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CHITONS (POLYPLACOPHORA) FROM PALEOGENE STRATA IN WESTERN WASHINGTON STATE, U.S.A.

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ABSTRACT—Recent collecting provided fossil chitons (Mollusca, Polyplacophora) from upper Eocene to lower Oligocene deposits of Washington State, U.S.A. The study material consists of 140 valves from six localities in the Quimper, Makah, Lincoln Creek, Crescent and Gries Ranch formations. The material is mostly incomplete or very fragmented and/or worn so that a precise appreciation of diagnostic features has been in many cases difficult if not impossible. Fourteen species were identified, seven are described as new: *Lepidopleurus propecajetanus* n. sp., *Leptochiton* sp., *Ischnochiton goederti* n. sp., *Ischnochiton*? sp. A, *Ischnochiton*? sp. B, *Stenoplax quimperensis* n. sp., *Stenoplax* sp. A, *Stenoplax* sp. B, *Lepidozona cowlitzensis* n. sp., *Lepidochitona lioplax* (Berry, 1922), *Lepidochitona washingtonensis* n. sp., *Lepidochitona squiresi* n. sp., *Lepidochitona* sp. and *Craspedochiton eernissei* n. sp. The only species previously described from the study area is *Lepidochitona lioplax* and it is also the most common chiton in the study material (67% of the total). No species other than *L. lioplax* has been found in more than one locality. In four of these localities only a single species has been collected. The basal Lincoln Creek Formation at the Porter Creek site supplied the richest and most diverse chiton assemblage with seven species and 86% of the valves. The discovery and formal identification of such a diverse Paleogene fauna from the northeastern Pacific provides a comparative base for a better appreciation of Polyplacophora biogeography and evolution.

INTRODUCTION

THE PALEONTOLOGICAL documentation of Polyplacophora from the Pacific margin of North America is quite scant and refers mostly to Plio-Pleistocene records (Berry, 1922). Older Tertiary records from same area are surprisingly few and include: 1) unidentified chiton fragments (probably *Stenoplax*) from the Eocene Tejon Formation, Tehachapi Mountains, southern California (Squires, 1989; Lindberg and Squires, 1990); 2) "amphineuran" plate (UCMP 35498) from the Quimper Formation (late Eocene) mentioned by Durham (1944, p. 191) but not further identified; 3) *Oligochiton lioplax* Berry, 1922: four plates from the Sooke Formation (late Oligocene or early Miocene) on southern Vancouver Island, British Columbia (Berry, 1922); 4) *Leptochiton alveolus* (Lovén, 1846): three articulated specimens and 37 separate plates from three localized cold-seep limestones on the Olympic Peninsula, Washington: Eocene Humptulips Formation near Humptulips; Oligocene Makah Formation at Shipwreck Point; Oligocene Lincoln Creek Formation at Canyon River (Squires and Goedert, 1995; Goedert and Campbell, 1995; Rigby and Goedert, 1996; Peckmann et al., 2002; Schwabe and Sellanes, 2010); 5) unidentified plate from the Oligocene San Lorenzo Formation, Walnut Creek, California (Clark, 1918; Berry, 1922); 6) *Leptochiton* sp. associated with wood in Oligocene deep-water strata, western Washington State: Makah, Pysht, and Lincoln Creek formations (Kiel and Goedert, 2006; Schwabe and Sellanes, 2010).

Recent fieldwork by James L. Goedert resulted in the collection of 140 chiton valves from six locaties in the Quimper, Makah, Lincoln Creek, Crescent and Gries Ranch formations in Washington State, U.S.A. (Fig. 1). These formations range in age from the late Eocene to the early Oligocene (Snavely et al., 1980; Prothero and Armentrout, 1985; Squires and Goedert, 1996; Prothero and Burns, 2001). Many of the taxa recovered from these strata are probably n. sp. but, because of the inadequacy of the valves found, some remain of taxonomic unclear position (Table 1).

The purpose of this article is to describe this chiton assemblage in order to supply the primary information needed to shed light on the evolution and biogeography of Polyplacophora from the long lasting convergent East Pacific margin.

MATERIAL AND METHODS

The collecting sites are described in Appendix 1.

Fossils were hand picked in the field and most of them are still on their matrix because excessive cleansing could irreparably damage the shell. The material under study is largely represented by incomplete, often very fragmented, and worn material so that a precise appreciation of diagnostic features has been in many cases difficult if not impossible.

Most plates have been imaged by Scanning Electron Microscopy using a JEOL mod. JSM-5200 SEM. The material is stored in the Zoological (now Evolution) Museum of the Bologna University, Italy.

Abbreviations used here include: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Northridge; JLG, J. L. Goedert locality; MZB, Zoological Museum of Bologna University (Italy); LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology, Los Angeles; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California, Museum of Paleontology, Berkeley; USGS, United States Geological Survey, Menlo Park, California.

SYSTEMATIC PALEONTOLOGY

We follow the systematics proposed by Sirenko (2006).

Class POLYPLACOPHORA Gray, 1821
Subclass LORICATA Schumacher, 1817
Order LEPIDOPLEURIDA Thiele, 1909
Family LEPTOCHITONIDAE Dall, 1889
Genus LEPIDOPLEURUS Risso, 1826

Type species.—*Chiton cajetanus* Poli, 1791, by subsequent designation (Herrmannsen, 1846).

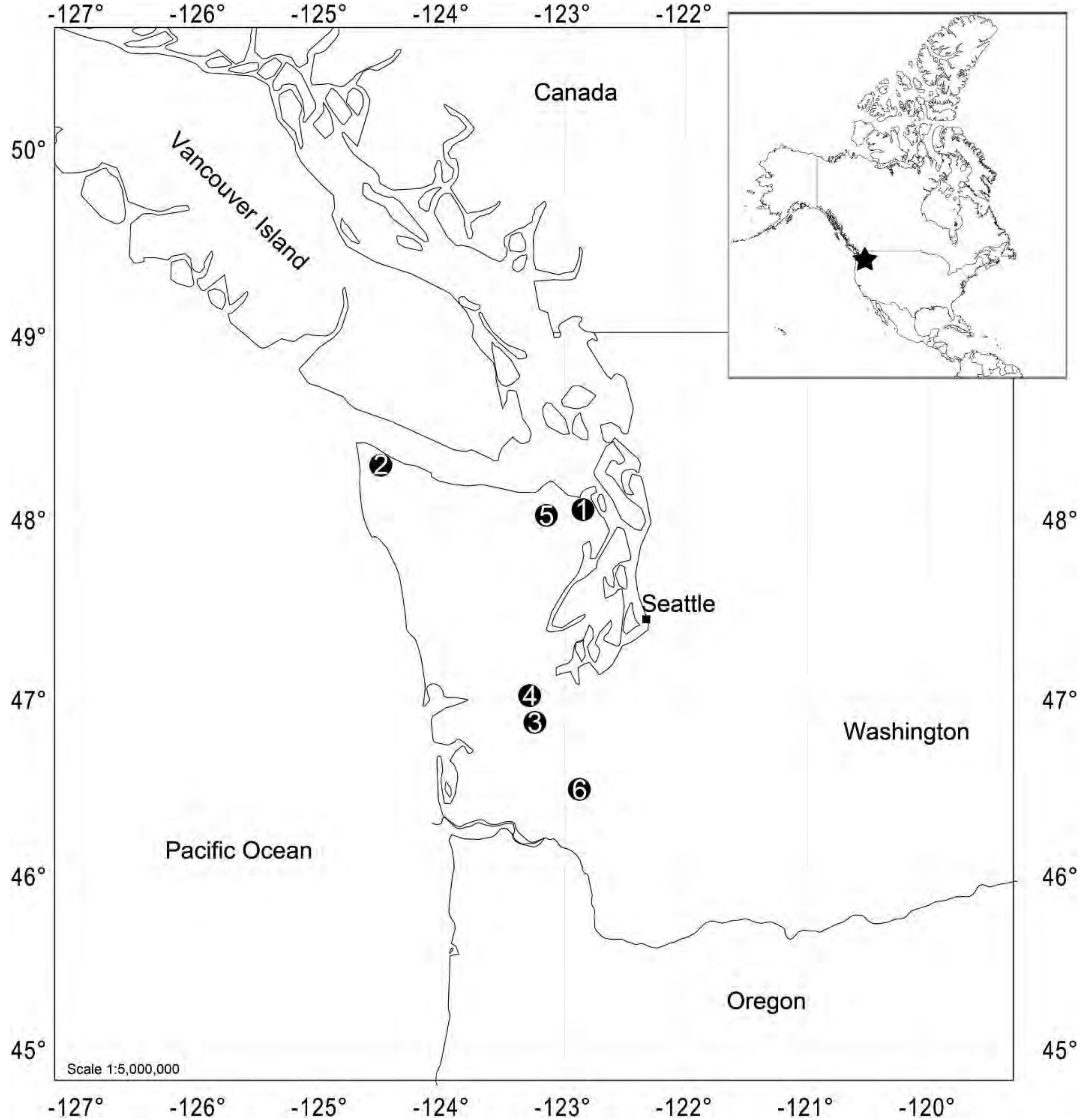


FIGURE 1—Location of study sites in Washington state, U.S.A. Numbers refer to localities described in Appendix 1.

LEPIDOPLEURUS PROPECAJETANUS new species
Figure 2.1–2.12

Diagnosis.—Head valve semicircular, sculptured with a series of large concentric folds. Intermediate valves rectangular, with a well developed apex and very elevated lateral areas, sculptured with longitudinal cords transversally intersected by thinner lamellae in central area, and with a series of large concentric folds in lateral areas. Articulamentum without insertion laminae, central depression with numerous transverse slits in jugal tract.

Description.—The only available head valve is incomplete. Sculpture of the tegmentum formed by a series of large concentric folds (Fig. 2.8).

Intermediate valve rectangular, subcarinate, moderately elevated, anterior margin nearly straight, posterior margin with a well-developed apex, lateral margins rounded, lateral area very elevated. Sculpture in lateral areas formed by a series of 6–8 large concentric folds, some of them very large and folded (Fig. 2.4, 2.5). Central areas present ~30 prominent longitudinal cords, formed by merged granules, locally

TABLE 1—Number of valves found by locality/species.

Species	Woodman's wharf	JLG214	Oakville	Porter creek	CSUN 1563	A-1424
Lepidopleurus propecajetanus n. sp.				14		
Leptochiton sp.				1		
Ischnochiton goederti n. sp.				7		
Ischnochiton? sp. A						1
Ischnochiton? sp. B				2		
Stenoplax quimperensis n. sp.	1					
Stenoplax sp. A		1				
Stenoplax sp. B						10
Lepidozona cowlitzensis n. sp.						1
Lepidochitona lioplax				94		
Lepidochitona washingtonensis n. sp.			4			
Lepidochitona squiresi n. sp.					1	
Lepidochitona sp.				1		
Craspedochiton eernissei n. sp.				2		
Total	1	1	4	121	1	12

anastomosed progressively coarser towards the lateral rims (Fig. 2.1). The cords are transversally intersected by thinner lamellae, providing a characteristic cancellate sculpture (Fig. 2.6). Individual granules with a single central megalaesthete (Fig. 2.6).

Tail valve unknown.

Articulamentum without insertion laminae. Apophyses not preserved, but suggesting a substantially large extension. One median and two lateral ditches are present next to the apical region that expands into a quadrangular region (Fig. 2.10). Central depression of intermediate valves with numerous transverse slits in jugal tract (Fig. 2.11).

Etymology.—The name recalls the morphological resemblance with the extant species *L. cajetanus*.

Types.—Porter Creek: 14 valves (1 head and 13 intermediate). Holotype, MZB 45652 (intermediate valve, Fig. 2.1–2.7), and 13 paratypes, MZB 45653 (head valve, Fig. 2.8, 2.9), MZB 45654 (intermediate valve, Fig. 2.10–2.12), MZB 45655 (11 intermediate valves, unfigured lot).

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—The available material consists of poorly preserved, worn and often incomplete valves. The species resembles the extant Atlantic-Mediterranean *Lepidopleurus cajetanus* (Poli, 1791) but it can be distinguished by various features. *Lepidopleurus propecajetanus* presents intermediate valves, which are more rectangular and subcarinate, have smaller dimensions (maximum width of intermediate valves is 4.2 mm in *L. propecajetanus* vs. more than 9 mm in *L. cajetanus*, Dell'Angelo et al., 2004, p. 26), stronger sculpture with lamellae intersecting well evident longitudinal cords in *L. propecajetanus* while they are less obvious in *L. cajetanus*, large concentric folds on lateral areas wider and flatter in *L. propecajetanus*, whereas they are denser, more elevated and never departing from the apex in *L. cajetanus*. Additional differences concern megalaesthete and many micraesthetes along the margins of granules (compare Eernisse and Reynolds, 1994, fig. 25B to Dell'Angelo and Smriglio, 1999, pl. 7L). Moreover, the structure formed by numerous transverse slits in the jugal tract of the central depression in intermediate valves is not present in *L. cajetanus*.

A few other taxa ascribed to *Lepidopleurus* have been reported for the Tertiary but all differ from the n. sp. *Lepidopleurus virgifer* (Sandberger, 1859) (=*Chiton subcajetanus* d'Orbigny, 1852) from the Oligocene–Miocene of Europe (Janssen, 1978; Dell'Angelo and Palazzi, 1989) is much larger and presents a finer sculpture characterised by subdued concentric folds. *Lepidopleurus scirpeus* Bielokrys, 2000, described from the upper Eocene of Ukraine is very close and potentially conspecific with *L. virgifer* (Bielokrys, 2000, p. 165).

The only living *Lepidopleurus* is *Lepidopleurus cajetanus*. Other species initially attributed to *Lepidopleurus*, *L. scrippsianus* Ferreira, 1980 from Baja California Sur, Mexico, *L. takii* Wu and Okutani, 1984, and *L. soyomaruae* Wu and Okutani, 1984 from Japan, and *L. bartlettae* Ferreira, 1986 from Caribbean Sea, were subsequently attributed to the genus *Ferreiraella* Sirenko, 1988 (Sirenko, 1997). The latter differs from *Lepidopleurus* by a sculpture presenting group of subsidiary caps protruding from aesthetes, and by differences in girdle (e.g., the naked ventral side) and radula.

Genus LEPTOCHITON Gray, 1847

Type species.—*Chiton cinereus* Montagu, 1803, non Linnaeus, 1767 (=*Chiton asellus* Gmelin, 1791), by subsequent designation (Gray, 1847).

LEPTOCHITON sp.
Figure 2.13–2.16

Description.—Intermediate valve broadly rectangular, anterior margin almost straight, lateral margin slightly rounded, apex probably not very conspicuous (the posterior margin is lacking), lateral areas little raised.

Sculpture of the tegmentum formed by roundish granules, forming subgranulose riblets, about 54 longitudinally disposed on the central area (27 estimated per side), and 15 radially arranged on the lateral areas (Fig. 2.13). Rows of longitudinal granules bent somewhat obliquely next to the marginal side. Interspaces between rows are quite narrow and not prominent. In each row, granules are joined by a narrow ridge, resulting in a "chained" ornamentation (Fig. 2.15). Equidimensional aesthetes visible on the granules, one central and others on the granules' margin (Fig. 2.16).

Articulamentum without insertion laminae. Apophyses widely separated, small, triangular (Fig. 2.14).

Material examined.—Porter Creek: one intermediate valve MZB 45656 incomplete.

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—The single valve, which is an incomplete intermediate valve, displays various features that somewhat resemble this taxon either as fossil or extant species belonging to *Leptochiton,* characterized by a sculpture of more or less circular granules, arranged in rows (longitudinal on central areas, radial on lateral and terminal areas). About ten species with such characteristics are known from Eocene/Oligocene deposits (see Appendix 2).

Our plate closely resembles *Leptochiton rugatus* (Carpenter in Pilsbry, 1892), an extant species inhabiting the western coast of North America (Ferreira, 1979). The sculptural features match our species (Ferreira, 1979, p. 147; "tegmental sculpture consists of microgranules linearly juxtaposed to form subgranulose riblets. These riblets are longitudinally disposed in the central areas [about 20–40 riblets per side], somewhat radially oriented in the end valves and lateral areas [about 10–15 per area]"). *Leptochiton rugatus* has one central megalaesthete and four micraesthetes per granule (Sirenko, personal commun.) and it is not known as a fossil. Because of the lack of adequate material, we do not define the nomenclature of our taxon.

The Miocene–Recent *Leptochiton cancellatus* (Sowerby, 1840) (=*Leptochiton sulci* [Bałuk, 1971]) shares some resemblance with the species here discussed from which it mainly differs in the lesser number of radial striae over the lateral areas (Dell'Angelo and Smriglio, 1999).

Leptochiton boettgeri (Šulc, 1934) (=*Leptochiton srameki* [Šulc, 1934]) from the Miocene of central Europe (Bałuk, 1971, 1984; Dell'Angelo and Palazzi, 1989) differs by having fewer rows of granules and wider interrow spaces.

Leptochiton clarki (Berry, 1922) from the Pleistocene of California has a higher number of rows of granules both longitudinal (55–60 per side) and radial (17–20). It also differs from the species discussed here and in Berry (1922) in the different shape and position of the sutural laminae and other minor details.

Order Chitonida Thiele, 1909
Suborder Chitonina Thiele, 1909
Family Ischnochitonidae Dall, 1889
Genus Ischnochiton Gray, 1847

Type species.—*Chiton textilis* Gray, 1828, by subsequent designation (Gray, 1847).

Ischnochiton goederti n. sp.
Figure 3.1–3.10

Diagnosis.—Intermediate valve rectangular, subcarinate, sculptured with longitudinal cords on each side of the central area crossed by coarse transverse lamellae, and by radial riblets on the lateral areas. Tail valve semielliptical, prominent central mucro, antemucronal area sculptured like the central area of intermediate valves, postmucronal area with an undetermined number of radial riblets. Articulamentum with a single slit by each side in intermediate valves.

Description.—Head valve not available. Intermediate valve rectangular, subcarinate, moderately elevated, anterior and posterior margins practically straight, apex not evident, lateral margins rounded, lateral areas pronounced. Sculpure represented by 18–20 longitudinal cords on each side of the central area, quite pronounced and crossed by coarse transverse lamellae forming an obvious reticulation, and by five radial riblets on the lateral areas (Fig. 3.1).

Tail valve semielliptical, anterior margin straight, prominent central mucro.

Sculpture represented by approximately 16 longitudinal cords on both sides of the central area, crossed by coarse transverse lamellae, and by an undetermined number of radial riblets on the postmucronal region (plates are very worn) (Fig. 3.8). Plates are densely covered by aequidimensional aesthetes, not separable as micraesthetes and megalaesthetes (Fig. 3.9–3.10).

Articulamentum rather worn, showing a single incision in intermediate valves (Fig. 3.2–3.3). Slits are not visible in tail valves. Apophyses wide, triangular in shape. Central depression of intermediate valves with numerous transverse slits in jugal tract.

Etymology.—The specific name honours James L. Goedert who collected the material and made it available to the authors.

Types.—Porter Creek: seven valves (four intermediate and three tail). Holotype, MZB 45657 (intermediate valve, Fig. 3.1–3.4), and 6 paratypes, MZB 45658 (intermediate valve, Fig. 3.5–3.7, 3.9–3.10), MZB 45659 (tail valve, Fig. 3.8), MZB 45660 (unfigured lot).

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—Available valves are worn and incomplete. The cancellate ornamentation is distinctly marked on the pleural area of intermediate valves (Fig. 3.9); holes are generated at the intersection between longitudinal cords and transversal lamellae (Fig. 3.10), with aesthetes thickly present both on the longitudinal cords and on the transversal lamellae. Fig. 3.6 and 3.7 show these "holes" seen from the top, pointed out as quadrangular structures, that at first sight should look like tubercles on the valve's surface.

Three *Ischnochiton* species have been previously described from Eocene/Oligocene deposits, but all differ sensibly from the new taxon here proposed: 1) *I. vectensis* Wrigley, 1943, from the Oligocene of Colwell Bay (Isle of Wight, England), displays a pattern sculpture formed by two sets of intersecting curved lines; 2) *I. cancellatus* Bielokrys, 1999, from the Eocene of Dniepr River (Dnepropetrovsk, Ukraine), displays a cancellate sculpture and coarser ribs; 3) *I. asper* Bielokrys, 1999, from the Eocene of Dniepr River (Dnepropetrovsk, Ukraine), shows a fine nodulose sculpture, with sinuous ribs.

Ischnochiton? sp. A
Figure 3.11–3.12

Description.—Intermediate valve worn, rectangular, subcarinate, moderately elevated, anterior and posterior margins straight, lateral areas subdued; central area smooth, 3–4 apparently radial ribs, very worn, visible on the lateral areas.

Material examined.—Loc. A-1424, Gries Ranch: one intermediate valve, MZB 45661.

Occurrence.—Gries Ranch Formation (latest Eocene or earliest Oligocene), on the Cowlitz River, Gries Ranch, Washington.

Discussion.—The only intermediate valve available is exceedingly fragile and in a very poor state of preservation. Also the attribution to the genus *Ischnochiton* cannot be defined with certainty on the basis of the available material. The morphological characteristics allow its separation from the other *Ischnochiton* taxa here described or discussed.

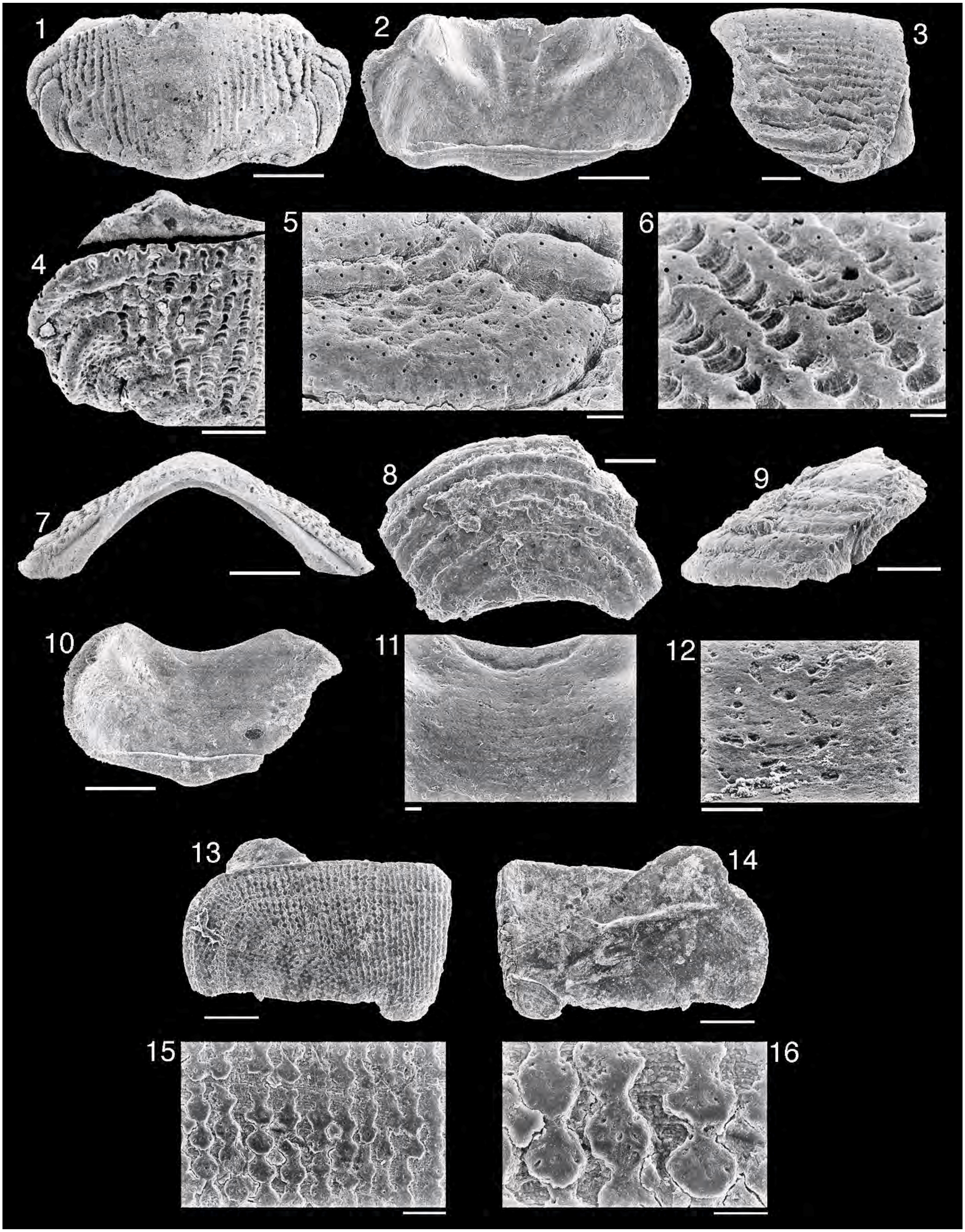
Ischnochiton? sp. B
Figure 3.13–3.15

Description.—The available material consists of two small fragments of intermediate plates. Some 4 to 5 riblets characterize a relatively pronounced lateral area.

The articulamentum displays 6 to 7 slit rays, and consequently an equal number of incisions on the insertion lamina should be expected (Fig. 3.14); because of their worn condition few of these incisions are evident near the border between the lateral and pleural areas.

Material examined.—Porter Creek: two intermediate valves, MZB 45662.

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.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Discussion.—Due to the scarce and worn material the attribution to the genus *Ischnochiton* cannot be defined with certainty. In spite of this, the species is mentioned as it has an unusual characteristic, i.e., the presence of 6 to 7 slits on the insertion lamina. To our knowledge, no living *Ischnochiton* species have been described with more than 4 slits, e.g., *Ischnochiton (Stenosemus) chiversi* Ferreira, 1981 (Ferreira, 1981, p. 325; Kaas and Van Belle, 1990).

The fossil Eocene/Oligocene *Ischnochiton* species have only one incision (*Ischnochiton vectensis* and *I. cancellatus*) or one to two (*I. asper*). This characteristic is however present in other Eocene species from the Paris basin, i.e., what Le Renard mentioned as *Tonicella semivittata* (Fossils website: http://www.somali.asso.fr/fossils/biotaxis.php). The genus *Tonicella* however, differs strongly from *Ischnochiton*, and is placed in another family (Tonicellidae Simroth, 1894).

Genus STENOPLAX Carpenter MS, Dall, 1879

Type species.—*Chiton limaciformis* Sowerby, 1832, by original designation.

STENOPLAX QUIMPERENSIS new species
Figure 4.1–4.2

Diagnosis.—Intermediate valve rectangular, moderately elevated, subcarinate, sculpture formed by approximately 60–70 longitudinal striae on each side of the central area, and by 11 radial striae in lateral areas. Apophyses rounded, covering about half of the anterior margin.

Description.—Intermediate valve rectangular, width ~33 mm, moderately elevated (dorsal elevation estimated 0.28), subcarinate (jugal angle of about 110°), anterior and posterior margins practically straight, apices inconspicuous, side margins rounded, lateral areas well evident but hardly raised.

Sculpture formed by approximately 60–70 longitudinal striae on each side of the central area (Fig. 4.2). The jugal area is worn but appears ornamented by longitudinal striae as well, tending to incline laterally, and by at least 11 radial striae in lateral areas. The sculpture is rather regular. Apophyses rounded, covering about the half of the anterior margin. Incisions not visible.

Etymology.—Named for the Quimper Formation, source of this new taxon.

Types.—Woodman's Wharf: one intermediate valve (Holotype, MZB 45663).

Occurrence.—Quimper Formation (late Eocene–upper Oligocene), north of Woodman's Wharf, Washington.

Discussion.—Only a single intermediate valve was found, preserved in matrix, thus the articulamentum is not visible. The attribution to the genus *Stenoplax* cannot be defined with certainty on the basis of the available material because the substantial differences with *Ischnochiton* regard the dimensions (Kaas and Van Belle, 1987, p. 124; "length 2 to 3 times the width" for *Stenoplax*, "length less than twice the width" for *Ischnochiton*). These measurements are not determinable with our available material, however, the valve characteristics and sculpture are in agreement with the attribution to the genus *Stenoplax*.

Four *Stenoplax* species are known from Eocene/Oligocene deposits. *S. anglica* and *S. selseiensis* Wrigley, 1943, both based on a single tail valve from the same Eocene locality (Medmery Farm, Selsey, England), with a sculpture nearly smooth. *S. sigillarius* Bielokrys, 1999, based on valves from the Eocene of Dniepr River (Dnepropetrovsk, Ukraine), with a sculture formed by nodulose ribs. *S. veneta* Dell'Angelo and Palazzi, 1992, based on head and tail valves from the Oligocene of Case Soghe (Vicenza, Italy), with a sculpture finely beaded by small granules.

The species shows some similarities with *Stenoplax conspicua* (Carpenter MS, Pilsbry, 1892), living along the western coast of North America and known as a fossil from Pliocene and Pleistocene rocks of California (Berry, 1922); but it differs in having less-raised lateral areas, finer sculpture, and an especially different apophyses' arrangement (very much larger in *S. conspicua*), with a consequently more reduced jugal sinus.

STENOPLAX SP. A
Figure 4.3

Description.—Intermediate valve rectangular, width ~23 mm, elevated (dorsal elevation estimated 0.28), carinate (jugal angle of about 80°), anterior and posterior margins practically straight, apices inconspicuous, side margins oblique resulting in a trapezoidal shape. Lateral areas evident and elevated. Sculpture not well detectable.

Material examined.—Loc. JLG214, Jansen Creek: one intermediate valve, MZB 45664.

Occurrence.—Makah Formation, Jansen Creek Member (latest Eocene or earliest Oligocene), at Jansen Creek, Washington.

Discussion.—Only a single intermediate valve was found, preserved in hard matrix, and so the articulamentum is not visible. The valve is poorly preserved and worn, with the sculpture not well evident. It is therefore not possible to make a specific determination but the valve characteristics are sufficient to allow its separation from *Stenoplax quimperensis* n. sp.

STENOPLAX SP. B
Figure 4.4–4.9

Description.—Head valve semi-oval. Intermediate valve rectangular, lateral margins slightly rounded, posterior margin straight, lateral area elevated, apices inconspicuous. Tail valve semi-elliptical, mucro subcentral, little elevated, postmucronal slope slightly concave. Tegmentum sculptured with many close set, rugose, hardly interrupted concentric riblets, extending in continuity on all valve's surface, also in the central areas. Articulamentum with insertion plates short, one slit per side in intermediate valves, slit rays weakly indicated.

Material examined.—Loc. A-1424, Gries Ranch: 10 valves (two head, five intermediate and three tail), MZB 45665–45667 (figured head valve, intermediate valve, tail valve, respectively), MZB 45668 (unfigured lot).

Occurrence.—Gries Ranch Formation (latest Eocene or earliest Oligocene), Cowlitz River, Gries Ranch, Washington.

Discussion.—The available valves are poorly preserved and worn. It is not therefore possible to make a specific determination but the valve characteristics are sufficient to

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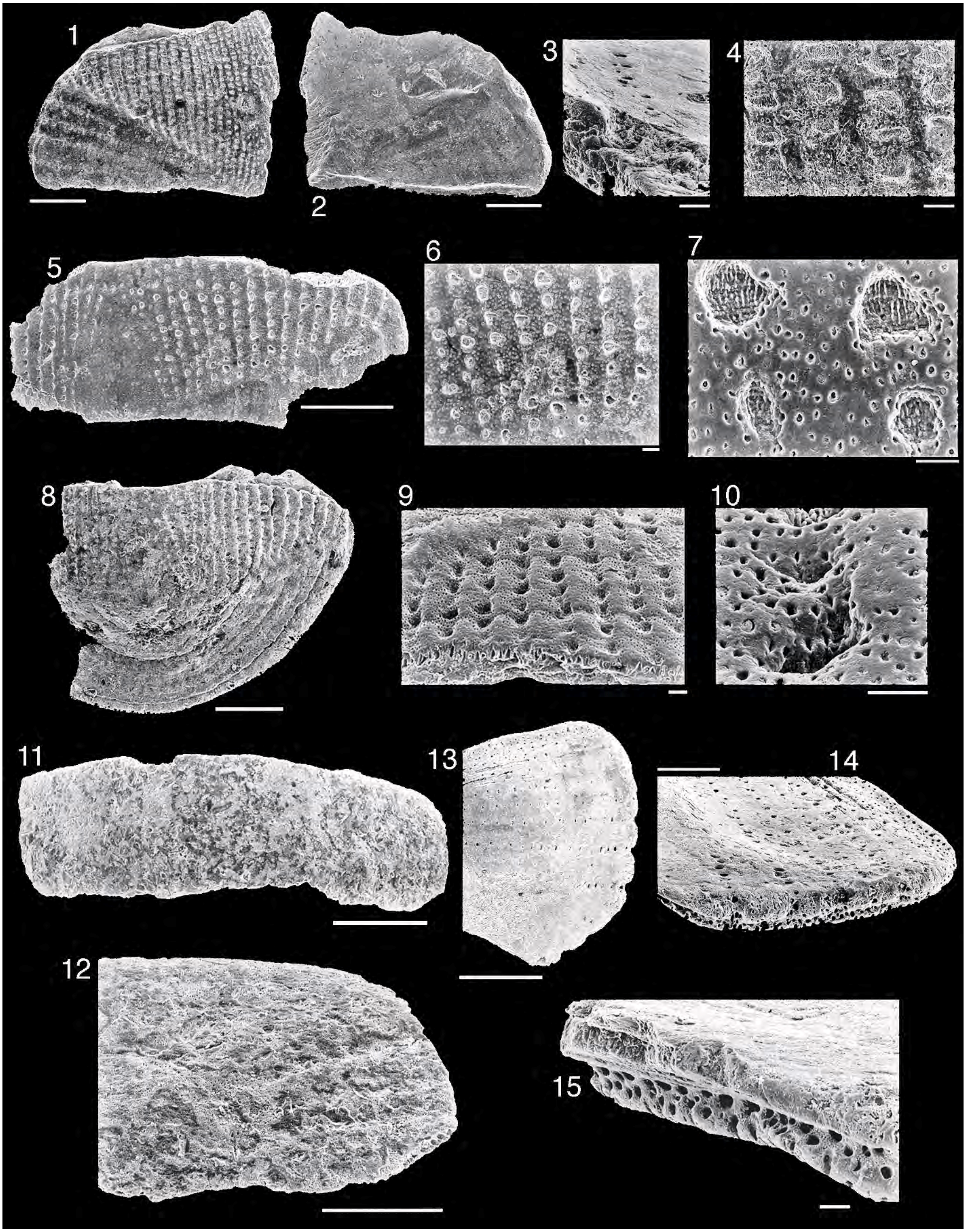
FIGURE 2—*1–12, Lepidopleurus propecajetanus* n. sp.: *1–7*, holotype, intermediate valve, MZB 45652; *1*, dorsal; *2*, ventral; *3*, *4*, lateral views; *5*, ornamentation of lateral area; *6*, ornamentation of central area; *7*, anterior view; *8–9*, paratype, head valve, MZB 45653: *8*, dorsal view, *9*, lateral view; *10–12*, paratype, intermediate valve, MZB 45654, ventral view: *11–12* detail of transverse slits in jugal tract; *13–16, Leptochiton* sp., intermediate valve, MZB 45656: *13–14,* dorsal, and ventral views, respectively; *15,* ornamentation of central area; *16,* close-up of Fig. 2.15, showing the granules. Scale bars: 1 mm: *1, 2, 7, 8, 10*; 500 µm: *3, 4, 9, 13, 14*; 100 µm: *5, 6, 11, 12, 15*; 50 µm: *16*.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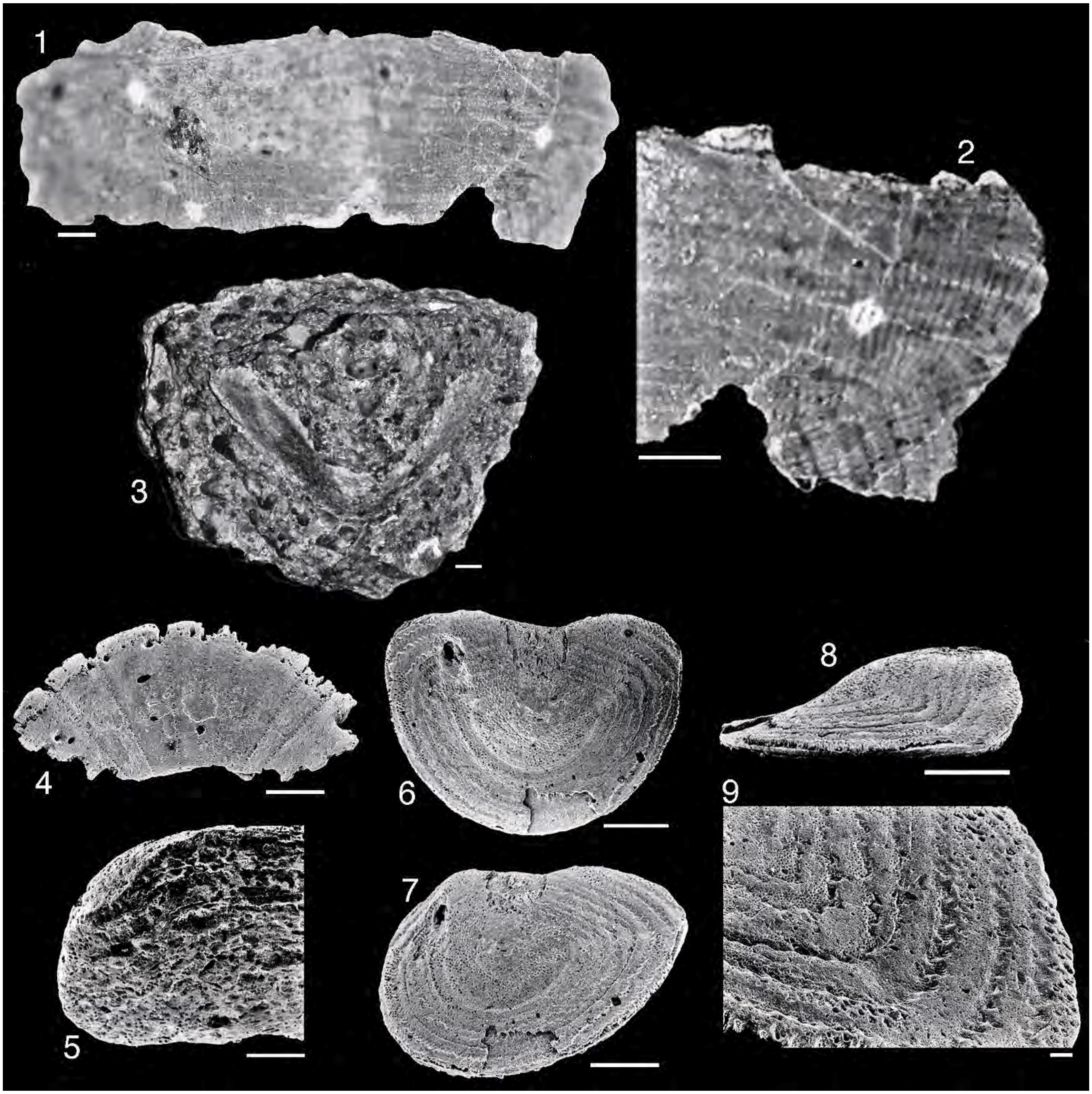

FIGURE 4—*1–2*, *Stenoplax quimperensis* n. sp., intermediate valve, holotype, MZB 45663, in matrix; *1*, dorsal view; *2*, close-up of half right valve; *3*, *Stenoplax* sp. A, intermediate valve, MZB 45664, in matrix; *4–9*, *Stenoplax* sp. B: *4*, head valve, MZB 45665, ventral view; *5*, half intermediate valve, dorsal view, MZB 45666; *6–9*, tail valve, MZB 45667; *6*, dorsal view; *7*, dorsal view, obliquely seen; *8*, lateral view, *9*, detail of the sculpture, at the contact between antemucronal and potmucronal areas. Scale bars: 2 mm: *1, 2, 3*; 1 mm: *4, 6, 7, 8*; 500 µm: *5*; 100 µm: *9*.

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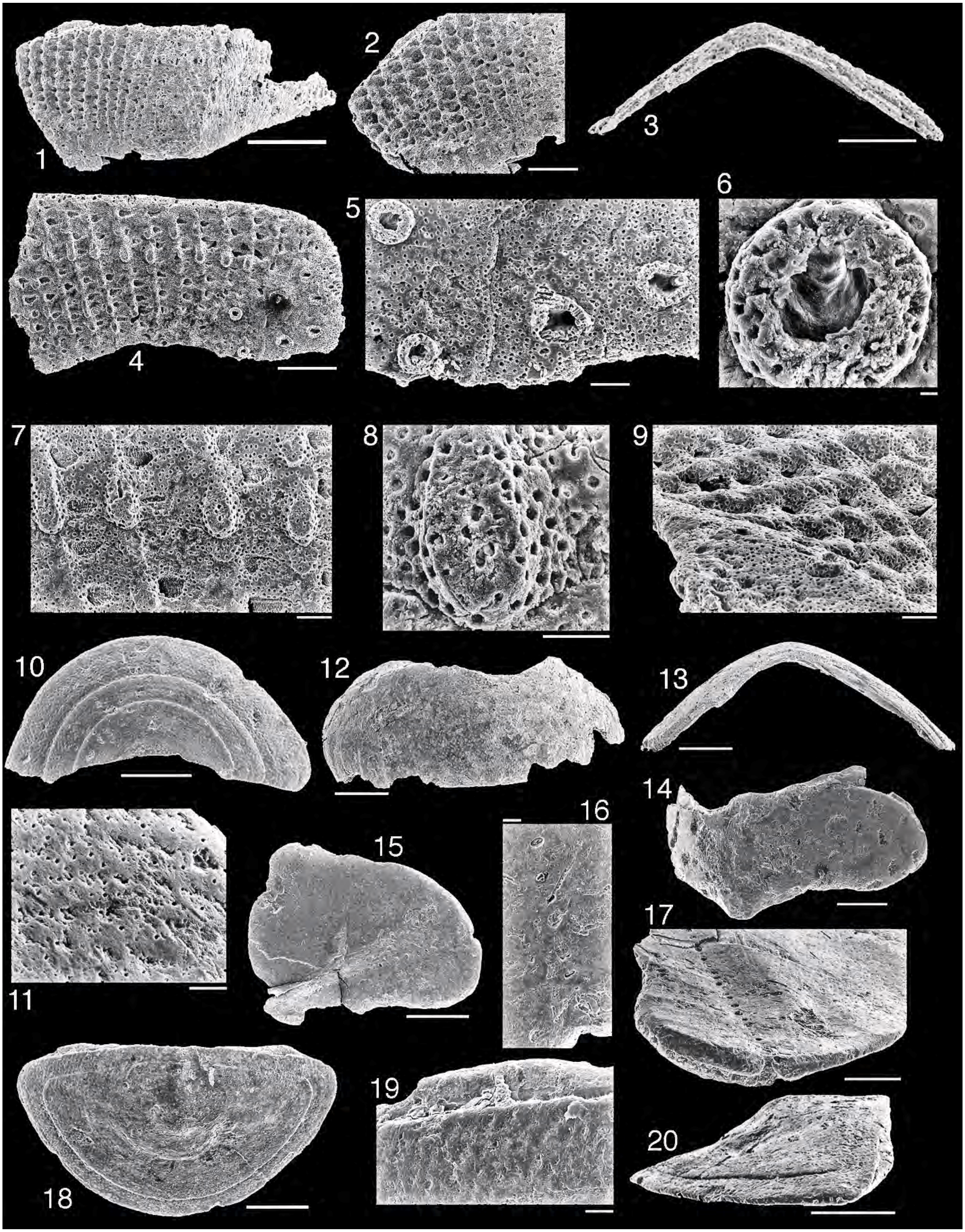
FIGURE 3—*1–10*, *Ischnochiton goederti* n. sp.; *1–4,* holotype, intermediate valve, MZB 45657; *1*, dorsal view; *2*, ventral view; *3*, detail of slit ray; *4*, ornamentation of central area; *5–7, 9–10,* paratype, intermediate valve, MZB 45658; *5*, dorsal view; *6–7,* ornamentation of central area, showing the holes pointed out as quadrangular structures, that at first sight should look like tubercles on the valve's surface; *9–10*, ornamentation of central area seen from a lateral view; *8,* paratype, tail valve, MZB 45659, dorsal view; *11–12*, *Ischnochiton*? sp. A., intermediate valve, MZB 45661, dorsal views; *13–15*, *Ischnochiton*? sp. B., intermediate valve, MZB 45662; *13*, ventral view; *14, 15*, ventro-lateral views, showing 6 to 7 slit rays. Scale bars: 1 mm: *1, 2, 5, 8, 11, 13*; 500 µm: *12, 14*; 100 µm: *3, 4, 6, 9, 15*; 50 µm: *7, 10*.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allow its separation from the four Eocene/Oligocene *Stenoplax* species described (reported in the discussion of *Stenoplax quimperensis* n. sp.) and the two other *Stenoplax* species reported in this paper.

Genus LEPIDOZONA Pilsbry, 1892

Type species.—*Chiton mertensii* Middendorff, 1847, by original designation.

LEPIDOZONA COWLITZENSIS new species
Figure 5.1–5.9

Diagnosis.—Intermediate valve rectangular, carinated, sculpture formed by ~13 longitudinal riblets per side on central area, the interspaces much wider, coarsely latticed, and by some rather large pustules (incompletely preserved), clearly separated, probably aligned in radial ribs on lateral areas. Articulamentum with a single incision in the lateral margin of the valve.

Description.—Intermediate valve rectangular, fragile, carinated, anterior margin slightly convex. Sculpture formed by ~13 longitudinal riblets per pleural area, the interspaces much wider, coarsely latticed. The longitudinal riblets formed by welldistanced, subdued and smoothed granules, elliptical in shape (Fig. 5.4). Lateral areas with some rather large pustules (incompletely preserved), clearly separated, measuring 100–120 μm in diameter, probably aligned in radial ribs (Fig. 5.5, 5.6). Pustules in the available intermediate valve are open, probably caused by erosion of the upper part. Tegmentum densely covered with aequidimensional aesthetes, not differentiating in macro- and micraesthetes (Fig. 5.7). Articulamentum worn, only a single incision can be detected. Apophyses are not visible.

Etymology.—Named for the Cowlitz River.

Types.—Loc. A-1424, Gries Ranch: one intermediate valve, holotype, MZB 45669.

Occurrence.—Gries Ranch Formation (latest Eocene or earliest Oligocene), Cowlitz River, Gries Ranch, Washington.

Discussion.—The attribution to the genus *Lepidozona* shows some problem, because some typical characters (i.e., the intermediate valves with a delicately denticulate jugal plate, separated from the apophyses by small notches) are not detectable in the available material. Other characters (Kaas and Van Belle, 1987, p. 166; "tegmentum usually sculptured with radial rows of pustules or graniferous ribs on end valves and lateral areas of intermediate valves, with longitudinal riblets, the interstices often latticed, on central areas") are consistent with the attribution to the genus. Also the dense covering of aesthetes on the whole tegmentum is compatible with the attribution to *Lepidozona*, as can be seen i.e., for *Lepidozona vietnamensis* Strack, 1991 (pl. 2, figs. 5, 6), so it is possible to attribute the valve to *Lepidozona* with a full agreement.

The only intermediate valve available is extremely fragile and was affected by cleavage during its preparation. Consequently the tegmentum peeled off from the whole half right valve which remained intact and was photographed as such. There are no other *Lepidozona* species described from Eocene or Oligocene strata, strengthening our diagnosis of this n. sp. The available specimens are very scarce and worn; however, the characters of this species are well defined.

Ischnochiton (Lepidozona) sanctaemonicae Berry, 1922 is known from the Pleistocene of Santa Monica, California, from which *L. cowlitzensis* n. sp. differs by the less numerous longitudinal riblets of the central areas (13 vs. 25–28 per side in *I. sanctamonicae*) and a minor elevation of intermediate valves (compare Fig. 5.3 with Berry, 1922, pl. 12, fig. 6).

Suborder ACANTHOCHITONINA Bergenhayn, 1930
Superfamily MOPALIOIDEA Dall, 1889
Family TONICELLIDAE Simroth, 1894
Genus LEPIDOCHITONA Gray, 1821

Type species.—*Chiton marginatus* Pennant, 1777 (=*Chiton cinereus* Linnaeus, 1767) by monotypy.

LEPIDOCHITONA LIOPLAX (Berry, 1922)
Figure 5.10–5.20

Oligochiton lioplax BERRY, 1922, p. 431, pl. 1, figs. 1–6; CLARK AND ARNOLD, 1923, p. 174; SMITH, 1960, p. I56, figs. 38/13a–c; FERREIRA, 1982, p. 133; SWEENEY AND ROPER, 1984, p. 76, 77, 81; SCOTT, HOCHBERG, AND ROTH, 1990, p. 6; COCKBURN, DUNLOP, AND LANDRY, 1999, p 30.

Lepidochitona (Spongioradsia) lioplax (Berry), VAN BELLE, 1981, p. 47.

Type material.—Holotype CAS 61805.46; paratype SBMNH 34398, one head valve attached to matrix (*fide* Scott et al., 1990, p. 6), not seen.

Description.—Head valve semicircular (Fig. 5.10). Intermediate valves rectangular, moderately elevated, dorsal elevation 0.33 in the valve illustrated (Fig. 5.13), not carinated, anterior margin nearly straight, lateral margins rounded, posterior margin with an evident apex (Fig. 5.14), slightly concave in both the sides, lateral areas flattened, hardly elevated (Fig. 5.12).

Tail valve semielliptical, anterior margin nearly straight, the mucro nearly median, little evident (Fig. 5.18). Tegmentum practically smooth except for a few weak, concentric growth lines. Aesthetes irregularly arranged (Fig. 5.11). Articulamentum worn, apophyses triangular always incomplete, well separated by a large jugal sinus. It is not possible to count exactly the incisions. Twelve slit rays can be seen in a better preserved but incomplete head valve, so it should be possible to infer 13 to 14 slits. Intermediate valves with a single slit (Fig. 5.15–5.17). Slits of tail valve unknown. The slit formula is therefore: 13–14/1/?. Central depression of intermediate valves with numerous transverse slits in jugal tract.

Material examined.—Porter Creek: 94 valves (10 head, 77 intermediate and seven tail), MZB 45670–45673 (figured head valve, two intermediate valves, half intermediate valve, tail valve, respectively), MZB 45674 (unfigured lot).

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—*Oligochiton lioplax* was described on the basis of four valves (one head, one intermediate and two tail) from the Oligocene Sooke Formation, conglomerates and sandstones found along the sea cliff between the mouths of Muir

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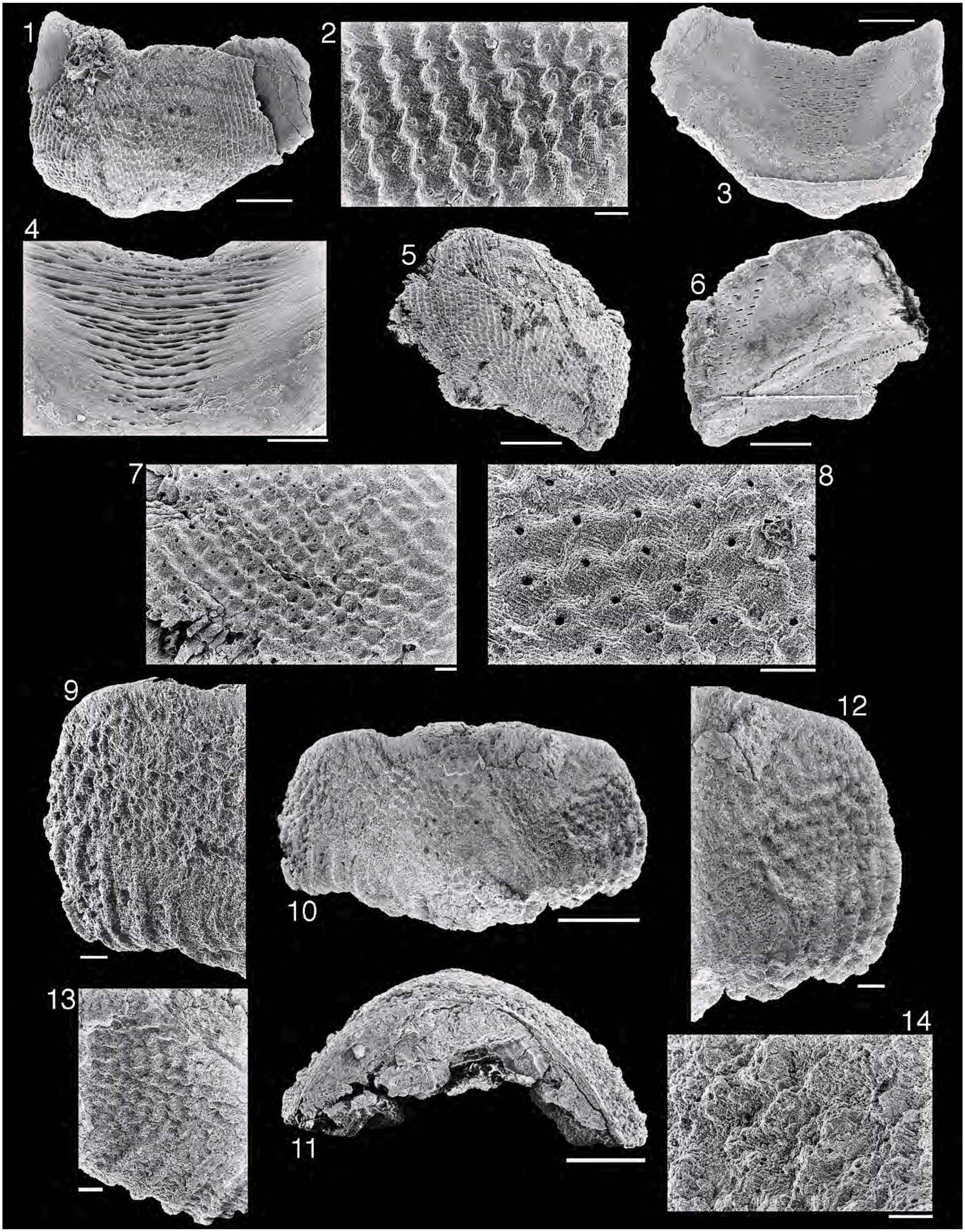
FIGURE 5—*1–9, Lepidozona cowlitzensis* n. sp.: *1–9*, intermediate valve, holotype, MZB 45669: *1–2,* dorsal view; *3*, anterior view; *4*, dorsal view of the tegmentum peeled off from the whole half right valve; *5–6*, ornamentation of lateral area; *7, 9*, ornamentation of central area, dorsal and dorso-lateral wievs, respectively; *8*, close-up of Fig. 5.7, showing a granule; *10–20*, *Lepidochitona lioplax* (Berry, 1922): *10–11*, head valve, MZB 45670; *10*, dorsal view; *11*, ornamentation; *12–13*, intermediate valve, MZB 45671, dorsal and anterior views, respectively; *14*, intermediate valve, MZB 45671a, dorsal view; *15–17*, half intermediate valve, MZB 45672, ventral view: *16*, slit ray; *17*, ventro-lateral view; *18–20*, tail valve, MZB 45673: *18*, dorsal view; *19*, apophyses; *20*, lateral view. Scale bars: 1 mm: *1, 3, 4, 5, 8, 10, 12, 14, 18, 19*; 500 μm: *7, 11, 13*; 100 μm: *6, 9, 15, 17, 19*; 50 μm: *2, 16*.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and Kirby creeks, west of Otter Point, southern Vancouver Island, British Columbia, Canada. This species has been only seldom recorded after its original description (Cockburn et al., 1999).

There are no valid reasons to consider *Oligochiton* as a genus distinct from *Lepidochitona*, which includes also smooth species, i.e., *Lepidochitona furtiva* (Monterosato, 1879), *L. turtoni* (Ashby, 1928), *L. dicksae* Sirenko and Hayes, 1999. The differences reported by Berry (1922, p. 433; "*Cyanoplax* and *Lepidochitona* have a differently formed tail valve, longer teeth, and a wider separation of the much better developed sutural laminae") may also be recognized in *Lepidochitona* species.

Van Belle (1981) considered the species belonging to *Lepidochitona*, subgenus *Spongioradsia* Pilsbry, 1894, on the basis of the presence of more incisions on insertion laminae in intermediate valves. This character allows the splitting of *Lepidochitona* into different subgenera (Kaas and Van Belle, 1985, p. 81) but this cannot be considered with certainty for *Oligochiton lioplax*. In fact, Berry reported in his original description "slits numerous…, probably 2 or 3 on a side in median valves" because he described a single intermediate valve "in situ" (Berry, 1922, l.c., pl. 1, fig. 3) and not visible in the ventral side. In our material, including 77 intermediate valves, a single incision per side is always present.

The shape of intermediate valves also differs in our material; the valves are less lengthened and with an evident apex. We think, however, that these slightly differences can be attributed to the scarce material available to Berry and to the poor conditions of preservation.

Lepidochitona washingtonensis new species
Figure 6.1–6.8

Diagnosis.—Intermediate valves solid, broadly rectangular, tegmentum uniformly covered with roundish granules, round-topped, arranged in quincunx. Each granule with a single central aesthete. Jugal tract with numerous transverse slits and a single slit ray per side.

Description.—Intermediate valves solid, broadly rectangular, posterior margin with a well developed apex. Tegmentum uniformly covered with roundish granules, little elevated, with the rounded top, arranged in quincunx (Fig. 6.7). A single central aesthete is present on the granules' top (Fig. 6.8). Articulamentum with apophyses not preserved. Insertion laminae no longer existing, but a single slit ray per side (Fig. 6.6) is visible. Central depression of intermediate valves with numerous transverse slits in jugal tract (Fig. 6.4).

Etymology.—Named for Washington State.

Types.—Oakville: four intermediate valves. Holotype, MZB 45675 (Fig. 6.1–6.4), and three paratypes, MZB 45676 (figured, Fig. 6.5–6.8), MZB 45677 (unfigured lot).

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), at Oakville, Washington.

Discussion.—Only four incomplete intermediate valves were found. It is very difficult to attribute fossil valves to *Lepidochitona* because of poor preservation, scarcity, and the convergence of some diagnostic characters. Notwithstanding these difficulties, the available material is well characterized and different by the other *Lepidochitona* species studied (*L. lioplax*, *L. squiresi* n. sp. and *Lepidochitona* sp.).

Several *Lepidochitona* species have been described for Eocene/Oligocene. *Lepidochitona defrancei* (de Rochebrune, 1883) from the Paris basin has the same sculpture in the central depression of intermediate valves, like *L. washingtonensis*, but is different in the tegmentum granules, more cylindrical and raised and with a central megalaesthete surrounded by several micraesthetes on the granule's edge (Fossils website). *Lepidochitona grinionensis* (Lamarck, 1802), from the Paris basin also exhibits more cylindrical and raised granules with a central megalaesthete and two lateral micraesthetes, and all the tegmentum is covered by micraesthetes, in contrast to *L. washingtonensis* (Fossils website). In addition, *L. grinionensis* does not present the transverse slits in the central depression of intermediate valves (based on the specimens present in Dell'Angelo collection).

In other species, i.e., *Lepidochitona corrugis* (Boettger, 1869) from Oligocene strata in Germany, the granules are more or less arranged in longitudinal series on the central area (Janssen, 1978, pl. 16, figs. 39–44).

Lepidochitona squiresi new species
Figure 6.9–6.14

Diagnosis.—Intermediate valve rectangular, rounded, moderately elevated, with a hardly evident apex. Tegmentum uniformly covered with very irregularly arranged and rather elevated roundish granules, randomly arranged. Granules with some irregularly disposed aesthetes. About ten raised lamellae on the lateral areas.

Description.—Intermediate valve rectangular, rounded, moderately elevated, anterior and posterior margins almost straight, with a scarcely evident apex, lateral margins rounded. Lateral areas not raised, there is not a clear separation with pleural areas (Fig. 6.10). Tegmentum uniformly covered with very irregularly arranged and rather elevated roundish granules, randomly disposed on the valve surface. Some irregularly disposed aesthetes are present on the granules top, up to seven (Fig. 6.14). About 10 raised lamellae, constituting structures similar to cords, (Fig. 6.9, 6.13), are present on the lateral areas. Articulamentum embedded in matrix, only a single incision is visible.

Etymology.—Named for Richard L. Squires, California State University, Northridge, for his many studies of Eocene North American mollusks.

Types.—Loc. CSUN 1563 (=LACMIP loc. 16655), Capitol Peak: one intermediate valve, Holotype, MZB 45678.

Occurrence.—Crescent Formation (middle early Eocene, "Capay" stage), at Capitol Peak, near Larch Mountain, Black Hills, Washington.

Discussion.—We have available only a unique intermediate valve, complete but with the ventral part filled by sediment, and consequently not visible. The attribution to the genus *Lepidochitona* cannot be defined with certainty on the basis of the available material but the uniform tegmentum granulation is a typical character of this genus (Kaas and Van Belle, 1985). The presence of lamellae on the lateral areas is, to our knowledge, not a characteristic of other *Lepidochitona* species.

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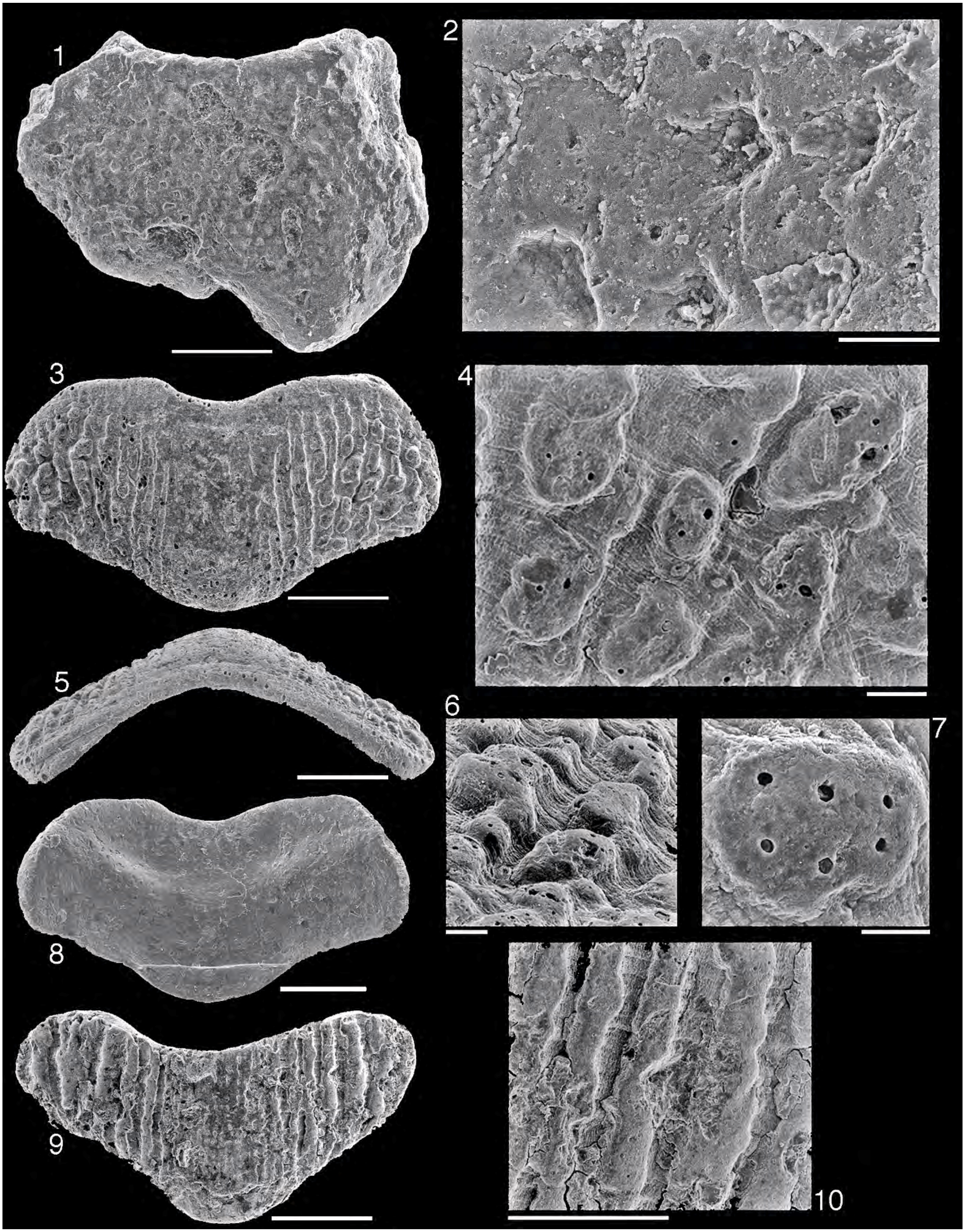
FIGURE 6—*1–8*, *Lepidochitona washingtonensis* n. sp.: *1–4,* holotype, intermediate valve, MZB 5675; *1,* dorsal view; *2,* ornamentation of central area; *3,* ventral view; *4,* ventral view, showing transverse slits in jugal tract; *5–8,* paratype, intermediate valve, MZB 45676; *5,* dorsal view; *6,* ventral view; *7–8,* dorsal views ornamentation of central area; *9–14*, *Lepidochitona squiresi* n. sp., holotype, intermediate valve, MZB 45678: *9,* left half valve; *10–11,* dorsal and anterior views, respectively; *12,* right half valve; *13,* lateral area with lamellae; *14,* ornamentation of central area. Scale bars: 1 mm: *1, 3, 5, 6*; 500 µm: *4, 10, 11*; 100 µm: *2, 7, 8, 9, 12, 13*; 50 µm: *14*.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LEPIDOCHITONA sp.
Figure 7.1–7.2

Description.—Only a small fragment of an intermediate valve with a well evident apex is available (Fig. 7.1). The sculpture is formed by rather irregular roundish granules, little raised, and with a central megalaesthete and several micraesthetes arranged along the granules's border (Fig. 7.2). A unique slit-ray is present on the ventral area.

Material examined.—Porter Creek: one intermediate valve, MZB 45679.

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—In spite of the very scarce material at our disposal, this species has characteristics that differentiate it from the other *Lepidochitona* species. It differs from *Lepidochitona washingtonensis* n. sp. particularly in the more irregular and rough granules and the different layout of the aesthetes. The ventral area is partially filled by sediment.

Superfamily CRYPTOPLACOIDEA H. and A. Adams, 1858
Family ACANTHOCHITONIDAE Simroth, 1894
Genus CRASPEDOCHITON Shuttleworth, 1853

Type species.—*Chiton laqueatus* Sowerby, 1841, by monotypy.

CRASPEDOCHITON EERNISSEI new species
Figure 7.3–7.10

Diagnosis.—Intermediate valves rectangular, sculptured with large raised tubercles of irregular oval shape, more roughly defined and coalesced in the pleural areas, even to form true irregular cords. Articulamentum with a single slit by each side, central depression with numerous transverse slits in jugal tract.

Description.—Intermediate valves rectangular, subcarinated, little raised, anterior margin concave in the jugal zone, posterior margin convex at both the sides with a well evident apex, lateral margins rounded, lateral areas not elevated. The sculpture consists of large raised tubercles of irregular oval to rectangular shape; highly variable both in shape (from regularly oval and separated tubercles to coalesced ones even to form true irregular cords) and for the degree of raising and density. The tubercles are more or less radially arranged in the lateral areas (Fig. 7.4, 7.6), while forming true irregular cords in the pleural areas (Fig. 7.10). The jugal area is smooth. The tubercles are rather worn, and the layout of the aesthetes is variable on their top, with 2 to 6 aesthetes discernible (Fig. 7.4, 7.7). The articulamentum is rather worn, a single slit on each side is hardly discernible (Fig. 7.8). Central depression of intermediate valves with numerous transverse slits in jugal tract.

Etymology.—The specific name honours our friend Douglas J. Eernisse, California State University, Fullerton, for his contribution to the study of Recent and fossil chitons.

Types.—Porter Creek: two intermediate valves. Holotype MZB 45680 (Fig. 7.3–7.8), paratype MZB 45681 (Fig. 7.9, 7.10).

Occurrence.—Lincoln Creek Formation (latest Eocene or earliest Oligocene), Porter Creek, Washington.

Discussion.—The genus attribution to *Craspedochiton* cannot be defined with certainty, because some characters that permit to differentiate the genus *Craspedochiton* from *Acanthochitona* (e.g., the presence of five radial ribs on the head valve, extending to the insertion lamina, and the insertion lamina of the tail valve with 6–10 rather irregular teeth, tending in some species to degenerate in a dense callus without slits) require the study of head and tail valves, not present in the available material (Smith, 1960; Dell'Angelo et al., 1999). Other characters (e.g., the general shape of intermediate valves and the stronger tubercle sculpturing) are consistent with genus attributes so it is possible to attribute this species to *Craspedochiton*.

If confirmed, this is the oldest record of *Craspedochiton*. Some *Craspedochiton* species were described from the central-eastern European and Mediterranean basins (revised by Dell'Angelo et al., 1999). The more common species is *C. altavillensis* (Seguenza, 1876) (found in the Miocene from Italy and central-eastern Europe and in the Plio-Pleistocene from some Italian and Spanish localities), which can be distinguished from *C. eernissei* by the greater dimensions, the different shape (trapezoidal) of the intermediate valves, and especially the presence of a large diagonal rib. C*raspedochiton minutulus* Bałuk, 1971 (found in the Badenian from Poland and in the Tortonian from Italy) show little carinated valves (maximum width 2 mm) with more dense and regular tubercles, and a different aesthetes layout (6–10 by each tubercle).

ADDITIONAL MATERIAL of unclear taxonomic position

Occurrence.—Humptulips Formation; LACMIP loc. 12385; middle Eocene. Small hill in an abandoned meander of the East Fork of the Humptulips River, northwest part of Sec. 4, T. 20 N., R. 9 W., N 47°15′19″, W 123°48′48.94″, Grays Harbor County, Washington.

Material examined.—One intermediate valve, MZB 45682.

Discussion.—The intermediate valve is incomplete, preserved in matrix, partially covered in the pleural area toward the anterior margin. It should be likely attributed to the genus *Lepidopleurus*, even if the articulamentum is not visible. It has a general appearance different from *Lepidopleurus propecajetanus* n. sp., i.e., the greater dimensions, more elevated, a greater number of longitudinal cords in the central area, but the material available does not permit a specific determination.

This particular locality is a deep-water cold seep deposit, one of those from which Squires and Goedert (1995) previously identified *Leptochiton alveolus.* These fossils need to be restudied to see if the identification of Squires and Goedert (1995) can be corroborated or to determine if more genera/species are present in these deposits.

Occurrence.—Makah Formation; early (?) Oligocene. From a concretion containing wood fragments, limpets, and teredinid tubes, found as float on beach terrace approximately 850 m northwest of the mouth of the Sekiu River, Sec. 5, T. 32 N, R. 13 W., N 48°17.639′, W 124°24.311′, Clallam County, Washington.

Material examined.—One intermediate valve, MZB 45683.

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FIGURE 7—*1–2*, *Lepidochitona* sp., intermediate valve, MZB 45679: *1*, dorsal view; *2*, ornamentation of central area; *3–10*, *Craspedochiton eernissei* n. sp.: *3–8,* holotype, intermediate valve, MZB 45680: *3,* dorsal view; *4,* ornamentation of lateral area; *5,* anterior view; *6,* dorso-lateral view ornamentation of lateral area; *7,* dorsal view of a tubercle with aesthetes; *8*, ventral view; *9–10*, paratype, intermediate valve, MZB 45681: *9,* dorsal view; *10,* ornamentation of pleural area. Scale bars: 1 mm: *3, 5, 8, 9*; 500 µm: *1*; 100 µm: *4, 6, 10*; 50 µm: *2*, *7*.

Discussion.—The intermediate valve is poorly preserved and worn, preserved in matrix, with the sculpture not well evident. It is not therefore possible to make a generic or specific determination.

Occurrence.—"Maynard Sandstone"; part of the Lyre Formation; late middle Eocene. Roadcut on the west side of highway 101, near the boundary between Secs, 23 and 24, T. 29 N., R. 2 W., N 47°59′43.95″, W 122°53′11.09″, near Maynard, Jefferson County, Washington.

Material examined.—One tail valve, MZB 45684.

Discussion.—The tail valve is poorly preserved and worn, in hard matrix. It should be attributed to the genus *Stenoplax* (see the discussion on *Stenoplax quimperensis* n. sp.) and is similar to *Stenoplax* sp. B, but it differs by valve layout and the greater number of close set, rugose, hardly interrupted concentric riblets in the postmucronal area.

Occurrence.—Lincoln Creek Formation; late Eocene. Basal sandstone exposed on the east bank of the Canyon River, near the center of the west half of Sec. 18, T. 21 N., R. 6 W., N 47°18′31.0″, W 123°29′59.90″, Mason County, Washington.

Material examined.—Two intermediate valves, MZB 45685.

Discussion.—The intermediate valves are very poorly preserved and worn, in hard matrix, with the sculpture not evident. It is not therefore possible to make a generic or specific determination.

CONCLUSIONS

Fossil molluscan assemblages from the Pacific Coast of North America have been studied for more than a century but reports of chitons as part of these assemblages are extremely scant. This preliminary report shows that chitons are consistently present in Eocene-Oligocene strata in western North America. The material examined comprises 14 species, coming from six different localities. No species has been found in more than one locality except for *Lepidochitona lioplax*, and in four of the localities only a single species has been collected (Table 1). One of the localities (Porter Creek) provided a reasonably diverse chiton fauna (seven species accounting for 86% of the valves here studied); however, 67% of the valves belong to a single taxon (*Lepidochitona lioplax*) while seven species are only represented by one single valve.

To date 79 identified species are known from the Paleogene (Appendix 2), 58 from Europe, 10 from Australia and New Zealand, and 11 from U.S.A., including the eight species reported herein. The remaining three species from U.S.A. are *Leptochiton alveolus* (Lovén, 1846) from the Eocene of Washington (Squires and Goedert, 1995; Goedert and Campbell, 1995), and two species from the eastern side of Nordamerican plate, *Chaetopleura tampaensis* (Dall, 1892), and *Chiton eocenensis* Conrad, 1856. *Chaetopleura tampaensis* was described from Florida (Ballast Point, Tampa Bay), Orthaulax Bed, lower Miocene (=Oligocene, *fide* Dall, 1915) based on only one head valve and one intermediate valve. *Chiton eocenensis* (syn. *Chiton conradi* Van Belle, 1980, nom. nov. pro *C. antiquus* Conrad, 1856, non Reeve, 1847; *Chiton*? *prostremus* De Gregorio, 1890) is known from a few valves from the Eocene (Claibornian) of Claiborne, Alabama, and was redescribed by Dall (1892).

Puchalski et al. (2008) considered a total of 900 fossil chitons known, of which 430 are named species known only as fossils, 123 are extant species that also have a fossil record, and 247 are indeterminate taxa. The 79 Paleogene chitons correspond to 14% of the named species. *Leptochiton algesirensis* and *L. alveolus* are the sole extant taxa with such old fossil records.

It appears that chitons are more widespread in the fossil record than previously thought as they are often overlooked by scholars (Puchalsky, 2005; Puchalsky et al., 2008). This research substantially contributes to the assessment of chiton diversity in a restricted geographic area and within a narrow time-span and therefore, we fully support the opinion of Puchalski et al. (2008) that the scarcity of Polyplacophora in the paleontological record is due to inadequate sampling.

The Paleogene chiton fauna described here forms the much-needed basis to begin understanding the post-Mesozoic Polyplacophora of this region. The Plio-Pleistocene to Recent fauna is quite well known, rich, and diverse. One major gap now exists in the overall appreciation of biogeography and evolution of northeastern Pacific Polyplacophora: Miocene chitons are still virtually unknown. It is our hope that this study will spur others to look for chiton fossils in the vastly understudied Pacific coast record in order to help fill the many geographic and temporal gaps on the related chiton fauna.

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APPENDIX 1—Collecting sites.

1. Woodman's Wharf (A-1802, UCMP loc.). Late Eocene (Quimper Formation). On beach a quarter mile north of Woodman's Station, Discovery Bay, SW¼ of NE¼ of Sec. 8, T. 29 N., R. 1 W., N 48°01′26.16″, W 122°49′87.94″, Jefferson County, Washington. (Durham, 1944).
2. JLG214. Latest Eocene (or earliest Oligocene), Makah Formation, Jansen Creek Member. Map: Sekiu River, WA USGS Quad., 7.5 minute, 1986 provisional edition. Blocks of greenish conglomerate containing mollusks, on beach terrace approximately 500 m southeast of mouth of Jansen Creek, approx. 200 m to the east of southwest corner of Sec. 25, T.33 N., R.14 W., N 48°19′18.55″, W 124°27′51.18″, Clallam County, Washington. (Squires, 1995).
3. Oakville (=LACMIP loc. 16934). Latest Eocene (or earliest Oligocene), basal Lincoln Creek Formation. Silty sandstone packed with shells, in between large basalt boulders, from a pocket on top of basalt in quarry on east side of Highway 9, N 46°51′00″, W 123°14′38.34″, just northwest of the town of Oakville, Grays Harbor County, Washington. Quarry activities completely removed this "pocket" of sediment in 1995. (Van Winkle, 1918 (mollusks from equivalent strata in basalt quarries in the same vicinity); Prothero and Armentrout, 1985).
4. Porter Creek (LACMIP loc. 16935). Latest Eocene (or earliest Oligocene), basal Lincoln Creek Formation. Glauconitic-basaltic sandstones in contact with basalt, banks of Porter Creek, approximately 500 m east and 220 m south of the northwest corner of Sec. 14, T. 17 N., R. 5 W., N 46°57′55.48″, W 123°16′39.22″, Grays Harbor County, Washington. (Rau, 1948; Prothero and Armentrout, 1985).
5. CSUN loc.1563 (=LACMIP loc. 16655). Middle early Eocene ("Capay" stage), Crescent Formation. Map: Capitol Peak USGS Quad., 7.5 minute, 1986 provisional edition. N 47°59′03″, W 123°8′12″. At elevation of 680 m, road cut on northeast side of logging road, 300 m north and 50 m east of the southwest corner of Sec.1, T.17 N., R.4 W., near Larch Mountain, Black Hills, Thurston County, Washington. (Squires and Goedert, 1996).
6. A-1424 (UCMP loc.). Latest Eocene (or earliest Oligocene), Gries Ranch Formation. South bank of Cowlitz River, at site of the old Gries Ranch, N 46°28′07.8″, W 122°52′83.9″, Lewis County, Washington. (Effinger, 1938; Prothero and Burns, 2001).

APPENDIX 2—Paleogene Polyplacophora reported in interature. This appendix lists all identified taxa reported in literature for the Paleogene, including taxa reported in the present paper. The list substantially agrees with the database of Cambrian to Pleistocene fossil chitons (Puchalski, 2005; Puchalski et al., 2008).

Species	Country	Geological period	Ref.
Fam. LEPTOCHITONIDAE Dall, 1889			
1 *Lepidopleurus eckelsheimensis* Gürs, 1992	EUROPE Germany	Oligocene	Gürs, 1992
2 *Lepidopleurus elaboratus* Bielokrys, 2000	EUROPE Ukraine	Eocene	Bielokrys, 2000
3 *Lepidopleurus jansseni* Gürs, 1995	EUROPE Germany	Oligocene	Gürs, 1995
4 *Lepidopleurus obsoletus* Cossmann and Pissarro, 1900	EUROPE France	Eocene	Cossmann and Pissarro, 1900
5 *Lepidopleurus paeninsulae* Gürs, 1992	EUROPE Germany	Oligocene	Gürs, 1992
6 *Lepidopleurus papillosus* Bielokrys, 2000	EUROPE Ukraine	Eocene	Bielokrys, 2000
7 *Lepidopleurus propecajetanus* n. sp.	USA Washington	Eocene–Oligocene	this paper
8 *Lepidopleurus pustuliferus* Bielokrys, 2000	EUROPE Ukraine	Eocene	Bielokrys, 2000
9 *Lepidopleurus scirpeus* Bielokrys, 2000	EUROPE Ukraine	Eocene	Bielokrys, 2000
10 *Lepidopleurus virgifer* (Sandberger, 1859)	EUROPE Germany	Oligocene–Miocene	Dell'Angelo and Palazzi, 1989
11 *Leptochiton algesirensis* (Capellini, 1859)*	EUROPE Germany	Oligocene–Recent	Dell'Angelo and Palazzi, 1989
12 *Leptochiton alveolus* (Lovén, 1846)	USA Washington	Eocene–Recent	Squires and Goedert, 1995
13 *Leptochiton chatticus* Janssen, 1978	EUROPE Germany	Oligocene	Dell'Angelo and Palazzi, 1989
14 *Leptochiton faksensis* Sigwart, Andersen and Schnetler, 2006	EUROPE Denmark	Paleocene	Sigwart et al., 2006
15 *Leptochiton fischeri* de Rochebrune, 1883	EUROPE France	Eocene	Dell'Angelo and Palazzi, 1989
16 *Leptochiton magnogranifer* Ashby, 1925	AUSTRALIA Vict.	Eocene	Ashby, 1925
17 *Leptochiton poirieri* (de Rochebrune, 1883)	EUROPE Germany, France	Oligocene	Dell'Angelo and Palazzi, 1989
18 *Leptochiton uhligi* (Koenen, 1892)	EUROPE Germany	Oligocene	Dell'Angelo and Palazzi, 1989
Fam. PROTOCHITONIDAE Ashby, 1925			
19 *Protochiton granulosus* (Ashby and Torr, 1901)	AUSTRALIA Vict.	Eocene	Ashby, 1925
Fam. HANLEYIDAE Bergenhayn, 1955			
20 *Hanleya glimmerodensis* Janssen, 1978	EUROPE Germany	Oligocene	Jannssen, 1978
Fam. ISCHNOCHITONIDAE Dall, 1889			
21 *Ischnochiton asper* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
22 *Ischnochiton cancellatus* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
23 *Ischnochiton goederti* n. sp.	USA Washington	Eocene–Oligocene	this paper
24 *Ischnochiton vectensis* Wrigley, 1943	EUROPE U.K.	Eocene	Wrigley, 1943
25 *Stenoplax anglica* Wrigley, 1943	EUROPE U.K.	Eocene	Wrigley, 1943
26 *Stenoplax quimperensis* n. sp.	USA Washington	Eocene–Oligocene	this paper
27 *Stenoplax selseiensis* Wrigley, 1943	EUROPE U.K.	Eocene	Wrigley, 1943
28 *Stenoplax sigillarius* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
29 *Stenoplax veneta* Dell'Angelo and Palazzi, 1992	EUROPE Italy	Oligocene	Dell'Angelo and Palazzi, 1992
30 *Lepidozona cowlitzensis* n. sp.	USA Washington	Eocene–Oligocene	this paper
Fam. CALLISTOPLACIDAE Pilsbry, 1893			
31 *Callistochiton zitteli* (de Rochebrune, 1883)	EUROPE Germany	Oligocene	Jannssen, 1978
Fam. CHAETOPLEURIDAE Plate, 1899			
32 *Chaetopleura tampaensis* (Dall, 1892)	USA Florida	Oligocene	Dall, 1915
Fam. LORICIDAE Iredale & Hull, 1923			
33 *Lorica bourdoti* (de Rochebrune, 1883)	EUROPE France	Eocene	Cossmann, 1888
34 *Lorica compressa* Ashby and Torr, 1901	AUSTRALIA Vict.	Eocene	Ashby, 1925
35 *Lorica houdasi* (Cossmann, 1922)	EUROPE France	Eocene	Cossmann, 1922
36 *Lorica radulifera* (de Rochebrune, 1883)	EUROPE France	Eocene	Fossils website
37 *Lorica rochebrunei* Cossmann, 1888	EUROPE France	Eocene	Cossmann, 1888
38 *Loricella gigantea* Ashby and Torr, 1901	AUSTRALIA Vict., Tasm.	Eocene–Miocene	Ashby, 1925
Fam. CALLOCHITONIDAE Plate, 1901			
39 *Callochiton chattonensis* Ashby, 1929	NEW ZEALAND	Oligocene	Ashby, 1929
Fam. CHITONIDAE Rafinesque, 1815			
40 *Chiton eocenensis* Conrad, 1856	USA Alabama	Eocene	Dall, 1892
41 *Chiton fossicius* Ashby and Torr, 1901	AUSTRALIA Vict.	Eocene	Ashby, 1925
42 *Chiton janshini* (Makarenko, 1969)	EUROPE Ukraine	Paleocene	Makarenko, 1976
43 *Chiton modestus* Rolle, 1862	EUROPE France	Oligocene	Rolle, 1862
44 *Lepidochitona moskvini* (Makarenko, 1969)	EUROPE Ukraine	Paleocene	Makarenko, 1976
45 *Chiton multicavus* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
46 *Rhyssoplax allanthomsoni* Mestayer, 1929	NEW ZEALAND	Oligocene	Mestayer, 1929
47 *Tonicia brasili* (Cossmann and Pissarro, 1900)	EUROPE France	Eocene	Cossmann and Pissarro, 1900
48 *Tonicia edwarsi* de Rochebrune, 1883	EUROPE France	Eocene	Fossils website
49 *Tonicia gaasensis* (Benoist MS) de Rochebrune, 1883	EUROPE France	Oligocene	Varone, 2008
50 *Tonicia lennieri* (Cossmann and Pissarro, 1905)	EUROPE France	Eocene	Cossmann and Pissarro, 1905
51 *Tonicia morgani* de Rochebrune, 1883	EUROPE France	Eocene	Cossmann and Pissarro, 1900
52 *Tonicia pannonica* Szots, 1953	EUROPE Hungary	Eocene	Szots, 1953
53 *Tonicia waltebledi* de Rochebrune, 1883	EUROPE France	Oligocene	de Rochebrune, 1883
Fam. SCHIZOCHITONIDAE Dall, 1889			
54 *Schizochiton baylei* (Briart and Cornet, 1887)	EUROPE Belgium, Ukraine	Paleocene	Makarenko, 1976
55 *Schizochiton carinatus* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
56 *Schizochiton hirtus* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
57 *Schizochiton parcus* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999
Fam. TONICELLIDAE Simroth, 1894			
58 *Lepidochitona bernayi* (Cossmann, 1888)	EUROPE France, U.K.	Eocene	Cossmann, 1888
59 *Lepidochitona corrugis* (Boettger, 1869)	EUROPE Germany	Oligocene	Jannssen, 1978
60 *Lepidochitona defrancei* (de Rochebrune, 1883)	EUROPE France	Eocene	Cossmann, 1888
61 *Lepidochitona grinionensis* (Lamarck, 1802)	EUROPE France	Eocene	Cossmann, 1888
62 *Lepidochitona lioplax* (Berry, 1922)	USA Canada, Washington	Oligocene	this paper
63 *Lepidochitona oligocaena* (Rolle, 1862)	EUROPE France	Oligocene	Rolle, 1862
64 *Lepidochitona squiresi* n. sp.	USA Washington	Eocene–Oligocene	this paper
65 *Lepidochitona vjalovi* Makarenko, 1969	EUROPE Ukraine	Paleocene	Makarenko, 1969
66 *Lepidochitona washingtonensis* n. sp.	USA Washington	Eocene–Oligocene	this paper
67 *Tonicella implumis* Bielokrys, 1999	EUROPE Ukraine	Eocene	Bielokrys, 1999

APPENDIX *2*—Continued.

Species	Country	Geological period	Ref.
68 *Tonicella tenuissima* (Sandberger, 1859)	EUROPE Germany	Oligocene	Jannssen, 1978
Fam. MOPALIIDAE Dall, 1889			
69 *Allochiton menneri* (Makarenko, 1969)	EUROPE Ukraine	Paleocene	Makarenko, 1976
70 *Plaxiphora concentrica* Ashby and Torr, 1901	AUSTRALIA Vict.	Eocene	Ashby, 1925
Fam. ACANTHOCHITONIDAE Pilsbry, 1893			
71 *Craspedochiton eernissei* n. sp.	USA Washington	Eocene–Oligocene	this paper
72 *Notoplax ashbyi* (Laws, 1932)	NEW ZEALAND	Oligocene	Beu and Raine, 2009
73 *Afossochiton rostratus* (Ashby and Torr, 1901)	AUSTRALIA Vict.	Eocene	Ashby, 1925
Gen.inquir.			
74 *Lepidopleurus bouryi* de Rochebrune, 1883	EUROPE France	Eocene	Dell'Angelo and Palazzi, 1989
75 *Lepidopleurus daubrei* de Rochebrune, 1883	EUROPE France	Oligocene	Dell'Angelo and Palazzi, 1989
76 *Lepidopleurus morleti* de Rochebrune, 1883°	EUROPE France	Eocene	Dell'Angelo and Palazzi, 1989
77 *Gymnoplax bourdoti* de Rochebrune, 1883	EUROPE France	Eocene	Cossmann, 1888
78 *Chiton damesi* Koenen, 1892	EUROPE Germany	Oligocene	Dell'Angelo and Palazzi, 1989
79 *Chiton (Tonicia) pissarroi* Cossmann, 1902	EUROPE France	Eocene	Cossmann, 1922

* = *Leptochiton maguntiacus* (de Rochebrune, 1883) *fide* Dell'Angelo and Palazzi (1989, p. 62).
° = *Lepidopleurus raincourti* de Rochebrune, 1883 *fide* Cossmann (1888, p. 17).