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Invertebrate Paleontology
Earth Sciences Division
Natural History MuseumTHE TETHYAN BIVALVE *ROUDAIRIA* FROM THE
UPPER CRETACEOUS OF CALIFORNIA

by M. X. KIRBY and L. R. SAUL

ABSTRACT. The Tethyan genus *Roudairia* is described for the first time from North America. A new species, *Roudairia squiresi*, occurs in the shallow-marine, basal beds of the San Francisquito Formation (uppermost Maastrichtian) at Warm Springs Mountain, Los Angeles County, California. The earliest representatives of the genus *Roudairia* are from the Cenomanian of north and west Africa. The genus later migrated westward to the western Tethyan Realm and into California during the latest Cretaceous. The presence of *R. squiresi* suggests warm water in California at the end of the Cretaceous. The taxonomic status of two closely related genera, *Cicatreia* and *Veniella*, in relation to *Roudairia*, remains unclear. However, among these three related taxa, there are at least two distinct generic groups present. The first is represented by *Veniella* and the second by *Roudairia*. Specimens from Africa and Madagascar, previously ascribed to '*Cicatreia*' *cordialis*, belong in the second group. Whether *Cicatreia cordialis* from India also belongs in this second group cannot be determined until additional specimens provide better morphological data.

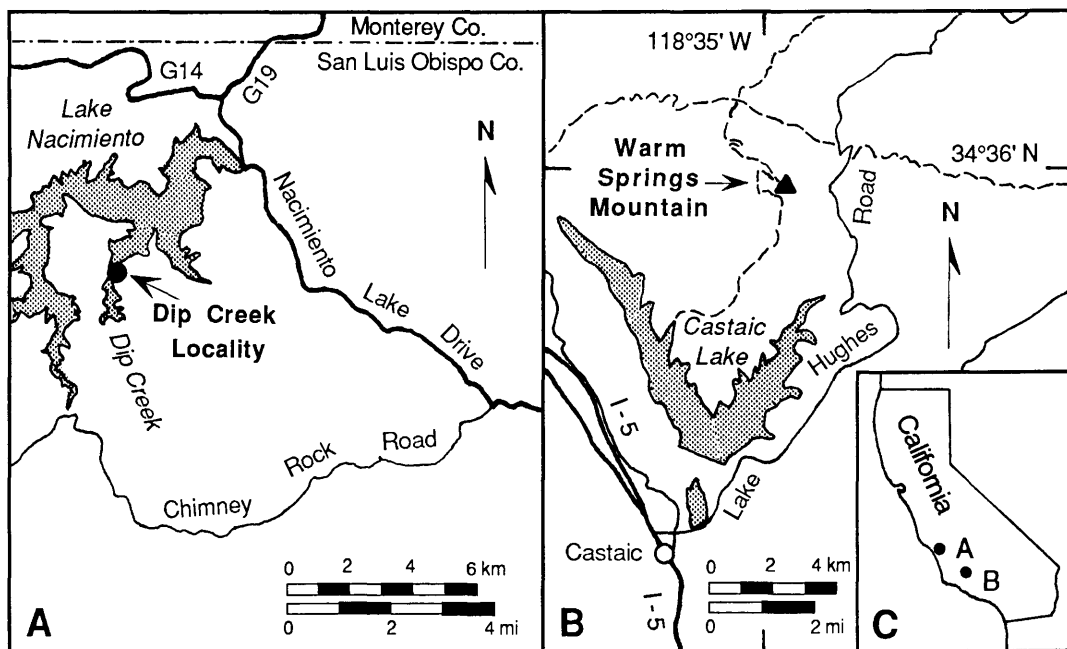
SEVERAL specimens of a new species, *Roudairia squiresi*, were collected from basal beds of the San Francisquito Formation on Warm Springs Mountain, in the San Gabriel Mountains, Los Angeles County, southern California (Text-fig. 1). Turrillid gastropods associated with *R. squiresi* at Warm Springs Mountain indicate a very late Maastrichtian age for the basal San Francisquito Formation (Saul 1983). The basal San Francisquito Formation at Warm Springs Mountain is part of a shallow-marine phase of a transgressive sequence that continued across the Cretaceous/Tertiary boundary into the Palaeocene (Kooser 1980; Kirby *et al.* 1991).

A fragment of a left valve that resembles *R. squiresi* was found in undifferentiated Upper Cretaceous rocks at Dip Creek, south shore of Lake Nacimiento, San Luis Obispo County, central California (Text-fig. 1). Associated Turrillid gastropods and an ammonite indicate a latest Maastrichtian age (Saul 1983).

Roudairia has not previously been reported from North America. One species is known from the Upper Cretaceous of Jamaica (Trechmann 1927), and four species are known from the Upper Cretaceous of Peru (Brüggen 1910; Lisson 1925; Olsson 1934, 1944). A closely related genus, *Veniella* Stoliczka, 1870, is present in Western Interior and Gulf Coast, North American deposits of Turonian to Maastrichtian age. Another closely related taxon, *Cicatreia* Stoliczka, 1870, is from the Upper Cretaceous of India.

The palaeobiogeographical distributions of *Roudairia*, *Veniella*, and *Cicatreia* are clouded by difficulties in determining their generic and specific characters. Many of the pioneering reports of species assignable to these genera failed to note important morphological features and were vague as to stratigraphical position. Darteville and Freneix (1957) considered *Roudairia* and *Cicatreia* to be synonyms of *Veniella*, and therefore placed their species in *Veniella*. They indicated the biogeographical provenance of these species, but did not reassess completely their stratigraphical positions.

A complete review is beyond the scope of this paper, but the work of Darteville and Freneix (1957), which delineates characters of four widely occurring species, '*Cyprina* (*Cicatreia*)' *cordialis* Stoliczka, 1870, '*Trigonia*' *auressensis* Coquand, 1862, *Roudairia drui* Munier-Chalmas, 1881, and '*Cyprina*' *forebesiana* Stoliczka, 1870, assists in assigning the first three of these species to *Roudairia* and the fourth to *Veniella*.



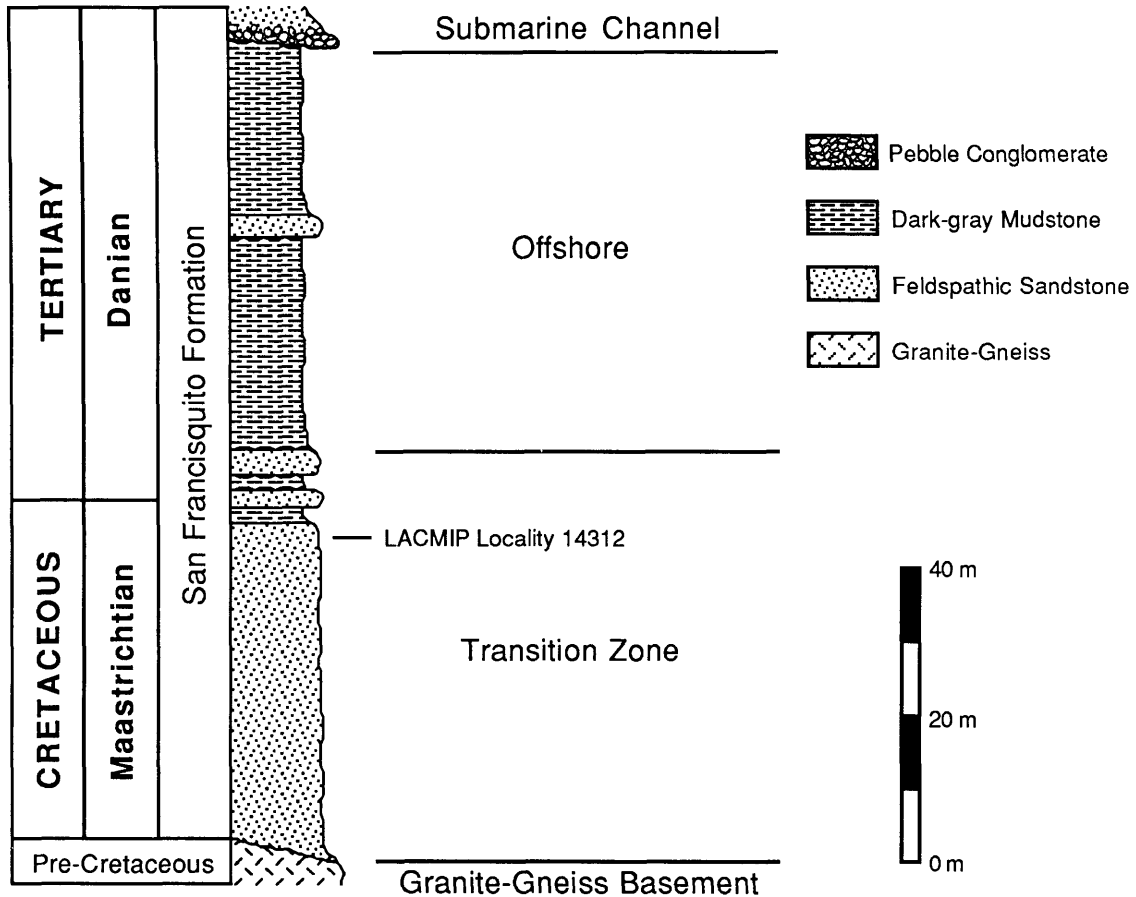
TEXT-FIG. 1. Locality maps showing (A) Dip Creek, (B) Warm Springs Mountain, and (C) California.

This paper describes the stratigraphy and depositional environments associated with *R. squiresi*, discusses the Late Cretaceous palaeobiogeography of the genus *Roudairia*, compares the generic characters of *Veniella* and *Cicatrea* with those of *Roudairia*, and concludes with the description of *R. squiresi*.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The most complete specimens of *R. squiresi* are from the lowermost San Francisquito Formation at Warm Springs Mountain (Text-fig. 2). The San Francisquito Formation ranges in age from late Maastrichtian to late Palaeocene (Dibblee 1967; Kooser 1980, 1982). At Warm Springs Mountain, the formation was deposited on a granite-gneiss basement that is cut by dykes of early Maastrichtian age (Joseph *et al.* 1982). The San Francisquito Formation represents a marine-transgressive sequence that consists of shallow-marine deposits grading upsection into deeper submarine-fan deposits (Kooser 1980; Kirby 1991). The lower part of the formation contains a conformable section across the Cretaceous/Tertiary boundary (Kirby *et al.* 1991), as defined by the *Turritella* zonation of Saul (1983). *Roudairia squiresi* was found 5 m below this boundary (Text-fig. 2).

Eight unabraded valves, including one right valve, three left valves, two articulated specimens, and one fragment, were found in a feldspathic sandstone at Warm Springs Mountain (Kirby 1991). The single-valved specimens had probably been transported a short distance, whereas the articulated specimens were most likely *in situ*. The specimens were associated with the gastropods *Turritella webbi* Saul, 1983, *Turritella chaneyi orienda* Saul, 1983, *Anchura?* sp., and with the bivalves *Cucullaea* sp. nov., *Brachidontes?* sp. nov., and *Callistalox fragilis* (Gabb, 1869). *Turritella webbi*, *Turritella chaneyi orienda*, and *Brachidontes* are characteristic of a shallow-marine environment (Keen 1971; Saul 1983).

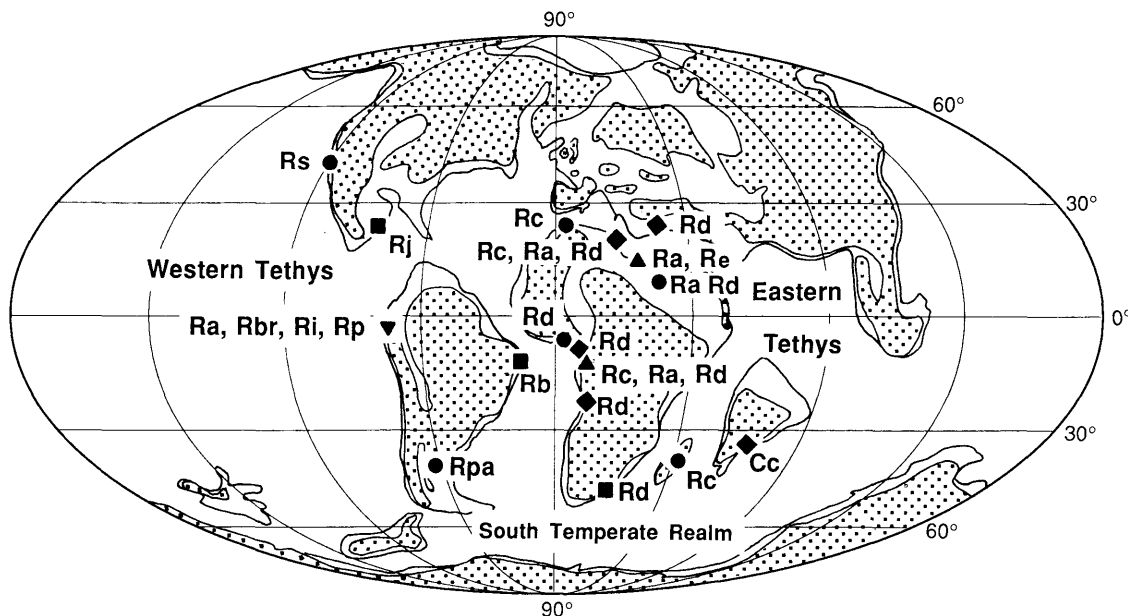


TEXT-FIG. 2. Stratigraphical section of the basal San Francisquito Formation, Warm Springs Mountain, California, showing chronostratigraphy, lithology, depositional environments, and stratigraphical position of *Roudairia squiresi* type locality (LACMIP locality 14312) (after Kirby 1991). Note transgressive nature of stratigraphical section.

Feldspathic sandstone crops out from the base of the San Francisquito Formation to 47 m above the base of the formation (Text-fig. 2). The sandstone is silty, very fine- to medium-grained, and poorly sorted. Although mostly structureless, the sandstone contains indistinct planar bedding locally. Bioturbation is very abundant. Fossiliferous lenses, up to 210 mm thick, are present throughout the feldspathic sandstone. These lenses are inferred to be storm-lag deposits (Kirby 1991).

Abundant bioturbation indicates deposition below fair weather wave base, and storm-lag deposits indicate deposition above storm wave base. Both these features indicate deposition of the feldspathic sandstone in the shallow-marine, transition zone (Kirby 1991).

These transition-zone deposits are part of a shallow-marine, transgressive sequence that grades upsection into offshore deposits. The underlying granite-gneiss basement and an overlying submarine-channel conglomerate stratigraphically bound the sequence (Text-fig. 2). This 110 m thick sequence is between 68.5 Ma and 63.8 Ma in age, based on the *Turritella* zonation of Saul (1983). Deposition of this transgressive sequence probably resulted from both basinal subsidence and eustatic transgression.



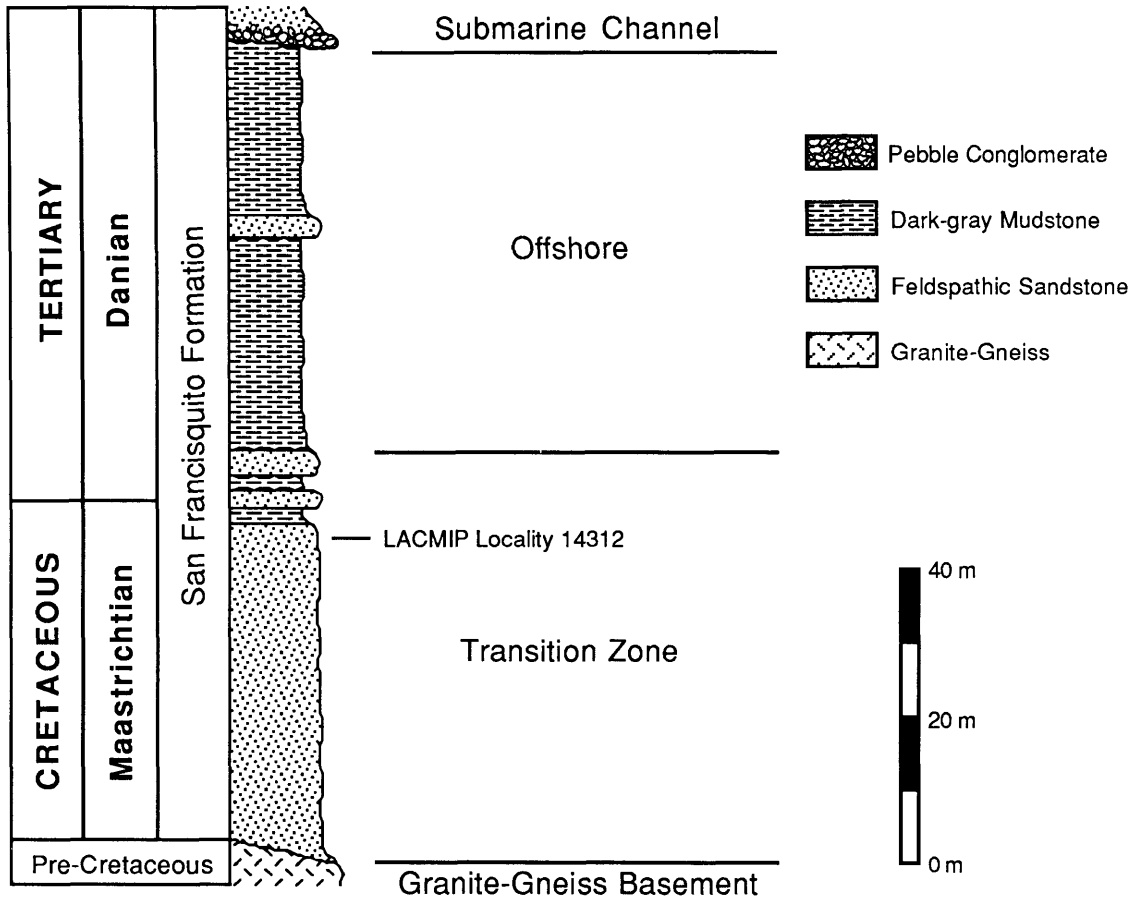
TEXT-FIG. 3. Palaeobiogeographical distribution of *Cicatrea* and *Roudairia* species on a Maastrichtian palaeogeographic map (Ziegler *et al.* 1982). Cretaceous palaeobiogeographical names after Kaufmann (1973). Plotted occurrences range from the Cenomanian to the Maastrichtian. Key to species: **Cc** = *Cicatrea cordialis* (Stoliczka 1870); **Ra** = *R. auressensis* (Coquand 1862) (Darteville and Freneix 1957); **Rb** = *R. brasiliensis* Maury, 1930; **Rbr** = *R. brüggeni* (Lisson 1925) (Olsson 1944); **Rc** = *R. cordialis* (Stoliczka 1870) (Douvillé 1904; Boule and Thevenin 1906; Darteville and Freneix 1957); **Rd** = *R. drui* Munier-Chalmas, 1881 (Rennie 1930; Darteville and Freneix 1957); **Re** = *R. elongata* Naldini, 1948; **Ri** = *R. intermedia* (Brüggen 1910) (Darteville and Freneix 1957; Willard 1966); **Rj** = *R. jamaicensis* Trechmann, 1927; **Rp** = *R. peruviana* Olsson, 1934; **Rpa** = *R. pampaensis* Lanza and Hünicken, 1970; **Rs** = *R. squirei* sp. nov. (this paper). Symbols indicate the age of the oldest specimens found at each locality: ▲ = Cenomanian; ▼ = Turonian; ■ = Campanian; ● = Maastrichtian; ◆ = Late Cretaceous.

A fragment of a left valve resembling *R. squirei* was found at Dip Creek. This fragment was found associated with turritellid gastropods and other shallow-water molluscs in very coarse-grained, conglomeratic sandstone and conglomerate beds. Grove (1986) interpreted these sandstone and conglomerate beds to be turbidites that were deposited in deep water.

Taliaferro (1944) referred the Dip Creek strata to his 'Dip Creek formation'. But Durham (1968) mapped outcrops along the north shore of Lake Nacimiento as unnamed Upper Cretaceous and Lower Tertiary rocks. Grove (1986) used this designation for the outcrops along the south shore of Lake Nacimiento. Confident assignment of the Dip Creek section to a formation can only be done after detailed geological mapping in the Lake Nacimiento area is undertaken (V. M. Seiders, pers. comm. 1992).

PALAEOBIOGEOGRAPHY

The genus *Roudairia* has a South Temperate to Tethyan distribution (Text-fig. 3. Cretaceous palaeobiogeographical names as defined by Kauffman 1973.) The genus *Veniella*, which as plotted by Darteville and Freneix (1957, text-fig. 3) included *Cicatrea* and *Roudairia*, has a South Temperate to North Temperate distribution. Text-figure 4 shows the biogeographical distributions of *Cicatrea*,

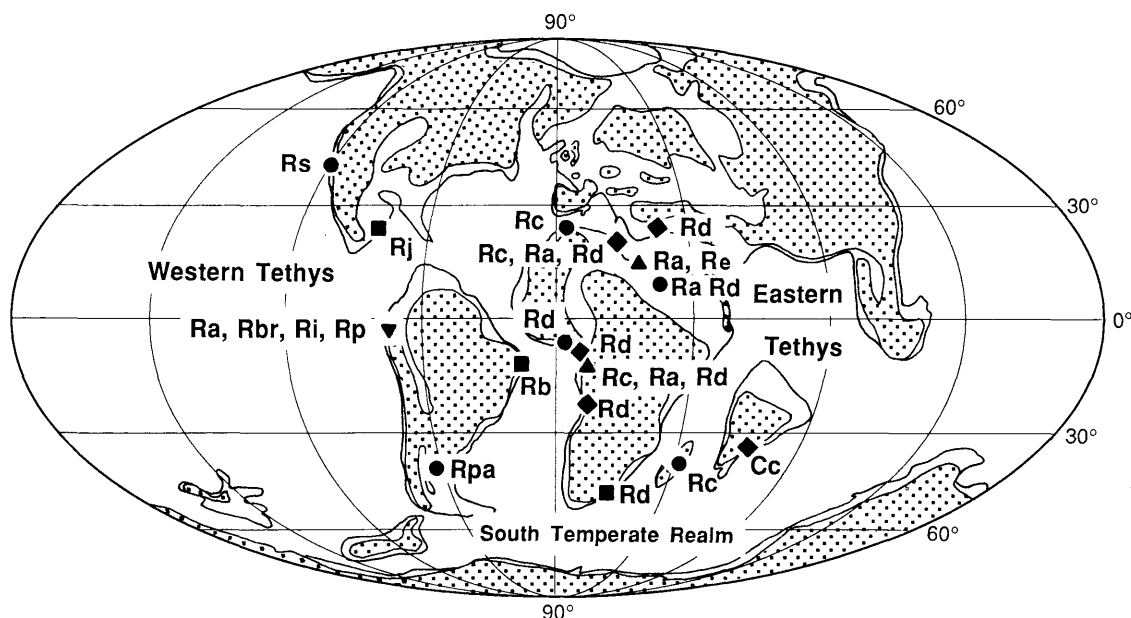


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Location Age	California	Peru	WI & GC USA	Jamaica	Argentina	Brazil	N. Africa	W. Africa	S. Africa	Madagascar	India
Maastrichtian	<i>R</i>	<i>R</i>	<i>V</i>		<i>R</i>		<i>R</i> <i>V</i>	<i>R</i> <i>V</i>		<i>R</i> <i>V</i>	<i>C</i>
Campanian		<i>R</i>	<i>V</i>	<i>R</i> <i>V</i>		<i>R</i>	<i>R</i> <i>V</i>	<i>R</i> <i>V</i>	<i>R</i> <i>V</i>		<i>C</i>
Santonian/ Coniacian		<i>R</i>	<i>V</i>				<i>V</i>	<i>R</i> <i>V</i>	<i>V</i>	<i>V</i>	<i>C</i> <i>V</i>
Turonian		<i>R</i>	<i>V</i>				<i>V</i>	<i>R</i> <i>V</i>	<i>V</i>	<i>V</i>	
Cenomanian							<i>R</i> <i>V</i>	<i>R</i> <i>V</i>			

TEXT-FIG. 4. Location of *Cicatrea* spp. (*C*), *Roudairia* spp. (*R*), and *Veniella* spp. (*V*) through time (based on Stoliczka 1870; Meek 1876; Douvillé 1904; Boule and Thevenin 1906; Trechmann 1927; Maury 1930; Rennie 1930; Olsson 1934, 1944; Naldini 1948; Darteville and Freneix 1957; Willard 1966; Leanza and Hünicken 1970). Note that ages are not to scale. WI = Western Interior. GC = Gulf Coast.

Roudairia, and *Veniella* through time. The earliest record of *Roudairia* is from the Cenomanian of north and west Africa (Naldini 1948; Darteville and Freneix 1957; Cooper 1978). Specimens from these areas range in age from Cenomanian to Maastrichtian. Willard (1966) reported *Roudairia* from the Turonian of Peru. In the Coniacian, *Roudairia* is found in Peru and west Africa (Olsson 1934, 1944; Darteville and Freneix 1957). In the Campanian, *Roudairia* is reported from Peru, Jamaica, Brazil, north Africa, west Africa, and south Africa (Trechmann 1927; Maury 1930; Rennie 1930; Olsson 1934, 1944; Darteville and Freneix 1957). In the Maastrichtian, *Roudairia* is reported from California (this paper), Peru, Argentina, north Africa, west Africa, and Madagascar (Douvillé 1904; Olsson 1934, 1944; Darteville and Freneix 1957; Leanza and Hünicken 1970).

Abbass (1962) described a new species of *Roudairia* from the Danian of Egypt. If his new species, *Roudairia awadi*, is indeed a *Roudairia*, then *Roudairia* evidently survived the Cretaceous/Tertiary mass extinction and lived on into the Palaeocene. His description and figures of *R. awadi*, however, permit doubt as to whether his specimens actually belong to *Roudairia*.

The palaeobiogeographical distribution of *Roudairia* suggests that the genus evolved either in the northern part of the South Temperate Realm or in the Tethyan Realm before or during the Cenomanian. The genus later migrated westward to the western Tethys during the Late Cretaceous. *Roudairia squiresi*, or one of its antecedents, migrated from Central or South America into California in the Maastrichtian (Text-figs 3–4). The migration of the Tethyan *Roudairia* into the northeastern Pacific at this time suggests the presence of warm water in California at the end of the Cretaceous.

Roudairia squiresi of California is most similar to *Roudairia peruviana* Olsson, 1934, which is present in the Maastrichtian Monte Grande Formation and undifferentiated rocks of Campanian to Maastrichtian age in northern Peru (Olsson 1934, 1944). *Roudairia peruviana* is older than *R. squiresi*. *Roudairia jamaicensis* Trechmann, 1927, from the Campanian of Jamaica (Trechmann 1927), is less similar to, and is also older than *R. squiresi*. The present findings extend the palaeobiogeographical range of *Roudairia* from Jamaica and Peru northward to California (Text-fig. 3). The age range of *Roudairia* in the eastern Pacific is extended to the latest Maastrichtian (Text-fig. 4).

SYSTEMATIC PALAEOLOGY

Abbreviations. The following abbreviations are used with catalogue and locality numbers mentioned in the text: CIT, California Institute of Technology; CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; PRI, Paleontological Research Institution; UCLA, University of California, Los Angeles. CIT and UCLA collections are currently at the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

Phylum MOLLUSCA Linnaeus, 1758
Class BIVALVIA Linnaeus, 1758
Order VENEROIDA Adams and Adams, 1856
Family ARCTICIDAE Newton, 1891
Genus ROUDAIRIA Munier-Chalmas, 1881

Type species. *Roudairia drui* Munier-Chalmas, 1881 from the Campanian and Maastrichtian of Tunisia.

Diagnosis. Inflated arcticid bivalves of trigonal to subquadrate outline with a strongly carinate posterior; sculpture of undulating ribs on the flank. Hinge of right valve with three cardinals and four laterals: 1 at the ventral hinge border, anterior to 3a; 3a dorsal to 1; 3b bifid; AI short, subtrigonal; AIII elongate. Hinge of left valve with two cardinals and two laterals; 2b obscurely bifid; 4b elongate, thin; AII chevron-shaped; PII elongate with transverse striations on both sides. Posterior adductor muscle scar bordered anteriorly by a strong myophoric flange.

Discussion. A number of problems with respect to the appropriate generic name for the specimens from Warm Springs Mountain cannot be solved solely on the basis of the Warm Springs Mountain specimens. Of the three generic taxa, *Veniella* Stoliczka, 1870 (type species *Veniella conradi* Morton, 1833), *Cicatrea* Stoliczka, 1870 (type species '*Cyprina*' (*Cicatrea*) *cordialis* Stoliczka, 1870), and *Roudairia* Munier-Chalmas, 1881, the specimens from Warm Springs Mountain are least like *Veniella*. Darteville and Freneix (1957) reviewed the status of the generic names *Veniella*, *Cicatrea*, and *Roudairia*. They considered *Cicatrea* and *Roudairia* to be synonyms of *Veniella* because: (1) the separation of *Veniella* and *Roudairia* required well-preserved adult hinges; (2) '*Cyprina*' *forbesiana* Stoliczka, 1870, was considered by Vokes (1954) to have a left valve hinge like *Roudairia* and a right valve hinge resembling *Veniella*; and (3) some species, such as the Indian *Cicatrea cordialis*, combine the hinge of *Veniella* and the external shape and sculpture of *Roudairia*. Although the type species of *Roudairia* and *Veniella* are sufficiently dissimilar to be recognized as representatives of distinct supraspecific taxa, Darteville and Freneix (1957) believed that '*Cyprina*' *forbesiana* and *Cicatrea cordialis* bridge this morphological gap. Vokes (1954) suggested that *Veniella* is a North American Late Cretaceous group, but he considered *Cicatrea cordialis*, from India and Madagascar, to be closer to *Veniella* than to *Roudairia*. The following discussion outlines what is known of the generic characters of *Veniella*, *Roudairia*, and *Cicatrea*.

The type species of *Veniella*, *V. conradi*, has been illustrated by Vokes (1954). Characters of the genus are discernable from his illustrations and from well-preserved specimens of the type species from the Ripley Formation of Tennessee (Pl. 2, figs 2–4). Exteriorly, the shell has a strong posterior

angulation. Commarginal sculpture anterior to the angulation consists of irregularly developed ridges, the strongest of which are flanged. In the right valve, *V. conradi* has three cardinals, one anterior lateral AIII, and two posterior lateral teeth (Pl. 2, fig. 2). In the left valve, *V. conradi* has two cardinals, one elongate to somewhat triangular anterior lateral AII, and one posterior lateral tooth (Pl. 2, fig. 3). *Veniella conradi* lacks an internal myophoric flange bordering the anterior side of the posterior adductor muscle scar. The *Treatise on invertebrate paleontology* illustration of the left valve of *V. conradi* is misleading (Casey 1969, p. N651, text-fig. E129, 6a). Cardinal 2b is never so bifid in mature specimens as depicted (see ontogenetic hinge changes in Vokes (1954, text-figs 1-4, 6-9)) and the adductor muscle scars are discrepant in size and shape. The posterior adductor muscle scar is actually larger and rounder than the semicircular anterior adductor muscle scar.

The nominal type species of *Roudairia*, *R. drui*, has been variously synonymized with the prior *Opis undatus* Conrad, 1852, and *Trigonia auressensis* Coquand, 1862. But Darteville and Freneix (1957, p. 141) rejected the synonymy of *R. drui* with *Roudairia undata* and *Roudairia auressensis*, and listed several characters, including a second posterior carina present in *R. undata* and finer, more uneven ribbing in *R. auressensis*, that separate these two species from *R. drui*. *Roudairia drui* has been recognized from several horizons and locations (Text-fig. 3), and not all of these specimens are conspecific (Darteville and Freneix 1957). This confusion and the poor preservation of some of the material has made generic characters of *Roudairia* difficult to determine. Exteriorly, *R. drui* has a carinate posterior angulation accentuated by a strongly raised keel. *Roudairia drui* is higher than long, and squarely truncated posteriorly. Commarginal ribbing on the anterior portion of the shell is strong and even near the beaks, but becomes more uneven ventrally. The commarginal ribs, although over-steepened, do not give rise to flanges. Vokes (1954) discussed the hinge teeth based on illustrations in Quaas (1902) and Pervinquier (1912). The hinge of *R. drui* differs from that of *V. conradi* in having a chevron-shaped anterior lateral AII in the left valve and a pustular anterior lateral AI in the right valve. In contrast, *V. conradi* has an elongate trigonal AII in the left valve and lacks AI in the right valve. Darteville and Freneix (1957) did not indicate whether *R. drui* has an internal myophoric flange along the anterior side of the posterior adductor muscle scar or not. But Quaas' figure (1902, pl. 24, fig. 22) of a left valve of *R. drui* indicates that such a flange is present.

Abbass (1962) described several *Roudairia* species from Egypt. Regrettably, he did not refer to Darteville and Freneix (1957), nor did he indicate the relationship of his Egyptian taxa to those discussed by Darteville and Freneix (1957). In order to settle discrepancies between Abbass (1962) and Darteville and Freneix (1957), we would need to examine and compare Abbass' specimens with those described by Darteville and Freneix (1957).

The type species of *Cicatreia*, *Cyprina (Cicatreia) cordialis* Stoliczka, 1870, has been recognized in various parts of Africa, as well as in India and Madagascar (Darteville and Freneix 1957) (Text-fig. 3). Discussions of the validity of *Cicatreia* (Douville 1904; Vokes 1954) refer to Stoliczka's figure (1870, pl. 10, fig. 2) of a left valve hinge to define generic characters. Darteville and Freneix (1957) did not figure a hinge for this species and did not have any available for study. Although they did not mention an internal myophoric flange, illustrations of specimens identified as *C. cordialis* by Darteville and Freneix (1957) clearly show the presence of an internal flange bounding the anterior side of the posterior adductor muscle scar. Exteriorly, *C. cordialis* has a high keel along the strong posterior angulation. This keel is particularly pronounced near the beaks. Commarginal sculpture on the anterior portion of the valve is even and roundly ripple-ribbed near the beaks. The commarginal ribs evanesce ventrally. Stoliczka's figure (1870, pl. 10, fig. 2) of the left valve hinge gives the impression of a double exposure. Two hinges appear to be present, one superposed on the other. One hinge is offset higher and to the left of the other hinge. Compared to *Veniella* and *Roudairia*, Stoliczka's figure is peculiar in having no upright, flanged posterior end to the nymph. Although broad ligament grooves are indicated, the usual nymph flange is not. Stoliczka (1870) did comment on its absence. If two valves are superposed, one set of the ligament grooves and subumbonal pits would be above and to the left of the other. Cardinal 2b is drawn as a moderately broad triangle and is more like 2b of *V. conradi* than of *R. squiresi* and *R. peruviana*. This broadly triangular cardinal 2b is somewhat surprising as *C. cordialis* is more elongate with a strong forward

twist to the shell. In *V. conradi*, mature shells of greater elongation and forward twist have a narrower, more elongate 2b, but shorter shells have a more trigonal 2b. The left anterior lateral AII is also peculiar. It is more equantly triangular than that of *V. conradi* and is drawn with the hint of a basal dimple suggesting the possibility of a socket for AI. If *C. cordialis* should be shown to have AI, then its hinge formula would be the same as that of *Roudairia*. Stoliczka (1870, p. 199) said that the base of cardinal 2b is united to the top of AII by a low rib. In *R. squiresi* and *R. peruviana*, a ridge drops from the tip of AII toward the base of 2b, but it encircles the socket for 1 and does not join 2b. Additionally, Stoliczka wrote (1870, p. 199), 'a distinct rib is seen in front of the anterior muscular impression, it has the appearance of an anterior lateral tooth, but has in reality nothing to do with hinge-teeth'. If this figure (Stoliczka, 1870, pl. 10, fig. 2) were drawn from superposed impressions of two shells, the 'distinct rib' would be the anterior margin of the upper, more leftward specimen. *Roudairia squiresi* has a raised anteroventral margin to the anterior adductor muscle scar, but this margin is not sufficiently raised to have the appearance of a tooth.

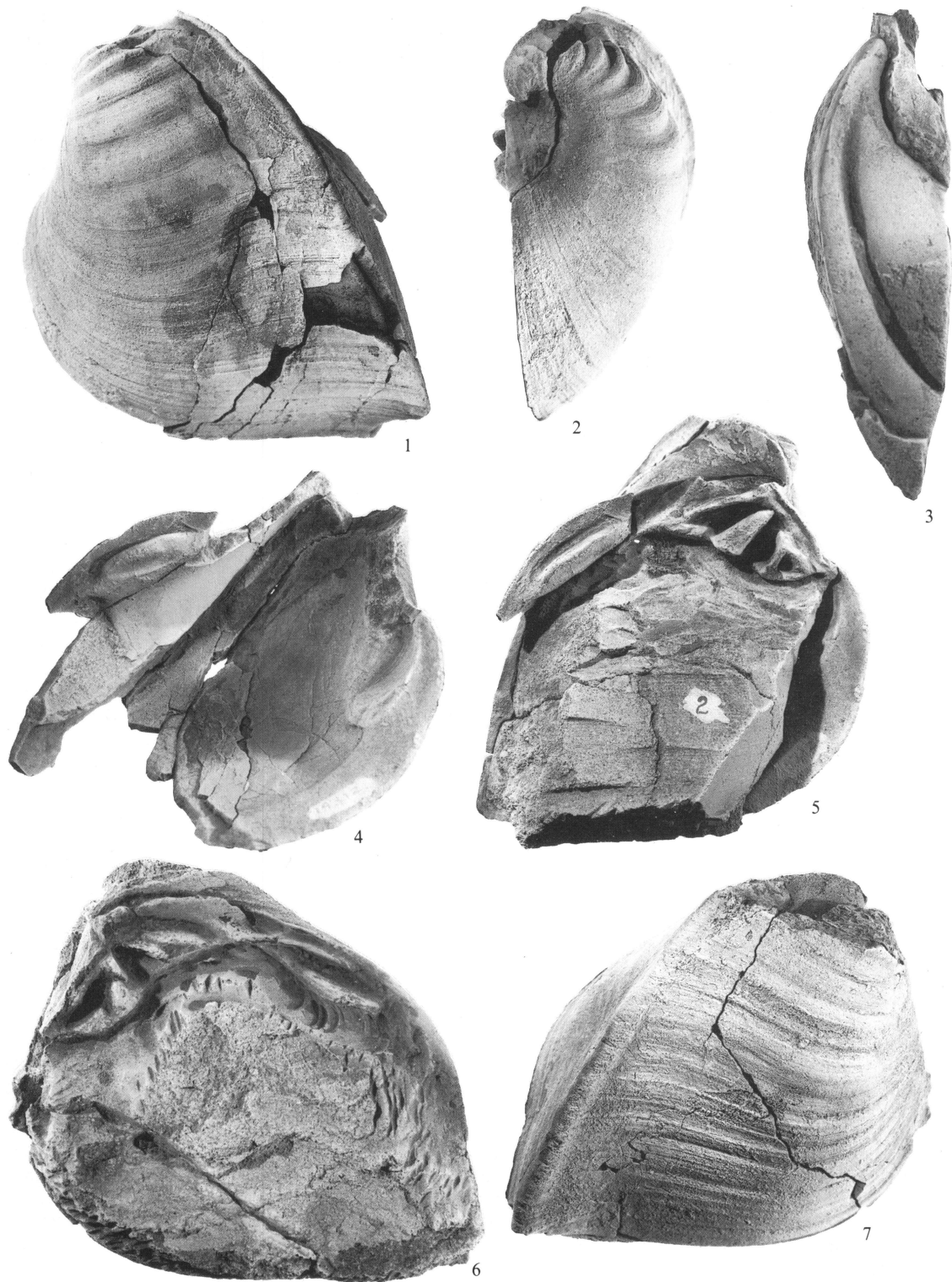
Drawings of *C. cordialis* credited to Douvillé are in Boule and Thevenin (1906, text-figs 4–6). The drawings are based on rock moulds from Madagascar. Their text-figure 6 of the left hinge greatly resembles Stoliczka's figure 2 (1870, pl. 10) in shape and position of hinge-teeth 2, 4 and AII, except that in Douvillé's text-figure 6, AII is depicted as having a chevron-shape with a well-developed socket for AI in its base. Douvillé's figures (Boule and Thevenin 1906, text-figs 4–6) do not depict any nymph or ligament groove. Their omission may have been caused by incomplete rock moulds.

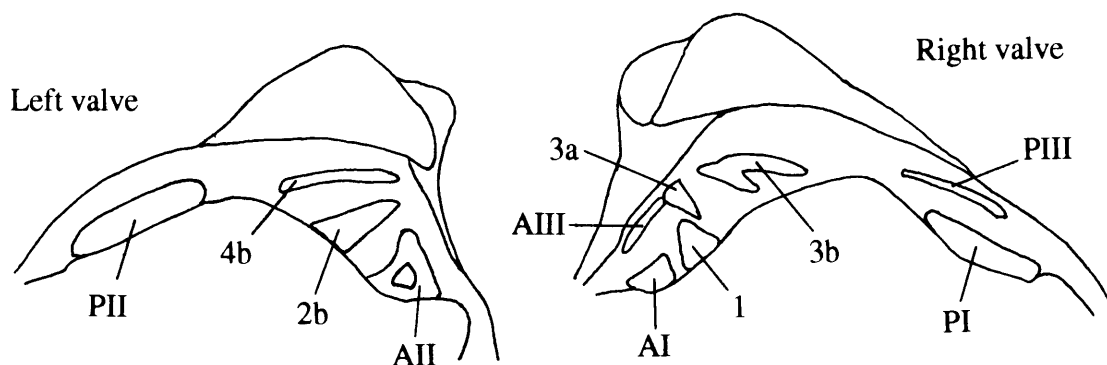
If Stoliczka's left hinge (1870, pl. 10, fig. 2) is drawn accurately, then the hinge of *Cicatrea* differs from that of *Roudairia* in the absence of an alate nymph and in having both 2b and AII broadly triangulate. But Douvillé's tooth AII (Boule and Thevenin 1906, text-fig. 6) is more like that of *Roudairia* and his right valve hinge (Boule and Thevenin 1906, text-fig. 4) shows a well-developed AI similar to that of *Roudairia* but much more elongate than that seen in *R. squiresi* or *R. peruviana*. Differences between illustrations of the Indian *C. cordialis* of Stoliczka and the Madagascan *C. cordialis* of Douvillé permit doubt as to whether they are both the same species, especially as the Indian specimens are probably of early Senonian age rather than the Maastrichtian age of the Madagascan specimens. Despite the comments of several palaeontologists (Douvillé 1904; Boule and Thevenin 1906; Rennie 1929; Cox 1952; Vokes 1954; Darteville and Freneix 1957), the generic characters of *Cicatrea* remain ambiguous. Adequate material from the type locality of *C. cordialis* is necessary to determine how closely Stoliczka's figure (1870, pl. 10, fig. 2) depicts the features these palaeontologists have variously reinterpreted. Based on available illustrations, specimens assigned to *C. cordialis* by Douvillé (Boule and Thevenin 1906) and Darteville and Freneix (1957) are herein referred to *Roudairia*.

In summary, the present taxonomic status of *Veniella*, *Roudairia*, and *Cicatrea* remains unclear due to the lack of well-preserved specimens of *Cicatrea*. Based on previous work (Boule and Thevenin 1906; Vokes 1954; Darteville and Freneix 1957), there are at least two distinct generic groups present. The first group, represented by *Veniella*, is characterized by uneven commarginal

EXPLANATION OF PLATE I

Figs 1–7. *Roudairia squiresi* sp. nov. LACMIP locality 14312, Warm Springs Mountain, California; San Francisquito Formation. 1–5, LACMIP 12204, holotype; left valve; 1, exterior showing strong carina on posterior angulation and rounded ripple ribs developed near beak; 2, anterior showing lunule and development of rounded ripple ribs near beak; 3, posterior, shell removed to show mark of internal myophoric flange on rock cast and posterior adductor muscle scar (rough area to right of myophore impression); 4, interior showing myophoric flange and position of adductor muscle scars; 5, hinge, nymph broken, posterior lateral PII, cardinal 4b elongate slender, cardinal 2b elongate trigonal with faint medial groove, anterior lateral AII chevron-shaped. 6–7, LACMIP 12205, paratype; right valve; 6, hinge, nymph nearly complete, anterior laterals AI and AIII, cardinal 1, 3a, and 3b, 3b bifid, posterior laterals PI and PII; 7, exterior showing strong carina on posterior angulation. All figures $\times 1$ and coated with ammonium chloride.





TEXT-FIG. 5. Left and right valve hinge areas of *Roudairia squiresi* with the hinge teeth labelled.

ribbing on the anterior margin that tends to develop flanges, by an angulate but not carinate posterior angulation, by the absence of the anterior-lateral tooth AI, and by the absence of an internal myophoric flange on the anterior side of the posterior adductor muscle scar. The second group, represented by *Roudairia*, is characterized by even commarginal ribbing which commonly becomes roundly ripple-ribbed on the anterior portion of the shell near the beaks and which evanesces toward the ventral margin in large specimens, by a strongly carinate posterior angulation that is accentuated by a keel, by the anterior-lateral tooth AI, and by an internal myophoric flange bordering the anterior side of the posterior adductor muscle scar. The specimens from Africa and Madagascar previously described as *Cicatrea* belong in this second group. The Indian specimens described as *Cicatrea* may also belong in this second group. But until better preserved specimens of *Cicatrea* from India are available, the relationship of *Cicatrea* to *Veniella* and *Roudairia* will remain unclear.

The specimens from Warm Springs Mountain are distinct from *V. conradi*. They are externally more similar to *R. drui* and *C. cordialis*. Internally, they are more similar to *R. drui*. Previous workers (e.g. Douvillé 1904; Olsson 1934; Vokes 1954) have used various stratagems to avoid replacing the more commonly used and better-based *Roudairia* Munier-Chalmas, 1881, with the enigmatic and ill-defined *Cicatrea* Stoliczka, 1870. Although the similarity of the Warm Springs

EXPLANATION OF PLATE 2

Fig. 1. *Roudairia squiresi* sp. nov. LACMIP 12209, paratype; articulated specimen, anterior view; LACMIP locality 14316, Warm Springs Mountain, California; San Francisquito Formation.

Figs 2–4. *Veniella conradi* (Morton). 2, LACMIP 12211, hypotype; right valve, interior view showing hinge, muscle scars, and lack of internal myophoric flange bordering posterior adductor muscle scar; LACMIP locality 8063, Coon Creek, Tennessee; Ripley Formation. 3–4, LACMIP 12212, hypotype; left valve; LACMIP locality 8063, Coon Creek, Tennessee; Ripley Formation; 3, interior view showing hinge, muscle scars, and lack of myophoric flange bordering posterior adductor muscle scar. 4, exterior with commarginal flanges developing into distant rib crests.

Figs 5–8. *Roudairia peruviana* Olsson. 5–6, PRI 3716, holotype; right valve; Monte Grande, Peru; Monte Grande Formation; 5, exterior with strong carina on posterior angulation and rounded ripple ribs near beak; 6, hinge, lunular margin and anterior portion of hinge damaged, nymph broken. 7, PRI 4825 (exterior figured by Olsson, 1944, pl. 2, fig. 7), hypotype; left valve, interior view, hinge damaged but shows nymph, cardinal teeth 4b and 2b, and chevron-shaped anterior lateral AII, also myophore along posterior muscle scar; Monte Grande, Peru; Monte Grande Formation, specimen not coated. 8, LACMIP 12210, hypotype; right valve, hinge with well-preserved nymph, anterior laterals AI and AIII, cardinals 1, 3a and 3b, 3b widely bifid, posterior laterals PI and PIII; UCLA locality 5261, north of Tortuga, Paita Peninsula, north-western Peru; **Baculites* beds*.

All figures $\times 1$ and coated with ammonium chloride, except where noted otherwise.