

## *Nipponolimopsis littoralis*, a New Species from Intertidal Boulder Shores in Japan, with a Systematic Review of the Genus (Bivalvia: Limopsoidea)

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**Abstract.** *Nipponolimopsis littoralis* n. sp. is described from the Pacific coast of central Japan and compared with other Recent and fossil species of the genus. The new species is distinguished from other members of the genus mainly in having (1) the periostracum composed of thick radially arranged bristles and thin commarginally lamellate membranes, (2) an obliquely oval outline without prominent posteroventral extension, (3) the hinge with three anterior and four posterior teeth, and (4) a finely pitted prodissoconch with a central depression and a marginal thickening. In addition, the habitat of the new species in the intertidal bolder shores is strikingly different from that of other lower subtidal species. This is the only species of *Nipponolimopsis* recorded from the intertidal zone.

### INTRODUCTION

The superfamily Limopsoidea comprises two families, Limopsidae and Philobryidae. The former is most successfully adapted to the subtidal to bathyal zone and also extends into abyssal depths (5,000 m and deeper) (e.g., Kundsén, 1970; Oliver & Allen, 1980; Oliver, 1981; Coan et al., 2000; Matsukuma, 2000; Amano & Lutaenko, 2004), while the latter is generally confined to the intertidal to shallow subtidal zones (Tevesz, 1977; Powell, 1979; Hayami & Kase, 1993; Lamprell & Healy, 1998; Coan et al., 2000; Malchus, 2006). Most limopsids prefer soft sediments, either being attached to coarse grains with a byssus or freely buried in sands or mud (e.g., Kondo, 1989); some species are epibyssately attached to hard substrates (Oliver, 1981: fig. 3), but such a mode of life is uncommon. The habitats of Philobryidae are less well examined, and philobryids have been recorded mainly from shallow-water rocky bottoms, including submarine caves.

The genus *Nipponolimopsis* has been treated as a member of the Limopsidae by most authors based on overall shell morphology (see below for details). The previously known species of the genus have been all collected from the lower subtidal zone, which seems consistent with the distinction between shallow-water philobryids and deeper-water limopsids. However, in

field sampling on the main island of Japan, we have collected an unidentified limopsid-like species from the undersides of boulders in the intertidal zone. Morphological observations revealed that it belongs to the genus *Nipponolimopsis* which has never been known from the intertidal zone. We describe this new species, review the records of previously known species of the genus, and discuss their taxonomic characters and implications for limopsid systematics.

### MATERIAL AND METHODS

The samples of a new species were collected from the undersides of boulders in the intertidal zone in Cape Manazuru, Kanagawa Prefecture (type locality: Figures 1, 2) and other localities (Figure 2). The shells with or without an intact periostracum were photographed with a binocular microscope and a scanning electron microscope (SEM: Hitachi S-2250N). The muscle scars inside of the shell are unclear in fresh specimens, but they were easily visible after the shell is soaked in 10% formalin for one day. Gross anatomy was investigated based on 22 samples: Two samples were collected from Oizura, Kitaibaraki City, Ibaraki Prefecture, five from Isozaki, Hitachinaka City, Ibaraki Prefecture and the other 15 from Tsumeki-zaki, Shimoda City, Shizuoka Prefecture. Live animals were relaxed in 7.5% MgCl<sub>2</sub>

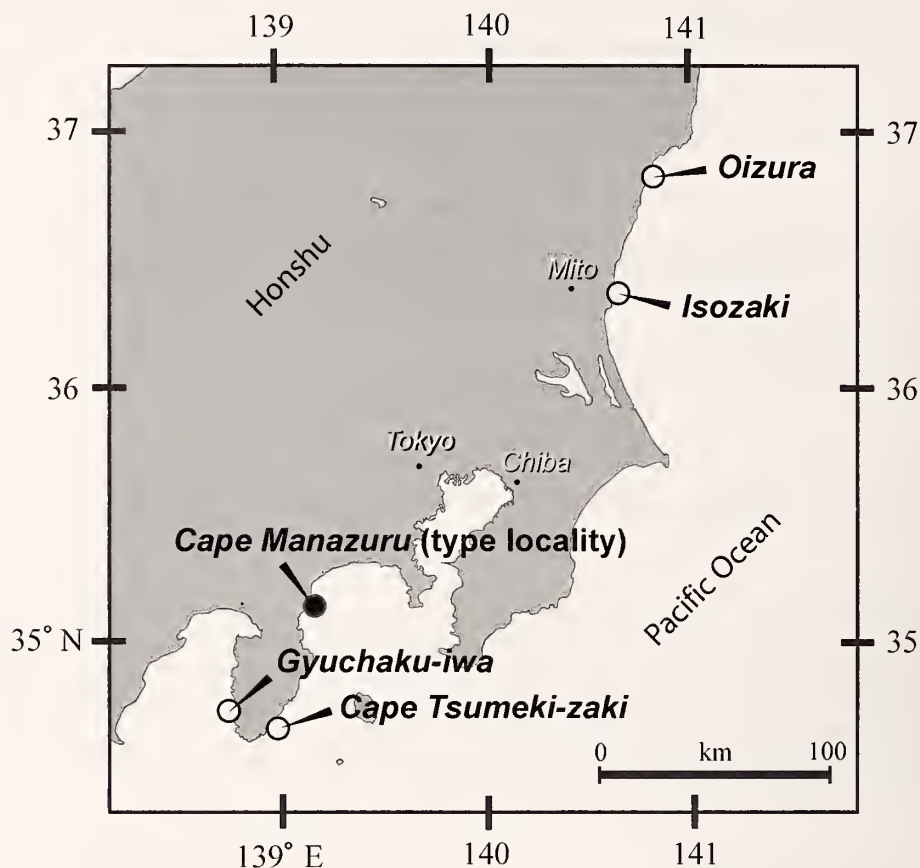


Figure 1. Localities of *Nipponolimopsis littoralis* n. sp.

solution, fixed with 10% neutralized sea water-diluted formalin for at least 3 days, rinsed in tap water for one hour, then preserved in 70% ethanol. The shells were dissolved by immersing in a diluted solution of HCl for several minutes, and dissected under a binocular microscope. Three samples were stained with eosin or toluidine blue for at least 30 min to evaluate tissue types. For taxonomic comparison, the type specimens described by Yokoyama (1910, 1922) were reinvestigated and photographed, since details were not given sufficiently in the original descriptions. The data from other species were reviewed and compiled from literature. The type specimens of new species are deposited in The University Museum, The University of Tokyo (UMUT) and the National Science Museum, Tokyo (NSMT).

#### SYSTEMATICS

Superfamily Limopsoidea Dall, 1895

Family Limopsidae Dall, 1895

Genus *Nipponolimopsis* Habe, 1951

**Type species:** *Limopsis nipponica* Yokoyama, 1922

(original designation) = *Cyrella decussata* A. Adams, 1862

**Diagnosis:** Shell small (less than 14 mm); surface finely and regularly reticulate; periostracum thick, densely hairy; anterior area of shell shorter than posterior; anterior arc of hinge teeth four or fewer in number, nearly vertical to hinge line; posterior arc of hinge teeth seven or fewer, oblique or subparallel to hinge line; anterior adductor muscle scar notably reduced in size below anteriormost hinge tooth; posterior adductor muscle scar much larger than anterior, remote from dorsal margin; inner ventral margin lacking crenulations.

**Remarks:** Following the majority of authors (e.g., Newell, 1969; Kuroda et al., 1971; Habe, 1977; Tevesz, 1977; Coan et al., 2000; Matsukuma, 2000), we tentatively allocate *Nipponolimopsis* to the Limopsidae rather than the Philobryidae. This treatment is mainly based on the presence of typical limopsid characters such as a finely reticulate sculpture, a thick hairy periostracum, prominent taxodont hinges both at the anterior and posterior sides. Oliver (1981:71) regarded the genus as a member of the Philobryidae, putting an



Figure 2. Habitat of *Nipponolimopsis littoralis* n. sp. in type locality. Arrow indicates approximate position where holotype was collected.

emphasis on a cap-shaped prodossoconch. The retention of the byssus at the adult stage, small size, and brooding habit may also support its closeness to philobryid members. The shell morphology of philobryids is highly variable in the hinge teeth, ligament, sculpture, and muscle scar (see Tevesz, 1977 for details), and the family might be a polyphyletic grade due to miniaturization and brooding, rather than a clade. Family-level systematics (cf. Oliver & Holmes, 2006: table 1) must be revised through phylogenetic analysis of all members of Limopsoidea.

*Nipponolimopsis littoralis* Sasaki & Haga n.sp.

(Figures 3–6)

**Material:** Holotype (2.0 mm in height, 1.6 mm in length, UMUT RM29331: Figure 3A), paratype #1 (UMUT RM29332: Figure 3B), paratype #2 (UMUT RM29333: Figure 3C–D): Cape Manazuru, Kanagawa Prefecture, Japan, July 21, 2005, collected by T. Sasaki; 3 paratypes (UMUT RM29334–29336); Oizura, Kitai-

baraki, Ibaraki Prefecture, Japan, July 9, 2002, collected by T. Haga; 9 paratypes (UMUT RM29337–29345): Isozaki, Hitachinaka, Ibaraki Prefecture, Japan, May 5, 2003, collected by T. Haga; 4 paratypes (UMUT RM29346–29349): Cape Tsumekizaki, Shimoda, Shizuoka Prefecture, Japan, May 8, 2005, collected by T. Haga; 2 paratypes, dead disarticulate valves from the subtidal zone, Gyuchaku-iwa, Kumomi, Matsuzaki, Shizuoka Prefecture, Japan, collected by Mr. Hisanao Nabeshima in 1990s (NSMT Mo73813, 73814).

**Diagnosis:** Shell height smaller than 3 mm; periostracum composed of radially arranged thick bristles and thin commarginally lamellate membranes; obliquely oval outline without prominent ventral extension; cancellate sculpture consisting of thicker radial ribs and thinner commarginal ridges; prodossoconch with weak collar-like marginal ridge, finely pitted sculpture, and deep umbonal depression; hinge teeth three in anterior and four in posterior row.

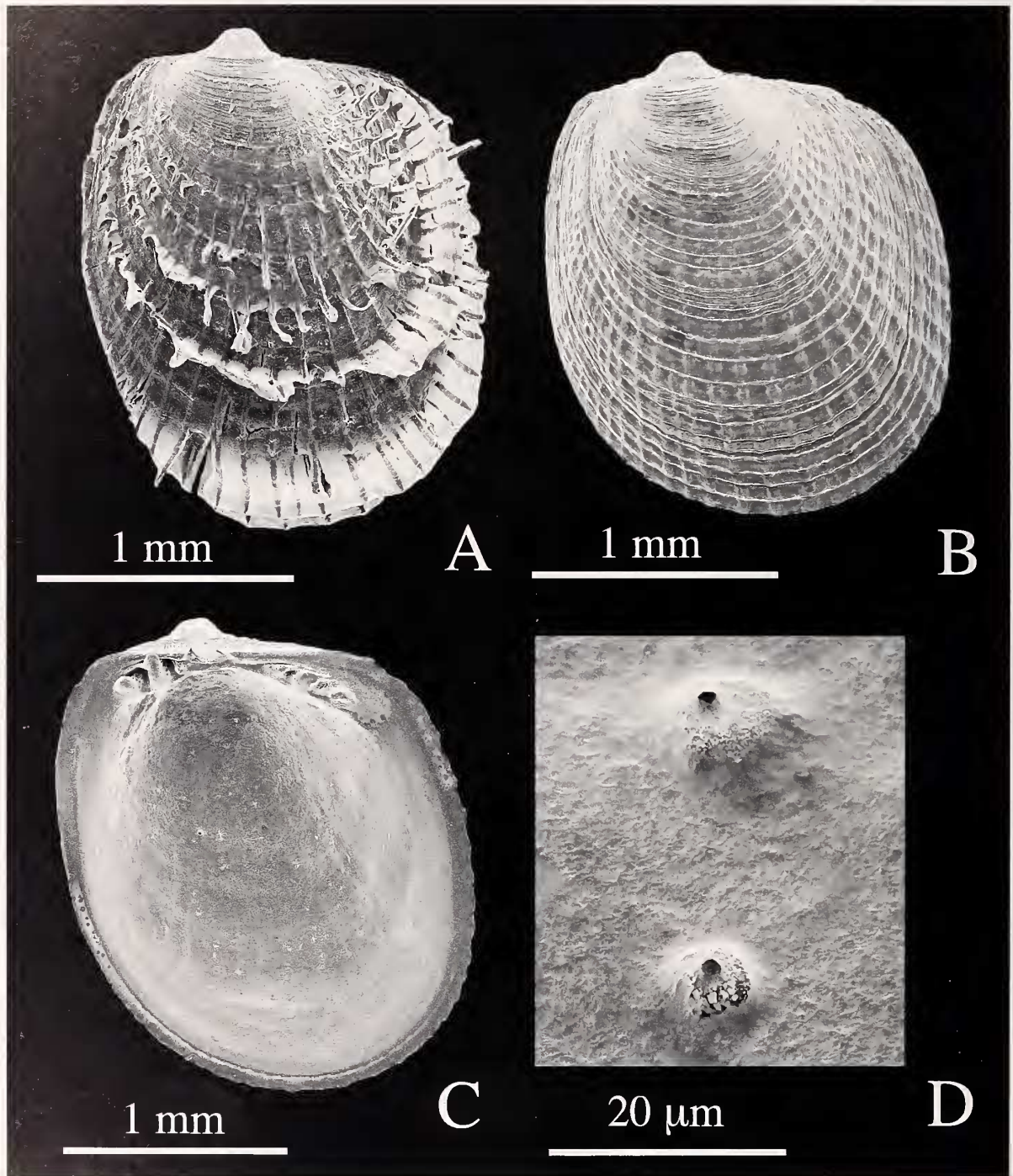


Figure 3. *Nipponolimopsis littoralis* n. sp. A. Holotype with complete periostracum. UMUT RM29333. B. Paratype #1 with periostracum artificially removed. UMUT RM29332. C. Inner view of paratype #2. UMUT RM29333. D. Enlarged view of shell pores on shell interior of paratype #2.

**Shell:** The shell is small for the family, subquadrate, inequilateral, and equivalve. The dorsal margin is straight. The anterior and posterior margins are almost parallel, slightly convex, roundly continuous with

a smoothly convex ventral margin. The umbo is located at 39% of the hinge line anteriorly (Figure 3), orthogyrate and projected dorsally. The periostracum consists of two elements (Figure 3A): (1) Sparse

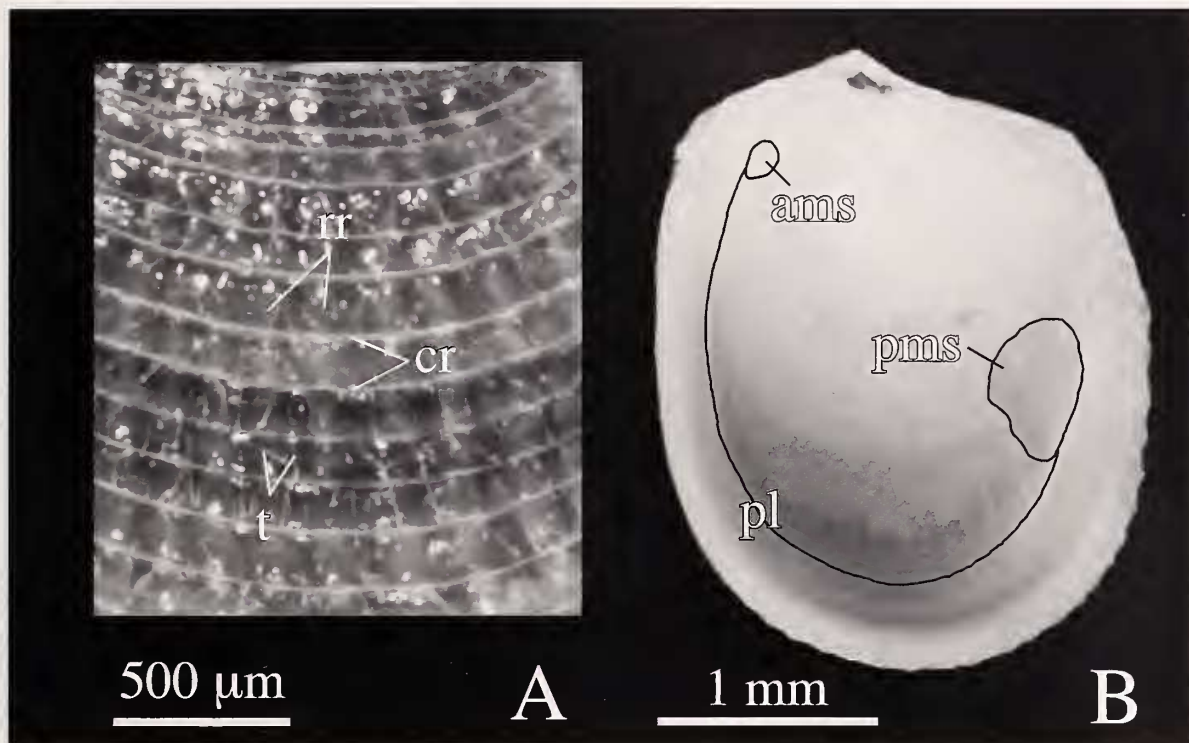


Figure 4. *Nipponolimopsis littoralis* n. sp. A. Enlarged view of outer surface after periostracum artificially dissolved. B. Inner view of shell showing position of muscle scars and pallial line. Paratype UMUT RM29334. Abbreviations: ams = anterior adductor muscle scar, cr = commarginal ridge, pl = pallial line, pms = posterior adductor muscle scar, rr = radial rib, t = tubule seen through shell.

periostracal bristles are arranged radially and project periodically along commarginal lines. (2) A thin filmy periostracum covers the entire shell surface and also connects periostracal bristles to form commarginal lamellate membranes. In gerontic specimens, the latter element of the periostracum is more easily worn away than the former. The outer surface of the shell is sculptured by ca. 30–40 radial ribs (rr) and also sharp commarginal ridges (cr: Figure 4A). When the periostracum is removed, microscopic tubules are visible as fine lines seen through the shell (t: Figure 4A; cf. Reindl & Haszprunar, 1996 for internal structure). The prodissoconch is discoidal in outline, 340 μm in length (Figure 5A), finely pitted on the surface (Figure 5B) and marked with a conspicuous depression (Figure 5C). The margin of the prodissoconch is thickened (Figure 5A). The hinge plate is straight dorsally, arcuate ventrally, and the thinnest below the umbo (Figure 5C). The hinge teeth are taxodont and consist of three anterior and four posterior teeth (Figure 5D). The teeth and sockets form a larger angle to the hinge axis at the anterior arc than the posterior; the posteriormost tooth is nearly parallel to the hinge axis. The ligament is alivincular, dorsally external; the resilium is small and triangular (Figure 5C). The cardinal area is

narrow and striated by fine vertical ridges. The inner surface of the shell is smooth except for microscopic pores (Figure 3D). The anterior adductor muscle scar (ams) is much smaller than the posterior (pms: Figure 4B). The pallial line (pl: Figure 4B) is nearly parallel to the shell margin. The inner margin is thickened with a commarginal ridge and smooth.

**Muscular system:** The animal is heteromyarian with a vestigial anterior adductor muscle (aam: Figure 6A) and a larger posterior adductor muscle (pam). Unlike most limopsids, an anterior pedal retractor muscle is absent. A small pedal protractor muscle (ppm) inserts beneath the anterior adductor muscle. The posterior adductor muscle is flanked by a well-developed posterior retractor muscle (prm) from which the byssal retractor element (bre) is independently branched out. The anterior part of the posterior retractor muscles covers most of the visceral mass.

**Mantle and pallial eyes:** Each mantle margin lacks pallial tentacles and comprises the outer, middle, and inner folds. A transparent periostracum protrudes from an incision between the outer and middle folds. Mantle fusion occurs only on both sides of a taxodont hinge, and there are no inhalant and exhalant apertures on the

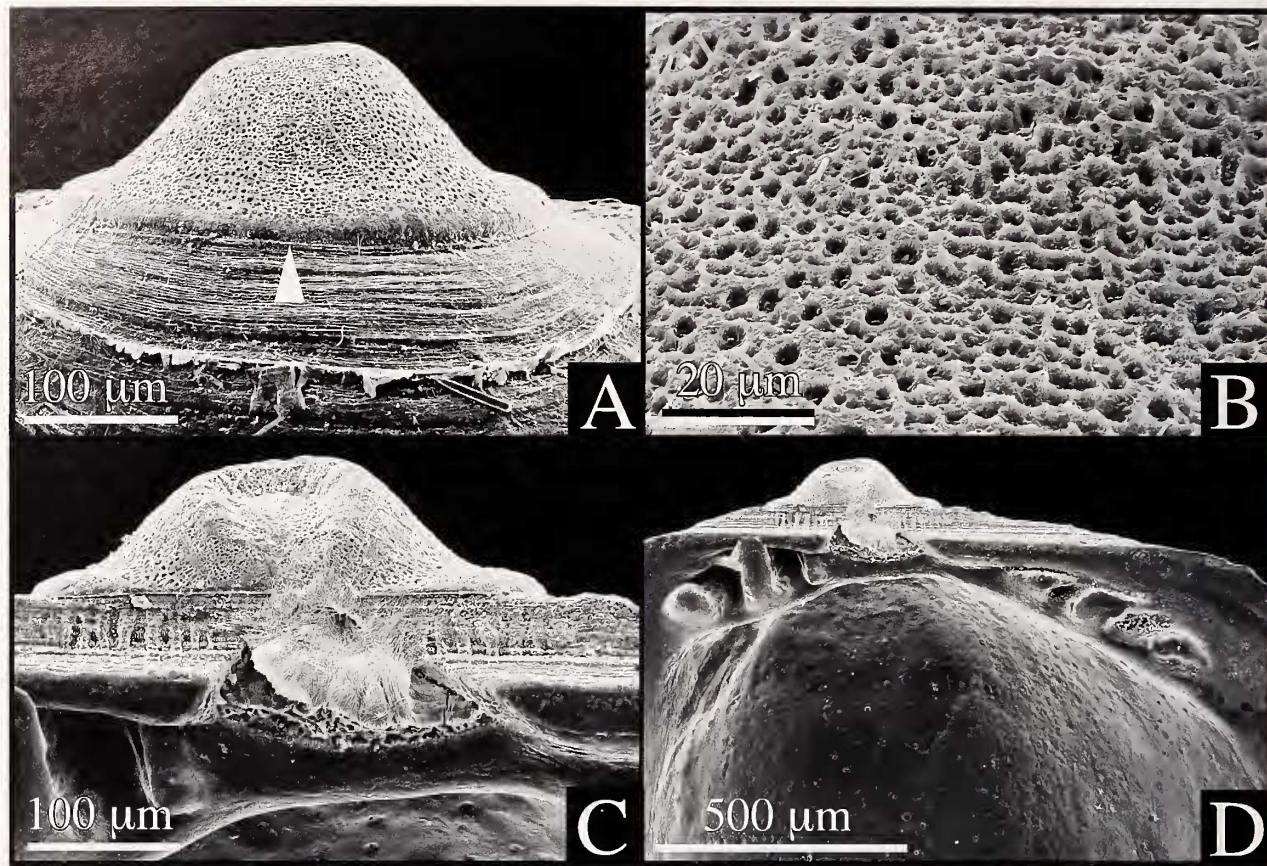
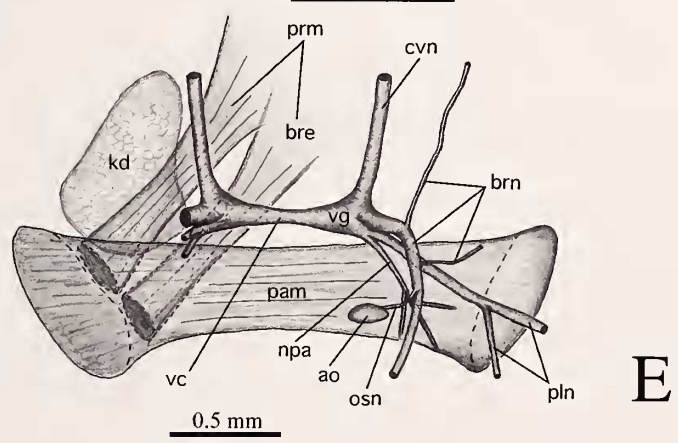
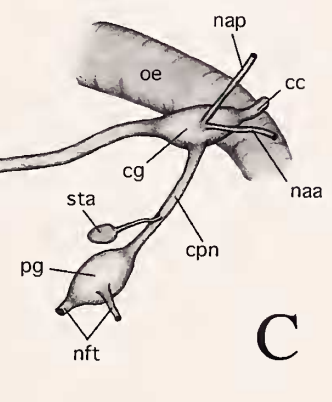
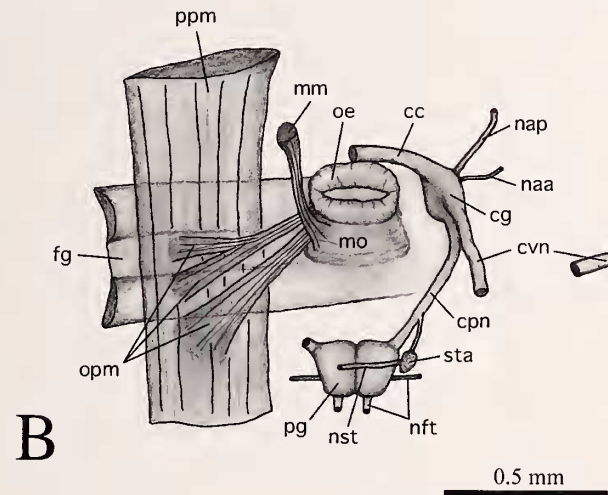
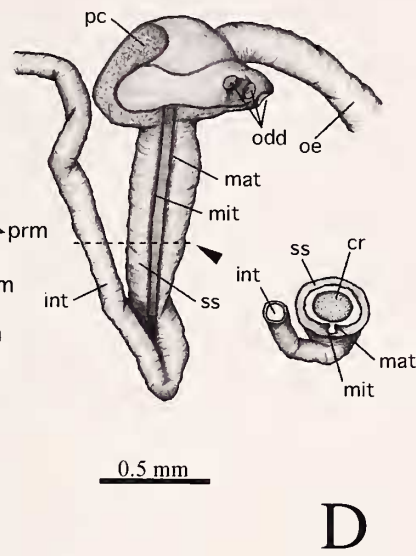
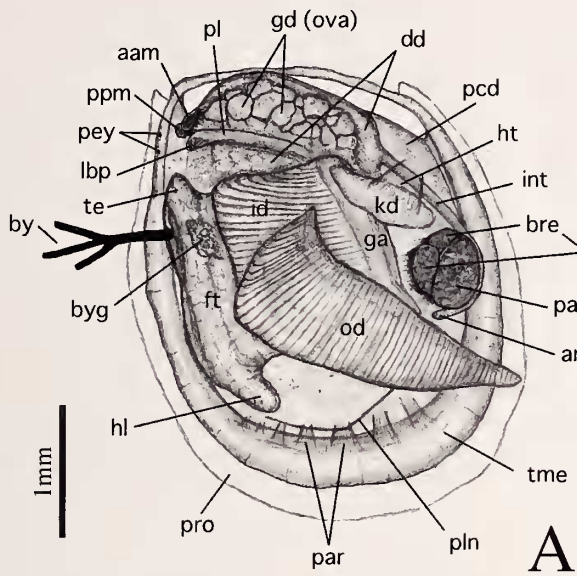


Figure 5. *Nipponolimopsis littoralis* n. sp. A. Prodissoconch of holotype. Arrowhead indicates boundary between prodissoconch and dissoconch. B. Enlarged view of prodissoconch sculpture. C. Hinge and umbonal part of paratype #2 (UMUT RM29333). D. Enlarged view of hinge teeth.

posterior mantle edge. The mantle margin is thickened (tme: Figure 6A) and few concentric muscle fibers are seen through it. The bundles of the pallial retractor muscle (par) are located on the inner side of a thickened mantle edge. They are innervated by the pallial nerves (pln) originating from the visceral ganglia (vg) via the

ventral part of the posterior adductor muscle. White granules, possibly mucous glands, are present on the inner side of each mantle wall close to the posterior end of the gill axes. In a narrow area of the outer fold, there are two to five brown-pigmented eyespots (pallial eyes; pey: Figure 6A) beneath the periostracum.

Figure 6. *Nipponolimopsis littoralis* n. sp. A. Left lateral view of animal with left valve and mantle removed. B. Anterior view of mouth, associated muscles, and circum-esophageal nervous system. C. Right lateral view of circum-esophageal nervous system. D. Right lateral view of digestive tract. Arrowhead indicates position of cross section which is shown on right side of figure. E. Posterior adductor muscle and adjacent nervous system seen from posterior side. Abbreviations: aam = anterior adductor muscle, an = anus, ao = abdominal organ, bre = byssal retractor element of posterior retractor muscle, brn = branchial nerve, byg = byssus groove, cc = cerebral commissure, cg = cerebral ganglion, cpn = cerebropedal nerve, cr = crystalline style, cvn = cerebrovisceral nerve, dd = digestive diverticulum, fg = food groove, ft = foot, ga = gill axis, hl = heel of foot, ht = heart, id = inner demibranch, int = intestine, kd = kidney, lbp = labial palp, mat = major typholosole, mit = minor typholosole, mm = muscular fiber supporting mouth, mo = mouth, naa = nerve to anterior adductor muscle, nap = nerve to anterior part of pallial line, nft = nerve to foot, npa = nerve to posterior adductor muscle, nst = nerve connecting statocysts, od = outer demibranch, odd = opening into digestive diverticulum, oe = esophagus, opm = muscular fiber originated from pedal protractor muscle, pam = posterior adductor muscle, par = pallial retractor muscle, pc = pigmented cell, pcd = pericardium, pey = pallial eyes, pg = pedal ganglion, pl = palps, pln = pallial nerve, ppm = pedal protractor muscle, prm = posterior retractor muscle, prm = posterior retractor muscle, ss = style sac, sta = statocyst, te = toe of foot, tme = thickened mantle margin, vc = visceral commissure, vg = visceral ganglion.



**Foot:** The foot is large, highly muscular, and laterally compressed with two terminal projections termed the toe (te) and the heel (hl; Figure 6A). On the ventral surface, there is a deep byssal slit anteriorly and a long but shallow byssal groove posteriorly. A relatively large byssal gland (byg) is visible in orange in living animals at the base of the mid-anterior region. The byssal threads are translucent, thin, slightly grayish.

**Ctenidia and labial palps:** The ctenidia are filibranchiate and consist of the outer (od) and inner demibranchs (id). The outer demibranchs are significantly smaller than the inner demibranchs. The anterior pallial space in front of the outer demibranchs is used to brood larvae. The posterior one-third of the outer demibranch is free from the visceral mass and highly mobile. When the animals are alive, the posterior tips of the ctenidia project beyond the shell edge.

Dorsally situated food grooves (fg; fig. 5B) are surrounded by the palps (pl) extended from the anterior ends of muscular gill axes (ga), and finally terminate as a laterally inflated, slit-like mouth. Small labial palps (lbp) are thick, triangular and corrugated with approximately five sorting grooves.

**Digestive system:** A slit-like mouth (mo) is located between the pedal protractor muscles (ppm) and well-developed food grooves. The ventral part of the mouth is supported by two muscular fibers (mm; Figure 6B). From this simple orifice, a long, slightly dorso-ventrally flattened oesophagus (oe) arises and is laterally supported by muscular fibers (opm; Figure 6B) originating from the wall of the visceral mass.

The stomach is mushroom-shaped and comprises two parts, *viz.* the dorsal chamber and the ventral tract. The anterior part of the dorsal chamber is connected to yellowish-gray digestive diverticula (dd) with two or three openings (odd) on the right side and one on the left. The digestive diverticula surround most of the stomach and spread into part of the oesophagus, but do not enter into the foot. The postero-ventral surface of the stomach bears bright brown-pigmented cells (pc; Figure 6D), and food tracts are traceable along a transparent area on the right stomach wall. These tracts fuse with the major and minor typhlosoles (mat, mit; Figure 6B) on the right side at the base of the style sac (ss). The major and minor typhlosoles are nearly equal in thickness, though the former is slightly stouter than the latter. The crystalline style (cr) is transparent, cylindrical and laterally flattened. The dorsal tip of the crystalline style in contact with the gastric shield is small and needle-shaped. Detailed inner morphology of the stomach was not observed.

The intestine (int) is long and ascends from the ventral right side of the style sac to the same level as the dorsal portion of the stomach, and finally turns in

a posterior direction. The intestine penetrates the heart and terminates as a simple anus (an; Figure 6A) below the middle portion of the posterior adductor muscle.

**Vascular and excretory systems:** The pericardium (pcd; Figure 6A) occupies the postero-dorsal portion of the visceral mass. The heart (ht) is almost transparent, membranous, and consists of the ventricle and laterally paired auricles. The ventricle is penetrated by the intestine.

The kidney (kd; Figure 6A) is large, translucent, membranous and comprising two components positioned laterally below the heart. The kidney ducts are significantly short and directly open into the supra-branchial cavity.

**Reproductive system:** Sexes are separate. The gonads (gd; Figure 6A) are distributed above the stomach and oesophagus, and extend towards the pedal ganglia along the wall of the visceral mass. The ovary and testis are both whitish, however, the former is distinguished from the latter by spherical shape and large size. The gonoducts were not observed in this study.

**Nervous system:** The cerebral ganglia are positioned lateral to the oesophagus. The pedal ganglia are embedded in the anterior portion of the foot. The visceral ganglia are located antero-ventral to the posterior adductor muscle.

The cerebral ganglia (cg; Figure 6B–C) are slender, cylindrical, and closely lateral to the anterior portion of the oesophagus. The cerebral commissure (cc) connects each cerebral ganglion beneath the oesophagus. Two small nerves ascend from the lateral surface of each ganglion: the ventral one is extended to the anterior portion of the pallial line (nap; Figure 6B–C) and another is to the anterior adductor muscle (naa). The pedal ganglia (pg; Figure 6B–C) are trapezoid, nearly equal in size to the cerebral ganglia, located at the anterior base of the foot, and connected to the cerebral ganglia with short cerebropedal nerves (cpn; Figure 6B–C). Since they are fused together, there is no commissure between them. From the pedal ganglia, two branches of small nerves are sent laterally and ventrally to the foot region (nft; Figure 6B–C). The statocysts (sta) are tiny, brownish, embedded in connective tissues on the wall of the visceral mass, and connected with the cerebropedal nerves and with each other by a small transverse commissure (nst). The inside of the statocysts were not observed in this study.

The cerebrovisceral nerves (cvn; Figure 6B–C) connect the cerebral and visceral ganglia. Large, dorso-ventrally flattened visceral ganglia (vg; Figure 6E) and their adjacent nerves form the most complicated part in the nervous system. The visceral ganglia are situated between the posterior end of the visceral mass and the posterior adductor muscle, and each ganglion is linked



with a thick and short visceral commissure (vc: Figure 6E). The visceral ganglia emit three nerves, viz. the branchial nerves (brn), the pallial nerves (pln), and nerves to the posterior adductor muscle. The branchial nerves are the most prominent element arising from the visceral ganglia, and the main thick nerves innervate the ctenidia along the muscular gill axes. The osphradial nerves (osn) are separated from the main ctenidial nerves and innervate the abdominal sense organ (ao) lying on either side of the anus. The pallial nerves (pln) are derived from the visceral ganglia dividing into two offshoots below the lateral margin of the posterior adductor muscle, descend along thickened mantle edges (tme), and finally reach the bundles of the mantle retractor muscles. The nerves to the posterior adductor muscle (npa: Figure 6E) bear three offshoots but they all terminate after a short distance.

**Type locality:** Cape Manazuru, Kanagawa Prefecture, Japan (35°08'35"N, 139°09'42"E) (Figures 1, 2).

**Distribution:** Pacific coasts of central Japanese mainland from Izu Peninsula to Ibaraki Prefecture.

**Habitat:** The new species byssally attaches to the undersides of partly buried, stable boulders in the upper to lower intertidal zone of open coasts exposed to waves.

**Etymology:** The species epithet is derived from the intertidal habitat of the species. The Latin word "*littoralis*" means "of the seashore."

*Nipponolimopsis decussata* (A. Adams, 1862)

*Cyrella decussata* A. Adams, 1862: p. 295.

*Limopsis nipponica* Yokoyama, 1922: p. 195, pl. 17, figs. 16–17.

*Limopsis skinoshitai* Kuroda, 1930: p. 18, figs. 24–25.

*Limopsis hilgendorfi* Thiele in Thiele & Jaeckel, 1931: pl. 6, figs. 21, 21a.

*Nipponolimopsis nipponica*: Habe, 1951: p. 45, figs. 83–84.

*Aspalima* (*Nipponolimopsis*) *decussata*: Habe, 1953: p. 206, pl. 29, figs. 20–21; Habe, 1961a: p. 112, pl. 50, fig. 7.

*Limopsis* (*Nipponolimopsis*) *nipponica*: Taki & Oyama, 1954: pl. 37, figs. 16–17 (reproduction of Yokoyama, 1922); Oyama, 1973: p. 76, pl. 21, figs. 21–22 (reproduction of Yokoyama, 1922).

*Nipponolimopsis decussata*: Kuroda et al., 1971: pp. 340–341, pl. 117, fig. 15; Habe, 1977: p. 50, pl. 9, figs. 4–5; Oliver, 1981: p. 67, figs. 11–12; Coan et al., 2000: p. 148–149, pl. 21; Matsukuma, 2000: pp. 856–857, pl. 426.

**Diagnosis:** Shell height 5 mm or smaller; anterodorsal margin truncate; posterior margin more roundly and

widely convex than anterior; hinge teeth three in anterior, four in posterior; hinge line and anterior margin variable, forming nearly right angle.

**Type specimen:** Unknown.

**Type locality:** Gotto Islands, 48 fathoms (= Goto Islands, northwestern Kyushu, Japan).

**Distribution:** Pleistocene: Kioroshi Formation, Kioroshi, Chiba, Japan (Yokoyama, 1922 as *Limopsis nipponica*). Recent: Indonesia (Thiele & Jaeckel, 1931 as *Limopsis hilgendorfi*); Iwate Prefecture to East China Sea, Sea of Japan, 40–400 m (Higo et al., 1997: 428, B262); southeastern Hokkaido to Kyushu, 50–100 m (Matsukuma, 2000:857); western Aleutian Islands, Alaska, 219–388 m (Coan et al., 2000:148).

**Remarks:** Although there are multiple problems concerning the true identity of this species, it is currently most practical to follow the conventional interpretation by Dr. Kuroda and Dr. Habe to avoid confusion. (1) The identify of this species is not unambiguous, because an unfigured type of Adams (1862) is missing (cf. Makiyama, 1929; Kuroda & Habe, 1954; Habe, 1961b, 1985; Higo et al., 2001 for types of A. Adams). Finding Adams's specimen is the most important thing in revising this species. (2) *Limopsis hilgendorfi* Thiele & Jaeckel, 1931 and "*N. decussata*" from outside of temperate Japanese waters may not belong to the same conspecific population, but this needs further investigation. (3) It is also possible that *Limopsis nipponica* Yokoyama, 1922 (Figure 7: lectotype) represents an independent extinct species, since it is more obliquely elongate than Recent specimens of *N. decussata* (and also than *N. littoralis*). (4) The holotype of *Limopsis skinoshitai* Kuroda, 1930 is missing (see Hanshin Shell Club, 1986; Kikuchi et al., 1996 for types of Kuroda).

*Nipponolimopsis azumana* (Yokoyama, 1910)

(Figure 8)

*Limopsis azumana* Yokoyama, 1910: p. 3, pl. 9, figs. 16–18; Yokoyama, 1920: p. 174–175, pl. 18, figs. 19–21. *Limopsis truncata* Yokoyama, 1910: p. 4, pl. 9, figs. 13–14.

*Aspalima* (*Nipponolimopsis*) *azumana*: Habe, 1953: p. 207, pl. 29, fig. 22–23.

*Limopsis* (*Nipponolimopsis*) *azumana*: Taki & Oyama, 1954: pl. 19, figs. 19–21 (reproduction of Yokoyama, 1920); Oyama, 1973: p. 76, pl. 21, figs. 12, 15, 19 (reproduction of Yokoyama, 1920)

*Nipponolimopsis azumana*: Kuroda et al., 1971: p. 341, pl. 71, figs. 21–22; Itoigawa et al., 1974: pp. 59–60, pl. 7, fig. 2; Itoigawa et al., 1981: pl. 4, fig. 3; Matsukuma, 2000: pp. 856–858, pl. 426; Ogasawara, 2001: p. 303.

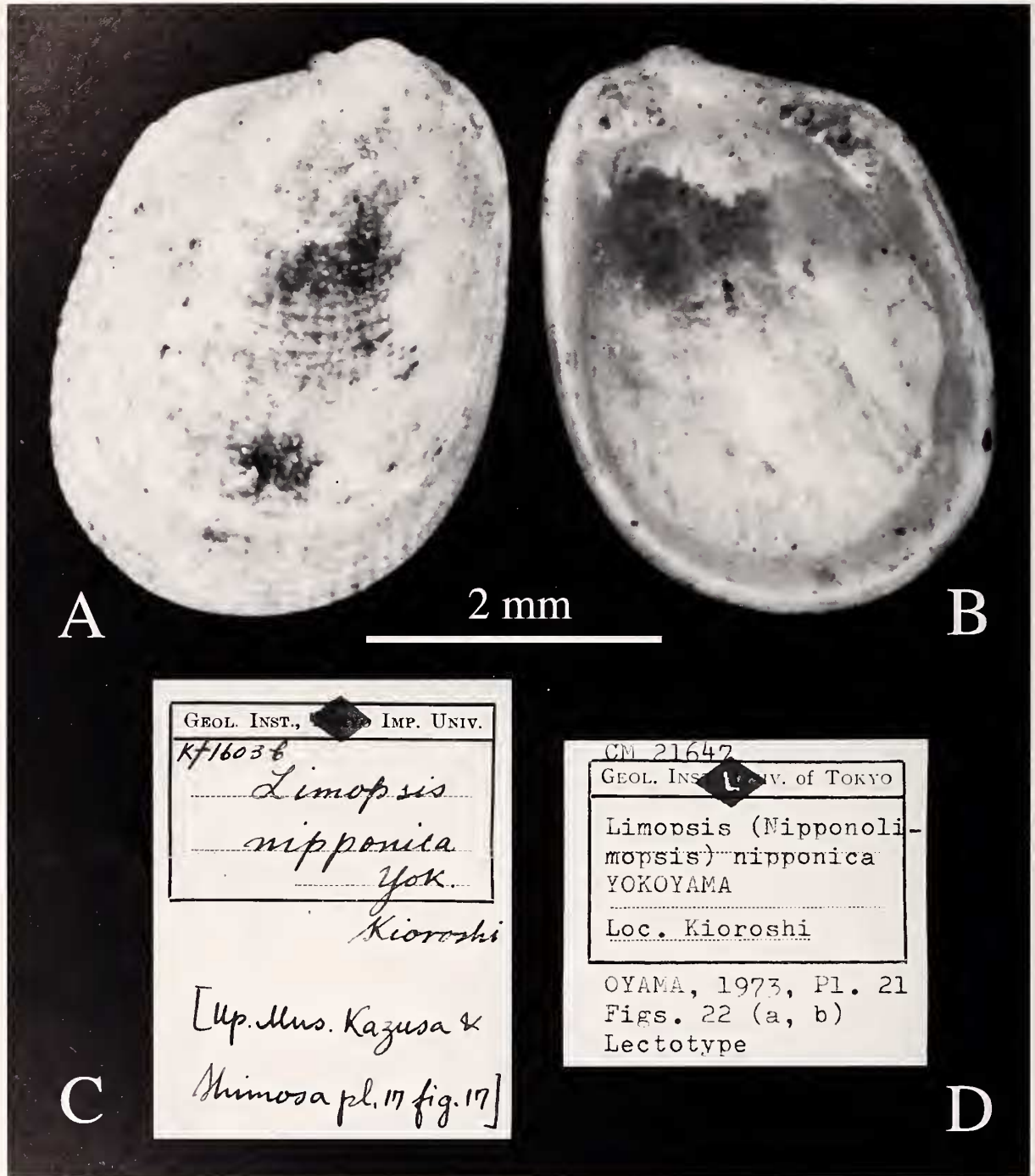


Figure 7. Lectotype of *Limopsis nipponica* Yokoyama, 1922. UMUT CM21647. A. Exterior. B. Interior. C–D. Labels attached to lectotype.

*Limopsis (Limopsis) azumana*: Tanabe, 1990: p. 637, fig. 3.

**Diagnosis:** Shell large for genus, 14 mm or less in height, markedly widened anteroventrally; posterior

margin markedly truncated, straight; anterior hinge teeth four in number, nearly vertical to hinge line; posterior hinge teeth seven, oblique to hinge line; anterior margin and hinge line forming right angle.

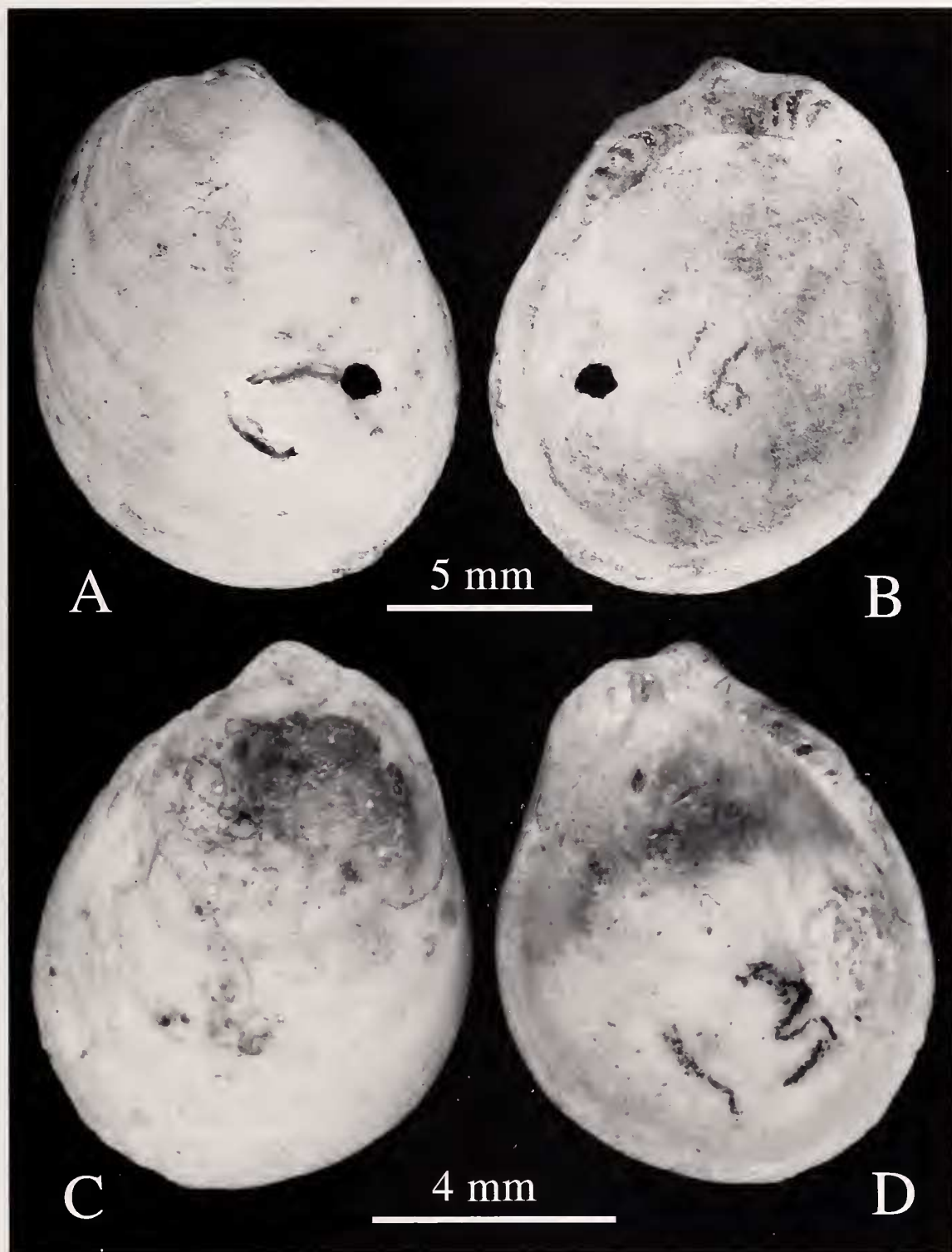


Figure 8. *Nipponolimopsis azumana* (Yokoyama, 1910). A–B. *Limopsis azumana* Yokoyama, 1910. One of syntypes here designated as lectotype. UMUT CM26403. C–D. *Limopsis truncata* Yokoyama, 1910. One of syntypes here designated as lectotype. UMUT CM26404.

**Type specimen:** Lectotype UMUT CM26403 (Figure 8A, B). See Appendix for paralectotypes.

**Type locality:** Koshiha (= Sea cliff of Shiba, Kanazawa-machi, Yokohama, Kanagawa Prefecture, Japan; 35°20'05"N, 139°38'06"E), Pleistocene.

**Distribution:** Miocene: Mizunami Group, Mizunami, Gifu, Japan (Itoigawa et al., 1974, 1981). Pleistocene: Koshiha Formation, Yokoyama, Kanagawa, Japan (Yokoyama, 1910, 1920), Lower Shimoda Formation, Ninomiya, Kanagawa, Japan (Tanabe, 1990). Recent: Sagami Bay to Kii Peninsula, 100–250 m (Higo et al., 1999:428, B263; Matsukuma, 2000:857).

**Remarks:** The type specimens of *Limopsis azumata* Yokoyama, 1910 and *Limopsis truncata* Yokoyama, 1910 had never been critically revised since their original description. We designate lectotypes of these two nominal species and illustrate them in Figure 8 to clearly define their identity. The surface of both lectotypes is smoothed by erosion.

*Nipponolimopsis kutekenensis* Noda, 1980

*Nipponolimopsis kutekenensis* Noda, 1980: pp. 78–79, pl. 12, fig. 11a, b; Ogasawara, 2001: 303.

**Diagnosis:** Shell extended anteroventrally; surface reticulate, roughened by dense concentric ribs; hinge teeth four in anterior, seven in posterior; angle between anterior margin and hinge line larger than 90°.

**Type specimen:** Holotype IGUT10338 (Institute of Geoscience, University of Tsukuba).

**Type locality:** Shinzato Formation, Chinen, Okinawa, Japan, Pliocene.

**Distribution:** Known only from the type locality.

**Remarks:** The species is most similar to *N. azumana* but different in having prominent concentric ribs and larger angle between the anterior margin and the hinge line (greater than 90°) (Noda, 1980: 78–79, pl. 12, fig. 11a, b).

*Nipponolimopsis* sp.

(Figure 9)

**Shell:** The outline is somewhat square (Figure 9A); the dorsal margin completely straight; the anterior margin at the right angle to the dorsal margin; the posterior margin is straight and oblique; the ventral margin is weakly convex. The surface is sculptured by conspicuous reticulate sculpture (Figure 9B). The number of the hinge teeth is four in the anterior and five in the posterior (Figure 9C). The prodissoconch at the beak is semicircular and fringed by an extremely thick ridge

(mr: Figure 9D); the initial center of the prodissoconch is also strongly ridged (cr: Figure 9D).

**Locality:** Off Tanabe, Wakayama Prefecture, Japan (R/V *Tansei-Maru*, cruise KT-05-30, station TN1(1), 33°39.05'N, 135°09.89'E–33°38.96'N, 135°10.16'E, 170.3–173.1 m deep).

**Remarks:** This species is different from any known members of *Nipponolimopsis* in its subsquare outline. The prodissoconch is characteristically margined by a conspicuous ridge in clear contrast to that of *N. littoralis* (Figure 5). This is probably another new species, but we obtained only a single dead valve so far.

## DISCUSSION

The new species is allocated to the genus *Nipponolimopsis* Habe, 1951 based on the combination of several characters such as (1) a small adult size, (2) a reticulate sculpture, (3) a thick periostracum, (4) an anteriorly positioned umbo, (5) a simple alivincular ligament (type C of Oliver, 1981), (6) a small number of taxodont hinge teeth (three anterior and four posterior teeth), (7) the anterior hinge teeth forming larger angles to the hinge axis than inclined posterior teeth, (8) the presence of the marginal locking groove along the inner ventral margin (cf. Oliver, 1981:fig. 12), and (9) a large prodissoconch associated with brooding habit (see Malchus & Warén, 2005 for prodissoconchs of various limopsids for comparison). In the original diagnosis, Habe (1951, 1977:49) mentioned a crenulated inner shell margin. However, such a character state is not confirmed in any species he assigned to the genus, and therefore, it is regarded as an erroneous observation.

By comparison with other described species, *N. littoralis* is diagnosed by four conchological characters. (1) The periostracum is the most distinctive character of the new species. It consists of sparsely and radially arranged, erected bristles and commarginally lamellate membranes. The periostracum of *N. decussata* (Habe, 1961a: pl. 50, fig. 7) and *N. azumana* (Kuroda et al., 1971: pl. 71, fig. 22; Matsukuma, 2000:856) is uniformly hairy and densely covers the shell surface. (2) The outline of the shell of *N. littoralis* is similar to that of *N. decussata* and *N. kutekenensis*, but distinguished from that of *N. azumana* which is more ventrally widened than dorsally (Figure 7). (3) The sculpture of the exterior is similarly reticulate in *N. littoralis*, *N. decussata*, and *N. azumana* (Matsukuma, 2000:856), but concentrically sharpened in *N. kutekenensis* (Noda, 1980: pl. 12, fig. 11a, b). (4) The prodissoconch of *N. littoralis* is characterized by a weak marginal ridge, a finely pitted sculpture, and a deep depression at the beak (Figure 4). This morphology is clearly in contrast to a smooth and rounded prodissoconch of *N. azumana* (Tanabe, 1990) and a more

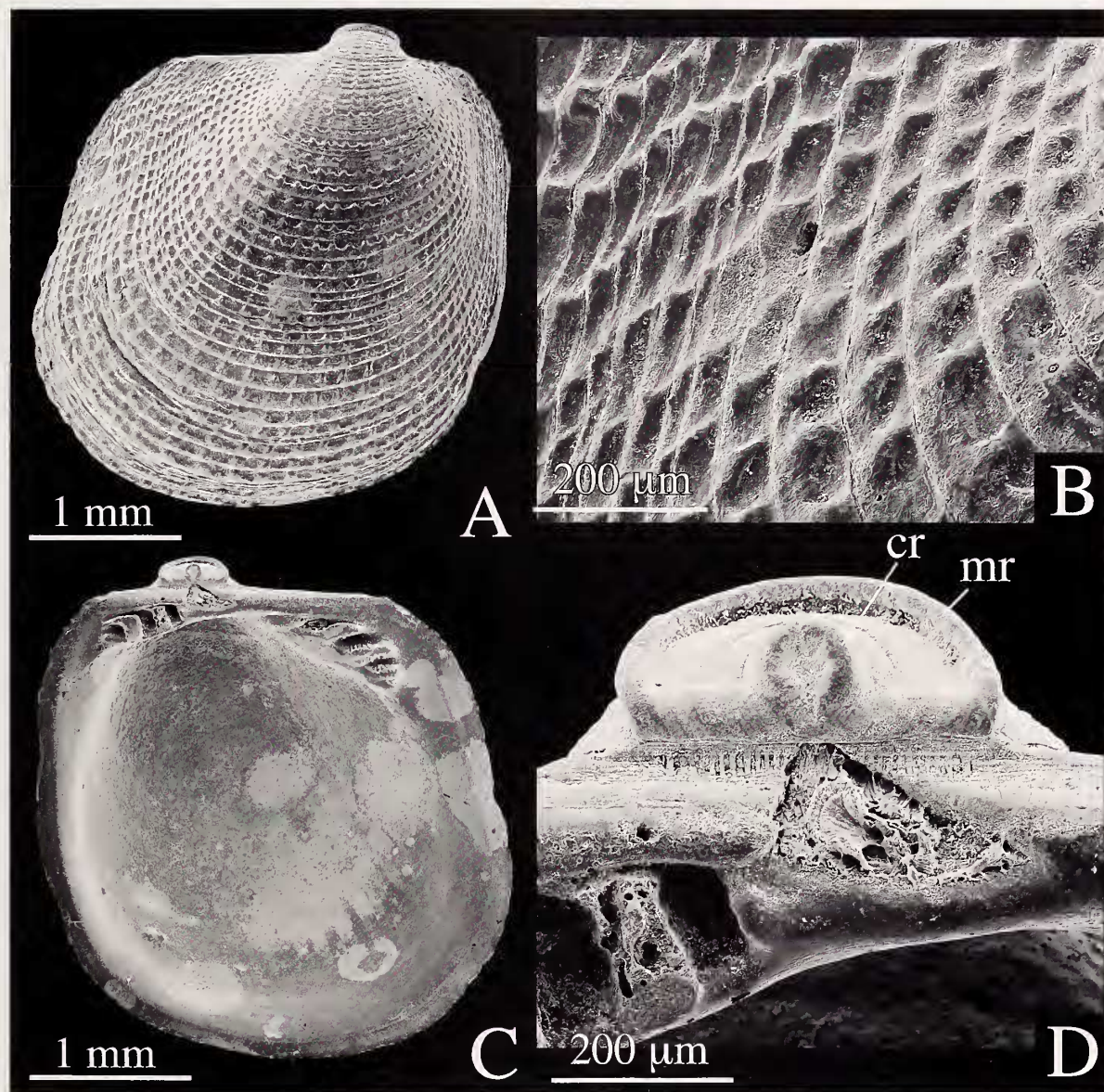


Figure 9. *Nipponolimopsis* sp. A. Shell exterior. B. Enlarged view of exterior sculpture. C. Shell interior. D. Enlarged view of prodissoconch. Disarticulated right valve from sediments dredged from off Tanabe, Wakayama Prefecture, Japan, w170.3–173.1 m deep. UMUT RM29350. Abbreviations: cr = central ridge, mr = marginal ridge.

depressed prodissoconch of *N. decussata* (Oliver, 1981:fig. 12). An unidentified species of *Nipponolimopsis* (Figure 9) also possesses a strikingly different prodissoconch with a sharply ridged fringe and a narrower depression. In addition to these differences in morphology, the new species is also separated by bathymetric distribution. The habitats of *N. decussata* and *N. azumana* range from 50 to 100 m and from 100 to 250 m, respectively (Matsukuma, 2000:857), while *N. littoralis* is confined to the intertidal zone.

At present, it is entirely uncertain whether anatomical characters are useful in diagnosing species, because

no comparable observations have been carried out for the genus. Compared to other limopsids, the ctenidia of *N. littoralis* are different in that the outer demibranchs are smaller than the inner demibranchs at the anterior side (Figure 5A). This morphology is functionally related to the brooding habit of the species. The anterior space of the pallial cavity where the outer demibranchs are lacking is used to brood eggs and larvae. The reduction of the anterior side, especially in the anterior adductor muscle, seems to be correlated with an epibyssate mode of life, as is found in other members of the Limopsidae (Oliver, 1981).

The habitat of the new species on the intertidal bolder shores is exceptional and noteworthy for *Nipponolimopsis*. Other extant species of the genus dwell in the lower subtidal zone (e.g., Oliver & Allen, 1980; Oliver, 1981; Coan et al., 2000; Matsukuma, 2000) and no member has been recorded from the intertidal rocky shores. In the family Philobryidae, most species are recorded from the shallow subtidal zone (Tevesz, 1977; Powell, 1979; Lamprell & Healy, 1998; Coan et al., 2000; Malchus, 2006), but their microhabitats are unknown except for the records from brown or red algae (Tevesz, 1977:30), sea-urchin spines (Janssen, 1997), undersides of stones (Morton, 1978), and submarine caves (Hayami & Kase, 1993). By contrast, *N. littoralis* dwells in the intertidal zone, hanging on the undersides of partly buried, stable boulders in wave-exposed coasts. In the localities (Figure 1), the same habitat is shared only with a limited number of bivalves (c.g., *Ostrea subucula* and *Porterius dalli*).

No ecological and developmental observations have been made on *Nipponolimopsis*. We confirmed that *N. littoralis* broods the larvae with fully developed prodissoconchs in the pallial cavity. This fact indicates lecithotrophic benthic development of this species without a planktonic stage. Tanabe (1990) inferred that *N. azumana* probably undergoes direct development or ovoviviparity based on the morphology and size of well-preserved prodissoconchs of juvenile fossil specimens. Our observation on an unidentified species of *Nipponolimopsis* (Figure 8) also shows a large prodissoconch I (410  $\mu\text{m}$  in length) without the formation of a prodissoconch II. Thus, the small adult size, a relatively large prodissoconch, brooding habit, and benthic development without a planktonic stage, might be a set of shared characters of the members of *Nipponolimopsis*. More detailed comparison on reproduction and development is necessary to evaluate these characters in future studies.

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## APPENDIX

Registration number, references, and present status of *Nippoulimopsis* specimens described by Yokoyama (1910, 1920, 1922).

*Limopsis nipponica* Yokoyama, 1922: UMUT CM21647: Yokoyama, 1922: p. 195, pl. 17, fig. 17 (as syntype); Taki & Oyama, 1954: pl. 37, fig. 17 (designated as holotype [to be lectotype]); Oyama, 1973: p. 76, pl. 21, fig. 22a, b (as lectotype). Present status: Lectotype, present in UMUT (Figure 5). UMUT CM21646: Yokoyama, 1922: p. 195, pl. 17, fig. 16 (as syntype); Taki & Oyama, 1954: pl. 37, fig. 16 (designated as paratype [to be Paralectotype]); Oyama, 1973: p. 76, pl. 21, fig. 21. Present status: Paralectotype, present in UMUT. UMUT CM21648: Yokoyama, 1922: p. 195, not figured (as syntype). Present status: Paralectotype, present in UMUT. UMUT CM21649: Yokoyama, 1922: p. 195, not figured (as syntype). Present status: Paralectotype, present in UMUT.

*Limopsis azumana* Yokoyama, 1910: UMUT CM24526: Yokoyama, 1910: p. 3, pl. 9, fig. 17 (as syntype). Present status: Paralectotype designated in this study, missing. UMUT CM26402: Yokoyama, 1910: p. 3, pl. 9, fig. 16 (as syntype). Present status: Paralectotype designated in this study, present in UMUT (Figure 6A, B). UMUT CM26403: Yokoyama, 1910: p. 3, pl. 9, fig. 18 (as syntype). Present status: Lectotype designated in this study, present in UMUT (Figure 6A, B). UMUT CM24544: Yokoyama, 1920: p. 174, pl. 18, fig. 19a–c; Taki and Oyama, 1954: pl. 19, fig. 19; Oyama, 1973: p. 76, pl. 21, fig. 12a–c (as paratype: error). Present status: Figured non-type specimen, missing. UMUT CM24545: Yokoyama, 1920: p. 174, pl. 18, fig. 20a–c; Taki and Oyama, 1954: pl. 19, fig. 20; Oyama, 1973: p. 76, pl. 21, fig. 15a–c (as paratype: error). Present status: Figured non-type specimen, missing. UMUT CM24546: Yokoyama, 1920: p. 174, pl. 18, fig. 21a–c; Taki and Oyama, 1954: pl. 19, fig. 21; Oyama, 1973: p. 76, pl. 21, fig. 19a–c (as

paratype: error). Present status: Figured non-type specimen, missing. UMUT CM20676: Yokoyama, 1920. p. 174, not figured. Present status: Unfigured non-type specimen, present in UMUT. UMUT CM20677: Yokoyama, 1920. p. 174, not figured. Present status: Unfigured non-type specimen, missing.

*Limopsis truncata* Yokoyama, 1910: UMUT CM26404: Yokoyama, 1910: p. 4, pl. 9, fig. 13 (as syntype). Present status: Lectotype designated in this study, present in UMUT (Figure 6C, D). UMUT CM26405: Yokoyama, 1910: p. 4, pl. 9, fig. 14. Present status: Paralectotype designated in this study, present in UMUT.