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

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**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 obscuratus* Golikov, 1985 = *Plicifusus maehirai* Tiba, 1980; *Colus okhotskana* Tiba, 1973 = *Plicifusus elaeodes* (Dall, 1907); *Tritonofusus* (Plicifusus) *aurantis* Dall, 1907 and *Plicifusus* (Aulacofusus) *rhysoides* Dall, 1918 = *Plicifusus rhysys* (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 of gastropods 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; cm2 – outer layer of circular muscle fibers; cm1 – 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; **lf** – longitudinal fold on the inner stomach wall; **lm1** – outer layer of longitudinal muscle fibers; **lm2** – inner layer of longitudinal muscle fibers; **lm** – lateral protractor of radula; **lt** – longitudinal folds on the inner stomach wall; **mo** – mouth opening; **mrr** – median radial retractor muscle; **n** – nerves; **nd** – nephridial duct; **nr** – nerve ring; **odr** – odontophoral retractor muscles; **ooe** – oesophageal opening; **op** – operculum; **os** – oesophagus; **ot** – oesophageal teeth; **p** – penis; **pdg** – opening of posterior duct of digestive gland; **pmu** – posterior mixing area; **poe** – posterior oesophagus; **pr** – proboscis; **prpp** – propodium; **prpg** – propodal groove; **prr** – proboscis retractors; **pw** – proboscis wall; **r** – radula; **rd** – rhynchodaenum; **re** – rectum; **ro** – siphon; **sd** – salivary duct; **sg** – salivary gland; **so** – male orifice; **sp** – seminal papilla; **st** – stomach; **sv** – siphonal valve; **tfl** – typhlosole; **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 Academy of Sciences, Moscow, Russia;
- NMC – National Museums of Canada;
- SMNH – Swedish Museum of Natural History, Stockholm, Sweden;
- SS – 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 Bucinidae Rafinesque, 1815**

**Subfamily Collinae Gray, 1857**

**Genus Plicifusus** Dall, 1902


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

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

**Type species:** *Fusus kroyeri* Möller, 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. Latereal 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 kroyeri** (Moller, 1842)  (Figs. 1, 2, 3 A-D, 4-7)

*Fusus kroyeri* Möller, 1842: 88.

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

*Sipho plicatus* A. Adams, 1863: 107.

*Fusus* (Tritonofusus) *kroyeri* var. major, pumila Mörch, 1869: 19.

*Fusus kroyeri* var. grossesstriata Aurivillius, 1885: 360.

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

*Plicifusus* kroyeri. – Dall, 1921: 92. – Galkin, Skarlato, 1955: 176, pl. XLVI, Fig. 3. – 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.


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

**Type localities:** *Fusus kroyeri* – 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*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Shell length</th>
<th>AL/H mean</th>
<th>D/H mean</th>
<th>Spiral sculpture</th>
<th>Axial sculpture</th>
<th>Salivary glands</th>
<th>Salivary ducts</th>
<th>Radula</th>
<th>Width / AL, %</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. kroeyeri</em> (41)</td>
<td>25-90</td>
<td>0.48</td>
<td>0.40</td>
<td>To 60 inconspicuous ribs</td>
<td>11-26</td>
<td>Medium-sized, separate</td>
<td>Thin, convoluted</td>
<td>3:3:3</td>
<td>1.33-1.46</td>
</tr>
<tr>
<td><em>P. bambusa</em> (8)</td>
<td>75-94</td>
<td>0.45</td>
<td>0.46</td>
<td>Multiple small ribs, abraded</td>
<td>To 16 S-shaped</td>
<td>Medium-sized, ventrally fused</td>
<td>Thin, convoluted</td>
<td>3:3:3</td>
<td>1.32</td>
</tr>
<tr>
<td><em>P. maehirai</em> (20)</td>
<td>32-64</td>
<td>0.42</td>
<td>0.42</td>
<td>~25 medium-expressed ribs</td>
<td>To 20, abraded</td>
<td>Small, rounded separate</td>
<td>Thick, convoluted</td>
<td>3:3:3</td>
<td>1.5</td>
</tr>
<tr>
<td><em>P. scissuratus</em> (10)</td>
<td>23-60</td>
<td>0.43</td>
<td>0.39</td>
<td>~20 ribs separated by deep grooves</td>
<td>About 14</td>
<td>Large, long, separate</td>
<td>Thin, convoluted</td>
<td>4:3:4</td>
<td>2.37-2.46</td>
</tr>
<tr>
<td><em>P. elaeodes</em> (8)</td>
<td>46-66</td>
<td>0.39</td>
<td>0.43</td>
<td>~30 small inconspicuous ribs</td>
<td>Low axial ribs/ incremental lines</td>
<td>Medium-sized, separate</td>
<td>Thick, convoluted</td>
<td>3:3:3</td>
<td>1.27</td>
</tr>
<tr>
<td><em>P. croceus</em> (2)</td>
<td>39-90</td>
<td>0.45</td>
<td>0.39</td>
<td>~25 flattened ribs</td>
<td>Ribs on last whorl obsolete</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>P. hastarius</em> (3)</td>
<td>56-88</td>
<td>0.32</td>
<td>0.37</td>
<td>Multiple spiral ribs</td>
<td>To 12 high S-curved</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>P. johanseni</em> (2)</td>
<td>52-53</td>
<td>0.48</td>
<td>0.38</td>
<td>~18 flattened ribs</td>
<td>Last whorl smooth</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>P. levis</em> (7)</td>
<td>22-32</td>
<td>0.51</td>
<td>0.45</td>
<td>absent</td>
<td>Most part of last whorl smooth</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>P. rhyssus</em> (10)</td>
<td>32-57</td>
<td>0.46</td>
<td>0.39</td>
<td>40-50 narrow ribs</td>
<td>12-16 more or less expressed</td>
<td>Large, sometimes fused ventrally</td>
<td>Thin, unevenly convoluted</td>
<td>3:3:3</td>
<td>1.77-2.42</td>
</tr>
<tr>
<td><em>P. oceanodromae</em> (3)</td>
<td>32-41</td>
<td>0.46</td>
<td>0.45</td>
<td>To 15 spiral ribs</td>
<td>To 20 frequent S-curved</td>
<td>Medium-sized, bean-shaped, separate</td>
<td>Thin, convoluted</td>
<td>3:3:3</td>
<td>1.83</td>
</tr>
<tr>
<td><em>P. olivaceus</em> (6)</td>
<td>28-43</td>
<td>0.51</td>
<td>0.49</td>
<td>~15 ribs separated by deep grooves</td>
<td>About 20 low orthocline</td>
<td>Medium-sized, oval, separate</td>
<td>Thin, convoluted</td>
<td>3:3:3</td>
<td>1.66-2.36</td>
</tr>
<tr>
<td><em>P. torquatus</em> (2)</td>
<td>30-40</td>
<td>0.46</td>
<td>0.5</td>
<td>To 20 spiral ribs</td>
<td>To 15</td>
<td>Small, rounded, separate</td>
<td>Thin, convoluted</td>
<td>3:4:3</td>
<td>1.27</td>
</tr>
</tbody>
</table>

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.
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
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**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.

**FIG. 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 µm 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 µm wide (1.45% AL). Central tooth with
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 \mu 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...
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 rhynchodaem to nerve ring. Proboscis retractors (Fig. 4 A,D, prr) 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 rhynchodaem 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-
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

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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*: A – вид сверху и B – сбоку, № 2 (раковина на Рис. 2 D, анатомия на Рис. 4), C – вид сверху и D – сбоку, № 1 (раковина на Рис. 2 B), E – вид сверху и F – сбоку, № 3 (раковина на Рис. 2 A).
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D-E); buccal mass spans less than half of proboscis length. Radula of no. 5 (Fig. 7 A-B) 400 µm 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 µm 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. 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 Г, радула на Рис. 7 С-Д). A – мягкое тело с вентральной и B – дорзальной сторон; C – мантя; D – передний отдел пищеварительной системы, вид справа; E – передний отдел пищеварительной системы, вид слева; F – хобот, вскрытый с дорзальной стороны; G – вскрытый желудок.
intestinal fold on inner stomach wall (ll) 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)


**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. Peristomal 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). 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 inversed into rhynchodaeum (Fig. 8 D,F,G). Buccal mass (Fig. 8H, bm) spans entire proboscis length. Numerous odontophoral retractor (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, prr). 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.

*Plicifusus maehirai* Tiba, 1980

(Figs. 1, 9 A-D, 10, 11 A-D)


**Types:** Holotype of *Plicifusus maehirai* – IMT-80-66 (Fig. 9A), holotype of *Plicifusus obtusatus* – ZIN 33732/1 (Fig. 9C).
Type localities: *Plicifusus maehirai* – off Kushiro, 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 Novoptyavlovski, st. 37D, 47°08’3N, 143°36’E, 146 m, mud, 23.09.1984. ZIN 58385, Sea of Okhotsk, R/V Poseidon, 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 Poseidon, 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 recurved to the left (Fig. 9 A-D). Aperture broad oval. Axial sculpture of closely spaced, curved, slightly to moderately prosoconine 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 rhynchodeaum 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 rhynchodeaum, 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 posterior 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. 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 plicatus* sensu Okutani, 2000: 465, pl. 231, fig. 61 (non *Sipho plicatus* A. Adams, 1863).


**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, 30.08.1948 (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 Е-Ф, анатомия на Рис. 12); F – *P. scissuratus* № 4, 23 мм (радула на Рис. 11 G-Н); 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 B, радула на Рис. 11 C-D). A – голова и передняя часть висцерального мешка; B – мягкое тело, вид с вентральной стороны; C – мантля; D – передний отдел пищеварительной системы, вид справа; E – передний отдел пищеварительной системы, вид слева, слюнные железы удалены; F – желудок, общий вид; G – вскрытый желудок; H – пенис № 3; I – хобот, вскрытый с дорзальной 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).
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.

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 siphalonal valve. Ctenidium spans 0.8 mantle length, oesophagus – 0.3. Ctenidium more than twice broader than oesophagus. Rectum terminates at mantle mid-length. Hypobranchial gland indistinct.

Dietary. 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, odtr) 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 haemocoele. 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-pyiform, 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) elaeoides Dall, 1907: 159-160.

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

Type localities: Tritonofusus (Plicifusus) elaeoides – 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, bionecosis 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,
closely spaced orthocline to slightly opisthoclinc axial ribs, often smoothed to nearly obsolete on last whorl and inconspicuous on whors 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
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 (prr) attach to bottom and lateral walls of body haemocoel. **Radu-**
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 (III) 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.


**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, which have very characteristic shell shape with strongly attenuated nearly straight canal. Conchologically it is somewhat similar to *Plicibuccinum declivis* (Habe et Ito, 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 Warin [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)


**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-
Revision of *Plicifusus* (Gastropoda: Buccinidae) 77

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.  


**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; *P. wakasanus* – Wakasa (Bay), Sea of Japan; *P. aurantisus* – Sea of Japan, USFC sta. 4982, 43°N, 140°10’30”E, 390-428 fms; *P. 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*, st. 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 periostracum color. It may be considered as a polymorphic species, or a complex of closely related species. Pedicle opening at mantle midly narrower than ctenidium. Hypobranchial gland 0.25 of width. Osphradium twice shorter and slightly curvilinear. Ctenidium spans 0.6 of mantle length and quarter of its span 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 oposis end 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 (lf). Opening of anterior duct of digestive gland (adg) at beginning of intestine, with two low typhlosoles (tlf) 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 sinusous 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. aurantisus* and *P. wakasanus* have shells of similar shape, proportions, size and spiral sculpture (despite that shell
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
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. rhys-sus*, had transitional characters: slender shell similar in outline to *P. rhyssoides*, bearing weakly expressed axial ribs like in *P. rhys-sus*. Its anatomy was identical to other three specimens. Taking into account high variability of axial sculpture in buc-cinids, we consider *P. rhyssoides* as junior synonym of *P. rhys-sus*, but for final decision additional mate-rial should be examined.

The major problem is *P. wakasanus*, that was described from Wakasa Bay (no more exact locality data), that is southward from the line between Noto and Bosso 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 charac-teristics between *P. aurantius* and *P. wakasanus*. In the absence of material of *P. wakasanus* from the type locality we follow the opinion of the mentioned authors. Thus, within the current morphological par-
FIG. 19. Anatomy of *Plicifusus rhysus* 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 rhysus* №№ 1-3. A – мягкое тело экз. № 2, вид с вентральной стороны; B – мантия экз. № 2; C – мягкое тело экз. № 1, вид с дорзальной 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 дорзально; 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. 21 C). 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. 21 C). 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 attached to bottom and lateral walls of body haemocoel (Fig. 21 D). Buccal mass (Fig. 21 E, *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. 21 E, *mrr*) originates at base of radula sac. Pair of buccal nerves (Fig. 21 E, *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. 21 G). Posterior mixing area small, lined with tall transverse folds (Fig. 21 F, *pma*). Inner stomach wall lined with oblique folds; smooth longitudinal fold (*flf*) 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.


**Distribution** – the Bering Sea, Eastern Kamchatka, USFC st. 3643, 51°16’00’’N, 158°03’00’’E, 100 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).

**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.

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.

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).

FIG. 22. Радулы *Plicifusus*: А – вид сверху и Б – сбоку *P. oceanodromae* № 1 (раковина на Рис. 20 В, анатомия на Рис. 21); С – вид сверху *P. olivaceus* № 1 (раковина на Рис. 20 Е); Д – 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).
Periostracum light-brown to dark-olive. 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, bd). Foot contracted, folded transversely, with narrow propodid separated by deep propodial groove, operculum oval with terminal nucleus. Penis long and narrow, bearing pointed seminal papilla, 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.

**Digestive system.** Proboscis completely inverted into rhynchodaemum. Proboscis retractors numerous, originate in proboscis wall, follow along rhynchodaemum 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 marginal 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 or mixing area small, lined with tall oblique folds (Fig. 23H). Outer stomach wall lined with tall transverse folds. Longitudinal fold on inner stomach wall follows from oesophageal opening to anterior duct of digestive gland, lined with low oblique folds (Fig. 23H, lf). 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.

**Differenteral 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)


**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-beige to dark-olive.

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

**Digestive system.** Proboscis partly inverted in rhynchodaeum. Numerous proboscis retractors situated on both sides of rhynchodaeum (Fig. 24 D-E, **prr**). Multiple odontophoral retractors originate at base of buccal mass, attaching to proboscis wall (Fig. 24F). **Radula** 380 μm 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 (bl) long and narrow, opening by short duct shortly behind nerve ring. **Stomach** spans ¼ 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 (hl) lined with low oblique folds, rest of inner stomach wall – with low transversal folds. Openings of posterior duct of digestive gland (pdg) large, situated near oesophageal opening. Opening of anterior duct (adg) at 1/3 of length from intestine; two well developed typhlosoles (tlf) 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 description. Types lack axial ribs on the shell, therefore we exclude the species from the genus *Plicifusus*. It is the type species of *Plicifusus* (*Helicofo- fusus*) Dall, 1916. Two other species were referred to this genus: *Tritonofusus* (*Plicifusus*) *rhyssus* Dall, 1907, which is here transferred to *Plicifusus* and *Helicofo- fusus luridus* Golikov in Golikov et Scarlato, 1985, which was considered as a junior synonym of *Latisiphos hallii* (Dall, 1873) [Kosyan, 2006a]. Since neither anatomy, nor radula of *P. laticordatus* are known, the status of *Helicofo- fusus* remains unclear.

*Plicifusus parvus* Tiba, 1980


**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


**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
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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.

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 johansenii* 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 oceandromea* 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 striaion.

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 phylogenies, 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 multicuspids [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 rachidians 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, plain 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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