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DESCRIPTIONS OF NEW CHILEAN ANT TAXA (HYMENOPTERA: FORMICIDAE)

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DESCRIPTIONS OF NEW CHILEAN ANT TAXA (HYMENOPTERA: FORMICIDAE)[1]

By ROY R. SNELLING[2]

ABSTRACT: One new species of *Solenopsis*, *dysderces*, is described. Two species, *bidentatus* Mayr and *denticulatus* Mayr, are removed from the genus *Nothidris*. A new species of *Nothidris*, *cekalovici*, is described and *Megalomyrmex bicolor* Ettershank is transferred to *Nothidris*. A key is given for the known species of *Nothidris*. A new genus, *Antichthonidris* (type species: *Monomorium denticulatum* Mayr 1887), is proposed for the two species removed from *Nothidris*.

The status of the two genera *Dorymyrmex* and *Araucomyrmex* is briefly discussed. A new species, *agallardoi*, of *Dorymyrmex* is described from Santiago Province. The following new species of *Araucomyrmex* are described: *hunti* (Antofagasta Prov.), *hypocritus* (Santiago Prov.), *incomptus* (Coquimbo Prov.), *pappodes* (Valparaiso Prov.) and *pogonius* (Ñuble Prov.).

All new taxa are illustrated. Primary types of new species are in the Natural History Museum of Los Angeles County (LACM), with paratypes of most in the Museo Nacional de Historia Natural, Santiago, and Universidad de Concepción, Concepción.

INTRODUCTION

A general taxonomic and ecological review of the ant fauna of Chile is now nearing completion. The following new taxa are described in order that the names may be available for use in that study in which all new and old taxa in the Chilean fauna will be separated by keys.

Most of the material for the present paper was collected by J. H. Hunt and deposited in the Natural History Museum of Los Angeles County (LACM). Important material from the collections of the Museo de Historia Natural de Santiago (MSTO) and from the collection of T. Cekalovic, Universidad de Concepción, Concepción (UCON), was also available. These institutions graciously have assented to deposit of primary types, based on their material, in the LACM; paratypic material will be deposited in all three collections.

The descriptions which follow utilize morphological terminology conventional in formicid taxonomy. The number in parenthesis following a measurement or index indicates the appropriate figure for the holotype or, in one case, the allotype. All measurements are in millimeters.

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MYRMICINAE

SOLENOPSIS Westwood

Solenopsis dysderces new species

Figures 1-2

Diagnosis. Worker: Size minute, HL less than 0.5 mm; apical antennomere longer than segments 2-8 combined; eye a single unpigmented facet; frontal punctures fine, sparse. FEMALE and MALE unknown.

WORKER. *Measurements.* HL 0.40-0.44 (0.44); HW 0.31-0.32 (0.32); SL 0.28-0.31 (0.30); WL 0.44-0.46 (0.45); PW 0.19-0.21 (0.20).

Head (fig. 1). Distinctly longer than broad, CI 70-76 (73), sides approximately parallel, slightly convergent above, occipital margin slightly concave. SI 87-98 (94), apex of scape short of occipital margin by about twice maximum diameter of scape; apical antennomere 1.20-1.30 (1.27) times combined lengths of segments 2-8. Eye unpigmented and barely discernible, consisting of a single facet. Clypeus with distinct carinal and paracarinal teeth projecting beyond apical margin. Mandibular formula 1+3, basal tooth distinctly displaced basad on upper margin.

Thorax (fig. 2). Slender, PW 0.44-0.46 (0.45) x WL. Thoracic dorsum, in profile, flattened; metanotal groove distinctly and sharply impressed. Propodeum, in profile, without differentiated basal and posterior faces.

Petiole, in profile, robust, anterior peduncle short; anteroventral tooth present, but small. Postpetiole, in profile, with node low, rounded. In dorsal view, nodes of petiole and postpetiole about equally broad.

Vestiture. Head, thorax and petiole with sparse, irregularly spaced erect hairs of variable length. Scape and tibiae with conspicuous short erect to suberect hairs.

Integument. Smooth and shiny. Frons with scattered fine punctures, separated by 4 x or more, a puncture diameter, hardly exceeding in diameter the hairs arising from them. Frontal lobe without conspicuous striae. Clypeus with bicarinate median lobe, otherwise unsculptured. Mandible with sparse fine punctures. Mesopleura without punctures or striae. Side of propodeum with two or three inconspicuous fine striae below.

Color. Pale yellowish, mandibular teeth, clypeal margin and thoracic sutures reddish.

FEMALE and MALE unknown.

Type Material. Holotype and five worker paratypes: CHILE, Prov. Aconcagua: ca. 3 km north of Zapallar, 28 Oct. 1972 (J. H. Hunt, #JHH 958). All type material in LACM.

Etymology. Gr., *dysderkes*, hardly seeing, so named because of the reduced, unpigmented eye.

Ecology. The few specimens known were removed from a small cell about 15 cm below the surface of the soil, while excavating a colony of *Araucomyrmex*.

The depigmentation, reduced eyes and minute size suggest that this species is probably entirely subterranean and may be associated with other ant species through cleptobiosis.

Discussion. This ant belongs to the group recognized formerly as the subgenus *Diplorhoptrum*, synonymized recently with *Solenopsis* by Ettershank (1966). Its affinities are uncertain, but the minute size, elongate tenth antennomere and reduced eye are suggestive of *S. pygmaea* Forel, an Antillean species. The latter ant is known to me only from the original description, which is sufficiently imprecise that no clear-cut distinction can be made at this time. I consider it unlikely, however, that the two are the same and have elected to describe the Chilean species as new.

The only other Chilean *Solenopsis* in which the tenth antennomere exceeds the combined lengths of segments 2-8 is *S. helena* Emery. In that species the eye is pigmented and consists of three or four facets. The punctures on the frons are two to three times the diameter of the hairs arising from them and are separated by two to three times their own diameter. The median clypeal lobe is more abruptly produced in *S. helena* and the node of the postpetiole, in profile, is more strongly elevated.

NOTHIDRIS Ettershank

Nothidris was established by Ettershank (1966) for three Chilean species assigned previously to *Monomorium*. The designated type species was *M. latastei* Emery, 1895. The two other included species were *N. bidentatus* (Mayr) and *N. denticulatus* (Mayr). Ettershank was unable to study the sexual forms of any of the species. Both sexes of all three species have been available to me and I am certain, after studying these, that the genus, as orginally constituted, is an unnatural one. I am removing *N. bidentatus* and *N. denticulatus* to a new genus, described below. Further, *Megalomyrmex bicolor* Ettershank, 1965, is transferred to *Nothidris* and one new species is described here.

Although Ettershank felt *M. bicolor* to be related to such *Megalomyrmex* species as *M. goeldii* Forel, I cannot agree that this is the case. In species of that group, the median lobe of the clypeus is not bicarinate, the head is more narrowed above than below, the antepenultimate and penultimate antennomeres are much longer than wide, the propodeal profile is different and the petiolar and postpetiolar nodes are much lower in profile. In all of these characters *M. bicolor* is very similar to *N. latastei*; the undescribed female of *M. bicolor* is also very much like that of *N. latastei*. The transfer of *Megalomyrmex bicolor* to *Nothidris* is a NEW COMBINATION.

Nothidris cekalovici new species

Figures 3-4

Diagnosis. Worker: Propodeum broadly rounded, without sharp projections; head narrow, CI 82-88; malar area no longer than maximum eye length; penultimate antennomere 1.2-1.5 times longer than wide. FEMALE and MALE unknown.

WORKER. *Measurements*. HL 0.86-1.10 (1.10); HW (excluding eyes, measured at level of top of eye) 0.71-0.96 (0.92); SL 0.78-0.99 (0.97); WL 1.13-1.48 (1.48); PW 0.51-0.71 (0.71).

Head (fig. 3). Distinctly longer than broad, CI 82-88 (84); in frontal view, sides approximately parallel in middle and convergent above and below; occipital margin nearly flat. Scape short, SI 103-111 (106); penultimate antennomere 1.2-1.5 (1.3) times longer than wide. Eye large, maximum diameter about 1.5 times minimum diameter; OMD 0.79-1.00 (0.95) x EL. Clypeus weakly longitudinally sulcate, sides of median lobe weakly carinate; median setae present; one pair intercarinal setae; first pair paracarinal setae shorter; a few lateral setae present. Dental formula 1+4. Palpal formula 4, 3.

Thorax (fig. 4). Of normal worker form for this genus, PW 0.43-0.48 (0.48) x WL. Promesonotum, in profile, strongly convex, abruptly sloping behind; promesonotal suture distinct to spiracle, above which and across dorsum, it is very faint. Metanotal groove distinctly impressed dorsally and on side. Mesothoracic dorsum, seen from above, distinctly narrowed behind. Propodeum longitudinally impressed; juncture of basal and posterior faces broadly rounded, not at all angulate. Propodeal spiracle small, round. Inferior propodeal plates large, with distinct angulation above. Metapleural gland large, distinct; posteroventrally with rounded protuberance bearing gland opening.

Nodes of petiole and postpetiole high, summits rounded in profile. Anterior peduncle of petiole ventrally carinate, carina ending truncately in front. Gastric profile biconvex.

Vestiture. Head, thorax and gaster with sparse, fine, long white hairs; scape with much shorter, suberect hairs; hairs appressed to subappressed on tibial extensor surfaces.

Integument. Entire ant smooth and shiny. Median lobe of clypeus bicarinate and with 1-3 short rugulae at side; a few fine rugulae in antennal fossa; malar area with distinct, coarse rugulae; mandible coarsely rugulose; mesokatepisternum with numerous fine, diagonal striae, some faint; metapleuron with a few short, coarse rugulae.

Color. Thorax, petiole, postpetiole, and legs (except basitarsi) light yellowish to light reddish; head, gaster and basitarsi light brown. Mandibles reddish yellow, teeth blackish.

FEMALE and MALE unknown.

Type Material. Holotype and 21 worker paratypes: CHILE, Prov. Aconcagua: Carretera Panamericana, km 206, 10 km north of Pichidangui, 23 Dec. 1963 (T. Cekalovic, No. 4174). Holotype and seven paratypes in LACM; 11 paratypes in UCON: three paratypes in MSTO.

Etymology. This species is dedicated to Tomás Cekalovic K., collector of the type series and many other fine samples of Chilean ants.

Discussion. The color pattern will serve to separate *N. cekalovici* from the other described species. Four specimens from Algarrobo, Valparaiso, 21 July 1951 (Kuschel and Peña; MSTO) resemble *N. cekalovici* in color pattern. These were recorded by Kempf (1970) as *Megalomyrmex bicolor*. Aside from the dark head and slightly more angulate propodeum they are very similar to *N. bicolor* and may represent a distinctive color phase of that species. These specimens differ from *N. cekalovici* in the sharply angulate propodeum and long malar area.

The three recognized species of *Nothidris* may be separated by the following key to the workers.

1. Head concolorous with thorax, gaster darker (if head is concolorous with gaster, malar area is at least 1.10 x EL); propodeum distinctly angulate or with sharp projections.. 2
   Head concolorous with gaster, thorax paler; malar area 0.79-1.00 x EL; propodeum rounded, not at all angulate at juncture of basal and posterior faces .... *cekalovici* Snelling
2. Propodeum angulate, but without sharp projections; penultimate antennomere 1.25-1.45 x longer than wide; malar area usually 1.2 or more x EL... *bicolor* (Ettershank)
   Propodeum at least sharply angulate, usually with distinct sharp projections; penultimate antennomere 0.77-1.20 x longer than wide; malar area usually less than 1.2 x EL... *latastei* (Emery)

ANTICHTHONIDRIS new genus

Diagnosis. Monomorphic: Median lobe of clypeus bicarinate, prolonged over apical margin in worker and female. Palpal formula, female and worker, 2, 2; male, 3, 2. Anterior tentorial pit about midway between antennal socket and lateral margin of clypeus. Male scape longer than third antennomere. Propodeum dentate or spinose. Promesonotum of worker, in profile, weakly convex or flattened. Mid and hind tibial spurs absent.

Type Species. *Monomorium denticulatum* Mayr, 1887, by present designation.

WORKER. Monomorphic, size variation small. Eye well developed, placed slightly below middle of side of head; ocelli absent. Antenna twelve-segmented, with well-defined three-segmented club; scape simple at base, its apex not exceeding occipital margin. Palpal formula 2, 2 (1*s*2*p*3, 1*s*2). Dental formula 1+4, mandible normal in *A. denticulatus*; modified in *A. bidentatus*; canthellus not meeting basal margin and trulleum distinct and open in *A. denticulatus,* both modified and reduced in *A. bidentatus*. Labrum cleft. Clypeus bicarinate (*A. denticulatus*) or flattened and modified (*A. bidentatus*, fig. 5.), apex of median lobe exceeding apical margin; median and paracarinal setae present. Promesonotum moderately convex (*A. denticulatus*) or flattened (*A. bidentatus*); promesonotal suture as in *Nothidris*. Metanotal groove distinct (*A. denticulatus*) or weak (*A. bidentatus*, fig. 6.). Middle and hind tibiae without apical spurs. Propodeum dentate or short-spinose. Propodeal spiracle round. Petiole distinctly pedunculate; nodes high and rounded in profile. Anterior and posterior subpostpetiolar process distinct.

FEMALE. Slightly larger than worker and similar except in possessing female thoracic segmentation. Forewing with M arising from Rs+M much anterior to r; cu-a meeting A at approximately right-angle, A continued beyond juncture.

MALE. Size similar to worker. Clypeus strongly convex. Mandible well developed, apex bidentate (fig. 9). Antenna thirteen-segmented, scape short, little longer than third antennomere; antennomeres elongate. Palpal formula 3, 2. Vertex strongly elevated above top of eye. Notauli and parapsides present, distinct (figs. 10, 11). Wings as in female. Petiole stoutly pedunculate; petiolar and postpetiolar nodes low, rounded in profile. Genitalic capsule fully retractile; parameres thickened, rounded apically.

Included Names.
bidentatus (Mayr 1887) (*Monomorium*). Chile, Argentina.
denticulatus (Mayr 1887) (*Monomorium*). Chile, Argentina.
= *navarinensis* (Forel 1904) (*Monomorium denticulatum* var.)
= *piceus* (Emery 1905) (*Monomorium denticulatum* var.)

Etymology. Gr., *antichthon* (southern hemisphere) + *idris* (the provident one, i.e., an ant).

Discussion. The two species included in this genus were originally described in the genus *Monomorium*; Emery (1915) placed them in his subgenus *Notomyrmex*. The Old World *Notomyrmex*, including the type species, were transferred to the synonymy of *Chelaner* by Ettershank (1966) who proposed the new genus *Nothidris* for the American species. However, the two species here placed in *Antichthonidris* have little in common with the type species of *Nothidris*.

The wing venation of the sexual forms, the longer scape of the male and the presence of distinct notauli on the male scutum require that these species be removed from *Nothidris*. The correct systematic placement of *Antichthonidris* is uncertain, but it is evident that these ants do not belong among the *Monomorium-Solenopsis* series of genera, since males of these groups lack notauli. The wing venation, clypeal form, lack of apical spurs on the middle and hind tibiae, and worker habitus are suggestive of *Stenamma* in the Pheidolini, but the male habitus is quite different. It seems best to leave *Antichthonidris* unassigned until all myrmicine genera can be re-evaluated.

DOLICHODERINAE

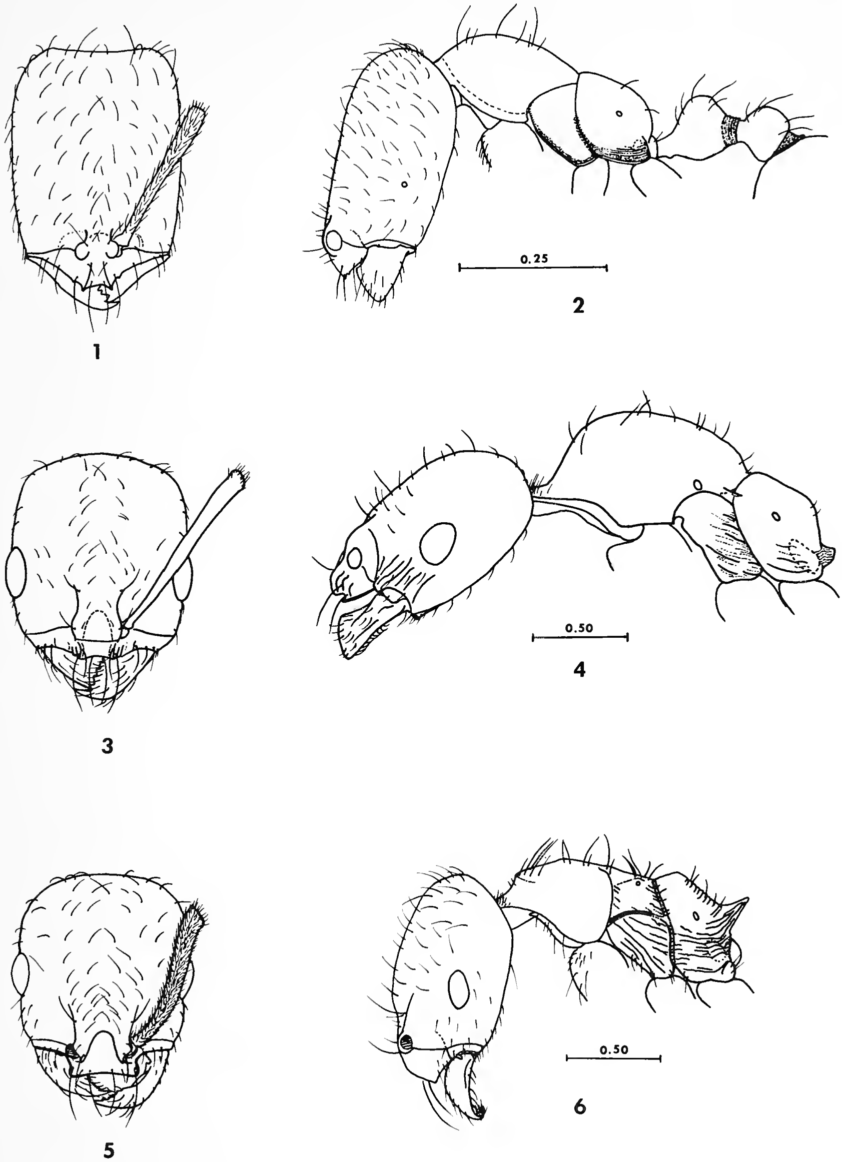
DORYMYRMEX Mayr

I am here using *Dorymyrmex* in the restricted sense suggested by Kempf (1972); i.e., the subgenera *Dorymyrmex*, *Psammomyrma* and *Spinimyrma*, but excluding *Ammomyrma*. *Ammomyrma*, ranked as a subgenus of *Dorymyrmex* by Kusnezov (1952) should, in my opinion, be transferred to *Araucomyrmex*. The latter group was also regarded as a subgenus by Kusnezov (1952), but later elevated to generic status by the same author (1959). *Ammomyrma* agrees with *Araucomyrmex* in thoracic and palpal structure.

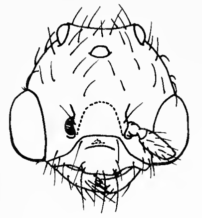
Dorymyrmex agallardoi new species

Figures 12-13

Diagnosis. Worker with prominent, posteriorly directed propodeal spine; side of propodeum with coarse, widely spaced rugulae; occiput densely punctulate. FEMALE and MALE unknown.



FIGURES 1-6. Head in frontal view, head and thorax in lateral view, of worker: 1-2, *Solenopsis dysderces*. 3-4, *Nothidris cekalovici*. 5-6, *Antichthonidris bidentatus*.



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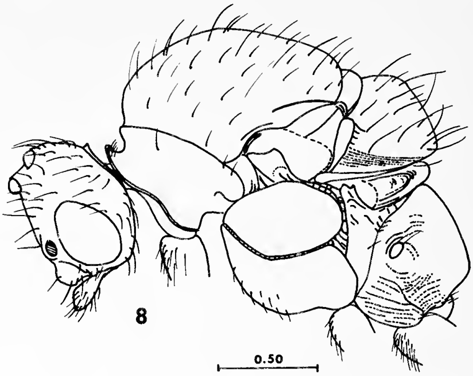

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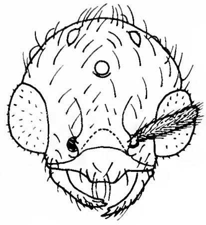

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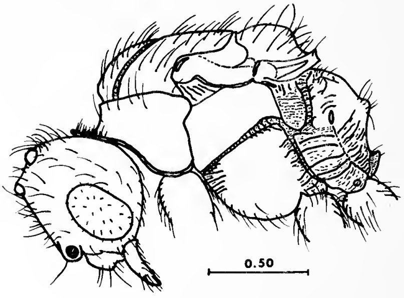

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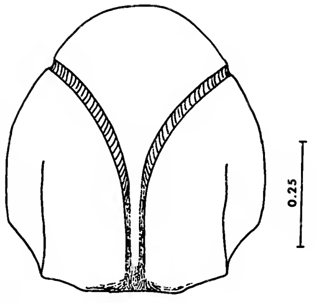

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FIGURES 7-10. Head in frontal view, head and thorax in lateral view, of male: 7-8, *Nothidris latastei*. 9-10, *Antichthonidris bidentatus*; 11, *A. bidentatus*, mesoscutum of male.

WORKER. *Measurements*. HL 1.05-1.22 (1.19); HW 0.92-1.06 (1.04); SL 1.08-1.23 (1.17); PW 0.60-0.69 (0.69); WL 1.73-1.99 (1.98).

Head. Distinctly longer than broad, CI 87-91 (87); HL a little less than to a little more than SL; SI 110-118 (112). In frontal view, HW greatest a little below midpoint, sides of head slightly convex; occipital margin distinctly concave.

Scape extending beyond occipital margin by about one-third its length. Apical margin of clypeus gently, evenly convex in frontal view. Eye on front of head, OMD 0.97-1.04 (1.04) x EL.

Thorax. Slender, PW 0.33-0.37 (0.35) x WL. From above, pronotum about twice as wide as mesonotum, about 1.3 x propodeum. In profile, meso- and metanota forming a continuous, steep slope from pronotum to propodeum, interrupted only by sharply projecting spiracles; posterior margin of metanotum depressed well below dorsal level of propodeum, so that anterior margin of propodeum is abruptly declivitous. Propodeal spine, from above, nearly parallel-sided, apex rounded; in profile, flattened and sharp at apex, base below upper level of propodeal dorsum, directed caudad. In profile, node of petiole with anterior face nearly vertical, dorsal face convex, posterior face strongly sloping; without ventral spines or teeth.

Vestiture. Erect setae general but sparse, variable in length on head, thorax and gaster; those of scape abundant, short, fine; those of tibiae long, acuminate.

Integument. Front of head mostly moderately shiny, lightly shagreened; malar area duller, more closely shagreened; occiput and vertex dull, closely punctulate; head with scattered, setigerous punctures, more numerous on occiput. Pronotum shinier than front of head, with scattered setigerous punctures. Pronotal neck and entire meso-metanotum dull, densely punctulate. Propodeal dorsum similar, but sides slightly shiny and with widely spaced, oblique rugulae. Posterior face of node of petiole with delicate, concentric striae which may be more or less obsolete. Gaster smooth and shiny.

Color. Head and thorax dull reddish; antenna and legs medium brown; gaster blackish.

FEMALE and MALE unknown.

Type Material. Holotype and four paratype workers: CHILE, Prov. Santiago: El Alfalfal, 25 Jan. 1968 (J. Moroni); five paratype workers: CHILE, Prov. Santiago: San José de Maipo, 29 Nov. 1969 (L. Alfaro). Holotype and two paratypes in LACM; five paratypes in MSTO; two paratypes in UCON.

Etymology. This species is dedicated to the late Angel Gallardo, a pioneer in the systematics and biology of South American ants.

Discussion. This is very likely the same species that Berg (1890) recorded from Santa Rosa de los Andes, Aconcagua, Chile, as *planidens* Mayr. Although it does resemble *planidens* in stature, the distinctly rugulose propodeal sides will separate it from that species. The red color is also much less bright than in *planidens*.

ARAUCOMYRMEX

This genus, as I interpret it, includes those species listed by Kempf (1972) under *Araucomyrmex* plus most of those included in the subgenus *Ammomyrma* of *Dorymyrmex*. I have seen most of the species placed in *Ammomyrma*, including the type species, *exsanguis* Forel; they are all *Araucomyrmex*, except for *emmaericaellus* Kusnezov, which is a true *Dorymyrmex*. Those species which I have not seen appear from their descriptions to be *Araucomyrmex* also.

Araucomyrmex hunti new species

Figures 14-15

Diagnosis. Worker: Dark brown to black; upper setae of psammophore below level of occipital foramen; frons conspicuously more shiny than occiput; propodeal tubercle high, acute; CI 77-84. FEMALE and MALE unknown.

WORKER. *Measurements.* HL 0.77-0.92 (0.88); HW 0.60-0.72 (0.70); SL 0.80-0.97 (0.90); PW 0.40-0.50 (0.50); WL 1.03-1.23 (1.17).

Head. Conspicuously longer than broad, CI 77-84 (79); in frontal view, widest at eye level, usually distinctly sinuate below eye level; occipital margin evenly convex. Scape about as long as head, SI 119-133 (129); extending beyond occiput by about 0.3 x its length. Eye large, OMD 0.86-1.17 (1.17) x EL. Apical margin of clypeus, in frontal view, slightly convex, weakly emarginate in middle.

Thorax. Slender, PW 0.38-0.43 (0.43) x WL. Mesonotum, in profile, straight or slightly convex, not angulate beyond middle. Propodeum, in profile, not depressed in front of tubercle; tubercle high, acute.

Vestiture. Head with sparse, appressed, whitish pubescence; thorax and gaster with appressed pubescence longer and a little denser; some cephalic pubescence, especially on frons may be decumbent; that of scape decumbent to erect.

Cephalic setae sparse, on face limited to clypeus and frontal lobes, none on occiput or vertex. Basalmost setae of psammophore below level of occipital foramen. Pronotum usually with a single pair of erect setae, which are shorter than apical width of scape; mesonotum and propodeum without erect setae. First gastric tergum with irregularly spaced, long, erect setae across summit of basal face and a row along posterior margin; remaining terga with sparse longer hairs. Scape without erect setae. Fore femur with three or four widely spaced setae along basal half of ventral margin; mid and hind femora without erect setae on dorsal margin; tibiae without setae.

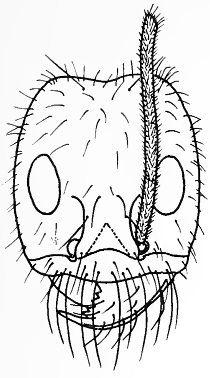
Integument. Clypeus moderately shiny, closely shagreened except along midline; frontal lobes and frons moderately shiny, lightly shagreened and with scattered micropunctures; vertex and occiput sharply duller, closely shagreened and with numerous micropunctures. Thorax similar to occiput, closely shagreened and with numerous micropunctures. Gaster moderately shiny, less closely shagreened than thorax, with numerous micropunctures and scattered coarser punctures.

Color. Dark brown to blackish; antenna and legs lighter.

FEMALE and MALE unknown.

Type Material. Holotype and 41 paratype workers: CHILE, Prov. Antofagasta: 2 km E Paposo, 300 m elev., 16 Nov. 1972 (J. H. Hunt, #994). Holotype and most paratypes in LACM; three paratypes each in MSTO and UCON.

Etymology. This species is dedicated to James H. Hunt, who collected numerous ant samples in Chile at my request.



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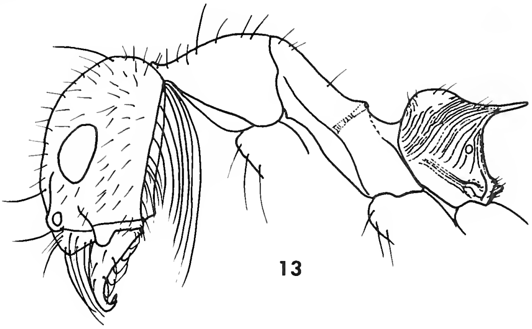

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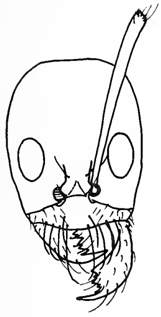

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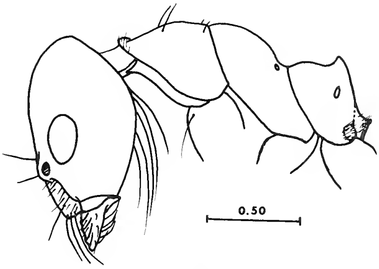

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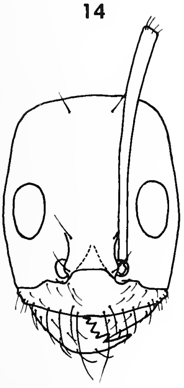

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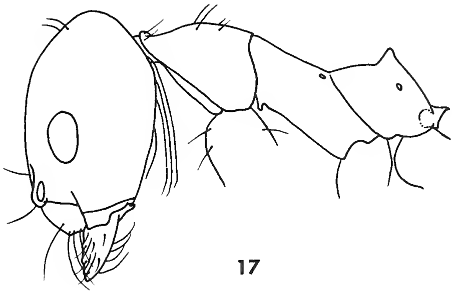

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FIGURES 12-17. Head in frontal view, head and thorax in lateral view, of worker: 12-13, *Dorymyrmex agallardoi*. 14-15, *Araucomyrmex hunti*. 16-17, *A. hypocritus*. All figures to same scale.

Araucomyrmex hypocritus new species
Figures 16-17

Diagnosis. Worker: Bicolored species with wholly ferruginous thorax; uppermost setae of psammophore below occipital foramen; occipital sculpture not sharply differentiated from that of frons; mesonotum, in profile, straight over posterior one-half; terga pubescent at sides. FEMALE and MALE unknown.

WORKER. *Measurements*. HL 1.03-1.08 (1.08); HW 0.83-0.92 (0.92); SL 1.17-1.23 (1.23); PW 0.57-0.62 (0.60); WL 1.43-1.57 (1.57).

Head. Conspicuously longer than broad, CI 81-85 (85); in frontal view, widest at eye level, slightly sinuate below eye level; occipital margin nearly flat in frontal view. Scape distinctly longer than head, extending beyond occipital margin by about 0.45 x its length; SI 134-140 (135). Eye large, OMD 1.06-1.25 (1.25) x EL. Apical margin of clypeus, in frontal view, nearly straight, with barely indicated median sinuosity.

Thorax. Slender, PW 0.38-0.41 (0.38) x WL. Mesonotum, in profile, nearly straight, not angulate beyond middle. Propodeum, in profile, not depressed in front of tubercle; tubercle high, acute.

Vestiture. Appressed pubescence short, sparse on fronsg denser on occiput; longer and denser on thorax; long and dense on gastric terga, including sides of first two segments; very scattered around antennal sockets and on sides of head; completely appressed on scape.

Clypeus with long setae on apical margin and a few on basal margin, disc with a few very short setae; frontal lobes with a seta pair near clypeal base and another at level of lower eye margin, the latter notably long; vertex with a single pair of short setae (apparently broken off in some specimens). Basalmost setae of psammophore below level of occipital foramen. Pronotum with a median seta pair and a preapical, much shorter pair; mesonotum and propodeum without erect setae. First tergum with a few scattered setae on posterior half of dorsal face; remaining terga with preapical seta row and a few, inconspicuous discal setae. Scape without setae except at apex. Fore femur with three or four setae on basal half of ventral margin; mid and hind femora without setae on dorsal margin; tibiae without setae.

Integument. Clypeus smooth and shiny along midline, closely shagreened and moderately shiny elsewhere; frontal lobes and frons slightly shiny, closely shagreened and micropunctate; vertex and occiput a little duller and more densely micropunctate, out blending into frons; malar area and gena shiny, lightly shagreened. Thorax similar to occiput, closely shagreened and moderately shiny, sides shinier. Gaster dull, very closely shagreened and with dull micropunctures.

Color. Head, including scape, and thorax bright ferruginous; gaster blackish; flagellum and legs dark brown.

FEMALE and MALE unknown.

Type Material. Holotype and four paratype workers: CHILE, Prov. Santiago: Fundo Santa Laura, near Cuesta la Dormida, 20 Oct. 1971 (J. H. Hunt, #453), all in LACM.

Etymology. The Latin, *hypocritus*, mime or dissembler, because of the similarity to such species as *goetschi* and *tener*.

Araucomyrmex incomptus new species

Figures 18-19

Diagnosis. Worker: Blackish, head more or less ferruginous; basalmost setae of psammophore below occipital foramen; vertex and occiput dull, sharply differentiated from shiny frons; basal face of propodeum, in profile, distinctly impressed in front of low, obtuse tubercle. FEMALE and MALE unknown.

WORKER. *Measurements.* HL 0.72-0.80 (0.78); HW 0.60-0.65; SL 0.73-0.80 (0.77); PW 0.40-0.43 (0.43); WL 0.97-1.03 (1.03).

Head. Conspicuously longer than broad, CI 79-85 (81); sides, in frontal view, widest at eye level, weakly sinuate below eye level or not sinuate; occipital margin flattened or very weakly convex in frontal view. Scape about as long as head, SI 121-128 (123), extending beyond occiput by about 0.25 x its length. Eye large, OMD 1.00-1.08 (1.00) x EL. Apical margin of clypeus, in frontal view, straight or weakly concave in middle.

Thorax. Slender, PW 0.40-0.43 (0.42) x WL. Mesonotum, in profile, evenly convex, not angulate beyond middle. Propodeum, in profile, distinctly depressed in front of tubercle; tubercle low, obtuse.

Vestiture. Pubescence short, scattered on most of head, conspicuous only on vertex and occiput; thoracic pubescence a little sparser than that of occiput; that of gaster similar but a little longer, becoming very sparse on sides of terga.

Cephalic setae sparse; apical clypeal margin only, with long setae, those of disc and basal margins short; frontal lobes with seta pair near clypeal base and a longer pair at level of lower eye margin; no occipital setae; basalmost setae of psammophore below level of occipital foramen. Pronotal disc with a single, median, seta pair; mesonotum and propodeum without setae. First gastric tergum with a few setae at about midlength of dorsal face and a few in preapical row; remaining terga with scattered discal and a few preapical setae. Scape without setae except at tip. Fore femur with two or three setae on basal half of ventral margin; mid and hind femora without setae on dorsal margin; tibiae without setae.

Integument. Midline of clypeus smooth and shiny, remainder lightly shagreened and moderately shiny; frontal lobes and frons moderately to very weakly shagreened, with scattered micropunctures, moderately shiny; vertex and occiput abruptly differentiated, closely shagreened and micropunctate, barely shiny; malar area and side of head moderately shiny, weakly shagreened. Thorax and gaster closely shagreened and micropunctate, slightly shiny.

Color. Head dark ferruginous, becoming lighter at sides and toward mandible, darkest (almost dark brown) on occiput; thorax and gaster blackish. Appendages dark brownish.

FEMALE and MALE unknown.

Type Material. Holotype and 11 paratype workers: CHILE, Prov. Coquimbo: Cerro Tololo, ca. 10 km W, 3 km S of Vicuña, 16 Oct. 1971 (J. H. Hunt, #439); holotype and most paratypes in LACM; two paratypes each in MSTO and UCON.

Etymology. L., *incomptus*, unadorned or simple, because of the reduced setation.

Araucomyrmex pappodes new species
Figures 20-21

Diagnosis. Worker: Basalmost setae of psammophore above lower margin of occipital foramen; front of head with numerous erect setae of various lengths on upper half; propodeal tubercle high, sharp; thorax wholly dark brown. FEMALE and MALE unknown.

WORKER. *Measurements.* HL 0.96-1.09 (1.09); HW 0.82-0.96 (0.96); SL 1.04-1.15 (1.15); PW 0.54-1.00 (1.00); WL 1.41-1.59 (1.59).

Head. Distinctly to a little longer than broad, CI 85-90 (88); in frontal view, widest at eye level, margins not sinuate below eye level; occiput, in frontal view, flat or weakly convex. Scape distinctly longer than head, SI 118-126 (120); extending beyond occiput by about 0.3 x its length. Eye large, OMD 1.10-1.20 (1.14) x EL. Apical margin of clypeus, in frontal view, weakly subangulate in middle.

Thorax. Slender, PW 0.37-0.40 (0.38) x WL. Mesonotum, in profile, weakly angulate beyond middle. Propodeum, in profile, weakly sinuate in front of tubercle; tubercle stout, high, summit rounded, but profile acute.

Vestiture. Appressed pubescence sparse on clypeus, malar area and gena; longer, dense, and partially obscuring surface, on frontal lobes, frons, vertex and occiput, some hairs subdecumbent. Thoracic pubescence less dense than that of occiput, mostly appressed, but some decumbent to suberect, especially on dorsum. Gastric pubescence dense, but not obscuring surface, mostly appressed, but some hairs subdecumbent.

Cephalic setae abundant; apical margin of clypeus with very long setae, basal margins and disc with much shorter setae; frontal lobes with apical seta pair and another at level of lower eye margin. Frons, vertex, occiput and margins of head with numerous short, fine setae generally distributed. Basalmost setae of psammophore arising well above lower margin of occipital foramen. Pronotum with a median pair of long (subequal to MOD), slender setae and a pair of much shorter setae near posterior margin; disc with numerous fine, much shorter, setae. Mesonotum with sparse, very short, fine setae. Discs of gastric terga with generally distributed, short, fine setae and preapical row of longer setae. Scape with abundant, fine, suberect to erect, very short setae. Fore femur with short, fine, suberect to erect setae along entire ventral margin. Femora and tibiae otherwise with generally distributed very short, fine, decumbent to erect setae.

Integument. Clypeus shiny, midline smooth and polished, remainder lightly shagreened; malar area and gena moderately shiny, lightly shagreened, with scattered micropunctures and a few coarser punctures; frontal lobes, frons, vertex and occiput slightly shiny, sharply shagreened and densely micropunctate. Thorax shinier than frons, less closely shagreened, about as densely micropunctate. Gastric terga about as shiny as frons and similarly sculptured.

Color. Head brownish ferruginous on occiput, becoming progressively paler toward mandible. Pronotal neck obscurely ferruginous, thorax otherwise very dark reddish brown. Gaster blackish brown. Appendages medium brown.

FEMALE and MALE unknown.

Type Material. Holotype and 37 paratype workers: CHILE, Prov.

Valparaiso: Maitencillo, 30 m elev., 10 Oct. 1971 (J. H. Hunt, #424). Holotype and most paratypes in LACM; three paratypes each in MSTO and UCON.

Etymology. Gr., *pappodes*, downy, in allusion to the abundance of fine pubescence rendering to this ant its distinctive appearance.

Araucomyrmex pogonius new species

Figures 22-28

Diagnosis. Worker: Basalmost setae of psammophore above lower margin of occipital foramen; vertex without seta pair; setae of pronotal pair less than 0.5 x MOD; head ferruginous. FEMALE. Unknown. MALE. CI 97-100; SI 71-77; interocellar distance equal to ocellocular distance; scape shorter than head.

WORKER. *Measurements.* HL 0.90-0.97 (0.93); HW 0.80-0.90 (0.87); SL 0.93-1.03 (1.00); PW 0.47-0.55 (0.53); WL 1.20-1.30 (1.27).

Head. Distinctly, to a little, longer than broad, CI 88-95 (92); in frontal view, widest at eye level, margins not sinuate below eye level; occiput, in frontal view, weakly concave in middle. Scape slightly longer than head, SI 114-122 (115); extending beyond occiput by about 0.3 x its length. Eye large, OMD 1.07-1.21 (1.21) x EL. Apical margin of clypeus, in frontal view, straight or very weakly convex in middle.

Thorax. Slender, PW 0.39-0.43 (0.42) x WL. Mesonotum, in profile, slightly convex, often weakly angulate beyond middle. Basal face of propodeum distinctly sinuate in profile; tubercle high, acute.

Vestiture. Appressed pubescence short, abundant on frontal lobes, frons vertex and occiput; very sparse on gena and malar area; some hairs subappressed or subdecumbent on side, above eye and on vertex. Thoracic pubescence general, mostly appressed, but some on pronotum subappressed to subdecumbent. Gastric terga including sides of segments with abundant appressed, and some subappressed, pubescence.

Cephalic setae sparse, vertex pair absent. Long setae present on apical margin of clypeus; shorter, sparse setae on disc and along basal margin; frontal lobes with seta pair near base of clypeus and another at level of lower eye margin. Basalmost setae of psammophore above level of lower margin of occipital foramen. Pronotal disc with median seta pair, setae less than 0.5 x MOD. Mesonotum and propodeum without setae. First tergum with sparse, short setae on basal half of dorsal face and usual preapical row; remaining terga with scattered, very short, discal setae and preapical row of widely spaced setae. Scape without setae, except near tip. Fore femur with two or three setae on basal half of ventral margin. Mid and hind femora without setae on dorsal margin. Tibiae without setae.

Integument. Midline of clypeus smooth and shiny, remainder shiny and lightly shagreened; gena and malar area moderately shiny, moderately shagreened and with scattered micropunctures; frontal lobes, frons, vertex and occiput slightly shiny, closely shagreened and densely micropunctate. Thorax slightly shiny, closely shagreened and densely micropunctate. Gastric terga slightly shiny, closely shagreened and densely micropunctate.

Color. Head and thorax pale ferruginous, propodeum slightly brownish. Gaster medium to dark brownish. Antennae yellowish brown, scape paler than flagellum; legs medium brown.

FEMALE. Unknown.

MALE. *Measurements.* HL 0.57 (0.57); HW 0.55-0.57 (0.57); SL 0.40-0.43 (0.40); PW 0.73-0.80 (0.73); WL 1.43-1.50 (1.50).

Head. As long as broad to slightly longer than broad, CI 97-100 (100), broadest at upper margins of eyes; occiput, in frontal view, flat, narrowly rounded onto sides of head. Scape shorter than head length, SI 71-77 (71); apex reaching about to occipital margin. Eye large, OMD 0.25-0.27 (0.25) x EL. Apical margin of clypeus convex in middle. Mandible with cutting margin oblique, with three teeth basad of apical tooth.

Thorax. Stout, PW 0.49-0.55 (0.49) x WL. Scutellum, in profile, strongly bulging, dorsal face flat. Propodeum evenly curved in profile.

Terminalia. Apical margin of subgenital plate broadly convex to slightly concave. Genital capsule (figs. 26, 27) broader than long; digitus elongate, straplike, extending to apex of gonocoxite; ventral margin of aedeagus (fig. 28) with very coarse teeth and a few fine teeth.

Vestiture. Appressed pubescence very sparse and inconspicuous on head. Pubescence a little more abundant on thorax, but still sparse; longest and most conspicuous on propodeum. Gastric terga with evenly distributed appressed pubescence, nowhere sufficiently dense to obscure surface; sterna similarly pubescent.

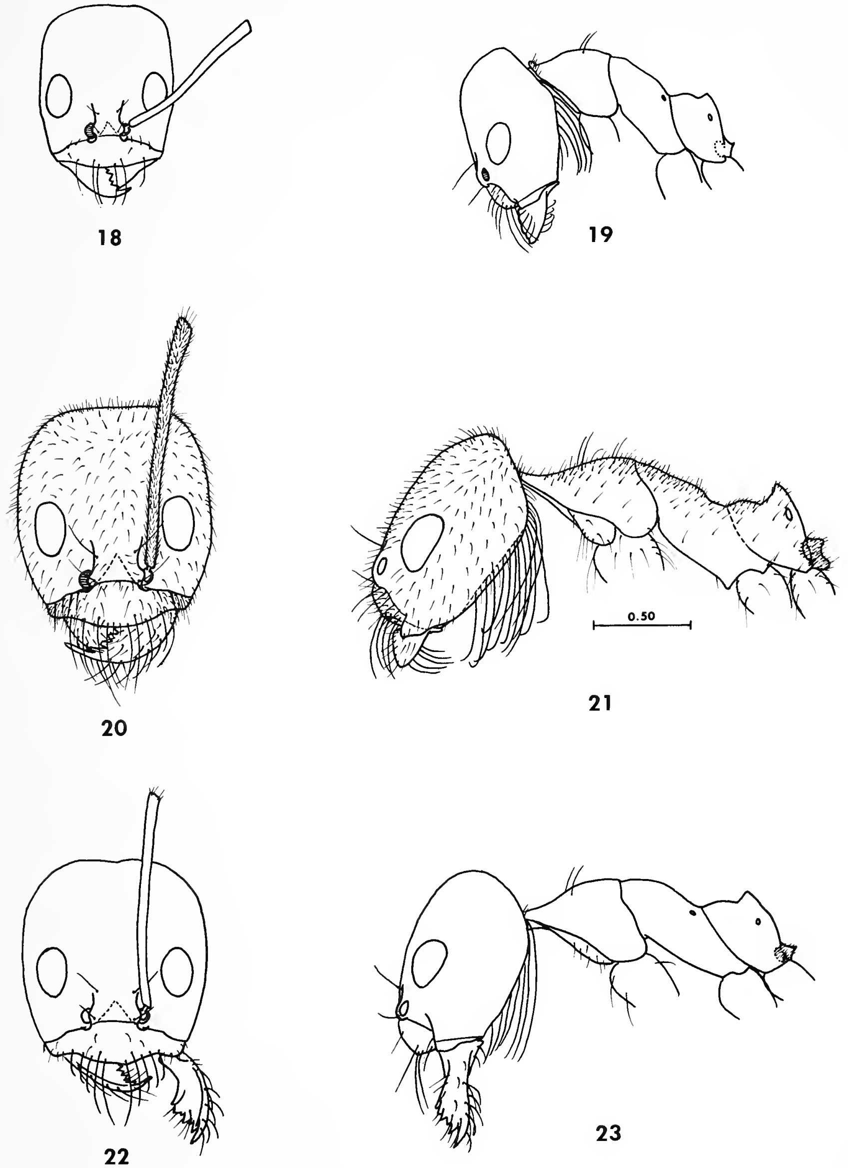
Clypeus with a few inconspicuous setae along apical margin and a longer pair on either side of median lobe; frontal lobe with a pair of very short setae a little above level of antennal sockets. Gastric sterna with a few short erect setae. Femora and tibiae without setae. Forewing without fringe hairs; hind wing with a few hairs on apical margin and a fringe on basal half of posterior margin.

Integument. Clypeus and frontal lobes shiny, lightly shagreened and with scattered micropunctures; frons, vertex and occiput less shiny, lightly shagreened, densely punctate with fine punctures of two sizes. Mesoscutum about as shiny as frons, similarly punctate anteriorly, punctures becoming coarser posteriorly; scutellum shiny between coarse, dense punctures; pleura similar to scutellum. Base of propodeum shiny, lightly shagreened and with scattered, obscure punctures which are finer than those of scutellum; sides less shiny, closely, finely punctate. Gastric terga moderately shiny, lightly shagreened, with sparse micropunctures and scattered coarser punctures.

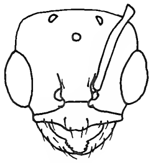
Color. Medium brown, with anterior half of scutellum lighter; antenna and legs light brown. Wings faintly whitish, veins and stigma yellowish to brownish yellow.

Type Material. Holotype worker, allotype male, 35 worker and 17 male paratypes: CHILE, Prov. Ñuble: Termas de Chillán, 20 Sept. 1969 (T. Cekalovic; #4187). Holotype, allotype, 15 worker and 7 male paratypes in LACM; 18 worker and 9 male paratypes in UCON; 2 worker and one male paratypes in MSTO.

Etymology. Gr., *pogon*, *-os*, beard, hence bearded, *pogonius*, in allusion to the long psammophore on the ventral surface of the worker head.



FIGURES 18-23. Head in frontal view, head and thorax in lateral view, of worker: 18-19, *Araucomyrmex incomptus*. 20-21, *A. pappodes*. 22-23, *A. pogonius*. All figures to same scale.



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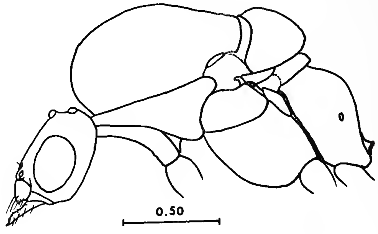

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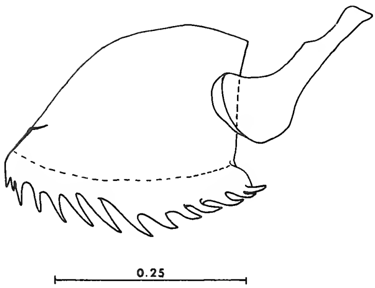

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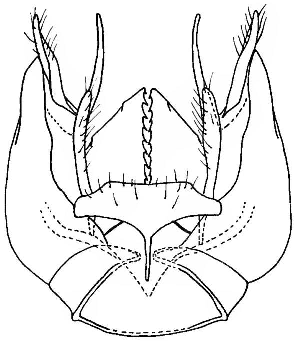

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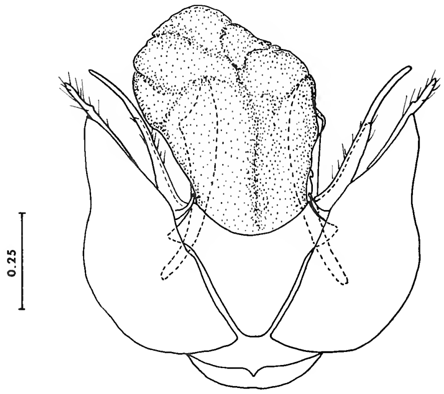

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FIGURES 24-28. *Araucomyrmex pogonius*, male. 24, head in frontal view; 25, head and thorax in lateral view; 26, genital capsule, ventral view, with attached subgenital plate; 27, genital capsule, dorsal view, with inflated penis; 28, aedeagus, lateral view.

RESUMEN

Se describe una nueva especie de *Solenopsis*, *dysderces*. Una nueva especie de *Nothidris*, *cekalovici*, es descrito y *Megalomyrmex bicolor* Ettershank es trasladado a *Nothidris*. Se presenta un clave para las especies conocidas de *Nothidris*. Dos especies, *bidentatus* Mayr y *denticulatus* Mayr, son transferidos a un nuevo género, *Antichthonidris*, con *denticulatus* como la especie típica.

El estado de los dos géneros *Dorymyrmex* e *Araucomyrmex* es tratado en breve. Una nueva especie, *agallardoi*, de *Dorymyrmex* es descrito de la Provincia de Santiago. Las nuevas especies siguientes de *Araucomyrmex* son descritas: *hunti* (Prov. Antofagasta), *hypocritus* (Prov. Santiago), *incomptus* (Prov. Coquimbo), *pappodes* (Prov. Valparaiso) y *pogonius* (Prov. Ñuble).

Todas las nuevas taxas son ilustradas. Los tipos primarios de las nuevas especies están depositados en el LACM, con los paratipos de la mayoría en el Museo Nacional de Historia Natural de Santiago, y Universidad de Concepción, Concepción.

LITERATURE CITED

BERG, C. 1890. Los formicidios argentinos, chilenos y uruguayos. Soc. Cient. Argent., An. 29:5-43.

EMERY, C. 1915. Noms de sous-genres et de genres proposés pour la sous-famille des Myrmicinae. Modification à la classification de ce group. Soc. Entomol. France, Bull. pp. 189-192.

ETTERSHANK, G. 1966. A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton*. Austr. Jour. Zool. 14:73-171.

KEMPF, W. W. 1970. Catalogo das formigas do Chile. Papeis Avulsos Zool., S. Paulo 23:17-43.

————. 1972. Catalogo abreviado das Formigas da Região Neotropical. Studia Entomol. 15:3-344.

KUSNEZOV, N. 1952. El estado real del grupo *Dorymyrmex* Mayr. Acta Zool. Lill. 10:427-448.

————. 1959. Die Dolichoderinen-Gattungen von Sud-Amerika. Zool. Anz. 162:38-51.

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NOTES ON THE HERPETOFAUNA OF WESTERN MÉXICO: NEW RECORDS FROM SINALOA AND THE TRES MARÍAS ISLANDS

By Roy W. McDiarmid, Joseph F. Copp and Dennis E. Breedlove

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NOTES ON THE HERPETOFAUNA OF WESTERN MÉXICO: NEW RECORDS FROM SINALOA AND THE TRES MARÍAS ISLANDS[1]

By Roy W. McDiarmid[2], Joseph F. Copp[3], and Dennis E. Breedlove[4]

Abstract: Two species of snakes, *Hypsiglena torquata* and *Tantilla bocourti*, are reported for the first time from the Tres Marías Islands. The salamander *Ambystoma rosaceum*, the frogs *Bufo cognatus* and *Rana tarahumarae*, the lizards *Eumeces parviauriculatus*, *Sceloporus poinsettii*, *S. spinosus* and *S. virgatus* and the snakes *Chilomeniscus cinctus*, *Tantilla bocourti* and *T. wilcoxi* are added to the fauna of Sinaloa. Each specimen is compared with individuals of the same species from other parts of its range. These records, together with deletions of two species and notes on six others, contribute to our knowledge of the variation, distribution and biogeography of the herpetofauna of western México.

INTRODUCTION

More is known about the distribution of the faunas of western México than of any other part of that country. This generalization is true especially of amphibians and reptiles where several major works (Bogert and Oliver 1945; Duellman 1958, 1961, 1965; Zweifel 1959, 1960; Hardy and McDiarmid 1969) have provided in-depth treatments of the faunal composition and species distributions in this biogeographically interesting area. As well known as the herpetofauna is, additional field work continues to produce significant specimens. In this paper range extensions, additions and deletions to the herpetofaunas of the Tres Marías Islands and of Sinaloa, México, are reported.

Most of the material from the Tres Marías Islands was collected by James R. Northern and Roy R. Snelling between 17 and 30 March 1964. Their expedition was sponsored by Richard F. Dwyer of the American Foundation of Oceanography in conjunction with the Natural History Museum of Los Angeles County (LACM). The field party visited Isla María Magdalena and Isla María Cleofas in the Tres Marías group and Isla Isabel, a small island located between the Tres Marías Islands and the Mexican mainland. The new material from Sinaloa is contained in several collections that became available after the manuscript on the herpetofauna of Sinaloa was submitted for publication (Hardy and McDiarmid 1969). One fairly large collection was made in the northeastern part of the state by Copp (JFC) and Breedlove during the dry seasons between 1967 and 1971. Animals were taken at several localities at various elevations

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and in different habitats along the road from Los Hornos (= El Orno of Gentry 1946) to Surutato (= Surotato of Gentry) and in adjacent canyons in the remote and rugged Sierra de Surutato. The specimens collected in México by Breedlove will be deposited in the collections of the California Academy of Sciences.

The vegetation of the Sierra de Surutato is composed of a diverse mixture of tropical and temperate forest types. Gentry (1946) gave a brief description of the vegetation and listed some major elements. At the lower elevations thorn forest and tropical deciduous forest are common. Some elements of seasonal evergreen forests are found in the outwashes of the major canyons such as the Cañon de Tarahumare. A riparian forest with *Platanus*, quite reminiscent of those found in the mountains of southern California, Arizona and Sonora, occurs along the canyons at middle elevations. At 1000 m the tropical deciduous forest grades imperceptibly into pine-oak forest, which at higher elevations becomes more mesic and includes *Juglans* and *Arbutus*. A forest reminiscent of evergreen cloud forests (Breedlove 1973; mesophytic mountain forest of Rzedowski and McVaugh 1966) occurs in a few moist, protected canyons at high elevations. This forest is composed of several genera of broadleaf evergreen trees, *Carpinus* and the conifer *Pseudotsuga*. The flora is characterized by a high degree of endemism. *Gentrya*, a Scrophulariaceae (Breedlove and Heckard 1970), is known to occur only here. This mountain range is also the northernmost station for many tropical and temperate-tropical species of plants.

SPECIES ACCOUNTS

LAS TRES MARÍAS AND ISABEL ISLANDS

Individuals of the following species known previously from the islands were collected during the 1964 trip or on earlier unreported expeditions. They include *Phyllodactylus tuberculosus saxatilis, Anolis nebulosus, Ctenosaura pectinata, Mastigodryas melanolomus slevini* and *Oxybelis aeneus* from María Cleofas; *Anolis nebulosus, Ctenosaura pectinata, Urosaurus ornatus lateralis, Cnemidophorus communis mariarum, Boa constrictor imperator, Mastigodryas melanolomus slevini* and *Masticophis striolatus* from María Magdalena; and *Ctenosaura pectinata, Sceloporus clarkii boulengeri, Cnemidophorus costatus huico* and *Lampropeltis triangulum nelsoni* from Isabel Island. In addition to these species, three snakes are worthy of separate consideration.

Hypsiglena torquata (Günther).—A single specimen of this nocturnal species was collected on Isla María Magdalena on 23 March 1964. The snake was moving over a rocky beach near the water's edge between 2200 and 2300 hours. The specimen (LACM 25247), a female, measures 434 mm total length, of which 63 mm (12.2%) is tail. It has the following scale characteristics: 179 ventrals, 44 subcaudals, divided anal plate, 21-21-17 dorsal scale rows, 8-8 supralabials, 10-10 infralabials, 1-1 preoculars, 2-3 postoculars, 1+2-1+2 temporals. There are 63 body blotches and 22 tail blotches on the dorsum; many of the dorsal blotches run together, especially on the tail. A dark brown collar involving eight scales on the midline continues well onto the parietal scales of the head as a thin stripe. The nuchal collar is bordered anteriorly by a narrow (1-3 scales), pale brown band that passes through the angle of the mouth. This anterolateral extension of the band separates the brown eye stripe from the dark collar. This pattern is more similar to *"ochrorhyncha"* types from Sinaloa (Hardy and McDiarmid 1969) than to specimens from Nayarit, which have *"torquata"* collar types with a wider, cream-colored band. The Tres Marías specimen also is more similar to Sinaloa than to Nayarit specimens in ventral, subcaudal and ventral plus subcaudal (V+Sc) counts. The V+Sc count (222) for the Tres Marías specimen is within the range for Sinaloa specimens (210-229; *"ochrorhyncha"* collar types $\bar{x}$ = 223; *"torquata"* collar types $\bar{x}$ = 220) but higher than for Nayarit specimens (208-219; $\bar{x}$ = 212, all *"torquata"* types).

This specimen is the first record of *Hypsiglena torquata* to be reported from the Tres Marías Islands. If the Tres Marías population is related more closely to Sinaloan populations to the north than to adjacent mainland populations, as indicated by certain scale characteristics and color pattern, then its distribution parallels that of *Urosaurus ornatus* (Zweifel 1960:118-120). Mertens (1934) pointed out that snakes from insular populations frequently have more ventral scales than do their mainland relatives. This same pattern was confirmed by Zweifel (1960) with respect to nearly all of the snake species that were known then from the Tres Marías Islands. Additional material is needed to clarify the relationship of this insular population of *Hypsiglena torquata.*

Leptophis diplotropis (Günther).—The field party, collecting in a canyon on Isla María Magdalena on 26 March 1964, between 1000 and 1100 hours, found a large specimen of *Leptophis* lying in a small water hole. The snake apparently was "drinking." Zweifel (1960) cited the presence of several species of snakes in close proximity to sources of permanent water on María Magdalena. This record (LACM 25248) represents the first report of *Leptophis diplotropis* from Isla María Magdalena. Unfortunately, the snake, which died several days later, was not preserved immediately. Although it is in relatively poor condition the following information is available: adult male, 189 ventrals, divided anal plate, incomplete tail, 8-8 supralabials, 9-9 infralabials, 1-1 loreal, 1-1 preocular, 2-2 postoculars, 1+2-1+2 temporals.

Tantilla bocourti (Günther).—A single specimen of *Tantilla bocourti* (LACM 25251) was collected in leaf litter along a dry stream bed on Isla María Cleofas on 29 March 1964. This specimen is the first record of the species from the Tres Marías and extends its known range about 240 kilometers to the west. That this is the first report of the species from a locality lower than 1500 meters elevation and from a habitat other than the pine and oak forests typical of many of the mainland localities is of even greater interest.

In attempting to allocate the Tres Marías snake to a known species of *Tantilla,* a large series of *T. bocourti* and specimens of several closely related species were examined. The known distribution of *Tantilla bocourti* is shown in figure 1.

The Tres Marías specimen is an adult female differing in some respects from other female *T. bocourti.* It has a slightly shorter tail and fewer ventrals and subcaudals than the average of the specimens examined. Data in Table 1 indicate that there is sexual dimorphism in the ratio of tail length to total length and in the numbers of ventral and subcaudal scales. However, the mean number of ventrals plus subcaudals is essentially the same for males and females. This pattern of dimorphism has been reported for other species of *Tantilla* as well (Hardy and Cole 1968; McDiarmid 1968). Other characteristics of the Tres Marías specimen are: 15-15-15 scale rows, 1-1 preoculars, 2-2 postoculars, 1+1-1+1 temporals, a posterior temporal as wide as long (scalelike), 7-7 supralabials, 6-6 infralabials, and no contact between the mental and chinshields. Two other specimens of *T. bocourti* have the mental and chinshields in contact. This last character probably is of little value in distinguishing species of *Tantilla* since it is

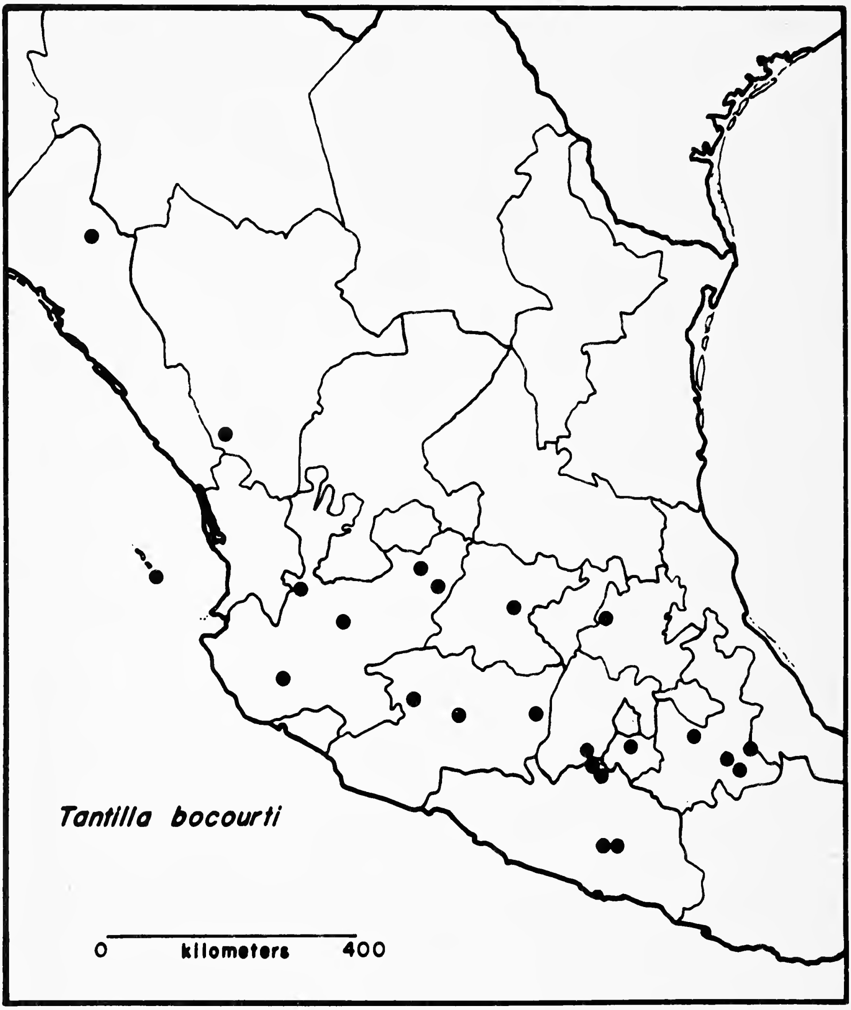

FIGURE 1. Map of central México showing known locality records of *Tantilla bocourti* (Günther).

TABLE 1

Selected character states of *Tantilla bocourti* from the Tres Marías Islands, Sinaloa, and of other specimens selected from localities throughout the range of the species.

	Sex	Tail Length/ Total Length in %	Ventrals	Subcaudals	V + Sc
Tres Marias	♀ (1)	17.6	171	45	216
Sinaloa	♀ (1)	21.5	179	59	238
Other[a]	♀ (13)	16.0-20.0 x̄ = 18.2	166-195 x̄ = 178.4	47-58 x̄ = 52.1	219-252 x̄ = 231.7
	♂ (9)	21.0-22.5 x̄ = 21.7	160-179 x̄ = 172.8	55-61 x̄ = 59.1	220-240 x̄ = 231.9

[a] Several authors record proportions and counts higher or lower than those reported here. Our re-examination of some of these specimens indicates that certain reports are in error; either specimens were incorrectly sexed or incorrectly measured or counted. Other reports (not included in Table 1) have not been verified for this study, including: ♂ subcaudals - 54 (Taylor and Smith 1939); ♀ subcaudals - 46 (Taylor 1940); ♀ subcaudals - 59, ♀ V + Sc - 216, and ♂ ventrals - 180, ♂ subcaudals - 48,65, ♂ V + Sc 219, 244 (Smith 1942); ♀ subcaudals - 41 and ♂ subcaudals - 43 and 51 (Davis and Dixon 1959); ♀ subcaudals - 44 and 45 and ♂ subcaudals - 53; ♀ tail/total length - 15.1, ♂ tail/total length 18.1-20.5 (Davis and Smith 1953).

variable in several of them. The cephalic coloration and scalation are shown in figure 2. We assign this snake to *T. b. bocourti* (see later discussion).

Although the Tres Marías specimen differs from other known mainland specimens in the lower number of ventral and subcaudal scales, the majority of other characteristics is typical of the species. As indicated above, most of the snakes on the Tres Marías average more ventral scales than their mainland counterparts. The only other exception to this rule is the other Tres Marías black-headed snake *Tantilla calamarina* that also has fewer ventrals than mainland individuals of the same species. It would be interesting to know whether this apparent reduction in ventral and/or subcaudal counts in insular populations of *Tantilla,* but not of other Tres Marías snakes when compared with their mainland counterparts, is an artifact of small sample size, is characteristic of snakes of the genus *Tantilla* only, or is associated with the ecologies of the species involved (*e.g.,* semifossorial versus terrestrial or arboreal).

SINALOA

The collection from the Sierra Surutato includes the following species: *Ambystoma rosaceum* (107 specimens), *Bufo occidentalis* (14), *B. punctatus* (1), *Pachymedusa dacnicolor* (1), *Hyla arenicolor* (18), *Rana pipiens* (11), *R. tarahumarae* (6), *Anolis nebulosus* (6), *Ctenosaura hemilopha* (1), *Holbrookia maculata* (8), *Sceloporus clarkii* (1), *S. horridus* (2), *S. spinosus* (2), *S. virgatus* (3), *S. poinsettii* (2), *S. jarrovii* (47), *S. nelsoni* (11), *Urosaurus bicarinatus* (5), *Eumeces callicephalus* (4), *E. parviauriculatus* (9), *Cnemidophorus costatus* (4), *Gerrhonotus kingii* (4), *Masticophis flagellum* (1), *M. striolatus* (1), *Salvadora bairdi* (1), *S. hexalepis* (1), *Storeria storerioides* (4), *Thamnophis cyrtopsis* (2), *Tantilla bocourti* (1), *T. calamarina* (1),

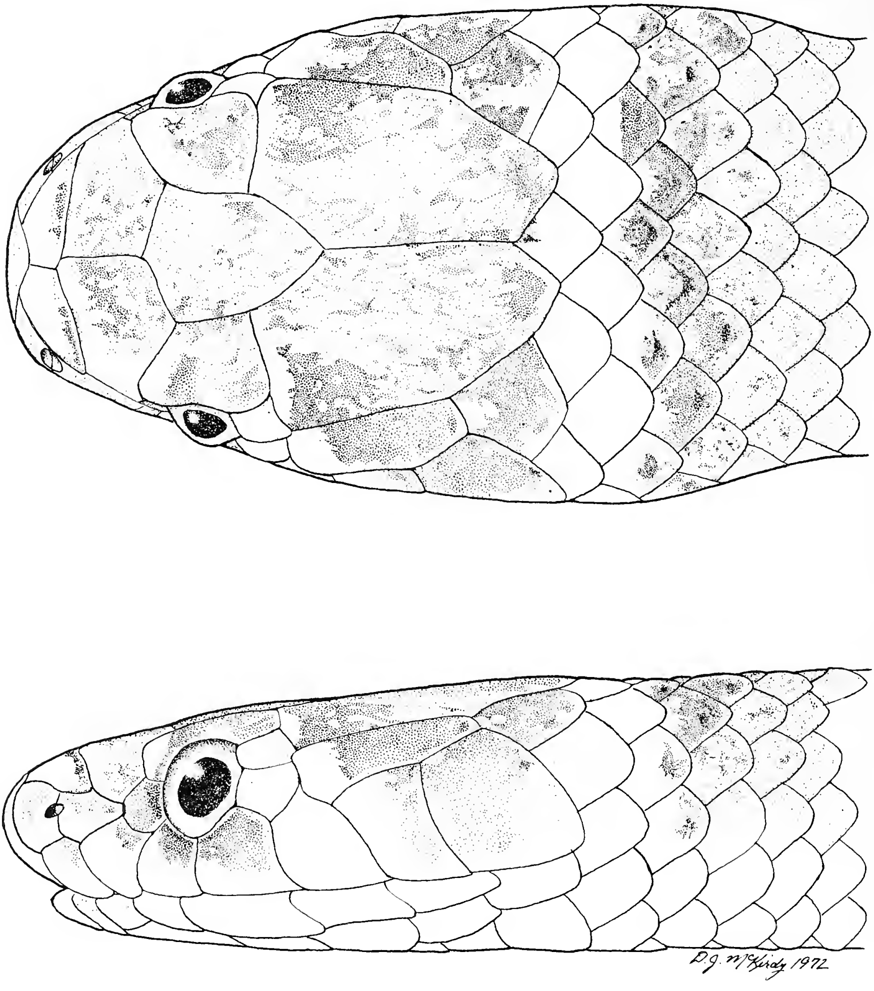

FIGURE 2. Dorsal and lateral view of the head of a female *Tantilla bocourti* (LACM 25251) from Isla María Cleofas, Tres Marías Islands.

T. wilcoxi (1). Several of these species represent important additions to the herpetofauna of Sinaloa or are of interest for other reasons. They are discussed below together with other species from the northern or southern part of the state.

Ambystoma rosaceum Taylor.—A large series of this salamander, including eggs, hatchlings, larvae and neotenes, was taken at several localities in the Sierra Surutato. This species appears to be restricted to small streams at higher elevations in the pine-oak-madrone forest. Thirty-five small larvae (16-30 mm total length; JFC uncataloged) were taken in two small tributaries of the Rio Sinaloa, 0.2 mi W Los Hornos and 0.4 mi N Los Hornos (elevation 1890 m) on 19 and 22 February 1968; and 24 eggs and hatchlings (JFC uncataloged) from a stream in the Arroyo Ocurahui (*ca.* 1920 m) were collected on 22 February 1969. The clustered eggs were attached to the underside of a large rock that had fallen into the stream. Other specimens are 15 larvae (83-117 mm; JFC 69-1 to 69-15) and one neotene (162 mm; JFC 69-16) taken in deep, spring fed pools at the source of a stream in the Arroyo de Rancho El Madroño, 6.1 mi by road NE La Cienega (*ca.* 2135 m) on 24 February 1969; 20 larvae (21.5-70 mm; JFC 71-1 to 71-18+2) and one neotene (142 mm; JFC 71-19) from Los Hornos (*ca.* 1890 m), 8 March 1971; and one larva (85 mm; JFC 71-20) from El Triguito (*ca.* 1860 m), 10 March 1971.

These specimens are interesting from several standpoints. They are the first salamanders to be reported from Sinaloa; the nearest known localities for *Ambystoma rosaceum* are about 100 kilometers to the east-northeast near El Vergel, Chihuahua, and about 310 kilometers to the southeast near Las Adjuntas, Durango (Anderson 1961). They represent the first report of eggs and hatchlings for this salamander as well as the first record of neoteny in the species, and they represent a population that breeds in February rather than at the beginning of the wet season in June or July, as is characteristic of other populations of *A. rosaceum.* Dr. James D. Anderson who currently is studying this material will provide more detailed information on these specimens in a later publication.

Bufo cognatus Say.—A single live specimen (UAZ 38720) was collected about 2200 hours by Mike Robinson on the road 9.2 mi SW San Blas on 6 June 1974. The road was dry and no rain had fallen. This is the first record of *Bufo cognatus* in Sinaloa and extends the range of this species about 110 kilometers southwest from previously known localities between Huatabampo and Navojoa, Sonora (McDiarmid 1966). McDiarmid (1966) predicted a southeastward extension of *B. cognatus* into Sinaloa in association with the extensive agricultural development along the lower Río Mayo and Río Fuerte drainages.

Rana tarahumarae Boulenger.—Two males (JFC 67-14 and 67-15) were collected on 26 March 1967 in a creek in pine-oak-madrone forest at Los Hornos (1890 m). These specimens were mentioned by Zweifel (1968) as representing the first records of this frog for Sinaloa as well as the southernmost locality for the species. They extend the known range of *Rana tarahumarae* approximately 95 kilometers to the southwest from Arroyo Tecolote de Los Loera, Chihuahua (Zweifel 1955). Four additional specimens were taken on 19 and 24 February 1969. Two (JFC 69-61 and 69-62) were collected in a riparian habitat below the pine-oak forest in Arroyo San Rafael at La Joya

(1370 m) and the others (JFC 69-63 and 69-64) were taken around spring-fed pools in a meadow surrounded by pine-oak-madrone forest at Arroyo de Rancho El Madroño (2135 m). One of these specimens is a gravid female measuring 102.4 mm body length. The latter two specimens were secured at an elevation about 300 m higher than previously recorded for this species (Zweifel 1968). Pertinent measurements and proportions are presented in Table 2.

TABLE 2

Pertinent measurements and proportions for Surotato specimens assigned to *Rana tarahumarae*.

No.	Sex	Body Length[a]	Tibia Length	Head Length	Head Width	HL/HW	TL/BL
67-14	♂	70.0	37.0	20.0	25.0	0.800	0.528
67-15	♂	72.0	37.0	21.5	27.0	0.796	0.514
69-61	♂	61.5	31.0	20.0	23.0	0.869	0.504
69-62	♀	102.4	47.4	32.4	39.5	0.820	0.463
69-63	♀	47.5	22.5	15.0	17.7	0.847	0.474
69-64	♀	82.5	44.2	27.0	32.0	0.844	0.536

[a] All measurements in mm; taken according to Zweifel (1955).

Welbourn and Loomis (1970) reported a single specimen of *Rana tarahumarae* from 8 km W Ameca, Jalisco as a host for a new species of chigger. This locality is within the range of *Rana pustulosa* but considerably south of the southernmost records for *R. tarahumarae*. The proportions of *R. tarahumarae*, the Surotato specimens and *R. pustulosa* are represented in Table 3. In both proportions the Surotato specimens are intermediate between *R. tarahumarae* and *R. pustulosa*. They are more similar to *R. tarahumarae* in HL/HW and more similar to *R. pustulosa* on TL/BL. Dorsolateral folds are present but faint in the three males and either very faint or absent in the females from Surotato. The tympanum is indistinct and covered by minute, white tubercles. In other details the Surotato frogs are more similar to *R. tarahumarae*, two of which were so referred by Zweifel (1968). However, the intermediate nature of the Surotato specimens in certain characteristics previously used to distinguish the two species, suggests that *R. pustulosa* and *R. tarahumarae* probably are conspecific. A detailed study of this group of frogs in Western México is needed.

TABLE 3

Proportions of samples of *Rana tarahumarae*, Surotato specimens and *Rana pustulosa*.

Samples	N	HL/HW	TL/BL
R. tarahumarae[a]	31	0.812±0.006(0.755-0.879)	0.486±0.004(0.418-0.522)
Surotato specimens	6	0.829±0.012(0.796-0.869)	0.503±0.012(0.463-0.536)
R. pustulosa[a]	66	0.851±0.004(0.755-0.923)	0.508±0.003(0.436-0.563)

[a] Data from Zweifel (1955); figures represent mean, standard error of mean and range.

Sceloporus spinosus Wiegmann.—Two immatures of this lizard were taken in the Sierra Surotato: JFC 68-33, from beneath a log in pine-oak-madrone forest, 0.4 mi by road N Los Hornos, *ca.* 1890 m, 22 February 1968; and JFC 69-67, collected on a fence post at Ocurahui, *ca.* 1920 m, 22 February 1969. These are the first specimens from Sinaloa and the westernmost localities reported for the species (Smith 1939). These also are the first records of this species from pine-oak-madrone forest habitat. Cole (1970) indicated that the species is found primarily in subtropical savanna and thorn scrub. They represent range extensions of approximately 355 km to the west-northwest from the nearest previously published locality, Durango, Durango (Smith 1939) and about 225 km in the same direction from Santiago Papasquiaro, Durango (JFC 66-78). Discovery of *Sceloporus spinosus* in the Surotato indicates that, contrary to the conclusion that Smith (1939:93) expressed, the elevated western margin of the Mexican Plateau has failed to present an effective barrier to the northwestward dispersal of this species. Pertinent data are 35.4, 44.1 mm snout-vent length; 28, 28 dorsal scales; 48, 46 ventral scales; 12-11, 12-12 femoral pores; 4-4, 4-4 supraoculars. The number of dorsals closely resembles the mean for the geographically nearby nominate subspecies as well as for the far-removed *S. s. apicalis* Smith and Smith of Oaxaca; the ventral and femoral pore counts most closely approach the means for *S. s. caeruleopunctatus* Smith of Guerrero and Oaxaca; and the number of supraoculars best fits the mean for *S. s. spinosus* (Smith 1939; Smith and Smith 1951). Since the data from our specimens is within the known range of variation for the nominate subspecies, and also on geographic grounds, we provisionally allocate the Sinaloan specimens to *S. s. spinosus.* A series of adults from this area will allow a more complete understanding of the relationships of this population to others of the species.

Sceloporus virgatus Smith.—Three specimens of this species include a juvenile, 25 mm SV length (JFC 69-133) and two adult males, 45.6 and 47.3 mm SV (JFC 70-12; 70-13). They are typical representatives of the species in details of scalation and general coloration (Cole 1968). These are the first records of *Sceloporus virgatus* for Sinaloa and extend the known range of the species about 170 kilometers south-southeast from between Cerocahui and Barranca de Urique, Chihuahua (Cole 1963). The lizards were taken near rocky streams at El Triguito, *ca.* 1860 m, on 4 November 1969 (JFC 69-133) and at a site 2 mi by road SE Los Hornos, 2075 m, on 4 October 1970 (JFC 70-12; 70-13).

Sceloporus poinsettii Baird and Girard.—Two specimens of this large sceloporine lizard (JFC 69-135, adult male, 125 mm SV and 69-134, adult female, 99 mm SV) were collected 1.1 mi by road SE La Cienega, *ca.* 1800 m, on 4 November 1969. The male is the largest known specimen of this species, exceeding the previous record by 8 mm in snout-vent length (Taylor & Knobloch 1940; Stebbins 1966). Both were taken during the day on a rocky road cut in pine-oak forest. These first records of *Sceloporus poinsettii* from Sinaloa help to fill the hiatus in the western range of the species in México. Previously, the specimens nearest to Sinaloa had been collected about 130 kilometers to the northeast near Guachochic, Chihuahua (Smith and Chrapliwy 1958) and about 315 kilometers to the southeast near El Salto, Durango (Smith and Chrapliwy 1958). Smith and Chrapliwy diagnosed *S. poinsettii macrolepis* from southwestern Chihuahua, southern Durango, and west-central Zacatecas as having fewer dorsal scales (85% with 26-29) than *S. p. poinsettii* (only 3% with less than 30). In this regard the two Sinaloan lizards with 30 and 32 dorsal scales are more similar to the northern subspecies of *S. p. poinsettii* than they are to populations from adjacent localities in the intervening area. The nearest specimens of the nominate subspecies are from northern and eastern Chihuahua, while those from the southwestern portion of the same state were assigned to *S. p. macrolepis*. Additional specimens from west-central Chihuahua were considered ". . . intergrades between *poinsetti* and *macrolepis,* tending strongly toward the latter race" (Smith and Chrapliwy 1958:268). In the same paper these authors characterized *S. p. polylepis* from southeastern Chihuahua and eastern Durango as possessing more dorsals (83% with 36-41) than *S. p. poinsettii* (only 4% with more than 35). At the same time they pointed out that *S. p. macrolepis* occurs at higher elevations than the nominate subspecies, while *S. p. polylepis* occupies desert foothills at comparatively low elevations. We suggest that the single character that serves to distinguish these three subspecies—the number of dorsal scales—may be merely a function of environmental temperature and aridity. If additional collecting in eastern Durango and eastern Sinaloa indicates the species to have a nearly continuous range (which we suspect), then the geographic and elevational distribution of the number of dorsal scales should be examined carefully.

Eumeces callicephalus Bocourt.—Four males of this species were taken on 19 and 20 February 1968 in the Sierra Surutato. Two (JFC 68-100; 68-101) are from beneath rocks along a stream in a logged-over valley surrounded by pine-oak-madrone forest 0.5 mi by road SE Los Hornos (*ca.* 1920 m); the others (JFC 68-102; 68-103), also beneath rocks, were found in the Cañon de Tarahumare between La Joya and Barranca de las Tahonitas (*ca.* 1310 m). The latter locality lies in an ecotone between riparian forest and tropical deciduous forest, immediately below pine-oak forest. The first specimen measures 58.5 mm in SV length and has the Y-shaped head-color pattern typical of *Eumeces callicephalus* as depicted by Stebbins (1966). However, the other three specimens (JFC 68-101; 68-102; 68-103) are very large males (72.0, 66.8, and 67.0 mm SV) and have either very faint head markings or lack them completely. The largest specimen is approximately 8 mm longer in SV length than the maximum reported for this species (Stebbins 1966). All specimens are representative of *E. callicephalus* in most other characteristics. Other salient data for these four specimens are: 27 or 28 (3) scale rows, the median dorsals unwidened; 56, 58 or 59 (2) dorsal scales (including nuchals); 7-7 supralabials; 6-6 infralabials; 2-2 loreals; 1-1 preoculars; 2-2 presuboculars; 2-2 postoculars; 4-4 postsuboculars; 1+2-1+2 temporals; 4-4 supraoculars; 5-8, 7-8 (2) or 8-8 supraciliaries. The prefrontals are separated (by contact of the frontal and frontonasal) in 68-100, fused (no seam) in 68-101, and touching (in contact) medially in 68-102 and 68-103. A postnasal is present on both sides in 68-100, absent on both sides in 68-101, and present on the left but absent from the right side of 68-102 and 68-103. The parietals are in contact behind the interparietal in 68-100 and 68-102 and separated in the others. A pair of scales separates the single postmental from the mental in 68-100; the other specimens have two postmentals. The scale bordering the medial margin of each postgenial is longer than wide. A distinct dorsolateral pale stripe is present on the smallest male but is faintly represented only on the anterior part of the body of the three large males. There are four dorsal scale rows between the dorsolateral stripes anterior to the insertion of the forelimbs. A dark lateral stripe is present on all animals, although it is faint in the large specimens. At midbody this dark lateral stripe involves from one and one-half to two and one-quarter scale rows. The paler dorsal color between the lateral dark stripes at midbody covers six full and two half scale rows, eight scale rows, or eight full and two quarter scale rows. Adpressed limbs of the smaller male touch; they do not touch in the other three specimens. Mr. Carl S. Lieb examined these specimens and confirmed our identifications.

Eumeces parviauriculatus Taylor.—Nine specimens of this small skink were collected at the following localities: 1 mi by road SE Los Hornos, *ca.* 1980 m, 26 March 1967 (JFC 67-17; 67-18); 0.4 mi by road N Los Hornos, *ca.* 1890 m, 22 February 1968 (68-104); 2.7 mi by road SE Los Hornos, 2135 m, 23 February 1969 (69-82); Arroyo El Pie la Cuesta, 1.8 mi by road NW Surutato, 1680 m, 23 February 1969 (69-85; 69-86); 1 mi by road E Buenas Juntas, 2075 m, 1 October 1970 (70-15; 70-16); Rancho El Madroño, 2135 m, 10 March 1971 (71-21). Most specimens were taken under rocks or in crevices in rocky cliffs in pine-oak forest. These are the first records for the state, realizing the prediction by Legler and Webb (1960) that *Eumeces parviauriculatus* would eventually be taken in northern Sinaloa. The specimens extend the known range of this species about 200 kilometers southeast from previously reported localities near Álamos, Sonora, and about 190 kilometers south-southeast from near Témores, Chihuahua (Legler and Webb, 1960). Four females (SV 43.2, 52.0, 53.1, 54.0 mm) contain developing eggs. Two (67-17, 67-18) have three eggs measuring 5 mm and a fourth measuring 2 mm; the others have a total of 7 and 8 very small eggs. The specimens range from 37 to 54 mm snout-vent length. In the two specimens with complete tails (male, 70-15; female, 67-18), the tail lengths are 61.4 and 64.9% of the total length. Other important diagnostic data are: 4 supraoculars, no postnasals, 1 postmental, parietals not in contact behind interparietals, frontal in contact with frontonasal, 20 scale rows, and 58 (damaged), 60, 62, 63 or 64 dorsal scales.

These specimens were compared with 5 specimens of *E. parviauriculatus* (MVZ 74187-90, 74198) from a streamside locality (elevation 2000 m) on the Sonora-Chihuahua border above Álamos, Sonora. The Sinaloan specimens are similar in most respects to this Sonoran material and to specimens reported in the literature (Taylor, 1933; Taylor and Knobloch, 1940; Legler and Webb, 1960). This new material increases the number of reported specimens of this small skink from five to nineteen.

Chilomeniscus cinctus Cope.—This first record of *Chilomeniscus* from Sinaloa is based on a specimen (LACM 121310) collected on 22 September 1975, at Rancho Palo Verde, 2.7 mi W Miguel Hidalgo Dam. Pertinent data are: juvenile female; 97 mm total length; 12 mm tail length; 15-13-13 dorsal scale rows; 111 ventrals; 24 subcaudals; 7-7 supralabials; 8-8 infralabials; 1-1 preoculars; 2-2 postoculars; 1+1-1+1 temporals. A loreal scale is present on the right side but absent on the left. There are 20 dorsal black crossbands, 15 on the body, 4 on the tail, and 1 across the head. The dorsal interspaces were reddish orange, with color restricted to the middle 5-7 scale rows. In most respects this specimen is similar to one from southern Sonora reported by Bogert and Oliver (1945). The occurrence of *C. cinctus* in Sinaloa is not unexpected as specimens are known from Sonora at localities 55 km to the northwest at Álamos (Bogert and Oliver, 1945) and 50 km to the west at a point 14.2 mi N Sinaloa-Sonora border on México Highway 15 (UMMZ 134106, W. Van Devender, personal communication).

Sonora aemula (Cope).—A third specimen of *Sonora aemula* from Sinaloa extends the known range (Hardy and McDiarmid, 1969) of this species about 400 kilometers southward. Its occurrence in the southern limits of the tropical semiarid forest is not surprising, as it is relatively common in this habitat in southern Sonora. The southern distribution of this snake parallels those of *Coleonyx variegatus* and *Salvadora hexalepis*. This specimen (LACM 51563) was found DOR by John K. Cross on 12 September 1967, on Highway 15, 40 mi S Mazatlán. It is a female measuring 280 mm in total length and 39 mm in tail length, with 149 ventrals, 34 subcaudals, 17-15-15 dorsal scale rows, 7-7 supralabials, 7-7 infralabials, 1 loreal (1 fused with preocular), 1-1 preoculars, 2-2 postoculars, and 1+2-1+2 temporals. The animal has a pale snout, black head cap, black collar, reddish ground color, four dyads and one triad on the body, two dyads on the tail, and the tail tip is black. Three of the body dyads are black-yellow-black, one is yellow-black-yellow and the triad is black-yellow-black-yellow-black. The highly variable color pattern is representative of the species.

Tantilla bocourti (Günther).—An adult female containing six enlarged ova (three on each side) is the first specimen from Sinaloa and extends the known range of the species (Fig. 1) about 345 kilometers northwest along the Pacific versant of the Sierra Madre Occidental from near Pueblo Nuevo in southwestern Durango (Webb and Baker 1962). The snake (JFC 68-111) was unearthed from rocky substratum during road repairs in pine-oak forest 1.1 mi by road N La Joya, *ca.* 1525 m, on 21 February 1968.

This specimen has more subcaudals and a longer tail than any other female examined (Table 1) but in other respects is representative of the species. Other pertinent data are: 349 mm total length; 75 mm tail length; 7-7 supralabials; 6-6 infralabials; 1-1 preoculars; 2-2 postoculars; and mental in contact with chinshields. The primary temporals are single and elongate (length is 3.5 times width); there is a small, scale-like secondary temporal (length about equal to width) on the left. On the right side the secondary temporal is lacking so that the parietal and seventh supralabial are in contact. The tertiary temporals are single and scale-like on both sides. Two ova on each side measure 6 mm in length while the anteromost on each side is smaller (3 mm). We assign this specimen to *Tantilla b. bocourti,* since it agrees with the nominate subspecies rather than *T. b. deviatrix* Barbour in all characters that have been used to differentiate the two forms. The ventral count is well above the known maximum for *T. b. deviatrix,* while the number of subcaudals falls below the minimum for the latter subspecies. The scale-like secondary temporal is characteristic of *T. b. bocourti* as opposed to the narrow, elongate condition in the other subspecies. Typical of the nominate subspecies is the widespread distribution of dark pigment on the head, which is markedly reduced in extent in *T. b. deviatrix.* This morphological evidence is consonant with the geographic picture, since *T. b. deviatrix* is known only from valley habitats in the distant state of San Luis Potosí.

Tantilla calamarina Cope.—A single male (JFC 69-91) of this small secretive snake was found in a rock crevice along a trail in mixed oak and tropical deciduous forest in the Cañon Tarahumares at Vado Ceboletas, *ca.* 1190 m, on 20 February 1969. This record extends the known range of the species about 275 kilometers north from near Mazatlán (Hardy and McDiarmid 1969). Pertinent data are: 147 mm total length; 29 mm tail length; tail 19.7% of total length; 136 ventrals; 44 subcaudals; 6-6 supralabials and infralabials; 1-1 preoculars and postoculars; and 1+1-1+1 temporals. The prefrontals and parientals are separated from the labials. Both the ventral and subcaudal counts (and, consequently, the V + Sc count) are higher than those previously reported for the species. In other respects, however, the scalation is typical of the species as described by Smith (1942) and others (*e.g.*, Peters 1954; Zweifel 1960).

This specimen is distinct in many aspects of coloration. The dorsal ground color is pale brown; the venter is grayish white. The lateral edges of the ventrals and subcaudals, the labials, and the mental have faint scattered tan flecks. A brown stripe extends middorsally from the head cap to the tail tip. Anteriorly it involves all of scale row eight and the adjacent edges of scale rows seven and nine from the head cap back to a position above ventral ten. From here the stripe is restricted to the central portion of scale row eight, gradually fading as it approaches the tail. Distinct lateral stripes are present. They consist of brown pigment spots on the upper third of the scales in row three and the posterior quarter of scales in row four. This arrangement gives the lateral stripes a zigzag appearance. In addition, there are dashes of brown pigment on the posteromedial parts of scales in rows one, two, five, and six. These dashes give the impression of discontinuous faint stripes, similar to the lateral stripes in a Tres Marías specimen (Zweifel 1960). The head cap is connected to the middorsal stripe but is separated from the lateral stripes by two crescent-shaped marks. These crescents arise on each side behind the parietals and extend anteriorly across the upper third to half of the secondary temporals, along the lateral edges of the parietals, through the upper third of the postoculars, and across the supraoculars and lateral parts of the prefrontals onto the internasals. These marks are white on the upper half of the scales in row five, the entire scale in row six, and most of the scale in row seven and clearly sets off the dark head cap from the ground color on the body. Anterior to the parietals, the crescentic marks gradually darken to the pale brown ground color. The lateral stripes continue onto the head where they broaden to form a dark eye mask that separates the crescents from the pale lower portions of the supralabials. The head cap is brown mottled with paler flecks that increase in size on the prefrontal, internasal, and rostral scales.

Much of the described variation in head coloration of specimens of *Tantilla calamarina* (Taylor 1937; Peters 1954; Zweifel 1960) is the result of a break up of the crescentic marks on the head. This specimen apparently has a much more discrete color pattern than any previous specimens and lends additional support to the suggestion that *Tantilla martindelcampoi* and *T. calamarina* are conspecific.

Tantilla wilcoxi Stejneger.—A single specimen of this relatively rare snake was collected in a rock crevice in a road cut in pine-oak-madrone forest 4.8 mi by road SE Los Hornos, 2075 m, on 19 February 1968. It is the first record for Sinaloa and extends the known range about 250 kilometers south from Mojárachic, Chihuahua (Smith 1942) and about 360 kilometers to the west-northwest from near Chorro, Durango (Webb and Hensley 1959). The specimen (JFC 68-112), an adult female, has the following characteristics: 295 mm total length; 70 mm tail length; tail 23.7% of total length; 157 ventrals; 63 subcaudals; 7-7 supralabials; 6-6 infralabials; 1-1 preoculars; 2-1 postoculars; 1+1-1+1+1 temporals; mental separated from chinshields. A continuous white collar one and one-half scales wide on the midline includes the posterior quarter of the parietals. The posterior dark border is irregular and only one-half scale wide. Most of the fifth supralabial and an adjacent part of each anterior temporal are white. Additional aspects of color pattern are essentially the same as described for other specimens of *Tantilla wilcoxi* by Smith (1942), Webb and Hensley (1959), and Stebbins (1966). In life, the dorsum was dark olive-green; the posterior two-thirds of the venter and entire underside of the tail was orange-red. Inasmuch as both ventral and subcaudal counts fall well within the reported ranges of variation for females of the nominate subspecies and above the ranges for *T. w. rubricata* Smith, and since the dorsal coloration is dark rather than reddish, we refer our specimen to *T. w. wilcoxi.* This snake adds further confirmation to the prediction by McCoy (1964) that in México the nominate subspecies occupies the Sierra Madre Occidental to the west, while *T. w. rubricata* occurs in the Chihuahua Desert to the east.

Crotalus stejnegeri Dunn.—Two specimens of this apparently rare rattlesnake have been collected in Sinaloa since Hardy and McDiarmid (1969) reported a specimen from near Santa Lucía. The first of these new specimens is a large male collected at night by Carlton Hall as it crossed Highway 40, 10 mi NE Concordia in August 1967. The specimen (LACM 37718) is 615 mm in total length. The tail is 91 mm long and 14.8% of the body length. In addition, this snake has the following pertinent characteristics: 176 ventrals of which ventral 97 and 103 are half scales; 48 subcaudals of which 41 are entire and the last seven divided; 27-23-29 dorsal scale rows; 15-15 supralabials; 16-15 infralabials; 2-2 preoculars; 4-4 postoculars; 3-3 suboculars; 32 dorsal body blotches; and more than 10 tail blotches. The posterior tail blotches are difficult to count due to darkening of the ground color. The matrix of the proximal rattle is black at its base; the rattle is complete, with four segments and a terminal button. In addition to being the largest specimen of the species reported in the literature, this snake has a slightly longer tail, fewer body blotches, and fewer dorsal scale rows at midbody than other known examples.

The second specimen (RS 901 HSH/RSS,NHSM) was collected on Highway 40 between 10 and 15 mi NE Concordia on 10 July 1972. The snake was found at a point where the road crosses a dry creek bed. It was dusk, the air temperature being about 24°C, and the road temperature about 27°C. According to the collector, this locality is about two miles west of the beginning of the pine forest, probably in subtropical dry forest (Hardy and McDiarmid 1969). Herbert S. Harris provided collecting data and the following information: juvenile female, 350 mm total length; 34 mm tail length; tail 9.5% of body length; 172 ventrals; 36 subcaudals; 27-27-20 dorsal scale rows; 14-15 supralabials; 18-17 infralabials; 2-2 preoculars; 4-4 postoculars; 2-3 suboculars; 40 body blotches; 10 tail blotches; 1 segment plus button comprising rattle.

QUESTIONABLE RECORDS FOR SINALOA

We take this opportunity to correct a statement concerning the southern limit of the range of *Uta stansburiana.* Tinkle (1969, Fig. 1) stated "The range of the southwestern race should extend slightly farther south into northern Sinaloa than shown

(Royce Ballinger, personal communication).'' In a recent letter concerning the accuracy of the map, Tinkle indicated that the comments in the caption were in error, and neither he nor Royce Ballinger know of any records of *Uta stansburiana* from Sinaloa.

In 1969 Peters and Donoso-Barros reported the distribution of *Mabuya mabouya alliacea* as ''Veracruz and Sinaloa, México to Costa Rica.'' Apparently their report of *Mabuya* from Sinaloa is based on Burger's (1952) incorrect transcription of the range of the species. He listed specimens from Colima but cited the distribution as ''México from the states of Veracruz on the Atlantic and Sinaloa on the Pacific coast. . . .'' We know of no verified records of *Mabuya mabouya* from Sinaloa. Some of the old records for northern states in México are vague and unsubstantiated and may well be based on misidentifications. Hobart Smith (personal communication) knows of neither specimens nor literature records for *Mabuya* in Sinaloa. We suggest that the report is in error; on the west coast of México, *Mabuya* is known from Colima south.

CONCLUSION

The report of *Hypsiglena torquata* and *Tantilla bocourti* from the Tres Marías brings the insular herpetofauna of this island group to a total of 21 species, including 2 frogs, 1 turtle, 5 lizards, and 13 snakes. The new records of amphibians and reptiles from Sinaloa, including the reports of *Enulius oligostichus* (McDiarmid and Bezy 1971) and *Hyla bistincta* (Duellman 1970) and the deletion of *Uta stansburiana* and *Mabuya mabouya,* bring the native terrestrial herpetofauna of that state to 133 species, including 1 salamander, 34 frogs, 5 turtles, 1 crocodilian, 35 lizards, and 57 snakes.

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RESUMEN

Desde Las Tres Marías nos viene por primera vez informe sobre dos especies de serpientes, a saber: *Hypsiglena torquata* y *Tantilla bocourti.* Como resultado de dicho informe y refiriéndonos únicamenta al susodicho grupo de islas, llega el total de la herpetofauna conocida a 21*a* especies, o sean 2 ranas, 1 tortuga, 5 lagartijas y 13 serpientes. La salamandra *Ambystoma rosaceum,* las ranas *Bufo cognatus* y *Rana* *tarahumarae,* las lagartijas *Eumeces parviauriculatus, Sceloporus poinsettii, S. spinosus* y *S. virgatus,* y las serpientes *Chilomeniscus cinctus, Tantilla bocourti* y *T. wilcoxi* se añaden a la fauna de Sinaloa. A cada especímen se le compara con otros miembros de la misma especie, procedentes de diferentes puntos del area de distribucíon geográfica de la especie. Estos datos, juntos con los apuntes sobre seis otras especies, añaden intensamente a nuestro conocimiento de la variedad, distribución, y biogeografía de la herpetofauna de México Occidental. Se suprimen de la fauna sinaloense *Uta stansburiana* y *Mabuya mabouya.* Resulta pues que la herpetofauna terrestre y oriunda de Sinaloa, se compone de 133 especies, a saber: 1 salamandra, 34 ranas, 5 tortugas, 1 cocodrilo, 35 lagartijas y 57 serpientes.

LITERATURE CITED

ANDERSON, J. D. 1961. The life history and systematics of *Ambystoma rosaceum.* Copeia, 1961:371-377.

BOGERT, C. M. AND J. A. OLIVER. 1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., 83:301-425.

BREEDLOVE, D. E. AND L. R. HECKARD. 1970. *Gentrya,* a new genus of Scrophulariaceae from Mexico. Brittonia, 22:20-24.

BREEDLOVE, D. E. 1973. The phytogeography and vegetation of Chiapas (Mexico), Chapter 5, *in* Vegetation and vegetational history of northern Latin America. Edited by Alan Graham. Elsevier, Amsterdam. 393 pp.

BURGER, W. L. 1952. Notes on the Latin American skink, *Mabuya mabouya.* Copeia, 1952:185-187.

COLE, C. J. 1963. Variation, distribution, and taxonomic status of the lizard, *Sceloporus undulatus virgatus* Smith. Copeia, 1963:413-425.

————. 1968. *Sceloporus virgatus.* Cat. Amer. Amphib. Rept., 72.1-72.2.

————. 1970. Karyotypes and evolution of the *spinosus* group of lizards in the genus *Sceloporus.* Amer. Mus. Novitates, 2431:1-47.

DAVIS, W. B. AND J. R. DIXON. 1959. Snakes of the Chilpancingo region, Mexico. Proc. Biol. Soc. Wash., 72:79-92.

DAVIS, W. B. AND H. M. SMITH. 1953. Snakes of the Mexican state of Morelos. Herpetologica, 8:133-143.

DUELLMAN, W. E. 1958. A preliminary analysis of the herpetofauna of Colima, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 589:1-22.

————. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148.

————. 1965. A biogeographic account of the herpetofauna of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:627-709.

————. 1970. The hylid frogs of Middle America. Monogr. Mus. Nat. Hist. Univ. Kansas, 1:1-753.

GENTRY, H. S. 1946. Notes on the vegetation of Sierra Surotato in northern Sinaloa. Bull. Torrey Bot. Club, 73:451-462.

HARDY, L. M. AND C. J. COLE. 1968. Morphological variation in a population of the snake, *Tantilla gracilis* Baird and Girard. Univ. Kansas Publ. Mus. Nat. Hist., 17:613-629.

HARDY, L. M. AND R. W. MCDIARMID. 1969. The amphibians and reptiles of Sinaloa, México. Univ. Kansas Publ. Mus. Nat. Hist., 18:39-252.

LEGLER, J. M. AND R. G. WEBB. 1960. Noteworthy records of skinks (genus *Eumeces*) from northwestern Mexico. Southwestn. Nat., 5:16-20.

MCCOY, C. J., JR. 1964. Notes on snakes from northern Mexico. Southwestn. Nat., 9:46-48.

McDiarmid, R. W. 1966. A study in biogeography: the herpetofauna of the Pacific Lowlands of western México. Masters Thesis, Univ. So. California. 296 pp.

________. 1968. Variation, distribution and systematic status of the black-headed snake *Tantilla yaquia* Smith. Bull. So. Calif. Acad. Sci., 67:159-177.

McDiarmid, R. W. and R. L. Bezy. 1971. The colubrid snake *Enulius oligostichus* in western México. Copeia, 1971:350-351.

Mertens, R. 1934. Die Insel-Reptilien, ihre Ausbreitung, Variation und Artbildung. Zool. Stuttgart, 84:1-209.

Peters, J. A. 1954. The amphibians and reptiles of the coast and coastal sierra of Michoacán, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 554:1-37.

Peters, J. A. and R. Donoso-Barros. 1970. Catalogue of the Neotropical Squamata: Pt. II. Lizards and amphisbaenians. U.S. Natl. Mus. Bull., 297:1-293.

Rzedowski, J. and R. McVaugh. 1966. La Vegetation de Nueva Gallica. Contr. Univ. Michigan. Herb., 9:1-123.

Smith, H. M. 1939. The Mexican and Central American lizards of the genus *Sceloporus*. Zool. Ser. Field Mus. Nat. Hist., 26:1-397.

Smith, H. M. 1942. A résumé of Mexican snakes of the genus *Tantilla*. Zoologica, New York, 27:33-42.

Smith, H. M. and P. S. Chrapliwy. 1958. New and noteworthy Mexican herptiles from the Lidicker collection. Herpetologica, 13: 267-271.

Smith, P. W. and H. M. Smith. 1951. A new lizard *(Sceloporus)* from Oaxaca, Mexico. Proc. Biol. Soc. Washington, 64:101-103.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Boston, Houghlin Mifflin. 279 pp.

Taylor, E. H. 1933. New species of skinks from Mexico. Proc. Biol. Soc. Washington, 46:175-182.

________. "1936" (1937). Notes and comments on certain American and Mexican snakes of the genus *Tantilla*, with descriptions of new species. Trans. Kansas Acad. Sci., 39:335-348.

________. "1939" (1940). Some Mexican serpents. Univ. Kansas Sci. Bull., 25:445-487.

Taylor, E. H. and I. W. Knobloch. 1940. Report on an herpetological collection from the Sierra Madre Mountains of Chihuahua. Proc. Biol. Soc. Washington, 53:125-130.

Taylor, E. H. and H. M. Smith. "1938" (1939). Miscellaneous notes on Mexican snakes. Univ. Kansas Sci. Bull., 25:239-258.

Tinkle, D. W. 1969. Evolutionary implications of comparative population studies in the lizard *Uta stansburiana*, pp. 133-154. *In:* Systematic Biology, Proc. Internat. Conf. Nat. Acad. Sci., 1969, Washington D.C.

Webb, R. G. and R. H. Baker. 1962. Terrestrial vertebrates of the Pueblo Nuevo area of southwestern Durango, Mexico. Amer. Midl. Nat., 68:325-333.

Webb, R. G. and M. Hensley. 1959. Notes on reptiles from the Mexican state of Durango. Publ. Mus. Michigan St. Univ., Biol. Ser., 1:249:258.

Welbourn, W. C., Jr. and R. B. Loomis. 1970. Three new species of *Hannemania* (Acarina, Trombiculidae) from amphibians of western Mexico. Bull. So. Calif. Acad. Sci., 69:65-73.

Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. Univ. California Publ. Zoöl., 54:207-292.

________. 1959. Additions to the herpetofauna of Nayarit, Mexico. Amer. Mus. Novitates, 1953:1-13.

________. 1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 9. Herpetology of the Tres Marías Islands. Bull. Amer. Mus. Nat. Hist., 119:77-128.

________. 1968. *Rana tarahumarae*. Cat. Amer. Amphib. Rept., 66.1-66.2.

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THE DISTRIBUTION OF RODENTS IN OWENS LAKE REGION, INYO COUNTY, CALIFORNIA[1]

By JOHN O. MATSON[2]

ABSTRACT: The distribution and relative abundance of rodents in Owens Lake Region, Inyo County, California are discussed. Seventeen species (18 subspecies) of rodents were recorded from 10 plant associations. Factors limiting the distribution of some rodents were soil texture *(Dipodomys deserti, Perognathus formosus* and *Peromyscus crinitus)* and vegetation *(Reithrodontomys megalotis, Microtus californicus* and *Mus musculus)*. The relative abundance of the other species may be influenced by either or both factors. The number of rodent species in each plant association was positively correlated with increased vegetative spatial heterogeneity. Faunal relationship values are compared for each plant association. Biogeographical comments are given.

INTRODUCTION

The Owens Valley of California is an area where vegetational elements common to northern and southern deserts come into contact. A shadscale vegetation zone, lying between the northern sagebrush zone and the southern creosote bush zone, occupies all but the most southern portion of Owens Valley (Billings 1949). Because of this Billings (1949) regarded the vegetation in Owens Valley as an ecotone between the northern and southern deserts.

Rodents are one of the most ecologically important factors in a community (Fautin 1946). Therefore, a study of rodent distributional patterns and abundance is an important aspect of community ecology. Information concerning mammalian distribution and abundance in the Owens Valley is scarce. Annotated checklists of the mammals from this area were given by Elliot (1904) and Grinnell (1933); however, their lists were incomplete giving only generalized information on distributional patterns. Most literature dealing with the mammals from this area basically is taxonomic, describing new forms or discussing the status of these forms (Merriam 1894 and 1897; Bailey 1898 and 1915; Elliot 1903; Hollister 1913 and 1914; Grinnell 1922; Hall and Dale 1939; and Lidicker 1960). More recently, various ecological studies (Kenagy 1972, 1973a, 1973b; Brown 1973; Brown and Lieberman 1973) have added to our knowledge of the rodent fauna of Owens Valley.

The purpose of this investigation was to study the distribution and relative abundance of rodents in the Owens Lake Region of Inyo County, California. The Owens Lake region was selected because of the ecotonal nature of vegetation and because the rodent distribution patterns had not been adequately studied.

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GENERAL DESCRIPTION OF THE STUDY AREA

The Owens Valley is located in west central Inyo County, California, with Owens Lake at the southern end of the valley. Owens Lake is bounded on the east by the Inyo Mountains and to the west by the Sierra Nevada Mountains. The majority of the study area is in the Upper Sonoran Life Zone (Merriam 1898), which is characterized by the presence of several species of *Atriplex* and *Sarcobatus*. An extension of the Lower Sonoran Life Zone is evident in the southern portion of the study area, characterized by the presence of Creosote bush *(Larrea divaricata)*. All of the study area is in the Mohavian Biotic Province of Dice (1943). In part, it is the Western Desert Scrub Formation of Clements (1920) with the major portion being the Basin Sagebrush Formation.

The entire Owens Valley is an alkali sink, becoming progressively more alkaline southward to Owens Lake (Gale 1915). With the completion of the Los Angeles Aqueduct, in 1913, Owens River water was diverted from the lake (Schumacher 1962). Today the lake is dry, except for a few salt marshes found along the former shoreline.

In the study area, the elevation extended from 3600 feet to 4249 feet; however, all field stations were located between 3600 feet and 3840 feet.

Climatic data were not available for the Owens Lake region itself since the nearest weather stations are at Independence, 15 miles to the north, and Haiwee, 5 miles to the south. Sprague (1941) recorded average January temperatures from these two weather stations as 39.0°F and 39.5°F, respectively. Average July temperatures were 78.3°F for Independence and 81.9°F for Haiwee. Average annual precipitation for a 40-year period at Independence was 4.49 inches, while at Haiwee it was 4.87 inches over a 16-year period (Sprague 1941). The differences were small between these two weather stations. Since Owens Lake is found between these stations, it may be assumed that the macroclimate is similar throughout the study area.

METHODS OF STUDY

Field stations were initially selected on the basis of apparent differences in habitat. Differences in plant species, number of plants per unit area, degree of rockiness, visibly different soil textures, and slope exposure were used as indicators of habitat distinctness.

A total of eleven field stations were studied (Fig. 1). Of these, ten were intensively studied during July and August 1971. The eleventh field station (Stream Side Association) was studied in October 1968.

PLANTS

A plant quadrat, 66 ft by 66 ft (20.1 m by 20.1 m), was staked out on each field station using a steel tape and compass. The perennial plants in each quadrat were identified and counted, except at stations 4 and 11 where most of the plants were too numerous to count. Notes were made of any other plants found at a field station but not occurring in the plant quadrat. Only the most prominent plants found

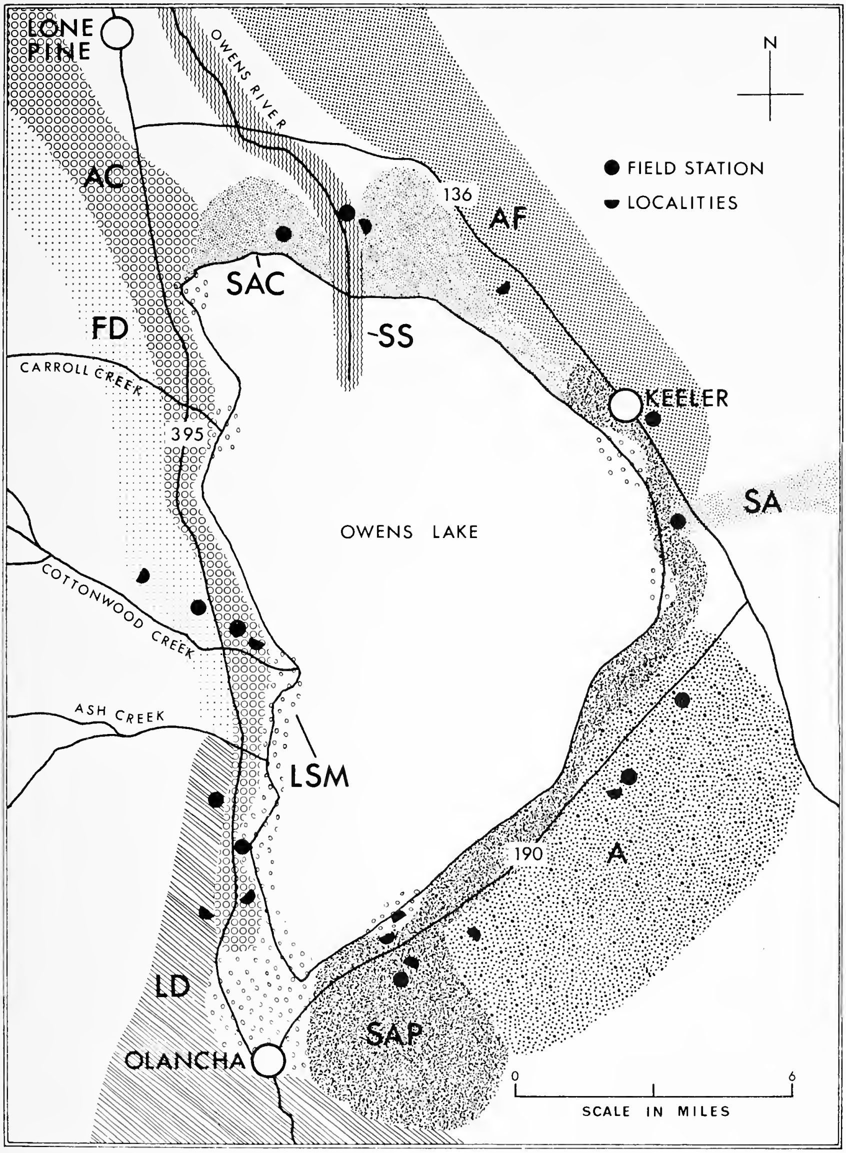

FIGURE 1. Map of study area showing trapping localities and distribution of plant association. See text for explanation of abbreviations.

in the plant quadrat were used in naming an association. The maximum height and width of each perennial plant was measured. The per cent cover area (Table 1) and volume (see Pianka 1966) were determined from these measurements.

Identification of plants was determined in the field using Munz and Keck (1959) and Jaegar (1941). Plant nomenclature follows that of Munz and Keck (1959). Numbers of plants per acre, by species, for each field station is given in Table 1.

SOILS

A soil sample was collected from each plant quadrat. A core sample was taken from the top six inches of soil and placed in an air-tight one-quart jar for subsequent analysis.

Texture analysis and the classes of soil texture follow those used by Hardy (1945). In order of decreasing particle size these are: granule gravel [passes through one-half inch (1.27 cm) mesh but not one-eighth inch (.32 cm)]; coarse sand [passes through one-eighth inch (.32 cm) mesh but not #20 mesh]; fine sand (passes through #20 mesh but not #80); and silt and clay (passes through the #80 mesh).

Field stations with rocks one-half inch or larger in diameter were assigned class numbers according to the degree of rockiness. Class #1 was relatively free of rocks. Class #2 contained rocks one-half inch to three inches (7.62 cm) in diameter. Class #3 had numerous rocks over three inches but less than twelve inches (30.48 cm) in diameter. Class #4 contained rocks over twelve inches in diameter. The results of the soil texture analysis are given in Table 2.

Results of soil analyses for levels of pH and soluble chlorides, sulfates and borates, by using a La Motte Soil Kit, are indicated in Table 3. Soil chemical analyses showed no direct correlation with rodent distribution or abundance, although Hardy (1945) did demonstrate indirect effect of soil chemicals as they affected plant distribution.

RODENTS

Trapping to determine the presence and relative abundance of rodents was carried on at irregular intervals from October 1968 through May 1969. An intensive trapping period using a quadrat-removal method (Bole 1939; Cahalane 1941) was conducted during July and August 1971.

The trapping carried on during 1968 and 1969 was accomplished using single traplines. Each line was set in a definite plant association but in different localities than the field stations. A trapline consisted of 20 to 35 trap stations set approximately 25 feet (7.62 m) apart with three traps per station. The total trapping results (combining both line and quadrate data) is given in Table 4.

A trapping quadrat was staked out at each field station using a steel tape and compass (Manville 1949). The quadrat consisted of three traplines set 50 feet (15.24 m) apart. Each line was composed of 20 trap stations placed 25 feet (7.62 m) apart with three traps per station (two museum specials and one Sherman live trap). A total of 180 traps per quadrat was used. This quadrat enclosed an area of 475 feet by 100 feet (144.78 m by 30.48 m) or about 1.1 acres (.445 ha).

TABLE 1

LIST OF ESTIMATED NUMBERS OF PLANTS PER ACRE[3]

Plants	Field Station[4] 1 (AC)	2 (FD)	3 (LD)	4 (LSM)	5 (SAP)	6 (A)	7 (A)	8 (AF)	9 (SA)	10 (SAC)	11 (SS)
Ephedra nevadensis	–	20	+	–	–	–	–	–	–	–	–
Larrea divaricata	–	–	500	–	–	10	–	–	–	–	–
Opuntia basilaris	–	–	20	–	–	–	–	–	–	–	–
Atriplex hymenelytra	–	–	–	–	–	40	10	–	130	–	–
Atriplex parryi	–	–	–	–	60	30	200	–	310	–	–
Atriplex confertifolia	820	+	–	–	–	100	20	250	–	150	–
Atriplex sp.	30	–	210	–	–	200	20	–	–	–	–
Grayia spinosa	+	+	80	–	–	30	30	100	–	–	–
Eurotia lanata	+	30	–	–	–	–	–	–	–	–	–
Sarcobatus vermiculatus	–	–	–	–	340	–	–	–	–	180	–
Suaeda torreyana	–	–	–	–	–	+	90	160	370	130	–
Lycium Cooperi	60	10	–	–	–	–	–	–	–	–	–
Dalea polyadenia	–	–	–	–	–	–	–	–	–	30	–
Dalea Fremontii	50	–	–	–	–	–	–	–	–	–	–
Populus Fremontii	–	–	–	+	–	–	–	–	–	–	+
Salix sp.	–	–	–	+	–	–	–	–	–	–	+
Hymenoclea salsola	70	80	50	–	–	–	–	–	–	–	–
Franseria dumosa	40	430	340	–	–	–	20	230	–	110	–
Haplopappus Cooperi	40	350	30	–	–	–	–	–	–	–	–
Chrysothamnus nauseosus	+	20	–	–	–	–	–	–	–	40	–
Artemisia dracunculus	–	–	–	+	–	–	–	–	–	–	+
Pluchea sp.	–	–	–	+	–	–	–	–	–	–	++
Typha sp.	–	–	–	++	–	–	–	–	–	–	++
Juncus sp.	–	–	–	++	–	–	–	–	–	–	++
Distichlis spicata	+	–	–	++	–	–	–	–	–	–	++
Polypogon monspeliensis	–	–	–	++	–	–	–	–	–	–	++
% Plant Cover	11.6	6.2	28.1	–	4.4	(1.7)		3.6	1.6	5.2	–
Plant Volume Diversity	1.68	1.21	1.74	low	1.42	(0.87)		1.13	0.28	1.52	high
Plant Species Diversity	1.47	1.81	2.15	high	0.61	(2.59)		1.92	1.47	2.37	high

[3] A "+" indicates a species found at field station but not in the plant quadrat. A "++" indicates plants too numerous to count.

[4] The abbreviations following Field Station numbers refer to the plant association (see text for explanation).

TABLE 2

SOIL TEXTURE IN PER CENT AND DEGREE OF ROCKINESS

	1	2	3	4	5	6	7	8	9	10	11
Field Station #	(AC)	(FD)	(LD)	(LSM)	(SAP)	(A)	(A)	(AF)	(SA)	(SAC)	(SS)
Granule Gravel	22.6	20.0	22.8	20.5	0.0	16.3	8.6	2.2	40.2	0.8	0.8
Coarse Sand	30.0	21.9	15.7	22.1	10.0	13.4	5.6	4.5	13.0	9.8	8.2
Fine Sand	31.6	31.0	27.6	35.9	67.3	40.7	49.6	56.8	21.1	50.6	55.3
Silt and Clay	15.8	27.1	33.9	21.5	22.7	29.6	36.2	36.5	25.7	38.8	35.7
Degree of Rockiness	1	4	3	2	1	2	2	1	3	1	1

TABLE 3

SOIL CHEMICALS IN PPM

	1	2	3	4	5	6	7	8	9	10	11
Field Station #	(AC)	(FD)	(LD)	(LSM)	(SAP)	(A)	(A)	(AF)	(SA)	(SAC)	(SS)
Chlorides	100	50	100	500	500	200	100	100	200	50	50
Sulfates	50	50	50	50	50	50	50	50	50	50	50
Borates	0	0	0	0.6	2.4	2.4	1.0	2.0	2.0	0.4	0.2
pH	8.0	8.6	8.4	8.8	9.0	8.8	9.0	9.2	9.2	9.0	9.0

TABLE 4

RELATIVE ABUNDANCE OF RODENTS PER 100 TRAP-NIGHTS (ALL DATA)[5]

Association	AC	FD	LD	A	SA	SAP	SAC	AF	SS	LSM
Ammospermophilus leucurus	0.15	0.26	1.15	0.24	–	0.41	1.03	0.15	+	+
Spermophilus beecheyi	–	+	+	–	–	–	–	–	–	–
Thomomys bottae operarius	–	–	–	–	–	–	–	–	–	+
Thomomys bottae perpes	+	+	–	–	–	–	–	–	+	+
Perognathus longimembris	2.27	1.60	1.28	0.96	0.18	0.10	0.39	0.15	–	–
Perognathus formosus	θ	0.26	1.67	–	0.56	–	–	–	–	–
Dipodomys microps	0.91	–	0.13	–	–	+	0.39	+	–	–
Dipodomys panamintinus	0.46	0.53	–	–	–	–	–	–	–	0.16
Dipodomys merriami	2.81	0.26	0.64	1.19	0.37	2.16	3.74	0.30	1.54	0.31
Dipodomys deserti	–	–	–	0.16	–	0.93	0.90	1.83	–	–
Reithrodontomys megalotis	0.08	–	–	–	–	–	–	–	1.54	0.93
Peromyscus maniculatus	0.61	–	0.38	–	–	0.82	1.80	0.46	2.85	1.40
Peromyscus crinitus	–	0.13	1.67	–	–	–	–	–	–	–
Peromyscus boylii	0.15	0.26	–	–	–	–	–	–	–	–
Onychomys torridus	0.15	–	0.13	0.08	–	–	0.13	–	0.22	–
Neotoma lepida	0.53	0.40	0.26	–	–	–	–	–	0.66	+
Microtus californicus	–	–	–	–	–	–	–	–	+	+
Mus musculus	–	–	–	–	–	–	–	–	0.88	–
Total number trap-nights	1317	752	780	1252	540	970	776	655	456	643
Total catch per 100 trap-nights	8.12	3.70	7.31	2.63	1.11	4.42	8.38	2.89	7.69	2.80

[5] A "+" indicates an observation or other record of occurrence of a species.

TABLE 5

RELATIVE ABUNDANCE OF RODENTS PER 100 TRAP-NIGHTS (SUMMER TRAPPING)[6]

Field Station #	1 (AC)	2 (FD)	3 (LD)	4 (LSM)	5 (SAP)	6 (A)	7 (A)	8 (AF)	9 (SA)	10 (SAC)	11 (SS)
Ammospermophilus leucurus	–	0.37	1.30	–	0.74	–	0.56	–	–	0.37	–
Perognathus longimembris	2.59	1.30	1.48	–	0.18	0.56	–	0.18	0.18	0.56	–
Perognathus formosus	–	0.18	2.41	–	–	–	–	–	0.56	–	–
Dipodomys microps	1.66	–	–	–	–	–	–	–	–	0.56	–
Dipodomys panamintinus	–	0.37	–	–	–	–	–	–	–	–	–
Dipodomys merriami	0.37	0.37	0.37	–	0.37	0.37	0.56	–	0.37	2.59	1.54
Dipodomys deserti	–	–	–	–	0.18	0.18	–	1.85	–	0.37	–
Reithrodontomys megalotis	–	–	–	0.93	–	–	–	–	–	–	1.54
Peromyscus maniculatus	–	–	0.56	0.93	0.18	–	–	0.18	–	0.18	2.85
Peromyscus crinitus	–	0.18	2.41	–	–	–	–	–	–	–	–
Peromyscus boylii	0.18	0.18	–	–	–	–	–	–	–	–	–
Onychomys torridus	0.18	–	0.18	–	–	0.18	–	–	–	–	0.22
Neotoma lepida	–	0.56	0.37	–	–	–	–	–	–	–	0.66
Mus musculus	–	–	–	–	–	–	–	–	–	–	0.88
Total Catch per 100 trap-nights	4.98	3.51	9.08	1.86	1.65	1.29	1.12	2.21	1.11	4.63	7.69

[6] Based upon 540 trap-nights at each Field Station, except Station 11 where 456 trap-nights were used.

Trapping was carried on for three consecutive nights at each field station (Bole 1939; Dice 1938). The traps, baited with rolled oats, were set in the afternoon of the first night. Traps were emptied and rebaited the following two mornings and afternoons. Thus, a total of 540 trap-nights was recorded for each field station, except for Station 11 where only 456 trap-nights were used. The results of quadrat trapping are shown in Table 5. Gopher traps were used to capture pocket gophers when burrows were observed.

Trapping results are recorded as the number of rodents per 100 trap-nights; these were assumed to reflect the relative abundance of rodents. Estimates of rodent populations are not attempted, but rather, a comparison of the relative abundance of each species was determined within an association and between associations.

The classification of rodents follows that of Hall and Kelson (1959). Original description and/or the latest revision of the taxa were consulted for all identifications. Specimens collected during this study were deposited in either the collections at California State University, Long Beach, or the Natural History Museum of Los Angeles County.

DESCRIPTIONS OF VEGETATION

Two distinct vegetation types composed of ten plant associations occur in the study area. The abbreviation, in parentheses, following an association name is the designation to be used throughout the text for that association.

DESERT SHRUB VEGETATION

The Desert Shrub Vegetation includes eight plant associations in this study area. It is characterized by plants that are widely spaced and adapted to xeric conditions. This community represents the major portion of the study area.

Atriplex confertifolia Association (AC).—This association covered almost all of the lower portion of what Knopf (1918) referred to as the alluvial piedmont slope of the eastern Sierra Nevada Mountains in the region of Owens Lake. On higher parts of the alluvium the rocky slopes became more prominent. Lower on the alluvium this association merged with the marshes along the lake shore. The area was dissected by the numerous washes of Carroll, Cottonwood and Ash Creeks. This association is irregularly distributed throughout the Owens Valley (Billings 1949). In general the slope gradient was about 2.5 per cent northeast. Field Station I was located in this association (Fig. 2).

Twelve species of rodents were recorded from this association (Table 4). The most abundant was *Dipodomys merriami,* followed by *Perognathus longimembris.*

Franseria dumosa Association (FD).—This association included the area above and west of AC. It merged to the south with the Larrea Association. The slope gradient at the field station was 10.8 per cent northeast. Field Station 2 was located in this association (Fig. 3).

Ten species of rodents occurred in this association (Table 4). The most abundant was *Perognathus longimembris* (Tables 4 and 5).

FIGURE 2. Field Station 1, Atriplex confertifolia Association.

Larrea Association (LD).—This association covered the southwestern portion of the study area, from about one mile south of Ash Creek to well south of Olancha. In the present study area it occurred only on the lower, more rocky slopes of the Sierra Nevada Mountains. It also occurred on the higher slopes of the Coso Mountains south of Owens Lake (outside the present study area). The slope gradient at

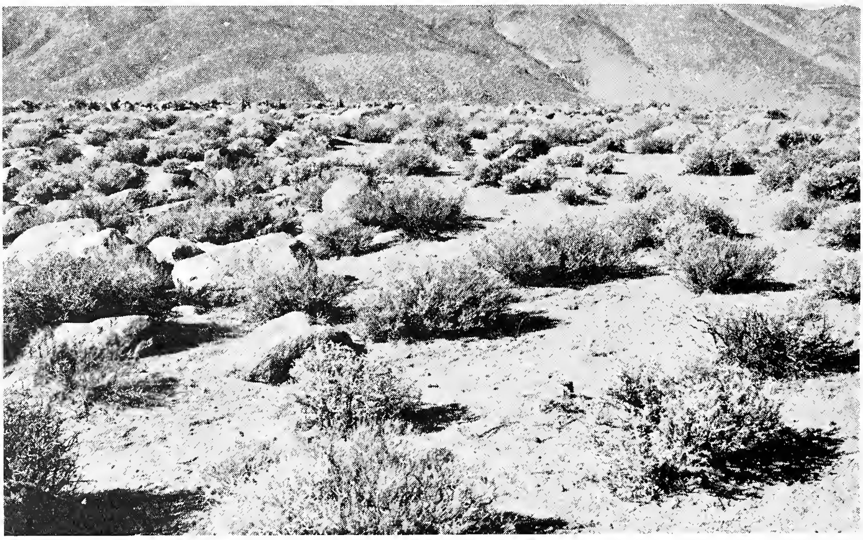

FIGURE 3. Field Station 2, Franseria dumosa Association.

the field station was 7.7 per cent southeast; in other areas it was nearly level. Field Station 3 was located in this association (Fig. 4).

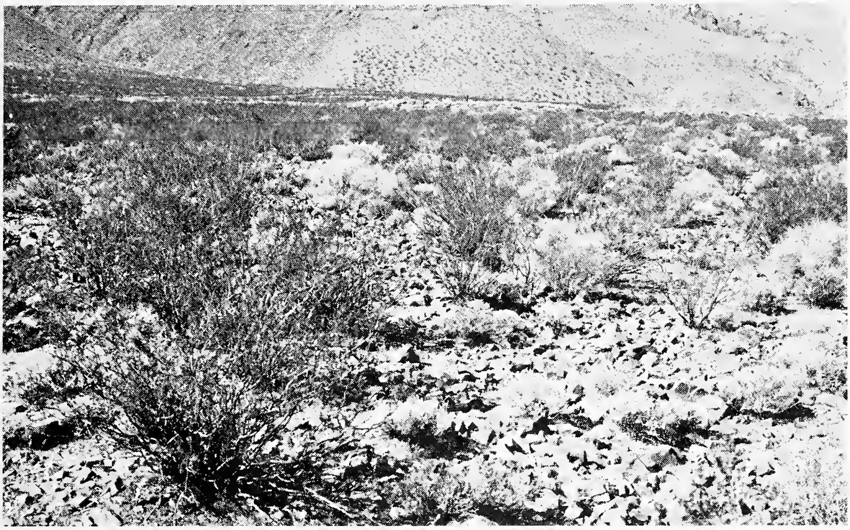

FIGURE 4. Field Station 3, Larrea Association.

In this association ten species of rodents were recorded (Table 4). The most abundant species were *Perognathus formosus* and *Peromyscus crinitus,* both occuring in about equal numbers. *Perognathus longimembris* was only slightly less abundant (Tables 4 and 5). Rodents were more numerous in this association during the summer of 1971 than in any other association.

Atriplex Scrub Association (A).—This association included most of the southern portion of the study area except the lake shore and the sand dunes areas. It merged with the creosote bush on the higher slopes of the Coso Mountains to the south. To the west it was bounded by the sand dunes. Its eastern limit was not determined, but was assumed to be on the lower slopes of the Inyo Mountains. The slope gradient at Field Station 6 is 5.6 per cent northwest, while Field Station 7 is somewhat steeper, 12 per cent northwest. Field Stations 6 and 7 are located in this association (Fig. 5).

Only five species of rodents were recorded from this association (Table 4), *Dipodomys merriami* being the most abundant. Station 6 seemed to be more productive in its rodent populations than did Station 7 (Table 5). This was probably because of the steeper slope and less dense plant cover at Station 7.

Suaeda-Atriplex Association (SA).—This association included a small area in the eastern portion of the study area, from about 2.5 miles south of Keeler to the Atriplex Scrub Association. It is part of the flood plain of the Malpais Mesa of the southern Inyo Mountains. The slope gradient was about 4 per cent west. Field Station 9 was located in this association (Fig. 6).

FIGURE 5. Field Station 6, Atriplex Scrub Association.

FIGURE 6. Field Station 9, Suaeda-Atriplex Association.

Only three species of rodents were recorded from this association (Table 4), *Perognathus formosus* being the most abundant.

Atriplex-Franseria Association (AF).—This association was irregularly distributed along the northeastern shore of Owens Lake. It merged in the north with the sand dunes and to the south with the Suaeda-Atriplex Association. For the most part, this association was found above the sand dunes on the western alluvium of

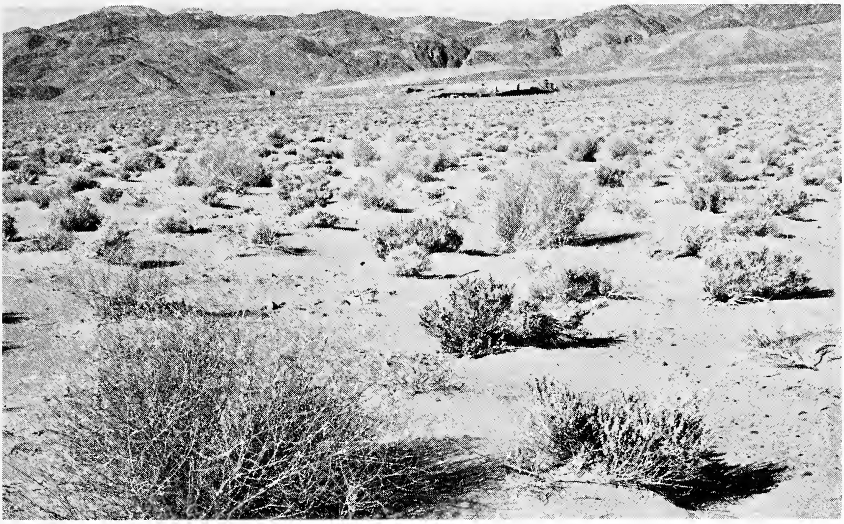

FIGURE 7. Field Station 8, Atriplex-Franseria Association.

the Inyo Mountains. In general, the slope gradient was southwest 5 per cent. Field Station 8 was located in this association (Fig. 7).

Six species of rodents occurred in this association (Table 4). The most abundant rodent was *Dipodomys deserti.*

Sarcobatus-Atriplex parryi Association (SAP).—This association occurred in the southern portion of the study area, from just east of Olancha to about the region of Keeler. It was a narrow strip, lying between the lake shore and the Atriplex Scrub Association. Its distribution was not continuous; instead, it occurred as isolated stands surrounded by other habitats. This association occurred on sand dunes and reached its optimum development about two miles east of Olancha, where the dunes may attain heights of over 50 feet above the surrounding terrain. The dunes in this area are apparently still in the process of active migration. Field Station 5 was located in this association (Fig. 8).

Six species of rodents occurred in this association (Table 4). The most abundant species was *Dipodomys merriami* followed by *D. deserti.*

Sarcobatus-Atriplex confertifolia Association (SAC).—This association occurred on the sand dunes at the northern end of Owens Lake. It was somewhat irregularly distributed along the eastern lake shore, eventually merging with the southern dunes near Keeler. These dunes are reportedly the old beach dunes of Owens Lake (Knopf 1918). They were smaller than those found at the southern end of the lake. Also, they do not appear to be actively migrating. Field Station 10 was located in this association (Fig. 9).

Seven species of rodents occurred in this association (Table 4). The same species occurred here as in the southern dunes with the addition of *Onychomys torridus.* Again, *Dipodomys merriami* was the most abundant.

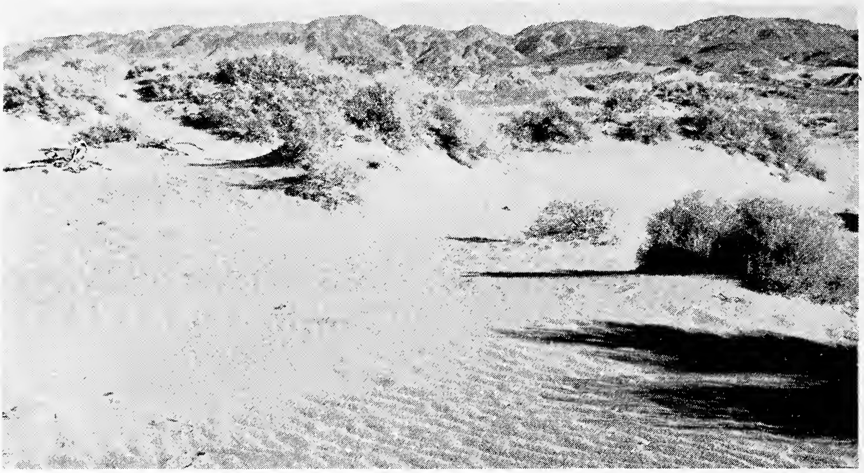

FIGURE 8. Field Station 5, Sarcobatus-Atriplex parryi Association.

FIGURE 9. Field Station 10, Sacrobatus-Atriplex confertifolia Association.

RIPARIAN VEGETATION

The Riparian Vegetation is separated into two associations. This vegetation type is characterized by plants which need abundant ground water. The main difference between the two associations was the number of trees present. The Stream Side Association contained relatively more cottonwoods and willows than did the Lake Shore Marsh.

Stream Side Association (SS).—This association reaches its optimum along the Owens River at the north end of the lake. There was also a more restricted Stream Side Association along Cottonwood Creek. Field Station 11 was located in this association (Fig. 10).

FIGURE 10. Field Station 11, Stream Side Association.

Nine species of the rodents were recorded from this association (Table 5). The most abundant was *Peromyscus maniculatus*.

Lake Shore Marsh Association (LSM).—This association was irregularly distributed around the lake. Field Station 4 was located in this association (Fig. 11).

FIGURE 11. Field Station 4, Lake Shore Marsh Association.

Eight species of rodents were recorded from this association (Table 4). One species, *Thomomys bottae,* was represented by two subspecies, *T. b. operarius* on the eastern shore, and *T. b. perpes* on the western shore of the lake. The most abundant species was *Peromyscus maniculatus* followed by *Reithrodontomys megalotis.*

ACCOUNTS OF SPECIES OF RODENTS

During the course of this study, a total of 8141 trap-nights produced 406 rodents (pocket gophers not included because of the different trapping procedures utilized). Of the 18 forms expected, I either collected or observed 17 forms. *Microtus californicus vallicola* was the only rodent not trapped or directly observed during this study.

Ammospermophilus leucurus leucurus (Merriam).—The antelope ground squirrel was the fourth most abundant rodent taken during this study, comprising 7.6 per cent of the total rodents captured. It was common throughout the study area and absent from only one association (SA Association).

Overall, the antelope ground squirrel was most abundant in the SAC Association (Table 4). During the summer of 1971, it was most abundant in the LD (Table 5), where large rocks and plants provided sufficient shelter against the summer heat. Summer activity of *A. l. leucurus* may be restricted to those areas supplying sufficient protection against extreme temperatures (Dawson 1955).

Spermophilus beecheyi parvulus (Howell).—The California ground squirrel was not taken during this study; however, visual observations were common. They were recorded from the western side of Owens Valley (Grinnell and Dixon 1919). I observed these squirrels only on the west side of Owens Valley and only in very rocky areas. They were never observed on the lower slopes of the alluvium, where large rocks are absent.

Seasons of peak activity in the study area seemed to be spring and early fall when ambient temperatures were moderate. California ground squirrels were observed in the LD and FD Associations during May 1969. They were also observed in the FD Association in early November 1968. They were not observed in February 1969, nor during the summer of 1971.

Thomomys bottae operarius Merriam.—The burrows of this subspecies of pocket gopher were quite numerous near the town of Keeler, during the summer of 1971. Surface activity of pocket gophers can be estimated from the number of burrows observed in an area (Crouch 1933). Surface activity also seems to be dependent on soil moisture (Crouch 1933; Miller 1948; Laylock 1957). The soil at Keeler was observably moister than in other areas, which probably accounted for the apparent high abundance of burrows observed.

Thomomys b. operarius was known only from the type locality—the town of Keeler on the eastern shore of Owens Lake (Merriam 1897; and Bailey 1915). During this study, specimens of *T. b. operarius* were taken at Keeler and at a locality three miles south of Keeler in sandy soils where salt grass *(Distichlis spicata)* was predominant. This was the same type of habitat that Grinnell (1933) recorded as preferred by this race of pocket gopher.

Thomomys bottae perpes Merriam.—This pocket gopher was found along the western side of Owens Valley (Bailey 1915; Grinnell 1933). The soils in this area were dry during the summer of 1971, which probably accounted for the noticeable lack of fresh burrows. Fresh burrows were observed during January, February and May, when winter rains had moistened the soils.

Pocket gophers in southwestern Utah may be restricted to areas with soils containing less than three per cent granule gravel (Hardy 1945). In the present study, burrows of *Thomomys b. perpes* were observed in the FD and AC Associations. Both of these associations have soils with over 20 per cent granule gravel.

Perognathus longimembris longimembris (Coues).—The little pocket mouse was the third most abundant rodent in the study area, 13.6 per cent of the total rodents. It was not taken during the colder months of the year, the earliest record being in late May 1969. Its latest record of occurrence was in late August 1971. It seemed unlikely that this pocket mouse could be inactive for more than a week at a time (Bartholomew and Cade 1957). Its absence from winter trapping records in the present study may have been the result of the irregularity of winter trapping periods. Specimens of *Perognathus l. longimembris* have been taken in all seasons of the year in other areas (Dean Harvey, personal communication). Specimens at the Los Angeles Museum have recorded dates of capture as late as November 23 (Cabazon, Riverside Co., California) and as early as April 3 (Mohave, Kern Co., California). Kenagy (1973b) found *P. l. longimembris* to be less active above ground in winter, but quite active within its burrows.

Perognathus l. longimembris occurred in greatest numbers in the AC Association (Tables 4 and 5). This was also recorded for *P. l. longimembris* in western Utah (Fautin 1946). *P. l. longimembris* in southwestern Utah was reported to prefer non-gravelly soils, soils with less than 10 per cent granule gravel (Hardy 1945). This was not found to be the case with *P. l. longimembris* of the Owens Lake region, where they occurred in greatest abundance on the gravelly soils (22.6 per cent granule gravel) of the AC Association.

Perognathus l. longimembris occurred in eight of the eleven field stations (Table 5), being absent from Stations 4 and 11 (Riparian Community) and Station 7 (A Association). It was present at Station 6 of the A Association. Steep slopes may be a limiting factor in the distribution of this species (Hardy 1945). Its absence from Station 7 (slope gradient of 12 per cent) and presence at Station 6 (slope gradient of 5.6 per cent) may be because of the steeper slope at Station 7.

Perognathus formosus mohavensis Huey.—The long-tailed pocket mouse was taken in only three associations (Table 4), all of which were in rocky habitats. This is in accord with what other authors have recorded as the preferred habitat for this species (Hardy 1945; Fautin 1946; Hall 1946).

Perognathus f. mohavensis was taken along with *P. l. longimembris* in the three associations. In two of the associations (L and SA), *P. f. mohavensis* was the more abundant of the two. This may be because more rocks were present at these two associations. In the FD Association, *P. l. longimembris* was more abundant than *P. f. mohavensis;* because there are relatively few rocks at this association, it is probably a marginal zone for the occurrence of *P. f. mohavensis.*

Trapping records were not complete enough for any generalizations concerning seasonal activity of this pocket mouse. They were absent from the LD Association in late May 1969 (212 trap-nights), this association producing the largest numbers of *P. f. mohavensis* during the summer of 1971. *P. f. mohavensis* was recorded as being equally active during all seasons in the Providence Mountains of California (Johnson, Bryant and Miller 1948).

Dipodomys microps microps (Merriam).—The chisel-toothed kangaroo rat was taken in all associations studied in western Utah by Fautin (1946) but seemed to prefer the shadscale and tetradymia associations. In southwestern Utah, it preferred gravelly or sandy soils and tended to shun rocky soils (Hardy 1945). In the present study, *Dipodomys m. microps* was most abundant on the gravelly soils of the AC Association (Tables 4 and 5), but was also taken in lesser numbers in the rocky LD Association and the sandy SAC Association. It is likely that the AC Association, with its gravelly soils, presents the optimum conditions for its existence. Recently, Kenagy (1972 and 1973a) had demonstrated the importance of saltbush *(Atriplex confertifolia)* in the diet of *D. m. microps* in Owens Valley.

Dipodomys panamintinus mohavensis (Grinnell).—The Panamint kangaroo rat was not abundant in the two associations where it occurred (Tables 4 and 5). It has been reported to prefer gravelly soils (Grinnell 1933; Johnson et. al. 1948). During the present study, it was taken on gravelly soils and in rocky areas, but it was absent from sandy soils. It was taken once from the edge of a LSM Association north of Olancha, probably as the result of wandering from a more typical habitat above the marsh.

Dipodomys p. mohavensis was reported to be absent from the east side of Owens Valley (Elliot 1904). This was also noted during the present study. It has been recorded from apparently sandy soils at the southern end of Owens Lake in association with *D. merriami* and *D. deserti* (Grinnell 1922). It may occur only marginally on sandy soils, where they merge with gravelly soils, as in the area at the southern end of the lake. If *D. p. mohavensis* does indeed tend to shun sandy soils, then its absence from the east side of Owens Valley can be explained, because soils in that area are predominantly sandy.

Dipodomys merriami merriami (Mearns).—Merriam's kangaroo rat was present in all plant associations studied (Table 4). It was most abundant in the SAC and AC Associations. Overall, it was the most abundant rodent in the study area, 30.5 per cent of the rodents being of this species. *D. m. merriami* was found to be the most widely distributed and abundant rodent in southwestern Utah (Hardy 1945). In southern Arizona, the distribution of *D. m. merriami* coincided with the distribution of creosote bush (Reynolds 1958), although it was present in other situations as well.

During the summer of 1971, *D. m. merriami* was about equally abundant in eight of the field stations, while being considerably more numerous at Station 10 (Table 5). It was absent from Stations 4 and 8 during the summer, but it was present in these associations during other trapping periods.

During the colder months of the year, *D. m. merriami* was one of the two most abundant rodents; *Peromyscus maniculatus* was the other. During the summer, however, its abundance was at a minimum, as was that of *P. maniculatus*. Possibly this was the result of the greater activity of the two species of *Perognathus*. In southern Arizona, *D. m. merriami* reached its highest densities in July (Reynolds 1958).

Dipodomys deserti deserti Stephens.—The desert kangaroo rat was reported to occur only where deposits of wind-blown sand are deep and easily workable (Grinnell 1914; Huey 1951; Durrant 1952). This was also apparent in the present study.

Dipodymus d. deserti was most abundant at Station 8, the AF Association (Tables 4 and 5) that had sandy soils. Overall, *D. d. deserti* was about twice as numerous in the AF Association as in the two associations found on the sand dunes; within the AF Association, it was about ten times more abundant than the other two rodents during the summer (Table 5).

Reithrodontomys megalotis megalotis (Baird).—In the Owens Lake region, *Reithrodontomys m. megalotis* was most abundant in the Riparian Vegetation (Table 4). It was taken only once in the Desert Shrub Vegetation (AC Association) where the trap-line was set about 100 yards from the SS Association at Cottonwood Creek. The SS Association had about one-half again as many harvest mice as the LSM Association (Tables 4 and 5).

The western harvest mouse is not confined to any one type of habitat, but did seem to prefer grassy areas near water (Long 1940; Hall 1946; Hooper 1952). It could be that the distribution of this mouse depends upon the presence of heavy vegetation (Hardy 1945).

Peromyscus maniculatus sonoriensis (Le Conte).—The deer mouse was the second most abundant rodent, 14.3 per cent of the rodents being of this species. It was absent from only three associations (Table 4); upon further study, it will probably be found to occur in them as well. It was most abundant in the Riparian Vegetation and in the SAC Association of the Desert Shrub Vegetation.

Its absence from the AC Association in the summer of 1971 coincided with the high abundance of *Perognathus longimembris* (Table 5). Whether this was the result of competition between the two species cannot be determined from present data.

Deer mice are usually one of the most abundant mammals in areas where they occur (Hall 1946; Manville 1949). However, in desert situations, it is usually outnumbered by heteromyid rodents (Baker 1968). Most species of *Peromyscus* usually have well defined habitat preferences, *P. m. sonoriensis* being the least restricted of all (Grinnell and Orr 1934; Baker 1968).

Peromyscus crinitus stephensi Mearns.—The canyon mouse was taken in only two associations, both of which were in rocky habitats (Table 5). It was most abundant in the LD Association, occurring in numbers equal to that of *Perognathus formosus* (Table 5), which was also restricted to rocky habitats. The canyon mouse is reportedly restricted to rocky habitats (Hardy 1945; Fautin 1946; Hall 1946).

Peromyscus boylii rowleyi (Allen).—Only four specimens of *Peromyscus b. rowleyi* were taken, two in the FD Association and two in the AC Association. The occurrence of this mouse on the desert floor was unexpected. However, they were quite numerous in nearby Cottonwood Canyon (Matson 1974). The two associations where *P. b. rowleyi* occurred were on the flood plain of Cottonwood Creek. It is possible that these mice moved down the canyon to the desert floor in response to population pressures. The brush mouse was reported to prefer areas of heavy vegetation (Bailey 1932; Grinnell 1933; Jameson 1951).

Onychomys torridus clarus Hollister.—During the present study, six specimens of *Onychomys t. clarus* were taken, five in the Desert Shrub Vegetation and one in the Riparian Vegetation (Table 4). They were found to occur on rocky, gravelly and sandy soils. There were no apparent differences in the amount of cover necessary, for they were taken at Station 6, with sparse vegetation, and at Station 11, with heavy vegetation. The southern grasshopper mouse in southwestern Utah seemed to prefer gravelly soils; however, there were too few data to make any generalizations (Hardy 1945). In New Mexico, the southern grasshopper mouse presumably preferred sandy soils (Bailey 1932). Grasshopper mice are reported to be primarily carnivorous, 90 per cent of their diet consisting of animal matter (Bailey and Sperry 1929). The predatory habits of this species may require it to forage over large areas with little or no regard for soil or plant types.

Neotoma lepida lepida Thomas.—The desert wood rat was taken in four associations and recorded (nests observed) for a fifth (Table 4). It was most abundant in the SS and AC Associations where rocks were not present, but was also taken in smaller numbers from two associations where large rocks were numerous (LD and FD Associations). In the Owens Lake region, the presence of rocks did not seem to be a requirement for the occurrence of *Neotomal. lepida.* The desert wood rat was reported to be most abundant in rocky habitats; but occurred in other situations as well (Hardy 1945; Fautin 1946; Hall 1946). It is probable that its occurrence is determined by the presence of adequate shelter material, vegetation or rocks.

Microtus californicus vallicola Bailey.—The California meadow mouse was not taken during this study. However, one specimen from the south shore of Owens Lake (LSM Association) is in the Bird and Mammal Museum, California State University at Long Beach. In addition, runways were observed in both associations of the Riparian Vegetation. In the Owens Valley, *Microtus c. vallicola* was reported to be especially abundant along the Owens River and its tributaries (Elliott 1904; Grinnell 1933). *M. c. vallicola* seemed to be restricted to the Riparian Vegetation.

Mus musculus Linnaeus.—The house mouse was taken in only one association (SS) that was at least five miles from the nearest human habitation. The house mouse was reported to be most commonly found in or near human dwellings; occasionally it occurred far from them (Ingles 1965). This species probably occurs in other associations within the study area, especially in areas where human dwellings are found, as at Keeler and Olancha.

DISCUSSION

DISTRIBUTION OF RODENTS

Soil texture has been considered to be a major factor influencing the local distribution of some small mammals (Hardy 1945; Fautin 1946 et. al.). This theory has recently been questioned by Rosenzweig and Winakur (1969:561), who ". . . could find no patterns of mammal density or diversity using soil depths or soil particle size''. They found structural aspects of the vegetation to be a major factor in the distribution of small mammals. I find that both soil texture and plant cover (or volume) are important. Three species *(Dipodomys deserti, Perognathus formosus* and *Peromyscus crinitus)* are apparently limited in their respective distributions by soil type. *D. deserti* is restricted to sandy soils, the latter two to rocky soils.

Though the data are not conclusive, there does seem to be a relation between relative abundance of some rodent species and soil texture. For example, *Dipodomys microps* shows a higher relative abundance in gravelly soils than other areas where it occurs; *Perognathus longimembris* was also more abundant on gravelly soils.

Structural aspects of vegetation was apparently a limiting factor for rodents normally inhabiting Riparian situations *(Mus musculus, Microtus californicus* and *Reithrodontomys megalotis).* Vegetation may also influence relative abundance of rodent species; for example, *Peromyscus maniculatus* was more abundant in the heavy vegetation of the Riparian than in Desert habitats. *Neotoma lepida* was apparently restricted to those areas where structural materials were available for shelter.

RODENT SPECIES DIVERSITY

Species diversity can be expressed in two main ways (MacArthur 1965): 1. simple species counts; 2. some method which takes into account the abundance of each species. The latter is usually considered to be a better method, because it differentially ranks species into importance classes. Thus, a rare or accidental species is not given as much importance as a more common species. Currently the most widely used index of diversity, derived by Shannon (1948), is $H = - \Sigma\, p_i \log p_i$. Utilization of H as a diversity index assumes a fairly reliable estimate of relative abundance. Pianka (1966) has pointed out that simple species counts may prove as useful as H, especially when there are seasonal and annual fluctuations in abundance.

Since my data are not sufficiently representative of each season, I consider the simple species count to be a more reliable index of diversity than H. I assume the total number of rodent species observed in each plant association is indicative of the rodent fauna of that association. Further study in some cases may add additional species to an association, but that should not significantly affect the general results of this study.

The number of rodent species was compared with plant species diversity from Table 1 and two aspects of vegetative spatial heterogeneity: per cent cover area and plant volume diversity. Plant volume diversity was determined in the same manner as described by Pianka (1966), utilizing H (Table 1). Only data from the Desert Vegetation were compared.

No apparent relationship exists between plant species diversity and the number of rodent species. This is essentially the same result as shown by Rosenzweig and Winakur (1969) for rodents in desert situations, MacArthur and MacArthur (1961) for birds and Pianka (1966) for desert lizards.

The number of rodent species is positively correlated with both per cent cover area (Fig. 12) and plant volume diversity (Fig. 13). Reasons for these apparent relationships are not readily observable. One can assume increased spatial heterogeneity

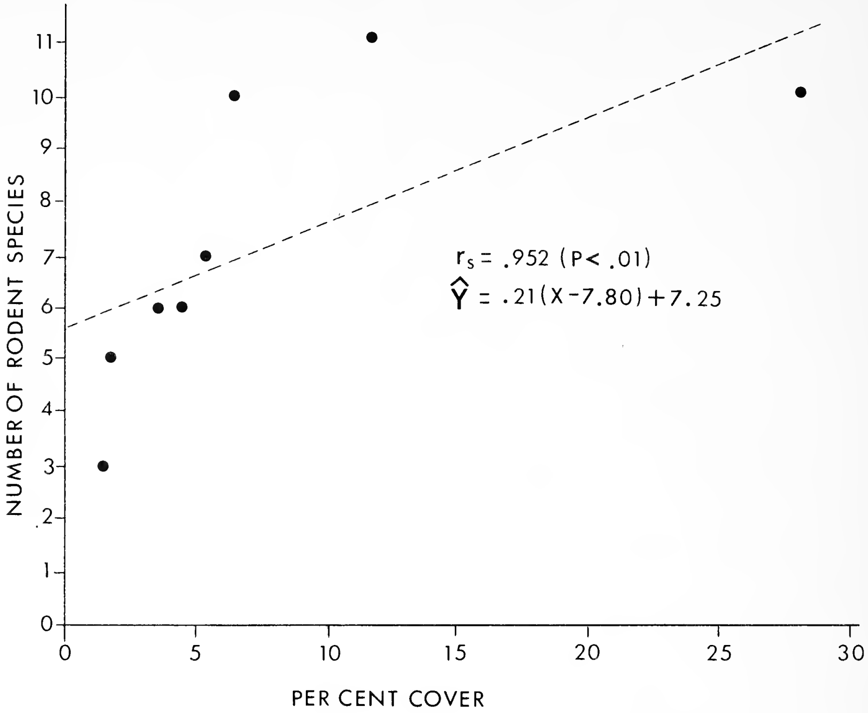

FIGURE 12. Number of rodent species versus per cent of plant cover. Spearman rank correlation coefficient (r_s) and linear regression equation are indicated.

(as shown by plant volume diversity) increases the number of "micro-habitats" available to the rodents. This increased habitat complexity would allow more rodent species to coexist.

FAUNAL RELATIONSHIPS BETWEEN ASSOCIATIONS

The faunal relationships that exist between various plant associations can be expressed by the following formula, utilized by Long (1963):

$$C(N_1 + N_2)(100)/2N_1N_2 = \text{percentage}$$

where C = the kinds common to both associations, N_1 = the number of kinds in one association, and N_2 = the number of kinds in the other association. This formula was intended primarily for comparing large physiographic regions. However, it can be utilized with good results on a smaller scale. Care must be taken when interpreting the results of this formula for a small geographic area. The mobility of small mammals will tend to obscure the faunal relationships between adjacent plant associations. A species will occasionally occur in an association it normally avoids if its preferred habitat is nearby; for example, *Dipodomys panamintinus* was recorded once from the LSM Association, which was close to the AC Association, its "preferred habitat". Situations such as this will tend to increase the faunal relationship

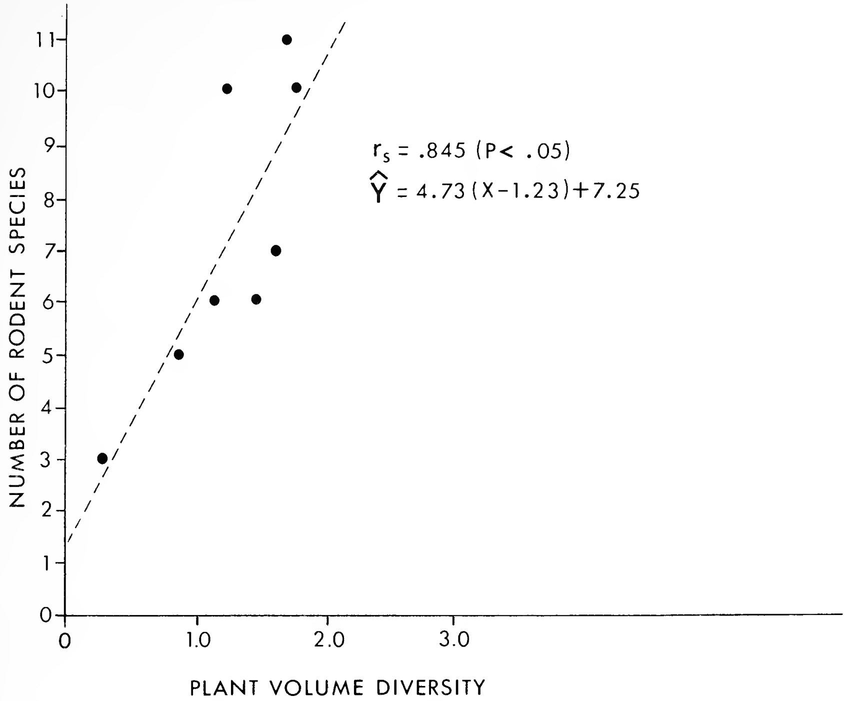

FIGURE 13. Number of rodent species versus plant volume diversity. Spearman rank correlation coefficient (r_s) and linear regression equation are indicated.

values. The results of faunal relationship analysis are given in Table 6 and graphically represented in figure 14.

TABLE 6

FAUNAL RELATIONSHIP[7]

	FD	LD	SA	A	SAP	SAC	AF	SS	LSM
AC	73	73	40	57	62	68	62	68	68
FD		70	65	45	40	36	40	42	53
LD			65	60	67	73	67	53	42
SA				53	50	48	50	22	22
A					73	86	73	47	31
SAP						93	100	42	42
SAC							92	51	38
AF								42	42
SS									78

[7] See text for explanation.

The greatest difference (lowest values) occurred between the Desert Shrub Vegetation (except SA) and the Riparian Vegetation. There are high values, indicating

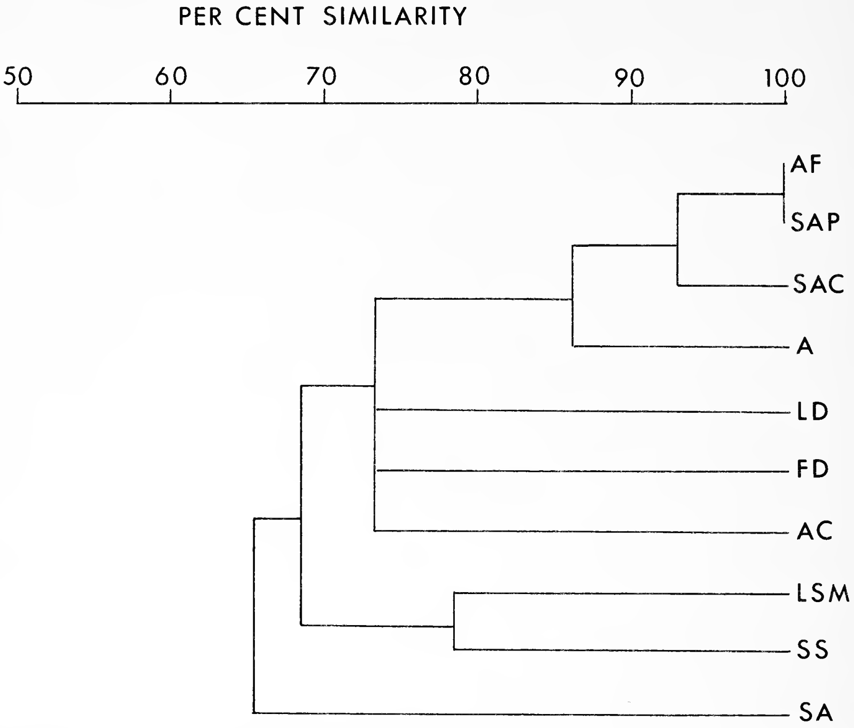

FIGURE 14. Similarity phenograms of rodent species in the plant associations (see text for explanation).

close relationships, between the AC Association and the two associations of the Riparian Community. This is probably caused by their proximity to one another.

Highest relationship values occurred in the three plant associations having sandy soils: SAP, SAC and AF Associations. Associations that occurred on rocky soils—FD, LD and SA—did not show such high values.

The greatest differences within the Desert Shrub Community occurred between associations found on different soil types (sandy versus rocky soils). The LD Association was an exception, showing a high relationship to associations with sandy soils.

The two associations occurring on gravelly soils (AC and A) had a low faunal relationship. This is probably because the A Association was the poorest producer of rodents.

The two associations of the Riparian Community showed a high faunal relationship, as would be expected.

BIOGEOGRAPHICAL COMMENTS

The 16 native species of rodents inhabiting the Owens Lake Region do not show the same ecotonal relationships as do the plants (see introductory paragraph).

Most species are of widespread occurrence in both northern and southern deserts. However, inspection of range maps in Hall and Kelson (1959) shows most of the species have their greatest distribution south of Owens Valley and may have invaded the valley from the south.

Two species, *Dipodomys microps* and *Peromyscus crinitus,* have more extensive ranges east and north of the valley and may have invaded from those directions.

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LITERATURE CITED

BAILEY, V. 1898. Descriptions of eleven new species and subspecies of voles. Proc. Biol. Soc. Washington, 12:85–90.

________. 1915. Revision of pocket gophers of the genus *Thomomys*. N. Amer. Fauna, 39:1–136.

________. 1932. Mammals of New Mexico. N. Amer. Fauna, 53:1–412.

BAILEY, V. AND C.C. SPERRY. 1929. Life history and habits of grasshopper mice, genus *Onychomys*. U.S.D.A. Tech. Bull., 145:1–20.

BAKER, R.H. 1968. Habits and distribution. pp. 98–126 *in* Biology of *Peromyscus* (Rodentia), J. A. King ed., Special Publ. no. 2, Amer. Soc. Mamm. 593 p.

BARTHOLOMEW, G. A. AND T. J. CADE. 1957. Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. J. Mamm., 38:60–72.

BILLINGS, W.D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. Amer. Midl. Nat., 42:87–109.

BOLE, B.P. 1939. The quadrat method of studying small mammal populations. Sci. Publ. Cleveland Mus. Nat. Hist., 5:15–77.

BROWN, J.H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology, 54:775–787.

BROWN, J.H. AND G.A. LIEBERMAN. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology, 54:788–797.

CAHALANE, V.H. 1941. A trap-removal census study of small mammals. J. Wildl. Manag., 5:42–67.

CLEMENTS, F.E. 1920. Plant indicators: the relation of plant communities to processes and practice. Carnegie Inst. Washington Publ., 290:1–388.

CROUCH, W.E. 1933. Pocket gopher control. U.S.D.A. Farmers Bull., 1709:1–20.

DAWSON, W.R. 1955. The relation of oxygen consumption to temperature in desert rodents. J. Mamm., 36:543–553.

DICE, L.R. 1938. Some census methods for mammals. J. Wildl. Manag., 2:119–130.

________. 1943. The biotic provinces of North America. Univ. Michigan Press, Ann Arbor, Mich., 78 p.

DURRANT, S. D. 1952. Mammals of Utah, taxonomy and distribution. Univ. Kansas Publ., Mus. Nat. Hist., 6:1–549.

ELLIOT, D. G. 1903. Descriptions of twenty-seven apparently new species and subspecies of mammals. Field Columb. Mus., Publ. 87, Zool. Ser., 3:239–261.

————. 1904. Catalogue of mammals collected by E. Heller in southern California. Field Columb. Mus., Publ. 91, Zool. Ser., 3:271–321.

FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr., 16:251–310.

GALE, H. S. 1915. Salines in the Owens, Searles, and Panamint basins, southeastern California. U.S. Geol. Sur. Bull., 580:251–323.

GRINNELL, J. 1914. An account of the mammals and birds of the lower Colorado Valley with especial reference to the distributional problems presented. Univ. California Publ. Zool., 12:51–294.

————. 1922. Geographical study of the kangaroo rats of California. Univ. California Publ. Zool., 24:1–124.

————. 1933. Review of the recent mammal fauna of California. Univ. California Publ. Zool., 40:71–234.

GRINNELL, J. AND J. DIXON. 1919. Natural history of the ground squirrels of California. Monthly Bull. State Comm. Hort. (Sacramento, California), 7:597–708.

GRINNELL, J. AND R. T. ORR. 1934. Systematic review of the californicus group of the rodent genus *Peromyscus*. J. Mamm., 15:210–220.

HALL, E. R. 1946. Mammals of Nevada. Univ. California Press, Berkeley, California, 710 p.

HALL, E. R. AND F. H. DALE. 1939. Geographic races of the kangaroo rat, *Dipodomys microps*. Occas. Pap. Mus. Zool., Louisiana St. Univ., 4:47–63.

HALL, E. R. AND K. R. KELSON. 1959. The mammals of North America. Ronald Press Co., New York, 2 vols. 1083 p.

HARDY, R. 1945. The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecol. Monogr., 15:71–108.

HOLLISTER, N. 1913. Three new subspecies of grasshopper mice. Proc. Biol. Soc. Washington, 26:215–216.

————. 1914. A systematic account of the grasshopper mice. Proc. U.S. Nat. Mus., 47:427–489.

HOOPER, E. T. 1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool., Univ. Michigan, 77:1–255.

HUEY, L. M. 1951. The kangaroo rats *(Dipodomys)* of Baja California, Mexico. Trans. San Diego Soc. Nat. Hist., 11:205–256.

INGLES, L. G. 1965. Mammals of the Pacific States. Stanford Univ. Press, Stanford, California, 506 p.

JAEGAR, E. C. 1941. Desert wildflowers. Stanford Univ. Press, Stanford, California, 322 p.

JAMESON, E. C., JR. 1951. Local distribution of white-footed mice, *Peromyscus maniculatus* and *Peromyscus boylei*, in the northern Sierra Nevada, California. J. Mamm., 32:197–203.

JOHNSON, D. H., M. D. BRYANT AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. Univ. California Publ. Zool., 48:221–376.

KENAGY, G. J. 1972. Saltbush leaves: excision of hypersaline tissue by a kangaroo rat. Science, 178:1094–1096.

————. 1973a. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology, 54:1201–1219.

————. 1973b. Adaptations for leaf eating in the Great Basin kangaroo rat, *Dipodomys microps*. Oecologia, 12:383–412.

KNOPF, A. 1918. A geologic reconnaissance of the Inyo Range and eastern slope of the southern Sierra Nevada. U.S. Geol. Sur., Prof. Paper 110.

LAYLOCK, W. A. 1957. Seasonal periods of surface inactivity of the pocket gopher. J. Mamm., 38:132–133.

LIDICKER, W. Z., JR. 1960. An analysis of intraspecific variation in the kangaroo rat *Dipodomys merriami*. Univ. California Publ. Zool., 67:125–218.

LONG, C. A. 1963. Mathematical formulas expressing faunal resemblance. Trans. Kansas Acad. Sci., 66:138–140.

LONG, W. S. 1940. Notes on the life histories of some Utah mammals. J. Mamm., 21:170–180.

MACARTHUR, R. H. 1965. Patterns of species diversity. Biol. Rev. 40:510–533.

MACARTHUR, R. H. AND J. MACARTHUR. 1961. On bird species diversity. Ecology, 42: 594–598.

MANVILLE, R. H. 1949. A study of small mammal populations in northern Michigan. Misc. Publ. Mus. Zool., Univ. Michigan, 73:1–83.

MATSON, J. O. 1974. Notes on the arboreal activities of *Peromyscus boylii* in Inyo County, California. Bull. So. California Acad. Sci., 73:51–52.

MERRIAM, C. H. 1894. Preliminary descriptions of eleven new kangaroo rats of the genera *Dipodomys* and *Perodipus*. Proc. Biol. Soc. Washington, 9:109–116.

________. 1897. Descriptions of eight new pocket gophers of the genus *Thomomys* from Oregon, California, and Nevada. Proc. Biol. Soc. Washington, 11:213–216.

________. 1898. Life zones and crop zones. U.S.D.A., Biol. Sur., Bull. no. 10:1–79.

MILLER, M. A. 1948. Seasonal trends in burrowing of pocket gophers *(Thomomys)*. J. Mamm., 29:38–44.

MUNZ, P. A. AND D. D. KECK. 1959. A California flora. Univ. California Press, Berkeley and Los Angeles, 1681 p.

PIANKA, E. R. 1966. Convexity, desert lizards and spatial heterogeneity. Ecology, 47:1055–1059.

REYNOLDS, H. G. 1958. The ecology of the Merriam kangaroo rat on the grazing land of southern Arizona. Ecol. Monogr., 28:111–127.

ROSENZWEIG, M. L. AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology, 50:558–572.

SCHUMACHER G., ed. 1962. Deepest valley. Vail-Ballou Press, Inc., Sierra Club, San Francisco, California, 206 p.

SHANNON, C. E. 1948. The mathematical theory of communication. pp. 3–91 *in* The mathematical theory of communication. Shannon and Weaver, eds., Univ. Illinois press, Urbana. 117 pp.

SPRAGUE, M. 1941. Climate in California. pp. 783–797 *in* Climate and man, U. S. D. A. Yearbook, 1941:1–1228.

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COMMENTS ON BATS NEWLY RECORDED FROM COSTA RICA

By ANDREW STARRETT

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COMMENTS ON BATS NEWLY RECORDED FROM COSTA RICA[1]

By Andrew Starrett[2]

Abstract: *Micronycteris nicefori, M. brachyotis,* and *Diphylla ecaudata* are reported for the first time from Costa Rica, and the ranges of these species are summarized. The molt pattern of *M. nicefori* is described and the two color phases of this species are explained on the basis of an apparent annual molt-hair discoloration sequence.

INTRODUCTION

In 1970 and 1971, more than 55 species of bats were collected in Costa Rica by students working in courses under the program of the Organization for Tropical Studies (OTS). Three, which are new to the recorded fauna of Costa Rica, are reported here. They were taken on the Osa Peninsula, Provincia de Puntarenas, in 1970, and at Finca Jiménez (Ministerio de Agricultura y Ganaderia, Estación Experimental "Finca Jiménez Nuñez"), Prov. Guanacaste, in 1971. Also included are specimens of two of these species which were collected at Finca La Pacífica, Prov. Guanacaste, by Theodore H. Fleming, and at Finca Jiménez, by Thomas B. Keyse, during the course of separate projects in 1971 and 1972. The specimens are now in collections at the Natural History Museum of Los Angeles County (LACM), the Museum of Southwestern Biology, University of New Mexico (MSB) and the University of Missouri, St. Louis (THF).

All measurements of specimens are in millimeters. Capitalized Forest Formation designations are those of L. R. Holdridge (Tosi 1969).

The sites of capture for the specimens from Finca Jiménez were in riparian forest along the Río Higuerón. Both Finca Jiménez and Finca La Pacífica are in the lowland Pacific Tropical Dry Forest region of western Costa Rica; the locality on the Osa Peninsula is in lowland Pacific Tropical Wet Forest, some 260 km to the southeast.

CAPTURES AND COMMENTS

Micronycteris nicefori Sanborn.—Two adult males were caught by O. T. S. students in nets set across the Río Higuerón (elev. 10 m) at Finca Jiménez. One was taken on the night of April 21-22, 1971, during the dry season when the river bed was for the most part dry; the second was caught on June 8, 1971, in the early part of the rainy season when the river was flowing. Three additional adult males were

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caught by Thomas B. Keyse, in May and June 1972, in the forest on the south side of the same river, not far from the place of capture of the first two.

In all essential characters and most measurements, the specimens from Costa Rica agree closely with those given in Sanborn's description of the species. In the original description, Sanborn (1949) indicated that his series of five specimens (in alcohol) showed "a gray and a red phase," the holotype being "near Olive Brown above" and the "darkest specimen near Walnut Brown above." He also mentioned "a faint light gray line" on the lower back of all specimens. No light gray line is present on any of the specimens from Costa Rica, and this character appears to be variable over the range of the species (Goodwin and Greenhall 1961; Ojasti 1966). The range of color in the five males from Costa Rica shows variation which apparently represents a molt and discoloration cycle similar to that described by Smith (1972) for *Pteronotus parnellii*. The specimens of *Micronycteris nicefori*, which were all taken from essentially the same locality on five different dates from late April to early June in two successive years, range from a "red phase" (April 22) through a reasonably date-correlated molt progression to a "gray phase" (June 8). One specimen was collected on a later date (June 30) and showed an active intermediate molt condition. The red phase pelage, which is somewhat more orange than Sanborn's "Walnut Brown" specimen (if the two copies of Ridgway 1912, which I consulted, and which differ one from the other in some colors, show the same colors seen in the copy used by Sanborn in 1949), seems to represent chemically altered coloration of the dark olive brown fur attained in what apparently is the single annual molt which takes place, in Costa Rica at least, from April through June or July. Sanborn's specimens (1 ♂, 4??) were collected in January and represent a similar series which would indicate an earlier molt for this species in Columbia. Five specimens caught in August in Amazonian Peru were "olivâtre" (Pirlot 1968), and three taken in Venezuela, a male and female in November and another female in May, were described as "marrón anaranjada" (Ojasti 1966, using Villalobos and Villalobos 1947, color designations). That these specimens represent the olive-brown and red color phases seems indicated, but whether they support the proposed interpretation of color phases in this species, perhaps modified by local factors and/or reproductive condition (Smith 1972), cannot be determined for certain with the limited information available. A relationship between reproductive state and molt pattern is suggested by the fact that in the specimens from Costa Rica which show hair replacement in progress, the chest gland is prominent and presumably active (representing reproductive activity?), whereas in the animal from June 8, which shows no remnant of red phase hair, the gland is not discernible from superficial examination. The timing of male activity is in line with that suggested by data presented by Fleming, Hooper and Wilson (1972) for other species in the same general locality.

In the Costa Rican series, dorsal molt progression begins around the eyes (already brown in the April specimen), then proceeds mainly by a gradual intermixture of new hairs and subsequent sloughing of old hairs over the head, and then from the shoulders and interscapular area posteriad, with the fur of the sides and middle back leading the progression. Ventrally, the molt pattern is more clearly defined with a loss-replacement sequence which starts below the ears and on the mid-abdominal area (light gray-brown hairs characteristic of gray phase ventral pelage present in the under-ear area and a few small patches on the abdomen in the April specimen), then expands laterad and posteriad from the throat and mid-venter, the orange fur under the wings between humerus and femur being the last to go. Especially noticeable dorsally is a frosted appearance caused by hairs with silvery-white tips (not noted by Sanborn 1949) which gradually change to a silvery-yellow in the red phase. During the molt sequence these hairs appear to be lost first, leaving dark-tipped red hairs that give the pelage a dull, worn look. In some areas the new silver-tipped brown hairs become apparent before the dull red pelage is gone, and closer examination shows the less obvious new darker-tipped brown hairs coming in as well. This intermixing of red and brown hairs gives the pelage an intermediate red-brown tone which suggests at first glance a third "color phase."

Selected measurements of the Costa Rica specimens are: (LACM 38542, 38543; MSB 32537, 32538, 32539) forearm, 36.4, 38.2, 38.7, 35.1, 37.5; (LACM specimens) metacarpal III, 33.3, 34.5; metacarpal IV, 30.8, 31.5; metacarpal V, 31.7, 33.0; (LACM 38543) greatest length of skull, 20.9; condylobasal length, 18.6; zygomatic width, 9.5; postorbital constriction, 4.5; maxillary tooth row, 7.4; width across upper canines, 3.4; width across M^3-M^3, 6.3.

Since Sanborn described *Micronycteris (Trinycteris) nicefori* from northern Colombia in 1949, it has been reported from Trinidad (Goodwin and Greenhall 1961), Guyana (Hill 1964), Venezuela (Ojasti 1966), Panama (Handley 1966) and the upper Amazon of Peru (Pirlot 1968). The locality nearest to the Costa Rican site reported here is Fort Gulick, Canal Zone (Handley 1966:760) some 600 km to the southeast.

Micronycteris brachyotis (Dobson) (=*M. platyceps* Sanborn).—An adult female (forearm 43) was caught in a net placed across the dry bed of the Río Higuerón, Finca Jiménez, on the night of April 21-22, 1971, and then banded and released. Three members of this species were also banded and released, in 1970-1971, at Finca La Pacífica (approx. elev. 40 m), some 20 km NNE of Finca Jiménez (Fleming et al. 1972), and two more, an adult male (forearm 41.0) and a weanling juvenile male (forearm 28) from the same locality, were saved as a skin and skull and alcoholic specimen, respectively (THF).

The yellow-throated bat was previously known from a scattering of localities in Oaxaca and Chiapas, Mexico (Davis et al 1964; Schaldach 1964), Guatemala (Jones 1966; Rick 1968), Nicaragua (Sanborn 1949), Panama (Handley 1966), Colombia (Marinkelle and Cadena 1972), Venezuela (Sanborn 1949), French Guiana (Sanborn 1949; Cayenne, type locality of *Schizostoma brachyote* Dobson), Trinidad (Sanborn 1949; Goodwin and Greenhall 1961; Guanapo, type locality of *Micronycteris (Lampronycteris) platyceps* Sanborn) and Brasil (Goodwin and Greenhall 1961: 231).

Diphylla ecaudata Spix.—An adult female was netted, on August 4, 1970, near the Tropical Science Center building and not far from the airstrip for Rincón de Osa. The net in which the animal was captured was set in relatively undisturbed forest, some 25 m from the Río Agua Buena (approx. elev. 15 m).

This species is known from a scattering of localities ranging from southern Texas (Reddell 1968) through Middle and South America to southern Brasil (Cabrera 1957; Hall and Kelson 1959; Villa-R. 1966). In Central America, it has been recorded previously from every country except Belize and Costa Rica (Goodwin 1942b; Burt and Stirton 1961; Handley 1966; Jones 1966; Jones et al 1971). Nowhere does it seem to be abundant, apparently being less influenced by concentrations of domestic animals than is *Desmodus*. It also appears to have more of a preference for humid environments than does the latter, being associated, in Central America, at least, with lowland evergreen forest.

The forearm measurement (57.2) of the Costa Rican specimen (LACM 33180) falls in the middle of the range for females given by Burt and Stirton (1961). I prefer to follow these authors (also Handley 1966, and Jones et al 1971) in considering *Diphylla ecaudata* monotypic, even though Ojasti and Linares (1971) have renewed support for the separate recognition of Middle American populations (based on a comparison of measurements of South American specimens with those given by Burt and Stirton 1961). The wide range of measurements shown by Villa-R. (1966) for this species in Mexico suggests the desirability of a more inclusive review of specimens from Middle America before basing any judgments on size characteristics.

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RESUMEN

Por primera vez se reportan tres epecies de murciélagos de Costa Rica: *Micronycteris brachyotis, Micronycteris nicefori* y *Diphylla ecaudata.* Las primeras dos especies provienan de localidades de la Provincia de Guanacaste, la tercera proviene de la Peninsula de Osa, Provincia de Puntarenas. En el presente informe se esquematiza la distribución de estas especies y se describe el patrón de muda para *M. nicefori.* Se sugiere que las dos fases de coloración en esta especie representan los extremos de una continua secuencia de muda y decoloración química del pelaje.

LITERATURE CITED

Burt, W. H., and R. A. Stirton. 1961. The mammals of El Salvador. Univ. Mich. Mus. Zool., Misc. Publ., No. 117:1-69.

Cabrera, A. 1957. Catalogo de los mamíferos de America del Sur. I. Mus. Argent. Cienc. Nat. ''Bernardino Rivadavia,'' Cienc. Zool., Rev., 4:1-307.

DAVIS, W. B., D. C. CARTER, AND R. H. PINE. 1964. Noteworthy records of Mexican and Central American bats. J. Mammal., 45:375-387.

FLEMING, T. H., E. T. HOOPER, AND D. E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles and movement patterns. Ecol., 53:555-569.

GOODWIN, G. G. 1942. Mammals of Honduras. Amer. Mus. Nat. Hist., Bull., 79:107-195.

————, AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. Amer. Mus. Nat. Hist., Bull., 122:187-302.

HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. Vol. I. Ronald Press, N.Y. 546 p.

HANDLEY, C. O., JR. 1966. Checklist of the mammals of Panama. pp. 753-795. *In* Wenzel, R. L., and V. J. Tipton, Ectoparasites of Panama. Field Mus. Nat. Hist., Chicago. 861 p.

HILL, J. E. 1964. Notes on bats from British Guiana, with the description of a new genus and species of *Phyllostomidae*. Mammalia, 28:553-572.

JONES, J. K., JR. 1966. Bats from Guatemala. Univ. Kans. Publ. Mus. Nat. Hist., 16:441-472.

————, J. D. SMITH, and R. W. TURNER. 1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. Mus. Nat. Hist., Univ. Kans., Occ. Pap., No. 2:1-35.

MARINKELLE, C. J., AND A. CADENA. 1972. Notes on bats new to the fauna of Colombia. Mammalia, 36(1):50-58.

OJASTI, J. 1966. Cuatro nuevos murciélagos para la fauna Venezolana. Acta Biol. Venez., 5:91-97.

————, AND O. J. LINARES. 1971. Adíciones a la fauna de murciélagos de Venezuela con notas sobre las especies del género *Diclidurus* (Chiroptera). Acta Biol. Venez., 7:421-441.

PIRLOT, P. 1968. Chiroptères du Perou, specialment de Haute-Amazonie. Mammalia, 32:86-95.

REDDELL, J. R. 1968. The hairy-legged vampire, *Diphylla ecaudata,* in Texas. J. Mammal., 49:769.

RICK, A. M. 1968. Notes on bats from Tikal, Guatemala. J. Mammal., 49:516-520.

RIDGWAY, R. 1912. Color standards and color nomenclature. Washington, D.C., publ. by author. 43 p., pl. I-LIII.

SANBORN, C. C. 1949. Bats of the genus *Micronycteris* and its subgenera. Field. Zool., 31: 215-230.

SCHALDACH, W. J., JR. 1964. Notas breves sobre algunos mamíferos del sur de México. Inst. Biol., Univ. México, An., 35:129-137.

SMITH, J. D. 1972. Systematics of the chiropteran family Mormoopidae. Univ. Kans. Mus. Nat. Hist., Publ. No. 56, 132 p.

TOSI, J. A., JR. 1969. Republica de Costa Rica, Mapa Ecológico. Tropical Science Center, San José.

VILLA-R., B. 1966. Los murciélagos de México. Inst. Biol., Univ. Nac. Auton. México. 491 p.

VILLALOBOS, D. O., AND J. VILLALOBOS. 1947. Altas de colores. El Ateneo, Buenos Aires, I-XV, 1-74, pl. 1-38 (citation from Ojasti, 1966).

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LIVING CHAMIDAE OF THE EASTERN PACIFIC (BIVALVIA: HETERODONTA)

By F. R. Bernard

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

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LIVING CHAMIDAE OF THE EASTERN PACIFIC (BIVALVIA: HETERODONTA)[1]

By F. R. BERNARD[2]

ABSTRACT: Nineteen species of Chamidae live in the American Eastern Pacific and occur predominantly in shallow warm waters. The extensive collections of the Allan Hancock Foundation, University of Southern California, provided the basis for this distributional and systematic review. It is concluded that the valve of attachment is genetically determined. A reinterpretation of hinge ontogeny is presented. *Pseudochama dalli* nom. nov. is proposed for a preoccupied name. Three new species, *Chama arcana, C. garthi,* and *C. tinctoria* are proposed.

INTRODUCTION

The Superfamily Chamacea is represented by the single family Chamidae, comprising epithetic (attached) dimyarian bivalves inhabiting shallow tropical to temperate waters. Maximum abundance is just sublittoral, though a few species have been collected down to 200 meters; deep records such as 2300 meters (Locard 1898) for *Chama nicoloni* Dautzenberg, 1892 are probably attributable to transported material (Clarke 1962). The largest and most diverse faunule is Indo-Pacific. Approximately 70 living species are represented world-wide of which 19 are eastern Pacific.

The amount of chamid literature is small and scattered. The modern comprehensive taxonomic treatment is that by Lamy (1927), while anatomical and systematic reviews by Odhner (1919) and Yonge (1967) reached somewhat contradictory conclusions. Bayer (1943) reviewed some Caribbean species. In the course of preparing a world-wide survey of the family, the large holdings of the British Museum (Natural History), the Paris Museum, the Stockholm Rijksmuseet, and the United States National Museum, were studied and compared, as well as material in the California Academy of Sciences, Los Angeles County Museum of Natural History, and the S. S. Berry collection. This paper is based upon the important West American collections made since 1931 by the Allan Hancock Foundation and its predecessor, the Hancock Pacific Expeditions, which have yielded new distributional records, three new species, and a sufficient series of juvenile specimens to clarify probable hinge ontogeny.

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Chamids are generally highly inequivalve, with strongly prosogyrate beaks. During development the beaks become separated, resulting in the longitudinal splitting of the substantial parivincular ligament. The external shell surface may be ornamented with regular lamellae or spines or may be entirely smooth, particularly in gerontic specimens. Cup-shaped outgrowths analogous to the hyote spines of some Indo-Pacific pycnodontid oysters are usually present on the cemented valve and probably serve as supports for sensory folds of mantle tissue (Rudwick 1965). The commissural outline is usually rounded but may be elongate, particularly in *Pseudochama*. In nearly all species the commissure margins display a flattened area set off at an obtuse angle from the general curve of the internal shell surface. This region is analogous to the commissural shelf of some oysters and consists of the outer and middle shell layers only, and may be crenulated or nodulose.

Chamids are either permanently cemented to the substrate or undergo a brief phase of attachment during development. In all genera the unattached valve carries a single laterally elongated tooth-like process that fits into a socket in the attached valve. While the juvenile dentition displays a generalized heterodont pattern, adult dentition is entirely different. Attempts to homologize the mature configuration to early dissoconch hinge structures have led to unsatisfactory conclusions and inability to resolve the systematic significance of the valve of attachment.

All the permanently attached chamids are strongly inequivalve, the free valve often being little more than a discoid operculum closing off the large cup-shaped attached valve. This group is extremely xenomorphic, moulding to the substrate and losing most external characters such as spines in mature specimens. The noncemented genus *Arcinella* displays a well-developed lunule that is absent in other taxa, but some attached chamids have a trace of an obscure escutcheon on the free valve. In all groups the ligament is external, but may be deeply sunk and overgrown by the outer shell layers.

Chamids are stenohaline nearshore inhabitants of rocky shores and coral reef communities. Their poor ability to withstand lowered salinity prevented their colonization of estuarine regions. Their distribution is limited to areas with little sedimentation, and habitats fall into two major categories. The greater number of species are cemented to massive rocks in exposed areas, from the mid-tidal zone to a few meters depth. These individuals are large, thick-shelled and bear little shell ornamentation. The other group comprises the smaller, thin shelled species with small areas of attachment and pronounced shell ornamentation. These individuals live as nestling epifauna, frequenting fissures and crannies, as well as the underside of boulders. This group has a wider bathymetric range than the first, frequently occurring in 20 or more meters, cemented to small pebbles, shells, or coral.

It is now well established that chamids and the extinct rudists had no common phylogenetic links, yet the distribution and ecological niche of the two taxa is strikingly similar. Dacqué (1915) noted the low latitude circumglobal distribution of rudists, an observation strengthened by Hamilton's (1956) discovery of rudists dredged from Cape Johnson guyot in the mid-Pacific.

Despite their wide tropical and subtropical distribution, chamids remained conservative in habitat selection, no representatives have been reported in such niches as mangrove roots or floating debris so successfully colonized by other cemented forms. The only experiment appears to be the pseudochamid-descended genus *Arcinella,* which adopted a free existence when adult. It is doubtful if this may be considered a true adaptation, as detachment is purely mechanical, the result of the initial small attachment zone. However, the nearly equivalve condition and the great development of the shell spines are probably contributive to successful free epiphetic existence. The experiment cannot be considered an unqualified success as *Arcinella* is very limited in distribution and is of rare occurrence.

ANATOMY

The gross morphology of the Chamidae is well known from the work by Grieser (1913), the comparative studies by Odhner (1919), and the functional interpretation of Yonge (1967). Only a brief summary is given here based upon observation of preserved *Chama squamuligera* Pilsbry and Lowe; *Pseudochama corrugata* (Broderip), and a single specimen of *Arcinella californica* (Dall).

Chamid soft parts, with the exception of *Arcinella,* are bilaterally asymmetrical, being hypertrophied on the side of attachment; the mantle, ctenidia, gonad and digestive diverticula are enlarged, though the balance of the alimentary, circulatory, and nervous systems are not affected. The ventral migration of the adult functional hinge results in the formation of a deep umbonal cavity, occupied by a prolongation of the mantle, gonad, and connective tissues, similar to that of some Ostreacea. The nature of this body asymmetry has been fully discussed by Yonge (1967).

The mantle is thin, with small marginal folds. Fusion is extensive but involves only the inner fold, except for the dorsal portions, where both the inner and middle folds are fused. The fused border is outside the hinge line and lies just below the ligament, so that an extensive epithelial sheet separates the opposing hinge elements. This interdental epithelium is fenestrated, the openings conforming to the protuberances on the teeth, which are analogous to vermiculate chomata (Stenzel 1971). The presence of a nacre-secreting mantle edge outside the hinge teeth is the main factor leading to the formation of an annular free valve with progressive centralization of the hinge teeth.

The fused mantle borders are furnished with irregularly distributed small tentacles, which are longest in *Arcinella.* Two small thin papillated siphons arise just below the posterior adductor muscle, while the pedal opening occupies most of the anterior face of the anterior adductor muscle. In *Arcinella* the pedal opening is smaller and more ventrally situated, the siphons larger and more muscular. The large adductor muscles are subequal and dorsoventrally elongated. The foot in *Chama* and *Pseudochama* is virtually vestigial and probably not functional. In *Arcinella* it is vermiform and capable of protrusion through the pedal opening.

Chamid ctenidial structure has been exhaustively covered by Menegaux (1890), Ridewood (1903), Grieser (1913), Odhner (1919) and others. This organ is remarkably uniform in all three genera, and consists of two complete demibranchs, the inner one larger than the outer. The lamellae are plicated, synaptorhabdic, with both interfilamentar and interlamellar junctions as well as intraplicatural fusions involving the distal ends of opposing filaments (Ridewood 1903). Ctenidial ciliation falls under "Type C" of Atkins (1937), and Yonge (1967) has dealt with ciliary currents.

The labial palpi are asymmetrically placed and small in *Chama* and *Pseudochama,* and much larger in *Arcinella.* The mouth is wide and overhung by protruding lips. The rest of the alimentary canal is similar in all taxa. A slender plicated oesophagus enters the anterior portion of the stomach, separated from the stomach main chamber by a conspicuous ventral ridge. Crystalline style-pouch and midgut are conjoined. The minor typhlosole terminates on the stomach's right posterior wall, while the major typhlosole, accompanied by the intestinal groove, curves over the left wall and terminates near the openings of the digestive diverticulae. A small dorsal hood is situated on the anterior left side of the stomach. The ducts of the digestive diverticula number about eight and are clustered into four groups. The gastric shield is small. The chamid stomach falls into "Type IV" of Purchon (1958).

The intestine is short, passes dorsally through the ventricle of the heart, then plunges ventrally along the outer surface of the posterior adductor muscle. The anus is removed from the exhalant siphon, so it is possible that faeces are transported by ciliary currents and discarded via the pedal aperture. Odhner (1919) reported variations in intestinal flexure; however, these are probably attributable to indifferent specimen preservation. The specimens examined for this report all conform to the description of Yonge (1967). Pelseneer (1911) claimed partial reversion of the alimentary canal in *Chama* and *Pseudochama;* however, Odhner (1919) did not support this view and Yonge (1967) showed that "inversion" involved the pallial structures only.

The family is dioecious, the extensive gonads occupying the lateral portions of the body, the umbonal cavity, and the dorsal mantle tissues. The eggs are small, fertilization occurs externally, and the larvae probably undergo a prolonged planktonic development (LaBarbera and Chanley 1971).

CEMENTATION

Cementation is usually associated with the monomyarian condition; living cemented dimyarians consist only of the Chamidae, *Myochama, Dimya* and the freshwater Etheriidae. In the Chamidae cementation occurs late in the dissoconch stage (sometimes termed the post-neanic), individuals being 0.5-5 mm total shell length, depending upon ultimate species size. Subsequent to planktonic development, larvae are mobile and temporarily attach by a single byssal thread (LaBarbera and Chanley 1971). Anthony (1905) believed cementations occurred either anteriorly or by the entire valve surface, resulting in an oblique elongated or rounded adult form. However, examination of large series of recently attached individuals and the report by LaBarbera and Chanley (1971) clearly show that cementation is not pleurothetic but involves the new growth margin and results in the anteroposterior axis being perpendicular to the substrate. A period of rapid idiomorphic growth occurs with a strong tangential component in the attached valve which undergoes a coiling growth. The early stages of cementation are presented diagrammatically in figure 1. The more rapid addition to the attached valve results in the progressive separation of the beaks, so that the dissoconch commissural planes come to lie at right angles to each other. The spatial displacement of the umbones causes the longitudinal splitting of the ligament, a process fully described by Owen (1953) and Yonge (1967).

The size of the cementation area bears a direct relationship to the curvature of the two shell valves. If it is extensive, the shell is highly inequivalve with a flat-

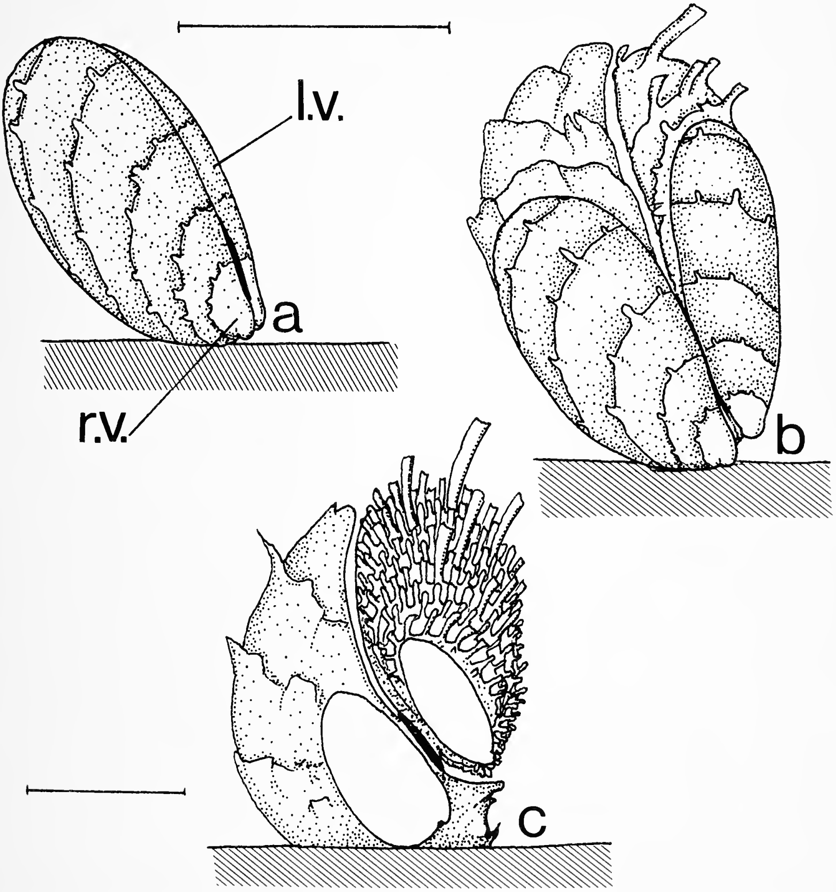

FIGURE 1. Cementation and early growth of *Pseudochama*. (a) Initial attachment; (b) period of rapid idiomorphic growth; (c) assumption of adult form. l.v. = left valve; r.v. = right valve. scale = 1 mm.

tened opercular free valve. Jackson (1890), in a largely overlooked paper, first concluded that mechanical constraints of cementation resulted in a cup-shaped attached valve. Subequivalve chamids such as *C. sordida* Broderip and *C. corallina* Olsson display small cementation zones as does the nearly equivalve genus *Arcinella.*

Lamarck (1819) segregated chamids according to which valve was cemented to the substrate, but Broderip (1835a) failed to distinguish between them, while Reeve (1847) stated that attachment was fortuitous. The systematic significance of left or right valve attachment has not been resolved, though Odhner (1919) divided the permanently cemented Chamidae into two genera. While agreeing that most representatives are consistently attached either by the left or right valve, Lamy (1927) placed all species in *Chama.* Yonge (1967) also rejected the taxonomic significance of attachment, but admitted the convenience of referring to *Chama* and *Pseudochama.*

Which valve is cemented to the substrate is genetically determined and apparent anomalies are nearly all referable to misidentifications. For example the type specimens of the Indo-Pacific *C. pulchella* said by Reeve (1847) to be indifferently attached (Syntypic Series BM(NH) 1950. 11.1 49-51) certainly consists of two species, the smaller individuals, the nominate species; and the larger specimen is *P. similis* Odhner 1917. The attached left and right valves figured by Palmer (1928), said to be *C. pellucida* Broderip, represent typical specimens of this species and of *P. exogyra* (Conrad), whose ranges overlap. Taylor and Kennedy (1969) repeated the observation that *C. pellucida* may sometimes attach by the right valve. I have examined long series of this species without noting a single case of anomalous attachment. Yonge (1967) stated that *Chama radians* Lamarck may be cemented by either valve, but I was unable to locate any material in the British Museum. Nicol (1952a) reported only one specimen of one thousand *A. arcinella* that appeared to be attached by the right valve.

HINGE DENTITION AND REVERSAL

Munier-Chalmas (1882) and Bernard (1895, 1897) examined the chamid hinge and attempted to homologize it with heterodonts while suggesting a dental formula notation. Dall (1903b) presented an illustration purporting to be a juvenile *C. pellucida* showing radiating cardinals and laterals. Odhner (1919) believed it to be a juvenile *Arcinella;* however I do not consider it to be chamid and have been unable to trace the specimen in the USNM. The first full description of the dentition of juvenile chamids is given by Anthony (1905) and its undoubted heterodont affinity revealed.

Munier-Chalmas (1882) demonstrated that dentition can be "normal" or "inverse" so that the arrangement of the teeth of the attached valve is similar; whether it be a right or left valve, and the dental elements are mirror images of each other (Yonge 1967). This inversion affects only the shell and hinge morphology; other systems (alimentary, nervous, etc.) are not reversed. Not only are attached bivalves very consistent in the valve by which they attach, but transposition of hinge elements is extremely rare. It has been suggested by various authors that at first adoption cementation may have occurred indifferently by either valve, but would become set later in the history of a species. Termier and Termier (1949) stated that Triassic oysters attached by either valve, but Newell and Boyd (1970) failed to find any well documented cases for Middle and Lower Triassic oyster-like bivalves. Odhner (1919, 1955) thoroughly reviewed the literature and correctly disposed of most reports of hinge reversal. Most inversions involve only part of the hinge structure and are probably teratological. Popenoe and Findlay (1933) could cite no example of complete transposition, though Hanna (1925) mentioned a case of complete inversion in an Eocene *Venericardia* and Eggleton and Davies (1961) noted a small percentage of reversion in some Sphaeriids.

DEVELOPMENT OF ADULT DENTITION

Adult dentition is different from the juvenile heterodont phase. Grant and Gale (1931) state that the hinge teeth ". . . are replaced by rather crude and heavy rugosities. . . ." Added to the impracticability of homologizing adult chamid teeth to the immature condition is the problem of the similarity of dentition of attached or free valves, whether they are right or left. Odhner (1919) accurately stated that current inversion theory "gives no satisfactory explanation of the process by which a right valve may acquire the characteristics of a left one. . . ."

The adult chamid hinge consists of a thick parivincular ligament sunk in a deep pit that may appear as an obtuse escutcheon on the free valve. Three distinct layers are present, consisting of an inner fibrous region covered with a partially calcified lamellar layer and a thin outer periostracal layer. The ligament is attached to substantial nymphs, whose lower margins are much thickened and reflected to envelop part of the ligament. The ligament is invariably more deeply inserted into the attached valve, and the nymphal margins of this valve are more developed than in the free counterpart. The ventral edge of the nymphal margin is crenulated and forms one side of the socket. It has been considered a tooth, and attempts have been made to homologize it with one of the juvenile cardinals. A schematic cross-section of the adult hinge showing the ligament and nymphal ridges is presented in figure 2.

The extensive Allan Hancock Foundation collections from the central eastern Pacific contain over 80 dissoconch and very recently settled chamids of several species. By careful comparison it was possible to assemble probable developmental stages of *Pseudochama* and *Chama*. Camera-lucida drawings are presented in figure 3 of *P. corrugata* Broderip and *Chama* cf. *C. pellucida* (Broderip).

In this material the very early dissoconch stages display two subumbonal cardinals and a smaller posterior lateral in each valve. During development only the lateral maintains its identity, or at least is a direct precursor of the adult structure. The three heterodont teeth remain distinct until cementation and the period of rapid idiomorphic growth. The pit between the cardinals of the free valve deepens and the teeth become buried by a general thickening of the pit edges; the ventral margin receives most deposition and ultimately forms the lateral peg of the free valve. The nymphal thickened margin originates as a group of tubercles that interdigitates with the accretionary mass of the posterior lateral of the free valve.

It is evident that juvenile dentition is identical in arrangement in left and right valve cemented chamids, so that no dental inversion occurs. Probably mechanical constraints, due to the more rapid coiling growth of the attached valve supporting an opercular free valve, lead to the development of a central socket in the attached valve, accommodating a single lateral tooth in its opposite number. This interpretation is essentially a development of Odhner's (1919) suggestion that similarity of arrangement of hinge elements is the result of growth characteristics, but he did

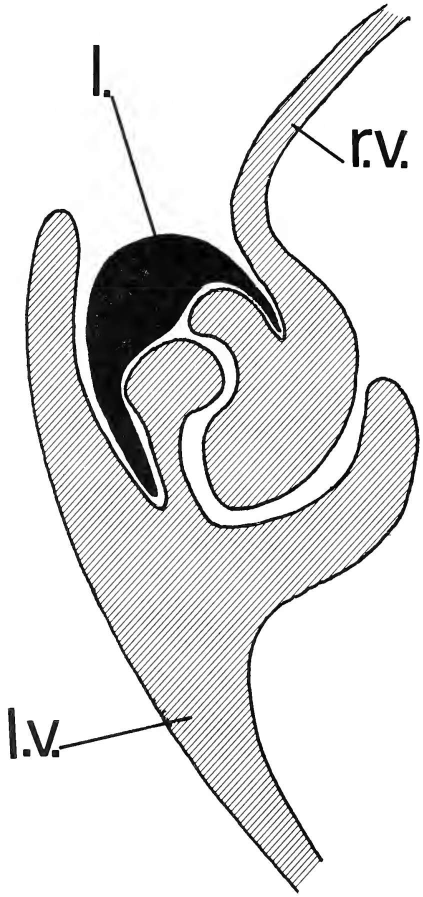

FIGURE 2. Schematic cross section of adult hinge of *Chama,* showing ligamental insertion and nymphal ridges. l. = ligament; l.v. = left valve; r.v. = right valve.

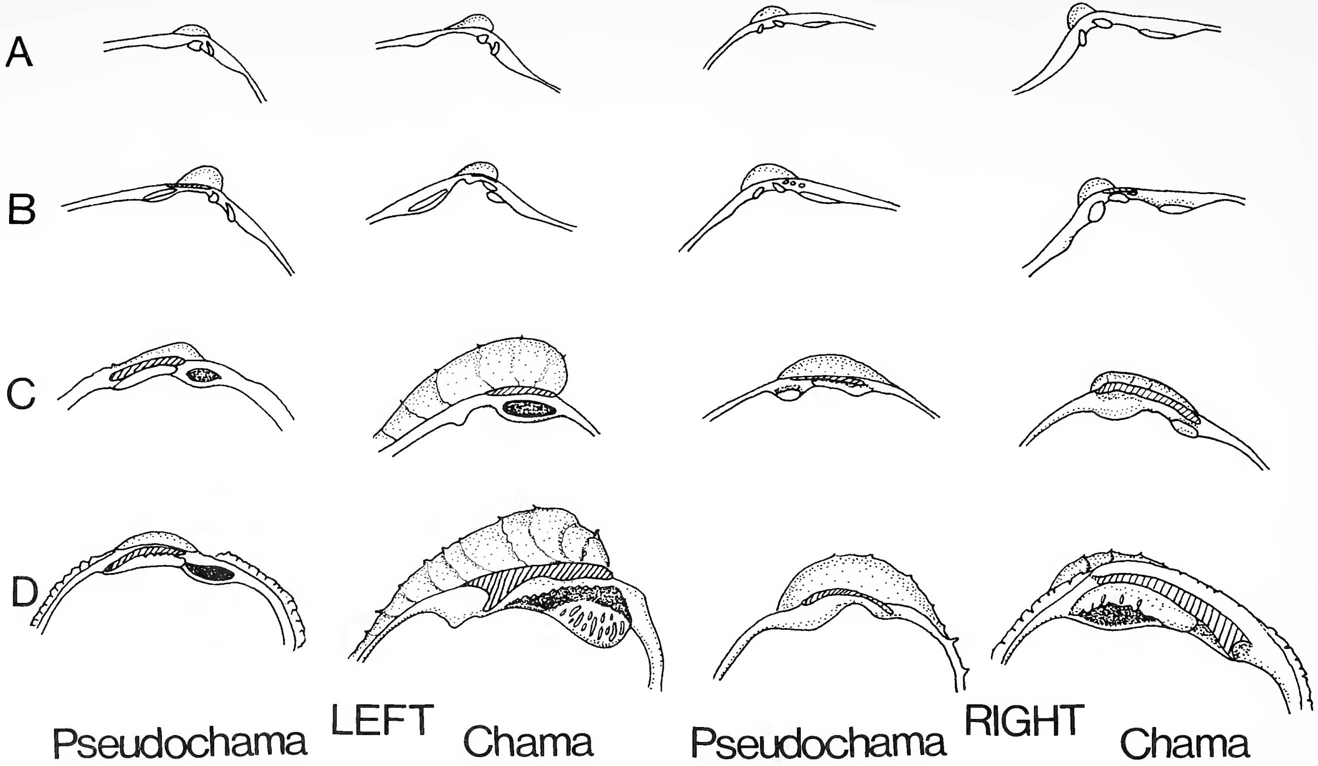

FIGURE 3. Schematic illustration of postulated hinge development in *Pseudochama* and *Chama*, prepared from camera-lucida drawings.

not recognize the basic identity of the juvenile dentition and proposed a diverse origin for the adult teeth of both groups, which he placed in separate genera.

The concept of separation of adult chamid hinge structures from the juvenile condition is strengthened by the fact that the majority of cemented bivalves are edentulous. Such structures as the sockets of *Spondylus* and the interlocking mechanisms of *Plicatula* and *Dimya* are secondary developments, as well as the loss of classical heterodont dental structures by the adult in *Anodonta* and the Thyasiridae. In these situations the early shell form may provide interesting phylogenetic insights, but the actual systematic placement is based upon adult morphology. Postponed assumption of adult characteristics does not influence generic placement, and it is on this basis that the cemented xenomorphic genus *Hinnites* is separated from *Chlamys,* though the juveniles are indistinguishable.

SHELL GROWTH AND FORM

Bivalve growth being accretionary, the shape of the generating curve is maintained. Shell formation, as Stasek (1963) phrases it, ". . . embodies a functional continuum of past and present." In the majority of bivalves the beaks are the point of origin and geometrical locus from which growth radiates. In chamids, the beaks are the point of origin, but their relative position changes, and finally, the growth origin is transferred to the commissural plane. The continuous secretory mantle border results in the dental elements not remaining marginal, a tendency carried to its extreme in the extinct rudists where the teeth of the free valve are placed subcentrally on the opercular disc.

Chamid growth form includes a pronounced tangential growth component (Yonge 1967). Observation of long developmental series confirms that one-half to three-quarter coiling of the shell occurs rapidly, but this growth pattern continues for a brief time only, and small specimens (3-5 mm) have attained the mature configuration. Subsequent growth is a simple increase in size. Coiling growth also occurs in a number of non-chamid taxa but the shell is usually equivalve, perhaps the earliest example being the Ordovician *Redonia* Rouault, assigned by Chavan (1966) to the carditaceans. The living *Isocardia* is also coiled (Owen 1953), as are some representatives of the Anomalodesmata, notably *Pecchiola,* which was originally considered to be a chamid. However, an elongate spiral design is incompatible with bivalve organization, which requires a large functioning pallial cavity to house the water pumping and food collecting ctenidial apparatus. The majority of bivalves maintain a constant ratio between ctenidial area and body size, however this is not true of spiriform taxa and those with a large subumbonal cavity. Large, old, chamids may nearly halve the proportion of ctenidium to body and there is no doubt this must have profound physiological implications. This problem was not encountered by the rudists, where the large attached valve was filled with porous calcitic deposits, effectively maintaining a proportionately constant shell cavity. Rudists developed further aids to maintaining adequate flow through the pallial cavity, which included perforated upper valves and siphonal notches (Vogel 1960).

SYSTEMATIC POSITION AND RELATIONSHIPS

The many common morphological characters and the ontogeny of the three living chamid genera are suggestive of a single phylogeny. While chamids have long been accepted as a homogenous group, their placement in the Class Bivalvia has been unsure. A marked similarity to the extinct rudists led support for their incorporation within the Hippuritacea (Odhner 1919, Newell 1965, Yonge 1967). Chamids have been thought to have descended from Silurian pachydonts which became cemented to the substrate by one valve in the manner of *Diceras* (Deschaseaux 1952). It is unlikely that the highly evolved porous-shelled Diceratidae could be ancestral to the modern Chamidae.

Rudists are considered to be heterodonts, primarily on dental homology, as no dissoconch stages have been identified from Mesozoic strata. Taylor and Kennedy (1969) and Taylor et al. (1969) confirmed earlier reports that though heterodonts are aragonitic in shell structure, *C. pellucida* Broderip and *P. exogyra* (Conrad) possess a superimposed external calcitic layer, a character shared with rudists. However, this cannot be considered conclusive evidence for affinity (Newell 1965, Yonge 1967). The general similarities to the Hippuritacea are probably the product of convergence as chamids occupied approximately the geographical range of rudists and appropriated the ecological niche vacated by their extinction.

Other authors have traced chamid descent from the Carditacea (Dall 1903b); the Crassatellacea (Böhm 1891); the Lucinacea (Nicol 1952a); and the Veneracea (Fischer 1886). Kennedy et al.(1970), in a wide survey of the shell structure and dental morphology of many fossil and living chamids discussed all these suggestions and demonstrated a most probable relationship to the byssate Carditacea.

Chamids have a comparatively short geological history, the earliest undoubted representatives occur in the Upper Cretaceous of Europe, and bear a strong resemblance to *C. pellucida* Broderip. A period of radiative expansion followed in the Eocene, together with the development of diverse ornamentation. Chamidae are abundant components of the tropical and subtropical shallow water faunules from the Pliocene. The genera *Chama* and *Pseudochama* are widely distributed, but *Arcinella,* which appeared in the Lower Miocene of Florida is endemic to Pacific and Atlantic central America.

EASTERN PACIFIC CHAMIDAE

The roughly north-south axis of the American west coast cutting across temperate and tropical waters yields a rich and diverse chamid faunule. The great majority of species were collected by Hugh Cuming and described by Broderip (1835a) with a few additions by Reeve (1847). Unfortunately the descriptions are overly short and type localities not clear. One problem results from the citation "Lord Hood's Island," which may be either South Pacific or West American. Cuming visited Polynesia in 1827-33 and collected at Lord Hood's Island, now known as South Marutea. The following years Cuming journeyed on the west coast of America collecting at the Pearl Islands, Panama and the Galapagos group, of which the southernmost island was originally Lord Hood's Island, now known as Hood or

Española Island. That Cuming in fact collected here is evidenced by Broderip and Sowerby (1832) in their description of *Stilifer astericola* with a type locality cited as "ad Insulas Galapagos (Lord Hood's Island)." The chamid species with doubtful type localities are *C. pacifica, C. imbricata,* and *C. spinosa.* I had occasion to examine the types and compare them to materials of known distribution and concluded that *C. pacifica* is a well established Indo-Pacific species, the center of distribution being the Solomon archipelago. Broderip states the species is identical to material of Samuel Stutchbury (1797-1859) who collected widely in Australia and Polynesia. A similar situation exists for *C. imbricata;* the type is identical to recently collected Indo-Pacific material and Broderip also mentions Stutchbury materials; however, Broderip also reports a variety of *C. imbricata,* citing the type locality as Insulas Galapagos. This specimen was separated by Reeve (1847) and described under the name *P. janus.* This species is well established in the Galapagos group and bears little resemblance to Broderip's *C. imbricata. C. spinosa* is distinguished by the uniform distribution of sparse spines and scales upon the free valve and resembles nothing in the eastern Pacific province, and is probably Indo-Pacific in origin. The western American chamid fauna appears to be endemic with little relationships to Indo-Pacific representatives, and despite free exchange until the end of the Miocene across the isthmus of Panama no western representatives extend into the Antillean region. The explanation may lie in the almost total extinction in the Pacific of the coral reef biotope.

In this review of eastern Pacific species, literature citations are furnished only to readily available works that are a help to identification. Because of many misidentifications and confusion, particularly in earlier works, published distribution data are to be viewed with reserve; those cited here have been verified with material. The terminology of higher taxa is taken from "Treatise on Invertebrate Paleontology" (R. C. Moore, ed. 1969).

Abbreviations for collections mentioned in the text are identified below:

AHF	Alan Hancock Foundation, University of Southern California
ANSP	Academy of Natural Sciences, Philadelphia
BM(NH)	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
LACM	Natural History Museum of Los Angeles County
MNHN	Museum National D'Histoire Naturelle de Paris
MCZ	Museum of Comparative Zoology, Harvard
SDSNH	San Diego Society of Natural History
USNM	National Museum of Natural History, Washington, D.C.

SYSTEMATIC REVIEW

SUPERFAMILY CHAMACEA LAMARCK 1809

Shell cemented, at least temporarily, to substrate. Umbones prosogyrate, ligament parivincular, adult dentition consisting of a large lateral process in the upper valve inserted in a deep pit on opposite valve. Sculpture generally well developed, consisting of spines sometimes conjoined into concentric frills. Pallial line entire, adductor muscle scars subequal. Upper Cretaceous to Recent.

FAMILY CHAMIDAE LAMARCK 1809

Shell characters as in Superfamily. Variable and xenomorphic. Predominantly among shallow warm water epifauna. The shell may be ponderously thickened in old specimens and external characters frequently obliterated by abrasion and the activity of shell borers. Anatomically this family is conservative. Mantle extensively fused except for a small pedal gape and two small delicate siphons formed solely from the inner mantle fold. Adductor muscles elongate, nearly subequal. Foot reduced, laterally compressed. Ctenidium comprising a large inner demibranch with a much smaller outer demibranch. Lamellae plicate, synaptorhabdic, filaments connected by substantial interfilamental junction. Interlamellar junctions short and numerous. Labial palp small, generally asymmetrical, with 12-20 palpar ridges. Mouth small, leading to short, longitudinally plicated oesophagus. Stomach large, divided by prominent ventral ridge. Style pouch and midgut conjointed. Intestine short, piercing heart ventricle.

The anatomical characteristic of the Chamidae suggests that they are adapted to waters with little suspended materials. The alimentary system is modified for the acception of fine particulate materials. Representatives of the family occur on hard substrates removed from zones of sedimentation. Geologically this group is probably indicative of warm water as those few representatives extending to cooler waters are all small and lack pronounced sculptural processes.

There are three West American genera.

GENERIC KEY TO THE WEST AMERICAN CHAMIDAE

1.	Shell nearly equivalve, lunule pronounced; not attached	*Arcinella*
	Shell inequivalve, no lunule; cemented	2
2.	Shell attached by left valve, nepionic shell small	*Chama*
	Shell attached by right valve, nepionic shell large	*Pseudochama*

GENUS *CHAMA* LINNÉ 1758

Type (subsequent designation: Schmidt 1818) *Chama lazarus* Linné 1758

Shell thick, porcellaneous, sometimes with waxy translucent outer layer. Shell cemented by left valve. External surface smooth or ornamented with irregularly placed concentric and radial processes. Attached valve with hyote-type spines. Commissural margin sometimes produced. Dentition consisting of a single broad tooth-like process in the right valve, fitting into socket in left valve. Nepionic shell small, with typical heterodont dentition, externally ornamented with concentric and radial sculpture. No abrupt transition of growth pattern at the post-neanic stage. Anatomy as for Superfamily.

Subgenera proposed in *Chama*, such as *Cipliacella* Vincent, 1928 (Type *C. pulchra* Ravn 1902) or *Psilopus* Poli 1795 (Type *C. gryphoides* Linné 1758) are based upon minor variations not significant above the species level.

Twelve species occur in the eastern Pacific, the majority in the Panamic province.

ARTIFICIAL KEY TO WEST AMERICAN *CHAMA*

1.	Interior shell not colored	2
	Interior of shell colored	8
2.	Both valves strongly arched, attachment area small	3
	Upper valve flat, attachment area large	4
3.	Exterior ornamented with many short narrow spines	*C. corallina*
	Exterior ornamented with few long broad arched spines	*C. sordida*
4.	Exterior ornamented, no distinct color pattern	5
	Exterior smooth, with uniform brown lines	*C. venosa*
5.	Shell waxy, with wide, minutely crenulated commissural shelf	6
	Shell porcellaneous with narrow, coarsely crenulated commissural shelf	7
6.	Shell laterally elongated, exterior with short uniform frills, fused into concentric wrinkles	*C. pellucida*
	Shell vertically elongated or round, exterior with irregular thin frills, not fused into concentric wrinkles	*C. arcana*
7.	Exterior white spines uniform, fusing into concentric frills	*C. squamuligera*
	Exterior colored, spines irregular, separate	*C. garthi*
8.	Internal color limited to narrow marginal band	9
	Internal color diffused	10
9.	External sculpture lacking or of narrow spines	*C. buddiana*
	External sculpture of broad, striated foliations	*C. frondosa*
10.	Internal color a diffuse marginal flush, or on anterior adductor muscle scar	*C. mexicana*
	Internal color extensive	11
11.	Interior purple, hinge teeth bright coral red	*C. echinata*
	Interior yellowish red, hinge teeth white	*C. tinctoria*

Chama arcana new species

Figures 4 a, b

Chama pellucida auctt., not Broderip 1835a:149; Keep 1888:182, fig. 155 (as of Sowerby); Arnold 1903:130 (Pliocene, Pleistocene of California); Arnold 1910:38 (Upper Miocene of California); Grant and Gale 1931:279; Soot-Ryen 1931:314 (Galapagos Islands); Smith and Gordon 1948:173.

Diagnosis: The new species can only be confused with *C. pellucida* Broderip, but the commissural shelf is wider and the latter lacks the streaks of bright color often present on the upper valve. The sculpture of *C. arcana* is irregular, thin, and periodically drawn out into longitudinally striated lamellae, which are not present in *C. pellucida,* where the sculpture is more uniform and subdued. The shell of *C. pellucida* is proportionately thicker and tends to be anteroposteriorly elongated, while in *C. arcana* it is subcircular or dorsoventrally elongated. A distinct, but small, pallial sinus is present just below the adductor muscle in *C. pellucida,* which is absent in the new species.

Description: Shell interior porcellaneous, white, exterior waxy translucent. Outline variable, depending upon habitat, either round or dorsoventrally elongated. Cemented to substrate by wide area of left valve. Exterior sculpture often abraded and encrusted, color white, sometimes with streaks of pink or red particularly on posterior of right valve. Sculpture of either valve consisting of close-set foliations irregularly joined into thin translucent concentric lamellae, with several radial rows of larger prolongations. Ligament deeply sunk and placed on a substantial nymph. Dental processes not highly developed, nymphal ridge of left valve with a strongly developed longitudinal groove. Shell margins minutely denticulated. Commissural shelf broad, lacking inner layer, sometimes iridescent. Adductor muscle scars large. Pallial lines shallow, entire.

Holotype measurement: Length 55, height 64, width 39 mm.

Type locality: Newport Bay, California (33°37′N, 117°55′W). Intertidal —Collected March 1965 by J. McLean.

Holotype deposition: LACM 1723.

Geographic range: Yaquina Point, Oregon (44°N) to San Juanico Bay, west coast of Baja California (26°N).

Bathymetric range: In Oregon and California this species occurs from the low intertidal level down to 50 meters. In its southern range it is always subtidal, down to 80 meters.

Habitat: Clear water, often in nooks and crannies in exposed zones. Attached to a solid substrate, rocks, pilings, breakwaters, subtidally often attached to gravel.

Etymology: The specific name is derived from the Latin adjective *arcanus* (secret), referring to the long hidden distinctness of this species from *C. pellucida.*

Discussion: This species is common in the California Province, first appearing in the Upper Miocene (Arnold 1910) and more frequently in the Pliocene and Pleistocene (Arnold 1903). It occurs higher in the intertidal zone than other chamids and is frequently found on pilings and other man-made objects. It has the most northern range of the genus, and, in common with some other cool water bivalves, extends down the coast of Baja California. Dall (1921) included the Galapagos Islands; this is probably not correct as USNM does not contain specimens from Galapagos. Soot-Ryen (1931) also recorded this species from the Galapagos group. *C. arcana* is entirely absent from the tropical Panamic province and its congener *C. pellucida* Broderip appears in similarly cool southern waters. These two species are closely related, but consistent differences in sculpture and shell shape separate them as discussed above.

Of the West American chamas, *C. arcana* and *C. pellucida* occupy the coolest waters. Lowenstam (1954) first noted the presence of an outer calcitic layer in *C. pellucida* and later suggested (Lowenstam 1963) that the aragonitic outer layer of warm water chamids is transformed to prismatic calcitic structure in a cool water environment. Taylor and Kennedy (1969) confirmed the calcitic external layer, but showed it to be an extra layer superimposed upon the normal aragonite shell of the Superfamily. This fact, coupled by their belief that *C. pellucida* is distributed transequatorially led Taylor and Kennedy to reject Lowenstam's hypothesis. In an appendix Taylor and Kennedy (1969) noted a calcitic layer in *Pseudochama exogyra* and suggested that this species is conspecific to *C. pellucida.* I cannot agree with these authors that the occurrence of a calcitic outer layer in these three species is sufficient grounds for combining them into a single taxon. It is well established that warm water bivalves tend to display a higher proportion of aragonite than cold water representatives, and Lowenstam's suggestion should be reconsidered, not on an individual ecomorphic basis but in a phylogenetic sense.

Chama buddiana C. B. Adams 1852

Figures 5 d, e

Chama buddiana C. B. Adams 1852:253 (Type locality: Panama Bay, 7°N. Syntypes MCZ); Turner 1956:36, pl. 20, figs. 7, 8 (designation of lectotype MCZ 190150); Olsson 1961:224, pl. 34, figs. 2-2c; Emerson and Hertlein 1964:348 (Pleistocene of Mexico); Keen 1971:147, fig. 346.

External surfaces pink to deep red, ornamented with irregular radial rows of small triangular white spines. Interior white with pinkish red marginal band. Shell margin finely crenate.

Discussion: The exterior coloration, the contrasting small triangular white spines interspersed with a few large ones in irregular rows, together with the marginal band of color distinguish this species.

This is the largest and most abundant chamid occurring off Panama but it is uncommon elsewhere. The Port Parker location, from the Allan Hancock Stations is a northward extension of the confirmed range. Dall's (1921) record of this species from California is certainly in error, probably stemming from the fact that Adams also cited material collected by Lt. Green at Guaymas. It is clear that Adams intended to describe those specimens personally collected at Panama but mentions material he considered identical.

Carpenter (1864) placed his *C. frondosa fornicata* in the synonymy of this species. After examining the types I consider that these species are in fact not synonymous, and that Carpenter's material is referable to *C. mexicana* Carpenter, 1857. *Chama rubropicta* Bartsch and Rehder, 1939 is an immature *C. buddiana* Adams, 1852.

C. buddiana is found in the low intertidal zone to 2 meters, generally attached to rock on large boulders. It ranges from Port Parker, Costa Rica (11°N) to Cape San Francisco, Ecuador (0°39′N). Also reported from Clipperton Island and the Galapagos Group (Albermarle, Narborough, and Indefatigable Islands). Emerson and Hertlein (1964) recorded this species from the Mexican Pleistocene.

Chamma corallina Olsson 1971

Figures 6 c-f

Chama corallina Olsson, 1971:39, figs. 7-10. (Type locality: Off Punta Escondido, Gulf of Panama, 7°59′N, 78°30′W, in 55 meters. Holotype USNM 701157); Keen 1971:197, fig. 346a.

Shell with both valves inflated, attachment area small. Exterior pinkish brown to red. Interior white. Surface sculpture of fine radial riblets with irregular sharp spines. Shell margin crenulated.

Discussion: The small size, rotundity of outline and concentric wrinkles with small sharp spines readily distinguish this rare species. Mr. and Mrs. E. E. Wahrenbrock collected several specimens from trash fish dumps in Mazatlan that had been trawled off the Sonora coast of Mexico.

This species is most frequently attached to small pebbles or calcareous polychaete tubes in 18 to 95 meters. It ranges from the Sonoran coast of Mexico (23°N) to Punta Escondido, Gulf of Panama (7°59′).

Chama echinata Broderip 1835

Figures 7 a-f

Chama echinata Broderip 1835a: 150 (Type locality: Puerto Portrero, Bay of Guayaquil, Ecuador, 2°11′S. Syntypes BM(NH) 1950. 11.1.20-22); Broderip 1835b:305, pl. 39, fig. 5; Reeve 1847: pl. 7, fig. 35; Stearns 1893:375; Clessin 1889:14, pl. 6, fig. 2; Keen 1971:147, fig. 347.

Chama coralloides Reeve 1847: pl. 4, sp. 18 (Type locality: Puerto Portrero, Ecuador, 2°11′S. Holotype BM(NH) no. number).

Chama delesserti Chenu 1846: pl. 6, fig. 4 (Type locality: Puerto Portrero, Bay of Guayaquil, Ecuador, 2°11′S. Holotype BM(NH) 1950.11.1.20).

Exterior yellowish white, sculpture of many short irregular spines, often totally abraded in mature specimens. Interior deep purple, hinge teeth bright coral red. Juvenile specimens display only the purple interior, the red hinge appearing later.

Discussion: Reeve (1847) illustrated *C. echinata* but separated two worn specimens of Broderip's type series to erect *C. coralloides*. Chenu (1846) reproduced Broderip's (1835b) figure of *C. echinata* under the new name *C. delesserti*. Carpenter (1857a) pointed out this confusion and correctly surmised that Chenu's species should also be placed in synonymy.

The deep purple of the interior, contrasting with the bright coral hue of the hinge teeth distinguishes this species from all other American chamids. The outside of the shell is frequently abraded and overgrown, attached to large rocks from the low intertidal zone to 25 meters. The geographical range is from Angel de la Guarda Island, Gulf of California (29°N) to Huanape Island, Northern Peru (8°34′S).

Chama frondosa Broderip 1835

Figures 8 a-c

Chama frondosa Broderip 1835a: 148 (Type locality: Isla La Plata, Ecuador, 1°18′S, BM(NH) 1950.11.1.55); Broderip 1835b:302, pl. 38, fig. 1; Reeve 1847: pl. 1, fig. 1a; Stearns 1893:375; Lamy 1927:314; Durham 1950:73, pl. 17, figs. 5, 6 (Pliocene to Recent of Mexico); Emerson 1960:6 (Shell middens of Mexico); Olsson 1961:225, pl. 34, figs. 1a, b, pl. 86, fig. 2; Keen, 1971:147, fig. 348.

Chama pacifica Carpenter (Gould MS) 1847, not Broderip 1834 (*fide* Carpenter 1857b).

Chama parasitica Rocheburne 1895:243 (Type locality: San Jose Island, Gulf of California, Mexico, 25°N. Holotype MNHN).

Shell heavy, pinkish white, external sculpture of wide radially striated foliations. Interior white, with narrow pink or purple marginal band.

Discussion: This infrequently encountered chamid is the only West American species with foliated spines. It occurs cemented to rocks and large boulders, extending from the subtidal zone to 25 meters. The geographic range is from southern part of the Gulf of California at La Paz (24°30′N) to Salango Bay, Ecuador (1°35′N). I have not seen genuine material from the Galapagos Islands and records from the outer coast of Baja California and California are certainly misidentifications. This is a warm water species and there is some doubt as to its northern extent, as the La Paz record is based upon a single specimen.

Chama garthi new species

Figures 9 a, b

Chama spinosa auctt., not Broderip 1835; Carpenter 1857a:90; Strong and Hanna 1930:15.

Diagnosis: The species may be confused with *C. squamuligera* Pilsbry and Lowe, but is easily distinguished by the bright external coloration and by the spines, which never fuse into crenulated frills.

Description: Shell small, rounded, exterior irregularly mottled with purplish red. Attachment area small. Left valve deeply cupped, right valve nearly flat. Right valve covered with dense radial rows of short imbricated free spines; left valve with fewer wider spines. Interior white or stained light brown; margins delicately crenulated.

Holotype measurement: Length 19.5, height 23.7, width 15 mm.

Type locality: Octavia Bay, Colombia (6°50′N, 77°41′10″W). Shallow water. Allan Hancock Station 435-35, January 28, 1935.

Type deposition: AHF 167 (Holotype). AHF 168 (Paratype).

Geographic range: Type locality and Salango Island, Ecuador (1°35′S).

Bathymetric range: Intertidal level to 22 meters.

Habitat: Rock and coral.

Etymology: The species is named for John S. Garth of the Allan Hancock Foundation in small recognition for his inestimable services to Central American malacology while accompanying all the Hancock Pacific Expeditions Velero III cruises (1931-1941).

Discussion: The external coloration and delicate imbricated spines make *C. garthi* the most elegant of West American chamids. There is a superficial similarity to juvenile *C. echinata* Broderip, but the new species displays a wide commissural shelf, entirely lacking in young *C. echinata* and the attached valve of *C. garthi* carries a few wide spines, rather than the many small spines of *C. echinata*.

Chama maculata Clessin 1889

Chama maculata Clessin 1889:43, pl. 4, figs. 4, 6.

The brief description and indistinguishable illustration relegate this species to a *nomen dubium* status. The type locality is the Strait of Magellan. It is highly improbable that these cold waters support any representative of the Chamidae. The literature yields no other mention of a chamid occurring south of approximately 33°S. Unfortunately the Clessin collection, housed in the Stuttgart Museum, was totally destroyed during the Second World War.

Chama mexicana Carpenter 1857

Figures 10 a-c

Chama frondosa mexicana Carpenter 1857a:87 (Type locality: Mazatlan, Mexico, 23°N. Syntypes BM(NH) Carpenter Collection Tablets 425-438); Hertlein and Strong 1955:114 (Galapagos Islands); Hertlein and Emerson 1956:165 (Pleistocene of Mexico); Keen 1971:147, fig. 349 (as *C. mexicana*).

Chama frondosa fornicata Carpenter 1857a:89 (Type locality: Mazatlan, Mexico, 23°N, Syntypes BM(NH) Carpenter Collection Tablets 439-443); Keen 1968:397, pl. 56, figs. 31 a, b, figs. 35 a, b.

Chama frondosa (*var β*) Broderip 1835a:149 (Type locality: Mazatlan, Mexico, 23°N. Type not located in BM(NH); Broderip 1835b:302, pl. 38, fig. 2.

Chama producta Broderip 1835a:150 (Type locality: Gulf of Tehuantepec, Mexico, 16°N. Holotype BM(NH) 1950.1.1.60); Broderip 1835b:305, pl. 39, fig. 4: Reeve 1847, pl. 3, fig. 13; Clessin 1889:20, pl. 10, fig. 1: Lamy 1927:314; Keen 1971:899 (Nomen oblitum).

Chama purpurascens Tryon (Conrad MS) 1872:117 (as synonym of *C. frondosa* Broderip 1835); Pilsbry and Vanatta 1902:551 (Galapagos Islands, as *Chama frondosa purpurascens* Conrad).

Chama compacta Clessin 1889:25, pl. 10, fig. 4 (Type locality: unknown. Type destroyed in WW. II).

Shell exterior pink to deep red, with many small, and two radial rows of larger spines. Interior white to yellowish. There is an indistinct flush of pinkish purple around the anterior adductor muscle scar and part of the shell margins. Gerontic specimens generally riddled by borers and with spines abraded.

Discussion: This species is readily separable from other West American chamids by the irregular internal purple red flush, which generally spreads to include the anterior adductor muscle scar.

There is some confusion in the literature concerning the type locality of *C. mexicana*. Carpenter (1857a) recognized that his specimens were identical to Broderip's *C. frondosa var β*, and intended merely to apply an acceptable name to it. In such a situation, Broderip's specimen must remain the type, unless a case can be made to suppress it entirely. Such a case can be made on the basis that symbols have no nomenclatural status or that Broderip's taxon may be considered a *species inquirenda*. The extreme brevity of Broderip's description would also favor considering it a *nomen dubium*. I was unable to locate *C. frondosa var β* in the Cuming Collection, and incline to accept Carpenter's material as syntypic, or at least plesiotypic.

Comparison of the paratype of *C. producta* Broderip (Fig. 10a) to the types of *C. frondosa mexicana* and *C. frondosa fornicata* convinced me they are synonymous and well removed from *C. frondosa* Broderip. However, Reeve (1847) thought *C. producta* to be identical to *C. iostoma* Conrad 1837, a species indigenous to Hawaii (Dall et al. 1938). Keen (1971) did not accept this view, and rejected *C. producta* on the basis of discrepancies in the description. Under guidelines adopted by the 1972 ICZN Commission meeting in Monaco the name is not available for nomenclatural purposes. In the unlikely event that it is proven desirable to reinstate *C. producta* Broderip, formal petition will have to be made to ICZN.

The species occurs on small cobbles and boulders, nearly always on a sandy substrate, from the middle intertidal zone to 80 meters. The geographical range is the head of the Gulf of California, Mexico (31°N) to San Jose point, Guatemala (13°46′N).

Chama pellucida Broderip 1835

Figure 4 c, d

Chama pellucida Broderip 1835a:149 (Type locality: Iquique, Chile, 20°13′S, in 17-20 meters. Syntypes BM(NH) 1950.11.1.63-65); Broderip 1835b:302, pl. 38, fig. 3; Reeve 1847: pl. 6, fig. 32: Clessin 1889:18, pl. 8, figs. 3-4; Lamy 1927:345; Olsson 1961:225, pl. 33, figs. 2, 2a, pl. 34, fig. 5; Marincovich 1973:11, fig. 10; *not* Smith and Gordon 1948:173; *part* Osorio and Bahamonde 1970:198 (Juan Fernandez Islands); *not* Hertlein and Grant 1972:227, pl. 43, figs. 12, 15.

Chama chilensis Philippi 1887:173, pl. 37, fig. 9 (Type locality: Pliocene of Laguna de Cahuil, Chile, 34°30′S, 72°01′W. Holotype MNHN no number).

Shell rounded, generally longitudinally elongated. Sculpture of short, translucent fluted spines, fused into concentric ridges. Exterior white or pink, sometimes dashed with red. Interior white, margins sharply crenulated. Commissural shelf wide. Small pallial sinus present.

Discussion: This species is close to the northern *C. arcana* new species, and possibly bears the same relationship to it as do Caribbean congeners of central eastern Pacific species. Both *C. arcana* and this species are inhabitants of cool waters, effectively separated by the warm equatorial zone since Miocene times. The more elongate form, proportionately thicker shell, and short concentric spines fused into ridges differentiate this species from its northern relative.

It appears that Keep (1888) first confused northern representatives with *C. pellucida* which is restricted to the Peruvian province and does not occur north of Paita. *Chama chilensis* Philippi from the Pliocene of Chile is certainly this species. Californian fossil materials, some as early as Late Miocene are all referable to *C. arcana* new species. Odhner's (1922) reference to *C. imbricata* Broderip, from the Juan Fernandez Islands, is actually to *C. pellucida.*

This species occurs high in the intertidal zone to 30 meters, most frequently nestling in fissures of rocks, or on pilings. The range is from Paita, Peru (5°15′S), to Tocopilla, Chile (22°S). It is also abundant in the low intertidal zone of the Juan Fernandez Islands (33°S).

Chama sordida Broderip 1835

Figures 6 a, b

Chama sordida Broderip 1835a:151 (Type locality: Isle of Cuna, Central America. Syntypes BM(NH) 1950.11.1.52-53); Broderip 1835b:306, pl. 39, figs. 8, 9; Keen 1971:149, fig. 35 (Right figure only).

Exterior reddish brown, the overall pattern of small radial riblets sparsely interspersed with large imbricated spines. The interior white, with the exterior color showing through. The margin is finely crenulated.

Discussion: The radial ribs and few large spines make it unlikely to confuse the identity of this elegant species. This is not *C. digueti* Rochebrune as suggested by a number of workers, which has an entirely different sculpture and should be assigned to *C. venosa* Reeve.

This species is generally attached to calcareous organisms and occurs from the subtidal zone to 45 meters. The geographic range is from Angel de Ia Guarda Island, Gulf of California, Mexico (29°39′N), to Gorgona Island, Colombia (3°01′N).

I have been unable to trace the original type location, given as Isla Cuna, America Centrali. The latter was in contemporaneous use for the region north of Panama Bay, approximately 9°N to 15°N. Isla Punta Icaco, Nicaragua (12°33′N, 87°16′W) is here designated the type locality.

Chama squamuligera Pilsbry and Lowe 1932

Figures 9 c, d

Chama spinosa auctt., not Broderip 1835a (in part).

Chama squamuligera Pilsbry and Lowe 1932:103, pl. 14, fig. 10 (Type locality; San Juan del Sur, Nicaragua, 11°15′N, 85°53′W. Holotype ANSP 155623, Paratypes SDSNH 475a,b); Durham 1950:73, pl. 17, fig. 3, 6 (Pliocene to Recent of Mexico); Hertlein and Allison 1966:139 (Clipperton Island 10°17′N, 109°13′W); Keen 1971:149, fig. 351.

Chama rubropicta Bartsch and Rehder 1939:13, pl. 3, figs. 6-10 (Type locality: Clipperton Island, 10°17′N, 109°13′W. Holotype USNM 472553)

Chama squamuligera rubropicta Bartsch and Rehder. Hertlein and Emerson 1953:350 (Clipperton Island); Salvat and Ehrhardt 1970:227 (Clipperton Island).

Shell small, pure white to yellowish. Exterior sculpture of thin broadly imbricated spines conjoined into concentric frills. In worn specimens the frills are reduced to concentric wrinkles. Interior white, margin finely crenulated. Commissural shelf wide, often granulose.

Discussion: This small nearly colorless species is characterized by the many spines, tending to fuse into irregular concentric lamellae.

When proposing this species Pilsbry and Lowe considered it very similar to *C. spinosa* Broderip (Fig. 9e), separating it on a purely geographical basis. *C. spinosa* has been listed in the West America fauna (Strong and Hanna 1930) —another legacy from the Cuming location "Lord Hood's Island," in fact South Marutea, as Broderip's species is clearly identifiable with South Pacific material and probably synonymous to *C. asperella* Lamarck 1835, which has a few months' priority. It is probable that *C. flavida* Clessin 1889 described from Panama with no suggestion whether Pacific or Caribbean will prove to be this species. Clessin's description and illustration do not match Caribbean materials I have examined; they do, however, conform to the yellowish phase of *C. squamuligera*. Should they prove synonymous Clessin's name will have priority, unless a case for treating it is as a *nomen oblitum* can be made.

This species is frequently found nestling in dead bivalve shells, or on small pebbles from the subtidal zone to 20 meters. It ranges from Gonzaga Bay, Gulf of California, Mexico (29°47′N), to Bahia Honda, Panama (7°43′N), also in the Galapagos Group (Indefatigable and Barrington Islands) and Clipperton Island.

Chama tinctoria new species

Figures 5 a-c

Chama pacifica auctt., not Broderip 1835 (Holotype BM(NH) 1950. 11.1.54, Indo-Pacific); Tryon 1872:119; Clessin 1889:15, pl. 7, fig. 2. Not *chama pacifica* Carpenter (Gould MS) 1857b (synonym of *Chama frondosa* Broderip 1835).

Chama broderipi auctt., not Reeve 1847 (Holotype BM(NH) 1952.4.9.1, Indo-Pacific); Tryon 1872:119; Lamy 1927:319 (as *Chama pacifica broderipi* Reeve 1847).

Diagnosis: This variable species can only be confused with *C. buddiana* Adams, but is more brightly colored and bears more spines on the upper valve, while the lower valve displays uniform radial costae never found on *C. buddiana*. Inside, the new species is more highly colored, and, though *C. buddiana* may be lightly maculated with pink or lilac, it never displays the bright rose brown. *C. tinctoria* has no colored marginal band.

Description: Shell very inequilateral, exterior of right valve brightly colored, with purple radial lines on anterior region, posterior white, central portions pink. Left valve exterior uniform brownish red. Sculpture of right valve consisting of short imbricated scales, white at the base and yellowish red at the tips. Left valve covered with shallow uniform radial costae, with sparse imbricated scales. Interior of right valve white, with a purple to brown patch. Interior of left valve white, flushed light brown to rose red with a darker border. Margin uniformly crenulated.

Holotype measurement: Length 32.5, height 37, width 29 mm.

Type locality: Bahia Honda, Panama, 7°43′16″N, 81°32′55″W, Allan Hancock Foundation ''Velero'' Station 249-34, in 28-37 meters.

Type deposition: AHF 169 (Holotype). AHF 170 (Paratype).

Etymology: Named from the Latin adjective *tinctorius*—of dyeing, to draw attention to the remarkable exterior and interior color combination.

Geographic range: Gulf of California (?). Tres Marias Islands, Mexico (21°26′N), to Bahia Honda, Panama (7°43′N).

Bathymetric range: 15 to 92 meters.

Habitat: Rocks and bivalve shells.

Discussion: Carpenter (1857b) cited ''*C. pacifica* Gould'' off the west coast of America and synonymized it with his *C. frondosa mexicana*. I have been unable to trace the specimen or any reference in Gould's publication to *C. pacifica* and consider it an MS name; however, it is possibly a *lapsus* for *C. pacifica* Broderip, which has appeared with its synonymous *C. broderipi* Reeve in eastern Pacific literature. Diguet in 1894 collected from the Gulf of California a large chamid he identified with *C. broderipi* Reeve, 1847. Lamy (1927) reviewing the collections in the Paris Museum cited Diguet's material as *C. pacifica broderipi* Reeve and accepted a pan-Pacific distribution. On examination of this specimen I concluded it is a distinct species with only superficial resemblance to Indo-Pacific representatives, and identical to two lots in the Allan Hancock Foundation collected off Mexico and the Gulf of Panama. As Diguet's material lacks a specific type locality and despite its large size, appears immature, I designate the Allan Hancock Foundation Panamic specimen as the type.

Chama venosa Reeve 1847

Figures 11 c-e

Chama venosa Reeve 1847: pl. 7, sp. 34 (Type locality: not stated. Syntypes BM(NH) 1950.11.1.4-6); Clessin 1889:36, pl. 16, fig. 6; Lamy 1927:341; Keen 1971:149, fig. 352.

Chama diqueti Rochebrune 1895:243 (Type locality: San Jose Island, Gulf of California, Mexico, 25°N. Syntypes MNHN); Keen 1971:149, fig. 350 (as *Chama sordida* Broderip 1835, left and center figures only).

Shell exterior smooth, with a few short scattered spines, white with an elegant pattern of fine reddish brown lines. Margins slightly and irregularly crenulated.

Discussion: This small species with parallel fine lines on the smooth shell cannot be mistaken. Superficially it is close to *P. janus* Reeve, but in this species the elegant fine lines are replaced by brown staining of the depths of radial striae and the upper valve demonstrates two distinct sculpture patterns. Keen (1971) illustrated the holotype of *C. digueti,* synonymizing it with *C. sordida* Broderip. Her illustration is one of three single specimens in the Paris Museum considered by Rochebrune when proposing his new species, but the description is based upon a syntypic cluster of 4 specimens. Lamy (1927) states this group to be the type lot and I believe Rochebrune drew attention to mutual fusion at the start of his description ''Testa aggregata . . .'' as the cemented nature of chamids was well established by then. I follow Lamy (1927) in considering *C. digueti* to be a junior synonym of *C. venosa* as it bears the flattened upper shell valve and reddish brown lines of the latter species and entirely lacks the bi-convex shape and long imbricated spines of *C. sordida.* A fine specimen in the d'Orbigny collection from Paita, Peru (BM(NH) 1954. 12.4.820) is undoubtedly this species.

This species has been collected on wharf pilings and dead shell from the subtidal zone to 4 meters. Distribution is centered in the Gulf of California, Mexico from 28°N and south possibly to Paita, Peru (5°S). Guaymas, Sonora, Mexico (29°52'N, 111°06'W), is here designated the type locality.

GENUS *ARCINELLA* SCHUMACHER 1817
(= *ECHINOCHAMA* FISHER 1887)

Type (monotype) *A. spinosa* Schumacher 1817 = *A. arcinella* Linné 1767.

Shell nearly equivalve, briefly cemented by right valve during early growth. Sculpture of radial rows of long, partially recurved spines, interspaces pitted, resulting in a reticulated appearance. Beaks prominent, prosogyrate. Lunule deeply impressed. Ligament short, deeply buried. Hinge elements as in *Chama* but more delicate. Nepionic shell distinctly demarcated, sculptured with concentric ridges.

Arcinella was first proposed by Oken (1815) for a carditid genus and is a senior homonym of *Arcinella* Schumacher 1817. In 1956 (Opinion 417) the ICZN rejected Oken as non-binomial, so *Arcinella* Oken no longer preoccupied Schumacher's genus. However, *Echinochama* Fischer 1887 is a synonym of *Arcinella* Schumacher; both cited *Chama arcinella* Linné 1767 as the type of the genus. Keen

(1962) summarized the situation, and pointed out that a rejected senior homonym has no status unless subsequently validated. On the basis of strict priority she proposed the use of *Arcinella* Schumacher. Nicol (1965) felt there may be some objection to adopting *Arcinella* and it could be considered a *nomen oblitum*. As no application has been made to the ICZN to retain *Echinochama* Fisher, and *Arcinella* Schumacher has appeared several times in the literature since Keen's 1962 article, it may be considered established in the taxonomy.

The gross external anatomy of *Arcinella* has already been discussed and appears very close to *Pseudochama*, except the foot is longer and the pedal aperture rather more ventral. The nepionic shell is similar to *Pseudochama* as is the abrupt post-neanic change in shell sculpture.

The taxon is confined to central America, appearing in the Early Miocene of Florida (Nicol 1952a). Speciation and distribution has occurred in the Caribbean, but the group is poorly developed on the Pacific side.

One eastern Pacific species:

Arcinella californica (Dall 1903)

Figure 6 g

Echinochama californica Dall 1903a:950, pl. 62, fig. 5 (figure only); Dall 1903b:1404, 1406. (Type locality: Cedros Island, Baja California, Mexico, 28°N, in 24 meters. Holotype USNM 96452); Keen, 1971:149, sp. 353 (as *Arcinella californica*).

Echinochama arcinella californica (Dall), Nicol 1952a:806, pl. 119, fig. 8; Olsson 1961:227, pl. 34, fig. 3.

Shell equivalve, whitish yellow, anterior portion produced into a lobe, lunule deep. Sculpture of symmetrical radial rows of long, sometimes recurved spines. Interior white, border finely crenulated.

Discussion: This rare species is closely related to the Caribbean *A. arcinella* (Linné 1767) but may be distinguished by the more produced anterior lobe, longer spines and more distinct surface pattern. Nicol (1952a) considered western representatives as only a subspecies of the Caribbean form and proposed a new subspecies *A.a. olssoni* for Pliocene or Pleistocene Pacific Panama material displaying particularly large flat spines.

The type locality of *A. californica* cited by Dall is Cerros (now Cedros) Island, situated on the outer coast of Baja California. Though Pilsbry and Lowe (1934) refer to single specimens dredged off Mexico at Manzanillo (19°N) and Acapulco (17°N) and the S. S. Berry collection contains several specimens from Angel de la Guarda Island, Gulf of California (29°N), the main distribution appears to be south of the Gulf of Tehuantepec (15°N). This species is represented in the Allan Hancock Foundation holdings by several small valves from Port Utria, Colombia (5°N). The geographic range is from Cedros Island, Mexico (28°N) to Port Utria, Columbia (5°58′N). Juveniles are generally attached to calcareous organic structures, particularly gastropod shells. The adults lie free on the substrate in 25 to 77 meters.

GENUS *PSEUDOCHAMA* ODHNER 1917

Type *Chama cristella* Lamarck 1819 (subsequent designation: J. Gardner 1926, see Nicol (1952b)).

Shell attached by right valve. Nepionic shell large, subquadrate. Other characters as of the family. Oligocene to Recent.

Seven eastern Pacific species:

ARTIFICIAL KEY TO WEST AMERICAN *PSEUDOCHAMA*

1.	Shell interior white, sometimes with brown patch	3
	Shell interior extensively streaked or uniformly colored	2
2.	Color streak rose or red	*P. clarionensis*
	Shell with extensive purple stain	*P. corrugata*
3.	Upper valve sculpture medially bisected	*P. janus*
	Upper valve sculpture not bisected	4
4.	Shell inner margins smooth or finely crenated	5
	Shell inner margins uniformly coarsely ridged	*P. saavedrai*
5.	Shell lacking obvious periostracum	6
	Shell with thin brownish periostracum	*P. dalli*
6.	Sculpture of numerous concentric lamellae and spines	*P. exogyra*
	Sculpture of irregular fluted broad spines	*P. panamensis*

Pseudochama clarionensis Willett 1938

Figures 12 e, f

Pseudochama clarionensis Willett 1938:48, pl. 4, figs. 1, 2 (Type locality: Off Clarion Island, Mexico, 18°22′N. Holotype LACM 1058, Paratype LACM 1058a); Keen 1971:151, fig. 354.

Shell exterior bright red, with scattered white, short, imbricated spines. The inner margin is delicately crenated. Interior white, clouded or streaked with bright rosy red.

Discussion: The short, white spines arising from the red exterior and the rich pinkish streaking of the interior distinguishes this elegant small species from all others. It is rarely collected and appeared endemic to Clarion Island until a specimen was collected in the Galapagos Islands (Keen 1971).

The species is generally cemented to small pebbles, or exists as colonies in fissures and on the underside of boulders in 27 to 55 meters. The northward range is Clarion Island, Mexico (18°22′N), extending southwards on the mainland coast to Isla del Tigre, Honduras (13°16′N). It is a frequent component of the rocky substrate epifauna of Barrington Island, Galapagos Group (0°51′S), but does not occur so far south on the mainland coast.

Pseudochama corrugata (Broderip 1835)

Figures 7 g, h

Chama corrugata Broderip 1835a:150 (Type locality: Corinto, Nicaragua, 12°29′N. Paratype BM(NH) 1950.11.1.23); Broderip 1835b:305, pl. 38, fig. 7; Reeve 1847: pl. 2, fig. 9; Clessin 1889:37, pl. 16, fig. 2; Lamy 1910:88.

Pseudochama corrugata (Broderip), Olsson 1961:226, pl. 34, fig. 4-4d; Keen 1971:151, fig. 355.

Shell highly variable, sculpture generally obscure, sometimes with broad foliations, exterior radially grooved, often with brown lines. Interior with extensive purple staining.

Discussion: This is the largest of western American *Pseudochama* and is easily recognized by the extensive purple staining of the shell interior. It is the commonest off the northern Peruvian coast, more rarely occurring off Panama, and sporadically to the Gulf of California, Mexico. It is a warm water species and does not extend into the cool water south of Point Aguja, Peru. The geographic range is from Sechura Bay, Peru (5°40′S), to Isla Partida, Mexico (28°52′N). *P. corrugata* is generally cemented to rock in exposed locations, more rarely on dead bivalve shell, in the intertidal zone to 5 meters.

Pseudochama dalli new name

Figure 12 d

Chama inermis Dall (Carpenter MS) 1871:148 (Type locality: unknown: not Puget Sound, Washington. Holotype USNM 24108). Not *Chama imbricata inermis* Deshayes 1863.

Pseudochama inermis (Dall), Palmer 1963:307, pl. 61, fig. 8-10; Keen 1971:151, fig. 356.

Shell smooth, covered by a thin adherent brownish yellow periostracum. Free valve may bear a purple ray. Interior white, sometimes with a purple brown patch. Margin smooth.

Discussion: This rare species is readily identifiable by the lack of exterior processes and the thin shining periostracum. It may possibly be a teratological specimen of *P. panamensis* (Reeve) but until more material is available the taxon must be retained. The holotype was obtained supposedly from Puget Sound, by J. Rowell, who collected from California to Panama. This material was deposited in the Smithsonian Institution and examined by P. P. Carpenter, who correctly surmised that it was tropical and not from Puget Sound. Because of the doubtful type locality Carpenter did not release his manuscript name and description for this species. Dall published the name; however, it is preoccupied by Deshayes (1863) for a variety of *Chama imbricata* Broderip 1835 from the Indian Ocean. Pilsbry and Lowe (1934) illustrate a fine specimen collected in 1930 from the Tres Marias Islands off Mexico. The species occurs from Panama Bay, Panama (9°N) to Tres Marias Islands, Mexico (21°26′N) and has been collected only from wooden pilings at the subtidal level to 5 meters. The type location, Tres Marias Islands, Mexico (21°26′N) is here designated.

Pseudochama exogyra (Conrad 1837)

Figures 10 d-f

Chama exogyra Conrad, 1837:356 (Type locality: Santa Barbara, California, 34°23′N. Syntypes BM(NH) 1961.5.20.155); Reeve 1847: pl. 7, fig. 38; Tryon 1872:117; Clessin 1889:26, pl. 10, fig. 5; Lamy 1927:337.

Pseudochama exogyra (Conrad), Durham 1950:73, pl. 17, figs. 4, 13 (Pliocene to Recent of Mexico); Addicott 1964:146 (Pleistocene of California); Yonge 1967:49; Smith and Gordon 1948:173.

Pseudochama granti Strong 1934:137, pl. 8, figs. 6, 7 (Type locality: Clarion Island, Mexico, 18°N. Holotype CAS 5808); Smith and Gordon 1948:137; Dibblee 1966:58 (Pleistocene of California).

Shell white, sometimes splashed with red, more rarely with green. Sculpture of concentric lamellae that may be produced into broad spines. Interior white, inner margin smooth; commissural shelf may be wide.

Discussion: This most northerly representative of *Pseudochama* may be difficult to recognize due to excessive abrasion and obliteration of the surface detail, but the plain shell margins and translucency of the exterior surface made it unlikely to be confused with other species. I consider *P. granti* Strong the subtidal form in which the sculpture tends to be smaller and more regular, less likely to be eroded. The type variant of *P. exogyra* is intertidal or just subtidal, and is distributed from central Oregon (approximately 44°N), to San Diego, California (32°40′N). *P. granti* occurs from 20 to 155 meters and extends from the southern British Columbia border (48°N) to San Benito Island, Mexico (28°N). In 1962 I collected a single specimen in 155 meters off the west coast of the Queen Charlotte Islands (53°N). Clarke and Clarke (1974) reported a single specimen of *P. exogyra* from a Nootka Indian shell midden on the west coast of Vancouver Island, British Columbia (49°35′N). A number of other molluscan species have been collected from time to time far from their normal range. These chance occurrences cannot be considered part of the normal distribution pattern as the errant specimens do not constitute established, breeding populations.

Odhner (1919) considered *P. exogyra* to be identical to *echama rotunda* Clessin, 1889 from the Gulf of Mexico. I do not agree with his conclusion.

Pseudochama janus (Reeve 1847)

Figure 11 a, b

Chama imbricata var α Broderip 1835a:149 (Type locality: Galapagos Islands. Syntypes BM(NH) 1950.11.1.36-38); Broderip 1835b:304, pl. 39, fig. 3; Soot-Ryen 1931:314.

Chama janus Reeve 1847: pl. 7, sp. 36 (Type locality: Galapagos Islands. Syntypes BM(NH) 1950.11.1.36-38); Clessin 1889:43, pl. 17, fig. 6; Lamy 1927:340.

Pseudochama janus (Reeve), Keen 1971:151, fig. 357.

Exterior with a uniform elegant brown striping. Upper valve medially bisected into two distinct surface patterns of ornamentation, the posterior section with brown lines and a few short scales. Interior white, margins crenulated only on dorsal posterior portion.

Discussion: The medial bisection of the free valve into two distinct pattern zones readily distinguishes this species from all other west American chamids.

There is no doubt that material from different locations was included by Broderip when he proposed *C. imbricata*. The nominate species is a common Indo-Pacific chamid, while var α is Galapagan and Reeve was correct in suggesting a new name. Odhner (1919) considered *P. janus* synonymous with *P. corrugata* (Broderip 1835), a totally unwarranted conclusion. The species appears endemic to the Galapagos Islands, cemented to molluscan shells in 10 to 25 meters. Osorio and Bahamonde (1970) record *C. imbricata* Broderip 1835 from the Juan Fernandez Islands (33°S), and the literature contains records of *P. janus* from Mexico. I have been unable to confirm these records and consider them probably due to misidentification of *P. panamensis* (Reeve 1847).

Pseudochama panamensis (Reeve 1847)

Figures 12 a-c

Chama panamensis Reeve 1847: pl. 8, sp. 45 (Type locality: Panama. Holotype (BM(NH) 1950.11.1.23); Clessin 1889:32, pl. 13, fig. 5; Lamy 1927:330.

Pseudochama panamensis (Reeve), Olsson 1961:225, pl. 33, fig. 1-1b; Keen 1971:151, fig. 358.

Shell generally dorsoventrally prolonged. Exterior white, with delicate lines of brown. Attached valve with a few hyote spines. Free valve with concentric rows of wide longitudinally ribbed imbricated spines and a small area of the dorsal posterior portion with concentric scales. Interior white, sometimes with patches of brown or yellow, shell margins smooth. Attachment area extensive.

Discussion: This species, though with a wide range, is of sporadic occurrence. The ribbed imbricated spines of the upper valve and small zone of concentric lamellae (''two-fold structure'' of Reeve) easily distinguish it from other chamids. However, specimens with poor sculpture and heavy brown striping may be mistaken for *P. janus* (Reeve). This species appears limited to clefts and fissures in massive rocks from the middle tidal level to 10 meters. The range is from Gonzaga Bay, Gulf of California, Mexico (29°50′N) to Cape San Francisco, Ecuador (0°40′N). The original type locality ''Panama'' is vague, so Punta Garachina, Panama (8°07′N, 78°39′W) is here designated the type locality.

Pseudochama saavedrai Hertlein and Strong 1946

Figures 8 d-f

Pseudochama saavedrai Hertlein and Strong 1946:110, pl. 1, figs. 1, 3, 8, 10. (Type locality: Manzanillo, Mexico, 19°00′N, in 45 meters. Holotype CAS 9189A.); Hertlein 1957:63 (Pleistocene of Mexico); Keen 1971:151, fig. 359.

Shell white to light yellow. Lower valve with concentric appressed lamellae. Upper valve ornamented with concentric longitudinally striated lamellae, prolonged into two radial rows of wide imbricated spines. Interior white, margins coarsely crenulated, comissural shelf wide. Attachment area small.

Discussion: The species is readily distinguished by the overlapping lamellae produced into two radial rows of spines. The holotype is a poor specimen and does not do justice to the beauty of this species. Material from Panama in the Allan Hancock Foundation holdings and other collections is more solid than Mexican representatives and the lamellae are shorter and coarser but it is undoubtedly this species.

P. saavedrai is frequently attached to dead shells in regions of small cobbles and rock fragments in the low intertidal to 55 meters. In ranges from Puerto Penasco, Gulf of California, Mexico (31°20′N) to Chacahua Bay, Mexico (15°55′N) and the Allan Hancock Foundation has material from Secas Island, Panama (7°58′N).

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My sincere appreciation is due to J. S. Garth, Senior Curator (now Professor Emeritus) of the Allan Hancock Foundation, for placing the chamid collection in my hands. As this material largely consists of detached, often juvenile, valves unsuitable for illustration, I am indebted to fellow workers, notably S. S. Berry, C. Angermeyer, and the late W. J. Eyerdam, who donated specimens that are now on deposit in the Los Angeles County Museum of Natural History. I am also indebted to K. M. Way of the British Museum (Natural History) for furnishing biographical details of certain nineteenth century collectors and to J. Rosewater of the United States National Museum for the loan of type material. I am grateful to E. V. Coan, A. M. Keen and J. H. McLean for generous advice and constructive criticism.

RESUMEN

Diecinueve especies de Chamidae viven en el Pacífico Oriental Americano y predominan en aguas templadas poco profundas. Las amplias colecciones de la Fundación Allan Hancock de la universidad del Sur de California proporcionan las bases para esta revisión sistemática y distributiva. Se concluye que se ha determinado genéticameente la valva de u ión. Se presenta una nueva interpretación de la ontogénesis principal. Se propone el nombre *Pseudochama dalli* para un nombre ya asignado. También se proponen tres nuevas especies *Chama arcana, C. garthi* y *C. tinctoria*.

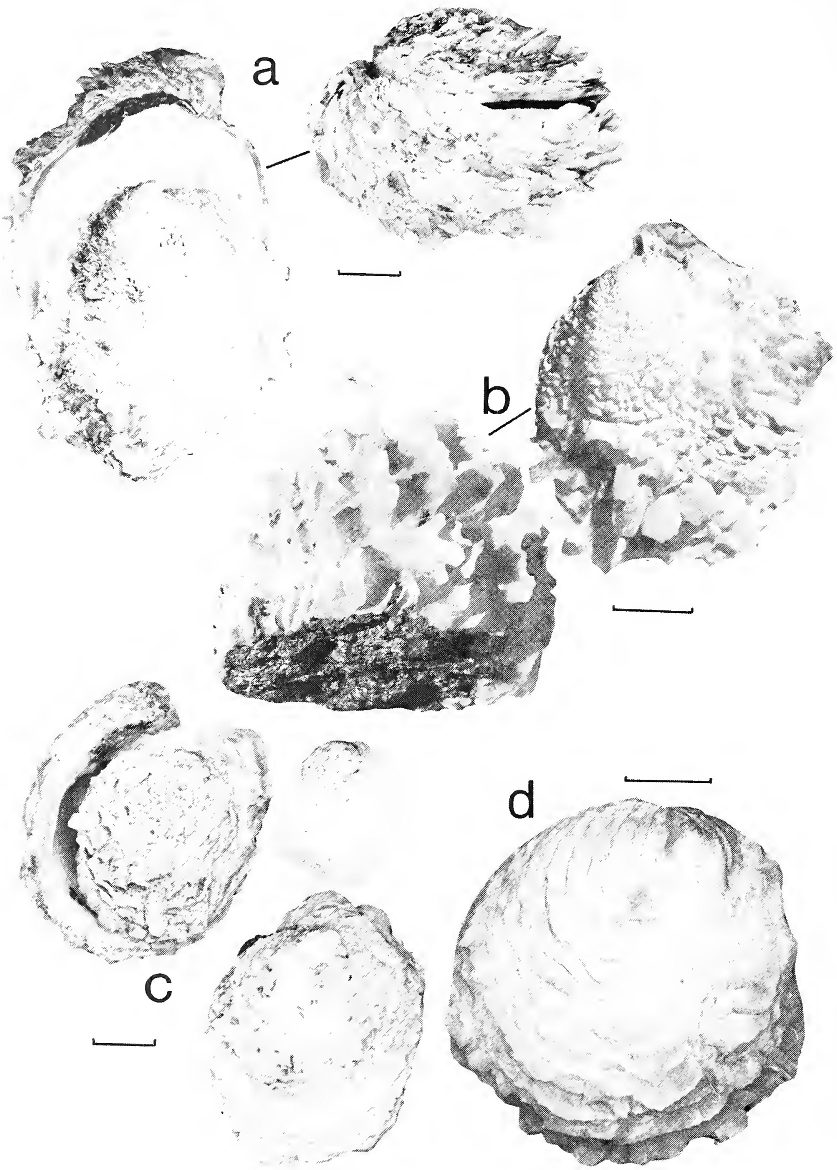

FIGURE 4. (a) *Chama arcana* new species, Newport Bay, California, holotype, LACM 1723; (b) *Chama arcana* new species, Monterey, California, LACM A8881.1; (c) *Chama pellucida Broderip, Iquique, Chile, topotypes, LACM A8881.2; (d) Chama chilensis* Philippi (= *C. pellucida*), Pliocene, Laguna de Cahuil, Chile, holotype, MNHN no number. Scale = 1 cm.

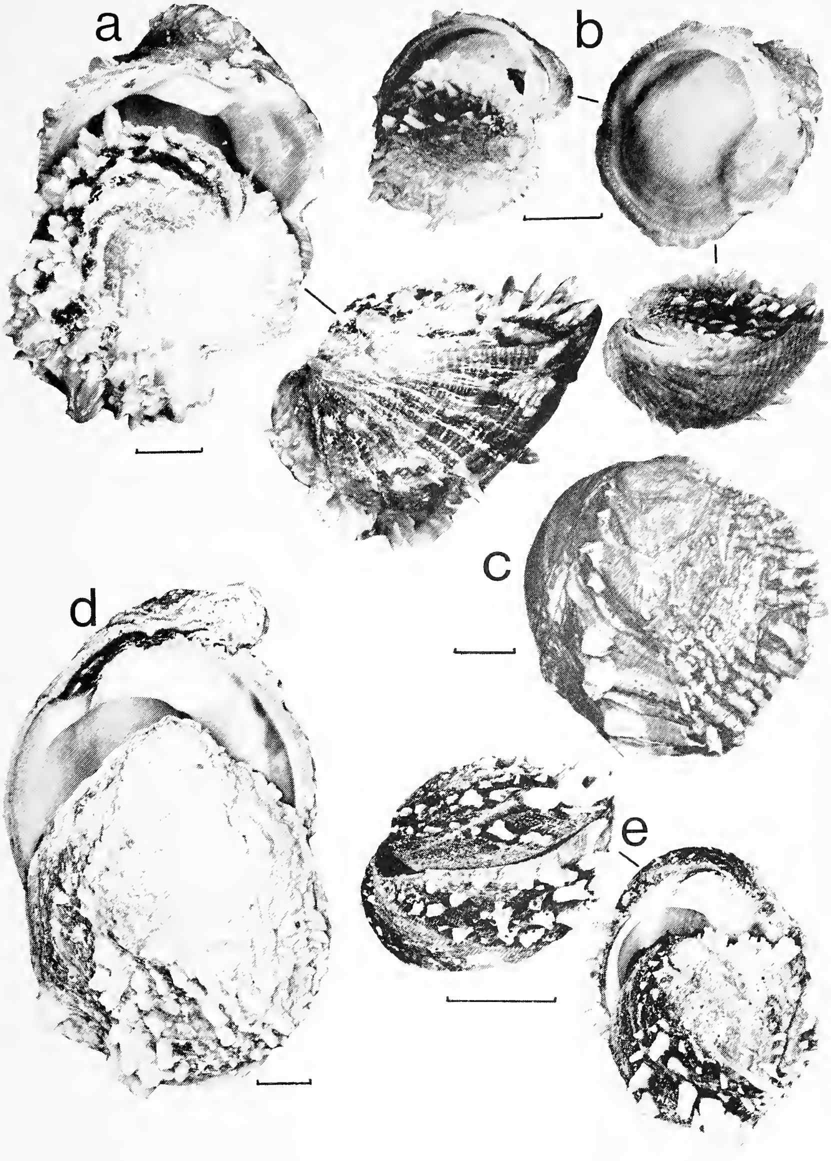

FIGURE 5. (a) *Chama tinctoria* new species, Bahia Honda, Panama, holotype, AHF 169; (b) *Chama tinctoria* new species, Bahia Honda, Panama, paratype, AHF 170; (c) *Chama tinctoria* new species, Panama Bay, Panama, MNHN no number; (d) *Chama buddiana* C. B. Adams, Isla del Rey, Panama Bay, Panama, LACM A8881.3; (e) *Chama buddiana* C. B. Adams, Albemarle Island, Galapagos Islands, Ecuador, LACM A8881.4. Scale = 1 cm.

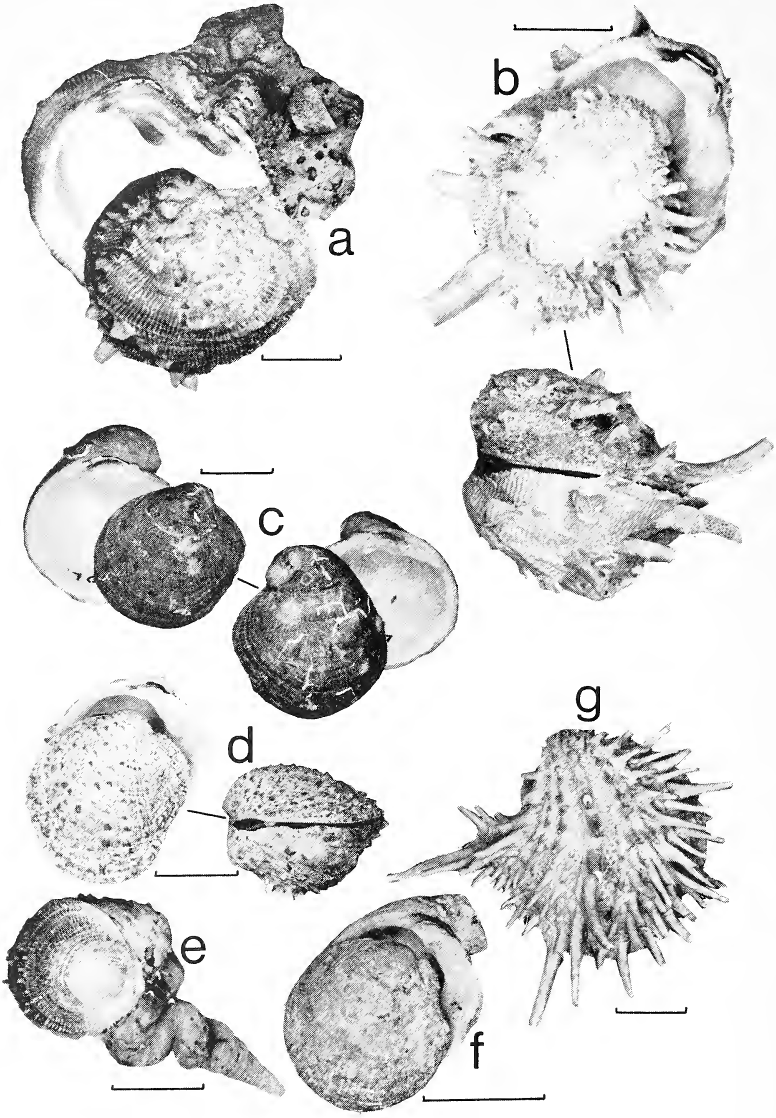

FIGURE 6. (a) *Chama sordida* Broderip, Isle of Cuna, Central America, syntype, BM(NH) 1950.11.1.52; (b) *Chama sordida* Broderip, Gorgona Island, Colombia, AHF 1262; (c) *Chama corallina* Olsson, Punta Escondido, Panama, holotype, USNM 701157; (d) *Chama corallina* Olsson, Isla Cinche, Bahia Honda, Panama, LACM A881.5; (e) *Chama corallina* Olsson, Gulf of California, Mexico, Mrs. E. E. Wahrenbrock; (f) *Chama corallina* Olsson, Punta Escondido, Panama, topotype, AHF 1264; (g) *Arcinella californica* (Dall), Cedros Island, Mexico, holotype, USNM 96252. Scale = 1 cm.

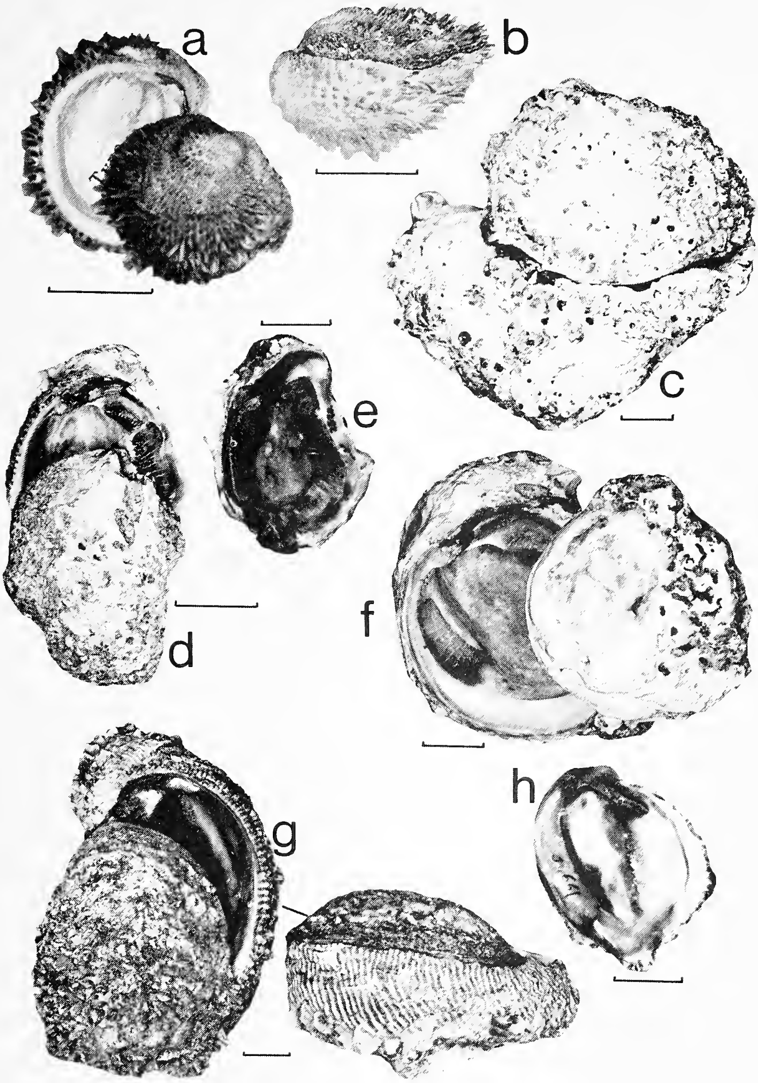

FIGURE 7. (a) *Chama echinata* Broderip, Puerto Portrero, Ecuador, syntype, BM(NH) 1950.11.1.21; (b) *Chama echinata* Broderip, Banderas Bay, Mexico, LACM A8881.6; (c) *Chama echinata* Broderip, Isla Bona, Gulf of Panama, Panama, LACM A8881.7; (d) *Chama echinata* Broderip, Banderas Bay, Nayarit, Mexico, LACM A8881.19; (e) *Chama echinata* Broderip, Cedros Island, Mexico, LACM A8881.8; (f) *Chama coralloides* Reeve (= *C. echinata*), Puerto Portrero, Ecuador, holotype, BM(NH) no number; (g) *Pseudochama corrugata* (Broderip), Tumbez, Peru, CAS 36666; (h) *Pseudochama corrugata* (Broderip), Caleto Mero, Peru, CAS 36661. Scale = 1 cm.

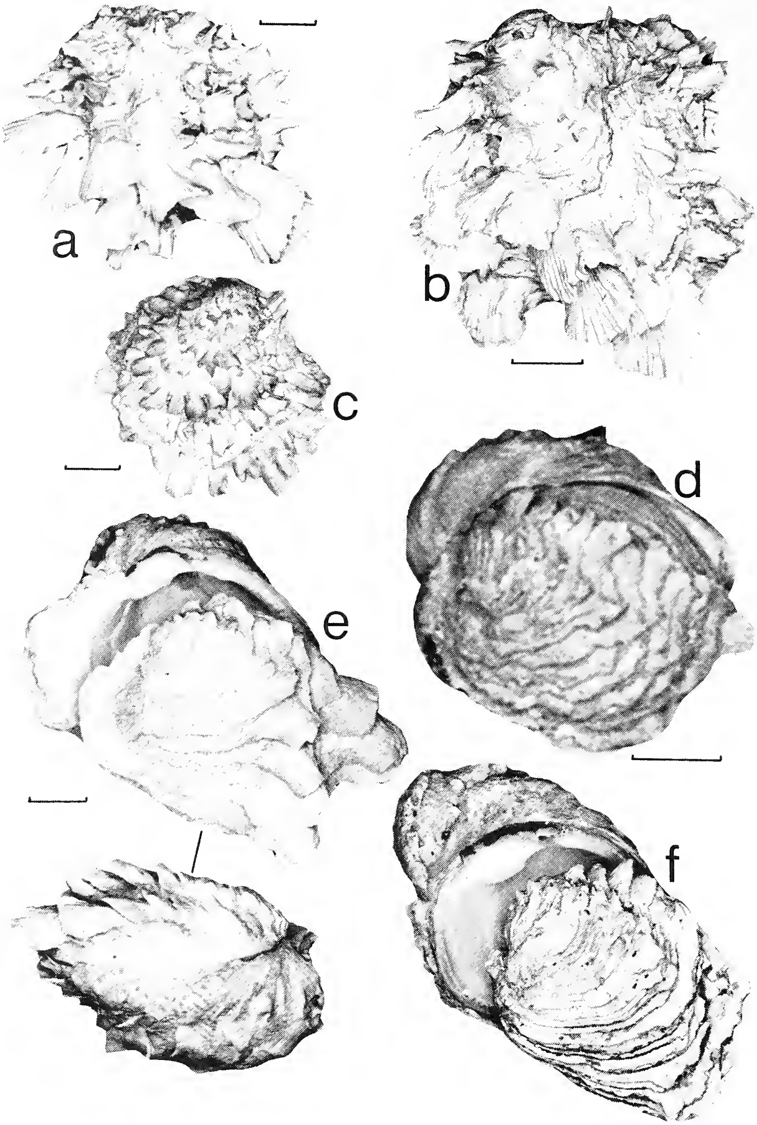

FIGURE 8. (a) *Chama frondosa* Broderip, Isla La Plata, Ecuador, holotype, BM(NH) 1950. 11.1.55; (b) *Chama frondosa* Broderip, Isla La Plata, Ecuador, paratype, BM(NH) 1950. 11.1.54; (c) *Chama parasitica* Rochebrune (= *C. frondosa*), San Jose Island, Mexico, holotype, MNHN no number; (d) *Pseudochama saavedrai* Hertlein and Strong, Manzanillo, Mexico, holotype, CAS 9189A; (e) *Pseudochama saavedrai* Hertlein and Strong, Manzanillo, Mexico, topotype, LACM A5498; (f) *Pseudochama saavedrai* Hertlein and Strong, Secas Island, Panama. LACM A8881.9. Scale = 1 cm.

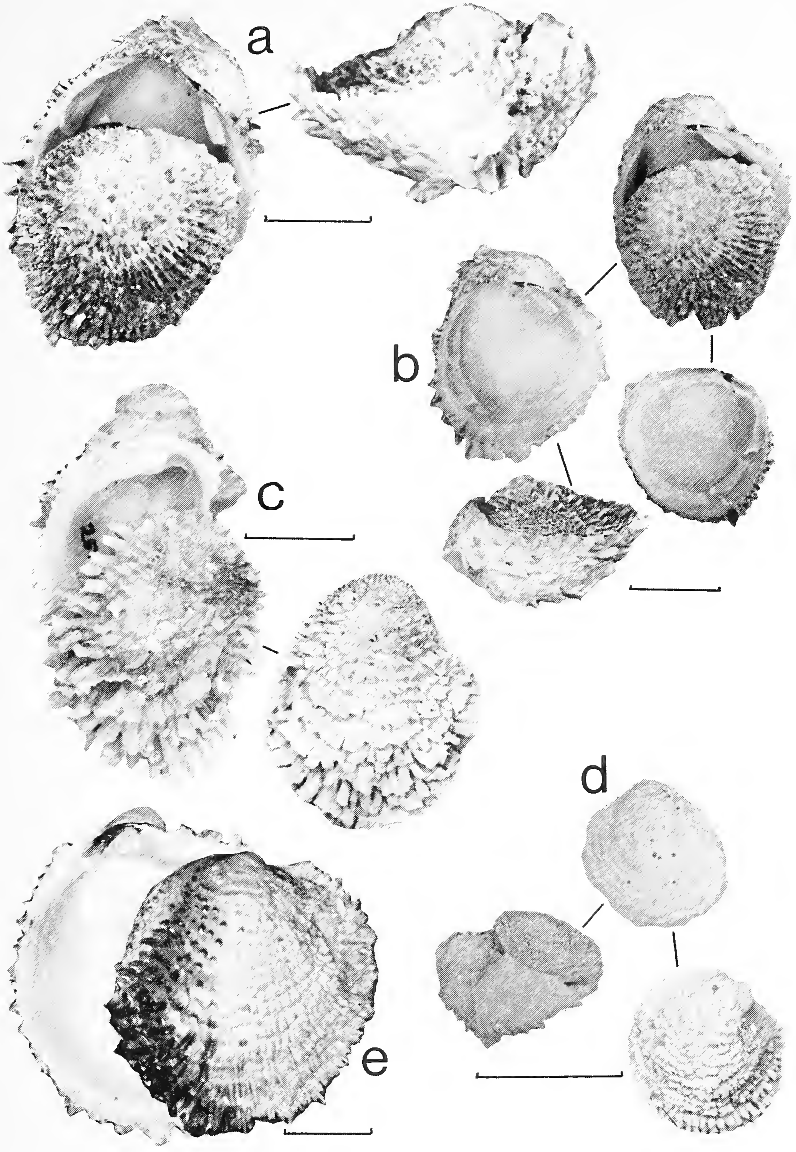

FIGURE 9. (a) *Chama garthi* new species, Octavia Bay, Colombia, holotype, AHF 167; (b) *Chama garthi* new species, Octavia Bay, Colombia, paratype, AHF 168; (c) *Chama squamuligera* Pilsbry and Lowe, Santa Cruz Island, Galapagos Islands, Ecuador, LACM A8881.10; (d) *Chama squamuligera* Pilsbry and Lowe, Barrington Island, Galapagos Islands, Ecuador, LACM A8881.11; (e) *Chama spinosa* Broderip, South Marutea (extralimital), holotype, BM(NH) no number. Scale = 1 cm.

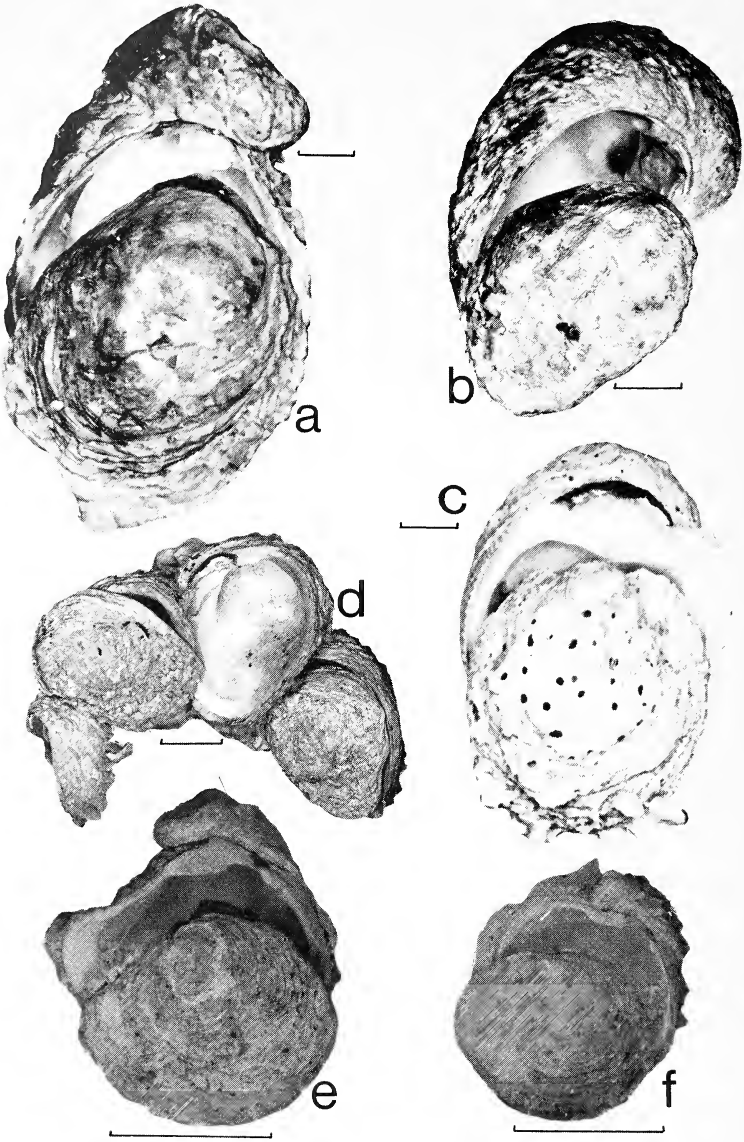

FIGURE 10. (a) *Chama producta* Broderip (= *C. mexicana*), Gulf of Tehuantepec, Mexico, holotype, BM(NH) 1950.11.1.60; (b) *Chama frondosa fornicata* Carpenter (= *C. mexicana*), Mazatlan, Mexico, syntype, BM(NH) Carpenter Collection 440; (c) *Chama mexicana* Carpenter, Bahia Concepcion, Baja California, Mexico, LACM A8881.12; (d) *Pseudochama exogyra* (Conrad), Santa Barbara, California, syntypes, BM(NH) 1961.5.20.155; (e) *Pseudochama exogyra* (Conrad), Vancouver Island, British Columbia, Canada, LACM A8881.13; (f) *Pseudochama exogyra* (Conrad), Catalina Island, California, LACM A8881.14; Scale = 1 cm.

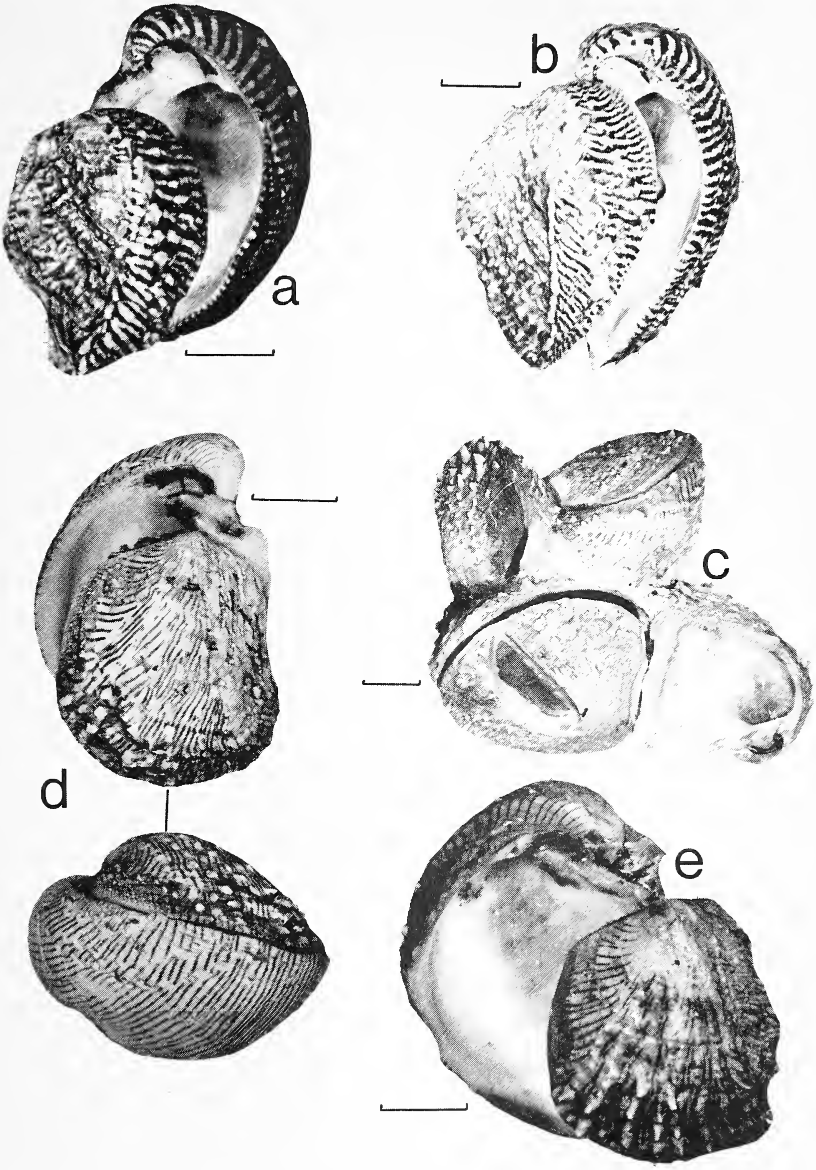

FIGURE 11. (a) *Pseudochama janus* (Reeve), Galapagos Islands, Ecuador, holotype, BM(NH) 1950.11.1.36; (b) *Pseudochama janus* (Reeve), Albemarle Island, Galapagos Islands, Ecuador, LACM A8881.15; (c) *Chama digueti* Rochebrune (= *C. venosa*), San Jose Island, Mexico, syntypes, MNHN no number; (d) *Chama venosa* Reeve, Guaymas, Gulf of California, Mexico, BM(NH) no number; (e) *Chama venosa* Reeve, locality unknown, holotype, BM(NH) 1950.11.1.4. Scale = 1 cm.

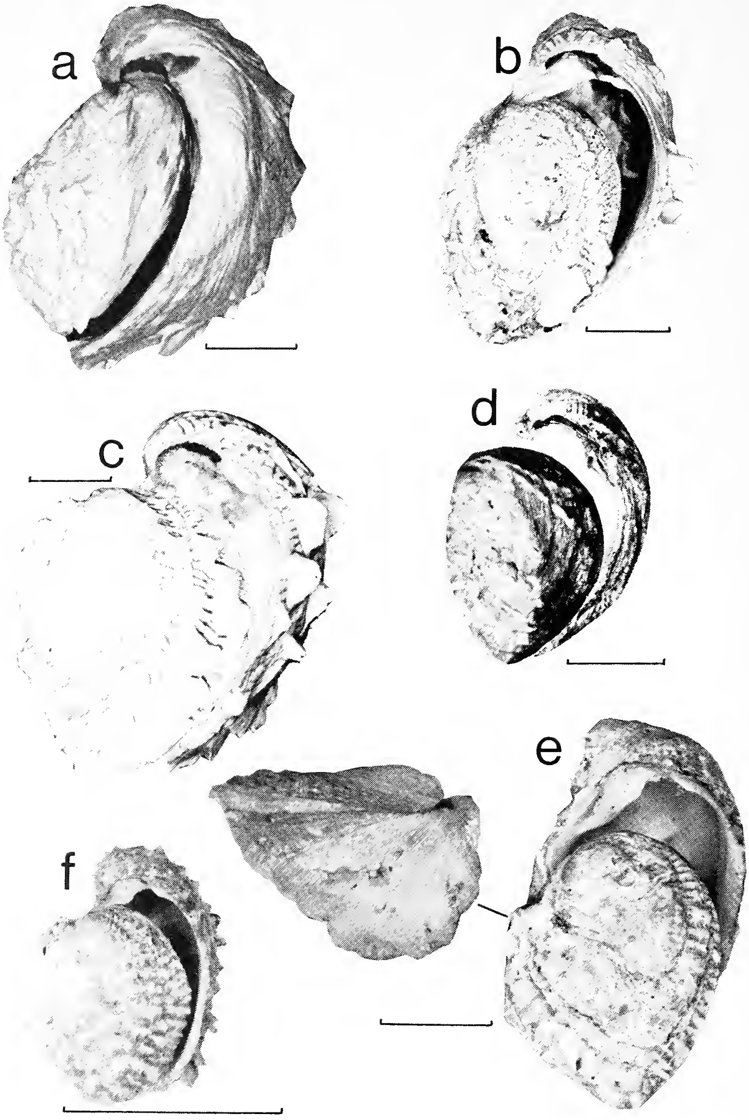

FIGURE 12. (a) *Pseudochama panamensis* (Reeve), Panama, holotype, BM(NH) 1950.11.1.23; (b) *Pseudochama panamensis* (Reeve), Bahia Gonzaga, Gulf of California, Mexico, LACM A8881.16; (c) *Pseudochama panamensis* (Reeve), La Paz, Baja California, Mexico, MNHN no number; (d) *Pseudochama dalli* new name (= *C. inermis*), Panama Bay, Panama, BM(NH) no number; (e) *Pseudochama clarionensis* Willett, Barrington Island, Galapagos Islands, Ecuador, LACM A8881.17; (f) *Pseudochama clarionensis* Willett, Clarion Island, Mexico, LACM A8881.18. Scale = 1 cm.

LITERATURE CITED

ADAMS, C. B. 1852. Catalogue of shells collected at Panama, with notes on synonymy, station, and habitat. R. Craighead, New York, viii + 334 pp.

ADDICOTT, W. O. 1964. Pleistocene invertebrates from the Dume Terrace, western Santa Monica Mountains, California. Bull. So. California Aca. Sci. 63(3):141-150, fig. 1, 2.

ANTHONY, R. 1905. Influence de la fixation pleurothetique sur la morphologie des mollusques acephales dimyaires. Ann. Sci. Nat. Zool. 1(9):165-396.

ARNOLD, R. 1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Mem. California Acad. Sci. 3:1-420, pls. 1-37.

———. 1910. Paleontology of the Coalinga District, Fresno and Kings Counties, California. U.S. Geol. Surv. Bull. 396:1-173, pls. 1-30.

ATKINS, D. 1937. On the ciliary mechanisms and interrelationships of Lamillibranchs Part III. Types of gills and their food currents. Quart. Jour. Microscop. Sci. 79:375-421.

BARTSCH, P., AND H. A. REHDER. 1939. Mollusks collected on the Presidential Cruise of 1938. Smithsonian Misc. Coll. 98(10):1-18, pls. 1-5.

BAYER, F. M. 1953. The Florida species of the family Chamidae. Nautilus 56(1):116-124.

BERNARD, F. 1895. Premiere note sur le développement et la morphologie de la coquille chez les Lamellibranches. Bull. Soc. Geol. France (3) 23:104-154.

———. 1897. Quatrième et dernière note sur le développement et la morphologie de la coquille chez les Lamellibranches. Bull. Soc. Geol. France (3) 25:559-566.

BÖHM, G. 1891. *Megalodon, Pachyerisma* und *Diceras.* Berliner Naturforsch. Gesellsch. 6:33-56.

BRODERIP, W. J. 1835a. Descriptions of some species of *Chama.* Proc. Zool. Soc. London for 1834:148-151.

———. 1835b. On the genus *Chama,* Brug., with descriptions of some species apparently not hitherto characterized. Trans. Zool. Soc. London 1; 301-306, pls. 38-39.

BRODERIP, W. J. AND G. B. SOWERBY. 1832. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. Proc. Zool. Soc. London for 1832:50-61.

CARPENTER, P. P. 1857a. Catalogue of the Reigen Collection of Mazatlan Mollusca in the British Museum. Oberlin Press, England. xii + 552 pp.

———. 1857b. Report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. Rept. 26th Meeting Brit. Ass. Adv. Sci., 1856:159-368, pls. 6-9.

———. 1864. Review of Prof. C. B. Adam's "Catalogue of the shells of Panama" from the type specimens. Proc. Zool. Soc. London 1863:339-369.

CHAVAN, A. 1966. Remarques sur l'origine des Lucinacea (Mollusques Pélécypodes). Soc. Géol. France Compt. Rendu 1966:163-164.

CHENU, J. C. 1842-53. Illustrations conchyliologiques, ou descriptions et figures de toutes les coquilles connues, vivantes et fosseles. Paris, 4 vols. 215 pp., 481 pls.

CLARKE, A. H. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. Canada Nat. Mus. Bull. 181: 114 pp.

CLARKE, L. R. AND A. H. CLARKE. 1974. Mollusk utilization by Nootka Indians, 2300 B.C. to A.D. 1966. Bull. American Malac. Union (1974), 15-16.

CLESSIN, S. 1889. Die Familie der Chamidae, *in* Martini and Chemnitz, Systematisches Conchylien Cabinet 8:1-56, pls. 1-20.

CONRAD, T. A. 1837. Descriptions of marine shells from Upper California, collected by Thomas Nuttall, Esq. Jour. Acad. Nat. Scie. Philadelphia 7(2):227-269, pls. 17-20.

DACQUÉ, E. 1915. Grundlagen und Methoden der Palaeogeographie. Gustave Fisher, Jena. 499 pp.

DALL, W. H. 1871. Descriptions of sixty new forms of mollusks from the west coast of America and the North Pacific Ocean, with notes on others already described. Amer. Jour. Conch. 7(2):93-160, pls. 13-16.

________. 1903a. Synopsis of the family Astartidae, with a review of American species. Proc. U.S. Nat. Mus. 26(1343):933-951, pls. 62-63.

________. 1903b. Contribution to the Tertiary fauna of Florida . . . Part VI. Trans. Wagner Free Inst. Sci. Philadelphia 3(6):1219-1654, pls. 48-60.

________. 1921. Summary of marine shellbearing mollusks of the northwest coast of America. Bull. U.S. Nat. Mus. 112:217 pp., 22 pls.

DALL, W. H., P. BARTSCH AND H. A. REHDER. 1938. A manual of the recent and fossil marine pelecypod mollusks of the Hawaiian Islands. Bishop Mus. Bull. 153:233 pp., 57 pls.

DESCHASEAUX, C. 1952. Classe des lamellibranches. *in* J. Piveteau. Traité de Paléontologie. Paris. 2, 790 pp.

DESHAYES, G. P. 1863. Catalogue des Mollusques de l'Ile de la Réunion (Bourbon) *In* L. Maillard. Notes sur l'Ile de la Réunion (Bourbon) 2nd ed. Paris 2 vols.

DURHAM, J. W. 1950. 1940 E. W. Scripps cruise to the Gulf of California, Part 2: Megascopic paleontology and marine stratigraphy. Geol. Soc. America Mem. 43:1-216, pls. 1-48.

EGGLETON, F. E. AND G. M. DAVIES. 1961. Hinge tooth reversal in populations of Ohio Sphaeriidae. Rep. Am. Malac. Un. Pacific Div. 1961. 19-20.

EMERSON, W. K. 1960. Results of the Puritan-American Museum of Natural History Expedition to western Mexico. 12. Shell middens of San Jose Island. American Mus. Novitates 2013:1-9, fig. 1-4.

EMERSON, W. K. AND L. G. HERTLEIN. 1964. Invertebrate megafossils of the Belvedere Expedition to the Gulf of California. Trans. San Diego Soc. Nat. Hist. 13(17):333-368, fig. 1-6.

FISCHER, P. H. 1880-1887. Manuel de Conchyliologie et de Paléontologie conchyliologique. Histoire naturelles des Mollusques vivants et fossiles, Paris, 1008 pp.

GARDNER, J. 1926. The molluscan fauna of the Alum Bluff group of Florida Part II. Astartacea, Carditacea, Chamacea. U.S. Geol. Surf. Prof. Paper 141-B:81-99, pls. 16, 17.

GRANT, U. S. AND H. R. GALE. 1931. Catalogue of the marine Pliocene and Pleistocene mollusca of California and adjacent regions. Mem. San Diego Soc. Nat. Hist. 1:1-1036, pls. 1-32.

GRIESER, E. 1913. Über die anatomie von *Chama pellucida* Broderip. Zool. JB. 4. Fauna Chilensis (Supp. 13):207-280.

HAMILTON, E. L. 1956. Sunken islands of the Mid-Pacific Mountains. Geol. Soc. America Mem. 64:1-97.

HANNA, M. A. 1925. Notes on the genus *Venericardia* from the Eocene of the West Coast of North America. Univ. Calif. Pub. Bull. Dept. Geol. Scie. 15:281-306.

HERTLEIN, L. G. 1957. Pleistocene and Pliocene fossils from the southern portion of the Gulf of California. Bull. So. Calif. Acad. Sci. 56(2):57-75, pl. 13.

HERTLEIN, L. G. AND E. C. ALLISON. 1966. Additions to the molluscan fauna of Clipperton Island. Veliger 9(2):138-140.

HERTLEIN, L. G. AND W. K. EMERSON. 1953. Mollusks from Clipperton Island (Eastern Pacific) with the description of a new species of gastropod. Trans. San Diego Soc. Nat. Hist. 11(13):345-364, pls. 26-27.

________. 1956. Marine Pleistocene invertebrates from near Puerto Penasco, Sonora, Mexico. Trans. San Diego Soc. Nat. Hist. 12(8):154-176, pl. 12.

HERTLEIN, L. G. AND U. S. GRANT. 1972. The geology and paleontology of the marine Pliocene of San Diego, California (Paleontology: Pelecypoda). Mem. San Diego Soc. Nat. Hist. 2(B):143-409, pls. 1-57.

HERTLEIN, L. G., AND A. M. STRONG. 1946. Eastern Pacific expeditions of the New York Zoological Society. Mollusks from the west coast of Mexico and Central America. Part IV. Zoologica 31:93-130, pl. 1.

________. 1955. Marine mollusks collected at the Galapagos Islands during the voyage of the *Velero III* 1931-1932. *In* Essays in the natural sciences in honor of Captain Allan Hancock. Univ. So. Calif. (Los Angeles):111-145, pl. A.

JACKSON, R. T. 1890. Phylogeny of the Pelecypoda. The Aviculidae and their allies. Mem. Boston Soc. Nat. Hist. 4(8):277-400, pls. 23-30.

KEEN, A. M. 1962. Nomenclatural notes on some west American mollusks, with proposal of a new species name. Veliger 4:178-180.

________. 1968. West American mollusk types at the British Museum (Natural History). IV. Carpenter's Mazatlan Collection. Veliger 10(4):389-439, pls. 55-59.

________. 1971. Sea Shells of tropical west America. 2nd Ed. Stanford Univ. Press, U.S.A. xiv + 1064 pp, 22 pls, approx. 3400 figs.

KENNEDY, W. J., N. J. MORRIS AND J. D. TAYLOR, 1970. The shell structure, mineralogy and relationships of the Chamacea (Bivalvia). Palaeontology 13(3):379-413, pls. 70-77.

KEEP, J. 1888. West coast shells. S. Carson Co., San Francisco. 230 pp.

LABARBERA, M. AND P. CHANLEY. 1971. Larval and postlarval development of the corrugated jewel box clam *Chama congregata* Conrad (Bivalvia: Chamidae). Bull. Mar. Sci. 21:733-744.

LAMARCK, J. B. DE. 1819. Histoire naturelle des animaux sans vertèbres. Paris. Vol. 6. 343 p.

LAMY, E. 1910. Mollusques marines recueillis par M. le Dr. Rivet a Payta (Perou). Mission pour la mesure d'un arc de meridien equatorial en Amerique du Sud (1899-1906). 9(3):78-91.

________. 1927. Revision des *Chama* vivants du Museum National d'Histoire Naturelle de Paris. Jour. Conchyl. 71:293-383.

LINNÉ, C. 1758. Systema naturae per regna tria naturae. Stockholm. Ed. 10, reformata, vol. 1, Regnum animale, 824 pp.

________. 1767. Systema naturae per regna tria naturae. Stockholm. Ed. 12, reformata, vol. 1, Regnum animale, part 2, p. 533-1327.

LOCARD, A. 1898. Expéditions Scientifiques du Travailleur et du Talisman . . . Mollusques Testacés, 2:369-482, pls. 15-18, 1 map.

LOWENSTAM, H. A. 1954. Environmental relationships of modification composition of certain carbonate-secreting marine invertebrates. Proc. Nat. Acad. Sci. 40:39-48.

________. 1963. Biological problems relating to the composition and diagenesis of sediments, *in* T. W. Donnelly. The Earth Sciences: Problems and progress in current research. University of Chicago Press: 138-195.

MARINCOVICH, L. 1973. Intertidal mollusks of Iquique, Chile. Natural History Museum Los Angeles County. Science Bull. 16, 49 pp. 102 figs.

MENEGAUX, A. 1890. Recherches sur la circulation des Lamellibranches marin. (Thesis) Besanzon. 296 pp.

MOORE, R. C. (ed.) 1969. Treatise on Invertebrate Paleontology. Pt. N. Mollusca 6:491-952, ill.

MUNIER-CHALMAS, E. 1882. Etudes critiques sur les rudists. Bull. Soc. Geol. France (3) 10: 472-494.

NEWELL, N. D. 1965. Classification of the Bivalvia. Amer. Mus. Novit. 2206. 25 pp.

NEWELL, N. D. AND BOYD, 1970. Oyster-like Permian Bivalvia. Bull. Amer. Mus. Nat. Hist. 143(4):217-282, figs. 1-34.

NICOL, D. 1952a. Revision of the Pelecypod genus *Echinochama*. Jour. Paleont. 26:803-817, pls. 118-119.

________. 1952b. Designation of the type species of *Pseudochama* (additional note). Jour. Wash. Acad. Sci. 42:248.

________. 1965. Nomenclatural note on *Arcinella* versus *Echinochama*. Nautilus 78(4): 115-116.

ODHNER, N. H. J. 1919. Studies on the morphology, the taxonomy, and the relations of recent Chamidae. K. Svenska. Vetensk-Akad. Handl. 59(3):1-102, pls. 1-8.

________. 1922. Mollusca of Juan Fernandez and Easter Island. *In* C. Skottsberg. The natural history of Juan Fernandez and Easter Island. 3:219-254.

________. 1955. Some notes on *Pseudochama*. Nautilus 69:1-6.

OKEN, L. 1815. Lehrbuch der Naturgeschichte. Zoologie. Leipzig. Vol. 3. 842 pp., 40 pls.

OLSSON, A. A. 1961. Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). Panamic-Pacific Pelecypoda. Paleont. Res. Inst. Ithaca, U.S.A., 574 pp., 86 pls.

________. 1971. Mollusks from the Gulf of Panama collected by R/V John Elliott Pillsbury, 1967. *In* F. M. Bayer & G. L. Voss (Eds) Studies in Tropical American Mollusks. Univ. Miami Press vii + 236 p.

OSORIO C. AND N. BAHAMONDE. 1970. Lista preliminar de Lamelibranquios de Chile. Bol. Mus. Nac. Hist. Nat. Chile 31:185-256.

OWEN, G. 1953. The biology of *Glossus humanus* (L) (*Isocardia cor* Lam.) Jour. Mar. Biol. Assoc. U.K. 33:85-106.

PALMER, K. V. W. 1963. Type specimens of marine Mollusca described by P. P. Carpenter from the west coast of Mexico and Panama. Bull. American Paleont. 46(211):289-400, pls. 58-70.

PALMER, R. H. 1928. The rudistids of southern Mexico. Occ. Pap. Calif. Acad. Sci. 14:1-137, pls. 1-18.

PELSENEER, P. 1911. Les Lamellibranches de l'expédition du Siboga. Partie anatomique. Siboga Exped. 53:1-125, pls. 1-26.

PHILIPPI, R. A. 1887. Die Tertiären und Quartaren Versteinerungen Chiles. Leipzig, 266 pp., 40 pls.

PILSBRY, H. A. 1934. West American Chamidae, *Periploma*, and *Glycymeris*. Nautilus 47:81-86, pl. 8.

PILSBRY, H. A. AND H. N. LOWE. 1932. West Mexican and Central American mollusks collected by H. N. Lowe 1929-31. Proc. Acad. Nat. Sci. Philadelphia 84:33-144, pls. 1-17.

PILSBRY, H. A. AND E. G. VANATTA. 1902. Papers from the Hopkins Stanford Galapagos Expedition, 1898-1899. XIII. Marine Mollusca. Proc. Washington Acad. Sci. 4:549-560, pl. 35.

POPENOE, W. P. AND W. A. FINDLAY. 1933. Transposed hinge structures in Lamellibranchs. Trans. San Diego Soc. Nat. Hist. 7:299-318.

PURCHON, R. D. 1958. The stomach in the Eulamellibranchia, stomach type IV. Proc. Zool. Soc. London 131:487-525.

REEVE, L. 1847. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Monograph of the genus *Chama*. Vol. 4. London.

RIDEWOOD, W. G. 1903. On the structure of the gills of the Lamellibranchia. Phil. Trans. Roy. Soc. (B) 195:147-284.

ROCHEBRUNE, A. T. DE. 1895. Diagnoses de mollusques nouveaux, provenant du voyage de M. Diguet en Basse-Californie. Bull. Mus. Hist. Nat. Paris 1:239-243.

RUDWICK, M. J. S. 1965. Sensory spines in the Jurassic brachiopod *Acanthothiris*. Palaentology 8:604-617.

SALVAT, B. AND J. P. EHRHARDT. 1970. Mollusques de l'Ile Clipperton. Bull. Mus. Natl. Hist. Nat. Paris (Sec 2) 42(1):223-231.

SCHUMACHER, C. F. 1817. Essai d'un nouveau système des habitations des vers testaces. Copenhagen. iv + 287 pp., pls. 1-22.

SMITH, A. G. AND M. GORDON. 1948. The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. Proc. Calif. Acad. Sci. 26:147-245.

SOOT-RYEN, T. 1931. Pelecypods from Floreana (Sancta Maria), Galapagos Islands. Myt. Mag. Naturv. Oslo 70:313-324, pls. 1, 2.

STASEK, C. R. 1963. Geometrical form and gnomonic growth in the bivalved mollusca. Jour. Morphol. 112:215-231.

STEARNS, R. E. C. 1893. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. XXV. Report on the mollusk-fauna of the Galapagos Islands with descriptions of new species. Proc. U.S. Nat. Mus. 16:353-450.

STENZEL, H. B. 1971. Oysters, *in* R. C. Moore, Treatise on invertebrate paleontology. Pt. N, Mollusca 6:953-1224.

STRONG, A. M. 1934. A new California *Pseudochama*. Nautilus 47(4):137, pl. 8.

STRONG, A. M. AND G. D. HANNA. 1930. Marine Mollusca of the Tres Marias Islands, Mexico. Proc. Calif. Acad. Sci. 19:13-22.

TAYLOR, J. D., AND W. J. KENNEDY. 1969. The shell structure and mineralogy of *Chama pellucida* Broderip. Veliger 11:391-398.

TAYLOR, J. D., W. J. KENNEDY AND A. HALL. 1969. The shell structure and mineralogy of the Bivalvia. Introduction: Nuculacea-Trigonacea. Bull. Brit. Mus. Nat. Hist. Zool. (3). 125 pp., 29 pls., 77 figs.

TERMIER, H. AND G. TERMIER, 1949. Role des Aviculopectinidae dans la morphogénès des dysodontes Mesozoiques. Mus. Natl. d'Hist. Nat. Paris Bull. 21:292-299.

TRYON, G. W. 1872. Catalogue of the family Chamidae. Proc. Acad. Nat. Sci. Philadelphia for 1872. 116-120.

TURNER, R. D. 1956. The eastern Pacific marine molluscs described by C. B. Adams. Occ. Pap. Mollusks Mu. Comp. Zool. Univ. Harvard 2(20): 21-135, pls. 5-21.

VOGEL, K. 1960. Struktur and funktion der "Siphonalpfeiler" der Hippuriten (Lamellibranchiata). Palaeont. Zeits. Stuttgart 34(3,4):275-294, pls. 21-25.

WILLETT, G. 1938. A new *Pseudochama* from Clarion Island. Nautilus 52:48-49, pl. 4.

YONGE, C. M. 1967. Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists. Phil. Trans. Roy. Soc. (B) 252:49-105.

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OSTEOLOGY AND RELATIONSHIPS OF THE ROOSTERFISH, *NEMATISTIUS PECTORALIS* GILL

By Richard H. Rosenblatt and
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OSTEOLOGY AND RELATIONSHIPS OF THE ROOSTERFISH, *NEMATISTIUS PECTORALIS* GILL[1]

By Richard H. Rosenblatt[2] and Michael A. Bell[3]

Abstract: The status of the roosterfish, *Nematistius pectoralis,* long has been in doubt. It alternatively has been considered a member of the Carangidae or to represent a monotypic family. An investigation of the osteology of *N. pectoralis* indicates that it should not be placed in the Carangidae, but merits separate familial status. *N. pectoralis* differs from members of the Carangidae in that the gas-bladder enters the skull through large foramina in the basioccipital and contacts the inner ear, the three anal spines are normally arranged, and the interosseus space of the shoulder girdle is well developed. The two families are similar, however, in most other skeletal features and are regarded as closely related.

Patterson's suggestion that the Carangidae have been derived independently from the Beryciformes is not supported. His primary indicator of relationships, caudal rays with forked bases that clasp the hypurals, has been developed independently in a number of unrelated lineages. Other resemblances between the Cretaceous berycoid genus *Aipichthys* and modern carangids are regarded as products of convergent evolution.

INTRODUCTION

Nematistius pectoralis, the roosterfish or papagallo, is a large, fast swimming, predaceous fish of the eastern tropical Pacific (Fig. 1). The most striking external feature of the species is the presence of elongate, free dorsal spines, which account for the generic and vernacular names.

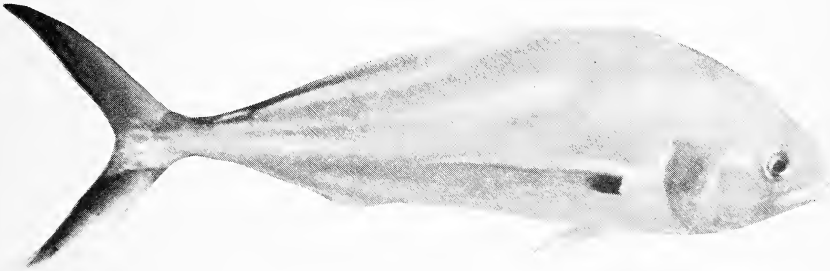

Figure 1. *N. pectoralis,* a living adult. In normal swimming the elongated dorsal spines are folded down. (Photograph by E. M. Hobson.)

The familial placement of *Nematistius* fairly can be termed an ichthyological football. It variously has been regarded as a member of the Carangidae (Boulenger 1910; Regan 1913; Greenwood et al 1966) or placed in a separate family (Gill 1864; Jordan and Evermann 1898; Berg 1947; Freihofer 1963). It will be noted that some of the most distinguished names in the history of ichthyology are ranged on either side of the question.

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Considering the unfavorable ratio of ichthyologists to fishes, it is perhaps not surprising that no one has attempted to settle the matter by an investigation of the internal anatomy of *Nematistius pectoralis.* Starks (1908) briefly described the connection between the inner ear and the gas bladder (otophysic connection, vide Greenwood et al 1966); Berg (1947) pointed out its possible taxonomic significance; and Freihofer (1963) indicated that the ramus lateralis accessorius nerve conformed to his Pattern 10, in distinction to the Carangidae, but that is all. An investigation of the osteology of *Nematistius* is made more meaningful by the recent publication of extensive descriptions of the osteology of a number of carangid genera and species (Suzuki 1962).

MATERIALS AND METHODS

Dried, partly disarticulated preparations as well as stained and cleared specimens were used. Details of the gas-bladder connection with the inner ear were worked out by dissecting specimens in which the gas-bladder had been filled with latex. In the following material list (S) refers to a stained specimen, and (D) to a dried preparation. The material used in this study is housed in the collections of the Scripps Institution of Oceanography (SIO), Biology Department, University of California, Los Angeles (UCLA) and the National Marine Fishery Service, Southwest Fisheries Center, La Jolla (BCF).

Nematistiidae-*Nematistius pectoralis:*SIO62-22, entire skeleton of an 886 mm (fork length) adult (D); SIO unnumbered, head and appendicular skeleton of an adult (D); UCLA S402, two neurocrania and vertebral columns (D); UCLA A-225 3 (32-79.5) (S); UCLA W53-297, 1 (17.5) (S).

Carangidae-*Caranx melampygus,* BCF422-26 (S); *Chloroscombrus chrysurus* BCF422-19 (S); *Decapterus* sp. SIO unnumbered (D); *Gnathanodon speciosus* BCF 422-17 (S); *Hemicaranx zelotes* BCF422-6 (S); *Selene oerstedi* BCF422-2 (S); *S. vomer* BCF422-22 (S); *Seriola dorsalis* SIO unnumbered (D); *S. mazatlana* SIO 57-16 (D); *Trachinotus carolinus* BCF422-5 (S); *T. falcatus* BCF422-21 (S); *T. goodei* BCF422-23 (S); *Vomer declivifrons* BCF422-11 (S); *V. setapinnis* BCF422-9, BCF422-20 (S).

Scombridae-*Sarda chiliensis,* SIO unnumbered (D); *Scomber japonicus,* SIO unnumbered (D); *Thunnus obesus,* SIO unnumbered (D).

Coryphaenidae-*Coryphaena hippurus* SIO54-160 (D).

Engraulididae-*Anchoa* sp. SIO unnumbered (S).

Stromateidae-*Peprilus* sp. SIO unnumbered (S).

Serranidae-*Mycteroperca jordani* SIO62-706 (D).

Kyphosidae-*Girella nigricans* SIO unnumbered (D); *Medialuna californiensis* SIO unnumbered (D).

OSTEOLOGY

Neurocranium.—(Figs. 2, 3). Bones of neurocranium relatively dense, except for cancellous areas along anterodistal margin of supraoccipital, dorsolateral portions of lateral ethmoids, and ventrolateral margins of frontals.

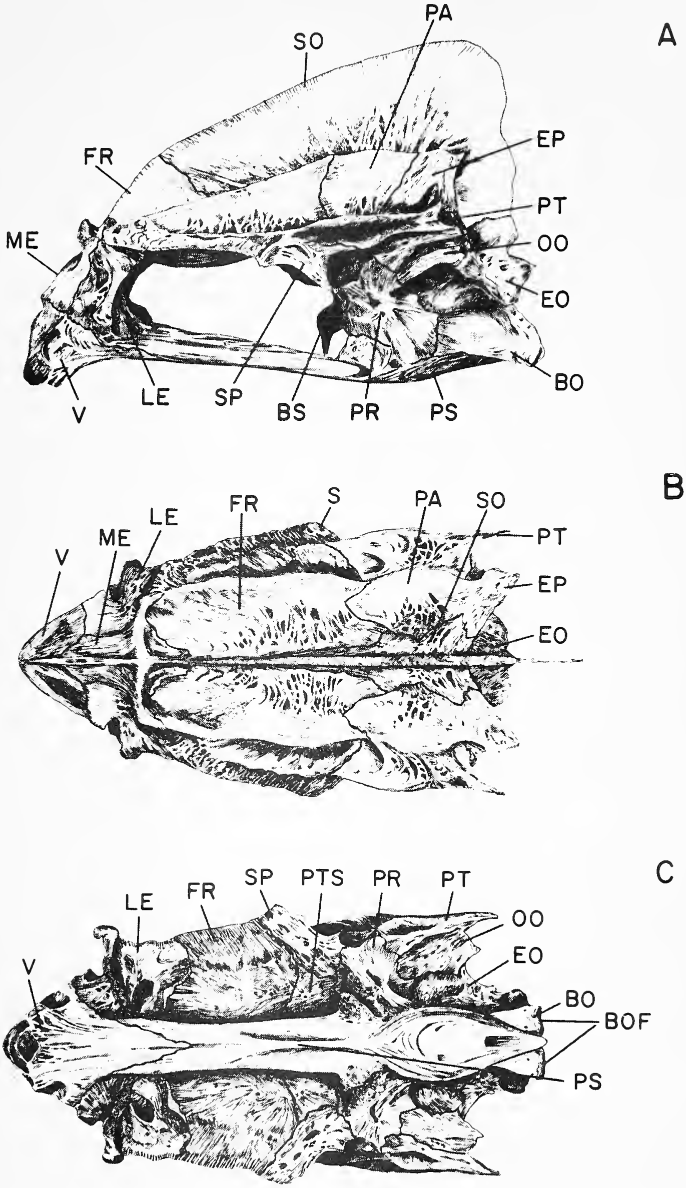

Figure 2. *N. pectoralis*, neurocranium. A—side view, B—top view, C—bottom view. Abbreviations: BO, basioccipital; BOF, basioccipital foramen; BS, basisphenoid; EO, exoccipital; EP, epiotic; FM, foramen magnum; FR, frontal; LE, lateral ethmoid; ME, mesethmoid; OO, opisthotic; PA, parietal; PR, prootic; PS, parasphenoid; PSF, parasphenoid foramen; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; V, vomer (prevomer).

Neurocranium deep, and relatively broad anteriorly; its outline subrectangular when viewed from above. The most prominent features are the lateral crests and median crest. The ventralmost crest is formed by the pterotic and frontal, the next by the epiotic, parietal and frontal, and the medial crest by the supraoccipital, frontals, and, to a minor extent, mesethmoid.

Mesethmoid roughly cruciform in anterior view, with dorsal ridges on the lateral arms and a pronounced median ridge that continues downward onto anterior face of vomer (prevomer). Vomer deep, with a relatively short shaft. Tooth patch ovoid. Lateral ethmoids with large openings for olfactory tracts. Nasals ligamentously attached to ethmoids.

Roof of orbital cavity formed mainly by frontals, pterosphenoids and sphenotics. Anterior opening of braincase bounded by pterosphenoids and basisphenoid. Pterosphenoids not meeting across midline, but with medial processes posteriorly, which almost come in contact. Basisphenoid in contact with pterosphenoids and prootic dorsally and parasphenoid ventrally. Myodome large and deep.

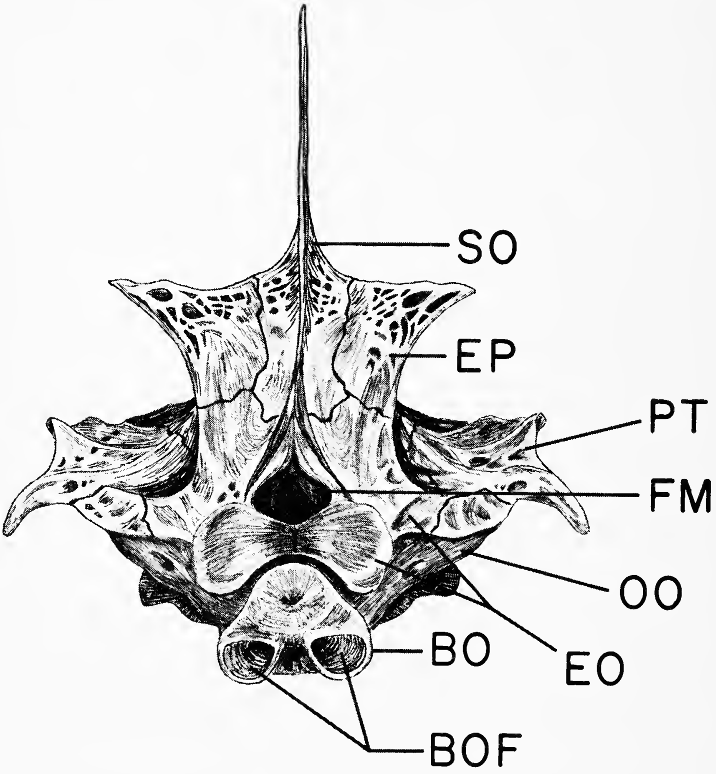

Figure 3. Neurocranium of *N. pectoralis*, rear view. Abbreviations as in figure 2.

Parasphenoid with a sharp keel to just behind level of orbital cavity, then expanded laterally and flattened. Parasphenoid in contact with vomer and lateral ethmoids anteriorly, and with prootic and basioccipital posteriorly. Posterior opening of myodome developed as a large canal bounded dorsolaterally by basioccipital and ventrolaterally by parasphenoid. Basioccipital contacting prootic anteriorly, parasphenoid ventrally, first vertebra posteriorly, and exoccipitals anteriorly.

On either side of basisphenoid, beneath and lateral to condyle, are two canals with posterior openings that lead into the auditory bulla. Each canal receives a process from the gas-bladder. These anterior processes of the gas-bladder extend forward to the region of the inner ear, but do not come in contact with it. Our observations thus confirm those of Starks (1908). The exoccipitals, bounded by the supraoccipital, epiotics, pterotics, opisthotics, prootics and basioccipital, are in contact along the midline, above and below the foramen magnum.

Opisthotic almost excluded from top of skull by the overlying pterotic and exoccipital. Pterotic with a strong backward projection, and a long socket which receives one facet of head of hyomandibular. At junction of the pterotic, epiotic and parietal there is an unossified area bridged by cartilage.

Prootic forming a major part of the posterolateral wall of the neurocranium. At its anterodorsal corner it, together with the sphenotic, forms a deep socket for an articular facet of the hyomandibular. Pars jugalis with but two openings, thus agreeing with other perciforms (Patterson 1964:434-438).

Supraoccipital with a high crest, which extends far forward over frontals, and posteriorly to exoccipital. Superficially frontals in contact for only a short distance; they are separated by the supraoccipital posteriorly and the mesethmoid anteriorly.

The general shape of the jaws is indicated in figure 4. The maxilla fits closely into the groove on the dorsolateral surface of the premaxilla and is braced anteriorly against the palatine. Supramaxilla rather loosely attached to maxilla. Premaxilla with two ascending processes anteriorly and a lower one posteriorly. The ascending (anteriormost) process contacts the mesethmoid and the posterior ones contact the maxilla. The premaxilla is very similar to those illustrated by Suzuki (1962) for various carangid genera. The lower jaw is of normal perciform type, except that the angular (retroarticular) is fused to the articular (angular).

Suspensorium.—(Fig. 5). Suspensorium and opercular bones well integrated. Posterolateral face of hyomandibular deeply grooved to receive ascending process of preopercle. Palatine with a narrow band of teeth.

Symplectic firmly joined to quadrate and metaptergyoid, and metapterygoid further united with hyomandibular and, on its inner face, with ectopterygoid.

Hyoid Apparatus.—(Fig. 6). Ceratohyal and epihyal firmly united by deep sutures on medial face. A well-developed, elongate-oval foramen in ceratohyal, from which a groove runs anteriorly and posteriorly along its lateral face. Posteriorly, this groove continues onto epihyal, forming a deep excavation. There are seven branchiostegals, three articulating with the inner face of the ceratohyal, two with its outer face, and two with the outer face of the epihyal.

Orbital Bones.—(Fig. 7). Six suborbital bones, including dermosphenotic (only the first four are figured). Lachrymal without the outward curvature described by

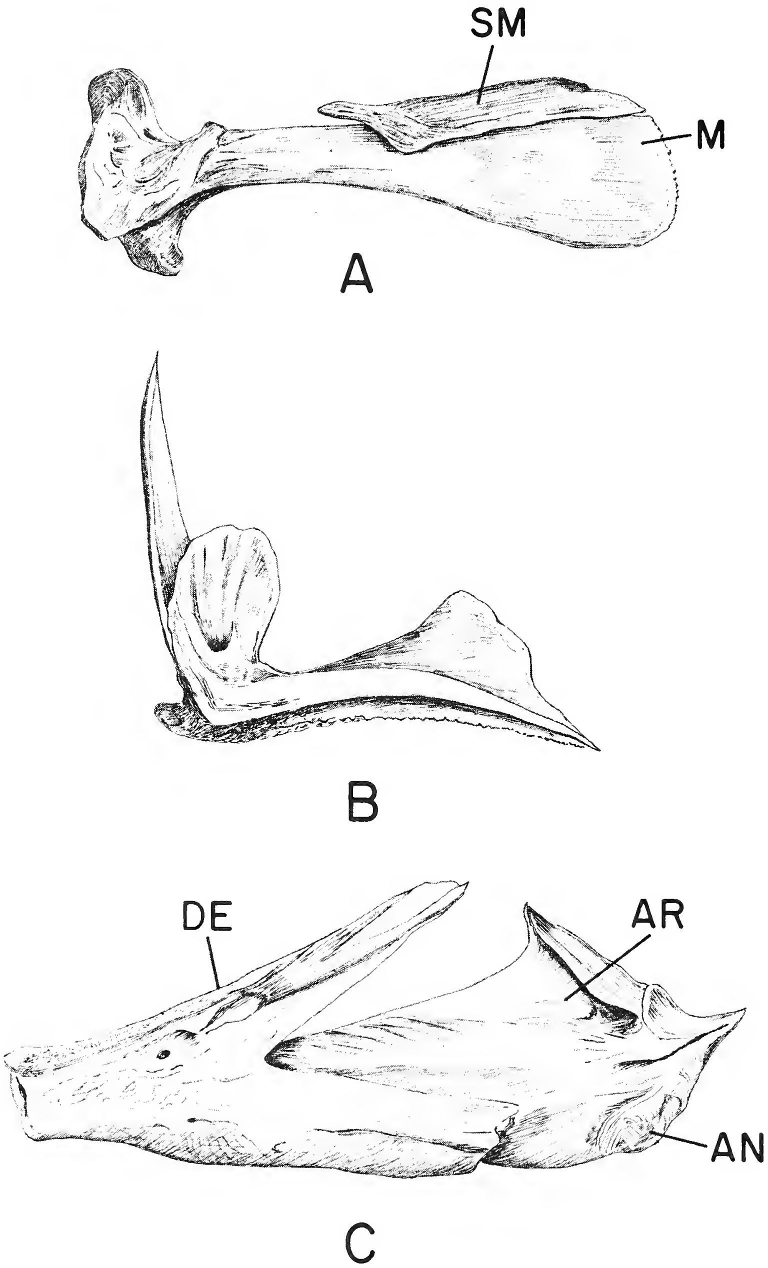

Figure 4. Jaws of *N. pectoralis*. A—maxilla and supramaxilla; B—premaxilla; C—lower jaw. Abbreviations: AN, angular (articular); AR, articular (retroarticular); DE, dentary.

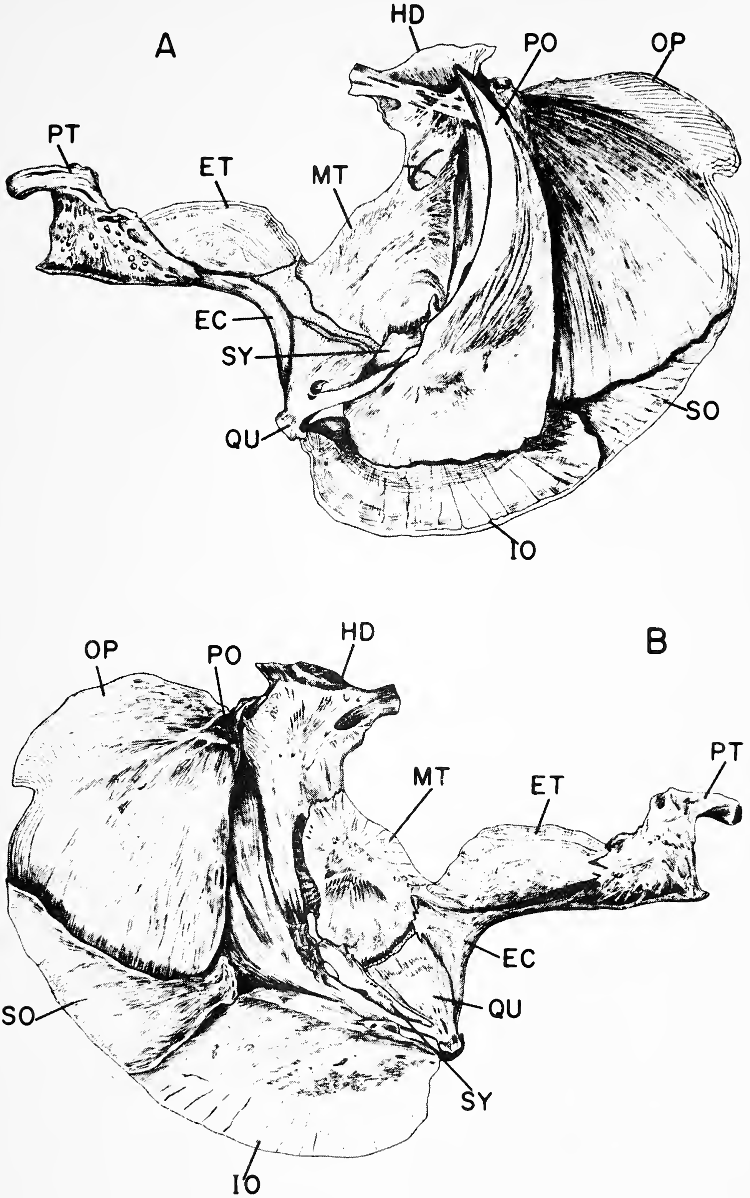

Figure 5. Suspensorium and opercular apparatus of *N. pectoralis*. A—outer face; B—inner face. Abbreviations: EC, ectopterygoid; ET, entopterygoid; HD, hyomandibular; IO, interopercle; MT, metapterygoid; OP, opercle; PO, preoperacle; PT, palatine; QU, quadrate; SO, subopercle; SY, sympletic.

Suzuki (1962) for many carangids, but anterior notch characteristic of the Carangidae weakly developed. Second suborbital trapezoidal and overlapping first, so that it contacts its outer face rather than its posterior edge for most of its length. Third circumorbital a thin, curved, inward directed lamina articulating with second along its upper inner border. Third suborbital forming major part of suborbital ring, in this respect agreeing with such carangid genera as *Elagatis* and *Naucrates*.

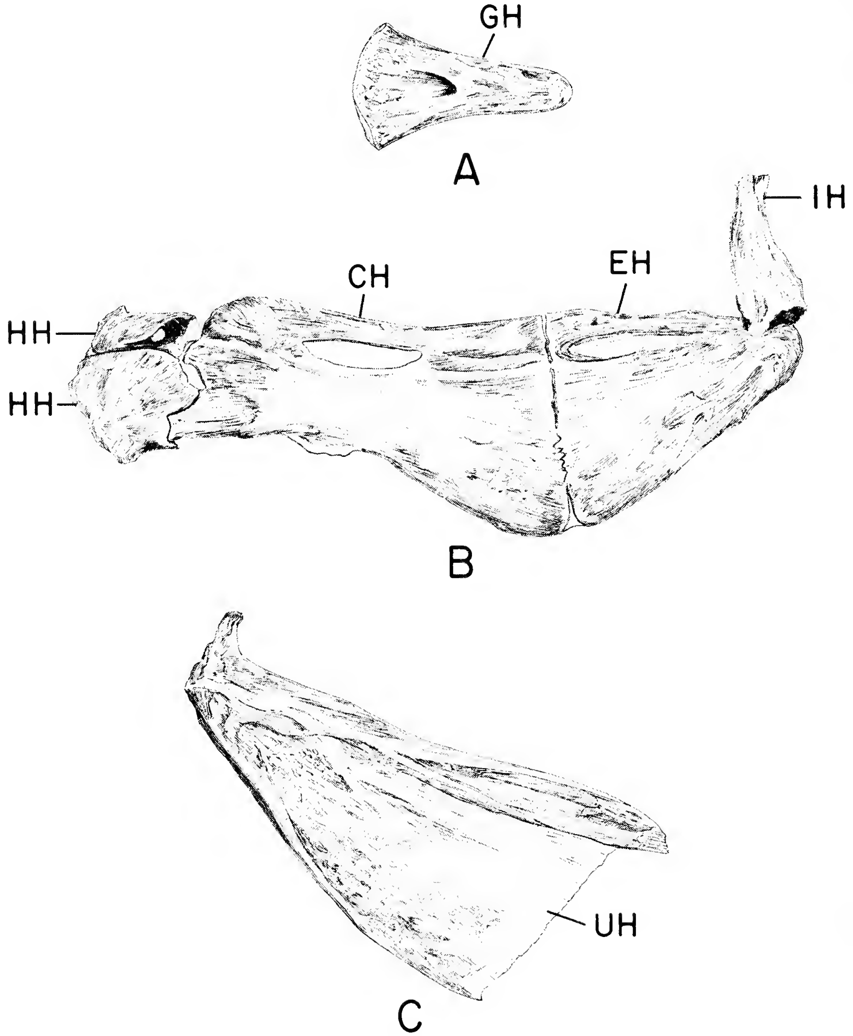

Figure 6. Hyoid apparatus of *N. pectoralis*. A—glassohyal, dorsal view. B—paired elements of hyoid arch. C—urohyal. Abbreviations: CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyals; IH, interhyal; UH, urohyal.

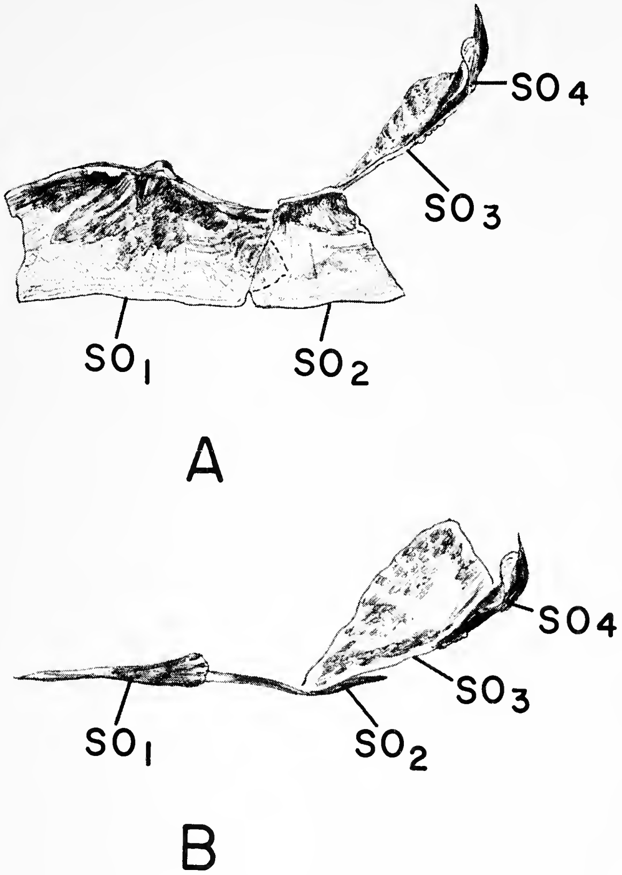

Figure 7. Orbital bones of *N. pectoralis*, SO_5 and dermosphenotic not shown. A—lateral view. B—top view.

Limb Girdles.—(Figs. 8, 9). Scapula with two foramina. Anteriorly is the normal perciform foramen. In *Nematistius*, the cleithrum forms part of the anterior border of this foramen on its lateral surface; medially the foramen is completely within the scapula. Behind this foramen is a second smaller one, which is absent in the Carangidae, as in all of the perciforms illustrated or described by Starks (1930) except *Cirrhites rivulatus* and *Scorpaenichthys marmoratus*.

All four actinosts borne on scapula. First short and hourglass shaped; remainder more elongate.

The pelvic girdle bears a striking resemblance to those illustrated by Suzuki (1962, Fig. 45). Pelvic plate thin and flattened and with lateral keel. Two sharp keels ventrally (subpelvic and interpelvic keels of Suzuki). Ischial processes long and curved.

Vertebral Column.—There are 10 precaudal and 14 caudal vertebrae, including the urostylar centrum. Articular facet of first vertebra for basioccipital condyle facing down and slightly forward, at an angle of approximately 45° to the axis of the body. Articular surfaces for exoccipital condyles facing almost straight forward. First neural arch autogenous. Second centrum about half as long as first and two thirds as long as third. First two neural spines curve forward and are in close contact. They appear fused in some specimens.

First epipleural rib articulating with first neural arch, second with second centrum, and remaining 5 are borne on pleural ribs. Pleural ribs eight; the first is associated with third vertebra. First three ribs sessile, remainder borne on

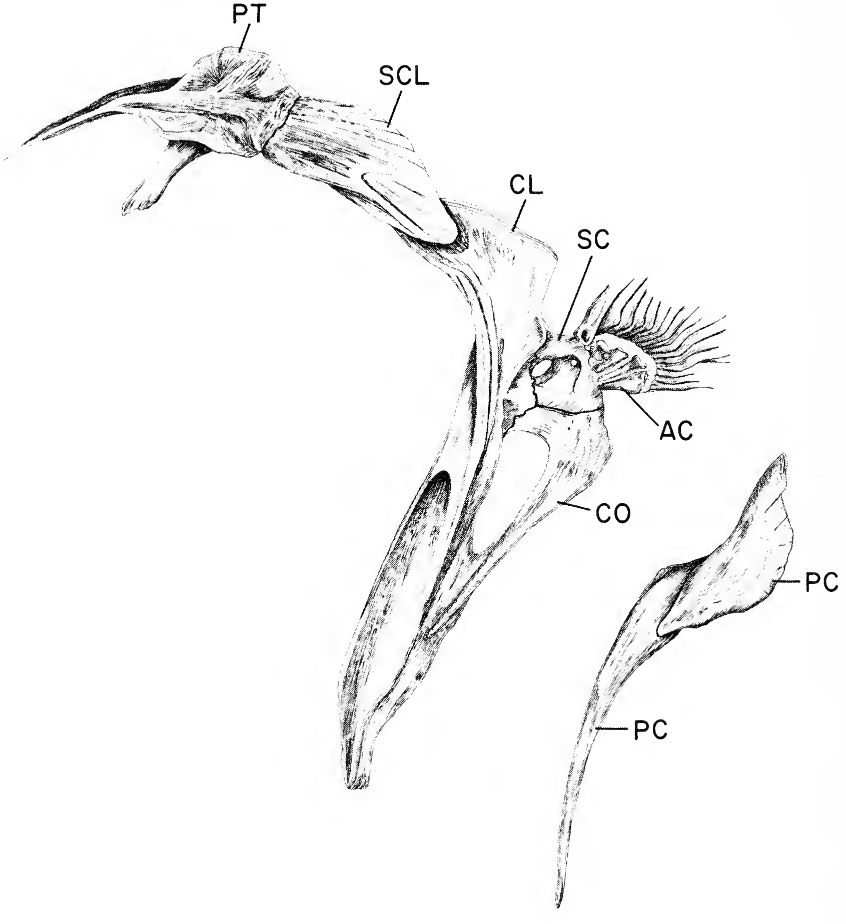

Figure 8. Pectoral girdle of *N. pectoralis*. Abbreviations: AC, actinosts; CL, cleithrum; CO, coracoid; PC, post-cleithra; PT, post-temporal; SC, scapula; SCL, supracleithrum.

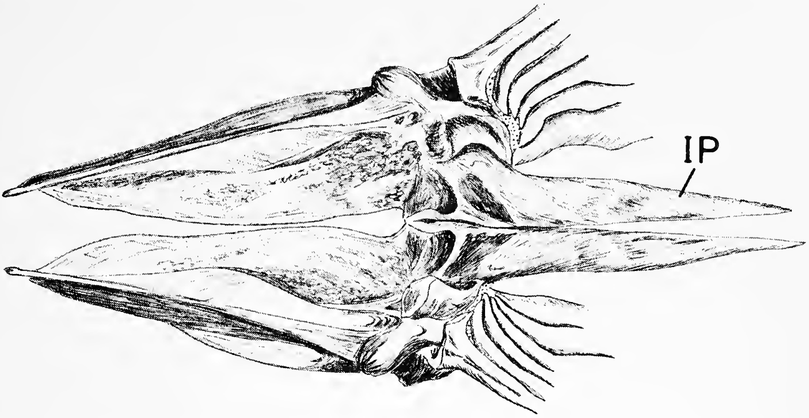

Figure 9. Pelvic girdles of *N. pectoralis.* IP, ischial process.

parapophyses. First vertebra with parapophyses is the fourth, first with a haemal arch the eighth. Inferior foramina of Starks (1911) lacking in parapophyses and haemal arches.

Ventral zygapophyses do not strongly interlock. Dorsal zygapophyses interlock strongly anteriorly, but become opposed by 17th vertebra.

Neural and haemal spines posterior to the 19th vertebra sloping strongly backward, increasing the rigidity of caudal peduncle.

Caudal Skeleton.—(Figs. 10, 11). Principal caudal rays 9 + 8. Caudal rays, except for middle two, cleft at the base and broadly overlapping skeletal supporting elements. Procurrent caudal rays borne by neural spine of antepenultimate vertebra and haemal spines of last two preural vertebrae. Two specimens with 10 procurrent rays above and 9 below, one with 9 and 8.

Elements associated with ural centrum forming a compact unit. Individual elements are difficult to distinguish in dried preparations, and more easily discerned in stained and cleared juveniles (contrast figures 10 and 11). Hypurals reduced by fusion to four. Upper and lower enlarged hypural plates each represent the fusion of two hypurals. In small juveniles there is a foramen in the lower expanded hypural plate, but this becomes obliterated with growth.

Dorsal and Anal Fins.—(Figs. 12, 13). Three median bones in advance of dorsal fin. We follow the terminology of Smith and Bailey (1961) who termed these structures predorsal bones. The first interneural element is an enlarged structure that bears two spines. The arrangement of three ray-less elements, followed by one which bears two rays is 0 -0 -0 -2 in the shorthand terminology of Smith and Bailey. For reasons given in the discussion, we regard the expanded element in *Nematistius* as representing the fusion of the first pterygiophore with the proximal and medial radials of the second pterygiophore. The first three anal spines are closely approximated, rather than unequally spaced as in the Carangidae, nor is the first anal pterygiophore as stout and expanded ventrally. However, the structure

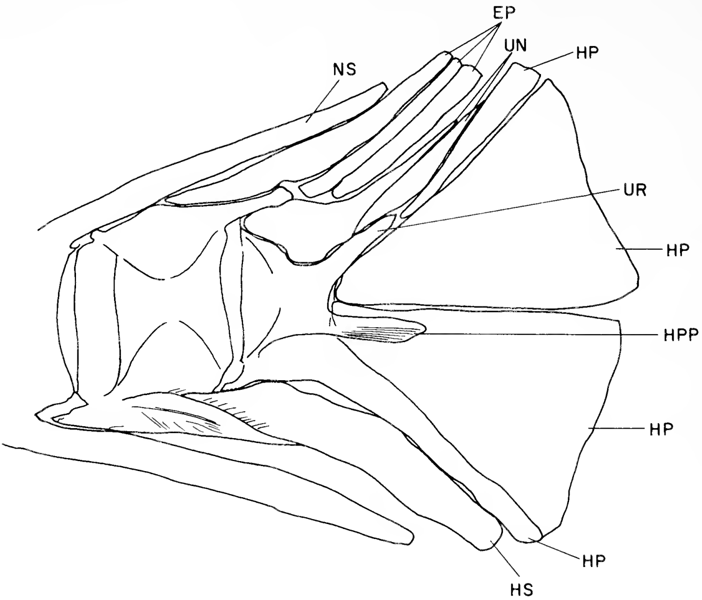

Figure 10. Caudal skeleton of a large juvenile *N. pectoralis* (dried preparation). Abbreviations: EP, epural; HP, hypural; HPP, hypurapophysis; HS, haemal spine; NS, neural spine; UN, uroneural; UR, urostyle.

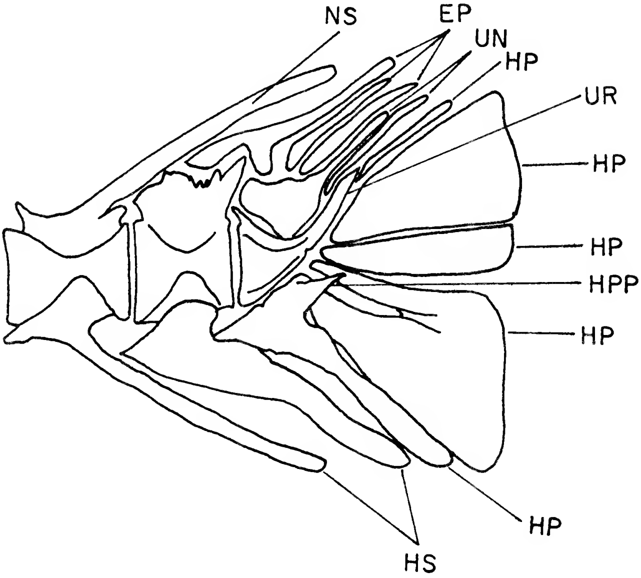

Figure 11. Caudal skeleton of a cleared and stained 32.5 mm juvenile of *N. pectoralis*. Abbreviations as in figure 10.

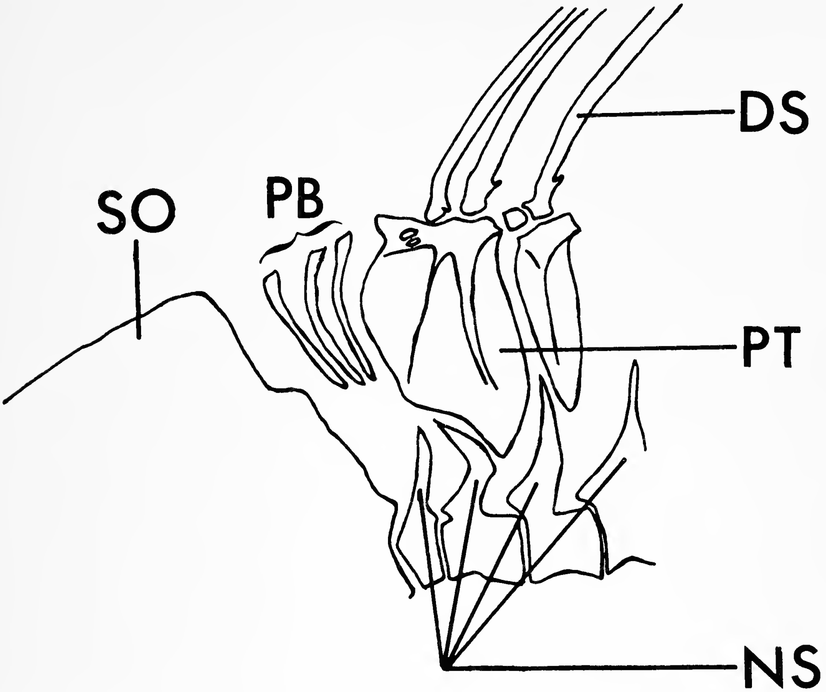

Figure 12. Anterior dorsal fin elements and supporting structures in a 27.5 mm *N. pectoralis*. Abbreviations: DR, dorsay ray; NS, neural spine; PB, predorsal bones; PT, pterygiophore.

fundamentally is not different from that found in carangids, and a moderate expansion of the ventral part of the pterygiophore could carry the first two anal spines away from the third.

CLASSIFICATION AND RELATIONSHIPS

Nematistius differs in several respects from the forms customarily placed in the family Carangidae. For comparative data on the Carangidae we have relied mainly on the important work of Suzuki (1962) and the descriptions of Starks (1911), although we have utilized skeletal and stained and cleared material as well.

The most important difference is the otophysic connection. The adaptive significance of this modification, which would serve to increase both the sensitivity of hearing and the range of frequencies perceived, is obvious. The formation of the otophysic connection has involved important changes in the configuration of the basioccipital and the gas bladder. It is of a type which is, so far as we have been able to determine, unique.

The remaining characters that serve to isolate *Nematistius* from the carangids are less fundamental. There are three normally arranged anal spines, rather than two spines detached from the anal and one at its base. This is not a character of obvious adaptive significance, although it is of great constancy in the Carangidae. The shoulder girdle, though composed of the same elements as in the Carangidae, is different in shape in *Nematistius*. In the Carangidae the coracoid is broad and flattened, and parallel to the cleithrum, from which the lower end sometimes diverges. As a result, the interosseous space (Starks 1930) is much reduced. In *Nematistius* the middle and lower parts of the coracoid are rodlike. The rodlike portion of the coracoid is well separated from the cleithrum, contacting it only ventrally, so that the interosseous space is large.

There is also a difference in the arrangement of the predorsal bones. In *Nematistius* there are two predorsals in advance of the first neural spine and one just behind its tip. In the carangids that we have examined either there is one predorsal before the first neural spine and two before the second, or each of the first three neural spines is preceded by a predorsal bone.

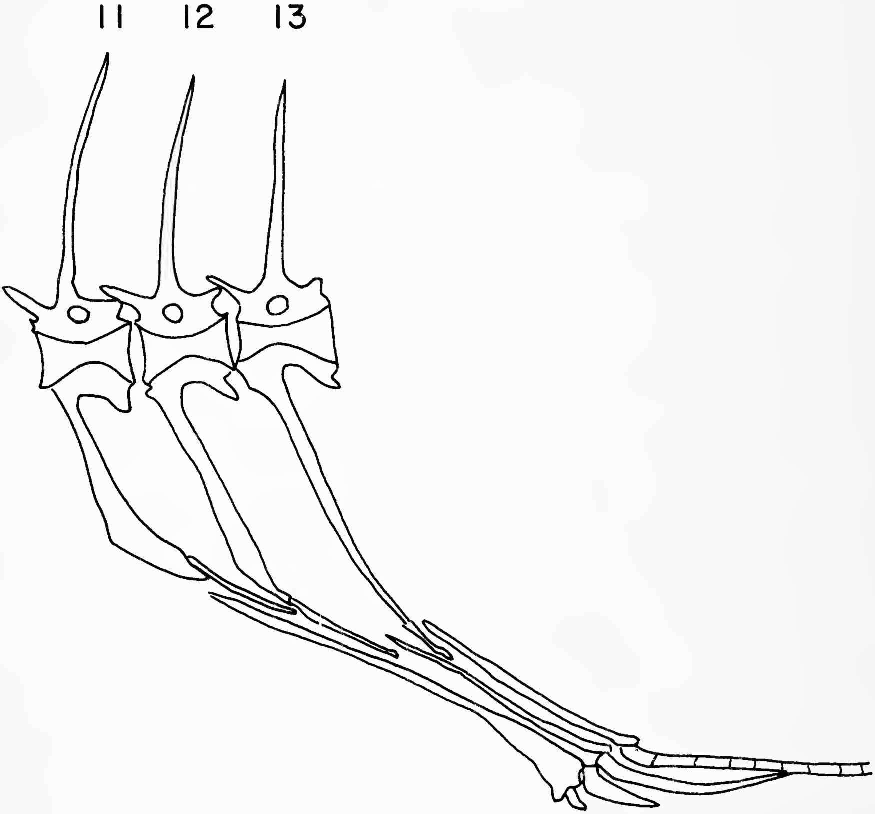

Figure 13. Anterior anal fin elements and associated supporting structures in a 27 mm *N. pectoralis*.

Nematistius also differs from many carangids in that the first pterygiophore is expanded greatly and platelike and bears two spines. The neural spines of the first two centra are crowded and curved forward to accommodate it. We regard this enlarged pterygiophore as the product of fusion of two pterygiophores. This is not in accord with the hypothesis put forward by Smith and Bailey (1961). According to their scheme, in a fish with 3 predorsals and 2 spines on the first proximal pterygiophore (0 -0 -0 -2), the first spine has been displaced backward from the third predorsal bone. However, this does not allow for the derivation of the 0 -0 -0 -2 condition from an ancestor with the 0 -0 -0 -1 condition. And the trends indicated in Smith and Bailey's plate I do not admit such a possibility. However, in the Carangidae both arrangements occur, as well as one not noted by Smith and Bailey, 0 -0 -0 -0 -2 in *Trachinotus*. (It should be noted that the arrangement in *Vomer setapinnis* is 0 -0 -0 -2, not 0 -0 -0 -0 -0 -0 -1 as indicated by Smith and Bailey).

It seems to us that it is simpler to derive the 0 -0 -0 -2 condition from the 0 -0 -0 -1 (especially in the Carangidae, in which the former condition appears to have been derived from the latter several times), by invoking a fusion of two pterygiophores, rather than the moving back of the spine and subsequent or simultaneous loss of the rayless pterygiophore. In *Trachinotus,* however, it is clear that the first spine has migrated backward, because its pterygiophore persists as a fourth predorsal bone. It is likely that studies of the ontogeny of the dorsal fin in carangids will help clarify this admittedly unsettled question.

The 0 -0 -0 -2 condition, however, has been derived independently in *Nematistius* and certain carangid genera, since primitive carangids such as *Seriola* and *Naucrates* have the 0 -0 -0 -1 condition.

We believe that the first three differences discussed above are sufficient to indicate the placement of *Nematistius* in a family distinct from the Carangidae. Nor does the set of features exhibited by *Nematistius* warrant its inclusion in any other fish family. However, the Nematistiidae does agree with the Carangidae in a number of features, and the families are closely related. The similarity in general appearance and in the deeply forked caudal, with the rays clasping the skeletal supporting elements, could be ascribed to convergence. The suite of osteological similarities displayed by the two groups, however, are not so easily explained on this basis.

The neurocranium of a carangid has a very characteristic appearance caused by the strong development of medial and lateral crests. The neurocranium of *Nematistius* is extremely similar to that of certain high-headed, short-snouted carangid genera. Only the tell-tale tunnels on the lateral faces of the basioccipital would allow the separation of a *Nematistius* skull from a group of carangid skulls. Even the peculiar posterior flattening of the parasphenoid of *Nematistius* is paralleled in *Trachinotus.* The circumorbital bones of carangids are likewise distinctive (Suzuki 1962, Figs. 35, 36; Smith and Bailey 1962, plate 3 Q), in that the third suborbital (2SO of Suzuki) bears a broad lamina and articulates with the second mainly along its upper inner edge, rather than posteriorly. The resemblance between the suborbital bones of *Nematistius* and such primitive carangid genera as *Elagatis, Naucrates* and *Seriola* is striking. Another pecularity shared by the two groups is in the structure of the pelvic girdle. In both, the anterior parts of the pelvic bone are thin but broad, with flanges produced ventrally to provide deep grooves for muscle attachment, and the posterior (ischial) processes are elongate and well developed. This characteristic facies can be seen in Suzuki's figures 45A-R, and our figure 9.

The otolith of *Nematistius* resembles that of *Seriola* and *Caranx* in that the rostrum is long and there is a deep notch above it. It further resembles that of *Seriola* in the form of the sulcus (*Caranx* differs somewhat from the other two genera in this respect) and in the serration of the lower margin. The otolith of *Nematistius* is more massive and more crystalline in structure than that of either carangid, but is not very different in either respect (compare figures 14 and 15).

Certain other points of similarity are perhaps of less value, but still serve to emphasize the overall similarity of *Nematistius* to the Carangidae. These include the presence of a well-developed foramen in the ceratohyal and the shape of the hyomandibular, which has a deep groove on its lateral face for the reception of the preopercle.

It is perhaps not surprising that the caudal skeleton of *Nematistius* should resemble that of carangids, considering the similarity of function. Although in most carangids there has been more fusion of elements (compare figures 10 and 11 and figure 16), the caudal skeleton of the primitive but specialized *Trachinotus* (Fig. 17) is like that of *Nematistius* in the retention of three epurals.

The differences between the Nematistiidae and the Carangidae are those of specialization and no feature militates against the derivation of *Nematistius* from a generalized carangid or protocarangid. However, no extant genus qualifies as an ancestor. All of the subfamilies considered primitive by Suzuki are specialized in having two detached anal spines. In the Chorineminae (=Scomberoidinae) the premaxillary is non-protractile, and in the Trachinotinae the supramaxillary has been lost, the pharyngeals are enlarged, and there is a lateral peg on the basioccipital for the attachment of a heavy ligament. Members of the Naucratinae are less specialized, but in addition to the aforementioned difference in arrangement of anal spines, the caudal skeleton of *Seriola* (the only naucratine genus examined osteologically by us) is specialized in fusion and loss of elements present in *Nematistius*.

Freihofer (1963) found that the Carangidae and Nematistiidae differ in the course of the nerves of the ramus lateralis accesorius (RLA), the former having pattern 9 and the latter pattern 10 (reduced). He believed that this means that the Carangidae and Nematistiidae are unrelated and that affinities should be sought among other groups with pattern 10. He stated that "*Nematistius pectoralis* most closely resembles *Medialuna californiensis* which also has pattern 10" and "Cursory examination of the skeletons of *Nematistius* and *Kyphosus* reveals enough general similarities falling within the entire conspectus implied by the Pattern 10 assemblage to leave the hypothesis stand as a good one for future testing."

We have compared the skeleton of *Nematistius* with those of *Medialuna californensis* and *Girella nigricans*. The general similarities indeed are sufficient to indicate an ordinal relationship. Neither form either exhibits or foreshadows the peculiarities of *Nematistius*. Without repeating them, neither are the peculiarities shared by the Nematistiidae and Carangidae found here. Noteworthy differences include the lack of lateral crests on the skull and the restriction of the supraoccipital

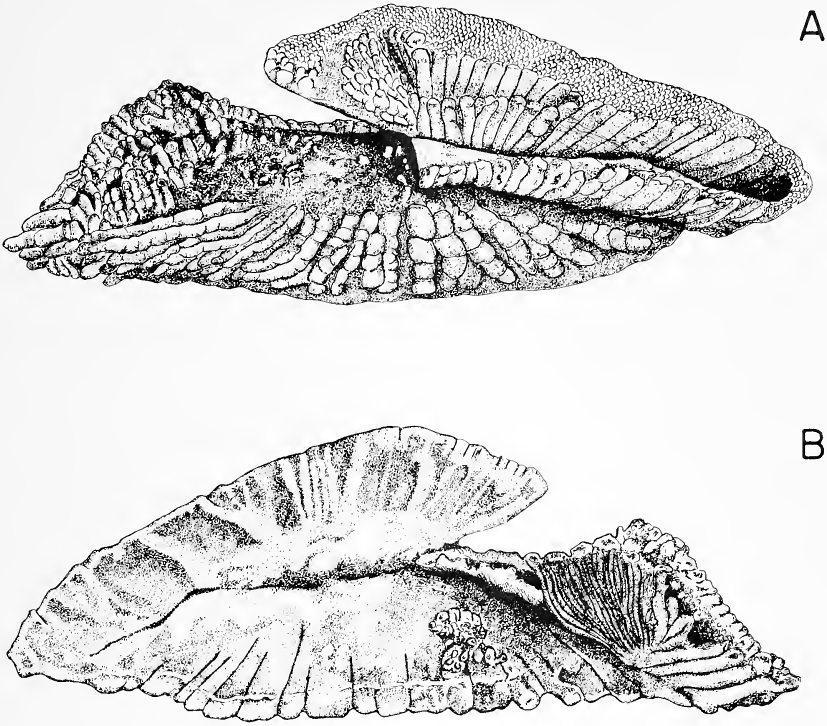

Figure 14. Right sagitta of *N. pectoralis*. A—medial face. B—lateral face.

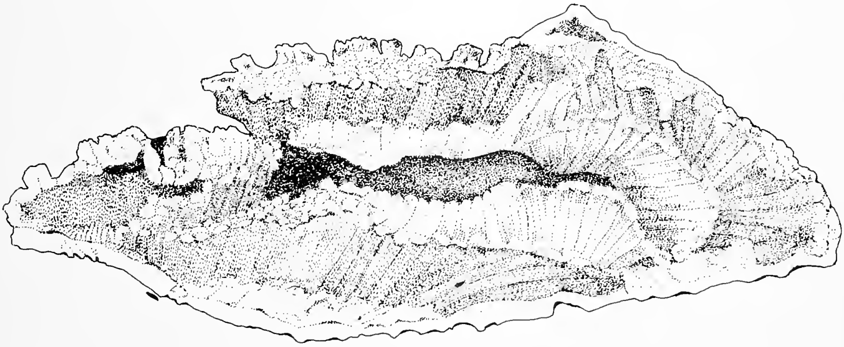

Figure 15. Right sagitta of *Caranx marginatus,* medial face.

crest, which does not encroach on the frontals, which in turn lack a crest. Also the shape of the jaw bones is very different in these nibbling forms. In short, once common perciform characteristics are eliminated, there is little in the osteology of *medialuna* and *Girella* to support the contention that they are especially closely related to *Nematistius*. There is only the evidence of the RLA pattern, and no convincing proof exists that it is the single characteristic by which teleost phylogenies are to be deduced.

Patterson (1964) has argued that the Carangidae (and by extension the Nematistiidae) are not perciform fishes, but that instead they have evolved independently from Beryciformes, and that their perciform characters are due to parallel evolution. This argument was repeated by Greenwood et al (1966:390) and supported by Patterson (1968).

This conclusion is based on a series of similarities between the Cretaceous dinopterygoid beryciform genus *Aipichthys* and certain carangids. Patterson (1964)

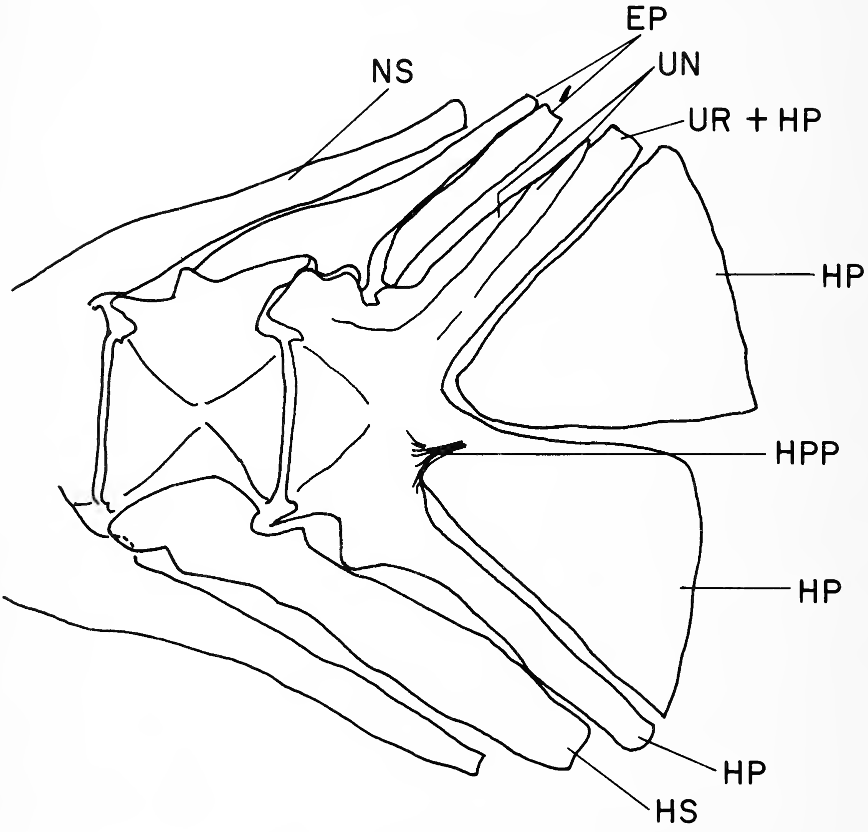

Figure 16. Caudal skeleton of a 50 mm juvenile of *Selene vomer*. Abbreviations as in figure 10.

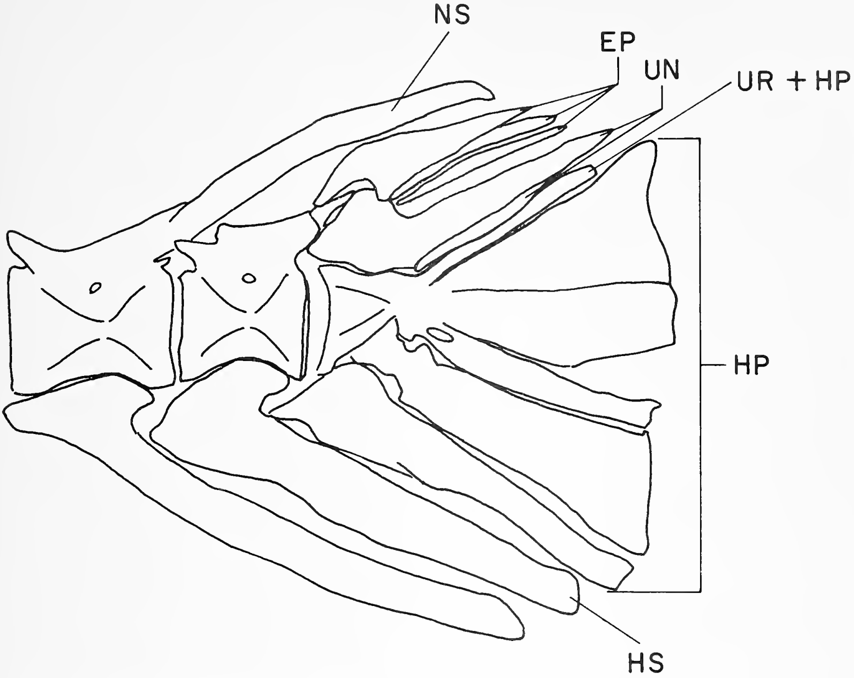

Figure 17. Caudal skeleton of a 73.5 mm juvenile of *Trachinotus glaucus*. Abbreviations as in figure 10.

did not cite the work of Suzuki (1962) or Starks (1911) and figured the osteology of *Vomer,* one of the most specialized and advanced genera of the Carangidae. His concept of the family thus was limited. According to him the chief characters linking *Aipichthys* with the Carangidae are the "deep trunk and long dorsal and anal fins, with few spines and with the anterior soft rays elongated. . . . the high supraoccipital crest. . . . the upturned highly protrusible mouth, the presence of an elongated supramaxilla, the number of vertebrae, the form of the cleithrum and coracoid, the characters of the radials of the dorsal and anal fins, the cycloid scales . . . , and, in particular, the deeply forked bases of the caudal fin-rays" (1964:397). The resemblances between *Aipichthys* and deep-bodied carangids such as *Alectis, Selene, Trachinotus* and *Vomer* were held to be especially close, and "too detailed to be due to convergence alone." The forked caudal rays that clasp the endoskeletal elements also were held to be an important character indicating relationships (1964: 470). Patterson's figure of *Aipichthys* is reproduced for comparison in figure 18.

To begin with, the deep-bodied carangid genera cited by Patterson were regarded by Suzuki (1962) as specialized and (with the exception of *Trachinotus*) advanced. Suzuki regarded the Naucratinae as the most generalized group of carangids and in this we concur. If, as the osteological evidence indicates, *Nematistius* represents an early offshoot from the carangid line, its features must also be accounted for. If phylogeny is to have any meaning, ancestral forms must resemble the generalized representatives of descendant lineages, not the most advanced and specialized ones.

Taking first a similarity utilized by Patterson (1964) that we believe to be more apparent than real, the supraoccipital crest of *Aipichthys* is very different from that of the Carangidae. It apparently stops at the back of the frontals and is not carried forward by them to the ethmoid as it is in carangids and *Nematistius*. A crest such as that of *Aipichthys,* termed the "chaetodontid type" by Gosline (1966), can be found in any number of perciforms with short, deep heads. Included would be several genera of embiotocids, *Calamus* (Sparidae), and *Medialuna* (Kyphosidae), certainly an unrelated assemblage. In fact, except that the head is less deep and foreshortened, the crest of *Aipichthys* is not basically different from that of certain polymixioid genera illustrated by Patterson (1964, Figs. 76-78). We concur with Gosline (1966) that it is unlikely that the sharp crest of carangids and *Nematistius* is derived from the broad crest of *Aipichthys*.

The nature of the articulation of the caudal rays to endoskeletal elements is a poor indicator of relationships. Caudal rays with forked bases that wrap around the

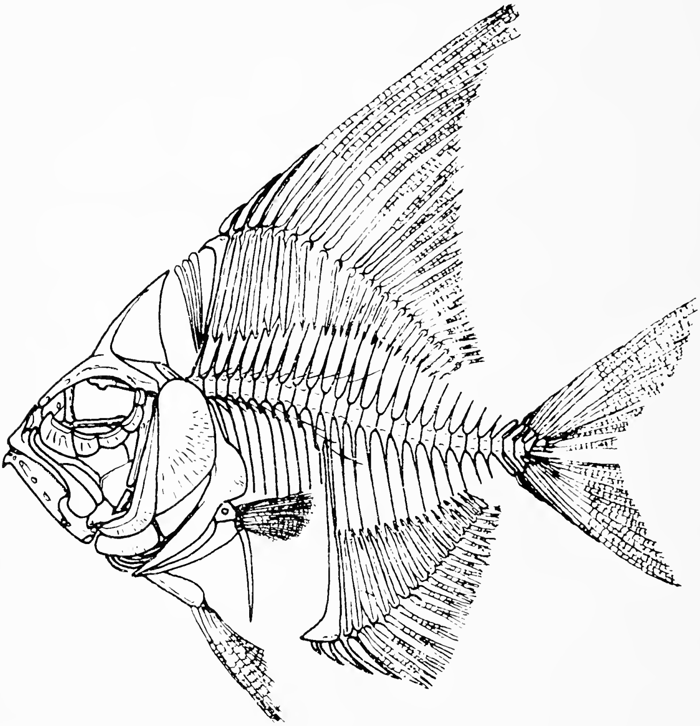

Figure 18. *Aipichthys velifer*. From Patterson, based on Smith Woodward.

tail skeleton are found in fish groups that differ greatly in other respects, and thus must have been evolved independently several times. Such "wrap-around" caudal rays are of course characteristic of the Scombroidei. They are also found in the Echeneiformes, some Atheriniformes (Exocoetoidei), and in the perciform suborder Stromateoidei (Haedrich 1967) (*Peprilus* sp. examined)—a quite unrelated assemblage. Weitzman (1967) has illustrated such rays (although not so dramatically developed) in malacopterygian teleosts such as *Vinciguerria* (Gonostomatidae), *Parasudis* (Paralepididae) and *Saurida* (Synodontidae), and they also occur in the Engraulididae (*Anchoa* examined). The list could be extended, but this should suffice to document our contention.

The upturned, highly protrusible mouth of *Aipichthys* is not a character shared with primitive carangids but with advanced and specialized ones. This sort of mouth, along with a modified suspensorium, appears in certain advanced carangids with scutes along the lateral line, a characteristic absent in *Aipichthys*.

Patterson did not specify the similarities in cleithrum and coracoid, but judging from his figure, the shoulder girdle of *Aipichthys* does not differ from that of most beryciforms, nor, for that matter, from that of generalized perciforms. The coracoid of *Aipichthys* certainly does not resemble the broad, almost straight coracoid of carangids. And, if Patterson's figure is correct, two pectoral actinosts are borne on the coracoid in *Aipichthys,* a character shared neither with the carangids nor most of the Beryciformes.

We are left, then, with a general resemblance in body form between *Aipichthys* and advanced carangids, and the shared characters of elongate and broad dorsal and anal pterygiophores, a low number of vertebrae and cycloid scales.

The superficial resemblances between *Aipichthys* and certain advanced carangids can be ascribed to convergent evolution in fishes with similar ecologies. Certainly the elongation and broadening of the pterygiophores is an obvious adaptation, which serves to stiffen the body in deep-bodied fishes, and is by no means restricted to *Aipichthys* and the Carangidae.

There thus does not seem to be sufficient basis for the removal of the Nematistiidae and the Carangidae from the Perciformes and the postulation of an independent origin of the perciform suite of characters. If the order Perciformes is to be dismembered, the process must begin elsewhere, and on firmer grounds.

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RESUMEN

La posición sistemática del papagallo, *Nematistius pectoralis,* ha estado en duda por largo tiempo. Ha sido considerado alternativamente como miembro de la familia Carangidae o como representante único de una familia monotípica. La investigación de la estructura ósea sugiere, sin embargo, que *N. pectoralis* no debería ser clasificado dentro de la familia Carangidae. *N. pectoralis* difiere de miembros de la familia Carangidae en cuanto a que su vejiga natatoria penetra al cráneo a través de grandes forámenes en los basioccipitales y toma contacto con el oído interno, a que el espacio interoseo de la cintura escapular está bién desarrallado y a que sus tres espinas anales están ubicadas normalmente. Sin embargo, ambas familias son similares en la mayoría de sus otras características óseas y, por lo tanto, se considera que están estrechamente relacionadas.

Se demuestra que la sugerencia de Patterson de que la familia Caragindae habría derivado independientemente de la familia Beryciformis carece de fundamentos: el principal índice de parentesco propuesto por él, rayos caudales con bases ahorquilladas que abrazan las estructuras hipurales, se ha desarrollado independientemente en various linajes no relacionados entre sí. Otras semejanzas entre el género bericoide *Aipichthys* del Cretáceo y carángidos modernos son considerades el producto de la evolución convergente.

LITERATURE CITED

BERG, L. S. 1947. Classification of fishes both recent and fossil. J. W. Edwards, Ann Arbor, Michigan, English Trans. 517 p.

BOULENGER, G. A. 1910. Fishes (Systematic account of Teleostei) In: The Cambridge Natural History (London), Harmer, S. F. and A. E. Shipley, Vol. 7 (viii+ 760 pp.), pp. 541-727.

FREIHOFFER, W. C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ich. Bull. 8(2):80-189.

GILL, T. 1864. Descriptive enumeration of a collection of fishes from the western coast of Central America. Proc. Acad. Nat. Sci. Philadelphia 1863, 15(4): 153-200.

GOSLINE, W. A. 1966. Comments on the classification of the percoid fishes. Pacific Science, 20(4):409-418.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. 131(4):341-455.

HAEDRICH, R. L. 1967. The stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. 135(2):31-139.

JORDAN, D. S. AND B. W. EVERMANN. 1898. The fishes of North and Middle America. Bull. U.S. Nat. Mus. 47(1):1-1240.

PATTERSON, C. 1964. A review of Mesozoic Acanthopterygian fishes, with special reference to those of the English Chalk. Phil. Trans. Roy. Soc. London, Ser. B. 247 (739):213-482.

________. 1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bull. Brit. Mus. (Nat. Hist)., Geol. 17(2):47-102.

REGAN, C. T. 1913. On the classification of the percoid fishes. Ann. Mag. Nat. Hist. (8)12(17):111-146.

SMITH, C. L. AND R. M. BAILEY. Evolution of the dorsal-fin supports of percoid fishes. Pap. Michigan Acad. Sci. Arts, Lett. 46:345-363.

________. 1962. The subocular shelf of fishes. Jour. Morph. 110(1):1-18.

STARKS, E. C. 1908. On a communication between the air-bladder and the ear in certain spiny-rayed fishes. Science 28(722):613-614.

________. 1911. Osteology of certain scombroid fishes. Leland Stanford Jr. Univ. Publ. Univ. Publ. No. 5. 49 pp.

________. 1930. The primary shoulder girdle of the bony fishes. Stanford Univ. Publ. Univ. Ser., Bio. Sci. 6(2):149-239.

SUZUKI, K. 1962. Anatomical and taxonomical studies on the carangid fishes of Japan. Rep. Fac. Fish. Prefectural Univ. Mie 4(2):45-232.

WEITZMAN, S. H. 1967. The origin of stomiatoid fishes with comments on the classification of salmoniform fishes. Copeia No. 3:507-540.

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ANATOMY OF XYLEM AND PHLOEM OF THE DATISCACEAE

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ANATOMY OF XYLEM AND PHLOEM OF THE DATISCACEAE[1]

By CHRISTOPHER DAVIDSON[2]

ABSTRACT: The woods of *Octomeles* and *Tetrameles* are similar in appearance and gross morphology. The large diameters and thin walls of the vessel elements and libriform fibers are responsible for the light-weight, non-durable quality of the woods; the small amount of wood parenchyma present probably does not contribute appreciably to this condition. The woods are quantitatively different in several respects, for instance in fiber length and vessel element diameter. The cambium is more conspicuously storied in *Tetrameles* than in *Octomeles*. The wood of *Datisca* is different from that of the two monotypic tree genera in the family and is similar to that of some other "woody herbs." The secondary phloem regions of *Octomeles* and *Tetrameles* are strikingly similar in the zone of functional sieve tube elements, but the amount and distribution of sclerenchyma in the zone of sieve tube obliteration are different.

INTRODUCTION

Lindley in 1846 suggested a relationship between *Datisca* and *Begonia* based on his knowledge of little more than the obvious morphological features, and even a detailed study of floral and vegetative parts by the present writer (Davidson 1973) permitted only an educated guess about the systematic position of the Datiscaceae and the closeness of interfamilial ties. Many of the same trends and features are present in Datiscaceae and Begoniaceae and in Flacourtiaceae, e.g., tendency toward an inferior ovary, monoecy and dioecy, separate stigmas, capsular fruits, numerous anatropous ovules and seeds, inflorescences with many flowers, tendency toward anemophily, valvate sepals, and nectar glands between gynoecium and androecium; but it is the plasticity of just such traditionally reliable characteristics in conjunction with the small size of the two families Datiscaceae and Begoniaceae that has made placement difficult, and not simply a lack of basic information.

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The four species of the Datiscaceae are trees or root perennials. *Datisca cannabina* L., a root perennial, has a range extending from the Middle East through Iran and Afghanistan and into Nepal. This species was not available for study, and therefore the California species, *D. glomerata* (Presl) Baill., which sometimes develops a small amount of wood, was used. *Octomeles sumatrana* Miq. and *Tetrameles nudiflora* R. Br. are monotypic genera of Indo-Malesian trees attaining heights of 150 to 180 feet. The former grows in rain forest and the latter in monsoon forest. Both trees are dioecious, a phenomenon explained (Davidson 1973) as a response to selection for maximum outbreeding in essentially insular situations; and this explanation could also account for dioecy in *D. cannabina* and androdioecy in *D. glomerata*.

In the present study, wood and phloem anatomy are compared among the three genera. Ontogeny of the xylem is analyzed, and comparison is made of the morphological variation in tracheary elements, fibers, and rays from primary to secondary xylem in each genus to see if a basic pattern is present despite the difference in habit between *Datisca* and the two trees. This search has not been entirely unrewarding, but interpretations based on this sort of data must be made with reservation because of the lack of comparable information from larger families that might be used to establish trends or at least the range of variation in a single group. Data derived from measurements of wood elements of *Octomeles* and *Tetrameles* are presented graphically to show size changes from the centers of the trees outward toward the cambia.

MATERIALS AND METHODS

Samples of *Datisca glomerata* were collected in Southern California *(Davidson 1002)*. Wood samples of *Octomeles* and *Tetrameles* were collected during a field trip to Malasia in 1970. Collection data for *Octomeles* is as follows: *Davidson 1124,* sapling, Gum Gum Forest Reserve, Sabah; *Davidson 1126,* seedling from Lungmanis grown in shade, Sabah; *Davidson 1482,* tree from Oomsis Cr., near Port Moresby, New Guinea. Data for *Tetrameles: Davidson 1413a,* tree from Pahang, W. Malaysia; *Davidson 1493,* tree from Brown River, Papua. Wood samples were taken across the diameter of the bole at a level just above the buttresses, at mid-point 30 to 60 ft above the ground, and at a level below the first branching. Samples from buttresses, limbs, and twigs were also included. Woods were kiln-dried and shipped to the U.S. with paraformaldehyde flake as a preservative. Cambia, phloem tissues, and twigs were preserved in alcohol.

All material was prepared by standard microtechnical procedures. Woods of the two trees sectioned poorly on the sliding microtome and had to be embedded in Parowax. Phloem was stained with safranin-fast green and with lacmoid, following the procedure of Cheadle et al. (1953). Fiber measurements were taken from macerations, but vessel elements were too large to macerate well and had to be studied in tangential sections. All figures represent the average of 50 measurements, except where stated otherwise.

OBSERVATIONS

Octomeles sumatrana Miq.

Xylem.—Fusiform cambial initials from the base of the New Guinea tree used in this study are storied, although the rows are not always perfectly even (Fig. 12). Cambial initials from the seedling and the four-meter sapling are not storied. Ray initials are storied, as are the vessel elements, though in the latter case this is inconspicuous because the vessels are solitary or paired; however, growth and adjustments related to it obscure storying in the rest of the wood elements. Average fusiform initial length and tangential width are 470 μ and 24 μ, respectively Corresponding values for ray initials are 780 μ and 110 μ. In the shade-grown seedling *(Davidson 1126)* the average size of fusiform initials is 250 μ long and 8 μ wide.

The following observations on primary xylem are based on serial radial sections and macerations of the xylem of seedling and sapling stems of *Octomeles*. Secondary xylem consisting mostly of libriform fibers arises from the cambium only a few centimeters proximal to the apex, apparently before stem elongation is completed; therefore, it is difficult to distinguish between early secondary elements and the late metaxylem. For convenience an arbitrary topographic boundary is used here. The first elements to arise from the interfascicular parts of the cambium are very long libriform fibers, and therefore, all elements included within the fiber zone opposite the original bundles are considered secondary. An ontogenetic study in depth has not been attempted, and the terms "proto-" and "metaxylem" are avoided. Instead, reference is made to the topographic relationships of the elements discussed as seen in radial sections and in incompletely macerated groups.

Tracheary elements of the primary xylem have annular and helical thickenings. The type of thickening may vary within a single element; and single, double, multiple, and singly-double helices are present in the peripheral part of the bundles (using the terminology of Bierhorst 1960). Perforation plates of the helically thickened elements may be simple (Fig. 1), or they may have a few thin bars.

Elements occurring in radial series adjust to the helically thickened vessel members have scalariform pitting with broad or narrow bars on all faces (Fig. 3). The helical thickenings of the preceding vessels are usually very closely spaced, and the gyres are nearly transverse (Fig. 2). Adjacent to the scalariformly pitted vessel elements are elements with alternate, closely spaced intervascular pits with wide borders and elliptical to narrow inner apertures; or there may be a series of transitional forms with more widely spaced bordered pits and larger apertures. Vessel-parenchyma pitting varies in this transitional region from scalariform with wide, horizontal bars to scalariform with thin, diagonal or variously oriented connections between the larger bars. These elements may be part of the late metaxylem or early secondary xylem. In vessel elements with closely spaced, alternate intervascular pits, the pits opposite parenchyma cells are unilaterally compound and half-bordered, and they are similar in most ways to the vessel-parenchyma pitting in the mature xylem at a greater distance from the pith. The chief difference is that the ray parenchyma near the pith consists mostly of upright cells, and the pits on the vessels are thus arranged in vertical rows. The perforation plates of the scalariformly pitted elements are almost always transverse, or nearly so, as are those of the first alternately pitted elements adjacent to them; and the ends of the elements are frequently tailed. The maturation pattern described here for the seedling is similar to that found in the xylem taken about two meters above the ground level in the sapling *(Davidson 1124)*.

The transition from the scalariformly pitted vessel elements to the first long, alternately pitted vessel elements and to the subsequent shorter, alternately pitted elements takes place within one millimeter of the pith in the sapling. Only a few measurements were possible, but they indicate that the helical elements are the longest (660 μ; 20 measurements) and that scalariformly pitted elements and the first alternately pitted types are similar in length (530 μ and 550 μ, respectively; 15 measurements each). The average diameter for both of these together is 130 μ (50 measurements). The long, alternately pitted members differ in several ways from the shorter ones found throughout the rest of the wood. The longer elements are narrow and have ends that are slightly constricted toward the rim of the perforation plate. In addition, as already mentioned, the vessel-parenchyma pitting pattern differs because of the vertical length of the axial parenchyma close to the pith.

Mature vessel elements are short with wide lumina and simple, transverse perforation plates and very thin walls (Fig. 13). Some elements have very large tails. Intervascular pitting is alternate, and the pits are crowded so that the chambers may appear slightly polygonal in face view (Fig. 19). Pit apertures are narrowly elliptical to slit-like and are oriented at a slightly oblique angle to the vessel axis. Pitting between vessel elements and axial parenchyma is half-bordered and unilaterally compound (Fig. 14). The border is on the vessel side, and up to eight vessel pits may be opposite a single parenchyma pit field. Often, however, there are several very fine, thickened bars extending across the parenchyma pit field, as well as similar bars in the membrane of the vessel element pit. The pit apertures are extremely irregular in shape and may be elliptical, reniform, or lenticular, with narrow, tapered ends (cf. *Tetrameles,* Fig. 26). When a single vessel pit is opposite a single pit field, the width of the pit field in any direction is usually slightly less than that of the pit membrane of the vessel pit. Occasionally pits to axial parenchyma cells are very small, round, and widely spaced (Fig. 13); this type of pitting can be found on radial and tangential walls but is apparently more common on the latter. Vessels are rarely in direct contact with procumbent ray cells, but in such instances the vessel member pits are similar to the intervascular pits, i.e., the apertures are narrow and the chambers are crowded together. These pits are arranged in conspicuous radial rows, however (Fig. 15). Transitions exist from this kind of pitting to that described for vessel walls in contact with axial parenchyma, just as there are transitions from axial parenchyma to procumbent ray cells. Both types can be found opposite a single parenchyma cell. Tyloses are present in varying numbers in heartwood and sapwood, but they are no more common in the former than in the latter. They are, however, very common (in 12 to 20 percent of the vessels) within a few millimeters of the pith. Pits on tylosis walls are simple and very small.

Figures in the following discussion represent the average of 50 measurements. There is hardly any change in vessel element length and width along a 45 cm radius from near the pith to the cambium. Along this radius element width varies from 220 μ to 330 μ, with a subtle increase radially; and vessel element length (including tails) fluctuates from 430 μ to 520 μ, with no radial correlation. Vessels may be solitary or in pairs. Near the pith up to half of them are in pairs, but along the rest of the diameter frequency varies from 10 to 25 percent. These data are summarized in figures 7 and 9. In transection vessel members are elliptical, with the long axis radially directed (Fig. 17). The vertical course of vessels is usually straight (Fig. 18), but it may be slightly sinuous.

Axial parenchyma is paratracheal vasicentric and forms a sheath two or more cells thick (Fig. 17). The cells adjacent to the vessel element, forming the inner strands, are very flat in transections and are square or broadly rectangular in face view (Figs. 14, 16). The strand ends are truncated. These cells may be divided by vertical or oblique walls as well as by the transverse walls formed in the original cambial derivatives. The number of cells in the inner strands varies from four to 16 but is generally around six; and in the outer strands, from two to four. Length of the strands varies from 500 μ to 600 μ. Although the inner strands have the greater numbers of cells, they are shorter than the outer strands and are the same length as the vessel elements. This is true regardless of the distance from the pith. Cells of the outer strands obviously intergrade with the libriform fibers.

Libriform fiber length increases from 800 μ near the pith to 1300 μ at five centimeters and then to 1700 μ at the outer end of the radius (Fig. 7). Fiber diameter increases from 35 μ near the pith to 50 μ at five centimeters and then decreases regularly to 30 μ at the end of the radius (Fig. 8). Morphologically the fibers can be divided into three zones: the two long, tapering ends and the central "body" having a nearly uniform lumen width throughout and comprising one half to one third of the total length. Pits are confined to the radial walls. The narrowly elliptical to very narrow, slitlike apertures of the simple pits are vertically oriented, and the very thin walls tend to fracture along the pit apertures in macerations. Gelatinous fibers are present in diffuse to concentrated, tangentially arranged groups (Fig. 17). Septae are infrequent in both types of libriform fibers and even in the wood of seedlings. Fibers adjacent to rays have broader lumina than normal, and those differentiating from fusiform initials that have "intruded" within a ray or between two rays are especially broad and are often rectangular in transection.

In the wood seen in this study, no apotracheal diffuse parenchyma is present, although it has been reported in some cases (Burgess 1966). The last source also mentions that the wood may be distinctly ring porous, but no cases of ring porousness were seen here.

Rays may be uniseriate or multiseriate (Fig. 18). Multiseriate rays are heterocellular (Fig. 20). Near the pith only 11 percent of the rays in this sample are uniseriate, and along the remainder of the radius they comprise from two to 15 percent of the total (Fig. 9). Neither abundance nor height of the uniseriate rays shows any distinct correlation with distance from the pith, but there are definite peaks in the abundance that may correspond to ontogenetic changes in the cambium. More work is necessary for a reliable demonstration of these changes. Multiseriate rays vary from 1400 μ high close to the pith to 1200 μ at the periphery of the bole, and the total range of variation is from 900 μ to 1400 μ. Again there is no correlation of this with position on the radius (Fig. 7). Width of the multiseriate rays, however, increases smoothly from 30 μ at the center to 100 μ at the periphery (Fig. 8).

Uniseriate rays are composed of erect cells only, and near the pith, of course, multiseriate rays are also composed of erect and square cells only. A few millimeters from the pith erect cells are found only at the margins of multiseriate rays, and they vary from narrow and upright to rather broad in radial sections. The maximum height of erect cells observed is about 100 μ. The average for all those measured (150) is 72 μ. Rays initials reaching the maximum apparently divide transversely and two rows of square or even slightly procumbent cells thus result. The several perfect radial sections seen show this change clearly. Changes in erect cells on one margin tend to parallel changes in those on the other margin. Whether the submarginal cells of the two-celled wing change ontogenetically to procumbent cells or to erect cells could not be determined. Height of the marginal cells after the division is from 40 to 50 μ. The rays may have very long wings of erect cells, and up to three multiseriate rays may be connected by uniseriate wings. The total height then often exceeds 3 mm. Wings and rays connected by wings are much more abundant in the inner part of the wood, e.g., wings were present on 25 percent of the rays near the pith in this sample, but none was seen in sections from the periphery of the bole. In other words, ray structure becomes simpler in a radial direction from the pith toward the cambium.

Phloem.—Sieve tube elements of *Octomeles* are arranged singly or in groups much like those of *Tetrameles* (see Fig. 28). They have simple to compound sieve plates and thick, nacreous walls (Fig. 21). Simple sieve plates are always transverse, but not all transverse plates are simple; compound ones are generally oblique, with two to ten sieve areas. The four to twenty-one companion cells are very narrow and deeply staining with fast green-safranin. In transections they are usually triangular and are easily distinguishable from the ordinary phloem parenchyma cells, which are slightly smaller in transectional area than the sieve tube elements and are highly vacuolate. Slime plug material in sieve tube elements is present on sieve areas opposite the lateral primary pit fields of the companion cells but not opposite those of the parenchyma cells. These lateral pit fields are elliptical to irregularly ovate, often with thin bars across the field, and thus they have a scalariform appearance. Pits between sieve tube elements and phloem ray cells are similar. Neither phloem parenchyma nor companion cells have nacreous walls, and both remain in chains in macerations. Cells of the phloem parenchyma strands may divide transversely, longitudinally, or obliquely.

Non-functional sieve tube elements are occluded by tylosoids (Fig. 22, on the right). These arise as expansions of the protoplast of a companion cell into the lumen of a sieve tube element, with a corresponding displacement of the nacreous wall of the latter. Frequently several arise from adjacent companion cells, and where they meet in the lumen, the cell faces are flat; otherwise, they are spheroidal to elongate. Soon after initial development, most of them acquire thick, lignified walls, as do the corresponding companion cells. Companion cells that do not give rise to tylosoids are still recognizable and apparently do not enlarge. Tylosoids may contain anisotropic crystals and spherites (see Metcalfe and Chalk 1950, p. 700, for a short account of this latter type of inclusion). Pits on and between the tylosoids are simple. Ultimately the entire lumen of a sieve tube element may be occluded by these structures or only a part of it, the rest being crushed by general expansion of the ground tissue.

Secondary phloem fibers and strands of brachysclereids occur in bundles that are tangentially elongate between the phloem rays and are rectangular in transection. In young stems the bundles are frequently radially directed as seen in transection because the rays are so much closer together. This sclerenchyma develops directly from cambial derivatives, and not through sclerification of non-functional sieve tube elements. The phloem fibers are very narrow and elongate, septate, and frequently mucilaginous. Their lumina are almost completely occluded, either by the mucilaginous walls or by lignified walls. Sclerenchyma in the bundles is frequently transitional between simple brachysclereids and elongate fibers; i.e., brachysclereids may have very narrow, elongate tails attached to a short, cylindrical body. These latter are transitional to short fibers that do not show a morphological zonation and have simple, circular pits. The long phloem fibers have slit-like pits that are oriented parallel to the long axis of each cell.

Phloem rays differ slightly from xylem rays. Derivatives of the erect ray initials divide transversely and all the phloem ray cells are thus procumbent, although there is much less radial elongation of these cells than in the xylem rays (Fig. 24).

Dilatation of the rays occurs in the same zone of the phloem tissue in which the tylosoids develop and comes about by both tangential elongation of and divisions in the ray cells (Figs. 22-23). No obvious dilatation meristem is present. Axial phloem parenchyma may divide, but ordinarily it takes little part in the expansion process. Conspicuous intercellular spaces are present in the ray tissue once it begins to expand, and the cells may contain starch, anisotropic crystals, and spherites. Nests of brachysclereids and solitary short-armed sclereids develop in the widening rays, especially adjacent to the strands of secondary phloem fibers. The sclereid nests may extend in either a tangential or a radial direction. The outer layer of procumbent ray cells in contact with the fiber strands is thus obscured (Fig. 23). Sometimes the axial phloem parenchyma strands sclerify, but this is uncommon.

Cambial initials from the cambium of the New Guinea tree used in this study are twice as long as those from the shade-grown seedling. The initials from just above the buttress level average 470 μ long and 24 μ in tangential width. In the seedling stem they average 240 μ and 250 μ long in two different regions of the cambium sampled, and 8 μ wide in a tangential direction. At the level of the buttresses, the sieve tube elements average 500 μ long in both macerated preparations and in tangential sections, and the average longest diameter is 84 μ. Their length corresponds to that of the cambial initials (also cf. vessel element length).

In the seedling the average sieve tube element length is 160 μ, or almost 100 μ less than that of the cambial initials, and the average longest diameter is 15 μ. This difference can be explained if some of the cambial derivatives divide transversely, or almost so, and the daughter cells undergo only slight elongation. Secondary phloem fibers in the bole from the same level as the sieve tube elements have an average length of 1600 μ and an average diameter of 40 μ, values corresponding to the dimensions of the libriform fibers in the outer xylem at that level (cf. Fig. 7). Cambial initials in a small branch about 2 cm in diameter average 352 μ long. The average length of the sieve tube elements in this stem is 307 μ, and the average diameter is 31 μ; phloem fibers average 1360 μ long and 29 μ in diameter. In this case the difference between the length of the initials and that of the mature elements possibly results in part from the measurement of slightly elongate derivatives. As mentioned before, the cambium of the small branches is non-storied and is difficult to locate precisely, unlike the storied cambium of the bole. The length of both elements of the phloem here are much shorter than those at the base of the tree. In the seedling two to six companion cells accompany each element, with an average of four. In the phloem at the base of the tree, an average of eight is found, and the most seen was 21.

Tetrameles nudiflora R. Br.

Xylem.—Fusiform cambial initials from the base of the tree from Papua are distinctly storied, as are the ray initials (Fig. 25). Fusiform initials from small branches are not storied. Storying is maintained in all elements of the wood including the rays, but it is not obvious in the vessel elements because they are generally solitary. Initials from the base of the tree have an average length of 520 μ and an average tangential width of 13 μ.

Primary xylem of *Tetrameles* shows a transitional series in wall thickenings slightly different from that in *Octomeles*. Annular thickenings are present in the earliest formed tracheary elements, but there are also elements with irregularly spiralled bands of very uneven thickness. Regular helical thickenings are single, double, or a combination of each. Complexity of the branching and anastomosis and tightness of the coils increases in a radial direction (Fig. 6). Thin connecting sheets of wall material sometimes unite the gyres of the helices of the morphologically more advanced elements, and vessel elements with scalariform-to-alternate pitting may be found directly adjacent to them (Fig. 4). Transitions in a comparable region in *Octomeles* are usually more abrupt, and vessel elements such as that on the far right in figure 6 are not present in macerations of the xylem of the latter. Often vessel elements with this scalariform-to-alternate pitting have a much greater diameter than the helically thickened elements, and the bars between the pits are very thin. The pits themselves may be hexagonal or polygonal in face view, which is an indication that the elements have been slightly stretched, according to Bierhorst and Zamora (1965). The pitting can be described as scalariform-reticulate in this case. Perforation plates are nearly always simple and vary from transverse to barely oblique, even on opposite ends of the same element (Fig. 5). Transitions from scalariform-to-alternate (scalariform-reticulate) pitted elements to mature, alternately pitted elements occur over a very short radial distance. The same sort of intermediate vessel members are present here as in comparable regions in *Octomeles* (i.e., comparable in terms of the radial sequence of secondary wall types). The intermediate vessel members are long with ends that are slightly constricted toward the perforation plates, and the pitting is almost identical to that seen in *Octomeles*.

The large, morphologically mature vessel elements are almost indistinguishable from those of *Octomeles* (Fig. 26). Intervascular pits are alternate and crowded closely together; vessel-axial parenchyma pits are unilaterally compound and half-bordered and have ovoid to lenticular or irregularly shaped chambers on the vessel element side. Perforation plates are simple and transverse, and the rim is very narrow. Inner apertures of intervascular pits are sometimes confluent by minute grooves, especially toward the ends of the elements, and very large tails may be present (Fig. 32). Pitting is less common on tangential walls, except when the vessels are in radial pairs; but occasionally normal vessel-parenchyma pit pairs are present on all faces. Vessel element to ray pitting is similar to that between vessels. Short radial files of very small vessel elements are infrequently present among the very large ones throughout the wood (Fig. 29, upper left). Pitting on these is similar to that on the large elements. No such small vessels are present in the wood of *Octomeles*. Lignified tyloses are common in heartwood and sapwood and have very large, simple pits. In transection vessel elements are circular to elliptical with the major axis oriented in a radial direction (Fig. 29), and the course of the vessels is straight to slightly sinuous.

Figures given represent the average of 50 elements measured. Measurements were taken at approximately six centimeter intervals along a 30 cm radius in a section of wood from just above the buttress level of the tree from Papua. Vessel elements of *Tetrameles* are similar in length to those of *Octomeles* but are slightly narrower. Vessel diameter increases hardly at all, as was the case in *Octomeles,* and the change in vessel element length is negligible (Fig. 33). Vessels are solitary or paired, with the pairs of vessels being a little more common than in *Octomeles* but still accounting for only ten to 25 percent of the total (Fig. 11). The number of vessels in a unit area, in this case 0.25 cm^2, decreases in a radial direction (Fig. 34).

Axial parenchyma is paratracheal, as in *Octomeles,* but the inner and outer strands are both storied and are the same length as the vessel elements (Fig. 30). Strands are mostly two to six cells long, and those nearest the rays are rounded in transection, more like the fibers, rather than tangentially flattened as they are in the rest of the sheath. The thin-walled tissue that appears in transection to be paratracheal, aliform parenchyma is actually composed of fibers, as seen from serial radial sections. Parenchyma is strictly vasicentric in the woods examined here. Axial parenchyma often contains large starch grains.

Libriform fibers increase in length from 910 μ near the pith to 1330 μ at the end of the radius 30 cm away (Fig. 33). Fluctuations in fiber diameter show no correlation with fiber length (Fig. 35). The fibers are similar in appearance to those of *Octomeles,* but the pits vary from slit-like and inconspicuous to large, with more noticeable pit membranes (Fig. 32). They show the same tendency to fracture along the pit lines, and the pits are confined to the radial walls. Gelatinous fibers occur in large, tangentially arranged groups, interspersed, of course, with the vessels.

Rays are uniseriate or multiseriate, and the latter are heterocellular (Figs. 30, 31), except near the pith, where the cells are square and erect only. The abundance of uniseriate rays varies from seven to 20 percent and shows no correlation with distance from the pith. There is a peak in abundance in the 18 to 24 cm region (Fig. 10). Multiseriate rays are 1200 μ high near the pith, 620 μ at 6 cm, and 690 μ at 30 cm (Fig. 33). The lowest multiseriate rays are only four cells high. Ray width remains fairly constant along the radius (Fig. 35). Near the pith multiseriate rays are composed almost entirely of erect and square cells, but the ontogenetic change to procumbent cells takes place over a very short distance. Erect sheath cells are rarely present. Uniseriate rays contain square and erect cells only, as seen in radial sections. Frequently a ray consists of two or three multiseriate regions connected by uniseriate wings. These "compound rays" are very numerous toward the pith and decrease in abundance in a radial direction. Wings on rays are also less common in the peripheral wood than near the pith, as was seen in *Octomeles*.

Phloem.—The appearance of the phloem zone with functional sieve-tube elements in *Tetrameles* is similar to that in *Octomeles*. Sieve-tube elements from the base of the tree from Papua (at the same level from which the xylem was taken) are distinctly storied and have thick, nacreous walls (Fig. 27). Sieve plates are transverse or slightly oblique and are either simple or compound. Most oblique sieve plates have two to four sieve areas. Pitting of the phloem elements is similar to that in *Octomeles*, and the arrangement of the elements in transection is the same. Companion cells average 12 in a strand, with a range from 7 to 17. Sometimes two rows of them accompany a single sieve-tube element, and the cells are occasionally divided longitudinally or obliquely. Ordinary phloem parenchyma strands are much larger in transectional area, though not longer than companion cell rows and contain four to eight cells. Sieve-tube elements contain very small starch grains, and the large parenchyma cells contain larger starch grains. Tylosoids are not present, but instead the sieve tubes are obliterated by a general expansion of the phloem parenchyma. Sieve plates, however, are still detectable in a transverse orientation far into the old phloem.

Secondary phloem fibers differentiate directly from cambial derivatives and are arranged in groups between the phloem rays (Fig. 28). The regular rectangular shape seen in transections of *Octomeles* phloem is absent, and small cells of axial and ray parenchyma adjacent to the fiber strands sclerify on their inner and radial walls only, forming what are sometimes referred to as "hippocrepiform" sclereids. These cells frequently contain large, cuboidal crystals, and they give the phloem in longisection a distinctive appearance quite different from that of *Octomeles*, where the adjacent cells are sclerified on all faces. The phloem fibers are usually septate or gelatinous or both.

Phloem rays are non-storied and are similar to those in *Octomeles* (Fig. 27). Expansion of the rays occurs in the zone of non-functional sieve-tube elements.

Ray cells adjacent to the fiber bundles sclerify, but large sclereid nests similar to those in *Octomeles* are infrequent. In general sclerification in the outer phloem region of the bole is not as pronounced as in *Octomeles*.

Cambial initials at the base of the tree have an average length of 520 μ and an average tangential width of 15 μ. Sieve-tube elements at the same level are 480 μ long and 65 μ on the longest diameter. Phloem fibers average 1230 μ long and 43 μ in diameter. Cambial initials from a young branch have an average length of 400 μ and an average tangential width of 12 μ. The average length of sieve-tube elements is 400 μ and the average greatest width, 49 μ; corresponding sizes for the phloem fibers in the young stem are 940 μ in length and 19 μ in diameter. Once again the phloem fibers are similar in length to the xylem fibers in the part of the wood closest to the phloem cambium.

Datisca glomerata

Xylem.—In the primary xylem of *Datisca,* a series of secondary wall thickening types similar to that in the other two genera is present. Annular and helical thickenings and scalariform pitting occur in vessel elements seen in radial sections and in macerations. The gyres of the helices are more frequently branched and tightly wound in vessel elements that are adjacent to elements with scalariform pitting. The transitional series from helical thickening to scalariform pits to alternate pits on intervascular walls is much less abrupt in *Datisca* than in *Octomeles* and *Tetrameles* because a considerable number of elongate pits and scalariformly pitted areas occur on the earliest alternately pitted vessel members. These areas of scalariform pitting are not necessarily localized at the ends of the elements toward the perforation plates, where the pitting of most vessel elements is frequently modified or distorted, but may occur anywhere on the intervascular face. In stems with a half inch of wood or more, vessel elements near the cambium have mostly alternate intervascular pits, with only a few elongate pits (Fig. 36). Intervascular pits may be widely spaced, but commonly they are very crowded, with chambers that are polygonal in face view and with inner apertures that are ovate to elliptical. The vessels may be arranged in distinct concentric bands or in more or less distinct diagonal bands that intergrade into a diffuse arrangement of vessels in different parts of the same stem.

Axial parenchyma is paratracheal in one or two layers, or around some vessels it is scanty. It is very difficult to recognize in transections because of the thick, lignified walls. The cells are often vertically elongate, and the half-bordered vessel-parenchyma pitting is thus more conspicuously scalariform than in *Octomeles* and *Tetrameles*. These pits are sometimes unilaterally compound. In places where a vessel is close to a ray, the axial parenchyma tends to be flatter and more nearly rectangular in transection, and the vessel-parenchyma pitting is almost identical to that in the two tree genera.

Libriform fibers are short and non-septate and have large, simple pits that are slit-like to elliptical with large, elliptical pit membranes. In some stems gelatinous fibers are absent, but in others they are far more common than non-gelatinous ones.

Rays are uniseriate or multiseriate (Fig. 38). Multiseriate rays are homocellular with erect and square cells in the first 7 mm of wood, but in the outer wood in thick stems there is a tendency for the central cells of the ray to be square and procumbent only. Pits in the tangential walls of procumbent and erect cells are tiny but numerous. Pits on the transverse or radial walls are much larger.

The average length of vessel elements is 200 μ, and the average greatest width, 96 μ. These measurements are taken from the outer xylem of a stem with 7 mm of wood *(Davidson 1002).* Libriform fibers are 430 μ long and 14 μ in diameter. The average height of multiseriate rays is 520 μ, and the average width, 40 μ. In a different stem from the same collection, this time with only 3 mm of wood, the average length of vessel elements is 240 μ, and the average greatest width, 72 μ. Libriform fibers in this stem have an average length of 420 μ and an average diameter of 23 μ; and the average height of multiseriate rays is 570 μ, and the average width, 45 μ.

Phloem.—Sieve-tube elements have thin, nacreous walls and transverse to slightly oblique sieve plates. Sieve plates are almost invariably simple. Very short-sieve-tube elements have a single companion cell, but the usual number is four. As in *Octomeles* and *Tetrameles,* sieve-tube elements are occasionally solitary in transections, but more often they are in irregular groups or radial rows, and they are generally larger in transverse section than the surrounding phloem parenchyma. The average length of sieve-tube elements is 180 μ, and the average greatest width is 53 μ. Secondary phloem fibers are absent. Dilatation of the rays occurs in the outer phloem where the sieve tubes are nonfunctional, and transections show large ''wedges'' of dilated ray tissue.

Cambial initials of *Datisca glomerata* are short and show a tendency toward storying (Fig. 39). The average length of the initials is 200 μ, and the average tangential width is 10 μ.

SUMMARY AND CONCLUSIONS

Woods of *Octomeles* and *Tetrameles* are rather similar in appearance and in physical properties. They are light-weight and nondurable and perish rapidly after attacks of fungi and beetles. When dry, they are very weak under most stresses. They have proved useful, therefore, in the manufacture of coffins, match sticks, dugout canoes, tea chests, and carved wooden ware (Burgess 1966; Desch 1941). Anatomically they are very specialized, consisting only of large vessel elements with simple perforation plates, thin-walled libriform fibers, axial parenchyma restricted to two paratracheal layers, and rays. The libriform fibers have very wide lumina and narrow, tapering ends; and they fracture in a nearly vertical direction in macerations, indicating a corresponding alignment or orientation of the cellulose fibrils in the wall. This is possibly a specialization for vertical strength, and a presumed lack of lateral strength resulting from the thin walls of the elements is then compensated by wall hydration. A reasonable assumption is that the wood is somewhat stronger in the living condition than when cut and ''green'' or dry, and that the rapid growth of these trees (at least of *Octomeles*) is correlated with this method (wall hydration in the libriform fibers) of attaining strength rather than one involving the production of thick, lignified fiber walls. Zones of gelatinous fibers in the wood are possibly also involved in this function.

The individual elements are similar not only in morphology but also in size. Vessel elements tend to be slightly smaller in radial diameter, however, in *Tetrameles* than in *Octomeles,* and libriform fibers of the former tend to be shorter. Also, vessels in *Tetrameles* are more frequently in radial pairs. The tendency for vessels to be in oblique rows in transections of *Tetrameles* wood mentioned by Lakhanpal and Verma (1965) was not evident in the woods in this study. Trends in the alteration of length and diameter of vessel elements and libriform fibers from the pith toward the exteriors of the boles of the two trees are similar. The most conspicuous difference is the greater amount of storying in *Tetrameles.* All elements of the secondary xylem are storied, including the libriform fibers, a feature that would appear to require a uniform and coordinated increase in the length of the fibers during the increase in girth of the trees. Support for this can be seen in figure 33, which shows a smooth increase compared to that in *Octomeles* (Fig. 7).

Cambial initials of *Datisca* average 200 μ in length and are less than half as long as those at the base of the bole in *Tetrameles* (520 μ) and *Octomeles* (470 μ). Carlquist (1966b) found the same relationship in Compositae: cambial initial length for all caudex perennials studied was half (152 μ) that of the trees (312 μ). Cumbie and Mertz (1963) found in *Sophora* a decreasing conspicuousness of storying in sequence from trees to subshrubs to herbaceous perennials, a situation similar to that in Datiscaceae. Cambia in *Octomeles* and *Tetrameles* are clearly storied, although some regions in the cambium of *Octomeles* do not show this as well as others; however, the cambium of *Datisca* is not distinctly storied but shows instead a tendency toward that condition, and the fusiform initials are short and similar to one another in length, which is usually the case when obvious storying is present.

The cambium is storied in a wide variety of plants, and the occurrence of this feature surely bears a relationship to habit and the amount of secondary growth that takes place, as pointed out by Cumbie and Merz (1963) and Carlquist (1966b). In *Octomeles* the shortest fusiform cambial initials are in seedlings (250 μ), the largest are in the cambium from the base of mature trees (470 μ), and intermediate sized initials are in twigs (352 μ). In this case the initials elongate considerably over seedling size, but an increasingly evident storied structure in this same sequence results from presumed radial longitudinal divisions. In twigs from a mature tree the vessel elements decrease in size from helical and scalariform (660 μ) to oppositely pitted elements (530 μ to 550 μ), and this apparently reflects a similar change in the fusiform initials.

Scarcity of data on cell lengths in actual storied cambia force one for the most part to extrapolate from vessel element lengths. When compared to published data from both vessel element and cambial initial lengths, these values for Datiscaceae do not appear to be unusual. The length for *Octomeles* is slightly larger than that given for *Hibiscus tiliaceus* L. (400 μ) and *Picraena excelsa* Lindl. (also 400 μ) (Beijer 1927); and that for *Datisca glomerata* is within the range for plants of comparable habit (90-200 μ) given by Beijer (1927) and close to that of *Hibiscus lasiocarpus* Cav. (210-212 μ) (Cumbie 1963). Webber (1934) gives the range for vessel element lengths in her material of *Hibiscus tiliaceus* as 59 to 456 μ (mostly 287 μ). Vessel element lengths are given by Hyde (1925) for the following tropical trees with light-weight woods: *Heliocarpus appendiculata* Turcz., 462 μ; *Apeiba aspera* Aubl., 510 μ; *Pachira barrigon* Seem., 280 μ; *Cavanillesia platanifolia* HBK., 675 μ; *Wercklea insignis* Pitt. & Standl., 300-600 μ; and *Cordia heterophylla* Poir., 276 μ.

Among the Senecioneae, 62 percent of the species studied by Carlquist (1962) had storied wood structure, and in these vessel element length varied from 463 μ in *Liabum klattii* Rob. & Greenm. and 445 μ in *Gynoxys hallii* Hieron. to 114 μ in *Tetradymia argyraea* Munz & Roos. The species of *Tetradymia,* all occupying a desert habitat, had the shortest vessel elements, and the diminution of elements in xerophytes is well documented in Compositae (Carlquist 1966b). Trees have the longest and caudex perennials, the shortest vessel elements, on the average, among the habit types found in this family. Only six percent of the annuals or biennials employed in this study had storied structure; however, 50 percent of each of the other habit categories, i.e., caudex perennial, shrub or subshrub, tree, and rosette tree or rosette shrub, had it.

From the extensive data of Carlquist (1960, 1962, 1965, 1966a) one can conclude that the degree of expression of storying in the wood is not necessarily related to the length of vessel elements (and hence, cambial initials). In the Astereae (Carlquist 1960) species with short fibers show storying more clearly than species with longer fibers, but storying is not always concerned with the amount of fiber elongation, but instead with the kind of elongation: differentially intrusive or coordinated. This can be seen clearly in *Tetrameles,* in which storying extends through all elements of the wood despite the considerable length of these elements. Presumably there is an upper limit above which the radial longitudinal divisions necessary for the formation and maintenance of a storied cambium are no longer feasible. This limit is obviously above 510 μ.

The trends of change in wood element sizes from the pith outward are interesting to note. Vessel element length remains almost unchanged in both trees throughout the 30 to 45 cm radii examined. In each case vessel element width increases slightly. A similar relationship is present in *Sophora* (Cumbie and Mertz 1963). In contrast fiber length increases 1.6 and 1.8 times the length of the cambial initials close to the pith in *Octomeles* and *Tetrameles,* respectively, and reaches a maximum of 2.7 and 3.8 times initial length at the ends of the radii. According to the table of Chattaway (1936) one might expect an enlargement of 2.0 to 2.3 times the size of the initials for species with initials between 450 μ and 500 μ long. The smaller amount of enlargement and the more uniform increase in length of the fibers in *Tetrameles* compared to *Octomeles* is no doubt at least partly responsible for the persistence of the storied condition in the wood. Fiber diameter in *Octomeles* decreases after a brief increase, but in *Tetrameles* no clear correlation with increasing girth is present. Height of multiseriate rays doubles in *Octomeles* but remains unchanged in *Tetrameles*. Changes in the percentages of uniseriate rays and vessel pairs present and in uniseriate and multiseriate ray height show subtle peaks and valleys on the graphs that are possibly correlated with environmental changes, especially because the peaks and valleys occur at similar distances from the pith (e.g., at 10 to 15 cm and 25 to 30 cm in *Octomeles;* and at 18 to 24 cm in *Tetrameles*). The number of vessel pairs in ¼ cm^2 as seen in transection decreases greatly. Ray width in mm and fiber diameter show hardly any change except for the slight peaks at 18 to 24 cm in *Tetrameles,* but ray width in *Octomeles* increases dramatically.

The woods of *Octomeles* and *Tetrameles,* although similar in appearance and gross morphology, are thus quantitatively different in numerous respects. The wood of *Datisca* differs both quantitatively and qualitatively from that of the two trees, but this does not necessarily support the recognition of two families, Datiscaceae and Tetramelaceae, as was done by Airy Shaw (1965). *Datisca* produces much less xylem and the mature wood pattern is much more slowly attained; thus one might expect little obvious correspondence between wood of herbaceous and arboreous members of the same family, as is the case here. The earliest secondary xylem in a stem of *Datisca* is, in fact, unlike that in the bole or even in twigs of *Octomeles* and *Tetrameles.* On the other hand, one might expect that if enough wood were eventually produced in plants with delayed maturation, a pattern resembling that found in trees of the same family would result. The outer wood produced in the largest stems of *Datisca* used in this study definitely has a configuration different from that close to the pith: rays contain a greater abundance of procumbent cells, intervascular pitting is alternate with only a very few transversely elongate pits, axial parenchyma is more conspicuously paratracheal, and the dimorphism in pitting between intervascular walls and vessel element-axial parenchyma walls is more pronounced.

A conspicuous difference in the wood of *Datisca,* however, is the arrangement of vessels in concentric or tangential bands. As far as can be determined, these bands do not correspond to growth rings. The vessel elements within the tangential groupings are all of approximately the same diameter, and the regions between bands are chiefly devoid of vessels; furthermore, definite concentric zones in which fiber diameter increases or decreases are not found either associated with the vessel groupings or in the zones between them. This feature of the xylem represents a major difference that can not be easily explained as simply the result of seasonality of the habitat. *Tetrameles* has been reported as occasionally having ring porous wood, although in the present study ring porousness was seen only in buttresses. An additional study of the buttress wood in *Tetrameles* is in progress.

Thus despite the difference in habits and the amount of wood produced, some correspondence between the woods of *Datisca* and the two Indo-Malesian genera can be noted; this is in addition to the storying or tendency toward it mentioned above.

A specimen of a fossil wood has been described by Lakhanpal and Verma (1965) and is tentatively included in the Datiscaceae as *Tetrameleoxylon prenudiflora.* It is from the Deccan Intertrappean beds near Nagpur in Central India and is possibly as old as early Eocene. As described and pictured, its anatomy approaches very closely that of *Tetrameles,* and the storied structure of the fossil is especially interesting. Storying of all wood elements is very uncommon (S. Carlquist, *personal communication,* 1972). However, several authors (Bailey 1924; Bancroft 1932) have pointed out some of the difficulties in identifying fossil woods and the treacherous convergences of xylem characteristics that may occur (Bailey 1957). In the 1957 paper Bailey stressed the importance of corroborative evidence in making statements about relationships even among living plants.

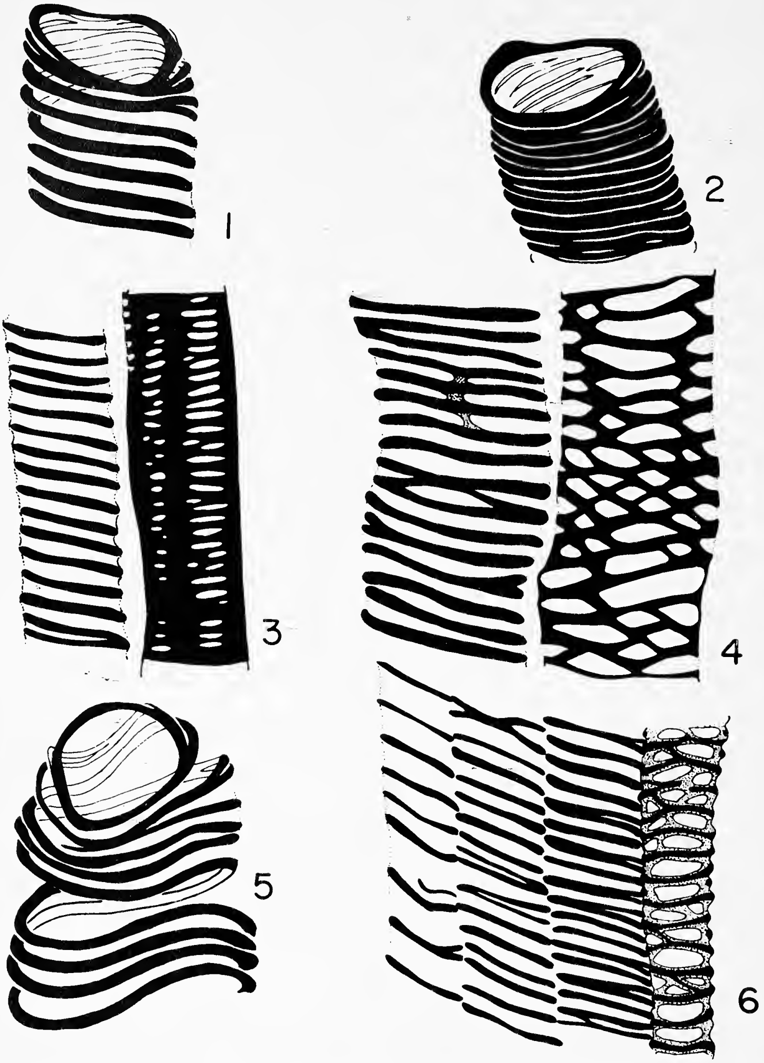
The anatomical and morphological characteristics of Datiscaceae indicate a fairly secure phylogenetic relationship with the Flacourtiaceae (Davidson 1973). The features of the xylem allow a modest refinement of this view. The level of specialization of the xylem in *Octomeles* and *Tetrameles* is greater than that in all Flacourtiaceae investigated so far. Values for the libriform fiber/vessel element ratio given by Miller (1975) are predominately below two. The values for Datiscaceae are: *Octomeles,* 3.95; *Tetrameles,* 2.77; and *Datisca,* 2.15. Vessel elements in Flacourtiaceae are smaller in diameter and in many species tend to be more angular in transection than in Datiscaceae. Fiber-tracheids are present in many species in addition to libriform fibers, and these elements generally have thick walls and narrow lumina.

Axial parenchyma is absent in secondary xylem of Flacourtiaceae and is absent or scanty in members of several other families considered to be related within the suborder Cistineae, and for which there is data: Cistaceae (Metcalfe and Chalk 1950), Violaceae (Taylor 1972), and Scyphostegiaceae (Metcalfe 1956). In these three families axial parenchyma, when present, is paratracheal as a few cells about the vessel elements. In Datiscaceae axial parenchyma is regularly paratracheal in two rows in *Octomeles* and *Tetrameles;* and in *Datisca* it is scanty or absent. Presence of abundant apotracheal axial parenchyma in *Paropsia* and *Soyauxia* indicates the possibility of an early and independent specialization in the xylem (preceding the subsequent and more obvious habit-related specializations) in Thorne's (1968) Caricineae because the tribe Paropsieae (Passifloraceae) is considered a morphologically unspecialized group in transitional between Flacourtiaceae and Passifloraceae (Ayensu and Stern 1964). A similar early specialization in the wood of Datiscaceae related to rapid growth is a possible consideration independent of the status of the proposed fossil *Tetrameleoxylon.*

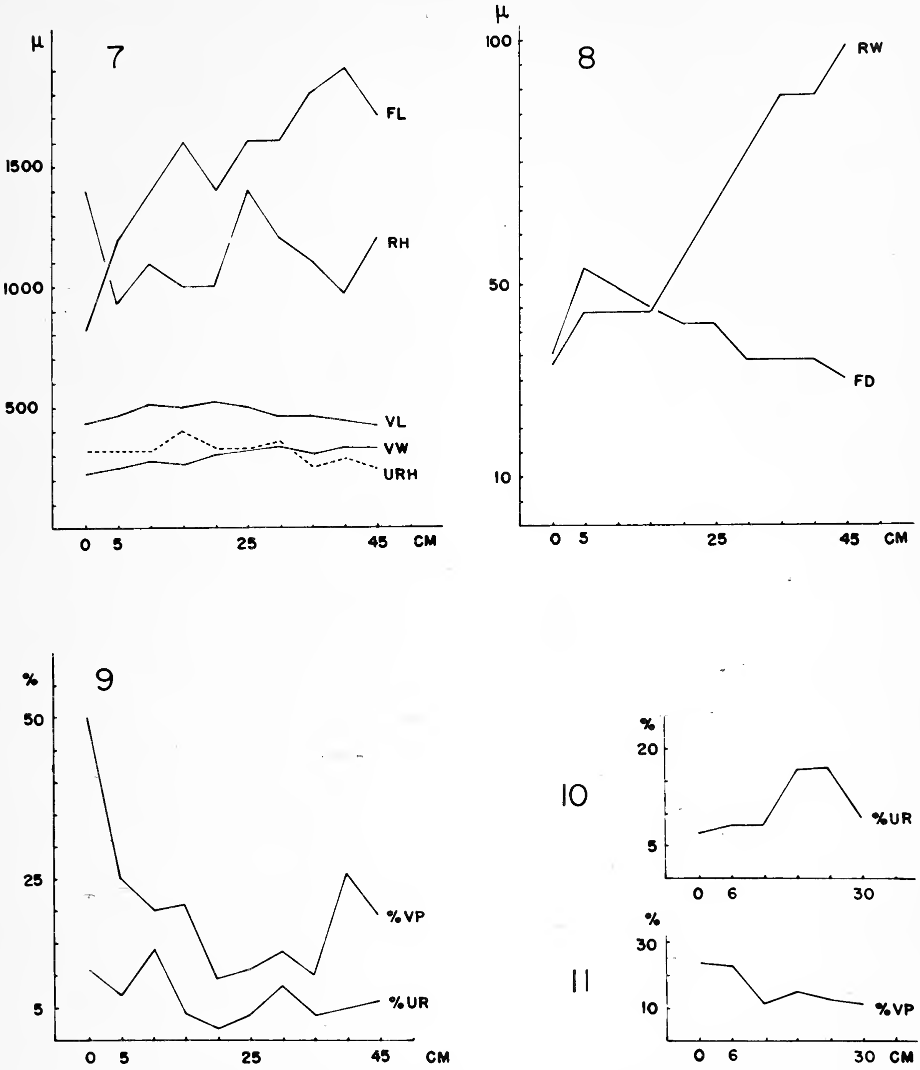
Secondary phloem regions of *Octomeles* and *Tetrameles* bear a striking resemblance to one another in the zone of functional sieve tube elements. In each genus the sieve tube elements have nearly the same average length (500 μ) and diameter (ca 70 μ) and have transverse and simple or slightly oblique and compound sieve plates. In addition the lateral walls thicken greatly, apparently as an artifact upon treatment with the fixative, and stain pearly green with fast green. The lumina of the sieve tubes may be almost completely occluded by these walls. Anatomists have referred to them as "nacreous" walls, and their presence appears to be a fairly common feature in the phloem (Esau 1969). Uncommon or infrequently reported, however, is the presence of a large number of companion cells in a single strand accompanying each sieve tube element. In *Octomeles* and *Tetrameles* up to 15 and even 20 may be present opposite a sieve tube element, and they are easily distinguishable from the other phloem elements in tangential, radial, and transverse sections. Secondary phloem fibers differentiate within the part of the phloem containing functional sieve tube elements. After dilation of the phloem rays has begun, the sieve tubes in *Octomeles* are ''invaded'' by tylosoids that grow out of the companion cells; however, tylosoids are lacking in the phloem of *Tetrameles,* in which the sieve tube elements are obliterated by general expansion of the phloem parenchyma. Moreover, the sclerenchyma that forms around the secondary phloem fibers in this region in *Tetrameles* is composed of ''hippocrepiform'' sclereids, i.e., they are horseshoe-shaped in transections because the outer cell walls remain unsclerified. Sclereids in a comparable region in *Octomeles* are sclerified on all faces. This is only a minor distinction between the two, but in longisection the outer phloem of each is easily distinguishable because of it.

In *Datisca* secondary phloem fibers are absent, a common feature of herbaceous plants, and the number of companion cells is four to five. Nacreous walls are present, but they are not nearly as thick as in the other two genera; and the sieve plates are almost exclusively simple.

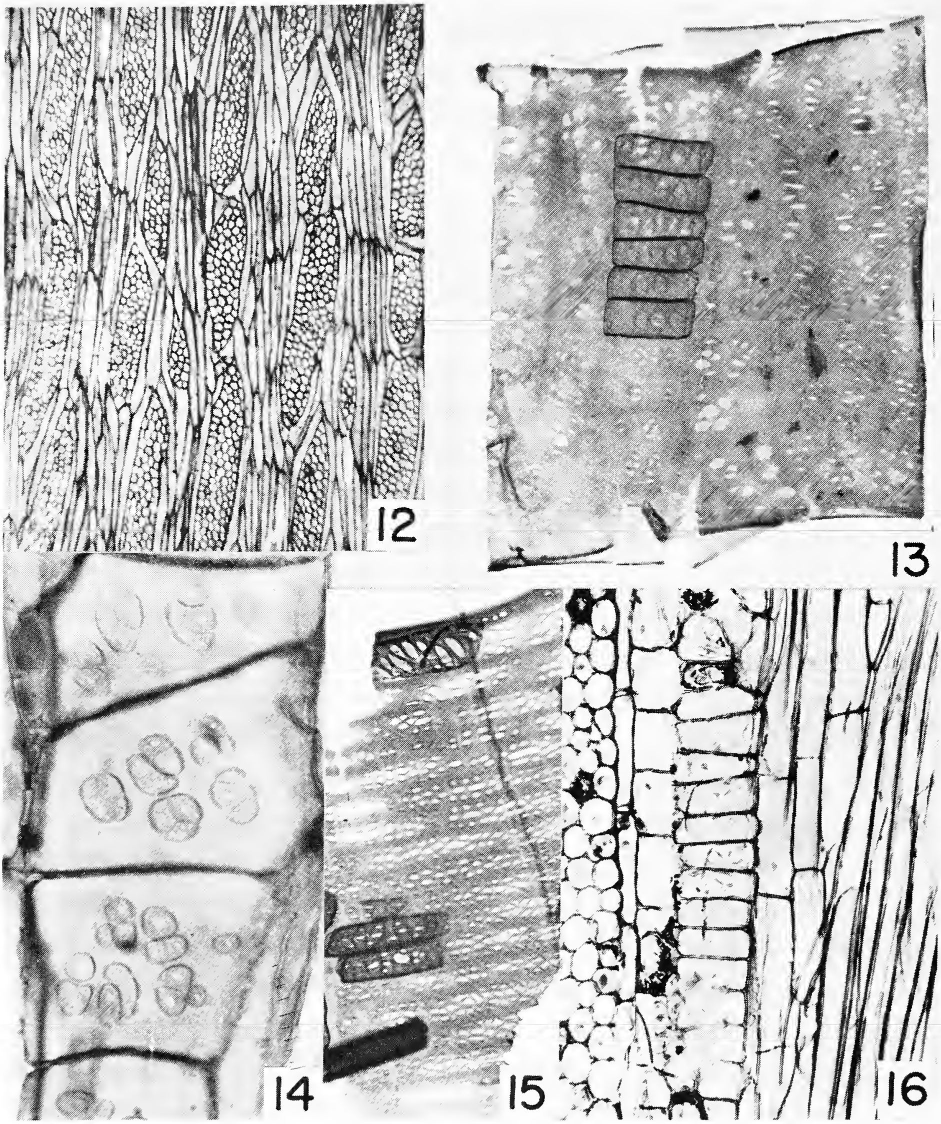
Evidence from anatomy and morphology supports the inclusion of these three genera in a single family. Subfamilial taxonomic ranking is possibly more a matter of personal preference here, but the present writer believes that the differences between Datisceae *(Datisca)* and Tetrameleae *(Tetrameles* and *Octomeles)* do not necessitate subfamily status for the two groups; rather, they are better treated as tribes, as was done by Warburg (1895) and Gilg (1925).



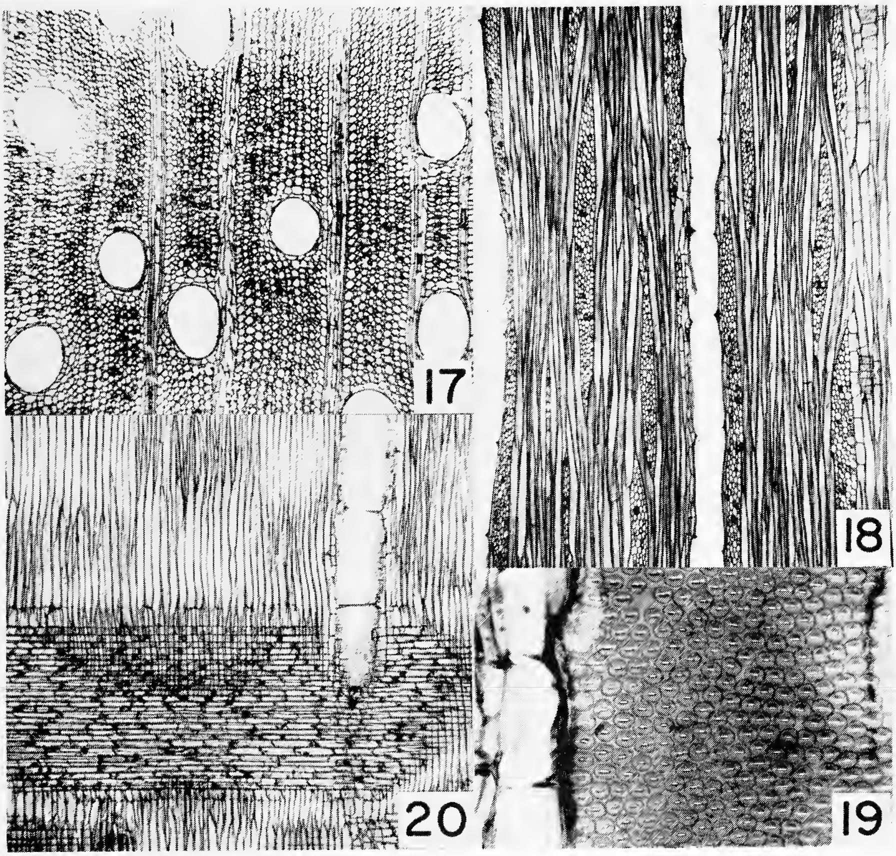
Figures 1-6. Primary and early secondary xylem elements, all from macerations. Figures 1-3. *Octomeles sumatrana. Davidson 1127.* Figures 4-6. *Tetrameles nudiflora. Davidson 1413a.* Drawn with camera lucida. Figure 1. Simple perforation plate on a vessel element with helical thickenings. × 1200. Figure 2. Vessel element. Very closely spaced gyres with complicated branchings. × 600. Figure 3. Two adjacent vessels, one with narrow, scalariform pits. Actual contact between these two elements was obscured. × 600. Figure 4. Two adjacent vessel elements. Note three thin connecting walls between the gyres. Parenchyma was present between the two elements. × 1200. Figure 5. Simple perforation plate. Note branches in the helix and one thickening band that ends blindly. × 1200. Figure 6. Four adjacent elements, each with a progressively more complex thickening pattern. Stippling indicates the wall is more lightly stained than the dark bands. × 1200.



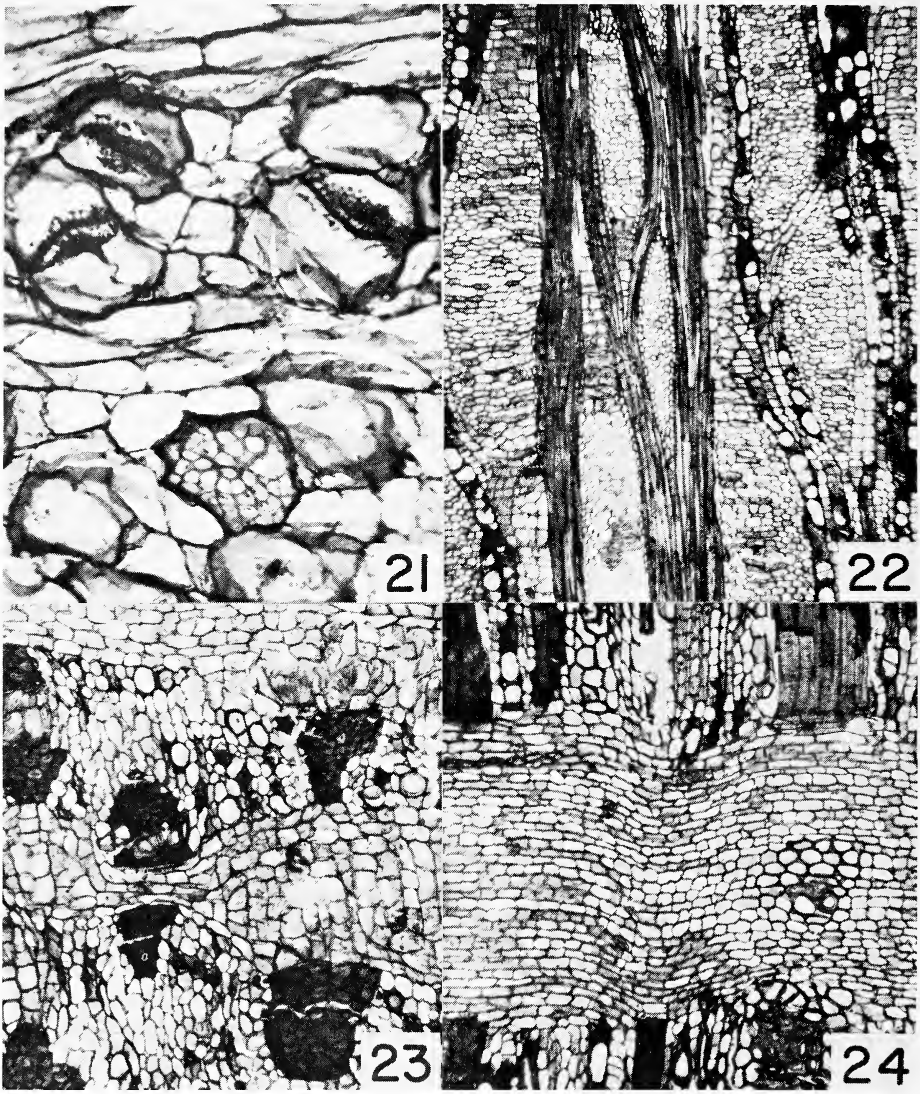
FIGURES 7-11. Graphs showing average lengths and percentages of certain xylem elements (ordinate) in relation to distance from the pith (abscissa) in cm. FD, fiber diameter; FL, fiber length; RH, ray height; RW, ray width; UR, uniseriate rays; URH, uniseriate ray height; VL, vessel element length; VW, longest width of vessel element; VP, vessel elements in pairs. FIGURES 7-9. *Octomeles sumatrana. Davidson 1482.* FIGURES 10-11. *Tetrameles nudiflora. Davidson 1493.* FIGURE 7. Note that fiber length increases but vessel element length changes very little. FIGURE 8. Fiber diameter decreases; width of multiseriate rays increases. FIGURE 9. Note rough correspondence of peaks between the percentages of uniseriate rays and vessel elements in pairs. FIGURE 10. Abundance of uniseriate rays shows a peak. FIGURE 11. Percentage of vessel elements in pairs decreases.



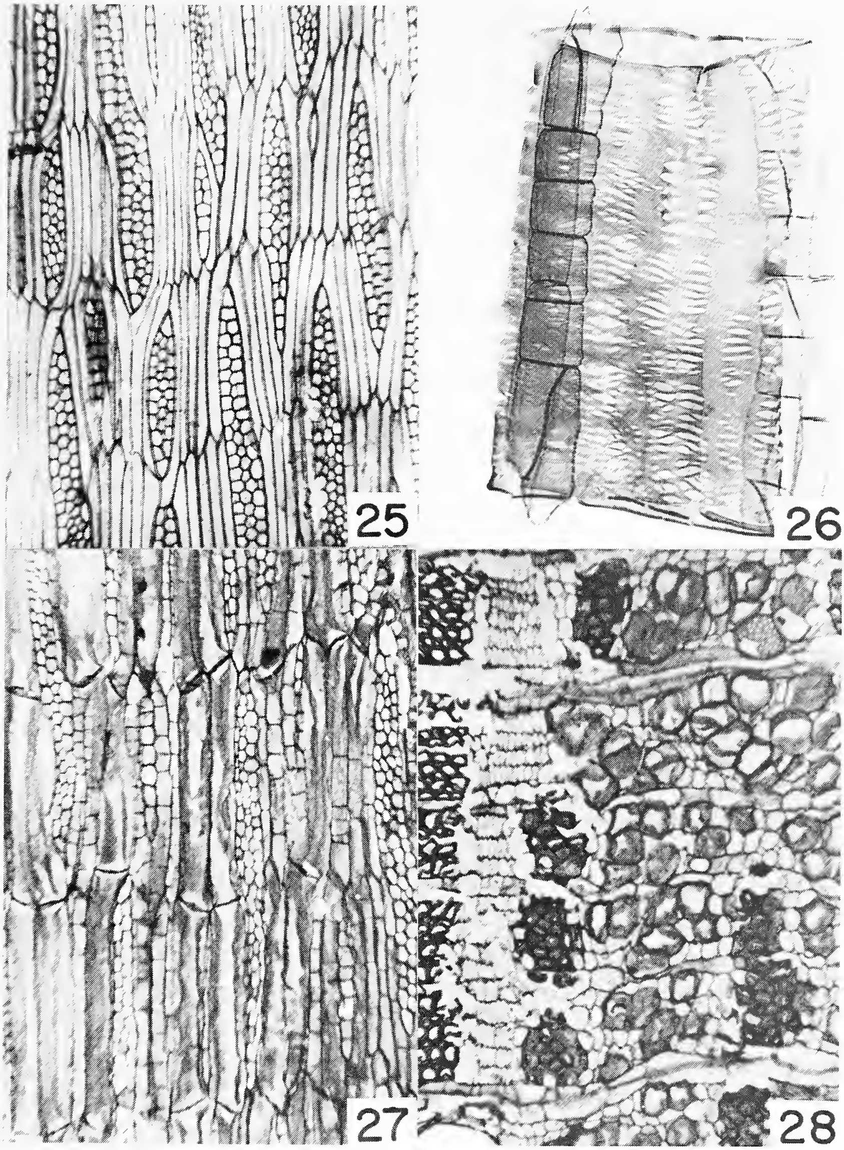
FIGURES 12-16. *Octomeles sumatrana. Davidson 1482.* FIGURES 13-16 from secondary xylem. FIGURE 12. Cambium. Storied condition is most evident on the right. Cambial derivatives are on the far left. × 45. FIGURE 13. Vessel element, flattened by the cover slip. Note unusually small vessel-parenchyma pits. × 155. FIGURE 14. Vessel-to-axial parenchyma pitting. These pits are half-bordered and unilaterally compound. × 560. FIGURE 15. Vessel pits opposite procumbent ray cells. × 155. FIGURE 16. Very long strand of axial parenchyma consisting of sixteen cells. Strand is directly adjacent to the vessel element. × 155.



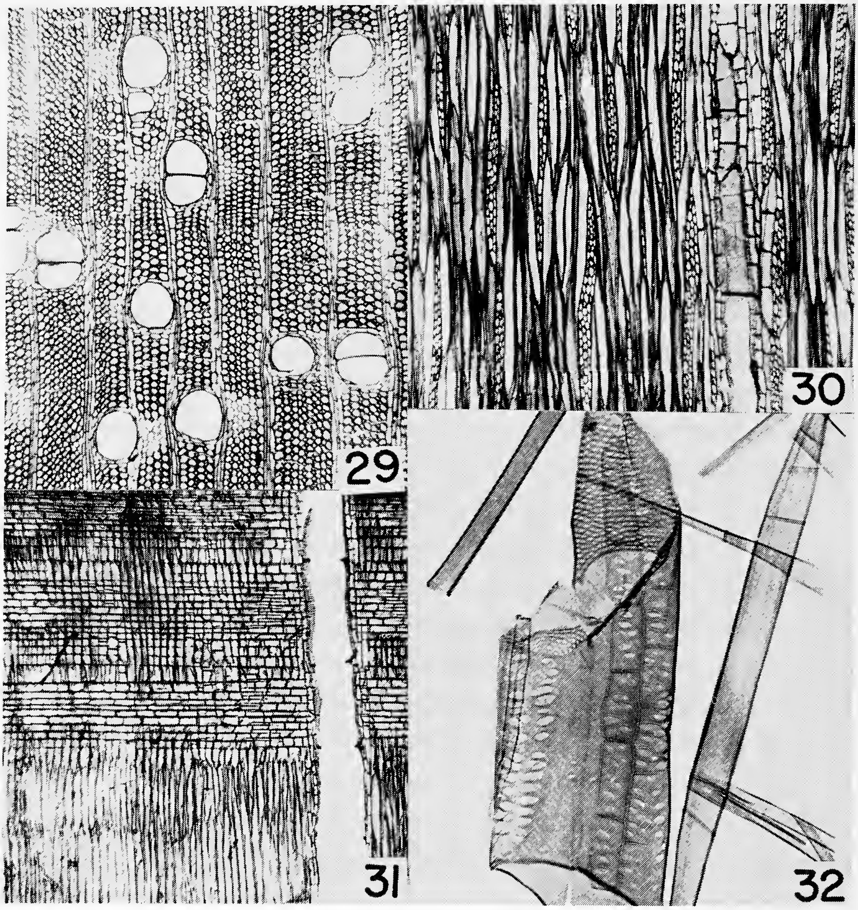
FIGURES 17-20. Secondary xylem of *Octomeles sumatrana. Davidson 1482.* FIGURE 17. Transection. Darkened patches are gelatinous fibers. × 40. FIGURE 18. Tangential section. × 40. FIGURE 19. Intervascular pitting. From a tangential section. × 360. FIGURE 20. Radial section. Note erect cells at the top of the ray. × 40.



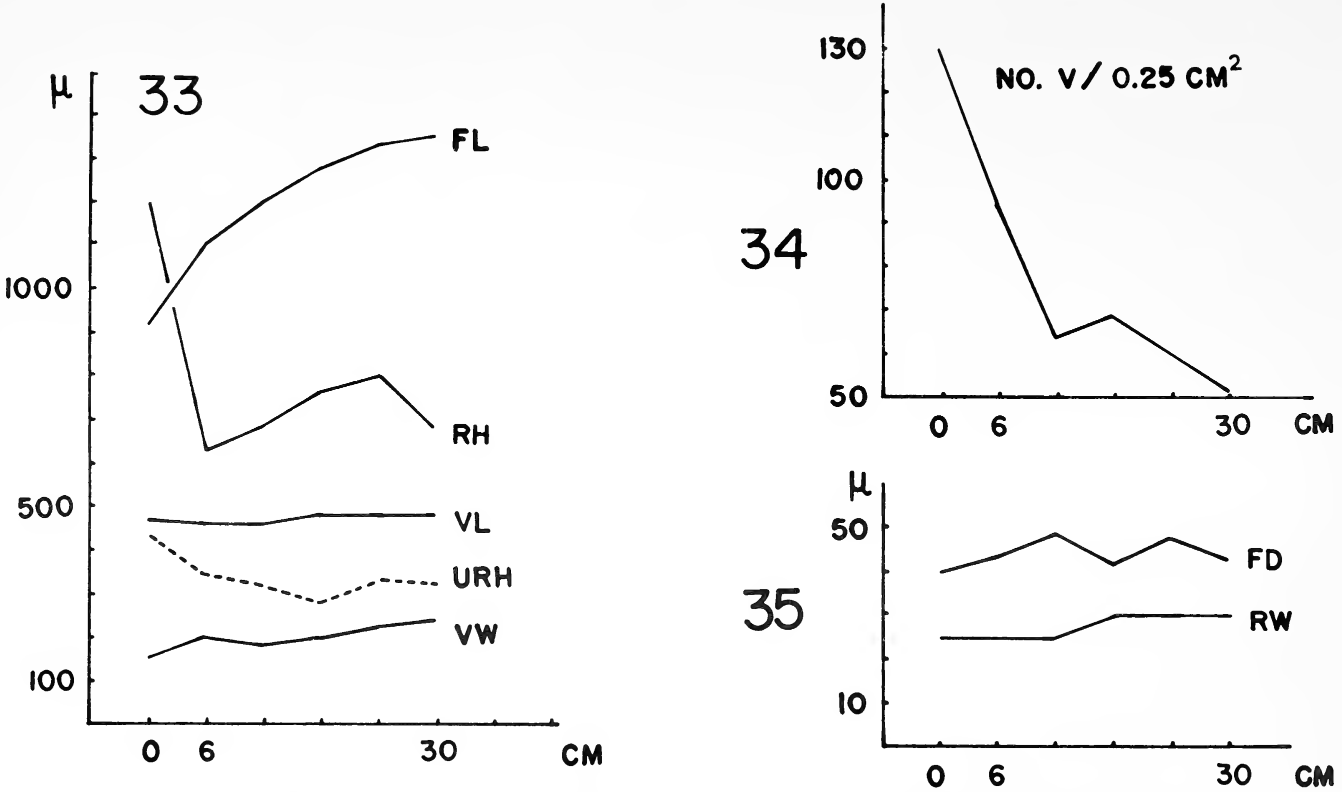
FIGURES 21-24. Phloem of *Octomeles sumatrana. Davidson 1482*. FIGURE 21. Transection of four sieve tubes, three with oblique sieve plates and one with a transverse sieve plate. Note appearance of the nacreous walls. × 920. FIGURE 22. Tangential section through several phloem rays, three of which are undergoing dilation. Secondary phloem fibers are in strands to left of center. Sieve tube elements occluded by tylosoids are to the right. × 60. FIGURE 23. Transverse section showing dilation of a phloem ray and the strands of secondary phloem fibers. × 60. FIGURE 24. Radial section through a phloem ray showing mostly procumbent cells on the left. Cambium is on the left, out of the picture. × 60.



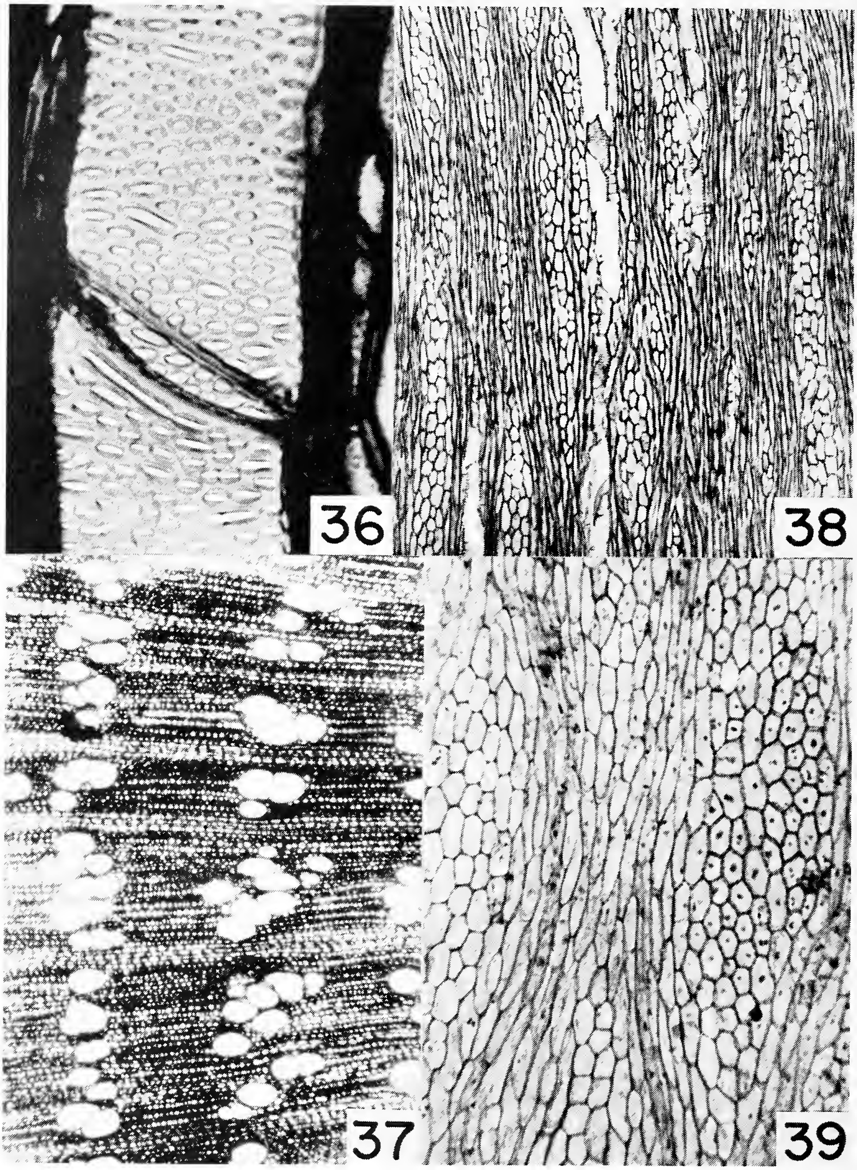
FIGURES 25-28. *Tetrameles nudiflora*. FIGURES 25-26. *Davidson 1493*. FIGURES 27-28. Davidson 1413. FIGURE 25. Tangential section of cambium region showing storied cambium. Cambial derivatives are on the far left. × 70. FIGURE 26. Vessel element from secondary xylem. Note lenticular pits opposite axial parenchyma cells. × 250. FIGURE 27. Tangential section of the secondary phloem showing storied sieve tube elements. × 80. FIGURE 28. Transverse section of the secondary phloem. Note sieve tube elements with nacreous walls and secondary phloem fibers. Cambium is to the left. × 105.



FIGURES 29-32. Secondary xylem of *Tetrameles nudiflora*. *Davidson 1493*. FIGURE 29. Transection. × 40. FIGURE 30. Tangential section. Note storied fibers and axial parenchyma. × 45. FIGURE 31. Radial section. × 52. FIGURE 32. Vessel element with a large tail and a few libriform fibers from a maceration. × 70.



FIGURES 33-35. *Tetrameles nudiflora. Davidson 1493.* Graphs showing average xylem component measurements and number of vessel elements (ordinate) in relation to distance from the pith (abscissa). Symbols are the same as in FIGURES 7-11. FIGURE 33. Note that fiber length increases, vessel element length and diameter hardly change. FIGURE 34. The number of vessel elements in a unit of area decreases greatly. FIGURE 35. Fiber diameter and multiseriate ray width change little.



FIGURES 36-39. *Datisca glomerata. Davidson 1002.* FIGURE 36. Intervascular pitting. From a tangential section of secondary xylem. Note simple perforation plate. × 340. FIGURE 37. Transection of secondary xylem showing the ring porous condition in a stem with a centimeter of wood. Pith is toward the right. × 55. FIGURE 38. Tangential section of secondary xylem. × 60. FIGURE 39. Tangential section of stem with one centimeter of wood, showing cambium. Note tendency toward storying of very short fusiform initials. × 110.

LITERATURE CITED

AIRY SHAW, H. K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis's 'Dictionary.' Kew Bull. 18:249-273.

AYENSU, E. S. AND W. L. STERN. 1964. Systematic anatomy and ontogeny of the stem in the Passifloraceae. Contr. U.S. Nat. Herb. 34:45-73.

BAILEY, I. W. 1924. The problem of identifying the wood of Cretacious and later dicotyledons: *Paraphyllanthoxylon arizonense*. Ann. Bot. (London) 38:439-451.

_________. 1957. The potentialities and limitations of wood anatomy in the study of the phylogeny and classification of Angiosperms. J. Arnold Arbor. 38:243-254.

BANCROFT, H. 1932. On the identification of isolated timber specimens with especial reference to fossil woods. Ann. Bot. (London) 46:353-365.

BEIJER, J. D. 1927. Die Vermehrung der radialen Reihen im Cambium. Rec. Trav. bot. néerland. 24:631-786.

BIERHORST, D. W. 1960. Observations on tracheary elements. Phytomorphology 10:249-305.

BIERHORST, D. W. AND P. M. ZAMORA. 1965. Primary xylem elements and element associations of angiosperms. Amer. J. Bot. 52:657-710.

BURGESS, P. R. 1966. Timbers of Sabah. Sabah Forest Records No. 6. Forest Department, Sabah, Malaysia.

CARLQUIST, S. 1960. Wood anatomy of Astereae (Compositae). Trop. Woods 113:54-84.

_________. 1962. Wood anatomy of Senecioneae (Compositae). Aliso 5:123-146.

_________. 1965. Wood anatomy of Eupatorieae (Compositae). Aliso 6:89-103.

CARLQUIST, S. 1966a. Wood anatomy of Anthemideae, Ambrosieae, Calenduleae, and Arctotideae (Compositae). Aliso 6:1-23.

_________. 1966b. Wood anatomy of Compositae: A summary, with comments on factors controlling wood evolution. Aliso 6:25-44.

CHATTAWAY, M. W. 1936. Relation between fiber and cambial initial length in dicotyledonous woods. Trop. Woods 46:16-20.

CHEADLE, V. I., E. M. GIFFORD AND K. ESAU. 1953. A staining combination for phloem and contiguous tissues. Stain Technol. 28:49-53.

CUMBIE, B. G. 1963. The vascular cambium and xylem development in *Hibiscus lasiocarpus*. Amer. J. Bot. 50:944-951.

CUMBIE, B. G. AND D. MERTZ. 1963. Xylem anatomy of *Sophora* (Leguminosae) in relation to habit. Amer. J. Bot. 49:33-40.

DAVIDSON, C. 1973. An anatomical and morphological study of Datiscaceae. Aliso 8:49-110.

DESCH, H. E. 1941. Manual of Malayan timbers. Vol. I. Malayan Forest Records No. 15. Federation Government of Malaya.

ESAU, K. 1969. The phloem. Gebrüder Borntraeger, Berlin.

GILG, E. 1925. Datiscaceae. pp. 543-547. *In* A. Engler and K. Prantl, Die Natürlichen Pflanzenfamilien. 2 ed., Vol. 21. Wilhelm Engelmann, Leipzig.

HYDE, K. C. 1925. Tropical light weight woods. Bot. Gaz. 79:380-411.

LAKHANPAL, R. N. AND J. K. VERMA. 1965. Fossil wood of *Tetrameles* from the Deccan Intertrappean beds of Mohgaonkalan, Madhya Pradesh. Paleobotanist 14:209-213.

LINDLEY, J. 1846. The vegetable kingdom. Vol. I Bradbury & Evans, London.

METCALFE, C. R. 1956. *Scyphostegia borneensis* Stapf. Anatomy of stem and leaf in relation to its taxonomic position. Reinwardtia 4:99-104.

METCALFE, C. R. AND L. CHALK. 1950. Anatomy of the dicotyledons. Vol. I. Clarendon Press, Oxford.

MILLER, R. B. 1975. Systematic anatomy of the xylem and comments on the relationships of Flacourtiaceae. J. Arnold Arbor. 56:20-102.

TAYLOR, F. H. 1972. The secondary xylem of the Violaceae: a comparative study. Bot. Gaz. 133:230-242.

THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6:57-66.

WARBURG, O. 1895. Datiscaceae. pp. 150-155. *In* A. Engler and K. Prantl, Die Natürlichen Pflanzenfamilien. Vol. III, pt. 6a. Wilhelm Engelmann, Leipzig.

WEBBER, I. E. 1934. The wood of *Hibiscus tiliaceus* L. Trop. Woods 37:14-17.

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