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D.W. Taylor,
Prof. (Retired) Ph.D.
(Eugene, Oregon, U.S.A.)

NEW DATA ON BIOGEOGRAPHY, CLASSIFICATION AND PHYLOGENY OF PHYSIDAE (GASTROPODA: HYGROPHILA)

Physidae – це родина прісноводних легеневих гастропод, яка включає близько 90-100 видів, котрі поділені на 23 роди, об'єднані у 7 триб та 4 класи. Дані морфологічні дослідження ведуть до відкриття багатьох нових параметрів. Деякі з них прогресивні, але є й ті, які відповідають певним критеріям для примітивних станів. Таким чином, можливо передбачити, що примітивні групи концентрувалися на Тихоокеанському узбережжі від Мексики до Коста Ріки, і розповсюдилися з цього регіону в інші частини світу.

Physidae, a world-wide family of freshwater snails with about 90-100 species, have been difficult to classify for some 200 years. Reasons are the lack of shell characters and lack of morphological study. Thus identifications based on shells are often at variance with those founded on morphology, and published information from most of the world is unreliable as to the species named.

Studies going beyond shell features began with the work by Möller [1], one of the first monographs of a mollusc species, illustrating the mantle projections in *Physa fontinalis*. Modern study began with description by Slugocka of the reproductive systems of the three species of Switzerland, including histological sections as well as gross morphology. Her conclusion [2:104] that the penis is a well-defined organ with characteristic shape in each species has not been valued sufficiently.

The family has been reclassified [3] 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 and other characters, many not recognized previously, has been possible only by the technique used in anesthetizing, fixing, and preserving. The basic procedure is 1, anesthetization with menthol. This reagent increases body turgor, so that often the preputium is extruded. 2, fixation in AFA (Lavdowsky's mixture: 10 ml formalin, 30 ml 95% ETOH, 60 ml distilled water, 2 ml glacial acetic acid); 3, transfer to 70% ETOH.

The two established subfamilies are divided into seven new tribes including 11 new genera, with diagnoses and lists of species referred to each. The simplest reproductive system in the family 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; (in) 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 tribes (Fig. 1). Superimposed on progressive changes in the penial complex are specializations unique to individual genera. Instances are the periostracal callus in *Ameancwta*; 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.

The characters defining all groups are morphological. Shell characters are nearly absent, except that Aplexinae in general have a steeper, more shallow suture than in Physinae. The many early Tertiary and Mesozoic fossils cannot be allocated to genera as now defined. Although the fossil record is thus of limited value, still it shows that distribution and size-range were greatly different in the past. On the basis of structural primitiveness, especially of prostate and radula, it is plausible that Physidae differentiated in the mid-Paleozoic from the earliest Hygrophila and their presumed opisthobranch ancestors.

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. Spawn of Physidae is most like that of Lymnaeacea amongst Hygrophila, but the prostate is of basically different structure, made up of follicles that each drain directly into the vas deferens, the most primitive condition in the Order. Spiral color bands and white streaks in the shell of *Mexinauta* recall those in Lencidae (Lymnaeacea), whereas the arrangement of the radular teeth in chevron-like rows of Physidae is like that of Chiliniidae. Physidae thus show affinities to various basal stocks of aquatic pulmonates; no clear-cut sister-group can be recognized. A dichotomous analysis of phylogeny, both of and within the family, is of dubious value.

Of 23 genera of Physidae, 17 occur in Pacific drainages of North and Central America; eight are 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 [4]. 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.

Preputial grand absent: PHYSINAE				PHYSINAE: Preputial grand present				
Penial sheath unipartite to Tripartite				Penial sheath unipartite		Penial sheath bipartite		
1.1. Stenophy- sini	Name uncertain <i>Afrophysa</i> <i>Stenophysa</i>							GRADE IV
Amecanautini	Name uncertain	Aplexini	Sibirenauta Aplexa Paraplexa	Physini	Physa Beringophysa	Physellini	Ultraphysella	GRADE III
	<i>Tropinauta</i> <i>Mayabina</i> <i>Mexinauta</i> <i>Amecanauta</i>		Amuraplexa		Laurentiphysa		Physella Archiphyse Utahphysa Costatella Petrophysa Chipaphysa	GRADE II
		Austrinautini	Caribnauta Austrinauta	1.2. Haiti- ini	Haitia			GRADE I

Interpretations of biogeography follow the methods of panbiogeography [5,6].

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.

Most species have a restricted range. Out of 55 with sufficiently detailed information for analysis, 25 are limited to a single 1°x1° 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. The following species are in precarious state or extinct: *Paraplexa ataxiaca* (France and Switzerland), *Haitia elegans* (Haiti), *Physa mirollii* (Italy), *Physella Columbians* and *P. hemphilli* (U.S.A.), genus uncertain *hordacea* (U.S.A.).

Some consequences of this study are unexpected. There is great 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 inappropriate name *Afrophysa* is based, is a species introduced from southern Brasil that is now called *Afrophysa brasiliensis*. The traditional *Aplexa hypnorum* of Europe is a composite of two species in two genera (*Aplexa hypnorum*, *Paraplexa ataxiaca*). Physidae are more diverse than Lymnaeidae, approaching Bulinidae and Planorbidae in numbers of genera, tribes and subfamilies.

Areas of study likely to prove rewarding in future are verification of species classification and ranges, especially in France, Russia, and Central and South America (exploration now in progress); studies of spawn, still unknown in most species; and refinement of inferred phylogeny.

Other features [31] 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.

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Тейлор Д.В. Новые данные биогеографии, классификации и филогении Physidae (Gastropoda: Hygrophila).

Physidae – это семейства пресноводных легочных гастропод, содержащие около 90-100 видов, которые разделены на 23 рода, объединены в 7 триб и 4 класса. Данные морфологические исследования ведут к открытию многих новых параметров. Некоторые из них прогрессивные, но есть и те, которые отвечают определенным критериям для примитивных форм. Таким образом, можно предположить, что примитивные формы концентрировались на Тихоокеанском побережье от Мексики до Коста Рики, и распространились из этого региона в другие части мира.

Taylor D.W. New data on biogeography, classification and phylogeny of Physidae (Gastropoda: Hygrophila).

Physidae are a family of freshwater pulmonate gastropods with about 90-100 named species, newly divided among 23 genera in seven tribes and four clades. Morphological studies resulted in discovery of many new characters, some of them progressive, yielding criteria for primitive versus advanced states. Thus it is possible to assert that primitive groups are concentrated on the Pacific coast from Mexico to Costa Rica, and to trace the spread of lineages from this region to other parts of the world.