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California Late Cretaceous Donaciform Bivalves

by

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Abstract. California donaciform bivalves of Late Cretaceous age occur sporadically, but locally abundantly, in coarse-grained sandstone. Where abundant, they indicate near strand-line deposition. Seven species are allocated among a new genus, ***Adelodonax***, and a new subgenus, ***Aliodonax***, in the Donacidae and a new genus, ***Califadesma***, in the Mesodesmatidae. The donacids are *Notodonax* (***Aliodonax***) ***hsui*** sp. nov. of Santonian age, *N.* (***A.***) ***bolsae*** sp. nov. of Campanian age, ***Adelodonax tectus*** sp. nov. of Santonian age, and ***A.*** *altus* (Gabb, 1864) of Maastrichtian age; the mesodesmatids are ***Califadesma aspris*** sp. nov. of Coniacian age, ***C. elaphium*** sp. nov. of Santonian age, and ***C. tuscanum*** sp. nov. of Campanian age.

Mactropsis Conrad, 1854, is a mactrid rather than a mesodesmatid. *Myadesma* Clark, 1922, is an anomalodesmacean and *Ceroniola* Wilckens, 1904, may be a donacid; both are excluded from the Mesodesmatidae and from the Mactracea.

INTRODUCTION

Although donacid bivalves have been recognized elsewhere in the Cretaceous, neither donacids nor mesodesmatids have previously been recorded from the California Cretaceous. Abundant donaciform bivalves from the Musty Buck Member of the Chico Formation at about 44 m above the base of the section on Chico Creek, Butte Co., California, proved, upon exposure of hinge lines, to belong to three genera in the Donacidae and Mesodesmatidae.

Cretaceous Donacidae include *Notodonax* (Feruglio, 1936) from the Maastrichtian of Argentina, and *Protodonax* (Vokes, 1945) proposed for species of Albian through Maastrichtian age from the Western Interior and Atlantic Coast of North America as well as the Aptian of Lebanon. STEPHENSON (1952) added two Cenomanian species from the Gulf Coast to *Protodonax*. The family has thus been recognized in the Early Cretaceous. The five California species herein added to the family range in age from Santonian to Maastrichtian. These species are more similar to Maastrichtian species from Chile and Argentina than to species described by VOKES (1945) and STEPHENSON (1952) from North America and the Near East.

The earliest mesodesmatid listed in the *Treatise on Invertebrate Paleontology* (Keen *in* MOORE, 1969) is *Ceroniola* Wilckens, 1904, from the Quiriquina Formation of Late Cretaceous age. WILCKENS (1904) apparently placed *Ceroniola* in the Mesodesmatidae because he considered the triangular depression beneath the beaks to be a resilifer, but the hinge teeth of *Ceroniola* show no relationship to those of *Mesodesma* Deshayes, 1832. *Ceroniola* is, as indicated by BEU (1971:124), an improbable ancestor for *Mesodesma*. Similarities between *Ceroniola* and ***Adelodonax*** gen. nov. suggest that *Ceroniola* may be a donacid.

The next oldest purported mesodesmatid (Keen *in* MOORE, 1969) is *Mactropsis* Conrad, 1854, from the Eocene of Alabama. DALL (1898:907) placed *Mactropsis* in the Mesodesmatidae because it has a very thick shell. He inferred that mesodesmatids were unlikely to be recognized earlier than Tertiary because of the stage of hinge development in *Mactropsis*, but *Mactropsis* appears more closely related to the mactrid *Spisula* Gray, 1837, than to *Mesodesma*.

The next younger genus included by Keen (*in* MOORE, 1969) in the Mesodesmatidae is *Myadesma* Clark, 1922, of Eocene to Miocene age from the Pacific Northwest. The lack of striated laterals and the probable lithodesma (CLARK, 1922) found within its chondrophore are sufficient to exclude it from Mesodesmatidae. BEU (1971) agrees with CLARK (1922) in placing it in Myadesmatidae but retains this family within the Mactracea. The rough and lamellar shell texture of *Myadesma* is more like that of *Entodesma* (*Agriodesma*) *saxicolum* Baird, 1863, of the Lyonsiidae, and the hinge structures resemble those of Periplomatidae. The tooth beneath the beak in each valve was interpreted as a cardinal by BEU (1971), but these are unduly inconstant for veneroid cardinal teeth and are not of mactracean form. Myadesmatidae has more in common with the anomalodesmacean families Lyonsiidae and Periplomatidae.

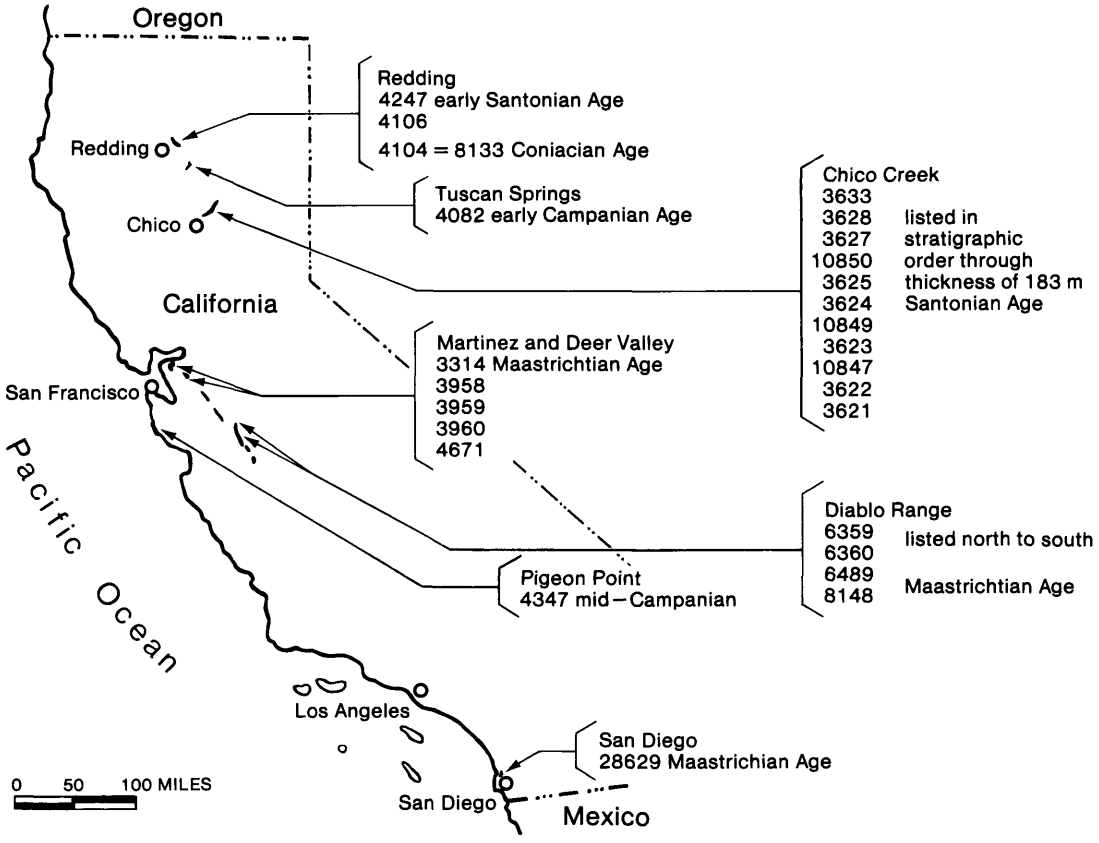


Figure 1

Index map to seven areas in California that have yielded donaciform bivalves of Late Cretaceous age. Localities listed for each area are described, or a reference to a description is given in Appendix 1—Localities Cited.

The hinge of the new genus ***Califadesma*** differs from that of *Mesodesma* Deshayes, 1832, in being less advanced but is indubitably that of a mesodesmatid. Unlike the hinge of *Mactropsis aequorea* (Conrad, 1833) (Figures 43, 44) with its resemblance to *Spisula,* the hinge of ***Califadesma*** is clearly homologous to those of Recent species of *Mesodesma,* such as *M. donacium* (Lamarck, 1818) (Figures 50, 51), *M. mactroides* Deshayes, 1855, and *M. (Ceronia) arctatum* (Conrad, 1830) (Figures 45, 46) and to those of the East Coast Miocene, *M. (C.) mariana* Glenn, 1904, and Pliocene, *M. (C.) spatha* Gardner, 1944. ***Califadesma*** is related to typical *Mesodesma* rather than to *Paphies* Lesson, 1831, which has smooth laterals and an austral distribution beginning as early as the early Miocene (BEU, 1971:117; BEU & DE ROOIJ-SCHUILING, 1982:212). ***Califadesma*** is thus the oldest known mesodesmatid.

Abbreviations used with locality and catalogue numbers are: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CIT, California Institute of Technology; LACM, Natural History Museum of Los Angeles County, Malacology; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCB, University of California, Berkeley; UCBMP, University of California, Berkeley, Museum of Paleontology; UCLA, University of California, Los Angeles.

DISTRIBUTION

The presence of both donacids and mesodesmatids in the California Upper Cretaceous is sporadic, and although specimens are abundant at some localities, they do not commonly constitute a major element of the faunas. They are abundant low in the Musty Buck Member of the Chico Formation on Chico Creek, Butte Co.; in a few beds of the Great Valley Series near Martinez and in Deer Valley, Contra Costa Co.; and in the Cabrillo Formation on Mt. Soladad, San Diego Co., California. They are locally common in the Redding Formation on the north side of Oak Run, Shasta Co., and in some beds of the Garzas Member of the Moreno Formation, Stanislaus Co., California. Donaciform bivalves, collected from localities in the seven areas indicated on Figure 1, have been studied for this report (see Appendix 1 for descriptions of localities). All of the mesodesmatids are from outcrops on the east side of the Sacramento Valley of northern California. Donacids occur with mesodesmatids in the northern California outcrops and additionally in central and southern California.

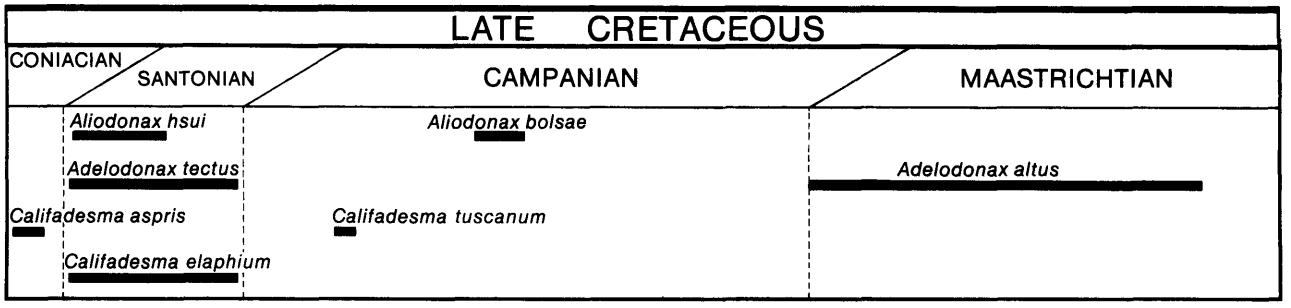


Figure 2

Geologic range chart for California Cretaceous species of Donacidae and Mesodesmatidae discussed in this paper.

The modern species of *Mesodesma* such as *M. donacium* of the Chilean coast and *M.* (*Ceronia*) *arctatum* of the northwest Atlantic coasts inhabit beaches to the south and north of the tropical to temperate donacids. Whether these Cretaceous records reflect a similar cooler water distribution for the mesodesmatids than for the donacids in the past or result from random preservation of sandy beach habitats is unclear.

Donacids are also longer ranging through the California Late Cretaceous than mesodesmatids. The presently known range of ***Califadesma*** is only from Coniacian through early Campanian, but that of the donacids is from Santonian into the late Maastrichtian. The geologic ranges of the species are shown in Figure 2.

Both *Notodonax*(***Aliodonax***) spp. and ***Califadesma*** spp. have relatively thick shells. An anteriorly compressed and posteriorly inflated shell, in several families, is an adaptation toward rapid burrowing (STANLEY, 1970), common among bivalves that frequently need reburying because they inhabit littoral substrates close to and within the surf zone. Rapid burrowers with thick shells (*Tivela, Mesodesma,* and *Donax*) occupy coarse, shifting substrate, where stability is essential (STANLEY, 1970:93).

Shells of ***Adelodonax*** spp. are of less than average thickness for donacids, and the paired valves have a more elongate, blade shape, which is efficient for rapid burrowing (STANLEY, 1970:59; VERMEIJ, 1987:312). Both sediment type and geologic occurrence agree with the morphologic implications of these clams and indicate that an abundance of either of these mesodesmatids or donacids is suggestive of a nearby shoreline.

Because the fossil record for such near-shore dwellers is relatively poor, VOKES (1945) expressed surprise at the number of Cretaceous donacid specimens that he was able to find. Most Cretaceous donacids have been described from the Atlantic basin; none of the species described from the Atlantic basin is closely related to the California species. California donacids resemble Maastrichtian species described from southern Argentina and Chile, and the mesodesmatids resemble typical late Cenozoic mesodesmatids of the Chilean coast. The lateral teeth of ***Califadesma*** are striate in the same manner as are those of *Mesodesma donacium* (Lamarck, 1818) (BEU & DE ROOIJ-SCHUILING, 1982:figs. 2b, c) and *M. mactroides* Deshayes, 1855, in that the dorsal sides of the laterals are more strongly striate than the ventral sides.

NARCHI (1981) indicated that paleontological records place the origin of the mesodesmatids in Australasia, but the geologically oldest is of Miocene age (BEU, 1971; BEU & DE ROOIJ-SCHUILING, 1982). *Mesodesma* is reported in the late Pliocene of Chile (HERM, 1969:94); it is inferred to have dispersed along the Patagonian coast during the Pleistocene, and *M. mactroides* to have only recently moved northward into Brazilian shores (NARCHI, 1981). The northern California specimens suggest a northern origin for the ancestors of typical *Mesodesma* and its north Atlantic subgenus *Ceronia* Gray, 1853.

Califadesma is first recognized in the Coniacian. Northern California Coniacian and Santonian faunas appear to reflect a cooler regime than do the earlier Turonian molluscan faunas or the later Campanian faunas (SAUL, 1986). ***Califadesma*** may have moved into northern California with the cooler water and left with the return of warmer water. ***Califadesma*** is a creditable ancestor for *Mesodesma,* despite the considerable time gap between the Late Cretaceous disappearance of ***Califadesma*** and the late Pliocene appearance of *Mesodesma.* The improbability that *Donacilla* (*Mesodesma*) *sakhalinensis* Kalishevich, 1967, from the late Eocene of Sakhalin can be included in *Mesodesma* is discussed under Mesodesmatidae. The Tertiary faunas of California are relatively well known and do not contain any *Mesodesma.* Their absence may reflect a paucity of sandy beach deposits. If ***Califadesma*** is ancestral to *Mesodesma,* the migration of this stock into southern waters might have been as early as Late Cretaceous but was not later than late Tertiary. The cool-water distribution of *Mesodesma* suggests that relatively cool periods during this time interval would have provided migration opportunities.

Donacids are unrecorded from Paleocene or between late Eocene and mid Pliocene in California, although another Recent sandy beach cohabiter, *Tivela,* is regularly represented in near-shore deposits beginning in the Oligocene. This lack of recorded donacids may result from the relatively small size of donacid shells and the uncom-

mon preservation of their sandy beach habitat which is usually sparsely fossiliferous when preserved and likely to be unexamined. Some ***Aliodonax*** shells preserve fine radial sculpture and structure, but none exhibits it to the extent usual among Holocene *Donax,* and none has denticulated valve margins. Possibly donacids were evolving the radial shell structure during the Late Cretaceous and Early Tertiary, but the absence of a better Early Tertiary record leaves the transition at present undocumented.

SYSTEMATIC PALEONTOLOGY

Order Veneroida H. & A. Adams, 1856

Superfamily TELLINACEA de Blainville, 1814

Family DONACIDAE Fleming, 1828

Although donacids appeared later than tellinids, POHLO (1967) suggested that the suspension-feeding donacids are unspecialized feeders and transitional to deposit-feeding tellinaceans. Donacids discussed in this paper have hinges with cardinal teeth that are not well separated from their lateral lamellae. These hinges are less advanced than those of tellinids of equivalent geologic age; thus, ancestors for tellinids must be sought elsewhere.

Genus *Notodonax* Feruglio, 1936

Type species by original designation *Donax annae-eugeniae* Feruglio, 1935.

The type species of *Notodonax* Feruglio, 1936, *Donax annae-eugeniae* from Patagonia, was described (FERUGLIO, 1935:90) from incomplete specimens interpreted to have two cardinals and an anterior lateral in each valve and two posterior laterals in the right valve and one in the left. The illustrations (FERUGLIO, 1936:pl 13, figs. 16–23) suggest that *Notodonax annae-eugeniae* bears considerable resemblance to *Notodonax* (***Aliodonax***) ***hsui*** sp. nov. and *N.* (*A.*) ***bolsae*** sp. nov. but has one more posterior lateral in each valve than is present in the California species. Additionally, the California species have one distinct cardinal in each valve, but the anterior cardinal is colaminal with the anterior lateral. Therefore the California species are placed in a new subgenus.

Aliodonax Saul, subgen. nov.

Type species *Notodonax* (***Aliodonax***) ***hsui*** Saul, sp. nov.

Diagnosis: ***Aliodonax*** is donaciform, solid, with a posterior angulation. Beaks are small, opisthogyral, and posterior to valve midline. Valve margin is smooth within. Ligament is in a deep groove behind short sturdy nymphs. Dentition consists of one posterior cardinal in each valve, 3b in right valve, 4b in left, and one posterior lateral in right valve. Anterior cardinals are not separated from anterior laterals, and in both valves the two form elongate colaminal anterior teeth, AIII-3a in right valve and AII-2 in the left. Right valve has long anterior "socket" into which thick and beveled anterior dorsal margin of left valve fits. Pallial sinus is short and rounded with dorsal arm sloping ventrally.

Discussion: The colaminal state of the anterior cardinals and laterals suggests a less evolved stage of hinge development than is described for *Notodonax s.s.* and *Protodonax* Vokes, 1945. Whereas in *Protodonax* the left valve hinge formula is AII 2 4b PII, in ***Aliodonax*** it is AII-2 4b (see Figure 3 for hinge diagrams and formulae). No complete right-valve hinge of *Protodonax* has been described. The two California species comprising ***Aliodonax*** have fewer and shorter laterals (especially posterior laterals), and a larger, more robust nymph than do species of *Protodonax.* VOKES (1945) did not find radial sculpture in *Protodonax* species nor is its presence mentioned by FERUGLIO (1936) in describing *Notodonax.* Fine radial sculpture and structure is present in the surficial shell layer of the posterior quarter of valves of *N.* (***A.***) ***hsui***. It has not been recognized in valves of *N.* (***A.***) ***bolsae***, but the shells of *N.* (***A.***) ***bolsae*** are so completely recrystallized that such structure and sculpture might have been obliterated. Radial structure is present in a medial shell layer of Holocene donacids from the eastern Pacific Panamic province (KEEN, 1971:234).

The name ***Aliodonax*** is compounded of the Latin *alius* meaning "another" or "other," and *Donax,* a bivalve genus. *Donax* is of masculine gender.

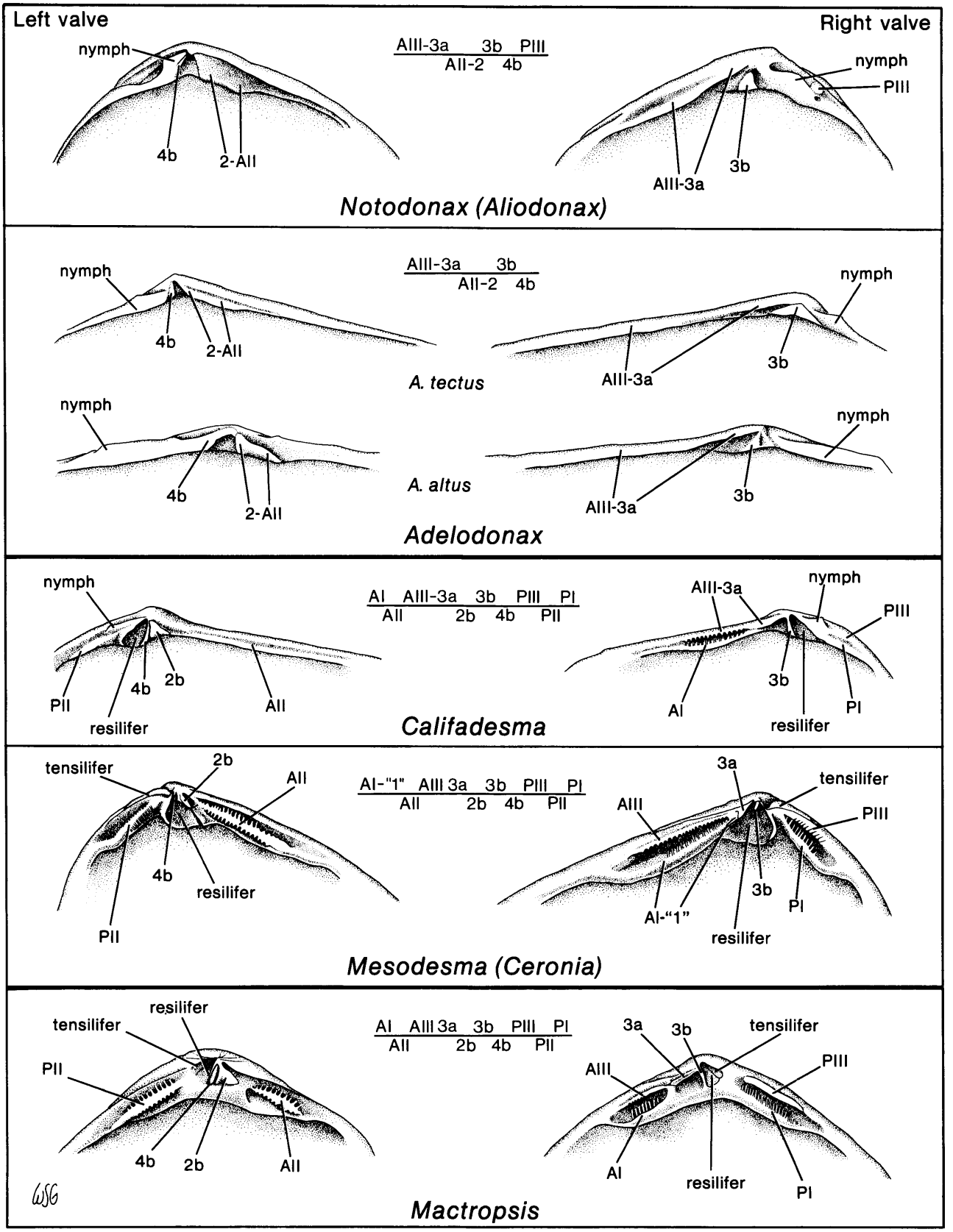
Notodonax (***Aliodonax***) ***hsui*** Saul, sp. nov.

(Figures 4–14)

Diagnosis: Elongate ***Aliodonax*** having the beak within the posterior third of the shell length. The hinge has, in the right valve aligned with the anterior hinge plate and valve margins, a long anterior colaminal tooth that is low adjacent to the beak and becomes high distally.

Description: Shell large for a donacid, thick. Valves elongate, compressed anteriorly, inflated and truncated posteriorly; anterodorsal margin nearly straight; anterior margin rounded, curving smoothly into ventral margin; ventral margin barely convex, angled abruptly into posterior margin; posterior margin nearly at right angle to ventral, rather straight, curving into very short posterodorsal margin; posterior angulation abrupt, parallel to and very near posterior margin. Beaks small, opisthogyral, very near posterior end; umbonal area blunt and broad. Lunule long, slightly depressed, bounded by low angulation. Exterior of valves with unevenly prominent growth lines and obscure radial ribbing on posterior quarter of shell.

Hinge with heavy, short nymph and deep ligament groove. Hinge of right valve with large, deltoid 3b vertically directed, immediately under beak; colaminal 3a-AIII very long, low and at valve margin dorsally, becoming high, bladelike, and aligned with hinge plate margin; long anterior "socket" for left valve anterior margin, dorsal to 3a-AIII; posterior lateral a low node just at base of ligament


Left valve
Right valve
nymph
AIII-3a 3b PIII
AII-2 4b
4b
2-AII
nymph
PIII
3b
AIII-3a
Notodonax (Aliodonax)
nymph
AIII-3a 3b
AII-2 4b
4b
2-AII
nymph
3b
AIII-3a
A. tectus
nymph
4b
2-AII
nymph
3b
AIII-3a
A. altus
Adelodonax
nymph
AI AIII-3a 3b PIII PI
AII 2b 4b PII
PII
4b
2b
resilifer
AII
AIII-3a
nymph
PIII
3b
AI
resilifer
PI
Califadesma
tensilifer
2b
AII
4b
resilifer
PII
AI-"1" AIII 3a 3b PIII PI
AII 2b 4b PII
3a
tensilifer
AIII
PIII
3b
PI
AI-"1"
resilifer
Mesodesma (Ceronia)
resilifer
tensilifer
PII
4b
2b
AII
AI AIII 3a 3b PIII PI
AII 2b 4b PII
3a
3b
tensilifer
AIII
PIII
AI
resilifer
PI
WSG
Mactropsis

groove. Pallial sinus extending just beyond line dropped from beaks, rounded; dorsal arm sloping ventrally from posterior adductor muscle scar; ventral arm partially confluent with pallial line. Muscle scars nearly equal, rather round; anterior scar distant from beaks; posterior scar very near beaks. Interior valve margin smooth.

Holotype: LACMIP 7813.

Paratypes: LACMIP 7814 from CIT loc. 1016, Chico Creek; 7861 from UCLA loc. 3621, Chico Creek; 7815–7817 from UCLA loc. 3622, Chico Creek; 7818 from UCLA loc. 3628, Chico Creek, Paradise Quadrangle, Butte Co.; 7819 from UCLA loc. 4247, south side of Oak Run, Millville Quadrangle, Shasta Co., California.

Dimensions: Of holotype, length 54 mm, height 30.5 mm, inflation of single valve 11 mm, length beak to posterior 12 mm; of paratype LACMIP 7815, length 24 mm, height 12 mm, inflation of single valve 4.4 mm, length beak to posterior 8.3 mm; of paratype LACMIP 7816, length 21.4 mm, height 9 mm, inflation of single valve 3.4 mm, length beak to posterior 6.3 mm; of paratype LACMIP 7819, length 21.9 mm, height 11.1 mm, inflation of single valve 4.3 mm, length beak to posterior 6.8 mm.

Type locality: UCLA loc. 3621, Chico Creek, Paradise Quadrangle, Butte Co., California.

Distribution: Musty Buck Member of the Chico Formation, from 370 to 450 m above the base of the section on Chico Creek (UCLA locs. 3621, 3622, 3625, CIT loc. 1016), Butte Co.; Redding Formation on south side of Oak Run (UCLA loc. 4247), Millville Quadrangle, Shasta Co., California.

Age: Santonian.

Remarks: The holotype is a large right valve. Large valves are strongly truncate posteriorly, but the growth lines indicate that the shape changes ontogenetically, and small valves are less truncate posteriorly and relatively less produced anteriorly. The pallial sinus is described from one of these small individuals. No left valve is available. Small individuals resemble both ***Califadesma elaphium*** sp. nov. and ***Adelodonax tectus*** sp. nov. with which they co-occur. Anterodorsal and ventral margins of *Notodonax* (***A.***) ***hsui*** slope toward each other, and the valves wedge anteriorly more than do those of ***Califadesma elaphium***; *N.* (***A.***) ***hsui*** lacks the double posterior angulation of ***C. elaphium***. *Notodonax* (***A.***) ***hsui*** differs from the similarly shaped ***A. tectus*** in having better developed hinge teeth, a shorter nymph, the ventral arm of the pallial sinus partially confluent with the pallial line, and radial riblets (Figure 7) on the posterior quarter of the valve.

The species is named for K. J. Hsu who assisted in measuring the Chico Creek section.

Notodonax (***Aliodonax***) ***bolsae*** Saul, sp. nov.

(Figures 16–21)

Diagnosis: Moderately elongate ***Aliodonax*** having beak more than a third of the shell length from the posterior margin. Hinge of right valve has a long anterior colaminal tooth, at an angle to the hinge plate and valve margins, that is relatively high adjacent to the beak.

Description: Shell large for a donacid; valves elongate, compressed anteriorly, inflated and truncated posteriorly; anterodorsal margin nearly straight; anterior margin rounded, curving smoothly into ventral margin; ventral margin broadly convex, angled abruptly into posterior margin; posterior margin at about 60° to ventral, rather straight, curving into very short posterodorsal margin; posterior angulation strong, parallel to and very near posterior margin. Beaks small, opisthogyral, near posterior third; umbonal area blunt and broad. Exterior of valves with unevenly prominent growth lines.

Hinge with heavy, short nymphs and deep ligament groove. Hinge of right valve with large, anteriorly slanted, deltoid 3b and long, thin, colaminal 3a-AIII; long, well developed anterior "socket" for margin of left valve; posterior lateral a low node just behind base of ligament groove. Hinge of left valve with posteriorly hooked, anteriorly directed, elongate 2-AII and short, lamellar, posteriorly directed 4b. Pallial sinus and muscle scars unknown. Interior valve margin smooth.

Holotype: LACMIP 7820.

Paratypes: LACMIP 7821–7824 from UCLA loc. 4347, near Bolsa Point, Pigeon Point Quadrangle, San Mateo Co., California.

Dimensions: Of holotype, somewhat crushed posteriorly, length 44.4 mm, height 27.5 mm, thickness 10 mm, distance of beak from posterior 14.3 mm; of paratype LACMIP 7821, length 37.4 mm, height 20.5 mm, thickness 6.4 mm, distance of beak from posterior 14.3 mm.

Type locality: UCLA loc. 4347, about 880 m north of

←

Figure 3

Diagrams of hinges and hinge formulae of supraspecific donacid and mesodesmatid taxa discussed in this paper. All hinges enlarged to approximately equal size. Both ***Aliodonax*** and ***Adelodonax*** have lucinoid-type hinges. These hinges are primitive in that cardinal tooth 2 is attached to lateral AII and cardinal 3a is attached to lateral AIII. ***Califadesma*** and *Mesodesma* have arcticoid-type hinges that are strongly modified by the submergence of the resilium and in *Mesodesma* by its forward rotation. In ***Califadesma*** the cardinal teeth, although crowded forward, are readily recognizable, but in *Mesodesma* the cardinals are vestigial and not easily seen without some magnification.

Bolsa Point, Pigeon Point Quadrangle, San Mateo Co., California.

Distribution: Known only from the type locality.

Age: Campanian.

Remarks: All five specimens of *Notodonax* (*A.*) ***bolsae*** are tectonically somewhat distorted and the shell material is recrystallized. *Notodonax* (*A.*) ***bolsae*** has a longer more sloping posterodorsal margin resulting in beaks that are more centrally positioned than in *N.* ***hsui.***

The species is named for its occurrence at Bolsa Point, San Mateo Co., California.

Genus *Adelodonax* Saul, gen. nov.

Type species ***Adelodonax tectus*** Saul, sp. nov.

Diagnosis: Valves of ***Adelodonax*** are smooth except for growth lines, elongate, and moderately inflated. Low beaks are slightly opisthogyral and posterior to the middle. Ligament is behind a long nymph. Hinge of right valve has one triangular cardinal (3b); a socket anterior to the cardinal, and an elongate, colaminal anterior tooth (AIII-3a). Left valve has one elongate, colaminal anterior tooth (AII-2) ventral to a long socket, a shallow socket beneath beak, and usually a low cardinal (4b) posterior to the shallow socket. Anterior adductor muscle scar is well impressed for such a thin shell and subtriangular in shape; posterior adductor muscle scar is plumply ovoid in shape. Pallial sinus is of moderate depth. U-shaped, and distant from pallial line.

Discussion: ***Adelodonax*** is doubtfully placed in the family Donacidae. The hinge teeth are delicate and difficult to expose from the matrix. They are reminiscent of juvenile hinges or an early stage in the development of the lucinoid hinge. In their indistinctness they resemble those of Quenstedtiidae Cox, 1929b; ***Adelodonax,*** however, has a ligament groove behind an alate nymph but does not have a ligament pit. The hinge teeth are somewhat better defined than those of Quenstedtiidae and might be derived therefrom, but to evolve a ligament seated in a groove behind an alate nymph from a ligament in a pit requires considerable change both to the shell attachment area and the structure of the ligament. ***Adelodonax*** has anterior laterals but not the long anterior and posterior laterals of Sowerbyiidae Cox, 1929b; anterior laterals are usually absent in Tancrediidae Meek, 1864 (Cox, 1929a). The nymph and ligament groove of ***Adelodonax*** are long for a donacid. The dorsal ends of the long colaminal teeth have not yet differentiated into cardinals, and ***Adelodonax*** differs from other Donacidae in having one rather than two cardinals in each valve and in lacking posterior laterals (see Figure 3 for hinge diagrams and formulae). The valves may gape slightly posteriorly.

Cox (1929a) and Chavan (1950) suggested that Donacidae are derived from Tancrediidae. Three supraspecific tancrediid taxa—*Palaeomya* Zittel & Goubert, 1861, *Isotancredia* Chavan, 1950, and *Paratancredia* Chavan, 1950—resemble ***Adelodonax*** in shape, but differ from ***Adelodonax*** in having posterior laterals and lacking a pallial sinus. Both *Isotancredia* and *Paratancredia* resemble ***Adelodonax*** in having an anterior colaminal tooth (AIII-3a) in the right valve. *Eodonax* Cox, 1929a, and *Protodonax* possess characteristics considered to be intermediate between the two families (Cox, 1929a; Vokes, 1945; Chavan, 1950) and the classification of each has oscillated between both families. ***Adelodonax*** also has characteristics that may be intermediate. The anterior colaminal teeth are suggestive of Tancrediidae, but an absence of posterior laterals suggests Donacidae. The hinge is more primitive than that of any other donacid and more primitive than that of most Tancrediidae, but the pallial sinus is deeper than that of tancrediids and suggests Donacidae.

Adelodonax bears a strong resemblance to *Ceroniola* Wilckens, 1904. Keen (*in* Moore, 1969:N609) follows Wilckens (1904) in considering this small, thin bivalve to be related to *Mesodesma,* and Stinnesbeck (1986) has reaffirmed this classification. The left valve hinge of ***Adelodonax*** differs from that of *Ceroniola* in lacking posterior laterals; in ***Adelodonax*** the depression between AII-2 and 4b is here interpreted as a socket for 3b; whereas, for *Ceroniola,* Keen (*in* Moore, 1969) and Stinnesbeck (1986) have interpreted this as a resilifer. The most prominent tooth in the right valve hinge of ***Adelodonax,*** cardinal 3b, is shaped and positioned to fit this socket. Illustrations of *Ceroniola* suggest that this area beneath the beak is the damaged portion of the right valve; if so, a resilifer has not been clearly demonstrated to be present in *Ceroniola,* and it and ***Adelodonax*** may be confamilial.

Adelodonax also resembles *Amphichaena* Philippi, 1847, in shape but the hinge teeth of *Amphichaena* are concentrated closer to the beaks, and the hinge is more advanced with a hinge formula of AI-3a 3b in the right valve and AII-2 4b in the left valve.

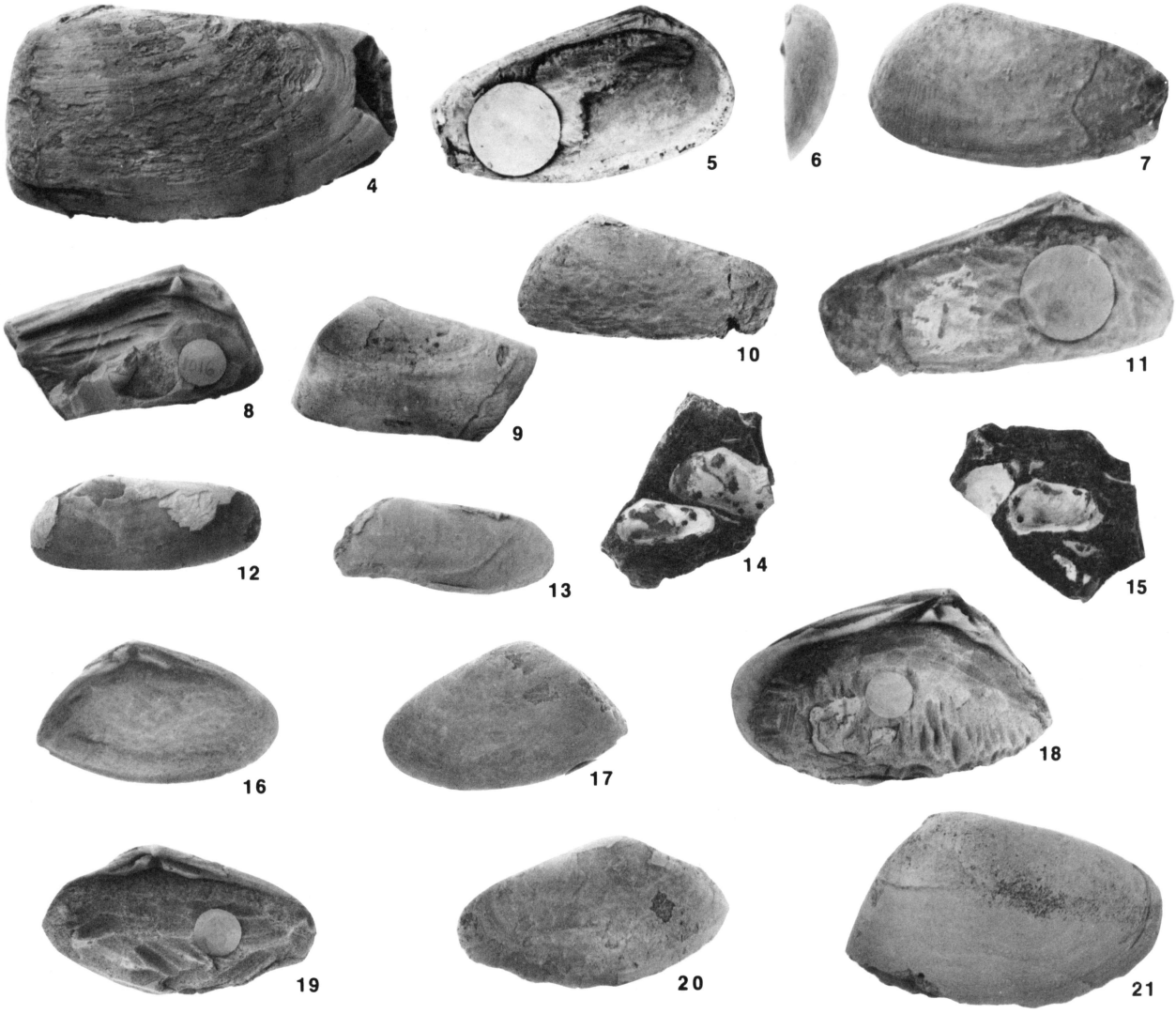
The name ***Adelodonax*** is compounded from the Greek *adelos,* meaning "unseen, unknown, obscure," and *Donax,* a bivalve genus of masculine gender.

Adelodonax tectus Saul, sp. nov.

(Figures 14, 22–28)

Diagnosis: ***Adelodonax*** having the beak very near the posterior end and a moderate posterior angulation.

Description: Shell thin, small; valves elongate, compressed and produced anteriorly, moderately inflated and truncated posteriorly; anterodorsal margin rather straight, anterior margin bluntly rounded, ventral margin barely convex, posterior margin truncated. Beaks opisthogyral, situated very near posterior end. Lunule depressed, long



Explanation of Figures 4 to 21

Figures 4–13. *Notodonax* (***Aliodonax***) ***hsui*** sp. nov., right valve. Figure 4: LACMIP 7813 from UCLA loc. 3621, holotype, ×1. Figures 5–7: LACMIP 7819 from UCLA loc. 4247, paratype, ×2; Figure 5, hinge, teeth worn; Figure 6, posterior; Figure 7, fine radial ribbing on dorsal half. Figures 8, 9: LACMIP 7814 from CIT loc. 1014, paratype, ×1; Figure 8, hinge, nymph chipped; Figure 9, exterior. Figures 10, 11: LACMIP 7815 from UCLA loc. 3622, paratype; Figure 10, exterior, ×1.5; Figure 11, hinge, ×2. Figure 12: LACMIP 7816 from UCLA loc. 3622, paratype, ×1.5. Figure 13: LACMIP 7818 from UCLA loc. 3628, paratype, ×1.5.

Figures 14, 15. Two sides of sandstone fragment Chico Formation, Musty Buck Member, UCLA loc. 3622, ×1. Figure 14: *Notodonax* (***Aliodonax***) ***hsui***, LACMIP 7817, and ***Adelodonax tectus*** sp. nov., LACMIP 7832. Figure 15: ***Califadesma elaphium*** sp. nov., LACMIP 7853.

Figures 16–21. *Notodonax* (***Aliodonax***) ***bolsae*** sp. nov., from UCLA loc. 4347. Figures 16, 17: LACMIP 7822, paratype, left valve, ×1; Figure 16, hinge; Figure 17, exterior. Figures 18, 21: LACMIP 7820, holotype, right valve slightly crushed posteriorly, ×1; Figure 18, hinge, nymph chipped; Figure 21, exterior. Figures 19, 20: LACMIP 7821, paratype, left valve, distorted longitudinally, ×1; Figure 19, hinge; Figure 20, exterior.

and very narrow; posterior angulation low. Exterior of valves polished, showing only growth lines.

Hinge with prominent nymph for ligament. Right valve with triangular, low rounded 3b with indistinct socket posterior to it and better defined socket anterior to it; colaminal AIII-3a very long, lamellar, extending from immediately in front of beak for nearly one-third length of anterodorsal margin. Left valve with elongate colaminal AII-2 and short obscure cardinal 4b on either side of the triangular, shallow, round-bottomed socket for 3b. Pallial line distant from valve margin anteriorly, becoming moderately close to margin posteriorly; pallial sinus U-shaped,