Cretaceous trichotropid gastropods from the Pacific slope of North America: Possible pathways to calyptraeid morphology

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ABSTRACT

Late Cretaceous gastropods belonging to genus *Lysis* Gabb, 1864, from the Pacific slope of North America, bridge the morphologic gap between turbiniform trichotropids and limpet-like calyptraeids. Development of the depressed and broadened inner lip/columella of *Lysis* resulted in a larger aperture that allowed more space for the foot to grasp a hard substrate. Pacific slope species of *Lysis* are represented by five species that collectively span an interval from late Coniacian to late Maastrichtian. They stem from two lineages of the trichotropine genus *Ariadnaria* Habe, 1961. The first lineage, which includes *Ariadnaria ainikta* new species of late Albian to Cenomanian age, *Ariadnaria stibara* new species of Cenomanian age, and *Ariadnaria obstricta* (White, 1889) of late Coniacian? and Santonian age, gave rise to the *Lysis duplicosta* group of neritiform to haliotiform, coarse-ribbed *Lysis*, including *Lysis mickeyi* new species (earliest *Lysis* in the world), *Lysis duplicosta* Gabb, 1864, *Lysis jalamaca* new species, and *Lysis lomaensis* new species. The second lineage of *Ariadnaria* consists of the Turonian *Ariadnaria aldersoni* new species, which gave rise to the *Lysis suciensis* (Whiteaves, 1879) group. Morphologically, this group, which show crepiduliform and fine ribbed shells, appears likely to be a stem group from which Cenozoic *Crepidula*-like genera evolved. *Garzasia* new genus, which ranges from late Campanian or early Maastrichtian age to the mid Maastrichtian, evolved from the *Lysis duplicosta* group and includes *Garzasia intermedia* (Cooper, 1894) and *Garzasia diabla* new species. The very broad, depressed spiraling inner lip of *Garzasia* is suggestive of *Calyptraea* Lamarck, 1799. We propose placement of *Lysis* and *Garzasia* in Lysinae new subfamily of the Trichotropidae. In addition to their occurrence along the Pacific Slope of North America, *Lysis* or *Lysis*-like gastropods are known from middle Santonian to lower Campanian strata in South Africa, upper Campanian in the Congo, and Maastrichtian strata in Mozambique and Japan.

Additional Keywords: Trichotropidae, Lysinae, Calyptraeidae, evolution, paleogeographical occurrence

INTRODUCTION

This study deals with the fossil record of the extinct genus *Lysis* Gabb, 1864, a small group of enigmatic gastropods which has received little or no study regarding its ancestry, point of origin in terms of time and geographic locale, and evolutionary history. Specimens have been found in shallow-marine Cretaceous deposits from southern Vancouver Island and neighboring Gulf Islands, British Columbia, Canada to northern Baja California, Mexico (Figure 1) and, although *Lysis*-like gastropods have been reported at a few locales in the world, its familial placement has been uncertain. This study brings new information about all of these items.

Material for this study included type specimens, additional collections from their type localities, and specimens of Late Cretaceous age (Coniacian to Maastrichtian) from previously unreported-upon localities. Figure 1 provides an index to areas which yielded specimens used in this study.

During the study we discovered undescribed species of the trichotropine genus *Ariadnaria* Habe, 1961, which appear to have given rise to two groups of *Lysis*, a neritiform coarse-ribbed group and a crepiduliform fine-ribbed group. As will be discussed under "Evolutionary Implications," we propose that the neritiform group evolved into *Garzasia* new genus, which appears to be a precursor to calyptraeiform genera.

A total of three genera (one of them new) and 11 species (seven of them new) make up this study. The taxa are: four species of *Ariadnaria* (three of them new), five species of *Lysis* (three of them new), and two species of *Garzasia* (one of them new). The ranges in time of all these species, as well as two recognizable groups of *Lysis*, are plotted on Figure 2. The *Lysis duplicosta* group consists of four species, spanning a total interval of late Coniacian to late Maastrichtian. This group was also the most geographically widespread, with specimens collected from British Columbia to Baja California. The *Lysis suciensis* group is known only from the Campanian to possibly early Maastrichtian, with specimens known from British Columbia to Baja California Sur. *Lysis* persisted for a total of approximately 18 million years in the study area.

The specimens studied here are mainly from fine-

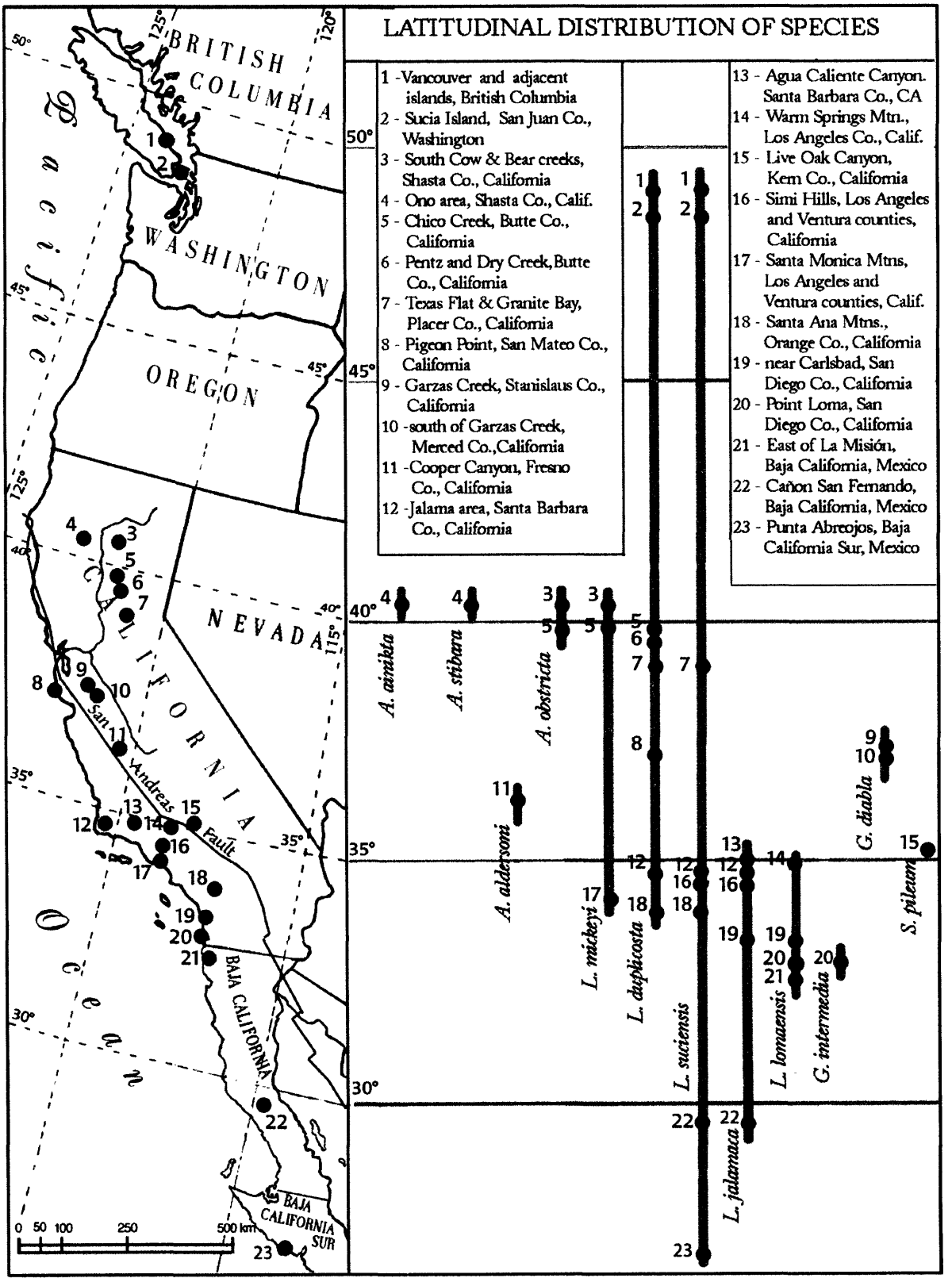


Figure 1. Index map of collecting localities.

grained argillaceous sandstone or siltstone that constitute shelfal deposits that accumulated at depths near or just below wave base.

Specimens are low in number and almost always incomplete. Protoconchs are rarely preserved, the larval shell is in part missing, its shape partially represented by its inner cast in all available specimens. Apertures are usually missing their anteriormost area. Adhering matrix, commonly consisting of well-cemented sandstone usually plugs the aperture, thereby necessitating careful cleaning.

As will be discussed under "Evolutionary Implications," the shape of *Lysis*, with the exception of *L. mickeyi* new species, approaches that of *Crepidula*, resulting from flattening of the aperture, development of a broad shelf, and lateral coiling of the spire. The crepiduliform shape, as well as the *Calyptraea*-like shape of *Garzasia*, pose problems for terminology used for describing certain figures of specimens, as well as for describing certain shell dimensions. For some specimens, a full view of the aperture could only be depicted by having the the shell tipped out of the plane of its axis. The true height of these shells, therefore, is not shown; hence, the "vertical dimension" of the view is given instead, and perpendicular to it is the "horizontal dimension." In most cases, the abapertural view is in the plane of the shell axis; hence, the terms "height" and "diameter" apply.

Abbreviations used in the text are: ANSP: Academy of Natural Sciences of Philadelphia; CAS: California Academy of Sciences, San Francisco; CGS: Geological Survey of Canada, Ottawa; CIT: California Institute of Technology, Pasadena (collections now housed at LACMIP); CSMB: California State Mining Bureau (specimen at CAS); IGM: Instituto de Geología, Universidad Nacional Autónoma de México; LACMIP: Natural History Museum of Los Angeles County; SDNHM: San Diego Natural History Museum; UCLA: University of California, Los Angeles (collections now at LACMIP); UCMP: University of California, Berkeley, Museum of Paleontology; USGS: United States Geological Survey, Menlo Park (collections now housed at UCMP); USNM: National Museum of Natural History, Smithsonian Institution.

PALEOBIOGEOGRAPHIC DISTRIBUTION OF *ARIADNARIA*, *LYSIS*, AND *GARZASIA*

Ariadnaria ranges from late Albian to Recent with its earliest appearance in Pacific slope deposits of North America, where it is found in strata ranging from late Albian to Santonian age. From Japan, Kase (1990) figured, as *Trichotropis*?, a possible *Ariadnaria* species of earliest Maastrichtian age.

Lysis ranges from the late Coniacian to late Maastrichitan, and that is also its range for the Pacific slope of North America. The genus apparently originated in California, with five species known from the Pacific slope of North America. Four additional probable species of *Lysis* are known elsewhere in the world. They are: *Lysis capensis* Rennie, 1930, from the middle Santonian to lower Campanian of South Africa (Kiel and Bandel, 2003); *Lysis congolensis* (Brébion, 1956) from upper Campanian of the Congo, Africa; *Lysis africana* (Cox, 1925) from the Maastrichtian (undifferentiated) of Mozambique; and *Lysis izumiensis* Kase, 1990, from the earliest Maastrichtian of Japan.

Rennie (1935) reported *Lysis caffra* Rennie, 1935, from the Upper Cretaceous near the eastern border of the Eastern Cape Province (Pondoland), southeast Africa, but its swollen naticiform shape with a very large, inflated body whorl and broad, non-depressed inner lip/columellar region, that appears to have a thin callus, are features not found in *Lysis*.

Garzasia ranges from late Campanian or early Maastrichtian to the mid Maastrichtian and is endemic to the Pacific slope of North America.

MODE OF LIFE OF *LYSIS*

Lysis has been found attached to a few specimens of large volutid gastropods. One specimen of *Longoconcha eumeka* Saul and Squires, 2008, from the Point Loma Formation near Carlsbad, California has two specimens of crepiduliform *Lysis jalamaca* new species on its shell, near the outer lip margin (Figure 34), as well as an attachment scar on the abapertural side of the shell. Specimens of *Lysis suciensis* from the Chatsworth Formation near Chatsworth, California, although not found in situ as are the younger Carlsbad specimens, have aperture shapes that could fit on the exterior of a specimen of *Volutoderma* Gabb, 1877. Indication of such an association is absent prior to middle Campanian. Whether the specimens of *Lysis* species were using dead shells as a substrate or had developed an association with living *Volutoderma* is undetermined.

Comparison to probable family members indicates that *Lysis* was a sedentary faculative ciliary feeder. Trichotropines, as well as calyptraeids, are ciliary feeders that live a sedentary life on hard substrates and are protrandrous hermaphrodites among whom brooding their young is common (Graham, 1954; Yonge, 1962). These mode-of-life characteristics have historically been used to classify trichotropines as being close to calyptraeids.

SYSTEMATIC PALEONTOLOGY

Superfamily Calyptraeoidea Lamarck, 1809

Discussion: The taxonomy of calyptraeoids, as with most gastropods, was traditionally based on shell morphology and later modified by increasing anatomical knowledge. The inclusion of patelliform Capulidae Fleming, 1822, turbiniform Trichotropidae, and coiled limpet-shaped Calyptraeidae in the superfamily Calyptraeoidea (e.g., Thiele, 1929; Wenz, 1940), has provided

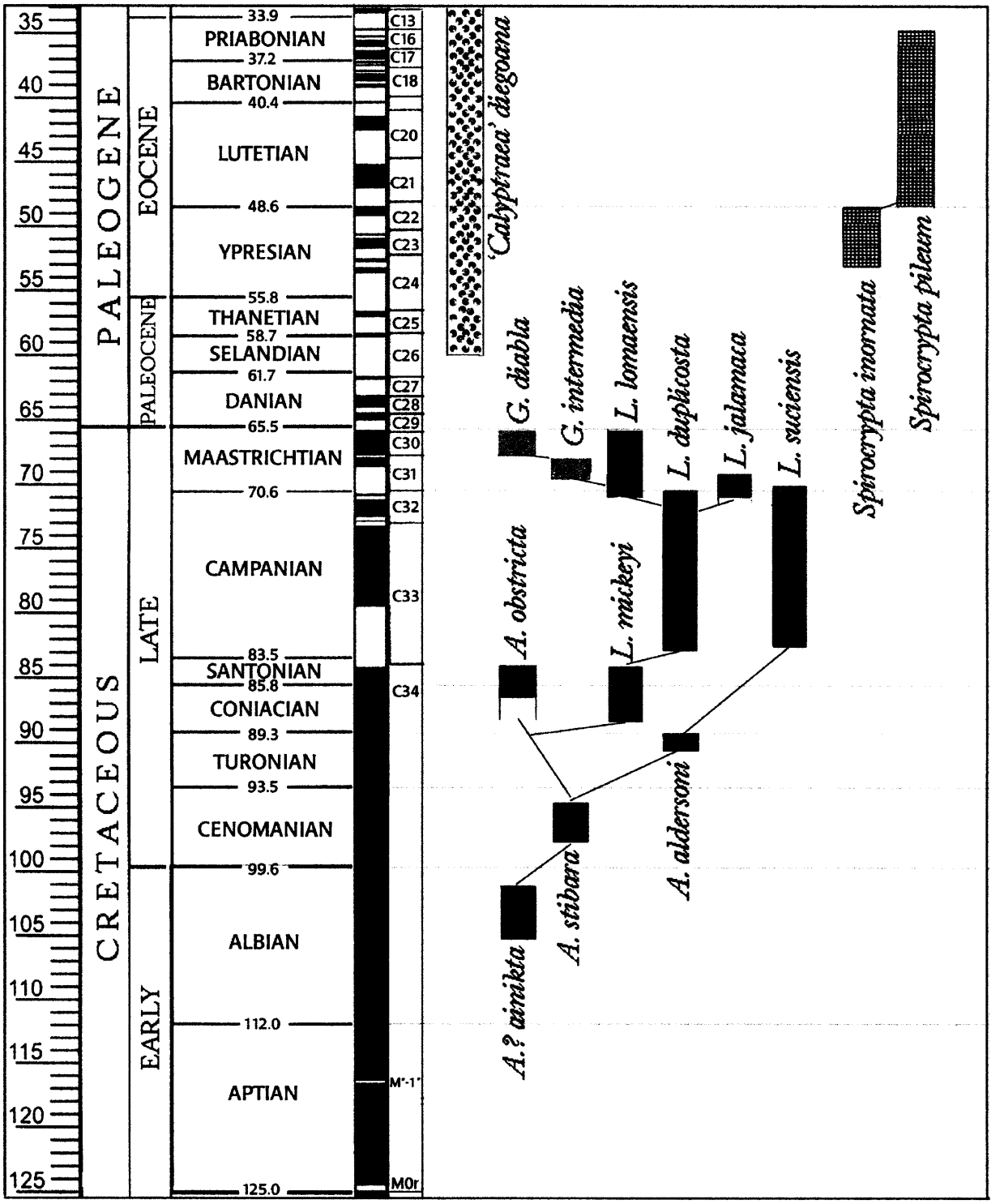


Figure 2. Age ranges of species of *Ariadnaria*, *Lysis*, *Garzasia*, *Calyptraea*, and *Crepidula* discussed in text. Lines connecting the species indicate inferred descent based on morphologic simiarity. *Lysis duplicosta* gave rise to two species one of which, *L. lomaensis*, produced proto-calyptraeform *Garzasia* and the other, *L. jalamaca*, is crepiduliform. An additional crepiduliform line was founded by *L. suciensis*. No known intermediate forms connect these Cretaceous calyptraeiform and crepiduliform gastropods to Tertiary species. The earliest known Pacific Slope calyptraeid, *'C.' diegoana* lacks the strong ribbing of *Garzasia*, but crepiduliform *Spirocrypta pileum* differs largely from *L. suciensis* in its small size. Time scale after Gradstein et al. (2004).

calyptraeoids a considerable morphological range and a somewhat complicated classification history (Bandel and Riedel, 1994). In addition to the above three families, Bandel and Riedel (1994), included Hipponicidae Troschel, 1861, in Calyptraeoidea, but Collin (2003: 632) rejected hipponicids from a close relationship with calyptraeids. Ponder and Warén (1988) and Ponder (1998), equated family Capulidae with family Trichotropidae Gray, 1850, on anatomical grounds, reducing the included families to two. Capulids, as exemplified by *Capulus* Montfort, 1810, have limpet-shaped shells; trichotropids, as exemplified by *Trichotropis* Broderip and Sowerby, 1829, usually have coiled shells; and calyptraeids, as exemplified by *Calyptraea* Lamarck, 1799, *Crepidula* Lamarck, 1799, and *Crucibulum* Schumacher, 1817, have limpet-shaped shells with an internal shelf of variable shape.

In her analysis of calyptraeids, Collin (2003a, 2003b) utilized shell characters, anatomical characters, and molecular characters. Collin (2003a) argued that although the so-called echinospira larva of *Capulus* and of *Trichotropis* do not appear to be "true" echinospira, the thickened and elaborate larval shell of these two groups is clearly different from the simple larval shell of extant calyptraeids, and she (Collin, 2003a, 2003b, 2005) has continued to recognize the families Capulidae Fleming, 1822, Calyptraeidae, and Trichotropidae. Collin (2003a) mentioned that despite the detailed studies done on calyptraeids, their taxonomy remains contentious and uncertain. Because specimens studied here show no resemblance to capulids but do, in part, resemble trichotropids, and calyptraeids such as *Calyptraea* and *Crepidula*, we follow Collin in recognizing families Calyptraeidae and Trichotropidae.

Family Trichotropidae Gray, 1850
Subfamily Trichotropinae Gray, 1850

Description: Small to medium sized (usually 15 to 25 mm, but up to 40 mm in height), coiled, high-conic to broad, low-conic, or nearly cap-shaped; spiral sculpture usually better developed than collabral sculpture and represented by distinct cords and/or keels; umbilicus broadly open to slit-like or completely closed; aperture variable in shape, ranging from irregularly triangular and broadly oval to elongate-oval; some forms with more or less attenutated canal; operculum small, horny; radula taenioglossate; periostracum forming combs, bristles, spines usually in places of intersection of spiral and collabral sculpture (from Egorov and Alexeyev, 1998).

Discussion: Trichotropids provide the geologically oldest representatives of the three families Trichotropidae, Capulidae, and Calyptraeidae. We did not follow Ponder and Warén (1988), Ponder (1998), and Bouchet and Rocroi (2005) in placing Trichotropidae in Capulidae because trichotropids, such as the high spired *Ariadnaria* spp. discussed herein, differ distinctly from cap–shaped capulids. Collin (2003b) referred to trichotropids plus capulids as the closest outgroup to calyptraeids, suggesting that she recognized these three as separate families. At present the geologic record finds trichotropids occurring earlier than capulids and also earlier than calyptraeids, and we suggest that based on species described herein, trichotropid-like gastropods gave rise to calyptraeids and that trichotropid specimens reported upon herein demonstrate a progressive development toward either a crepiduliform or a calyptraeiform shell.

Atresius Gabb, 1869, of Early Cretaceous (Valanginien to Hauterivian) age is the earliest trichotropine recognized by Wenz (1940), but its sole named species *A. liratus* Gabb, 1869, is a prominent constituent of chemosynthetic paleocommunities in northern California and probably not a trichotropid. *Lirpsa* Stephenson, 1952, of Cenomanian age from the Woodbine Formation of Texas may be the earliest previously known trichotropine. The earliest reported cap-shaped capulid is *Capulus verus* (Böhm, 1885) of Late Cretaceous (early Campanian) age from Aachen, Germany.

Genus *Ariadnaria* Habe, 1961
[= *Ariadna* Fischer, 1864; *non* Audouin, 1826].

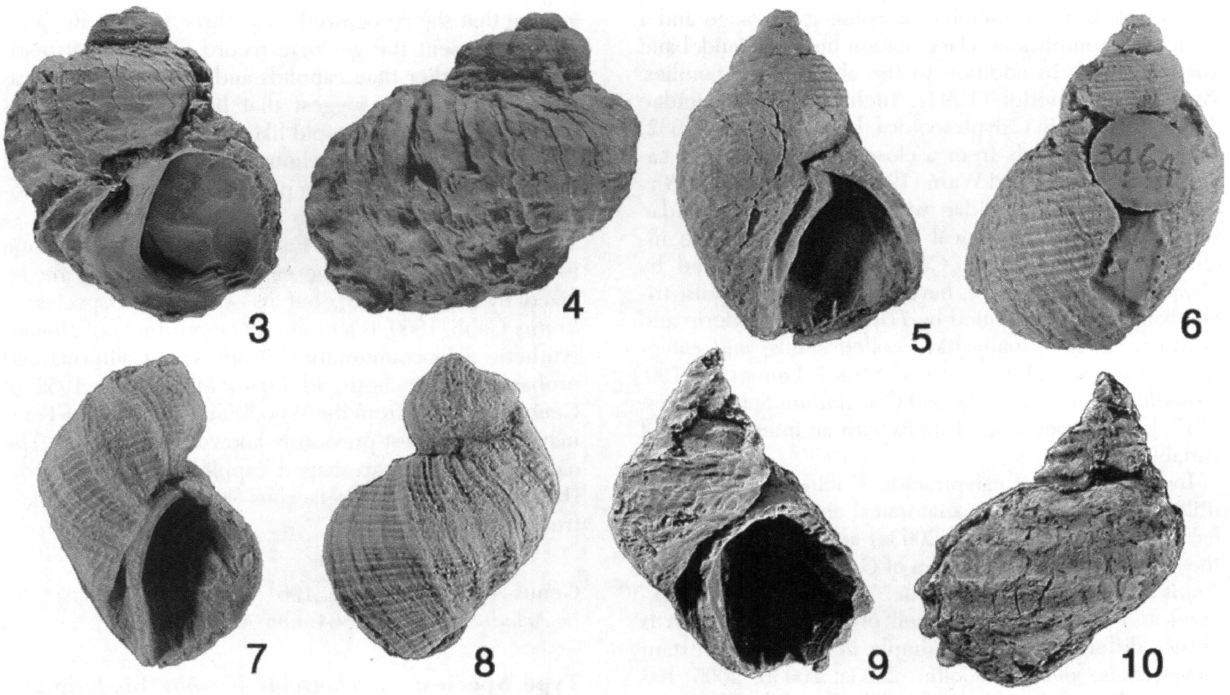
Type Species: *Trichotropis borealis* Broderip and Sowerby, 1829, by monotypy; boreal Arctic circumpolar (Egorov and Alexeyev, 1998) and cool temperate seas: northern North Atlantic south to Northumbria and all Scottish coasts (Fretter and Graham, 1962) and Massachusetts Bay (Emerson and Jacobson, 1976); the Bering Sea and north Pacific south to British Columbia (LACM collection, Forrester Island).

Description: Shell turbiniform (oval-conic) with raised spire; spiral sculpture well developed and consisting of raised cords separated by interspaces of variable width; collabral sculpture consisting of raised growth lines; aperture wide; inner lip slightly concave; canal short and straight; umbilicus slit-like; operculum thin; periostracum forming long, closely spaced bristles on spiral ribs.

Discussion: No prior records of *Ariadnaria* as a fossil were found by us. *Ariadnaria* differs from *Trichotropis* Broderip and Sowerby, 1829, by having an umbilicus. *Turbinopsis* Conrad, 1860, a turbiniform trichotropid of late Campanian or early Maastrichtian age from Mississippi, differs from *Ariadnaria* by having a wider umbilicus (profound according to Conrad, 1860), a last whorl that is more inflated and is tabulate, and having a very oblique fold near the basal margin of the columella.

Ariadnaria ainikta new species (Figures 3-4)

Diagnosis: Medium-size *Ariadnaria* with sturdy shell, rounded whorls, strong sculpture with nine spiral cords widely spaced; collabral sculpture thickly foliate; umbili-



Figures 3–10. *Ariadnaria* species. Specimens coated with ammonium chloride. **3–4.** *Ariadnaria ainikta* new species, holotype CAS 61794.00, CAS loc. 61794, height 20 mm, diameter 17 mm. **3.** Apertural view. **4.** Abapertural view. **5–6.** *Ariadnaria stibara* new species, holotype LACMIP 13371, LACMIP loc. 23464, height 19 mm, diameter 13.5 mm. **5.** Apertural view. **6.** Abapertural view. **7–8.** *Ariadnaria aldersoni*, holotype LACMIP 13372, LACMIP loc. 26370, height 12 mm, diameter 8.5 mm. **7.** Apertural view. **8.** Abapertural view. **9–10.** *Ariadnaria obstricta* (White, 1889), hypotype LACMIP 13373, LACMIP loc. 28717, height 21 mm, diameter 15 mm. **9.** Apertural view. **10.** Abapertural view.

cus elliptical; inner lip broad, expanded anterior and posterior to umbilicus.

Description: Shell medium (approximately 22 mm height), sturdy, turbiniform, spire moderately high, approximately 36% of total shell height; apical angle 110°; most of protoconch missing, remanent low and apparently smooth; teleoconch whorls three, whorls well rounded and enlarging very rapidly; suture appressed but appearing channeled; umbilicus open, deep, and elliptical; growth line prosocline; spiral sculpture consisting of regularly spaced and equally narrow cords; four cords on penultimate whorl; nine cords on last whorl, becoming stronger and more raised near umbilicus; spiral cords on last whorl widely spaced and occasionally with spiral thread in interspaces, especially anterior of periphery; collabral sculpture consisting of thickly foliate ridges coincident with growth checks, especially near outer lip; aperture D-shaped; inner lip broad, expanded anteriorly and posteriorly of umbilicus; abapertural edge of inner lip delineated by sharp ridge; basal lip broadened.

Holotype: CASG 61794.00, height 20 mm, diameter 17 mm, spire height 7.5 mm.

Type Locality: CASG loc. 61794 [=CASG loc. 1346-A].

Distribution: Basal Bald Hills Member of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

Geologic Age: Late Albian.

Discussion: Only the holotype is known. It evidently had a very foliate, thick shell. What remains is riddled with endobiont borings. Remnants of the protoconch are present, there is no clear evidence of an anterior sinus to the aperture, and the shell does not appear to have been nacreous.

The new species most resembles the trichotropid *Turbinopsis hilgardi* Conrad, 1860 (Conrad, 1860: 289, pl. 46, fig. 29; Sohl, 1960: 91, pl. 10, figs. 17, 18) from the upper Campanian/lower Maastrichtian Ripley Formation of Tippah Co., Mississippi, except *A. ainikta* has a smaller umbilicus and narrower cords with much wider interspaces. Additionally, the inner lip of *A. ainikta* is more expanded both anterior and posterior to the umbilicus.

Ariadnaria ainikta and *A. stibara* new species are similar in that there is no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. stibara* by having a less elongate shell, wider penultimate whorl, stronger spiral cords with much wider interspaces, a shorter umbilicus that is oval rather than slit-like, foliate

collabral sculpture, and no parietal swelling on the inner lip. *Ariadnaria ainikta* differs from *A. aldersoni* new species by being larger, having much stronger spiral cords with much wider interspaces, a well rounded last whorl (not angulate), shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. *Ariadnaria ainikta* differs from *A. obstricta* (White, 1889) by having a lower spire, wider penultimate whorl, round last whorl (not angulate) more spiral cords, foliate collabral sculpture, shorter umbilicus that is oval rather than slit-like, and no ridge separating the umbilicus from the inner lip. The strong spiral ribbing of *A. ainikta* resembles that of *A. obstricta*.

Etymology: *Ainiktos*, Greek, meaning: baffling, obscure, or enigmatic.

Ariadnaria stibara new species
(Figures 5-6)

Diagnosis: A medium size sturdy *Ariadnaria* with rounded whorls, medium strong sculpture with many spiral cords moderately closely spaced; collabral sculpture very fine and lattice-like on spire whorls; umbilicus chink-like; inner lip with low parietal swelling.

Description: Shell medium small (height approximately 20 mm), sturdy, turbiniform, somewhat elongate, spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch not present; teleoconch whorls four, whorls well rounded and enlarging rapidly; last whorl tapering anteriorly; suture appressed, appearing channeled, and rapidly descending near aperture; umbilicus narrow, chink-like and present only adjacent to medial and posterior parts of inner lip; growth line prosocline, with several irregularly spaced growth checks near outer lip; spiral sculpture consisting of numerous fine subequal rounded cords; approximately ten closely spaced cords on penultimate whorl with interspaces of nearly equal width; approximately 18 cords on last whorl with interspaces slightly wider than cords; cords strongest, most widely spaced, and occasionally with spiral thread in interspaces on medial and anterior portions of last whorl; collabral sculpture consisting of thin, raised growth lines, forming nearly microscopic lattice-like pattern on spire whorls; aperture D-shaped, moderately large, oblique, narrowed at posterior end by low parietal swelling; inner lip broad, somewhat excavated (concave) medially and flattened anteriorly; abapertural edge of inner lip delineated by low but distinct ridge; basal lip broadened.

Holotype: Holotype LACMIP 13371, height 19 mm (incomplete), diameter 13.5 mm, spire height 9 mm.

Type Locality: LACMIP loc. 23464 is also type locality of *Turrilites dilleri* Murphy and Rodda, 1960.

Distribution: Bald Hills Member (unit IV of Matsumoto, 1960) of the Budden Canyon Formation, (area 4) Ono area, Shasta Co., California.

Geologic Age: Middle Cenomanian.

Discussion: Only the holotype is known, and it lacks the protoconch and the anterior end of the teleoconch. Whether or not an anterior siphonal notch was present is unknown, but the shape of the last whorl suggests that at least a small one was present. The species is assigned to *Ariadnaria* based on shell shape, but it differs from typical *Aradnaria* in its very sturdy shell, the fineness of its sculpture, and the presence of a parietal swelling at the posterior end of the aperture.

Ariadnaria stibara differs from *A. ainikta* by having a more elongate shell, narrower penultimate whorl, much weaker spiral cords with much narrower interspaces, longer and narrower umbilicus, parietal swelling on inner lip, and absence of foliate collabral sculpture. *Ariadnaria stibara* differs from *A. aldersoni* by larger size, less elongate shell, more rounded whorls that are not lax in their coiling, coarser spiral ribs, lattice-like very fine collabral sculpture on spire whorls, parietal swelling on inner lip, less delineated abapertural edge of inner lip, and no fasciole-like flange bounding the umbilicus. *Ariadnaria stibara* differs from *A. obstricta* by having rounded whorls, many more spiral ribs that are much weaker and much more closely spaced, and a less well demarked abapertural edge of the inner lip.

Etymology: Named for its sturdy shell, *stibaros*, Greek, meaning strong or sturdy.

Ariadnaria aldersoni new species
(Figures 7-8)

Diagnosis: Small Ariadnaria with elongate shell and last whorl medially subangulate, coiling stretched axially, whorls bearing many very fine and closely spaced ribs, umbilicus chink-like, spiral sculpture very fine, abapertural edge of inner lip well delineated and raised, umbilicus bordered by fasicole-like flange.

Description: Shell small (approximately 13.5 mm height, estimated); elongately turbiniform, with medially subangulate whorls; upper spire missing; teleoconch whorls enlarging rapidly; suture apparently appressed on earlier whorls, becoming channeled on penultimate whorl, rapidly descending; umbilicus chink-like, bounded by strong rounded fasciole-like ridge; growth line prosocline, well marked with numerous growth welts on last whorl; spiral sculpture consisting of fine, well spaced ribs of unequal strength crossing irregular growth welts; interspaces between ribs wider than ribs; aperture D-shaped, narrowed posteriorly but not angled, with short, broad anterior sinus; outer lip thin, simple; inner lip moderately narrow, abapertural edge raised and well demarked.

Holotype: LACMIP 13372, height 12 mm (incomplete), diameter 8.5 mm.

Type Locality: LACMIP 26370.

Distribution: Panoche Formation, (area 11) Alcalde Hills, Fresno Co., California.

Geologic Age: Late Turonian.

Discussion: Only the holotype is known. It is incomplete, consisting only of the last two whorls, and its small size may indicate that it is not mature. The elongate shape is a distinctive characteristic of this species. *Ariadnaria aldersoni* apparently had a relatively high spire, and the coiling is lax and reminiscent of *Lirpsa* Stephenson, 1952. It somewhat resembles *Lirpsa teres* Stephenson, 1952, but the new species has a narrow, chink-like umbilicus.

Ariadnaria aldersoni is most similar to *A. stibara* and differs by being smaller, having a more elongate shell, angulated whorls that are lax in their coiling, much weaker spiral ribs, abapertural edge of inner lip better delineated, fasciole-like ridge bounding the umbilicus, absence of lattice-like very fine collabral sculpture on spire whorls, and absence of parietal swelling on inner lip. *Ariadnaria aldersoni* differs from *A. ainikta* by being smaller, having much weaker spiral cords with much narrower interspaces, angulate last whorl, longer umbilicus that is slit-like rather than oval, and having a ridge separating the umbilicus from the inner lip. *Ariadnaria aldersoni* differs from *A. obstricta* by being smaller and having fewer and much weaker spiral cords with much narrower interspaces.

In some respects *A. aldersoni* is similar to *Lysis suciensis*. Both have fine ribbing, a relatively high spire, rather lax coiling, and a somewhat slower increase of whorl diameter. Whereas the suture of *A. obstricta* and *Lysis mickeyi* is very close to or at the perimeter of the previous whorl, in *A. aldersoni* and *Lysis suciensis* the suture is usually abapical to the previous whorl's perimeter.

Etymology: The species is named for John M. Alderson who collected the holotype from Cooper Canyon.

Ariadnaria obstricta (White, 1889)
(Figures 9-10)
Stomatia obstricta White, 1889: 18-19, pl. 4, figs. 10-11.

Diagnosis: Medium size *Ariadnaria* with high spire and angulate last whorl, sculpture of a few widely spaced strong cords, umbilicus chink-like or covered.

Description: Shell medium size (approximately 21.4 mm height), elongate turbiniform; whorl profile rounded with slight angulation at third strong cord on last whorl; spire high and approximately 50% of total shell height; apical angle approximately 67°; protoconch missing; teleoconch whorls four, enlarging rapidly and last whorl tapering anteriorly; suture appressed, anterior to subangulate periphery; umbilicus chinklike or covered by inner lip expansion; bounded abaperturally by strong ridge; growth line prosocline; sculpture of three strong, widely spaced cords on spire, five or six on body whorl; interspaces commonly with mid thread; aperture large and ovate with abapertural edge raised and sharply demarked; outer lip apparently simple; inner lip somewhat expanded and standing high along umbilical chink; basal lip barely drawn out into slight spout-like sinus.

Holotype: USNM 20124.

Type Locality: Little Cow Creek but additional specimens have not been found there. The species is abundant at some localities along South Cow Creek, Shasta Co., California.

Hypotype: LACMIP 13373, height 20 mm, diameter 15 mm from LACMIP loc. 28717.

Distribution: Redding Formation, Bear Creek Sandstone Member, especially (area 3) along South Cow Creek and Bear Creek, Shasta Co.; Chico Formation, Musty Buck Member, (area 5) Chico Creek, Butte Co., California.

Geologic Age: Late Coniacian? to Santonian.

Discussion: The above description is based on 16 specimens; all but one are from LACMIP loc. 28717. Most specimens are poorly preserved, and specimens with the shell surface preserved are difficult to find. The primary cords are strong and almost flange-like.

White's species is here assigned to *Ariadnaria* based on shell shape, sculpture, umbilicus, and presence of a small spout-like sinus in the aperture. This would be the earliest unquestioned occurrence of this genus that previously was known only from the Recent (Wenz, 1940).

In shape and probably sculpture (preservation makes comparison difficult) *A. obstricta* resembles illustrations of *Trichotropis*? sp. in Kase (1990: 568, figs. 2.26, 2.27). Kase's specimen was from the Izumi Group of Japan of early Maastrichtian age.

Ariadnaria obstricta is very similar to *Lysis mickeyi* new species, but *A. obstricta* has more regular spiral ribs, a slighly higher spire, the strong spiral delimiting an umbilical chink, and a free standing inner lip. *Ariadnaria obstricta* differs from *Ariadnaria ainikta* by having a higher spire, narrower penultimate whorl, angulate last whorl, fewer spiral cords, shorter umbilicus that is slit-like rather than oval, ridge separating the umbilicus from the inner lip, and an absence of foliate collabral sculpture. *Ariadnaria obstricta* differs from *A. aldersoni* by being larger, having fewer spiral cords that are much stronger and much more widely spaced, and lacking a fasciole-like ridge bounding the chink-like umbilicus. *Ariadnaria obstricta* differs from *A. stibara* by having angulate whorls, fewer spiral ribs that are much stronger and much more widely spaced, and a more demarked abapertural edge of the inner lip.

Subfamily Lysinae new subfamily

Description: Small to moderately large (15 to 80 mm in height), low turbiniform to almost haliotiform, barely siphonate shells with spiral ribbing. Final whorl somewhat to greatly enlarged; spire very short; aperture large, nearly circular to elongate oval; columella and inner lip flattened, expanded, and depressed to form a shelf within the aperture; some with shelf that spirals into an "umbilicus."

Discussion: The subfamily Lysinae includes *Lysis*

Gabb, *Garzasia* new genus, and probably *Spirogalerus* Finlay and Marwick, 1937. These gastropods are intermediate in form between trichotropines and calyptraeids. If their characteristics were better known, some other species such as those discussed under Global Distribution of Cretaceous Lysiform Gastropods, probably could be included here, some as *Lysis* or *Garzasia* others in as yet undescribed genera.

Genus *Lysis* Gabb, 1864
Tropidothais Cox, 1925: 213-214.

Type Species: *Lysis duplicosta* Gabb, 1864, by monotypy (Stewart, 1927: 345); Campanian of Pacific slope of North America.

Description: Turbinate to crepiduliform gastropods with a rapidly expanding whorl diameter having the columella/inner lip flattened, expanded, and submerged to form a narrow to broad shelf or deck. Shell sculptured by spiral cords or smooth. Nonumbilicate. Aperture with very slight anterior siphonal notch.

Discussion: *Lysis* differs from *Trichotropis* and *Ariadnaria* in having the inner lip completely appressed to the columella. Typical *Lysis* (i.e., the group of *L. duplicosta*) has a carinated whorl in the juvenile stage and a few moderately strong to strong spiral cords. The stronger spirals are typically scaly. Included in this group is *L. duplicosta* and the following new species: *Lysis mickeyi*, *L. jalamaca*, and *L. lomaensis*. The group of *Lysis suciensis* has a more rounded whorl profile and more subdued, finer spiral sculpture; included in it is *L. suciensis*.

Group of *Lysis duplicosta*

The genus *Lysis* was proposed by Gabb (1864) for a low-spired, turbiniform gastropod with a depressed inner lip. He had only immature specimens of a single species (i.e., the type species) and did not recognize their similarity to genus *Crepidula* Lamarck, 1799. He gave no indication of the familial affinities of *Lysis*, other than stating the general form is like genus *Stomatia* Helbling, 1779.

During the last 127 years, *Lysis* has been placed in at least 11 families scattered among "archaeogastropods" to the neogastropods. A review of this placement history is given here. Species that were eventually placed in *Lysis* were originally placed in *Stomatia* of the Stomatellidae Gray, 1840, by Whiteaves (1879, 1903) and White (1889). Stoliczka (1867-1868: 157-158) suggested that *Lysis* should be placed near *Separatista* Gray, 1847, in the Trichotropidae Gray, 1850, in the event that *Lysis* does not belong in either the Naticidae Guilding, 1834, or the Velutinidae Gray, 1840. Fischer (1885) placed *Lysis* in the Naticidae near *Eunaticina* Fischer, 1885. Tryon (1884: 112) did not hesitate to refer *Lysis* to the Muricidae Rafinesque, 1815 (as *Murexia*) [= Purpuradae Children, 1823], but on page 208 Tryon suggested a relationship to *Velutina* Fleming, 1821, of the Lamellariidae d'Orbigny, 1841. Cossmann (1903) wrote that *Lysis* could not be a muricid but must be placed near *Fossarus* Philippi, 1841, presumably in the Fossaridae Adams, 1860, where Stewart, 1927, Rennie (1930), Wenz, 1940, and Anderson (1958) also put it. Cossmann (1925) considered *Lysis* to be a subgenus of *Micreschara* Cossmann (1891) in the family Vanikoroidae Gray, 1840. Dall in Eastman (1913) and Packard (1922) placed *Lysis* in the "Thaisiidae" (=Thaididae) Suter, 1909. Saul (1959) and Saul and Alderson (1981) placed *Lysis* in Calyptraeidae, and, in 1990, Saul included it in superfamily Calyptraeoidea. Kase (1990) discussed previous taxonomic treatments of *Lysis* and suggested that, based on its inner lip shelf, the genus should be placed within the Calyptraeidae Lamarck, 1799. Bandel and Riedel (1994) and Kiel and Bandel (2003) supported this placement. Cox (1925) named and described genus *Tropidothais* Cox, 1925, which is a junior synonym of *Lysis*. He based *Tropidothais* on *T. africana* Cox, 1925, from the Maastrichtian of Mozambique [formerly Portuguese East Africa] and tentatively placed his genus in the Thaididae Jousseaume, 1888. Upon realizing its similarity to *Lysis*, Cox (in Rennie, 1935) synonomized the two genera and placed *Lysis* in the Stomatellidae. In this present paper, we place *Lysis* in the family Trichotropidae, subfamily Lysinae because *Lysis* appears to have evolved from trichotropids by expanding the columella/inner lip area (width and length) to form an interior shelf suggestive of the calyptraeid *Crepidula*.

Lysis mickeyi new species.
(Figures 11-16)

Diagnosis: A relatively high spired *Lysis* with eight or nine strong cords on last whorl; shelf moderately broad, somewhat depressed, and shallowly concave.

Description: Shell medium small (height approximately 20 mm), turbiniform; whorl profile overall rounded with medial angulation on last whorl; spire moderately low and approximately 30% of total shell height; apical angle approximately 90°; protoconch 1.5 whorls, low and smooth; teleoconch whorls 3.5, moderately expanding and last whorl tapering anteriorly; suture abutting and becoming laxly channeled on later whorls; sculpture of strongly raised cords, either moderately closely spaced or widely spaced; penultimate whorl with two to six and last whorl with eight or nine strong spirals, with variable number (two to five) of finer spirals in interspaces; both cords and interspaces crossed by fine collabral ribs, producing beaded appearance; angulation moderately strong on last whorl, coincident with strongest spiral cord; spiral cord anterior to angulation nearly same strength, thereby producing bicarinate appearance to medial part of last whorl; aperture large, oblique, barely notched anteriorly; outer lip simple; shelf moderately broad, somewhat depressed, and shallowly concave.

Holotype: LACMIP 13374, height 13 mm, diameter 9.5 mm, spire height 5 mm.

Paratypes: LACMIP 13375 from LACMIP loc. 23617 and 13376 and 13377 from LACMIP loc. 10757.