

Revision of the genus *Retifusus* Dall, 1916 (Gastropoda: Buccinidae)

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ABSTRACT. The genus *Retifusus* was revised on the basis of conchological characters, radular morphology, foregut and stomach anatomy. Ten previously described and one new species are recognized as valid: *R. jessoensis* (Schrenck, 1863 in 1862-63), *R. virens* (Dall, 1877), *R. olivaceus* (Bartsch, 1929), *R. laticingulatus* (Golikov et Gulbin, 1977), *R. roseus* (Dall, 1877), *R. parvus* (Tiba, 1981), *R. attenuatus* (Golikov et Gulbin, 1977), *R. similis* (Golikov et Gulbin, 1977), *R. iturupus* (Golikov et Sirenko, 1998), *R. latericeus* (Möller, 1842), and *R. latiplicatus* sp. nov. *Chrysodomus brunneus* Dall, 1877 was synonymized with *R. jessoensis*; *Belayanarii* Yokoyama, 1926 – with *R. virens*; *Plicifusus saginatus* Tiba, 1980 and *Retifusus semiplicatus* Golikov in Golikov et Scarlato, 1985 – with *R. parvus*.

The taxonomy of the subfamily Colinae is in the state of flux, mostly due to high conchological variability of included species. Vast majority of species from North Pacific in the XIX and first half of the XX centuries have been described purely on conchological grounds, rarely the morphology of operculum was taken into account, even more rarely the radular characters. The situation is worsened by the rarity of many species and declining of collecting activities. As a result, although large amount of material was accumulated in the Russian museums and research institutes, it was collected long before the “molecular revolution”, and it is not feasible that any significant material will be available for molecular phylogenetic studies in near future. Nevertheless there is strong need of reliable tool for species identification as well as the “working” classification of the subfamily. In the current situation the use of anatomical and morphological characters remain the only applicable (although with reservations) approach to the alpha-taxonomy of many gastropod groups.

Among North Pacific Buccinidae there is a large number of small to medium-sized species with pronounced axial sculpture. They were attributed to one of the three genera – *Retifusus*, *Mohnia* and *Retimohnia*, although there is still no consensus on

the generic position and validity of many species, that were often transferred from one genus to another by different authors and usually without sufficient arguments [Tiba, Kosuge, 1992; McLean, 1995; Higo *et al.*, 1999; Okutani, 2000; Kantor, Sysoev, 2006; Kosyan, Kantor, 2009; Kantor, 2009; Hasegawa, 2009].

One of the taxa with complicated taxonomic history is *Retifusus*, proposed by W.H. Dall [1916, 1918] without any diagnosis or comments as a subgenus of *Plicifusus*. Originally it included three sections: *Latifusus* (type species *Chrysodomus griseus* Dall, 1889), *Microfusus* (type species *Chrysodomus acutispiratus* Sowerby, 1913, now accepted as *Nassaria acutispirata*) and *Helicofusus* (type species *Plicifusus laticordatus* Dall, 1907). Besides type species *Tritonium (Fusus) jessoense* Schrenck, 1863, Dall later [1921, 1925] attributed to *Retifusus* five species: *Plicifusus (Retifusus) oceanodromae* Dall, 1919, *Plicifusus (Retifusus) incisus* Dall, 1919, *Plicifusus (Retifusus) scissuratus* Dall, 1918, *Chrysodomus brunneus* Dall, 1877 (within the section *Microfusus*) and *Chrysodomus virens* Dall, 1877. Subsequent authors considered *Retifusus* either as a full genus [Golikov *et al.*, 2001; Kantor, Sysoev, 2005, 2006] or subgenus of *Plicifusus* [Higo *et al.*, 1999; Okutani, 2000]. *Chrysodomus brunneus*, *Chrysodomus virens* and *Mohnia okhotskana* were placed in *Mohnia* by Tiba and Kosuge [1992] based on operculum with somewhat subspiral nucleus. *Para-retifusus tenuis* (Okutani, 1966) was attributed to *Retifusus* by Kantor and Sysoev [2005, 2006]. Besides the above mentioned, five more species were included into *Retifusus* by Kosyan and Kantor [2009]: *Mohnia frielei* Dall, 1891, *Mohnia similis* Golikov et Gulbin, 1977, *Mohnia iturupa* Golikov et Sirenko, 1998, *Mohnia attenuata* Golikov et Gulbin, 1977, *Chrysodomus roseus*, Dall, 1877.

The revision of the entire genus has never been conducted before, anatomical and radular features of majority of the species remained unknown. The purpose of this paper is to fill this gap by newly obtained conchological, anatomical and radulae data and critically reevaluate the scope of the genus.

Material and methods

The examined material is stored in the collections of Russian Institutions (ZIN, IO, ZMMU). The radulae were extracted by gross dissection, cleaned using diluted bleach (NaOCl), air-dried, coated with gold and examined with a Tescan TS5130MM Scanning Electron Microscope (IPEE RAS).

Abbreviations of the depositories and conventions: BNHM – the Natural History Museum, London, UK; FV – fishery vessel; IMT – Institute of Malacology of Tokyo, Japan; IO – P.P. Shirshov Institute of Oceanology of RAS, Moscow, Russia; RV – research vessel; UKM – Rikuzentakata City Museum, Rikuzentakata, Iwate, Japan; UMUT – University Museum of the University of Tokyo; USNM – the Natural History Museum, Smithsonian Institution, Washington, DC, USA; ZIN – Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia; ZMMU – Zoological Museum of Moscow State university, Moscow, Russia; ZMUC – Zoological Museum, University of Copenhagen, Denmark.

Abbreviations on the figures: **adg**, opening of anterior duct of digestive gland; **AL**, aperture length; **ao**, anterior aorta; **aoe**, anterior oesophagus; **bm**, buccal mass; **cg**, capsule gland; **cm**, columellar muscle; **ct**, ctenidium; **dg**, digestive gland; **dgl**, duct of gland of Leiblein; **eye**, eye; **fo**, female orifice; **ft**, foot; **gl**, gland of Leiblein; **H**, height of the shell, **h**, height of the last whorl; **hd**, head; **hg**, hypobranchial gland; **int**, intestine; **kd**, kidney; **lfl**, longitudinal fold on inner stomach wall; **mrr**, medial retractor of radula; **n**, nerves; **nr**, nerve ring; **oeo**, oesophageal opening; **odn**, odontophore nerves; **odr**, odontophore retractors; **op**, operculum; **os**, osphradium; **p**, penis; **pdg**, opening of posterior duct of digestive gland; **pma**, posterior mixing area; **poe**, posterior oesophagus; **pr**, proboscis; **prp**, propodium; **prpg**, propodial groove; **prrr**, proboscis retractors; **pw**, proboscis wall; **r**, radula; **rd**, rhynchodaeum; **re**, rectum; **s**, siphon; **sd**, salivary duct; **sg**, salivary gland; **sp**, seminal papilla; **so**, seminal opening; **ss**, salivary pouches; **st**, stomach; **va**, vagina; **vl**, valve of Leiblein.

Systematics

Order Neogastropoda Wenz, 1938
Family Buccinidae Rafinesque, 1815
Subfamily Colinae Gray, 1857

Genus *Retifusus* Dall, 1916

Plicifusus (*Retifusus*) Dall, 1916: 8.

Type species – *Tritonium jessoense* Schrenck, 1867, by original designation.

Diagnosis. Shell rather small comparing to other genera of Colinae, from 8 to 36 mm in height, broad or elongated-fusiform, with moderately or quickly increasing whorls' diameter; last whorl comprises about 0.75 of shell height, with moderately long, straight or slightly curved to left siphonal canal. Aperture moderately high, about 0.5 of shell height; outer lip evenly arcuate. Operculum oval with terminal nucleus, strongly dislodged leftward. Axial sculpture represented by prominent varying in number orthocline axial ribs, becoming obsolete on lower part of shell base, up to 15 on penultimate whorl; in *R. roseus* axial sculpture absent, in *R. attenuatus* present only on upper whorls. Spiral sculpture represented by multiple cords (from 5 in *R. laticingulatus* to 10 in *R. jessoensis*), sometimes secondary striae present (*R. virens*).

Rachidian teeth of radula with 5-6 (*R. jessoensis* and *R. laticingulatus*), 3-4 (*R. olivaceus* and *R. virens*) or 3 (*R. roseus*, *R. attenuatus*, *R. similis*, *R. iturupus*, and *R. latiplicatus* sp. nov.) sharp cusps on the rounded posterior edge of basal plate; length of cusps diminishes from center to periphery of the plate; seldom the cusps are of equal length. Lateral teeth normally have three nearly equal in length cusps, but this number may increase up to 5 in *R. jessoensis* and *R. laticingulatus*. The width of radula relatively to aperture length diminishes with age. Salivary glands of *R. jessoensis*, *R. olivaceus*, *R. virens* and *R. laticingulatus* are small, not fused, with rather thick and weakly twisted salivary ducts. Salivary glands of the rest of included species are large, about two thirds of proboscis length, with very thick, not twisted salivary ducts, forming salivary pouches in some species (*R. parvus*, *R. roseus*, *R. latericeus* and *R. latiplicatus* sp. nov.) Stomach comparing to proboscis large, with small posterior mixing area. Penis of *R. jessoensis* and *R. olivaceus* with small and thin narrowing to the tip seminal papilla, while that of *R. parvus*, *R. roseus*, *R. atiplicatus* sp. nov. and *R. attenuatus* – with large conical papilla, situated on upper lateral side of penis, with seminal opening surrounded by tiny papillae, not visible with naked eye.

From *Neptunea* Röding, 1798, *Colus* Röding, 1798, *Aulacofusus* Dall, 1918, *Latisipho* Dall, 1916 the genus *Retifusus* differs by smaller size and presence of defined axial ribs; from *Plicifusus* Dall, 1902 – by smaller sizes and radula with similar in length cusps of lateral teeth; from *Pararetifusus* Kosuge, 1967, *Fusipagoda* Habe and Ito, 1965, and *Mohnia* Friele, 1879 – by presence of axial ribs and operculum with terminal nucleus. From most similar genus *Retimohnia* McLean, 1995 species of *Retifusus* differ by lateral teeth of radula, which have unequally sized cusps in *Retimohnia*, and operculum with terminal nucleus, versus subspiral nucleus in the latter genus.

Remarks. As accepted here, *Retifusus* is rather heterogeneous, somewhat loosely defined genus broadly distributed in North Pacific and Arctic Oceans. While the type species, *R. jessoensis* as well as *R. laticingulatus* possess rather characteristic radulae with multicuspid rachidians, there are species with only three cusps on the rachidian. Several species – *R. parvus*, *R. roseus*, *R. latericeus*, *R. atiplicatus* sp. nov., *R. attenuatus*, *R. iturupus* and *R. similis* differ from the rest of *Retifusus* species in having penis with large papilla and lateral radular teeth with shorter and thicker cusps. *R. parvus*, *R. roseus*, *R. latericeus*, and *R. atiplicatus* sp. nov., in their turn, are distinct in possessing salivary pouches of salivary ducts. Thus, it is not impossible, that currently accepted scope of *Retifusus* include several phylogenetic groups, although at the current state we are not able to prove it confidently.

Retifusus jessoensis Schrenck
(Schrenck, 1863 in 1862-63)
(Figs. 1, 2A-E, 3-5, 6A-C, 7)

- Tritonium (Fusus) jessoense* Schrenck, 1863 in 1862-1863: 513. – Schrenck, 1867: 426, t. 17, figs. 8-10.
Fusus (Sipho?) manchuricus E. A. Smith, 1875: 422.
Chrysodomus brunneus Dall, 1877: 1, **syn. nov.**
Sipho brunneus – Tryon, 1881: 130, pl. 53, fig. 343.
Sipho jessoensis – Tryon, 1881: 131, pl. 53, fig. 345-346.
Tritonofusus (Plicifusus) brunneus – Dall, 1902: 525, pl. 34, fig. 1.
Plicifusus (Microfusus) brunneus – Dall, 1921: 93. – Abbott, 1974: 216.
Retifusus brunneus – Golikov, Gulbin, 1977: 187. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 199, pl. 101 K.
Mohnia brunneus – Tiba, Kosuge, 1992: 3-5.
Plicifusus (Retifusus) brunneus – Higo *et al.*, 1999: 230.
Plicifusus (Retifusus) jessoensis – Higo *et al.*, 1999: 230.
Mohnia (Retimohnia) yanamii – Okutani *et al.*, 2000: 463, pl. 230, fig. 46 (non Yokoyama, 1926).
Retifusus jessoensis – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 199, pl. 101 G. – Sirenko *et al.*, 2013: 162.
Mohnia yanamii – Kantor, Sysoev, 2005: 133. – Kantor, Sysoev, 2006: 188, pl. 93 C (non Yokoyama, 1926).
Retifusus yanamii – Sirenko *et al.*, 2013: 162 (non Yokoyama, 1926).

Types: syntypes of *Tritonium (Fusus) jessoensis* – not traced; four syntypes of *Fusus (Sipho?) manchuricus* – BNHM 1873.8.6.23; syntypes of *Chrysodomus brunneus* – USNM 108984, 635708.

Type localities: *Tritonium (Fusus) jessoensis* – Hakodate, Hokkaido, Japan; *Fusus (Sipho?) manchuricus* – eastern Honshu, 42°58'N, 145°24'E, 88 m, sand and mud; *Chrysodomus brunneus* – Etolin cape, Nunivak Island, Bering Sea, 15 m..

Material examined: 10 lots (36 specimens). ZIN 34121/16, Sea of Japan, Peter the Great Bay(?), coll. Derugin, 1926 (spm. no. 1 dissected). ZIN uncataloged, RV *Toporok*, sta. 149, 47°00'N, 143°40'E, south-east Sakhalin, transect from

Siraura, 103 m, 1.10.1949 (3 spms, nos. 2-4 dissected). ZIN uncataloged, RV *Poseidon*, Sakhalin, Pogranichnoye village, transect 2, sta. 14, 78 m, 03.07.1978 (14 spms., no. 5 dissected). ZIN uncataloged, RV *Toporok*, southern Sakhalin, Tatar Strait, sta. 46, transect from Tomarioru, 61-89 m. 26.08.1949 (no. 6 dissected). ZIN 32450/15, RV *Toporok*, Kurile-Sakhalin expedition, sta. 120, transect Shikotan – Kunashir, 63 m, sand, 22.09.1949 (12 spms., no. 7 dissected). ZIN 58415, north Kurile Islands, RV *Gidrolog*, sta. 16, 100 m, sand with pebble, 14.10.1952 (no. 8 dissected). IO, northern Okhotsk Sea, RV *Vityaz*, sta. 56, 57°12.5'N, 152°23.0'E, 397 m (no. 9 dissected). IO, eastern Kamchatka, RV *Vityaz*, sta. 1347, 53°1'N, 160°9'E, 152 m, 20.05.1952 (spm. no. 10 dissected). IO, southern Kamchatka, RV *Vityaz*, sta. 1331, 51°50'N, 158°13'E, 83 m, 16.05.1952 (spm. no. 11 dissected). IO, north-western Bering Sea, RV *Vityaz*, sta. 1541, 62°6'N, 179°28'E, 110 m 18.06.1952 (spm. no. 12 dissected).

Description. Shell from 18 to 35 mm in height (Table 1), broad to elongate fusiform, solid, with well defined, medium long, slightly curved leftwards siphonal canal (Fig. 1, 2 A-E). Periostracum from light beige to dark brown in color; shell under periostracum white. Spiral sculpture represented by distinct spiral cords, about 10 on penultimate whorl. Spiral cords often covered by secondary spiral striae. Axial sculpture consists of well visible incremental lines and from straight to S-shaped axial ribs (10-15 on penultimate whorl).

Soft body. Mantle spans one whorl, kidney – 0.25, the remaining whorls occupied by digestive gland and gonad (Fig. 3A). Head wide and short, with broadly spaced short and thick contracted tentacles (Fig. 3E). Large brown eyes situated on small lobes in basal part of tentacles. Foot folded transversely, with deep propodial groove, isolating rather wide propodium. Operculum oval with terminal nucleus dislodged leftward. Penis situated on the right of head (Fig. 3E). It is elongated, tapering towards end; small seminal papilla, represented by thin elongated cone, situated in small deepening on its top. Capsule gland (Fig. 3B, **cg**) large, comprising about half mantle length, with ventrally situated vagina and large slit-like female orifice (Fig. 3B, **fo**). **Mantle** length slightly exceeds width, siphon long (Fig. 3B). Osphradium crescent-curved, occupies less than half mantle length and ¼ of its width. Ctenidium is ¼ of width and ¾ length of mantle. Hypobranchial gland represented by low transverse folds, covered with particles of mucus and silt. Rectum spans half mantle length.

Digestive system. Proboscis straight within rhynchodaeum. Mouth opening surrounded by three inflated lips. Paired proboscis retractors detach from both sides of rhynchodaeum in its anterior part (Fig. 3 D,F, **pr**). Buccal mass occupies whole length of proboscis. Multiple muscular bands of odontophore retractors come out of buccal mass base and attach to proboscis walls (Fig. 3C, **odr**). Well noticeable medial retractor of radula starts from posterior part of radular sac (Fig. 3C, **mrr**).



FIG. 1. Shells of *Retifusus jessoensis*. **A** – syntype of *Sipho manchuricus*: eastern Honshu, 42°58'N, 145°24'E, 88 m. **B** – no. 1, Sea of Japan, Peter the Great Bay(?) (radula on Fig. 4A). **C-E** – south-east Sakhalin, transect from Siraura, 103 m, **C** – no. 2, radula on Fig. 4B; **D** – no. 3, radula on Fig. 4C; **E** – no. 4 (radula on Fig. 4E-F). **F** – no. 5: Sakhalin, Pogranichnoye village, 78 m (radula on Fig. 4D). **G** – no. 6: Kurile Islands, transect from Tomarioru, 61-89 m (radula on Fig. 5A). **H-I**: Southern Kurile Islands, transect Shikotan – Kunashir, 63 m, **H** – no. 7, radula on Fig. 5C-D, anatomy on Fig. 3; **I** – no radula, anatomy on Fig. 3). **K** – no. 8: North Kurile Islands, 100 m (radula on Fig. 5B, anatomy on Fig. 3). Scale bar 10 mm.

РИС. 1. Раковины *Retifusus jessoensis*. **A** – синтип *Sipho manchuricus*, восточный Хонсю, 42°58'N, 145°24'E, 88 м. **B** – № 1: Японское море, Залив Петра Великого(?) (радула на Рис. 4A). **C-E** – юго-восточный Сахалин, разрез от Сираура, 103 м, **C** – № 2 (радула на Рис. 4B), **D** – № 3 (радула на Рис. 4C), **E** – № 4 (радула на Рис. 4E-F). **F** – № 5: Сахалин, пос. Пограничное, 78 м (радула на Рис. 4D). **G** – № 6: Курильские острова, разрез от Томари, 61-89 м (радула на Рис. 5A). **H-I**: Южные Курильские острова, разрез Шикотан – Кунашир, 63 м, **H** – №7, радула на Рис. 5C-D, анатомия на Рис. 3А, С-Н; **I** – анатомия на Рис. 3. **K** – № 8: Северные Курильские острова, 100 м (радула на Рис. 5B, радула на Рис. 3). Масштабный отрезок 10 мм.

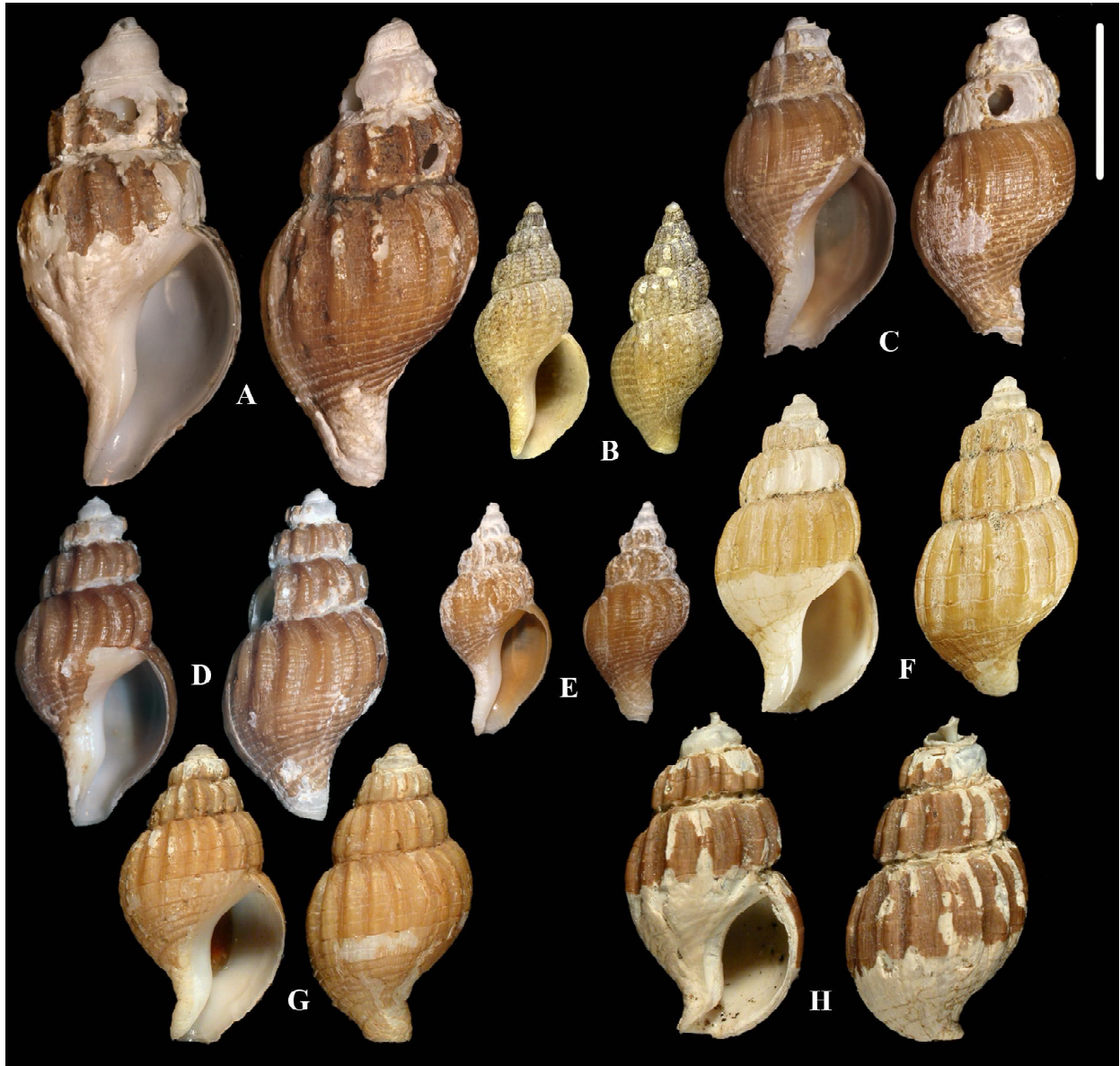


FIG. 2. Shells of *Retifusus*: **A** – *R. jessoensis* no. 9: northern Okhotsk Sea, 57°12.5'N, 152°23.0'E, 397 m (radula on Fig. 5E). **B** – holotype of *Chrysodomus brunneus*, Etolin cape, Nunivak Island, Bering Sea, 15 m. **C** – *R. jessoensis* no. 10: eastern Kamchatka, 53°1'N, 160°9'E, 152 m (radula on Fig. 5F). **D** – *R. jessoensis* no. 11: southern Kamchatka, 51°50'N, 158°13'E, 83 m (radula on Fig. 6A-B). **E** – *R. jessoensis* no. 12: north-western Bering Sea, 62°6'N, 179°28'E, 110 m (radula on Fig. 6C). **F** – holotype of *R. laticingulatus*: Shikotan, Kurile Islands, 181 m. **G-H** – paratypes of *R. laticingulatus*: transect from Shikotan (South Kurile Islands) to the ocean, 170 m (**G** – paratype 1, radula on Fig. 6D; **H** – paratype 2). Scale bar 10 mm.

РИС. 2. Раковины *Retifusus*: **A** – *R. jessoensis* № 9: северная часть Охотского моря, 57°12.5'N, 152°23.0'E, 397 м (радула на Рис. 5E). **B** – голотип *Chrysodomus brunneus*, мыс Этолин, о. Нунивак, Берингово море, 15 м. **C** – *R. jessoensis* № 10: восточная Камчатка, 53°1'N, 160°9'E, 152 м (радула на Рис. 5F). **D** – *R. jessoensis* № 11: южная Камчатка, 51°50'N, 158°13'E, 83 м (радула на Рис. 6A-B). **E** – *R. jessoensis* № 12: северо-западная часть Берингова моря, 62°6'N, 179°28'E, 110 м (радула на Рис. 6C). **F** – голотип *R. laticingulatus*. **G-H** – паратипы *R. laticingulatus*: разрез от о-ва Шикотан (Южные Курилы) в океан (**G** – паратип 1, радула на Рис. 6D; **H** – паратип 2). Масштабный отрезок 10 мм.

Radula (Figs. 4, 5, 6 A-C) is slightly shorter than odontophore. Rachidian teeth bear 4-6 cusps of unequal length: median cusp(s) the longest, neighboring cusps – a bit shorter, and marginal cusps – the shortest. The cusps are situated on crescent-curved base in a fan-like way. Lateral teeth large: their basal parts are equal or wider than rachidian bases, with three (sometimes 4) large cusps on

them. The details of studied radulae summarized in Table 1.

Pair of buccal nerves and buccal artery between them leave buccal mass and follow ventrally along anterior oesophagus towards nerve ring (Fig. 3I). Anterior oesophagus twisted. Valve of Leiblein large, much broader than oesophagus; posterior oesophagus and anterior aorta equal in diameter. Salivary

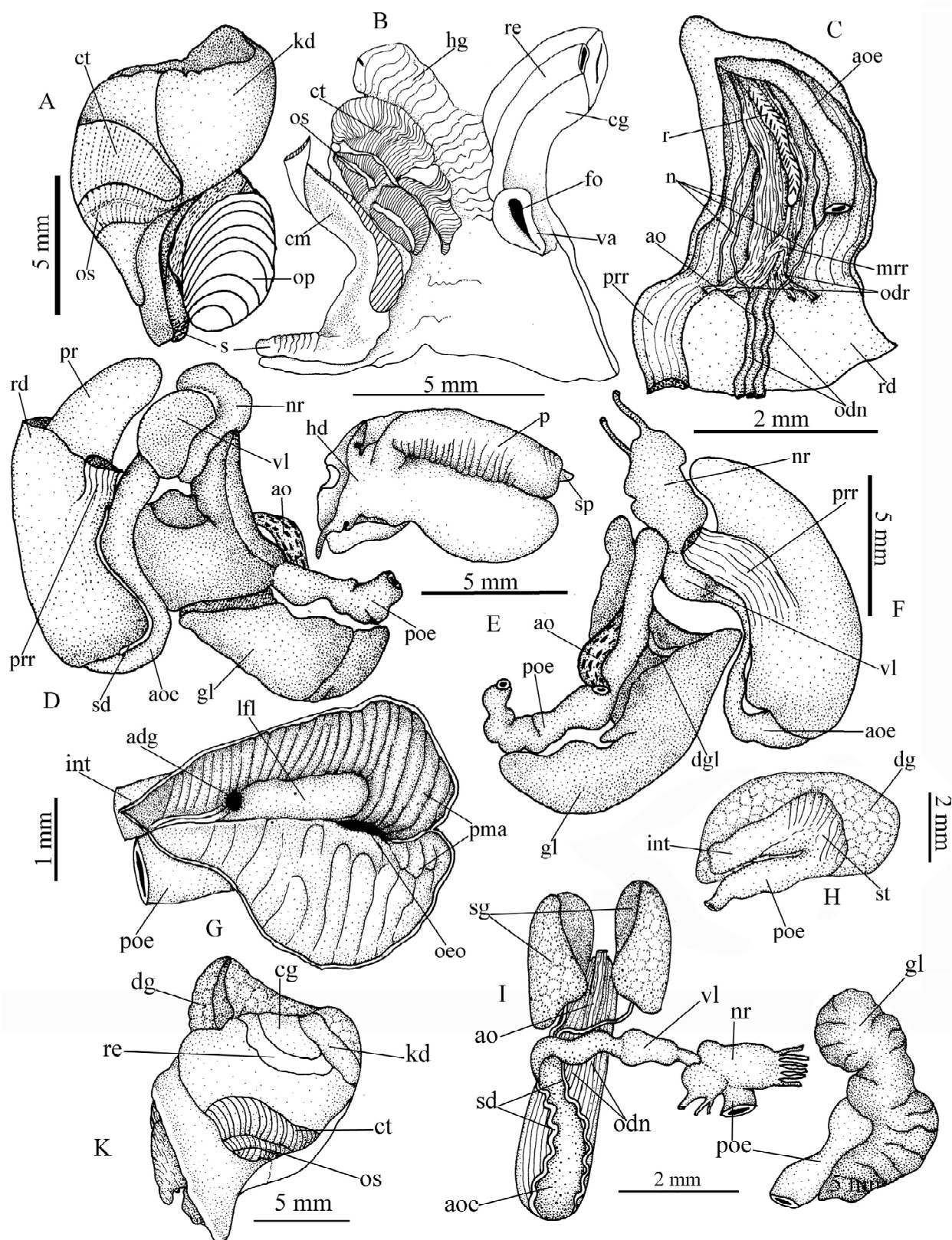


FIG. 3. Anatomy of *R. jessoensis* no. 7 (A, C-H) (shell on Fig. 1H, radula on Fig. 5C-D), no. 8 (I-K) (shell on Fig. 1K, radula on Fig. 5B) and female spm. from ZIN (B) (shell on Fig. 1I). A – soft body, pulled out of the shell, ventral view; B – mantle; C – proboscis, opened dorsally; D, F – lateral views of foregut; E – cephalopodium, dorsal view; G – stomach, opened dorsally; H – stomach, general view; I – foregut, ventral view; K – soft body, dorsal view.

РИС. 3. Анатомия *R. jessoensis* № 7 (A, C-H) (раковина на Рис. 1H, радула на Рис. 5C-D), № 8 (I-K) (раковина на Рис. 1K, радула на Рис. 5B) и самки из ЗИНа (B) (раковина на Рис. 1I). A – мягкое тело, вид с вентральной стороны; B – мантия; C – хобот, вскрытый дорсально; D, F – латеральные виды переднего отдела пищеварительной системы; E – цефалоподиум, вид с дорсальной стороны; G – желудок, вскрытый дорсально; H – общий вид желудка; I – передний отдел пищеварительной системы, вид с вентральной стороны; K – дорсальный вид мягкого тела.

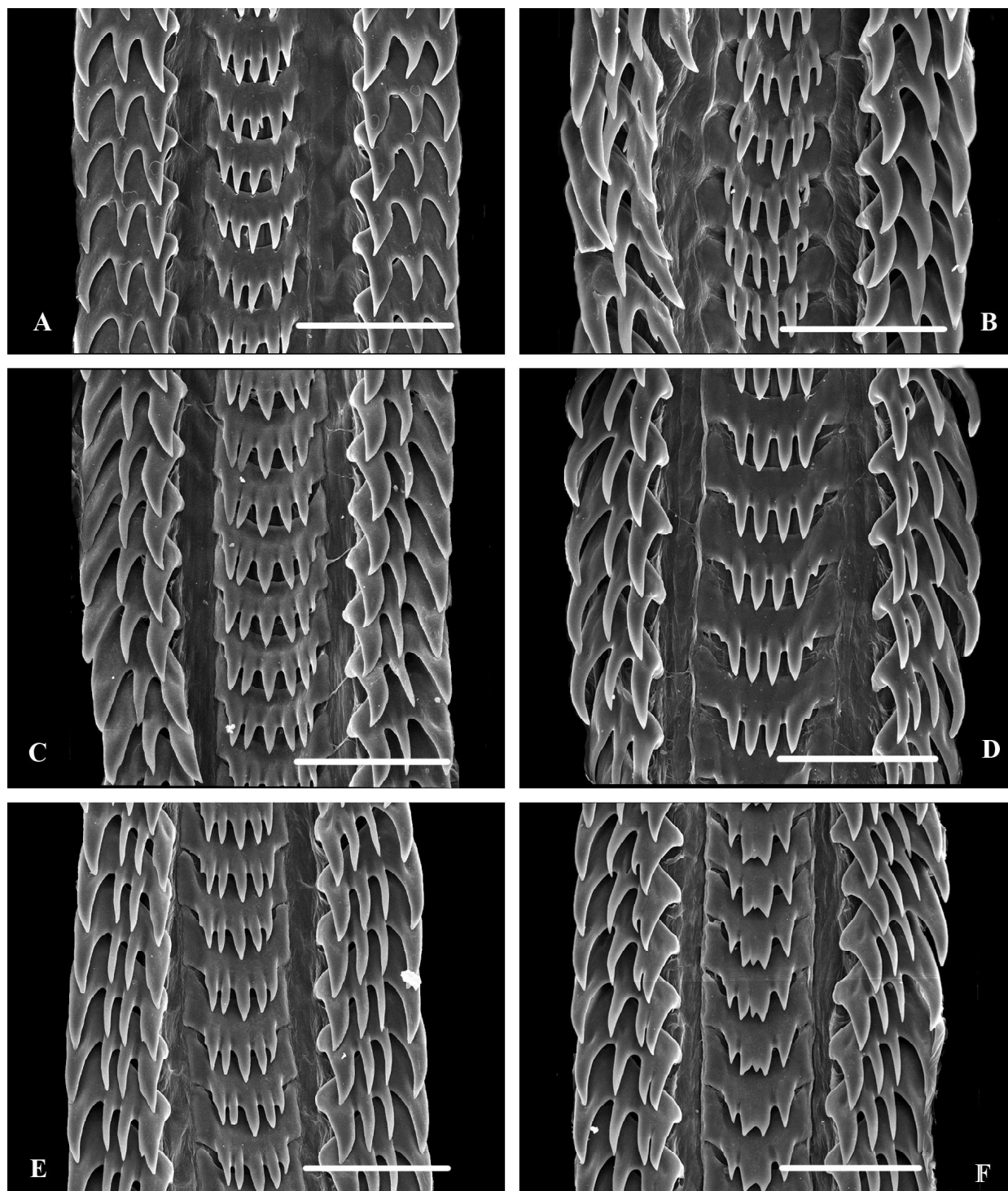


FIG. 4. Radulae of *Retifusus jessoensis*: **A** – no. 1 (shell on Fig. 1B), **B** – no. 2 (shell on Fig. 1C), **C** – no. 3 (shell on Fig. 1D), **D** – no. 5 (shell on Fig. 1F), **E-F** – no. 4 (shell on Fig. 1E). Scale bars 100 μ m.

РИС. 4. Радулы *Retifusus jessoensis*: **A** – № 1 (раковина на Рис. 1B), **B** – № 2 (раковина на Рис. 1C), **C** – № 3 (раковина на Рис. 1D), **D** – № 5 (раковина на Рис. 1F), **E-F** – № 4 (раковина на Рис. 1E). масштабный отрезок 100 μ m.

glands of medium size, separate, rounded, situated on both sides of nerve ring (Fig. 3I). Salivary ducts rather thick, weakly twisted and running along anterior oesophagus. Large gland of Leiblein situated beneath salivary glands, opening into oesophagus by rather long thin duct immediately behind the nerve ring.

Stomach spans 0.25 of whorl, bordering the digestive gland (Fig. 3H). Posterior mixing area small but well-defined, lined with high transverse folds, each with fine transverse striation (Fig. 3G, **pma**). Oesophageal opening situated ventrally in deepening. Opening of posterior duct of digestive gland is in the same deepening, but closer to central

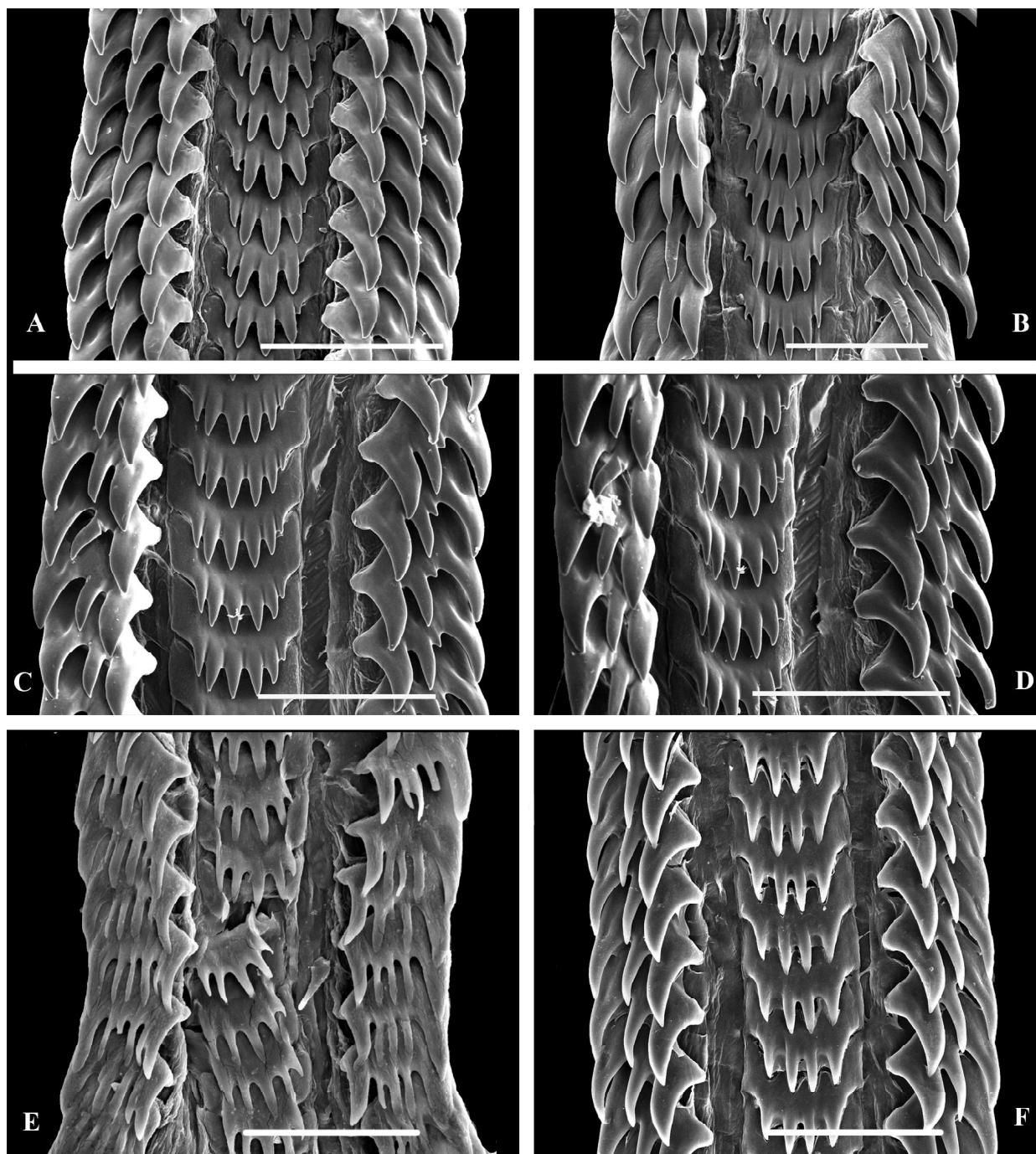


FIG. 5. Radulae of *Retifusus jessoensis*: A – no. 6 (shell on Fig. 1G), B – no. 8 (shell on Fig. 1K, anatomy on Fig. 3), C–D – no. 7 (shell on Fig. 1H, anatomy on Fig. 3), E – no. 9 (shell on Fig. 2A), F – no. 10 (shell on Fig. 2C). Scale bar 100 μ m.

РИС. 5. Радуды *Retifusus jessoensis*: А – № 6 (раковина на Рис. 1Г), В – № 8 (раковина на Рис. 1К, анатомия на Рис. 3), С–D – № 7 (раковина на Рис. 1Н, анатомия на Рис. 3), Е – № 9 раковина на Рис. 2А), F – № 10 (раковина на Рис. 2С). Масштабный отрезок 100 μ m.

stomach area. Longitudinal fold (Fig. 3G, **lfl**) with light oblique striation is situated on inner stomach wall in its central part. Large opening of anterior duct of digestive gland is situated at anterior end of longitudinal fold closer to intestine. Inner wall near intestine is lined with low oblique folds. Outer stomach wall lined with high S-shaped transverse folds.

Differential diagnosis. From the most similar *R. olivaceus*, which is conchologically nearly in-

distinguishable, differs by rachidian with 4-5 cusps (in *R. olivaceus*, rachidians are tricuspidate). From close species *R. virens* differs by shell shape and rachidian.

Distribution – Bering, Okhotsk and Japan Seas, Kurile Islands, Pacific coast of Japan, 15-397 m (Fig. 7).

Remarks. Here we treat *R. jessoensis* as broadly distributed, highly variable species. Although some

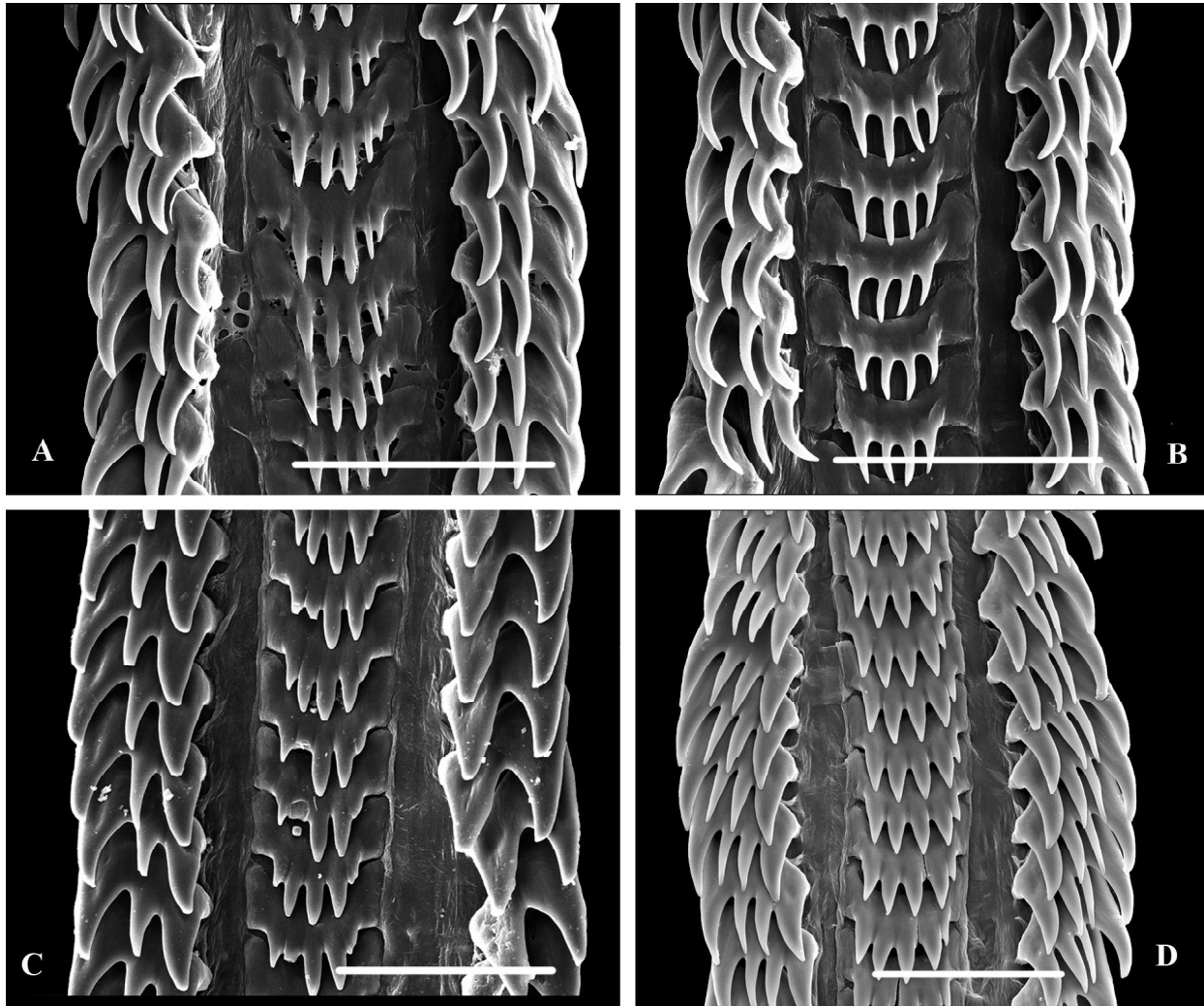


FIG. 6. Radulae of *Retifusus*: **A-B** – *R. jessoensis* no. 11 (shell on Fig. 2D), **C** – *R. jessoensis* no. 12 (shell on Fig. 2E, anatomy – Fig. 3), **D** – *R. laticingulatus* (paratype 1, shell on Fig. 2G). Scale bar 100 μ m.

РИС. 6. Радулы *Retifusus*: **A-B** – *R. jessoensis* № 11 (раковина на Рис. 2D), **C** – *R. jessoensis* № 12 (раковина на Рис. 2E), **D** – *R. laticingulatus* (паратип 1, раковина на Рис. 2G). Масштабный отрезок 100 μ m.

of the specimens are quite different from the typical ones (eg. Fig. 1 H-K), there is a number of intermediate specimens, on one hand, and still rather limited material on the other. Sometimes the specimens from the same lot have rather different outline (eg. Fig. 1, D and E – specimens from the same station). Therefore we abstain from describing some forms as separate species pending additional material that could allow clarifying the situation.

The species is highly variable, both in conchological characters and radular morphology, what may be caused by its vast distribution throughout the North Pacific and relatively shallow-water habitats.

The species was at least twice described under different names, although already Tryon [1881] supposed that *Fusus* (*Sipho*?) *manchuricus* E.A. Smith, 1875 was a junior synonym of *Tritonium jessoense* Schrenck, and speculated about close similarity of the latter with *C. brunneus* and *C.*

virens. Although the types of Schrenck were not traced, judging from his illustration of *Tritonium jessoense*, the close similarity of both species is rather obvious. Both were collected from eastern Honshu. We accept this opinion.

The position of *Chrysodomus brunneus* is ambiguous. The species was attributed to different genera (*Sipho* [Tryon, 1880], *Plicifusus* [Dall, 1902, 1921], *Mohnia* [Tiba, Kosuge, 1992]), but neither radula, nor anatomy was ever examined. Conchologically it is rather similar to other *Retifusus*, differing in less twisted columella and less pronounced and slightly narrower axial ribs. Nevertheless, the variability of the species, represented only by syntypes, is unknown and it may represent deviated form of *R. jessoensis*. We have at our disposal specimen of *R. jessoensis* from northern Bering Sea (Fig. 2E), that is somewhat intermediate between the typical *jessoensis* and *brunneus*. In the absence of the specimens from type locality of *Chryso-*

Table 1. Shell and radulae measurements of *Retifusus jessoensis*.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, μ m	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
1	26.0	19.2	13.9	230	1.65	3:5:3	4A
2	24.9	18.0	13.0	220	1.69	4:6:3	4B
3	34.8	26.1	20.4	230	1.13	3:5:3	4C
4	30.3	22.9	17.4	250	1.44	4:5:4	5E-F
5	29.8	23.0	16.9	250	1.50	3:4:4	4D
6	24.6	-	12.3	200	1.63	3:4:3	5A
7	19.0	14.6	10.0	210	2.10	3:6:4	5C-D
8	24.5	17.8	14.1	230	1.63	3:6:4	5B
9	35.2	26.5	21.0	250	1.19	6:5:5	5E
10	23.3	18.2	13.9	250	1.80	3:4:3	5F
11	24.7	18.6	13.8	200	1.45	3:6:3	6A-B
12	26.0	19.6	14.8	230	1.55	3:5:2	6C

domus brunneus, available for radulae examination we conditionally synonymize it with *R. jessoensis*.

Within the defined here species, the axial sculpture may be of frequent (Fig. 1 B, F) or rare (Fig. 1I), straight (Fig. 1 F, K) or S-shaped (Fig. 1B, 2D) axial ribs, outer lip may be evenly rounded (Fig. 1 B, D, K; 2B) or more convex in upper part (Fig. 1 C, E, 2C), siphonal canal straight or curved to left, periostracum color from yellowish to olive and brown. The radula varies in number of cusps on rachidian (4-6) and lateral teeth (2-5) (Table 1), even in the same specimen (Fig. 4 E-F). Ratio of radula width to aperture length (Table 1) is also extremely different, varying from 1.19 to 2.10%, but this may be ontogenetic variability, since there is clear negative correlation with shell height.

Retifusus laticingulatus

Golikov et Gulbin, 1977

(Figs. 2 F-H, 6D, 7)

Golikov, Gulbin, 1977: 188-189, Figs. 6, 17(4). – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 199, pl. 101 D-D'.

Plicifusus (Retifusus) laticingulatus – Higo *et al.*, 1999: 231.

Retifusus laticingulatus – Sirenko *et al.*, 2013: 162.

Holotype: ZIN 28255/1, “*Toporok*”, sta. 91, Pacific coast of Shikotan Island, 181 m, 12.09.1949.

Type locality: Shikotan, Kurile Islands, 181 m.

Material examined: ZIN 33749/4, paratypes, RV *Toporok*, sta. 90 (67), Pacific Ocean, transect from Shikotan (south Kurile Islands) to the ocean, 43° 47' N, 146° 51' E, 170 m, 12.09.1949 (2 spms., no. 1 dissected).

Description. Shell (Fig. 2 F-H) about 20 mm in height, broad-fusiform, covered with yellowish-brown periostracum. Shell under periostracum light-beige. Spiral sculpture consists of wide very flat and fewer cords, about 5-7 the penultimate whorl, separated by very narrow and shallow grooves.

Axial sculpture represented by narrow high, slightly curved ribs, extending to shell base and becoming obsolete on canal, about 12 on the last whorl. Operculum with terminal nucleus dislodged leftwards. Measurements: no. 1: H 19.5 mm, h 15 mm, AL 11.5 mm.

Radula (Fig. 6D) 2.65 mm long and 100 μ m wide (1.05 % AL), consisting of 84 tooth rows, 3 nascent; length of 5 transverse rows of teeth comprises 1.27 % of AL. The shape of rachidian is the same as in *R. jessoensis*: there are 5 sharp cusps, situated on crescent-curved tooth base in a fan-like way. Lateral teeth with four cusps, outer longest and two median shortest of same length.

Remarks. The species is most similar to *R. jessoensis* in shell and radular structure. Golikov and Gulbin [1977] pointed out a distinct spiral sculpture of the species, consisting of unusually wide cords (5 on penultimate whorl of the holotype), which thus was its main distinguishing character. We consider that hydractinian colony, spreading its stolons in the spiral grooves of holotype, might have deepened them and thus made spiral structure more prominent in comparison with paratypes. In the dissected paratype the spiral sculpture was closer to *R. jessoensis* and consisted of 8 cords on the penultimate whorl. Nevertheless, we prefer to treat *R. laticingulatus* as a separate species until more data is available.

Distribution – southern Kurile Islands, 129-188 m (Fig. 7).

Retifusus olivaceus (Bartsch, 1929), **comb. nov.** (Figs. 7-12)

Plicifusus olivaceus Bartsch, 1929: 138-139, pl. 4, fig. 8.

Mohnia okhotskana Tiba, 1981: 86, pl. 30, figs. 6-7. – Tiba,

Kosuge, 1992: 15-16. – Kantor, Sysoev, 2005: 133. –

Kantor, Sysoev, 2006: 187, pl. 93 F-G.

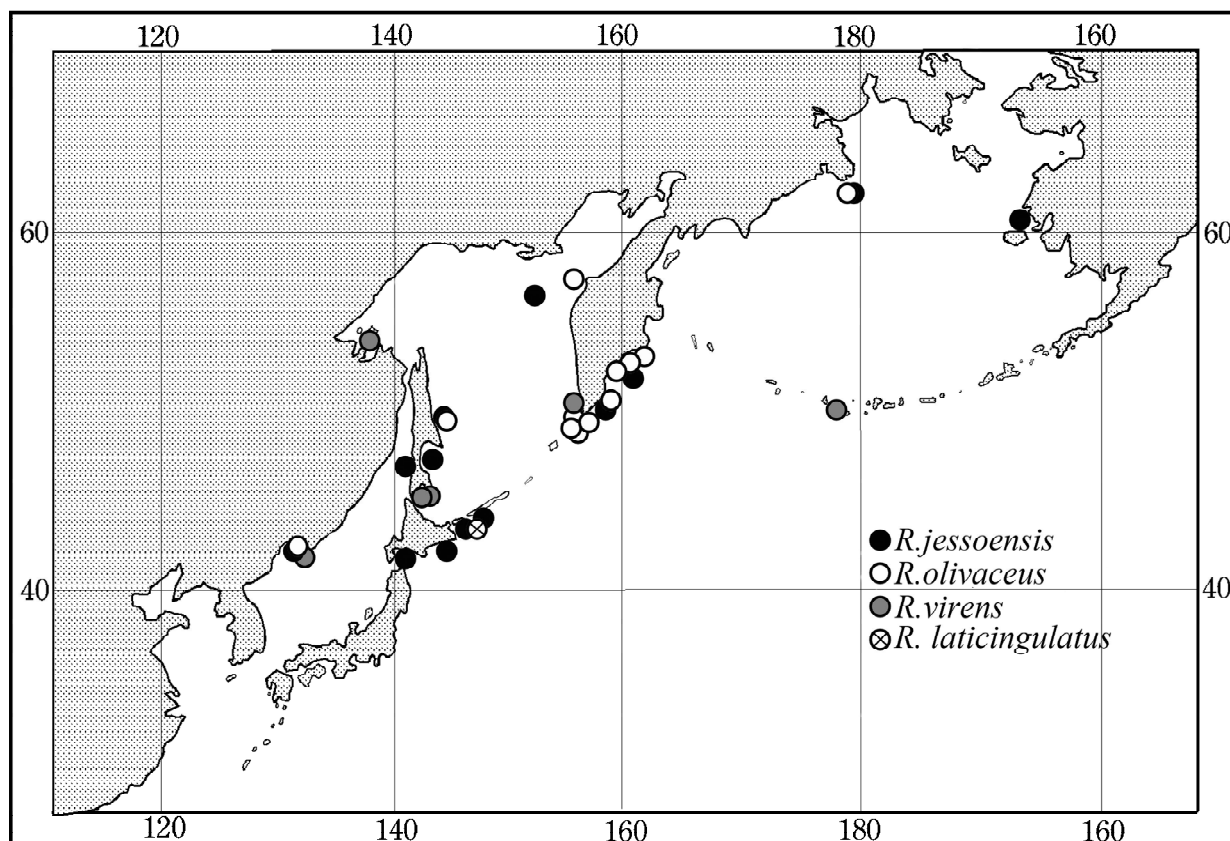


FIG. 7. Geographical distribution of *Retifusus jessoensis*, *R. laticingulatus*, *R. olivaceus* and *R. virens*.

РИС. 7. Географическое распространение *Retifusus jessoensis*, *R. laticingulatus*, *R. olivaceus* и *R. virens*.

Retimohnia olivacea – Kantor, 2009: 68, fig. 2A-C (holotype illustrated). – Sirenko *et al.*, 2013: 162.

Non *Retifusus olivaceus* (Aurivillius, 1885) sensu Kantor, Sysoev [2005, 2006] = *Plicifusus olivaceus* (Aurivillius, 1885) [Kosyan, Kantor, 2012].

Types: holotype of *P. olivaceus* – USNM 369037; holotype of *M. okhotskana* – UKM-MO-48910.

Type localities: *P. olivaceus* – at Vladivostok; *M. okhotskana* – north-western part of the Sea of Okhotsk (near Kamchatka).

Material examined: 9 lots (24 specimens). ZIN uncataloged, RV *Poseidon*, Sakhalin, Pogranichnoye village, transect 2, sta. 14, 78 m, muddy sand with pebble and boulders (10 spms., no. 1 dissected). ZIN 28437/12, north Kurile Islands, Paramushir Island, RV *Krylatka*, sta. 16, 76 m, 10.07.1955 (no. 2 dissected). ZIN, north Kurile expedition, Paramushir Island, 165-156 m, 19.07.1954 (spm. no. 3 dissected). ZIN 56034/41, southern Kamchatka, RV *Academic Oparin*, 50°26.1'N, 156°55.9'E, 132 m, muddy sand, 15.08.1986, (7 spms., no. 4 dissected). ZIN uncataloged, RV *Raduga*, eastern Kamchatka, Olga Bay, 148 m, muddy sand, 18.08.1975 (spm. no. 5 dissected). IO, southern Kamchatka, RV *Vityaz*, sta. 1327, 51°26'N, 158°7'E, 148 m, 16.05.1952 (spm. no. 6 dissected). IO, south-eastern Kamchatka, RV *Vityaz*, sta. 1354, 53°50'N, 160°14'E, 104 m, 21.05.1952 (spm. no. 7 dissected). IO, south-eastern Kamchatka, RV *Vityaz*, sta. 1341, 52°56'N, 159°30'E, 85 m, 20.05.1952 (spm. no. 8 dissected). IO, north of the Bering Sea, RV *Vityaz*, sta. 1541, 62°6'N, 179°28'E, 110 m, 18.06.1952 (spm. no. 9 dissected).

Description. Shell. Holotype was in details described by Kantor [2009]. Shell height from 16 to 33 mm (Table 2), broad to elongate-fusiform, solid, with well defined, medium long, slightly curved leftwards siphonal canal (Figs. 8-9). Periostracum olive, yellowish-brown or brown; shell under periostracum from white to creamy. Spiral sculpture represented by distinct spiral cords, 8-12 on penultimate whorl. Axial sculpture consists of straight to slightly left-curved axial ribs (10-15 on penultimate whorl) (Figs. 8-9). Operculum with terminal nucleus shifted to left.

Soft body. 1.5 whorls extracted from the shell. Head rather small, short thick tentacles pulled together; propodium wide. Mantle with short siphon (Fig. 10D, s), osphradium and ctenidium as above described for *R. jessoensis*; penis with small tapering seminal papilla (Fig. 10B).

Digestive system. Foregut and stomach are similar to *R. jessoensis* (Fig. 10E-H). **Radula** equal to odontophore in length. Rachidian bears 3 cusps, median cusp usually slightly longer than marginal cusps (Figs. 11-12). Lateral teeth are similar to *R. jessoensis*, with three (sometimes two) large cusps. The details of all studied radulae are summarized in Table 2.

Distribution. Bering, Okhotsk and Japan Seas, south-east of Kamchatka, 76-165 m (Fig. 7).

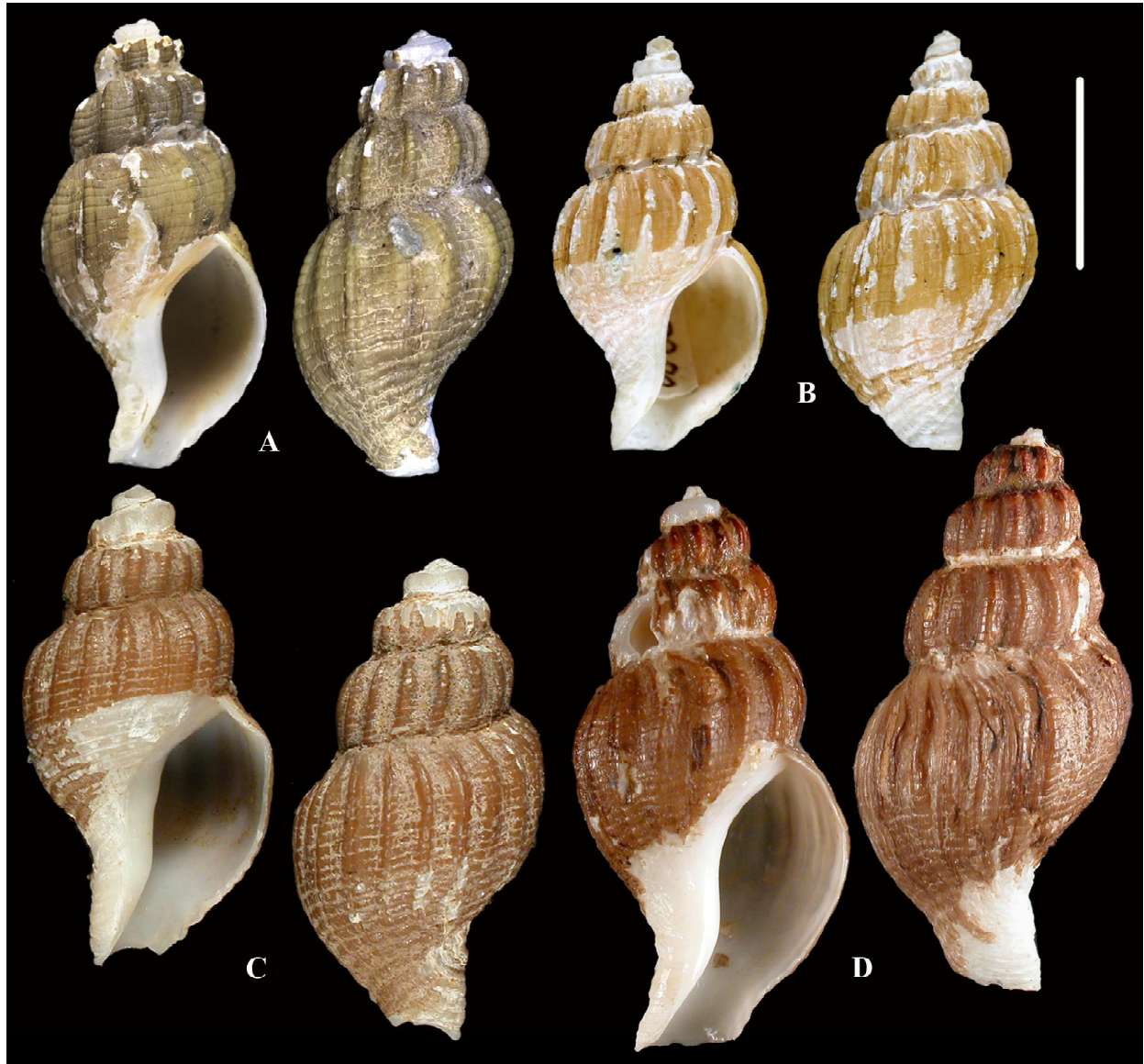


FIG. 8. Shells of *Retifusus olivaceus*: **A** – holotype of *Plicifusus olivaceus* Bartsch, 1929, Vladivostok. **B** – holotype of *Mohnia okhotskana* Tiba, 1981, north-western part of the Sea of Okhotsk (near Kamchatka). **C** – no. 1: Sakhalin, Pogranichnoye village, 78 m (radula on Fig. 11A). **D** – no. 2: North Kurile Islands, Paramushir, 76 m (radula on Fig. 11B). Scale bar 10 mm.

FIG. 8. Раковины *Retifusus olivaceus*: **A** – голотип *Plicifusus olivaceus* Bartsch, 1929, Владивосток. **B** – голотип *Mohnia okhotskana* Tiba, 1981, северо-западная часть Охотского моря (около Камчатки). **C** – № 1: Сахалин, пос. Пограничное, 78 м (радула на Рис. 11A). **D** – № 2: Северные Курильские острова, о. Парамушир, 76 м (радула на Рис. 11B). Масштабный отрезок 10 мм.

Remarks. *Plicifusus olivaceus* Bartsch, 1929 was forgotten and the name was never used (surprisingly even in Russia although the original description was in Russian periodical and in Russian) after its original description, probably due to rarity of the publication. The name was resurrected by Kantor [2009], who discovered and illustrated the holotype from USNM. Although the species name was not used in current literature, the species was recorded in the Far-East seas of Russia under the other name, *Mohnia okhotskana* Tiba, 1981. The latter species was described from north-western part of the Okhotsk Sea (near Kamchatka Peninsula,

also found in the Kurile Islands and in the Japan Sea (type locality of *Plicifusus olivaceus* Bartsch). Kantor [2009] placed *R. olivaceus* within *Retimohnia*, but due to radula features and operculum we believe it should be transferred to *Retifusus*.

The species is conchologically variable and very similar to *R. jessoensis*, often being found in the same haul, obviously living in the same habitat and in the same geographic area. The species can be differentiated by the morphology of rachidian radular teeth, which are tricuspidate in *R. olivaceus*, while have 4-6 cusps in *R. jessoensis*.



FIG. 9. Shells of *Retifusus olivaceus* Bartsh, 1929. **A** – no. 3: North Kurile Islands, Paramushir, 165-156 m (radula on Fig. 11C, anatomy on Fig. 10). **B** – no. 4: southern Kamchatka, 50°26.1'N, 156°55.9'E, 132 m (radula on Fig. 11D). **C** – no. 5: eastern Kamchatka, Olga Bay, 148 m (radula on Fig. 11E). **D** – no. 6: southern Kamchatka, 51°26'N, 158°7'E, 148 m (radula on Fig. 11F). **E** – no. 7: south-eastern Kamchatka, 53°50'N, 160°14'E, 104 m (radula on Fig. 12A). **F** – no. 8: south-eastern Kamchatka, 52°56'N, 159°30'E, 85 m (radula on Fig. 12B). **G** – no. 9: northern Bering Sea, 62°6'N, 179°28'E, 110 m (radula on Fig. 12C). Scale bar 10 mm.

FIG. 9. Раковины *Retifusus olivaceus* Bartsh, 1929. **A** – № 3: Северные Курильские острова, о. Парамушир, 165-156 м (радула на Рис. 11C, анатомия на Рис. 10). **B** – № 4: южная Камчатка, 50°26.1'N, 156°55.9'E, 132 м (радула на Рис. 11D). **C** – № 5: восточная Камчатка, бухта Ольги, 148 м (радула на Рис. 11E). **D** – № 6: южная Камчатка, 51°26'N, 158°7'E, 148 м (радула на Рис. 11F). **E** – № 7: юго-восточная Камчатка, 53°50'N, 160°14'E, 104 м (радула на Рис. 12A). **F** – № 8: юго-восточная Камчатка, 52°56'N, 159°30'E, 85 м (радула на Рис. 12B). **G** – № 9: северная часть Берингова моря, 62°6'N, 179°28'E, 110 м (радула на Рис. 12C). Масштабный отрезок 10 мм.

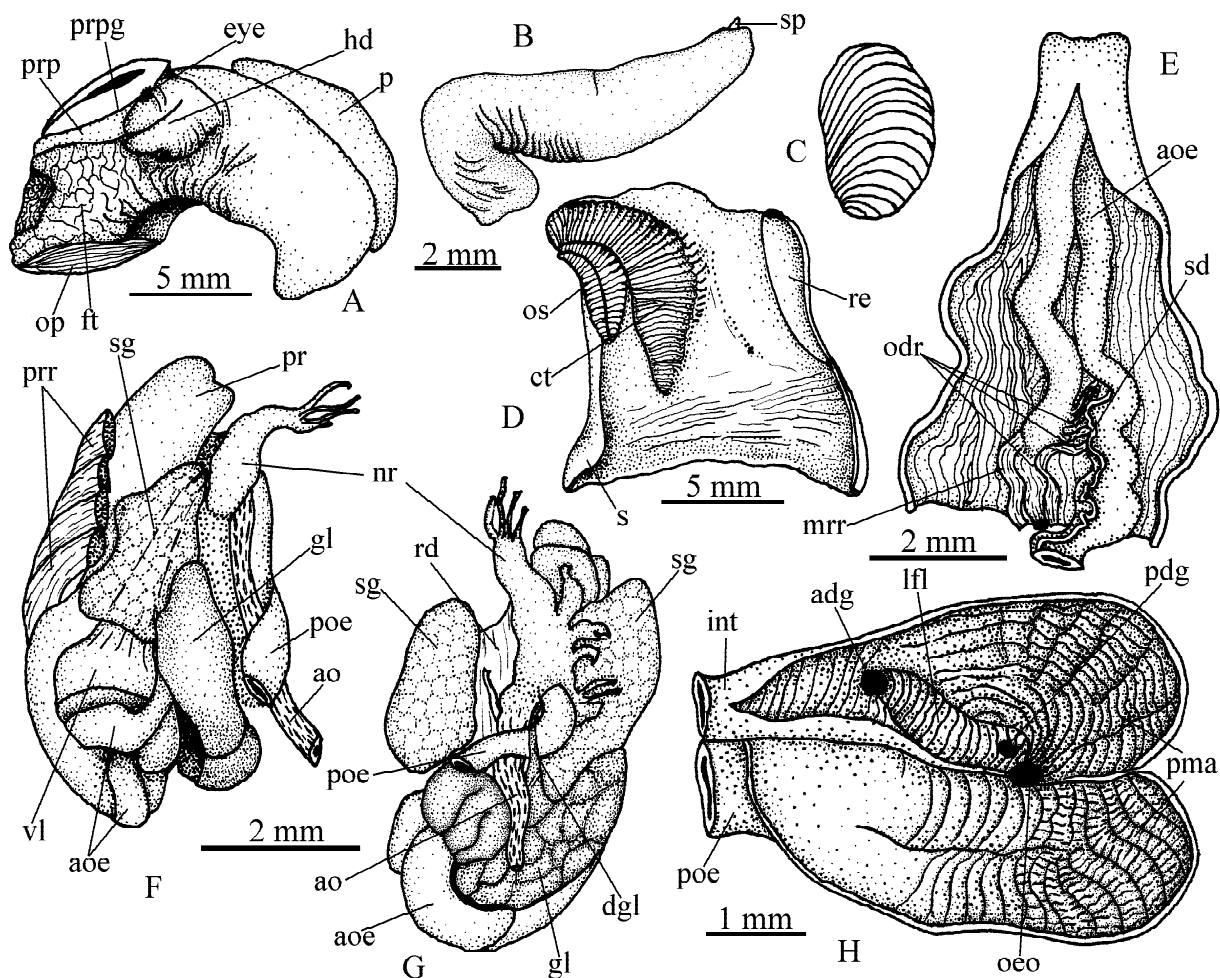


FIG. 10. Anatomy of *Retifusus olivaceus* no. 3 (shell on Fig. 9A, radula on Fig. 11C). A – cephalopodium, lateral view. B – penis. C – operculum. D – mantle. E – proboscis, opened dorsally. F-G – foregut, ventral- lateral views. H – stomach, opened dorsally.

FIG. 10. Анатомия *Retifusus olivaceus* № 3 (раковина на Рис. 9A, радула на рис. 11C). А – цефалоподиум, вид сбоку. В – пенис. С – крышечка. D – мантия. E – хобот, вскрытый дорсально. F-G – передний отдел пищеварительной системы, вентро-латеральный вид. H – желудок, вскрытый дорсально.

Retifusus virens (Dall, 1877) (Fig. 7, 13-15)

Chrysodomus virens Dall, 1877: 1.

Sipho virens – Tryon, 1881: 130, pl. 53 fig. 347.

Tritonofusus (Plicifusus) virens – Dall, 1902: 525, pl. 36, f. 8.

Plicifusus (Retifusus) virens – Dall, 1921: 93. – Higo *et al.*, 1999: 230.

Bela yanamii Yokoyama, 1926: 261, pl. 32, fig. 11.

Mohnia yanamii – Makiyama, 1958, pl. 44, fig. 11. – Higo *et al.*, 1999: 227.

Mohnia virens – Tiba, Kosuge, 1992: 25-26.

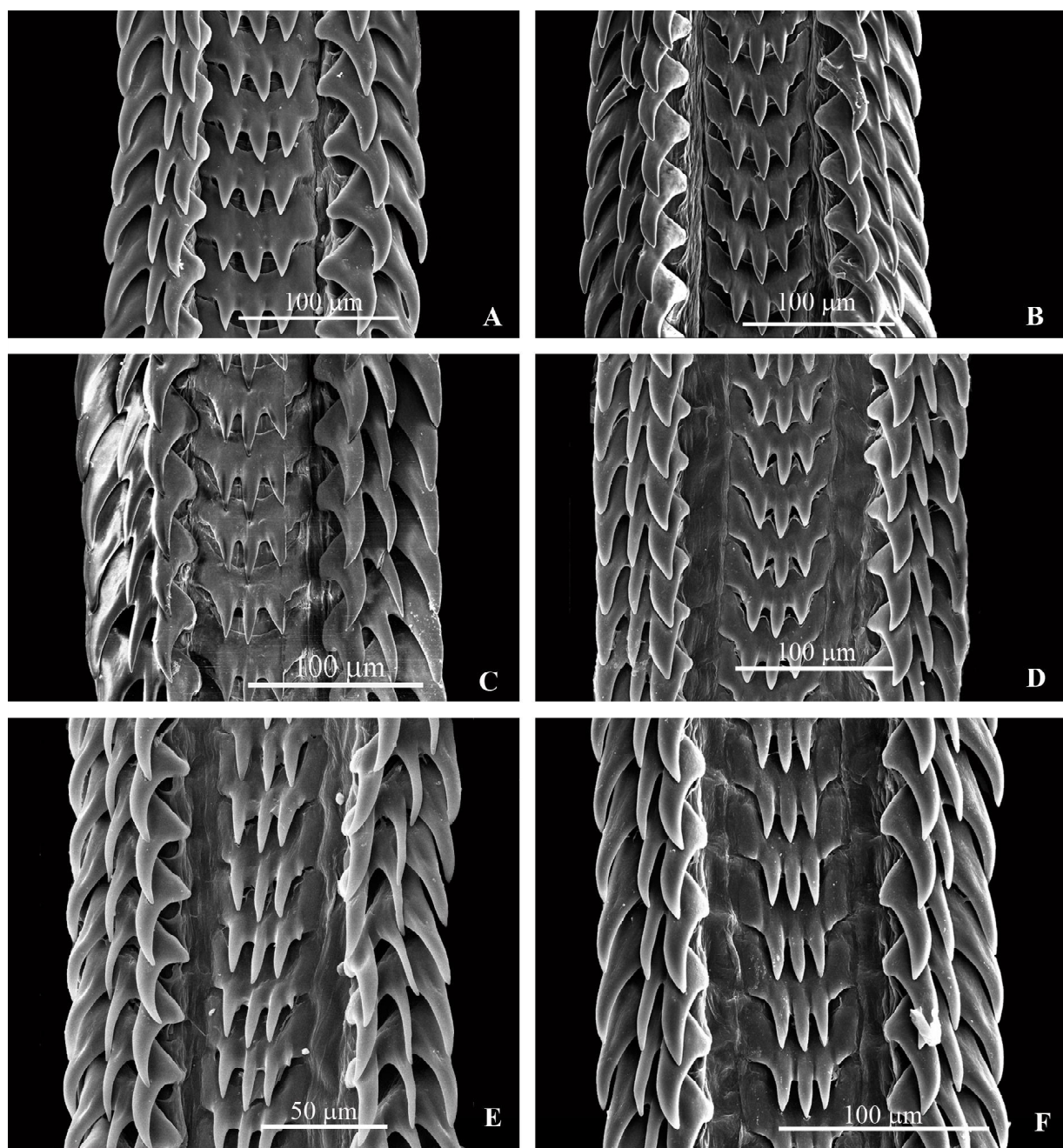
Retifusus virens – Kantor, Sysoev, 2005: 139. – Kantor, Sysoev, 2006: 200, pl. 102 E-F. – Hasegawa, 2009: 307, fig. 231. – Sirenko *et al.*, 2013: 162.

Types: holotype of *Chrysodomus virens* Dall 1877 – USNM 108982; syntypes of *Bela yanamii* UMUT CM 23085 http://umdb.um.u-tokyo.ac.jp/DKoseibu/specimens/en/23085_.html

Type localities: *C. virens* – Kyska Harbor, Kiska Island, Aleutian Islands, 18 m; *B. yanamii* – Yanami, Akumi district, northern Honshu, fossil.

Material examined: 5 lots (7 specimens). ZIN uncatalogued, north-western part of the Sea of Okhotsk, RV *Poseidon*, XVIII cruise, sta. 226, 54°42'N, 137°27'E, 24 m, 20.08.78 (2 spms, no. 1 dissected). ZIN 56036, Paramushir Island, RV *Academic Oparin* 7 cruise, 50°12'N, 156°35'E, 312 m, 26.06.1988 (2 spms., no. 2 dissected). ZIN uncatalogued, Kurile-Sakhalin expedition, Sea of Okhotsk, Aniva Bay, sta. 30(10), 47-55 m, 27.08.1947 (no. 3 dissected). ZIN uncatalogued, Kurile-Sakhalin expedition, Sea of Okhotsk, Aniva Bay, sta. 26, 95 m, 17.08.1947 (spm. no. 4 dissected). ZIN 28827, Sea of Japan, Peter the Great Bay, RV *Tamingo*, transect from Lichachev cape, 42°41'N, 132°51.2'E, sta.17, 65 m, 15.08.1970 (spm. no. 5 dissected).

Description. Shell height from 10 to 30 mm (Table 3), with rather long, well-defined slightly left-curved, nearly straight siphonal canal and rapidly increasing diameter of whorls. Shell white or creamy, covered with green (holotype) to yellowish-brown or beige periostracum (Fig. 13). Spiral sculpture consists of well pronounced spiral cords, up to 15 on the penultimate whorl, each with secondary fine spiral striation. Axial sculpture repre-

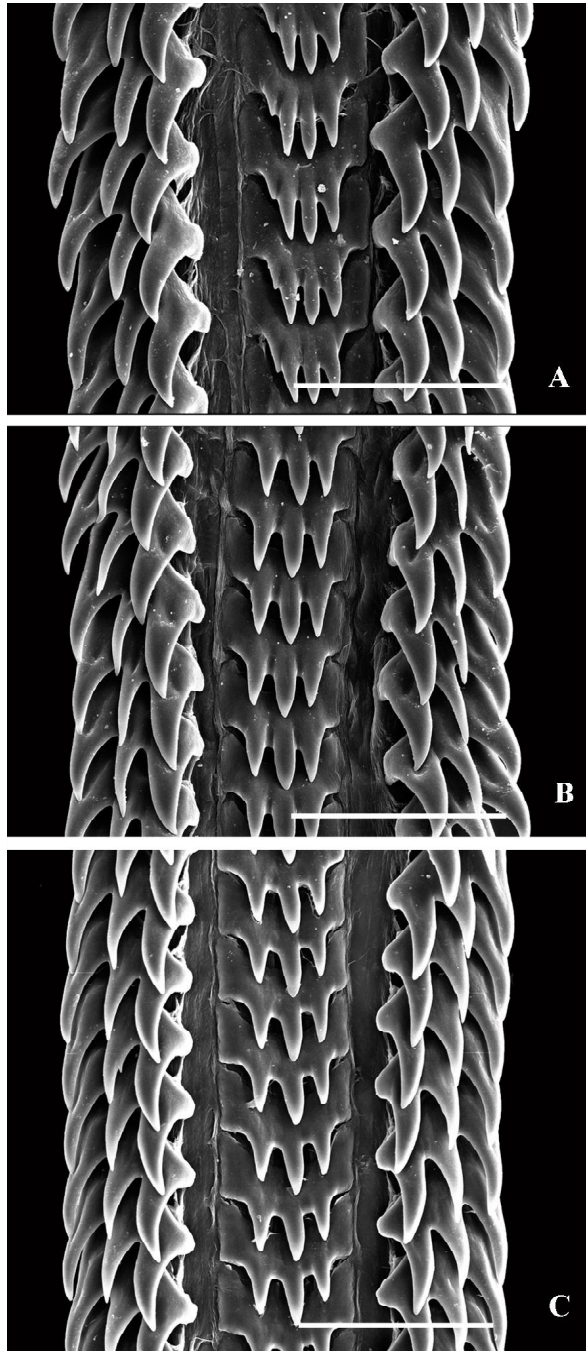


11. Radulae of *Retifusus olivaceus*: **A** – no. 1 (shell on Fig. 8C). **B** – no. 2 (shell on Fig. 8D). **C** – no. 3 (shell on Fig. 9A, anatomy on Fig. 10). **D** – no. 4 (shell on Fig. 9B). **E** – no. 5 (shell on Fig. 9C). **F** – no. 6 (shell on Fig. 9D).

11. Радулы *Retifusus olivaceus*: **A** – № 1 (раковина на Рис. 8C). **B** – № 2 (раковина на Рис. 8D). **C** – № 3 (раковина на Рис. 9A, анатомия на Рис. 10). **D** – № 4 (раковина на Рис. 9B). **E** – № 5 (раковина на Рис. 9C). **F** – № 6 (раковина на Рис. 9D).

Table 2. Shell and radulae measurements of *Retifusus olivaceus*.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, µm	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
1	28.4	22.3	17.2	180	1.05	3:3:2	11A
2	33.2	25.0	16.6	200	1.20	3:3:3	11B
3	21	16.0	11.0	200	1.82	3:3:3	11C
4	24.2	18.6	14.1	220	1.56	3:3:3	11D
5	16.2	12.7	10.1	170	1.68	3:3:3	11E
6	21.5	16.4	12.6	200	1.59	3:3:3	11F
7	26.8	20.5	16.0	200	1.25	3:4:3	12A
8	25.6	19.2	14.6	200	1.37	3:3:3	12B
9	24.5	18.6	14.7	220	1.50	3:3:3	12C



12. Radulae of *Retifusus olivaceus*: A – no. 7 (shell on Fig. 9E). B – no. 8 (shell on Fig. 9F). C – no. 9 (shell on Fig. 9G).

12. Радулы *Retifusus olivaceus*: A – № 7 (раковина на Рис. 9E). B – № 8 (раковина на Рис. 9F). C – № 9 (раковина на Рис. 9G).

sented by well pronounced high shallowly S-shaped ribs, about 10–14 on the last whorl.

Soft body. Head large and broad (Fig. 14A, **hd**), tentacles long, with large black eyes situated on small lobes at tentacles' bases. Foot folded transversely, with wide propodium (**prp**), separated by deep propodial groove (**prpg**). **Mantle** slightly longer

than wider, with long ($3/4$ mantle length) and narrow (about $1/4$ mantle width) ctenidium and osphradium (about half ctenidium length and $2/3$ ctenidium width). Rectum narrow and short (half ctenidium length); capsule gland not developed (juvenile female). Operculum oval, thin and semitransparent, with terminal nucleus shifted to left.

Digestive system. Proboscis not coiled within the rhynchodaeum (Fig. 14 D-E, **pr**). Proboscis retractors (Fig. 14D, **prrr**) originate at ventro-lateral side of rhynchodaeum and attach to lateral walls of body haemocoel. Buccal mass occupies the whole length of dissected proboscis, attached to its wall by multiple odontophoral retractors coming off buccal mass base (Fig. 14F, **odr**). **Radula** is similar to that of *R. olivaceus*. There are 3–4 cusps on rachidian (intermediate cusps are slightly longer than marginal ones), and 3 long cusps on the lateral teeth (Table 3, Fig. 15).

Two buccal nerves and anterior aorta come out of the buccal mass and follow along ventral side of rhynchodaeum. Valve of Leiblein large, covered with connective tissue. Gland of Leiblein (Fig. 14E, **gl**) very large and massive, adjoining to the left salivary gland. Salivary glands small and rounded, left one situated a bit more anterior than the right one (Fig. 14 D-E).

Stomach spans approximately one third of whorl. Posterior mixing area moderately large (Fig. 14G, **pma**). Outer stomach wall lined with high transverse folds, inner wall lined with lower transverse folds, becoming oblique closer to intestine orifice; central part of inner wall occupied by longitudinal smooth fold (Fig. 14G, **lfl**). Posterior oesophagus opens into stomach ventrally by narrow orifice, where epithelial folds are especially high. Openings of digestive gland ducts not found (stomach damaged).

Distribution – Aleutian Islands, Sea of Okhotsk, Sea of Japan (Peter the Great Bay), 18–312 m (Fig. 7).

Remarks. The group of specimens, which we attribute to *R. virens*, is rather heterogeneous regarding shell size and shape. We consider them conspecific tentatively based predominantly on shell shape characterized by rapidly increasing diameter of whorls and long siphonal canal, differing from above described *Retifusus jessoensis*, *R. laticingulatus* and *R. olivaceus*. From conchologically similar *R. similis* and *R. iturupus*, the species differs by morphology of lateral radular teeth with three thick and rather short, wide-spread large cusps, and anatomy with twice larger salivary glands and thicker salivary ducts. The secondary spiral striation found in some examined specimens, is also a distinct feature, but usually can hardly be observed due to erosion of the shell surface in majority of specimens.



FIG. 13. Shells of *Retifusus virens*: **A** – holotype of *Chrysodomus virens*, Kyska Harbor, Kiska Island, Aleutian Islands, 18 m. **B** – no. 1, north-western part of the Sea of Okhotsk, 54°42'N, 137°27'E, 24 m. **C**, **H** – Paramushir Island, 50°12' N, 156°35'E, 312 m (**C** – no. 2, radula on Fig. 15A, anatomy on Fig. 14). **D** – syntype of *Bela yanamii*, Yanami, Akumi district, Northern Honshu, fossil. **E** – no. 3, southern part of the Sea of Okhotsk, Sakhalin, Aniva Bay, 47-55 m (radula on Fig. 15B). **F** – no. 4, southern part of the Sea of Okhotsk, Sakhalin, Aniva Bay, 95 m (radula on Fig. 15C, anatomy on Fig. 14). **G** – no. 5, Sea of Japan, Peter the Great Bay, 42°41'N, 132°51.2'E, 65 m (radula on Fig. 15D). Scale bar 10 mm.

РИС. 13. Раковины *Retifusus virens*: **A** – голотип *Chrysodomus virens*, гавань Кыска, Алеутские острова, 18 м. **B** – № 1, северо-западная часть Охотского моря, 54°42'N, 137°27'E, 24 м. **C**, **H** – о. Парамушир, 50°12' N, 156°35'E, 312 м (**C** – № 2, радула на Рис. 15А, анатомия на Рис. 14). **D** – синтип *Bela yanamii*, Янами, р-н Акуми, северный Хонсю, ископаемый. **E** – № 3, южная часть Охотского моря, Сахалин, залив Анива, 47-55 м (радула на Рис. 12В). **F** – № 4, южная часть Охотского моря, Сахалин, залив Анива, 95 м (радула на Рис. 15С, анатомия на Рис. 14). **G** – № 5, Японское море, залив Петра Великого, 42°41'N, 132°51.2'E, 65 м (радула на Рис. 15D). Масштабный отрезок 10 мм.

Table 3. Shell and radulae measurements of *Retifusus virens*.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, μ m	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
1	23.7	18.3	13.6	200	1.47	3:3:3	-
2	15	12.0	10.0	150	1.25	3:4:3	15A
3	11.3	8.7	6.8	150	2.21	3:4:3	15B
4	29.7	21.7	19.4	170	0.88	3:3:3	15C
5	10.7	9.0	7.5	125	1.67	3:3:3	15D

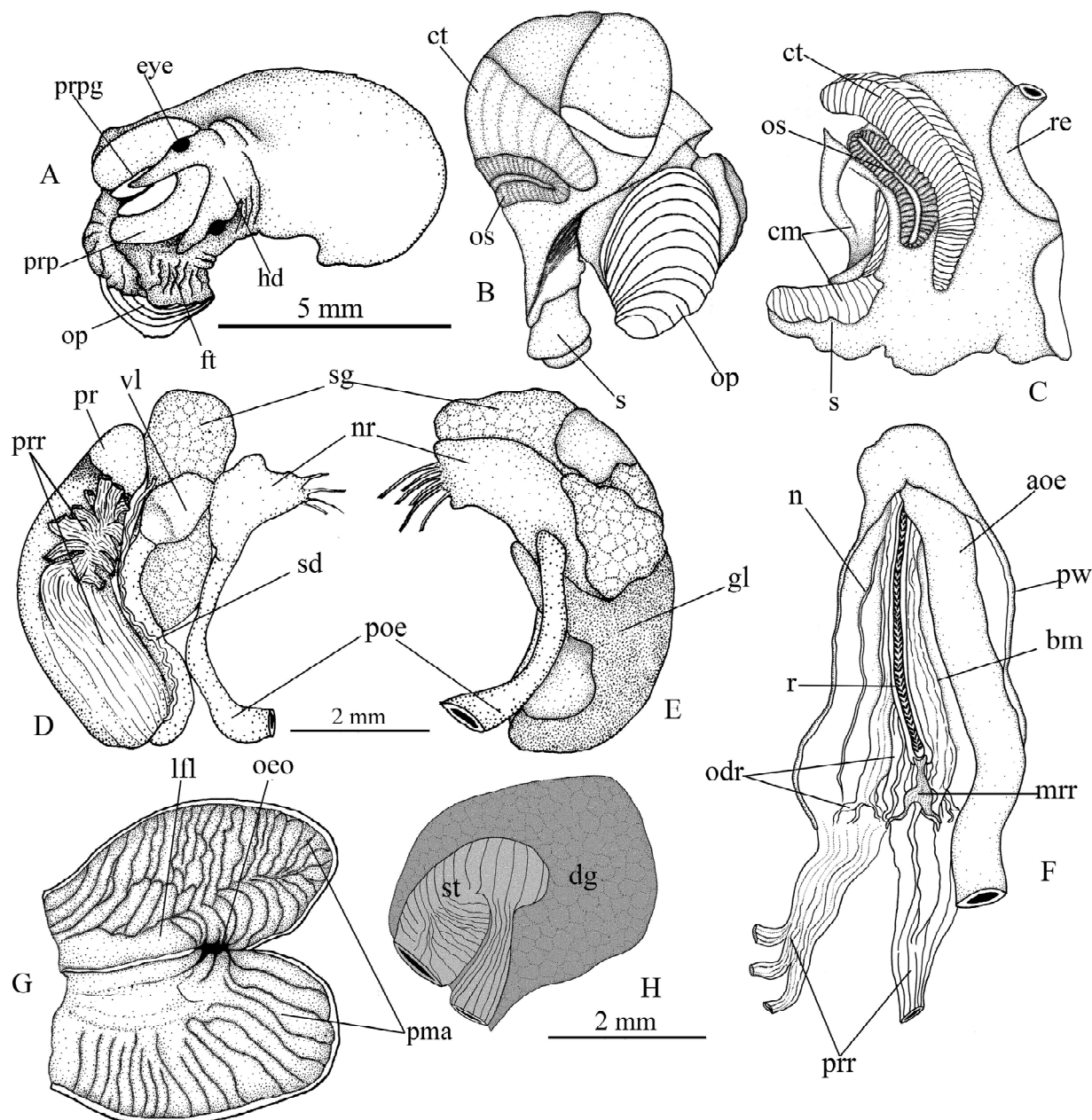


FIG. 14. Anatomy of *Retifusus virens* no. 2 (A, D, E, G, H) and 4 (B, C, F). **A** – cephalopodium, dorsal view; **B** – soft body, ventral view; **C** – mantle; **D–E** – foregut, lateral views; **F** – proboscis opened dorsally; **G** – stomach, opened dorsally; **H** – stomach, general view.

РИС. 14. Анатомия *Retifusus virens* № 2 (A, D, E, G, H) и 4 (B, C, F). **A** – цефалоподиум, вид с дорсальной стороны. **B** – вентральный вид мягкого тела. **C** – мантия. **D–E** – передний отдел пищеварительной системы, вид сбоку. **F** – хобот, вскрытый с дорсальной стороны. **G** – желудок, вскрытый с дорсальной стороны. **H** – общий вид желудка.

Retifusus parvus (Tiba, 1980), **comb. nov.**
(Figs. 16-21)

Plicifusus parvus Tiba, 1980: 47-48, pl 12, figs. 1-8. – Tiba, Kosuge, 1980: 15-16. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 197-198, pl. 100 J-K.

Plicifusus saginatus Tiba, 1980: 49, pl. 13, figs. 1-7, **syn. nov.** – Tiba, Kosuge, 1980: 25-26. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 198, pl. 100 H-I.

Retifusus semiplicatus Golikov in Golikov et Scarlato, 1985: 405, fig. 6, **syn. nov.** – Kantor, Sysoev, 2005: 139. – Kantor, Sysoev, 2006: 198, pl. 102 A.

Types: holotype of *Plicifusus parvus* – UKM-MO-84841; holotype of *Plicifusus saginatus* – UKM-MO-29181; holotype of *Retifusus semiplicatus* – ZIN 33735/1.

Type locality: of *Plicifusus parvus* – off Dalnegorsk, Sea of Japan (?), 400 m; of *Plicifusus saginatus* – Sakhalin, 400 m; of *Retifusus semiplicatus* – south-eastern Sakhalin, 78 m.

Material examined: 13 lots, more than 80 specimens. ZIN uncataloged, Tatar Strait, RV *Poseidon*, XVIII cruise, sta. 226, 54°42'N, 137°27'E, 24 m, 20.08.78 (4 spms., no. 1

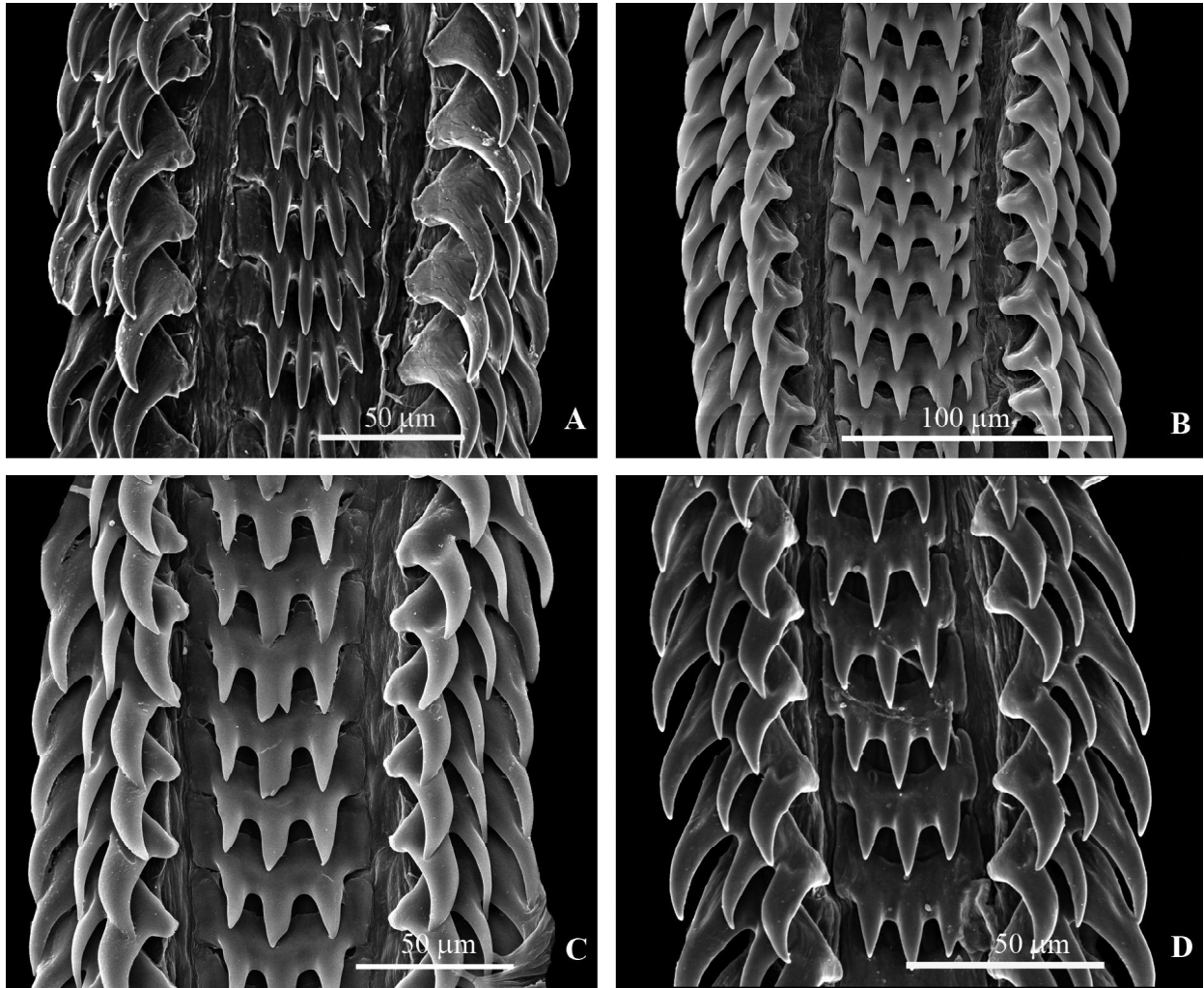


FIG. 15. Radulae of *R. virens*: **A** – no. 2 (shell on Fig. 13C, anatomy on Fig. 14). **B** – no. 3 (shell on Fig. 13E). **C** – no. 4 (shell on Fig. 13 F, anatomy on Fig. 14). **D** – no. 5 (shell on Fig. 13G).

РИС. 15. Радуды *R. virens*: **A** – № 2 (раковина на Рис. 13 C, анатомия на Рис. 14). **B** – № 3 (раковина на Рис. 13E). **C** – № 4 (раковина на Рис. 13F, анатомия на Рис. 14). **D** – № 5 (раковина на Рис. 13G).

dissected). ZIN uncataloged, RV *Toporok*, Nemuro, 44°15'N, 145°20'E, 60 m, 03.09.1948 (11 spms., no. 2 dissected). ZIN uncataloged, Kurile-Sakhalin expedition, Sea of Okhotsk, Aniva Bay, 95 m, 17.08.1947 (30 specimens, nos. 3 and 8-10 dissected). ZIN uncataloged, RV *Poseidon*, transect 2, sta. 14, Sakhalin Island, Pogranichnoye village, 78 m, 03.07.1978 (12 specimens, no. 5 dissected). ZIN uncataloged, RV *Toporok*, Tatar Strait, transect from Sakayjakan, sta. 67, 46°48'N, 143°51'E, 144 m, 05.09.1947 (no. 7 dissected). IO, northern part of the Sea of Okhotsk, RV *Vityaz*, sta. 1866, 57°49.7'N, 141°53.6'E, 142 m, 20.10.1952 (spm. no. 6 dissected). IO, northern part of the Bering Sea, RV *Vityaz*, sta. 1006, 63°59.9'N, 177°38.6'W, 87 m, 12.10.1951 (2 spms, no. 4 dissected). ZIN 58797, Sea of Japan, RV *Academic Oparin* 13 cruise, sta. 176, 43°04.4'N, 134°30.8'E, 90 m, 09.06.1991 (spm. no. 11 dissected). ZIN 58411, RV *Blucher*, Tatar Strait, 110 m, 21.07.1933 (spm. no. 12 dissected). ZIN uncataloged, Shantar expedition, RV *Poseidon*, sta. 82, transect 5, northern Sakhalin, Elisabeth's cape, 88 m, 20.07.1978 (1 specimen). ZIN uncataloged, North Kurile Islands, Shumshu Island, Babushka Bay, sta. 36, 40-50 m, 02.07.1954 (1 spm.). RV *Vityaz*, sta. 1329, 51°44'N, 158°24.7'E, 285 m, 16.05.1952 (5 spms). ZIN uncataloged, Arctic Ocean, Wrangel Island,

Ice-breaker *Litke*, sta. 32, 70°42'N, 175°37'W, 66.5 m, coll. Ushakov, 24.08.1929 (6 spms.).

Description. Shell height from 18 to 31 mm (Table 4), elongated to broad-fusiform, with more or less attenuated spire, covered with yellowish, olive, light-beige to brown periostracum, shell under periostracum white to yellowish-beige and light orange (Figs. 16-17). Siphonal canal short to medium-long, slightly curved leftward; outer lip evenly rounded, sometimes concave in lower part, marking the transition into siphonal canal. Spiral sculpture consists of wide flattened cords, separated by deep, often wide grooves. Sometimes cords are additionally lined with shallower spiral grooves. There are 12-15 cords on the penultimate whorl. Axial sculpture represented by axial ribs (up to 20 on the last whorl), which may be well expressed on entire shell surface (Fig. 16) or be significantly weaker on the last whorl (Fig. 17).

Soft body: two whorls extracted from the shell.

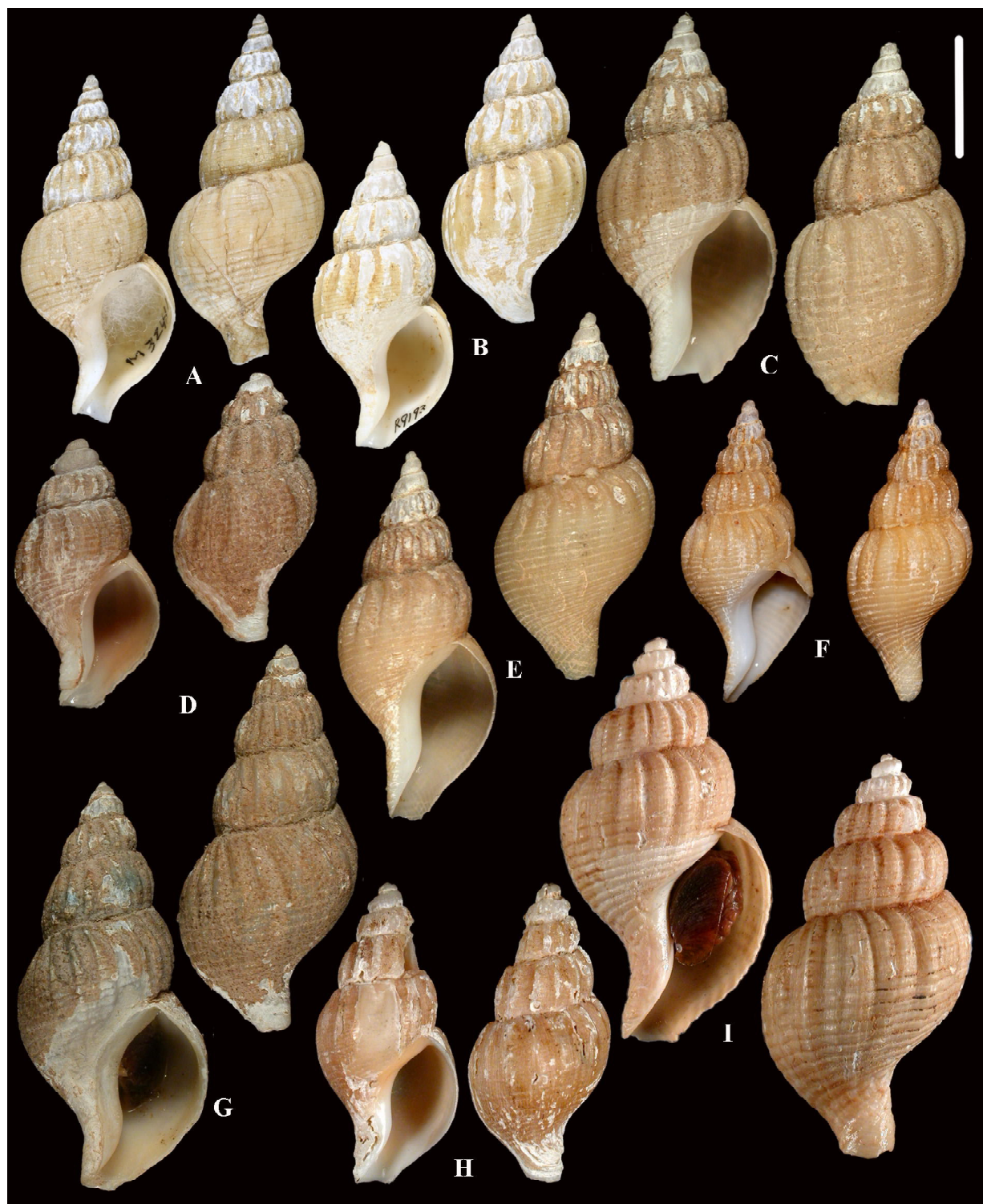


FIG. 16. Shells of *Retifusus parvus*: **A** – holotype of *P. parvus* Tiba, 1980, off Dalnegorsk, Sea of Japan (?), 400 m. **B** – holotype of *P. saginatus* Tiba, 1980, Sakhalin, 400 m. **C** – no. 1, Sea of Okhotsk, Tatar Strait, 54°42'N, 137°27'E, 24 m (radula on Fig. 19A). **D** – no. 2, Sea of Okhotsk, Nemuro, 44°15'N, 145°20'E, 60 m (radula on Fig. 19B). **E** – no. 3, Sea of Okhotsk, Aniva Bay, 95 m (radula on Fig. 19C). **F** – no. 4, northern part of the Bering Sea, 63°59.9'N, 177°38.6'W, 87 m (radula on Fig. 19D). **G** – no. 5, Sakhalin Island, Pogranichnoye village, 78 m (radula on Fig. 19E). **H** – no. 6, northern part of the Sea of Okhotsk, 57°49.7'N, 141°53.6'E, 142 m (radula on Fig. 19F). **I** – no. 7, Sakhalin, section from Sakayjakan, 144 m (radula on Fig. 20A). Scale bar 10 mm.

РИС. 16. Раковины *Retifusus parvus*: **A** – голотип *P. parvus* Tiba, 1980, от Дальнегорска, Японское море (?), 400 м. **B** – голотип *P. saginatus* Tiba, 1980, Сахалин, 400 м. **C** – № 1, Охотское море, Татарский пролив, 54°42'N, 137°27'E, 24 м (радула на Рис. 19A). **D** – № 2, Охотское море, Немуро, 44°15'N, 145°20'E, 60 м (радула на Рис. 19B). **E** – № 3, Охотское море, залив Анива, 95 м (радула на Рис. 19C). **F** – № 4, северная часть Берингова моря, 63°59.9'N, 177°38.6'W, 87 м (радула на Рис. 19D). **G** – № 5, Сахалин, с. Пограничное, 78 м (радула на Рис. 19E). **H** – № 6, северная часть Охотского моря, 57°49.7'N, 141°53.6'E, 142 м (радула на Рис. 19F). **I** – № 7, Сахалин, разрез от Сакайякана, 144 м (радула на Рис. 20A). Масштабный отрезок 10 мм.



FIG. 17. Shells of *Retifusus parvus*: **A** – holotype of *P. semiplicatus* Golikov in Golikov et Scarlato, 1985, south-eastern Sakhalin, 78 m. **B-D** – Sea of Okhotsk, Aniva Bay, 95 m: **B** – no. 8 (radula on Fig. 20B), **C** – no. 9 (radula on Fig. 20C), **D** – no. 10 (radula on Fig. 20D). **E** – no. 11, Sea of Japan, 43°04.4' N, 134°30.8' E, 90 m (radula on Fig. 20E, anatomy on Fig. 18). **F** – no. 12, Sea of Okhotsk, Tatar Strait, 110 m (radula on Fig. 20F, anatomy on Fig. 18). **G** – ZIN uncatalogued, north part of the Sea of Okhotsk.

РИС. 17. Раковины *Retifusus parvus*: **A** – голотип *P. semiplicatus* Golikov in Golikov et Scarlato, 1985, юго-восточный Сахалин, 78 м. **B-D** – Охотское море, залив Анива, 95 м: **B** – № 8 (радула на Рис. 20B), **C** – № 9 (радула на Рис. 20C), **D** – № 10 (радула на Рис. 20D). **E** – № 11, Японское море, 43°04.4' N, 134°30.8' E, 90 м (радула на Рис. 20E, анатомия на Рис. 18). **F** – № 12, Охотское море, Татарский пролив, 110 м (радула на Рис. 20F, анатомия на Рис. 18). **G** – ЗИН не каталогизировано, северная часть Охотского моря.

Mantle spans one whorl, kidney – 0.2, digestive gland and gonad the remaining part of visceral mass (Fig. 18 A-B). Head large, with thick contracted tentacles and folded short neck. Small black eyes sit at small lobes at tentacles' bases. Foot contracted, propodium rather wide, separated by deep propodi-

al groove. Operculum oval, with terminal nucleus shifted to left.

Mantle as wide as long, with long siphon (Fig. 18C). Ctenidium crescent-curved, occupying whole mantle length and about quarter of its width. Osphradium is equal to ctenidium in width and

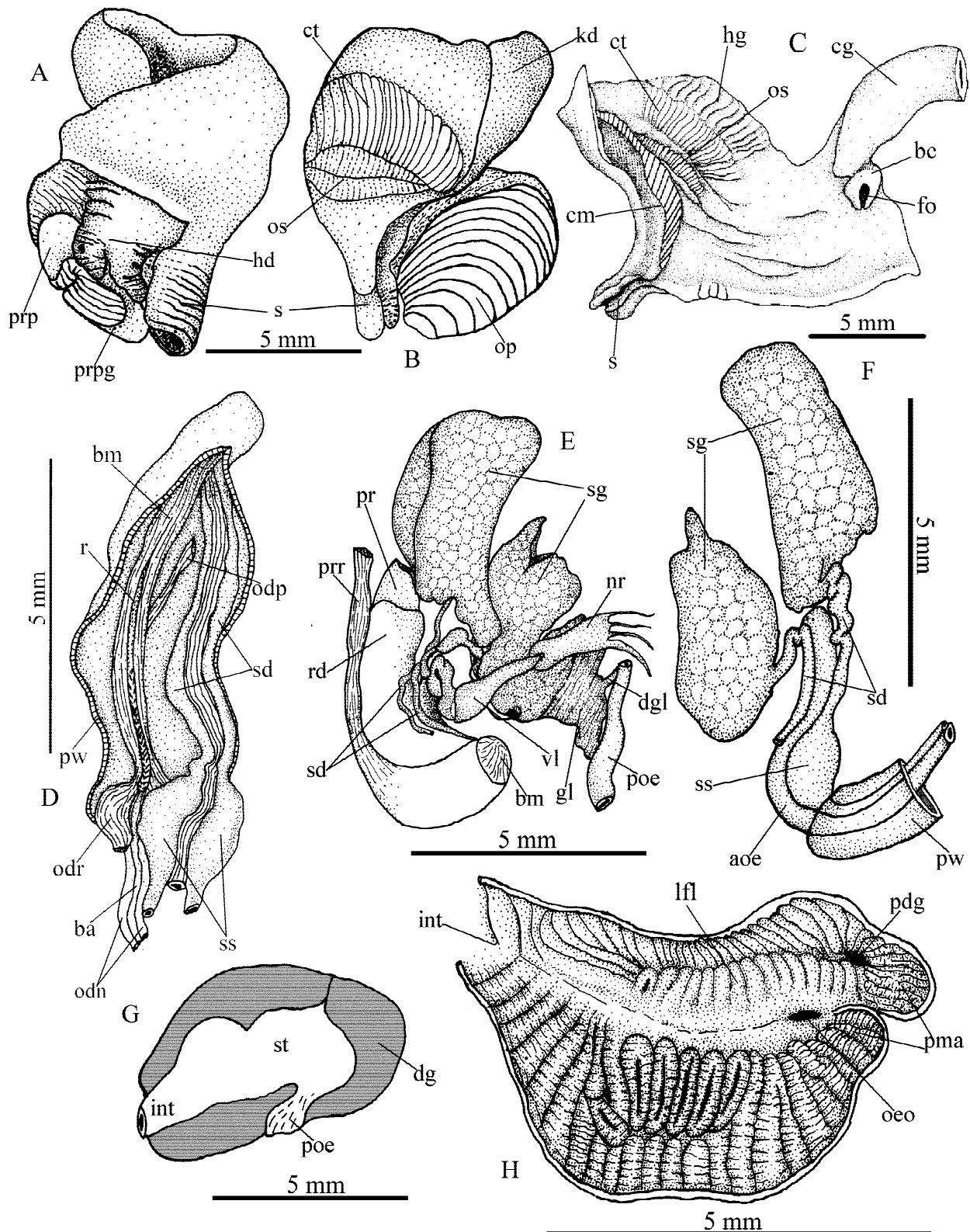


FIG. 18. Anatomy of *Retifusus parvus* no. 11 (A-C, E-H, shell on Fig. 17E, radula on Fig. 20E) and no. 12 (C-D, shell on Fig. 17F, radula on Fig. 20F): A – soft body dorsal view, B – soft body ventral view, C – mantle, D – proboscis opened dorsally, E – foregut ventro-lateral view, F – part of foregut showing salivary pouches, G – stomach general view, H – opened stomach.

РИС. 18. Анатомия *Retifusus parvus* № 11 (A-C, E-H, раковина на Рис. 17E, радула на Рис. 20E) and № 12 (C-D, раковина на Рис. 17F, радула на Рис. 20F): A – дорсальный вид мягкого тела, B – вентральный вид мягкого тела, C – мантия, D – хобот, вскрытый дорсально, E – вентро-латеральный вид мягкого тела, F – фрагмент переднего отдела пищеварительной системы, показывающий слюнные протоки со слюнными мешками, G – общий вид желудка, H – вскрытый желудок.

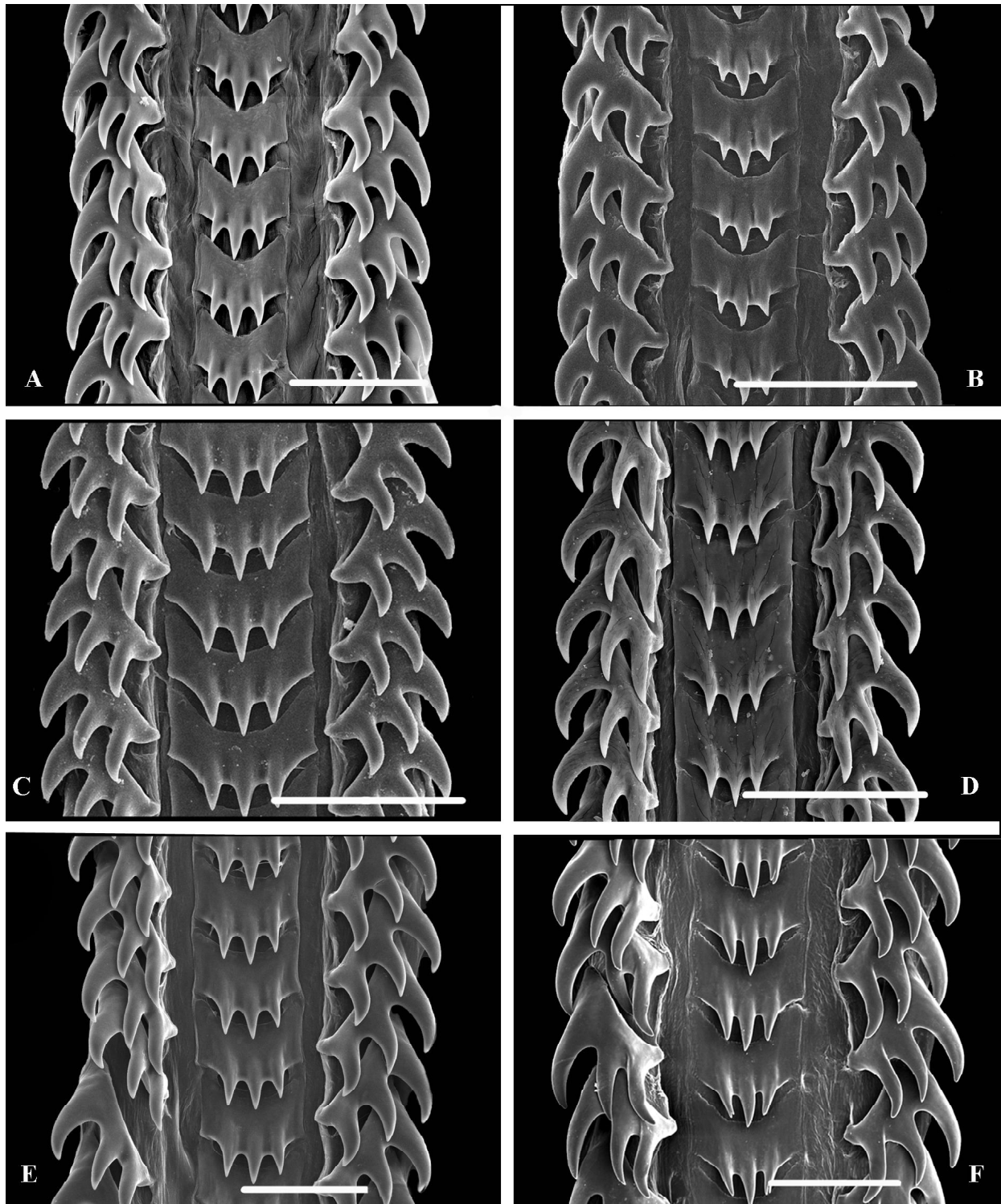


FIG. 19. Radulae of *Retifusus parvus*. **A** – no. 1 (shell on Fig. 16C). **B** – no. 2 (shell on Fig. 16D). **C** – no. 3 (shell on Fig. 16E). **D** – no. 4 (shell on Fig. 16F). **E** – no. 5 (shell on Fig. 16G). **F** – no. 6 (shell on Fig. 16H). Scale bar 100 μ m.

РИС. 19. Радулы *Retifusus parvus*. **A** – № 1 (раковина на Рис. 16C). **B** – № 2 (раковина на Рис. 16D). **C** – № 3 (раковина на Рис. 16E). **D** – № 4 (раковина на Рис. 16F). **E** – № 5 (раковина на Рис. 16G). **F** – № 6 (раковина на Рис. 16H). Масштабный отрезок 100 μ m.

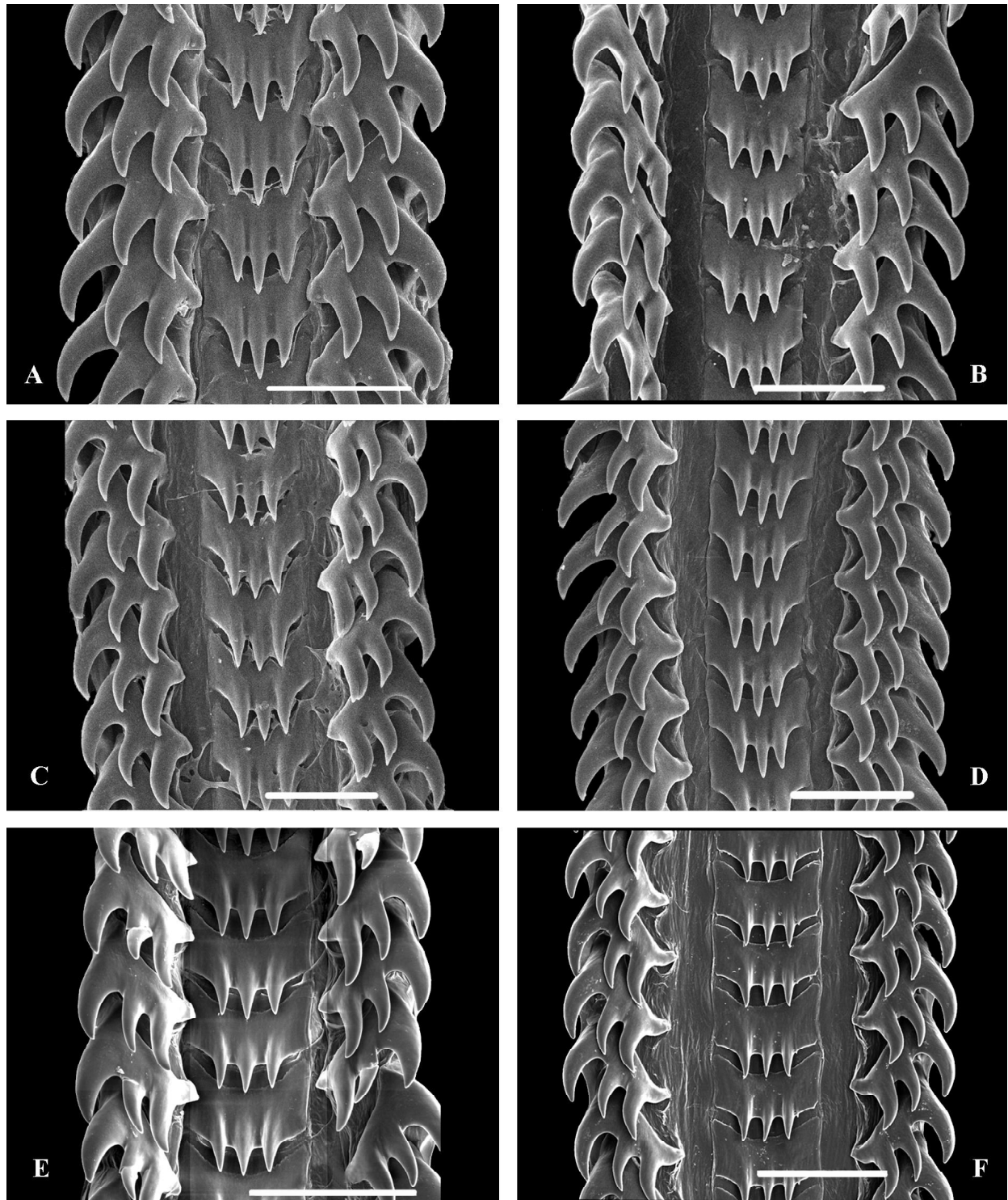


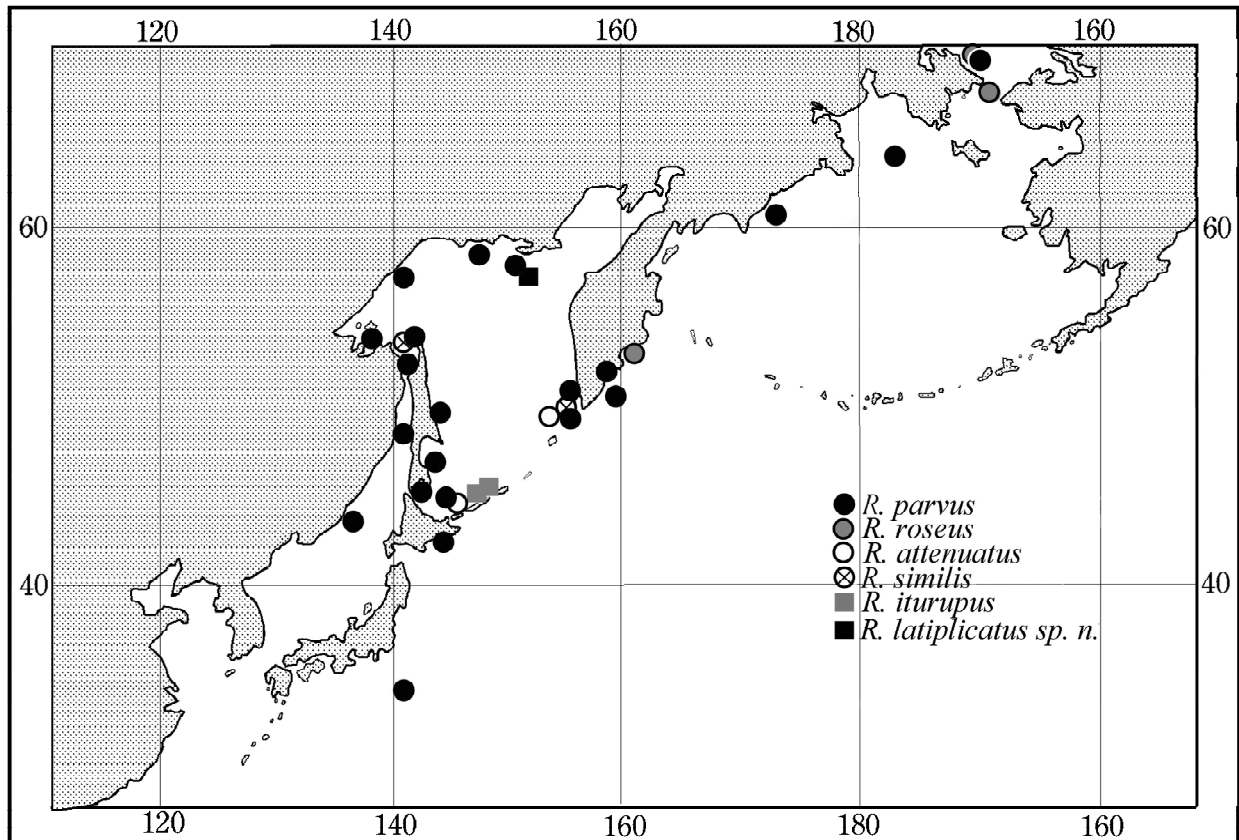
FIG. 20. Radulae of *Retifusus parvus*. **A** – no. 7 (shell on Fig. 16I). **B** – no. 8 (shell on Fig. 17B). **C** – no. 9 (shell on Fig. 17C). **D** – no. 10 (shell on Fig. 17D). **E** – no. 11 (shell on Fig. 17E, radula on Fig. 20E, anatomy on Fig. 18). **F** – no. 12 (shell on Fig. 17F, radula on Fig. 20F, anatomy on Fig. 18). Scale bar 100 μ m.

РИС. 20. Радулы *Retifusus parvus*. **A** – № 7 (раковина на Рис. 16I). **B** – № 8 (раковина на Рис. 17B). **C** – № 9 (раковина на Рис. 17C). **D** – № 10 (раковина на Рис. 17D). **E** – № 11 (раковина на Рис. 17E, радула на Рис. 20E, анатомия на Рис. 18). **F** – № 12 (раковина на Рис. 17F, радула на Рис. 20F, анатомия на Рис. 18). Масштабный отрезок 100 μ m.

comprises 0.6 of its length. Rectum short, spans half of mantle length, covered by well-developed capsule gland (**cg**) occupying $\frac{3}{4}$ of mantle length. *Bursa copulatrix* (**bc**) situated ventrally on capsule gland, female orifice elongated and wide (Fig. 18C, **fo**). Penis (nos. 3, 8-9, not figured) terminated in

large rounded cone-shaped papilla with small semi-nal opening on the top. Papilla not encircled by a fold of skin and obviously non-retractile.

Digestive system. Proboscis not folded within rhynchodaeum, buccal mass slightly extends from rear of proboscis (Fig. 18 E-F). Proboscis retrac-

FIG. 21. Geographical distribution of *Retifusus parvus*, *R. roseus*, *R. iturupus*, *R. similis*, *R. attenuatus* and *R. latiplicatus*.РИС. 21. Географическое распространение *Retifusus parvus*, *R. roseus*, *R. iturupus*, *R. similis*, *R. attenuatus* и *R. latiplicatus*.Table 4. Shell and radulae measurements of *Retifusus parvus*.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, μm	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
1	27.5	19.2	13.9	300	2.16	3:3:3	19A
2	17.6	13.7	10.3	200	1.94	3:3:3	19B
3	27.0	19.1	14.2	220	1.55	3:3:3	19C
4	24.5	17.1	13.1	200	1.53	3:3:3	19D
5	28.4	22.3	17.2	320	1.86	3:3:3	19E
6	22.0	17.0	13.0	300	2.30	3:3:3	19F
7	30.5	23.4	17.3	250	1.45	3:3:3	20A
8	20.7	16.0	11.4	320	2.80	3:3:3	20B
9	21.0	16.9	12.8	300	2.34	3:3:3	20C
10	23.3	17.9	13.6	300	2.21	3:3:3	20D
11	30.0	21.0	16.0	230	1.35	3:3:3	20E
12	24.6	18.7	14.3	250	1.47	3:3:3	20F

tors situated on both sides of rhynchodaeum and attach to lateral walls of body haemocoel. Odontophore is attached to proboscis walls by several bands of odontophoral retractors. **Radula** similar in all examined specimens (Figs. 19-20). Rachidian is tricuspidate, median cusp sometimes slightly longer than marginal ones. Lateral teeth with three large cusps, shorter and thicker than in the previous species, their basal parts are equal or wider than

rachidian bases. Details of radulae of examined specimens are summarized in Table 4.

Median radula retractor detaches from basal part of radula sac. Several buccal nerves follow along ventral side of proboscis wall. Thick salivary ducts follow along anterior oesophagus and open in anterior part of buccal cavity. They form widening – salivary pouches – after leaving proboscis (Fig. 18F, ss). Salivary glands very large, equal to pro-

boscis length, situated within body haemocoel ventrally and anteriorly to proboscis (Fig. 18E). Valve of Leiblein long and narrow; gland of Leiblein very large, situated posteriorly to salivary glands, duct of the gland opens into oesophagus at a distance posterior to nerve ring (Fig. 18E, **gl**).

Stomach occupies third part of whorl and situated at an angle to its longitudinal axis (Fig. 18G). Posterior mixing area small, rounded. Outer stomach wall lined with high transverse folds (Fig. 18H). Longitudinal fold on inner stomach wall lined with transverse folds, the rest part of the wall lined with oblique folds. Opening of posterior duct of digestive gland (**pdg**) situated above oesophageal opening, near end of longitudinal fold. Opening of anterior duct not found.

Distribution. Pacific coast of Japan, Sea of Japan, Sea of Okhotsk, eastern Kamchatka, Bering and Chuckchi (Wrangel Island) seas, 24-400 m (Fig. 21).

Remark. As a result of examination of a large number of specimens we came to the conclusion, that *Plicifusus parvus*, *P. saginatus*, and *Retifusus semiplicatus* represent the same species, widely distributed in north Pacific. The shell morphology varies from elongated-fusiform shells with high axial ribs represented on entire shell surface ("*R. parvus*" and "*R. saginatus*") to broad-fusiform shells with less expressed axial ribs, usually well pronounced only on the spire ("*R. semiplicatus*"). The intermediate forms are common and sometimes are found in the same sample. Radular structure and anatomical characters (especially presence of salivary pouches on salivary ducts) are uniform among conchologically different specimens of the species.

Retifusus roseus (Dall, 1877) (Figs. 21-24)

Chrysodomus roseus Dall, 1877: 2.

Aulacofusus roseus – Dall, 1921: 94. – 1925: 13, pl. 26, fig. 2.

– Kantor, Sysoev, 2005: 130. – Kantor, Sysoev, 2006: 181, pl. 89 I-J.

Retifusus roseus – Sirenko *et al.*, 2013: 162.

Types: holotype of *Chrysodomus roseus* – USNM 108985.

Type locality: Bering Strait.

Material examined: 4 lots, 38 specimens. ZIN 57884/1,

Ice-breaker *North Pole*, northern part of East-Siberian Sea, 42 m, sta. 27/33, 72°34'N, 171°51'E, 18.08.1946 (spm. no. 1 dissected). ZMMU, eastern Kamchatka, RV *Equator*, sta. 119, 53°18.6'N, 160°20.5'E, 850 m, 08.12.1972 (no. 2 dissected). ZIN 56657/84, Kara Sea, western coast of Yamal peninsula, RV *Rusanov*, 71°54'N, 67°45'E, 40 m, sta. 10, 09.08.1931 (33 specimens, no. 3 dissected). ZIN 56940/106, south-eastern Barents Sea, RV *Persey*, sta. 133, 70°38'N, 52°08'E, 165 m 23.07.1924 (3 specimens, no. 4 dissected).

Description. Shell height from 18 to 24 mm (Table 5), broad-fusiform, with more or less attenuated spire, and short and broad siphonal canal, covered with yellow to brown periostracum (Fig. 22). Shell under periostracum white or beige. Spiral sculpture consists of wide flattened cords (about 13-17 on penultimate whorl), separated by deep, narrow grooves. Axial sculpture represented only by incremental lines. Operculum oval with terminal nucleus, turned to left.

Soft body. Two whorls extracted from the shell. Mantle spans one whorl, kidney 0.25, digestive gland and gonad – remaining part of visceral mass (Fig. 23 A-B). Head with contracted closely situated tentacles (Fig. 23D). Large black eyes situated on lobes at tentacles' bases. Foot is half-folded transversely, rather wide propodium (Fig. 23B, **prp**) is separated by deep propodial groove (**prpg**). Operculum oval, with terminal nucleus dislodged to the left (Fig. 23A).

Mantle width equals its length (Fig. 23C). Siphon short, contracted, with well expressed siphonal valve at its base. Crescent curved osphradium large (0.5 of mantle length); ctenidium occupies 0.75 of mantle length, its width equals that of osphradium. Folds of hypobranchial gland not expressed, its area filled with mucus. Rectum flattened, thin-walled, occupies 0.6 of mantle length.

Reproductive system. Penis long (Fig. 23E) and wide, terminating in large rounded cone-shaped papilla (**sp**) with small seminal opening (**so**) on the top. Papilla not encircled by a fold of skin and obviously non-contractible. Prostate gland very well developed, with thick walls.

Digestive system. Proboscis straight, not folded (Fig. 23G, **pr**). Buccal mass (Fig. 23F, **bm**) equals proboscis in length; attached to proboscis wall by several strongly contracted odontophoral retractors (**odr**). **Radula** in radular sac equal to odontophore in length, with long median retractor

Table 5. Shell and radulae of *Retifusus roseus*.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, µm	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
1	18.8	15.0	6.7	130	1.94	3:3:3	24A
2	19.2	14.4	11.8	130	1.10	3:3:3	24B
3	20.2	15.2	11.0	200	1.82	3:3:3	24C
4	23.2	16.0	12.2	200	1.64	3:3:3	24D



FIG. 22. *Retifusus roseus* shells: **A** – holotype of *Chrysodomus roseus* Dall, 1877, Bering Strait. **B** – no. 1, northern part of East-Siberian Sea, 42 m (radula on Fig. 24A, anatomy on Fig. 23). **C** – no. 2, eastern Kamchatka, 53°18.6'N, 160°20.5'E, 850 m (radula on Fig. 24B). **D** – no. 4, south-east Barents Sea, 70°38' N, 52°08'E, 165 m (radula on Fig. 24D). **E-F** – Kara Sea, western coast of Jamal peninsula, 71°54'N, 67°45'E, 40 m, (**F** – no. 3, radula on Fig. 24C). Scale bar 10 mm.

РИС. 22. Раковины *Retifusus roseus*: **A** – голотип *Chrysodomus roseus* Dall, 1877, Берингов пролив. **B** – № 1, северная часть Восточно-Сибирского моря, 42 м (радула на Рис. 24А, анатомия на Рис. 23). **C** – № 2, восточная Камчатка, 53°18.6'N, 160°20.5'E, 850 м (радула на Рис. 24В). **D** – № 4, юго-восточная часть Баренцева моря, 70°38' N, 52°08'E, 165 м (радула на Рис. 24D). **E-F** – Карское море, западный берег п-ва Ямал, 71°54'N, 67°45'E, 40 м, (**F** – № 3, радула на Рис. 24С). Масштабный отрезок 10 мм.

(**mrr**). Rachidian (Fig. 24 A-D) with 3 cusps of equal or unequal length (median cusp the longest). The cusps are situated on crescent-curved base. Lateral teeth as in *P. parvus*. Radular morphology is summarized in Table 5.

Anterior oesophagus inside proboscis thin-walled and narrow. Salivary ducts thick, equal in width to anterior oesophagus. (Fig. 23F, **sd**). They widen abruptly after leaving proboscis and form salivary pouches on both sides of buccal mass (Fig 23F, **ss**). Salivary glands (Fig. 23G, **sg**) large, nearly

equal to proboscis in length, situated on its both sides. Proboscis retractors (Fig. 23 F-G, **prr**) paired, thick, contracted, detached from rhynchodeum approximately in the middle of proboscis and attached to lateral walls of body haemocoel. Valve of Leiblein (**vl**) short, swollen, with nerve ring located immediately after it. Posterior oesophagus narrower than anterior one, follows along well-developed gland of Leiblein (**gl**), tapering posteriorly to an ample. Narrow duct of gland of Leiblein opens into oesophagus close to nerve ring.

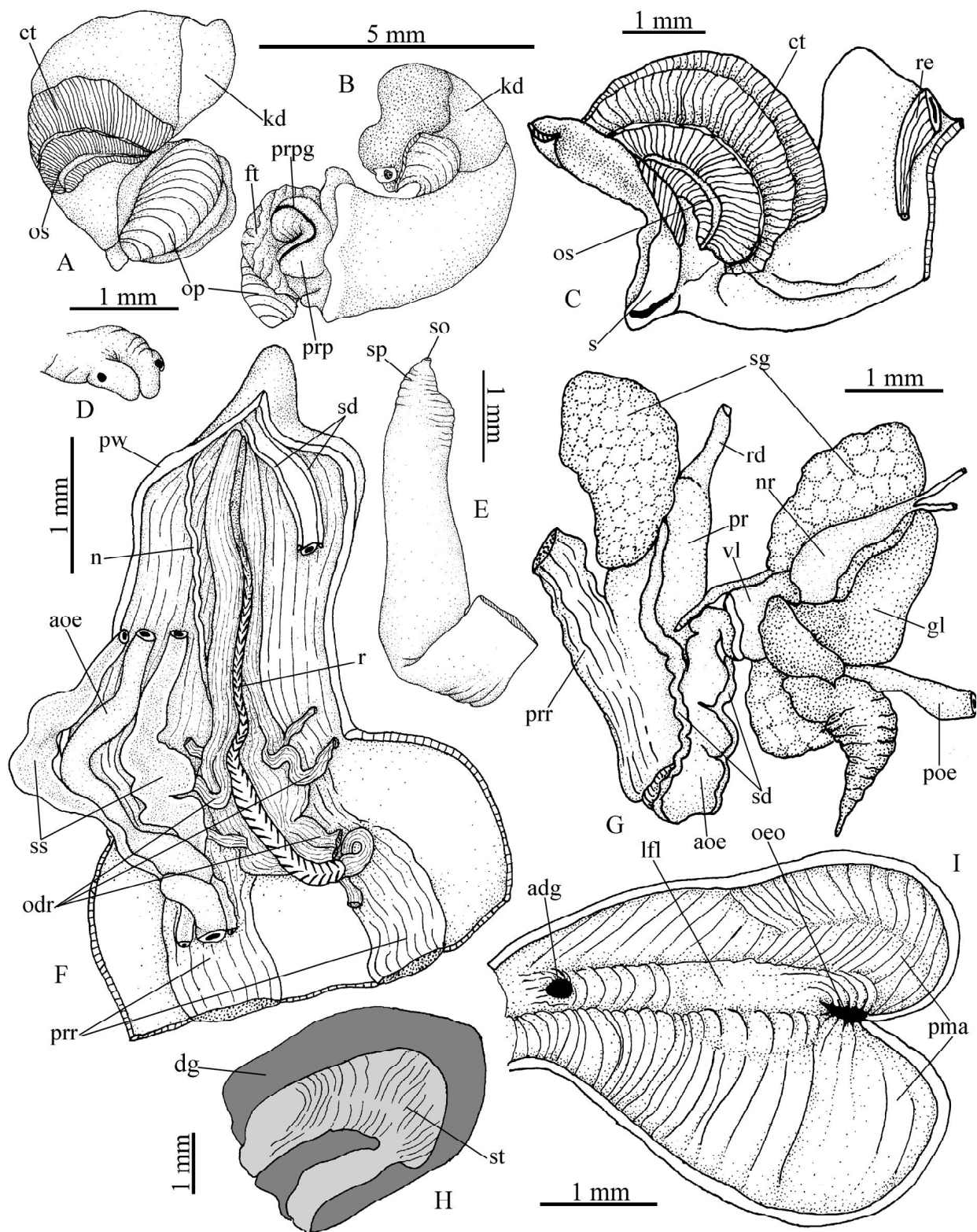


FIG. 23. Anatomy of *Retifusus roseus* no. 1 (shell on Fig. 22B, radula on Fig. 24A). A – soft body ventral view; B – soft body lateral view; C – mantle; D – head; E – penis; F – proboscis opened dorsally; G – foregut ventro-lateral view; H – stomach general view; I – opened stomach.

РИС. 23. Анатомия *Retifusus roseus* № 1 (раковина на Рис. 22B, радула на Рис. 24A). А – мягкое тело, вид с вентральной стороны; В – мягкое тело, латеральный вид; С – мантия; D – голова; Е – пенис; F – хобот, вскрытый с дорсальной стороны; G – вентро-латеральный вид переднего отдела пищеварительной системы; H – общий вид желудка; I – вскрытый желудок.

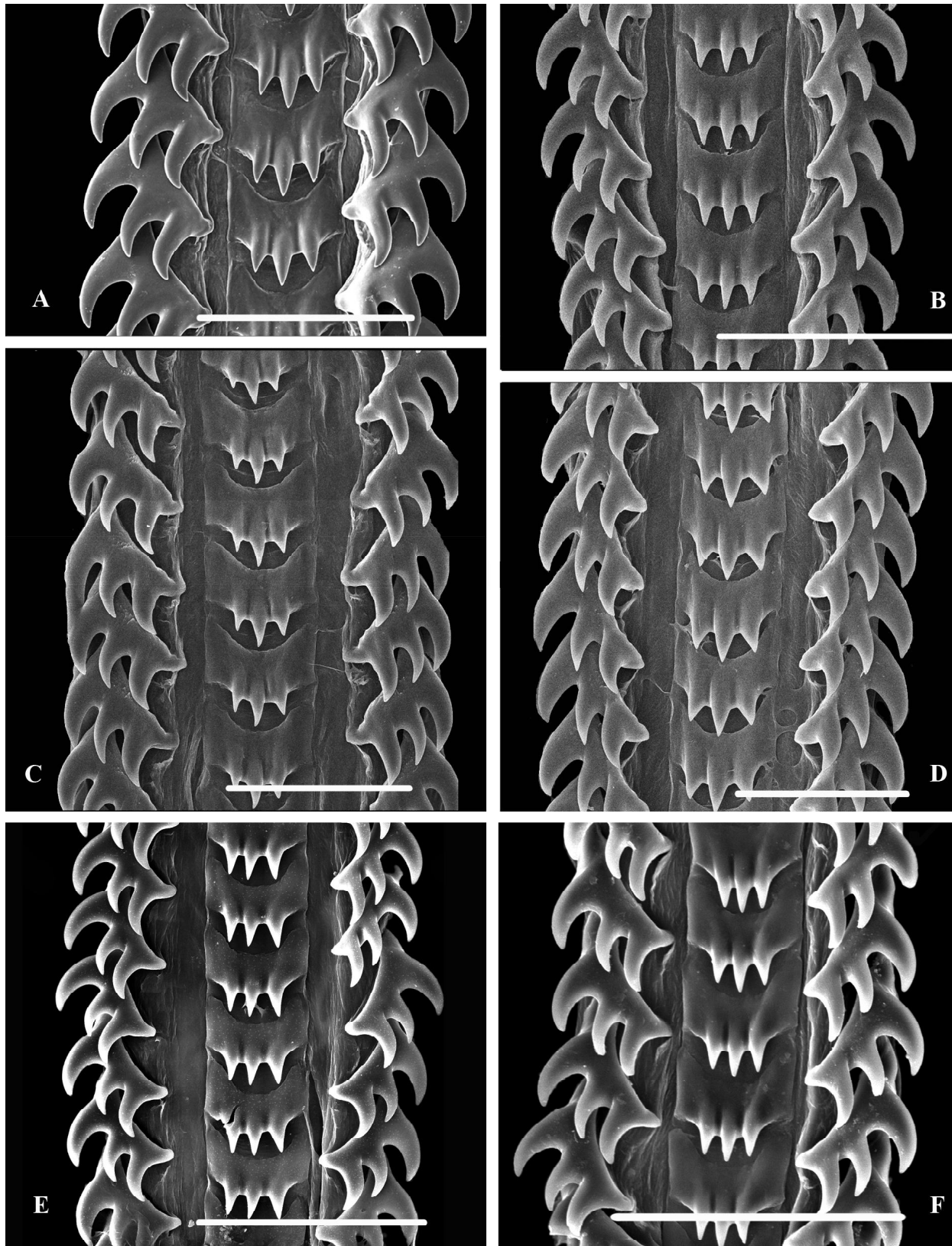


FIG. 24. Radulae of *Retifusus*. **A** – *R. roseus* no. 1 (shell on Fig. 22B, anatomy on Fig. 23). **B** – *R. roseus* no. 2 (shell on Fig. 22C). **C** – *R. roseus* no. 3 (shell on Fig. 22F). **D** – *R. roseus* no. 4 (shell on Fig. 22D). **E** – *R. latericeus* no. 1 (shell on Fig. 25A, anatomy on Fig. 26). **F** – *R. latericeus* no. 2 (shell on Fig. 25B). Scale bar 100 μm .

РИС. 24. Радулы *Retifusus*. **A** – *R. roseus* № 1 (раковина на Рис. 22B, анатомия на Рис. 23). **B** – *R. roseus* № 2 (раковина на Рис. 22C). **C** – *R. roseus* № 3 (раковина на Рис. 22F). **D** – *R. roseus* № 4 (раковина на Рис. 22D). **E** – *R. latericeus* № 1 (раковина на Рис. 25E, анатомия на Рис. 26). **F** – *R. latericeus* № 2 (раковина на Рис. 25B). Масштабный отрезок – 100 μm .

Stomach spans 1/3 of visceral whorl, situated parallelly to its longitudinal axis, and has thin semi-transparent walls with transverse folds visible through them (Fig. 23H). Posterior mixing area small, rounded, lined with transverse folds (Fig. 23I, **pma**). Inner stomach wall in its posterior part lined with two rows of oblique folds, joining at obtuse angle, while anteriorly the wall is lined with uniform oblique folds. Longitudinal fold on inner stomach wall rather large, ends near opening of anterior duct of digestive gland (Fig. 23I, **adg**). Opening of posterior duct of digestive gland situated in the deepening of oesophageal opening. Outer stomach wall lined with multiple transverse folds.

Differential diagnosis. From most similar *Retifusus jessoensis*, *R. roseus* differs by less pronounced spiral cords, absence of axial ribs, radula morphology and foregut anatomy; from *R. similis* and *R. attenuatus* by the presence of salivary pouches.

Distribution – the Barents, Kara, East-Siberian and Bering seas, eastern Kamchatka, 40–850 m.

Remarks. The deep-water specimen from Kamchatka (Fig. 22C) differs from the rest of material in shape and is attributed to *R. roseus* only tentatively, based on similar shell sculpture, anatomy and radula morphology. Since Dall [1921], the first record of the species (within the genus *Aulacofusus*) has been made by Kantor and Sysoev [2005, 2006] based on the single specimen from the East-Siberian Sea. Bouchet and Warén [1985, p. 231, figs. 634–636] illustrated two specimens of *Colus latericeus*, one typical and another rather different from the type, i.e. with more rounded shell with lower spire and lacking axial ribs. We found several specimens from the Barents and Kara Seas in the collections of ZIN, greatly reminding that latter specimen, and attribute them to *Retifusus roseus*.

Retifusus latericeus (Möller, 1842),

comb. nov.

(Figs. 24E–F, 25, 26)

Fusus latericeus Möller, 1842: 88.

Fusus pellucidus Hancock, 1846: 330, pl. 5, fig. 3.

Fusus pullus Reeve, 1848: pl. 21, fig. 89.

Tritonium incarnatum M. Sars, 1851: 191–192.

Neptunea (Sipho) pertenuis Sykes, 1911: 339, fig. page 340.

Lectotype [Bouchet, Warén, 1985]: ZMUC GAS-72.

Type localities: of *Fusus latericeus* – west Greenland (Igaliko Fjord or Godthaab); of *Fusus pellucidus* – deep inlet on the west coast of the Davis Strait, 68°N, 66°30'W, 12–15 fms; of *Fusus pullus* – Newfoundland; of *Tritonium incarnatum* – Tromsø and Havörsund, 20–30 fms; of *Neptunea (Sipho) pertenuis* – Porcupine Expedition 1869, sta. 51.

Material examined: 8 lots, 8 specimens. ZMMU 18275,

Barents Sea, RV *A. Otkupschikov*, sta. 54, 190 m (no. 1 dissected). ZMMU 18273 Barents Sea, RV *A. Otkupschikov*, sta. 9, 69°10'N, 36°00'E, 80–88 m (no. 2 dissected). ZMMU 18272, Barents Sea, RV *A. Otkupschikov*, sta. 12, 69°20'N, 36°00'E, 182 m (1 spm.). ZMMU 18274, Barents Sea, RV *A. Otkupschikov*, sta. 29, 69°22.5'N, 35°40'E, 180 m (1 spm.). ZMMU 18270, White Sea, 34 m (1 spm.). ZIN 37308/23, White Sea, Lovozero Gulf, sta. T-25, 26 m, 17.06.1974 (1 spm.). ZIN 37309/24, White Sea, Onezhsky Gulf, sta. 1, 65°18'N, 35°00'E, 25–30 m, 10.07.80 (1 spm.). ZIN 55691/52, White Sea, Solovetsky Islands, 26 m, 18.07.1895 (1 spm.).

Description. Shell 10–25 mm in height, elongated-fusiform, with high spire, covered with thin light-beige periostracum; shell under periostracum white or rosy-beige (Fig. 25). Spiral sculpture represented by flattened spiral cords (10–17 on penultimate whorl) separated by three times narrower deep grooves between them. Axial sculpture consists of medium high axial ribs, present on all whorls in small specimens and only on upper whorls in large ones. Operculum oval with terminal nucleus, slightly shifted to the left. Measurements: no. 1 H 17.4 mm, h 11.7 mm, AL 9.0 mm; no. 2 H 23.0 mm, h 14.8 mm, AL 9.7 mm.

Soft body. Head large, tentacles long and thick, with large black eyes situated at their bases on small lobes. Mantle with ctenidium comprising 0.3 of mantle width, and almost symmetrical, bipectinate osphradium. Both dissected specimens were mature females with thick capsule gland.

Digestive system. Proboscis straight, buccal mass pulled into proboscis haemocoel (Fig. 26). Proboscis retractors attached to both sides of rhynchodaeum as a few muscle bands. Radula has the same morphology as in *R. roseus*, but median cusps of rachidian are almost equal in length to outermost cusps. Radula of no. 1 is 150 µm wide (1.67% of AL); of no. 2 – 130 µm wide (1.34% of AL) (Figs. 24 E–F respectively). Salivary glands large, comprising about 0.4 of proboscis length. Salivary ducts inside proboscis as wide as anterior oesophagus, widening at basal part of buccal mass and forming salivary pouches (Fig. 26). The ducts open into salivary glands soon after coming out of proboscis. Valve of Leiblein not large, pear-shaped; gland of Leiblein medium large, dark brown, following parallel to posterior oesophagus.

Distribution. West Greenland, Newfoundland, 91–1417 m [Rosenberg, 2009 – Malacolog 4.1.1.]; the White and Barents Seas, 25–190 m.

Remarks. *R. latericeus* and *R. roseus* have similar anatomy with salivary pouches of salivary ducts, similar radulae morphology and sympatric distribution in Arctic waters, thus probably being closely related. Nevertheless, *Retifusus latericeus* was found in warmer waters of North Atlantic and the part of the Barents Sea, influenced by Gulf-stream, whereas *R. roseus* was found only in cold Arctic waters and North Pacific.

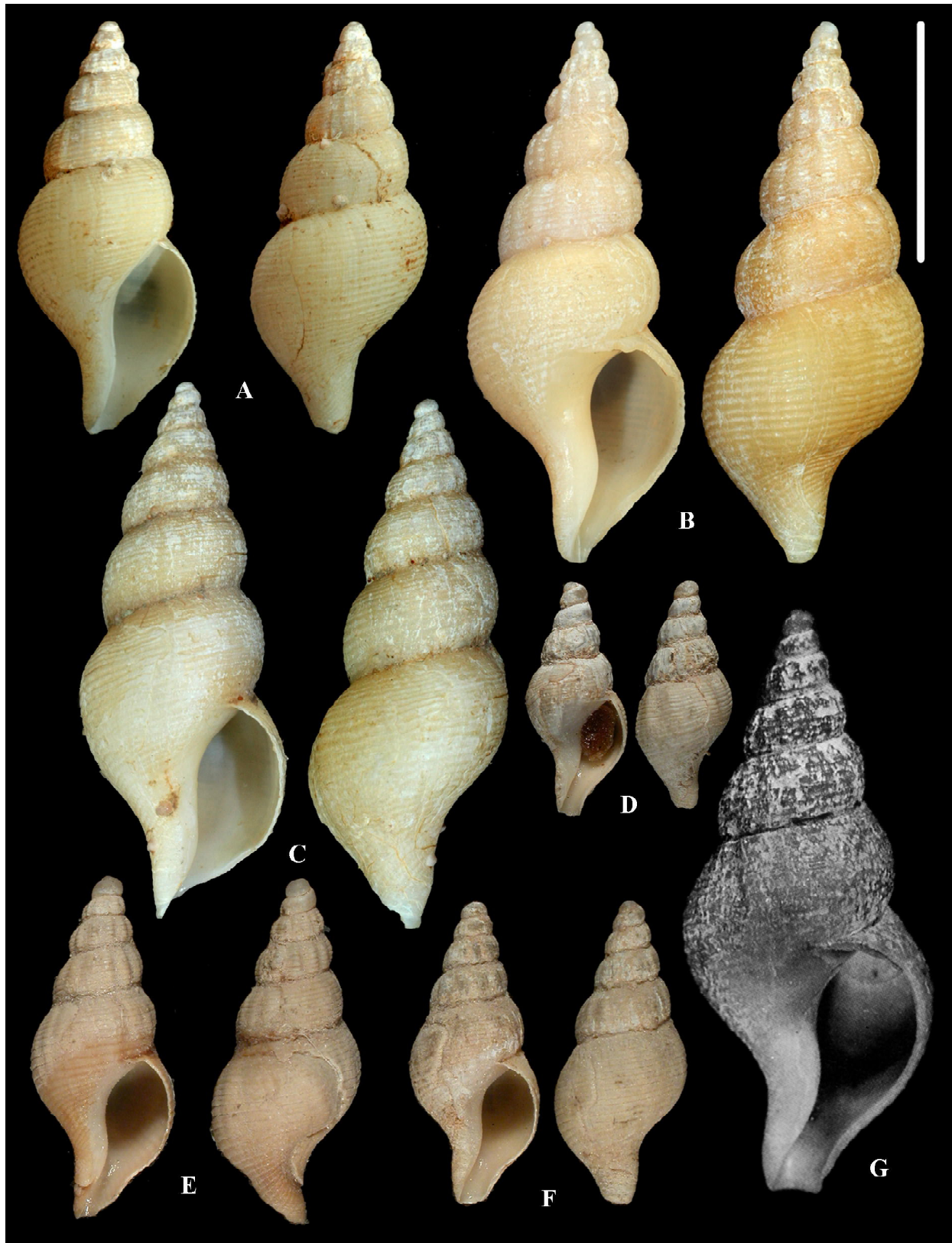


FIG. 25. Shells of *Retifusus latericeus*. **A** – no. 1, Barents Sea, 190 m (radula on Fig. 24E, anatomy on Fig. 26). **B** – no. 2, Barents Sea, 69°10'N, 36°00'E, 80–88 m (radula on Fig. 24F). **C** – Barents Sea, 69°22.5'N, 35°40'E, 180 m. **D** – White Sea, Lovozero Gulf, 26 m. **E** – White Sea, Solovetsky Islands, 26 m. **F** – White Sea, Onezhsky Gulf, 25–30 m. Scale bar 10 mm.

РИС. 25. Раковины *Retifusus latericeus*. **A** – Баренцево море, 190 м, № 1 (радула на Рис. 24Е, анатомия на Рис. 26). **B** – Баренцево море, 69°10'N, 36°00'E, 80–88 м, № 2 (радула на Рис. 24F). **C** – Баренцево море, 69°22.5'N, 35°40'E, 180 м. **D** – Белое море, Ловозерская губа, 26 м. **E** – Белое море, Соловецкие острова, 26 м. **F** – Белое море, Онежский залив, 25–30 м. Масштабный отрезок 10 мм.

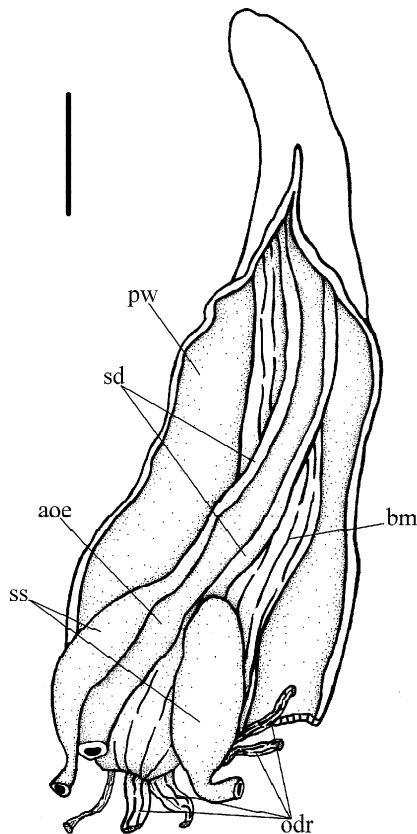


FIG. 26. Opened proboscis of *Retifusus latericeus* no. 1 (shell on Fig. 25A, radula on Fig. 24E). Scale bar 1 mm.

РИС. 26. Вскрытый хобот *Retifusus latericeus* №1 (раковина на Рис. 25А, радула на Рис. 24Е). Масштабный отрезок 1 мм.

Retifusus attenuatus
(Golikov et Gulbin, 1977)
(Figs. 21, 27 A-C, 28, 29B)

Mohnia attenuata Golikov, Gulbin, 1977: 178-179, Fig. 1. – Higo *et al.*, 1999: 228. – Kantor, Sysoev, 2005: 133. – Kantor, Sysoev, 2006: 186, pl. 93 L.
Retifusus attenuatus. – Sirenko *et al.*, 2013: 161.

Holotype: ZIN 28231/1.

Type locality: Ekaterina Strait (between Kunashir and Iturup Islands), 250 m.

Material examined: ZIN 28233, RV *Lebed*, Paramushir Island, off Jumen cape, sta. 77, 198 m, pebble, sand, mud (1 specimen, dissected).

Description. Shell 20-25 mm in height, thin-walled, elongated-fusiform, with poorly convex whorls and attenuated spire, covered with light-beige periostracum (Fig. 27 A-C). Spiral sculpture consists of flattened cords, separated by shallow grooves, up to 15 cords on penultimate whorl. Axial sculpture on last and penultimate whorls represent-

ed only by incremental lines, some weak axial ribs are seen on upper whorls. Operculum oval, with terminal nucleus, slightly shifted to left. Measurements: H 20.7 mm, h 15.0 mm, AL 11.0 mm. Juvenile male.

Soft body. Head wide, contracted, tentacles pointed towards lateral parts of head, with eyes sitting on small lobes at their bases (Fig. 28B). Foot folded transversely, propodium moderately wide separated by deep propodial groove. Penis small, situated at right side of head, distinct seminal papilla absent. (Fig. 28A, p). **Mantle** length equal to width, siphon moderately thick and long (Fig. 28C). Ctenidium very long, occupies almost entire mantle length. Folds of hypobranchial gland comprise the rest part of mantle between ctenidium and rectum. Osphradium slightly shorter than ctenidium, occupies 0.75 of length and about 0.2 width of mantle. Rectum occupies half mantle length.

Digestive system. Proboscis straight within thin-walled rhynchodaeum (Fig. 28A). Proboscis retractors situated on both sides of rhynchodaeum in middle part of its length attaching to lateral walls of body haemocoel (Fig. 28 E-F, prr). Buccal mass occupies entire proboscis length; multiple bands of odontophoral retractors arise from its base (Fig. 28A, bm, odr). **Radula** is 6 mm long and 120 µm wide (0.86 % AL), consists of 116 rows of teeth, 6 nascent (Fig. 29B). Central tooth of radula bears three narrow cusps of subequal length. Lateral teeth of the same morphology as in *R. roseus* and *R. parvus*. Large median radula retractor arises from radula sac base, splits in two bundles before attaching to rhynchodaeum walls (Fig. 28A, mrr). Ramifying nerve fibers follow along inner proboscis walls (n). Anterior oesophagus, after leaving proboscis, coiled anterior to medium-sized valve of Leiblein. Nerve ring situated next to the valve. Posterior oesophagus wide; gland of Leiblein large, well-developed, situated beneath salivary glands along posterior oesophagus. Duct of the gland not found. Salivary glands very large, equal to proboscis length (Fig. 28 E-F, sg). Wide salivary ducts follow parallel to anterior oesophagus and open into buccal cavity. Salivary pouches absent.

Stomach spans 0.3 whorl and situated parallelly to its longitudinal axis (Fig. 28D). Posterior mixing area not large, tapering. Posterior oesophagus opens into stomach ventrally. Outer stomach wall lined with transverse folds. Further inner structure of stomach not examined.

Distribution – southern Kurile Islands, 150-414 m (Fig. 21).

Remarks. Shell clearly differs from the majority of *Retifusus* species by absence of axial ribs on two last whorls. From *R. roseus* differs by more elongated shell shape and absence of salivary pouches of salivary ducts.



FIG. 27. Shells of *Retifusus*: **A** – holotype of *R. attenuatus*: Ekaterina Strait (between Kunashir and Iturup Islands), 250 m. **B** – *R. attenuatus*, ZIN. **C** – *R. attenuatus* no. 1: North Kurile Islands, Paramushir, off Jumen cape, 198 m (radula on Fig. 29B, anatomy on Fig. 28). **D** – holotype of *R. similis*: Paramushir Island, Kurile Islands, 300 m. **E** – *R. similis* no. 1, Paramushir Island, Vasiliev gulf, 53 m (radula on Fig. 29C, anatomy on Fig. 30). **F** – *R. similis* no. 2: Sea of Okhotsk, Sakhalin Bay, 54°31.8'N, 140°44'E, 82 m (radula on Fig. 29A). **G-H** – *R. similis*, ZIN. **I** – holotype of *R. iturupus* in scale: Kurile Islands, Iturup Island, 44°47.7'N, 148°55.5'E, 660 m; **I'** – twice enlarged. Scale bar 10 mm.

РИС. 27. Раковины *Retifusus*: **A** – голотип *R. attenuatus*: пролив Екатерины (между о-вами Кунашир и Итуруп), 250 м. **B** – *R. attenuatus*, ЗИН. **C** – *R. attenuatus* № 1: Северные Курилы, о-в Парамушир, от м. Юмен, 198 м (радула на Рис. 29B, анатомия на Рис. 28). **D** – голотип *R. similis*, Курильские острова, Парамушир, 300 м. **E** – *R. similis* № 1, Парамушир, бухта Васильева, 53 м (радула на Рис. 29C, анатомия на Рис. 30). **F** – *R. similis* № 2: Охотское море, Сахалинский зал., 54°31.8'N, 140°44'E, 82 м (радула на Рис. 29A). **G-H** – *R. similis*, ЗИН. **I** – голотип *R. iturupus* в масштабе, Курильские острова, Итуруп, 44°47.7'N, 148°55.5'E, 660 м. **I'** – увеличен вдвое. Масштабный отрезок 10 мм.

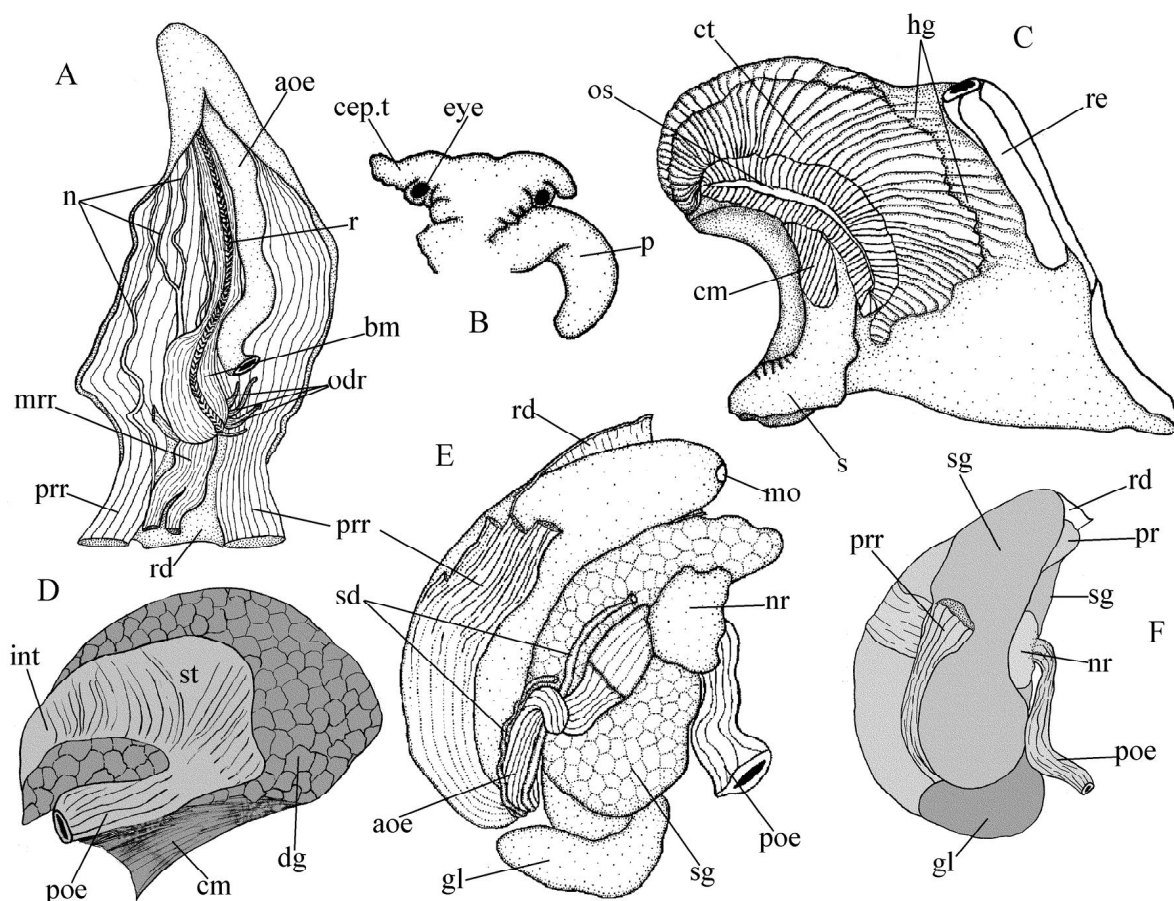


FIG. 28. Anatomy of *Retifusus attenuatus* no. 1 (shell on Fig. 27C, radula on Fig. 29B). **A** – proboscis opened dorsally; **B** – head and penis; **C** – mantle; **D** – stomach general view; **E** – foregut, right salivary gland removed; **F** – foregut, right salivary gland present.

РИС. 28. Anatomy of *Retifusus attenuatus* № 1 (раковина на Рис. 27C, радула на Рис. 29B). **A** – proboscis opened dorsally; **B** – head and penis; **C** – mantle; **D** – stomach general view; **E** – foregut, right salivary gland removed; **F** – foregut, right salivary gland present.

Retifusus similis (Golikov et Gulbin, 1977)
(Figs. 21, 27 D-H, 29 A, C, 30)

Mohnia similis Golikov, Gulbin, 1977: 179-180, Fig. 2. – Higo *et al.*, 1999: 228. – Kantor, Sysoev, 2005: 133. – Kantor, Sysoev, 2006: 198, pl. 93 B.
Retifusus similis – Sirenko *et al.*, 2013: 162.

Holotype: ZIN 28236/1.

Type locality: Paramushir Island, Kurile Islands, 300 m.

Material examined: ZIN 28237, RV *Lebed*, Paramushir Island, Vasiliev's gulf, sta. 65, 53 m, pebble, 11.07.1954 (no. 1 dissected). ZMMU 18301, FV *Popov*, Sakhalin Bay, 54°31.8'N, 140°44'E, 82 m, 15.07.1985 (no. 2 dissected).

Description. Shell 12-34 mm in height, elongated-fusiform, covered with yellowish to light-brown periostracum (Fig. 27 D-H). Siphon well-defined, slightly left-curved, moderately long. Spiral sculpture consists of prominent spiral cords, up to 15 on penultimate whorl; axial sculpture represented by more or less pronounced axial ribs, up to

15 on last whorl. Operculum oval, with terminal nucleus, shifted to left. Measurements: no. 1 H 15.6 mm, h 12.4 mm, AL 9.5 mm; no. 2. H 33.3 mm, h 22.7 mm, AL 16.1 mm.

Soft body: three whorls extracted from the shell. Mantle spans 1 whorl, kidney – 0.5, the rest – digestive gland and gonad (Fig. 30 A-B). Head large, with large thick tentacles bearing large black eyes at their bases. Foot contracted, of medium sizes, propodium separated by deep propodial groove. **Mantle** length slightly exceeds width (Fig. 30C). Ctenidium and osphradium crescent-curved and equal to each other, occupying 0.6 of length and 0.2 of mantle width. Capsule gland not large, occupies 0.6 of mantle length and terminates by small female orifice (**cg**). Rectum covered by capsule gland.

Digestive system. Proboscis long and narrow. Two lateral bands of proboscis retractors attached to rhynchodeum at proboscis base (Fig. 30H, **prr**). Buccal mass attached to basal part of proboscis wall by multiple odontophoral retractors (Fig. 30D,

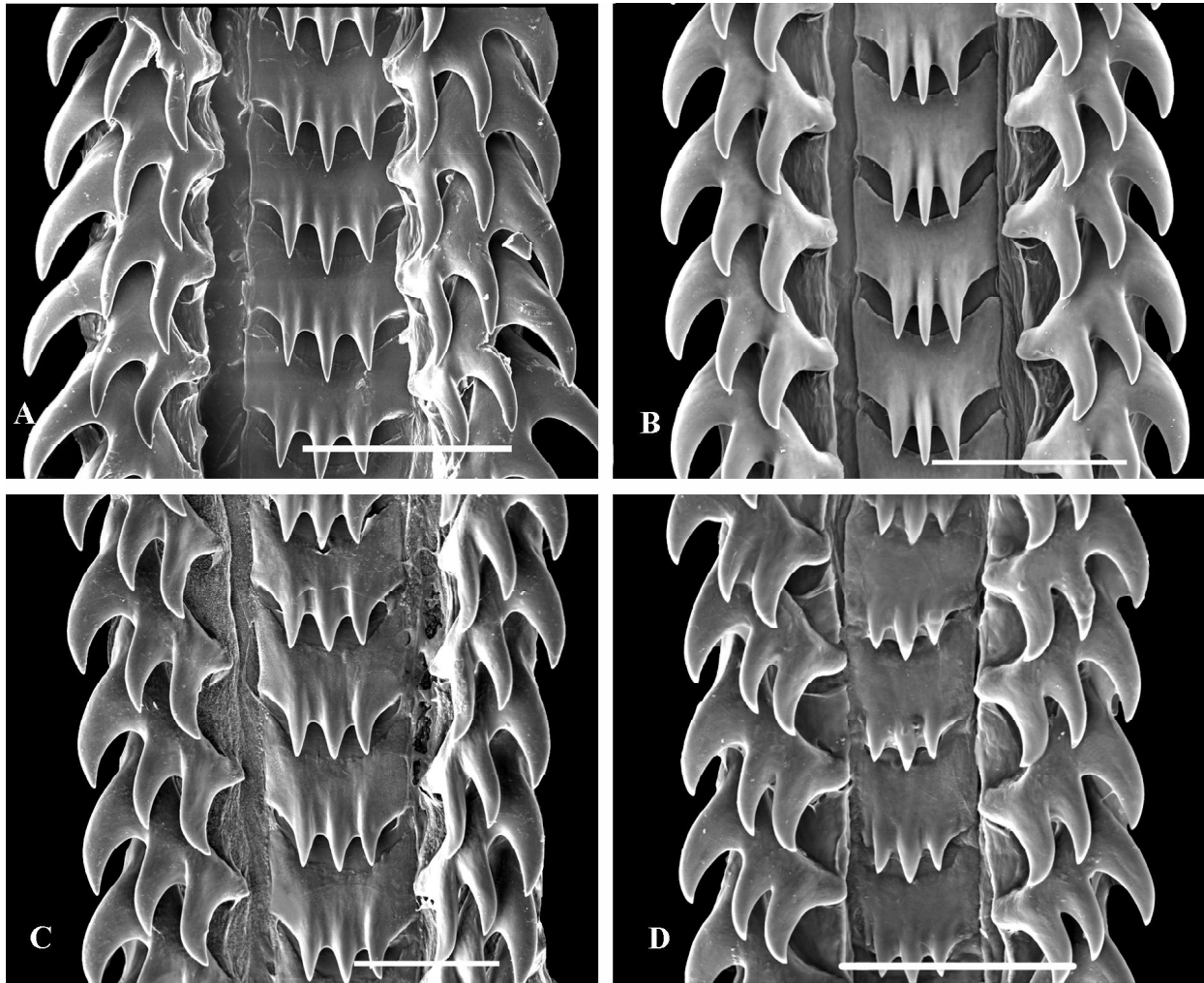


FIG. 29. Radulae of *Retifusus*: **A** – *R. similis* no. 2 (shell on Fig. 27 F); **B** – *R. attenuatus* no. 1 (shell on Fig. 27 C, anatomy on Fig. 28); **C** – *R. similis* no. 1 (shell on Fig. 27 E, anatomy on Fig. 30); **D** – *R. iturupus* no. 1 (anatomy on Fig. 31). Scale bar 50 µm.

РИС. 29. Радулы *Retifusus*: **A** – *R. similis* № 2 (раковина на Рис. 27 F); **B** – *R. attenuatus* № 1 (раковина на Рис. 27 C); **C** – *R. similis* № 1 (раковина на Рис. 27 E); **D** – *R. iturupus* № 1. Масштабный отрезок 50 µm.

odr). **Radula** in radula sac attached to rhynchodaeum by bifurcating median retractor. Radula width of specimen no. 1 is 150 µm (1.58 % AL), of no. 2 – 130 µm (0.81 % of AL) (Fig. 29 A, C). Rachidian tricuspidate, cusps of equal size in spm. no. 1, median cusp slightly longer than marginals in spm. no. 2. Lateral teeth of the same morphology as in *R. parvus*, *R. roseus* and *R. attenuatus*. Valve of Leiblein of moderate size, oval (Fig. 30 G, I, **vl**). Gland of Leiblein large, well-developed (**gl**); small narrow duct of gland of Leiblein opens into oesophagus soon posterior to nerve ring (Fig. 30 I, **dgl**). Salivary glands very large, longer than proboscis (Fig. 30 G–H, **sg**); salivary ducts follow along anterior oesophagus and open into buccal cavity; salivary pouches absent.

Stomach spans 0.25 of visceral whorl and situated at 45° to its longitudinal axis (Fig. 30 F). Posterior mixing area not large, rounded, lined with medium high transverse folds on inner stomach wall.

Outer stomach wall lined with high transverse folds (Fig. 30 E, **pma**). There is oblique longitudinal fold (**lf**) on inner stomach wall, lined with low transverse folds; opening of anterior duct of digestive gland situated at anterior end, and openings of oesophagus and posterior duct of digestive gland – on posterior end of longitudinal fold. The rest of inner stomach wall lined with oblique folds.

Distribution – Kurile Islands, northern Sakhalin, 50–300 m (Fig. 21).

Remarks. The species very much resembles *R. parvus*, differing by absence of salivary pouches on salivary ducts.

Retifusus iturupus (Golikov et Sirenko, 1998)
(Figs. 21, 27 I, 29 D, 31)

Mohnia iturupa Golikov, Sirenko, 1998: 113, figs. 7 I, 15 F, M. – Kantor, Sysoev, 2005: 133. – Kantor, Sysoev, 2006: 187, pl. 93 H–H'.

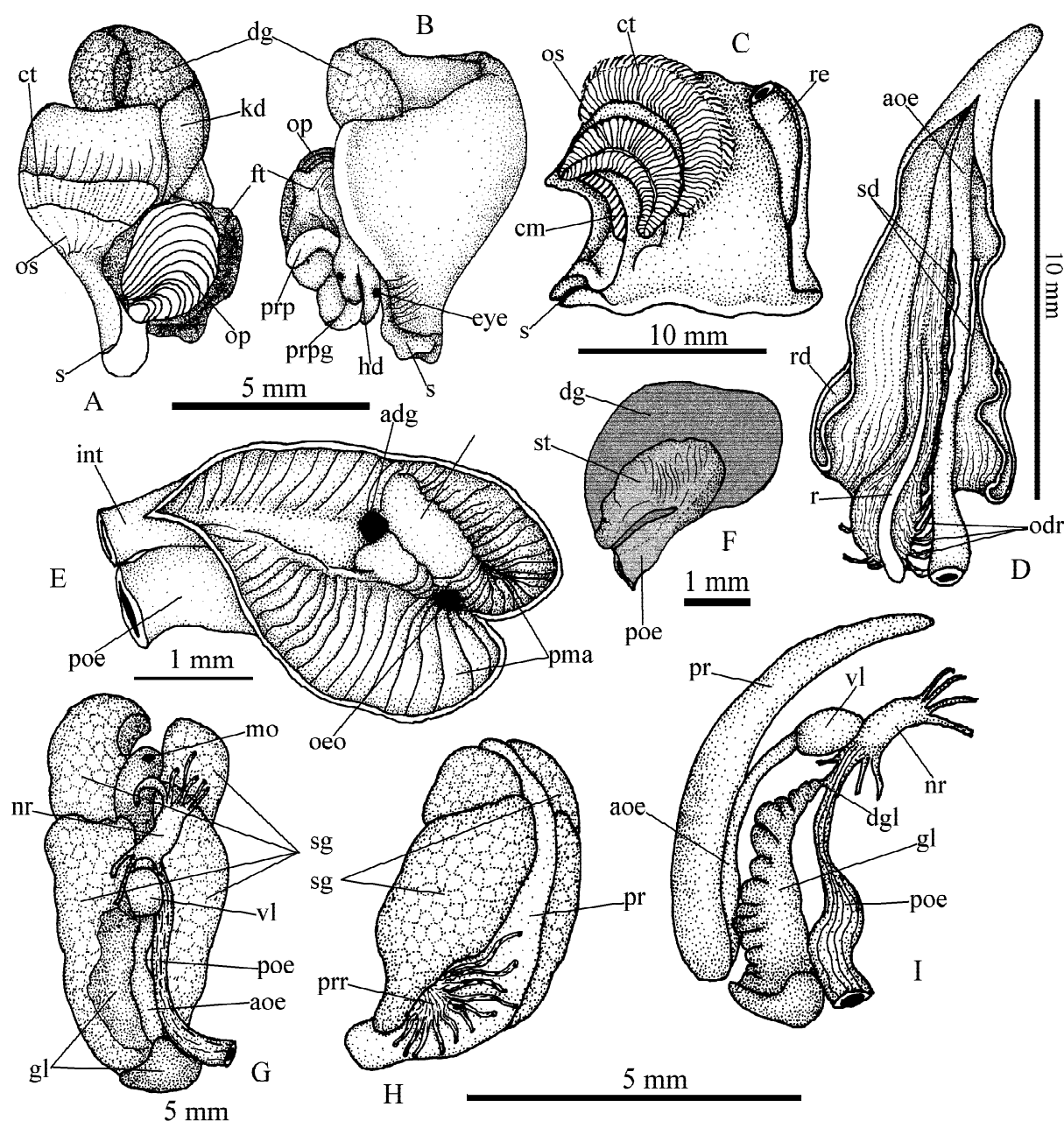


FIG. 30. Anatomy of *Retifusus similis* no. 1 (shell on Fig. 27E, radula on Fig. 29C). A – soft body ventral view; B – soft body dorsal view; C – mantle; D – proboscis opened dorsally; E – opened stomach; F – stomach general view; G – ventral view of foregut; H – dorsal view of foregut; I – lateral view of foregut, salivary glands removed.

РИС. 30. Анатомия *Retifusus similis* № 1 (раковина на Рис. 27Е, радула на Рис. 29С). А – вентральный вид мягкого тела; В – дорсальный вид мягкого тела; С – мантия; D – хобот, вскрытый с дорсальной стороны; Е – вскрытый желудок; F – общий вид желудка; G – вентральный вид переднего отдела пищеварительной системы; H – дорсальный вид переднего отдела пищеварительной системы; I – латеральный вид переднего отдела пищеварительной системы, слюнные железы удалены.

Retifusus iturupus – Sirenko et al., 2013: 162.

Holotype: ZIN 57499/1

Type locality: Iturup Island, 44°47.7'N, 148°55.5'E, 660 m.

Material examined: ZIN 57891, RV *Odissey*, Iturup Island (Kurile Islands), 44°46.8'N, 149°06.7'E, 880 m, 26.07.1984 (2 spms., no. 1 dissected).

Description. Shell 8-10 mm in height, broad-fusiform, with fast increasing diameter of whorls;

covered with thin light-brown periostracum, shell under periostracum light-beige (Fig. 27 I-I'). Spiral sculpture consists of wide flat spiral cords (about 10 on penultimate whorl), axial sculpture represented by well-pronounced incremental lines on last whorl and low axial ribs on spire.

Operculum oval with terminal nucleus moved to left. Measurements: H 8.7 mm, h 6.8 mm, AL 5.5 mm. Juvenile male.

Soft body consists of four whorls: mantle spans

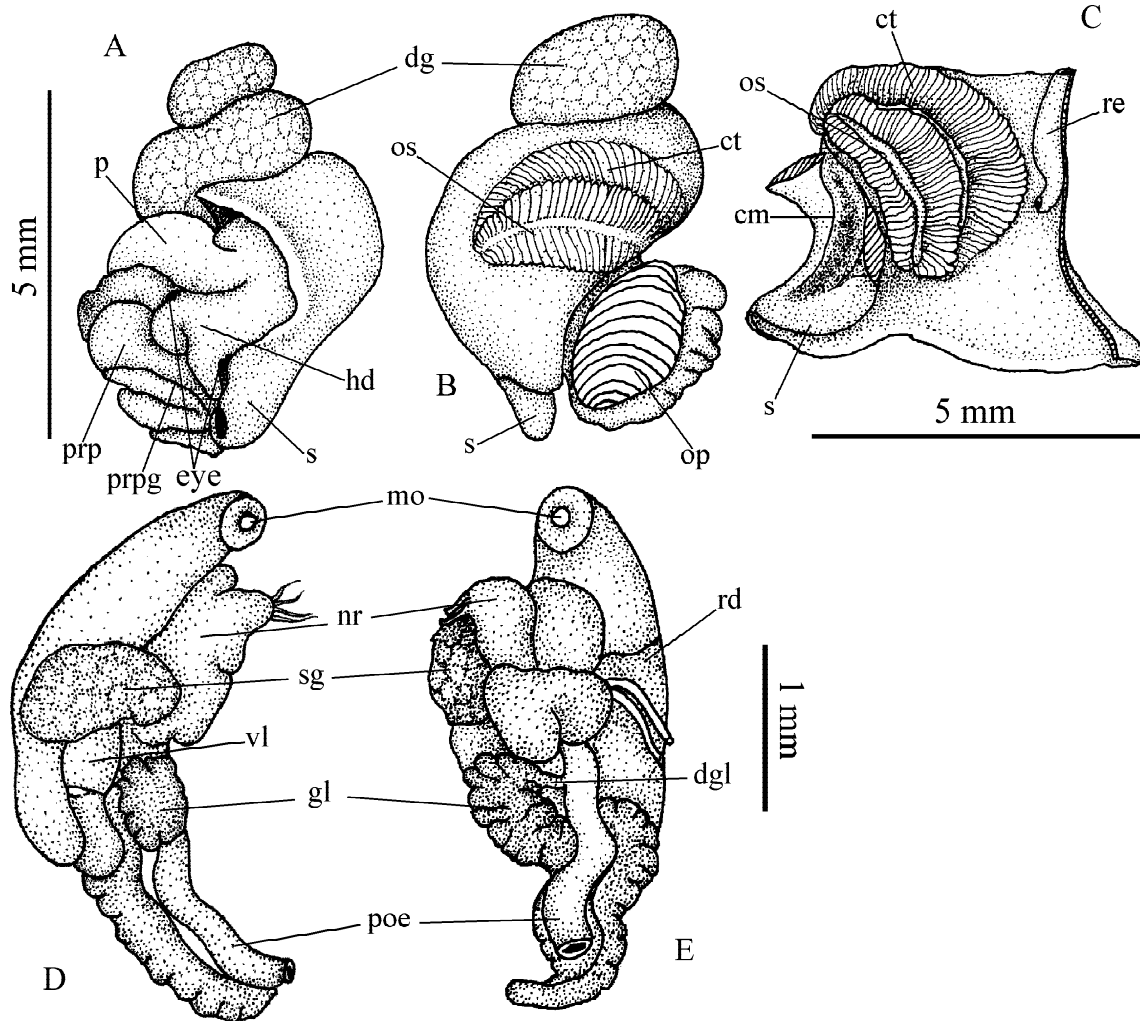


FIG. 31. Anatomy of *Retifusus iturupus* no. 1 (radula on Fig. 29D). **A** – soft body dorsal view; **B** – soft body ventral view; **C** – mantle; **D-E** – lateral and ventro-lateral view of foregut.

РИС. 31. Анатомия *Retifusus iturupus* № 1 (радула на Рис. 29D). **A** – дорсальный вид мягкого тела; **B** – вентральный вид мягкого тела; **C** – мантия; **D-E** – передний отдел пищеварительной системы.

1 whorl, kidney 1/3, digestive gland and gonad the rest of visceral mass (Fig. 31 A-B). Head large, with thick contracted tentacles and large black eyes at their bases (Fig. 31, **eye**). Foot contracted, wide propodium separated by deep propodial groove. Operculum oval, with terminal nucleus (Fig. 31B, **op**, broken). Penis large, seminal papilla absent (Fig. 41A, **p**). **Mantle** length slightly exceeds width (Fig. 31C). Siphon moderately long and wide. Osphradium very large, with wide lamellae, occupying 0.75 length and 0.3 width of mantle. Crescent-curved ctenidium slightly narrower than osphradium, occupies 0.75 length and 0.25 width of mantle. Rectum less than half mantle length, narrow.

Digestive system. Proboscis partially protracted. Mouth opening rounded, situated terminally (Fig. 31 D-E, **mo**). Buccal mass occupies whole proboscis length. **Radula** is 2 mm long and 80 µm wide (1.13% AL), consisting of 74 rows of teeth. Central

tooth with three cusps, with median one slightly longer than marginal (Fig. 29D). Lateral teeth of the same morphology as in *R. parvus*, *R. roseus*, *R. attenuatus* and *R. similis*. Anterior oesophagus follows along ventral side of proboscis forming large valve of Leiblein (Fig. 31D, **vl**). Massive nerve ring (**nr**) is situated immediately behind the valve. Gland of Leiblein (**gl**) large, massive, long, S-curved, running along posterior oesophagus. Duct of gland of Leiblein opens shortly posterior to nerve ring (Fig. 31E, **dgl**). Salivary glands not large, about 0.3 proboscis length, rounded, situated on both sides of nerve ring.

Stomach not studied.

Distribution – Pacific coast of Iturup Island, 660-920 m (Fig. 21).

Remark. The species was obviously described from a juvenile specimen. It is much similar to *R. similis* from which it differs by its peculiar shell shape with quickly increasing diameter of whorls.

Retifusus latiplicatus sp. nov.

(Figs. 21, 32-34)

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Holotype: ZMMU Lc 40338, paratypes ZMMU Lc 40339.**Type locality:** northern part of the Sea of Okhotsk, 57°12.5'N, 152°23.0'E, 415 m.**Type material:** 1 lot, 9 specimens, IO, Sea of Okhotsk, RV *Vityaz*, sta. 56, 57°12.5'N, 152°23.0'E, 415 m, 27.08.1948 (holotype, paratype 1 and spm. no. 1. dissected).**Etymology.** The name is derived from *latus* (Latin: wide) and *plicae* (Latin: folds), regarding the peculiarities of axial sculpture.**Description.** Shell small-sized, broad-fusiform, relatively thin-walled, but solid, not-translucent, with long, well-defined, slightly left-curved rather narrow siphonal canal (Fig. 32, Table 6). Protoconch and upper whorls eroded, the rest of shell consists of 3 whorls (holotype). Periostracum thin, pale-beige to creamy; shell under periostracum white or creamy. Teleoconch whorls strongly convex, periphery of last whorl more convex apically, whorl gradually tapering to siphonal canal. Aperture high, oval, tapering posteriorly beneath impressed suture; outer lip unevenly rounded, somewhat swollen in the upper part. Inner lip is concave, smooth, covered with thin callus, extending on parietal part of whorl. Dominant sculpture of strong to faint axial ribs on upper half of whorl, becoming obsolete in some specimens, 9-10 on last whorl; spiral sculpture represented by well-pronounced unevenly wide spiral cords (15 to 20 on penultimate whorl). Operculum oval with terminal nucleus shifted leftward.[**Диагноз.** Раковина маленькая, широко-веретеновидная, сравнительно тонкостенная, но твердая, с длинным, хорошо обособленным, слегка повернутым влево, довольно узким сифональным выростом. (Рис. 32, Табл. 6). Протоконх и верхние обороты эродированы, остальная часть раковины состоит из двух оборотов. Периостракум тонкий, от бледно-бежевого до кремового. Обороты телеоконха сильно выпуклые, периферия последнего оборота более выпуклая в его верхней части, оборот постепенно сужается к сифональному каналу. Устье высокое, овальное, постепенно сужающееся к вдавленному шву. Наружняя губа неравномерно округлая, несколько вздутая в верхней части. Внутренняя губа вогнутая, гладкая, покрытая тонким каллусом, заходящим на париетальную

часть оборота. Преобладающая скульптура представлена более или менее выраженными осевыми ребрами на верхней половине последнего оборота и на всей поверхности остальных оборотов, ребра могут быть слегка скошенными (отклоненными вправо). Число осевых ребер 9-10 на последнем обороте. Спиральная скульптура представлена хорошо выраженными неравномерно широкими спиральными ребрами (15-20 на предпоследнем обороте). Крышечка овальная со смещенным влево терминальным ядром.]

Soft body: 1.5 whorls extracted from the shell. Head large, with long and thick tentacles, adpressed to each other, and small black eyes sitting on lobes at bases of tentacles. Foot contracted, with wide propodium, separated by deep propodial groove (Fig. 33A). Penis large, slightly tapering and bearing large seminal papilla on the top, encircled by fold of skin. Male orifice surrounded by rather large, visible with naked eye, high papillae (Fig. 33C). **Mantle** with long siphon; ctenidium spans almost whole mantle length and 0.2 of its width; osphradium slightly wider than ctenidium and occupies about 0.75 of its length (Fig. 33B). Narrow rectum occupies less than half of mantle length,**Digestive system.** Proboscis rather long and straight (Fig. 33 D-E). Buccal mass spans whole proboscis length. **Radula** similar in all examined specimens (Table 6, Fig. 34), rachidian with three cusps, of which median shifted forward on arcuate basal plate. Lateral teeth with three cusps, outermost slightly longer, than two innermost, of approximately same size. Anterior oesophagus follows along ventral part of rhynchodaeum and folds twice before forming large pear-shaped valve of Leiblein. Salivary glands medium-sized, situated on both sides of rhynchodaeum. Salivary ducts thick, straight, follow from salivary glands on both sides of anterior oesophagus and form medium-sized salivary pouches before entering proboscis. Gland of Leiblein rather thin, long, enters by long narrow duct immediately after nerve ring (Fig. 33 D-E, **dgl**).**Stomach** of medium size, with small posterior mixing area, lined by multiple transverse folds (Fig. 33F). Outer stomach wall bears longitudinal fold (Fig. 33G, **lfl**) lined with semicircular low transverse folds, the rest part of stomach wall lined with less frequent transverse folds. Oesophageal opening deep and not large. Rather large opening of anterior duct of digestive gland situated almost inTable 6. Shell and radulae measurements of *Retifusus latiplicatus* sp. nov.

No. of specimen	H, mm	h, mm	AL, mm	Width of radula, μ m	% of AL	Teeth formula (number of cusps on left lateral: rachidian: right lateral)	Figure of radula
Holotype	18.2	14.4	11.1	180	1.62	3:3:3	34A
Paratype 1	17.5	14.3	10.8	160	1.48	3:3:3	34B
no. 1	20.1	16.1	12.0	190	1.58	3:3:3	34C

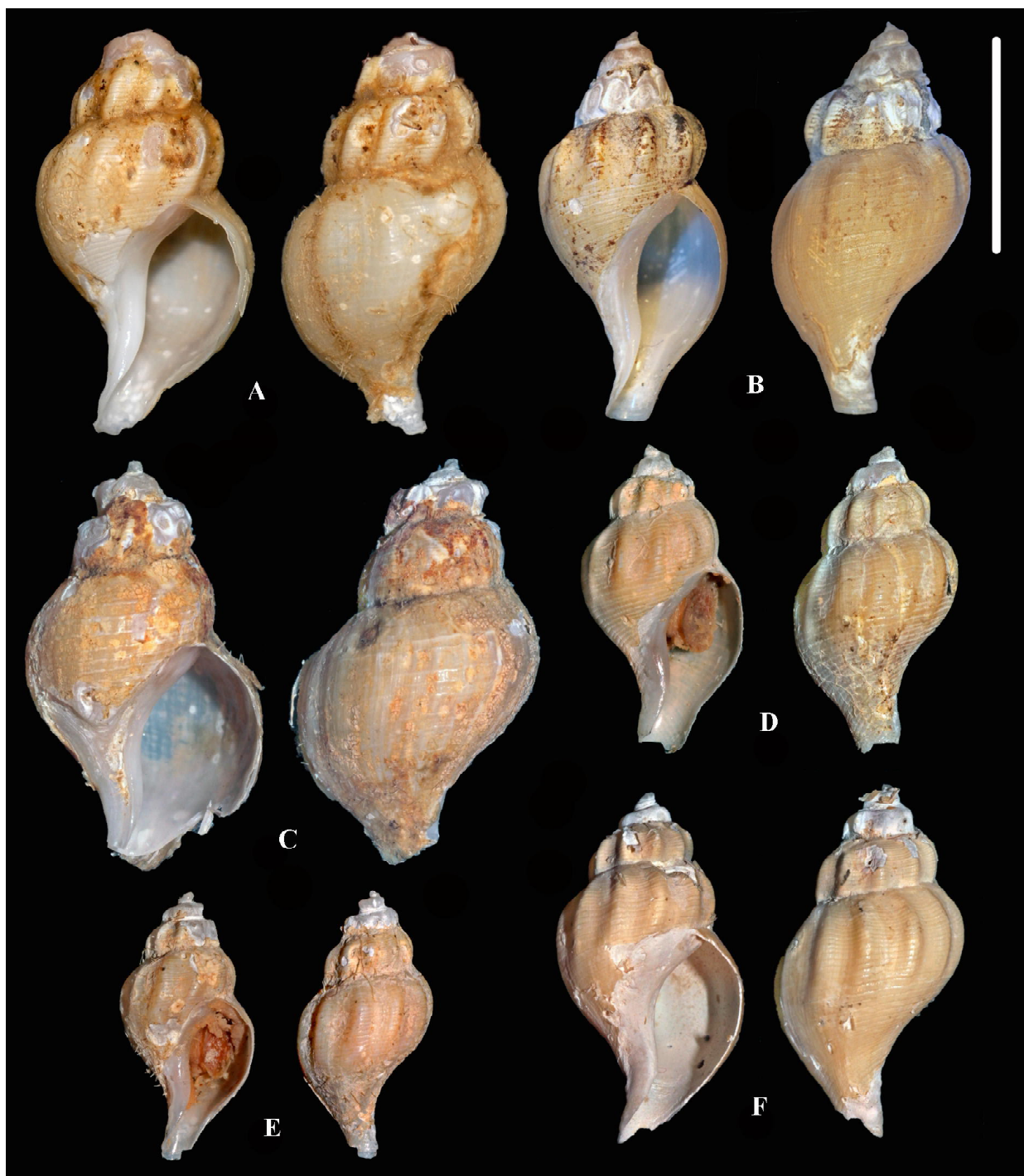


FIG. 32. Shells of *Retifusus latiplicatus* sp. nov., Sea of Okhotsk, 57°12.5'N, 152°23.0'E, 415 m: **A** – holotype, ZMMU Lc 40338 (radula on Fig. 34A, anatomy on Fig. 33); **B** – paratype 1, ZMMU Lc 40339 (radula on Fig. 34B), **C** – no. 1 (radula on Fig. 34C), **D-F** – paratypes 2-4, ZMMU Lc 40339.

РИС. 32. Раковины *Retifusus latiplicatus* sp. nov., Охотское море, 57°12.5'N, 152°23.0'E, 415 м: **A** – голотип, ZMMU Lc 40338 (радула на Рис. 34А, анатомия на Рис. 33); **B** – паратип 1, ZMMU Lc 40339 (радула на Рис. 34В); **C** – № 1 (радула на Рис. 34С), **D-F** – паратипы 2-4, ZMMU Lc 40339.

the middle part of inner stomach wall. The area between anterior duct of digestive gland and intestine opening is lined with longitudinal folds. The area of inner stomach wall corresponding to longitudinal fold on outer stomach wall lined with low straight transverse folds. Opening of posterior duct of digestive gland not found.

Distribution. Known only from the type locality.

Remarks. The new species may be easily recognized from other *Retifusus* species by peculiar shell shape with long siphonal canal and slightly swollen in upper parts periphery of the whorls, as well as axial sculpture consisting of large widely

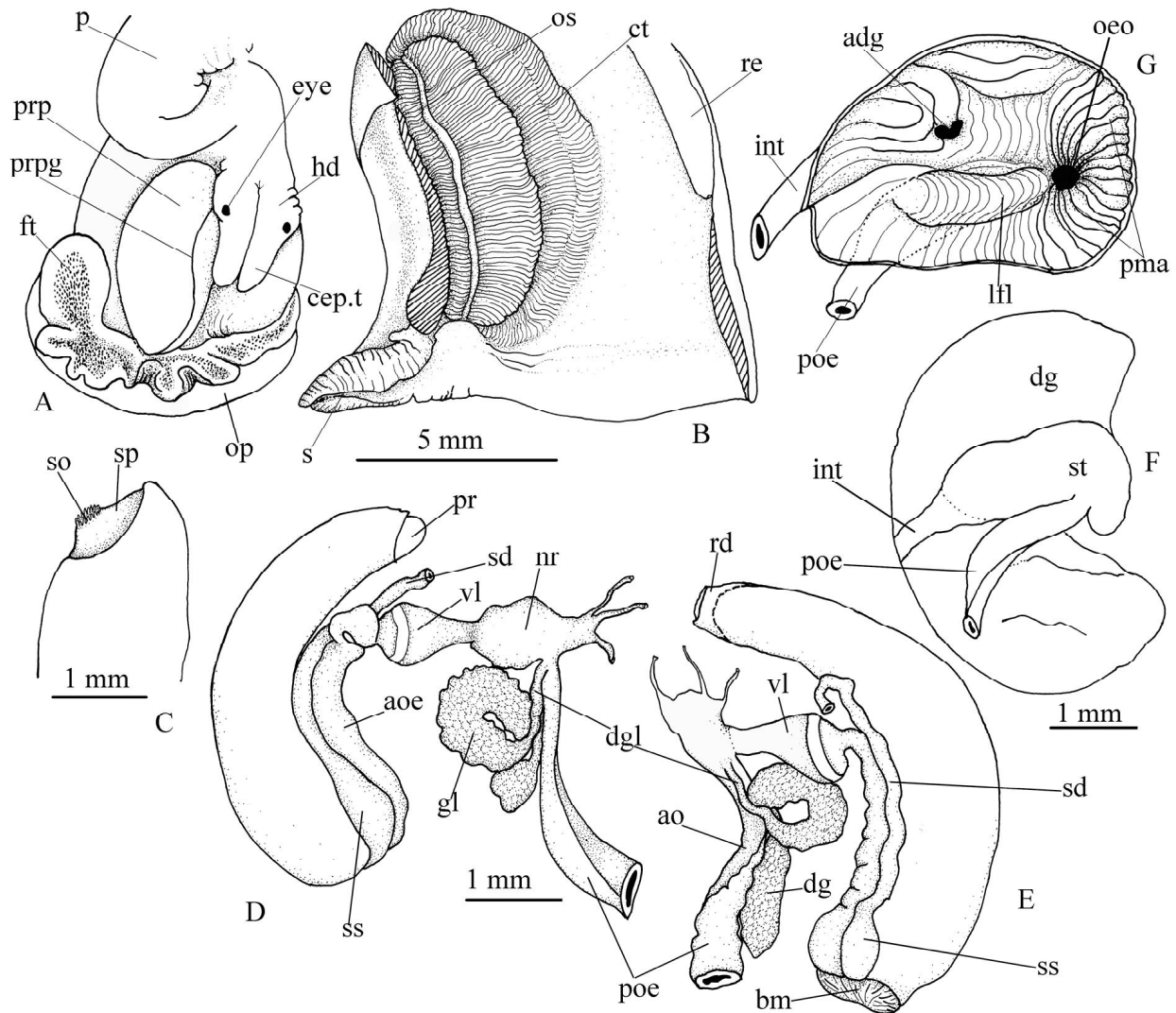


FIG. 33. Anatomy of holotype of *Retifusus latiplicatus* (shell on Fig. 32A, radula on Fig. 34A). A – cephalopodium front view; B – mantle; C – upper part of penis; D-E – foregut, right and left views; F – stomach general view; G – opened stomach.

РИС. 33. Анатомия голотипа *Retifusus latiplicatus* (раковина на Рис. 32А, радула на Рис. 34А). А – цефалоподиум, вид спереди; В – мантия; С – апикальная часть пениса; D-E – передний отдел пищеварительной системы; F – общий вид желудка; G – вскрытый желудок.

spaced axial ribs. The species has salivary pouches and radula morphology similar to that in *R. parvus*, *R. roseus* and *R. latericeus*, and is probably related to these species.

Discussion

Retifusus was often considered as a subgenus of *Plicifusus* Dall, 1902. This is a result of lack of original diagnosis, rather variable shell, in many respects similar to small-sized representatives of *Plicifusus*, and partially because of unclear boundaries of the latter genus. Recent revision of *Plicifusus* [Kosyan, Kantor, 2012] revealed characteristic radular morphology, allowing its clear separation from *Retifusus*. The radulae of *Plicifusus* nor-

mally with three-cuspidate lateral teeth, with smallest intermediate cusps, while in all here considered species of *Retifusus* lateral teeth possess three large nearly equal-sized cusps. The other two genera, besides *Retifusus* comprising a large number of small-sized species possessing axial sculpture, are poorly studied deep-water *Mohnia* and *Retimohnia*, obviously representing heterogeneous groups in need of revision.

Besides the radula, the genus *Retifusus* is characterized by operculum with terminal nucleus, shifted to the left. This type of operculum may be considered transitional between clear subspiral, found in all known *Mohnia*, *Retimohnia* and *Fusipagoda* [Kosyan, unpublished] species, and clear terminal, typical for the rest genera of Colinae (*Plicifusus*,

Colus, *Neptunea*, *Latisipho*, *Aulacofusus*). We suggest that this transitional form is closer to subspiral type, because in *Retimohnia bella* (Ozaki, 1964) we found larger (and, probably, older) specimens bearing operculums with terminal nucleus shifted leftwards, while other, smaller and younger specimens possessed operculums with subspiral nuclei. Within the species possessing operculums with subspiral nuclei, the location of the nucleus may be different: if it is situated closer to the posterior margin of operculum, it may be several times broken during lifetime. As a result, we see terminal nuclei, shifted to the left. This type of operculum is known in *Pararetifusus tenuis* and *P. kosugei*, while *P. kantori* has subspiral operculum.

Based on radula morphology, the species, considered here as *Retifusus*, may be divided into two groups: the first (*R. jessoensis*, *R. laticingulatus*, *R. olivaceus* and *R. virens*) has 3-6 cusps on rachidian and lateral teeth with three long and thin, gradually tapering cusps. The second group (*R. roseus*, *R. parvus*, *R. atiplicatus* sp. nov., *R. attenuatus*, *R. similis*, *R. iturupus* and *R. latericeus*) has three cusps on rachidian and lateral teeth with shorter and thicker cusps, than in the first group. Four species of the second group also possess very peculiar anatomy of the salivary ducts that form salivary pouches. We do not know the function of these structures, but may suggest that they serve for accumulation of large volumes of saliva. Transverse sections of salivary ducts of *R. parvus* show the presence of a rather thick outer layer of circular muscle fibers [Kosyan, 2007], which indicates the possibility of peristaltic contractions. Probably, the saliva contains poison (often found in *Neptunea* species) and may be delivered during predation.

Shell characters appear to be of the least use both for generic and specific identification of *Retifusus*. *R. jessoensis* and *R. olivaceus*, as well as *R. parvus* and *R. similis* are conchologically similar and can not be distinguished from each other without radula (in the first case) or anatomy (in the second case) examination. The difference between these two pairs of species is also very weak: generally, *R. jessoensis* – *R. olivaceus* possess more coarse spiral sculpture and lower spires than *R. parvus* – *R. similis*. It is interesting, that *R. jessoensis*, *R. olivaceus* and *R. parvus* are often found syntopic.

The species that we exclude herein from *Retifusus* and were attributed previously to it by different authors are shown in Table 7.

In the result of current revision we recognize 11 valid species of the genus *Retifusus*:

R. jessoensis (Schrenck, 1863, in 1862-63) – Bering, Okhotsk and Japan Seas, Kurile Islands, Pacific coast of Japan, 15-397 m.

R. laticingulatus (Golikov, Gulbin, 1977) – south-

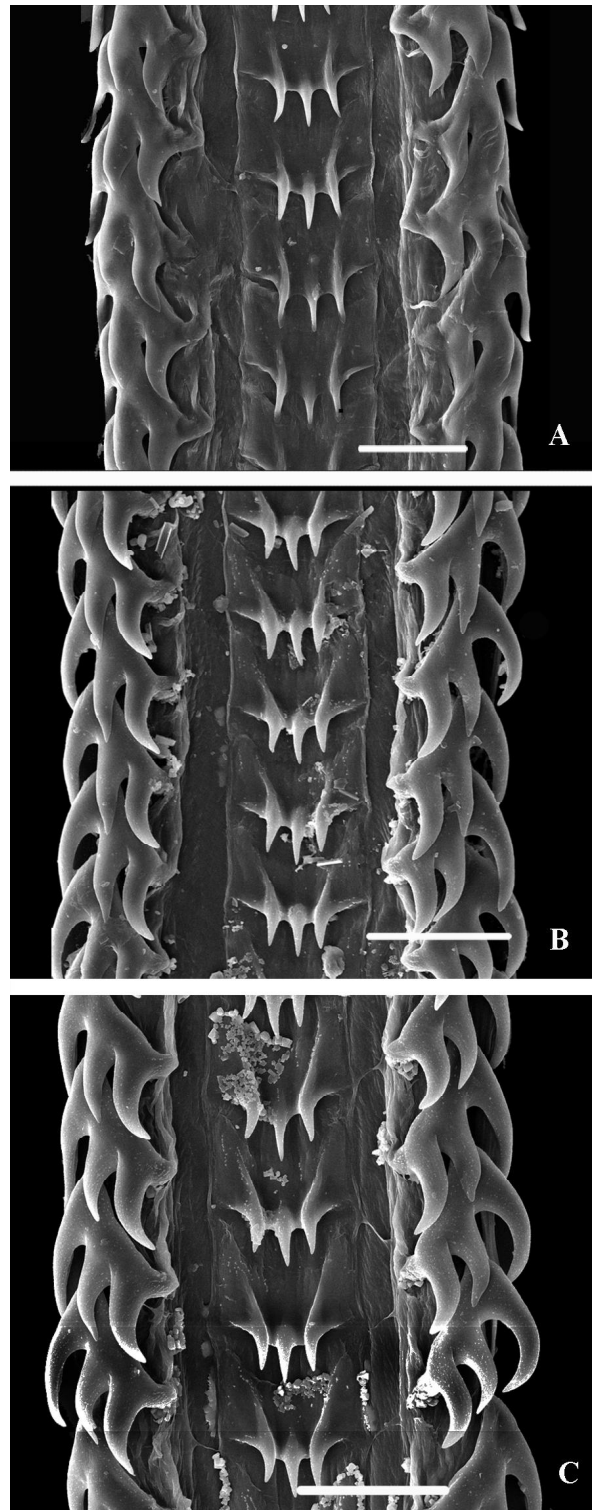


FIG. 34. Radulae of *Retifusus laticingulatus*: A – holotype (shell on Fig. 32A, anatomy on Fig. 33), B – paratype 1 (shell on Fig. 32B), C – no. 1 (shell on Fig. 32C). Scale bar 50 μ m.

РИС. 34. Радуды *Retifusus laticingulatus*: А – голотип (раковина на Рис. 32А, анатомия на Рис. 33), В – паратип 1 (раковина на Рис. 32В), С – № 1 (раковина на Рис. 32С). Масштабный отрезок 50 μ m.

ern Kurile Islands, Peter the Great Bay (Sea of Japan) 129-188 m.

R. olivaceus (Bartsch, 1929) – Bering, Okhotsk

Table 7. Species excluded from *Retifusus*.

Original binomen	Attributed to <i>Retifusus</i> by:	Current generic position	Reference
<i>"Phymorhynchus" tenuis</i> Okutani, 1966	Kantor, Sysoev, 2005, 2006	<i>Pararetifusus</i>	Kosuge, 1967
<i>Plicifusus scissuratus</i> Dall, 1918	Golikov et al., 2001; Kantor, Sysoev, 2005, 2006	<i>Plicifusus</i>	Kosyan, Kantor, 2012
<i>Fusus (Sipho) olivaceus</i> (Aurivillius, 1885)	Golikov et al., 2001; Kantor, Sysoev, 2005, 2006	<i>Plicifusus</i>	Kosyan, Kantor, 2012
<i>Plicifusus (Retifusus) incisus</i> Dall, 1919	Golikov et al., 2001; Kantor, Sysoev, 2005, 2006	Junior synonym of <i>Plicifusus olivaceus</i> (Aurivillius, 1885)	Kantor, Sysoev, 2005, 2006; Kosyan, Kantor, 2012
<i>Plicifusus (Retifusus) oceanodromae</i> Dall, 1919	Dall, 1921, 1925	<i>Plicifusus</i>	Kosyan, Kantor, 2012
<i>Mohnia frielei</i> Dall, 1891	Kosyan, Kantor, 2009	<i>Retimohnia</i>	McLean, 1995; Kantor, 2009

and Japan Seas, south-eastern Kamchatka, 76-165 m.

R. virens (Dall, 1877) – Aleutian Islands, Sea of Okhotsk, Sea of Japan (Peter the Great Bay), 18-312 m.

R. parvus (Tiba, 1980) – Pacific coast of Japan, Sea of Japan, Sea of Okhotsk, eastern Kamchatka, Bering Sea, 24-400 m.

R. roseus (Dall, 1877) – the Barents, Kara, East-Siberian and Bering Seas, eastern Kamchatka, 40-850 m.

R. latericeus (Moeller, 1842) – west Greenland; Newfoundland, White and Barents seas, 25-1417 m.

R. attenuatus (Golikov, Gulbin, 1977) – southern Kurile Islands, 150-414 m

R. similis (Golikov, Gulbin, 1977) – Kurile Islands, northern Sakhalin, 50-300 m.

R. iturupus (Golikov, Sirenko, 1998) – Pacific coast of Iturup Island, 660-920 m

R. atiplicatus sp. nov. – northern part of the Sea of Okhotsk, 415 m.

The majority of species are found in shallow waters, from subtidal to upper bathyal (not exceeding 450 m), except for *R. roseus* and *R. iturupus*, that penetrate the lower bathyal: the range of the first species is 40-850 m, the range of the second one – 660-920 m. *R. latericeus* is found in North Atlantic; *R. roseus* appears to be nearly circumpolar, the rest of the *Retifusus* species have Pacific boreal distribution.

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Ревизия рода *Retifusus* Dall, 1916 (Gastropoda: Buccinidae)

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РЕЗЮМЕ. Род *Retifusus* ревизован на основании признаков раковины, радулы и анатомии мягкого тела. В результате в состав рода включены 10 ранее описанных видов и один новый: *R. jessoensis*

(Schrenck, 1863 in 1862-63), *R. virens* (Dall, 1877), *R. olivaceus* (Bartsch, 1929), *R. laticingulatus* (Golikov et Gulbin, 1977), *R. roseus* (Dall, 1877), *R. parvus* (Tiba, 1981), *R. attenuatus* (Golikov et Gulbin, 1977), *R. similis* (Golikov et Gulbin, 1977), *R. iturupus* (Golikov et Sirenko, 1998), *R. latericeus* (Moeller, 1842), и *R. latiplicatus* **sp. nov.** *Chrysodomus brunneus* Dall, 1877 синонимизирован с *R. jessoensis*; *Bela yanamii* Yokoyama, 1926 – с *R. virens*; *Plicifusus saginatus* Tiba, 1980 и *Retifusus semiplicatus* Golikov in Golikov et Scarlato, 1985 – с *R. parvus*.

