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Cover illustration: . Copy of a Kodachrome 35-mm slide (taken by the author) of the apertural view of the missing holotype of *Ancistrolepis carolineae* Squires, 1984 from the “Stewart bed” at LACMIP Locality 40374, measuring length 32 mm, width 20 mm.

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The earliest *Ancistrolepis* (Gastropoda: Buccinidae) and its geologic implications

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The buccinid gastropod *Ancistrolepis carolineae* Squires, 1984 is the earliest known and shallowest marine species belonging to the extant genus *Ancistrolepis* Dall, 1895, which is endemic to the North Pacific region. This species is of late early Eocene (Ypresian Stage) age and is about 7 million years older than the previously oldest known record (late Eocene) of the genus. This rare species occurs at several localities in a 1-m thick bed (“Stewart bed”) of fossiliferous shallow-marine sandstone within the Llajas Formation, on the north side of Simi Valley, Ventura County, southern California. The “Stewart bed” contains a rich fauna of subtropical mollusks and other invertebrates, which lived just below effective wave base, at the distal edge of a braid delta, immediately adjacent to an upper bathyal prodelta/slope environment, where a rich microfauna of calcareous nannofossils and benthic foraminifers lived. Dispersal of *A. carolineae* would have been either via drifting of buoyant “pouches” containing its non-planktonic eggs or by rafting of its adults in buoyant plant-material debris. The dispersal of *A. carolineae* northward coincided with the cooling of the North Pacific waters during the late Eocene, thereby providing the opportunity for *Ancistrolepis* to adapt to living in bathyal waters and also to living in association, in some cases, with chemosynthetic (methane) cold seeps.

Keywords: Early Eocene, California, shallow marine, subtropical, Llajas Formation

INTRODUCTION

A restudy of specimens of the the buccinid gastropod *Ancistrolepis* (Dall, 1891), from the upper lower Eocene (upper Ypresian Stage) part of the Llajas Formation, north side of Simi Valley, Ventura County, southern California (Fig. 1), allows for better identification of this gastropod. Formerly identified as *Ancistrolepis? carolineae* Squires, 1984, it is now identified unquestionably as being an *Ancistrolepis*, thereby extending significantly the earliest occurrence of this genus from the late Eocene to the latest early Eocene age (late Ypresian Stage). *Ancistrolepis carolineae* is found only in a single bed, called the “Stewart bed,” which, as discussed below, was deposited in a subtropical, shallow-marine environment at the distal edge of a braid delta. This genus is extant and endemic to the North Pacific region. The geographic distribution of its living species are very close to that of its fossil species, namely, in southern California, Japan,

Sea of Okhotsk, Kamchatka, Bering Sea, Alaska, and Washington. The habitat occurrences of its living species are also very close to that of nearly all of its fossil species, namely, in deep offshore and bathyal waters, including some Eocene, Oligocene, and Miocene cold seeps (Amano and Oleinik 2016).

MATERIAL AND METHODS

Seventeen specimens were used in this present project in order to re-evaluate the identification of the gastropod originally identified as *Ancistrolepis? carolineae* Squires, 1984. A few of these specimens were collected by the late W.P. Popenoe in 1946 and 1950, and they were placed in the UCLA Collection, later accessioned by LACMIP. The rest of the specimens were collected by the author between 1977 and 1980, and most of them were placed in the CSUN Collection, later accessioned by LACMIP (Groves et al. 2003). A few of the specimens collected by

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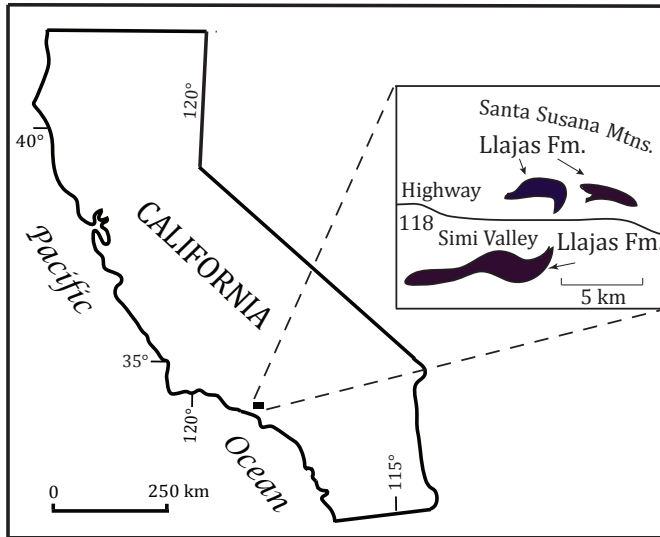


Figure 1. Index map of the Simi Valley, Ventura County, southern California and distribution of the outcrops of the Eocene Llajas Formation.

the author were retained for his personal collection. The best preserved ones of these had their aperture plugged with well-cemented rock matrix. Recently, the author cleaned these particular specimens by the careful use of very sharp needles. This cleaning was the key to exposing critical morphologic information about this species and its identification as to genus.

In this present paper, the term “northeast Pacific” refers to southern Alaska, Washington, Oregon, and California; the term “northwest Pacific” refers to Japan, Kuril Islands, Sea of Okhotsk, Kamchatka, and the Bering Sea; and the term “North Pacific” refers to both regions together. The classification system of Kantor et al. (2021) is used. Morphologic terms are from Cox (1960a). Depositional-environment terms are from Reineck and Singh (1980).

Institutional Abbreviation— CSUN, California State University, Northridge, California (collection now stored at LACMIP). LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology. UCLA, University of California, Los Angeles (collection now stored at LACMIP).

GEOLOGIC SETTING OF THE “STEWART BED”

Stratigraphy and Depositional Environment

An overview of the vertical succession of the sedimentary depositional environments (facies) of the Llajas Formation is given in Figure 2. The conglomeratic section at the base of the formation was originally interpreted

as a coastal-alluvial deposit (Squires, 1981, 1983, 1984), but a revised interpretation, given here for the first time, is that it is a fluvial deposit deposited by an ancestral river that emanated from western region of the North American continent, prograded into the Pacific Ocean, and created a braid delta. McPherson et al. (1987) coined the term “braid delta,” which is a gravel-rich delta that forms where a braided river system progrades into a standing body of water. The upper part of the Llajas fluvial conglomerate interfingers with the immediately overlying shallow-marine beds. Upsection from this interfingering is the thickest part of the Llajas Formation, namely, shallow-marine beds that accumulated as lower shoreface deltaic sandstone, with scattered molluscan fossils concentrated by wave action (Figs. 2, 3).

The “Stewart bed” caps the thick shallow-marine-sandstone section. This informally named bed is 1-m thick, mappable, and has a lateral extent of 10 km. It consists of poorly sorted (silt-to-granule), angular to sub-angular, glauconitic, subarkosic fossiliferous sandstone. It contains a diverse subtropical macrofauna (Squires 1984, 2001), which represents an mollusk-dominated indigenous death assemblage that underwent a much smaller amount of post-mortem transport, as well as

	Facies	Thickness (m)	Lithology
braid delta	shallow marine (progradational)	66	mostly bioturbated silty sandstone with few shells
	upper bathyal prodelta/slope channelized turbidites	124	siltstone rich in microfossils turbidite sandstone in two vertically stacked channels (both 180 m wide and 20 m thick, separated by siltstone)
braid delta	“Stewart bed” ↗ shallow marine (progradational)	280	see text very fine sandstone: numerous repetitions of storm beds (laminated sandstone) and fair-weather (bioturbated) sandstone and scattered lentils of shells
	shallow marine interfingering w/ fluvial	30	pebble conglomerate and fossiliferous sandstone with worn, broken shells in small channels
	fluvial	20 to 40	quartzite cobble-boulder conglomerate (80%) and fine to granule sandstone (20%)

Figure 2. Overview of the depositional environments (facies) of the Llajas Formation. Data from Squires (1981, 1983) and updates in the present paper.

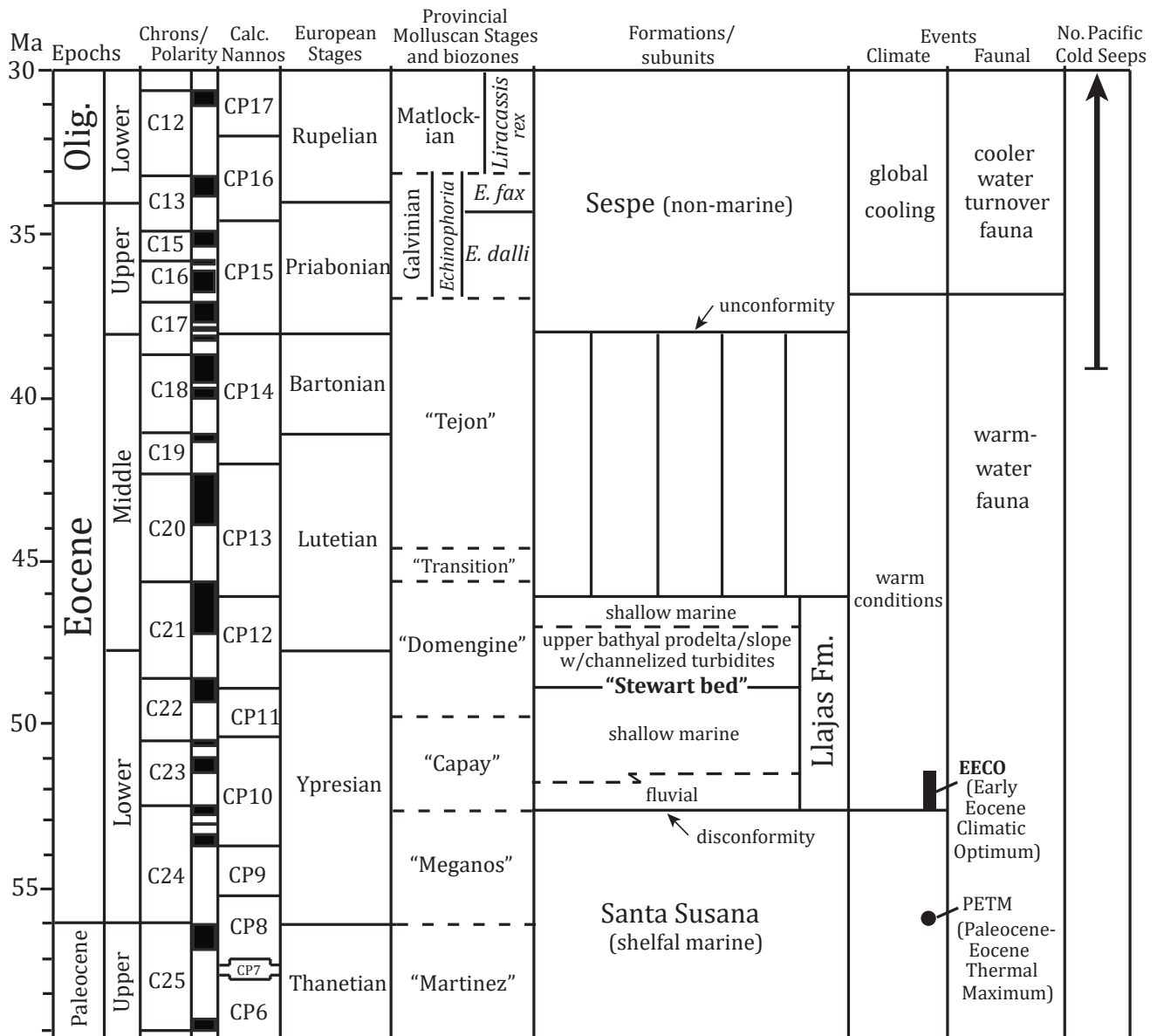


Figure 3. Chronostratigraphic diagram showing the depositional environments (facies) of the Llajas Formation and the underlying and overlying formations (from Squires 1981, 1983, 1984, and updates made, in the present paper, by the author). Geologic time scale, chrons/polarity, calcareous nannofossil Zones, European Stages, and timing of global climate events from Gradstein et al. 2012: fig. 28.11). Northeast Pacific provincial molluscan stages from Squires (2003: fig. 2.1). Timing of the beginning of the “Cooler water turnover fauna” from Squires (2003: fig. 2.1). Earliest record of North Pacific cold seeps from Goedert and Squires (1990).

much less winnowing, in comparison to the fossiliferous assemblages in the underlying shallower marine deposits (Squires 1981). Locally the “Stewart bed” can approach being an *in situ* paleocommunity, and a reconstruction of this community is shown by Squires (1983: fig. 13). Specimens of *Ancistrolepis carolineae* are present only in the “Stewart bed.” They were found at four localities, and the majority of the specimens are from LACMIP Locality 40374. At this locality, a few wood fragments (up to 5 cm in length) have been found.

The “Stewart bed,” located at the distal edge of the aforementioned braid delta, is directly overlain by siltstone that makes up the majority of the prodelta/slope sedimentary section (Fig. 2). This siltstone unit was formerly referred to as “outer shelf to slope” deposits by Squires (1981, 1983, 1984, 2001). The contact at the base of the siltstone unit is transitional with the “Stewart bed,” based on the presence of local lentils (20 cm thick) containing “Stewart bed”-like lithology and similar, but much less diverse, fossil content, interbedded within the lower

few meters of the overlying siltstone. The prodelta/slope deposits have a paucity of macrofossils but contain a richly diverse microfossil fauna, including cassidulinid, gryoidinids, and agglutinated benthic foraminifers, all of which are indicative of “inner neritic to upper bathyal” depths (Schymiczek 1983). A few displaced and broken mollusks, as well as some wood fragments (Squires 1981), are present in the turbidite-filled channels in the lower part of the prodelta/slope section (Figs. 2, 3).

The prodelta/slope section accumulated when the rate of deposition of the braid delta decreased and was exceeded by the rate of subsidence of the sedimentary basin. The progradation of the braid delta resumed again during the deposition of the uppermost part of the Llajas Formation, which consists of a relatively thin section of mainly bioturbated shallow-marine silty sandstone and much fewer macrofossils relative to the shallower-depth sandstone section in the lower part of this formation (Squires 1984, 2001).

Macrofossils

The Llajas Formation has a richly diverse shallow-marine macrofossil fauna. Approximately 145 species (including some subspecies) have been reported (Squires 1984, 2001; Nyborg et al. 2017). Approximately 75 percent of these occur in the “Stewart bed,” and the highest diversity is at LACMIP Locality 40374, where most of the specimens of *Ancistrolepis carolineae* were found. Other macrofossils found at this locality are: solitary corals, scaphopods, many gastropods (especially turritellids) and bivalves, nautiloids, burrowing echinoids, and shark teeth. In addition, some “macro-sized” discocylinid orbitoid foraminifers are found in at LACMIP Locality 40374.

Age

The age of the “Stewart bed” is well constrained, based on the presence of calcareous nannofossils, which are among the most precise geologic age indicators of marine strata. Filewicz and Hill (1983: table 2) reported that the “Stewart bed” is correlative with the lower part of the calcareous nannofossil zone CP12. Using Gradstein et al. (2012: fig. 28.1), zone CP12 is equivalent to the late early Eocene part of the Ypresian Stage (Fig. 3). Very similar age assignments obtained by the use of benthic foraminifers were reported by Schymiczek (1983) and obtained by the use of paleomagnetic procedures were reported by Bottjer et al. (1991). More generalized assignments obtained by the use of mollusks were reported by Saul (1983) and by Squires (1983, 1984).

Paleoclimate

The Llajas Formation fauna is indicative of subtropical temperatures (Squires 1987). The early Eocene Climatic Optimum (EECO), which was the warmest time of the Cenozoic, coincided with the lower part of the Llajas Formation (Fig. 2) and warm-water conditions continued throughout the deposition of the rest of the formation.

Paleobiogeographic implications

Some of the thermophilic gastropods present in the Llajas Formation are very similar morphologically (i.e., species pairs) to those found in similar age strata in Western Europe, and it is likely that these molluscan taxa were dispersed by means of a current emanating from the Old World Tethys Sea into the California region. Examples of these gastropods are found among strombids (Squires 2013), cassids (Squires 2019), and ficids (Squires 2014).

Post-Eocene Tectonic Influences

The present-day geographic position of the Llajas Formation bears little resemblance to its original position. This is the result of complex tectonism and associated rotation, which began about 18 million years ago during the Miocene, when the Pacific and North American plates first made contact with one another (Hornafius et al. 1986). At that time, the Simi Valley region and adjacent areas began to be tectonically rotated clockwise and also began northward tectonic displacement via the San Andreas fault system. These movements took place as separate adjacent pieces, rather than as a single rigid block of the Earth's crust. This dynamic tectonic situation is still on-going today. In sum, as illustrated by Onderdonk (2005: fig. 1), the Llajas Formation area has moved northwestwardly from 33°33'N to 34°18'N and has been rotated a total of 90°. The adjacent Eocene-age component parts, all of which were similar in their shallow deltaic environments grading into deeper water prodelta/slope and bathyal environments, were originally laterally adjacent and in a southerly aligned “belt” of depocenters along the Pacific Coast. This “belt” became fragmented and geographically separated by the tectonic movements. Today, from west to east, the Eocene strata making up these various depocenters are referred to as the Juncal Formation, the Matilija Formation, and the Llajas Formation. These formations are exposed as uplifted strata in a 115 km-long “belt” known as the western part of the Transverse Ranges, extending from Point Conception area eastward to the Santa Ynez Mountains and the Simi Valley area (see Squires 1987).

SYSTEMATIC PALEONTOLOGY

GASTROPODA CUVIER, 1795
 CAENOGASTROPODA COX, 1960B
 NEOGASTROPODA WENZ, 1938
 BUCCINOIDEA RAFINESQUE, 1815
 BUCCINIDAE RAFINESQUE, 1815

Remarks—The family Buccinidae, which consists of numerous genera of predatory carnivores, originated during the Early Cretaceous (mid-Albian Stage) (Taylor et al., 1980: fig. 7, with no accompanying geographic data). In the northeast Pacific region, the earliest known buccinid is the Late Cretaceous *Eripachya* Gabb, 1869. It was endemic to California and formed a lineage of three species (Squires and Saul 2003), whose members occurred intermittently only during the warm times of the Turonian and Campanian but not during the cooler times of the Coniacian and Santonian (Squires 2018).

PARANCISTROLEPIDINAE HABE, 1972

Remarks—Kantor et al. (2021) noted that subfamily Parancistrolepidinae Habe, 1972 has priority over Ancistrolepidinae Habe and Sato, 1973. For a list of genera included in Parancistrolepidinae, see Kantor et al. (2021: p. 31).

ANCISTROLEPIS DALL, 1895 SENSU STRICTO

Type species—By original designation. *Chrysodomus eucosmius* Dall, 1891. Dall (1891) did not figure the type species of this genus, but Dall (1895: pl. 29, fig. 7) provided an apertural view. Egorov and Barsukov (1994) provided a synonymy of *Ancistrolepis eucosmius* (Dall). The type species is extant and lives in deep, cold waters in the following areas: Bering Sea area (Dall 1891), north of Unalaska in the Bering Sea (Dall 1891), off the coast of Oregon (Dall 1895), and off San Diego, southern California (Dall 1895, 1919, 1925).

Geologic range of genus—Late early Eocene (late Ypresian Stage = early “Domengine Stage”), Ventura County, southern California (new information) to Recent: from the South China Sea to the East China Sea, the Sea of Japan, Kurile Islands, Sea of Okhotsk, Bering Sea, Aleutian Islands, southern Alaska (Egorov and Barsukov 1994), as well as Washington, Oregon, and off the coast of San Diego, southernmost California (Dall, 1895, 1919, 1925).

Differential diagnosis—Protoconch low (one to two whorls), smooth. Teleoconch small to medium size (height range 25 to 135 mm). Fusiform to elongate

fusiform and with approximately six to eight convex whorls. Whorls can be rounded or shouldered. Spire approximately 50 percent or less of shell height. Sculpture mostly spiral ribs (rarely nodular locally) or cords, can be relatively few (on upper spire) or moderately numerous, triangular to square, thin to moderately thick (keel-like), interspaces somewhat narrow to moderately wide, commonly flat-bottomed. Sutural area impressed. Axial sculpture mostly only growth lines. Last whorl approximately 50 percent or more of shell height. Aperture moderately wide, interior smooth or showing spiral impressions. Columella smooth. Outer lip entire or marginated, rarely thickened. Siphonal canal short and twisted backward, slightly or somewhat strongly. Radula hamiglossate. Periostracum well developed, can be hairy, and with well developed and numerous growth lines. Operculum horny (can be substantially smaller than aperture width).

Remarks—The name *Ancistrolepis* is feminine and derived from Greek: *ankrison*, for fishhook and *lepis* for scale.

ANCISTROLEPIS CAROLINEAE SQUIRES, 1984
 FIG. 4A–I

Ancistrolepis? carolineae Squires, 1984. p. 30, figs. 8d–e. Groves and Squires. 2021. p. 191.

Primary type material—Holotype LACMIP 10554 [originally UCLA 59401], LACMIP Locality 7242.35. Paratype LACMIP 10555, LACMIP Locality 7242.36; paratype LACMIP 10556, LACMIP Locality 7242.37; and paratype LACMIP 10557, LACMIP Locality 22312.14. These three paratypes were originally referred to as lot UCLA 59402, which was, at some point in the past, split into the three lots listed here. LACMIP Locality 7242 is equivalent to UCLA Locality 22312 (originally UCLA Locality 2312 (collected by W.P. Popenoe classes, April 19, 1946 and 1950).

Dimensions of holotype—Length 32 mm, width 20 mm (specimen is missing most its anterior siphonal canal).

Secondary type material—LACMIP hypotype 14904, LACMIP Locality 40444.2; LACMIP hypotype 14905, LACMIP Locality 40374.75; LACMIP hypotype 14906, LACMIP Locality 40374.76; and LACMIP hypotype LACMIP 14907, LACMIP Locality 40374.77.

Number of specimens examined—Seventeen specimens. All are from four localities (7242, 40374, 40444, and 40479) in the “Stewart bed” of the Llajas Formation on the north side of Simi Valley, Ventura County, southern California. Nearly all the specimens are from the Las

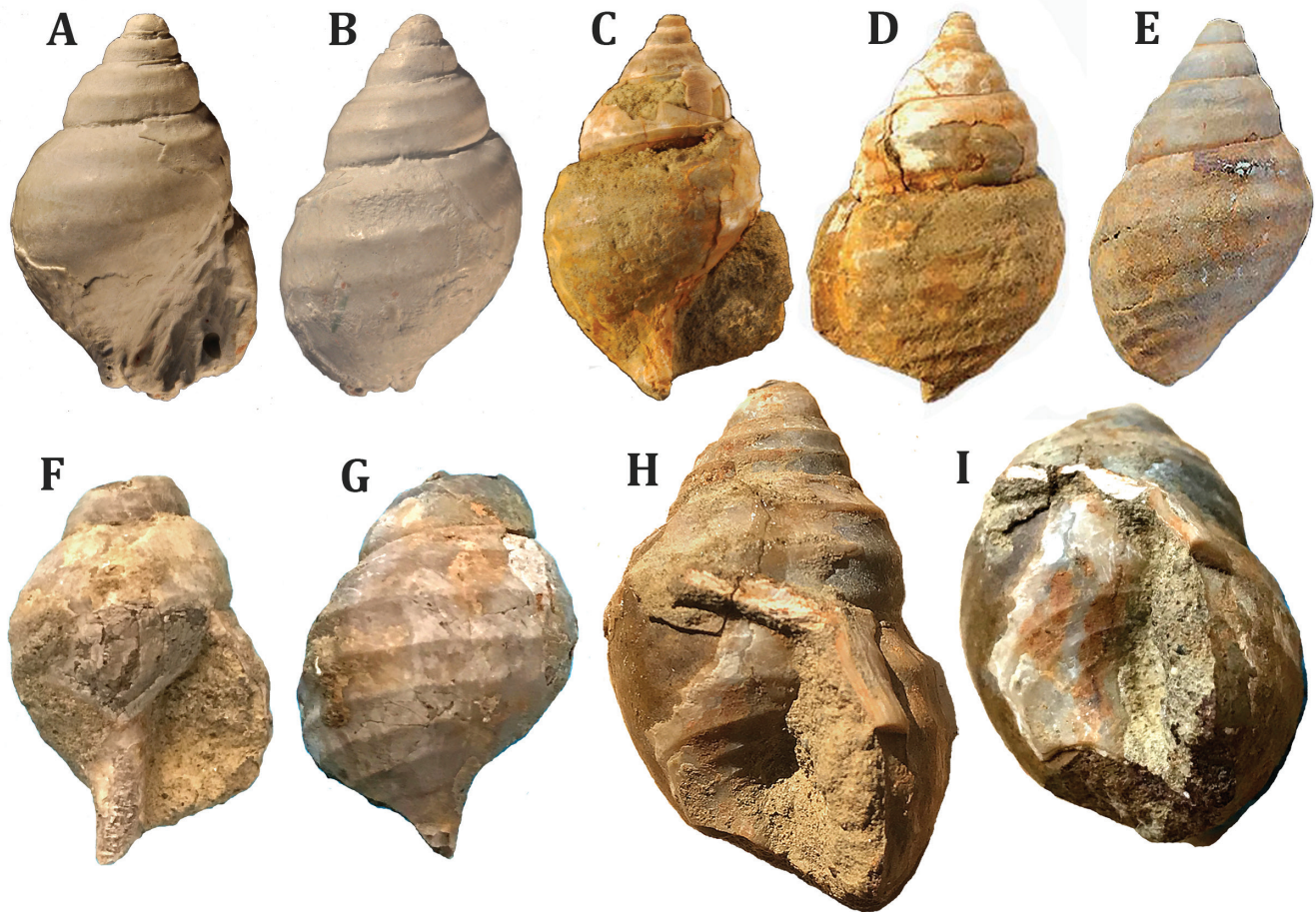


Figure 4A-I. *Ancistrolepis carolineae* Squires, 1984. “Stewart bed,” Llajas Formation, north side of Simi Valley, Ventura County, southern California. Apertural (A) and abapertural (B) views, 1.7x, length 32 mm, width 20 mm, plasto-holotype, LACMIP 10554 [=UCLA 59401], Locality LACMIP 7242.35. Apertural (C) and abapertural (D) views, x1.8x, length 28.8 mm, width 18.4 mm, hypotype, LACMIP 14904, LACMIP Locality 40444.2. Apertural (E) view, 1.8x, length 26.3, width 14.9, hypotype, LACMIP 14905, LACMIP 40374.75. Apertural (F) and abapertural (G) views, x2.3, length 22 mm, width 15.8 mm, hypotype, LACMIP 14906, LACMIP Locality 40374.76. Right-lateral apertural, with aperture end tilted up slightly (H) and oblique lower columellar (I) views, x2.5, length 28.5 mm, width 29.8 mm, hypotype, LACMIP 14907, LACMIP Locality 40374.77.

Llajas Canyon area: LACMIP Localities 7242 and 40374, which are in the immediate vicinity of each other, and Locality 40444, which is a short distance northwestwardly. The one exception is a specimen from LACMIP Locality 40479, approximately 3 km westwardly of the localities in Las Llajas Canyon.

Description—Shell ovate fusiform, shell very thin (“paper thin”), up to 30.4 mm height and 17.7 mm width, with corresponding $h/w = 1.72$; average h/w of all specimens = 1.59. Protoconch/shell apex missing, upper spire incomplete on most specimens. Teleoconch up to 5 whorls; commonly only four teleoconch whorls present. Suture impressed and coincident with spiral rib. Only spiral ribs (widely spaced); no radial sculpture. Earliest two teleoconch whorls smooth (ribs apparently eroded off), 2 ribs on pre-ante penultimate whorl, 2

ribs on ante-penultimate whorl, 3 ribs on penultimate whorl, and 6 (on most specimens) to 8 (rarely) ribs on last whorl. Several widely spaced secondary spiral ribs can be present inside of surface of apertural area and represent continuations of primary ribs on main surface of last whorl. Spacing of spirals usually consistent at 3 mm apart but can be as much as 4 mm apart, even on a single specimen. Spiral ribs beveled (not square-edged); interstitially (especially on columellar inner lip) with five bands of spiral microscopic threads alternating with bands of five spiral submicroscopic threads; comprising a grand total of 25 threads. Columella has almost none to only slight twist to left; no columellar teeth; anterior part of columella can have a few intermediate-strength ribs, becoming obsolete anteriorward and interiorward. Siphonal canal moderately long. Outer lip “terminal

varix," 3 mm thick, smooth, solid, and flattish but with beveled on both outermost and innermost edges; minute threads axially parallel to edge of outer lip.

Remarks—The holotype has been missing for several decades. A copy of a Kodachrome 35-mm slide of the holotype, taken by the author 30 years ago, is shown on the "Cover" of this present paper. The specimens of *A. carolineae* all have moderately poor to poor preservation because of weathering, which has caused some of the shells, which had thin shells to begin with, to become to steinkerns or nearly so. Weathering has probably caused the spiral ribs to be somewhat rounded.

Four of the 17 Llajas Formation specimens of *A. carolineae* have an obvious, relatively wide, flat, and sturdy thickening (callus) of the outer lip (terminal varix) of the aperture. A search of the available literature revealed that no other ancistrolepine (fossil or extant) has such a wide and flat outer lip callus, although a few extant species can have a very thin, narrow ridge callus. A terminal "varix" is common in warm, shallow-marine gastropods, but is rare in polar and deep-marine habitats (Webster and Vermeij 2017), therefore, the presence of this feature on *A. carolineae* might be another indication that *A. carolineae* lived in an environment quite different than the extant *Ancistrolepis* spp.

Ancistrolepis carolineae most closely resembles *Ancistrolepis rategiensis* Titova, 1993 (p. 12, figs. 2A–2D) from the upper Eocene Rategian Formation at Podkagernaya Bay, northwestern Kamchatka. The Llajas Formation species is similar in its ovate-fusiform shell shape, approximately five rounded whorls, rounded base on last whorl, subtriangular to triangular spiral ribs, about seven spiral ribs (can be variously spaced) on last whorl, and interstitial ribs on last whorl of some specimens. *Ancistrolepis carolineae* differs from this Kamchatka species by having a smaller size shell, fewer spiral ribs on the spire whorls, many fewer and much less closely spaced spiral ribs on the siphonal canal, and the presence of a terminal varix on the outer lip.

Titova (1993) reported that *Ancistrolepis rategiensis* Titova, 1993 shows much similarity to *Ancistrolepis matchgarensis* (Makiyama, 1934: p. 165, pl. 7, figs. 56, 57) from the upper Oligocene Asagai Sandstone near Matchgar in northern Sakhalin. The Llajas Formation species is similar, therefore, to *A. matchgarensis*, but this latter species, which has a small shell (like *A. carolineae*) has rather poor preservation (interstitial threads not visible) and its siphonal canal is missing. The Llajas Formation species differs by having a "terminal varix"

on the outer lip. *Ancistrolepis matchgarensis* occurs with calcareous concretions containing *Turritella*, which is a shallow-marine gastropod.

Ancistrolepis carolineae, *A. rategiensis*, and *A. matchgarensis* differ from most other species of this genus by having subtriangular spiral ribs, rounded whorls, and a rounded shell base. Four other species, all from the Kuschiro coal fields in Japan, that share these particular properties are *A. chizuzenensis* (Matsui, 1958); *A. onbet-suensis* (Matsui, 1959); *A. subcarinata* (Matsui, 1958); and *A. ezoana* Takeda, 1953.

Previous workers (Titova 1993, Egorov and Barsukov 1994) have placed various species of *Ancistrolepis* into two informal groups, referred commonly to as the *eucosmius* "stock" and the *grammatus* "stock." The *eucosmius* "stock," bearing the name of the type species of *Ancistrolepis*, is supposedly characterized by relatively small shells with relatively few spiral ribs, which are narrow and have a square shape. The *grammatus* "stock," has larger shells with much stronger spiral ribs, commonly referred to as "T" ribs

DISCUSSION

Overview of the Geologic History of *Ancistrolepis* in the northeast Pacific region

From Paleocene through middle Eocene time, nearly all the marine gastropods on the west coast of North America were shallow-water, warm-water forms and buccinids were scarce (Squires 2003). During the early and middle Eocene, the thermal gradient between the equator and the poles was low (Evans et al. 2018). The most northerly known molluscan fauna during this time interval is the late middle Eocene molluscan fauna is found in the Tolstoi Formation, in the Alaskan Peninsula (Marincovich 1988). The Tolstoi molluscan fauna represents an extremely shallow-water (not greater than 20 m depths), warm-temperate to subtropical-marine environment. No specimens of *Ancistrolepis* have been reported from that formation. One reason for the presence of warm-water mollusks in such a northerly location as the Tolstoi fauna is because the connection between the Arctic and Pacific oceans had not been yet established (Oleinik and Marincovich 2003). The Tolstoi molluscan fauna has close affinities with middle Eocene faunas of southern California (e.g., Tejon Formation) and the Cowlitz Formation in southwestern Washington. The Tolstoi molluscan fauna has lesser affinities with middle and upper Eocene faunas of West Kamchatka. None of the Tolstoi mollusks have been reported in the Japanese

literature (Marincovich 1988).

Prior to the recognition of late early Eocene *Ancistrolepis carolineae* as the earliest known member of this genus, the earliest reported records of *Ancistrolepis* were of late Eocene age in northern Japan, Sakhalin, and Kamchatka (Titova 1993, Amano and Oleinik 2016). The interval of time between these records of occurrence and that of *A. carolineae* is approximately 7 million years. The dispersal of *Ancistrolepis* would have required considerable time because buccinids, including *Ancistrolepis*, are gonochoristic and fertilization is internal. Kantor (1988) reported that up to eight eggs of *Ancistrolepis* (*Clinopegma*) are enclosed within a [leathery] “pouch” (length 52–60 mm) with a stalk (length 195–205 mm) attached to hard substrate, and on the concave side of the capsule there is an operculum for the release of hatching juveniles. As a result of *Ancistrolepis* having direct development, its juveniles emerge out their eggs as crawling young (Egorov and Barsukov 1994). This kind of nonplanktotrophic larval development has little potential of long-distance dispersal (Shuto 1974), yet *A. carolineae* achieved considerable dispersal in the northern Pacific region. One conceivable method of dispersal of *Ancistrolepis* could have been via drifting, if its leathery “pouch” became prematurely detached. Floatation of a “pouch” have been enhanced if any of eggs had already died because any gas generated by their decay would have filled the “pouch,” thereby rendering the whole mass buoyant.

Another plausible and effective mode of widespread dispersal of marine invertebrates, like *Ancistrolepis*, which do not have a pelagic larval phase, was discussed by Winston (2012). It is the rafting of recently hatched young animals or even adults via floating wood (or algal) debris. It is relevant to mention that fragments (up to 5 cm in length) of wood are present in the “Stewart bed.” Wood fragments, up to 18 cm in length, have been found in the upper part of the shallow-marine deposits of the Llajas Formation on the south side of Simi Valley, where unfortunately, the “Stewart bed” is not exposed. At one of these south-side localities, 90 moderately well preserved specimens of a species of raninid crab were seen in one small area in association with pieces of driftwood debris located slightly downsection from the stratigraphic level of the “Stewart bed” (Squires 2001: p. 25).

Dispersal of *A. carolineae*, by drifting and/or rafting, would have been advantageous because of the nearby access to deep waters at the distal edge of the Llajas Formation braid delta. The dispersal history of *Ancistrolepis*

is similar to that of the Miocene buccinid *Chauvetia Monterosato, 1884*, a shallow-marine dweller (no more than 20–30 m depth) with non-planktonic development. *Chauvetia* emigrated (possibly via rafting) from the Caribbean (Venezuela) to the Azores region in the eastern Atlantic Ocean, west of the coast of Portugal (Laudau et al. 2015). A similar case history was the dispersal via vegetation of late Pliocene or Pleistocene “invader” shelled mollusks being transported long distances across portions of oceans or across entire oceans (Vermeij and Rosenberg 1993).

At the beginning of the late Eocene, several faunal turnovers occurred in a stepwise fashion in the northeast Pacific region, when cooler-water taxa appeared (Squires 2003, Oleinik and Marincovich 2003, Nesbitt 2003, Hickman 2003). Shallow-marine gastropods changed stepwise, from predominantly cosmopolitan to more locally distributed taxa (Oleinik and Marincovich 2003). The onset of global cooling has traditionally been the proposed reason for these faunal changes. Vermeij et al. (2018) recognized correctly that there many “mysteries” about the details of the geographical origins of clades in the North Pacific during the transformation of this region from a subtropical ocean during the early Eocene to the cold ocean of today. The new discoveries of the late early Eocene origin of *Ancistrolepis carolineae* in intermediate-latitude, shallow-marine subtropical waters in southern California are strongly suggestive that a northward dispersal of *Ancistrolepis* into higher latitude and into associated cooler waters coincided with the cooling of the entire North Pacific region.

Another interesting aspect of the evolution of *Ancistrolepis* is that most of its fossil species lived in sublittoral deep-waters (Amano and Oleinik 2016). In the late Eocene, there was a sudden and significant increase in the occurrence of cold-seep sites (Kiel 2009), as a result of changes in the rate of plate-tectonics-related subduction in the northern region. Locally during the late Eocene, *Ancistrolepis* began to live in the cold-seep environment. The earliest record, to date, of a cold-seep *Ancistrolepis* is the late Eocene *Ancistrolepis modestoideus* (Takeda, 1953) from Hokkaido (Amano and Oleinik 2016). It is important to mention, however, that *Ancistrolepis* is not a chemosymbiotic organism; instead, it is a predator and/or scavenger that feeds on chemosymbiotic organisms (e.g., tube worms and bivalves). Since the late Eocene, all mollusks, including *Ancistrolepis*, diversified rapidly and spread geographically within the northern Pacific (Titova 1993, 1994). The highest biodiversity today of buccinids is in the temperate northern Pacific (Okutani 2017).

Kantor et al. (2021: p. 61) did a thorough review of the Cenozoic routes of migration/colonization of the buccinids in the North Pacific and adjacent oceans. They concluded that the northern Pacific buccinids, as a group, invaded the Arctic and Atlantic oceans, but only after the opening of the Bering Strait during Pliocene time (3.5 Mya). *Ancistrolepis*, however, was not a member of this invasion (Amano et al. 1996).

Most of the the living species of *Ancistrolepis* live today in deep-cold bathyal waters between 88 and 890 m depth in boreal regions between approximately 43°N and 60°N. More specifically, these areas are in northern Japan, Sea of Okhotsk, Sakhalin, Kurile Islands, Kamchatka, Bering Sea, and the Aleutian Islands of Alaska (Egorov and Barsukov 1994; Honda 2000), but not in the Arctic Ocean. *Ancistrolepis californicus* Dall, 1919 (p. 313; 1925: pl 2, pl. 3, fig. 9), the only other occurrence of this genus from southern California, lives in bathyal waters (984 fathoms) at Cortes [Cortez] Bank, off the coast of San Diego. *Ancistrolepis vietnamensis* Sirenko and Goryachev, 1990 is the only living species of this genus found in the tropical realm, in the Sea of China at 11°N, 108°55'E, but at a depth of 460 m (Egorov and Barsukov 1994: see caption of fig. 18).

Titova (1993) and Vermeij et al. (2018) considered that cool-water buccinids had a western North Pacific origin, and given the previously known fossil record of *Ancistrolepis*, such an assumption was logical. The newly established earliest occurrence of this genus in the eastern North Pacific (California) during late Eocene time, however, establishes that this buccinid genus does not fit the general rule.

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