**PACIFIC SLOPE OF NORTH AMERICA RECORD OF THE CRETACEOUS APORRHAIID GASTROPOD TESSAROLAX: EVOLUTIONARY TRENDS, MODE OF LIFE, AND PALEOBIOGEOGRAPHY OF THE GENUS**

**LOUELLA R. SAUL** and **RICHARD L. SQUIRES**

**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 southern Baja California, Mexico. Its longest geographic range (late Hettnerian 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; *T. bollardi*, middle Coniacian to early Campanian; *T. grahami*, early Campanian; *T. louellae*, middle Coniacian; and *T. 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) siliclastics, where warm-temperate waters were deeper/calmer and slightly cooler relative to more nearshore environments. *Tessarolax* gabbii new name is provided for *Heliculina bicarinata* Gabb, 1869, a junior secondary homonym of *T. bicarinata* (Deshayes in Leymerie, 1842). *T. gabbii* is the oldest recognized species. Although the pre-Albian global record of *Tessarolax* is sparse, the genus was most widespread during the Albion, 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. *T. 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 aporrhaid genera does not apply to the Jurassic and Cretaceous, during which they were geographically more widespread (Korotkov, 1992; Kiel, 2002). Aporrhaid genera 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 aporrhaid species 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 *Cathpholesium* Pfeiffer, 1876.

One of the more distinctive Cretaceous aporrhaid genera is *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 aoporrhaid 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...
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, which is devoted to strombid gastropods, proved to be a very useful research tool because it provided critical information about taxonomy and morphology of fossil aporrhaid 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 midway on a carina of some species. Gabb (1864:1126) 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, angly ventrally, flangeform-callus deposit along the abacterial 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 bicornata 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 Piettea Cossmann, 1904 [e.g., Piettea cretacea Kase in Kase and Maseda, 1980].

ABBREVIATIONS

Locality and/or catalog numbers

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<td>ANSP</td>
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<td>(collections now housed at UCMP)</td>
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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 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.

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

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<tr>
<th>Species</th>
<th>Location</th>
<th>Age</th>
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<tr>
<td><em>T. gahbi</em> n. nom.</td>
<td>Late Hauterivian to late Barremian</td>
<td>Vancouver Island to northern California</td>
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<tr>
<td><em>T. nequina</em> Camacho, 1953</td>
<td>Late Hauterivian</td>
<td>West-central Argentina</td>
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<tr>
<td><em>T. gigantea</em> (Kase, 1984)</td>
<td>Late Aptian</td>
<td>Northern Japan</td>
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<tr>
<td><em>T. cf. “ehlersi”</em> (de Loriol) of Kase (1984)</td>
<td>Late Albian</td>
<td>Northern Japan</td>
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<tr>
<td><em>T. aff. trinalis</em> Murphy and Rodda, 1960</td>
<td>Late Albian to early Cenomanian</td>
<td>Northern Kazakhstan</td>
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<tr>
<td><em>T. retusa</em> Sowerby in Litton, 1836</td>
<td>Early Cenomanian</td>
<td>Northern Japan</td>
</tr>
<tr>
<td><em>T. trinalis</em> Murphy and Rodda, 1960</td>
<td>Mid-Cenomanian</td>
<td>Southeastern Alaska to southern California</td>
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<tr>
<td><em>T. distorta</em> Gabb, 1864</td>
<td>Late Turonian to early Coniacian</td>
<td>Northern Japan, Sakhalin Island, Russia</td>
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<tr>
<td><em>T. incrustata</em> Anderson and Hanna, 1935</td>
<td>Coniacian</td>
<td>Vancouver Island to southern California</td>
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<tr>
<td><em>T. huttoni</em> White, 1883</td>
<td>Coniacian</td>
<td>California to northern Baja</td>
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<tr>
<td><em>T. japontica</em> Yabe and Nagao, 1928</td>
<td>Coniacian</td>
<td>Vancouver Island</td>
</tr>
<tr>
<td><em>T. acutimarginata</em> Nagao, 1932</td>
<td>Coniacian or Santonian</td>
<td>Northern California</td>
</tr>
<tr>
<td><em>T. biullardi</em> n. sp.</td>
<td>Coniacian or Santonian</td>
<td>Northern California</td>
</tr>
<tr>
<td><em>T. bitzii</em> White, 1883</td>
<td>Late Albian</td>
<td>Northern California, Sakhalin Island, Russia</td>
</tr>
<tr>
<td><em>T. grabanu</em> n. sp.</td>
<td>Late Albian to early Cenomanian</td>
<td>Vancouver Island to southern California</td>
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<tr>
<td><em>T. distorta</em> Gabb, 1864</td>
<td>Early Cenomanian</td>
<td>Vancouver Island to southern California</td>
</tr>
<tr>
<td><em>T. insculpta</em> Anderson and Hanna, 1935</td>
<td>Early Campanian</td>
<td>Canada to northern Baja</td>
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<tr>
<td><em>T. alaskana</em> n. sp.</td>
<td>Early Campanian</td>
<td>Vancouver Island</td>
</tr>
<tr>
<td><em>T. loiiellae</em> n. sp.</td>
<td>Middle late Campanian</td>
<td>Northern California</td>
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<tr>
<td><em>T. teleos</em> n. sp.</td>
<td>Latest Campanian to early Maastrichtian</td>
<td>Northern California</td>
</tr>
<tr>
<td><em>T. gahbi</em> n. nom.</td>
<td>“Mid” Maastrichtian</td>
<td>&quot;Mid” Maastrichtian</td>
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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 Pquoi Formation, upper lower to lower upper Maastrichtian.

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., Popoeno, 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 Kolen, 1889; Pterocerclidae Bandel, 2007; and Pugnellidae Kiel and Bandel, 1999 (including its subfamily, Tunderrandae Bandel, 2007).

Bandel (2007) referred Jurassic stromboideans to “Alariidae” Kolen (1889), but, as noted by Bouchet and Rocroi (2005:22) and by Kollmann (2009:49), Alarta of Morris and Lycett, 1850, is a junior primary homonym of both Alarta Schrank, 1788 (a parasitic flatworm), and of Alarta Duncan, 1801 (a flower moth), and is thus unavailable in Gastropoda. Bouchet and Rocroi (2005) have indicated Athrogoninae Popoeno (1983) [“Alariidae” Kolen, 1889] and Dicroloaminae Korotkov, 1992, and that Athrogonia 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 stromboids and aporrhaids 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 aporrhaids developed diverse forms of outer lips, which have been used to infer phylogenetic relationships among aporrhaids. 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 Tessoralax in Aporrhaidae but suggest that Tessoralax is closer to Dicroloa Gabb, 1868, than to Phylochelites Gabb, 1868.

Kiel and Bandel (1999) proposed Pugnellidae for nine genera previously assigned to Aporrhaidae or Stromboidea and indicated that Tessoralax; Ceratosiphon Gill, 1870; Tindora Stephenson, 1941; and Lispesthede White, 1877, might, with further study, also be included in Pugnellidae. They noted, however, that Tessoralax 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, 1830

**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 aporhaid subfamily Pterocerellinae Bandel, 2007, to which Bandel (2007) and Kollmann (2009) assigned *Tessarolax* based mainly on the presence of a callus coat. In pugnelline 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 Pugnellininae. 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 predecessor 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 whors, _Dicroloma_ lacks the posterior outer lip digitation of _Tessarolax_.

_Genus Tessarolax_ Gabb, 1864

[= _Ornithopus_ Gardner, 1875a, not Hitchcock, 1848, a reptile].


**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 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 carina 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 _T. 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 Folkstone, 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 aporrhais (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, 7), 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.

Blagovetshensky and Shumilkin (2006:39) placed Tessarolax retusa (J. de Sowerby in Fitton) in genus Trilemma Blagovetshensky 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 Blagovetshensky 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 fivactavix) is actually not truly opposite the outer lip. The fivactavix on Tessarolax leans “forward” so that its outer margin and the forward bending of the outer lip rest on the substrata. 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 Protobohemichnos pusquenis 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 Protobohemichnos a junior subjective synonym of Tessarolax. The overall shape of Protobohemichnos pusquenis is somewhat similar to Dicroloma zelandica Marshall (1919:228, pl. 15, fig. 16), but P. pusquensis 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 Hemichnophora 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 Albain 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 Albain 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) actimumarginatus [sic] (Nagao, 1932) from the Bibai area, Hokkaido, northern Japan. Maeda (1986) misspelled the species name, which should read actimumarginata. Maeda’s specimens are associated with the ammonite Desmoscera (Pseudouhligella) japonicum (Yabe), which, according to Matsumoto (1959:39), 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. actimumarginata Nagao, illustrated by Hayami and Kase (1977:pl. 6, fig. 14b). We believe that Maeda’s specimens represent Tessarolax sp. but are not Tessarolax actimumarginata (Nagao, 1932:pl. 6, figs. 14a, b), which is of Comanian or Santonian in age.

Aporrhais ebrayii Plamadalia (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 Plamadalia’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 Tundora and Tundora in Aporrhais. 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 fivactavix, 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 Roding, 1798.

The geologic range of Ceratosiphon moreausiana is contradic-torily 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. moreaiisiana*. 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. moreaiisiana*, *Ceratosiphoii* is not a synonym of *Tessarolax*.

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

*Pterocera beckettii* Mantell (1851:443, ligg. 40) from Atherfield, England, has priority over Gardner's *A. moreaiisiana* (d'Orbigny), and thus *Aporrhais gardneri* Pchelnistev (1927:298, unfig.), also from Atherfield, is a junior synonym. Name-wise, Pchelnistev'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 *Ceratosiphoii moreaiisiana* (d'Orbigny) and *Ceratosiphoii beckettii* (Mantell) are placed in *Ceratosiphoii* because they have long digitations with flanges (i.e., thin calcified "membranes") and can have additional rostral digitations. Flanges consisting of thin calcified "membranes" on digitations, as in Gardner's (1875b) figures of *Ceratosiphoii moreaiisiana* (pl. 7, fig. 3) and *C. fittioni* (pl. 7, fig. 4), are characteristic of *Ceratosiphoii*.

Blagovetshenskiy and Shumilkin (2006:39) assigned "*Tessarolax moreaiisiana* (d'Orbigny)" and "*Tessarolax ebrayi* (de Loric)" to their new genus *Trilemma*. Neither species appears to resemble *Aporrhais striato carinatus* Sznov, 1880, the type species of *Trilemma*. Based on discussions in the present article, both species cited by Blagovetshenskiy and Shumilkin (2006) belong to *Ceratosiphoii*.

Kollmann (2005, 2009) agreed with Bandel (2007) that *Ceratosiphoii* belongs in Pterocerellinae Bandel, 2007, but Kollmann (2009) disagreed with Bandel (2007) and reported that *Tessarolax* and *Ceratosiphoii* are separate genera, belonging in different subfamilies, and we agree. *Ceratosiphoii* 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 *Ceratosiphoii* by having only four, shorter, unbranched, and "unflanged" calcarulate 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 spine, 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 *Ceratosiphoii*.

*Tessarolax*, furthermore, occurs in both the Old World and the New World, whereas *Ceratosiphoii* is known only from the Old World and the Orient.

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

"*Ceratosiphoii* 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-channel 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 *Ceratosiphoii*. 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? giganteus* (Kase).

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

*Aporrhais (Tessarolax) antarctica* Cox (1953:6, pl. 2, figs. 9-11) from Aptian deposits on Alexander 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 side 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. acuticalinatus* (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 arraloorenis* Stolizcka (1867:28, pl. 2, figs. 2, 2a) from the Senonian Arraloid Group of southern India was placed by Coissmann (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*. 
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.

Sitrculites (uncertainly assigned to Tessarolax by Stewart (1927:365-366, pi. 23, fig. 2), was reported from the “Martinez Group” near Martinez, Contra Costa County, California, by Gabb (1869), Stanton (1895:364-365, pi. 23, fig. 6), and Anderson, 1938:64, 134; Imlay, 1960:180. Not Rostellaria retusa J. de Sowerby in Fitton, 1836:344, pi. 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 abalabral 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. 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)
Tessarolax sp., aff. T. trinalis Murphy and Rodda, 1960
Figures 14, 15

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 whors are generally uncinurate with several intercalated weak spiral ribs. Immature-stage last whorl with seven widely spaced spiral ribs; posteriorior rib weakest, next three are of nearly equal strength (posterioriormost 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, Brewericeras bulenense 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 later immature individual consisting of five whors. The specimens are too immature to have digitations or callus, and they differ from juveniles of T. gabbii in being
Tessarolax trinalis Murphy and Rodda, 1960
Figures 16–21

Tessarolax trinalis Murphy and Rodda, 1960:842, pi. 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 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.

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 adapically from neck toward tip of spire. Fictavari.x incipient and coincident with bulge of callus near apertural edge of ventral-glaze callus.

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, Desmoeceras (Psehodugbligella) dasseni 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 flanged-form.

DESCRIPTION. Shell up to 39 mm high and 20 mm wide (missing digitations). Pleuroconch unknown. Teleoconch consisting of at least five whorls (tip missing). Suture slightly impressed. Immature shell: Turriculate, consisting of approximately four whorls, early spire whorls uncarinate and finely ribbed; later spire whors 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 thick, expanded into four canaliculate 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 Talkeetna 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] Matanuksa Formation, lower part, Hicks Creek, southeastern Talkeetna 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 Subprionocyclocus 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 whors (tip missing). Suture and immature shell callused over. Immature shell: Turriculate, consisting of four whors, early spire whors unicarinate and finely ribbed. Mature shell: Consisting of last whorl, bicarinate, with carinae noded and parallel. Single mid-ril 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 canaliculate 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.EH1201.001.002, loc. 12, near Chemainus, Nanaimo, Vancouver Island, British Columbia [Area 12].

PARATYPES. GSC 5791 [specimen labeled by Whiave's (1879:123) as “unfig'd. hypotype” from Trent River, “below the
Tessarolax grahami 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 unincarnate and finely ribbed. Mature shell: Consisting of last whorl, bicarinate, carinate subparallel and without nodes; posterior carina weakest and thin; anterior carina near center or dorum with several (commonly three) short spines (middle one longest) that form high crest on thin, approximately five whorls, early spire whorls unicarinate and finely sculpted. 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 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;
somewhat knob-shaped, extending ventrally to support abradial 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] question-able 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 communica-tion, 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 contemporaneous sandstone. The Northwest Bay section is late early Campanian in age, based on the concurrent ranges of the bivalve Yaadia tryoniana (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 fichtavix that also projects farther than the fichtavix in *T. bullardi*, and a weaker posterior carina on the last whorl. The fichtavix on *T. grahami* is narrow and knob-shaped, similar to that of *T. distorta*, but on *T. grahami* the fichtavix is commonly longer.

Whereas *T. distorta* has a dorsal spine, *Tessarolax grahami* has a more flange-like dorsal expansion on the anterior carina. In *T. distorta*, the two carinae are commonly noticeably closer together at the base of the dorsal spine.
small, narrow, ear-shaped with sulcus on dorsal side, ultimately extending somewhat laterally perpendicular to shell surface.

**HOLOTYPE.** UCMP 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 CAM- PANOIAN: [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...
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 factavarix of T. distorta does not coalesce with the ablabral callus and differs from T. lonellae in lacking the anteriorward extension of the ablabral flange anterior of the anterior carina.

**Tessarolax lonellae** 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 factavarix 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 whors. 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 canalicate 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 factavarix. Growth line opisthocline.

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**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 incrustedata** Anderson and Hanna, 1935

Figures 3, 72-84

**Tessarolax incrustedata** 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.

**DIAGNOSIS.** Mature last whorl biconcave, dorsal spine prominent; callus extensive over entire shell with digitations thickly callused; factavarix flange shaped and extending ventrally to form broad stabilizer.
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 teleconch 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 biconcave, with carinae nodded, carina on shoulder strongest. Suture calloused over. Aperture moderately wide. Outer lip expanded into four long and curving canaliculate 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 embosses. Rostrum 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 ablabrally; 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 glassy 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. Abalabal-callus process either slightly set off from ventral callus by indentations or merging with it to form thin, flange-shaped fictavarium 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 K6/b1 [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 Panche Formation [Uhalde Formation], Salt Creek, Merced County, northern California; [Area 30] upper Panche 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; [Area 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, centralCalifornia.

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

Poorly preserved specimens of T.? incrusta 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 Pancho-Moreno contact” and of latest Campanian or
earliest Maastrichtian age. Poorly preserved specimens of T.
? incrusta 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


DIAGNOSIS. Mature last whorl wide and bicarinata; 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, bicarinata
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
bicarinata. 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].

GEOL OGY. “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 minten-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.
incrusta, but T. teleos differs in having its carinae closer
together and an apaxalward-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 uncarinate 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
gabbi 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 abalabral callus deposit but
no fictavarix. During the Albion, 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 Albion through early
Coniacian species have a fictavarix (or incipient fictavarix),
they lack a large dorsal callus structure. An Albion-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 Albion Tessarolax retusa in
Gardner (1875b) show neither a fictavarix nor dorsal incrusteration
of the spire, but a well-developed fictavarix is present on the
western European Albion species of “Pterocea” bicarinata
D’Orbigny (1843:pl. 208, figs. 3–5) [reprinted by Kollmann
(2005:132) as Ceratosiphon retusa]. The PSNA specimens of T.
trinalis (latest Albion to middle Conenomanian 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 Albion age is fully
mature, and none shows a well-developed fictavarix such as that on
“Pterocea” 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
lateral flangiform.
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. grabami) and eventually to a longer dorsal spine (e.g., T. distorta, T. lottellae, and T. incrustata). Also during this interval, the callus coating remained overall thin (very thin on T. bullardi but somewhat thicker on T. grabami), 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 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 abdalbral side as the shell perched above the substrate by means of the anchoring digitations and by means of the abdalbral-callus deposits. The fictavarix on T. distorta was ear-shaped, not coalescing with the abdalbral callus.

During the latest Campanian and into the Maastrichtian, there was extensive callus over the entire shell, and the abdalbral 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 (Saül, 1989). *Tessarolax mcristata*, 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 aperrhaid animals (see Solsona et al., 2000; pl. 1) in consisting of three smooth whors. It is likely that modern aperrhaid animals have planktotrophic larval development; thus, they have a high capacity for geographical dispersion (Thiriot-Quievreux, 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 turriculated and without an expanded outer lip and therefore are like modern immature aperrhaid animals (see Barnes and Bagenal, 1952; Perron, 1978b). As the outer lip is gradually developed during growth, modern aperrhaid animals live a shallow-burrowing mode of life and tend to live near the surface (Barnes and Bagenal, 1952). It seems doubtful 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 aperrhaid animals (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 abdalbral 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 abdalbral and apical calluses, and the fictavarix.

The arched digitations and callus buildup of *Tessarolax* appear capable of having positioned the body of the shell well above the substrate in a lifestyle different than that of both *Ceratostomphal* and *Pterocoevela*, 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 aperrhaid animals 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 Folkstone 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 fine-grained sandstone interbedded between black shales, and *T. cf. ebrayi* (Kiel, 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 Eocenian 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 *Horny* 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 (1971:833), 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 (Saül, 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., Saül 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.

**PALEOBIogeography of Tessarolax**

The global occurrences of the 19 species (16 known and three questionable) of *Tessarolax* (Table 1) are shown geographically
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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); 3, Kase (1984); 4, Sowerby in Fitton (1836); 5, Gardner, 1875b; Kollmann (2005); 6, Kiel (2006); 7, Cox (1925); 8, Plamadiala (1982). 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).

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. gahbi* from the PSNA. *Tessarolax*? *neuguenensis* (Camacho) is of late Hauterivian age in west-central Argentina. *Tessarolax*? *gahbi* 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 Aptian 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 *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 *Tessarolax hillardi* 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
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 Schmiditerranum *schmidttii* 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 gahbi* 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 *Tessarolaxi*) 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 callus coating (new term, in reference to the flangiform-callus deposit along the abradial side of the shell). The geologically older PSNA *Tessarolax* spp. have less callus. There is none dorsally on *T. gahbi*, 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. lonelae*, and the thickest, most complete callus coat on *T. incrustata*. Sculpture otherwise remained modest, with either a bicarinare or a tricarinare last whorl.

The *callus* first appeared during the Albian (i.e., coincident with *T. retusa* in England); the dorsal sculpture appeared during the late Coniacian to early Maastrichtian (i.e., coincident with *T. bullardi*), as did the adding of more callus (including the callus knob). The digitations, *callus*, 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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