
Restoration of the genus *Squamophora* (Mollusca: Polyplacophora: Loricidae)

B.I. SIRENKO

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab.1, St. Petersburg, 199034,
RUSSIAN FEDERATION; E-mail: marine@zin.ru

ABSTRACT. I propose to restore the old genus name *Squamophora* for *S. oviformis* and the described herein *S. nierstraszi* sp. nov.. A new emendation of the genus *Squamophora* is provided, taking into account the main features of the shell, girdle and radula that distinguish it from the closely-related genus *Loricella*. The new species differs from the type species by the sculpture of the dorsal scales and the shape of the radula teeth.

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Восстановление рода *Squamophora* (Mollusca: Polyplacophora: Loricidae)

Б.И. СИРЕНКО

Зоологический институт Российской Академии наук,
Университетская наб. 1, Санкт Петербург, 199034,
РОССИЯ, E-mail: marine@zin.ru

РЕЗЮМЕ. Предложено восстановить название *Squamophora* для *S. oviformis* и вновь описываемого вида *S. nierstraszi* sp. nov. Составлен новый диагноз рода *Squamophora*, учитывающий основные признаки раковины, перинотума и радулы, отличающие его от близкого рода *Loricella*. Новый вид отличается от типового вида рода скульптурой дорсальных чешуек и формой зубов радулы.

Introduction

The genus *Squamophora*, described by Nierstrasz [1905], had a very short existence in the taxonomic history of Polyplacophora. After its description, the genus was only mentioned twice in the works of Thiele [1909, 1929], who found out that the species has a tricuspid head of major lateral tooth of radula and placed *Squamophora* together with *Loricella* Pilsbry, 1893 as subgenera of the genus *Lorica* H. & A. Adams, 1852. Only 49 years later in the fundamental work on the revision of the class Polyplacophora Van Belle [1978, 1983] considered *Squamophora* as junior synonym of the genus *Loricella*. This observation was subsequently confirmed by Kaas [1985] and Kaas *et al.* [2006]. Saito [2005] was the first who noticed significant differences between *Loricella scissurata* (Xu, 1990) and *L. oviformis*

(Nierstrasz, 1905). Unfortunately, he only stated the differences at the species level, but did not discuss the generic importance.

A careful examination of the holotype of *Squamophora oviformis* and the three specimens of a new species of this genus revealed little-known but significant morphological features. The features of the shell, the ventral part of the girdle, the dorsal spicules, as well as the radula teeth indicate differences to *Loricella* and justify a restoration of *Squamophora*. The genus *Squamophora* is here redefined and a second species from New Caledonia and the Solomon Islands is here introduced under the new conception.

Material and methods

Three specimens have been collected during the EXBODI (doi.org/10.17600/11100080) and SALOMON 2 (doi.org/10.17600/4100090) expeditions of the MNHN. The holotype of *Squamophora oviformis* (ZMA.MOLL.138609), collected near Philippines, the Sulu Sea, 73 m, was studied. The specimen treatments follow Sirenko [2018]. Bathymetric ranges are reported as inner values of the shallowest and deepest stations as suggested by Bouchet *et al.* [2008].

Abbreviations: BL, body length. IEE RAS, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia. MNHN, Muséum National d'Histoire Naturelle, Paris, France. Stn., station. ZISP, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia. ZMA, Zoologisch Museum Amsterdam, Netherlands, but now material is held in Naturalis Biodiversity Center, Leiden.

Taxonomy

Class Polyplacophora Gray, 1821
 Subclass Neoloricata Bergenhayn, 1955
 Order Chitonida Thiele, 1909
 Family Loricidae Iredale & Hull, 1923

Genus *Squamophora* Nierstrasz, 1905

Type species: *Squamophora oviformis* Nierstrasz, 1905, by original designation.

Genus distribution. South of Philippines, New Caledonia and Solomon Islands, 73–355 m.

Since Nierstrasz [1905] placed *Squamophora* in the family Mopaliidae, he compared this new genus with the rest of the genera in the family Mopaliidae and not the family Loricidae. The first person to note the relationship between *Squamophora* and *Loricella* was Thiele [1929]. Based on new data obtained by study of the type species and new species on SEM, here I propose a new diagnosis for *Squamophora*.

Diagnosis. Medium sized, broadly oval, head valve large and more than twice as wide as tail valve, intermediate valves very short and wide, mucro terminal. Pits of tegmentum arranged in a random manner. Slit formula 16–23/1–(rare 2)/sinus. Girdle widest in front and with a slit behind, dorsally covered with solid scales and rare tufts of short needles. The tufts are located on the perinotum closer to the edge of the girdle. There is very wide mantle fold, which partly covers small head and foot. Mantle fold covered with longitudinally ribbed scales with rolled edges and with short, pointed, distal spike. Hyponotum scales long rectangular with longitudinal ribs. Central tooth of radula short, tulip shaped, head of major lateral tooth tricuspid.

Squamophora differs from congenial *Loricella* with five currently known species *L. angasi* (H. Adams in H. Adams & Angas, 1964) (Fig. 1D, E), *L. profundior* (Dell, 1956), *L. vanbellei* Sirenko, 2008, *L. eernissei* Sirenko, 2008 and *L. dellangeloi* Sirenko, 2008 in having dorsal scales without tubular hollow (vs tubular hollow in dorsal girdle scales in all species of *Loricella*), tuft of needles in the girdle (vs tuft of bristles in all species of *Loricella*), head of major lateral teeth with three denticles (vs with two denticles in all species of *Loricella*), wide mantle fold partially covering the narrow head and foot (Fig. 1C) (vs narrow mantle fold and wide head in all species of *Loricella*) (Fig. 1F), the mantle fold covered with unusual longitudinally-ribbed scales with rolled edges and a short pointed spike at the distal end (vs mantle fold covered with simple longitudinally-ribbed scales in all species of *Loricella*), ribbed ventral scales (vs smooth ventral scales in all species of *Loricella*), pits of tegmentum in head valve and lateral areas of intermediate valves arranged in a random manner. (vs pits of tegmentum arranged in radial rows in all species of *Loricella*).

Squamophora nierstraszi sp. nov. (Figs 1A–C, 2–5)

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Type material. Holotype (MNHN IM-2013-66498) now disarticulated, consisting of mount of part of girdle and radula, vial with valves, part of radula and part of girdle, and 1 paratype (MNHN IM-2013-49566).

Type locality. New Caledonia, EXBODI, stn. CP 3900, 22°17'S, 168°41'E, depth 355–357 m.

Etymology. Named in honour of H. F. Nierstrasz who described the genus *Squamophora*.

Material examined. **New Caledonia.** EXBODI, stn. CP 3898, 22°18'S, 168°42'E, 340–346 m, paratype (MNHN IM-2013-49566), BL 21 mm (without tail part), 20.09.2011; EXBODI, stn. CP 3900, 22°17'S, 168°41'E, 355–357 m, holotype (MNHN IM-2013-66498), BL 26 mm 20.09.2011; **Solomon Islands,** SALOMON2, stn. DW 2255, 8°07.7'S, 157°02.1'E, 185–196 m, 1 spm, (MNHN IM-2013-67013), BL 16 mm, 03.11.2004.

Distribution. New Caledonia and Solomon Islands, 196–355 m.

Diagnosis. Chiton of medium size, broadly oval, shell solid, rather low, carinated, valves not beaked. Head valve with about 40 weakly radial ribs, valve II widest, tegmentum of central area sculptured with 5–7 short narrow folds on both sides of the jugum. Lateral areas of intermediate valves sculptured like head valve and bearing up to 6–7 weakly radial ribs. Tail valve more than twice as narrow as head valve, mucro terminal. Apophyses connected with rather long, not interrupted jugal plate. Slit formula 23/1–2/sinus. Dorsal scales solid, with 28–30 narrow longitudinal ribs. Several dozens of tufts with short needles. Major lateral tooth with tricuspid head, denticles pointed, the inner one much shorter than others.

Description. Holotype 26.0 x 20.0 mm, valves low elevated (dorsal elevation 0.26), carinated, not beaked. Color of tegmentum ivory-white with numerous brown flecks.

Head valve very large, semicircular, twice as wide as tail valve, hind margin notched in the middle, tegmentum sculptured with about 50 weak radial ribs with vague granules crossed by a few growth line. Intermediate valves broadly rectangular, front margin almost straight at both sides of a narrow, roundish, forwardly produced jugal part, side and posterior margins almost straight, central areas sculptured with 5–7 short narrow folds on both sides of the jugum, lateral areas weakly raised, sculptured like head valve, with diagonal rib and 6–7 weak radial ribs with vague granules. Tail valve with terminal mucro, antemucronal slope slightly concave, antemucronal area sculptured like central area, postmucronal area very narrow. There are many pits of different size

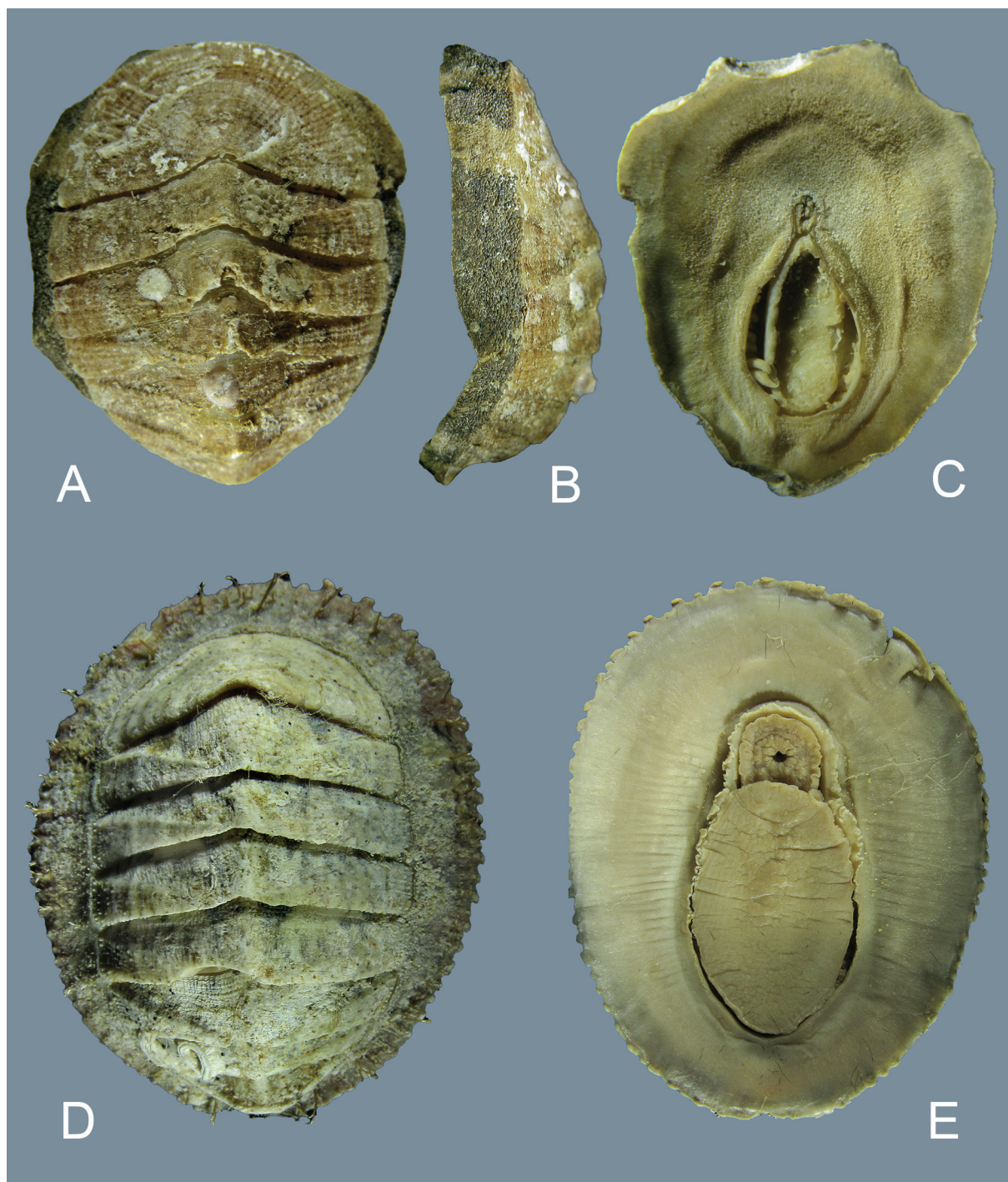


FIG. 1. *Squamophora nierstraszi* sp. nov., holotype (MNHN IM-2013-66498), New Caledonia, BL=26.0 mm (A–C) and *Loricella angasi* (ZISP 2394) South Australia, intertidal, BL=60.0 mm (D, E). A, D. Dorsal view; B. Lateral view; C, E. Ventral view.

РИС. 1. *Squamophora nierstraszi* sp. nov., голотип (MNHN IM-2013-66498), Новая Каледония, BL=26.0 мм (A–C) и *Loricella angasi* (ZISP 2394) Южная Австралия, литораль, BL=60.0 мм (D, E). A, D. Вид сверху; B. Вид сбоку; C, E. Вид снизу.

from 15 to 30 μm which arranged in a random manner in all areas of tegmentum. There is one row of large pits (50 μm) along the diagonal ridge between central and lateral areas.

Articulamentum white, smooth, solid, apophyses very wide, rounded to subtrapezoidal, short, triangu-

lar, connected with rather long, not interrupted jugal plate. Slit formula 23/1–(rare 2)/sinus, two slits in valve II, slit rays obsolete, not prominent, teeth short, finally grooved on the upper side, eaves narrow.

Girdle expanded anteriorly, narrowing posteriorly, with a narrow, deep mantle slit (2.4 mm wide

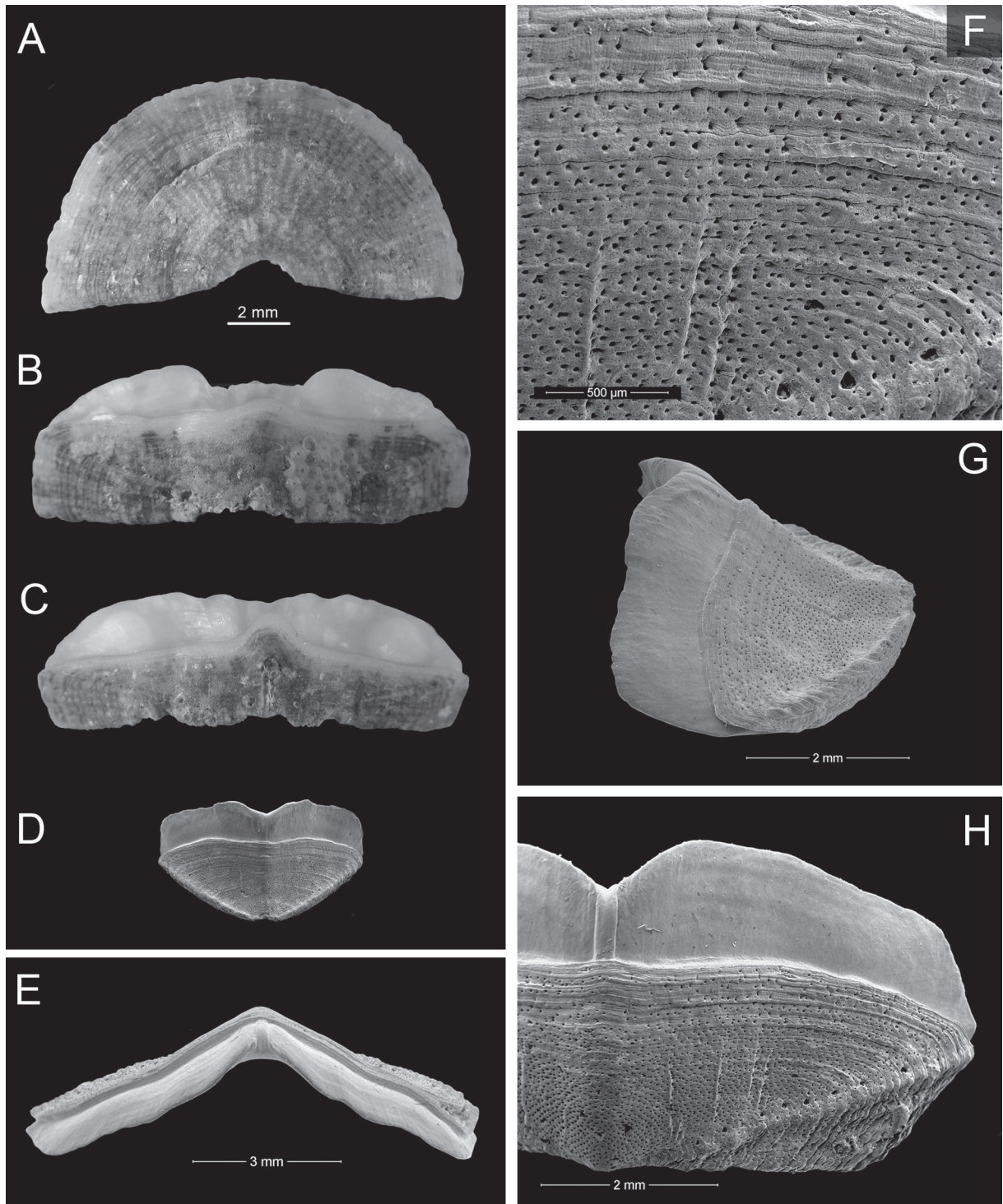


FIG. 2. *Squamophora nierstraszi* sp. nov., holotype (MNHN IM-2013-66498), New Caledonia, BL–26.0 mm. **A.** Head valve, dorsal view; **B.** Valve II, dorsal view; **C.** Valve IV, dorsal view; **D.** Valve VIII, dorsal view; **E.** Valve VII, rostral view; **F.** Valve VII, central area **G.** Valve VIII, lateral view; **H.** Valve VII, dorsal view.

РИС. 2. *Squamophora nierstraszi* sp. nov., голотип (MNHN IM-2013-66498), Новая Каледония, BL–26.0 мм. **A.** Головной щиток, вид сверху; **B.** Щиток II, вид сверху; **C.** Щиток IV, вид сверху; **D.** Щиток VIII, вид сверху; **E.** Щиток VII, вид спереди; **F.** Щиток VII, центральное поле; **G.** Щиток VIII, вид сбоку; **H.** Щиток VII, вид сверху.

near valve IV), umber with ivory spots, dorsally covered with solid, rectangular, slightly bent scales (130–149 x 170–180 μm), the scales longitudinally ribbed (28–30 ribs), near margin scattered tufts of

short straight needles (220–240 x 25–29 μm). There is a marginal fringe of sharp-topped, straight, ribbed needles (415 x 34 μm). Ventrally girdle covered with long rectangular scales (75 x 24 μm) near the margin

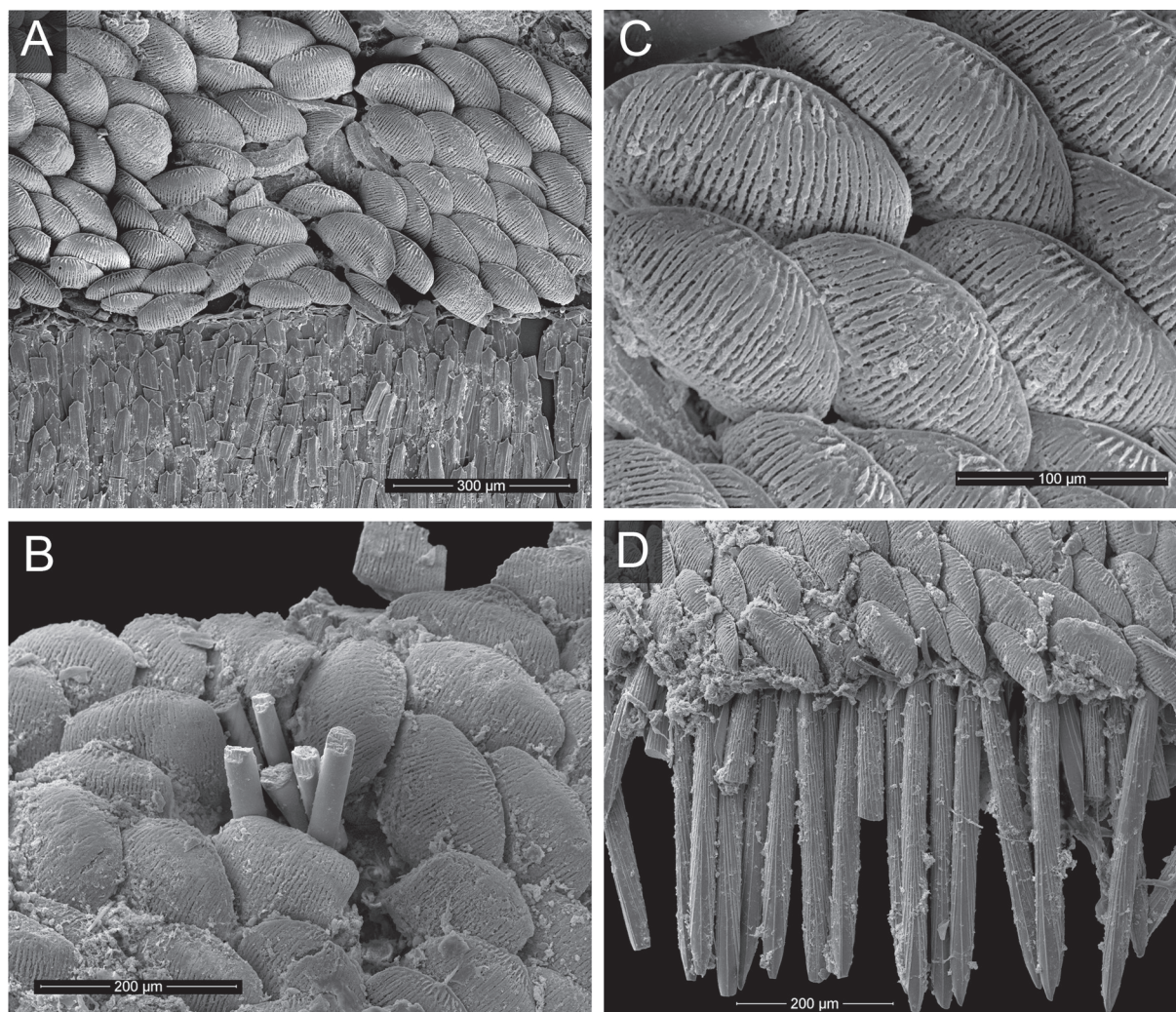


FIG. 3. *Squamophora nierstraszi* sp. nov., holotype (MNHN IM-2013-66498), New Caledonia, BL–26.0 mm. A. Dorsal and ventral scales; B. Dorsal scales and tuft of needles; C. Dorsal scales; D. Dorsal scales and marginal needles.

РИС. 3. *Squamophora nierstraszi* sp. nov., голотип (MNHN IM-2013-66498), Новая Каледония, BL–26.0 мм. А. Дорсальные и вентральные чешуйки; В. Дорсальные чешуйки и пучок игл; С. Дорсальные чешуйки; D. Дорсальные чешуйки и маргинальные иглы.

and (170 x 24 μm) in other part of hyponotum, the scales longitudinally ribbed and with small short spike on distal part. Around the head and foot, partially covering them, is a broad mantle fold covered with unusual longitudinally ribbed scales with rolled edges and with a short pointed spike at the distal end.

Radula of holotype 4.1 mm long with 42 transverse rows of mature teeth. Central tooth short, tulip shaped, first lateral tooth short, wide with small cusp on top, head of major lateral tooth tricuspid, interior denticle the smallest, central denticle the largest, major uncinial tooth long, fan-shaped, stalk thick.

Gills adanal. Twenty gills per side arranged from valve III to valve VII. Nephridiopore and gonopore arrange between third and fourth and between fourth and fifth gills, respectively.

The digestive tract was empty, it is short (about 22

mm), which indicates that animal flesh is predominant in this species [Saito, Okutani 1992].

Remarks. The new species is very similar to *Squamophora oviformis*, but differs from it in having dorsal scales with ribs (vs dorsal scales with sharp spikes in *S. oviformis*) (Fig. 6). The smaller paratype and specimen from Solomon Islands have the same ribs on the dorsal scales, which indicates the stability of this feature, first lateral tooth of radula is almost the same length as the central one (vs the lateral tooth is almost twice as long as the central one in *S. oviformis*), 23 slits of insertion plate in head valve (vs. 16 slits in *S. oviformis*).

Discussion

As noted in the introduction, the name *Squa-*

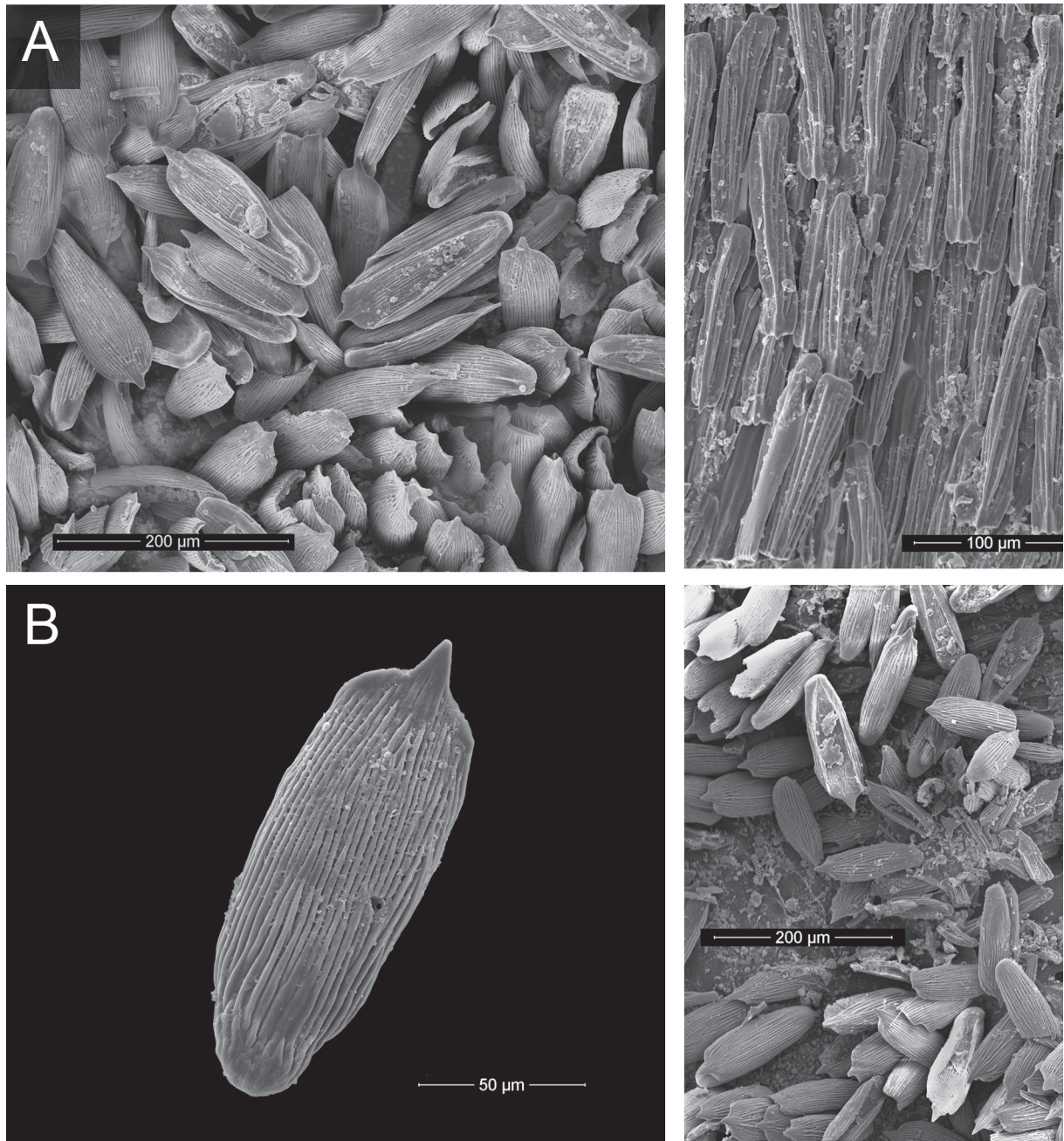


FIG. 4. *Squamophora nierstraszi* sp. nov., holotype (MNHN IM-2013-66498), New Caledonia, BL–26.0 mm. **A.** Scales of front part of mantle fold; **B.** Scale of mantle fold; **C.** Ventral scales; **D.** Scales of mantle fold and ventral scales at the border between mantle fold and hyponotum in the front of the body.

РИС. 4. *Squamophora nierstraszi* sp. nov., голотип (MNHN IM-2013-66498), Новая Каледония, BL–26.0 мм. **A.** Чешуйки передней части мантийной складки; **B.** Чешуйка мантийной складки; **C.** Вентральные чешуйки; **D.** Чешуйки мантийной складки и вентральные чешуйки на границе между мантийной складкой и гипонотумом в передней части тела.

mophora became synonymous with the name *Loricella*. Indeed, the species of these two genera are very similar in appearance. They are connected by the wide shape of the shell, presence of the dorsal scales, the caudal sinus of the girdle and the general appearance of the radula. Kaas [1985] considered *Paricoplax profundior* and *Componochiton raceki* Milne, 1963 as junior synonyms of the species *Loricella oviformis*. He also referred two new findings

from Indonesia and New Caledonia to this same species. However, in my research, I identified them as *L. profundior* (Indonesia, “Corindon”-Makassar-Expedition, 1980, stn. CH229) and *L. vanbellei* (New Caledonia, “Vauban”, 1978-79, stn. 16). Kaas’ [1985] drawings, labeled as *Loricella oviformis*, show three different species from two genera (figs 41–45 *L. vanbellei*, 46, 47 *Squamophora oviformis*, 48–54 *L. profundior*).

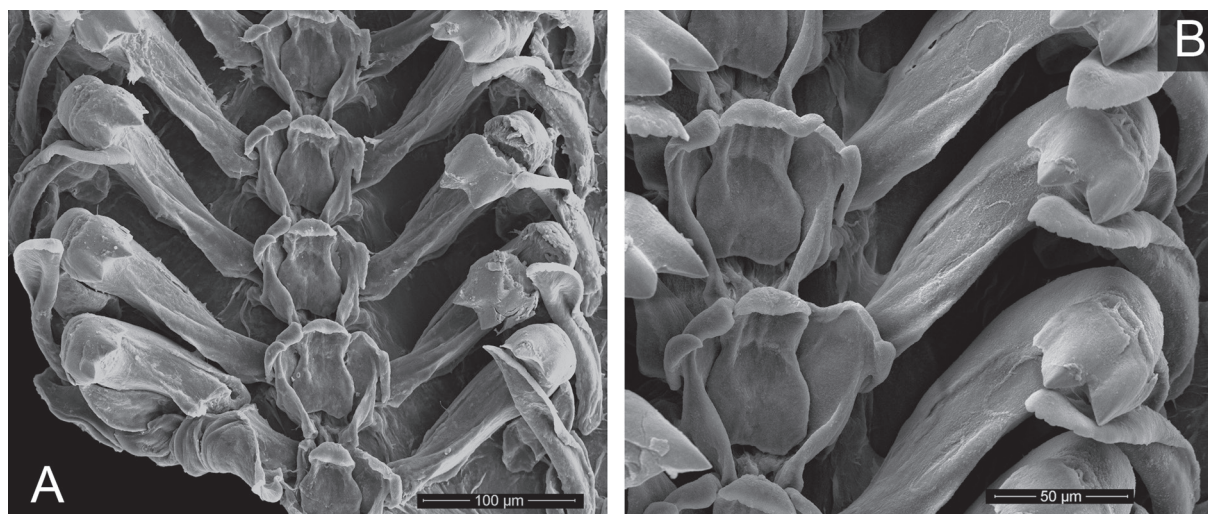


FIG. 5. *Squamophora nierstraszi* sp. nov., holotype (MNHN IM-2013-66498), New Caledonia, BL–26.0 mm. A. Part of radula; B. Central, first lateral, major lateral and major uncinal teeth of radula.

РИС. 5. *Squamophora nierstraszi* sp. nov., голотип (MNHN IM-2013-66498), Новая Каледония, BL–26.0 мм. А. Часть радулы; В. Центральные, первые латеральные, крючковые и большие унциальные зубы радулы.

In 1995 I studied the holotype of *S. oviformis*. It was a 20 mm long and 13 mm wide specimen with separated I, II, III, IV and VIII valves. I found the features noted in the description of this species and some new features not mentioned in the original description, so I find it useful to describe them. The dorsal elevation of valve IV is 29. Head valve has 52 radial ribs with granules, central area of intermediate valves and antemucronal area of tail valve sculptured with several short narrow folds on both sides of the jugum. Jugal sinus of intermediate and tail valves is deeper than in *S. nierstraszi* sp. nov. Slit formula is 16/1 (rare 2)/0. Valve II has 2 slits while the other intermediate valves have a single slit on both sides. Eaves are narrow and finely porous. There are about 40 tufts of short, straight needles were located on the perinotum closer to its edge. Dorsal scales are slightly bent and covered with sharp spikes (Fig. 6). Ventrally the holotype has wide mantle fold, the head is about twice as narrow as the foot. The mantle fold is covered with scales that have a short pointed spike at the distal end. The hyponotum is covered with long, rectangular, narrow scales. The major lateral teeth of radula has tridentate head, inner denticle is smaller. First lateral teeth are about twice as long as central one. The holotype has 17 gills per side arranged from valve III to valve VII. Nephridiopore and gonopore arrange between third and fourth and between fourth and fifth gills, counted from the last one, respectively. Thiele [1909] was first who studied radula of the holotype of *S. oviformis*. He was the first to show that the head of the major lateral tooth is tricuspidate. However, the first lateral tooth was only slightly longer than the central one in his drawing, which is at odds with my observations, according to

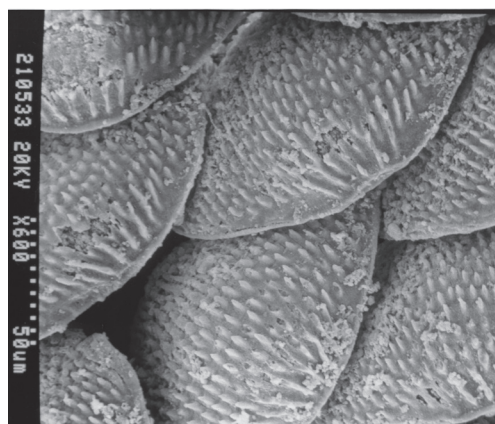


FIG. 6. *Squamophora oviformis*, holotype (ZMA. MOLL.138609), Sulu Sea, BL–20.0 mm, dorsal scales.

РИС. 6. *Squamophora oviformis*, голотип (ZMA. MOLL.138609), море Сулу, BL–20.0 мм, дорсальные чешуйки.

which the first tooth is almost twice as long as the central one.

When describing *Squamophora*, Nierstrasz [1905] placed the new genus in the family Mopaliidae Dall, 1889. The main features that persuaded Nierstrasz [1905] to place the new genus in the family were broad valves like in *Placiphorella* Dall, 1879 and especially the shape of the last valve like in *Mopalia* Gray, 1847, *Placiphorella* and *Plaxiphora* Gray, 1847. Later, Thiele [1929] transferred *Squamophora* to the genus *Lorica* H. & A. Adams, 1852, as a subgenus where he placed together with *Lorica* s.s. and *Loricella* also completely unrelated groups such as *Lepidozona* Pilsbry, 1892 and *Callistochiton* Dall,

1879. Finally, Van Belle [1978] placed *Squamophora* as a junior synonym to *Loricella*.

Squamophora strongly resemble *Placiphorella* and *Craspedochiton* Shuttleworth, 1853, in body shape. The similarity between *Squamophora* and *Craspedochiton* is particularly striking. In both species, in addition to the broad body shape, the mantle folds that hide part of the head are strongly developed. Given that the groups listed above belong to predatory chitons belonging to completely unrelated families and even orders we can state surprising examples of convergent similarity first noted by Saito and Okutani [1992].

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