

Revision of the genus *Plicifusus* Dall, 1902 (Gastropoda: Buccinidae)

A.R. KOSYAN¹, Yu.I. KANTOR²

*A.N. Severtsov Institute of Ecology and Evolution, 119071, Leninsky prospekt, 33, Moscow, RUSSIA,
e-mails: ¹kosalisa@rambler.ru; ²kantor@malaco-sevin.msk.ru*

ABSTRACT. The genus *Plicifusus* Dall, 1902 has been revised on the basis of available anatomical data. Thirteen valid recent species are recognised, for 9 of them detailed descriptions of anatomy are provided. Four names were synonymized: *Plicifusus obtusatus* Golikov, 1985 = *Plicifusus maehirai* Tiba, 1980; *Colus okhotskana* Tiba, 1973 = *Plicifusus elaeodes* (Dall, 1907); *Tritonofusus (Plicifusus) aurantius* Dall, 1907 and *Plicifusus (Aulacofusus) rhyssoides* Dall, 1918 = *Plicifusus rhyssus* (Dall, 1907). *Plicifusus parvus*, Tiba, 1980 and *Plicifusus saginatus* Tiba, 1980 are considered as junior synonyms of *Retifusus roseus* (Dall, 1877). *Plicifusus laticordatus* (Dall, 1902) is excluded from the genus *Plicifusus*.

Buccinidae is a large and diverse family of predatory marine gastropods, widely spread in polar, temperate and tropical waters of the World Ocean. Buccinids are also one of the most abundant groups in the Russian Far-Eastern waters, comprising more than 30% of total number of gastropod species [Kantor, Sysoev, 2006]. Six subfamilies are present in the North-Western Pacific, with subfamily Colinae Gray, 1857 (previously commonly known under the name Neptuneinae Stimpson, 1865) being the most diverse in terms of the number of genera and species [Kantor, Sysoev, 2005, 2006]. It includes 16 of 34 genera and 116 of 263 species of Buccinidae recorded in the fauna of Russia.

The best known representative of the subfamily Colinae is a genus *Neptunea* represented mostly by the species with large and medium-sized shells, which was already revised twice [Golikov, 1963; Fraussen, Terryn, 2007]. Other genera, with species that do not attain commercial size, have not attracted sufficient attention of malacologists. *Latisipho* Dall, 1916 and *Pararetifusus* Kosuge, 1967 have been revised by Kosyan [2006, a,b]; several conchologically similar genera, namely, *Colus* Röding, 1798, *Plicifusus* Dall, 1902, *Aulacofusus* Dall, 1918, *Retifusus* Dall, 1916, *Mohnia* Friele in Kobelt, 1878 and *Retimohnia* McLean, 1995, still need revision.

Taxonomy of Buccinidae is still mostly based on

conchological characters with occasional use of the radulae. Only few buccinids were used in molecular phylogenetic studies [eg. Hayashi, 2005; Kosyan *et al.*, 2009]. The major reason is unavailability of properly preserved material, especially on boreal and arctic species. Therefore morphology and conchology at the moment remain the principal approach to buccinid alpha-taxonomy.

The aim of this publication is to revise taxonomic composition of the genus *Plicifusus* on the basis of conchological, anatomical and radular characters.

Material and methods

The material for the study was predominantly obtained from the collections of Russian museums: Zoological Institute of Russian Academy of Sciences, St.-Petersburg; P. P. Shirshov Institute of Oceanology of RAS, Moscow; and the Zoological Museum of the Moscow State University, Moscow. In total, 140 specimens were studied, 24 specimens dissected. The type specimens of species described by Dall in the collections of the National Museum of Natural History, Smithsonian Institution were mostly studied by the second author.

While processing this material, standard zoological methods were used, such as manual dissection, histology and scanning electron microscopy for the radulae examination.

Terminology of the stomach morphology is given after Kantor [2003].

The dissected specimens are numbered in *Material* section of species descriptions. Measurements in the descriptions are provided for dissected specimens only. The size ranges for species are provided in Table 1.

Abbreviations: **adg** – opening of anterior duct of digestive gland; **agl** – ampule of gland of Leiblein; **AL** – aperture length; **ao** – anterior aorta; **aoe** – anterior oesophagus; **ba** – buccal artery; **bc** – bursa copulatrix; **bh** – body haemocoel; **bm** – buccal mass; **bn** – buccal nerves; **cep.t** – cephalic tentacles; **cg** – capsule gland; **cm** – cut mantler edge; **cm1** – outer layer of circular muscle fibers; **cm2** – inner layer of

muscle fibers; **cnt** – connective tissue; **ct** – ctenidium; **cte** – transverse folds on the outer stomach wall; **dg** – digestive gland; **dgl** – duct of gland of Leiblein; **eye** – eye; **ep**, epithelium; **fo** – female orifice; **ft** – foot; **gl** – gland of Leiblein; **gon** – gonad; **H** – height of the shell; **h** – height of the last whorl; **hd** – head; **hg** – hypobranchial gland; **ht** – heart; **int** – intestine; **kd** – kidney; **lfl** – longitudinal fold on the inner stomach wall; **lm1** – outer layer of longitudinal muscle fibers; **lm2** – inner layer of longitudinal muscle fibers; **lpr** – lateral protractor of radula; **lti** – longitudinal folds on the inner stomach wall; **mo** – mouth opening; **mrr** – median radular retractor muscle; **n** – nerves; **nd** – nephridial duct; **nr** – nerve ring; **odr** – odontophoral retractor muscles; **oeo** – oesophageal opening; **op** – operculum; **os** – osphradium; **ot** – oesophageal tensors; **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; **ro** – siphon; **sd** – salivary duct; **sg** – salivary gland; **so** – male orifice; **sp** – seminal papilla; **st** – stomach; **sv** – siphonal valve; **tfl** – typhlosoles; **va** – vagina; **vd** – vas deferens; **vl** – valve of Leiblein.

Abbreviations of depositories:

BMNH – Natural History Museum, London, UK;
IBM – Institute of Marine Biology, Russian Academy of Sciences, Vladivostok, Russia;
IMT – Institute of Malacology, Tokyo, Japan;
IO – P.P. Shirshov Institute of Oceanology, Russian Ac. Sci., Moscow, Russia;
NMC – National Museums of Canada;
SMNH – Swedish Museum of Natural History, Stockholm, Sweden;
SSM – Sea and Shell Museum, Rikuzen-Takada, Iwate prefecture, Japan;
USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA;
ZIN – Zoological Institute of Russian Academy of Sciences
ZMUC – Zoological Museum of the University of Copenhagen, Denmark.
ZMMU – Zoological Museum of Moscow State University, Russia

Systematics

Order Neogastropoda Wenz, 1938
Family Buccinidae Rafinesque, 1815
Subfamily Colinae Gray, 1857
Genus *Plicifusus* Dall, 1902

Tritonofusus (*Plicifusus*) Dall, 1902: 523.

Parasipho Dautzenberg et Fischer, 1912: 37, 82, 100 (Type species: *Fusus kroeyeri* Møller, 1842, by original designation).

Quasisipho Petrov, 1982: 43 (Type species: *Quasisipho torquatus* Petrov, 1982; by original designation; Kamchatka, Russia, Pleistocene).

Type species: *Fusus krøyeri* Møller, 1842, by original designation.

Shell elongated, fusiform, small to medium-sized, with short to medium long siphonal canal, sculpture of well developed axial ribs and spiral cords or

narrow riblets (from 15 to 60 on penultimate whorl). Operculum with terminal nucleus, usually turned to the left. Central tooth of radula large and broad, with two to four (usually three) sharp cusps. Lateral teeth usually with three or four cusps, with central cusps always smaller than lateral ones. Salivary ducts thin and convoluted. Stomach large, in comparison to proboscis, narrow, with small posterior mixing area.

Remarks: *Plicifusus* was described by Dall [1902] as subgenus of *Tritonofusus* Mörch, 1857, which is an objective synonym of *Colus* Röding, 1798, since it is based on the same type species, *Murex islandicus* Mohr, 1786. *Plicifusus* has been treated as a distinct genus by the majority of subsequent authors.

Morphological differences between species of the genus are summarized in Table 1.

Plicifusus kroeyeri (Møller, 1842) (Figs. 1, 2, 3 A-D, 4-7)

Fusus krøyeri Møller, 1842: 88.

Fusus arcticus Philippi, 1850: 119, pl. 5, fig. 5.

Sipho plicatus A. Adams, 1863: 107.

Fusus (*Tritonofusus*) *krøyeri* vars. *major*, *pumila* Mörch, 1869: 19.

Fusus krøyeri var. *grossestriata* Aurivillius, 1885: 360.

Tritonofusus (*Plicifusus*) *polypleuratus* Dall, 1907: 159

Plicifusus kroeyeri. – Dall, 1921: 92. – Galkin, Skarlato, 1955: 176, pl. XLVI, Fig. 3. – Golikov, Gulbin, 1977: 186. – Matsukuma *et al.*, 1991: 83, pl. LXXXI, fig. 1. – Alexeev, 2003: 93, pl. XXXII-4,5. – Kantor, Sysoev, 2005: 137. – Kantor, Sysoev, 2006: 197, pl. 100 A-B.

Plicifusus arcticus. – Dall, 1921: 93. – Dall, 1925: 24, pl. 22, fig. 4. – Matsukuma *et al.*, 1991: 83, pl. LXXXI, fig. 9. – Alexeev, 2003: 93, pl. XXXII-2, 3.

Plicifusus polypleuratus. – Dall, 1925: 25, pl. 34, fig. 7. – Tiba, Kosuge, 1980: 17-18, figs. 1-10. – Higo *et al.*, 1999: 230. – Kantor, Sysoev, 2006: 198, pl. 101 H.

Colus kroeyeri. – Bouchet, Warén, 1985: 231, figs 631-633.

Plicifusus (*Plicifusus*) *kroeyeri*. – Higo *et al.*, 1999: 230.

Plicifusus (*Plicifusus*) *arcticus*. – Higo *et al.*, 1999: 230.

Plicifusus plicatus. – Golikov, Skarlato, 1967: 57-58, pl. 2, fig. 9. – Golikov, Gulbin, 1977: 186. – Alexeev, 2003: 94, pl. XXXII-6. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 198, pl. 101 A-C; 196, pl. 99 F.

Types: lectotype of *Fusus kroeyeri* (designated by Bouchet, Warén, 1985) – ZMUC GAS-61 (Fig. 2C); possible syntypes of *Sipho plicatus* – BMNH 20030809 (Fig. 3 A,B,D); holotype of *Tritonofusus* (*Plicifusus*) *polypleyratus* – USNM 110476 (Fig. 2F).

Type localities: *Fusus kroeyeri* – Western Greenland; *Fusus arcticus* – Spitzbergen; *Sipho plicatus* – Sakhalin, Aniwa Bay, 30 m; *Tritonofusus* (*Plicifusus*) *polypleuratus* – Sea of Japan, Albatross sta. 4996, 45°35'N, 140°55'E, 86 fms.

Distribution – circumpolar (not present in Norway and Iceland), the Bering Sea and the Sea of Okhotsk, eastern coast of Kamchatka, Kurile Is-

Table 1. Summary of conchological and morphological characters of species of *Plicifusus*.Табл. 1. Конхологические и морфологические признаки видов *Plicifusus*.

Species ¹	Shell length ²	AL/H mean	D/H mean	Spiral sculpture ³	Axial sculpture ⁴	Salivary glands	Salivary ducts	Radula ⁵	R. width /AL, %
<i>P. kroeyeri</i> (41)	25-90	0.48	0.40	To 60 inconspicuous spiral ribs	11-26	Medium-sized, separate	Thin, convoluted	3:3:3 3:3:4 3:2:3 4:3:3	1.33-1.46
<i>P. bambusa</i> (8)	75-94	0.45	0.46	Multiple small ribs, abraded	To 16 S-shaped	Medium-sized, ventrally fused	Thin, convoluted	3:3:3	1.32
<i>P. maehirai</i> (20)	32-64	0.42	0.42	~25 medium-expressed ribs	To 20, abraded	Small, rounded separate	Thick, convoluted	3:3:3	1,5
<i>P. scissuratus</i> (10)	23-60	0.43	0.39	~20 ribs separated by deep grooves	About 14	Large, long, separate	Thin, convoluted	4:3:4 3:3:3	2.37-2.46
<i>P. elaeodes</i> (8)	46-66	0.39	0.43	~30 small inconspicuous ribs	Low axial ribs/incremental lines	Medium-sized, separate	Thick, convoluted	3:3:3	1.27
<i>P. croceus</i> (2)	39-	0.45	0.39	~25 flattened ribs	Ribs on last whorl obsolete	-	-	-	-
<i>P. hastarius</i> (3)	56-88	0.32	0.37	Multiple spiral ribs	To 12 high S-curved	-	-	-	-
<i>P. johanseni</i> (2)	52-53	0.48	0.38	~18 flattened ribs	Last whorl smooth	-	-	-	-
<i>P. levis</i> (7)	22-32	0.51	0.45	absent	Most part of last whorl smooth	-	-	-	-
<i>P. rhyssus</i> (10)	32-57	0.46	0.39	40-50 narrow ribs	12-16 more or less expressed	Large, sometimes fused ventrally	Thin, unevenly convoluted	3:3:3	1.77-2.42
<i>P. oceanodromae</i> (3)	32-41	0.46	0.45	To 15 spiral ribs	To 20 frequent S-curved	Medium-sized, bean-shaped, separate	Thin, convoluted	3:3:3	1.83
<i>P. olivaceus</i> (6)	28-43	0.51	0.49	~15 ribs separated by deep grooves	About 20 low orthocline	Medium-sized, oval, separate	Thin, convoluted	3:3:3	1.66-2.36
<i>P. torquatus</i> (2)	30-40	0.46	0.5	To 20 spiral ribs	To 15	Small, rounded, separate	Thin, convoluted	3:4:3	1.27

¹In brackets – number of measured specimens; ² Size range is shown for all studied specimens, including published data;³Numbers indicate spiral ribs on the penultimate whorl; ⁴Numbers indicate axial ribs on the last whorl; ⁵Numbers show number of cusps on the teeth in each of the three longitudinal rows

lands, western and northern part of the Sea of Japan, 0-225 m (Fig. 1).

Material: 8 lots (41 specimens): ZMMU, R/V *D. Peskov*, Tatar strait, st. 63, 46°55.2'N, 141°21'E, 699 m, 17.03.2003 (specimen **no. 1** dissected). ZIN, Eastern Kamchatka, Karaginsky Bay, Litke's Strait, 52 m, mud, sand, shelly material, stones, 01.08.1975 (specimens **nos. 2, 3** dissected). ZIN uncatalogued, Sea of Okhotsk, R/V *Novouljanovsk*, trawl 35D, around 47°00'N, 143°21'E, 55 m, grey mud, 23.09.1984. ZIN uncatalogued, Sea of Okhotsk, R/V *Lebed*, transect from Neprochodimiy cape sta. 51, 50°09'7N, 156°29'4E, 240-146 m, muddy sand, 06.07.1954. ZIN 13804, R/V *Lebed*, Shumshu Island, transect from Lopatka cape, st.131, 50°32.5'N, 157°00'E, 118-120 m, 02.08.1954 (specimen **no. 4** dissected). ZIN, R/V *Toporok*, sta. 26, 22-35 m, Sea of Japan, transect from cape Vstrechniy, 48°7.2'N, 139°41.4'E, rough sand with pebble, slightly mudded,

19.08.1949, t 3.8°C (specimen **no. 5** dissected). ZIN 58384, collected by scuba diving on Iturup Island, Kasatka Bay, 7-18 m, 17.08.1969 (specimen **no. 6** dissected). ZIN R/V *Academik Oparin*, 13 cruise, Sea of Japan, 42°47.8'N, 133°34.7'E, 31 m, 05.06.1991.

Description. *Shell* (Fig. 2, 3 A-D) is rather variable: from narrowly fusiform with 11-17 axial ribs on the last whorl (named for convenience "*plicatus*" form as closest to that of possible syntypes of *Sipho plicatus*) to widely-oval with 15-26 axial ribs (named "*kroeyeri*" form, as closest to lectotype of *Fusus kroeyeri*). Siphonal canal attenuated, narrow to broad, slightly curved to the left. Aperture narrow to broad oval. Axial ribs curved, from nearly orthocline to slightly prosocline. Spiral sculpture of very thin inconspicuous riblets, up to 60 on penultimate

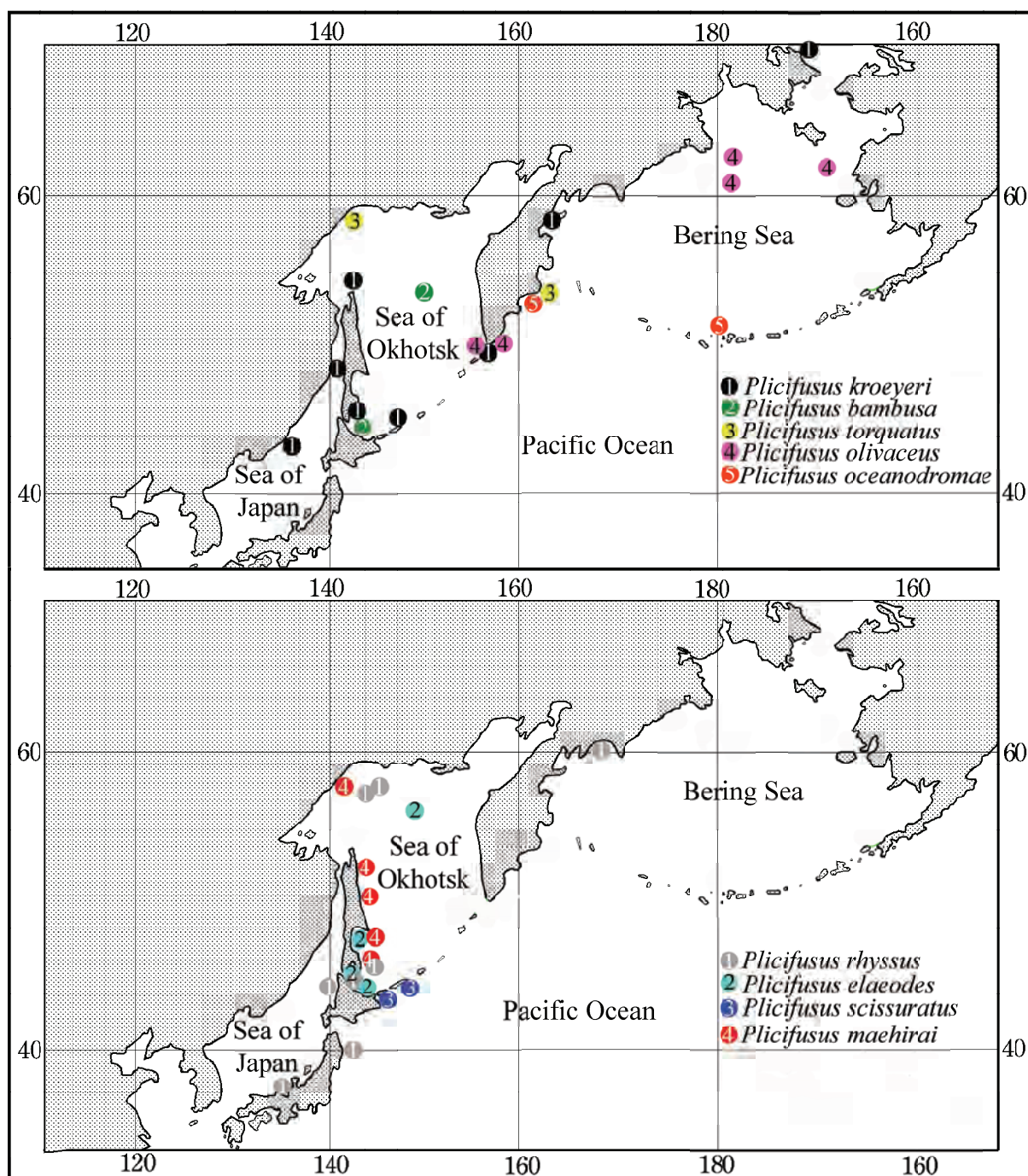


FIG. 1. Distribution of *Plicifusus* species. Type localities and examined lots shown.

РИС. 1. Распространение видов *Plicifusus*. Указаны типовые местонахождения и точки, откуда был исследован материал.

whorl. Periostracum light-brown, thin, easily peeling. Shell grayish-pink to brownish. Measurements: **no. 1.** H 68 mm, h 44 mm, AL 30.3 mm; **no. 2.** H 57.2 mm, h 38.2 mm, AL 27.6 mm; **no. 3.** H 69.2 mm, h 46 mm, AL 32.5 mm; **no. 4.** H 39.8 mm, h 27 mm, AL 21.6 mm; **no. 5.** H 56.8 mm, h 36.2 mm, AL 25.5 mm; **no. 6.** H 55.6 mm, h 33.7 mm, AL 24 mm.

Morphological description of nos. 2 and 3 with "kroeyeri" shell form. Soft body (Fig. 4) **Head** very short and broad, with long thick tentacles.

Black eyes well-noticeable, on small lobes at tentacles' base. **Foot** folded transversely, with narrow propodium and deep propodial groove. Operculum oval, with terminal nucleus. **Mantle** (Fig. 4B) length 1.5 times width. Siphon short, medium-wide, slightly extending beyond mantle edge, with well expressed siphonal valve. Rectum lacks anal papilla, opens at mid mantle length. Ctenidium (**ct**) 2.5 wider than osphradium; osphradium (**os**) narrow, symmetrical. Large whitish capsule gland (**no. 3**)



FIG. 2. *Plicifusus kroeyeri*. A – no. 3, 69.2 mm (radula on Fig. 5 E-F); B – no. 1, 68 mm (radula on Fig. 5 C-D); C – lectotype of *Fusus kroeyeri* ZMUC GAS-61, 68 mm; D – no. 2, 57.2 mm (anatomy see Fig. 4, radula – Fig. 5 A-B); E – no. 4, 39.8 mm; F – holotype of *Tritonofusus (Plicifusus) polypleuratus* USNM 110476; G – no. 6, 55.6 mm (anatomy see Fig. 6, radula – Fig. 7 C-D). All shells at the same scale.

РИС. 2. *Plicifusus kroeyeri*. A – № 3, 69,2 мм (радула на Рис. 5 E-F); B – № 1, 68 мм (радула на Рис. 5 C-D); C – лектотип *Fusus kroeyeri* ZMUC GAS-61, 68 мм; D – № 2, 57,2 мм (анатомия на Рис. 4, радула на Рис. 5 A-B); E – № 4, 39,8 мм; F – голотип *Tritonofusus (Plicifusus) polypleuratus* USNM 110476; G – № 6, 55,6 мм (анатомия на Рис. 6, радула на Рис. 7 C-D). Все раковины в одном масштабе.

with visible longitudinal folds on right to rectum, of two lobes with slit-like channel between them. Female orifice large, leading to vagina with multiple longitudinal epithelial folds. Penis (**no. 2**) small, underdeveloped (Fig. 4C).

Digestive system. Proboscis almost completely inverted (Fig. 4D). Buccal mass short, occupying

half of proboscis length (Fig. 4A, **bm**). **Radula** slightly shorter than odontophore. Radula of **no. 1** (Fig. 5 C-D) 300 μ m wide (1.33% AL). Central tooth tricuspid, with median cusp slightly longer than marginal cusps. Lateral teeth tricuspid, with the smallest median cusp. Radula of **no. 2** (Fig. 5 A-B) 400 μ m wide (1.45% AL). Central tooth with



FIG. 3. *Plicifusus kroeyeri* (A-D) and *P. bambusa* (E-F): A, B, D – possible syntypes of *Sipho plicatus* BMNH 20030809, 57.8 mm, 59.3 mm and 42.0 mm; C – no. 5, 56.8 mm (radula on Fig. 7 A-B); E – holotype of *Plicifusus bambusa*, 76 mm; F – no. 1, 82.6 mm (anatomy on Fig. 8, radula on Fig. 7 E-F). All shells at the same scale.

РИС. 3. Раковины *Plicifusus kroeyeri* (A-D) и *P. bambusa* (E-F): A, B, D – возможные синтипы *Sipho plicatus* BMNH 20030809, 57,8 мм, 59,3 мм и 42,0 мм; C – № 5, 56,8 мм (радула на Рис. 7 A-B); E – голотип *Plicifusus bambusa*, 76 мм; F – № 1, 82,6 мм (анатомия на Рис. 8, радула на Рис. 7 E-F). Все раковины в одном масштабе.

three closely spaced cusps, median cusp longer and narrower than lateral ones. Lateral teeth of same morphology as in previous specimen. Radula of **no. 3** (Fig. 5 E-F) 460 μ m wide (1.42% AL). Median cusp of tricuspid central tooth much shorter than

marginal cusps, lateral teeth of right longitudinal row with four cusps. Median radular retractor originates at base of radular sac (Fig. 4A, **mrr**). Lateral radular protractors (**lpr**) attach to radular sac at its mid-length. Odontophoral retractors (**odr**) originate

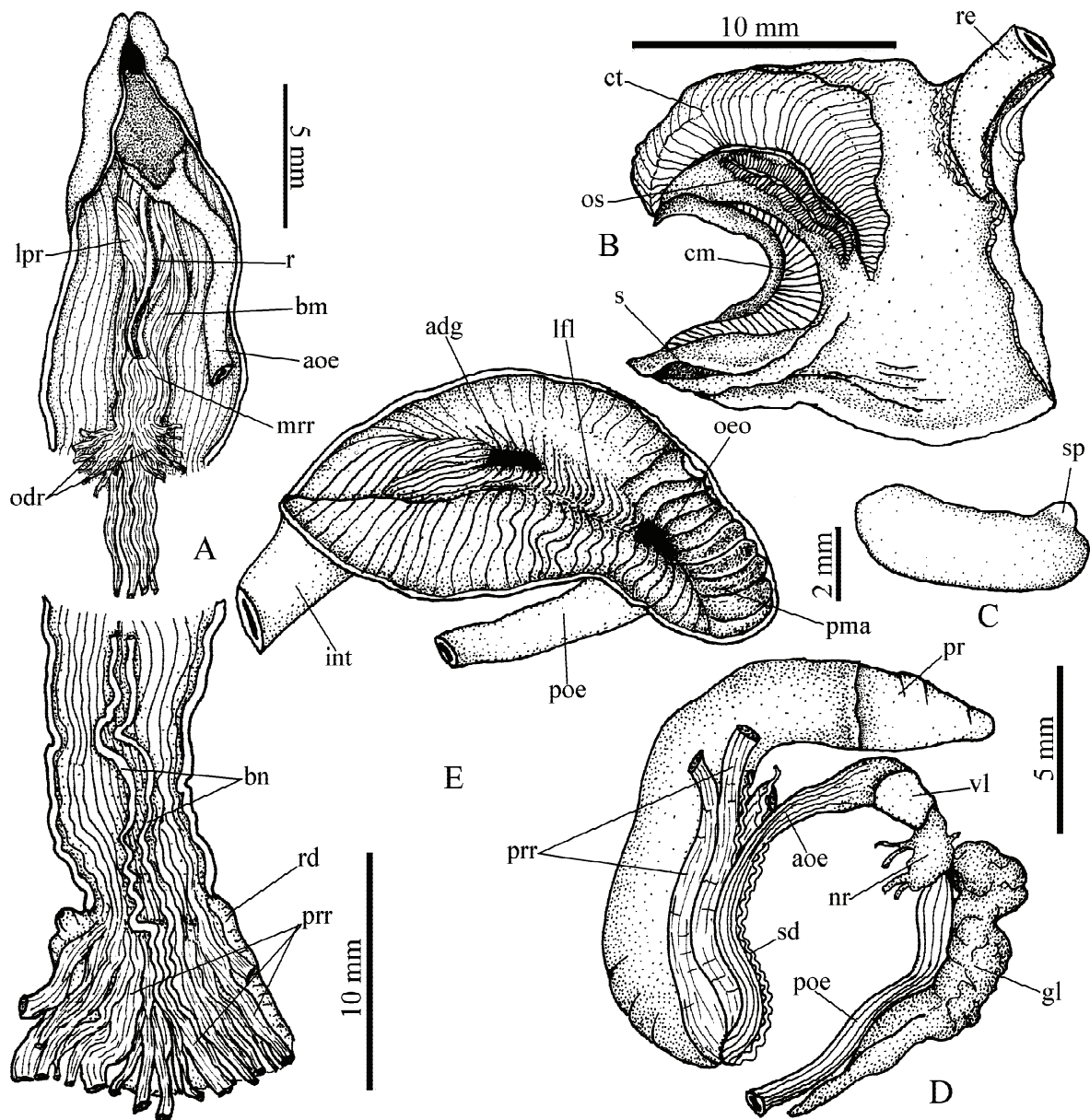


FIG. 4. Anatomy of *Plicifusus kroeyeri* no. 2 (shell on Fig. 2 D, radula on Fig. 5 A-B). A – proboscis and part of everted rhynchodaeum, opened dorsally; B – mantle; C – penis; D – foregut, right view; E – opened stomach.

РИС. 4. Анатомия *Plicifusus kroeyeri* № 2 (раковина на Рис. 2 D, радула на Рис. 5 A-B). А – хобот и часть вывернутого ринходеума, вскрытые дорзально; В – мантия; С – пенис; D – передний отдел пищеварительной системы, вид справа; Е – вскрытый желудок.

at base of buccal mass to fuse with proboscis wall. Paired buccal nerves (**bn**) follow along ventral side of proboscis, continue along ventral side of rhynchodaeum to nerve ring. Proboscis retractors (Fig. 4 A,D, **pr**) form two bands, splitting in multiple muscular fibers. These fibers originate in proboscis wall at a level of buccal mass, detach from wall, follow along ventral side of rhynchodaeum at both sides of oesophagus to attach to roof of body haemocoel in its dorsal-median part. Strongly coiling salivary ducts (Fig. 4D, **sd**) follow freely along anterior oesophagus. Valve of Leiblein (**vl**) round-pyriform, in front of nerve

ring. Gland of Leiblein (**gl**) dark brown, narrowing towards its end. Duct not traced.

Stomach rather large, occupying approximately one third of whorl. Posterior mixing area well developed, comprising one third of entire stomach length (Fig. 4E, **pma**), with tall transversal folds on its inner wall. Posterior oesophagus opens into stomach ventrally. Opening of anterior duct of digestive gland (**adg**) very large, situated almost at mid length of stomach. Longitudinal fold on inner stomach wall lined with low transverse folds. Rest of inner stomach wall lined by oblique folds, replaced by longitudinal ones closer to intestine. Outer stom-

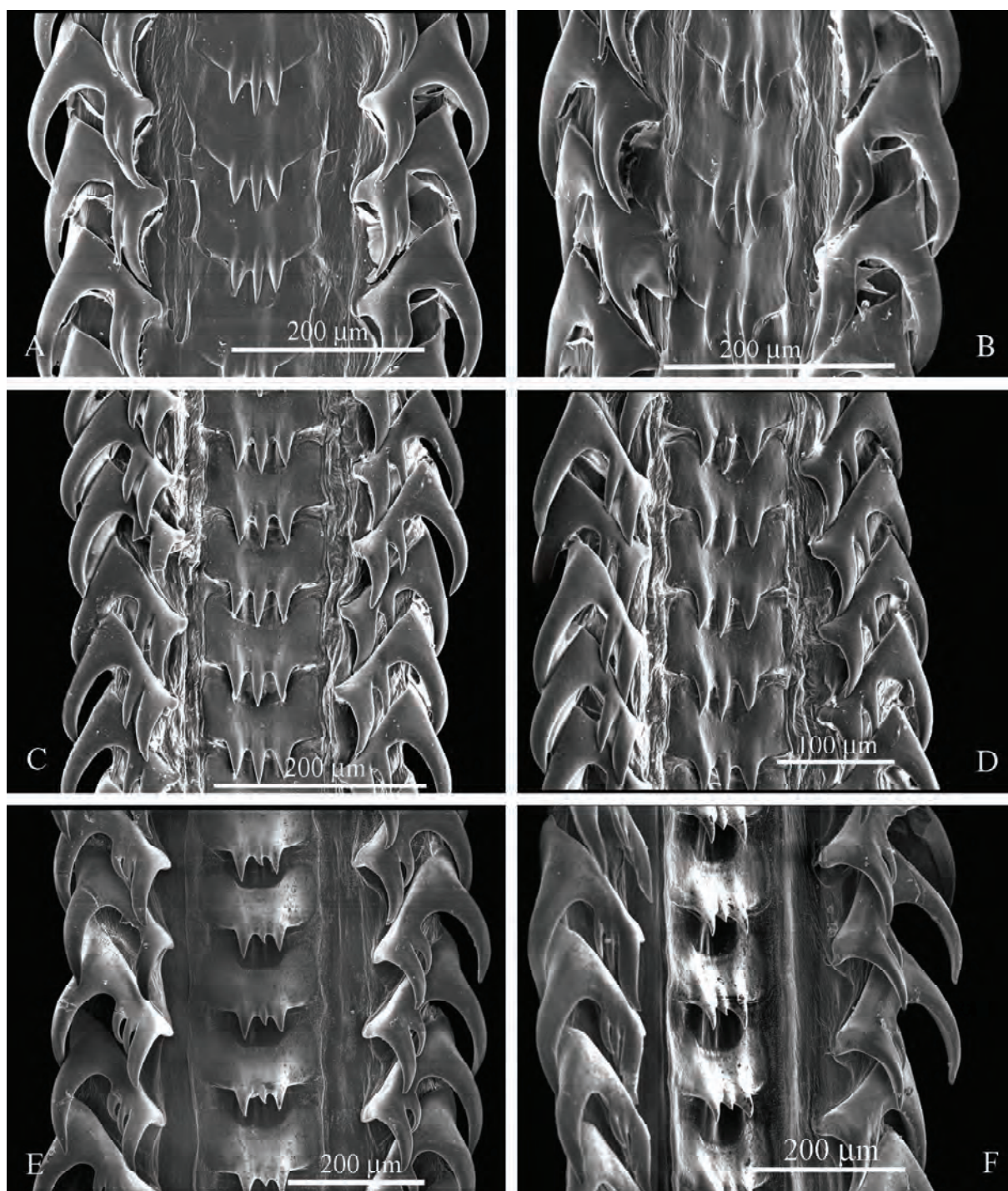


FIG. 5. Radulae of *Plicifusus kroeyeri*: A – dorsal and B – lateral view of no. 2 (shell on Fig. 2 D, anatomy on Fig. 4), C – dorsal and D – lateral view of no. 1 (shell on Fig. 2 B), E – dorsal and F – lateral view of no. 3 (shell on Fig. 2 A).

РИС. 5. Радулы *Plicifusus kroeyeri*: А – вид сверху и В – сбоку, № 2 (раковина на Рис. 2 D, анатомия на Рис. 4), С – вид сверху и D – сбоку, № 1 (раковина на Рис. 2 B), Е – вид сверху и F – сбоку, № 3 (раковина на Рис. 2 A).

ach wall lined by tall oblique folds. Opening of posterior duct of digestive gland not found.

Brief morphological description of no. 6 and radulae descriptions of no. 4-5 (“*plicatus*” form). **Soft body** and **mantle** of same morphology structure as in above described specimen; osphradium

slightly wider and shorter. Narrow hypobranchial gland represented by low oblique folds of mantle epithelium. Capsule gland (Fig. 6C, **cg**) spans 0.6 length and 0.3 width of mantle. Female orifice (**fo**) medium-sized, narrow elongated. Vagina passes into lobes of capsule gland and covers *bursa copulatrix*. **Digestive system.** Proboscis partly everted (Fig. 6

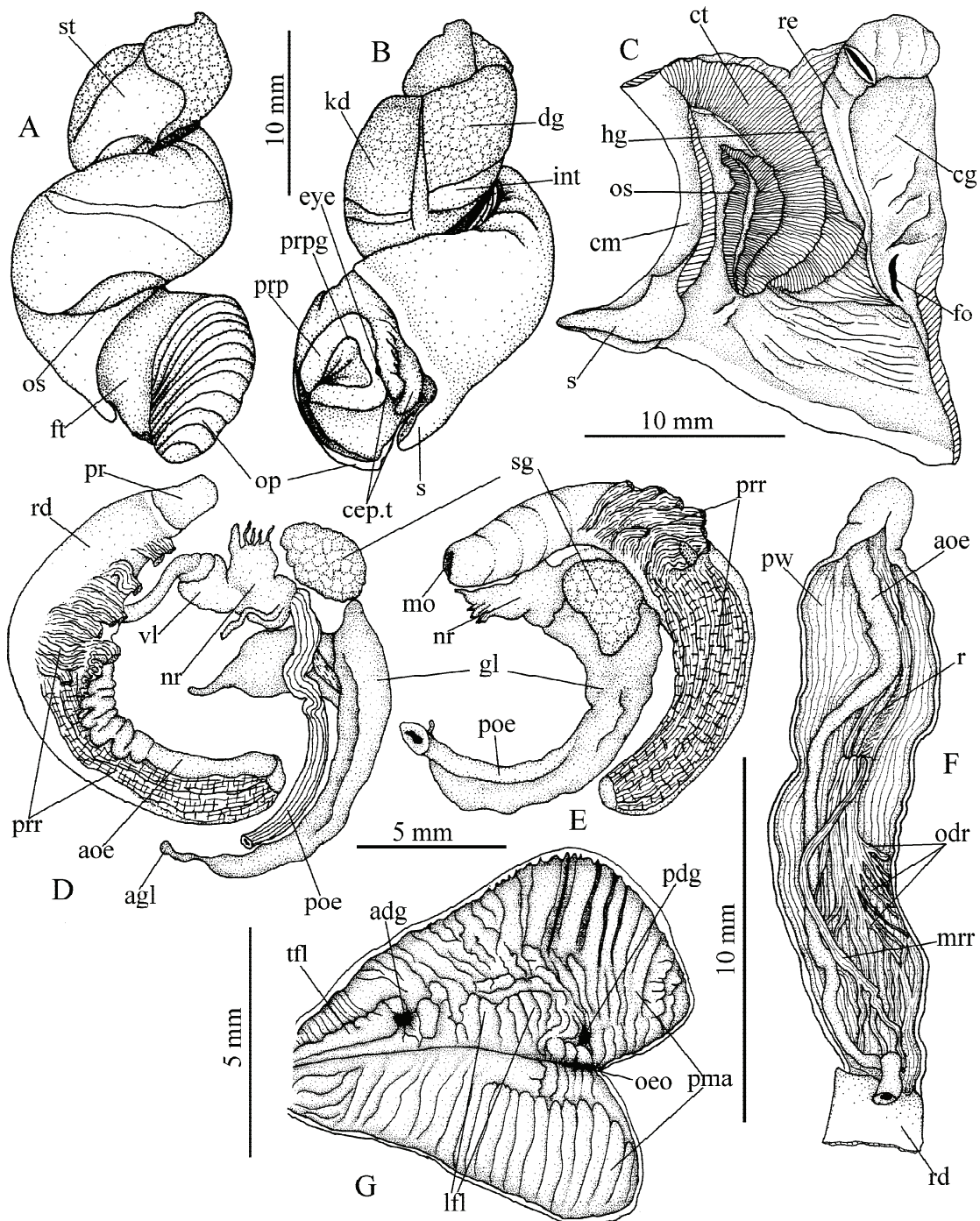


FIG. 6. Anatomy of *Plicifusus kroeyeri* no. 6 (shell on Fig. 2 G, radula on Fig. 7 C-D). A – ventral and B – dorsal views of soft body; C – mantle; D – foregut, right view; E – foregut, left view; F – proboscis, opened dorsally; G – opened stomach.

РИС. 6. Анатомия *Plicifusus kroeyeri* № 6 (раковина на Рис. 2 G, радула на Рис. 7 C-D). А – мягкое тело с вентральной и В – дорсальной сторон; С – мантия; D – передний отдел пищеварительной системы, вид справа; Е – передний отдел пищеварительной системы, вид слева; F – хобот, вскрытый с дорсальной стороны; G – вскрытый желудок.

D-E); buccal mass spans less than half of proboscis length. Radula of **no. 5** (Fig. 7 A-B) 400 μ m wide (1.45% AL). Central tooth with two lateral cusps, and very reduced median one. Lateral teeth tricuspid. Radula of **no. 6** (Fig 7 C-D) 12 mm long and 350 μ m wide (1.46% of AL), of 114 rows of teeth, 19 nascent. Rachidian tricuspid, median cusp slightly longer than

marginal ones. Lateral teeth of left longitudinal row with four cusps, of right – with three, of which intermediate the shortest. **Stomach** similar to **no. 2** in size and anatomy (Fig. 6G); opening of posterior duct of digestive gland (**pdg**) small, near entrance of oesophagus into stomach. Wide typhlosole (**tfl**) running from anterior opening of digestive gland into

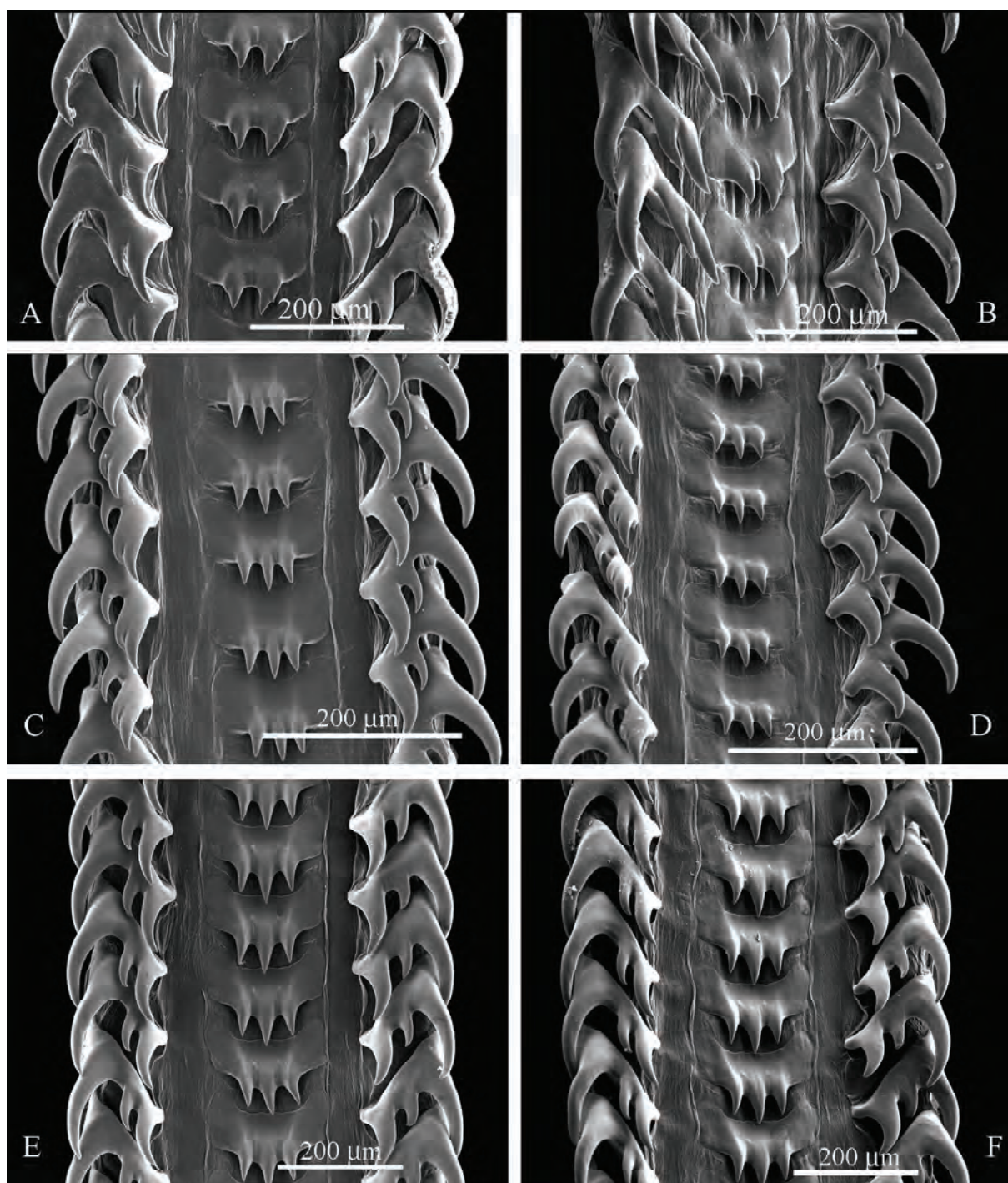


FIG. 7. Radulae of *Plicifusus*: A – dorsal and B – lateral view of *P. kroeyeri* no. 5 (shell on Fig. 3 C); C – dorsal and D – lateral view of *P. kroeyeri* no. 6 (shell on Fig. 2 G, anatomy on Fig. 6); E – dorsal and F – lateral view of *P. bambusa* no. 1 (shell in Fig. 3 F, anatomy on Fig. 8).

РИС. 7. Радулы *Plicifusus*: А – вид сверху и В – сбоку *P. kroeyeri* № 5 (раковина на Рис. 3 С); С – вид сверху и D – сбоку *P. kroeyeri* № 6 (раковина на Рис. 2 G); Е – вид сверху и F – сбоку *P. bambusa* № 1 (раковина на Рис. 3 F, анатомия на Рис. 8).

intestine. Longitudinal fold on inner stomach wall (lf1) lined with low transverse folds.

Differential diagnosis. *Plicifusus kroeyeri* differs from similar species *P. maehirai* by more numerous and less pronounced spiral cords; from *P.*

bambusa – by less massive and more slender shell ($D/H = 0.40$ and 0.46 respectively, see Table 1), from *P. hastarius* – by higher aperture (0.48 and 0.32 respectively, Table 1).

Remarks. This rather variable species was de-

scribed under several names, among which *Sipho plicatus* was repeatedly used in literature, although already Tryon [1881] considered it as a possible synonym of *P. kroeyeri*. Moreover, Tryon probably illustrated one of Adams' syntypes (Plate 53, fig. 351), illustrated here in Fig. 3 B. As is discussed below, many of the references to *P. plicatus* belongs to *P. scissuratus*.

The specimens that are usually treated as *plicatus* have in general more pronounced higher axial ribs, the highest on last whorl shoulder. Number of folds on the last whorl averaged 14. In shells more close to typical *P. kroeyeri* the axial ribs are less pronounced, the highest on the median part of the whorl. Average axial ribs number on the last whorl is 18–20.

The shell surface of type specimens of *Sipho plicatus* is strongly abraded and the spiral sculpture is indistinguishable. The only character differing the two larger syntypes of *S. plicatus* (Fig. 3 A–B) from lectotype of *Fusus kroeyeri* (Fig. 2C) is number of axial ribs on the last whorl, while the third, smallest syntype (Fig. 3D) is similar in this respect to lectotype of *F. kroeyeri*. Number of axial ribs is a strongly intraspecific variable character [Kantor, 1990; Golikov, 1963; Goryachev, 1978]; moreover, we examined several specimens with transitional characters, which could hardly be attributed to one or another “form”. Anatomy of studied specimens of both “forms” is similar, while radulae are rather variable, precluding use of radular characters for species delimitation (compare radulae of two specimens of *P. kroeyeri*, Figs. 5 A–B and E–F). Taking all this into account, we confirm that *S. plicatus* is a junior synonym of *F. kroeyeri*.

The holotype of *Tritonofusus (Plicifusus) polypleuratus* (Fig. 2F) is strongly damaged with siphon broken. In general shell shape and axial sculpture the specimen is rather similar to many specimens of *P. kroeyeri*. It was collected off northern Hokkaido, close to Sakhalin, the type locality of *S. plicatus*. In the absence of additional material we consider species as a synonym of *P. kroeyeri*.

Plicifusus bambusa Tiba, 1980 (Figs. 1, 3 E–F, 7 E–F, 8)

Tiba, 1980b: 74, pl. 21, figs. 1–6. – Tiba, Kosuge, 1980: 31–32. – Higo *et al.*, 1999: 230. – Kantor, Sysoev, 2005: 137. – Kantor, Sysoev, 2006: 195, pl. 99 E.

Holotype: originally in IMT-80-65, transferred to Coral and Shell Museum (Anonymous, 2001).

Type locality – off Monbetsu, northern Hokkaido.

Distribution – Hokkaido, the Sea of Okhotsk, 194 m (Fig. 1).

Material examined: ZIN 58381, ?Sea of Okhotsk, 194 m (specimen **no. 1** dissected). Mature female.

Description. *Shell* large, broad-fusiform, with strongly convex whorls (Fig. 3 E–F). Siphonal canal distinctly attenuated, narrow. Aperture broad oval. Spiral sculpture of inconspicuous narrow ribs, abraded on most part of shell surface. Axial sculpture of S-shaped low folds, up to 16 on last whorl. Periostracum pale-yellow. Measurements: **no. 1.** H 82.6 mm, h 53.5 mm, AL 38 mm.

Soft body. Mantle spans one whorl, kidney 0.3, digestive gland and gonad – rest of visceral mass (Fig. 8 A–B). **Head** wide, with thick, contracted tentacles and small black eyes situated on tentacles lobes. **Foot** folded transversely, with narrow propodium, separated by deep propodial groove. Operculum oval, with terminal nucleus. **Mantle** length exceeds width (Fig. 8C). Siphon moderately long, siphonal valve (**sv**) well developed. Osphradium small, slightly asymmetrical, spans 0.3 mantle length and three times narrower than ctenidium. Ctenidium 0.8 mantle length. Rectum on inner side of strongly developed capsule gland and opens at middle of mantle. Hypobranchial gland forms numerous folds. Pallial oviduct of large two-lobed capsule gland (Fig. 8C, **cg**) and vagina (**va**). Vagina with thick walls, situated ventrally of capsule gland.

Digestive system. Proboscis completely inverted into rhynchodaeum (Fig. 8 D,F,G). Buccal mass (Fig. 8H, **bm**) spans entire proboscis length. Numerous odontophoral retractors (**odr**) attach to proboscis walls at level of posterior part of buccal mass. Median radular retractor large, bifurcating. **Radula** (Fig. 7 E–F) 13.7 mm long, 500 µm wide (1.32% AL), of 106 rows of teeth, 5 nascent. Rachidian tricuspid, central cusp slightly longer than marginal cusps. Lateral teeth with three cusps, intermediate cusp smallest. Proboscis retractors situated ventro-laterally on both sides of anterior part of rhynchodaeum (Fig. 8 D,F, **pr**). Salivary glands (**sg**) large, about third of rhynchodaeum length, situated on both sides of rhynchodaeum and fusing ventrally of valve of Leiblein. Salivary ducts thin and strongly convoluted. Large oval valve of Leiblein embraced by salivary glands (Fig. 8D, **vl**), immediately anterior to nerve ring. Duct of gland of Leiblein (**dgl**) opens rather posterior to nerve ring. Gland of Leiblein brownish, of medium length. **Stomach** U-shaped (Fig. 3E), spans 0.25 of whorl. Internal anatomy not studied.

Differential diagnosis. The species is very similar to *P. kroeyeri*, differing in less pronounced axial ribs. It may be a junior synonym of *P. kroeyeri*. In the absence of additional material we prefer to consider it a separate species.

Remarks. The only available specimen was collected probably in the Kurile Islands (the exact locality on the label is missing). Our specimen is very close to holotype.

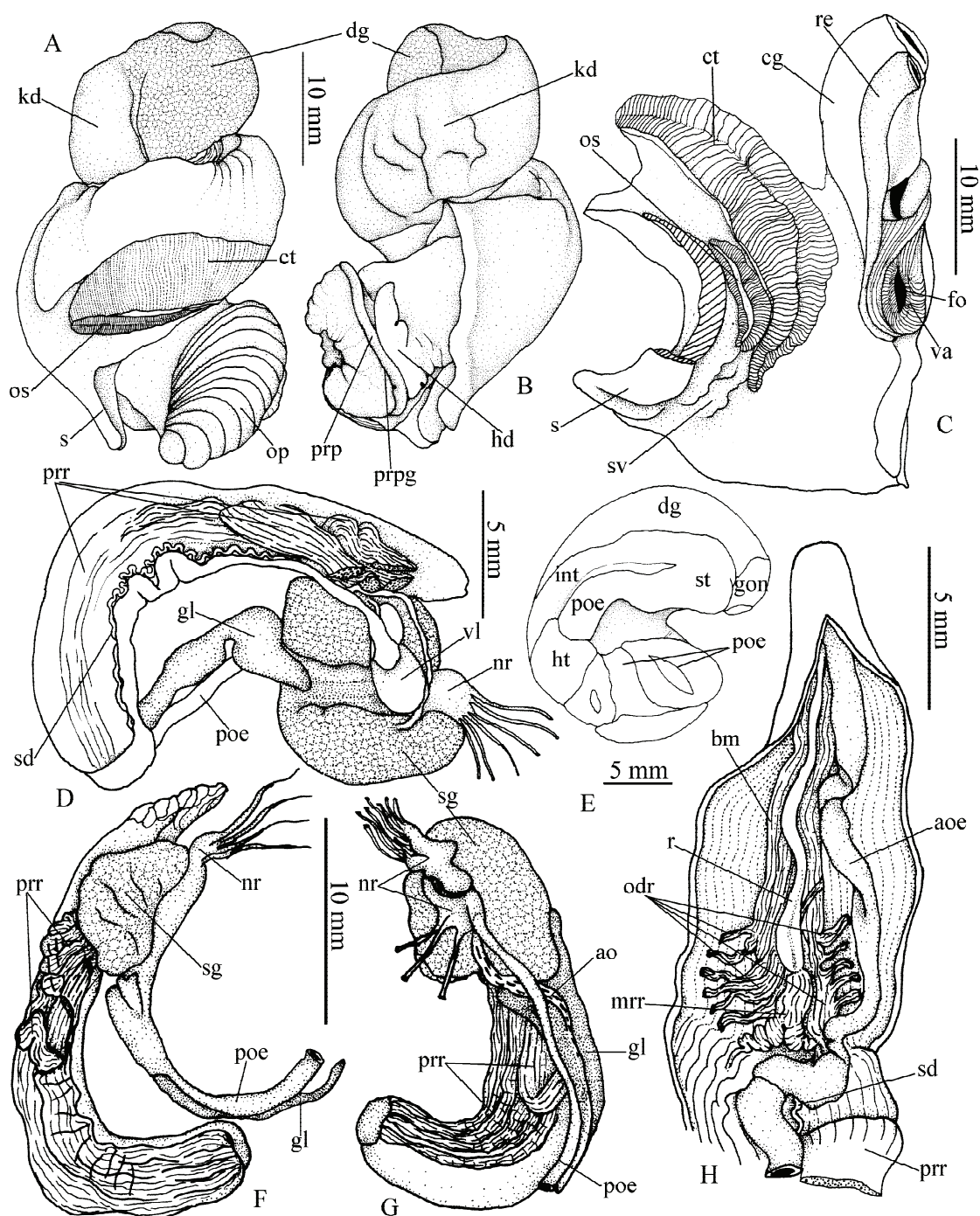


FIG. 8. Anatomy of *Plicifusus bambusa* no. 1 (shell on Fig. 3 F, radula on Fig. 7 E-F). A-B – soft body; C – mantle; D – foregut, right view, salivary gland displaced to show valve of Leiblein; E – visceral mass, general view; F-G – foregut, right and left view; H – proboscis, opened dorsally.

РИС. 8. Анатомия *Plicifusus bambusa* № 1 (раковина на Рис. 3 F, радула на Рис. 7 E-F). A-B – мягкое тело; C – мантия; D – передний отдел пищеварительной системы, вид справа, слюнная железа отогнута, чтобы показать клапан Лейблейна; E – общий вид висцеральной массы; F-G – правый и левый вид переднего отдела пищеварительной системы; H – хобот, вскрытый с дорсальной стороны.

Plicifusus maehirai Tiba, 1980
(Figs. 1, 9 A-D, 10, 11 A-D)

Tiba, 1980: 75, pl. 22, figs. 1-6. – Tiba, Kosuge. 1980: 33-34.
Plicifusus obtusatus Golikov in Golikov, Scarlato, 1985: 404,
fig. 5. – Alexeev, 2003: 91, pl. XXXI-5. – Kantor, Sysoev,

2005: 137. – Kantor, Sysoev, 2006: 197, pl. 100 L,
syn.nov.

Types: Holotype of *Plicifusus maehirai* – IMT-80-66 (Fig. 9A), holotype of *Plicifusus obtusatus* – ZIN 33732/1 (Fig. 9C).

Type localities: *Plicifusus maehirai* – off Kushi-ro, eastern Hokkaido; *P. obtusatus* – Terpeniya Bay, Sakhalin Island, 53 m.

Distribution: Northern part of the Sea of Japan, Southern Kurile Islands, the Sea of Okhotsk, Eastern Kamchatka; 25–200 m.

Material: 5 lots (21 specimens) examined. ZIN 30062/72, F/V *SRTM 8.452*, eastern coast of Sakhalin Island, sta. 54, 51°51'N, 143°54'E, 60 m, rough sand, with shelly material, 03.07.1975 (specimen **no. 1** dissected). IO, northern Sea of Okhotsk, R/V *Vityaz*, sta. 1866, 57°49'7"N, 141°53'6"E, 142 m, 20.10.1952 (specimen **no. 2** dissected). ZIN 58385/1, Sakhalin Island, 80 m. ZIN, uncataloged, Sea of Okhotsk, R/V *Novouljanovsk*, st. 37D, 47°08'3N, 143°36'E, 146 m, mud, 23.09.1984. ZIN 58385, Sea of Okhotsk, R/V *Poseydon*, sta. 4, Sakhalin Island, 51°42'N, 143°13'E, Sigsbi trawl, 80 m, muddy sand, 15.07.1978. ZIN 58386, Sea of Okhotsk, R/V *Poseydon*, north-eastern Sakhalin, off Katangli village, approximately 51°42'N, 143°45'E, 60 m, commercial trawl, 14.07.1978.

Description. *Shell* broad fusiform, thick-walled, with attenuated narrow siphonal canal, slightly re-curved to the left (Fig. 9 A-D). Aperture broad oval. Axial sculpture of closely spaced, curved, slightly to moderately prosocline axial ribs, usually eroded in adults; about 20 on last whorl. Spiral sculpture of well pronounced flattened ribs, about 25 on penultimate whorl. Shell covered with adhering light- or dark-olive periostracum. Measurements: **no. 1.** H 54.6 mm, h 36.6 mm, AL 27 mm; **no. 2.** H 36 mm, h 26.5 mm, AL 24 mm.

Soft body (**no.1**, shell on Fig. 9B). **Head** (Fig. 10A, **hd**) contracted, with thick tentacles. Small black eyes on lobes at base of tentacles. Operculum oval, with terminal nucleus. **Mantle** with rather long muscular siphon (Fig. 10C, **s**). Ctenidium spans 0.75, osphradium – 0.5 of mantle length. Ctenidium twice broader than osphradium. Rectum opens at middle of mantle length. Hypobranchial gland not expressed. **Penis** (**no.2**, Fig. 10H) laterally flattened and strongly contracted. Seminal papilla (**sp**) rounded, on antero-dorsal side of penis, surrounded by circular fold.

Digestive system. Proboscis rather long. Multiple proboscis retractors attach laterally to rhynchodaeum and to lateral walls and roof of body haemocoel (Fig. 10 D-E). Buccal mass slightly shorter than retracted proboscis (Fig. 10I, **bm**). Multiple odontophoral retractors originate from base of buccal mass and attached to proboscis walls. Anterior oesophagus within proboscis attached to its wall by multiple tensors. **Radula** of **no. 1** (Fig. 11 C-D) 350 µm wide (1.5% AL). Central tooth tricuspid, central cusp being slightly shorter, than lateral ones; lateral teeth tricuspid with shortest median cusp. **Radula** of **no. 2** (Fig. 11 A-B) 9 mm long and 360 µm wide (1.5% AL), of 85 teeth rows, 5 nascent. Rachidian tricuspid, with equal cusps. Lateral teeth as in **no. 1**. Anterior oesophagus (**aoe**) follows along ventral

side of rhynchodaeum, tightly pressed to anterior aorta (Fig. 10 D-E). Salivary glands small, rounded, not fusing. Salivary ducts rather thick, coiled, running on both sides of anterior oesophagus. Valve of Leiblein short and broad. Gland of Leiblein very long, with U-folded anterior part, embracing salivary glands. Posterior part of gland terminates with ampoule. Duct of gland of Leiblein opens into oesophagus slightly posterior to nerve ring. Posterior-most part of oesophagus strongly widens before entering stomach. **Stomach** not large (Fig. 10F). Posterior mixing area small (Fig. 10G), lined with high and thick transverse folds. Longitudinal fold on inner stomach wall lined with shallow oblique grooves. Rest of inner wall is lined with low oblique folds oriented in upper and lower parts in opposite directions. Opening of anterior duct of digestive gland near beginning of intestine; opening of posterior duct not found. Outer stomach wall lined with high transverse folds.

Differential diagnosis. *P. maehirai* in shell shape resembles *P. kroeyeri*, differing in more pronounced and less numerous spiral ribs. In spiral sculpture *P. maehirai* is most similar to *P. scissuratus*, but has more numerous and less pronounced spiral cords, more numerous axial ribs on the last whorl, abrading with age, and slightly broader shell with broader aperture.

Remarks. Holotypes of *P. maehirae* and *P. obtusatus* are conchologically very similar, and little doubts of their conspecificity exist.

Plicifusus scissuratus Dall, 1918 (Figs. 1, 9 E-G, 11 E-H, 12)

Plicifusus (*Retifusus*) *scissuratus* Dall, 1918: 226.

Plicifusus (*Retifusus*) *plicatus* sensu Habe, 1965: 90, pl. 29, fig. 5 (non *Sipho plicatus* A. Adams, 1863).

Plicifusus scissuratus. – Tiba, Kosuge, 1980: 27–29. – Okutani et al., 1988: 105.

Plicifusus (*Plicifusus*) *scissuratus*. – Higo et al., 1999: 230.

Plicifusus plicatus sensu Okutani, 2000: 465, pl. 231, fig. 61 (non *Sipho plicatus* A. Adams, 1863).

Retifusus scissuratus. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 198, pl. 102 A.

Petifusus scissuratus. – Golikov, Gulbin, 1977: 187–188 (misspelling in *Retifusus scissuratus*).

Lectotype [designated by Tiba, Kosuge, 1980]: USNM 274071 (Fig. 9G).

Type locality – Nemuro, Japan.

Distribution – Hokkaido, Southern Kurile Islands, 49–400 m (Fig. 1).

Material: 2 lots (10 specimens) examined. ZIN 34444, R/V *Toporok*, sta. 67, transect from Mosbes, Tatar strait, 49 m, 30.08.1949 (specimens **no. 1–3** dissected). ZIN 28449, R/V *Toporok*, sta. 44, Pacific coast of Iturup island, 143 m, t +2,1°C, 06.09.1948 (specimen **no. 4** dissected).

Description. *Shell* (Fig. 9 E-G) elongate fusiform, with long narrow siphonal canal slightly curved



FIG. 9. Shells of *Plicifusus maehirai* (A-D) and *P. scissuratus* (E-G): A – holotype of *P. maehirai*, 47 mm; B – *P. maehirai*, no. 1, 54.6 mm (radula on Fig. 11 C-D, anatomy on Fig. 10); C – holotype of *P. obtusatus* ZIN 33732/1, 48.8 mm; D – *P. maehirai* no. 2, 36.0 mm (radula on Fig. 11 A-B); E – *P. scissuratus* no. 2, 41.2 mm (radula on Fig. 11 E-F, anatomy on Fig. 12); F – *P. scissuratus* no. 4, 23 mm (radula on Fig. 11 G-H); G – lectotype of *Plicifusus* (*Retifusus*) *scissuratus*, USNM 274071, 54 mm. All shells at the same scale.

РИС. 9. Раковины *Plicifusus maehirai* (A-D) и *P. scissuratus* (E-G): A – голотип *P. maehirai*, 47 мм; B – *P. maehirai* № 1, 54,6 мм (радула на Рис. 11 C-D); C – голотип *P. obtusatus* ZIN 33732/1, 48,8 мм; D – *P. maehirai* № 2, 36,0 мм (радула на Рис. 11 A-B); E – *P. scissuratus* № 2, 41,2 мм (радула на Рис. 11 E-F, анатомия на Рис. 12); F – *P. scissuratus* № 4, 23 мм (радула на Рис. 11 G-H); G – лектотип *Plicifusus* (*Retifusus*) *scissuratus* USNM 274071, 54 мм. Все раковины в одном масштабе.

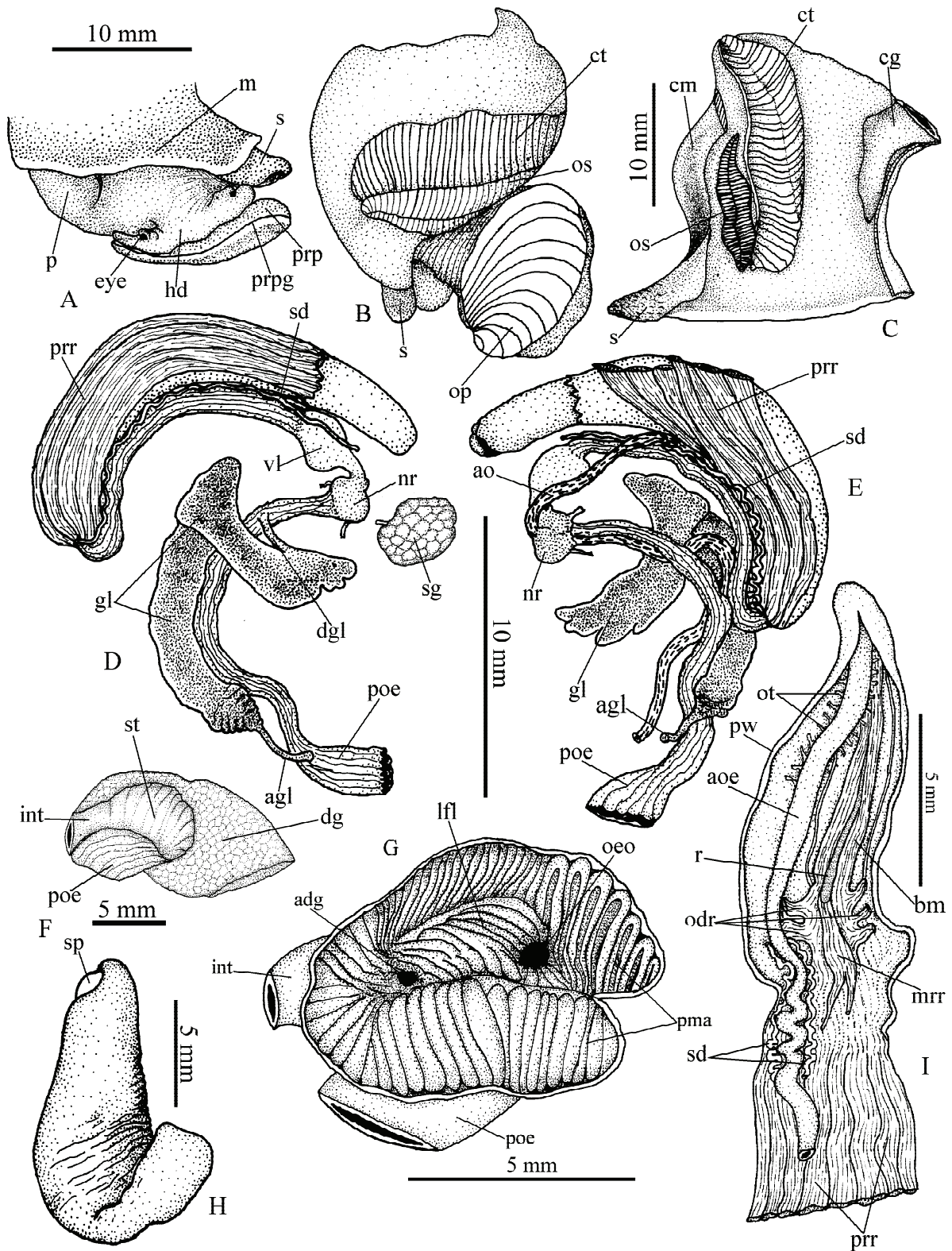


FIG. 10. Anatomy of *Plicifusus maehirai* no. 1 (shell on Fig. 9 B, radula on Fig. 11 C-D). A – cephalopodium; B – soft body, ventral view; C – mantle; D – foregut, right view; E – foregut, left view, salivary glands removed; F – stomach, general view; G – opened stomach; H – penis of no. 3; I – proboscis, opened dorsally.

РИС. 10. Анатомия *Plicifusus maehirai* № 1 (раковина на Рис. 9 В, радула на Рис. 11 С-Д). А – голова и передняя часть висцерального мешка; В – мягкое тело, вид с вентральной стороны; С – мантия; Д – передний отдел пищеварительной системы, вид справа; Е – передний отдел пищеварительной системы, вид слева, слюнные железы удалены; F – желудок, общий вид; G – вскрытый желудок; H – пенис № 3; I – хобот, вскрытый с дорсальной стороны.

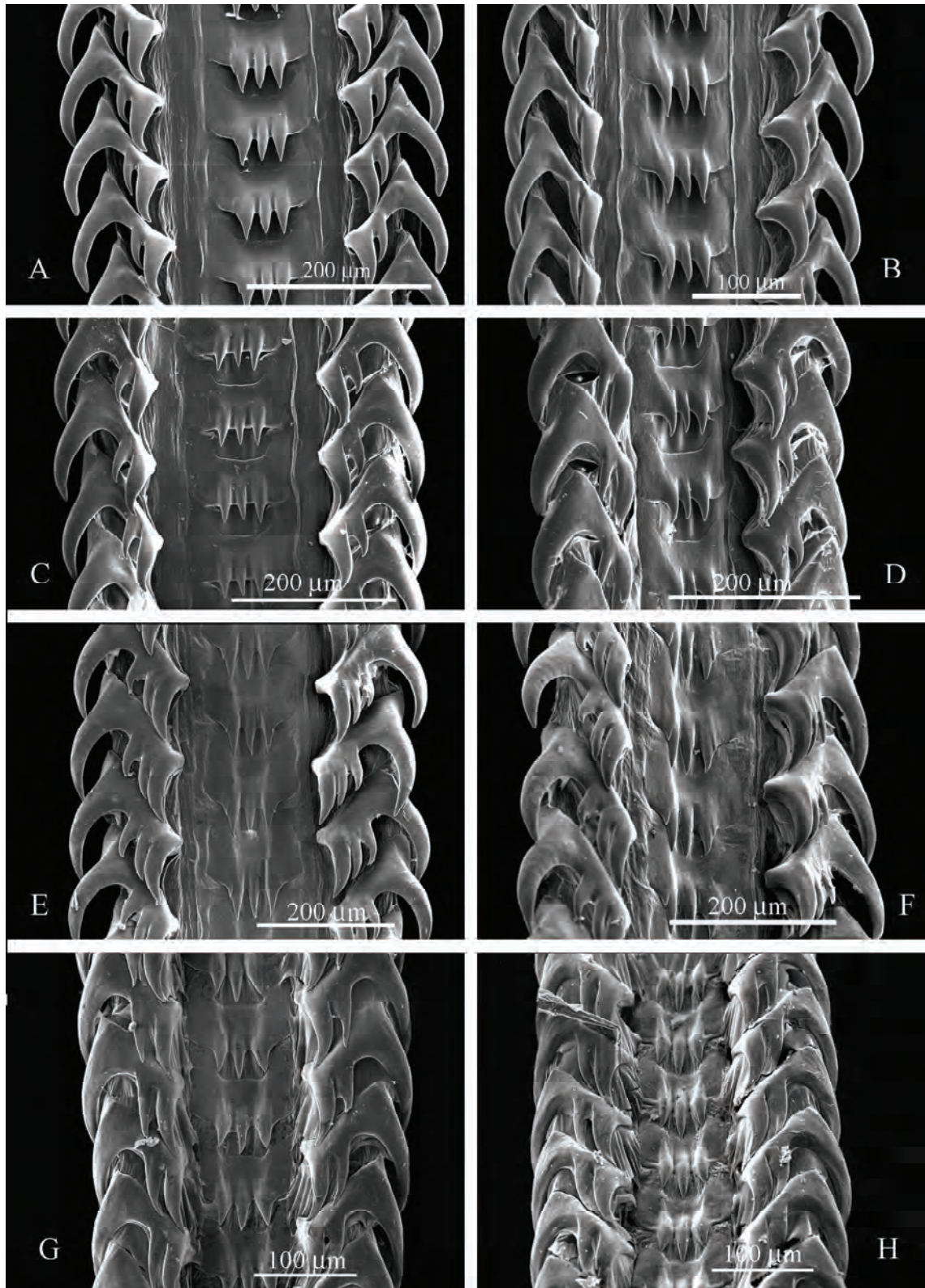


FIG. 11. Radulae of *Plicifusus maehirai* (A-D) and *P. scissuratus* (E-H): A – dorsal and B – lateral view of *P. maehirai* no. 2 (shell on Fig. 9 D); C – dorsal and D – lateral view of *P. maehirai* no. 1 (shell on Fig. 9 B, anatomy on Fig. 10); E – dorsal and F – lateral view of *P. scissuratus* no. 2 (shell on Fig. 9 E, anatomy on Fig. 12); G-H – *P. scissuratus* no. 4 (shell on Fig. 9 F).

РИС. 11. Радулы *Plicifusus maehirai* (A-D) и *P. scissuratus* (E-H): А – вид сверху и В – сбоку *P. maehirai* № 2 (раковина на Рис. 9 D); С – вид сверху и D – сбоку *P. maehirai* № 1 (раковина на Рис. 9 B, анатомия на Рис. 10); Е – вид сверху и F – сбоку *P. scissuratus* № 2 (раковина на Рис. 9 E, анатомия на Рис. 12); G-H – *P. scissuratus* № 4 (раковина на Рис. 9 F).

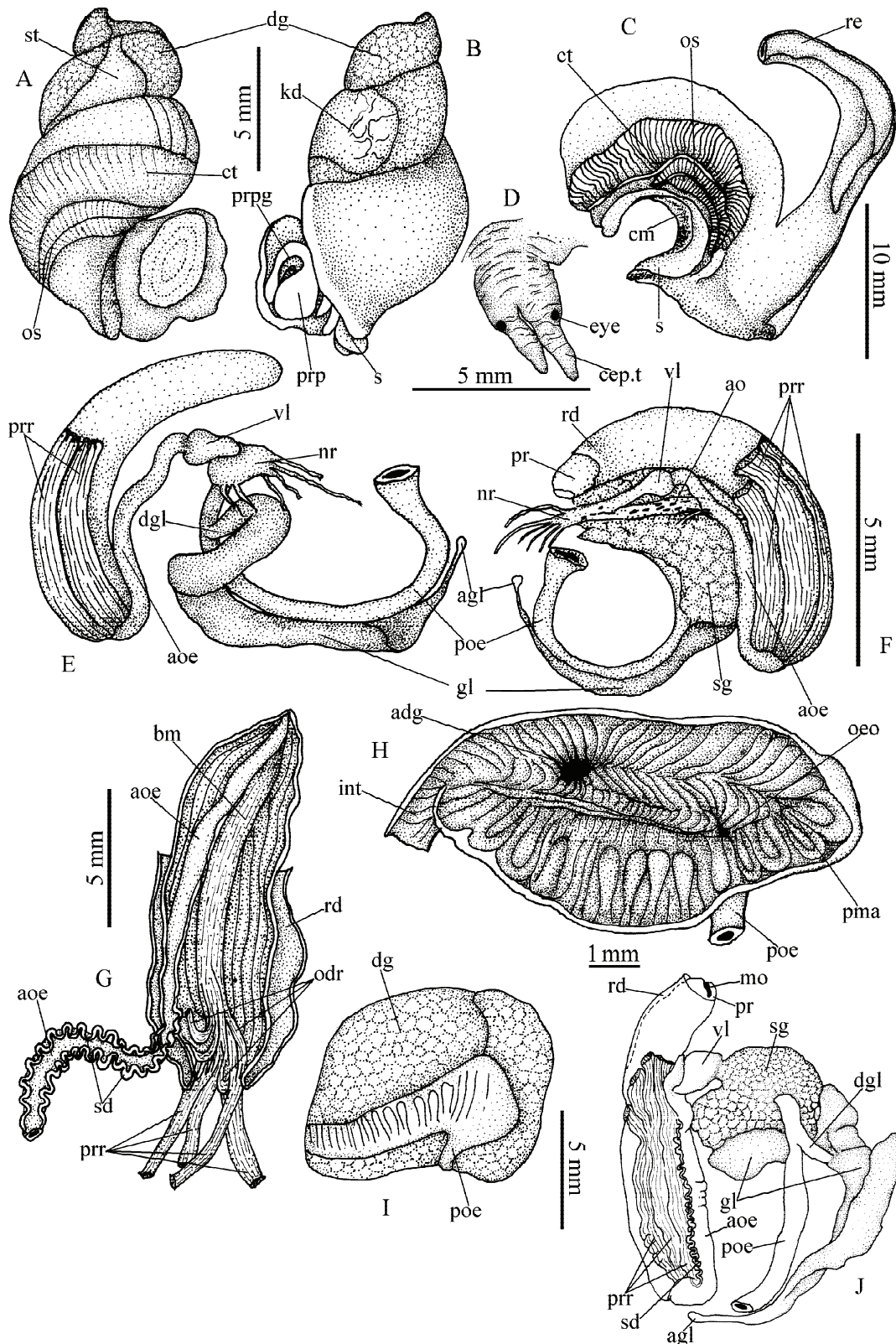


FIG. 12. Anatomy of *Plicifusus scissuratus* no. 2 (shell on Fig. 9 E, radula on Fig. 11 E-F). A – soft body, ventral view, operculum removed; B – soft body, dorsal view; C – mantle; D – head; E – foregut, right view, salivary glands removed; F – foregut, left view; G – proboscis, opened dorsally; H – opened stomach; I – stomach, general view; J – foregut of no. 4, right view.

РИС. 12. Анатомия *Plicifusus scissuratus* № 2 (раковина). А – Мягкое тело, вид с вентральной стороны, крышечка удалена; В – мягкое тело, вид с дорсальной стороны; С – мантия; D – голова; Е – передний отдел пищеварительной системы, вид справа, слюнные железы удалены; F – передний отдел пищеварительной системы, вид слева; G – хобот, вскрытый дорсально; H – вскрытый желудок; I – желудок, общий вид; J – передний отдел пищеварительной системы № 4, вид справа.

to the left. Aperture narrow elongate. Axial sculpture of distinct, tall, nearly prosocline, curved ribs, usually broadly spaced, up to 14 on last whorl. Spiral sculpture of well pronounced wide flattened ribs. On last whorl periphery and shell base spiral ribs usually subdivided by shallower groove in two. In upper parts of whorls this subdivision may be absent. Periostracum dark-olive to brown, tightly adhering. Measurements: **no. 1.** H 47 mm, h 29.4 mm, AL 20.7 mm. **no. 2.** H 41.2 mm, h 21.5 mm, AL 16.9 mm. **no. 3** (siphon is broken). H 43 mm, h 27.3 mm, AL 18 mm. **no. 4.** H 23 mm, h 15.8 mm, AL 12.2 mm.

Soft body (no. 2): mantle spans one whorl, kidney – 0.25, digestive gland and gonad – 1.5 whorls (Fig. 12 A-B). **Head** rather large; its width equals length (Fig. 12D) without tentacles. Tentacles long and thick; eyes large, black, round, on small lobes at tentacles base. **Mantle** long (Fig. 12C). Siphon medium long, with distinct siphonal valve. Ctenidium spans 0.8 mantle length, osphradium – 0.3. Ctenidium more than twice broader than osphradium. Rectum terminates at mantle mid-length. Hypobranchial gland indistinct.

Digestive system. Proboscis thin, short, completely inverted into rhynchodaeum, pigmented (Fig. 12F). Buccal mass spans entire proboscis length (Fig. 12G, **bm**). **Radula** of **no. 2** (Fig. 11 E-F) 12.5 mm long and 400 µm wide (2.37% AL), of 82 transverse rows of teeth, 7 nascent. Radula of **no. 4** (Fig. 11 G-H) 8.5 mm long and 300 µm wide (2.46% AL), of 82 transverse rows of teeth, 16 nascent. Central tooth tricuspid, with the median cusp very slightly longer than marginal ones. Lateral teeth with four cusps in specimen **no. 2** and with three – in specimen **no. 4**, with intermediate cusp(s) smaller than marginal. Odontophoral retractors (Fig. 12G, **odr**) leave buccal mass base to fuse with proboscis wall at its transition to rhynchodaeum. Fibers of proboscis retractors originate in proboscis wall at level of mid-length of buccal mass, detach from wall at transition of proboscis wall to rhynchodaeum, and follow along dorso-lateral sides of rhynchodaeum anteriorly, forming several tufts attached to roof of body haemocoel. Walls of buccal cavity lined with thick cuticle. Large (0.5 of proboscis length) elongated salivary glands situated on both sides of proboscis. Strongly coiling salivary ducts follow parallel to anterior oesophagus. Valve of Leiblein (**vl**) elongated-pyriform, followed by large nerve ring. Gland of Leiblein (**gl**) very long, coiled anteriorly, gradually narrowing and terminating with ampoule (**agl**). Duct of gland of Leiblein wide, opening into oesophagus slightly behind nerve ring. Anterior oesophagus (**aoe**) follows along ventral side of rhynchodaeum, accompanied with anterior aorta (**ao**). **Stomach (no. 2)** (Fig. 12I) with medium-sized posterior mixing area. Posterior mixing

area lined with tall oblique folds (Fig. 12H). Longitudinal fold on inner stomach wall lined with low oblique smaller folds. Inner stomach wall lined with low oblique folds oriented in upper and lower parts in opposite directions; outer stomach wall with deep oblique folds. Posterior oesophagus opens into stomach ventrally. Oesophageal groove passing into intestinal groove. Opening of anterior duct of digestive gland not large, situated at mid-length of stomach; opening of posterior duct not found.

Juvenile male (**no. 4**) with shell with more numerous axial ribs (shell on Fig. 9F) was dissected. Penis of medium size; prostate well developed, vas deferens – with single loop. Salivary glands small, situated behind and dorsally to nerve ring, fused together (Fig. 12J). In other details its morphology is similar to described above.

Differential diagnosis. In shell shape and axial sculpture, the species resembles elongated form of *P. kroeyeri*, differing in well pronounced and more wide spiral cords. In spiral sculpture it is similar to *P. maehirai*, but has less numerous axial ribs on the last whorl. The species was several times erroneously cited as *P. plicatus* (Adams) (see the synonymy).

Plicifusus elaeodes (Dall, 1907) (Figs. 1, 13, 14, 15 A-B)

Tritonofusus (Plicifusus) elaeodes Dall, 1907: 159-160.

Colus okhotskana Tiba, 1973: 65-66, 67, pl. 6. figs. 1-5, **syn. nov.**

Plicifusus elaeodes. – Tiba, Kosuge, 1980: 7-9. – Higo *et al.*, 1999: 230. – Kantor, Sysoev, 2005: 137. – Kantor, Sysoev, 2006: 196, pl. 99 H.

Plicifusus okhotskana. – Tiba, Kosuge, 1980: 7-35. – Okutani, 2000: 467, fig. 64. – Alexeev, 2003: 92, pl. XXXII-1. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 197, pl. 100 G.

Types: Holotype of *Tritonofusus (Plicifusus) elaeodes* — USNM 110477 (Fig. 13A), holotype of *Colus okhotskana* – SSM R13226 (Fig. 13B).

Type localities: *Tritonofusus (Plicifusus) elaeodes* – Sakhalin Island, Aniwa Bay, USFC sta. 5011, 42 fms; *Colus okhotskana* – northern part of the Sea of Okhotsk, 300 m.

Distribution – the Sea of Okhotsk, Sakhalin Island, Southern Kurile Islands, western Kamchatka, northern part of the Sea of Japan, 80-500 m (Fig. 1).

Material: 2 lots (3 specimens) examined. ZIN 52056, R/V *Toporok*, Sea of Okhotsk, Sakhalin Island, Terpeniya Bay, 80 m, biocenosis of *Leda*, 1949 (specimen **no. 1** dissected). ZIN 34146/11, eastern Sakhalin Island, off Siraura, 82 m, 1.10.1949.

Description. *Shell* (Fig. 13) elongate-fusiform, thick-walled, with attenuated canal, from nearly straight to slightly recurved to the left. Aperture broadly ovate. Axial sculpture of slightly arcuate,



FIG. 13. Shells of *Plicifusus elaeodes*: A – holotype of *Tritonofusus (Plicifusus) elaeodes* USNM 110477, 51.5 mm; B – holotype of *Colus okhotskana* R-13226, C – paratype of *Colus okhotskana* R-13225, photos taken from: www.city.rikuzentakata.iwate.jp; D – *P. elaeodes* no. 1, 51.2 mm (radula on Fig. 15 A-B, anatomy on Fig. 14); E – *P. elaeodes* ZIN 34146/11, Sakhalin, Siraura, 82 m, 53.2 mm. All shells at the same scale.

РИС. 13. *Plicifusus elaeodes*. A – голотип *Tritonofusus (Plicifusus) elaeodes*, USNM 110477, 51,5 мм; B – голотип *Colus okhotskana*, R-13226, C – паратип *Colus okhotskana* R-13225, фото взяты с сайта: www.city.rikuzentakata.iwate.jp; D – *P. elaeodes* № 1, 51,2 мм (радула на Рис. 15 A-B, анатомия на Рис. 14); E – *P. elaeodes* ZIN 34146/11, Сахалин, Сираура, 82 м, 53,2 мм. Все раковины в одном масштабе.

closely spaced orthocline to slightly opisthoclinal axial ribs, often smoothed to nearly obsolete on last whorl and inconspicuous on whorls of spire. Spiral sculpture of numerous inconspicuous flattened cords, up to 30 on penultimate whorl. Periostracum thin, light-olive, tightly adhering. Measurements: **no. 1.** H 51.2 mm, h 33.2 mm, AL 15.5 mm.

Soft body. **Head** short and broad (Fig. 14 A,F, **hd**), with long tentacles and large black eyes on lobes at tentacles base. **Foot** folded transversely, with narrow propodium. Operculum oval, with terminal nucleus. **Penis** long and thick (Fig. 14F, **p**), with conical seminal papilla (**sp**), surrounded by circular fold. **Mantle** length twice its width with

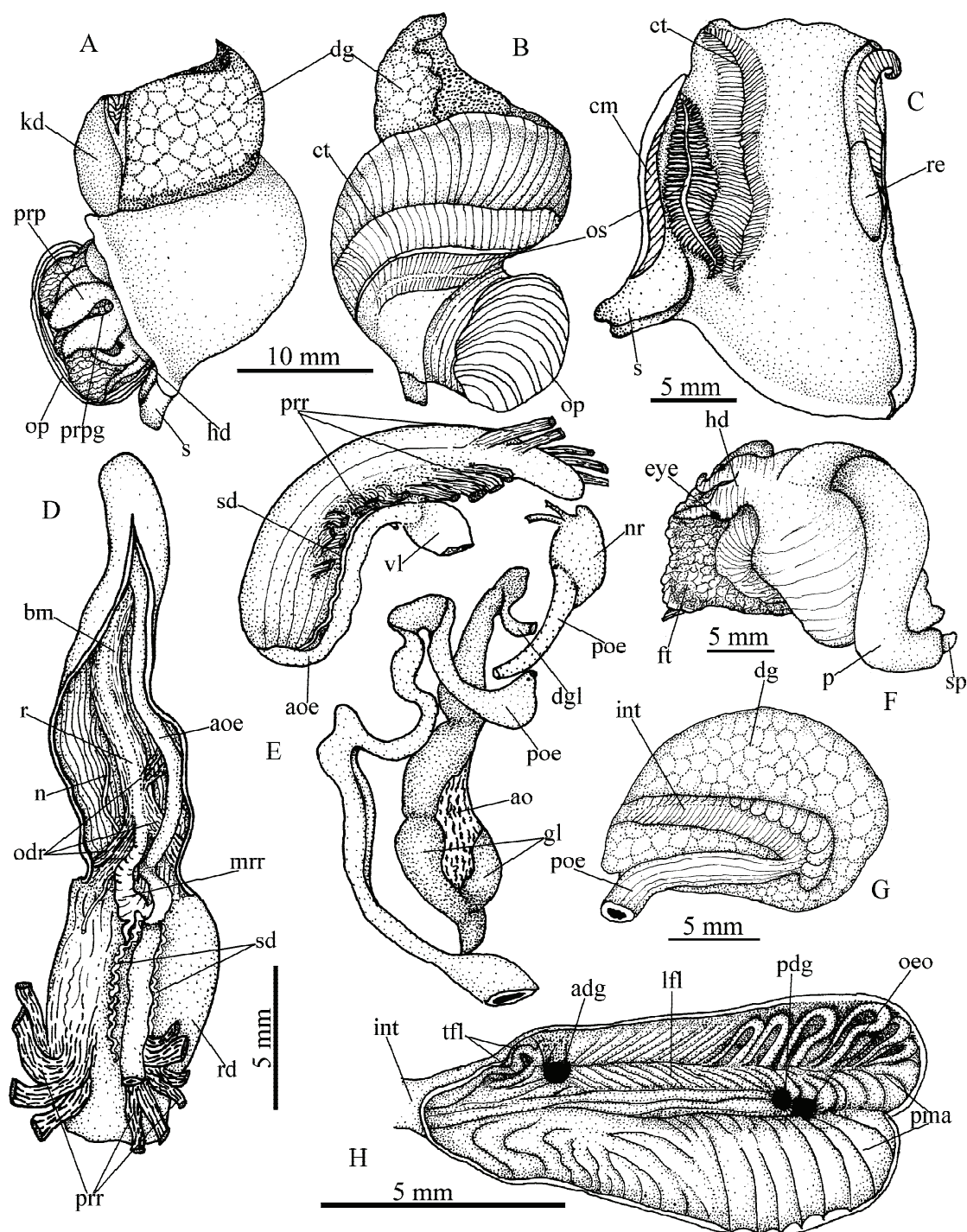


FIG. 14. Anatomy of *Plicifusus elaeodes* no. 1 (shell on Fig. 13 D, radula on Fig. 15 A-B). A – soft body, dorsal view; B – soft body, ventral view; C – mantle; D – proboscis, opened dorsally; E – foregut, right view, salivary glands removed; F – dorsal view of cephalopodium, mantle removed; G – stomach, general view; H – opened stomach.

РИС. 14. Анатомия *Plicifusus elaeodes* № 1 (раковина на Рис. 13 D, радула на Рис. 15 A-B). А – мягкое тело, вид с дорзальной стороны; В – мягкое тело, вид с вентральной стороны; С – мантия; D – хобот, вскрытый с дорзальной стороны; E – передний отдел пищеварительной системы, вид справа, слюнные железы удалены; F – тело моллюска с дорзальной стороны, мантия удалена; G – желудок, общий вид; H – вскрытый желудок.

narrow thickened free mantle edge (Fig. 14C). Muscular siphon medium long. Ctenidium large, equals to osphradium in width and about 1.5 times exceeds osphradium length. Rectum terminates at mantle mid-length. Hypobranchial gland indistinct.

Digestive system. Proboscis completely inverted into rhynchodaeum. Buccal mass long, spans entire inverted proboscis length (Fig. 14D, **bm**). Multiple tufts of proboscis retractors (**prp**) attach to bottom and lateral walls of body haemocoel. **Radu-**

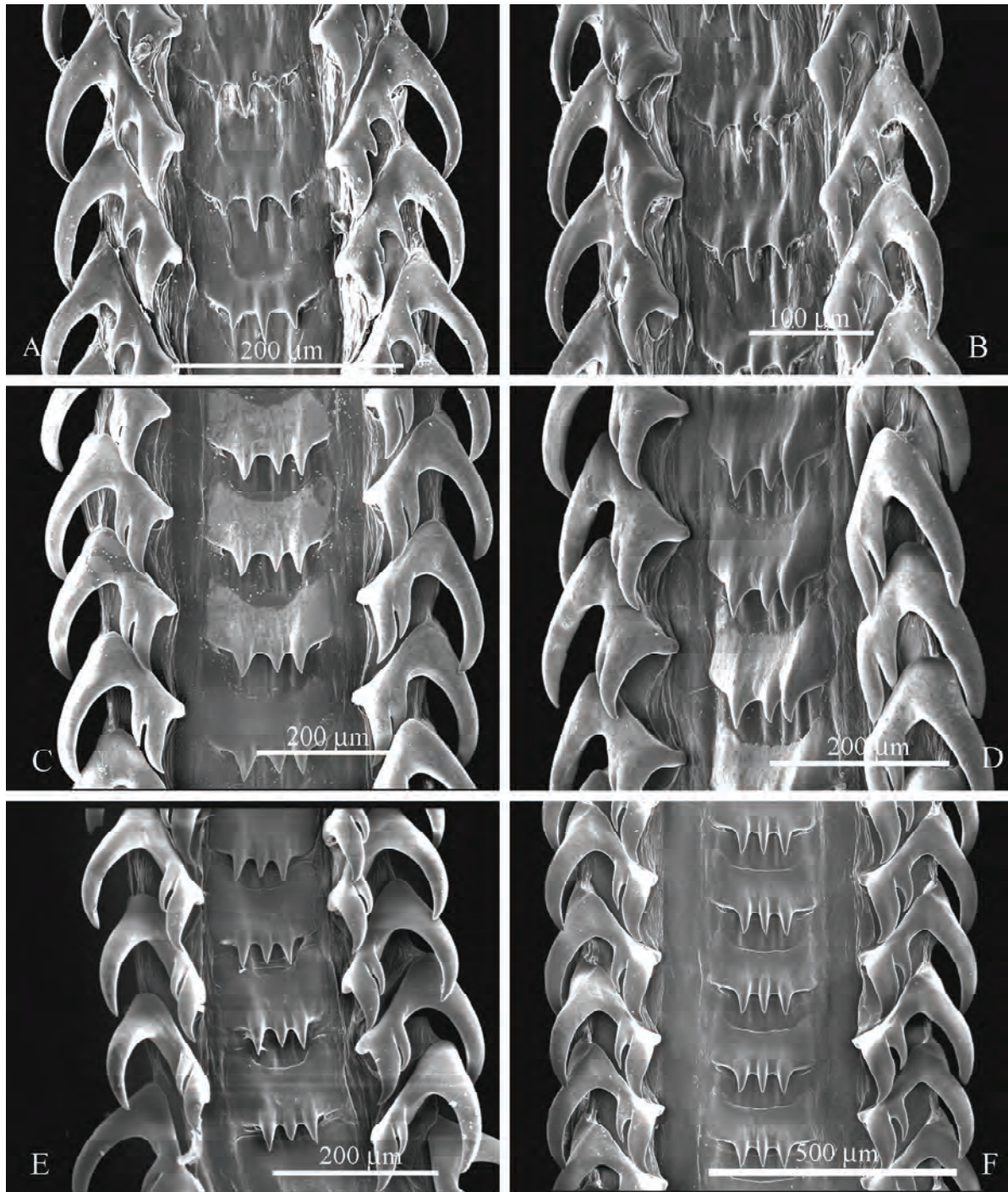


FIG. 15. Radulae of *Plicifusus elaeodes* and *P. rhyssus*: A – dorsal and B – lateral view of *P. elaeodes* no. 1 (shell on Fig. 13D, anatomy on Fig. 14); C – dorsal and D – lateral view of *P. rhyssus* no. 3 (shell on Fig. 18D), E – dorsal view of *P. rhyssus* no. 2 (shell on Fig. 18C), F – dorsal view of *P. rhyssus* no. 4 (shell on Fig. 17 B).

РИС. 15. Радулы *Plicifusus elaeodes* (A-B) и *P. rhyssus* (C-F): A – вид сверху и B – сбоку *Plicifusus elaeodes* № 1 (раковина на Рис. 13D, анатомия на Рис. 14); C – вид сверху и D – сбоку *Plicifusus rhyssus* № 3 (раковина на Рис. 18D), E – вид сверху *P. rhyssus* № 2 (раковина на Рис. 18C), F – вид сверху *P. rhyssus* № 4 (раковина на Рис. 17 B).

la (Fig. 15 A-B) 11 mm long and 300 µm wide (1.27% AL). Central tooth tricuspid, with slightly longer median cusp. Lateral teeth tricuspid on left side and with four cusps on right side, median cusp(s) shortest. Anterior oesophagus (**aoe**) follows along

ventral side of rhynchodaeum (Fig. 14E). Valve of Leiblein (**vl**) elongated-pyriform, followed by large nerve ring. Gland of Leiblein (Fig. 14E, **gl**) long, medium-thick, tightly attached to anterior aorta (**ao**) by connective tissue, opens into oesophagus shortly

posterior to nerve ring (**dgl**). Posterior oesophagus (**poe**) strongly convoluted. Salivary glands of medium size, not fused, with thick coiled ducts, following along anterior oesophagus. **Stomach** long (Fig. 14G). Upper part of outer stomach wall lined with low oblique folds, more pronounced in lower part. Posterior mixing area not large (Fig. 14H). Opening of posterior duct of digestive gland small, situated near oesophagus opening. Inner stomach wall with longitudinal fold (**lfl**) lined with oblique folds. Upper part of inner wall lined with oblique folds, oriented in opposite direction to those on longitudinal fold. Opening of anterior duct of digestive gland near entrance to intestine, in lateral sulcus. Two typhlosoles follow from anterior duct of digestive gland to intestine. Oesophageal groove with two tall and narrow longitudinal folds.

Differential diagnosis. *P. elaeodes* differs from conchologically similar *Plicifusus kroeyeri* in lower axial ribs and twice broader spiral cords; from *P. maehirai* – by less pronounced spiral sculpture; from *P. scissuratus* – by shell shape and more numerous axial ribs.

Remarks. *Colus okhotskanus* Tiba, 1973, described from Okhotsk Sea (Fig. 13 B-C) is conchologically indistinguishable from *Plicifusus elaeodes*.

Plicifusus croceus (Dall, 1907)
(Fig. 16 B)

Tritonofusus (Plicifusus) croceus Dall, 1907: 161.

Plicifusus croceus. – Tiba, Kosuge, 1980: 7-8, figs. 1-6. – Okutani *et al.*, 1988: 104. – Higo *et al.*, 1999: 230. – Okutani, 2000: 465, pl. 231, fig. 63.

Lectotype [designated by Tiba, Kosuge, 1980]: USNM 110491 (Fig. 17B).

Type locality – central part of the Sea of Japan, USFC sta. 4982, 43°N, 140°10'30"E, 390 fms.

Distribution: northern part of the Sea of Japan, Okhotsk Sea, 150-700 m [Higo *et al.*, 1999; Okutani, 2000].

Remarks. Although Okutani *et al.* [1988] and Okutani [2000] recorded the species from the Okhotsk Sea, it is not present in our material. Specimens from ZIN, identified as *P. croceus*, belong to *P. maehirae*. Nothing is known about anatomy and radula of the species, it may be distinguished from other species by its relatively small size (up to 42 mm), and thin shell with numerous narrow axial folds.

Plicifusus hastarius Tiba, 1980
(Fig. 16 A)

Tiba, 1980a: 49-50, pl. 13, figs. 8-11. – Tiba, Kosuge, 1980: 7-11. – Higo *et al.*, 1999: 230. – Kantor, Sysoev, 2005: 137. – Kantor, Sysoev, 2006: 196, pl. 99 F-G.

Holotype: IMT-80-19 (Fig. 17A).

Type locality – off Kushiro, Hokkaido, at about 80-100 m.

Distribution – Kurile Islands, Pacific coast of Japan, 7-100 m [Higo *et al.*, 1999] (Fig. 1).

Remark. Although Higo *et al.* [1999] recorded this species from Kurile Islands, it is not present in our material. The single specimen from ZIN, erroneously identified as *P. hastarius*, significantly differs from type specimen; and we attribute it to *P. kroeyeri*. Nothing is known about anatomy and radula of the species, which has very characteristic shell shape with strongly attenuated nearly straight canal. Conchologically it is somewhat similar to *Plicibuccinum declivis* (Habe *et al.*, 1976), but differs in having operculum with terminal nucleus [Tiba, 1980], not concentric as in *P. declivis*.

Plicifusus johanseni Dall, 1919
(Fig. 16 C-D)

Dall, 1919b: 21A, pl. III. – Dall, 1921: 93.

Type locality: Point Burrow sandpit and Icy Cape, Alaska, sta. 24.

Syntypes: NMC 4117, USNM 27475A.

Distribution: type locality.

Remarks: The species was erroneously recorded in the Sea of Okhotsk [Golikov *et al.*, 2001] basing on a single erroneously identified specimen from ZIN (No. 13777/1, Okhotsk Sea, Shelekhov Bay, 61°23.0' N, 158°01' E, 75 m), belonging to *Plicifusus kroeyeri* [Kantor, Sysoev, 2006]. Bouchet and Warén [1985, p. 231] reduced *P. johanseni* to junior synonym of *P. kroeyeri*. Although the types of *P. johanseni* are dead collected and have strongly worn shells, the original drawing and studied syntype in USNM clearly demonstrates different from *P. kroeyeri* pattern of sculpture – absence of axial ribs on the last whorl and broad flattened spiral cords. It is not clear whether the species is actually Recent or fossil and in the lack of additional information we consider it as a valid species.

Plicifusus levis Tiba, 1980
(Fig. 16E)

Tiba, 1980a: 47, pl. 11, figs. 1-8. – Tiba, Kosuge, 1980: 13-14. – Higo *et al.*, 1999: 230.

Type locality: off the coast of Rikuzen, Iwate Pref., Honshu, 250-300 m.

Holotype: SSM R 13258 (Fig. 17E).

Distribution: northeastern Honshu (Iwate Prefecture (off Kuji; off Yagi; off Ayari); off Miyagi prefecture), 200-300 m [Higo *et al.*, 1999].

Remarks: The species is not present in our material and neither anatomy nor radula were studied. Conchologically it is rather similar to small species originally described within *Plicifusus* – *P. parvus* and *P. saginatus* Tiba, 1980, both transferred to *Reti-*

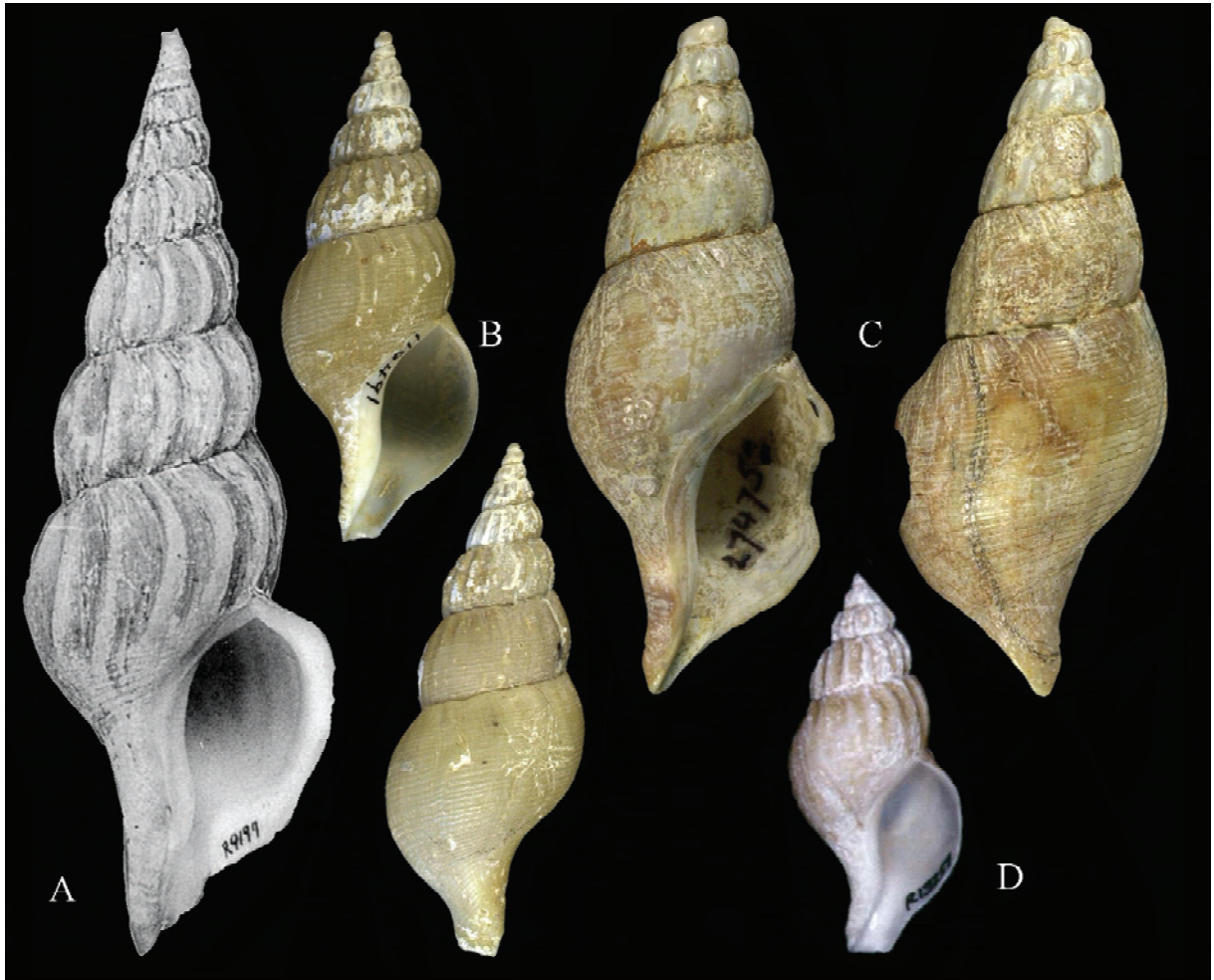


FIG. 16. A – holotype of *Plicifusus hastarius* IMT-80-19; B – lectotype of *P. croceus* USNM 110491, 37.9 mm, courtesy of USNM; C – syntype of *P. johanseni* USNM 27475A, 53 mm; D – holotype of *Plicifusus levis* SSM.R 13258, 31 mm. All shells at the same scale.

РИС. 16. А – голотип *Plicifusus hastarius* IMT-80-19; В – лектотип *P. croceus* USNM 110491, 37,9 мм; С – синтип *P. johanseni* USNM 27475A, 53 мм; D – голотип *Plicifusus levis* SSM.R 13258, 31 мм. Все раковины в одном масштабе.

fusus (see below). Nevertheless, according to the original description *P. levis* lacks spiral sculpture, that differs it from both mentioned species and other species of the genus. The species attains 32 mm in length (holotype) that makes it the smallest known *Plicifusus*. In the absence of the data on radula and anatomy we consider it conventionally as *Plicifusus*.

Plicifusus rhyssus (Dall, 1907) (Figs. 1, 15 C-F, 17; 18, 19)

Tritonofusus (*Plicifusus*) *rhyssus* Dall, 1907: 160.

Plicifusus rhyssus. – Dall, 1925: 25, pl. 33, fig. 7.

Tritonofusus (*Plicifusus*) *aurantius* Dall, 1907: 160-161, **syn. nov.**

Plicifusus (*Helicofusus*) *aurantius*. – Dall, 1925: 24, pl. 34, fig. 1.

Plicifusus (*Latifusus*) *wakasanus* Dall, 1918: 227.

Plicifusus (*Aulacofusus*) *rhyssoides* Dall, 1918: 227, **syn. nov.**

Helicofusus rhyssus. – Habe, 1965: 90, pl. 29, fig. 6. – Alexeev, 2003: 95, pl. XXXIII-1. – Kantor, Sysoev, 2005: 132. – Kantor, Sysoev, 2006: 184-185, pl. 91 I.

Plicifusus aurantius. – Tiba, Kosuge, 1980: 3-4. – Okutani *et al.*, 1988: 103. – Okutani, 2000: 465, pl. 231, fig. 62. – Kantor, Sysoev, 2005: 137. – Kantor, Sysoev, 2006: 195, pl. 99 A-B.

Plicifusus rhyssus. – Dall, 1925: 25, pl. 33, fig. 7. – Tiba, Kosuge, 1980: 21-22. – Okutani *et al.*, 1988: 102. – Okutani, 2000: 467, pl. 231, fig. 65.

Plicifusus (*Plicifusus*) *aurantius*. – Higo *et al.*, 1999: 230.

Plicifusus (*Plicifusus*) *rhyssus*. – Higo *et al.*, 1999: 230.

Type specimens: lectotype of *Tritonofusus* (*Plicifusus*) *rhyssus* [designated by Tiba, Kosuge, 1980]: USNM 110489 (Fig. 17C); lectotype of *Tritonofusus* (*Plicifusus*) *aurantius* [designated by Tiba, Kosuge, 1980]: USNM 110490 (Fig. 17D); holotype of *Plicifusus* (*Latifusus*) *wakasanus*: USNM 274068 (Fig. 18 E); syntypes of *Plicifusus* (*Aulacofusus*) *rhyssoides*: USNM 274069 (Fig. 18A).

Type localities: *Plicifusus rhyssus* – Aniwa Bay, Sakhalin Island, USFC sta. 5013, 46°17'N, 143°09'E, 43 fms); *Plicifusus wakasanus* – Wakasa (Bay), Sea of Japan; *Plicifusus aurantius* – Sea of Japan, USFC sta. 4982, 43°N, 140°10'30"E, 390-428 fms; *Plicifusus rhyssoides* – Rikuzen, Japan.

Distribution – the Bering Sea, the Sea of Okhotsk, Kurile Islands, northern part of the Sea of Japan; eastern and western coasts of Honshu, 52-500 m (Fig. 1).

Material: 5 lots (30 specimens) examined. ZIN 34166, Sea of Okhotsk, R/V *Toporok*, st. 147-149, transect from Siraura, 47°51'06"N, 142°31'00"E, 82-103 m, 01.10.1949 (specimen **no. 1** dissected). IO, Sea of Okhotsk, R/V *Vityaz*, sta. 1861, 58°21'9"N, 143°15'6"E, 144 m, 20.10.1952 (specimen **no. 2** dissected). ZIN 34102, R/V *Toporok*, sta. 32, Sakhalin, cape Aniwa, 46°06'1 N, 142°34'8 E, 4-82 m, pebble, mud. 27.08.1947 (specimen **no. 3** dissected). ZMMU 14829, Kamchatka, Olutorsky Bay, 60°06'7 N, 168°09'9 E, 140-145 m, 12.08.1988 (specimen **no. 4** dissected). IO, R/V *Vityaz*, 12 cruise, Sea of Okhotsk, sta. 1841, 57°24.7'N, 144°57.6'E, 160 m, 16.10.1952.

Description. *Shell* (Figs. 17, 18) broad to elongate fusiform, with convex whorls and often pronounced rounded shoulder. Canal short, broad, recurved to the left and often on dorsal shell side. Aperture elongate to broad oval. Axial sculpture of poorly to more or less pronounced slightly arcuate orthocline or slightly prosocline ribs, from 12 to 16 on last whorl, sometimes nearly obsolete. Spiral sculpture of narrow, well pronounced sinuous, closely spaced spiral cords, from 40 to 50 on penultimate whorl. Periostracum from light-yellow to dark-brown, tightly adhering. Measurements: **no. 1:** H 49.6 mm, h 36.3 mm, AL 30.9 mm, male. **no. 2:** H 37.7 mm, h – 28 mm, AL 19.8 mm, female. **no. 3:** H 39 mm, AL 18.6 mm. **no. 4:** H 55 mm, h 40.5 mm, AL 31 mm.

Soft body. Four specimens were dissected: **no. 1** (Fig. 17A) having the shell most close to the types of *P. rhyssus* (Fig. 17D), **no. 2** (Fig. 18C) most close to the type of *P. wakasanus*, **no. 3** (Fig. 18D) – close to the type of *P. rhyssoides*, and **no. 4** (Fig. 17B) – close to the type of *P. aurantius*. The morphology of all dissected specimens was similar, therefore generalized description is given.

Head (Fig. 19C, **hd**) very broad, large, contracted. Tentacles long, with large black eyes on lobes at tentacles bases. **Foot** folded transversely, with wide propodium and deep propodial groove. **Operculum** oval, with terminal nucleus. **Mantle** length equals to its width (Fig. 19B). Siphon medium long, muscular. Ctenidium spans 0.6 of mantle length and 0.25 of width. Osphradium twice shorter and slightly narrower than ctenidium. Hypobranchial gland not pronounced. Rectum opening at mantle mid-length, covered by capsule gland. Capsule gland (**no. 2**) spans half of mantle length and quarter of its

width (Fig. 19B, **cg**). Female orifice (**fo**) of medium size, narrow, vagina short. Penis large, terminated with large seminal papilla (**sp**), surrounded by circular fold of skin. Male orifice surrounded by low ridge (Fig. 19D).

Digestive system. Proboscis deeply inverted into rhynchodaeum, and buccal mass protruded into body haemocoel (Fig. 19 E, J-K). Mouth opening slit-like. Buccal mass attached by multiple retractors to wall of proboscis base. Median radula retractor attached together with proboscis retractors in posterior third of rhynchodaeum (**mrr**). On opposite ends proboscis retractors attached to lateral walls of body haemocoel. **Radula** of **no. 2** (Fig. 15E) 350 µm wide, (1.77% AL), of 78 transverse rows of teeth, 4 nascent. Central tooth tricuspid, median cusp slightly shorter than marginal ones; lateral teeth tricuspid, with shortest median cusp. Radula of **no. 3** (Fig. 15 C-D) 400 µm wide (2.15% AL), of 135 transverse rows of teeth, 6 nascent. Teeth morphology identical to previous specimen. Radula of **no. 4** (Fig. 15F) 750 µm wide (2.42% AL). Cusps of central tooth equal-sized; lateral teeth same as in the previous specimens. Anterior oesophagus (**aoe**) follows along ventral side of rhynchodaeum. Valve of Leiblein (**vl**) not large, elongated (Fig. 19 E, J), followed by large nerve ring. Gland of Leiblein (**gl**) long and narrow, opens into oesophagus immediately posterior to nerve ring by long and thick duct (Fig. 19E, **dgl**). Posterior oesophagus of same diameter as anterior, widening at opening ventrally into stomach. Salivary glands large and thick, situated on both sides of the nerve ring. In specimen **no. 3** they equal in length to proboscis, and fused ventrally of rhynchodaeum (Fig. 19J, **sg**). Salivary ducts very thin and convoluted, with left one being more coiled than right one, within proboscis follow in walls of anterior oesophagus. **Stomach** (Fig. 19H) with small posterior mixing area that is lined with high transverse folds on outer wall and low oblique transverse folds on inner wall (Fig. 19I, **pma**). Rest of inner stomach wall with several wide transverse folds and with longitudinal fold in median part (**lfl**). Opening of anterior duct of digestive gland (**adg**) at beginning of intestine, with two low typhlosoles (**tfl**) running from anterior duct into intestine. Opening of posterior duct of digestive gland not found.

Differential diagnosis. Despite high variability, the species is easily distinguishable by spiral sculpture, represented by distinct numerous sinuous ribs.

Remarks. The species is extremely variable in number and shape of the axial ribs, shell shape and periostracum color. It may be considered as a polymorphic species, or a complex of closely related species.

Type specimens of *P. rhyssus*, *P. aurantius* and *P. wakasanus* have shells of similar shape, proportions, size and spiral sculpture (despite that shell



FIG. 17. Shells of *Plicifusus rhyssus*: A – *P. rhyssus* no. 1 (radula on Fig. 15 E, anatomy on Fig. 19 C-I), B – *P. rhyssus* no. 4 (radula on Fig. 15 F), C – lectotype of *P. rhyssus* USNM 110489, 48.3 mm; D – lectotype of *Tritonofusus* (*Plicifusus*) *aurantius* USNM 110490, 45.4 mm. All shells at the same scale.

РИС. 17. Раковины *Plicifusus rhyssus*: А – *P. rhyssus* № 1 (радула на Рис. 15 Е, анатомия на Рис. 19 С-I), В – *P. rhyssus* № 4 (радула на Рис. 15 F), С – лектотип *P. rhyssus* USNM 110489, 48,3 мм; D – лектотип *Tritonofusus* (*Plicifusus*) *aurantius* USNM 110490, 45,4 мм. Все раковины в одном масштабе.

surface of *P. aurantius* is eroded, the spiral sculpture is preserved on shell's dorsal side). Some authors [Tiba, Kosuge, 1980; Kantor, Sysoev, 2005] have already considered *P. wakasanus* as junior synonym of *P. aurantius*, but without morphological evidence.

Dissected specimens possessing shells similar to type specimens of the three species, did not show significant differences. At the same time this can not be considered as ultimate proof, since all dissected specimens originated from the Sea of Okhotsk

and even eastern Kamchatka and therefore are not close to type localities of *P. aurantius* and *P. rhyssoides*. Nevertheless, *P. rhyssus*, *P. aurantius* and *P. rhyssoides* were described from Japanese low boreal area, which is characterised by many species, distributed within entire area [Golikov, 1980]. Types of *P. rhyssoides* and *P. rhyssus* conchologically are rather similar, that was mentioned by Dall himself [1918: 227]. The main, although slight differences are the shell proportions (more elongated in *P. rhyssoides*, with slower increasing whorls diameter and



FIG. 18. Shells of *Plicifusus rhyssus*: A – syntype of *Plicifusus rhyssoides* USNM 274069, 47.3 mm; B – *P. rhyssus* ZIN, uncatalogued, C – *P. rhyssus* no. 2 (anatomy on Fig. 19 A-B), D – *P. rhyssus* no. 3 (radula on Fig. 15 C-D, anatomy on Fig. 19 J-K), E – lectotype of *Plicifusus wakanus* USNM 274068, 39 mm. All shells at the same scale.

РИС. 18. Раковины *Plicifusus rhyssus*: A – синтип *Plicifusus rhyssoides* USNM 274069, 47,3 мм; B – *P. rhyssus* ZIN, не занесен в каталог; C – *P. rhyssus* № 2 (анатомия на Рис. 19 A-B), D – *P. rhyssus* № 3 (радула на Рис. 15 C-D, анатомия на Рис. 19 J-K), E – лектотип *Plicifusus wakanus* USNM 274068, 39 мм. Все раковины в одном масштабе.

less convex whorls), and axial sculpture (in *P. rhyssoides* it is more prominent). Dissected specimen no. 3, found in the same locality as type of *P. rhyssus*, had transitional characters: slender shell similar in outline to *P. rhyssoides*, bearing weakly expressed axial ribs like in *P. rhyssus*. Its anatomy was identical to other three specimens. Taking into account high variability of axial sculpture in buccinids, we consider *P. rhyssoides* as junior synonym of *P. rhyssus*, but for final decision additional material should be examined.

The major problem is *P. wakanus*, that was described from Wakasa Bay (no more exact locality data), that is southward from the line between Noto and Boso peninsulas. This line is considered as a southern border of the Boreal province [Golikov, 1980]. Tiba and Kosuge [1980] illustrated a large series of specimens, which have transitional characters between *P. aurantius* and *P. wakanus*. In the absence of material of *P. wakanus* from the type locality we follow the opinion of the mentioned authors. Thus, within the current morphological par-

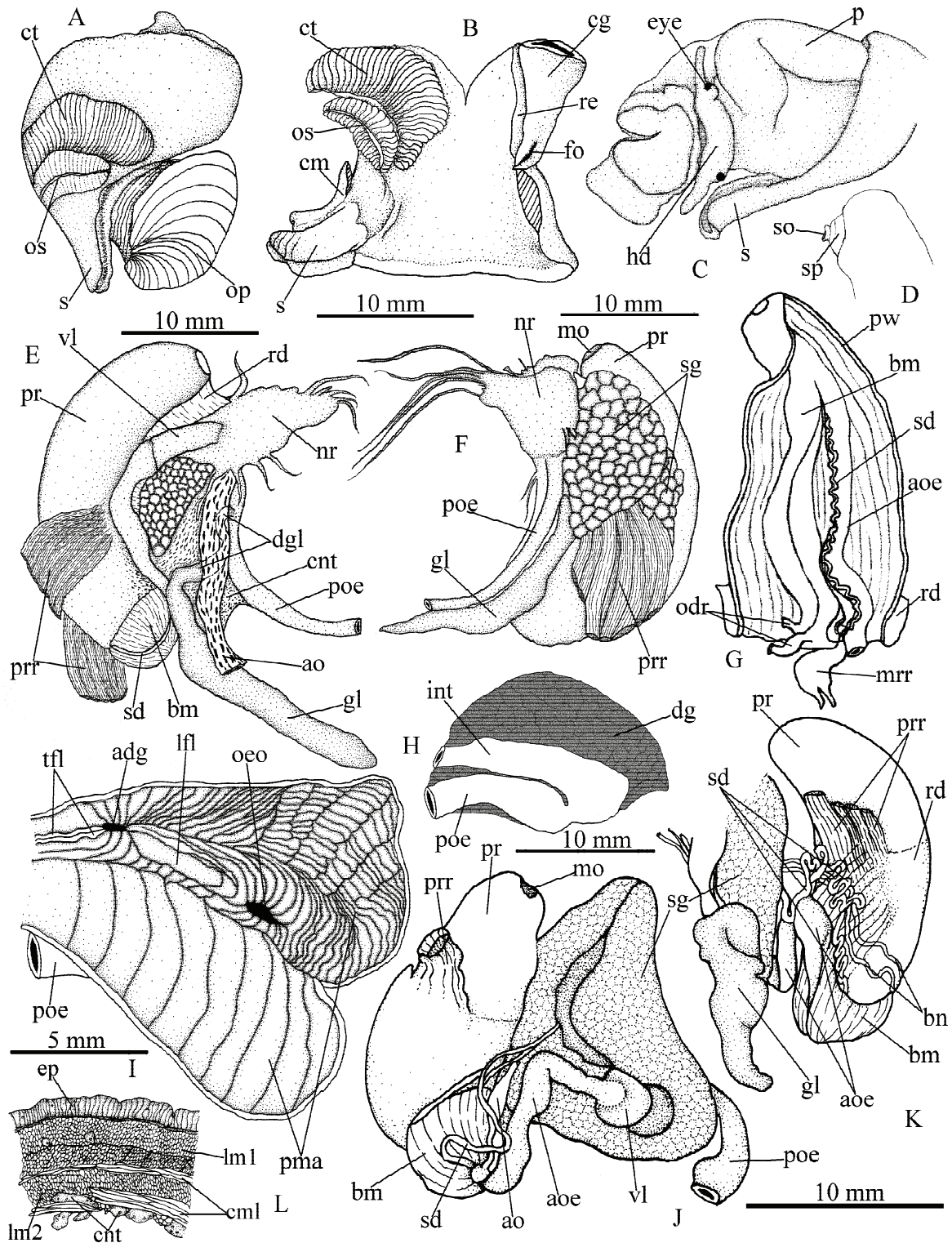


FIG. 19. Anatomy of *Plicifusus rhyssus* nos. 1-3. A – soft body of spm. no. 2, ventral view; B – mantle of spm. no. 2; C – soft body of spm. no. 1, dorsal view; D – tip of penis of spm. no. 1; E – foregut of spm. no. 1, right view, right salivary gland removed; F – foregut of spm. no. 1, left view; G – proboscis, opened dorsally; H – stomach of spm. no. 1, general view; I – opened stomach of spm. no. 1; J – foregut of spm. no. 3, right view; K – foregut of spm. no. 3, left view; L – transverse section of proboscis wall of spm. no. 1.

РИС. 19. Анатомия *Plicifusus rhyssus* №№ 1-3. А – мягкое тело экз. № 2, вид с вентральной стороны; В – мантия экз. № 2; С – мягкое тело экз. № 1, вид с дорсальной стороны; D – верхняя часть пениса экз. № 1; E – передний отдел пищеварительной системы экз. № 1, вид справа, правая слюнная железа удалена; F – передний отдел пищеварительной системы экз. № 1, вид слева, G – хобот, вскрытый дорсально; H – общий вид желудка экз. № 1; I – вскрытый желудок экз. № 1; J – передний отдел пищеварительной системы № 3, вид справа; передний отдел пищеварительной системы экз. № 3, вид слева; L – поперечный срез стенки хобота экз. № 1.

adigm we consider *P. rhyssus* as broadly distributed polymorphic species. *Tritonofusus (Plicifusus) rhyssus* and *Tritonofusus (Plicifusus) aurantius* were described by Dall in the same publication [1907]. As the first revisers we consider *P. rhyssus* as senior synonym on the reasons that the species name is more often used in literature and the better preservation conditions of the types.

Plicifusus oceanodromae Dall, 1919
(Figs. 1, 20 A-B, 21, 22 A-B)

Plicifusus (Retifusus) oceanodromae Dall, 1919a: 314. – Dall, 1921: 93. – Kantor, Sysoev, 2005: 137-138. – Kantor, Sysoev, 2006: 197, pl. 100 C-D.

Syntypes: USNM 205923.

Type locality – Petrel Bank, Bering Sea, USFC sta. 4777, 52°11'N, 179°49'E, 43-52 fms.

Distribution – the Sea of Okhotsk, Eastern Kamchatka, Aleutian Islands, 129-180 m (Fig. 1).

Material examined: 2 specimens, ZIN 56031, Eastern Kamchatka, Morzhovaya Bay, 53°16'0"N, 159°57'51"E, R/V *Raduga*, 180 m, muddy sand, 17.07.1975 (specimen no. 1 dissected).

Description. *Shell* (Fig. 20 A-B) broadly fusiform, stout, with medium convex whorls and short and broad canal, slightly curved to the left. Aperture broad oval. Axial sculpture of closely spaced, slightly arcuate prosocline axial ribs, obsolete on shell base, up to 20 on last whorl. Spiral sculpture of well pronounced, nearly flat, closely spaced spiral cords (up to 15 on penultimate whorl), which may have secondary shallow grooves. Periostracum light brown, peeling. Shell color white to light pink. Measurements: **no. 1:** H 32.4 mm, h 23.4 mm, AL 16 mm.

Soft body. Mantle spans one whorl, kidney – 0.2, digestive gland and gonad – rest of visceral mass (Fig. 21 A-B). **Head** of medium size, with thick contracted tentacles. Small black eyes on small lobes at tentacles bases. Foot contracted, folded transversely, with rather narrow propodium and deep propodial groove. Operculum oval with terminal nucleus. **Mantle** length slightly exceeds its width (Fig. 21C). Siphon medium-long, wide and muscular. Osphradium symmetrical, spans one third of mantle length. Ctenidium 0.75 of mantle length, equals to osphradium in width, consisting of wide triangular lamellae. Hypobranchial gland represented by irregular shaped folds covered with mucus. Narrow rectum is semi-covered by well developed capsule gland (Fig. 21C, **cg**). Large elongated female orifice situated ventro-laterally and surrounded by relatively thin wall of vagina (**va**).

Digestive system. Proboscis almost completely inverted into rhynchodaeum. Proboscis retractors situated on both sides of rhynchodaeum and at-

tached to bottom and lateral walls of body haemocoel (Fig. 21D). Buccal mass (Fig. 21E, **bm**) equals to proboscis length, multiple odontophoral retractors attached to proboscis walls. **Radula** (Fig. 22 A-B) 5.5 mm long and 300 µm wide (1.83% AL). Central tooth tricuspid, with median cusp longest, lateral teeth tricuspid, with median cusp shortest. Median radular retractor (Fig. 21E, **mrr**) originates at base of radula sac. Pair of buccal nerves (Fig. 21E, **bn**) follow ventrally of rhynchodaeum to nerve ring. Salivary glands not large, bean-like, situated on both sides of large nerve ring; salivary ducts strongly convoluted. Valve of Leiblein not large; gland of Leiblein long, folded anteriorly and tubular posteriorly; duct of gland (**dgl**) opens immediately behind nerve ring. **Stomach** spans about ¼ of whorl (Fig. 21G). Posterior mixing area small, lined with tall transverse folds (Fig. 21F, **pma**). Inner stomach wall lined with oblique folds; smooth longitudinal fold (**lfl**) runs from oesophageal opening to anterior duct of digestive gland. Opening of posterior duct of digestive gland not found. Outer stomach wall is lined with tall transverse folds.

Differential diagnosis. The species is very close to *P. olivaceus*, slightly differing in stronger prosocline axial ribs. It is possible that both species are synonyms, but the present limited material does not allow us to draw a final conclusion, therefore we consider both species valid at the moment.

Plicifusus olivaceus (Aurivillius, 1885)
(Figs. 1, 20 C-D, F, 22 C-D, 23)

Fusus (Sipho) olivaceus Aurivillius, 1885: 366-367, 380, Tafl. 13, fig. 10.

Plicifusus (Retifusus) incisus Dall, 1919a: 314. – Dall, 1921: 93. – Dall, 1925: 13, pl. 3, f. 1. – Higo *et al.*, 1999: 231. *Retifusus incisus*. – Golikov, Gulbin, 1977: 187.

Plicifusus incisus. – Alexeev, 2003: 90, pl. XXXI-3.

Retifusus olivaceus. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 199-200, pl. 101 E.

Types: 11 syntypes of *Fusus (Sipho) olivaceus* — SMNH Type-3852 (Fig. 20 C); holotype of *Plicifusus (Retifusus) incisus* — USNM 225614.

Type localities: *Fusus (Sipho) olivaceus* – northern Bering Sea, Anadyrsky Bay, 62°39'N, 177°05'W, 55 fms, *Vega* expedition sta. 1068; of *Plicifusus (Retifusus) incisus* – E Siberia, SE coast Kamchatka, USFC st. 3643, 51°16'00"N, 158°03'00"E, 100 fms (the depth given according to the original description).

Distribution – the Bering Sea, Eastern Kamchatka, Northern Kurile Islands, 103-318 m (Fig. 1).

Material: 3 lots (15 specimens). ZIN 5488, R/V *Academik Oparin*, 2 cruise, sta. 93, south-eastern Kamchatka, 50°26.1'N, 156°55.9'E, 132 m, muddy sand, pebbles, 15.08.1986, (specimen no. 1 dissected). ZIN 57886/13, R/V *Academik Oparin*, 7 cruise Paramushir Island, Kurile Islands,



FIG. 20. Shells of *Plicifusus*: A – syntype of *P. oceanodromae* USNM 205923, 40.5 mm; B – *P. oceanodromae*, no. 1 (radula on Fig. 22 A-B, anatomy on Fig. 21), C – syntype of *P. olivaceus*, SMNH-3852, 40 mm; D – *P. olivaceus* no. 2 (radula on Fig. 22 D, anatomy on Fig. 23), E – *P. olivaceus* no. 1 (radula on Fig. 22 C); F – *P. torquatus* no. 1 (radula on Fig. 22 E-F, anatomy on Fig. 24). All shells at the same scale.

РИС. 20. Раковины *Plicifusus*: А – синтип *P. oceanodromae* USNM 205923, 40,5 мм; В – *P. oceanodromae*, по. 1 (радула на Рис. 22 А-В, анатомия на Рис. 21), С – синтип *P. olivaceus* SMNH-3852, 40 мм; D – *P. olivaceus* № 2 (радула на Рис. 22 D, анатомия на Рис. 23), E – *P. olivaceus* № 1 (радула на Рис. 22 C), F – *P. torquatus* № 1 (радула на Рис. 22 E-F, анатомия на Рис. 24). Все раковины в одном масштабе.

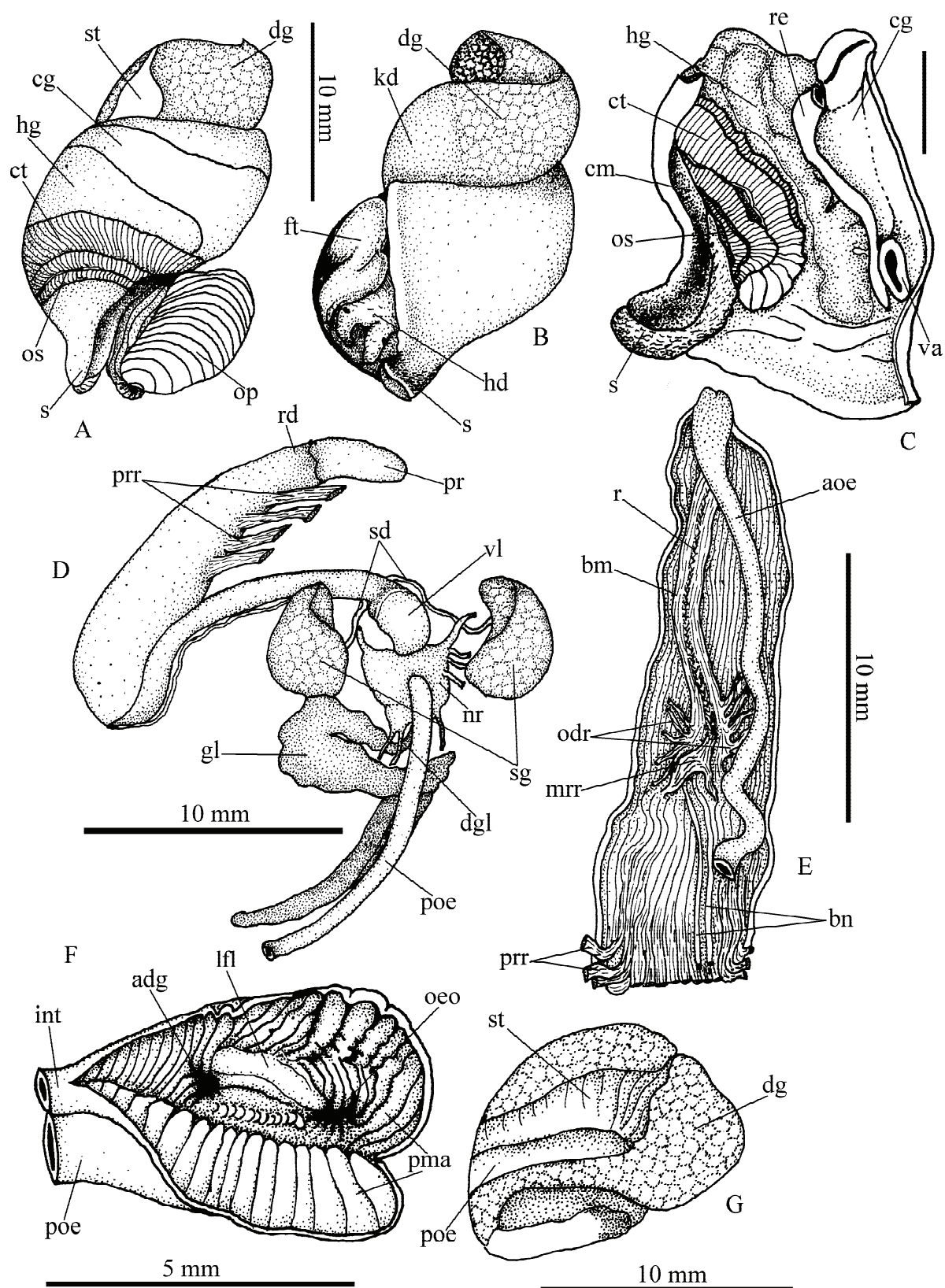


FIG. 21. Anatomy of *Plicifusus oceanodromae* no. 1 (shell on Fig. 20 B, radula on Fig. 22 A-B). A – soft body, ventral view; B – soft body, dorsal view; C – mantle; D – foregut; E – proboscis, opened dorsally; F – opened stomach; G – stomach, general view.

РИС. 21. Анатомия *Plicifusus oceanodromae* № 1 (раковина на Рис. 20 B, радула на Рис. 22 A-B). А – мягкое тело, вид с вентральной стороны; В – мягкое тело, вид с дорзальной стороны; С – мантия; D – передний отдел пищеварительной системы; E – хобот, вскрытый с дорзальной стороны; F – вскрытый желудок; G – общий вид желудка.

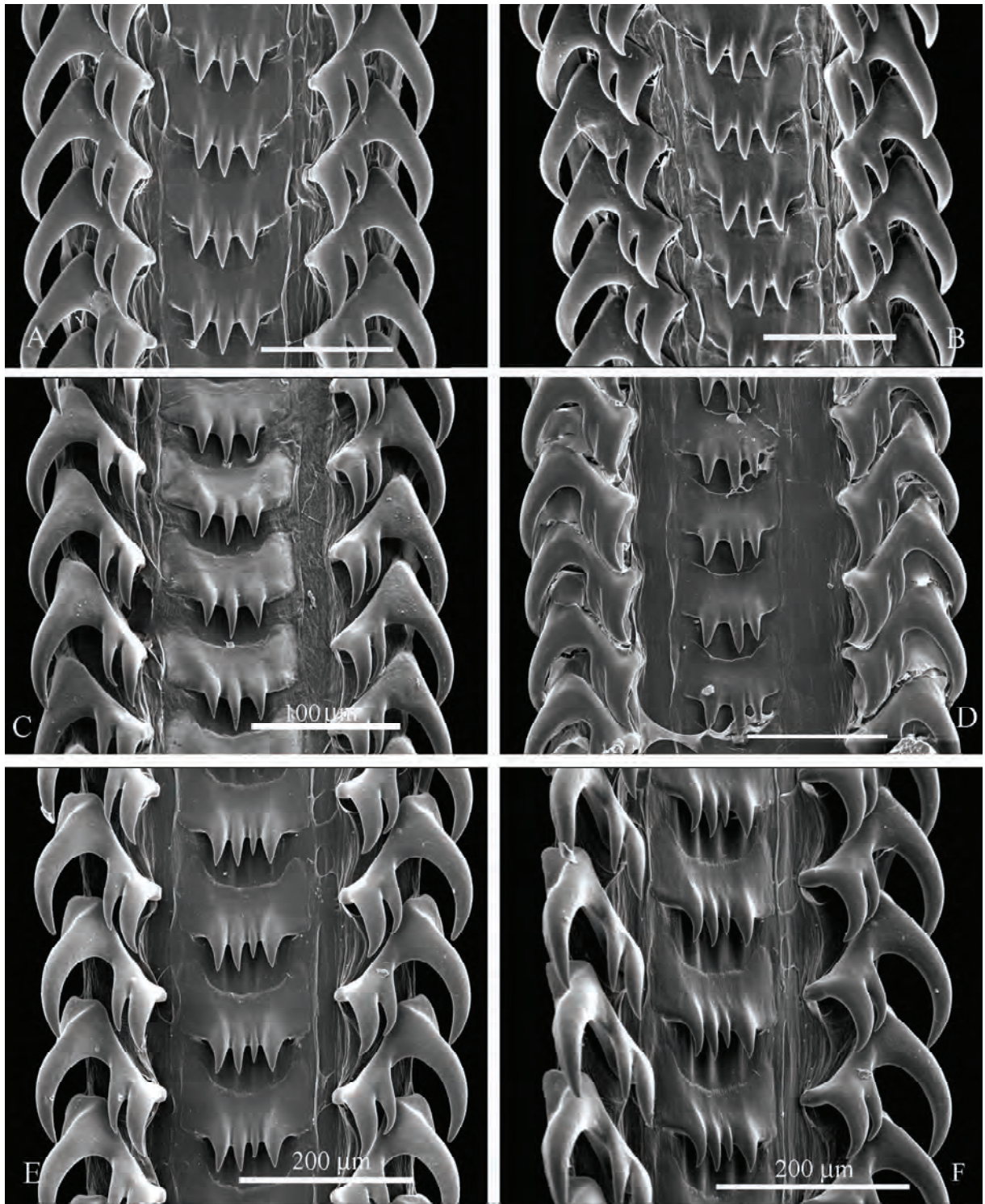


FIG. 22. Radulae of *Plicifusus*: A – dorsal and B – lateral view of *P. oceanodromae* no. 1 (shell on Fig. 20 B, anatomy on Fig. 21); C – dorsal view of *P. olivaceus* no. 1 (shell on Fig. 20 E); D – dorsal view of *P. olivaceus* no. 2 (shell on Fig. 20 D, anatomy on Fig. 23); E – dorsal and F – lateral view of *P. torquatus* no. 1 (shell on Fig. 20 F, anatomy on Fig. 24).

РИС. 22. Радулы *Plicifusus*: А – вид сверху и В – сбоку *P. oceanodromae* № 1 (раковина на Рис. 20 В, анатомия на Рис. 21); С – вид сверху *P. olivaceus* № 1 (раковина на Рис. 20 Е); D – вид сверху *P. olivaceus* № 2 (раковина на Рис. 20 D, анатомия на Рис. 23); Е – вид сверху и F – сбоку *P. torquatus* № 1 (раковина на Рис. 20 F, анатомия на Рис. 24).

50°12'N, 156°35'E, 312 m, 26.06.1988 (specimen **no. 2** dissected). IBM 4733, R/V *Lebed*, sta. 114, 280-301 m, transect from Lopatka cape, around 50°51'53"N, 156°39'54"E, pebble with sand, 22.07.1954.

Description. *Shell* (Fig. 20 C-D, F) broad fusiform, stout, with moderately convex whorls and attenuated short, nearly straight canal. Aperture elongate oval. Axial sculpture of closely spaced, narrow, low, slightly arcuate, nearly opisthocline axial ribs, more than 20 on last whorl. Spiral sculpture of well pronounced flattened to slightly rounded on top spiral cords (to 15 on the penultimate whorl), separated by deep grooves. Secondary shallow grooves can be present on some cords. Periostracum light beige, peeling. Measurements: **no. 1.** H 29 mm, h 21 mm, AL 15.1 mm; **no. 2.** H 43.5 mm, AL 21.2 mm.

Soft body. Mantle spans one whorl, kidney – 0.25, digestive gland and gonad – rest of visceral mass (Fig. 23 A-B). Head short, with long thick tentacles (Fig. 23A, **hd**). Foot contracted, folded transversely, with narrow propodium separated by deep propodial groove, operculum oval with terminal nucleus. Penis long and narrow, bearing pointed seminal papilla, surrounded by circular fold (Fig. 23E). Mantle length slightly exceeds width (Fig. 23C); siphon short. Osphradium and ctenidium of similar width, osphradium length 0.6 of ctenidium. Hypobranchial gland forms distinct folds. Rectum narrow, opens at mid-length of mantle, lacking papilla.

Digestive system. Proboscis completely inverted into rhynchodaeum. Proboscis retractors numerous, originate in proboscis wall, follow along rhynchodaeum to join the roof of body haemocoel (Fig. 23F, **pr**). **Radula** of **no. 1** (Fig. 22C) 6.5 mm long and 250 µm wide (1.66% AL), of 86 rows of teeth, 13 nascent. Central tooth tricuspid with median cusp slightly longer than marginal cusps. Lateral cusps tricuspid, with nearly equal inner and median cusps. Radula of **no. 2** (Fig. 22D) 8.1 mm long and 500 µm wide (2.36% AL), of 91 rows of teeth, 15 nascent. Marginal cusps of rachidian slightly differ in length; median cusp of lateral teeth much shorter than inner cusp. Anterior oesophagus convoluted, followed by anterior aorta. Salivary glands not large, oval. Salivary ducts thin, strongly convoluted, following along anterior aorta (Fig. 23 F,I). Valve of Leiblein large, pyriform. Nerve ring large. Gland of Leiblein very long, with folded walls, not coiled, widened anteriorly. Duct of gland of Leiblein opens slightly posterior to nerve ring (Fig. 23F, **dgl**). Posterior oesophagus slightly wider than anterior, with longitudinal epithelial folds visible through its wall, strongly widens, approaching stomach and narrowing immediately before opening ventrally into stomach. **Stomach** spans ¼ of whorl (Fig. 23G). Posterior mixing area small, lined with tall oblique folds (Fig. 23H). Outer stomach wall lined with tall trans-

verse folds. Longitudinal fold on inner stomach wall follows from oesophageal opening to anterior duct of digestive gland, lined with low oblique folds (Fig. 23H, **lfl**). Upper part of inner stomach wall lined with tall transversal folds. Opening of anterior duct of digestive gland situated close to intestine, opening of posterior duct – above oesophageal opening.

Differential diagnosis. *P. olivaceus* is most similar to *P. oceanodromae*, for differences see the latter species.

Remarks. *Plicifusus incisus* was already synonymized with *Fusus olivaceus* by Sysoev and Kantor [2002]. Among our material one specimen significantly differs from others in less convex whorls and slower growing whorls diameter, but most of all in strongly attenuated siphon, markedly curved to the left. Kantor and Sysoev [2006] illustrated this specimen (plate 101 F) and admitted the possibility that it may belong to separate, still unnamed species. Anatomically it appeared to be similar to other examined specimen of *P. olivaceus*, that is conchologically close to typical specimens. Therefore pending obtaining additional material we still consider it as a deviant form of *P. olivaceus*.

Plicifusus torquatus (Petrov, 1982) (Figs. 1, 20 E, 22 E-F, 24)

Quasisipho torquatus Petrov, 1982: 43, pl. 3, Figs. 3-13.

Plicifusus torquatus. – Fraussen, Jakubzik, 2000. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 198, pl. 101 M.

Holotype: Geological Institute of Russian Ac. Sci., Moscow 3829/5-3.

Type locality – eastern Kamchatka, late Pliocene – early Pleistocene.

Distribution – the Sea of Okhotsk, Northern Kurile Islands, Eastern Kamchatka, 142 m (Fig. 1).

Material examined: 1 lot with 20 spms. IO, northern Sea of Okhotsk, R/V *Vityaz*, sta. 1866, 57°49.7'N, 141°53.6'E, 142 m, 20.10.1952 (specimen **no. 1** dissected).

Description. *Shell* (Fig. 20 E) broad fusiform, stout, with poorly convex whorl and strong subsutural rim. Canal slightly attenuated, short and broad, nearly straight. Aperture broadly ovate. Axial sculpture of orthocline arcuate axial ribs, becoming obsolete on periphery of last whorl and lower part of spire whorls. Ribs most pronounced on subsutural rim where they form large nodes. Up to 15 folds on last whorl. Spiral sculpture of well pronounced, closely spaced flattened cords, up to 20 on penultimate whorl. Periostracum light-brown to dark-olive. Measurements: **no. 1:** H 35 mm, h 25.5 mm, AL 30 mm. Juvenile female.

Soft body (Fig. 24): mantle spans one whorl, kidney – 0.25, digestive gland and gonad rest of

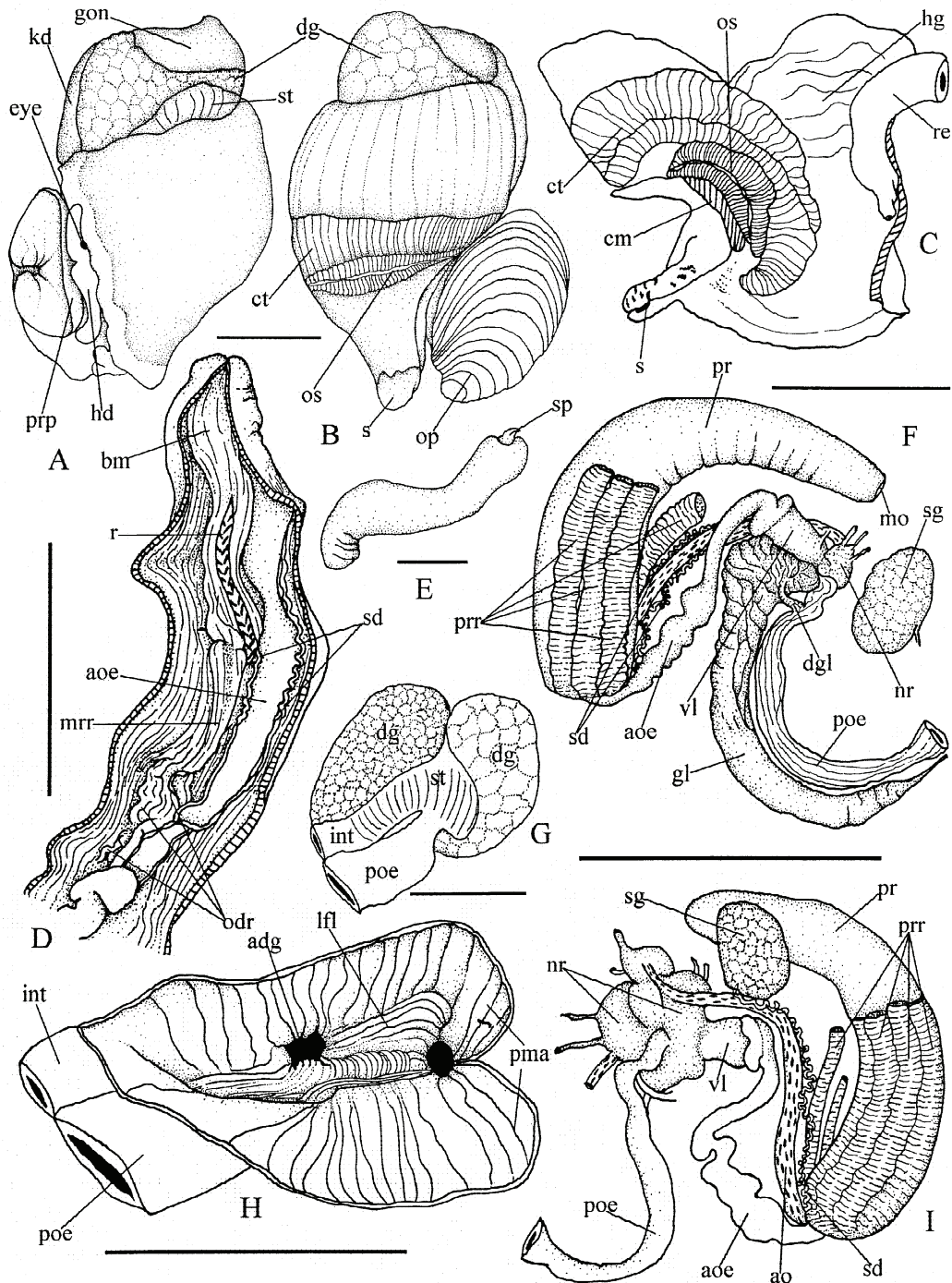


FIG. 23. Anatomy of *Plicifusus olivaceus* no. 2 (shell on Fig. 20D, radula on Fig. 22D). A – soft body, dorsal view; B – soft body, ventral view; C – mantle; D – proboscis, opened dorsally; E – penis; F – foregut, right view; G – stomach, general view; H – opened stomach; I – foregut, left view. Scale bar – 5 mm.

РИС. 23. Анатомия *Plicifusus olivaceus* № 2 (раковина на Рис. 20D, радула на Рис. 22D). А – мягкое тело, вид с дорзальной стороны; В – мягкое тело, вид с вентральной стороны; С – мантия; D – хобот, вскрытый с дорзальной стороны; E – пенис; F – передний отдел пищеварительной системы, вид справа; G – общий вид желудка; H – вскрытый желудок; I – передний отдел пищеварительной системы, вид слева. Длина масштабного отрезка – 5 мм.

visceral mass. **Head** short and broad (Fig. 24B, **hd**), with very thick contracted tentacles. Black eyes on small distinct lobes at tentacles base. Foot folded transversely, with rather wide propodium (**prp**) and

deep propodial groove (**prpg**). Operculum oval, with terminal nucleus. **Mantle** length equals its width (Fig. 24C). Ctenidium 0.8 mantle length and 0.3 mantle width, osphradium 0.6 length and 0.5 width

of ctenidium. Hypobranchial gland of sinuous folds. Rectum opens at mid-length of mantle.

Digestive system. Proboscis partly inverted in rhynchodaeum. Numerous proboscis retractors situated on both sides of rhynchodaeum (Fig. 24 D-E, **pr**). Multiple odontophoral retractors originate at base of buccal mass, attaching to proboscis wall (Fig. 24F). **Radula** 380 μ m wide (1.27% AL), of 78 transverse rows of teeth, 6 nascent (Fig. 22 E-F). Central tooth with four unequal cusps. Lateral teeth tricuspid, with shortest median cusp. Median radular retractor (Fig. 24F, **mrr**) originates at base of radula sac and attached to rhynchodaeum slightly behind its transition into proboscis wall. Salivary glands small, oval, salivary ducts strongly coiled. Valve of Leiblein elongated, pyriform, followed by nerve ring. Posterior oesophagus widens in its distal part approaching stomach. Gland of Leiblein (**gl**) long and narrow, opening by short duct shortly behind nerve ring. **Stomach** spans $\frac{1}{4}$ of whorl (Fig. 24H). Posterior mixing area very small. Outer stomach wall lined with tall transverse folds (Fig. 24G). Longitudinal fold on inner stomach wall (**lfl**) lined with low oblique folds, rest of inner stomach wall – with low transversal folds. Opening of posterior duct of digestive gland (**pdg**) large, situated near oesophageal opening. Opening of anterior duct (**adg**) at $\frac{1}{3}$ of stomach length from intestine; two well developed typhlosoles (**tfl**) follow from duct to intestine.

Differential diagnosis. The species is rather uniform in shell characters and can be easily distinguished from other species of the genus by characteristic well pronounced subsutural rims and axial ribs, forming crown of nodes on the rim. The surface of all studied shells was covered by *Hydractinia* (Hydrozoa).

Excluded species:

Plicifusus laticordatus (Dall, 1907)

Tritonofusus (*Plicifusus*) *aurantius* var. *laticordatus* Dall, 1907: 161.

Chrysodomus laticaudatus (misspelling) – Dall, 1916: 8. – Dall, 1918: 221.

Plicifusus laticordatus. – Dall, 1925: 25, pl. 1, fig. 4.

Type locality: Bristol Bay, Alaska, R/V *Albatross*, sta. 3279, 56°25'40"N, 162°39'15"W, 41 fms.

Syntype: USNM 122664.

Distribution: Bering Sea [Dall, 1907].

Remarks. The species is characterized by “deeply orange-tinted shell, with four whorls, strongly recurved, short canal, but with the spirals about twice as wide as in the type, flat above and with distinctly channeled interspaces in which the incremental lines are strong” [Dall, 1907, p. 161]. The species has never been referred since Dall’s de-

scription. Types lack axial ribs on the shell, therefore we exclude the species from the genus *Plicifusus*. It is the type species of *Plicifusus* (*Helicofusus*) Dall, 1916. Two other species were referred to this genus: *Tritonofusus* (*Plicifusus*) *rhyssus* Dall, 1907, which is here transferred to *Plicifusus* and *Helicofusus luridus* Golikov in Golikov et Scarlato, 1985, which was considered as a junior synonym of *Latisipho hallii* (Dall, 1873) [Kosyan, 2006a]. Since neither anatomy, nor radula of *P. laticordatus* are known, the status of *Helicofusus* remains unclear.

Plicifusus parvus Tiba, 1980

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.

Type locality: Sakhalin.

Holotype: IMT-80-17.

Distribution: the East Siberian and Bering seas, the Sea of Okhotsk, the Sea of Japan, Kamchanka, Sakhalin Island, 42-400 m.

Remark. The species is a junior synonym of *Retifusus roseus* (Dall, 1877) [Kosyan, 2007; Kosyan, Kantor, 2009].

Plicifusus saginatus Tiba, 1980

Tiba, 1980: 49, pl. 13, figs. 1-7. – Tiba, Kosuge, 1980: 25-26. – Kantor, Sysoev, 2005: 138. – Kantor, Sysoev, 2006: 197-198, pl. 100 J-K.

Type locality: Sakhalin.

Holotype: IMT-80-42.

Distribution: the East Siberian and Bering seas, the Sea of Okhotsk, the Sea of Japan, Kamchanka, Sakhalin Island, 42-400 m.

Remark. The species is a junior synonym of *Retifusus roseus* (Dall, 1877) [Kosyan, 2007; Kosyan, Kantor, 2009].

Discussion

Composition of the genus

In the result of current revision we recognize 13 valid species of the genus:

Plicifusus kroeyeri (Møller, 1842) – circumpolar, the Bering Sea and the Sea of Okhotsk, eastern coast of Kamchatka, Kurile Islands, western and northern part of the Sea of Japan, 0-225 m;

Plicifusus bambusa Tiba, 1980 – Hokkaido, ?Kurile Islands;

Plicifusus maehirai Tiba, 1980 – northern part of the Sea of Japan, Southern Kurile Islands, the Sea of Okhotsk, Eastern Kamchatka; 25-200 m;

Plicifusus scissuratus (Dall, 1918) – Hokkaido, Southern Kurile Islands, 49-400 m;

Plicifusus elaeodes (Dall, 1907) – the Sea of

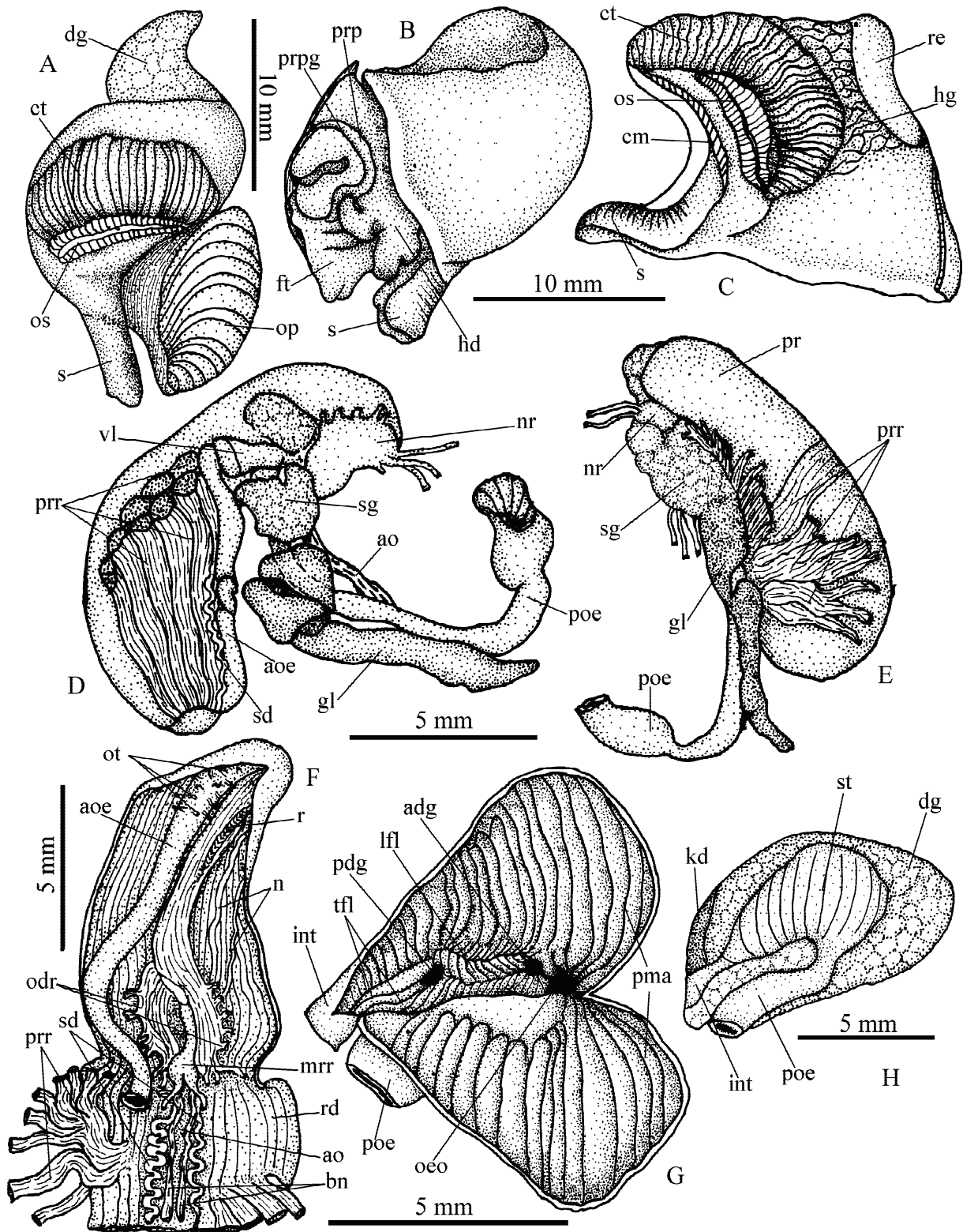


FIG. 24. Anatomy of *Plicifusus torquatus* no. 1 (shell on Fig. 20 F, radula on Fig. 22 E-F). A – soft body, ventral view; B – soft body, dorsal view; C – mantle; D – foregut, right view; E – foregut, dorso-lateral left view; F – proboscis, opened dorsally; G – opened stomach; H – stomach, general view.

РИС. 24. Анатомия *Plicifusus torquatus* № 1 (раковина на Рис. 20 F, радула на Рис. 22 E-F). А – мягкое тело, вид с вентральной стороны; В – мягкое тело, вид с дорзальной стороны; С – мантия; D – передний отдел пищеварительной системы, вид справа; E – передний отдел пищеварительной системы, дорзо-латеральный вид слева; F – хобот, вскрытый с дорзальной стороны; G – вскрытый желудок; H – общий вид желудка.

Okhotsk, Sakhalin, Southern Kurile Islands, Kamchatka, northern part of the Sea of Japan, 80-500 m;

Plicifusus croceus (Dall, 1907) – northern part of the Sea of Japan, Okhotsk Sea, 150-700 m;

Plicifusus hastarius Tiba, 1980 – Kurile Islands, Pacific coast of Japan, 7-100 m;

Plicifusus johanseni Dall, 1919 – Alaska;

Plicifusus levis Tiba, 1980 – northeastern Honshu, 200-300 m;

Plicifusus rhyssus (Dall, 1907) – the Bering Sea, the Sea of Okhotsk, northern part of the Sea of Japan; eastern coast of Japan, 52-500 m;

Plicifusus oceanodromae Dall, 1919 – the Sea of Okhotsk, Eastern Kamchatka, Aleutian Islands, 129-180 m;

Plicifusus olivaceus (Aurivillius, 1885) – the Bering Sea, Eastern Kamchatka, North Kurile Islands, 103-318 m;

Plicifusus torquatus (Petrov, 1982) – the Sea of Okhotsk, North Kurile Islands, Eastern Kamchatka, 140 m.

Majority of species are Pacific boreal ones, except single broadly distributed *Plicifusus kroeyeri*, that is circumpolar and reaches the Sea of Japan in the Pacific. Protoconch of the species [illustrated by Bouchet, Warén, 1985: fig. 633] suggests direct development, as in other cold-water Buccinidae. Therefore the extremely broad distribution of *P. kroeyeri* may indicate the presence of a complex of conchologically similar species. Future studies with use of molecular techniques might probably resolve this problem. Nevertheless at the moment we are not able to demonstrate clear distinctions between Arctic, north Atlantic and Pacific specimens and consider *P. kroeyeri* as a single highly variable species.

The single Recent species described originally from fossil material – *Quasisipho torquatus* Petrov, 1982 from upper Pliocene-lower Pleistocene of eastern Kamchatka [Petrov, 1982]. Petrov established a monotypical genus for it. Later the species was found in Recent fauna and its anatomy confirms that the species belongs to *Plicifusus*.

Conchological variability of *Plicifusus* and comparison with other genera of Colinae

Anatomical characters can hardly be used for species differentiation in Buccinidae, although together with conchological characters, they are applicable on generic level [Kosyan, Kantor, 2009].

The species of *Plicifusus* are rather well defined conchologically due to possession of more or less well pronounced numerous axial ribs together with fusiform or elongate fusiform shell. Axial sculpture is most variable in terms of the degree of development of axial ribs (within species they can be nearly obsolete to well defined, e.g. in *P. rhyssus*), and in

number of ribs per whorl. Spiral sculpture is more conservative, and not very variable in *Plicifusus*. Two main types can be defined – thin sinuous cords or rather riblets (*P. kroeyeri*, *P. rhyssus*) or more or less equal in width flattened broader ribs (most of species), sometimes with secondary striation.

Still the species differentiation is based mostly on shell characters, subjected to rather high intraspecific variability. Besides few well defined and easily recognizable species (*P. rhyssus* and *P. torquatus*), it is still difficult to prove the validity of some species within the current morphological/conchological paradigm. The situation is worsened by the fact, that many species are rather rare and it is impossible to ascertain confidently the degree of intraspecific variability. Alternative methods, such as molecular phylogeny, probably could help to resolve the problem, but there are no properly fixed specimens. Therefore we generally accepted conservative “valid until proved otherwise” concept.

Most of species were described within (sub)genus *Plicifusus*, few in *Retifusus*. The genus *Retifusus* is the most similar conchologically, and some species considered here as *Plicifusus* were attributed to *Retifusus* by different authors [e.g. Golikov *et al.*, 2001; Kantor, Sysoev, 2006]. Generally, species of *Retifusus* have pronounced axial ribs, although the siphonal canal is usually more attenuated and recurved, while species attain smaller adult sizes. Both genera can be reliably differentiated by the radular anatomy. In *Retifusus* lateral teeth have similar size of all cusps (in *Plicifusus* central cusp(s) is always shorter) and central teeth are multicuspid [Kosyan, 2007].

Other genera of Colinae do not have characteristic axial ribs and can not be confused with *Plicifusus*.

Anatomy and its variability in *Plicifusus*

The anatomy of the soft body is rather uniform throughout the genus. Small variations are observed in number and length of radula cusps (more than three cusps may appear on central and lateral teeth, median cusp of rachidian may be longer or shorter than marginal ones); size and shape of salivary glands (small to large, separated or fused); thickness and shape of salivary ducts (more or less convoluted, thin or thick), size of posterior mixing area (small or medium-sized), and relative sizes of pallial organs (wider or narrower, shorter or longer osphradium comparing to ctenidium) (Table 1).

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References

- Adams A., 1863. On the species of Fusidae which inhabit the seas of Japan. *Journal of the proceedings of the Linnean Society of London, Zoology*, 7: 105-108.
- Alexeev D.O., 2003. *Gastropod seashells of Russia*. VNIRO Publishing, Moscow, 254 p.
- Anonymous, 2001. Transfer of the holotypes. *Bulletin of the Institute of Malacology of Tokyo*, 3(8): 130.
- Aurivillius C. W. S., 1885. Översigt öfver de af Vega-Expeditionen insamlade arktiska Hafsmollusker. II. Placophora och Gastropoda. *Vega-Expeditionens Vetenskapliga Jakffagelser*, Stockholm, IV: 313-383, 2 Taf.
- Bouchet P., Warén A. 1985. Revision of the northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). *Bollettino Malacologico*, Supplement 1: 121-296.
- Dall W. H., 1902. Illustrations and descriptions of new, unfigured or imperfectly known shells, chiefly American, in the U. S. National Museum. *Proceedings of the United States National Museum*, 24(1264): 499-566, pls. 27-40.
- Dall W. H., 1907. Descriptions of new species of shells, chiefly Buccinidae, from dredging of the U.S.S. "Albatross" during 1906, in the northwestern Pacific, Bering, Okhotsk, and Japanese Seas. *Smithsonian Miscellaneous Collections*, 50, part 2, no. 1727: 139-173.
- Dall W. H., 1916. Prodrome of a revision of the chrysodomoid whelks of the boreal and arctic regions. *Proceedings of the Biological Society of Washington*, 29: 7-8.
- Dall W. H., 1918. Notes on *Chrysodomus* and other mollusks from the North Pacific Ocean. *Proceedings of the United States National Museum*, 54: 207-234.
- Dall W. H., 1919a. Descriptions of new species of Mollusca from the North Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum*, 54(2295): 293-371.
- Dall W. H. 1919b. The Mollusca of the Arctic Coast of America collected by the Canadian Arctic Expedition west from Bathurst Inlet with an Appended Report on a Collection of Pleistocene Fossil Mollusca. *Report of the Canadian Arctic Expedition*. 8(a): 4a, 6a, 9a, 21a, pl. 3.
- Dall W. H., 1921. Summary of the marine shell-bearing mollusks of the Northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species. *United States National Museum Bulletin*, 112: 1-217.
- Dall W. H., 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum. *Proceedings of the United States National Museum*, 66(2554): 1-41, pls. 1-36.
- Fraussen K., Jakubzik H., 2000. The discovery of living specimens of *Quasisipho torquatus* Petrov, 1982 (Gastropoda, Buccinidae), and its transfer to the genus *Plicifusus* Dall, 1902. *Novapex*, 1(1): 29-31.
- Fraussen K., Terryn Y., 2007. *A Conchological Iconography. The Family Buccinidae. Genus Neptunea*. ConchBooks, 319 p.
- Galkin Yu.I., Scarlato O.A., 1955. Gastropod mollusks – Gastropoda. In: Strelkov A.A., ed. *Atlas of invertebrates of Far Eastern seas of USSR*. Published by Academy of Science of USSR. Moscow-Leningrad: 167-175 [In Russian].
- Golikov A.N., 1963. Gastropod mollusks of the genus *Neptunea* Bolten. *Fauna of USSR. Mollusks*. Leningrad: Nauka, 5(1): 1-218 [In Russian].
- Golikov A.N., 1980. Mollusks Buccininae of the World Ocean. *Fauna of USSR, Mollusks*. Leningrad, Nauka, 5(2): 1-466. [In Russian].
- Golikov A.N., Gulbin V.V., 1977. Gastropod prosobranch mollusks (Gastropoda, Prosobranchiata) of shelf of Kurile Islands. II Orders Hamiglossa – Homoestrophia. In: *Fauna of coastal zones of Kurile Islands*. M.: Nauka: 172-268. [In Russian].
- Golikov A.N., Scarlato O.A., 1967. Mollusks of the Posiet Bay (Sea of Japan) and their ecology. *Molluscs and their role in biocenosis and fauna formation. Trudy Zoologicheskogo Instituta ANSSSR*, 42: 5-154 [In Russian].
- Golikov A.N., Scarlato O.A., 1985. Shell-bearing gastropod and bivalve mollusks of the shelf of southern Sakhalin and their ecology. In: *Biocenoses and fauna of the shelf of south Sakhalin. Issledovaniya Fauny Morei*, 30(38): 360-487. [In Russian].
- Golikov A.N., Sirenko B.I., Gulbin V.V., Chaban E.M., 2001. Checklist of shell-bearing gastropods of the northwestern Pacific. *Ruthenica*, 11(2): 153-174.
- Goryachev V. N., 1978. *Gastropod mollusks of the genus Neptunea Röding from the Bering Sea*. Moscow, Nauka, 90 p. [In Russian].
- Habe T., 1965. *Shells of the Western Pacific in color*. 2. Hoikusha, Osaka, 233 p.
- Hayashi S., 2005. The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the complete mitochondrial 16S rRNA gene sequences of selected representatives. *Molluscan Research*, 25(2): 85-98.
- Higo S., Callomon P., Goto Y. 1999. *Catalogue and bibliography of the marine shell-bearing Mollusca of Japan*. Elle Scientific Publications, Osaka, 749 p.
- Kantor 1990. *Gastropod mollusks of the World Ocean: subfamily Volutopsiinae*. Moscow, Nauka, 178 p. [In Russian].
- Kantor Yu.I., Sysoev A.V., 2005. *Catalogue of mollusks of Russia and adjacent countries*. KMK Scientific Press Ltd. Moscow, 627 p. [In Russian].
- Kantor Yu.I., Sysoev A.V., 2006. *Catalogue of mollusks of Russia and adjacent countries*. KMK Scientific Press Ltd. Moscow, 372 p., 140 tables.
- Kosyan A.R., 2006a. Anatomy and taxonomic composition of the genus *Latisipho* Dall (Gastropoda: Buccinidae) from the Russian waters. *Ruthenica*, 16(1-2): 17-42.

- Kosyan A.R., 2006b. Two new species of the genus *Pararetifusus* Kosuge, 1967 (Buccinidae: Colinae), with notes on the morphology of *Pararetifusus tenuis* (Okutani, 1966). *Ruthenica*, 16(1-2): 5-15.
- Kosyan A.R. 2007. *Morphology and taxonomy of the gastropods of the subfamily Colinae Neogastropoda: Buccinidae of the Far-East seas of Russia*. PhD dissertation. A.N.Severtzov Institute of Ecology and Evolution, Russian Ac. Sci., Moscow, 223 p. [In Russian].
- Kosyan A.R., Kantor Yu. I. 2009. Phylogenetic analysis of the subfamily Colinae (Neogastropoda: Buccinidae) based on morphological characters. *The Nautilus*, 123(3): 83-94.
- Kosyan A.R., Modica M.V., Oliverio M. 2009. The anatomy and relationships of *Troschelia* (Neogastropoda: Buccinidae): New evidence for a closer fasciolarid-buccinid relationship? *The Nautilus*, 123(3): 95-105.
- Matsukuma A., Okutani T., Habe T., 1991. *World sea-shells of rarity and beauty*. National Science Museum, Tokyo, 206 p.
- Møller H. P. C., 1842. Index Molluscorum Groenlandia. *Naturhistorisk Tidsskrift*, 4(1): 76-97.
- Mörch O.A.L., 1869. Catalogue des mollusques du Spitzberg recueillis par le Dr H. Kroyer pendant le voyage de la corvette La Recherche en juin 1838. *Mémoires de la Société malacologique de Belgique*, 4: 7-32.
- Okutani T. (Ed.), 2000. *Marine molluscs of Japan*. Tokai University Press, 1173 p.
- Okutani T., Tagawa M., Horikawa H., 1988. *Gastropods from continental shelf and slope around Japan*. Japan Fisheries Resource Conservation Association, 204 p, 160 pls.
- Petrov O.M., 1982. Marine mollusks of Quaternary of the Northern Pacific. *Trudy Instituta Geologii Akademii Nauk SSSR*, 357: 1-144 p. [In Russian].
- Philippi R. A., 1850. *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien*, 3. Cassel, T. Fischer, 138 pp.
- Tiba R., 1973. Descriptions of two new species of the genus *Colus* (Buccinidae). *Venus* (32)3: 65-69.
- Tiba R., 1980a. Descriptions of four new species of the genus *Plicifusus* (Buccinidae, Gastropoda). *Bulletin of the Institute of Malacology, Tokyo*, 1(3): 47-50, pl. 11-13.
- Tiba R., 1980b. Descriptions of a new species of the genus *Colus* and two new species of the genus *Plicifusus* (Buccinidae, Gastropoda) from the Northern Pacific Ocean. *Bulletin of the Institute of Malacology, Tokyo*, 1(5): 74-76, pl. 21-23.
- Tiba R., Kosuge S., 1980. North Pacific shells. 7. Genus *Plicifusus* Dall, 1902. *Occasional Publication of the Institute of Malacology of Tokyo*, 36 p.
- Tryon G. W. 1881. *Manual of Conchology*. 3. Philadelphia, 310 pp., 87 pls.

Ревизия рода *Plicifusus* Dall, 1902 (Gastropoda: Buccinidae)

А.Р. КОСЬЯН, Ю.И. КАНТОР

Институт проблем экологии и эволюции им. А.Н.Северцова РАН, Ленинский проспект 33, Москва 119071, РОССИЯ

РЕЗЮМЕ. С использованием анатомических данных проведена ревизия рода *Plicifusus* Dall, 1902. В состав рода включены 13 валидных рецентных видов, для 9 из них приведены подробные анатомические описания. 4 названия сведены в синонимы: *P. obtusatus* Golikov, 1985 = *Plicifusus maehirai* Tiba, 1980; *Colus okhotskana* Tiba, 1973 = *Plicifusus elaeodes* (Dall, 1907); *Tritonofusus (Plicifusus) aurantius* Dall, 1907 и *Plicifusus (Aulacofusus) rhyssoides* Dall, 1918 = *Plicifusus rhyssus* (Dall, 1907). *Plicifusus parvus*, Tiba, 1980 и *Plicifusus saginatus* Tiba, 1980 сведены в синонимы *Retifusus roseus* (Dall, 1877). *Plicifusus laticordatus* (Dall, 1902) исключен из состава рода *Plicifusus*.

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