THE VELIGER
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The Veliger 33(3):305-316 (July 2, 1990)

First Occurrence of the Tethyan Bivalve *Nayadina* (*Exputens*) in Mexico, and a Review of All Species of This North American Subgenus

by

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Abstract. The malleid bivalve *Nayadina* (*Exputens*) has Old World Tethyan affinities but is known only from Eocene deposits in North America. *Nayadina* (*Exputens*) is reported for the first time from Mexico. About 50 specimens of *N.* (*E.*) ***batequensis*** sp. nov. were found in warm-water nearshore deposits of the middle lower Eocene part of the Bateque Formation, just south of Laguna San Ignacio, on the Pacific coast of Baja California Sur.

The new species shows a wide range of morphologic variability especially where the beaks and auricles are located and how much they are developed. A review of the other species of *Exputens,* namely *Nayadina* (*E.*) *llajasensis* (Clark, 1934) from California and *N.* (*E.*) *ocalensis* (MacNeil, 1934) from Florida, Georgia, and North Carolina, revealed that they also have a wide range of morphologic variability. *Nayadina* (*E.*) *alexi* (Clark, 1934) is shown, herein, to be a junior synonym of *N.* (*E.*) *llajasensis.*

The presence of a byssal sinus is recognized for the first time in *Exputens.* An epifaunal nestling mode of life, with attachment by byssus to hard substrate, can now be assumed for *Exputens.*

INTRODUCTION

The macropaleontology of Eocene marine deposits in Baja California Sur, Mexico, is largely an untouched subject. Recent collecting by the author and Robert Demetrion from outcrops of the Eocene Bateque Formation in this area has resulted in the discovery of a varied and rich macrofauna. During field work, numerous specimens of the malleid bivalve *Nayadina* (*Exputens*) ***batequensis*** sp. nov. were found. *Exputens,* a warm-water bivalve with Old World Tethyan affinities (PALMER, 1967), is restricted to North America. Although two uncommon species had been reported from California, these two species are herein shown to be the same. *Exputens* is known also from one, uncommon species in the southeastern United States. Discovery of this interesting but scarce subgenus in Baja California Sur, therefore, represents a significant new find.

Attempts to identify the *Exputens* material of the Bateque Formation at the specific level were met with difficulty because of the incomplete knowledge of the existing species. It became necessary to thoroughly examine them, and after such a study, it was found that the Bateque material belongs to a new species.

The intent of this paper is not only to report the new stratigraphic and geologic occurrence of a new species of *Exputens* but also to revise the description of this subgenus, as well as the description of each of its other species. These revisions are based on new material, as well as a restudy of type material. Recognition of previously undetected morphologic features common to all these species also allows for new insights as to how *Exputens* lived. In addition, the wide range in morphologic variation in the other species is photographically documented.

Abbreviations used for catalog and locality numbers are as follows: CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Autónoma Museum de México; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCLA, University of California, Los Angeles (collections

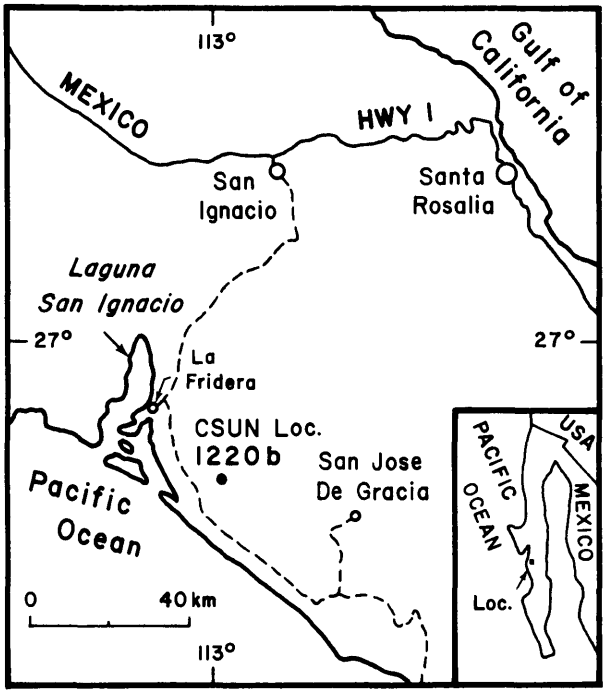


Figure 1

Index map to California State University, Northridge (CSUN) collecting locality 1220b, Bateque Formation, Baja California Sur, Mexico (after SQUIRES & DEMETRION, 1989).

now housed at the Natural History Museum of Los Angeles County); UCMP, University of California Museum of Paleontology, Berkeley; UCR, University of California, Riverside; UF, Florida Museum of Natural History, University of Florida, Gainesville; USNM, U.S. National Museum of Natural History, Smithsonian Institution.

MATERIALS

A total of 50 specimens of *Nayadina* (*Exputens*) ***batequensis*** were found in the Bateque Formation at locality CSUN 1220b, which is about 75 km southwest of San Ignacio, Baja California Sur, Mexico (Figure 1). Ten of these specimens were too fragmental to be useful. Of the remaining specimens, there are about equal numbers of left and right valves. Two specimens are articulated.

A total of 35 specimens of *Nayadina* (*E.*) *llajasensis* (Clark, 1934) were studied. Five of the specimens are the primary type material from locality UCMP 7004, northern Simi Valley, southern California. The other specimens, except for one, are from this same locality and include 25 specimens borrowed from LACMIP and four more collected by the author. A single specimen was collected by the author from locality CSUN 473, also in northern Simi Valley. Four of the specimens were too fragmental to be useful. Of the remaining specimens, there are roughly equal numbers of left and right valves. Eight specimens are articulated.

Only four specimens of *Nayadina* (*E.*) *alexi* (Clark, 1934) were available for study, and they represent the primary type specimens from locality UCMP A-1007, central California. Three of the specimens are left valves and one is a right valve.

A total of 19 specimens of *Nayadina* (*E.*) *ocalensis* (MacNeil, 1934) were studied. Three of these are the primary type material from localities USGS 6812 and 12751, northern Florida, and the rest came from various localities examined by the University of Florida, Gainesville. Five of the specimens have well-indurated matrix covering the ligamental area. Of the remaining specimens, four are left valves and 10 are right valves.

DEPOSITIONAL ENVIRONMENT AND GEOLOGIC AGE OF THE BATEQUE SPECIMENS

The specimens of *Nayadina* (*E.*) ***batequensis*** in the Bateque Formation were found at locality CSUN 1220b, which is between 96 and 145 m above the base of the exposures of the formation in this area. The specimens were found in several lenses of fossiliferous, very fine-grained sandstone surrounded by bioturbated, very fine-grained sandstone. Associated macrofauna included stromatolites, coralline algae, calcareous sponges, colonial and solitary scleractians, encrusting and branching bryozoans, thick-shelled gastropods and bivalves, nautiloids, crabs, spatangoids, and sea urchin spines. A new species of calcareous sponge (SQUIRES & DEMETRION, 1989), new species of gastropods (SQUIRES & DEMETRION, 1990), and new taxa of bivalves (SQUIRES & DEMETRION, in press; SQUIRES, in press) have been described from this locality. The fossiliferous lenses represent storm-deposit concentrations in an inner shelf warm-water environment, and the amount of post-mortem transport was not great (SQUIRES & DEMETRION, in press). Lack of transport is also supported by the presence of articulated specimens of *N.* (*E.*) ***batequensis***, as well as by the approximately equal number of unabraded left and right valves of this bivalve.

The fossiliferous lenses at locality 1220b contain planktonic foraminifera indicative of the early Eocene *Globorotalia aragonensis* or *G. pentacamerata* Zone of STAINFORTH *et al.* (1975), which is equivalent to the P8 or P9 Zone as used by BERGGREN *et al.* (1985) (SQUIRES & DEMETRION, 1990).

MODE OF LIFE OF *Exputens*

Of the previous workers, only CLARK (1934:271) offered an opinion as to how *Exputens* lived. He concluded that it was probably a nestler, based on surface irregularities in the shell, variability in form, generally elongate shape, and the lack of any well-defined byssal sinus. Presumably, he considered *Exputens* to be an unattached nestler.

In the present study, however, a byssal sinus is recognized for the first time in *Exputens*. Furthermore, it is present in all the species of this subgenus, which may have

been byssate epifaunal nestlers or, possibly, byssate fissure dwellers. Such bivalves commonly inhabit nearshore, shallow-water environments where firm substrate is available, as in reefs or on the roots of marine plants (KAUFFMAN, 1969).

Abundant fragments of reef corals are associated with *Nayadina* (*E.*) ***batequensis*** in the Bateque Formation. In addition, there is a strong possibility that marine plants were associated as well, because *Pycnodonte* oysters with possible scars of marine plants were found with *Exputens* at locality CSUN 1220b (SQUIRES & DEMETRION, in press). All valves of *N.* (*E.*) ***batequensis*** have a distinct groove that shows the former position of the byssal sinus. The distinctness of the groove indicates that the byssus was robust. In the relatively high-energy nearshore environment in which this species lived, a robust byssus would have been necessary to provide adequate attachment.

Abundant shell debris could have served as firm substrate for the numerous specimens of *Nayadina* (*E.*) *llajasensis* from the "Stewart bed" at locality UCMP 7004 in the Llajas Formation. SQUIRES (1981, 1984) reported that the macrofossils in the "Stewart bed" at this locality (=locality CSUN 374) represent a shelf-slope break paleocommunity consisting of at least 50 species of mollusks. Many bivalves, including *Exputens,* are articulated and large. They were able to grow to maturity in this moderately calm-water environment. Many valves of *N.* (*E.*) *llajasensis* have only a weakly developed groove that shows the former position of the byssal sinus. The weak development of the groove indicates that the byssus was not very robust. In the moderately calm-water environment in which this species lived, a moderately robust byssus would have provided adequate attachment for most of the specimens.

No detailed information is available concerning the paleoenvironment of *Nayadina* (*E.*) *ocalensis.* However, it is likely that *N.* (*E.*) *ocalensis* lived in a relatively high-energy environment much like that of *N.* (*E.*) ***batequensis*** because the groove that shows the former position of the byssal sinus is distinct in both. The presence of small pebbles of calcareous material and foraminiferal coquina matrix that fills the interior of some of the valves of *N.* (*E.*) *ocalensis* also supports a relatively high-energy environment interpretation.

Some modern malleids are byssate and epifaunally attached to other shells or coralline rock (BOSS & MOORE, 1967; YONGE, 1968; KEEN, 1971). Two of the most commonly occurring examples are *Malleus* (*Malleus*) *malleus* (Linné) and *M.* (*Malvufundus*) *regula* (Forskål). Both are widely distributed in the tropical Indo-Pacific area. The shells of these species are vertically disposed, rest on the umbonal-byssal surface (*i.e.,* dorsal surface), and are firmly attached to rocky surfaces (YONGE, 1968). Their shells in the ligamental area are somewhat similar to those of *Exputens,* although they have a byssal sinus that is much stronger than in *Exputens* and deep and long enough to qualify as a notch.

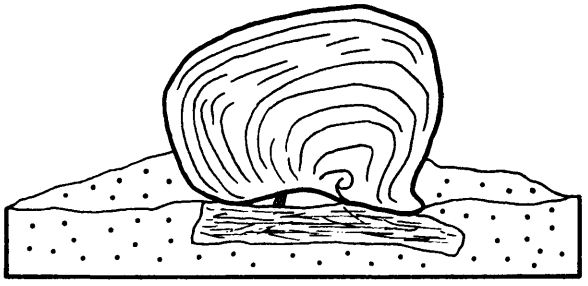


Figure 2

Reconstruction of the living position of *Nayadina* (*Exputens*). Right-valve exterior view, ×2.1, shows the dorsal side of shell attached by a byssus to a shell fragment (*i.e.,* hard substrate). Diagram is based on paratype, IGM 5114 of *N.* (*E.*) ***batequensis*** sp. nov., shown in Figures 14–16.

Based on morphologic similarities between *Exputens* and modern byssate malleids, as well as on available paleoecologic data concerning *Exputens,* a reconstruction of the living position of *Nayadina* (*Exputens*) is given in Figure 2. Having *Exputens* rest on its dorsal surface is also in keeping with the fact that articulated and even some single-valve specimens of *Exputens* are stable in that position.

SYSTEMATIC PALEONTOLOGY

Family MALLEIDAE Lamarck, 1819

Genus *Nayadina* Munier-Chalmas, 1864

Type species: By monotypy, *Nayadina herberti* Munier-Chalmas, 1864.

Subgenus *Exputens* Clark, 1934

Type species: By subsequent designation (VOKES, 1939), *Exputens llajasensis* Clark, 1934.

Description: Small to large size, subquadrate elongate to triangular shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and laterally inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated with anterior end laterally inflated. In a few specimens, both ends of shell elongated and both posterior and anterior dorsal margins raised and inflated, causing dorsal margin of shell to appear depressed in ligamental area. Valves smooth or with irregular commarginal lamellae. Beaks prosogyrate, very low to very inflated, usually in posterior half of shell but ranging from extreme posterior end to slightly anterior of center. Single auricle on each valve very low to very projecting, usually in posterior half of valve but ranging from very near posterior end to slightly anterior of center. Auricles offset from and usually posterior to beaks, just anterior to the beaks, directly above them, or even covering them. Auricles connected to beak area by one curved or fairly straight ridge.

Ligamental area projected along hinge line, forming an overhanging platform. Posterior part of ligamental area flat to concave to ridgelike, triangular, and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, deep to moderately deep, with apex near beak. Ligamental pit mostly or, in rare cases, entirely anterior to beak. Length of ligamental pit (measured parallel to hinge line) approximately one-eighth to one-fourth of valve length. Margins of ligamental pit straight or undulatory. Anterior margin of ligamental pit commonly strongly raised with one dorsally directed toothlike projection on hinge line. Byssal groove equally developed on each valve, just anterior to raised anterior margin of ligamental pit and extending from beak to hinge line. Byssal groove narrow, shallow, distinct to fairly distinct, becoming more pronounced ventrally where it ends in small, shallow byssal sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually inflated and, in some cases, very strongly inflated. Monomyarian. Muscle scar subcircular to elongate, near ventral margin and below ligamental area, but posterior to byssal sinus. Rarely, one pallial rib in region posterior from ligamental pit area to dorsoposterior corner of muscle scar. Prismatic outer shell underlaid by nacreous lamellar layer. Shell length up to 53.8 mm, shell height up to 29 mm.

Discussion: A revised description of *Exputens* is given above because of new findings made during the present study. The most important of these findings is the presence of a byssal sinus, which is best developed in *Nayadina* (*E.*) ***batequensis*** and *N.* (*E.*) *ocalensis*. As the shell grew, the byssal sinus in each valve was continually infilled with shell material and became a groove. The sinus itself is a small indentation of the hinge line and is only observable in a dorsal view of the hinge line.

Some modern-day members of the family Malleidae, such as *Malleus* (*M.*) *malleus* and *M.* (*Malvufundus*) *regula*, have a byssal notch located anterior to the ligamental area and anterior to the adductor muscle scar. By analogy, it is interpreted that these same relationships hold for *Exputens*. Such observations now allow for an understanding of the proper orientation of the valves of *Exputens*. As noted by MacNeil (1934) and Nicol & Shaak (1973), there has been much confusion in the literature regarding which is the anterior end and which is the posterior end of the shell of *Exputens*. Most authors have mainly relied on the assumption that the beaks and auricles are in the anterior part of the shell. With few exceptions, however, just the reverse is true: usually the beaks and auricles are located in the posterior part of the shell.

Prosogyrate beaks and an outer prismatic shell layer in *Exputens* are recognized for the first time in this report.

Clark (1934) and Hertlein & Cox (1969) reported that *Exputens* is dimyarian. In this study, however, no specimens of *Exputens* were observed to have more than a single muscle scar.

The relationship between ligamental pit length and valve length in *Exputens* is different for each species. Within each species, the relationship is fairly uniform, regardless of specimen size.

There is a wide range of variability in *Exputens* in terms of where the beaks and auricles are located and how inflated and projecting they are. There is also much variability as to which part of the shell is elongate, raised, or inflated.

Previously, Hertlein & Cox (1969) reported *Exputens* only from the middle Eocene of California and Jamaica. Unfortunately, they did not cite the source for the Jamaican occurrence, and it could not be found during the course of this study.

Material: *Exputens* includes *Nayadina* (*E.*) *llajasensis* (Clark) [which includes *N.* (*E.*) *alexi* (Clark)], *N.* (*E.*) *ocalensis* (MacNeil), and *N.* (*E.*) ***batequensis***.

Distribution: Middle lower Eocene ("Capay Stage," equivalent to Ypresian Stage) to lower middle Eocene ("Domengine Stage," equivalent to lower Lutetian Stage) on the west coast of North America; upper Eocene (Jackson Stage, equivalent to upper Bartonian to Priabonian Stages) in the southeastern United States.

Nayadina (*Exputens*) ***batequensis*** Squires, sp. nov.

(Figures 3–25)

Diagnosis: Small size, triangular to elliptical shape, spirally curved short auricles usually near posterior end of shell, beaks and auricles anterior of center of shell in some specimens, margins of ligamental pit straight, and in both valves a distinct groove showing former positions of byssal sinus.

Description: Mostly small size, triangular to elliptical shape, less commonly subquadrate elongate shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated. Rarely, both ends of shell elongated and both posterior and anterior dorsal margins raised, causing dorsal margin of shell to appear depressed in ligamental area. Valves nearly smooth with closely spaced growth lines or rough owing to low commarginal lamellae accentuated by weathering. Beaks prosogyrate, fairly prominent, usually in posterior half of shell, but range from extreme posterior end to slightly anterior of center. Short auricle on each valve usually small but moderately prominent to very projecting, usually in posterior half of valve but ranging from near the posterior end to slightly anterior of center. Auricles offset from and usually posterior to beaks, but occasionally just anterior to beaks or directly above them. In most specimens, auricles

connected to beak area by prominent spiral ridge along anterior margin of ligamental pit.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flat or ridgelike, triangular, and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, usually very prominent, and mostly or, in rare cases, entirely anterior to beak. Length of ligamental pit slightly less than approximately one-fourth of valve length. Margins of ligamental pit straight. Byssal groove equally developed on each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, shallow, distinct, becoming more pronounced ventrally where it ends in small, shallow sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually strongly inflated. Rarely, one pallial rib in region posterior from ligamental pit area to dorsoposterior corner of muscle scar. Muscle scar subcircular to elongate, near ventral margin, below ligamental area, and posterior to byssal sinus. Shell length up to 36 mm (most not over 20 mm), shell height up to 23 mm (most not over 12 mm).

Discussion: Seven variants were found. The triangular form of the holotype (Figures 3–5) is the most common variant. This variant is also shown in Figures 6–8. The other variants, with the beak area becoming progressively more anteriorly located, are shown in Figures 14–25. Most of these variants, except for the one shown in Figure 13, are confined to either single specimens or only a few specimens. The most unusual variant, shown in Figures 20–25, has the beak anterior to the center of the shell and can have a very projected auricle.

Nayadina (*E.*) ***batequensis*** differs from *N.* (*E.*) *llajasensis* in its smaller size, forms with a triangular shape, smaller and more spirally curved auricles, posterior part of ligamental area that can be ridgelike, beaks and auricles that can be slightly anterior of the center of the shell, auricles that are never covered by the beaks, and in both valves a more common occurrence of a distinct groove that shows the former position of the byssal sinus.

Nayadina (*E.*) ***batequensis*** differs from *N.* (*E.*) *ocalensis* in having smaller size, forms with a triangular shape, auricles that can be anterior to the beaks, auricles less rectangularly shaped, auricles that can be more projecting, dorsal margin of shell immediately anterior to byssal sinus more strongly inflated, length of ligamental pit slightly less than approximately one-fourth rather than one-eighth of valve length, and straight margins along the ligamental pit.

Holotype: IGM 5108 = plastoholotype, LACMIP 8294.

Type locality: Locality CSUN 1220b, just south of Laguna San Ignacio, Baja California Sur, Mexico.

Paratypes: IGM 5109–5119 = plastoparatypes, LACMIP 8295–8305.

Distribution: West Coast "Capay Stage," equivalent to middle lower Eocene (Ypresian Stage): Bateque Formation, Baja California Sur, Mexico, locality CSUN 1220b.

Nayadina (*Exputens*) *llajasensis* (Clark, 1934)

(Figures 26–46)

Exputens llajasensis CLARK, 1934:270–271, pl. 37, figs. 11–18; VOKES, 1939:51.

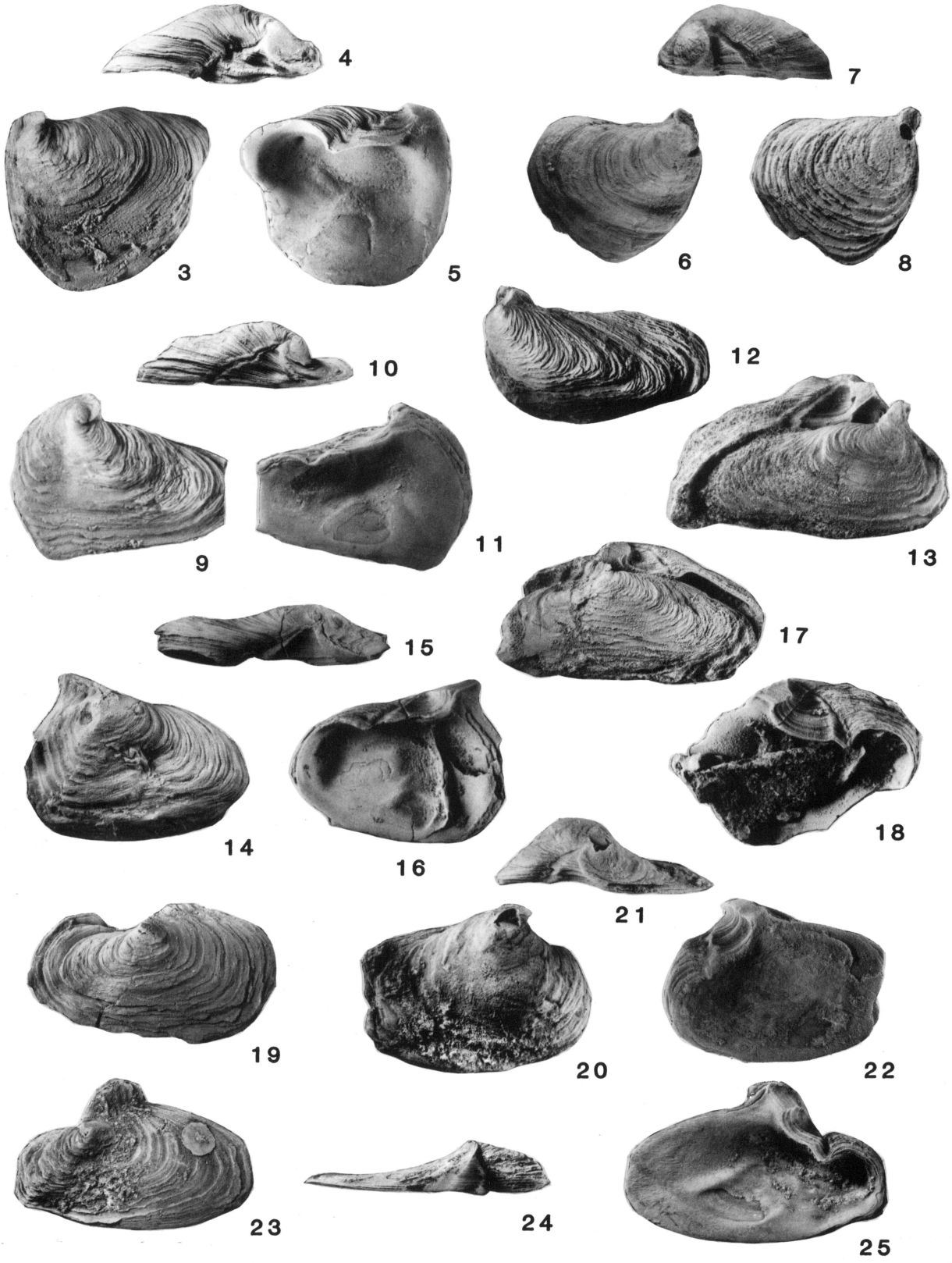
Exputens alexi CLARK, 1934:271–272, pl. 37, figs. 19–24; VOKES, 1939:51, pl. 2, figs. 2, 5, 9.

Nayadina (*Exputens*) *llajasensis* (Clark): HERTLEIN & COX, 1969:331, fig. C55-7; GIVENS, 1974:44, pl. 1, fig. 9; MOORE, 1983:A86–A87, pl. 26, figs. 10, 13; SQUIRES, 1984:43, figs. 10h–i.

Nayadina (*Exputens*) *alexi* (Clark): MOORE, 1983:A86, pl. 26, figs. 8–9.

Supplementary description: Mostly large size, subquadrate elongate shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and laterally inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated with anterior end laterally inflated. Occasionally, both ends of shell elongated and both posterior and anterior dorsal margins raised and inflated, causing dorsal margin of shell to appear depressed in ligamental area. Valves with closely spaced growth lines and rough with irregular commarginal lamellae, especially in posterior part of shell. Beaks prosogyrate, very low to very inflated, usually in posterior half of shell but ranging from extreme posterior end to center. Single auricle on each valve bladelike, low to prominent, usually in posterior half of valve or at the center. Auricles usually offset and posterior to beaks. In some specimens, exterior of auricles partially or completely covered by beaks. Auricles usually connected to beak by straight or curving ridge.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flat or rarely concave and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, usually very deep, and mostly anterior to beak. Length of ligamental pit approximately one-fourth of valve length. Margins of ligamental pit straight. Byssal groove developed equally on each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, shallow, and usually weakly developed, becoming more pronounced ventrally where it ends in broad, shallow sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually inflated. Muscle scar elongate, large, near ventral margin, below ligamental area, and slightly posterior to byssal sinus. Prismatic outer shell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layer underlaid by nacreous lamellar layer. Shell length up to 53.8 mm (many about 50 mm), shell height up to 29 mm.

Discussion: Five variants of this species were found. The form of the holotype is the most common variant (Figures 26–30, 38–46). The other variants are mainly confined to single specimens, shown in Figures 31–36, with the beak area becoming progressively more anteriorly located. In the most unusual variant the anterior and posterior ends are equally elongate, only the anterior end is laterally inflated, and the projecting beaks engulf the auricles (Figures 35, 36).

CLARK (1934) also commented on the variability of this species and recognized three variants (A–C). CLARK's (1934) variant A is the form of the holotype. In this present report, Clark's variant B is included with the form of the holotype, but his variant C is regarded as distinct (Figure 33). CLARK (1934) reported that variant C is opisthogyrate, but actually it is prosogyrate.

The muscle scar of this species, previously unknown, is illustrated for the first time in Figure 29.

The four primary type specimens of *Nayadina* (*E.*) *alexi* show only a small amount of variation in morphology. All have the form of the holotype of *N.* (*E.*) *llajasensis* and are determined, for the first time, to be conspecific with *N.* (*E.*) *llajasensis*. The holotype of *N.* (*E.*) *alexi*, shown in Figures 38–40, is very similar to a specimen of *N.* (*E.*) *llajasensis* (Figure 41). A paratype of *N.* (*E.*) *alexi* (Figure 42) is essentially identical to a specimen of *N.* (*E.*) *llajasensis* (Figure 43), and another paratype of *N.* (*E.*) *alexi* (Figures 44, 45) is very similar to a specimen of *N.* (*E.*) *llajasensis* (Figure 46).

CLARK (1934) reported that *Nayadina* (*E.*) *alexi* could be distinguished from *N.* (*E.*) *llajasensis* on the basis of the following: the auricles are above the beaks in *N.* (*E.*) *alexi* but are offset from the beaks in *N.* (*E.*) *llajasensis*, the ligamental pit in *N.* (*E.*) *alexi* is less concave, and *N.* (*E.*) *alexi* is smaller. Actually, the auricles are offset from the beaks in *N.* (*E.*) *alexi*, and the amount of offset is similar to that in the holotype of *N.* (*E.*) *llajasensis*. The difference in concavity of the ligamental pit is just the result of specimen size. The average shell height of *N.* (*E.*) *alexi* is 12 mm whereas in *N.* (*E.*) *llajasensis* it is 24 mm. The amount of ligamental pit concavity in the holotype of *N.* (*E.*) *alexi* (Figure 40) is 2.7 mm (measured vertically from the apex of the auricle to the ventral surface of the ligamental pit). The amount of ligamental pit concavity in an average specimen of *N.* (*E.*) *llajasensis* (Figure 28) is 5.5 mm. This paratype of *N.* (*E.*) *llajasensis* is twice the size of the holotype of *N.* (*E.*) *alexi* and, hence, has twice the amount of concavity in the ligamental pit.

The primary type specimens of *Nayadina* (*E.*) *alexi* represent juvenile forms whereas those of *N.* (*E.*) *llajasensis* are fully mature specimens. When specimen age is taken into consideration, any distinction between *N.* (*E.*) *alexi* and *N.* (*E.*) *llajasensis* is removed.

Nayadina (*E.*) *llajasensis* differs from *N.* (*E.*) ***batequensis*** in having larger size, no triangular forms, more bladelike auricles, larger and straighter auricles, beaks and auricles that are never anterior of center of the shell, beaks that can cover the auricles, posterior parts of ligamental area not ridgelike, and in both valves usually a less distinct groove that shows the former position of the byssal sinus.

Nayadina (*E.*) *llajasensis* differs from *N.* (*E.*) *ocalensis* in having beaks and auricles never anterior of center of the shell, beaks that can cover the auricles, length of ligamental pit approximately one-fourth rather than one-eighth of valve length, straight margins along the ligamental pit, posterior parts of ligamental area not ridgelike, and in both valves usually a less distinct groove that shows the former position of the byssal sinus.

Holotype: UCMP 32391. [Note: Holotype of *N.* (*E.*) *alexi* is UCMP 32386.]

Type locality: *Nayadina* (*E.*) *llajasensis*: Locality UCMP 7004, Las Llajas Canyon, just north of Simi Valley, Ventura County, southern California. [Note *Nayadina* (*E.*) *alexi*: Locality UCMP A-1007, Los Gatos Creek, Fresno County, central California.]

Paratypes: *Nayadina* (*E.*) *llajasensis*: UCMP 32389–32390, 32392–32393. *Nayadina* (*E.*) *alexi*: UCMP 32384–32385, 32387.

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Explanation of Figures 3 to 25

Figures 3–25. *Nayadina* (*Exputens*) ***batequensis***, CSUN locality 1220b. Figures 3–5: holotype, IGM 5108, right valve, ×2.3; Figure 3, exterior; Figure 4, dorsum; Figure 5, interior. Figures 6–7: paratype, IGM 5109, left valve, ×2.2; Figure 6, exterior; Figure 7, dorsum. Figure 8: paratype, IGM 5110, left valve exterior, ×3.5. Figures 9–11: paratype, IGM 5111, right valve, ×2; Figure 9, exterior; Figure 10, dorsum; Figure 11, interior. Figure 12: paratype, IGM 5112, right valve exterior, ×2.5. Figure 13: paratype, IGM 5113, left valve exterior, ×2.4. Figures 14–16: paratype, IGM 5114, right valve; Figure 14, exterior, ×2.1; Figure 15, dorsum, ×2.2; Figure 16, interior, ×2.1. Figure 17: paratype, IGM 5115, right valve exterior, ×1.8. Figure 18: paratype, IGM 5116, partial left valve interior, ×1.6. Figure 19: paratype, IGM 5117, left valve exterior, ×2.2. Figures 20–22: paratype, IGM 5118, right valve, ×1.9; Figure 20, exterior; Figure 21, dorsum; Figure 22, interior. Figures 23–25: paratype, IGM 5119, left valve; Figure 23, exterior, ×1.1; Figure 24, dorsum, ×1.2; Figure 25, interior, ×1.2.

Distribution: West Coast "Capay Stage" and "Domengine Stage," equivalent to middle lower to lower middle Eocene (Ypresian to lower Lutetian Stages). "Capay Stage": Juncal Formation, *Turritella uvasana infera* fauna, Pine Mountain area, Ventura County, southern California, locality UCR 4659 (GIVENS, 1974). "Domengine Stage": "Stewart bed," middle Llajas Formation shallow-marine (transgressive) facies, Simi Valley, Ventura County, southern California, at and in the vicinity of locality UCMP 7004 [=locality UCLA 2312 = locality CSUN 374], as well as at and in the vicinity of locality CSUN 473 (CLARK, 1934; SQUIRES, 1984); Domengine Formation, Fresno County, central California, locality UCMP A-1007 (CLARK, 1934).

Nayadina (*Exputens*) *ocalensis* (MacNeil, 1934)
(Figures 47–60)

Vulsella ocalensis MACNEIL, 1934:43, figs. 5–11; HARRIS, 1951:14, pl. 6, figs. 7, 7'.
Exputens ocalensis (MacNeil): NICOL & SHAAK, 1973:72–73, figs. 1–3; TOULMIN, 1977:316–317, pl. 56, fig. 6; PALMER & BRANN, 1965:143 (lectotype designated).

Supplementary description: Mostly medium size, subquadrate elongate shape, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated. In one specimen, only the anterior dorsal area inflated. Valves smooth or with irregular commarginal lamellae. Beaks prosogyrate, low to moderately prominent and usually in posterior half of shell but ranging from near posterior end to, in rare cases, anterior part. Single auricle on each valve usually bladelike, usually with right-angle bend at dorsal posterior corner, low to moderately strongly projecting, usually in posterior half of valve or slightly anterior to center. Auricles offset and posterior to beaks, rarely directly above beaks. Auricles connected to beak by straight to curving ridge.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flattish to ridgelike and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, very prominent, and mostly anterior to beak. Length of ligamental pit approximately one-eighth of valve length. Margins of ligamental pit commonly markedly undulatory. Anterior margin of ligamental pit commonly strongly raised with one dorsally directed toothlike projection on hinge line. Byssal groove equally developed in each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, usually distinct, becoming more prominent ventrally where it ends in small, shallow byssal sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually moderately inflated. Muscle scar subcircular to elongate, along ventral margin, below ligamental area, and slightly posterior of byssal sinus. Shell length up to 47.6 mm, shell height up to 24 mm.

Discussion: Four variants of this species were found. The form of the lectotype is the most common variant (Figures 47–50). This form is also shown in Figure 51. The other variants are mainly confined to single specimens and are shown in Figures 52–60. The most unusual variant, shown in Figures 58–60, has the beak and auricle in the anterior part of the shell, and has an inflated anterodorsal part of the valve.

MACNEIL (1934) reported that the muscle scar of this species is anterior to the beak. Actually, it is posterior to the beak.

Nayadina (*E.*) *ocalensis* differs from *N.* (*E.*) ***batequensis*** in having no triangular forms, auricles never anterior to the beaks, auricles commonly more rectangular shaped, dorsal margin of shell immediately anterior to byssal sinus less strongly inflated, length of ligamental pit approximately one-eighth rather than slightly less than one-fourth

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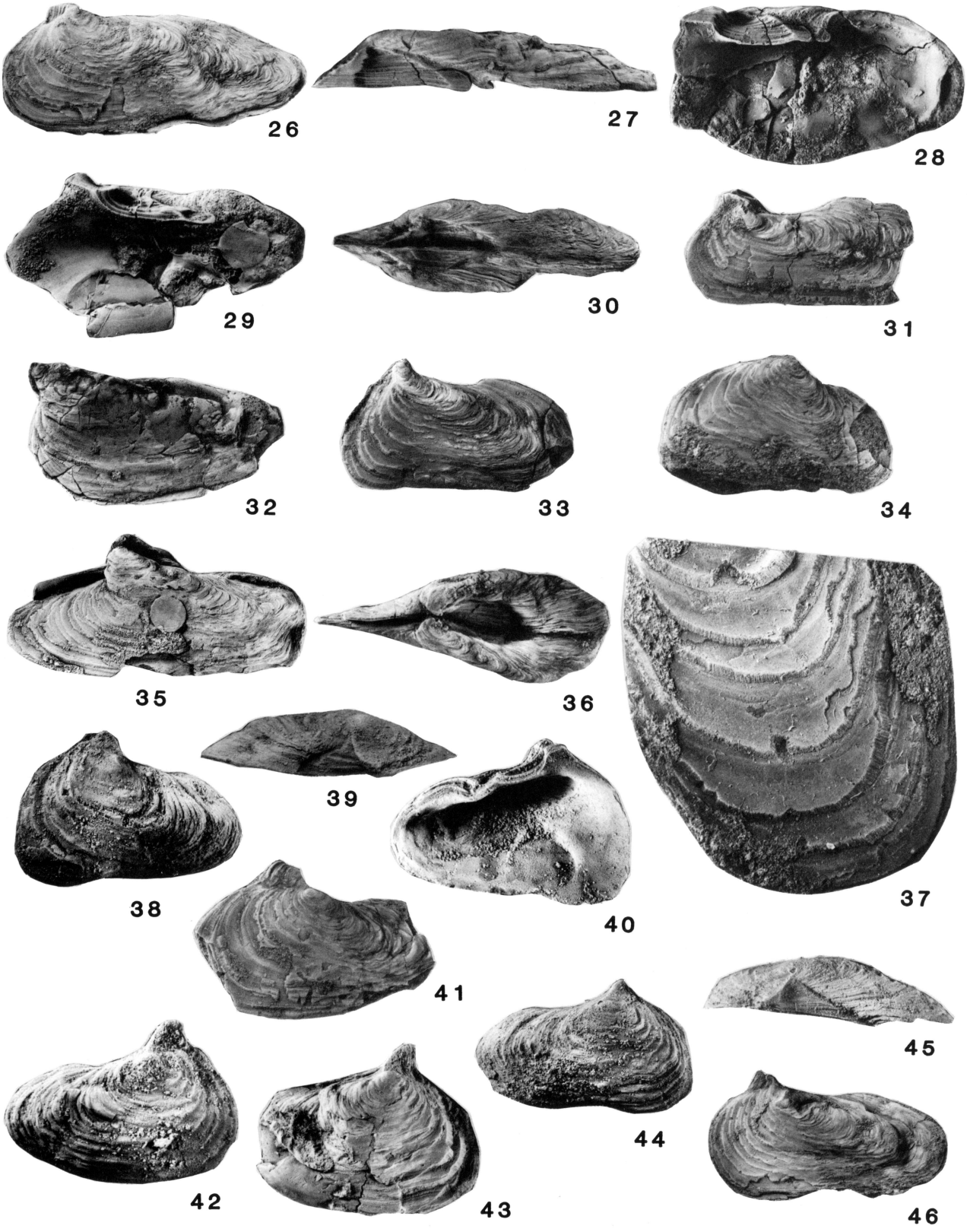
Explanation of Figures 26 to 46

Figures 26–46. *Nayadina* (*Exputens*) *llajasensis* (Clark, 1934), locality UCMP 7004, unless otherwise noted. Figure 26: holotype, UCMP 32391, right valve exterior, ×1. Figures 27–28: paratype, UCMP 32389, left valve; Figure 27, dorsum, ×1.5; Figure 28, interior, ×1.3. Figure 29: hypotype and topotype, LACMIP 8306, left valve interior, ×1.3. Figure 30: holotype, UCMP 32391, complete specimen, dorsum, ×1. Figure 31: hypotype and topotype, LACMIP 8307, right valve exterior, ×1.2. Figure 32: paratype, UCMP 32392, right valve exterior, ×1.2. Figure 33: paratype, UCMP 32390, right valve exterior, ×1. Figure 34: hypotype and topotype, LACMIP 8308, right valve exterior, ×1. Figures 35–36: hypotype and topotype, LACMIP 8309, ×1; Figure 35, right valve exterior; Figure 36, complete specimen, dorsum. Figure 37: hypotype and topotype, LACMIP 8310, partial right valve exterior showing outer prismatic layer, ×3. Figures 38–40: holotype, UCMP 32386 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, right valve; Figure 38, exterior, ×2; Figure 39, dorsum, ×2.4; Figure 40, interior, ×2.2. Figure 41: hypotype and topotype, LACMIP 8311, right valve exterior, ×1. Figure 42: paratype, UCMP 32384 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, left valve exterior, ×2.4. Figure 43: hypotype, LACMIP 8312, locality CSUN 473, left valve exterior, ×2.4. Figures 44–45: paratype, UCMP 32385 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, left valve; Figure 44, exterior, ×1.9; Figure 45, dorsum, ×2.2. Figure 46: paratype, UCMP 32393, right valve exterior, ×0.8.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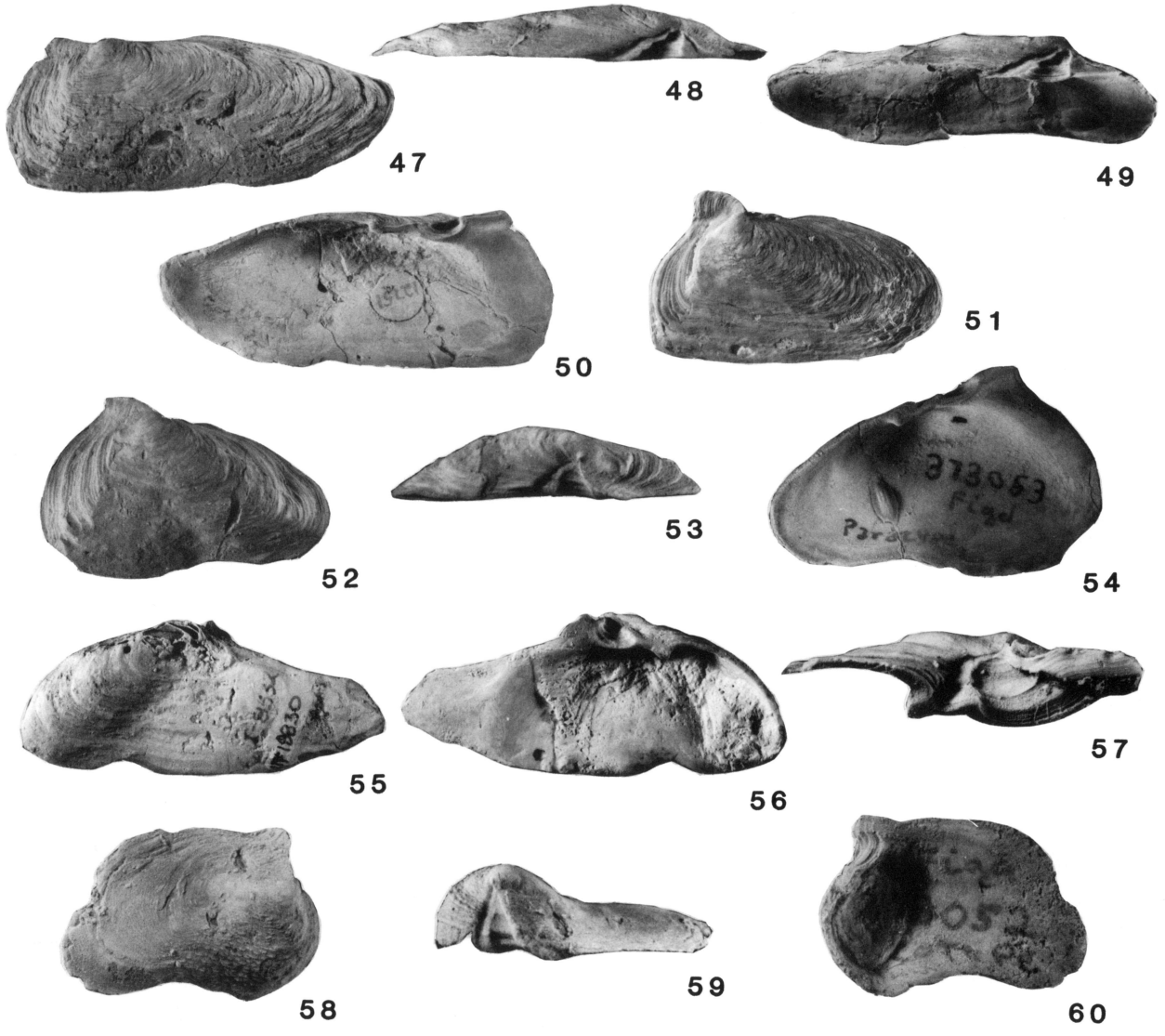

Explanation of Figures 47 to 60

Figures 47–60. *Nayadina* (*Exputens*) *ocalensis* (MacNeil, 1934). Figures 47–50: lectotype, USNM 373052, locality USGS 12751, right valve; Figure 47, exterior, ×1.1; Figure 48, dorsum, ×1.2; Figure 49, oblique view of dorsum, ×1.2; Figure 50, interior, ×1.2. Figure 51: hypotype, UF 3481, quarry west of U.S. 441 at south edge of Kendrick, Marion County, Florida, right valve exterior, ×1.5. Figures 52–54: paratype, USNM 373053, locality USGS 6812, right valve; Figure 52, exterior, ×1.5; Figure 53, dorsum, ×1.6; Figure 54, interior, ×1.7. Figures 55–56: hypotype, UF 18830, Bell 1 quarry, Gilchrist County, Florida, left valve; Figure 55, exterior, ×1.1; Figure 56, interior, ×1.2. Figure 57: hypotype, UF 5709, Dickerson Limerock Mines, Alachua County, Florida, right valve dorsum, ×2.5. Figures 58–60: paratype, USNM 373052, locality USGS 12751, right valve; Figure 58, exterior, ×3; Figure 59, dorsum, ×3.2; Figure 60, interior, ×3.1.

of valve length, and undulatory margins along the ligamental pit.

Nayadina (*E.*) *ocalensis* differs from *N.* (*E.*) *llajasensis* in having beaks and auricles that can be anterior of center, auricles that are never covered by the beaks, posterior part of ligamental area that can be ridgelike, length of ligamental pit approximately one-eighth rather than one-fourth of valve length, undulatory margins along the ligamental pit, and in both valves a more common occurrence of a distinct groove that shows the former position of the byssal sinus.

Lectotype: USNM 373052, figs. 10–11 of MacNeil (1934); designated by Palmer & Brann (1965:143).

Type locality: Locality USGS 12751, Sumter Rock Co. quarry, just northeast of Sumterville, Sumter County, northern Florida.

Paratypes: USNM 373052 (=figs. 5-6 of MACNEIL [1934]) and USNM 373053.

Distribution: Southeastern United States Jackson Stage, equivalent to upper Eocene (upper Bartonian and Priabonian Stages). Jackson Stage: Crystal River Formation (=Ocala Limestone, restricted, according to PURI [1957]), northern Florida, localities USGS 6812 and 12751 (MACNEIL, 1934), Kendrick quarry (NICOL & SHAAK, 1973), unspecified localities in Columbia, Suwannee, Dixie, Gilchrist, Alachua, Levy, Marion, Citrus, and Sumter Counties, northern Florida (NICOL & SHAAK, 1973), and the following new localities: Newberry Corp. Pit 1, Dickerson Limerock Mines, Buda 1 Quarry, all from Alachua County, Florida, and Bell 1 Quarry, Gilchrist quarry, Florida; Toulmin collection locality Fla-1 (TOULMIN, 1977); Ocala Limestone, southwestern Georgia (NICOL & SHAAK, 1973); Castle Hayne Marl, unspecified localities in Pender and Wayne Counties, southeastern and north-central North Carolina (NICOL & SHAAK, 1973).

ACKNOWLEDGMENTS

R. S. Vernis and R. R. Quintana (Departamento de Geología, Universidad Autónoma de Baja California Sur, La Paz) kindly arranged for permission for geologic studies and paleontologic collecting in Baja California Sur. M. C. Perrilliat (Instituto de Geología, Universidad Nacional Autónoma Museum de México) graciously provided type-specimen numbers.

Robert Demetrion helped in collecting the Baja specimens. D. R. Lindberg (University of California, Berkeley), G. L. Kennedy (Natural History Museum of Los Angeles County), R. W. Portell (Florida Natural History Museum), and J. W. M. Thompson (National Museum of Natural History) efficiently provided for loan of requested specimens. R. W. Portell also kindly loaned previously unstudied specimens of *Nayadina* (*E.*) *ocalensis* that he selected from the University of Florida, Gainesville, collection.

This paper benefited from helpful comments made by two anonymous reviewers.

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APPENDIX

Localities Cited

CSUN 473: At elevation of 503 m (1650 ft) on a ridge, 320 m (1050 ft) north and 701 m (2300 ft) west of southeast corner of section 30, T3N, R17W, Santa Susana 7.5-minute quadrangle, 1969, northern Simi Valley, Ventura County, California. Locality is in the "Stewart bed" (SQUIRES, 1984:61). Llajas Formation. Age: Early middle Eocene ("Domengine Stage"). Collector: R. L. Squires.

CSUN 1220b: North side of a minor canyon, at an elevation of 120 m, on the west side of Mesa La Salina, 100 m above the bottom of the exposures of the Bateque Formation, approximately 1.25 km southeast of the intersection of 113°00'W and 26°45'N, San Jose de Gracia, Baja California Sur, Mexico, 1:50,000 quadrangle map (number G12A64), issued in 1983 under the authority of the Direccion General de Geografia. Bateque Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: R. L. Squires and Robert Demetrion.

UCMP A-1007: Coarse sandstone reef, underlying and overlying shale, outcropping about 100 m from the mouth of a small gulley on the north bank of Los Gatos Creek, which is a few kilometers north of the town of Coalinga and in the NE ¼, sec. 10, T20S, R14E (CLARK, 1934: 272), Alcalde Hills 7.5-minute quadrangle, 1969, Fresno County, central California. Domengine Formation. Age: Early middle Eocene ("Domengine Stage"). Collector: Alex Clark.

UCMP 7004: At elevation of 518 m (1700 ft) on a small cliff on south side of a side canyon to Las Llajas Canyon, 594 m (1950 ft) north and 556 m (1825 ft) east of southeast corner of section 29, T3N, R17W, Santa Susana 7.5-minute quadrangle, 1969, northern Simi Valley, Ventura County, southern California. Locality is in the "Stewart bed" and is equivalent to localities UCLA 2312 and CSUN 374 (SQUIRES, 1984:58). Llajas Formation. Age: Early middle Eocene ("Domengine Stage"). Collectors: B. L. Clark and R. L. Squires.

UF locality Newberry Corp. Pit 1: SW ¼, SE ¼, sec. 13, T9S, R17E, Newberry quadrangle, Alachua County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality Dickerson Limerock Mines (Haile Complex): T9S, R17E, Newberry quadrangle, Alachua County, northern Florida. Inglis/Crystal River Formation. Age: Late Eocene. Collectors: D. S. Jones and students; D. Nicol and others.

UF locality Buda 1 Quarry (bed 3): NE ¼, NE ¼, sec. 32, T8S, R17E, High Springs SW quadrangle, Alachua County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality Bell Quarry (bed 6): SE ¼, NW ¼, sec. 24, R14E, T8S, Bell quadrangle, Gilchrist County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality quarry west of U.S. 441 at south edge of Kendrick: NW ¼, sec. 25, T14S, R21E, Marion County, northern Florida (NICOL & SHAAK, 1973). Crystal River Formation. Age: Late Eocene. Collectors: University of Florida, Gainesville, staff.

USGS 6812: Cummer Lumber Company, 2 km south of Newberry, Alachua County, northern Florida (MACNEIL, 1934:431). Crystal River Formation. Age: Late Eocene. Collector: C. W. Cooke.

USGS 12751: Sumter Rock Co. quarry, about 3.2 km (2 mi.) northeast of Sumterville, Sumter County, northern Florida (MACNEIL, 1934:431). Crystal River Formation. Age: Late Eocene. Collectors: W. C. Mansfield and G. M. Ponton.

Toulmin's (1977) collection, Fla-1: Mayo quarry, 7.5 km northwest of Mayo on U.S. Highway 27 and about 0.8 km south of Mayo fire tower in SE ¼, sec. 32, T4S, R11E, Lafayette County, northern Florida (TOULMIN, 1977:388). Crystal River Formation. Age: Late Eocene. Collector: L. D. Toulmin.