

"River Amur, coll. Goshkevich, 1859" (2 specimens). These three samples belong in our opinion to 3 different species. Majority of authors, more recently Dvoriadkin [1980]; Bogatov and Zatravkin [1991], regarded "Orig. No. 3" as the main type series of *P. centrifugus*. Moreover, Bogatov and Zatravkin [1991] designated a specimen from this series as "lectotype". However, the third series was not mentioned in original Westerlund's description and, correspondingly, it does not belong to the type series of the species. It is evident that the name *Anisus centrifugus* cannot be applied to Amurian species and we propose to substitute it by *Anisus centrifugops* *nom. nov.* pro *Anisus centrifugus* Bogatov et Zatravkin, 1991 ("1990"), p. 142, fig. 32 e-z, non *Planorbis centrifugus* Westerlund, 1897. Accordingly, the "lectotype" of *A. centrifugus* designated by Bogatov and Zatravkin becomes the holotype of *A. centrifugops*. The "Orig. No. 1" belongs to *A. stroemi*. The "Orig. No. 2" contains species differing from all other Siberian species and having no other

names. It differs sharply from *A. stroemi*, *A. kamschaticus*, and *A. centrifugops* (Fig. 3, F) by higher rate of increasing of whorls and must be regarded as true *A. centrifugus*. We fix the application of the name by designation of lectotype of *Planorbis centrifugus* Westerlund, 1897 (Fig. 3, G).

Lectotype of *A. (G.) centrifugus* (Fig. 3, F) has dimensions (in mm): SW — 6.1, SH — 1.9, HA — 3.0, WA — 2.5, WU — 2.0, WTLbas — 2.2, NW — 4.45.

A. centrifugus is distributed in the Kolyma drainage area (except its upstream parts) and lives in permanent waterbodies on plants and ground.

Holotype of *A. (G.) centrifugops* (Fig. 3, E) has dimensions (in mm): SW — 5.9, SH — 2.0, HA — 2.5, WA — 2.2, WU — 2.3, WTLbas — 2.2, NW — 4.6.

A. centrifugops is distributed in the Amur drainage area (from uppermost reaches to the mouth) and in Primorye Region. It lives in permanent and semipermanent waterbodies on plants and ground.

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Composition and phylogenetic relations of the Cochlicellidae (Gastropoda, Pulmonata)

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Genera *Monilearia*, *Prietocella* *gen. nov.* and *Cochlicella* form a natural taxon — the Cochlicellidae family. Illustrated anatomical descriptions of *Monilearia phalerata* (Webb et Berthelot), *M. lemniscata* (Webb et Berthelot), *Prietocella barabara* (Linnaeus) and *Cochlicella acuta* (Müller) are given. On the ground of comparative and functional analysis of the organisation of reproductive apparatuses the possible ways of the evolution of the Cochlicellidae are reconstructed. In part, drastic enough differences in the structure of both female and male divisions of *Prietocella* and *Cochlicella* are connected with the change of method of stimulation of a partner before mating. Phylogenetic scheme of the cochlicellid evolution is suggested. Family Cochlicellidae is placed in the superfamily Xanthonychoidea.

Состав и филогенетические связи Cochlicellidae (Gastropoda, Pulmonata)

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Роды *Monilearia*, *Prietocella* *gen. nov.*, *Cochlicella* образуют естественный таксон — семейство Cochlicellidae. Приведены иллюстрированные анатомические описания *Monilearia phalerata* (Webb et Berthelot), *M. lemniscata* (Webb et Berthelot), *Prietocella barbara* (Linnaeus) и *Cochlicella acuta* (Müller). На основании сравнительного и функционального анализа строения репродуктивного аппарата реконструированы возможные пути эволюции Cochlicellidae. В частности, довольно резкие различия в строении как женского, так и мужского отделов полового аппарата *Prietocella* и *Cochlicella* связаны, в конечном счете, со способом стимуляции партнера перед спариванием. Предлагается филогенетическая схема морфологической эволюции кохлицеллид. Cochlicellidae помещены в надсемейство Xanthonychoidea.

The genus *Cochlicella* has been traditionally placed and is still often placed in the subfamily Helicellinae of the family Helicidae, in spite of the fact that the highly conical shell is not characteristic of xerophilous Hygromiidae, and peculiarities of the sexual apparatus were revealed as far back as the middle of the

19th century [Moquin-Tandon, 1855; Schmidt, 1855]. Significant anatomical differences of *Cochlicella acuta* (Müller, 1774) from other "Helicellinae" gave the ground for separation of a subfamily Cochlicellinae within Hygromiidae [Schileyko, 1972]; later this decision has been supported by Forcart [1976].

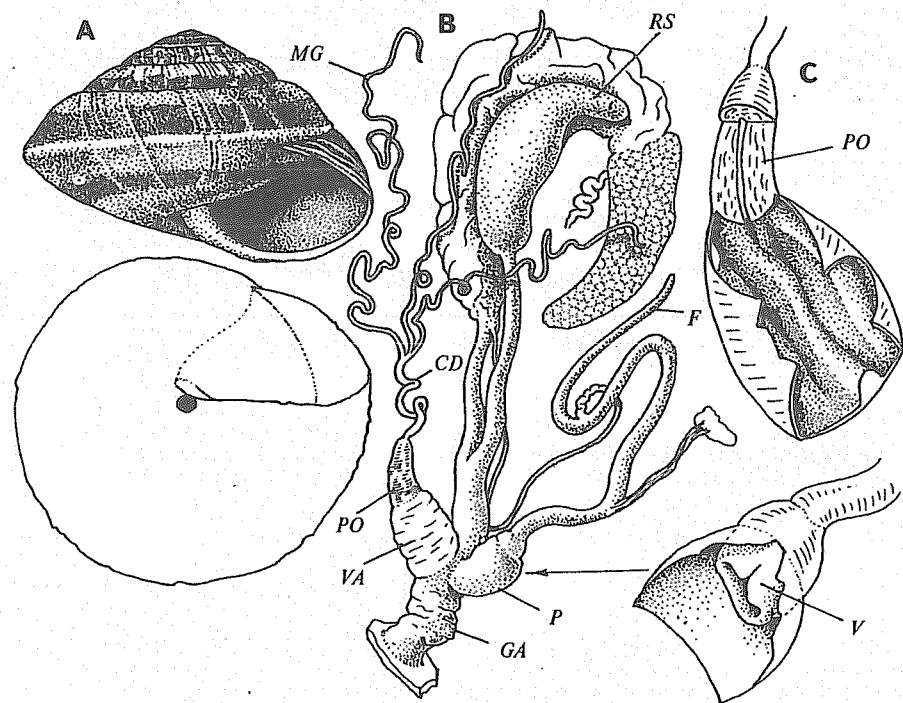


FIG. 1. *Monilearia phalerata* (Webb et Berthelot, 1833). A — shell; B — sexual apparatus and opened penis; C — inner structure of vaginal appendix. CD — common duct of mucus glands; F — flagellum; GA — genital atrium; MG — mucus gland; P — penis; PO — propulsatory organ; RS — reservoir of spermatheca; V — verge; VA — vaginal appendix.

РИС. 1. *Monilearia phalerata* (Webb et Berthelot, 1833). А — раковина; В — половой аппарат и вскрытый penis; С — внутреннее строение вагинального придатка; CD — общий проток слизистых желез; F — флагеллум; GA — половой атриум; MG — слизистая железа; P — penis; PO — пропульсаторный орган; RS — резервуар семеприемника; V — папилла пениса; VA — вагинальный придаток.

Hesse [1911] dissected *Monilearia phalerata* (Webb et Berthelot, 1833) and uttered an opinion on taxonomic relations between *Cochlicella* and *Monilearia*. At the same time, Hesse had no doubt in assigning both genera to Helicidae sensu Hesse.

Subsequently, Nordsieck [1987], admitting the relations between *Cochlicella* and *Monilearia*, placed them in the tribe Cochlicellini of Monachinae (Hygromiidae); the diagnosis of the tribe, after Nordsieck, being as follows: "Eine Appendicula, mit zerteilten Anhang, Drüsen des Reizapparatus fehlend; Ommatophorenretraktor neben den Endwegen verlaufend" [op. cit.: 32]. In our point of view, the placement of Cochlicellini in Monachinae is purely formal, because the structure of vaginal appendices in members of these taxa is quite different.

Finally, Schileyko [1991a] advanced a hy-

pothesis on the origin of "*Cochlicella* (and *Monilearia*?) from some very ancient and fully extinct xanthonychoid ancestors whose various groups were widely represented on the northern shores of the Tethys." [op. cit.: 215], and expressed a conviction that in any case these taxa deserve the status of a separate family.

As one of the unique peculiarities of *Cochlicella acuta* and *C. conoidea* (Draparnaud, 1801) is specific inner structure of the penis (mainly the presence of calcareous envelope of the penial verge), Schileyko supposed that the question of taxonomic relations of *Cochlicella* will be clearer when the inner structure of the penis of *Monilearia* is known. However, in that time the author did not know the book by Prieto Sierra [1986], where the genus *Acalchlicella* has been established. Unfortunately, this book

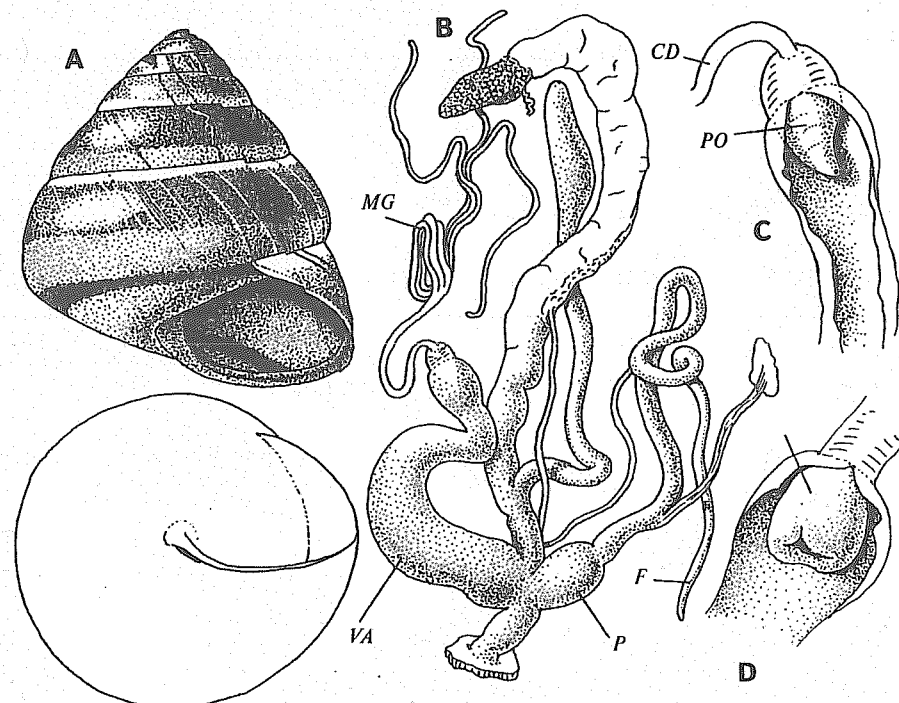


FIG. 2. *Monilearia lemniscata* (Webb et Berthelot, 1833). A — shell; B — sexual apparatus; C — inner structure of vaginal appendix; D — opened penis. Abbreviations as in Fig. 1.

РИС. 2. *Monilearia lemniscata* (Webb et Berthelot, 1833). А — раковина; В — половой аппарат; С — внутреннее строение вагинального придатка; D — вскрытый penis. Обозначения как на рис. 1.

is not a publication in the sense of International Code of Zoological Nomenclature, being a photocopy of thesis, which does not meet the requirements of Art. 8 (d) (II), (III) and Art. 9 (3). Therefore, the name *Acalchlicella* is unavailable.

As for connections amongst *Monilearia*, *Acalchlicella* and *Cochlicella*, their relationship is based on the presence of vaginal appendix in representatives of all three genera; to the top of the appendix the tubular slender gland(s) is attached, the latter consisting of one to three (four?) trunks which are sometimes fused at various distances from the apex of appendix [Hesse, 1911; Odhner, 1931]. Inner structure of the penis in the species of *Monilearia*, as it was mentioned above, is still unknown.

One of us (H.M.) has collected several specimens of two species of *Monilearia*, including the type species of the genus, in

April, 1988. After descriptions of species the discussion will be continued.

Genus *Monilearia* Mousson, 1872

Mousson, 1872: 39 (*Helix* sect.); Hesse, 1911: 161; Odhner, 1931: 81; Hesse, 1934: 31.

TYPE SPECIES — *Helix phalerata* Webb et Berthelot, 1833; by subsequent designation of Pilsbry, 1895.

DIAGNOSIS. Shell depressed to trochoidal, more or less angulate at periphery, with dark spiral bands. Embryonic whorls smooth, post-nuclear sculpture of radial striation; delicate spiral, incised, wavy striae at shell base. Aperture margins not reflexed or expanded. Umbilicus minutely open to nearly closed.

Flagellum long. Penis small, subglobose in appearance, containing a short closed verge

with central canal, without calcareous envelope. Highly muscled propulsatory organ with very narrow duct attached apically to thin-walled vaginal appendix; long, slender, tubular, trilobate gland opening in top of propulsatory organ. Genital atrium long.

Monilearia phalerata
(Webb et Berthelot, 1833)

(Fig. 1)

Webb, Berthelot, 1833: 325; Hesse, 1911: fig. 3 (reproductive anatomy); Odhner, 1931: 82, 88, Abb. 38 A, B (description of sexual apparatus and drawing of columellar musculature).

Three specimens: Grand Canary, 2 km S of Fataga, April 6, 1988.

Flagellum somewhat shorter than cylindrical epiphallus. Penis rather small, thin-walled. Internal canal of short verge wide, occupying central position inside verge. Penial retractor attached to epiphallus above penis/epiphallus junction. Elongate sac (vaginal appendix) with longitudinal folds on inner surface is attached to lower section of vagina opposite penis. Muscled propulsatory organ sits on apex of vaginal appendix; this organ represents thickening of basal portion of tubular gland, splitted into three branches at some distance above thickening. Basal portion of spermathecal shaft not enlarged. Reservoir of spermatheca voluminous, its upper end somewhat narrowed, demarcation between shaft and reservoir quite well expressed. Upper portion of vagina ("free oviduct") of nearly same length as lower one.

Monilearia lemniscata
(Webb et Berthelot, 1833)

(Fig. 2)

Webb, Berthelot, 1833: 317; Odhner, 1931: 82 (description of anatomy without drawing).

Two specimens: Gran Canaria, San Lorenzo, 5 km NW of Tafira, April 5, 1988.

Flagellum 1.5-2 times shorter than cylindrical epiphallus. Penis thin-walled, rather small. Canal of globose verge rather broad, occupying central position within organ. Penial retractor attached to epiphallus well above penis. Vaginal appendix long, with almost smooth inner surface. Basal muscled section of mucus gland (propulsatory organ) ovate-conical or pear-shaped, strongly separated off and deeply protruded into cavity of vaginal appendix. Common duct of mucus gland, as in *M. phalerata*, divided into three branches at rather long distance from its base. Basal portion of spermathecal shaft not enlarged. Reservoir of spermatheca somewhat narrowed, passing into shaft without clear boundary. Up-

per section of vagina longer than lower one approximately by two times.

For the comparison, we present also diagnoses of genera "*Acalchlicella*" and *Cochlicella*.

Prietocella
Schileyko et Menkhorst, gen. nov.

(Fig. 3)

Prieto Sierra, 1986: 231, 234 (*Acalchlicella*, unavailable name; type species - "*Acalchlicella barbara* (Draparnaud, 1801)"; by original designation).

TYPE SPECIES — *Helix barbara* Linnaeus, 1758.

DERIVATIO NOMINIS. The name is given in honour of our colleague Carlos Enrique Prieto Sierra, who has discovered highly interesting anatomical features of the type species of the genus.

DIAGNOSIS. Shell conical, radially striate, without peripheral angle. Umbilicus covered with reflexed columellar margin of aperture, other margins of aperture sharp and simple.

Flagellum very short. Penis voluminous, bulky, containing rather long cylindrical verge, lacking calcareous envelope. At upper portion of vaginal appendix there are three or four thickenings ("nodules"), in each of them one tubular gland opens; separate glands could be biramous. Genital atrium rather short.

[ДИАГНОЗ. Раковина коническая, радиально исчерченная, без периферического угла. Пупок закрыт колумеллярным краем устья, остальные края устья простые и острые.

Флагеллум очень короткий, Пенис объемистый, с довольно длинной цилиндрической папиллой, без известковой оболочки. В верхней части вагинального придатка располагаются три или четыре утолщения, в каждое из которых открывается трубчатая железа; отдельные железы могут быть двуветвистые. Половое атриум довольно короткий.]

REMARK. It is important to reveal what are the "nodules", occupying the top of vaginal appendix: whether these are simple local alveolar widenings or muscled propulsatory organs, corresponding to those of species of *Monilearia*. Judging by original description and drawing [Prieto Sierra, 1986: 233, fig. 6], the latter proposition seems to be more probable, and all further reconstructions are based on this assumption.

Cochlicella Ferussac, 1821

(Fig. 4)

Ferussac, 1821: 56 (Opinion 335); Schmidt, 1855: 41, Taf. X, Fig. 78, 79 (details of anatomy of *C. acuta* and *C. conoidea*); Schileyko, 1972: 39, fig. 7 (anatomy of *C. acuta*); Forcart, 1976: 139, Abb. 1 (anatomy of *C. acuta*).

TYPE SPECIES — *Helix conoidea* Draparnaud, 1801; by subsequent designation of Gray, 1847.

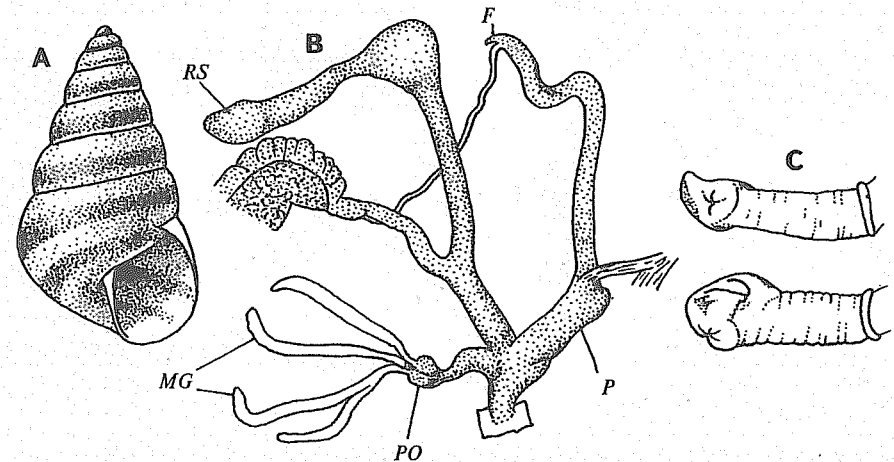


FIG. 3. *Prietocella barbara* (Linnaeus, 1758). A — shell; B — sexual apparatus; C — verge [after Prieto Sierra, 1986]. Abbreviations as in Fig. 1.

РИС. 3. *Prietocella barbara* (Linnaeus, 1758). А — раковина; В — половой аппарат; С — папилла пениса [по Prieto Sierra, 1986]. Обозначения как на рис. 1.

DIAGNOSIS. Shell elongate conical, with dark spiral bands or radial streaks, without peripheral angle. Embryonic whorls smooth, postembryonic ones radially striate, with elements of malleate sculpture; no spiral striation.

Flagellum very short. Penis voluminous, bulky, approximately cylindrical in shape. Penial verge consists of distal and proximal portions, with superficial groove. Verge surrounded by calcareous envelope. Rather short tubular gland enters subapically top of thick-walled vaginal appendix. No propulsatory organ. Gland simple or forked at upper end. Genital atrium very short.

DISCUSSION

We need to consider three problems. 1. Whether the genera *Monilearia*, *Prietocella* and *Cochlicella* comprise a taxonomic unit. 2. If so, what are phylogenetic relations of this taxon, and what is its rank. 3. What are interrelations between these genera within the taxon.

1. On the taxonomic unity

We are inclined to answer this question positively for reasons as follows. Shells of members of all three genera form a mor-

phological series from common hygromioid depressed shape to high-spined ones: *Monilearia phalerata* — *M. lemniscata* — *Prietocella barbara* — *Cochlicella acuta*. All other species of these genera fit this series. It is characteristic for all the species that there are 1-2 (it is probable, primarily 3) dark spiral bands, which could be sometimes represented by rows of spots.

The sexual apparatus bears more important and highly characteristic signs of similarity. The most eminent feature is the presence of more or less long vaginal appendix, to whose apex three slender tubular glands are attached. In the lower part these glands could fuse with each other, forming a common united duct. The base of the common duct could be somewhat swollen, which is the basis for the formation of a muscled propulsatory organ. So we think that Hesse [1911, 1934] was correct in drawing together *Monilearia* and *Cochlicella*.

Objectively the taxonomic unity could be characterized by a formal diagnosis, which can be given as follows.

Family Cochlicellidae
Schileyko, 1972

Schileyko, 1972: 39 (as subfamily of Hygromiidae).

Shell moderately depressed to elongate

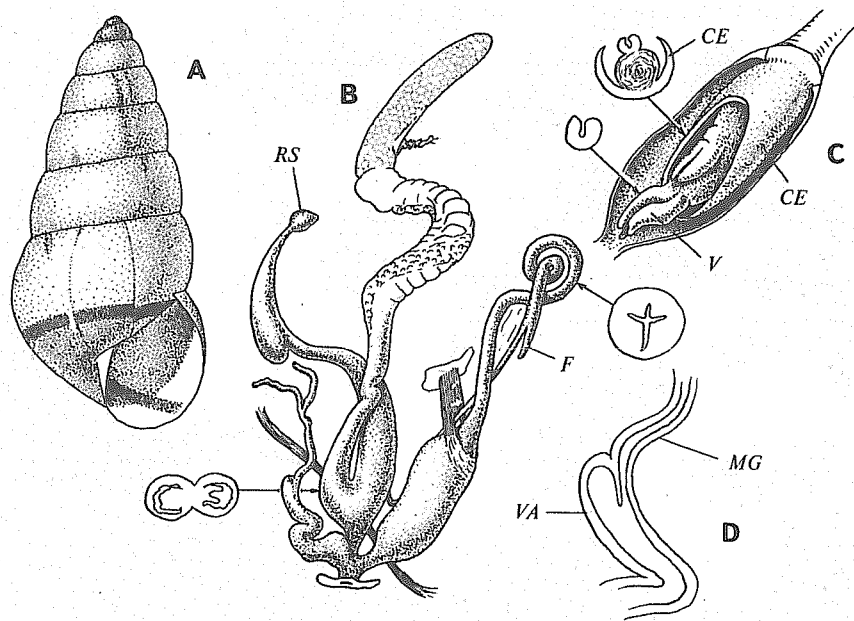


FIG. 4. *Cochlicella acuta* (Müller, 1774). A — shell; B — sexual apparatus; C — opened penis; D — longitudinal section of vaginal appendix (scheme) [after Schileyko, 1972]. CE — calcareous envelope of penial verge; other abbreviations as in Fig. 1.

РИС. 4. *Cochlicella acuta* (Müller, 1774). А — раковина; В — половой аппарат; С — вскрытый пенис; D — продольный разрез пениального придатка (схема) [по Шилейко, 1972]. CE — известковая оболочка пениальной папиллы; другие обозначения как на рис. 1.

conical, rather small, with 1-3 dark spiral bands. Aperture margins, except columellar, straight, simple, not expanded or reflexed. No apertural teeth. Umbilicus narrowly open or closed.

Flagellum of various length, but always present. Penis containing closed or partially open verge; in latter case verge consisting of proximal and distal parts and coated by calcareous envelope. Vagina with well developed appendix, in its top 1-3 tubular simple or biramous mucus glands open.

2. On the phylogenetic relations of Cochlicellidae

This problem is more complex and more arbitrary. Amongst hygromioid groups no taxon is known which could be considered as a relative of Cochlicellidae without stretching the point. Unanimous placing of the Cochlicellidae (-inae, -ini) in Hygromiidae (or Helicidae) is connected, as it seems to us, with the fact that this taxon inhabits Western Palearctic — the kingdom of hygromioids; besides,

shells of various Cochlicellidae do not fit to any other West-Palearctic group of snails except Hygromiidae.

At the same time a vast group exists in the nature, for which the presence of stylophore and tubular or alveolar glands, located upon it, is highly characteristic, that is Xanthonychoidea [see Schileyko, 1991a]. We do not see any serious obstacles for including Cochlicellidae in Xanthonychoidea, except geographical reason: Xanthonychoidea distributed predominantly in South-Eastern Asia, South, Central and southern parts of North America; in western Palearctic this superfamily is represented by a single species, *Bradybaena fruticum* (Müller, 1774). Judging from the fact that *B. fruticum* has spacious area and does not differ in any respect from Asian Bradybaenidae, it must have come to Europe not so long ago — probably in Pleistocene or early Holocene. However this does not mean that in early Tertiary some individual representatives of the Xanthonychoidea were not be able to penetrate far westward. By the way, some ancient members of also South

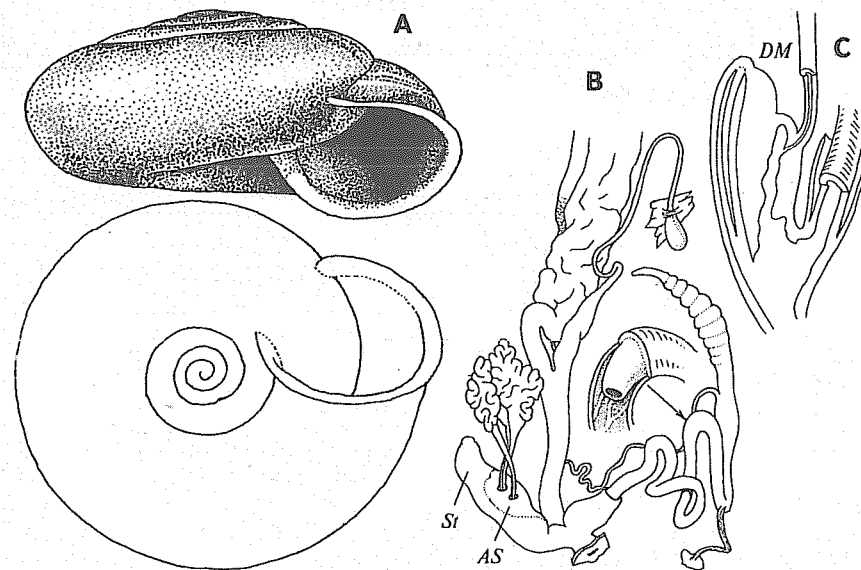


FIG. 5. *Aegista subchinensis* (Moellendorff, 1884) from Taiwan, SW of Yeh-liu, Taipei Co., May 14, 1988, coll. et det. C.C. Coney and P.F. Liu. A — shell; B — sexual apparatus and opened penis; C — longitudinal section of stylophore. AS — additional sac of stylophore; DM — duct of mucus gland; Sr — stylophore. Other abbreviations as in Fig. 1.

РИС. 5. *Aegista subchinensis* (Moellendorff, 1884) из Тайваня, ЮЗ от Е-лю, округ Тайпей, 14 мая 1988, сбор и опр. С.С. Коней, П.Ф. Лиу. А — раковина; В — половой аппарат и вскрытый пенис; С — продольный срез стилофора; AS — дополнительный мешок стилофора; DM — проток слизистой железы; Sr — стилофор. Другие обозначения как на рис. 1.

Asian superfamily Ariophantoidea are distributed in south-western Palearctic, where they have formed the family Sphincterochilidae [Schileyko, 1991a, b].

If we adopt this hypothesis, one may indicate even the concrete group amongst Xanthonychoidea, namely Aegistinae (Bradybaenidae), as the most related to the Cochlicellidae. In establishing the connections between Aegistinae-like group and Cochlicellidae we have to adopt what members of Cochlicellidae are least specialized. Undoubtedly it is *Monilearia*, specifically the low-spined species, as, for example, *M. phalerata*, because the shell of this species still retains its initial helicoid appearance, basal section of mucus gland is still not turned into a specialized propulsatory pyriform organ, and penial verge is primitive and represents an expanded sphincter separating the cavities of penis and epiphallus. It is essential also that the range of *Monilearia* is restricted only by Canary Islands.

If we compare the reproductive apparatus of *M. phalerata* with that of such repre-

sentatives of Aegistinae as *Aegista awajensis* (Gude, 1910) or *A. kobensis* (Schmacker et Boettger, 1890) [see Azuma, 1982: 286, figs 409 and 411], then, except some secondary differences in the structure of flagellum (they are connected with complication of spermatophore), we do not find any principal differences in the structure of sexual apparatus: there is a couple of simple non-branched tubular glands attached to an additional sac. This sac is a widening of the basal section of the stylophore. The latter contains a dart of simple structure. Reduction of the dart down to complete disappearance is a common enough phenomenon in Xanthonychoidea as a whole, and in the case of shifting of additional sac to the terminal position, this reduction will be an inevitable consequence of the process, because the dart would be neither formed nor functional if the duct of the gland will open in the dart base. In other words, the loss of the dart is a natural result of shifting of mucus gland base to the apical position.

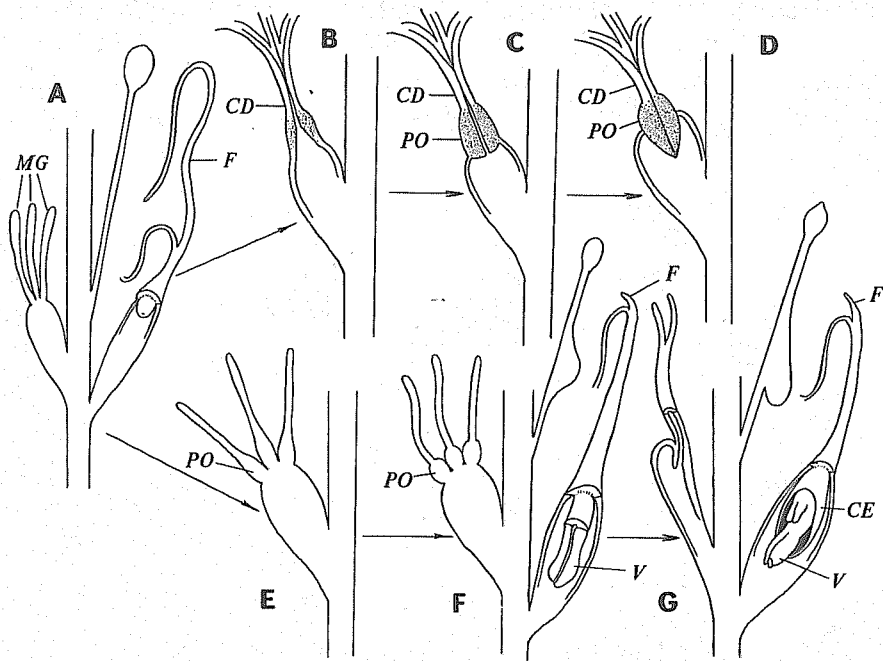


FIG. 6. Scheme of phylogenetic relationships in Cochlicellidae. A — hypothetical ancestral form, related to some ancient "pre-Aegistinae"; B — derivative of this ancestral form, intermediate link to *Monilearia*; C — *Monilearia phalerata*; D — *M. lemniscata*; E — derivative of ancestral form, intermediate link to *Prietocella*; F — *Prietocella*; G — *Cochlicella*. CE — calcareous envelope of penial verge; other abbreviations as in Fig. 1.

РИС. 6. Схема филогенетических связей в сем. Cochlicellidae. А — гипотетическая предковая форма, связанная с древними "pre-Aegistinae"; В — производный вариант от этой предковой формы, переходное звено к *Monilearia*; С — *Monilearia phalerata*; D — *M. lemniscata*; E — производный вариант от предковой формы, переходное звено к *Prietocella*; F — *Prietocella*; G — *Cochlicella*. CE — известковая оболочка пениальной папиллы; другие обозначения как на рис. 1.

We had the opportunity to dissect one specimen of *Aegista subchinensis* (Moellendorff, 1884) from Taiwan and discovered a minute closed penial verge with a broad inner canal (Fig. 5). Despite this species has an alveolar but not tubular structure of mucus glands, it is noteworthy that these glands are three in number and their lower portions are tubular.

We would like to stress that we are speaking by no means on the origin of Cochlicellidae from any Recent members of Aegistinae, and the given examples are just illustrations of possibility of historical succession between some hypothetical pre-Aegistinae and ancient *Monilearia*-like Cochlicellidae.

Seemingly the role of the stylophore as well as of various vaginal appendages consists in stimulation of a partner before mating. The dart acts as a tool of transferring of

the secret of mucus glands into the skin of a partner [Adamo, Chase, 1990], but a number of instances of dart reduction (disappearance) in helicoid and xanthonychoid groups indicate that in the present geological time not only a dart but also mucus glands in many cases are being lost. This allows to suggest that the vaginal appendix in ancestors of the Cochlicellidae contained a dart, i.e. this appendix is a homologous to xanthonychoid stylophore.

3. On the historical connections of genera within Cochlicellidae

If we are based on really existing variants of structure, we can reconstruct a hypothetical form from which the recent Cochlicellidae have originated. This form had a depressed banded shell; three tubular glands, attaching

separately to the apex of vaginal appendix; long flagellum; long genital atrium; short closed penial verge without calcareous coating (Fig. 6, I).

Historical development of this organism proceeded in two directions. The first direction: with retaining of all features of ancestral form, the basal portions of mucus glands were fused into a united common duct (Fig. 6, II), and this fusing created a definite ground for origin and differentiation of a powerful propulsatory organ. The stages of differentiation of the organ can be seen in Recent *Monilearia phalerata* (Fig. 6, III) and *M. lemniscata* (Fig. 6, IV). At the same time the shell becomes more elongate.

The second direction: shape of the shell becomes elongate too, but independently of *Monilearia*. Each of three mucus glands, retaining independence from each other, forms in its basal part its own propulsatory organ, still weakly differentiated (Fig. 6, V). Further elongation of the shell, lengthening of the penial verge and appearance of well-expressed propulsatory organs of each gland lead to the origin of *Prietocella* (Fig. 6, VI).

To understand the beginning of the final stage of this morphological series we have to estimate the role vaginal appendix and peculiarities of the structure of the penis from functional point of view. Above we have come to the conclusion that the vaginal appendix seems to be homologous to stylophore of some ancient pre-Aegistinae, and stressed that the role of dart consists in transferring of feromones contained in the mucus. In case of dart reduction the transferring of the secret must be fulfilled by another mechanism. We suppose that the origin of propulsatory organs at the bases of mucus glands is just the mechanism which has come instead the darts. This organ, judging by its structure, must be capable to inject strongly the secret of mucus gland — either to the lumen of vaginal appendix or, if the appendix everts during copulation, immediately outside, where the partner could estimate the degree of readiness of the individual to mating. Seemingly, the appearance of only one powerful propulsatory organ

at the base of common duct of mucus glands (as in *Monilearia*) is more efficient functionally than the presence of three or four smaller ones (as in *Prietocella* — Fig. 6, VI). In the latter case the propulsatory organs could not be very large because the problem of their spacing arises, while for efficient action of "injectors" some minimal muscular mass is necessary.

It seems to us that the shortening of genital atrium in *Prietocella* and *Cochlicella* in comparison to *Monilearia* is connected with the same factor, because shorter way outside facilitates the leading out of the secret by less powerful mechanism of injection.

As further evolution in this direction leads to a dead end, the only possibility remains: to change the mean of stimulation of a partner once more, using for this purpose some other mechanisms, for example, the distal part of male division. So we think that the origin of calcareous envelope of the penial verge in *Cochlicella* is connected just with the loss of stimulatory function by vaginal appendix. It is not accidental that in *Cochlicella* the calcareous envelope of verge arises simultaneously and parallel to the reduction in number of mucus glands down to one, and this gland is weakly developed and lacking a propulsatory organ (Fig. 6, VII).

Thus the differences in the structure of sexual apparatus between *Prietocella* and *Cochlicella*, which at the first glance seem to be deep enough, are connected with the same process of change of the method of partner stimulation and do not present any obstacle to admit the phylogenetic succession between *Prietocella* and *Cochlicella* (Fig. 6, VI-VII). It is essential in this connection that the flagellum in both genera is much reduced and the reservoir of spermatheca is differentiated into a sac-like lower part and a small globular reservoir.

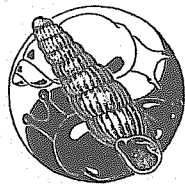
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Variability of the respiratory apparatus in *Bathydoris* Bergh, 1884 (Gastropoda, Doridida)

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The mantle complex of the primitive group of nudibranchiate molluscs, *Bathydoris*, was studied. The respiratory apparatus of few-gilled species is highly variable. The variability of other systems of organs was revealed. The evolution of the mantle complex of bathydoridids was also considered. A new genus *Prodoris* was described.

Изменчивость дыхательного аппарата *Bathydoris* Bergh, 1884 (Gastropoda, Doridida)

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Исследован мантийный комплекс примитивной группы голожаберных моллюсков *Bathydoris*. Дыхательный аппарат маложаберных видов сильно варьирует. Резкой изменчивости подвержены и другие системы органов. Рассматривается эволюция мантийного комплекса батидоридид. Выделен новый род — *Prodoris* gen. nov.

Among gastropod molluscs the advanced nudibranchiate forms, including some orders classified previously in the order Nudibranchia, are of special interest. The formation of the Nudibranchia occurred as a result of detorsion, that is shifting of mantle complex along the right side of the body. In different phylogenetic lineages the initial stages of this process were similar, but the further destiny of mantle organs was different. The detorsion process reaches its maximum in Doridida-like forms, where the anus and nephroproct are in the terminal position. The shift of the mantle complex to the dorsal position and the polymerization of primary gill were significant in the evolution of Doridida [Minichev, 1970]. The first stages of formation of perianal corolla (characteristic of Doridina) can be traced in Bathydoridina, comprising a parallel phylogenetic lineage of Doridina [Baranetz, Minichev, 1994]. A few species of *Bathydoris* (*Bathydoris clavigera* Thiele, 1912, *B. obliquata* Odhner, 1934, *B. argentina* Kaiser, 1980, and *B. vio-*

lacea Baranetz, 1993) have retained this exceptional peculiarity in their structure, with an asymmetric mantle complex which has an arc of 1-3 gills on the right side of anal papilla. We will designate individuals with similar morphotype as few-gilled forms. Individuals having 4-5 asymmetrically arranged gills may also be included in this group. Beside gills, the mantle complex of lower representatives of *Bathydoris* has nephroproct on the right side of anus and the pore of secretory organ on the left side. The mantle gland was not found in many-gilled species of *Bathydoris*, which have a ring respiratory apparatus. The symmetric corollae of true doridids do not have multicellular gland structure. However, other groups similar to doridids (Corambidae and Okadaidae) possess multicellular mantle glands [Baba, 1937; Slavoshevskaja, 1971]. Possibly, the secretory organ in the mantle complex is homologous to hypobranchial gland of ancestral forms and is preserved only in primitive Doridida [Minichev, Baranetz, 1994].