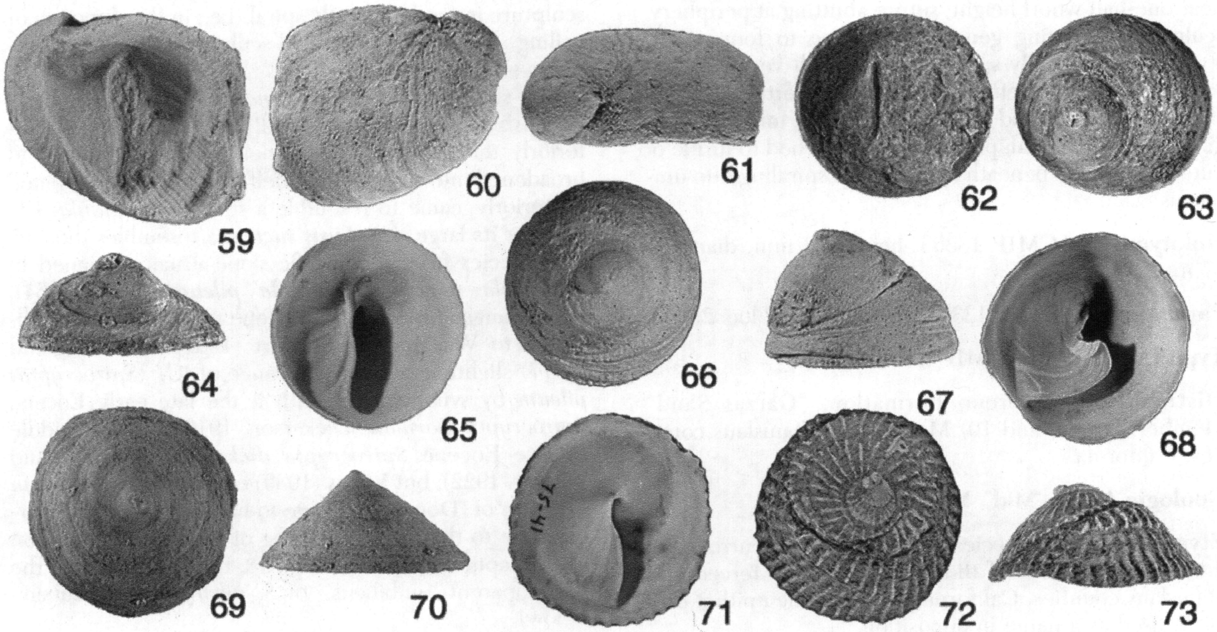
Kleinpell and Weaver (1963, pl. 24, fig. 11). Weaver's (1943: 724, pl. 71, fig. 16) illustration of *Calyptraea diegoana* (Conrad) is a lapsus and is a posterior-end-up, apertural view of *'Crepidula' pileum*. On page 356 he correctly lists the figure as *Crepidula pileum*. Gabb's (1864: pl. 29, fig. 233a) and Stewart's (1927, pl. 29, fig. 3) show the shelf. Gabb's figure is a fascimile and Stewart's is a photograph that has been reproduced in other discussions of *Spirocrypta* (e.g., Wenz, 1940: 903, fig. 2660a). Gabb's and Stewart's figures are based on lectotype ANSP 4221, but, unfortunately, the shelf of this specimen is broken. Both figures create the false impression that there is a sinus near both ends of the shelf and that the middle part protrudes and is concave. An additional representative specimen (hypotype LACMIP 13395) was cleaned by the senior author and is illustrated in Figures 59-61. Its shelf (Figure 59), which is unbroken, is slightly sigmoidal and long on the left side (or anterior end) and shorter on the right side (or posterior end). There is also a slight convexity of the somewhat sinuous shelf as it approaches the posterior end of the aperture and the shelf margin spirals over slightly to form an indication of an umbilicus. In addition, the shelf is also narrower and closer to the shell margin on the left/anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior. The shelf of *'C.' pileum* thus, as noted by Gabb (1864), spirals inward toward the apex. Gabb's figure (pl. 29, fig. 233b) in part illustrates this, as does Figure 59. Although Stewart (1927) synonomized *Spirocrypta* with *Crepidula*, Gabb's description of *Spirocrypta* recognizes this very important characteristic, which helps to distinguish *Spirocrypta* from *Crepidula*. In modern *Crepidula fornicata*, the shelf does not spiral into the whorl apex.

Aperture/shelf features of *Spirocrypta pileum* and *S. inornata* resemble those of the early Paleocene *Spirogalerus lamellaria* Finlay and Marwick, 1937, from New Zealand, in that the shelf of *S. lamellaria* is also narrower and closer to the shell margin on the left/anterior and noticeably farther from the shell margin (deeper into the aperture) on the right/posterior.

Our proposed evolutionary relationship between trichotropines and calyptraeids differs from any previous author's proposal. Hoagland (1977), for example, in her study of *Crepidula* Lamarck, 1799, rejected trichotropids as direct ancestors of calytraeids and crepidulids. Hoagland (1977) opined that although *Trichotropis* Broderip and Sowerby, 1829, and *Crepidula* had a common an-



Figures 59–73. Fossil Calyptraeidae. **59–64.** Comparative Eocene *Crepidula* and *Calyptraea* species. **59–61.** *Spirocrypta pileum* (Gabb, 1864), hypotype LACMIP 13395, LACMIP loc. 22386, vertical dimension 3 mm, diameter 9 mm. **59.** Apertural view. **60.** Abapertural view. **61.** Lateral view. **62–64.** *'Calyptraea' diegoana* (Conrad, 1855), hypotype LACMIP 13458, LACMIP loc. 22340. **62.** Apertural view, vertical dimension 29 mm, diameter 31 mm. **63.** Apical view, diameter 31 mm. **64.** Right lateral view, height 13 mm, diameter 31 mm. **65–67.** *'Calyptraea' aperta* Solander *in* Brander, 1766, hypotype LACMIP 13396, LACMIP loc. 7333. **65.** Apertural view, vertical dimension 11 mm, diameter 11 mm. **66.** Apical view, diameter 11 mm. **67.** Right-lateral view, height 7 mm, diameter 11 mm. **68–70.** *Calyptraea chinensis* (Linnaeus, 1758), Recent, type-species, hypotype LACM 161651, Cherbourg (Manche), Normandie, France. **68.** Apertural view, vertical dimension 15 mm, diameter 14.5 mm. **69.** Apical view, diameter 14.5 mm. **70.** Right-lateral view, height 6 mm, diameter 14.5 mm. **71–73.** *Trochita trochiformis* (Born, 1778), Recent, type-species, LACM loc. lot 75-41, Pumalin, west of Isla Telcon, Gulf of Corcovado, Chiloe Province, Chile – intertidal. **71.** Apertural view, vertical dimension 40 mm, diameter 38 mm. **72.** Apical view, diameter 38 mm. **73.** Right-lateral view, height 18 mm.

cestor, *Trichotropis* has no direct relationship to *Crepidula* because *Trichotropis* is boreal, living in cold and deep water and has rough sculpture, whereas *Crepidula* had its origin in the Panamic region and is relatively smooth sculptured. Her implications that *Trichotropis* is a deep, cold-water gastropod and that *Crepidula* is a shallow, warm-water gastropod are misleading. Modern *Trichotropis cancellata* (Hinds, 1843) is intertidal in Alaska, British Columbia, and Washington to depths of 104 m off Alaska, 165 m off British Columbia, and 274 m off Washington (LACM Malacology collection). In the southern part of *T. cancellata*'s range, it is in cool-temperate, not boreal waters. The question is, however, not where trichotropids live now but where they were during the Late Cretaceous, when there were no polar ice caps and the subtropical and temperate zones were much wider. Trichotropids and calyptraeid-like gastropods co-existed during the Late Cretaceous in the study area, and both forms lived in relatively warm, shallow waters. Although the Coniacian-Santonian faunas of northern California are noticeably cooler than Turonian faunas (Saul and Squires, 2008) of that area, they would have been temperate. Hoagland (1977) mentioned that anatomical features of *Trichotropis* suggest affinities to calyptraeids, but she believed that similarities of life history and niche between *Trichotropis* and *Crepidula* are convergent. She suggested that *Crepidula* is derived from some form of "calyptraeid stock" that, in turn, was derived from *Trochita* Schumacher, 1817, reported by Wenz (1940) to range from Eocene to Recent. She did not provide any geologic time parameters as to when these derivations took place, but indicated that Shimer and Shrock (1959) recorded the first calyptraeids as "lower Cretaceous." The "lower" seems to be a minor lapsus; all printings of Shimer and Shrock from first 1944 to last 1989 list range of *Calyptraea* and *Crepidula* as "U. Cret.-Recent" and *Crucibulum* as "Tert.-Recent." Wenz (1940: 902), however, questionably included the peculiar looking genus *Galericulus* Seeley, 1861 from the Upper Greensand (Lower Cretaceous upper Albian) of England in calyptraeids. It does not resemble any calyptraeid we have studied. Seeley (1861) named *Crepidula cooksoniae* also from the Upper Greensand, but Hoagland (1977: 395) found it "unconvincing" as a calyptraeid.

The Campanian to Maastrichtian *Damesia* Holzapfel, 1888, of Europe and Tennessee, has been regarded as a calyptraeid by some workers (e.g., Sohl, 1960), but Dockery (1993) assigned *Damesia* to the pyramidelloids.

Bandel and Riedel (1994) reviewed placement and content of Calytraeoidea, and in comparison to Hoagland's (1977) study, they arrived at a different familial content and different relationships between the families. Their Calyptraeoidea consisted of two families: Calyptraeidae containing genera *Calyptraea*, *Crucibulum*, and *Crepidula*; and Hipponicidae containing *Cheilea*, *Hipponix*, *Neojanaca*, and *Thylacus*; but both families excluded trichotropids. According to Bandel and Riedel (1994), all genera in Calyptraeidae lack a probosis and are obligatory filter feeders. However, in Hawaii Ulbrick (1969) reported algae grazing, in addition to filter feeding by *Crucibulum spinosum* Sowerby, 1824.

Cretaceous trichotropines probably had several characteristics that lysines would have inherited from them: 1) filter feeding, 2) living epifaunally, probably on a hard substrate, 3) brooding egg capsules from which planktotrophic larvae hatch, and 4) being protandrous hermaphrodites. Characteristics the lysines would pass on to calyptraeids. Lysines' first recognizable difference from the trichotropines is the increase in expansion rate of the whorl, especially of the last whorl, resulting in an enlarged aperture in which the columella is broadened. The earliest broadening and enlargement were moderate and only become striking as geologically younger species began to have a very distinctive morphology. Until connected with its ancestry, *Lysis* was difficult to classify. The shell also became more flattened and limpet-like, as the aperture enlarged.

Hoagland (1977) credited *Crepidula hochstetteriana* Wilckens (1922: 5-6, pl. 1, figs. 9a, b) as being the earliest *Crepidula* because it was reported from the calcareous conglomerate stratigraphic unit of the Lower "Amuri Group" in the "Amuri Bluff" area, northeastern South Island, New Zealand (Wilckens, 1922: Warren and Speden, 1978). Modern spelling of "Amuri" is Haumuri, and the Cretaceous strata are referred to the Mata Series. Woods (1917) reported that these strata at Haumuri Bluff contain the bivalves *Inoceramus australis* Woods, 1917 and *Inoceramus pacificus* Woods, 1917, which according to Wellman (1959) are limited to the Piripauan Stage of latest Coniacian to Santonian age.

Warren and Speden (1978) noted "problems" with the early collections from this area but nevertheless, listed *Maoricrypta hochstetteriana* (Wilkens, 1922) from the Campanian Okarahia Sandstone of the Mata Series. Described conditions of collecting suggested a strong possibility of co-mingling of material from different strata and that the only known specimens of *M. hochstetteriana* might not be from the Mata Series. In search of the type specimen, we contacted three extraodinarily helpful New Zealanders: A. G. Beu, A. Grebneff, and J. D. Stilwell. Their email communications (2006) indicated that *M. hochstetteriana* is not from the Okarahia Sandstone, and is not of Cretaceous age. Beu found the type specimen (GNS TM2608) in the New Zealand Geological Survey collections. Fortunately, the type specimen was in a large enough block of matrix to take a sample for microfossil dating. He enlisted the aid of G. Wilson who dated the dinoflagellates as late Oligocene, at the oldest. Ian Raine, who looked at the rich spore-pollen assemblage also from the sample, found *Acacia* pollen, which is not known earlier than Miocene in New Zealand. Miocene strata crop out above the Mata Series, and some of the original material sent to Wilkens was apparently from beach boulders derived from younger strata overlying the Cretaceous Mata Series. This Neogene age for Wilckens' species is much more likely considering that the shelf covers nearly one-half of the aperture (Hoagland, 1977: 380).

Hoagland published more papers on *Crepidula* and, in 1986, she revised several items of her 1977 paper but did not design a new evolutionary pathway. We differ from Hoagland (1977) in that we believe it is difficult to go from the centrally oriented apex plan of *Trochita* (Figure 71) or *Calyptraea* (Figure 68) with its spiraling shelf and get to *Crepidula* with its eccentric spire and apparently unspiraled deck. Whether or not *Lysis* species are ancestral to any modern *Crepidula*, younger species of *Lysis* achieved a crepiduloid form with a respectable shelf by wrapping the posterior end of the shelf onto the inside of the outer whorl. Furthermore, from this, the calyptraeid form appears to have evolved with the development of an "umbilicus" in *Garzasia intermedia* making Cooper's specific name remarkably prescient.

At about the Campanian/Maastrichtian boundary, development of the spiral shelf of *Garzasia* resulted in a shelf that appears to be a pattern for development of shelves in *Calyptraea* and perhaps *Crucibulum*. The very broad, depressed spiraling inner lip of *Garzasia* appears to provide a likely pattern for development of the shelf of *Calyptraea* or *Crucibulum*, not for the more decklike shelf of *Crepidula*.

The earliest reported *Calyptraea* on the Pacific slope is *'Calyptraea' diegoana* (Conrad, 1855) which ranges from middle Paleocene to Oligocene and occurs from California to Washington and easternmost Russia (Squires, 1987). A representative specimen from the Tejon Formation Eocene is shown in Figures 62-64. Figure 62 displays the shelf of this species, which is similar to that of *'Calyptraea' aperta* Solander in Brander, 1766 from the Eocene of Europe (Figures 65-67). Both of these species have often been referred to *Trochita* Schumacher, 1817 (type species *Turbo trochiformis* Born, 1778), but their shelves (Figures 62 and 65) spiral from an off-center position roughly a quarter of the diameter in from the aperture edge. A so-called pseudoumbilicus at the upper end of the shelves in Figures 62 and 65 could result from reduction of an umbilicus such as that of *Garzasia*. The shelves of *'C.' diegoana* and *'C.' aperta* are narrower than shelves of *Garzasia* and expand across about one third of the aperture. They differ distinctly from that of *Trochita* (Figures 71-73), which has a sturdy spiraling internal shelf extending from the centered axis of coiling to the outer shell margin, giving the impression of dividing the circular aperture in half.

'Calyptraea' diegoana does not appear to be a direct descendent of *Garzasia*. Its similarity to *'C.' aperta* suggests an ancestor in the Old World Tethyan Sea and, like many of the other Early Cenozoic mollusks (Squires, 1987, 2003), it probably arrived onto the Pacific slope via a circum-equatorial current. These species *'C.' diegoana* and *'C.' aperta* do not have shelves similar to that of *Calyptraea chinensis* (Linnaeus, 1758), the type species of *Calyptraea*. In *C. chinensis*, the thin fragile shelf (Figure 68) occupies about a quarter of the apertural circle. It arises from the apex with a folded-over edge that forms the umbilicus. At the open end of the umbilicus, the shelf edge abruptly veers counter to coiling direction and approaches the apertural margin at an acute angle. The total shelfal edge is sickle-shaped with a short handle (the umbilical edge) and a long curved blade (the outer margin of the shelf). This leaves a deep notch between the attachment of the shelf to the shell and a delicate, lobate shelf.

Trochita is present in modern eastern Pacific slope faunas from Mazatlan, Mexico to Valpariso, central Chile. It occurs in lower to middle Miocene strata as far north as the La Panza Range, San Luis Obispo Co., is present in the Kern River section, Kern Co. (Addicott, 1970) and the Topanga Formation, Santa Monica Mountains, Los Angeles Co., California. It has a thick shell with protractive ribbing and, as mentioned above, a sturdy shelf.

GLOBAL DISTRIBUTION OF CRETACEOUS LYSIFORM GASTROPODS

Both *'Crepidula'* and *'Calyptraea'* have been reported from Campanian and Maastrichtian age strata from throughout the world. Preservation of most specimens makes identification of them problematical. Some of these gastropods have proven to belong to other families or not to be of Cretaceous age. Others need verification. Our tally of occurrences is doubtless incomplete.

Although stated above as "throughout the world," these gastropods are recovered from areas that were probably temperate to tropical. Verified lysines are all younger than Turonian and older than Eocene. Classing *Spirogalaerus* as a lysine provides the only Paleocene record of this subfamily. Late Cretaceous occurrences suggest that the calyptraeids developed in several geographic places from widely distributed trichotropids evolving into Lysinae. An example of this is the evolving shape of *Lysis*. Although on the Pacific Slope calyptraeiform calyptraeoids developed from a crepiduliform calyptraeoid, the calyptraeiform has been recognized more widely geographically, but not earlier than Coniacian.

Cretaceous calyptraeiform calyptraeoids are more widely recognized geographically than are crepiduliform calyptraeoids. Europe has calyptraeiform occurrences but no crepiduliform occurrences. Africa has calyptraeiform occurrences in the north and crepiduliform occurrences in the south. African occurrences are close in time to those of the Pacific Slope. North America (exclusive of the Pacific Slope) has a very few reports along the Gulf Coast of calyptraeiform specimens. The Pacific Slope has both calyptraeiform *Garzasia* and crepiduliform *Lysis*. South America has calyptraeiform species. Japan somewhat mirrors the Pacific Slope. Its known lysine is of early Maastrichtian age, but the additional presence of a trichotropid (Kase, 1990) similar to *A. obstricta* suggests that lysines were developing there roughly synchronously with those along the Pacific Slope. New Zealand has no

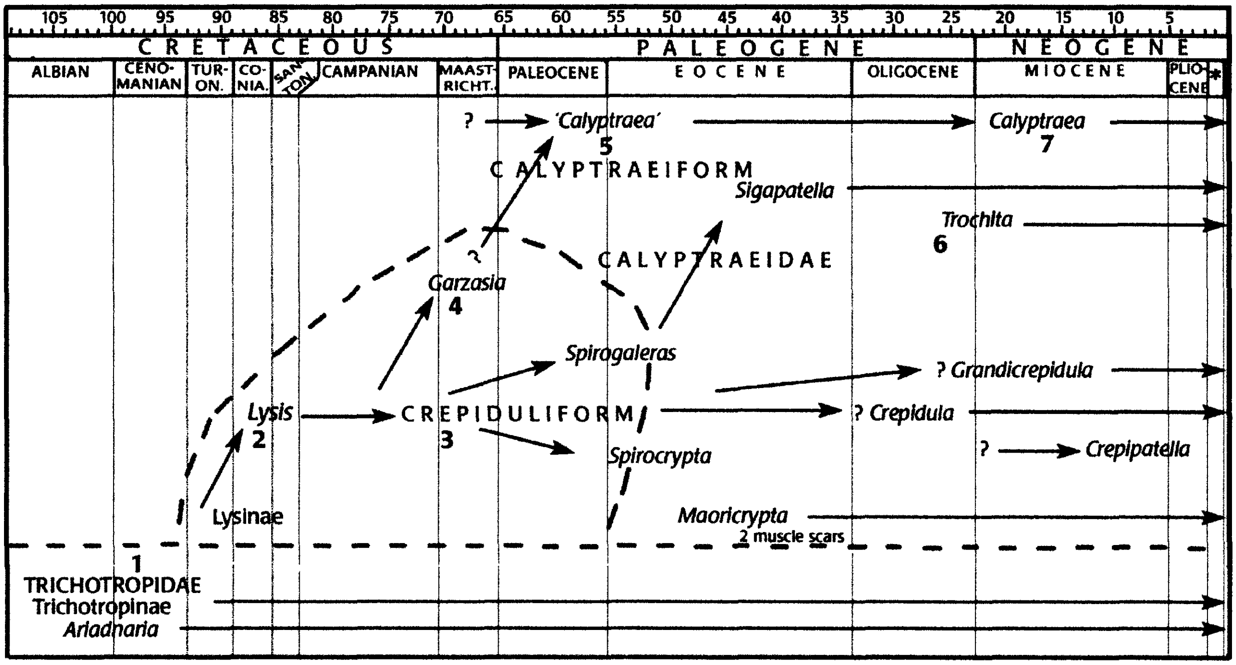


Figure 74. Generalized proposed evolutionary trends of calyptraeoids. Time scale after Gradstein et al., 2004. Calyptraeids and crepidulids probably evolved from several trichotropids. *Lysis* or *Lysis*-like fossils of Coniacian to Maastrichtian age have been described from California, and from Campanian to Maastrichtian age from southern Africa and Japan. **1.** Turriculate gastropods having gill capable of filter feeding, sedentary adult life on hard substrate. Probably capable of copulation, protandrism, and brooding of young. **2.** Broadening of columella and inner lip. Enlarging final whorl. **3.** Attachment of posterior shelf end to interior of outer lip to develop crescentic shelf. **4.** Some species developed "umbilicus" in spiraling shelf as in *Garzasia*. **5.** "Umbilicus" closed or nearly so in Eocene '*Crepidula*' and moving toward more central position in more circular base. **6.** Broad shelf, spiraling from near center of base. Shelf edge nearly straight. **7.** Spiral shell with low spire, round base. Shelf edge extremely sigmoidal. * = Pleistocene. Stages abbreviated are Turonian, Coniacian, Santonian, Maastrichtian.

known Cretaceous lysines but does have the youngest known calyptraeiform lysine.

EUROPE: *Crepidula mytiloidea* Bellardi and Michelotti, 1840 from Villavernia near Tortona Italy was listed among Nomina Dubia by Hoagland (1977) as being from the Cretaceous. Bellardi and Michelotti were describing a Tertiary fauna. Because the specimen and illustrations are so small, Hoagland could not verify that this species was a *Crepidula*.

Calyptraea cretacea (d'Orbigny, 1842: 390, pl. 234, figs. 1–3) [*Infundibulum*] was examined by Kollmann (2005) who determined that d'Orbigny's material was from Campanian of Charente-Maritime, southern France, and that the specimen identified as *C. cretacea* by Delpey (1942: 165, fig. 1) was from Maastrichtian of southwestern France. Poor preservation of d'Orbigny's type caused Kollmann (2005: 172, pl. 18, fig. 18) to refer to it as "*Calyptraea s. lato cretacea* (d'Orbigny, 1843), *species dubia*." Delpey's illustration shows no shelf. Kollmann considered both specimens to be only *Calyptraea* sensu lato. These specimens expand their whorl diameter much less rapidly and have much higher spires than specimens of *Lysis* and *Garzasia* from the Pacific Slope of North America.

Calyptraea depressa Delpey, 1942 (p. 165, fig. 2) from Maastrichtian southwestern France, has a spiraling shelf similar to that of Eocene '*Calyptraea*' *aperta* except that its shelfal margin is concavely arcuate between rim and whorl center.

Kollmann and Odin (2001: 446, pl. 1, figs. 18–19) recorded *Calyptraea* sp. of Maastrichtian age from southwestern France, but the preservation of the specimens appears to be too poor to allow positive generic identification.

AFRICA: As figured, '*Calyptraea*' *bouéi* (Pervinquière, 1912: 10–11, pl. 1, figs. 7–11) from the Maastrichtian of Tunisia externally resembles some forms assigned to '*C.*' *aperta*. The shape of the shelf of '*C.*' *bouéi* shown in figure 9 is difficult to determine, but appears to have a straight edge and probably resembles that of '*C.*' *aperta*.

Galerus libyca Quaas, 1902, was described from upper Maastrichtian/ possibly Danian strata (*Exogyra overwegi* beds) from the Ammonite Hills, Great Sand Sea, Egypt (Quaas, 1902: 238, pl. 25, figs. 26–29). It has been reported also from the Congo (Dartevelle and Brébion, 1956: 29–30, pl. 1, figs. 9–10), and from Libya, Egypt, Congo, and Madagascar (Bandel and Riedel, 1994: 339–340, pl. 7, figs. 2–3). Bandel and Riedel reported Quaas' original specimens lost in World War II and figured the exterior of a subsequently collected specimen of 'Calyptraea' *libyca* which resembles '*C.*' *aperta*. They did not figure the shelf, but described it too briefly as "a flat spiral shelf like that of modern *Calyptraea*."

A *Crepidula* chain was reported by Brébion (1956) in describing *Crepidula congolensis* Brébion, 1956, from the upper Campanian of the Congo, Africa. This African species resembles a *Lysis* more than it does a modern *Crepidula*, in that *C. congolensis* has coiling similar to *Lysis* and a depressed inner lip that barely wraps onto the labral side of the aperture. *Lysis*? *congolensis* (Bré bion, 1956: 89, fig. 1; pl. 1, fig. 7a, 7b) is most similar to *L. jalamaca* in shape and sculpture but appears to have much finer ribbing than *L. jalamaca*.

'*Calyptraea*' *primogenita* Kiel and Bandel (2003: 460, fig. 4.14–4.16) and *Lysis capensis* (Rennie, 1930) illustrated by Kiel and Bandel (2003: 460, fig. 6.1–6.2) are from the upper Santonian/lower Campanian, Umzamba Formation. '*Calyptraea*' *primogenita* was described from a single worn and broken specimen. Its ribbing (except on last quarter-whorl) is protractive as in *Trochita*, and it has a thick shell as does *Trochita*. Its whorl shape is more trochiform than in *Trochita* or *Calyptraea*, it consists of more whorls than a *Trochita* or a *Calyptraea*, the last whorl lacks the notable enlargement of a *Trochita* or a *Calyptraea*, and unlike *Trochita* or *Calyptraea*, it has a small open umbilicus and "the columellar lip bears a strong plate" (Kiel and Bandel, 2003).

Lysis capensis is very similar in shape and sculpture to *L. duplicosta*, but its inner lip seems narrower and more similar to that of *L. mickeyi*. *Lysis duplicosta* is generally lower spired and has a broader inner lip/columella.

Rennie (1945: 50, 116, pl. 3, fig. 10) figured a *Calyptraea* sp. from the Upper Cretaceous Senonian of Angola, Africa. A more precise age is unknown and, although the shape and angle of suture in the figure resemble *Calyptraea*, the base and aperture are not illustrated, thereby making generic assignment indeterminate.

NORTH AMERICA (exclusive of the Pacific Slope): *Crucibulum*? sp. of Sohl (1960: pl. 10, fig. 21) is an immature, incomplete specimen from the upper part of the Ripley Formation (Maastrichtian) in Mississippi. Sohl indicated that its incomplete shell suggested a close relationship to *Crucibulum*, and that it definitely appeared to belong in the Calyptroidea. The specimen is too incomplete to determine its genus, its similarity to *Crucibulum* could be a result of the way it is broken, but its spire does suggest Calyptraeoidea.

Sohl (1960) classed *Thylacus cretaceous* Conrad, 1860 in Capulidae, but Dockery (1993) moved it to Calyptraeidae and Bandel and Riedel (1994) included Conrad's species in Hipponicidae. It apparently lived attached to the columella within the aperture of empty gastropod shells. It differs from *Lysis* and *Garzasia* in the way *Thylacus* muscles were attached. At the end of juvenile coiling and beginning of expansion of the last whorl, *Thylacus* deposited left and right prongs instead of modifying the inner lip/columella into a shelf as in *Lysis*. Sohl (1960: pl. 10, fig. 4) and (Dockery (1993: pl.18, figs. 1 and 4) provided good illustrations of the early development which does seem more hipponicid than calyptraeid. When developed to maturity a horseshoe-shaped muscle scar resulted. Dockery's (1993) specimens were from the Coffee Sand of Campanian age and Sohl's (1960) from the Ripley Formation of Maastrichtian age.

SOUTH AMERICA: '*Calyptraea*' *aperta* (Solander *in* Brander, 1766), a European Eocene species (see Figures 65–67 for a representative late Eocene specimen from the Paris Basin, France), was identified by Olsson (1944: 248–249, pl. 9, figs. 10–13) from northern Peru. Olsson's placement of the Tortuga fossil beds below his Radiolite sandstones with *Baculites* suggests a Maastrichtian age. As he provided only exterior views and no description of the shelf, this identification needs further verification. Specimens identified as '*Calyptraea*' *aperta* from Europe and the American Gulf Coast range widely as to whorl height and sculpture which varies from smooth to spinose. The Peruvian specimens increase in diameter at a slower rate and they have more strongly impressed sutures than Eocene specimens, suggesting that the Peruvian specimens are probably not '*C.*' *aperta*.

Calyptraea laevis (Philippi, 1887) from Maastrichtian of central Chile was described as *Trochita laevis* Philippi (1887: 92, pl. 11, fig. 3; referred to *Galeropsis* by Wilckens (1904: 195–196, pl. 17, figs. 9a, b) because of its high spire, and to *Calyptraea (Trochita)* by Bandel and Stinnesbeck (2000: 763–764, pl. 1, fig. C). Bandel and Stinnesbeck provided a view of the exterior only, and described the shelf as "a flat concave shell like that of modern *Calyptraea*." Although "flat concave shell" might partially describe a *Trochita* shelf, it is not an acurate description of the shelf in *Calyptraea chinensis* (Figure 68). Wilckens (1907: 13, pl. 3, fig. 6) also reported *Calyptraea* aff. *laevis* Philippi of Maastrichtian age from southern Patagonia, but the preservation of the specimen appears to be too poor to allow positive generic identification.

Calyptraea pileolus d'Orbigny, 1841 was indicated by Hoagland (1977: 354) to have been recorded from Lower Cretaceous strata of Argentina by von Ihering (1907), but the species was listed by Feruglio (1937: 187) from the Patagoniano (Tertiary) of Lago Argentino, Argentina.

JAPAN: As noted earlier, *Lysis izumiensis* Kase, 1990 has been described from the earliest Maastrichtian of Japan. It resembles the group of *Lysis duplicosta* and appears from the illustrations (Kase, 1990: figs. 2.11–2.12) to be most similar to *L. duplicosta* in strength of sculpture and development of innerlip/columellar expansion. Kase (1990) also recorded a trichotropid similar to *Ariadnaria obstricta* from the Izumi Group in Japan.

NEW ZEALAND: The early Paleocene (Danian) *Spirogalaerus* Finlay and Marwick, 1937, from New Zealand is *Lysis*-like, especially as to growth line, and this similarity requires further study to determine whether it results from common ancestry, convergent evolution, or parallel evolution. Finlay and Marwick (1937) assigned *Spirogalerus* to family Calyptraeidae and based their genus on *Spirogalerus lamellaria* Finlay and Marwick, 1937, which resembles *L. suciensis* except that *L. suciensis* lacks the "pseudoumbilicus" described for *Spirogalerus*. Finlay and Marwick (1937) and Boshier (1960) opined that *Spirogalerus lamellaria* could represent the evolutionary link between crepidulids and calyptraeiform *Sigapatella* Lesson, 1830.

Classification of *Spirogalerus* has been inconsistent. Wenz (1940) made it a subgenus of *Calyptraea* Lamarck, 1799. Beu and Maxwell (1990) made *Spirogalerus* a subgenus of the calyptraeid *Sigapatella* Lesson, 1830, but Stilwell and Zinsmeister (1992) separated *Sigapatella* from *Spirogalerus* because the latter has a strongly exerted spire. Collin (2003a) noted that *Sigapatella* has a shell and anatomy similar to the calyptraeid genera *Calyptraea*, *Trochita* Schumacher, 1817, and *Zegalerus* Finlay, 1926. Collin (2003b) considered *Sigapatella* to be monophyletic but did not mention *Spirogalerus*. Marshall (2003) recognized *Sigapatella* (=*Zegalerus*) as a distinct genus based on its shelf edge being broadly and evenly concave instead of sigmoidal. This is a very different shelf than that of *Calyptraea chinensis* (Figure 68). The differences between *Spirogalerus* and *Sigapatella* are similar to those found between *Lysis* and *Garzasia*, and the New Zealand forms also record an evolutionary pattern of enlargement of the last whorl and the aperture, with broadening of the columella/inner lip area into a shelf within a limpetiform shell. Thus, these two genera were probably not links from actual crepidulids, but represent links from lysines to calyptraeids.

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APPENDIX 1

LOCALITIES CITED

Localities are LACMIP, unless otherwise noted. All quadrangle maps are U. S. Geological Survey maps. Bracketed numbers are areas shown on Figure 1.

[4] CASG 61794. [= CAS 1346-A]. In conglomeratic sandstone 1.6 km (1 mi.) above mouth of Huling Creek, North Fork Cottonwood Creek, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Budden Canyon Formation, Bald Hills Member. Late Albian.

7333. Le Fayel, Paris Basin, France. Late Eocene (Bartonian Stage).

[18] 10095. [=CIT 83]. Fine sandstone just above shale, sectionline fence gate on old road 0.4 km (1/4 mi.) W of Schulz Ranch, 122 m (400 ft.) S. of northeast corner of section 19, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1968), south side of Williams Canyon, Santa Ana Mountains, Orange Co., California. Coll.: B. N. Moore, 1 January, 1926. Ladd Formation, uppermost Holz Shale Member. Early Campanian.

[16] 10711. [=CIT 1158]. Approximately 1.84 km (1.5 mi.) due west of Los Angeles-Ventura Co. line on the boundary (extended) between T. 1 N and T. 2 N, north bank of Bell Canyon, southeast slope of Simi Hills, Calabasas Quadrangle (7.5 minute, 1952), Ventura Co., California. Coll.: W. P. Popenoe, 18 July, 1935. Chatsworth Formation. Middle Campanian.

[3] 10757. [=CIT 1593]. Massive sandstones in bed of North Fork Bear Creek, approximately 777 m (2550 ft.) south and 533 m (1750 ft) east of northeast corner of section 5, T. 31 N, R. 1 E, Whitmore Quadrangle (15 minute, 1956), Shasta County, California. Coll.: W. P. Popenoe and W. M. Tovell, 12 Sept., 1941. Redding Formation, Bear Creek Sandstone. Coniacian.

[5] 10846. [=CIT 1014]. Concretions in sandstone, right bank of Chico Creek about 1.6 km (1 mi.) upstream from the little bridge across creek below Mickey house and about 4.16 km (2.5 mi.) N6°W of 14-mile house on Humboldt Road, NW 1/4, SE 1/4 of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll: W. P. Popenoe and D. W. Scharf, 16 August, 1931. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian.

[23] 11944. Approximately 10 km N of Punta Abreojos (SW of San Ignacio), in first ridges N of arroyo that crosses Punta Abreojos road (dirt) just S of Campo Rene turnoff, approx. 2 km NW of road. Approx. 2–3 km up ravine, hill .5 km to east is pachydiscid loc., Viscaiano Peninsula, Baja California Sur, Mexico. Coll.: R. Demetrion, 1987, 1989. Valle Formation. Middle? Campanian, with *Hoplitoplacenticeras*?

[14] 14310. About 450m north and 70m west of lookout at summit of Warm Springs Mountain at elev. of 1052 m (3450 ft.), at base of Kirby's (1991, M. A. Thesis) measured section no. 2, Warm Springs Mountain Quadrangle (1958), Los Angeles County, California. Coll.: M. X. Kirby. Basal San Francisquito Formation. Late Maastrichtian.

22340. Gritty conglomeratic sandstone lenses in fine-grained sandstone and shales, east side Grapevine Canyon about 0.8 km (0.5 mi.) south of its north end, about 0.4 km (0.25 mi.) east of, and 30.48 m (100 ft.) above the abandoned highway roadbed on east side of canyon, at about 648 m (2100 ft.) contour, about 91 m (300 ft.) northwest of Tejon/granite fault contact. Locality is 3048 m (10,000 ft.) N24°W of 3174 ft. BenchMark at old Fort Tejon, Tejon Quadrangle, Kern County, California. Coll: W. P. Popenoe, 9 December, 1946. Tejon Formation. Middle Eocene.

22386. Prominent shell bed at crest of ridge on east side of Live Oak Canyon, about 0.4 m (0.25 mi.) south of its mouth, T 10 N, R 19 W, Pastoria Creek Quadrangle, 7.5', 1958, photorevised 1974, Kern County, California. Coll.: W. P. Popenoe, 13 March, 1947. Tejon Formation, Metralla Sandstone Member. Middle to upper Eocene ("Tejon Stage").

[10] 22588. About 2/3 of the way to the top of a gully on southwest slope of a northwest-trending hill on south side of Garzas Creek, where the creek enters the San Joaquin Plain, approximately 610 m south and 183 m west of northeast corner of section 19, T 8 S, R 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, west side of San Joaquin Valley, Stanislaus Co., California. Coll.: W. P. Popenoe and T. Susuki, April, 1950. Moreno Formation, "Garzas Sand" member. Middle Maastrichtian.

[4] 23464. [PR1] Up small creek from Sulivan Ranch Rd. crossing, and 1.28 km (0.8 mi.) north of ranch, near Gas Point Rd., 701 m (2300') N 75°E from mouth of Huling Creek, 579 m (1900') S, 488 , (1600') E of NW corner of section 16, T. 30 N, R. 6 W, Ono Quadrangle (15 minute, 1952), Shasta Co., California. Coll.: P. U. Rodda and M. A. Murphy, May 1955. Budden Canyon Formation, Bald Hills Member, unit iv in Matsumoto, (1960). Middle Cenomanian, probably *Turrilites costatus* Zone.

[5] 23617. Fossil in hard, blue-gray concretion in gray-weathering buff sandstone approximately 15.2 m (50 ft.) below highest conglomerate, approx. 0.8 km (0.5 mi.) upstream from Mickey house on west side of Chico Creek, 1.52 m (5 ft.) above stream, 716.28m (2350 ft.) north, 609.6 m (2000 ft.) west of southeast corner of section 1, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte Co., California. Coll.: R. B. Saul, 14 August, 1955. Chico Formation, top of Ponderosa Way Member. Late Coniacian or early Santonian.

[5] 23639. In concretions in massive, greenish-gray sandstone, east bank of Chico Creek, west of meadow with large flat-topped, lava block at north edge near road, 373.38 m (1225 ft.) south and 292.6 m (960 ft.) west of northeast corner of section 23, T. 23 N, R. 2 E, Paradise Quadrangle (15 minute, 1953), Butte County, northern California. Collectors: L. R. Saul and R. B. Saul, 20 August, 1952. Chico Formation, lowermost part of Ten Mile Member. Early Campanian.

[12] 24122. Fine- to coarse grained buff sandstone; 76.2 m (250 ft.) north of jeep trail in Jalama Canyon; elevation 190 m (625 ft.), 6.58 km (4.11 mi.) east and 1.1 km (0.69 mi.) south of Jalama Ranch Headquarters; 0.93 km (0.58 mi.) west and 0.66 km (0.41 mi.) north of southeast corner of topo, Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: D. Dailey, August, 1959. Jalama Formation. Late Campanian-early Maastrichtian.

[12] 24128. Dark gray conglomerate in first small canyon east of Ramajal Canyon, elevation 167.6 m (550 ft.), 0.54 km (0.34 mi) south, 3.25 km (2.03 mi.) east of Jalama Ranch Headquarters, 1.22 km (0.76 mi.) north 4.27 km (2.67 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: D.

Dailey, August 1958. Jalama Formation. Late Campanian-early Maastrichtian.

[12] 24237. Medium-grained, buff, arkosic sandstone, 396.2 m (1300 ft.) north of Jalama Creek, elevation 160 m (525 ft.), 0.48 km (0.30 mi.) south, 3 km (1.88 mi.) east of the Jalama Ranch Headquarters, 1.28 km (0.80 mi.) north, 4.59 km (2.87 mi.) west of southeast corner of Lompoc Hills Quadrangle (7.5 minute, 1959), Santa Barbara Co., California. Coll.: W. P. Popenoe, September 1938. Jalama Formation. Late Campanian-early Maastrichtian.

[6] 24340. Penz vicinity, conglomerate beds cropping out just below a drainage canal, southeast side of new Oroville Hwy, about 1.2 km (0.75 mi.) northeast of intersection with Pentz-Magalia-Oroville road, 426.7 m (1400') S., 182.9 m (600') W of the northeast corner of section 36, T. 21 N, R. 3 E, Cherokee quad. (7.5 minute, 1949), Butte Co., California. Coll.: W. P. Popenoe, 1960. Chico Formation, Musty Buck Member. Early Campanian.

[8] 24349. [=USGS M8601 and USGS M8745]. In place? large angular block of sandstone surrounded by sand at shoreline in covelet on north side of elongate seaward-pointing rock; approx. N30°W of Pigeon Point lighthouse, just south of Bolsa Point, Pigeon Point Quadrangle (7.5 minute, 1952), San Mateo County, California. Coll.: L. R. and R. B. Saul, October 11, 1960. Pigeon Point Fm. Middle Campanian.

[16] 26020. [=CIT 1158]. Hard sandstone slabs in fine-grained sandstone, cropping out on high bare cliff, north bank of Bell Canyon, just east of mouth of large gully, and 152.4 m (500') S, 2743.3 (9000') west of northeast corner of section 4, T. 1 N, R. 17 W, Calabasas Quadrangle (7.5 minute, 1952), Simi Hills, Ventura Co., California. Coll.: W. P. Popenoe, 11 Feb., 1972. Chatsworth Formation. Middle Campanian.

[10] 26353. Approximately 1.2 km south of Garzas Creek, 671 m south and 114 m east of northwest corner of section 20, T 8 S, R 8 E, Howard Ranch Quadrangle, 7.5', 1953, photorevised 1971, Stanislaus County, California. Coll.: R. B. Stewart and W. P. Popenoe, 1944. Moreno Formation, "Garzas Sand" member. Late early to early late Maastrichtian.

[11] 26370. Reworked fossiliferous Turonian blocks in upper Campanian conglomerate lens in shale, northeast side of Cooper Canyon, approx. 411.5 m (1350') n, 670.6 m (2200') W of southeast corner of section 2, T. 21 S, R. 14 E, Alcalde Hills Quadrangle (7.5 minute, 1969), Alcalde Hills, Fresno Co., California. Coll.: J. Alderson, 18 June, 1977. Panoche Formation, "Alcalde Shale" Member. Late Turonian (with juvenile *Subprionocyclus* sp.).

[18] 26951. Small sandstone lens approx. 6.1 m (20 ft.) above road in roadcut on north side of Silverado Truck Trail, 274.3 m (900 ft.) south of northeast corner of section 18, T. 5 S, R. 7 W, El Toro Quadrangle (7.5 minute, 1949), Orange Co., California. Coll.: A. A. Almgren, 4 Dec., 1981. Ladd Formation, uppermost Upper Holz Shale Member. Late early Campanian.

[17] 26967. Small exposure of coarse-grained, poorly sorted sandstone at bottom of northwest-flowing tributary to main fork of Garapito Creek, 449.6 m (1475 ft.) and 2835 m (9380 ft.) east of northwest corner of section 5, T. 1 S, R. 16 W, Topanga Quadrangle (7.5 minute, 1952, photorevised, 1981), Santa Monica Mountains, Los Angles County, California. Coll.: J. M. Alderson, 31 Dec., 1981. Tuna Canyon Formation. Coniacian.

[3] 28717. South Cow Creek Valley, sandstone associated with conglomerate, lower South Cow Creek Valley, about 152.4 m (500 ft.) downstream from old bridge site across creek, and about 1.6 km (1 mi.) due west of buildings on Hunt Ranch, NE 1/4 of section 17, T. 31N, R. 2W, Millville Quadrangle, Shasta Co., California. Coll.: W. P. Popenoe, 27 Oct., 1971. Redding Formation, Oak Run Conglomerate Member of Haggart, 1986. Late Santonian.

[19] SDNHM 3403. Taylor Made Golf Facility at Salk Drive and College Blvd., elevation 45.1 m (148 ft.) along College Blvd., lat. 33°8'25' N, long. 117°16'56' W, [in general = SDNHM 3402, 3404, 4071, 4073], Carlsbad Research Center, Site 29, San Luis Rey Quadrangle 7.5' (1968), San Diego Co., California. Coll.: B. O. Riney, 26 April, 1987. Point Loma Formation. Late Campanian/?early Maastrichtian.

[19] SDNHM 3405. Carlsbad Research Center, 1.6 km north and 2.7 km west of southeast corner of San Luis Rey Quadrangle 7.5' (1968), indicated area along west side of College Blvd, starting about 0.32 km from intersection with El Camino Real extends southward for 0.15 km, San Diego Co., California. Coll.: B. O. Riney, 1987. Point Loma Formation. ?Late Campanian/early Maastrichtian.

[18] UCMP 2167. 3.2 km (2 mi.) N 10°W of BM 1271, Corona Quadrangle (1902), at a gate about 0.8 km (0.5 mi) below Modjeska Springs in Williams Canyon, Santa Ana Mountains, Orange Co., California. Ladd Formation, uppermost Holz Shale. Middle? Campanian.