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РЕЗЮМЕ. По результатам конхологических и анатомических исследований рассмотрен систематический состав рода *Lindholmomeme* Haas, 1936. Род включает в себя шесть видов, ареал которых охватывает Восточный Казахстан, Южную Сибирь и Приморский край. *L. notophila* обитает на юге Приморья. *L. turbinatum* в Восточном Казахстане и на Юго-западном Алтае. Остальные четыре вида (*L. rhysoya*, *L. altaica*, *L. nordenskioldi* и *L. westerlundii* sp.nov.) — на юге Сибири. Для определения видов составлен ключ.

Boreolestes gen. nov., a new genus of carnivorous slugs from Western Caucasus, and some considerations on the phylogeny of Trigonochlamydidae (Pulmonata)

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ABSTRACT. *Boreolestes* gen. nov. with 2 species, *B. likharevi* sp. nov. (type species) and *B. sylvestris* sp. nov. from NW Caucasus is described. The new genus is characterized by a very large mantle covering most of animal back and by the presence of a well-developed perivaginal gland. The new genus is similar to cave-dwelling *Troglolestes* Ljovushkin et Matekin, 1965, but differs from the latter by a well-pigmented mantle, presence of perivaginal gland, and absence of vaginal accessory organ at the base of spermathecal stalk. It is suggested that Trigonochlamydidae derived from a zonitoid ancestor. An attempt has been made to reconstruct the probable phylogenetic relationships in Trigonochlamydidae.

pigmented, leaden-colored; indistinct blotches with whitish dots in centre seen at magnification. Horse-shoe-like groove on mantle normally developed or presented by only right branch. Orifice of genital atrium situated slightly behind right tentacle base. Eyes normally developed.

Shell composed of thickened nucleus and very delicate, fragile spatula.

Throat length about 1/4 of body length. Numerous retentors attached to throat obliquely-laterally, along one irregular line. Radula of normal "carnivorous" type, but teeth relatively small. Jaw rudimentary, transparent, exceptionally thin.

Lung cavity very small. Venation scarcely visible.

Reproductive apparatus without accessory organs except for perivaginal gland. Penis sheath absent.

The genus is similar to *Troglolestes* Ljovushkin et Matekin, 1965 in possessing a very large mantle and in the absence of penis sheath and "spermatophores" in penis. *Boreolestes* differs from *Troglolestes* in the presence of intensive pigmentation of the mantle and perivaginal gland, the absence of distinct papillae on the mantle surface and additional vaginal sac at the base of spermathecal stalk.

Distribution. NW Caucasus. 2 sp. Mollusks live on open slopes under stones, at wet conditions.

Etymology. *Boreo-* (L., northern, indicating the area of the genus at northern border of the family range) plus *-lestes* (a robber, traditional ending of generic names in Trigonochlamydidae). Gender masculine.

Диагноз. Фиксированные животные удлиненно-овальной формы, закругленные на обоих концах. Мантия очень большая, закрывает почти всю спину животного. Поверхность мантии покрыта неясными или четкими папиллами. Пневмостом расположен близ заднего края мантии. Капюшон занимает немного меньше 1/3 длины мантии. Верхняя поверхность мантии сильно пигментирована, имеет свинцовую окраску; при увеличении заметны нечеткие пятнышки с белесыми точками в центре. Подкововидная борозда на мантии развита нормально или представлена лишь

A peculiar family Trigonochlamydidae consists of obligatory carnivorous slugs. Its range is of a relict type, occupying Caucasus and adjacent territories of Iran and Turkey. Up to date, 7 monotypic genera of the family have been known [Ljovushkin, Matiokin, 1965; Likharev, Viktor, 1980; Schileyko, 1988]. Here we describe the eighth genus composed of 2 species.

Systematic account

Trigonochlamydidae Hesse, 1882

Hesse, 1882: 32 (as subfam. Trigonochlamyidina).

Trigonochlamydiniae Hesse, 1882

Boreolestes Schileyko et Kijashko, gen. nov.

Type species — *Boreolestes likharevi* Schileyko et Kijashko, sp. nov.

Diagnosis. Preserved animals elongated-ovate, rounded at both ends. Mantle very large, covering nearly entire back of slug. Mantle surface covered with vague or quite distinct small papillae. Pnevmostome situated not far from posterior end of mantle. Hood occupying somewhat less than 1/3 of mantle length. Upper surface of mantle strongly

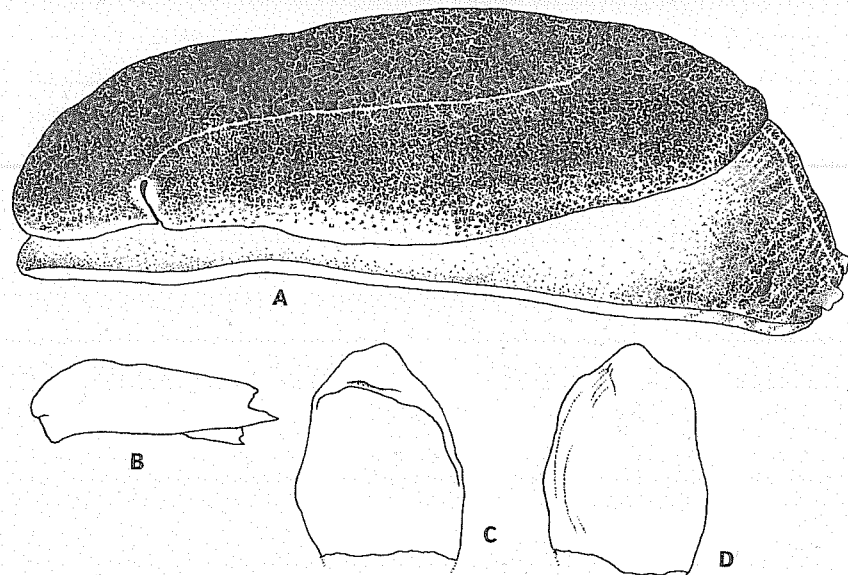


FIG. 1. *Boreolestes likharevi* sp. nov. Holotype. A — external appearance; B, C, D — shell.

РИС. 1. *Boreolestes likharevi* sp. nov. Голотип. А — внешний вид, В, С, D — раковина.

правой ветвью. Отверстие атриума располагается позади основания правого глазного щупальца.

Глаза нормально развиты.

Раковина состоит из слегка утолщенного ядра и тонкой, хрупкой ступалы.

Глотка занимает около 1/4 длины тела. Многочисленные ретенторы прикрепляются к глотке косолатерально, вдоль одной линии. Радула нормального "хищного" типа, но зубы относительно маленькие. Челюсть рудиментарная, прозрачная, очень тонкая.

Легочная полость очень маленькая. Венозная сеть еле заметна.

Половой аппарат лишен придаточных органов, кроме перивагинальной железы. Пениальный чехол отсутствует.]

Boreolestes likharevi

Schileyko et Kijashko, sp. nov.

(Figs. 1, 2)

Type locality — Oshten-Fisht Mountains, western part of Great Caucasus, about 2000 m above the sea level.

Material. NW Caucasus, Oshten-Fisht Mountains, west-facing slope of Mount Oshten, saddle, under stones, June 24, 1997; coll. P.V. Kijashko (holotype and paratype); — west-facing slope of Mount Oshten, environs of Psheno-Dakh Lake, July 5, 1997; coll. P.V. Kijashko (3 paratypes);

— west-facing slope of Mount Oshten, environs of Psheno-Dakh Lake, isthmus between Mount Oshten and Pshekha-su, July 5, 1997; coll. G.B. Bakhtadze (1 paratype).

Holotype and the paratype from the type locality are stored in the Zoological Institute of Russian Academy of Sciences (Saint-Petersburg), other paratypes are in the Zoological Museum of Moscow State University, Nos. Lc-23371, Lc-23372.

Description. Body length of preserved holotype (the largest specimen) 10.6 mm.

Albumen gland bulky, of irregular shape. Spermatheca. Vas deferens tightly adhering to penis. Penis rather long, internally with two broad longitudinal pilasters covered with numerous minute papillae. Glandular pads and "spermatophores" in penis absent. Penial retractor attached to penis terminally. Free oviduct rather short, about same length as vagina. Perivaginal gland well developed, surrounding the vagina and base of spermatheca. Spermathecal stalk short, slender, reservoir ovate.

Distribution. NW Caucasus (Oshten-Fisht Mountains).

Etymology. The species is named in honour of Prof. Ilya M. Likharev, who made a considerable contribution to studying of land mollusks, slugs in particular.

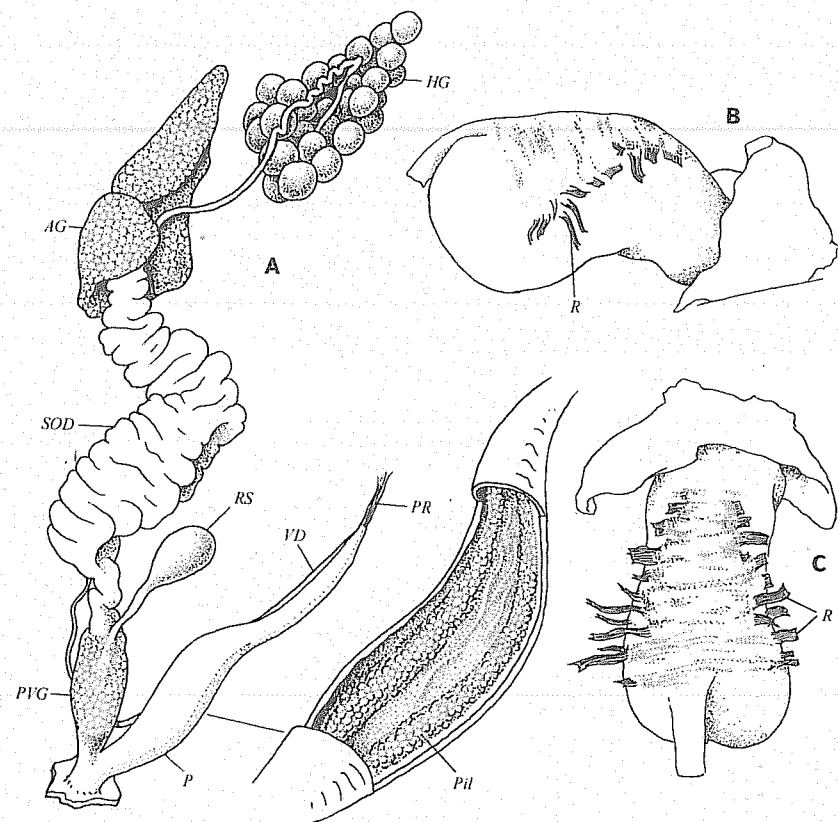


FIG. 2. *Boreolestes likharevi* sp. nov. Holotype. A — reproductive tract and interior of penis; B, C — throat (B — lateral view, C — dorsal view). AG — albumen gland; HG — hermaphroditic gland; P — penis; Pii — pilasters inside penis; PR — penial retractor; PVG — perivaginal gland; R — retentors; RS — reservoir of spermatheca; SOD — spermoviduct; VD — vas deferens.

РИС. 2. *Boreolestes likharevi* sp. nov. Голотип. А — репродуктивный тракт и вскрытый пенис; В, С — глотка (В — вид справа, С — вид со спинной стороны). АГ — белковая железа; НГ — гермафродитная железа; Р — пенис; Рii — пиластры внутри пениса; РR — пениальный ретрактор; РVГ — перивагинальная железа; R — ретенторы; RS — резервуар семеприемника; SOD — спермовидукт; VD — семепровод.

[**Диагноз.** Длина тела фиксированного голотипа (самый большой экземпляр) 10.6 мм.

Белковая железа большая, неправильной формы. Спермовидукт объемистый. Камера оплодотворения скрыта в тканях белковой железы. Семепровод плотно прилегает к пенису. Пенис довольно длинный, внутри с двумя широкими пиластрами, покрытыми многочисленными маленькими папиллами. Железистые подушки и "сперматофоры" внутри пениса отсутствуют. Половой ретрактор крепится к пенису терминально. Свободный яйцевод довольно короткий, примерно той же длины, что и вагина. Перивагинальная железа

хорошо развита, окутывает вагину и основание протока семеприемника. Проток семеприемника короткий, резервуар овальный.]

Boreolestes sylvestris Kijashko, sp. nov.

(Figs. 3, 4)

Type locality — environs of Ghooscriple, Molchepa riverside (right tributary of Belaya River), NW Caucasus.

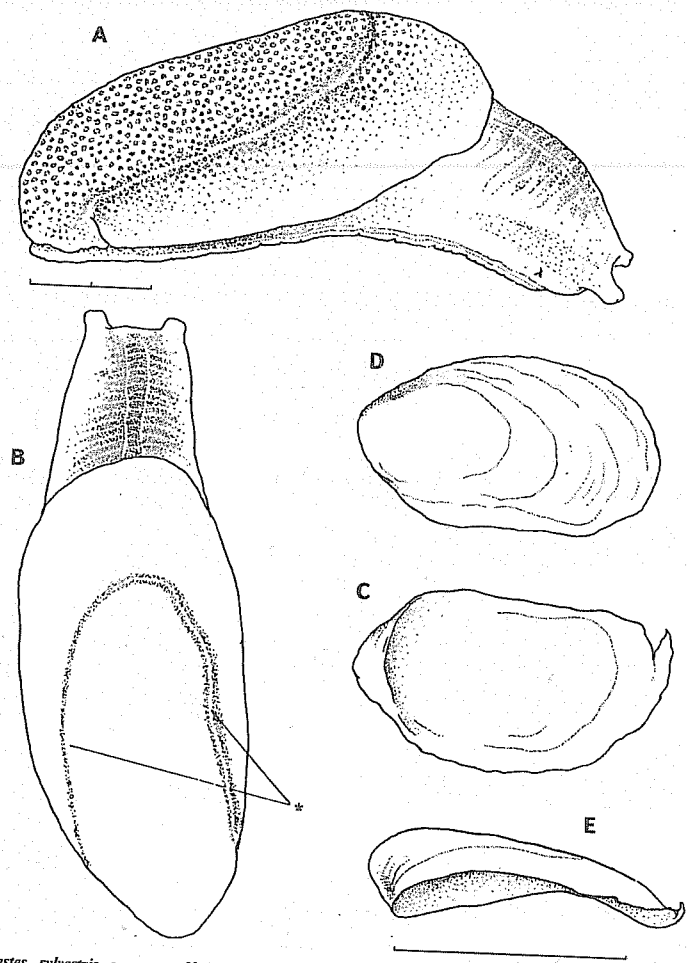


FIG. 3. *Boreolestes sylvestris* sp. nov. Holotype. A, B — external appearance; C, D, E — shell. Asterisk — horse-shoe-like groove.

РИС. 3. *Boreolestes sylvestris* sp. nov. Голотип. А, В — внешний вид; С, D, E — раковина. Звёздочка — подкововидная борозда.

Material. NW Caucasus, Molchepa riverside (right tributary of Belaya River), 6 km from Ghooseripl, mixed coniferous-broad-leaved forest (*Fagus orientalis*, *Abies nordmanniana*), July 1, 1998, coll. P.V. Kijashko (holotype and 6 paratypes); — near the same place, July 2, 1998, coll. P.V. Kijashko (13 paratypes).

Holotype and 5 paratypes are stored in the Zoological Institute of Russian Academy of Sciences (Saint-Petersburg), 6 paratypes are in the Zoological Museum of Moscow State University, No. Lc-24424; 7 paratypes are in the Museum of scientific collections of Zoological department of Rostov State University.

Description. Body length of holotype (the largest specimen) 10.0 mm. Both branches of horse-shoe-like groove on mantle normally developed. Surface of mantle covered with numerous, small, distinct papillae.

Albumen gland irregularly triangular. Spermo-viduct and talon as in *B. likharevi*. Vas deferens not adhering to penis. Penis moderately long, internally with 2 longitudinal pilasters; inner surface of penis and pilasters covered with minute papillae. Glandular pad and "spermatophores" inside penis

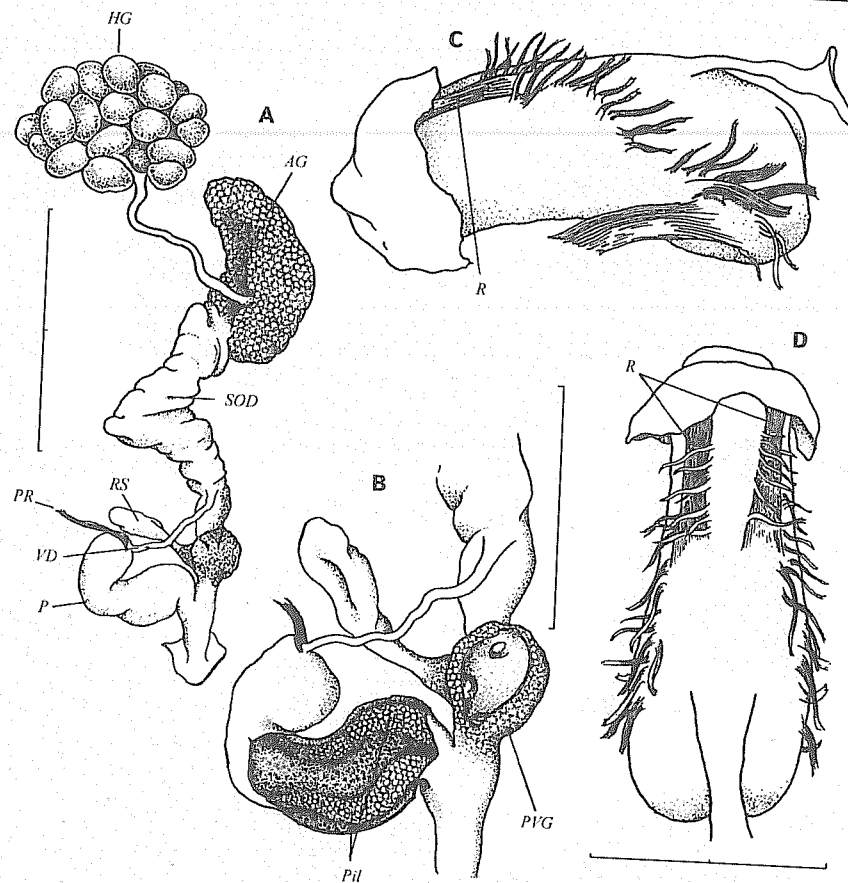


FIG. 4. *Boreolestes sylvestris* sp. nov. Holotype. A — reproductive tract; B — interior of penis and vagina; C, D — throat (C — lateral view, D — dorsal view). Abbreviations as in Fig. 2. Scale bars — 1 mm.

РИС. 4. *Boreolestes sylvestris* sp. nov. Голотип. А — половой аппарат; В — внутреннее строение пениса и вагины; С, D — глотка (С — вид слева, D — вид со спинной стороны). Обозначения как на рис. 2. Масштабные линейки — 1 мм.

wanting. Penial retractor attached to penis at base of vas deferens. Free oviduct somewhat longer than vagina. Upper portion of vagina markedly enlarged and surrounded by perivaginal gland along with base of short spermathecal stalk. Reservoir of spermatheca rather small, elongate.

Distribution. NW Caucasus (upper part of Belaya River basin).

Diagnosis. Вид близок *B. likharevi*, внешне отличается более светлой окраской, наличием явственных папилл на поверхности мантии (даже у фиксированных экземпляров) и тем, что обе ветви подкововидной борозды нормально развиты. Анатомически отличается

главным образом тем, что вагина в области перивагинальной железы образует заметное расширение).

Discussion

Trigonochlamydidae are evidently a very peculiar and ancient family. Its ancient age is indicated, in particular, by the fact that seven of eight genera of the family are monotypic (only *Boreolestes* consists of 2 species), and the family is composed of two subfamilies, one of which (*Selenochlamydininae* Likharev et Wiktor, 1980) is also monotypic.

To reconstruct possible phylogenetic relation-

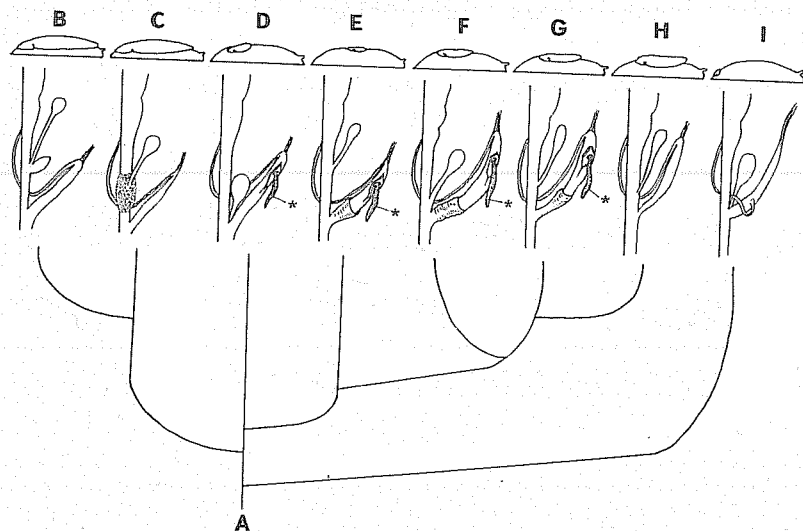


FIG. 5. Possible phylogenetic relationships in Trigonochlamyidae. A — zonitid ancestor; B — *Troglolestes*; C — *Boreolestes*; D — *Parmacellilla*; E — *Trigonochlamys*; F — *Hyrcanolestes*; G — *Drilolestes*; H — *Lesticulus*; I — *Selenochlamys*. Asterisk — "spermatophores" inside penis.

РИС. 5. Возможные филогенетические связи внутри Trigonochlamyidae. A — зонитидный предок; B — *Troglolestes*; C — *Boreolestes*; D — *Parmacellilla*; E — *Trigonochlamys*; F — *Hyrcanolestes*; G — *Drilolestes*; H — *Lesticulus*; I — *Selenochlamys*. Звездочка — "сперматофоры" внутри пениса.

ships among genera, we need to discuss the archetype of pre-trigonochlamydid organization. We think that the family has originated from a zonitoid ancestor for the following reasons:

1. The very unusual structures inside penis in some Trigonochlamyidae are traditionally designated as "spermatophores", but they are not actually spermatophores, because they are not transferred to a partner during copulation, and there is no mechanism which could provide the transfer of the "spermatophores" content to a partner. Besides, it is unclear how the semen fluid could get in this "spermatophore". At the same time, the penis of *Spinophallus* (Zonitidae) has conspicuous structures inside [Riedel, 1960], which resemble trigonochlamydid "spermatophores". Muratov [1998, this volume] suggested that "spermatophores" of such kind are filled with carbonate buffer and probably supply the recipient spermatheca with this buffer.

2. One of conspicuous characters of Zonitidae is the presence of perivaginal gland. In species of *Boreolestes* we have also found a well developed perivaginal gland of quite traditional zonitid structure.

3. Both Zonitidae (at least, Zonitini and Oxy-

chilini) and Trigonochlamyidae usually have a short spermathecal stalk lacking a diverticle.

4. Penial retractor in representatives of both taxa is attached to penis (or to flagellum) terminally or subterminally.

5. Although there are no obligatory predators among Zonitidae, most of them are omnivorous (not herbivorous), their radulae are of universal type, and the closely related family Daudebardiiidae is composed of predators only.

6. Shells of many Zonitidae are thin and sometimes show a tendency to reduction down to vitrinoid stage (*Godwinia*, *Vitrinizonites*). Likharev and Wiktor [1980: 97], when discussing the origin of Trigonochlamyidae, wrote: "Judging by their internal shell, in which the nucleus is shifted leftward from longitudinal axis and growth lines on the spatula are shifted to the right, these slugs... originated from snails with succinoid shells". We do not agree with this viewpoint, because, if we imagine the stage of reduction next to that of *Vitrinizonites*, we get a shell, much resembling those of *Daudebardia*, and the next step would be the trigonochlamydid shell.

7. In addition, skin of the upper surface of cephalopodium of large Zonitidae often has characteristic bluish-lead color; back of cephalopo-

dium of some Trigonochlamyidae (*Parmacellilla*, *Trigonochlamys*, *Hyrcanolestes*, *Drilolestes*) is similarly colored.

Schileyko [1982, 1986] suggested that Trigonochlamyidae have ancient connections with South African endodontoid genus *Trachycystis* because the penis of *Trachycystis* contains structures that are somewhat similar to those of some Trigonochlamyidae [Sigel, 1980]. This hypothesis, however, contradicts the above-considered facts and should be rejected.

There are two groups in Trigonochlamyidae (Fig. 5): species with (rather) small mantle (*Parmacellilla*, *Trigonochlamys*, *Hyrcanolestes*, *Drilolestes*, and *Lesticulus*), and species with enormously large mantle, covering most of animal back (*Boreolestes* and *Troglolestes*). In the first group the mantle may be either posterior (*Parmacellilla*) or medial in position (rest genera). As the posterior position of the mantle is probably an initial condition (compare with Daudebardiiidae which are immediate derivatives of Zonitidae), *Parmacellilla* is seemingly the most archaic member of Trigonochlamyidae. Besides, the shell of *Parmacellilla filipowitschi* Simroth, 1910 retains the distinct traces of spiral coiling (Fig. 6).

The next stage of mantle transformation was its shift forward, a state occurring in all other Trigonochlamyidae. Therefore, the median position of the mantle is an advanced feature.

Thus we consider *Parmacellilla* as the most archaic genus of the Recent trigonochlamydid taxa. *Selenochlamys*, retaining the primitive position of mantle, early deviated from *Parmacellilla*-like lineage, lost the "spermatophores", and changed the internal structure of penial tube [Likharev, Wiktor, 1980].

Trigonochlamys, having very small and shifted forward mantle, is probably a more or less direct descendant of *Parmacellilla*. *Drilolestes* is the next stage of evolution, because it has somewhat enlarged mantle, while retaining all main characters of *Trigonochlamys*. *Hyrcanolestes* has a peculiar character: the penis sheath is attached to penis at both ends. This is undoubtedly a secondary character and that is why we think that *Hyrcanolestes* is a descendant of *Drilolestes*. *Hyrcanolestes*, *Trigonochlamys* and *Drilolestes* are united by the presence

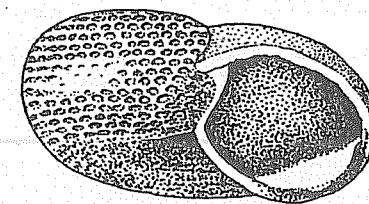


FIG. 6. Shell of *Parmacellilla filipowitschi* Simroth, 1910. N Iran, Mazenderan Prov., near Meshkhed, right bank of Babul River. Naturhistorisches Museum Basel, No. 3960a.

РИС. 6. Раковина *Parmacellilla filipowitschi* Simroth, 1910. Сев. Иран, пров. Мазендеран, близ Мешхеда, правый берег р. Бабул. Музей естественной истории, Базель, No. 3960a.

of penial sheath which is absent in all other Trigonochlamyidae.

Lesticulus is a highly specialized troglobiont slug lacking coloration and eyes. Nevertheless, it differs anatomically from mentioned genera mainly by the absence of "spermatophores" in the penis and penis sheath. This is probably a result of secondary simplification, and this genus is historically connected with some extinct forms closely related to *Drilolestes*.

As it has been noted, *Troglolestes* and *Boreolestes* have an enormous mantle and lack penis sheath. Hence, they are related to each other, although the former is colorless and lives deeply in caves, whereas the latter is normally pigmented and inhabits open slopes (lives under stones). We suggest that the succession of habitats indicates that *Boreolestes* is an ancestor of *Troglolestes*. Moreover, *Boreolestes* is the only representative of the family which retains perivaginal gland, an evidence of origin of Trigonochlamyidae from zonitoid ancestor. As far as the strange "additional sac" in *Troglolestes* is concerned, it is unclear whether it is a glandular organ. If it is shown to be glandular, this "sac" is probably a derivative of perivaginal gland.

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Boreolestes gen. nov., новый род хищных слизней из Западного Кавказа и соображения по филогении Trigonochlamyidae (Pulmonata)

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Описание **Boreolestes** gen. nov. из северо-западного Кавказа с 2 видами — *B. likharevi* sp. nov. (типовой вид) и *B. sylvestris* sp. nov. Новый род характеризуется очень большой мантией, закрывающей почти всю спину животного, и присутствием хорошо развитой перивагинальной железы. Новый род сильно напоминает пещерного *Troglolestes* Ljovushkin et Matekin, 1965, но отличается интенсивной пигментацией мантии, наличием перивагинальной железы и отсутствием дополнительного вагинального органа при основании протока семеприемника. Предполагается, что Trigonochlamyidae произошли от зонитонидного предка. Сделана попытка реконструировать возможные филогенетические связи внутри Trigonochlamyidae.

A new genus and two new species of land snails of the family Ariophantidae from North Vietnam

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ABSTRACT. A new genus, *Laocaia* gen. nov., with two species, *L. attenuata* sp. nov. and *L. obesa* sp. nov., are described and illustrated.

During collecting trips to North Vietnam (Lao Cai, Sa Pa) in November-December 1996 two new species of land molluscs were found, both belonging to a new genus.

Laocaia Kuzminykh, gen. nov.

Type species — *Laocaia attenuata* sp. nov.

Diagnosis. Small slugs with non-coiled visceral hump, rounded posteriorly, lying in "V"-shaped body groove. Body cavity not extending into tail. Tail keeled posteriorly, with caudal gland and hooked caudal horn. Foot sole narrow, divided into three parts. Mantle with large hood. Pneumostome located medially. Shell very thin, non-spiral, internal, hemispheric, completely covering visceral hump, with small calcified part, consisted of minute calcareous granules and situated in front of respiratory orifice.

Jaw oxygnathous, without median projection.

Penis short, bulbous, with large stimulator inside. Epiphallus and additional organs absent. Spermatheca entering atrium between vagina and penis.

[Диагноз. Небольшие слизи с висцеральным мешком, не погруженным в толщу ноги, закругленным сзади, лежащем в V-образном углублении на спине. Полость тела не продолжается в заднюю часть ноги. Нога в задней части с отчетливым килем. Подошва узкая, трехраздельная. Кaudальная ямка с нависающим над ней каудальным рогом хорошо развиты. Мантия с крупным капюшоном, пневмостом лежит медially. Раковина внутренняя, очень тонкая, неспиральная, полусферическая, целиком покрывает внутренностный мешок, в передней части с небольшой известковой пластинкой, состоящей из известковых зерен и со слабо заметными линиями нарастания.

Челюсть оксигнатная, без срединного выступа. Пенис короткий, вздут, внутри с крупным стимулятором. Эпифаллус и придаточные органы отсутствуют. Семеприемник впадает в атриум между вагиной и пенисом.]

Remarks. A number of genera of ariophantoid slugs are known from South-Eastern Asia.

Cryptogirasia Cockerell, 1891 from India has visceral hump more deeply submerged in body groove, than in *Laocaia* gen. nov., and slightly protruded over dorsum, pointed behind, not rounded; the colour is orange-pink. Unfortunately, the internal anatomy has not been studied.

Myotesta Collinge, 1901 from Tonkin is externally very similar to the new genus, but anatomical data show considerable differences. The jaw of *Myotesta* is composed of several plates, the epiphallus is well developed (in *M. fruhstorferi* with accessory organs), the penis has a papilla (not a stimulator), the spermatheca enters the vagina. Moreover, Simroth [1901], describing the genus *Ostracolethe* (a synonym of *Myotesta*), indicated that the shell was barely visible through the posterior of the mantle hump.

Minyongia Godwin-Austen, 1916 differs from the new genus mainly in the presence of accessory organs on the penis and in the shape of shell.

Muangnua Solem, 1966 has a more calcified shell with a remnant of coiling. Unfortunately, the description of genitalia was based on an immature specimen, but there are considerable differences in their structure.

The genus *Papuarion* Van Mol, 1973 from New Guinea is rather similar to the *Laocaia* gen. nov. in characters of genitalia but it has a well-developed external shell.

At present it is difficult to determine the exact relationships of *Laocaia*. Further collections are needed to clarify the problem.

Derivatio nominis. The genus is named after the type locality — Lao Cai Province. Gender: feminine.

Laocaia attenuata Kuzminykh, sp. nov. (Fig. 1)

Locus typicus. North Vietnam, Lao Cai province, Sa Pa district, Fan Si Pan massif, 5 km SW of Sa Pa town, 1900-2000 m above sea level, coll. M.V. Kalyakin and L.P. Korzun, 30.11.1996.

Material. Holotype (No. Lc-23419) and 4 paratypes (2 immature) from the type locality (No. Lc-23420) are deposited in the Zoological Museum of Moscow State University.