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Introduction to Physidae (Gastropoda: Hygrophila); biogeography, classification, morphology

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Abstract: Physidae, a world-wide family of freshwater snails with about 80 species, are reclassified by progressive characters of the penial complex (the terminal male reproductive system): form and composition of penial sheath and preputium, proportions and structure of penis, presence or absence of penial stylet, site of pore of penial canal, and number and insertions of penial retractor muscles. Observation of these characters, many not recognized previously, has been possible only by the technique used in anesthetizing, fixing, and preserving. These progressive characters are the principal basis of 23 genera, four grades and four clades within the family. The two established subfamilies are divided into seven new tribes including 11 new genera, with diagnoses and lists of species referred to each. Proposed as new are: in Aplexinae, Austrinautini, with *Austrinauta g.n.* and *Caribnauta harryi g.n., nom.nov.*; Aplexini; Amecanautini with *Amecanauta jaliscoensis g.n., sp.n., Mexinauta g.n.*, and *Mayabina g.n.*, with *M. petenensis, polita, sanctijohannis, tempisquensis spp.nn., Tropinauta sinusdulcensis g.n., sp.n.*; and Stenophysini, with *Stenophysa spathidophallus sp.n.*; in Physinae, Haitiini, with *Haitia moreleti sp.n.*; Physini, with *Laurentiphysa chippevarum g.n., sp.n., Physa mirollii nom.nov.*; and Physellini, with *Chiapaphysa g.n.*, and *C. grijalvae, C. pacifica spp.nn., Utahphysa g.n., Archiphysa g.n.*, with *A. ashmuni, A. sonomae spp.nn., Physella hemphilli sp.n.*, and *Ultraphysella sinaloae g.n., sp.n.*

The simplest reproductive system is found in *Austrinauta* of the Aplexinae; its penial complex approaches that in the related family Lymnaeidae. Within Physinae a close approximation is found in *Haitia*. By these two genera the two subfamilies are drawn close together. Four grades of progressive complexity are recognized: (I) penial sheath entirely muscular; (II) penial sheath with both glandular and muscular tissue; (III) penis with penial stylet or other specialization of the tip of the penis; and (IV) pore of penial canal lateral rather than terminal as in the lower grades. In both subfamilies there are clades with glandular tissue in the penial sheath, a penial sheath subdivided into two parts, and tip of penis specialized in various ways. These clades are formalized as new tribes.

Of 23 genera of Physidae, 17 occur in Pacific drainages of North and Central America, eight of these restricted to the region. Concentration of primitive genera along the Pacific coast from Mexico to Costa Rica conforms to previous observations that primitive pulmonate families are concentrated within, or along the continental margins of, the Pacific Ocean. An ancestral origin of Physidae along an ancient eastern Pacific coast is probable. From this region the several lineages have spread north, south and east in the Americas, and through Siberia to Europe.

Although Physinae have fewer genera than Aplexinae (11 v. 12), they have more species (47 v. 34). Greater land area in the temperate zone has provided more opportunity for speciation of Physinae, in contrast to the generally tropical and warm-temperate range of Aplexinae. Furthermore, 10 species of Physinae are localized in individual lakes, whereas Aplexinae are not lake-dwellers.

Both well-developed egg strings and capsular strings are found in the spawn of *Sibirenauta elongatus*. These structures have been known in Lymnaeidae, but not hitherto in Physidae; they are a link with some marine groups, such as Siphonariidae. Spiral color bands and white streaks in the shell of *Mexinauta* recall those in Lancidae (Lymnaeacea), whereas the radula of Physidae is like that of Chilinidae. Physidae thus show affinities to various basal stocks of aquatic pulmonates; no clear-cut sister-group can be recognized.

Most species have a restricted range; out of 55 with sufficiently detailed information for analysis, 25 are limited to a single 1ºx1º quadrangle. Only a few species are widespread, on one or even two continents. Accordingly, more species of Physidae are threatened by habitat destruction than in other families of Hygrophila with generally wider distributions.

Other features are a key to genera; catalog of more than 430 names applied to living Physidae, with original reference, type locality, and location of type specimens; summary of museums with types; and glossary.

Key words: Physidae, classification, biogeography, new species, new genera, new tribes.

Physidae are common freshwater snails in the North Temperate to Arctic Zones and throughout the Americas, in readily accessible habitats such as ditches, ponds, lakes, small streams, and rivers. They can be collected easily and maintained in an aquarium. The family has been recognized as such for more than a century. Yet there has been no classification in which relationships between genera are clarified, no agreement on what characters are primitive or advanced, and no consistent ranking. Scarcity of careful morphological studies is a principal cause.

Lack of shell characters means that it is not only previous classifications, entirely or largely based on shells, that are deficient. Identification of species, except in rare cases, has been practically impossible. In the thousands of local lists, keys, handbooks, and other citations published during the last 200 years, species identifications are simply untrustworthy. This in a group often encountered by not only collectors, but by all those with a general interest in freshwater habitats, or those engaged in some applied study. Generalizations as to diversity in a region, species distributions, and ecology are correspondingly suspect. The species composition of a country or region has been understood only where the fauna is sparse (as in the British Isles and northwestern Europe), or where there has been morphological verification of the species (as in Connecticut and New York: Jokinen, 1983, 1992).

Advances of this work over previous studies are due principally to the technique used in anesthetizing and fixing. This permitted examination of material in far better condition for detailed study than was available to most earlier writers. Then, too, I have had the advantage of collecting widely (extensively in the western United States, also Minnesota, Wisconsin, Alabama and Florida; in British Columbia; in many states of Mexico; Guatemala and Costa Rica; in the West Indies in Jamaica, Dominican Republic, Barbados, and Trinidad; Argentina, Hawaii, Singapore, and England) and have had well-preserved material of more genera at my disposal than have any others. Frustratingly, virtually all preserved specimens borrowed from museums (albeit with gratitude) have been of wretched quality, more tantalizing than informative. Only such a quantity and quality of well-preserved samples allowed recognition of progressive characters in the male reproductive system that are fundamental to the present classification (Figs. 1-3). In addition, I have been able to see many more characters overall than have previous students of Physidae. Indeed, an implicit message of this work is an appeal for more and thorough morphological studies and for more detailed illustrations.

Naturally, with this foundation, new biogeographic conclusions have been possible. The more primitive Physidae are concentrated in Pacific drainage from southern Mexico to Costa Rica, and the primitive pulmonates with which Physidae share some traits are also found along the eastern Pacific coast. Perhaps ancient adaptation to fresh waters in this region accompanied differentiation of the modern families. In any case, one can trace lineages of Physidae from this area, to Europe, Asia, North and South America, and the West Indies.

Beyond morphology, I have tried to stabilize nomenclature by preparing a catalog of the more than 430 nominal species (p. 208-251), finding many preoccupied names in the process. Type localities have been refined by allocating the species to expeditions or voyages, tracing routes and itineraries (under Museum Collections, p. 198-207). The taxonomist's common question is, "Where is the _ _ _ _ type?" Sherborn (1940), in "Where is the _ _ _ _ collection?," helped much in this respect; now there are many catalogs of types in various museums that are of great assistance. And yet, not always. The zeal of some curators who were also "type collectors" has led to the supposed existence of multiple holotypes or lectotypes in several cases. I have merely recorded such information without attempting a resolution of the matter.

The new classification (Fig. 1) is based almost entirely on the terminal male reproductive

Preputial gland absent: APLEXINAE			PHYSINAE: Preputial gland present		
Penial sheath unipartite to tripartite			Penial sheath unipartite	Penial sheath bipartite	
Stenophysini: Name uncertain; *Afrophysa*; *Stenophysa*					GRADE IV
Amecanautini: Name uncertain	Aplexini	*Sibirenauta*; *Aplexa*; *Paraplexa*	Physini: *Physa*; *Beringophysa*	Physellini: *Ultraphysella*	GRADE III
Amecanautini: *Tropinauta*; *Mayabina*; *Mexinauta*; *Amecanauta*	Aplexini	*Amuraplexa*	Physini: *Laurentiphysa*	Physellini: *Physella*; *Archiphysa*; *Utahphysa*; *Costatella*; *Petrophysa*; *Chiapaphysa*	GRADE II
	Austrinautini	*Caribnauta*; *Austrinauta*	Haitiini: *Haitia*		GRADE I

Fig. 1. Classification of Physidae, with division into grades and clades, based on progressive changes in penial complex and its musculature.

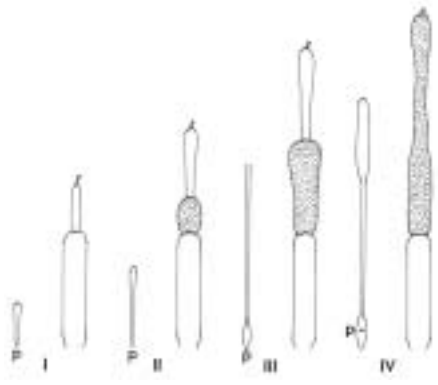

Fig. 2. Progressive changes in penial complex (diagrammatic). No particular species are illustrated, but all are Aplexinae (lacking a preputial gland). p, pore of penial canal.

system (the penial complex), including its retractor muscles. Many features useful in distinguishing genera and even species are found in other structures and systems: in the hermaphroditic and female reproductive tracts, in shell, mantle, prostate, spawn, and external body pigmentation. In none of these, however, are progressive characters found consistently. For simplicity of presentation, most information on these other features is omitted.

Criteria for primitive v. specialized states are based on comparison with the related family Lymnaeidae, and on geometric or structural simplicity or complexity. Thus the following character-states can be classified as primitive (0) or specialized (1). Some are gradational (states varying "to"), others discrete ("or") (see Fig. 3 for terminology of reproductive system).

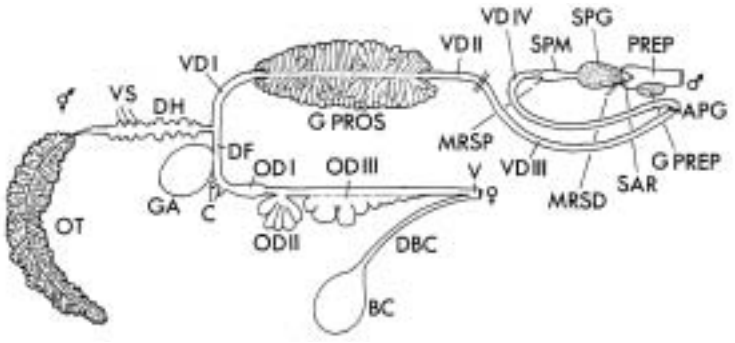

Fig. 3. Reproductive system of Physidae (diagrammatic), showing terminology and abbreviations. Nomenclature is that of Duncan (1959, 1960) with minor exceptions.

APG, paragonoporal angle of vas deferens; BC, bursa copulatrix; C, caecum or fertilization pocket; CAV, wall of body cavity; DBC, duct of bursa copulatrix; DF, female duct; DH, hermaphroditic duct; GA, albumen gland; G PREP, preputial gland; G PROS, prostate gland; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD I, OD II, OD III, oviduct; OT, ovotestis; PREP, preputium; SPG, glandular penial sheath; SPM, muscular penial sheath; SAR, sarcobelum; V, vagina; VD I, vas deferens behind prostate gland; VD II, vas deferens in front of prostate within body cavity; VD III, vas deferens within body wall; VD IV, vas deferens in cavity of head-foot; VS, seminal vesicles.

Preputium (A):

A1. Without a gland (0) or with gland (1).
A2. Straight (0) or flexed and appressed against penial sheath (1).
A3. Without (0) or with (1) retractor muscle from columellar muscle.
A4. Without (0) or with (1) a band from the distal retractor muscle of the penial sheath.

Penial sheath (B):

B1. Relatively short (0) to long (1).
B2. Entirely muscular (0) or with glandular tissue (1).
B3. Unitary (0), or bipartite or tripartite (1).
B4. Straight (0) or flexed and appressed against preputium (1).

Penis (C):

C1. Wider at head than at exit of penial canal (0); or wider at mid-length (1).
C2. Obviously tapered to flagellar (0) or tubular (1).
C3. Tip of penis simple (0) or with stylet or other modification (1).
C4. Pore of penial canal terminal (0) or lateral (1).

By these criteria, each genus (and any that may be discovered in future) can be allocated to one of the following grades: (I) penial sheath entirely muscular; (II) penial sheath with both glandular and muscular tissue; (III) penis with penial stylet or other specialization of the tip; and (IV) pore of penial canal lateral rather than terminal as in the lower grades (Fig. 2).

Clades in Physinae are defined easily. In Physini glandular tissue is added progressively from the *proximal* end of the penial sheath, whereas in Physellini it is added from the *distal* end. In these two clades, formalized as tribes, there is a progressive increase in glandular tissue from *Laurentiphysa* to *Physa*, and from *Chiapaphysa* to the advanced Physellini. Similarly in Amecanautini of the Aplexinae, glandular tissue in the sheath is increased from *Amecanauta* to *Tropinauta*. Stenophysini, the most advanced of all Physidae in having a lateral rather than terminal pore of the penial canal, show increasing complexity of both penial tip and penial sheath from *Stenophysa* to *Afrophysa*. In Austrinautini, the large terminal bulb and sarcobelum of *Caribnauta* are clear specializations relative to *Austrinauta*. In Aplexini, *Paraplexa* differs from the other two

genera by the spindle-shaped penis with elongate, narrow tip.

Rank of the various groups is determined as follows: each group within a given clade and grade is a genus; no genus includes members of more than one grade. Accordingly, Physidae consist of 23 genera, 11 in Physinae, 12 in Aplexinae. This number is far greater than that in previous classifications: seven (Starobogatov, 1970); four, with three other subordinate groups (Te, 1980); two, with several subgenera (Zilch, 1959-1960). The extreme of conservatism is by Hubendick (1978), who recognized only two genera, *Physa* and *Aplexa*, doubting that the latter was "truly" distinct. The reason for the larger number of genera is the greater number of additional characters used herein, characters unknown to previous authors, and the recognition of clades and grades. It is no exaggeration to state that examination of all genera has been necessary for an appreciation of characters in Physidae. Time and again I have begun study of an unfamiliar species, only to find that it revealed a new character-state, or even a new character, unique in the family. This is in striking contrast with the related family Lymnaeidae, in which the shell, mantle, external body, and reproductive system are, by comparison, stereotyped. No doubt study of Physidae still unknown morphologically will bring new surprises.

Superimposed on progressive changes in the penial complex are specializations unique to individual genera. Instances are the periostracal callus in *Amecanauta*, and ribbed shell of *Costatella*; small, auriform shell, vestigial eyes, blunt tentacles, and hypertrophied preputial gland and penial sheath in *Petrophysa*; spindle-shaped penis in *Paraplexa*; and transversely folded prostate with special prostatic chamber and discrete vagina with external papilla in *Sibirenauta*. Others could be cited.

Some consequences of this study are unexpected. One is the diversity of genera in the American tropics, still so little explored that further novelties may be expected. Another is bringing into relation the superficially dissimilar *Costatella*, *Petrophysa*, and *Utahphysa*. In Puerto Rico there are two genera of Aplexinae, the widespread *Stenophysa* and the local *Caribnauta*. The African species of Aplexinae, on which the name *Afrophysa* is based, is a species introduced from southern Brasil, now called *Afrophysa brasiliensis* (Küster, 1844). The traditional *Aplexa hypnorum* of Europe is a composite of two species in two genera.

Physidae are less widespread than the other major families of Hygrophila (Lymnaeidae, Bulinidae, Planorbidae). They are not native in Africa, Australia, or south and east Asia, whereas those other groups occur over all continents. Yet Physidae occur at higher latitudes than any other freshwater snails, and also are diverse in the tropics as well as boreal regions. Thus they are further distinct from Lymnaeidae (diverse in cool-temperate regions, sparse in the tropics), and from Bulinidae and Planorbidae (diverse in tropical and temperate regions, marginal in boreal regions).

Any attempt to compare diversity in Physidae with the other principal families of Hygrophila meets the obstacles of varied opinions as to ranking of groups, their relationships and nomenclature. Some authors would recognize few or even only one genus in Lymnaeidae, with various subgroups. These number 22 living groups to Zilch (1959-60), but 18 to Starobogatov (1970). Neither phylogeny nor relationships of the groups are established. In Bulinidae Starobogatov listed 33 living genera and subgenera (I think 25 would be closer), with several subfamilies; and in Planorbidae 39 (30 or fewer is more likely), again with several subfamilies. It seems that Physidae are certainly more diverse than Lymnaeidae, and more nearly equal to Bulinidae and Planorbidae.

In the Northern Hemisphere highest-latitude records for Aplexinae are: *Sibirenauta depressior* to nearly 73.5ºN on the Taimyr Peninsula, Russia; *S. pictus* at 72ºN, on Banks Island, in the Canadian Arctic Archipelago; and *S. sibiricus* at 71º54'N along the estuary of the Yenisei River, Russia. For Physinae the extreme records are *Physa streletzkajae* at 64º53'N in the Chukotsk National Region, Siberia; and *P.*

TABLE 1

Life cycles in Physidae. Nomenclature of species modernized. "Distinct" generations are those in which the adults reproducing in the spring die during that year; the young over-winter to reproduce the following year. "Indistinct" are those in which some adults live until a second year. All observations come from temperate regions, and it is questionable whether the cycle of widespread species is uniform throughout the range

Species	Source	Generations	Reference
Aplexinae			
Aplexa hypnorum	Netherlands	1/yr	Hartog & Wolf (1962)
Sibirenauta pictus	Arctic Canada	1/yr	Holyoak (1983)
Physinae			
Archiphysa parkeri	Michigan	1/yr	Cort *et al.* (1941)
Haitia acuta	England	2/yr, indistinct	Duncan (1959)
Haitia acuta	France	1yr	Duncan (1959)
Haitia acuta	New York	2/yr, indistinct	Herrmann & Harman (1975)
Haitia integra	Iowa	2/yr, indistinct	Clampitt (1970)
Haitia integra	New York	1/yr	Eckblad (1973)
Haitia mexicana	Texas	3/yr, distinct	McMahon (1975)
Physa fontinalis	England	1/yr,	Duncan (1959) 2/yr, indistinct
Physa fontinalis	Scotland	1/yr,	Russell-Hunter (1961) 2/yr, indistinct
Physa fontinalis	Netherlands	2/yr, distinct	Wit (1955)
Physella gyrina	Iowa	2/yr, distinct and	Clampitt (1970) indistinct
Physella gyrina	Michigan	1/yr,	DeWitt (1955) 2/yr, indistinct

skinneri, 69º21'N at Umiat, Alaska. In the Southern Hemisphere the ranges of both subfamilies are far less extensive. Aplexinae in South America reach 35ºS in Argentina, and Physinae to 33º05'S (*Haitia venustula*, Valparaiso, Chile).

Corresponding extremes of altitudinal range for some species are as follows: The maximum elevation known for any species of Physidae is *Mayabina carolita* at 3 200 m, Huamachuco, Peru. In the Rocky Mountains of the western United States *Physa skinneri* occurs at about 9 540 ft/2 908 m, and *Sibirenauta elongatus* at over 8 100 ft/2 469 m. *Haitia mexicana* attains its highest elevation of more than 2 500 m in cloud forest of the Sierra Juarez, Oaxaca, Mexico.

Biological studies of Physidae began with the monograph by Dawson (1911). Since then they have been focused principally on the leech-avoidance reaction (unique to Physidae), and on life cycles (Table 1). At present the most

thoroughly studied species is *Stenophysa marmorata* of the West Indies, for which there are detailed field and laboratory studies, ecology, biogeographic interpretations, water chemistry (Harrison & Rankin, 1976a,b, 1978; Rankin & Harrison, 1979; Ross & Harrison, 1977) and morphology (Paraense, 1986) from St. Vincent, the type locality.

Degner (1921) first observed the strong reaction of *Physa* to contact with leeches. Later studies have been by Wrede (1927) and Frieswijk (1957, 1973); the observations are restricted to *Physa fontinalis* (indigenous) and *Haitia acuta* (introduced) in Germany and the Netherlands. When *Physa* contacts another snail (either *Physa* or some other), the reaction is a rapid twisting of the shell back and forth to dislodge the other. The muscle used is the "physid muscle" (Harry & Hubendick, 1964), not found in other Hygrophila, which therefore do not show the reaction. The leech-avoidance reaction carries the action one step further: on contact with a leech the snail twists its shell violently and detaches its foot from the substratum as well.

Frieswijk studied the reaction of two species of Physids to various species of leeches and to various salts. In *Haitia acuta* the avoidance reaction was much lower than in *Physa fontinalis*. The highest percentage of reactions in *Physa* were obtained with the two species of leeches that feed chiefly on snails. The nature of the substance that produces the reaction is undetermined, but presumably is a protein.

METHODS

Detailed topographic maps were available in the field in the United States (1:24 000); these are inconvenient for locating a collection site by latitude and longitude, and the land-net system of section, township and range has been cited. In England, maps were available at scale 1:25 000, and in Costa Rica and parts of Guatemala at 1:50 00. Localities in these countries are cited by latitude and longitude as precisely as possible. Localities in Mexico, where maps used were at scale 1:250 000, are cited to the nearest .1 minute. Altitudes are given only when over 100 m. Administrative subdivisions are abbreviated as Prov. (Provincia), Depto. (Departamento) and Dépt. (Département); states (state or estado) have no prefix, nor do Canadian Provinces. Often no such subdivision is cited for major cities. Websites with useful geographic information are the U.S. Geological Survey Geographic Names Information System (mapping.usgs.gov/www/gnis) within the United States, and for outside of the United States the U.S. National Imagery and Mapping Agency (www.nima.mil).

Collections were made by hand-picking or by hand-held sieve. In some habitats Aplexinae could be collected by walking through submergent vegetation, then harvesting the animals when they floated to the surface.

Counts of whorls are made as tubular rather than suture whorls, *i.e.*, as the coils of a tube (the whorls of the shell) and not the suture where the whorls adjoin. Numbers are therefore .5 whorl greater than whorls of the suture. Shell measurements are by ocular micrometer, or by calipers accurate to .01 mm. Measurements are given as L, length; LPer, length of peritreme; W, width.

Observation of morphological details essential to study depends on technique of anesthetizing, fixing and preserving. The method of choice is as follows: (1) Anesthetization with menthol. This has the advantage over other reagents of increasing turgor pressure so that frequently the preputium is extruded as in copulation. Time required for anesthetization varies according to concentration of menthol, ratio of snails to unit volume of water, length of time from collection site to laboratory, and changes in temperature. During the process the snails must be free from vibration or jarring of the container, or they are likely to retract into their shells. This basic procedure is, like cooking, an art rather than science, and despite many years of experience I do not always achieve satisfactory results. (2) Fixation in FAA, preferably Lavdowsky's mixture. Its formula: 10 ml formalin, 30 ml ETOH (approximately 95%),

60 ml distilled water, 2 ml glacial acetic acid. Time needed for fixation depends on the body volume of the specimen. For animals 30-40 mm long, 24 hrs; for those 5-10 mm, 6 hrs; and for intermediate sizes 10-12 hrs. (3) Transfer to 70% ETOH. This procedure is satisfactory for gross morphological study, but not for histological work. Less desirable methods that will yield less satisfactory results are to kill the animals with hot (but not boiling) water, then transfer to alcohol; or to kill them by gradual freezing, then transfer to alcohol. Observation of structures was aided as necessary by staining with methylene blue.

In a few cases the only material available was severely contracted and desiccated. Specimens were treated by a solution of trisodium phosphate (TSP)(Van Cleave & Ross, 1947). The resulting material was then merely inadequate, rather than impossible, for dissection. Too late for the present study, I learned of a method developed in the Zoology Department of the Natural History Museum, London: A solution of "decon 90" (brand name) detergent and water is prepared in approximate concentration 1:20; exact proportions are not necessary for good results. After an average of three days in the solution (with changes to fresh solution if it becomes discolored), specimens become suitably rehydrated. A final transfer to water for one day is necessary for thorough rinsing and prevents expulsion of the rehydrant.

For study of spawn, small groups of living specimens were maintained for short periods in clear plastic sacs, on which they deposited capsules. Pieces of the plastic were then cut to size for microscopic examination by direct and transmitted light.

In this connection another technique is worth mentioning, even though not used in the present study. Paraense (1986) found that by feeding snails for several days with colored gelatin, the digestive gland takes up color and distinction between gland and ovotestis is accentuated.

Life studies are highly desirable. Even with optimal results in preservation, there will be tissue contraction. Proportions of tentacles and mantle projections are especially sensitive to fixation.

Line drawings are based on camera lucida sketches except as noted. Illustrations of living animals are composites from a shell or preserved specimen and sketches from life.

As many names as possible have been allocated to genera and species, including *nomina nuda*. These were assembled from various sources, mostly incomplete: summaries by Küster & Clessin (1841-1886), Paetel (1888-1890), and Sowerby (1873-1874); the "Zoological Record," and "Index Animalium" by C. D. Sherborn; for the intervening period, "Index to the species of Mollusca introduced from 1850 to 1870" (Ruhoff, 1980); and of course references within works consulted. Despite effort, some publications have not been accessible for examination (citations marked with #), and no doubt a few names have been overlooked. Some names treated as *nomina nuda* herein may have been proposed validly in publications I have missed.

Taxonomic references and catalogs of types are cited in the "Catalog of Physidae" (p. 208 ff.).

Type localities (abbreviated as TL) have been modernized as to spelling and present political units so far as possible, but some proved obscure. No explanation is provided in the case of minor differences of spelling, otherwise revisions are in square brackets after the original form.

The lists of species and synonyms surely include errors, but types or topotypes of most forms have not been accessible. For those species already named and redescribed herein, references are limited to original description, new combinations, and relatively significant information.

Terminology of the reproductive system (Fig. 3) is that used by Duncan (1959, 1960) with minor modifications; that of spawn, by Bondesen (1950).

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My long-time friends Wendell O. Gregg (1898-1979) and Allyn G. Smith (1893-1976) generously donated their collections of Physidae. This material included not only specimens historically valuable, but also some unique series.

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H. Nesemann, Universität für Bodenkultur, Vienna, Austria.

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R. K. Sinha, Patna University, Patna, India.

A. Skoptsov, Tambov State Teacher's Training Institute, Tambov, Russia.

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In April, 1992, I spent a week at the Museum of Comparative Zoology, Harvard University, where K. J. Boss facilitated access to specimens and library. The former curator, William J. Clench, had specialized early in Physidae and brought together a substantial amount of type material in addition to that of his own species.

Two weeks at the Natural History Museum, London, in May 1998, gave opportunity to consult scarce publications and to review the collection. F. Naggs and J. Pickering were

of special help in the Mollusca Section. On this trip also I had the assistance of G. Douglas in consulting rare works in the library of the Linnean Society.

In the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, S. E. Miquel made available the collection of Physidae and aided with scientific literature.

The timely appearance of "Panbiogeography" by R. C. Craw, J. R. Grehan, and M. J. Heads (1999) permitted important additions in biogeography.

My colleagues the late J. Gray, University of Oregon, and A. J. Boucot, Oregon State University, took time from their own researches to contribute advice on the manuscript.

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CLASSIFICATION

For each genus, its grade and general distribution (native) are indicated. The list includes only living species that can be assigned to a genus in the present classification. Some will prove to be synonyms of other species, and some may be composite. Others, surely distinct but *incertae sedis*, need morphological study to determine their relationships. Type localities (TL) are given first, then range. Of 81 species listed, the following are most likely to be synonyms: *Haitia jamaicensis*, *H. lacustris*, and *Physella microstoma*.

I believe that there are at least two or three genera of Aplexinae in Argentina, but they cannot be linked to the named species without topotypes. Two appear as "Name uncertain" in Fig. 1. The traditional identification of these forms has been *Physa* or *Aplexa marmorata* (*Stenophysa marmorata* herein), but the specimens I have examined, and published illustrations, show that they belong to different genera.

The present version of classification will change with discovery of additional genera and species, reduction of some species listed herein to others as synonyms, allocation of forms *incertae sedis* to a probable assignment, study of species that may show some are composite, and by changes in weighting of characters. The fauna of Siberia, central Asia, and South America is scarcely known, and there are many uncertainties concerning the Physidae of other regions, including the United States.

Superfamily **Physacea** Harry & Hubendick, 1964
Family **Physidae** Fischer & Crosse, 1886
Subfamily **Aplexinae** Starobogatov, 1967
Tribe **Austrinautini**, new tribe

Austrinauta g.n. (**I**), northwestern Mexico (Nayarit).

1. *Austrinauta elatus* (Gould, 1853); TL "Lower California" [in error]. Nayarit, Mexico.

Caribnauta g.n. (**I**), West Indies in Puerto Rico and Virgin Islands.

2. *Caribnauta harryi g.n.,nom.nov.*; TL river west of Las Piedras, Municipio Las Piedras, Puerto Rico. Puerto Rico and the Virgin Islands.

Tribe **Aplexini**, new tribe

Amuraplexa Starobogatov, Prozorova & Zatravkin, 1989 (**II**), eastern Siberia.

3. *Amuraplexa amurensis* (Starobogatov & Prozorova, 1989); TL Konstantinovka [48º35'N, 135º27'E], Khabarovsk region, Russia. Eastern Siberia.

Paraplexa Starobogatov, 1989 (**III**), southwestern Europe.

4. *Paraplexa cornea* (Massot, 1845); TL Perpignan [42º41'N, 2º53'E], Dépt. Pyrénées-Orientales, France. Southwestern Europe in southern France, western Switzerland, northeastern Spain, and northern Italy.

Aplexa Fleming, 1820 (**III**), Europe and western Siberia.

5. *Aplexa hypnorum* (Linnaeus, 1758); TL Sweden. Western and northern Europe, eastward to western Siberia.

Sibirenauta Starobogatov & Streletskaya, 1967 (**III**), Siberia and northern North America.

6. *Sibirenauta depressior* (Middendorff, 1851); TL Ichl, and near Falchudda Lake [neither locality traced], Taimyr Peninsula, Russia. Eastern Siberia.
7. *Sibirenauta elongatus* (Say, 1821); TL "shores of Illinois" opposite St. Louis, Missouri. Canada and northern United States.
8. *Sibirenauta pictus* (Krause, 1883); TL tundra pond north of Lavrentija Zaliv

[Lawrence Bay, 63º35'N, 171º00'W], and mouth of a small stream entering the west end of that bay, Chukotka, Russia. Extreme eastern Siberia, Alaska, and northern Northwest Territories, Canada.

9. *Sibirenauta sibiricus* (Westerlund, 1876); TL Bukhta Sopochnaya Karga [71º54'N, 82º43'E], Taimyr Peninsula, Russia.
10. *"Sibirenauta" tuwaensis* Starobogatov & Zatravkin, *in* Starobogatov *et al*., 1989; TL Toora-Khem [52º28'N, 96º09'E], Tuvinsk Autonomous Region, Russia. Tuvinsk Autonomous Region, Russia, and adjacent Mongolia.

Tribe **Amecanautini**, new tribe

Amecanauta g.n. (**II**), northwestern Mexico (Jalisco).

11. *Amecanauta jaliscoensis sp.n.*; TL delta of Río Ameca [20º41.48'N, 105º13.95'W], forming the boundary between Nayarit and Jalisco, Mexico.

Mexinauta g.n. (**II**), humid coastal plains of Mexico south to southwestern Costa Rica; Ecuador and Peru.

12. *Mexinauta aurantia* (Carpenter, 1857); TL "Mazatlan," surely in error; most likely Acapulco [16º5'N, 99º55'W]. Jalisco and Guerrero, Mexico, and Río Tempisque, Costa Rica.
13. *Mexinauta gracilentus* (Fischer & Crosse, 1886); TL Cobán [15º29'N, 90º19'W], Depto. Vera Paz, Guatemala.
14. *Mexinauta impluviatus* (Morelet, 1849); TL Guatemala City [13º40'N, 88º13'W], Guatemala. Southeastern Mexico (Chiapas) to southern Guatemala.
15. *Mexinauta laetus* (Martens, 1898); TL Depto. Vera Paz, Guatemala.
16. *Mexinauta nicaraguanus* (Morelet, 1851); TL "Nicaragua."
17. *Mexinauta nitens* (Philippi, 1841); TL "Mexico," probably in the vicinity of Veracruz [32º25'N, 115º05'W]. Coast of the Gulf of Mexico from extreme southern Texas [where now extinct] to western Campeche, Mexico.
18. *Mexinauta peruvianus* (Gray, 1828); TL swamps between Lima and Callao, Peru. Ecuador to central Peru.
19. *Mexinauta princeps* (Phillips, 1846); TL "Yucatan." Peninsula of Yucatán, Mexico, to northern Guatemala.

Mayabina g.n. (**II**), Oaxaca and Veracruz, Mexico, to northernmost Chile.

20. *Mayabina bullula* (Crosse & Fischer, 1882); TL Tuxpan [20º57'N, 97º24'W], Veracruz, Mexico. Veracruz state, Mexico.
21. *Mayabina carolita* (Jousseaume, 1887); TL San Nicolás, Cantón Mejía, Prov. Pichincha, Ecuador. Ecuador to northernmost Chile.
22. *Mayabina nitidula* (Clessin, 1886); TL "Honduras."
23. *Mayabina obtusa* (Clessin, 1885); TL "Honduras."
24. *Mayabina petenensis sp.n.*; TL Aguada at NE side of La Libertad [16º47.30'N, 90º6.49'W], Depto. Petén, Guatemala. Depto. Petén, Guatemala.
25. *Mayabina pliculosa* (Martens, 1898); TL Río Reventazon, Ujarrás [9º50'N, 83º50'W], Prov. Cartago, Costa Rica. Central Costa Rica.
26. *Mayabina polita sp.n.*; TL 1.5 km S of Mex. 186 toward Zopo Norte, 17º39.6'N, 92º24.7'W, Tabasco, Mexico. Tabasco and northernmost Chiapas to Quintana Roo, Mexico.
27. *Mayabina sanctijohannis sp.n.*; TL Barra del Colorado, 10º46.37'N, 83º35.27'W, Prov. Limón, Costa Rica.
28. *Mayabina spiculata* (Morelet, 1849); TL Campeche [19º51'N, 90º32'W], Campeche, Mexico. Peninsula of Yucatán, Mexico.
29. *Mayabina tapanensis* (Crosse & Fischer, 1882); TL San Pedro Tapanatepec [16º21'N, 94º12'W], Oaxaca, Mexico. Southeastern Oaxaca, Mexico, to southern Guatemala.
30. *Mayabina tempisquensis sp.n.*; TL Parque Nacional Palo Verde, 10º20.68'N, 85º20.60'W, Prov. Guanacaste, Costa Rica. Río Tempisque drainage, Costa Rica.

Tropinauta g.n. (**II**), southeastern Costa Rica.

31. *Tropinauta sinusdulcensis sp.n.*; TL Stream 3 km SE Golfito, 8º36.68'N, 83º8.48'W, Prov. Puntarenas, Costa Rica.

Tribe **Stenophysini**, new tribe

Stenophysa Martens, 1898 (**IV**), West Indies except Cuba; eastern Costa Rica to Panama; ?northeastern South America.

32. *Stenophysa marmorata* (Guilding, 1828); TL St. Vincent, Lesser Antilles. West Indies except Cuba; eastern Costa Rica and Panama.
33. *Stenophysa spathidophallus sp.n.* TL Singapore, doubtless introduced, perhaps from northeastern South America.

Afrophysa Starobogatov, 1967 (**IV**), southern Brasil.

34. *Afrophysa brasiliensis* (Küster, 1844); TL "Brasil," herein restricted to Porto Alegre [30º04'S, 51º11'W]. Southern Brasil, in the state of Rio Grande do Sul.

Subfamily **Physinae** Starobogatov, 1967
Tribe **Haitiini**, new tribe

Haitia Clench & Aguayo, 1932 (**I**), North America from southernmost Canada through the West Indies and Central America; Andean South America as far south as central Chile.

35. *Haitia acuta* (Draparnaud, 1805); TL Garonne River and its tributaries, France [introduced]. Maritime Canada, New England and north Atlantic United States; widely introduced in Europe and Africa.
36. *Haitia cubensis* (Pfeiffer, 1839); TL Cuba, probably in the vicinity of La Habana, 23º08'N, 82º22'W. West Indies.
37. *Haitia elegans* (Clench & Aguayo, 1932); TL Lake Miragoane, two miles SE of Miragoane [18º27'N, 73º06'W], Haiti.
38. *Haitia integra* (Haldeman, 1841); TL Indiana, probably from the vicinity of New Harmony [38º07'47"N, 87º56'06"W], Posey County. Great Lakes region from Canada to midwestern United States.
39. *Haitia jamaicensis* (C. B. Adams, 1851); TL Tank at Malvern [17º58'N, 77º42'W], in the Santa Cruz Mountains, St. Elizabeth Parish, Jamaica. West Indies in Jamaica and St. Croix.
40. *Haitia lacustris* (Clessin, 1886); TL Lago Coatepeque, El Salvador. Possibly only an ecophenotype of *mexicana*.
41. *Haitia mexicana* (Philippi, 1841); TL Mexico, probably in the vicinity of the capital. Western and south-central United States through Mexico to Costa Rica at least, perhaps even as far as Colombia.
42. *Haitia moreleti sp.n.*; TL Lago Petén-Itzá, Santa Elena, 16º55.30'N, 89º53.40'W, Depto. El Petén, Guatemala. Vicinity of Lago Petén-Itzá, Guatemala.
43. *Haitia natricina* (Taylor, 1988); TL Snake River, SW 1/4 SE 1/4 sec. 21, T. 6 S., R. 13 E., Gooding County, Idaho. Snake River, southern Idaho.
44. *Haitia patzcuarensis* (Pilsbry, 1891); TL Lago de Pátzcuaro [19º35'N, 101º35'W], Michoacán, Mexico.
45. *Haitia pomilia* (Conrad, 1834); TL Randons Creek, near Claiborne [31º32'24"N, 87º30'56"W], Monroe County, Alabama. Southern Alabama to Florida.
46. *Haitia porteri* (Germain, 1913); TL brackish waters of Prov. Antofagasta, Chile. Perhaps a synonym of *H. venustula*.
47. ?*Haitia solidissima* (Pilsbry, 1920); TL Laguna de Chapala, Jalisco, Mexico. Generic reference uncertain; possibly *Physella?*
48. *Haitia spelunca* (Turner & Clench, 1974); TL Lower Kane Cave, Big Horn County, Wyoming.
49. *Haitia venustula* (Gould, 1847); TL Lima [12º03'S, 77º03'W], Prov. Lima, Peru. Northern Peru to central Chile.

Tribe **Physini**, new tribe

Laurentiphysa g.n. (**II**), Great Lakes region of United States east to Newfoundland, Canada, and Long Island, New York.

50. *Laurentiphysa chippevarum sp.n.*; TL SW 1/4 SE 1/4 sec. 31, T. 43 N., R. 2 W., Ashland County, Wisconsin. Northern Wisconsin.

51. *Laurentiphysa vernalis* (Taylor & Jokinen, 1985); TL "Bluebird Pond," Windham Township, Windham County, Connecticut. Great Lakes region of United States east to Newfoundland, southern New England, and Long Island, New York.

Beringophysa Starobogatov & Budnikova, 1976 (**III**), Siberia to vicinity of James Bay, Canada.

52. *Beringophysa jennessi* (Dall, 1917); TL ponds near Bernard Harbour [68º47'N, 114º47'N], District of Mackenzie, Northwest Territories, Canada. Eastern Siberia to Alaska, southeast through Northwest Territories, Canada, to vicinity of Hudson Bay and James Bay, Quebec.

Physa Draparnaud, 1801 (**III**), Europe, Siberia and northern North America.

53. *Physa arachleica* Starobogatov & Prozorova *in* Starobogatov *et al*., 1989; TL Lake Arakhlei [52º12'N, 112º52'E], Chitinsk District, Russia.
54. *Physa dalmatina* Küster, 1844; TL three localities in Dalmatia, Croatia: See von Boccagnazo bei Zara (=Bokanjacko Blato, north of Zadar), the Salona at Spalato (=Split), and in marshes of the Cettina (=Cetina) at Almissa (not traced). Balkans to western Siberia.
55. *Physa fontinalis* (Linnaeus, 1758); TL vicinity of Uppsala [59º52'N, 17º38'E], Sweden. Europe to western Siberia.
56. *Physa hankensis* Starobogatov & Prozorova, *in* Starobogatov *et al*., 1989; TL pool near Kaktokovsk lake [not traced], Khabarovsk region, Russia. Eastern Siberia.
57. *Physa megalochlamys* Taylor, 1988; TL lily pond beside US highway 26-89-187, NW 1/4 sec. 19, T. 45 N., R. 114 W., Teton County, Wyoming. Southwestern Canada and western United States.
58. *Physa mirollii nom.nov.*; TL Lago Maggiore, Italy.
59. *Physa skinneri* Taylor, 1954; TL Pleistocene, SE corner sec. 6, T. 5 N., R. 28 E., Beaver County, Oklahoma. Alaska to central United States.
60. *Physa streletzkajae* Starobogatov & Budnikova, 1976; TL Vakarevo [64º53'N, 171º37'E], Chukotka, northeastern Siberia.
61. *Physa taslei* Bourguignat, 1860; TL "Très-commune dans un petit ruisseau provenant de la fontaine de Limoges, à 2 kilomètres de Vannes," Brittany, France. France.

Tribe **Physellini**, new tribe

Chiapaphysa g.n. (**II**), southeastern Mexico (Chiapas) and northwestern Costa Rica (Prov. Guanacaste).

62. *Chiapaphysa grijalvae sp.n.*; TL Río Suchiapa, 2 km SE Suchiapa, 16º36.4'N, 93º5.0'W, Chiapas, Mexico. Chiapas, southeastern Mexico.
63. *Chiapaphysa pacifica sp.n.*; TL Río Tenorito, Hacienda La Pacífica, 10º29.02'N, 85º9.58'W, Guanacaste, Costa Rica. Prov. Guanacaste, northwestern Costa Rica.

Costatella Dall, 1870 (**II**), Clear Lake, California.

64. *Costatella costata* (Newcomb, 1861); TL Clear Lake, Lake County, California.

Petrophysa Pilsbry, 1926 (**II**), Zion National Park, Utah.

65. *Petrophysa zionis* (Pilsbry, 1926); TL Zion Canyon [37º09'54"N, 113º00'40" W], Utah.

Utahphysa g.n. (**II**), Fish Lake, Utah.

66. *Utahphysa microstriata* (Chamberlin & Berry, 1930); TL Fish Lake, Sevier County, Utah.

Archiphysa g.n. (**II**), southernmost Canada, northern and western United States.

67. *Archiphysa ashmuni sp.n.*; TL Ojo del Gallo, 35º07'20"N, 107º52'32"W, San Rafael, Cibola County, New Mexico (now extinct). One or two other populations, at localities not yet recovered, are of uncertain status. New Mexico.
68. *Archiphysa laphami* (F. C. Baker, 1928); TL Hancock [44º08'01"N, 89º31'23"W],

Waushara County, Wisconsin. Wisconsin and adjacent Michigan.

69. *Archiphysa latchfordi* (F. C. Baker, 1928); TL Meach Lake [45º31'N, 75º52'W], Quebec.
70. *Archiphysa lordi* (Baird, 1863); TL "Lake Osoyoos, British Columbia," Canada; but probably Pend Oreille River, Seneacquoteen [48º09'06"N, 116º45'16"W], Bonner County, Idaho. Southern British Columbia; formerly in northern Idaho.
71. *Archiphysa parkeri* (Currier, *in* DeCamp, 1881); TL Houghton Lake [44º18'53"N, 84º45'53"W], Roscommon County, Michigan. Lower Peninsula of Michigan.
72. *Archiphysa sonomae sp.n.*; TL artificial pond in sec. 30, T. 9 N., R. 9 W., Sonoma County, California. Native range uncertain, but presumably in that county.
73. *Archiphysa zomos* (Baily & Baily, 1952); TL Pyramid Lake, Nevada.

Physella Haldeman, 1843 (**II**), southeastern Alaska and Canada over most of the United States.

74. *Physella ancillaria* (Say, 1825); TL Delaware River, near Easton [40º41'18"N, 75º13'16"W], Northampton County, Pennsylvania. Great Lakes region to New England, New York, and Pennsylvania.
75. *Physella columbiana* (Hemphill, 1890); TL Columbia River, Astoria [46º11'17"N, 123º49'48"W], Clatsop County, Oregon. Probably extinct.
76. *Physella globosa* (Haldeman, 1841); TL mouth of Nolichucky River, Greene County, Tennessee.
77. *Physella gyrina* (Say, 1821); TL Boyer Creek, Pottawatomie County, Iowa. Southeastern Alaska and Canada over most of the United States.
78. *Physella hemphilli sp.n.*; TL Coeur D'Alene Lake, Idaho. Possibly extinct.
79. *Physella microstoma* (Haldeman, 1840); TL Kentucky and Ohio (no precise localities). Kentucky, Ohio and Tennessee.
80. *Physella vinosa* (Gould, 1847); TL "Lake Superior region."

Ultraphysella g.n. (**III**), Northwestern Mexico.

81. *Ultraphysella sinaloae sp.n.*; TL pool at road 2.5 mi from Villa Unión toward Siqueiros [23º13.4'N, 106º12.5'W], Sinaloa, Mexico. Sinaloa and Nayarit, northwestern Mexico.

PHYLOGENY

Phylogenetic position of Physidae within the Hygrophila rests on comparative studies by previous authors such as Duncan (1960a,b), Harry (1964a), and Starobogatov (1967). The family has been considered a relatively primitive group from structure of the egg capsules (Bondesen, 1950). Duncan (1960b) concluded that "the genital system of the Physidae is nearest to the ancestral condition" of Basommatophora and shows resemblances to that in the Chilinidae. From comparison of the copulatory organ in such primitive pulmonates as Chilinidae and Ellobiidae, Starobogatov (1967:297) concluded that the archetypal form was a simple tubular penis, covered by a sheath twice as long, the proximal part comprising the penial sheath, and the distal part the preputium; this condition is closely approximated amongst some Physidae. In the radula, the chevron-like arrangement of teeth, unique in Hygrophila, is a trait shared with the Chilinidae and has been interpreted (Harry, 1964a) as retention of the primitive condition.

Interestingly, Chilinidae and Physidae are ecological equivalents, as well as being almost mutually exclusive in distribution. In southern South America "Within their area, the Chilinidae are abundant snails in all suitable stations, as Physidae are in the north. They swarm in springs, small streams, lakes, and in some places the margins of rivers. They are most abundant southward, becoming rarer and local toward the northern borders of their range" (Pilsbry, 1911).

The combination of conspicuous color bands and white streaks in the shell is rare in Hygrophila, known only in *Lanx* (Lancidae, northwestern United States) and in *Mexinauta* (Physidae) of Mexico to Peru. Color bands in both groups are simple strips, unlike the

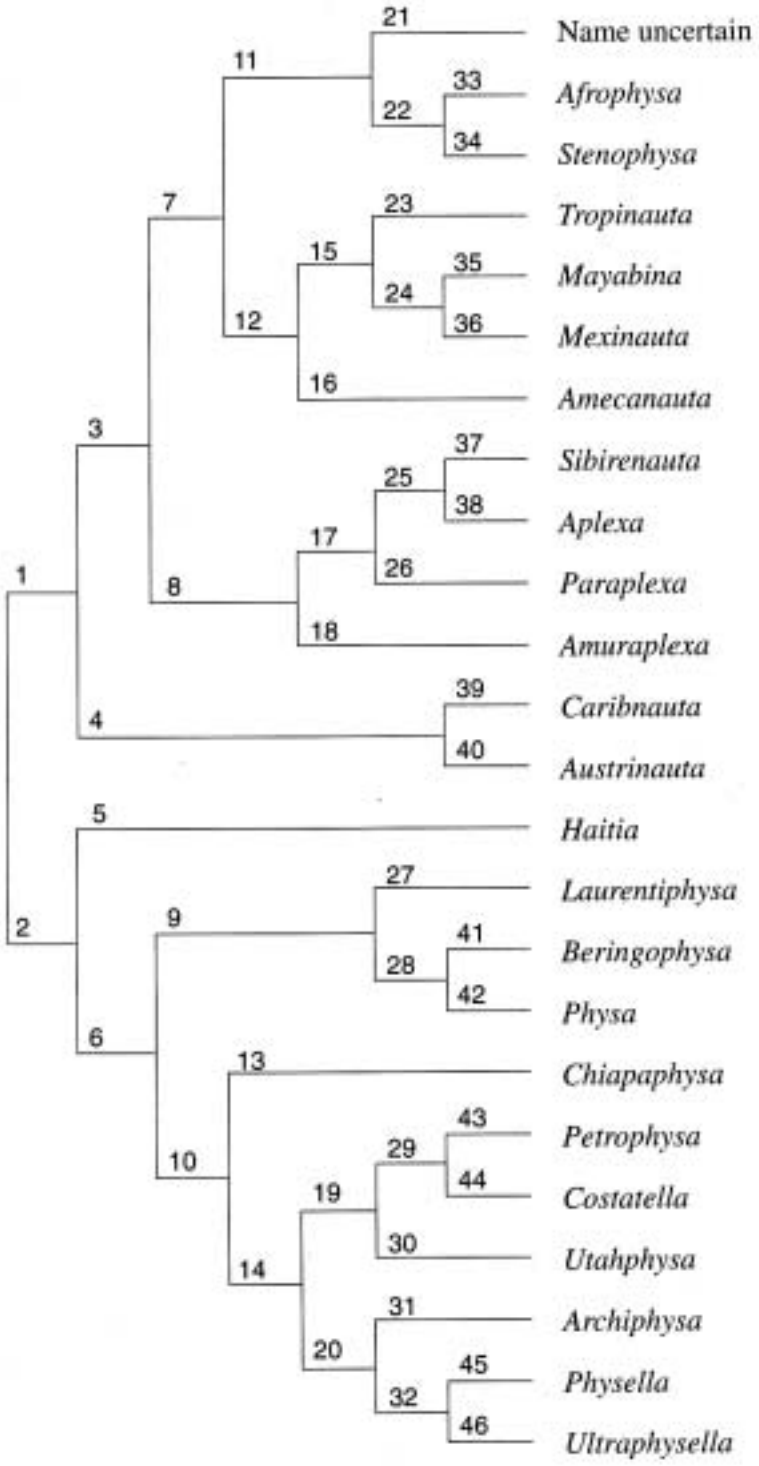


Fig. 4. Phylogeny of Physidae, shown as a dichotomous trellis diagram.

chevron-like pattern found in Chilinidae, but like the simple pattern found in some Acteonidae (Architectibranchia), Siphonariidae (Thalassophila), and some Ellobiidae (Actophila).

Thus various features of Physidae link them to diverse groups, some marine (Acteonidae, Siphonariidae), some freshwater (Chilinidae), some strand-dwellers (Ellobiidae). No clear-cut ancestry of Physidae can be discerned; rather, they are part of a complex including basal stocks of several lineages of pulmonates. Those yearning for "sister-groups" within a dichotomous analysis of relationships should take into account the extent to which emphasis on a particular structure or organ-system influences the conclusions. If the radula is taken as primary, then Chilinidae are the sister-group; if the prostate or sinistral body, then Planorbacea; if the spawn, then Lymnaeacea; if color bands and white streaks in the shell, then Lancidae (Lymnaeacea) and Siphonariidae (Thalassophila). Indeed, any scheme or technique that identifies a particular group as "sister" to Physidae needs be an over-simplification.

Phylogeny within Physidae (Fig. 4) has been inferred almost entirely on the basis of 12 progressive character-states of the penial complex (p. 4, Table 2). Numbers correspond to those in Fig. 4. Imposition of a dichotomous relationship between various groups is satisfactory in some cases (Aplexinae - Physinae), but less so in others, and artificial in still others (Physellini).

1,2. Preputial gland absent (1, Aplexinae) or present (2, Physinae).

3,4. Glandular tissue present in penial sheath (3, Stenophysini, Amecanautini and Aplexini) or absent (4, Austrinautini).

5,6. Glandular tissue absent in penial sheath (5, Haitiini) or present (6, Physini and Physellini).

5,6. Penial sheath bipartite or tripartite (5, Stenophysini and Amecanautini) or unipartite (6, Aplexini).

7,8. Penial sheath bipartite with both muscular and glandular tissue, pore of penial canal lateral or terminal (7, Amecanautini and Stenophysini); or penial sheath unipartite,

TABLE 2

Physidae scored as primitive (0) or specialized (1) according to 12 character-states of penial complex, not all of equal significance. Information is lacking in some groups

	A1	A2	A3	A4	B1	B2	B3	B4	C1	C2	C3	C4
Austrinauta	0	0	0	0	0	0	0	0	0	0	0	0
Caribnauta	0	0	0	0	0	0	0	0	0	0	0	0
Amuraplexa	0	0	0	0	0	1	0	0	0	0		0
Paraplexa	0	0	0	0	0	1	0	0	1	0	1	0
Aplexa	0	0	0	0	0	1	0	0	0	0	1	0
Amecanauta	0	0	0	1	0	1	1	0	0	0	0	0
Mexinauta	0	0	0	0	1	1	1	0	0	0	0	0
Mayabina	0	0	0	0	1	1	1	0	0	0	0	0
Tropinauta	0	1	1	0	1	1	1	1	0	0	0	0
Sibirenauta	0	0	0	0	1	1	1	0	0	1	1	0
Stenophysa	0	0	0	0	1	1	1	0	0	0	1	1
Afrophysa	0	0	0	0	1	1	1	0	0	0	1	1
Haitia	1	0	0	0	0	0	0	0	0	0	0	0
Laurentiphysa	1	0	0	0	1	1	0	0	0	0	0	0
Beringophysa	1	0	0	0		1	0	0	0	0	1	0
Physa	1	0	0	0	1	1	0	0	0	0	1	0
Chiapaphysa	1	0	0	0		1	1	0	0	0	0	0
Petrophysa	1	0	0	0	1	1	1	0	0	0	0	0
Costatella	1	0	0	0	1	1	1	0	0	0	0	0
Utahphysa	1	0	0	0	1	1	0	0	0	0	0	
Archiphysa	1	0	0	0	1	1	1	0	0	0	0	0
Physella	1	0	0	0	1	1	1	0	0	0	0	0
Ultraphysella	1	0	0	0	1	1	1	0	0	0	1	0

entirely glandular, or bipartite or tripartite with both muscular and glandular tissue and elaborate distal ornament of penis (8, Aplexini).

9,10. Penial sheath unipartite (9, Physini) or bipartite (10, Physellini).

11,12. Pore of penial canal lateral (11, Stenophysini) or terminal (12, Amecanautini).

13,14. Muscular portion of penial sheath strongly tapered to glandular portion, and glandular portion less than one-third of length of sheath (13, *Chiapaphysa*); or glandular portion of sheath far more bulky than muscular portion, or with muscular portion not strongly tapered (14).

15,16. Penis flagelliform (15, most Amecanautini) or slender but obviously tapered (16, *Amecanauta*).

17,18. Penis tubular with tapered end, or spindle-shaped, with terminal narrowing of penial canal (17); or tapered, with no terminal specialization (18, *Amuraplexa*).

19,20. Penis with broad proximal end, and obviously tapered (19), or with narrow proximal end, less obviously tapered (20).

21,22. Not as in 22 (21, name uncertain); or penis with conspicuous terminal structure, and lateral opening of penial canal distant from tip of penis (22, *Stenophysa*, *Afrophysa*).

23,24. Penial sheath flexed 180º and preputium flexed 90º (23, *Tropinauta*) or neither flexed (24, *Mayabina, Mexinauta*).

25,26. Shaft of penis a stout tube, with narrow conical tip at least slightly set off from shaft (25, *Sibirenauta*, *Aplexa*); or spindle-shaped, wider in the middle than at the proximal end, and with penial canal narrow in narrow terminal end (26, *Paraplexa*).

27,28. Penis without terminal stylet (27, *Laurentiphysa*) or with terminal stylet (28, *Beringophysa*, *Physa*).

29,30. Mantle not broadly reflected over shell and with at least vestigial projections of margin (29, *Petrophysa* and *Costatella*); or mantle broadly reflected over shell, with smooth margin (30, *Utahphysa).*

31,32. Penis with simple tip; bursal duct leaves bursa on medial aspect; shell medium to large-sized, often obovoid (31, *Archiphysa*); or bursal duct leaves bursa at anterior end; shell small to medium-sized (32, *Physella* and *Ultraphysella*).

33,34. Penial sheath and penis tripartite (33, *Afrophysa*) or bipartite (34, *Stenophysa*).

35,36. Penial sheath glandular in about 40% of length (35, *Mayabina*) or about 20% (36, *Mexinauta*).

37,38. Penis tubular with tapered end (37, *Aplexa*) or spindle-shaped, with terminal narrowing of penial canal (38, *Paraplexa*).

39,40. Penial sheath with large terminal bulb (39, *Caribnauta*), or a simple tube (40, *Austrinauta*).

41,42. Penial stylet ovoid (41, *Beringophysa*) or lanceolate (42, *Physa*).

43,44. Shell smooth, posterior end of foot broad, mantle with vestigial projections only, and tentacles short and blunt (43, *Petrophysa*); or shell ribbed, posterior end of foot acutely pointed, mantle projections in two groups of triangles, columellar and left posterior, and tentacles slender and pointed (44, *Costatella*).

45,46. Tip of penis simple, tapered gradually (45, *Physella*), or tip of penis narrowed, and penial canal enlarged within (46, *Ultraphysella*).

Sequence of character-states is determined by their degree of uniformity within lower-level clusters. Thus progressively increased amounts of glandular tissue are found in the penial sheath whether the sheath is unipartite (11, Physini) or bipartite (12, Physellini), and presence of glandular tissue is accepted as antecedent. Development of a terminal stylet or other modification of the tip of the penis is found in various genera (*Afrophysa*, *Stenophysa*, *Sibirenauta*, *Aplexa*, *Beringophysa*, *Physa*, *Ultraphysella*) that are otherwise distinct and share characters with other genera, and is interpreted as significant only at the generic level. In all the family I have found only one instance of character-state reversal. *Physa mirollii* lacks a preputial gland, the only exception to presence of this structure in Physinae.

BIOGEOGRAPHY

Physidae are a world-wide family, found on all continents but Antarctica and on many remote islands. Much of this range is due to modern artificial introduction, however: all occurrences in Africa, Australia, New Zealand, southeast Asia, Japan, and islands in the Indian and Pacific Oceans. Criteria for recognition of introduced occurrences (mostly from Harry, 1964b) are (1) detailed knowledge of the circumstances of introduction, (2) time of importation estimated from previous knowledge of the area, (3) lack of close relatives in the area, (4) restriction to habitats much affected by human activity, (5) local restriction to the new area, (6) known introductions in other areas, (7) enormous population densities in the new home, and (8) lack of a fossil record, even in archeological sites.

The earliest introduction was by the early 19th century, when *Haitia acuta* of northeastern North America was found in France (1805) and probably also England (1807). Occurrences on the island of Réunion (1827) in the Indian Ocean, and in North Africa and the Canary Islands might date to approximately the same time. Shipboard transport in water casks would seem likely.

Another early introduction was that of *Afrophysa brasiliensis* from southern Brasil (once a Portuguese colony) to Africa. The earliest documented occurrence is in the former Portuguese colony of Lourenço Marques (now part of Mozambique), southeastern Africa (1886). Transport in water casks by ships engaged in the black ivory trade seems plausible. Later, sporadic occurrences in West and South Africa might be due to independent introductions, but the lack of faunistic knowledge in such early times leaves open a range of possibilities.

Transport to Hawaii from the western United States by 1845 is documented by the freshwater snail *Tryonia protea* (Gould, 1855) (Hydrobiidae). The species was named from Hawaii by Mighels (1845) as *Paludina porrecta*. Types of the latter were destroyed by fire many years ago, but illustration of the species by Küster (1852-1853), and comparison with series from mainland United States and from Hawaii (in B. P. Bishop Museum, Honolulu) render the identification confident. This date of introduction, by 1845, is likely to apply also to *Haitia mexicana* of the western United States, now on all the larger Hawaiian Islands.

The modern development of air cargo transport, and a popular aquarium trade in fishes, have opened a far greater range of opportunities for artificial introduction of snails. A clear instance is that of *Stenophysa spathidophallus*, described herein from Singapore, a major center in the tropical fish trade. Its native range is unknown, probably in northeastern South America, but it was in Singapore from at least 1975 to 1985.

Eliminating occurrences due to importation reduces the range to that shown in Figs. 5-10. With new criteria for recognition of primitive groups, one can state that they are concentrated along the Pacific coast from Mexico (Sinaloa and Nayarit) to Costa Rica. *Amecanauta*, *Austrinauta*, and *Chiapaphysa*, all three the most primitive of their lineages, are restricted to this region. In addition *Haitia* and *Stenophysa*, similarly primitive, are found here. These account for the roots of five out of the seven tribes of Physidae. Furthermore, *Amuraplexa*, most primitive of the four genera of Aplexini, is found in the Maritime Region of Russia, along the northwestern Pacific. The family accordingly fits the previous generalization (Taylor, 1988a:525-529) that the more primitive pulmonates, marine, freshwater, and terrestrial, are concentrated within or around the margins of the Pacific. There are also characters of some Physidae linking them to other families: to Chilinidae, of southern South America, and to Lancidae, of northwestern United States. Thus the differentiation of Physidae, along with some related families, and perhaps with progressive adaptation to freshwater habitats, along an ancient eastern Pacific coast is probable. Dating of this origin is necessarily speculative, but some time in the first half of the Paleozoic seems plausible.

Fig. 5. Distribution of some Aplexinae. 1, *Austrinauta*; 2, *Amecanauta*; 3, *Mexinauta*; 4, *Caribnauta*. Heavy bar connects disjunct range of *Mexinauta*.

Fig. 6. Distribution of some Aplexinae. 1, *Mayabina*; 2, *Stenophysa marmorata*; 3, *Afrophysa*; 4, two or more genera hitherto confused as "*Aplexa marmorata*". Unnumbered solid dot, *Tropinauta*.

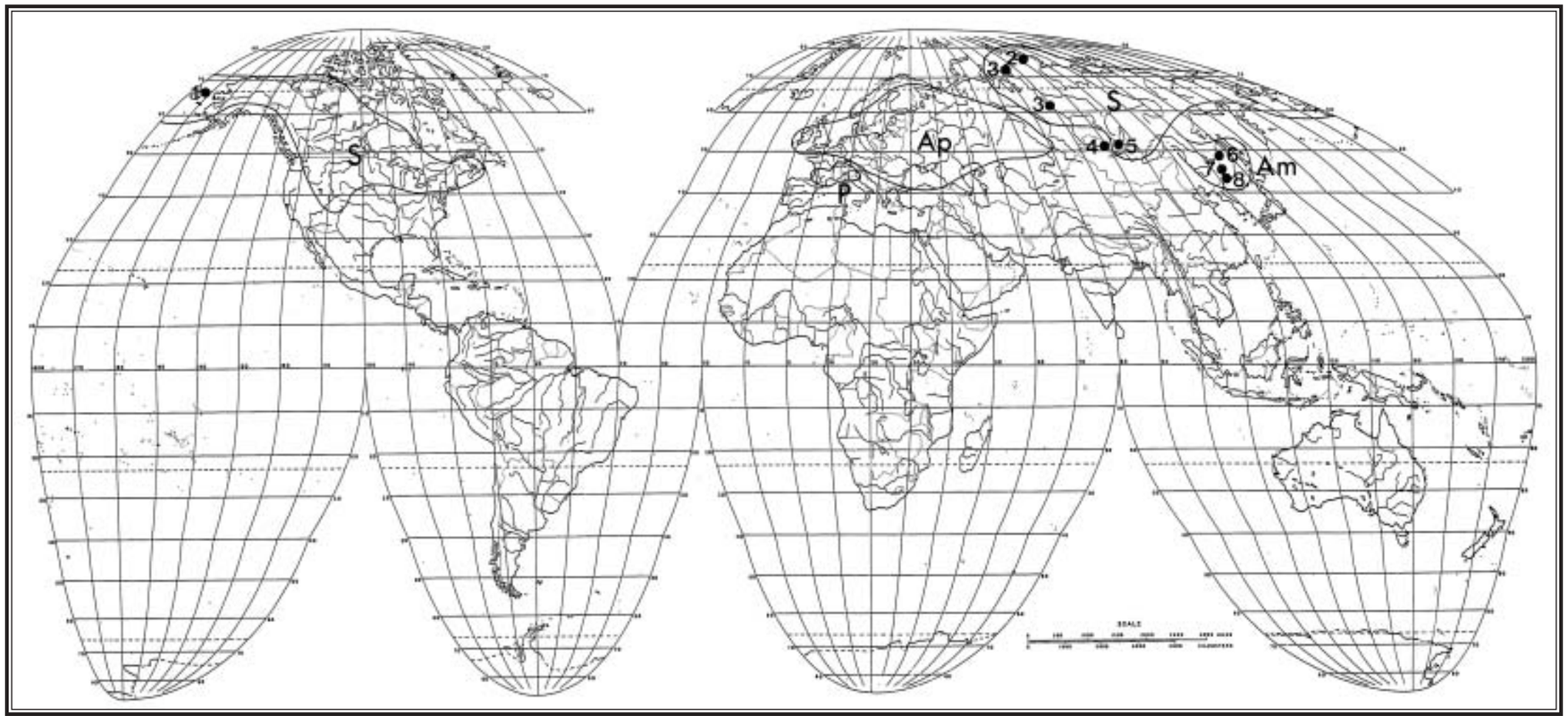


Fig. 7. Distribution of Aplexinae: Aplexini. Solid dots, type localities, shown only in Asia. 1, *Sibirenauta pictus*; 2, *depressior* and *sibiricus*; 3, *polaris*; 4, *tuwaensis*; 5, *kultukiana*; 6, *Amuraplexa amurensis*, *orientalis*; 7, *aphallica*; 8, *moskvichevae*. Am, *Amuraplexa*; Ap, *Aplexa*; P, *Paraplexa*; S, *Sibirenauta*. Ranges are given in general terms only by Starobogatov *et al.* (1989) and the Russian part of the map is not accurate in detail. The westward range of *Amuraplexa* may overlap that of *Sibirenauta*. *S. tuwaensis* does not belong to that genus.

Fig. 8. Distribution of Physinae: Haitiini, with the sole genus *Haitia*.

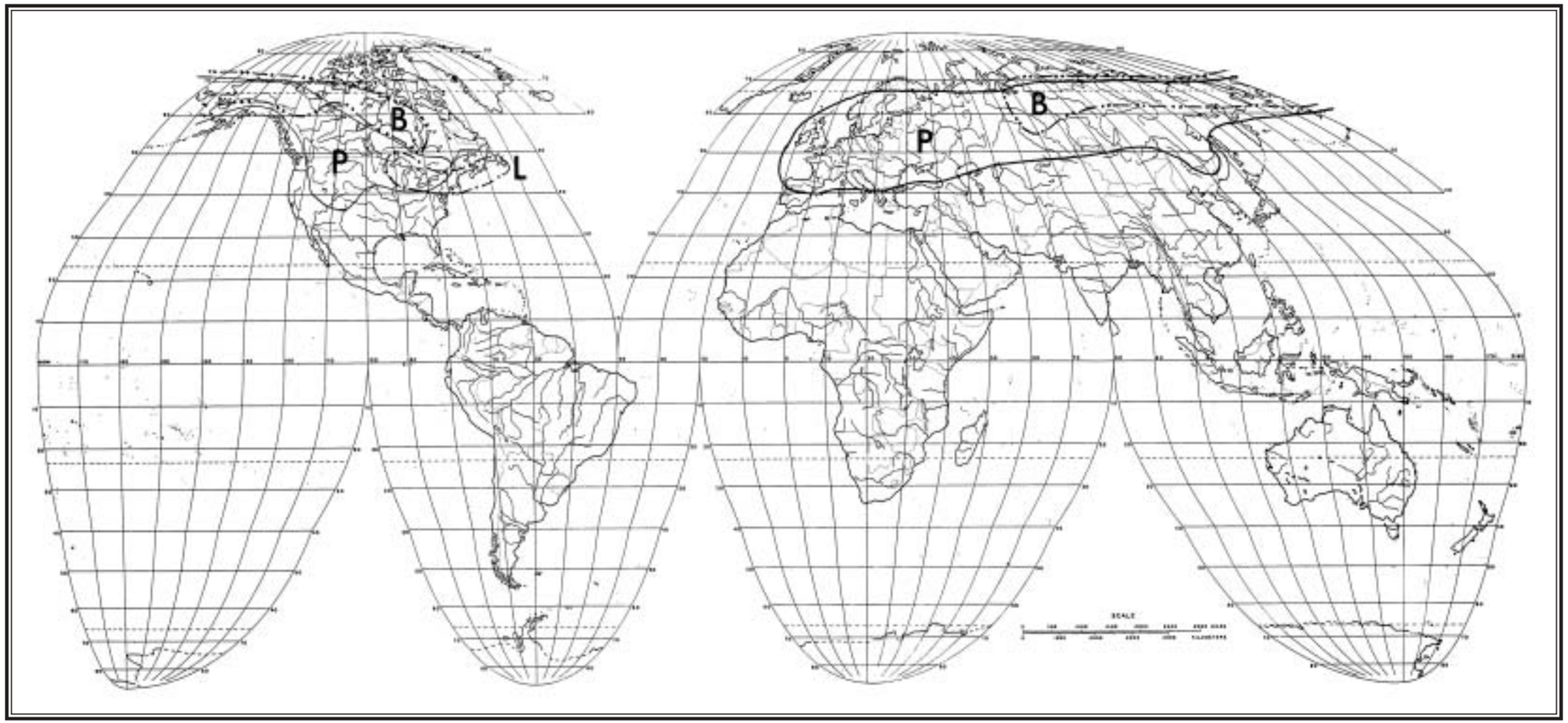


Fig. 9. Distribution of Physinae: Physini. B, *Beringophysa*; L, *Laurentiphysa*; P, *Physa*.

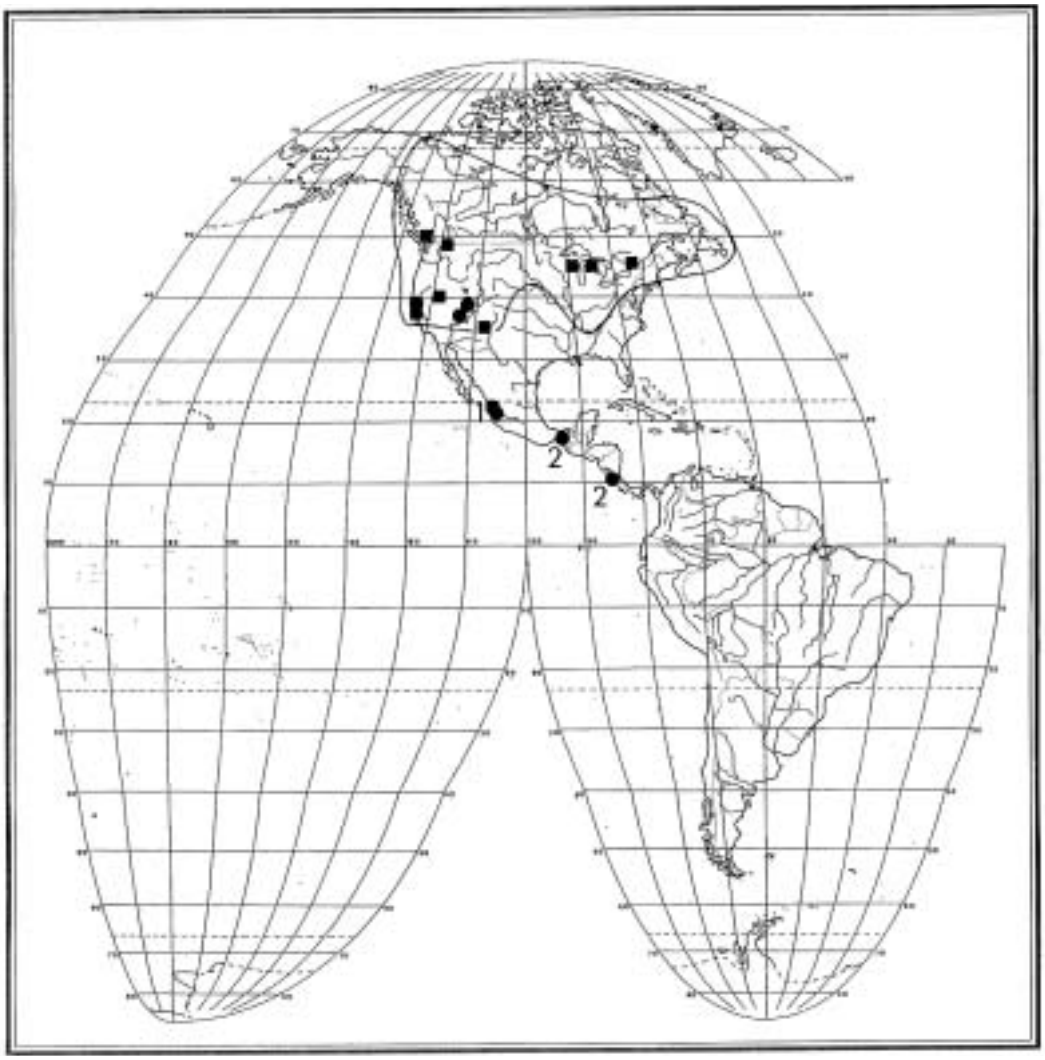


Fig. 10. Distribution of Physinae: Physellini. *Physella* enclosed within solid line. Solid squares, *Archiphysa* (for more detail see Fig.176); solid circles, three local genera *Costatella*, *Petrophysa*, and *Utahphysa* (for more detail see Fig. 11); 1, *Ultraphysella* (for more detail see Fig. 15); 2, *Chiapaphysa* (for more detail see Fig.165).

Assuming segregation of Physidae as such along the shores of the tropical eastern Pacific, one can trace the spread of several lineages accompanied by increasing specialization: Austrinautini, to the Caribbean with *Caribnauta*; Aplexini, in Eurasia with *Amuraplexa* in southeastern Siberia, *Paraplexa* in southwestern Europe, *Aplexa* in western Siberia and Europe, and *Sibirenauta* in Siberia and northern North America; Amecanautini, to the Caribbean coast, spreading north in Mexico, south to Ecuador, Peru and Chile (*Mexinauta*, *Mayabina*); Stenophysini, from the Caribbean (*Stenophysa*) to southeastern South America (*Afrophysa*); Physini, in temperate eastern North America (*Laurentiphysa*), thence to Siberia (*Beringophysa*) and as far as Europe (*Physa*); Physellini, from *Chiapaphysa* of Mexico and Costa Rica into the western United States, where three local relicts (*Petrophysa, Costatella*, *Utahphysa*), then in both western and eastern United States, *Archiphysa*, sporadic in lakes of both areas, and *Physella*, widespread in Canada and the United States, and lastly, *Ultraphysella*, of Sinaloa and Nayarit, Mexico.

These interpretations entirely neglect the fossil record. But that record is of little help in deciphering history of Physidae. Shells are inadequate guides to the genera as now limited, and some early fossils may be Bulinidae rather than Physidae. Yet one thing is clear: distribution and size-range were different in the past. The Eocene *Physa pleromatis* White (1877a), from the Rocky Mountains of the United States, attained a length of over 65 mm, the greatest size and body volume known for the family; the maximum length known for any living species is less than 40 mm. *P. copei* White (1877b), from the Upper Cretaceous Judith River Formation, Montana, reached a length of 50 mm, as did *P. lacteana* Russell (1935) of the Upper Cretaceous Milk River Formation, Alberta, Canada; *P. doeringi* Doello Jurado (1927; see Parodiz, 1969), of the Paleocene in Patagonia, Argentina, 38 mm. So late as the Pleistocene, Physidae are documented from China, although none has been reported living there: *Physa assuturalis* Wang (1995), from the Luwangfen Formation of Henan. Other fossil Physidae, unrelated to anything in their regions, include *P. bajandaica* Martinson (1956), from the upper Miocene or lower Pliocene in the vicinity of Irkutsk, Siberia; *P. efremowi* Martinson (1957), from the Upper Cretaceous of Mongolia; *P. meigsi* Dall (1890, *in* Dall, 1890-1903), from the Pliocene of Florida; and the curious *Haliotis*-like *Hannibalina dorrisensis* Hanna & Gester (1963), from the Pliocene of northern California. Most of these are probably Physinae, but precise relationships are speculative.

Modern distribution of Physidae is known imprecisely in most cases, hence no detailed review is possible. On present evidence there are no major breaks in distribution between continents.

Numbers of genera and species in major geographic areas are as follows (native occurrences only); those restricted to the given area are indicated by an asterisk (*).

	Genera	Species
North America	16 (*9)	45 (*38)
Central America	6 (*1)	19 (*13)
South America	8 (*4)	13 (*11)
West Indies	3 (*1)	5 (*4)
Europe	3 (*1)	6 (*3)
Asia	6 (*2)	12 (*7)

These numbers do not match the text precisely, because the tabulation includes some species *incertae sedis*, and genera thought to be new, but not named.

The predominance of North America (Canada, United States, Mexico) in the world fauna is evident. At the generic level Pacific drainages of North and Central America are the region of greatest diversity. The following 17 genera (of 23 in the family) occur in this region; those eight marked with an asterisk (*) are known only here.

**Amecanauta*
Archiphysa
**Austrinauta*
Beringophysa
**Chiapaphysa*
**Costatella*
Haitia
Mayabina
Mexinauta
**Petrophysa*
Physa
Physella
Sibirenauta
Stenophysa
**Tropinauta*
**Ultraphysella*
**Utahphysa*

Central America has been little explored for Physidae except in Costa Rica, hence comparisons among the various countries would be pointless. Yet it is still remarkable that this small country has eight species of Physidae (practically 10% of the world fauna) and one endemic genus. This richness in Physidae is in strong contrast to the other families of Hygrophila and indeed of all freshwater molluscs, that are absent or poorly represented in Costa Rica. Comparison is made with Brasil, a very large country of little habitat diversity and including vast regions of tannin-rich waters not habitable by Physidae, little explored, with taxonomy of Physidae poorly known; the United States (48 conterminous states), a very large country of great habitat diversity, moderately well explored, with taxonomy of Physidae moderately well known; Mexico, a large country of great habitat diversity, moderately well explored, with taxonomy of Physidae moderately well understood; and Guatemala, a small country of great habitat diversity, not well explored, with taxonomy of Physidae moderately well understood.

Country	Area (km^2)	Genera	Species	(Species/ km^2) x 10^6
Brasil	8 511 965	2 (*1)	2 (*1)	.24
U.S.	7 827 625	10 (*3)	28 (*16)	36
Mexico	1 972 546	7 (*3)	15 (*9)	76
Guatemala	108 889	3	8 (*4)	73
Costa Rica	50 900	6 (*1)	8 (*5)	157

* Restricted to the country

Costa Rican species of Physidae are as follows:
Mexinauta aurantia
*Mayabina *pliculosa*
*Mayabina *sanctijohannis*
*Mayabina *tempisquensis*
**Tropinauta *sinusdulcensis*
Stenophysa marmorata
Haitia mexicana
*Chiapaphysa *pacifica*

Discontinuities in the ranges of species are rare. A conspicuous exception is *Stenophysa marmorata*. It is found throughout the Greater Antilles except for Cuba, through the Lesser Antilles to Trinidad at least, in the western Caribbean on Providence Island, and in eastern Costa Rica (for localities and distribution map see under the species). More information is presented for this species than for others, to document its widespread occurrence in the West Indies. Convinced that identifications based on shells were unreliable (in most cases, I still am), I collected on several islands, fully expecting to find distinct species in at least the more distant localities. Yet all have proved to be the same, and also the same as that in Costa Rica. Some may appeal to the old standby, accidental transportation by birds, to account for this distribution. But Rankin & Harrison (1979) found in laboratory studies that the species is very sensitive both to desiccation, and to lack of food after only two days.

Those authors (Harrison & Rankin, 1976b), considering principally the freshwater fauna of the eastern Lesser Antilles, were firm in opposing any interpretation of adventitious transport

over the sea. Furthermore, how could this one species be so transported, but no other Aplexinae, as shown by the several local species on the mainland; and how explain its absence in Cuba and southern Florida? An alternative view is to suppose that the species is older than present geography, older than the present separation of the West Indian islands from one another, and from eastern Costa Rica. A plausible date for such a time would be in the early Tertiary at the latest, if one accepts the interpretation of extensional structure of the Caribbean (Carey, 1976, 1988). Another strong argument against accidental transportation is that the range of *S. marmorata* is by no means unique. It fills much of a standard pattern of distribution of other organisms encircling the Caribbean that Croizat (1976) called the "Antillean Ring."

Breaks in the ranges of genera are rare. Two such are shown by *Mexinauta*, found from Mexico to Costa Rica, then again from coastal Ecuador to central Peru (Fig. 5); and *Mayabina*, also Mexico to Costa Rica, reappearing mostly at moderate to high altitudes from Ecuador to Chile (Fig. 6). The gap in range may be due partly to lack of exploration in Colombia; but a similar gap is known in other organisms, so that it may well be actual. *Haitia* is found widely in North America southward to Costa Rica, then from Colombia to Chile; likewise the gap in Panama (not shown in Fig. 8) might be due to collecting failure, but has precedents in other groups.

The subfamilies Aplexinae and Physinae have generally different ranges although they overlap broadly (Figs. 5-10). The difference is marked especially in diversity of species and higher groups. Aplexinae are principally a group of the American tropics and warm-temperate zone, Physinae of the temperate and boreal Northern Hemisphere. Partly for this reason there are more species of Physinae (47) than of Aplexinae (34): greater land area within the range of Physinae has provided more opportunities for speciation.

Another factor affecting richness in species of the two groups is lacustrine endemism. No Aplexinae are lake-dwellers. By contrast, ten modern Physinae are restricted to individual lakes:

Species	Lake
Archiphysa zomos	Pyramid, Nevada
Costatella costata	Clear, California
Haitia elegans	Miragoane, Haiti
?Haitia lacustris	Coatepeque, El Salvador
Haitia patzcuarensis	Pátzcuaro, Mexico
Haitia? solidissima	Chapala, Mexico
Physa arachleica	Arakhlei, Russia
Physa mirollii	Maggiore, Italy
Physella hemphilli	Coeur D'Alene, Idaho
Utahphysa microstriata	Fish, Utah

Evolution of these localized species has been restricted to young lakes with low diversity of molluscs and low endemism. There are no endemic Physidae in such rich, old lakes as Baikal and Ohrid, for example.

Other local Physidae too are found in habitats where there are few or no other localized molluscs. Extreme instances are *Haitia spelunca* in Lower Kane Cave, Wyoming, and *Petrophysa zionis* on steep rock faces in Zion National Park, Utah (Fig. 11). These and others less extreme are as follows:

CANADA:	
British Columbia:	*Archiphysa lordi*
Quebec:	*Archiphysa latchfordi*
UNITED STATES:	
California:	*Archiphysa sonomae*
Idaho:	*Haitia natricina*
Michigan:	*Archiphysa parkeri*
New Mexico:	*Archiphysa ashmuni*
Tennessee:	*Physella globosa*
Utah:	*Petrophysa zionis*
Washington/Oregon:	*Physella columbiana*
Wisconsin:	*Archiphysa laphami*
	Laurentiphysa chippevarum
Wyoming:	*Haitia spelunca*
MEXICO	
Chiapas:	*Chiapaphysa grijalvae*
Jalisco:	*Amecanauta jaliscoensis*
Nayarit:	*Austrinauta elatus*

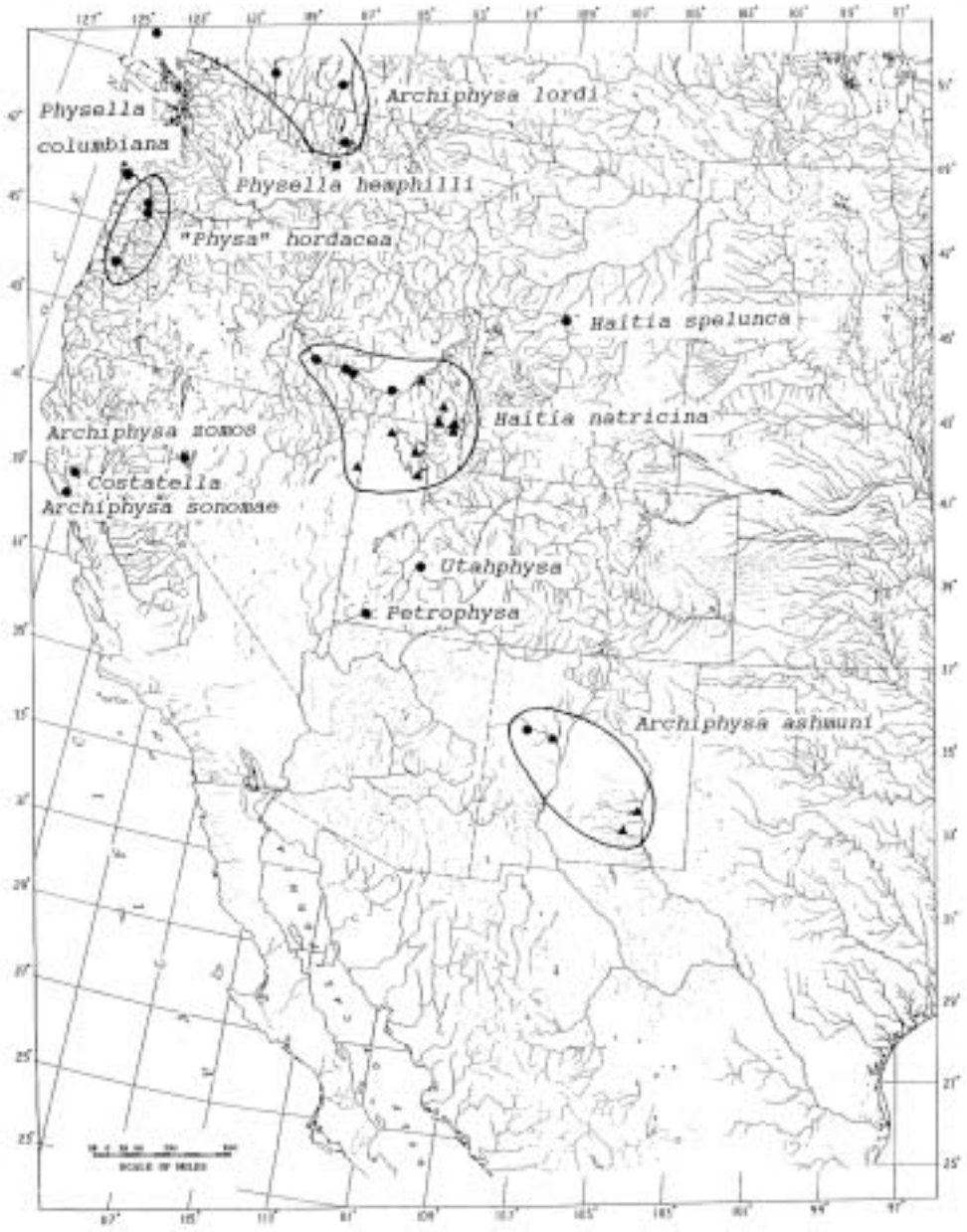


Fig. 11. Distribution of local Physidae in western United States.

Sinaloa/Nayarit:	*Ultraphysella sinaloae*
Veracruz:	*Mayabina bullula*
Yucatan Peninsula:	*Mayabina polita*
	Mayabina spiculata
	Mexinauta princeps
GUATEMALA:	*Haitia moreleti*
	Mayabina petenensis
	Mexinauta gracilentus
	Mexinauta laetus
HONDURAS:	*Mayabina nitidula*
	Mayabina obtusa
NICARAGUA:	*Mexinauta nicaraguanus*
COSTA RICA:	*Chiapaphysa pacifica*
	Mayabina pliculosa
	Mayabina sanctijohannis
	Mayabina tempisquensis
	Tropinauta sinusdulcensis
WEST INDIES:	*Caribnauta harryi*
VENEZUELA:	*"Aplexa" simoni*
	"Aplexa" venezuelensis
ECUADOR/PERU:	*Mexinauta peruvianus*
CHILE:	*Haitia porteri*

Physidae have been analyzed biogeographically (Fig. 12) according to methods developed by Craw *et al.* (1999), that are in turn refinements of those used by Croizat (1958 and later). The state of knowledge of the family is hazy over some large areas (especially Russia) with respect to both taxonomy and distribution, and greater precision will be possible in future. The graph shows distribution in only a crude way (for more details see Figs. 5-10), but instead emphasizes the lineages of the tribes and location of the most advanced genus in each. It was constructed as follows (numbers correspond to those in Fig. 4):

Aplexinae are rooted to Austrinautini (4), overlapping with *Haitia* (5), most primitive of the Physinae, on the Pacific coast of western Mexico (large circle). This is then, by this method, the root home of Physidae as a whole.

Austrinautini consist of the primitive *Austrinauta* (40) and the more advanced *Caribnauta* (39). A track links the two; *Caribnauta* has a terminal, 1º vertex, that is, a vertex with a single link, indicated by the larger symbol.

Aplexini include the more primitive genus *Amuraplexa* (18) and three more advanced genera. The center of diversity of *Paraplexa* (26, one species) is in southern France; of *Aplexa* (38), also with one species, in the region of eastern Europe. The most advanced genus, *Sibirenauta* (37), has a vaguely located center of diversity "somewhere" in Siberia, marked by a terminal, 1º, vertex. Certainly there are more species here than the two in North America, but morphology, distribution and taxonomy are a hazy blur. The track leads back from *Sibirenauta* to *Aplexa*, then *Paraplexa* and *Amuraplexa*, and across the Pacific to the root of Aplexinae (1). This track is the only one with a Pacific Ocean baseline.

Amecanautini are rooted in *Amecanauta* (16), and the track leads on to *Tropinauta* (23), most advanced of the tribe.

Stenophysa (34) has one species that fills most of the Antillean Ring around the Caribbean, and another presumed to be native in northeastern South America; the vertex of greatest diversity is located at a poorly determined intermediate site. *Afrophysa* (33), relatively advanced, is known only in southern Brasil. A "name uncertain" group (21) is more distinct than either of the other Stenophysini, and further information is necessary to evaluate its status. Tentatively it receives a 1º vertex and larger symbol.

Haitiini include the widespread genus *Haitia* (5), more diverse on the mainland of North America as far south as Guatemala than elsewhere. No center of diversity is shown, only its overlap with *Austrinauta* (large circle).

Physini are a northern group. The most primitive, *Laurentiphysa* (27), has its center of diversity in northern Wisconsin where the ranges of the two species approach one another. The next advance is *Beringophysa* (41), with a single species widespread on both sides of the Bering Straits; its center of diversity is accordingly placed on these straits. The most advanced genus, *Physa* (42), has a center of diversity located vaguely in Siberia like that of *Sibirenauta* and for the same reasons.

Physellini include seven genera, more than any other tribe. The group is rooted in

Chiapaphysa (13), known by one species in southern Mexico and another in Costa Rica– the latter not shown for cartographic convenience. The lineage proceeds to a group of three monotypic genera, *Utahphysa* (30), *Petrophysa* (43) and *Costatella* (44), then to *Archiphysa* (31) and *Physella* (45), at last returning to Mexico with *Ultraphysella* (46).

As further exploration of biogeographic method, a map was prepared for three local genera of Physellini (Fig. 13), including fossil occurrences. It illustrates how addition of fossils changes a map based on modern distribution only. The map was drawn first for the living species of the three monotypic genera *Costatella, Petrophysa* and *Utahphysa*; C and U are 1º vertices. Adding fossil occurrences (all *Costatella*, C) reduces the modern occurrence of C from a 1º vertex to 3º. The long track C-P would disappear, and P and U are linked to the eastern end of the C-track. The combined map shows that the track of C is from central California to the northern Great Basin, whereas P and U are from just outside the Great Basin, on its eastern margin. Despite the closer geographic occurrence of *Petrophysa* and *Utahphysa* to one another, they are not morphologically more similar to one another than to *Costatella*. Indeed, in the character of mantle projections the vestigial projections of *Petrophysa* relate it to the more distant *Costatella* rather than to the nearer *Utahphysa*.

Most Physidae are of only local distribution. This is demonstrated by plotting species according to occurrence in 1º x 1º quadrangles (Table 3, Fig. 14). Restriction of the data to species found in fewer than 22 quadrangles is imposed by limitations of knowledge. The number of species (55) includes some that are *incertae sedis* but thought to be valid. More precision would be attained by use of quadrangles of equal area, because those based on latitude and longitude shrink with higher latitude. The present knowledge of species distributions is so scanty, however, that 1º quadrangles are adequate for rough generalization.

Many species cannot be assigned to 1º quadrangles throughout their range because of inadequate information. Some are probably localized in only a few quadrangles, but do not have even a precise type locality. All widespread species are omitted. A few occur in well over 100 or even 200 quadrangles, but distribution is known only in general and published identifications are unreliable. Four species are restricted to lakes divided by quadrangle borders: *Archiphysa zomos* in Pyramid Lake, Nevada; *Costatella costata* in Clear Lake, California; *Haitia? solidissima* in Laguna Chapala, Mexico; and *Physa mirollii* in Lago Maggiore, Italy. These are assigned to two quadrangles even though their lakes would fit within a single quadrangle, thus the predominance of single-quadrangle species is reduced.

A few species are moderately widespread, but sporadic, and so occur in few quadrangles. The graph is thus different from a classification based on distance between known localities.

Even if increased knowledge permitted inclusion of more species, including those that are widespread, the shape of the graph would not change its general asymptotic form, skewed strongly to the left. It shows a real aspect of distribution of the species: most are of limited range. Accordingly, more species of Physidae are threatened by habitat destruction than those of other families of Hygrophila with generally wider specific ranges.

MORPHOLOGY

Only parts of the body are considered in this paper, principally the reproductive system and mantle. For general morphology see various manuals on the fauna of a given country or state.

Mantle

All Physidae have a mantle more or less reflected over the shell, except in the northern genera *Aplexa* and *Sibirenauta*. Usually the mantle has two lobes, one on the right over the columellar-parietal area, and the other left-posterior, at the posterior angle of the aperture. Along the margin both lobes have projections in the form of broad or narrow triangles, acute or

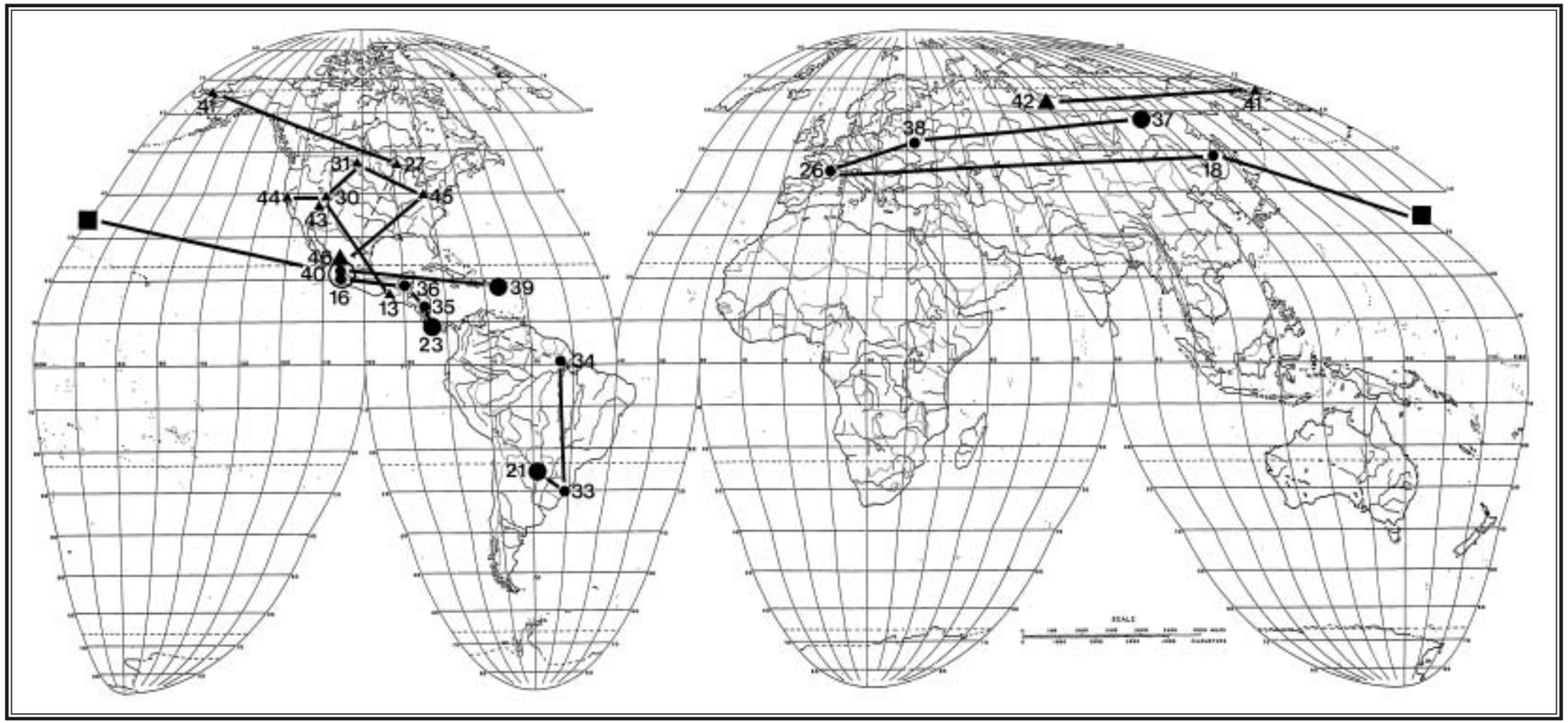


Fig. 12. Biogeographic analysis of Physidae. Tracks are oriented by phylogeny (Fig. 4), with larger symbols at terminus of the inferred lineage, *i.e.*, the genus interpreted as most advanced; numbers correspond to genera in that figure. Methodology from Craw *et al.* (1999). Solid dots, Aplexinae; triangles, Physinae; square, baseline of Aplexini.

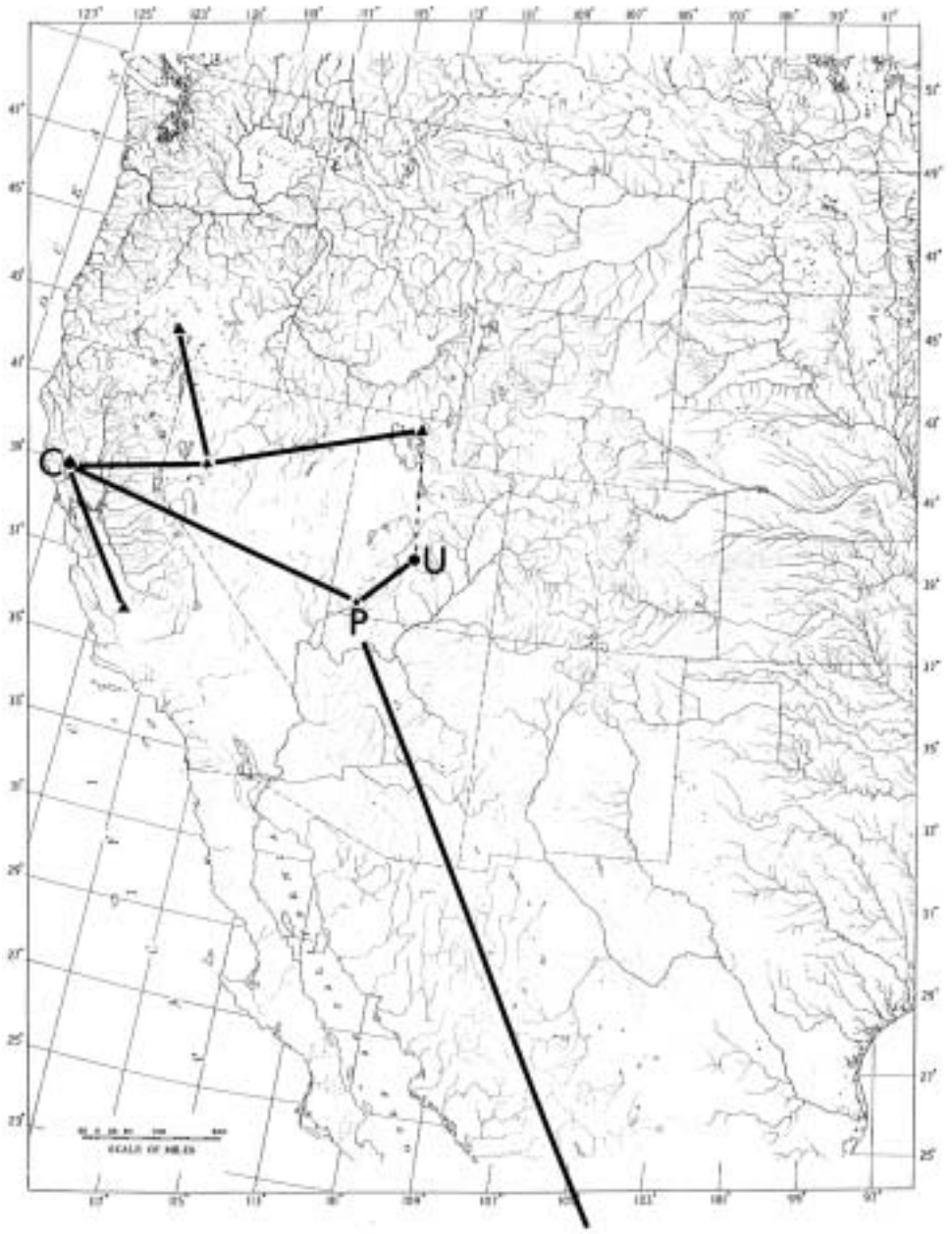


Fig. 13. Distribution of three local genera of Physellini.: C, *Costatella* (solid dot, modern; triangles, fossil); P, *Petrophysa*; U, *Utahphysa*. Tracks between the three are unoriented: there are no criteria for stating one genus is more primitive/advanced than another, nor for the species of *Costatella*.Unlabeled track leading off map is to *Chiapaphysa* (Mexico in Chiapas, and in Costa Rica), most primitive of Physellini and much like the presumed common ancestor of the three genera mapped. In principle, another member of the series of genera might be found near the Pacific Ocean/ Gulf of Mexico drainage divide in northwestern Mexico. Distribution of fossil *Costatella* from Taylor & Smith (1981). See text for fuller explanation.

TABLE 3
Physidae allocated to 1ºx1º quadrangles

Quadrangles (number of species)		Species
1	(25)	*Afrophysa brasiliensis*
		Amecanauta jaliscoensis
		"Aplexa" simoni
		"Aplexa" venezuelensis
		Archiphysa ahmuni
		Archiphysa latchfordi
		Archiphysa sonomae
		Austrinauta elatus
		Haitia elegans
		Haitia lacustris
		Haitia moreleti
		Haitia porteri
		Haitia patzcuarensis
		Haitia spelunca
		Mayabina sanctijohannis
		Mayabina tempisquensis
		Mexinauta gracilentus
		Mexinauta nicaraguanus
		Petrophysa zionis
		Physa arachleica
		Physella columbiana
		Physella globosa
		Physella hemphilli
		Tropinauta sinusdulcensis
		Utahphysa microstriata
2	(12)	*Archiphysa parkeri*
		Archiphysa zomos
		Caribnauta harryi
		Chiapaphysa grijalvae
		Chiapaphysa pacifica
		Costatella costata
		Haitia? solidissima
		Laurentiphysa chippevarum
		Mayabina bullula
		"Physa" hordacea
		Physa mirollii
		"Sibirenauta" tuwaensis
3	(4)	*Haitia natricina*
		Mayabina petenensis
		Mexinauta aurantia
		Mexinauta peruvianus
4	(3)	*Archiphysa lordi*
		Mayabina tapanensis
		Ultraphysella sinaloae
5	(2)	*Mayabina pliculosa*
		Mexinauta impluviatus
6	(2)	*Archiphysa laphami*
		Mayabina carolita
7	(2)	*Mayabina spiculata*
		Mexinauta princeps
8	(1)	*Mexinauta nitens*
11	(2)	*Mayabina polita*
		Physa megalochlamys
12	(1)	*Haitia venustula*
21	(1)	*Laurentiphysa vernalis*

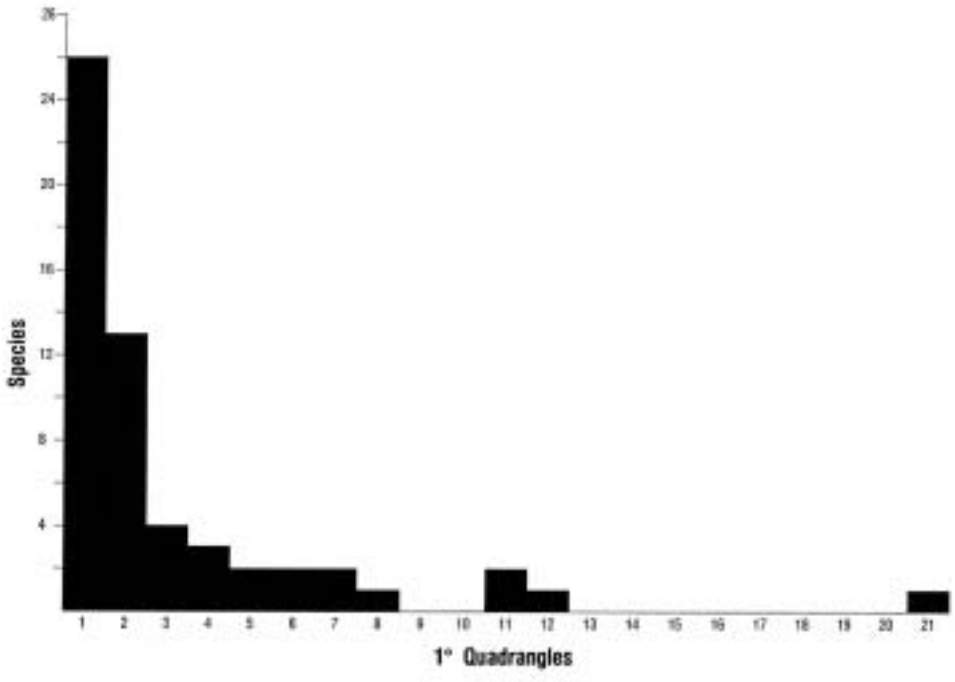


Fig. 14. Distribution of species of Physidae by 1º quadrangles.

rounded; or broad, rounded scallops. The posterior lobe may be distinct on the left side, or may be united with the anterior border of the mantle with no separation. Rarely the mantle has no projections, and is reflected over the shell with a smooth margin.

Reproductive System

The reproductive system of Physidae (shown diagrammatically in Fig. 3) is divided into three parts, *hermaphroditic, male, and female.*

The *hermaphroditic* portion begins with the *ovotestis* (OT), embedded in the columellar aspect of the digestive gland in the spire. Its numerous follicles discharge ova and spermatozoa into a *common collecting canal* (CC), that leads into a tube, the *hermaphroditic duct* (DH), with simple or compound outpocketings, the *seminal vesicles* (VS) on both sides. At its end the hermaphroditic duct divides into male and female gonoducts. Close to this division, there may be a ventral pore, whose constancy of occurrence remains to be studied.

The *male* portion is a long duct, the *vas deferens* (VD), that leads spermatozoa to the male gonopore and on which are various accessory structures. Its first part, *vas deferens I* (VD I), leads to the *prostate gland* (G PROS), an elongate-ovoid organ whose numerous follicles discharge the prostatic secretion directly into the *prostatic vas deferens*. Beyond the prostate gland, *vas deferens II* (VD II) courses within the body cavity next to the terminal part of oviduct III and the vagina, and then enters the body wall as *vas deferens III* (VD III). This runs as a nearly straight tube to a site behind the male pore (junction of body wall and terminal end of preputium), where it leaves the wall to enter the body cavity again. Here begins *vas deferens IV* (VD IV) at an angle, the *paragonoporal angle* (APG), that is a useful point of reference. Structures anterior to vas deferens IV form the *penial complex*. Vas deferens IV leads to the *penial sheath* (SP), formed of one or two sacs. In either case there may be a *glandular* part (SPG) and another *muscular* part (SPM). Within the sheath lies the *penis* (PEN). The terminal part of

the male system is the *preputium* (PREP), a sleeve with muscular but flaccid walls and, only in the subfamily Physinae, a gland, the *preputial gland* (G PREP). The *male pore* lies close behind the left post-tentacular flap. Within the preputium at the end of the sheath is a structure usually of hemispherical to conical form, the *sarcobelum* (SAR), forming the tip of the preputium during copulation, when the preputium is everted from the body. In copulation the animal opens the male pore by relaxation of the circular muscles, the swollen preputium is extruded from the body cavity by the action of its muscles and hydrostatic pressure, and the penis is extruded from the penial sheath and enters the vagina. After copulation, penial sheath and preputium are withdrawn into the body cavity by the action of two groups of retractor muscles. The *penial retractor muscles*, usually two, are the *proximal retractor muscle* (MRSP) that is inserted on the proximal end of the sheath, and the *distal retractor muscle* (MRSD), inserted on the distal end of the sheath. These two retractor muscle bands, sometimes with cross-connections, lead from the columellar muscle immediately below the female pore; of the two, the distal retractor is the wider. Less often a single *common retractor* of the sheath (MRS) leaves the columellar muscle and divides into proximal and distal retractor muscles. In previous works there are different terminologies for orientation of the penial complex. In this work the structures are considered in relation to the apex of the body and not to an external observer. Thus the preputium is the most *distal* structure of the penial complex, not the most proximal. The *retractor muscles of the preputium* are considered in relation to orientation of the body; thus the muscles that draw the preputium toward the head are *protractors* (MP), and those that draw it toward the rear are *retractors* (MR). These muscles of the preputium tie it to the body wall. One could consider also both groups as retractors, because they aid in withdrawing the preputium within the body after extrusion. A *connective of the penial sheath and preputium* (MCPS) has a band that leads to the ganglionic complex; this band carries the penial innervation; and in those forms with a long penial sheath, the connective brings the proximal end of the sheath closer to the preputium.

The *female* part of the reproductive system is shorter than the male part, and is contained within the upper part of the body. From the hermaphroditic duct arises a tube that receives the products of various accessory structures that provide the fertilized eggs with different nutritive fluids and protective layers for development of the embryo. The first is the *albumen gland* (GA), through which runs the *female duct* (DF) receiving directly the secretions of the gland, that is, the gland has no separate duct. Secretion from the albumen gland is "the fluid with which the embryo is surrounded and constitutes its only food supply until hatching" (Duncan, 1958:77). From the wall of the female duct arise one or two small blind sacs, the *caeca* (singular, *caecum*) (C), and then shortly begins *oviduct I* (OD I), discharging into *oviduct II* (OD II), a many-lobed sac where the internal and external membranes around each embryo are secreted. *Oviduct III* (OD III) forms the greater part of the oviduct; it is a canal with a series of large pouches arising along one side, where the mucous mass in which the egg capsules are embedded is secreted, as well as the wall of the spawn mass. These pouches diminish gradually, and the oviduct then receives the *duct* of the *bursa copulatrix* (DBC). The thickness of the *pallium gelatinosum* around the spawn mass is such that it cannot be secreted in that form within OD III. Bondesen (1950:126) suggested that it absorbs water after deposition of the spawn mass. The *vagina* is the common duct between the junction of oviduct III and bursal duct, and the *female pore*; usually it is not a discrete structure. This definition of vagina is to permit measurement or comparison of length to other structures, but a histological definition would be more useful from the standpoint of function. The female pore lies on the left side of the body, on the body stalk. Only in *Sibirenauta* is the pore located on a discrete structure, an external papilla. The *bursa copulatrix* (BC) is a thin-walled sac that receives spermatozoa from the partner.

OUTLINE OF CHARACTERS

The characters that have been found useful in Physidae are mentioned below, with examples of their presence or variation in various genera. More detailed study would surely reveal additional characters.

Shell

(see Plates)

Form

Generally ovoid to elongate ovoid, but ranging from turriform (*Sibirenauta*) to globose (*Petrophysa*). The body whorl flares into a wing-like expansion in *Haitia elegans*.

Texture

Dull to polished. The shell is more often dull in Physinae, more often polished in Aplexinae, but with exceptions in both groups.

Sculpture

Macrosculpture is rare, except for axial growth lines. Prominent ribs occur uniquely in *Costatella*. Microsculpture is usually present; it is formed by spirally aligned series of short, straight or crescentic wrinkles, convex in the direction of growth.

Color and pattern

Hue is generally a uniform pale yellow-brown to brown, but in some species of *Mexinauta* it is deep red-brown. White streaks in axial or spiral arrangement are present in the calcareous part of the shell in *Sibirenauta*, and these white streaks together with numerous spiral color bands occur in *Mexinauta*. Color bands are conspicuous only in *Mexinauta*, present but inconspicuous in *Stenophysa*. These white streaks and color bands are like those in the related family Lancidae, and the color bands recall those in the marine Siphonariidae.

Apex

Nearly always acute. *Physa* is unique in having a broadly rounded apex, and *Laurentiphysa* and *Beringophysa* in having an obtuse apex. *Sibirenauta* has a bulbous apex.

Parietal callus

The parietal callus is applied as a thin calcareous layer over part of the body whorl in correlation with extent of the mantle. In species with a broadly reflected mantle there is usually a broad parietal callus, and in those with little or no reflection of the mantle there is a narrow callus. Within a given genus there may be considerable variation in extent of reflection of the mantle (for example, *Physa*), and the extent of the parietal callus is of no more than specific value.

Periostracal callus

Uniquely in *Austrinauta* there is a periostracal callus in addition to the usual parietal callus. A thin layer of periostracum is applied over the parietal callus and part of the body whorl, adding a glossy texture to that part of the shell.

Columellar fold

A single, simple fold is present in most species but may be absent in those with a relatively straight columella.

Mantle

Reflection

In *Aplexa* and *Sibirenauta*, perhaps also in *Amuraplexa* and *Paraplexa*, the mantle is not reflected over the shell. In most Physinae the only reflection of the mantle is by two small lobes with projections, on the columellar-parietal surface and next to the posterior end of the aperture. In many Aplexinae and in *Utahphysa* and a few species of *Physa*, the mantle may be reflected extensively over the shell on the right side and over the anterior and outer lip. Rarely, in some specimens of a few species (*Austrinauta elatus, Physa megalochlamys*), the mantle may even cover the whole shell.

Lobes

A posterior lobe of the mantle may be discrete on the left side, or fused with the anterior mantle with no evident separation. It may lie entirely on the left, or may overlap the shell broadly on either side of the spire.

Margin

The mantle margin is simple and without projections only in *Aplexa* (and perhaps *Amuraplexa* and *Paraplexa*), *Austrinauta*, *Sibirenauta*, *Tropinauta*, and *Utahphysa*. In other genera there are projections in the form of scallops or triangles; their general shape (scallops, broad or narrow triangles) is ordinarily consistent within species. Scallops are found only in Aplexinae, triangles in both Aplexinae and Physinae. Most commonly the projections are restricted to two lobes of the mantle, columellar-parietal on the right side, and left posterior at the posterior end of the aperture. Number of mantle projections is not characteristic of a given species. Variation of this character has been studied by F. C. Baker (1898-1902) in several North American species, and especially by Pelseneer (1920) in the European *Physa fontinalis*.

Pigmentation

A concentration of melanin is commonly present as a diffuse-edged spot in the mantle projections of Aplexinae.

External body

The foot is a long, narrow triangle in outline in nearly all species, but broad with a posterior rounded end in *Petrophysa*. The tip may be acuminate in *Stenophysa*.

Color pattern

The head and foot are usually of uniform tone with no pattern. In *Stenophysa* a median posterior stripe in the last quarter of the foot may be present, and the head bears a characteristic pattern of spots and blotches of melanin.

In *Haitia natricina* the tentacles have melanin pigment as a core in the distal half, in contrast to the nearly unpigmented body. The usual tapered, sharply pointed tentacles are reduced to short, wide, blunt stubs in *Petrophysa*.

Hermaphroditic duct

Seminal vesicles along the duct vary in size and spacing. They may be shorter than the width of the duct, or longer; simple or bilobed or even trilobed; widely spaced or crowded; and uniform along the duct, or smaller or even absent along its distal and proximal portions.

Male reproductive system

Prostatic vas deferens

This segment of the vas is usually straight, but in *Sibirenauta* it is folded transversely.

Prostatic follicles

These may be longer or shorter, branched or unbranched, arranged along the vas deferens in a single row, or in multiples; and may be widely spaced or densely crowded.

Prostatic chamber

This structure, unique to *Sibirenauta*, is a capacious enlargement of the vas at the proximal end of the prostate.

Vas deferens IV

Relative length of this segment of the vas varies greatly, in correlation with length of the penial sheath and whether the sheath is flexed or not. In *Laurentiphysa* and *Petrophysa* there is a short VD IV and a bulky, flexed penial sheath. In *Sibirenauta elongatus* there is a long but unflexed penial sheath, and an exceptionally long VD IV. This section of the vas may or may not bear melanin flecks.

Penial sheath

Length relative to preputium: The sheath may be markedly shorter than the preputium, as in *Austrinauta*, or several times longer.

Form: Unitary (a single sac) as in *Austrinauta*, *Haitia* and *Physa*, to clearly bipartite (two sacs) as in Physellini, and tripartite in *Sibirenauta* and *Afrophysa*; flexed and appressed against preputium (*Tropinauta*), or unflexed.

Composition: Entirely muscular (*Austrinauta*, *Caribnauta*, *Haitia*) to entirely glandular (*Physa*), with much variation in relative proportion of intermediate states. The sheath may be glandular in the proximal part only

(*Beringophysa, Laurentiphysa*) or distal part only (Physellini).

Pigmentation: Black melanin flecks may be present or absent. No granules of another color have been observed.

Penis

Form: Obviously tapered from a broad proximal end to distal tip (*Haitia, Austrinauta*); flagelliform with simple tip (*Chiapaphysa, Mexinauta*); tubular (*Aplexa, Sibirenauta*); with terminal stylet (*Physa, Beringophysa*); or even with a broad, spatulate distal end in *Stenophysa spathidophallus*. In *Afrophysa* the penis is tripartite, with a sac-like initial part, central shaft, and a distal swollen, asymmetrical tip. Uniquely in *Paraplexa* there is a narrow head, broader body, and narrow tip, so that the form as a whole is spindle-shaped.

Composition: A specialized tip of the penis may have no differentiation in tissue, or there may be a cuticular tip (*Physa*).

Pore of penial canal: The pore is at the tip of the penis in all genera except Stenophysini (*Stenophysa* and *Afrophysa*), in which it is lateral.

Preputium

This structure is a distensible and contractile sleeve, variable according to the state of preservation. In the retracted state it contains two internal pilasters; these disappear when the preputium is everted.

Form: Uniquely in *Tropinauta* the proximal third is bent sharply at right angles, and appressed to the penial sheath.

Preputial gland: The gland when present is on the central posterior face of the preputium. It is diagnostic of Physinae, present in all species except *Physa mirollii* of Italy, with little variation. Size of the gland is notably large in *Petrophysa*.

Sarcobelum: The tubular penial sheath meets the tubular preputium by entering it, and the conical or hemispherical structure within the proximal end of the preputium is the sarcobelum. A papilla may be present on the tip of the sarcobelum, or lacking.

Musculature: Uniquely in *Tropinauta* there is a muscle band from the columellar muscle to the preputium, in addition to the two retractors of the penial sheath. Again uniquely, in *Amecanauta* there is a band from the distal retractor to the preputium.

Pigmentation: The preputium is the most heavily pigmented part of the penial complex. It may have a dusting of melanin even when other parts of the complex lack pigmentation.

Penial retractor muscles

A common state is two independent retractor bands from the columellar muscle: a wider band to the distal end of the penial sheath, the distal retractor; and a narrower band to the proximal end of the penial sheath, the proximal retractor. Variation is principally in whether origins of the bands are separate or not, whether cross-connections are present, and in number and location of insertions.

Origin: The retractor bands may originate as a single band that splits in two at a variable distance from the origin, or as two bands with independent but adjacent origin.

Insertions: The common state is one insertion of each retractor muscle, on the proximal and distal ends of the sheath. There is consistently an insertion on the proximal end of the sheath, but number and location of other insertions vary.

Two insertions of the proximal retractor are found in *Amecanauta*. One insertion is on the proximal end of the sheath, the other on the distal portion, close to insertion of the distal retractor muscle.

Insertion of the distal retractor may be shifted away from the preputium onto a bulky terminal portion of the penial sheath, as in *Caribnauta, Laurentiphysa* and *Petrophysa*. In *Amecanauta* the distal portion of the distal retractor also gives origin to retractor muscles of the preputium.

Cross-connections: There is a muscle band connecting the proximal and distal retractor muscles in *Austrinauta, Tropinauta,* and (inconsistently) in *Sibirenauta*.

Pigmentation: Melanin flecks on the muscle bands may be present or absent.

A connective between the penial sheath and preputium may be present. It originates on the proximal end of the sheath and is inserted on the distal part of the preputium; this muscle band holds the end of the sheath close to the preputium, and bears also the penial nerve.

Female reproductive system

Female pore

In *Sibirenauta* the pore is situated on a discrete papilla; in other groups there is no such papilla.

Junction of bursal duct, oviduct, and vagina

Commonly the bursal duct and oviduct are simple tubes that meet at a low angle, then join to continue as the vagina. Some genera have unique variations, as follows. In *Tropinauta* the bursal duct joins a large swelling on the end of the oviduct. In *Sibirenauta* the two ducts meet at approximately 180º, and from their junction proceeds the vagina in the form of a discrete narrow tube, narrower than either bursal duct or oviduct. In *Stenophysa* the oviduct joins the bursal duct at about 60º, and only the bursal duct leads straight into the vagina. *Afrophysa* has an exceptionally narrow bursal duct that joins a terminal swelling of the oviduct. In *Archiphysa* the bursal duct is stout and muscular; its junction with both bursa and oviduct is clearly set off.

Bursa copulatrix

The bursa is usually a spherical, ovoid, or elongate sac, variably distinct from its duct. In *Archiphysa* the duct leaves the medial aspect of the bursa, instead of the anterior margin as in all other genera. The duct may be a uniform tube throughout its length, or may leave the bursa as a wider structure not clearly set off, and then become narrower. In nearly all genera it is a flaccid, thin-walled tube, but in *Archiphysa* stout and muscular.

Spawn

Spawn capsules provide a large number of characters. These include form and degree of curvature of the mass; the prominence and location of wisps at the ends; the thickness of the various layers; the number of eggs and their arrangement within the capsule; and the membranes surrounding the egg. Particularly striking is the pallium gelatinosum in *Sibirenauta*, not a uniform layer as in all other genera studied, but with a lengthwise greatly thickened band. The spawn mass ranges from a narrow, irregular elongate mass with no regular coil in *Mexinauta* through the spiral coil of *Mayabina* to the short, elongate capsule of *Aplexa*. Uniquely in *Sibirenauta* the spawn may not be in one plane, but coiled so that the posterior end overrides the anterior.

KEY TO GENERA

1. Preputium without a gland. Subfamily Aplexinae 2
1'. Preputium with a posterior gland. Subfamily Physinae 13
2. Penial sheath entirely muscular. Tribe Austrinautini 3
2'. Penial sheath with glandular tissue 4
3. Penial sheath a simple muscular tube little more than half length of preputium; western Mexico . . . . . *Austrinauta*
3'. Penial sheath nearly as long as preputium, with a large terminal bulb in distal third; Puerto Rico . . . . . *Caribnauta*
4. Opening of penial canal at distal end of penis 5
4'. Opening of penial canal lateral, not at distal end of penis. Tribe Stenophysini 12
5. Penial sheath bipartite, with both muscular and glandular parts. Tribe Amecanautini 6
5'. Penial sheath unipartite and entirely glandular; or if bipartite or tripartite, with a stout tubular penis bearing a narrow conical introvert set off from the shaft by annular ornament. Tribe Aplexini 9
6. Penis slender, obviously tapered; glandular part of penial sheath about twice as wide as muscular part and half as long; western Mexico . . . . . *Amecanauta*
6'. Penis flagelliform 7
7. Glandular part of penial sheath flexed 180º; preputium flexed 90º; glandular part of penial sheath about 3 times as wide as muscular part and half as long; Costa Rica . . . . . *Tropinauta*

7'. Neither penial sheath nor preputium flexed; glandular part of penial sheath only 1.5 - 2 times as wide as muscular part 8
8. Glandular part of penial sheath about 1.5 times as wide as muscular part, and no more than 1/4 as long; mantle projections are broadly rounded scallops; penial retractor muscles with independent origins; Mexico to northern Peru . . . . . .*Mexinauta*
8'. Glandular part of penial sheath about twice as wide as muscular part and half as long; mantle projections triangular; penial retractor muscles originate as single band; Mexico to northernmost Chile . . . . . .*Mayabina*
9. Penis tapered to simple tip; far eastern Russia . . . . . .*Amuraplexa*
9'. Penis spindle-shaped, or with tubular shaft 10
10. Penis spindle-shaped, with narrow but not conical tip; western Switzerland, southern France and adjacent Spain . . . . . .*Paraplexa*
10'. Penis with tubular shaft, set off from narrow conical introvert by annular swelling 11
11. Penial sheath unipartite, glandular; conical introvert set off from shaft by annular swelling; Europe and western Siberia . . . . . .*Aplexa*
11'. Penial sheath bipartite or tripartite; conical introvert set off from shaft by annular rings or constrictions; penial sheath bipartite or tripartite, not wholly glandular; Siberia and northern North America . . . . . .*Sibirenauta*
12. Muscular part of penial sheath a slender tube; exit of penial canal at about 60% of length of penis; penis distal to penial canal with enlarged, specialized tip; Costa Rica, West Indies and northern South America . . . . . .*Stenophysa*
12'. Muscular part of penial sheath bipartite, with proximal thin-walled part and distal thick-walled part; exit of penial canal at about 90% of length of penis, on an enlarged specialized tip; Rio Grande do Sul, Brasil . . . . . .*Afrophysa*
13. Penial sheath entirely muscular. Tribe Haitiini. North America and West Indies to Peru and Chile; widely introduced on other continents . . . . . .*Haitia*
13'. Penial sheath at least partly glandular 14
14. Proximal part of penial sheath glandular. Tribe Physini 15
14'. Distal part of penial sheath glandular, sharply set off from proximal muscular part. Tribe Physellini 17
15. Penis flagellar, with simple tip; Great Lakes region of North America east to Atlantic coast . . . . . .*Laurentiphysa*
15'. Penis flagellar, with terminal stylet 16
16. Penial stylet ovoid; penial sheath glandular in proximal part only; Siberia and northern North America . . . . . .*Beringophysa*
16'. Penial stylet narrow, elongate; nearly all of penial sheath glandular; Eurasia and North America . . . . . .*Physa*
17. Mantle margin with triangular projections in two groups, columellar-parietal and at posterior end of aperture .19
17'. Mantle margin smooth, penis obviously tapered 18
18. Mantle broadly reflected over medium-sized shell on both sides; Fish Lake, Utah . . . . . .*Utahphysa*
18'. Mantle not reflected over tiny shell; Zion Canyon, Utah . . . . . .*Petrophysa*
19. Distal glandular part of sheath $^1/_3$ or less of length of penial sheath; Chiapas, Mexico, and Costa Rica . . . . . .*Chiapaphysa*
19'. Distal glandular part of sheath $^1/_2$ or more of length of penial sheath 20
20. Shell ribbed; penis obviously tapered; Clear Lake, California . . . . . .*Costatella*
20'. Shell not ribbed; penis slender but not obviously tapered 21
21. Penis with simple, tapered tip 22
21'. Tip of penis narrowed; penial canal expanded within; western Mexico . . . . . .*Ultraphysella*
22. Shell obovoid, medium sized to large; duct of bursa leaves bursa on medial aspect; North America . .*Archiphysa*
22'. Shell ovoid to elongate, small to medium-sized; duct of bursa leaves bursa at anterior end; North America . . . . . .*Physella*

SYSTEMATICS

Sinistral coiling, pointed foot, and slender tentacles distinguish all Physidae readily, and the group has been understood in its present scope for many years. Haldeman (1842-45) is the nomenclatural author of Physidae (as Physadae), although earlier group names had been proposed (Physoidea Fitzinger, 1833; Physina Gray, in Turton, 1840). The family was then heterogeneous by present standards, and Dall (1870) still included some Bulinidae in his concept of Physidae. Fischer & Crosse (1870-1902, 2:82 [1886]) explicitly separated Physidae from Bulininae of the Planorbidae, and Physidae reached the modern concept of the group. Harry & Hubendick (1964) distinguished Physidae as a superfamily Physacea, adding new characters.

Among many earlier studies a few papers are noteworthy. Müller (1781) published one of the first monographs of a mollusc species, illustrating the mantle projections in *Physa fontinalis*. North American species of Physidae were described and illustrated by Haldeman (1842-1845); his illustrations remain among the best ever published for the family. The monograph of the French fauna by Moquin-Tandon (1855) is illustrated in the beautiful fashion so characteristic of French works of that period, and describes and illustrates the shell, external morphology, reproductive system, jaw and spawn, giving also observations on behavior, eclosion, and habitat.

The two conchological monographs of Physidae, by Küster & Clessin (1841-1886) and by Sowerby (1873-1874), added species names, but contributed nothing to an understanding of the group, like all other shell-based studies, whether modern or ancient.

Modern morphological study began with description by Slugocka (1913) of the reproductive systems of the three species of Switzerland, including histological sections as well as gross morphology. Her conclusion (p. 104) that the penis is a well defined organ with characteristic shape in each species has not been appreciated sufficiently. The most careful morphological description of a species of Physidae thus far is by Paraense (1986), whose work deserves emulation.

The first author to subdivide Physidae above the level of genus was Starobogatov (1967), who characterized a subfamily Aplexinae. Hitherto there have been no subdivisions between the rank of subfamily and genus.

In the present work groups have been defined principally by unique combinations of characters of the penial complex and its retractor muscles (Fig. 3, terminology of reproductive system). A consequence of this definition is that several are monotypic, but others have few or many species. This is an aspect of differentiation in the family. Within Physidae there is no group with numerous species such as *Gyraulus* or *Biomphalaria* (Planorbidae), or *Bulinus* (Bulinidae), even though these genera too are defined narrowly by morphological characters.

Some nominal species cannot be allocated to one of the genera described herein without morphological study; others listed as synonyms may prove to be valid. With allowance for species yet to be discovered, the number of modern species in the family is estimated at 90-100. This total is half the estimate of 200 by Boss (1971), but double the 48 of Te (1980). The number of genera is likely to increase from the 23 named herein to about 30.

The shell rarely has characters permitting identification to genus, hence practically no fossil species can be allocated in the present classification. The exceptions are three Pliocene species of *Costatella*, distinguished by their ribbed shells.

In the accounts of species, specimens studied or verified morphologically are marked (**M**). For samples I collected, usually no collector is cited, only date and catalog number (for example, T88-1204).

Family **PHYSIDAE** Fischer & Crosse, 1886

Body and shell have an evident spire, low or high, consistently coiled to the left. The

shell is usually thin, in a few genera with a color pattern of spiral bands. Tentacles are rod-like, with the eyes at their inner bases. The foot tapers to an acute hind end.

Male and female tracts are completely separate. The male gonopore lies just behind the left post-tentacular flap, the female pore on the left side of the body stalk just within the mantle cavity. From the ovotestis the hermaphroditic duct leads to the pont of separation of the male and female tracts next to the albumen gland; along the duct are numerous seminal vesicles. Along the male tract within the body cavity is the prostate, consisting of a mass of follicles discharging directly into the vas deferens; there is great variation in size and number of follicles, but never a common envelope. Within the cavity of the head-foot is the penial complex, in simplest form a penial sheath and penis that join the extrusible preputium. Relative size and glandular development of the sheath are greatly variable, and the penis may display terminal specializations.

Along the female tract are the various structures that provide nutrient and covering for the fertilized eggs: albumen gland and swollen portions of the oviduct, OD I, OD II, OD III; none of these structures has a separate duct. A bursa copulatrix is connected by its duct to OD III, close to the terminal end of that structure and shortly within the female pore.

Spawn is a gelatinous capsule with a slimy coating, the pallium gelatinosum, over the capsular wall. The capsule is coiled to the right at least slightly, except when it contains few eggs; in extreme cases the coil exceeds 360º. Individual egg capsules are surrounded by both an internal and external membrane. Only rarely are egg-strings and capsular strings present.

The radula has rows of teeth in chevron-like arrangement. The central tooth has a mesocone and several smaller ectocones. Lateral and marginal teeth total over a hundred on each side of the central, all with a broad lateral flange, and all diminishing in size toward the sides of the radular ribbon. Cusps on the lateral and marginal teeth are dagger-like blades, with smaller cusps intercalated between larger ones.

PHYSIDAE, Species *Incertae Sedis*

The following names cannot be allocated to a particular subfamily; some may even apply to Bulinidae.

bernardii "Récluz" Paetel, 1889; no locality. *Nomen nudum.*

crassula Dillwyn, 1817; "Inhabits Virginia. *Lister*. West Indies. *Chemnitz*." Not recognizable.

foeniculum Rigacci & Rigacci, 1866; no locality. *Nomen nudum*.

mascotica Rigacci & Rigacci, 1866; no locality. *Nomen nudum*.

minima "Frey." Rigacci & Rigacci, 1866; no locality. *Nomen nudum*.

oblonga Potiez & Michaud, 1838; "Hab...?" Not recognizable.

vitrea "Frey." Rigacci & Rigacci, 1866; no locality. *Nomen nudum*.

Subfamily **APLEXINAE** Starobogatov, 1967

Starobogatov, 1967:289; as subfamily for *Aplexa*, *Stenophysa*, and *Sibirenauta*.

Preputium without a gland (the only trenchant character). In general the shell has a steeper, more shallow suture than in Physinae, and is more highly polished.

Twelve genera, allocated to four tribes: Austrinautini, with *Austrinauta* and *Caribnauta*; Aplexini, with *Amuraplexa*, *Paraplexa*, *Aplexa* and *Sibirenauta*; Amecanautini, with *Amecanauta*, *Mexinauta*, *Mayabina*, and *Tropinauta*; and Stenophysini, with *Stenophysa* and *Afrophysa*. Most of these are found in the tropical or warm-temperate areas of the Americas, but Aplexini are restricted to temperate and arctic Eurasia and northern North America.

APLEXINAE, Species *Incertae Sedis*

abbreviata Beck, 1838. Substitute for *Physa rivalis, var.* as recorded from Argentina by d'Orbigny, near the Río Batel [not traced], Prov. Corrientes; and in Patagonia, not far from the Río Negro [locality doubtful].

antonii Küster, 1844; TL "Peru."

>*peruviensis* "Mühlfeldt" Anton, 1838, *nomen nudum*; TL "Peru."

aspii Holmberg, 1909; TL Laguna de los Murciélagos, Prov. Formosa, Argentina.

chilensis Clessin, 1886; TL "Chile," but locality probably wrong.

cornea Preston, 1907; TL Mérida [8º36'N, 71º08'W], Mérida, Venezuela.

hartwigi "Dunker" Paetel, 1889, *nomen nudum*. "Parana" [Río Paraná, Argentina - Brasil - Paraguay; or the city of Paraná, Prov. Entre Ríos, Argentina].

loosii Holmberg, 1909; TL ciénaga at the foot of Sierra Pie de Palo, Prov. San Juan, Argentina.

rivalis var. minor d'Orbigny, 1837; TL restricted here to the locality described by d'Orbigny as "la source de la petite rivière voisine du Cerro, dans la baie de Montevideo," Uruguay, identified by Formica Corsi (1900-1901) as Arroyo Pantanoso.

panamensis "Megerle von Mühlfeldt" Anton, 1838, *nomen nudum*; TL "Panama."

panamensis "Mühlfeldt" Küster, 1844; TL "Panama."

rivalis Potiez & Michaud, 1838; TL Lima [12º03'S, 77º03'W], Prov. Lima, Peru.

tuwaensis Starobogatov & Zatravkin, 1989; TL Toora-Khem [52º28'N, 96º09'E], Tuvinsk Autonomous Region, Russia.

venezuelensis Martens, 1860; TL Lagunilla near Mérida [probably Lagunillas, 8º30'N, 71º26'W], Mérida, Venezuela.

purpurostoma var. ventricosa Tate, 1870, *nomen nudum*; TL San Nicolás, in the drainage of Lake Nicaragua, Nicaragua [locality not traced, probably in Depto. Chontales].

Tribe **AUSTRINAUTINI**, new tribe

Mantle reflected over outer lip of shell in a narrow band, or broadly, so as to cover nearly all the shell. Mantle margin smooth; or there may be triangular projections in two groups, columellar-parietal on the right, and left posterior. Penial sheath entirely muscular. Penis tapered to a simple tip with terminal pore.

Two genera, both monotypic: *Austrinauta g.n.*, in northwestern Mexico (Nayarit); and *Caribnauta g.n.*, in the West Indies (Puerto Rico).

Austrinauta g.n.

Type species: *Physa elata* Gould, 1853, Nayarit, Mexico.

Name: Latin *australis*, southern, and *Nauta* (masculine, a sailor), a synonym of *Aplexa*; *i.e.*, the southern *Aplexa*.

Diagnosis: Shell narrowly ovoid to fusiform, attaining a length of 25 mm with 6 whorls. Surface silky to polished, with sculpture of fine growth lines and spiral series of minute arcs. A thin periostracal layer applied as a secondary callus on the ventral surface of the shell adjacent to the calcareous parietal callus, giving the surface a luster. Profile of aperture broadly convex in direction of growth; anterior end rounded. Parietal callus narrow, apex acute. Inconspicuous color bands and white streaks in the shell commonly present.

Mantle reflected extensively over the shell on both sides, covering all but 1/3 to 1/4 whorl, margin smooth.

Penial complex: Preputium (PREP) without a gland, and more than twice as long as penial sheath. Penial sheath (SP) unitary, muscular, slightly wider at the proximal end, and tapered slightly. Penis (PEN) shorter than its sheath, and tapered conspicuously from a wider proximal end to a simple blunt tip with terminal pore but no thickening. A web of muscle fibers (MS) around the distal end of the penial sheath gives the appearance that the sheath is enlarged, but in fact it narrows within the

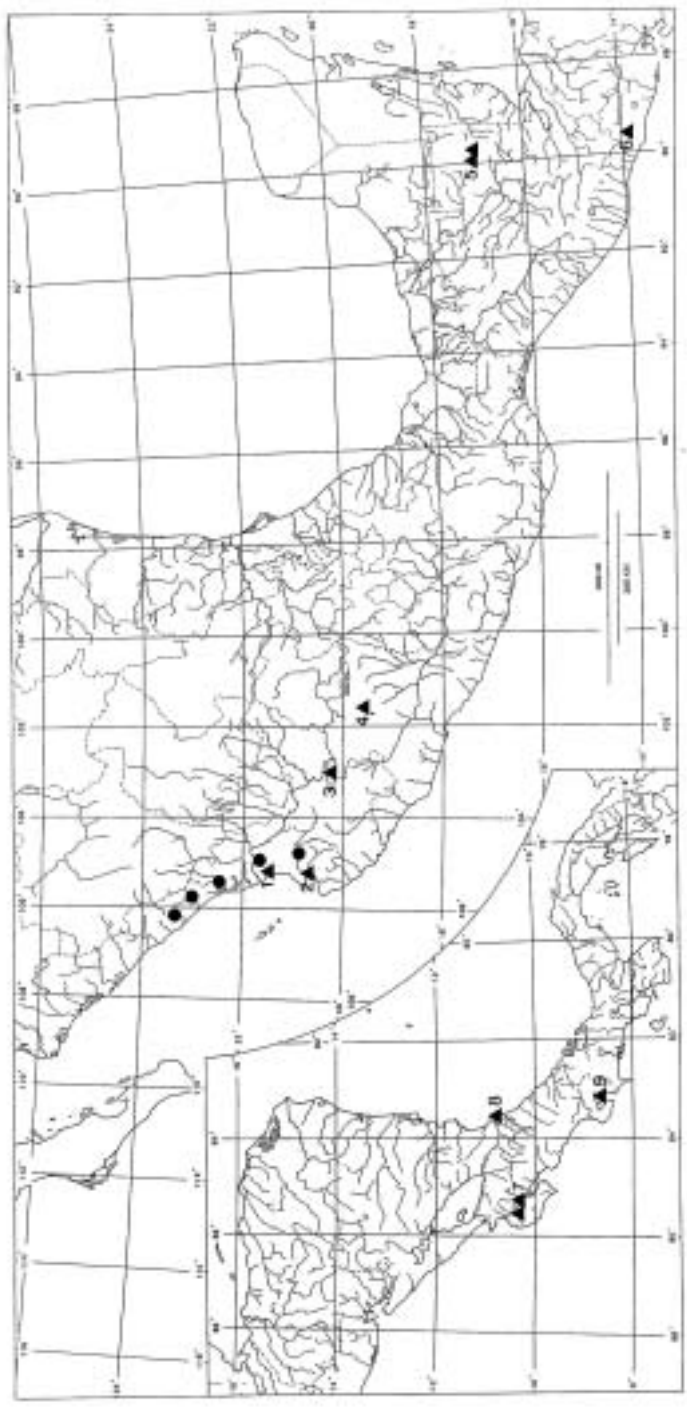


Fig. 15. Distribution of some local Physidae in Mexico and Central America, and of *Ultraphysella*. Numbered triangles: 1, *Austrinauta elatus*; 2, *Amecanauta jaliscoensis*; 3, *?Haitia solidissima*; 4, *H. patzcuarensis*; 5, *H. moreleti*; 6, *H. lacustris*; 7, *Mayabina tempisquensis*; 8, *M. sanctijohannis*; 9, *Tropinauta sinusdulcensis.* Solid circles: *Ultraphysella sinaloae.*

proximal end of the preputium, where it is bound to a thick-walled, short sarcobelum (SAR) with conical papilla. Vas deferens (VD) between paragonoporal angle (APG) and penial sheath shorter than preputium.

Two principal retractor bands, with a cross-connection, run separately from the columellar muscle to the penial complex. The wider distal retractor (MRSD) is inserted on the muscular sheath that surrounds the distal end of the sheath, with fibers running also onto the preputium. The narrower band, the proximal retractor (MRSP), gives off a band to the distal retractor, and is inserted on the proximal end of the penial sheath.

Female system: Bursa copulatrix (BC) an elongate sac, widest at its proximal end; bursal duct (DBC) a stout tube, about three-fourths as long as bursa, from which it is slightly set off. Vagina (V) short and wide, even wider than long, consisting of a short continuation of bursal duct and oviduct III; W/L vagina about 1.4.

Distribution: The one species is found on the Pacific coast of northwestern Mexico in Nayarit state, perhaps also in Sinaloa (Fig. 15).

Comparisons: *Austrinauta* is distinct in having an entirely smooth mantle margin, and a mantle broadly reflected over the shell, even covering it almost entirely. It has a short, muscular penial sheath that is a simple tube about half the length of the preputium, the smallest relative size known in the family. The periostracal callus of the shell is a character unknown in other Physidae.

Austrinauta elatus (Gould, 1853)

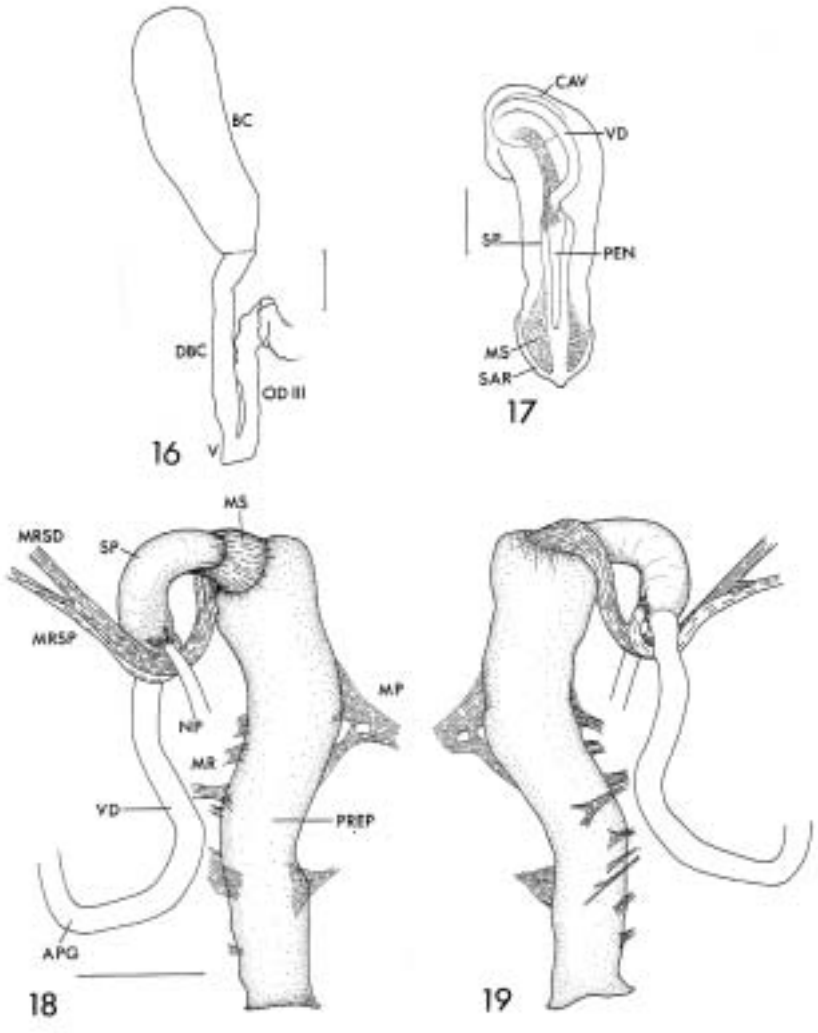
Figs. 16-19, Pl. 1, fig. 1. Distribution Map, Fig. 5

Physa elata Gould, 1853:379, pl. 14, fig. 4; TL Lower California, *Major Rich* [surely a locality error].
Bulinus elatus Gould: H. & A. Adams, 1858, 2:259.
Aplexa elata Gould: Carpenter, 1857b:180; Mazatlán, Sinaloa, *Frederick Reigen*.
Aplecta elata Gould: Fischer & Crosse, 1870-1902, 2:92, pl. 32, fig. 2.
Aplexus elatus Gould: Paetel, 1888-1890, 2:409.
Stenophysa elata (Gould): Starobogatov, 1970:259; endemic species of East [sic!] Mexican Province.

Lectotype (Johnson, 1964:71, pl. 44, fig. 9) MCZ 169 130; 2 lectoparatypes MCZ 169 131; 2 lectoparatypes USNM 56 414; *Major William Rich*.

Name: Latin *elatus*, high, tall.

Description: The shell is narrowly ovoid to fusiform, with an acute spire and broadly rounded anterior end. The profile of the aperture is broadly convex in the direction of growth, but not regularly curved; it is commonly almost plane in the middle, and markedly retractive to the suture. The columella is heavy, white to pale lavender, with a weak fold. The parietal callus is a thin wash, continuous between the ends of the aperture, broadly expanded adjacent to the columella. The spire whorls are weakly convex, separated by an indistinct or distinct but shallow suture. The lateral profile of the spire is weakly concave to weakly convex. The shell surface is polished and shining to silky. A thin layer of periostracum overlies the ventral aspect of the body whorl, from the edge of the parietal callus for as much as one-eighth to one-quarter whorl, applying a polish over the otherwise silky or less shining surface. Shell color is pale brown to medium brown, with a narrow pale band at the suture, and a broader dark brown or reddish-brown band immediately below. Numerous other narrow, inconspicuous spiral color bands with diffuse edges are present. Irregular white streaks may occur in spiral or axial arrangement, either as fine lines or aggregates of streaks forming broad bands; these are usually inconspicuous. Surface sculpture consists of fine axial growth lines and coarser wrinkles. Spiral sculpture consists of minute wrinkles either straight or weakly convex in the direction of growth that are arranged in spiral series. These may be more abundant on the posterior part of the whorl.



Figs. 16-19. *Austrinauta elatus*, p. 45. Mexico, Nayarit: south end of Matanchén Beach. 16, distal part of female system; 17, penial complex, extruded, seen in transparency; 18-19, medial (18) and lateral (19) views of one specimen. APG, paragonoporal angle; BC, bursa copulatrix; CAV, edge of body cavity; DBC, duct of bursa copulatrix; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRSD, distal retractor muscle of penial complex; MRSP, proximal retractor muscle of penial complex; MS, muscular sheath; NP, penial nerve; OD III, terminal portion of oviduct; PEN, penis; PREP, preputium; SAR, sarcobelum; SP, penial sheath; V, vagina; VD, vas deferens. Scale 1 mm.

TABLE 4
Measurements and descriptive statistics of shells of Austrinauta elatus *from Matanchén Beach, Nayarit, Mexico (T71-1801). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	20.47	15.58	.761	10.50	.513	5.36
Range	17.9-25.3	13.5-19.6	.71-.80	9.3-13.1	.48-.53	5-6
S. D.	1.56	1.36	.021	.810	.014	
S. E.	.285	.248	.004	.148	.003	

Living specimens have a lanceolate foot that extends behind the shell apex. Body color is jet black in most specimens, a few very dark gray. The mantle envelops the shell broadly on both sides, and covers the ventral tip of the spire but rarely a part of the dorsal tip. At the extreme only a narrow dorsal strip of the shell is visible; more commonly about 1/3 to 1/4 whorl is exposed. The mantle edge is smooth, with no trace of scallops.

Variation: Incidence of white streaks and lines is the most conspicuous variable. Pale color bands are inconspicuous and diffuse, hence difficult to count; there may be 20-40 within the aperture.

Localities and material examined: MEXICO, Nayarit: Freshwater marsh beside Matanchén-Santa Cruz road, at south end of Playa Matanchén, 21º29.6'N, 105º11.7'W, 25-I-1971 (T71-1801)(**M**).

Sinaloa: "Mazatlán" (MCZ 4 673, 45 324, and three sets uncataloged; MCZ 4 387, labeled only "Mexico," agrees in texture and preservation).

Habitat: The one sample came from a pond fed by a small stream; *Austrinauta* was in marginal pools and lateral channels among grasses, dead wood, and some *Typha*, but not in the main pond. The only other mollusc found was *Gundlachia radiata* (Guilding).

Remarks: The MCZ collection includes six lots that are surely or probably from the Reigen collection. Five are labeled "Mazatlan;" of these, three lots have the printed label used in distribution of the Reigen collection, and one other has the initials "P.P.C." (P. P. Carpenter). Texture and preservation of all these specimens are so similar that they probably came from the original Reigen sample. Three specimens of four in MCZ 4 387 retain the original shell texture and show the periostracal callus diagnostic of the species. Most specimens are bleached and dirty as if from a dried marsh or ditch. All these sets agree with the lectotype and lectoparatypes localized as "Lower California," where of Physidae only *Haitia mexicana* has ever been found subsequently. I think it likely that Major Rich obtained his specimens from Reigen at Mazatlan.

The periostracal callus is a character not seen in any other Physidae. It is an instance of a repeated phenomenon in the family: a structure or organ in a given species or genus displays unique features, whereas the same structure is nearly uniform in all others. This callus permits identification of the sample from Nayarit with the type series.

Caribnauta g.n.

Type species: *Caribnauta harryi nom.nov.*; West Indies in Puerto Rico, and probably formerly on St. Croix.

Name: Caribbean Sea, and Latin *Nauta* (masculine, a sailor), a synonym of *Aplexa*; *i.e.*, the Caribbean *Aplexa*.

Diagnosis: Shell ovoid-fusiform, polished, with no evident sculpture except growth lines. Profile of aperture weakly convex in direction of growth. Parietal callus narrow, apex acute. Length to 14 mm. Shell without color bands or white streaks.

Mantle narrowly reflected over outer lip of the shell and columellar-parietal region. Margin with narrow triangular projections in two groups, columellar-parietal (C) and left posterior (P); C 3, P 3.

Penial complex: Penial sheath muscular, thin and slender in proximal two-thirds, tapered distally to a massive terminal bulb more than twice as wide as head of penial sheath; sheath about 1.5 times length of preputium; W/L sarcobelum about 1.2. Penis slender, tapered to simple tip with terminal pore.

Penial retractor muscles inserted on proximal ends of penial sheath and of preputium.

Distribution: West Indies, in Puerto Rico; Virgin Islands, but identified by shells only, and records need substantiation (Fig. 5).

Comparisons: *Caribnauta* is distinguished especially by the large terminal bulb of the penial sheath. The mantle is reflected

only narrowly over the outer lip of the shell. Its margin is unlike nearly all Aplexinae by having two groups of narrow, triangular, projections, as in Physinae.

Remarks: No preserved material has been available for study; the preceding diagnosis is based principally on information from Harry & Hubendick (1964).

From Puerto Rico, Richards (1964) described as "*Aplexa marmorata*" a mixture of *Stenophysa marmorata* and *Caribnauta*. "*Aplexa*, small variety" is partly *Caribnauta* as shown by the narrow reflection of the mantle over the shell and its short, narrow projections (Richards, 1964, figs. 4-6). The spawn mass (Richards, 1964, fig. 18) is sharply distinct from that of the other species (*Stenophysa marmorata* in the present work) that he included in "*Aplexa marmorata*."

Caribnauta harryi nom.nov.

Fig. 20, Pl. 1, fig. 2. Distribution Map, Fig. 5

Physa marmorata Guilding [misidentified]: Harry & Hubendick, 1964:13, figs. 9, 11, 13, 16, 24, 72, 110.
Aplexa, small variety: Richards, 1964:1025, figs. 4-6, 18.

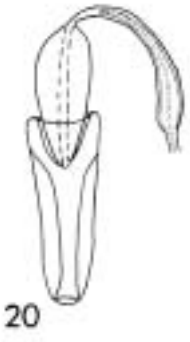


Fig. 20. *Caribnauta harryi*. Penial complex, copied from Harry & Hubendick (1964).

Holotype: The shell figured by Harry & Hubendick (1964, fig. 72) from a stream west of Las Piedras, Municipio Las Piedras, Puerto Rico, length 15.0 mm, width 8.4 mm. Thinking that the holotype may still be in the Göteborgs Museum, Göteborg, Sweden, I wrote to the museum for information. No reply was received. Paratypes might be in the Houston Museum of Natural Science, Houston, Texas, where Harry's collection is deposited. I wrote to the museum asking for loan of the relevant specimens, but received the reply that other duties prevented the curator from aiding me.

Name: For Harold W. Harry (1921-1995).

Localities and material examined: The following material in MCZ collections, all dry shells, is likely to represent *Caribnauta harryi*, but without morphological support a definite reference is not possible. I visited St. Croix in May, 1996, for the purpose of collecting the species, but could find no native living molluscs. Recent hurricanes had devastated the island, and it is questionable how much of the fauna has survived.

ST. CROIX: Hogensborg [17º42'41"N, 64º50'50"W], *H.A. Beatty*. Canaan stream, Concordia, *H.A. Beatty*. Fairplain [not traced], *H.A. Beatty*. Crique stream [not traced], *H.A. Beatty*. Crique stream, below dam, *H.A. Beatty*. Jealousy stream [not traced], *H.A. Beatty*. Two Friends [17º44'55"N, 64º49'55"W], *H.A. Beatty*. Caledonia [Caledonia Valley is 17º45'57"N, 64º52'54"W], *H.A. Beatty*. Williams [Williams Delight is 17º42'07"N, 64º50'09"W], *H.A. Beatty*. Estate New Works [not traced], *R.M. Bond*, IV-1954. St. Georges [not traced], *H.A. Beatty*. La Grange [17º43'16"N, 64º52'44"W], *H.A. Beatty*.

ST. THOMAS: No precise locality, *H.A. Beatty*.

GUANA ISLAND: No precise locality, *G.T. Dewey* (MCZ 110 134, one specimen, collected as weathered, empty shell).

Some of the series of probable *Caribnauta* were mixed lots including also *Haitia cubensis*, but no *Stenophysa marmorata*. Thus it is likely that *Caribnauta* and *Stenophysa* occur in different habitats and have different distributions in the islands where both occur.

Remarks: Morphological information demonstrates that in Puerto Rico there are two genera of Aplexinae, rather than only one as previous authors supposed. The two are difficult to distinguish by shell, but are widely different in mantle, reproductive system, and spawn. Review of MCZ collections (dry shells only) revealed no *Caribnauta* in most of the West Indies, and none among the material recorded by Clench (1936, 1939).

Description of both the new species and genus is based on the descriptions and figures of the authors cited. In fact, none of them understood what they were studying. Harry & Hubendick (1964) described the present species, but identified it as *Stenophysa marmorata* (in current nomenclature). In view of the great differences between the two species, it seems that they investigated very few samples. Richards (1964), with ample materials, recognized two "varieties" of *S. marmorata*. Again, considering the differences between the two, it seems that he investigated morphology of only the larger "variety," that is, the true *Stenophysa marmorata*.

Tribe **APLEXINI**, new tribe

Penial sheath unitary to bipartite or tripartite. Penis tapered, tubular or spindle-shaped, with terminal pore. Penial retractor muscles inserted on ends of penial sheath.

Four genera, all monotypic except *Sibirenauta*: *Amuraplexa* Starobogatov, Prozorova & Zatravkin, 1989, eastern Siberia; *Paraplexa* Starobogatov, 1989, southwestern Europe; *Aplexa* Fleming, 1820, northern and central Europe and western Siberia; and *Sibirenauta* Starobogatov & Streletskaya, 1967, Siberia and northern North America.

Both *Aplexa* and *Sibirenauta* have a tubular penis with narrow, conical tip set off from the penial shaft. The two are so similar in this respect that their many differences in size, form, and composition of penial sheath are interpreted as of secondary value. Both are unlike *Paraplexa* in the shape and terminal end of the penis, hence one supposes that *Paraplexa* represents an independent lineage from *Amuraplexa*.

Amuraplexa Starobogatov, Prozorova & Zatravkin, 1989

Starobogatov *et al*., 1989:64; type species (by original designation): *Aplexa (Amuraplexa) amurensis* Starobogatov & Prozorova, 1989, Maritime Region of Russia. As subgenus of *Aplexa*.

Name: Amur River, and *Aplexa*.

Diagnosis: This group and its nominal species, like all others proposed in the work cited, were described with insufficient detail. As described, the shell is like that of *Aplexa*. The penial sheath is unitary; its composition was not mentioned, but may be glandular, judging by its large size relative to the penis. Penis tapered to a simple tip. Sarcobelum bearing a papilla.

Distribution: Far eastern Russia, in drainages of the Amur and Ussuri (Fig. 7); surely in China, in the basin of L. Khanka on the Manchurian-Russian border, although there are no records of any living Physidae in China.

Comparisons: *Amuraplexa* is distinct by the simple, tapered penis, and form of sarcobelum. Detailed relationships are uncertain in

the absence of an adequate description, but it seems that *Amuraplexa*, with simple penial tip, is at Grade II and thus less advanced than the other genera of the tribe.

Referred species:

Amuraplexa amurensis (Starobogatov & Prozorova, 1989); TL Konstantinovka [48º35'N, 135º27'E], Khabarovsk region, Russia.

>*orientalis* Starobogatov & Prozorova, *in* Starobogatov *et al*., 1989; TL Konstantinovka [48º35'N, 135º27'E], Khabarovsk region, Russia.

>*moskvichevae* Starobogatov & Zatravkin, *in* Starobogatov *et al*., 1989; TL overflows of the river Artemovka [near Artëm, 43º22'N, 132º13'E], southern Maritime Region, Russia.

>*moskvichevae aphallica* Starobogatov & Zatravkin, *in* Starobogatov *et al*., 1989; TL Vladimiro-Petrovka [44º40'N, 132º06'E], Lake Khanka region of Maritime Region, Russia.

Paraplexa Starobogatov, 1989

Starobogatov, *in* Starobogatov *et al*., 1989:63; type species (by original designation) *Physa ataxiaca* Fagot, "1844" [1883], southern France. As subgenus of *Aplexa.*

Name: Greek *para*, beside, near, and *Aplexa*.

Diagnosis: Penis narrowly spindle-shaped, tapered at distal end, with lumen of penial canal narrowed within, but with no terminal thickening, stylet, or ornament.

Paraplexa was proposed as a subgenus of *Aplexa* with inadequate differentia and description. "Shell as in the nominate subgenus, but with a little more closely coiled whorls, preputium with weak sarcobelum and pilasters, penis of uniform thickness, but with a strong hold-fast thickening at the end." The sketch of the penial complex is of a specimen from Russia, showing a penis with arrowhead-like tip, identified by shell characters with *Physa ataxiaca* from the south of France. This dubious procedure in a group with such poorly-marked shell characters is badly founded, and to me the Russian material is doubtless *Aplexa hypnorum*.

Scarcely anything is known of *Paraplexa* beyond description of the penis by Slugocka (1913). That penis is widely different from any other known in Physidae: narrower at the head than at mid-length, and spindle-shaped, with the penial canal narrowed within a tip lacking any stylet or ornament. Distinctive characters may be expected in other structures of the reproductive system and the spawn. Other descriptions and illustrations that may apply to *Paraplexa* are by Germain (1930-1931) and Cesari and Orlandini (1984). None of those authors provided illustrations with sufficient detail for identification. Although Germain described the penis as cylindrical, with median thickening, he may have relied on Slugocka's work without independent observations.

Slugocka's material, so different from *Aplexa hypnorum*, came from the vicinity of Geneva. On the assumption that this species has a southern range distinct from that of *Aplexa*, various named forms are grouped under the name *cornea* (Massot, 1845), as being the oldest likely to apply. Among these names is *Physa ataxiaca*, type species of the poorly described *Paraplexa*. It is hardly more than a guess that the species will eventually bear the name *Paraplexa cornea*. No specimens have been available for study, and in any case working out the range limits and nomenclature of the species will require someone able to collect fresh material at various type localities. *Aplexa hypnorum* is found in southeastern England (Kent), hence it probably occurs also in Belgium, and in France at least in the northwest. Considering the commonly exclusive distribution of related groups of Physidae, I have assumed the range of *Paraplexa* lies to the south of *Aplexa*.

Distribution: The vicinity of Geneva, Switzerland, is the only certain locality for *Paraplexa*. I have grouped under this name the nominal forms from the Rhône drainage of France and western Switzerland, and those of

southern France. It is presumably this species that has been recorded as *"Aplexa hypnorum"* in northern Italy and northeastern Spain (Catalonia; Haas, 1929). Other names listed herein under *Aplexa hypnorum* may also be found to apply. Eastern limits of distribution are speculative.

Referred species:

A single species, *Paraplexa cornea* (Massot, 1845); TL Perpignan [42º41'N, 2º53'E], Dépt. Pyrénées-Orientales, France.

>*hypnorum major* Charpentier, 1837; TL "Un petit marais au bord du Rhône, près du hameau du Diabley en Vallais," Switzerland.

>*hypnorum intermedia* Locard, 1880; TL vicinity of Lyon [45º45'N, 4º51'E], Dépt. Rhône, France.

>*hypnorum rufula* Locard, 1880; TL in Rhône drainage, France.

>*ataxiaca* Fagot, 1883; TL Campagne-les-Bains, between Quillan and Limoux, Dépt. Aude, France.

?>*etruricus* "Porro" Paetel, 1889, *nomen nudum*; TL Etruria, Italy.

>*thermalis* "Fagot" Locard, 1893; TL "Eaux thermales de Campagne (Aude)," France.

>*hypnorum var. cornea* "Monterosato" Coen, 1945, *nomen nudum*; TL Castel Goffredo [45º18'N, 10º28'E], Mantova, Italy.

Paraplexa cornea (Massot, 1845)

Fig. 22

Physa cornea Massot, 1845:236, fig. 4.

Physa (Aplexa) hypnorum: Slugocka, 1913:101, pl. 4, fig. 36; fossé du Lignon (près de Châtelaine), Canton Genève, Switzerland; reproductive system.

Holotype: Not extant?, from Perpignan [42º41'N, 2º53'E], Dépt. Pyrénées-Orientales, France.

Name: Latin *corneus*, of horn, presumably in reference to the color of the shell.

Description: The few details known are given under the generic heading.

Aplexa Fleming, 1820

Fleming, 1820, *in* Brewster's Edinburgh Encyclopaedia, 14:617 [cited from Kennard & Woodward, 1926]; type species (by monotypy): *Bulla hypnorum* Linnaeus, 1758, northern Europe.

=*Nauta* Leach, *in* Turton, 1831:129. Cited as *Nauta hypnorum* Leach in synonymy of *Physa hypnorum*.

=*Aplexus* Gray, *in* Turton, 1840:255; emendation of *Aplexa*.

=*Amplexa* "Fleming" T. Brown, 1844:31; error for *Aplexa*.

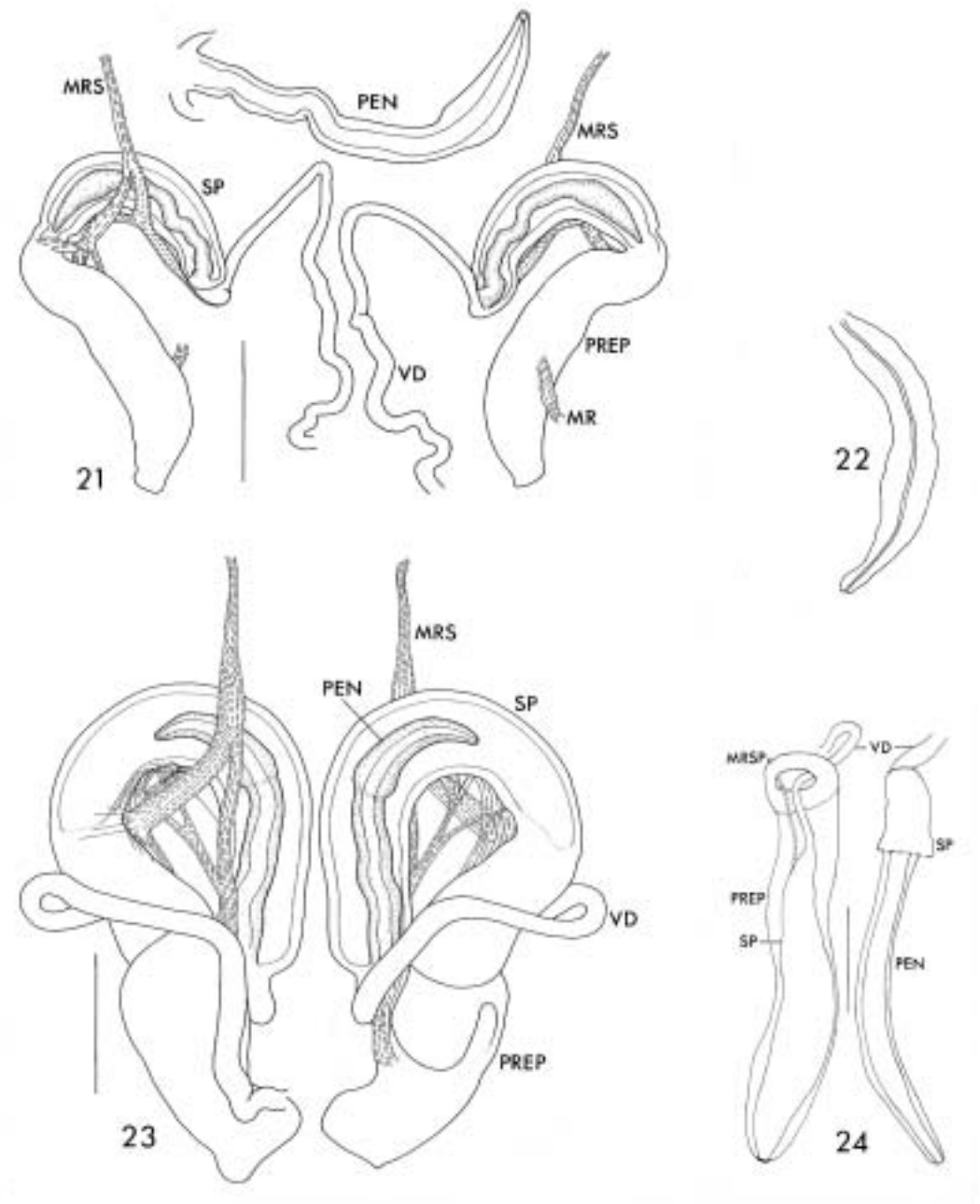
=*Aplecta* Herrmannsen, 1846-1849, 1:65 [1846]; emendation of *Aplexa* Fleming. Not of Guenée, 1838.

Name: Greek *a*, not, without, *plexis*, fold, plait; *i.e.*, lacking the mantle projections of *Physa*.

Diagnosis: Shell narrowly elongate, with flattened whorl outline, polished, with axial sculpture of fine growth lines only, and spiral microsculpture of series of fine wrinkles. Aperture less than half of shell length, its profile broadly convex in direction of growth. Suture and parietal callus narrow, apex acute. Length to about 15 mm.

Mantle not reflected over shell, its margin entirely smooth, with no scalloping or digitations.

Penial complex: Entire complex small, all on left side of body. Penial sheath unitary, glandular, shorter than preputium; not set off sharply from vas deferens.



Figs. 21, 23-24. *Aplexa hypnorum*, p. 54. 21, 23, Sweden, Uppland: 900 m WSW of Lohärad church (SMNH 7144). Penial complex, lateral (left) and medial right views of a single specimen, scale 1 mm; in 21, penis removed, scale .5 mm. 24, ditch in Kent, England (T98-301). Extruded penial complex (left), scale 1 mm; penis removed (right), scale .5 mm. MR, retractor muscle of preputium; MRS, common retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PREP, preputium; SP, penial sheath; VD, vas deferens.
Fig. 22. *Paraplexa cornea*, p. 51. Canton Genève, Switzerland. Penis, redrawn from Slugocka (1913, pl. 4, fig. 36).

Penis tubular, with distal end tapered to a blunt tip, with or without a slight expansion at the beginning of the taper. Vas deferens between paragonoporal angle and penial sheath about equal to combined length of preputium and penial sheath.

Penial retractor muscles have either a common origin, or separate but adjacent origins, and are inserted on ends of the penial sheath; rarely a cross-connection may be present.

Distribution: Northern and central Europe, from the British Isles and Scandinavia, eastward to Siberia in the Altai (Fig. 7).

Comparisons: *Amuraplexa* has been so poorly described that few comparisons can be made. Unlike *Aplexa*, the penis tapers to a simple tip, and the sarcobelum bears a papilla. *Paraplexa* is compared under that heading.

Berëzkina & Starobogatov (1988) provided the only clear illustration of *Aplexa hypnorum* in the sense used herein. The penis of their Russian material is not at all like that figured by Slugocka. Starobogatov *et al*. (1989) illustrated the penis in what they considered to be three different species from Russia. The sketches are so diagrammatic that they are of little value, but show an arrowhead-like end of the penis that might be an exaggeration of the structure seen in Swedish specimens and illustrated herein. Earlier illustrations by Grossu (1987), Soós (1917), and Stadnichenko (1990) lack sufficient detail for specific identification, but samples from Ukraine confirm the species as *Aplexa hypnorum*.

Referred species:

Aplexa hypnorum (Linnaeus, 1758); TL Sweden. British Isles and Scandinavia to the Netherlands and probably northern France, eastward to Russia and Ukraine; in Siberia as far as the Altai.

>*turritus* Müller, 1774; TL Frederiksdal, Randers, Denmark.

>*achatina* Gmelin, 1791; no locality.

>*marmorata* Gmelin, 1791; TL Strasbourg [48º35’N, 7º45’E], Dépt. Bas-Rhin, France.

=*turrita* A. E. de Férussac, 1814; substitute for *hypnorum* Linnaeus, 1758.

>*hypnorum normalis* Beck, 1838.

>*hypnorum rhenanus* Beck, 1838; TL Austria and Germany.

>*hypnorum var. fasciata* Küster, 1844; TL Hesse, Germany.

>*hypnorum var. pulchella* Moquin-Tandon, 1855; TL Dijon [47º19’N, 5º01’E], Dépt. Côte d’Or, France.

>*hypnorum minor* De Malzine, 1867; TL “Le bois l’Abbesse,” Belgium.

>*hypnorum var. rubra* Van den Broeck, 1871; TL near Selzaete [Zelzate, 51º12’N, 3º48’E], Belgium.

>*hypnorum forma major* Westerlund, 1885; no locality.

>*hypnorum forma minor* Westerlund, 1885; TL Stockholm [59º20’N, 18º03’E], Sweden.

>*alixiana* Servain, 1887; TL Lac de Grand-Lieu [47º06’N, 1º40’E], Dépt. Loire-Atlantique, France.

=*hypnicola* Chatenier, 1888; emendation of *hypnorum* Linnaeus (1758), but the locality cited is Chavannes [45º05’N, 4º51’E], Dépt. de la Drôme, France, likely to be outside the range of *hypnorum*.

>*hypnorum var. cuprella* Cockerell, 1889, *nomen nudum*; TL Sussex, England.

>*hypnorum albescens* “Mörch” Westerlund, 1897.

>*hypnorum mut. parva* Babor & Novák, 1909; TL Bohemia, Czech Republic.

>*hypnorum var. rubra* “Tryon” Schlesch, 1937, *nomen nudum*; TL Kleboniskes [Kleboniškiai] near Kaunas [54º54’N, 23º54’E], Lithuania.

>*hypnorum var. gratiosa* “Monterosato” Coen, 1945, *nomen nudum*; TL Interlaken [46º41’N, 7º51’E], Canton Berne, Switzerland.

>*hypnorum var. pulchella* “Monterosato” Coen, 1945, *nomen nudum*; TL Innsbruck [47º16’N, 11º24’E], Austria.

>*hypnorum var. rubra* “Taylor” Coen, 1945, *nomen nudum*; TL England.

Aplexa hypnorum (Linnaeus, 1758)

Figs. 21, 23-30, Pl. 1, fig. 4

Cochlea testa pellucida flava ovata sinistrorsa, apertura ovata-lanceolata, spira producta: Linnaeus, 1746:373, no. 1303.
Bulla hypnorum Linnaeus, 1758:727; with reference to Fauna Suecica no. 1303.
Bulimus hypnorum: Bruguiére, 1789, 1:301.
Physa hypnorum Draparnaud, 1801:52.
Aplexa hypnorum (L.): Fleming, 1820:617 [cited from Kennard & Woodward,1926]. Berëzkina & Starobogatov, 1988:173, figs. 9, 171; Russia; morphology, spawn.
Nauta hypnorum Leach: Turton, 1831:129; in synonymy.
Bulinus (Aplexa) hypnorum (L.): Beck, 1838:116.
Aplexus hypnorum: Gray, *in* Turton, 1840:255, pl. 9, fig. 113.
Aplecta hypnorum: Fischer & Crosse, 1870-1902, 2:85 [1886].

Holotype: Not extant, from Sweden.

Name: Latin; genitive plural of *Hypnum*, a genus of mosses, hence, the *Aplexa* of mosses.

Diagnosis: Penis a tube of uniform diameter with tapered distal end set off from the shaft by a low, asymmetrical swelling and ending in a simple, blunt tip without cuticular thickening. Sarcobelum globular, without papilla. Terminal portion of oviduct III heavily pigmented, nearly tubular and sharply set off from the unpigmented vagina by a constriction.

Description: Hermaphroditic duct: The duct is not sharply distinct from the collecting canal (CC) of the ovotestis. It enlarges gradually to about three times the width of the canal, and bears small seminal vesicles (VS) that are simple, unbranched, and attain a length of less than half the width of the duct. No vesicles are evident in the distal fifth of the duct.

Male system:

Penial complex: The whole penial complex is relatively small for Physidae, and lies entirely on the left side of the body.

In the extruded state the penial sheath (SP) is obviously shorter than the preputium (PREP). It is glandular, widest in the distal part, and tapered gradually to the distal end, that lacks a papilla. At the proximal end the sheath is not as sharply set off from the vas deferens (VD) as usual in Physidae, and enlarges gradually.

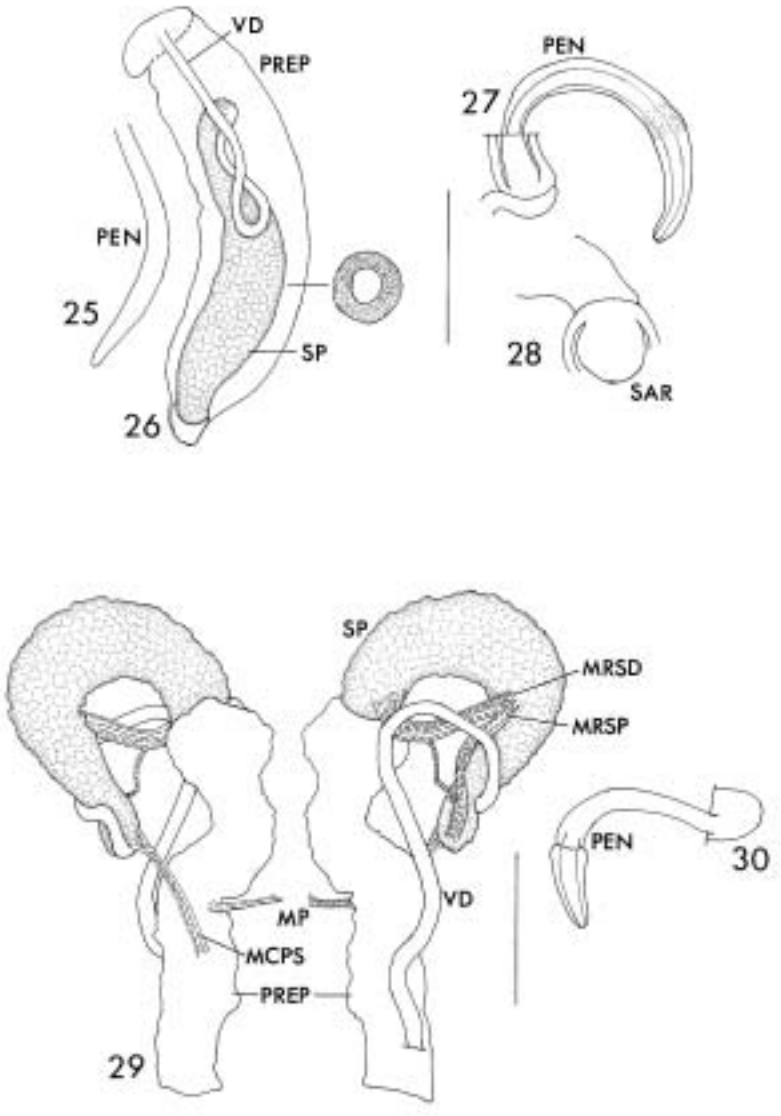
In the retracted state, the preputium shows a marked swelling at its proximal end, where it receives the penial sheath. On dissection the swelling can be seen as associated with a large, globular sarcobelum with terminal pore but no papilla.

The penis (PEN) is a tubular structure with broad penial canal. Where the distal end of the penis begins to taper, it is commonly set off by a slight enlargement that is asymmetrical, and may be either inconspicuous or marked by a low ring.

Penial retractor muscles have either a common or separate but adjacent origins from the columellar muscle, and are inserted on the ends of the penial sheath.

Female system: The albumen gland is appressed against the shell wall, and hence lacks the plump, subovoid form in other groups. The caeca are heavily melanin-pigmented. The outstanding character of the female system is that the terminal part of oviduct III is a heavily pigmented, almost tubular structure that is distinct from the upper parts of that same oviduct by its pigmentation, and is sharply separated by a constriction from the narrower and unpigmented vagina; the female pore is not on a papilla. The bursa copulatrix is a plump sac, its width only slightly less than half its length, widest in the posterior half, and sharply distinct from its duct, that is approximately equal in length to the bursa.

Distribution: British Isles in Ireland, England, and Wales; Scotland on the Inner Hebrides and the main island little north of 56º N. Lat. (Ellis, 1926). Southern Sweden as far



Figs. 25-30. *Aplexa hypnorum*, p. 54. 25-26, 29-30, ditch, Kent, England (T98-301). 27-28, ditch, Kent, England (T98-201). Scale 1 mm except .5 mm for 27-28. 25, penis removed from specimen illustrated in 26. 26, preputium extruded. 27, penis removed from sheath; stippled area shows extent of slight raised area. 28, sarcobelum dissected free. 29, medial (left) and lateral (right) views of a single penial complex. 30, penis dissected from specimen illustrated in 29. MCPS, muscle connecting penial sheath and preputium; MP, protractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens.

north as Jämtlands Län (Hubendick, 1947). Finland to 65º (Ehrmann, 1956). European Russia on the Kola Peninsula and in the basin of the Northern Dvina (Zhadin, 1952). South through Denmark and the Netherlands at least; presumably in northern France; replaced in western Switzerland and probably southern France by *Paraplexa*. Austria; Hungary to Ukraine (Stadnichenko, 1990); on the Balkan Peninsula only in the north (Croatia) (Ehrmann, 1956), but in Greece (Willmann & Pieper, 1978). Vicinity of Ankara, Turkey (Germain, 1936). Vicinity of Poti, Georgia, on the Black Sea (Retowski, 1914; cited by Germain, 1936). Southern West Siberia as far east as the Altai (Starobogatov *et al.*, 1989).

Localities and material examined:

SWEDEN, Uppland: 900 m WSW of Lohärad church, *H. W. Waldén*, 20-VI-1959 (SMNH 7 144, five specimens)(**M**).

DENMARK, Ærø: Grøft ved 6.2 km Stenen på Vejen til Ærskøbing - Marstal, *K. Stephensen*, 20-VIII-1940(**M**). København: Amager Fælled, *Doc. Stamm*, 1912-1915. Østjylland: Ø Tørslev Kær, *Hj. Ussing*.

NETHERLANDS, Gelderland: gemeente Winterswijk, Ratum, *A. W. Janssen*, 26-VII-1966 (**M**).

ENGLAND, Kent: Ditch, TR993 285, 51º01.66' N, 0º50.65' E, 19-V-1998 (T98-301) (**M**). Ditch, TR015 318, 51º03.43' N, 0º52.74' E, 18-V-1998 (T98-201)(**M**).

AUSTRIA: Danubian riverine forest, Vienna, *H. Nesemann*, 1-V-2001 (**M**).

UKRAINE: More than 75 samples from northern Ukraine, from the Khmel'nits'ka, Kyivs'ka, and Vinnits'ka Districts, and especially from Zhitomirs'ka District (**M**).

Remarks: The preserved material from western Europe, all more or less contracted and decayed except for the sample from Austria, was inadequate for resolution of most details of the reproductive system but sufficient to show its similarity to the English specimens.

Sibirenauta
Starobogatov & Streletskaya, 1967

Starobogatov & Streletskaya, 1967:234; type species (by original designation) *Physa kultukiana* Dybowski, 1913, Kultuk [51º44'N, 103º42'E], Lake Baikal, Siberia; as genus of Physidae.

Name: Siberia, and Latin *Nauta* (masculine; a sailor), a synonym of *Aplexa; i.e.*, the Siberian *Aplexa*.

Diagnosis: Shell narrowly elongate, with flattened whorl outline, polished, with axial sculpture of fine growth lines only. Spiral microsculpture of fine incised lines, and white spiral or axial streaks may be present. Profile of aperture broadly convex in direction of growth. Parietal callus narrow, apex acute to bulbous. Length to about 20 mm.

Mantle not reflected over shell; its margin entirely smooth, with no scalloping or digitations.

Prostate: A large prostatic chamber at the proximal end. Thereafter, the prostatic vas deferens is elongate, folded transversely, and set with long, tubular prostatic follicles that are widely spaced and bent double once or twice.

Penial complex: Penial sheath tripartite, with a narrow proximal muscular portion (SPP) about one-fifth of total length, slightly broader at proximal end, and scarcely tapered. Distal portions glandular, or mixed muscular and glandular; roughly cylindrical; or with narrow distal portion and thicker central portion. Penis long and tubular, with tapered distal end set off from shaft by constrictions or rings. Sarcobelum short, without papilla.

Retractor muscles, sometimes interconnected, originate from a single band or from separate but adjacent origins in the columellar muscle, and are inserted on ends of the penial sheath.

Vagina a discrete, tubular structure, not formed merely by junction of bursal duct and

oviduct. Female pore on an external papilla (at least in *S. elongatus*).

Distribution: Siberia to northern United States.

Comparisons: The shell is scarcely to be distinguished from that of *Aplexa*, but the numerous unique and striking features of the reproductive system show it is widely different. The following characters in *S. elongatus* are unknown in other Physidae: prostatic chamber of the prostate, transverse folding of the prostatic vas deferens, very long and folded prostatic follicles, vas deferens between paragonoporal angle and penial sheath longer than combined lengths of penial sheath and preputium, discrete tubular vagina, external papilla on which the female pore is situated, well-developed egg strings and capsular strings in the spawn, enormous thickening of the pallium gelatinosum in a lengthwise band on the spawn capsule, and coiling of the capsule in more than one plane. In these respects *Sibirenauta* is the most advanced of all Physidae. Stenophysini are more advanced only by the single criterion of a lateral penial pore, pointing to deficiency in the simple classification of the family into four grades. Perhaps presentation of the classification in two-dimensional form (Fig. 1) is at fault.

Referred species:

Sibirenauta depressior (Middendorff, 1851); TL Ichl, and near Falchudda Lake, Taimyr Peninsula, Russia [neither locality traced]. Eastern Siberia.

?>*hypnorum var. polaris* Westerlund, 1876; TL Schaitanskoj, 71º65' [near Mys Schaytanskiy, 72º05'N, 82º20'E]; Mesenkin [not traced], 71º20'; and Vorogovo, 60º50' [61º02'N, 89º35'E], all along the Yenisei River, Krasnoyarsk District, Russia.

?>*kultukiana* B. Dybowski, 1913; TL Kultuk [51º44'N, 103º42'E], Lake Baikal, Irkutsk District, Russia.

Sibirenauta elongatus (Say, 1821); TL "shores of Illinois" opposite St. Louis, Missouri. Canada and northern United States.

>*glabra* De Kay, 1843; TL Lake Champlain, New York.

>*elongatina* Lewis, 1855; TL Massachusetts and New York.

>*tryoni* Currier, 1867; TL Grand Rapids [42º58'N, 85º40'W], Kent County, Michigan.

>*elongata var. arctica* Clessin, 1885; TL Hudson Bay, Canada.

>*hypnorum pilsbryi* Brooks, 1935; TL pond near Whiterocks River at Paradise Creek (about sec. 36, T. 3 N., R. 17 E.; original data are irreconcilable), Uintah County, Utah.

Sibirenauta pictus (Krause, 1883); TL tundra pond north of Lavrenty (Lawrence) Bay, and mouth of a small stream entering the west end of that bay, Chukotka, Russia. Extreme eastern Siberia, Alaska, northern Yukon and Northwest Territories, Canada.

Sibirenauta sibiricus (Westerlund, 1876); TL Bukhta Sopochnaya Karga [71º54'N, 82º43'E], Taimyr Peninsula, Russia.

Species wrongly referred to Sibirenauta:

"Sibirenauta" tuwaensis Starobogatov & Zatravkin, *in* Starobogatov *et al*., 1989; TL Toora-Khem [52º28'N, 96º09'E], Tuvinsk Autonomous Region, Russia. Tuvinsk Autonomous Region, Russia, and adjacent Mongolia.

This species does not belong to *Sibirenauta*, as indicated by the enormous sarcobelum (W/L about .6), and the penis that widens in its distal half to more than twice the width of the proximal half, ending in a blunt, rounded tip.

Physa (?) aenigma Westerlund, 1877:104. TL mouth of Podkamennaya Tunguska at the Yenisei, Krasnoyarsk Region, Russia, *Dr. Théel, Swedish Expedition to Siberia*, 6-VII-1876. Referred to *Sibirenauta* by Starobogatov *et al*. (1989). The holotype, a unique specimen, is SMNH 1 652. Westerlund noted its resemblance to a sinistral *Cochlicopa lubrica*, but nevertheless described it as a new *Physa* (?). With the specimen is a note by N. H. Odhner, dated 1933, identifying it as a sinistral *Cochlicopa lubrica*. I certainly agree it is terrestrial, and not one of the Physidae. Whether the *Sibirenauta* described and illustrated by

Starobogatov *et al*. (1989) as *S. aenigma* from the vicinity of Krasnoyarsk and Bijsk, southern Yakutia, and northern Mongolia will prove to be *Sibirenauta*, and whether it is a single species, depends on more morphological information.

Sibirenauta ?depressior (Middendorff, 1851)

Fig. 34, Pl. 5, fig. 4

Physa hypnorum var. depressior Middendorff, 1851:298 [138], pl. 30, figs. 18-19.

?*Physa (Aplexa) hypnorum var. polaris* Westerlund, 1876:100. Westerlund, 1877:56, fig. 12. Martens, 1880-1885, 2:184, pl. 33, figs. 28-29 [1885].

?*Physa (Nauta) kultukiana* B. Dybowski, 1913:207, pl. 5, fig. 30.

?*Aplexa hypnorum var. kultukiana* W.[sic] Dybowski: Kozhov, 1936:126, pl. 2, figs. 20-21.

?Sibirenauta elongata (Say) [misidentified]: Starobogatov & Budnikova, 1976:81 in part, figs. 4IIa-e; northern West Siberia, East Siberia, Chukotka.

Holotype: If extant, presumably in ZIP. TL Ichl, and near Falchudda Lake, Taimyr Peninsula, Russia [neither locality traced].

Name: Latin, lower, more depressed.

Diagnosis: A species of *Sibirenauta* with fusiform shell, not consistently distinguishable from *S. elongatus*. Penial sheath with proximal thin muscular walls, gradually enlarging to a much longer portion with thick glandular walls. Penis with a tapered distal end, behind which is a narrow shaft that appears inserted into it (Starobogatov & Budnikova, 1976).

It remains to be verified by morphological studies of topotypes whether *kultukiana* and *polaris* are synonyms of *S. depressior*. The latter name is used here as the oldest from the region that is possibly applicable.

The species illustrated as *S. elongatus* by Starobogatov & Budnikova (1976, fig. 4, II; redrawn herein as Fig. 34) from the basin of the river Amguyema, in the Chukotsk region of eastern Siberia, has a penial tip with short, slender haft inserted into it, and behind the isthmus so formed a broad elevation— widely distinct from the structure of *elongatus.* Other morphological details are not clear from their sketch.

I have examined four syntypes of *polaris*, SMNH 1 653, from Schaitanskoj [near Mys Schaytanskiy, 72º05'N, 82º20'E]. None agrees with the illustrations by Westerlund (1877) nor by Martens (1880-1885). The specimens show slightly flattened whorls, but not shouldered as in Westerlund's illustration, a spire relatively longer than in Martens' figure, and have a polished surface and blunt, slightly bulbous apex. One juvenile specimen was not measured; the others are as follows:

Length	Width	LPer	Whorls	
10.2	5.6	6.2	5	Pl. 5, fig. 4
Last whorl broken away			5	
8.0	4.2	3.9	5 $^{1}/_{2}$	

Final disposition of this form will depend upon morphological study of material from the vicinity of the localities cited by Westerlund.

Figs. 31-33, 35-44. *Sibirenauta elongatus*, p. 61. Scale 1 mm except 10 mm for 38. 31, hermaphroditic duct; 32, penial complex; 33, penis; 34, *Sibirenauta* ? *depresior*, p. 58. Russia, Chukota: River Amguyena. Tip of penis, redrawn from Starobogatov & Budnikova (1976); 35, prostate stretched, 36, prostate; 38-41, spawn; 42, 44, female tract; 43, hermaphroditic duct. 31-32, 35, 38-40, Penticton, British Columbia (T90-3401); 33, Bannock County, Idaho (T75-4005); 36, 41-44, Bear River, Utah (T88-4202). APG, paragonoporal angle; BC, bursa copulatrix; C1, C2, caeca; CP, capsule wall; CVD, chamber of prostatic vas deferens; DBC, duct of bursa copulatrix; DF, female duct; DGA, duct of albumen gland; DH,

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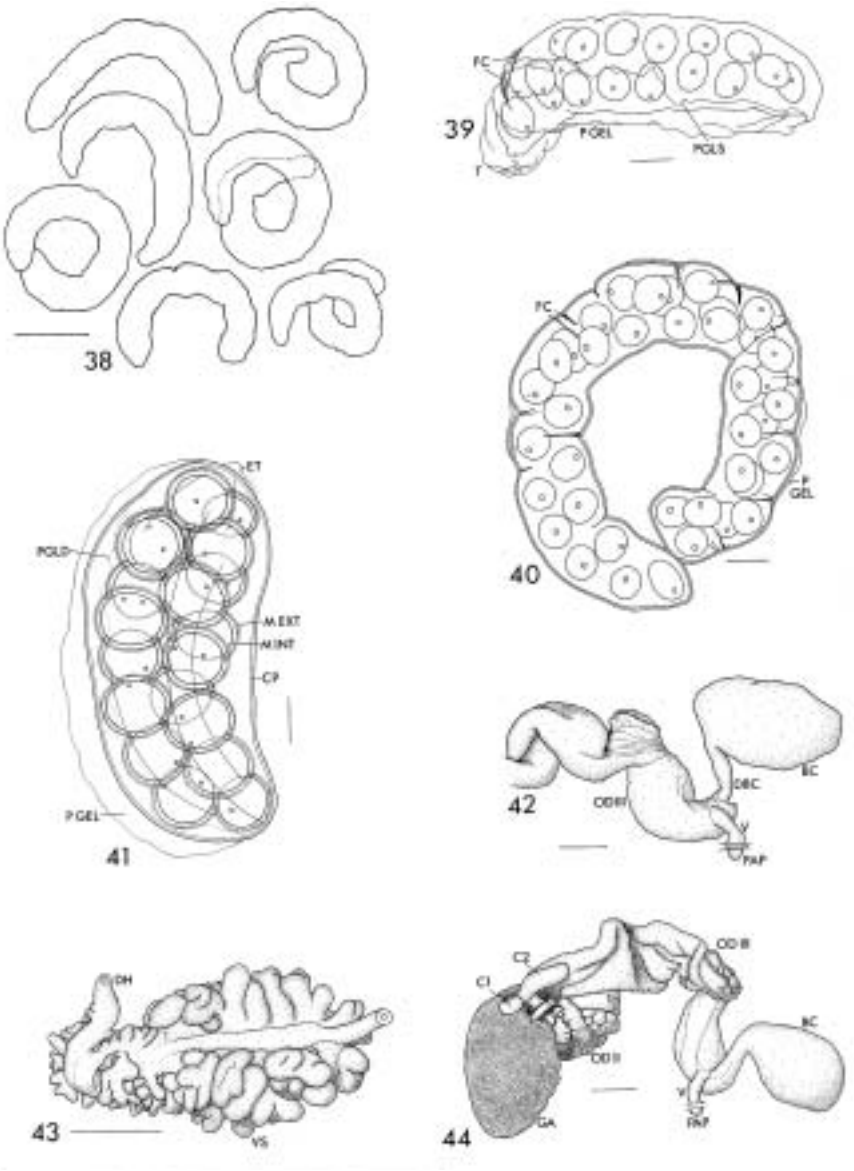


Figs. 38-44…*viene de página anterior*.

hermaphroditic duct; ET, terminal wisp; FC, capsular strings; FP, follicles of prostate; GA, albumen gland; MCPS, muscle band connecting proximal end of penial sheath to preputium; M EXT, external membrane; M INT, internal membrane; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD II, OD III, oviduct; PAP, papilla; P GEL, pallium gelatinosum; PGLD, right margin of pallium gelatinosum; PGLS, left margin of pallium gelatinosum; PREP, preputium; PV, ventral pore; SAR, sarcobelum; SPD, distal muscular portion of penial sheath; SPG, glandular portion of penial sheath; SPP, proximal muscular portion of penial sheath; T, tip of pallium gelatinosum; V, vagina; VD, vas deferens; VDP, prostatic vas deferens; VS, seminal vesicles.

Sibirenauta elongatus (Say, 1821)

Figs. 31-33, 35-44, Pl. 4, figs. 2-3

Physa elongata Say, 1821:171.
Bulinus elongatus Jay [sic]: H. & A. Adams, 1858:259.
Nauta elongata Say: Morse, 1864:44.
Stenophysa elongata: Starobogatov, 1963:302.
Sibirenauta elongata (Say): Starobogatov, 1970:241. Starobogatov & Budnikova, 1976:81 in part; not Siberian material described and illustrated.
Aplexa elongata (Say): Te, 1980:182.

Holotype: ANSP 21 208a. Illinois: shores of Mississippi River opposite St. Louis [38º38'N, 90º11'W], Missouri, *Thomas Say*, VI-1819.

Name: Latin, elongate.

Diagnosis: A species of *Sibirenauta* with fusiform shell, attaining a length of 20 mm. Penial sheath with proximal and distal narrower portions, and a sharply distinct medial portion with thick glandular walls. Penis with a tapered tip, set off by a circular flange at its base.

Description: Shell as in the generic diagnosis, not consistently identifiable as to species, but attaining a larger size than other species of the genus.

Body and tentacles dark gray to black.

TABLE 5
Measurements and descriptive statistics of shells of Sibirenauta elongatus *from Penticton, British Columbia (T90-3401). Measurements to nearest .128 mm, except for L, .1 mm. N = 25*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	20.53	11.74	.574	9.10	.445	6.9
Range	16.3-23.2	10.1-13.3	.53-.63	7.7-10.4	.39-.49	$6\ ^1/_4$ - $7^1/_2$
S.D.	1.59	.805	.030	.647	.022	
S.E.	.306	.155	.006	.125	.004	

TABLE 6
Measurements and descriptive statistics of shells of Sibirenauta elongatus *from Bear River valley, Utah (T88-4202). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	17.60	9.84	.560	7.70	.439	6.5
Range	16.0-20.4	9.0-11.3	.48-.63	6.7-8.7	.38-.50	6 - $7^1/_2$
S.D.	1.14	.670	.037	.504	.027	
S.E.	.208	.122	.007	.092	.005	

TABLE 7
Measurements and descriptive statistics of shells of Sibirenauta elongatus *from Crow Wing County, Minnesota (T92-2404). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	12.75	6.42	.505	5.35	.420	6.3
Range	11.5-14.6	5.8-7.8	.46-.55	4.7-6.3	.38-.47	6 - 7
S.D.	.676	.431	.026	.331	.022	
S.E.	.123	.079	.005	.060	.004	

Mantle with a thickened collar, but no broad thickened area (as in *S. pictus*). It is deep black or with faint irregular lighter patches, but in overall tone dark gray to black, without patterning as conspicuous as in *S. pictus*.

Male system: The prostatic vas deferens is distinctive, consisting of an initial straight, capacious chamber (CVD), and thereafter a tube folded transversely. Prostatic follicles are long tubules, usually unbranched, single, bent double once or twice, and widely spaced along most of the length of the prostatic vas deferens. Thus the structure is unlike the usual prostate of Physidae, in which the follicles are branched once or twice, not bent, and set closely and in numbers along a simple, nearly straight, tubular, prostatic vas.

The vas deferens is bound to the preputium at the paragonoporal angle, and then lies free within the cavity of the head for an enormous distance. The segment of the vas between paragonoporal angle (APG) and penial sheath is longer than the combined lengths of preputium and penial sheath, a relative length greater than known in any other Physidae.

Penial retractor muscles originate in the columellar muscle, and pass as separate bands to ends of the penial sheath, with variation in discreteness of the bands and number of insertions. There may be cross-connections between the retractors, and the distal retractor may branch into several bands. The insertion may be simple, onto the distal end of the sheath; multiple, onto the distal end of the sheath only, or onto both sheath and proximal end of preputium; a branch of the distal retractor may even be inserted onto the proximal end of the sheath in addition to the normal proximal retractor.

The preputium is a simple tubular sac with no gland, shorter than the penial sheath.

The penial sheath is tripartite, with a central enlarged glandular portion, and narrower proximal and distal portions. The proximal portion, narrowest of the three, is slightly swollen at the proximal end, generally cylindrical, and slightly over one-fourth or even over one-third the length of the penial sheath. It is sharply set off from the central glandular portion, that expands abruptly to about three times the width of the proximal portion. The distal portion, less than a fifth the length of the penial sheath, is about twice the width of the proximal portion. The glandular central portion tapers distally so that width of the penial sheath does not change abruptly at limit of the central and distal portions. The glandular portion is opaque cream, with weak melanin flecking. The distal portion, and distal end of the proximal portion, are heavily dusted with melanin, dark gray to black.

The penis is a long tubular shaft; at about 80% of length there is a ring-shaped low swelling, or more usually a sharp-edged ridge. Speculatively, this marks the limit to which the penis is inserted within the female aperture.

Sarcobelum (SAR) simple, with no papilla, varying from a low swelling to mammiform.

Female system (Figs. 42, 44): The bursa copulatrix (BC) is a plump sac, widest in the middle, sharply set off from its stout duct (DBC). The duct is shorter than the bursa, joining the tip of oviduct III above the vagina. The vagina (V) is a discrete tube, shorter than the bursal duct leading from oviduct III, not formed as usual by a simple union of oviduct and bursal duct. The female pore lies on a discrete papilla on the outer surface of the body wall.

Spawn: studied in several hundred capsules from each of two localities: north of Driggs, Idaho, and from the Bear River valley east of Sage Creek Junction, Utah; and in a lesser number (47) from Penticton, British Columbia. The capsule is sausage-shaped, curved clockwise, in the samples from Idaho and Utah generally through 90º to 180º. It is not flattened on the ventral side, but roughly circular in cross-section, *i.e.*, no trace of appression to the substratum is evident. With few eggs (10 or less) curvature may not be evident, and with a larger number curvature may be greater. In one capsule the coil was a full 360º, with the ends of the capsule on a radius from the center but not meeting. A small closed

wisp may be evident at either or both ends of the capsule, on the right side. The capsule wall is about .06 mm thick, exclusive of the pallium gelatinosum (Figs. 39, 41). The pallium is a film about .03 mm thick over most of the capsule surface, thickened greatly but irregularly in a lengthwise ventrolateral strip, up to 1.6 mm thick on the ventral surface, about one-fourth the circumference of the capsule and on the left (convex) side. The eggs are nearly regular, slightly elongate-ovoid, 1.12 x .98 mm, and overlapping, usually in a double series, less often in three rows. The external membrane is well developed and divided in the middle into two layers of equal thickness, that in plan appear as an outer, more coarsely layered and an inner, more finely layered part. An egg navel is present but not conspicuous. Egg strings were not seen.

Snails from north of Driggs attained a smaller size than those from Bear River valley, and produced capsules that were generally smaller, with fewer eggs, and with eggs in a double series only, even with a large number of eggs (more than 25). Furthermore, the initial end of the capsule was generally wider than the terminal end. In contrast, capsules laid by snails from Bear River valley had similar ends, or a wider terminal end, and three rows of eggs were often present, even when the number of eggs was small (14).

Several hundred capsules were laid in the laboratory in smooth-walled plastic containers. Virtually all were found lying free on the bottom, less than half a dozen adhering weakly to the wall or, more commonly, to the bottom. The capsule is not appressed to the substratum and so can readily be dislodged.

The sample from Penticton consisted of larger snails that laid larger capsules. These showed distinctive features not present in the other samples, but whether the differences are due entirely to size or to geographical variation as well is unknown. The capsules were almost always coiled helically rather than spirally, *i.e.*, not in one plane, and the initial end of the capsule was raised above the terminal end, or even overlapped it (Fig. 38). The degree of coiling was commonly 270º to more than 360º; in a sample of 47 mean coil was 300º, range 60º-520º. In the one specimen coiled through 520º, diameter 14.0 mm, there were 67 eggs. Maximum number of eggs (86) was in a capsule coiled through 400º, diameter 14.9 mm. Closeness of coiling varied so that the capsules with greater linear dimensions were not those with greater coil. These capsules from Penticton differed from the other samples not only in size and coiling but in having continuous egg strings in many cases, and capsular strings in most cases. Like the helical coiling of the capsule, neither of these features has been observed previously in Physidae; and relative to the structures in Lymnaeidae described by Bondesen (1950) they are vestigial.

Egg strings were mostly reduced to short wisps or were invisible, but in not a few cases there was a continuous string passing from one egg to another in series. In no capsule were all eggs linked by a continuous string. As emphasized by Bondesen, egg strings in Lymnaeidae (and now in Physidae) are reminiscent of the condition in some marine Opisthobranchia.

Capsular strings (Figs. 39-40) when present are short, and irregular in structure and occurrence. When most strongly developed, they form a thin crescentic flange projecting into the lumen of the capsule to a maximum of .1-.2 its diameter, and are restricted to the dorsal and lateral walls. In length they are usually less than half the circumference of the capsule. The capsular strings are commonly single, or in groups of two, but may occur in groups of three or even four. They are usually present at a slight constriction of the capsular wall, that is common in the Penticton sample but was not observed in the other samples studied. The strings were more common on the exterior (convex) wall than on the inner (concave) wall of the coil, and were found almost entirely in the terminal half of the capsule. Usually they occur between eggs of the dorsal series within the capsule. Number of capsular strings per capsule was tabulated in a sample of 36 capsules; on the exterior wall range was 0-18, mean

8.8; on the interior wall 0-5, mean 1.8. These numbers do not allow for the repetition of capsular strings in groups, so that the numbers would be higher if the individual small strings were counted. Unlike the capsular strings described in Lymnaeidae by Bondesen (1950), these in *Sibirenauta* from Penticton are not forked at each end, nor do they occur between each pair of eggs. Their irregular occurrence and structure are consistent with the interpretation that they are vestigial, derived from an ancestral form with capsular strings like those of some Lymnaeidae.

Compared with the capsule of *Aplexa* as described by Bondesen (1950), that of *Sibirenauta elongatus* differs by its regular clockwise coil, by attaining a larger size with more eggs, and by the regular arrangement and nearly regular form of the eggs. Initial and terminal wisps may also be present. In contrast to *Aplexa* and to all other Physidae and Lymnaeidae, the pallium gelatinosum is not a uniform film or envelope over the entire capsule, but is greatly thickened in a ventrolateral lengthwise strip about one-fourth as wide as the circumference of the capsule. As in *Aplexa* but unlike *Physa*, the external membrane of the egg is divided into an outer, more coarsely layered, and an inner, more finely layered, envelope.

The thickened pallium gelatinosum leads one to speculate as to possible function. Ross & Harrison (1977) suggested that it may act as a calcium store. Speculatively, then, the young might survive temporarily in a low-calcium environment after hatching, by ingesting some of the pallium. A common habitat of the species is ponds and ditches that are filled with dead vegetation, a source of humic acid that would be concentrated as the water body dried. The matter is readily amenable to laboratory study on account of the wide range of the species.

Distribution: North West Territories, Canada, from vicinity of Great Slave Lake southeast (south of Hudson Bay) to Anticosti Island, Quebec, and Nova Scotia; south through British Columbia, eastern Washington and eastern Oregon to southernmost Utah and Colorado; east across the Great Plains from northeastern Colorado through northern Nebraska to central Illinois, through Indiana and Ohio to Pennsylvania and eastern Massachusetts. In Illinois and Ohio there are early records from south of the modern known range. Perhaps these show the effects of forest clearing in later times.

Limits of range in southern New England and New York are uncertain because of confusion with *Laurentiphysa vernalis*. Most of the reports from Connecticut, Rhode Island, and Long Island, New York, probably refer to that species. The northwestern range limit is uncertain because of confusion with *Sibirenauta pictus*. Distribution of *S. elongatus* as described above is based on the assumption that the two species are mutually exclusive.

The preserved specimens studied are from southern British Columbia, Colorado, Idaho, and Utah. They agree with one another and with descriptions by F. C. Baker (1928) of specimens from Wisconsin.

Localities and material examined (in west to east order)**:** The specimens listed are samples examined or measured, and those along the southern limit of range. All specimens examined from New England are listed, documenting the few localities known. Published records from that area require confirmation.

BRITISH COLUMBIA, Kootenay District: Ditch on east side of B.C. Highway 3, 0.25 mi N of road E to Morrissey Station, between Fernie and Elko, 23-VI-1963 (T63-5001)(**M**). Yale District, Similkameen Division: Sedge-cattail swale 100 feet E of Okanagan River, Penticton [49º30'N, 119º35'W], in park above head of river rafting concession, 15-VIII-1990 (T90-3401)(**M**).

OREGON, Grant County: Ditch beside US highway 395, 1.0 mile N of Silvies, NE 1/4 NE 1/4 sec. 1, T. 18 S., R. 31 E., 2-VII-1975 (T75-10903). West Myrtle Creek W of road, SW 1/4 SE 1/4 sec. 31, T. 18 S., R. 30 E., 2-VII-1975 (T75-10702).

Harney County: Ditch 1 800 ft W, 200 ft S, sec. 7, T. 23 S., R. 31 E., 4-VI-1975 (T75-2202). Marshes W of Harney Lake, 2 400 ft W,

400 ft N, sec. 33, T. 26 S., R. 29 E., 4-VII-1975 (T75-11509). Sedge pond 2 200 ft W, 1 000 ft S, sec. 4, T. 27 S., R. 29 E., 4-VII-1975 (T75-11607). Roadside ditch, 1 400 ft E, 1 700 ft S, sec. 31, T. 31 S., R. 32 1/2 E., 7-VII-1975 (T75-12704).

Malheur County: Ditches at US highway 20, E of Juntura, SE 1/4 NE 1/4 sec. 17, T. 21 S., R. 38 E., 27-VI-1975 (T75-8904). Swale on S side US highway 20, center E 1/2 sec. 27, T. 20 S., R. 39 E., 27-VI-1975 (T75-8804).

IDAHO, Bannock County: Marsh on S side of road W from Downey, on E side of Marsh Creek valley, NW1/4 sec. 31, T. 11 S., R. 37 E., 13-VI-1975 (T75-4005)(**M**).

Teton County: Ditch off state highway 33, north-central sec. 35, T. 6 N., R. 45 E., 16-VII-1988 (T88-4001)(**M**).

NEVADA, Eureka County: Dry stream bed, U.S. 50, T. 20 N., R. 52 E., *Robert P. Sharp*, 1-VIII-1939.

UTAH, Rich County: Sedge-cattail belt on W side Bear River valley along Sage Creek Canal, S side state highway 30, sec. 23, T. 12 N., R. 7 E., 18-VII-1988 (T88-4202)(**M**).

Washington County: St. George [37º06'15"N, 113º35'00"W, 2761 ft], swamp along Virgin River, *J. D. Vasquez, W. H. Behle*, XII-1939 (Jones, 1940:41).

COLORADO, Alamosa County: San Luis Lake [37º40'27"N, 105º43'21"W], *J. Henderson*, 1-IX-1923 (JH sta. 499) (UCM 12 283). Three miles N Alamosa, *S. C. Bishop*, 19-VI-1930 (ANSP 151 783). Roadside ditch 3 300 ft W of SE corner sec. 33, T. 39 N., R. 9 E., 24-V-1981 (T81-10105)(**M**). Roadside ditch 1 700 ft N of SE corner sec. 12, T. 38 N., R. 9 E., 24-V-1981 (T81-10205). Roadside pond at US highway 285, 6 miles S of Alamosa, *S.-K. Wu*, 12-VI-1974 (UCM 27 132). La Jara Creek, 3 miles E, 7 miles S of Alamosa, sec. 7, T. 36 N., R. 11 E., *S.-K. Wu, P. A. Unger*, 25-V-1978 (UCM 29 083).

NEBRASKA, Arthur County: Three Mile Lake, 12.2 miles E, 6.7 miles N of Arthur, *S.-K. Wu, J. F. Saunders*, 29-IV-1979 (UCM 29 310). Creek 2.7 miles S Collins Lake, *S.-K. Wu, J. F. Saunders*, 29-IV-1979 (UCM 29 325).

Brown County: Drainage ditches in NW corner sec. 34, T. 30 N., R. 22 W., 18-VI-1953 (T53-1003).

Cherry County: Dewey Lake, *R. H. Wolcott* (UMMZ 115 683). Marsh Lake [42º18'16"N, 101º00'06"W], *R. H. Wolcott* (UMMZ 115 684).

Rock County: Ditch 2.8 miles W of Bassett, NE 1/4 SW 1/4 sec. 18, T. 30 N., R. 19 W., 16-VI-1953 (T53-206).

Sheridan County: Roadside seepage at state highway 2, entrance of Crescent Lake, .8 mile E of Lakeside, *S.-K. Wu, J. F. Saunders*, 29-IV-1979 (UCM 29 326).

MINNESOTA, Crow Wing County: Ditch by highway 49, NE1/4 sec. 32, T. 134 N., R. 31 W., 15-VII-1992 (T92-2404).

IOWA, Dickinson County: West Okoboji Lake [1396 ft] (MCZ 4 390, ex R. E. Call colln.). Small creek tributary to Little Millers Bay, West Okoboji Lake, *T. C. Stephens*, 24-VII-1913 (TCS 77a). Swamp back of Millers Bay Hotel, Lake Okoboji, *T. C. Stephens*, 3-VII-1918 (CAS uncat.). Slough near Lake Okoboji, *T. C. Stephens*, 9-VII-1915 (TCS 114a) (CAS uncat.). Slough at base of sand spit, Millers Bay, *T. C. Stephens*, 3-VIII-1942 (TCS 370a) (CAS uncat.). Schoolhouse road W of laboratory on Lake Okoboji, *T. C. Stephens*, 9-VII-1915 (CAS uncat).

Scott County: Davenport [41º32'N, 90º41'W], *D. S. Sheldon* (Tryon, 1865:68).

Winnebago County: No precise locality (MCZ 4 314, 86 588, 161 327). Crystal Lake [41º48'56"N, 90º34'43"W] (MCZ 55 296, ex D. Smith).

ILLINOIS, St. Clair County: "Shores of Illinois," opposite St. Louis [38º38'N, 90º11'W], Missouri, *Thomas Say*, VI-1819 (type locality).

INDIANA, Fayette County: Connersville [not traced] (MCZ 55 285, *ex* USNM).

Hendricks County: Danville [not traced], *C. Dallas* (MCZ 75 336).

Marion County: Little swamp along East River, Indianapolis, *R. E. Call* (MCZ 4 311).

OHIO, Hamilton County: vicinity of Cincinnati [39º06'N, 84º31'W], *J. G. Anthony* (Anthony, n.d.).

PENNSYLVANIA, Centre County: Erie Railroad ditch, Howard Junction [not traced], *W. E. Burnett*, 15-VI-1927 (MCZ 58 765).

NEW YORK, Westchester County: Lake Waccabuc [not traced], *A. G. Smith*, 24-V to 2-VI-1914 (AGS 1 343).

VERMONT, Chittenden County: Burlington [44º28'33"N, 73º12'45"W], *R. K. Smith, W. F. Clapp*, 7-V-1910 (MCZ 15 343).

Windsor County: Hartland [43º32'26"N, 72º23'58"W, 587 ft], *D. H. Eaton, C. F. Tracy* (MCZ 15 935); *C. O. Enos*, 1886 (CAS uncat., *ex W. J. Raymond* 1816).

NEW HAMPSHIRE, Hillsborough County: Hollis [42º44'35"N, 71º35'32"W], *W. Carter* (MCZ 153 119).

MAINE, Cumberland County: Westbrook [43º40'37"N, 70º222'18"W] (MCZ 45 316, 55 284, 161 360). "Westbrook near l. s.," *E. C. Bolles* (MCZ 161 332; 5 *S. elongatus* mixed with 6 *Laurentiphysa vernalis*).

Knox County: North Warren [Warren is 44º07'13"N, 69º14'26"W], *N. W. Lermond* (MCZ 104120). Rockland [44º06'13"N, 69º06'34"W], *R. K. Smith, W. F. Clapp* (MCZ 18 738). Old lime quarry, Thomaston [44º04'44"N, 69º10'56"W], *N. W. Lermond*, 16-V-1910 (MCZ 104 194).

Washington County: Woodland [45º09'25"N, 67º24'19"W], *O. O. Nylander* (MCZ 180 885).

York County: Kennebunk [43º23'02"N, 70º32'43"W], *J. A. Swan* (MCZ 161 333). Saco [43º30'03"N, 70º26'36"W], *Dwight Blaney* (MCZ 176 499), *H. W. Winkley*, 1906 (MCZ 19 302).

MASSACHUSETTS, Berkshire County: No precise locality, *Mayo* (MCZ 45 317).

Hampshire County: Westfield [42º07'30"N, 72º45'00"W]; "collected June 1854. The ground has had a coating of ashes and guano in the spring of 1853 & 1854" (MCZ 45 314).

Middlesex County: Groton [42º36'40"N, 71º34'30"W], *W. N. Souther*, 1916 (MCZ 31 580); no date (MCZ 132 656). Lexington [42º26'50"N, 71º13'30"W] (MCZ 163 168, ex J. R. Miller colln.). North Cambridge [42º23'45"N, 71º07'50"W], *W. J. Clench*, 12-X-1916 (MCZ 55 305). Cambridge [42º22'N, 71º06'W], *R. K. Smith, W. F. Clapp*, 1903 (MCZ 15 372). Glacialis pond, Cambridge, *R. K. Smith, W. F. Clapp*, 1-V-1912 (MCZ 17 185). Riverside, Charles River; *R. K. Smith, W. F. Clapp*, 11-IV-1910 (MCZ 15 346).

Suffolk County: Blue Hills, Milton [42º14'58"N,71º04'00"W], *W. F. Clapp*, 14-IV-1910 (MCZ 15 344).

CONNECTICUT, Fairfield County: Ponds behind Marcus Dairy, Rte. 7, Danbury, *S. L. H. Fuller, R. M. Fenn* II, V-1960 (MCZ 228 991).

VIRGINIA: Greene County: No precise locality (Beetle, 1973:25). The locality is so remote from others that confirmation is desirable.

Habitat: East and west of the limit of forest in the mid-continent, *Sibirenauta* lives in different habitats, that have been studied principally in the east.

Regarding the more northern coniferous forest I have traced only one mention of habitat. Dawley (1947) recorded the species "in temporary pools in coniferous forests especially in the northern part of the state" [Minnesota].

Notes on habitat and studies of ecology have been concentrated in the deciduous forest region around the Great Lakes. Near Ottawa, Ontario, Heron (1880) noted that the species "is found everywhere during summer in dried-up ponds with *Sphaerium occidentale*, under leaves and rubbish, but still alive. Many of the shells are very large… A few of my specimens were as much as eight-tenths of an inch [20 mm] in length." Similar habitat has been reported in Wisconsin: "It is especially abundant in woodland pools which become dry in summer, in company with *Stagnicola caperata, Physella hildrethiana* [<*Physella gyrina*], and *Sphaerium occidentale*. It occurs in some localities (as in a ravine bordering the Mississippi River near St. Paul, Minn.) in small clean brooks where the water is a few cm. deep and the bottom of mud" (F. C. Baker, 1928).

The temporary woods-pool habitat has been studied most thoroughly by Kenk (1949)

in southern Michigan, where Pond I, nine miles northeast of Ann Arbor, "probably resembles the original woodland pools of southern Michigan more closely than any one of the other three ponds investigated." The locality has been modified by clearing of the forest, so that the pond is exposed on the east but shaded on the west by trees that partly overhang its surface. During the investigation the pond was dry during summer and fall, and overgrown by a dense growth of rooted hydrophytes. In winter water began to accumulate, although the surface was frozen for about three months, and after melting of the ice-cover water lasted only until near the end of June. Although "*Aplexa hypnorum*" was common from May to June, it was not found in dry bottom samples either before filling in the fall or just after drying in early summer.

At 40 localities where I collected *Sibirenauta elongatus* from 1950-1988, mostly in the Rocky Mountain region or intermountain west, associated mollusc species ranged in number from 0-14, mean 4.26. This shows that it is not usually found in rich localities with a high diversity of mollusc species. Most common associates were *Lymnaea elodes* Say at 27 sites, followed by *Promenetus umbilicatellus* (Cockerell) at 17, *Physella gyrina* (Say) and *Gyraulus circumstriatus* (Tryon) at 15 each, *Gyraulus parvus* (Say) and *Lymnaea caperata* Say at 13 each. Twenty-five other species were associated at eight or fewer localities, twelve of these at only one site each. All localities were ditches, marshes, or other situations in or near flowing water. This is in contrast to habitats in the Plains of Canada and the north-central United States, where ponds and lake margins are the usual habitat (Cvancara, 1983).

In the Rocky Mountains the species is known to elevations over 8 100 ft (2 500 m). This is not nearly as high as the limit of some species with which it is commonly associated (*e. g., Lymnaea caperata*). The difference in distribution is evidently due to the absence of suitable flowing-water habitats at high elevations, whereas other species can live in ponds.

Sibirenauta pictus (Krause, l883)

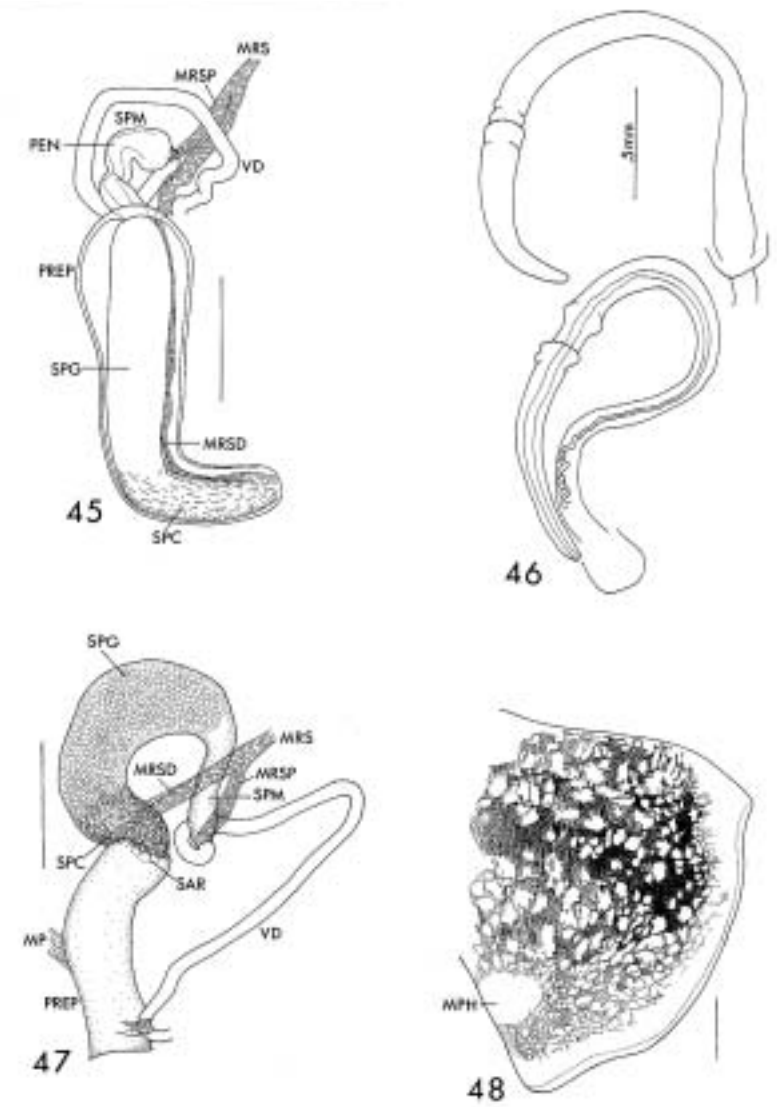
Figs. 45-48, Pl. 4, fig. 1

Physa hypnorum var. picta Krause, 1883:33. Martens, 1880-1885, 2:l84, pl. 33, figs. 25-27.
Nauta hypnorum v. picta Krause: Westerlund, 1890:156.
Sibirenauta picta (Krause): Starobogatov & Budnikova, 1976:80, figs. 4Ia-b.
Sibirenauta pictus: Taylor, 1988a:531.
Sibirenauta elongata (Say) [misidentified]: Starobogatov & Streletskaya, 1967:234, in part, fig. 28.
Aplexa hypnorum (Linnaeus) [misidentified]: Clarke, 1973:383, in part; not pl. 13, fig. 2 or pl. 24, fig. 11; western Arctic populations in northern North West Territories and Yukon, Canada. Clarke, 1981:172, in part, not fig. 65. Holyoak, 1983:260; near Sachs Harbour, Banks Island, N.W.T., ecology.

Types: Four syntypes ZMB 36 330. TL tundra pond north of Lavrentija Zaliv [Lawrence Bay, 63º35'N, 171º00'W], and mouth of a small stream entering the west end of that bay, Chukotka, Russia.

Name: Latin *pictus*, painted, in reference to the white spiral and axial streaks in the shell.

Diagnosis: A species of *Sibirenauta* weakly distinguished in shell features from *S. elongatus* by slightly shorter and broader body whorl and aperture, by attaining lesser size, and by variable presence of white streaks in axial or spiral arrangement. Trenchant differences are in the penial complex: the penial sheath has a proximal part with thin muscular wall, central part thick and glandular, and distal end mixed muscular and glandular. Penis with tapered tip set off from the shaft by annuli and a shallow constriction.



Figs. 45-48. *Sibirenauta pictus*, p. 67. Nome, Alaska. 45, penial complex with preputium extruded; 46, two penes; 47, penial complex in retracted state; 48, anterior portion of mantle. MP, protractor muscles of preputium; MPH, attachment of physid muscle; MRS, common retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor of penial sheath; PEN, penis; PREP, preputium; SAR, sarcobelum; SPC, mixed muscular and glandular portion of penial sheath; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm except as indicated.

Description: The head-foot is pale gray to dark gray, with dorsal aspect of the head often darker than the rest of the body. Mantle margin simple, with no scalloping or digitations. Below the pulmonary cavity, the mantle is greatly thickened all around, pale gray in contrast to the dark rim. Mantle pigmentation (Fig. 48) consists of a network of melanin enclosing diffuse-edged cream to pale gray open areas that are roughly equidimensional. Consistently there is a more heavily pigmented band in the posterior half. A narrowly elongate unpatterned, or weakly patterned area outlines the physid muscle (PHM), and the fan muscles

radiating therefrom are indicated by faint lineation of the pigmentation.

The penial complex was studied in one specimen with preputium everted, nine retracted as usual.

The glandular part of the penial sheath can be accommodated entirely in the everted and distensible preputium. Internal details are visible only on dissection through the dark gray and opaque preputium.

Muscles of the penial complex consist of a medial protractor (MP) inserted on the preputium, and two retractors (MRSD, MRSP) with origin in the columellar muscle and insertions on the penial sheath. After leaving the unpigmented columellar muscle, the retractor bands are pigmented for their entire lengths. From a common, pigmented origin (MRS) they diverge, one to insert on the proximal end of the penial sheath (MRSP), the other at the distal end of the sheath (MRSD). In one specimen there was a cross-connective between the two, about one-third as wide as the two roughly equal bands. Commonly the distal retractor is a wide strip at its insertion, but may divide in two; in two instances the distal retractor was double.

The vas deferens is bound to the distal end of the preputium, and relatively long for Physidae, but shorter than the penial complex. It is a weakly pigmented tube of uniform diameter between body wall and penial sheath.

The penial sheath is tripartite, consisting of a proximal muscular portion (SPM) and a longer and thicker distal glandular portion (SPG). The muscular portion is commonly set off distinctly from the glandular area by an abrupt increase in diameter of the latter, and usually has a slightly swollen head. Its pigmentation is weak proximally, becoming heavy at the distal end. The length varies from about one-third to one-fifth of the entire sheath.

The distal glandular portion of the sheath is of either uniform width or tapered slightly. Its distal end (SPC) is nearly black, with muscle fibres running through external glandular tissue from the inner muscular tube to external sheathing on which the retractor muscle is inserted and which connects also to the end of the preputium. This distal part of the sheath is set off from the middle glandular segment by the muscle fibres that, being pigmented, also contrast with the weaker melanin dusting of the middle segment.

Internally in the preputium is a weak, short sarcobelum.

Form of penis is evidently variable, but could not be studied satisfactorily in all specimens. The tapered tip is set off from the shaft usually by an isthmus, sometimes a group of two or three annuli. Distal to the isthmus there may be only one ring, that may be oblique. In one extreme case the isthmus between two annuli was as long as the whole tapered tip.

Comparisons: The differentia given for the species by Starobogatov & Budnikova (1976) included the proportions of preputium; these seem so dependent on quality of preservation and state of contraction as to be unreliable. Those authors further described the distal end of the penial sheath as muscular; I have found it to be glandular and thick-walled with an intermixture of musculature. The isthmus of the distal part of the penis was illustrated by them, although not described, so that I believe there is no doubt of the species.

Sibirenauta elongatus differs from *S. pictus* by a uniformly dark mantle over the pulmonary cavity, or it has a few faint spots of weak pigment in the generally intense melanin. It has a thin mantle collar, without the thick, broad muscular ring of *S. pictus*. Internally the more obvious differences are in the length of vas deferens between paragonoporal angle and penial sheath (longer in *elongatus*); penial sheath (with narrow, muscular distal portion in *elongatus*), and penis (distal ring and no isthmus in *elongatus*).

Distribution: Chukotka in the basin of the river Kolyma, eastward to Lawrence Bay [Lavrentii Zaliv]. Alaska, principally in the north, also offshore on St. Matthew Island. Canada in the northern Yukon, and Northwest Territories on the arctic coast, ranging northward to Banks and Victoria Islands of the Arctic Archipelago.

Localities and material examined:

RUSSIA, Yakut Autonomous Region: Pokhodsk [69º06'N, 160º59'E], in the delta of the Kolyma River (Starobogatov & Streletskaya, 1967).

Chukotsk National Region: Basin of the river Amguyema, at 94, 105, and 107 km along the Egvekinot-Iul'tin road, *L. Budnikova, I. Chereshnev*, VII-VIII-1973. Vicinity of Chaplinsk lake, *L. Budnikova, T. Vshivkova*, VII-IX-1974. Ust'-Chaun, *E. Streletskaya*, 31-VII-1972 (all from Starobogatov & Budnikova, 1976). In a freshwater lake on the tundra north of Lawrence Bay, as well as in the broadened mouth of a small stream flowing into the west end of Lawrence Bay, *A. & A. Krause*, 1881 (type locality).

ALASKA: Pools of beaded stream which enters lagoon just south of Navy Camp, Point Barrow, *John Koranda*, 13-VIII-1955 (Hanna, 1956). Ikroavik Lake [71º13'58"N, 156º38'00"W], *Ira L. Wiggins*, 15-VII-1956 (CAS 38983). First large lake south of Ikroavik Lake, about six miles south of Point Barrow, *Frs. E. J. Long, John Ostdiek*, 1955 (Hanna, 1956). Lake near Meade River Village, *Fr. E. J. Long*, 10-VII-1955 (Hanna, 1956). Half Moon Three Ranch [=Alaktak], *Frs. E. J. Long, John Ostdiek*, 1955 (Hanna, 1956). Ninuluk Creek, 20 miles SW of Umiat (Hanna, 1956). Pond at foot of Red Hill, Umiat, *Edward Reed, Frederick Jackson*, 16-VII-1955 (Hanna, 1956). Fifteen miles north of junction of Anaktuvik and Colville Rivers, *Edward Reed, Frederick Jackson*, 26-VII-1955 (Hanna, 1956). Oliktok Point, *Edward Reed, Frederick Jackson*, 25-VIII-1955 (Hanna, 1956). Lake and pond at Konganevik, Camden Bay, *Frits Johansen, Canadian Arctic Expedition*, 25, 26-VI, 4-VII-1914 (Dall, 1919). Ponds at Collinson Point, *Frits Johansen, Canadian Arctic Expedition*, 1914 (Dall, 1919). Lake at Demarcation Point, *Frits Johansen, Canadian Arctic Expedition*, 15-V-1914 (Dall, 1919). Brackish pond near Teller, *Frits Johansen, Canadian Arctic Expedition*, 3-VIII-1913 (Dall, 1919). Nome [64º30'N, 165º24'W]; west side of road from Bureau of Public Roads camp into Nome via NE end of Nome Airport, from shallow roadside ponds, *R. D. Reger*, 20-VII-1968(**M**). 60-75 miles N of Rampart House, *J. M. Jessup* (USNM). Nulato River, *W. H. Dall* (USNM 43 377). Mouth of Porcupine River, *Robert Kennicott* [1861-1862] (CAS 50 649, ex Josiah Keep colln.; MCZ 184 150; UMMZ 216 442). Nushagak River, *Arnheim* (USNM 180 298). Freshwater lake near center of north shore, St. Matthew Island, *G. D. Hanna* (USNM 332 774).

YUKON: Pond, 69º40'N, 141ºW, *J. M. Jessup* (USNM 251 935). Ponds on Herschel Island, *Frits Johansen, Canadian Arctic Expedition*, 14-VIII-1914, 29-VII-2-VIII-1916 (Dall, 1919).

NORTHWEST TERRITORIES: Near Sachs Harbour, Banks Island [about 72ºN, 125ºW; this is the record farthest north], *Fisheries Research Board*, 1958 (Clarke, 1973); *D. T. Holyoak*, 1981 (Holyoak, 1983). Pond, Colville Mts., Victoria Island [near 69º35' N, 115º35' W], *Canadian Arctic Expedition*, 1915-1916 (Dall, 1919). Waterholes on tundra, Cape Bathurst, *Frits Johansen, Canadian Arctic Expedition*, 26-VII-1916 (Dall, 1919). Pond and river at Bernard Harbour [68º45' N, 114º45' W], *Canadian Arctic Expedition*, 1915-1916 (Dall, 1919). Lake opposite Bernard Harbour [68º47'N, 114º47'N], *Canadian Arctic Expedition*, 1915-1916 (Dall, 1919). Spring run-off pool near Coppermine River [67º49'N, 115º06'W], *Fisheries Research Board*, 1957 (Clarke, 1973).

One preserved series was available from Nome, Alaska, *R. D. Reger*, anesthetized and fixed in formalin. Most details of the penial complex could be studied adequately, although as usual in formalin-fixed specimens the contraction of tissues affects observations. Morphological descriptions are based on 10 specimens.

Habitat: R. D. Reger kindly supplied habitat notes with the collection from Nome. The snails are from small ponds no deeper than four ft, associated with *Lymnaea* and *Gyraulus*. The

latter two were almost exclusively on submerged vegetation with no evident distribution by depth. In contrast, *Sibirenauta* was almost restricted to water less than one foot in depth, on debris and vegetation.

Field notes of the Canadian Arctic Expedition published by Dall (1919) indicate the species was collected in lakes, tundra ponds, and streams. These were all fresh, except for a "brackish tundra-pond" near Teller, Alaska.

Holyoak (1983) described the habitat on Banks Island, in the Canadian Arctic Archipelago. The snails were found only in small, shallow, unshaded pools, mostly less than 1 m in diameter, and depth 0.1-0.5 m. The pools are warmed substantially above air temperature during the summer, but are frozen for eight to nine months of the year. During warm sunny weather the animals fed actively at and close to the water surface.

Sibirenauta sibiricus (Westerlund, 1876)

Pl. 5, fig. 5

Physa (Isidora?) sibirica Westerlund, 1876:100; 1877:55, fig. 13. Sopochnaya Karga, 71º40', Taimyr Peninsula, Russia, *A. Stuxberg, Swedish Novaya Zemlya-Yenisei Expedition*, 22-VIII-1875.

Sibirenauta sibiricus is known surely from the original locality only. As represented in Westerlund's collection it is a composite of two species. SMNH 1 651 includes one specimen, slightly bleached, with broken outer lip, probably collected as an empty shell (Pl. 5, fig.5). It does not match Westerlund's illustration. Measurements:

Length	Width	W/L	LPer	LPer/L	Whorls
9.4	5.0	.53	5.8	.62	4 3/4

The relatively obese form of this specimen is widely different from that of other species of *Sibirenauta*.

Westerlund collection 12:31 (in SMNH) includes three small specimens, one with a fourth tiny shell in its aperture. The label reads "*Ph. sibirica* W. Kap Sopotschnaja Korga. Sibir."

Length	Width	W/L	Length peritreme	LPer/L	Whorls
4.1	2.2	.54	2.3	.56	3 1/2
3.9	2.2	.56	2.2	.56	3 1/2
3.8	2.1	.55	2.2	.58	3 1/4

These retain the periostracum, and were apparently collected as living specimens. They have a more narrowly conical form than the preceding specimen, besides being proportionally smaller, and represent another species of *Aplexa* or *Sibirenauta*. All specimens have a polished surface with obsolete spiral sculpture, proving that I was wrong in identifying Westerlund's species with *Beringophysa jennessi* (Taylor, 1988b).

Again, systematic allocation of this nominal form will need morphological study of material from the type locality.

Tribe **AMECANAUTINI**, new tribe

Penial sheath bipartite, consisting of a proximal, tubular, muscular part and a distal glandular part. Glandular part much stouter than and as long as the proximal portion, or relatively minor; and clearly set off from the muscular portion or not. Penis slender and distinctly tapered or flagelliform, with simple tip (non-cuticularized and without ornament), or with terminal, slightly swollen introvert. Mantle edge reflected over outer lip of the shell or not, with margin either scalloped or smooth.

Five genera: *Amecanauta g.n.*, monotypic, in northwestern Mexico (Jalisco); *Mexinauta g.n.*, about eight species from both coastal plains of Mexico to Costa Rica, and Ecuador to Peru; *Mayabina g.n.*, 11 species from Oaxaca and Veracruz, Mexico to Costa Rica, and Ecuador to northernmost Chile; *Tropinauta g.n.*, monotypic, in southeastern Costa Rica; and a "name uncertain" group in Argentina (Fig. 1).

Amecanauta g.n.

Type species: *Amecanauta jaliscoensis sp.n.*

Name: Río Ameca, and Latin *Nauta* (masculine; a sailor), a synonym of *Aplexa*.

Diagnosis: Shell fusiform to narrowly elongate, polished, with sculpture of axial growth lines and spiral series of minute arcs, convex in direction of growth. Profile of aperture broadly convex in direction of growth. Parietal callus narrow, apex acute. Length to about 18 mm. Inconspicuous pale spiral bands and axial or spiral white streaks in the shell may be present.

Mantle reflected broadly over shell on both sides, leaving exposed about 1/3 - 1/4 whorl. Posterior lobe distinct on right side of shell, but on left fused completely with anterior mantle. Mantle projections consist of broad, shallow scallops, with a diffuse patch of melanin in each, on columellar-parietal lobe (C), and on posterior lobe on both right (PD) and left (PS) sides; C 5-8, PD 2-3, PS 2. The hind end of the mantle reaches the ventral tip of the apex, but does not envelop it.

Penial complex: Preputium (PREP) thrice or more as long as penial sheath. Penial sheath bipartite, consisting of a tubular, muscular, proximal portion (SPM), only slightly enlarged at proximal end; and a glandular distal portion (SPG), short and abruptly expanded to about twice the width of proximal portion. Within preputium a wide but short, broadly convex sarcobelum (SAR), with blunt papilla (PAP). Penis (PEN) distinctly tapered from wider proximal end to simple tip and terminal pore. Vas deferens between paragonoporal angle (APG) and penial sheath about twice as long as penial sheath.

Penial retractor muscles originate as a common band, divided at mid-length or even farther towards the penial sheath. Distal retractor (MRSD) inserted on distal end of sheath. Proximal retractor (MRSP) divided into two equal bands, one inserted on proximal end of sheath, the other towards the distal end, above insertion of distal retractor. No cross-connections between proximal and distal retractor muscles. A retractor muscle of the preputium (MRPR) originates in the distal part of the distal retractor of the penial sheath, and is inserted on the proximal portion of the preputium.

Female system: Bursa copulatrix (BC) much as in *Austrinauta*: an elongate, plump sac, wider at its proximal end, sharply distinct from the duct (DBC), and longer. Distal end of oviduct III only about twice as wide as bursal duct. Vagina very short, wider than long, consisting of a short continuation of bursal duct and oviduct; W/L about 1.3.

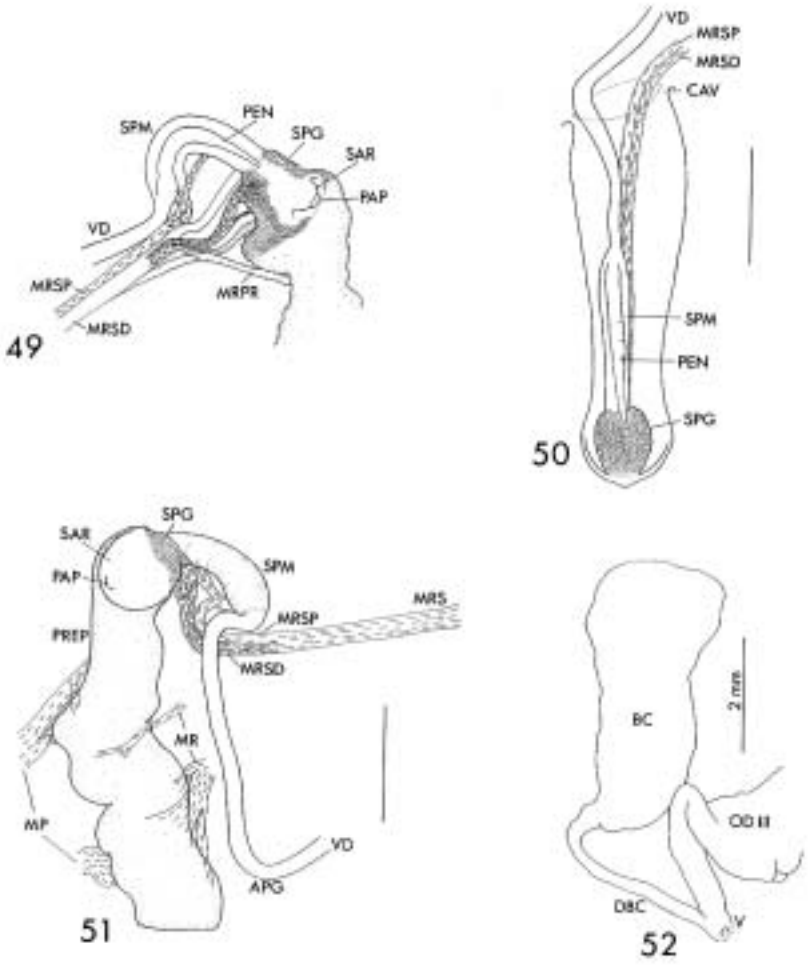
Distribution: Northwestern coast of Mexico, at the mouth of Río Ameca, forming the boundary between the states of Nayarit and Jalisco. It is striking that so close together on the coast of Mexico occur the most primitive genera of the Austrinautini (*Austrinauta*) and of the Amecanautini (*Amecanauta*).

Comparisons: *Amecanauta* is the most primitive of the Amecanautini in the short penial sheath, small glandular portion of the sheath, relatively short and obviously tapered penis, and short, broad sarcobelum. The penis has a simple tip as in *Austrinauta*, but the penis is more slender.

Amecanauta jaliscoensis sp.n.

Figs. 49-52, Pl. 1, fig. 3
Distribution Map, Fig.15

Holotype: CAS 114813. Mexico, Jalisco: Roadside ditch on W side of Mex. 200 opposite entrance to "Modulo de Abasto" de Puerto Vallarta, 2.2 km NE of entrance to airport, 20º41.48'N, 105º13.95'W, 16-IX-1987 (T87-901). Paratypes CAS 114 800 (10), BMNH 20001306 (10), MCZ 302596 (4), ZIBM CNMO 1159 (10).



Figs. 49-52. *Amecanauta jaliscoensis*. Mexico, Jalisco: 2.2 km NE of Puerto Vallarta airport. 49, detail of part of penial complex. 50, penial complex, extruded, seen in transparency. 51, penial complex in retracted state. 52, distal part of female system. APG, paragonoporal angle; BC, bursa copulatrix; CAV, edge of body cavity; DBC, duct of bursa copulatrix; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRPR, retractor muscle from MRSD to preputium; MRS, common retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; MS, muscular sheath; NP, penial nerve; OD III, terminal portion of oviduct; PAP, papilla; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale 1 mm except as indicated.

Name: From the state.

Description: The shell can be described most easily by comparison with that of *Austrinauta elatus*, because they are practically identical. Shells of *Amecanauta jaliscoensis* are far more fragile, pale tan rather than brown, and attain a slightly smaller size. No periostracal callus was seen, either because it is absent, or so thin as to be unrecognized. The columellar fold is often weaker or absent, and the junction of columellar and parietal margins of the aperture less marked.

A representative large specimen measures length, 16.4 mm; length peritreme, 12.8; width, 8.4 mm; whorls 5. The shells are so fragile that most of those collected were broken, and no series could be measured.

Habitat: The habitat was part of the extensive marshy area fed by Río Ameca. Here the snails were among grasses in water generally less than 6 in (15 cm) deep; only *Biomphalaria* was associated.

Mexinauta g.n.

Type species: *Physa nitens* Philippi, 1841.

Name: Mexico, and Latin *Nauta* (masculine; a sailor), a synonym of *Aplexa*, *i.e.*, the Mexican *Aplexa*.

Diagnosis: Shell fusiform to narrowly elongate, polished and without evident sculpture, or silky with microsculpture of spiral series of minute arcs, convex in the direction of growth. Profile of aperture broadly convex in direction of growth. Parietal callus narrow, apex acute. Length to about 35 mm. Spiral color bands and axial or spiral white streaks in the shell may be present.

External body (head, tentacles, foot, external mantle) gray to very dark gray. Mantle reflected over shell in two lobes, on the right with a large lobe over the columellar-parietal area, and as a ventral posterior lobe on both sides of the ventral aspect of the spire. Mantle projections on both lobes are in the form of scallops or broad, obtuse triangles.

Hermaphroditic duct convoluted in proximal 40%, with seminal vesicles sparse and small; broad in the next 50%, with numerous, closely crowded seminal vesicles shorter than the width of the duct that may be branched; and in the distal 10% diminishing in width, but still with numerous seminal vesicles.

Penial complex: Preputium longer or shorter than penial sheath. Penial sheath bipartite, consisting of a long, tubular muscular, proximal portion (SPM), only slightly enlarged at the proximal end, about 80-90% of total sheath; and a glandular distal portion (SPG), narrowly cylindrical. Sarcobelum with a small terminal papilla. Penis (PEN) long and flagellar, with simple tip and terminal pore. The vas deferens between paragonoporal angle (APG) and penial sheath is longer or shorter than the sheath.

Origin of retractor muscles of the penial sheath is side by side on the columellar muscle. The proximal retractor (MRSP) is inserted on the proximal end of the sheath, the distal retractor (MRSD) on the distal end.

Female tract: Oviduct III contracts into a slender tube in its distal portion, where it is little wider than the bursal duct. The bursa is a plump sac about twice as long as wide, longer than its duct, and sharply set off from it. The bursal duct and terminal portion of oviduct III are about of equal width, with W/L vagina about .50 - 1.0.

Distribution (Figs. 5, 53)**:** The two coastal plains of Mexico, on the west as far north as Jalisco, on the east barely into Texas, in the vicinity of Brownsville (now eradicated there); south through Guatemala and Nicaragua to northwestern Costa Rica; coastal Ecuador and Peru.

Comparisons: *Mexinauta* is distinctive especially by its large size, shell with color bands and axial white markings, in having a scalloped mantle margin on the columellar-

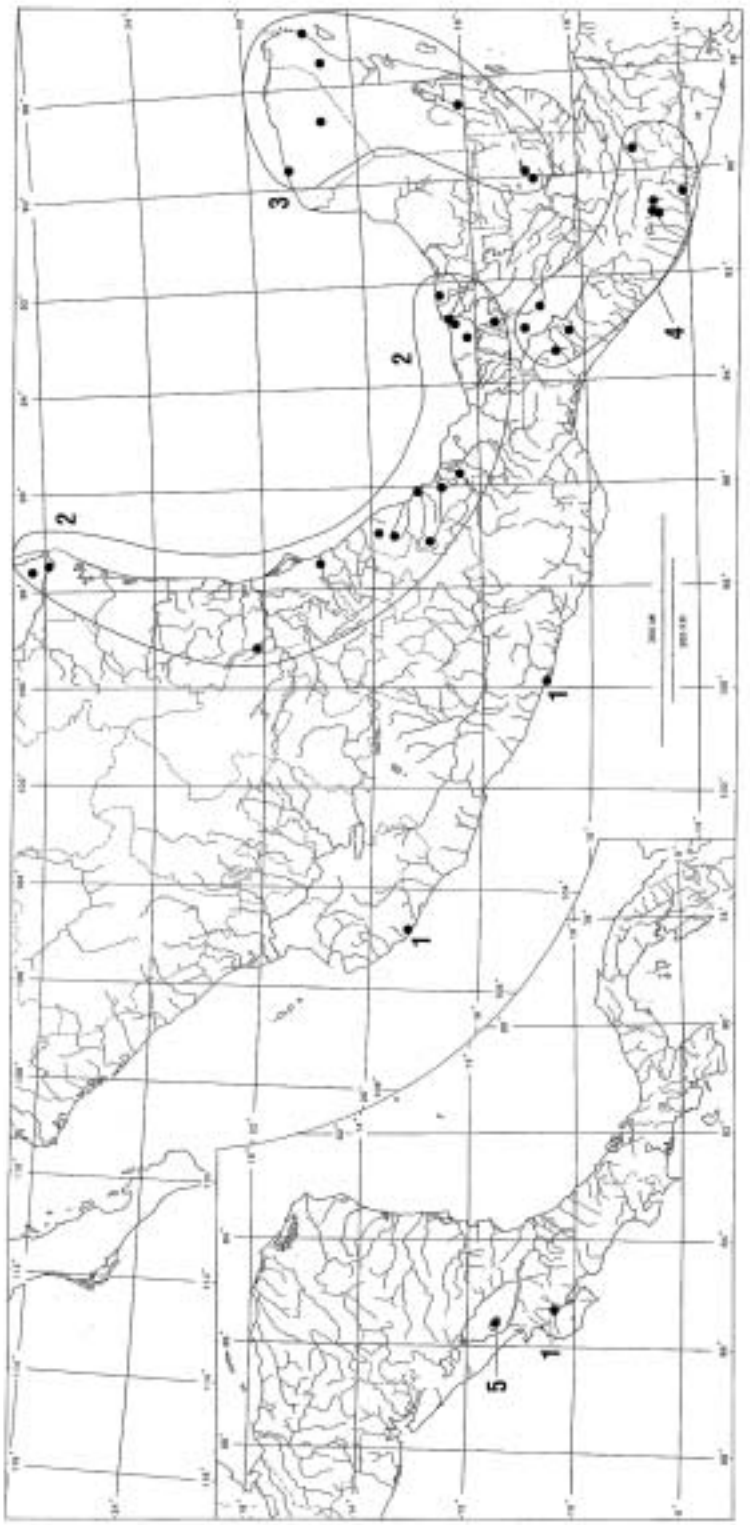


Fig. 53. Distribution of some species of *Mexinauta*, p. 74. 1, *aurantia*; 2, *nitens*; 3, *princeps*; 4, *impluviatus*; 5, *nicaraguanus*. Not shown: *gracilentus* and *laetus*, of which I have seen no material, and *peruvianus* of South America. For general range see Fig. 5.

parietal lobe, a penial sheath consisting of a long, narrow, tubular, muscular portion about 80-90% of length and short, slender, glandular portion, and flagelliform penis with simple tip. The genus includes the largest living species of the family. Fischer & Crosse (1870-1902, 2:89) reported shells of *M. nitens* up to 36 mm long, and the maximum length of a specimen of *Mexinauta aurantia* that I have examined was 36.3 mm (after erosion).

Referred species:

Mexinauta aurantia (Carpenter, 1857); TL "Mazatlán," surely in error, probably from Acapulco [16º5'N, 99º55'W]. Jalisco and Guerrero, Mexico, and Río Tempisque, Prov. Guanacaste, Costa Rica.

>*aurantia var. glandiformis* (Fischer & Crosse, 1886); TL near Acapulco [16º5'N, 99º55'W], Guerrero, Mexico.

Mexinauta gracilentus (Fischer & Crosse, 1886); TL Cobán [15º29'N, 90º19'W], Depto. Vera Paz, Guatemala.

Mexinauta impluviatus (Morelet, 1849); TL Guatemala City [13º40'N, 88º13'W], Guatemala. Chiapas, Mexico, to central Guatemala.

>*fuliginea* Morelet, 1851; TL Antigua [14º34'N, 90º44'W], Depto. Antigua, Guatemala.

>*purpurostoma* Tristram, 1861; TL Lake of Dueñas [now Laguneta Quilisimapa], Depto. Antigua, Guatemala.

=*influviata* "Morelet" Sowerby II, 1873; error for *impluviata* Morelet, 1851.

>*stolli* Clessin, 1885; TL "Guatemala."

>*aurantia var. bocourti* Fischer & Crosse, 1886; TL Cobán [15º29'N, 90º19'W], Depto. Vera Paz, Guatemala.

>*fuliginosa* "Morelet" Fischer & Crosse, 1886; error or emendation of *fuliginea* Morelet, 1851.

=*impluvialis* "Morelet" Paetel, 1889; error for *impluviata* Morelet, 1851.

Mexinauta laetus (Martens, 1898); TL Depto. Vera Paz, Guatemala.

Mexinauta nicaraguanus (Morelet, 1851); TL Lake Nicaragua, Nicaragua. Nicaragua.

Mexinauta nitens (Philippi, 1841); TL "Mexico," probably in the vicinity of Veracruz [32º25'N, 115º05'W], Veracruz. Coast of the Gulf of Mexico from extreme southern Texas to western Campeche, Mexico.

>*suturalis* Beck, 1838, *nomen nudum*; "Mexico."

>*berlandierianus* Binney, 1865; TL near Brownsville [25º54'04"N, 97º29'50"W], Cameron County, Texas.

>*conspicua* "Uhde" Martens, 1865; published in synonymy of *nitens* from Veracruz [32º25'N, 115º05'W], Veracruz, Mexico.

>*nitens var. acutalis* Fischer & Crosse, 1886; TL Cazones [20º43'N, 97º19'W], Veracruz, Mexico.

>*nitens var. gigantea* Fischer & Crosse, 1886; TL subfossil, Veracruz [32º25'N, 115º05'W], Veracruz, Mexico.

Mexinauta peruvianus Gray, 1828; TL swamps between Lima and Callao, Peru. Coastal Ecuador to central Peru.

=*major* d'Orbigny, 1837; new name for *peruviana* Gray.

>*gualbertoi* Cousin, 1887; TL Mapasingue [2º09'S, 79º54'W], Prov. Manabí, Ecuador.

Mexinauta princeps (Phillips, 1846); TL Yucatán, Mexico. Peninsula of Yucatán, Mexico, to northern Guatemala.

>*maugeriae* "Gray" Beck, 1838, *nomen nudum*; Mexico.

>*maugeriae* "Quoy" Sowerby II, 1873; TL "Jamaica."

Mexinauta aurantia (Carpenter, 1857)
Figs. 54-55, Pl. 2, figs. 4-9
Distribution Map, Fig. 53

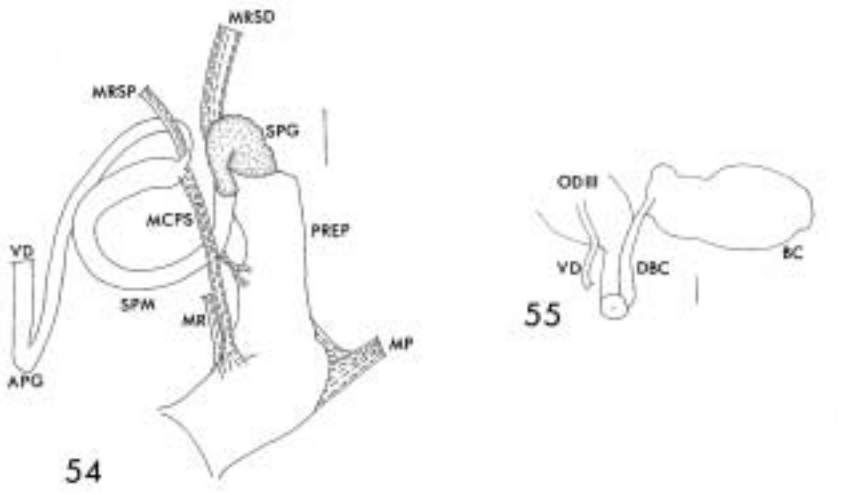
Aplexa aurantia Carpenter, 1857b:179.
Physa aurantia: Carpenter, 1864:541. Stearns, 1901:288; Acapulco.
Bulinus aurantius Carpenter: Binney, 1865:97, figs. 166, 167.
Aplecta aurantia: Tryon, 1882-1884, 1:200.
Stenophysa aurantia (Carpenter): Taylor, 1966:111.

Types: 22 syntypes BMNH 815-819; 4 paratypes MCZ 55 580, from the collection assembled at Mazatlán by Frederick Reigen, 1846-1848. Type locality "Mazatlán," Sinaloa; but surely from some place far to the south. Of the known localities, the types are most likely to have come from Acapulco [16º5'N, 99º55'W].

Name: Latin *aurantium*, orange.

Diagnosis: Shell often with spiral color bands and axial white markings, W/L .43-.54, length up to 36 mm; penial sheath longer than preputium; W/L vagina about 1.0.

Description: The shell is narrowly oval with an acute spire and broadly rounded anterior end. The profile of the aperture is broadly convex in the direction of growth, markedly retractive to the suture. The columella is heavy, white to pale lavender, with a fold conspicuous or not evident. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but not incised suture. The lateral profile of the spire is weakly concave. The shell surface is polished and shining, its color pale brown to deep redddish-brown, with a narrow pale band at the suture, and a broader dark brown or deep purple-brown band immediately below. Other spiral color



Figs. 54-55. *Mexinauta aurantia*. Parque Nacional Palo Verde, Costa Rica (T92-7601). 54, medial view of penial complex; 55, terminal portion of female tract. APG, paragonoporal angle; BC, bursa copulatrix; DBC, duct of bursa copulatrix; MCPS, connective between penial sheath and preputium; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor of penial sheath; MRSP, proximal retractor of penial sheath; OD III, oviduct III; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

TABLE 8
Measurements and descriptive statistics of shells of Mexinauta aurantia *from Bahía Tenacatita, Jalisco, Mexico (T87-1201). Measurements to nearest .16 mm. N = 20*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	25.26	18.9	.790	13.21	.522	6.2
Range	22.2-29.1	16.5-21.8	.714-.819	12.0-16.3	.469-.573	6-6$^1/_2$
S. D.	1.71	1.25	.015	1.11	.015	
S. E.	.381	.278	.006	.248	.006	

TABLE 9
Measurements and descriptive statistics of shells of Mexinauta aurantia *from Puerto Marques, Guerrero, Mexico (T87-1301). Measurements to nearest .16 mm. N = 6*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	19.36	15.28	.790	10.11	.522	5.3
Range	17.6-20.6	14.1-16.3	.770-.812	9.0-11.2	.509-.543	5-5$^1/_2$
S. D.	1.09	.721	.015	.767	.015	
S. E.	.443	.294	.006	.313	.006	

TABLE 10
Variation in numbers of mantle projections of Mexinauta aurantia *from Puerto Marques, Guerrero, Mexico (T87-1301). N = 14.*

	Columellar	Posterior
Mean	7.43	4.79
Range	6 - 9	4 - 6
S.D.	1.223	.699
S.E.	.327	.187

TABLE 11
Measurements and descriptive statistics of shells of Mexinauta aurantia *from Parque Nacional Palo Verde, Costa Rica (T92-7601). Measurements to nearest .1 mm. N = 30. Apex of the shells was slightly eroded, preventing a count of whorls, and making the ratios relative to length slightly in error*

	Length	LPer	LPer/L	Width	W/L
Mean	31.67	25.01	.765	15.79	.483
Range	30.3-36.3	23.2-28.0	.72-.83	13.6-17.7	.43-.52
S. D.	5.99	1.15	.026	.893	.022
S. E.	1.094	.210	.005	.163	.004

bands, all diffuse-edged, may be present. Fine, irregular white streaks, either continuous or discontinuous in short segments, occur in both axial and spiral arrangement. These may be inconspicuous, or so numerous as to give a chalky tone to much of the shell. Surface sculpture consists of fine axial growth lines and coarser wrinkles. Spiral sculpture consists of minute wrinkles either straight or weakly convex in the direction of growth that are arranged in spiral series, more strongly developed over the posterior part of the whorl, and discontinuous and less common on the anterior part of the whorl. When these are developed strongly they form a fine beadwork next to the suture. A finer spiral sculpture consists of incised lines that are discontinuous, and do not cut the axial wrinkles but may cut the growth lines.

The external body (head, tentacles, foot, external mantle) is uniformly very dark gray. In life the mantle is reflected over the shell in a narrow band of less than .1 whorl over the outer lip and anterior end of the shell, more broadly on the right side, but less than .25 whorl. In dorsal view the mantle is visible on the right anterior surface, and sometimes all along the left side of the body whorl. On the ventral side the mantle usually extends to the penultimate whorl, but may reach the tip of the spire; the tip is not enveloped. The mantle margin is smooth on the left side and anterior end, with projections on the two mantle lobes, at least in smaller specimens.

Both of the large series available are fully adult, and the characters of scalloping of the mantle margin so evident in *Mexinauta impluviatus*, *nitens* and *princeps* are not evident, perhaps because of wear or predation. A series of smaller specimens from Puerto Marques, Guerrero, Mexico (Table 10) showed the characteristic projections with internal melanin smudges. These smudges are diffuse and follow the contour of the mantle margin, unlike *M. princeps*, and are more diffuse than in the other species examined.

Variation: In the shell, color hue and banding are the most conspicuous variables besides the variation in form. Pale brown shells grade into deep reddish brown, almost dark purple-brown. Banding is commonly present, but subtle, with all bands diffuse-edged and usually inconspicuous except for the dark band below the suture. The hue of the bands is an intensification of the overall tone, with darker bands in darker shells. There may be up to twenty or thirty diffuse bands within the aperture. Form of shell is fairly uniform (Tables 8-10).

Comparisons: *Mexinauta aurantia* of the Pacific Coast is scarcely distinct morphologically from *M. nitens* of the Gulf Coast, but is usually narrower. The periphery is at about mid-length of the aperture, whereas in *M. nitens* the periphery is often more anterior. The two species form a pair like *Mayabina tapanensis* and *M. polita* of the two coasts of Mexico.

Spawn: The animals laid egg capsules freely on the sides of containers, but facilities for detailed observation were not available. The shape is ordinarily a long sausage in an open irregular curve, roughly half to three-quarters of a circle, 15-20 mm long. Ends of the capsule are blunt and subequal. Form varied from a quarter-circle to full circle, with many irregular curved shapes in addition. Number of eggs probably attains 150 in a capsule.

Distribution: Pacific coastal margin of southern Mexico in Jalisco and Guerrero; northwestern Costa Rica in the marshes of the lower Río Tempisque, Guanacaste Province.

Localities and material examined:

MEXICO, Jalisco: Marsh at Bahía Tenacatita, 1.4 km south of Mex. 200, 19º18.3'N, 104º48.4'W, 19-IX-1987 (T87-1201)(**M**).

Guerrero: "Acapulco" or "near Acapulco" [16º5'N, 99º55'W] (MCZ 49 732, 55 119, 76 852, 76 853, and uncat.), evidently *R. E. C. Stearns*, 1868. Llano Largo, 3 km NE Puerto Marques, 24, 27-IX-1987 (T87-1301) (**M**).

COSTA RICA, Prov. Guanacaste: Parque Nacional Palo Verde, edge of marshes 100 m E of W end of airstrip, 10º20.68'N, 85º20.60'W, 16-XI-1992 (T92-7503). Quebrada La Mula, 10º21.00'N, 85º16.94'W, 17-XI-1992 (T92-7601)(**M**). Other localities in the immediate vicinity are represented in INBio and UCR.

Habitat: At Bahía Tenacatita, the marsh is bordered by mangrove and carrizo (*Phragmites*); at the time of collection *Salicornia* was covered by brown fresh water. *Lemna* and abundant empty shells were floating on the surface. Evidently the marsh had been filled with water by the seasonal rains, and may be dry or even brackish much of the year. *Mexinauta* was abundant, several per m^2, climbing on stems or crawling on the lower surface of the water film. Few snails were visible before disturbance of the habitat, but stirring the vegetation and bottom caused the buoyant snails to rise to the surface. Associated molluscs were *Biomphalaria*, *Drepanotrema lucidum* (Pfeiffer), and *Planorbella*. Bivalves were sought but not found.

Quebrada La Mula is a sluggish channel with neither current nor discrete margin evident, filled entirely with emergent aquatic and floating vegetation. *Mexinauta* was abundant; the sample of 221 specimens came from an area of about 7 m^2, in water depth of 1-2 ft. Only one juvenile was found, and only one specimen of another species, *Drepanotrema lucidum* (Pfeiffer). *Mexinauta* here is the major invertebrate component of biomass.

Remarks: The largest recorded specimen of any living Physidae is from Quebrada La Mula (36.3 mm long). The shell was slightly eroded, so that the measured length is about .2 mm less than the length when intact.

Mexinauta impluviatus (Morelet, 1849)

Figs. 56-57, Pl. 3, figs. 9, 11-12
Distribution Map, Fig. 53

Physa impluviata Morelet, 1849-1851, 1:18 [1849].
Bulinus impluviatus Morelet: H. & A. Adams, 1858, 2:259.
Aplecta impluviata Morelet: Fischer & Crosse, 1870-1902, 2:91, pl. 30, fig. 3, pl. 39, fig. 5.

Types: Three syntypes BMNH uncat., three in MHNP (Chevallier, 1965:25). Guatemala: ditches in Guatemala City [13º40'N, 88º13'W], *Arthur Morelet*, 1847.

Name: "This name, given by Morelet, is derived from the Latin word *impluvium*, a reservoir of water or cistern in the atrium of an old Roman house, referring to *pluvia*, rain...." (Martens, 1890-1901).

Diagnosis: A species of *Mexinauta* with penial sheath longer than preputium, and W/L vagina about .50. The shell often has spiral color bands and axial white markings; W/L .48-.55, length up to 26 mm.

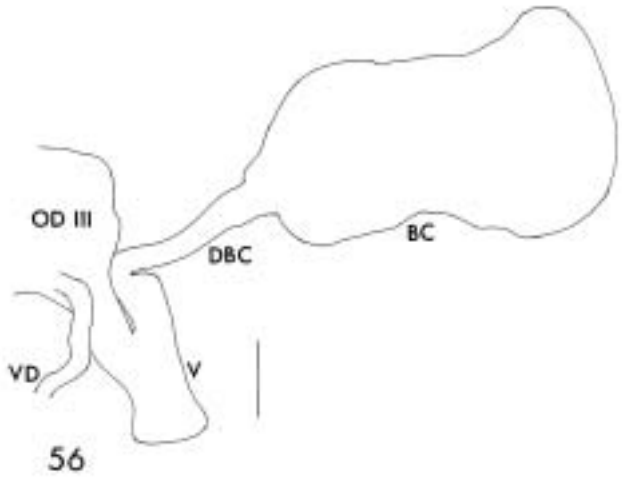
Description: Shell form, color and sculpture are as in *Mexinauta aurantia*. The exposed body (head, foot, tentacles, external mantle) is very dark gray. The mantle has two broad

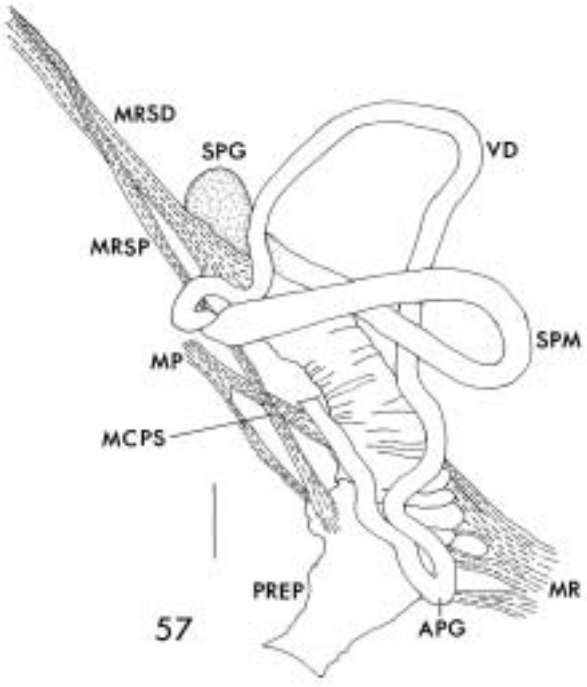
TABLE 12
Measurements and descriptive statistics of shells of Mexinauta impluviatus *from Laguneta Quilisimate, Guatemala (T91-1801). N = 17. Measurements to nearest .1 mm. Apex of the shells was eroded, preventing a count of whorls, and making the ratios relative to length slightly in error. The sample consists of two size-classes, of which only the larger was measured*

	Length	LPer	LPer/L	Width	W/L
Mean	23.17	16.51	.711	11.67	.504
Range	20.0-25.9	14.2-21.5	.65-.83	10.3-13.0	.48-.55
S. D.	1.54	1.71	.039	.782	.021
S. E.	.375	.415	.010	.190	.005

TABLE 13
Variation in numbers of mantle projections of Mexinauta impluviatus *from Laguneta Quilisimate, Guatemala (T91-1801). N = 30*

	Columellar	Posterior
Mean	8.83	5.07
Range	5 - 11	2 - 6
S.D.	1.341	.980
S.E.	.245	.179





Figs. 56-57. *Mexinauta impluviatus*, p. 80. Laguneta Quilisimate, Guatemala. 56, distal portion of female tract; 57, lateral view of penial complex. APG, paragonoporal angle; BC, bursa copulatrix; DBC, duct of bursa copulatrix; MCPS, connective between penial sheath and preputium; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD III, oviduct III; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale 1 mm.

lobes, one columellar-parietal, the other posterior, on the ventral aspect of the spire. Mantle projections are broadly rounded scallops in larger specimens, but in those half-grown they are broad, obtuse triangles with rounded tips; in all cases there is a smudge of melanin just within the pale edge of the mantle. The shell is much like that of *M. aurantia* and *M. nitens*, but attains lesser size. As in *M. aurantia*, the penial sheath is longer than the preputium, but the vagina is about twice as long as in *M. aurantia, nitens*, or *princeps*.

Distribution: Eastern Chiapas, Mexico, to southern Guatemala.

Localities and material examined:

MEXICO, Chiapas: Pond at Pueblo Nuevo Solistahuacán [17º06'N, 92º53'W], 5 800 ft, *D. E. Breedlove*, 12-XII-1972 (CAS 52 432, 079 121)(**M**). San Cristobal de las Casas [16º45'N, 92º38'W], 2 200 m, *I. J. Cantrall*, 14-IV-1941 (UMMZ 151 427); 7 000 ft, *Eugene Hunn*, 13-XI-1971 (CAS 52 408). 65 km S of Tuxtla Gutierrez along road to Nueva Concordia, 2700 ft, *D. E. Breedlove*, 12-IX-1974 (CAS uncat.). 15 km S of Ocozocuautla along road to Villa Flores, 2 800 ft, *D. E. Breedlove*, 13-IX-1974 (CAS uncat.).

GUATEMALA, Depto. Chimaltenango: Yepocapa [14º30'N, 90º57'W], in fountain, *H. Elishewitz*, 15-IX-1944 (MCZ 155 092). Parque Nacional Los Aposentos, 2.5 km S Chimaltenango, 14º38.00'N, 90º48.83'W, 1720 m, 16-XI-1991 (T91-1704)(**M**). =Ditch near Park Chimaltenango, *W. Bullock, F. Aguila*, 15-IV-1963 (MCZ 246 731).

Depto. Guatemala: Laguna El Naranjo, Finca El Naranjo, ca. 5 km NW of Ciudad Guatemala, 14º38.8'N, 90º33.82'W, 1560 m, 12-XI-1991 (T91-1401)(**M**). Environs of Guatemala City [13º40'N, 88º13'W], *A. Morelet*, 1847 (BMNH uncat.). Guatemala City; from F. R. Latchford collection 18770 (UMMZ 193 667).

Depto. Sacatepéquez: Antigua, *A. Morelet*, 1847 (BMNH 1893.2.4.663-665). Antigua [14º34'N, 90º44'W], in fountain, *G. B. Fairchild* (MCZ 155 481). Laguneta Quilisimate, between Santiago Zamora and Santa Catarina Barahona, 14º32.57'N, 90º47.46'W, 1460 m, 16-XI-1991 (T91-1801)(**M**). From a small stream running into the Lake of Dueñas above Santiago Zamora, *O. Salvin*, 31-VII-1873 (BMNH 1901.6.22.1228-1236).

Depto. Santa Rosa: Río Taxisco, Taxisco 14º04'N, 90º28'W], *D. T. Dalmat* (MCZ 210 578).

Depto. Zacapa: Zacapa [14º58'N, 89º32'W], *J. Bequaert* (MCZ 110737).

Remarks: The fountains in the plazas of Antigua no longer have snails. The water supply is chlorinated heavily for protection of the inebriates who drink thirstily from the fountains at night.

Mexinauta nitens (Philippi, 1841)
Figs. 58-65, Pl. 1, figs. 5-7
Distribution Map, Fig. 53

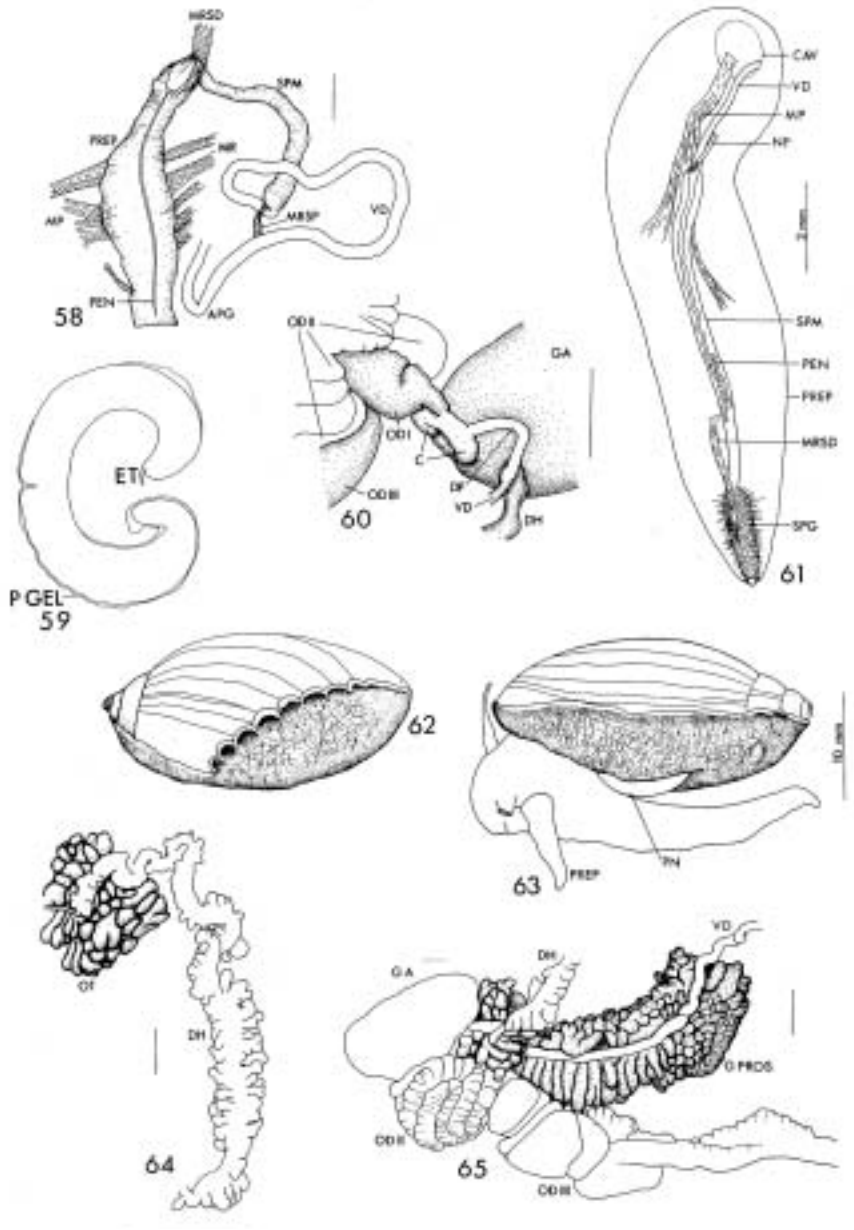
Physa nitens Philippi, *in* Martini & Chemnitz, 1837-1918, 32:5, pl. 1, figs. 1-2 [1841]; "in Mexiko," no precise locality. Martens, 1865:57; Veracruz, *Uhde*; *Aplexa suturalis* Beck as synonym. Martens, 1890-1901:357, pl. 19, fig. 19 [1898]; Veracruz, San Juan, and Jalapa, state of Veracruz; not Yucatán locality.

Bulinus nitens Philippi: Binney, 1865:98, fig. 168.

Aplecta nitens Philippi: Fischer & Crosse, 1870-1902, 2:88, pl. 39, fig. 1-1b [1886]; ditches, canals and swamps of the state of Vera Cruz.

Aplexus nitens Philippi: Paetel, 1888-1890, 2:410 [1889].

Aplexa nitens: Berry, 1949:4; near Brownsville, Texas; molluscacidal susceptibility. Von Brand *et al*., 1950:267; laboratory-reared from specimens collected near Brownsville, Texas; anaerobic metabolism. P. McMahon *et al*., 1957:220, 232; polysaccharide content of albumen gland in lab-reared specimens from Texas stock.



Figs. 58-65. *Mexinauta nitens*, p. 82. 58, 60-65, Mexico, Tabasco: road to Playa Miramar (T88-1502). 59, Buenos Aires, Veracruz (T89-401). 58, penial complex, lateral view, with penis (shown by transparency) extruded through nearly the whole length of the preputium. 59, freehand sketch of spawn. 60, detail of separation of hermaphroditic, male, and female tracts. 61, penial complex extruded, seen by transparency. 62-63, right and left sides of one specimen with preputium extruded; most of left tentacle removed. 64, hermaphroditic duct. 65, detail of proximal portion of female system and vas deferens. APG, paragonoporal angle of vas deferens; C, caecum; CAV, edge of body cavity; DF, female duct; DH, hermaphroditic duct; ET, terminal tail; GA, albumen gland; G PROS, prostate; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRSD, distal penial retractor; MRSP, proximal penial retractor; NP, penial nerve; OD I, OD II, OD III, oviduct; OT, ovotestis; P GEL, pallium gelatinosum; PEN, penis; PN, pneumostome; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm except as indicated.

TABLE 14
Measurements and descriptive statistics of shells of Mexinauta nitens *from Buenos Aires, Veracruz, Mexico (T89-401). Measurements to nearest .1 mm. N = 30. Apex of shells eroded; whorls not counted*

	Length	LPer	LPer/L	Width	W/L
Mean	30.45	23.15	.760	17.13	.563
Range	27.7-35.0	21.6-26.4	.69-.82	15.5-19.1	.51-.61
S. D.	1.70	1.31	.029	.969	.024
S. E.	.310	.239	.005	.180	.004

TABLE 15
Measurements and descriptive statistics of shells of Mexinauta nitens *from near road to Playa Miramar, Tabasco, Mexico (T88-1502). Measurements to nearest .1 mm. N = 25. Apex of shells eroded; whorls not counted*

	Length	LPer	LPer/L	Width	W/L
Mean	29.58	23.13	.782	15.48	.524
Range	27.7-32.9	20.7-25.5	.72-.85	14.0-17.2	.49-.57
S. D.	1.44	1.25	.028	.843	.020
S. E.	.289	.249	.006	.169	.004

Holotype presumably destroyed in SMF. Type locality "In Mexiko." Veracruz [32º25'N, 115º05'W], the major seaport within the range of the species, is probably the original locality.

Name: Latin *nitens*, polished, shining.

Diagnosis: Shell often with spiral color bands and axial white markings, W/L .46-.61, length up to 35 mm; penial sheath shorter than preputium; W/L vagina about 1.1 - 1.9.

Description: The external body (head, tentacles, foot, external mantle) is jet black. The mantle lobes reflected over the shell are so thin that the white-lined shell can be seen vaguely through them in some specimens, and the sinuses leading to the mantle edge are outlined in black, contrasting with the dark gray areas between. On the columellar-parietal margin of the mantle either the tips only, or the whole extent, of the broad, shallow scallops are black, and in paler individuals the black tips contrast with the rest of the mantle.

Degree of reflection of the mantle over the shell, and extent of scalloping, vary. The extreme of coverage seen in about 60 live specimens from near Playa Miramar, Tabasco (T88-1502) was broad lobes on either side of the shell, leaving only about 1/6 of the dorsal surface of the shell exposed, and covering the apex. The mantle is reflected over the shell in three lobes. At the anterior end of the shell is a narrow reflection continuous with the lobe on the left side, the largest, that extends continuously to the apex, usually on the ventral surface only but sometimes enveloping it. The margin of the left lobe is smooth but irregular, and towards the apex there may be 2-4 weak, shallow scallops. On the right side the mantle is divided into two lobes, separated at about 2/3 the length of the body whorl; the division may be sharp and deep or shallow and indistinct. Scallops are more conspicuous on the anterior of the two right lobes, numbering 8-10; even when they are weakly developed they are highlighted by a concentration of melanin in the form of an elongate curved aggregation next to the creamy margin.

Male system: the many crowded follicles of the prostate are simple, or branch 1-3 times. Vas deferens (VD) between paragonoporal angle (APG) and penial sheath shorter or longer than sheath. Up to three-fourths of the distal, glandular portion (SPG) of the sheath is inserted into the preputium, where it is bound by a web of muscle fibers.

Aphally was encountered in one specimen (T88-1502). The vas deferens was normal in

the upper part of the prostate, becoming vestigial within the prostate, and not found thereafter. The preputium was of normal size and form, even though without vas deferens or penis.

Female system: The female duct passes along the surface of the albumen gland, in which it is mostly embedded, then widens, giving off two caeca, and meets the narrow entrance to oviduct I (OD I).

The bursa copulatrix is an elongate sac, longer than wide, with its duct sharply set off and leaving at the anterior end of the bursa. The duct is short, shorter than the vagina. Length of the vagina was measured from the junction of OD III and bursal duct to the female pore, and the width across the upper end immediately below the junction of the two ducts; W/L 1.1 to 1.9.

Spawn: Two spawn masses were observed. Both were a clear, gelatinous sausage, coiled through about 180º and more than 360º; eggs numbered about 90 and 225, respectively, in three layers and 3-4 rows. Ends of the masses were blunt, in one case with a narrow terminal wisp (Fig. 59). The pallium gelatinosum is a thin and generally uniform layer, but somewhat lumpy.

Behavior: Copulation was observed in four cases. In two the functional male was larger than the partner, in one case about equal in size, and in a fourth case the functional male was the smaller. No courtship, play, or stimulation was observed; the preputium was everted, extended, and then it probed for the female pore. There followed some quick dorso-ventral shaking of the shell, perhaps with emission of sperms. The mobile and extensible preputium is nearly colorless and translucent; within it the long, narrow, pale muscular portion of the penial sheath can be seen, contrasting with the cream-colored glandular portion.

Comparisons: See under *Mexinauta aurantia*.

Distribution: Coastal lowlands along the Gulf of Mexico from the vicinity of Brownsville, Texas, to western Campeche.

Localities and material examined (in NW to SE order):

Texas, Cameron County: Fifteen miles N Brownsville, *Jay Weber* (CAS 49 960). Vicinity of Matamoros, *J. L. Berlandier*, 1830-1851 (type locality of *berlandierianus*).

MEXICO, Tamaulipas: Hacienda Acuña, 2 650 ft (808 m) elevation [locality not traced], *Robert G. Webb*, 1-VIII-1966.

San Luis Potosí: Seven miles W Micos [22º08'N, 99º11'W] (MCZ 55 265).

Veracruz: Charco at Buenos Aires, 20º57.5'N, 97º30.0'W, 19-III-1989 (T89-401)(**M**). Misantla [19º56'N, 96º50'W] (MCZ 210 537). Veracruz [32º25'N, 115º05'W], *Luis Mazzotti* (MCZ 172 523). Jalapa [19º32'N, 96º55'W], *Höge* (BMNH 1901.6.22.1177-1178). Córdoba [18º53'N, 96º56'W], *A. Sallé* (BMNH uncat., *ex* Cuming collection). Cerro de las Mesas, between Ignacio de la Llave and Piedras Negras, *M. Stirling* (CAS 51 058, MCZ 184 112). Cosamaloapan [18º22'N, 95º48'W], *Luis Mazzotti* (MCZ 172 522).

Tabasco: Pasture pond at km 21.1, NW of Taxco, on road Nacajuca to Villahermosa, 18º8.6'N, 93º0.4'W, 14-II-1988 (T88-1801)(**M**). Ponds beside Mex. 180, 1 km N of road to Ignacio Allende, 18º23.9'N, 92º47.9'W, 14-II-1988 (T88-1602)(**M**). Pasture pool beside Mex. 180, 2.3 km NE of road to Playa Miramar, 18º28.3'N, 92º44.6'W, 13-II-1988 (T88-1502)(**M**). Roadside marsh about 1 km N of junction of Tacotalpa-Tapijulapa road with road to Teapa, 17º34.9'N, 92º49.4'W, 20-II-1988 (T88-3002). Pasture pond beside Jalapa-Tacotalpa road 2 km S of road to Guanal, N of Rancho Nuevo, 17º38.2'N, 92º49.2'W, 20-II-1988 (T88-3102)(**M**).

Campeche: Ditch beside Mex. 180 0.5 km E Nuevo Progreso, 18º37.2'N, 92º17.1'W, 18-II-1988 (T88-2702).

Habitat: At six localities associated mollusc species ranged in number from one to six. *Pomacea flagellata* (Say) was present at all six localities; *Biomphalaria* sp. and *Drepanotrema lucidum* (Pfeiffer) at five localities each. Other species were found at only one locality each.

Mexinauta peruvianus (Gray, 1828)

Pl. 3, fig. 8

Physa peruviana Gray, 1828:5, pl. 6, fig. 10.
Aplexa peruviana (Gray): Beck, 1838:117. Larrea *et al.*, 1990:40-41; distribution in Depto. Lima, Peru.
Bulinus peruvianus, Gray: H. & A. Adams, 1858:259.
Aplecta peruviana, Gray: Fischer & Crosse, 1870-1902:85 [1886].
Stenophysa peruviana peruviana (Gray): Te, 1980:182.

Holotype: BMNH 1950.5.24.3. Swamps between Lima and Callao, Peru, *Rev. W. Hannah.* The series of four (1950.5.24.3-6) is labeled syntypes, but within the aperture of one is a printed label "Type;" this specimen was figured by Gray and is accepted as the holotype.

Name: From the locality.

Description: The type series retained original dirt within, and apparently was collected as empty shells. They are slightly bleached, but retain some purple coloring, and when fresh would have been much like *Mexinauta aurantia* in this respect. The shell is polished, with obscure white spiral bands, and narrow, irregular axial streaks that are concentrated toward the suture on the last two whorls. The apex is a rich, dark, ruby-red. Sculpture consists of fine axial growth lines, and microsculpture of sparse, minute, short raised lines, either straight or convex toward the aperture, arranged in spiral series. This spiral sculpture may be more closely crowded and stronger toward the suture.

Type	Length	Width	W/L	Whorls
1	23.4	11.9	.51	6
2	22.1	11.3	.51	6
3	22.3	11.9	.53	5 3/4
4	21.2	11.6	.55	---

Localities and material examined:

ECUADOR: Guayaquil [2º10'S, 79º54'W], *R. B. Hinds, H.M.S. Sulphur*, 1836 (BMNH 1851.12.2.257, 3 specimens, from Capt. Belcher's collection). Mapasingue [2º09'S, 79º54'W], Prov. Manabí (type locality of *gualbertoi* Cousin).

PERU, Swamps between Lima and Callao (type locality). "Peru," with no more data, from Cuming collection; perhaps part of original sample (BMNH uncat., 7 specimens).

Mexinauta princeps (Phillips, 1846)

Figs. 66-67, Pl. 2, figs. 1-3, Pl. 3, fig. 13
Distribution Map, Fig. 53

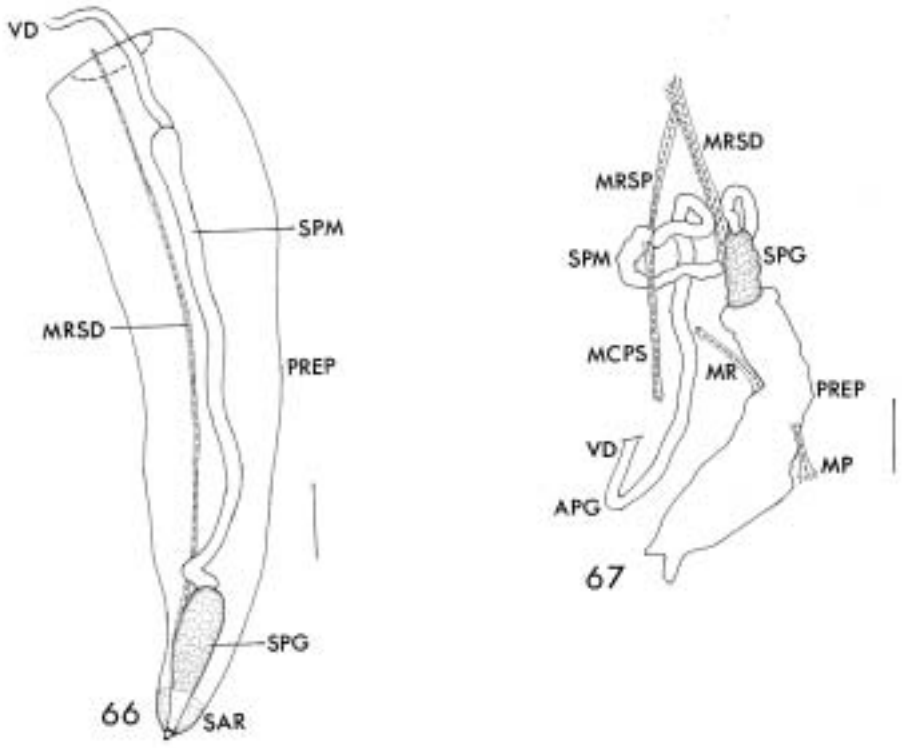
Physa princeps Phillips, 1846:66, pl. 1, fig. 11.
Bulinus princeps Phillips: Gould, 1870:486.
Aplexa princeps (Phillips): Bequaert & Clench, 1933:539.
Stenophysa princeps (Phillips): Rehder, 1966:280.

Holotype: ANSP 21 184a (H. B. Baker, 1964:155). Yucatan [Peninsula], no precise locality, *B. M. Norman*.

Name: Latin *princeps*, chief, leader, probably in reference to the relatively large size.

Diagnosis: Only one shell series has been available for study, and all shells are exceptionally slender. No diagnosis can be prepared.

Description: Head, tentacles, dorsum of foot, and pneumostome medium gray. The



Figs. 66-67. *Mexinauta princeps*, p. 86. Guatemala, Depto. Petén: 4.5 km S of La Libertad-San Francisco road. 66, preputium extruded and penial sheath within, seen by transparency. 67, penial complex. APG, paragonoporal angle; MCPS, connective between penial sheath and preputium, insertion removed and muscle moved to one side; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

external mantle is very pale gray and translucent, so that it appears brown over the tan shell. The columellar-parietal mantle lobe has low projections varying from convex scallops to broad obtuse triangles. The melanin smudge within each projection does not parallel the mantle edge; the farthest extent of the melanin concentrations is in a nearly straight line, so that the pale mantle border is wider at the apex of each projection. Sinuses in the mantle are outlined by a delicate border of melanin.

The posterior mantle lobe is a broad, fan-shaped structure on the ventral aspect of the spire, extending onto both sides of the spire. Projections are broad obtuse triangles, as with the other mantle lobe having the farthest limit of the melanin concentrations aligned. The ventral lobe passes smoothly into the smooth-edged, reflected mantle on the left side; toward the posterior end this portion covers about 1/10 of a whorl, narrowing toward the anterior end, where a mantle reflection is barely discernible. Along the margin of the smooth-edged mantle segment there is a nearly continuous, narrow, diffuse strip of melanin, that has not been seen in other species of the genus. Mantle projections on the columellar-parietal lobe (C) and posterior lobe (P) varied from C 9-11, P 6-7, in three specimens.

Penial complex: The preputium is longer than the penial sheath. The glandular portion of the sheath, only a small part of the sheath, is variable in proportions. In four specimens preserved with preputium extruded, the glandular

portion could be seen readily through the preputium; its W/L ranged from .16 to .33. The sarcobelum is longer than wide, and bears a small papilla. Preputium, retractors of preputium, penial sheath, penial retractors, and even the distal portion of the vas deferens are flecked with melanin, the distal, glandular portion of the sheath most heavily.

Penial retractors have adjacent but separate origins. The distal retractor is inserted on the distal, glandular portion of the sheath, the proximal retractor on the proximal end of the sheath. The female system has the general proportions seen in other species of the genus, but in the one specimen examined the vagina is wider than long.

Distribution: Yucatan Peninsula, from Yucatán and Quintana Roo, Mexico through northern Guatemala to Belize.

Localities and material examined:

MEXICO, Quintana Roo: Marsh .5 km W Puerto Morelos, 20º50.8'N, 86º52.9'W, 2-X-1987 (T87-1801). Laguna de Cobá, Cobá, 20º29.38'N, 87º44.08'W, 3-X-1987 (T87-2002). Río Hondo, *D. B. Parson* (MCZ 76 851).

Yucatán: Dried pond at Pemex plant 4 km S of Puerto Progreso, 21º15.0'N, 89º39.5'W, 19, 24-IV-1986 (T86-502). Dzadz Cenote, 6 1/2 mi SW Chichén Itzá, *E. P. Creaser* (MCZ 59 762).

GUATEMALA, Depto. El Petén: Aguada 4 1/2 km from La Libertad road to San Francisco, 16º48.1'N, 90º0.3'W, 22-XI-1991 (T91-3001)(**M**). Small drying aguada just SW of San Benito (opposite Flores on mainland), *Henry van der Schalie*, 22-II-1935 (MCZ 99 303).

BELIZE, Corozal District: Louisville forest, *R. W. Neck*. Orange Walk District: Orange Walk [17º16'N, 88º47'W] (BMNH 1897.7.6.12-15).

Habitat: At the Pemex plant south of Puerto Progreso, there were two ponds, one on either side of the raised entrance road, similar in shallow depth. To the north there was a little water, with *Mayabina spiculata*; to the south there remained only dried mud and empty shells, with *Mexinauta princeps* but no *M. spiculata*. Among the cattails (*Typha*) the mud was locally moist, and beneath the mat of fibrous roots and rhizomes under an individual plant there were one or two empty shells of *M. princeps*. From their location, these snails had burrowed into the moist mud, then followed the moisture as it dried.

The Guatemala locality was in an artificial excavation about 50x100 ft, with water 1 ft deep over dead leaves and firm mud, and sparse emergent aquatic vegetation throughout. It was different from all other aguadas seen in the area by being so small and heavily shaded; this was the only site where Conchostraca were noted. The shells found here are more slender than any others seen, but are connected by intermediates to the stouter shells from Yucatán.

Mayabina g.n.

Type species: *Physa cisternina* Morelet (1851), <*Mexinauta spiculatus* (Morelet, 1849).

Name: El Mayab, the region inhabited by the Mayas.

Diagnosis: Shell small to medium sized, slender, to about 25 mm. Mantle projections usually are round-ended triangles (scallops in *M. bullula*), in two groups, columellar-parietal (C) and left posterior (P) on a strong, fan-shaped lobe; numbers of projections are greatly variable.

Penial complex: Penial sheath bipartite, consisting of a long, slender, proximal, muscular tube forming about 60-80% of sheath, and a wider, cylindrical, distal, glandular portion varying from 2-5 times as wide as the muscular portion. Penis flagelliform, with simple tip and terminal pore.

Penial retractor muscles arise usually as a single band from the columellar muscle. The proximal retractor (MRSP) arises from the

common band at less than 5% to 25% of length. Whether origins are separate or common, the proximal retractor is inserted on the proximal end of the sheath, the distal retractor (MRSD) on the distal glandular portion of the sheath.

Distribution: From Oaxaca and Veracruz, Mexico, to Costa Rica; Ecuador to northernmost Chile (Figs. 6, 68, 69).

Comparisons: *Mayabina* is distinct by the slender, cylindrical distal glandular portion making up about 20-40% of the penial sheath, and flagelliform penis with simple tip and terminal pore. Commonly but not invariably there are roughly triangular mantle projections in two groups, with a large left posterior lobe; and origin of penial retractor muscles as a single band.

Referred species:

Mayabina bullula (Crosse & Fischer, 1882); TL Tuxpan [20º57'N, 97º24'W], Veracruz, Mexico. Veracruz state, Mexico.
=*bullatus* "Crosse et Fischer" Paetel, 1889; error for *bullula* Crosse & Fischer, 1882.

Mayabina carolita (Jousseaume, 1887); TL San Nicolás, Cantón Mejía, Prov. Pichincha, Ecuador. Ecuador to northernmost Chile.
=*martinidella* Cousin, 1887; same TL.

Mayabina nitidula (Clessin, 1886); TL Honduras, no precise locality.

Mayabina obtusa (Clessin, 1885); TL Honduras, no precise locality.

Mayabina petenensis sp.n.; TL Aguada at NE side of La Libertad, 16º47.30'N, 90º6.49'W, 200 m, Depto. El Petén, Guatemala. Northern Guatemala.

Mayabina pliculosa (Martens, 1898); TL Río Reventazon, Ujarrás [9º50'N, 83º50'W], Prov. Cartago, Costa Rica. Central Costa Rica.
>*nitens var. minor* Strebel, 1874; TL Laguna Redonda [not traced], Candelaria, Costa Rica.
>*impluviata var. gracilior* Martens, 1898; TL vicinity of San José [9º56'N, 84º05'W], Costa Rica.
>*fuliginea var. hoffmanni* Martens, 1898; TL Laguna Redonda [not traced], Candelaria, Costa Rica.

Mayabina polita sp.n.; TL 1.5 km S of Mex. 186 toward Zopo Norte, 17º39.6'N, 92º24.7'W, Tabasco, Mexico. Tabasco to Yucatán, Mexico.
>?*cisternina var. abbreviata* Fischer & Crosse, 1886; TL Mérida [20º58'N, 89º37'W], Yucatán, Mexico.
>*cisternina var. gracilis* Fischer & Crosse, 1886; TL Mérida [20º58'N, 89º37'W], Yucatán, Mexico.
>*cisternina var. minor* Fischer & Crosse, 1886; TL Mérida [20º58'N, 89º37'W], Yucatán, Mexico.
>*cisternina var. ventrosior* "Morelet" Martens, 1898.

Mayabina sanctijohannis sp.n. TL Barra del Colorado, 10º46.37'N, 83º35.27'W, Prov. Limón, Costa Rica.

Mayabina spiculata (Morelet, 1849); TL Campeche [19º51'N, 90º32'W], Campeche, Mexico. Peninsula of Yucatán, Mexico.
>*cisternina* Morelet, 1851; TL Mérida [20º58'N, 89º37'W], Yucatán, Mexico.
=*speculosa* Martens, 1873; error for *spiculata* Morelet, 1849.
>*princeps var. pallens* Martens, 1898; TL Yucatán, Mexico.

Mayabina tapanensis (Crosse & Fischer, 1882); TL San Pedro Tapanatepec [16º21'N, 94º12'W], Oaxaca, Mexico. Southeastern Oaxaca, Mexico, to southern Guatemala.
?>*tapanensis var. guatemalensis* Fischer & Crosse, 1886; TL Plateau of Guatemala.

Mayabina tempisquensis sp.n.; TL 10º20.68'N, 85º20.60'W, in Parque Nacional Palo Verde, Prov. Guanacaste, Costa Rica. Prov. Guanacaste, Costa Rica.

The species of *Mayabina* in Mexico fall into two discrete species-groups on the basis of size, the species in each group being geographically

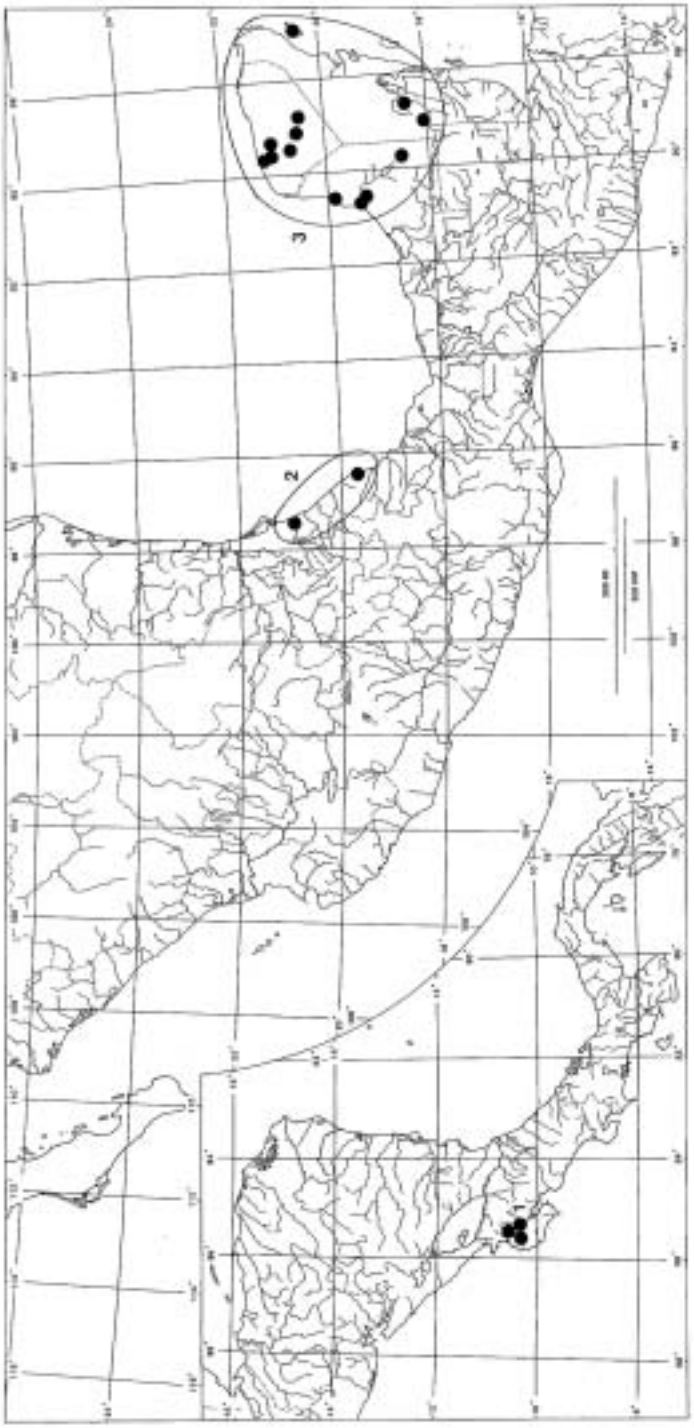


Fig. 68. Distribution of some species of *Mayabina*, p. 88. 1, *M. tempisquensis*; 2, *bullula*; 3, *spiculata*.

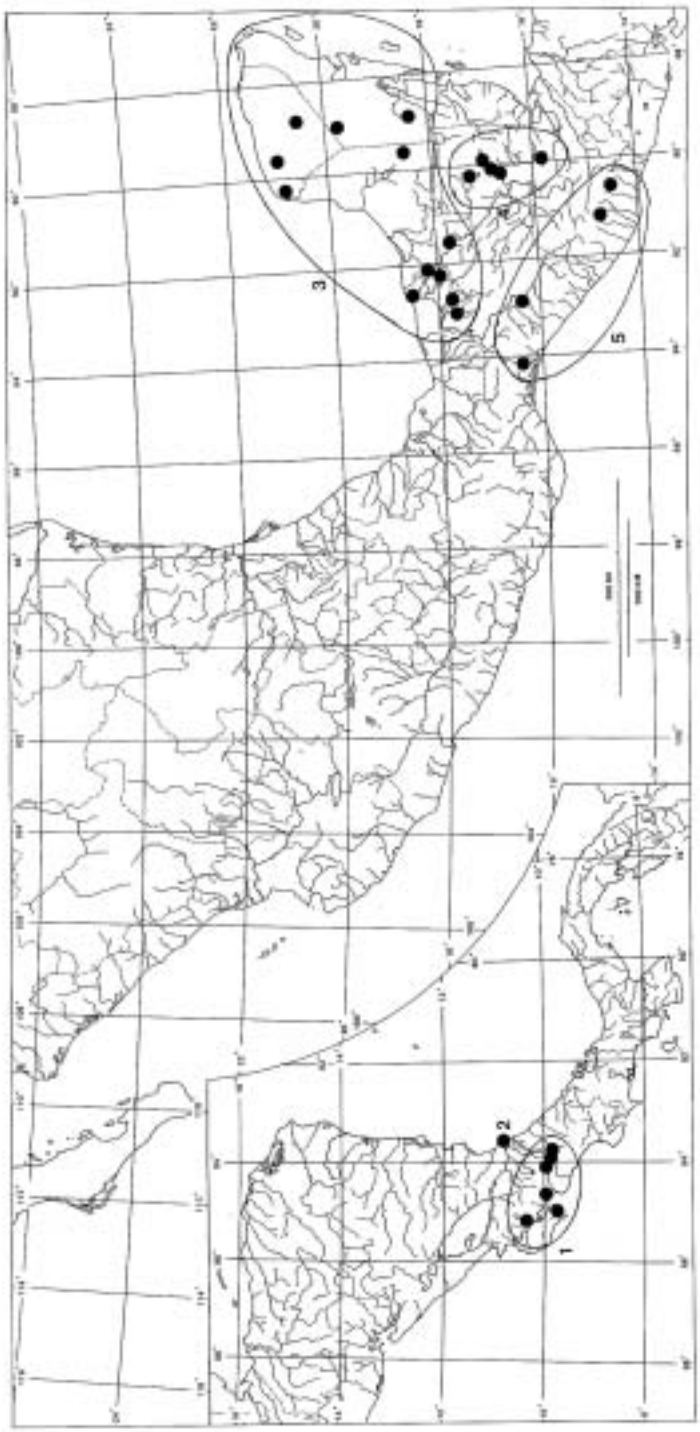


Fig. 69. Distribution of some species of *Mayabina*, p. 88. 1, *M. pliculosa*; 2, *sanctijohannis*; 3, *polita*; 4, *petenensis*; 5, *tapanensis*.

distinct. *M. spiculata* of the Yucatan peninsula is most like *M. bullula*, found also on the eastern coastal plain, in Veracruz state; both species are relatively large. *M. tapanensis*, southeastern Oaxaca to Guatemala on the Pacific slope, is most like *M. polita*, Tabasco to the Yucatan peninsula, on the eastern coastal plain; these two are relatively small. *M. polita* overlaps in range with *M. spiculata* and is sometimes found associated with it.

This same grouping into larger and smaller species can be recognized also in Honduras, with the barely known *M. nitidula* and *M. obtusa*. But in Guatemala and Costa Rica the species cannot be assigned readily to a *spiculata*-group and a *tapanensis*-group. The South American *M. carolita*, hardly known as yet, belongs to the *tapanensis*-group on the basis of size. Its penial retractor muscles originate from a common band as in most of the northern species. Except for *M. polita* and *M. spiculata* as noted above, all of the species have separate ranges, as is characteristic in other genera of Physidae.

The differences between the species are sometimes in shell characters (the strong sculpture and color bands of *spiculata*), sometimes in the mantle projections (scallops in *bullula*, triangles in the other species; square-tipped projections often in *petenensis*), but principally in the penial sheath. The relative proportions of the glandular and muscular portions provide the most characteristic specific differences.

Mayabina bullula (Crosse & Fischer, 1882)

Figs. 70-75, Pl. 3, figs. 1-3
Distribution Map, Fig. 68

Aplecta bullula Crosse & Fischer, 1882:334. Fischer & Crosse, 1870-1902, 2:91, pl. 39, figs. 6-6b [1886].

Holotype: not in MHNP (Chevallier, 1965:25). Mexico, Veracruz: Tuxpan [20º57'N, 97º24'W], *Auguste Sallé*.

Name: Latin *bulla*, bubble, and the diminutive; a little bubble.

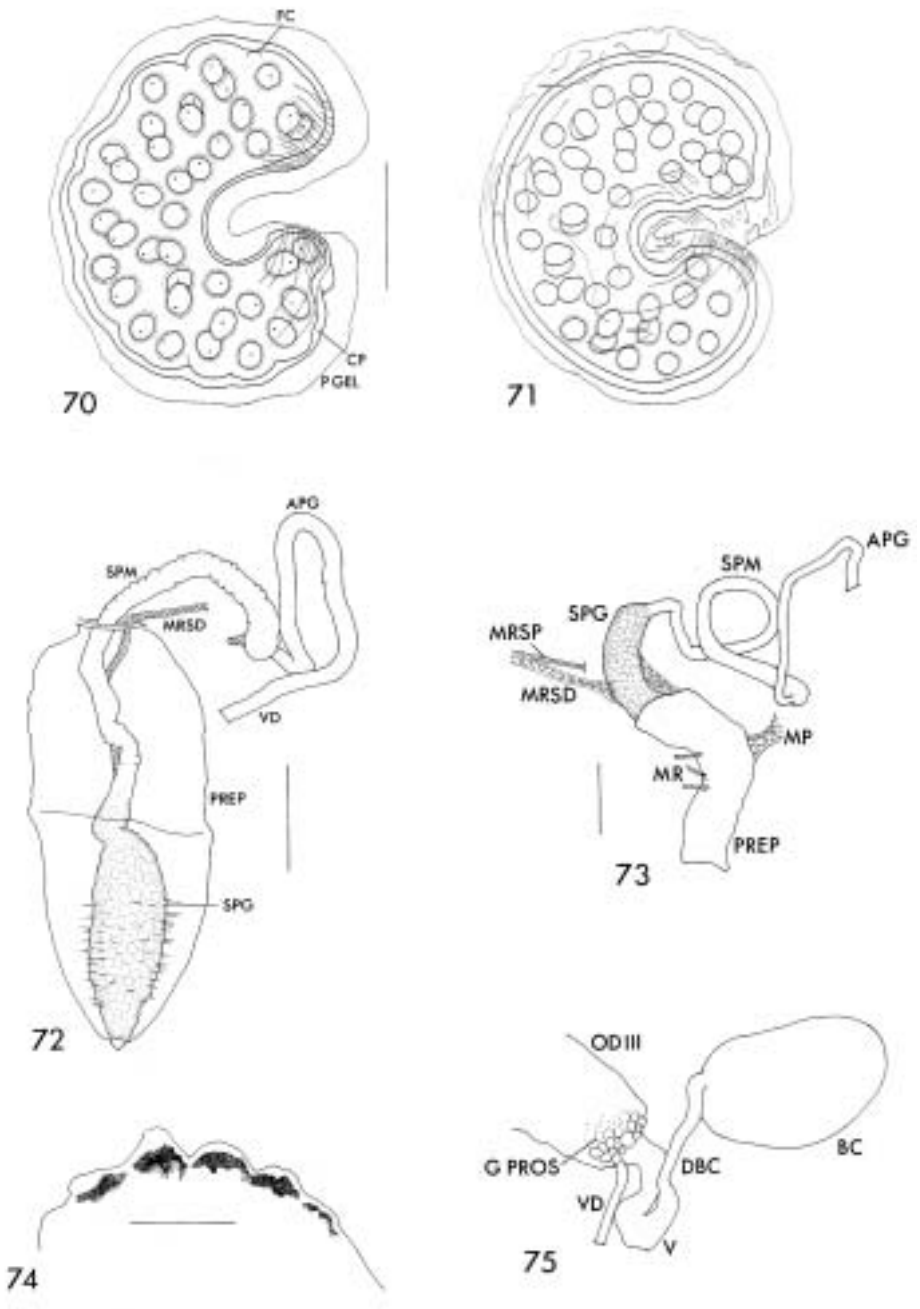
Diagnosis: A large species of *Mayabina* with length about 16-21 mm, W/L .46-.52, and 5 1/4 - 6 whorls. The glandular portion is about 1/3 of the total length of the sheath, and more than three times as wide as the muscular portion. Mantle projections are in the form of scallops, and penial retractor muscles have independent but adjacent origins in the columellar muscle.

Description: Mantle projections are in the form of broad scallops on the columellar-parietal and posterior lobes of the mantle; C 6, P 5.

Penial complex: There is a light sprinkle of melanin flecks overall, but lighter on the vas deferens. Penial retractor muscles have independent but adjacent origins. The distal penial retractor (MRSD) is inserted on the distal end of the penial sheath, the proximal retractor (MRSP) on the proximal end of the sheath. The distal glandular portion (SPG) is about 1/3 of the total length of the sheath, and more than three times as wide as the muscular portion. The preputium is about half the length of the

TABLE 16
Measurements and descriptive statistics of shells of Mayabina bullula *from north of Río Actopan, Veracruz, Mexico (T89-1101). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	17.65	12.81	.728	8.64	.489	5.65
Range	15.8-21.6	11.4-14.7	.66-.78	7.8-10.0	.46-.52	5 1/4 - 6
S. D.	1.39	1.13	.027	.528	.018	
S. E.	.254	.207	.005	.096	.003	



Figs. 70-75. *Mayabina bullula*, p. 92. Pool 8.8 km N of Río Actopan, Veracruz, Mexico (T89-1101). Figs. 70-71, capsule, scale 5 mm. Fig. 72, preputium extruded. Fig. 73, penial complex; the penial sheath has been pulled to the right, and the proximal penial retractor broken. Fig. 74, mantle projections on posterior lobe. Fig. 75, terminal portion of female system. APG, paragonoporal angle; BC, bursa copulatrix; CP, capsule wall; DBC, duct of bursa copulatrix; FC, vestigial capsule string; G PROS, prostate gland; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor of penial sheath; OD III, oviduct III; P GEL, pallium gelatinosum; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale 1 mm except as noted.

penial sheath, and bears a strong protractor muscle as well as several minor retractors. The vas deferens between the paragonoporal angle (APG) and the penial sheath is less than half the length of the sheath.

Female system: The bursa copulatrix (BC) is a plump sac less than twice as long as its width. Its duct (DBC) is well set off from the bursa, less than the length of the bursa, and widens in its distal fourth. Bursal duct and oviduct III join at a low angle, forming a vagina (V) with W/L about 2.0.

Four laboratory-reared specimens were studied alive. Overall body tone is dark olive; a diffuse darker median band may be present in the posterior end of the foot. The mantle overlaps the shell on the left and in front as a narrow, unscalloped band less than 1/20 whorl; the posterior lobe is ventral, extending onto both sides of the midline, and thus unlike that structure in the other species of the genus with a large posterior lobe on the left side only. Mantle projections are scallops on both the columellar and posterior lobes that are shallow, with a moderate concentration of melanin within, and a pale margin.

Spawn: The capsule wall (CP) is about .15-.20 mm thick, but the pallium gelatinosum (P GEL) is more variable. It may be only a thin film, .03 mm thick, or more than 1 mm. Form of the capsule is usually C-shaped, with a narrow concavity on the right, or closed with the pallium gelatinosum of both arms in contact; degree of coiling was from about 90º to 360º. Ends of the capsule are blunt, of subequal size; wisps are sometimes present. The largest capsule (of 36 both field- and laboratory-laid) was 15.4 x 12.8 mm, with 40 eggs; but the capsule with most eggs (over 65) was only 13.2 m long. These differences in dimensions are due partly to variation in thickness of the pallium gelatinosum. Number of eggs was counted in 36 specimens; range was 12 to more than 65, mean 36.8, S.D. 11.6.

One specimen (Fig. 70) had constrictions of the capsular wall within the smoother pallium gelatinosum, and suggestions of capsular strings at four places. These were not septa as in *Sibirenauta elongatus*, but only lines that stained like the capsular wall in methylene blue; yet from their location they seem homologous with the vestigial capsular strings of that species. These capsules in *Mayabina bullula* are distinct from those of *Mexinauta aurantia* by having a regular coil and especially by the proportionally much thicker pallium gelatinosum.

Distribution: Veracruz state, Mexico.

Localities and material examined:

MEXICO, Veracruz: Tuxpan (type locality). Pool on W side Mex. 180, 8.8 km N Río Actopan, 19º33.1'N, 96º23.6'W, 24-III-1989 (T89-1101)(**M**).

Remarks: *Mayabina bullula* is like *Mexinauta* in that the mantle projections are scallops instead of triangles, and the penial retractor muscles have independent origins. In size, shape, and color of shell, and in relative proportions of the muscular and glandular portions of the penial sheath, however, it is like *Mayabina spiculata*, and the spawn mass is unlike that known in *Mexinauta*.

Mayabina carolita (Jousseaume, 1887)

Fig. 76, Pl. 4, figs. 6, 9

Aplecta carolita Jousseaume, 1887:184, pl. 3, fig. 5. Reibisch, 1897:61.
Aplecta martinidella Cousin, 1887:76.

Holotype: presumably in MHNP. San Nicolás, Canton Mejía, Prov. Pichincha, Ecuador, *Charles Martin*.

Name: Derivation uncertain.

Diagnosis: A medium-sized species, length about 8-15 mm, W/L .48-.54, with 4-5 1/2 whorls. Surface of shell polished and shining; microsculpture conspicuous only near the suture, becoming obsolete toward the anterior end.

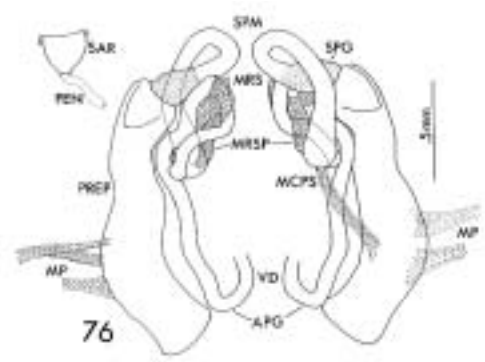


Fig. 76. *Mayabina carolita*, p. 94. Peru, Arequipa: Baños de Jesús. Penial complex of one specimen, in lateral (L) and medial (R) views; inset, sarcobelum with end of penis extruded. APG, paragonoporal angle; MCPS, connective between preputium and penial sheath; MP, protractor muscle of preputium; MRS, retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens.

Localities and material examined:

ECUADOR, Prov. Guayas: Chanduy [2º25'S, 80º40'W], *R. W. Barker* (BMNH 1932.5.30.1-20). Prov. El Oro: Santa Rosa [3º27'S, 79º58'W], in dried ponds, *Theodor Wolf* (Reibisch, 1897). Prov. Pichincha, Canton Mejía: San Nicolas, *Charles Martin* (type locality)

PERU, Depto. Arequipa: Baños de Jesús [16º25.11'S, 71º28.48'W, 2650 m], 7 km E Arequipa, *Percy Sladen Trust Expedition to Lake Titicaca*, 4-X-1937 (BMNH uncat., preserved in alcohol). For references to the thermal springs, *see* Waring (1965:95).

Depto. Cajamarca: Santa Rosa near Cajamarca, 2 700 m, in lukewarm spring water, *W. Weyrauch* (FMNH 30 711). ?=Los Baños del Inca, 7º9.51'S, 78º27.68'W, 2667 m. For references to the thermal springs see Waring (1965:94).

Depto. La Libertad: Huamachuco [7º48'S, 78º04'W], 3 200 m, *W. Weyrauch* (FMNH 30 900).

Depto. Paita: 2 mi west of Sullana, Prov. Piura, *D. H. Frizzell*, 1938 (CAS uncat.).

CHILE, Prov. Tarapaca: Miñi-miñi [19º11'S, 69º41'W], *G. Kuschel*, 1948 (MACN 30 192; one fresh juvenile, one broken adult shell, referred on the basis of range).

Remarks: The preserved specimens examined are of indifferent quality, and might not all represent a single species. Better material from near the type locality and from Peru will be necessary to verify the relationships of the populations. Whether the samples I have examined are *M. carolita* is uncertain. There is no trace of the pinkish band below the suture mentioned in Jousseaume's description of the species from Ecuador, and according to his measurements LPer/L is .63, slightly less than in the measured series from Peru (Tables 14-15).

TABLE 17

Measurements and descriptive statistics of shells of Mayabina carolita *from Santa Rosa near Cajamarca, Peru (FMNH 30711). Measurements to nearest .128 mm. N = 10*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	12.21	8.37	686	6.25	.514	4.88
Range	10.24-15.10	7.30-10.50	.66-.71	5.38-7.81	.48-.53	$4\ ^1/_2$ - $5\ ^1/_2$
S. D.	1.32	.921	.017	.687	.014	
S. E.	.418	.291	.005	.217	.005	

TABLE 18

Measurements and descriptive statistics of shells of Mayabina carolita *from Baños de Jesús, Peru (BMNH uncat). Measurements to nearest .064 mm. N = 5*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	8.61	5.95	.692	4.43	.514	4.50
Range	8.00-9.79	5.50-6.59	.67-.73	3.90-5.06	.48-.54	4 - $4\ ^3/_4$
S. D.	.728	.400	.024	.413	.022	
S. E.	.326	.178	.011	.185	.010	

Mayabina petenensis sp.n.

Fig. 77, Pl. 3, fig. 10
Distribution Map, Fig. 69

Aplexa cisternina (Morelet) [misidentified]: Goodrich & van der Schalie, 1937:34.
Aplexa spiculata Morelet [misidentified]: van der Schalie, 1940:7.
Stenophysa spiculata (Morelet) [misidentified]: Covich, 1976:55, fig. 3D.

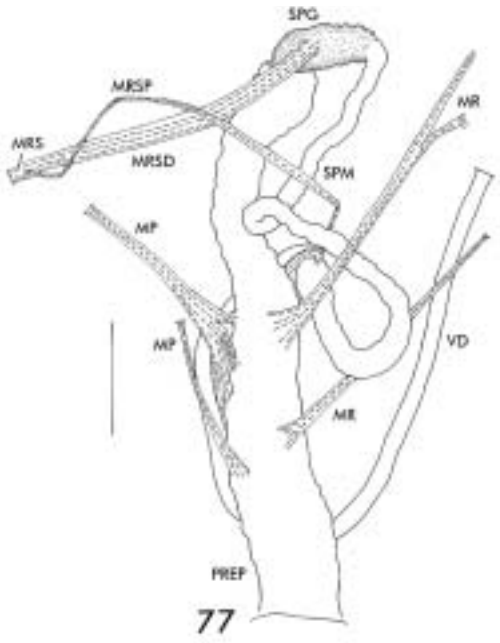


Fig. 77. *Mayabina petenensis*. Guatemala, El Petén: La Libertad (T91-2401). Penial complex; the penial retractors have been turned to the left, although in life they would be to the right. MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRS, retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

Holotype: CAS 114811. Guatemala, Depto. El Petén: Aguada at NE side of La Libertad, 16º47.30'N, 90º6.49'W, 200 m, 22-XI-1991 (T91-2401). Paratypes CAS 114 823 (10), BMNH 20001310 (10).

Name: From Depto. Petén, Guatemala.

Diagnosis: A medium-sized species of *Mayabina* with polished shell attaining a length of about 9 - 13.5 mm with 4 1/2 to 5 1/2 whorls; W/L about .4 - .5. The glandular portion of the sheath is only about 1/6 of the total length of sheath, and twice as wide as the muscular portion. Mantle projections vary in form from acute-triangular to square-tipped; there may be a large melanin smudge within a projection, or none.

Description: External body medium gray, except dark gray on upper hind end of foot. Often the mantle projections are roughly square-tipped, a form not seen in any other Physidae. Penial sheath longer than preputium; glandular portion (SPG) only about 1/6 of total length of sheath, and twice as wide as muscular portion (SPM). There are exceptionally strong and numerous retractors of the preputium (MP, MR). The common retractor of the sheath (MRS) is only about 1/10 the length of the distal retractor (MRSD).

TABLE 19
Measurements and descriptive statistics of shells of Mayabina petenensis *from type locality (T91-2401). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	10.83	7.46	.689	5.11	.473	4.85
Range	8.96-13.57	6.27-9.86	.636-.733	4.35-6.66	.434-.507	$4\ ^1/_2$- $5\ ^1/_2$
S. D.	1.299	.898	.023	.558	.016	.268
S. E.	.237	.164	.004	.102	.003	.049

TABLE 20
Variation in numbers of mantle projections of Mayabina petenensis *from type locality (T91-2401). N = 30*

	Columellar	Posterior
Mean	8.43	5.33
Range	4-11	4-8
S.D.	1.94	.92
S.E.	.355	.168

Distribution: Northern Guatemala.

Localities and material examined:

GUATEMALA, Depto. Alta Verapaz: Río Pasión [now Río Sebol] at first arroyo [Quebrada Cacao] on east below mouth of Río San Simón, *H. van der Schalie*, 16-IV-1935 (MCZ 99 319). First arroyo [Río Mabilá] below Río Chajmaic Cajbón, *H. van der Schalie*, 14-IV-1935 (MCZ 99 320). Marsh, headwaters of Río Seniso, 1 km W of hacienda, Finca Chamá, *L. C. Suart*, 9-VI-1938 (UMMZ 132 342).

Depto. Petén: Río El Subín, Santa Teresa, *H. van der Schalie*, 3-IV-1935 (MCZ 99 304). Aguada .5 km NE of El Subín, 16º38.46'N, 90º10.81'W, 135 m, 22-XI-1991 (T91-2701). Río El Subín, El Subín, 16º38.14'N, 90º10.93'W, 130 m, 22-XI-1991 (T91-2502). Laguneta El Sos, *H. van der Schalie*, 4-III-1935 (MCZ 99 321). Small aguada across road from Aguada Jalal, 16º48.89'N, 90º4.02'W, 190 m, 22-XI-1991 (T91-2301)(**M**). Aguada at NE side of La Libertad, 16º47.30'N, 90º6.49'W, 200 m, 22-XI-1991 (T91-2401)(**M**). Aguada 10.4 km SSW of La Libertad, 16º42.16'N, 90º9.13'W, 175 m, 22-XI-1991 (T91-2801)(**M**). Aguada El Progreso, La Libertad, 16º47.41'N, 90º6.97'W, 190 m, 22-XI-1991 (T91-2901). Río San Pedro, Paso Caballos, *H. van der Schalie*, 10-III-1935 (MCZ 99305). Tributary of Río San Pedro about 1/2 mile NW of Laguna de Yalac, *H. van der Schalie*, 16-III-1935 (MCZ 99318). Marshy border of Lago Petén-Itzá, Piedra Blanca, 16º59.68'N, 89º41.60'W, 110 m, 24-XI-1991 (T91-3603)(**M**). L. Petén, Flores, *H. van der Schalie*, 13-II-1935 (MCZ 99 301). Marshy border of L. Petén-Itzá, Santa Elena, 16º55.30'N, 89º53.40'W, 110 m, 21-XI-1991 (T91-2101, 2110)(**M**). =Shore of L. Petén at National Airways Field S of Flores, *H. van der Schalie*, 8-II-1935 (MCZ 99 308). South arm of L. Petén, near Flores, *H. van der Schalie*, 17-II-1935 (MCZ 99 302). Aguada de San Antonio, 12.5 km SW of Flores, 16º51.97'N, 89º59.52'W, 190 m, 22-XI-1991 (T91-2201)(**M**). South side of easterly island in L. de Eckixil, *H. van der Schalie*, 18-II-1935 (UMMZ 65 804).

Mayabina pliculosa (Martens, 1898)

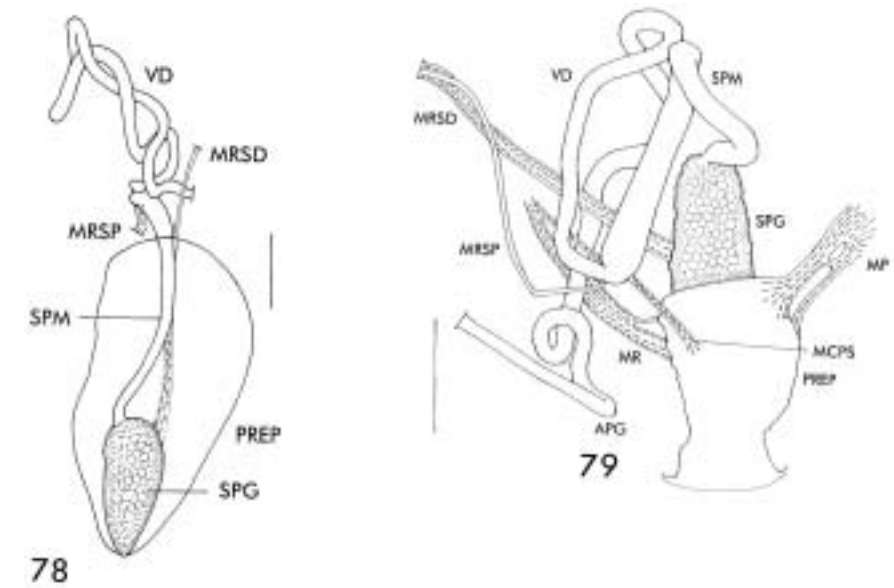
Figs. 78-79, Pl. 4, figs. 10-11
Distribution Map, Fig. 69

Physa fuliginea var. pliculosa Martens, 1890-1901:361, pl. 20, figs. 11-12 [1898].
Stenophysa pliculosa Martens: Tonn *et al*., 1964:60.
Aplexa fuliginea [misidentified]: Monge-Nájera, 1984:69 ff.; ecology and behavior.

Lectotype (Kilias, 1961) ZMB 51237a. Costa Rica, Prov. Cartago: Río Reventazón at Ujarrás [9º50'N, 83º50'W], *P. Biolley*.

Name: Latin, with little folds.

Diagnosis: A medium-sized species of *Mayabina*, length about 15-19 mm, W/L about .45-.5, with 5-5 3/4 whorls. The glandular portion of the penial sheath is about 30% of the



Figs. 78-79. *Mayabina pliculosa*, p. 97. Costa Rica, Prov. Cartago: Quebrada Barahona (T92-7005). 78, penial complex, extruded; 79, penial complex. Scale 1 mm. APG, paragonoporal angle; MCPS, connective between preputium and penial sheath; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens.

TABLE 21

Measurements and descriptive statistics of shells of Mayabina pliculosa *from Quebrada Barahona, Cartago, Costa Rica (T92-7005). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	16.09	11.46	.712	7.95	.493	5.4
Range	14.6-18.8	10.2-13.3	.68-.75	6.9-9.3	.45-.52	5 - 5 $^{3}/_{4}$
S. D.	1.03	.762	.024	.648	.020	
S. E.	.189	.139	.004	.118	.004	

TABLE 22

Variation in numbers of mantle projections of Mayabina pliculosa from Quebrada Barahona, Costa Rica (T92-7006). N = 30

	Columellar	Posterior
Mean	6.00	3.97
Range	3-8	2-6
S.D.	1.26	.85
S.E.	.230	.155

total length of the sheath, and four to five times as wide as the muscular portion.

Description: The external body is a very pale gray from a dusting of melanin, except for the darker, medium-gray tentacles. Unlike other species of the genus, the front of the head is not darker than the rest of the exposed body. Mantle projections are broad to narrow round-ended triangles, with a moderate smudge of melanin within each.

Penial retractor muscles have adjacent but separate origins. The glandular portion of the sheath (SPG) is about 30% of the total length of the sheath, and four to five times as wide as the muscular portion.

Eight specimens were preserved with the preputium extruded. In that state the sheath is longer than the preputium, and the glandular portion of the sheath varies from about 40-65% of the length of the preputium. It is a cream-colored stout cylinder tapered at the distal end, or fusiform, slightly wider in the middle. Length of the vas deferens from the paragonoporal angle to the sheath is greater than the length of the sheath.

Distribution: Western Costa Rica, from the Central Valley northwestward to the southern tip of Nicoya Peninsula (Prov. Puntarenas) and Prov. Guanacaste.

Localities and material examined:

COSTA RICA, Prov. Alajuela: Sarchí Sur [10º05'N, 84º21'W], Grecia, *Rodrigo Brenes*, 24-VII-1953 (MCZ 211 211).

Prov. Cartago: Río Turrialba, Turrialba [9º54'N, 83º41'W], *Rodrigo Brenes*, 27-IX-1953 (MCZ 211 212). Turrialba, *C. Gans* (MCZ 212 403). Alto de Ochomogo, *B. Malkin*, 20-IX-1955 (MCZ 210 586). Aguas Calientes near Cartago, *J. Zetek*, 3-III-1919 (MCZ 66 957, 66 958). Quebrada Barahona, 9º51.32'N, 83º58.78'W, 1380 m, 14-XI-1992 (T92-7005)(**M**). Juan Viñas [9º54'N, 83º45'W] (BMNH uncat.).

Prov. Guanacaste: Roadside ditches .3-.4 km toward Hacienda La Taboga from Cañas-Bebedero road, 10º22.31'N, 85º11.12'W, 9-XI-1991 (T91-1304).

Prov. Puntarenas: Pasture of La Hacienda, 1 km SW of Concepción-Pochote road, 9º45.08'N, 85º0.44'W, 24-XI-1990 (T90-4903)(**M**). Barranca [9º59'N, 84º43'W], *J. Monge-Nájera, Z. Barrientos*, 4-X-1988 (UCR).

Prov. San José: Pavas [9º57'N, 84º08'W], *B. Morera*, X-1984 (UCR). Uruca [9º57'N, 84º06'W], *P. Biolley* (MCZ 211 219). San José, *P. Biolley* (MCZ 21 127). San José, *A. Alfaro*, 1938 (MCZ 77 600). Río Torres, San José (La Sabana), *Rodrigo Brenes*, 7-IV-1956; and Río Torres, *P. Biolley* (MCZ 211 194, two sets combined). Río Torres, *Henry Gongoro* (CAS 23 271, *ex* F. Baker). Ocloro [not traced], 1 160 m, *A. Alfaro* (MCZ 75 606).

Mayabina polita sp.n.

Figs. 80-84, Pl. 5, figs. 1-2
Distribution Map, Fig. 69

?*Aplecta cisternina var. abbreviata* Fischer & Crosse, 1870-1902, 2:95, pl. 30, fig. 9 [1886]; with the typical form at Mérida, Yucatán, *Arthur Morelet*.

Aplecta cisternina var. gracilis Fischer & Crosse, 1870-1902, 2:95, pl. 30, figs. 10-10b [1886]; vicinity of Mérida, *Arthur Morelet*.

Aplexa spiculata var. gracilis (Fischer and Crosse): Bequaert & Clench, 1936:70, pl. 2, figs. 5-8.

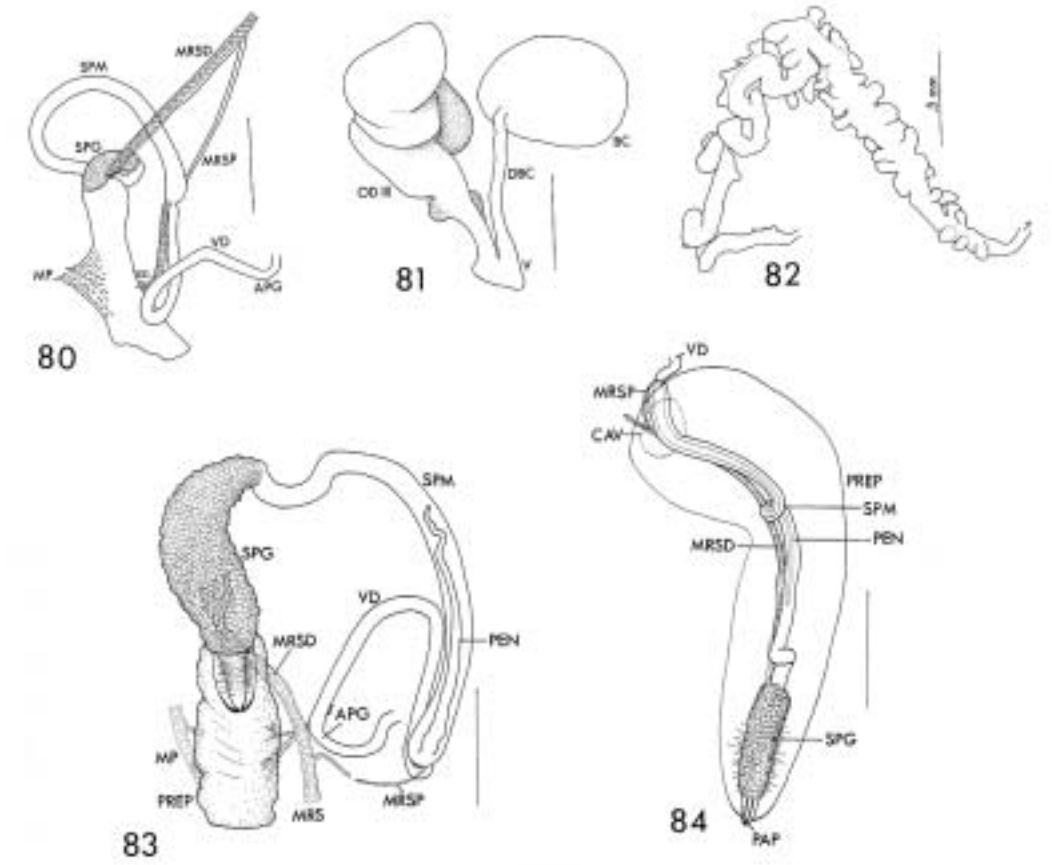
Aplecta cisternina var. minor Fischer & Crosse, 1870-1902, 2:95, pl. 30, fig. 8 [1886]; no locality cited.

Holotype: CAS 114 783. Mexico, Tabasco: Pasture pool 50 m W Río Tulija, 1.5 km S of Mex. 186 toward Zopo Norte, 17º39.6'N, 92º24.7'W, 22-II-1988 (T88-3602). Paratypes CAS 114 817(10), BMNH 20001311 (10), ZIBM CNMO 1160 (10).

Name: Latin, polished.

Diagnosis: A small species of *Mayabina* with narrow, polished shell attaining a length of about 9-14 mm, W/L about .4-.5; with 5-6 whorls. The glandular portion of the penial sheath varies from about 20-40% of the total length of the sheath, and 2-5 times as wide as the muscular portion.

Description: The shell is fusiform, with a narrow, acute spire and broader, narrowly rounded anterior end. The profile of the aperture is broadly but weakly convex in the



Figs. 80-84. *Mayabina polita*, p. 99. Mexico, Tabasco: 1.5 km S of Mex. 186 (T88-3602). 80, 83, penial complex; 81, distal portion of female system; 82, hermaphroditic duct; arrow points away from ovotestis; 84, penial complex in extruded state. Scale 1 mm except as noted. APG, paragonoporal angle; BC, bursa copulatrix; CAV, wall of body cavity; DBC, duct of bursa copulatrix; MCPS, connective between preputium and penial sheath; MP, protractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD III, oviduct III; PAP, papilla; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens.

TABLE 23

Measurements and descriptive statistics of shells of Mayabina polita *from type locality (T88-3602). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	10.67	6.89	.646	4.96	.468	5.3
Range	9.1-14.0	5.6-9.5	.58-.68	4.0-7.0	.41-.51	$4\,{}^{3}/_{4}$ - 6
S. D.	1.17	.801	.025	.613	.021	
S. E.	.213	.146	.005	.112	.004	

TABLE 24
Variation in numbers of mantle projections of Mayabina polita *from type locality (T88-3602). N = 50*

	Columellar	Posterior
Mean	6.70	4.52
Range	0-10	0-6
S.D.	1.98	1.23
S.E.	.280	.174

TABLE 25
Measurements and descriptive statistics of shells of Mayabina polita *from east of Laguna Celestún, Yucatán, Mexico (T86-703). Measurements to nearest .0794 mm. N = 13*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.54	4.60	.703	3.35	.513	4.17
Range	5.32-8.10	3.57-5.72	.67-.75	2.70-4.13	.49-.54	$3\,{}^{3}/_{4}$ - $4\,{}^{1}/_{2}$
S. D.	1.01	.722	.022	.519	.016	
S. E.	.279	.200	.006	.144	.004	

direction of growth, evenly retractive to the suture. The columella is thin, pale tan, with a fold absent, or rarely, scarcely evident. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but not incised suture. The lateral profile of the spire is plane to weakly concave. The shell surface is shining, its color pale yellow-brown, with a narrow pale band at the suture, and a broader brown band immediately below. Numerous inconspicuous, spiral, fine, diffuse-edged whitish bands are commonly present. Surface sculpture is inconspicuous, consisting of fine axial growth lines and coarser wrinkles, and spiral sculpture. The latter is formed by irregular minute wrinkles, straight or weakly convex in the direction of growth. These are arranged in short, discontinuous, spiral series that are more common on the posterior surface of the whorl, and are stronger and more closely crowded toward the suture.

Mantle projections vary greatly in form, from barely perceptible to acute-triangular. Usually there is a dense concentration of melanin in the tip of each projection. A small patch of melanin may be present even when the projection is barely discrete and broadly rounded, and triangular projections may lack melanin. The posterior group is borne on a strong fan-shaped lobe, present even when no projections are evident. Number of projections in a sample from the type locality (Table 24) varied greatly, C 0-10, P 0-6.

Hermaphroditic tract: Hermaphroditic duct composed of an initial thick-walled, convoluted portion about one-fourth of duct length; then thickly set with bud-like seminal vesicles once or twice as long as wide, and rarely branched once. Distal one-fifth of duct a simple, narrow tube.

Penial complex: The entire complex is flecked with melanin, that may be present also on the penial retractor muscles. Retractor muscles of the penial sheath have either separate origins in the columellar muscle, or a common origin. The narrow proximal retractor (MRSP) is inserted on the head of the penial sheath; the distal retractor (MRSD) on the distal half of the glandular portion (SPG), where the muscle bands are splayed widely. Relative proportions of the glandular and muscular portions of the sheath vary widely. The glandular portion ranges from about 20% to 40% of total length of sheath, and 2-5 times as wide as the muscular portion. The glandular portion continues inside the sheath as a cylindrical sarcobelum of variable size, with a terminal papilla (PAP).

Female tract: OD III and bursal duct join at an acute angle, forming a short vagina, W/L .5. The bursa, equal in length to is duct, is sharply set off from it.

Distribution: Southeastern Mexico, in Tabasco and northern Chiapas through the Yucatán Peninsula in eastern Campeche, Yucatán and Quintana Roo.

Localities and material examined:

MEXICO, Tabasco: Marsh beside Jonuta-Frontera road, 8.45 km S Mex. 180, 18º26.8'N, 92º38.5'W, 18-II-1988 (T88-2802)(**M**). Lagoon off Río Chico 2 km NNE Cocoyolar, 17º57.6'N, 92º8.5'W, 22-II-1988 (T88-3302). Roadside pond at petroleum camp Campo José Colomo, 17º59.7'N, 92º25.2'W, 16-II-1988 (T88-2202). 4.3 km N Ciudad Pemex, 17º55.4'N, 92º28.9'W, 16-II-1988 (T88-2302)(**M**). Along Ciudad Pemex-Jonuta road, .1 km, 17º58.1'N, 92º17.1'W (T88-1901)(**M**), .9 km, 17º58.0'N, 92º17.7'W (T88-2001), and 2.6 km, 17º57.9'N, 92º18.4'W (T88-2101)(**M**), W of road to Monte Grande, all 16-II-1988. 3.9 km N Jalapa, 17º45.0'N, 92º50.1'W, 16-II-1988 (T88-2501)(**M**). 2.8 km SW Macuspana, 17º44.6'N, 92º37.0'W, 16-II-1988 (T88-2402)(**M**). Ditch beside Mex. 195 at Rancho La Trinidad, about km 36.9, 17º39.5'N, 92º57.2'W (T88-2901)(**M**). Roadside marsh beside Tacotalpa-Tapijulapa road about 1 km N road to Teapa [with *Mexinauta nitens*], 17º34.9'N, 92º49.4'W, 20-II-1988 (T88-3003)(**M**). Roadside ditches beside Mex. 186, 200 m W of road to Microondas Tulija, 17º41.1'N, 92º21.6'W, 22-II-1988 (T88-3502). Pasture pool 50 m W Río Tulija, 1.5 km S of Mex. 186 toward Zopo Norte, 17º39.6'N, 92º24.7'W, 22-II-1988 (T88-3602)(**M**). Laguna Leona Vicario, 10 km S Balancán, 17º42.3'N, 91º32.6'W, 23-IV-1986 (T86-1206).

Campeche: Roadside ditch along Mex. 180, 3.7 km W Puerto Rico, 18º37.1'N, 91º58.4'W, 18-II-1988 (T88-2602). Roadside pond 1 km NNE Jonuta toward Palizada, 18º5.9'N, 92º7.9'W, 22-II-1988 (T88-3402). Fifty-eight miles [93 km] east of Silvituc, *University of Colorado Yucatan Expedition*, 29-VI-1964 (UCM 27 483) [with *spiculata*].

Chiapas: Pasture pond beside Mex. 195, 1.5 km NE of bridge over Río Pichucalco, 17º31.9'N, 93º5.0'W, 20-II-1988 (T88-3201)(**M**).

Yucatán: Charco beside highway 25 at km 44.5, 17.3 km east of Laguna Celestún, 20º51.4'N, 90º13.4'W, 21-IV-1986 (T86-703). Mérida, *Arthur Morelet*, 1847 (MCZ 4 385, a mixture of nine *spiculata* and three *polita*). Xtolok Cenote near Chichén-Itzá, *E. P. Creaser* (MCZ 59 760). Great Cenote, Chichén Itzá [20º40'N, 88º34'W], *L. J. Cole*, 4-III-1904 (MCZ 47201).

Quintana Roo: Laguna Om [18º26'N, 89º08'W], near San José [San José Aguilar], *O. J. Polaco*, 1-III-1982. Laguna Chichancanab [19º54'N, 88º46'W], *R. T. Hatt* (MCZ 157 916).

Habitat: Marshes and ponds at lower elevations, either seasonal or perennial.

Remarks: Of the varietal names given by Fischer and Crosse *abbreviata, gracilis,* and *minor* are all preoccupied. It is not quite certain that *var. abbreviata* refers to the present species, because the authors (like most) paid little attention to shell microsculpture.

Mayabina sanctijohannis sp.n.

Fig. 85, Pl. 3, figs. 5-6
Distribution Map, Figs. 15, 69

Holotype: CAS 114790. Costa Rica, Prov. Limón: Barra del Colorado, 10º46.37'N, 83º35.27'W, 11-XI-1993 (T93-3002). Paratypes CAS 114780 (11), BMNH 20001312 (10), INBio (10), UCR (10).

Name: From Río San Juan drainage.

Diagnosis: The smallest species of *Mayabina*, distinguished by its short, stout shell with length about 6-8 mm, W/L .51-.57, with four whorls, and shining surface. The

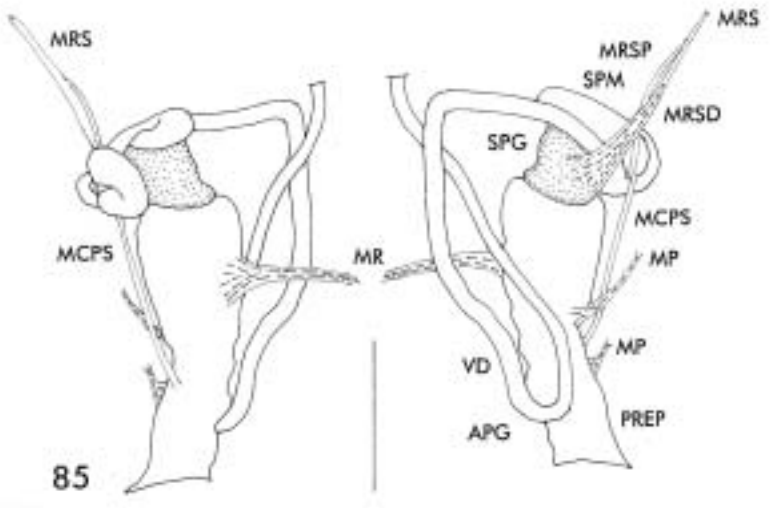


Fig. 85. *Mayabina sanctijohannis*, p. 102. Costa Rica, Prov. Limón: Barra del Colorado (T93-3002). Penial complex, in lateral (left) and medial (right) views. APG, paragonoporal angle; MCPS, connective between penial sheath and preputium; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRS, retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

TABLE 26
Measurements and descriptive statistics of shells of Mayabina sanctijohannis *from type locality (T93-3002). Measurements to nearest .064 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.91	4.89	.709	3.75	.544	4.09
Range	5.95-7.94	4.42-5.76	.66-.76	3.26-4.48	.51-.57	$3\ ^{3}/_{4}$ - $4\ ^{1}/_{2}$
S. D.	.465	.337	.028	.271	.019	
S. E.	.085	.062	.005	.050	.004	

TABLE 27
Variation in numbers of mantle projections of Mayabina sanctijohannis *from type locality (T93-3002). N = 30*

	Columellar	Posterior
Mean	7.7	4.9
Range	4-10	3-7
S.D.	1.39	.96
S.E.	.254	.175

glandular portion of the penial sheath is about 20% of the total length of the sheath, and about 1.3-3 times as wide as the muscular portion.

Description: The shell is fusiform, with a short, blunt spire and narrowly rounded anterior end. The profile of the aperture is broadly but weakly convex in the direction of growth, evenly retractive to the suture. The columella is thin, pale tan to white, with a weak fold or none. The parietal callus is a thin wash, continuous between the end of the aperture, expanded broadly adjacent to the columella.

The spire whorls are moderately convex, separated by a distinct but not incised suture. The lateral profile of the spire is plane to barely concave. The shell surface is shining, its color yellow-brown, with a narrow pale band at the suture and a narrow darker band immediately below. Numerous fine, diffuse-edged, indistinct, spiral white threads are often present. Surface sculpture is inconspicuous, consisting of fine axial growth lines and wrinkles, and fine spiral sculpture. This sculpture consists of short, straight, irregular, minute wrinkles in short spiral series, coarser and more conspicuous toward the suture; these spiral series of wrinkles are scattered irregularly over the shell, but are more abundant on the posterior part of the body whorl.

Overall tone of body, foot, mantle and pneumostome is a medium gray, paler on ventral surfaces, more intense on the front of the head. Mantle projections (Table 27) are broad triangles with rounded ends, roughly equal in width and length. A slightly stronger concentration of melanin within some projections may be present. Posterior projections are on a broad lobe; from this lobe forward the mantle is reflected over the shell on the left side about .05 whorl as a smooth-edged band. The reflected mantle continues narrowly over the anterior end of the shell to the more broadly expanded columellar lobe. On the left ventral aspect a broad and deep, smooth-edged gap separates the two mantle lobes.

Penial complex: The entire complex, retractor muscles and VD IV are lightly flecked with melanin. Retractor muscles of the penial sheath have separate but adjacent origins in the columellar muscle. The narrow proximal retractor of the sheath (MRSP) is inserted on the head of the sheath; the distal retractor (MRSD) on the distal half of the glandular portion, where the muscle bands are splayed widely. A delicate connective of the penial sheath and preputium (MCPS) is present, but not illustrated. The long and slender muscular portion of the sheath (SPM) is about three-fourths of the glandular portion (SPG) in width; the glandular portion (outside the preputium) is about 20% of the total length of the sheath. This glandular portion continues inside the sheath as a stout, conical sarcobelum (SAR) with no terminal papilla; W/L about 75%. The vas deferens between the paragonoporal angle and the sheath is conspicuously longer than the total length of the sheath.

Localities and material examined:

COSTA RICA, Prov. Limón: Barra del Colorado, 10º46.37'N, 83º35.27'W, 11-XI-1993 (T93-3002)(**M**). Marsh on left bank of Río Colorado, 10º46.10'N, 83º36.14'W, 12-XI-1993 (T93-3102).

Mayabina spiculata (Morelet, 1849)

Figs. 86-87, Pl. 3, figs. 4, 7

Distribution Map, Fig. 68

Physa spiculata Morelet, 1849-1851, 1:18 [1849]. Martens, 1890-1901:366 [1898].

Aplecta spiculata Morelet: Fischer & Crosse, 1870-1902, 2:93, pl. 27, fig. 13 [1886].

Aplexa spiculata Morelet: Bequaert & Clench, 1936:69, pl. 2, figs. 1-4; *cisternina* as synonym. H. G. Richards, 1937:256. Harry, 1950:23.

Physa (Aplexa) spiculata Morelet: Branson & McCoy, 1965:12.

Stenophysa spiculata (Morelet): Rehder, 1966:280.

Aplexa nitens var. spiculata Morelet: Pilsbry, 1891:325.

Stenophysa peruviana spiculata (Morelet): Te, 1980:182.

Physa cisternina Morelet, 1849-1851, 2:15 [1851].

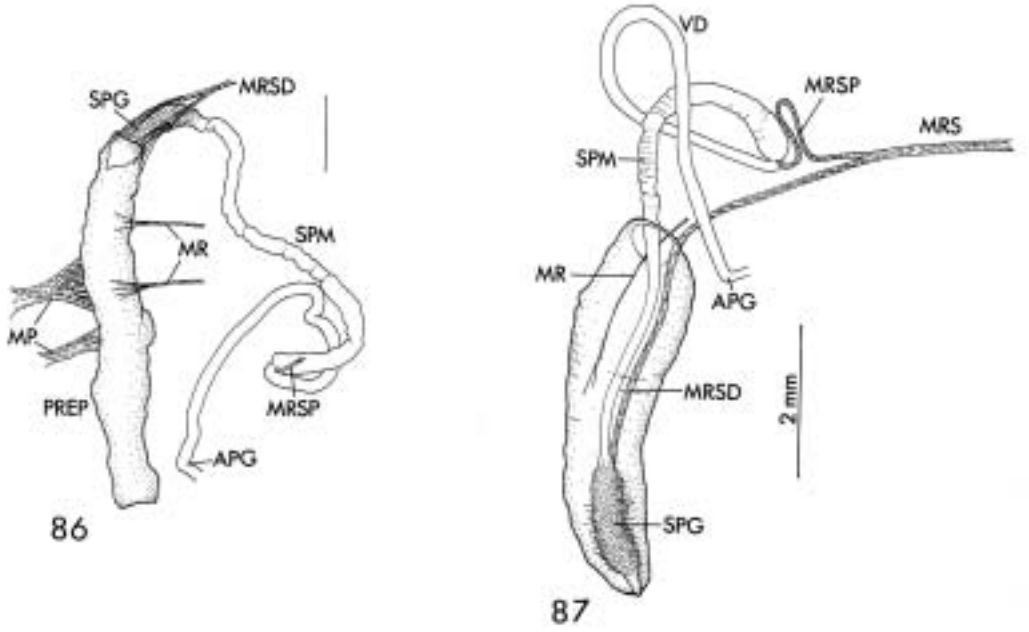
Aplecta cisternina Morelet: Fischer & Crosse, 1870-1902, 2:94, pl. 30, fig. 7 [1886]. Pilsbry, 1891:325.

TABLE 28
Measurements and descriptive statistics of shells of Mayabina spiculata *from 4 km south of Puerto Progreso, Yucatán, Mexico (T86-505). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	20.62	15.12	.733	10.56	.513	5.83
Range	18.6-25.0	13.4-18.8	.70-.77	9.1-12.7	.47-.62	$5\ ^1/_2$ - $6\ ^1/_4$
S. D.	1.72	1.28	.021	.914	.027	
S. E.	.314	.234	.004	.167	.005	

TABLE 29
Variation in numbers of mantle projections of Mayabina spiculata *from 4 km south of Puerto Progreso, Yucatán, Mexico (T86-505). N = 30*

	Columellar	Posterior
Mean	9.3	6.1
Range	7-12	4-9
S.D.	1.34	1.17
S.E.	.245	.214



Figs. 86-87. *Mayabina spiculata*, p. 104. Mexico, Yucatán: 4 km S of Puerto Progreso (T86-507). Penial complex retracted (86) and extruded (87). Scale 1 mm except as noted. APG, paragonoporal angle; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRS, retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens.

Types: No type material in BMNH. TL Campeche [19º51'N, 90º32'W], Campeche, Mexico, *Arthur Morelet*, 1847.

Name: Latin *spiculatus*, sharpened to a point.

Diagnosis: A large species of *Mayabina*, attaining a length of about 25 mm with 6 whorls, W/L about .5-.6. Shell color varies from pale yellow-brown to dark purple-brown; white streaks are often present in spiral and axial arrangement. Surface sculpture is well-developed, consisting principally of spiral series of irregular minute wrinkles. The glandular portion of the sheath is only about 20% of the total length of the sheath, and twice as wide as the muscular portion.

Description: The shell is subfusiform, with a narrow, acute spire and broader, narrowly rounded anterior end. The profile of the aperture is broadly but weakly convex in the direction of growth, evenly retractive to the suture. The columella is moderately heavy, white to pale lavender, with a fold absent, or rarely, scarcely evident. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but not incised suture. The lateral profile of the spire is plane to barely convex. The shell surface is silky and dull to shining, its color pale yellow-brown to dark purple-brown, with a narrow pale band at the suture, and a narrower or broader pale brown to dark purple-brown band immediately below. Other spiral color bands, all diffuse-edged and inconspicuous, may be present. Fine, irregular white streaks, either continuous or discontinuous in short segments, occur in both axial and spiral arrangement. These may be inconspicuous, or so numerous as to give a chalky tone to much of the shell. Surface sculpture is conspicuous, consisting of fine axial growth lines and coarser wrinkles, and conspicuous spiral sculpture. The latter is formed by irregular minute wrinkles, either straight or weakly convex in the direction of growth, that are arranged in spiral series covering most or all of the whorl, and are less strongly developed on the anterior part of the whorl.

The mantle is reflected over the outer lip of the shell as a narrow strip less than 1/10 whorl wide, its margin smooth. Mantle projections are round-ended broad triangles in the usual two groups, columellar-parietal (C) and posterior (P). The posterior projections are on a strong, distinct lobe; C 7-12 (mean 9.3), P 4-9 (mean 6.1), in a sample of 30 from north of Mérida (Table 29). Overall body color is nearly black to dark gray. In life the posterior end of the foot extends behind the shell about 1/4 of the shell length.

Penial retractor muscles have a common origin, and diverge at about 1/4 of the combined length of the common muscle (MRS) and distal retractor (MRSD). The glandular portion of the sheath (SPG) is relatively small, only about 20% of the total length of the sheath, and twice as wide as the muscular portion (SPM). Even in the extruded state, the preputium is shorter than the penial sheath; it has strong protractor muscles but weak retractors. The vas deferens from the paragonoporal angle to the sheath is about equal to the length of the sheath.

Variation: In the shell, color hue and form are the most conspicuous variables. Pale yellow-brown shells grade into purple-brown. Banding is commonly present, but subtle, with all bands diffuse-edged and inconspicuous except for the dark band below the suture. The hue of the bands is an intensification of the overall tone, with darker bands in darker shells. There may be up to ten or twenty diffuse bands visible within the aperture.

Distribution: Yucatán Peninsula in eastern Campeche, Yucatán, and Quintana Roo, Mexico.

Localities and material examined:

MEXICO, Campeche: Campeche (Morelet, 1849-1851). Pantel Aguada near Champotón (Bequaert & Clench, 1936). Aguada 3.5 miles S of Champotón (Branson & McCoy, 1965:11, as *Physa princeps*). 26 km [airline] SE of Champotón, *O. J. Polaco*, 26-II-1982 (Laboratorio de Paleozoología, Depto. de Prehistoria, México, D.F.). 58 miles [93 km] east of Silvituc [=Colonia Lopez Mateos],

University of Colorado Museum Yucatan Expedition, 29-VI-1964 (UCM 27 483).

Quintana Roo: San Gerbacio, Isla Cozumel (H. G. Richards, 1937). Ruinas Kuhunlich [18º25'N, 88º47'W], *O. J. Polaco*, 2-III-1982. Potreros at Tomás Garrido [18º01'N, 89º04'W], *O. J. Polaco*, 15-VII-1981 (both sets in Laboratorio de Paleozoología, Depto. de Prehistoria, México, D.F.).

Yucatán: Cienaga near [2 km SW of] Progreso, [at] Cerro Isla, *E. P. Creaser* (MCZ 5 976). South side of cienaga near Progreso, and irrigation cistern about 3 miles north of Mérida (Harry, 1950). Charcos at Pemex plant 4 km south of Puerto Progreso, 21º15.0'N, 89º39.5'W, IV-1986 (T86-505, 507)(**M**). Izamal [20º56'N, 89º01'W], Mérida, Cenote Shkolak, and Tekanto [21º01'N, 89º06'W] (Pilsbry, 1891). Halal Aguada [Hallal is 20º27'N, 89º58'W] near Mérida, *A. S. Pearse* (MCZ 59 759). Yunku Aguada near Yunku [20º34'N, 89º37'W]; hacienda at Chichén-Itzá [20º40'N, 88º34'W] (Bequaert & Clench, 1936). Aguada 1.5 miles south of Libre Unión (Branson & McCoy, 1965).

Remarks: *Mayabina spiculata* is the most heavily sculptured of all Aplexinae. The spiral series of fine wrinkles are stronger even than in some species of Physinae.

Mayabina tapanensis (Crosse & Fischer, 1882)

Figs. 88-89, Pl. 4, fig. 7
Distribution Map, Fig. 69

Aplecta tapanensis Crosse & Fischer, 1882:334. Fischer & Crosse, 1870-1902, 2:93, pl. 30, figs. 6-6b [on legend of plate as *Aplecta spiculata var. tapanensis*] [1886].
Physa spiculata var. tapanensis: Martens, 1890-1901:367, in part.
Aplexa tapanensis guatemalensis (Crosse & Fischer): Hinkley, 1920:38.

Holotype: not in MHNP (Chevallier, 1965:25). Mexico, Oaxaca: near Tapana [San Pedro Tapanatepec, 16º21'N, 94º12'W], *Francisco Sumichrast*.

Name: From the locality.

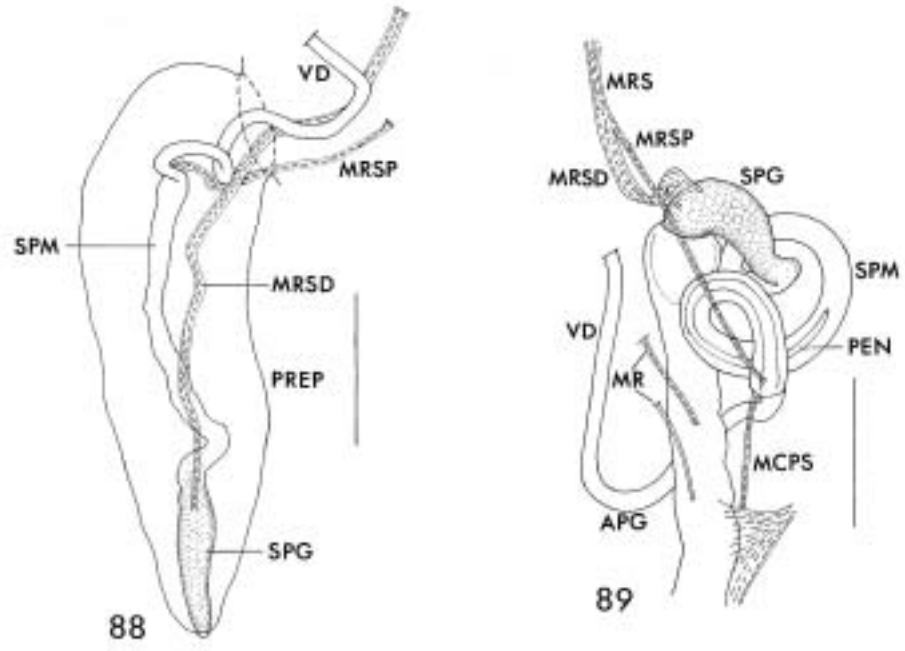
Diagnosis: Shell similar to *M. polita*, but with fewer whorls at the same size. Proportions of the figured shell are: L, 10.11 mm; LPer, 7.55; LPer/L, .75; W, 5.12; W/L, .51; 4 1/2 whorls. The glandular portion of the penial sheath is about 20-30% of the total length of the sheath, and 1.5-2 times as wide as the muscular portion.

Description: Mantle projections are acute, round-ended triangles; C 1-9, P 0-6. In the one preserved series studied, the melanin concentration within the projections usual in the genus is absent in nearly all cases.

Penial complex: All parts flecked with melanin, the muscular portion of the sheath and the vas deferens less so than the other parts. Retractor muscles of the penial sheath originate as a single band (MRS), dividing into distal retractor (MRSD) and proximal retractor (MRSP) at approximately 40% of the combined length of MRS and MRSD. The glandular

TABLE 30
Variation in numbers of mantle projections of Mayabina tapanensis *from Río San Buenaventura, Guatemala (T91-1502). N = 30*

	Columellar	Posterior
Mean	5.9	3.5
Range	1-9	0-6
S.D.	1.96	1.28
S.E.	.359	.234



Figs. 88-89. *Mayabina tapanensis*, p. 107. Río San Buenaventura, Guatemala (T91-1502). 88, preputium extruded; 89, penial complex, medial view. APG, paragonoporal angle; MCPS, connective between penial sheath and preputium, exceptionally in this specimen with insertion on a web of muscle fibers instead of on the preputium; MR, retractor muscles of preputium; MRS, common retractor of penial sheath; MRSD, distal retractor of penial sheath; MRSP, proximal retractor of penial sheath; PEN, penis; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

portion of the penial sheath varies from about 20-30% of the total length of the sheath, and 1.5-2 times as wide as the muscular portion. The sheath is shorter than the preputium, and the vas deferens between the paragonoporal angle (APG) and the head of the sheath is far shorter than the muscular portion of the sheath (SPM).

Distribution: Southeastern Oaxaca, Mexico, to southern Guatemala.

Localities and material examined:

MEXICO, Oaxaca: San Pedro Tapanatepec, in the northern part of the town, in a marsh 100 m E of the 90 km post on Mex. 190, 16º22.2'N, 94º11.7'W, 19-X-1988 (T88-6001).

Chiapas: 65 km S of Tuxtla Gutierrez along road to Nueva Concordia, *D. E. Breedlove*, 12-IX-1974 (CAS 079 137).

GUATEMALA, Depto. Guatemala: pools along railroad across L. Amatitlán from Laguna Station, *A. A. Hinkley* (Hinkley, 1920:38).

Depto. Sololá: Río San Buenaventura, 1 km NW Panajachel, 14º44.92'N, 91º9.86'W, 1565 m, 13-XI-1991 (T91-1502)(**M**). L. Atitlán at mouth of Río Catarata, 1.5 km NW Panajachel, 14º44.81'N, 91º10.03'W, 1562 m, 14-XI-1991 (T91-1605).

Habitat: The type locality is a perennial marsh, but with seasonal changes of level. Other molluscs found were *Drepanotrema anatinum* (d'Orbigny) and *D. kermatoides* (d'Orbigny). At the time of collecting, all the specimens were above water level as empty shells on the ground. The rains had ended a month previously.

In Guatemala, one collection was from a small stream with fluctuating amounts of water, depending on irrigation diversions. Associated species were *Pisidium casertanum*

(Poli) and *Lymnaea parva* Lea. In the varying availability of moisture, this habitat may be like the railroad pools where Hinkley collected; those pools were no longer in existence in 1991. The collection from L. Atitlán is from a large, perennial lake; here the population was small, perhaps maintained only by immigration from tributary streams.

Remarks: Nearly all of the specimens were preserved in alcohol, and the shells were mostly dissolved in fixation, so that no detailed information on the shells is available.

Mayabina tempisquensis sp.n.

Fig. 90, Pl. 4, fig. 4
Distribution Map, Figs. 15, 68

Holotype: CAS 146092. Costa Rica, Prov. Guanacaste: Parque Nacional Palo Verde, edge of marshes 100 m E of W end of airstrip, 10º20.68'N, 85º20.60'W, 16-XI-1992 (T92-7503). Paratypes INBio (10) UCR (10).

Name: From Río Tempisque.

Diagnosis: A medium-sized, slender species with a glandular portion of the penial sheath only about 10% of the total length of the sheath, and twice as wide as the muscular portion.

Description: Proportions of the figured paratype (a slightly broken shell) are: L, 12.7 mm; LPer, 9.6; LPer/L, .76; W, 6.1; W/L, .48; 4 1/2 whorls.

External body pale gray, front of head and tentacles medium gray. Inconsistently the dorsal part of the hind end of the foot may be medium gray also.

Mantle projections are broad triangles with rounded tips, C 4-11, P 3-6 in three specimens from the type locality, and C 4-11, P 4-7 in 12 from Liberia. The columellar and posterior lobes are pale, and the mantle projections difficult to resolve. Indistinct clusters of melanin are present in a minority of the projections.

Penial retractor muscles have separate but adjacent origins. The glandular portion of the sheath is about 10% of total length of the sheath, and twice as wide as the muscular portion. The preputium is about as long as the sheath. Vas deferens between paragonoporal angle and sheath also about as long as sheath.

Spawn: Egg masses were found at the type locality, on the under surfaces of lily pads. Facilities for study were not available, and only rough notes were possible. Coiling was similar to that described in *M. bullula*, in nine capsules ranging from 90º to 360º, from kidney-shaped through an open C-shape to a full turn with a small open space in the middle. Both ends were blunt, the terminal end most often wider than the initial end.

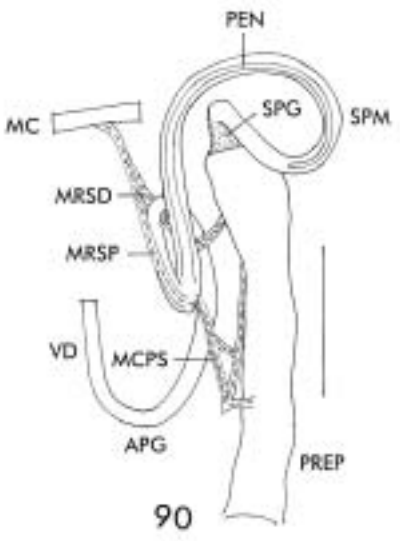


Fig. 90. *Mayabina tempisquensis*. Costa Rica, Prov. Guanacaste: Parque Nacional Palo Verde (T92-7503). Penial complex, medial view. APG, paragonoporal angle; MC, columellar muscle; MCPS, connective between penial sheath and preputium; MRSD, distal retractor of penial sheath; MRSP, proximal retractor of penial sheath; PEN, penis; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

TABLE 31
Variation in numbers of mantle projections of Mayabina tempisquensis *from Liberia, Costa Rica (T92-7701). N = 12*

	Columellar	Posterior
Mean	8.25	5.58
Range	4-11	4-7
S.D.	2.05	.996
S.E.	.592	.288

Localities and material examined:
COSTA RICA, Prov. Guanacaste: Parque Nacional Palo Verde, edge of marshes 100 m E of W end of airstrip, 10º20.68'N, 85º20.60'W, 16-XI-1992 (T92-7503)(**M**). Ornamental pool inside Hotel Las Espuelas near the bar, 2 km SE Liberia, 10º36.81'N, 85º26.09'W, 17-XI-1992 (T92-7701)(**M**). Río Cañas 9 km S Cartagena, 10º19.00'N, 85º39.73'W, 19-XI-1992 (T92-8007)(**M**).

Tropinauta g.n.

Type species: *Tropinauta sinusdulcensis sp.n.*
Name: Tropic, and Latin *Nauta* (masculine; a sailor), a synonym of *Aplexa, i.e.*, a tropical *Aplexa*.
Description: Shell stoutly spindle-shaped, short-spired with shallow sutures. White streaks or bands in the shell not evident. Length to about 10 mm.

Mantle reflected over shell on both sides, on the left about .1 whorl, on the right as a broad lobe over the columellar-parietal area; margin entire all around, with no projections or scalloping. Head and foot are nearly uniform gray, without patterning.

The hermaphroditic duct (DH) is set with closely crowded, blunt seminal vesicles on both sides along most of its length; these vesicles are shorter than or slightly longer than the width of the duct.

Male system: The prostate is a bulky mass of simple tubular follicles, in length up to about five times their diameter; W/L .37. Rather than being simply appressed against the distal oviduct (OD III) as usual, the prostate is half enfolded by it.

Penial complex: The preputium is approximately equal in length to the penial sheath, flexed through 90º in its proximal portion. The penial sheath is bipartite, with a proximal, tubular muscular portion (SPM), forming about 60% of length, and a distal, thick-walled, glandular portion (SPG) about three times as wide as the proximal portion. The distal portion is flexed through 180º, and appressed to the proximal end of the preputium. The penis (PEN) is flagellar, with simple tip and terminal pore. The sarcobelum (SAR) is massive, W/L .50, about 40% of the length of the distal glandular portion of the sheath.

Penial retractor muscles originate at a common source on the columellar muscle. The proximal retractor muscle (MRSP) is inserted on the proximal end of the penial sheath, the distal retractor (MRSD) on the distal end of the sheath. A columellar-preputial muscle (MCP) originates at the common source of the penial retractor muscles, and divides into two bands that have different insertions on the preputium distal to its right-angled flexure.

The vas deferens between the paragonoporal angle (APG) and penial sheath is equal in length to the preputium.

Female system: The bursa copulatrix (BC) is a simple ovoid sac; the duct (DBC) leaves at the anterior margin. The duct widens gradually and conspicuously toward its junction with the oviduct, and is clearly set off at each end. At the junction the duct enters a conspicuous muscular swelling, not seen in other Physidae. The vagina is short, wider than long; W/L 3.0.

Distribution: Known only from a single locality (Fig. 15).

Comparisons: *Tropinauta* is unique in Physidae by having a preputial retractor muscle from the columellar muscle, a flexure of 180º in the penial sheath, and of 90º in the adjacent part of the preputium. Other characteristics are the uniformly entire mantle margin, bulky distal glandular portion of the penial sheath, the enfolding of the prostate by the lower oviduct, the tapered bursal duct, and the muscular knot at the distal end of the bursal duct. *Tropinauta* is the most advanced of Amecanautini in Grade II.

Tropinauta sinusdulcensis sp.n.

Figs. 91-94

Holotype: CAS 146095. Costa Rica, Prov. Puntarenas: small stream in pasture 3 km SE of Golfito, 8º36.68'N, 83º8.48'W, 6-XI-1992 (T92-5703), and later. Paratypes INBio.

Name: Latinized from Golfo Dulce.

Description: As above for the genus. Only one adult specimen, the holotype, was available for dissection. Application of pesticides in the marsh had eliminated adult animals when the locality was visited on two occasions after the original collection.

Habitat: An unnamed rivulet from the hills above spreads through a pasture, and at the lower end is partly dammed by an abandoned railway grade to form a marshy area among emergent grasses. Other molluscs associated were *Pisidium jamaicense* Prime, *Aroapyrgus costaricensis* (Mörch), *Pyrgophorus parvulus* (Guilding), *Biomphalaria*, *Drepanotrema anatinum* (d'Orbigny), *D. lucidum* (Pfeiffer), and *Gundlachia radiata* (Guilding).

Tribe **STENOPHYSINI**, new tribe

Penial sheath consisting of a muscular proximal part and a shorter, bulkier, distal glandular part. Pore of penial canal lateral, in distal half of penis; muscular tip solid. Mantle edge reflected broadly over both sides of shell.

Three genera: *Stenophysa*, with one species in the West Indies except Cuba, and in eastern Costa Rica, another perhaps in northeastern South America; *Afrophysa*, monotypic, Rio Grande do Sul, southern Brasil; and a "name uncertain" group in Argentina and perhaps adjacent countries.

Stenophysa Martens, 1898

Martens, 1890-1901:362 [1898]; type species (by original designation): *Physa sowerbyana* d'Orbigny, 1841, Guadeloupe, <*Physa marmorata* Guilding, 1828.

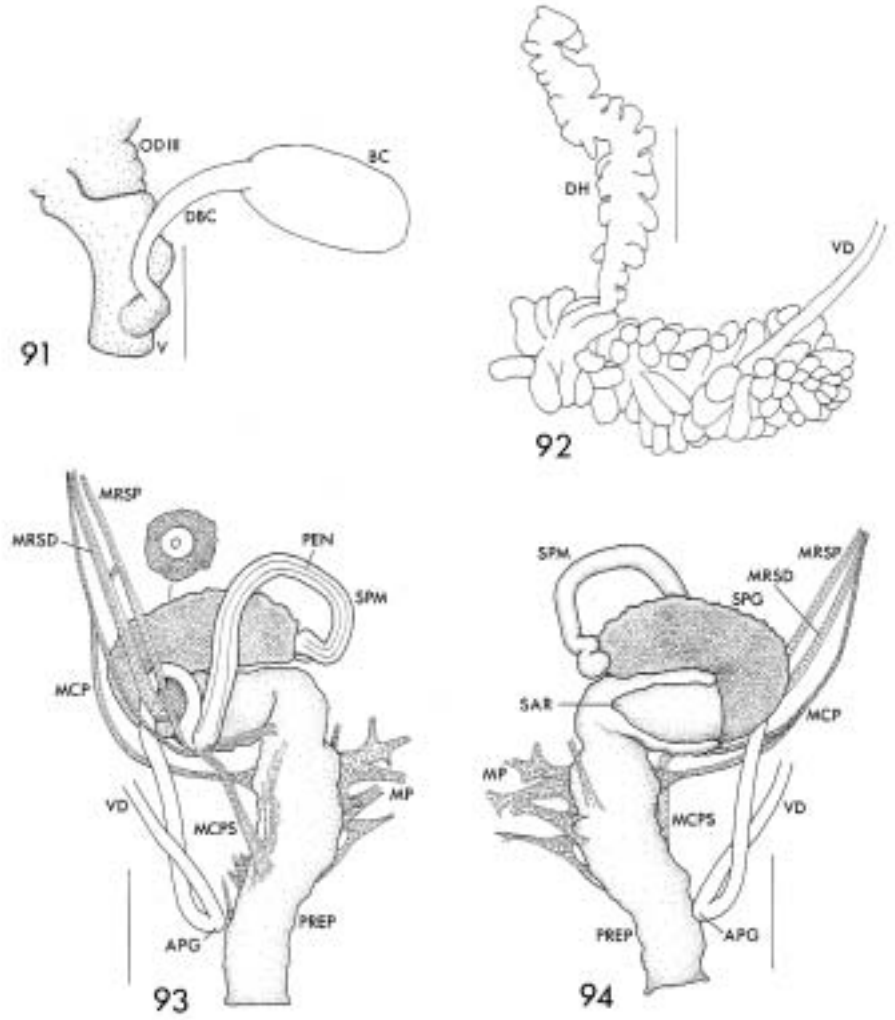
Name: Greek *stenos*, narrow, and *Physa*; *i.e.*, narrow *Physa.*

Diagnosis: Shell ovoid-fusiform, polished, with slightly flattened body whorl. Parietal callus narrow, apex acute. Length to 16 mm. Color bands in the shell faint or absent.

Mantle broadly reflected on both sides; the margin with triangular projections in two groups, columellar-parietal (C) and left posterior (P); C 6-10; P 4-6.

Foot with a median stripe of melanin in its posterior one-fourth. Posterior tip narrowly triangular to acuminate. Head bearing a pattern of irregular black spots and blotches.

Penial complex: Preputium about as long as penial sheath. Penial sheath bipartite, consisting of a long muscular tube (SPM) in proximal two-thirds to three-quarters, of which the proximal end is slightly swollen; it enlarges gradually in the glandular portion to more than twice the width of the proximal portion.



Figs. 91-94. *Tropinauta sinusdulcensis*, p. 111. Holotype. Costa Rica, Puntarenas: 3 km E Golfito. 91, terminal female system; 92, hermaphroditic duct and prostate; 93-94, medial (93) and lateral (94) views of penial complex. APG, paragonoporal angle of vas deferens; BC, bursa copulatrix; DBC, duct of bursa copulatrix; DH, hermaphroditic duct; MCP, muscle bands from columellar muscle to preputium; MCPS, muscle connecting proximal end of penial sheath to preputium; MP, protractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD III, terminal portion of oviduct; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale 1 mm.

Glandular portion (SPG) continued into a conical sarcobelum inside preputium. Penis bipartite, slender and cylindrical up to the exit of the penial canal, its tip either elongate, distensible, and slightly swollen, or broadly spatulate. Pore of penial canal lateral, at about 50-60% of length of penis. Vas deferens between paragonoporal angle (APG) and penial sheath shorter than sheath, and longer or shorter than proximal muscular portion of penial sheath.

Penial retractor muscles originate from the columellar muscle as a single band that divides into two muscles; the narrower proximal retractor (MRSP) is inserted usually on the proximal end of the penial sheath, but with much variation, and the wider distal retractor (MRSD) is

inserted on the distal end. Cross-connections between the retractor bands may be present.

The connective of penial sheath and preputium (MCPS) originates on the proximal end of the sheath, and is inserted on the distal part of the preputium.

Distribution: Two species, one in the West Indies except Cuba, from Jamaica to Trinidad; eastern Costa Rica; probably also on Isla Providencia and in Panama (*S. marmorata*); another in northeastern South America? (*S. spathidophallus*). Identity of the one or more species in eastern Brasil remains unresolved.

Comparisons: *Stenophysa* is distinct especially by the color pattern on the head, slender penis behind a lateral opening of the penial canal, and elaborate tip of the penis.

Nomenclature: *Physa sowerbyana* d'Orbigny (1841), type species of *Stenophysa*, was based on the species illustrated as *Lymnea rivalis* by Sowerby (1821-1834), who cited Guadeloupe as the only locality he knew. This fixes the type locality, and the name *Stenophysa* is thus tied to the species of Guadeloupe. H. B. Baker (1930) considered *Bulla rivalis* Maton & Rackett (1807) as an older name for *Stenophysa sowerbyana*, but to me it is rather a synonym of *Haitia acuta*.

Referred species:

Stenophysa marmorata (Guilding, 1828); TL St. Vincent, Lesser Antilles.

>*rivalis* Sowerby I, 1822; TL Guadeloupe, Lesser Antilles.

>*rivalis antillarum* Beck, 1838; substitute for *rivalis* Sowerby I, 1822, Guadeloupe, Lesser Antilles.

?>*ventricosior* Beck, 1838, *nomen nudum*; TL "Panama."

>*sowerbyana* d'Orbigny, 1841; substitute for *rivalis* Sowerby I, 1822.

>*acuminata* "Parreyss" Villa & Villa, 1841, *nomen nudum*; St. Thomas, U.S. Virgin Islands.

>*ventricosa* "Guilding" Jay, 1850, *nomen nudum*; TL St. Vincent, Lesser Antilles.

>*salleana* Dunker, 1853; TL savanna in the vicinity of Bávaro, Prov. La Altagracia, Dominican Republic.

>*margaritacea* "Shuttleworth" Martens, 1873; published in synonymy of *Physa rivalis* Maton. Antigua, British Virgin Islands.

>*acuminata* "Gray" Sowerby II, 1873; TL St. Thomas, U.S. Virgin Islands.

>*ventricosa* "Guilding" Sowerby II, 1873; TL St. Vincent, Lesser Antilles.

>*guadeloupensis* "Grateloup" Clessin, 1885; TL Guadeloupe, Lesser Antilles.

?> *simoni* Jousseaume, 1889; TL Laguna de Espino, near Caracas, Venezuela.

Stenophysa spathidophallus sp.n. TL Singapore, doubtless introduced, perhaps from northeastern South America.

Stenophysa marmorata (Guilding, 1828)

Figs. 95-108, Pl. 5, fig. 3
Distribution Map, Fig. 109

Physa marmorata Guilding, 1828:534. Paraense, 1986:459, figs. 1-33; beautiful morphology.
Aplexa marmorata (Guilding): Clench, 1936:337, pl. 25, fig. 6.
Aplexa (Stenophysa) marmorata (Guilding): Aguayo, 1938:269, pl. 18, fig. 5.
Physa (Stenophysa) marmorata Guilding: Aguayo, 1966:10.
Stenophysa marmorata (Guilding): Starobogatov, 1970:258.

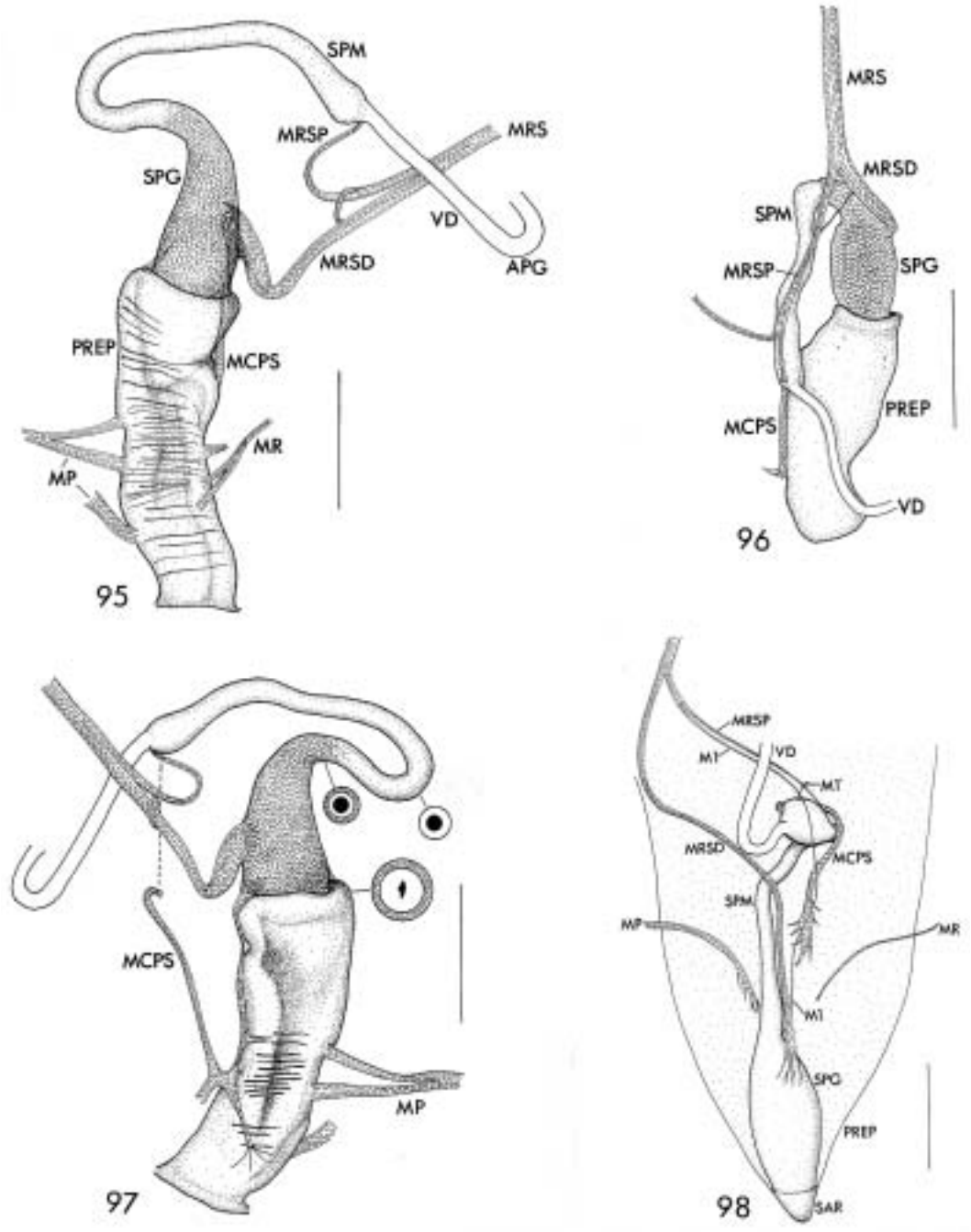
Holotype: probably lost; from St. Vincent, Lesser Antilles.

Name: Latin, marbled.

Diagnosis: Penis terminating in an elongate, distensible swelling.

Description: External features of the head-foot are as in the generic diagnosis.

The mantle is broadly reflected over the shell on both sides, on the left about 1/10 whorl. The mantle margin bears triangular projections



Figs. 95-108. *Stenophysa marmorata*, p. 113. 95, penial complex, retracted, and 98, extruded and laid open. 95, lateral and 97, medial views of one specimen, Mare Tombeau, Guadeloupe. 96, Little London, Jamaica. 98, Mare Tombeau, Guadeloupe. 99, penial complex, extruded, Cabarete, Dominican Republic; 100, penial complex, retracted, medial view, El Socorro Road, Trinidad; 101-102, medial (L) and lateral (R) views of penial complex, retracted, Cabarete, Dominican Republic; 102, 103, 107, terminal female system; 104, penial complex; 105, 106, 108, entire animal. 102, Little London, Jamaica; 103, 104, 106, 108, El Socorro Extension Road, Trinidad; 105, Cabarete, Dominican Republic; 107, Mare Tombeau, Guadeloupe.

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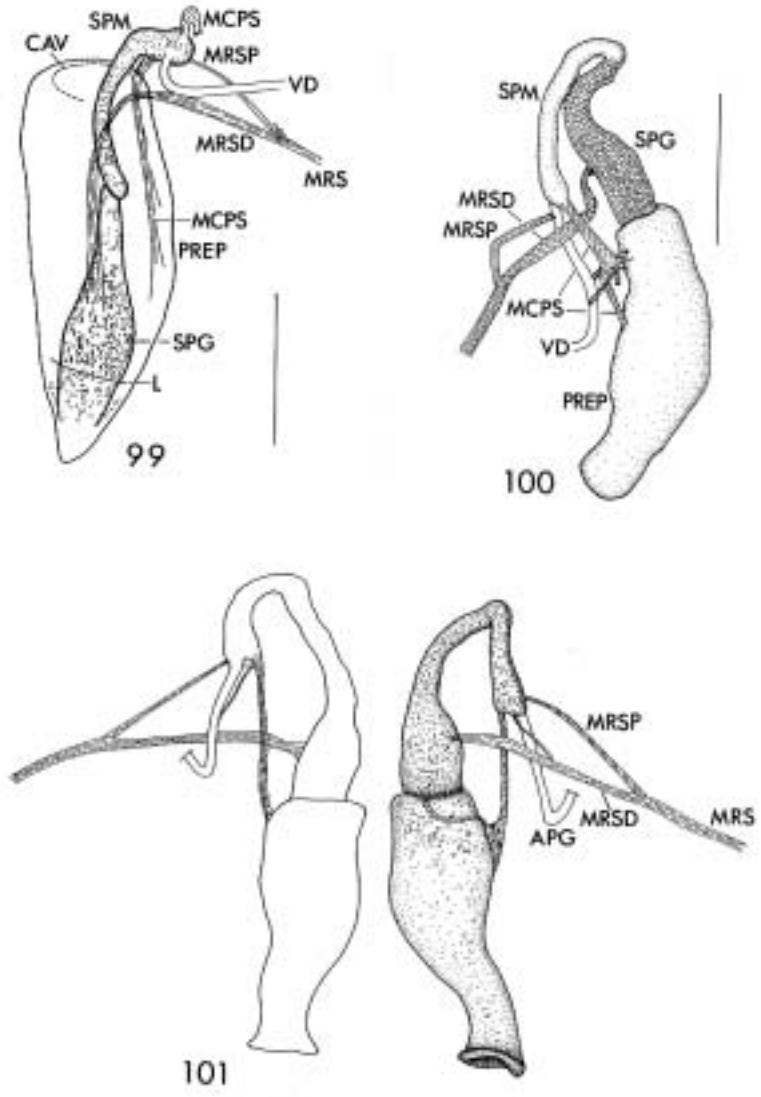

Figs. 99-101. APG, paragonoporal angle of vas deferens; BC, bursa copulatrix; CAV, limit of body cavity; DBC, duct of bursa copulatrix; L, limit of sarcobelum; M1, M1', accessory muscles; MCPS, muscle band connecting proximal end of penial sheath to preputium; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRS, retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD III, terminal portion of oviduct; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale 1 mm.

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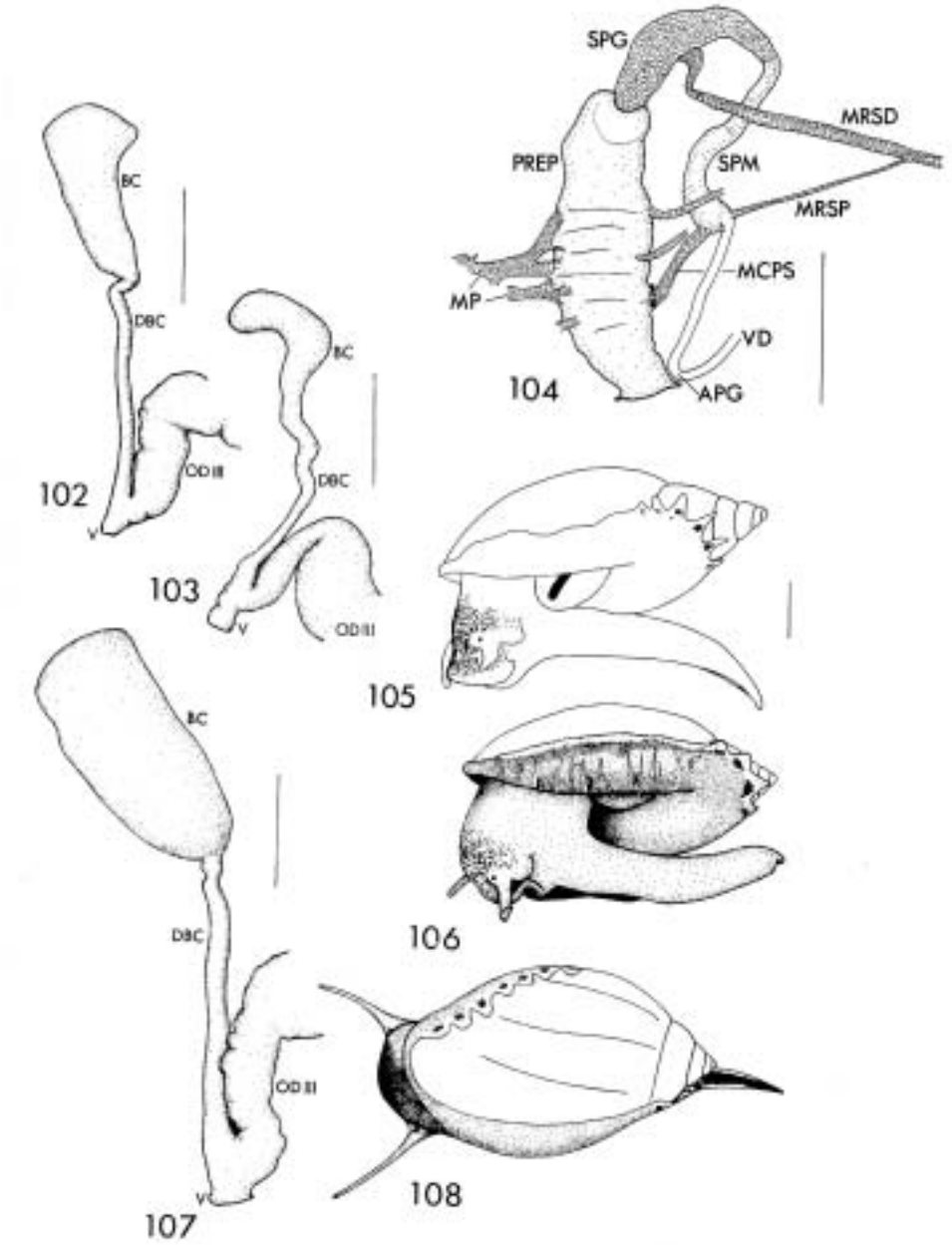
SPG
MRSD
PREP
SPM
MRSP
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APG
104
BC
DBC
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Figs. 102-108.

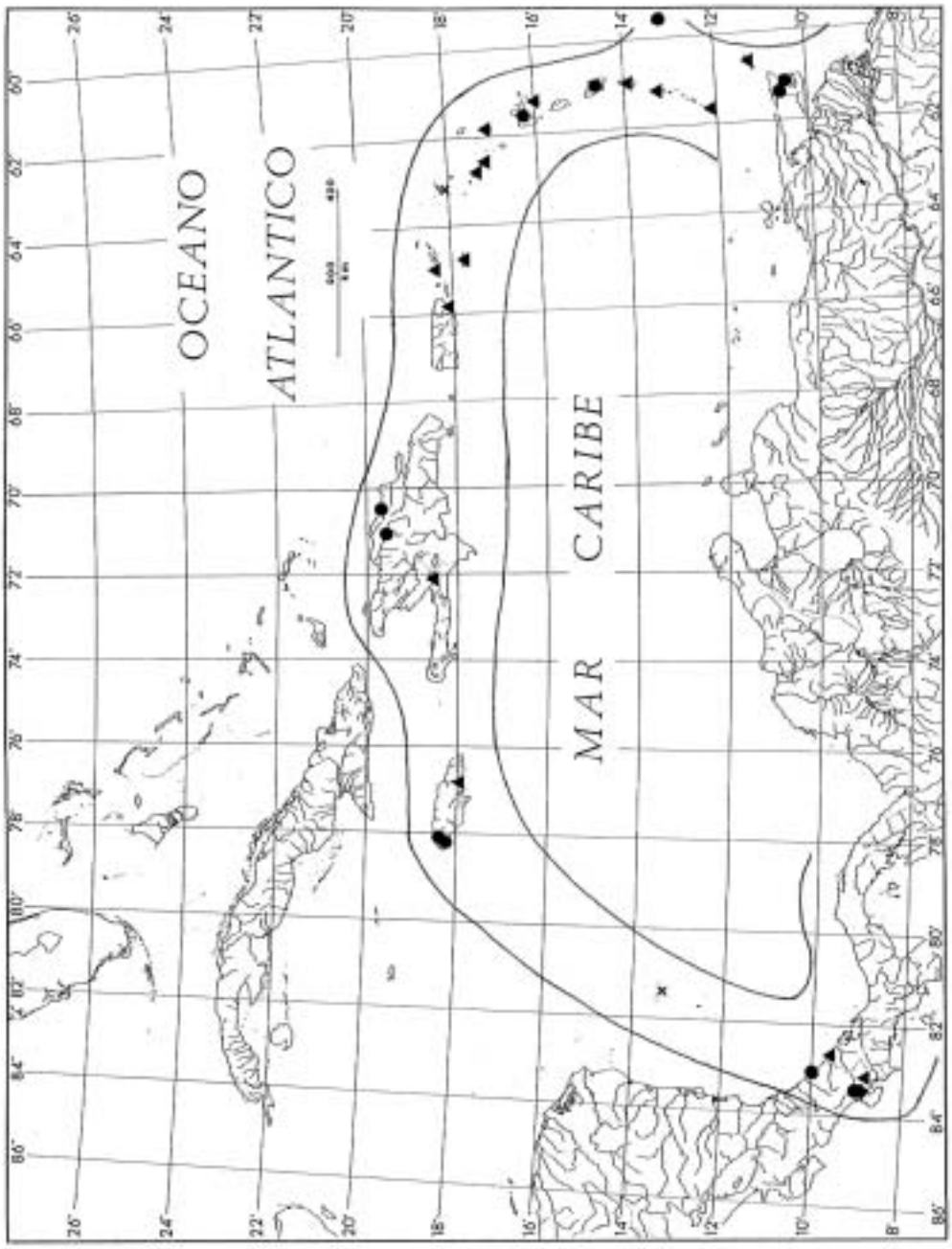


Fig. 109. Distribution of *Stenophysa marmorata*, p. 113. Solid dots, specimens verified morphologically; solid triangles, shells only; x, literature records.

TABLE 32
Measurements and descriptive statistics of shells of Stenophysa marmorata *from Cabarete, Dominican Republic (T89-5601). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	12.28	8.25	.672	6.34	.517	5.1
Range	11.1-15.0	7.2-9.7	.62-.73	5.8-7.4	.49-.56	$4\,^{3}/_{4}$ - $5\,^{3}/_{4}$
S.D.	.905	.542	.029	.418	.016	
S.E.	.165	.099	.005	.076	.003	

TABLE 33
Measurements and descriptive statistics of shells of Stenophysa marmorata *from south of El Socorro Waterworks, Trinidad (T89-4102). Measurements to nearest .128 mm. N = 15*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	11.05	8.17	.740	6.14	.556	4.6
Range	10- 12.3	7.4-9.3	.70-.81	5.8-7.4	51-.58	4 - 5
S.D.	.738	.533	.037	.420	.018	
S.E.	.191	.138	.010	.108	.005	

in two groups, columellar-parietal (C) and left posterior (P); C 7-11, P 5-7. The posterior projections reach nearly to the tip of the shell, sometimes even enveloping it. In form the projections are generally round-tipped triangles, wider than long, but may be longer than wide, or even semicircular.

Penial complex: The penial sheath, slightly longer than the preputium, is composed of a proximal muscular portion and distal glandular portion. The proximal portion is in the form of a tube, slightly wider at the proximal end, and usually longer than the glandular portion. The distal glandular portion is not sharply distinct from the muscular portion; it enlarges gradually at first, and may then swell abruptly into a terminal bulb, or simply enlarge gradually throughout its length. The glandular portion of the penial sheath enters the preputium, forming a conical sarcobelum.

The penis is a slender rod in its proximal two thirds, at the end of which is the lateral opening of the penial canal. The distal portion widens into a swollen tip that is roughly elliptical in plan.

The length of the vas deferens from the paragonoporal angle to the penial sheath is less than that of the muscular portion of the sheath.

The penial retractor muscle originates as a single band (MRS) from the columellar muscle; it is distinct by its melanin flecks. At a variable distance, usually 40-60% of length, it gives off the narrow fibre of the proximal penial retractor (MRSP). Between the proximal and distal penial retractors there is rarely a cross-connection. Insertion of the distal retractor (MRSD) is on the terminal bulb of the penial sheath, well above the preputium. Insertion of the proximal retractor is predominantly on the proximal end of the sheath, but sometimes with extraordinary variation; it may be inserted instead on the preputium, terminal bulb of the sheath, or on the vas deferens; and there may be additional insertions as well.

The connective of the penial sheath and preputium (MCPS) originates on the proximal end of the sheath, where it is wider than the proximal penial retractor, and is inserted by a wider band on the preputium, with a narrower band to the webbing of the cephalic cavity. All muscle bands of the penial complex are melanin-flecked.

Female system: The bursa copulatrix (BC) is an elongate sac, generally two to three times as long as wide. It is shorter than its duct

(DBC), from which it is usually well set off. The duct expands slightly at its distal end, joining the much broader opening of oviduct III. The latter joins the bursal duct at right angles; beyond the oviduct, the vagina (V) is short and about equidimensional.

Variation: The most conspicuous variation is in the proximal penial retractor muscle, both as to number and location of insertions. In a sample of ten from Trinidad (El Socorro Extension Road), insertion of the muscle was on the proximal end of the sheath (as usual) in six, on the preputium in one, on the distal end of the sheath in one, and on the vas deferens above the sheath in two. I have never found such variation in any other species of Physidae.

Distribution: West Indies, from Jamaica to Trinidad; probably on Isla Providencia of the western Caribbean; eastern Costa Rica; probably Panama. From Trinidad there are two biogeographic tracks toward the west. One leads through the coastal islands offshore of Venezuela to Aruba. Not one of these islands provides an adequate freshwater habitat for the species. The other track leads to mainland Venezuela. Perhaps *S. marmorata* was described from Caracas as *Physa simoni* (Jousseaume, 1889), but morphological study is necessary for confirmation.

H. B. Baker (1930:36, pl. 39, figs. 1-7, as *Aplexa rivalis* from Bejuma, Carabobo, Venezuela) described what may be *Stenophysa*. Features in agreement with *S. marmorata* are the elongate, narrow bursa copulatrix, and multiple insertions of the penial retractor muscles; but the junction of bursal duct and oviduct III is farther from the female pore than in any specimens of *Stenophysa* that I have examined. In the absence of information as to composition of penial sheath and form of penis, no identification is possible.

Stenophysa marmorata has been recorded repeatedly in eastern Brasil, but in the absence of morphological information no confirmation is possible.

Localities and material examined:

GREATER ANTILLES: Jamaica, Cornwall County, Hanover Parish: Pasture pond about 200 yards NNE Flint River crossing by Montego Bay-Lucea highway, 4-XI-1989 (T89-1901)(**M**). Manchester Parish: Mandeville [18º02'N, 77º30'W] (MCZ 62876, *ex* F. C. Baker). Westmoreland Parish: Overflowing pond beside Glasgow-Cessnock road, 5-XI-1989 (T89-2001)(**M**). Side channel of Cabarita River at Grange Hill-Frome road, 5-XI-1989 (T89-2103)(**M**). Pond on S side of Negril-Little London road, W of Little London, 7-XI-1989 (T89-2501)(**M**). Pond about 500 ft N of Negril-Little London road, W of Little London, 7-XI-1989 (T89-2601)(**M**). Little London, in pond divided by causeway of road to Savanna-La-Mar, 7-XI-1989 (T89-2701)(**M**). Drainage ditch at road, S of main intersection in Little London, 7-XI-1989 (T89-2801)(**M**). Bluefields (MCZ 91 327, *ex* USNM). Surrey County, St. Andrew Parish: Kingston [18º00'N, 76º48'W], *E. Chitty* (BMNH uncat., *ex* C. B. Adams colln.).

Dominican Republic, Prov. Puerto Plata: Marsh in west side of Cabarete, 19º44.0'N, 70º23.3'W, 26-XI-1989 (T89-5601)(**M**). Prov. Valverde: Side channel of Río Yaque del Norte at Esperanza-Mao road, north of Mao, 19º36.84'N, 71º4.20'W, 23,24-XI-1989 (T89-5303)(**M**). Many other localities are cited by Gomez *et al.* (1986).

Haiti: widespread (Robart *et al.*, 1977). Miragoane, *P. J. Darlington* (MCZ 108 589).

Puerto Rico (Harry & Hubendick, 1964; Richards, 1964). Humacao (BMNH uncat., from Cuming collection).

VIRGIN ISLANDS: St. Thomas, no precise locality (BMNH 1841.4.28.233-237, and two sets uncat.; UMMZ 124190, 143216, both from Kent Scientific Institute).

Tortola, no precise locality (UMMZ 157 539, from W. F. Webb through B. Walker collection).

St. Croix: No precise locality, *H. A. Beatty* (MCZ 179 095, 196 134). Bethlehem stream, *H. A. Beatty*, 1935 (MCZ 91 341, ex USNM). Christiansted [17º44'55"N, 64º42'13"W], *H. A. Beatty*, XI-1942 (MCZ 196 135).

LESSER ANTILLES: St. Martin (Coomans, 1967).

St. Kitts: No precise locality, *R. W. Jackson* (MCZ 172 074); *C. W. Branch* (BMNH 1908.7.10.380), *W. A. Hoffman* (UMMZ 167 300).

Nevis: No precise locality (MCZ 91 337, *ex* USNM).

Antigua (no precise locality): *F. Watts* (BMNH 1895.1.29.30); *J. W. Gregory* (BMNH 1899.12.23.85-88, 1899.12.23.89-91); *C. A. Barber* (BMNH 1892.12.1.4-5). Hodge Point, *D. Stingley* (MCZ 189 166). Between English Harbor and Parham (MCZ 91 321, *ex* USNM).

Guadeloupe: widespread (Pointier, 1975). Mare Tombeau, *J. P. Pointier*, 29-III-1987(**M**). Marshy area behind mangrove, Jacquot; *J. P. Pointier*, 20-XI-1986 (**M**).

Marie Galante: Rivière de St. Louis (MCZ 91 349, *ex* USNM).

Martinique: widespread (Guyard & Pointier, 1979). Mare Cap Chevallier, *J. P. Pointier*, 14-X-1982(**M**).

St. Lucia (McKillop *et al.*, 1981; Sturrock, 1974). Cul de Sac Valley, *R. F. Sturrock* (MCZ 257 109).

St. Vincent (Rankin & Harrison, 1979). No precise locality (BMNH 1839.9.15.122-137, purchased from *L. Guilding*; 1839.9.15.140-150). Brighton [13º08'N, 61º10'W], *H. H. Smith* (BMNH 1895.6.17.426-432). Three Rivers, *H. H. Smith* (BMNH 1895.6.17.433-440).

Barbados, Christ Church Parish: Graeme Hall Swamp, 13º04.27'N, 59º34.84'W, 19,20-XI-1989 (T89-4703, 5002)(**M**).

Grenada (Smith, 1895). No precise locality, *H. H. Smith* (BMNH 1895.6.14.1-7).

Tobago: Cocoa Walk, *Mrs. J. Longstaff* (BMNH uncat.).

Trinidad: No precise locality, *R. J. L. Guppy* (BMNH 1866.1.3.9). Port of Spain, *A. Lutz* (UMMZ 123942, from B. Walker collection). Caroni County, Cunupia Ward: Marshy ditch on E side Uriah Butler Highway, 500 m N of Caroni Bird Sanctuary turnoff, 12-XI-1989 (T89-3701). Borrow-pit pond at Caroni Bird Sanctuary flyover, on SE side Uriah Butler highway, 13-XI-1989 (T89-3901). Caroni Bird Sanctuary, about 250 m S of headquarters buildings, 12-XI-1989 (T89-3803)(**M**). St. Andrew County, Turure Ward: N end of Nariva Swamp, MP 39 3/4, 15-XI-1989 (T89-4501)(**M**). St. Ann's Ward: Ditch about 100 m S of S end El Socorro Extension Road No. 2, S of El Socorro Waterworks, 13-XI-1989 (T89-4102)(**M**).

WESTERN CARIBBEAN: Isla Providencia (Pilsbry, 1930).

COSTA RICA, Prov. Limón: Hotel Matama, 2 km NE of Moín, 10º0.53'N, 83º3.74'W, 18-XI-1993 (T93-3704)(**M**). Parque Nacional Cahuita, western edge, 9º44.13'N, 82º50.41'N, *D. W. Taylor*, 6,7-XI-1997 (INBio).

Prov. Puntarenas: Drainage canal about 1/4 km E of Río Coto Colorado and about 1 km NE of Kilómetro 20 in the palm-oil plantation, perhaps Finca 63, 8º37.80'N, 83º3.61'W, 7-XI-1992 (T92-6201)(**M**). Marshy puddles along road, .1-.5 km W of Río Pejeperro, 8º26.22'N, 83º23.74'W, 30-X-1995 (T95-1702, INBio). Estación Esquinas, *Marianella Segura*, 9-IV-1994 (INBio 1 001 467 154). Palmar Sur, at airport, 8º57.20'N, 83º28.14'W, 9-XI-1993 (T93-2801)(**M**). Roadside pool 3.5 km N of Sierpe, 8º53.75'N, 83º28.59'W, 5-XI-1996 (T96-601, INBio)(**M**).

PANAMA, Canal Zone: Juan Mina Station [not traced], *G. B. Fairchild* (MCZ 125 103).

GUYANA, probably introduced: No precise locality, *J. J. Quelch* (BMNH 1897.3.20.24-35). Botanical Gardens, Georgetown (Clench, 1936). Perhaps both records refer to the same population. Georgetown, "Curaçao" (UMMZ 123940, from J. R. LeB. Tomlin through B. Walker collection).

Biology: Rankin & Harrison (1979) compared field and laboratory populations in four stocks from different sites on St. Vincent. Each population included three groups with different growth trends, each group contributing differently to survival, viability, and stability of the population. Width/length ratio of shells in all groups was .51, with low S.D., so that the authors considered it a specific character [But it

may not be diagnostic; W/L in a small sample of *S. spathidophallus* is .52]. *S. marmorata* is very sensitive to direct sunlight, lack of oxygen, desiccation, and lack of food after even two days. As in other species of Hygrophila studied, crowding of the snails in containers reduced the number and size of the spawn masses produced, and the production of viable eggs.

In the cultivated dasheen (*Colocasia*) marshes of St. Lucia *S. marmorata* occurs with several other species, whereas on St. Vincent it is virtually the only gastropod (McKillop *et al*., 1981). The precarious existence it leads on St. Lucia seems due to the widespread occurrence of the Hydrobiid *Pyrgophorus parvulus* (Guilding, 1828). The latter, a fine-particle feeder, is always present to compete for food with *S. marmorata*, a browser on organic film.

Effects on embryonic development of deprivation of calcium were studied by Ross & Harrison (1977). Embryos were able to develop to maturity in only .22 mg/l of calcium, a concentration too low for the survival of adults and one hardly ever encountered in nature. Evidently the wall of the egg capsule can regulate ionic concentrations of the capsular fluid much like a true cell membrane. In 105 spawn masses studied there were 653 eggs, an average of 6.2 per mass. Time for hatching of all living embryos in an individual spawn mass varied from one to three days.

Remarks: No spawn were available for study. Paraense (1986) reported an egg string in his stock from St. Vincent, but as described and illustrated it does not approximate the egg strings I have studied. As a bulbous prolongation of the outer membrane, however, it may well be a vestigial part of an egg string.

Stenophysa spathidophallus sp.n.

Figs. 110-116, Pl. 8, fig. 9

Holotype: CAS 114 804. Singapore: ditch from Seletar Reservoir, 100 m west of Upper Thompson Road, 13-XII-1985 (T85-1403).

Name: Greek *spathe*, *-idos*, a paddle for stirring; and *phallus*.

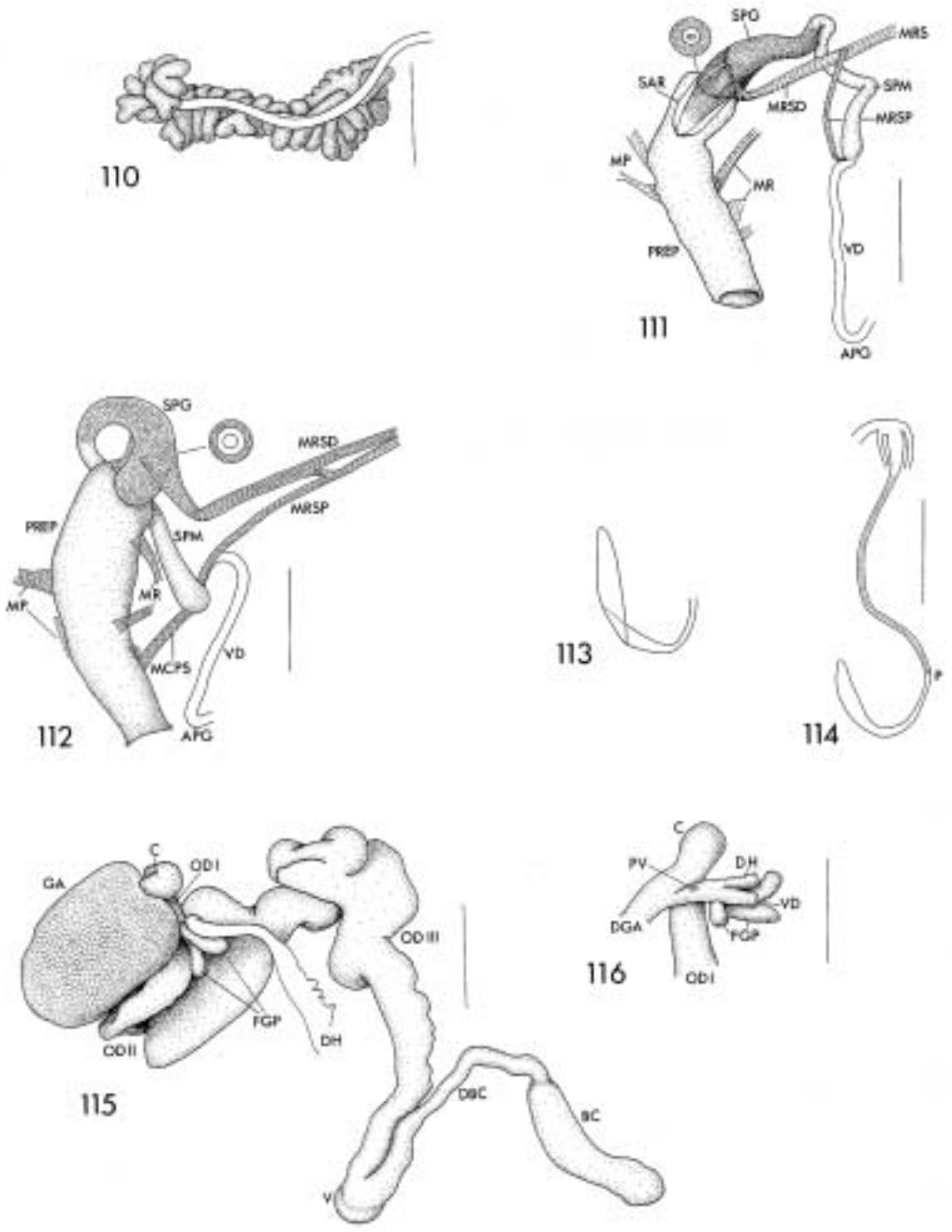
Diagnosis: Penis terminating in a broad, flat blade with rounded tip.

Description: The shell is elongate-ovate, with an acute spire and narrowly rounded anterior end. The aperture has a narrowly rounded anterior end and acute posterior end. The profile of the aperture is broadly convex in the direction of growth, with no retraction to the suture. The columella is narrow, white, with no evident fold. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but not incised suture. The lateral profile of the spire is plane. The shell surface is polished and shining, its color pale yellow-brown, with a narrow white band at the suture. Axial white lines and scattered dots are present but sparse. Spiral bands are numerous but diffuse and obscure, recognizable only by slight contrast in the overall tone of the shell. Surface

TABLE 34

Measurements and descriptive statistics of shells of Stenophysa spathidophallus *from Singapore (T85-1403). Measurements to nearest .079 mm. N = 7*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	8.78	6.34	.723	4.59	.524	4.36
Range	7.23-10.40	5.40-7.54	.69-.75	3.81-5.40	.50-.55	4-4 $^{3}/_{4}$
S.D.	.999	.647	.021	.473	.015	
S.E.	.378	.245	.008	.179	.006	



Figs. 110-116. *Stenophysa spathidophallus*, p. 121. Singapore.110, prostate; 111-112, penial complex, lateral view; 113, tip of penis with blade folded over itself; 114, penis; 115, female tract; 116, detail of structures at separation of male and female tracts. APG, paragonoporal angle of vas deferens; BC, bursa copulatrix; C, caecum; DBC, duct of bursa copulatrix; DGA, duct of albumen gland; DH, hermaphroditic duct; FGP, follicles of prostate gland; GA, albumen gland; MCPS, connective between preputium and penial sheath; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD I, OD II, OD III, oviduct I, II, and III; p, pore of penial canal; PREP, preputium; PV, ventral pore; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens. Scale .5 mm except detail, .05 mm.

sculpture consists of fine axial wrinkles, distributed irregularly. Near the suture the wrinkles are stronger and closer, and cut into short segments, straight or slightly curved in the direction of growth, that are arranged in spiral series and give the shell surface a tessellated appearance.

The mantle is reflected over the shell on the left as a smooth-edged band, 1/10 whorl or less in extent. Both columellar-parietal (C) and posterior (P) lobes have round-tipped projections, each usually with a patch of melanin within; C 8-10, P 6-7. The posterior lobe is weakly or not discrete on the left side.

Penial complex: The preputium is about as long as the penial sheath. The penial sheath consists of a proximal, slender muscular tube (SPM) that is swollen slightly at its proximal end, and is not sharply set off from the distal glandular portion. The glandular portion (SPG) is about 30-40% of the total length of the sheath, but bulkier than the rest; it enlarges gradually until it enters the preputium. Within the preputium, the penial sheath tapers sharply inside a large sarcobelum without papilla. The penis is a slender rod in its proximal two thirds, at the end of which is the lateral opening of the penial canal. The distal portion widens gradually into a thin, flat, blade with rounded tip, unique in Physidae.

The vas deferens between the paragonoporal angle and the penial sheath is shorter than the sheath, but longer than the muscular portion.

Penial retractor muscles originate usually as a single band (MRS) from the columellar muscle; they divide into a wider band, the distal retractor (MRSD), inserted on the glandular portion of the sheath well above the preputium, and a narrower band, the proximal retractor (MRSP), inserted on the proximal end of the sheath. Length of the common band is about 10-50% of the distal retractor. Less often the penial retractors originate independently, from adjacent origins in the columellar muscle. A cross-connection between the bands may be present.

Localities and material examined:

Singapore: ditch from Seletar Reservoir, 100 m west of Upper Thompson Road, 13-XII-1985 (type locality).

Habitat: The ditch had a slow stream about 30 ft wide over mud bottom between grassy banks at the times of visit. Other molluscs associated were *Thiara tuberculata* (Müller), *Pila ?scutata* (Mousson), *Gyraulus*, and *Planorbella duryi* (Wetherby). In a second attempt to collect the species, 26-I-1987, not one specimen could be found. The most likely explanation of the occurrence of this species is that it was transported through the trade in tropical fishes, and formed a temporary colony after an aquarium was emptied into the ditch or reservoir above. No commercial fish farm existed in the immediate area.

Distribution: On the assumption that this species has a range distinct, but not far distant, from that of *Stenophysa marmorata*, I speculate it may occur in northeastern South America.

Remarks: Evidently the species has been in Singapore for more than twenty years. Two specimens (BMNH uncat.) were found on aquatic plants from Singapore at Manchester Airport, 21-VIII-1975, by British authorities and submitted to BMNH for identification.

Afrophysa Starobogatov, 1967

Starobogatov, 1967:295; type species (by original designation): *Physa waterloti* Germain, 1911. As genus of Physidae.

Name: From Africa, and *Physa*.

Diagnosis: Shell narrow-ovoid to ovoid-fusiform, polished, with no evident sculpture except growth lines. Profile of aperture convex in direction of growth. Parietal callus narrow, apex acute. Length to 16 mm with five whorls. Numerous faint color bands in shell.

Mantle broadly reflected on both sides, reaching apex of shell. Wide, blunt, scalloped projections in two groups, along most of the right side (C) and left posterior (P), C about 15, P 0-4.

Vas deferens between paragonoporal angle (APG) and penial sheath shorter than sheath.

Penial retractor muscles with independent but adjacent origins, inserted on ends of penial sheath, with no interconnections. A connective between head of sheath and distal end of preputium.

Penial complex: Penial sheath tripartite, consisting of proximal muscular portion (SPM) and distal glandular portion (SPG). Muscular portion again subdivided, made up of a wider, thin-walled section (SPM 1), and a narrower but longer thick-walled tube (SPM 2) passing gradually into glandular portion. Distal portion enlarged gradually, nearly to diameter of preputium, consisting of glandular external sheath around a muscular tube. Glandular sheath tapered gradually, disappearing within a large, conical sarcobelum inside preputium.

Penis tripartite, consisting of a proximal elongate sac with thin walls, a long, narrow, thick-walled shaft, and an asymmetrical, solid, swollen tip. The penial canal opens through a wide pore on the dorsal surface of the swollen tip, at about mid-length.

Distribution: State of Rio Grande do Sul, Brasil; widely but sporadically introduced in western and southern Africa.

Comparisons: *Afrophysa* is distinct especially by the tripartite penis with lateral opening of the penial canal on the bilaterally asymmetrical terminal portion of the penis, and by the penial sheath with a muscular portion composed of two distinct parts.

Referred species:

One species, *Afrophysa brasiliensis* (Küster, 1844).

>?*rivalis brasiliana* Beck, 1838, *nomen nudum*; TL Rio de Janeiro [22º54'S, 43º15'W], Brasil.

>*mosambiquensis* Clessin, 1886; TL Tete [16º13'S, 33º35'E], Mozambique, southeast Africa.

>*waterloti* Germain, 1911; TL Porto Novo [6º29'N, 2º37'E], Dahomey, West Africa.

Afrophysa brasiliensis (Küster, 1844)

Figs. 117-125, Pl. 4, figs. 5, 8

Physa brasiliensis "Koch" Küster, *in* Küster & Clessin, 1841-1886 (47):10, pl. 1, figs. 18-20 [1844].

Aplecta brasiliensis Koch: Fischer & Crosse, 1870-1902(2):86 [1886]

Physa waterloti Germain: Ranson & Cherbonnier, 1951:391, figs. 1-6, A-F; Dahomey, West Africa; morphology (very bad).

Aplexa waterloti (Germain): D. S. Brown, 1994:249, figs. 115b-d.

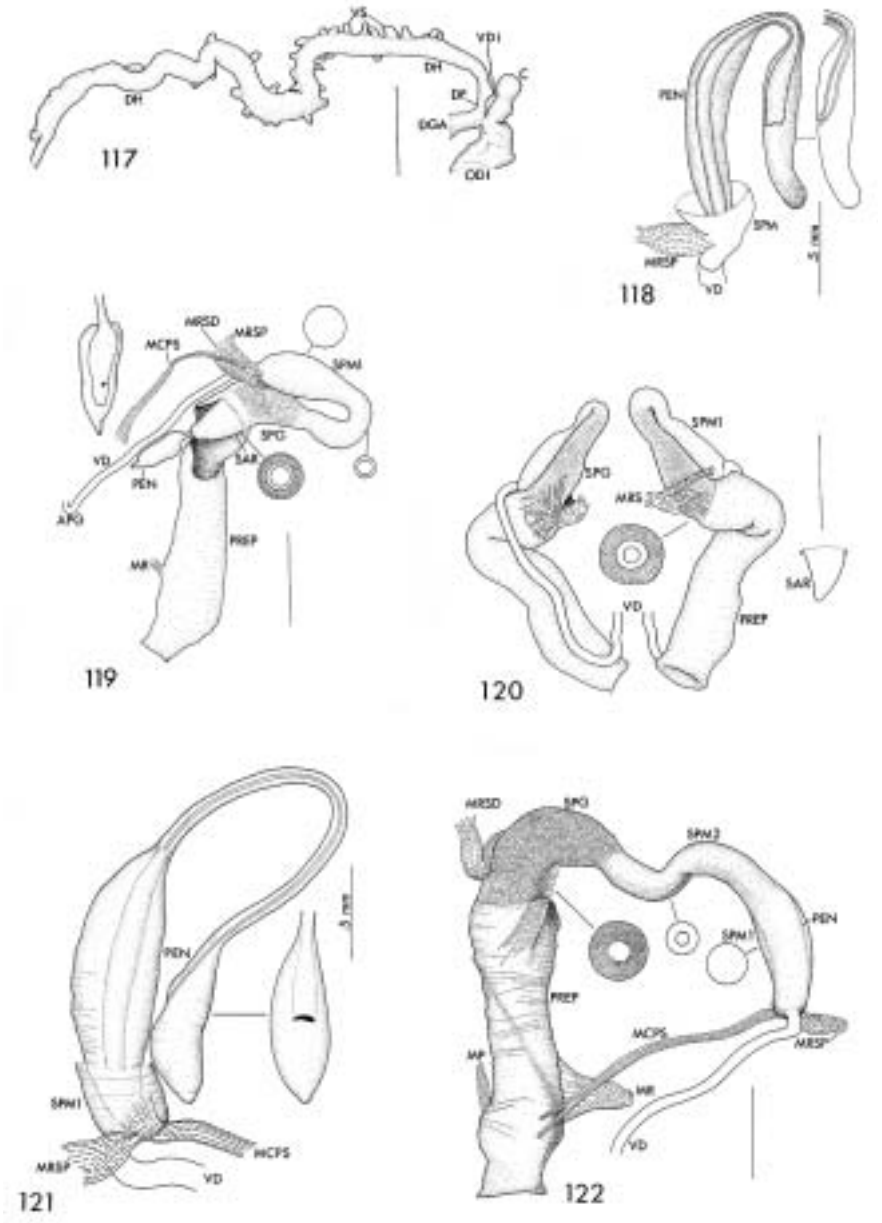
Aplexa marmorata (Guilding) [misidentified]: Appleton *et al*., 1989:340, figs. 1B, 2A (not 2B), 4, 5B; Natal, South Africa; sketch of reproductive system; external morphology; radula. Appleton, 1996:35, fig. 51.

Holotype: Destroyed in SMF in war of 1939-1945, localized only as from "Brasil." Type locality here restricted to Porto Alegre [30º04'S, 51º11'W], Rio Grande do Sul.

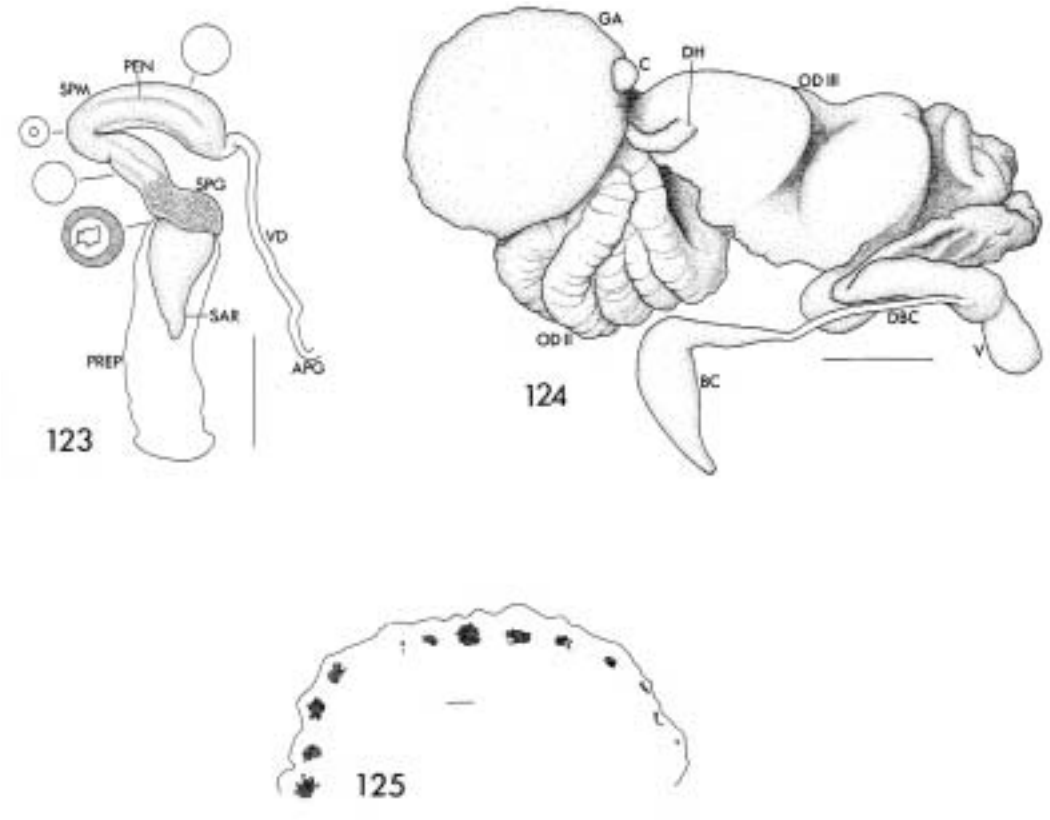
Name: From the locality.

Description: Overall body color is a wash of dark gray. There is no color pattern on the head, nor posterior stripe on the foot, as in *Stenophysa*. The mantle is broadly reflected over the outer lip of the shell on the left in a band with smooth margin. The edge of the mantle bears scallops in two groups: on the right side (C), and left posterior (P); C about 6-8, P 3. The posterior mantle lobe is slightly distinct on the right, not on the left.

Penial complex: The preputium is shorter than the penial sheath. The sheath is muscular in the proximal two-thirds, glandular in the distal third. The proximal portion is composed of recognizably distinct sections. The head, less than ten percent of total length, is muscular, opaque, and moderately thick-walled. This segment passes into a muscular, thin-walled, translucent portion (SPM 1) within which the penis is visible, forming about forty percent of the proximal muscular portion of the sheath. Next the sheath narrows to a thick-walled, opaque, muscular tube (SPM 2), whose lumen is only about forty percent of its diameter. This tube is more heavily dusted with melanin than the more proximal



Figs. 117-125. *Afrophysa brasiliensis*, p. 124. 117, hermaphroditic duct and structures adjacent to caecum; 118, penis; 119, penial complex, medial view; the preputium has been cut open and the penis, extruded through the sarcobelum, has ben lifted out; 120, penial complex, lateral (L) and medial (R) views; 121, penis; 122, penial complex, lateral view;123, penial complex, lateral view; sarcobelum shown by transparency; 124, female system; 125, mantle margin. 120, Kubeasi pool, Ghana; 117-119, 121-124, Porto Alegre, Brasil (MCN 309, 3426); 125, Tzaneen, South Africa. Scale 1 mm except as noted. APG, paragonoporal angle; BC, bursa copulatrix; C, caecum; DBC, duct of bursa copulatrix; DF, female duct; DGA, duct of albumen gland; DH, hermaphroditic duct; GA, albumen gland; MCPS, connective between preputium and penial sheath; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial complex; OD I, OD II, OD III, oviduct; OT, ovotestis; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, SPM1, SPM2, muscular portion of penial sheath; V, vagina; VD, vas deferens.



Figs. 123-125.

region, and passes gradually into the glandular distal portion of the sheath (SPG). The distal portion enlarges gradually almost to the diameter of the preputium, with a glandular sheath around a muscular tube within. Both structures continue within the preputium, in a large, conical sarcobelum without papilla.

The vas deferens between the paragonoporal angle and the penial sheath is shorter than the sheath, and about as long as the muscular portion.

The retractor muscles have independent but adjacent origins in the columellar muscle. Insertions of the two penial retractors are on the ends of the sheath; there are no cross-connections. The connective from the preputium to the sheath (MCPS) runs from the head of the sheath to the distal part of the preputium. All muscles are flecked with melanin.

The penis is composed of three sections. The proximal section, thirty percent of total length, consists of an elongate inflated sac with thin muscular walls. Within its voluminous lumen runs a thick-walled, opaque, penial canal about one-third the diameter of the penis; the canal is suspended by a web of muscle fibers. The second and longest section of the penis, about half its total length, is a narrow tubular shaft. Within it the penial canal is a thick-walled tube. The tip of the penis, about one-fifth the total length, is a swollen muscular structure, shorter and narrower than the proximal sac-like portion. It is bilaterally symmetrical in dorsal view, but asymmetrical in

side view; internally it is filled with spongy muscular tissue. There is no cuticle. The penial canal widens, and continues through a lengthwise dorsal swelling of the penial tip, exiting on the dorsal surface at mid-length of the swollen tip.

The description is based principally on six specimens from Porto Alegre, Brasil (MCN 3426). All material available was contracted to varying extent, and some features were not observable.

Variation: In one specimen (MCN 3426) the penial sheath was composed of four parts. A second, thin-walled muscular portion occurred between the glandular distal portion and the thick-walled muscular portion. In this specimen the tip of the penis also differed from the usual form, in being longer, blunt-tipped, and less swollen in the proximal region.

The penial retractor muscles usually have independent but adjacent origin; rarely they begin as a single band.

Localities and material examined:

BRASIL, Rio Grande do Sul: Chafaris da Facultad de Agronomia, Porto Alegre, *Dr. Morán*, 13-V-1971 (MCN 3 426)(**M**). Jardim Botânico, Porto Alegre, *R. G. Soares, N. T. Schröder*, 29-IV-1986 (MCN 9 127)(**M**). Porto Alegre [30º04'S, 51º11'W], no precise locality; from *Dr. Morán* (MCN 3 309)(**M**). Temporary pools near Porto Alegre (UMMZ 156 458, 156 465). Reservoir near Porto Alegre (UMMZ 156 460).

GHANA: Kubeasi pool, *R. F. Sturrock, Imperial College Ghana Expedition*, 4-VIII-1958 (British Museum Experimental Taxonomy Unit 482)(**M**), provided through the courtesy of D. S. Brown. Adeiso near Nsawam, N of Accra, *J. C. Bequaert*, 1943-1944 (MCZ 163 593). Epe, on the lagoon shore, *Dr. Onobamiro* (BMNH 1953.4.8.1-8). Weija, *E. G. Berry*, 22-I-1952 (UMMZ 246 509). Stream along road from Kumasi to Bokrom, *E. G. Berry*, 28-II-1952 (UMMZ 246 510).

NIGERIA: Oshon stream that crosses Abeokuta Road, *ca*. 1/2 km from road, Ibadan, *P. T. LoVerde*, 2-VII-1974 (UMMZ 232 969).

SOUTH AFRICA, Transvaal: Artificial pond at S. Annecke Research Institute, Tzaneen, *C. C. Appleton*, I-1988 (**M**).

Remarks: Application of *brasiliensis* to this species avoids proposal of a new name, although there is no certainty that the original material came from Porto Alegre. Measurements as given by Küster (converted from lines) are L 12.0 mm, W 5.8, LAp 8.5, whorls 4 1/2, W/L .48, and LAp/L .71. These are within the range of variation observed in material from Porto Alegre.

Subfamily **PHYSINAE** Starobogatov, 1967

Starobogatov, 1967:289; as subfamily for *Physa, Physella, Afrophysa,* and *Petrophysa*. This is the earliest ranking as subfamily within Physidae.

Shell globose to fusiform, dull to polished, to about 25 mm. Mantle margin reflected over shell on left side or not, usually with elongate digitations in two groups, one columellar-parietal, the other left posterior. Preputium with a posterior gland (the only trenchant character), with exception of *Physa mirollii*.

Eleven genera, allocated to three tribes: Haitiini with *Haitia*; Physini with *Laurentiphysa*, *Beringophysa* and *Physa*; and Physellini with *Chiapaphysa*, *Costatella*, *Petrophysa*, *Utahphysa*, *Archiphysa*, *Physella*, and *Ultraphysella*. Distributions of these tribes overlap, but are broadly different: Haitiini from temperate North America through Central America and the West Indies, southward to central Chile (Fig. 8); Physini in Europe, Siberia, and temperate to arctic North America (Fig. 9); and Physellini in North America, as far south as the Pacific coast of Mexico in Nayarit, Sinaloa and Chiapas, and in Costa Rica (Fig. 10).

PHYSINAE, Species *Incertae Sedis*

These nominal forms are referred to Physinae but cannot be assigned more precisely at present:

Alampetis Martens, 1898; type species (subsequent designation by F. C. Baker & Cahn, 1931) *Physa osculans* Haldeman, 1841, an unrecognizable species. Not of Thomson, 1878 (Coleoptera).

=*Alampetista* Zilch, 1956:85; type species (subsequent designation by Zilch, 1959-1960) *Physa osculans* Haldeman, 1841. Substitute for *Alampetis* Martens, 1898.

aequata "Parreyss" Paetel, 1889; TL North America; *nomen nudum*.

bullata Potiez & Michaud, 1838; no locality; not recognizable.

clarkei Ingersoll, 1875; no locality, but apparently from the western United States; *nomen nudum.*

hordacea Lea, 1864; TL Vancouver Island, Clark County, Washington. Columbia River and southward in Willamette River valley, Oregon. Probably extinct.

küsteri Clessin, 1886; no locality; not recognizable.

minor Beck, 1838; TL Lake Ontario; *nomen nudum*.

niagarensis Lea, 1864; TL Niagara River, New York.

nigricans callosa Rigacci & Rigacci, 1866; TL Ohio; *nomen nudum.*

oarium "Bourguignat" Servain, 1880; TL Italy; *nomen nudum*.

osculans Haldeman, 1841; TL "Middle, Eastern and Western States;" not recognizable.

philippii Küster, 1844; TL "North America;" not recognizable.

ruscinonensis "Loutr." Astre, 1921; TL presumably in France; *nomen nudum.*

thiarella Rigacci & Rigacci, 1866; TL "America;" *nomen nudum.*

Tribe **HAITIINI**, new tribe

Penial complex simple, with unitary, muscular penial sheath. Penis tapered obviously from broader proximal end to simple tip with terminal pore. Mantle edge with triangular projections in two groups, columellar-parietal on the right, and left posterior. Mantle not reflected over outer lip of the shell. One genus, with about 15 species in North, Central, and South America, and in the West Indies.

Haitia Clench & Aguayo, 1932

Clench & Aguayo, 1932:37; type species (by original designation): *Physa elegans* Clench & Aguayo, 1932, Lake Miragoane, Haiti. As subgenus of *Physa.*

Name: From the country.

Diagnosis: Shell with broadly rounded anterior end and acute spire, narrow to broad in general shell form. Surface dull to silky but not polished or glossy, with spiral crescentic microsculpture evident or obsolete. Aperture less than or more than half of shell length, with profile weakly convex in direction of growth. Parietal callus narrow. Suture strongly impressed to weakly incised; apex acute. Length to about 20 mm.

Mantle not reflected over outer lip of shell, with triangular projections in two groups, columellar-parietal (C) and left posterior (P); C generally 5-8, P 3-4, but variable.

Penial complex: Preputium with posterior gland. Length of preputium greater than to slightly less that of penial sheath. Penial sheath unitary, entirely thin-walled and muscular, tapered from a broader proximal end. Penis shorter than sheath, tapered from a broader proximal end to a simple acute tip with no thickening or special structure. Sarcobelum large or insignificant, with or without papilla. Vas deferens between paragonoporal angle and penial sheath longer than or much shorter than preputium.

Penial retractor muscles inserted on ends of penial sheath, with no cross-connections or multiple insertions.

Distribution: Tropical and temperate North America, Central America, and the West Indies; South America in Colombia, and along the Pacific slope from Peru to central Chile (Fig. 8).

Two or more species (*H. acuta* and *mexicana*, for the most part) have been introduced widely, and are now in Europe, Asia Minor,

Africa, the Mascarene and Macaronesian Islands, India, Nepal, marginal East Asia, Australia, New Zealand, Polynesia, Brasil and Argentina.

Comparisons: The simple, muscular penial sheath and tapered penis with simple tip distinguish *Haitia* from other groups of Physinae, and show relationship with *Austrinauta* of the Aplexinae. The simplicity of the penial complex in *Haitia* means that in the absence of shell characters little is left to distinguish species. At present form and proportions of sarcobelum are the more useful criteria.

The greatly flared, wing-like body whorl of *Haitia elegans*, type species of the genus, is unique in the family (Fig. 126). No material for morphological study has been available. Classification of this species with the others called *Haitia* is based partly on geographic distribution, partly on the characters of immature shells that are much like high-spired *Haitia mexicana*. Lack of characters, as well as of material, make this summary of *Haitia* among the least satisfactory of all genera in the family.

Referred species:

Haitia incertae sedis

heterostropha peninsulae Pilsbry, 1899; TL Miami [25º46'N, 80º12'W], Dade County, Florida.

>*cubensis peninsulare* "Pilsbry" Thompson, 1984; error for *peninsulae* Pilsbry, 1899.

papaveroi Leme, 1966; TL Parque D. Pedro II, São Paulo [23º32'S, 46º37'W], Brasil.

Haitia acuta (Draparnaud, 1805); TL Garonne River and its tributaries, France. Maritime Canada, New England and north Atlantic United States; widely introduced in Europe and Africa.

=*fluviatilis* Férussac, 1807; unnecessary substitute for *acuta* Draparnaud, 1805.

?>*rivalis* Maton & Rackett, 1807; TL Hampshire, England.

>*heterostropha* Say, 1817; TL Delaware River, Philadelphia, Pennsylvania.

>*subopaca* Lamarck, 1822; TL Montpellier [43º36'N, 3º53'E], Dépt. Hérault., France.

>*sayi* Blainville, 1826; unnecessary substitute for *heterostropha* Say, 1817.

>*borbonica* Férussac, 1827; TL Réunion, Indian Ocean.

>*striata* Menke, 1828; TL near Goshen [42º26'25"N, 72º48'00W, 1450 ft], Hampshire County, Massachusetts.

>*acutus minuta* Beck, 1838; TL southern France.

=*acutus normalis* Beck, 1838; new name for typical *acuta* Draparnaud, 1805.

>*arctistropha* "Cristofori & Jan" Beck, 1838; probably a label error for *heterostropha* Say, 1817.

>*nana* Potiez & Michaud, 1838; TL Réunion, Indian Ocean.

>*fontana* Haldeman, 1841; TL Pennsylvania.

>*inflata* Lea, 1841; TL between Salt Sulphur Springs [37º34'13"N, 80º33'30"W, 1896 ft] and Sweet Springs [37º37'42"N, 80º14'30"W, 2029 ft], Monroe County, West Virginia.

>*borbonica* Sganzin, 1842; TL Réunion, Indian Ocean.

>*plicata* De Kay, 1843; TL Manhattan Island, New York, New York.

>*acuta gibbosa* Moquin-Tandon, 1843; TL Fonsorbes [43º32'N, 1º14'E], Dépt. Haute-Garonne, France.

>*perrisiana* Dupuy, 1849; TL France (no precise locality).

>*rivularia* Dupuy, 1849; TL France (no precise locality).

>*elliptica* "Parreyss" Dupuy, 1850; published in synonymy of *acuta* Draparnaud, 1805.

>*mediana* "Parreyss" Dupuy, 1850; published in synonymy of *subopaca* Lamarck, 1822.

>*buschi* Küster, 1850; TL Santa Cruz, presumably in Canary Islands.

>*charpentieri* Küster, 1850; TL Baltimore [39º17'25"N, 76º36'45"W], Baltimore County, Maryland.

>*venetzi* "Charpentier" H. & A. Adams, 1855, *nomen nudum*; no locality.

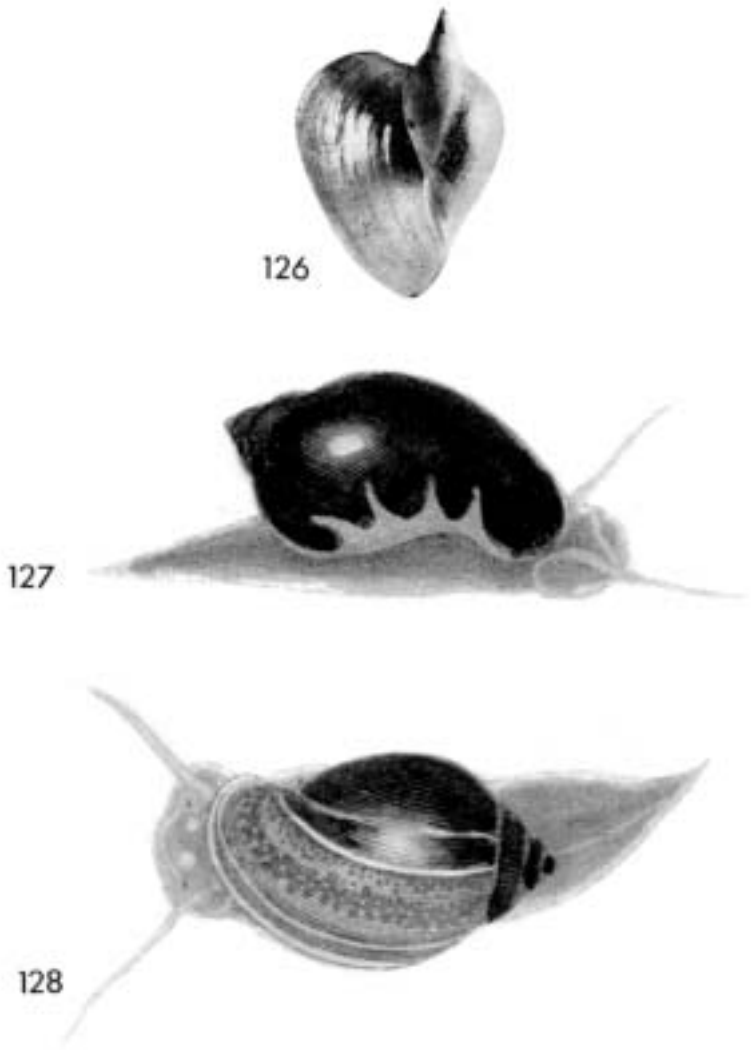


Fig. 126. *Haitia elegans*, p. 129, type species of *Haitia*. Lake Miragoane, Haiti; copied from Clench (1936). Figs. 127-130. *Haitia acuta*, p. 135. Figs. 127-128, living animal, copied from Haldeman (1842-1845).

>*acuta var. minor* Moquin-Tandon, 1855; TL Dijon [47º19'N, 5º01'E, Dépt. Côte d'Or], Poitiers [46º35'N, 0º20'E, Dépt. Vienne], and Bordeaux [44º50'N, 0º34'W, Dépt. Gironde], France.

>*acuta var. subacuta* Moquin-Tandon, 1855; TL Dépt. Sarthe, France.

>*acuta var. ventricosa* Moquin-Tandon, 1855; TL canal du Languedoc, Toulouse [43º36'N, 1º26'E], Dépt. Haute-Garonne, France.

>*acuta var. minor* Bourguignat, 1864; TL Mostaganem [35º51'N, 0º07'E], Algeria.

>*lata* Tryon, 1865; TL Juniata River, Hollidaysburg [40º25'38"N, 78º23'21"W], Blair County, Pennsylvania.

>*primeana* Tryon, 1865; TL Long Island, New York.

>*pisana* Issel, 1866; TL ditch a little way from the Porta a Lucca, Pisa [43º43'N, 10º23'E], Toscana, Italy.

>*fusca* “Rossmässler” Rigacci & Rigacci, 1866, *nomen nudum*; no locality.

>*heterostropha var. gibbosa* Rigacci & Rigacci, 1866, *nomen nudum*; TL “America.”

>*heterostropha var. minor* Rigacci & Rigacci, 1866, *nomen nudum*; TL Bethlehem [40º37’33”N, 75º22’15”W], Northampton County, Pennsylvania.

>*acuta var. acutior* Gassies, 1867, *nomen nudum*; TL “Les prés salés, à La Teste [-de-Buch, 44º38’N, 1º09’W], Le Teich, Audenge [44º41’N, 1º31’W], etc. Arès [44º46’N, 1º08’W] (*M. Durieu*), Andernos [Andernos-les-Bain, 44º44’N, 1º6’W] (*Gassies*),” Dépt. Gironde, France.

>*acuta var. minor* Gassies, 1867, *nomen nudum*; TL Pinchourlin, Lége [46º53’N, 1º36’W], Dépt. Loire-Atlantique, France.

>*melitensis* Mamo *in* Caruana, 1867, *nomen nudum*; TL Floriana Gardens, Malta.

>*seychellana* Martens, 1869; TL Seychelles.

>*tenerifae* Mousson, 1872; TL Tenerife, Canary Islands.

>*tenerifae var. fuerteventurae* Mousson, 1872; TL Fuerteventura, Canary Islands.

>*tenerifae var. gomerana* Mousson, 1872; TL Gomera and San Sebastian, Canary Islands.

>*tenerifae var. grancanariae* Mousson, 1872; TL El Monte, Gran Canaria, Canary Islands.

>*tenerifae var. palmaensis* Mousson, 1872; TL Palma, Canary Islands.

>*mamoi* Benoit, 1875, *nomen nudum*; TL Malta.

>*elliptica var. minor* Benoit, 1875, *nomen nudum*; TL Malta.

>*letourneuxi* Bourguignat, 1879; TL “Damahour [Damanh_r, 31º02’N, 30º28’E, Prov. Al-Buhayra],” Egypt.

>*lhotellerii* Bourguignat, 1879; TL “Damahour [Damanh_r, 31º02’N, 30º28’E, Prov. Al-Buhayra],” Egypt.

>*burriana* Kobelt, 1880, *nomen nudum*; TL Spain.

>*acuta var. fusca* “Rossmässler” Kobelt, 1880; TL Cartagena [37º36’N, 0º59’W], Spain.

>*acuta var. septentrionalis* Kobelt, 1880; TL Ostend [Oostende, 51º13’N, 2º55’E], Belgium.

>*acuta major* Locard, 1880; TL “La Mouche au sud de Lyon [45º45’N, 4º51’E, Dépt. Rhône],” France.

>*dilucida* “Letourneux” Servain, 1880, *nomen nudum*; TL “Îles Ioniennes.”

>*martorelli* Servain, 1880; TL “Pedralbas à Sarria, près Barcelone,” Cataluna, Spain.

>*achaiae* Westerlund, 1881; TL Pátrai [38º15’N, 21º44’E], Greece.

>*solidior* A. Costa, 1882; TL “Confluenti del Flumendosa nelle valli del Gennargento,” Sardinia, Italy.

>*acuta var. brevispira* Paulucci, 1882; TL “Convive col tipo a Cagliari [39º13’N, 9º06’E] in un fosso presso la ferrovia, rio Sixerri, Zinnigas nelle sorgenti, nei dintorni di Sarroch, S. Lucia e nel Flumendosa presso S. Vito,” Sardinia, Italy.

>*acroxa* Fagot, 1883; TL “Nous n’avons trouvé encore que trois exemplaires de cette espèce: l’un dans un vivier de la commune d’Avignonet [Avignonet-de-Lauragais, 43º22’N, 1º48’E], quartier de Craman; l’autre dans un vivier de la commune de Villefranche-Lauragais [Villefranche-de-Lauragais, 43º24’N, 1º44’E], et le troisième dans une fontaine de la commune d’Odars [43º31’W, 1º36’E], tous en compagnie des *Physa subopaca* et *Mamoi*” [all Dépt. Haute Garonne, France].

>*saint-simonis* Fagot, 1883; TL “Le canal du Midi, aux écluses de Gardouch, de Laval, et de Renneville, près Villefranche” [France].

>*acuta var. minima* Cockerell, 1889; TL hot spring at Salut [Bagnères-de-Bigorre, 43º04'N, 0º09'E], near Bigorre, Dépt. Hautes-Pyrénées, France.

>*acuta var. minuta* "Parreyss" Paetel, 1889, *nomen nudum*; TL Egypt.

=*aurata* "Draparnaud" Paetel, 1889, probably an error for *acuta* Draparnaud, 1805; "Tirol."

>*dilucida* "Letourneux" Locard, 1893; TL "Rennes (Aude)," France.

>*gallica* "Bourguignat" Locard, 1893; TL "Var, Charente, Aude, Charente-Infér., Loire-Infér., Rhône, Isère," France.

>*massoti* "Penchinat" Locard, 1893; TL La Preste [Les Bains de La Preste, 42º24'N, 2º24'E, Dépt. Pyrénées-Orientales], France.

>*salteli* "Saint-Simon" Locard, 1893; TL Livinhac-le-Haut [44º35'N, 2º14'E], Dépt. Aveyron, France.

>*heterostropha var. alba* Crandall, 1901; TL Cedar Lake, near Capachet [not traced], New York.

>*subopaca var. nilotica* Pallary, 1902; TL marshes bordering the White Nile, at the level of Gebelein [now Al-Jabalayn, 12º36'N, 32º48'E, Prov. An-Nil Al-Azraq], Sudan.

>*castanea globosa* Germain, 1903; TL "La Maine, en Reculée" [Promenade de Reculée, Angers (47º28'N, 0º33'W), Dépt. Maine-et-Loire], France.

>*castanea major* Germain, 1903; TL "La Maine, à la tour Guilloux, à Angers [47º28'N, 0º33'W]," Dépt. Maine-et-Loire, France.

>*gibbosa rubella* Germain, 1903; TL "La tour Guilloux à Angers [47º28'N, 0º33'W]," Dépt. Maine-et-Loire, France.

>*acuta var. bulla* Schlesch, 1907; TL Botanical garden, Copenhagen [55º40'N, 12º35'E], Denmark.

>*acuta var. castanea* Schlesch, 1907; TL Botanical garden, Copenhagen [55º40'N, 12º35'E], Denmark.

>*syriaca* Germain, 1911; TL River Barada, Hidachariyé [not traced], Syria.

>*caliban* Vanatta, 1911; TL Pembroke Marsh, Hamilton [32º17'N, 64º46'W], Bermuda.

>*acuta var. thermalis* Boettger, 1913; TL thermally influenced water in the Pipe, a stagnant arm of the Oder River, Oppeln, Silesia, Germany [now Opole, 50º41'N, 17º55'E, Slaska, Poland].

>*subopaca var. minor* Pallary, 1920; TL Foum Sefrou and Aïn Sfa (Beni Znassen), Fès, Morocco.

>*acuta var. thermalis* "Dupuy" Astre, 1921, *nomen nudum*; TL Barbotan-les-Thermes, Dépt. Gers, France.

>*borbonicensis* "Férussac" Germain, 1921; emendation of *borbonica* Férussac, 1827.

>*semiopaca* Annandale, 1922; error for *subopaca* Lamarck, 1822.

>*acuta botanica* "Monterosato" Coen, 1945, *nomen nudum*; TL botanical garden of Palermo [38º07'N, 13º21'E], Sicily, Italy.

>*acuta brevispira thermalis* "Monterosato" Coen, 1945, *nomen nudum*; TL "Sorgenti termali di Giers" [?Barbotan-les-Thermes, Dépt. Gers, France].

>*acuta brevispira vinacea* "Monterosato" Coen, 1945, *nomen nudum*; TL Cagliari [39º13'N, 9º06'E], Sardinia, Italy.

>*acuta nostra* "Monterosato" Coen, 1945, *nomen nudum*; TL Villa Igea, Palermo [38º07'N, 13º21'E], Sicily, Italy.

>*acuta panormitana* "Monterosato" Coen, 1945, *nomen nudum*; TL Palermo [38º07'N, 13º21'E], Sicily, Italy.

>*opaca* "Lamarck" Coen, 1945, probably error for *subopaca* Lamarck, 1822; TL "Attica," Greece.

?>*tonollii* Mirolli, 1958; TL Lago di Mergozzo and Lago Maggiore, Italy.

Haitia cubensis (Pfeiffer, 1839); TL Cuba, probably in the vicinity of Havana [La Habana, 23º08'N, 82º22'W]. West Indies.

>*orbignyi* Mazé, 1883; substitute for *Physa acuta* as identified by d'Orbigny in the West Indies.

?>*bermudezi* Aguayo, 1935; TL Pálpite [22º19'32"N, 81º11'07"W], near Ciénaga de Zapata, Prov. Matanzas, Cuba.

>*havanensis* "Pfeiffer" Clench, 1936; published in synonymy of *cubensis* Pfeiffer, 1839.

Haitia elegans (Clench & Aguayo, 1932); TL Lake Miragoane, two miles SE of Miragoane [18º27'N, 73º06'W], Haiti.

Haitia integra (Haldeman, 1841); TL Indiana, probably from the vicinity of New Harmony [38º07'47"N, 87º56'06"W], Posey County. Great Lakes region from Canada to midwestern United States.

>*brevispira* Lea, 1864; TL Ottawa River, Ontario, Canada.

>*billingsi* Heron, 1880; TL Billings' Bridge, near Ottawa [45º25'N, 75º42'W], Ontario, Canada.

>*walkeri* Crandall, 1901; TL Petoskey [45º22'24"N, 84º57'19" W], Emmet County, Michigan.

?>*ancillaria var. crassa* Walker, 1901; TL Higgins Lake [44º28'30"N, 84º43'00"W], Roscommon County, Michigan.

>*oneida* F. C. Baker, 1919; TL Oneida Lake, Brewerton [43º14'17"N, 76º08'28"W], Onondaga County, New York.

>*michiganensis* Clench, 1926; TL stream 1 mile west of Geddes [42º16'01"N, 83º40'04"W], Washtenaw County, Michigan.

Haitia jamaicensis (C. B. Adams, 1851); TL tank at Malvern [17º58'N, 77º42'W], in the Santa Cruz Mountains, St. Elizabeth Parish, Jamaica. West Indies in Jamaica and St. Croix.

Haitia lacustris (Clessin, 1886); TL Lago Coatepeque [13º52'N, 89º33'W], El Salvador (Fig. 15). Possibly only an ecophenotype of *mexicana*.

Haitia mexicana (Philippi, 1841); TL Mexico, probably in the vicinity of the capital. Western and south-central United States through Mexico to Costa Rica at least, possibly even to Colombia. Introduced in Hawaii at an early date; now also in eastern Asia and locally in the West Indies.

?>*solida* Philippi, 1841; TL New Orleans [29º58'N, 90º07'W], Jefferson Parish, Louisiana.

>*squalida* Morelet, 1851; TL marshes of Río Usumacinta around Balancán [17º48'W, 91º32'W], Tabasco, Mexico.

>*humerosa* Gould, 1855; TL Pleistocene or Holocene, Colorado Desert, California.

>*virgata* Gould, 1855; TL Gila River, Arizona, and San Diego, California.

>*anatina* Lea, 1864; TL northern tributary of Arkansas River, Kansas.

>*forsheyi* Lea, 1864; TL near Rutersville [29º56'51"N, 96º47'49"W], Fayette County, Texas.

>*grosvenori* Lea, 1864; TL "Santa Rita Valley, Kansas?"; probably Santa Rita Creek, Haskell County, Oklahoma.

>*halei* Lea, 1864; TL Alexandria [31º18'40"N, 92º26'42"W], Rapides Parish, Louisiana.

>*parva* Lea, 1864; TL Verdigris River, Kansas.

>*striata* Lea, 1864; TL "Salt Lagoon, near Monterey [36º36'01"N, 121º53'37"W]," California.

?>*tenuissima* Lea, 1864; TL Alexandria [31º18'40"N, 92º26'42"W], Rapides Parish, Louisiana.

>*traski* Lea, 1864; TL Los Angeles River, Los Angeles, California.

>*mexicana var. minima* Martens, 1865; TL Jalapa [17º43'N, 92º49'W], Veracruz, Mexico.

>*mexicana var. minor* Martens, 1865; TL "Río de Colipa, bei der Stadt Colipa [19º55'N, 96º42'W, Veracruz]...; Río

de Octopan..., Mexico und Veracruz," Mexico.

>*mexicana ovalis* "Wiegmann" Martens, 1865; TL Jalapa [17º43'N, 92º49'W], Veracruz, Mexico.

>*mexicana var. parva* Martens, 1865; TL Orizaba [18º51'N, 97º06'W], Veracruz, Mexico.

>*distinguenda* Tryon, 1865; TL Stockton [37º57'28"N, 121º17'23"W], San Joaquin County, California.

>*politissima* Tryon, 1865; TL Sacramento [38º34'54"N, 121º29'36"W], Sacramento County, California.

>*sparsestriata* Tryon, 1865; TL San Joaquin Valley, California.

>*dorbigniana* Lea, 1867; substitute for *striata* Lea, 1864, preoccupied.

>*ambigua* Pease, 1870; TL Hawaii.

>*compacta* Pease, 1870; TL Oahu, Hawaii.

>*berendti* "Dunker" Strebel, 1874; TL vicinity of Veracruz [32º25'N, 115º05'W], Veracruz, Mexico.

>*mexicana minor* Strebel, 1874; TL Mexico City, Mexico.

>*boucardi* Crosse & Fischer, 1882; TL the former lake in the Valley of Mexico, Mexico.

>*strebeli* Crosse & Fischer, 1882; TL Veracruz [32º25'N, 115º05'W], Veracruz, Mexico.

>*tehuantepecensis* Crosse & Fischer, 1882; TL Isthmus of Tehuantepec, Mexico.

>*polakowskyi* Clesssin, 1886; TL "Guatemala."

>*mexicana var. acutissima* Fischer & Crosse, 1886; TL the former lake in the Valley of Mexico, Mexico.

>*mexicana var. conoidea* Fischer & Crosse, 1886; TL the former lake in the Valley of Mexico, Mexico.

>*berendti var. intermedia* Fischer & Crosse, 1886; TL Putla [Putla de Guerrero, 17º02'N, 97º56'W; despite the name it is in Oaxaca], Oaxaca, Mexico.

>*mexicana var. plicata* Fischer & Crosse, 1886; TL near Mexico City, Mexico.

>*mexicana var. tolucensis* Fischer & Crosse, 1886; TL Toluca [19º17'N, 99º40'W], Mexico, Mexico.

>*cupreonitens* Cockerell, 1889; TL hot springs at Wellsville [38º29'12"N, 105º54'34"W, 6844 ft], Fremont County, Colorado.

>*heterostropha var. penicillata* Hemphill, 1890, *nomen nudum*; TL Potrero Valley, San Diego County, California.

>*osculans rhyssa* Pilsbry, 1899; TL Saltillo [25º25'N, 101º00' W], Coahuila, Mexico.

>*rhomboidea* Crandall, 1901; TL Muddy Creek, Sedalia [38º42'16"N, 93º13'41"W], Pettis County, Missouri.

>*virgata mut. alba* Cockerell, 1902; TL Salt River, Tempe [33º24'53"N, 111º54'31"W], Maricopa County, Arizona.

>*gabbi var. orbignyana* "Lea" Keep, 1904; error for *dorbigniana* Lea, 1867.

>*crandalli* F. C. Baker, 1906; substitute for *rhomboidea* Crandall, 1901, preoccupied.

>*balteata* Preston, 1907; TL Oaxaca [17º03'N, 96º43'W], Oaxaca, Mexico.

>*bottimeri* Clench, 1924; TL Comanche Springs [30º52'53"N, 102º52'42"W], Fort Stockton, Pecos County, Texas.

>*marci* F. C. Baker, 1924; TL "Little Valientia Spring (hot sulphur spring), Santa Barbara National Forest, California;" probably an error for Little Caliente Spring, SW 1/4 sec. 4, T. 5 N., R. 26 W., Santa Barbara County.

>*humerosa interioris* Ferriss, 1920, *nomen nudum*.

>*interioris* "Ferriss" Pilsbry, 1932; TL west branch of Navajo Creek, Coconino County, Arizona.

?>*californica* "Monterosato" Coen, 1945, *nomen nudum*; TL "California."

Haitia moreleti sp.n. TL Guatemala, Depto. El Petén: Marshy border of L. Petén-Itzá, Santa Elena, 16º55.30'N, 89º53.40'W, 110 m. Vicinity of L. Petén-Itzá, Guatemala.

Haitia natricina (Taylor, 1988); TL Snake River, SW 1/4 SE 1/4 sec. 21, T. 6 S., R. 13 E., Gooding County, Idaho. Snake River, southern Idaho (Fig. 11).

Haitia patzcuarensis (Pilsbry, 1891); TL Lago de Pátzcuaro [19º35'N, 101º35'W], Michoacán, Mexico (Fig. 15).

>*ventricosa* "Uhde" Martens, 1865, preoccupied.

>*mexicana var. coniformis* Strebel, 1874, preoccupied.

Haitia pomilia (Conrad, 1834); TL Randons Creek, near Claiborne [31º32'24"N, 87º30'56"W], Monroe County, Alabama. Southern Alabama to Florida.

=*pumilus* Beck, 1838; emendation of *pomilia* Conrad, 1834.

>*showalteri* Lea, 1864; TL Uniontown [32º26'58"N, 87º30'51"W, 305 ft], Perry County, Alabama.

>*pomilia ariomus* Clench, 1925; TL Gastonburg [32º12'26"N, 87º26'15"W], Wilcox County, Alabama.

>*pomilia hendersoni* Clench, 1925; TL Yemassee [32º41'24"N, 80º51'03"W], Hampton County, South Carolina.

>*barberi* Clench, 1925; TL canal embankment, West Palm Beach [26º42'54"N, 80º03'13"W], Palm Beach County, Florida; described as Pleistocene, but most likely modern material dragged up from the canal in the process of cleaning or deepening it.

>*hendersoni floridana* "Pilsbry MS" Te, 1980, *nomen nudum*; no locality other than that implied by name.

Haitia porteri Germain, 1913; TL brackish waters of Prov. Antofagasta, Chile.

Haitia? solidissima (Pilsbry, 1920); TL Laguna de Chapala, Jalisco, Mexico (Fig. 15).

Haitia spelunca (Turner & Clench, 1974); TL Lower Kane Cave, Big Horn County, Wyoming (Fig. 11).

Haitia venustula (Gould, 1847); TL Lima [12º03'S, 77º03'W], Prov. Lima, Peru. Northern to central Peru; and also central Chile if the nominal forms described from Chile are correctly assigned here.

?>*medianus* "Férussac" Beck, 1838, *nomen nudum*; TL Lima [12º03'S, 77º03'W], Prov. Lima, Peru.

?>*mediana* "Férussac" Clessin, 1886; TL Lima [12º03'S, 77º03'W], Prov. Lima, Peru.

>*nodulosa* Biese, 1949; TL Río Illapel, Illapel [31º37'51"S, 71º09'55"W], Prov. Coquimbo, Chile.

>*nodulosa forma albina* Biese, 1949; TL Río Elqui, Algarobito [not traced], Prov. Coquimbo, Chile.

Haitia acuta (Draparnaud, 1805)

Figs. 127-130, Pl. 6, figs. 8-10

Physa acuta Draparnaud, 1805:55, pl. 3, figs. 10-11. Moquin-Tandon, 1855, 2:452, pl. 32, figs. 14-23, pl. 33, figs. 1-10. Slugocka, 1913:75 ff., pls. 3-4; Switzerland; morphology.

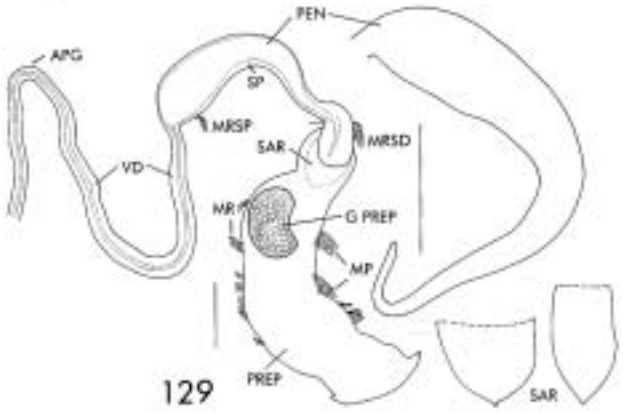
Physella acuta (Draparnaud): Starobogatov, 1970:49, 145.

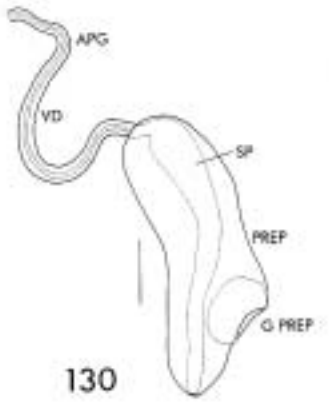
Holotype: NMW, Draparnaud collection, 1820/XXVI/45 (Adensamer, 1937:131). Garonne River, France.

Diagnosis: A species of *Haitia* attaining a length of about 13 mm, with dull to silky surface texture. Sarcobelum usually longer than wide.

Description: Penial complex: Pigmentation consists of a light dusting of melanin on the preputium and preputial gland, with practically none on either penial sheath or vas deferens.

The preputium is a generally cylindrical body, with the preputial gland entirely within





Figs. 129-130, penial complex. 129, CONNECTICUT, Litchfield County: Lake Wononscopomuc, Salisbury, *E. H. Jokinen*, 10-VI-1977. Fig. 130, Mt. Tom Pond, Morris, *E. H. Jokinen*, 21-VI-1978. Scale 1 mm. APG, paragonoporal angle; G PREP, preputial gland; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens.

the proximal half. The penial sheath is unitary, consisting of a muscular thin sheath about three-fourths or more as long as the preputium. It tapers gradually from a broader proximal end to a kink or abrupt curve at about four-fifths of total length, then widens. The penis tapers likewise from a broader proximal end to a slender, simple tip with no stylet or internal thickening. Within the preputium there is a large, elongate sarcobelum with a minute papilla at the apex (as preserved). In the ten specimens studied from Lake Wononscopomuc, the sarcobelum was longer than wide in eight; broadly convex and about as wide as long in two. Penial retractor muscles are inserted on ends of the penial sheath. The proximal muscle is a narrow band about half as wide as the distal retractor. No cross-connections between the muscles are present. The vas deferens between the paragonoporal angle and

the penial sheath is about three-fourths the length of the penial complex.

Distribution: Native in northeastern United States and adjacent Canada. Further range to the west and south is so poorly known as to be speculative.

Localities of preserved material examined:

CONNECTICUT, Litchfield County: Lake Wononscopomuc, Salisbury, *E. H. Jokinen*, 10-VI-1977 (**M**). Penial complex studied in ten of the less contracted specimens. Mt. Tom Pond, Morris, *E. H. Jokinen*, 21-VI-1978 (**M**). Hartford County: Mattabesset River, Berlin, *E. H. Jokinen*, 23-IX-1979 (**M**). Middlesex County: Black Pond, Middlefield, *E. H. Jokinen*, 1-IX-1978 (**M**). These three series were less well preserved than the first, and only five specimens from each were examined. The series were fixed in formalin, accounting for apparent change in diameter of the vas deferens on either side of the paragonoporal angle. Contraction of the muscles in the body wall compresses the vas within, whereas within the body cavity no such contraction takes place. Tolland County: Impoundment of tributary to Dunham Pond Brook on E side Maple Road, S of Storrs; Maple Road Pond A, EHJ site 202, *D. W. Taylor, E. H. Jokinen*, 20-V-1990 (T90-501). Windham County: Pond along Frog Brook, between Jerusalem Road and Indian Hollow Road, Windham, *D. W. Taylor, E. H. Jokinen*, 19-V-1990 (T90-301).

ENGLAND, Surrey: Old water-lily tank, Royal Botanic Garden, Kew [51º28'N, 0º17'W], Richmond, *B. Verdcourt*, V-1998.

Comparisons: The shell is scarcely distinguished from that of *Haitia mexicana*, but the elongate sarcobelum is a feature not seen in that species.

Haitia cubensis (Pfeiffer, 1839)

Figs. 131-134, Pl. 6, fig. 5

Physa cubensis Pfeiffer, 1839:354. Clench, 1936:339, pl. 25, fig. 2. Harry & Hubendick, 1964:15, figs. 12, 14-15, 17-18, 22-23, 71, 111; Puerto Rico; morphology. Pointier, 1975:919, fig. 13B, pl. 3, fig. 30; sketch of penial complex. Paraense, 1987:15 ff., figs. 1-7; Havana, Cuba; morphology.
Physodon cubensis: Starobogatov & Budnikova, 1976:82.
Physella (Costatella) cubensis (Pfeiffer): Te, 1980:184.

Holotype: destroyed?; five cotypes MCZ 73 619. Cuba [presumably in the vicinity of Havana], *C. Pfeiffer*, 1839.

Name: From the locality.

Distribution: West Indies. Bahamas; Cuba; Jamaica; Hispaniola; Puerto Rico; less abundant in the Lesser Antilles, where reliably reported as far south as Martinique. Whether it occurs on the mainland of the United States in Florida and perhaps elsewhere requires morphological confirmation, and also whether the species of the Bahamas is indeed the same as that of the Greater Antilles. So far as known, the range of *Haitia cubensis* overlaps that of *Stenophysa marmorata* in most of the Greater Antilles, but is generally more northern. It is found in Cuba and the Bahamas, where *Stenophysa* is absent, and reaches only the northern Lesser Antilles, where it is less common than *Stenophysa*, which ranges southward.

Localities and material examined:

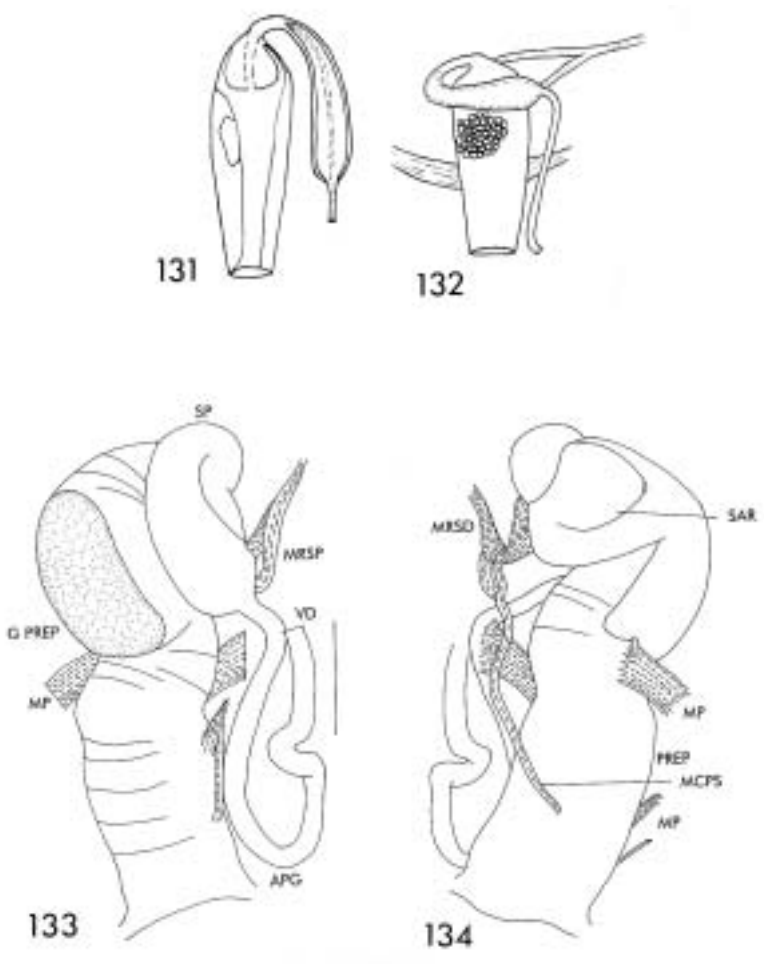
BAHAMAS

Grand Bahama Island: West end of island, *W. J. Clench, J. C. Greenway*, II-V-1936 (MCZ 116 118). Dundee Bay Pond, 3 mi NE of SW point, *W. J. Clench, J. C. Greenway*, II-V-1936 (MCZ 116 119). Eight-mile Rock, *W. J. Clench, J. C. Greenway*, II-V-1936 (MCZ 116 120).

New Providence: Two mi W of Adelaide, *W. J. Clench*, II-V-1936 (MCZ 116 121).

Eleuthera: No precise locality, *C. C. Allen* (MCZ 79 435).

Andros Island: Mangrove Cay, *O. Bryant* (MCZ 24 100, 24 101). Five mi NW of Fresh



Figs. 131-134. *Haitia cubensis*, p. 137. Penial complex. Figs.131-132, Puerto Rico; copied from Harry & Hubendick (1964). Figs. 133-134, Dominican Republic, Prov. Monte Cristi: Río Gurabo at Mao-Guayubin road, 24-XI-1989 (T89-5401). Scale 1 mm. APG, paragonoporal angle; G PREP, preputial gland; MCPS, connective between preputium and penial sheath; MP, protractor muscle; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens. Note the great difference in the shape of the sarcobelum in the specimens figured from Puerto Rico by Harry & Hubendick, and those from the Dominican Republic.

Creek, *F. G. Thompson*, XI-1963 (MCZ 250 633). Two mi SE of Androstown, *F. G. Thompson*, X-1963 (MCZ 250 624). Three and one-half mi S of Androstown, *F. G. Thompson*, X-1963 (MCZ 250 630).

Cat Island: Pond 2 mi NW of Arthurstown, *Clench, Russell, Huntington*, 5-VIII-1935 (MCZ 100 960). One-half mi due E of Arthurstown, *Clench, Russell, Huntington*, VII-VIII-1935 (MCZ 107 174).

Great Exuma: Hog Cay, near SE corner, *R. Robertson* (MCZ 214 674).

Acklins Island: Pompey Bay Settlement, *R. Robertson, A. Scott*, 31-VIII-1958 (MCZ 223 633). Two and one-half mi S of Chesters, *R. Robertson, A. Scott*, 19-IX-1958 (MCZ 223 633).

GREATER ANTILLES

CUBA: "It is the most common fluviatile mollusc in Cuba, found in practically all the streams and waterbodies of the island, as well

as in the Isle of Pines" (Aguayo, 1938). Clench (1936) cited many localities.

JAMAICA, St. Catherine Parish: Hunts Bay. St. Andrew Parish: Buff Bay (both from Clench, 1939).

HISPANIOLA, Haiti, Dépt. de la Grande Anse: Lake Miragoane 2 mi SE of Miragoâne, *W. J. Eyerdam* (MCZ 83 737). Dépt. de l'Ouest: Near Damien [18º36' N, 72º18' W], *C. R. Orcutt* (MCZ 91 338, *ex* USNM). Port au Prince, *C. R. Orcutt* (MCZ 91 342, *ex* USNM). Furcy [18º25' N, 72º18' W], *W. M. Mann*, 1912-1913 (MCZ 23 410). Shore of Lake Azuei (MCZ 91 335, *ex* USNM). Stream, Fond Parisien, *R. M. Bond* (MCZ 110 629). Not traced: Diguini, *W. M. Mann* (MCZ 31 799). Clench (1939) cited additional localities. Robart *et al*. (1977) did not cite this species in their inventory of the freshwater molluscs of Haiti. In view of the previously published records as well as my examination of specimens, it seems they confused it with *Stenophysa marmorata*.

Dominican Republic, Prov. Monte Cristi: Río Gurabo at Mao-Guayubin road, 24-XI-1989 (T89-5401)**(M)**. Prov. Santiago: Below San José de Las Matas, *ca*. 1000 ft, *P. J. Darlington, Jr.* (MCZ 90 730). Other localities were cited by Gomez & Malek (1986).

PUERTO RICO: La Muda, Río Piedras, *W. A. Hoffman* (MCZ 119 496). Widespread (Harry & Hubendick, 1964).

VIRGIN ISLANDS

St. Thomas: No precise locality, *E. Hartwig, ex C. B. Adams* (MCZ 177 267); *H. A. Beatty* (MCZ 110 346).

St. Croix: River [17º44'32"N, 64º48'52"W] (MCZ 110 302). Canaan stream, Concordia, *H. A. Beatty* (MCZ 110 304). West end of Concordia, *H. A. Beatty* (MCZ 110 311). Pond bush, La Grange [17º43'16"N, 64º52'44"W], *H. A. Beatty* (MCZ 110 301). Diamond school [17º42'46"N, 64º49'50"W], *H. A. Beatty* (MCZ 110 305). Fredericksted Reservoir, *P. Bartsch*, 1927 (MCZ 91 322, *ex* USNM). Jealousy stream [not traced], *H. A. Beatty* (MCZ 91 332, *ex* USNM; and 179 105). Crique [not traced], *H. A. Beatty* (MCZ 110 306).

LESSER ANTILLES

St. Eustatius: Lily pond, Oranjestad [17º28'N, 62º59'W], *G. A. Seaman*, 18-IV-1968 (MCZ 271 674).

St. Kitts: Phillips, 500 ft, *G. A. Seaman* (MCZ 213 545). No precise locality, *ex R. W. Jackson* (MCZ uncat.).

Nevis: No precise locality (Clench, 1939).

Antigua: Willoughby Bay; between English Harbor and Parham (Clench, 1939).

Guadeloupe: Known from only a few localities (Pointier, 1975; distribution map, fig. 16 N).

Marie-Galante: Rivière de Saint-Louis (Clench, 1939).

Martinique: small stream tributary to rivière Roxellane near Saint-Pierre (Guyard & Pointier, 1979).

Remarks: Neither diagnosis, description, nor reliable distribution can be given to this form, on account of the lack of morphological information. Paraense (1987) provided morphological information for specimens from the type locality in Cuba, but omitted the critical features of the sarcobelum. Harry & Hubendick (1964) illustrated the sarcobelum in a specimen from Puerto Rico; it is widely different from the material I have seen from the Dominican Republic, or anywhere else. Thus one does not know whether there is more than one species in the West Indies, nor what their characters are, nor their distribution. The locality data given above are for specimens from the West Indies, this range being probably the basis of all previous identifications.

Haitia integra (Haldeman, 1841)

Fig.135, Pl. 6, figs. 6-7

Physa integra Haldeman, 1842-45(3):cover p. 3 [1841]; (6):33, pl. 4, figs. 7-8 [1843]. Cvancara, 1983:82, pl. 4, fig. 10.
Bulinus integer Haldeman: H. Adams & A. Adams, 1858:260.
Isidora integra Haldeman: Chenu, 1859:481, fig. 3556.
Physella integra (Haldeman): F. C. Baker, 1928(1):460, figs. 190, 198, pl. 28, figs. 24-31.

Holotype: ANSP 280 023a, Indiana; sent by *Mrs. Say*, hence likely from the vicinity of New Harmony [38º07'47"N, 87º56'06"W], Posey County.

Name: Latin *integer*, whole, sound.

Diagnosis: A species of *Haitia* attaining a length of over 12 mm, with short spire and slightly convex profile of spire; commonly almost white, with multiple white bands representing former calluses within the outer lip. Sarcobelum elongate, slightly produced at tip.

Distribution: Great Lakes region and South Dakota (F. C. Baker, 1928:462); North Dakota (Cvancara, 1983). The range may more extensive, but morphological confirmation is virtually lacking.

Localities and material examined:

MINNESOTA, Crow Wing County: Round Lake, sec. 2, T. 134 N., R. 29 W.; 6-VII-1992 (T92-604, 606) (**M**.).

MICHIGAN, Cheboygan County: Grapevine Point cove, Douglas Lake, sec.28, T. 37 N., R. 3 W.; 28-VI-1952 (T52-2208). East side Lancaster Lake, sec. 8, T. 37 N., R. 3 W.; 7-VII-1952 (T52-2704). NE side Munro Lake, secs. 4, 9, T. 37 N., R. 3 W.; 4-VII-1952 (T52-2605).

Comparisons: Scarcely any preserved material has been available for study, and the constancy of the following characters is uncertain. Compared to *H. mexicana*, the sarcobelum is more elongate, and the shell is paler, with a short spire with convex profile. The body whorl may be wider than in *H. mexicana*, and the incidence of white callus bands within the shell is far more frequent.

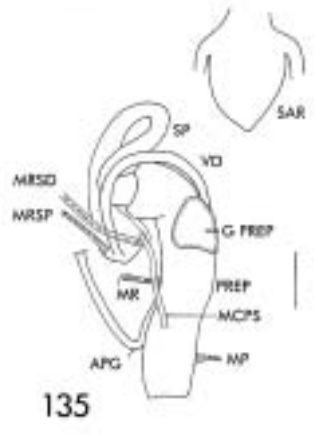


Fig. 135. *Haitia integra*. Round Lake, Crow Wing County, Minnesota. Penial complex. Scale 1 mm. APG, paragonoporal angle of vas deferens; G PREP, preputial gland; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens.

Haitia mexicana (Philippi, 1841)

Figs. 136-139, Pl. 7, figs.1-15

Physa mexicana Philippi, *in* Martini & Chemnitz, 1837-1918(32):5, pl. 1, figs. 3-4 [1841]. Strebel, 1874:50, pl. 6, figs. 26a-d, f. Fischer & Crosse, 1870-1902(2):100, pl. 30, figs. 12-12b.
Aplexus mexicanus Philippi: Paetel, 1888-1890(2):410.

Holotype: destroyed in SMF during 1939-45 war; "In Mexiko," presumably from the vicinity of the capital.

Name: From the country.

Diagnosis: A species of *Haitia* with thin shell, dull to polished, usually with little or no

TABLE 35
Measurements and descriptive statistics of shells of Haitia mexicana *from Xochimilco, D. F., Mexico (T87-201). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	16.45	12.48	.759	10.22	.622	4.65
Range	14.8-18.3	11.0-14.0	.67-.81	9.0-11.5	.56-.67	$4\ ^1/_4$ - $5\ ^1/_2$
S.D.	.858	.691	.030	.647	.024	.291
S.E.	.157	.126	.005	.118	.004	.010

TABLE 36
Measurements and descriptive statistics of shells of Haitia mexicana from Los Angeles County, California (T46-1002). Measurements to nearest .128 mm. N = 30

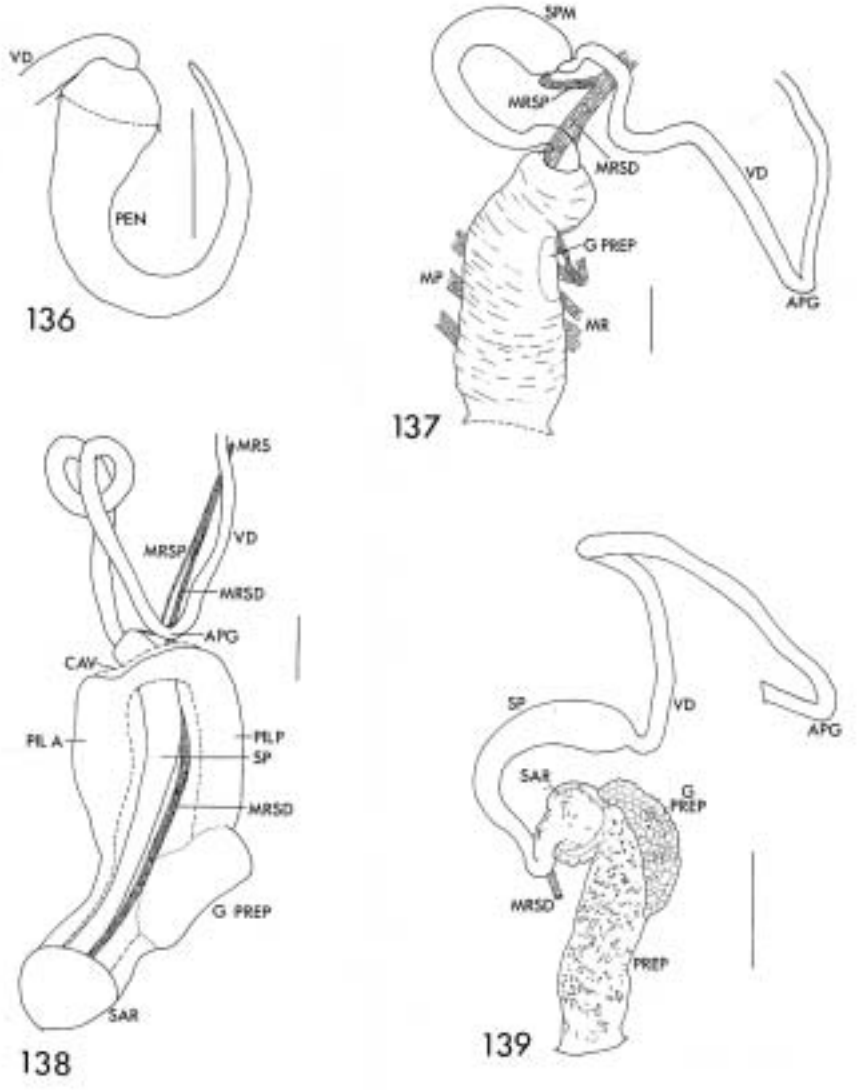
	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	14.25	9.60	.674	7.92	.557	5.14
Range	13.4-15.9	8.6-11 .8	.60-.74	7.4-9.0	.50-.61	$4\ ^3/_4$ - $5\ ^1/_2$
S.D.	.552	.651	.034	.456	.030	.224
S.E.	.101	.119	.006	.083	.005	.041

TABLE 37
Measurements and descriptive statistics of shells of Haitia mexicana *from Texas, Pecos County: Wilbank Spring (T67-2904). Measurements to nearest .128 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	15.97	11.27	.706	9.70	.608	5.3
Range	14.6-18.8	10.2-13 68	.61-.78	8.7-11.1	.55-.65	5 - 6
S.D.	.917	.798	.042	.582	.032	.222
S.E.	.167	.146	.008	.106	.006	.041

sculpture of the spirally aligned arcs characteristic in many species, and with an acute spire three-fourths as long as the aperture or longer. Shell features are greatly variable with habitat; the one diagnostic feature is the large mammiform sarcobelum, usually about equidimensional.

Description and variation: Shell features vary in relation to current, available lime, other dissolved solids, and temperature. In the usual small-stream habitat of the species it has a high spire often with concave outline, the shell is thin, polished, and the characteristic Physid sculpture of spirally aligned crescents is less evident than in *Physella gyrina*. In the limestone terrain of south Texas the shells are thick, and often have multiple apertural thickenings, appearing as white bands on the shell. Habitats with a high gypsum content, as in the Pecos River valley of southeastern New Mexico and Texas, may yield thick shells of unusual outline. One extreme is narrow, elongate shells with shouldered spire whorls reminiscent of *Bulinus*; such a set is from a spring 12 miles east of Roswell, New Mexico (UCM 6 733). Another variant is a large, thick-shelled form with exceptionally dark animal. Such a form is found in Diamond Y Draw, Pecos County, Texas; although the snails are quite different outwardly, they are only *mexicana* within, albeit heavily pigmented. Some specimens (Pl. 7, fig. 14) are like *Physa humerosa*, described from subfossil specimens from the Colorado Desert, as is true also of fossil shells from near Las Vegas, New Mexico, illustrated by Springer (1902). The specimen illustrated in Pl. 7, fig. 13 is close to *Physa bottimeri* Clench, named from Comanche Spring about 9 miles south of Diamond Y Draw. It is 13.2 mm



Figs. 136-139. *Haitia mexicana*, p. 140. 136, penis; 137, penial complex in retracted state, both from same specimen; 138, preputium extruded and opened laterally; 139, penial complex in retracted state. 139, Strike Reservoir, Owyhee County, Idaho; others from Diamond Y Draw, Pecos County, Texas. Scale 1 mm. APG, paragonoporal angle of vas deferens; G PREP, preputial gland; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRS, retractor muscle of penial sheath; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PIL A, anterior pilaster; PIL P, posterior pilaster; PREP, preputium; SAR, sarcobelum; SPM, muscular penial sheath; VD, vas deferens.

long and so about twice the size of the four specimens on which *P. bottimeri* was based, but agrees in large aperture, short spire, and sculpture. The shell in Pl. 7, fig. 12, 15.0 mm long, is thinner-shelled, lacks shouldering of the whorls, and conforms to other series in the region from slow-moving water. The three specimens figured (Pl. 7, figs. 12-14) are all from one sample in an area less than 1 ft square. Fig. 15 shows the extreme (in Diamond Y Draw) of high spire. The specimen is from the mouth of Leon Creek, about 1 000 ft from the site at which the preceding three were found, and is 17.3 mm long. This narrow elongate form is found to the north especially in more rapid streams, when shell length is only about half that of the specimen illustrated. To the south, in the lower Rio Grande valley, even larger but similarly elongate specimens of *Haitia mexicana* have been found. Populations in Diamond Y Draw are more variable in shape than any others seen. In the specimen illustrated (Fig. 137) with preputium retracted, one unusual feature is seen. Usually the preputial gland projects from the posterolateral face of the preputium as an oval body. In this and other specimens from Diamond Y Draw the gland is confined within the preputium, evidently in correlation with the unusually thick and muscular preputial wall. Size of the gland is as usual for the species.

From extensive field experience, the observation of shell variability, and the dissection of series from dozens of localities over the geographic range, I conclude the basis on which most species have been based is insubstantial.

The question of intra-specific variation in other features remains open. Springer (1902) reported differences in radular characters in *Physa virgata*, *P. rhomboidea*, and supposed *P. lordi*. All her material represents *H. mexicana*, as interpreted herein.

Physa spelunca Turner & Clench (1974), from a warm cave stream in Wyoming, is evidently closely related to *Haitia mexicana*, but further details are needed to assess its status. It is a northern isolated population of the generally southern group *Haitia*, perhaps representing survivors of *H. mexicana* that were once in the region.

Distribution: Continuous from the Central Valley of California southward over the Plateau of Mexico to Oaxaca and Tabasco, south at least as far as Costa Rica and perhaps to Colombia; eastward through southern Nevada, central and southern Utah, Arizona and New Mexico across the southern Great Plains from Colorado to Illinois, Missouri, and Louisiana. North of the generally continuous distribution there are isolated or patchy occurrences in western Washington and Oregon. The records in British Columbia are all from artificial habitats where the species was evidently introduced, but a former native presence in the area cannot be excluded. Another isolated area of occurrence is in the Snake River valley of southwestern Idaho and adjacent eastern Oregon. In southeastern Mexico (Chiapas) it is replaced by *Chiapaphysa*, likewise in northwestern Costa Rica; elsewhere in Costa Rica it is found in the Central Valley, and also in the extreme southeast. In the Yucatán Peninsula it seems to be absent. I did not find it in Guatemala, but *Physa polakowskii*, described only from "Guatemala", is not distinguishable in shell features from *mexicana* of both to the north and south.

Localities and material examined: *Haitia mexicana* is the most common freshwater mollusc in a large part of the United States and Mexico. A very large number of samples has been examined; in northern Mexico this species is the only one of the Physidae in the peninsula of Baja California, and in the states of Chihuahua, Coahuila, Durango, Nuevo Leon, and Sonora. The following list of material examined includes only the extremes of range. Northern localities listed are those along the northern range limit, southern localities those of southern Mexico and southward.

Northern marginal localities (W to E):

CANADA, BRITISH COLUMBIA, Cameron District: Hillier Water Gardens, Qualicum Beach, 10-VII-1989 (T89-2201)(**M**). New Westminster District: Van

Dusen Botanical Garden, Vancouver, 25-VI-1990 (T90-603)(**M**). Victoria District: Crystal Garden, Victoria, 9-VII-1989 (T89-2001)(**M**).

UNITED STATES, WASHINGTON, Clark County: Buckmire Slough W of N end of Vancouver Lake, 25-VIII-1984 (T84-301).

King County: Southwest end of Bow Lake, NE 1/4 SE 1/4 sec. 33, T. 23 N., R. 4 E., 18-VII-1989 (T89-3601) **(M)**.

OREGON, Columbia County: Cut-off pond from Columbia River on Willow Bar Island, 3300 ft E, 700 ft N, sec. 23, T. 3 N., R. 1 W., 27-VIII-1984 (T84-501).

Curry County: Indian Creek, 1400-1600 ft W, 1200-1400 ft N, sec. 30, T. 36 S., R. 14 W., 24-VIII-1977 (T77-7702) **(M)**. Saunders Creek, 2200-2500 ft E, 2400 ft N, sec. 21, T. 36 S., R. 14 W., 24-VIII-1977 (T77-7805). Rogue River, NE 1/4 NE 1/4 sec. 16, T. 36 S., R. 14 W., 24, 25-VIII-1977 (T77-7906). Rogue River, Tenmile Rapids, 1500 ft E, 1300 ft S, sec. 30, T. 34 S., R. 11 W., 27-VIII-1977 (T77-9006)(**M**). Rogue River, 100 ft W, 3000 ft S, sec. 36, T. 35 S., R. 14 W., 26-VIII-1977 (T77-8105).

Josephine County: Rogue River 200-300 ft above (S of) Galice Creek, 1000 ft E, 1300 ft S, sec. 1, T. 35 S., R. 8 W., 23-IX-1977 (T77-10003).

Lane County: Coast Fork of Willamette River at mouth of Row River, NW 1/4 sec. 22, T. 20 S., R. 3 W., 24-VIII-1984 (T84-203).

Linn County: Little Muddy Creek and minor unnamed stream at mouth, 2000 ft E, 1900 ft N, sec. 4, T. 15 S., R. 3 W., 2-III-1986 (T86-202).

Malheur County: Snake River, 1300 ft E, 1100 ft S, sec. 19, T. 15 S., R. 46 E., 15-VIII-1981 (T81-12401)(**M**).

IDAHO, Canyon County: Gravel pit pond, 1250 ft E, 900 ft S, sec. 16, T. 4 N., R. 3 W., 15-V-1982 (T82-802)(**M**).

Owyhee County: Snake River, SW 1/4 NW 1/4 sec. 32, T. 5 S., R. 4 E., 21-VIII-1981 (T81-13603)(**M**). C. J. Strike Reservoir at pumping plant, SW 1/4 sec. 8, T. 6 S., R. 5 E., 23-VIII-1981 (T81-14003)(**M**). Snake River, upper end of C. J. Strike Reservoir, NW 1/4 sec. 4, T. 6 S., R. 6 E., 23-VIII-1981 (T81-14104)(**M**).

NEVADA, Lyon County: Spring 900 ft W, 300 ft S, sec. 34, T. 13 N., R. 23 E., 31-X-1970 (T70-16503)(**M**).

Mineral County: Spring beside U.S. highway 95, 13.2 mi NW of road to Candelaria, 1-IX-1950 (T50-6101). Spring 2600 ft E, 1700 ft S, sec. 17, T. 5 N., R. 28 E., 7-VII-1970 (T70-13003)(**M**).

UTAH, Beaver County: Beaver River 1/4 mi above narrows at irrigation ditch intake above Minersville, center NW 1/4 sec. 8, T. 30 S., R. 9 W., 27-IX-1975 (T75-13604)(**M**). Beaver Creek near Beaver, *Vasco M. Tanner* (UCM 17919).

Emery County: Flood pool, San Rafael River, 16 mi SW Green River [town], *Hugh B. Leech*, 3-VIII-1964 (AGS 10 878).

Juab County: Fish Springs, Fish Springs National Wildlife Refuge, 17-19-VII-1986 (T86-59)(**M**).

San Juan County: Outflow of artificial pond 1/2 mi NW Bluff, 2700 ft W, 1200 ft N, sec. 24, T. 40 S., R. 21 E., 18-IX-1984 (T84-2401)(**M**).

Washington County: Santa Clara River, U.S. highway 91, Shivwits Shebit Indian Reservation, 24-VI-1946 (T46-101). Springs and irrigation ditch at Danish Ranch, 2000 ft W, 2600 ft N, sec. 33, T. 40 S., R. 14 W., 13-XI-1984 (T84-6202)(**M**). Magotsu Creek, Mountain Meadow Historical Monument, 150 ft E, 300 ft N, sec. 15, T. 38 S., R. 16 W., 15-XI-1984 (T84-6601)(**M**).

Wayne County: Artificial pond, Waterpocket Canyon, 200 ft E, 2300 ft N, sec. 10, T. 30 S., R. 7 E., 18-IX-1984 (T84-2301)(**M**).

COLORADO, Weld County: Two Mile Creek 1 mi NW of state highway 21, NW 1/4 sec. 36, T. 11 N., R. 57 W., 3-VIII-1950 (T50-2001).

Southern localities (southern Mexico and southward):

MEXICO, Campeche: Río Candelaria, Puente Candelaria, Carretera 186, Buenavista, 18º15.8'N, 91º18.3'W, 23-IV-1986 (T86-1303)(**M**).

Colima: Colima [19º14'N, 103º43'W], in an irrigation ditch, *M. E. Bourgeois*, 20-II-1945 (USNM 592 486). Colima, *Gustav Glückert* (MCZ uncat.).

Distrito Federal: Canals of Xochimilco [19º16'N, 99º06'W] , about 2240 m, 11-III-1987 (T87-201)(**M**). Canal at Nativitas, Xochimilco, *Creaser*, 1930 (MCZ uncat.). Xochimilco, *M. K. Jacobson*, 20-VII-1950 (MCZ 210 594).

Guerrero: Chilapa [22º51'N, 104º26'W], road on south side, *M. E. Bourgeois*, 28-II-1946 (USNM 591 595).

Michoacán: Río Duero .5 km E bridge at Cumuato, 20º15.5'N, 102º35.0'W, 2-X-1988 (T88-4401)(**M**). Canal at km 17, highway Quiroga-Pátzcuaro, 4 km from Pátzcuaro, 19º33.2'N, 101º34.7'W, 13-III-1987 (T87-501)(**M**).

Oaxaca: Huajuapan de León, in a small irrigation ditch on the north side of town [17º48'N, 97º46'W], *M. E. Bourgeois*, I-1946 (USNM 591 579). Vistahermosa, in a ditch above San Agustín Etla, 17º11.5'N, 96º45.7'W, 9-X-1988 (T88-5001)(**M**). Reservoir of San Agustín Etla, 17º10.9'N, 96º45.8'W, 9-X-1988 (T88-5101)(**M**). Ditch beside Carretera 175, 3.55 km N La Cumbre, 5.1 km S El Punto, slightly over 2500 m elevation (the highest known), in cloud forest, 10-X-1988 (T88-5201)(**M**). Arroyo de Monjas, about 100 m E Carretera 175, 16º21.8'N, 96º38.0'W, 12-X-1988 (T88-5301)(**M**). Ojo de San Bernardo Miahuatlán, 16º21.5'N, 96º41.9"W, 12-X-1988 (T88-5402)(**M**). Canal, Carretera 200, 10 km WSW Juchitán, 16º23.5'N, 95º7.1'W, 18-X-1988 (T88-5702)(**M**). Canal 2.5 km W Ixtaltepec, 250 m S road Comitancillo-Ixtaltepec, 16º28.8'N, 95º4.7'W, 18-X-1988 (T88-5901)(**M**). Ditch at canal beside Carretera 190, 7.5 km ENE La Ventosa, 16º34.3'N, 94º53.1'W, 19-X-1988 (T88-6101)(**M**).

Tabasco: Laguna Leona Vicario, 10 km S Balancán, 17º42.3'N, 91º32.6'W, 23-IV-1986 (T86-1205)(**M**).

COSTA RICA, Prov. Cartago: Parque Nacional Tapantí, 1150 m, *R. Delgado*, 26-IX-1994 (INBio 1 001 479 750, 479 751, in alc.). Quebrada Barahona 6 km W of center of Cartago, 9º51.32'N, 83º58.78'W, 1380 m, 14-XI-1992 (T92-7003). Las Concavas, Cartago, *Z. Barrientos*, 25-X-1988 (UCR uncat.).

Prov. Heredia: Santo Domingo de Heredia, *J. L. Jiménez*, 22-IX-1991, 22-X-1991 (UCR).

Prov. Puntarenas: Roadside ditch, 9º27.22'N, 84º8.36'W, 21-XI-1995 (T95-2803, INBio)(**M**). Drainage ditch on S side of Av. 2, Quepos, 9º25.84'N, 84º9.95'W, 21-XI-1995 (T95-2601, INBio)(**M**). Quebrada Laguna at SE edge of Golfito, 8º37.09'N, 83º8.70'W, 5-XI-1992 (T92-5601)(**M**).

Prov. San José: San Isidro Coronado, *J. L. Jiménez*, 31-VIII-1991 (UCR 6-003, 6-004). Parque La Sabana, San José, 9º56.14'N, 84º6.34'W, 1130 m, 17-XI-1990 (T90-4302, UCR)(**M**). Río Tiribí, bridge Los Anonos west of San José, *Rodrigo Brenes*, 14-IV-1956; and Río Tiribí, *P. Biolley* (MCZ 211 204, two sets combined). Río Tiribí, *P. Biolley* (MCZ 102 198). San José, *A. Alfaro* (MCZ 77 622). San Pedro Montes de Oca, collector unspecified, 9-XI-1991 (UCR). Juncales, Desamparados, *Rodrigo Brenes*, 14-IV-1956; and San Antonio Desamparados, "salitral" (aguas termales), *Rodrigo Brenes*, 21-IV-1956 (MCZ 211 235, two sets combined)[For information on the springs, see Waring (1965:64)]. Las Nubes, Coronado, *J. Monge-Nájera*, 21-VI-1992 (UCR).

COLOMBIA, Depto. Antioquía: Medellín [6º15'N, 75º35'W], 1540 m, *E. Osorno*, XII-1943 (MCZ 147 229).

Depto. Boyacá: Cuincha [not traced], near Muzo, 780 m, *E. Osorno* (MCZ 147 228).

Depto. Cundinamarca: Laguna de Tomine [not traced], ca. 9 000 ft elev., ca. 15 km N of Bogotá, *P. R. Craig*, 27-IX-1964 (CAS 079 590, 3 specimens in alcohol).

Depto. Norte de Santander: Agua Azul, Cúcuta, *Cesar Uribe-Priedrahita* (MCZ 157 437). Cúcuta [7º54'N, 72º31'W], *Apólinar María* (MCZ 157 884).

Examination of one of the three preserved specimens from Colombia revealed no features

separating it from *H. mexicana*, but the material is inadequate for specific identification. So far as the shells are concerned, they may well be *mexicana*.

Habitat: Perennial waters, nearly always flowing; seepages, small brooks, creeks, and rivers; less often in ponds or reservoirs.

In the western United States, generally *Haitia mexicana* occurs in more arid areas, at lower elevations and in smaller water bodies, than *Physella gyrina* (Say), the only other widespread and common Physid of the region. Ordinarily one replaces the other, although I have found a few marginal joint occurrences. At the eastern and northeastern margin of range, where the distribution has not been studied, there seems to be a zone of overlap with *P. gyrina* from eastern Kansas eastward to Illinois, and perhaps in Nebraska. Whether the two species are found together, or partition the local habitats, remains for study. So much published information is either unreliable or clearly wrong that details of habitat and distribution are uncertain. On present information it seems that *H. mexicana* is the only species of the family in Texas and in most of Oklahoma.

In the southeastern part of its range, in Mexico, *Haitia mexicana* occurs at far higher elevations than in the United States. In the Distrito Federal it is found at an elevation of about 2240 m, and in the Sierra Juarez of Oaxaca at more than 2500 m.

Biology: *Haitia mexicana* is a tolerant species except for requiring permanent water, and occurs in waters naturally high in gypsum, other salts, natural thermal waters, and those polluted by wastes as well as thermal effluent. Studies of the upper limit of thermal tolerance have investigated adults only, and the upper limit at which the life cycle can be completed may be lower than the experimental limits given: New Mexico, 38.7ºC (Brues, 1928:203, as *Physa virginea*); 43ºC (Beames & Lindeborg, 1969, as *P. anatina*); Texas, 43.93ºC (R. F. McMahon, 1975, 1976, as *P. virgata*). In the sewage treatment plant of Urbana-Champaign, Illinois, *Haitia mexicana* was studied by T. F. Brown (1937, as *P. anatina*). The snails achieved very high population density, requiring semiannual cleaning of the conduits, and apparently bred in the sprinkling filters. Peaks of reproductive activity (measured by percentage of individuals that laid eggs) occurred in spring and fall, when 75-80 percent of the snails produced eggs.

Transplant experiments were carried out in west Texas by Malone (1965, as *Physa anatina*). The species evidently can be transported passively into suitable isolated habitats, but the carrier (waterfowl, or insects) is unknown.

Haitia moreleti sp.n.

Fig.140, Pl. 6, fig. 2
Distribution Map, Fig. 15.

Physa squalida Morelet [misidentified]: Goodrich & van der Schalie, 1937:34, in part.
Aplexa cisternina Morelet [misidentified]: Goodrich & van der Schalie, 1937:34, in part.

Holotype: CAS 114821. Guatemala, Depto. El Petén: Marshy border of L. Petén-Itzá, Santa Elena, 21-XI-1991 (T91-2104, 2109).

Name: For Arthur Morelet (1809-1892), the first to obtain molluscs in the area. He spent over six weeks in Flores in 1847, on an island in L. Petén-Itzá, but during this time was recovering from an injury and fever, and his collections were made by schoolchildren. That he did not receive the new Physidae in the area is probably due to lack of interest by the collectors.

Diagnosis: A species of *Haitia* attaining a length of about 10 mm, with dense microsculpture over the entire shell surface; the sculpture

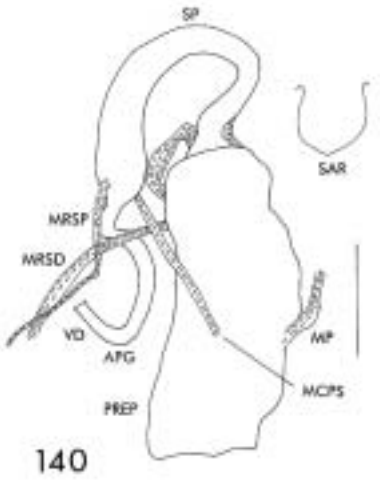


Fig. 140. *Haitia moreleti*, p. 146. Penial complex. Marshy border of L. Petén-Itzá, Santa Elena, Guatemala. 21-XI-1991 (T91-2104). Scale 1 mm. APG, paragonoporal angle; MCPS, connective between penial sheath and preputium; MP, protractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens.

consists of spirally aligned, short, raised ridges, either straight or convex in the direction of growth. The vas deferens between the paragonoporal angle and the penial sheath is only about 2/3 the length of the sheath. The stout sarcobelum is equally as long as wide, without terminal papilla.

Distribution: Northern Guatemala, from L. Petén-Itzá eastward in tributary streams or adjacent basins, but with few known localities outside of the lake proper.

Localities and material examined:

GUATEMALA, Depto. El Petén: Río Ixlú at Flores-Tikal road, 16º58.38'N, 89º41.18'W, 130 m, 24-XI-1991 (T91-3705)(**M**). Marshy border of L. Petén-Itzá, Piedra Blanca, 16º59.68'N, 89º41.60'W, 110 m, 24-XI-1991 (T91-3604)(**M**). Río Naranjo at Flores-Tiquinsacán road, 16º57.16'N, 89º35.42'W, 180 m, 24-XI-1991 (T91-3302). Arroyo Manantial, at Manantial, 16º56.73'N, 89º32.22'W, 240 m, 24-XI-1991 (T91-3203)(**M**). Quebrada El Zapote, El Zapote, 16º56.89'N, 89º30.96'W, 240 m, 24-XI-1991 (T91-3102)(**M**). L. Petén, Flores, *H. van der Schalie*, 8-II-1935 (MCZ 99 298); *H. van der Schalie*, 13-II-1935 (MCZ 99 301; 7 mixed with 33 *Mayabina petenensis*). South arm of L. Petén, near Flores, *H. van der Schalie*, 17-II-1935 (MCZ 99 302; 3 mixed with 11 *M. petenensis*). Marshy border of L. Petén-Itzá, Santa Elena, 16º55.30'N, 89º53.40'W, 110 m, 21-XI-1991 (T91-2104, 2109)(**M**). =Shore of L. Petén at National Airways Field south of Flores, *H. van der Schalie*, 8-II-1935 (MCZ 99 308; 5 mixed with 28 *M. petenensis*). South side of easterly island in Laguna de Eckixil, *H. van der Schalie*, 18-II-1935 (UMMZ 65 804; 10 mixed with 69 *M. petenensis*).

Haitia natricina (Taylor, 1988)

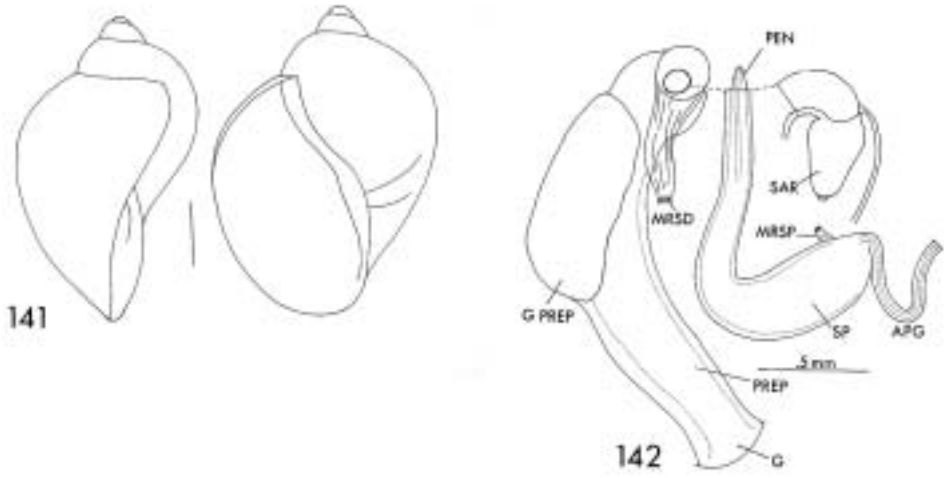
Figs. 141-142

Physa (Haitia) natricina Taylor, 1988:67, fig. 6; references, description, distribution.

Holotype: CAS 114 795, the shell dry, body preserved in alcohol. Gooding County, Idaho; Snake River, in rapids along the east side, SW 1/4 SE 1/4 sec. 21, T. 6 S., R. 13 E., 27-VII-1980.

Name: *Natrix*, a genus of water snakes, in reference to the Snake River.

Diagnosis: Shell with inflated body whorl, planes of aperture and growth lines conspicuously oblique to axis of coil, and coarse axial sculpture of crowded, irregular, raised threads. Body nearly colorless; tentacles with a dense black core of melanin in the distal half. Penial complex unitary, muscular; preputial gland about one-third length of preputium; penial sheath only slightly longer than preputium; sarcobelum massive, pyriform, with a terminal papilla.



Figs. 141-142. *Haitia natricina*, p. 147. Holotype. 141, shell; 142, penial complex, dissected. Scale 1 mm except as indicated. APG, paragonoporal angle; G PREP, preputial gland; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PREP, preputium; SAR, sarcobelum; SP, penial sheath. From Taylor (1988b).

Description: Shell ovoid, solid, with broadly rounded anterior end and acute spire; 3-3 1/2 convex whorls separated by a well-impressed suture; body whorl ventricose, greatest width anterior to mid-length. Aperture roughly ovate, broadly rounded anteriorly, angular posteriorly, about 3/4 of shell length. Outer lip simple, thin; parietal wall covered by a narrow callus. Growth lines and plane of aperture oblique to axis of coil at about 40º. In more coarsely sculptured individuals the body whorl bears numerous irregular, crowded, uninterrupted raised axial threads. Less coarsely sculptured shells bear axial sculpture of fine, low, raised threads broken into series of spirally aligned weakly curved arcs, convex toward the aperture, and 3-6 times as long as wide. This crescentic sculpture is characteristic on early whorls, and may be retained in the adult or replaced by coarser uninterrupted threads. Periostracum thin, amber to brown.

Penial complex (Fig. 142) known only from two specimens; measurements given are first those of the holotype, and in parentheses those of the other specimen dissected. The entire complex lacks pigmentation. The vas deferens .06 (.08) mm in diameter leads into a thick, opaque penial sheath, swollen proximally, .32 (.44) in greatest diameter. As preserved, it is bent just above the middle, and so divided into two parts: a proximal swollen part tapered strongly, and a distal part that tapers gradually to .13 (.32) mm diameter. By transmitted light the sheath can be seen as a thin, muscular envelope of uniform thickness that surrounds the thick, opaque, muscular penis. The penial canal can be discerned only toward its distal end; the tip of the penis is simple.

The preputium is nearly as long as the penial sheath, and bears a gland that is about one-third its length. Exclusive of the preputial gland, the preputium is roughly cylindrical, .34 (.43) mm in diameter distal to the gland. Through the thick, muscular walls of the preputium little can be seen; within are two pilasters. Within the proximal end is a massive, roughly pyriform sarcobelum, .24 (.30) mm in greatest diameter, bearing a terminal papilla.

Penial retractor muscles are inserted on ends of the penial sheath.

Remarks: List of localities and discussion of variation are provided in the original description. The species has been found living only in the Snake River, southern Idaho. It is known only in the main-stem river, not in any of the tributary streams, and so is one of the few Physidae that are restricted to a large river.

Haitia patzcuarensis (Pilsbry, 1891)

Figs. 143-144, Pl. 6, fig. 1
Distribution Map, Fig. 15

Physa osculans var. Patzcuarensis Pilsbry, 1891a:9; 1891b:323, pl. 15, fig. 5.
Physella patzcuarensis (Pilsbry): Starobogatov, 1970:259.
Physella (Costatella) patzcuarensis (Pilsbry): Te, 1980:184.

Holotype: ANSP 61 629 (not mentioned by H. B. Baker, 1964), Lago de Pátzcuaro [19º35'N, 101º35'W], Michoacán, Mexico, *F. C. Baker, ANSP Expedition*, 1-V-1890.

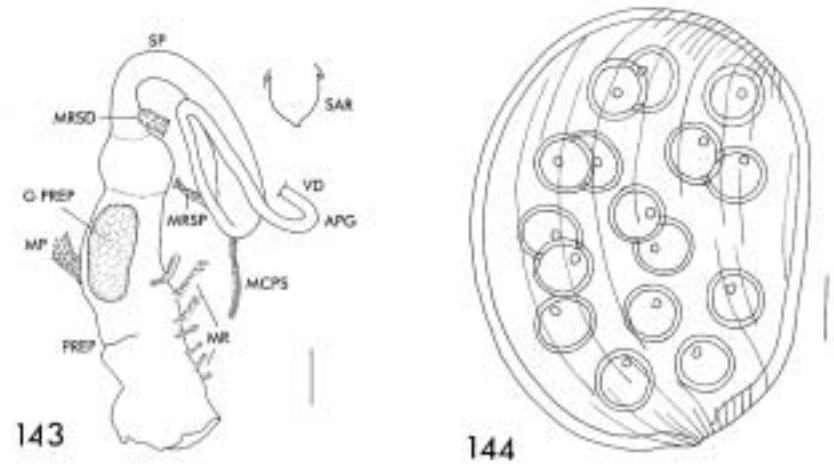
Name: For the lake.

Diagnosis: A species of *Haitia* attaining a length of over 17 mm, with a greatly expanded body whorl. The spire is very short, with a concave profile.

Description: Penial complex: Vas deferens between paragonoporal angle (APG) and penial sheath (SP) longer than sheath. Sheath about as long as preputium (PREP). Sarcobelum (SAR) slightly longer than wide. Penial retractor muscles (MRSD, MRSP) are inserted on the ends of the penial sheath.

TABLE 38
Measurements and descriptive statistics of spawn masses of Haitia patzcuarensis *from L. Pátzcuaro, Michoacán, Mexico. Measurements to nearest .064 mm. N = 12.*

	Length	Width	Eggs/capsule
Mean	7.57	4.63	16.9
Range	5.50-9.09	3.90-5.38	11-21
S.D.	1.38	.368	3.20
S.E.	.399	.111	.925



Figs. 143-144. *Haitia patzcuarensis*. Mexico, Michoacán: Lago de Pátzcuaro, Pátzcuaro, 13-III-1987 (T87-301). 143, penial complex; 144, capsule. Scale 1 mm. APG, paragonoporal angle; G PREP, peputial gland; MCPS, connective between preputium and penial sheath; MP, protractor muscle; MR, retractor muscle; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SAR, sarcobelum; SP, penial sheath; VD, vas deferens.

Localities and material examined:

MEXICO, Michoacán: Lago de Pátzcuaro, Pátzcuaro, 19º32.7'N, 101º37.1'W (T87-301) and Ihuatzio, 19º33.8'N, 101º37.1'W (T87-402), 13-III-1987(**M**). Tzintzuntzan, *S. N. Rhoads*, IV-VI-1899 (MCZ 78 450). No locality other than the lake, *S. N. Rhoads* (MCZ 86 380).

Spawn: Twelve spawn masses from laboratory-reared specimens were studied. Both ends of the capsule are broadly rounded, the anterior end slightly narrower. A terminal wisp was present in only one instance. The left side is broadly convex, the right side nearly straight to weakly concave. The pallium gelatinosum is a thin film less than .06 mm in thickness, too small to illustrate at the scale of the figure (Fig. 144). Within the capsule, the eggs overlap. Length of the capsules ranged from 5.50-9.09 mm, with 11-21 eggs.

Haitia pomilia (Conrad, 1834)

Figs. 145-146, Pl. 6, fig. 3

Physa pomilia Conrad, 1834:343. Tryon, 1870-1871:152, pl. 8, figs. 9-10.
Physella (Costatella) heterostropha pomilia (Conrad): Te, 1980:184.

Holotype: Probably lost; formerly in ANSP and illustrated by Tryon (1870-1871), but not listed by H. B. Baker (1964). TL Randons Creek, near Claiborne, Monroe County, Alabama.

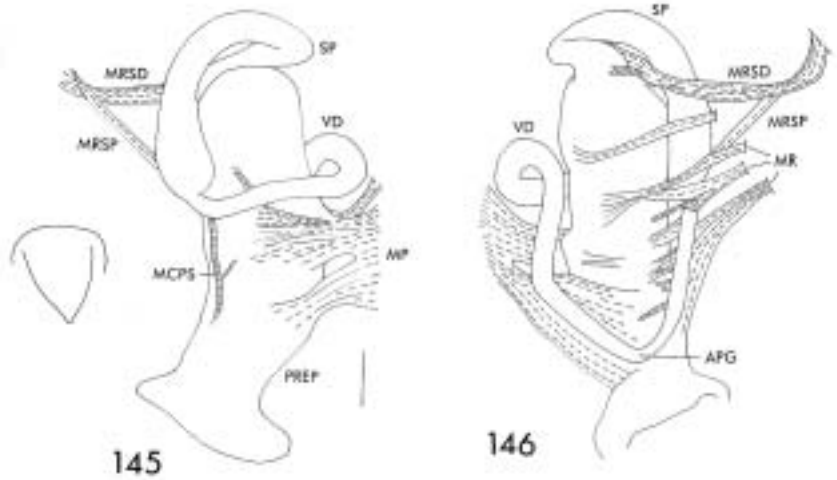
Name: Perhaps from Latin *pomum*, fruit or apple.

Diagnosis: A species of *Haitia* attaining a length of 18 mm, in such cases with a high, narrow spire with slightly convex profile. Sarcobelum elongate, produced into a narrow tip without papilla.

Distribution: Southeastern United States, in Alabama and Florida at least. Morphological studies are necessary to verify the range.

Localities and material examined:

ALABAMA, Baldwin County: Gulf State Park, highway 59, Gulf Shores; 7-V-1993



Figs. 145-146. *Haitia pomilia*. Alabama, Wilcox County: Pond by highway 28, NE 1/4 sec. 11, T. 14 N., R. 6 E.; 5-V-1993 (T93-401)**.** 145, penial complex, medial view; 146, lateral view. Inset: sarcobelum. Scale 1 mm. APG, paragonoporal angle; MCPS, connective between preputium and penial sheath; MP, protractor muscle; MR, retractor muscle; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PREP, preputium; SP, penial sheath; VD, vas deferens.

(T93-801). Ditch by US 90-98, by Meaher State Park; 8-V-1993 (T93-1003). Marengo County: Dry Creek, highway 25, NE 1/4 NE 1/4 sec. 36, T. 16 N., R. 4 E.; 4-V-1993 (T93-301). Cottonwood Creek, highway 25, NE 1/4 NE 1/4 sec. 5, T. 17 N., R 5 E.; 4-V-1993 (T93-205). Monroe County: Roadside ditch, center N 1/2 sec. 21, T. 6 N., R. 7 E.; 5-V-1993 (T93-501). Wilcox County: Pond by highway 28, NE 1/4 sec. 11, T. 14 N., R. 6 E.; 5-V-1993 (T93-401) **(M)**.

FLORIDA, Wakulla County: St. Marks River, Newport, NE corner sec. 25, T. 3 S., R. 1 E.; 3-XI-1969 (T69-7308).

Haitia venustula (Gould, 1847)

Pl. 6, fig. 4

Physa venustula Gould, 1847:215; 1852-1856:115, pl. 8, figs. 134-134b. Tantaleán *et al*., 1974:244 ff. Larrea *et al.*, 1990:40-41; distribution in Depto. Lima, Peru.

Aplexa venustula Gould: Weyrauch, 1964:169; *Physa nodulosa* Biese as synonym.

Physella (Costatella) venustula (Gould): Te, 1980:184.

Holotype: USNM 5 534, paratype MCZ 151 590. Lima [12º03'S, 77º03'W], Prov. Lima, Peru, *J. P. Couthouy, U.S. Exploring Expedition*, 1839.

Name: Latin *venustus*, lovely, graceful, and the diminutive.

Distribution: Peru to central Chile, generally along the coast.

Localities and material examined:

PERU, Depto. Ica: Lake La Huega near Ica [14º04'05"S, 75º43'32"W], *Angel Maldonado*, 1941 (FMNH 17 113)(**M**). Tambo de Mora [13º28'S, 76º12'W], Provincia de Chincha (Tantaleán *et al*., 1974).

Depto. Junín: San Ramon, Valle Chanchamayo, 800 m, *W. Weyrauch*, 1939 (MCZ 125 099).

Depto. Lambayeque: 10 km S of "Chiclare" [probably error for Chiclayo, 6º46'S, 79º50'W], *E. S. Ross*, 21-III-1951 (CAS uncat.).

Depto. La Libertad: Hacienda "El Cortijo," Provincia de Trujillo (Tantaleán *et al*., 1974).

Depto. Lima: Lima [12º03'S, 77º03'W], *W. Weyrauch* (MCZ 157 400). Lima - Chorillos, *W. Weyrauch* (MCZ 177508). Villa, Distr. Chorrillos, near Lima, *Angel Maldonado*, 1941 (FMNH 17 276). Huacho, Chancay, near Lima, *W. Weyrauch* (MCZ 110 146). Laguna Villa, near Lima, *W. Weyrauch*, 1939 (MCZ 177 512). Callao [12º04'S, 7º09'W], *W. Weyrauch* (MCZ 139 470). Torna Mesa [11º54'S, 76º31'W], 4 600 ft, *G. B. Fairchild* (MCZ 176 980).

Depto. Piura: Redondo, waterhole in Quebrada Pasul, *Mr. and Mrs. D. L. Frizzell*, 1-I-1939 (MCZ 89 075). Río Pariñas, Talara [4º34'33"S, 81º16'09"W], *G. B. Fairchild*, 12-XII-1943 (MCZ 176 979).

Remarks: The shells I have seen cannot be distinguished from the widespread and variable *H. mexicana*. The preserved material

TABLE 39

Measurements and descriptive statistics of shells of Haitia venustula *from Villa, Lima, Peru (FMNH 17276). Measurements to nearest .064 mm. N = 27*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	7.76	5.56	.717	4.64	.597	4.12
Range	6.78-9.21	4.80-6.66	.68-.75	3.90-5.50	.54-.64	$3\,{}^{3}/_{4}$ - $4\,{}^{1}/_{2}$
S.D.	.711	.516	.017	.426	.025	
S.E.	.137	.099	.003	.082	.005	

examined represents *Haitia*, but is not of sufficient quality to show diagnostic characters. The series from Peru are all grouped under the name *venustula* on a geographic basis.

Tribe **PHYSINI**, new tribe

Penial sheath unitary, with glandular tissue in proximal part of sheath at least. Penis flagelliform, with simple tip in *Laurentiphysa*, but a terminal stylet in *Beringophysa* and *Physa*. Mantle edge with triangular or rounded projections in two groups, columellar-parietal on the right, and left posterior. Mantle not reflected over outer lip of shell in *Laurentiphysa* and *Beringophysa*, but in *Physa* reflected as a narrow band, or broadly on both sides so as even to cover the shell.

The three genera all live in temperate or arctic regions. *Laurentiphysa*, most primitive, is found in Newfoundland, Canada, and in the United States from the Great Lakes to New England; *Beringophysa*, intermediate, arctic Siberia and North America; and *Physa*, most advanced, temperate to arctic Europe, Siberia, and North America (Fig. 9).

Laurentiphysa g.n.

Type species: *Physa vernalis* Taylor & Jokinen, 1985, Great Lakes region of the United States to Newfoundland, New England, and Long Island, New York.

Name: From Laurentian Great Lakes, and *Physa*.

Diagnosis: Shell narrow-ovoid to ovoid-fusiform, dull to shining, with spiral crescentic microsculpture. Profile of aperture weakly convex in direction of growth. Parietal callus narrow, apex blunt. Length to 11 mm.

Mantle not reflected over outer lip of the shell, with narrow triangular projections in two groups, columellar-parietal (C) and left posterior (P); C 3-10, P 1-9.

Penial complex: Penial sheath bipartite; greatly enlarged, glandular, and thick-walled proximally, non-glandular and thin distally, and longer than preputium. The terminal part of the distal muscular portion of sheath consists of an elongate bulb, swollen proximally, that enters the preputium for about half its length. Penis flagellar, with simple tip.

Proximal penial retractor muscle inserted on proximal end of penial sheath, distal retractor on proximal end of terminal bulb of sheath.

Distribution (Fig. 147)**:** Newfoundland, Canada, and in the United States from the Great Lakes region (Wisconsin, Michigan and Ohio) to southern New England and Long Island, New York. Collecting in seasonal habitats, commonly not searched in the past, is likely to increase the range to other provinces (Canada) and states (United States).

Comparisons: *Laurentiphysa* shares several characters with *Beringophysa*. The penial sheath is glandular in the proximal portion only; the shell apex is blunt, not rounded; the mantle is not reflected over the outer lip of the shell; and the penis is flagellar. It differs most conspicuously by the terminal bulb of the sheath. Other differences are that the proximal glandular portion of the penial sheath is greatly enlarged, the penis lacks a stylet, and the distal penial retractor is inserted on the terminal bulb.

Referred species:

Laurentiphysa chippevarum g.n., sp.n.; northern Wisconsin.

Laurentiphysa vernalis (Taylor & Jokinen, 1985); TL "Bluebird Pond," Windham Township, Windham County, Connecticut. Great Lakes region of United States east to Newfoundland, southern New England, and Long Island, New York.

>*aplectoides* Sterki, 1900, *nomen nudum*; TL Portage and Tuscarawas Counties, Ohio.

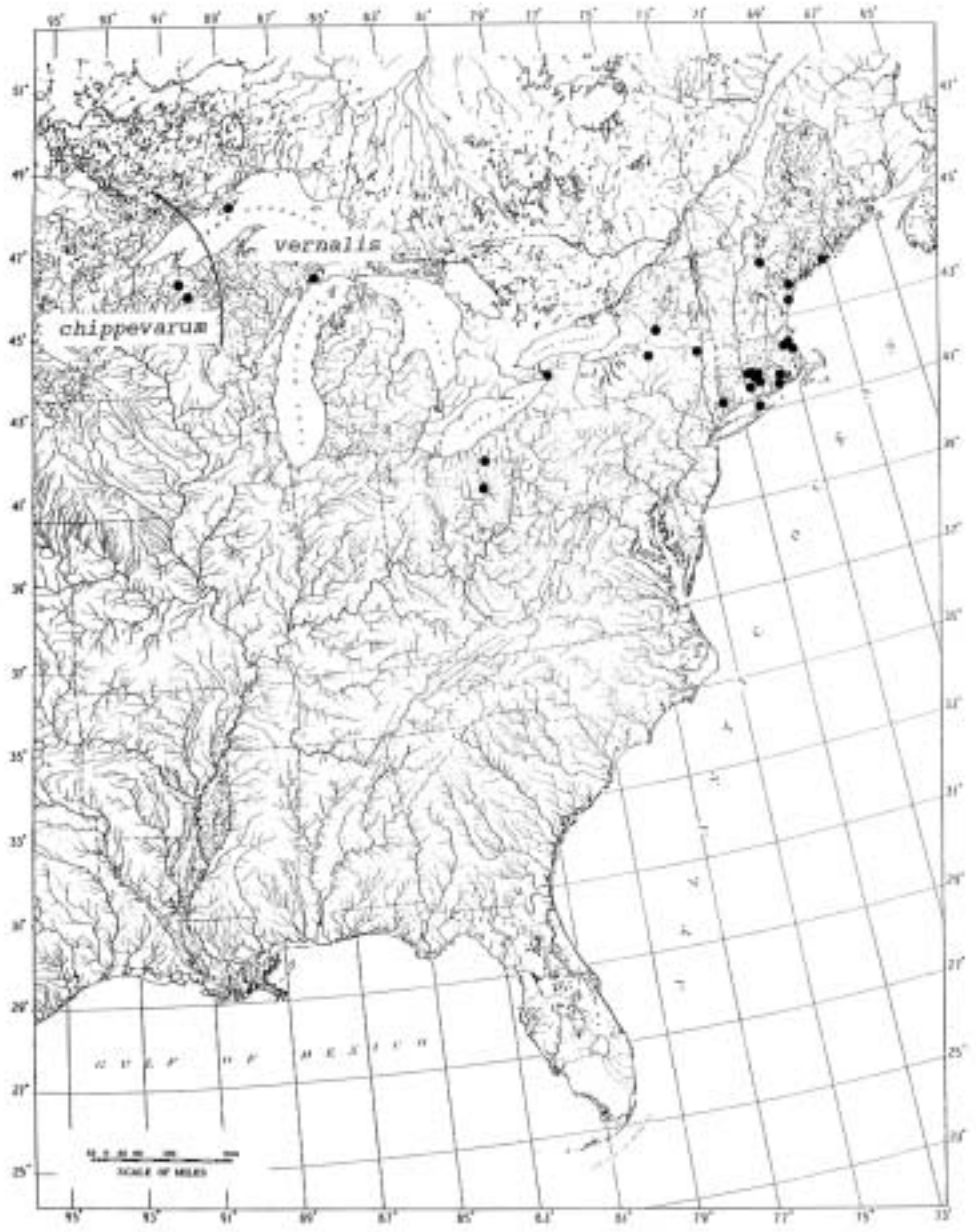


Fig. 147. Distribution of *Laurentiphysa*, p. 152. A locality of *L. vernalis* in Newfoundland is off the map to the northeast.

Laurentiphysa chippevarum sp.n.

Figs. 148-152, Pl. 8, fig. 1
Distribution Map, Fig. 147

Holotype: CAS 146089, an undissected specimen with preputium extruded, preserved in alcohol. Wisconsin, Ashland County: ditch on N side of highway 77, 1.85 mi W of highway 13, SW 1/4 SE 1/4 sec. 31, T. 43 N., R. 2 W., 1530 ft, 7, 14-VII-1992 (T92-803). Paratypes CAS 146090 (10), BMNH 20001309 (10).

Name: Latinized, of the Chippewa, the regional native American nation.

Diagnosis: The shell is narrowly elongate-ovoid, with peritreme little more than half of shell length, attaining a length of 8 mm with 4 1/2 whorls. Fine, irregular spiral white bands about equal in width to their interspaces occur through most of the shell. The penial sheath is glandular through nearly its proximal three-fourths, and tapers gradually from a wide proximal end to a narrow muscular isthmus, that is succeeded by a slender, glandular terminal bulb.

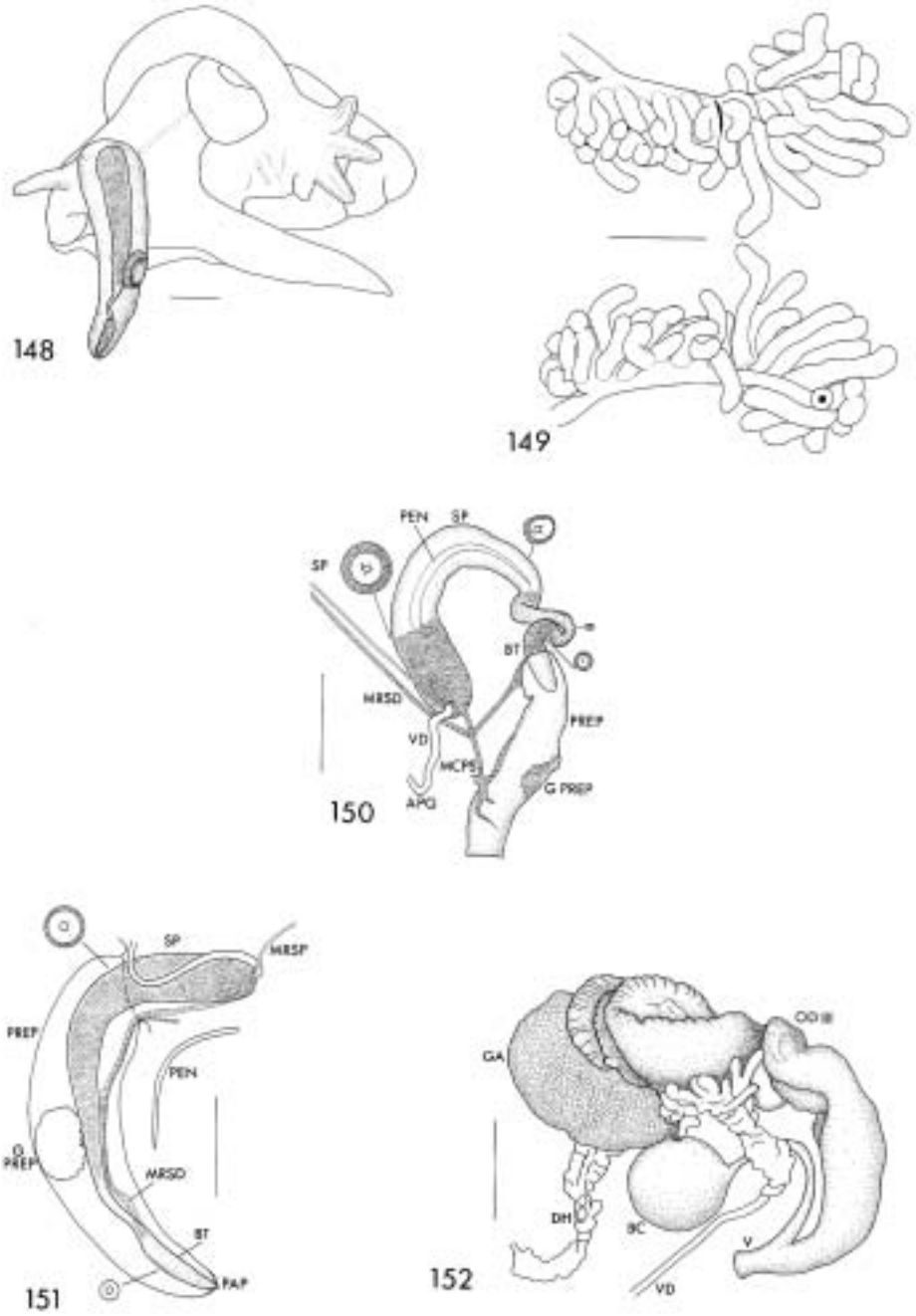
Description: The shell is narrowly elongate-ovoid with a narrow, blunt spire and broader, narrowly rounded anterior end. The aperture has a narrowly rounded anterior and acute posterior end. Its outer profile is broadly but weakly convex in the direction of growth, evenly retractive to the suture. The inner margin consists of a regularly concave parietal segment, and a straight columellar segment sharply set off from the parietal segment but merging gradually into the anterior end. The columella is thin, white to pale brown, with a fold absent or scarcely evident. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but not incised suture. The lateral profile of the spire is gently convex, strongly so toward the blunt apex. The shell surface is silky to shining, dark brown, with a narrow pale band at the suture. Throughout nearly all the calcareous part of the shell are fine white spiral bands, about equal in width to their interspaces, often interrupted and finely waved. Surface sculpture consists of fine axial growth lines, and spiral series of irregular minute wrinkles over all the

TABLE 40
Measurements and descriptive statistics of shells of Laurentiphysa chippevarum *from type locality (T92-803). Measurements to nearest .064 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.32	4.10	.649	3.24	.512	3.88
Range	5.57-7.30	3.46-4.86	.57-.71	2.88-3.78	.49-.55	3.25-4.25
S.D.	.398	.343	.038	.199	.016	
S.E.	.073	.063	.007	.036	.003	

TABLE 41
Variation in numbers of mantle projections in Laurentiphysa chippevarum *from type locality (N=91)*

	Columellar	Posterior
Mean	6.63	5.39
Range	4-10	2-9
S.D.	1.324	1.020
S.E.	.139	.107



Figs. 148-152. *Laurentiphysa chippevarum*, p. 154. Wisconsin, Ashland County: ditch by highway 77 (type locality). 148, preserved specimen with preputium extruded; 149, two views of prostate; 150, penial complex; 151, penial complex with preputium extruded and penis removed; 152, female system. Scale 1 mm except .5 mm for prostate. APG, paragonoporal angle; BC, bursa copulatrix; BT, terminal bulb; DH, hermaphroditic duct; GA, albumen gland; G PREP, preputial gland; MCPS, muscle connecting proximal end of penial sheath to preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD III, oviduct; PAP, papilla; PEN, penis; PREP, preputium; SP, penial sheath; V, vagina; VD, vas deferens.

surface; these wrinkles are either straight or weakly convex in the direction of growth.

The largest shell collected had the tip broken, but would have been about 8 mm long, with 4 1/2 whorls.

Overall body color is a pale gray wash. Within the mantle projections the central blood sinuses appear pale in contrast to the gray areas adjacent. Within the tentacles is a central rod-like core of melanin.

Mantle projections are in two groups, columellar-parietal (C) and posterior (P); C 4-10, P 2-9. In a juvenile specimen mantle projections were C 3, P 2.

Hermaphroditic duct with simple, blunt, unbranched seminal vesicles up to three times the width of the duct. The duct is enveloped by melanin-pigmented connective tissue.

Male system: The prostate consists of a double row of about 30 tubular follicles along a generally straight prostatic vas deferens. The follicles are rarely branched once, .08 mm in diameter, and up to 8 times as long as wide. The posterior follicles lap onto not only OD II but also onto the albumen gland.

Penial complex: Penial sheath, preputium, and retractor muscles are all melanin-flecked. Penial retractor muscles originate from the columellar muscle. Proximal and distal muscles originate as one, separating shortly thereafter, or have separate but adjacent origins; in one case the two retractors were fused as one. The distal retractor muscle (MRSD), twice or thrice as wide as the proximal retractor, is inserted on the proximal end of the preputium. The proximal retractor (MRSP) is inserted on the proximal end of the penial sheath adjacent to the vas deferens.

The length of the vas deferens between the paragonoporal angle (APG) and the penial sheath is less than one-third of the length of the sheath.

Ten specimens were preserved with the preputium swollen and extruded from the body (the common reaction to menthol crystals as an anesthetic). The thin preputial wall is transparent, and structures within can be seen readily. The preputial gland (G PREP) is relatively small, shorter than the terminal bulb (BT) of the sheath within, and is located on the posterior face of the preputium distal to the midlength of the preputium as extruded. The penial sheath is longer than the preputium, even in its extruded and distended state, with about 5-10% of the length of the sheath remaining in the body cavity. The sheath is made up of a proximal glandular, long, narrow, carrot-shaped portion, widest at the proximal end, that tapers into a slender, non-glandular tube about 1/8 of the diameter of the widest part of the sheath, and a slender, muscular terminal bulb.

Female system: Observations were limited by a high incidence of parasitism that had destroyed the system in most individuals. One caecum is present. The bursa (BC) is a globular sac, well set off from its duct. Bursal duct (DBC) about twice the length of the bursa, joining OD III at a low angle, and about half the width of OD III. Width/length of vagina (V) about .5.

Distribution: North-central Wisconsin, where known from only three localities, in Ashland and Price Counties (Fig. 147).

Localities and material examined: In addition to the type locality, the species was found at only two other sites in the region, despite search of many ditches with cattail growth similar to the type locality.

WISCONSIN, Ashland County: ditch, highway 77, SE 1/4 SW 1/4 sec. 32, T. 43 N., R. 2 W., 11-VII-1992 (T92-1507, two specimens. This site is close to the type locality, but not connected with it by continuous water in the ditch). Price County: ditch, highway 70, NE 1/4 NW 1/4 sec. 10, T. 39 N., R. 1 E., 10-VII-1992 (T92-1404, two specimens).

Habitat: The type locality is a roadside ditch similar to many others sampled in the area, drying at the time of collection, with standing brown water in discontinuous pools up to three ft wide and a few inches deep among growth of cattails and sedges. Here *Laurentiphysa* was the most abundant gastropod. Associated molluscs were *Pisidium casertanum* (Poli), *P. ventricosum* Prime, *Valvata*

sincera Say, *Sibirenauta elongatus* (Say), *Lymnaea modicella* Say, and *Gyraulus deflectus* (Say). From these associates it seems that the habitat probably does not dry entirely, but retains at least a little water in the deeper parts of the ditch.

Laurentiphysa vernalis

(Taylor & Jokinen, 1985)
Figs. 153-155, Pl. 8, fig. 2
Distribution Map, Fig. 147

Physa vernalis Taylor & Jokinen, 1985:190, figs. 1-3, 6, 7 description, distribution, references.

Holotype: MCZ 294 071, a specimen preserved in alcohol, but in the collection of dry shells; laboratory-reared from stock collected in "Bluebird Pond," along unnamed tributary of Frog Brook, between Jerusalem Road and Indian Hollow Road, Windham, Windham County, Connecticut.

Name: Latin, pertaining to springtime.

Diagnosis: Shell narrowly elongate, thin, pale brown, with weak spiral crescentic sculpture, attaining a length of 11 mm with 5 1/2 whorls. Mantle margin with two groups of digitate projections, one on the parietal surface, one at the posterior end of the aperture. At the anterior end and left side the mantle barely expands over the shell margin. Male reproductive system with a penial sac swollen proximally, tapering to a large terminal bulb inserted about halfway into the preputium; penial sheath about half glandular. Penis shorter than sac, flagellar, with no terminal swelling or papilla.

Description: Shell thin, ovoid-fusiform, pale brown, with aperture two-thirds of shell length. Apex blunt; spire with weakly convex whorls separated by a shallow, broadly attached suture. Aperture elongate-oval, rounded anteriorly, acute posteriorly, widest at mid-length. Outer lip thin, sharp, slightly advanced in middle. Parietal wall with a thin, white, closely appressed callus. Columellar lip a rounded ridge that forms a low plait as it enters the whorl cavity. Surface texture silky to shining. Axial sculpture of fine threads or lines, crossed by spirally arranged series of crescentic or arcuate fine ridges.

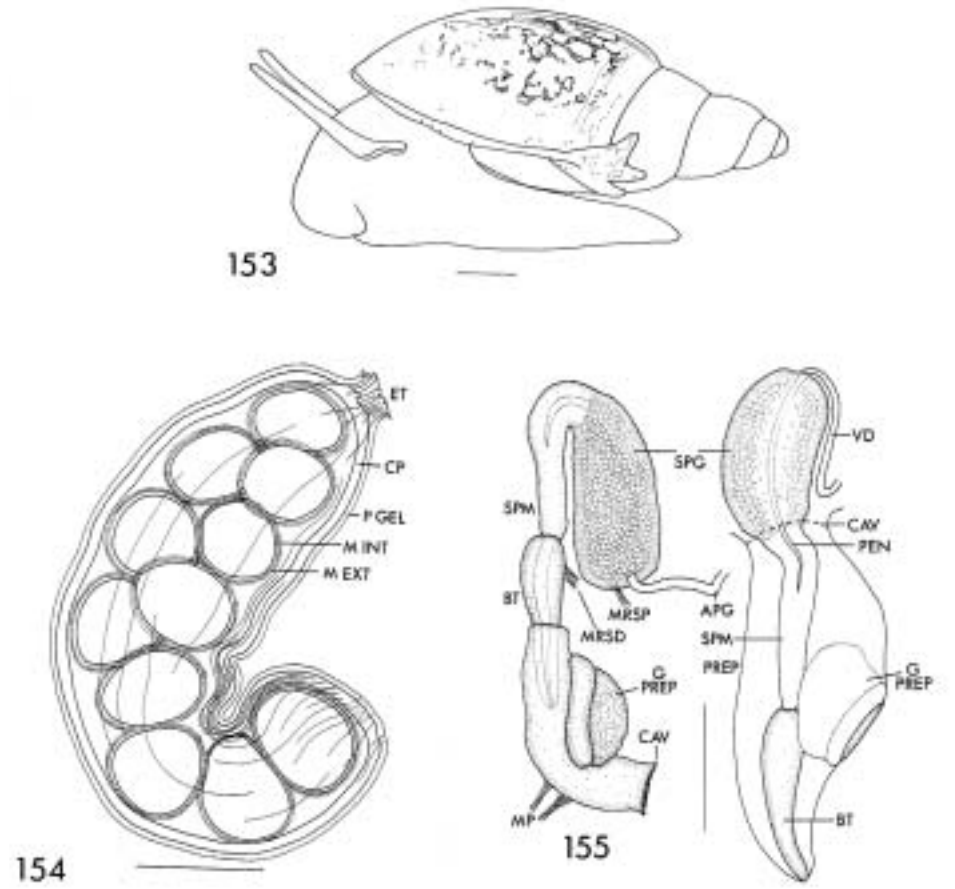
The two largest specimens seen measured 10.9 mm with 5 1/2 whorls and 10.4 with 5 1/4 whorls; aperture 68% and 67% of shell length, respectively.

The penial complex (Fig. 155) was studied in one specimen in life when the preputium was extruded, and in that specimen and others (total = eight specimens with preputium extruded, five retracted) after preservation. In extruded state the preputium is transparent, and internal structures can be discerned readily. The non-glandular distal part of the penial sheath is transparent, the massive terminal bulb opaque creamy-white. In preserved material the distal non-glandular part of the penial sheath is cloudy but translucent, and contrasts with the opaque, glandular, proximal part of the penial sheath.

Mantle projections were P 1-3 (mean 2.7), C 3-5 (mean 4.2), N = 30.

Distribution: Great Lakes region of United States east to Newfoundland, southern New England, and Long Island, New York (Fig. 147).

Remarks: References, list of localities and discussion of variation are provided in the original description.



Figs. 153-155. *Laurentiphysa vernalis*, p. 157. Connecticut, Windham County: "Bluebird Pond" (type locality). From Taylor & Jokinen (1985). 153, animal; 154, spawn; 155, penial complex with preputium retracted (left) and extruded (right). APG, paragonoporal angle; BT, terminal bulb; CAV, limit of body cavity; CP, capsule wall; ET, terminal tail of capsule; G PREP, preputial gland; M EXT, external membrane; M INT, internal membrane; MP, protractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; P GEL, pallium gelatinosum; PREP, preputium; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

Beringophysa Starobogatov & Budnikova, 1976

Starobogatov & Budnikova, 1976:82; type species (by original designation): *Physa ampullacea chukchensis* Starobogatov & Budnikova, 1976, Chukotka, Siberia, <*P. jennessi* Dall, 1919, North West Territories, Canada. As subgenus of *Physa*.

Name: From Bering Straits, and *Physa*.

Diagnosis: Shell narrow-ovoid, having a dull surface with spiral crescentic microsculpture. Profile of aperture weakly convex in direction of growth. Parietal callus narrow, apex blunt. Length to about 9 mm. (Pl. 8, fig. 5).

Mantle not reflected over outer lip of shell, with narrow triangular projections in two groups, columellar-parietal (C) and left posterior (P); C 6, P 4.

Penial complex: Penial sheath unitary, glandular and thick-walled proximally, non-glandular and thin distally, longer than preputium. Preputium with blunt, massive sarcobelum. Penis flagellar, with ovoid terminal stylet.

Proximal penial retractor muscle inserted on proximal end of penial sheath, distal retractor on proximal end of preputium (?).

Distribution: The one species is found from central Siberia to Arctic North America, from Alaska and the Arctic coast of Yukon Territory southeastward to the borders of Hudson Bay, including James Bay, Ontario and Quebec (Fig. 9).

Comparisons: *Beringophysa* shares several characters with *Laurentiphysa*: the penial sheath is glandular in the proximal portion only; the shell apex is blunt, not rounded; the mantle is not reflected over the outer lip of the shell; and the penis is flagellar. It differs by the blunt, ovoid, penial stylet; insertion of the distal penial retractor muscle on the preputium (?); and absence of terminal bulb.

Remarks: Morphological information is from Starobogatov & Budnikova (1976) and Clarke (1973).

Referred species:

Beringophysa jennessi (Dall, 1919); TL ponds near Bernard Harbour [68º47'N, 114º47'N], District of Mackenzie, Northwest Territories, Canada.

>*chukchensis* Starobogatov & Budnikova, 1976; TL Ust'-Chaun [68º47'N, 170º30'E], Chukotka, Russia.

>*kuvaevi* Starobogatov & Prozorova, 1989; TL lake near Anadyr [64º45'N, 177º29'E] airport, Chukotsk Autonomous Region, Russia.

>*tei* Starobogatov & Prozorova, 1989; TL same as preceding.

Physa Draparnaud, 1801
Draparnaud, 1801:31, 52.

#>*Exydra* Hübner, 1810 [cited from Menke, 1848].

=*Physina* Rafinesque, 1815:144; unnecessary substitute for *Physa*.

=*Phyza* Risso, 1826:96; emendation of *Physa*.

>*Rivicola* Fitzinger, 1833:110; type species (by monotypy) *Rivicola fontinalis* Fitzinger, =*Bulla fontinalis* Linnaeus.

=*Echemythes* Gistel, 1848:X; unnecessary substitute for *Physa*.

=*Enydra* Hübner: Dall, 1905:99; error for *Exydra*.

>*Mediterraneophysa* Starobogatov & Budnikova, 1976:82; type species (by original designation): *Physa taslei* Bourguignat, 1860. As subgenus of *Physa*.

>*Ussuriphysa* Starobogatov & Prozorova, 1989:71; type species (by original designation): *Physa hankensis* Starobogatov & Prozorova, 1989. As subgenus of *Physa*.

Type species: (by designation of International Commission on Zoological Nomenclature, Opinion 94 and Direction 72) *Physa fontinalis* (Linnaeus, 1758), Europe.

Name: Greek *physao*, to blow out; thus, a bubble.

Diagnosis: Physinae with shell ovoid to elongate-ovoid, silky to polished and shining, with inconspicuous spiral sculpture. Aperture more than half to nearly all of shell length; profile of aperture weakly to strongly convex in direction of growth. Parietal callus broad or narrow. Suture shallow to inconspicuous. Apex broadly rounded. Length to about 12 mm.

Mantle reflected over the shell on both sides, in extreme cases even enveloping the entire shell, with narrowly elongate to broadly rounded digitations. Digitations in two groups, columellar-parietal (C) and left posterior (P). Modal numbers were C 8 (range 1-11), P 5 or 6 (range 1-8), in a sample of 1000 adult *Physa fontinalis* from Belgium studied by Pelseneer (1920:74-90). Means for *P. skinneri* from Colorado were C 6.9 (range 6-8), P 4.9 (range 4-6; N = 15); and for *P. megalochlamys* from Wyoming C 8.1 (range 2-17), P 5.4 (range 0-9; N = 35).

Penial complex: Penial sheath unitary, entirely glandular, tapered at first gradually from a broad proximal end, more rapidly in the distal third, and attaining minimum diameter at the distal one-fifth; enlarged in the distal one-tenth. Penis thin and flagellar, with a terminal, lanceolate stylet. A well-developed sarcobelum is present, in the form of a prolate hemisphere; a terminal papilla is inconspicuous. Vas deferens between paragonoporal angle and penial sheath shorter than preputium.

Penial retractor muscles are inserted on the ends of the penial sheath, with no cross-connections.

Distribution: Temperate to Arctic Eurasia and North America.

Comparisons: The broadly rounded shell apex is a feature unique in Physidae. The wide reflection of the mantle over both sides of the shell, together with series of projections along the mantle edge, is diagnostic within Physinae, but is not found in all species of the genus (for example, *P. skinneri*). Internally, unique characters of the group are the wholly glandular penial sheath and lanceolate stylet.

Ussuriphysa Starobogatov & Prozorova (1989) was defined by trivial characters, as follows: "Shell thin-walled, ovoid, with rather short spire, penial sheath thin-walled in distal third, with muscular thickening next to junction with preputium, sarcobelum moderately developed, without distinct papilla, between parietal and palatal groups of mantle digitations a deep but not wide gap." Descriptions and illustrations of the three referred species do not distinguish them convincingly from one another.

Mediterraneophysa has as type species *Physa taslei*, a species not known from near the Mediterranean. It was described thus: "Shell polished, shining, rather high and solid. Penial sheath almost completely glandular except for the muscular, distal one-fifth. It narrows rather sharply near the middle, the distal part is narrow. Penis very slender, longer than the sheath, preputial gland sharply set off, the massive sarcobelum without a distinct papilla at the tip."

The locality cited for the specimens illustrated is Lake Achikol'. I have not traced its location, but evidently it is a long way from the type locality in Brittany. The shell is distinct by a wide parietal callus and blunt spire, like *P. dalmatina*, and I doubt that the Russian material is *P. taslei*. But concerning the French *taslei* there are many uncertainties. In proposing the species Bourguignat described the shell as having a slightly obtuse apex, and emphasized that the species was more like *P. fontinalis* than *acuta*. Germain (1930-1931) too described the apex as obtuse. Nevertheless, the illustrations by both authors look to me more like *acuta*. As in many other cases, morphological studies of topotypes are necessary to resolve the matter.

Referred species:

Physa arachleica Starobogatov & Prozorova in Starobogatov *et al*., 1989; TL L. Arakhlei [52º12'N, 112º52'E], Chitinsk District, Russia.

Physa dalmatina Küster, 1844; TL three localities in Dalmatia, Croatia: See von Boccagnazo bei Zara (=Bokanjacko Blato, north of Zadar), the Salona at Spalato [=Split, 43º31'N, 16º27'E], and in marshes of the Cettina [=Cetina] at Almissa (not traced). Balkans to western Siberia.

>*fontinalis forma succinea* Hesse, 1913; TL canal of Marotza at "Phillipol" [Philippopolis, now Plovdiv, 42º09'N, 24º45'E], Bulgaria.

>*sartlandinensis* Mozley, 1934; TL L. Sartlan, Novosibirsk District, Russia.

Physa fontinalis (Linnaeus, 1758); TL vicinity of Uppsala [59º52'N, 17º38'E], Sweden. Europe and western Siberia.

>*bulla* Müller, 1774; TL Frederiksdal, Randers, Denmark.

>*gelatinus* Müller, 1774; no locality.

>*adversus* Da Costa, 1778; TL several localities in southeastern England.

>*perla* Müller, 1781; unnecessary substitute for *bulla* Müller, 1774.

>*pellucida* Razoumowsky, 1789; TL L. Geneva, Switzerland.

>*gelatinosa* Gmelin, 1791; emendation of *gelatinus* Müller, 1774.

>*bullaoides* Donovan, 1803; TL Lincolnshire, England.

>*fluviatilis* Turton, 1819; unnecessary substitute for *bullaoides* Donovan.

>*fluviatilis* T. Brown, 1827; TL Clonoony, King's County, Ireland [Clonony, County Offaly, 53º14'N, 7º55'W].

>*fontinalis obtusata* Beck, 1838; TL Denmark.

>*fontinalis producta* Beck, 1838; based on previous references from England and France.

>*fontinalis subacuta* Beck, 1838; based on previous references from Germany and France.

>*fontinalis var. amnica* "Ziegler" Parreyss, 1849, *nomen nudum*; TL Laxenburg [40º04'N, 16º21'E], Niederösterreich, Austria.

>*fontinalis var. inflata* Moquin-Tandon, 1855; TL Nantes [47º13'N, 1º33'W], Dépt. Loire-Atlantique, France.

>*fontinalis var. lepida* Moquin-Tandon, 1855; TL Nantes [47º13'N, 1º33'W], Dépt. Loire-Atlantique, France.

>*fontinalis var. minor* Moquin-Tandon, 1855; TL "dans les Vosges," France.

>*canariensis* Bourguignat, 1856; new name for *fontinalis* as identified from the Canary Islands by Webb & Berthelot (1833) and d'Orbigny (1839).

>*fontinalis var. albina* Jeffreys, 1862; TL Birkenhead [53º24'N, 3º02'W], Cheshire, England.

>*fontinalis var. curta* Jeffreys, 1862; TL Clonony [53º14'N, 7º55'W], County Offaly, Ireland.

>*fontinalis var. oblonga* Jeffreys, 1862; TL Anglesea, England [?Anglesey, Wales], and Naas [53º13'N, 6º39'W], County Kildare, Ireland.

>*minima* "Kutschig" Brusina, 1866, *nomen nudum*; TL Krka [43º37'45"N, 16º45'16"E], Dalmatia, Croatia.

>*fontinalis var. aplexoides* Colbeau, 1868; TL Saint-Gilles [50º49'N, 4º20'E], near Brussels, Belgium.

>*fontinalis var. curta* Van den Broeck, 1869; TL Saint-Gilles [50º49'N, 4º20'E], near Brussels, Belgium.

>*fontinalis normalis* Westerlund, 1871; TL Ronneby [56º12'N, 15º18'E], Sweden.

>*fontinalis oblonga* Westerlund, 1871; TL Sweden and Norway (no precise locality).

>*semiglobosa* Westerlund, 1871; TL Nacka [59º18'N, 18º10'E] near Stockholm, Sweden.

>*fontinalis typica* Westerlund, 1871; TL Höje å Skåne, Sweden.

>*stabilei* Lessona, 1880; TL L. d'Azeglio, Piemonte, Italy.

>*fontinalis major* Locard, 1880; TL "Saint-Fons [45º42'N, 4º52'E], Rhône," France.

>*fontinalis rufula* Locard, 1880; TL vicinity of Grenoble [45º10'N, 5º43'E, Dépt. Isère], France.

>*coronadoi* Servain, 1880; TL alluvia of Río Guadalaviar, near Valencia [39º28'N, 0º22'W], Spain.

>*acutespira* "Bourguignat" Servain, 1882; TL "Dans le ruisseau au pied de la colline de Privas," Dépt. de l'Ardèche, France.

>*taciti* "Bourguignat" Servain, 1882; TL "Dans l'Erdre, à Nantes [47º13'N, 1º33'W, Dépt. Loire-Atlantique], dans la Loire-Inférieure," France.

>*fontinalis var. bulla forma grandis* Westerlund, 1885; TL Ronneby [56º12'N, 15º18'E], Sweden.

>*subglobosa* "Westerlund" Clessin, 1886; error for *semiglobosa* Westerlund, 1871.

>*canarium* "Bourguignat" Paetel, 1889; error for *canariensis* Bourguignat, 1856.

>*fontinalis var. flava* Cockerell, 1893; TL Herne Bay [51º23'N, 1º08'E], Kent, England.

>*fontinalis major* Licherdopol, 1903, *nomen nudum*.

>*fontinalis var. junior* Astre, 1921; TL Oise valley, France.

>*fontinalis subflava* Clench, 1926; substitute for *fontinalis inflata* Moquin-Tandon, 1855, preoccupied.

Physa hankensis Starobogatov & Prozorova, *in* Starobogatov *et al*., 1989; TL pool near Kaktokovsk lake [not traced], Khabarovsk region, Russia. Eastern Siberia.

>*jarochnovitschae* Starobogatov & Zatravkin *in* Starobogatov *et al*., 1989; TL delta of the Kolyma River at Pokhodsk [69º06'N, 160º59'E], Yakutsk Autonomous Republic, Russia.

>*khabarovskiensis* Starobogatov & Zatravkin *in* Starobogatov *et al*.,

1989; TL pool near Kaktokovsk lake [not traced], Khabarovsk region, Russia.

Physa megalochlamys Taylor, 1988; TL lily pond beside US highway 26-89-187, NW 1/4 sec. 19, T. 45 N., R. 114 W., 6815 ft, Teton County, Wyoming. Southwestern Canada and western United States.

>*Physa megachlamys* "Taylor" Wu & Brandauer, 1982; *nomen nudum*.

Physa mirollii nom.nov.; TL L. Maggiore, Italy.

Physa skinneri Taylor, 1954; TL Pleistocene, SE corner sec. 6, T. 5 N., R. 28 E., Beaver County, Oklahoma. Alaska to central United States. Possibly in Siberia also.

>*fontinalis canadensis* Beck, 1838, *nomen nudum*; TL Canada.

>*elliptica minor* Crandall, 1901, preoccupied; TL Grand Rapids [42º57'48"N, 85º40'05"W], Kent County, Michigan.

Physa streletzkajae Starobogatov & Budnikova, 1976; TL Vakarevo [64º53'N, 171º37'E], Chukotka, northeastern Siberia.

Physa taslei Bourguignat, 1860; TL "Très-commune dans un petit ruisseau provenant de la fontaine de Limoges, à 2 kilomètres de Vannes," Brittany, France. France.

Physa fontinalis (Linnaeus, 1758)

Figs. 157-158

Bulla fontinalis Linnaeus, 1758:727.

Physa fontinalis: Draparnaud, 1801:52. Moquin-Tandon, 1855:451, pl. 32, figs. 9-13; description and illustration of shell and living animal; notes on spawn; synonymy. Slugocka, 1913:75 ff., pl. 4, figs. 26, 31, 32, 35; Switzerland, morphology. Soós, 1917:138, figs. 5-8; Hungary, morphology. Germain, 1930-1931:509, fig. 519, pl. 14, fig. 406; France, description, synonymy, illustration and notes on morphology. Mandahl-Barth, 1949:57, figs. 23, 24, 26; Denmark, illustration of shell, radula, genitalia. Duncan, 1958:55 ff., illus.; England; morphology and anatomy. Adam, 1960:163, figs. 30 B, 31 B, 32 B; Belgium; illustration of shell, live animal and reproductive system. Starobogatov, 1967:288, fig. 9; Russia; sketch of penial complex. Berëzkina & Starobogatov, 1988:41, 177, figs. 8, 72; vicinity of Smolensk, Russia; illustration of reproductive system, spawn.

Limnea (Physa) fontinalis: Sowerby, 1821-1834, *Limnea*, fig. 8 [1822]. An example preserved in the Linnean cabinet was figured by Sowerby, according to Hanley (1855:208).

Holotype: no longer extant. As to locality, Linnaeus specified only "Habitat in Lacuum plantis subaquaticis" in his description of 1758, but cited the Fauna Suecica (1746, no. 1302) where he stated "Habitat… praesertim Upsaliae." The type locality can therefore be accepted as the vicinity of Uppsala [59º52'N, 17º38'E], Sweden.

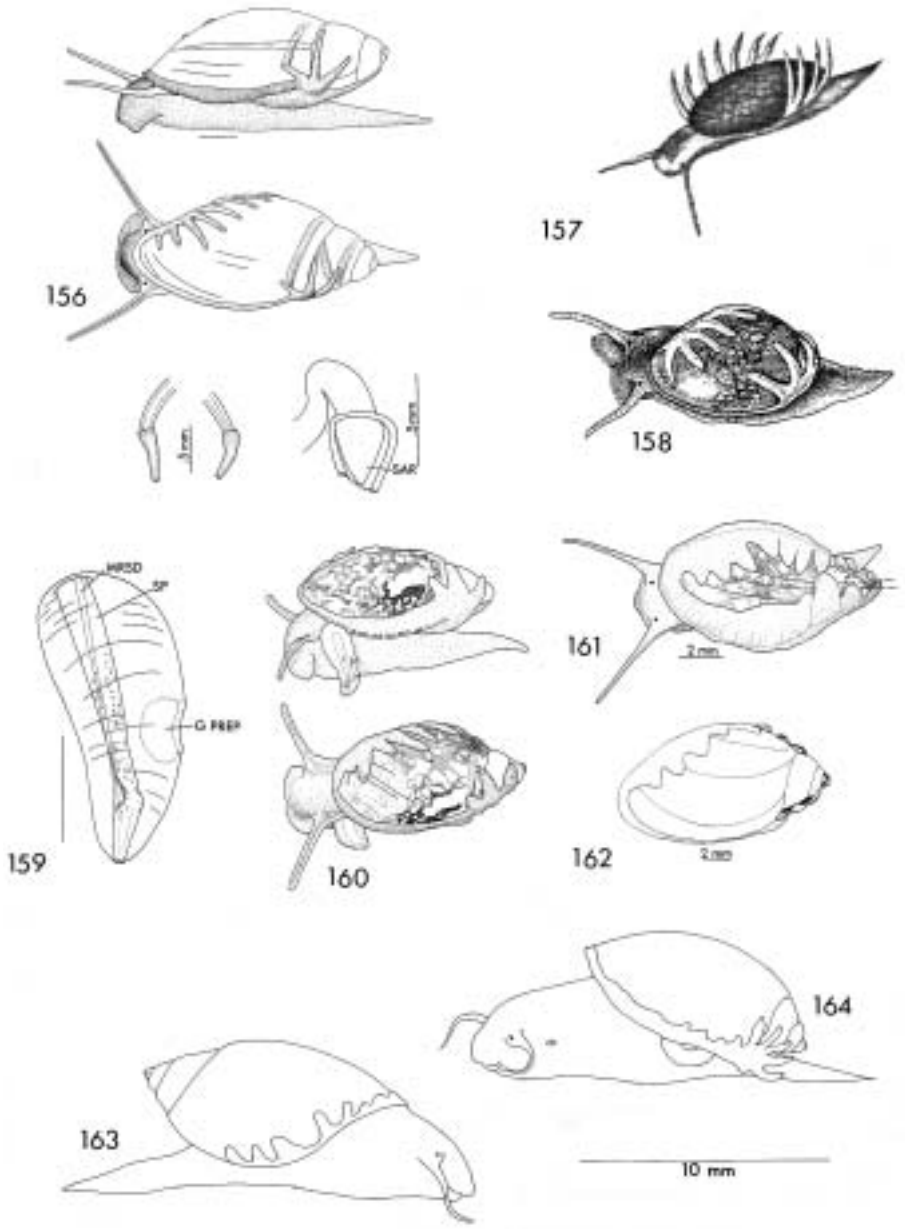
Name: Latin *fons*, *fontis*, m., a spring. Linnaeus named his two species of Physidae according to habitat. This is the species of springs, whereas the other, *Bulla hypnorum*, is the species of mosses.

Description: The bulky penial sac fills much of the anterior body cavity, and extends well to the right of the midline. It tapers gradually from the wide proximal end to about 1/10 of its length, then enlarges slightly before entering the preputium; through the entire length it is glandular, although in the narrowest segment the glandular cells form only a thin layer. Length of the penial sac is far greater than that of the preputium. The penis is flagelliform, bearing a lanceolate stylet at its tip. Length of vas deferens IV is about 1/2 the length of the penial sac and preputium, in correlation with the flexed state of the sac.

Penial retractor muscles take adjacent but separate origins from the columellar muscle, and insert on the ends of the penial sac, without cross-connections. The distal retractor, stronger of the two, divides close to its distal end, and inserts on either side of the penial sac at its union with the preputium.

Localities and material examined:

AUSTRIA: Danubian riverine forest, Vienna, *H. Nesemann*, 1-V-2001 (**M**).



Figs. 156-164. 156, *P. skinneri*, p. 166. 157-158, *Physa fontinalis*, p. 162. 159-162, *P. megalochlamys*, p. 164. 163-164, *P. mirollii,* p. 165. Scale 1 mm except as noted.

Figs. 157-158. *Physa fontinalis*.157, Denmark; from Müller (1781); 158, Belgium; from Adam (1960). These two illustrations demonstrate the progress in technique of printed illustrations over almost 200 years. Müller's illustration is the earliest that shows the animal of any Physidae; despite its crudity in some respects, it shows a plausible number of mantle projections on each side, and the color pattern of the mantle within the shell.

Figs. 159-162. *Physa megalochlamys*. 159, preputium extruded. 160. Two views of one specimen. 161-162. External views of two specimens. From Taylor (1988b).

Fig. 156. *Physa skinneri*. Two views of living animal, Sevier County, Utah, and (insets) details of penial stylet and sarcobelum. From Taylor (1988b).

Figs. 163-164. *Physa mirollii*. L. Maggiore, Italy. Redrawn from Mirolli (1958).

ITALY, FRIULI - VENEZIA GIULIA, Prov. Gorizia: Lago Doberdò, *M. Bodon*, 30-III-1991(**M**; eight). Prov. Udine: Irrigation ditch Mortesina, loc. Borgo Modena (Cervignano), *F. Stoch*, 9-V-1988(**M**; one). Canal Cornuzze, bridge road Precenicco-Lignano Precenicco), *F. Stoch*, 28-V-1987(**M**; five). Irrigation ditch Velicogna, loc. Stroppagallo (Pocenia), *F. Stoch*, 21-VII-1987(**M**; two). River Muzzanella, loc. Muzzana (Muzzana), *F. Stoch*, 21-VII-1987(**M**; one). River Turgnano upstream Boschi Muzzana (Palazzolo), *F. Stoch*, 21-VII-1987(**M**; two).

LAZIO, Prov. Rieti: Lake of Ripa Sottile, loc. S. Nicola, *S. Cianfanelli, M. Calcagno*, 10-VIII-1989(**M**; four, coll. *Cianfanelli*, Firenze).

LOMBARDIA, Prov. Brescia: Lake of Garda at Campione del Garda, *S. Cianfanelli*, 23-VIII-1986(**M**; one, coll. *Cianfanelli*, Firenze). Lake of Idro at north of Vestone, *M. Bodon*, 18-IX-1991(**M**; six). Prov. Como: River Adda near Airuno, *M. Bodon*, 27-VI-1991(**M**; one). River Adda, Paderno d'Adda, *S. Cianfanelli, M. Calcagno*, 21-II-1988(**M**; one, coll. *Cianfanelli*, Firenze).

TOSCANA, Prov. Lucca: Canal at Viale dei Tigli at Viareggio, *S. Cianfanelli, Manfredi*, 14-II-1982(**M**; two, coll. *Cianfanelli*, Firenze).

VENETO, Prov. Padova: Stream Muson Vecchio, Massanzago, *P. Turin*, 19-VII-1990(**M**; two). Prov. Treviso: Stream Piavesella, *P. Turin*, 25-III-1988(**M**; one). Prov. Venezia: River Lemene at Portogruaro, *M. Bodon*, 19-IX-1991(**M**; three).

Remarks: The references listed might be to a composite species. According to Starobogatov *et al*. (1989) *Physa fontinalis* has a penial sheath that tapers gradually to the preputium, and a shell with very low spire. A second species has a penial sheath that narrows abruptly between the proximal third and the mid-length, then narrows more gradually to the preputium; and a shell with more elevated spire. Whether the differences are constant or whether they may be only an artifact of preservation deserve further investigation; but in both cases the penial sheath is illustrated as much longer than the preputium, and far bulkier, with a proximal end twice the diameter of the preputium. A similarly large penial sheath is illustrated by the following authors: Adam (1960, fig. 32B; Belgium); Berëzkina & Starobogatov (1988, fig. 8, Russia); Germain (1930-1931, fig. 519; France); Mandahl-Barth (1949, fig. 24; Denmark); Soós (1917, figs. 6-8; Hungary). Slugocka (1913:99) emphasized with description and measurements that the penial sheath (deuxième poche) in her specimens from near Geneva was twice as long and twice as wide as the preputium. If the species in the traditional sense should indeed prove to be composite, then topotypes of the various named species will need to be examined.

Physa megalochlamys Taylor, 1988

Figs. 159-162, Pl. 8, fig. 3

Physa (s.s.) megalochlamys Taylor, 1988:55, fig. 3; references, morphology, distribution.

Holotype: CAS 114 779, preserved in alcohol; Teton County, Wyoming; lily pond beside US 26-89-187, NW 1/4 sec. 19, T. 45 N., R. 114 W., 23-VII-1963. Paratypes UCM 30 260.

Name: Greek, signifying large mantle.

Diagnosis: A species of *Physa* with elongate-ovoid shell, narrow spire, blunt apex, and wide parietal callus, attaining a length of about 12 mm. The mantle is broadly reflected over the shell on both sides, even covering the entire shell, with broadly rounded projections.

Description: Shell thin and fragile, ovoid-fusiform, with aperture about three-fourths of shell length. Apex obtusely rounded; spire bluntly rounded with weakly convex

whorls separated by a shallow, broadly attached suture. Aperture elongate oval, rounded anteriorly, narrowed abruptly to an acute angle posteriorly, widest about one-third length from anterior end. Outer lip thin, sharp, convex in the direction of growth, strongly retractive to the suture. Parietal wall and ventral-anterior aspect of body whorl with with a broad, thin, translucent, closely appressed callus. In a profile view of the aperture, the callus is visible on the body whorl; the edge of the callus crosses the axis of the shell opposite a point three-fourths or more of the apertural length from the anterior end. Columellar lip a rounded ridge that enters the whorl cavity forming a low plait. Surface texture silky, less often shining. Axial sculpture of fine growth lines and weak raised threads. Spiral sculpture formed by spiral series of straight to weakly arcuate fine ridges, convex in the direction of growth.

The largest shells seen, from the type locality, have an eroded apex and whorl counts are not possible. The largest specimen with apex entire measure L 11.5, LAp 8.6, W 6.7, whorls 4 1/2.

Penial complex: The preputium is translucent, melanin-flecked, shorter than the penial sheath; on its posterior side it bears a preputial gland less than one-third the length of the preputium. The long penial sheath is entirely glandular, opaque creamy-white, and flecked all over with wisps of melanin; no contrast in intensity of pigmentation with preputium, vas deferens, or muscle bands is evident. The sheath is widest in the proximal third, gradually narrows, then in the distal fifth abruptly narrows to the minimum diameter, and enlarges in the distal tenth. The penis is narrow, flagellar, about two-thirds the length of the penial sheath, and bears an elongate stylet not sharply set off from the shaft (Fig. 159). Within the preputium is a large sarcobelum, usually about three-fourths as wide as long, forming a prolate hemisphere; a small terminal papilla is present. Retractor muscles are inserted on the ends of the penial sheath, with no cross-connections. The distal penial retractor may be divided into separate bands for much of its length. Length of the vas deferens between the paragonoporal angle and the penial sheath is less than one-fourth the length of the sheath.

Variation: The most conspicuous external variate is number of mantle projections and to a lesser extent their shape and location (Figs. 160-162). The projections are broadly rounded, varying from semicircular to elongate with broadly convex tips, or to spoon-shaped, with the base narrower than the tip. Less often they are broadly triangular, two to three times as long as wide, with rounded tips. Outer margins are nearly always smooth, rarely scalloped. Projections are

Remarks: References and list of localities were provided in the original description. The most similar species seems to be the Eurasian *P. dalmatina*, of which I have seen no specimens.

Physa mirollii nom.nov.

Figs. 163-164

Physa fontinalis (L.): Mirolli, 1958:245, pl. 24, figs. 1-5; pl. 26, figs. 1-3; L. Maggiore and adjacent L. di Mergozzo, Italy; not *P. fontinalis* (Linnaeus).

Holotype: The shell illustrated by Mirolli (1958, pl. 24, fig. 1). Whether this specimen or any others studied by Mirolli survive is doubtful.

Name: For Maurizio Mirolli.

Diagnosis: A species of *Physa* distinguished from *P. fontinalis* by the longer, subacute apex of the shell, relatively shorter and narrower aperture, narrow parietal callus, many short, rounded mantle projections on the columellar side, and most notably by absence of the preputial gland. Whether a stylet on the penis may be present is unresolved; it was neither described nor illustrated by Mirolli.

Remarks: Some illustrations of *Physa* are oriented so as not to show the preputial gland, but authors mention its presence (Germain,

1930-1931, fig. 519, France; Stadnichenko, 1990, fig. 35, *2*; Ukraine). The preputial gland seems to be consistently present in all populations of all Physinae except for these in northern Italy, which moreover differ from *Physa fontinalis* in other characters.

The question naturally arises whether this species is to be classified as a *Physa*. Against this are the subacute apex and absence of preputial gland, perhaps also lack of a penial stylet. Can this be a species of Aplexinae? But the inclination of the shell suture is wholly that of Physinae, and the penial sheath is that of *Physa*. I have been unable to obtain material of the species, that is probably extinct, and leave the species as *Physa*.

Physa skinneri Taylor, 1954
Fig. 156

Physa skinneri Taylor, 1954:9, 1960:63, pl. 3, figs. 5,6,9-11.
Physa (s.s.) skinneri Taylor, 1988:45, fig. 1; references, morphology, distribution.

Holotype: UMMZ 181 292. Pleistocene, Beaver County, Oklahoma. SE corner sec. 6, T. 5 N., R. 28 E. (Berends local fauna), *C. W. Hibbard et al*., 1950. Paratypes MCZ 198 177 (68), UMMZ 177 533 (31), USNM 562 010 (12).

Name: For paleontologist-stratigrapher Morris F. Skinner (1906-1989).

Diagnosis: A species of *Physa* with slender, elongate-ovoid shell, attaining a length of about 8 mm, moderately wide parietal callus, and mantle reflected narrowly on the left. Mantle projections are narrow and elongate (Fig. 156).

Description: Shell thin, narrowly ovoid to ovoid-fusiform, with aperture about 60% of shell length. Apex obtusely rounded; spire blunt with weakly convex whorls separated by a shallow, broadly attached suture. Aperture elongate-oval, rounded anteriorly, acute posteriorly, widest about one-third length from anterior end. Outer lip thin, sharp, sometimes with a white band of callus thickening within, convex in the direction of growth.

The largest specimen seen, from Ruby Lake, Nevada, measured L 8.8 mm, LAp 6.1, W 5.2, whorls 4.

Penial complex: The preputium is translucent, melanin-flecked, shorter than the penial sheath; on its posterior face it bears a preputial gland one-fourth to one-half the length of the preputium. The long penial sheath is entirely glandular, opaque creamy-white, and flecked all over with melanin. No contrast in intensity of pigmentation with preputium, vas deferens or muscle bands is evident. The penial sheath is widest in the proximal third, then narrows gradually to its minimum diameter at about nine-tenths of length, then enlarges toward the preputium. The penis is narrow, flagellar, one-half to two-thirds the length of the sheath, and bears an elongate stylet sharply set off at its base from the shaft (Fig. 156). Sarcobelum large, more than twice as long, forming a prolate hemisphere; a terminal papilla is present but may be inconspicuous. Retractor muscles are inserted on the ends of the penial sheath, with no cross-connections or multiple insertions.

Distance from the paragonoporal angle to the penial sheath is one-third or less the length of the sheath.

Spawn: Laboratory-laid spawn from a population in Comins Lake, Nevada, was measured (N = 25) with the following results:

	Length	Width	Eggs/capsule
Mean	3.14	1.81	3.12
Range	2.12 - 4.33	1.52 - 2.18	2-5
S.D.	.580	.169	
S.E.	.116	.034	

Distribution: From Alaska southeast to Ontario, Canada, and to Michigan; in the western

United States to eastern Washington, Nevada, southern Colorado, and northern Nebraska. Whether the species indeed occurs in Siberia, as indicated in the original description, remains for morphological confirmation.

Remarks: References, list of localities, and discussion of variation were provided by Taylor (1988). *Physa skinneri* is similar to the European *P. fontinalis* in the slender, elongate mantle projections, but is less globose in form. Whether the species indeed occurs in Siberia, as indicated in that paper, remains for morphological confirmation.

This species is one of a small number in North America first described as fossil, and only later recognized as living.

Tribe **PHYSELLINI**, new tribe

Penial sheath bipartite, with proximal muscular portion distinctly set off from a distal glandular portion. Penis with simple tip in *Chiapaphysa*, *Costatella*, *Petrophysa*, *Archiphysa*, and *Physella*, but tip with narrow stylet within which the penial canal is narrowed in *Ultraphysella*. Mantle edge with triangular projections in two groups, columellar-parietal on right, and left posterior, with exception of *Petrophysa* and *Utahphysa*. Mantle not reflected over outer lip of shell, except in *Utahphysa*.

Seven genera: *Chiapaphysa*, most primitive, with two species on the Pacific coast in Chiapas, southern Mexico, and in northwestern Costa Rica. Three local monotypes are *Costatella* in Clear Lake, California, *Petrophysa* in Zion Canyon, Utah, and *Utahphysa*, Fish Lake, Utah. *Archiphysa* includes five species in southern Canada and western and northern United States. *Physella*, with six species, is widely distributed in Canada and the United States. *Ultraphysella*, most advanced, is known only in the states of Sinaloa and Nayarit, on the Pacific coast of northwestern Mexico (Fig. 10).

Chiapaphysa g.n.

Type species: *Chiapaphysa grijalvae sp.n.*

Name: Chiapas, and *Physa*.

Diagnosis: Shell ovoid, dull to silky, but not polished or glossy, with crescentic microsculpture. Aperture usually more than half of shell length, its profile weakly convex in the direction of growth. Parietal callus narrow. Suture distinct, either well impressed or scarcely impressed. Apex acute. Length to about 12 mm with 4 3/4 whorls.

Mantle not reflected over outer lip of shell, with narrow triangular projections in two groups, columellar-parietal (C) and left posterior (P); C 4-6, P 1-2.

Penial complex: Preputium shorter than penial sheath. Penial sheath bipartite, with a small glandular distal portion, and longer muscular proximal portion. Glandular distal portion shorter than and less bulky than muscular portion. Within the glandular portion a muscular tube fluted lengthwise. Proximal muscular portion swollen at proximal end. Penis shorter than sheath as a whole, longer than proximal muscular portion, muscular, tapering from broader proximal end to simple tip with no enlargement or cuticular tip. Sarcobelum elongate, with strong papilla. Vas deferens between paragonoporal angle and penial sheath shorter than or as long as glandular portion of sheath.

Penial retractor muscles with separate adjacent origins in columellar muscle, inserted on ends of penial sheath, with no cross-connections or multiple insertions.

Distribution: *Chiapaphysa grijalvae sp.n.*, southeastern Mexico, in the state of Chiapas, and *C. pacifica sp.n.*, northwestern Costa Rica, in Guanacaste Province (Fig. 165).

Chiapaphysa grijalvae sp.n.

Figs. 166-167, Pl. 8, fig. 7
Distribution Map, Fig. 165

Holotype: CAS 114 818. Mexico, Chiapas: Río Suchiapa, 2 km SE Suchiapa, 16º36.4'N, 93º5.0'W, 7-II-1988. Paratypes CAS 114 787 (10), BMNH 20001308 (10), MCZ 302 595 (4), ZIBM CNMO 1161 (10).

Name: From Río Grijalva, in which drainage occur most of the localities.

Diagnosis: A species of *Chiapaphysa* with mantle projections C 4, P 1-2. The muscular portion of the penial sheath (SPM) is tapered from a broad head to the glandular portion (SPG); the vas deferens between paragonoporal angle (APG) and glandular portion of sheath is less than half as long as the muscular portion.

Description: The shell is elongate-ovoid, with an acute spire and broad, narrowly rounded anterior end. The profile of the aperture is broadly but weakly convex in the direction of growth, evenly retractive to the suture. The columella is moderately heavy, pale tan, with a strong fold. The parietal callus is a thin wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly to moderately convex, separated by a distinct but not incised suture. The lateral profile of the spire is weakly concave. The shell surface is shining, pale brown, with an inconspicuous narrow pale band at the suture. Surface sculpture is inconspicuous, consisting of fine axial growth lines; and spiral microsculpture of irregular minute wrinkles, either straight or slightly convex in the direction of growth, that are arranged in spiral series, discontinuous and irregular in distribution.

Morphology is described under the generic heading.

Variation and Comparisons: Shape is the most conspicuous variable. Some specimens have a slightly flattened last whorl as in *Ultraphysella sinaloae*, but others can be confused easily with *Haitia mexicana*, the Mexican species most similar in shell. Many specimens of *Chiapaphysa grijalvae* can be mistaken for *H. mexicana*, but others show a flattened whorl outline and narrower anterior end that distinguishes them. As usual with shells of many Physidae, diagnostic characters are poorly marked.

Distribution: Southeastern Mexico, in the state of Chiapas, in drainage of both the Pacific Ocean and Gulf of Mexico.

Localities and material examined:

MEXICO, Chiapas: Río La Venta, Las Flores, Mex. 190, 18 km E Cintalapa, 16º41.6'N, 93º33.5'W, 5-II-1988 (T88-401)(**M**). Río Suchiapa, 2 km SE Suchiapa, 16º36.4'N, 93º5.0'W, 7-II-1988 (T88-502; type locality)(**M**). Río Santo Domingo, Puente Santo Domingo, 9 km S of Cupía, 16º37.4'N, 92º59.8'W, 4-II-1988 (T88-102). Río Santo Domingo 2 km NE of Julián Grajales, 16º30.0'N, 92º57.4'W, 4-II-1988 (T88-201)(**M**). Río Quemado [or Río Salado] about 1 km SW Vicente Guerrero, 16º25.7'N, 92º43.5'W, 8-II-1988 (T88-1203). Baños del Carmen on Río Quemado [or Río Salado]

TABLE 42
Measurements and descriptive statistics of shells of Chiapaphysa grijalvae *from type locality (T88-502). Measurements to nearest .125 mm. N = 30*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	9.51	7.16	.753	5.81	.612	4.54
Range	8.45-12.42	6.14-9.86	.70-.83	4.86-8.06	.57-.66	$4\,{}^{1}/_{4}$ - $4\,{}^{3}/_{4}$
S.D.	.850	.754	.030	.620	.027	
S.E.	.155	.138	.006	.113	.005	

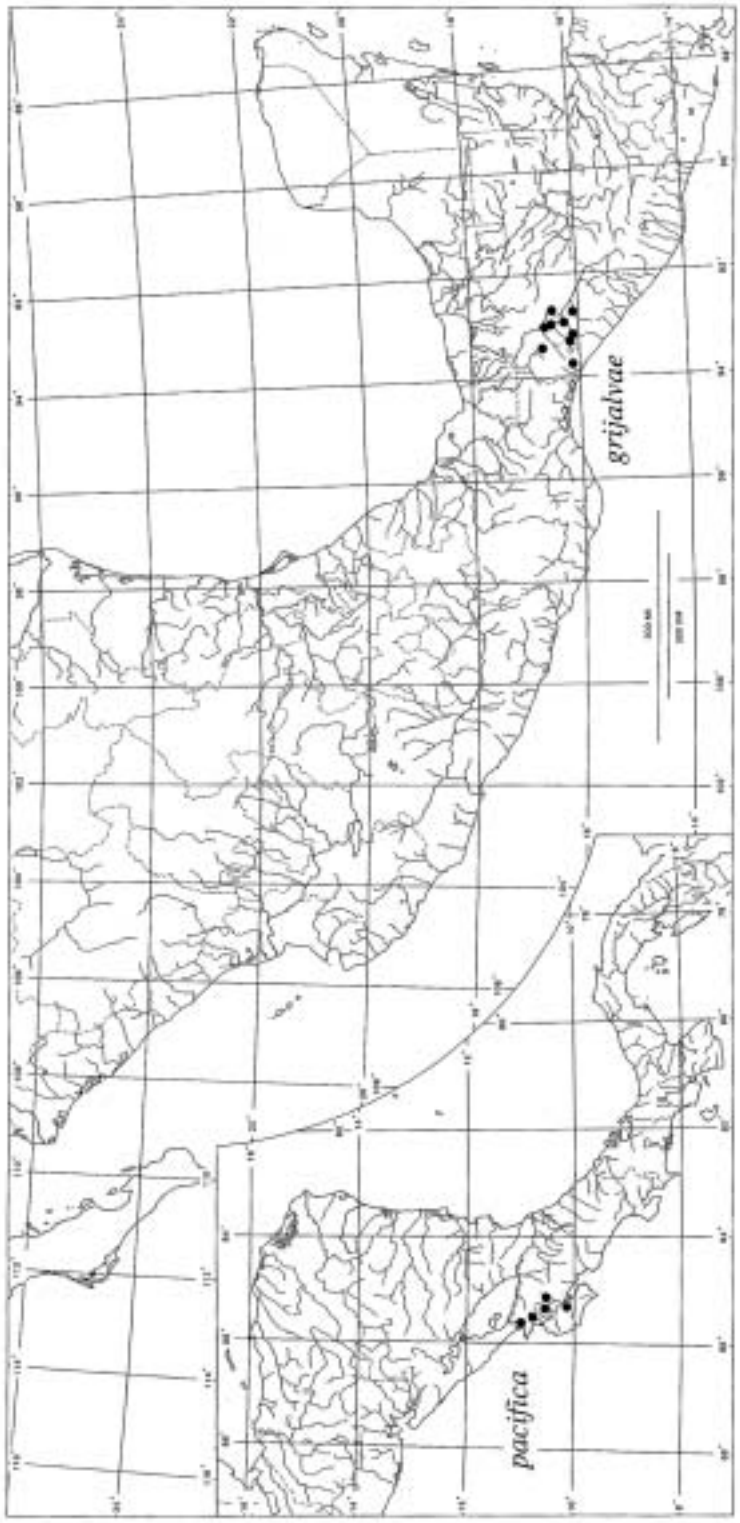
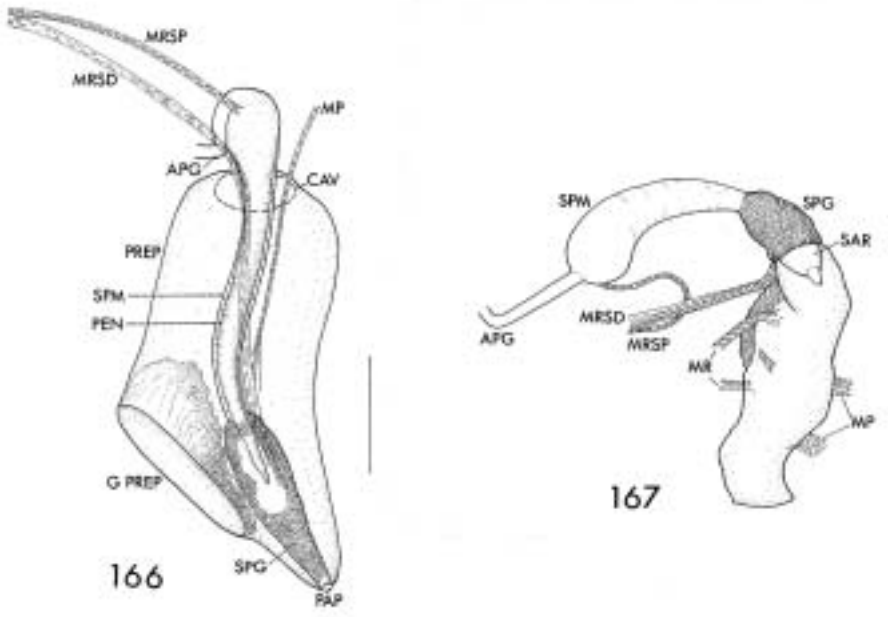


Fig. 165. Distribution of *Chiapaphysa*, p. 164.



Figs. 166-167. *Chiapaphysa grijalvae*, p. 168. Mexico, Chiapas: 2 km SE Suchiapa (type locality). Penial complex extruded and greatly swollen (166), and in retracted state (167). APG, paragonoporal angle; CAV, limit of body cavity; G PREP, preputial gland; MP, protractor muscles of preputium; MR, retractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PAP, papilla; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath. Scale 1 mm.

about 1 km from paved road to La Angostura, 16º25.4'N, 92º43.0'W, 8-II-1988 (T88-1303). Río San Francisco Ocotal, Mex. 200, 16º7.6'N, 93º47.7'W, 5-II-1988 (T88-301). Río Los Amates, Puente Los Amates, Villa Flores, 16º14.3'N, 93º1.0'W, 7-II-1988 (T88-601). Río Pando 1.5 km S of Villa Flores, 16º12.8'N, 93º16.1'W, 7-II-1988 (T88-701). Río Ningunito 1 km SW of Revolución Mexicana, 16º9.6'N, 93º4.8'W, 7-II-1988 (T88-801). Río Custepeques 2 km SE of Independencia, 16º4.6'N, 92º49.8'W, 7-II-1988 (T88-901). Irrigation ditch overflow about 1.5 km WNW of Independencia, 16º5.8'N, 92º51.7'W, 7-II-1988 (T88-1001)(**M**).

Remarks: Specimens of *Ultraphysella sinaloae* may be much larger than *Chiapaphysa grijalvae*. In all samples of *Ultraphysella* studied, there is a silky shell surface with conspicuous microsculpture, and usually a shorter spire with shallower suture, weak columellar fold, and flattened whorl outline.

Chiapaphysa pacifica sp.n.

Fig. 168, Pl. 8, fig. 8
Distribution Map, Fig. 165

Holotype: CAS 114 784. Costa Rica, Prov. Guanacaste: Río Tenorito, Hacienda La Pacífica, 10º29.02'N, 85º9.58'W, 7,8-XI-1991. Paratypes INBio (10).

Name: From Hacienda La Pacífica.

Diagnosis: A species of *Chiapaphysa* with triangular, round-tipped mantle projections, C 4-6, P 3. The muscular portion of the penial

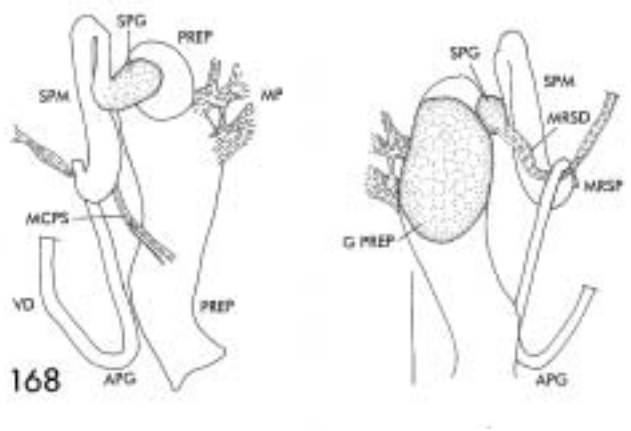


Fig. 168. *Chiapaphysa pacifica*, p. 170. Costa Rica, Prov. Guanacaste: Río Tenorito, Hacienda La Pacífica, 7-XI-1991 (T91-905). APG, paragonoporal angle; G PREP, preputial gland; MCPS, connective between penial sheath and preputium; MP, protractor muscles of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm.

sheath (SPM) is more than four times as long as the glandular portion (SPG) in retracted state, and tapered from the head more gradually than in *C. grijalvae*. The preputium is slightly shorter than the penial sheath, and bears a large preputial gland on its posterior face that is about 1/4 the length of the preputium. The vas deferens between the paragonoporal angle (APG) and the penial sheath is about as long as the muscular portion of the sheath.

Distribution: Northwestern Costa Rica, in Guanacaste Province.

Localities and material examined:

COSTA RICA, Prov. Guanacaste: Río Salina 1 km NW Soley, 11º1.05'N, 85º40.46'W, 20-XI-1992 (T92-8401)(**M**). Parque Nacional Guanacaste, Quebrada Aserradero, 10º53.82'N, 85º33.74'W, *D. García et al.*, 22-IX-1994 (INBio 1 001 480 039). Parque Nacional Santa Rosa, Sendero Las Mesas, 10º50.95'N, 85º35.65'W, 230 m, *D. García*, 13-II-1995 (INBio 1 001 483 872). Parque Nacional Santa Rosa, Sendero Los Patos, 10º49.57'N, 85º37.84'W, 260 m, *Z. Barrientos et al.*, 2-XI-1994 (INBio 1 001 480 370). Río Tempisquito, Vado Esperanza, 10º47.38'N, 85º33.11'W, *M. Lobo*, 4-III-1995 (INBio 1 001 483 744). Río Cabuyo, 10º29.86'N, 85º22.72'W, *Z. Barrientos et al.*, 29-VII-1994 (INBio 1 001 474 754). Río Tenorito, Hacienda La Pacífica, at road to "Ecomuseo," 10º29.02'N, 85º9.58'W, 7,8-XI-1991 (T91-905; type locality)(**M**). Hacienda La Pacífica, in irrigation ditch 0.9 km W of Lechería, 10º28.19'N, 85º8.97'W, 7-XI-1991 (T91-804). Rivulet 1.65 km S of headquarters of Parque Nacional Barra Honda, 10º9.92'N, 85º22.84'W, 24-XI-1992 (T92-9904)(**M**).

Costatella Dall, 1870

Dall, 1870:355; type species (by original designation): *Physa costata* Newcomb, 1861. As subgenus of *Physa*.
=*Costella*, Dall: Meek, 1876:603-604. Error for *Costatella*.

Name: Latin *costata*, ribbed, and the diminutive; loosely, a little ribbed *Physa*.

Diagnosis: Shell ovoid with dull texture, and sculpture of prominent axial rounded ribs. Aperture more than half of shell length, profile

weakly convex in direction of growth. Parietal callus narrow. Suture impressed, apex acute. Length to about 7 mm (modern), 15 mm (fossil).

Mantle not reflected over outer lip of shell, with elongate projections in two groups, columellar-parietal (C) and posterior (P); C 1-5, P 0-3.

Penial complex: Length of preputium less than that of penial sheath. Penial sheath bipartite, with slender, tapering, muscular proximal portion (SPM) set off from a slightly shorter but far bulkier thick, glandular, distal portion (SPG). Penis (PEN) shorter or longer than muscular portion of penial sheath, tapered to a slender tip with no terminal stylet or thickening. Sarcobelum narrowly conical, with prominent papilla. Vas deferens (VD) from paragonoporal angle to penial sheath less than half the length of penial sheath.

Penial retractor muscles (MRSD, MRSP) inserted on ends of penial sheath without cross-connectives. Three or four conspicuous retractor muscles of the preputium (MR) on the proximal two-thirds of the preputium.

Vagina very short, wider than long. Bursa copulatrix an asymmetrical plump sac, wider than long, set off clearly from duct. Bursal duct only slightly longer than bursa.

Distribution: Western United States. The one living species is restricted to Clear Lake and the nearby Blue Lakes, California (Fig.13). Other species, all Pliocene, are found in California, Nevada, Oregon, and Utah. In all cases, modern and Pliocene, the species are in lakes with a fauna showing distinctive endemism in other groups of molluscs. This is the only genus with shell characters so distinctive that fossil species can be referred to it with confidence.

Comparisons: *Costatella* is most closely related to *Petrophysa*, of Zion Canyon, Utah, in the tapered penis with simple tip lacking a stylet or internal thickening. In external features the two are widely different.

Referred species (distribution map in Taylor & Smith, 1981)**:**

costata Newcomb, 1861; living, Clear Lake (1026 ft) and the nearby Blue Lakes, Lake County, California.

+*harpa* Taylor, 1981; Pliocene, Cache Valley Formation, Box Elder County, Utah.

+*humboldtiana* Taylor, 1981; Pliocene, upper Truckee Formation, Mopung Hills, Churchill County, Nevada.

+*wattsi* Arnold, 1910; Pliocene, Tulare Formation, Kettleman Hills, California.

Costatella costata (Newcomb, 1861)

Figs. 169-171, Pl. 9, fig. 4

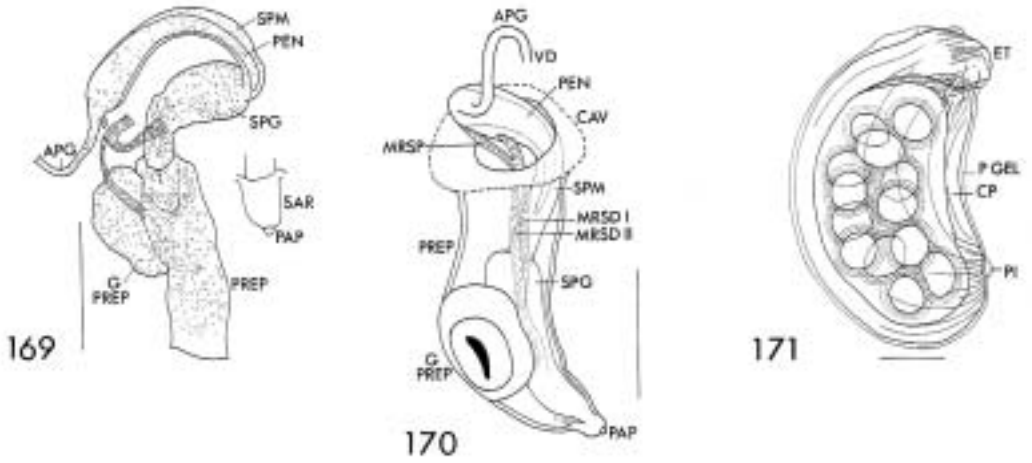
Physa costata Newcomb, 1861:104; Clear Lake, California, *J. A. Veatch*.
Physella (Costatella) costata (Newcomb): Starobogatov, 1970:48.

Lectotype: in PRI. California, Lake County: Clear Lake, *J. A. Veatch*.

Name: Latin *costatus*, ribbed, indicating the unique sculpture.

Diagnosis: The one living species of *Costatella*, with shouldered body whorl bearing about 9-18 rounded ribs, and shell attaining a length of nearly 7 mm with 3 1/2 whorls.

Description: Shell thin, ovoid-conical, pale brown, with aperture three-quarters of shell length. Apex acute; spire with increasingly convex to shouldered whorls separated by an impressed suture. Aperture roughly a flattened oval, rounded anteriorly, right-angled posteriorly, widest at mid-length. Outer lip thin, sharp, furthest advanced at the suture, or below the suture at the shoulder. Parietal wall with a thin, white, closely appressed callus. Columellar lip a sharp ridge that forms a rounded plait as it enters the whorl cavity. Surface texture dull. Axial sculpture of irregularly arranged raised threads, superimposed on broad swollen ribs that are strongest over the shoulder and disappear usually before reaching



Figs. 169-171. *Costatella costata*, p. 172. California, Lake County: Clear Lake. 169, penial complex (retracted); 170, penial complex, extruded; 171, capsule. Some structures are seen by transparency. Scale 1 mm. APG, paragonoporal angle; CAV, wall of body cavity; CP, capsule wall; ET, terminal end; G PREP, preputial gland; MRSD I, MRSD II, distal retractor muscles of penial complex; MRSP, proximal retractor muscle of penial complex; PAP, papilla; PEN, penis; P GEL, pallium gelatinosum; PI, initial end; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens.

TABLE 43
Measurements and descriptive statistics of shells of Costatella costata *from Clear Lake, California. Measurements to nearest .128 mm. N = 10*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.07	4.65	.767	4.30	.709	3.4
Range	5.38-6.66	4.22-4.99	.73-.79	3.97-4.61	.68-.74	3 .25 - 3.5
S.D.	.342	.249	.021	.202	.023	
S. E.	.114	.079	.007	.064	.008	
		Ribs/body whorl				
Mean		14.3				
Range		9-18				

TABLE 44
Variation in numbers of mantle projections of Costatella costata. *N=13*

	Columellar	Posterior
Mean	2.8	1.8
Range	1-5	0-3
S.D.	1.01	.93
S.E.	.281	.257

suture or mid-length of whorl. Spirally arranged series of arcuate fine ridges continue over the major elements of axial sculpture, becoming obsolete on the body whorl.

The mantle does not project beyond the peritreme, except for the mantle digitations arranged in a columellar-parietal (C) and a posterior (P) group as usual in Physinae. The

digitations are roughly triangular with rounded tips. C 1-5 (mean 2.8), P 0-3 (mean 1.8) in a sample of 13 from Clear Lake.

Overall tone of the body as seen through the shell is dark brown. General proportions of head, foot, and tentacles are as in the common species *Physella gyrina* and *Haitia mexicana*. The dorsal aspect of the head and body stalk is dark gray, from melanin wisps and internal organs. Borders of the head-foot, palps, and tentacles are paler gray, with fewer wisps of melanin. Sugary white granules are common within the tissue of the head-foot, tentacles, and mantle margin, including the digitate projections. The largest granules are about five times (in greatest dimension) the size of the smallest.

Penial complex: The preputium is shorter than the penial sheath, and the sheath is divided into proximal muscular and distal glandular portions. Flecks of melanin are scattered uniformly over preputium and both portions of penial sheath, on muscle bands, and on the vas deferens. The thin-walled muscular portion of the penial sheath is translucent, permitting observation of the penis within. The glandular portion of the penial sheath and preputial gland are opaque creamy white. The preputium is transparent except for its gland, making visible the sarcobelum and pilasters within.

Spawn: The capsule is thick-walled, relative to the size of the egg, as in *Physa fontinalis*. Shape of the capsule is distinctive; it may be kidney-shaped, or with straight right side and strongly convex left side. Ends of the capsule are blunt and subequal. With a small number of eggs (ten or less) the form is ovate or flask-shaped. Curvature of the capsule is commonly 45 degrees or less, greater than in *P. fontinalis*, but less than in other species of *Physa*. Both initial tip and terminal end are consistently on the right; one or both may be strong, but more often the terminal end is conspicuous and formed into a spout, even when no initial tip is discernible. The eggs overlap within the capsule, even with as few eggs as four and an ovate capsule. In 244 capsules examined, length ranged up to 7.0 mm, and number of eggs from 4-34.

Eggs are pear-shaped to elongate, irregular to regularly ovoid, with terminal depression, egg navel, and stout internal membrane. The external membrane is composed of fine lamellae, and is divided in the middle by a relatively strong lamella that is thinner than the internal membrane. Out of 25 measured, the largest two eggs were 1.01 mm x .72 and 1.00 x .76. Mean size was .89 x .66. Capsular strings (*fila capsulae*) were detected only rarely.

Localities and material examined: California, Lake County: north shore of Clear Lake, 1.0 mile east of Bartlett Springs Road (just east of the town of Nice), 11-X-1966, 5-VIII-1984, VIII-1988.

Habitat: At the later times of collection Clear Lake was several feet below extreme high-water level. Snails and spawn were not uncommon on the lower surfaces of subangular cobbles and small boulders in 1-2 ft depth, thus in water well oxygenated by wave action but not exposed to air or direct force of waves. No other molluscs were associated, and as *Costatella* was found on other occasions at lower water with *Valvata* and *Helisoma* it is likely that they had come into shallower water to spawn.

Petrophysa Pilsbry, 1926

Pilsbry, 1926:328; type species (by original designation): *Physa zionis* Pilsbry, 1926. As "new subgenus or section" of *Physa*.

=*Pterophysa* Pilsbry: Starobogatov, 1967:289; error for *Petrophysa*.

Name: Greek *petra*, rock, and *Physa*; the rock *Physa*, from its habitat on vertical cliffs.

Diagnosis: Shell globose, with obtuse spire less than one-fifth the length of the large auriform aperture, less than 5 mm long. Surface dull, with sculpture of axial fine growth lines only.

Mantle not reflected over shell, and nearly even around entire margin. Projections reduced to a few inconspicuous bluntly rounded projections on columellar surface.

Penial complex: Preputium about 40 percent of length of penial sheath, with large posterior gland (G PREP) about two-thirds as long as preputium. Penial sheath bipartite, consisting of a longer, narrower, muscular proximal portion (SPM) tapering gradually from wider proximal end; and shorter, much bulkier, glandular, distal portion (SPG) wider than preputium.

Penis (PEN) shorter than muscular portion of penial sheath, tapering from a broad proximal end to simple tip with no thickening or change in structure. Sarcobelum (SAR) massive and roughly conical, with small papilla. Vas deferens from paragonoporal angle to penial sheath shorter than muscular portion of penial sheath. Entire penial complex flecked sparsely with wisps of melanin, rather than (as in some species) with a contrast between one or both parts of the penial sheath and preputium.

Penial retractor muscles inserted on proximal end of sheath and on glandular portion of penial sheath at about mid-length, with no cross-connections.

Distribution (Fig. 13)**:** The one species is known only in Zion Canyon, Washington County, southwestern Utah.

Comparisons: *Petrophysa* is most like *Costatella* in having an obviously tapered penis, with broad proximal end. These two localized and presumably relictual groups, so different in gross appearance, are more closely related to one another than either is to the widespread *Physella*.

Other characters of *Petrophysa* are associated with its relatively sedentary life on rock surfaces, and changes in general body proportions. These include the broad foot, relatively short, blunt tentacles with large post-tentacular flaps, reduced eyes, reduced mantle projections, and insertion of distal penial retractor higher on the penial sheath than usual.

Petrophysa zionis (Pilsbry, 1926)

Figs. 172-173, 175

Physa zionis Pilsbry, 1926:326, pl. 11, fig. 5-6; Zion Canyon, Utah; type of new subgenus or section *Petrophysa*.
Physa (Petrophsa) [sic] zionis Pilsbry: Ng & Barnes, 1986:310 ff; local distribution and habitat in Zion Park.
Petrophysa zionis (Pilsbry): F. C. Baker, 1928:416. Woodbury, 1933:177; a predominant species in hanging gardens communities.
Physella (Petrophysa) zionis (Pilsbry): Te, 1980:183.

Holotype: ANSP 140 235a. Utah, Washington County: Zion Canyon [37º09’54”N, 113º00’40”W], *H. A. Pilsbry*.

Name: From Zion Canyon.

Description: As in the generic diagnosis.

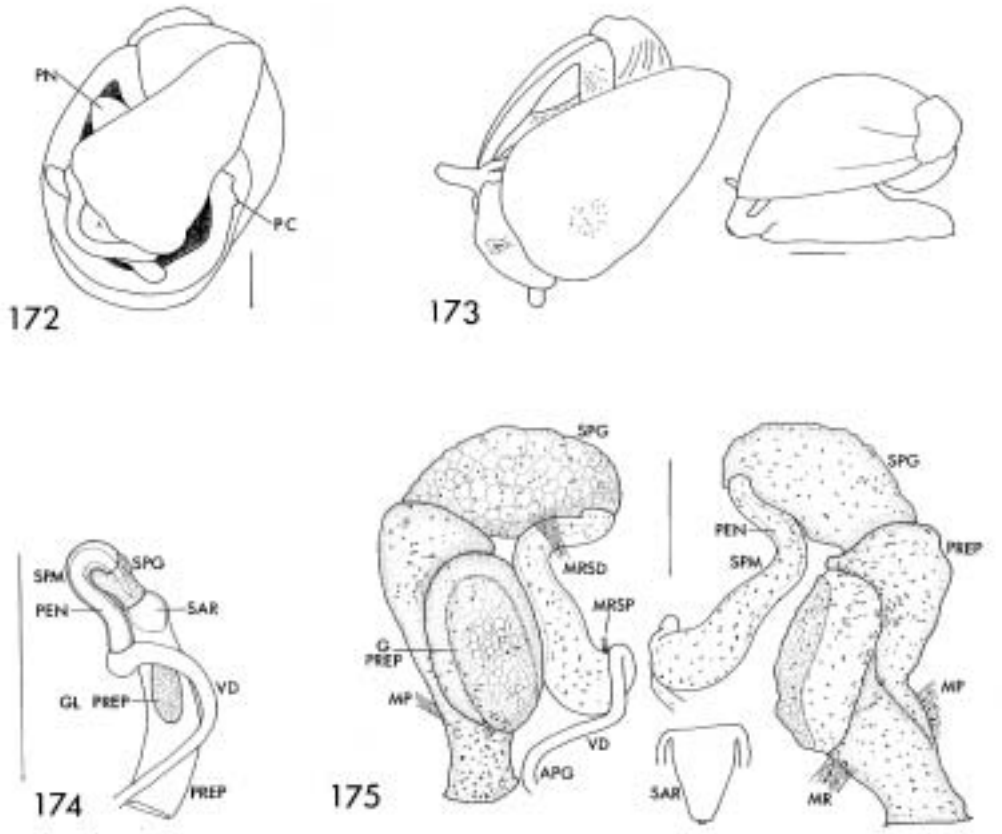
Localities and material examined: a small series collected by S. D’Vincent, San Diego Museum of Natural History, in 1970. Most specimens did not survive transport. One remained active, and was anesthetized, fixed, and preserved, providing the basis for the drawings.

Utahphysa g.n.

Type species: *Aplexa microstriata* Chamberlin & Berry, 1930; Fish Lake, 8843 ft, Sevier County, Utah; Fig. 174.

Name: The state, and *Physa*.

Diagnosis: Mantle reflected broadly over the shell on the columellar side, reaching to the dorsal midline in the anterior third of the shell; reflected over the outer lip about 1/10 whorl, and less so over the anterior end. A posterior lobe is smooth-edged like the rest of the mantle margin.



Figs. 172-173, 175. *Petrophysa zionis*, p. 175. Zion Canyon, Utah. 172, animal after preservation showing the vestigial mantle projections. 173, two views of same specimen living but moribund. 175, lateral (L) and medial (R) views of penial complex of same specimen; inset, sarcobelum removed. APG, paragonoporal angle; G PREP, preputial gland; MP, protractor muscle of preputium; MR, retractor muscle of preputium; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; PC, mantle projection; PEN, penis; PN, pneumostome; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; VD, vas deferens. Scale 1 mm. Fig. 174. *Utaphysa microstriata*, p. 175. Fish Lake, Utah. Penial complex after rehydration.

Penial complex: Preputium (PREP) approximately equal in length to the penial sheath. Penial sheath bipartite, with a tubular, thin-walled, proximal muscular portion (SPM), and a shorter and broader distal glandular portion (SPG). Penis moderately stout, tapered to a simple tip. Sarcobelum broad, W/L 1.0.

Distribution (Fig. 13)**:** Known only from the type locality.

Comparisons: *Utahphysa* differs conspicuously from all other Physellini in the broadly reflected, smooth-edged mantle. In the form of penis and extent of glandular tissue in the penial sheath it is approximately intermediate between *Costatella* and *Petrophysa*, and the more advanced *Archiphysa*, *Physella*, and *Ultraphysella*.

Referred species: Only the type species is known.

Remarks: Only a few badly preserved specimens were available for study. It seems that only thoroughly desiccated material reached either CAS or FMNH, the museums holding the specimens I have examined. Paratypes in both institutions are so dried I could not rehydrate them with TSP. Fourteen immature specimens, FMNH 186548/23, were

less desiccated than the paratypes and were partly rehydrated; two of these were stained, transferred to glycerine, and could be dissected for the penial complex, but all other structures were obscure. The diagnosis thus is based on one penial complex (illustrated), another partial penial complex, and what could be made out of the mantle in the paratypes.

Archiphysa g.n.

Physella lordi group: F. C. Baker, 1928:424.

Type species: *Physa lordi* Baird, 1863; southern British Columbia, Canada.

Name: Greek *archon*, chief, ruler, in reference to the large size of the species and to the name *lordi*; and *Physa*.

Diagnosis: Shell obovate, with very short, broad spire that may have a plane or even concave outline, rounded anterior end, and relatively large and often shouldered body whorl; surface texture dull, with spiral microsculpture. Aperture semicircular to ovate-pyriform, about three-fourths or even more of shell length. Parietal callus narrow. Suture inconspicuous to weakly incised; apex acute. Length up to 26 mm.

External body color a pale gray wash overall, tentacles paler, an off-white. Mantle collar, mantle projections and pneumostome pale gray like the body, or even paler. Mantle not reflected over outer lip of shell, with round-tipped triangular projections in two groups, columellar-parietal (C) and left posterior (P). Behind the collar the mantle is pigmented in a reticulum of dense black enclosing diffuse-edged openings, pale gray to off-white. The openings are roughly equidimensional, circular to oval to elongate-quadrangular in form, with widths up to several times as wide as the enclosing black reticulum.

Hermaphroditic duct thickly set with seminal vesicles along its whole length. Near the ovotestis the vesicles are small and simple, shorter than the width of the duct. For most of its length they are up to twice or more as long as the width of the duct, and have two to three lobes.

Male system: Prostate gland a bulky mass of numerous simple, tubular follicles. In the posterior half, where they are better developed, they are up to five times as long as wide.

Penial complex: Preputium shorter than penial sheath, about as long as glandular portion. Penial sheath bipartite, with a short, tubular, thin-walled, proximal muscular portion; and a bulky distal glandular portion more than twice as long as the proximal portion. Penis moderately slender but not flagelliform, tapered to a simple tip with no stylet or internal narrowing of penial canal. Sarcobelum broad.

Penial retractor muscles have separate but adjacent origins in the columellar muscle, and are inserted on ends of the penial sheath.

Vas deferens from paragonoporal angle to penial sheath shorter than length of sheath.

Female system: Bursa copulatrix exceptionally large, roughly quadrangular in outline. The bursal duct originates on the medial aspect of the bursa, and not (as usual) at the distal margin; it is shorter than the length of the bursa, stout and clearly set off at both ends. The duct joins the oviduct so close to the female pore that the vagina is short, wider than long (based on 10 specimens of *A. lordi* from Ruby Lake, Sechelt Peninsula, British Columbia).

Spawn: In *A. parkeri* the mass is usually about 12-18 mm long, reaching a maximum of 50x12 mm. Number of eggs per mass ranged from 5 to 161 in 22 counts, mostly 40 to 80 (Cort *et al*., 1941).

Distribution (Fig. 176)**:** Sporadic in southernmost British Columbia, Canada, western United States, and Great Lakes region of United States and Canada, principally in lakes.

Comparisons: *Archiphysa* has a penis with simple tip that is more slender than the broadly tapered structure in *Chiapaphysa*, *Costatella* and *Petrophysa*. The bursa is relatively large, its duct leaving on the medial aspect of the bursa, and the duct stout and muscular instead of the usual flaccid tube. The vagina is very short.

Referred species:

Archiphysa ashmuni sp.n.; TL New Mexico, Cibola County: Ojo del Gallo, 1 650 ft N, 4 150 ft E, sec. 3, T. 10 N., R. 10 W. [35º07'20"N, 107º52'32"W,], 6450 ft, a former large spring in the small town of San Rafael, 23-X-1980. Holotype CAS 146087, paratypes CAS 146088 (10), BMNH 20001307 (10). Status of one or two other populations in New Mexico remains uncertain, as well as precise localities.

Archiphysa laphami (F. C. Baker, 1928); TL Hancock [44º08'01"N, 89º31'23"W, 1089 ft], Waushara County, Wisconsin. Wisconsin and adjacent Michigan. Shell, Pl. 10, figs. 5-6.

Archiphysa latchfordi (F. C. Baker, 1928); TL Meach Lake [45º31'N, 75º52'W], Quebec. Shell, Pl. 9, figs. 2-3.

Archiphysa lordi (Baird, 1863); TL "Lake Osoyoos, British Columbia," Canada; but probably Pend Oreille River, Seneacquoteen [48º09'06" N, 116º45'16" W, 2101 ft], Bonner County, Idaho. Southern British Columbia; formerly in northern Idaho.

Archiphysa parkeri (Currier, in DeCamp, 1881); TL Houghton Lake [44º18'53"N, 84º45'53"W], Roscommon County, Michigan. Lower peninsula of Michigan. F. C. Baker (1928) provided some morphological details. Shell, Pl. 9, figs. 6-7.

Archiphysa sonomae sp.n. TL California, Sonoma County: artificial pond 2500 ft S, 4300 ft W, sec. 30, T. 9 N., R. 9 W.

Archiphysa zomos (Baily & Baily, 1952); TL Pyramid Lake, Nevada. Shell, Pl.10, figs. 9-10.

Archiphysa ashmuni sp.n.

Pl. 10, figs. 1-3
Distribution Map, Fig. 176

Physa lordi Baird [misidentified]: Dall, 1905:102, in part, not fig. 80; San Rafael, New Mexico. Clench, 1925:9, in part; New Mexico.

Holotype: CAS 146087. New Mexico, Cibola County: Ojo del Gallo, 1650 ft N, 4150 ft E, sec. 3, T. 10 N., R. 10 W. [35º07'20"N, 107º52'32"W], 6450 ft, a former large spring in the small town of San Rafael; shells on spoil heaps left after excavation of the spring as it dried up from lowering of the water-table by groundwater pumping, 23-X-1980 (T80-805). Paratypes CAS 146088 (10), BMNH 2001307 (10).

Name: For Rev. Edward Houghton Ashmun (1853-1904).

Description: Shell roughly ovoid to obovoid, with acute spire that widens rapidly to the expanded body whorl. Lateral profile of spire concave. Body whorl broadly rounded, base narrowly rounded. Posterior angle of aperture about 60-80º. Parietal callus a thin, continuous wash. Suture distinct but not incised.

Surface texture shining but not polished; periostracum not preserved in type series. Spiral surface sculpture weak, consisting of short, discontinuous series of fine spirally aligned short raised ridges, either straight or weakly crescentic, with crescents convex in direction of growth. Axial sculpture consists of irregular growth ridges.

The series from "near Bland" retain a pale tan periostracum, and show variation in sculpture. Some shells have a silky texture, with spiral sculpture over the entire body whorl. Others have little sculpture, hence a smooth, shining texture. Size and shape of series from the type locality and "near Bland" differ little.

Comparisons: *Archiphysa ashmuni* differs from *A. lordi* by attaining lesser size, the periostracum is paler, there is no dark brown callus within the outer lip, and the body whorl is not subangular.

Localities and material examined: New Mexico, Cibola County: San Rafael, *E. H.*

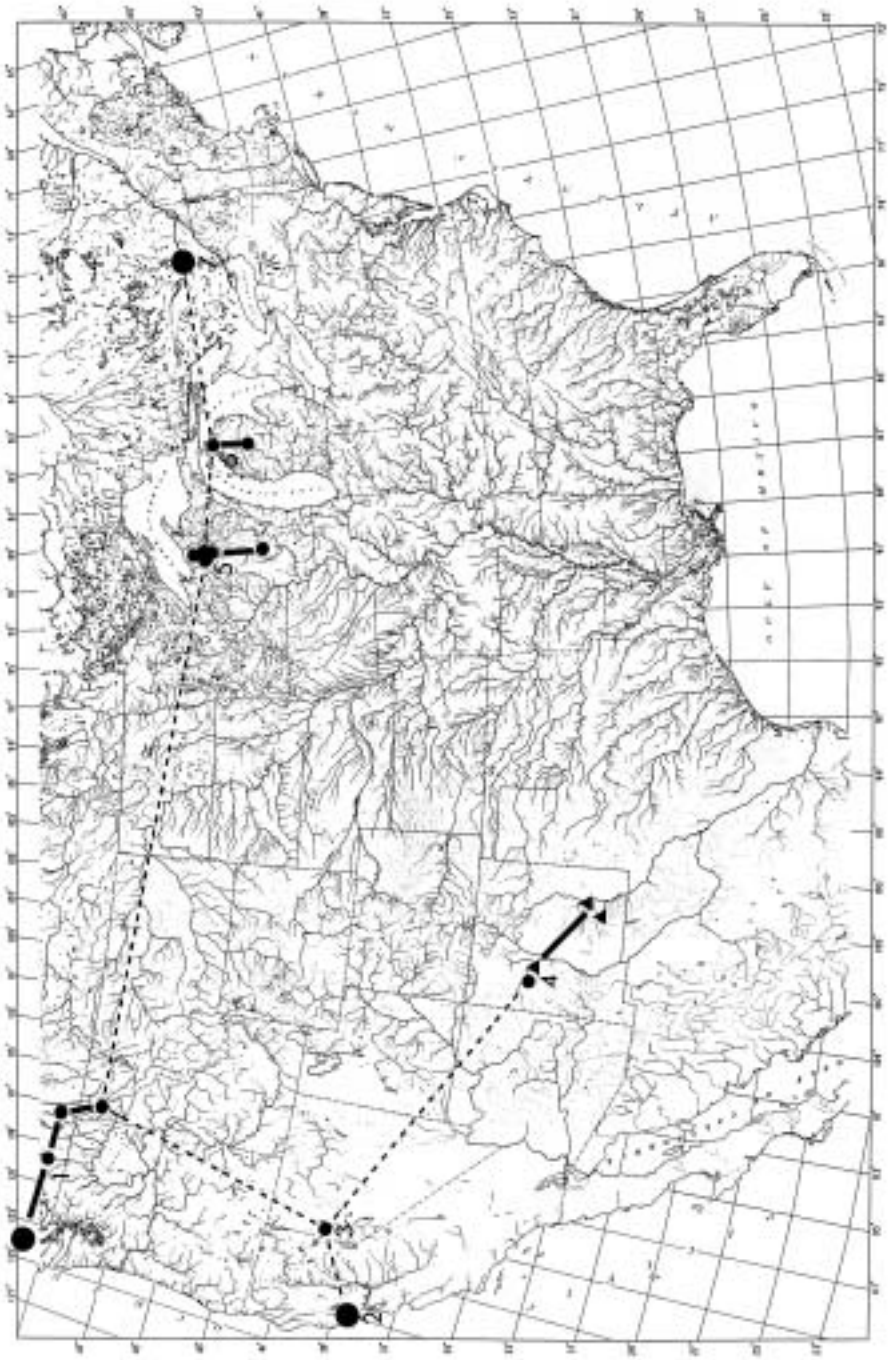


Fig. 176. Distribution of *Archiphysa*, p. 177. All tracks are unoriented. Solid lines connect localities of a single species; dashed lines, of different species. Larger symbols, terminal 1∞ vertices; triangles, Pleistocene; solid dots, modern. Track 1-5 is slightly longer than distance 4-5, and is preferred on the basis of other distributions, whereas 4-5 would be in accord with a minimal spanning tree (Craw *et al*. 1999). Note that with the addition of fossils the 1º terminal vertex in 4 would be shifted from the modern occurrence (solid dot) to fossil occurrences. Species: 1, *lordi*; 2, *sonomae*; 3, *zomos*; 4, *ashmuni*; 5, *laphami*; 6, *parkeri*; 7, *latchfordi*.

TABLE 45
Measurements and descriptive statistics of shells of Archiphysa ashmuni *from type locality (T80-805). Measurements to nearest .128 mm. N = 15*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	14.97	12.46	.832	10.80	.723	4.35
Range	13.6-16.5	10.9-14.3	.70-.88	9.2-12.0	.67-.79	4 - 4.5
S.D.	.776	.951	.044	.825	.036	
S.E.	.201	.246	.011	.213	.009	

TABLE 46
Measurements and descriptive statistics of shells of Archiphysa ashmuni *from "Block Ranch," near Bland, New Mexico (SSB 2086). Measurements to nearest .128 mm. N = 8*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	16.03	13.15	.821	11.30	.705	4.69
Range	15.3-17.6	13.1-17.9	.79-.84	10.6-12.8	.66-.75	$4\ ^{1}/_{2}$ - 5
S.D.	.880	.492	.020	.737	.028	

Ashmun (CAS 6 763, SDMNH 46 130, 59 729).

County?: "Block Ranch. N. M." (A. G. Smith 7 537, from E. H. Ashmun collection); "Block R., near Bland, New Mexico, *E. H. Ashmun*" (S. S. Berry 2 086); "Black Ranch, New Mexico" (CAS 51 566, 51 572, 51 592, originally R. E. Coats 2 579 and 2 590, purchased from J. Q. Burch). All these sets are apparently from a single source, and a locality not yet traced. "Anderson's"? [label not clear], *E. H. Ashmun* (MCZ uncat., *ex* 12 275 B. Walker colln., now in UMMZ; four specimens, one identified by Clench as *Physa lordi utahensis*). Whether the material from "Anderson's" represents a second population is unknown.

Habitat: A relatively large spring is the only identified modern locality. The fossil localities also represent outflow of springs.

Fossil record: Holocene also in tributaries of the Pecos River, southeastern New Mexico. Chaves County: Banks of Rio Peñasco, .85 mile W of state highway 24 on U.S. highway 82, .05 mile W of roadside picnic area, *A. L. Metcalf*, 23-IV-1973 (UTEP 3 412). Banks of Rio Peñasco, .5 mile W of state highway 24 on U.S. highway 82, *A. L. Metcalf*, 15-IV-1963 (UTEP 4 397). Valencia County: Suwanee Spring, NE 1/4 NE 1/4 sec. 10, T. 8 N., R. 3 W., *John S. Applegarth*, 6-VIII-1978 (UTEP 6 878).

Remarks: The only fresh specimens of the species that I have seen were collected by E. H. Ashmun in the last century. Status of the population at "Block Ranch" remains uncertain. The mining town of Bland (now abandoned) was in Sandoval County, and presumably it was the nearest population center at the time of collection.

Archiphysa lordi (Baird, 1863)

Figs. 177-182, Pl. 10, figs. 8, 11-13
Distribution Map, Fig. 176

Physa lordi Baird, 1863:68; Lake Osoyoos, British Columbia. Binney, 1865:76, figs. 125-127; "E. of Ft. Colville, W. T." [Washington Territory of that time].
Physella (Physella) lordi (Baird): Te, 1980:183.

Types: three syntypes BMNH 1863.2.4.1. "Lake Osoyoos, British Columbia," but probably at or near the outlet of Lake Pend Oreille, Bonner County, Idaho.

Name: For John Keast Lord (1818-1872), Naturalist to the British North American Boundary Commission.

Description: Shell roughly ovoid to obovoid, with acute spire that widens rapidly to the expanded body whorl. Lateral profile of spire concave. Body whorl broadly rounded to subangular, base narrowly rounded. Posterior angle of aperture about 45º-60º. Parietal callus a thin, continuous wash. In full-grown specimens a dark brown callus within the outer lip. Suture distinct but not incised.

Periostracum tan, surface texture silky. Spiral surface sculpture consists of fine spirally aligned short raised ridges, either straight or weakly crescentic, with crescents convex in direction of growth; sculpture usually covers the entire shell surface. Axial sculpture consists of irregular growth ridges.

Length to 23.3 mm with six whorls, W/L .63-.73, in the eight largest specimens seen (three syntypes; five RBCM 991-95-3).

Variation: Shells from Kootenay Lake and the syntypes are larger than the series from Ruby Lake, but fall within the range of variation of the latter in shape and sculpture.

Morphological features in ten specimens from Ruby Lake varied as shown by the following statistics:

	C	P	V W/L	G PROS W/L	SAR W/L
Range	2-8	2-4	.8-3.6	.29-.59	.61-1.3
Mean	4.6	2.9	2.07	.40	.92
S. D.	1.61	.640	.883	.109	.238

Penial retractor muscles ordinarily take separate but adjacent origins in the columellar muscle. In one specimen the proximal retractor separated from the distal retractor a short distance from the columellar muscle. The course of the distal retractor is ordinarily direct to the distal end of the glandular portion of the penial sheath, but in one instance it ran to the proximal end of the muscular portion, there looped around the connective between the preputium and penial sheath, and thence to the usual insertion.

The relation of the bursal duct and the oviduct varies. Usually the stout, muscular bursal duct joins the oviduct above the female pore, leaving a short vagina; the angle of the junction varies, and in some cases it appears that the penis may be inserted into the bursal duct and not into the oviduct. This appearance is reinforced by the condition in one specimen, in which the oviduct joined the bursal duct, leaving the vagina as a much narrower structure than usual.

The bursal duct leaves the bursa on its medial aspect in most cases. In only one specimen was the origin of the duct at the distal margin of the bursa, as usual in Physidae.

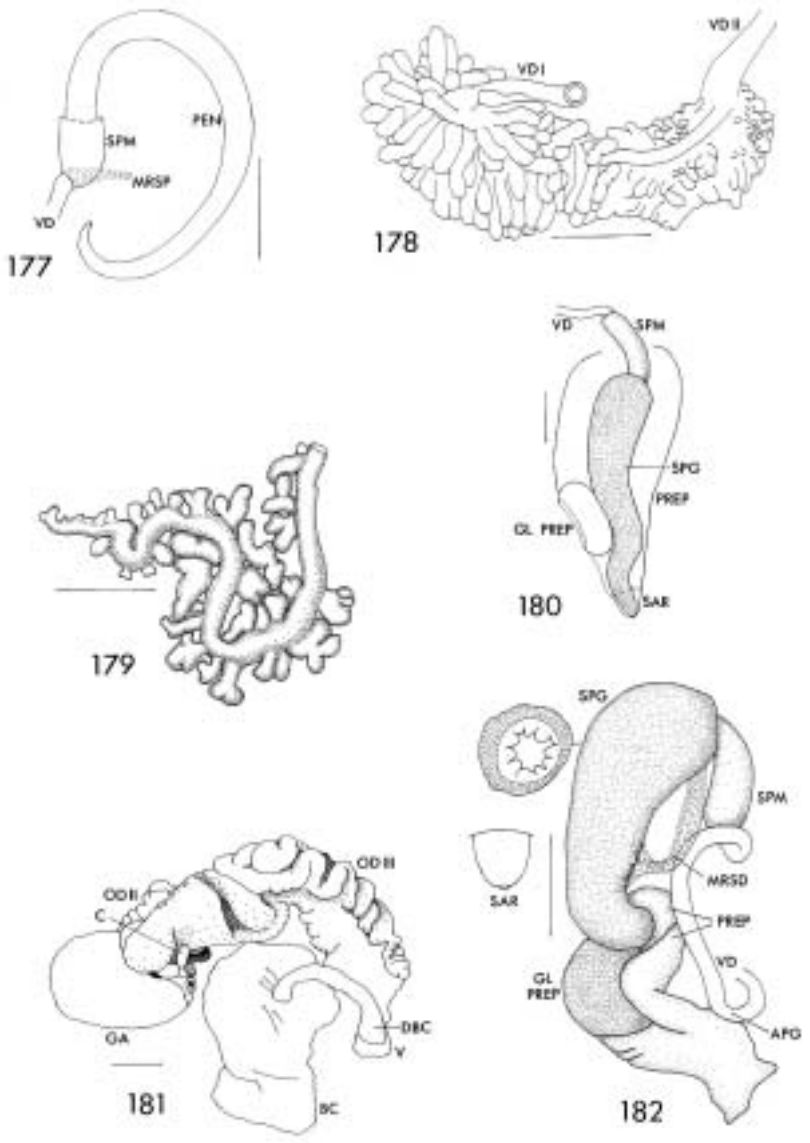
Localities and material examined:

British Columbia, Kootenay District: Kootenay Lake near Nelson [49º29'N, 117º17'W], from *Dr. Rose*, 12-V-1933 to C. F. Newcombe (RBCM 991-95-3). Nelson, *ex* E. N. Drier (MCZ 112138).

New Westminster District: Ruby Lake (two sites), Sechelt Peninsula, on the Pacific Coast, 12, 13-VIII-1992 (T92-3001, 3202).

Yale District, Osoyoos Division: Okanagan Lake, Okanagan Lake Park, 15-VIII-1990 (T90-3305, two immature specimens, not certainly identified).

Washington [probably Idaho]: "east of Fort Colville." Binney (1865) cited specimens as USNM 9 310; these were not found when sought some time before 1964. Two specimens from W. G. Binney are MCZ 79 811. "Lake Osoyoos," British Columbia, *J. K. Lord*; BMNH 1863.2.4.1, five adult specimens much like the syntypes; 1863.2.4.3, four adults smaller than the syntypes.



Figs. 177-182. *Archiphysa lordi*, p. 180. Ruby Lake, Sechelt Peninsula, British Columbia. 177, penis; 178, prostate; 179, hermaphroditic duct; 180, preputium extruded and penial sheath seen by transparency; 181, female system; 182, penial complex and sarcobelum removed. APG, paragonoporal angle; BC, bursa copulatrix; C, caecum; DBC, duct of bursa copulatrix; GA, albumen gland; GL PREP, preputial gland; MRSD, distal retractor muscle of penial sheath; MRSP, proximal retractor muscle of penial sheath; OD II, OD III, portions of oviduct; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath; V, vagina; VD, vas deferens; VD I, VD II, vas deferens proximal and distal to prostate. Scale 1 mm.

Habitat: Known localities of the species are all large or medium-sized oligotrophic lakes.

Remarks: The type locality as originally published is wrong. Both the British and American Commissions of the Northwest Boundary Survey obtained the species, from "Lake Osoyoos" by the British, but from "east of Fort Colville" [now Colville, Washington] by the Americans. One of the localities seems surely an error, because the data are irreconcilable.

A probable locality where both parties might have obtained the species is the Pend Oreille River at or near a former ford at Seneacquoteen [48º09'06"N, 116º45'16"W, 2101 ft, Laclede 7.5' map], Bonner County, Idaho, now flooded by waters of Lake Pend Oreille. This was the site of a supply depot for the survey parties, published as "Syniakwateen Depot." The three syntypes have an inflated shell and expanded body whorl, are bleached and retain a few sand grains within. Evidently they were collected as empty shells, probably at or below the outlet of former Lake Pend Oreille.

Contemporary information that might resolve the locality has been lost. Molluscs collected by J. K. Lord, Naturalist of the British Commission, were studied by William Baird, who published the new species and at least began a fuller illustrated report. This report is known through comments by Carpenter (1864:604), who stated that the new species had "been drawn on stone by Sowerby," mentioned a proof-copy of the illustrations, and published revised identifications of the collection. Thanks to Carpenter, Binney (1865) was able to publish copies of the illustrations. I have been unable to find further mention of Baird's report, or whether it was ever completed.

The account by Lord (1866) of his travels is valuable mainly in providing itinerary, because the section on molluscs contains little specific locality data and in this respect is inferior to Carpenter's summary. In describing Lake Osoyoos, Lord (1866, 2:75) noted that "The shore is sandy, like a seabeach, and, strewn thickly with freshwater shells along the ripple line, has quite a tidal aspect." He mentioned a new species of *Succinea* found at the lake, but not *Archiphysa lordi*— a suspicious omission. The appendix on molluscs in Lord's work mentions the species, but only in quotation from Baird's published description. J. G. Cooper collected in Lake Osoyoos ("Lake Oyosa") during the Pacific Railroad Surveys (W. Cooper, 1859), but found there only *Physa bullata* [<*Physella gyrina*].

The American Commissioner of the Northwest Boundary Survey was Archibald Campbell; C. B. R. Kennerly served as surgeon and naturalist. Loss of manuscript, confusion of localities, and subsequent loss of specimens characterize the American efforts just as those of the British. Commissioner Campbell subsequently borrowed the final draft of the report covering the four years of American effort, and the report has never been seen since (Goetzmann, 1959:429).

Archiphysa sonomae sp.n.

Pl. 10, figs. 4, 7
Distribution Map, Fig. 176

Holotype: CAS 114 807. California, Sonoma County: artificial pond 2 500 ft S, 4 300 ft W, sec. 30, T. 9 N., R. 9 W., *A. G. Smith*, 16-IX-1967. Three paratypes CAS 114 803.

Name: From the county.

Description: Shell obovoid, with acute spire that widens rapidly to the expanded body whorl. Lateral profile of spire concave. Body whorl broadly rounded, gently convex on the side, more narrowly so at the posterior end, base narrowly rounded. Posterior angle of aperture about 60-80º. Parietal callus a thin continuous wash. No callus within outer lip. Suture distinct but not incised.

Periostracum pale tan, surface silky to shining but not polished. Spiral surface sculpture consists of fine spirally aligned short raised ridges, either straight or weakly crescentic, with crescents convex in direction of growth; sculpture usually covers the entire surface. Axial sculpture consists of irregular growth ridges.

Variation: Three immature specimens have a white callus marking the position of a

TABLE 47
Measurements and descriptive statistics of shells of Archiphysa sonomae *from type locality. N = 3*

	L	W	W/L	Whorls
Holotype	10.8	7.8	.72	4.75
Paratype	10.6	8.6	.81	4.5
Paratype	8.7	6.8	.78	4.25
Mean	10.04	7.72	.770	4.5
Range	8.7-10.8	6.8-8.6	.72-.81	4.25 - 4.75
S. D.	1.14	.917	.045	
S. E.	.659	.530	.026	

former lip; in two there is a dark tan band immediately in front of the callus.

Comparisons: *Archiphysa sonomae* is distinct by its small size, and the narrow rounding of the body whorl near its posterior end.

Remarks: The material consists of 13 specimens, most immature; of four paratypes, two have the apex broken, thus reducing the measurements to those of the holotype and two paratypes. I visited the locality with Allyn Smith, but was unsuccessful in finding more specimens. The pond is a small artificial pond for stock, and there seems no other possibility but to suppose the snails were carried by insects or birds, or perhaps introduced with plants. In any case, they seem unlikely to have come from any great distance.

Physella Haldeman, 1843

Haldeman, 1842-1845(6):14; type species (by monotypy) *Physa globosa* Haldeman, mouth of Nolachucky River, Tennessee. As subgenus of *Physa*.

>*Physodon* Haldeman, 1842-1845(6):14; type species (by monotypy) *Physa microstoma* Haldeman, Kentucky and Ohio. Not of Müller & Henle, 1839 (Pisces). As subgenus of *Physa*.

Name: *Physa* and the diminutive *-ella*; *i.e.*, little *Physa*.

Diagnosis: Shell ovoid to subfusiform, dull to silky, but not polished or glossy, with crescentic microsculpture. Aperture usually more than half of shell length, profile weakly convex in direction of growth. Parietal callus narrow. Suture distinct, but either well impressed or scarcely impressed. Apex acute. Length to about 25 mm.

Mantle not reflected over outer lip of shell, with triangular projections in two groups, columellar-parietal (C) and left posterior (P).

Penial complex: Preputium shorter than penial sheath. Penial sheath bipartite, with glandular distal portion and muscular proximal portion. Glandular distal portion usually longer than muscular portion, and of far greater bulk, widened abruptly at proximal end, and tapered gradually to preputium. Within glandular portion a muscular tube fluted lengthwise. The proximal muscular portion may be slightly enlarged at its proximal end. Penis shorter than sheath as a whole, but longer than proximal muscular portion, muscular throughout its length. It tapers from a broader proximal end to a narrow, simple tip. Sarcobelum massive. Vas deferens between paragonoporal angle and penial sheath shorter than preputium.

Penial retractor muscles inserted on ends of penial sheath, with no cross-connections or multiple insertions.

Distribution: Seven species from southeastern Alaska through Canada and most of the United States, but not as far north as *Physa* (Fig. 10). *Physella gyrina* has recently been introduced into Ireland (Anderson, 1996).

Comparisons: In the reproductive system, *Physella* is most like *Archiphysa*, differing by the bursal duct, that is thin-walled as in most Physinae, and leaves the bursa on its distal end. The shells are of the subovoid form usual in Physinae, not obovate as in *Archiphysa*.

Fig. 184. *Physella globosa*, p. 185. Tennessee, Greene County: mouth of Nolichucky River. Copied from Haldeman (1840-1845, *Physa* pl. 5, fig. 11). Length of life-size figure, 6.7 mm.
Figs. 185-186. *Physella microstoma*, p. 187. All figures copied from Haldeman (1842-1845).

Referred species:

Physella ancillaria (Say, 1825); TL Delaware River, near Easton [40º41'18"N, 75º13'16"W], Northampton County, Pennsylvania. Great Lakes region to New England, New York, and Pennsylvania.

>*subarata* Menke, 1830; TL near Cincinnati [39º06'N, 84º31'W], Hamilton County, Ohio.

>*fragilis* Mighels, *in* Mighels & Adams, 1842; TL Monmouth [44º14'19"N, 70º02'10"W], Kennebec County, Maine.

=*ampularia* "Say" Hayden, 1859; error for *ancillaria* Say, 1825.

>*subrotunda* Sowerby II, 1873; TL "North America."

Physella columbiana (Hemphill, 1890); TL Columbia River, Astoria [46º11'17"N, 123º49'48"W], Clatsop County, Oregon (Fig. 8). Probably extinct.

>*columbella* "Hemphill" Keep, 1904; error for *columbiana*.

Physella globosa (Haldeman, 1841); TL mouth of Nolichucky River, Greene County, Tennessee. Fig. 184

Physella gyrina (Say, 1821); TL Boyer Creek, Pottawatomie County, Iowa. Southeastern Alaska and Canada over much of the United States.

>*elliptica* Lea, 1834; no locality.

>*crassulus typica* Beck, 1838; TL Missouri River.

>*aurea* Lea, 1838; TL Hot Springs [37º59'58"N, 79º49'55"W, 2238 ft], Bath County, Virginia.

>*sayi* Tappan, 1839; TL Lake Pipin, Franklin Township, Portage County, Ohio.

>*margarita* Lesson, 1840; TL Newfoundland, Canada.

>*concolor* Haldeman, 1841; TL "Oregon," *i.e.*, Oregon Territory of that time.

>*hildrethiana* Lea, 1841; TL lake in Illinois.

>*troostensis* Lea, 1841; TL near Nashville [36º09'57"N, 86º47'04"W, 440 ft], Davidson County, Tennessee.

>*cylindrica* De Kay, 1843; TL Red Creek, Wayne County, New York.

>*fragilis* De Kay, 1843; TL West Point [41º23'29"N, 73º57'23"W], Orange County, New York. Published in synonymy of *aurea* Lea, 1838.

>*obesa* De Kay, 1843; TL Mohawk and Hoosic Rivers, Rensselaer County, New York.

>*troostiana* Lea, 1844; emendation of *troostensis* Lea, 1841.

>*virginea* Gould, 1847; TL Mountain Lake [37º47'17"N, 122º28'12"W], San Francisco, California.

>*bullata* Gould, 1855; TL Osoyoos Lake, British Columbia-Washington.

>*triticea* Lea, 1856; TL Shasta County, California.

>*gabbi* Tryon, 1863; TL Mountain Lake [37º47’17”N, 122º28’12”W], San Francisco, California.
>*altonensis* Lea, 1864; TL Alton [38º53’26”N, 90º11’03”W], Madison County, Illinois.
>*blandi* Lea, 1864; TL California, no precise locality.
>*crocata* Lea, 1864; TL LaFayette [34º42’17”N, 85º16’55”W], Walker County, Georgia.
>*febigeri* Lea, 1864; TL Logan County, Ohio.
>*hawni* Lea, 1864; TL Verdigris River, Kansas.
>*nicklini* Lea, 1864; TL Callaghan [37º48’43”N, 80º04’28”W], Alleghany County, Virginia.
>*nuttalli* Lea, 1864; TL “Lewis’ River, Oregon,” *i.e.*, Snake River, Idaho.
>*saffordi* Lea, 1864; TL Lebanon [36º12’29”N, 86º17’28º] Wilson County, Tennessee.
>*smithsoniana* Lea, 1864; TL Loup River, Nebraska.
>*venusta* Lea, 1864; TL near Fort Vancouver [45º37’32”N, 122º39’25”W], Clark County, Washington.
>*warreniana* Lea, 1864; TL Loup River, Nebraska.
>*whitei* Lea, 1864; TL LaFayette [34º42’17”N, 85º16’55”W, 823 ft], Walker County, Georgia.
>*ampullacea* Gould *in* Binney, 1865; new name for *bullata* Gould, 1855, preoccupied.
>*cooperi* Tryon, 1865; TL spring in Crane Lake Valley (Crane Lake is now Cowhead Lake), Modoc County, California.
>*diaphana* Tryon, 1865; TL Oakland [37º48’16”N, 122º16’11”W], Alameda County, California.
>*malleata* Tryon, 1865; TL “Hell Gate River, Oregon,” most likely Columbia River in northeast Washington.
>*occidentalis* Tryon, 1865; TL Umpqua River, Oregon.
>*propinqua* Tryon, 1865; TL Jordan Creek, Owyhee County, Idaho.
>*coniformis* Tryon, 1866; TL Humboldt River, Nevada.
>*oleacea* Tryon, 1866; TL Bridgeport [34º56’51”N, 85º42’52”W], Jackson County, Alabama.
>*deformis* Currier, 1867; TL Grand Rapids [42º57’48”N, 85º40’05”W], Kent County, Michigan.
>*carltoni* Lea, 1869; TL near Antioch [38º00’18”N, 121º48’17”W], Contra Costa County, California.
>*wolfiana* Lea, 1869; TL Hot Sulphur Springs [40º04’23”N, 106º06’47”W], Grand County, Colorado.
>*amygdalus* Sowerby II, 1873; TL “Texas.”
>*binneyana* Ancey, 1886; new name for *diaphana* Tryon, 1865, preoccupied.
>*elliptica var. decollata* Cockerell, 1888; TL close to White Earth Creek, Powderhorn [38º16’37”N, 107º05’43”W], Gunnison County, Colorado.
>*heterostropha var. heterostrophella forma brevis* Cockerell, 1889; TL Westcliffe [38º08’05”N, 105º27’55”W, 7888 ft], Custer County, Colorado.
>*heterostropha var. heterostrophella forma elongata* Cockerell, 1889; TL Westcliffe [38º08’05”N, 105º27’55”W, 7888 ft], Custer County, Colorado.
>*staffordi* “Lea” Paetel, 1889; error for *saffordi* Lea, 1864.
>*albofilata* “Ancey” Sampson, 1894; TL West Leatherwood Creek, Eureka Springs [36º24’04”N, 93º44’16”W], Carroll County, Arkansas.
>*smithi* F. C. Baker, 1919; TL Largest Teller Lake (now simply Teller Lake), sec. 12, T. 2 S., R. 74 W. [39º53’24”N, 105º36’50”W], Gilpin County, Colorado.
>*smithiana* F. C. Baker, 1920; new name for *smithi* F. C. Baker, 1919, preoccupied.
>*lordi utahensis* Clench, 1925; TL Utah Lake 2 miles south of Lehi, Utah County, Utah; Holocene.

>*goodrichi* Clench, 1926; TL South Fork of Powell River, Big Stone Gap [36º52'54"N, 82º44'50"W], Wise County, Virginia.

>*johnsoni* Clench, 1926; TL Middle spring, Hot Sulphur Springs, Banff [51º10'N, 115º34'W], Alberta, Canada.

>*gyrina byersi* Crabb, 1927; *nomen nudum*.

>*bayfieldensis* F. C. Baker, 1928; TL Pike Creek, near Bayfield, Bayfield County, Wisconsin.

>*chetekensis* F. C. Baker, 1928; TL Moose Ear Creek, between Taber and Chetek Lakes, Barron County, Wisconsin.

>*obrussoides* F. C. Baker, 1928; TL Hatchery Bay, Winnebago Lake, Oshkosh [44º01'29" N, 88º32'33" W], Winnebago County, Wisconsin.

>*plena* Clench, 1930; TL Reed Spring, Centerville [37º26'06"N, 90º57'30"W, 742 ft], Reynolds County, Missouri.

>*remingtoni* Clench, 1930; TL Round Spring [37º16'57"N, 91º24'27"W], 12 miles north of Eminence, Shannon County, Missouri.

>*salina* Clench, 1930; TL Brackish spring, Skeen's Ranch, Promontory, Box Elder County, Utah.

>*gouldi* Clench, 1935; TL Mouse River, 6 miles north of Towner, McHenry County, North Dakota.

>*jennessi athearni* Clarke, 1973; TL Horseshoe Lake, about 10 miles SE of Jasper, Alberta, Canada.

>*wrighti* Te & Clarke, 1985; TL Alpha Stream, Liard Hot Springs Provincial Park, British Columbia, Canada.

Physella hemphilli sp.n.; TL Coeur D'Alene Lake, Idaho (Fig. 8). Possibly extinct.

Physella microstoma (Haldeman, 1840); TL Kentucky and Ohio (no precise localities). Kentucky, Ohio and Tennessee. Figs. 185-186.

Physella vinosa (Gould, 1847); TL "Lake Superior region."

>*ancillaria var. magnalacustris* Walker, 1901; TL Frankfort [44º38'01"N, 86º14'04"W], Benzie County, Michigan.

Remarks: Whether application of the name *Physella* to this genus is valid depends on morphological study of the type species, *P. globosa*. I have seen no material of that form nor of *P. microstoma*, type species of *Physodon* and a probable member of the group, possibly even a synonym of *P. gyrina*.

Physella ancillaria (Say, 1825)

Fig. 183, Pl. 8, figs. 4, 6

Physa ancillaria Say, 1825:124.
Physella ancillaria (Say): F. C. Baker, 1928, 1:424, figs. 180, 183-184, 186, pl. 25, figs. 9-17, 22, 23.

Holotype: ANSP 20 895a. Delaware River near Easton [40º41'18"N, 75º13'16"W], Northampton County, Pennsylvania, *Benjamin Say*.

Name: Latin; probably in the sense of auxiliary, *i.e.*, additional to the species Say had described previously.

Diagnosis: A species of *Physella* with short, broad spire, and shouldered to rounded body whorl; shell polished, pale straw color, without strong axial sculpture. Length to about 20 mm.

Description: Penial complex: The muscular portion of the sheath is shorter than glandular portion of sheath (SPG), and far less bulky. The preputium is far shorter than the penial sheath as a whole, and bears a preputial gland on its posterior face. Within the preputium, the sarcobelum (SAR) is elongate, produced to a narrow tip, without papilla. The penis tapers gradually from a swollen head to a simple end, without any swelling or specialization of the

tip. The vas deferens between the paragonoporal angle (APG) and the penial sheath is far shorter than the sheath as a whole, about equal in length to the muscular portion (SPM). Penial retractor muscles are inserted on the ends of the penial sheath.

Distribution: Southern Quebec and New Brunswick; Wisconsin to New York and New England, south to Ohio and Pennsylvania; perhaps to the Potomac River, Virginia. The northern and western range is given in irreconcilable ways by various authors.

Localities and material examined:

MINNESOTA, Crow Wing County: Edna Lake, sec. 3, T.135 N., R. 29 W., 6-VII-1992 (T92-701) (**M)**. Round Lake, sec. 2, T. 134 N., R. 29 W., 6-VII-1992 (T92-608) (**M**.).

MAINE, Waldo County: Lake Winnecook, Unity, *S. S. Berry*, 16-IV-1910 (SSB 2547).

MASSACHUSETTS, Nantucket County: South end of North Head of Long Pond, 17-VII-1948 (T48-1803). Miacomet Pond, 25-VIII-1952 (T52-4104).

CONNECTICUT, Windham County: Roseland Lake, Woodstock, *E. H. Jokinen*, 1979 (multiple collections) (**M**.).

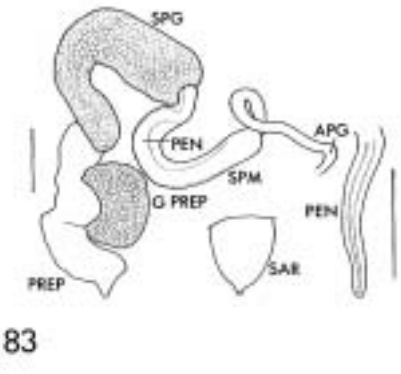


Fig. 183. *Physella ancillaria*. Connecticut, Windham County: Roseland Lake. Penial complex, lateral view, and sarcobelum and tip of penis of same specimen. Scale 1 mm. APG, paragonoporal angle; G PREP, preputial gland; PEN, penis; PREP, preputium; SAR, sarcobelum; SPG, glandular portion of penial sheath; SPM, muscular portion of penial sheath.
Copied from Taylor & Jokinen (1985).

Remarks: Only scanty information, and scarcely any preserved material, has been available. Even the geographical range is quite uncertain.

Physella gyrina (Say, 1821)

Pl. 9, fig. 8; Pl. 11, figs. 1-5

Physa gyrina Say, 1821:171. Binney, 1865:77, fig. 130. Clampitt, 1970:114 ff., fig. 4; Iowa; ecology, life history.
Physella gyrina (Say): F. C. Baker, 1928(1):449, fig. 196; pl. 27, figs. 30-35, 37-40; pl. 28, figs. 1, 5, 6.

Holotype: ?ANSP 20 968a. Boyer Creek, Pottawatomie County, Iowa, *Thomas Say*, 1819-1820.

Name: Greek *gyrinos*, tadpole.

Diagnosis: The shell is roughly ovoid, and attains a length of up to 25 mm. It varies in outline from high-spired to low-spired, or even nearly globose, with whorls rounded or shouldered, and generally a shallow suture. Usually the crescentic microsculpture is conspicuous. As in all species of wide distribution found in a variety of habitats, the shell characters are variable.

Distribution: Temperate and sub-Arctic North America. Southern Alaska and northwestern Canada (but not in the extreme north) east and southeast to central Labrador [on advice from J. E. Maunder], western New England and the vicinity of New York City; south to central California, Nevada, Utah, and Colorado; to the central Great Plains in eastern Kansas and eastern Oklahoma; east to the southern Appalachian Mountains. Southward at higher elevations in discontinuous areas on the Mogollon Plateau and White Mountains, Arizona; Jemez, San Juan, Sangre de Cristo, and Zuni Mountains, New Mexico.

Habitat: Lakes, ponds, streams, ditches, and marshes. Although the species is found in a variety of habitats, in the southern parts of the range where *Haitia mexicana* is found close by, the two species show segregation by habitat: *Physella gyrina* is ordinarily in ponds and marshes, and *H. mexicana* in flowing water.

Biology: As a widespread, common species *Physella gyrina* has been the subject of numerous studies.

In northwestern Iowa Clampitt (1970) studied comparative ecology of *Physella gyrina* and *Haitia integra* (revised nomenclature) to elucidate differences in local distribution. Dense populations of *gyrina* were found in ponds, in rocky lake-shore areas, and in habitats of intermediate type, but always in shallow water. Growth and reproductive activity was greatest in the spring, there was considerable mortality in summer, and growth was slight during winter. Food is a wide variety of materials, determined chiefly by what can be scraped loose and ingested. *P. gyrina* can withstand high temperatures (35ºC, 40ºC) and desiccation longer than *H. integra*. Partly for this reason the lake species *H. integra* is excluded from ponds. Larger size and more rapid growth of *P. gyrina*, with resultant need for atmospheric oxygen, may limit it in summer to very shallow water, while the smaller, slower-growing *H. integra* is not so restricted. Active dispersion of *P. gyrina* (field and laboratory) was also significantly greater than in *H. integra*.

Passive dispersion while the snails were floating or hanging on the surface film of a creek was observed by Marsh (1980) in Minnesota. Over 21 months the density of *P. gyrina* on the bottom averaged 1 417/m^2, reaching a maximum of 9 256/m^2. Highest stream drift occurred under normal stream flow conditions, and was interpreted as a behavioral response to crowding. The rate was calculated at 533 000 individuals per m^3/sec, "far in excess of previously reported drift rates for any mollusc."

Exceptional abundance of *P. gyrina* was studied near Decatur, Illinois, by Agersborg (1930, 1932) and by Agersborg & Downer (1931) in the effluent of a corn products manufacturing plant. A nearly constant temperature of 29ºC was maintained in the flow through the winter. Organic wastes (sugar and some starch) supported an abundant but species-poor growth of flora and fauna. The fungus *Sphaerotilus natans* was the food of *P. gyrina*, that in these exceptional conditions swarmed so as to cover the bottom of the ditch in many places. Shut-down of the manufacturing plant in May, 1929, returned the ditch water to ambient temperature, when the fungus practically ceased to grow and *Physella* nearly disappeared. Reproduction continued throughout winter under the summer-like artificial conditions. As a whole the fauna and flora of the ditch was poor, due to abnormally high temperature, the concentration of organic wastes, and the swift current. *P. gyrina* was one of the dominant Metazoa and only mollusc.

Similar effects on population dynamics were found by Sankurathri & Holmes (1976), who studied *P. gyrina* in Lake Wabamun, Alberta, in the effluent and near the intake of a power plant. In the warm effluent water rate of development of eggs and growth of snails was greater than near the intake; reproductive activity was continuous year-round. Eggs of *P. gyrina* do not survive prolonged laboratory exposure to temperature of 5ºC, and the species is maintained in winter by mostly immature and some mature snails in the natural environment near the intake. Oviposition occurred from May to September, when water temperatures reached 10-12ºC.

In southeastern Michigan *P. gyrina* has been the subject of two Ph.D. dissertations in the University of Michigan. Dawson (1911) studied local distribution, mucous thread-spinning, food, respiration, and behavior. She found that dense submergent vegetation precludes the species, and that an optimum pond habitat is one that dries sufficiently to kill pond weeds but has a dense enough substratum so that the snails can survive buried. "If a pond has no clay in its bed and is subject to drying, *Physa* is likely to die off with the pond weeds

because it but rarely forms a mucous epiphragm" (p. 38).

DeWitt (1954a, b, c, 1955) studied ecology, life history and growth of *P. gyrina*. Field observations in a permanent and temporary pond showed different life histories, correlated with available water. "In a permanent pond in southern Michigan, oviposition occurred in the spring when water temperatures reached 10 to 12ºC. The adult population died shortly thereafter. Snails born in the spring may reach sexual maturity that fall, but most oviposition is delayed by low temperatures until the following spring. Within the Scio population a shell length of seven mm was determined to be the size below which snails are believed to be sexually immature. Those individuals seven or more millimeters in length are capable of ovipositing under favorable environmental conditions. The life span of individuals in the field is from twelve to thirteen months. The life history of *P. gyrina* in a permanent pond 300 miles north of the above-mentioned habitat differed only in that oviposition took place three to four weeks later in the spring. Temporary ponds, located in southern Michigan, are usually dry from mid-June until November. Estivation forced upon *P. gyrina* living in such habitats delays growth, and the snails rarely attain sexual maturity by the fall of the year in which they hatch. The time to reach maturity the following spring is dependent upon the length of estivation. If the dry period is unusually long, the snails may overwinter a second year. Thus the life span in such situations may be considerably longer than in permanent ponds" (DeWitt, 1955:44).

In the state of Washington McNeil (1963) studied winter survival of snails in irrigation canals of the Columbia Basin. *Physella gyrina* (as *Physa propinqua*) is left stranded in numbers when the canal waters are withdrawn after irrigation season. None survived overwintering on dry culvert walls (in contrast to the associated *Lymnaea*), confirming observations in Michigan by Dawson (1911). In pans containing water, earth and rock, simulating a canal bottom, *Physella* survived; although in far fewer numbers than *Lymnaea* when the pans froze completely in brief cold spells.

Schistosome dermatitis in Cultus Lake, southern British Columbia, led to a study of the two species of vector snails by Howard & Walden (1965). They studied the lake fauna using SCUBA, thus making "it possible to observe snail populations directly at all water depths and to study migration, breeding habits and habitat preferences." *Physella gyrina* (as *Physa ampullacea, P. coniformis*, and *P. occidentalis*) was found from the surface to 50 ft depth. The life span is about 13-16 months. Even when water temperature was still low in February-March, the snails begin to disperse from the preferred substratum type; breeding began almost immediately and apparently continues for most of the year, for small juveniles were found in samples collected from December through February. No migration toward shore is evident; egg masses are laid at depth. Dermatitis was caused in Cultus Lake partly by cercariae "of the *C. physellae* type" from *Physella gyrina*.

Physella hemphilli sp.n.

Pl. 9, fig. 5

Distribution Map, Fig. 8

Physa heterostropha var. brevispira Lea: Hemphill, 1890:19.

Holotype: CAS 116 331, paratypes 114 824, 114 825. Idaho, Kootenai County: Coeur D'Alene Lake, *Henry Hemphill*.

Name: For Henry Hemphill (1830-1914).

Diagnosis: Shell ovoid, with short spire only 10-15% of length, less than 8 mm long,

yellowish-tan, with polished surface and sculpture of fine axial striae.

Description: The shell is ovoid with a short, obtusely pointed spire, shallow suture, and a broad, ovate-pyriform aperture more than 85% of shell length. The surface is polished, yellowish-tan, with axial sculpture of numerous, irregularly spaced striae. Microsculpture, that may be evident only near the suture, consists of spiral series of short, raised ridges. At the narrowly rounded anterior end, shortly within the aperture, there is usually a white callus spreading from the white columella. The outer lip is not thickened. The parietal callus is a thin wash, narrow, with no color contrast with the rest of the shell. The columellar plait is white and prominent.

Localities and material examined: Coeur D'Alene Lake, *H. Hemphill*: CAS 114 825 (formerly H. Hemphill 6 788, five specimens); CAS 114 824, from Stanford University (15); Hemphill's label reads *"Physa brevispira* Lea." Same locality, *L. B. Elliott, ex B. Shimek*: MCZ uncat. (six). These differ from the type series by having a dull rather than glossy surface, pale tan rather than pale yellow brown color, body whorl with a tendency to shouldering, and coarser sculpture.

Remarks: The broad spire and polished shell surface are reminiscent of the east American *Physella ancillaria*, but the surface sculpture and larger aperture distinguish the new species.

The two series, one directly from the Hemphill collection, and the other from Stanford University, agree precisely in all details of color, texture, size, and surface dirt, and are surely part of one sample. The disparity in number of specimens (15 compared to five) reflects the value that Ida Shepard Oldroyd of Stanford University placed on her "curation" of Hemphill's material.

Ultraphysella g.n.

Type species: *Ultraphysella sinaloae sp.n.*

Name: Latin *ultra*, beyond, and *Physella*; advanced beyond *Physella*.

Diagnosis: The shell has a flattened whorl outline, and characteristic dense microsculpture of spirally arranged arcs and fine axial growth lines. The reproductive system is similar to that in *Physella*, with a slender proximal muscular portion of the penial sheath, and a longer and far more bulky distal glandular portion. The flagelliform penis is longer than the muscular portion of the sheath, and is unique in the family by the specialized tip of the penis: the tip is narrowed, and within it the penial canal is enlarged.

Distribution: The single species is known only in Sinaloa and Nayarit, northwestern Mexico.

TABLE 48
Measurements and descriptive statistics of shells of Physella hemphilli *type series (CAS 114824, 114825). Measurements to nearest .064 mm. N = 19*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.66	5.91	.888	4.62	.695	3.32
Range	5.31-7.68	4.86-7.04	.85-.92	4.03-5.50	.54-.76	3 - 3 $^1/_2$
S.D.	.603	.545	.020	.406	.045	
S.E.	.138	.125	.005	.093	.010	

Ultraphysella sinaloae sp.n.

Figs. 187-191, Pl. 9, fig. 1
Distribution Map, Fig. 15

Holotype: CAS 146096. Mexico, Sinaloa: pool at road 2.5 mi from Villa Unión toward Siqueiros, 23º13.4'N, 106º12.5'W, 21-I-1971 (T71-1001).

Name: from the locality.

Description: The shell is narrowly ovoid with a short, acute spire and distinct but not incised suture. The aperture is narrowly ovate-pyriform, commonly flattened on the outer side, 65-75% of shell length. The surface is dull yellow-brown, with microsculpture of fine axial growth lines and closely spaced, spiral series of fine raised elements of short threads either straight or convex toward the aperture, giving a silky texture. The parietal callus is a thin wash. Within the aperture the columellar plait is thin and distinct.

Most shells had either an eroded spire or an encrusted spire, precluding all measurements of adults. In four half-grown specimens of sample T71-2003, 4-4 1/4 whorls, measurements ranged as follows:

	L	LPer	LPer/L	W	W/L
Mean	7.49	5.28	.705	4.29	.578
Range	6.66-7.81	4.80-5.63	.67-.73	3.97-4.42	.57-.60
S.D.	.557	.356	.027	.216	.015

Two adults, in which a count of whorls was not possible, measured 14.6 mm in length, and over 16 mm (as restored).

Mantle projections are in two groups, columellar-parietal (C) and posterior (P); in shape they are narrow, elongate, round-tipped triangles, about three times as long as their basal width. C8, P5 in one representative specimen.

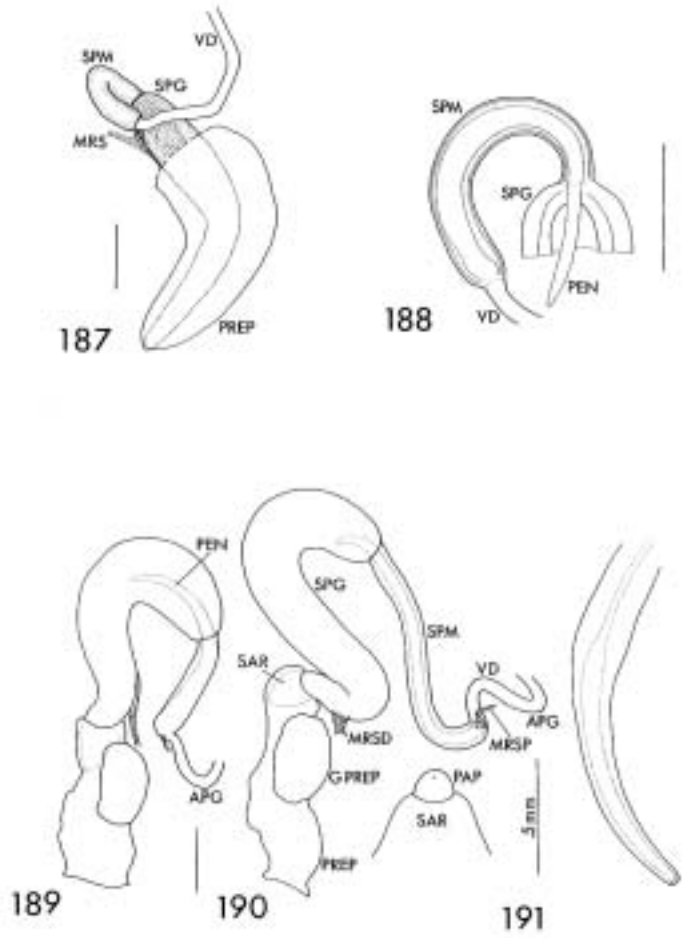
Penial complex: The proportions of the penial sheath are widely variable; the proximal muscular portion (SPM) may be as long as the glandular portion (SPG), or only half as long; the glandular portion is a bulky, sausage-shaped structure, far larger in volume than the muscular portion. The penis is long and flagelliform, longer than the muscular portion of the sheath, with a gradually narrowed tip. Within the tip, the penial canal is expanded, and gradually narrows to the terminal opening. The vas deferens between the paragonoporal angle (APG) and the penial sheath is half or less than half the length of the muscular portion of the sheath (SPM). Penial retractor muscles are inserted on the ends of the sheath.

Localities and material examined:

MEXICO, Sinaloa: Pool in culvert beneath road from Villa Unión to Siqueiros, 2.5 miles (4.2 km) from Mex. 15 in Villa Unión, 23º13.4'N, 106º12.5'W, 21-I-1971 (T71-1001; type locality)(**M**). Stream at Mex. 15, 2.5 mi NW Rincón Verde, 22º55.7'N, 105º49.7'W, 22-I-1971 (T71-1202). Marshy pool beside Mex. 15, 4.3 miles (7 km) S Ojo de Agua de Palmillas and 24.7 miles (41 km) S Escuinapa, 22º33.6'N, 105º35.0'W, 29-I-1971 (T71-2003).

Nayarit: Río de Palillo, El Palillo, 21º38.3'N, 105º8.4'W, 24-I-1971 (T71-1502)(**M**). Borrow-pit pond beside Mex. 68D, 0.7 km E of exit to San Pedro Lagunillas, 0.1 km E of km 16 post, 21º12.3'N, 104º45.1'W, 17-IX-1987 (T87-1001)(**M**).

Remarks: In all four series collected the dense microsculpture and flattened whorls are usually but not always present. These features may be found also in the widespread and variable *Physella gyrina*, but are rare in that species.



Figs. 187-191. *Ultraphysella sinaloae*, p. 192. Mexico, Sinaloa: between Villa Unión and Siqueiros (type locality). Some structures are seen in transparency. Scale 1 mm except for two insets. 186, penial complex with preputium extruded; 187, proximal part of penial complex; 188, lateral view of penial complex; 189, lateral view of penial complex; 190, detail of sarcobelum and detail of tip of penis from that specimen, showing enlargement of penial canal within. Scale 1 mm except as noted. APG, paragonoporal angle of vas deferens; G PREP, preputial gland; MRS, retractor muscle of penial sheath; MRSD, distal retractor of penial sheath; MRSP, proximal retractor of penial sheath; PEN, penis; PREP, preputium; SPG, glandular portion of penial sheath; SAR, sarcobelum; SPM, muscular portion of penial sheath; VD, vas deferens.

Incertae Sedis

"Physa" hordacea Lea, 1864

Distribution Map, Fig. 8

Physa hordacea Lea, 1864:116; Lea, 1867:176, pl. 24, fig. 102. Taylor, 1960:64, pl. 3, figs. 1-4. Starobogatov & Budnikova, 1976:82; possibly a subspecies of *Sibirenauta elongata* (Say).
Bulinus hordaceus, Lea: Tryon, 1865:172.
Aplexus hordaceus Lea: J. G. Cooper, 1867:20.
Physa venusta var. hordacea Lea: J. G. Cooper, 1870:97.
Physa (Aplexa?) hordacea Lea: Dall, 1905:103, 107.
Aplexa hordacea (Lea): Walker, 1918:116; "its generic position still remains to be definitely settled by an examination of the animal."
Sibirenauta hordacea (Lea): Starobogatov, 1970:246.
Physella (Physella) hordacea (Lea): Te, 1980:183.

Types: USNM 170 764, holotype and 111 paratypes, collected by *Sir George Simpson*, 1841; 3 paratypes MCZ 55 263, 2 paratypes MCZ uncat.; 7 paratypes CMN 55 081. ANSP 123 965, from the C. M. Wheatley collection, and labeled only "Oregon," is a series of probable paratypes. BMNH 41.2.18.124-174 are from the original collection, but not paratypes.

Type locality: Vancouver Island, Fort Vancouver [45º37'32"N, 122º39'25"W], Clark County, Washington.

Name: Latin *hordeaceus*, of barley, from *hordeum*, barley; presumably indicating the shell is like a barley-grain.

Diagnosis: The shell is narrowly elongate-ovoid, with acute apex, and peritreme about 65-75% of shell length, attaining a length of 6 mm with 3 $^{1}/_{2}$ whorls. Surface texture is silky, with spiral microsculpture near the suture that may be well-developed over most of the body whorl. Profile of the spire is plane to slightly convex, with weakly convex whorls separated by a shallow suture.

Description: The shell is narrowly elongate-ovoid with a short spire, acute apex, and narrowly rounded anterior end. The aperture has a narrowly rounded anterior and acute posterior end. Its profile is weakly convex in the direction of growth, but not evenly so; the posterior third, posterior to the periphery, may be nearly straight to the suture, or evenly retractive. The inner margin consists of a gently convex parietal segment, distinct from the nearly straight columellar segment. The columella is thin and white, with a low fold clearly or barely evident. The parietal callus is a white wash, continuous between the ends of the aperture, expanded broadly adjacent to the columella. The spire whorls are weakly convex, separated by a distinct but shallow suture. The lateral profile of the spire is plane to slightly convex, evenly so to the acute apex. The shell surface is silky and shining, pale brown, with a narrow pale band at the suture. Surface sculpture consists of fine axial growth lines, and spiral series of irregular minute wrinkles. These wrinkles are either straight, or weakly convex in the direction of growth; they may be dense over the entire body whorl, or evident only near the suture.

A thick, brown apertural callus may be present within the outer lip, between the columella and posterior end of the aperture. In some specimens more than one callus may be evident.

Distribution: From the Columbia River southward in the Willamette River valley, Oregon.

Localities and material examined:

BRITISH COLUMBIA, Victoria District: Brayfast, Victoria; from Stanford University collection, probably from *Rev. G. W. Taylor* (CAS uncat., 20 specimens) [The locality could not be traced in July, 1989, despite efforts by the British Columbia Archives or Royal British Columbia Museum personnel].

WASHINGTON, Clark County: Vancouver Island, Fort Vancouver [45º37'32"N,

TABLE 49
Measurements and descriptive statistics of shells of Physa hordacea *from $^1/_2$ mile N Veneta, Lane County, Oregon (AGS 10 973). Measurements to nearest .064 mm. N =20*

	Length	LPer	LPer/L	Width	W/L	Whorls
Mean	6.36	4.42	.695	3.49	.549	3.50
Range	5.44-8.00	3.39-5.70	.62-.76	2.82-4.54	.518-.568	3 $^1/_4$-3 $^3/_4$
S.D.	.708	.547	.033	.422	.015	.18
S.E.	.158	.122	.007	.094	.003	.041

122º39’25”W], *Sir George Simpson, Hudson’s Bay Company*, 1841 (type locality).

OREGON, Lane County: One-half mile N of Veneta [44º02’56”N, 123º20’59”W] and about 3/4 mile S of Elmira, *H. E. Vokes, D. A. Myers*, 23-VII-1948 (AGS 10 973). Multnomah County: Small stream entering Willamette River 6 miles above Portland, *J. A. Allen*, 1912-1913 (ANSP 112 435, one specimen).

Habitat: That so few localities are known indicates that this species lived in a habitat not widely available. At two localities only it was found in numbers, probably in seasonal ponds or marshes formed by high water runoff along large streams: at Fort Vancouver, and near Veneta, Oregon. Construction of dams has eliminated the habitat along both the Willamette and Columbia Rivers, and along the lower Long Tom River near Veneta where the habitat was eradicated by construction of Fern Ridge Reservoir. The locality above Portland may have been close to such a seasonal pond, but in any case the growth of the city of Portland has destroyed suitable habitats in that area. “Brayfast, Victoria” remains a puzzle. Was “Brayfast” a collector? or a district in Victoria whose name has been lost? No seasonal ponds along large streams could have been found in the city. Was this a temporary introduction? And if so, whence? My attempts to find the species in western Oregon, southeastern Washington, Vancouver Island and the Sechelt Peninsula of British Columbia have been uniformly unsuccessful.

Remarks: In hope of obtaining information about the original locality and collection, I sought information about the itinerary of the collector. Sir George Simpson (1792?-1860) had an outstanding career in the Hudson’s Bay Company, rising to become one of the joint governors. He founded Fort Vancouver on the Columbia River, now the city of Vancouver, Washington. Simpson traveled around the world for pleasure in 1841-1842, leaving an entertaining account of his trip (Simpson, 1847), but without mention of molluscs. Simpson gave the shells he obtained at various places in the course of this journey, including Fort Vancouver, to Lady Katherine Douglas.

Lady Katherine Jane Douglas (d. 30 Sept. 1863) was the youngest daughter of Thomas Douglas, 5th Earl of Selkirk (1771-1820). She married Loftus Tottenham Wigram, Q.C., M.P. for Cambridge, 1850-1859, on 23 January 1849. The Earl of Selkirk had close ties with the Hudson’s Bay Company through establishment of a colony in the Red River Valley, in what is now Manitoba. This is evidently the link between Sir George Simpson and Lady Douglas, and indeed the reason why Simpson bothered to obtain shells in the first place. This almost casual collection provided what was one of the first samples from the Pacific Northwest (Carpenter, 1857a:192). Either directly from Lady Douglas, or from the British Museum, samples of the freshwater shells reached Isaac Lea.

Published reports of the species from localities other than those listed above are based on misidentifications. I have examined the specimens (UCM) reported from Whidbey Island, Washington, by Craig (1927:72) and Henderson (1929:153); they are immature *Physella gyrina* in my opinion. Similarly, the illustration by Clarke (1981:168, fig. 61) of a specimen from Vancouver Island, British Columbia, represents *P. gyrina*.