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On the anatomy of Orculidae with special reference to the spermatophores (Gastropoda Pulmonata, Stylommatophora)

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ABSTRACT. The structure of reproductive tract of 15 species and subspecies (forms) of European (mainly Alpine) and South African Orculidae has been studied. For 12 of them the spermatophores were discovered and described or the characters undoubtedly indicating presence of spermatophore have been found (inner structure of the epiphallus). The presence of spermatophores as such is established for 5 species. Hypotheses about the possible historical relationships among subfamilies and genera of Orculidae and among species in the genus *Orcula* are presented.

Introduction

The family Orculidae (except for the subfamilies Lauriinae and Argninae whose taxonomic position is not undisputed) includes 3 subfamilies (Odontocycladinae, Orculinae, Pagodulininae), 15 taxa of generic rank and more than 80 species and subspecies. The area of the family consists of two widely isolated parts: northern (including West Europe, Mediterranean countries and Central Asia), and southern (South Africa, Madagascar).

The structure of reproductive tract of different Orculidae has been studied by several authors [Hesse, 1924; Soós, 1924; Steenberg, 1925; Schileyko, 1976, 1984; Páll-Gergely, 2011]; the main sources are the articles by Gittenberger [1978] and Hausdorf [1996]. In total the anatomy of 40 species and subspecies has been studied. In the article by Hausdorf I have not found indications of the presence of spermatophores in any species of the genera *Orculella, Alvariella* and *Schileykula*. In *Sphyradium* spermatophores are seemingly absent as well. Gittenberger [1978] has established that spermatophores in some *Orcula* species exist, and gave the photo of the spermatophore of *O. dolium dolium*. Among South African Orculidae at least 2 species [*Fauxulus* (*Anisoloma*) *grayi* Van Bruggen et Meredith, 1983 and *Fauxulus* (*Anisoloma*) *glanvillianus darglensis* (Burnup, 1911)], judging from the drawings and the text, have spermatophores [Van Bruggen, Meredith, 1983, p. 313, 314, Fig. 2; Gittenberger, 1978, p. 8, Fig. 3]; besides, Gittenberger [1978] has dissected 3 specimens of *Fauxulus* (*Fauxulus*) *ovularis* (Küster, 1841) but has not mentioned the spermatophores in this species.

Of 14 known genera of Orculidae (without Lauriinae, Argninae, and Pagodulininae) for 3 genera (*Orculella*, *Schileykula*, and *Sphyradium*) spermatophores are unknown. I have found the spermatophores or structures speaking on the presence of spermatophores in nearly all studied species of the European genus *Orcula* and South-African *Fauxulus*, *Fauxulella*, and *Anisoloma*.

Results

Spermatophore structure in Orculidae

In general, spermatophore of Orculidae is a thin tubule, in most cases equipped with scale-like protrusions of various shape on anterior and/or posterior end(s). One can select two basic types of spermatophores in Orculidae:

1. A long, slender tubule with smooth walls, pointed anterior part and open posteriorly. Anterior and posterior ends of the spermatophore are equipped with scale-like lamellate protuberances, or protrusions directed perpendicular to the spermatophore axis. Judging from known data, the shape, number and arrangement of these outgrowths are probably species specific. This type takes place in all Orculinae except for *Pilorcula*.

2. Tubule with spirally directed, rounded, smoothed, longitudinal riblets; seemingly, posterior end bears some semicircular lamellar protrusions (*Pilorcula*) (judging from fragment of spermatophore) [Schileyko, 1984, p. 119, fig. 49 I and III].

Anatomical descriptions

Abbreviations in illustrations:

E – epiphallus. *ES* – slits in epiphallus where protrusions of spermatophore are formed. *FO* – free oviduct. *P* – penis. *PC* – penial caecum. *PR* – penial retractor. *SF* – spermatophore. *SR* – spermathecal reservoir. *SS* – spermathecal stalk. *V* – vagina. *VD* – vas deferens.

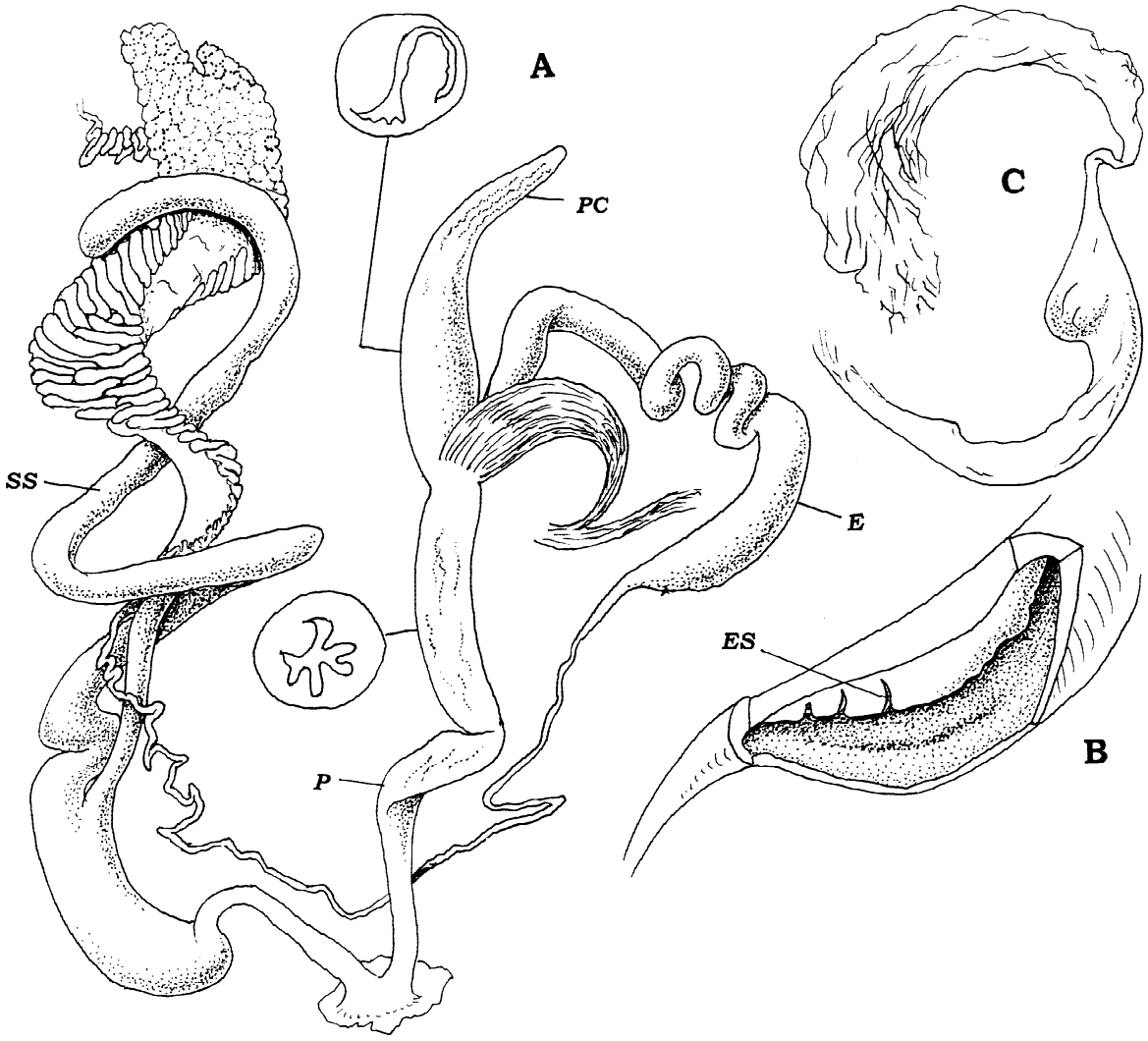

FIG. 1. *Fauxulus kurrii*. W Cape: Cape Agulhas Nat. Res. A – reproductive tract; B – inner structure of epiphallus; C – remnants of spermatophore extracted from spermatheca.

РИС. 1. *Fauxulus kurrii*. Запад Мыса Доброй Надежды, природный заповедник Кейп Агульяс. A – репродуктивный тракт; B – внутреннее строение эпифаллуса; C – частично лизированный сперматофор, извлечённый из семеприемника.

Fauxulus kurrii (Krause in Pfeiffer, 1842)
Fig. 1

Pfeiffer, 1842: 54 (*Pupa*).

Locus typicus: "Promont. bon. spei." [Cape of Good Hope].

Material. W Cape: Cape Agulhas Nat. Res. (34.813° S, 20.012° E), limestone fynbos, aestivating on vegetation (*Restios* etc.), 10.II.2000, leg. et det. D. Herbert. Natal Museum, V 7762 LP (2 specimens).

Vas deferens very long, thin, twisted, entering epiphallus not terminally, without sharp boundary. Epiphallus is rather thick, twisted, internally with three semicircular slits in proximal part. Penis little shorter than epiphallus, internally with 5-6 longitudinal pilasters. Penial caecum is conical, internally with a very strong axial pilaster in lower portion and many delicate, corrugated folds in upper section which are visible without dissection of the organ. Penial retractor strong, attached to penis/epiphallus junction at base of caecum. Free oviduct is about twice shorter than vagina. Latter consists of two nearly equal parts: lower slender and much expanded upper. Widened part thick-walled, its inner surface with numerous smoothed short axial folds. Spermathecal stalk sleeve-like, without differentiated reservoir, attending albumen gland.

Spermatophore was found in the spermathecal duct of seminal receptacle, but it was in a bad condition (partly lysed). However the presence of three semicircular slits inside proximal part of epiphallus testifies the occurrence of three lamellar protrusions on posterior end of the spermatophore.

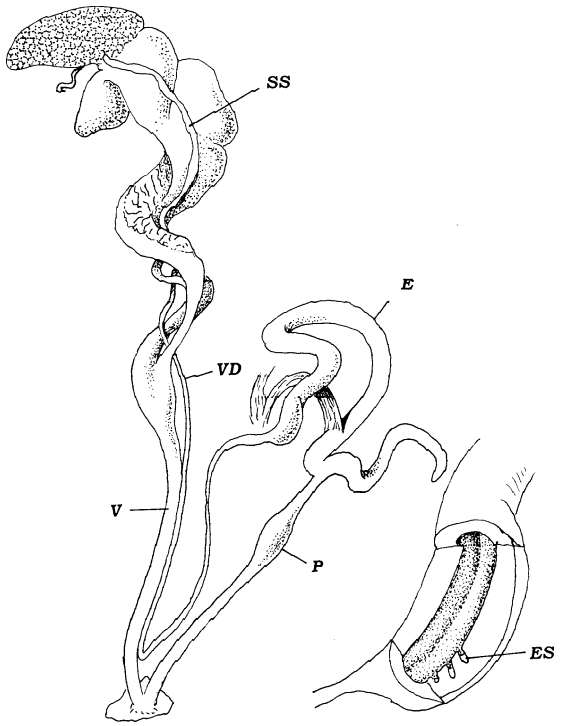

FIG. 2. *Fauxulella pamphorodon*. W Cape: Cape Peninsula, Silvermine Nat. Res. Reproductive tract and inner structure of epiphallus.

РИС. 2. *Fauxulella pamphorodon*. Запад Мыса Доброй Надежды, природный заповедник Силвермайн. Репродуктивный тракт и внутреннее строение эпифаллуса.

Remark. It is unclear whether this species is a synonym of the type species of genus *Fauxulus* – *Pupa capensis* Küster, 1841. Anyway, these two taxa are closely related and the data given above, most probably, are also valid for *Fauxulus capensis*.

Fauxulella pamphorodon (Benson, 1864)
Fig. 2

Benson, 1864: 495 (*Pupa*).

Locus typicus: Cape Peninsula at Simonstown, in the ravine behind the Admiralty House.

Material. W Cape: Cape Peninsula, Silvermine Nat. Res., old mule track above St. James (34.11977° S, 18.44658° E), fynbos, beneath shrubs, 02.X.2007, leg. et det. D. Herbert & L. Davis. Natal Museum, W 5709 LP T (1 specimen).

Vas deferens very long, slender, scarcely expanded in distalmost section, entering the epiphallus subterminally; inside proximal part of epiphallus there are three semicircular slits. Penis slender, with fusiform thickening a little above its middle, is approximately 1.5 times shorter than epiphallus; internally with vague axial foldlets. Penial caecum slender, subcylindrical, with pointed apex. Penial retractor attached to epiphallus markedly above caecum. Free oviduct is about twice shorter than vagina. Spermathecal stalk unusually thin, without visible reservoir, attending basal part of albumen gland.

Spermatophore not found, but the presence of three semicircular slits in epiphallus testifies the existence of three lamellar protrusions on posterior end of the spermatophore.

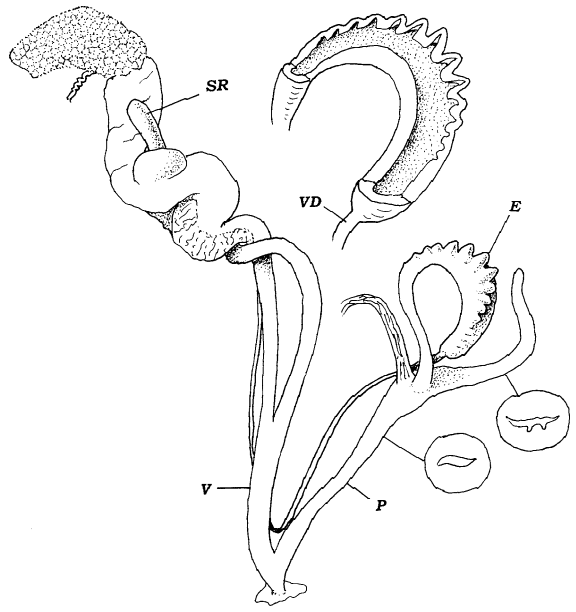

FIG. 3. *Anisoloma mcbeaniana*. KwaZulu-Natal: Injasuthi. Reproductive tract and inner structure of epiphallus.

РИС. 3. *Anisoloma mcbeaniana*. Квазулу-Наталь: Инджасути. Репродуктивный тракт и внутреннее строение эпифаллуса.

Anisoloma mcbeaniana (Melvill et Ponsonby, 1901)
Fig. 3

Melvill, Ponsonby, 1901: 319, pl. 2, fig. 9;

Locus typicus: Karkloop Bush.

Material. KZN [KwaZulu-Natal]: Injasuthi (29º06'6" S : 29º26'5" E), 1700 m a.s.l., montane *Podocarpus* forest patch, in leaf-litter, 08.XII.1998. Leg. et det. Herbert, Seddon & Tottersfield. Natal Museum, Moll. V 8009 (1 specimen).

Vas deferens is uniformly slender, entering epiphallus terminally, with visible boundary. Epiphallus comparatively short, with unusually distinct protuberances, containing narrow slits. These slits correspond to outgrowths of spermatophore. The largest protuberances are observed in the middle, and their size decreases toward both ends of epiphallus. Epiphallus becomes narrower near penis. Penis slender, without swellings, with slit-like lumen in cross-section. Penial caecum is subcylindrical, nearly equal

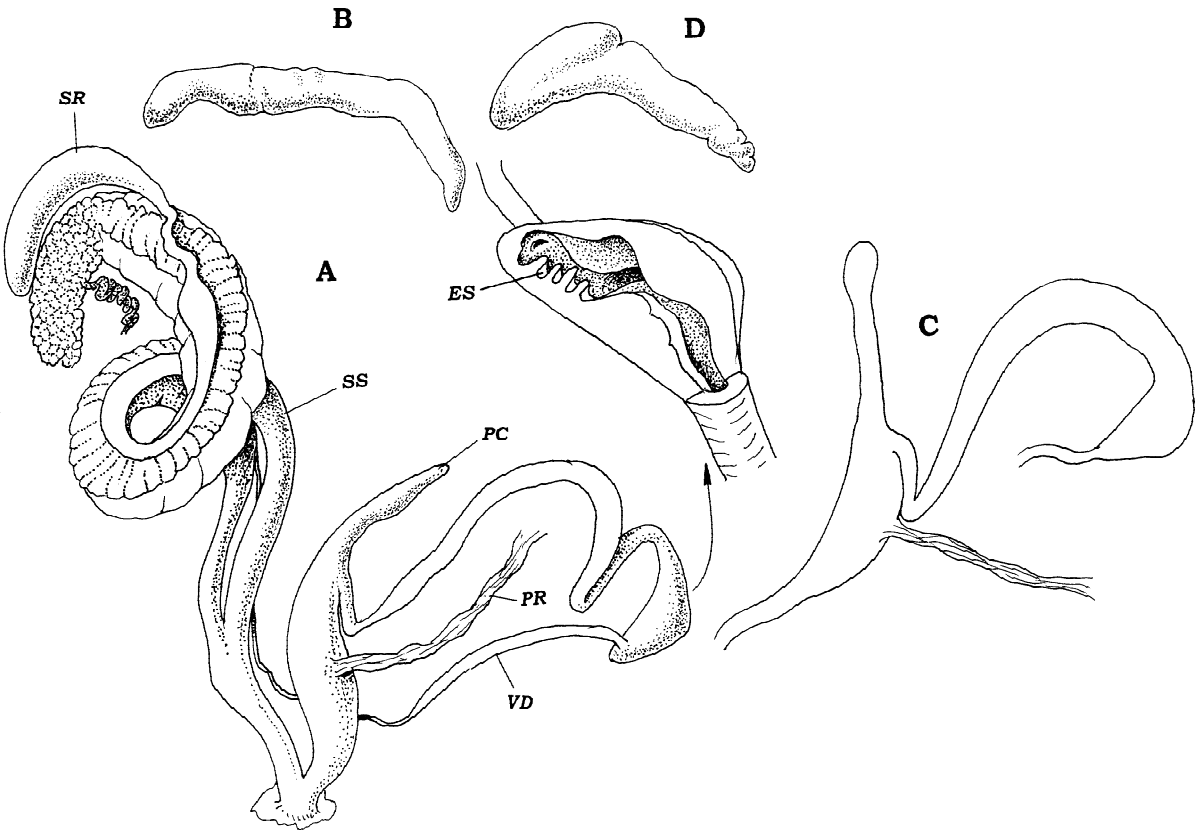

FIG. 4. *Orcula conica*. Trögener Klamm, Koschuta Mt., Karawanken, Krain, Austria. A – reproductive tract and inner structure of epiphallus. B – sperm mass taken from reservoir of spermatheca. C, D – distal part of male division and sperm mass of another specimen.

РИС. 4. *Orcula conica*. Ущелье Трегенер, гора Кошута, хребет Караванкен, Австрия. A – репродуктивный тракт и внутреннее строение эпифаллуса. B – конгломерация спермиев, извлечённая из резервуара семеприемника. C, D – дистальная часть мужского отдела и конгломерация спермиев другого экземпляра.

in length to penis, internally with two longitudinal grooves. Penial retractor attached to penis at the base of epiphallus. Free oviduct and vagina are of about equal length. Spermathecal duct uniformly cylindrical. Reservoir externally not differentiated from the duct, not attending albumen gland.

Spermatophores have not been found, but the structure of epiphallus clearly indicates, that spermatophore is short, and nearly all its surface bears large lamellar protrusions (14-15 in number).

Orcula conica (Rossmässler, 1837)
Fig. 4

Rossmässler, 1837: 17 (*Pupa*); Gittenberger, 1978: 20, Fig. 12; Harl et al., 2011: 178, Pl. 4, Fig. A (photo of syntype).

Locus typicus: Krain, Voralpen um Laibach [Kranjska (formerly part of Austria), Lower Alps near Ljubljana].

Material. Trögener Klamm, Koschuta Mt., Karawanken, Krain, Austria, 29.VII.2009, coll. et leg. J. Harl (3 specimens).

Distal section of vas deferens slightly expanded, enters epiphallus laterally, remaining very short "flagellum". Proximal end of epiphallus is much swollen, having nearly triangular outline, internally with strong axial pilasters and 3-4 transversal semicircular slits. Epiphallus forms a distinct curvature ("fracture") near entering the penis. Short section of epiphallus after bending tightly adjacent to penis, in result the caecum looks as a continuation of penis. Penis is rather short, fusiform. Penial caecum is moderately long, thin-walled, conical or slightly clavate, with a little thickened tip. Penial retractor attached approximately to the middle of penis, well below insertion of epiphallus. Free oviduct and vagina nearly equal in length. Lower half of spermathecal duct stout, than narrowed and may form a spindle-shaped thickening near reservoir. Latter lies on albumen gland.

Spermatophores in my specimens have been ly-

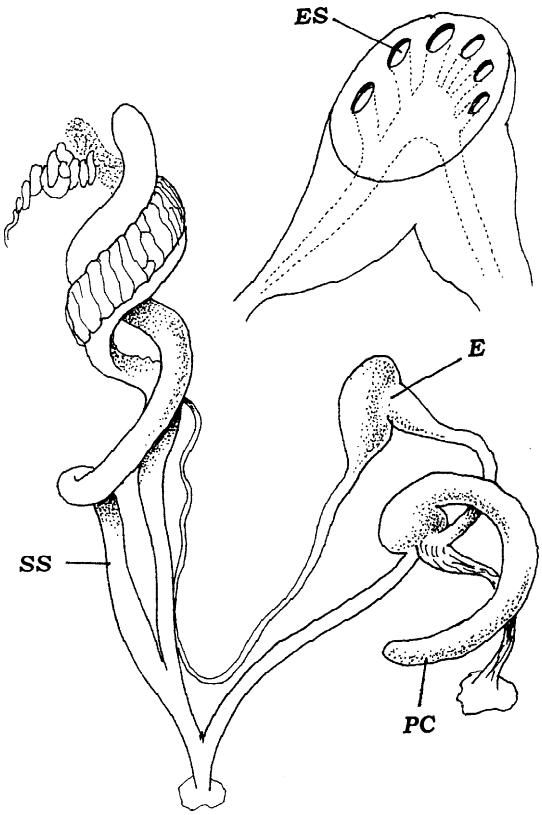

FIG. 5. *Orcula fuchsi*. Niederösterreich, Turmmauer, Kernhof (type locality). Reproductive tract and inner structure of epiphallus.

РИС. 5. *Orcula fuchsi*. Нижняя Австрия, Турммауэр, Кернхоф (типовое местонахождение). Репродуктивный тракт и внутреннее строение эпифаллуса.

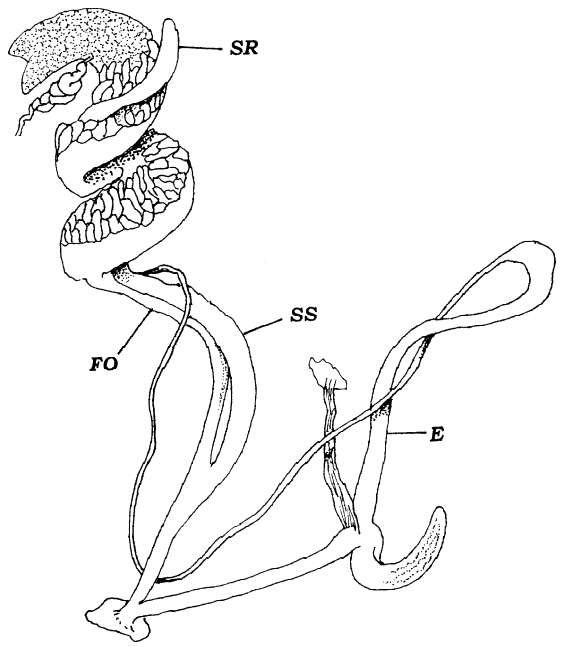

FIG. 6. *Orcula dolium gracilior*. Semmering-Gebiet. Reproductive tract.

РИС. 6. *Orcula dolium gracilior*. Земмеринг. Репродуктивный тракт.

sed, but in two individuals content of the spermatophores in form of dense whitish mass has been found in the spermatheca. Judging by inner relief of the epiphallus, posterior end of the spermatophore bears 3 or 4 transversal lamellar protrusions.

Remarks. 1. In the specimen depicted by Gittenberger [1978], penial retractor was attached to the bending of epiphallus, not to penis.

2. *O. conica* differs from all other members of the genus not only by shell shape, but by anatomical characters as well: position of caecum and peculiar shape of proximal end of epiphallus. Perhaps it deserves to be in a separate subgenus.

Orcula fuchsi Zimmermann, 1931
Fig. 5

Zimmermann, 1931: 44, Taf. VI, Fig. 3-5; 1932: 39; Gittenberger, 1978: 19-20, Fig. 10-11; Harl et al., 2011: 183, Pl. 1, Fig. A (photo of syntype).

Locus typicus: Niederösterreich, Turmmauer bei Kernhof.

Material. Niederösterreich, Turmmauer, Kernhof, X.1967 (topotype). (1 specimen). Niederösterreich, Mariazell, Gölber-Nord, 741 m a.s.l., 5.V.2009 (1 specimen).

Vas deferens of moderate length, very slightly and gradually expanded in distal section, entering swollen, bulb-like part of epiphallus. Inside this part of epiphallus there is a series (6 in total) of cavities rounded in cross-section, in which processes of spermatophore are formed. From this inflate portion subcylindrical distal part of epiphallus branches off laterally. Penis thin, slender, cylindrical, somewhat longer than epiphallus. Penial caecum long, subcylindrical, with markedly swollen basal part; this part is thick-walled, with narrow lumen. Retractor of penis attached to penis/epiphallus junction, at the base of caecum. Free oviduct is 2-3 times longer than vagina. Spermathecal stalk thick, slightly twisted, without clear reservoir, attending albumen gland.

Spermatophore in spermatheca has not been found. Judging by the length of epiphallus and shape of mentioned cavities in epiphallus, one can suggest that spermatophore itself is rather short, and protrusions on its posterior end have not lamellar but sooner needle-like shape.

Orcula dolium gracilior Zimmermann, 1932
Fig. 6

Zimmermann, 1932: 22 (pro “forma localis”); Gittenberger,

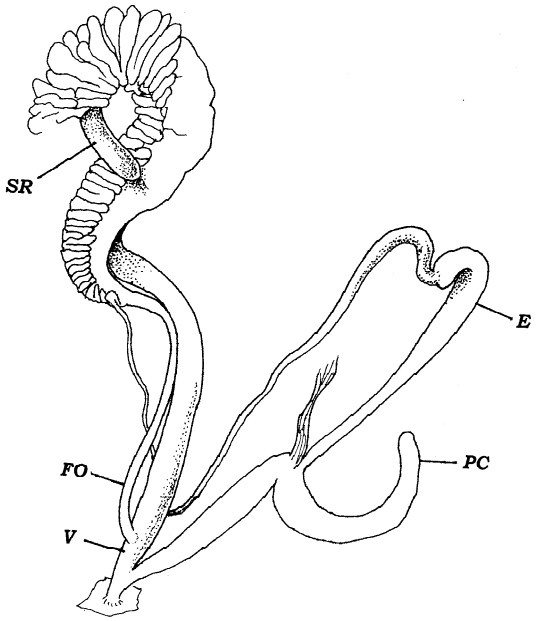

FIG. 7. *Orcula dolium edita*. Niederösterreich, Baumgartnerhaus, Luzboden. Reproductive tract.

РИС. 7. *Orcula dolium edita*. Нижняя Австрия, Баумгартнерхаус, Луцбоден. Репродуктивный тракт.

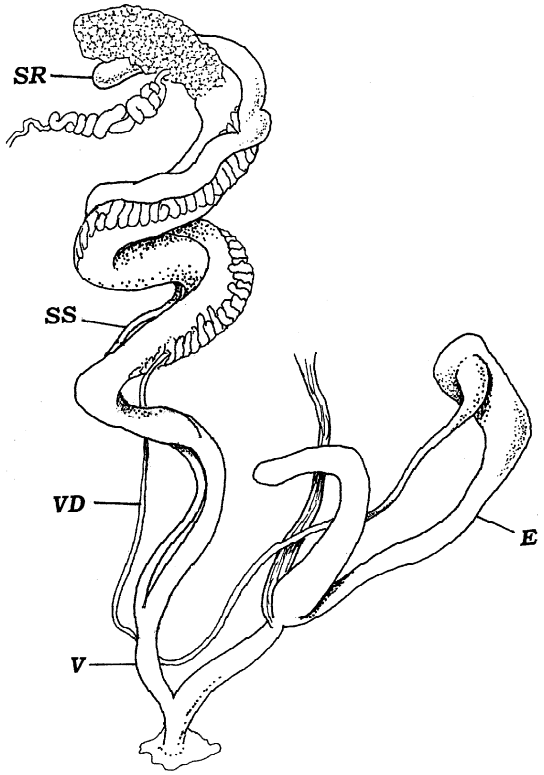

FIG. 8. *Orcula dolium infima*. Niederösterreich, St. Andrä/Wörden, Hagenbachklamm. Reproductive tract.

РИС. 8. *Orcula dolium infima*. Нижняя Австрия, Ст. Андре/Верден, ущ. Хагенбах. Репродуктивный тракт.

1978: 25, Fig. 19; Harl et al., 2011: 180, Pl. 2, Fig. D (photo of syntype).

Locus typicus: Niederösterreich, Semmering, Adlitzgraben.

Material. Austria, Semmering-Gebiet, VII.1970. Leg. O. Paget, det. W. Klemm. NHMW No. 79144 (1 specimen).

Vas deferens very long, uniformly thin, entering epiphallus apically. Epiphallus long, slender, the most proximal part of epiphallus little expanded. Penis rather thin, cylindrical, 1.5 times shorter than epiphallus. Penial caecum curved, with rounded apex. Penial retractor attached to penis/epiphallus junction just opposite to the base of caecum. Free oviduct is 2-3 times longer than very thin vagina. Spermathecal stalk comparatively thin, without distinct reservoir, attends lower part of albumen gland.

Spermatophore not found; on the drawing by Gittenberger [1978, p. 26, Fig. 19] one can see 12 or 13 short transversal slits inside expanded proximal part of epiphallus.

Orcula dolium edita Ehrmann, 1933
Fig. 7

Zimmermann, 1932: 17 (*Orcula dolium* morpha *edita*, nom. nud.); Ehrmann, 1933: 50 (*Orcula dolium* forma *edita*); Harl et al., 2011: 179, Pl. 2, Fig. B (photo of syntype).

Locus typicus: Niederösterreich, [Mt.] Schneeberg, [gorge] Eng (1000 m).

Material. Niederösterreich, Baumgartnerhaus, Luzboden, 1891. Leg. R. Sturany, det. E. Gittenberger. NHMW No. 73948 (1 specimen).

Vas deferens is rather long, thin, gradually expanding in distal third, entering epiphallus apically, with abrupt boundary. Epiphallus clavate, with expanded upper end. Penis subcylindrical, 1.5 times shorter than epiphallus. Penial caecum curved, with rounded apex. Retractor of penis attached to penis/epiphallus junction just opposite to the base of caecum. Free oviduct is about 5 times longer than vagina, and besides it seems that spermathecal stalk looks like the continuation of the vagina, and free oviduct branches off from this stalk to the side. Reservoir of spermatheca not expressed, attending albumen gland.

Spermatophore not found.

Remark. Unfortunately, I dissected only one specimen; if in the future the constancy of described topography of the spermathecal stalk, free oviduct, and vagina is confirmed, this form, perhaps, should be considered as a separate species.

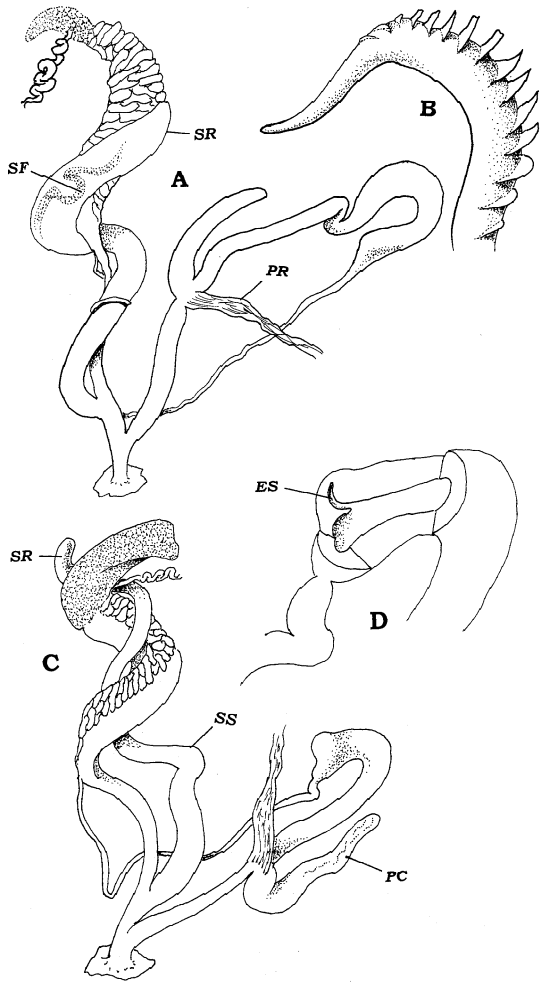

FIG. 9. *Orcula dolium dolium*. A, B – Austria, Styria, Gesäuse, Langgrießgraben, N of Johnsbach. A – reproductive tract. B – anterior part of spermatophore taken from spermatheca. C, D – Upper Austria, Dachstein, Wiesbergalm, Wiesberghaus. C – reproductive tract. D – inner structure of epiphallus.

РИС. 9. *Orcula dolium dolium*. A, B – Австрия, Штирия, Национальный парк Гезойзе, Ланггрисграбен, севернее Йонсбаха. A – репродуктивный тракт. B – передний конец сперматофора, извлечённый из семеприемника. C, D – Верхняя Австрия, Дахштайн, Визбергальм, Визбергхаус. C – репродуктивный тракт. D – внутреннее строение эпифаллуса.

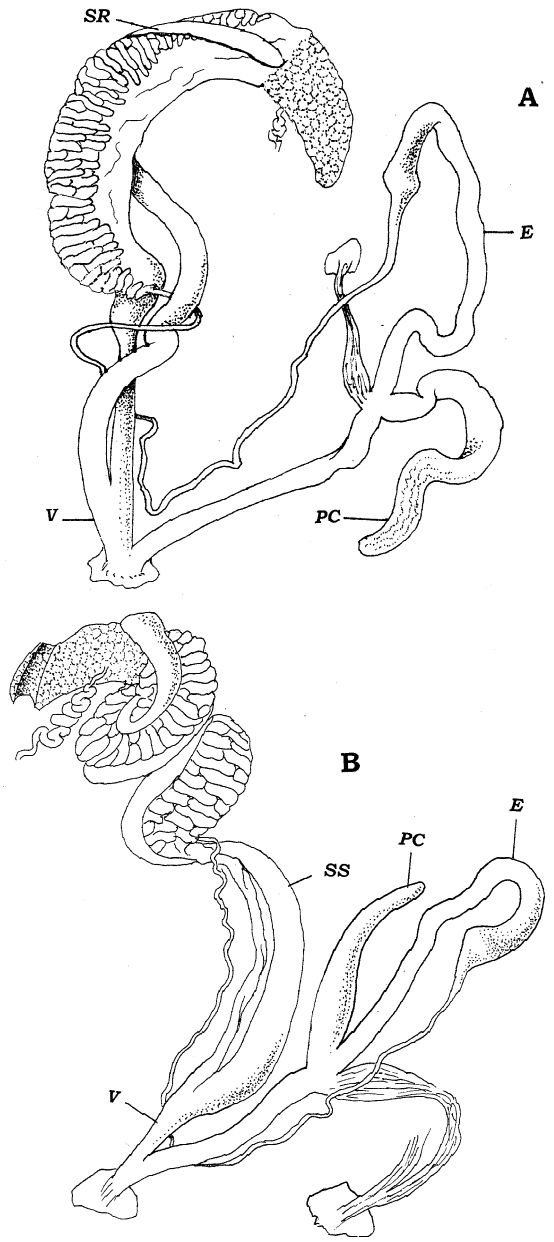

FIG. 10. *Orcula dolium dolium*. A – Austria, Karintia, Gailtaler Alpen, Kreuzen, Gailwaldbachgraben. Reproductive tract. B – Austria, Styria, Gesäuse, Johnsbachtal, Kaderalpl. Reproductive tract.

РИС. 10. *Orcula dolium dolium*. A – Австрия, Каринтия, Гайлталерские Альпы, Кройцен, Гайлвальдбахграбен. Репродуктивный тракт. B – Австрия, Штирия, Национальный парк Гезойзе, долина Йонсбаха, Кадеральпль. Репродуктивный тракт.

Moreover, it should be noted that *edita* has an unusually short vagina.

Orcula dolium infima Ehrmann, 1933
Fig. 8

Zimmermann, 1932: 14 (*Orcula dolium* morpha *infima*; nom. nud.); Ehrmann, 1933: 50 (*Orcula dolium* f. *infima*); Harl et al., 2011: 180, Pl. 2, Fig. H (photo of syntype).

Locus typicus: Niederösterreich, Kierling bei Klosterneuburg.

Material. NÖ-Wienerwald, St. Andrä/Wördern, Hagenbachklamm, 48°18,660 N, 16°12,582 E, 191 m, 26.03.2007. NHMW (1 specimen).

Vas deferens long, thin, markedly expanded in distalmost part, entering epiphallus laterally. Epiphallus clavate, with much thickened proximal end. Penis slender, about 2.5 times shorter than epiphallus. Penial caecum is rather long (longer than penis), with rounded apex. Penial retractor attached to

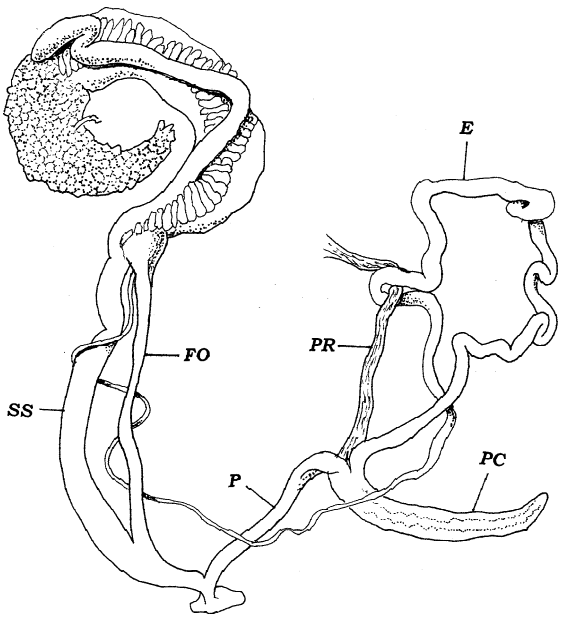

FIG. 11. *Orcula* sp. (ex gr. *dolium*) Austria, Kaisergebirge, Wilder Kaiser, Gamsanger. Reproductive tract.

РИС. 11. *Orcula* sp. (ex gr. *dolium*) Австрия, Кайзергебирге, Вильдеркайзер, Гамзангер. Репродуктивный тракт.

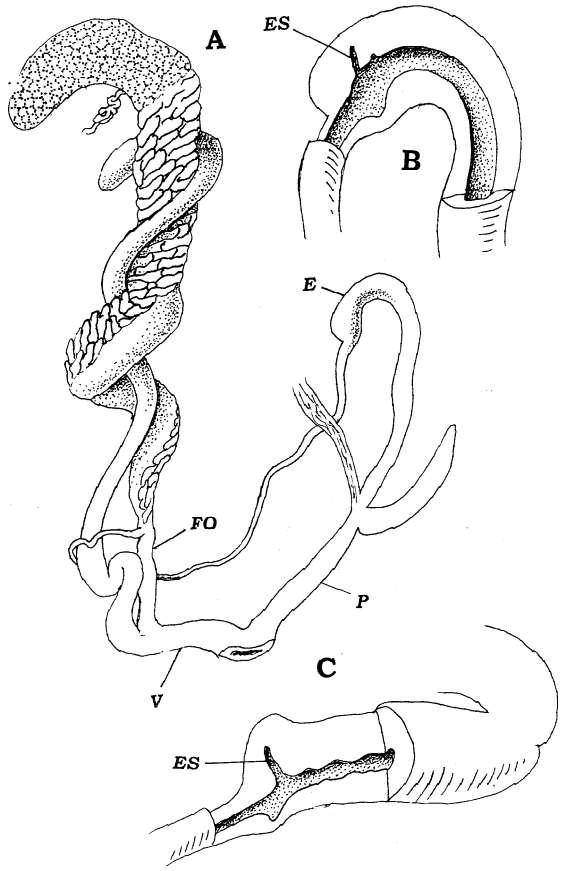

FIG. 12. *Orcula spoliata*. Sfruz, Credai, Valle de Non, Trentino [N Italy]. A, B – reproductive tract and inner structure of epiphallus. C – inner structure of epiphallus of another specimen.

РИС. 12. *Orcula spoliata.* Сфруз, Кредаи, долина р. Нон, Тренчино [сев. Италия]. А, В – репродуктивный тракт и внутреннее строение эпифаллуса. С - внутреннее строение эпифаллуса другого экземпляра.

penis/epiphallus junction, at base of caecum. Free oviduct is about 3 times longer than vagina. Spermathecal stalk narrowed in distal third, reservoir not differentiated, attends albumen gland.

Spermatophore not found.

Remark. I dissected only one specimen of *infima*, so it is hard to say whether it is a local form (or subspecies?) of *dolium*, or it is a separate species.

Orcula dolium dolium (Draparnaud, 1801)
Fig. 9, 10

Draparnaud, 1801: 62 (*Pupa*); Gittenberger, 1978: 25, Fig. 16, 17; Harl et al., 2011: 179, Pl. 2, Fig. A (photo of syntype).

Locus typicus: France (from title).

Material. Austria, Styria, Johnsbachtal, Gesäuse, Langgrießgraben, 17.IX.1996. Leg. & det. A. Schileyko (6 specimens).

Austria, Styria, Johnsbachtal, Gesäuse, Kaderalpl, 634 m, 24.IV.2008. Leg. & det. A. Schileyko (4 specimens).

Gailtaler Alpen, Kreuzen, Gailwaldbachgraben, Kärnten, 19.06.2007 (2 specimens).

Oberösterreich, Dachstein, Wiesbergalm, Wiesberghaus, 1685 m, 47°31,529 N, 13°37,493 E, 12.05.2008 (1 specimen).

Grazer Bergland, Semriach, Augraben, Steiermark, 503 m, 30.04.2008 (1 specimen).

Vas deferens enters slightly widened end of epiphallus apically. Epiphallus more or less curved. Penis equal to epiphallus in length or somewhat shorter. Penial caecum longer than penis. Retractor of penis attached to the penis at insertion of caecum. Free oviduct is 3-4 times longer than vagina. Spermathecal duct is stout, poorly differentiated reservoir lies on lower half of albumen gland or does not attend the gland.

Spermatophore has been found in spermatheca. Its anterior end provided with about 15 lamellar semilunar and triangular protrusions. Judging by inner structure of the epiphallus, posterior end of spermatophore bears one lamellar protrusion. Gittenberger [1978, Taf. I, Fig. 1] showed the photo of nearly intact spermatophore within spermatheca as it seen in translucent light. This specimen came from Spital near Semmering, Styria. On this figure one can see that the anterior section of spermatophore is a long (of about a half of spermatophore

length), smooth tubule; farther a section bearing lamellar protrusions (13-16 in number) follows; than there is a smooth-walled widened ampula; posterior end very short, with, seemingly, one protrusion.

Remarks. It should be paid attention to the anatomical variability of *Orcula dolium* s. lat. One can recognize at least two variants of reproductive tract structure.

1. "Normal" *O. dolium*, whose reproductive tracts are shown in Fig. 10, and by Gittenberger (1978: 24, Figs 16 and 17).

2. Two specimens from Langgrießgraben differ by unusually short and stout spermathecal stalk which does not reach albumen gland (Fig. 9A). They are typical *dolium*, just differ from "normal" by comparatively short shell.

At present it is hard to estimate taxonomical status of these variants; it is not excluded that these are different species.

It should be added that nobody dissected *Orcula dolium* from France that is why we do not know the anatomy of genuine *dolium*. Moreover, in the original description Draparnaud had not indicated exact type locality, and we can not dissect at least topotypes.

Orcula sp. (ex gr. *dolium*)
Fig. 11

Conchologically the specimen is typical *dolium*, but smaller: shell height 5.8 mm, width 2.8 mm.

Material. Kaisergebirge, Wilder Kaiser, Gamsanger, 1938 m, 47º33,682 N, 12º18,428 E, 31.07.2007 (1 specimen).

This specimen differs from *dolium* (sensu authors) by extraordinarily long epiphallus which is about 5-6 times longer than penis. Besides, vas deferens passes into epiphallus so gradually that it is impossible to determine real boundary between these ducts.

Spermatophore has not been found.

Orcula spoliata (Rossmässler, 1837)
Fig. 12

Rossmässler, 1837: 18 (*Pupa gularis* var.); Zimmermann, 1932: 35; Gittenberger, 1978: 22, Fig. 15.

Locus typicus: Tiroler Alpen [Südtirol/Alto Adige, Alps].

Material. Struz-Credai, Struz, Valle di Non, Trentino, 23.V.2010. Leg. et det. J. Harl (3 specimens).

Vas deferens moderately long, entering epiphallus slightly laterally (not terminally). Epiphallus forms a small widening in proximal part. Internally widened part of epiphallus contains one slit-like transversal cavity. Penis is about 1.5 times shorter than epiphallus, thin, slender. Penial caecum is not long, sleeve-like, with a little pointed apex. Penial retractor attached to penis/epiphallus junction, at base of caecum. Free oviduct and vagina are comparatively short, of approximately equal length. Spermathecal stalk uniformly cylindrical, without visible reservoir, attending albumen gland.

Spermatophore has not been found, but, judging by inner structure of proximal section of epiphallus, on posterior end of the spermatophore there is one lamellar protrusion.

Remark. The specimens dissected by me, are different from those have been studied by Gittenberger (1978: 22-23, Fig. 15). After Gittenberger, the topography and shape of distal end of epiphallus similar to that of *O. conica*, i.e. tightly adjacent to penis. Besides, in Gittenberger's specimens "Nach dem Lumen des Epiphallus ist der Spermatophor ähnlich wie bei *O. dolium* (Taf. I Fig. I) gebaut, nur ist Teil IV stumpf und nicht mit Septa versehen; Teil II trägt etwa 24 Septa." [According to the lumen of the epiphallus there is a spermatophore which is similar to that of *O. dolium* (Plate I. Figure I), only part IV is blunt and not equipped with septa, part II contains about 24 septa].

Orcula gularis (Rossmässler, 1837)
Fig. 13

Rossmässler, 1837: 17 (*Pupa*); Gittenberger, 1978: 27, Fig. 21, 22; Harl et al., 2011: 183, Pl. 1, Fig. I-J (photos of syntypes).

Locus typicus: "Loibl in Kärnthen".

Material. Austria, Styria, Langgrießgraben, N of Mt. Reichenstein, N of Johnsbach, 17.09.1996. Leg. & det. A. Schileyko (5 specimens).

Austria, Styria, Johnsbachtal, Gesäuse, Kaderalpl, 634 m, 24.04.2008. Leg. & det. A. Schileyko (5 specimens).

Austria, Weyer [Weyer Markt]. NHMW No. 73.950 (1 specimen).

Vas deferens is long, passes into epiphallus gradually, without abrupt boundary. Epiphallus long, subcylindrical to somewhat fusiform. Penis thin, 3-4 times shorter than epiphallus. Penial caecum more or less conical, curved. Penial retractor attached to penis/epiphallus junction or to very distal section of epiphallus. Free oviduct very long, 5-7 times longer than vagina. Spermathecal stalk thick, more or less twisted, reservoir is expressed to varying degrees, lies on upper part of spermoviduct or reaches albumen gland.

Spermatophore has been found in the spermatheca. Its very anterior end is smooth, elongate-conical, followed by the section, equipped with 14-20 triangular and almost rectangular outgrowths. Median part of spermatophore smooth, lacks any armament. Posterior end of the spermatophore bears 10-12 triangular protrusions.

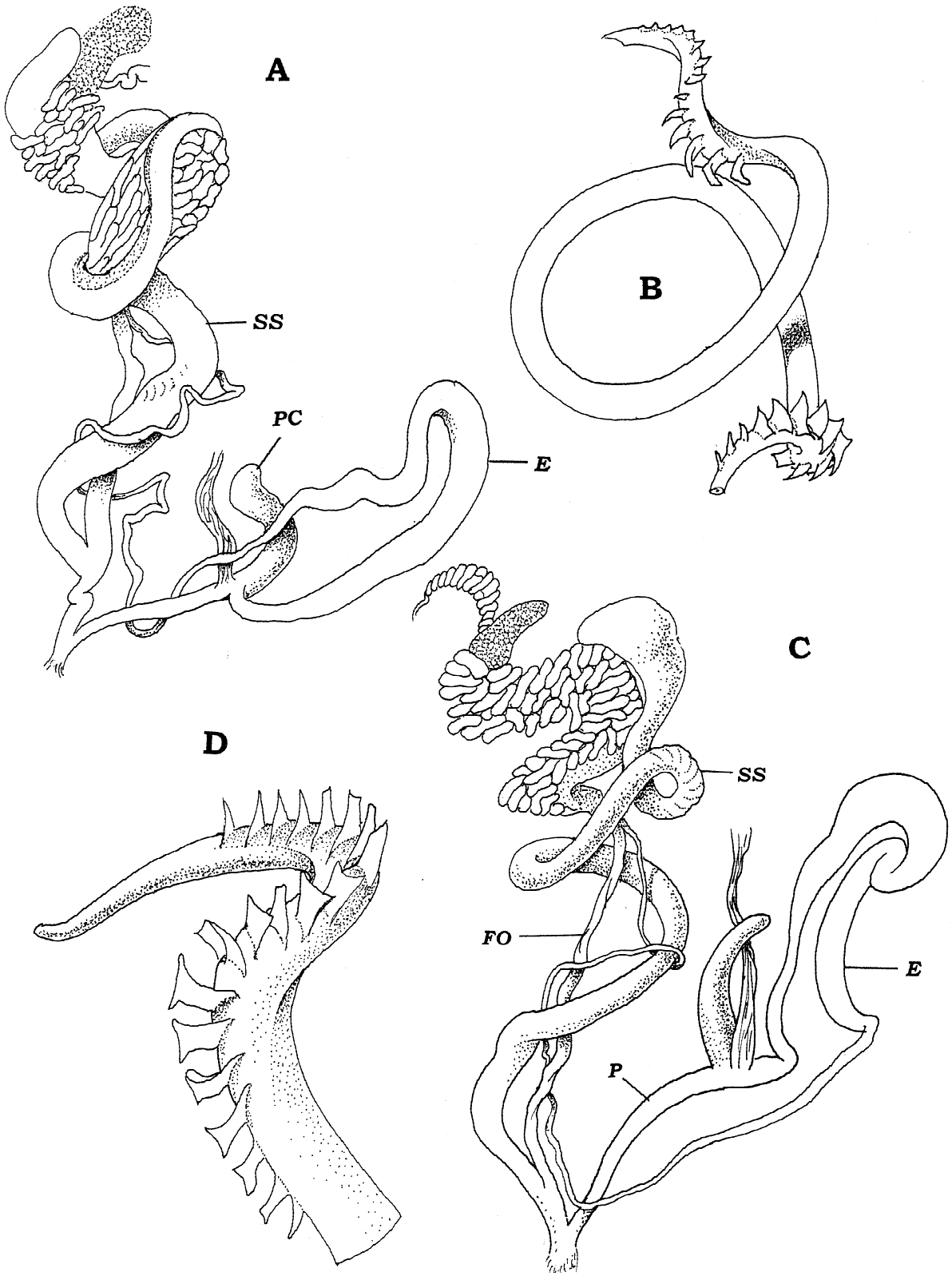

FIG. 13. *Orcula gularis*. A, B – Austria, Styria, Langgrießgraben, N of Johnsbach. A – reproductive tract. B – spermatophore taken from spermatheca. C, D – Austria, Styria, Gesäuse, Johnsbachtal, Kaderalpl. C – reproductive tract. D – anterior part of spermatophore taken from spermatheca.

РИС. 13. *Orcula gularis*. A, B – Австрия, Штирия, Ланггрисграбен, севернее Йонсбаха. A – репродуктивный тракт. B – сперматофор, извлечённый из семеприемника. C, D – Австрия, Штирия, Национальный парк Гезойзе, долина р. Йонсбах, Кадеральпль. C – репродуктивный тракт. D – передняя часть сперматофора, извлечённая из семеприемника.

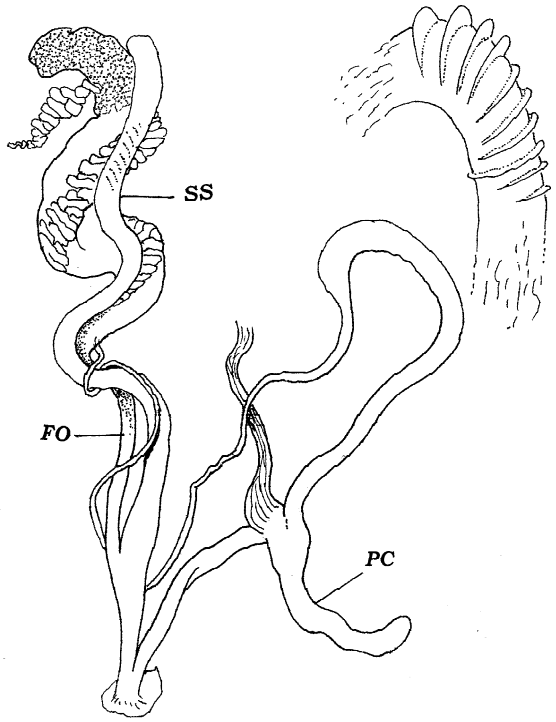

FIG. 14. *Orcula austriaca austriaca*. Austria, Gutenstein. Reproductive tract and fragment of spermatophore taken from spermatheca.

РИС. 14. *Orcula austriaca austriaca*. Австрия, Гутенштайн. Репродуктивный тракт и фрагмент сперматофора, извлечённый из семеприемника.

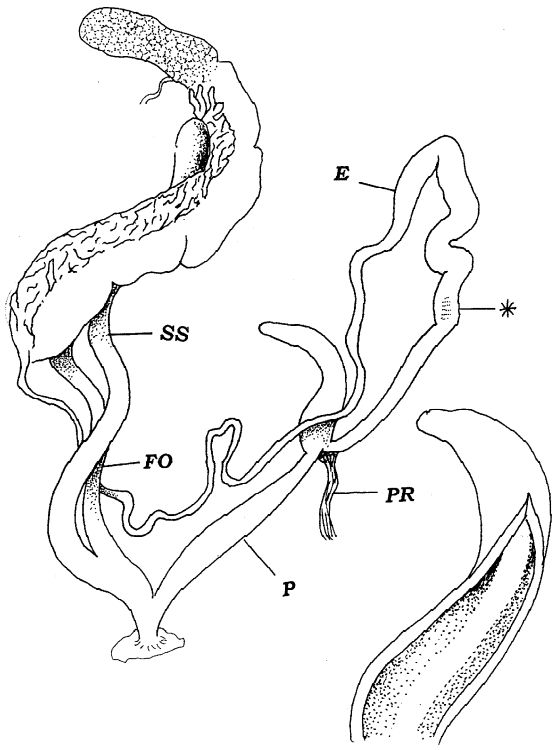

FIG. 15. *Orcula austriaca pseudofuchsi*. Niederösterreich, Ternitz, Gösing-Westwand. Reproductive tract and inner structure of penial caecum. *Asterisk* – inner structure of epiphallus seen through the wall of the organ.

РИС. 15. *Orcula austriaca pseudofuchsi*. Нижняя Австрия, Терниц, Гёзинг-Вестванд. Репродуктивный тракт и внутреннее строение пениального цекума. *Звёздочка* – внутренняя структура эпифаллуса, просвечивающая сквозь стенку органа.

Orcula austriaca austriaca Zimmermann, 1932
Fig. 14

Zimmermann, 1932: 37 (*O. spoliata* subsp.); Gittenberger, 1978: 30, Fig. 25, 26; Harl et al., 2011: 177, Pl. 1, fig. G (photo of syntype).

Locus typicus: Niederösterreich, Lilienfeld.

Material. Niederösterreich, Baumgartnerhaus, Luzboden, 1891. Leg. R. Sturany, det. E. Gittenberger. NHMW No. 73.948 (1 specimen).

Gutenstein [ca. 50 km SW of Vienna], 1935. NHMW No. 73.949 (1 specimen).

Vas deferens long, thin, little expanded near epiphallus. Epiphallus slightly thickened at proximal end, is about twice longer than subcylindrical penis. Penial caecum is not very long, irregularly cylindrical, with rounded summit. Retractor of penis attached to penis at base of caecum. Free oviduct is twice longer than vagina. Spermathecal duct is stout, nearly cylindrical, reservoir attending middle part of albumen gland.

Spermatophore. Fragment of spermatophore in spermatheca has been found. Armament of the spermatophore consists of several (10 in one of the dissected specimen) low lamellar protrusions of semilunar shape, these outgrowths are visible through wall of spermatheca as narrow dark lines. Anterior and posterior ends of the spermatophore have been lysed.

Orcula austriaca pseudofuchsi Klemm, 1967
Fig. 15

Klemm, 1967: 107; Harl et al., 2011: 178, Pl. 1, Fig. B (photo of holotype).

Locus typicus: Niederösterreich, bei Ternitz, oberste Felswände des Gösingberges (800 m).

Material. Niederösterreich, Ternitz, Gösing-Westwand, 04.V.2009. Leg. et det. A. Schileyko (2 specimens).

Vas deferens is long, thin, entering epiphallus terminally and very gradually. Epiphallus is long, slightly narrowed at both ends, internally with transversal lamellar structure; this structure is very weak except in the portion below middle of the organ (*asterisk* in Fig. 15), where it is visible through the wall of epiphallus. Penis rather thin, approximately twice shorter than epiphallus. Penial caecum is not

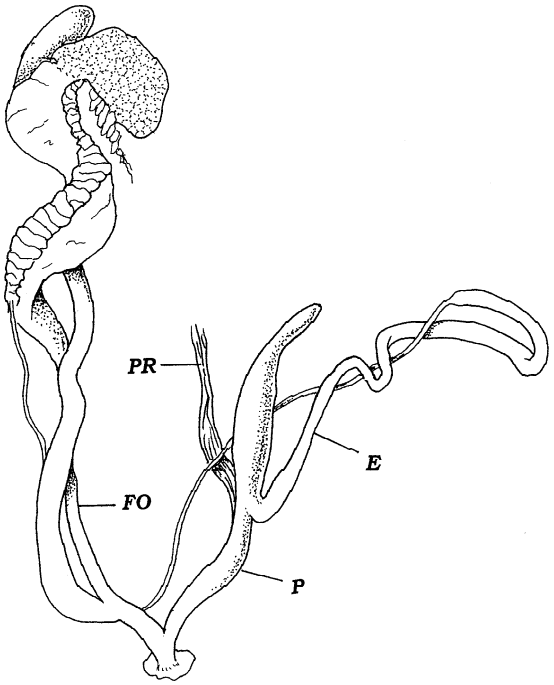

FIG. 16. *Orcula austriaca faueri*. Karawanken, Hochobirmassiv, Freibachgraben. Reproductive tract.

РИС. 16. *Orcula austriaca faueri*. Караванкен, Хохобирмассив, Фрайбахграбен. Репродуктивный тракт.

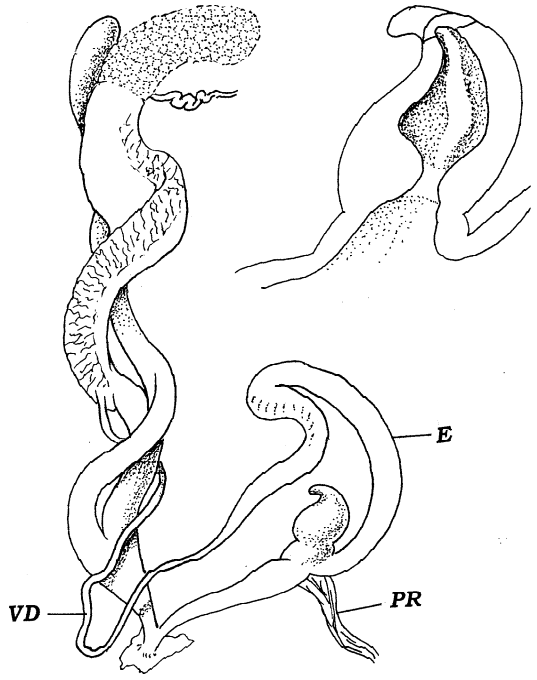

FIG. 17. *Orcula wagneri*. S Albania, Maja e Tomorit Mt. Reproductive tract and inner structure of penial caecum.

РИС. 17. *Orcula wagneri*. Ю. Албания, гора Майа-е-Томорит. Репродуктивный тракт и внутреннее строение пениального цекума.

long, irregularly conical, with rounded apex; internally contains one strong longitudinal fold. Retractor of penis comparatively weak, attached to penis/epiphallus junction just below basal section of caecum. Free oviduct is 2-2.5 times longer than vagina. Spermathecal duct rather stout, with poorly expressed reservoir, slightly not attending albumen gland.

Spermatophore not found, but judging by the inner structure of epiphallus, protrusions on the surface of spermatophore are small and densely arranged (at least in the middle portion of the spermatophore).

Orcula austriaca faueri Klemm, 1967
Fig. 16

Klemm, 1967: 101; Gittenberger, 1978: 32, Fig. 27; Harl et al., 2011: 178, Pl. 1, Fig. F (photo of holotype).

Locus typicus: Kärnten, Karawanken, Hochobirmassiv, Westfuss des Kuhberges, Freibachgraben (ca. 900 m).

Material. Karawanken, Hochobirmassiv, Freibachgraben, 808 m, 46°29,025 N, 14°26,049 E, 21.VI.2007 (1 specimen).

Vas deferens enormously long, uniformly thin, entering epiphallus terminally through a weak widening. Epiphallus thin, about 3 times longer than penis. Penis subcylindrical. Penial caecum a little longer than penis. Penial retractor attached to place of junction penis, epiphallus, and caecum. Free oviduct is about 4 times longer than vagina. Spermathecal duct rather stout, reservoir attending lower portion of albumen gland.

Spermatophore not found; judging by external appearance of epiphallus, spermatophore must be long, slender, with much reduced armament or without it.

Orcula wagneri
Sturany in Sturany et Wagner, 1914
Fig. 17

Sturany, Wagner, 1914: 45, Taf. 15, Fig. 82a-b; Harl et al., 2011: 186, Pl. 5, Figs. A (photo of holotype).

Locus typicus: Albanien, Mirdita [Mirditë], Berg Munela bei Oroshi [Orosh].

Material. "Tomorr 2200 m" [Maja e Tomorit Mt., S Albania]. NHMW 73.951 (1 specimen).

Vas deferens moderately long, uniformly thin, gradually entering epiphallus. Inside proximal section of epiphallus there are 10-11 slit-like semicircular cavities. Penis rather short. Penial caecum short, swollen, subglobular, with hook-like curved tip. Internally upper part of caecum supplied with a

short axial pilaster and sphincter-like thickening in basal part. Penial retractor attached to penis/epiphallus junction just opposite to the basal section of caecum. Free oviduct is twice longer than vagina. Spermathecal stalk nearly cylindrical, with poorly differentiated reservoir, attending basal part of albumen gland.

Spermatophore in spermatheca has not been found, but in the proximal end of epiphallus one can see 10 or 11 slit-like structures which correspond to the lamellar protrusions of the spermatophore.

Remark. *O. wagneri* is closely related to *O. schmidtii* (Küster, 1843) [see Gittenberger, 1978: 34, Figs. 30, 31]: both species have peculiar and similar shape of penial caecum. The material studied by Gittenberger came from Macedonia.

It should be mentioned that this applies only to the nominative subspecies of *O. schmidtii*, because caecum of *O. schmidtii transversalis* (Westerlund, 1894) of the island of Epirus (Greece) has a traditional shape [Hausdorf, 1987]. Perhaps, *transversalis* is a separate species, as originally described.

Remarks on genealogy of Orculidae

At the subfamily and generic level

It is hard to say who could be an ancestor of Orculidae, but with a high probability one can assume that it had elongated shell with a long columellar lamella, and a standard pupilloid set of accessory organs of the reproductive tract [Schileyko, 1984]. Full set consists of penial appendix (PA), penial caecum (PC), diverticle of spermathecal stalk (DSS), and flagellum (F). The presence of this set is, in my opinion, initial (plesiomorphic) and characteristic for the suborder Pupilloidei.

It is essential that this hypothetical ancestor lived, most likely, in mesophilous or hygrophilous conditions, since aridization of Western Palearctic started, by geological scale, not so long ago.

Among the Recent Orculidae no species which would have a full set of listed accessory organs; these organs in different taxa are present in various combinations.

In reality, the following combinations exist:

PA+PC+DSS – in the genus *Pilorcula* [Hudec, Lezhawa, 1969; Schileyko, 1984] and *Alvearella* [Hausdorf, 1996].

PC+DSS+F (flagellum rudimentary) – in *Pagodulina* (*Pagodulina*) [Schileyko, 1984, p. 130, fig. 60; Páll-Gergely, 2011: 474, Fig. 8].

PC+DSS – in *Odontocyclas* [Gittenberger, 1978]

PA+PC – in *Walklea* [Gittenberger, 1978], *Orculella*, *Schileykula* (part.) [Hausdorf, 1996; Páll-Gergely, 2011].

DSS+F (flagellum rudimentary) – in *Pagodulina* (*Crystallifera*) [Schileyko, 1984, p. 132, fig. 61].

Only PA – in *Agardhiella* [Gittenberger, 1974].

Only PC – in *Fauxulella*, *Anisoloma*, *Fauxulus*, *Orcula*, *Sphyradium, Schileykula* (part.) [Gittenberger, 1978; van Bruggen, Meredith, 1983; Hausdorf, 1996; Schileyko, 1984; Páll-Gergely, 2011].

Thus, among the Recent Orculidae the features of the genus *Pilorcula* correspond to those of the hypothetical ancestor (except for the flagellum). This is the basis for placing this genus near the common ancestor of the family Orculidae (Fig. 18). Noteworthy that the structure of spermatophores of *Pilorcula* differs from those of *Orcula*: although we do not know the structure of whole spermatophore (one can judge about its structure just from its fragment), it is known that part of it bears spirally directed smoothed riblets, without protuberances, and posterior end has semicircular lamellae (it follows from inner structure of epiphallus) [Schileyko, 1984, p. 119, Fig. 49 I and III]. It should be added that the species of *Pilorcula* live in the forest (i.e. not dry) habitats.

Apparently, the initial system "flagellum – penial appendix – penial caecum – diverticle of spermathecal stalk" in the hypothetical "proto-orculids" was functionally a single entity [Schileyko, 1984] which provided the formation and transfer of spermatophores.

Most likely, spermatophore is initially appeared as an isolating mechanism that prevents introgression. However, this mechanism is irrational because it is *post-copulatory*, and thus leads to waste of gametes. In case when the recipient chooses a wrong partner and receives the spermatophore, the location, shape and number of protuberances on it appeared not to be species specific and the nervous apparatus provides a signal to lysis of the spermatophore together with its contents.

Subsequently the morphological mechanisms preventing introgression have been simplified and replaced by more adequate and more economical behavioral (i.e. *pre-copulatory*) mechanisms (about which we know very little), and at the present time we see that in the most progressive groups (for example, *Sphyradium*) the spermatophores have disappeared.

As a result, the functional relationships between these accessory organs were gradually destroyed, and now we see that the listed organs in the members of different taxa disappear in any combinations [Schileyko, 2003; see below]. Moreover, sometimes in the limit of one genus some definite organ may be present or totally absent (for example – species of the genus *Schileykula* have, as a rule, a rudimentary penial appendix, but in *Sch. aculeata* Gittenberger et Menkhorst, 1993 the appendix is totally absent [Páll-Gergely, 2011].

It is appropriate to recall that similar processes of reduction (down to full disappearance) of acces-

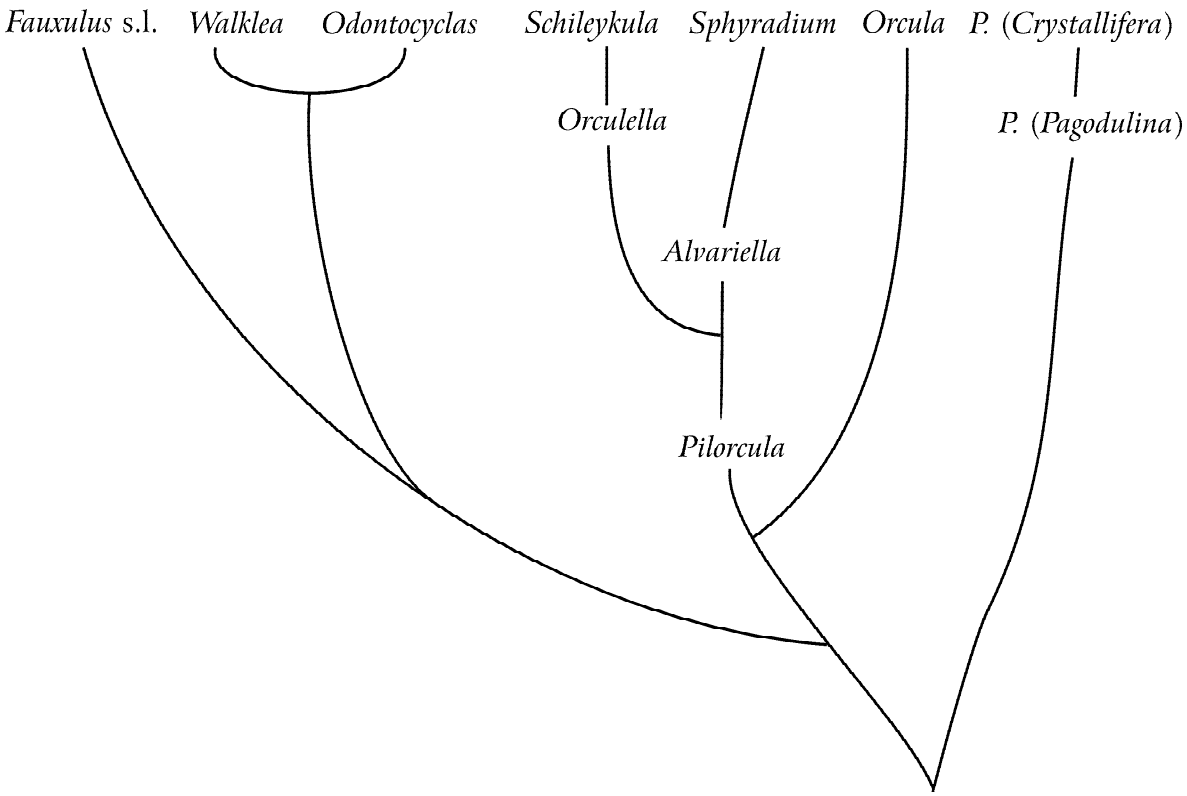

FIG. 18. Phylogenetic scheme of Orculidae.

РИС. 18. Филогенетическая схема Orculidae.

sory organs of the reproductive tract observed in some other Stylommatophora (Helicarionidae, Hygromiidae, many helicoid groups) [Schileyko, 1991a, b; 2004].

From ancient "proto-orculids" to which *Pilorcula* is close two branches originated: Pagodulininae and Odontocycladinae+Orculinae.

Pagodulininae, maintaining a rudimentary flagellum and diverticle of spermathecal stalk, lost penial appendix, and subgenus *Crystallifera* – also caecum, whereas in *Pagodulina* s. str. caecum preserved [Schileyko, 1984; Gittenberger, Pieper, 1984]. Judging from inner structure of epiphallus, in Pagodulininae spermatophores are absent, although in their direct ancestors spermatophores existed (rudimentary flagellum). Recent Pagodulininae, like the common ancestor of Orculidae, live in fairly humid forest habitats. So, I think, Pagodulininae originated directly from some "proto-orculids": they lost penial appendix but retained penial caecum (in *Pagodulina* s. str.), diverticle of spermathecal duct, and rudiment of flagellum.

Odontocycladinae, having preserved the elongated columellar lamellae, have acquired apomorphous characters in the form of secondary elements of aperture, which are formed only in subadult age (armament of superficial type).

With regard to the reproductive tract, in *Walklea* diverticle of spermathecal stalk has disappeared, in *Odontocyclas* – penial appendix, and in *Fauxulus* s. lat. both of these organs; penial caecum has preserved in all Odontocycladinae.

Apropos, it should be noted, that such a character as the presence/absence of penial caecum is not suitable for phylogenetical reconstructions, because it is present in all Orculidae, except for *Argna* and *Pagodulina lederi* (but in *P. pagodula* it is present).

Orculinae – currently the most flourishing taxon of Orculidae – is a group of genera, the historical connections between which mostly can be traced rather confident.

Thus, the monotypic genus *Alvariella* retained all three accessory organs (penial appendix, caecum and diverticle) and can be derived directly from *Pilorcula*. At the same time *Alvariella* got very peculiar characters: within the last whorl there are 3-4 palatal folds and the distal part of the penis in *A. multiplicata* sharply narrowed [Hausdorf, 1996]. The presence of such a peculiar structure of the penis brings *Alvariella* together with the genus *Sphyradium*, which, however, lost all appendages of the reproductive tract, except for a small caecum. It is important that just the genus *Sphyradium* (with a single species – *C. doliolum*), which has

lost almost all additional organs, is currently the most prosperous taxon of Orculidae.

On the evolutionary flourishing of this species testifies its huge area, covering the Mediterranean (including North Africa, Asia Minor, the Crimea and the Caucasus), a large part of Europe, northern Iran and Central Asia.

The genus *Orculella* originated, most likely, from the direct ancestor of *Alvariella* (but not from *Alvariella* itself) by the loss of diverticle of spermathecal stalk. The genus *Schileykula* is derived directly from *Orculella*, since it distinguished from the latter only in that the penial appendix in *Schileykula* is clearly rudimentary. The species of both genera (*Orculella* and *Schileykula*) live in regions with arid climate.

At the same time *Alvariella* has some very peculiar characters which differ this genus from *Sphyradium*: 1. In *Alvariella* penis as such is much reduced; 2. *Alvariella* has enormously developed penial appendix; 3. *Alvariella* has diverticle of spermathecal stalk; 4. Shell of *Alvariella* has deeply lying palatal plicae.

Since the species of the genus *Orcula* live in mesophilous or hygrophilous (sometimes very wet) conditions, it is appropriate to search for their ancestors among the archaic Orculidae. I would suggest that *Orcula* derived from *Pilorcula*-like ancestor due to the loss of all accessory organs, except for the penial caecum.

Thus, there is a reason to assume that the main direction of evolution of Orculidae was the reduction of additional organs of the reproductive tract – just as in many other stylommatophoran groups [Schileyko, 1991, 2003; see above]. In addition, in some cases there have been cases of secondary complications îf aperture armament (Odontocycladinae, *Alvariella*), but this process did not have significant evolutionary consequences.

The cladogram presented by Hausdorf [1996: 9] shows possible phylogenetic relationships within Orculidae. In general, I agree with this scheme, but I doubt in some particular points. So, my conclusions coincide with opinion of Hausdorf in the estimation of South-European *Odontocyclas* and *Walklea* as related to South-african taxa; in somewhat isolated position of *Orcula* in comparison with other Euroasiatic genera; in close connection between the genera *Alvariella* and *Sphyradium*.

On the reasons why I disagree with the phylogenetic position of some taxa see above.

The main reason for discrepancies between Hausdorf's cladogram and the scheme proposed here is different taxonomic evaluation of the weight of characters. More precisely, Hausdorf generally avoids the procedure of weighting evidence, recognizing, in effect, weight of all the characters to be equal. Hausdorf operates by 14 characters, of which 6 are associated with reproductive tract, and 8 – with shell.

In fact, the features are not equal, because, for example, the disappearance of any of accessory organs of the reproductive tract can occur in different branches of Orculidae independently. The same can be said about some elements of the aperture armature, in particular, about the degree of tooth development in the angular region. At the same time such a character, as a narrowed penis, in this case has considerable weight, since it means a lack of spermatophore, and, as a consequence, serious changes in the method of the transfer of sperm.

Another phylogenetically important feature is the type of penial appendix (pupilloid or orculoid). In all Orculidae, except for Argninae, the appendix is orculoid meanwhile in Argninae it is pupilloid. By the way, Hausdorf [1996] in the legend to his phylogenetical scheme indicates the character 2 with variants: 2(O) – pupilloid type, 2(1) – orculoid type, 2(-) – appendix is reduced or absent; however, variant 2(O) in the scheme is absent, although it corresponds to Argninae (Hausdorf considers this taxon to be a separate family).

In the genus *Orcula*

Klemm [1973: 124], on the base of conchological characters, has suggested the genealogical scheme of the genus *Orcula*. According to this scheme, the genus is a bouquet of 9 species (*conica*, *restituta*, *tolminensis*, *gularis*, *dolium*, *faueri*, *spoliata*, *pseudofuchsi*, *fuchsi*). Each species originated independently from some generalized "*Orcula*". From some species, in turn, branch off the taxa of lower rank (subspecies, forms). Situation with *pseudofuchsi* in this scheme remains unclear, since Klemm designates it as "infrasubspezifische" form, but does not write to which species this form belongs.

In my opinion, the main disadvantage of Klemm's scheme is that it implies an independent radiation of all basic species from a common ancestor, and ignores the fact that in some cases the relations "ancestor-descendant" take place in reality and the existence of some groups of species looks natural.

Indeed, within the genus *Orcula* it is possible to recognize two groups of species that differ from one another by the different ways of contact of the vas deferens with epiphallus.

Representatives of the first group are characterized by the presence of clear, often abrupt, boundary between vas deferens and epiphallus (*O. conica*, *O. fuchsi*, *O. restituta, O. spoliata, O. dolium*). Somewhat isolated position in this complex occupies *O. fuchsi*, since boundary between vas deferens and epiphallus in it is expressed especially clear, and proximal swelling of the epiphallus contains an unusual and complicated structure, where tail part

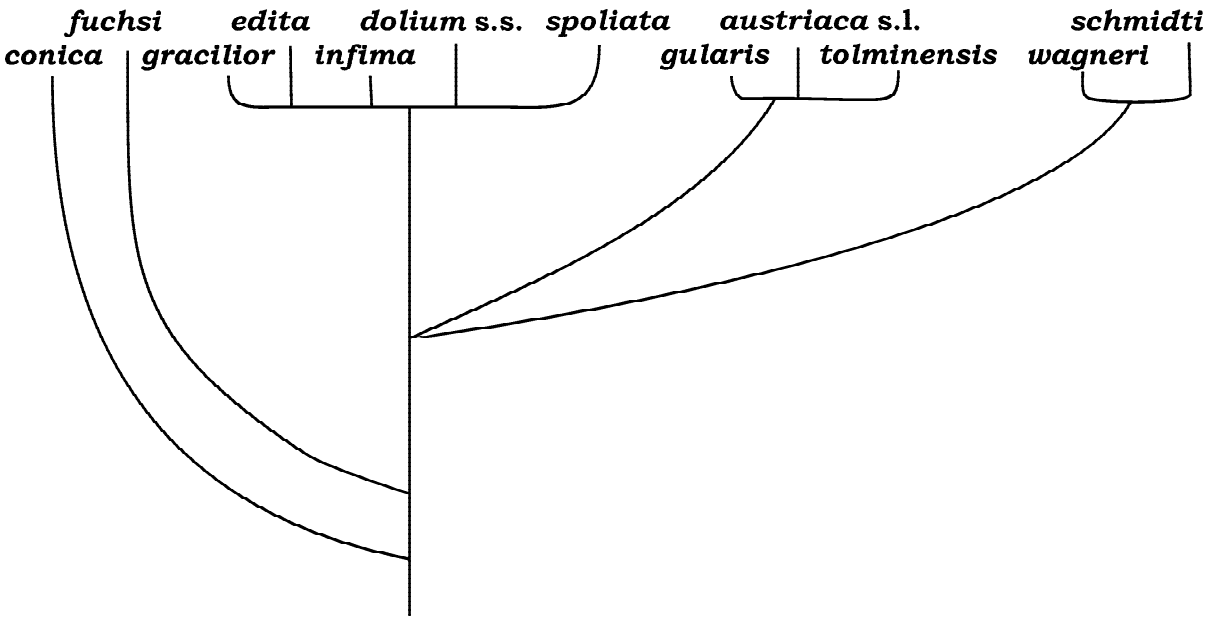

FIG. 19. Phylogenetic scheme of the genus *Orcula*.

РИС. 19. Филогенетическая схема рода *Orcula*.

of spermatophore is formed. The other flank in this part of genealogic tree occupies *O. conica*: it has peculiar (nearly triangular) shape of proximal end of epiphallus, characteristic "fracture" of epiphallus near caecum, and, besides, unusual for the genus conical shape of the shell.

In the members of the second group of species vas deferens passes into epiphallus gradually, without visible boundary (*O. gularis*, *O. austriaca*, *O. tolminensis*, *O. wagneri*, *O. schmidti*). Marginal position in this complex occupied by closely related species *O. wagneri* and *O. schmidti*, because of similar and peculiar shape of penial caecum (Fig. 17). Note in passing that some species of the genus *Schileykula* have a similar shape of penial caecum [Páll-Gergely, 2011].

It should be noted that there is no clear delimitation between these two groups: for some forms of *O. dolium* sensu lato it is hard to decide, to which group one can refer this form.

The problem is which of these groups is more archaic. I think that the ancient ancestor of Orculidae had a flagellum (see above). In the members of the first group the swelling of proximal part of epiphallus topographically and functionally (because the spermatophore is formed inside this part) corresponds to flagellum; thus, it is reasonable to assume that this section of the epiphallus is a homologue of flagellum. Based on these considerations I think that species belonging to the first group are more ancient.

Independently of these two groups, in the genus *Orcula* one can select five clusters:

1. *conica* (shell shape; peculiar position of penial caecum)
2. *fuchsi* (unique structure of epiphallus)
3. *dolium* s. lat.+*spoliata* (no special characters; clear boundary between vas deferens and epiphallus present)
4. *austriaca* s. lat.+*tolminensis*+ *gularis* (differs from No.3 just by the absence of clear boundary between vas deferens and epiphallus)
5. *schmidti*+*wagneri* (peculiar shape of penial caecum)

As said above, these clusters grouped in two species complexes: the first complex includes clusters No. 1-3 (clear boundary between vas deferens and epiphallus exists), the second – clusters 4-5 (no visible boundary between these two ducts). Possible relationships between species are shown on Fig. 19.

This genealogic scheme is based on above ideas. In Fig. 19 not included what I conventionally called "*Orcula* sp. (ex gr. *dolium*)" (see Fig. 11) because this is a strange form: its shell is very similar to *O. dolium dolium*, but the structure of its reproductive tract is very similar to *O. austriaca*.

Finally, few words on the taxonomic impor-

tance of the spermatophores. At the present there is not enough material to judge to what extent the spermatophores structure can be used to solve the taxonomic problems in the genus *Orcula*, but it is obvious that the spermatophores of different species are morphologically distinct. They differ by the number, shape, and topography of protrusions at anterior and posterior ends of the spermatophore.

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Об анатомии Orculidae со специальным рассмотрением сперматофоров (Gastropoda Pulmonata, Stylommatophora)

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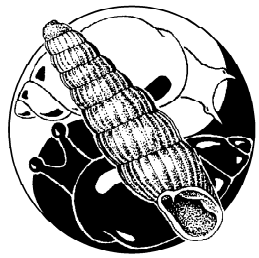
РЕФЕРАТ. Исследовано строение репродуктивного тракта 15 видов и подвидов (форм) южноафриканских и европейских (альпийских) Orculidae. У 12 из них обнаружены и описаны сперматофоры или найдены признаки, указывающие на то, что сперматофоры несомненно имеются (внутреннее строение эпифаллуса). Присутствие сперматофоров как таковых установлено для 5 видов Orculidae. Представлены гипотезы о возможных исторических связях между подсемействами и родами Orculidae и между видами рода *Orcula*.



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