilsbry & Hinkley (1910) gave measures of four shells which are also figured. Pilsbry & Hinkley (1909) described together with the species, a small form named var. *pilula*. Pilsbry (1956: 33) selected and marked a lectotype and its companion paratypes. The ANSP lot (99564) is labeled as secondary type and paratypes. This designation is not valid and according to the Code they have the status of paralectotypes.

Table 31. Shell parameters of the type material of *Pachychilus pila* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	19	16.5	13				
	20	15.5	13				
	19	17	13.5	12.25			
	20	17	13	10			
LT (ANSP 99559)	19.73	16.95	13.42	9.73	17.95	19.73	3
PLT (ANSP 99559), mean of four shells	16.98	16.10	12.02	8.54	15.98	8.67	2.25
PLT (ANSP 99564), mean of three shells	9.91	8.32	7.21	4.6	8.71	6.14	2.67
PLT (ZMB 61707), mean of four shells	14.93	13.91	10.88	7.19	13.84	11.71	2.75
PLT (ZMB 61706), mean of five shells	8.69	7.68	6.21	3.91	7.65	6.35	3

pila Pilsbry, 1956

Amnipila pila Pilsbry, 1956: 38, pl. 4, fig. 7-9. Thompson, 2008: 106.

Type locality. “San Luis Potosi: Ingenio Agua Buena in power canal and communicating rills and ditch. Puente de Dios near Tamasopo” (Mexico).

Remarks. According to Pilsbry (1956), the type species of *A. pila* is the same *Pachychilus pila* Pilsbry & Hinkley, 1910. The former erected a new genus for *P. pila* based on the complete absence of side cusps on all the radular teeth. Pilsbry (1956) described *Amnipila pila*’s radula as very long, with a central tooth slightly wider than long, and lateral teeth that resembled those of *Pachychilus* except that there is a single very broad cusp.

pilsbryi Martens, 1899

Pachychilus (Potamanax) pilsbryi Martens, 1899: 463, pl. 44, fig. 8. Thompson, 2008: 131.

Pachychilus pilsbryi – Martens, 1901: 646. Goodrich & v.d. Schalie, 1937: 18, 19, 42. Morrison, 1954: 365.

Pachychilus (Pachychilus) potamanax pilsbryi – Thiele, 1928: 399.

Pachychilus (Potamanax) pilsbryi – Thiele, 1929: 189.

Pachychilus pilsbryi – Pilsbry, 1956: 34, pl. 4, fig. 11-12.

Type locality. “Mountains of Poana, State of Tabasco” (Mexico).

Type material. Not examined.

Remarks. Martens (1899) assigned this new name to *Potamanax rovirosai* because “... as there is a *Pachychilus glaphyrus* var. *rovirosai*, mentioned on a preceding page in Pilsbry’s paper (loc. cit. p. 339), the name *Potamanax rovirosai* must be changed...”. Martens (1901), Pilsbry (1956) and Thompson (2008), listed *P. (Potamanax) rovirosai* as synonym of *P. pilsbryi*, but the latter remarks that the generic and familial affinities of this species remain to be resolved. According to Thompson (2008) the type material are two cotypes ANSP 63386 (which are the type series of *P. rovirosai* Pilsbry, 1892).

Additional localities. Mexico: Santa Gertrudis in Tabasco (Martens, 1899). Guatemala: Usumacinta River; small creek tributary to Rio de la Pasion, east Sebol (Martens, 1899; Goodrich & v.d. Schalie, 1937).

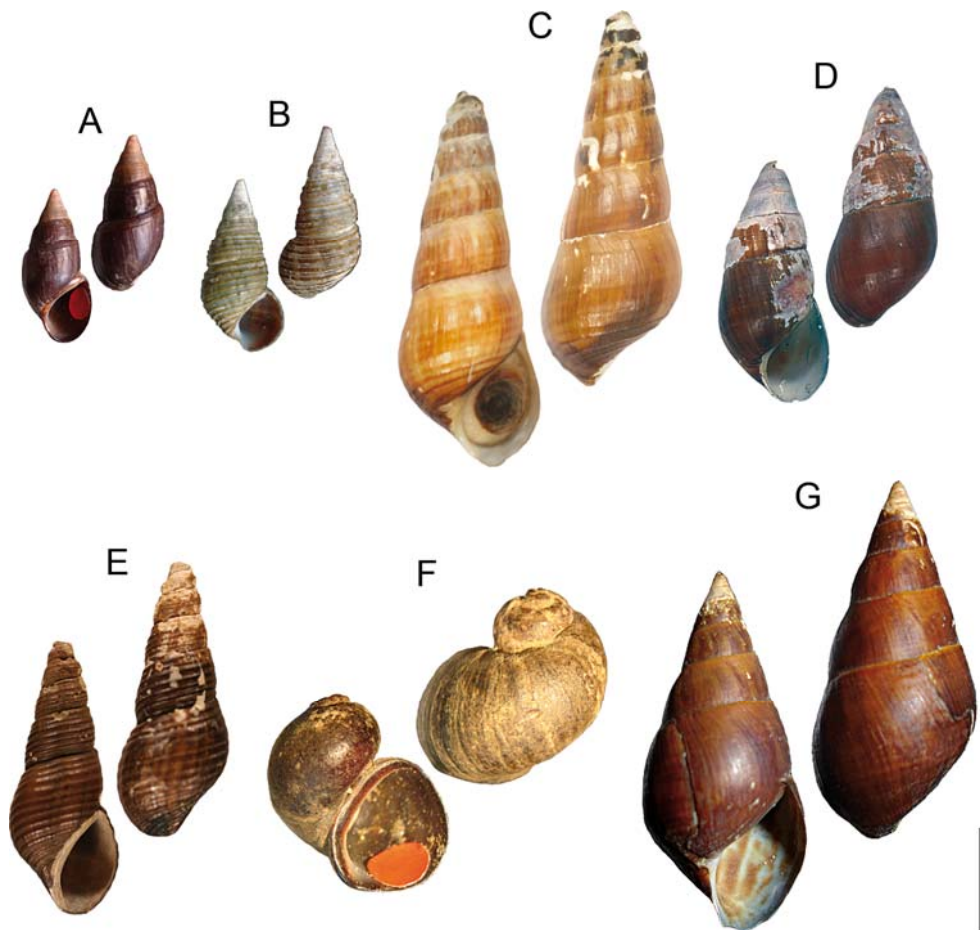


Fig. 5 A-G. Types of Pachychilidae from Mesoamerica (*Melania*, *Pachychilus*).

A. Lectotype of *Pachycheilus monachus* Pilsbry & Hinkley, 1910 (ANSP 99581), bar = 2 cm; – B. Syntype of *Pachycheilus olssoni* Pilsbry, 1950 (ANSP 186101), bar = 2 cm; – C. Syntype of *Pachychilus opiparis* Morelet, 1851 (BMNH 1893.2.4.1759); – D. Syntype of *Melania panucula* Morelet, 1851 (MNHN), bar = 2 cm; – E. Syntype of *Melania petenensis* Tristram, 1863 (MHNG 120), bar = 1 cm; – F. Lectotype of *Pachycheilus pila* Pilsbry & Hinkley, 1910 (ANSP 99559), bar = 1 cm; – G. Paratype of *Pachychilus planensis* Lea, I., 1858 (USNM 119725), bar = 1 cm.

planensis (Lea, I. 1858)

Melania planensis Lea, I., 1858: 118. Lea, I., 1867: 127, pl. 22, fig. 26. Brot, 1868: 5. Brot, 1870: 277. Brot, 1875: 33, pl. 4, fig. 3. Paetel, 1890: 384.

Melania (Pachychilus) planensis – Kobelt, 1886: 299.

Pachychilus ørstedii var. *planensis* – Martens, 1899: 459.

Pachychilus (Pachychilus) ørstedii planensis – Thompson, 2008: 113.

Pachychilus planensis – Goodrich & v.d. Schalie, 1937: 42.

Type locality. “Plan and Omoa, Valley of Ulua River, Atlantic slope, Honduras”.

Type material. Two paratypes USNM 119725 (Tab. 32, Fig. 5G).

Remarks. Original description corresponds to a shell h = 57.66 mm; w = 22.86 mm; wn = 9. Lea (1867) probably due to an edition mistake, referenced Plan and Omas as type locality, spelling which is kept by Brot (1875). Lea (1867) stated that *P. planensis* is nearly allied to *P. largillierti*, but is not so slender and has not the lines at the base. Goodrich & v.d. Schalie (1937) made a quotation for *P. planensis*, which stated that "... this author [Martens], for unexplained reasons, makes *planensis*, the earlier named species, a variety of *ördstedti* Mörch, which was described in 1860...". None of the specimens of the type series match with the measurements of the original description.

Additional localities. Central America (Kobelt, 1886). Mexico (Paetel, 1890). Guatemala: Puerto Barrios (Goodrich & van der Schalie, 1937; Thompson, 2008). Honduras (Brot, 1868, 1870).

Table 32. Shell parameters of the paratypes of *Pachychilus planensis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
PT (USNM 119725), mean for two shells	28.86	14.22	13.36	7.16	18.59	24.28	7.50

pleurotomus Pilsbry & Hinkley, 1910

Pachycheilus pleurotoma Pilsbry & Hinkley, 1910: 530, pl. 24, fig. 13-15.

Pachychilus pleurotoma – Pilsbry, 1956: 37.

Pachychilus (Oxymelania) pleurotoma – Thompson, 2008: 127 [emendation for *pleurotoma*].

Type locality. "first rill on the road to the Moctezuma River" (Mexico).

Type material. Lectotype and three paralectotypes ANSP 99592a; four paralectotypes ZMB 61702 (Tab. 33, Fig. 6A).

Remarks. Pilsbry & Hinkley (1910) published measurements of two shells and figured three. Pilsbry (1956) stated that although some shell differences between *P. pleurotoma* and *P. dalli*, the former would be include under the sub-genus *Pilsbrychilus*. Pilsbry (1956) also established that *P. pleurotoma* has teeth of the same general type as *P. pluristriatus*. The latter author remarks that he himself selected the lectotype and its paralectotypes.

Additional localities. Mexico: Rio Axtla; Xilitla (Pilsbry, 1956).

Table 33. Shell parameters of the type material of *Pachychilus pleurotoma* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	36.35	12.35	11.5				10
	29	10.5	9.70				10
LT (ANSP 99592a)	36.38	13.53	10.80	7.44	17.48	26.35	10
PLT (ANSP 99592a), mean of three shells	27.38	10.43	9.31	5.81	13.96	20.40	8.67
PLT (ZMB 61702), mean of four shells	25.70	11.20	9.63	6.04	14.47	20.39	7.25

pluristriatus (Say, 1831)

Melania pluristriata Say, 1831: 15. Say, 1858: 140. Brot, 1862: 43. Brot, 1870: 276. Brot, 1875: 44. Paetel, 1890: 385.

Melania (Pachychilus) pluristriata – Kobelt, 1886: 300.

Melania planistriata – Martens, 1865: 71 [emendation for *pluristriata*].

Pachychilus pluristriatus – Fischer & Crosse, 1892: 370. Pilsbry, 1956: 31.

Pachychilus (Glyptomelania) pluristriatus – Martens, 1899: 449, pl. 26, fig. 1.

Pachycheilus pluristriatus – Pilsbry & Hinkley, 1910: 523, pl. 23, fig. 1-5 [emendation for *Pachychilus*].

Pachycheilus pluristriatus longus – Pilsbry & Hinkley, 1910: 524, pl. 23, fig. 11-12. Pilsbry, 1956: 33.

Pachychilus (Oxymelania) pleurostriatus longus – Thompson, 2008: 126 [emendation for *pluristriatus*].

Pachychilus pleurostriatus – Goodrich & van der Schalie, 1937: 39, pl. 1, fig. 3 [emendation for *pluristriatus*].

Pachychilus (Oxymelania) pleurostriatus pleurostriatus – Thompson, 2008: 126.

Pachychilus pleurostriatum – Thompson, 1967: 26 [emendation for *pluristriatus*].

Type locality. “Mexico”.

Type material. Lectotype and one paralectotype ANSP 99583 (Tab. 34, Fig. 6B).

Remarks. The shell described is h = 31.8 mm; w = 14 mm; wn = 8-10. Say’s work (1840) was published by his wife Lucy Say, who explains that *P. pluristriatus* (among others), was originally published in the Disseminator, a weekly periodical published at New Harmony, Indiana, but it was not included into the American Conchology. Consequently, the publication of 1840 is considered sometimes as the original description. For Brot (1875) the shell resembles those of *P. schiedeanus*. Fischer & Crosse (1892) stated that *P. pluristriatus* is probably not a *Pachychilus* but a *Goniobasis*. Martens (1899) and Pilsbry

& Hinkley (1910) synonymized *P. rubidus* and *Melania labiosa* Deppe to *P. pluristriatus*. Pilsbry & Hinkley (1910) established the subspecies *longus* for shells which are longer than *P. pluristriatus* and with the keel above the suture more prominent. Both authors published measurements and illustrations of two shells (h = 36-37.3 mm; w = 14.3-14.5 mm; la = 13.3-13.5 mm; wn = 9.5-12), and Pilsbry (1956: 33) selected its lectotype and paralectotypes. Thompson (2008) synonymized *P. rubidus* Lea to *P. pluristriatus*, and rejects the idea of the Chapala Lake as a place where the snail could be found. According to Barber (1928), it is probable that all of the Mexican forms described by Say without more definite locality than “Mexico”, were collected along the old road between Vera Cruz, Jalapa, Mexico City and Tacuba.

Additional localities. Mexico: Laguna de Chapala; San Luis Potosi, Coy River (Martens, 1899; Pilsbry & Hinkley, 1910; Thompson, 2008), Ganina River three miles southwest of San Dieguito (Pilsbry & Hinkley, 1910). Thompson (2008) established that the correct name of the locality is “Gallina River” instead Ganina.

Table 34. Shell parameters of the type material of *Pachychilus pluristriatus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
LT (ANSP 99583)	36.95	15.48	13.56	9.00	20.22	28.78	8
PLT (ANSP 99583)	36.86	14.56	13.89	8.46	20.86	28.65	8

polygonatus (Lea, I. & Lea, H. 1850)

Melania polygonata Lea & Lea, 1850: 195. Reeve, 1859: pl. 3, fig. 11. Brot, 1862: 43. Paetel, 1890: 385.

Pachychilus (Glyptomelania) glaphyrus var. *polygonata* – Fischer & Crosse, 1892: 351.

Pachychilus (Glyptomelania) glaphyrus polygonatus – Thompson, 2008: 117 [emendation for *polygonatus*].

Pachychilus glaphyrus var. *polygonatus* – Martens, 1899: 444.

Melania immanis unnamed variety – Brot, 1874: 21.

Melania immanis var. *polygonata* – Kobelt, 1886: 290.

Type locality. “Copan, Central America” (Honduras).

Type material. One syntype USNM 119569; two syntypes BMNH 1893.2.4.1757-59 (Tab. 35, Fig. 6C).

Remarks. The shell described is h = 88.9 mm and w = 33.02 mm. Reeve (1859) was the first on depicted *P. polygonatus* from Cuming’s collection. Brot (1868) explains that according to Morelet, *P. polygonatus* is the same as *P. immanis*. Consequently, Brot

(1874) and Kobelt (1886) assumed *P. polygonatus* as variety of *P. immanis*. Fischer & Crosse (1892) and Martens (1899) treated *P. polygonatus* as variety of *P. glaphyrus*. Thompson (2008) synonymized *P. glaphyrus rovirosai* Pilsbry to *P. polygonatus*. The latter also stated that if the locality of *P. polygonatus* is really Copan and not Coban, then *rovirosai* can not be synonym of *polygonatus*.

Regarding to the type material, there is an exemplar at the USNM collection originally labeled as “*Melania*” *polygonata* and relabeled as *Pachychilus glaphyrus*. Since the shell at the USNM is like Reeve’s *P. polygonatus* figure, and the name “*Melania polygonata*” is the older at the label, the USNM 119596 exemplar is syntype of *P. polygonatus*. The BMNH types are labeled as *Pachychilus polygonatus* Lea (*M. opiparis* Morelet). Here again, the shells are either the type of *P. polygonatus* or the type of *P. opiparis*. Comparison with Reeve’s figures shows that the BMNH is a mixed lot with one specimen resembling *P. opiparis* and two specimens more similar to *P. polygonatus*.

Additional localities. Central America (Paetel, 1890). Guatemala, Coban; Dolores (Brot, 1862; Brot, 1874; Fischer & Crosse, 1892; Martens, 1899; Thompson, 2008). Mexico: Tabasco, Limon (Martens, 1899; Thompson, 2008).

Table 35. Shell parameters of the type material of *Pachychilus polygonatus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (USNM 119596)	61.99	25.57	22.07	12.98	33.36	49.04	7
ST (BMNH 1893.2.4.1757-58)	72.83	27.15	26.08	13.80	37.88	55.98	7
	71.60	30.52	29.86	16.03	40.96	59.53	7

potamarchus Pilsbry, 1893a

Pachychilus glaphyrus potamarchus Pilsbry, 1893a: 340, pl. 14, fig. 7. Pilsbry, 1893b: 63, pl. 3, fig. 7. Martens, 1899: 446.

Pachychilus glaphyrus var. *potamarchus* – Martens, 1899: 446

Pachychilus glaphyrus var. *bicarinatus* – Martens, 1901: 645

Pachychilus (Glyptomelania) glaphyrus bicarinatus – Thompson, 2008: 116.

Pachychilus (Glyptomelania) potomarchus – Thompson, 2008: 122 [emendation for *potamarchus*].

Type locality. “Tabasco, Mexico”.

Type material. Two syntypes ANSP 63387 (Tab. 36, Fig. 6D).

Remarks. Pilsbry (1893a) described the species based on two shells, but only the larger was figured. He stated that is one of the largest forms of *Pachychilus* known and the most aberrant from the *glaphyrus* stock.

Table 36. Shell parameters of the syntypes of *Pachychilus glaphyrus potamarchus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	99	33					10-11
	87	29					
ST (ANSP 63387)	98.40	34.30	32.92	17.09	48.68	70.53	10
	87.88	33.03	31.06	16.90	43.39	64.22	9

pottsianus Hinkley, 1920

Pachycheilus pottsianus Hinkley, 1920: 54.

Pachychilus pottsianus – Hinkley, 1920: 47.

Pachychilus (Pachychilus) pottsianus – Thompson, 2008: 114.

Type locality. “... two rills on hillsides, in dense woods” (back of Jocolo, Guatemala).

Type material. Not examined.

Remarks. Four shells varying between h = 40-44 mm; w = 16-17 mm; la = 14-15 mm; wa = 7.5-8 mm were described. The name was established for shells that resembles *P. indiorum*, from which differed by a more solid texture and a smaller and different shell aperture. According to Hinkley (1920) the samples were found together with *P. pyramidalis*, from which they differ in being smaller and without any sculpture.

pyramidalis (Morelet, 1849)

Melania pyramidalis Morelet, 1849: 25, species number 63. Hanley, 1854-1858: pl. 4, fig. 31. Reeve, 1859: pl.5, fig. 25. Brot, 1862: 43. Brot, 1870: 276. Paetel, 1890: 386.

Pachychilus (Glyptomelania) glaphyrus var. *pyramidalis* – Fischer & Crosse, 1892: 353, pl. 52, fig. 1 a-c.

Pachychilus (Glyptomelania) glaphyrus pyramidalis – Thompson, 2008: 118.

Pachychilus glaphyrus var. *pyramidalis* – Martens, 1899: 445, pl. 25, fig. 2-3.

Pachychilus glaphyrus pyramidalis – van der Schalie, 1940: 7.

Pachycheilus pyramidalis – Hinkley, 1914: 1. Hinkley, 1920: 42, 43 [emendation for *Pachychilus*].

Pachychilus pyramidalis – Hinkley, 1920: 45, 47, 49, 50. Bequaert, 1957: 225.

Melania immanis unnamed variety – Brot, 1874: 21.

Melania immanis var. *pyramidalis* – Kobelt, 1886: 290.

Type locality. “rivulos in interiore prov. Tabascensis” (streams of the interior of the Tabasco province, Mexico).

Type material. Three syntypes MNHN (Tab. 37, Fig. 6e).

Remarks. v.d. Schalie (1940) considered *P. glaphyrus pyramidalis* more a form rather than a subspecies, but kept the sub-species named and stated that the shells have an intermediate sculptured between *P. lacustris* and *P. largillierti*. Bequaert (1957: 225) cited a var. *maximus* (Lea, 1851) from Lake Tzibal, Chiapas.

Additional localities. Mexico: Tabasco; Tenocique; Chiapas, Meyapoc, Rancho El Edén, Palenque (Reeve, 1851-1870; Brot, 1862, 1874; Paetel, 1890; Fischer & Crosse, 1892; Martens, 1899; Bequaert, 1957; Thompson, 2008). Guatemala: Livingston; Plantera; Jocolo; Esmeralda; Panzos; Polochic Valley; Chama; San Luis; Lake Peten; Coban (Fischer & Crosse, 1892; Martens, 1899; Hinkley, 1920; v.d. Schalie, 1940; Thompson, 2008). Nicaragua: Managua Lake (Martens, 1899).

Table 37. Shell parameters of the syntypes of *Pachychilus pyramidalis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	86	26-28					11
ST (MNHN), mean of three shells	79.32	28.24	25.61	13.22	37.65	55.20	12

radix (Brot, 1872)

Melania radix Brot, 1872: 31, pl. 2, fig. 16. Martens, 1872: 134. Brot, 1874: 30, pl. 3, fig. 6.

Melania (Pachychilus) radix – Kobelt, 1886: 301.

Type locality. “Amérique centrale” (Central America).

Type material. One syntype MHNG 176; two syntypes MHNG 177 (Tab. 38, Fig. 6F).

Table 38. Shell parameters of the syntypes of *Pachychilus radix* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	42	18	16	8.5			9.5
ST (MHNG 176)	41.08	18.24	16.14	9.21	23.26	32.58	9
ST (MHNG 177), mean of two shells	29.98	14.50	13.59	6.96	18.66	25.91	6.5

rasconensis Thiele, 1928

Pachychilus rasconensis Thiele, 1928: 383, pl. 8, fig. 11.

Type locality. “bei der Hazienda Rascon (S. Luis Potosi)” (close to the hacienda Rascon, San Luis Potosi, Mexico).

Type material. Not examined.

Remarks. The species name was erected for black, spiral sculptured shells. The type is h = 33–35 mm and w = 10 mm.

renovatus (Brot, 1862)

Melania renovata Brot, 1862: 43. Brot, 1875: 41, pl. 5, fig. 5. Paetel, 1890: 386.

Melania (Pachychilus) renovata – Kobelt, 1886: 301.

Type locality. “Coban. Am. Centr.” (Cobán, Guatemala).

Type material. Four syntypes MHNG 109; six syntypes MHNG 110 (Tab. 39, Fig. 6G).

Remarks. Brot (1862) published the name into a list without type locality or description. Later, Brot (1875) described and illustrated the shell. Brot (1875) listed *P. cumingii* and *P. graphium* as possible synonyms, although he also established that *P. graphium* and *P. renovata* have to be separated. For Paetel (1890) there is a var. *cumingii* from Central America. “*Melania*” *renovata* was proposed by Brot as a way to avoid confusions between *Pachychilus cumingii* from Honduras and *Melania cumingii* from Philippines (for a discussion see under *cumingii*).

Additional localities. Central America (Kobelt, 1886).

Table 39. Shell parameters of the syntypes of *Pachychilus renovatus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	33	12	11	7			12
ST (MHNG 109), mean of four shells	31.95	12.63	11.62	6.31	16.69	23.97	10
ST (MHNG 110), mean of six shells	25.38	9.28	9.39	4.38	14.18	19.75	10.5

rovirosai Pilsbry, 1893a

Pachychilus glaphyrus rovirosai Pilsbry, 1893a: 339. Pilsbry, 1893b: 62, pl. 1, fig. 9-10.

Type locality. “spring which gushes from the western brow of the little ridge of the Limon, State of Tabasco, Mexico”.

Type material. Six syntypes ANSP 62938 (Tab. 40, Fig. 7A).

Remarks. Pilsbry (1893a) stated that by the time he published his *Pachychilus polygonatus rovirosai* (Pilsbry, 1892), he was not aware that Morelet’s name *glaphyrus* antedated *polygonatus* Lea, which makes *P. polygonatus rovirosai* invalid. Thus, Pilsbry (1893a) decide to change the name to *P. glaphyrus rovirosai*, establishing that this species is allied to *P. glaphyrus* typical and to the var. *scamnata*, but different from both.

rovirosai Pilsbry, 1892

Pachychilus (Polygonatus) rovirosai Pilsbry, 1892: 153, pl. 8, fig. 9-10.

Type locality. “Collected from a spring which gushes from the western brow of the little ridge of the Limon, State of Tabasco, Mexico by Prof. José N. Rovirosa”.

Type material. Six syntypes ANSP 62938 (Tab. 40, Fig. 7A-B).

Remarks. The species was described based on two different shells (one a half-grown specimen and the other an adult). Pilsbry (1892) established that *P. rovirosai* is associated with Lea’s *polygonata*.

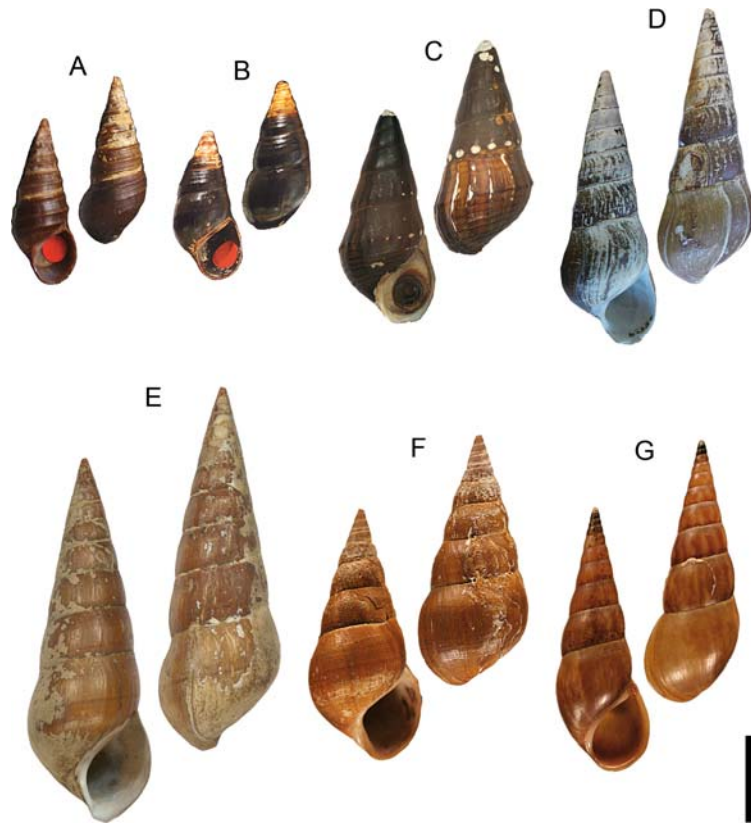


Fig. 6 A-G. Types of Pachychilidae from Mesoamerica (*Pachychilus*).

A. Lectotype of *Pachychilus pleurotomus* Pilsbry & Hinkley, 1910 (ANSP 99592a), bar = 2 cm; – B. Lectotype of *Pachychilus pluristriatus* Pilsbry & Hinkley, 1910 (ANSP 99583), bar = 2 cm; – C. Syntype of *Pachychilus polygonatus* Lea & Lea, 1850 (USNM 119569), bar = 3 cm; – D. Syntype of *Pachychilus glaphyrus potamarchus* Pilsbry, 1893 (ANSP 63387), bar = 3 cm; – E. Syntype of *Pachychilus pyramidalis* Morelet, 1849 (MNHN), bar = 2 cm; – F. Syntype of *Pachychilus radix* Brot, 1872 (MHNG 176), bar = 1.5 cm; – G. Syntype of *Pachychilus renovatus* Brot, 1862 (MHNG 109), bar = 1 cm.

Table 40. Shell parameters of the syntypes of *Pachychilus rovirosai* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	55	20	20	12.5			8
	78	28	25	18			9
ST (ANSP 62938), mean of six shells	59.38	22.23	13.26	18.95	30.34	44.57	8.17

rovirosai Pilsbry, 1893

Potamanax rovirosai Pilsbry, 1893a: 341, pl. 14, fig. 8-9.

Pachychilus (Potamanax) rovirosai – Pilsbry, 1893b: 64, pl. 3, fig. 8-9. Wenz, 1938: 686, fig. 1970. Thompson, 2008: 131.

Type locality. “Mountains of Poana, State of Tabasco”.

Type material. Holotype and one paratype ANSP 63386 (Tab. 41, Fig. 7C).

Remarks. The original description was made for two shells: an “old” exemplar with h = 20 mm; w = 12 mm, and a “young” exemplar h = 16.5 mm; w = 9.75 mm. Pilsbry (1893a) considered these shells allied to *Melania brevis* from Cuba and suggests that *Potamanax* could be a subgenus of *Hemisinus* rather than a distinct genus of Pachychilidae. According to Wenz (1938), *Potamanax rovirosai* is the same as *Pachychilus (Potamanax) pilsbryi* Martens.

Table 41. Shell parameters of the holotype and paratype of *Potamanax rovirosai* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
HT (ANSP 63386)	16.51	10.11	8.63	4.86	12.11	15.28	5
PT (ANSP 63386)	19.33	12.04	9.58	5.59	14.33	18.67	4

rubicundus (Reeve, 1860)

Melania rubicunda Reeve, 1860: vol. 12, pl. 31, fig. 206.

Type locality. Not given.

Type material. Not examined.

Remarks. Reeve (1860) published this species without locality, but with a short note stating that is “... a small species of the *Pachycheilus* section, which can not be referred to any of those previously described...”. This species can be either from Central America or from Asia, because the other species described in the same plate are from India and Borneo. In 1886, Kobelt synonymized this name to *P. largillierti* and from this moment on, subsequent authors cited the species for Central America.

rubidus (I. Lea, 1856)

Melania rubida I. Lea, 1856: 145. I. Lea, 1857: 5. Martens, 1865: 71. I. Lea, 1867: 121, pl. 22, fig. 16. Paetel, 1890: 387.

Melania (Pachychilus) rubida – Kobelt, 1886: 302.

Pachychilus rubidus – Fischer & Crosse, 1892: 371. Brot, 1877: 341, pl. 34, fig. 2.

Type locality. “Mexico” (San Luis Potosi, Mexico).

Type material. Two paratypes USNM 119713 (Tab. 42, Fig. 7D).

Remarks. Original description only give details about the shell and the locality. The measurements of the type material was given on Lea's 1867. Brot (1877) stated that he maintain the shell in the "*Melania*" group because he does not where to placed it. The lot is originally labeled as holotype and paratype, but the specimen labeled as holotype does not match with Lea's measurements. It could be possible that the holotype was misplaced in the collection or Lea selected another shell as type.

Table 42. Shell parameters of the paratypes of *Pachychilus rubidus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	33.02	14.48					
PT (USNM 119713), mean of two shells	30.18	14.87	12.14	7.84	18.15	24.73	6.50

rusticolus (von dem Busch, 1858)

Melania rusticola von dem Busch, 1858: 36.

Melania largillierti unnamed variety – Brot, 1874: 32, pl. 4, fig. 1c.

Type locality. Not given.

Type material. Lectotype GSUB 14882; one paratype GSUB 14906 (Tab. 43, Fig. 7E).

Remarks. von dem Busch (1858) established that the sample came to him as a present from Herr Landauer, without specification of the locality. The author remarks also that *P. rusticolus* keep a distant similarity with *M. nigrita* Morelet. At the original labels of both types appear *M. largillierti* var. *rusticola*. Despite both shells belong to Landauer's lots, the dimensions of the types do not match with the original description.

Table 43. Shell parameters of the lectotype and paratype of *Pachychilus rusticolus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	32.71		10.90	5.45			12
LT (GSUB 14882)	37.01	14.09	12.66	6.34	19.04	27.94	10
PLT (GSUB 14906)	34.55	14.07	11.55	6.16	17.46	25.69	8

sallei (Reeve, 1860)

Melania sallei Reeve, 1860: pl. 19, fig. 133 a-c. Brot, 1862: 43. Paetel, 1890: 387.

Pachychilus (Pachychilus) laevisissimus var. *sallei* – Fischer & Crosse, 1892: 329.

Type locality. “Central America”.

Type material. Not examined.

Remarks. Reeve (1860) described under *sallei* three different shells with 6-7 whorls. The shells were grouped based mainly on their similarity on color pattern (profusely streaked and spotted) and belong to Mexico, Florida and Venezuela. For Brot (1868) is impossible to distinguish *P. sallei* from *P. laevissimus*. Paetel (1890) considered *P. sallei* the same as *P. gassiesii* Reeve.

Additional localities. Mexico: Veracruz, San Andres Tuxtla (Fischer & Crosse, 1892).

salvini (Tristram, 1863)

Melanoides salvini Tristram, 1863: 413, species 72.

Melania salvini – Brot, 1868: 5. Brot, 1870: 276.

Melania salwini – Brot, 1874: 27. Paetel, 1890: 387.

Melania (Pachychilus) salvini – Kobelt, 1886: 302.

Pachychilus (Cercimelania) salvini – Fischer & Crosse, 1890: 362.

Pachychilus (Glyptomelania) largillierti var. *salvini* – Martens, 1899: 451, pl. 26, fig. 3.

Type locality. “Rio de la Paçon, Vera Paz” (Rio de la Pasion, Guatemala).

Type material. Not examined.

Remarks. The shell described is h = 63 mm; w = 19 mm; la = 13 mm; wa = 8 mm; wn = 10-11. For Brot (1874) *P. salvini* is the same as an unnamed variety of *P. lacustris* Brot. Probably the type of *P. salvini* is lost since it could not be found at the collections where material from Tristram was deposited.

Additional localities. Guatemala: Vera Paz, Rio de la Pasion; small streams near Lake Izabal; Lake Amatitlan (Paetel, 1890; Kobelt, 1886; Martens, 1899).

sargi (Crosse & Fischer, 1875)

Melania sargi Crosse & Fischer, 1875: 226; 1876: 385, pl. 11, fig. 4. Brot, 1877: 335, pl. 34, fig. 12, 12a. Paetel, 1890: 387. [non *Melania sargi* Paetel, 1890].

Melania (Pachychilus) sargi – Kobelt, 1886: 303.

Pachychilus (Pachychilus) sargi – Fischer & Crosse, 1892: 338, pl. 51, fig. 6, 6a, 7.

Pachychilus (Potamanax) sargi – Martens, 1899: 463.

Type locality. “Guatemala”.

Type material. Holotype MNHN (Tab. 44, Fig. 7F).

Remarks. The shell was figured later by Crosse & Fischer (1876). The same authors established that this species is close to *P. corvinus*. Brot (1877) supports author’s idea and raise also the possibility that *P. sargi* could be a local variety of *P. corvinus*. At the MNHN there is another specimen labeled as syntype, which is here not considered.

Additional localities. Guatemala: Coban; Cahabon (Brot, 1877; Fischer & Crosse, 1892; Martens, 1899).

Table 44. Shell parameters of the holotype of *Pachychilus sargi* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	16	10	9	6			4-5
HT (MNHN)	15.78	10.79	9.81	5.16	12.78	15.11	5

saussurei (Brot, 1860b)

Melania saussurei Brot, 1860b: 11, pl. 17, fig. 11. Brot, 1862: 43. Martens, 1865: 71. Brot, 1870: 276. Martens, 1874: 358. Brot, 1875: 43, pl. 5, fig. 7. Paetel, 1890: 387.

Melania (Pachychilus) saussurei – Martens, 1874: 36, pl. 4, fig. 43-43a. Kobelt, 1886: 303.

Pachychilus (Oxymelania) saussurei – Fischer & Crosse, 1892: 368. Martens, 1899: 462. Thompson, 2008: 128.

Pachychilus saussurei – Pilsbry, 1956: 31.

Type locality. “Mexique, route de Tampico à Mexico, bois du Rio Grande” (Mexico, way from Tampico to Mexico, forest of the Rio Grande, Hidalgo, Mexico). According to Martens (1899), this river runs into the lagoon of Meztitlan, the road from Tampico to Mexico City crosses it between Zacualtipan and Atotonilco, in Hidalgo.

Type material. One syntype MHNG 125; three syntypes MHNG 124; one syntype ANSP 26850 (Tab. 45, Fig. 7G).

Remarks. Brot (1860b) related *P. saussurei* with *P. schiedeanus*. Fischer & Crosse (1892) established that *P. saussurei* is a variety of *P. schiedeanus*. Thompson (2008) stated that *P. saussurei* is probably extinct because it was not found at the type in 2000.

Additional localities. Mexico (Brot, 1862, 1870; Kobelt, 1886; Paetel, 1890); Creek Palpoala near Misantla (Martens, 1874); swamps in the woods bordering the Rio Grande, between Tampico and Mexico (Thompson, 2008).

Table 45. Shell parameters of the syntypes of *Pachychilus saussurei* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	26	9	8	5			10
ST (MHNG 125)	25.88	9.18	8.30	4.86	13.06	19.34	9.5
ST (MHNG 124), mean of three shells	16.73	7.09	5.90	3.76	8.96	12.87	7.33
ST (ANSP 26850)	17.14	7.29	6.15	3.28	9.09	12.84	8

schiedeanus (Philippi, 1843)

Melania schiedeana Philippi, 1843: 62, pl. 2, fig. 11. Reeve, 1859: pl.15, fig. 101. Brot, 1862: 43. Brot, 1870: 276. Martens, 1874: 358. Brot, 1875: 42, pl. 5, fig. 6, 6a. Paetel, 1890: 388.

Melania (Pachychilus) schiedeana – Martens, 1865: 51. Kobelt, 1886: 303.

Melania (Pachychilus) schiedeana – Strebel, 1874: 35, pl. 4, fig. 37-37a.

Pachychilus schiedeanus – Troschel, 1858: 116, pl. 9, fig. 3. Fischer & Crosse, 1892. Martens, 1899: 462. Pilsbry, 1956: 31.

Pachychilus (Oxymelania) schiedeanus – Fischer & Crosse, 1892: 366, pl. 50, fig. 10 a-b. Martens, 1874: 358. Thiele, 1929: 189. Morrison, 1951: 8.

Pachychilus (Oxymelania) schiedeanus var. *strebelianus* – Fischer & Crosse, 1892: 369. Martens, 1899: 462.

Pachychilus (Oxymelania) schiedeanus strebelianus – Thompson, 2008: 128.

Pachychilus (Oxymelania) schiedeanum – Wenz, 1938: 685, fig. 1967.

Pachychilus (Oxymelania) schiedianus – Morrison, 1954: 365.

Pachychilus (Pachychilus) (sectio Oxymelania) schiedeanus – Thiele, 1928: 399.

Pachychilus (Oxymelania) schiedeanus schiedeanus – Thompson, 2008: 127.

Type locality. “Rivuli et fossae circa urbem Mexico” (Rivers and channels close to Mexico City).

Type material. Two syntypes ZMB 112952 (Tab. 46, Fig. 7H).

Remarks. Shell described is h = 23.9 mm; w = 8.7 mm; wn = 10-11. Philippi (1843) related *P. schiedeanus* with the North American Pleuroceridae *P. virginiana*. Brot (1868) and Martens (1899) synonymized *Melania variegata* M. Reg. Berol. (Wieg. Mss.) to *P. schiedeanus*. For Thompson (2008), *P. saussurei* Brot and var. *strebelianus* Fischer & Crosse are synonyms of *P. (Oxymelania) schiedeanus strebelianus*. The ZMB specimens are labeled as “Mexico prope urbem” (Proper Mexico City).

Additional localities. Central America (Wenz, 1938). Mexico (Brot, 1862, 1870; Paetel, 1890); in streams and ditches at the suburbs of the city of Mexico (Reeve, 1851-1870; Thompson, 2008); Rio Misantla; stream of Palpoala (Martens, 1865, 1899; Brot, 1875; Fischer & Crosse, 1892; Thompson, 2008); creek Arroyo de la Vieja, three miles from Misantla, Veracruz (Strebel, 1874; Martens, 1899); Coatepec (Martens, 1899; Thompson, 2008); Cordoba (Thompson, 2008).

Table 46. Shell parameters of the syntypes of *Pachychilus schiedeanus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
ST (ZMB 112952)	21.95	8.70	7.49	4.83	11.91	17.46	7
	19.51	7.69	6.76	3.91	10.70	15.53	8

schumoi Pilsbry, 1931

Pachychilus schumoi Pilsbry, 1931: 84, pl. 7, fig. 1.

Pachychilus (Pachychilus) schumoi – Thompson, 2008: 114.

Type locality. “Rio Negro (a head stream of the Rio Usumacinta) at Chamá” (Guatemala).

Type material. Holotype and three paratypes ANSP 76231 (Tab. 47, Fig. 8A).

Remarks. According to the author the shell possess a thick callous and is more shortly conic than *P. panuculus* or *P. tumidus*.

Table 47. Shell parameters of the holotype and paratypes of *Pachychilus schumoi* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	39.3	20.5					5
HT (ANSP 76231)	39.43	21.85	19.36	11.62	28.25	36.66	5
PT (ANSP 76231), mean of three shells	34.09	21.13	17.95	10.63	24.60	31.76	4.67

subexaratus Crosse & Fischer, 1891

Pachychilus subexaratus Crosse & Fischer, 1891: 216. Fischer & Crosse, 1892: 350, pl. 52, fig. 6, 6a.

Type locality. “in rivulis, propè lacum Izabal, et in lacu Amatitlan, Guatemalae” (at small brooks, the Lake Izabal and the Lake Amatitlán, Guatemala).

Type material. Holotype and one paratype MNHN; two paratypes MNHN; one paratype MNHN (Tab. 48, Fig. 8B).

Remarks. Fischer & Crosse (1892) published the same original description of Crosse & Fischer (1891) and depicted one shell. At the MNHN there are another two lots labeled as syntypes.

Table 48. Shell parameters of the holotype and paratypes of *Pachychilus subexaratus* (mm and whorl number).

	H	w	la	wa	lwl	ltw	wn
Original description	49	19	20	11			5
HT (MNHN)	49.11	19.94	20.02	9.97	28.58	43.49	5
PT (MNHN)	43.70	19.79	18.72	9.64	27.14	39.64	4.5
PT (MNHN), mean of two shells	40.00	19.29	17.98	9.64	26.15	37.54	3.50
PT (MNHN)	47.42	20.60	19.74	9.19	28.56	42.75	5

subnodosus (Philippi, 1847)

Melania subnodosa Philippi, 1847: 173, pl. 4, fig. 18. Brot, 1862: 43. Brot, 1870: 276. Brot, 1874: 29, pl. 3, fig. 5. Paetel, 1890: 390.

Melania (Pachychilus) subnodosa – Kobelt, 1886: 305.

Pachychilus (Cercimelania) subnodosus – Fischer & Crosse, 1892: 365.

Pachychilus (Glyptomelania) subnodosus – Martens, 1899: 450, pl. 25, fig. 11, 13. Thompson, 2008: 122.

Type locality. “America Centralis” (Central America).

Type material. Not examined.

Remarks. The shell described is h = 45.6 mm; w = 20.63 mm, sculptured with folds at the penultimate whorl and knots at the body whorl. According to Martens (1899) this species is similar to *P. lacustris*.

Additional localities. Guatemala (Brot, 1874; Fischer & Crosse, 1892). Nicaragua: Managua (Martens, 1899). Costa Rica (Martens, 1899).

suprastriatus Pilsbry & Hinkley, 1910.

Pachycheilus atratus suprastriatus Pilsbry & Hinkley, 1910: 526. – Thompson, 2008: 123.

Type locality. “Valles River at Mecos falls, and some rapids two miles west of Mecos, State of San Luis Potosi, Mexico”.

Type material. Lectotype and two paratypes ANSP 99575a; three syntypes ZMB 61704 (Tab. 49, Fig. 8C).

Remarks. This variety name was established for shells with pale spiral bands on the ridges, (which seems to be only product of erosion) and also partially because it is the only species of *Pachychilus* found around the Mecos falls. Pilsbry & Hinkley (1910) depicted five shells and gave measures of four. Pilsbry (1956: 33) figured and designated the lectotype. Thompson (2008) synonymized this species with *Pachychilus (Oxymelania) atratus*. As the currently type series is composed by a large number of shells, here we present dimensions of only three (the lectotype and the biggest and the smallest shell of the series).

Table 49. Shell parameters of the type material of *Pachychilus atratus suprastratus* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	28	18	13.5	10			3.5-6
	27	17	14	12			
	25	18.5	14.35	12			
	25	16.5	14	10.35			
LT (ANSP 99575a)	30.32	15.98	13.11	8.42	19.13	26.31	6
PLT (ANSP 99575a)	19.33	9.63	9.19	4.58	13.43	17.31	5
	27.99	13.95	12.06	7.24	18.37	23.98	7
PLT (ZMB 61704), mean of three shells	26.32	14.03	11.53	7.42	17.27	22.51	6

suturalis Pilsbry & Hinkley, 1910

Pachycheilus suturalis Pilsbry & Hinkley, 1910: 529, pl. 24, fig. 16-20.

Pachychilus suturalis – Pilsbry, 1956: 37.

Pachychilus (Oxymelania) suturalis – Thompson, 2008: 129.

Type locality. “Creek near Tampamolón” (San Luis Potosí, Mexico).

Type material. Lectotype and five paralectotypes ANSP 99585a; four syntypes ZMB 61696 (Tab. 50, Fig. 8D).

Remarks. The original description gives measures of four shells and depicted five. Pilsbry & Hinkley (1910) additionally gave measures of two largest examples from Moctezuma river (h = 34–33.2 mm; w = 15–12.2 mm; la = 13–12 mm; wn = 4–7.5), and of two specimens from Coxcatlán (h = 18.2–20 mm; w = 7–7.3 mm; wn = 6.2–7) which were

found living together with *P. pleurotoma*. According to Pilsbry & Hinkley (1910) *P. suturalis* is related to *P. pleurotoma* and to *P. saussurei*. Pilsbry (1956) remarks that he selected a lectotype and the respectively paratypes. Although Pilsbry (1956) mentioned four paratypes, the lot is currently composed by five shells.

Additional localities. Mexico: Also found in the creek at Coxcantlan, a creek one mile above the ford of the Moctezuma River, and in the first and second brooks crossed on the road through the mountains to the Moctezuma River, State of San Luis Potosi (Pilsbry & Hinkley, 1910); Tamazunchale and a creek south Huichihuayan; Coxcatlan; creek ca. 7 miles S of Huichihuayan (Thompson, 2008).

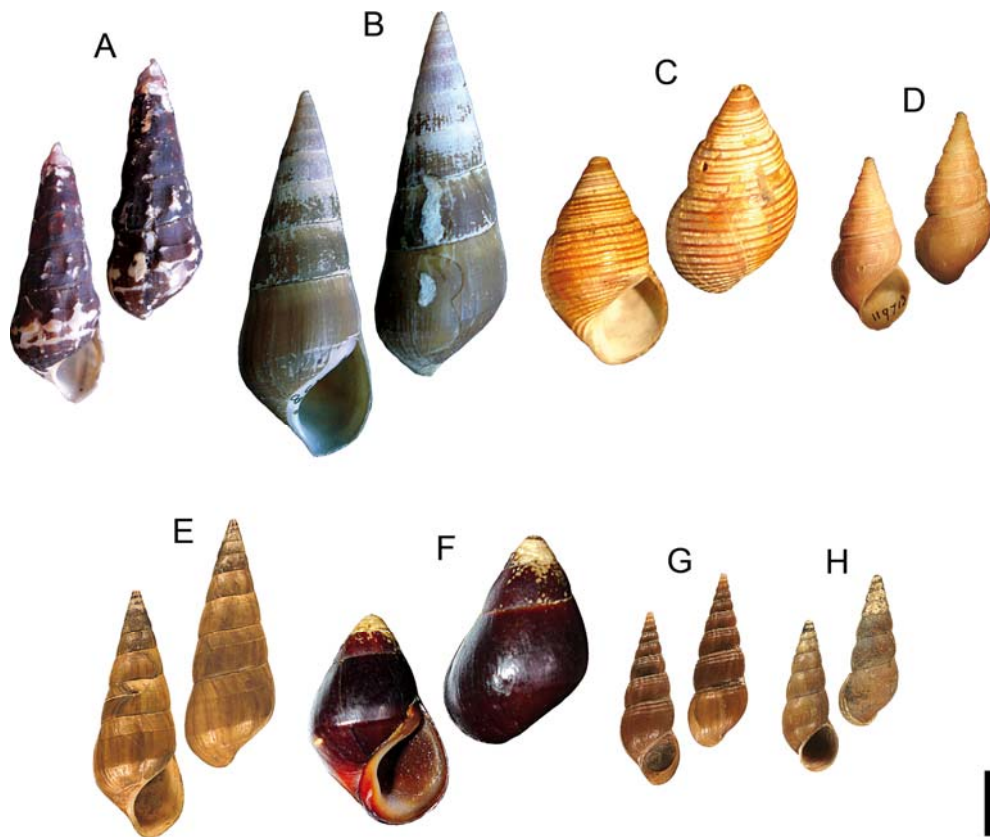


Fig. 7 A-H. Types of Pachychilidae from Mesoamerica (*Pachychilus*, *Potamanax*).

A-B. Two syntypes of *Pachychilus rovirosai* Pilsbry, 1892 (ANSP 62938), bar = 2 cm, 1 cm respectively; – C. Holotype of *Potamanax rovirosai* Pilsbry, 1893 (ANSP 63386), bar = 0.5 cm; – D. Holotype of *Pachychilus rubidus* Lea, I., 1856 (USNM 119713), bar = 1 cm. – E. Lectotype of *Pachychilus rusticolus* von dem Busch, 1858 (GSUB 14882), bar = 1 cm; – F. Holotype of *Pachychilus sargi* Crosse & Fischer, 1875-1876 (MNHN), bar = 0.5 cm; – G. Syntype of *Pachychilus saussurei* Brot, 1860 (MHNG 125), bar = 1 cm; – H. Syntype of *Pachychilus schiedeanus* Philippi, 1843 (ZMB 112952), bar = 1 cm.

Table 50. Shell parameters of the type material of *Pachychilus suturalis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	28	13	11				5.5
	28	11.5	11				6.5
	24.5	11	10				6.5
	26	11.35	9.35				7
LT (ANSP 99585a)	25.69	11.68	9.39	6.73	14.98	21.33	7
PLT (ANSP 99585a), mean of five shells	25.54	11.80	10.10	6.39	15.46	21.66	6.80
ST (ZMB 61696), mean of four shells	24.22	11.72	9.61	5.81	14.33	20.29	7

tomasopensis Pilsbry & Hinkley, 1910

Pachycheilus pluristriatus tomasopensis Pilsbry & Hinkley, 1910: 524, pl. 23, fig. 6-10.

Pilsbry, 1956: 36, pl. 4, fig. 3.

Pachychilus (Oxymelania) pleurostriatus tomasopensis – Thompson, 2008: 127 [emendation for *pluristriatus*].

Type locality. “Small stream north of the mill of the Tamasopo Sugar Co., San Luis Potosi” (Mexico).

Type material. Lectotype and one paralectotype ANSP 99584 (Tab. 51, Fig. 8E).

Remarks. This sub-species was established for shells that resemble those of *P. pluristriatus* but possess weaker sculpture tending to smooth. Pilsbry & Hinkley (1910) published measurements of three “typical” plus two “perfect adult” shells. Four of these shells are depicted. Additionally, the authors figured one shell with the apex completely eroded in order to remark that *P. pluristriatus tomasopensis* can be confused with another species. Pilsbry (1956: 33) selected a lectotype and three paratypes, but the lot is composed only by two shells.

Table 51. Shell parameters of the lectotype and paralectotype of *Pachychilus pluristriatus tomasopensis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Typical shells	36.5	17	14				5.5
	38	15	15				7.5
	34	13	14				7.5
Perfect adult shells	25	13	11.7				3
	26.5	15.2	11				4.5
LT (ANSP 99584)	32.78	16.57	14.13	9.01	20.09	28.28	6
PLT (ANSP 99584)	25.90	13.60	11.23	6.72	16.24	23.35	4

tristis Pilsbry & Hinkley, 1910

Pachycheilus tristis Pilsbry & Hinkley, 1910: 522, pl. 24, fig. 7-10. [not *Melania tristis* Reeve, 1860 from Java]. Kobelt, 1886: 307. Branson & McCoy Jr., 1963: 105.

Pachychilus tristis – Thiele, 1928: 383, pl. 35. Pilsbry, 1956: 33.

Pachychilus (Oxymelania) tristis – Thompson, 2008: 129.

Type locality. “Tamosopo River above and below the “Natural Bridge”, near Verastagu, State of San Luis Potosi” (Mexico).

Type material. Lectotype and paralectotype ANSP 99566; four syntypes ZMB 61705 (Tab. 52, Fig. 8F).

Remarks. Species described based on four shells. For Pilsbry & Hinkley (1910) *P. tristis* differs from *P. pila* by the brown color, bluish-white aperture and white columella. Pilsbry (1956: 33) selected and marked a lectotype and three paratypes. Nowadays, the ANSP lot selected by Pilsbry (1956) is composed by the lectotype (which is labeled as holotype) and only one paralectotype.

Additional localities. Salto River, San Luis Potosi, Mexico (Branson & McCoy Jr., 1963).

Table 52. Shell parameters of the lectotype, paralectotype and syntypes of *Pachychilus tristis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	21	13.7	11.5	9			3-4
	20	14	11.2	9.2			
	23.5	16	12.5	10			
	16.2	12.5	9.5	8			
LT (ANSP 99566)	23.29	16.23	12.79	8.49	18.91	23.29	3
PLT (ANSP 99566)	17.37	12.25	9.91	6.30	13.79	16.93	3.33
ST (ZMB 61705), mean of four shells	24.22	11.72	9.61	5.81	14.33	20.29	7

tumidus (Tristram, 1863)

Melanoides tumida Tristram, 1863: 413, species 70.

Melania tumida – Brot, 1868: 5. Brot, 1870: 276. Brot, 1874: 23. Paetel, 1890: 393.

Melania (Pachychilus) tumida – Kobelt, 1886: 308. [not *Melania tumida* Gredler, 1885].

Pachychilus (Cercimelania) tumidus – Fischer & Crosse, 1892: 357.

Pachychilus panucula var. *tumidus* – Martens, 1899: 458, pl. 25, fig. 5.

Type locality. “Lake Peten, Vera Paz” (Guatemala).

Type material. Not examined.

Remarks. Shell originally described is h = 65 mm; w = 32 mm; la = 23 mm; wa = 15 mm; wn = 7-8. Brot (1874) assumed that *P. tumidus* is the same *P. immanis* unnamed variety Brot. Probably the type of *P. tumidus* is lost since it could not be found at the collections where material from Tristram was deposited.

Additional localities. Central America (Kobelt, 1886). Guatemala: Lake Peten (Martens, 1899).

turati (Villa, 1854)

Melania turati Villa, 1854: 113. Brot, 1862: 43. Brot, 1868: 6, pl. 3, fig. 11-12. Brot, 1870: 277. Brot, 1875: 39, pl. 5, fig. 2, 2a. Paetel, 1890: 393.

Melania (Pachychilus) turati – Kobelt, 1886: 308.

Pachychilus (Cercimelania) turatii – Fischer & Crosse, 1892: 345, pl. 51, fig. 1, 1a.

Pachychilus (Pachychilus) turatii – Martens, 1899: 454, pl. 26, fig. 10-20.

Pachychilus (Pachychilus) turati – Thompson, 2008: 114.

Type locality. Not given.

Type material. Not examined.

Remarks. Brot (1868; 1875) established that *P. turati* is related with *P. corvinus* and both can be easily confused. For Martens (1899) and Thompson (2008) *P. gassiesi* Strebel is synonym of *P. turati*. Martens (1899) related *P. liebmanni* to *P. turati*.

Additional localities. USA: Louisiana Mexico (Brot, 1870). Mexico: Vera Cruz; Atoyac River; Jamapa River; Orizaba; Jalapa; Cordova (Brot, 1870; Kobelt, 1886; Fischer & Crosse, 1892; Martens, 1899)

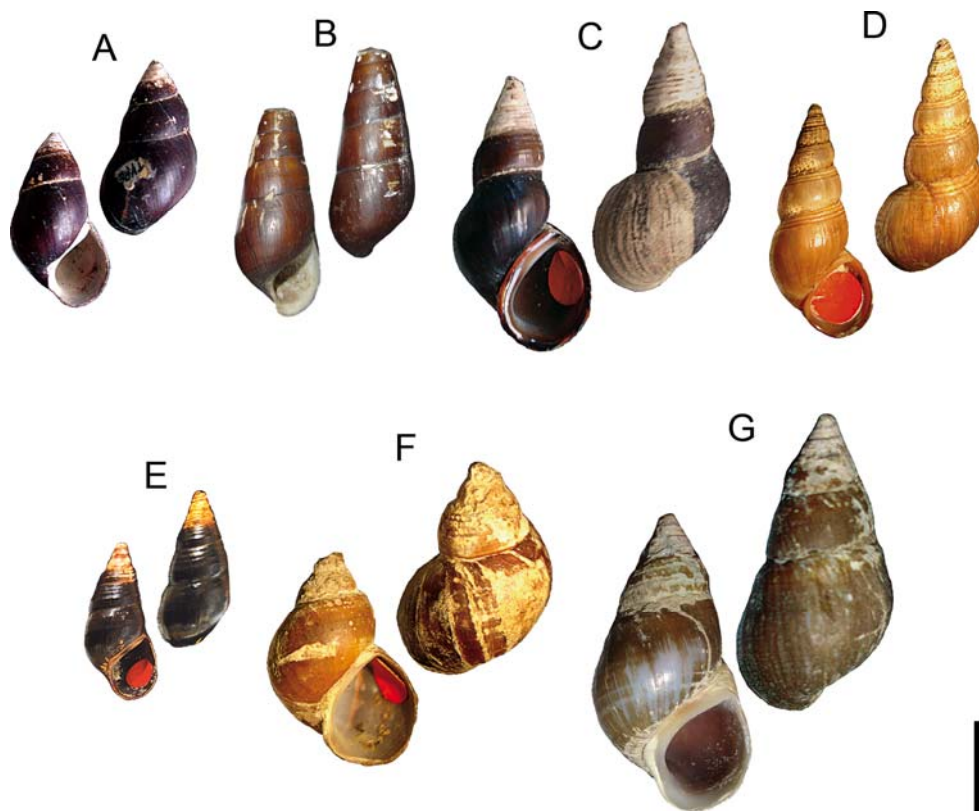


Fig. 8 A-G. Types of Pachychilidae from Mesoamerica (*Pachychilus*).

A. Holotype of *Pachychilus schumoi* Pilsbry, 1931 (ANSP 76231), bar = 2 cm; – B. Holotype of *Pachychilus subexaratus* Crosse & Fischer, 1891 (MNHN), bar = 2 cm; – C. Lectotype of *Pachychilus atratus suprastratus* Pilsbry & Hinkley, 1910 (ANSP 99575a), bar = 1 cm; – D. Lectotype of *Pachychilus suturalis* Pilsbry & Hinkley, 1910 (ANSP 99585a), bar = 1 cm; – E. Lectotype of *Pachychilus pluristriatus tomasopensis* Pilsbry & Hinkley, 1910 (ANSP 99584), bar = 2 cm; – F. Lectotype of *Pachychilus tristis* Pilsbry & Hinkley, 1910 (ANSP 99566), bar = 1 cm; – G. Lectotype of *Pachychilus vallesensis* Hinkley, 1907 (ANSP 96592), bar = 1 cm.

vallesensis Hinkley, 1907

Pachycheilus vallesensis Hinkley, 1907: 25, pl. 5, fig. 1-10. Pilsbry & Hinkley, 1910: 528.

Pachychilus vallesensis – Goodrich & van der Schalie, 1937: 39, pl. 1, fig. 2. Pilsbry, 1956: 37.

Pachychilus (Oxymelania) vallesensis vallesensis – Thompson, 2008: 129.

Type locality. “Valles River, Valles, State of San Luis Potosi, Mexico”.

Type material. Lectotype and one paralectotype ANSP 96592; one syntype ZMB 59631; four syntypes ZMB 61695 (Tab. 53, Fig. 8G).

Remarks. According to Hinkley (1907) this is the only *Pachychilus* species living so far north in Mexico. The author also established that *P. vallesensis* resembles short forms of *P. laevissimus*. In the original description figure 1 was designated as type. Later, Pilsbry (1956: 33) designated one lectotype (ANSP 96592). Currently this ANSP lot is composed by two shells which have to be lectotype and one paralectotype.

Additional localities. Mexico: Tamaulipas: Temesí River, Rio Guayalejo system, Rio Frio, Gomez Farias; San Luis Potosi: Rio Panuco, Rio Moctezuma at the ford south Tampamolón, Pujal (Pilsbry, 1956; Thompson, 2008).

Table 53. Shell parameters of the type material of *Pachychilus vallesensis* (mm and whorl number).

	h	w	la	wa	lwl	ltw	wn
Original description	32	16					6-8
	33	19					
LT (ANSP 96592)	32.02	17.53	14.46	8.60	22.45	29.03	6
PLT (ANSP 96592)	26.21	14.83	13.79	7.95	19.20	23.95	5.75
ST (ZMB 59631)	26.18	15.14	13.93	7.30	19	23.51	7
ST (ZMB 61695), mean of four shells	24.36	14.18	11.80	6.50	17.72	21.70	6.25

vulneratus Fischer & Crosse, 1892.

Pachychilus (Cercimelania) chrysalis var. *vulneratus* Fischer & Crosse, 1892: 342, pl. 51, fig. 9, 9a, 10, 10a.

Pachychilus vulneratus – Pilsbry, 1900: 139. Martens, 1901: 646.

Type locality. “San Pedro Gineta, in isthmo Tehuantepecensi, provinciae Chiapas, reipublicae Mexicanae” (in San Pedro Gineta, Isthmus of Tehuantepec, Chiapas province, Republic of Mexico).

Type material. Not examined.

Remarks. The name was originally published as a variety of *chrysalis* for a shell with h = 60 mm; w = 22 mm; la = 24 mm; wa = 14 mm; wn = 8. Pilsbry (1900) cited *Pachychilus vulneratus* as a distinct species from Upper Puyacatengo River, near Teapa (Mexico). Pilsbry (1900) also stated that in Morelet’s collection *P. vulneratus* is labeled as *P. helleri*, and that the form differs considerably from *P. chrysalis* which proves its distinctiveness. Martens (1901), in disagree with Pilsbry (1900) stated that the shell of *vulneratus* is extremely eroded. Thompson (2008: 108) treated *P. vulneratus* as a synonym of *P. chrysalis*.

5.2 A case study: *Pachychilus* in Guatemala

Introduction

The Pachychilidae are represented in Mesoamerica by the genera *Pachychilus*, *Potamanax*, *Lithasiopsis* and *Amnipila*. Of 76 *Pachychilus* species described for this whole region, Guatemala accounts for 27.6% of the total number.

Guatemala is a Central American country bordered by Mexico to the north and west, the Pacific Ocean to the southwest, Belize and the Caribbean Sea to the northeast, and Honduras and El Salvador to the southeast (Chapter 2.2, Fig. 1). The Guatemalan topography is characterized by a series of isolated mountain ranges and lowlands, with flat areas on the Caribbean and Pacific coasts, as well as around Lake Izabal. In the middle of the country there is one mountain range system surrounding Lake Izabal. Southeast of the lake another series of mountains extends to the Honduras and El Salvador borders. In the north, the lowlands of Peten give place to the north-west Maya Mountains of Belize (Schuster & Cano, 2006). This highly variable topography and the fact that some of the basins are isolated have resulted in many different and sometimes fragmentary habitat types. Consequently, in this region areas of endemism that are determined by geographic features are recognized for different groups of plants and animals (Goodrich & v.d. Schalie, 1937; Rosen, 1979; Bermingham & Martin, 1998; Schuster & Cano, 2006).

In Guatemala, endemism studies have mostly been based on phenetic analyses (freshwater mollusks, amphibians and reptiles), while only few phylogeographic analyses (Scarabaeoidea and poeciliid fishes) have been done (Goodrich & v.d. Schalie, 1937;

Rosen, 1979; Schuster & Cano, 2006). Phylogeography is a young and fast growing field that analyzes the geographical distribution of genealogical lineages, seeking to test the congruence between the evolutionary, demographic, and distributional histories of taxa against the particular geological and ecological setting of a given region (Bermingham & Moritz, 1998; Emerson & Hewitt, 2005). Phylogeographic analyses are used as a tool to solve endemisms because they allow to compare evolutionary responses across different historical isolates, can provide evolutionary and geographical context for communities, and can direct conservation strategies (Bermingham & Moritz, 1998).

As it is also stated in Chapter 5.1, there are many uncertainties regarding generic affiliation and species names in the Neotropical Pachychilidae. Due to their quite variable shells and the confused older taxonomic literature, the species are not clearly delimited and their identification is difficult. For example, in Guatemala up to five different shell morphotypes, which can be found inhabiting the same locality, have been usually treated as different species. On the other hand, organisms from distant localities living in different conditions have often been identified as a single species. Since it is difficult to recognize species from shell characters only, radula comparisons and phylogenetic analyses of the mitochondrial genes 16S and COI were carried out. Additionally, the first phylogenetic approximation of freshwater mollusks assemblages from Mesoamerica is here described for Pachychilidae species from Guatemala. Also, some relationship patterns between Guatemalan species and pachychilid representatives of Mexico and Cuba are shown. These analyses constitute a first step towards a phylogeographic study of Neotropical freshwater gastropods.

Specific material and methods

The Pachychilidae used in this study were collected by K. Schneider in several field trips to Guatemala and Cuba between 2005–2008. Additional material from Mexico was obtained through exchange with the Universidad Autónoma de Mexico (UNAM). The samples were directly fixed in ethanol after collection. Prior to preservation, the shell spire was perforated in order to avoid incorrect fixation of the tissues by closure of the operculum. 63 specimens were used for this study. Each shell was measured according to the methodology previously described (see Chapter 3.2), and photographically documented. The shells were compared with the original description as well as with the available type material, and provisional species names were assigned. The animal was extracted from the shell and pieces of the foot were used for the molecular analysis (see Chapter 3.4). The radula was also removed and prepared as described in Chapter 3.3. The molecular procedure, the sequence alignment and the phylogenetic analysis were carried out by co-workers of the molecular laboratory of the Museum of Natural History –

Humboldt University (Berlin) as described in Chapters 3.4 and 3.5. Trees for the 16S (Fig. 2) and COI (Fig. 3) genes were constructed using MrBayes 3.1.2.

Results

For most of the specimens, the names previously assigned based on shell comparisons do not correspond with the arrangements of the phylogenetic tree topologies as will be discussed below. Comparisons of the radulae show that these are scarcely differentiable between organisms and localities, and therefore do not allow to clearly and consistently separate species, as can be observed in Fig. 1.

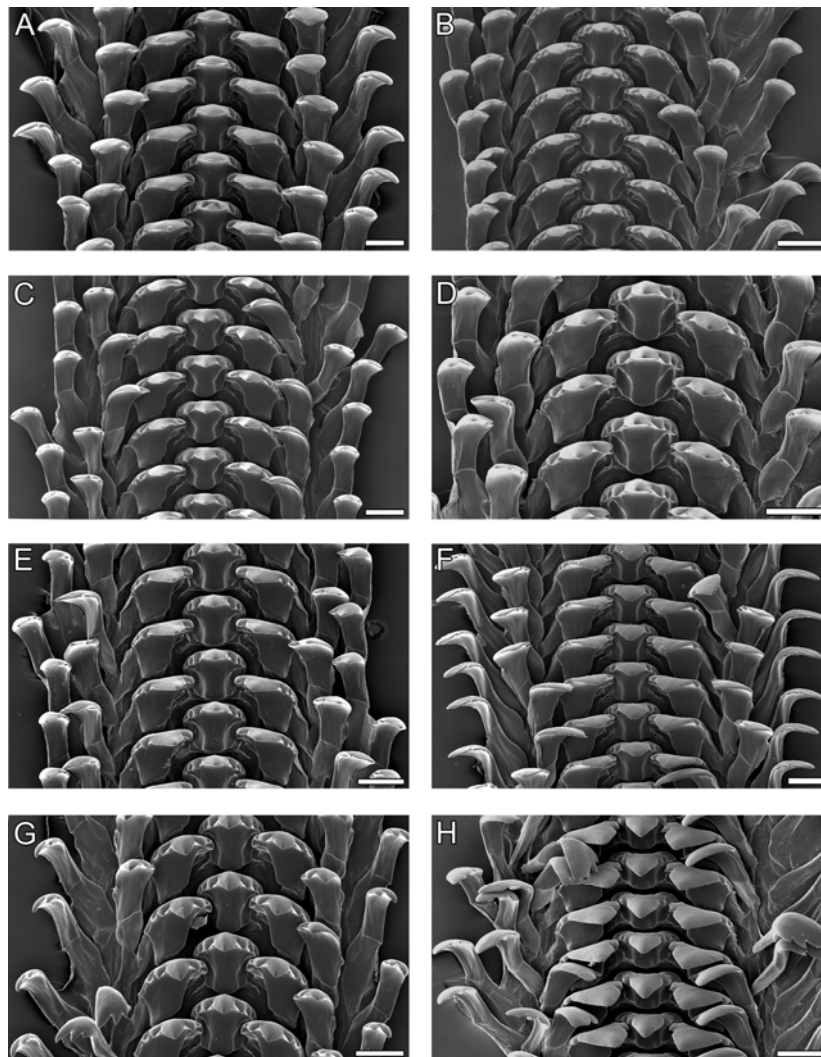


Fig. 1 A-H. Radular morphology of Pachychilidae from Mesoamerica. All the radular segments viewed from above.

A. *Pachychilus vallesensis* from Semococh River, Guatemala (ZMB 113147); – B. *Pachychilus* sp. from Polochic River, Guatemala (ZMB 113145); – C. *Pachychilus* sp. from Livingston, Guatemala (ZMB 113149); – D. *Pachychilus* sp. from Raxrujaj, Guatemala (ZMB 113144); – E. *Pachychilus radix* from Livingston, Guatemala (ZMB 113148); – F. *Pachychilus corvinus* from Campamic River, Guatemala (ZMB 113146); – G. *Pachychilus planensis* from Dolores River, Guatemala (ZMB 113140); – H. *Pachychilus atratus* from San Luis Potosi, Mexico (ZMB 113159). Bars = 100 μ m.

Both 16S and COI gene topologies show almost identical phylogenetic relationship topologies (Fig. 2, 3). A concatenated tree is dismissed since not for all specimens it was possible to sequence the two genes. Nodes support, indicated by Bayesian posterior probabilities, is high for most clades.

The 16S sequence data set comprises a total of 63 sequences (Fig. 2). The tree was rooted using two Australian species (Pachychilidae: *Pseudopotamis supralirata* and *Pseudopotamis semoni*) as outgroup. It is remarkable that (a) *Pachychilus vallesensis* (ZMB 113147) from the Semococh River in south-east Guatemala appears as the sister group of *Pachychilus conicus* from Cuba (ZMB 200290), and (b) that there is a clade composed of specimens from Mexico, Guatemala and Honduras. This clade is, in turn, composed of two well-defined clades: one comprising organisms from San Luis Potosi and Tamaulipas (Mexico, clade A in Fig. 2), and a second including all the Guatemalan specimens and representatives of southern Mexico and eastern Honduras (clades B-F in Fig. 2).

Concerning the central Mexican clade (San Luis Potosi and Tamaulipas), it is composed of three well-discriminated species: *Pachychilus atratus*, *P. pila* and *P. suturalis* (clade A in Fig. 2).

The clade comprising specimens from southern Mexico, Guatemala and Honduras is composed of five different clades: (i) one clade grouping *Pachychilus planensis* from Dolores and Copala rivers (Guatemala), *P. polygonatus* (Honduras), *P. corvinus* from Sesajal and Campamic rivers (Guatemala), *P. indiorum* from Lagartero River (Guatemala) and Chiapas (south Mexico), and *P. hellerii* from Chiapas (south Mexico) (clade B in Fig. 2, Appendix 3).

(ii) A well-supported group formed by *Pachychilus indifferens* from Sesajal River in Guatemala (clade C in Fig. 2, Appendix 3).

(iii) A clade of presumably one species (*P. radix*) composed of two specimens from Quebrada Grande and Las Escobas rivers, and of two specimens from Livingston River, which all drain into Amatique Bay, Guatemala (clade D in Fig. 2, Appendix 4).

(iv) A clade comprising specimens from Raxrujay, Trece Aguas, Seebitz, La Puente, Mopan, Ixbobo, San Pablo, Livingston and Candelaria rivers (central and north-eastern Guatemala, and south of Lake Izabal, respectively) (clade E in Fig. 2, Appendix 4).

(v) A well-defined and separate clade composed of specimens with sculptured shells from Lake Izabal basin and rivers draining into Amatique Bay, north and south of the lake. Its

sister group is a weakly supported clade comprising Livingston and Trincheras specimens (clade F in Fig. 2, Appendix 5).

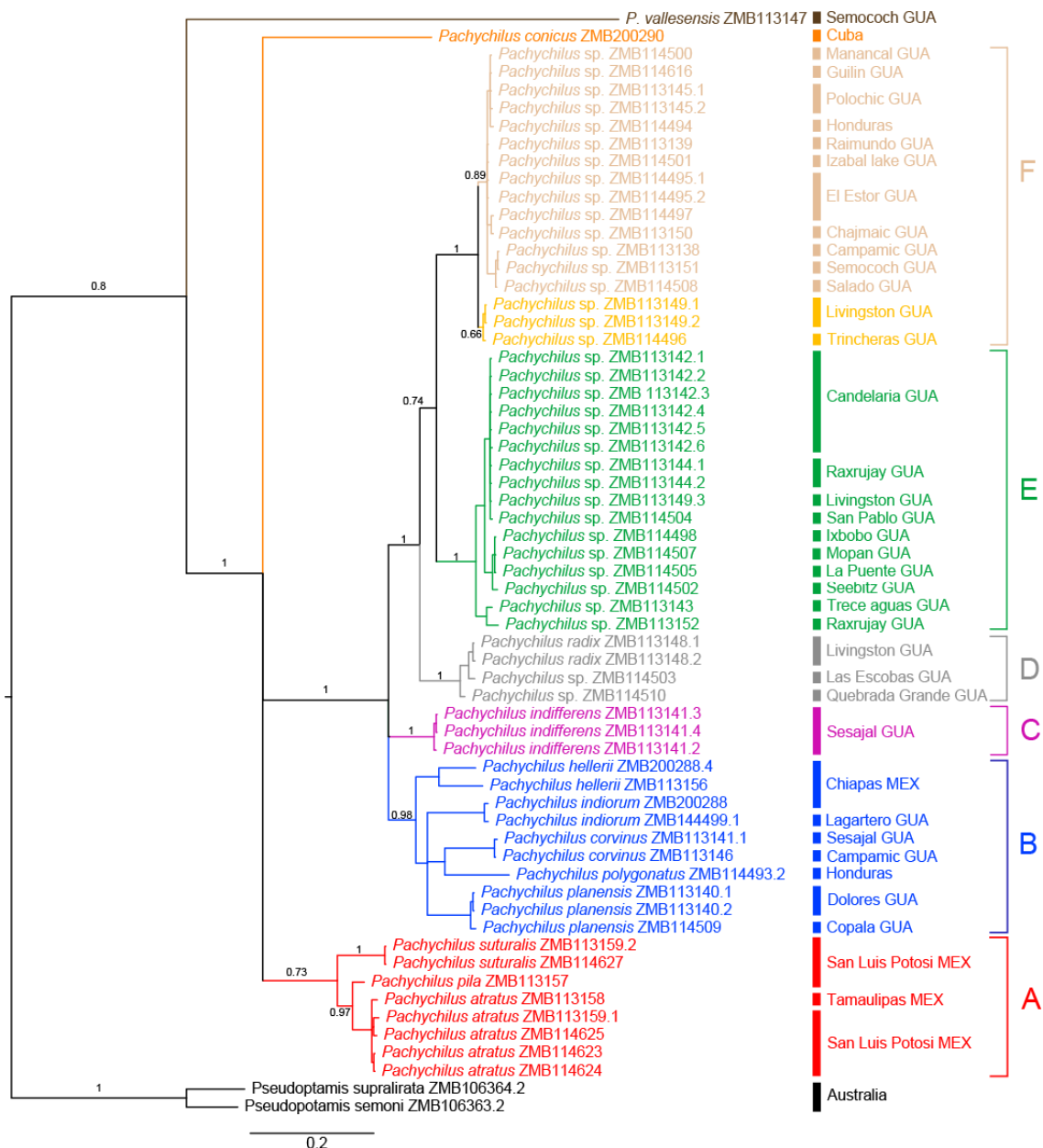


Fig. 2 Bayesian phylogram (mtDNA, 16S) of Pachychilidae specimens from Cuba and Mesoamerica (Bayesian posterior probability values indicated). Color bars are indicating localities.

B-E include specimens with a “smooth” shell, F specimens with a “sculptured” shell, see text for details. Abbreviations: GUA, Guatemala; MEX, Mexico.

The COI sequence data set comprises a total of 66 sequences (Fig. 3). The tree was rooted using two Australian species (Pachychilidae: *Pseudopotamis supralirata* and *Pseudopotamis semoni*), and two Indonesian species (Pachychilidae: *Tylomelania neritiformis* and *T. perfecta*) as outgroup. Here, the Cuban species (*P. conicus* and

Pachychilus sp2.) are the sister group of the rest of the Mesoamerican specimens. As the Cuban species are not monophyletic, *Pachychilus* sp.2 is probably a different species (Fig. 3).

In this analysis, *P. vallesensis* is consistently separated and different from the rest of the Mesoamerican representatives. The COI tree suggests that this could be the older lineage of the Mesoamerican group (Fig. 3).

Regarding the Mexican clade, two more specimens than in the 16S analysis were included in this analysis. Nevertheless, the clade is still consistent with the 16S topology, suggesting that it is composed of three different species (clade A in Fig. 3).

In the COI-tree topology the species clustering is the same but the relationships among species and/or groups of species are different. However, for comparative reasons the names of the 16S clades (capital letters) are kept here disregarding the order.

(i) This clade consistently shows *Pachychilus planensis* from Dolores and Copala rivers (Guatemala), and *P. corvinus* from Sesajal and Campamic rivers (Guatemala) as monophyletic groups, but the sequences of *Pachychilus hellerii* are lacking. The COI topology disagrees with the 16S topology in *P. polygonatus* from Honduras, which is grouping with one representative of *P. indiorum* from Chiapas, while the other two specimens of *P. indiorum* from Lagartero River (Guatemala) and Chiapas are grouping together. This topology shows *P. indiorum* as a polyphyletic group and suggests that the specimen of *P. polygonatus* is either a different species, or that the specimen previously identified as *P. indiorum* is really *P. polygonatus* (clade B in Fig. 3).

(ii) As in the 16S topology, *P. indifferens* from Sesajal River is a well-defined clade, appearing here as the sister group of the rest of the specimens from southern Mexico, Guatemala and Honduras, meanwhile in the 16S it is not (clade C in Fig. 3).

(iii) This clade is consistently conformed of two specimens from Quebrada Grande and Las Escobas rivers, and two specimens from Livingston. Although the specimens identified as *P. radix* are grouping together as in the 16S topology, the other two specimens are not resolved in this tree, prohibiting to draw a conclusion about the identity or the number of species within the clade (clade D in Fig. 3).

(iv) The results of the COI analysis shows complete consistency with those of the 16S, and strongly suggest that this clade, comprising specimens from Raxrujay, Trece Aguas, Seebitz, La Puente, Mopan, Ixbobo, San Pablo, Livingston and Candelaria rivers, is composed of three different species (clade E in Fig. 3).

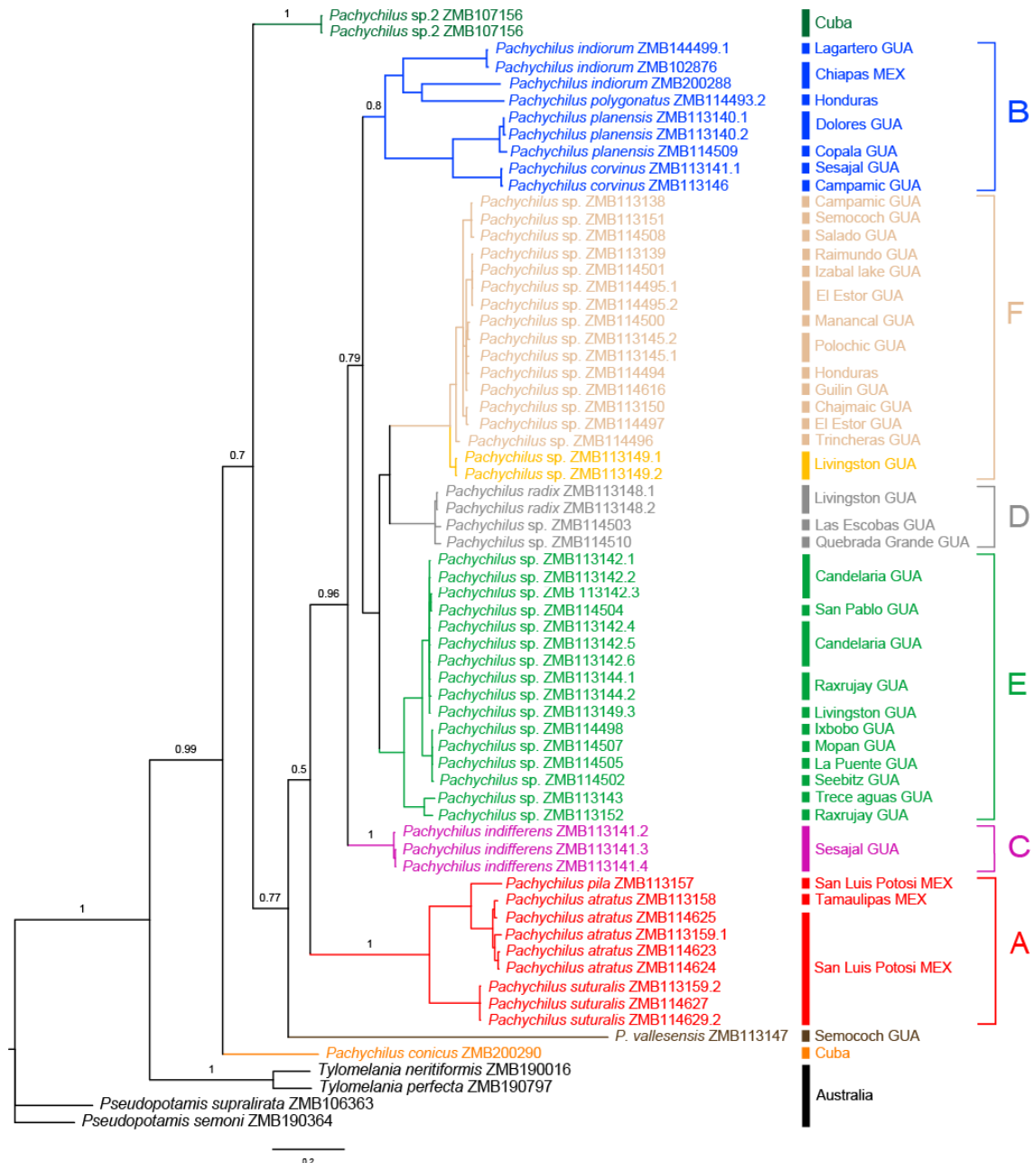


Fig. 3 Bayesian phylogram (mtDNA, COI) of Pachychilidae specimens from Cuba and Mesoamerica (Bayesian posterior probability values indicated). Color bars are indicating localities.

B-E include specimens with a “smooth” shell, F specimens with a “sculptured” shell, see text for details. Abbreviations: GUA, Guatemala; MEX, Mexico.

(v) The specimens with sculptured shells from Guatemala are also here a monophyletic group. Nevertheless, the relationships of the specimens within this clade are poorly supported and even an approximate number of species can not be established (clade F in Fig. 3).

Discussion

The shell as diagnostic character

The gastropod shell is traditionally used in classifications and taxon descriptions because it is accessible even from dry material. Shell morphometry and sculpture are regarded as essential for species discrimination (Köhler, 2003). As regards to the Neotropical freshwater mollusca, Goodrich & v.d. Schalie (1937) established that the central, northern and southern areas of Peten and Alta Vera Paz (Guatemala) are areas that comprise three well-defined groups of mollusk assemblages which do not overlap. These two authors use as differentiating character the sculptural emphasis of the shells: while one group has shells without sculpture other than the growing lines, another exhibits axial plicae, and a third revolving striae. In this study shell characters are supported two main clades, a “smooth” clade in which shells have a poorly developed sculpture in form of ridges or faint growing lines, and a “sculptured” clade, comprising shells with striae, ribs, tubercles or even incipient spines. The “smooth” clade is divided into four different Guatemalan subclades. Only the representatives of the central Mexican clade exhibit shells with revolving striae, but are not grouping together with the Guatemalan specimens. For the Cuban and Mesoamerican Pachychilidae, the results here presented indicate that the shells exhibit a high degree of similarity between some of the specimens, and that there is no complete correspondence between molecular clustering and shell-defined species. Hence, in spite of the “sculptural” differences, the shells are not a good taxonomical character for the identification of the Mesoamerican Pachychilidae. Nevertheless, it can be hypothesized that the possession of a smooth shell is a convergent character which has evolved at least twice in the region, while a sculptured shell is a synapomorphy.

The radula as diagnostic character

The molluscan radula is generally considered a conservative character with little variation on the species level (Fretter & Graham, 1994). Nevertheless, the importance of radular characteristics at least in higher level classifications has been emphasized very early by Troschel (1856-1863). Among the Mesoamerican Pachychilidae, the results show that this is not an anatomical useful character and that, consequently, species can not be reliably separated by means of the radular morphology.

Molecular phylogenies

Both 16S and COI topologies reveal two different *Pachychilus* species from Cuba and *P. vallesensis* as sister groups of two well defined clades: one comprises organisms from

central Mexico, and another includes all the Guatemalan specimens and representatives of southern Mexico and eastern Honduras.

The Cuban specimens were collected in the central part of the island, from different localities belonging to the same river basin. Nevertheless, they are clearly different entities with *Pachychilus conicus* basal to *Pachychilus* sp.2. With regards to *P. vallesensis*, its constant position as sister group of the rest of the Mesoamerican Pachychilidae suggests that this species could represent the origin of the group in the region and should be addressed as key species. It is also possible that these species, as well as the species of the central Mexican clade, belong to genera other than *Pachychilus*.

It is supposed that some time between the Late Paleocene to Middle Eocene, terranes from western and central Cuba were detached from the Yucatan peninsula (Iturralde-Vinent & MacPhee, 1999). Additionally, geological evidence suggests that central Cuba remained subaerial since the beginning of the Oligocene (see Chapter 2.3.1). If this is true, according to the 16S topology of the molecular analyses, and in contrast to the Greater Antilles *Hemisinus* (see Chapter 4.2), the Cuban Pachychilidae are a product of vicariance. Hence, the ancestral Pachychilidae population from Guatemala became fragmented with its descendants surviving in central Cuba and Mesoamerica. But according to the COI topology, the Cuban species are the sister group of the Mesoamerican Pachychilidae including *P. vallesensis*, and are also older than the latter. In this case two hypotheses can be made. In one scenario the ancestral population, occupying the terranes that subsequently detached from Yucatan peninsula, survived in what is now central Cuba, with its descendants remaining on the continent. The other option is that, by means of vicariance, the Cuban species differentiated into two distinct lineages on the island and then one of these lineages recolonized the continent through dispersal, which is evidenced by mammals with poor dispersal abilities (Dávalos, 2007). Nevertheless, nothing can be assured until more anatomical evidence will be collected and a molecular clock can be calibrated.

The representatives of central Mexico are consistently separated from the specimens of southern Mexico, Guatemala and Honduras. This clade is composed of three different species exhibiting strong intraspecific shell variation. While in *Pachychilus suturalis* there are pronounced differences in aperture shape between adults and juveniles, *P. atratus* shells are varying from smooth to grooved shells independent of the age of the organism. Despite both *P. suturalis* and *P. atratus* having ornamented shells, the distribution and sculpture pattern is different, keeping them separated. The third species of the clade is *P. pila*, the smooth, globose and short spire shells of which are clearly different from the

other two species. The fact that this clade appears consistently separate in the two molecular analyses performed suggests that the three species could belong to a different genus or at least a subgenus of *Pachychilus*. Evidence coming from the geological history of the region they inhabit also suggests a long time of isolation. San Luis Potosi and Tamaulipas lies at the Mesa Central in Mexico, a geological feature limited to the south by the Transmexican Volcanic Belt (TVB), whose activity during the mid-Cenozoic contributed most to shaping the present land, which could represent at least 20 Ma of separation of the Mexican species from the Central American pachychilids.

Regarding to the clade comprising organisms from Chiapas (southern Mexico), Guatemala and Honduras, Goodrich & v.d. Schalie (1937) already pointed out that the species of the northern and southern areas of Alta Verapaz province (Guatemala) are closely related with, and some times indistinguishable from, those of the lower Usumasinta River system. In the case of the genus *Pachychilus*, these identities possibly point to ancient drainage connections that have now disappeared. I found the same relationship between specimens from Alta Vera Paz province (Sesajal, Campamic, Dolores and Copala rivers) and specimens from the lower Usumasinta River system (Chiapas), but this work includes also specimens from the upper Mezcalapa basin (Lagartero river, Guatemala) and Warunta basin (Honduras). This clade is characterized by medium sized, thick shells, without other sculpture than the growing lines, which clearly separates it from the rest of the specimens, indicating that they constitute a group of at least four different but closely related species. Along the two phylogenetic analyses *P. planensis* and *P. corvinus* are consistently monophyletic, while the identity of *P. polygonatus* and *P. indiorum* remains unresolved.

According to shell comparisons and the monophyly shown by the two molecular analyses, the three specimens from Sesajal River can be assigned to *Pachychilus indifferens*, which is a monophyletic species. Nevertheless, there is another specimen from Sesajal River grouping within the clade B, which clearly is a different species than *P. indifferens*. Sesajal River is part of the Usumasinta basin and drains into the Chixoy River, the course of which alternates between subterranean and subaerial passages. This geographical particularity could determine the presence of two different, not directly related species in the same locality.

The tree supports the evidence that the taxa from Livingston (Guatemala), which is located at the north-eastern Lake Izabal close to the coast, are presumably three different entities because they belong to distantly separated clades. One Livingston species (*P.*

radix) clusters with two specimens from rivers draining into the Amatique Bay (Guatemala). The other Livingston specimens are more closely related to specimens inhabiting Trincheras River in the southern basin of Lake Izabal, while the remaining specimens belong to clade B.

Although there is no correspondence between traditional species identification and the results of the molecular analyses, it is possible that the three specimens of the clade D comprising Livingston's *P. radix* and specimens from Las Escobas and Quebrada Grande are the same species, since they are forming a monophyletic group and are closely related.

It seems that in Raxrujay the same pattern prevails as in the Livingston specimens. In Raxrujay there are two closely related but different species inhabiting the same locality because its representatives, in spite of being in the same clade, are not grouping together within it. Since clade E is divided into three clades, it could be supposed that it is probably composed of three different species: one species constituted by specimens from Trece Aguas and Raxrujay; a second species comprising organisms from Ixbobo, Mopan, La Puente and Seebitz; and a third species composed of Candelaria, San Pablo, Raxrujay and Livingston representatives. However, further anatomical and shell morphometrical analyses of these specimens are required in order to assign a name to them.

In Campamic, specimens belonging to the “sculptured” clade and to one of the “smooth” clades are occupying the same locality. Here it is clear that they are two different, not closely related entities. Concerning the “sculptured” clade, there is no good support for the internal relationships, and there is also no correspondence between the traditional species identification and the results of the phylogenetic analyses. Consequently, the exact number of species in this clade can not be determined.

Conclusions

To understand the identification problem of the Mesoamerican Pachychilidae, I used traditionally anatomical features as well as molecular analyses of two mitochondrial genes. The results suggest a high degree of homoplasy in shell and radula features. Consequently, these anatomical characters, which were traditionally considered to be informative to distinguish species, are not reliable and useful for this Neotropical group. However, given that there are several cases of correspondence between traditional species identification and molecular data, the latter could be useful to identify species where shell characters are useless. These findings also indicate the need for detailed

studies of the internal anatomy in order to search for sufficiently robust anatomical features that allow us to identify the species. As shown in Chapter 4.2, anatomical data of the midgut and the pallial gonoduct could help to separate species of this group. It is also possible that the Mexican species from San Luis Potosi and Tamaulipas, the two species from Cuba and *Pachychilus vallesensis*, may belong to genera or subgenera different than *Pachychilus*, given the high molecular distance that characterize them. Geological, biogeographical and molecular data suggest a vicariant origin of the Cuban Pachychilidae, and a dispersal origin of the continental members of the family from a central Guatemalan ancestor.

6. Synopsis

Traditionally, invertebrates are underrepresented in biological studies such as, for instance, on phylogeography. Freshwater mollusks are not an exception and the lack of comprehensive studies for most of its groups have hampered many insights into their systematics, evolution and biogeography. Despite the Caribbean region being well known due to its natural richness and suitability for biogeographical studies, its molluscan fauna has received but little attention. Our knowledge is mainly based on 19th century's works when many valuable papers on land- and freshwater-snails from the region were published. However, these studies usually omitted to record the special habitats of the species, and suggested a profuse number of species names and descriptions based solely on shell characters. Since then, the number of published works has hardly increased and the "conchological" approximation was maintained.

The focus of this work was to study the systematics, phylogeny and biogeography of freshwater gastropods belonging to the families Thiaridae and Pachychilidae from Mesoamerica and the Greater Antilles. The goal was to unravel the identity and characteristics of the species in order to establish relationship patterns among them and within the Cerithioidea. Although both families share part of their histories, and their members having been found to inhabit the same areas, for practical reasons I will summarize the two groups separately.

6.1 Conclusions on Thiaridae

During the last decades, research efforts in the Neotropics have focused on invasive thiarid species due to their suitability as biological control of native gastropods, which are intermediate host of parasites, while the native species *per se* have been totally neglected. After over a century of "conchological" works, this study is the first to describe in detail the internal anatomy of Greater Antilles representatives of the Thiaridae, establishing diagnostic features other than the shell for the genus *Hemisinus*. Also, it is the first to conduct genetic and phylogenetic analyses in order to investigate intra- and interspecific relationships.

Taxonomy

Most of the Thiaridae species of the Greater Antilles belong to *Hemisinus*, a genus which is at present restricted to the archipelago and the Darien region in northern South America. While it was previously thought that the genus in the Greater Antilles comprises two different species in Jamaica and five species in Cuba, in this work I provide

morphological, anatomical and genetic evidence for the existence of only a single species in Jamaica (*H. lineolatus*, which is the type species of the genus), and two distinct species in Cuba (*H. cubanianus* and *Cubaedomus brevis*), plus a still doubtful species on the latter island (*H. martorelli*).

Anatomy

Members of the genus *Hemisinus* are characterized by sexual dimorphism; a short osphradium; midgut with shallow caecum, large and textured accessory pad, two caecal folds, and two apertures of the digestive gland; male pallial gonoduct laterally open almost all along its length, females with pallial oviduct half open, exhibiting conspicuous glands and undivided dorsal brood pouches containing up to five juveniles.

Intra- and interspecific differences in size or complexity of the anatomical structures were observed in both *H. lineolatus* and *H. cubanianus*, which seem to be determined either by local environmental conditions or by the particular history of each lineage. Nevertheless, morphological variability displayed by specimens of *H. lineolatus* could reflect an ongoing ecological speciation, which is not the case in *H. cubanianus*.

Another important finding is that *Hemisinus* shares anatomical and morphological features with African-Asian families other than the Thiaridae, which might indicate a common ancestry with an Oriental freshwater cerithioidean lineage of Gondwanan origin.

Phylogeny and biogeography

At the intraspecific level, the monophyly of the different species in Jamaica and Cuba is well supported, despite populations of the Cuban *H. cubanianus* exhibiting different haplotypes and also a high variability in the shell's color patterns.

For the Greater Antilles, the molecular phylogeny reveals a well-supported monophyletic group composed of *H. lineolatus*, *H. cubanianus* and *Cubaedomus brevis*, with *H. lineolatus* from Jamaica diverging first. This “most derived” condition of the Cuban representatives is also confirmed by their anatomy. Moreover, according to the phylogenetic analyses, it is highly probable that the Cuban species usually assigned to the genus *Cubaedomus* is a member of *Hemisinus*.

At a larger scale, the Jamaican *H. lineolatus* is more closely related to *Hemisinus* sp. from the Darien region in northern South America than to its Cuban relatives. The results of the molecular analysis together with the geological evidence suggest that Jamaica was colonized from continental source populations some time during the Oligocene, with the fauna reaching Cuba during the Pliocene. Hence, this argument could also support the Inter-American origin of the Caribbean Plate.

Ecology and conservation

According to historical records and recent field collections, *Hemisinus* spp. preferably inhabit running water environments that are undisturbed or only little affected by human activity. These preferences, as well as their competitive inferiority to introduced thiarids (i.e. *Tarebia granifera*), are responsible for the displacement or elimination of the species from their original areas of distribution. As there are no ecological studies on the different *Hemisinus* species, their ecological niches and specific requirements are completely unknown.

6.2 Conclusions on Pachychilidae

Phylogenetics as taxonomical tool

For Mesoamerican Pachychilidae, five genera, four subgenera and 116 species names have been described based on shell characters. All of these are valid names under the rules of the Code, but their real status as true species have yet to be proven. So far, phylogenetic analyses of mitochondrial genes (16S and COI) of Pachychilidae show two different *Pachychilus* species from Cuba and *P. vallesensis* as sister groups of two well-defined and -supported clades: a Mexican clade composed of three species with strong intraspecific variation (*P. atratus*, *P. suturalis* and *P. pila*), which probably do not belong to the genus *Pachychilus*, and a clade comprising organisms from south Mexico, Guatemala and Honduras. Regarding this latter clade, it is six consistently subdivided in six clades (i) one comprising at least four different but closely related species, with *Pachychilus corvinus*, *P. planensis* and *P. indiorum* consistently clustering in the two phylogenetic analyses; (ii) a well-supported group formed by *Pachychilus indifferens*; (iii) a clade of presumably two species from basins draining to Amatique Bay in Guatemala; (iv) a clade composed of specimens from the northern and southern Lake Izabal; (v) a clade of specimens from the south of Lake Izabal, central Guatemala and northeastern Guatemala, which are presumably three different species; and (vi) another clade of sculptured shells from Lake Izabal basin.

Anatomy

The Neotropical representatives of the Pachychilidae are oviparous and non-parthenogenetic species, with sexual dimorphism evidenced by the shape and the length of the genital groove. Concerning the shells, while Pachychilidae in the Greater Antilles have small and smooth shells, the representatives of the family on the nearby continent (e.g. Mesoamerica) have large and strong shells, which vary from smooth to ornamented with tubercles or ribs. In Guatemala, there are two shell groups, one with smooth shells and another with sculptured shells. Although shell sculpture may be used to determine

groups, this character is not always useful to separate species. For instance, for this Mesoamerican group it can be hypothesized that the possession of a smooth shell is a convergent character, which has evolved at least twice in the region, while the sculptured shell is a synapomorphy. With regards to the radula, the pachychilids of this region have a radula with square and strong teeth with few cusps, with scarce differences among the whole group.

These results thus suggest a high degree of homoplasy in shell and radula character evolution. Consequently, these anatomical characters, which were traditionally considered to be informative to distinguish species, are far from being ideal for this Neotropical group. These findings clearly indicate the need for detailed studies of the internal anatomy in order to search for sufficiently robust anatomical features that allow us to identify the species.

Ecology

As opposed to the Caribbean Thiariidae, members of the Pachychilidae are found both in lotic and lentic ecosystems. Hardly anything is known about their ecology and there is also no information regarding their conservation status.

Biogeography

My results suggest that in Mesoamerica it is the geography that mainly determines the distribution of Pachychilidae species. Geological, biogeographical and molecular data suggest a vicariant origin of the Cuban Pachychilidae, which could have occurred at some time between the Late Paleocene to Middle Eocene, and a dispersal origin of the continental members of the family from a central Guatemalan ancestor, which could have taken place before the Oligocene.

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Appendix 1 – 5

Biogeography

The pros and cons of dispersal vs. vicariance

From Darwin's time until the 1960s, oceanic dispersal was the answer to explain why particular terrestrial and freshwater taxa have geographical distributions that are divided by oceans. During the '60s and '70s, validation of the plate tectonic theory and the spread of cladistic thinking led to a vicariance biogeography, also called cladistic biogeography (Glaubrecht, 2000; de Queiroz, 2005). In this concept it is assumed that the correspondence between taxonomic relationships and area relationships is biogeographically informative. Area cladograms are constructed by replacing the names of terminal taxa in a cladogram with the names of the areas in which they occur. Comparisons between area cladograms derived from different plant and animal taxa occurring in a certain region allow to elucidate general patterns (Morrone & Crisci, 1995; Glaubrecht, 2000). Vicariance now is losing ground because the extrapolation of the rigorous cladistic concept to the geography dismisses any condition of parallel evolution of traits subsequent to divergence. Moreover, vicariance denied the existence of centers of origin, ignoring that allopatric speciation may also result from successful migrations of organisms across geographic barriers. In addition, vicariance hypotheses require that speciation and the corresponding fragmentation of areas must occur at the same time, assuming that all of the clades under consideration diversified simultaneously. Thus, incomplete information on the absolute timing of speciation events avoid distinguishing groups that diversified during the same time period from those that diversified during different time periods and require different causal explanations. As a consequence, the match between area cladograms and the history of fragmentation of areas are also in doubt (Briggs, 1981; Smith, 1989; Donoghue & Moore, 2003; de Queiroz, 2005; Upchurch, 2007).

It has been stated that evolution is primarily a function of dispersal because of the ability of populations to geographically expand their range (Smith, 1989). However, dispersal explanations as well as phylogenetic biogeography are considered as irrefutable hypotheses that do not provide a general theory to explain distributional patterns (Morrone & Crisci, 1995). Phylogenetic biogeography is considered the study of the history of monophyletic groups in time and space, taking into account cladogenesis, anagenesis (see definitions in Chapter 1), allopatry (vicariance), sympatry (dispersal) and paleogeographical events (de Queiroz, 2005). But yet, new support for oceanic dispersal is arising from information on the timing of speciation fuelled by the development of

molecular methods and by the increasing evidence coming from different groups of organisms. The current tendency is to build a more synthetic theory where both processes, dispersal and vicariance, contribute to the distribution patterns of the species (Smith, 1989; Glaubrecht, 2000; Page *et al.*, 2005).

Historical summary: colonization of the West Indies

Based on comparisons of biogeographical and tectonic patterns, the colonization events of the West Indies can be summarized as follows: by the Late Cretaceous one vicariance event filled all West Indian islands with anuran amphibians. This event, followed by eight independent dispersals from the South and Central America mainlands, represents the origin of the current amphibian fauna (Hedges, 1996). During the Cenozoic, evidence from fossil mammals suggests many overwater colonization events. Pollen grains from the Paleocene and Eocene of Jamaica resemble those from Guatemala, Colombia and Venezuela, indicating a probable proximity of both terranes (Buskirk, 1985). During the Eocene or earlier, dispersal of Scarabaeine beetles, danaid butterflies, Helicinidae snails and alpha anoles lizards from North America and Mexico colonized Cuba, Hispaniola and Puerto Rico. At the same time, a larger colonization event of Central American groups affected Jamaica, a phenomenon which is now elucidated by vertebrate fossil assemblages, flowering plants, monotypic Scarabaeinae, Xenodontinae snakes, *Sphaerodactylus* geckos, as well as anguid and beta anolis lizards (Buskirk, 1985; Iturralde-Vinent & MacPhee, 1999). In the Oligocene, Camaeniidae snails with an early Cenozoic North American ancestor radiated on Cuba and Puerto Rico (Buskirk, 1985; Hedges, 1996; Iturralde-Vinent & MacPhee, 1999). In the Late Oligocene or Early Miocene, evidence from hystricognath rodents suggests that their origin was a single trans-oceanic dispersal event from South America, colonizing first Puerto Rico and then moving to Hispaniola and Cuba. In the Miocene, a subsequent introduction of South American groups to the Lesser Antilles, Hispaniola and Puerto Rico (with some reaching Cuba but not Jamaica), is represented by the presence of *Anolis cristatellus-bimaculatus* groups. New evidence from Caribbean bats indicates that they mostly reached the islands by over-water dispersal during this period (Buskirk, 1985). Also in the Miocene, the subdivision of block-terranes of the Greater Antilles may have been significant biogeographically if it caused island-island vicariance. During the Miocene-Pliocene, there was a radiation of Camaeniidae land snails from Cuba and Puerto Rico to Jamaica and the Lesser Antilles. In the Quaternary, alder trees appeared in sediments of Jamaica and the northern South American Andes indicating long distance dispersal (Buskirk, 1985; Hedges, 1996, 2006; Iturralde-Vinent & MacPhee, 1999; Heaney, 2007).

The Greater Antilles

Vertebrates. In general, the vertebrate fauna of the Greater Antilles exhibits high levels of endemism and has a taxonomic composition characteristic of more isolated oceanic islands (Buskirk, 1985; Hedges, 1996; Rosenberg & Muratov, 2005). In fishes it is possible that the native Jamaican species which are a monophyletic group, resulted from a single colonization event from Cuba in the Miocene (Hedges, 1996). Concerning the herpetofauna, phylogenetic analyses of amphibians and *Anolis* lizards in the Greater Antilles revealed that most of the species are more closely related to other species on the same island than to species on other islands, implicating local species production as the key process. These analyses also showed that throughout the Cenozoic, colonization and extinction rates of both taxa were extremely low and approximately homogeneous (Ricklefs & Bermingham, 2008). In mammals, fossil evidence and the divergence pattern of mitochondrial markers of short-faced bats (which have rather poor dispersal abilities), provide evidence for a two-way invasion and recolonization. According to Dávalos (2007), a common short-faced bat ancestor from Mexico and/or Central America reached Cuba and/or Jamaica during a period of low sea levels (15-23 Ma). This colonizer differentiated in the Caribbean while, following diversification into two distinct lineages on the islands, a single lineage recolonize the continent and gave rise to the genera that today range from Mexico to central South America.

Land mollusks. The Greater Antilles present an astonishingly rich and diversified land snail fauna, which is well studied since the middle of the 19th century, allowing to elucidate some biogeographical patterns. It is noteworthy that the present distribution of land snails in the Greater Antilles and adjacent land areas shows close parallels in certain respects to the distribution of plants and reptiles (Russell-Hunter, 1955). In earlier times, Bland (1871) stated that the fauna of the islands on the northern side of the Caribbean Sea, from Cuba to the Virgin and Anguilla banks, was derived from Mexico and Central America. On the other hand, the fauna of the islands of the eastern side, from Antigua and St. Christopher banks to Trinidad, was derived from tropical South America. The marked differences, both generic and specific, between the present land mollusk faunas of the north-west islands and those of the south, may be taken as evidence for their early and continued separation (Bland, 1871). From nearly 600 peculiar species of operculated land snails in the Archipelago, only two Cuban species are shared with the continent, while Jamaica and Hispaniola has no species in common with it. Although the proportion of operculated land snails species is roughly similar in Jamaica, Cuba and Hispaniola, the snail faunas of Cuba and Hispaniola show greater affinities within restricted genera, and both are more

associated with Puerto Rico but none of them with Jamaica (Bland, 1866a, b, c; Russell-Hunter, 1955). In addition, Jamaican land snails do not only show a high sympatric diversity, but also a high allopatric diversity with many species having limited ranges (Rosenberg & Muratov, 2005).

The Lesser Antilles

Vertebrates. In amphibians, *Leptodactylus* frogs which now occur on Dominica and Montserrat, exhibit an unexpected distribution because the two islands have never been joined and most of the species are endemic to one island. But historical records have suggested that this species had, through dispersal from South America to the Lesser Antilles (~27-28 Ma), a wider distribution in the past, occurring also on St. Kitts, Antigua, Guadeloupe, Martinique and St. Lucia (Hedges & Heinicke, 2007). Birds' molecular data suggest that their colonization was entirely by episodic events of overwater dispersal, which is easy since the distance between the islands and the continent is shorter compared to that of the Greater Antilles. Besides, this group indicates that conditions affecting colonization and extinction have not been homogeneous, suggesting that the history of the Lesser Antilles is far more complex than originally thought (Miller & Miller, 2001; Ricklefs & Bermingham, 2008).

Invertebrates. Biogeographic studies of the invertebrate fauna in the Lesser Antilles are rare. Land molluscs, ticks, Rhysodine beetles and butterflies evidence that genera and species are chiefly allied to those of continental northern South America (Bland, 1871; Bell, 2001; de la Cruz, 2001; Miller & Miller, 2001).

On the most general level, Antillean snail faunas share several sub-families and genera with Central America, rather few with tropical South America, and very few with continental America north of Tehuantepec. Similar degrees of affinities are found in the Caribbean reptile fauna, which also exhibits high levels of allopatric species richness, as is characteristic of monophyletic groups within oceanic archipelagos (Heaney, 2007).

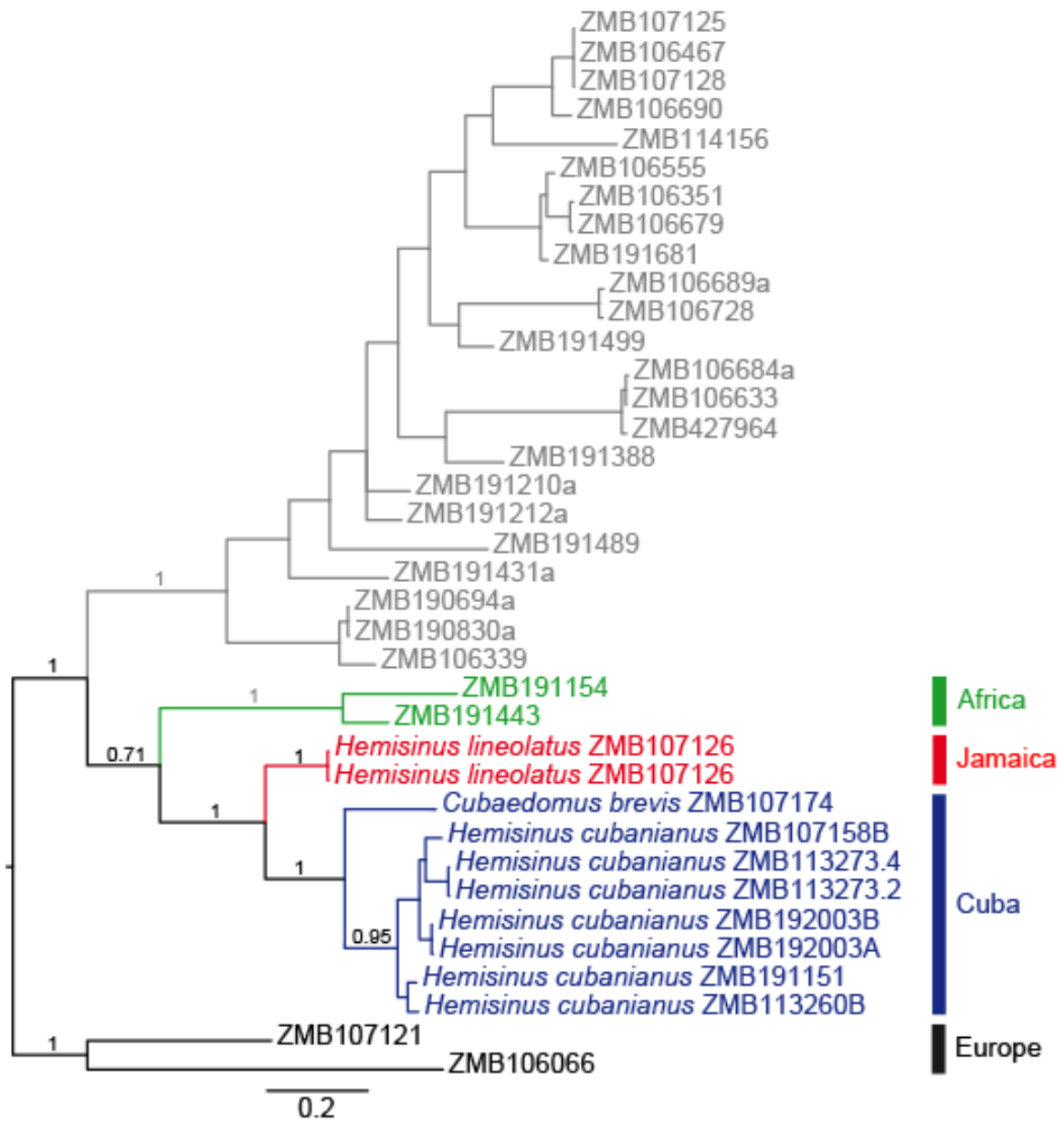
Mesoamerica

Freshwater biota. It is assumed that the freshwater biota of the region have been changed by intense vicariant events associated with the geological history, like the uplift of the cordilleras, and non-vicariant events such as post-dispersal speciation and also post-speciation dispersal (Dominguez-Dominguez et al., 2006; Huidobro et al., 2006). Freshwater fishes of the genus *Roeboides* in Lower Central America (LCA) contain species representing a colonization episode from South America during the Late Cretaceous to early Cenozoic. Gene flow and/or geography have provided little

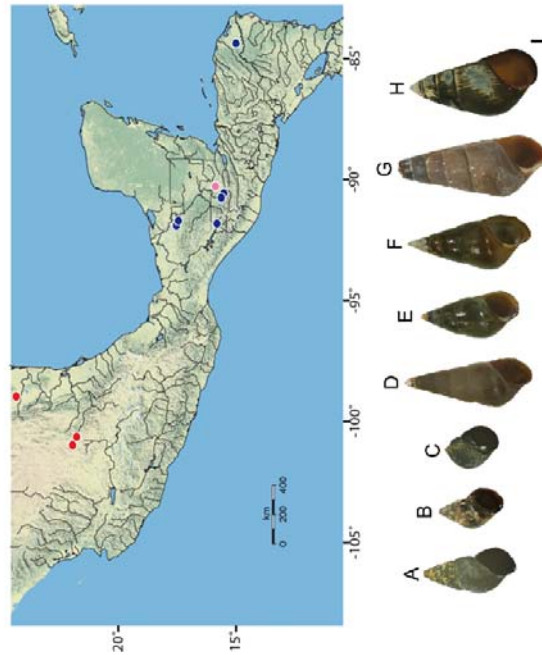
opportunity for its diversification, but phylogeographic patterns suggest that many LCA freshwater drainages harbor unique evolutionary lineages that originated at least 1-3 Ma ago. On average, Atlantic slope drainages appear to be historically more isolated and harbor greater mtDNA endemism than Pacific slope drainages (Bermingham & Martin, 1998).

African-Mesoamerican distributions are known for the region among plants, insects, and freshwater fishes and mollusks (Cyrenidae, *Eupera*, *Neritina*, Amnicolidae, Thiaridae). Nevertheless, these groups constitute a distributional enigma. The absence of Neotropical Thiaridae and pea clams from the fossil record of European Mesozoic and Cenozoic faunas, and the young age estimate for lineages of the endemic lacantunid freshwater fishes of south Mexico reject a Gondwanan vicariance (Pilsbry & Bequaert, 1927; Lundberg *et al.*, 2007). Several hypothesis like the Beringian land bridge (suspected for plants, dinosaurs, plethodontid salamanders, mammals, and some fishes including ictaluroid catfishes), or the Thulean or De Geer land bridges between eastern North America and Western Europe (suspected for tropical Malpighiaceae, hummingbirds and fossil freshwater fishes), proposed an explanation of the distribution of these groups. But lack of direct fossil evidence, renders these hypotheses speculative (Pilsbry & Bequaert, 1927; Lundberg *et al.*, 2007).

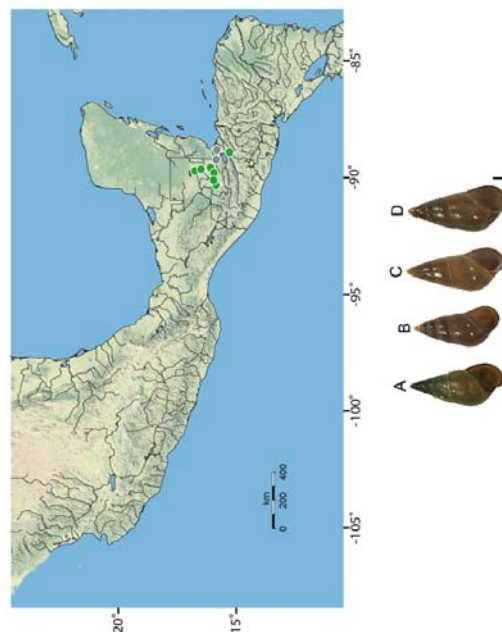
Land biota. Land mollusks from islands close to the Honduras coast reveal that almost all their endemic species are more closely related to mainland forms than to those of the West Indies, evidencing a definitely Central American relationship (Richards, 1938).



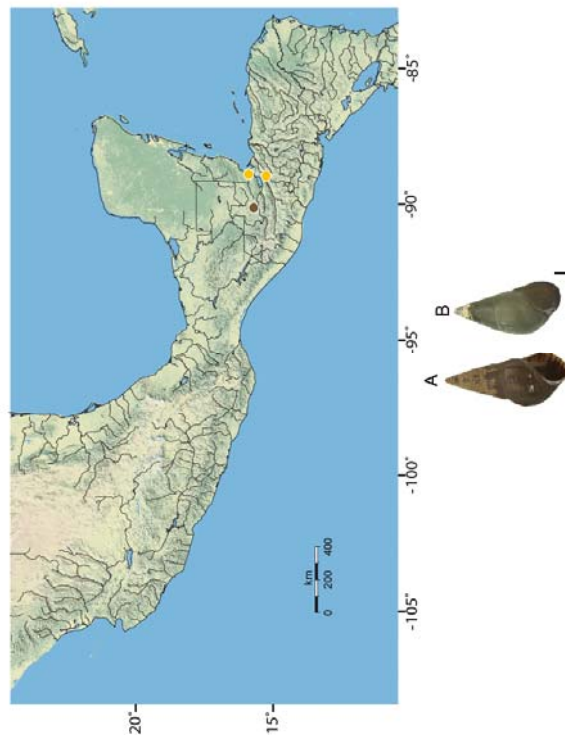
Appendix 2. Bayesian phylogram (mtDNA, COI) of Thiaridae specimens from Cuba, Jamaica, Africa and Asia (Bayesian posterior probability values indicated). Color bars are indicating localities. The tree was rooted using two Melanopsidae species from Europe: *Holandriana holandri* (ZMB 107121) and *Melanopsis praemorsa* (ZMB 106066).



Appendix 3. Distribution in Mesoamerica of the members of the clades A-C (16S).– A. *Pachychilus suturalis* (ZMB 113159); – B. *P. atratus* (ZMB 114625); – C. *P. pila* (ZMB 113157); – D. *P. polygonatus* (ZMB 114493); – E. *P. planensis* (ZMB 113140); – F. *P. corvinus* (ZMB 113146); – G. *P. indiorum* (ZMB 200288); – H. *P. indifferens*. Scale bar = 0.5 mm. ● = clade A; ● = clade B; ● = clade C.



Appendix 4. Distribution in Mesoamerica of the members of the clades D-E (16S). – A. *Pachychilus cf. radix* (ZMB 114503); – B. *Pachychilus* sp. (ZMB 113143); – C. *Pachychilus* sp. (ZMB 114502); – D. *Pachychilus* sp. (ZMB 114504). Scale bar = 0.5 mm. ● = clade D; ● = clade E.



Appendix 5. Distribution in Mesoamerica of the members of the clade F and *Pachychilus vallesensis* (16S). – A. *Pachychilus* sp. (ZMB 114495); – B. *Pachychilus vallesensis* (ZMB 113147). Scale bar = 0.5 mm. ● = clade F; ● = *P. vallesensis*.

Eigenständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Maria Isabel Gomez

Berlin, 03.06.2009