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New Late Cretaceous Epitoniid and Zygopleurid Gastropods from the Pacific Slope of North America

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Abstract. Seventeen species of epitoniid gastropods are discussed from Upper Cretaceous shallow-marine rocks in British Columbia, California, and northern Baja California. Eleven of the species are new: *Opalia* ***atra,*** *Opalia* ***cavea,*** *Amaea* ***trifolia,*** *Amaea* ***cerva,*** *Amaea* ***pentzia,*** *Belliscala* ***petra,*** *Belliscala* ***meta,*** *Acirsa* ***alpha,*** *Acirsa* ***beta,*** *Acirsa* ***delta,*** and *Acirsa* ***epsilon.*** The genera *Amaea, Belliscala,* and *Acirsa* have not been previously reported from Cretaceous rocks in this region. Generic assignment, age, and distribution of *Opalia*? *mathewsonii* (Gabb, 1864), *Belliscala suciense* (Whiteaves, 1879), *Acirsa obtusa* (White, 1889), *Acirsa nexilia* (White, 1889), and *Confusiscala newcombii* (Whiteaves, 1903) are discussed. *Claviscala* sp. is recognized, and it represents the first confirmed Late Cretaceous occurrence of this genus in this region.

The very rare and large ***Zebalia*** n. gen. *suciensis* (Packard, 1922), from Upper Cretaceous rocks in Washington and southern California, is an epitoniid-like zygopleurid gastropod and the first Late Cretaceous record of zygopleurids.

INTRODUCTION

As far as we know, this is the first paleontologic study anywhere in the world that has focused on Late Cretaceous epitoniid gastropods. It is certainly the first detailed study of Late Cretaceous epitoniid gastropods from shallow-marine rocks in a region extending from Vancouver Island, British Columbia, Canada, to northern Baja California, Mexico (Figure 1). The only other study devoted entirely to epitoniids from this region is Durham's (1937) study of Mesozoic and Cenozoic species, with an emphasis on the latter. He listed only five Mesozoic epitoniid taxa, two of Early Cretaceous age and three of Late Cretaceous age. Studies by Saul & Popenoe (1993) and by us indicate that of these five, only two are unequivocal epitoniids: *Opalia* (*Confusiscala*) *mathewsonii* (Gabb, 1864) and *Opalia* (*Confusiscala*) *mathewsonii* (Gabb)?. The former is herein identified as *Opalia*? *mathewsonii,* and the latter is the same as *Confusiscala*? *sulfurea* Saul & Popenoe, 1993.

Over the last few years, while examining the collections of Late Cretaceous fossils at the Natural History Museum of Los Angeles County, we detected 11 new species of epitoniids and a new genus of an epitoniid-like zygopleurid gastropod, formerly known as "*Cerithium*" *suciaensis* Packard, 1922. Also included in this paper is a restudy of the poorly known *Opalia*? *mathewsonii* Gabb, 1864, as well as the description augmentation, generic reassignment, and biostratigraphic analyses of the following four other previously named species of Late Cretaceous epitoniids from the study area: *Cerithium lallierianum,* var. *suciense* Whiteaves, 1879; *Mesalia obtusa* White, 1889; *Ceratia nexilia* White, 1889; and *Mesostoma newcombii* Whiteaves, 1903. *Cirsotrema tenuisculptum* Whiteaves, 1879, is not an epitoniid. The chronostratigraphic positions of the new and restudied taxa are shown in Figure 2. Most of these taxa occur between the Santonian and late Campanian, and this peak in epitoniid diversity is coincident with a cooling of the waters in this region when warm-temperate seas were the norm, relative to the warmer seas of the Turonian and the Maastrichtian (Saul, 1986).

Much of this present study stems from collections made by Saul (1959) in the Chico Formation of northern California. Her detailed stratigraphic locality data have made it possible to sort out and arrange chronologically, similar faunas of different ages. In addition, collections of epitoniids made by various collectors from the Chatsworth Formation of southern California are also very valuable.

The family Epitoniidae Berry, 1910, is a group of marine gastropods popularly referred to as "wentletraps." It is a relatively large family with more than 600 Recent species and an additional 300 or 400 fossil species. Epitoniids can be found worldwide, from the intertidal zone

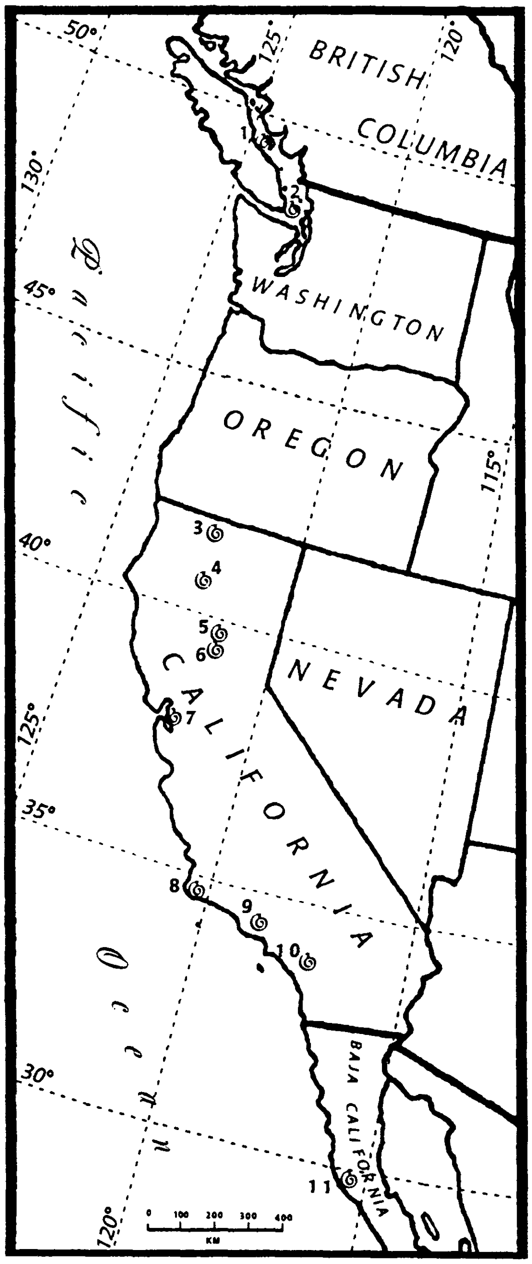


Figure 1. Index map of the study area's geographic place names mentioned in text. 1 = Hornby Island. 2 = Sucia Island. 3 = Yreka area. 4 = East of Redding. 5 = Chico Creek. 6 = Pentz. 7 = Martinez. 8 = Jalama Creek. 9. = Simi Hills. 10. = Santa Ana Mountains. 11. = Arroyo Santa Catarina.

to deep water but are rare in the abyssal zone (> 6000 m depth). They are particularly common in shallow, warm waters of the continental shelf. Some epitoniids have planktotrophic larval stages (Bouchet & Warén, 1986), hence wide dispersal. Members of the family are predators or parasites on sea anemones or corals (Bouchet & Waren, 1986; Weil et al., 1999), and most epitoniid species seem to be loosely associated with their prey or host species (Bouchet & Warén, 1986).

According to Cossmann (1912), the earliest known epitoniid is the Middle Jurassic (Bathonian) *Proacirsa inornata* (Terquem & Jourdy, 1869; Wenz, 1940:fig. 2290) from Lorraine, France. According to Clench & Turner (1950), the greatest generic/subgeneric diversities of epitoniids took place during the Eocene and Miocene. On the Pacific slope of North America, however, the greatest generic/subgeneric diversities were during the Oligocene (Durham, 1937:481–483) and Pliocene (DuShane, 1979: 95), with seven genera/subgenera during both times. In comparison, during the Eocene and Miocene in this region, there were three and six genera/subgenera, respectively (Durham, 1937:481–483). The greatest generic diversity of Cretaceous epitoniids from the Pacific slope of North America was during the early to middle Campanian, with six genera present (Figure 2). On a worldwide scale, it is very difficult to assess Cretaceous epitoniid generic diversity because many of the specimens illustrated in the literature do not show the critical views of the aperture and basal part of the last whorl. In addition, diversity studies are difficult because early workers used very broadly defined generic names (e.g., *Scala* Bruguière, 1792; *Scalaria* Lamarck, 1801) that have been replaced by a multitude of other generic names. Very few modern workers have attempted to do additional collecting and restudy of these faunas.

The higher classification system used here follows that of Bandel (1991). Abbreviations used for catalog and locality numbers are: ANSP, Academy of Natural Sciences, Philadelphia; GSC, Geological Survey of Canada, Ottawa, Ontario; CIT, California Institute of Technology, Pasadena [collections now housed at LACMIP]; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP, University of California, Museum of Paleontology, Berkeley; USGS, United States Geological Survey, Menlo Park [collections now housed at UCMP]; USNM, United States National Museum, Washington, D. C.

STRATIGRAPHY

The geologic ages of most of the formations/members cited in this paper have been summarized by Saul (1982), Haggart & Ward (1984), and Squires & Saul (2001, 2003). Cited literature in these papers includes relevant information on lithostratigraphy and depositional environments. Stratigraphic information mentioned below concerns either those rock units not discussed in recent literature or additional pertinent biostratigraphic details.

Osburger Gulch Sandstone Member of Hornbrook Formation

This Cenomanian to lower Coniacian member crops out in northern California and southwestern Oregon and

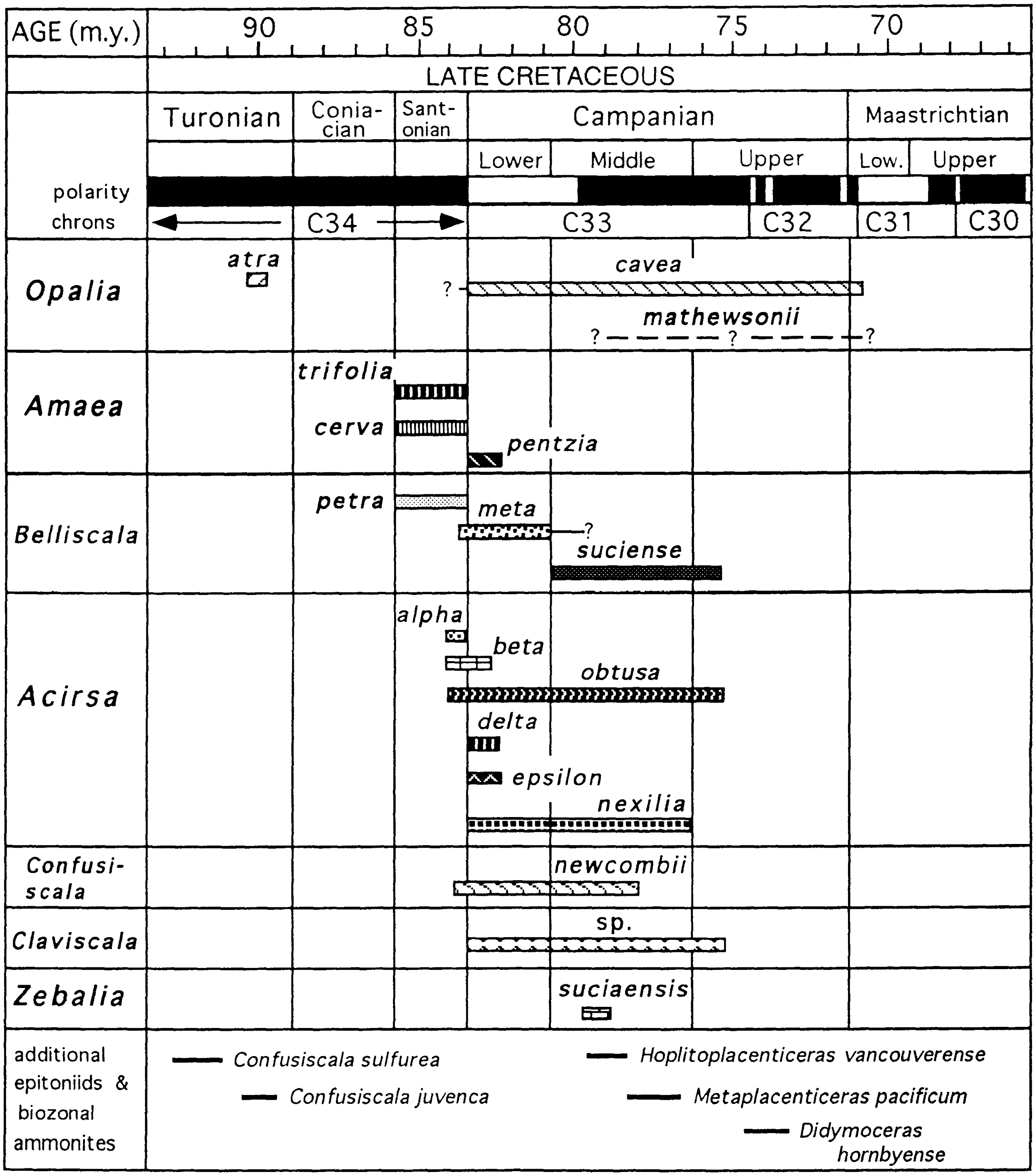


Figure 2. Chronostratigraphic positions of the new and restudied Late Cretaceous epitoniid and zygopleurid gastropods from the Pacific slope of North America. Geologic ages, polarities, and chrons after Gradstein et al. (1994). Ammonite biozones after Matsumoto (1959, 1960) and Elder & Saul (1996).

is primarily a high-energy nearshore deposit containing abundant molluscan fossils (Nilsen, 1984). The type locality of *Opalia* ***atra*** is in this member in the Yreka area (Figure 1), and this locality has also yielded the gastropods *Carota dilleri* (White, 1889) and *Turritella hearni* Merriam, 1941. The former is indicative of the early to late Turonian (Saul & Popenoe, 1993), and the latter is indicative of the late Turonian to possibly early Coniacian (Saul, 1982). Based on the overlapping geologic ranges of these two species, the age of the type locality beds of *O.* ***atra*** is late Turonian.

Redding Formation

This formation crops out east of Redding, Shasta County, northern California (Figure 1) and consists of several shallow-marine members deposited during the Turonian to Santonian stages. The members that concern this paper are Members V and VI of Popenoe (1943). These members were also utilized by Murphy et al. (1957), Matsumoto (1959, 1960), and Trujillo (1960), with some modification of outcrop distribution of members V and VI by Murphy et al. (1957:pl. 3) and Matsumoto (1960:fig. 2). Haggart (1986) named Members IV to V, but his units do not directly correspond to those of Popenoe. Haggart included in his Hooten Gulch Mudstone Member the mudstones of Members IV and VI. The thick conglomerate at the base of Member V along Oak Run, Haggart referred to his Oak Run Conglomerate Member, but he did not discuss his concept of the stratigraphic equivalency of the remaining part of Member V. Conversion of Popenoe's (1943) version of the Redding Formation stratigraphy to Haggart's version would require a more detailed map than available in Haggart (1986: fig. 4) and a detailed integration of previous workers' biostratigraphic data.

All the specimens of *Amaea* ***trifolia*** sp. nov. and *Belliscala* ***petra*** sp. nov., as well as those specimens of *Amaea* ***cerva*** sp. nov. from east of Redding, were collected by Popenoe, and the recorded locality descriptions reflect his view of the stratigraphy. The first two of these species are both present in Members V and VI, and the localities (LACMIP 10794 and 24217 for both, as well as 24246 for *B.* ***petra***) they were found at correspond to the Santonian (Popenoe et al., 1987; Popenoe & Saul, 1987; Saul, 1988; Saul & Popenoe, 1992). Most of the specimens of *Amaea* ***cerva*** are of late Santonian age and from the upper part of the Musty Buck Member of the Chico Formation, but a few specimens are from LACMIP loc. 10786 in Member V (lower part), and the rocks at this locality are of early Santonian age (Saul, 1988).

"Trent River Formation"

This broad stratigraphic unit is equivalent to several formations that crop out along the eastern side of Vancouver Island from Hornby Island, British Columbia, on the north, to Sucia Island, Washington, on the south (Mustard, 1994). These formations, which include the Haslam, Extension, Pender, Protection, and Cedar District, range in age from Santonian to middle Campanian (Haggart, 1991).

Ten Mile Member of Chico Formation

The stratigraphically highest strata of the Chico Formation exposed along Big Chico and Butte creeks, Butte County, northern California (Figure 1) constitute the Ten Mile Member of Saul (1959, 1961), which was formalized by Haggart & Ward (1984). This silty sandstone member ranges in age from Santonian to early Campanian, and epitoniids are from the part recognized by Saul (1959) to be of early Campanian age. The member is quite fossiliferous, and on the basis of mollusks, the maximum-water depth of the member was 90 m (Saul, 1961).

Spray Formation

This formation, which was named by Usher (1952) for thin-bedded shale and sandstone outcrops on Hornby Island, east coast of Vancouver Island, British Columbia, is a sparsely fossiliferous, outer shelf to upper slope deposit (Haggart, 1991). Muller & Jeletzky (1970) subdivided the formation into a lower part, correlative to the ammonite *Metaplacenticeras pacificum* biozone, and an upper part, correlative to the ammonite *Didymoceras hornbyense* biozone. In modern usage, the *M. pacificum* biozone is equivalent to the upper middle Campanian to lower upper Campanian, and the *D. hornbyense* biozone is equivalent to the middle upper Campanian (Figure 2).

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1797

Superorder CAENOGASTROPODA Cox, 1959

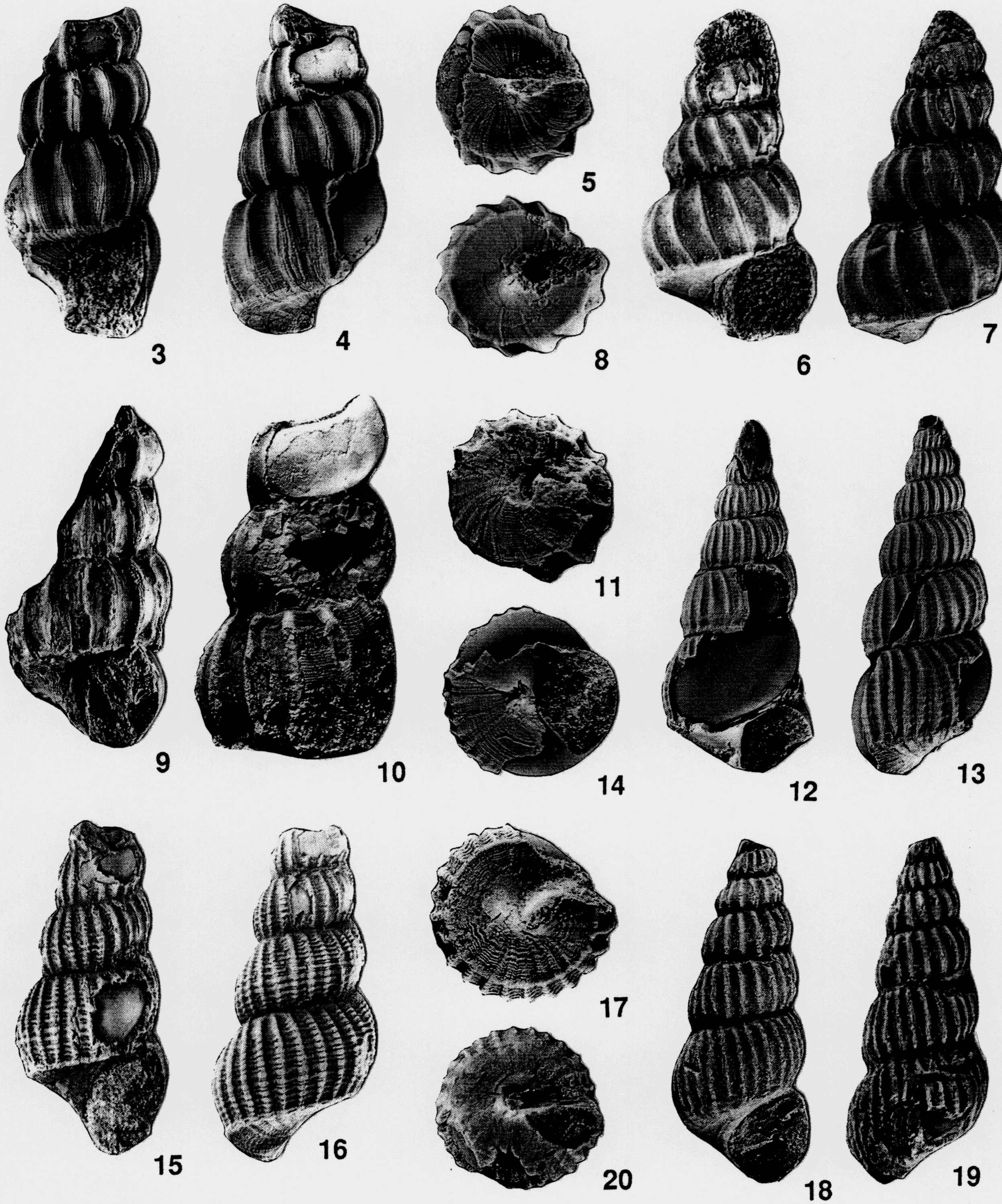
Order PTENOGLOSSA Gray, 1853

Superfamily JANTHINOIDEA Lamarck, 1812

Family EPITONIIDAE Berry, 1910

Discussion: We follow the convention of most modern workers in using Berry (1910) as the author of family Epitoniidae. According to Garvie (1996:64), however, the first author to actually use the family name Epitoniidae seems to have been Suter (1913). This discrepancy needs to be officially resolved.

All the current classifications of this family are still based on shell characters, and the present state of knowledge of epitoniids allows for only a provisional classification scheme because the nomenclatural history of this family is chaotic, particularly above the species level (Weil et al., 1999). Much of this confusion is the result of the early French worker de Boury, who named many genera and subgenera but who provided, in many cases, no more than just type designations for the names. Some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of these type species are obscure European ones. Even when the type species can be examined, it is not always possible to differentiate the genera or subgenera. It must be realized that many of his names are probably superfluous or questionable, and that a rather broad interpretation of the better known taxa is the most practical approach until such time as the family can be thoroughly revised (Clench & Turner, 1950; Maxwell, 1992).

Kilburn (1985) reported that in scanning the Epitoniidae for synapomorphies that might be useful in formulating a classification, he received the impression that most lineages have arisen through the genetic "reshuffling" of a limited number of characters and that convergence is rampant. He also reported that radula studies have yielded little of value, and one must, at present, rely on shell characters. Bouchet & Warén (1986), however, reported that there are radular differences among the family, as well as some differences in the operculum. At present, only two major shell characters appear to be of "taxonomic value"; namely, the presence of a pitted intritacalx (or chalky layer external to the primary shell) and, especially, the protoconch form of those species with planktotrophic type of larval shell (Kilburn, 1985; Bouchet & Warén, 1986). Unfortunately, the intritacalx and protoconchs are rarely preserved in fossil epitoniids, especially those from the Cretaceous of the Pacific slope of North America.

Genus *Opalia* H. Adams & A. Adams, 1853

Type species: *Scalaria australis* Lamarck, 1822, by subsequent designation (de Boury, 1886); Recent, New South Wales to Western Australia.

Diagnosis: Shell solid, whorls joined, and not umbilicate. Axial ribs usually strong, broad, and occasionally angulated or nodulose. Spiral sculpture usually consisting of exceedingly fine incised threads, finely pitted or not. Intritacalx pitted and present on unworn specimens. Basal keel usually present and strong. Basal disk present or absent; transverse ribs absent on base. Operculum thin, corneous, paucispiral, and littorinoid in shape (Clench & Turner, 1950; Neville, 2001).

Discussion: One of the most diagnostic characters of *Opalia* is the pitted intritacalx, which consists of microscopic sculpture in a very thin and soft outer layer of calcium carbonate that is quickly lost in worn specimens. This feature is easily eroded and rarely preserved in fossil specimens (Bouchet & Warén, 1986). Although *Opalia* generally has axial ribs, all transitions seem to exist between species with strong axial sculpture and species with no axial sculpture at all.

Wenz's (1940:fig. 2297) illustration of the type species of *Opalia* shows transverse ribs on the base. Clench & Turner (1950), as well as other authors, have maintained that *Opalia* is distinctive for its lack of transverse ribs on the base. We have examined specimens of *O. australis* stored in the Natural History Museum of Los Angeles County, Malacology Section, and found them to be lacking transverse ribs on the base, just like the specimen of this species illustrated by Wells & Bryce (1985:fig. 148).

Opalia is morphologically very similar to *Confusiscala* de Boury, 1909, and future work may show them to be the same. The two new species of *Opalia* described below have narrow axial ribs, as well as very weak to nearly obsolete spiral ribbing, and are more similar to the type species of *Opalia,* than they are to the type species of *Confusiscala,* which has swollen axial ribs and relatively strong spiral ribbing. *Opalia*? *mathewsonii* (Gabb, 1864), which is also included in this present report, generally resembles *Opalia* but cannot be positively placed in this genus because of poor preservation of the available material.

According to Bouchet & Warén (1986), *Opalia* is morphologically indistinguishable from *Gregorioiscala* Cossmann, 1912, and *Punctiscala* de Boury, 1890, both of which are found today only in bathyal and abyssal habitats. Bouchet & Warén (1986), however, preferred to treat *Opalia* as distinct from these two genera because *Gregorioiscala* and *Punctiscala* are bathymetrically distinct.

As will be discussed below, the two new species of *Opalia* described here, and especially *Opalia* ***cavea,*** are very similar to an array of other Cretaceous *Opalia* found throughout the world. These Cretaceous species are, in

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Figures 3–20. Specimens coated with ammonium chloride, unless otherwise stated. Figures 3–5. *Opalia* ***atra*** Squires & Saul, sp. nov., holotype LACMIP 12898, LACMIP loc. 25401, Yreka area, ×3.6. Figure 3. Apertural view. Figure 4. Abapertural view. Figure 5. Basal view. Figures 6–8. *Opalia* ***cavea*** Squires & Saul, sp. nov., holotype LACMIP 12990, LACMIP loc. 2853, Arroyo Santa Catarina, ×3.3 Figure 6. Apertural view. Figure 7. Abapertural view. Figure 8. Basal view. Figures 9–11. *Opalia*? *mathewsonii* (Gabb, 1864), holotype ANSP 4220, Martinez area, specimen uncoated. Figure 9. Apertural view, ×2.7. Figure 10. Right-lateral view, ×3.7. Figure 11. Basal view, ×3.4. Figures 12–14. *Amaea* ***trifolia*** Squires & Saul, sp. nov., holotype LACMIP 12991, LACMIP loc. 24217, east of Redding. Figure 12. Apertural view, ×2.9. Figure 13. Left-lateral view, ×2.9. Figure 14. Basal view, ×3.5. Figures 15–17. *Amaea* ***cerva*** Squires & Saul, sp. nov., holotype LACMIP 12992, LACMIP loc. 10849, Chico Creek. Figure 15. Apertural view, ×2.7. Figure 16. Abapertural view, ×2.7. Figure 17. Basal view, ×3.3. Figures 18–20. *Amaea* ***pentzia*** Squires & Saul, sp. nov., holotype LACMIP 12993, LACMIP loc. 24340, Pentz area, ×2. Figure 18. Apertural view. Figure 19. Abapertural view. Figure 20. Basal view.

turn, very similar to the *Opalia australis*, the living type species of *Opalia*.

The geologic range of *Opalia* sensu lato is Late Jurassic to Recent (Durham, 1937).

Opalia ***atra*** Squires & Saul, sp. nov.

(Figures 3–5)

Diagnosis: An *Opalia* with slightly sinuous and slightly prosocline axial ribs, approximately 11 to 12 of them on middle-spire whorls. Spiral striae very fine. Basal keel strong.

Description: Shell medium small (up to 14.7 mm high), turriculate, with high spire. Pleural angle approximately 23° (estimated). Protoconch and upper spire unknown. Teleoconch whorls approximately six (estimated), rounded, suture moderately impressed. Axial ribs stronger than spiral sculpture. Axial ribs narrow to moderately broad, moderately spaced, extending from suture to suture, not aligned from whorl to whorl, slightly prosocline, occasionally sinuous posteriorly, usually reflexed leftward near posterior suture, approximately 13 on last whorl, 12 on penultimate whorl, and approximately 11 on ante-penultimate whorl. Spiral sculpture consisting of numerous, very closely spaced spiral striae crossing axial ribs. Basal keel prominent, slightly swollen where axial ribs meet it. Basal disk with microscopic spiral ribs and some raised growth lines; axial ribs obsolete. Aperture ovate, anterior end twisted slightly to left.

Dimensions of holotype: Incomplete specimen of three whorls, height 14.7, diameter 7 mm.

Holotype: LACMIP 12989.

Type locality: LACMIP loc. 25401, 41°51′30″N, 122°30′W.

Geologic age: Late Cretaceous (late Turonian).

Distribution: Hornbrook Formation, Osburger Gulch Sandstone Member, Siskiyou County, northern California.

Discussion: Only two specimens are known. Both are partial specimens, with one of them consisting of only the last whorl, without its base. The new species is very similar to *Opalia* ***cavea*** sp. nov. but differs from it by having a slightly narrower pleural angle; broader and fewer axial ribs that are more sinuous; and spiral striae that are more prominent. *Opalia* ***atra*** is somewhat similar to *Confusiscala*? *juvenca* Saul & Popenoe (1993:359–360, figs. 25, 26) from the Turonian Frazier Siltstone Member of the Redding Formation, Redding area, Shasta County, northern California. *Opalia* ***atra*** differs from *C.*? *juvenca* by having much narrower and more numerous axial ribs, much weaker spiral striae, and probably a narrower pleural angle.

Etymology: The specific name *atra* is Latin, meaning black, and refers to Black Mountain in the type-locality area.

Opalia ***cavea*** Squires & Saul, sp. nov.

(Figures 6–8)

Diagnosis: An *Opalia* with a 28° pleural angle. Axial ribs prosocline, approximately 14 to 15 on middle-spire whorls. Spiral striae nearly obsolete. Basal keel strong.

Description: Shell medium small (up to 19.2 mm high), turriculate, with high spire. Protoconch and upper spire unknown. Pleural angle approximately 28°. Teleoconch whorls approximately six (estimated), rounded, suture moderately impressed and with or without a subsutural cord. Axial ribs stronger than spiral sculpture. Axial ribs narrow, moderately spaced, extending from suture to suture, generally aligned from whorl to whorl on upper spire but becoming less so on more mature whorls, prosocline, occasionally reflexed leftward near posterior suture, 14 on last whorl, and 15 on penultimate and antepenultimate whorls. Spiral striae between axial ribs nearly obsolete, except for very faint striae (especially near anterior suture) on some whorls. Basal keel prominent, noded where axial ribs meet it. Basal disk with very faint, closely spaced spiral striae and some raised growth lines. Aperture subcircular, inner lip with thin callus.

Dimensions of holotype: Incomplete specimen of 3.5 whorls, height 16.2 mm, diameter 8.6 mm.

Holotype: LACMIP 12990.

Type locality: LACMIP loc. 2853, 29°36′N, 115°15′W.

Geologic age: Late Cretaceous (latest Santonian?, Campanian to early Maastrichtian).

Distribution: UPPERMOST SANTONIAN: Tentatively in the Chico Formation, Musty Buck Member, Chico Creek, Butte County, northern California; LOWER CAMPANIAN: Chico Formation, Ten Mile Member, Chico Creek, Butte County, northern California. MIDDLE CAMPANIAN: Tentatively in the Cedar District Formation, Sucia Island, San Juan County, Washington. LOWER UPPER CAMPANIAN: Jalama Formation, Santa Barbara County, southern California. UPPER CAMPANIAN TO LOWER MAASTRICHTIAN: Upper part of Chatsworth Formation, Lang Ranch area, western Simi Hills, Ventura County, southern California; Rosario Formation, "Ammonite Ravine," Arroyo Santa Catarina, northern Baja California, Mexico.

Discussion: The new species is known from approximately 20 specimens. Preservation is mostly poor, but a few specimens have moderately good preservation.

The new species is very similar to *Opalia* ***atra*** sp. nov. but differs from *O.* ***atra*** by having a slightly wider pleural angle; narrower, more numerous axial ribs that are more prosocline; and nearly obsolete spiral striae between axial ribs.

The new species is very similar to *Opalia*? *mathewsonii* (Gabb, 1864), discussed below. The new species differs from *O.*? *mathewsonii* by having axial ribs that are unnoded, more prosocline and more uniform in width; nearly obsolete spiral striae between axial ribs; finer spiral sculpture; and obsolete axial ribs on basal disk.

The new species is very similar to *Opalia* (*Opalia*?) *fistulosa* Sohl (1964:320–321, pl. 52, figs.1, 2) from Maastrichtian strata in Mississippi. The new species differs from Sohl's species by having an absence of fine punctae on the spiral lines covering the whorl sides and having weaker spiral sculpture on the basal disk.

Opalia ***cavea*** is also very similar to *Opalia* (*Opalia*) sp. A Perrilliat et al. (2000:16, fig. 6.15) and *Opalia* (*Opalia*) sp. B Perrilliat et al. (2000:16, fig. 6.17), both from lower Maastrichtian strata of southern Mexico. *Opalia* ***cavea*** differs from these two species by having spiral striae that are nearly obsolete. *Opalia* (*O.*) sp. A and *O.* (*O.*) sp. B both have spiral ribs covering the whorl sides and crossing the axial ribs. In the former species, the spiral ribs are fine in strength, whereas in the latter species, they are medium in strength.

Opalia ***cavea*** is also very similar to *Epitonium faearium* Dockery (1993:84, pl. 26, fig. 13; pl. 27, figs. 10, 11; pl. 41, figs. 4, 5) from Campanian strata of Mississippi. Perrilliat et al. (2000) reported *Epitonium* cf. *faearium* from Maastrichtian strata of southern Mexico. *Opalia* ***cavea*** differs from *E. faearium* by having a wider pleural angle and axial ribs that are more prosocline.

Opalia ***cavea*** sp. nov. is similar to *Confusiscala uchauxensis* Roman & Mazeran (1920:39, pl. 4, fig. 21) from Turonian strata of the Uchaux basin in southwestern France. Comparison is difficult because Roman & Mazeran only figured the dorsal view of their species. The new species differs from *C. uchauxensis* by having a more rounded last whorl and possibly one more axial rib per whorl on the more mature whorls.

Webster (1983) provided a detailed index map of the type locality area of the new species.

Etymology: The specific name *cavea* is Latin, meaning a cage for animals, and refers to the resemblance of the shell to an elongate cage for birds.

Opalia? *mathewsonii* (Gabb, 1864)

(Figures 9–11)

Scalaria (*Opalia*) *mathewsonii* Gabb, 1864:212, pl. 32, fig. 278; 1869, p. 223.

Epitonium (*Confusiscala*) *mathewsonii* (Gabb). Stewart, 1927:321–322, pl. 24, fig. 20.

Opalia (*Confusiscala*) *mathewsonii* (Gabb). Durham, 1937: 504, unfig.

Not *Opalia* (*Confusiscala*) *mathewsonii* (Gabb)?. Durham, 1937:504, pl. 56, fig. 23 (= holotype of *Confusiscala*? *sulfurea* Saul & Popenoe, 1993).

Supplementary description: Shell medium (up to 27.8 mm high), turriculate. Pleural angle approximately 22° (estimated). Protoconch and upper spire unknown. Teleoconch whorls approximately seven to eight (estimated), rounded, suture slightly impressed and undulatory. Axial ribs stronger than spiral sculpture; axial ribs narrow, minutely noded, moderately spaced, extending from suture to suture, not aligned from whorl to whorl, slightly prosocline to orthocline, occasionally reflexed leftward near posterior suture, and approximately 15 (estimated) on last whorl. Spiral ribs very fine, very closely spaced, and crossing axial ribs. Basal keel prominent. Basal disk with very fine spiral ribs and irregularly spaced, weak and narrow axial ribs. Aperture subcircular.

Dimensions of holotype: Incomplete specimen of five whorls, height 22.1 mm, diameter 9.2 mm.

Holotype: ANSP 4220.

Type locality: Great Valley Series near Martinez, Contra Costa County, northern California (see "Discussion" below).

Geologic age: Late Cretaceous (probably Campanian to early Maastrichtian).

Distribution: MIDDLE CAMPANIAN: Tentatively in the Chatsworth Formation, Bell Canyon, eastern Simi Hills, Ventura County, southern California. EARLY TO LATE CRETACEOUS GREAT VALLEY SERIES: Cretaceous rocks near Martinez, Contra Costa County, northern California.

Discussion: The location of the type locality of *O.*? *mathewsonii* is uncertain, as it was given as "near" Martinez, Contra Costa County, northern California. Cretaceous rocks in the vicinity of Martinez are in fault slivers and range in age from Albian to Maastrichtian. A partial specimen of a medium-large, poorly preserved individual from LACMIP loc. 26020 in the middle Campanian part of the Chatsworth Formation at Bell Canyon, eastern Simi Hills, southern California, is tentatively identified as *O.*? *mathewsonii*. Only two and one-half whorls are present, and they show 16 axial ribs, of variable width, crossed by fine spirals, and there appears to be remnants of axial nodes. This specimen lends support to the type locality of *O.*? *mathewsonii* being in Upper Cretaceous rocks rather than in Lower Cretaceous rocks. Saul & Popenoe (1993) surmised that the holotype of *O.*? *mathewsonii* is probably of Maastrichtian age.

Opalia? *mathewsonii* is included in this present paper because it is similar to the two new species of *Opalia* illustrated and discussed here. The right-lateral and basal views (Figures 10, 11) of the holotype (ANSP 4220) are illustrated here for the first time.

Genus *Amaea* H. & A. Adams, 1853, *sensu lato*

Type species: *Scalaria magnifica* Sowerby, 1844, by subsequent designation (Boury, 1909); Recent, Pacific coast of Japan.

Diagnosis: Shell acuminate, whorls joined, and not umbilicate. Protoconch smooth, conical, and polygrate. Suture impressed. Sculpture consisting of both axial and spiral ribs, usually cancellate (occasionally a few irregular varices). Basal keel prominent or weak (only a line and visible, or not, next to suture). Basal-disk sculpture similar to or unlike that on rest of teleoconch, axial ribs occasionally passing onto basal disk. Aperture ovate to quadrate (Clench & Turner, 1950; DuShane, 1974, 1979; Kilburn, 1985; Garvie, 1996; Neville, 2001).

Discussion: Sixteen subgenera of *Amaea* were recognized by Wenz (1940), and eight subgenera of this genus were recognized by Weil et al. (1999). Attempts by us to place the following three new species into subgenera proved to be tenuous at best and overall most unsatisfactory. It seems that many of these subgenera were based on descriptions of single species. Some of them, especially extinct genera like *Coniscala* de Boury, 1887 and *Unidiscala* de Boury, 1909, are rare, poorly preserved, not fully described, and poorly illustrated. Their definitions are very narrowly construed and impractical to use for intermediate forms, like those encountered in this study. Pending a thorough revision of the definitions of these subgenera, so that they include the concepts of variation and of incorporating similar species into one genus, we believe it to be prudent to heed the advice of Clench & Turner (1950) and use a rather broad interpretation of the better known taxa. In this paper, therefore, we use *Amaea* sensu lato. Its geologic range is late Early Cretaceous (Albian) to Recent (Wenz, 1940).

Amaea ***trifolia*** Squires & Saul, sp. nov.

(Figures 12–14)

Diagnosis: An *Amaea* with axial ribs strong, closely spaced, and reflected leftward near posterior suture. Spiral ribs weak, moderately widely spaced, not crossing axial ribs. Subsutural rib and sulcus posterior to subsutural rib. Basal keel weak, and weak axial ribs crossing onto basal disk.

Description: Shell medium small (up to 28.3 mm high), turriculate, with high spire. Pleural angle approximately 25°. Protoconch unknown. Teleoconch whorls approximately nine (estimated), rounded, suture moderately impressed and usually containing a subsutural rib, with a sulcus posterior to subsutural rib. Axial ribs stronger than spiral sculpture; axial ribs moderately strong, closely spaced, half as broad as interspaces, occasionally irregularly spaced, extending from suture to suture, somewhat aligned on early whorls but much less so on later whorls, opisthocyrt, reflexed leftward near posterior suture, and approximately 22 on last whorl, penultimate, and antepenultimate whorls. Spiral ribs weak and closely spaced, approximately as broad as interspaces; spiral ribs much weaker and more closely spaced than axial ribs; spiral ribs faint to obsolete? on upper spire whorls, with a tendency to become stronger on later whorls; and spiral ribs extending onto sides of axial ribs but not across them. Basal keel weak, same width as axial ribs and noded where crossed by them. Basal disk with axial ribs much thinner than on last whorl with some becoming obsolete toward axis of shell; spiral ribs on basal disk crenulated, very fine, thinner, and more closely spaced than elsewhere on shell. Aperture ovate; inner lip with a smooth callus (at least in parietal region).

Dimensions of holotype: Incomplete specimen of 6.5 whorls; height 19.4 mm, diameter 8.13 mm.

Holotype: LACMIP 12991.

Type locality: LACMIP loc. 24217, 40°36′40″N, 122°4′20″W.

Geologic age: Late Cretaceous (Santonian).

Distribution: Redding Formation, Members V and VI of Popenoe (1943), east of Redding, Shasta County, northern California.

Discussion: The above description is based on six specimens. Although much of the shell is missing on the last whorl and penultimate whorl of the holotype, the preservation of the remaining shell is very good and much better than the other specimens, which are incomplete and more weathered. The pleural angle is somewhat difficult to measure on the holotype because the penultimate whorl is crushed. Spiral ribs were not observed on the uppermost spire whorls of this species, but this might be a result of preservation.

The new species is most similar to *Amaea* ***pentzia*** sp. nov. and differs from it by having opisthocyrt axial ribs (rather than nearly straight ones), narrower axial ribs, subsutural rib and associated sulcus, basal keel, and no microscopic spiral striae and associated banding.

The new species is similar to *Amaea* ***cerva*** sp. nov. and differs from it by having a subsutural rib and associated sulcus, a weaker basal keel, less prominent spiral ribs, and, therefore, an absence of subcancellate ornamentation. In addition, the new species differs from *A.* ***cerva*** by having spiral ribs that are narrower, more uniform in width, not crossing the axial ribs, and without interribs.

Etymology: The specific name *trilofia* is Latin, meaning clover, and refers to the type locality in Clover Creek.

Amaea ***cerva*** Squires & Saul, sp. nov.

(Figures 15–17)

Diagnosis: An *Amaea* with subcancellate sculpture (axial ribs stronger than spiral ribs); narrow interspaces with occasional spiral interrib. Basal keel prominent.

Description: Shell medium (up to 31.5 mm high), turriculate, with high-acuminate spire. Pleural angle approximately 23°. Protoconch unknown. Teleoconch whorls approximately nine to 10 (estimated), rounded, suture moderately impressed. Sculpture subcancellate, with axial ribs stronger than spiral ribs. Axial ribs moderately strong, moderately spaced, and half as broad as interspaces. Axial ribs extending from suture to suture, not usually aligned from whorl to whorl, mostly straight (orthocline), occasionally slightly reflexed leftward near posterior suture (especially on later whorls), and approximately 20 to 22 on last whorl, penultimate, and ante-penultimate whorls. Spiral ribs numerous, crossing axial ribs, flat, variable width, narrower and more closely spaced on posterior part of whorls near suture, wide and straplike especially on medial part of whorls, very closely spaced, and narrow interspaces with occasional interrib. Basal keel prominent. Axial ribs cross weakly onto basal disk, with some axial ribs becoming obsolete toward axis of shell; spiral ribs on basal disk crenulate, thinner and more closely spaced than elsewhere on shell. Aperture ovate; outer lip thin, without a thickened varix; inner lip thicker, reflected, and with thin callus wash extending onto basal disk.

Dimensions of holotype: Incomplete specimen of 3.5 whorls, height 20 mm, diameter 9.2 mm.

Holotype: LACMIP 12992.

Type locality: LACMIP loc. 10849, 39°52′35″N, 121°42′15″W.

Geologic age: Late Cretaceous (Santonian).

Distribution: Redding Formation, Member V (lower part) of Popenoe (1943), east of Redding, Shasta County, northern California; Chico Formation, Musty Buck Member, Chico Creek, Butte County, northern California.

Discussion: The above description is based on approximately 30 fragmental specimens. Preservation is moderately poor to poor, and no specimen has a complete, undamaged aperture.

The new species is most similar to *Acrilla* (*Unidiscala*) *lolakensis* Durham (1937:509–510, pl. 56, fig. 22) from the Paleocene Martinez Formation, stratigraphically situated near the lower-upper Paleocene boundary at Lower Lake, Lake County, northern California (see Squires, 1997). The new species differs from Durham's species by having much wider spiral ribs with much narrower interspaces, and a secondary spiral rib only rarely in these interspaces.

Amaea ***cerva***, sp. nov. is very similar to *Amaea reticulata* (Solander in Brander, 1766; Castell, 1975:pl. 17, fig. 6) from the upper middle to lower upper Eocene Bracklesham-Barton Beds, Hampshire basin, southern England. The new species differs by having larger size, wider and stronger axial and spiral ribs, fewer and much stronger spiral interribs, and spiral ribs that cross the axial ribs.

The new species resembles somewhat *Amaea* ***trilofia***, sp. nov. but differs from it by having subcancellate sculpture; stronger, more closely spaced, straighter, and flatter spiral ribs with an occasional interrib; no subsutural rib and associated sulcus; and a stronger basal keel.

Etymology: The specific name *cerva* is Latin, meaning deer or buck, and refers to the Musty Buck Member.

Amaea ***pentzia*** Squires & Saul, sp. nov.

(Figures 18–20)

Diagnosis: An *Amaea* with axial ribs strong, closely spaced, and nearly straight. Spiral sculpture consisting of microscopic spiral striae occurring in bands; spiral groove near change in sculpture on basal part of last whorl.

Description: Shell medium (up to 28.2 mm high), turriculate, with high spire. Pleural angle approximately 23°. Protoconch unknown. Teleoconch whorls approximately seven to eight (estimated), rounded, suture moderately impressed. Axial ribs narrow, prominent, relatively closely spaced, and approximately two-thirds as broad as interspaces. Axial ribs extending from suture to suture, somewhat aligned on later whorls but much less so on early whorls, nearly straight, slightly prosocline, occasionally slightly reflexed leftward near posterior suture, 28 on last whorl, 23 on penultimate whorl, and 17 on ante-penultimate whorl. Spiral striae microscopic, not crossing axial ribs, numerous, very closely spaced, occurring in white and yellow narrow bands, with both types becoming wider, and white bands becoming slightly elevated on penultimate and last whorls. Basal part of last whorl with narrow-spiral groove; axial ribs extending short distance beyond spiral groove and transitioning into faint axial ribs extending toward axis of shell but becoming obsolete before reaching axis; anterior end of base of last whorl with some fine, closely spaced spiral ribs. Aperture ovate; inner lip with smooth callus.

Dimensions of holotype: Incomplete specimen of 5.5 whorls, height 28.2 mm, diameter 11.3 mm.

Holotype: LACMIP 12993.

Type locality: LACMIP loc. 24340, 39°39′08″N, 121°35′50″W.

Geologic age: Late Cretaceous (early Campanian).

Distribution: Chico Formation, Pentz Road Member, Pentz area, Butte County, northern California.

Discussion: The above description is based on a single specimen, whose preservation is generally good. The last whorl has been subject to abrasion, resulting in the spiral striae not being discernible there, even when viewed by means of a microscope. The spiral bands, nevertheless, are evident on the last whorl.

The new species resembles *Amaea* ***trifolia***, sp. nov. but differs from it by having larger size, straighter and wider axial ribs, microscopic spiral striae and associated banding, no subsutural rib and associated sulcus, and a narrow-spiral groove rather than a basal keel.

Etymology: The specific name *pentzia* refers to the type locality near the hamlet of Pentz.

Genus *Belliscala* Stephenson, 1941

Type species: *Belliscala rockensis* Stephenson, 1941, by original designation; Upper Cretaceous (Campanian to Maastrichtian), Texas.

Diagnosis: Shell conical-turriculate, whorls joined, rounded, and not umbilicate. Suture impressed. Sculpture consisting of rounded axial ribs and weaker spiral threads. Base rounded without a well developed disk (Stephenson, 1941; Dockery, 1993).

Discussion: Sohl (1964) indicated that the lack of a distinct basal disk in *Belliscala* suggests placement close to *Acirsa* Mörch, 1857.

Prior to this study, *Belliscala* had only been reported from Upper Cretaceous (near the boundary of the lower/middle Campanian to Maastrichtian) rocks of the southern United States (east Texas and northeast Mississippi) (Stephenson, 1941; Sohl, 1964; Dockery, 1993). The new occurrences reported here extend the geologic range of this genus back to the Coniacian and extend its geographic range to the Pacific slope of North America, as far north as Sucia Island, Washington. Although at least one of the southern United States Campanian species of *Belliscala* closely resembles one of the Pacific coast species (see "Discussion" of *Belliscala* ***meta***, sp. nov. below), the southern United States Maastrichtian species of *Belliscala* differ from the Pacific slope ones by having very weak spiral ribs that do not cross the axials and an absence of nodes on the whorls.

Perrilliat et al. (2000) reported a *Belliscala* sp. from Maastrichtian strata of southern Mexico. Although the figured specimen of *Belliscala* sp. Perrilliat et al. (2000: fig. 6.16) is incomplete, its very convex whorls, nonrounded axial ribs, and very weak spiral threads strongly suggest that it is an *Opalia*.

Belliscala ***petra*** Squires & Saul, sp. nov.

(Figures 21–25)

Diagnosis: A *Belliscala* with approximately 18 axial ribs on last whorl, axial and spiral ribs moderately spaced and moderately swollen. Strong development of a finer interrib between spiral ribs on most of shell. Intersections of axial and spiral ribs with low nodes. Axial ribs weak to moderately weak on base of last whorl.

Description: Shell small (up to approximately 16.6 mm high), conical, with moderately high spire. Pleural angle approximately 34°. Protoconch unknown. Teleoconch whorls approximately eight (estimated), flatly rounded medially, with a slight subsutural ramp and glossy surface; suture moderately impressed. Whorls with subcancellate sculpture, axial ribs stronger than spiral sculpture, intersections of ribs with low nodes, usually elongate but occasionally swollen-beaded on shoulder of last whorl. Axial ribs broadly rounded, extending from suture to suture, not usually aligned from whorl to whorl, straight, prosocline, and becoming more irregular and numerous near outer lip. Axial ribs on immature specimens (less than 13 mm in height) approximately 16 on last whorl, and 13 to 14 on penultimate and ante-penultimate whorls. Axial ribs on mature specimens moderately spaced, approximately 18 on last whorl, and 13 to 14 on penultimate and ante-penultimate whorls. Spiral ribs on spire and posterior part of last whorl moderately spaced, crossing axial ribs, narrower than interspaces, and usually with one finer

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Figures 21–38. Specimens coated with ammonium chloride. Figures 21–25. *Belliscala* ***petra*** Squires & Saul, sp. nov., east of Redding. Figures 21–23. Holotype LACMIP 12994, LACMIP loc. 24246, ×4.2. Figure 21. Apertural view. Figure 22. Abapertural view. Figure 23. Basal view. Figure 24. Paratype LACMIP 12995, LACMIP loc. 24246, apertural view, ×3.3. Figure 25. Paratype LACMIP 12996, LACMIP loc. 10794, apertural view, ×4.2. Figures 26–33. *Belliscala* ***meta*** Squires & Saul, sp. nov. Figures 26–27. Holotype LACMIP 12997, LACMIP loc. 23635, Chico Creek, ×3.3. Figure 26. Apertural view. Figure 27. Abapertural view. Figure 28. Paratype LACMIP 12998, LACMIP loc. 23634, basal view, ×3.2. Figures 29–30. Paratype USNM 46851, USGS Mesozoic loc. M8610, Pigeon Point, slightly crushed, ×5.1. Figure 29. Apertural view. Figure 30. Abapertural view. Figures 31–32. Paratype LACMIP 12999, LACMIP loc. 23648, Chico Creek, ×4.4. Figure 31. Apertural view. Figure 32. Abapertural view. Figure 33–38. *Belliscala suciense* (Whiteaves, 1879). Figure 33. Lectotype GSC 5764b, Sucia Island, abapertural view, ×4.7. Figure 34. Hypotype GSC 5930, Sucia Island, apertural view, ×4.2. Figures 35–36. Hypotype LACMIP 13000, LACMIP loc. 10449, Sucia Island, ×3.9. Figure 35. Apertural view. Figure 36. Basal view. Figure 37. Hypotype LACMIP 13001, Sucia Island, abapertural view, ×4.8. Figure 38. Hypotype LACMIP 13002, LACMIP loc. 10715, Simi Hills, abapertural view, ×3.9.