

# PACIFIC SLOPE OF NORTH AMERICA RECORD OF THE CRETACEOUS APORRHAIID GASTROPOD *TESSAROLAX*: EVOLUTIONARY TRENDS, MODE OF LIFE, AND PALEOBIOGEOGRAPHY OF THE GENUS<sup>1</sup>

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**ABSTRACT.** The Cretaceous aporrhaid *Tessarolax* Gabb, 1864, is a widespread but uncommon marine gastropod whose mature shell is very distinctive with four long and narrow digitations. Its most species-rich record is from the Pacific slope of North America (PSNA), where it has been found from southern Alaska to northern Baja California, Mexico. Its longest geologic range (late Hauterivian to early late Maastrichtian) occurs in the PSNA and is represented by 10 species, five of them new: *Tessarolax alaskana*, late Turonian to early Coniacian; *Tessarolax bullardi*, middle Coniacian to early Campanian; *Tessarolax grahami*, early Campanian; *Tessarolax louellae*, middle late Campanian; and *Tessarolax teleos*, “mid” Maastrichtian.

Nondigitate immature specimens of *Tessarolax* were infaunal, whereas digitate mature specimens were epifaunal. In maturity, shells also developed a callus coat, partial in Early Cretaceous and becoming overall by Late Cretaceous. Through time, part of the mature ventral surface thickened into a projecting stabilizer (herein newly termed “fictavarix”), and other distinctive callus structures developed dorsally and ventrally on the shell. Some exceptional specimens provide three-dimensional views of fragile projecting features, thereby allowing for the first insights as to mode of life. In the PSNA region, specimens are most common in fine-grained offshore (outer sublittoral) siliciclastics, where warm-temperate waters were deeper/calmer and slightly cooler relative to more nearshore environments.

*Tessarolax gabbi* new name is provided for *Helicaulax bicarinata* Gabb, 1869, a junior secondary homonym of *Tessarolax bicarinata* (Deshayes in Leymerie, 1842). *Tessarolax gabbi* is the oldest recognized species. Although the pre-Albian global record of *Tessarolax* is sparse, the genus was most widespread during the Albian, where it is best represented in western Europe. It was localized thereafter, with post-Cenomanian occurrences mainly in the PSNA and, to a lesser degree, in Japan, southern Sakhalin, and Montana. *Tessarolax teleos* is the youngest known species.

## INTRODUCTION

The family Aporrhaidae Gray, 1850, is an extant group of marine gastropods characterized by a highly modified apertural margin. Modern species are restricted to the western and eastern Atlantic, the Mediterranean, the Black Sea, and western Africa (Mauritania/Senegal to Angola/Namibia) (Kronenberg, 1991), with the recognized number of species depending largely on an author’s predilection for morphologic conformity. The present-day distribution of aporrhaides does not apply to the Jurassic and Cretaceous, during which they were geographically more widespread (Korotkov, 1992; Kiel, 2002). Aporrhaides reached their maximum geographic distribution and taxonomic diversity during the Late Cretaceous. The end-Cretaceous mass-extinction event removed a majority of the genera, and aporrhaides have been of decreasing diversity since the beginning of the Paleogene (Roy, 1994). According to Simone (2005), possibly one of the modern species belongs to the Jurassic genus *Cuphosolenus* Piette, 1876.

One of the more distinctive Cretaceous aporrhaides is genus *Tessarolax* Gabb, 1864, whose mature shell has four long and narrow, curving digitations that are channeled and unbranched. Despite its distinctiveness, identification of this genus and discrimination of its species have been difficult because specimens are rarely preserved intact, a problem exacerbated by the incomplete holotype of the type species. Incomplete specimens of Early Cretaceous

*Tessarolax* resemble incomplete specimens of the aporrhaid genus *Ceratosiphon* Gill, 1870. Confusion between the two genera has been common in the literature.

Despite being widespread, *Tessarolax* has not received a detailed study of its morphology or of its biostratigraphy encompassing a substantial interval of time. This article aims at establishing the first evolutionary study of *Tessarolax*, based mainly on specimens from the Pacific slope of North America (PSNA), a region extending southward from southern Alaska to the vicinity of Arroyo Santa Catarina, Baja California, Mexico (Fig. 1). Based on this present study, the best-known record of *Tessarolax* is from the PSNA, where 10 species are recognized: five new, three previously named, and one renamed; one that has affinity to a named species might be new but is represented only by immature specimens. The latitudinal and temporal distributions of the PSNA species are shown in Figure 2. Supplementary descriptions and refined biostratigraphic records of the three previously named species and the renamed species are provided here. Other aims of the study are to offer the first insights about the mode of life of *Tessarolax* based on well-preserved specimens with all their digitations intact and to present the first global overview of the paleobiogeography of *Tessarolax*.

## MATERIAL AND METHODS

Specimens were borrowed from major museums having extensive collections of Cretaceous PSNA fossils, especially the Natural History Museum of Los Angeles County. The studied material is from approximately 60 localities collected over the years since 1864. Compared to many other molluscan genera present in the PSNA faunas, *Tessarolax* specimens occur at relatively few localities and in small numbers. Most specimens were collected from fine-grained, well-cemented rocks. Digitations tend to be missing because they are fragile and are prone to mechanical breakage during collecting. Grinding away adhering rock matrix is time intensive and can result in additional breakage. Quick-drying glue is essential in preparation. Stating a definite number of studied specimens of *Tessarolax* is difficult because of

<sup>1</sup> URL: [www.nhm.org/scholarlypublications](http://www.nhm.org/scholarlypublications)

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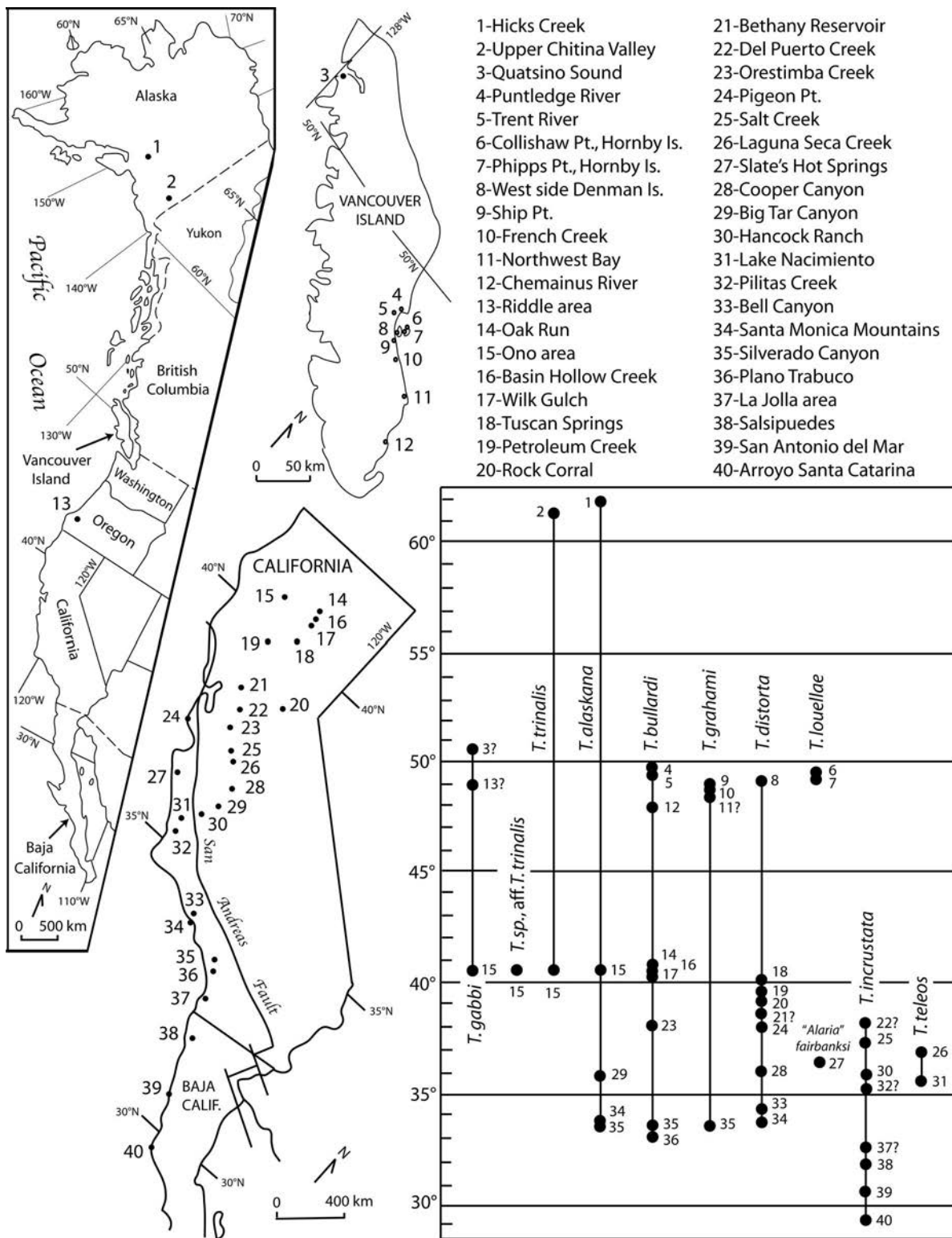


Figure 1 Localities/areas of occurrence and latitudinal distribution of studied *Tessarolax* species. Question mark indicates tentative identification of species.

the amount of breakage but includes more than approximately 142 specimens.

Early collectors found some nearly complete specimens of late Campanian to early Maastrichtian age from Baja California. Members

of the Victoria Palaeontology Society also found some broken but otherwise well-preserved *Tessarolax* of late Santonian to late Campanian age from the Nanaimo Basin of British Columbia. They skillfully reconstructed the broken pieces into nearly complete specimens.

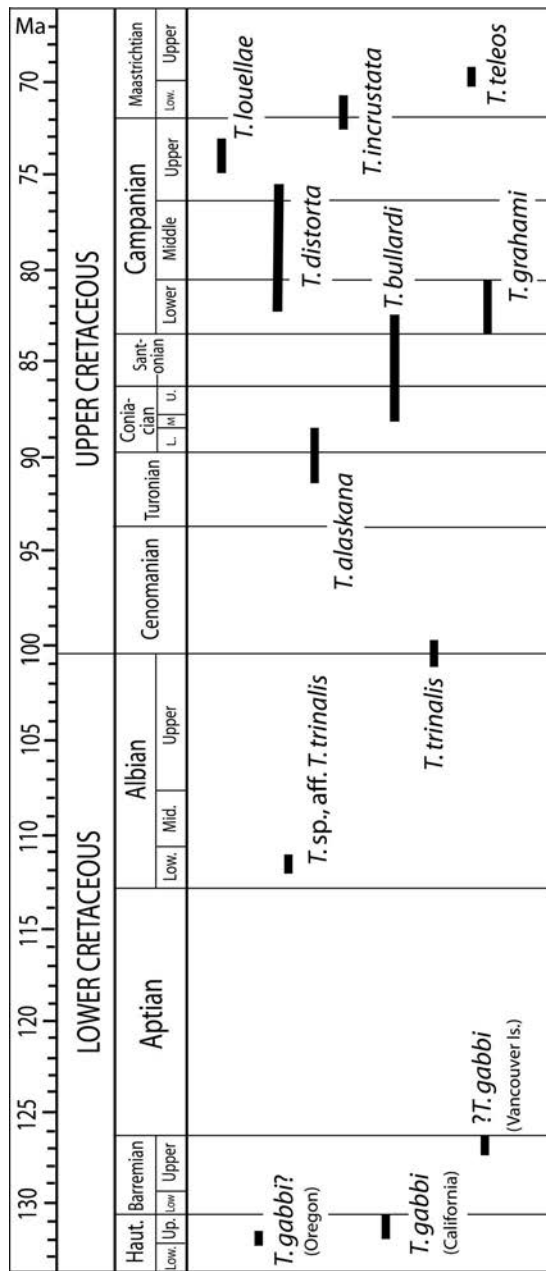


Figure 2 Geological ranges of the Pacific slope of North America (PSNA) species of *Tessarolax*. Ages of stage boundaries from Gradstein et al. (2012).

The website [www.stromboidea.de](http://www.stromboidea.de), which is devoted to stromboid gastropods, proved to be a very useful research tool because it provided critical information about taxonomy and morphology of fossil aporrhoids as well as accompanying excellent digital images of many genera and species from all over the world.

Table 1, which lists the global occurrences of species of *Tessarolax*, is based on a comprehensive but not exhaustive literature search. A few of these species cannot be identified with certainty because the specimens are broken, poorly preserved, and/or inadequately illustrated.

MORPHOLOGICAL TERMS

The terms used in describing *Tessarolax* are illustrated in Figures 3 and 4. Although the digitations are referred to as “spikes” by some

authors (e.g., Bandel, 2007), they are not straight, sharp spikes but are bent, elongately channeled digits. There can be, however, a true dorsal spine present about mid-back on a carina of some species. Gabb (1864:126) used the terms “varix-like” and a “short, clavate process” for a feature found on some species of *Tessarolax*. Gardner (1880) used the term “varix” when describing this feature. We substitute the new term “fictavarix” for the axially elongate, angled ventrally, flangiform-callus deposit along the ablabral side (i.e., on the side opposite the outer lip) of the shell (Fig. 3). In shape and placement, a fictavarix somewhat resembles a varix but is not one because the fictavarix was neither formed nor abandoned by the outer lip. A fictavarix on *Pterocera bicarinata* of d’Orbigny (1843:pl. 208, figs. 3, 5) [specimen referred to by Kollmann (2005:132) as *Ceratosiphon retusus*] was called a “varice” by Kollmann (2005). A possible fictavarix is also present on species of *Pietteia* Cossmann, 1904 [e.g., *Pietteia cretacea* Kase in Kase and Maseda, 1980].

ABBREVIATIONS

Locality and/or catalog numbers

- ANSP Academy of Natural Sciences at Drexel University, Philadelphia, PA
- CAS California Academy of Sciences, San Francisco, CA
- CIT California Institute of Technology, Pasadena, CA (collections now housed at LACMIP)
- GSC Geological Survey of Canada, Ottawa, Canada
- LACMIP Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, CA
- RBCM Royal British Columbia Museum, Victoria, Canada
- SDSNH San Diego Society of Natural History, San Diego, CA
- UCMP University of California, Berkeley, Museum of Paleontology, Berkeley, CA
- USGS United States Geological Survey, Menlo Park, CA (collections now housed at UCMP)

LOCALITIES

Locality information given below is in abbreviated format for LACMIP and UCMP localities, and complete information about these localities can be accessed, respectively, through their website links: [http://ip.nhm.org/ipdatabase/locality\\_show](http://ip.nhm.org/ipdatabase/locality_show) and <http://ucmpdb.berkeley.edu>. More detailed information, where available, is provided below for CAS, GSC, RBCM (this institution does not issue museum-locality numbers), SDSNH, and USGS. Numbers in brackets refer to “Area” numbers of Figure 1.

**Manuscript Localities** (pertaining to RBCM specimens, all from the east coast of Vancouver Island and associated smaller islands, British Columbia, Canada): [4] **Locality 4.** Siltstone on northern bank of Puntledge River at the Van Arcs Farm, near Courtenay, lower Haslam Formation, upper Santonian. Collector: T. Bullard, August 17, 2001. [5] **Locality 5.** Near where Inland Highway crosses Trent River, a few kilometers south of Courtenay, lowermost Haslam Formation, lower upper Santonian. Collector: R. Graham, September 23, 2007. [6] **Locality 6.** Collishaw Point, northwestern Hornby Island, Northumberland Formation, uppermost Campanian or lowermost Maastrichtian. Collector: R. Graham, June, 1997. [7] **Locality 7.** Phipps Point, Hornby Island, Northumberland Formation, uppermost Campanian to possibly lowermost Maastrichtian. Collector: R. Graham, May 28, 2005. [8] **Locality 8.** “White House Site” western Denman Island, upper Cedar District Formation, upper middle Campanian. Collector: T. Bullard, May 26, 2001. [9] **Locality 9.** Ship Point, eastern side of Ship Peninsula, southeast of Fanny



**Table 1** Occurrences of known and questionable species of *Tessarolax*, listed in ascending geologic age.

Species	Location	Age
<i>T. gabbi</i> n. nom.	Late Hauterivian to ?late Barremian	Vancouver Island to northern California
<i>T.?</i> <i>neuquensis</i> Camacho, 1953	Late Hauterivian	West-central Argentina
<i>T.?</i> <i>gigantea</i> (Kase, 1984)	Hauterivian or Barremian	Northern Japan
<i>T.</i> cf. “ <i>ebrayi</i> ” (de Loriol) of Kase (1984)	Late Aptian	Northern Japan
<i>T.</i> aff. <i>trimalis</i> Murphy and Rodda, 1960	Early Albian	Northern California
<i>T. retusa</i> Sowerby in Fitton, 1836	Early to late Albian	Western Europe, Mozambique, Madagascar
<i>T. trimalis</i> Murphy and Rodda, 1960	Late Albian to early Cenomanian	Southeastern Alaska to northern California
<i>T.?</i> <i>ebersini</i> (Plamadiala, 1982)	Early Cenomanian	Northern Kazakhstan
<i>T.</i> sp. (see Maeda, 1986)	Middle Cenomanian	Northern Japan
<i>T. alaskana</i> n. sp.	Late Turonian to early Coniacian	Southeastern Alaska to southern California
<i>T. japonica</i> Yabe and Nagao, 1928	Coniacian or Santonian	Northern Japan
<i>T. acutimarginata</i> Nagao, 1932	Coniacian or Santonian	Northern Japan, Sakhalin Island, Russia
<i>T. bullardi</i> n. sp.	Mid-Coniacian to early Campanian	Vancouver Island to southern California
<i>T. hitzii</i> White, 1883	Early Coniacian	Montana
<i>T. grahami</i> n. sp.	Early Campanian	Vancouver Island to southern California
<i>T. distorta</i> Gabb, 1864	Mid-early to early late Campanian	Vancouver Island to southern California
<i>T. incrustata</i> Anderson and Hanna, 1935	Latest Campanian to early Maastrichtian	California to northern Baja
<i>T. louellae</i> n. sp.	Middle late Campanian	Vancouver Island
<i>T. teleos</i> n. sp.	“Mid” Maastrichtian	Northern California

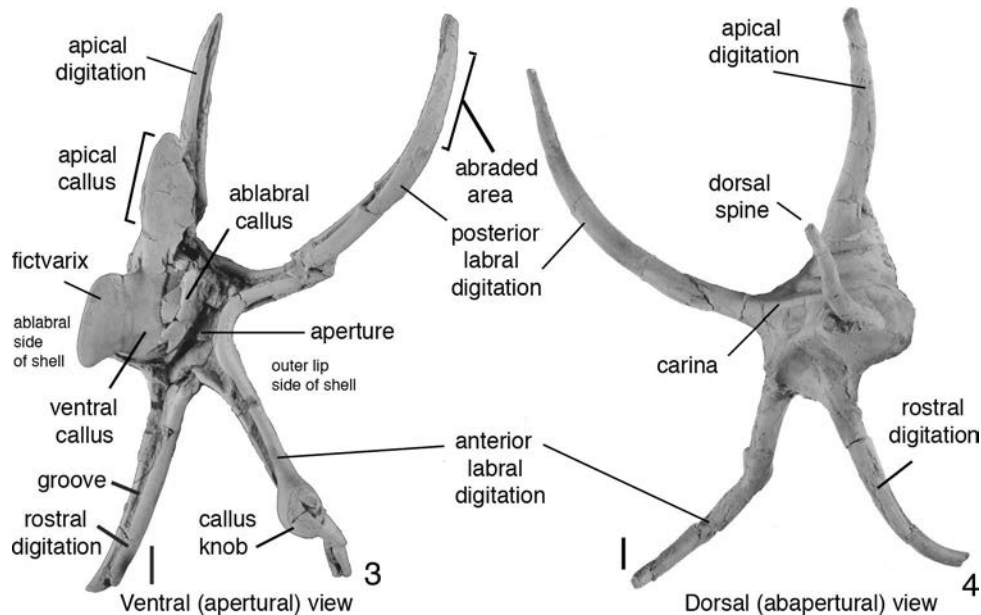
Bay, Cedar District Formation, upper middle Campanian. Collector: R. Graham and T. Bullard, September, 2005. [10] **Locality 10.** South bank of French Creek near Coombs, Nanaimo District, Pender Formation or Cedar District Formation, upper middle Campanian. Collector: R. Graham, August 4, 2006. [11] **Locality 11.** Northwest Bay, east of Parksville, Nanaimo District, Pender Formation or Cedar District Formation, lower Campanian. Collector: J. Haegert, 2000. [12] **Locality 12.** Downstream end of high-siltstone exposure along bank of Chemainus River, south and west of town of Chemainus, Nanaimo, east coast of Vancouver Island, British Columbia, lower Haslam Formation, upper Santonian. Collector: R. Graham and T. Bullard, June 15, 1997.

**CAS:** [39] 1430. Vicinity of San Antonio del Mar (i.e., Johnson’s Ranch), Baja California, Mexico, Rosario Formation, uppermost Campanian to lowermost Maastrichtian. [23] 27854. Orestimba

Creek, Stanislaus County, California, lower Panoche Formation, lower Turonian or Coniacian. [15] 27862. Thin bed of conglomerate, on Roaring River, Ono, Shasta County, California, Budden Canyon Formation, Gas Point Member, Turonian or Coniacian. [15] 62534. Upper North Fork Cottonwood Creek, Ono, Shasta County, California, Budden Canyon Formation, Ogo Member, upper Hauterivian. [32] 42920. North side Santa Margarita Lake, San Luis Obispo County, California, unnamed formation, upper Campanian.

**GSC:** [3] 23280. Mouth of Kewquodie Creek, Quatsino Sound area, northern Vancouver Island, British Columbia, upper Barremian strata.

**LACMIP:** [England] 14843. Sea cliff just east of Folkestone (Kent), southeastern England. Upper Gault, upper Albian. [1] 25110. Hicks Creek, southeastern Talkeenta Mountains,



**Figures 3, 4** Morphological terms applied to *Tessarolax*. 3. *Tessarolax incrustata* ventral view of hypotype LACMIP 13591. 4. *Tessarolax louellae* n. sp., dorsal view of holotype RBCM.EH2011.007.0015. Scale bars = 5 mm.

southern Alaska, lower Matanuska Formation, upper Turonian or lower Coniacian. [2] 31483. [= USGS loc. M1366], upper Chitina Valley, Wrangell Mountains, southern Alaska, unnamed formation, upper Albian to Cenomanian. [14] 26934. Oak Run, Shasta County, California, Redding Formation, Member IV, Coniacian. [15] 22785. North Fork Cottonwood Creek area, Ono, Shasta County, California, Budden Canyon Formation, Ogo Member, upper Hauterivian. [15] 22787. North Fork Cottonwood Creek, Ono, Shasta County, California, Budden Canyon Formation, Ogo Member, upper Hauterivian. [15] 23052. North Fork of Cottonwood Creek, Ono, Shasta County, California, Budden Canyon Formation, Ogo Member, upper Hauterivian. [15] 23464. Gas Point Road, Ono area, Shasta County, California, Budden Canyon Formation, Bald Hills Member, uppermost Albian to lowermost Cenomanian. [15] 23763. North Fork Cottonwood Creek, Ono, Shasta County, California, Budden Canyon Formation, Bald Hills Member, uppermost Albian to lowermost Cenomanian. [15] 23896. Upper Horse Creek area, southwest of Redding, Shasta County, California, Budden Canyon Formation, Chickabally Mudstone Member, upper lower Albian. [15] 29185. Southwest of Redding, Shasta County, California, Budden Canyon Formation, Ogo Member, upper Hauterivian. [18] 24082. Tuscan Springs about 16 km northeast of Red Bluff, Tehama County, California, Chico Formation undifferentiated (possibly Ten Mile Member?), middle lower Campanian. [20] 28764. Rock Corral north of Folsom, east of Sacramento, Sacramento County, California, Chico Formation, upper lower or upper middle Campanian. [26] 8147. 10 km south of Mervel Ave., Laguna Seca Creek, Merced County, California, Moreno Formation, Tierra Loma Member, Maastrichtian. [30] 26337. Cottonwood Creek, Hancock Ranch, Monterey County, California, Panoche Formation, uppermost Campanian to lower Maastrichtian. [31] 30141. North shore of Lake Nacimiento, San Luis Obispo County, California, El Piojo Formation, Maastrichtian. [34] 4818. Santa Ynez Canyon, Santa Monica Mountains, Los Angeles County, California, Tuna Canyon Formation, upper middle Campanian. [34] 11656. Rustic Canyon/Temescal Canyon divide, Santa Monica Mountains, Los Angeles County, California, lower Tuna Canyon Formation, upper Turonian. [35] 1250. Silverado Canyon, Santa Ana Mountains, Orange County, California, Ladd Formation, upper Baker Canyon Member, uppermost Turonian to lowermost Coniacian. [35] 10091. Silverado Canyon, Santa Ana Mountains, Orange County, California, Ladd Formation, Holz Shale, lower Campanian. [35] 10093. Harding Canyon, Santa Ana Mountains, Orange County, California, Ladd Formation, middle Holz Shale Member, lower Campanian. [36] 8184. Plano Trabuco, Santa Ana Mountains, Orange County, California, formation?, uppermost Santonian. [39] 22414. Arroyo San Antonio, northern Baja California, Mexico, Rosario Formation, uppermost Campanian to lowermost Maastrichtian. [39] 27149. Vicinity of San Antonio del Mar, northern Baja California, Mexico, Rosario Formation, uppermost Campanian to lowermost Maastrichtian.

**SDSNH:** [38] 1010. Float below beach cliffs, 0.4 km north of west end Salsipuedes exit, north of Ensenada, northwestern Baja California, Mexico, Rosario Formation, uppermost Campanian to lowermost Maastrichtian. Collector: N. Brown, December 8, 1978. Rosario Formation. Age: Latest Campanian to earliest Maastrichtian.

**UCMP:** [27] A-919. About 6.5 km north of Slate's Hot Springs, upper San Antonio Creek, Monterey County, California, unnamed formation, probably upper Campanian. [31] A-3368. Cantinas Creek, Lake Nacimiento area, San Luis Obispo County, California. El Piojo Formation, upper lower to lower upper Maastrichtian.

**USGS:** [15] USGS 1092. Vicinity of Paskenta, Tehama County, California, Budden Canyon Formation, upper Hauterivian.

## SYSTEMATICS

Class Gastropoda Cuvier, 1797

Superfamily Stromboidea Rafinesque, 1815

**REMARKS.** Several authors have lately revised various families and subfamilies of the superfamily Stromboidea (e.g., Popenoe, 1983; Korotkov, 1992; Roy, 1994; Kiel and Bandel, 1999; Bouchet et al., 2005; Bandel, 2007; Kollmann, 2009). Bandel (2007) discussed 12 stromboidean families, of which the following three are mentioned herein: Alariidae Koken, 1889; Pterocerellidae Bandel, 2007; and Pugnellidae Kiel and Bandel, 1999 (including its subfamily, Tundorinae Bandel, 2007).

Bandel (2007) referred Jurassic stromboideans to "Alariidae" Koken (1889), but, as noted by Bouchet and Rocroi (2005:22) and by Kollmann (2009:49), *Alaria* of Morris and Lycett, 1850, is a junior primary homonym of both *Alaria* Schrank, 1788 (a parasitic flatworm), and of *Alaria* Duncan, 1801 (a flower moth), and is thus unavailable in Gastropoda. Bouchet and Rocroi (2005) have indicated Arrhoginae Popenoe (1983) [= "Alariidae Koken, 1889" and Dicrolomiatidae Korotkov, 1992] and that Arrhoginae has a range of Jurassic to Recent.

Stromboidea is in part characterized by leaping locomotion (Miller, 1974; Perron, 1978a, b), various versions of which have been described for living stromboids. Leaping locomotion is reflected in the shape of many stromboid shells. The dorsal knob on the back of the final whorl has been credited with tipping the shell toward landing on either side rather than on its back (Savazzi, 1991), thus placing the foot nearer the substrate and providing a speedier return to leaping position and escape. The leap is defensive rather than offensive, as living strombids and aporrhoids are herbivorous and detritivorous.

Family Aporrhaidae Gray, 1850

**REMARKS.** Aporrhoids are characterized by determinate-shell growth because after the shell attains mature size, the aperture undergoes a substantial change in shape, especially in regard to the extended outer lip, the margin of which can be lobe-like or highly digitated. Late Jurassic and Cretaceous aporrhoids developed diverse forms of outer lips, which have been used to infer phylogenetic relationships among aporrhoids. These outer lips also suggest differing adjustments to substrate, water depth, currents, and food sources.

Korotkov (1992:fig. 1) split Aporrhaidae into four families and mentioned variations of the outer lip as important in defining his families. But in his families Aporrhaidae, Dicrolomidae, Perissopteridae, and Spinigeridae, he grouped together genera having very different outer lip structures and separated genera with similar structures. We agree with his inclusion of *Tessarolax* in Aporrhaidae but suggest that *Tessarolax* is closer to *Dicroloma* Gabb, 1868, than to *Phyllocheilus* Gabb, 1868.

Kiel and Bandel (1999) proposed Pugnellidae for nine genera previously assigned to Aporrhaidae or Strombidae and indicated that *Tessarolax*; *Ceratosiphon* Gill, 1870; *Tundora* Stephenson, 1941; and *Lispodesthes* White, 1877, might, with further study, also be included in Pugnellidae. They noted, however, that *Tessarolax* has spiral sculpture and lacks the collabral sculpture common among pugnellids; has apertural digitations whose lengths greatly exceed those of pugnellids; has a bicarinate whorl suggestive of *Aporrhais* da Costa, 1778; and, as in *Aporrhais*, has

digitations that splay out and up (away from substrate) rather than curl somewhat inward and down (toward substrate).

Bandel (2007) included *Tessarolax* despite its having four long and unbranched digitations, with the apical digitation adnate on the spire, in the aporrhaid family Pterocerellidae Bandel, 2007, which Kollmann (2009) changed to a subfamily of Aporrhaidae. The type genus of Pterocerellidae is *Pterocerella* Meek, 1864, and it has six flanged digitations, forming a complex, extended “wing-like” outer lip (see Dockery, 1993). The posterior outer lip digitation of *Pterocerella* is unlike *Tessarolax* by not being adnate on the spire.

#### Subfamily Aporrhainae Gray, 1850

**REMARKS.** Aporrhainae are characterized by having an outer lip bearing several digitations that are medially bent with their distal end directed ventrally, the posteriormost digitations adnate on the more or less high spire, whorl shape convex (inflated), and a rostrum that is relatively short. These characteristics ally *Tessarolax* with Aporrhainae rather than with the aporrhaid subfamily Pterocerellinae Bandel, 2007, to which Bandel (2007) and Kollmann (2009) assigned *Tessarolax* based mainly on the presence of a callus coat. In pugneline genera, however, the anterior outer lip digitation either is the smaller of the outer lip digitations or is absent. The morphological characters of *Tessarolax* beneath the callus are more similar to those of Aporrhainae than to Pugnellinae. For example, *Tessarolax* has four long digitations, each of which is bent differently and all of which are channeled and lack flattened lateral expansions. In addition, *Tessarolax* has callus on the anterior outer lip digitation, possession of a fictavarix, lack of flanges, and persistently spiral sculpture.

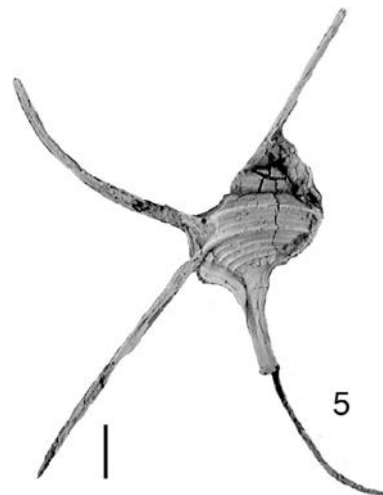
*Dicroloma* Gabb, 1868, which Kollmann (2009) included in Aporrhainae, is a possible Jurassic precursor for *Tessarolax*. On its last whorl, *Dicroloma* has two carinae that extend into outer lip digitations. Its rostrum is elongate and bent as in *Tessarolax*, and both the anterior outer lip digitation and the elongated rostral digitation are twisted to face their channels away from the substrate (Kaim, 2004), a maneuver consonant with that of the digitations of *Tessarolax*. Several species of *Dicroloma* have been described from Middle and Upper Jurassic strata of northern Europe. Kaim (2004:figs. 54, 55) figured early whorls of two species, both of which have two carinae on the last whorl, but, as in *Tessarolax*, there is a single carina showing on the spire whorls. *Dicroloma* lacks the posterior outer lip digitation of *Tessarolax*.

#### Genus *Tessarolax* Gabb, 1864

[= *Ornithopus* Gardner, 1875a, not Hitchcock, 1848, a reptile].  
?[= *Protohemichenopus* Camacho, 1953].

**TYPE SPECIES.** *Tessarolax distorta* Gabb, 1864, by monotypy; middle early to early late Campanian, Vancouver Island area, British Columbia to southern California. The type species of *Ornithopus* Gardner, 1875a:395, is *Rostellaria retusa* Sowerby in Fitton, 1836:344, by subsequent designation (Jukes-Brown, 1877:495), late Albian, England. The type species of *Protohemichenopus* Camacho, 1953, is *Protohemichenopus nequensis* Camacho, 1953, by monotypy, late Hauterivian, west-central Argentina.

**DIAGNOSIS.** Mature shell with four, long, curved, unbranched, widely spaced, unflanged, canaliculate (internally channeled) digitations: three extending from outer lip and one engulfing rostrum. Apical digitation considerably exceeds height of spire and extends from apical corner of aperture on outer lip side of shell, angles across spire, and leaves spire near tip on a



**Figure 5** *Tessarolax retusa* Sowerby in Fitton, 1836, hypotype, LACMIP 13573, LACMIP loc. 14843 (Folkestone, England). Scale bar = 5 mm.

trajectory away from substrate (both this digitation and its adjoining apical-tip area became encrusted in Late Cretaceous). Posterior and anterior outer lip digitations represent continuous extensions of posterior and anterior carinae of last whorl; ventral side of latter digitation with localized callus knob on post-early Coniacian species. Rostral digitation engulfs rostrum and becomes very elongate; spiral ornamentation predominates.

**REMARKS.** Gabb (1864) did not provide an explanation of the derivation of the name *Tessarolax*. “*Tessar*” is a Greek prefix meaning “four,” an obvious reference to its four digitations. Brown (1956:353) indicated that “*laxus*” is Latin for “loose, slack, or unstrung.” Gabb was indicating perhaps that the four digitations bend in various directions. The root “*lax*” is an adjective modifying “*tessar*”; hence, “*lax*” does not inherently have a gender, even though Cossmann (1904:363) incorrectly stated that it is neuter. According to the International Commission on Zoological Nomenclature (1999), Article 30.1.4.2 and 30.2.3, when the word itself does not indicate its gender, the combination that the original author used can be taken into account. *Tessarolax* would then be feminine because Gabb treated it as such.

Gabb (1868:146) claimed knowledge of only two species belonging to *Tessarolax*: *T. distorta* from the PSNA and *T. bicarinata* (Deshayes in Leymerie, 1842) from western Europe. The latter species, originally placed in genus *Rostellaria* Lamarck, 1799, has a complicated nomenclatural history (see last entry in synonymy of *T. gabbi* new name). *Tessarolax bicarinata* is now recognized by most modern workers (e.g., Cox, 1925; Stewart, 1927; Casey, 1961; Kiel, 2006; present study) as a junior synonym of *Tessarolax retusa* (J. de Sowerby in Fitton, 1836). An illustration is provided in Figure 5 of *T. retusa* from the upper Albian part of the Gault at Folkestone, southeastern England. Gardner (1880) also recognized that *retusa* and *distorta* belong to *Tessarolax*.

D’Orbigny’s (1843:307, pl. 208, figs. 3, 5) figures of *bicarinata* show four slender digitations and a fictavarix (i.e., fig. 5). These structures are typical of *Tessarolax retusa*. The fictavarix shown in d’Orbigny, however, is not present on any other illustrated specimens of *T. retusa*. Whether d’Orbigny’s specimen is *retusa* or not, it is a *Tessarolax* with a prominent fictavarix similar to that found on a specimen (Figs. 23–24) of *T. alaskana* n. sp.



Gardner (1875b:52) placed Cretaceous aporrhoids (especially those of England) into several “Groups,” and he labeled *Aporrhais retusa* (J. de Sowerby in Fitton) as the type of “Group 1.” Gardner (1875a:395) included *retusa* in the new genus *Ornithopus* Gardner, 1875a. In addition to Gardner (1880), Cossmann (1904) and Wenz (1940) correctly noted that *Ornithopus* is a junior subjective synonym of *Tessarolax*. Kase and Maeda (1980), Kase (1984), and Kollmann (2005), however, believed *Ornithopus* Gardner, 1875b, to be a synonym of *Ceratosiphon*.

Gardner (1875b:pl. 3, fig. 2) showed the channel (groove) of the anterior outer lip digitation of *Tessarolax retusa* passing directly through the middle of the ventral side of the callus knob. On the PSNA specimens of *Tessarolax* (see Figs. 3, 79), however, this groove passes around the side of the callus knob and is never on the ventral surface of the callus knob. Gardner (1880:50) considered that the complete encrustation of the spire of *Tessarolax* and the various tubercles were only rarely and abnormally present and that these “rare” coatings and “tubercles” constitute abnormal morphological features that should not be included in specific characteristics. This present study has found, however, that the “missing” dorsal callus on Early Cretaceous *Tessarolax* reflects evolution of this genus from relatively unencrusted Neocomian species toward total encrustation of Campanian and Maastrichtian species.

Blagovetshenskiy and Shumilkin (2006:39) placed *Tessarolax retusa* (J. de Sowerby in Fitton) in genus *Trilemma* Blagovetshenskiy and Shumilkin, 2006. *Tessarolax* differs from *Trilemma*, however, by having much narrower digitations without a wing-like “membrane” between the outer lip digitations and having a longer apical digitation that also hugs the spire and extends beyond it. Although Blagovetshenskiy and Shumilkin (2006) characterized *Tessarolax* as having a projection on the side of the shell opposite to the wing-like extension of the outer lip, this projection (referred to herein as the *fictavarix*) is actually not truly opposite the outer lip. The *fictavarix* on *Tessarolax* leans “forward” so that its outer margin and the forward bending of the outer lip rest on the substrate. In summary, *Tessarolax retusa* does not have the tall, wide spire or the wing-like extension of the outer lip bearing two broad digitations, especially the anterior outer lip digitation, that characterize *Trilemma*.

Camacho (1953) illustrated two specimens of *Protohemichenopus neuquensis* Camacho (1953:191–192, figs. A, B) from the Agrio Formation in west-central Argentina. Lazo (2006) reported that this formation is late Hauterivian in age. Camacho’s (1953) figured specimens are small for mature *Tessarolax* but are similar to *Tessarolax* in whorl shape and ornament and in having four digitations: posterior digitation adnate on the spire and extending beyond it, posterior and anterior outer lip digitations emanating from two carinae, and a rostral digitation. The aperture is not illustrated. The specimens have a wider pleural angle, but this difference might be the result of crushing. Based on available figures and descriptions, we questionably make *Protohemichenopus* a junior subjective synonym of *Tessarolax*. The overall shape of *Protohemichenopus neuquensis* is somewhat similar to *Dicroloma zelandica* Marshall (1919:228, pl. 15, fig. 16), but *P. neuquensis* has an apical digitation, and *D. zelandica* does not. Nielsen (2005:1123–1124, figs. 2.6–2.8) and Bandel (2007:114) placed *D. zelandica* in genus *Hemichenopus* Steinmann and Wilckens, 1908.

*Tessarolax ebrayi* (de Loriol, 1882:25–28, pl. 3, figs. 16–20) was reported by Cossmann (1904:58) as a species of *Tessarolax* from the Albian of France, but this species is a *Ceratosiphon*. All of its mature type specimens, except the one shown in de Loriol’s figure 18 (i.e., a different species?), have a thin “spike”

branching from the anterior canal. Kase (1984:144, pl. 22, fig. 6) reported a single specimen of the so-called *Ceratosiphon* sp., cf. *C. ebrayi* (de Loriol), from upper Aptian strata in northeastern Honshu, northern Japan. Although this specimen is not a *Ceratosiphon ebrayi* (de Loriol, 1882:25–28, pl. 3, figs. 16–20), which is named for specimens from the Albian of France, we believe that Kase’s specimen is a *Tessarolax*.

Maeda (1986:pl. 1, figs. 6, 8, 9) reported a so-called *Aporrhais* (*Tessarolax*) *actimarginatus* [sic] (Nagao, 1932) from the Bibai area, Hokkaido, northern Japan. Maeda (1986) misspelled the species name, which should read *acutimarginata*. Maeda’s specimens are associated with the ammonite *Desmoceras* (*Pseudoubligella*) *japonicum* (Yabe), which, according to Matsumoto (1959:59), is temporally correlative to the “main part of the Cenomanian.” Maeda’s figured specimens represent two juveniles (figs. 8, 9) and an incomplete young adult (fig. 6). The two spiral ribs on the young adult are more prominent compared to the type specimen of *T. acutimarginata* Nagao, illustrated by Hayami and Kase (1977:pl. 6, fig. 14b). We believe that Maeda’s specimens represent *Tessarolax* sp. but are not *Tessarolax acutimarginata* (Nagao, 1932:pl. 6, figs. 14a, b), which is of Coniacian or Santonian in age.

*Aporrhais ebersini* Plamadiala (1982:184–185, pl. 18, figs. 5–8) is known from lower Cenomanian strata of the northern Caspian Sea area, northern Kazakhstan. The material appears to be peels of external molds of small (up to 28 mm high) and somewhat incomplete specimens. Of the four illustrated specimens, three have two prominent spiral carinae on the last whorl. Based on their incompleteness and their small size for mature *Tessarolax*, we questionably place Plamadiala’s species in *Tessarolax*.

According to Kiel and Bandel (2002), *Tessarolax* and *Tundora* appear closely related. *Tundora tuberculata* Stephenson (1941:313–314, pl. 59, figs. 1–4), the type species of *Tundora* Stephenson, 1941, known from upper Campanian to lower Maastrichtian strata of the Gulf Coast, does resemble *Tessarolax*. Both genera have four long digitations of similar length, spiral sculpture beneath the callus coatings, and (see Dockery 1993:pl. 40, figs. 1, 2) a ventrally located callus pad or knob on the anterior outer lip digitation. Based on these features, as well as the fact that *Tundora tuberculata* also resembles *Aporrhais pachysoma* Gardner (1875b:pl. 7, fig. 8) of Cenomanian age from England, we include *Tessarolax* and *Tundora* in Aporrhainae. Although the immature spiral sculpture of *Tessarolax* and *Tundora* is similar to that of *Ceratosiphon*, their outer lip developments are not. *Tessarolax* differs from *Tundora* by having a much larger shell, a turriculate rather than a rotund spire, a *fictavarix*, and an absence of spirally arranged rows of prominent tubercles over much of the callused surface of the shell.

Several workers (e.g., Cossmann, 1904; Stewart, 1927; Wenz, 1940; Casey, 1961; Kase and Maeda, 1980; Kiel, 2006; Bandel, 2007) have misunderstood the morphology of *Tessarolax* and considered it to be the senior synonym of *Ceratosiphon*, a genus whose type species was selected by Gill (1870:pl. 139) as *Pterocera moreausiana* d’Orbigny (1843:301, pl. 211, figs. 1, 2). D’Orbigny (1843) originally used the name *Pterocera* Lamarck, 1799, for material of supposedly Albian age from Atherfield, England. According to Vaught (1989), *Pterocera* is no longer a valid name, and its accepted name is now *Lambis* Röding, 1798.

The geologic range of *Ceratosiphon moreausiana* is contradictorily known from the Hauterivian, not Aptian, rocks in France (see Kollmann, 2005:128–129). Kollmann (2005) searched available collections for d’Orbigny’s type material of *Pterocera moreausiana* but was unable to find adequately preserved specimens from localities indicated by d’Orbigny. The type locality of *P. moreausiana*, therefore, remains elusive, as neither

of the two small specimens discussed by Kollmann (2005) is from a locality linked by d'Orbigny to *P. moreausiana*. Kollmann (personal communication, 2010) informed us that “d'Orbigny wrote explicitly that the figure (pl. 211, fig. 1) is that of a complete specimen kept in the collection Moreau, and that it can therefore be supposed that it is more or less correctly reproduced.” If the figure in d'Orbigny is representative of *P. moreausiana*, *Ceratosiphon* is not a synonym of *Tessarolax*.

Gardner (1875b:292–293, pl. 7, fig. 3) illustrated a specimen of what he referred to as *Aporrhais moreausiana* (d'Orbigny). Wolleemann (1900:171, unfig.) noted that the specimen Gardner illustrated is not d'Orbigny's species, but Wolleemann inexplicably retained the name “*Aporrhais moreausiana*.”

*Pterocera becklesii* Mantell (1851:443, lign. 40) from Atherfield, England, has priority over Gardner's *A. moreausiana* (d'Orbigny), and thus *Aporrhais gardneri* Pchelinstev (1927:298, unfig.), also from Atherfield, is a junior synonym. Name-wise, Pchelinstev's 1927 “*A. gardneri*” is a junior synonym of *Aporrhais* (*Tessarolax*) *gardneri* Keeping (1883:pl. 2, figs. 2a, 2b). Keeping (1883) based his species, which is from Aptian beds at Upware, England, on a small fragment of an aporrhaid and also on the specimen of *Tessarolax* n. sp. of Gardner (1880:50, pl. 3, fig. 2). The generic assignment of these two specimens, however, is indeterminate. Both *Ceratosiphon moreausiana* (d'Orbigny) and *Ceratosiphon becklesii* (Mantell) are placed in *Ceratosiphon* because they have long digitations with flanges (i.e., thin calcified “membranes”) and can have added rostral digitations. Flanges consisting of thin calcified “membranes” on digitations, as in Gardner's (1875b) figures of *Ceratosiphon moreausiana* (pl. 7, fig. 3) and *C. fittoni* (pl. 7, fig. 4), are characteristic of *Ceratosiphon*.

Blagovetshenskiy and Shumilkin (2006:39) assigned “*Tessarolax moreausiana* (d'Orbigny)” and “*Tessarolax ebrayi* (de Loriol)” to their new genus *Trilemma*. Neither species appears to resemble *Aporrhais striatocarinata* Sinzow, 1880, the type species of *Trilemma*. Based on discussions in the present article, both species cited by Blagovetshenskiy and Shumilkin (2006) belong to *Ceratosiphon*.

Kollmann (2005, 2009) agreed with Bandel (2007) that *Ceratosiphon* belongs in Pterocerellinae Bandel, 2007, but Kollmann (2009) disagreed with Bandel (2007) and reported that *Tessarolax* and *Ceratosiphon* are separate genera, belonging in different subfamilies, and we agree. *Ceratosiphon* commonly has four or more commonly flanged digitations: two long outer lip digitations divided along their sides and only very rarely a rhombic-shaped pad at the anterior terminus of the anterior outer lip digitation, one short apical digitation that is not adnate on the spire, and one long spike-like rostral digitation that commonly can be branched. *Tessarolax* differs from the pterocerelline *Ceratosiphon* by having only four, shorter, unbranched, and “unflanged” canaliculate digitations (one apical digitation that is adnate on the spire, two outer lip digitations, and one rostral digitation). *Tessarolax* also differs in other respects: nearly all Albian and all younger species of *Tessarolax* have a fictavarix, and post-early Coniacian and younger species of *Tessarolax* have a shorter spire, arched digitations, and either dorsal nodes (Fig. 37), a dorsal saw-toothed flange (Figs. 45, 46), or a dorsal spine (Fig. 63). Additionally, post-early Coniacian *Tessarolax* commonly has callus glaze on the last whorl and spire of mature specimens and a callus knob on the anterior outer lip digitation. These arched digitations and callus buildups of *Tessarolax* appear capable of having raised the body of the shell higher above the substrate than would have the digitations of *Ceratosiphon*. *Tessarolax*, furthermore, occurs in both the Old World and

the New World, whereas *Ceratosiphon* is known only from the Old World and the Orient.

The digitations of *Ceratosiphon* are similar to those of *Pterocerella* Meek, 1864, the type genus of family Pterocerellinae Bandel, 2007. Both genera have flanged digitations and, commonly, multiple rostral spines, but neither possess *Tessarolax*'s digitation that is adnate on the spire. *Ceratosiphon* differs from *Pterocella* in having simpler, smaller, and fewer lateral expansions on its digitations. Early Cretaceous *Ceratosiphon* have simpler versions of the outer lip flanges in comparison to the Late Cretaceous pterocerellids.

“*Ceratosiphon*” *giganteus* Kase (1984:143–144, pl. 22, figs. 2–5) from upper Neocomian strata in Honshu, northern Japan, is based on incomplete specimens missing much of the anterior siphonal-canal area. The specimens are represented by rubber casts of four external molds. Kase mentioned that the holotype of his species has a trace of a spine branching from the upper part of the anterior siphonal canal, but the “spine” is not discernible in any of the figures. An additional rostral “spine” would definitely place this species in *Ceratosiphon*. Based on the illustrated material and its similarity to *Tessarolax* but tempered by the questionable presence of an additional rostral “spine,” we questionably identify Kase's species as *Tessarolax*? *gigantea* (Kase).

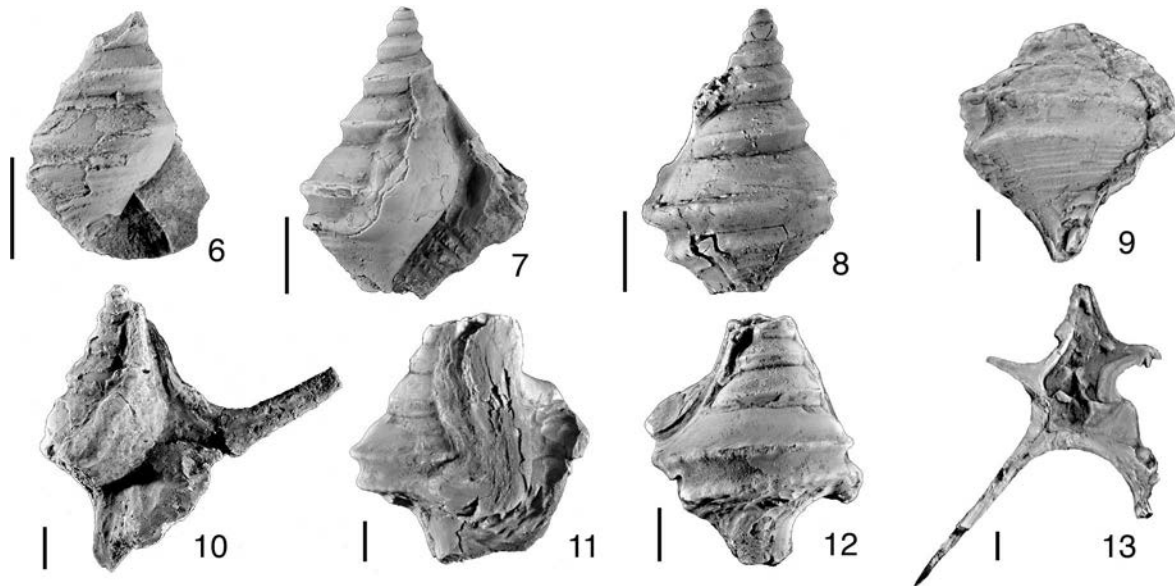
*Aporrhais bicarinatoides* Wolleemann (1903:33, pl. 4, figs. 16, 17; 1906:292, pl. 10, figs. 6, 7) from Albian strata in northern Germany was identified by Wolleemann (1908:192) as *Aporrhais* (*Tessarolax*) *bicarinatoides*. This species is based on juvenile specimens that show no digitations. Complete specimens are needed for generic determination. It resembles Albian *Ceratosiphon* in having callus on the side of the spire, but it might also be *Tessarolax retusa*. Wolleemann (1903) said that his species is similar to *Aporrhais bicarinata* (Deshayes in Leyermie), but he reported that Deshayes species is of Neocomian age rather than of Albian age. Blagovetshenskiy and Shumilkin (2006:39) questionably assigned Wolleemann's species to *Trilemma*.

*Aporrhais* (*Tessarolax*) *antarctica* Cox (1953:6, pl. 2, figs. 9–11) from Aptian deposits on Alexander I Island, Falkland Islands Dependencies, is based on six molds, all more or less incomplete. All spires are very tall for *Tessarolax*, the posterior carina has stronger nodes than have been otherwise seen on *Tessarolax*, and the outer anterior lip digitation is wider than that of *Tessarolax*. These features suggest that Cox's species is a *Pietteia* Cossmann, 1904. Cox's species (1953:pl. 2, fig. 10) might have a small fictavarix-like structure on the left side of its last whorl. Genus *Pietteia* can have a fictavarix, as shown by the Early Cretaceous species *Pietteia cretacea* Kase in Kase and Maseda (1980:311–313, pl. 36, figs. 4–10, text-fig. 9), which has a small but distinct, spine-like fictavarix on its last whorl.

*Tessarolax* cf. *acuticalinatus* Nagao, 1932, was reported by Nagao (1939:225–226, pl. 22, fig. 6) from northern Hokkaido, Japan, as a single, small imperfect specimen that shows no digitations. It is clear from his synonymy that Nagao (1939) is tentatively identifying this as his 1932 species *T. acutimarginata* (misspelled as *acuticalinatus* in his 1939 synonymy). The spire of this 1939 specimen is too high and too narrow to be a *Tessarolax*. The specimen is also from older strata (Cenomanian), but the specimen's exact stratigraphic position is not known.

*Aporrhais arrialoorensis* Stolizcka (1867:28, pl. 2, figs. 2, 2a) from the Senonian Arrialor Group of southern India was placed by Cossmann (1904) and Wenz (1940) in *Tessarolax*. Stolizcka (1867) recorded a single incomplete specimen, and its illustration does not show digitations. Its weak collabral ribbing, a feature not seen on any other *Tessarolax* species, discourages placement of this species in *Tessarolax*.





Figures 6–13 *Tessarolax gabbi* new name (Ono area). 6. Hypotype, LACMIP 13568, LACMIP loc. 23052, apertural view. 7, 8. Hypotype, LACMIP 13569, LACMIP loc. 22785. 7. Ventral view. 8. Dorsal view. 9. Hypotype LACMIP 13570, LACMIP loc. 29185, dorsal view. 10. Hypotype LACMIP 13571, LACMIP loc. 22787, ventral view. 11, 12. Hypotype LACMIP 13572, LACMIP loc. 29185. 11. Ventral view. 12. Dorsal view. 13. Hypotype CAS 62534.01, CAS loc. 62534, cross-section dorsal view. Scale bars = 5 mm.

*Tessarolax?* sp. was reported from Cenomanian strata at the Kassenbery quarry in Germany by Kiel and Bandel (2004:121, fig. 7L) in their caption but reported as *Aporrhais?* sp. in their text. Its outer lip forms a wide, flat, and protruding platform (wing?), not seen in *Tessarolax*.

*Surcula* (*Surculites*) *inconspicua* (Gabb, 1869:151, pl. 26, fig. 29), questionably assigned to *Tessarolax* by Stewart (1927:365–366, pl. 23, fig. 2), was reported from the “Martinez Group” near Martinez, Contra Costa County, California, by Gabb (1869), Stanton (1896:1029), and Dickerson (1914:88, 110) as of Paleocene age. Much of the “Martinez” strata in this area is of Paleocene age (Weaver, 1953). Stewart indicated that if this species is really a *Tessarolax*, it should be from Cretaceous beds. Faulted blocks of Great Valley Group strata crop out in the Franklin Canyon area near Martinez (see Squires and Saul, 2006:88). Weaver (1953) supplied long fauna lists but did not record finding this species in Paleocene rocks of this area. This species is known only from its holotype, which is small (approximately 11 mm in height). When compared to immature *Tessarolax* specimens, *S. (S.) inconspicua* has a narrower pleural angle and a more turriculoid shape. Immature *Tessarolax* shells have more widely expanding whorls. These differences indicate that *S. (S.) inconspicua* is probably not a *Tessarolax*.

#### *Tessarolax gabbi* new name

Figures 6–13

*Helicaulax* n. sp. Gabb, 1868:145.

*Helicaulax bicarinata* Gabb, 1869:166–167, 226, pl. 27, fig. 47.

?*Helicaulax bicarinata* Gabb. Diller and Stanton, 1894:446–447.

?*Helicaulax* [?] *bicarinata* Gabb. Stanton, 1895:22.

?*Aporrhais* sp. Stanton, 1895:72.

*Tessarolax bicarinata* (Gabb). Stewart, 1927:364–365, pl. 23, fig. 6; Anderson, 1938:64, 134; Imlay, 1960:180.

Not *Rostellaria retusa* J. de Sowerby in Fitton, 1836:344, pl. 18, fig. 22 [= *Rostellaria bicarinata* Deshayes in Leymerie,

1842:14, 31, pl. 17, figs. 14a, b = *Pterocera bicarinata* (Deshayes in Leymerie) of d’Orbigny (1843:307, pl. 208, figs. 3, 5); = *Aporrhais retusa* (J. de Sowerby in Fitton) of Gardner (1875b) = *Ceratosiphon retusus* (J. de Sowerby in Fitton) of Kollmann (2005:132; 2009:53)].

**DIAGNOSIS.** Mature last whorl bicarinate, carinae with many small nodes; callus over ventral face becoming massively thick at ablabral edge, crossing carinae, and extending up spire and along edge of apical digitation.

**DESCRIPTION.** Shell up to 44 mm high (apical and rostral digitations incomplete) and 58 mm wide (only posterior outer lip digitation complete). Pleural angle approximately 40 degrees. Protoconch unknown. Teleoconch of at least six whorls (tip missing). Suture moderately impressed. **Immature shell:** Turriculate, consisting of five whorls, unicarinate; numerous spiral threads on whorls, threads more widely spaced on ramp. Penultimate whorl carina with weak nodes. **Mature shell:** Consisting of very wide last whorl, strongly bicarinate, carinae with many small nodes, posterior carina stronger, interspace covered with spiral ribs. Aperture wide. Outer lip thickened with callus, expanded into four slender canaliculate digitations. Apical digitation extending along spire at angle to shell axis and crossing below tip of shell. Posterior and anterior outer lip digitations extending from their respective carinae. Rostral digitation apparently straight. Callus deposit over ventral face of shell becoming massively thick on ablabral edge, forming thick ridge that crosses carinae and continuing up spire along edge of apical digitation; tip of spire free of callus, but tip missing from specimens with most callus. Base of last whorl free of callus, flattish, with spiral threads immediately anterior to anterior carina. Apertural side of neck with some light callus glaze.

**HOLOTYPE.** ANSP 4282, crushed specimen, “Shasta Group, Cottonwood Creek, Shasta County” (Gabb 1869:167), Ono, northern California. Stanton (1895) referred these strata to the “Horsetown beds.” Murphy (1956) and Murphy et al. (1969)

recovered this species only from Ono [Area 15] in the Budden Canyon Formation, Ogo Member, upper Hauterivian *Hertleinites aguila* zone.

**HYPOTYPES.** All from near Ono [Area 15]. LACMIP 13568–13572: [13568, LACMIP loc. 23052; 13569, LACMIP loc. 22785; 13570, LACMIP loc. 29185; 13571, LACMIP loc. 22787; 13572, LACMIP loc. 29185] and CAS 62534.01, CAS loc. 62534.

**GEOLOGIC RANGE.** Late Hauterivian to late Barremian?

**GEOGRAPHIC RANGE.** Near northern tip of Vancouver Island, British Columbia to northern California.

**STRATIGRAPHIC DISTRIBUTION.** UPPER HAUTERIVIAN: [Area 15] Budden Canyon Formation, near base of Ogo Member, *Hertleinites aguila* zone (see Imlay, 1960), near Ono, southwest of Redding, Shasta County, California, and questionably [Area 13] Myrtle Group, Days Creek Formation, *Hollisites dichotoma* zone (see Imlay, 1960), near Riddle, Douglas County, Oregon. UPPER BARREMIAN?: [Area 3] unnamed strata, Quatsino Sound, near the northern tip of Vancouver Island, British Columbia, Canada.

**REMARKS.** Twelve specimens were examined, and five are immature. All specimens were found in hard, black mudstone. Shell preservation is generally good, but all specimens are broken. Only one specimen (hypotype CAS 62534.01) is nearly complete. It is adjacent to a very hard siltstone nodule, and the specimen cannot be extracted without risking damage. Its shell outline, however, is visible (Fig. 13). Some of the best specimens are from LACMIP locs. 22785, 22787, and 29185, all from the Budden Canyon Formation, Ono [Area 15]. Murphy (1956) plotted all of these localities on his geological map and columnar sections.

Originally, Gabb (1868:145) included four species in his genus *Helicaulax*. Three of them were named and represented western European species. From these three named species, Cossmann (1904) chose *Rostellaria ornata* d'Orbigny (1843:pl. 209, figs. 1, 2) as the type species of *Helicaulax*. D'Orbigny's (1843) species has a tall narrow spire and a relatively narrow outer lip extending into an outrigger style wing, similar to that of *Anchura* Conrad, 1860, but very different from that of *Tessarolax*. In 1869, Gabb named the fourth species *Helicaulax bicarinata*, based on specimens from Cottonwood Creek near Ono [Area 15], but Gabb's species is quite unlike *Helicaulax ornata* (d'Orbigny, 1843). Gabb's specimens of *Helicaulax bicarinata* are incomplete, and he did not recognize that they had four long, slender, curved outer lip digitations, like those found on genus *Tessarolax*. Gabb's (1869:pl. 27, fig. 47) only illustration of the holotype of *Helicaulax bicarinata* from Cottonwood Creek shows just the apertural view of an immature specimen. Stanton (1895:72) noted that Gabb's description and figure of *H. bicarinata* are inaccurate because the whorls of the spire are distinctly angular instead of flat-sided. He also noted that better-preserved specimens of this species from the Cottonwood Creek area show long and slender digitations. Stewart (1927:364–365) agreed with Stanton (1895) that the holotype of *Helicaulax bicarinata* Gabb is not well preserved, and Stewart (1927:pl. 23, fig. 6) provided a photograph of the abapertural view of a mature specimen.

Diller and Stanton (1894:447) and Stanton (1895:18, 22, 72) listed *H. bicarinata* Gabb from localities in the Knoxville and Horsetown beds, but subsequent work by Bailey et al. (1964) referred these strata to the Great Valley Series, Budden Canyon Formation [Area 17]. Stanton (1895:72) suggested that one of these specimens from “the uppermost layers of the Knoxville beds” (i.e., specimen USNM 23082) is a species distinct from *H. bicarinata* “though probably closely related.” He identified it as *Aporrhais* sp. (unfigured) from USGS loc. 1092, which he considered to be of Valanginian age and from the Knoxville Formation [Area 15] but

which Imlay (1960:190) assigned to the upper Hauterivian Budden Canyon Formation (*Hertleinites aguila* zone).

Stanton (1895:22) indicated the occurrence of *Helicaulax bicarinata* Gabb (i.e., probably *Tessarolax gabbi*) at several southern Oregon localities near Riddle, Douglas County, Oregon (Area 13). Imlay (1960:177) referred these localities to the Myrtle Group, Days Creek Formation, of early late Hauterivian age (*Hollisites dichotoma* zone).

Available specimens of *Tessarolax gabbi* (new name for *Helicaulax bicarinata*) indicate that it did not deposit callus dorsally and lacked a dorsal spine. It has four digitations and a very thick abapertural callus. Deformation of the available specimens has disrupted the four digitations, which were apparently elongate and bent but whose spatial paths are as yet undetermined. The deformation also obscured the callus shape, and a clearly differentiated fictavarium has not been recognized.

A specimen of ?*T. gabbi* is known from GSC loc. 23280 in upper Barremian unnamed strata of Quatsino Sound, near the northern tip of Vancouver Island, British Columbia [Area 3]. This specimen is the same one identified as “*Pterocera*” sp. indet. by Jeletzky (1976:88). Kollmann (2009:58) referred to it as *Ceratosiphon*. Based on a photograph of Jeletzky's specimen (H. Kollmann, personal communication, 2010), the specimen is incomplete and appears to be a mold of the outer lip area of *Tessarolax gabbi*. The specimen, which shows three digitations and part of the right side of the whorl adjacent to the outer lip, preserves incomplete but longer impressions of the outer lip digitations and rostral digitation, all of which have not been adequately preserved in California specimens of *T. gabbi*.

**ETYMOLOGY.** A new name honoring W. M. Gabb, the first paleontologist of the Geological Survey of California, is provided for *Helicaulax bicarinata* Gabb, 1869, because Gabb's original name for this species became a junior secondary homonym when Stewart (1927) recognized that *Rostellaria bicarinata* Deshayes in Leymerie, 1842, is conspecific with *Tessarolax retusa* (Sowerby in Fitton, 1836). Although Stewart (1927) recognized the need for a new name, he did not provide one because the holotype of *H. bicarinata* (Gabb) is poorly preserved and the exact location of the type locality is not known.

*Tessarolax* sp., aff. *T. trinalis* Murphy and Rodda, 1960  
Figures 14, 15

*Tessarolax* sp., aff. *T. trinalis* Murphy and Rodda, 1960:842.

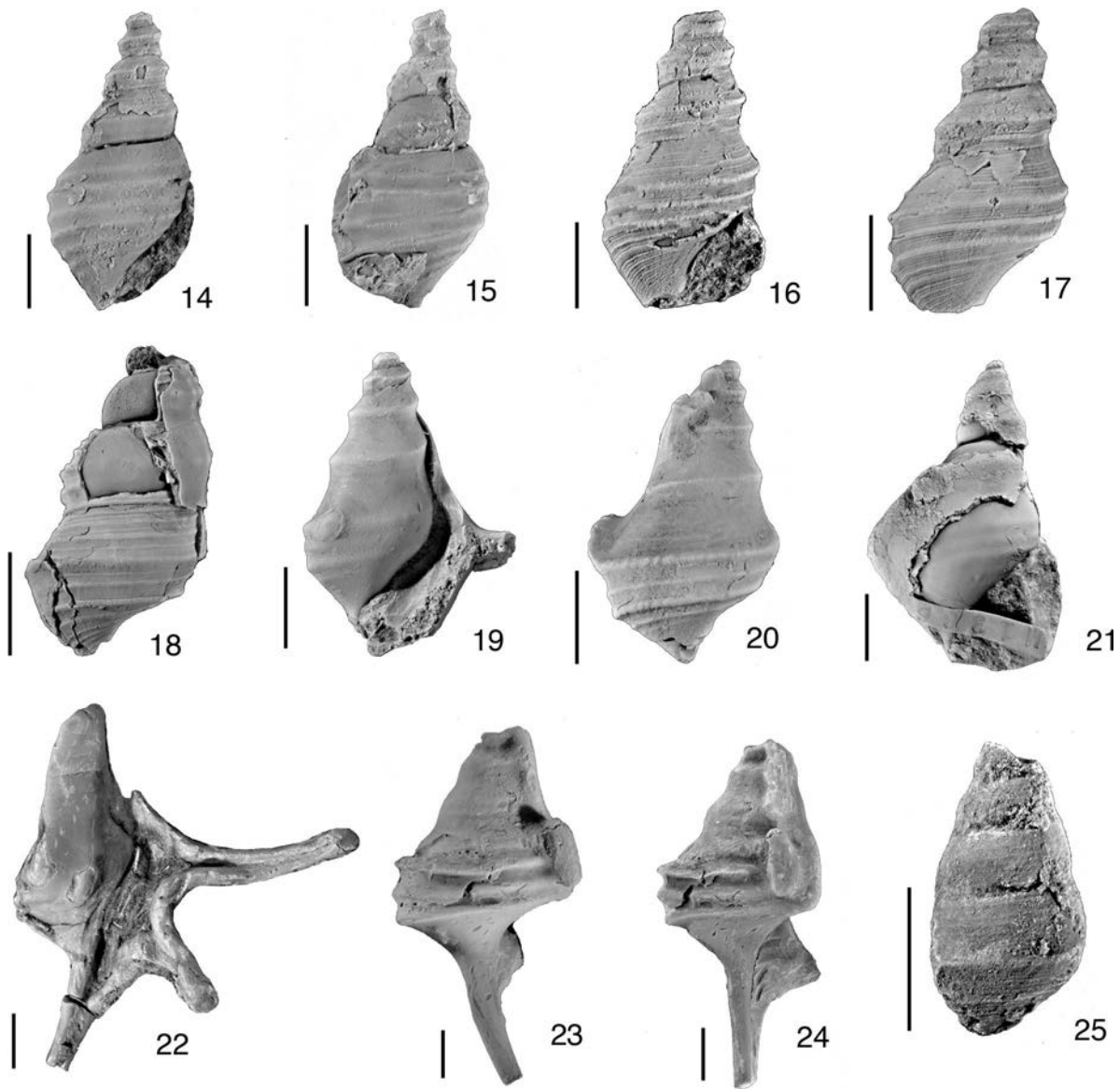
**DESCRIPTION.** Shell up to 19 mm high and 8 mm wide. Pleural angle 35 degrees. Protoconch unknown. Teleoconch of at least five whorls (tip missing). **Immature shell:** Earliest teleoconch whorls rounded and smooth, whereas other spire whorls are generally uncarinate with several intercalated weak spiral ribs. Immature-stage last whorl with seven widely spaced spiral ribs; posteriormost rib weakest, next three are of nearly equal strength (posteriormost of these slightly stronger), and three weak ribs on anterior whorl slope.

**HYPOTYPE.** LACMIP 13574, LACMIP 23896, near Ono (Area 15).

**GEOLOGIC RANGE.** Late early Albian.

**STRATIGRAPHIC DISTRIBUTION.** [Area 15] Budden Canyon Formation, Chickabally Mudstone Member, *Breweriaceras hulenense* zone, Ono area, Shasta County, California.

**REMARKS.** Six specimens were examined. All are immature individuals and found in hard black mudstone at LACMIP loc. 23896 [Area 15]. Five are early immature individuals, and the sixth one (Figs. 14, 15) is a late immature individual consisting of five whorls. The specimens are too immature to have digitations or callus, and they differ from juveniles of *T. gabbi* in being



Figures 14–25 Various species of PSNA *Tessarolax*. 14, 15. *Tessarolax* sp., aff. *T. trinalis* Murphy and Rodda, 1960, hypotype LACMIP 13574, LACMIP loc. 23896. 14. Apertural view. 15. Dorsal view. 16–21. *Tessarolax trinalis* Murphy and Rodda, 1960. 16, 17. Paratype LACMIP 9827, LACMIP loc. 23763. 16. Apertural view. 17. Dorsal view. 18. Hypotype LACMIP 13575, LACMIP loc. 23464, left-lateral view. 19, 20. Holotype LACMIP 9826, LACMIP loc. 23763. 19. Apertural view. 20. Dorsal view. 21. Hypotype LACMIP 14426, LACMIP loc. 31483, apertural view. 22–25. *Tessarolax alaskana* n. sp. 22. Paratype CAS 27862.01?, CAS loc. 27862. 23, 24. Holotype LACMIP 13576, LACMIP loc. 25110. 23. Dorsal view. 24. Left-lateral view. 25. Paratype LACMIP 13577, LACMIP loc. 11656, right-lateral view. Scale bars = 5 mm.

less bicarinate and somewhat taller relative to width. Differences suggest that these late early Albian specimens represent a distinct species, but additional and more mature specimens are needed for description and naming of a new species. They are most similar to immature *Tessarolax trinalis*, especially in having three prominent spiral ribs on the medial part of the last whorl, but *T. sp.*, aff. *T. trinalis*, differs by having only a few strong spiral ribs on the base rather than having numerous spiral threads.

*Tessarolax trinalis* Murphy and Rodda, 1960  
Figures 16–21

*Tessarolax trinalis* Murphy and Rodda, 1960:842, pl.103, figs. 1–3.

**DIAGNOSIS.** Early mature last whorl tricarinate, carinae can be beaded; callus glaze only on venter of shell, spire tip not covered over; fictavarix incipient.

**DESCRIPTION.** Shell up to 26 mm high and 16 mm wide (digitations missing). Pleural angle approximately 43 degrees. Protoconch unknown. Teleoconch with at least six whorls (tip missing). Suture moderately impressed. **Immature shell:** Turriculate, consisting of approximately five whorls. Spire whorls appearing unicarinate, carina noded. Ramp with spiral threads or three weak and noded spiral ribs crossed by raised growth lines, imparting a very weak cancellate pattern; anterior to carina, one to two moderately strong spiral ribs with interspaces that bear spiral threads; single weak spiral rib in interspaces flanking carina. Last whorl with broad ramp



covered by spiral threads, medial area with three equally spaced prominent spiral ribs, interspaces of which bear spiral threads; with growth, posteriormost rib becoming slightly stronger and noded. Base/rostral neck covered with moderately strong spiral threads; posteriormost ones intercalated with two weak spiral ribs. Aperture narrow. **Early mature shell:** Consisting of last whorl, moderately narrow, tricarinate with broad ramp covered with spiral threads, carinae equally spaced, can be beaded, posteriormost one slightly stronger. Base/rostral neck with several widely spaced, weak spiral ribs, posteriormost one strongest. Apical digitation adnate on most of spire but not attached in tip area. Posterior outer lip digitation narrow. Callus glaze on ventral side only, extending apically from neck toward tip of spire. Fictavarix incipient and coincident with bulge of callus near abapertural edge of ventral-callus glaze.

**HOLOTYPE.** LACMIP 9826, LACMIP loc. 23763, Budden Canyon Formation, Bald Hills Member, Ono area, California [Area 15].

**PARATYPE.** LACMIP 9827, LACMIP loc. 23763, near Ono [Area 15].

**HYPOTYPES.** LACMIP 13575, LACMIP loc. 23464, near Ono [Area 15], and LACMIP 14426, LACMIP loc. 31483, upper Chitina Valley [Area 2].

**GEOLOGIC RANGE.** Latest Albian to earliest Cenomanian.

**GEOGRAPHIC RANGE.** Southern Alaska to northern California.

**STRATIGRAPHIC DISTRIBUTION.** [Area 2] UPPERMOST ALBIAN: Unnamed formation, *Desmoceras* (*Pseudoughligella*) *dawsoni* zone, upper Chitina Valley, southeast of Nizina Glacier, Wrangell Mountains, southern Alaska. LOWERMOST CENOMANIAN: [Area 15] Budden Canyon Formation, Bald Hills Member, *Turrilites dilleri* zone, Ono area, Shasta County, California.

**REMARKS.** Five specimens were examined. Preservation is good, but specimens are incomplete. All specimens were found in mudstone or in silty very fine-grained sandstone. Available specimens of *T. trinalis* are mostly immature, and only the most mature of these specimens exhibit what appears to be an incipient (developing) fictavarix (Figs. 19, 21).

#### *Tessarolax alaskana* new species

Figures 22–25

**DIAGNOSIS.** Mature last whorl strongly tricarinate; callus glaze thin on dorsum, thicker on venter; fictavarix short and laterally flangiform.

**DESCRIPTION.** Shell up to 39 mm high and 20 mm wide (missing digitations). Pleural angle 47 degrees. Protoconch unknown. Teleoconch consisting of at least five whorls (tip missing). Suture slightly impressed. **Immature shell:** Turriculate, consisting of approximately four whorls, early spire whorls unicarinate and finely ribbed; later spire whorls with three (possibly four?) spiral ribs, all equally moderately strong, closely spaced, and weakly noded. **Mature shell:** Consisting of last whorl, having three strong closely spaced spiral ribs, plus one weaker spiral rib located posteriorly; neck and base of last whorl smooth. Aperture moderately narrow. Outer lip expanded into four canalicate digitations. Apical digitation adhering to spire, except in tip area. Callus light on dorsum, thicker on venter, and extending onto spire. Fictavarix short and flange-like.

**HOLOTYPE.** LACMIP 13576, LACMIP loc. 25110, lower Matanuska Formation, Hicks Creek, southeastern Talkeenta Mountains, southern Alaska [Area 1].

**PARATYPES.** LACMIP 13577–13582: 13577–13580, LACMIP loc. 11656, Santa Monica Mountains [Area 34]; 13581–13582, LACMIP loc. 1250, Silverado Canyon [Area 35], and CAS 27862.01; and CAS loc. 27862, near Ono [Area 15].

**GEOLOGIC RANGE.** Late Turonian to early Coniacian.

**GEOGRAPHIC RANGE.** Southern Alaska to southern California.

**STRATIGRAPHIC DISTRIBUTION.** UPPER TURONIAN: [Area 29] One specimen from a boulder yielding redeposited Turonian fossils in Panoche Formation conglomerate of Eocene age, Big Tar Canyon, Kings County, California; [Area 34] Tuna Canyon Formation, Rustic Canyon-Temescal Canyon divide, Santa Monica Mountains, Los Angeles County, California; [Area 15] Budden Canyon Formation, probably Gas Point Member, Roaring River, Shasta County, Ono area, California. UPPER TURONIAN OR LOWER CONIACIAN: [Area 1] Matanuska Formation, lower part, Hicks Creek, southeastern Talkeenta Mountains, southern Alaska; [Area 35] Ladd Formation, probably upper Baker/Holz transition or lower Holz Shale Member, Silverado Canyon, Santa Ana Mountains, Orange County, California.

**REMARKS.** Thirteen specimens were examined. Many of the specimens are too immature to have digitations or callus, and all were found in calcareous mudstone containing fragments of the ammonite *Subprionocyclus* sp. and carbonized wood. The holotype is well preserved, but a layer of strongly adherent matrix obscures details of shell sculpture and makes ribbing appear stronger than it is. Attempts to remove this layer resulted in removal of bits of shell surface.

Mature *Tessarolax alaskana* somewhat resembles mature *T. trinalis*, but *T. alaskana* differs by having three much stronger carinae, a smooth neck and base, and a better-developed fictavarix. Within the study area, this species has the greatest north-to-south distribution of any *Tessarolax* (Fig. 1).

**ETYMOLOGY.** Named for the state of Alaska, from which the holotype was collected.

#### *Tessarolax bullardi* new species

Figures 26–31, 33–41

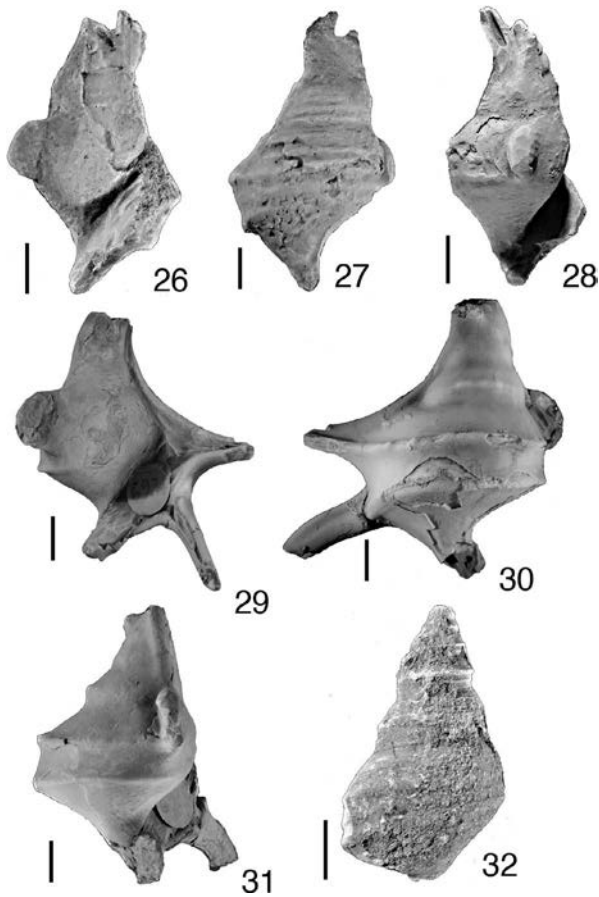
*Tessarolax distorta* Gabb. Whiteaves, 1879:123.

**DIAGNOSIS.** Mature last whorl bicarinate, anterior carina forming low crest of slightly elevated nodes in dorsal area; callus generally thin; fictavarix short, flange-shaped, and extending ventrally to form short stabilizer.

**DESCRIPTION.** Shell up to 113 mm high and 60 mm wide (almost complete). Protoconch unknown. Teleoconch at least five whorls (tip missing). Suture and immature shell callused over. **Immature shell:** Turriculate, consisting of four whorls, early spire whorls unicarinate and finely ribbed. **Mature shell:** Consisting of last whorl, bicarinate, with carinae noded and parallel. Single mid-rib present between carinae dying out about at mid-dorsum. Posterior carina with lower, more discrete nodes. Anterior carina with coalescent stronger nodes, which near center of dorsum are slightly to moderately elevated and form low crest with four or five prominent nodes. Aperture moderately narrow. Outer lip thick, expanded into four canalicate digitations. Apical digitation slightly curved, extending along spire but diverging away from tip of shell. Posterior and anterior outer lip digitations long, strongly curved, and extending from their respective carinae. Anterior outer lip ventrally bearing callus knob. Rostral digitation long and slightly curved. Callus covering shell, obscuring ornamentation except for carinae on last whorl. Callus on venter forms flat, thin surface with sharp edges. Ablabral-callus process flange-shaped; more set off from ventral surface on younger specimens than on more adult ones, on which ablabral callus merges somewhat with ventral callus. Fictavarix extending ventrally to form short stabilizer.

**HOLOTYPE.** RBCM.EH2011.007.0002, loc. 12, near Chemainus, Nanaimo, Vancouver Island, British Columbia [Area 12].

**PARATYPES.** GSC 5791 [specimen labeled by Whiteaves (1879:123) as “unfig’d. hypotype” from Trent River, “below the



Figures 26–32 Various species of PSNA *Tessarolax*. 26–31. *Tessarolax bullardi* n. sp. 26–28. Paratype CAS 27854.01, CAS loc. 27854. 26. Apertural view. 27. Dorsal view. 28. Left-lateral view. 29–32. Paratype LACMIP 13583, LACMIP loc. 26934. 29. Apertural view. 30. Dorsal view. 31. Left-lateral view. 32. *Tessarolax grabami?* n. sp. (juvenile), hypotype RBCM.EH.2011.007.0001, loc. 11, dorsal view. Scale bars = 5 mm.

falls” [Area 5], not listed as type by Bolten (1965)]; CAS 27854.01, CAS loc. 27854, Orestimba area [Area 23]; LACMIP 13583, LACMIP loc. 26934, Oak Run [Area 14]; LACMIP 13584 (three unfigured specimens), all from LACMIP loc. 8184, Plano Trabuco [Area 36]; RBCM.EH2011.007.0003 from loc. 12, Chemainus River [Area 12]; RBCM.EH2011.007.0004–RBCM.EH2011.007.0005 from loc. 4, Puntledge River [Area 4]; RBCM.EH2011.007.0006 from loc. 12, Chemainus River [Area 12]; and RBCM.EH2011.007.0007 from loc. 5, Trent River [Area 5].

**GEOLOGIC RANGE.** Middle Coniacian to early Campanian.

**GEOGRAPHIC RANGE.** Vancouver Island to southern California.

**STRATIGRAPHIC DISTRIBUTION.** MIDDLE CONIACIAN: [Area 23] Panoche Formation (lower part), Orestimba Creek, Stanislaus County, California; [Area 14] Redding Formation, Oak Run, Shasta County, California. SANTONIAN: [Area 4] Haslam Formation, Puntledge River, Vancouver Island; [Area 12] Chemainus River, Vancouver Island; [Area 16] Redding Formation, Basin Hollow Mudstone (Haggart and Ward, 1984), Basin Hollow, east of Redding, Shasta County, California; [Area 17] Redding Formation, Wilk Gulch, east of Redding, Shasta County, California;

[Area 35] Ladd Formation, middle Holz Shale, Silverado Canyon, Santa Ana Mountains, Orange County, California; and [Area 36] ?Ladd Formation, south side of Plano Trabuco, Santa Ana Mountains, Orange County, California. LOWER CAMPANIAN: [Area 5] Pender Formation or possibly Cedar District Formation, Trent River “below the falls,” Vancouver Island, British Columbia (Squires and Graham, 2014).

**REMARKS.** Twenty-eight specimens were examined, including a so-called specimen of *Tessarolax distorta* reported by Whiteaves (1879:123). *Tessarolax bullardi* is most similar to the geologically slightly younger *T. grabami* new species. *Tessarolax bullardi* differs from *T. grabami* by having a much less elevated noded crest on the dorsum, a less projecting fictavarix, and a better-developed posterior carina.

Matsumoto (1960) recognized *Baculites schencki* Matsumoto, 1959, and other ammonites as indicative of possible Coniacian age for the Redding Formation, Member IV, in Oak Run, northern California [Area 14]. In the Chemainus River region of British Columbia [Area 12], *T. bullardi* is found with abundant megafossils, including many fragments of ammonites indicative of late Santonian age (Haggart, 1989). At the Puntledge River locale of British Columbia [Area 4], *T. bullardi* is also found with abundant megafossils, including the gastropod *Pseudocymia? wardi* Saul, 1988, of Santonian age, as well as the heteromorph ammonite *Eubostriochoceras elongatum* (Whiteaves, 1903). Jeletzky (1970), who used the name *Bostrychoceras elongatum* (Whiteaves, 1903) for this ammonite (see Haggart, 1989:199), indicated that it occurs in the Haslam and “lower Trent River” stratigraphic units, and he considered *E. elongatum* indicative of late Santonian age.

Whiteaves (1879:123) reported one specimen of so-called *Tessarolax distorta* Gabb from below the falls on the banks of the Trent River, Vancouver Island, British Columbia. We examined the specimen and found it to be a *T. bullardi*. Squires and Graham (2014:fig. 2) correlated this locale to lower Campanian strata in the Pender Formation or possibly in the Cedar District Formation.

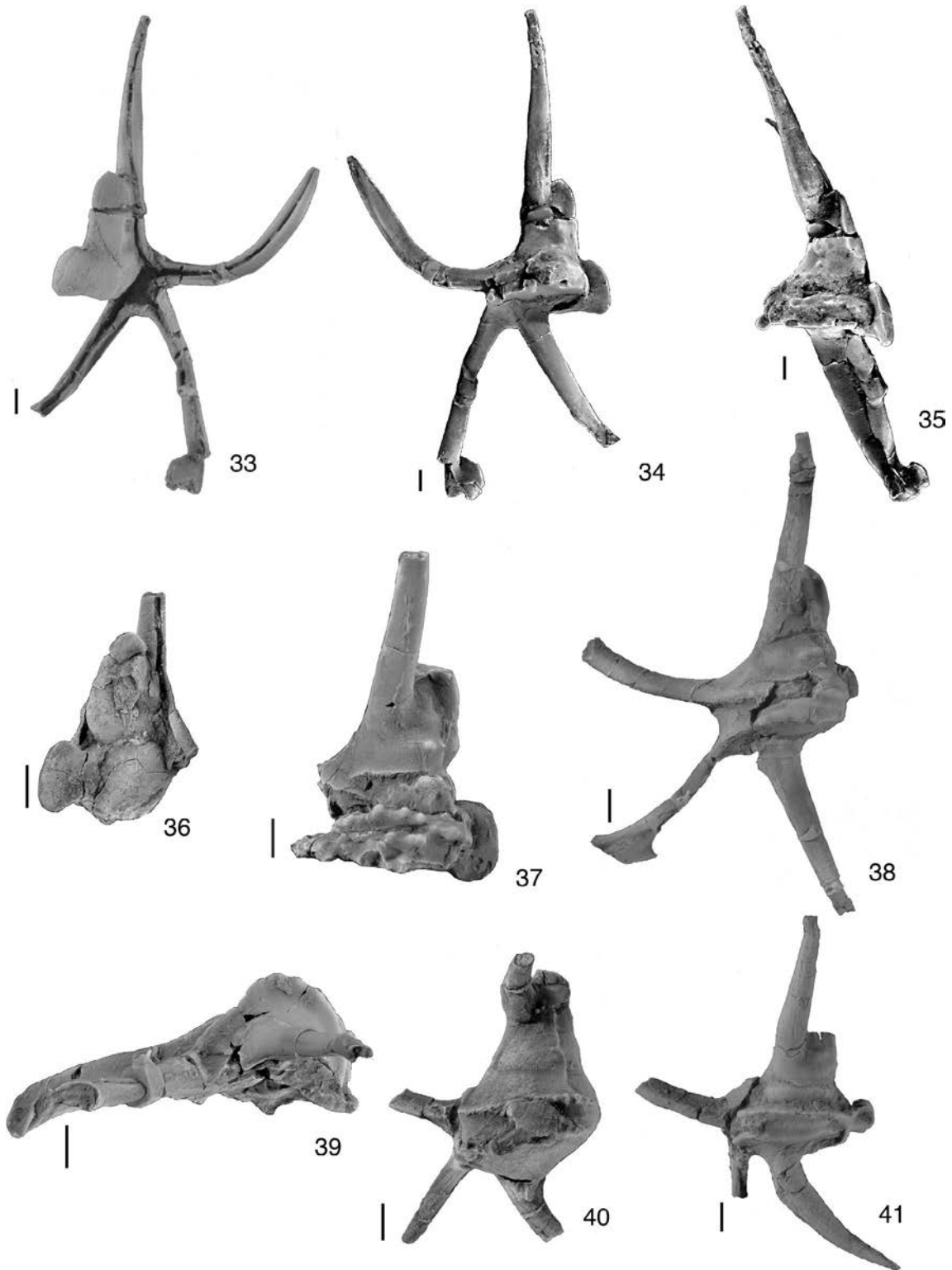
**ETYMOLOGY.** The species is named for Timon Bullard, who collected and prepared many of the specimens.

#### *Tessarolax grabami* new species

Figures 32, 42–49

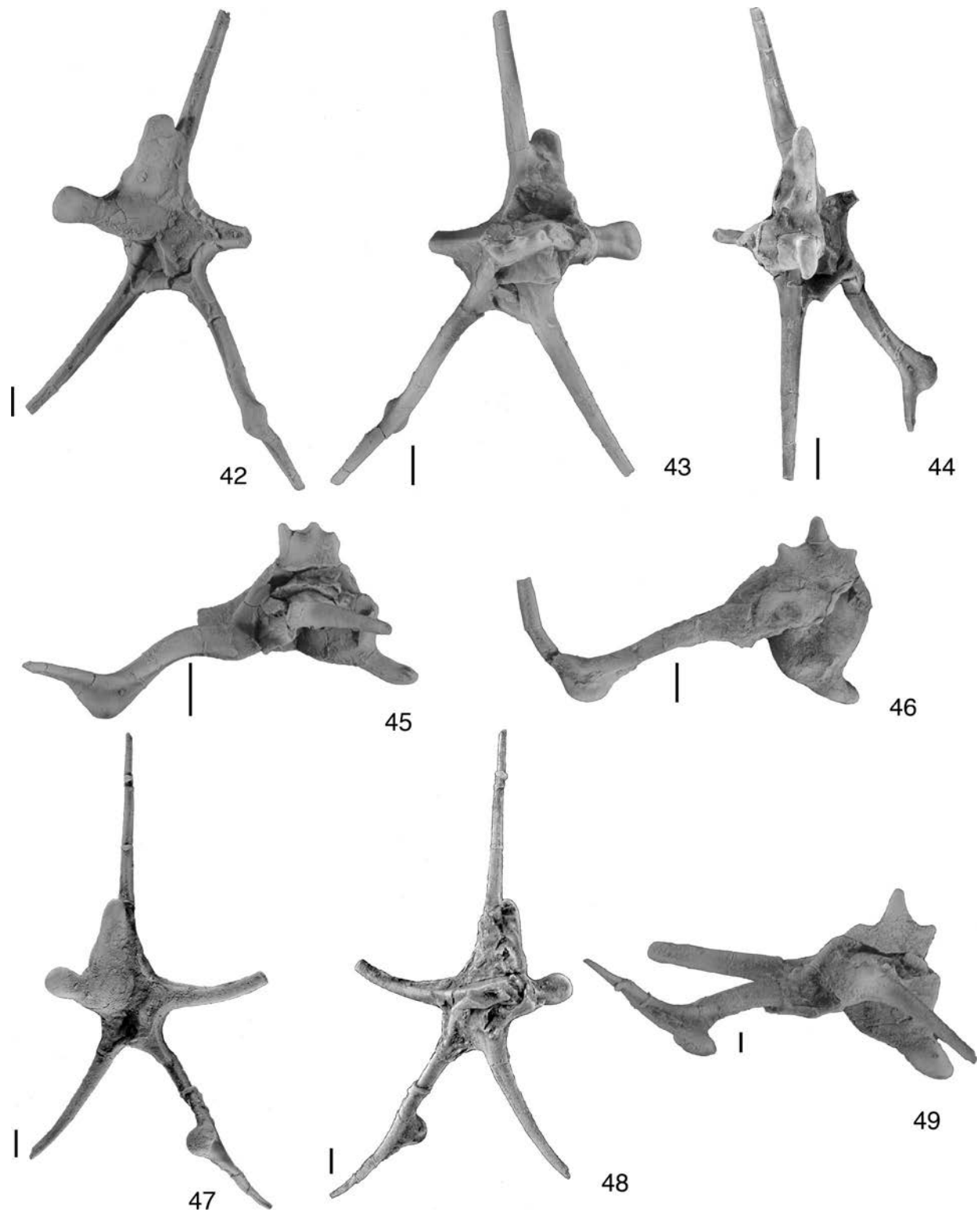
**DIAGNOSIS.** Mature last whorl bicarinate, anterior carina forming high crest of three short spines (middle spine largest) on elevated thin dorsal septum; callus covering shell; fictavarix narrow and somewhat knob-shaped, extending ventrally to form stabilizer.

**DESCRIPTION.** Shell fragile and thin, up to 87 mm high and 43 mm wide (essentially complete). Pleural angle 30 to 40 degrees. Protoconch unknown. Teleoconch approximately six whorls. Suture callused over. **Immature shell:** Turriculate, consisting of approximately five whorls, early spire whorls unicarinate and finely ribbed. **Mature shell:** Consisting of last whorl, bicarinate, carinae subparallel and without nodes; posterior carina weakest and thin; anterior carina near center or dorsum with several (commonly three) short spines (middle one longest) that form high crest on thin, projecting septum. Aperture moderately narrow. Outer lip expanded into four canalliculate digitations. Apical digitation straight, extending along spire but diverting from tip of shell. Posterior and anterior outer lip digitations long and curved and extending from their respective carinae. Anterior outer lip digitation straight and bearing callus knob that can be elongate. Rostral digitation slightly curved. Callus covering shell, obscuring ornamentation except for carinae on last whorl. Callus on venter forms flattened surface. Fictavarix narrow and projecting, not merging with ventral callus;



Figures 33–41 *Tessarolax bullardi* n. sp. 33–35. Holotype RBCM.EH2011.007.0002, loc. 12. 33. Apertural view. 34. Dorsal view. 35. Left-lateral view. 36. Paratype RBCM.EH2011.007.0003, loc. 12, apertural view. 37. Paratype RBCM.EH2011.007.0004, loc. 4, dorsal view. 38, 39. Paratype RBCM.EH2011.007.0005, loc. 4. 38. Dorsal view. 39. Basal view. 40. Paratype RBCM.EH2011.007.0006, loc. 12, dorsal view. 41. Paratype RBCM.EH2011.007.0007, loc. 5, height 60 mm, width 39 mm, dorsal view. Scale bars = 5 mm.





Figures 42–49 *Tessarolax grahami* n. sp. 42–45. Holotype RBCM.EH2011.007.0008, loc. 10. 42. Apertural view,  $\times 1.2$ . 43. Dorsal view,  $\times 1.2$ . 44. Left-lateral view. 45. Basal view. 46. Paratype RBCM.EH2011.007.0009, loc. 9, basal view. 47–49. Paratype RBCM.EH2011.007.0010, loc. 9. 47. Apertural view. 48. Dorsal view. 49. Basal view. Scale bars = 5 mm.

somewhat knob-shaped, extending ventrally to support ablabral side of shell aperture.

**HOLOTYPE.** RBCM.EH2011.007.0008, loc. 10, French Creek, Vancouver Island, British Columbia, Cedar District Formation, French Creek, Vancouver Island, British Columbia [Area 10].

**PARATYPES.** RBCM.EH2011.007.0001 from Northwest Bay [Area 11]; RBCM.EH2011.007.0009–RBCM.EH2011.007.0010, both from loc. 9, Ship Point [Area 9]; and LACMIP 13585 (three unfigured specimens), LACMIP loc. 10093, Silverado Canyon [Area 35].

**GEOLOGIC RANGE.** Early Campanian.

**GEOGRAPHIC RANGE.** Vancouver Island to Southern California.

**STRATIGRAPHIC DISTRIBUTION.** [Area 9] Ship Point, Cedar District Formation, Vancouver Island; [Area 10] French Creek, Cedar District Formation, French Creek, Vancouver Island; [Area 35] Ladd Formation, upper Holz Shale Member, near Modjeska Canyon and Silverado Canyon, Santa Ana Mountains, Orange County, California; and [Area 11] questionable juvenile specimen from the Pender Formation, Northwest Bay, Vancouver Island.

**REMARKS.** Fourteen specimens were examined, of which only two are nearly complete. Of the other specimens, two have been crushed, and the remainder are fragments. Most of the specimens are mature forms. Four immature specimens from the Santa Ana Mountains [Area 35] are probably *T. grahami*, as is probably the only specimen (Fig. 32) available to us from Northwest Bay, eastern side of Vancouver Island [Area 11]. This particular specimen is a turriculate juvenile whose earliest whorls are rounded and whose later whorls are angled by carinae formed by spiral ribs. There are traces of fine spiral ribs on the ramp, and there are three moderate spirals on the rounded base. At present, no juvenile specimens associated with *T. bullardi* n. sp. or *T. grahami* n. sp. are available for direct comparison to this one from Northwest Bay. Several juveniles are associated with *T. distorta*, but those shells are fragile and have been variously bent from their original configuration. On the subsutural-whorl slope of the specimen from Northwest Bay, there is a stronger spiral rib than is present on juveniles associated with *T. distorta*. Based on fieldwork by T. Bullard and R. Graham (personal communication, 2011), the specimen of *T. grahami*? from the Northwest Bay specimen is from coarse-grained siltstone in the middle part of a 53-m-thick section of the Pender Formation, whose upper part at this locale consists of concretionary sandstone. The Northwest Bay section is late early Campanian in age, based on the concurrent ranges of the bivalve *Yaadia tryoniiana* (Gabb, 1864) in the lowermost and uppermost parts of the section and the gastropod *Forsia popenoei* Saul, 1988, in the middle part of the section.

This new species is most similar to *T. bullardi*, the other “crested” *Tessarolax*. *Tessarolax grahami* differs from *T. bullardi* by having the carinae subparallel dorsally, with a serrate crest elevated on a thin septum on the anterior carina. The crest is commonly three-pointed with the middle point projecting farthest, a knob-shaped fictavarix that also projects farther than the fictavarix in *T. bullardi*, and a weaker posterior carina on the last whorl. The fictavarix on *T. grahami* is narrow and knob-shaped, similar to that of *T. distorta*, but on *T. grahami* the fictavarix is commonly longer.

Whereas *T. distorta* has a dorsal spine, *Tessarolax grahami* has a more flange-like dorsal expansion on the anterior carinae. In *T. distorta*, the two carinae are commonly noticeably closer together at the base of the dorsal spine.

Specimens from the Santa Ana Mountains (LACMIP locs. 10091 and 10093) [Area 35] are from below the uppermost Holz Shale. At LACMIP loc. 10093, the specimens occur with *Canadoceras yokoyamai* (Jimbo) (*vide* Matsumoto 1960:102) and could be of early Campanian or late Santonian age.

**ETYMOLOGY.** The species is named for Raymond Graham, who found many of the specimens of this new species and provided valuable biostratigraphic information about them.

*Tessarolax distorta* Gabb, 1864

Figures 50–60

*Tessarolax distorta* Gabb, 1864:126–127, pl. 20, figs. 82, 82a, 82b; Gabb, 1868:146, pl. 4, figs. 18, 19.

Not *Tessarolax distorta* Gabb; Whiteaves 1879:123 [= *T. bullardi* n. sp.].

Not *Tessarolax distorta* Gabb; Whiteaves, 1895:127 [= *T. louellae* n. sp.].

Not *Tessarolax distorta* Gabb; Whiteaves, 1903:358 [= *T. louellae* n. sp.].

*Chenopus* (*Tessarolax*) *distortum* (Gabb); Cossmann, 1904:364.

*Tessarolax distorta* Gabb; Grabau and Shimer, 1909:754, fig. 1097 (after Gabb); Stewart, 1927:363, pl. 23, figs. 4, 5;

Shimer and Shrock, 1944:pl. 204, p. 499, figs. 12, 13 (after Stewart); Elder and Saul, 1993:177, table 1, pl. 2, fig. 23.

*Aporrhais* (*Tessarolax*) *distorta* (Gabb); Wenz, 1940:916, fig. 2690 (after Gabb).

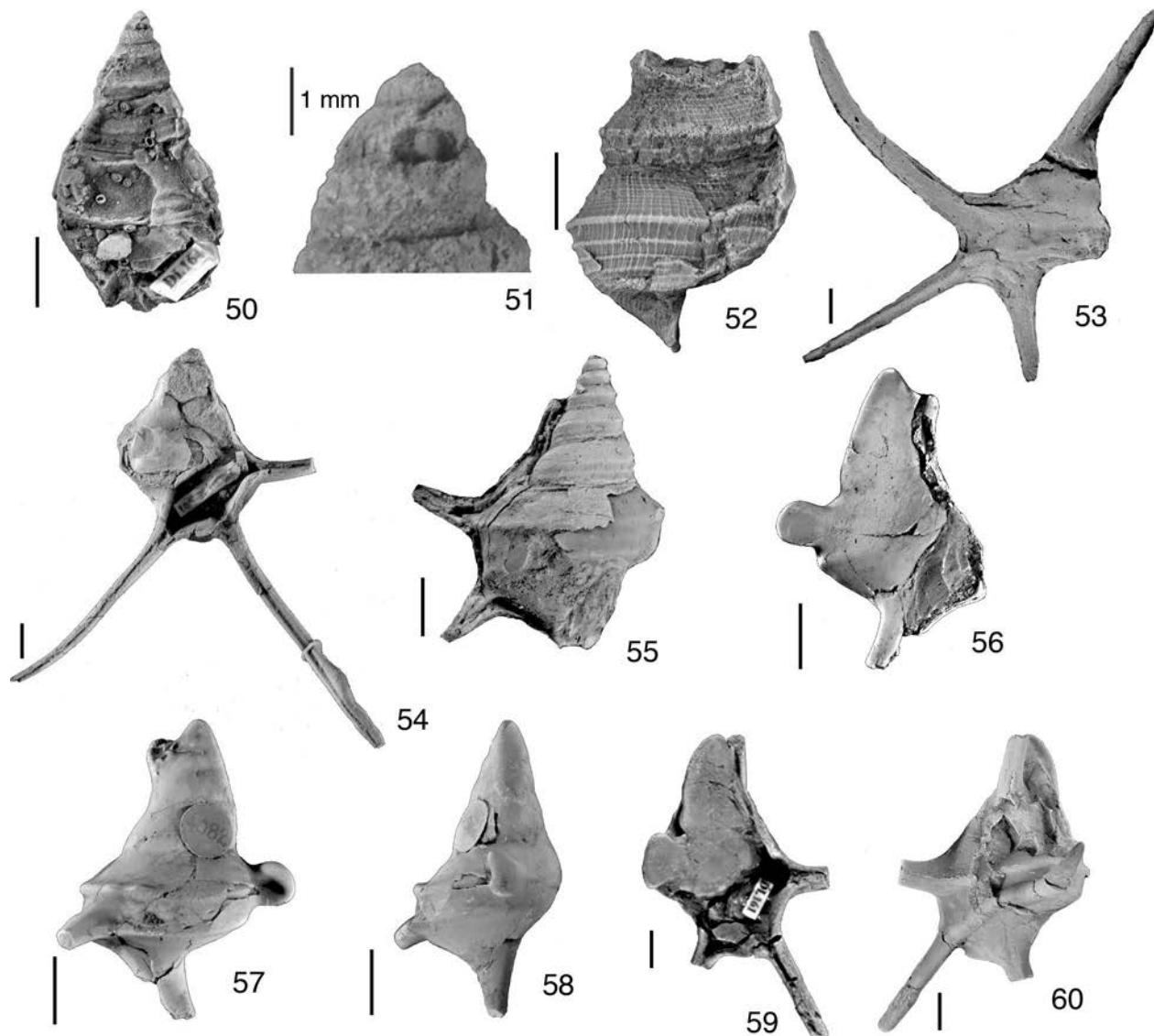
Not *Tessarolax* aff. *T. distorta* Gabb; Saul, 1986:27, figs. 17, 18 [= *T. teleos* n. sp.].

Not *Tessarolax distorta* Gabb; Ludvigsen and Beard, 1994:98, fig. 6 (three views); [= *T. louellae* n. sp.].

Not *Tessarolax distorta* Gabb; Ludvigsen and Beard, 1997:117, fig. 74 (three views) [= *Tessarolax louellae* n. sp.].

**DIAGNOSIS.** Mature last whorl bicarinate, posterior carina noded; dorsal spine (spike-like) prominent; callus glaze extensive over entire shell; fictavarix narrow, ear-shaped when small, enlarging and extending laterally, but not coalesced with ablabral callus.

**DESCRIPTION.** Shell up to 60 mm high (estimated) and 57 mm wide (digitations nearly complete). Pleural angle 37 to 41 degrees. Protoconch conical and consisting of three smoothish whorls. Teleoconch up to six whorls. Suture slightly impressed. **Immature shell:** Turriculate, consisting of approximately five whorls having steeply sloped, barely concave ramp bearing fine spirals crossed by spaced raised growth lines (producing cancellate effect), three strong spirals beaded where crossed by growth lines, five medium spirals on rounding part of base, followed by finer spirals on base and rostrum, early spire whorls unicarinate (suture on third spiral), later spire whorls with two additional spiral ribs. **Mature shell:** Consisting of last whorl, wide, strongly bicarinate, with small nodes prominent on posterior carina. Aperture moderately wide. Outer lip expanded into four long and curving canalicate digitations. Apical digitation straight, extending along spire but diverting away from tip of spire. Posterior and anterior outer lip digitations long and somewhat curved, extending from their respective carinae. Anterior outer lip digitation ventrally bearing small callus knob. Rostral digitation long and generally straight. Dorsal spine (spike-like) emanating from anterior carina on last whorl; spine commonly midway between fictavarix and outer lip but can be closer to either. Callus glaze extensive over entire shell, obscuring ornamentation except for spirals on two carinae of last whorl. Tongue of callus on venter of upper spire expands beyond tip, and apical callus envelops tip of shell in callus tongue. Fictavarix



Figures 50–60 *Tessarolax distorta* Gabb, 1864. 50, 51. Hypotype RBCM.EH2011.007.0011. 50. Apertural view, crushed. 51. Enlarged tip (2.5 mm), showing protoconch and early teleoconch whorls. 52. Hypotype RBCM.EH2011.007.0012, loc. 8, juvenile sculpture. 53. Hypotype LACMIP 13588, LACMIP loc. 4818, latex peel of external mold, dorsal view. 54. Hypotype RBCM.EH2011.007.0013, loc. 8, apertural view. 55. Hypotype LACMIP 13586, LACMIP loc. 28764, dorsal view. 56–58. Hypotype LACMIP 13587, LACMIP loc. 24082. 56. Apertural view. 57. Abapertural view. 58. Right-lateral view. 59, 60. Hypotype RBCM.EH2011.007.0014, loc. 8. 59. apertural view. 60. dorsal view. Scale Bars = 5 mm, except where otherwise noted.

small, narrow, ear-shaped with sulcus on dorsal side, ultimately extending somewhat laterally perpendicular to shell surface.

**HOLOTYPE.** UCMF 31394 from Tuscan Springs, Tehama County, northern California [Area 18].

**PARATYPES.** According to ANSP records: ANSP 4279-4280, Tuscan Springs [Area 18].

**HYPOTYPES.** RBCM.EH2011.007.0011–RBCM.EH2011.007.0014, all from loc. 8, “White House Site,” western Denman Island [Area 8]; LACMIP 13586, LACMIP loc. 28764, Rock Corral [Area 20]; LACMIP 13587, LACMIP loc. 24082, Tuscan Springs [Area 18]; and LACMIP 13588, LACMIP loc. 4818, Santa Monica Mountains [Area 34].

**GEOLOGIC RANGE.** Late early Campanian to early late Campanian.

**GEOGRAPHIC RANGE.** Vancouver Island to southern California.

**STRATIGRAPHIC DISTRIBUTION.** UPPER LOWER CAMPANIAN: [Area 18] Chico Formation, Tuscan Springs, Tehama County, California; MIDDLE CAMPANIAN: [Area 20] Chico Formation, Rock Corral, north of Folsom, Placer County, California; [Area 19] Forbes Sandstone, Petroleum Creek east of Rumsey, Yolo County, California; [Area 28] Panoche Formation, Cooper Canyon, Alcalde Hills, Fresno County, California; [Area 24] Pigeon Point Formation, San Mateo Coast beaches, San Mateo County, California; [Area 33] Chatsworth Formation, upper Bell Canyon, Simi Hills; [Area 34] Tuna Canyon Formation, Santa Ynez Canyon, Santa Monica Mountains, Los Angeles County, California; and questionably



[Area 21] Joaquin Ridge Sandstone, upper part, near Bethany Reservoir, Alameda County, California. LOWER UPPER CAMPANIAN (= approximately the *Metaplacenticerias pacificum* zone): [Area 8] Cedar District Formation, "White House site," west side of Denman Island, off east coast of Vancouver Island.

**REMARKS.** Twenty-six specimens were examined. The holotype is incomplete, and its digitations are either incomplete or completely broken off. Its fictavarix, however, is intact. Five of the other examined specimens are immature, but on three of them, the sculpture is obscured by a mineral coating. The remaining two of the immature specimens are somewhat crushed; the better specimen (Fig. 52) has a strong carina with fine spiral striae posterior to the carina and anterior to the carina two to four noticeable spirals, the most anterior of which is strongest. The suture is at or immediately below the anterior carina. The last whorl has at least three fairly strong ribs anterior of the anterior carina and fine ribs on the base of the rostrum. None of the immature specimens has a complete rostrum. In mature specimens, a flange of callus was deposited up the ablabral side of the shell, over the apex, and covering the protoconch before the exterior of the last whorl was coated.

*Tessarolax distorta* differs from *T. grahami* in having a dorsal spine (spike-like) rather than a crest of three short spines on a thin septum. The fictavarix of *T. distorta* does not coalesce with the ablabral callus and differs from *T. louellae* in lacking the anteriorward extension of the ablabral flange anterior of the anterior carina.

#### *Tessarolax louellae* new species Squires

Figures 4, 61–70

*Tessarolax distorta* Gabb. Whiteaves, 1895:27; Whiteaves, 1903:358; Ludvigsen and Beard, 1994:98, fig. 63 (three views); Ludvigsen and Beard, 1997:116–117, fig. 74 (three views).

**DIAGNOSIS.** Mature last whorl tricarinate, dorsal spine prominent; callus extensive over entire shell; ablabral callus, ventral callus, and fictavarix merge to form long, blade-shaped callus structure.

**DESCRIPTION.** Shell fragile and thin, up to 88 mm high and 56 mm wide (essentially complete). Pleural angle approximately 37 degrees. Protoconch covered by callus deposit. Teleoconch of six whorls. Suture callused over. **Immature shell:** Essentially unknown due to callus coverage. **Mature shell:** Consisting of last whorl, tricarinate, carinae (not noded) equally spaced and nearly of equal strength. Base of last whorl with several weak and moderately widely spaced spiral ribs, decreasing in strength anteriorly. Entire last whorl covered with numerous microscopic and very closely spaced spiral threads between carinae and prominent spiral rib. Aperture moderately narrow. Outer lip extended into four narrow canalicular digitations. Apical digitation curved, extending along spire but diverting from tip of shell. Posterior and anterior outer lip digitations long, strongly curved, and extending from their respective carinae. Posterior outer lip digitation bending posteriorly. Anterior outer lip digitation extending forward to callus knob, then bending away from substrate. Rostral digitation nearly straight or curved into wide U-shape. Dorsal spine, long and slender, prominently emanating from at or near anterior carina on middle of dorsal side of last whorl and commonly bent. Callus covering shell obscuring two carinae on last whorl and hiding ornamentation. Callus on venter can accentuate convexity (plumpness) of last whorl. Ablabral callus elongate, narrow, extending over apex in small curl, and merging with ventral callus to form long and blade-shaped fictavarix. Growth line opisthocline.

**HOLOTYPE.** RBCM.EH2011.007.0015, Phipps Point, Hornby Island, Vancouver Island area, British Columbia [Area 7].

**PARATYPES.** GSC 5936a–c [specimens of Whiteaves (1895:27; 1903:358)], Hornby Island [Area 7], and RBCM.EH2011.007.0016–RBCM.EH2011.007.0018, all from loc. 6, Collishaw Point, Hornby Island [Area 6].

**GEOLOGIC RANGE.** Middle late Campanian.

**GEOGRAPHIC RANGE.** Vancouver Island area, British Columbia to questionably northern California.

**STRATIGRAPHIC DISTRIBUTION.** [Area 6] Northumberland Formation, Collishaw Point, Hornby Island off east coast of Vancouver Island; [Area 7] Northumberland Formation, Phipps Point, Hornby Island off east coast of Vancouver Island.

**REMARKS.** Eight specimens were examined, including specimens of so-called *Tessarolax distorta* reported by Whiteaves (1895:127; 1903:358). Although most of the examined specimens are broken, a few are complete and show very good preservation, especially the holotype (Figs. 4, 61–64). Mature specimens have callus obscuring the spiral sculpture. Even on the apertural face of the shell, the carinae are obscured and are mainly hidden. Sculpture is seen only in places from which the callus has broken away. This new species is most similar to *T. incrustata* but differs in the following: one-half the shell size (versus the largest *incrustata*), more slender spire, thinner callus overcoat, and in having the ablabral callus merged with the ventral callus to form the broadly tongue-shaped callus that extends from above the spire tip to below the anterior carina. *Tessarolax louellae* is slightly higher spired than *T. distorta* and commonly has a long, slender, and bent dorsal spine rather than a nearly straight dorsal spike. *Tessarolax louellae* also has a more axially elongate ablabral callus that extends beyond the anterior carina, whereas that of *T. distorta* does not reach the anterior carina.

The poorly preserved holotype (Fig. 71) of "*Alaria*" *fairbanksi* Davis (1913:456, fig. 1), from UCMP loc. A-919, just north of Slate's Hot Springs, Monterey County, northern California [Area 27], resembles somewhat *T. louellae*. In comparison to the latter, however, the holotype of "*Alaria*" *fairbanksi* is too tall relative to its girth but appears to have had its surface resculptured and its original shape altered by deformation. The poor state of preservation and the incompleteness of the holotype renders any specific identification a matter of speculation. "*Alaria*" *fairbanksi* was originally inferred to be of probable Jurassic age based on some associated plant fragments described by Fontaine (1905). Nomland and Schenck (1932) believed the gastropod might be an *Anchura* of Cretaceous age, but Elder and Saul (1993:381) suggested that it bears a greater similarity to *Tessarolax*. Impressions of the ammonite *Baculites anceps* Lamarck from the same strata indicate an age in the later part of the Campanian (Matsumoto, 1960:74).

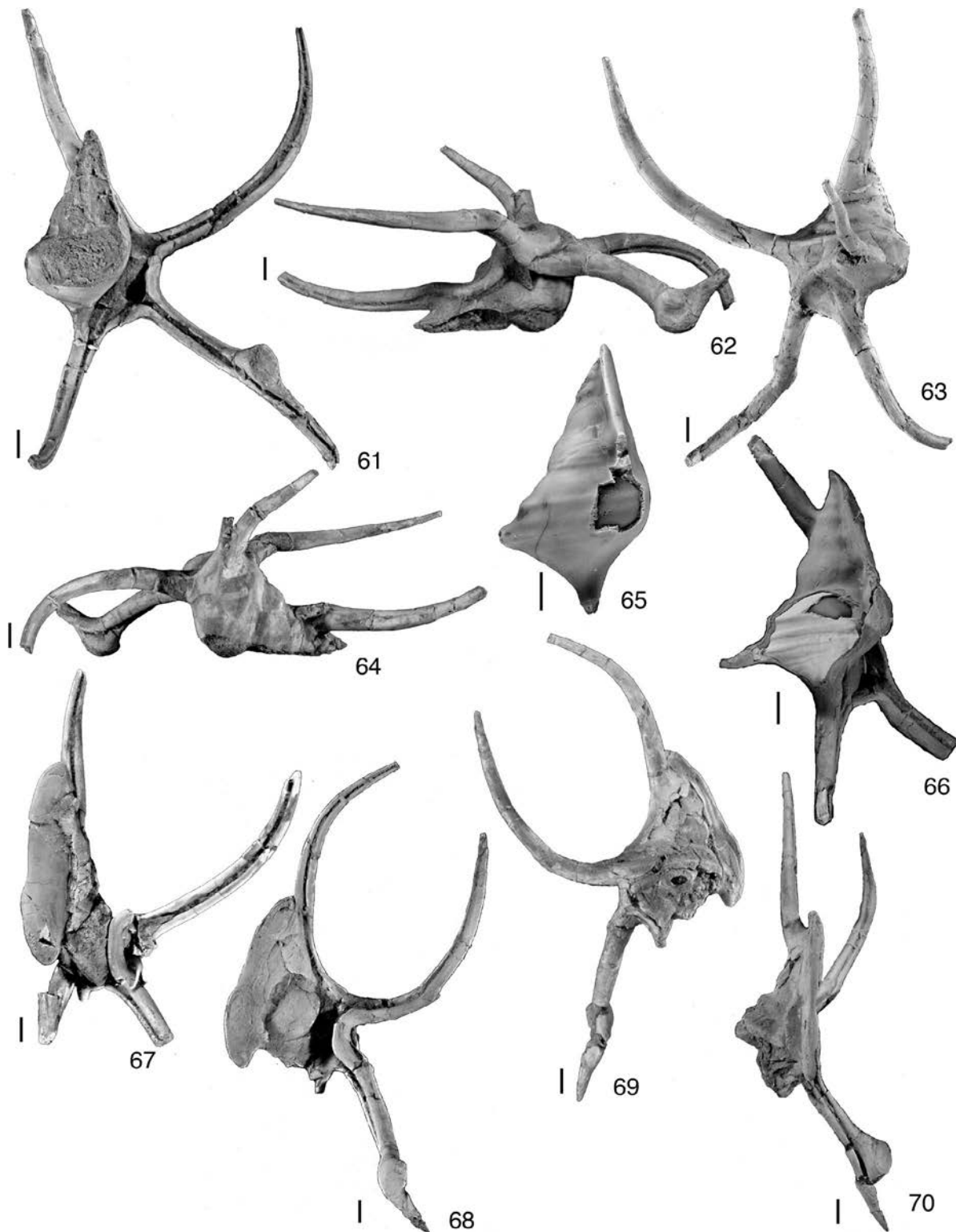
**ETYMOLOGY.** The junior author names this species in honor of Louella R. Saul for all her many contributions devoted to establishing highly useful details of the geological history of numerous Cretaceous gastropods and bivalves.

#### *Tessarolax incrustata* Anderson and Hanna, 1935

Figures 3, 72–84

*Tessarolax incrustata* Anderson and Hanna, 1935:27, pl. 9, figs. 4, 5; Perrilliat, 1989:168, fig. 57a (after Anderson and Hanna, 1935); Saul, 1989:20, unnumbered fig.  
? *Tessarolax* sp. Sundberg, 1979:fig. 2.

**DIAGNOSIS.** Mature last whorl bicarinate, dorsal spine prominent; callus extensive over entire shell with digitations thickly callused; fictavarix flange shaped and extending ventrally to form broad stabilizer.



Figures 61–70 *Tessarolax louellae* n. sp. Squires. 61–64. Holotype RBCM.EH2011.007.0015, Phipps Pt., Hornby Island. 61. Apertural view. 62. Lateral view of outer lip side, living position. 63. Dorsal view. 64. Lateral view of ablabral side, living position. 65. Paratype GSC 5936, Hornby Island, British Columbia. 66. Paratype RBCM.EH2011.007.0016, Collishaw Pt., Hornby Island, ablabral view with fictivarix. 67. Paratype RBCM.EH2011.007.0017, Collishaw Pt., Hornby Island, apertural view. 68–70. Paratype RBCM.EH2011.007.0018, Collishaw Pt., Hornby Island. 68. Apertural view. 69. Dorsal view. 70. Left-lateral view. Scale bars = 5 mm.



Figure 71 “*Alaria*” *fairbanksi* (Davis, 1913), holotype UCMP 32297, UCMP loc. A919, possibly left-lateral view. Scale bar = 5 mm.

**DESCRIPTION.** Shell up to 114 mm high and 92 mm wide (digitations nearly complete). Pleural angle 41 degrees. Protoconch consisting of two, low whorls encased in callus. Teleoconch of five whorls. **Immature shell:** Turriculate, consisting of four whorls. Suture impressed. Second whorl of teleoconch with traces of spirals about mid-whorl. Third whorl with strong sharp carina near mid-whorl and two spirals anterior; second spiral barely above suture. Fourth whorl with strong sharp carina mid-whorl and two anterior spirals, second spiral barely above suture, ramp covered with fine and closely spaced spirals, and base/neck covered with fine spirals. **Mature shell:** Consisting of wide last whorl, strongly bicarinate, with carinae noded, carina on shoulder strongest. Suture callused over. Aperture moderately wide. Outer lip expanded into four long and curving canalicate digitations. Apical digitation long and generally straight, extending along spire but in most specimens diverting away from tip of shell and tilted slightly upward at narrow angle to shell axis with its channel remaining on apertural side of digitation. Posterior and anterior outer lip digitations long and curved, coincident with their respective carina. Posterior outer lip digitation slopes toward substrate, bends posteriorly, and, near its distal end, turns away from substrate; channel along digitation begins on apertural side but migrates to abapertural side; distal third of digitation, but not including final-upward portion, flattened and appears abraded on substrate side. Anterior outer lip digitation slopes more abruptly toward substrate, then more abruptly reverses slope and bends upward; channel in digitation begins on apertural side, runs along anterior side of digitation at bend, and migrates back to outer lip side along its upturned portion; rounded, thick callus knob abraded on its substrate side embellishes bend. Rostral digitation, commonly moderately straight (remains nearly in plane of shell axis but distally has somewhat downward slope), engulfs rostrum by extending anteriorly and curving more or less ablaterally; rostral digitation rarely U-shaped. Channel remains on apertural side of digitation, and rostral digitation is not worn, abraded, or flattened. Digitations layered by coats of callus. Dorsal spine arises from strong anterior carina of last whorl and forms relatively straight prong pointing away from substrate; dorsal spine prominent, can be as long as apical digitation, and rarely bent in angle, toward anterior of shell. Callus glaze extensive over entire shell, totally obscuring ornamentation but not carinae. Callus on venter of shell

thick, forming thick tongue from neck to beyond tip of spire. Ablabral-callus process either slightly set off from ventral callus by indentations or merging with it to form thin, flange-shaped fictavarix extending ventrally to form broad stabilizer.

**HOLOTYPE.** CAS 1430.02 [= CAS 4262], CAS loc. 1430, Johnson’s Ranch, San Antonio del Mar, northern Baja California, Mexico [Area 39].

**PARATYPE.** CAS 1430.03 [= CAS 4263], CAS loc. 1430, San Antonio del Mar [Area 39].

**HYPOTYPES.** LACMIP 13589 (unfigured) from LACMIP 26337, Hancock Ranch [Area 30]; SDSNH 20269 from SDSNH loc. 1010, Salsipuedes [Area 38]; LACMIP 13590–13591 from LACMIP 27149, San Antonio del Mar [Area 39]; and LACMIP 13592–13593 from LACMIP 22414, San Antonio del Mar [Area 39].

**GEOLOGIC RANGE.** Latest Campanian to early Maastrichtian. *Tessarolax incrustata* occurs with the bivalve *Inoceramus shikotanensis* Nagao and Matsumoto, 1939, which is an *Inoceramus* zone marker for the lower Maastrichtian Japanese Zone K6b1 [correlative to the ammonite *Pachydiscus* (*Neodesmoceras*) *japonicus* Zone].

**GEOGRAPHIC RANGE.** Northern California to northern Baja California, Mexico.

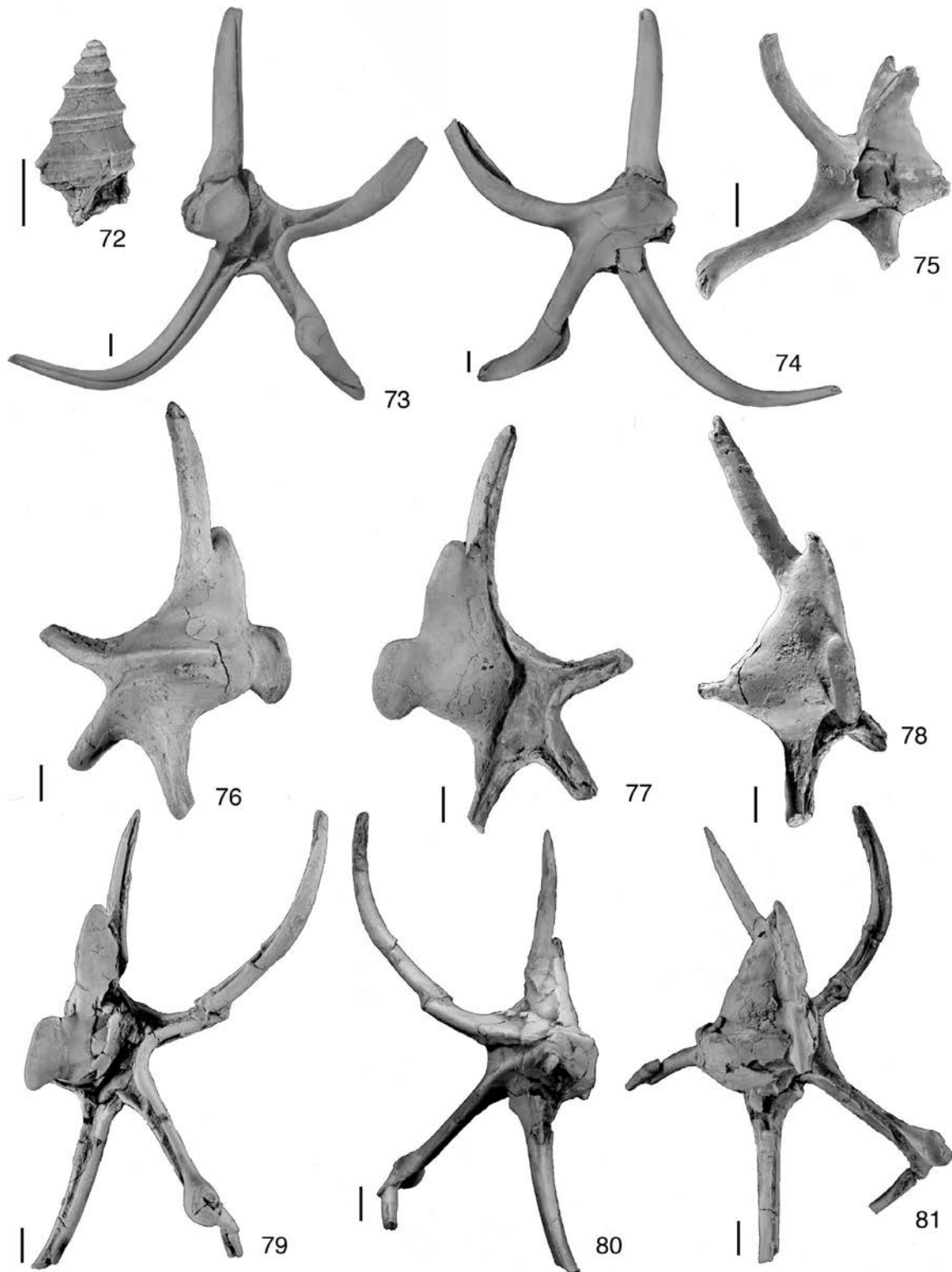
**STRATIGRAPHIC DISTRIBUTION.** [Area 25] Moreno Formation or below top of Panoche Formation [Uhalde Formation], Salt Creek, Merced County, northern California; [Area 30] upper Panoche Formation, deep-water strata?, west side Cottonwood Creek, Hancock Ranch, Monterey County, northern California; and [Area 38] Rosario Formation, Salsipuedes, north of Ensenada, Baja California, Mexico; [Area 37] a *Tessarolax* specimen not seen by us was reported by Sundberg (1979) from Point Loma Formation, near La Jolla, San Diego County, southern California; [39] Rosario Formation near San Antonio del Mar, northwestern Baja California, Mexico; [Area 40] Rosario Formation, Arroyo San Antonio and Arroyo Santa Catarina, northwestern Baja California, Mexico; questionably [Area 22] CAS loc. 29666, lower Moreno Formation, Del Puerto Creek, Stanislaus County, central California; and questionably [Area 32] CAS loc. 42920, unnamed formation, Pilitas Creek Pozo area, San Luis Obispo County, central California

**REMARKS.** Approximately 15 specimens, as well as numerous fragments, were examined. Most of the specimens were found in micaceous fine-grained sandstone. The largest and best-preserved specimens are from LACMIP locs. 22414 and 27149 in the Rosario Formation, Baja California [Area 39].

Anderson and Hanna (1935) based their *T. incrustata* on specimens collected by C. H. Sternberg in 1928, who provided a minimum of geographic information. Anderson and Hanna (1935:27) reported the type locality as “from Johnson’s ranch, midway between Rosario and Santa Catarina Landing.” Their description is in general agreement with the CAS locality catalog for the type locality for *T. incrustata*: “CAS loc. 1430 at Johnson’s Ranch, 20 miles below Rosario.” The earliest map in the LACM Map collection that indicates the position of Johnson’s Ranch is the “Map of Lower California and the Northeastern States of Mexico,” drawn by E. E. Knight and published in 1930 by Areg-Jones Co. in San Diego, California. On this map, Johnson’s Ranch is near San Antonio del Mar, about 160 km south of the U.S./Mexico border. In summary, the type locality of *T. incrustata* is confirmed herein as being in the vicinity of San Antonio del Mar [Area 39], which is roughly halfway between El Rosario and Arroyo Santa Catarina, northern Baja California [Area 40]. For additional background information on this locality, see Saul (1983:93).

*Tessarolax incrustata* has a much sturdier shell with digitations of greater diameter than any of the older species discussed. This





Figures 72–81 *Tessarolax incrustata* Anderson and Hanna, 1935. 72. Hypotype LACMIP 13590, LACMIP loc. 27149, apertural view. 73, 74. Hypotype LACMIP 13593, LACMIP loc. 22414. 73. Apertural view. 74. Dorsal view. 75. Hypotype LACMIP 13592, LACMIP loc. 22414, right-lateral view. 76–78. Hypotype LACMIP 13594, LACMIP loc. 22414. 76. Apertural view. 77. Dorsal view. 78. Left-lateral view. 79–81. Hypotype LACMIP 13591, LACMIP loc. 27149. 79. Apertural view. 80. Dorsal view. 81. Left-lateral view. Scale bars = 5 mm.

sturdiness results from deposition of a thicker callus coating, as the immature shell and even those just beginning to develop the coating are thin shelled and frail. Of the examined specimens, only one is an immature specimen.

A hypotype of *T. incrustata* (Fig. 75) has its callus broken away, thereby providing a view of the noded carinae, strong noded mid-rib of the last whorl, and spiral ribs on the base. Internal structure of the glaze consists of a thick cross-lamellar layer directly above the unglazed shell, overlain by a thin lamellar layer.

Specimens of *T. incrustata* from Salsipuedes in Baja [Area 38] differ from most specimens of *T. incrustata* in higher and narrower spires, a more club-shaped fictavarix that is less connected to the ablabral flange, and more arcuate apical and posterior outer lip digitations.

Poorly preserved specimens of *T. incrustata* are from CAS loc. 29666, in Del Puerto Creek in central California [Area 22], and they occur with the ammonite *Didymoceras vancouverense* (Gabb), which was indicated by Matsumoto (1960:89) to be from “above Panoche-Moreno contact” and of latest? Campanian or earliest Maastrichtian age. Poorly preserved specimens of *T. incrustata* are also from CAS loc. 42920, in an unnamed formation in the Pilitas Creek area in central California [Area 32].

#### *Tessarolax teleos* new species

Figures 85–91

*Tessarolax* aff. *T. distorta* Gabb. Saul, 1986:27, figs. 17–19.

**DIAGNOSIS.** Mature last whorl wide and bicarinate; dorsal spine stout; callus glaze extensive; fictavarix “mitten-like.”

**DESCRIPTION.** Shell up to 37 mm high and 27 mm wide (digitations missing). Pleural angle approximately 55 degrees. Protoconch unknown. Teleoconch up to six whorls. Suture impressed. **Immature shell:** (LACMIP 13596): Turriculate, consisting of five whorls. Ramp broad, whorl surfaces covered with many closely spaced spiral threads alternating in strength. First two teleoconch whorls rounded and possibly smooth. Remaining immature whorls with carina located anterior of mid-whorl and suture nearly coincident with moderately strong spiral rib. **Mature shell:** Consisting of wide last whorl, bicarinate with very weak spiral rib on interspace visible where callus is thinned. Aperture moderately wide. Outer lip expanded into four canaliculate digitations. Apical digitation extending along spire but diverted away from tip of spire. Posterior and anterior digitations coincident with their respective carina. Rostral digitation mostly incomplete. Dorsal spine stout (thick) and arising from anterior carina. Callus glaze over entire shell (including tip of spire) and obscuring ornamentation except for bicarinae. Callus on venter of shell moderately thick, forming continuous sheet from neck to tip of spire. Fictavarix moderately long, narrow, and “mitten-like.”

**HOLOTYPE.** UCMP 38033, UCMP loc. A-3368, El Piojo Formation, Lake Nacimiento, San Luis Obispo County, California [Area 31].

**PARATYPES.** UCMP 38032, UCMP loc. A-3368 [Area 31]; LACMIP 13595–13596 (two specimens), all from LACMIP loc. 8147 [Area 26]; and LACMIP 13597 (unfigured), LACMIP loc. 301410 [Area 31].

**HYPOTYPES.** LACMIP 13594, 13595, and 13596, all from LACMIP loc. 8147 [Area 26].

**GEOLOGIC RANGE.** “Mid” Maastrichtian [= late early to early late Maastrichtian].

**GEOGRAPHIC RANGE.** Northern California.

**STRATIGRAPHIC DISTRIBUTION.** [Area 26] Moreno Formation, Tierra Loma Member, Laguna Seca Creek, Merced County, northern California; [Area 31] El Piojo Formation, Cantinas Creek, Lake Nacimiento area, San Luis Obispo County, northern California.

**REMARKS.** Six specimens were examined, and all are incomplete. Preservation is generally poor. Digitations and dorsal spine are incompletely preserved on the two most mature specimens. A fictavarix is well preserved only on the holotype (Figs. 89–91), a small adult. It extends outward and apexward, appearing mitten-like, and does not extend anteriorly to the anterior carina. Its attachment area to the spire is unusually short. On other specimens, the fictavarix is obscured by chipping, breakage, and adherence of large sand grains, thereby making determination of the exact shape uncertain. Mature or early mature individuals from LACMIP loc. 8147 Laguna Seca Creek, California [Area 26] have apparently lost sufficient callus glaze (through weathering? or removal with matrix?) to reveal spire sculpture and lose mature appearance.

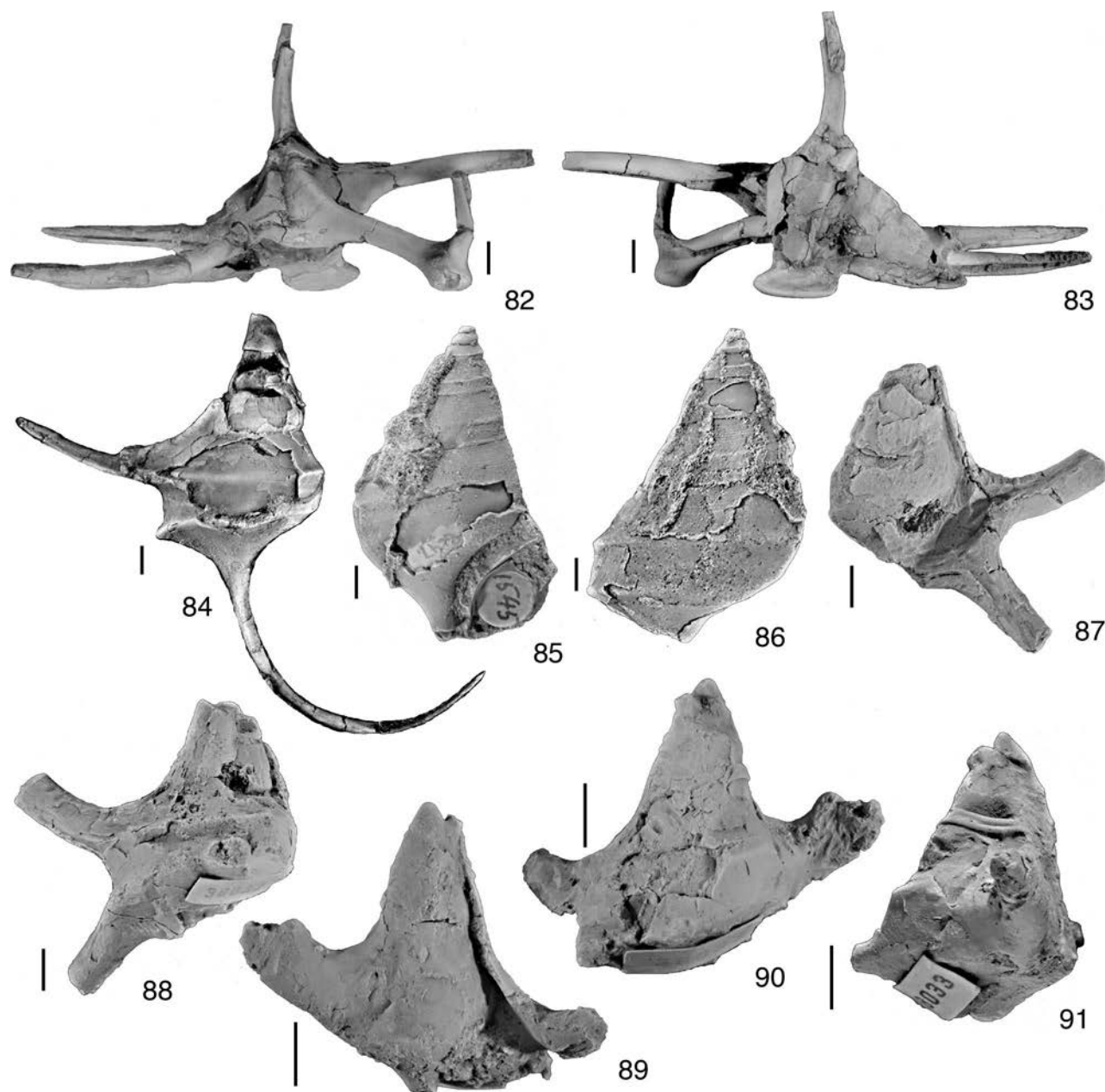
In spire shape and size, *T. teleos* most closely resembles *T. incrustata*, but *T. teleos* differs in having its carinae closer together and an apexward-bent fictavarix that is smaller and does not extend anteriorly of the anterior carina, nor is it adjacent to the shell spire.

**ETYMOLOGY.** The species name is derived from the Greek *teleos*, meaning “having reached its end” or “finished,” signifying the end of the *Tessarolax* lineage.

#### EVOLUTIONARY TRENDS

Immature *Tessarolax* show no evolutionary trend because their shells are all morphologically very similar in having a turriculate shape with generally unicarinate whorls and lacking outer lip digitations. Mature *Tessarolax* show evolutionary trends that primarily involve callus encrustation and development of associated callus-related features, as summarized below.

Mature specimens of the geologically oldest species, *Tessarolax gabbii* of late Hauterivian age, have modest sculpture and no overall callus coat (none dorsally), are generally less encrusted than later species, and possess a thick ablabral callus deposit but no fictavarix. During the Albian, mature *Tessarolax* shells began to display development of a fictavarix and a thick tongue of callus (apical callus) that extends along the inner lip and adapically beyond the spire. Although Albian through early Coniacian species have a fictavarix (or incipient fictavarix), they lack a large dorsal callus structure. An Albian-age specimen of *T. retusa* from the Gault (Fig. 5) displays the lack of callus on the shell’s dorsal side. The callus coat of *T. retusa* is predominantly on the apertural side. Illustrations of Albian *Tessarolax retusa* in Gardner (1875b) show neither a fictavarix nor dorsal encrustation of the spire, but a well-developed fictavarix is present on the western Europe Albian specimen of “*Pterocera*” *bicarinata* d’Orbigny (1843:pl. 208, figs. 3–5) [reprinted by Kollmann (2005:132) as *Ceratosiphon retusus*]. The PSNA specimens of *T. trinalis* (latest Albian to middle Cenomanian age) are all immature, but they have a thin callus glaze on the venter of the shell, although the spire tip was not covered up. Also, there is an incipient fictavarix on the most mature ones. None of the available PSNA *Tessarolax* specimens of Albian age is fully mature, and none shows a well-developed fictavarix such as that on “*Pterocera*” *bicarinata* d’Orbigny. During the late Turonian to early Coniacian, callus glaze was thicker on the venter but thin on the dorsum of *T. alaskana*, and the fictavarix was short and laterally flangiform.



Figures 82–91 Various species of PSNA *Tessarolax*. 82–84. *Tessarolax incrustata* Anderson and Hanna, 1935. 82, 83. Hypotype LACMIP 13591, LACMIP loc. 27149. 82. Lateral view of outer lip side, in living position. 83. Lateral view of ablabral side, in living position. 84. Paratype SDSNH 20269, SDSNH loc. 1010, dorsal view, dorsal spine missing. 85–91. *Tessarolax teleos* n. sp. 85, 86. Paratype LACMIP 13595, LACMIP loc. 8147, earliest whorl (about 1.3 mm wide) is possibly last whorl of protoconch. 85. Apertural view. 86. Dorsal view. 87, 88. Paratype UCMP 38032, UCMP loc. A-3368, rostral area missing. 87. Apertural view. 88. Dorsal view. 89–91. Holotype UCMP 38033, UCMP loc. A-3368. 89. Apertural view. 90. Dorsal view. 91. Left-lateral view. Scale bars = 5 mm.

Post-early Coniacian species developed a sequence of dorsal (abapertural) callus deposits arising medially from the anterior carina on the last whorl. This sequence involved a gradual evolutionary change in the sculpture from a lowly elevated, noded crest on the dorsum (e.g., *T. bullardi*) to a more elevated crest of short spines (e.g., *T. grahami*) and eventually to a longer dorsal spine (e.g., *T. distorta*, *T. louellae*, and *T. incrustata*). Also during this interval, the callus coating remained overall thin (very thin on *T. bullardi* but somewhat thicker on *T. grahami*), and, at

halfway to two-thirds of its length from the aperture, the anterior outer lip digitation developed a callus. The rostral digitation at maturity extended and strengthened the short juvenile rostrum and leaned slightly dorsally near the shell. It retained a ventrally facing channel but did not develop evidence of contact with the substrate.

During the late early to early late Campanian, the callus coating became thick enough to cover the original spiral ornamentation of *T. distorta*, and Gabb (1864) mentioned this



overall callus in his generic description. The fictavarix evolved to form a prop or stabilizer on the ablabral side as the shell perched above the substrate by means of the arching digitations and by means of the ablabral-callus deposits. The fictavarix on *T. distorta* was ear-shaped, not coalescing with the ablabral callus.

During the latest Campanian and into the Maastrichtian, there was extensive callus over the entire shell, and the ablabral callus, ventral callus, and fictavarix all merged to form a long, blade-like structure. A dorsal spike-like spine also continued to be present. The entire mature shell of Campanian and younger species is callus coated, and on a shell of approximately 3 cm height, the digitation span commonly exceeds 11 cm (Saul, 1989). *Tessarolax incrustata*, of latest Campanian to early Maastrichtian age, has the thickest, most complete callus coat.

#### MODE OF LIFE AND HABITAT PREFERENCE OF *TESSAROLAX*

The protoconch of *Tessarolax* is similar to that of modern aporrhoids (see Solsona et al., 2000:pl. 1) in consisting of about three smooth whorls. It is likely that modern aporrhoids have planktotrophic larval development; thus, they have a high capacity for geographical dispersion (Thiriot-Quévieux, 1969). The wide paleobiogeographical distribution (see “Paleobiogeography of *Tessarolax*” section herein) and great longevity of *Tessarolax* can be best explained if this genus also had planktotrophic larval development.

As mentioned earlier, immature *Tessarolax* shells are turriculate and without an expanded outer lip and therefore are like modern immature aporrhoids (see Barnes and Bagenal, 1952; Perron, 1978b). As the outer lip is gradually developed during growth, modern aporrhoid animals live a shallow-burrowing mode of life and tend to live nearer the surface (Barnes and Bagenal, 1952). It seems doubtless that immature *Tessarolax* did likewise. The mature shape of *Tessarolax*, however, does not resemble gastropods that either burrow within soft substrate or clamp down on hard substrate. The long, curved digitations of *Tessarolax* appear unlikely to promote burrowing. The fictavarix, apical callus, and bend of the anterior outer lip digitation also would have prevented clamping down onto a substrate.

Figures 62, 64, 82, and 83 are the first pictures ever shown of nearly complete *Tessarolax* in living position. The curving outer lip digitations and fictavarix supported the shell above the substrate and provided space for mobility of the foot and for food gathering. The rostral digitation extended forward and above the proboscis and inhalant area. By bending toward the substrate, the anterior outer lip digitation propped the rostrum and aperture margin above the substrate. The anterior outer lip digitation also formed a callus pad at the substrate contact point and turned the remaining third (or more) of its length upward away from the substrate, making it, in effect, a sled runner with its forward point upturned to prevent digging into the surface over which it could slide. *Tessarolax* would have perched most of its shell and its aperture above the substrate in order to graze on its food source, which, based on studies of modern aporrhoids (Solsona et al., 2000), would have probably been benthic diatoms, decaying macroalgae, and other detritus.

The channels of the digitations of *Tessarolax* (Fig. 3) were kept open (not filled in by callus), perhaps in order to facilitate repairs or add a thicker callus coating. By its placement, the fictavarix supported the ablabral side of the shell, thereby stabilizing and maintaining a position for the aperture above the substrate. Abraded areas of shell are present only on the ventral side of shells where they would have contacted the substrate, such as the distal portion of posterior outer lip digitation, the ventral side of

callus knob on anterior outer lip digitation, the more ventralward surfaces of ablabral and apical calluses, and the fictavarix.

The arched digitations and callus buildups of *Tessarolax* appear capable of having positioned the body of the shell well above the substrate in a lifestyle different than that of both *Ceratosiphon* and *Pterocerella*, whose digitations were more likely to have “floated” the shell on a soft substrate.

The perched position suggests that *Tessarolax* would have lived distally enough to be out of strong currents and below wave base. This observation is compatible with Kollmann’s (2009) reporting that aporrhoids lived on the distal inner shelf to proximal outer shelf, as these environments would be below wave base. The fine-grained sediments that enclose specimens of *Tessarolax* reinforce this observation. In England, *Tessarolax retusa* is found in sandy and glauconitic sediments of the Lower Greensand Formation at the upper Aptian Upware locality and the lower Albian Folkestone locality. In Madagascar, *T. retusa* is also found in glauconitic sandstone in lower Albian rocks (Kiel, 2006). Glauconite is restricted mainly to sediments that accumulate in continental-shelf settings where there is low turbulence, low rate of sedimentation, and some organic matter (Beel and Goodell, 1967). In Mozambique, *Tessarolax* cf. *retusa* is found in dark brown sandy limestone in upper Albian rocks (Cox, 1925). In northern Japan, *T. gigantea* (Kase, 1984) is found in fine-grained sandstone interbedded between black shales, and *T. cf. ebrayi* (Kase, 1984) is found in dark gray sandy siltstone in upper Neocomian and upper Aptian strata.

On Vancouver Island and Gulf Islands, British Columbia, *Tessarolax* occurs with large scaphopods illustrated by Whiteaves (1879:134, pl. 16, figs. 10, 10a) as *Entalis cooperi* Gabb, 1864. This name, however, is based on specimens of Eocene age (Anderson and Hanna, 1935). When Anderson and Hanna (1935) described *Dentalium (Entalis) whiteavesi* Anderson and Hanna, 1935, from the Rosario Formation in Baja California, Mexico, they also stated that they were “renaming” Whiteaves’s Hornby and Vancouver Islands specimens of *Entalis cooperi*. In British Columbia and in Baja California, *Tessarolax* occurs in some abundance in fine-grained sandstone with *D. (E.) whiteavesi*. According to Keen (1971:883), modern scaphopods live mostly offshore away from areas of rigorous wave action. The occurrence of large scaphopods with *Tessarolax* suggests an offshore habitat of little turbidity.

The fact that post-Albian species of *Tessarolax* deposited thicker layers of callus over more and more of their shells would have provided defense (Saul, 1990) against durophagous predators such as crabs and especially predatory gastropods, whose drill holes are not found on *Tessarolax*. The development during the Campanian and Maastrichtian of substantial dorsal crests and a long dorsal spine also would have provided defense, especially against predaceous fish.

Other Cretaceous molluscan faunas found on the PSNA indicate that warm-temperate ocean conditions prevailed there during the Late Cretaceous (e.g., Saul and Squires, 2008:fig. 3). As mentioned above, *Tessarolax* preferred to live in outer sublittoral depths in calmer waters where muds and silts accumulated. The water temperature in these deeper depths would have been inherently slightly cooler than those in the shallower depths nearshore. *Tessarolax* lived at a depth where temperature differences were most likely “evened out”; thus, it is not the best indicator of paleotemperature of a specific region.

#### PALAEOBIOGEOGRAPHY OF *TESSAROLAX*

The global occurrences of the 19 species (16 known and three questionable) of *Tessarolax* (Table 1) are shown geographically

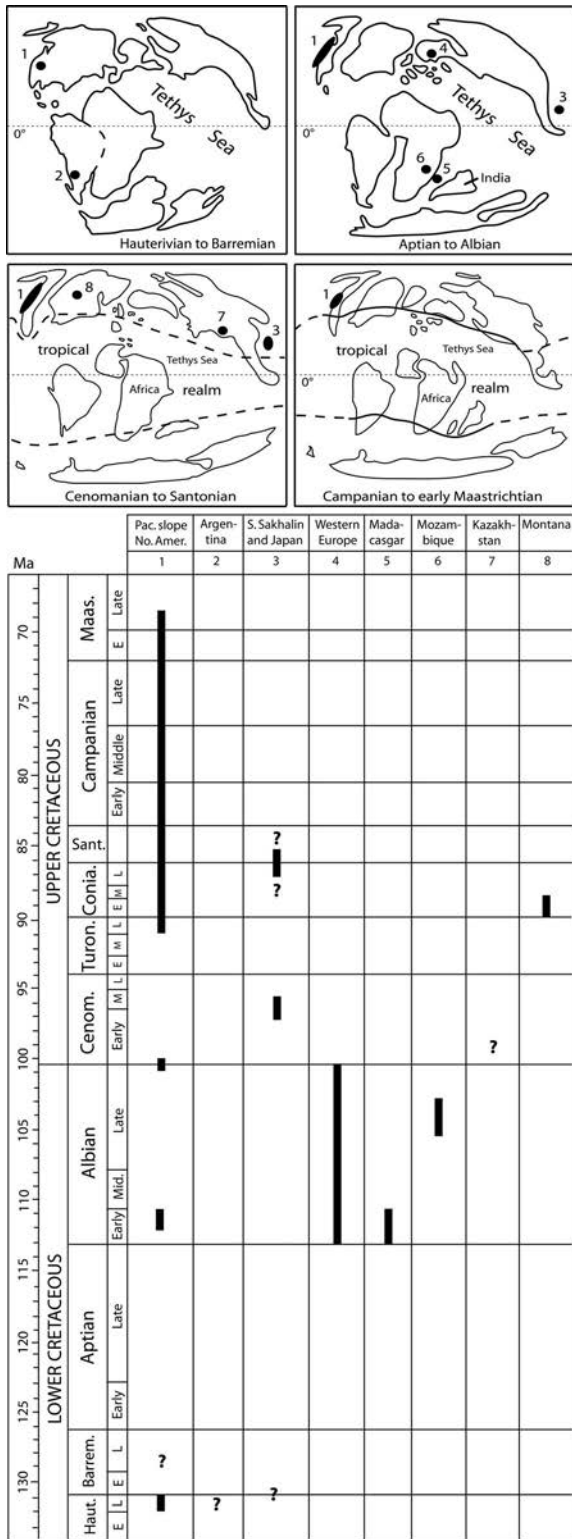


Figure 92 Global paleogeographic distribution and temporal occurrences of genus *Tessarolax* shown in order of first-appearance datum. Ages from Gradstein et al. (2012). Questionable occurrences shown by question marks. Maps modified from Smith et al. (1994). Heavy solid line shows tropical realm (after Kiel, 2002:fig. 2); heavy dashed line indicates imperfectly known tropical realm. Numbers at top of columns refer to geographic regions and sources of data: 1, this study. 2, Camacho (1953).

and temporally in Figure 92. The best control is the PSNA because there, the genus has its longest geologic range (approximately 60 million years) and is represented by 10 species. Elsewhere, the global record is sparse and represented by nine species, including the three questionable species. Western European Lower Cretaceous deposits, especially the finer-grained terrigenous deposits, provide a good record of *Tessarolax*, but *Tessarolax* spp. are largely lacking from chalk deposits of later Cretaceous age.

Based on available data, the Hauterivian was the time of origination and initial geographic dispersal of *Tessarolax*. The earliest confirmed occurrence of *Tessarolax* is the late Hauterivian *T. gabbi* from the PSNA. *Tessarolax? neuquensis* (Camacho) is of late Hauterivian age in west-central Argentina. *Tessarolax? gabbi* is of late Barremian age near the northern tip of Vancouver Island.

Except for *Tessarolax* cf. “*ebrayi*” (de Loriol) of Kase (1984) from upper Aptian deposits in Japan, there are no other records of Aptian *Tessarolax*. Based on ammonites, inoceramids, and microfossils, it seems that deposition along the PSNA during the Aptian was possibly either too deep or too shallow for *Tessarolax*. Also, Aptian outcrops are not extensive in the PSNA, and many of the available outcrops are complexly faulted and poorly studied.

Figure 92 shows the Albian to have been the time of widest distribution of *Tessarolax*. Albian-age *Tessarolax* are known mostly from western Europe, Mozambique, and Madagascar. The Albian record is based primarily on *T. retusa* (Sowerby in Fitton, 1836), which represents the most widespread species of *Tessarolax*. Most reports are from the middle to upper Albian Gault beds in England (Gardner, 1875b; Casey, 1961) and from Albian beds of similar lithology in France and western Switzerland (Kollmann, 2005). Kiel (2006) reported *T. retusa* from northwestern Madagascar. Cox (1925) reported it as *T. aff. retusa* from Mozambique. The latest Albian occurrence of *Tessarolax trinalis* is known from the PSNA.

Cenomanian and Turonian records of *Tessarolax* are sparse. The latest Albian to earliest Cenomanian *Tessarolax trinalis* occurs in the PSNA region from southern Alaska to northern California. There are questionable Cenomanian occurrences of *Tessarolax* in Japan and Kazakhstan. The late to early Coniacian Turonian *Tessarolax alaskana* n. sp. is known from southern Alaska to southern California and is the most widespread *Tessarolax* on the PSNA. The northernmost occurrence of this species is in the lower Matanuska Formation of southern Alaska [Area 1]. As discussed by Squires (2010:913), this formation is part of the Wrangelia-composite terrane complex that was probably located just off the coast of southern Canada during the deposition of this formation.

During the Coniacian and/or Santonian, *Tessarolax* was moderately widespread, with occurrences in the PSNA, the Western Interior basin of the United States, and the Japan region. In the first region, the genus is represented by the late Coniacian to Santonian *Tessarolax bullardi* n. sp., known from Vancouver Island to southern California. In the Western Interior basin, the genus is represented by *Tessarolax hitzii* White (1883:29–30), based on a mold from Fort Shaw, west of Great Falls, Cascade County, northwestern Montana. Sohl (1967:9) reported this

←  
3, Kase (1984); Maeda (1986). 4, Sowerby in Fitton (1836); Gardner, 1875b; Kollmann (2005). 5, Kiel (2006). 6, Cox (1925). 7, Plamadiala (1982). 8, White (1883); Sohl (1967, 1971).

species from the ammonite *Scaphites preventricosus* Zone, and Gradstein et al. (2012:fig. 27.6) reported this zone to be early Coniacian in age. *Tessarolax hitzii* is apparently the only North American *Tessarolax* known east of the PSNA. Sohl (1967, 1971) suggested that *Tessarolax* emigrated from Canada (no specimens known) into Montana. Then, according to him, the genus moved progressively southward in succeeding time intervals. It supposedly reached Colorado in the early Campanian and reached New Mexico in the middle Campanian. This scenario was based not only on *T. hitzii* but also on undescribed species of *Tessarolax* he was working on prior to his death.

*Tessarolax japonica* Yabe and Nagao (1928:94–95, pl. 17, figs. 9, 10) and *Tessarolax acutimarginata* Nagao (1932:42–43, pl. 6, figs. 10, 15) [= *T. cf. acuticalinatus* Nagao, 1939, spelling error for *T. acutimarginata*] are known from Upper Yezo Group strata in the Abeshinai River area of northern Hokkaido, Japan. The latter species is also known from the Kawakami area of southern Sakhalin Island, Far East Russia. The type material of both species is imperfect. Their type localities are not precisely known; hence, their geological age is uncertain. Hayami and Kase (1977:58, pl. 6, figs. 13a, 13b), who erroneously placed both species in genus *Aporrhais*, assigned them either a Coniacian or a Santonian age. Nagao (1932) mentioned that a southern Sakhalin specimen of *T. japonica* was found in rocks correlative to the *Schmidticerasmus schmidtii* zone. Based on magnetostratigraphy, this zone has been variously reported as being late Santonian in age (Verosub et al., 1989), late Santonian to earliest Campanian (Ward et al., 2012), early late Campanian (Yazykova, 2004), or latest Campanian (Kodama et al., 2000). We favor the Santonian age assignment because the specimens of *T. japonica* and *T. acutimarginata* have considerable callus coatings and overall morphology like that of *T. bullardi* of late Coniacian to late Santonian age.

Campanian and Maastrichtian *Tessarolax* are known with certainty only from the PSNA. This restricted distribution corresponds well with the temperate North Pacific Province shown by Kiel (2002:fig. 2) for the palaeogeographic reconstruction of Campanian-gastropod provinces. This temperate region was areally restricted in comparison to the very broad tropical realm, which includes the Tethys Sea (Fig. 92). The PSNA Campanian species and also those that straddle the Campanian/Maastrichtian boundary are mostly widespread, from Vancouver Island to the southern California region. The two exceptions are *Tessarolax grahami*, which is known only from Vancouver Island, and *T. incrustata*, which is known only from southern California and northern Baja California. The youngest known species of *Tessarolax* is the “mid” Maastrichtian *T. teleos*, which is known only from northern California.

## CONCLUSIONS

*Tessarolax* belongs to the subfamily Aporrhinae of family Aporrhaidae. *Tessarolax* is a separate genus from *Ceratosiphon*. Poorly preserved specimens of both genera have been commonly misidentified as one another, resulting in some taxonomic confusion.

There are 16 known and three questionable species of *Tessarolax*. *Tessarolax* was widely distributed prior to the Cenomanian but afterward was confined to just the Northern Hemisphere. The best record of *Tessarolax* is from the PSNA, where the genus has its longest geologic range (60 million years) and its best biostratigraphic control, namely, from the late Hauterivian to the middle part of the Maastrichtian. Of the 10 PSNA species, five are new and are described herein. Specimens of these 10 species occur at relatively few localities in small

numbers. *Tessarolax gabbi* n. name, from northern California and the northern tip of Vancouver Island, is the earliest known *Tessarolax*, and *T. teleos* n. sp., from central California is the youngest known *Tessarolax*. Some of the specimens from the Vancouver Island area and from northern Baja California are remarkably nearly complete. Other species of *Tessarolax* (including questionable *Tessarolax*?) are known sparsely from west-central Argentina, western Europe, Mozambique, Madagascar, Kazakhstan, the northern Japan region, and Montana. The Albian *Tessarolax retusa* (J. de Sowerby in Fitton, 1836) was the most globally widespread of any *Tessarolax* species. In the PSNA region, *Tessarolax trinalis* and *T. alaskana* n. sp. have been found as far north as southern Alaska, but the Alaskan material has undergone postdepositional transport.

Among all species, immature *Tessarolax* are very similar looking. They lacked digitations and were infaunal. Mature *Tessarolax* were epifaunal and possessed four long, curving outer lip digitations. Evolution of mature *Tessarolax* included development of dorsal crests and a dorsal spine, adding encrusting callus coating and a callus knob on the anterior outer lip digitation, and development and subsequent modification of a fictavarix (new term, in reference to the flangiform-callus deposit along the ablabral side of the shell). The geologically older PSNA *Tessarolax* spp. have less callus. There is none dorsally on *T. gabbi*, very thin and incomplete callus dorsally on *T. trinalis* and *T. alaskana*, more complete on *T. bullardi*, complete and thick enough to cover original spiral ornamentation on *T. distorta* and *T. louellae*, and the thickest, most complete callus coat on *T. incrustata*. Sculpture otherwise remained modest, with either a bicarinate or a tricarinate last whorl.

The fictavarix first appeared during the Albian (i.e., coincident with *T. retusa* in England); the dorsal sculpture appeared during the late Coniacian to early Campanian (i.e., coincident with *T. bullardi*), as did the adding of more callus (including the callus knob). The digitations, fictavarix, and callus knob on the anterior outer lip digitation supported, in a perched position, the *Tessarolax* shell above the substrate and provided space for mobility of the foot and for food gathering. The PSNA species preferred the slightly cooler offshore (outer sublittoral) depths of warm-temperate waters where fine-grained siliciclastics accumulated. The occurrence of *Tessarolax* in this area appears to be linked as much to temperate waters as to offshore terrigenous substrates. *Tessarolax* in other parts of the world seemed to prefer fine-grained sandy and glauconitic sediments.

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