

The *Tonicella lineata* (Wood, 1815) species complex (Polyplacophora: Tonicellidae), with descriptions of two new species

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Abstract: Four species of lined chitons from the Pacific coast of North America (two of them new) formerly regarded as *Tonicella lineata* (Wood, 1815) are described and discussed. *Tonicella lineata*; *T. undocaerulea* Sirenko, 1973; *T. lokii* Clark, *spec. nov.*; and *T. venusta* Clark, *spec. nov.* are differentiated by characteristics of their shells, girdle elements and radulae.

Key Words: *Tonicella lineata* complex, chitons, Polyplacophora

For many years chiton workers on the Pacific coast of North America have been aware of two or three varieties of lined chitons of the genus *Tonicella* Carpenter, 1873 that differed markedly from typical *T. lineata* (Wood, 1815). In 1973, Sirenko described *T. undocaerulea*, a species from the northern Sea of Japan that he believed to be the western Pacific Ocean counterpart of the eastern Pacific *T. lineata*. However, soon after its description, several workers recognized *T. undocaerulea* as one of the forms they had been encountering in the waters of Washington and British Columbia. In his revision of the family Lepidochitonidae of the eastern Pacific Ocean, Ferreira (1982) concluded that *T. undocaerulea* and the other lined forms were varieties of a single, widely distributed species properly referred to as *T. lineata*, a view echoed by Kaas and Van Belle (1985). My own preliminary investigations revealed many consistent differences between the various forms. These differences suggested the probability of a complex of several closely related species. Further investigation has produced evidence for the presence of four sibling species that overlap broadly in their ecological habitats as well as in their geographic and bathymetric ranges.

MATERIALS and METHODS

Several hundred specimens of *Tonicella* were exam-

ined and their characters and distributional patterns were compared. Valves, girdle elements and radulae were studied with light and scanning electron microscopes. Several specimens of each of four nominal species were immersed in a heated 10% solution of KOH until all that remained were the shell plates, radulae and epidermal layers (hypernotum & hyponotum) of the girdle; these were then rinsed thoroughly in distilled water. The shell plates were placed in a 50% solution of household bleach for 30 minutes, rinsed and air dried. Radulae and epidermal layers of the girdle were separately rinsed, dehydrated in an acetone series, and air dried. The specimens were then mounted on SEM stubs with colloidal silver paint, sputter coated with gold for two minutes, and examined at 5 or 10 KV with an Hitachi S-2100 scanning electron microscope at the Department of Biology at Southern Oregon University, Ashland, Oregon.

Abbreviations used in the text are: LACM, Los Angeles County Museum of Natural History; LACMIP, Los Angeles County Museum of Natural History-Invertebrate Paleontology; USNM, United States National Museum of Natural History, Washington, D.C.; CAS, California Academy of Sciences, San Francisco; SBMNH, Santa Barbara Museum of Natural History; ZISP, Zoological Institute, Saint Petersburg, Russia; RBCM, Royal British Columbia Museum, Victoria British Columbia, Canada; RMNH, Rijksmuseum van Natuurlijke Historie, Lciden; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; UAF, University of Alaska, Fairbanks; RNC, Private collection of the author.

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SYSTEMATICS

Higher chiton systematics are presently in a state of flux. The widely used and variously modified scheme of Thiele (1909-1910) is based primarily on the characters of the shell plates. However, Sirenko (1993) has proposed a new scheme based on gill placement and the shape of egg hull processes. A very similar system of relationships had been noted earlier by Eernisse (1984). The new scheme appears to be an advancement and is herein adopted.

Order: CHITONIDA Thiele, 1929

Suborder: ACANTHOCHITONINA Bergenhayn, 1930

Superfamily: Tonicelloidea Simroth, 1894

Family: Tonicellidae Simroth, 1894

Subfamily: Tonicellinae Simroth, 1894

Genus: *Tonicella* Carpenter, 1873

Type species: *Chiton marmoreus* Fabricius, 1780, subsequent designation by Dall (1878).

Tonicella lineata (Wood, 1815)

(Figs. 1-8, 33)

Chiton lineatus Wood, 1815:15, pl. 2, figs. 4-5

Chiton (*Stenosemus*) *lineatus* Wood var. *fusca* Von Middendorff, 1847:110

Lepidochitona lineata: Oldroyd, 1927: 255, 256 (in part).

Tonicella lineata: Berry, 1917: 233 (in part); Sirenko, 1974: 995; Ferreira, 1982: 124, figs. 78-81 (in part); Baxter, 1983: 66; Kaas & Van Belle, 1985: 142-144, fig. 65, map 24 (in part); Baxter, 1987: 105.

Diagnosis: Chitons of medium size (to 5.0 cm), oval to elongate-oval, valves convex to subcarinate, beaked; tegmentum smooth (shiny) except for faint growth lines; color orange-salmon or maroon, with alternating white and dark maroon-brown lines; lines on head valve forming forwardly directed gothic arch or arrowhead shape.

Description: Medium-sized chitons, often reaching 40-45 mm in length; largest specimen examined 52.5 mm (RNC 959, Ogden Point Breakwater, Victoria, British Columbia, Canada, leg. George P. Holm, 17 May, 1991). Shell (neotype, herein designated) (fig. 1) oval to elongate-oval, valves subcarinate to convex, beaked; tegmentum smooth (shiny), with faint growth lines. Head valve (fig. 2) semicircular, posterior margin widely V-shaped. Intermediate valves (fig. 3) broadly rectangular, lateral areas very slightly raised, side margins slightly rounded. Tail valve (figs. 4, 5) less than semicircular, about twice as wide as long, with mucro in anterior 1/5-1/3, post-mucronal slope

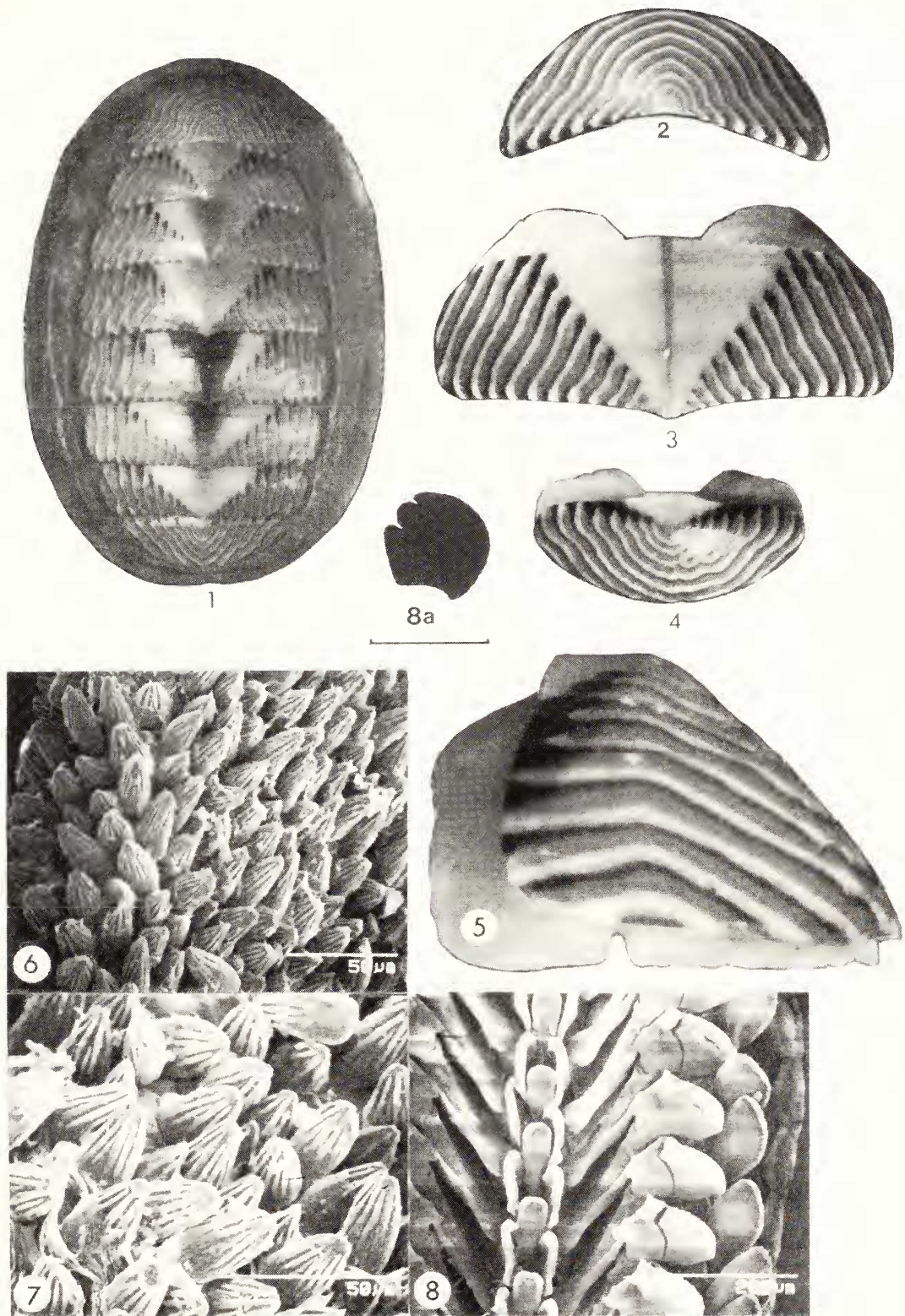
straight to convex. Articulamentum white, with pink stain under central areas; sutural laminae short, wide, about 1/2 length of valve five tegmentum, moderately to strongly rounded; insertion teeth short, thick, finely rugose on anterior surface. Slit formula 8/1/9. Color: orange-salmon or maroon, with alternating white and dark, maroon-brown (often nearly black) lines on terminal valves and lateropleural areas of intermediate valves; lines on head valve always forming forwardly directed arrowhead shape; jugal triangles delineated, usually of darker hues than ground color. Girdle of medium width, about 1/4 width of valve five tegmentum; usually light brown (in alcohol), often with paler bars but occasionally unicolored; dorsal surface covered with very minute, fairly broad, pointed scales (fig. 6), scales strongly ribbed on distal 1/2-3/4, about 28 μ m long and 13 μ m wide at base; ventral surface covered with similar but slightly larger scales (fig. 7) about 32 μ m long and 15 μ m wide. Radula (fig. 8) rachidian tooth narrow, elongate, sides nearly parallel along distal 3/4, distal end rounded; denticle cap of major lateral teeth (fig. 8a) broad, rounded, about 200 μ m x 175 μ m with deep notch on inner edge defining a small, thumb-like denticle, often with a smaller secondary notch above it. Ctenidia merobranchial, abanal, extending 4/5 length of foot.

Range of morphological variation: Some specimens have one or more dark maroon valves. Some specimens are nearly totally (except for subjugal markings) orange-salmon or maroon [var. *fusca* von Middendorff, 1847 (fig. 33), see discussion], but specimens nearly always have at least one white, dark maroon-brown, or black line on the head valve and often on the tail valve as well. Completely white "albino" specimens are infrequent.

Type locality: "Their country is unknown" (Wood, 1815: 16). Subsequently designated as Sitka, Alaska (Sirenko, 1974: 994). Here restricted to Old Sitka (Starrigaven Bay), 10 km N of Sitka, Baranof Id., Alexander Archipelago, SE Alaska (57°08'N, 135°55'W). Ferreira (1982: 125) designated Monterey Bay, California as the type locality, apparently unaware that Sirenko had already designated Sitka as the type locality.

Type material: Lost (Ferreira, 1982). Neotype LACM 2734 (fig. 1) here designated from type locality (leg. RNC, intertidal beneath cobble encrusted with coralline algae; 19 May, 1983); 35 mm x 22.5 mm x 6.5 mm (ex-RNC 496).

Additional material: Alaska: 1, CAS 41449, Montague Id.; 1, RNC 659, Navy breakwater, Kuluk Bay, Adak Id., Aleutian Islands, +0.5 m; 1, RNC 666, Nazan Bay, Atka Id., Aleutians, 0 m; 3, RNC 398, Chernofski



Figs. 1-8. *Tonicella lineata* (Wood, 1815). 1. Whole animal, Neotype, LACM 2734; Old Sitka, Baranof Island, Alaska. 35 mm x 22.5 mm x 6.5 mm. 2-8. RNC 430, Cape Arago, Oregon. 2. Head Valve; width 9.0 mm. 3. Intermediate valve five; width 12.2 mm. 4, 5. Tail valve; width 6.3 mm. 6. Dorsal girdle scales. 7. Ventral girdle scales. 8. Radula. 8a. Denticle Cap of Major Lateral Tooth. Bar = 200 μ m.

Harbor, Unalaska Id., Aleutians, 0 m; 5, Eider Point, Unalaska Id., Aleutians, 0 m; 2, RNC 901, Herendeen Bay, SE Bering Sea, 0 m; 3, RNC 146, Chiniak Bay, Kodiak Id., 0 m; 4, RNC 442, Kachemak Bay, Kenai Peninsula, 0 m; 2, RNC 496, Old Sitka, Baranof Id., 0 m; 9, RNC 975, Petersburg, Mitkof Id., 0-1 m; 5, RNC 1295, Petersburg, Mitkof Id., 1 m; 6, CAS 083452, Edena Bay, Kosciusko Id.; 4, RNC 1236, N. Vallinar Rocks, Gravina Id., 3-5 m; 77, CAS 013454, N of Ketchikan, Revillagigedo Id.; 3, RNC 970, Saxman, Revillagigedo Id., 0-1 m; 3, RNC 969, Rotary Beach, Revillagigedo Id., 0-1 m; 3, RNC 1191, Mountain Pt., Revillagigedo Id., 0-1 m; 12, RNC 5450, Metlakatla, Annette Id., 0-2 m; 9, RNC 544, Brownson Bay, Prince of Wales Id., 0-1 m; 24, CAS 013121, Rose Inlet, Dall Id., British Columbia: 2, CAS 013590, Portage Inlet, 1 m; 5, RNC 934, Bowen Id., 3-5 m; 3, RNC 320, Victoria, Vancouver Id., 0-2 m; 1, RNC 959, Victoria, Vancouver Id., 0-1 m. Washington: 2, CAS 013346, Marrowstone Id., Jefferson Co.; 2, RNC 344, Indian Id., Jefferson Co., 0-1 m; 2, RNC 642, Neah Bay, Clallum Co., 0-1 m; 5 RNC 13, Tacoma Narrows, Pierce Co., 0-1 m. Oregon: 2, RNC 430, N Cove, Cape Arago, Coos Co., +1 m; 5, RNC 4, Cape Blanco, Curry CO., 0 m; 1, RNC 979, Port Orford, Curry Co., 2 m; 1, RNC 999, Island Rock, Curry Co., 17 m; 4, RNC 963, Brookings, Curry Co., 0 m. California: 4, CAS 060413, Trinidad, Humboldt Co.; 28, CAS 009294, S of Cape Mendocino, Humboldt Co.; 3, CAS 013396, Shelter Cove, Mendocino, Co., 0-1 m; 1, CAS 013374, Fort Ross, Sonoma Co.; 2, CAS 077112, Bodega Head, Sonoma Co.; 3, CAS 069442, Bodega Bay breakwater, Sonoma Co.; 4, CAS 034724, Duxbury Reef, Marin Co.; 2, CAS 078781, Marin Co.; 1, CAS 077028, Angel Id., San Francisco Bay; 3, CAS 001933, Fort Mason, San Francisco Co.; 2, CAS 007149, Franklin Point, San Mateo Co.; 1, CAS 007148, Ano Nuevo Point, San Mateo Co.; 1, CAS 000219, Davenport Landing, Santa Cruz Co.; 3, CAS 013361, China Point, Monterey Co.; 2, RNC 1233, Coast Guard breakwater, Monterey Bay, 3-5 m.

Distribution: *Tonicella lineata* is a North American boreal species endemic to the Aleutian and Oregonian provinces (Fig. 37). The species occurs continuously from the central Aleutian Islands to central California in depths ranging from +2 to 17 m. The westernmost record is Navy breakwater, Kuluk Bay, Adak Island, Aleutian Islands, Alaska (51°45'N, 176°45'W) (LACM 86-00.0, RNC 659, leg. Rae Baxter, 12 August, 1286, intertidal); the northernmost record is Montague Island, Prince William Sound, Alaska (60°10'N, 147°15'W) (CAS 41449), and the southernmost record is the United States Coast Guard breakwater, Monterey Bay, Monterey County, California (36°45'N, 121°55'W) (RNC 1060; leg. RNC, with SCUBA, 23 March, 1992, 5 m). These animals are abundant at some localities,

with population densities often exceeding 50 per square m. This species fairly common at the Navy breakwater at Adak Island (Rae Baxter, pers. comm., Nov. 1988) but is abruptly absent west of that locality. In the southern portion of its range, it becomes uncommon from Mendocino County, California southward, where it begins to overlap with the similar *Tonicella lokii*; it is quite rare in Monterey County.

Habitat and ecology: Lives on cobbles, boulders and bedrock encrusted with purple-pink coralline red algae (*Lithothamnion* spp.) or unidentified rust-brown encrusting bryozoans

Fossil record: Valves of *Tonicella lineata* have been identified from Pleistocene deposits in southern Oregon and northern California (LACMIP loc. 2636, Coquille Point, Coos Co., Oregon; LACMIP loc. 2641, Cape Blanco, Curry Co., Oregon; LACMIP loc. 3955, Battery Formation, Crescent City, Del Norte Co., California; LACMIP loc. 4816 & 10770 & USGS loc. M7824, Point Arena, Mendocino Co., California). These specimens have been radiometrically dated at 80,000-85,000 years before present (BP). Specimens from Moonstone Beach, Humboldt Co., California (LACMIP loc. 3942) have been dated at 700,000-1,000,000 years BP (George L. Kennedy, pers. comm. Oct. 1992).

Remarks: *Tonicella lineata* is remarkably similar to *T. undocaerulea* Sirenko, 1973 and *T. lokii* Clark, spec. nov. (see comments for those species).

Tonicella undocaerulea Sirenko, 1973

(Figs. 9-16, 35, 36)

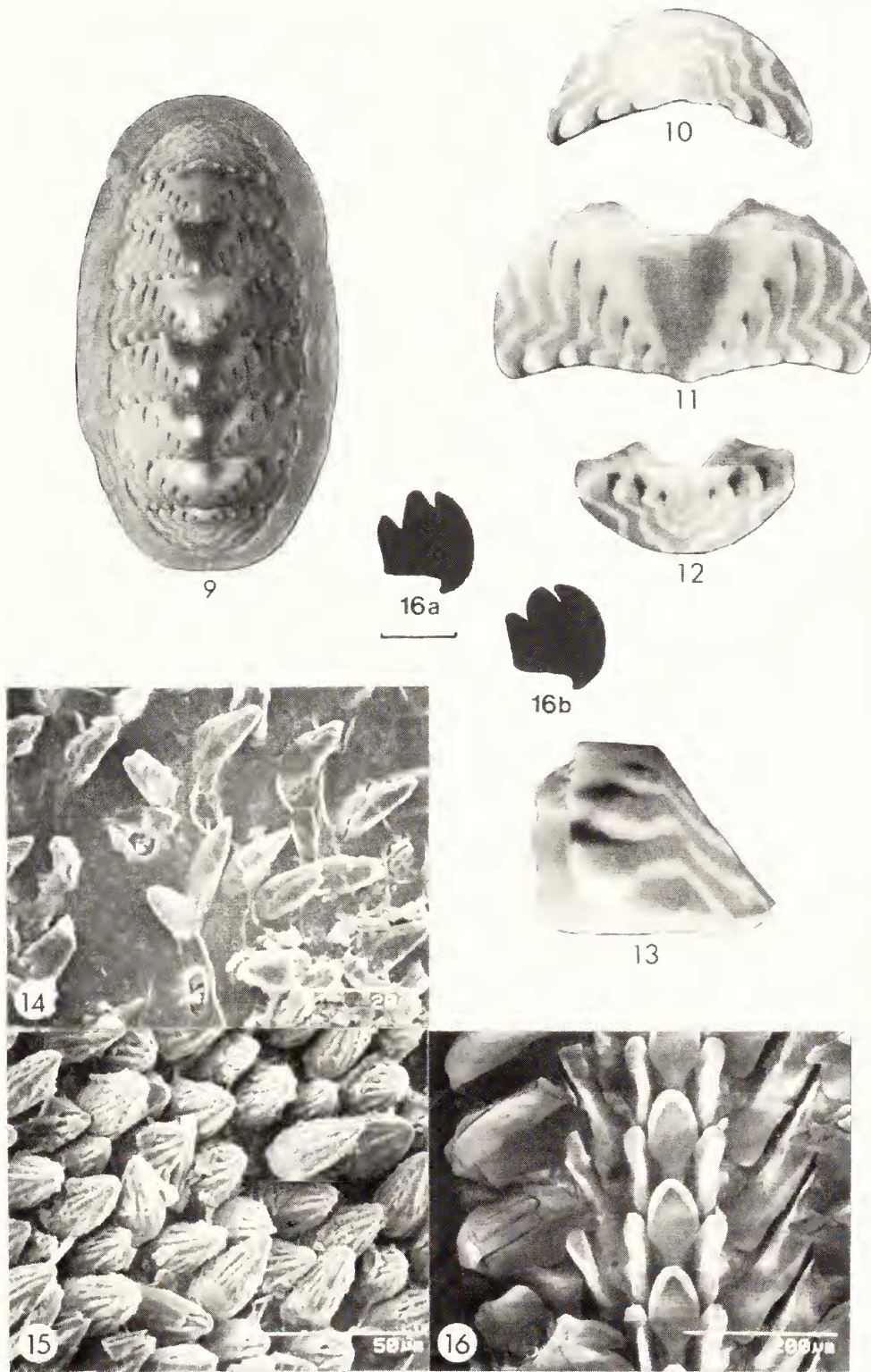
Lepidochitona lineata, non Wood: Oldroyd, 1927: 255, 256 (in part).

Tonicella lineata, non Wood: Taki, 1938: 331; Yakovleva, 1952: 56, 61-62 (in part); Itoigawa *et al.*, 1978 (Fossil): 150-153, pl. 16, figs. 2-7; Ferreira, 1982: 124-126 (in part); Kaas & Van Belle, 1985: 142-144, fig. 65-5, 6, map 24 (in part).

Tonicella undocaerulea Sirenko, 1973: 663, figs. 3/1-7, 9-13; Baxter, 1983: 66; Baxter, 1987: 105.

Diagnosis: Chitons of relatively small size [(to 3.8 cm), Asian specimens smaller]; shell oval to elongate-oval; valves subcarinate to round, beaked; tegmentum smooth, shiny; color (in alcohol) light orange with white zigzag lines, often with short, dark maroon streaks on edges of pleural areas.

Description: Relatively small chitons, rarely exceeding 25 mm in North American waters and 16 mm in



Figs. 9-16. *Tonicella undocerulea* Sirenko, 1973. 9. Whole animal, RNC 2222; Vallinar Rocks, Gravina Id. (near Ketchikan) Alaska. 25.0 mm x 14.0 mm x 4.5 mm. 10-16 RNC 255; Neah Bay, Clallum County, Washington. 10. Head valve; width 4.5 mm. 11. Intermediate valve five; width 6.7 mm. 12, 13. Tail valve; width 4.0 mm. 14. Dorsal girdle scales. 15. Ventral girdle scales. 16. Radula. 16a. Denticle Cap of Major Lateral Tooth (Asian specimen). 16b. Denticle Cap of Major Lateral Tooth (North American specimen). Bar = 100 μ m.

Asian waters. Largest specimen examined 38.0 mm (RNC 287b, Ogden Point breakwater, Victoria, British Columbia, *leg.* RNC, 12 July, 1987). Shell oval to elongate-oval (often egg-shaped)(fig. 9), valves subcarinate to round, beaked; tegmentum smooth, shiny, usually lacking noticeable growth lines. Head valve (fig. 10) semicircular, posterior margin widely V-shaped to nearly straight. Intermediate valves (fig. 11) broadly rectangular, lateral areas indistinct to slightly raised, side margins slightly rounded. Tail valve (figs. 12, 13) oval, mucro in anterior 1/3, post-mucronal slope convex to (rarely) slightly concave. Articulation white, stained with intense rose-maroon under central areas; sutural laminae short, wide, about 1/3 length of valve five tegmentum, rounded; insertion teeth short, solid; slit formula 8/1/8-9. Color light orange, terminal valves with concentric, white zigzag lines radiating from apices; lateropleural areas with white zigzag lines, those on pleural areas often bordered beneath with short, dark maroon streak; jugal areas with delineated triangles of maroon, yellow, orange, or white. Girdle narrow, less than 1/4 width of valve five tegmentum, appearing nude; dorsal surface covered with minute, rather narrow, pointed, smooth scales (fig. 14), about 18-20 μm long and 5 μm wide, with single groove (often obscured) extending from apex to about mid length of scale; ventral surface covered with minute, tear-drop shaped scales (fig. 15), about 25 μm long and 12 μm wide, ribbed along proximal 1/2-1/3. Radula (fig. 16) rachidian tooth very broadly dilated anteriorly, forming distinctive spoon shape; denticle cap of major lateral teeth (16a & b) tridentate, about 120 μm x 130 μm , central cusp the largest, inner cusp slightly smaller, and outer cusp about 1/2 length of the central one. Ctenidia mero-branchial, abanal, extending about 3/4 to 4/5 length of foot.

Range of morphological variation: *Tonicella undocaerulea* varies somewhat in shape and size from one locality to another in American waters, some specimens being quite egg-shaped in outline, whereas others are very elongate. The slope of the shell also varies from straight and nearly carinate to very convex. The valves of some specimens may be completely maroon, or suffused with maroon on the lateropleural areas; the ground color of some specimens may be yellow.

Type Locality: Russia, Bay of Minonosok, Posjet Strait, Sea of Japan (42°39'N, 130°54'E), by original designation (Sirenko, 1973).

Type material: Holotype ZISP 1905; paratypes ZISP 1906 & 1907.

Additional material: Russia: 3, RNC 103, Vostok Bay, Sea of Japan, 1-2 m; 3, RNC 118, Vostok Bay, Sea of

Japan, 1 m; 2, CAS 077081, Vostok Bay, Sea of Japan, 1-22 m; 7, CAS 013448, Vostok Bay, Sea of Japan, 2-3 m; 12, LACM 91-91, Vostok Bay, Sea of Japan, 0-3 m; 4, LACM 91-94, Vostok Bay, Sea of Japan, 3-10 m; 1, LACM 91-89, Popova Id., Amusky Bay, Sea of Japan, 0-2 m. Japan: 8, LACM 82-12, Mutsu Bay, Honshu Id., 3-10 m; 1, RNC 725, Oshoro, Hokkaido, 1-3 m; 1 valve, RNC F-1 (fossil), Soli, Kisarazu City, Chiba Prefecture, Kioroshi Formation, Shimosa group, Middle Pleistocene. Alaska: 2, RNC 501, Naked Id., Prince William Sound, 3-6 m; 1, CAS 013449, Kodiak Id.; 1, RNC 1196, Chiniak Bay, Kodiak Id., 1 m; 1, RNC 679, Hesketh Id., Kachemak Bay, Kenai Peninsula, 9 m; 6, RNC 348, Kachemak Bay, Kenai Peninsula, 1-2 m; 6, RNC 348, Kachemak Bay, Kenai Peninsula, 1-2 m; 6, RNC 144, Sitka, Baranof Id., 1-2 m; 1, LACM 73-13, Sitka, Baranof Id., 1-5 m; 1, LACM 73-15, Pirate Cove, Baranof Id., 3-12 m; 2, RNC 1192, Petersburg, Mitkof Id., 5-6 m; 25 CAS 013331, Edena Bay, Kosciusko Id.; 5 RNC 2222, Vallinar Rks., 3-5 m; 3 RNC 940, Saxman, Revillagigedo Id., 0-2 m; 5, RNC 1031, Rotary Beach, Revillagigedo Id., 0-1 m; 4, RNC 241, Mountain Pt., Revillagigedo Id., 1-3 m; 10, RNC 1189, Mountain Pt., Revillagigedo Id., 0-5 m; 9, RNC 425, Metlakatla, Annette Id., 0-2 m; 1, RNC 1198, Washington Monument, Revillagigedo Channel, 5-8 m. British Columbia: 1, RNC 222, Port Hardy, Vancouver Id., 1-2 m; 1, CAS 002414, Quiet Bay, Vancouver Id.; 11, RNC 287, Victoria, Vancouver Id., 0-2 m. Washington: 5, RNC 136, San Juan Id., 12-18 m; 2, RNC 337, Port Gable, Hood Canal, Kitsap Co., 1 m; 2, RNC 255, Neah Bay, Clallum Co., 1-2 m. Oregon: 5, RNC 973, Island Rock, Curry Co., 30 m; 1, RNC 141, Brookings, Curry Co. California: 9, LACM 71-106, Tolo Bank, Mendocino Co., 21-30 m; 1, LACM 64-20, Salt Point Ranch, Sonoma Co., 3-5 m; 1, CAS 008948, SE Farallon Id.; 4, CAS 013350, Monterey Bay, Monterey Co., 18 m; 9, LACM 60-22, Del Monte, Monterey Bay, 18 m; 6, RNC 1027, Coast Guard breakwater, Monterey Bay, 3-15 m; 3, LACM 63-3, Coast Guard breakwater, Monterey Bay, 4-12 m; 2, CAS 083441, Chace Reef, Monterey Co., 12-13 m; 1, LACM 60-24, Carmel Submarine Canyon, Monterey Bay, 3-15 m; 3, LACM 63-3, Coast Guard breakwater, Monterey Bay, 4-12 m; 2, CAS 083441, Chace Reef, Monterey Co., 12-13 m; 1, LACM 60-24, Carmel Submarine Canyon, Monterey Bay, 12-38 m; 2, LACM 38-153, San Luis Obispo Bay, San Luis Obispo Co., 15-26 m; 1, LACM 38-162, San Miguel Id., Channel Islands, 9-27 m.

Distribution: *Tonicella undocaerulea* has a discontinuous distribution. In Asian waters it has been reported from the Sea of Japan (Sirenko, 1973; Saito, 1994) from Mutsu Bay, Honshu Id. Japan (42°20'N, 140°55'E) to near Uglegorsk, SE Sakhalin Id., Russia (49°00'N, 142°31'E)

and the Okhotsk Sea (Sirenko, 1973) from Iturup Id., Kurile Is., Russia (approx. 45°00'N, 147°30'E) at depths of 1-27 m (Sirenko, 1973). In American waters it is found from Kodiak Id., Alaska (57°50'N, 152°30'W)(RNC 1196) and Naked Id., Prince William Sound, Alaska (60°37.8'N, 146°23'W)(RNC 501) to San Miguel Id., California (34°01'N, 120°24'N)(LACM 38-162) (Fig. 37) at depths of 0-38 m.

Habitat: *Tonicella undocaerulea* lives on encrusting coralline algae (*Lithothamnion* spp.) on pebbles, cobbles, boulders and bedrock.

Fossil record: Valves of *T. undocaerulea* have been found in the middle Pleistocene deposits on the Boso Peninsula, Honshu Id., Japan (Itoigawa *et al.*, as *T. lineata*).

Remarks: *Tonicella undocaerulea* has long been confused with the similar *T. lineata* and *T. lokii* because of its lined color pattern and habitat of encrusting *Lithothamnion*. However, it may be distinguished from both of these species by its lack of maroon-brown "black" lines on the valves.

North American specimens of *Tonicella undocaerulea* are considerably larger than Asian specimens, attaining a length of up to nearly 40 mm, whereas the largest specimen recorded from Asia is 16 mm (Sirenko, 1973). Also, the denticle cap of the major lateral teeth of North American specimens have very rounded cusps, in Asian specimens they are quite triangular. However, all other characters of North American and Asian specimens are identical. Because of the differences in size and distribution, and the shape of the denticle caps, North American specimens should perhaps be considered a subspecies.

***Tonicella lokii* sp. nov.**

(Figs. 17-24)

Tonicella lineata, non Wood: Berry, 1922: 433, pl. 2 figs. 1-5 (fossil); Burghardt and Burghardt, 1969: 36 (in part, pl. 4, no. 76); of authors (from Monterey Bay and central California).

Lepidochitona lineata, non Wood: Oldroyd, 1927: 255, 256 (in part).

Diagnosis: Chitons of medium size (to 5.0 cm), shell low to moderately elevated; valves salmon to light orange, with white and dark maroon-brown (black), zigzag lines on terminal valves and lateropleural areas of intermediate valves; jugal areas with dark orange, pink, or maroon triangles; tail valve with concave post-mucronal slope; girdle with alternating light and dark bars.

Description: Holotype (fig. 17) 32.3 mm x 21.0 mm x 5.5 mm; body oval in outline, slightly elevated; valves subcarinate, smooth. Head valve (fig. 18) semicircular, posterior margin widely V-shaped. Intermediate valves (fig. 19) rectangular, length about 1/3 width, slightly beaked. Tail valve (figs. 20-21) oval, more than twice as wide as long, mucro in anterior 1/3, post-mucronal slopes concave. Articulation white, with light brown rays on slit rays, often with triangular pink stain under central areas; slit formula 9/1/11; sutural laminae short, about 1/2 length of valve five tegmentum; jugal sinus rather narrow; insertion teeth short, thick, those on head valve crenulated on exterior surface. Girdle moderately wide, about 1/4 width of valve five tegmentum; dorsal surface appearing smooth, actually clothed with very minute non-imbricating, broad, smooth, bluntly pointed scales (fig. 22) 22-25 µm long and 10-12 µm wide, rarely with a barely perceptible groove extending from apex to mid-length of scale; ventral surface covered with minute, densely packed, broad scales (fig. 23) 2/3 length. Radula (fig. 24) 9.7 mm long, bearing 53 mature rows of teeth; rachidian tooth about 100 µm long, narrow at base dilated anteriorly to broad, spatula shape about 50 µm wide and slightly recurved at distal end; denticle cap of major lateral teeth (24a) broad, rounded, slightly longer than wide, about 120 µm x 135 µm, with deep notch on inner edge defining a small thumb-like denticle. Ctenidia merobranchial, abanal, extending 4/5 length of foot, about 25 plumes per side.

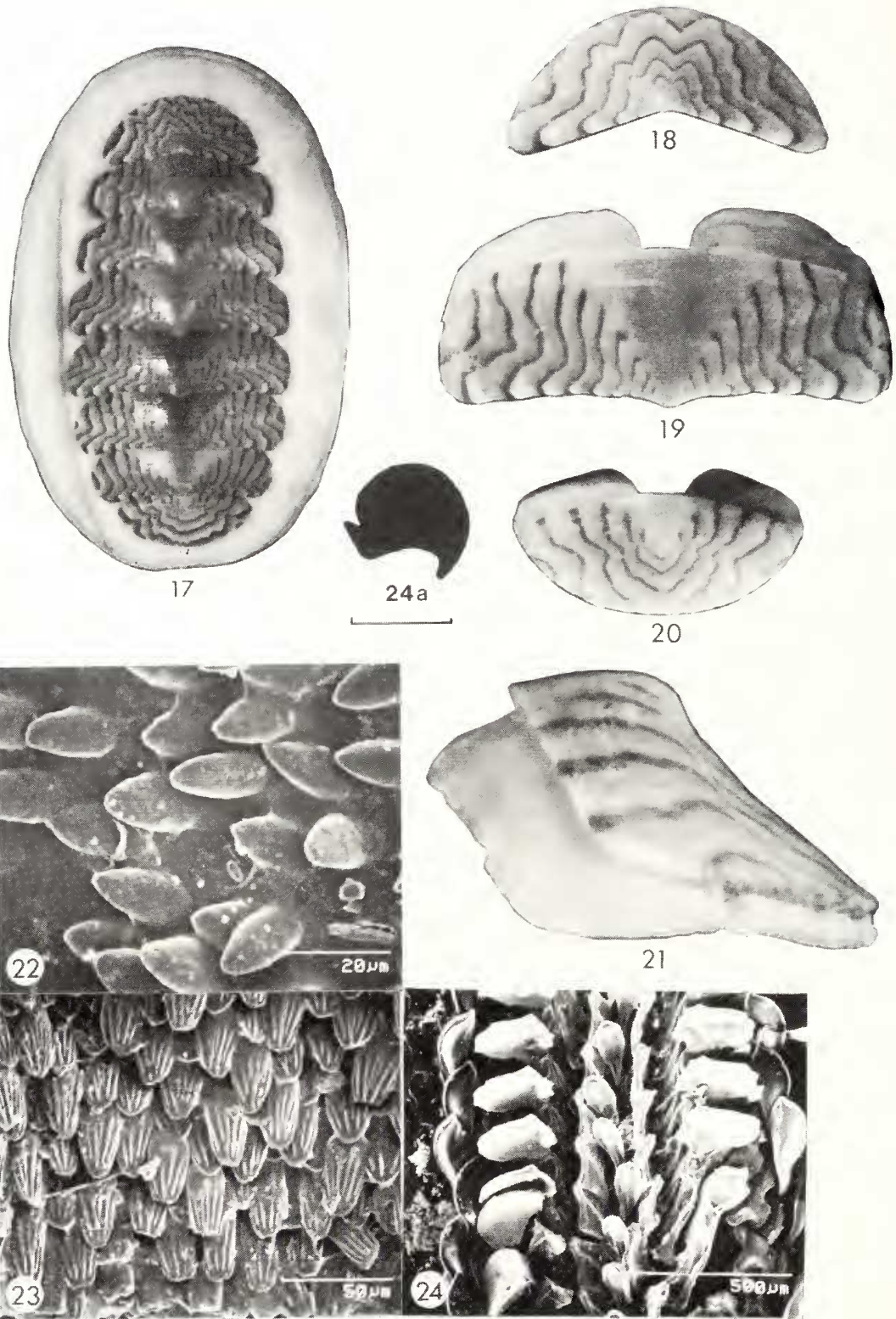
Range of morphological variation: As is the case with several members of this genus, individual valves may be uniformly white or dark maroon. However, unlike other *Tonicella* spp., the central portion of the articulation is often unstained, and when stain is present it may be pink, rose, or light brown.

Type locality: Coast Guard breakwater, Monterey Bay, Monterey County, California (36°45'N, 121°55'W), 0-13 m.

Type material: Holotype (LACM 2623) and 36 paratypes (2, LACM 2624 & 2625); (2, USNM 880067); (2, CAS 103560); (2, SBMNH 141109); (1, UMMZ 252868); (2, RMNH 9360); (3, ZISP 1933); (22, RNC 1056 & 1191).

Type material preserved flat and fully extended, all but seven in 70% ethanol or 70% isopropyl alcohol; remaining seven specimens glycerin-dried. Type material collected 16 & 23 March, 1992 by RNC (9 specimens) and 26 March, 1993 by RNC and Bob Abela (28 specimens).

Additional material: California: 1, CAS 013583, Shelter Cove, Humboldt Co.; 1, CAS 013798, N of West-



Figs. 17-24. *Tonicella lokii* Clark, spec. nov. 17. Whole animal, Holotype, LACM 2623; 32.3 mm x 21.0 mm x 5.5 mm. 18-24. Paratype, RNC 1056. 18. Head valve; width 9.4 mm. 19. Intermediate valve five; width 13.2 mm. 20, 21. Tail valve; width 8.8 mm. 22. Dorsal girdle scales. 23. Ventral girdle scales. 24. Radula. 24a. Denticle Cap of Major Lateral Tooth. Bar = 100 μ m.

port Landing, Mendocino Co.; 3, CAS 013459, Buckhorn Cove, Mendocino Co., 0.5 m; 5, CAS 013453, Albion Head, Mendocino Co.; 10, LACM 49-3, Salmon Point, Mendocino Co., 0.5 m; 20, LACM 50-11, Fort Ross, Sonoma Co., 0.5 m; 8, CAS 043848, Stewart's Point, Sonoma Co.; 3, CAS 069441, Bodega Bay breakwater, Sonoma Co.; 1, CAS 043485, Tomales Point, Marin Co.; 18, CAS 008948, SE Farallon Id.; 1, CAS 069445, S of Pescadero Point, San Mateo Co.; 1, CAS 007065, Pigeon Point, San Mateo Co.; 1, CAS 000217, Davenport Landing, Santa Cruz Co.; 5, CAS 013350, Monterey Bay, Monterey Co., 18 m; 6, CAS 013361, China Point, Monterey Co.; 2, CAS 013364, Cannery Row, Monterey Bay, 10 m; 7, LACM 63-58, Mission Point, Monterey Co., 0.5-2 m; 2, RNC 342, Point Pinos, Monterey Co., 0-1 m; 4, RNC 656, Carmel, Monterey Co., 0-1 m; 2, CAS 056335, 6.4 km N of San Simeon, San Luis Obispo Co.; 2, RNC 402, Cayucos, San Luis Obispo Co., 0.5 m; 1 CAS 013586, Purisima Point, Santa Barbara Co.; 1, CAS 020482, Surf, Santa Barbara Co.; 1, LACM 64-28, S side of Anacapa Id., Channel Is., 15-24 m; 7, LACM 67-38, SE of Bay Point, San Miguel Id., Channel Is., 0-8 m.

Distribution: *Tonicella lokii* occurs between latitudes 40°N and 34°N, on the northern and central coast of California (Fig. 37) at depths of 0-24 m. The northernmost record is Shelter Cove, Humboldt County (40°01.5'N, 124°45'W)(CAS 013583), and the southernmost record is SE of Bay Point, San Miguel Id., California (34°02'N, 120°18'W)(LACM 67-38). Only one specimen of *T. lokii* has been recorded from Humboldt County, and the species is not common in adjacent Mendocino County to the south, but it becomes more abundant closer to the Monterey County distribution center.

Habitat and ecology: *Tonicella lokii* lives on cobbles, boulder, and bedrock encrusted with coralline algae (*Lithothamnion* spp.).

Fossil record: Valves of *T. lokii* have been identified from Pleistocene deposits in southern California (LACMIP Loc. 11004, First Terrace, Army Camp Beach, San Nicholas Island), at a San Pedro area terrace (Berry, 1922, as *T. lineata*), and from northern Baja California, Mexico (LACMIP loc. 10131, Lighthouse Terrace, Bahia el Playon, Punta Banda, and LACMIP loc. 10619, Lighthouse Terrace, near tip of Punta Banda). The specimens have been dated at 80,000-85,000 years BP (G. L. Kennedy, pers. comm., 1992).

Etmology: Named for Loki, the Norse God of mischief and deception, appropriate for a species that long has deceived biologists as to its true identity.

Remarks: *Tonicella lokii* is often found with the morphologically similar and apparently closely related *T. undocerulea*, but it can be easily distinguished from the latter by the presence of dark maroon-brown lines on its valves. *Tonicella lokii* may also be found with *T. lineata*, from which it can be distinguished by the concentric zigzag lines on the head valve (those on *T. lineata* form a very distinctive gothic arch) and by the concave post-mucronal slope of its tail valve.

Tonicella venusta sp. nov.

(Figs. 25-32, 34)

Tonicella rubra, non Linnaeus: Berry, 1917: 233 (in part); Smith and Gordon, 1948: 205; Burghardt and Burghardt, 1969: pl. 4, fig. 79.

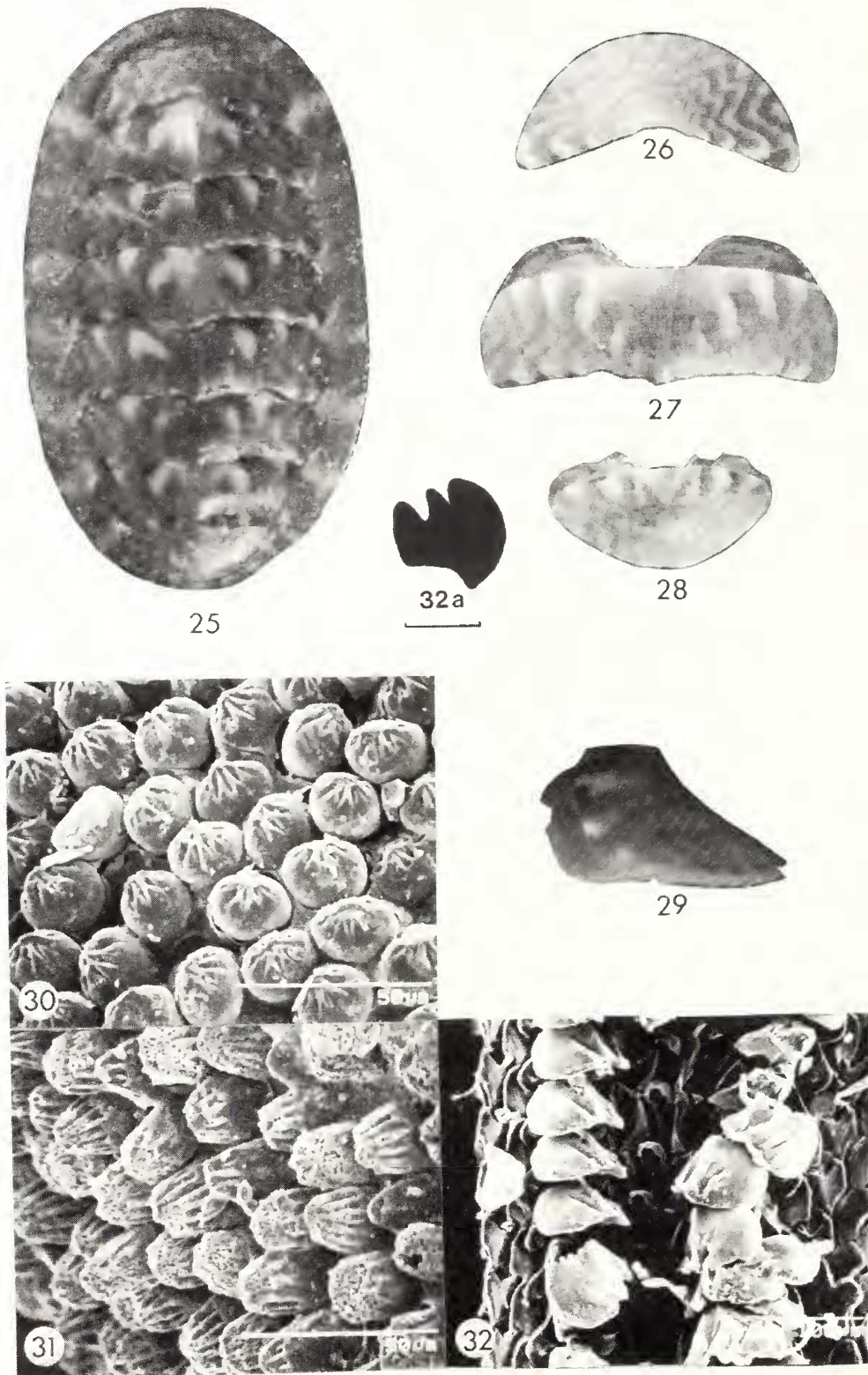
Lepidochitona lineata: Oldroyd, 1927: 255, 256 (in part).

Lepidochitona ruber, non Linnaeus: Oldroyd, 1927: 256-257 (in part).

Tonicella marmorea, non Fabricius: Baxter, 1983: 66.

Diagnosis: Chitons of small size (to 1.7 cm), oval, shell low to moderately elevated, subcarinate; valves light orange or pink, terminal valves and lateral areas of intermediate valves with white, zigzag lines; pleural areas with 2-5 large white flammules; jugal areas with orange, pink, white or maroon triangles; post-mucronal slope of tail valve concave.

Description: Holotype (fig. 25) preserved dry, flat and fully extended, 10.5 mm x 6.0 mm x 1.8 mm; body oval in outline, slightly elevated; valves subcarinate, smooth. Head valve (fig. 26) semicircular, posterior margin widely V-shaped. Intermediate valves (fig. 27) rectangular, length about 1/3 width, beaked; lateral areas poorly defined. Tail valve (figs. 28-29) oval, length about 1/2 with; mucro anterior 1/3, post-mucronal slope concave. Articulamentum white or pale pink, with triangular maroon stain under central area; sutural laminae short, about 1/3 length of valve five tegmentum; jugal sinus about 1/5 valve width; insertion teeth short, fairly thick; slit formula 8/1/11. Girdle of moderate width, about 1/4 width of valve five tegmentum, of sandy appearance, clothed dorsally with relatively large, closely packed, erect, smooth, rotund, mammillate scales (fig. 30) about 45 µm long and 28 µm wide; mammillae with 8-10 heavy ribs; ventral surface of girdle covered with closely packed, rather broad, bluntly tapering scales (fig. 31) about 30 µm long and 16 µm wide, strongly ribbed on proximal 1/3-1/2. Radula (fig. 32) 3.2 mm long, with 53 mature rows of teeth; rachidian tooth spatulate, about 75 µm long and 12 µm wide at base, dilating proximally to about 30 µm wide at working edge, thickened on



Figs. 25-32. *Tonicella venusta* Clark, spec. nov. 25. Whole animal, Holotype, LACM 2626: 10.5 mm x 6.0 mm x 1.8 mm. 26-32. Paratype, RNC 1033 26. Head valve; width 4.0 mm. 27. Intermediate valve five; width 5.0 mm. 28, 29. Tail valve; width 3.2 mm. 30. Dorsal girdle scales. 31. Ventral girdle scales. 32. Radula. 32a. Denticle cap of major lateral tooth. Bar = 50 μ m.

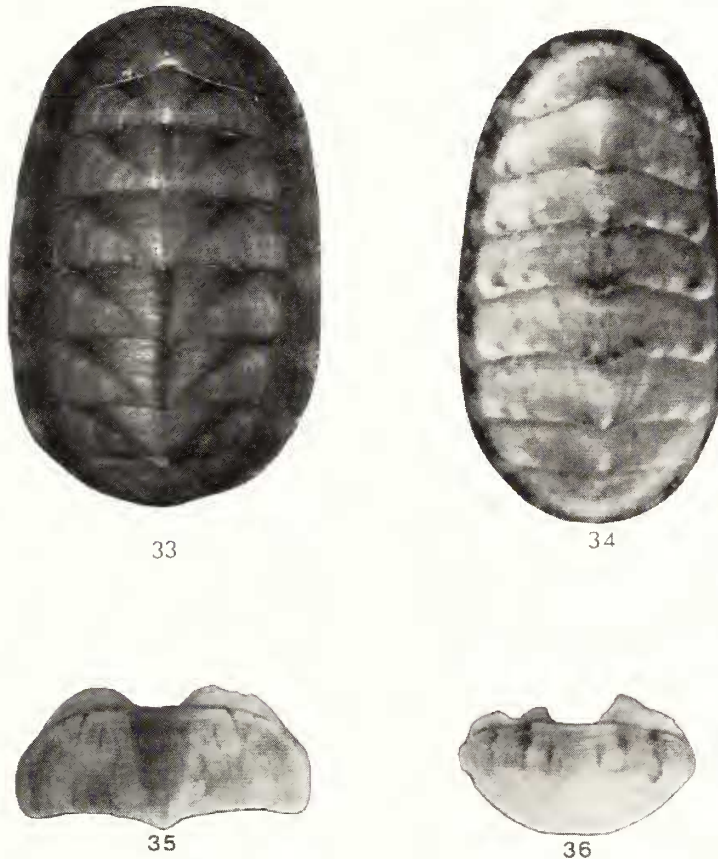


Fig. 33. *Tonicella lineata* var. *fusca* (von Middendorff, 1847) ? RNC 934, Tunstal Bay, Bowen Id., near Vancouver, British Columbia, 6 m. 38.0 mm x 23.0 mm x 6.0 mm. **Fig. 34.** *Tonicella venusta* Clark, spec. nov., RNC 194, Neah Bay, Clallum Bay, Washington, 0-1 m. 8.0 mm x 4.0 mm x 2.0 mm (Albino). **Figs. 35 & 36.** *Tonicella undocaeerulea* Sirenko, 1973; fossil intermediate and tail valves, middle Pleistocene, Boso Peninsula, Honshu Id., Japan (Photos: courtesy of A. Naruse). Scale bar 5.0 mm.

lateral edges and notched at center at proximal end; denticle cap of major lateral teeth (32a) broad, tridentate, about 65 μ m x 75 μ m, rounded on outer edge, denticles about equal in length (inner one only slightly smaller). Ctenidia merobranchial, abanal, extending about 3/4 length of foot, 16 plumes per side.

Range of morphological variation: Some specimens have a dark maroon-brown, central area bordered by a diagonal white band at the edge of the lateral areas on valve two. Rare albinistic specimens (fig. 34) are gray-white with a few darker gray blotches at the posterior edges of the plates. Some specimens are nearly uniformly, light pink, and one southern specimen has the color pattern of the lateropleural areas extending across the jugal areas.

Type locality: Mountain Point, 8 km S of Ketchikan, Revillagigedo Island, Alexander Archipelago, SE Alaska (55°17'35"N, 131°32'20"W), 1-10 m.

Type Material: Holotype (LACM 2626) and 41 paratypes (2, LACM 2627, 2628); (2, CAS 103559); (1, SBMNH 141110); (2, USNM 880068); (1, RMNH 9361); (1, ZISP 1934); (2, UAF MO-5572); (1, UMMZ 252870); (29, RNC 1026, 1033, 1140).

Type material preserved flat and fully extended. Holotype and 17 paratypes preserved dry (with glycerin), collected 24-25 June, 1991 by RNC & Alan Murray; Twenty-four additional paratypes preserved in 70% ethanol, 8 collected 3 September, 1992 by RNC, Alan Murray, Kurt Morin & David Zwick, and 16 collected 26-30 September, 1993 by RNC, David Zwick & Kurt Morin.

Additional Material: Alaska: 1, CAS 025595, Knight Id., Prince William Sound; 5, LACM 83-106, Hesketh Id., Kachemak Bay, Kenai Peninsula, 12-16 m; 3, RNC 435, Kachemak Bay, 0-2 m; 2, RNC 1193, Chiniak Bay, Kodiak Id., 1 m; 7, RNC 200, Sitka, Baranof Id., 0-1 m; 1, RNC 1193, Chiniak Bay, Kodiak Id., 1 m; 7, RNC

200, Sitka, Baranof Id., 0-1 m; 1, RNC 1197, Petersburg, Mitkof Id., 8-10 m; 2, SBMNH 36067, Forrester Id.; 6, RNC 1010, Rotary Beach, Revillagigedo Id., 0-1 m; 9, RNC 1033, Mountain Pt., Revillagigedo Id., 1 m; 9 RNC 579, Metlakatla, Annette Id., 42 m; 1, RNC 912, Saxman, Revillagigedo Id., 1 m; 9, RNC 1199, Washington Monument (submerged pinnacle), Revillagigedo Channel, 5-30 m. British Columbia: 1, SBMNH 36069, Departure Bay, Vancouver Id.; 3, RNC 251, Tofino Harbor, Vancouver Id., 1-2 m; 8, RBCM 7516, Tofino Harbor, Vancouver Id., 1-2 m; 2, RNC 397 Saanach Inlet, Vancouver Id., 18 m; 2, RNC 349, Victoria, Vancouver Id., 1-2 m. Washington: 6, RNC 194, Neah Bay, Clallum Co., 0-1 m. Oregon: 1, RNC 972, Port Orford breakwater, Curry Co., 5 m; 1 RNC 971, Island Rock, Curry Co., 30 m. California: 1, CAS 013476, Shelter Cove, Mendocino Co.; 1, RNC 1226, Coast guard breakwater, Monterey Bay, Monterey Co., 10-12 m; 3 SBMNH 36073, N of San Simeon, San Luis Obispo Co.; 1, Hanselman Coll., Gaviota, Santa Barbara Co., 18 m; 1, LACM 41-195, E of Carwell Point, San Miguel Id., Channel Is., 38 m; 3, SBMNH 36066, Dago Bank, off San Pedro, Los Angeles Co.; 1, CAS 025200, Catalina Id., 79-140 m; 1, CAS 083447, Point Fermin, Los Angeles Co., 30 m; 3, LACM 65-3, S of Los Angeles Harbor, Los Angeles Co., 27 m; 2, LACM 65-2, SW of Point Fermin, Los Angeles Co., 29 m; 1, LACM 57-53, NW of Point Vincent Light, Los Angeles Co., 18 m; 24, LACM 72-91, off San Pedro, Los Angeles Co., 22 m; 1, CAS 083442, Cortez Bank, Channel Is., 12-27 m; 1, RNC. 264, Point Loma, San Diego Co., 15 m; 2, Hanselman Coll., Point Loma, San Diego Co., 15 m. Baja California, Mexico: 1,

CAS 083446, Bahia de Todos Santos; 1, LACM 67-52, Arbolito, S side of Punta Banda, 15 m; 1, LACM 67-46, Puerto Santo Tomas, 13 m; 1, LACM 71-151, NE end of Isla Cedros, 5-12 m.

Distribution: *Tonicella venusta* occurs continuously from south-central Alaska to Isla Cedros, Baja California, Mexico (Fig. 37) at depths of 0-140 m. The northernmost record is Knight Island, Prince William Sound, Alaska (60°15'N, 147°44'W)(CAS 025595), the westernmost record is Chiniak Bay, Kodiak Id., Alaska (57°41'15"N, 152°24'00"W), and the southernmost record is Isla Cedros, Baja California (28°17'N, 115°8'W)(LACM 71-151).

Habitat and Ecology: *Tonicella venusta* lives on pebbles, cobbles, boulders, shells, and bedrock encrusted with coralline algae (*Lithothamnion* spp.) and bryozoans of unknown identity.

Fossil record: No fossil specimens of *Tonicella venusta* have been found. This is probably due to the small size and fragile nature of the valves.

Etymology: The name is Latin, and means lovely. The species is so named for the brilliant coloration of the valves in live animals, which are pink or lavender with blue or purple markings.

Remarks: Because of its small size and sandy girdle, *Tonicella venusta* has previously been confused with *Tonicella beringensis* (Yakovleva, 1952) [as *Tonicella*

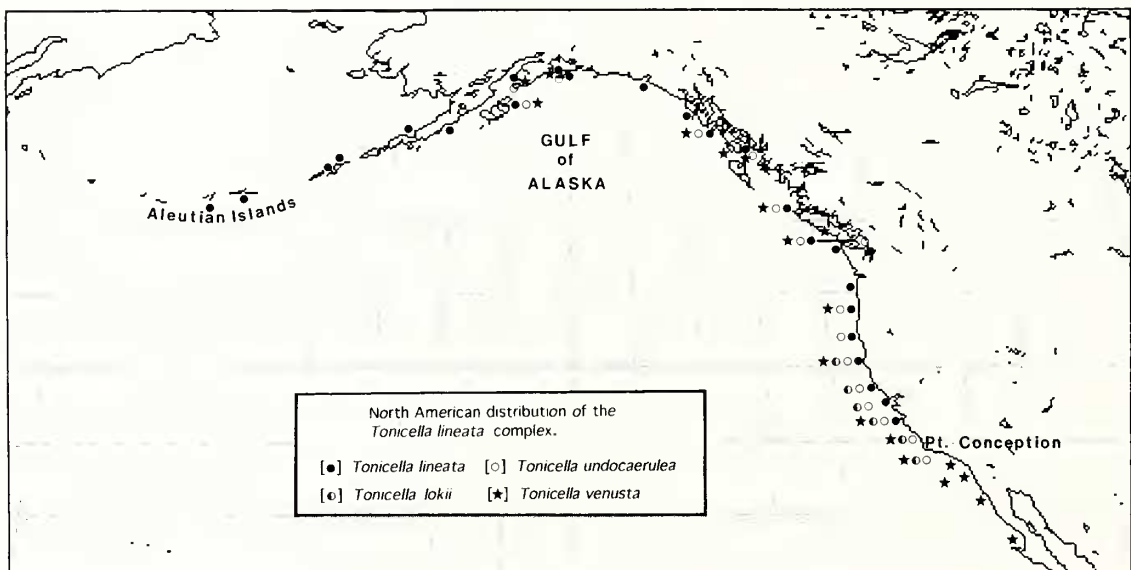


Fig. 37. Distribution of the *Tonicella lineata* complex.

rubra (Linnaeus, 1767), see discussion] from which it may be distinguished by its anterior mucro, concave post-mucronal slope and color pattern. *Tonicella venusta* has also been confused with *T. marmorea* (Fabricius, 1780), from which it is distinguished by the sandy girdle and the color pattern; with juveniles of *T. lineata*, from which it may be distinguished by the post-mucronal slope of the tail valve, sandy girdle and the color pattern; and with *Lepidochitona beanii* (Carpenter, 1855), from which it is distinguished by lacking large spicules in the girdle at the valve sutures.

DISCUSSION

The similarities in color pattern and habitat between the members of the *Tonicella lineata* complex are remarkable, and explain why the four taxa have been confused. Yet they differ in line pattern, post-mucronal slope of the tail valve and the morphology of the girdle elements and radula (Table 1). In addition to morphological characters of the valves, girdle elements and radula, these species also have distinct differences in the number of gills. In specimens of the same size, *Tonicella lokii* has slightly more numerous gills than *T. lineata*, and these two species both have more numerous gills than *T. undocaerulea* and *T. venusta*. *Tonicella venusta* has the fewest gills of the four (figure 38).

Berry (1917) was apparently misled by these similarities, as an examination of Berry's material from Forrester Island, Alaska revealed that he identified specimens of *Tonicella undocaerulea* as juveniles of *T. lineata*, but remarked that the "juveniles" were found off shore in 15-20 fathoms (27-36 m) and "adults" were found only on the shore. Additionally Berry identified both "*Tonicella rubra*" (see below) and *Tonicella venusta* as "*Tonicella*

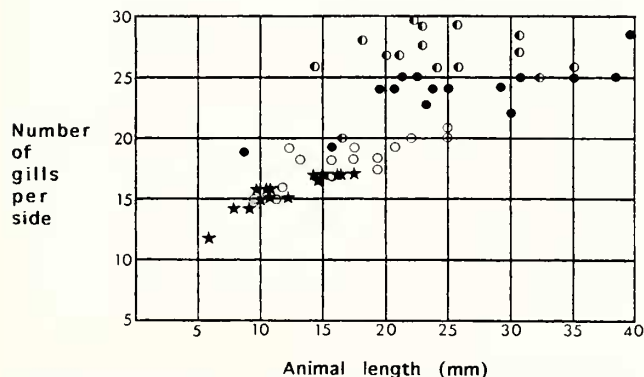


Fig. 38. Number of gills as a function of length (N = 15 specimens). *Tonicella lineata* [●]; *T. undocaerulea* [○]; *T. lokii* [◐]; *T. venusta* [★].

Table 1. Characters of taxa in the *Tonicella lineata* species complex.

Taxa/Character	<i>T. lineata</i>	<i>T. undocaerulea</i>	<i>T. lokii</i>	<i>T. venusta</i>
Dorsal girdle scales	ribbed	smooth w/ groove	smooth	rotund w/ apical pleats
Dimensions of scales (μm)	40 x 18	20 x 10	22 x 12	30 x 18
Central tooth of radula	narrow/elongated	broad/spoon-shaped	narrow/spoon-shaped	narrow/cupped head
Major lateral teeth	rounded/w 1-2 notches	tridentate	rounded/w 1 notch	tridentate
Brown lines on head valve	yes	no	yes	no
Head valve line pattern	gothic arch	zigzag	zigzag	zigzag
Flammules on pleural areas	no	no	no	yes
Post-mucronal slope of tail valve	+ / - straight	variable	concave	concave

rubra." Berry's specimens are preserved at the Santa Barbara Museum of Natural History.

The identity of

merly LACM); Darlene Southworth, Southern Oregon University, Ashland, Oregon; Hiroshi Saito, National Science Museum, Tokyo, Japan; Atsushi Naruse, Mizunami Fossil Museum, Mizunami City, Japan; Alan J. Murray, David Zwick and Kurt Morin, Ketchikan, Alaska; Robin C. Harrison National Marine Fisheries Service, Seattle, Washington. A specimen and numerous photographs (figs. 35 & 36) were received through the kindness of Dr. Atsushi Naruse of the Mizunami Fossil Museum, Mizunami City, Japan. I also Thank James H. McLean and Douglas J. Eernisse for critically reviewing the manuscript. The comments of three anonymous reviewers were also very helpful.

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