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CANINE FUNCTION IN *SMILODON* (MAMMALIA; FELIDAE; MACHAIRODONTINAE)

William A. Akersten[1]

ABSTRACT. A number of sabertoothed mammal features, exemplified by *Smilodon* from Rancho La Brea, cannot be reconciled with hypotheses that the upper canines were used for stabbing or slashing: the relatively dull sabers which would require enormous force to penetrate the hide of a prey animal, the robust mandible with functional but small canines, the geometric relationships of the skull and the reconstructed head-depressing musculature, and the presence of canine opposition (necessary for biting but not for stabbing or slashing). It is also difficult to envision intermediate steps of behavior and morphology in the multiple evolution of stabbing or slashing from biting ancestors. These apparent anomalies can be resolved (and other features can be explained) by hypothesizing that the upper canines were employed in a shearing, as opposed to puncturing, bite accomplished by depressing the cranium against immobilized mandibles. The probable area of attack was the abdomen. Most, if not all, other sabertoothed mammals appear to possess canine opposition and probably employed some variation of the attack methodology suggested for *Smilodon.* Several lines of evidence suggest that *Smilodon* possessed some degree of cooperative social behavior. The attack methods of the extant Komodo dragon, *Varanus komodoensis,* appear to be analogous to those hypothesized for *Smilodon* and the extinct giant varanids of Australia may have preempted the niche occupied by sabertoothed mammals on other continents.

INTRODUCTION

The suite of unusual specializations which typify sabertoothed mammals has intrigued researchers for decades. Practically every possible mode of saber use has been postulated, including using them as "can-openers" for glyptodonts (Brandes, 1900) or for slicing carrion (Bohlin, 1940). Matthew (1901) refers to earlier suggestions (without citation) that sabertooths used their canines to grub for marine molluscs as walruses supposedly do, as tree climbing aids, or (in forms with reduced mandibular flanges) to stab with the mouth closed.

More recent studies (e.g., Hough, 1949; Miller, 1969; Gonyea, 1976; Martin, 1980; and Emerson and Radinsky, 1980) have firmly established sabertooths as active predators well adapted to catching prey and eating meat. Presently accepted hypotheses concerning saber function usually center about their use in stabbing and/or slashing, probably at the throat of their prey. While these interpretations appear to be consistent with many sabertooth specializations, other considerations have led me to question the efficacy of this type of attack.

One difficulty I have with accepting a stabbing or slashing attack by *Smilodon* involves the problem of forcing a pair of such weapons into the hide and flesh of a prey animal. As compressed and seemingly sharp as the sabers may be, they are far from being equivalent to a steel knife. Forcing even a slightly dulled steel knife through the hide of a large mammal can be very difficult. Other mammalian carnivores with conical canines use the opposing force of the lower canines to facilitate penetration of the upper canines (and vice versa) during an attack. If they simply tried to force the upper canines into their prey without using the lower canines, they would fail. Similarly, if *Smilodon* were to try to stab or slash without an opposing force, considerable momentum would have to be built up by the time the sabers contacted the prey. I believe that the problem of developing enough force to drive a pair of rather dull sabers into hide and flesh raises serious questions about any stabbing or slashing hypothesis.

An important theoretical point involves the fact that sabertooth adaptations arose independently within at least four different groups of mammals—borhyaenid marsupials, creodonts, nimravids, and felids. As the normal kill method in all living mammalian carnivores (and, presumably, all ancestors of sabertoothed types) is the canine bite, postulating a slash or stab requires the multiple, convergent development of a radically different method of kill behavior. I find it impossible to envision the necessary intermediate combinations of morphology and behavior that would be required by a gradualistic model of evaluation and equally impossible to accept that such a complex combination of changes could occur even once within the framework of punctuated models.

These and other difficulties with the slashing/stabbing hy-

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potheses raised the question of whether the peculiar specializations of sabertoothed mammals have resulted in more radical interpretations of saber function than is necessary. In an effort to address this question, I studied the large Rancho La Brea sample of *Smilodon* in the collections of the George C. Page Museum (specimen prefixes LACMHC and LACMRLP), a branch of the Natural History Museum of Los Angeles County (LACM).

MORPHOLOGY

Three character complexes were most important in the development of the various slashing/stabbing hypotheses: (1) the apparently weak mandible with a reduced canine which does not appear to have been of much use during an attack, (2) the evidence for powerful head-depressing muscles which could be used in a stabbing or slashing action, and (3) the striking hypertrophy of the upper canines which immediately conjures up images of the edged weapons man uses to slash or stab. Re-examination of these characters and consideration of other morphologic features yield additional information not always in agreement with previous interpretations.

OVERALL STRUCTURE

The *Smilodon* from Rancho La Brea approximated the size of a modern African lion but had very powerful forelimbs, a proportionately larger head, and a short tail. The forelimbs, with their large, retractile claws (Gonyea, 1976), would have been very well suited to pulling down and immobilizing fairly sizable prey animals. Limb and foot structure and proportions (Merriam and Stock, 1932; Gonyea, 1976; Martin, 1980; Shaw and Tejada-Flores, in press) and vertebral structure (Merriam and Stock, 1932; Slijper, 1946) indicate that *Smilodon* was not cursorial but probably was capable of short, rushing attacks. Most recent authors generally agree that *Smilodon* probably stalked close to its potential prey, then rushed a short distance from ambush. I believe that the massive forelimbs were employed in grasping the upper part of the prey's body from the side and pulling it down towards the attacker so that the abdomen would be exposed on the opposite side. This method of bringing down prey is similar to that often used by many of the larger living felids when attacking large prey except that they may also employ their teeth in the attack (Leyhausen, 1979; Schaller, 1967, 1972).

MANDIBULAR COMPLEX

The greatly reduced coronoid process has been repeatedly used as evidence for a relatively weak bite (e.g., Matthew, 1910; Merriam and Stock, 1932) because it would have provided less leverage for the temporalis muscle. Emerson and Radinsky (1980), elaborating on the work of Kurtén (1952), showed that the probable bite strength during carnassial occlusion was roughly equivalent to that of comparably sized living felids, but at full gape, it was undoubtedly rather weak. This resulted not only from the poor lever arm for the temporalis but also from the reduction of the masseter. They also determined that the relative cross-sectional area of the mandible below the carnassial was about equivalent in sabertooths and living felids. The diastemal region superficially appears weaker in *Smilodon* because it is relatively shallow. However, Figures 1A, B compare cross sections cut through the shallowest part of the diastema in a young adult African lion (*Panthera leo*) and a young adult *Smilodon* of about the same size. Not only is the relatively greater breadth of this area in *Smilodon* readily apparent, but the outer layer of compact bone is far thicker. If anything, the mandible of *Smilodon* appears much stronger than that of the lion. Several longitudinally sectioned and many broken mandibles in the Rancho La Brea collections at the George C. Page Museum demonstrate that this very strong internal construction characterizes the entire *Smilodon* mandible. In overall appearance, the *Smilodon* mandible is stouter than that of the lion with a massive, very rugose symphyseal region (Fig. 1C) most similar to that of *Panthera* among the type III symphyses described by Scapino (1981). The major differences between the two appear in the outline of the symphyses and the distribution of the largest rugosities. In *Smilodon* these occur toward the ventral portion at or near the ventral tubercle while in *Panthera* they are found near the posterior margin. The evidence strongly indicates that powerful forces impinge upon the mandible and that it was not simply used for shearing at the carnassials or pulling flesh off prey in conjunction with the incisors, the only other postulated uses for the mandibular dentition (Emerson and Radinsky, 1980; Miller, 1969).

Forces acting on the mandible have major components transmitted through the condyloid process to the glenoid

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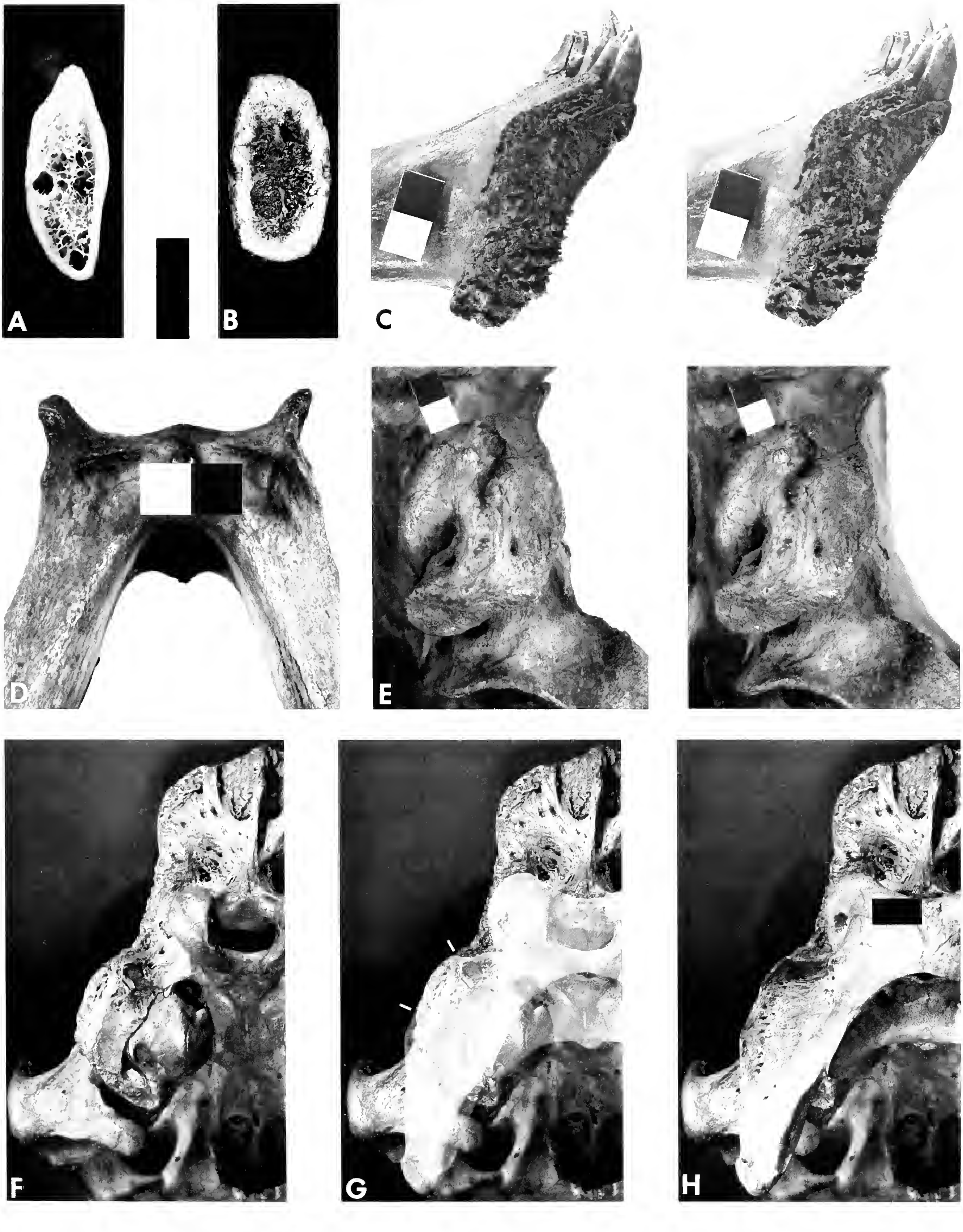
Figure 1. *Panthera leo.* **A.** Cross section through diastema of mandible, LACMRLB JGT2. Rest are *Smilodon.* **B.** Cross section through diastema of mandible, LACMHC 7108. **C.** Stereopair of left mandibular symphysis, LACMRLP R11258. **D.** Ventral view of anterior mandible, LACMHC 2001-2, showing anterior projection of flanges. **E.** Stereopair of right mastoid process, LACMHC 2001-2 (retroarticular process at bottom). **F, G, H.** Posteroventral views of left portion of cranium, LACMRLP 20273, and associated atlas, LACMRLP 20276, depicting relationships of atlas and mastoid process. **F.** Cranium only. **H.** Cranium with atlas articulated and rotated to extreme anteroventrad position. **G.** Same as H but with "ghost image" of ammonium chloride coated atlas in double exposure. Note the alignment of portions of the lateral margins of atlas wing and mastoid process between white marks in G. Scales: A, B, F, G, H, scale bar = 2 cm (bar between A and B applies to both and bar on H also applies to F and G). C, D, E in cm.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fossa of the squamosal. This region independently reflects the gross magnitude of such forces. In comparison to the African lion, the neck of *Smilodon*'s condyloid process is much stouter and the condyle is wider with a considerably larger articular surface. In the cranium of *Smilodon,* the retroarticular process is thick and stout, the entire zygoma is very well developed and the base of the zygomatic process of the temporal provides massive support for the glenoid fossa. The entire articular complex and supporting structures demonstrate again that the mandible of *Smilodon* was subjected to very strong forces during some portion of its use.

While the lower canines of *Smilodon* are relatively small in comparison to body size, they are far from vestigial. They approximate the size of canine found in a medium-sized mountain lion (*Felis concolor*) but they appear even smaller because of their proximity to the very large incisors. The lower canines are stout, sharp, and recurved posteriorly with strong roots and relatively thick enamel. Their posterior and medial margins bear sharp, finely serrate ridges (see Merriam and Stock, 1932: pl. 13, figs. 8, 8a). While the medial serrate ridge may have functioned with the incisor battery in worrying loose chunks of meat as described by Miller (1969), the only apparent function for the posterior serrate ridge would have been to facilitate puncturing. Thus, the reduced lower canines of *Smilodon* were still capable of functioning like those of living felids in penetrating the hide and flesh of prey animals, but would not have produced as large or deep wounds as the lower canines of an equivalent-sized true cat. The large roots and the heavy bone surrounding them are evidence that the canines were also subjected to considerable stress.

One often discussed feature of the mandible is the anteroventral mandibular flange. The ventral development of this flange in *Smilodon* is relatively slight, when compared to many other sabertoothed mammals, and quite variable. It has been suggested that a highly developed ventral flange served to protect the sabers from breakage or to protect the neck from accidental injury by the sabers (Scott and Jepsen, 1936; Martin, 1980). A more plausible explanation has recently been advanced by Dawn A. Adams and Daniel B. Adams (pers. comm., 1983), which relates the ventrad development of the flange to a powerful digastric musculature required by forms with nearly vertical occiputs. Several studies (e.g., Schultz et al., 1970) have suggested that the flange became reduced in *Smilodon* to allow stabbing with the mouth closed. This appears to be improbable because there would then be no function for that portion of the posterior serrations on the upper canine which extend dorsad to the ventral border of the closed mandible all the way to the gum line. Furthermore, if the sabers were used to stab with the mouth closed, the proximal serrations should wear smooth more slowly than the distal serrations. None of the La Brea specimens display such differential wear. Also, a major potential problem would result from the shock transmitted to occluding upper and lower teeth (particularly the interlocking incisors) when the mandible struck the prey in a closed mouth stab.

In contrast to the moderate and variable ventral development of the flanges, they are consistently well developed anteriorly. The anterior portions of the flanges flare laterally and become slightly thickened at their margins. In ventral view, the anterior outline of the symphyseal region is strongly concave with the symphysis situated at the axis of a considerable depression (Fig. 1D). As described below, I believe that the anterior development of the flange played an important part during *Smilodon*'s attack.

INCISOR BATTERY

The basic form and function of the upper and lower incisors have been well described by Merriam and Stock (1932) and Miller (1969). Overall, they are very large, sharp, recurved posteriorly, and bear huge roots. The bone anterior and posterior to the alveoli is very stout. The incisor battery appears very prognathous with the sharp apices of the upper and lower incisors (and the lower canines) completely interlocking when the jaw is closed (Fig. 2). All tend to bear ridges on their medial and lateral margins. These ridges are usually very finely serrate in unworn teeth with the serrations becoming progressively better developed from the medial (where they may be absent) to the lateral incisors. The ridges curve posteriad toward the bases of the crowns to form cingula which frequently bear small cuspules. Placement of the cingular cusps is such that they provide additional shear against the tips of the opposing incisors when the jaw is completely closed. If the incisors were used to gnaw flesh from bones as suggested by Miller (1969), one would expect to find wear on the anterodistal portions of the crowns. None of the examined specimens exhibited such wear. As noted by Merriam and Stock (1932) and further elaborated by Miller (1969), the incisor battery, including the lower canines, forms an immensely powerful puncturing and gripping device. I would add that it was also capable of developing considerable shear between opposing teeth.

HEAD-DEPRESSING MUSCULATURE

A number of osteological characters indicative of powerful head-depressing muscles in various sabertoothed mammals have been cited as evidence supporting a stabbing or slashing attack (Matthew, 1910; Merriam and Stock, 1932). Emerson and Radinsky (1980) question these interpretations, noting that the insertion scars for the rectus capitus ventralis and longus capitus (at the basioccipital-basisphenoid suture) are not unusually well developed and asserting that "the sternomastoid and the cleidomastoid do not leave discrete scars on the mastoid process." While it is true that the insertion scars for the rectus capitus ventralis and the longus capitus are only modestly developed in *Smilodon,* the broad tip of the mastoid process is very rugose with several deep pits (Fig. 1E) which may coalesce to form a large groove. I agree with Merriam and Stock (1932:33) that this area probably served as the insertion for well-developed sternomastoid and cleidomastoid muscles. In addition, the manubrium of the sternum (origin of the sternomastoid) is relatively robust in *Smilodon.* The enlarged mastoid processes would give these muscles considerably more leverage to depress the head than in typical felines. Another possible explanation for at least a portion of the apparent muscle scars at the tip of the mastoid process is that they served as the area of origin for a very well developed digastric musculature (Dawn A. Adams and Daniel B. Adams, pers. comm., 1983).

There is evidence for additional, and even more powerful, head-depressing muscles in *Smilodon.* The entire posterolateral portions of the enlarged mastoid processes appear to be covered with very large muscle scars (Fig. 1E). Matthew (1910) believed that this area provided attachment for the sternomastoid which had shifted from its normal attachment area at the tip of the mastoid process. However, if the atlas of *Smilodon* is rotated anteroventrally about the atlantooccipital articulation, the parts of the lateral margins of its wings not only align quite well with posterolateral muscle scars of the mastoid processes but would also effectively block other muscles of posterior origin which might potentially insert on these scars (Figs. 1F, G, H). Modern felids and canids possess tiny mastoid processes with only very minute muscles extending between them and the atlas wings. Descriptions of modern felid and canid anatomy often ignore, or are not consistent in the terminology and interpretations of, these muscles. Though quite different in detail, the highly developed mastoid processes of the giant panda, *Ailuropoda,* more closely approximate those of *Smilodon* and their anatomical relationships have been thoroughly described by Davis (1964). He states that the rectus capitus lateralis inserts on the "posterior surface of the mastoid process near its outer edge" (p. 170). The obliquus capitus anterior is described as inserting "just above the mastoid process" (p. 170) but on his figure 20, its insertion is shown as including much of the posterior surface of the mastoid process. Both muscles originate on the ventral surface of the tip of the atlas wing which, in *Smilodon,* is posteriorly elongated and deflected ventrad (Figs. 3A, B; 5A). Thus, it appears highly probable that very well developed muscles (which may or may not be homologous with those of *Ailuropoda*) extended from the ventral surfaces of the atlas wings to the posterolateral margins of the mastoid processes. The enlargement of the atlas wings and mastoid processes in *Smilodon* would give this atlantomastoid musculature increased length and considerable leverage to depress the head about the atlantooccipital articulation. I consider them to have been more important in this action than other head-depressing muscles. Additional evidence for the presence of powerful muscles originating from the ventral portion of the atlas wings is provided by the large attachment area on the axis for the obliquus capitus posterior, which originates from the entire neural arch and inserts on the dorsal surface of the atlas wings (Davis, 1964). This muscle functions to rotate the atlantoaxial articulation and prevents the atlas wings from being drawn anteriad during contraction of the atlantomastoid musculature. In comparison to *Panthera,* the neural arch of the axis in *Smilodon* (Fig. 3C) is proportionately larger and extends more posteriad relative to the centrum indicating a well-developed obliquus capitus posterior. Reconstructions of the major head-depressing muscles are depicted in Figure 5A. Overall ventrad movement of the head and neck would have been aided by a powerful scalene musculature indicated by the enlarged transverse processes on the cervical vertebrae (Matthew, 1910).

All available evidence leads to the almost inescapable conclusion that *Smilodon* possessed strongly developed muscles for head depression, especially those which rotate the atlantooccipital articulation. While these have been used as powerful evidence for a stabbing or slashing mode of saber use, it is not impossible that powerful head depression could have served some other purpose, as will be proposed below.

UPPER CANINES

The saber morphology of *Smilodon* has been well described by Merriam and Stock (1932). To review briefly, they are long, slender, recurved, blade-like teeth with an extremely thin veneer of enamel (Fig. 4). The enamel extends to the gum line along the posterior margin but its extent is variable on the rest of the tooth, averaging only about two thirds as far. Very fine enamel serrations extend from the tip to the gum line on the posterior margin and, variably, between one half to two thirds as far from the tip on the anterior margin. The posterior margin is more compressed than the anterior, especially toward the base of the exposed portion. Here, the anterior margin becomes quite rounded proximal to the termination of the anterior serrations. The serrations are frequently worn, even smooth, in older individuals. Although this wear indicates that the canines were not used simply for display, I believe that the fineness of the serrations and the very thin enamel layer covering the saber in *Smilodon* demonstrate relatively infrequent use (such as during the kill but not regularly during feeding). More frequent use, resulting in more severe wear, should have required thicker enamel and strongly developed serrations. The large root of the upper canine, about 40% of its total length, undoubtedly reflects the need for support during strenuous use.

The bone surrounding the canine alveolus is relatively thin along the medial surface, but this area is braced to some extent by the palatal portions of the maxillary and premaxillary bones. On the lateral surface, it is thin at the alveolar margin but thickens a little toward the root region, especially adjacent to the long axis of the alveolus. Heavier bone occurs along the anterior and posterior margins of the alveolus, indicating more anterior and posterior stress on the canine. In individuals with fully developed canines, very thick bone surrounds the pointed tip of the canine root and extends from the tip along the anterior margin for a short distance. The canine root does not extend as far posteriad as the convex surface on the external portion of the maxillary suggests, but terminates above or slightly anterior to the infraorbital foramen. Younger specimens, in which the canine root is still forming, have alveoli with broadly U-shaped terminations surrounded by relatively thin bone. These canine alveoli also extend farther posteriad, almost to the posterior margin of the maxillary bone. Thus, thickening of the bone is accomplished by a filling in of the alveolus as the root becomes fully formed. The mass of bone at the tip and along the proximal anterior edge of the root is consistent with the need

Figure 2. Anterior view of *Smilodon* skull and mandible, LACMHC 2001-1, showing interlocking of incisors. Scale bar = 3 cm. From Merriam and Stock (1932: pl. 2, fig. 3) with permission, Carnegie Institution of Washington.

to provide support for fairly strong forces developed by pushing the tip against a resistant object. If the sabers were used regularly in anterior or posterior slicing actions, I would expect to find more bone supporting the distal portions of the anterior and posterior alveolar margins.

The importance of the sabers to *Smilodon* is illustrated by the similar morphology of the deciduous upper canines which are, however, concave on their medial surfaces in order to accommodate considerable eruption of the permanent canines before the deciduous canines are lost (Merriam and Stock, 1932). Unlike modern felines, in which there is a brief period of time when the deciduous canines have become too weak to use and the permanent canines have not yet erupted to the point of becoming functional (Leyhausen, 1979), *Smilodon* always maintained functional upper canines (Tejada-Flores and Shaw, 1984).

As briefly, mentioned in the introduction, the supposed knife-like appearance of the sabers is only valid when compared to a typical conical carnivore canine, not when compared to a genuine steel knife. Cross sections through a typical saber (Fig. 4) more nearly resemble somewhat flattened ovals than sections through a metal blade. The very tips of the upper canines, which would initiate penetration of a prey animal's hide and flesh, are rounded both transversely and anteroposteriorly (Figs. 5B, C). Comparison with the upper canines of *Panthera leo* shows that the saber tips of *Smilodon* are little, if any, sharper. The force required to drive one, let alone two, of these formidable looking weapons into a large prey animal would be enormous.

PALATE

The palate of *Smilodon* (Fig. 5D) exhibits a pattern of longitudinal ridges and grooves (Merriam and Stock, 1932:35–36). A highly variable medial ridge usually occurs from the premaxillary-maxillary suture to the posterior margin of the palatines. In some individuals, this ridge may extend more anteriorly while in others, parts or all of it may be very reduced or absent. A lateral ridge occurs on each side of the medial ridge. These are more consistently developed and extend posterolaterad from the anterior margins of the anterior palatine foramina to terminate between the middle and posterior of the palatines. The anterior portions of the lateral ridges bear sharp crests which frequently flare laterally. Posterior to the palatine-maxillary suture, the lateral ridges become subdued and broadened before merging with the palatine surface. A prominent broad groove with a roughened bottom exists between each lateral ridge and the adjacent alveolar margin of the palate. Merriam and Stock (1932:36) suggested that these grooves served as conduits to ingest sucked blood. This appears to be improbable in that the posterior portions of the grooves trend laterally and terminate just medial to the M^{1}s, not at mid-palate. In addition, it would be very difficult to seal off the front of the mouth for effective sucking unless the pool of blood was quite deep (Bohlin, 1940).

If the mandible is articulated with the cranium in a closed position (Fig. 5E), however, the rather sharp diastemal crests align exactly with the middle of the palatal grooves with about 4 cm of clearance. This alignment of the palatal ridges and grooves and the diastemal crests of the mandible could serve as a very effective gripping device for thick pieces of flesh held in the anterior of the mouth. Galapagos finches have similar longitudinal ridges and grooves in the horny palate which line up with the margins of the mandibular tomia in order to grip and crush seeds (Bowman, 1961). Use of the palate for gripping would require a much stronger palatal construction than exists in cats with conical canines. In fact, the palate of *Smilodon* is far sturdier than in modern felids of similar size; the bone is thicker, the corrugations

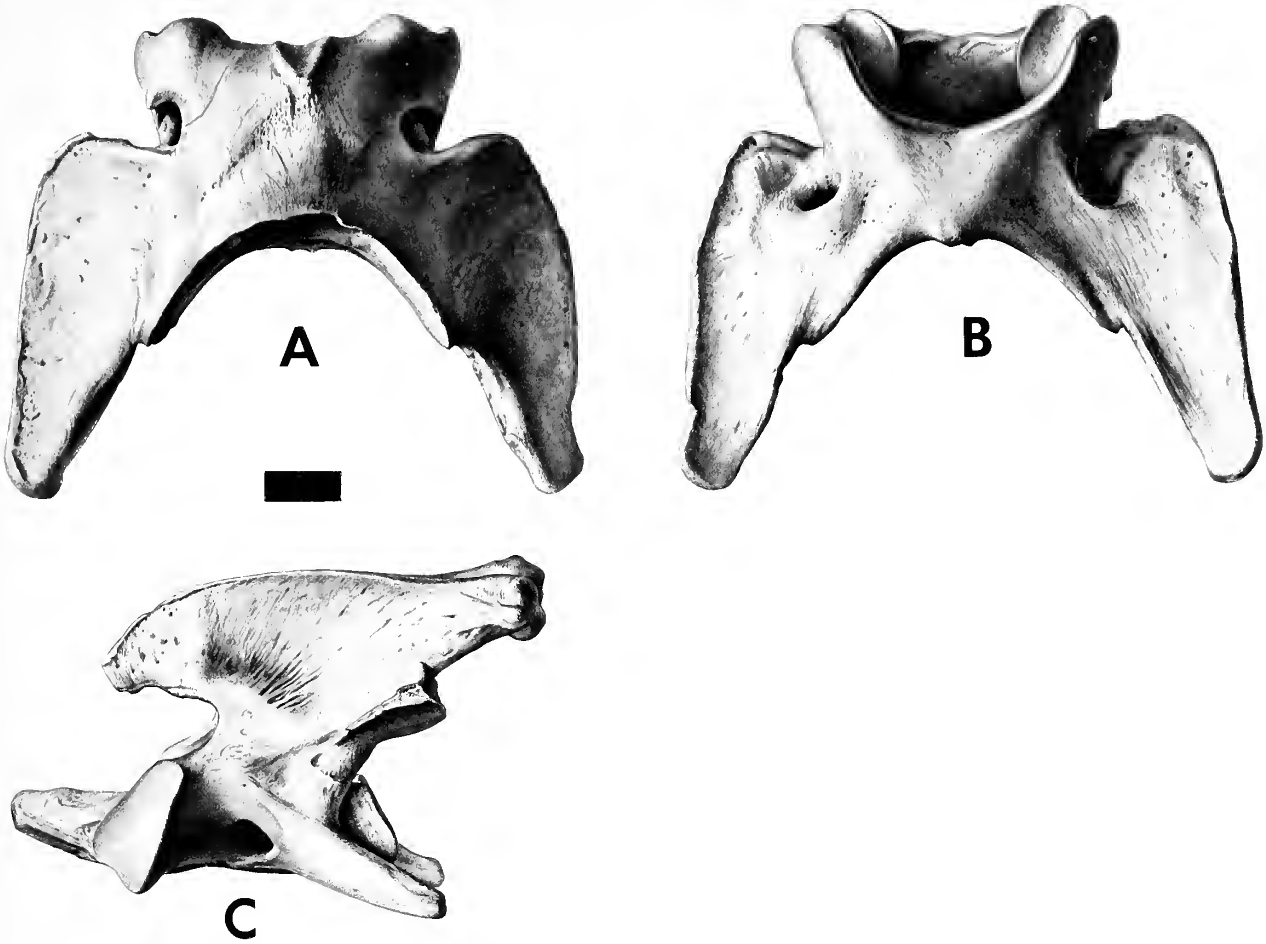

Figure 3. *Smilodon.* Atlas, LACMHC 2038-5: **A.** Dorsal view. **B.** Ventral view. Axis, LACMHC 2039-1: **C.** Lateral view. Scale bar = 2 cm. All from Merriam and Stock (1932: pl. 17, figs. 4, 7, 3) with permission, Carnegie Institution of Washington.

would also serve to reinforce this area, and the palate is partially braced along the midline by the vomer.

CRANIUM-MANDIBLE GEOMETRY

The most important task in determining mode of saber usage is the investigation of types of motion permitted or excluded by the geometric relationships of cranium and upper dentition to mandible and lower dentition. The extent of the gape in *Smilodon* has often been discussed. I agree with Emerson and Radinsky (1980) that the maximum possible gape was about 90 to 95 degrees. As they further point out, this maximum gape results in about the same amount of absolute clearance between the upper and lower canines as does the maximum gape in modern felids of similar size.

In a detailed study of possible modes of saber use by *Smilodon,* Simpson (1941) concluded that the momentum needed for a stabbing attack could be generated by an initial leap. As the sabertooth struck its prey, body momentum would be transferred to the skull which would whip ventrad to drive the sabers home. Simpson omitted the mandible from his figures and calculations, however, stating that inclusion of the mandible would not have altered his conclusions. If the mandible is added to all of his diagrams and the outline of the prey animal's body is extended in a rounded curve, it is obvious that the mandible, even at maximum possible gape, would strike the prey well before or at least simultaneously with the upper canines. This would either abruptly close the mouth or prevent canine penetration. Bohlin (1947) also showed that when the amount of posterodorsad cranial flexion necessary to generate momentum for a stab is considered, the head would be drawn so far back that the attacker could not have seen its prey, much less the intended area of attack (see his fig. 1). Kurtén (1952) suggested that sabertooths pressed the mouth at full gape against the body of their prey then nodded the head ventrad to stab. While this removes potential problems which would be created by impact of the mandible or inability to see the intended prey, there would now be far too little force for the sabers to penetrate.

Initial penetration of a tapered, sharp blade is best facilitated by motion in the direction of its long axis. Any deviation from the axial direction when the target is struck will

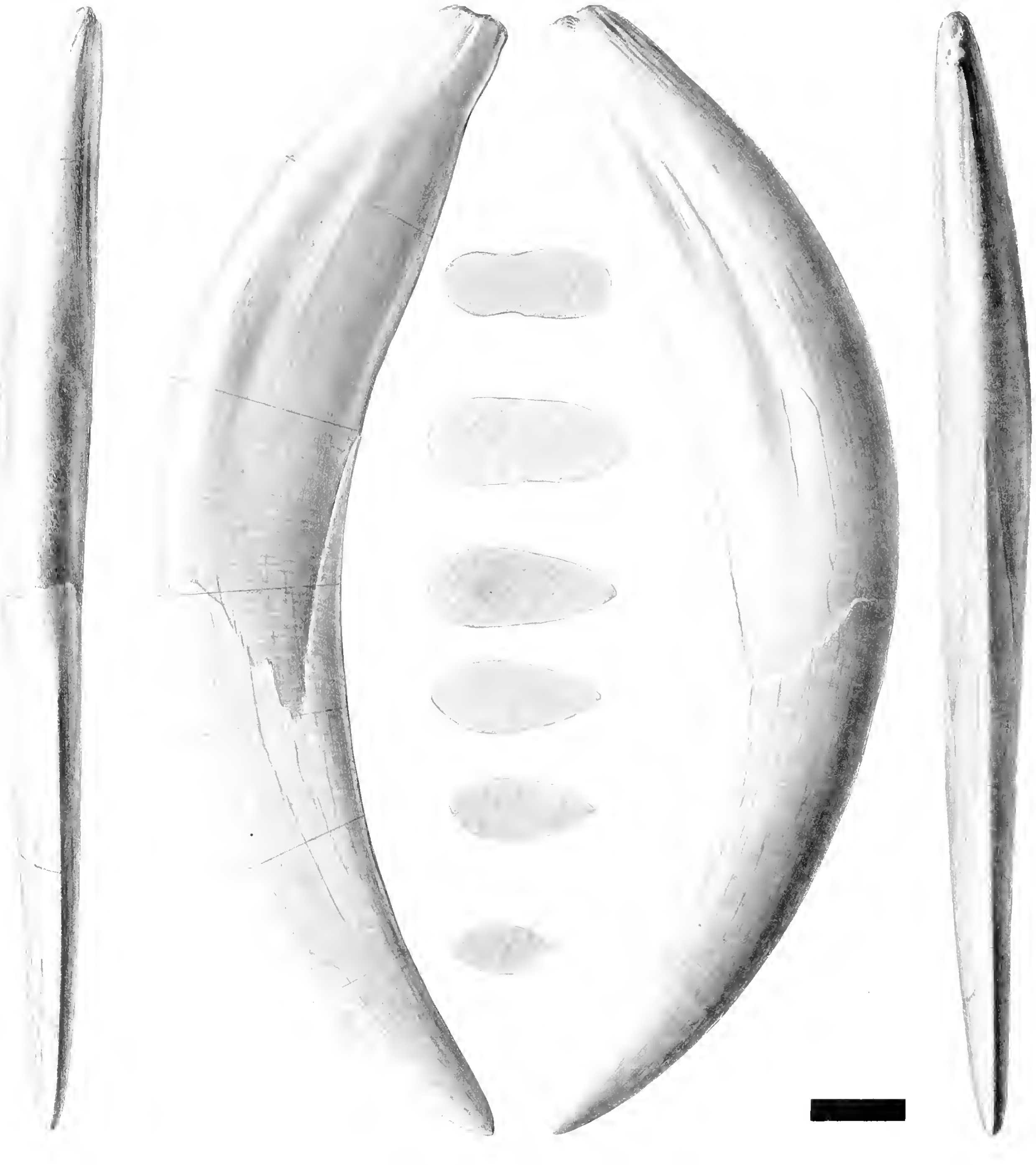

Figure 4. *Smilodon* right upper canine, LACMHC 2000-R.9. From left to right: anterior, medial, cross-sectional, lateral, and posterior views. Scale bar = 2 cm. From Merriam and Stock (1932: pl. 12, fig. 1) with permission, Carnegie Institution of Washington.

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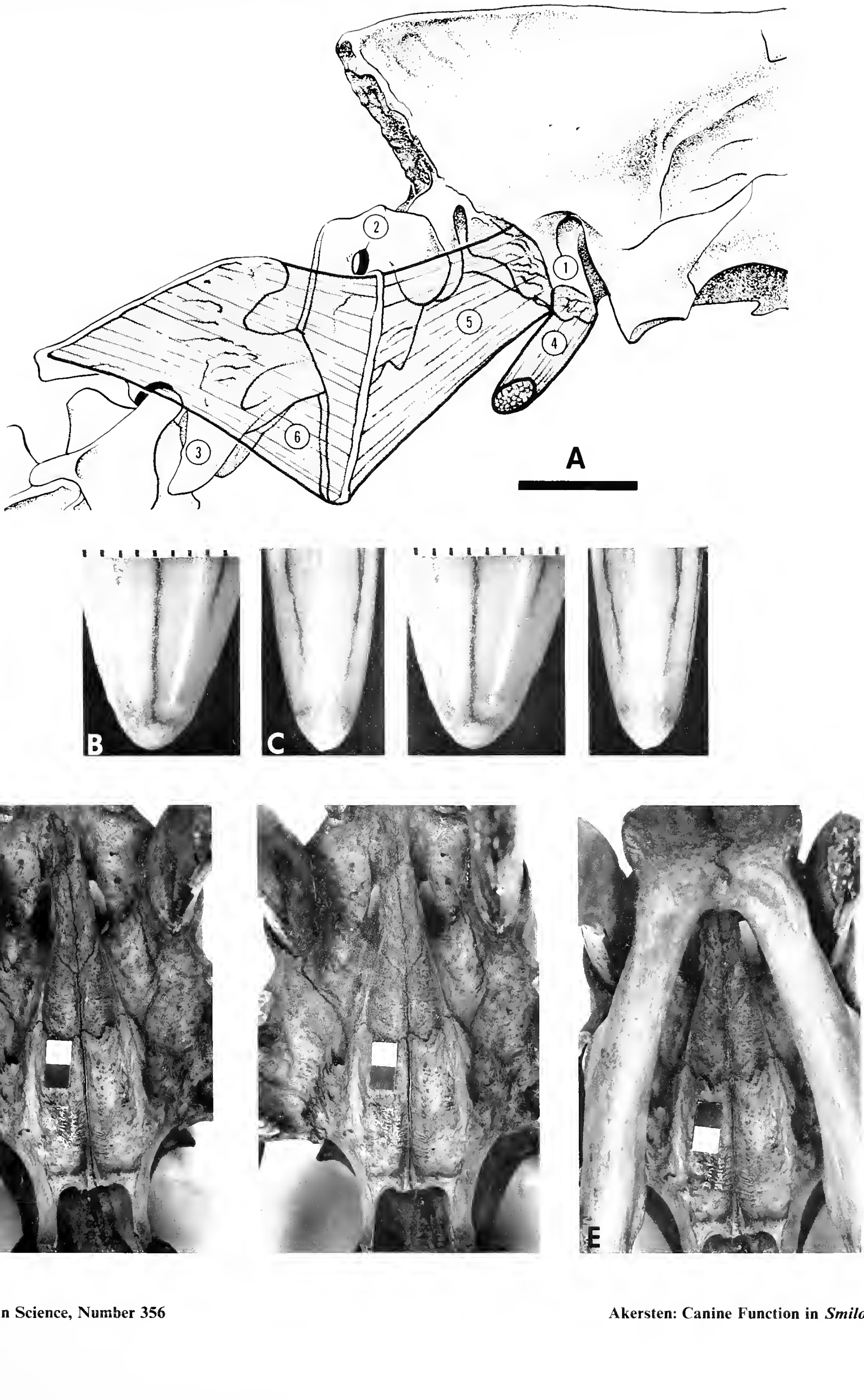
Figure 5. *Smilodon.* **A.** Reconstruction of major head-depressing muscles (1 = mastoid process, 2 = atlas, 3 = axis, 4 = sternomastoid/cleidomastoid, 5 = atlantomastoid musculature, 6 = obliquus capitus posterior) drawn by Mark Hallett. **B, C.** Lateral and posterior stereopairs of right upper canine tip, LACMHC 2000-R.31. **D.** Stereopair of palate, LACMHC 2001-2. **E.** Palatal view of LACMHC 2001-2 with articulated mandible. Scales: A, bar = 5 cm. B, in mm. C, same as B. D, E, in cm.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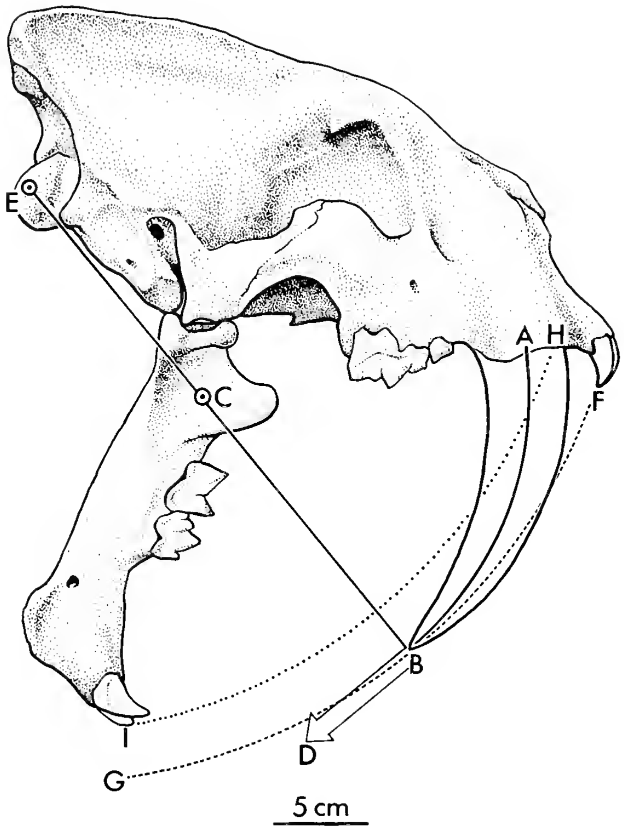

Figure 6. Geometric relationships of *Smilodon* cranium and mandible based on LACMHC 2001-2. See text for explanation. Drawn by Mark Hallett.

result in a larger area of contact and require more initial force to begin a puncture. As noted by Simpson (1941), angulation of the saber axis during a stabbing motion by *Smilodon* would also place a potentially dangerous strain on the saber and its alveolus. Figure 6 illustrates the long axis of the saber and other geometric relationships of the skull and mandibles in *Smilodon.* Arc A–B represents the axis of the upper canine, essentially a perfect segment of a circle with its center at C. The line B–D is tangent to A–B at B and indicates the direction that the tip of the saber must be moving at the moment it contacts a prey animal if it is to achieve the most efficient initial penetration. Clockwise rotation about any point along the radian C–B or its posterodorsal extension will result in the required instantaneous force along the direction B–D. The posterodorsal extension of C–B extends through E, the center of rotation for the atlantooccipital articulation. Thus, the powerful atlantomastoid musculature will rotate the head in precisely the proper motion for most efficient initial penetration of the upper canines. While this configuration may appear to confirm a stabbing mode of attack, further geometric considerations show stabbing to be very improbable, if not impossible. Rotation about point E would result in the tip of the saber moving through the arc F–B–G and the tip of the lower incisors, through the arc H–I. Obviously, the body of a prey animal would have to extend inside of arc F–B–G to be struck at all by the tip of the saber but, if the prey's body extended inside the arc H–I, the lower incisors or mandible would impact before the sabers. As the distance between these arcs is less than 3 cm, a very precise motion would be required to stab or slash without abruptly closing the mouth. Even if this could be accomplished, the curvature of a large prey animal's body would result in the axis of the saber being very oblique to its target and only a glancing blow could be delivered.

If the action of the other head- and neck-depressing muscles were included in a stabbing or slashing action, the center of the resulting complex motion probably could not be represented by a single point. The general area about which movement would center would, however, be farther posteriad and ventrad. This would result in a slightly greater clearance between the paths described by the motions of the tip of the saber and the anterior end of the mandible. It would also result in the long axis of the sabers being at an angle to the direction of force with concomitant loss of efficiency during initial penetration. In the most extreme case of a vertical stab (Simpson, 1941: fig. 1A), only about 12 cm of clearance could be generated. This would still not be enough for a reasonably safe attack using a stabbing or slashing action.

The Rancho La Brea collections of the LACM include at least 600 fairly complete crania of *Smilodon* but their sabers are not as well preserved as the rest of the specimens. The sabers are usually broken off, shattered, or have slipped out of the alveoli. In addition, very few crania have associated lower jaws. As a result, only one cranium with associated mandible (LACMHC 2001-2) contains an almost complete saber in original position and can be used to determine accurately the relationships of the upper and lower canines during closure of the mouth. Manipulation of the specimen immediately demonstrates that, as the tips of the canines pass each other, the tip of the lower passes just interior and anterior to the tip of the upper (Fig. 7B)—exactly the same mode of canine opposition which allows other mammalian carnivores to bite with their canines.

The questions of canine opposition and whether or not sabertoothed mammals could bite with their canines have been addressed by several earlier workers. Pomel (1843) interpreted wear facets on the lateral surfaces of lower canines in *Felis meganthereon* as indicative of canine opposition in that form. In discussing several Old World taxa of saber-

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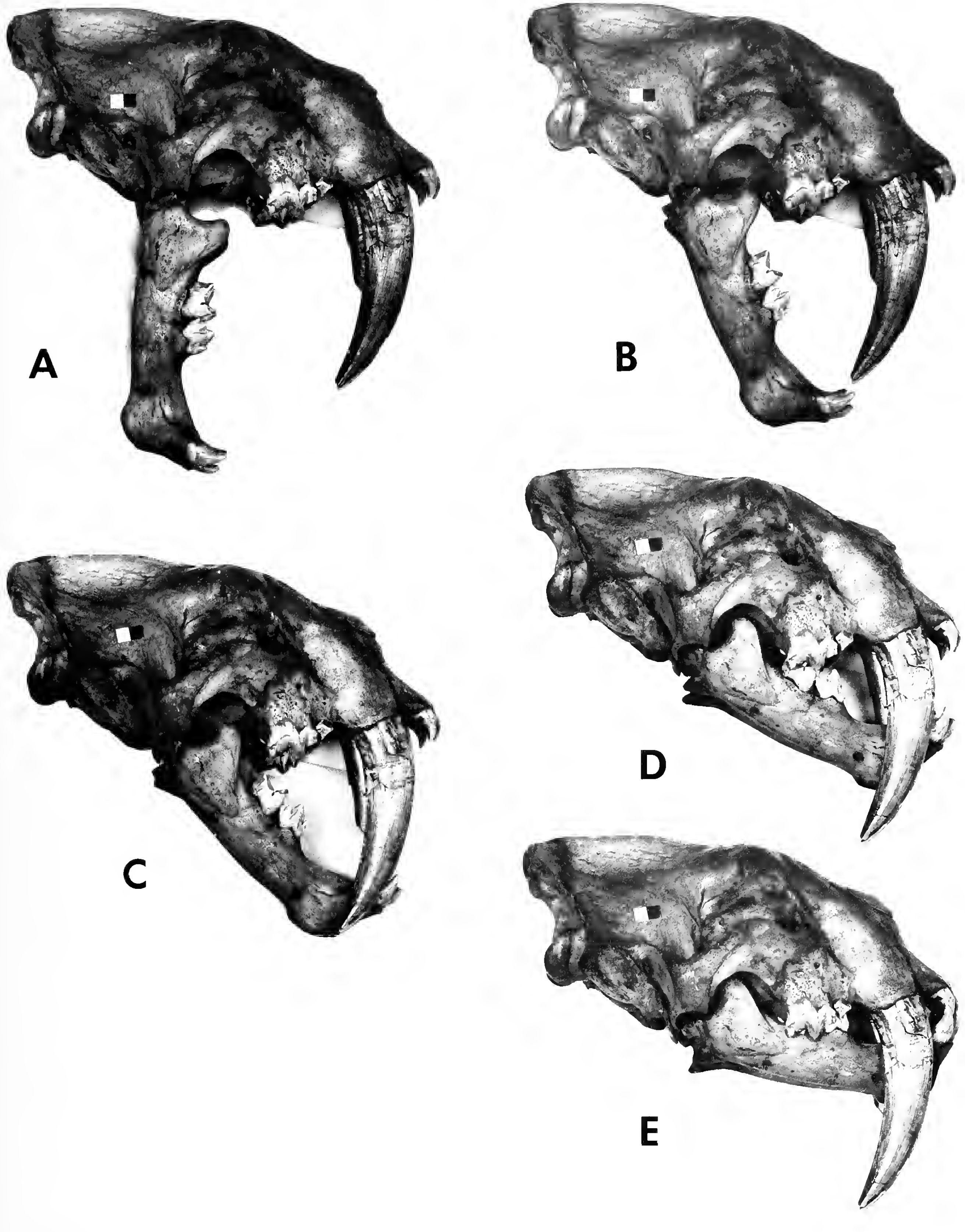
Figure 7. Associated *Smilodon* cranium and mandible, LACMHC 2001-2, depicting mouth closing sequence. **A.** At maximum gape. See text for explanation of others. Scales in cm.


A
B
C
D
E

tooths, Fabrini (1890) appeared to believe that canine opposition occurred in all and hypothesized a mode of attack in which a bite was used to pierce the body of the prey then the head was pulled posteriad to shear through the mouthful of flesh. He also described an upper canine of *Machairodus nestianus* which bore a facet on its medial surface formed by wear against the lower canine. Matthew (1901), however, denied that canine opposition could have occurred in any sabertooth. Schaub (1925) noted the presence of canine opposition in *Machaerodus crenatidens* but believed that it did not occur in *Machaerodus aphanistis, Machaerodus cultridens,* and *Smilodon.* (Taxonomic designations used above are those given by the cited authors and may not reflect currently used synonymies.) Marinelli (1938) specifically stated that *Smilodon* was incapable of biting with the canines. The potential for canine opposition and canine biting in sabertooths appears to have largely disappeared from consideration in subsequent work except for passing mention by Bohlin (1940) and a comment by Kurtén (1963) that the Smilodontini evidently used their sabers exclusively in stabbing, whereas the Homotheriini used them in biting as well as stabbing and slashing. The retention of canine opposition in *Smilodon,* in spite of all the other structural modifications, strongly indicates that biting with the canines was very important. If stabbing or slashing were the primary mode of attack, I would expect canine opposition to have been lost and a different relationship, more efficiently adapted for stabbing or slashing, to have evolved. A similar point was made by Bohlin (1940) in that the curvature of the sabers was not suited for a stabbing attack. Can the various adaptations of *Smilodon,* then, be explained in terms of a biting mode of attack?

The arc of lower canine movement centers at the temporomandibular articulation while the center of canine curvature lies several centimeters ventral to this articulation as previously described (Fig. 6). The non-coincidence of these centers results in a constantly changing relationship of the upper and lower canines during closure of the mouth as shown in Figure 7. As the mouth closes beyond the point where the tips of the canines pass, the lower canine moves anteriad relative to the upper or it can be stated that the saber progressively moves posteriad relative to the mandible, ultimately all but filling the diastema. As a result, the distance between the tip of the lower canine and the serrate posterior margin of the upper canine progressively increases. In Figure 7B, the shortest distance between the tip of the lower canine and the posterior edge of the upper canine is about 10 mm, in Figure 7C, 30 mm, in Figure 7D, 45 mm, and in Figure 7E, 55 mm. If a piece of flesh were anchored by the tips of the lower canines (and, perhaps, also by the sharp lower incisors and the opposing corrugations of the palate and the sharp diastemal crests of the mandible), closure of the mouth would result in the upper canines shearing through that piece of flesh. I propose the term "canine shear-bite" for this type of bite as opposed to the "canine puncture-bite" used by living mammalian carnivores.

As is readily obvious from the above photographic sequence, normal individuals of *Smilodon* could not develop wear facets between the upper and lower canines. However, only a slight developmental error would result in their contact. One left saber, LACMHC 7037, exhibits wear from the lower canine on its medial surface (Fig. 9D). The slightly arcuate facet is longitudinally striated and about 6.5 cm in total length but only the most distal 4 cm is deep enough to expose the dentine.

MECHANICS OF THE CANINE SHEAR-BITE

This mode of attack involves more than simple closure of the mouth with the mandibular musculature. As *Smilodon* pressed its gaping mouth against the body of a prey animal and began to close the mandible, the tips of the opposing canines started to fold the skin and flesh of the prey (Fig. 8A). By the time that the tips of the canines approached each other, they produced a strong fold in the anterior region of the mouth and began to penetrate the "neck" of that fold (Fig. 8B). At about this stage, the poor lever arm of the coronoid process and reduced masseteric muculature resulted in *Smilodon* being unable to close its mouth further by using only the mandibular musculature and the mandible became nearly stationary relative to the body of the prey. It was then anchored by the mandibular musculature and by pressing the well-developed anterior portions of the mandibular flanges against the prey. This pair of laterally flared, narrow ridges would have provided a very good grip when pressed against an animal, more so than if the entire anterior of the mandible protruded anteriorly. Completion of the bite was accomplished by using the head-depressing muscles to drive the cranium against the immobilized mandible with the upper canines shearing through the lateral margins of the fold of flesh (Figs. 8C, D). The serrate distal portion on the anterior margin of the saber facilitated initial penetration while the rounded, non-serrate proximal portion prevented anterior enlargement of the wound at the expense of posterior shear during later stages of the bite. There may have been a sequential use of the head-depressing muscles with the atlantomastoid musculature, best oriented for initial saber penetration, acting first. Those which move the axis of the saber more obliquely would, perhaps, contract in later bite stages. The short lower canines, with probably some assistance from the tips of the lower incisors, could only penetrate deeply enough to anchor the fold. At some intermediate stage, the opposing ridges and grooves of the palate and the diastemal ridges of the mandible gripped and helped to stabilize the fold of flesh. As the head was depressed, the posterior of the mandible would also move ventrad and rotate the anterior so that more of the mandibular flange would contact the prey. This anchored the mandible even more firmly to oppose head depression and resulted in the incisors rotating away from the prey to stretch and thin the neck of the flesh fold. During the final stages of the bite, the upper and lower incisor batteries (which now functionally included the lower canines) punctured the neck of the flesh fold with a closely spaced series of perforations. *Smilodon* could then free the entire

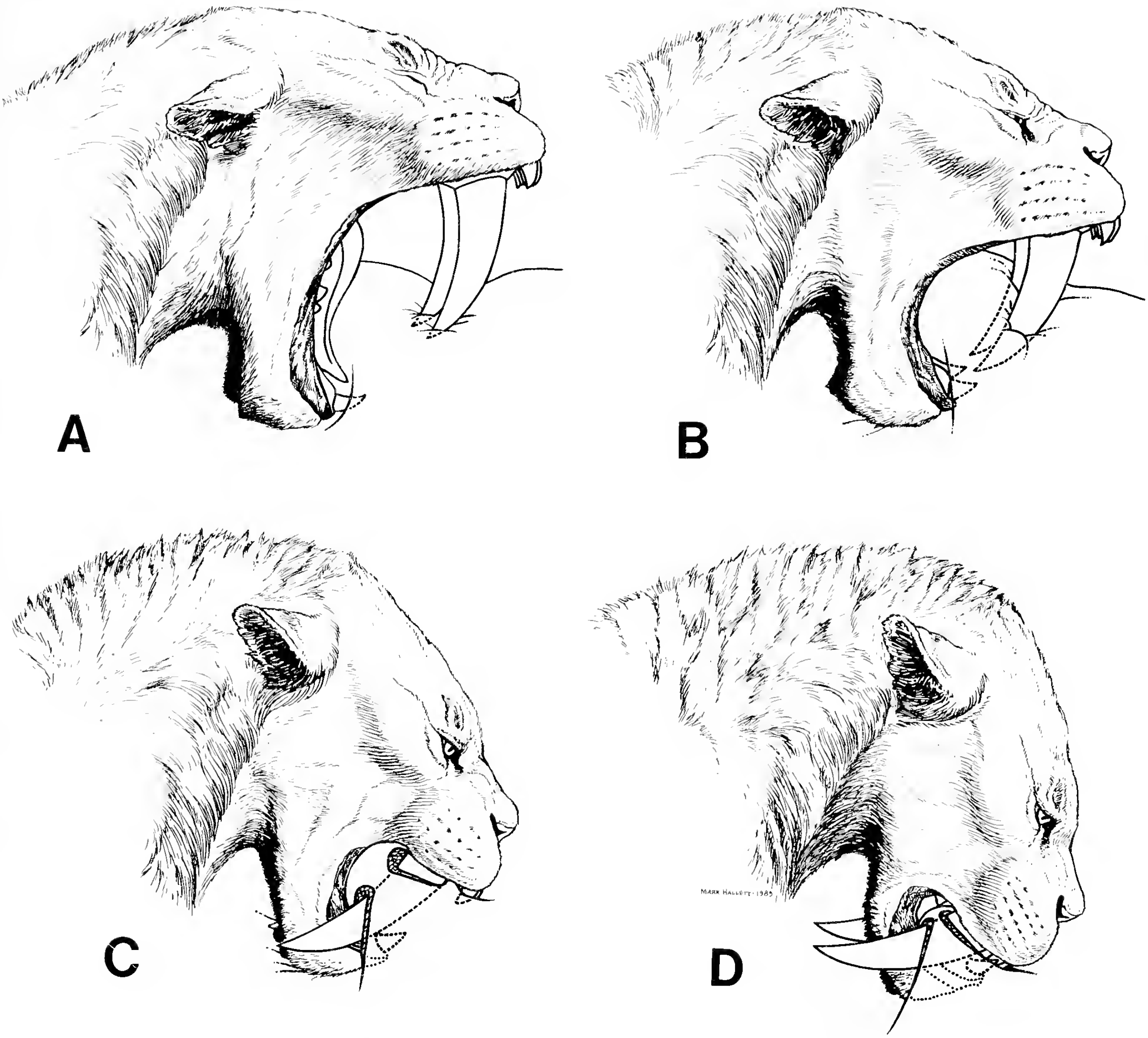


Figure 8. Reconstruction of canine shear-bite sequence in *Smilodon*. See text for explanation. Drawn by Mark Hallett.

fold of flesh with only a modest pull, leaving a major wound in the body of its prey.

SUPPOSED EVIDENCE OF STABBING FROM WOUNDS FOUND IN SKULLS

Three specimens have been described as bearing wounds attributed to stabbing by sabertoothed mammals. Scott and Jepson (1936) described a skull of *Nimravus* with an obliquely directed, elongate, and partially healed wound to the left frontal. They noted that the size and shape of the wound conformed to the upper canine of *Eusmilus* and concluded that this specimen provided evidence that *Eusmilus* stabbed with its sabers. The size and shape of the injury appear to be consistent with damage inflicted by a saber, but the specimen lacks conclusive evidence—part of a saber within the wound. Even if we assume that a saber caused the damage, it need not have resulted from a stab. A saber puncture could have just as easily, or more easily, been accomplished with a bite. The head of *Nimravus* appears to be small enough to have been taken into the mouth of *Eusmilus* and bitten. This specimen does not provide any solid evidence regarding the mode of attack used by sabertooths.

Miller (1969, 1983) used the above specimen and two others from Rancho La Brea to support a stabbing attack for

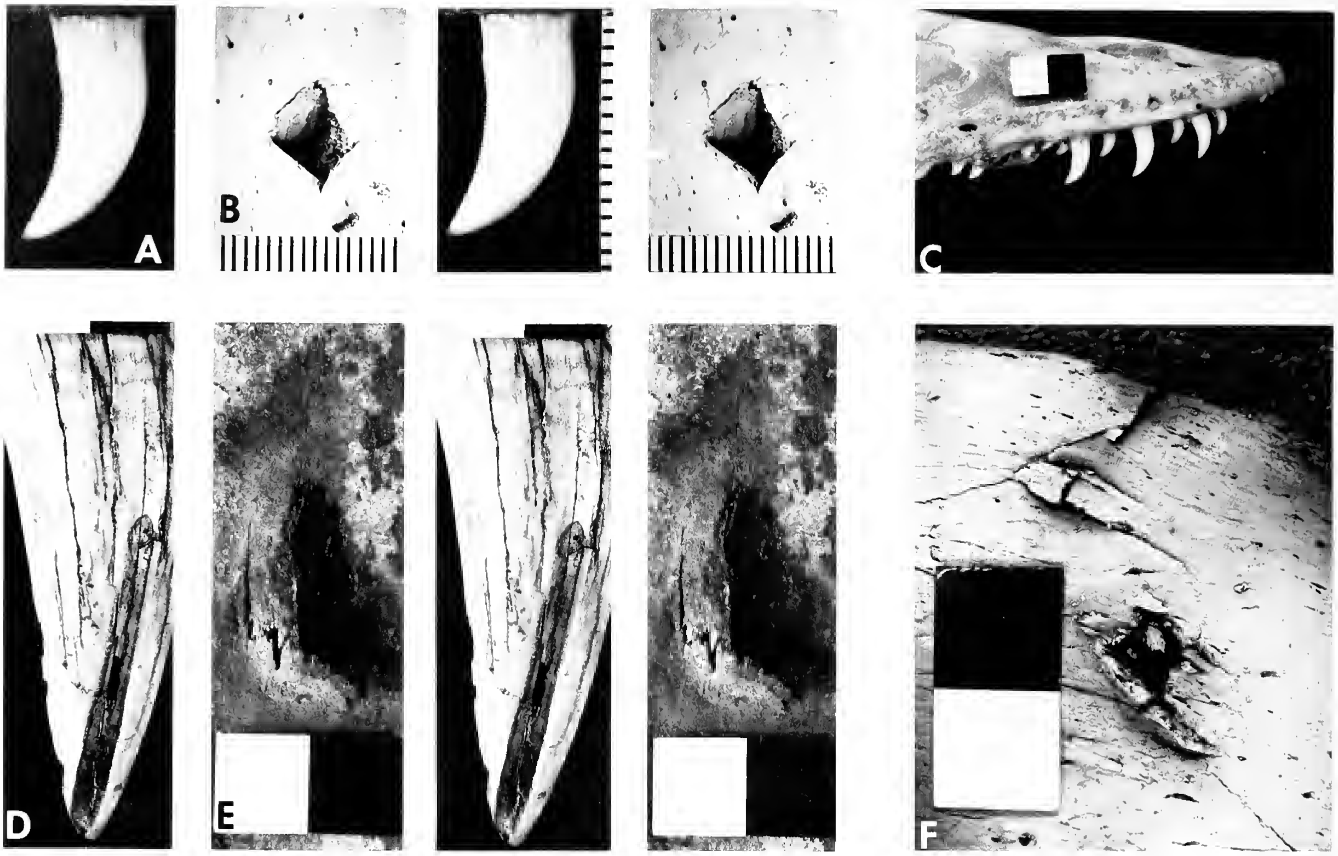


Figure 9. *Varanus komodoensis*, LACM Herpetological Collections 121971. **A.** Stereopair of upper tooth. **C.** Upper dentition. Damage to *Smilodon* scapulae inflicted by a square-ended pick about 1915. **B.** LACMHC K-50, stereopair of pick entry hole. **E.** LACMHC K-232, stereopair of oblique blow from pick. **F.** LACMHC K-50, reverse side of different pick hole from that shown in B. Note depressed bone flake, lack of bone flake detachment, and splintery fractures usually typical of damage to fresh bone. **D.** Stereopair of medial surface of *Smilodon* left upper canine showing wear facet from lower canine. Scales: A and B in mm, others in cm. B and F coated with ammonium chloride.

sabertooths. The only information available for one of the latter specimens is a brief mention by Moodie (1923:128) "A skull of a young wolf the brain case of which is cut through by the tooth of a tiger, the saber being broken off and imbedded in the preserved skull, is on exhibition at the University of California." Since this specimen has never been illustrated or adequately described and cannot presently be located in the Berkeley collections (J.H. Hutchison, pers. comm., 1983), it does not provide useful information about mode of saber use. The other La Brea specimen cited by Miller (1983) is a *Smilodon* skull (LACMHC 2001-24) with an elongate, anteroposteriorly oriented perforation of the left frontal. Relative to the skull orientation, this injury has a rounded posterior margin and a pointed anterior margin, very similar to the cross section of a saber oriented so that the anterior margin of the saber is at the posterior margin of the perforation. An isolated saber, however, can be inserted from either direction. S. Shermis (pers. comm., 1983) conducted a pathology study of this specimen and concluded that characteristics of the injury are compatible with insertion of a saber from the anterior of the individual while the animal was still alive. In Rancho La Brea specimens, however, damage known to be of recent origin often has characteristics considered to be indicative of injury which occurred during life or soon after death (Figs. 9B, E, F). This probably results from the unusually good preservation of collagen in bones from Rancho La Brea (Ho, 1965; Doberenz and Wyckoff, 1967).

While the conclusive evidence of a broken saber in the wound is again lacking, the evidence does indicate that an upper canine of *Smilodon* could have caused the damage. But is this evidence for stabbing? With a maximum 3-cm clearance between the arcs described by the tip of the canine and the tip of the mandible, the position of the injury does not allow sufficient clearance for either an anterior or posterior attack without the attacker first striking its mandible against the skull. In order to determine if any method of stabbing would be feasible, the injured specimen was manipulated with another skull bearing mandibles mounted at maximum gape. All four attack possibilities were attempted: posterior stab with left saber, posterior stab with right saber, anterior stab with left saber, and anterior stab with right saber. In both the posterior stab with left saber and the anterior stab with right saber, the opposite saber contacted the skull in the area mediad to the right postorbital process and prevented insertion of the attacking saber. In both posterior attacks, contact of the mandible with the posterior of the injured cranium prevented the attacking saber from striking the skull at the proper angle to produce the observed injury, but a more elongate perforation could have been produced. Both types of frontal attacks had similar results from the mandible striking the anterior of the head. The observed injury could not have been the result of an open-mouthed stab by another *Smilodon*. It could, however, have been the result of a canine blow struck with the mouth closed. An upper canine of *Smilodon* inserted in the injury does penetrate to the depth consistent with the maximum length of exposure ventral to a closed mandible. Therefore, it seems plausible that (if one assumes that a saber was actually responsible for the perforation) the injury may have been caused by an accidental blow struck with the mouth closed during intraspecific combat.

A specimen recently collected by the Rancho La Brea Project deserves mention here. The left third rib of a *Smilodon* (LACMRLP R25876) had the very tip of a *Smilodon* upper canine (separately cataloged as LACMRLP R25877) imbedded in its anterolateral surface. This specimen was found with the left fourth rib of a *Smilodon* in very close to life position but no other elements can be reasonably associated with the two ribs. The puncture produced by the canine appears to have been made in green bone. Its long axis is nearly transverse to the length of the rib with the anterior end (relative to rib orientation) slightly dorsad to the posterior end. The saber tip is obliquely broken; the distance from the tip to the break is between 3 and 6 mm. The margin with the greatest portion remaining appears to be the posterior and occurred in the posterior margin of the puncture. Therefore, the bite was probably made from a posterior and slightly ventrad orientation. Depending on the forelimb orientation of the bitten individual, the saber may have passed through the posterior part of the scapula. None of the *Smilodon* left scapulae from this area of the excavation exhibits possible saber damage but several lack the posterior portion. Other specimens from Rancho La Brea also suggest intraspecific strife (S. Shermis, pers. comm., 1983).

It is interesting that all of the specimens which supposedly show some evidence of damage inflicted by the upper canines of sabertooths are from carnivores. The lack of herbivore specimens displaying saber injury is indirect evidence that bony areas were avoided during predation. Intraspecific or interspecific combat among carnivores is quite different from predatory attack behavior (e.g., Schaller, 1972; Bertram, 1978; Leyhausen, 1979). Therefore, even if the wounds in these specimens were actually caused by sabers during life, they should not be considered as indicative of sabertooth predatory behavior.

SOCIAL STRUCTURE IN *SMILODON*

Hunting techniques employed by various predators are dependent in part upon whether they seek prey in a group with cooperative behavior or alone (except for a female with young). Although this is almost impossible to interpret for extinct forms which do not have close living relatives, a few inferences can be drawn about social structure in *Smilodon* from the fossil record at Rancho La Brea. As Gonyea (1976) pointed out, the large numbers of *Smilodon* preserved at this locality strongly suggest that they lived in groups or prides.

The LACM made a large collection of fossil vertebrates, now termed the Hancock Collection, from Rancho La Brea between 1913 and 1915. Few of these specimens have been exchanged or lost so that the relative numbers of the larger taxa presently in this collection should be a very close approximation to the preserved thanatocenose. Only about one third of the Hancock Collection, roughly 260,000 specimens, has been cataloged to date. A number of years will be required to complete the task and produce a definitive census of the megafauna, but it is obvious that larger taxa with the lowest proportion of cataloged elements are coyote and *Smilodon*. Marcus (1960) used the catalogs plus complete counts of *Bison* and *Camelops* in his census of the megafauna and arrived at a total of 1029 as the minimum number of *Smilodon* in the collection. Miller (1968), however, estimated about 2100 individuals of *Smilodon* based on cranial elements.

Unpublished data, briefly reviewed by Akersten, Shaw, and Jefferson (1983), from a recent excavation at Rancho La Brea indicate that entrapment in shallow asphalt seepages was the primary mode of producing the rich fossil deposits at Rancho La Brea. An episode of entrapment apparently began when one large animal (probably an herbivore since these would be most common in natural large mammal populations) blundered into a shallow puddle of asphalt. The helpless or dead herbivore would then attract a number of opportunistic carnivores, thus accounting for the fact that carnivores make up about 90% of the larger mammals found at this locality. The total number of large herbivores should closely approximate the total number of entrapment episodes. Marcus (1960) counted 423 individuals of large herbivores (*Bison, Camelops, Nothrotheriops, Glossotherium,* and *Equus*). Allowing for a few proboscidians and uncataloged or lost specimens, the maximum number of individual herbivores and, consequently, the number of entrapment episodes represented in the Hancock Collection is considerably fewer than 600. Therefore, an average of 1.7 to 3.5 *Smilodon* were caught during each entrapment episode, depending on the count used for *Smilodon*. As it is unlikely that all entrapped herbivores lured *Smilodon* in equal numbers, as many as six or eight may have been caught during a single entrapment episode—a period of weeks or several months at the most. This ratio would be improbable if *Smilodon* were a solitary hunter unless, unlike living large predators, a number of individuals shared overlapping hunting areas. The best explanation of these data, providing that the mode of entrapment is correctly interpreted, is that *Smilodon* was a social animal and may have hunted in groups.

Another way of looking at the same data is to compare the relative numbers of *Smilodon* at Rancho La Brea with those of other predators, whose social structure is known or can reasonably be inferred. The other very common predator is *Canis dirus* Leidy with at least 1646 individuals represented in the Hancock Collection (Marcus, 1960), approximately equal to *Smilodon.* Though *C. dirus* is extinct, its morphology is quite similar to the extant *C. lupus* and a reasonable conclusion would be that it also hunted in fairly large groups. The other common, but smaller, predator is the extinct *C. latrans orcutti* (Merriam), very closely related to the living coyote (Nowak, 1979). Marcus accounted for 239 coyotes in the Hancock Collection but, as previously noted, much of the coyote material has not been cataloged. Coyotes are also social animals but usually form smaller groups than wolves. Carnivores which do not hunt in packs, *Felis concolor, Panthera onca* (Jefferson, 1983), *Ursus americanus, Ursus arctos, Lynx rufus, Urocyon cinereoargenteus,* and *Taxidea taxus,* are comparatively rare at Rancho La Brea. Thus, if the relative abundance of carnivores preserved at Rancho La Brea reflects hunting behavior, *Smilodon* must be included among the social forms. As the American lion, *Panthera atrox* (Leidy), is relatively uncommon with 76 individuals reported by Marcus, the same line of reasoning suggests that this predator was either a solitary hunter or, if it hunted cooperatively, groups did not often frequent the area.

Finally, evidence that *Smilodon* may have been a social animal derives from the relatively high frequency of individuals from Rancho La Brea which either could not have killed prey or would have had great difficulty in doing so. Seven adult skulls in the collection had only one saber during life as shown by the undeveloped or secondarily lost alveolus for the other. The remaining canine alveolus in one of these specimens is small and distorted. One or both canines in several skulls were broken off and subsequently worn during life. Individuals lacking one or both canines would probably experience difficulty making a kill. Many postcranial elements of *Smilodon* in the Hancock Collection exhibit pathology, some very severe (Moodie, 1926, 1927, 1930). At least one limb was all but useless in some individuals; vertebral abscesses and fusions would have hampered or crippled many more. A number of skulls also have badly worn cheek teeth (Miller, 1968). Solitary carnivores possessing such major disabilities soon perish unless they manage to survive by scavenging. These same disabilities, however, would place them at an extreme disadvantage when competing with healthy individuals for carrion. Most living large carnivores regularly attempt to appropriate carcasses from other predators. Social carnivore groups, on the other hand, frequently allow incapacitated individuals to feed on kills made by other pack members. Schaller (1972) and Bertram (1978) describe a number of occasions when African lions (especially females) incapacitated by age or injury, survive by feeding on kills made by other pride members. Even aged nomadic males may survive as members of nomadic groups or by being allowed to feed at the kills of other nomads (e.g., Schaller, 1972:81). Schaller (1972:358) even considers that one function of the lion's social system is to provide "life insurance" for individuals unable to hunt for themselves but the selective advantage of this is difficult to envision. Kruuk (1972) noted that older female members of spotted hyaena clans, no longer able to run well, feed from kills made by other clan members. The African wild dog appears to have the most highly developed social structure among the fissiped carnivores. Estes and Goddard (1967:68) report that the pack provides food for "sick and old adults unable to kill for themselves."

It has been suggested that the frequency of pathologic *Smilodon* specimens from Rancho La Brea was a result of crippled individuals specializing in feeding from the carcasses of trapped animals (Bohlin, 1947). However, if one assumes that the Hancock Collection represents only 10% of the total individuals of all species that were once trapped in these deposits, the 600 episodes of entrapment represented by this collection become 6000, spread over at least 25,000 years or an average of no more than one every four years. Even allowing for a probable clustering of entrapment episodes through time, this could hardly represent a dependable source of food, especially considering the hazards of scavenging at such a place and the necessity of competing with healthy carnivores for carrion.

Although the data regarding *Smilodon*'s social behavior are far from conclusive, they are more easily explained by a cooperative model than by a solitary model. It is not possible, however, to draw inferences about the extent of cooperation during the hunt. They may have merely hunted the same area with each attack made by an individual acting on its own, then fed as a group, or they may have cooperated to a greater degree throughout the hunt.

PREY SPECIES

It has generally been assumed that the sabers of *Smilodon* and other sabertooths were adaptations for attacking large, relatively thick skinned prey such as ground sloths or proboscidians. The only direct evidence available comes from the Late Pleistocene fauna of Friesenhahn Cave in Texas (Evans, 1961; Meade, 1961; Lundelius and Slaughter, 1971; Graham, 1976, pers. comm., 1983; Rawn-Schatzinger, 1983). This cave appears to have been a denning site for *Homotherium* to judge from the number of individuals recovered and especially from the occurrence of several very juvenile specimens. Scores of juvenile proboscidians, primarily mammoths, were also found but adult proboscidians and other large carnivores are rare. This association of an apparent denning site with the remains of juvenile proboscidians strongly suggests that *Homotherium* preferentially hunted juvenile proboscidians and brought their remains back to its lair. Perhaps the coarsely serrate margins of *Homotherium*'s sabers and other teeth facilitated dismembering the carcasses into more easily carried chunks. The incisors, in particular, are almost shark-like with very serrate margins.

If the herd and parental behavior of extinct proboscidians were similar to those of modern African elephants, hunting juveniles could have been a hazardous occupation. Many or all of a herd of elephants will defend or aid any juvenile; they may even continue to defend the body several days after death (Douglas-Hamilton and Douglas-Hamilton, 1975). Even if mammoth behavior were more like that of Indian elephants with separate nursing and juvenile care units, as suggested by Graham (1976, pers. comm., 1983), attacking predators would have had to be cautious. Whatever the case, *Homotherium* probably waited for an ideal opportunity and retreated immediately after even a successful attack on a juvenile until the adults left the area.

It is certainly tempting to extend this interpretation of *Homotherium*'s prey to *Smilodon* (and other sabertooths), but the two genera have different morphologies (Meade, 1961; Churcher, 1966), even different dental eruption sequences (compare Rawn-Schatzinger, 1983, with Tejada-Flores and Shaw, 1984). In addition, the shear-bite of *Smilodon* would have been equally effective on smaller, thin-skinned prey. The powerful build of *Smilodon* indicates that they probably could have successfully attacked any of the larger herbivores found at Rancho La Brea except for adult proboscidians. They were certainly attracted to entrapped non-proboscidians because they are quite common in many La Brea deposits that totally lack proboscidian remains. I doubt that *Smilodon* fed exclusively on members of any one taxon—no living large predator does—but they may have more commonly hunted juvenile proboscidians than did the other Carnivora found at Rancho La Brea.

AREA OF ATTACK

Most researchers have concluded that the upper canines of sabertooths were too fragile to be used on bony areas of their prey but Gonyea (1976), rebutted by Emerson and Radinsky (1980), thought that a stab at the back of the neck or skull was more likely. Even though the sabers of *Smilodon* are much heavier than a knife, they still have a rather slender cross section in comparison to their length. Because of their length, it seems likely that relatively little lateral force near the tip would cause breakage. If they were used in an attack on a bony area, one saber would probably contact bone before the other, resulting in considerable lateral torque and probable breakage (Bohlin, 1947). Repeated contact with bone would also cause wear on the tips of the canines. Leyhausen (1979:33) notes that even the much stouter conical canines, with thicker enamel, of modern cats readily splinter from normal use.

The curated portion of the Hancock Collection was surveyed for sabers with well-preserved tips and fully formed roots. Of 54 adult sabers, one displayed a minute wear facet on the enamel of the tip, two had wear that barely penetrated to the dentine, and only one had an appreciably wear facet: 2 mm wide by 2.5 mm long. Three others exhibited breakage of the very tip with some subsequent wear; this suggests that the one specimen with a larger wear facet may have also resulted from wear after breakage. All of the sabers with tip wear are isolated specimens exhibiting moderate to extreme wear of the serrations and appear to come from older individuals. This information supports the interpretation that the sabers were not employed in attacks on bony areas. The sabers with broken and worn tips, the occurrence of a saber tip in a *Smilodon* rib, and the skulls with more severely broken sabers showing post-breakage wear do show that mistakes were occasionally made. Of the 17 juvenile sabers located, 10 had appreciable wear facets on the tips and one had a minute facet. The larger facets tended to be oblique with more wear toward the lateral margins. Perhaps *Smilodon* kittens were less careful with their sabers than adults.

If the interpretation is correct that the canine shear-bite of *Smilodon* was normally directed toward areas in which bone would not be encountered, only the throat and abdomen are possible targets. The throat has been suggested as the focus for a stabbing or slashing attack because of the shallow carotid artery and jugular vein and because most modern felids typically employ a nape or throat bite (Martin, 1980; Emerson and Radinsky, 1980). It seems to me that a throat bite would have to be delivered with precision in order to sever these blood vessels without encountering the cervical vertebrae or, in short-necked juvenile proboscidians, without striking the posterior of the mandible or the anterior of the humerus. Because the tips of the sabers are well outside the visual area of *Smilodon*, a throat bite would be potentially hazardous to these teeth. Leyhausen (1979) states that the neck bite in living felids results from a taxis oriented toward an indentation (the neck) between a large cylinder (the body) and a smaller one (the head). This taxis does not discriminate between throat and nape orientations; the nape bite used by smaller felids is learned. Larger felids may use either nape or throat bites (other points and methods of attack less commonly), possibly depending on prey size or on the learned behavior of the individual. One interesting variation is the bite to the posterior of the cranium employed by jaguars in killing capybaras (Schaller and Vasconcelos, 1978). A jugular/carotid attack by *Smilodon* would require a much more specific taxis than occurs in modern felids, because the process of learning the exact point to bite by trial-and-error would be far too hazardous to the sabers. I also find it difficult to explain the development of extremely elongate sabers in *Smilodon* and other dirktooths in terms of a throat attack. The shorter sabers of scimitartooths should be more than sufficient to sever the major blood vessels.

The elongate sabers of *Smilodon* appear to be adapted for causing massive damage with a single bite. The large, bone-free abdominal region, with a rich supply of blood vessels and a variety of vital organs, would be a more logical area to wield these weapons. Furthermore, unlike the neck, there would be relatively little muscle tissue for the incisors to penetrate at the end of the bite. The type of accuracy needed in order to sever the jugular/carotid blood vessels without striking bone would not be required, simply a taxis directed toward the region anterior to the hind legs. Most authorities agree that, while large, living felids rarely attack the abdomen, they do typically begin feeding there (e.g., Leyhausen, 1979; Schaller, 1972). African lions, after pulling down large prey such as rhinoceros and hippopotamus, are known to occasionally attack the abdomen instead of the throat (J. Kingdon, pers. comm., 1983). Wolves (Young, 1944; Mech, 1970), African wild dogs, golden jackals (van Lawick-Goodall and van Lawick-Goodall, 1971), and spotted hyaenas (Kruuk, 1972) frequently kill by attacking the abdomen. This is probably the only vulnerable area easily available to such

Figure 10. Reconstruction of initial stages of attack by *Smilodon.* Left, pulling down young mammoth. Right, beginning of canine shear-bite to abdomen. Drawn by Mark Hallett.

packs of relatively small predators which lack the claws and bulk to pull down their prey in order to attack other vital areas. Even so, it does show that abdominal attack can be effectively used by modern mammalian carnivores.

Martin (1980) considered an abdominal attack by saber-toothed cats, especially by dirktoothed forms such as *Smilodon,* to be very improbable. He argued that the prey would not be killed immediately and, unless it went into total shock, would try to escape from the attacker which was not adapted to pursue an escaping animal. He also claimed that the abdomen can be defended by the head of the prey and that stabbing a broad, gently sloping abdominal area would be difficult at best. I concur with the last point; however, the canine shear-bite is perfectly adapted for attacking such areas. Furthermore, it is difficult to visualize how the forms which were potential prey for *Smilodon* at Rancho La Brea could have used their heads to defend their abdomens while stretched out on the ground. Figure 10 depicts *Smilodon* pulling down a juvenile mammoth and initiating a canine shear-bite to its abdomen.

In regard to the prey attempting to escape, Schaller (1972: 266) stated that prey pulled down by lions and not yet bitten appeared to go into shock and rarely struggled to any extent. He went on to describe an uninjured buffalo that lay on its side while its tail was chewed by a lioness. Auffenberg (1981) credited shock as being important in the lack of struggle evinced by downed but not yet killed prey of *Varanus komodoensis.* Furthermore, tigers are easily able to control large, struggling prey after bringing them down (Schaller, 1967). I doubt that prey would make much of an attempt to escape after the shock of being pulled down by *Smilodon* and having a huge chunk of the abdominal region torn out. The claws and powerful forelimbs of *Smilodon* would easily be able to control any who might try to struggle. Even if an occasional prey animal could escape after the attack, its severe injuries would prevent it from running very fast or very far.

A POSSIBLE KILL SCENARIO

Events in a typical attack sequence might have taken the following course, assuming that *Smilodon* did cooperate to a minor extent during the hunt, that the prey in this particular case was a juvenile mammoth, and that mammoth social behavior was similar to that of modern Indian elephants (Graham, 1976, pers. comm., 1983).

A pride of sabertooths scatter out while approaching a herd of adult female and juvenile mammoths, targeting one pair of juveniles who were playing a short distance from the rest. While several of the predators distract the herd, one makes a short rush from concealment and pulls one juvenile down toward itself with the retractile claws and powerful forelimbs. Quickly orienting itself to the posterior of the abdomen, the sabertooth opens a gaping wound with a canine shear-bite, then flees before the mother and the rest of the herd can retaliate. The pride regroups at a distance and waits for the critically injured juvenile to die and for the rest of the herd to leave. Once the dead animal is abandoned, the sabertooths (including aged or incapacitated members of the pride) return to feed. They tear the carcass apart with their prognathus incisors and occasionally employ a canine shear-bite to open up a new area. The rather long lips of sabertooths allow them to take chunks and strips of flesh into the side of the mouth so that the highly developed carnassials can slice the meat into pieces small enough to swallow (Miller, 1969; Martin, 1980).

A MODERN ANALOG, THE KOMODO DRAGON

A major problem in interpreting the mode of attack in sabertooths has always been the lack of a modern analog. No living mammalian predator has teeth comparable to the sabertooth canine and none is known to consistently kill its prey by first pulling it down then biting open the abdomen, as I hypothesize for *Smilodon*. If one looks at non-mammalian predators, however, one very interesting modern reptilian analog stands out: the Komodo dragon (*Varanus komodoensis*). Auffenberg (1978, 1981) has thoroughly studied this large active predator, which may grow up to 3 m long and 60 kg in weight. Its dentition consists of mediolaterally flattened, sharp, recurved teeth with serrations on the entire posterior margins and about the distal one fourth of the anterior margins. Although this reptile has numerous teeth in both upper and lower dentitions, the individual teeth quite closely resemble the canines of *Smilodon*, even in the distribution of serrations (Figs. 9A, C).

The usual prey of the Komodo dragon consists of deer and boar. Recorded kills include deer of up to 80 kg and boar up to 40 kg, but villagers report kills of deer up to 200 kg. The Komodo dragon typically kills these prey by ambush along game trails or in bedding areas. Because it lacks prehensile forelimbs, it grasps them with the mouth, pulls or wrestles them down, then bites open the abdomen. Small individuals may be picked up in the powerful jaws and shaken. Attacks on tethered goats indicate that they appear to be in shock prior to their abdomens being ripped open; death probably results from "massive viscaral bleeding" (Auffenberg, 1981: 247). As Auffenberg further notes, visceral bleeding could be enhanced by physiological shock resulting from the violent attack.

Successful attacks on larger prey, such as tethered or free water buffalo up to 590 kg, apparently follow a different initial pattern. The Komodo dragon lacks the strength to bring down such large prey but a few individuals learn to repeatedly bite and slash at the legs until the animal is crippled by the severing of its tendons and collapses. Available indirect evidence indicates that the kill is again accomplished by biting open the abdomen (Auffenberg, 1981:261). Unlike *Smilodon*, the Komodo dragon can afford to attack bony areas such as lower legs because it has numerous and replaceable teeth; however, it still makes the killing bite to the soft abdomen after bringing the animal down. That it can easily bite open the abdomen of a large water buffalo with saber-like teeth only 2 cm or less in height surely shows that the sabers of *Smilodon* could very effectively function in a similar manner. The method of biting also differs in that the Komodo dragon delivers repeated bites with backward jerks at the same spot. Despite the number of differences, I suggest that this reptile is the closest living analog to *Smilodon* in kill methodology.

Other indirect evidence tends to support the analogy. The prey animals of the extant Komodo dragons appear to have been introduced by man. Pleistocene deposits on the island of Flores (within the present range of the Komodo dragon) appear to contain only two large animals, both miniature stegodont elephants (Hooijer, 1972a). On Timor, east of the Komodo dragon's present range, Pleistocene deposits have yielded large varanid vertebrae similar to *Varanus komodoensis* in association with the same proboscidians and giant tortoises (Hooijer, 1972b). Large varanid vertebrae are also known from the Pleistocene of Java (Hooijer, 1972b) with a more varied fauna including proboscidians. These data led Auffenberg (1981:289) to suggest that the ancestors of Komodo dragons once fed on small proboscidians. Thus, a tentative parallel can be drawn between the prey of Pleistocene Komodo dragons and, at least, *Homotherium*.

In addition, Australia stands out as the only temperate continent which lacks the remains of some type of sabertoothed mammal. This seems odd because the carnivorous marsupials there underwent as extensive a radiation as did the South American marsupials which did evolve a sabertoothed form. Varanids are, however, known in Australian faunas by the Middle or Late Miocene and underwent a major radiation, culminating in the giant, Late Pleistocene *Megalania prisca* Owen which reached a total length of perhaps 7 m and a maximum weight of 600 to 620 kg (Hecht, 1975). The teeth of *Megalania* closely resemble (but are larger than) those of *Varanus komodoensis*, suggesting a similar, highly predaceous mode of life. Hecht believed that *Megalania* was the major predator of the Late Pleistocene giant marsupials of Australia. Perhaps *Megalania* and other large fossil Australian varanids occupied a niche similar enough to sabertoothed mammals that they precluded marsupial carnivores from that adaptive zone.

CONCLUSIONS

The hypothesis that *Smilodon* pulled down its prey, then killed with a canine shear-bite to the abdomen, appears to be consistent with all of the observed morphology relevant to use of the upper canines and eliminates several anomalies introduced by stabbing or slashing hypotheses. The powerful head-depressing muscles function to bite by means of depressing the cranium against an essentially stationary mandible, held in place by pressing the anterior margins of the mandibular flanges against the prey. The mandible needs to be very robust to resist the developed forces but does not require a long coronoid process in order to bite with the canines. The lower canines are relatively small because they need only penetrate enough to anchor the fold of flesh taken into the mouth until the very end of the bite, then they function with the incisor battery. In the shear-bite model, a tremendous force is no longer needed to drive the sabers into the prey. The geometric relationships of the cranium, mandible, and dentition are far easier to explain. The palatal ridges and grooves serve as gripping devices in the absence of most of the premolars. One could even speculate that the retracted nose of *Smilodon* (Miller, 1969) was an adaptation to avoid friction burns from rubbing against the hair of its prey during the head depressing stages of the canine shear-bite. The problem of structural and behavioral intermediates between biting and stabbing/slashing forms disappears. The similarities between the kill behavior hypothesized here for *Smilodon* and that observed in the living *Varanus komodoensis,* plus the correspondence in dental morphologies between the two, add the dimension of a modern analog.

Examination of fairly complete and undistorted specimens, casts, and figures of other sabertoothed mammals indicates that they all very probably possessed upper and lower canine occlusion similar to that of *Smilodon.* Therefore, I believe that the canine shear-bite was utilized by all, even though the details of its use must have differed as demonstrated by the variety of other morphologic features exhibited by various taxa. The shorter sabers of *Homotherium* may have been more useful in a throat attack and the coarser nature of their serrations may indicate that these teeth were more frequently employed for some purpose (such as to dismember carcasses) in addition to the kill. In *Thylacosmilus,* the lack of upper incisors, the ever-growing upper canines, the blunt lower canines which honed the uppers, and the longer series of cheek teeth (Riggs, 1934; Turnbull, 1978) clearly show that the canine shear-bite of this genus must have differed in many details. The morphological differences between other sabertooths and *Smilodon* are many, but I believe that they do not negate the hypothesis that all employed some variation of the canine shear-bite to kill prey.

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CONTRIBUTIONS IN SCIENCE

SYSTEMATICS AND DISTRIBUTION OF THE SKINKS ALLIED TO *EUMECES TETRAGRAMMUS* (SAURIA: SCINCIDAE)

Carl S. Lieb

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SYSTEMATICS AND DISTRIBUTION OF THE SKINKS ALLIED TO *EUMECES TETRAGRAMMUS* (SAURIA: SCINCIDAE)

Carl S. Lieb[1]

ABSTRACT. The distributions and relationships of the three species in the *Eumeces brevilineatus* Group, *E. brevilineatus, E. callicephalus,* and *E. tetragrammus* are re-evaluated. *E. brevilineatus* and *E. tetragrammus* are sympatric over a narrow zone in southern Texas, and intermediates in color pattern occur at some localities. The presence of intermediates and lack of other morphological differences between the two taxa suggest that gene exchange occurs in the area of contact.

The third member of the species group, *callicephalus,* is the most distinctive in scalation and color pattern. It is allopatric to the distributions of *brevilineatus* and *tetragrammus,* but populations of *brevilineatus* that are geographically nearest to the range of *callicephalus* contain some individuals with the distinctive traits of the latter form. The expression of these characteristics within the westernmost populations of *brevilineatus* is interpreted as evidence of former gene flow that was interrupted by Pleistocene alterations in the habitat and climate of the western Chihuahuan Desert.

The three nominal species of the *E. brevilineatus* Group are relegated to subspecies of *tetragrammus* (Baird). Salient features of coloration and scalation of the polytypic *tetragrammus* ally it with *anthracinus* and *septentrionalis* of the *E. anthracinus* Group. A total of 13 species groups in the genus are now recognized; a key to these groups and a list of the constituent species are provided.

RESUMEN. En su monografía del género *Eumeces,* Taylor (1935b) asignó tres especies de lagartijo escincidos a La Especie-Grupo *Eumeces brevilineatus: E. brevilineatus* de la parte norte de México y Tejas, *E. callicephalus* de la parte oeste de México y sur de Arizona, y *E. tetragrammus* de la parte nordeste de México y sur de Tejas. Las especies *E. brevilineatus* y *E. tetragrammus* fueron clasificadas por diferencias en deseño de las coloración, poseiendo *E. brevilineatus* bandas y rayas sobre el cuerpo más cortas que *E. tetragrammus.* Aún cuando las dos son escencialmente idénticas en sus escamas, Taylor las clasifico como especies diferentes porque el no encontró invididuos intermedios, y porque supuso la existencia de una área grande simpatrica en sus distribuciónes geográficas. Sin embargo, una revista de las distribuciónes de estas dos especies revela que su área de distribución geográfica simpátrica esta confinada a una zona estrecha en el sur de Tejas. Además, el examen de especímenes obtenidos hasta el presente, indica que rangos intermedios en coloración existen, y por eso, es posible que las dos formas intercambien material genético en la área de contacto.

El tercer miembro de las especie-grupo, *Eumeces callicephalus,* tiene una distribución geográfica que es alopatrica a las distribuciónes de *E. brevilineatus* y *E. tetragrammus. E. callicephalus* se localiza en elevaciones bajas y moderaciones al oeste de la Division Continental, desde la zona central de Jalisco hasta el Sur de Arizona. De los tres miembros del Grupo *E. brevilineatus, E. callicephalus* es el más distinto en sus escamas y coloración. Empero, poblaciones de *E. brevilineatus* que se encuentran más proximas en su posición geográfica a poblaciones de *E. callicephalus,* poseen individuous que tienen alguna de estas cualidades distintas de *callicephalus.* La expresión de estas caracteristicas dentro de las poblaciones más occidentales de *E. brevilineatus* es interpretada como evidencia de una distribución continua anterior, de poblaciones intermedias la cual fue interrupida recientemente por alteraciones Pleistocénicas en el habitat y clima de la parte norte del Desierto Chihuahuense.

A causa de estas observaciones e interpretaciones, la asignación taxonómica de los tres especies nominal del Grupo *E. brevilineatus* a subespecies de *Eumeces tetragrammus* (Baird) es recomendada. Rasgos salientes de coloración y escamación de la politipica *E. tetragrammus* claramente la une con *Eumeces anthracinus* y *E. septentrionalis* de el Especie-Grupo *E. anthracinus.* El Grupo *E. anthracinus* es una de las trece especie-grupos en el género *Eumeces,* y está asocido aprentemente con un grupo que incluye los escíncidos de Las Especies-Grupos *E. fasciatus* y *E. multivirgatus.*

INTRODUCTION

In E.H. Taylor's (1935b) monograph of the scincid genus *Eumeces,* the species were arranged into 15 species groups on the basis of shared color patterns and scalation features. One of the New World assemblages, the *E. brevilineatus* Species Group, included three species: *callicephalus* Bocourt, 1879, of Arizona and western Mexico, and *brevilineatus* Cope, 1880, and *tetragrammus* (Baird) 1858, of Texas and northern Mexico. In contrast to most other species groups erected by Taylor, species of the *E. brevilineatus* Group evinced a high

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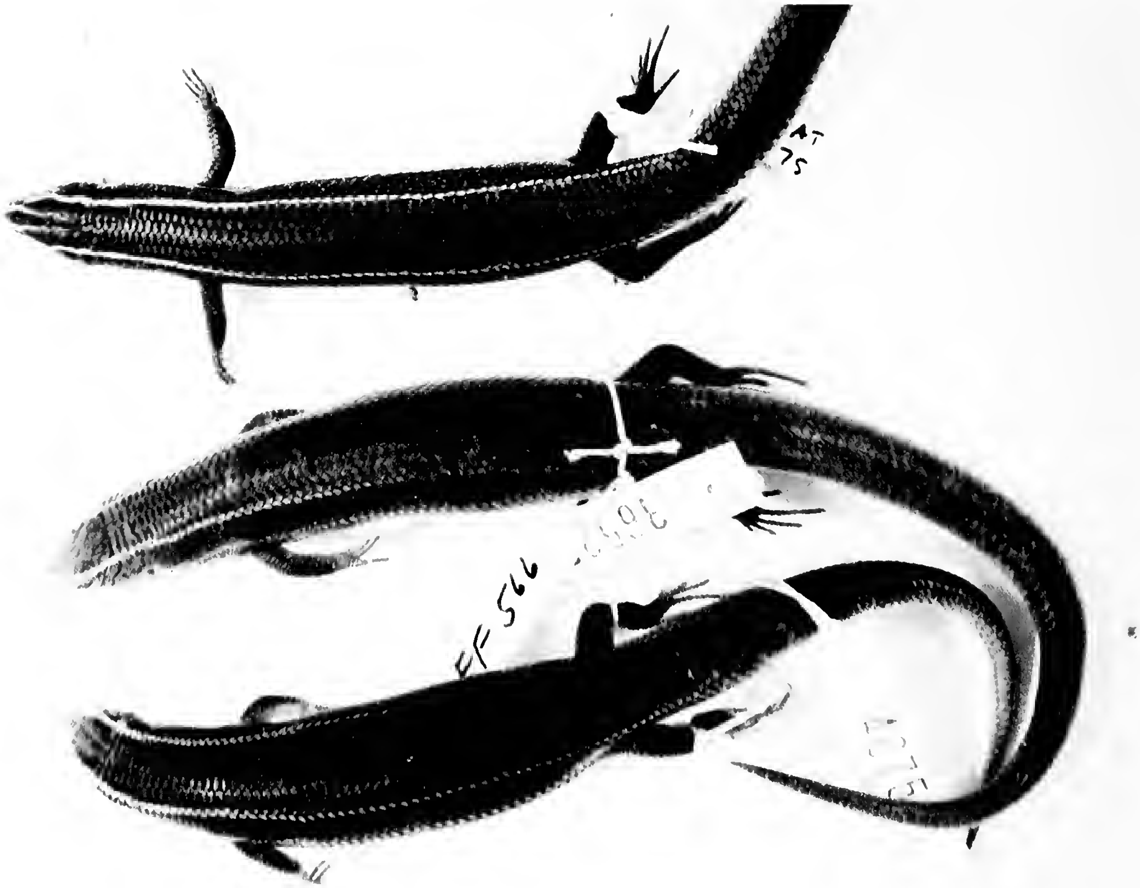

Figure 1. Pattern variation in *Eumeces tetragrammus.* Top: Young adult (TCWC 45496; Querétaro: El Trapiche); Middle: Old adult with faded posterior striping (TCWC 36535; Texas: Hidalgo Co.); Bottom: Adult with broad neck lines (TCWC 40751; Coahuila: vic. Cuatro Cienegas).

degree of intraspecific variation in usually conservative scale features.

The systematic results of the present study served as a partial requirement for a Master's degree at Texas A&M University (Lieb, 1973), and were partly incorporated into Conant's (1975) field guide. Taxonomic arrangements appearing in the latter work thus anticipated the publication of the present account. Here I document the evidence and rationale for these proposed taxonomic conclusions and review the geographic distribution and morphological variation. Changes are proposed at the intragroup and intergroup levels within the genus.

MATERIALS AND METHODS

I have examined over 600 specimens of skinks of the *E. brevilineatus* Group. Data concerning individual and geographic variation were compiled on the following scalation features (terminology after Taylor, 1935b; Robinson, 1979): number of postmentals, presence of postnasals, contact of primary temporals and parietals, enclosure of interparietal by parietals, number of postlabials, number of longitudinal dorsal rows, number of latitudinal rows around midbody, number of nuchal pairs, number of supralabials, number of supraciliaries, and contact of prefrontals. In addition, data on individual, geographic, and where possible, ontogenetic variation in the following color pattern features were also collected (terminology after Dixon, 1969): expression of median light line, dorsolateral light lines, dark lateral stripes, lateral light lines, and upper secondary dark lines. Two aspects of gross morphology, axilla-groin/snout-vent length ratio and adpressed limb overlap, were also evaluated. This data base has been discussed elsewhere (Lieb, 1973), and only data relevant to the interpretation of relationships among *E. brevilineatus* Group taxa are presented here. Moreover, new data acquired since 1973 have also been incorporated

Figure 2. Pattern of *Eumeces brevilineatus* and intermediates with *E. tetragrammus.* Top: Typical short-lined pattern of *E. brevilineatus;* Middle: Sympatric zone intermediate form with lengthened body striping (TCWC 39265; Texas: McMullen Co.); Bottom: Possible intermediate from Sierra Madre foothills (MVZ 185746; Nuevo León: vic. Ranchitos).

into this study. Unless otherwise noted, all specimens cited by museum number have been examined by me.

RELATIONSHIPS BETWEEN *EUMECES BREVILINEATUS* AND *E. TETRAGRAMMUS*

Eumeces tetragrammus and *brevilineatus* are distinguished only by differences in the striped pattern on the body (Taylor, 1935b). They are much more similar morphologically to each other than either is to *callicephalus.* In strongly patterned *tetragrammus,* the striping consists of a dark lateral stripe bordered above and below by light lines (dorsolateral and lateral light lines). This stripe extends from the neck throughout the length of the body to the groin or base of the tail (Fig. 1). In *brevilineatus,* the same striping (lateral stripe, dorsolateral, and lateral light lines) terminates on the body just posterior to the shoulder (Fig. 2). In hatchlings, the dorsum may be as dark as the lateral stripe. In both *tetragrammus* and *brevilineatus,* the dorsal ground color becomes distinctly lighter than the lateral stripe with increasing age. In the largest skinks, the light lines may also fade, resulting in only faint traces of dorsolateral and lateral light lines. The striping may also be obscured on the posterior dorsum by prolonged tenure in formalin; such conversion of fully lined individuals of *tetragrammus* to morphs similar to *brevilineatus* has been observed in several specimens. Fortunately, even in the most blackened specimens, enough pattern usually persists to make positive identification possible.

Taylor (1935b) found no evidence of intergradation between *tetragrammus* and *brevilineatus,* but his distributional data suggested a substantial zone of geographic sympatry in Texas. Later (Taylor, 1943) he reported a specimen of *brevilineatus* from Tamaulipas, Mexico, thus indicating an expanded zone of overlap with *tetragrammus* that included not only southern and central Texas (from Burnet Co. southward), but also a large section of northeastern Mexico. This broad zone of overlap was further substantiated by Smith

Figure 3. Hatchling *Eumeces tetragrammus* (TCWC 41555–61) from a clutch found with a fully lined female, 2 mi. W Bruni, Webb Co., Texas (TCWC 39271). Note the dark coloration and the incomplete expression of the dorsolateral light lines. Photograph by Richard J. Baldauf.

(1946), who provided distribution maps that indicated overlap; Brown (1950), who reported a specimen of *tetragrammus* from Bexar Co., Texas (immediately south of the Edwards Plateau), and specimens of *brevilineatus* from Cameron and Hidalgo cos. (in the lower Rio Grande Valley); Conant (1958), who published distribution maps indicating the overlapping ranges; Anderson (1962), who reported a specimen of *brevilineatus* from San Luis Potosí; Holman (1968), who reported a Pleistocene fossil *tetragrammus* from Kendall Co. (on the Edwards Plateau); Raun and Gehlbach (1972), who published a county distribution map for *brevilineatus* in Texas with a record for Cameron Co. (probably that of Brown, 1950), and examined specimens from Hidalgo Co. Raun and Gehlbach (1972) also accepted the Bexar Co. *tetragrammus* record, rejected literature records for western and northern Texas, and doubted the validity of the central Edwards Plateau Burnet Co. record.

Strecker (1909a) reported *tetragrammus* from an isolated locality in Burnet Co., to the north of the range. Taylor (1935b) questioned this record, apparently a single specimen in the Strecker Museum. The specimen is not now in the museum nor are there records that it was preserved, retained or exchanged (pers. comm., D. Lintz, Strecker Museum). It could have been a misidentified *septentrionalis.* The two forms are superficially similar, and it is clear elsewhere that Strecker (1908, 1909b; Strecker and Williams, 1927) could not readily distinguish the two.

Taylor (1943) reported a very small specimen of *brevilineatus* from the coastal plain of Tamaulipas. This individual (UIMNH 22443) was found to be a desiccated hatchling of *tetragrammus* in which the light lines are poorly defined and partially obscured by skin creases. Hatchlings often have such truncated light lines (Fig. 3).

Brown (1950) did not cite specimen numbers or museums for Texas records, and the reports of *tetragrammus* from Bexar Co. and *E. brevilineatus* from Hidalgo and Cameron cos. are unverifiable. I have not seen specimens of *tetragrammus* from Bexar Co., but I have examined a series of *brevilineatus* reportedly from Cameron Co. (FMNH 27215–17). Brown could have utilized these specimens, as he did examine some FMNH holdings. These, however, are the only representatives of the short-lined form from the lower Rio

Grande Valley seen by me. The specimens examined in the B.C. Brown private collection from Hidalgo Co. that were catalogued as *brevilineatus* (BCB 2402, 2 specimens) are aged *tetragrammus* with faint light lines. Similarly, Anderson's (1962) record of *brevilineatus* for San Luis Potosí (AMNH 66999) is a specimen of *tetragrammus* that has been over-preserved in formalin.

The allocation of a Pleistocene fossil to *tetragrammus* was based upon dentary tooth characters (Holman, 1968). Although I have not examined the fossil material (Univ. Texas Bureau Econ. Geol. 40450-1666), the allocation is dubious in that study of several cleared and stained specimens of both taxa does not corroborate Holman's observed differences in the spaeing and robustness of the teeth. Furthermore, even if *tetragrammus* occurred in the area during the Pleistocene, it does not now occur there.

The county-based maps and distributional summaries of Raun and Gehlbach (1972) were based upon literature records, examined specimens, and in some cases, museum catalogue files. The presumed distributional errors for *brevilineatus* of Brown (1950) were thus perpetuated, and other museum records from the lower Rio Grande Valley of Texas were also accepted. Besides the BCB specimens from Hidalgo Co. mentioned above, a misidentified series from this county at a second museum (TCWC 18169–73, 18176–82, verified as *tetragrammus* by me) was also apparently utilized by Raun and Gehlbach (1972) for the *brevilineatus* distribution map.

Thus, extant material with acceptable locality data indicate that the major area of sympatry of *brevilineatus* and *tetragrammus* occurs in the coastal plain of southern Texas, north of the Rio Grande Valley and south of the Edwards Plateau escarpment. Plotting of locality data (Fig. 4) further suggests that actual sympatry in southern Texas occurs only in the vicinity of the Nueces River drainage system, from the mouth of the river west and then north to the edge of the Pleateau. The two forms may also occur together in the Rio Grande drainage in the vicinity of Laredo (Webb Co.). There is a specimen of *brevilineatus* from this area (UMMZ 114253), and Werler (1951) reported on the hatchlings of a clutch of eggs from a female *tetragrammus* from Laredo (specimens not examined). Nevertheless, these regions mark the northernmost limit of the range of *tetragrammus*, and the southern extent of the Gulf Coastal Plain populations of *brevilineatus*. *E. brevilineatus* do occur in northern Mexico, but are known only from the Sierra del Nido of Chihuahua and the Coahuila Folded Belt of Coahuila and Nuevo León. These populations occur in rocky habitats within pinyon-juniper, oak woodland, or piedmont areas similar to those in western Texas. Within the northern Chihuahuan Desert, *brevilineatus* may occur in low desert mountain ranges where the appropriate mesic habitats are found. On the other hand, *tetragrammus* are primarily associated with the coastal plain lowlands, particularly riparian or mixed grassland-brushy areas with sandy substrata. Toward the southern part of its range in Mexico, the species also occurs in rocky habitats in the foothills of the Sierra Madre Oriental and in the isolated coastal plain ranges of Tamaulipas (Sierra de Tamaulipas, Sierra San Carlos). The distributional ranges of *tetragrammus* and *brevilineatus* should make contact in northeastern Nuevo León, in areas where the foothill habitats of the Coahuila Folded Belt and northern Sierra Madre abut those of the Tamaulipan Coastal Plain. However, only two specimens are known from this region. Their significance is discussed below.

A presumably disjunct population of *tetragrammus* occurs in the Cuatro Cienegas Basin of Coahuila (Zweifel, 1958); the four specimens from this population (AMNH 77316, TCWC 40750–52) are all from riparian or other mesic habitats in the floor of the basin. The two adult specimens are distinctive in having comparatively wide dorsolateral light lines on the neck (Fig. 1), and a dorsal ground color of a pale shade of gray or gray-brown. The other two specimens are juveniles with coloration and color pattern similar to other *tetragrammus* populations; the scalation of all four individuals is fairly typical of the species (Table 1). *E. brevilineatus* is known to occur in a low mountain range approximately 75 km (air) north of the Cuatro Cienegas area, but because of the habitat specificity described above, such desert range populations are almost certainly isolated from the riparian enclave of *tetragrammus* in the Cuatro Cienegas Basin. The occurrence of a disjunct population of *tetragrammus* in this basin is thus interesting in a biogeographic sense, but does not appear to represent sympatry with *brevilineatus*. Other taxa of obvious Tamaulipan affinities are also found in the Cuatro Cienegas area (e.g., the snakes *Drymarchon corais* and *Drymobius margaritiferus*), as are riparian species with close relatives in the Gulf Coast lowland/Salado River drainage to the east (see Morafka, 1977).

What would otherwise be a reasonably clear-cut habitat difference between the two species breaks down south of the Edwards Plateau in south-central Texas. In this area, and southward into the zone of sympatry with *tetragrammus*, *brevilineatus* occupy non-rocky brushland, grassland, and riparian habitats that are essentially identical to those utilized by *tetragrammus*. Moreover, within this area of sympatry, color pattern intermediates have been observed. In the intermediates, the body striping pattern extends posterior to transverse dorsal row 30 and terminates at or before the midbody region (Fig. 2). In *brevilineatus* outside the sympatric zone, such elongated stripes do not occur. In *tetragrammus*, both within and outside of the sympatric zone, the body striping is continuous from neck to groin, although it may be somewhat faded posterior to the midbody in old adults (Fig. 1). As mentioned earlier, some *tetragrammus* hatchlings have shortened body lines. In these individuals, however, the fully lined pattern seems to develop ontogenetically before a snout-vent length of 45 mm is reached. Even though most small juveniles of *tetragrammus* are fully lined, the allocation of individual skinks to intermediate status is thus possible only for adults and subadults over 45 mm in snout-vent length.

In a series of six specimens from southern Live Oak Co. (TAIC), one is fully lined (*tetragrammus*, No. 117), four are "short" lined (*brevilineatus*, 258.1–.2, 123.2–.3), and the sixth is intermediate (123.1). A second sample, a series of five individuals from the northwestern edge of the sympatric zone in south-central Uvalde Co. (TCWC), contains one *tetra-*

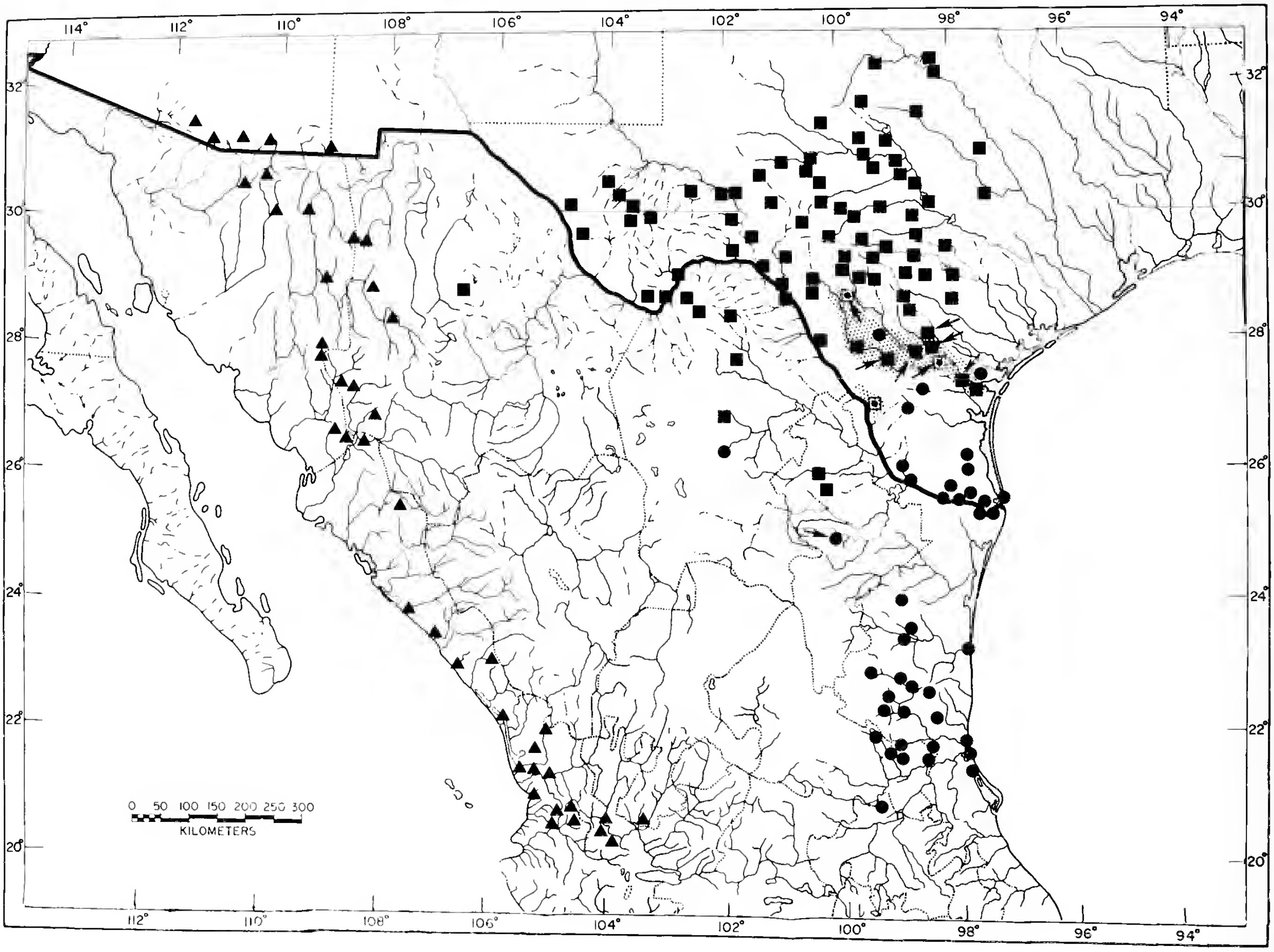

Figure 4. Distribution of *Eumeces brevilineatus* Group taxa in southwestern North America. Circles indicate *Eumeces tetragrammus;* squares *E. brevilineatus;* triangles *E. callicephalus.* Stippled areas mark the regions of presumed sympatry between *brevilineatus* and *tetragrammus,* the circle within squares indicating localities where both forms are known to occur together, and arrows indicating populations that contain intermediate forms (see text).

grammus (44175), two *brevilineatus* (44173–74), and two intermediates (44171–72). The fully lined individual (a female) was taken under a rock in copulo with one of the short-lined males (R.A. Thomas, pers. comm.). The two lizards obligingly repeated their act in the laboratory for photographs (Fig. 5), and the eight subsequent eggs produced only fully lined offspring (TCWC 44176–83).

Other intermediates between *brevilineatus* and *tetragrammus* are known from individual specimens collected in Jim Wells Co. (KU 8812), LaSalle Co. (TAIC 643), Live Oak Co. (TCWC 10537), and McMullen Co. (LACM 134855, TCWC 39265, TNHM 28836); their occurrence spans most of the coastal plain drainage of the Nueces River. In addition to the typical short-lined specimens of *brevilineatus* from Live Oak (TAIC) and Uvalde (TCWC) cos., other short-lined individuals within the Nueces drainage have been examined from Dimmit Co. (KU 8195), McMullen Co. (TCWC 39266–67), Nueces Co. (TCWC 18175), and elsewhere in Live Oak Co. (TCWC 10535–36, 10538). A fully lined *tetragrammus* is known from Frio Co. (CM 10558). Over the entire Nueces River drainage area, the total observed numbers of fully lined, intermediate, and short-lined individuals were 3, 9, and 13, respectively. Although the short-lined form seems to predominate, there are still relatively few specimens available from this poorly sampled region.

As mentioned previously, another area of potential contact of *tetragrammus* and *brevilineatus* is in northeastern Nuevo León. Only two specimens (MVZ) are known from this region, both from the same locality about 35 km SE of Ciudad Monterrey. One specimen (185745) is a typical fully lined *tetragrammus,* the other (185746) has the shortened light lines that are typical of the condition in south Texas intermediate populations (Fig. 2). In this "intermediate" specimen, however, there are distinct traces of a complete dark

Table 1. **Geographic variation in six characters for the nominal forms of *Eumeces tetragrammus*. Frequencies are followed (in parentheses) by sample sizes. Letters correspond to geographic regions mapped in Figure 6. Asterisks indicate a condition that is expressed on at least one side of the head.**

	Postmental divided	Postnasals present*	Interparietal enclosed	Primary temporal contacts parietal*	Postlabials single*	Nuchal Y-mark present
A: NE Mexico						
tetragrammus	0.10 (51)	0.04 (51)	0 (51)	0.18 (50)	0.03 (39)	0 (42)
B: Cuatro Cienegas						
tetragrammus	0 (4)	0 (4)	0 (4)	0.25 (4)	0.25 (4)	0 (4)
C: South Texas						
tetragrammus	0.15 (74)	0.01 (74)	0 (73)	0.19 (72)	0.06 (71)	0 (68)
D: Sympatric zone	0.03 (33)	0.10 (32)	0 (24)	0.25 (24)	0.03 (31)	0 (13)
E: West-central Texas						
brevilineatus	0.05 (151)	0.07 (149)	0.02 (149)	0.21 (149)	0.14 (139)	0.01 (68)
F: East-central Texas						
brevilineatus	0.18 (33)	0.21 (33)	0.03 (33)	0.30 (33)	0.26 (35)	0 (23)
G: Coahuila–West Texas						
brevilineatus	0.17 (47)	0.09 (45)	0.04 (47)	0.31 (45)	0 (47)	0.60 (47)
H: Sierra del Nido						
brevilineatus	0 (4)	0 (4)	0.33 (3)	0.67 (3)	0.33 (3)	0.25 (4)
I: USA–NW Mexico						
callicephalus	0.96 (80)	0.58 (79)	0.64 (80)	0.67 (76)	0.99 (67)	0.87 (61)
J: West Mexico						
callicephalus	0.59 (41)	0.83 (41)	0.89 (38)	0.87 (39)	0.96 (28)	0.77 (30)

lateral stripe extending posterior to the termination of the light lines. Such extension of the dark lateral band was not observed in any of the southern Texas intermediates, although such a characteristic could be obscured in some individuals by a long period of preservation. Nevertheless, in the absence of more information on the distribution of short-lined forms in the region, the assignment of the specimen to intermediate status is provisional.

Evidence for conspecificity of the forms *tetragrammus* and *brevilineatus* arises from the following observations: 1) the extremely close morphological similarity between the two forms in southern Texas; 2) the apparent lack of behavioral pre-mating isolating mechanisms where the two occur in sympatry; and 3) the presence of color pattern intermediates in the sympatric zone. This evidence is further supported by the lack of significant overlap in the distributions of the two forms, and by a lack of ecological segregation in the principal area of geographic contact and sympatry.

Alternatively, the two forms could be acting as parapatric species that only rarely hybridize. As noted before, copulation of a short-lined male and a long-lined female were observed under field and laboratory conditions, and that the resultant offspring were all fully lined. Assuming that the short-lined individual was indeed the male parent, then the expression of the long-lined pattern of *tetragrammus* would seem to be dominant over the short-lined pattern of *brevilineatus*. Such a dominance relationship in the inheritance of color pattern, however, does not readily explain how the intermediate condition arises, or why there is an apparent preponderance of short-lined individuals in the sympatric zone. On the other hand, should the gene pools of *brevilineatus* and *tetragrammus* be separated by post-mating isolating mechanisms, then the presence of occasional intermediates in the contact zone might represent sterile F_1's incapable of backcrossing to the parental stocks.

My studies on *brevilineatus* and *tetragrammus* clarify some aspects of the relationships of the two forms (particularly in distribution), but offer little in the way of an objective decision as to their specific status. From the material I have examined and the characters I have inspected, I feel that for the present the two nominal forms should be considered subspecies of a single species. Full resolution of their status, however, will require larger samples from the contact zone and a complete genetic analysis of the populations involved.

DISTRIBUTION AND STATUS OF *EUMECES CALLICEPHALUS* BOCOURT

When compared with both *tetragrammus* and *brevilineatus*, *callicephalus* differs significantly in several aspects of cephalic scutellation. These characters are as follows (frequencies of *tetragrammus* and *brevilineatus* in parentheses, respectively; N > 100 in all cases): postmental scale divided, 0.91 (0.14

Figure 5. Male *brevilineatus* (TCWC 44173) and female *tetragrammus* (TCWC 44175) copulating under laboratory conditions. Both individuals are from 8 mi. N Uvalde, Uvalde Co., Texas; they were also observed copulating when captured. Photograph by Robert A. Thomas.

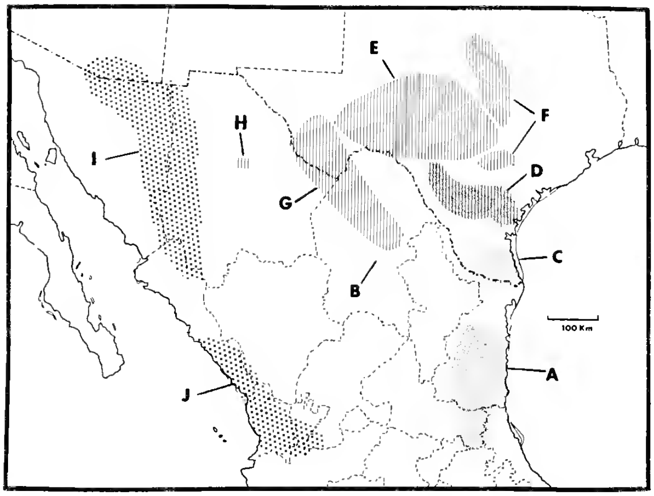

Figure 6. Geographic areas for combined samples indicated in Table 1. A, B, C: *Eumeces tetragrammus;* D: principal sympatric zone of *E. tetragrammus* and *E. brevilineatus* in southern Texas; E, F, G, H: *E. brevilineatus;* I, J: *E. callicephalus.*

and 0.08); postnasal scales present on at least one side of the head, 0.68 (0.03 and 0.09); enclosure of interparietal scale by parietals or azygous scales, 0.62 (0 and 0.03); primary temporal contacting parietal on at least one side of the head, 0.77 (0.17 and 0.25); and single (rather than double or triple) postlabials on at least one side, 0.97 (0.05 and 0.12). However, the frequencies of these characters vary geographically (Table 1, Fig. 6) and are discussed further below.

Most of the vividly patterned specimens of *callicephalus* vary from the basic *tetragrammus/brevilineatus* stripe pattern in having a persistent dark lateral stripe from neck to groin, faded dorsolateral and lateral light lines posterior to the shoulder, and a light median line on the anterior dorsum that bifurcates on the nuchal scales (Fig. 7). In some adults, particularly those from the southern part of the range, the color pattern is faded, with concomitant loss of the bifurcating Y-mark and median light line, and a general obscuring of the lateral stripe and other light lines. Such faded specimens seem to have been the basis for the original recognition of *humilis* Boulenger 1887, a name based on patternless individuals of *callicephalus* (Robinson, 1979).

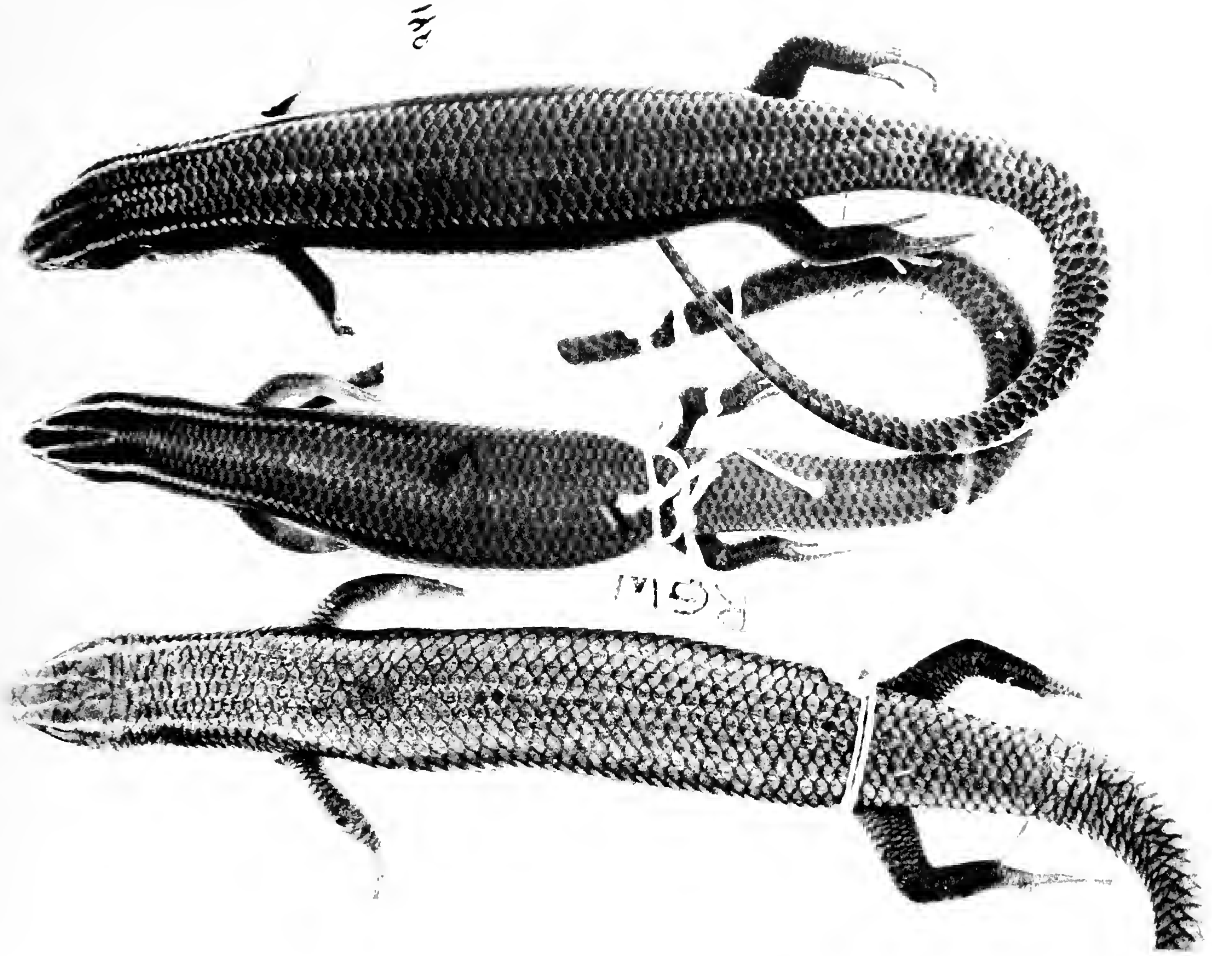

Figure 7. Pattern of *Eumeces callicephalus* and western *E. brevilineatus*. Top: *E. callicephalus* with typical pattern, including nuchal Y-mark (BYU 14260; Chihuahua: Cuiteco); Middle: *E. brevilineatus* from western part of range, with faint nuchal Y-mark present (UAZ 16816; Coahuila: vic. Piedra Blanca); Bottom: *E. callicephalus* with faded dorsal pattern (UTEP 4865; Sinaloa: vic. Mazatlan).

The geographic range of *callicephalus* in Mexico has been somewhat overestimated. Bocourt (1879) described the species from a specimen (MNHP 1643, not examined) sent to him in the mid-1800's by Alfrédo Dugés of Guanajuato, Mexico. Later authors, particularly Cope (1887) and H.M. Smith and Taylor (1945), assumed the city of residence of the collector to be the type locality of the species. There are also two specimens of *callicephalus* studied by Cope (ANSP 13604–05) that bear tags reading only "Guanajuato, Mexico . . . Dugés." The original type description, however, does not clearly give the collection locality as the city or state of Guanajuato, but only associates the specimen with the collector who resided there. Additional information is contained in a paper by Dugés (1889) on a comparison of the herpetofauna of the Guanajuato region with that of the Guadalajara (Jalisco) area. Here, he specifically associates *callicephalus* with the Jalisco capital, citing *lynxe* as characteristic of his own locale. This condition still pertains, and it is likely that the type specimen of *callicephalus* (as well as the ANSP material) originated from near Guadalajara or from some other locality farther to the west. Taylor (1935b) indicated that the remaining material in the Alfrédo Dugés Museum in Guanajuato bears the label "San Blas," presumably referring to the coastal town in Nayarit. Specimens of *callicephalus* are known from within 50 km of Guadalajara.

E. callicephalus has also been reported from Querétaro, Mexico (Smith and Taylor, 1945). H.M. Smith (Univ. Colorado, pers. comm.) has advised me that this is another of Dugés's specimens, but I have been unable to locate either the original citation or the specimen. The locality is "Huaxteca Potosina," which is more applicable to a general region in the northeastern part of the state than to any specific locality. *E. tetragrammus* occurs in the Huaxteca area, and the report could be based upon a specimen of this species.

Two additional localities, records of Taylor (1935b), have already been questioned and corrected: Tombstone, Arizona (see Zweifel, 1962) and "Ciudad" (=La Ciudad de Rocas) in Durango. The latter record, based upon a specimen (British Mus. Nat. Hist. 83.413, not examined) collected by Forrer in the early 1800's, is a *callicephalus* (in litt., R.G. Webb, UTEP). However, La Ciudad is higher in elevation (more than 2400 m) than other records for the species in western Mexico, and only *brevirostris* occur there. Conant (1969:86) has discussed problems involving confused localities for other specimens credited to Forrer, and it seems likely that this specimen actually came from a much lower elevation somewhere along the trail between Ventanas and La Ciudad. Thus, the geographic range of *callicephalus* is confined to low and moderate elevations west of the Continental Divide, extending from the general area west of Guadalajara north to southern Arizona and adjacent New Mexico.

The geographic range of *callicephalus* is allopatric to those of the other *Eumeces brevilineatus* Group members. *E. brevilineatus* occur in the Sierra del Nido of Chihuahua, approximately 140 km east of the nearest locality for *callicephalus* (Chihuahua: 8 mi. W Matachic, AMNH 68295). This Chihuahua *brevilineatus* population is known from four specimens (MVZ 70702–03, LACM 116401, UTEP 62), all of which were collected in Cañon de Santa Clara on the eastern slope of the range. The LACM and MVZ specimens have the typical color pattern of *brevilineatus*, whereas the UTEP specimen has traces of the *callicephalus*-like bifurcating head lines on an otherwise typical *brevilineatus* pattern. Such traces also occur in some individuals of *brevilineatus* from the western part of the range, but do not occur in eastern populations nor in *tetragrammus*. One specimen (MVZ 70702) is badly damaged, and most scalation features could not be determined (postmental entire, postnasals absent). In MVZ 70703, the postmental is entire, the postnasals absent, the interparietal not enclosed, the primary temporal contacts the parietal on the right side, and the postlabials are double. The LACM specimen is similar, except that neither primary temporal contacts a parietal. UTEP 62 has an entire postmental, no postnasals, an enclosed interparietal, contact of the primary temporal with the parietal on the left side, and a single postlabial on the right side.

The small series from the Sierra del Nido thus contains two individuals (MVZ 70702, LACM) that are typical of eastern *brevilineatus* populations in color pattern and scalation, one (UTEP) that contains a mixture of *brevilineatus* and *callicephalus* color pattern and scalation similarly contained in western *brevilineatus*, and one (MVZ 70703) that has the typical *brevilineatus* color pattern and approaches the *callicephalus* scalation condition only in the contact of a primary temporal and a parietal (occurs at an overall frequency of 0.77 in *callicephalus* and 0.25 in more easterly *brevilineatus*). A similar trend is seen in other western *brevilineatus* populations (ca. 250–450 km to the east) for which larger series are available. Overall in the samples from Trans-Pecos Texas and Coahuila (Fig. 6; Table 1), the Y-shaped bifurcating head lines occur in 60 percent (N = 47) of the individuals, and the frequencies of two of the five scale characters typical of *callicephalus* are higher than those in the central Texas *brevilineatus* populations. Slightly higher frequencies of *callicephalus*-like scale features also occur in *brevilineatus* populations in the northeastern Edwards Plateau and along its southeastern periphery (Fig. 6, Table 1). The bifurcating head lines observed in many western *brevilineatus*, however, do not occur in the more easterly populations, nor in *tetragrammus*.

These data indicate a pronounced tendency for the westernmost populations of *brevilineatus* to express a color pattern feature otherwise more characteristic of *callicephalus*, and suggest similarities in some scalation features as well. The Trans-Pecos and Coahuila populations of *brevilineatus*, however, are separated from the range of *callicephalus* by 400 km of unsuitable Chihuahuan Desert habitats. There are no authenticated distributional data for *callicephalus* east of the Continental Divide, so it is unlikely that the observed trends in western *brevilineatus* populations could be due to hybridization with the other form. These patterns do suggest, however, that intermediate populations between *brevilineatus* and *callicephalus* probably extended across much of the now intervening desert during the pluvial past. The estimated extent of pinyon-juniper woodlands during the Wisconsin glacial maximum (ca. 20,000 years B.P.) is to elevations as low as 300–600 m at the 25th parallel, and 600–900 m at the 30th parallel (see Morafka, 1977, for review). Such displacements would have provided suitable corridors for these skinks across much of Chihuahua and Coahuila north of the Arteaga and Parras anticlines. Thus the differentiation of *callicephalus* and *brevilineatus* may be the result of interruption of a continuous gene pool by climate and vegetation changes of the last 10,000 years. Further studies on the variation and distribution of both *brevilineatus* and *callicephalus* in Chihuahua are needed, particularly in regard to the discontinuous areas of pinyon-juniper and oak habitats from which neither form is known. The degree of similarity of western Texas and Coahuila populations of *brevilineatus* to *callicephalus*, however, suggests that the two forms should be considered allopatric members of a single species, and that *callicephalus* be retained as a distinct subspecies.

TAXONOMIC AND DISTRIBUTIONAL SUMMARY

The three forms recognized as distinct species of the *Eumeces brevilineatus* Group of Taylor (1935b) are herein considered subspecies that are distributed in a discontinuous arc from western Mexico north to the southwestern United States and south again into eastern Mexico. The oldest available name for the three taxa is *Eumeces tetragrammus* (Baird). The following accounts summarize information on variation and distribution for the species and its three subspecies.

Eumeces tetragrammus (Baird)

Plestiodon tetragrammus Baird, 1858:256.
Eumeces callicephalus Bocourt, 1879:431–433.
Eumeces brevilineatus Cope, 1880:18–19, 44, 46.
Eumeces humilis Boulenger, 1887:377.
[*Eumeces tetragrammus*] var. *funebrosus* Cope, 1900:630, 661.

Type specimens. The type series originally consisted of 12 or more specimens from Matamoros, Tamaulipas (USNM 3124; Taylor, 1935b). Taylor designated 3124A as the lectotype (now USNM 165662, examined; the remaining specimens in the original type series were not seen).

Diagnosis. Maximum snout-vent length 74 mm, dorsal scales around body subequal, in 26 or 28 parallel rows at midbody; scale lying medial to postgenial scale longer than wide (see Robinson, 1979); supraoculars four; body striping present in all but old adults, striping terminates anterior to the midbody region or on tail within three to five scales posterior to vent; single dark lateral stripe at least two scale rows wide present on each side, bordered above and below by light lines; dorsolateral light lines occupy third and fourth, or fourth only, lateral scale rows of neck; lateral light line passes through auricular opening; median light line, if present, bifurcates on the nuchal scales and extends posteriorly no more than a third of the body length; distal portions of tails in hatchlings and juveniles bright blue.

Variation. Supranasal scales usually in contact; prefrontals in contact or not; parietals may or may not enclose interparietal; postnasals present or absent; supraciliaries vary from six to nine, usually seven or eight; postsuboculars vary from two to four, usually three; postlabials single or double; postmental single, or divided by a transverse suture; dorsal scales from occiput to above vent 52–60; lamellae under fourth toe of hind limb 10–18; upper secondary dark lines (see Dixon, 1969) present or absent; complete pattern loss may occur in very large or old adults.

Most patterned individuals may be identified to subspecies as follows:

1a. Dark lateral stripe extends from axilla to groin 2
1b. Dark lateral stripe terminates anterior to midbody region .... *E. t. brevilineatus*
2a. Postlabials single; median light line anteriorly bifurcating on nuchals to form a Y-shaped head marking .... *E. t. callicephalus*
2b. Postlabials double; median line absent, no bifurcating lines on nuchals .... *E. t. tetragrammus*

Distribution. Southwestern United States, northeastern and western Mexico (Fig. 4).

Eumeces tetragrammus tetragrammus (Baird)

Type specimens. See species account.

Diagnosis. Postlabial scales usually double; postnasals usually absent; interparietal usually not enclosed by parietals; dark lateral stripes, dorsolateral and lateral light lines present throughout body length in adults and juveniles; median light line absent.

Variation. Some hatchlings have poorly expressed or truncated light lines. With the exception of the population at Cuatro Cienegas, Coahuila, there is little geographic variation in color pattern. As noted earlier, adults from this area have a relatively pale dorsal color and slightly wider dorsolateral light lines on the neck (Fig. 1). These characteristics are not evident, however, in the two juveniles from the same area. Additional specimens are needed to evaluate the ontogeny of color pattern in this unique geographic variant.

Distribution. See Figure 4.

Habitat. This subspecies is most abundant in brushlands and grasslands with sandy substrata, but it also occurs in tropical deciduous forest, palm forest, subtropical brushlands with rocky substrates, and in mesic forests associated with riparian areas. The known elevational range is sea level to 1060 m.

Eumeces tetragrammus brevilineatus (Cope)

Type specimens. There are two syntypes from Helotes, Bexar Co., Texas (USNM 10159A and 10159B). Taylor (1935b) designated 10159B as the lectotype.

Diagnosis. Postlabials usually double; interparietal usually not enclosed by parietals; body striping terminates between shoulder and midbody.

Variation. Ground color in adults varies from dark gray to greenish-gray to brown, with or without dark edges on the dorsal scales. Specimens from far western populations often possess a light bifurcating mark on the nuchals (Fig. 7).

Distribution. See Figure 4.

Habitat. *Eumeces t. brevilineatus* is most abundant in xerophilous woodlands with rocky substrata. It also inhabits grasslands and brushlands with sandy substrata and riparian woodlands through xeric areas. Reported elevations range from about 150 m to 2300 m.

Eumeces tetragrammus callicephalus (Bocourt)

Type specimen. The holotype (MNHP 1643, not examined) was sent from Guanajuato to Paris by Alfrédo Dugés in 1868, but it was probably collected elsewhere.

Diagnosis. Postlabials usually double, postnasals usually present, dark lateral stripe usually present throughout body length, light bifurcating head lines and short median light line usually present.

Variation. Color of adults in preservative is gray or gray-green dorsally, with dark brown to red-brown lateral stripes. The median light line, and the dorsolateral and lateral light lines, may be faded or absent (Fig. 7).

Distribution. See Figure 4.

Habitat. This subspecies seems to be most abundant in wooded rocky canyons in the northern part of its range, usually within an elevational range of 900 to 1700 m. In southwestern Mexico, they occur in mesic foothill forests and tropical deciduous lowland habitats. In the southern part of the range it is replaced at higher elevations by *Eumeces brevirostris* and by *E. multilineatus* in the north. Habitats on the eastern slopes of the Sierra Madre Occidental in Durango and Zacatecas, as well as across the southern margin of the Mexican Plateau that would appear suitable for *E. t. callicephalus*, are inhabited by *E. lynxe*. Suitable habitats in western New Mexico and western Chihuahua are apparently unoccupied.

SPECIES GROUP STATUS

Taylor (1935b) defined 15 species groups of *Eumeces*, but did not fully indicate his criteria for recognizing all groups. Moreover, the relationships between the species groups were largely unstated, and were essentially confined to a phylogenetic tree (p. 38) with little comment or explanation. It is clear from this tree, as well as from the key to the species and from the text, that Taylor's groups were based upon shared features of color pattern and/or scalation. How he arrived at many of his conclusions is not easily determined.

Taylor's phylogeny indicated that the *E. brevilineatus* Group (i.e., *Eumeces tetragrammus* as defined above) was closely related to the *E. fasciatus* Group, an assemblage of 12 nominal species widely distributed in eastern Asia and the southeastern United States. The unifying feature of the *E. fasciatus* Group is primarily the presence of five dorsal light lines on the body and tail in all juveniles and many adults. In *tetragrammus,* only parts of this *E. fasciatus*-type pattern are present: the median light line is absent (or present only anteriorly), and the paired light lines are absent on the distal tail and/or reduced on the body. *E. fasciatus* Group species also differ from *tetragrammus* in the following (characteristics of the latter in parentheses): larger body sizes attained, with snout-vent lengths in excess of 80 mm typical of most species (observed snout-vent maximum 76 mm); interspecific variation in scales around body ranging from 22 to 26 (26–28 intraspecifically); postnasals usually present in eight of the 12 species (usually present in one of three subspecies). However, in these features of color pattern, body size, and scalation, *tetragrammus* is much less similar to any *E. fasciatus* Group form than it is to members of the *E. multivirgatus* and *E. anthracinus* species groups.

The *E. multivirgatus* Group was defined by Taylor (1935b) as follows: *multivirgatus, gaigei, humilis, parviauriculatus,* and *parvulus.* Subsequent studies have considerably altered the original composition of the species group. *E. gaigei* is now a junior synonym of *multivirgatus,* and the *gaigei* specimens that Taylor utilized are now *E. m. epipleurotus* (Taylor, 1935a; Axtell, 1961; Mecham, 1980). *E. humilis* was based on patternless *multivirgatus* from the United States (H.M. Smith, 1942; Mecham, 1957), and on patternless *callicephalus* from Mexico (Robinson, 1979). Robinson (1979) also removed *parviauriculatus* and *parvulus* from the *E. multivirgatus* Group and allocated them to the *E. brevirostris* Group (sensu Dixon, 1969). One species, *multilineatus* (known only from a small area in the high elevations of the Sierra Madre of Chihuahua), was added to the *E. multivirgatus* Group at the time of its description (Tanner, 1957). It is similar to *multivirgatus,* and was independently described as *E. multivirgatus mexicanus* Anderson and Wilhoft, 1959 (see Legler and Webb, 1960). The present composition of the *E. multivirgatus* Group consists of only *multilineatus* and *multivirgatus.*

Individuals of *multilineatus* have the fully developed five-lined dorsal pattern characteristic of the *E. fasciatus* Group, as do juveniles of some populations of the polytypic species, *multivirgatus.* Most of the populations of the latter form, however, have modified five-lined patterns in adults. The predominate modifications are patternless (unicolor), four-lined, and five-lined patterns that lack the nuchal Y-mark, as well as the multiple-lined pattern, the source of the scientific and common names (Many-lined Skink). *E. tetragrammus* resembles the species of the *E. multivirgatus* Group in body size and scalation features, and the color pattern of *E. t. tetragrammus* and the four-lined *multivirgatus* are similar. However, the great variation in color pattern in the *E. multivirgatus* Group and the tendency for reduced number of scales around the body (24) are absent in *tetragrammus.*

Greater resemblance to *tetragrammus* is found with the *E. anthracinus* Group. As defined by Taylor, the *E. anthracinus* Group contained three species: *anthracinus, copei,* and *septentrionalis.* At present, however, only *septentrionalis* and *anthracinus* remain in this group; *copei* was removed by Dixon (1969) and placed in the *E. brevirostris* Group. *E. septentrionalis* is a grassland species that is locally abundant over much of central North America from Manitoba to coastal Texas; *anthracinus* is a relatively rare forest species distributed discontinuously in the eastern United States. The principal diagnostic characters for the two (P.W. Smith and H.M. Smith, 1952) are the placement of the light lateral line in the auricular region (through the ear opening in *anthracinus,* above it in *septentrionalis*) and the condition of the postmental scale (entire in *anthracinus,* divided in *septentrionalis*). *E. tetragrammus* resembles these species in their essentially four-lined color patterns, comparable body size and proportions, and similar scalation (including 26–28 scale rows around body). Moreover, the position of the body striping is identical in *anthracinus, septentrionalis,* and *tetragrammus,* except the striping extends well onto the tail instead of terminating at the shoulder (*E. t. brevilineatus*) or within two to five scales posterior to the vent (*E. t. tetragrammus, E. t. callicephalus*). Some individuals of both *E. anthracinus* Group species possess traces of middorsal light lines as well. When present, this line occurs as an indistinct postnuchal light stripe with or without a dark border; no trace of a bifurcating Y-mark is ever present.

The resemblance of *E. tetragrammus* to the *E. anthracinus* Group is so marked that continued placement of *tetragrammus* in a separate species group is unwarranted. The three species, *anthracinus, septentrionalis,* and *tetragrammus* represent a fairly homogenous group within the genus, particularly when compared with such diverse assemblages as the *E. fasciatus, E. multivirgatus,* and *E. brevirostris* groups.

In the nearly five decades since the appearance of Taylor's generic monograph, a substantial number of taxonomic changes have occurred in the species or species groups of *Eumeces.* Only one of the subsequently introduced species names (*multilineatus*) has persisted as part of the North American fauna. Most studies have resulted in the reallocation of various taxa to other species or species groups. In order to summarize the relationships of *tetragrammus,* I provide in Table 2 a revised group classification of the genus *Eumeces.* This classification and species group terminology is in large based upon the arrangement of Taylor (1935b:35–39), but it incorporates subsequent changes. Additionally, I have incorporated the following new changes: the use of subgeneric nomenclatural categories for species series and sections above the level of species groups; the *E. longirostris* Group and the *E. obsoletus* Group are combined into the same species series. Taylor placed the *E. longirostris* Group

Table 2. A classification of the genus *Eumeces* (modified from Taylor, 1935b). Pertinent literature is indicated by the citations in parentheses.

- Genus *Eumeces*
  - *Eumeces* Section
    - *E. schneiderii* Species Series
      - *E. schneiderii* Species Group (Eiselt, 1940; Mertens, 1946)*
        - *E. algeriensis*
        - *E. pavimentatus*
        - *E. princeps*
        - *E. schneiderii*
    - *E. taeniolatus* Species Series
      - *E. taeniolatus* Species Group
        - *E. poonaensis* (Sharma, 1970)
        - *E. taeniolatus*
      - *E. schwartzei* Species Group
        - *E. altamirani*
        - *E. managuae*
        - *E. schwartzei*
  - *Pariocela* Section
    - *E. obsoletus* Species Series
      - *E. longirostris* Species Group
        - *E. longirostris*
      - *E. obsoletus* Species Group
        - *E. chinensis*
        - *E. coreensis* (Doi and Kamita, 1937; Smith et al., 1975)
        - *E. kishinouyei*
        - *E. obsoletus* (Hall, 1976)
    - *E. lynxe* Species Series
      - *E. lynxe* Species Group (Parker, 1960; Webb, 1968)
        - *E. lynxe*
      - *E. sumichrasti* Species Group (Smith and Etheridge, 1953)
        - *E. sumichrasti*
    - *E. fasciatus* Species Series
      - *E. anthracinus* Species Group
        - *E. anthracinus* (Smith and Smith, 1952)
        - *E. septentrionalis* (Smith and Slater, 1949)
        - *E. tetragrammus*
      - *E. fasciatus* Species Group (Davis, 1969; Hikada, 1978a; Murphy et al., 1983)
        - *E. barbouri*
        - *E. capito* (Smith et al., 1975)
        - *E. elegans*
        - *E. fasciatus*
        - *E. inexpectatus*
        - *E. laticeps*
        - *E. latiscutatus*
        - *E. marginatus*
        - *E. okadae* (Hikada, 1978b)
        - *E. oshimensis*
        - *E. stimsoni*
        - *E. tamdaoensis* (Bourret, 1937)
        - *E. tunganus*

Table 2. Continued.

- *E. multivirgatus* Species Group (Tanner, 1957; Robinson, 1979)
  - *E. multilineatus* (Tanner, 1957; Legler and Webb, 1960)
  - *E. multivirgatus* (Lowe, 1955; Mecham, 1957, 1980)
- *E. brevirostris* Species Series
  - *E. brevirostris* Species Group (Dixon, 1969; Robinson, 1979)
    - *E. colimensis*
    - *E. copei*
    - *E. brevirostris*
    - *E. dugesii*
    - *E. ochoteranae*
    - *E. parviauriculatus*
    - *E. parvulus*
  - *E. egregius* Species Group
    - *E. egregius* (Mount, 1965, 1968)
  - *E. skiltonianus* Species Group (Rodgers and Fitch, 1947)
    - *E. gilberti*
    - *E. lagunensis*
    - *E. quadrilineatus*
    - *E. skiltonianus*

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* Although Eiselt, and later Mertens, proposed a *schneideri* "Rassenkreis" to include the species listed here as subspecies of a single form (*Eumeces schneiderii*), it is now clear from karyological data (Kupriyanova, 1973; Talliuri, 1975; J.W. Wright, LACM, pers. comm.) that at least two different karyotypes are involved among these nominal taxa. The *E. schneiderii* Species Group is thus in need of taxonomic re-evaluation with respect to this new information.

into its own section (Section II) and allocated the *E. obsoletus* Group to Section III. In my classification, only two sections are recognized: the *Eumeces* Section (Taylor's Section I) and the *Pariocela* Section (Taylor's II and III). Taylor's placement of the *E. longirostris* Group into a separate section arose from his emphasis upon its unique arrangement of preanal scales. My combination of the *E. longirostris* Group with the *E. obsoletus* Group is based upon a shared arrangement of lateral scales that is otherwise unique in the genus. Thirdly, I retain separate the *E. lynxe* and *E. sumichrasti* groups, but unite them at the species series level. I concur with others (Smith and Etheridge, 1953; Parker, 1960) that the species involved are related, but perceive the differences between the two groups to be of a magnitude greater than that found within the species group levels in the rest of the genus.

The overall phenetic basis for the erection of the various categories above the species group level is indicated in the following key to those groups.

1a. Median row(s) of dorsal scales conspicuously wider than adjacent scale rows .... *Eumeces* Section ... 2
1b. Median row(s) of dorsal scales not noticeably wider than scales of adjacent rows .... *Pariocela* Section ... 4
2a. Most of the enlarged median dorsal scales in a single row at midbody .... *E. taeniolatus* Series ... 3

2b. Two rows of enlarged dorsal scales at midbody . . . . *E. schneideri* Species Group and Series

3a. Two presuboculars posterior to second loreal . . . . *E. taeniolatus* Species Group

3b. Three presuboculars posterior to second loreal . . . . *E. schwartzei* Species Group

4a. Inferior lateral body scales in parallel rows 6

4b. Inferior lateral body scales in oblique rows . . . . *E. obsoletus* Series . . . 5

5a. Ground color of juveniles and subadults black, labials white-spotted; dorsal scales of adults yellow to greenish-gray with black scale margins; black scale margins occasionally expanded into dark body stripes . . . . *E. obsoletus* Species Group

5b. Juveniles and subadults with distinct dark lateral stripes and dorsolateral light lines; dorsum of adults bronze or greenish with black suffusions on the anterior-medial portions of most dorsal scales . . . . *E. longirostris* Species Group

6a. A middorsal light line present anteriorly or throughout body length in juveniles and patterned adults; line extending anteriorly on head terminating or bifurcating on the posterior part of the frontal scale . . . . *E. lynxe* Series . . . 7

6b. Middorsal light line absent in juveniles and patterned adults; or, if present, terminating or bifurcating on nuchal scales 8

7a. Middorsal light line extending posteriorly no more than a third of the body length . . . . *E. lynxe* Species Group

7b. Middorsal light line extending posteriorly throughout body length to tail . . . . *E. sumichrasti* Species Group

8a. Scale lying medial to postgenial scale longer than wide, dorsal median light line present or absent 9

8b. Scale lying medial to postgenial scale wider than long, dorsal median light line invariably absent 10

9a. Dorsolateral light lines occupying second and third lateral scale rows on the neck just anterior to shoulder 10

9b. Dorsolateral light lines absent, or occupying third and fourth, or fourth only, lateral scale rows on the neck region just anterior to shoulder 12

10a. Postnasal scales absent 11

10b. Postnasal scales present . . . . *E. skiltonianus* Species Group

11a. Supraocular scales four, or if less than four, postmental scale entire . . . . *E. brevirostris* Species Group

11b. Supraoculars three, postmental divided by a transverse suture . . . . *E. egregius* Species Group

12a. Scales around body in more than 24 rows 14

12b. Scales around body 24 or less 13

13a. Keeled lateral postanal scales present . . . . *E. fasciatus* Species Group, in part

13b. Keeled lateral postanal scales absent . . . . *E. multivirgatus* Species Group, in part

14a. Single dark lateral stripe present on each side of the body, terminating at the shoulder, at midbody, or on the tail within three to five scales posterior of vent . . . . *E. anthracinus* Species Group, in part

14b. Single dark lateral stripe absent or extending throughout body length and onto tail for a distance considerably more than five scale-lengths posterior to vent 15

15a. Postnasal scales present 16

15b. Postnasal scales absent 17

16a. Scales around body 26 13

16b. Scales around body 28 or more . . . . *E. fasciatus* Species Group, in part

17a. Middorsal light line present in patterned adults and juveniles, line bifurcating on the nuchals and extending throughout body length 13

17b. Middorsal light line absent, or, if partially expressed, does not form a bifurcating mark on the nuchals 18

18a. Postmental scale divided by a transverse suture *and* the light lateral line passes through the ear opening . . . . *E. multivirgatus* Species Group, in part

18b. Postmental scale entire, or, if divided, the light lateral line above the ear opening . . . . *E. anthracinus* Species Group, in part

SPECIMENS EXAMINED

Eumeces tetragrammus tetragrammus (Specimens examined, 162). MEXICO. COAHUILA: 3 mi. W Cuatro Cienegas (AMNH 77316); 3 mi. NW Cuatro Cienegas (TCWC 40750–51); 12.9 mi. E Cuatro Cienegas (TCWC 40752). NUEVO LEÓN: Arroyo de las Vacas, 2 km W Hwy 85 at Ranchitos (MVZ 185745). QUERÉTARO: 9.3 mi. E Jalpan, 3500 ft. (TCWC 29546); El Trapiche (TCWC 45494–97); 11 mi. N Jalpan, 2300 ft. (TCWC 32289–90). SAN LUIS POTOSÍ: 4 mi. (by rd to Oviedo) SSW Ajinche (LSUMZ 2374, 2376); 10 mi. S Antiguo Morelos (FMNH 105277); 1 mi. W Chantol (TCWC 59971); 3.5 mi. W Chantol, Rancho Pago Pago (TCWC 59969); Ebano (LSUMZ 343); 7 mi. W El Naranjo (BCB 61-878); 7 mi. N Valles, Los Sabinos (AMNH 66999); 8 mi. N Valles (UMMZ 118200); 5.4 mi. S, 1.1 mi. E Valles off Hwy 85 (TCWC 59904). TAMAULIPAS: 0.4 mi. SW Altamira (TNHM 28903–04); 0.3 mi. SW Rancho Carricitos, 1950 ft. (TCWC 49978); 1.3 mi. WSW Rancho Carricitos, 2500 ft. (TCWC 49779); 1 mi. E Chamal (UMMZ 101433); 6 mi. NW Chamal (BCB 68-49); 8 mi. NW Chamal (BCB nh8-908, -909); La Clementina (FMNH 105225); 3.5 mi. WSW Gavilan (TCWC 49780); Gomez Farias (UMMZ 110801); 24 mi. SW Jiminez (BCB 3238); Jaumave (UMMZ 95227); 3 mi. NW Limon (BCB 68-44); 19 mi. N Limon, 500 ft. (BCB 7323); 26 km N El Limon (UIMNH 22443); 12 mi. NW Llera (BCB 66-107); 22 mi. SE Manuel (BCB 6751); Matamoros (USNM 165662, lectotype); Padilla (TCWC 6937–38); San Jose (UMMZ 69252); Sierra San Carlos, 1.5 mi. NW Tinaja, 1800 ft. (TCWC 38666–67); Sierra de Tamaulipas, Hacienda Acuña (UMMZ 101431–32); 18 mi. N Ciudad Victoria (SM 6973); 19 mi. N Cd. Victoria, Rio Corona (BCB 11710); 21 mi. N Cd. Victoria, Rio Corona (BCB 11711); 22 mi. N Cd. Victoria, Rio Corona (BCB nhv67-470–nhv67-472); Zaragoza (BCB 68-45). USA. TEXAS: *Cameron Co.:* 2 mi. S Bluetown, 50 ft. (BCB 3447–51); 2 mi. W Bluetown, 40 ft. (BCB 4749–51); Brownsville (AMNH 102620; FMNH 5499; KU 69025; TAIC 2413 [2]; TCWC 8969–72); Brownsville, Fort Brown (AMNH 79091; USNM 52301); 6 mi. N Brownsville on Los Fresnos Rd (TNHM 13617–23); 5 mi. SE Brownsville (TAIC 2516); 9 mi. SE Brownsville (AMNH 79089–90; ANSU 6039); 10 mi. SE Brownsville, 25 ft. (BCB 3283–86); 17 mi. E Brownsville (BCB 25); 20 mi. N Brownsville (KU 7754–58); 1 mi. E Los Fresnos (TNHM 14998–99); 4 mi. W Los Fresnos (TNHM 11924–26); Harlingen (FMNH 94823–24); 1 mi. E Harlingen, 40 ft. (BCB 19); Padre Island (AMNH 8160); 3 mi. SE Santa Maria, near La Feria Pump Sta. (TNHM 13624); Southmost Palm Grove (TCWC 38759–60); *Duval Co.:* Freer (LSUS 3222); *Frio Co.:* 11 mi. W Dilley (CM 10558); *Hidalgo Co.:* 5 mi. S Alamo (LSUMZ 18214, 18266); 13 mi. N Edinburg, La Coma Ranch (TCWC 36524–31); 0.5 mi. N Hidalgo, FmRd 1962 (TCWC 18176–80); 1 mi. S Hidalgo, near Rio Grande River (TCWC 18181–82); *Kenedy Co.:* King Ranch, Norias Div., Rudolf Gate Area (TCWC 38855); *Live Oak Co.:* 8 mi. W Jct. FmRd 624 & US Hwy 281 (TAIC 117); *Starr Co.:* Arroyo Los Alamos, 3 mi. SE Rio Grande City (FMNH 105226); Arroyo El Salado (KU 7747); 6 mi. W El Sauz (BCB 68-841, 842); *Uvalde Co.:* 8 mi. N Uvalde (TCWC 44175, 77176–83); *Webb Co.:* 0–2 mi. W Bruni, along RR tracks (TCWC 39270–76, 41555–61; UTEP 8759); *Willacy Co.:* Raymondville (TCWC 35558); 3 mi. N Raymondville (MVZ 68402). Other significant localities represented by unexamined specimens include: TAMAULIPAS: 1 mi. NW La Pesca (Baker and Webb, 1967). VERACRUZ: Tampico (Taylor, 1935b); 39 mi. and 34 mi. S Tampico (Darling and Smith, 1954). Specimens examined for which the locality data are questionable include: MCZ 93177 (Mategalpa, Nicaragua [sic]); USNM 78581 (TEXAS: Rio Grande, Brule)—I have been unable to locate this placename within a modern county; WW unnumbered, four specimens (TEXAS: *San Patricio Co.:* Welder Wildlife Refuge, HQ area)—circumstances surrounding the capture of the specimens (E. Blacklock, pers. comm.) strongly suggests they were accidentally imported in ornamental vegetation from the lower Rio Grande Valley.

Eumeces tetragrammus brevilineatus (Specimens examined, 330). MEXICO. CHIHUAHUA: 5 mi. N Cerro La Campana (MVZ 70702–03); Santa Clara Canyon, 4.5 mi. (by rd) E MX Hwy 45 (LACM 116401); Sierra del Nido, 4.7 mi. (by rd) W Encinillas (UTEP 62). COAHUILA: 21 mi. NW Ciudad Melchor Muzquiz (EAL 3139); 16 mi. E, 18 mi. N Ocampo (KU 38073); 5 mi. W Piedra Blanca, 5000 ft. (MVZ 58338); 5.3 mi. E Piedra Blanca (UAZ 16815–17); 8 mi. SW Piedra Blanca, 7000 ft. (MVZ 58337); Sierra Madera Jardin (SRSU 864); 2 mi. S Villa Acuña (UIMNH 27136); NUEVO LEÓN: near Sabinas Hidalgo (UIMNH 22441). USA. TEXAS: *Atascosa Co.:* 4 mi. W Jordanton (USL 15433); near Lytle (KU 15564); *Bandera Co.:* 9 mi. S Medina (TCWC 15065); 7 mi. SW Medina on W Fork Medina River (TNHM 1410); 18 mi. NW Medina, Sutton's Ranch (TNHM 1898); 8.4 mi. N Vanderpool on Hwy 187 (LSUMZ 10359); 10.4 mi. W Vanderpool, Hwy 337 (USL 13133); 14.7 mi. W Jct. Hwy 462 on Hwy 470 (USL 13133, 13551, 15680); *Bell Co.:* 7.2 mi. NE Holland along Salado Creek (TCWC 23064); *Bexar Co.:* Helotes (KU 7744, 7764; USNM 10527 [2], 13628); Marnock's Ranch, near Helotes (KU 69018; USNM 10159-B, lectotype, and 10159-A, syntype); 1 mi. N Helotes (MVZ 68397); 7 mi. SE Lytle (CM 18406); 6 mi. NW Rio Medina (CM 58465); San Antonio (KU 8703, 8810–11, 15565); San Antonio, Brackenridge Park (CM 18392); 9 mi. S San Antonio (CM 8466); 8 km ENE Shavano Park, Voight Ranch (UTEP 8873); Somerset (KU 8703); 2.5 mi. N Somerset (BCB 2257); 6 mi. N Somerset, Medina River (CM 18425); 8 mi. SW Somerset (BCB 3351); Von Ormy (CM 18377); *Blanco Co.:* 4.5 mi. SE Johnson City (TCWC 8942); 6 mi. S and 3.4 mi. E Johnson City (UTEP 165); *Bosque Co.:* 2 mi. S Mosheim, Mid Fork Bosque River (TCWC 36932, 38740–43); 3 mi. N Osage (TCWC 14242); *Brewster Co.:* Alpine (SRSU 223, 343); 3 mi. SW Alpine (KU 7768–70); 20 mi. S Alpine (SRSU 453); Big Bend Natl. Park (BBNP), Boquillas Ranger Station (UNM 9974); BBNP, base of Burro Mesa (UNM 9972–73); BBNP, Casa Grande (TCWC 16052); BBNP, Government Springs (UNM 20843); BBNP, Government Wells (UNM 18239–40); BBNP, Grapevine Springs (TCWC 16045); BBNP, south of Moss Well, 5000 ft. (UNM 5900); BBNP, Oak Canyon, 4000 ft. (UNM 20846); BBNP, Panther Jct. (UNM 6555); Chisos Mts., E slope (KU 13200); Chisos Mts., Basin, 6000 ft. (TCWC 1113); Chisos Mts., Green Gulch (TCWC 16050); Chisos Mts., Mt. Emory, 8000 ft. (KU 12748); Chisos Mts., Pine Canyon (TCWC 14269); 16.2 mi. NW La Linda, Coahuila (EAL 3238); 60 mi. S Marathon, Black Gap Wildlife Mgmt. Area (TCWC 20161; TNHM 12939, 12987); Glass Mts., 5 mi. N Marathon (KU 13199); Strumbere Ranch (SRSU 3605); *Brown Co.:* 4 mi. W Bangs, US Hwy 67 (TCWC 23446–48); 4 mi. W Brownwood (KU 11387); *Burnet Co.:* "Burnet County" [no further data] (USNM 5877); Burnet (CAS 7409); 8 mi. W Burnet (TCWC 4499–501); *Callahan Co.:* 19 mi. W Cross Plains (TNHM 9738); *Comal Co.:* New Braunfels, Water Rec. Dist. #2 (TCWC 15064); *Comanche Co.:* 5 mi. N DeLeon (TCWC 15266); *Crockett Co.:* 11 mi. E Ozona, US Hwy 290 (ANSU 148); *Dimmit Co.:* near Carrizo Springs, Nueces River (KU 8195–96); *Edwards Co.:* 24 mi. NE Rocksprings (TCWC 4502); *Gillespie Co.:* 15 mi. NE Fredricksburg (TCWC 5545–46); *Hays Co.:* Fern Bank Springs, Little Arkansas (TCWC 31486–87, 36534, 38744); 10 mi. S Oak Hill on Big Bear Creek (TNHM 21179); Pollard Wildlife Refuge (TCWC 38745–49); 4 mi. W San Marcos (TCWC 8941); 7 mi. W San Marcos (FSM 3579); 2 mi. E Wimberly on Cypress Creek (TNHM 8794); 4 mi. E Wimberly (TCWC 27320–24); *Irion Co.:* 11 mi. NW Mertzon (ANSU 2768–69, 2771, 2773, 2790); 12 mi. NW Mertzon (ANSU 4535); 13 mi. NW Mertzon (ANSU 629–30, 871–73); *Jeff Davis Co.:* Cherry Valley (MCZ 12822); 10.6 mi. N Fort Davis, Jones Ranch (TCWC 26108); Nations Canyon (SRSU 688); *Kendall Co.:* 0.5 mi. W Century Caverns (TCWC 38739); 0.5–1.0 mi. S Camp Alzafar (TCWC 30172, 38737–38); *Kerr Co.:* 4 mi. NE Centerpoint (TCWC 181); Kerrville (USL 1716); 15 mi. SE Kerrville (LSU 13676); Kerr Wildlife Mgmt. Area (TCWC 13806); *Kimble Co.:* 2–4 mi. N Cleo (TCWC 38750–53); 2 mi. SW Junction on US Hwy 377 (UTEP 8583); 10 mi. W Junction (ANSU 7153); 15 mi. NW Junction (ANSU 8132); 2.3 mi. S Junction, Schriener Ranch (TNHM 7065); Telegraph, Point Creek and Schiener Ranches (TNHM 7003–05); *Kinney Co.:* Ft. Clark (USNM 25445); *Live Oak Co.:* 6 mi. E George West on Nueces River (TAIC 258.1–.2); 3 mi. W Three Rivers (TCWC 10535–36, 10538); 8 mi. W Jct. FmRd 624 & US Hwy 281 (TAIC 123.2–.3); *Mason Co.:* 20 mi. ESE Mason (TCWC 31047–50); 8 mi. S Mason (TCWC 3105); 10 mi. S Mason (TCWC 31052–53; *Maverick Co.:* Mangus Ranch, S of Eagle Pass (TAIC 2473, [2]); *McClennan Co.:* Bluff Creek, 0.5–2 mi. W Crawford (FMNH 46757–58, 46762); near Crawford (FMNH 46759); *McMullen Co.:* 5.6 mi. W Whitsett (TCWC 39267); 7.9 mi. W Whitsett (TCWC 39266); *Medina Co.:* "Medina County" [no further data] (USNM 42307); 5 mi. N Hondo (TCWC 14621); 3 km ENE Mico, 1200 ft. (UTEP 9481); *Nueces Co.:* 10 mi. W Corpus Christi (TCWC 18175); *Palo Pinto Co.:* BSA Camp Constantine (TCWC 25271); 10 mi. W Graford (ANSU 7154); 10 mi. S Mineral Wells (TCWC 406); 2.8 mi. N Palo Pinto (TNHM 13503); *Pecos Co.:* 11 mi. E Bakersfield (SRSU 771); Fort Stockton (SRSU 1412); near Iraan (TNHM 33380); 1.4 mi. W Sheffield on US Hwy 290 (UTEP 8584); *Presidio Co.:* Chinati Mts., Pinto Canyon (SRSU 524); 11 mi. W Valentine, CE Miller Ranch (TNHM 1124, 2876, 3257, 3298–99, 3395, 4256, 4283); *Regan Co.:* Best (ANSU 2745–47); 15 mi. W Big Lake (ANSU 528); 9 mi. W, 12 mi. S Big Lake, 2500 ft. (ANSU 7166–69, TCWC 31355–58); *Real Co.:* 14.4 mi. E Jct. US Hwy 83 on FmRd 337 (USL 16378); *San Saba Co.:* Gorman Falls Camp, 6 mi. SE Bend (ANSU 141, 144, 2799–800, 5525, 5629, 5264); San Saba (ANSU 2916, 4064–74); 1 mi. S San Saba (ANSU 2968); 12 mi. E San Saba (TNHM 28837); 20 mi. NNW San Saba (TNHM 9697); *Schleicher Co.:* "Schleicher County" [no further data] (ANSU 2729); 5 mi. S Christoval (ANSU 145); 12 mi. S Christoval (ANSU 146); *Shackleford Co.:* 20 mi. N Albany, Matthews Ranch (UNM 9049); *Sutton Co.:* 5 mi. S Sonora (TNHM 33381); 10 mi. S Sonora (MVZ 38199–200); 26 mi. SE Sonora (USNM 6529); *Terrell Co.:* 27 mi. ESE Dryden (USL 15432); 13 mi. S Sheffield (TNHM 7588, 7612, 7678, 7777); 15 mi. S Sheffield, Blackstone Ranch (TNHM 7105); 18 mi. S Sheffield (TNHM 8131–33); 21 mi. S Sheffield (TNHM 7920, 7948); 30 mi. S Sheffield, Chandler Ranch (SRSU 303, 316, 325, 338–40, 2201; TNHM 8314–18, 8054); *Tom Greene Co.:* Christoval (ANSU 1180, 2108–10, 5579); 3 mi. E Christoval, Toe Nail Trail (ANSU 140, 142); 4 mi. S Christoval, Concho River (ANSU 5561); 4.5 mi. S Christoval, Head of River Ranch (ANSU 147, 150); 5 mi. S Christoval (ANSU 149); N Concho Lake (ANSU 279, 3114–15, 3161); Fort Concho (USNM 12777); 4 mi. N Log Cabin Steakhouse Club (ANSU 5274); Nasworthy Lake (ANSU 3035–36); San Angelo (ANSU 3140, 8131); 4 mi. S San Angelo, near Nasworthy Dam (ANSU 143); *Travis Co.:* Austin, Texas Univ. Campus (TNHM 25727); 1 mi. NW Austin, Bull Creek Rd (TNHM 33375); 4 mi. SSW Austin (TNHM 9877); 5 mi. SW Austin, Barton Creek (TNHM 1693, 1936, 5870, 5942); 6 mi. SE Austin (TNHM 32195); 1.5 mi. SE Manchaca (TNHM 21683; Shoal Creek (TNHM 13074–75); 1 mi. upriver from Zilker Park (TNHM 13501); *Uvalde Co.:* near Concan, Bludworth Ranch (SM 5024); 3 mi. E Concan (BCB 7161); 3 mi. N Sabinal (TNHM 4873); 8 mi. N Uvalde (TCWC 44173–74); *Val Verde Co.:* 3 mi. W Comstock, along RR (ANSU 7161); 5.2 mi. N Comstock at Pecos River (ANSU 7156); 12 mi. N Comstock at Pecos River (ANSU 7157–60); 12 mi. S, 11 mi. E Comstock (ANSU 7165); 19.5 mi. SE Comstock (ANSU 7155); 20 mi. SE Comstock, under US Hwy 90 (ANSU 7162–64); near mouth of Devils River (KU 7748); Dolan Falls, Devils River (UNM 5973); Dolan Springs, Fawcett Ranch (UNM 5971–72); 12 mi. NW Del Rio (TNHM 32495); 50 mi. NW Del Rio (MVZ 68398); 60 mi. SW Ozona (ANSU 5448); *Webb Co.:* Laredo (UMMZ 114253); *Wilson Co.:* Cibolo River bottoms (SM 4353, 4355). Other significant localities represented by unexamined specimens include: MEXICO. COAHUILA: 33 mi. N, 8 mi. W San Geronimo (KU 33502); NUEVO LEÓN: 4 mi. W Sabinas Hidalgo (Taylor, 1935b); 31 mi. S Sabinas Hidalgo (Taylor, 1935b). TEXAS: *Coke Co.:* 2 mi. S Blackwell (Brown, 1950); *Coleman Co.:* 22 mi. S Valera, Day Ranch (TCWC 53456–61); *Kinney Co.:* 18.0 mi. N Bracketville (TCWC 46527); *Llano Co.:* 19 mi. SW Llano, FmRd 2323 (TCWC 58480–81); *McCulloch Co.:* 8 mi. N Brady (TCWC 18925); *Menard Co.:* 2.5 mi. E Ft. McKavett, 1800 ft. (TCWC 51196); *Throckmorton Co.:* 19 mi. NW Albany (KU 61796–97). Specimens examined for which the locality data are questionable include: FMNH 106623–26 ("large spring near Sabinas, Hidalgo")—the locality may refer to Sabinas Hidalgo in Nuevo León; TNHM 27810 (OKLAHOMA: 5 mi. SW Colbert); FMNH 27215–17 ("Probably Brownsville, Texas"); BCB nH69-1237, -2181 (TEXAS: *Henderson Co.:* 10 mi. S Athens); FMNH 46760–61 (TEXAS: *Limestone Co.:* between Oletha and Thronton).

Eumeces tetragrammus tetragrammus* × *brevilineatus (Specimens examined, 10). MEXICO. NUEVO LEÓN: Arroyo de las Vacas, 2 km W Hwy 85 at Ranchitos (MVZ 185746). USA. TEXAS: *Jim Wells Co.:* Casablanca, Nueces River (KU 8812); *La Salle Co.:* 2.8 mi W Jct. FmRd 624, FmRd 468, and FmRd 469 (TAIC 643); *Live Oak Co.:* 3 mi. W Three Rivers (TCWC 10537); 8 mi. W Jct. FmRd 624 and US Hwy 281 (TAIC 123.1); *McMullen Co.:* 17 mi. S Charlotte (TNHM 28836); 6.9 mi. S Tilden on State Hwy 16 (LACM 134855); 8 mi. W Whitsett (TCWC 39265); *Uvalde Co.:* 8 mi. N Uvalde (TCWC 44171–72).

Eumeces tetragrammus callicephalus (Specimens examined, 106). MEXICO. CHIHUAHUA: Bavispe River below Three Rivers, Sonora–Chihuahua line (BYU 13145–49, 14233); ca. 2 mi. E Cerocahui (BYU 14248–49); Cuiteco (BYU 14259–61, 14608–10); Guasaremos (MCZ 43389–90); Madera (MCZ 15928); Madronoi, W Rim, between Urique and Cerocahui (BYU 14338); 8 mi. W Matachic (AMNH 68295); Pacheco (MVZ 46672); 3 mi. NE Temoris (KU 51462). JALISCO: 38.2 mi. NW Guadalajara on MX Hwy 15 (FSM 12844–45); Hostotipaquillo (AMNH 17943); near

Magdalena (FMNH 106357–58); 3 mi. NE Magdalena (KU 38069). NAYARIT: 6 mi. SE Ahucatlan (UMMZ 118530); 7.1 mi. N Compostela, 3200 ft. (FSM 28999); Rosamorada (AMNH 15488); Mt. San Juan Tepec (FMNH 106359); Laguna Santa Maria del Oro, 2350 ft. (AMNH 96608); 19.6 mi. E Santa Cruz (CAS 95518); Santiago Ixcuintla (AMNH 19305–06); 12 mi. SW Santiago Ixcuintla (FSM 19305–06); 5 mi. NE Sentispac (AMNH 87673–77, 87974); 23.1 mi. E Tepic (MVZ 71259); 29 mi. SW Tepic at Crater Lake (BCB 64-1331). SINALOA: 16 km NNE Choix, 1700 ft. (KU 73745); vic. El Dorado (BCB 66-1381); La Cruz (LACM 6768); 1 mi. N Mazatlan (UTEP 4863–65); 2 mi. E Mazatlan (CAS 104975–77); 5 mi. N Mazatlan, along Sabalo Beach Rd (AMNH 87672); Sierra Surutato, 0.5 mi. (by rd) SE Los Hornos, ca. 1920 m (CAS 155910, 155913); Sierra Surutato, Canon de Tarahumare between La Joya and Baranca de las Tahonitas, ca. 1310 m (CAS 155911–12); Teacapan (LACM 6769–70); 24.8 mi. (by MX Hwy 40) E Jct. MX Hwy 15 (CAS 11483). SONORA: Alamos (AMNH 64219; UAZ 3468); 7 mi. SE Alamos, Arroyo Cuchujaqui (MVZ 72602); N Slope Alamos Mt., Las Higueras Creek (UAZ 3472); stream above Alamos on Sonora–Chihuahua border (MVZ 74186); Arispe, 840 m (UAZ 3471, 3473–74); Guirocoba, Cienigitas (MVZ 50735); 9 mi. NNE Imuris, 1000 m (KU 50633); 9.4 mi. by rd from Huertas (UAZ 11310–11); ca. 28 mi. E Nacozari, Presa de Rebeico (UAZ 11309); 36 mi. ENE Nuri, 3600 ft. (UAZ 3467); upper fork Nutria Creek (BYU 13140–41); 2 mi. E Santa Ana on rd to Yecora (UAZ 28193–94); above Santa Maria Mine (UMMZ 78124); 0.5–1.0 mi. SW Yecora (UAZ 16598); Rio Zatachi, 2930 ft. (UAZ 3475). USA. ARIZONA: *Cochise Co.:* Huachuca Mts. (CAS 48095–96, 80747); Huachuca Mts., Ash Canyon (KU 6473–76); Huachuca Mts., Copper Canyon (FMNH 46117); Huachuca Mts., Hunter Canyon, 5640 ft. (UAZ 16734); Huachuca Mts., Ramsay Canyon (UMMZ 71029); N Ridge Hunter Canyon, Short Springs (UAZ 16737); *Pima Co.:* Baboquivari Mts., Brown Canyon (AMNH 86573); Baboquivari Mts., Elkhorn Ranch, 3750 ft. (UAZ 7166); *Santa Cruz Co.:* Pajarito Mts., Peña Blanca Canyon (AMNH 15063); Pajarito Mts., Peña Blanca Springs (MVZ 49838, 53877; CAS 84125); Pajarito Mts., Walker Canyon, 1.5 mi. N Ruby Rd, Rockwell Camp, 3750 ft. (UAZ 19834, 30607–08); Santa Rita Mts., Madera Canyon (AMNH 64342; LACM 5929); Sycamore Canyon, 3800–3960 ft. (UAZ 3466, 3419; MVZ 50736). NEW MEXICO: *Hidalgo Co.:* Guadalupe Mts., Guadalupe Canyon, 4500 ft. (KU 74332–34). A significant locality represented by an unexamined specimen is: MEXICO. ZACATECAS: Mesquital del Oro (Taylor, 1935b). Specimens examined for which the locality data are questionable include: ANSP 13604–05 (MEXICO. GUANAJUATO: Guanajuato).

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CONTRIBUTIONS IN SCIENCE

SYSTEMATICS OF THE SOUTH AMERICAN FRESHWATER FISH GENUS *ADONTOSTERNARCHUS* (GYMNOTIFORMES, APTERONOTIDAE)

Francisco Mago-Leccia, John G. Lundberg, and
Jonathan N. Baskin

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SYSTEMATICS OF THE SOUTH AMERICAN FRESHWATER FISH GENUS *ADONTOSTERNARCHUS* (GYMNOTIFORMES, APTERONOTIDAE)

Francisco Mago-Leccia,[1] John G. Lundberg,[2] and Jonathan N. Baskin[3]

ABSTRACT. The apteronotid fish genus *Adontosternarchus* Ellis, 1912, is revised, and characters are presented as evidence for the monophyly of the genus and of the interrelationships of its member species. Four species are recognized of which two are described as new: *A. sachsi* (Peters, 1877), *A. balaenops* (Cope, 1878), *A. devenanzii* new species, and *A. clarkae* new species. The known distribution of each species is plotted and a key to species is provided. Recent collections in channels of the lower Orinoco River show *A. sachsi* and *A. devenanzii* to be extremely abundant.

RESUMEN. Este trabajo es una revisión sistemática del género apteronótido *Adontosternarchus* Ellis, 1912, e incluye la presentación de caracteres que evidencian su condición monofilétiea, asi como también una hipótesis explícita de interrelaciones entre sus especies integrantes. Se reconocen cuatro especies en el género, de las cuales dos son nuevas para la ciencia: *A. sachsi* (Peters, 1877), *A. balaenops* (Cope, 1878), *A. devenanzii* sp. n. y *A. clarkae* sp. n. La distribución geográfica conocida para cada especie se muestra en mapas. Asi mismo, se señala que colecciones recientes hechas en los canales del Bajo Orinoco revelaron la extraordinaria abundancia de las especies *A. sachsi* y *A. devenanzii.*

INTRODUCTION

The genus *Adontosternarchus* was established by Ellis (1912: 424) to distinguish apteronotids characterized by "Teeth wanting; lower jaw with a distinct V-shaped median groove for the reception of the pointed decurved upper jaw." The type species, by monotypy, and subsequent designation, is *Sternarchus sachsi,* a species described by Peters (1877) based on specimens collected by Dr. Carl Sachs from the Venezuelan llanos, near San Fernando de Apure. Ellis referred to *A. sachsi* all material of *Adontosternarchus* available to him from the Amazon basin. In 1942 Eigenmann and Allen added *Adontosternarchus balaenops* (Cope), a species based on a single poorly preserved specimen from Perú.

Recently we made large collections of *Adontosternarchus* from the Orinoco Delta and middle Orinoco that disclosed the presence there of two species. Further study demonstrated a basis for recognizing four species in the genus. Only part of the material treated by Ellis represents *A. sachsi.* The fish he illustrated (1913: pl. 22, fig. 3; see our Fig. 9) as *A. sachsi,* and others in the same series, are *A. balaenops,* although he referred the name *balaenops* to *Sternarchella.* We redescribe *A. sachsi* and *A. balaenops,* and describe two additional species as new. One of these is the common middle Orinocan form modern workers have called *A. sachsi* (Mago-Leccia, 1967, fig. 10; 1970). The other was discovered among specimens provided to us by Ms. Kate Clark from the Río Negro, Venezuela, near the Brazilian border, and now is known to be widespread in the Amazon system.

METHODS AND MATERIALS

Specimens, carefully straightened and pinned down, were measured with Helios dial calipers. Head measurements were made under low power magnification. Gymnotiform fishes often suffer damage (predation) to the tail region. Most wounded fish are recognized by their truncated, or abruptly narrowed and/or abruptly depigmented tails, but some individuals often remarkably regenerate the lost tail and fins. Despite careful external examination, apparently nearly complete regeneration occurred in some individuals in our measured samples. These fish are recognized as outliers on the low ends of the scales for measurements involving the tail but otherwise they have near average measurements. This problematic element of morphometric variation makes difficult both the preparation and the use of identification keys. Persons working with gymnotiform fishes should be aware of cryptically damaged but partly regenerated fish. The di-

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agnostic measurements are: Total length (abbreviated TL), length from snout to end of base of anal fin (abbreviated LEA), length of anal fin base, distance from tip of snout to origin of dorsal thong (a fleshy, ray-less filament attached to back over about last third of anal fin and the tail base; minor dissection is often necessary to locate thong's origin), length of tail (starting from posterior end of anal fin base), length of caudal peduncle, distance from snout to origin of anal fin, snout to vent distance, greatest body depth, head length (taken to upper end of soft opercular membrane), eye diameter, distance from snout tip to rictus, and size of branchial opening.

Counts of anal, caudal, and pectoral fin rays were taken with strong transmitted light and include all elements. Vertebral counts (all from radiographs) begin with the first free vertebra behind the compound Weberian complex. This is the first one bearing a full neural spine. The last one counted has its hemal spine immediately behind the base of the last anal fin ray.

Abbreviations used for various institutions are: Academy of Natural Sciences, Philadelphia (ANSP), American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Carnegie Museum (CM, material now at FMNH), Duke University (DU), Field Museum of Natural History (FMNH), Ministerio de Agricultura y Cría, Estación de Puerto Ayacucho, Venezuela (MAC-PAY), Museo de Biología de la Universidad Central de Venezuela (MBUCV), Museum of Comparative Zoology, Harvard University (MCZ), Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP), National Museum of Natural History, Smithsonian Institution (USNM), Natural History Museum of Los Angeles County (LACM), University of Michigan Museum of Zoology (UMMZ), and Berlin Museum (ZMB).

Adontosternarchus Ellis

Adontosternarchus Ellis, 1912:424 (in Ellis, 1912, type species: *Sternarchus sachsi* Peters, 1877, designated subsequently in Ellis, 1913:155 by monotypy).

The valid name *Adontosternarchus* was first published by Ellis (1912) in Eigenmann's monograph on the freshwater fishes of British Guiana. The name and diagnostic characters appeared just once in a key to genera said to inhabit Guianan waters. No *Adontosternarchus* species has been recorded from British Guiana. In his 1913 revision of gymnotiform fishes Ellis provided what he clearly intended to be the original description of this genus and discussion of the only recognized species, *A. sachsi.*

DIAGNOSIS. Apteronotid fishes with a unique beak-like, terminal mouth in which the margin of lower jaw is strongly curved to form a V-shaped notch across the mandibular symphysis flanked by elevated flanges and, in turn, the snout is curved downward into notch of mandibles, and the margin of the upper jaw is concave to received the lower. Other diagnostic features are the absence of teeth at least in individuals over about 30 mm TL, and the slightly to markedly bulbous chin.

DESCRIPTION. Body compressed and moderately elongate; dorsal profile of body nearly straight to gently convex; ventral profile of body strongly convex to nearly angular at anal fin origin, nearly straight behind; anal fin origin about under branchial opening; lateral line complete.

Head small, slightly compressed to rounded; its dorsal profile variable, ventral profile nearly straight; mouth small; rictus in advance of center or margin of small eye; chin rounded to bulbous and projecting. The margin of lower jaw is strongly curved to form a V-shaped notch across the mandibular symphysis flanked by elevated flanges and, in turn, the snout is curved downward into notch of mandibles and the margin of the upper jaw is concave to receive the lower.

Eye small; anterior nostril located about midway between tip of snout and anterior margin of eye, opening at end of a short tube; posterior nostril without a tube and located above and slightly in front of anterodorsal margin of eye; branchial membranes joined to isthmus; branchial opening restricted to a short oblique slit in front of base of pectoral fin; anus and short urogenital papilla (both sexes) adjacent, located in large adult fish between raised rims of united branchial membranes, their positions shift relatively forward with growth (Fig. 12).

Anal fin elongate with 135–185 rays (Table 2); caudal and pectoral fins small with 10–22 rays and 12–18 rays respectively (Table 1); body and base of caudal fin scaled; head, fin membranes, and dorsal thong lacking scales; 4–8 rows of enlarged cycloid scales along the flanks, including the pored lateral line scale row; small scales above large scales to dorsal midline, below to anal fin base and onto breast; scales of lower flanks with free ventral or ventroposterior margins, other scales with free posterior margins.

Salient osteological features of *Adontosternarchus* are: premaxillary bone small and connected to maxillary by a long ligament; maxillary bone elongate (Figs. 2A,3); infraorbital series represented only by bony, superficial tubes; supratemporal and pterotic canals of the laterosensory system of the head represented by free bony tubes (Fig. 3); posttemporal fossae absent; cranial fontanelles present, the interfrontal shorter and broader than the interparietal; lateral ethmoids and vomer present; mesopterygoid bone short, edentulous and with a well-developed, ascending process which articulates with orbitosphenoid; preopercular bone broad (Fig. 3); pectoral girdle without mesocoracoid (Fig. 6); cleithrum broad; scapular foramen absent; coracoid with a long ventral process which fails to reach the cleithral symphysis; posttemporal fused to supracleithrum; 4 pectoral radials; 5 branchiostegal rays, the last two greatly broadened, the three anterior more slender (Fig. 4); urohyal small; gill-rakers reduced to small bony nodules covered by cartilage; 3 infrapharyngobranchials, the posteriormost one cartilaginous; 5 epibranchials, the fifth one cartilaginous; upper pharyngeal tooth plate present, strongly connected by a ligament to epibranchial 3 (Fig. 5); 53–64 vertebrae to base of last anal fin ray (Table 4); Weberian apparatus without claustrum.

ETYMOLOGY. Greek *a* = without + *odons* = tooth + *sternon* = breast + *archos* = anus. Gender masculine.

MONOPHYLY AND RELATIONSHIPS. It is not our purpose in this paper to accomplish a phylogenetic analysis

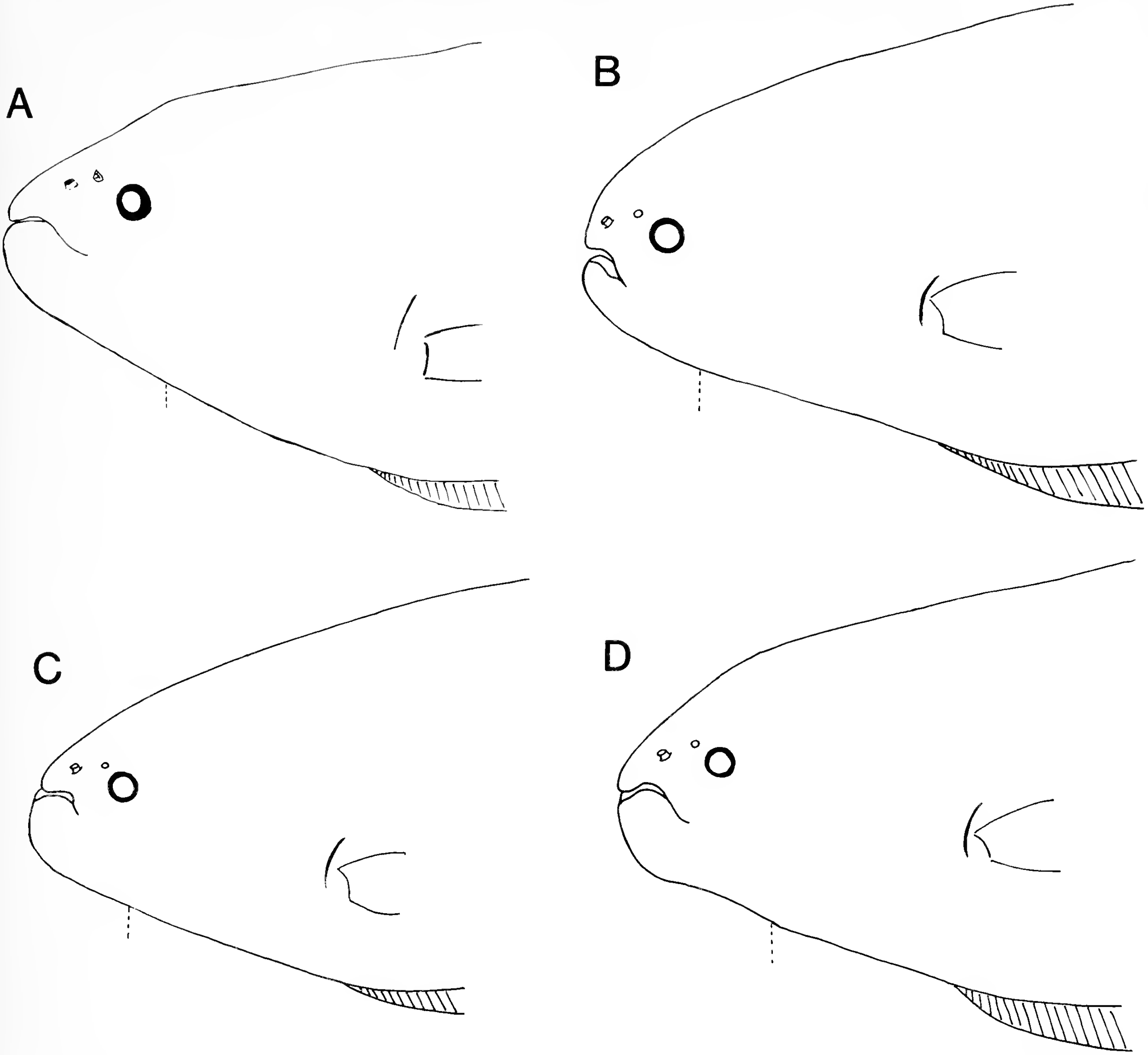


Figure 1. Head profiles of *Adontosternarchus* species. A, *A. balaenops;* B, *A. devenanzii;* C, *A. clarkae;* D, *A. sachsi.* Dotted line indicates position of anus.

of the Apteronotidae. One of us (FML) is engaged in a study of that broader subject. However, it is important for future phylogenetic work to point out the evidence for the monophyly of the genus *Adontosternarchus.* The hypothesis of exclusive common ancestry of the four species of *Adontosternarchus* is supported by the two features used by Ellis to erect the genus, i.e., (1) the form of the beak-like snout, bulbous chin and curved mouth (Fig. 1), and (2) the much reduced dentition (Figs. 2, 3). The odd form of the chin is due to the presence of an accessory electric organ formed from sensory nerve fibers (Bennett, 1971). Additionally, we mention the small size of the upper jaw elements, and the elongate premaxillary-maxillary ligament (Figs. 2, 3). Based upon comparisons with other apteronotids and gymnotiforms these characteristics appear to be uniquely shared by the species of *Adontosternarchus.* Of these features only the nearly complete absence of teeth (present only in juveniles) is approached by some other apteronotids (e.g., *Sternarchogiton* and an undescribed form from the lower Orinoco have lost upper jaw teeth but retain dentary teeth) but these taxa do not present facial or gnathal similarities to *Adontosternarchus* which can be interpreted as synapomorphies.

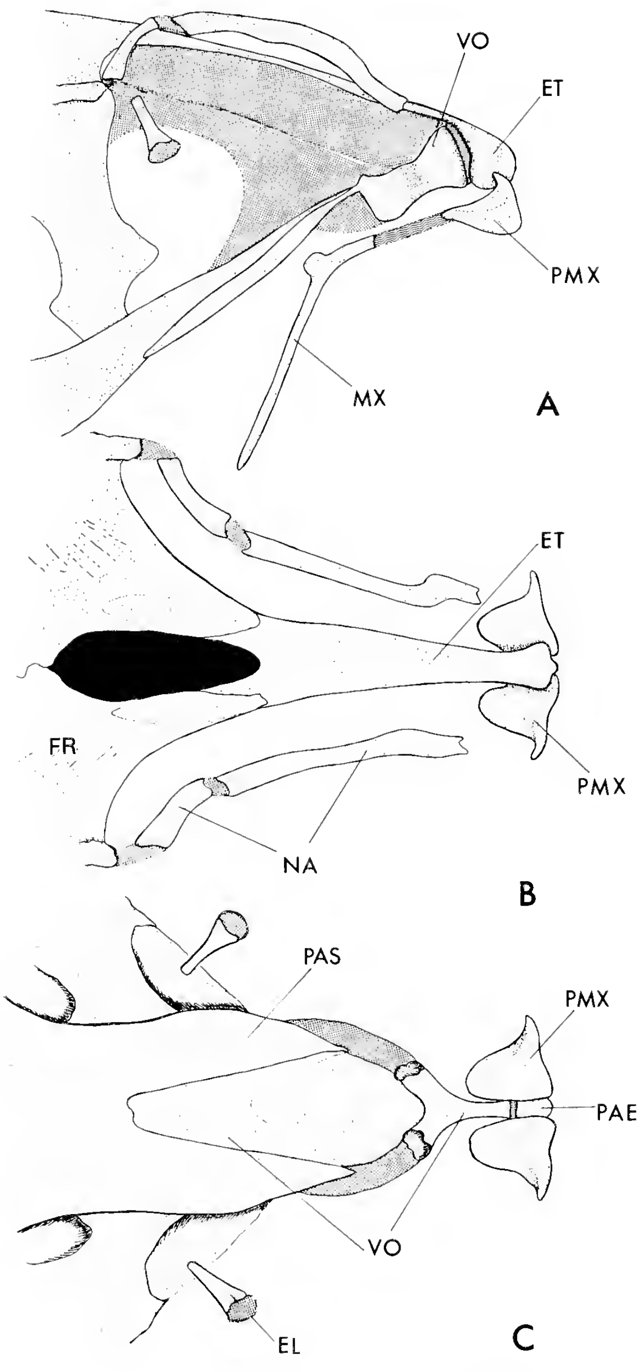


Figure 2. Snout region of *Adontosternarchus devenanzii* sp. n. 120.0 mm TL, MBUCV-V-4772. A, lateral view; B, dorsal view; C, ventral view. EL lateral ethmoid, ET ethmoid (=mesethmoid), FR frontal, MX maxillary, NA nasal, PAE anterior piece of ethmoid, PAS parasphenoid, PMX premaxillary, VO vomer.

Certain aspects of morphometric and coloration diversity among the species of *Adontosternarchus* suggest the following hypothesis of interrelationships. *A. sachsi* is taken to be the sister taxon of the three species *A. balaenops, A. devenanzii,* and *A. clarkae* which share a distinctive, boldly mottled color pattern on the back and sides (Figs. 7, 8, 14, 16). The pigmented blotches of this pattern are irregular in outline and generally cover areas larger than a single scale. *A. sachsi* has a nearly uniform coloration of the sides (Fig. 19) although the scale margins are often darker than their centers. This uniform pattern appears certainly to be the primitive condition in *Adontosternarchus* based on outgroup comparison to other apteronotids (*Apteronotus, Porotergus, Sternarchella, Sternarchogiton, Sternarchorhamphus,* and *Sternarchorhynchus*). The relatively deep body form and short tails of *A. balaenops* and *A. devenanzii* (Figs. 10, 11 and species diagnoses) are considered shared derived similarities based on outgroup comparisons; thus these are hypothesized to be sister species. *A. clarkae* and *A. sachsi* are shallower in relation to length and their tails are relatively long, more like the other apteronotids examined. *A. balaenops* and *A. devenanzii* each have their own phyletically advanced color pattern element. *A. balaenops* possesses black anal and pectoral fin membranes. *A. devenanzii* has a narrow pale or yellow stripe along the midline from the chin or snout to the base of the dorsal thong. Other *Adontosternarchus,* most other apteronotids (some species of *Apteronotus* and *Sternarchorhamphus* have black fin membranes; *Apteronotus albifrons* and *Sternarchorhynchus curvirostris* have broad, light, mid-dorsal stripes), sternopygids and rhamphichthyids lack these species-specific novelties. At this time we have not identified uniquely derived character states for either *A. clarkae* or *A. sachsi.*

In the context of our hypothesis on species interrelationships and their geographic ranges, *A. balaenops* (central Amazon) and *A. devenanzii* (middle and lower Orinoco) are sister species which arose in allopatry. Because *Adontosternarchus* is not present in the Guianas it seems likely that the Casiquaire served as the dispersal route for the common ancestor of *balaenops* and *devenanzii* between the Orinoco and Amazon although the basin of its origin is uncertain. Collection records suggest that these species are restricted now to lowland large rivers and lagoons, and perhaps the steeper gradients of the upper Orinoco mitigate against secondary contact.

A. clarkae is widespread in the upper parts of major Amazon tributaries. This species is sympatric with *A. sachsi* in the Río Negro and with *A. balaenops* in the Peruvian Amazon. *A. sachsi* is known to occur with *A. devenanzii,* both in great numbers, and *A. sachsi* is expected to be found with *A. balaenops.* The broader distributions of the phylogenetically older species of *A. clarkae* and *A. sachsi* do not suggest simple hypotheses on their speciation pattern and biogeographic history.

KEY TO SPECIES OF *ADONTOSTERNARCHUS*

1a. Tail short (character not applicable to damaged or regenerated individuals), head length contained less than two times in caudal peduncle length; body depth below origin of dorsal thong greater than or equal to least distance between eye and pectoral fin base; anal and pectoral fin membranes dark, or, a pale stripe on dorsal midline 2

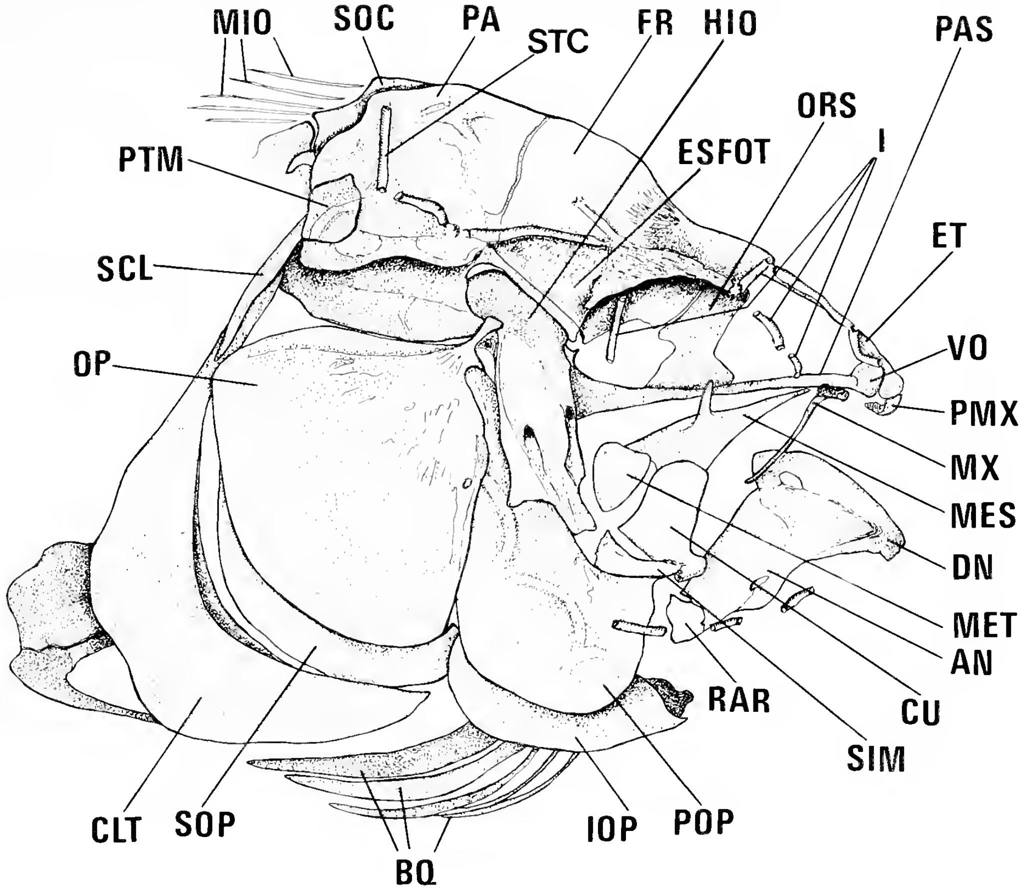


Figure 3. Head skeleton and pectoral girdle of *Adontosternarchus devenanzii* sp. n. 120.0 mm TL, MBUCV-V-4772. Lateral view of right side. AN angular, BQ branchiostegal rays, CLT cleithrum, CU quadrate, DN dentary, ET ethmoid (=mesethmoid), ESFOT sphenotic, FR frontal, HIO hyomandibular, I infraorbitals, IOP interopercular, MES mesopterygoid, MET metapterygoid, MIO intermuscular bones, MX maxillary, OP opercular, ORS orbitosphenoid, PA parietal, PAS parasphenoid, POP preopercular, PMX premaxillary, PTM posttemporal, RAR retroarticular, SCL supracleithrum, SIM symplectic, SOC supraoccipital, SOP subopercular, STC supratemporal sensory canal, VO vomer.

1b. Tail long, head length usually contained more than two times in caudal peduncle length; body depth below origin of dorsal thong less than or equal to least distance between eye and pectoral fin base; anal and pectoral fin membranes hyaline and no pale stripe on dorsal midline 3

2a. Interradial membranes of anal and pectoral fins darkly pigmented with black or brown melanophores; no pale stripe on dorsal midline; chin bulbous, often projecting beyond snout; head profile nearly straight (Fig. 1A) .. .. *A. balaenops* (Cope), Amazon Basin

2b. Interradial membranes of anal and pectoral fins hyaline; a pale (yellow in life) stripe present on dorsal midline, from snout (chin in most specimens) to near origin of dorsal thong; chin rounded and little projected; head profile rounded (Fig. 1B) .... *A. devenanzii* new species, Orinoco Basin

3a. Back and sides mottled with brown spots; anal rays (135?) 143–163 (Table 2); total pectoral rays 12–15 (Table 1); snout length usually greater than interorbital distance (snout 1.04–1.28 times interorbital width); body deeper, maximum depth contained 3.6 to 5.1 times in distance from snout to origin of dorsal thong (Fig. 9) .... *A. clarkae* new species, Amazon Basin

3b. Back and sides nearly uniform brown (scale margins have denser concentration of melanophores); anal rays 153–185 (Table 2); total pectoral rays 14–17 (Table 1); snout length usually less than interorbital distance (snout 0.80–1.04 times interorbital width); body shallower, maximum body depth contained 4.5–5.8 times in distance from snout to origin of dorsal thong (Fig. 9) .... *A. sachsi* (Peters), Orinoco and Amazon Basins

Adontosternarchus balaenops (Cope, 1878)

Figures 1A, 7–13

Sternarchus balaenops Cope, 1878:682 (original description, single specimens). Eigenmann and Eigenmann, 1891:62 (listed).

Sternarchella balaenops. Eigenmann and Ward, 1905:164

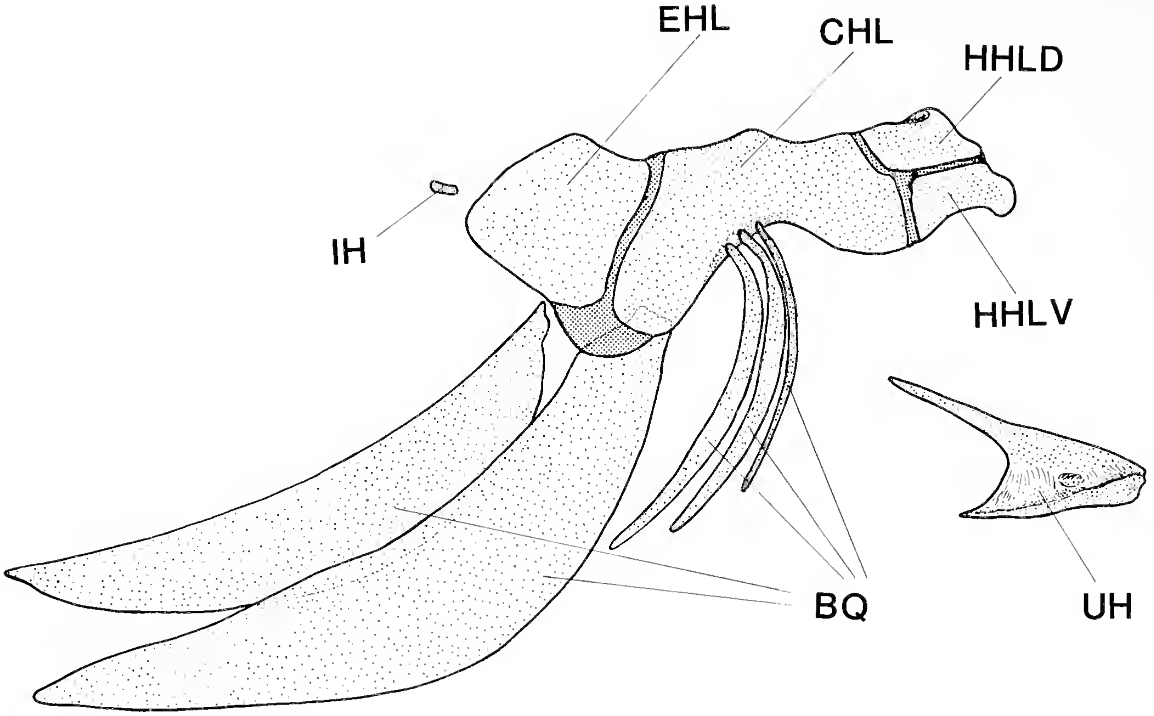


Figure 4. Lateral view of the right lower hyoid apparatus of *Adontosternarchus devenanzii* sp. n. BQ branchiostegal rays, CHL ceratohyal, EHL epihyal, HHLD dorsal hypohyal, HHLV ventral hypohyal, UH urohyal, IH interhyal.

(new combination, listed). Eigenmann, 1910:448 (listed). Ellis, 1913:152 (copy of original description, bibliography). Fowler, 1915: second page (characters). Fowler, 1943:121, fig. 68 (profile of type, bibliography). Fowler, 1945:184, fig. 68 (reprint of Fowler, 1943). Fowler, 1951:428 (bibliography).

Adontosternarchus sachsi. Ellis, 1913:156, pl. xxii, fig. 3 (in part, Bolivia, San Joaquin, Río Machupo). Eigenmann and Allen, 1942:326 (in part, Perú, Iquitos). Fowler, 1939:278 (characters of single specimen, Perú, near Contamana, Río Ucayali). Fowler, 1951:423, fig. 465 (copied from Ellis, 1913).

Adontosternarchus balaenops. Eigenmann and Allen, 1942: 327 (new combination, bibliography).

MATERIAL EXAMINED. Holotype of *Sternarchus balaenops:* ANSP 21462, ca. 165 mm; Perú, Loreto State, Pebas, Amazon River.

PERU: ANSP 83968, TL 138 (tail broken), Loreto State, Ucayali River near Contamana.

BRAZIL: MBUCV-V-11522, 2, LEA 173.8 mm (other length measurements not recorded due to damage); Amazonas State, Lago Janauacá. MBUCV-V-13219, 1, TL 168.9 mm, LEA 150.0 mm (both measurements below normal due to damage and regeneration), and MBUCV-V-13220, 2, TL 190–232 mm; Amazonas State, Rio Solimões, Ilha Marchanteria, Lago Camaleão, 25 km SE of Manaus, María Gercilia Mota. MCZ 9338, 1, TL 182 mm (measurement below normal due to damage and regeneration); Amazonas State, Rio Solimões, Manacapuru. MZUSP 6896, TL 146.8 mm, LEA 138.6 mm (both measurements below normal due to damage and regeneration); Amazonas State, Rio Madeira, 25 km below Nova Olinda. MZUSP 24954, 3, TL 168.1–188.9 mm, LEA 154.2–167.8 mm (measurements below normal due to damage and regeneration); Amazonas State, Rio Solimões, Lago Janauacá and vicinity. USNM 261385, 2,

Table 1. Frequency distributions of pectoral fin ray and caudal fin ray counts in *Adontosternarchus*.

	Pectoral fin rays (one fin counted per fish)							Caudal fin rays												
	12	13	14	15	16	17	18	10	11	12	13	14	15	16	17	18	19	20	21	22
balaenops				2	5	2	1				1		2			3	1	1		
devenanzii			13	11	6								1	4	5	9	7	6	1	2
clarkae	5	7	6	3				1		2	1	6		4						
sachsi			11	19	12	1						1	7	9	6	10	2	1		1

TL 151–163 mm, and USNM 229407, 1, TL 148.8 mm, LEA 136.4 mm (measurements below normal due to damage and regeneration); Amazonas State, Lago do Janauari, Lago Terra Preta.

BOLIVIA: FMNH 54568 (formerly CM 3199), 5 (originally 6), TL 122.6–163.7 mm, LEA 113.5–139.5 mm (both measurements below normal due to damage and regeneration); Beni State, San Joaquin, Machupo. UMMZ 204883, 9, TL 106–124 mm; Beni State, Río Baures, 2 km above mouth.

DIAGNOSIS. Tail and caudal peduncle short, head length contained less than two times in peduncle; dorsal thong does not reach end of anal fin; body deep, maximum depth 222–385 thousandths of length to origin of dorsal thong (see Fig. 9); depth below origin of dorsal thong exceeds or equals least distance between eye and pectoral base; head angular, its dorsal profile sloping in nearly straight or slightly concave line to snout; chin projecting (Figs. 1A, 8), interorbital distance does not reach from eye to tip of chin; distance to anal fin origin 172–233 thousandths of length to origin of dorsal thong; 143–179 anal rays (Table 2); 15–18 pectoral rays (Table 1); 13–21 caudal rays (Table 1); back and sides irregularly marked with spots and blotches; no pale dorsal midline stripe; pectoral and anal fin interradial membranes dark brown or black.

DESCRIPTION. Measurements in thousandths of reference dimension. Body depth about 162–196 of LEA, 225–315 of length to origin of dorsal thong, 190–228 of anal fin base 1108–1521 of head length; depth at nape 152–214 of length to origin of dorsal thong, 767–1032 of head length; dorsal profile of body gently convex, more so behind the head; preanal fin distance 137–167 of LEA, 156–195 of anal fin base, 171–242 of length to origin of dorsal thong (Fig. 11); caudal peduncle 114–161 of LEA, 133–184 of anal fin base.

Head somewhat compressed, its length 171–223 of length to origin of dorsal thong; distance from snout tip to rictus 673–1056 of snout length; chin rounded; end of snout bluntly pointed; snout length 254–295 of head length, 818–1111 of interorbital distance; both jaws edentulous in adults.

Eye diameter 75–115 of head length, 272–406 of snout length, 269–377 of interorbital distance; interorbital distance 254–323 of head length; branchial opening 197–345 of depth at nape, 169–293 of head length; distance from tip of snout to vent 82–95 of LEA, vent shifts relatively anteriad with growth (Fig. 12).

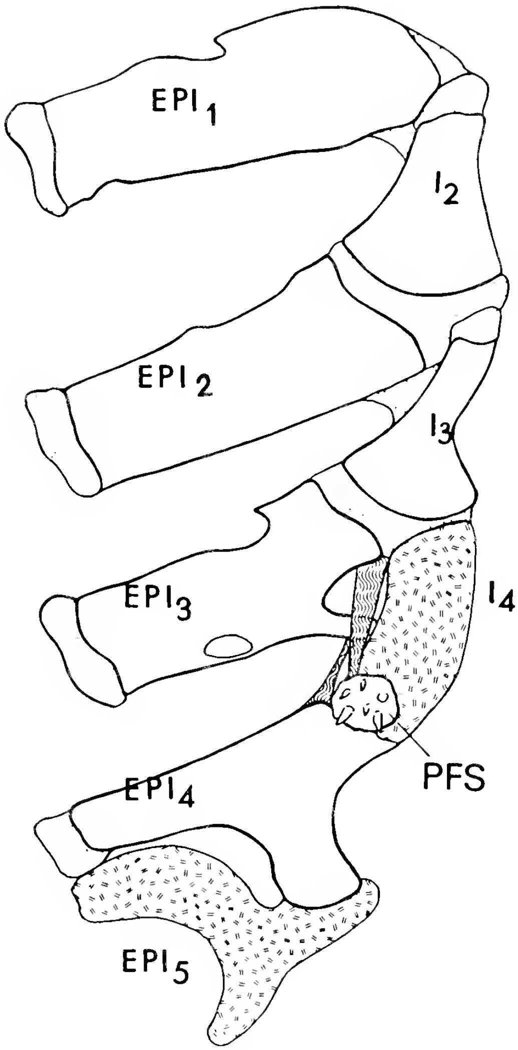


Figure 5. Upper pharyngeal tooth plate (PFS) and associated bones of *Adontosternarchus devenanzii* sp. n. EPI 1–5 epibranchials, I 2–4 infrapharyngobranchials. EPI 5 and I 4 are cartilaginous. I 1 is absent.

Anal fin base about 857–913 of LEA; length of pectoral fin 725–965 of head length.

53–60 vertebrae to base of last anal fin ray.

Background color in alcohol tan to brown; sides and back mottled with brownish-black chromatophores; spots and large

Table 2. Frequency distribution of anal fin rays in *Adontosternarchus*.

	Anal fin rays (grouped by twos)																									
	135	**137**	**139**	**141**	**143**	**145**	**147**	**149**	**151**	**153**	**155**	**157**	**159**	**161**	**163**	**165**	**167**	**169**	**171**	**173**	**175**	**177**	**179**	**181**	**183**	**185**
balaenops					1		1	2	3	2			1	2	1		1	2					1			
devenanzii							2	2	2	8	5	6	4	5		2				1						
clarkae	1				1	3		2	1	6	1	2	2		2											
sachsi										1	1	1		2	4	3	4	4		3	5	3	7		1	1

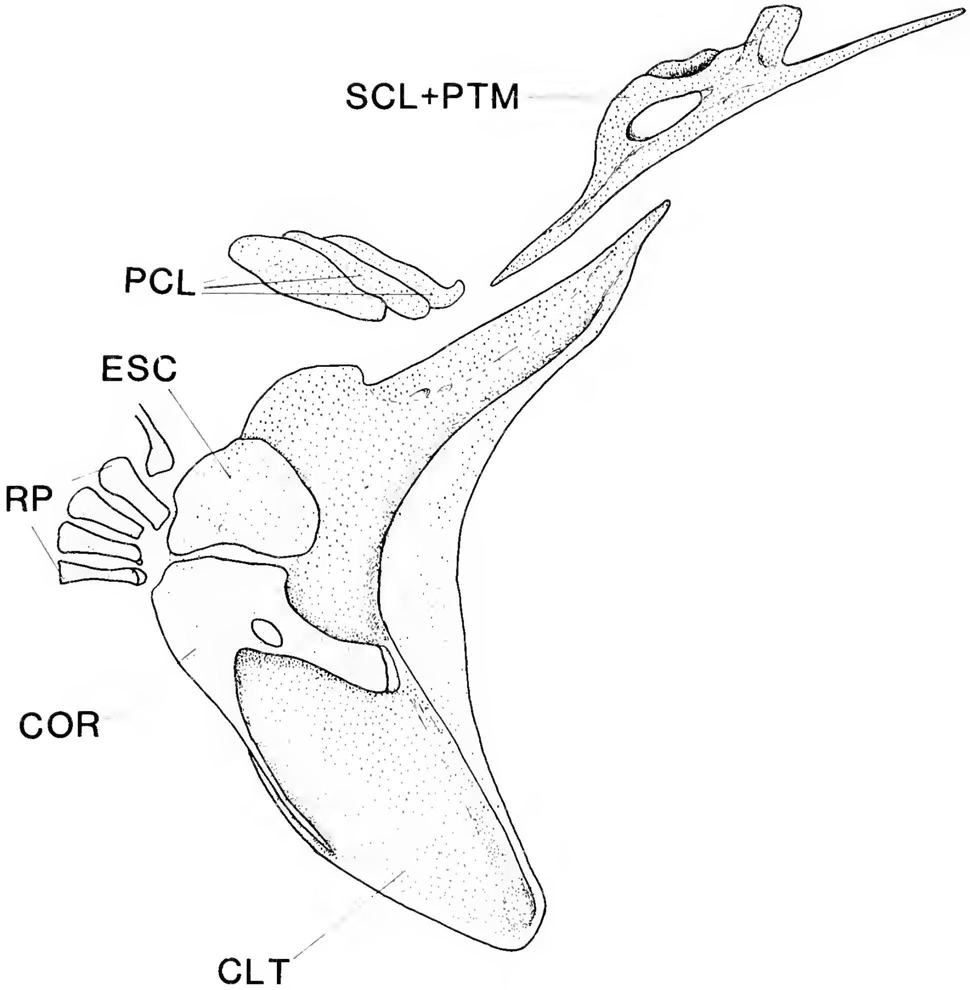


Figure 6. Medial view of the left pectoral girdle of *Adontotosternarchus devenanzii* sp. n. CLT cleithrum, COR coracoid, ESC scapula, PCL postcleithra, PTM posttemporal, RP pectoral radials, SCL supracleithrum.

dense blotches scattered irregularly on sides and dorsum; dorsal midline without a pale stripe; dorsal thong with hyaline ground color but otherwise colored as the back; lateral line sensory canal evident as a thin pale broken line on sides; lower sides with scattered superficial spots underlain with numerous dark, ventroposteriorly oblique lines formed by deep chromatophores and spaces between anal bases; anal fin membrane mostly black but few or no chromatophores over rays; caudal fin (all regenerated in material examined) mostly hyaline or with a light peppering of chromatophores at the base; anal and pectoral fin membranes mostly black except over the rays; top and upper sides of head pigmented as the body, tip of snout with a pale area; chin dusky or pale; lateral margin of upper lip pale; sides and under surface of

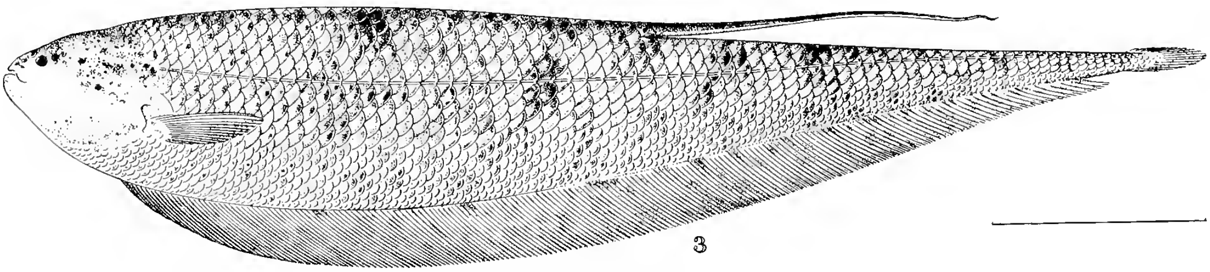


Figure 7. Lateral view of *Adontosternarchus balaenops* (CM 3199, 140 mm); reproduced from Ellis (1913, plate XXII, fig. 3) with permission of the Carnegie Museum.

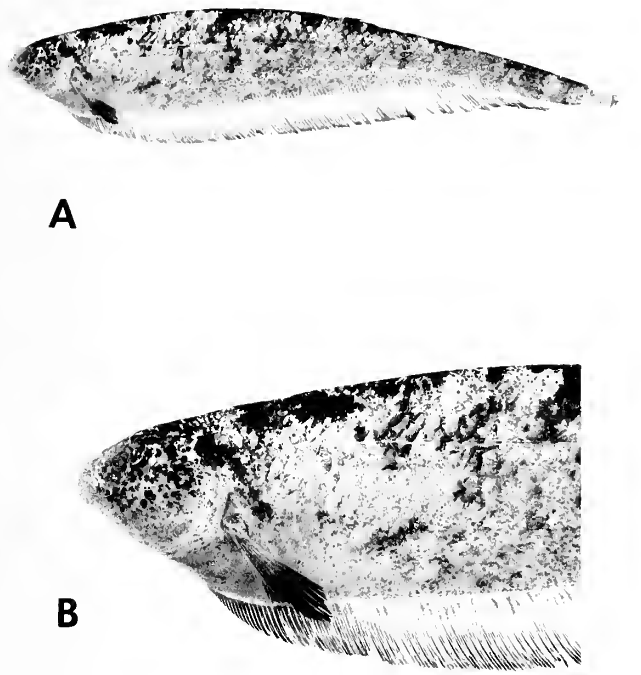


Figure 8. *Adontosternarchus balaenops* (Cope), 174.0 mm TL, Lago Janauacá, Rio Solimões, Amazonas, Brazil. A, entire fish; B, close up of head.

head paler, with variable amount of scattered chromatophores; tube of anterior naris immaculate.

DISTRIBUTION. *Adontosternarchus balaenops* is thus far known from the lowlands (< ca. 200 m elevation) of the Amazon River Basin of Brazil, Perú, and Bolivia (Fig. 13).

REMARKS. The original description of *A. balaenops* was based on a single specimen that had become severely distorted and damaged through desiccation. Ellis, following Eigenmann and Ward (1905), assigned the species to *Sternarchella*, a genus defined in part by the presence of small teeth in both jaws. The holotype, however, shows neither gnathal dentition, nor the nearly straight dorsal profile of *Sternarchella* (Ellis, 1913:151, fig. 14), but does exhibit features of the distinctive snout and jaws of *Adontosternarchus* (Fig. 1). Without explicit justification Eigenmann and Allen (1942) transferred *balaenops* to *Adontosternarchus*. One feature of

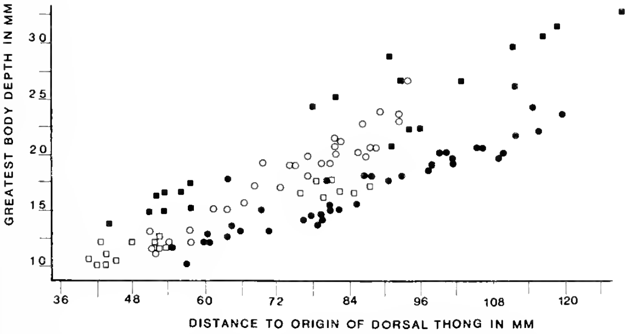


Figure 9. Greatest body depth versus distance to origin of dorsal thong in *Adontosternarchus;* closed squares, *balaenops;* open squares, *clarkae;* closed circles, *sachsi;* open circles, *devenanzii.*

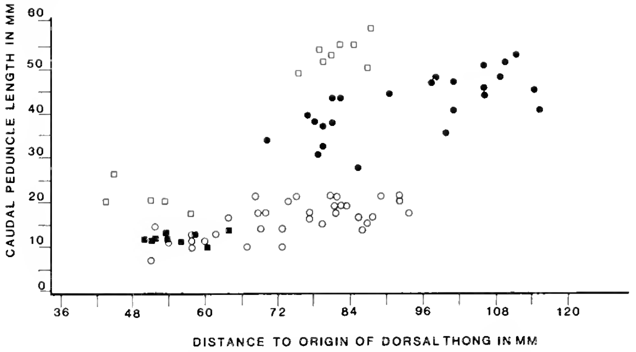


Figure 10. Caudal peduncle length versus distance to origin of dorsal thong in *Adontosternarchus;* closed squares, *balaenops;* open squares, *clarkae;* closed circles, *sachsi;* open circles, *devenanzii.*

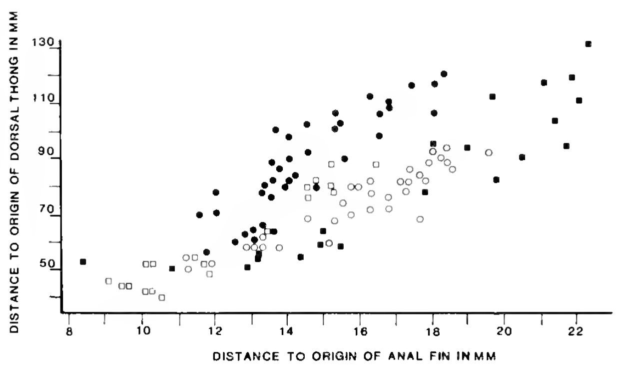


Figure 11. Length to origin of dorsal thong versus distance to origin of anal fin in *Adontosternarchus;* closed squares, *balaenops;* open squares, *clarkae;* closed circles, *sachsi;* open circles, *devenanzii.*

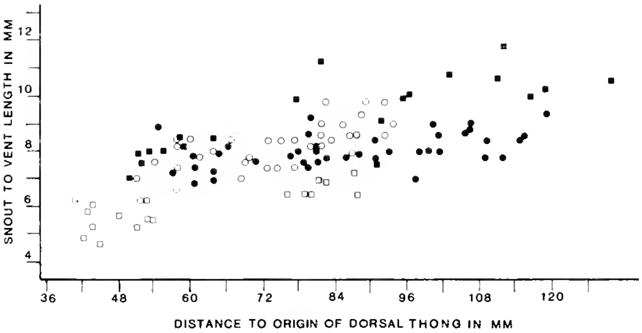


Figure 12. Snout to vent length versus distance to origin of dorsal thong in *Adontosternarchus;* closed squares, *balaenops;* open squares, *clarkae;* closed circles, *sachsi;* open circles, *devenanzii.*

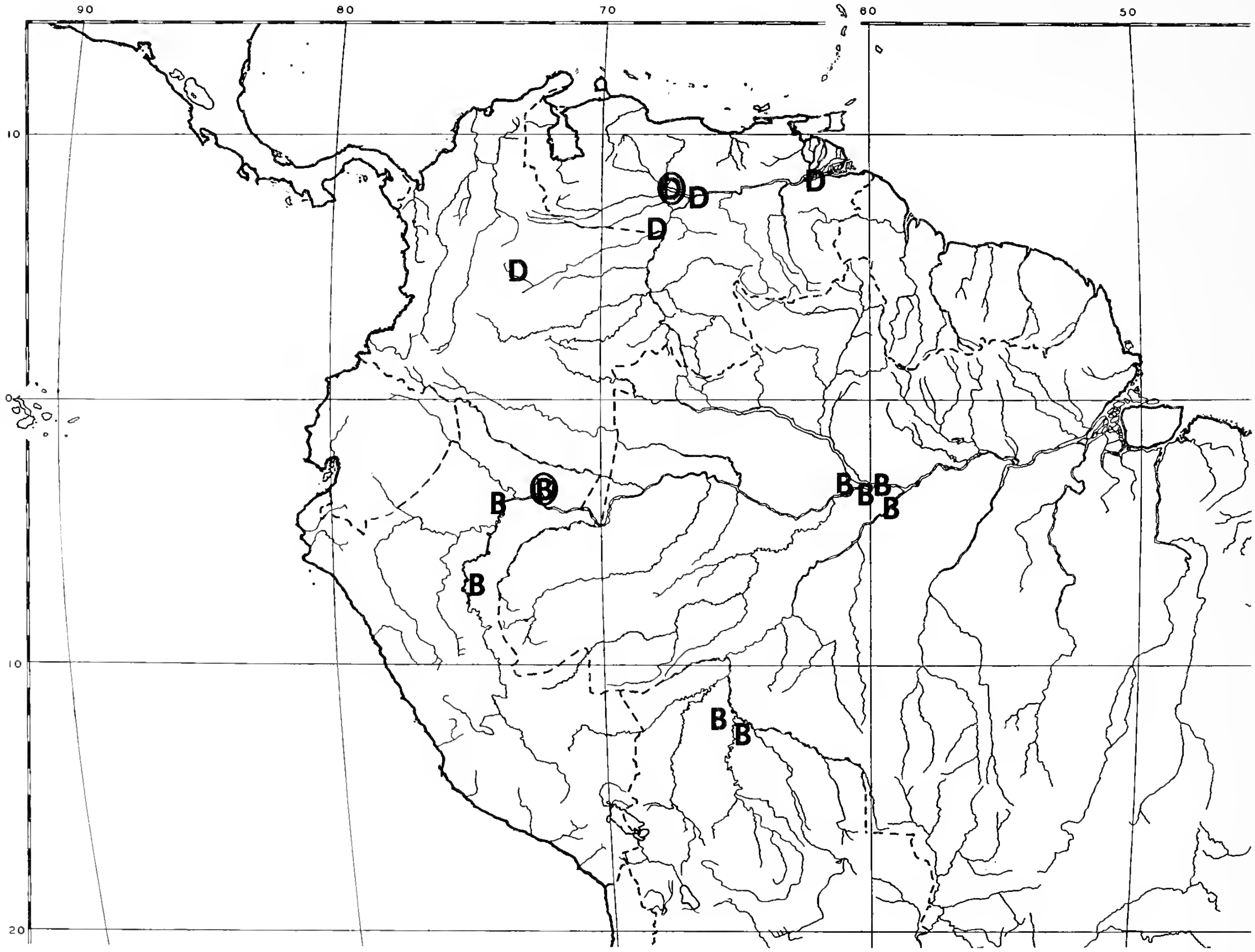


Figure 13. Geographic distribution of *Adontosternarchus balaenops* (B) and *A. devenanzii* (D); circled symbols = type localities; some symbols represent more than one collection locality or lot of specimens (see especially text section on distribution under *A. devenanzii* and Fig. 15).

the holotype that early concerned us as not being a character of *Adontosternarchus* is its concave, rather than bulbous chin. This, however, is clearly a result of desiccation at some point in the specimen's history; we find exactly the same concave chin shape with projecting lower lip in purposely dried specimens of *Adontosternarchus*. We fully agree with Eigenmann and Allen's generic placement of *balaenops*.

Cope's description of the type of *balaenops* offers little help in determining its relationship to the material examined by us. He wrote (1878:682),

> "Profile oblique, with a depression between the orbits; snout short and much narrowed; lower jaw large, projecting beyond the upper both anteriorly and laterally, enclosing the latter somewhat as in a whalebone whale. The fissure of the mouth is short, only reaching the vertical line from the anterior nostril. Eyes small, without free border, much nearer the snout than the gill-opening, one twelfth the length of the head, which latter enters the length without the caudal fin, 8.5 times. The depth at the base of the dorsal thong is equal to the length of the head. Anal radii 171. Scales very large, in only nine longitudinal rows at the base of the dorsal thong. Color olivaceous, with a pale dorsal band which reaches the dorsal thong, and a pale narrow band on each side near the dorsal band. Length 165 mm.; length to origin of anal 20 mm.; length to base of dorsal thong 96 mm.
>
> This species resembles remotely the *S. schotti* of Steindachner, but differs from it and from all the other species in the much enlarged mandible and large scales."

Most of these features suggest only *Adontosternarchus* in general, with some added specimen damage. Cope's count of 171 anal radials (the fin is missing) may be accurate but it falls within the anal fin ray count range of the two of the other three species recognized herein. (Our count of 156 radials and length measurement of 143 mm indicates that a part of the tail is now missing.) Cope's color notes could be positively misleading since the pale dorsal bands are created by exposed connective tissue of myosepta; these are not part of the integumentary pigmentation and thus bear no similarity to the pale dorsal band of *A. devenanzii.* In fact, given the poor state of the type nothing can be said of its skin or fin pigmentation. Contrary to Cope's remark, the depth of the body at the base of the dorsal filament does not nearly equal the head length unless he intended to exclude snout and eye. This depth, however, exceeds the least distance between the eye and pectoral base, a character which we have found to be diagnostic of some species. Furthermore, the maximum body depth is contained a little less than 4½ times in the length to the origin of the dorsal thong (Fig. 9). These two expressions of a relatively deep body characterize two otherwise distinguishable species of *Adontosternarchus:* the Orinocan *A. devenanzii,* and the central Amazonian species to which we here apply the name *A. balaenops.* Our decision is based on the depth measurements and known geographic distribution of the two species. Other possible diagnostic features are not preserved in the type. Ours is a conservative course that avoids coining a likely superfluous binomen. We do recognize that, if the two species are someday found sympatric and no other diagnostics are discovered, *balaenops* might become a *nomen dubium.*

Table 3. Measurements in mm and thousandths of length to end of anal fin base (LEA), and counts of meristic characters for holotypes of *Adontosternarchus devenanzii* and *A. clarkae.*

	A. devenanzii MBUCV-V-7513		*A. clarkae* MBUCV-V-12703	
Measurements	mm	mils LEA	mm	mils LEA
Total length	133.4	1181	172.0	1536
LEA	113.0	–	112.0	–
Maximum body depth	16.6	147	17.4	155
Head depth at nape	12.9	114	13.4	120
Length to origin of anal fin	17.6	156	15.1	135
Caudal peduncle length	13.2	117	52.9	472
Tail length	20.4	181	55.0	491
Length to origin of dorsal thong	68.2	608	80.9	722
Head length	16.0	142	12.7	113
Snout length	4.5	40	3.4	30
Eye diameter	1.7	15	1.4	13
Interorbital distance	4.8	42	3.9	35
Postorbital length	10.4	92	8.5	76
Size of branchial aperture	3.1	27	2.2	20
Length to anus	7.6	67	6.9	62
Length of anal fin base	99.0	876	101.2	904
Pectoral fin length	12.5	111	10.8	96
Pectoral fin rays	ii, 13–14		ii, 10	
Anal fin rays	153		154	
Caudal fin rays	20		16	

Adontosternarchus devenanzii new species

"De Venanzi's knifefish"

Figures 1B, 2–7, 9–15

Adontosternarchus sachsi. Mago-Leccia, 1967:257, fig. 10 (Venezuela). Mago-Leccia, 1970:77 (listed). *Adontosternarchus* sp. López, Lundberg, and Marsh, 1984:333 (Venezuela, Río Orinoco Delta).

HOLOTYPE. MBUCV-V-7513, 1, TL 133.4 mm, LEA 113.0 mm (see Table 3); Venezuela, Caño Caujarito, tributary of Río Portuguesa, 3 km above La Unión, Guarico State, 23 Aug. 1974, J.N. Baskin, J.O. Silva, and L. Aguana.

PARATYPES. VENEUZUELA: MBUCV-V-4772, 20, TL 71.2–159.8 mm; Cãno Caracara tributary of Río Meta, Apure State, 10 March 1967, F. Mago-Leccia and J. Mosco (4 specimens cleared and stained). MBUCV-V-5139, 1, TL 106.8 mm; Caño Cocuiza, Tabirito bridge, near Caicara del Orinoco, Bolivar State, 27 Feb. 1969, F. Mago-Leccia and party. MBUCV-V-5984, 1, TL 116.5 mm; Esteros de Camaguan, Guarico State, 6 Aug. 1971, A. Machado. MBUCV-V-7516, 4, TL 111.0–135.9 mm; Boca Ruido lagoon, Río Portuguesa system, Guarico State, 8 Aug. 1971, F. Mago-Leccia. MBUCV-V-9301, 5, TL 85.9–123.7 mm; Modulos de Mantecal, Apure State, 1 June 1974, L. Aguana and A. Machado. MBUCV-V-12701, 4, TL 146.2–186.2 mm; Esteros de Camaguan, Guarico State, 25 April 1980, F. Provenzano, O. Castillo, and L. Aguana. The following material collected by J.N. Baskin, J.G. Lundberg, and F. Mago-Leccia. MBUCV-V-10385, 3, TL 154.6–162.5 mm; Río Orinoco, Los Castillos, southside of channel, Delta Amacuro Territory, 16 Feb. 1978. MBUCV-V-10486, 1, TL 137.7 mm; Río Orinoco, main channel North of Isla Tres Caños, at Caño Araguaíto, Delta Amacuro Territory, 19 Feb. 1978. MBUCV-V-10497, 6, TL 115.1–144.5 mm; Río Orinoco, upstream from Caño Tres Caños, Delta Amacuro Territory, 19 Feb. 1978. MBUCV-V-10528, 1, TL 152.9 mm; Río Orinoco, 2 km downstream from Barancas, Delta Amacuro Territory, 17 Feb. 1978. MBUCV-V-10535, 3, TL 126.8–174.7 mm; Río Orinoco, Los Castillos, Delta Amacuro Territory, 16 Feb. 1978. MBUCV-V-10580, 1, TL 125.6 mm; Río Orinoco, Tapatapa lagoon in Isla Tapatapa, Delta Amacuro Territory, 16 Feb. 1978. MBUCV-V-10588, 2, TL 103.4–159.0 mm; Río Orinoco, Brazo Imataca, Delta Amacuro Territory, 22 Feb. 1978. MBUCV-V-10595, 3, TL 110.8–132.0 mm; Río Orinoco, main channel N of Isla Tres Caños at Caño Araguaíto, Delta Amacuro Territory, 19 Feb. 1978. USNM

Table 4. Frequency distributions of number of vertebrae to base of last anal fin ray in *Adontosternarchus.*

	57	58	59	60	61	62	63	64
balaenops	2	1	4	2				
devenanzii				2	3	2	2	2
clarkae	2	2	4	1	1			
sachsi			1	1	2	4		3

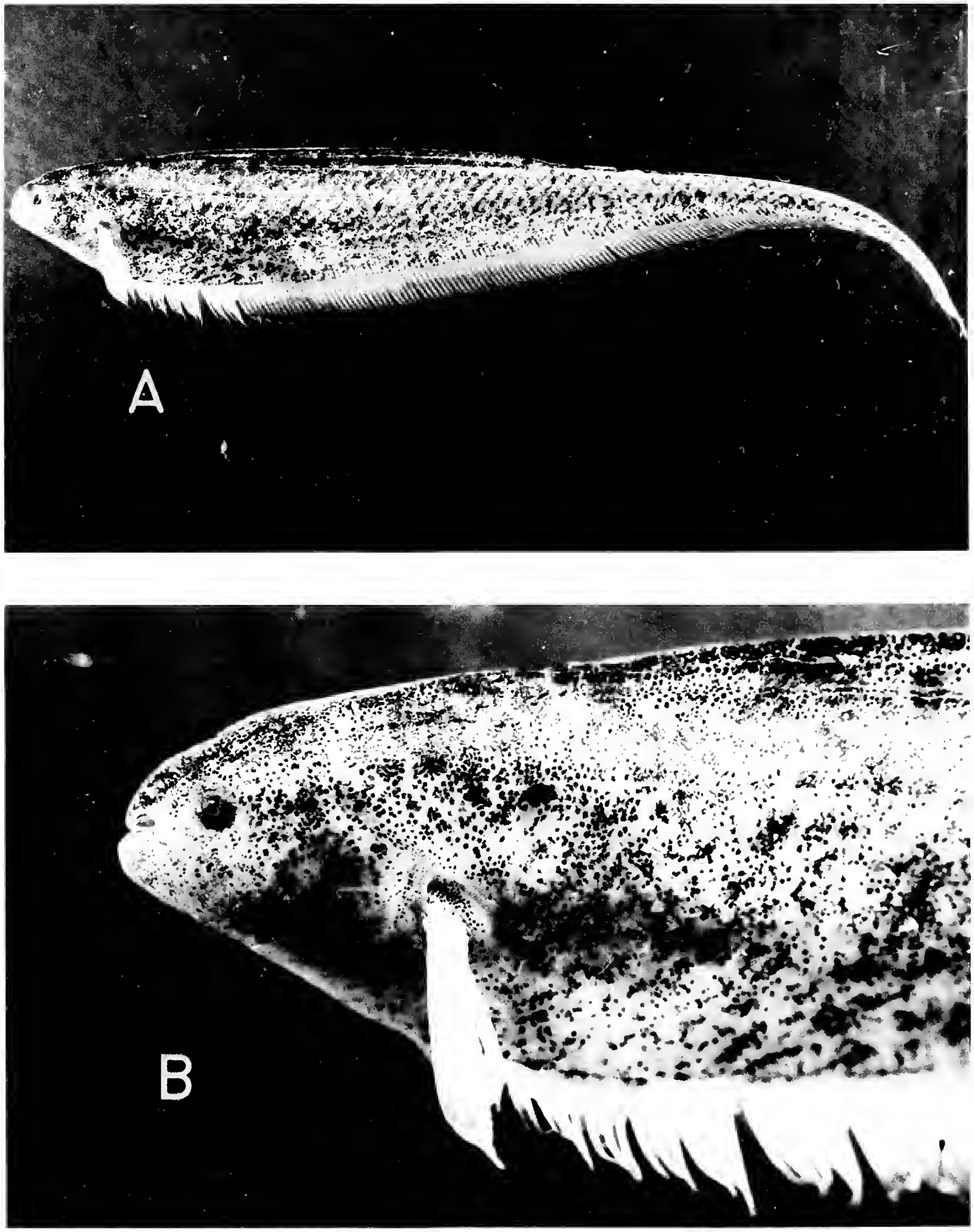
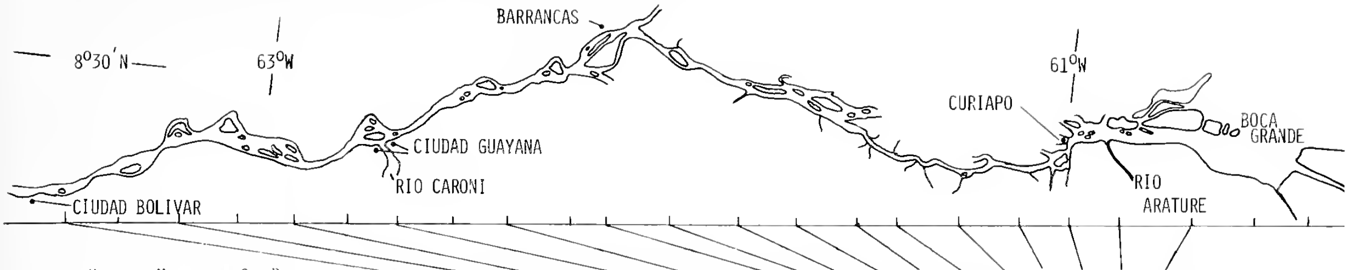


Figure 14. *Adontosternarchus devenanzii* sp. n., 154.6 mm TL, MBUCV-V-10385, paratype, Orinoco River, Los Castillos, Venezuela. A, entire fish; B, close up of head.

264839, 68, LEA 84–117 mm; Río Orinoco, main channel S of Isla Portuguesa, Delta Amacuro Territory, 20 Feb. 1978. LACM 43103-1, 75, LEA 90–147 mm; Río Orinoco, main channel N of Isla Fajardo, Delta Amacuro Territory, 14 Feb. 1978. FMNH 94909, 12, LEA 82–130 mm; Río Orinoco, main channel N of Isla Tres Caños, 19 Feb. 1978. CAS 54328, 24 LEA 82–124 mm; Río Orinoco, main channel near Caño Remolina, 25 Feb. 1978. LACM 43295-1, 27, LEA 67–84 mm; Río Orinoco, north shore at Isla Portuguesa in Caño Anabata, Delta Amacuro Territory, 16 Nov. 1979.

COLOMBIA: ANSP 128203, 8, TL 88–130 mm, LEA 76–111 mm; Meta State hacienda Mozambique, Laguna Mozambique, N shore, 20 March 1971, J.E. Böhlke. ANSP 131836, 1, TL 127 mm, LEA 114 mm, Meta State, Quebrada Venturosa between La Balsa and Puerto López, 4°05′N, 72°58′W, 21 March 1975, J.E. Böhlke. ANSP 138859, 1, TL 123 mm, LEA 109 mm; Meta State, Río Metica, N bank of river SW of Laguna Mozambique, 20 Feb. 1972, J.E. Böhlke.

OTHER MATERIAL. Additional material of *A. devenanzii* comprising 89 lots and 4594 individuals was collected



Nautical Miles from Sea Buoy:			240	230	220	210	200	190	180	170	160	150	140	130	120	110	100	90	80	70	60	50	40	%
Feb 1978 (Low water)	devenanzii (n=2438)	Deep River							82		52	28	35	1103	851	11	12	111	57	65	1			98.8
		Shallow River									23													0.9
		Near Shore										3	2			1		1						0.3
	sachsi (n=652)	Deep River							67		73	111	19	120	162	1	1	30	36	6	10	16		100.0
		Shallow River																						
		Near Shore																						
Nov 1979 (High water)	devenanzii (n=2184)	Deep River												1	4	1								0.3
		Shallow River					2		12		6		4	2031	99				10					99.1
		Near Shore							3			3	2	1				5						0.6
	sachsi (n=1359)	Deep River												5	4	7							8	1.8
		Shallow River	1				14		117		7			1014	100				18		5	37		96.9
		Near Shore							21			1												1.6

Figure 15. Longitudinal and habitat distribution of *Adontosternarchus sachsi* and *A. devenanzii* in the lower Orinoco River in 1978 and 1979. Values in the table are numbers of specimens taken in the indicated habitat (rows) at the indicated site (columns). (See text section on distribution under *A. devenanzii* for discussion.)

in 1978 and 1979 in the Orinoco River delta region, Venezuela, by J.N. Baskin, J.G. Lundberg, and F. Mago-Leccia from R/V EASTWARD, then of Duke University. This material is deposited in the following institutions: USNM, LACM, FMNH, UMMZ, ANSP, AMNH, and MCZ.

DIAGNOSIS. Tail and caudal peduncle short, head length contained in peduncle less than twice; dorsal thong usually does not reach end of anal fin (sometimes extends slightly beyond); body deep, maximum body depth 208–286 thousandths of length to origin of dorsal thong (Fig. 9); depth below origin of dorsal thong exceeds or equals least distance between eye and pectoral fin base; head chubby and rounded, its dorsal profile distinctly convex; chin not markedly projecting (Figs. 1B, 14), interorbital distance reaches from eye to tip of chin or beyond; distance to origin of anal fin 170–256 thousandths of length to origin of dorsal thong; 147–173 anal rays (Table 2); 14–16 pectoral rays (Table 1); 15–22 caudal rays (Table 1); a pale (yellow in life) stripe from chin tip and snout to near origin of dorsal thong (this stripe is occasionally obscured by dark spots or is very rarely obsolescent); pectoral and anal fins hyaline.

DESCRIPTION. Measurements in thousandths of reference dimension. Body depth 131–179 of LEA, 208–283 of length to origin of dorsal thong, 138–206 of anal fin base and 104–160 of head length; depth at nape 85–124 of LEA, 137–206 of length to origin of dorsal thong, 90–140 of anal fin base, 765–1020 of head length; dorsal profile of body gently convex, more so behind the head (Fig. 14); preanal fin distance 119–159 of LEA, 195–256 of distance to origin of dorsal thong (Fig. 11), 126–183 of anal fin base; caudal peduncle length 79–204 of LEA, 131–313 of distance to origin of dorsal thong (Fig. 10), 90–228 of anal fin base and 70–168 of total length; tail length 121–236 of LEA, 194–386 of distance to origin of dorsal thong, 133–267 of anal fin base, 108–191 of total length; length to origin of dorsal thong 583–716 of LEA.

Head rounded; head length 107–138 of LEA, 164–209 of distance to origin of dorsal thong, 113–158 of anal fin base and 578–1435 of caudal peduncle; dorsal profile of head convex, smoothly continuous with contour of back (Fig. 14), except in individuals ca. 100 mm TL in which there is often a shallow concavity at the nape; distance from snout tip to rictus 600–953 of snout length; chin rounded (Fig. 1B); end of snout bluntly pointed; snout length 260–298 of head length, 771–1040 of interorbital distance; both jaws edentulous in adults, but carrying conical teeth in juveniles up to ca. 26 mm TL.

Eye diameter 86–142 of head length, 317–500 of snout length, 265–500 of interorbital distance; interorbital distance 250–361 of head length; branchial opening 153–291 of depth at nape, 152–244 of head length; distance from tip of snout to vent 58–99 of LEA, vent shifts relatively anteriad with growth (Fig. 12).

Anal fin base 802–976 of LEA; length of pectoral fin 829–969 of head length.

56–64 vertebrae to base of last anal fin ray.

Background color in alcohol pale tan to yellowish-white; sides and back densely mottled with brownish-black chromatophores; spots and large dense blotches scattered irregularly on sides and dorsum; dorsal midline with a pale stripe from chin and snout to near origin of dorsal thong, irregularly obscured by dark spots or rarely obsolescent; dorsal thong with a hyaline ground color but superficially spotted; lateral line sensory canal evident as a thin, pale broken line on sides; lower sides with scattered superficial spots underlain with numerous dark, ventroposteriorly oblique lines formed by deep chromatophores and spaces between anal fin bases; anal fin membrane hyaline except usually a few chromatophores present over rays; caudal fin usually with scattered chromatophores, particularly on its base; pectorals hyaline; top and upper sides of head pigmented as the body, the pale stripe of the dorsal midline extending onto tips of snout and chin where it is surrounded by a dark U-shaped band; sides and under surface of head paler, with scattered chromatophores; lateral margin of upper lip pigmented; tube of anterior naris always bears a few chromatophores.

Color in life: background color dark brownish, mottled; head yellow ocher and dark brown; dorsal midline with a yellow stripe; fins all hyaline, except the caudal which is pigmented with a darker area on its base; opercles darker than surrounding areas; snout with dark areas on each side of the midline stripe; chin with a dark U-shaped band.

ETYMOLOGY. The name *devenanzii* is for Dr. Francisco De Venanzi, former Rector of the Universidad Central de Venezuela, Caracas, who encouraged the first author to study fishes.

DISTRIBUTION. This new species is quite common throughout the Venezuelan and Colombian Low Llanos, the main course of the Río Orinoco and its large tributaries (Fig. 13).

Collections made by us in the Orinoco Delta region in 1978 and 1979 reveal that *Adontosternarchus* are more abundant than prior sampling suggested. In our survey work collections were made with trawls from R/V EASTWARD in deep river channels (10–80 m) and from smaller craft in shallower areas (ca. 10 m), as well as with conventional collecting gear in near shore habitats. The 1978 expedition was in February during the middle of the low water (dry) season; the 1979 expedition was in November near the end of the high water (wet) season. Large numbers of *A. devenanzii* and *A. sachsi* were collected in both years and their distributions along the transects were similar (Fig. 15).

Between 46% and 96% of the total sample of each species in each year were collected between channel markers 120 n,mi and 140 n,mi, the 20 n,mi stretch of river just below the head of the delta (channel markers and lights of the shipping lanes are labelled with distances from the sea buoy which is located about 30 n,mi off Boca Grande). *A. devenanzii* was not taken downstream from the 60 n,mi marker or above the 201 n,mi marker, but *A. sachsi* was found further downstream to the 42 n,mi marker (just 7 n,mi above the transition to brackish water) and further upstream at 241 n,mi. Despite the between-year similarity in longitudinal distribution, both species appear to shift habitat between low and high water seasons. In 1978 (low water) 88.7% of the *A. devenanzii* and 100% of *A. sachsi* were collected in bottom trawls in mid-river channels usually much greater than 10 m in depth. In 1979 only 11.5% of *devenanzii* and 28.6% of *sachsi* were collected in deep channels even though trawling effort in this habitat was greater in that year (151 vs. 186 deep channel trawls). The largest numbers of *Adontosternarchus* collected in 1979 (57.7% of *devenanzii* and 62.9% of *sachsi*) were taken with a small trawl pulled by a dugout canoe in lagoons and shallow places of the river between about 30 and 110 m from shore (López, Lundberg, and Marsh, 1984). In both years these fishes were rarely captured in near shore habitats. Overall then, it appears that *Adontosternarchus* are bottom-oriented fishes of large rivers and lagoons and that they make marked seasonal movements between the deep channels and the shallow channels and lagoons. The biological significance of this movement remains to be investigated.

Adontosternachus clarkae new species

"Clark's knifefish"

Figures 1C, 9–12, 16–17

HOLOTYPE. MBUCV-V-12703, TL 172.0 mm, LEA 112.0 mm (see also Table 3); Venezuela, Raudal (Rapids) de Mavahate, Río Negro, near San Carlos de Río Negro, Amazonas Territory, 6 May 1981, Edgar Armas.

PARATYPES. VENEZUELA: MAC-PAY-0369, 3, TL 172–186 mm, LEA 110–119 mm; paratopotypes taken with the type specimen. MBUCV-V-11218, 2, TL 158.6–172.5 mm; rapids downstream from the mouth of the Casiquiare in the Río Negro, about 10 km N of San Carlos de Río Negro, Amazonas Territory, 2 May 1978, Kate Clark and Raimundo Videra. MBUCV-V-11293, 1, TL 162.4 mm; San Carlos de Río Negro, Amazonas Territory, Nov. 1980, Kate Clark. MBUCV-V-11936, 2, TL 168.1–168.5 mm; paratopotypes (one specimen stained).

COLOMBIA: FMNH 94263, 5, TL 73.1–94.8 mm, LEA 68.1–77.4 mm; Amazonas State, Amazon River above Leticia, Nov. 1973, J. Thomerson.

PERU: MZUSP uncatalogued, 2, TL 88.3–133.8 mm, LEA 72.5–109.0 mm; Ucayali State, Río Ucayali, Masisea, H. Ortega, Oct. 1975.

ECUADOR: FMNH 94264, 1, TL 105.3 mm, LEA 75.5 mm; Río Tiputini at confluence with Río Napo, 0°48.9′S, 75°32.5′W, Dec. 1981, D.J. Stewart.

BRAZIL: MCZ 46877, 141, TL 85.0–104.2 mm, LEA 65.3–80.5 mm; Terr. Roraima, Rio Negro near confluence with Rio Branco and lower 30 miles of Rio Branco, 1°24′S, 61°27′W, March–April 1967, Alpha Helix. USNM 266551, 3, TL 95–127 mm; same data as preceding lot. MCZ 46872, 41, TL 60.4–90.9 mm, Rio Negro at 1°24′S, 61°27′W, 2 miles below confluence with Rio Branco, 27–28 March 1967, Alpha Helix. LACM 43645-1, 3, TL 74.1–94.1 mm; same data as preceding lot.

DIAGNOSIS. Tail and caudal peduncle long, head length contained in peduncle twice or more; dorsal thong reaches beyond end of anal fin; body depth moderate relative to other species of the genus, maximum body depth 196–278 thousandths length to origin of dorsal thong (Fig. 9); depth below origin of dorsal thong less than or equal to least distance between eye and pectoral base; head angular, its dorsal profile straight or slightly convex; chin projecting (Figs. 1C, 16), interorbital distance reaches from eye to chin tip; distance to origin of anal fin 167–256 thousandths of length to origin

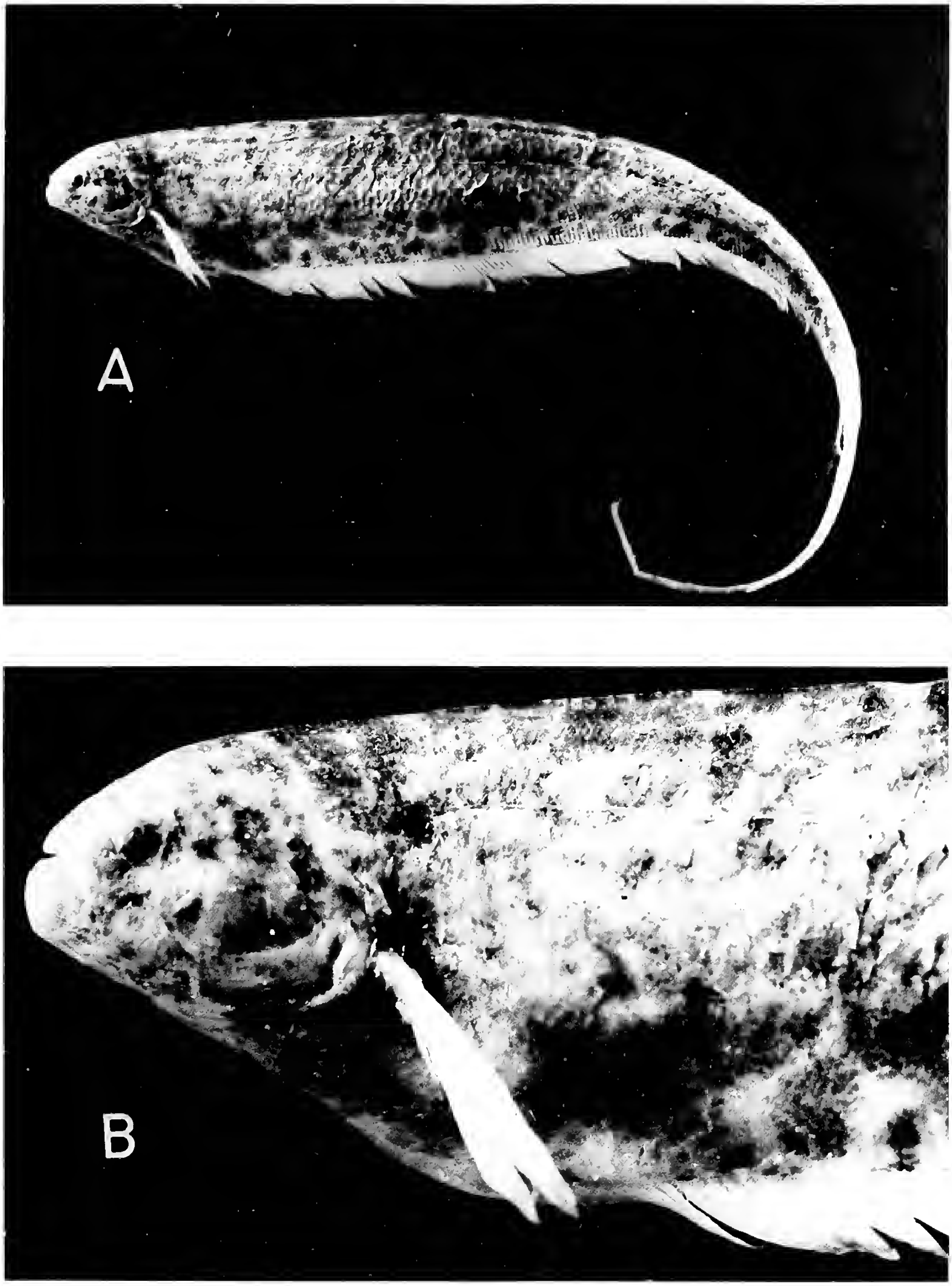


Figure 16. *Adontosternarchus clarkae* sp. n., 172.5 mm TL, MBUCV-V-11218, paratype, Río Negro, Amazonas Territory, Venezuela. A, entire fish; B, close up of head.

of dorsal thong; (135 partly regenerated?) 144–164 anal fin rays (Table 2); 12–15 pectoral fin rays (Table 1); 10–16 caudal fin rays (Table 1); back and sides mottled with light and dark brown, oddly shaped spots; no pale dorsal midline stripe; pectoral and anal fins hyaline.

DESCRIPTION. Measurements in thousandths of reference dimension. Body depth 138–170 of LEA, 195–278 of length to origin of dorsal thong, 154–199 of anal fin base, 1149–1458 of head length; depth at nape 92–127 of LEA, 126–183 of length to origin of dorsal thong, 105–149 of anal fin base, 730–1118 of head length; dorsal profile of body gently convex more so behind the head (Fig. 16); preanal distance 115–154 of LEA, 166–259 of distance to origin of dorsal thong (Fig. 11), 133–175 of anal fin base; caudal peduncle length 258–495 of LEA, 379–679 of distance to origin of dorsal thong (Fig. 10), 293–549 of anal fin base, 194–318

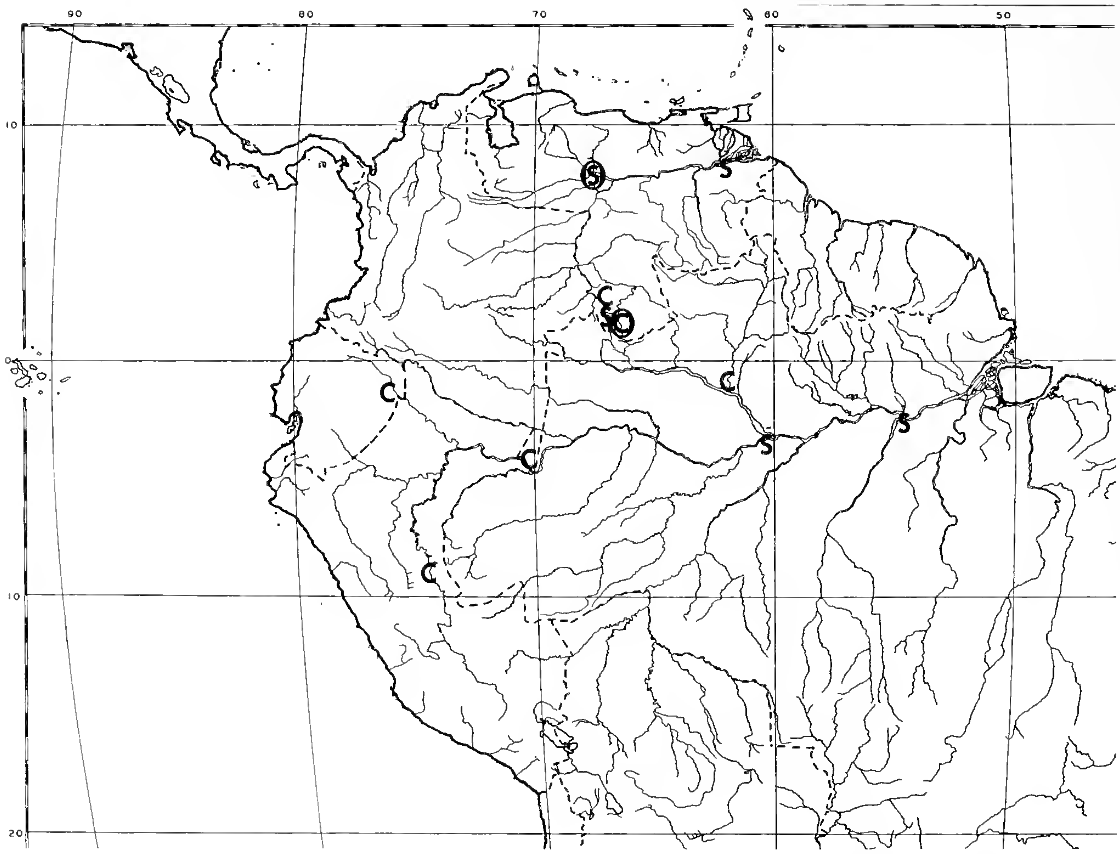


Figure 17. Geographic distribution of *Adontosternarchus clarkae* (C) and *A. sachsi* (S); circled letters = type localities; some symbols represent more than one collection locality or lot of specimens (see especially text section on distribution under *A. devenanzii* and Fig. 15 for additional information on *A. sachsi*).

of total length; tail length 310–565 of LEA, 454–765 of distance to origin of dorsal thong, 351–633 of anal fin base, 243–361 of total length; distance to origin of dorsal thong 595–756 of LEA.

Head rounded (head length 104–140 of LEA, 139–228 of length to origin of dorsal thong, 117–158 of anal fin base, 213–495 of caudal peduncle); dorsal profile of head slightly convex, smoothly continuous with contour of back (Fig. 1C); distance from snout tip to rictus 543–1000 of snout length; chin bulbous; end of snout bluntly pointed; snout length 253–303 of head length, 775–1000 interorbital distance; both jaws edentulous in adults.

Eye diameter 85–130 of head length, 294–500 of snout length, 267–458 of interorbital distance; interorbital distance 270–345 of head length; branchial opening 128–268 of depth at nape, 137–242 of head length; distance from tip of snout to vent 54–90 of LEA, vent shifts relatively anteriad with growth (Fig. 12).

Anal fin base 851–919 of LEA; length of pectoral fin 833–1021 of head length.

57–61 vertebrae to base of last anal fin ray.

Background color in alcohol pale tan to yellowish-white; sides and back densely mottled with irregularly scattered, brownish-black blotches; dorsal midline without a pale stripe; dorsal thong with a hyaline ground color but superficially with dark brown blotches; lateral line sensory canal evident as a thin pale broken line on sides; anal fin membrane hyaline except for a few chromatophores present over rays; caudal fin pigmented with small spots and chromatophores more concentrated over its base; pectoral fins hyaline; top and upper sides of head with blotches as the body; lower sides and undersurface of head with scattered blotches and dots; tip of snout, margin of upper lip, tip of chin, and tube of anterior naris always immaculate.

ETYMOLOGY. The name *clarkae* is for Ms. Kate Clark, collector of this new species from the Río Negro, Venezuela.

DISTRIBUTION. *Adontosternarchus clarkae* is distributed in the upper parts of the Amazon River Basin of Brazil, Venezuela, Colombia, Ecuador, and Perú (Fig. 17). There are no records of it from the lower Amazon. The Venezuelan specimens were collected in black waters near rapids.

Adontosternarchus sachsi (Peters)
"Sachs' knifefish"

Figures 1D, 9–12, 15, 17–19

Sternarchus sachsi Peters, 1877:473 (original description, type locality: San Fernando de Apure, Venezuela). Sachs, 1879:

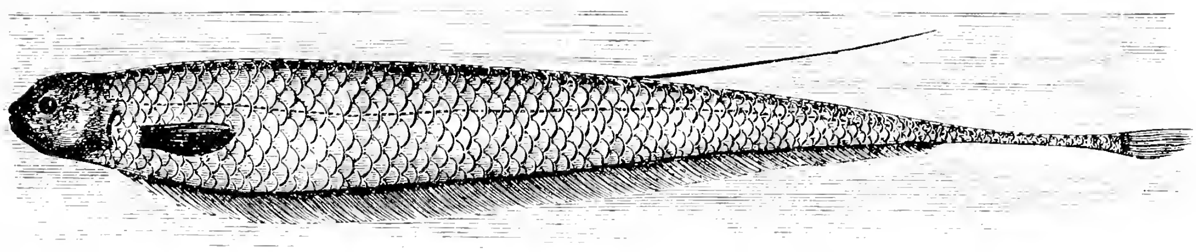


Figure 18. *Adontosternarchus sachsi* (Peters) (exact origin and disposition of specimen unknown) reproduced from Sachs (1879:279).

153, 367, fig. on p. 279 (Apure). Eigenmann and Eigenmann, 1891:62 (listed). Röhl, 1942:377, fig. 189 (copied from Sachs).

Sternarchogiton sachsi. Eigenmann and Ward, 1905:165 (new combination). Ihering, 1907:275 (listed). Eigenmann, 1910: 448 (listed).

Adontosternarchus sachsi. Ellis, 1913:156 (in part). Fowler, 1939:278 (Perú, Contamana). Schultz, 1949:74 (listed, characters). Fowler, 1943:124 (listed). Fowler, 1945:185 (reprint of Fowler, 1943). Fowler, 1951:423 (listed).

MATERIAL EXAMINED. VENEZUELA: Photograph of holotype of *Sternarchus sachsi;* ZMB No. 10044; Venezuela, Apure State, San Fernando de Apure. MBUCV-V-11292, 1, TL 165.6 mm; Venezuela, Río Negro, Amazonas Territory, near San Carlos de Río Negro. MBUCV-V-4643, 1, TL 120.8 mm; Río Orinoco, Quiritare, Amazonas Territory. MBUCV-V-10377, 3, TL 152.8–200.5 mm; Río Orinoco, Brazo Imataca, Delta Amacuro Territory. MBUCV-V-10417, 2, TL 190.8–203.0 mm; Río Orinoco, old shipping channel, S of Isla Portuguesa, Delta Amacuro Territory. MBUCV-V-10431, 3, TL 211.1–222.9 mm; Río Orinoco, near Isla Iguana, Delta Amacuro Territory. MBUCV-V-10441, 2, TL 193.4–202.6 mm, Río Orinoco, along S shore by Caño Guine, Delta Amacuro Territory. MBUCV-V-10445, 1, TL 186.4 mm; Venezuela, Río Orinoco, along S shore by Caño Guine, Delta Amacuro Territory. MBUCV-V-10470, 1, TL 169.9 mm; Río Orinoco, main channel E of Isla Portuguesa, Delta Amacuro Territory. MBUCV-V-10495, 3, TL 147.8–180.7 mm; Río Orinoco, Caño Tres Caños, Delta Amacuro Territory. MBUCV-V-10506, 1, TL 200.0 mm; Río Orinoco, near Los Castillos, Delta Amacuro Territory. MBUCV-V-10554, 13, TL 145.5–321.8 mm; Venezuela, Río Orinoco, Isla Veradero, Delta Amacuro Territory (4 specimens stained). LACM 43295-2, 29, LEA 57–85 mm; Rio Orinoco, north shore at Isla Portuguesa in Caño Anabata, Delta Amacuro Territory.

BRAZIL: MZUSP 24925, 2, TL 138.2–160.2 mm, LEA 129.4–141.6 mm Rio Solimões, Lago Janauacá and vicinity. FMNH 54569 and 15187, 15188, 15189, 15190, 15191 (formerly CM 3200), 55, TL 93.4–116.6 mm, LEA 83.2–108.3 mm; Pará State, Santarém.

OTHER MATERIAL. Additional material of *A. sachsi* comprising 89 lots and 2011 individuals was taken in 1978 and 1979 in the Orinoco River Delta region, Venezuela, by J.N. Baskin, J.G. Lundberg, and F. Mago-Leccia from R/V EASTWARD, then of Duke University. This material is deposited in the following institutions: USNM, LACM, FMNH, UMMZ, CAS, ANSP, AMNH, and MCZ.

DIAGNOSIS. Tail and caudal peduncle long, head contained in peduncle twice or more; dorsal thong reaches beyond end of anal fin; body shallow, maximum body depth 172–222 thousandths of distance to origin of dorsal thong (Fig. 9); depth below origin of dorsal thong less than or equal to least distance between eye and pectoral base; head angular, its dorsal profile variable but not strongly convex; chin projecting (Fig. 1D, 19), interorbital distance not reaching from eye to chin tip; distance to origin of anal fin 137–213 thousandths of distance to origin of dorsal thong; 154–185 anal rays (Table 2); 14–17 pectoral rays (Table 1); 14–22 caudal rays (Table 1); back and sides nearly uniform brown, except for dark margins of some scales; no pale midline stripe; pectoral and anal fins hyaline.

DESCRIPTION. Measurements in thousandths of reference dimension. Body depth 116–143 of LEA, 174–218 of distance to origin of dorsal thong, 126–174 of anal fin base, 953–1548 of head length; depth at nape 79–106 of LEA, 119–163 of distance to origin of dorsal thong, 85–129 of anal fin base, 733–1087 of head length; dorsal profile of body scarcely convex to straight (Fig. 19); preanal distance 86–146 of LEA, 137–214 of distance to origin of dorsal thong (Fig. 11), 93–169 of anal fin base; caudal peduncle length 219–366 of LEA, 327–524 of distance to origin of dorsal thong (Fig. 10), 236–404 of anal fin base, 170–257 of total length; tail length 287–426 of LEA, 411–628 of distance to origin of dorsal thong, 306–468 of anal fin base, 217–299 of total length; distance to origin of dorsal thong 621–710 of LEA.

Head slightly compressed (head length 92–135 of LEA, 135–205 of length to origin of dorsal thong, 99–164 of anal fin base, 296–460 of caudal peduncle); dorsal profile of head angular, with a shallow concavity at the nape at all sizes (Fig. 19); distance from snout to rictus 611–1083 of snout length; chin bulbous; snout sharply pointed; snout length 267–323 of head length, 935–1241 of interorbital distance; both jaws edentulous in adults.

Eye diameter 90–136 of head length, 293–484 of snout length, 314–500 of interorbital distance; interorbital distance 242–315 of head length; branchial opening 155–337 of depth at nape, 153–271 of head length; distance from tip of snout to vent 47–143 of LEA, vent shifting anteriad with increasing size (Fig. 12).

Anal fin base 778–951 of LEA; length of pectoral fin 885–1000 of head length.

59–64 vertebrae to base of last anal fin ray.

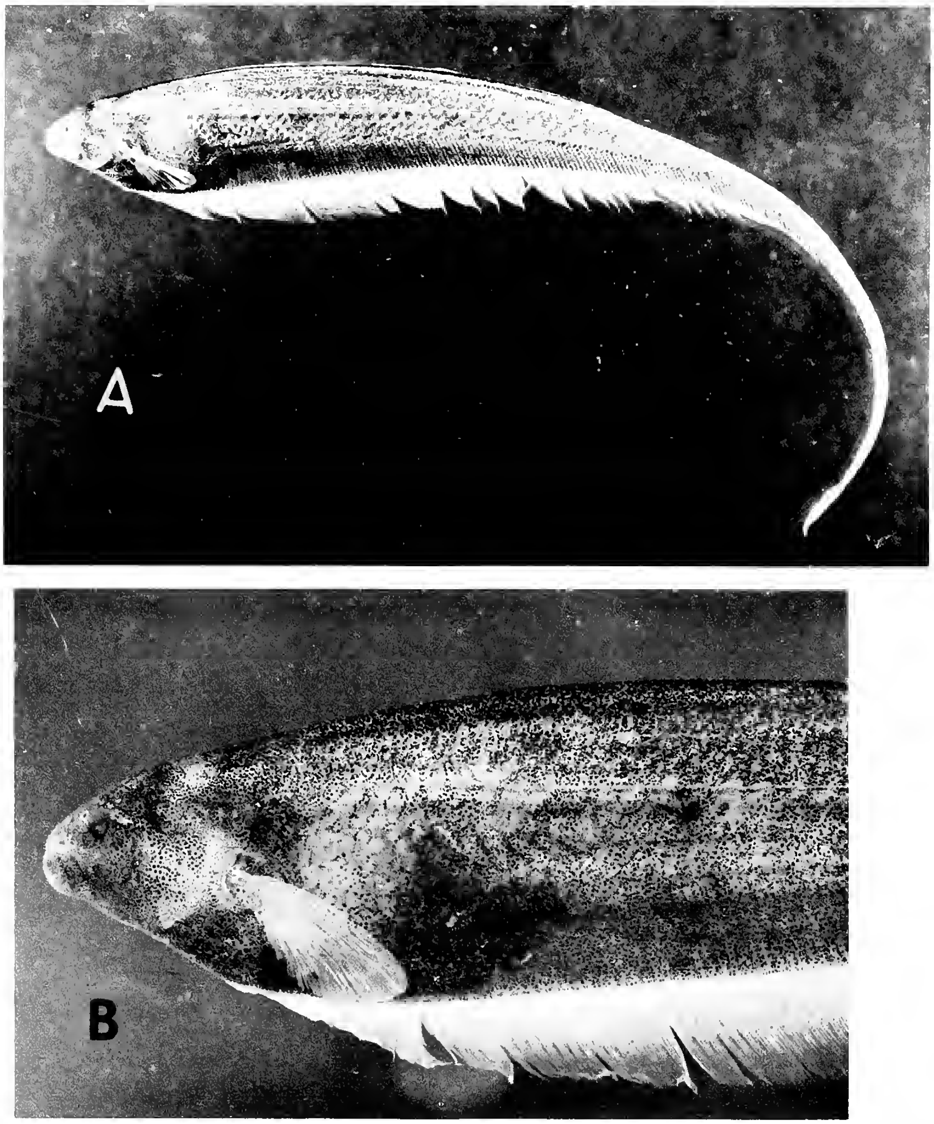


Figure 19. *Adontosternarchus sachsi* (Peters) 205.0 mm TL, MBUCV-V-10441, Orinoco River, Caño Guine, Venezuela. A, entire fish; B, close up of head.

Background color in alcohol pale tan to brown; sides and back densely and almost uniformly peppered with brownish-black chromatophores; chromatophores of mid-sides often arranged as oblique bands along scale margins; mid-doral pale stripe absent; dorsal thong with a hyaline ground color but superficially covered with chromatophores; lateral line sensory canal evident as a thin pale line on sides; superficial chromatophores of lower sides sometimes forming ventro-posteriorly oblique lines and underlain with numerous corresponding dark lines formed by deep chromatophores and spaces between anal fin basals; anal fin membrane hyaline but usually a few chromatophores present over rays; caudal fin dusky at base and centrally, its distal end hyaline; pectoral fins hyaline; top and upper sides of head pigmented as the anterior part of the body; lower sides and undersurface of head paler, with scattered chromatophores; tip of snout, margin of upper lip, tip of chin and tube of anterior naris almost always immaculate.

DISTRIBUTION. *Adontosternarchus sachsi* is found in the middle and lower parts of the Orinoco and Amazon rivers (Fig. 17). Data on its detailed distribution in the Orinoco Delta region was presented above in connection with *A. devenanzii* (p. 14 and Fig. 15).

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CONTRIBUTIONS IN SCIENCE

BIOMECHANICAL IMPLICATIONS OF THE VARIATION IN *SMILODON* ECTOCUNEIFORMS FROM RANCHO LA BREA

Christopher A. Shaw and Antonia E. Tejada-Flores

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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BIOMECHANICAL IMPLICATIONS OF THE VARIATION IN *SMILODON* ECTOCUNEIFORMS FROM RANCHO LA BREA

Christopher A. Shaw and Antonia E. Tejada-Flores[1]

ABSTRACT. Of 517 *Smilodon* ectocuneiforms examined from the late Pleistocene Rancho La Brea asphalt deposits, the typically hook-like plantar process is unfused in 23.8 percent. The plantar tuberosity of felid ectocuneiforms develops from a separate center of ossification than that of the main body of the ectocuneiform. Tendons of the *M. tibialis posterior* and *M. peroneus longus*, extensors of the hind limb, interact with the plantar process of the ectocuneiform and affect the development of this bone. The frequency of unfused plantar tuberosities is greater in geologically younger localities at Rancho La Brea and is correlative with an overall increase in *Smilodon* body size. This increase in body mass through time placed greater stress (produced by proportionately more powerful extensor muscles) on the developing plantar process of larger *Smilodon* individuals, preventing fusion to the body of the ectocuneiform. Lever-arm ratios, adjusted for body mass, indicate that *Smilodon* had mechanically more powerful hind limbs than living lions and was able to attack prey by stalking and leaping.

INTRODUCTION

Osteologically, *Smilodon floridanus* is one of the most completely known extinct species from the late Pleistocene of Rancho La Brea in southern Californa. Between 1913 and 1915, field parties from the Los Angeles County Museum of Natural History (LACM) excavated extensively in what is now Hancock Park. From 1029 to over 2000 estimated individuals of *Smilodon* are represented in the collections (Marcus, 1960; Miller, 1968) housed at the George C. Page Museum.

In a comparative osteologic study of the felids from Rancho La Brea, Merriam and Stock (1932) noted two morphologic varieties of *Smilodon* ectocuneiforms. The more common variety (Fig. 1A) has a hook-like plantar tuberosity, fused to the body along a broad area; this process is often truncated, the hook being reduced or absent in the less common variety (Fig. 2A). Merriam and Stock (1932) examined 120 ectocuneiforms and found that 70.8 percent bore a well-developed tuberosity. This percentage is 76.2 in our study of 517 specimens. Six of 11 (54.5%) *Smilodon* ectocuneiforms from asphalt deposits of Talara, Peru, have well-developed, fused plantar tuberosities (C.S. Churcher, written comm.).

The plantar (posterior) end of truncated ectocuneiforms also exhibits two distinct morphologies. In our sample of 123 specimens, 37 (30.1%) bear a facet (Fig. 2A, right) for apparent articulation with a small nodule of bone, representing the missing plantar process. The remainder have a roughened surface for tendinous or ligamentous attachment similar to that of the fully developed process; furthermore, nine of these specimens (7.3%) exhibit unexplained pathologic bone growth. Four of the five truncated ectocuneiforms from Talara bear a nodular facet (C.S. Churcher, written comm.).

Until recently, the nodule of bone assumed to be associated with the truncated *Smilodon* ectocuneiforms by Merriam and Stock (1932) had not been recognized from Rancho La Brea. Twenty specimens have now been identified in the collections. Seven (LACMHC 10791, 10792, 10795, 10805, 10806, LACMRLP R36931, R51053) are hook-like in shape, identical in morphology to the fused plantar process of complete ectocuneiforms (Fig. 3A); four (LACMHC 10791, 10792, 10805, LACMRLP R36931) bear an articular facet and three do not. The other 13 specimens (LACMHC 10790, 10793, 10794, 10796 through 10803, 10807) do not have a articular facet and are oval and globular in shape. The dorsal (anterior) surface bears an oval rugosity where articulation with or fusion to the body of the ectocuneiform would be expected (Fig. 3B).

Ectocuneiforms of extinct felids (other than *Smilodon*) from Rancho La Brea and those of several extant species from the comparative collections of the American Museum of Natural History, LACM, and the George C. Page Museum (RLB) were examined. Of 40 *Felis atrox* specimens one was truncated; the plantar projection is small and rounded, with a smooth surface texture and no articular facet (Fig. 2C). Small

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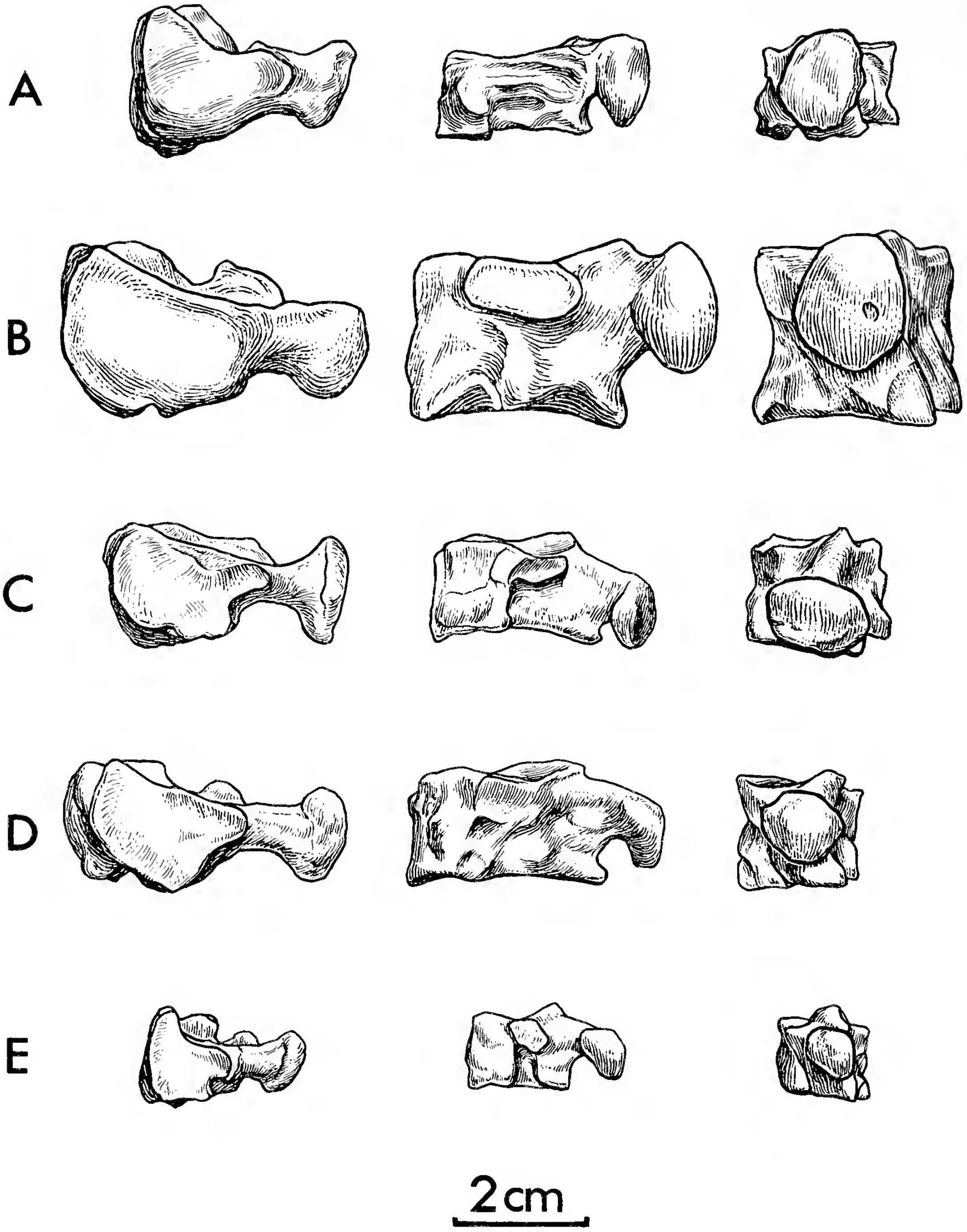

Figure 1. Normally developed left ectocuneiforms of *Smilodon* and four species of *Felis:* proximal (left), lateral (center), and plantar (right) views. A. *Smilodon* (LACMHC Q4602). B. *F. atrox* (LACMHC 10788). C. *F. tigris* (RLB 8). D. *F. leo* (LACM M1144). E. *F. concolor* (LACM M1456). Line drawing by Mark Hallett.

samples of extant felid species (*F. leo* (20), *F. tigris* (2), *F. concolor* (6), *F. cattus* (4), and *Lynx rufus* (4)) were also examined; only one *F. tigris* ectocuneiform was found to have an unfused plantar process. The prominently hooked plantar tuberosity of this specimen occurs as a separate accessory bone articulated to the body of the ectocuneiform (Figs. 2B and 3C). The articular facets are large and oval. Furthermore, in this individual, the plantar tuberosity of the ectoeuneiform is fused on the left side but not on the right.

It is likely that the plantar process is an ontogenetic center of ossification separate from the main body of the ectocuneiform. Thus far no specific mention of the occurrence of

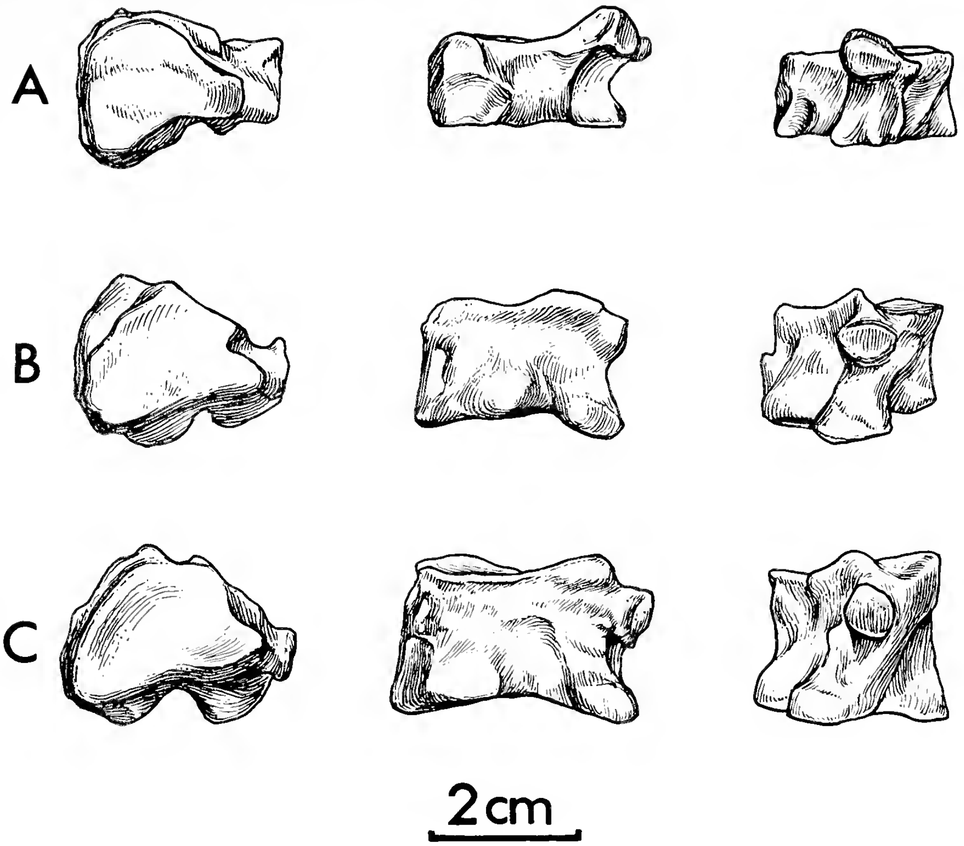

Figure 2. Truncated right ectocuneiforms of *Smilodon* and two species of *Felis:* proximal (left), medial (center), and plantar (right) views. A. *Smilodon* (LACMHC Q4445). B. *F. tigris* (RLB 8). C. *F. atrox* (LACMHC 10789). Line drawing by Mark Hallett.

accessory or supernumerary bones associated with the ectocuneiform in mammals has been found in the literature. However, other accessory or supernumerary tarsal elements are apparently common in some mammals (Davis, 1964; Grant and Basmajian, 1965). Two centers of ossification could account for the asymmetry seen in the *F. tigris* individual, with fusion taking place on the left side but not on the right.

ANATOMY

Descriptions of *Smilodon* and *Felis atrox* ectocuneiforms are provided by Merriam and Stock (1932). The body of the ectocuneiform in *F. atrox* is very similar to that of all extant felids, but that of *Smilodon* is very different. The proximal surface of the plantar process, between the body and hooked tuberosity, forms a very broad and flat neck in *Smilodon.* This neck consistently equals or exceeds the width of the proximal articular surface nearest the area of fusion to the body (Fig. 1A). In all other felids examined, this neck is medio-laterally constricted and proximo-distally rounded (oval to circular in cross section). It is smooth and flares transversely into the hooked or rounded area of tendon attachment. In the unfused specimen of *F. tigris,* the neck is flared and rugose around the area of articulation. The hook-like character of the plantar tuberosity in *Smilodon,* mentioned by Merriam and Stock (1932), is highly developed in *F. tigris,* less developed in *F. leo* and *F. concolor,* and poorly developed in *F. atrox* (Fig. 1). A summary of ectocuneiform measurements is provided in Table 1.

The variation observed in *Smilodon* ectocuneiforms may be attributed to muscular forces exerted on this bone. Two muscles interact with the ectocuneiform in modern felids, the *M. tibialis posterior* and the *M. peroneus longus.* These have been reconstructed for *F. atrox* and *Smilodon* (Fig. 4). The *M. tibialis posterior* originates on the entire medial surface of the head of the fibula and between the oblique ridges of the posterior surfaces of the tibia. The muscle ends in a slender flat tendon that passes through the dorsal groove on the medial surface of the tibia, then turns onto the plantar surface of the foot and passes through a groove on the ventral surface of the navicular. It inserts on the posterior surface of the plantar tuberosity of the ectocuneiform and the lateral tuberosity of the navicular. This muscle is an extensor of the foot (Reighard and Jennings, 1951; Crouch, 1969). The *M. peroneus longus,* a flexor of the foot, originates from two areas of the fibula, the lateral surface of the head and the proximal half of the lateral surface. This muscle terminates in a slender tendon which passes through the groove on the lateral surface of the lateral malleolus, then passes through peroneal grooves of the calcaneum, cuboid, and ectocunei-

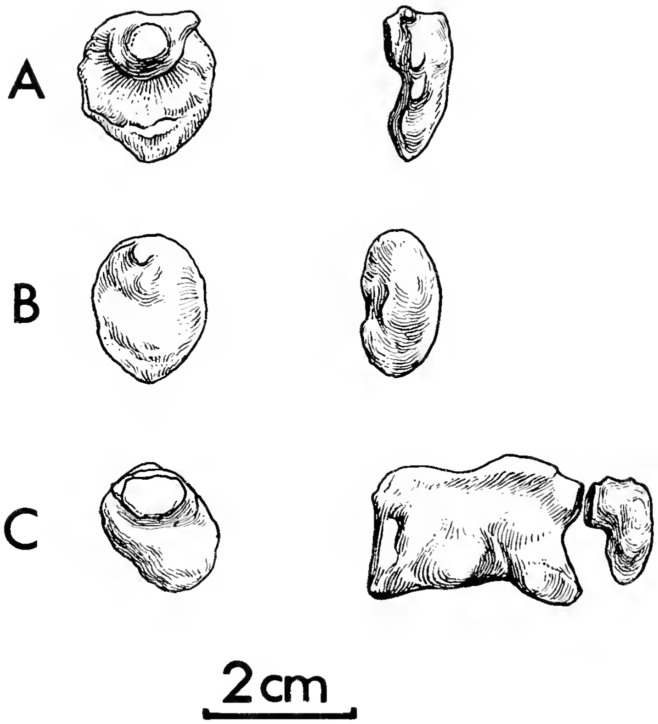

Figure 3. Unfused plantar processes of *Smilodon* and *Felis tigris:* dorsal (left) and medial (right) views. A. *Smilodon* (LACMHC 10791), hooked process with articular facet. B. *Smilodon* (LACMHC 10790), ovoid process without articular facet. C. *F. tigris* (RLB 8). Line drawing by Mark Hallett.

form. Large branches insert on the proximo-posterior bases of the first and fifth metatarsal and slender branches insert similarly on the other metatarsals (Reighard and Jennings, 1951; Crouch, 1969). In addition, the plantar tuberosity of the ectocuneiform serves as the attachment of the plantar navicularicuneiform ligaments (Davis, 1958).

BIOMECHANICS

Comparison of fore and hind limb size and strength in machairodonts has been discussed by many authors. Schaub (1925) and Bohlin (1940, 1947) assert that the heavily developed fore limbs were not balanced by equally developed hind limbs, therefore, *Smilodon* could not initiate a leaping attack on a prey animal. However, Merriam and Stock (1932) and Simpson (1941) state that the hind limb is weak only relative to the fore limb and that this genus probably began its attack by lunging or leaping.

A more exact comparison can be made by analyzing relative lever-arm ratios in the hind limbs of *Smilodon* and true cats. Any mechanical action can be described by the following equation,

$$F_o = F_i \times L_i/L_o$$

where F_o = out-force, F_i = in-force, L_i = length of the in-lever, and L_o = length of the out-lever (Hildebrand, 1974).

The out-force, in-lever, and out-lever may be calculated or directly measured for extinct species. The out-force is defined as the resistance (in this case, the body mass of the animal) that must be overcome by a muscular system to obtain momentum. Assuming only the hind limbs are employed to propel the animal forward and each foot bears an equal load, F_o equals one half of the body mass (M/2). Body

Table 1. Summary of measurements (in mm) of normally developed (normal) and truncated ectocuneiforms of *Smilodon* and *Felis atrox* from Rancho La Brea. Abbreviations: N = sample size, OR = observed range, x̄ = mean, s = standard deviation, V = coefficient of variation, Dr-Pl = dorso-plantar, Px = proximal, Dt = distal. Measurements taken after Merriam and Stock (1932).

	N	OR	x̄	s	V
		Smilodon			
Normal					
Dr-Pl depth	182	31.4–45.6	39.0	2.539	6.510
Px-Dt length	187	15.1–23.6	18.8	1.491	7.931
Dt width	184	21.0–28.6	24.7	1.461	5.915
Truncated					
Dr-Pl depth	123	26.8–36.6	31.5	2.013	6.390
Px-Dt length	122	15.1–23.0	17.8	1.461	8.006
Dt width	122	20.8–27.9	25.1	1.384	5.514
		Felis atrox			
Normal					
Dr-Pl depth	38	43.6–58.0	51.1	3.589	7.023
Px-Dt length	39	20.6–33.5	26.9	2.297	8.539
Dt width	40	24.1–33.4	29.1	2.236	7.684
Truncated					
Dr-Pl depth	1	33.5			
Px-Dt length	1	23.4			
Dt width	1	26.2			

Table 2. Measurements (in mm) of the minimum antero-posterior diameter of *Smilodon* and *Felis atrox* femora. The pits are ranked by order of descending mean weight (in kg) which is calculated using the allometric constants of Alexander et al. (1979). Abbreviations as in Table 1.

	N	OR	x̄	s	x̄ weight
		Smilodon			
Pit					
3	121	27.4–36.6	31.9	1.921	154.3
61/67	92	25.4–36.6	31.5	1.851	149.0
4	78	27.7–35.1	30.8	1.636	139.9
77	61	26.0–33.6	30.5	2.003	136.2
13	36	26.2–32.9	30.4	1.461	134.9
Total sample	415	25.4–36.9	31.3	1.947	146.3
		Felis atrox			
Total sample	23	30.8–43.7	35.1	3.450	201.2

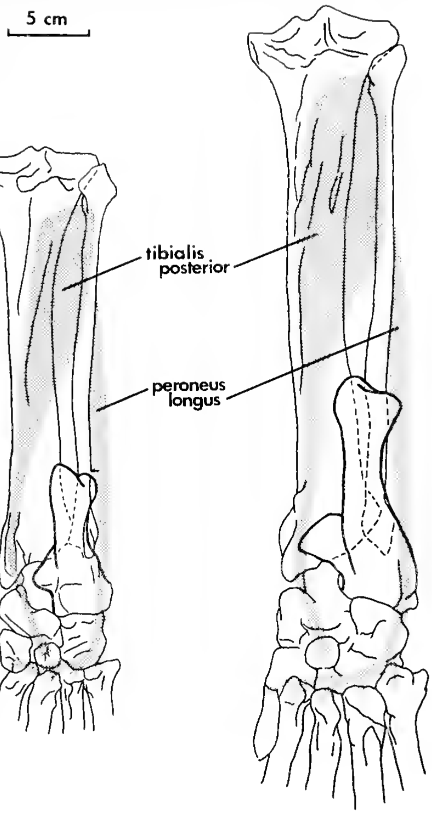

Figure 4. Posterior view of distal hind limb showing the origin and insertion of the *M. tibialis posterior* and *M. peroneus longus* in *Smilodon* (left) and *Felis atrox* (right). Illustration by Mark Hallett.

mass was calculated from the minimum antero-posterior femur midshaft diameter of *Smilodon* and *F. atrox* (Table 2) using the allometric constants of Alexander et al. (1979). Lengths of the in-lever (distal end of calcaneum to calcaneal pivot at tibia, L_i) and out-lever (calcaneal pivot to end of metatarsal III, L_o) were calculated from mean lengths of the calcaneum, navicular, ectocuneiform, and metatarsal III for *Smilodon, Felis atrox,* and *F. leo* (Tables 3 and 4).

The in-force is produced by contraction of extensors of the lower hind limb and will approximate the minimum amount of contractile force required to overcome the inertia of the body mass. These muscles include the *M. gastrocnemius, M. soleus, M. plantaris, M. peroneus brevis,* and *M. tibialis posterior.* The large *M. gastrocnemius* arises from the patella and femoral sesamoids and inserts on the distal calcaneum. The *M. plantaris* has a similar origin but crosses the tuber calcis to insert on the plantar aponeurosis of the foot. The other muscles originate along portions of the tibia and/or fibula and insert on the distal calcaneum (*M. soleus*) or on palmar areas of the foot. Using the mechanical equation above, F_i was calculated for *Smilodon, Felis atrox,* and *F. leo* (Table 4).

The out-force will become greater as the in-force or in-lever length is increased or as the out-lever length is decreased. The mean lever ratio (L_i/L_o) is nearly equal in *Felis atrox* and *F. leo.* Because the L_o of *Smilodon* has been appreciably shortened and the L_i lengthened, this ratio is proportionately much greater, increasing the potential out-force capability of hind foot extension. Adjusting for allometric differences in mass (M) between comparable species by using $M/2 = F_o$ and solving the mechanical equation gives the minimum amounts of in-force (F_i) necessary to overcome inertia. The smaller the value F_i, the more powerful the muscular contraction; the larger the value of F_i, the more rapid the

Table 3. Proximo-distal length measurements (in mm) of hind foot elements of *Smilodon, Felix atrox,* and *F. leo.* Statistics on metatarsal III of *Smilodon* taken from Menard (1947). Abbreviations: Pv-Dt = pivot to distal, * = approximately. Other abbreviations as in Table 1.

	N	OR	$\bar{x}$	s	V
		Smilodon			
Calcaneum					
Total length	50	84.6–101.5	93.5	3.628	3.879
Pv–Dt length	50	20.8–28.8	24.4	1.999	8.188
Navicular	30	16.6–21.5	18.6	1.198	6.429
Ectocuneiform	187	15.1–23.6	18.8	1.491	7.931
Metatarsal III	759	*85–112	97.8	*4.7	*4.8
		Felis atrox			
Calcaneum					
Total length	56	108.0–140.4	125.3	7.792	6.219
Pv–Dt length	56	34.1–48.9	40.9	3.579	8.744
Navicular	54	15.9–20.7	18.5	1.321	7.140
Ectocuneiform	39	20.6–33.5	26.9	2.297	8.539
Metatarsal III	49	132.0–157.8	145.7	7.292	5.004
		Felis leo			
Calcaneum					
Total length	20	90.9–114.9	103.5	6.736	6.508
Pv–Dt length	20	28.9–37.7	34.0	2.708	7.965
Navicular	20	14.1–18.2	15.8	1.151	7.287
Ectocuneiform	19	18.7–23.0	21.1	1.259	5.969
Metatarsal III	19	112.4–139.0	126.8	8.107	6.393

Table 4. Lever-arm statistics used to determine relative hind limb lever strength between *Smilodon, Felis leo,* and *F. atrox* where $F_o = F_i \times L_i/L_o$. Abbreviations: $\bar{x}$ = mean, L_i = in-lever, L_o = out-lever, M = mass, F_o = out-force, F_i = in-force. Weight of *F. leo* from Schaller (1972).

	Smilodon	***Felis leo***	***Felis atrox***
$\bar{x}$ L_i (mm)	69.1	69.5	84.4
$\bar{x}$ L_o (mm)	159.6	197.7	232.9
ratio $\bar{x}$ L_i/$\bar{x}$ L_o	0.43	0.35	0.36
$\bar{x}$ M/2 (kg) (=F_o)	72.9	81.0	100.6
minimum F_i	169.5	231.4	279.4

Table 5. Ectocuneiform samples and radiocarbon dates on bone collagen from Pits 3, 4, 13, 61/67, and 77. The sites from Rancho La Brea are ranked from oldest to youngest. Specimen data from Talara, Peru, provided by C.S. Churcher (written comm.) and radiocarbon dates from Churcher (1966). Abbreviations: Lt = left, Rt = right, % = percent of sample from the site. Other abbreviations as in Table 1.

		Normal				**Truncated**					
Pit	**Total N**	N	%	**Lt**	**Rt**	N	%	**Lt**	**Rt**	N	**OR dates**
77	169	157	92.9	81	76	12	7.1	6	6	3	28,200–33,100
4	44	32	72.7	16	16	12	27.3	6	6	12	13,500–36,000
3	141	80	56.7	40	40	61	43.3	31	30	9	12,650–21,400
13	33	30	90.9	16	14	3	9.1	2	1	4	14,310–15,360
61/67	56	36	64.3	17	19	20	35.7	14	6	5	11,130–13,600
Other pits	74	64	79.7	37	22	15	20.3	7	8	—	—
Total sample	517	394	76.2	207	187	123	23.8	66	57	33	11,130–36,000
Talara	11	6	54.5	3	3	5	45.5	2	3	4	13,616–14,418

muscular contraction. Of the three species examined (Table 4), *Smilodon* exhibits the smallest F_i, indicating a more powerful hind limb than *F. atrox* and *F. leo*. Obviously, *Felis leo* is adept at running, leaping and in-place wrestling when pursuing prey. *Smilodon*, with an even more powerful foot leverage system and less body mass, was able to propel itself more powerfully than living lions. The robust forelimbs of *Smilodon* appear to be yet more powerfully organized and constructed than the hind. Therefore, although the hind limb is "weaker" than the fore limb as Schaub (1925) and Bohlin (1940, 1947) state, and proportioned differently than in most true cats (as argued by Merriam and Stock, 1932, and by Simpson, 1941), both are clearly more powerful appendages than those of large living cats. In addition, the minimum F_i (Table 4) shows that the La Brea lion (*F. atrox*) had a disproportionately weaker (read "speedier") foot leverage system for its body mass than the smaller modern lion (*F. leo*). Thus in the La Brea ecosystem, the roles of large felids were played by the smaller, more powerfully legged sabertooth and the larger, speedier-legged lion.

CHANGES THROUGH TIME

Morphologic change during Pleistocene time is documented in many mammalian lineages. In some taxa (e.g., *Felis onca*), size is the main difference between fossil and living forms (Kurten, 1973). Many felid taxa exhibit a gradual overall size reduction throughout the Pleistocene; in contrast, the size of *Smilodon* increased (Kurten, 1965).

Samples of *Smilodon* ectocuneiforms are available from several radiocarbon dated localities (pits) at Rancho La Brea. Most sites accumulated fossil specimens within one or two brief, definable periods spanning about 3000 years or less. These are fairly evenly spaced between 11,000 and 36,000 years B.P. (Akersten et al., 1983; Marcus and Berger, 1984). The most reliable radiocarbon dates from Rancho La Brea are those measured on bone collagen (Ho et al., 1969; Akersten et al., 1983). In many instances collagen dates can be reliably correlated with stratigraphic depth within a single pit. Specimens from Pits 3, 4, 13, 61/67, and 77 have been radiocarbon dated and these sites contained the largest samples of ectocuneiforms (Table 5).

The frequency of normally developed (versus truncated) ectocuneiforms is distinct in each of these five sites (Table 5). The chi-square values show significant differences between all sites except between Pits 3 and 61/67 and between 13 and 77 (Table 6). In addition, pits in which high frequency of truncation is observed are roughly correlative to younger radiocarbon horizons (Table 5 and Fig. 5) and increased body mass (Table 2). As observed, Pits 3 and 61/67, with high

Table 6. Chi-square values comparing frequencies of normally developed and truncated *Smilodon* ectocuneiforms from five pits at Rancho La Brea. * = P < 0.05, ** = P < 0.01. Probabilities interpolated from Zar (1974).

Pit	3	61/67	4	13
61/67	0.36			
4	**	*		
13	**	**	**	
77	**	**	**	0.45

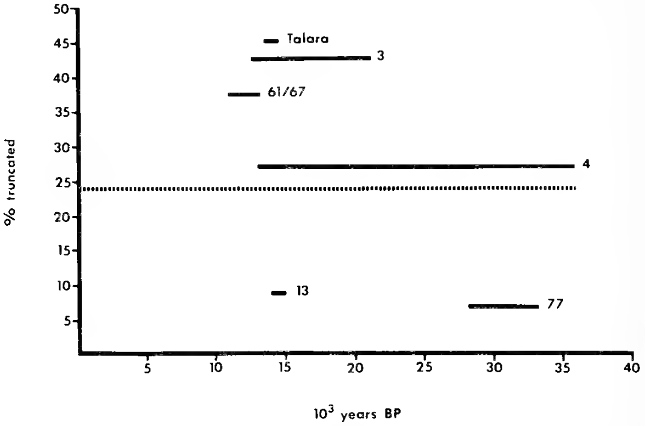

Figure 5. Change in frequency of *Smilodon* ectocuneiform truncation through time of the samples from five localities at Rancho La Brea and one from Talara, Peru. Dotted line represents the mean ectocuneiform truncation for the total sample from Rancho La Brea.

truncation frequencies, are of relatively young radiocarbon age and contain *Smilodon* with the largest mean body size. The small sample of comparable age from Talara (Table 5) also has a high frequency of ectocuneiform truncation. The sample from Pit 4 was accumulated throughout the time span represented at Rancho La Brea and, as expected, the ectocuneiform truncation frequency and mean body mass are most similar to the entire sample (Tables 5 and 6). Pit 77, which contains animals with relatively small body mass and low ectocuneiform truncation frequency, is one of the oldest sites of fossil accumulation; *Smilodon* body mass and truncation frequency is similar in Pit 13, although radiocarbon dates indicate it to be a much younger deposit, comparable in age to Pits 3 and 61/67.

The similarity between Pits 13 and 77 is unexpected. Radiocarbon dates of specimens from these pits do not appear inaccurate (Marcus, pers. comm.). The sample of *Smilodon* from Pit 13 is the least variable in observed range and standard deviation of all samples from Rancho La Brea (Tables 2 and 5; Menard, 1947). Its temporal range is also the most restricted, only spanning approximately 1000 years of accumulation (Table 5). Furthermore, the body mass calculations (Table 2) indicate a depositional episode biased toward the entrapment of small individuals. When excavating Pit 13, Wyman (1914) remarked that the *Smilodon* materials "appear to average small as compared to those from other pits," which is consistent with the low frequency of ectocuneiform truncation and the small body mass measured from femoral diameters. Thus, the low frequency of ectocuneiform truncation in Pit 13 near the terminal Pleistocene is due to an accumulation bias selectively entrapping small individuals of *Smilodon.*

DISCUSSION

Several factors may have contributed to the observed increase in frequency of plantar process truncation in *Smilodon* ectocuneiforms from Rancho La Brea. An important consideration is the effect of allometric increase of muscle and tendon size through time and the increased stress in the relatively small area of insertion on (and interaction around) the plantar tuberosity. As the *M. tibialis posterior* and *M. peroneus longus* became more massive, so did their tendons. The area of insertion of the *M. tibialis posterior* on normally developed ectocuneiforms is about equal in *Smilodon* and *Felis atrox* (a considerably larger animal); similarly, the groove for the *M. peroneus longus* is the same absolute size in both taxa (Figs. 1A and 1E). These features imply that both muscles in each taxon were of comparable size. However, the proximo-distal length of the ectocuneiform is much shorter in *Smilodon* (Table 1) and the neck connecting the plantar process is flattened and less robust. If the plantar process and body of the ectocuneiform were ontogenetically two centers of ossification, movement of a large *M. peroneus longus* tendon and the contraction of a powerful *M. tibialis posterior* would tend to continually pull the plantar process away from the body, preventing fusion. When two centers of ossification develop close together, an articular facet forms in the area of syndesmotic attachment between the bone surfaces (Fig. 3A); if they ossify further apart the ovoid plantar process (Fig. 3B) would likely function as a sesamoid within the *M. tibialis posterior* tendon. With increase of *Smilodon* body mass through time, the increased muscular stress on the plantar process of the ectocuneiform could explain the observed lower frequency of fusion between these centers of ossification.

It is interesting to note that the Felidae possess the most robust plantar tuberosity of all living mammals. Within this family, its degree of development is roughly negatively associated with cursorial behavior. It is characteristic that less cursorial felids have a large *M. tibialis posterior* (Ginsberg, 1961) and a robust plantar process with a pronounced hook for its insertion (e.g., *Felis tigris, F. onca*); the most cursorial felid (*Acinonyx*) has a reduced *M. tibialis posterior* and a reduced plantar process, very similar to canids. *F. leo* and *F. atrox* fall between these extremes. Morphologically, the plantar process of *Smilodon* is most like that of *F. tigris* and *F. onca.*

Of the large living cats, *Felis onca* is most similar to *Smilodon* in limb proportions (Gonyea, 1976a). Though digitigrade, both taxa share several features of the hind limb (short, stocky tibia and fibula, large *M. tibialis posterior,* and short, slightly splayed metatarsals) characteristic of plantigrade carnivores (Ginsberg, 1961). Ginsberg (1961) noted that *F. onca* rarely employs a "rapid pursuit phase" in prey capture, but usually leaps with a single bound, overpowering its victim; he suggests identical predatory behavior in machairodonts. Gonyea (1976b) stated that *Smilodon* probably used ambush and stalking techniques to capture prey, immobilizing it with the powerful front limbs. Similar limb proportions between *Felis onca* and *Smilodon* have been interpreted as indicative of habitat (Gonyea, 1976b); this similarity, however, is more likely to reflect a common prey capture technique. This is supported by the *Smilodon* limb mechanics presented here.

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A REVIEW OF THE GOBIID FISH GENUS *MONISHIA* SMITH, 1949, FROM THE WESTERN INDIAN OCEAN AND RED SEA, WITH DESCRIPTION OF A NEW SPECIES

Menachem Goren

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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A REVIEW OF THE GOBIID FISH GENUS *MONISHIA* SMITH, 1949, FROM THE WESTERN INDIAN OCEAN AND RED SEA, WITH DESCRIPTION OF A NEW SPECIES

Menachem Goren[1]

ABSTRACT. Five species have been included in the gobiid fish genus *Monishia* Smith, 1949: *M. william* (Smith, 1947); *M. oculata* Smith, 1959; *M. sordida* Smith, 1959; *M. ochetica* (Norman, 1927); *M. bulejiensis* Hoda, 1983. These species are compared and redescribed. *M. adamsoni,* a new species from Pakistan, is described; it is characterized by having 12 segmented dorsal rays, 22 pectoral rays (upper 6 free) and 38–39 scales along the body.

INTRODUCTION

The genus *Monishia* Smith, 1959, is known from the western Indian Ocean and the Red Sea (Smith, 1959; Miller, 1973; Goren, 1979); Smith (1959) included three Indian Ocean species: *M. william* (Smith, 1947), type species; *M. oculata* Smith, 1959; and *M. sordida* Smith, 1959. Other species subsequently assigned to *Monishia* are: *Gobius ocheticus* Norman, 1927, from the Suez Canal (Miller, 1973, 1978), and *Cabillus anchialinae* Klausewitz, 1975, from the northern Red Sea (Goren, 1979). The latter is synonymized with *M. ochetica* in this paper. An additional species, *M. bulejiensis* Hoda, 1983, was described from Pakistan. Yet another species discovered during a study of gobies from the Pakistan coast, is herein described.

Smith (1960) placed in *Monishia* the South African species *Gobius saldanha* Barnard, 1927; Talbot and Penrith (1965) transferred it to *Ctenogobius.* Winterbottom (1976), who placed it in "the overladen catchall genus *Gobius,*" noted that *G. saldanha* shows certain similarities to *Monishia* and may ultimately be placed in that genus. Miller (1978) suggested the removal of *saldanha* to *Caffrogobius* or *Gobius;* Hoese and Winterbottom (1979) assigned the species to *Nematogobius.* Further research is needed to clarify the taxonomic affinities of *saldanha;* however, I do not consider the species to be a member of *Monishia.* Miller (1978) suggested that *Ctenogobius godavariensis* Rao, may belong to *Monishia;* unfortunately, I could not obtain specimens to confirm or reject this suggestion. Hoese and Winterbottom (1979) provisionally included *Acentrogobius simulus* Smith, 1960, in *Monishia;* however, I do not place it there as it has a scaled predorsal and the upper rays in its pectoral fins are not free.

The species of *Monishia* resemble each other in morphology and color pattern, probably due to the similarity of the habitats they populate. The fishes that belong to this genus are small, usually 30–40 mm in total length, never longer than 60 mm. The genus is characterized by having the upper rays of the pectoral fins free (at least partly) and filamentous. The pelvic fins are fully united with a well-developed fraenum. The caudal fin is rounded and shorter than the head. Scales along the body 26–40. Most of the scales are ctenoid; only the anterior ones are cycloid. The scales reach a line from the upper base of the pectoral to a point on the first dorsal fin base, usually its insertion. The head, predorsal, and prepelvic regions are naked. Vertebrae (including ural centrum) 27 (in two individuals of *O. ochetica,* 28). The lateral line system consists of cephalic canals with pores and rows of sensory papillae. The cephalic pore system consists of the following: a pair of nasal pores; unpaired anterior and posterior interorbital pores; pairs of supra-otic, anterio-otic, posterio-otic, and intertemporal pores. All of these pores open along a continuous canal. The anterior and posterior temporal pores open in a separate canal, except in *M. sordida* in which all of the above-mentioned pores are connected. Three preopercular pores, on the posterior margin of the preopercle, are connected by a canal. The sensory papillae are arranged mostly in vertical rows with two horizontal rows on the cheek, two on the opercle, and a discontinuous row above the opercle and the pectoral base. The strueture of the lateral line system of each species is illustrated in the figures.

The genus *Monishia* is closely related to *Hetereleotris* Bleeker, 1874, and *Coryogalops* Smith, 1958. Each of the three genera has a depressed head, unscaled head and nape, 4–6 vertical, and 1–2 horizontal rows of papillae on the cheek

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Table 1. A summary of selected diagnostic characters in six species of *Monishia*.

	ochetica n = 47	*oculata* n = 6	*sordida* n = 8	*william* n = 10	*adamsoni* n = 3	*bulejiensis* n = 5
Scale alone body	26–31	30–33	34–36	34–36	38–39	31–33
Transverse scale rows	8–9	11	12–13	9–10	10–11	9–10
Segmented rays in second dorsal fin	10–11 (12)	9	11	(10) 11	12	11
Segmented rays in anal fin	9–10	8	9	9	9	9
Pectoral rays	16–18	17–18	22	22–23	22	20
Free pectoral rays	2	3–4	5	6–7	6	5
Gill rakers	1+1+5	1+1+4	1+1+6	1+1+4	1+1+6	1+1+6
Vertebrae (including urostyle)	27 (28) (n = 14)	27	27	27	27	27
Scales on pectoral base	–	–	+	–	–	–

arranged in a similar pattern. In addition the first gill slit of *Heterelеotris* is closed by a membrane as in *Monishia* (at least partly). The cephalic pore system of *Coryogalops* is similar to that of *Monishia william*. *Monishia* differs from *Hetereleotris* in possessing ctenoid scales (vs. cycloid or naked body), in having gill rakers on the anterior gill arch (vs. none) and in the interorbital pore being always unpaired holes (vs. tubular, mostly paired pores). *Coryogalops* differs from *Monishia* in having the first gill arch completely free, posterior nostril a hole (vs. tubular) and pelvic fins completely separated, with the tips of the rays free.

Little is known of the biology of the species of *Monishia*. My specimens were all taken in shallow water, usually less than 2 m deep, although a few specimens of *M. ochetica* were collected at a depth of 8 m (in artificial reefs). The fish seems to be resistant to extreme ecological conditions. *M. ochetica* was found in Lake Timsah, Suez Canal, where temperatures fluctuate from 14 to 26.5°C and salinity from 30 to 50 parts per thousand (Miller, 1978). *M. anchialinae* was found for the first time in the hyperhaline water bodies of the Cracks at Ras Muhammad, Sinai Peninsula (Klausewitz, 1975). *M. william* was found in brackish water at the mouth of Nora River, southeast Africa, as well as in other localities and habitats (Winterbottom, 1976). The species that is described here as new was found in tidal pools. The diet of *M. william* consists of amphipods, isopods, polychaetes, and occasional decapods and mollusks (Winterbottom, 1976). Very little is known about the reproductive behavior of the genus. The only available information refers to *M. sordida:* "... apparently male, indicates buccal incubation, for its mouth is full of eggs, similar to those found in a female" (Smith, 1959: 207).

METHODS AND MATERIALS

Specimens from the collections of the following institutions were studied: British Museum (Natural History), London (BMNH); Hebrew University of Jerusalem (HUJ); Natural History Museum of Los Angeles County (LACM); J.L.B. Smith Institute of Ichthyology, Grahamstown (RUSI); Senckenberg Museum of Frankfurt (SMF); Zoological Museum of Tel Aviv University (TAU).

Counts of vertebrae were made from X-ray photographs taken for all the listed material in this work excluding *M. ochetica*, of which only 14 specimens were photographed (TAU 7606, 5 spec.; TAU 6206 + TAU 6211, 5 spec.; TAU 5592, 1 spec.; HUJ 7571, 3 spec.).

X-ray photographs were also used to verify the counts of the spines and rays in the dorsal and anal fins.

All measurements and counts given in the text and the tables are based on the material examined and listed. Measurements are given in mm. In cases in which the total length could not be measured due to a damaged caudal fin, TL is followed by ?.

The lists of synonyms include only publications in which the taxonomy of a species is discussed or changed, or in which additional information about the species is provided.

COUNTS. A, D, P, V—anal, dorsal, pectoral, and pelvic fins, respectively; the posterior bifid ray of second dorsal and anal ray counted as one.

MEASUREMENTS. BD—body depth at the insertion of the first dorsal fin; GR—number of gill rakers on anterior gill arch; HL—head length from snout tip to upper attachment of opercular membrane; LS—longitudinal scale counts from upper attachment of the opercular membrane to the end of the hypural; SL—standard length; TL—total length; TR—number of transverse scale rows, counted from the origin of second dorsal fin.

KEY TO SPECIES OF *MONISHIA*

1. Pectoral fin base with scales. .... *M. sordida* Smith
–. Pectoral fin base naked 2
2. Dorsal segmented rays 9; anal segmented rays 8 .... *M. oculata* Smith
–. Dorsal segmented rays 10–12; anal segmented rays 9–10 3

3. LS scales 38–39; segmented dorsal rays 12 .... *M. adamsoni* n. sp.
–. LS scales fewer than 37; segmented dorsal rays 10–11 (rarely 12, but then LS fewer than 32) 4
4. LS scales 26–30; pectoral fin rays 16–18 .... *M. ochetica* (Norman)
–. LS scales 32–36; pectoral fin rays 20–22 5
5. A tentacle on posterior part of upper margin of eye ... . *M. bulejiensis* Hoda
–. No tentacle on posterior part of upper margin of eye .. .. *M. william* (Smith)

Species are also distinguished in Table 1.

SPECIES ACCOUNTS

Monishia adamsoni new species

Figures 1a, 2, 4a

MATERIAL EXAMINED. Holotype. LACM 38320-23, TL 41.4 mm, SL 35.0 mm; Pakistan, Sind, small cove 4.8 km west of Nuclear Power Plant, 13.II.1979, in shallow water (to 2 m), rocky bottom with sandy pockets. Paratypes. TAU 8800, TL 42.1 mm, SL 35.5 mm, data as for holotype; LACM 38310-26, TL 36.3 mm, SL 30.7 mm; Pakistan, Sind, Beluji Point, 27.I.1979, tidepool, shallow water (to 60 cm), conglomerate bed with rocky rubble.

ADDITIONAL MATERIAL. RUSI 74-91 (part), 1 ex., TL 20.5 mm, SL 17.1 mm, South Africa, Beauchamp, 1 mile E on road near Taeotet Bay, 0.3 miles E of St. Marie Bridge at jutting head of the island, 6.III.1971.

ETYMOLOGY. This species is named in honor of Thomas A. Adamson (formerly of the Natural History Museum of Los Angeles County) for his genuine interest in Indo-West Pacific fishes and his valuable contributions to ichthyology.

DIAGNOSIS. A *Monishia* with 12 segmented rays in second dorsal fin; pectoral rays 22, the upper 6 free; filamentous; scales along body 38–39; gill rakers 1+1+6. In addition *adamsoni* has a distinctive arrangement of the rows of sensory papillae on head (Fig. 4a). Comparisons are presented in Table 1.

DESCRIPTION (based on holotype and 2 paratypes). Body elongate and compressed. Head depressed, its upper profile moderately convex. Mouth almost horizontal. Maxillary reaches level of front of eye. Three to four rows of teeth on each jaw, outer teeth on both jaws and inner teeth on lower jaw enlarged. A pair of curved canines on the sides of the outer teeth row on lower jaw. Tongue truncate with a slight median emargination. Posterior nostril a short tube at front of eye. Anterior nostril a long tube, with a tentacle on top, overhanging labial groove. Eyes of moderate size, interorbital space narrow. Gill opening restricted, reaching to below pectoral base. Gill rakers short 1+1+6.

Body proportions presented in Table 2.

Fins. D VI, I 12; A I 9; P 22—upper 6 rays free; the first fin is little shorter than the second, which is about two thirds of body depth. Pectoral fins rounded, not reaching level of insertion of the second dorsal fin. Pelvic fins fully united with a well-developed fraenum. The pelvics do not reach the anus. Anal fin inserts below third segmented dorsal ray. Its height about two thirds of body depth. Caudal fin rounded.

Scales. LS 38–39; TR 10–11; body scales ctenoid, except for the three–four anterior transverse rows. Predorsal and prepelvic regions, pectoral base, and mid belly completely naked. Vertebrae (including ural centrum): 27.

Cephalic lateral line system. Position and number of pores and papillae as in Figure 4a.

Color (preserved). Body and head brownish, covered with irregular dark speckles. A dark blotch on the upper base of the pectorals and a vertical dark band on the base of the caudal fin. First dorsal fin with two oblique large dark bands. The upper tip of the fin white. Second dorsal fin brownish.

Monishia bulejiensis Hoda, 1983

Figures 1b, 3, 4b

Monishia bulejiensis Hoda, 1983a:111–115; 1983b:143–147.
Type locality: Karachi coast, Pakistan.

MATERIAL EXAMINED. LACM 38310-27 (2 ex.), TL 35.5–38.1 mm, SL 29.8–31.5 mm; TAU 8801 (2 ex.), TL 32.7–36.5 mm, SL 27.2–30.1; LACM 38309-22, TL 31.3

Table 2. Measurements and body proportions of the types of *Monishia adamsoni* n. sp.

	Holotype (LACM 38320-23)	Paratype (TAU 8800)	Paratype (LACM 38310-26)
Total length (mm)	41.4	42.1	36.3
Standard length (mm)	35.0	35.5	30.7
Body depth (mm)	7.2	7.6	6.1
Head length (mm)	10.6	11.2	8.5
Head width (mm)	8.6	8.7	6.7
Standard length (% of TL)	84.5	84.3	84.5
Body depth (% of SL)	20.5	21.4	19.7
Head length (% of SL)	30.3	31.5	27.7
Head width (% of SL)	24.6	24.5	21.8
Head depth (% of SL)	20.0	19.1	18.6
Distance between snout and first pectoral fin (% of SL)	39.1	37.4	38.1
Distance between snout and second pectoral fin (% of SL)	57.4	58.3	57.0
Distance between snout and anal fin (% of SL)	62.8	61.9	62.3
Eye diameter (% of SL)	8.0	8.7	8.4
Longest pectoral ray (% of SL)	19.1	19.1	18.2
Longest spine in first dorsal fin (% of SL)	11.1	12.9	12.0
Longest ray in second dorsal fin (% of SL)	12.8	14.6	13.7
Longest anal ray (% of SL)	14.0	14.3	13.0
Head width (% of HL)	81.1	77.6	78.8
Eye diameter (% of HL)	26.4	27.6	26.8

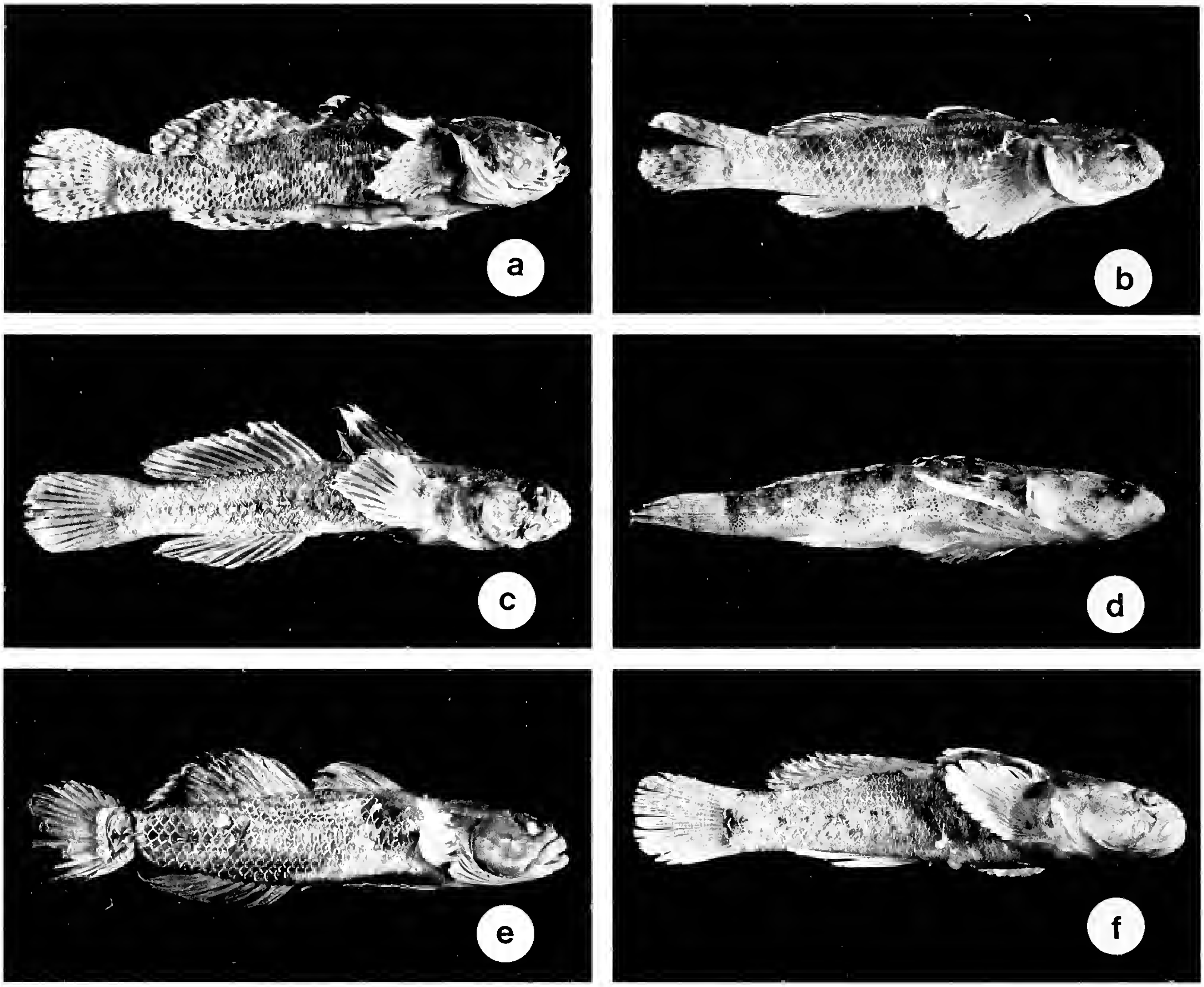

Figure 1. Photographs of six species of *Monishia.* a) *M. adamsoni* n. sp. Holotype LACM 38320, SL 35.0 mm. Sind; Pakistan. b) *M. bulejiensis* LACM 38310, SL 31.5 mm. Sind; Pakistan. c) *M. ochetica* TAU 7607, SL 45.7 mm. Ras Muhammad, Sinai Peninsula. d) *M. oculata* RUSI 830 (Paratype), SL 20.5 mm. Baixo Pinda. e) *M. sordida* RUSI 823 (Paratype), SL 37.5 mm. Inhaca Islands. f) *M. william* TAU 8803 (formerly RUSI 74-329), SL 32.5 mm. Coffee Bay. Photographs by L. Maman.

mm, SL 26.3 mm; LACM 38210 and TAU 8801 were collected in Pakistan, Sind, Beluji Point, 27.I.1979, in shallow water (to 60 cm) (tidepool), conglomerate bed with rocky rubble. LACM 38309 was collected in Pakistan, Sind, Beluji Point (300 m WNW of the point), shallow water (tidepool—0.15 cm), conglomerate bed, 27.I.1979.

DIAGNOSIS. A *Monishia* with 11 segmented rays in second dorsal fin and 9 in anal fin; pectoral rays 20, the upper 6 free and filamentous; scales along body 31–33; transverse scale rows 9–10; a small tentacle on the upper posterior edge of the eye. Possession of this tentacle distinguishes *M. bulejiensis* from all known *Monishia.* In addition *M. bulejiensis* has a distinctive arrangement of the rows of sensory papillae (Fig. 4b). Comparisons are presented in Table 1.

DESCRIPTION (based on all specimens listed). Body elongate and compressed. Head depressed, its upper profile convex. Mouth oblique. Maxillae reach to level of mid eye. On the upper posterior part of eye, just within the margin, is a short cylindrical pointed tentacle, an outgrowth of the sclerotic coat, its length equal to the length of the anterior nostril. Each jaw with 3–4 rows of teeth, the outer teeth on each jaw enlarged. No canines. Tongue truncate. Gill opening restricted, reaching to below pectoral base. Gill rakers 1+1+6. Vertebrae (including ural centrum): 27.

Cephalic lateral line system. Position and number of papillae as in Figure 4b.

Body proportions presented in Table 3.

Fins. D VI, I 11; A I 9; P 20, upper 5 rays free. First dorsal

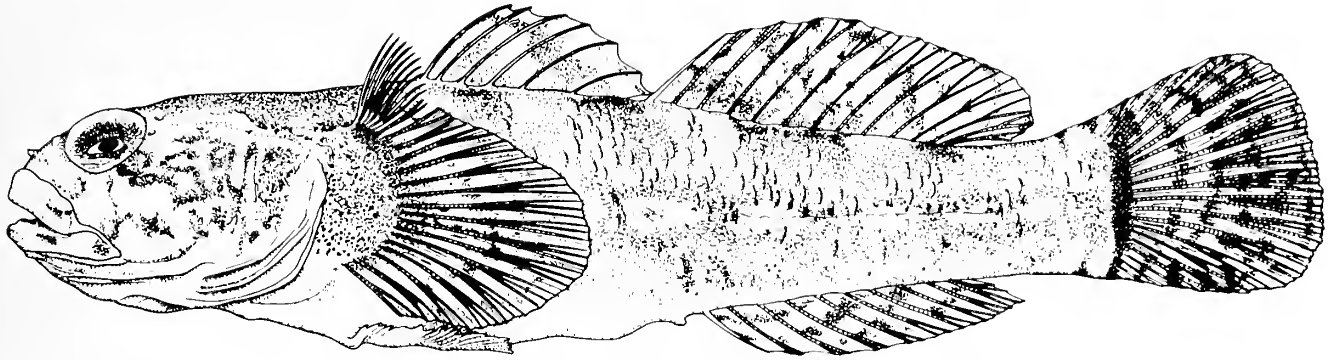

Figure 2. *Monishia adamsoni* n. sp. Holotype LACM 38320, SL 35.0 mm. Sind; Pakistan. Drawing by W. Ferguson.

fin little shorter than second dorsal fin, which is about two thirds of body depth. Anal fin inserted below second dorsal segmented ray. Pectoral fin rounded, reaching to below sixth dorsal spine. Pelvic fins fully united with a well-developed fraenum. Caudal fin rounded.

Scales. LS 31–33; TR 9–10. The body is covered with ctenoid scales except those on belly and three–four anterior rows on body which are cycloid. No scales on the median line of the belly, on predorsal, pectoral base, and prepelvic regions.

Color (preserved). Brownish, irregular dark speckles. A series of light spots along the midlateral scale row. First dorsal fin dark with upper margin white (about one quarter of its height). Second dorsal fin and anal fin dark with a light line along their edges. Pectoral fin dusky. Caudal fin with irregular vertical dark rows.

Monishia ochetica (Norman, 1927)

Figures 1c, 4c

Gobius ocheticus Norman, 1927:381, figs. 92–93. Type locality: Suez Canal.
Pomatoschistus (*Ninnia*) *ocheticus:* De Buen, 1930:132.
Coryphopterus ocheticus: Smith, 1959:211, pl. 93H.
Monishia ochetica: Miller, 1973:501; Miller, 1978:38–58.
Cabillus anchialinae Klausewitz, 1975:203–207.
Monishia anchialinae: Goren, 1979:46–48.

MATERIAL EXAMINED. BMNH 1925.9.19.114–123, (syntypes of *G. ocheticus*), 7 ex., TL 18.2–32.4 mm, SL 16.2–28.2 mm, Suez Canal, Lake Timsah, 1924; BMNH 1925.12.31.54–58 (syntypes of *G. ocheticus*), 4 ex., TL 21.5–33.0 mm, SL 18.2–27.0 mm, Suez Canal, 1924; SMF 13229 (holotype of *Cabillus anchialinae*), TL 41.1 mm, SL 33.4 mm; SMF 13230–13232 (paratypes of *C. anchialinae*), 3 ex., TL 26.7–34.5 mm, SL 23.2–28.6 mm, Sinai Peninsula, Cracks at Ras Muhammad (detailed description of the biotope in Por and Tsurnamal, 1973), VI.1972; TAU 7606, 5 ex., TL 33.1–51.0 mm, SL 28.0–45.7 mm, Cracks at Ras Muhammad, 16.X.1969; 26 ex., around Sinai Peninsula (detailed list in Goren, 1979, as *Monishia anchialinae*), TL 24.0–47.0 mm, SL 20.0–38.4 mm; HUJ E 62/532, Southern Red Sea, Nocra, 1 ex., TL 24.0 mm, SL 20.0 mm, 23.III.1962.

DIAGNOSIS. A *Monishia* with 10–11 segmented rays in second dorsal fin and 9–10 in anal fin; pectoral rays 16–18, upper 2 partly free; scales along body 23–31; transverse scale

Table 3. Selected body proportions of *M. ochetica, M. oculata, M. sordida, M. william,* and *M. bulejiensis.*

	ochetica n = 47	***oculata*** n = 6	***sordida*** n = 8	***william*** n = 10	***bulejiensis*** n = 5
Total length (mm)	24.0–51.0	15.5–25.6	32.7–43.3	27.8–41.2	31.3–38.1
Standard length (mm)	20.0–45.7	12.8–21.3	27.9–37.5	22.9–34.0	26.3–31.5
Standard length (% of TL)	81.0–84.2	81.4–83.2	82.2–86.8	81.5–83.9	82.5–84.0
Head length (% of SL)	27.8–30.5	27.9–29.1	29.6–32.9	29.4–30.2	28.5–30.4
Body depth (% of SL)	18.1–23.2	15.9–16.7	19.7–20.6	18.3–21.1	17.6–20.8
Distance between snout and first dorsal fin (% of SL)	34.2–36.8	35.4–37.4	35.3–36.5	36.1–37.6	35.4–39.0
Distance between snout and second dorsal fin (% of SL)	52.3–56.0	54.3–56.3	54.6–56.6	54.4–58.2	52.2–56.2
Distance between snout and anal fin (% of SL)	52.7–56.2	54.6–56.3	56.6–58.6	54.4–57.3	57.0–60.4
Head width (% of HL)	61.1–71.2	51.2–53.0	70.2–71.4	68.5–71.4	71.4–75.0
Eye diameter (% of HL)	25.4–30.1	25.0–26.0	25.0–26.1	24.2–25.0	25.0–27.5

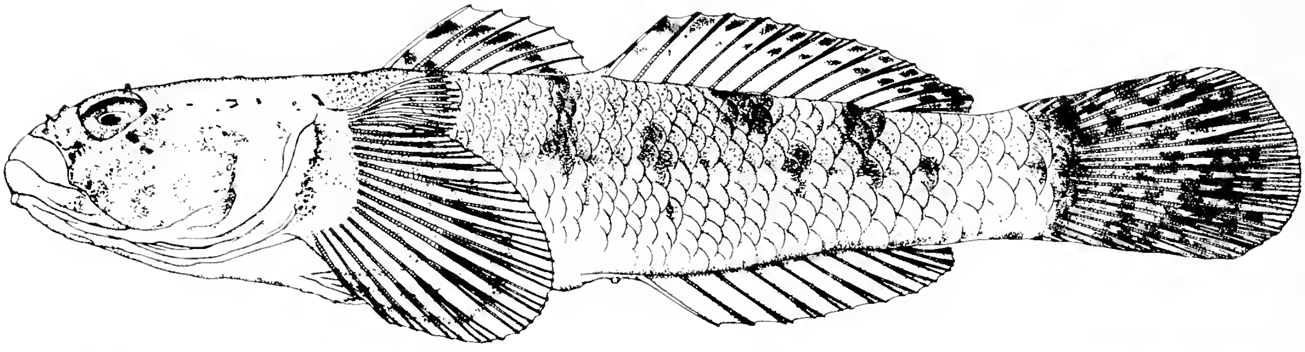

Figure 3. *Monishia bulejiensis* LACM 38310, SL 31.5 mm. Sind; Pakistan. Drawing by W. Ferguson.

rows 8–9; gill rakers 1+1+7. Comparisons are presented in Table 1.

DESCRIPTION (based on the above listed material). Body elongate and compressed. Head slightly depressed. Mouth small, oblique. Three–four rows of teeth on each jaw; outer teeth larger, inner a little curved backward. Tongue bilobed. Posterior nostril a very short tube, in front of eye. Anterior nostril tubular, close to upper lip. Interorbital space narrow, about one half pupil diameter. Gill opening restricted. Gill rakers 1+1+5–7, relatively short.

Cephalic lateral line system. Position and number of pores and papillae as in Figure 4c.

Body proportions presented in Table 3.

Fins. D VI, I 10–11; A I 9–10; P 16–18, 2 upper rays partly free. In the isolated population at the Cracks at Ras Muhammad (the type locality of *M. anchialinae*) two specimens were found with seven spines in first dorsal fin and 12 segmented dorsal rays. First dorsal fin high relative to that of the other *Monishia* species. Longest dorsal spines equal to body depth; second dorsal fin reaches almost the same height. Anal fin inserts below second dorsal segmented ray. Pectoral fins rounded, each to below the insertion of the second dorsal fin. Pelvic fins fully united. Fraenum weak. Caudal fin rounded.

Scales. LS 26–31; TR 8–9. Body covered with ctenoid scales except those on belly which are cycloid. The scales reach a line from the insertion of the first dorsal fin to the upper part of pectoral base. No scales on predorsal and prepelvic areas, and none on pectoral base.

Vertebrae. 27 including ural centrum (28 in 2 specimens from the Cracks at Ras Muhammad, not those with 7 spines or 12 segmented dorsal rays).

Color. Body and head brownish. Dark blotches along median line of the body. Irregular darker bands on body. Head darker than body. Back of the body and the upper part of head darker than the rest of the body. First dorsal fin with two large diagonal black bands. In several specimens the first dorsal fin is uniformly dark with its tip white. Second dorsal fin and anal fin dusky with white edges. Pelvic fins dark. Caudal fin with vertical irregular lines of dark spots.

REMARKS. In a previous paper (Goren, 1979) I noted that *M. anchialinae* is in fact a synonym of *M. ochetica*, but I left the two species separate as I had some hestitation that arose from apparently contradictory information concerning the habitats of the two nominal species. A further study in which fresh material from the Cracks at Ras Muhammad was included, as well as many observations in the Red Sea during the last four years, settled the question. These fish were observed always on or near hard substratum which in most of the occasions was located in sandy areas. In certain cases it was a small coral knoll, but usually the fish were observed in or near small coral heads, mollusk shells, and even artificial objects such as bottles and tins. The fish searched for food on the sand in close proximity to the hard substratum and hid in holes when disturbed. I conclude that when specimens of *M. ochetica* were collected from what seemed to be soft bottom, hard substratum was actually part of the habitat. Thus, on the basis of these new observations and additional examinations of material, I regard *M. anchialinae* as a junior synonym of *M. ochetica.*

Monishia oculata Smith, 1959

Figures 1d, 4d

Monishia oculata Smith, 1959:206. Type locality: Mahé; Miller, 1978:56.

MATERIAL EXAMINED. RUSI 830, paratypes, 3 ex., TL ?, SL 15.3–20.5 mm, Baixo Pinda, 10.IX.1956; RUSI 74-95 (part), 3 ex., TL 15.5–25.9 mm, SL 12.8–21.3 mm, Beauchamp, 1 mile E on road near Jacotet Bay, 0.3 miles E of St. Marie Bridge at jutting head of island, 6.III.1971.

DIAGNOSIS. A *Monishia* with a wide dark band from eye to lower edge of preopercle. Second dorsal fin with 9 segmented rays. Anal fin with 8 segmented rays; pectoral rays 17–18, upper 3–4 free; scales along body 30–33; transverse scale rows 11; first gill slit closed by a membrane. *M. oculata* can be distinguished from all its congeners by a diagonal dark band below eye. Comparisons are presented in Table 1.

DESCRIPTION (based on the above listed material). Body elongate and compressed. Head depressed. Mouth little oblique. Maxillae to level of mid eye. Three to four rows of teeth on each jaw. Outer teeth enlarged. The two lateral pairs of teeth in the inner row of the lower jaw are caniniform. Tongue bilobed. Posterior nostril a short tube, in front of eye. Anterior nostril tube above lip. No flaps on nostrils. Gill

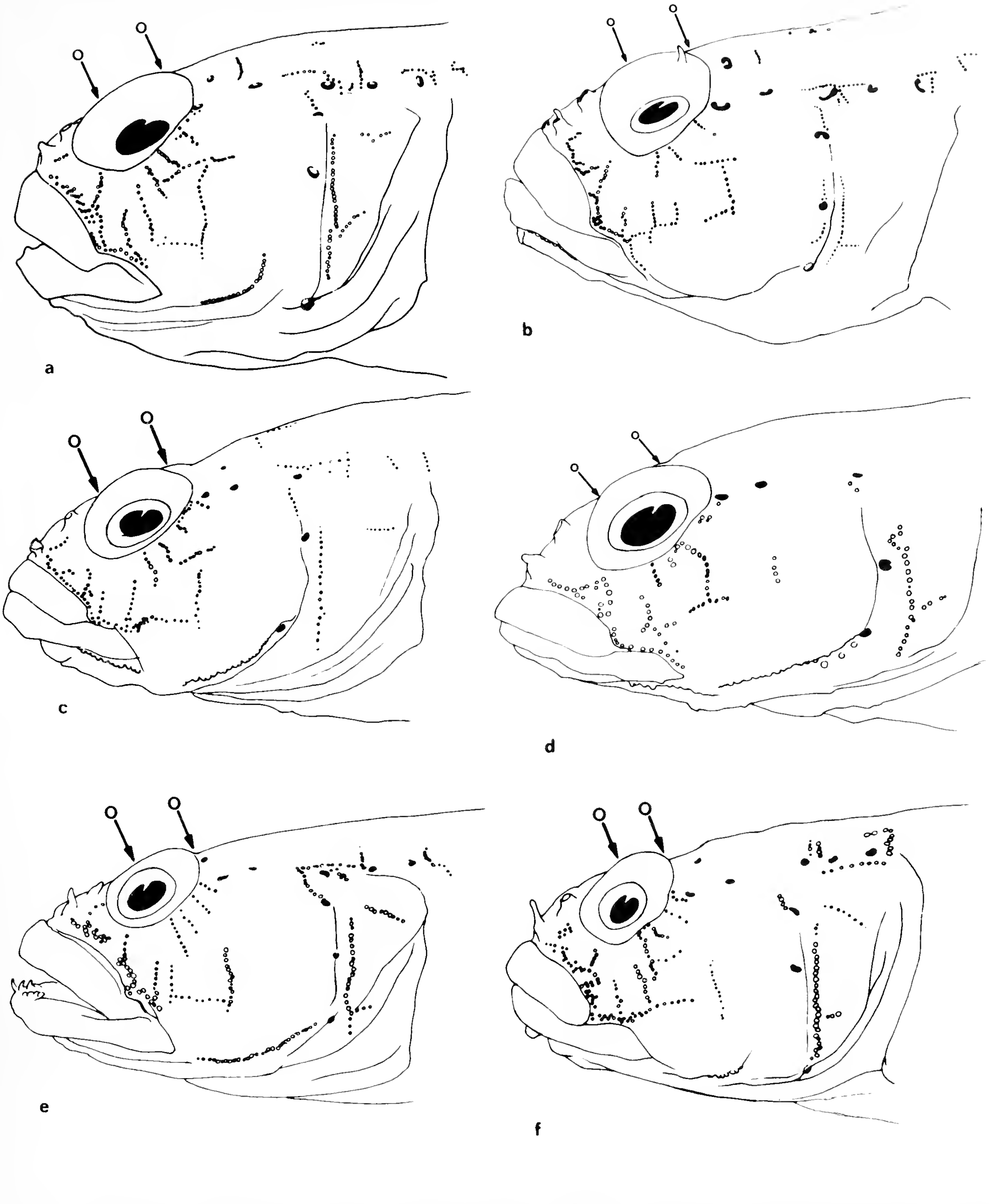

Figure 4. Lateral line sensory papillae and canal pores in six species of *Monishia*. a) *M. adamsoni* n. sp. Holotype LACM 38320. Sind; Pakistan. b) *M. bulejiensis* LACM 38310. Sind; Pakistan. c) *M. ochetica* TAU 7606, Ras Muhammad, Sinai Peninsula. d) *M. oculata* RUSI 830 (Paratype). Baixo Pinda. e) *M. sordida* RUSI 823 (Paratype). Inhaca Islands. f) *M. william* TAU 8803 (formerly RUSI 74-329). Coffee Bay. Drawing by W. Ferguson.

opening restricted. First gill slit closed by a membrane. Gill rakers 1+1+4, very short.

Vertebrae (including ural centrum). 27.

Cephalic lateral line system. As shown in Figure 4d.

Body proportions are presented in Table 3.

Fins. D VI, I 9; A I 8; P 17–18, upper 3–4 rays free. Dorsal fin height less than body depth. Pectoral fins rounded, reaching to below second dorsal segmented rays. Upper pelvic rays free. Pelvic fins fully united, almost reaching the anus. Fraenum developed. Caudal fin rounded.

Scales. LS 30–33; TR 11. Ctenoid scales on body, reaching to a line from second dorsal spine to upper part of pectoral base. No scales on mid belly, pectoral base, prepelvic and predorsal regions.

Color (preserved). Body yellowish with four vertical wide and irregular brown bands; that on caudal base much darker. A dark wide band runs from eye down and backward to preopercle margin. Two oblique dark bands on first dorsal fin. Dark spots form irregular vertical lines on second dorsal and anal fins. Pelvic fins colorless to dark. Caudal fin colorless.

Monishia sordida Smith, 1959

Figures 1e, 4e

Monishia sordida Smith, 1959:206–207. Type locality: Inhaca; Miller, 1978:55–56.

MATERIAL EXAMINED. RUSI 823, paratypes, 3 ex., TL 38.1–43.3 mm, SL 32.3–37.5 mm, Mozambique, Inhaca Islands, VIII.1948; TAU 8802 (out of RUSI 3018), 5 ex., TL 32.7–41.7 mm, SL 27.9–34.0 mm, Mozambique, Lourenco Marques, Ponte Maone, X.1953.

DIAGNOSIS. A *Monishia* with 2–3 vertical rows of scales on pectoral base; scales along the body 34–36, transverse scale rows 12–13; segmented rays in second dorsal fin 11 and in anal fin 9; pectoral rays 21–22, the upper 5 free. *Monishia sordida* differs from all its congeners in having scales on pectoral base. Comparisons are presented in Table 1.

DESCRIPTION (based on the above listed material). Body elongate and compressed. Head depressed. Snout convex, little shorter than eye diameter. Mouth oblique. Maxillae reach to level of mid eye, 3–4 rows of teeth on each jaw, the outer enlarged. At the middle of the inner row of the upper jaw two large canines directed backward. Two to three curved canines on each side of inner row on lower jaw. Tongue slightly emarginate. Posterior nostril a short tube at the front of eye. Anterior nostril, a tube with a flap, hanging above lip. Gill opening restricted. Gill rakers relatively long, 1+1+6.

Vertebrae (including ural centrum). 27.

Cephalic lateral line system. As in Figure 4e.

Body proportions presented in Table 3.

Fins. D VI, I 11; A I 9; P 22 (5 free). The two dorsal fins are the same height, which is about two thirds of body depth. Pectoral fins rounded, reaching to below insertion of second dorsal fin. Pelvic fins fully united with a weak fraenum. The pelvics reach 65–80 percent of the distance between the anus and the pelvic fin base. Caudal fin rounded.

Scales. LS 34–36; TR 12–13. The body covered with scales posteriorly from a line from the first dorsal fin insertion to the upper base of the pectoral fin. Scales in the anterior 2–3 transverse rows are cycloid, the rest are ctenoid. Belly and pectoral base covered with cycloid scales. No scales on prepelvic and predorsal regions.

Color (preserved). Body brownish. A black blotch on the upper part of the pectoral base. Two wide diagonal dark bands on first dorsal fin. Dark dots form diagonal lines on the second dorsal fin and vertical lines on the caudal fin.

REMARKS. Winterbottom (1976) found prepelvic scales in some specimens of *M. sordida* "(Not in all individuals)," but I found none.

Monishia william (Smith, 1947)

Figures 1f, 4f

Bathygobius william Smith, 1947:340. Type locality: Xora River Mouth, Transkei (lectotype by Winterbottom, 1976).
Monishia william: Smith, 1959:206–207; Winterbottom, 1976:1–11; Miller, 1978:49–56.

MATERIAL EXAMINED. RUSI 74-348, 1 ex., TL 39.0 mm, SL 32.5 mm, Chaka's Rocks, Natal, 3.IX.1974; RUSI 77-12, 2 ex., TL 34.1–37.5 mm, SL 27.8–30.5 mm, Port Edward, 31.V.1977; RUSI 74-322, 2 ex., TL 27.8–28.8 mm, SL 22.9–23.4 mm, Tshani, Transkei, VIII.1974; TAU 8803 (formerly RUSI 74-329), 5 ex., TL 32.5–41.2, SL 27.0–34.0 mm, Coffee Bay, 6.VIII.1974.

DIAGNOSIS. A *Monishia* with 11 (rarely 10) segmented rays in second dorsal fin and 9 in anal fin. Scales along body 34–36; transverse scale rows 9–10; pectoral fin with 22–23 rays, upper 6–7 free; first gill slit closed by a membrane; gill rakers very short (1+1+4). Comparisons are presented in Table 1.

DESCRIPTION (based on the above listed material). Body elongate and compressed. Head slightly depressed. Snout oblique-convex. Posterior nostril a short tube in front of eye. Anterior nostril a moderate tube (about one third diameter of pupil) with a skin flap at its hind margin. Mouth little oblique. Maxillae reach to below mid eye. Two to three rows of teeth on both jaws. Outer teeth on upper and lower jaws enlarged and pointed. A pair of canines at the side of the lower jaw. Tongue rounded. Interorbital space narrow, about one third diameter of pupil. Gill opening restricted, reaching lower part of pectoral base. First gill slit closed by a membrane. Gill rakers short, 1+1+4.

Vertebrae (including ural centrum). 27.

Cephalic lateral line system. As in Figure 4f.

Body proportions presented in Table 3.

Fins. D VI, I 11 (10 in one); A I 9; P 22–23, the upper 6 or 7 rays free. Dorsal fins of equal height; longer spines and rays reach about two thirds of body depth. Second dorsal fin inserting above anus. Anal fin inserting below second dorsal segmented ray, its height about two thirds of body depth. Pectoral fins rounded, reaching to below insertion of second dorsal fin. Pelvic fins fully united, fraenum well developed. Caudal fin rounded.

Scales. LS 34–36; TR 9–10. Body covered with scales to a line from insertion of first dorsal fin to upper base of pectoral fin. Scales in anterior 3–4 transverse rows and those on belly are cycloid, the rest are ctenoid. Mid belly, pectoral bases, and predorsal and prepelvic regions unscaled.

Color (preserved). Body brownish with 4–6 irregular dark vertical bands. Black blotches along median line of body. Dark vertical half-moon blotch on the base of the caudal fin. A dark blotch on the upper part of the pectoral base; first dorsal fin with two diagonal wide dark bands. Rows of black spots form vertical lines on the caudal fin and diagonal lines on second dorsal and anal fin.

Remarks. The counts presented in this work are very close to those given in the original description of *M. william* (Smith, 1947) but differ from those given in subsequent publications (Smith, 1959, 1960). The reason for this discrepancy is the inclusion of specimens of *Bathygobius fuscus* in the material of *M. william* as found by Winterbottom (1976).

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CONTRIBUTIONS IN SCIENCE

THE SYSTEMATICS OF THE HYLAEINE BEES (HYMENOPTERA: COLLETIDAE) OF THE ETHIOPIAN ZOOGEOGRAPHICAL REGION: THE GENERA AND SUBGENERA WITH REVISIONS OF THE SMALLER GROUPS

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THE SYSTEMATICS OF THE HYLAEINE BEES (HYMENOPTERA: COLLETIDAE) OF THE ETHIOPIAN ZOOGEOGRAPHICAL REGION: THE GENERA AND SUBGENERA WITH REVISIONS OF THE SMALLER GROUPS

Roy R. Snelling[1]

ABSTRACT. The genera and subgenera of hylaeine bees of the Ethiopian Region are characterized and separated by a key; pertinent morphological features are illustrated. Within *Hylaeus* four subgenera are recognized: *Deranchylaeus* Bridwell and *Metylaeus* Bridwell, as well as two new subgenera, *Alfkenylaeus* and *Cornylaeus*. *Nothylaeus* Bridwell (=*Anylaeus* Bridwell n. syn.) is regarded as a genus apart from *Hylaeus*. Two new genera are described: *Calloprosopis* in Kenya and *Psilylaeus* in Cape Province. All groups except *Deranchylaeus* and *Nothylaeus* are revised in this part. *Prosopis albonasata* Strand is a synonym of the Palaearctic species, *H. signatus* (Panzer) and is probably incorrectly cited from "Kapland." The following species, described as hylaeines, are all allodapine anthophorids: *Prosopis gracilis* Bingham, *P. pernix* Bingham, *P. quadrilineata* Cameron, *P. 5-lineata* Cameron, and *P. sandaracta* Bingham.

INTRODUCTION

This is the first of three parts treating the hylaeine bees of the Ethiopian zoogeographical region. For purposes of this study, the Ethiopian zoogeographical region encompasses all of the African continent below the Sahara Desert, including the Cape Region, but excluding the Malagasy Region. This introductory part includes keys to the genera and subgenera, revisions of all groups except *Hylaeus*, subgenus *Deranchylaeus*, and the genus *Nothylaeus*. The second part will revise the genus *Nothylaeus* and the final part will treat the species here assigned to the subgenus *Deranchylaeus* of *Hylaeus*.

Early work on these bees consisted of descriptions of various species in papers by J.D. Alfken, P. Cameron, T.D.A. Cockerell, H. Friese, F. Smith, and E. Strand (see Literature Cited); these species were described, for the most part, under the old generic name *Prosopis*, though some of the works by Cockerell employed *Hylaeus*. In 1919 J.C. Bridwell attempted to organize the, by then numerous, species into genera and subgenera. He recognized three genera: *Nothylaeus*, *Metylaeus*, and *Hylaeus*. *Nothylaeus* was further divided into two subgenera, *Nothylaeus* and *Anylaeus*. Those species assigned to *Hylaeus* were all placed in his new subgenus *Deranchylaeus*.

In this same study, Bridwell relied heavily on characteristics of the male genitalia. But, since he was unfamiliar with many of the previously described forms, placement of these in his scheme was based on imperfect descriptions and he was not always correct. Cockerell (1942) noted some difficulty in recognizing Bridwell's groupings. In the main, however, the classification proposed by Bridwell is sound and provides a basis on which the present study was constructed. At the time this revision began, there were 93 species-group names applied to Ethiopian Region hylaeines.

The first part of this study, in addition to recharacterizing the previously described genera and subgenera, describes two new genera and two new subgenera of *Hylaeus*. These smaller groups are revised. Regrettably, these small groups appear to consist of species that are mostly rare or uncommon and the amount of material available is limited.

Hylaeine bees commonly nest in hollow plant stems, apparently utilizing already excavated sites. Unfortunately, there have been no studies of the nesting biology of the African species. Similarly, there are scanty records of the flower visitations for African species. Such data as are available are cited under each species.

TERMINOLOGY AND MEASUREMENTS

Figures 1–5

Antennal socket diameter (ASD). The maximum diameter, between the outer margins, at a right angle to the longitudinal axis of the head in frontal view.

Basal clypeal width (BCW). The distance between the subantennal sutures along the basal margin of the clypeus.

Clypeal length (CL). The median length of the clypeus from the basal margin to the apical margin; this differs from Houston's (1975) measurement, which extends to the level of the

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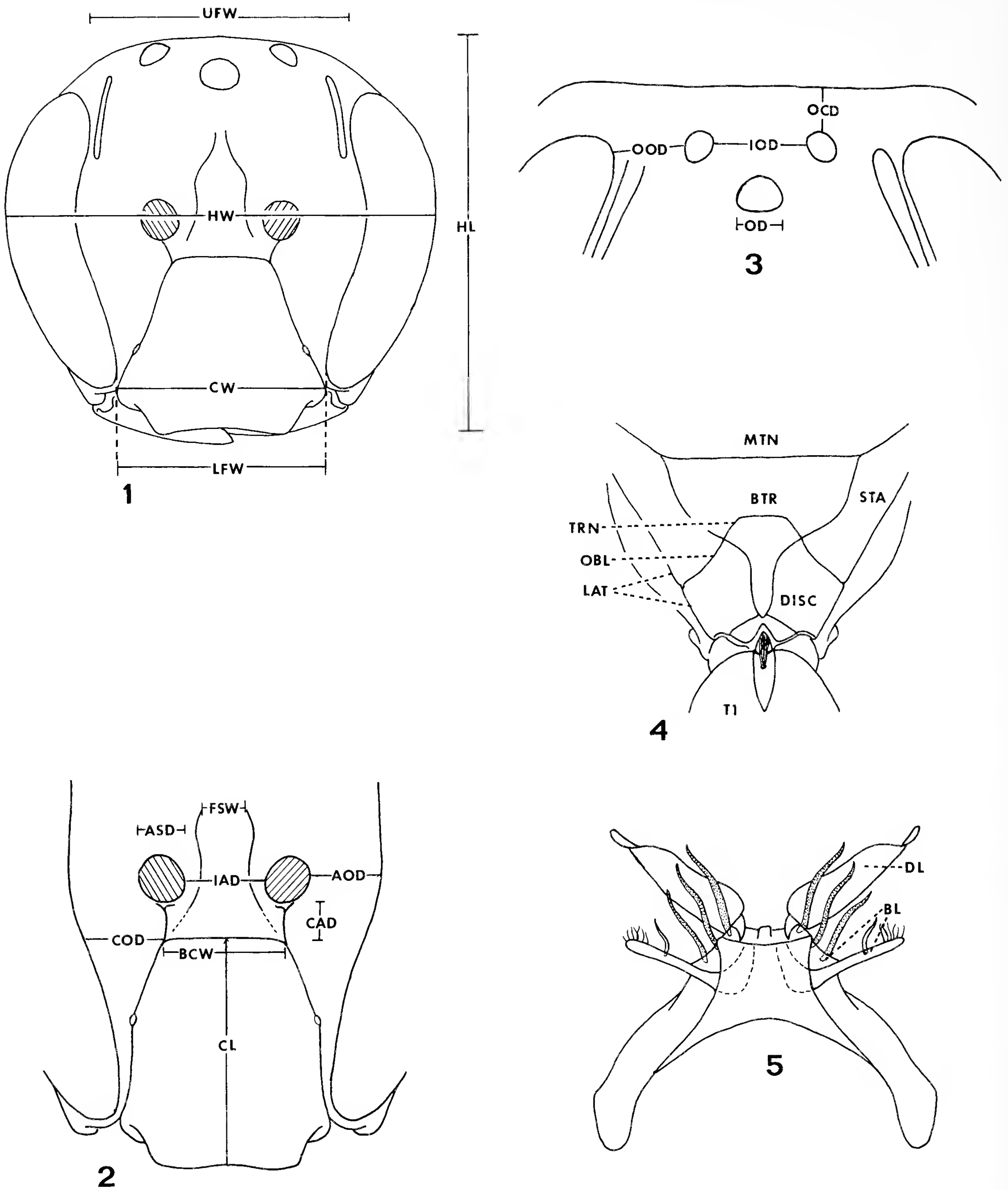

Figures 1–5. Taxonomic characters of Hylaeinae. **1,** frontal view of female head; **2,** lower face of female; **3,** ocellocular area, dorsal view; **4,** posterodorsal view of propodeum; **5,** male sternum 7 (lateral teeth stippled). Abbreviations: AOD, antennocular distance; BL, basal lobe; BTR, basal triangle; CAD, clypeoantennal distance; CW, clypeal width; DL, distal lobe; LAT, lateral carina; MTN, metanotum; OBL, oblique carina; OCD, ocelloccipital distance; STA, stigmatal area; T1, tergum 1; TRN, transverse carina. See text (Terminology and Measurements) for remaining abbreviations.

lowermost extremity of the clypeus, but is consistent with my prior usage.

Clypeo-ocular distance (COD). The minimum distance between the laterobasal angle of the clypeus and the inner eye margin.

Frontal shield (FS). For the usually elevated and marginate area of the face above and between the antennal sockets, Houston (1975) has proposed "elevations of the interantennal area." This is cumbersome and I prefer to use the simpler "frontal shield." The frontal shield is elevated above the frons and is distinctly margined and usually widened at about the midpoint. Houston has noted that the width of the frontal shield (FSW) at its apex on the frons, when compared to the diameter of the antennal socket (ASD), is useful as a specific character.

Head length (HL). The maximum midline distance between the occipital margin and the apical margin of the clypeus, in frontal view.

Head width (HW). The maximum breadth, across the eye, of the head in frontal view.

Interantennal distance (IAD). The minimum distance between the inner margins of the antennal sockets.

Interocellar distance (IOD). The minimum distance between the posterior ocelli.

Lower facial width (LFW). The minimum distance between the eyes at their lower end. This term is utilized in its relationship to UFW (q.v.) to express degree of convergence of the inner eye margins: *weakly convergent*—UFW 1.01–1.29 × LFW; *moderately convergent*—UFW 1.30–1.49 × LFW; *strongly convergent*—UFW 1.50–1.70 × LFW; *very strongly convergent*—UFW more than 1.70 × LFW.

Ocellar diameter (OD). The transverse diameter of the anterior ocellus.

Ocellocular distance (OOD). The minimum distance between a posterior ocellus and the inner eye margin.

Pilosity. The distribution of hairs on hylaeine bees, whether simple or short-plumose, is monotonously uniform, and pilosity is not accorded attention here except when it offers useful differences between species. The following characteristics apply generally throughout the Ethiopian Region fauna and will receive no further mention.

The hairs are uniformly whitish; those on the inner surface of the tarsal segments are usually yellowish, and the extremely short hairs of the face are often brownish yellow; females may have a few long dark brown or blackish hairs on the last tergum and/or sternum.

Very short, simple, suberect to erect hairs are very sparsely distributed over the surfaces of the head and thorax. Similar, but slightly longer, appressed to suberect hairs are present on the abdominal segments and they may be abundant on the apical terga.

Short, short-plumose, suberect to erect hairs are present on the face above the level of the antennal sockets, on the gena (where they become longer toward the mandibular base and toward the gula), on the side of the thorax, on the side and disc of the propodeum and on the sides of the abdominal terga, as well as on the discs of the third and following segments. They are sparse on all areas except the side and disc of the propodeum where they are conspicuously more abundant.

Relatively long, erect, short-plumose hairs are present around the antennal sockets, on the vertex, around the wing bases, on the side and center of the thorax, and on the apical terga and sterna. They are most abundant around the antennal sockets and wing bases and on the thoracic venter.

Slightly shorter, mixed barbulate and short-plumose hairs are present on the mandible, antennal scapes, and the legs. They are sparse on those segments and are usually suberect to erect, often moderately curved.

Important specific characters of pilosity are: the presence of long, erect, short-plumose hairs on the lower face, the mesoscutum, and the discs of the abdominal terga; the presence of a transverse fascia of short, appressed, short-plumose hairs on the pronotal collar; the presence of long, ereet, short-plumose hairs at the juncture of the anterior and dorsal faces of the first tergum and/or at the side of that segment; the presence of fasciae, entire or not, of short, appressed, short--plumose hairs preapically on any of the abdominal terga. Although other differences between species do exist, they are often too subtle to be useful and are, therefore, ignored here.

Pronotal lobes. Houston (1975) proposed to call the dorsal and posterior lobes of the pronotum the "pronotal collar" and "pronotal tubercles," respectively. Since Michener (1965) has already utilized the former following a tradition established by earlier workers, the usage is continued here, as it has been in my earlier papers. In place of "pronotal tubercles," I still prefer the older term "pronotal lobes," for they are lobes and not tubercles.

Propodeum. The hylaeine propodeum is useful in determining group relationships, and it is convenient to refer to specific subdivisions in the descriptions. In dorsal view, the most obvious feature is the more or less horizontal basal or dorsal face; a pair of sutures extends from the antero-lateral margin, converging toward the postero-median margin of the basal area. The resultant somewhat triangular area is the *basal triangle,* the apex of which is situated on the posterior, more or less vertical surface, here called the *propodeal disc;* the disc is divided by a median groove, the sides of which are continuous with the margins of the basal triangle. The lateral margin of the disc, at its juncture with the *side* of the propodeum, is often marked by a low carina, the lateral carina, which may extend forward to the anterior margin of the propodeum, but usually does not. At the point where the lateral carina reaches the basal face there may be another low carina which extends obliquely mesad to join the side of the triangle; this is the *oblique carina.* The area mesally bounded by the margin of the triangle, posteriorly by the oblique carina and laterally by the lateral carina (or its imaginary extension) is the *stigmatal area* (after Benoist, 1959) and is equivalent to the "lateral area" of Dathe (1980).

Punctation. I prefer to use puncture in preference to Houston's (1975) "pit"; the former is long established and consistent with general terminology used in apoid systematics. Houston illustrated his various terms (minute, fine, small, medium, large, coarse) to express relative size of punctures, but I prefer more absolute definitions. Puncture diameters are measured, by means of an ocular micrometer, at 120×, and the following terminology applies to various puncture diameters:

minute	0.010–0.019 mm
fine	0.020–0.035 mm
moderate	0.036–0.055 mm
coarse	0.056–0.070 mm
very coarse	over 0.070 mm

Since punctures are rarely of one size on a given segment or stipulated area, they may be described as "fine to moderate" (puncture diameter varying between 0.020 and 0.055 mm), though usually a more limited size range, such as "moderate" prevails.

The relative density of the punctation on a given segment is often different in closely related and otherwise similar species. The commonly applied terms such as close, dense, sparse, etc., are usually not defined and subject to considerable latitude of interpretation. I have attempted to standardize my terminology for ease in comparison and, perhaps, encourage some degree of accepted usage. Because the interspaces within an indicated area are somewhat variable in extent, the stated condition in descriptions is that which is prevalent:

Contiguous punctures are so close that they are often deformed; their interspaces are greatly compressed and sharp edged.

Subcontiguous punctures are separated by more or less flat-topped interspaces up to about 0.25 puncture diameters; at its lower extreme this merges into contiguous.

Dense punctures are separated by more or less flat-topped interspaces varying from about 0.30 to about 0.70 puncture diameters; most commonly about 0.50 puncture diameters.

Close punctures are separated by more or less flat-topped interspaces varying from about 0.70 to about 1.50 puncture diameters.

Sparse punctures are separated by distances from 2.00 to about 3.00 puncture diameters.

Scattered punctures are separated by very irregular interspaces, from about 3.00 to as much as 6.00 puncture diameters, often with extensive areas devoid of punctation.

Since size and density of punctation are often not uniform on all areas of a given segment, the following comments are necessary. The description of clypeal punctation is derived from the basal one-third of that segment; punctures usually are somewhat coarser toward the apex and often are sparser along the midline. Genal punctation is finest on the upper one-third and becomes gradually coarser, closer and more distinct toward the base of the mandible.

The mesoscutal punctation is described from the area between the midline and the parapsidal line at the level of the tegula; punctures become finer and, often closer, anterior to this area; often coarser and somewhat sparser in the posteromedian area, but very fine and dense along the mesoscutal-scutellar suture. Scutellar and metanotal punctation are described from the mesal one-third of each segment. The middle of the mesopleural disc is the standard for that segment as is also true for the side of the propodeum.

Scape length (SL). The standard measurement, exclusive of the basal condyle.

Scape width (SW). The maximum width of the scape.

Sculpture. Except for the obvious differenees related to punctation, I have not devoted much attention to superficial texture. My main reason is simply that the superficial texture varies considerably within a species, and the differences between closely related species are often so subtle that descriptions are useless and/or largely subjective. So, I use "tessellate" generally to describe the surface: "lightly tessellate" corresponds approximately to Houston's "lineo-reticulate" and "closely tessellate" is approximately equivalent to his "pit-reticulate"; lineolate is the same as his "transversely lineo-reticulate."

Total length (TL). This is the least satisfactory of measurements used here; it is certainly the least exact. The method used here differs from the conventional ones, but seems less subject to the vagaries resulting from wide variations in the death posture of the specimen or its final, mounted condition. The TL is derived by adding the following: HL + thoracic length (in dorsal view, along the midline, from the anterior margin of the pronotal collar to the posterior margin of the dorsal or basal face of the propodeum) + length of tergum 1 (dorsal view along the midline, with the summit of the basal face just occluding the basal attachment) + length of tergum 2 (along midline, from gradulus to apical margin).

Upper facial width (UFW). The *minimum* distance between the eyes above, at about the level of the anterior ocellus, or somewhat below, but *not* at the point of greatest width as Houston (1975) has it. The usage here is consistent with that in my earlier papers.

Wing length (WL). The length of the anterior wing, from the tegular margin to the wing apex.

DESCRIPTIONS

The descriptions of genera and subgenera are divided into three sections. First is a Diagnosis, a brief statement of the outstanding features of the taxon. This is followed by the Description. The Description consists of numbered statements, and they are directly comparable at the appropriate (i.e., generic or subgeneric) level. Concluding is another statement, supplemental to the Description, of additional characteristics of taxonomic interest.

The species descriptions are more detailed than those of the genera and subgenera. Although the statements are not numbered, a uniform descriptive format is used, so descriptions of species are comparable.

Previously described species are usually not redescribed. In most instances the characteristics noted in keys and discussions should be ample. All new species are fully described.

ABBREVIATIONS OF MUSEUMS

AMNH	American Museum of Natural History, New York, New York, U.S.A.
BMNH	British Museum (Natural History), London, U.K.

CAS	California Academy of Sciences, San Francisco, California, U.S.A.
CORN	Cornell University, Ithaca, New York, U.S.A.
DEI	Deutsches Entomologisches Institüt, Eberswalde bei Berlin, D.D.R.
GEMB	Faculté des Sciences Agronomiques de l'état, Gembloux, Belgium
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
MRAC	Musée Royal de l'Afrique Central, Tervuren, Belgium
PRET	National Collection of Insects, Pretoria, South Africa
SAM	South African Museum, Cape Town, South Africa [In 1981 the Hymenoptera collections of the National Museum of Rhodesia (now Zimbabwe), Bulawayo, were transferred to the South African Museum, Cape Town. Material borrowed from the Rhodesian National Museum is, therefore, included herein under SAM.]
UKAN	University of Kansas, Lawrence, Kansas, U.S.A.
USNM	National Museum of Natural History, Washington, D.C., U.S.A.

LIST OF EXCLUDED SPECIES

The following species are excluded for reasons stated under each name.

Prosopis albonasata Strand, 1912. Described from a single male from "Kapland." The type has been examined, and I conclude that the locality may be spurious. This is a synonym of the Palaearctic species, *Hylaeus* (*Prosopis*) *signatus* (Panzer) (NEW SYNONYMY).

Prosopis gracilis Bingham, 1903. Described from a female presumably from Durban, Natal, in BMNH. According to Michener (1975), a synonym of *Braunsapis facialis* (Gerstaecker) (Anthophoridae).

Prosopis pernix Bingham, 1903. Described from a female from Port Natal, Natal. According to Michener (1975), this is a valid species in *Allodape* (Anthophoridae).

Prosopis quadrilineata Cameron, 1905. Described from a female from Grahamstown, Brak Kloof, in BMNH. Michener (1975) treats this as a valid species in *Allodape.*

Prosopis 5-lineata Cameron, 1905. Described from a female from Stellenbosch, Cape Province, in BMNH. According to Michener (1975), this is a synonym of *Allodape pictifrons* F. Smith.

Prosopis sandaracta Bingham, 1903. Described from a female from Durban, Natal, in BMNH. Friese (1909) stated that this is a synonym of *Hylaeus purpurisata* (Vachal) of Algeria, but there is no evidence that he actually saw the type. According to Cockerell (1934), this is a synonym of *Allodapula variegata* (F. Smith) (Anthophoridae) with which Michener (1975) concurs.

KEY TO GENERA AND SUBGENERA OF ETHIOPIAN REGION

1. Integument of both sexes black, red or both, never strongly metallic; metatibia of female without raised glabrous area at base; male genitalia with well-developed, cup-like base 2

– Integument of both sexes metallic blue to blue-green; metatibia of female with raised glabrous area at base; male genitalia with gonobase reduced to a basal ring (Fig. 61) .... *Calloprosopis,* new genus

2. Supraclypeal area elevated between antennal sockets and laterally marginate; propodeum with defined basal area and usually coarsely rugose or roughened or sharply punctate, at least in part 3

– Supraclypeal area gently sloping from midline to antennal sockets, not laterally marginate; propodeum smooth, densely tessellate, without defined basal area; entire body densely tessellate, without conspicuous punctures .... *Psilylaeus,* new genus

3. Apical margin of mandible transverse or oblique, bi- or tridentate, mandible short and broad (Figs. 12–15) (*Hylaeus*) 4

– Apical margin of mandible acute, without distinct teeth, mandible elongate and slender (Figs. 16–17) .... *Nothylaeus* Bridwell

4. Integument variously punctate; scutellum and metanotum without lateral spines; occipital carina often absent; mesepisternum not sharply carinate, but sometimes with obscure ridge at juncture of lateral and anterior faces 5

– Integument very coarsely punctate; scutellum and metanotum each usually with a pair of spines; occipital carina present, sharp; mesepisternum sharply carinate at juncture of anterior and lateral faces .... subg. *Metylaeus* Bridwell

5. Male, antenna 13-segmented, gaster with 7 visible segments 6

– Female, antenna 12-segmented, gaster with 6 visible segments 9

6. Gonocoxite abruptly narrowed over apical one-third or more (Figs. 31, 36, 40, 45) 7

– Gonocoxite terminating bluntly at level of apex of aedeagus (Figs. 21, 50) 8

7. Face and first tergum coarsely, closely punctate; lateral lobes of sternum 7 thin, strap-like, very short (Fig. 29); apex of gonocoxite without barbulate setae .... *Alfkenylaeus,* new subgenus

– Face finely punctate, punctures obscured by tessellation; lateral lobes of sternum 7 bifurcate, basal lobule with a few coarse teeth on margin (Figs. 5, 6); apex of gonocoxite with two or three barbulate setae ....subg. *Deranchylaeus* Bridwell (part)

8. All terga with abundant erect, fine, white hairs, these becoming longer and denser caudad (Fig. 18); clypeus

black or with median yellow stripe which tapers toward apex, but not reaching apical margin; terga 1 and 2 coarsely, closely punctate; basal lobule of sternum 7 short, without lateral teeth ...... *Cornylaeus,* new subgenus

– Discs of terga 1–3 usually with few or no erect hairs (if any present, they are short, separated by their own lengths or more and often dark); clypeal marks variable, but rarely as described above, clypeus usually entirely pale; terga 1 and 2 often without evident punctures; basal lobule of sternum 7 often elongate and always laterally dentate ....subg. *Deranchylaeus* Bridwell (part)

9. Mandibular apex bi- or tridentate, dorsal border usually not flattened and expanded, but if flattened, conspicuously punctate and only slightly shiny *and* pronotal collar sharply marginate in middle; clypeal marks various, often greatly reduced or absent; tergal fasciae and punctation various 10

– Mandibular apex bidentate, dorsal border flattened and expanded, shiny and impunctate (Fig. 12); lateral face mark full, clypeus black or with median stripe, pronotal stripe complete; first tergum conspicuously punctate; terga 1 and 2 with apical pubescent fasciae, broadly interrupted in middle; pronotal collar not marginate in middle .... *Cornylaeus,* new subgenus

10. Clypeus flat preapically without conspicuous transverse or quadrate impression 11

– Clypeus with pronounced median, preapical quadrate or somewhat transverse depression ....subg. *Deranchylaeus* Bridwell (part)

11. Clypeus coarsely, closely punctate; pronotum sharply marginate in middle; lateral face mark complete, but not extending above level of antennal socket; legs and clypeus often ferruginous ..... *Alfkenylaeus,* new subgenus

– Clypeus usually finely and sparsely punctate; pronotum usually rounded in middle; if clypeus and pronotum as above, *then* lateral face mark absent or reduced to narrow stripe along eye margin; legs and clypeus not ferruginous, *or,* if ferruginous, then clypeus finely punctate and lateral face mark absent ....subg. *Deranchylaeus* Bridwell (part)

Hylaeus Fabricius

Hylaeus Fabricius, 1793:302. Type-species: *Apis annulata* Linnaeus, 1758; designation of Latreille, 1810.

DIAGNOSIS

Body mostly dull black, with or without pale marks on head and thorax; frontal shield present; mandibles stout, bi- or tridentate; at least head and thorax usually conspicuously punctate.

DESCRIPTION

(1) Mandible stout, bidentate in male, bi- or tridentate in female. (2) Labral tubercle, when present, small, midbasal, often depressed along center. (3) Tentorial pit usually at midpoint of clypeal length. (4) First flagellar segment, and often second as well, short and transverse. (5) Frontal shield present and sharply margined. (6) Lateral carina of propodeum usually present, oblique carina usually absent in our fauna. (7) Sulcus of first tergum long or short. (8) Gradulus of second tergum gently arched, usually evanescent laterad. (9) Third tergum of male without sublateral pubescent fovea. (10) Male sternum 7 normally with distinct basal and apical lobules. (11) Male sternum 8 usually with distal process long and slender; dorsal tubercle usually near base of distal process. (12) Male gonocoxite usually broad and not extending much beyond penis valves, but may be elongate and slender.

DISCUSSION

Hylaeus is a virtually cosmopolitan genus with many species arrayed within numerous subgenera. The European species have been recently reviewed by Dathe (1980), and many of the Nearctic species by Snelling (1966a–c, 1968, 1970). The hylaeines of Australia are presently being revised by Houston (1975, 1981). The extensive Neotropical and Asian faunas are essentially unstudied.

The above description is drawn entirely from the species of the Ethiopian Region and will not apply, in all particulars, to *Hylaeus* from other Regions. Species are mostly small black bees with limited whitish or yellowish marks on the head and thorax, especially in the males. A few species have limited red marks, particularly on the clypeus and legs.

After removing some species to *Nothylaeus* and *Metylaeus,* Bridwell (1919) placed all remaining Ethiopian hylaeines in his subgenus *Deranchylaeus.* Many of those included were known to Bridwell only from their original descriptions. It is not surprising, therefore, to find that some will not fit within Bridwell's scheme. For these species, new subgeneric or generic names are proposed. At the same time, Bridwell's genus *Metylaeus* is treated as a subgenus of *Hylaeus.*

Most species still remain in *Deranchylaeus,* a large and diverse subgenus, apparently restricted to the Ethiopian Region. *Deranchylaeus* may be derived from the large Holarctic subgenus *Prosopis,* or at least from a similar stock. However, until the taxa within *Hylaeus* can be studied on a worldwide basis, this must be presumption only.

Subgenus *Deranchylaeus* Bridwell

Hylaeus subg. *Deranchylaeus* Bridwell, 1919:136–137. Type-species: *Prosopis curvicarinata* Cameron, 1905; original designation.

DIAGNOSIS

Mandibles short, broad, bi- or tridentate at apex; preoccipital carina absent; mesepisternum not carinate between anterior and lateral faces; scutellum and metanotum unmodified; male

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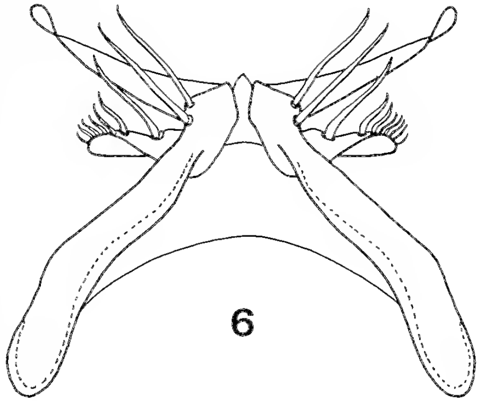
Figures 6–11. Sterna 7 and 8, genital capsule (right half dorsal, left half ventral views) of: **6–8,** *H.* (*Deranchylaeus*) sp., scale line = 0.25 mm; **9–11,** *H.* (*Nothylaeus*) *heraldicus,* scale line = 0.50 mm.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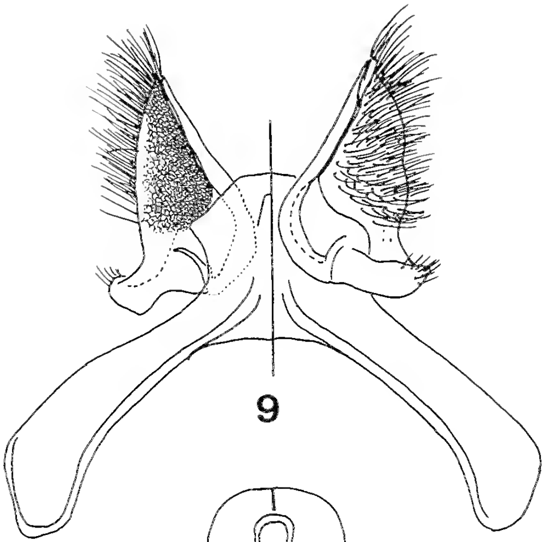
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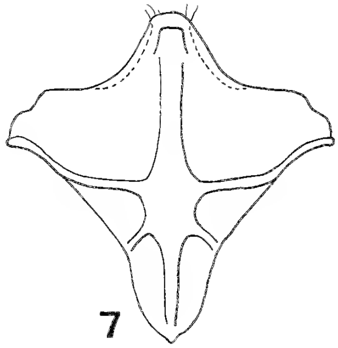
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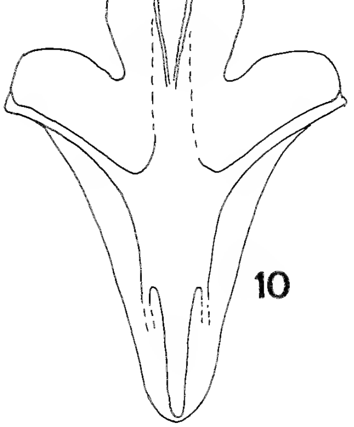
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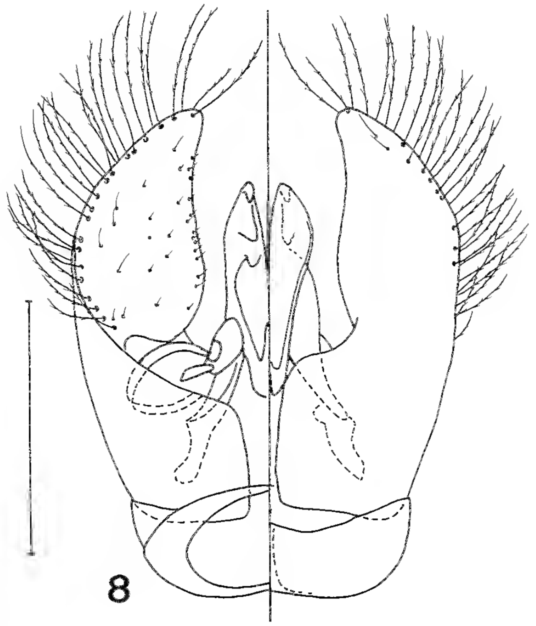
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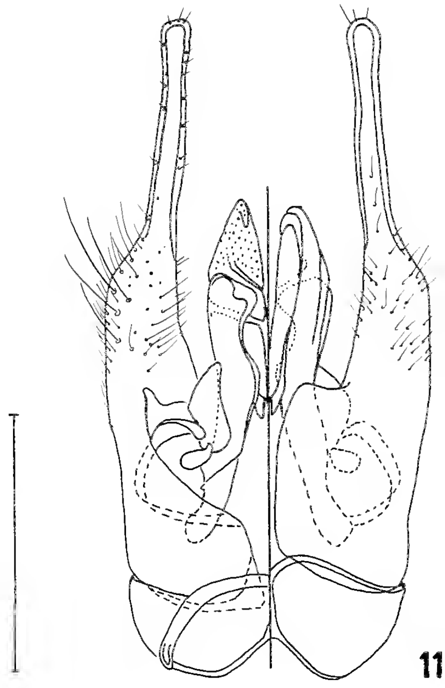
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sternum 7 with lateral margin of basal lobule dentate; male gonocoxite stout, ending at about level of penis valves.

DESCRIPTION

(1) Mandible broad, usually bidentate, but tridentate in some females. (2) Clypeus flat or with distinct preapical depression; punctures minute to fine, usually sparse but may be close. (3) Preoccipital carina or ridge absent. (4) Pronotal collar usually rounded on dorsal surface, rarely somewhat marginate. (5) Mesepisternum without carina between anterior and lateral faces. (6) Lateral carina of propodeum usually present, oblique carina usually absent. (7) Sulcus of tergum 1 one-third or less as long as basal face. Tergum 2 with punctiform lateral fovea. Male sterna 2 and 3 usually not tuberculate. (10) Male sternum 7 with teeth along lateral margin of basal lobule. (11) Male gonocoxite broad, blunt, extending little, if any, beyond level of apex of penis valves.

Dorsal border of mandible usually not flattened, but if so, expanded area is densely punctate and only slightly shiny; scutellum and metanotum simple.

DISCUSSION

This is the largest group of hylaeines in the Ethiopian Region. Many of the species appear to be common and widespread. These wide-ranging species are subject to considerable variation in the intensity and distribution of pale face marks, with many trivial forms named on the basis of slight color differences. There are 10 clearly recognizable species groups.

LIST OF INCLUDED SPECIES NAMES

absonulus Cockerell, 1936a
abjunctus Cockerell, 1936a
alfkeni (Friese, 1913)
atriceps (Friese, 1911)
bequaertianus Bridwell, 1919
capicola (Alfken, 1914)
clavigerus Cockerell, 1936b
corpana (Warncke, 1972)
curvicarinatus (Cameron, 1905)
dominae Cockerell, 1936a
dregei (Strand, 1912)
extensicornis Cockerell, 1936a
flaviscutum (Alfken, 1914)
gabonica (Vachal, 1899)
graafi Cockerell, 1936a
haygoodi Bridwell, 1919
immarginatus (Alfken, 1914)
kasindensis Cockerell, 1936a
krebsianus (Strand, 1912)
lemuriae (Benoist, 1946)*
leucolippa (Friese, 1913)
lightfooti Bridwell, 1919
lineaticeps (Friese, 1913)
longula (Friese, 1913)
major (Strand, 1912)
malagassa (Benoist, 1946)*
melanosomus Cockerell, 1920
ogilviei Cockerell, 1936
perater Cockerell, 1936a
perdensus Cockerell, 1936a
promontorii Meade-Waldo, 1923
punctifrons Cockerell, 1936a
punctiferus Cockerell, 1936a
reditus Cockerell, 1936a
rhodognathus Cockerell, 1936a
robertiana (Cameron, 1906)
rugipunctus (Alfken, 1914)
sanctus Cockerell, 1936a
simplex (Bingham, 1912)
simplior Meade-Waldo, 1923
simulans Cockerell, 1942
stictifrons (Cockerell, 1936b)
sublucens Cockerell, 1936a
subreditus Cockerell, 1942
tenuis (Alfken, 1914)
tinctulus Cockerell, 1932
varians Cockerell, 1936a
vau Cockerell, 1936a
xanthostoma (Alfken, 1914)

Cornylaeus, new subgenus

Type-species: *Prosopis aterrima* Friese, 1911.

DIAGNOSIS

Mandible bidentate, that of female with upper margin flattened, expanded, shiny and impunctate; mesepisternum not carinate between anterior and lateral faces; scutellum and metanotum simple; macula of pronotal collar complete; male with abundant fully erect hairs on discs of abdominal segments; male sternum 7 without teeth on lateral margin of basal lobule; male gonocoxite stout, ending at about level of apex of aedeagus.

DESCRIPTION

(1) Mandible bidentate at apex, upper border flattened and expanded in female, expanded portion shiny and impunctate. (2) Clypeus flat, without preapical impression. (3) Preoccipital ridge or carina absent. (4) Pronotal collar rounded above. (5) Mesepisternum without carina between anterior and lateral faces. (6) Oblique carina absent, lateral carina present in its lower half only. (7) Sulcus of tergum 1 about one-third as long as basal face. (8) Tergum 2 with punctiform lateral fovea. (9) Male sternum 3 conspicuously tuberculate, or not.

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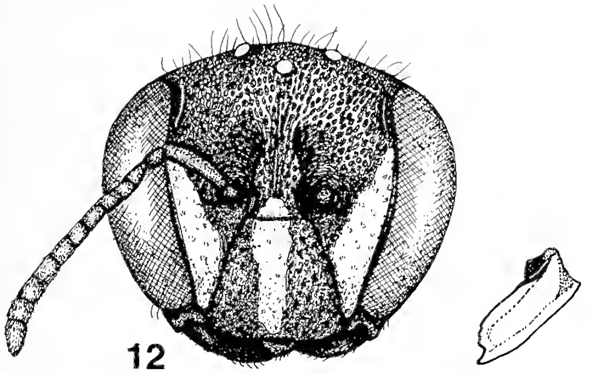
* Known only from Madagascar.

Figures 12-17. Frontal view of head of female and male of: **12-13,** *H.* (*Cornylaeus*) *aterrimus;* **14-15,** *H.* (*Cornylaeus*) *proteae*; **16-17,** *Nothylaeus heraldicus*. Scale line = 1.00 mm. Figures by R.A. DeNicola.



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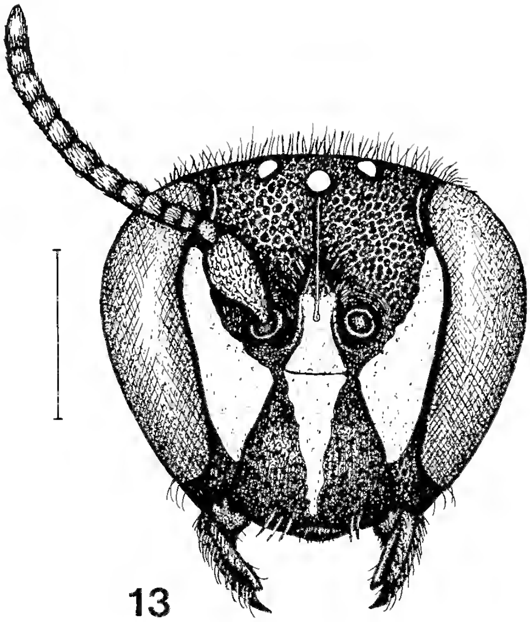

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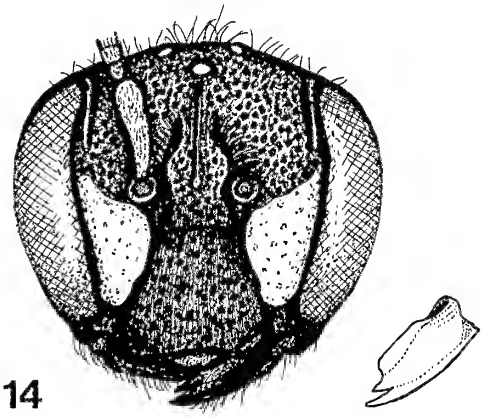

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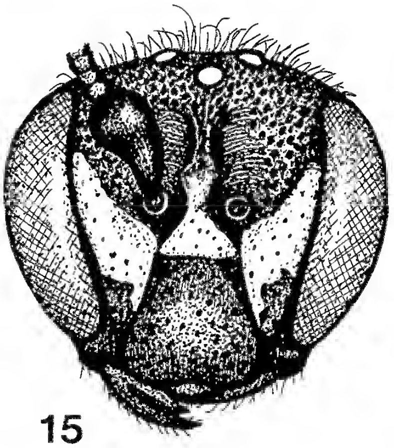

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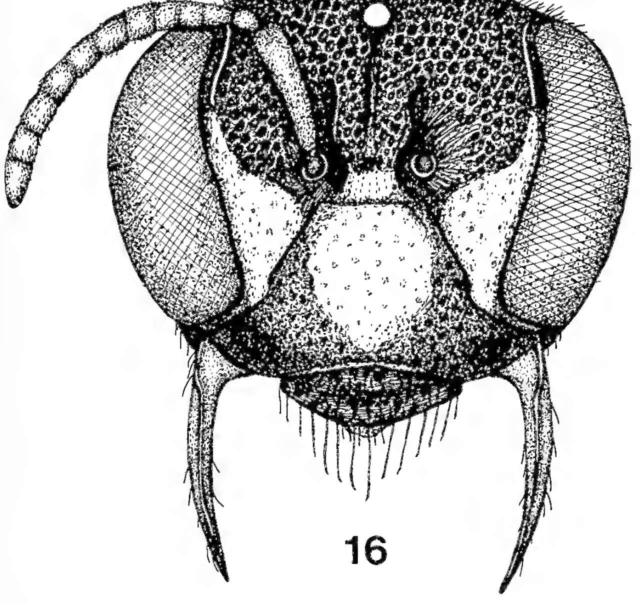

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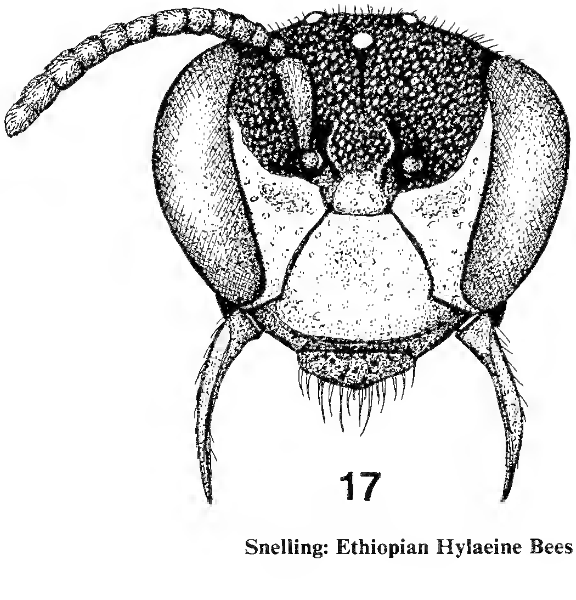

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(10) Male sternum 7 without teeth along lateral margin of basal lobule. (11) Male gonocoxite broad, blunt, ending slightly beyond apex of penis valves.

Male labrum without median tubercle; IAD about 0.66 × COD; subantennal sutures about as long as ASD; upper end of female facial fovea slightly separated from inner eye margin; first flagellar segment slightly broader than long, longer than second segment; male mesepisternum with longitudinal tubercle below.

DISCUSSION

This subgenus is proposed for two apparently uncommon, rather large and robust forms. Although Bridwell (1919) included the type species in his subgenus *Deranchylaeus,* there is no evidence that he actually saw any specimens. Males are easily recognizable by the presence of abundant long erect hairs on the discs of the abdominal segments. In most males, too, there are conspicuous tubercles on the third sternum.

The males of at least one species, *H. aterrimus,* are polymorphic, exhibiting a wide range of variation in the development of the tubercles of sternum three. In this species, tubercles may also be present on the third tergum. In general, degree of development of the tubercles is correlated with body size, but there is no consistency. So far as known, males of *H. proteae* always possess a large, somewhat asymmetrical process on the third sternum, but too few specimens have been seen for there to be any certainty about this.

Females of *Cornylaeus* are less easily recognized, but the mandibular structure is unlike that of any *Deranchylaeus.* In addition, the basal face of the first tergum has numerous fully erect white hairs, usually long and conspicuous. These hairs are subject to wear and are sometimes absent. A few *Deranchylaeus* do possess hairs on the basal face of the first tergum but do not have the mandibular structure characteristic of *Cornylaeus.*

ETYMOLOGY

The subgenerie name is derived by combining the Latin word for horn, or tubercle (*cornus*), with the name *Hylaeus.*

SYNONYMIC LIST OF SPECIES

aterrimus (Friese)
  =*quinquedentata* Friese
  =*pondonis* Cockerell, NEW SYNONYMY
proteae Cockerell

KEY TO SPECIES OF *CORNYLAEUS*

1. Female, antenna 12-segmented 2
– Male, antenna 13-segmented 3
2. Clypeus with median stripe; supraclypeal area maculate .... *aterrimus* (Friese)
– Clypeus and supraclypeal area black .. *proteae* Cockerell
3. Clypeus with longitudinal stripe; metatibia with basal pale mark; tergum 3 often with lateral tubercles; sternum 3 tuberculate or not; scape longer than broad .... *aterrimus* (Friese)
– Clypeus black or with a minute preapical median spot; metatibia wholly dark; tergum 3 always without lateral tubercles; sternum 3 with a large median swelling; scape rotund, as broad as long .... *proteae* (Cockerell)

Hylaeus (*Cornylaeus*) *aterrimus* (Friese)

Figures 12–13, 18–21

Prosopis aterrima Friese, 1911:120. ♂, ♀. SOUTH AFRICA: Shilouvane, N. Transvaal, Feb. (♀), Oct. (♂) (MNHU) [examined].

Prosopis quinquedentata Friese, 1911:132. ♂. SOUTH AFRICA: Shilouvane, N. Transvaal (*Junod*) (MNHU) [examined].

Hylaeus pondonis Cockerell, 1942:10. ♂. SOUTH AFRICA: Port St. John, Pondoland, Oct. 1923 (*R.E. Turner*) (BMNH) [examined]. NEW SYNONYMY.

Three cotypes are available from MNHU. Of these, the male, which agrees with Friese's original description, is selected as lectotype. Of the two females, the smaller is designated allolectotype and the larger paralectotype; all specimens are in MNHU.

Alfken (1914) first recognized that *H. quinquedentata* was a junior synonym of *H. aterrima.* I have examined the type and concur. Cockerell's *H. pondonis* is based on a male lacking tubercles on the third tergum. It falls well within the range of variation of *H. aterrimus,* as I understand the species.

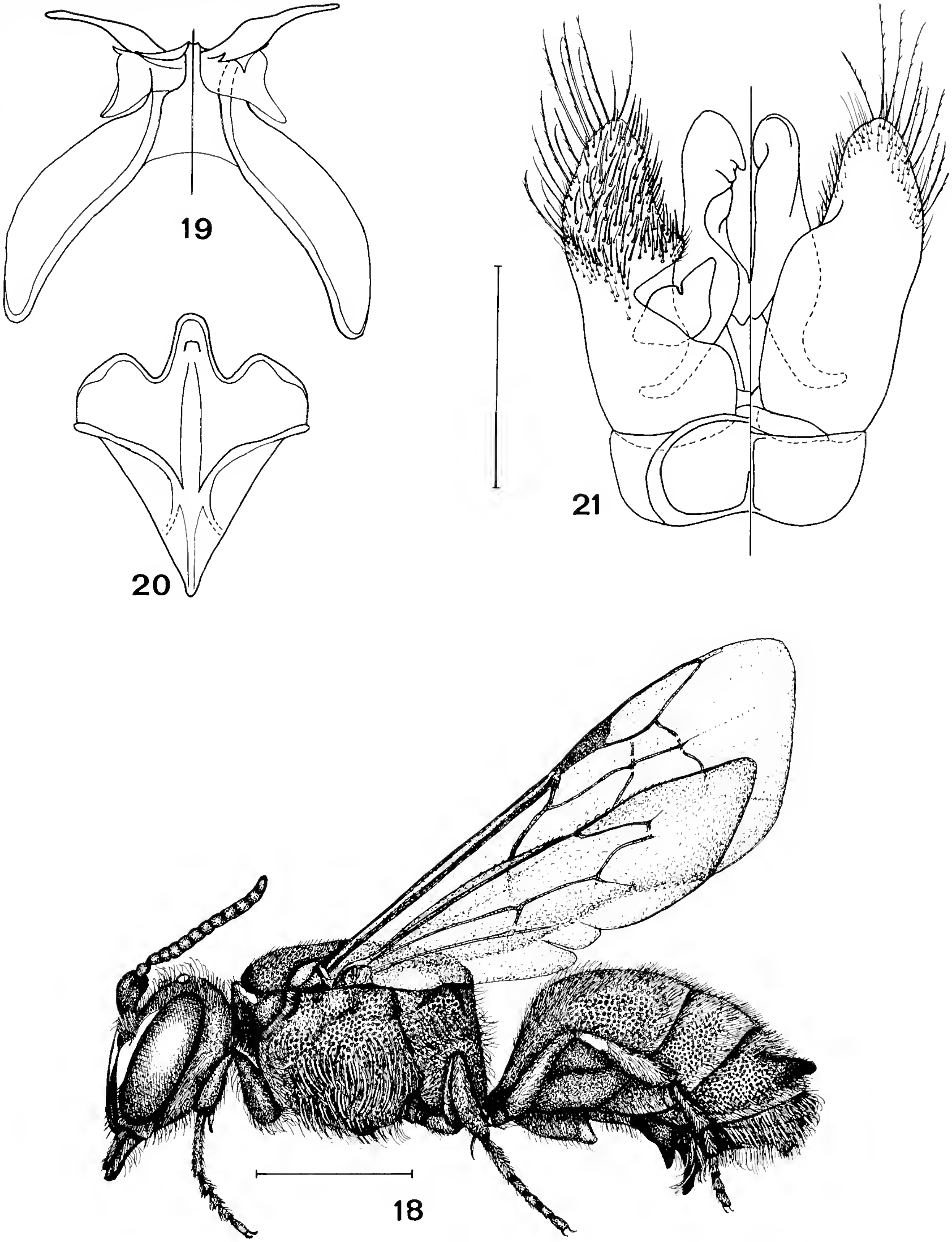
MATERIAL EXAMINED

CONGO REPUBLIC: 2♂♂, 10 mi. S Kapona, 1570 m elev., 13 Jan. 1958 (*E.S. Ross & R.E. Leech;* CAS). ZIMBABWE: 1♀, 1♂, Salisbury, no date (*D. Dodds;* SAM, AMNH); 1♂, Burnside, Bulawayo, 28 Sept. 1952 (*no name;* SAM); 2♂♂, Bulawayo, 24 Apr. 1916 (*no name;* SAM); 1♀, Bulawayo, Apr. 1916 (*no name;* SAM); 1♀, Bulawayo, 29 Apr. 1916 (*no name;* SAM); 1♂, Bulawayo, 6 June 1925 (*R.H.R. Stevenson;* SAM); 1♂, Bulawayo, 7 Sept. 1954 (*no name;* SAM); 1♀, Hope Fountain, 7 May 1916 (*no name;* SAM); 1♂, Salisbury, Mar. 1906 (*G.A.K. Marshall;* BMNH); 2♂♂, Umtali Heights, 1420 m elev., 13 Mar. 1958 (*E.S. Ross & R.E. Leech;* CAS). SOUTH AFRICA: 1♀, Port St. John, Pondoland, 1–17 Mar. 1924 (*R.E. Turner;* BMNH); 1♂, same locality and collector, Jan. 1924 (BMNH); 1♀, same locality and collector, Oct. 1923 (BMNH); 2♂♂, Hilton, Natal, 2 Aug. 1966 (*J.S. Taylor;* USNM), on *Protaea;* 2♂♂, Hellabella, 2200 ft. elev., 12 mi. SW Richmond, 13 Jan. 1967 (*C.D. Michener & D.J. Brothers;* UKAN); 1♂, 2♀♀, Shilouvane, Transvaal, no date (*Junod;* MNHU, cotypes of *P. aterrima*); 1♂, same data (MNHU, type of *P. quinquedentata*); 1♂, Wolkberg, Transvaal, 13 Apr. 1974 (*R.H. Watmough;* PRET); 1♀, Long Tom Pass, 25°07′S, 30°35′E, Transvaal, Jan. 1977 (*E.F. Whitehead;* PRET), "yellow bowl trap."

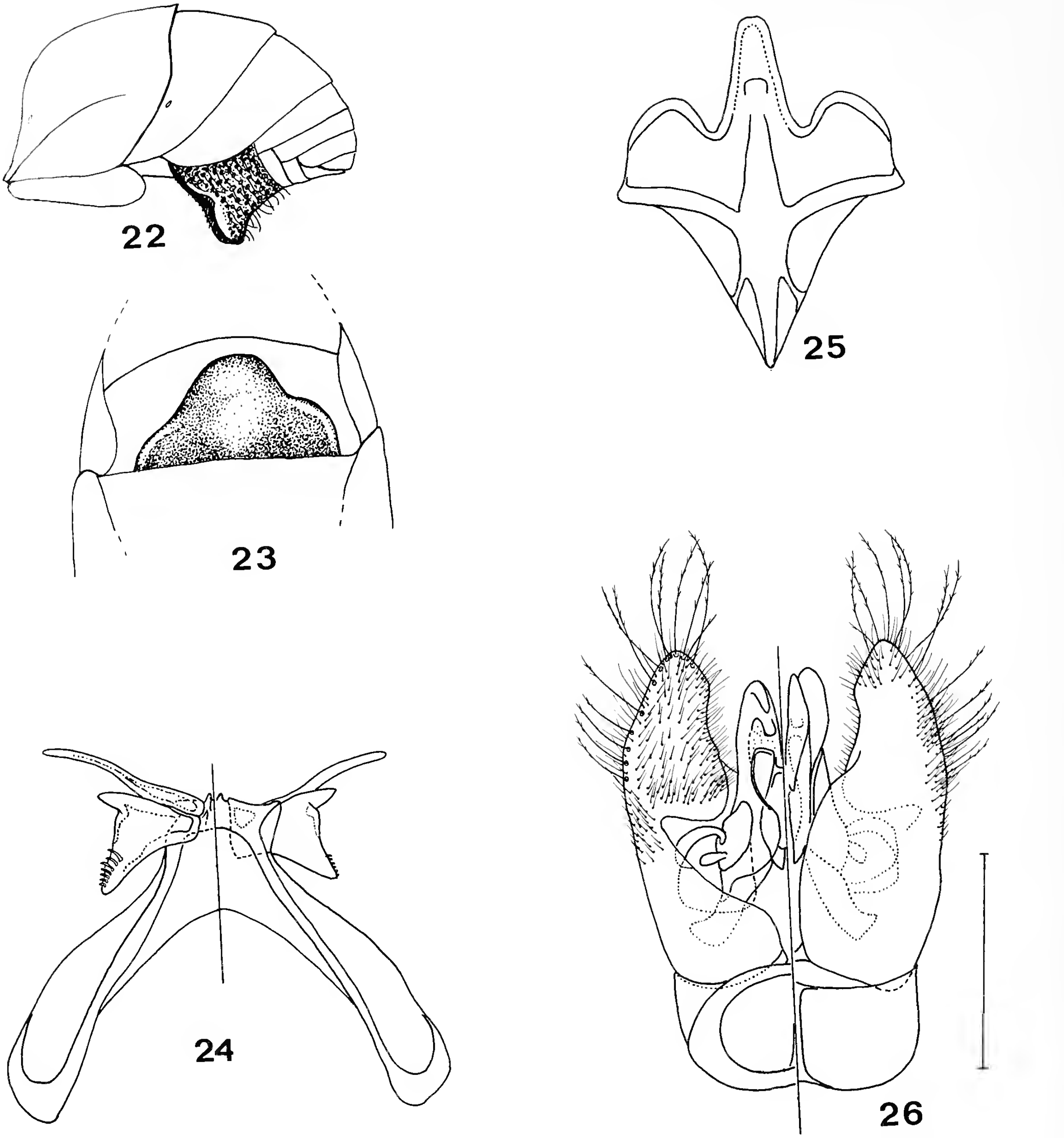
Hylaeus (*Cornylaeus*) *proteae* Cockerell

Figures 14–15, 22–26

Hylaeus proteae Cockerell, 1942:11–12. ♂. SOUTH AFRI-



Figures 18-21. Male, *H.* (*Cornylaeus*) *aterrimus:* **18,** lateral habitus (scale line = 2.00 mm); **19-21,** sterna 7 and 8, genitalic capsule (scale line = 0.50 mm). Figure 18 by R.A. DeNicola.



Figures 22–26. Male, *H.* (*Cornylaeus*) *proteae:* **22,** abdomen, lateral view; **23,** sternum 3, ventral view; **24–26,** sterna 7 and 8 genitalic capsule (scale line = 0.50 mm, 24–26 only). Figures 22 and 23 by R.A. DeNicola.

CA: Port St. John, Pondoland, Oct. 1923 (*R.E.Turner*) (BMNH) [examined].

The male of *H. proteae* is easily recognized by the combination of black clypeus, externally globose scape, densely pubescent abdomen and enormous tubercle on the third sternum. In the female the cutting margin of the mandible is oblique behind the second tooth, the blade is broad, the clypeus is black, and the pronotal collar has a continuous yellow band.

MATERIAL EXAMINED

ZIMBABWE: 1♀, Vumba Mts., 27 Feb. 1938 (*no name;* SAM); 2♀♀, same locality, 12 Aug. 1956 (*no name;* SAM). SOUTH AFRICA: 2♀♀, 4♂♂, Port St. John, Pondoland, Oct. 1923 (*R.E.*

Turner; BMNH, SAM, including 2 cotype ♂♂), on *Protaea;* 1♀, Magaliesberg, Tonguani Kloof, Transvaal, 2 Feb. 1975 (*P.H. Watmough;* PRET), in "open grassland."

***Alfkenylaeus*, new subgenus**

Type-species: *Hylaeus namaquensis* Cockerell, 1942.

DIAGNOSIS

Male with gonocoxite abruptly narrowed over distal one-third or more; seventh sternum with apical lobule virtually absent, basal lobule strap-like and without teeth. Female mandible weakly tridentate; gradulus of second tergum weakly curved, deflected at side; pregradulus of third sternum elevated and extended caudad in middle. In both sexes, head, thorax (except propodeum in one species) and first two terga coarsely and closely punctate; pronotal collar carinate.

DESCRIPTION

(1) Male mandible bidentate at apex, that of female weakly tridentate. (2) Clypeus gently arched, without preapical impression. (3) Occipital margin acute, but preoccipital ridge absent. (4) Pronotal collar carinate on its dorsum. (5) Mesepisternum without carina between anterior and lateral faces. (6) Oblique and lateral propodeal carinae absent. (7) Sulcus of tergum 1 broad at base, at least half as long as basal face, depressed and marginate. (8) Tergum 2 with broadly oval lateral fovea; gradulus gently bowed in middle, weakly deflected at side. (9) Male sternum 3 with or without transverse swelling. (10) Male sternum 7 with distal lobules reduced or absent, basal lobules strap-like and without teeth (Figs. 29, 34, 38). Male gonocoxite abruptly narrowed in distal one-third or more, ending much beyond apex of penis valves (Figs. 31, 36, 40), usually protruding from genital opening in dry specimens.

IAD subequal to (*H. namaquensis*) or much less than (*H. acariphorus* and *H. psaenythioides*) COD; frontal shield high, narrow (more so in males), sharply marginate and reflexed at sides; female facial fovea ending nearer eye than ocellus; first two flagellar segments transverse, subequal in length or second slightly longer; pregradulus of tergum 3 elevated and narrowly, triangularly extended distad in middle; distal process of male sternum 8 elongate, narrow, and slightly broadened at apex (Figs. 30, 35, 39).

ETYMOLOGY

This subgenus is dedicated to J.D. Alfken whose early work on *Hylaeus* has contributed greatly to our understanding of the Old World forms.

DISCUSSION

This subgenus is proposed to accommodate a few coarsely punctate species of distinctive habitus. The unusually large basal sulcus of the first tergum is apparently a modification to accommodate the mites often found on these bees. The elevated pregradular area of the third segment may be similarly adaptive.

The following key to species of *Alfkenylaeus* includes both sexes of *H. arnoldi* (Friese), although this bee does not belong to this subgenus. In the key to genera and subgenera, however, *H. arnoldi* will come out with the *Alfkenylaeus* species and so it seems most convenient to include the species here; *H. arnoldi* is discussed following treatment of the species of *Alfkenylaeus.*

SYNONYMIC LIST OF SPECIES

acariphorus, new species
infulatus, new species
namaquensis Cockerell
psaenythioides, new species

KEY TO SPECIES OF *ALFKENYLAEUS*

1. Female, antenna 12-segmented 2
– Male, antenna 13-segmented 6
2. Apical protarsal segment broadest at apex, evenly narrowed toward base; bristles of protarsus slightly or not at all flattened, their apices acuminate; terga 1–2 coarsely, closely punctate 3
– Apical protarsal segment narrowest basad, broadened to basal one-third, evenly narrowed apicad; protarsal bristles strongly flattened, apices bluntly rounded; second tergum either without evident punctures or punctures fine and obscure .... *arnoldi* (Alfken)
3. Clypeus entirely black; legs brownish, metatibia with basal one-third more or less yellowish; terga 2–5 with conspicuous preapical pubescent fasciae 4
– Clypeus largely ferruginous; legs entirely ferruginous; terga 3–5 with short, inconspicuous hairs, a little denser on side of first and second segments .... *acariphorus,* new species
4. Punctures along middle of clypeus fine to moderate, separated by one-half, or more, puncture diameters; pronotal collar maculate; hairs on basal face of tergum 1 long, fully erect, and continuous across summit .... *namaquensis* Cockerell
– Punctures along middle of clypeus coarse and contiguous to subcontiguous; pronotal collar immaculate; hairs of basal face of tergum 1 subappressed and limited to margin of sulcus, none across summit .. *infulatus,* new species
5. Clypeus entirely pale or pale with apical area ferruginous; lateral face mark filling most of space between eye and clypeus; thorax often dull, punctural interspaces densely tessellate 6
– Clypeus black on basal two-thirds, apical one-third ferruginous; transverse stripe between antennal sockets and clypeal base yellowish; thoracic interspaces shiny, polished on dorsum .... *psaenythioides,* new species
6. Sternum 3 flat, without mediobasal glabrous swelling; base of metatibia and entire metatarsus whitish 7
– Sternum 3 with low, semicircular glabrous swelling at base; legs wholly ferruginous .. *acariphorus,* new species

7. Lateral face mark ending at level of upper margin of antennal sockets; scape maculate beneath; third and following terga without preapical pubescent fascia .... *arnoldi* (Alfken)
- Lateral face marking ending midway between antennal sockets and top of eye; scape immaculate beneath; tergum 3, at least, with preapical pubescent fascia .... *namaquensis* Cockerell

Hylaeus (*Alfkenylaeus*) *acariphorus*, new species

Figures 27–31

DIAGNOSIS

Male: Sternum 3 with large, flat, glabrous swelling in middle of base; legs wholly ferruginous; clypeus yellow and ferruginous; interspaces of frons and thoracic dorsum slightly shiny, distinctly tessellate. Female: Terga 2 and 3 with pubescent fasciae, interrupted in middle; interspaces of frons and thoracic dorsum dull, densely tessellate; clypeus red and black, legs wholly red.

DESCRIPTION

MALE (HOLOTYPE). Measurements. HL 1.74; HW 1.97; SL 0.74; WL 4.9; TL 7.3 mm.

Head. Broad, HW 1.1 × HL; scape moderately long, 2.3 × longer than wide, SL 0.42 × HL. Eyes strongly convergent below, UFW 1.53 × LFW. Clypeus slightly longer than wide at apex, sides regularly divergent to maximum width, BCW 0.48 × CW; BCW:COD:CAD:ASD:IAD = 10:10:8:6:5. OD:IOD:OOD = 5:12:7.5. Frontal shield very narrow between antennal sockets, sides reflexed, transparent. First flagellar segment shorter than either pedicel or second flagellar segment. Entire face coarsely punctate, punctures about 0.06 mm diam.; interspaces in maculate areas slightly shiny and lightly tessellate, in immaculate areas dull, closely tessellate.

Thorax. Pronotal collar sharply carinate in front, carina extending laterad to base of pronotal lobe; humeral ridge present. Mesoscutum 1.35× wider than long. Scutellum flat, about 0.37 × length of scutum. Metanotum flat, sloping, about half as long as scutellum. Basal face of propodeum gently curved into declivitous face; basal triangle sharply marginate. Sides of pronotal collar coarsely, closely punctate; scutum, scutellum, pleura coarsely, almost contiguously punctate; sides and stigmatal area of propodeum closely punctate, punctures about one-half size of mesopleural punctures; basal triangle rugosoreticulate. Integument barely shiny, interpunctural spaces lightly to densely tessellate.

Abdomen. Tergum 1, from above, about 1.4× wider than long, basal sulcus sharply margined, deep, over half length of basal face, apical band broad, a little depressed at sides; apical band about twice as wide on second segment, strongly depressed at sides; first two terga coarsely, closely punctate; sternum 3 with large, flat, semicircular, mediobasal, glabrous tumescence occupying about ⅓ of segment; sternum 7 without hairs on apical lobes; sternum 8 abruptly broadened preapically, apex angulate; gonocoxite evenly narrowed, apex slightly broadened.

Pilosity. Clypeus with numerous short, erect hairs; sides and front of face with hairs conspicuously longer, weakly plumose, especially around antennal insertions; genal hairs sparse, mostly reclinate. Thoracic dorsum with short, sparse erect hairs, except around wing bases and sides of scutellum and metanotum where they are much longer; pleura with hairs short, sparse above, becoming longer ventrad; propodeal hairs sparse, moderately long. Tergum 1 with a few short simple hairs near base and with fine, appressed plumose hairs on sides of apical depression; tergum 2 with sparse simple, erect hairs and dense, plumose, appressed hairs in apical depression, narrowly interrupted in middle; remaining terga with sparse simple hairs of variable length, appressed to fully erect; sterna with scattered, erect, weakly plumose hairs, more abundant caudad.

Color. Black; mandible, lower sides of face, apical third of clypeus (except median stripe), scape, flagellum, and legs light ferruginous; minute basal spot on mandible, basal third of clypeus and broad median intrusion into apical two-thirds, supraclypeal area, sides of face to slightly above level of antennal sockets, all light yellowish. Upper side of scape and flagellum brownish. Tegula testaceous. Wings clear, veins and stigma brownish.

FEMALE (ALLOTYPE). Measurements. HL 1.89; HW 2.05; SL 0.37; WL 4.8; TL 7.8.

Head. Broad, HW 1.08 × HL; scape short, SL 0.19 × HL. Eyes moderately convergent below, UFW 1.41 × LFW. Clypeal length and apical width subequal; BCW 0.54 × CW; BCW:COD:CAD:ASD:IAD = 13:12:6:5:7. OD:IOD:OOD = 5:12.5:9. Mandible broad, tridentate, inner tooth small. Clypeus coarsely and closely punctate, frons a little more coarsely punctate; interspaces dull, densely tessellate. Facial fovea ending about ⅓ of distance between eye and ocellus.

Thorax. As in male, but pleural punctures a little finer, no sparser above than below.

Abdomen. Similar to that of male, with usual sexual differences; no tumescence on sternum 3.

Pilosity. Much as in male, but a little denser in all areas.

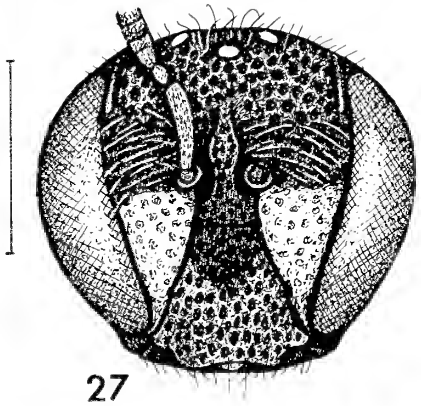
Color. Black; lower sides of face, mandible, clypeus except black basal third, under side of scape and flagellum, legs, all ferruginous. Side of face with broad yellowish macula ending abruptly above at level of antennal sockets. Upper side of scape and flagellum brownish. Tegula translucent brownish. Wings clear, veins and stigma light brown. First tergum with reddish areas laterally and basally.

TYPE MATERIAL

Holotype male and allotype: Khami, ZIMBABWE, 11 Dec. 1932 (*no name*), from collection of the National Museum of Zimbabwe, deposited in SAM: Paratype: 1♀, Pretoria, Transvaal, SOUTH AFRICA, 9 Jan. 1980 (*S.J. van Tonder;* PRET).

ETYMOLOGY

Latin, *acarus* (mite) plus the suffix *-phorus* (to bear), in reference to the presence of a mite-bearing chamber at the base of the first tergum.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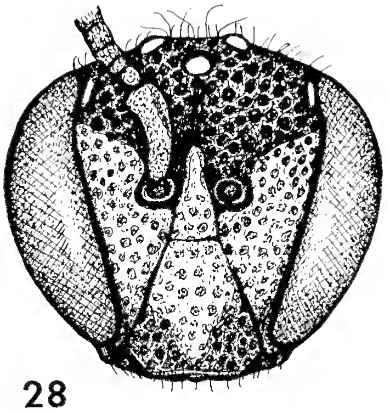
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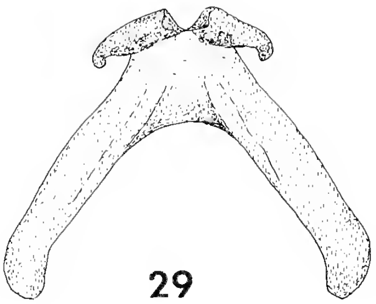
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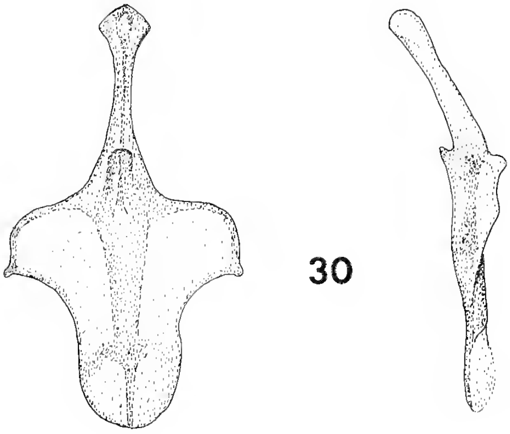
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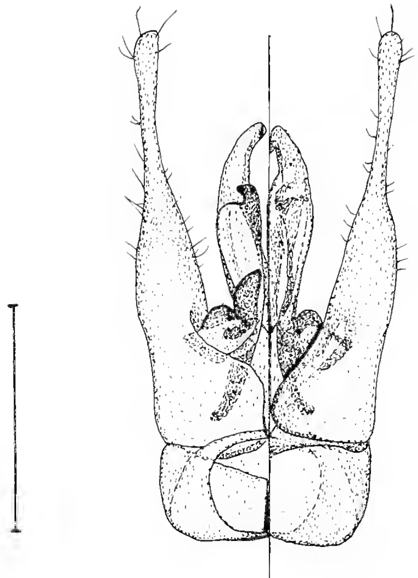
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Figures 27–31. *H.* (*Alfkenylaeus*) *acariphorus:* **27–28,** frontal view of head of female and male (scale line = 1.00 mm); **29–31,** male sterna 7 and 8, genitalic capsule (scale line = 0.50 mm). Figures by R.A. DeNicola.

DISCUSSION

This species is easily recognized by the diagnostic characters given above. The Zimbabwe specimens possess hypophal mites in the modified basal sulcus of the first tergum.

Two additional females, which may be this species, have been seen. Both are from Mombasa, KENYA, collected 12 Dec. 1982 by T.L. and R.T. Griswold, and are in Mr. Griswold's collection. They differ from the allotype in having the first tergum ferruginous rather than black. The punctures laterad on the metanotum are separated by about one-half a puncture diameter, the basal area of the propodeum is very weakly rugulose and the entire propodeum is matt. In one specimen the punctures of the second tergum are separated by up to a puncture diameter and the punctures, instead of being deep and sharply defined, slope upward to the tergal surface along their posterior portions.

Possibly these represent another species, but this is uncertain in the absence of males, and because there are so few specimens that I have no idea of the limits of infraspecific variation. For the time being it seems best to tentatively assign these two Kenyan specimens to *H. acariphorus.* One of these females has hypophal mites in the sulcus of the first tergum.

Hylaeus (Alfkenylaeus) infulatus, new species

DIAGNOSIS

Female only: Terga 1–5 with complete apical pubescent fasciae; clypeus immaculate and coarsely, contiguously to subcontiguously punctate in middle. Male unknown.

DESCRIPTION

FEMALE (HOLOTYPE). Measurements. HW 1.84; HL 1.71; SL 0.45; WL 4.4; TL 7.0 mm. Paratype: HW 1.87; HL 1.74; SL 0.44; WL 4.3; TL 6.3 mm.

Head. Broad, HW 1.08 × HL; scape moderately long, SL 0.26 × HL. Eyes moderately convergent below, UFW 1.45 × LFW. Clypeus about as long as broad, sides regularly divergent to broadest point, BCW 0.58 × CW; BCW:COD:CAD:ASD:IAD = 32:24:17:13:18. OD:IOD:OOD = 11:33:20. Frontal shield narrow, sides nearly straight and strongly convergent above. First flagellar segment transverse, slightly shorter than pedicel and about as long as second segment. Entire clypeus coarsely and contiguously to subcontiguously punctate, interspaces tessellate and moderately shiny, bottoms of punctures shiny. Remainder of front of head similar, but interspaces of frons and vertex shiny, becoming more distinctly tessellate in preoccipital area. Gena moderately shiny between contiguous moderate to coarse punctures.

Thorax. Pronotal collar sharply carinate across front, carina extending across front of lateral lobe. Mesoscutum about 1.6× broader than long. Scutellum flat, about 0.36 × length of mesoscutum. Metanotum, in profile, weakly convex, its dorsum on same level as scutellum, about one-half as long as scutellum. Basal face of propodeum sharply curved into declivitous face; basal triangle sharply marginate. Side of pronotal collar shiny between irregularly spaced fine punctures; mesoscutum moderately shiny between subcontiguous coarse punctures; scutellum similar but a little shinier and punctures distinctly more separated in middle; metanotum coarsely and subcontiguously punctate, interspaces moderately shiny. Mesopleuron moderately shiny between coarse, subcontiguous punctures; metapleuron slightly shiny between subcontiguous to close moderate punctures. Propodeal triangle dull, appearing almost granulose, and sharply reticulorugose; stigmatal area and side dull, moderately rugosopunctate; disc dull, finely rugosopunctate.

Abdomen. Tergum 1, in dorsal view, about 1.4× broader than long; basal sulcus extending above middle of anterior face; disc shiny between coarse, subcontiguous punctures; pregradulus of second tergum moderately shiny between subcontiguous to close, fine to moderate punctures; disc of tergum 2 moderately shiny between subcontiguous to close moderate to coarse punctures. Remaining terga moderately shiny and finely tessellate between close to sparse fine punctures.

Pilosity. Lower frons with conspicuous long, subappressed, plumose hairs near antennal sockets; pronotal collar with dense pubescent fascia; terga 1–5 with complete apical pubescent fasciae; tergum 1 without erect hairs across summit of anterior face.

Color. Black; antenna (lighter beneath), tegula and legs dark brownish. The following pale yellowish: large lateral face mark, filling area between clypeus and eye, ending at level of lower margin of antennal socket; small tegular spot; basal spot on protibia and larger spot on metatibia. Wings clear, veins and stigma brownish.

TYPE MATERIAL

Holotype female: Konkoyo, 22 km W Kebemer, SENEGAL, 4 Aug. 1979 (A. Pauly, #10) in GEMB. Paratype female: Dingasso, near Bobo, UPPER VOLTA, 28 Sept. 1979 (A. Pauly), on *Ziziphus mauritiana,* in LACM.

ETYMOLOGY

From Latin, adorned with a fillet or band, referring to the abdominal fasciae.

DISCUSSION

Only the two female specimens are known. The paratype is very similar to the holotype: HW 1.07 × HL; UFW 1.43 × LFW; BCW 0.59 × CW; BCW:COD:CAD:ASD:IAD = 33:23:16:13:21. OD:IOD:OOD = 10:34:22.

Although very similar to *H. namaquensis,* females of *H. infulatus* are more coarsely punctate; this is especially evident on the clypeus, as noted in the key. The male of *H. infulatus* is unknown but probably will run to *H. namaquensis* in the key above.

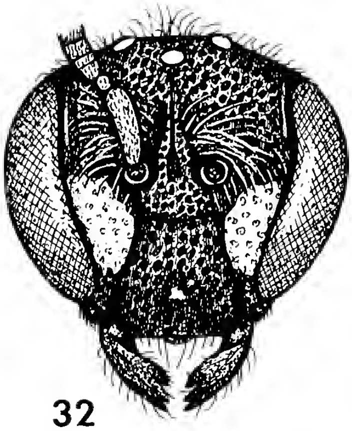
Hylaeus (Alfkenylaeus) namaquensis Cockerell

Figures 32–36

Hylaeus namaquensis Cockerell, 1942:12–13. ♀ ♂. SOUTH WEST AFRICA: Aug., Jan. 1930 (*R.E. Turner*) (BMNH) [examined].

DISCUSSION

This species is easily recognized, in the female by the combination of coarse punctation, extending to the second tergum, black clypeus, but with two lateral marks on face and pubescent fasciae on the second to fifth terga. The male has the lower half of the face yellow, the third sternum without a glabrous swelling, coarse punctation, and third to sixth terga with preapical pubescent fasciae; the fasciae of the fourth and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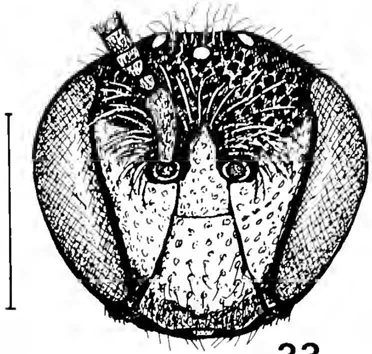
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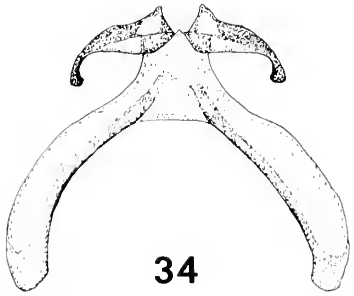
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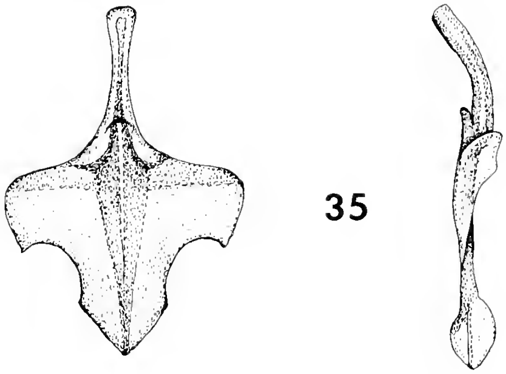
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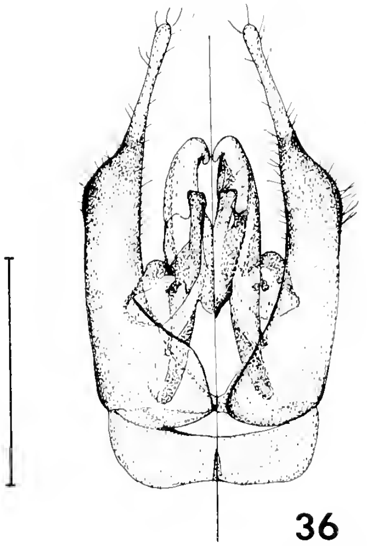
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Figures 32-36. *H.* (*Alfkenylaeus*) *namaquensis:* **32-33,** frontal view of head of female and male (scale line = 1.00 mm); **34-36,** male sterna 7 and 8 (ventral and lateral), genitalic capsule (scale line = 0.50 mm). Figures by R.A. DeNicola.

following segments may be absent due to abrasion. In this species the propodeum is sharply and densely tessellate, with fine, dense punctures; the basal triangle is rugosoreticulate at the base.

SOUTH WEST AFRICA: 10♂♂, 14♀♀, Aug., Jan. 1930 (*R.E. Turner;* BMNH, incl. cotypes); 1♂, Aug., Dec. 1929 (*R.E. Turner;* BMNH); 1♂, Windhoek, 12 Dec. 1933 (*J. Ogilvie;* BMNH); 1♂, Kaoko Otavi, Mar. 1926 (*no name;* SAM). One additional female, surely mislabelled, is in the BMNH: Mahdatha, 60 mi. NE Mecca, ARABIA, Jan. 1945 (*B.P. Uvarov*).

Hylaeus (*Alfkenylaeus*) *psaenythioides*, new species

Figures 37–40

DIAGNOSIS

Male only: Face with transverse yellow band between inner orbits above clypeal base; punctation coarse. Female unknown.

DESCRIPTION

MALE (HOLOTYPE). Measurements. HL 1.68; HW 1.74; SL 0.68; WL 4.3; TL 6.5 mm.

Head. Broad, HW 1.06 × HL; scape moderately long, twice longer than wide, SL 0.40 × HL. Eyes strongly convergent below, UFW 1.62 × LFW. Clypeus slightly longer than wide at apex, sides evenly divergent from base; BCW 0.58 × CW; BCW:COD:CAD:ASD:IAD = 11:8:7:5:5:5. OD:IOD:OOD = 5:11:8. Cephalic punctures uniformly coarse, about 0.08 mm diam., often irregularly shaped, subcontiguous, interspaces polished; genal punctures a little smaller, interspaces less shiny, faintly tessellate.

Thorax. Pronotal collar with thin crest along anterior margin, reduced in middle, extended laterad along front of pronotal lobe nearly to lower margin of lobe; humeral ridge sharp. Mesoscutum about 1.3× wider than long. Scutellum flat, about 0.4 × length of scutum. Metanotum half as long as scutellum, anterior margin raised above posterior margin of scutellum, sloping to propodeal base. Basal area of propodeum oblique, evenly rounded onto posterior face; basal triangle almost entirely on basal face, sharply marginate; median groove deep and narrow. Entire thorax with coarse, subcontiguous punctures, those of mesoscutum about 0.06 mm diam., on mesopleura a little finer, propodeal punctures coarser above than below; interspaces smooth and shiny and dorsal areas, lightly tessellate and slightly shiny on pleura and sides of propodeum.

Abdomen. Enlarged basal sulcus about ¾ length of basal face of tergum 1; apical impunctate band of tergum 1 broad, sharply depressed; tergum 2 with apical impunctate band broader, more depressed, especially at sides; tergum 3 with apical impunctate band about as broad as on second, lightly depressed; sternum 3 with low, inconspicuous shiny swelling at base. First two terga coarsely punctate, punctures about 0.06 mm diam., interspaces smooth and shiny; remaining terga slightly shiny, transversely lineolate and with sparse, irregular, fine punctures; sterna shiny, very lightly tessellate and with scattered fine punctures which are coarser than on tergum 3. Sternum 7 with apical process expanded distally, apical margin rounded; sternum 8 with apical lobes narrow, apices reflexed, with a few setae along distal margin; gonocoxite evenly narrowed, apices not broadened.

Pilosity. Specimen apparently rubbed. Short simple hairs on front of head, a few longer, plumose hairs around antennal sockets, upper inner orbits, occipital margin, and head. Thoracic dorsum with short simple erect hairs, longer, plumose hairs at wing bases and sides of scutellum, metanotum, and stigmatal area; pronotal collar with band of dense, appressed, short plumose hairs and pronotal lobe margined by similar hairs; pleura with only short simple hairs (longer, plumose hairs may have once been present); propodeum with a few long, plumose hairs at sides of posterior face. Tergum 1 with moderately long simple hairs in sulcus, shorter simple hairs at sides and on disc; tergum 2 with similar, longer hairs on disc and sides; third and following terga with longer, more abundant simple hairs. Sterna with sparse, long, simple hairs. Tergum 1 with short, dense, appressed, plumose hairs on each side of apical margin.

Color. Black, abdomen obscurely reddish basally and ventrally; mandible, labrum, apical fourth of clypeus, lower sides of face, and most of legs reddish; underside of scape and flagellum dull yellowish red, dorsal surfaces brownish. Meso- and metafemora and tibiae mostly brownish. Tegula transparent brownish. Wings clear, veins light brown, stigma darker. Supraclypeal area and adjacent side of face light yellowish, so that face has transverse yellow band (Fig. 37).

TYPE MATERIAL

Holotype male: 13 mi. S Malindi, KENYA, 26 May 1967 (*C.D. Michener*), in UKAN.

ETYMOLOGY

This name was suggested by the presence of the transverse facial mark, as in the Neotropical bee genus *Psaenythia* (Andrenidae), to the name of which is added the suffix, *-oides*, resembling.

DISCUSSION

The species is easily recognized by the transverse facial mark, apparently unique among the hylaeines of the Ethiopian Region. The female possibly will be similarly marked, though it seems more likely that the supraclypeal area will be dark in this sex.

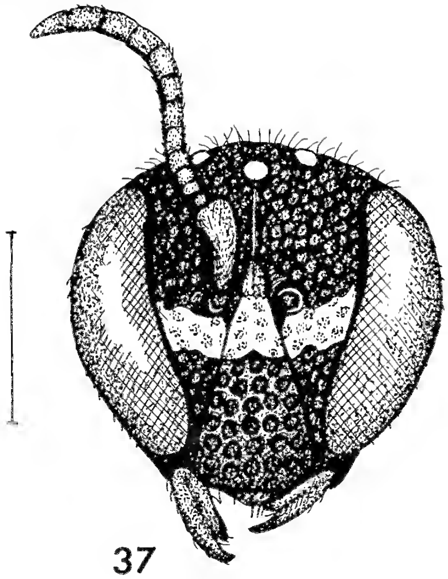
Subgenus uncertain

Although *Hylaeus arnoldi* will key to the subgenus *Alfkenylaeus* it is not, in my opinion, a member of that subgenus. In particular, I am impressed by the very different male sternum 8 (Fig. 44) and the shape of the male gonocoxite (Fig. 45). At present *H. arnoldi* does not fit within any of the existing subgenera. I am, however, presently unwilling to erect a monotypic subgenus for this species.

Hylaeus arnoldi (Friese)

Figures 41–45

Prosopis arnoldi Friese, 1913:574. ♂. ZIMBABWE: Bulawayo, 28 Sept. 1912 (*G. Arnold*) (MNHU) [examined].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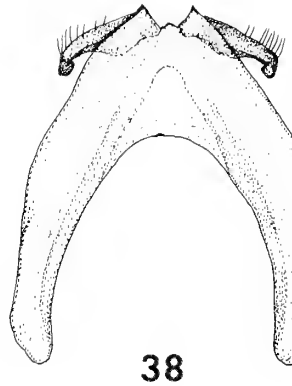
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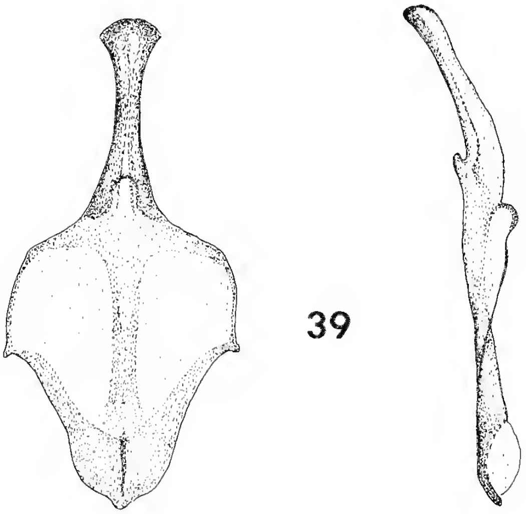
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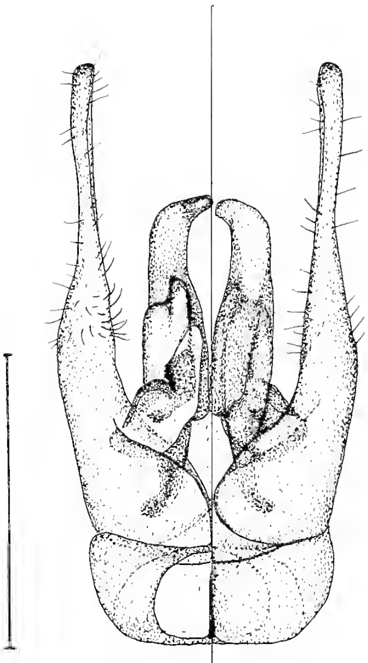
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Figures 37-40. Male, *H.* (*Alfkenylaeus*) *psaenythioides:* **37,** frontal view of head (scale line = 1.00 mm); **38-40,** sterna 7 and 8 (ventral and lateral views), genitalic capsule (scale line = 0.50 mm). Figures by R.A. DeNicola.

Prosopis xanthopus Alfken, 1914:107. ♀. ZIMBABWE: Bulawayo, 28 Sept. 1912 (*G. Arnold*) (MNHU) [examined].

DISCUSSION

Bridwell (1919) correctly recognized that Alfken's *P. xanthopus* was a synonym of *P. arnoldi.* His assignment of this bee to *Deranchylaeus* appears to have been based on the descriptions alone. The male terminalia are different from those of *Deranchylaeus;* the lobules of sternum 7 lack teeth, sternum 8 is profoundly bilobed and the gonocoxites are sharply narrowed toward their apices and extend well beyond the level of the apices of the penis valves. The shape of sternum 8 will immediately separate this species from those assigned here to the new subgenus *Alfkenylaeus.* The female cannot be separated from those of the few species of *Alfkenylaeus.*

SPECIMENS EXAMINED

ZIMBABWE: 1♂, 1♀, Bulawayo, 28 Sept. 1912 (*G. Arnold;* MNHU, types of *P. arnoldi* and *P. xanthopus,* respectively); 4♂♂, same data as *P. arnoldi* type (MNHU, SAM); 1♂, Bulawayo, 21 Sept. 1913 (*G. Arnold;* BMNH); 1♂, Bulawayo, 19 Oct. 1924 (*R.H.R. Stevenson;* AMNH); 1♂, Bulawayo, 5 Oct. 1924 (*no name;* SAM). SOUTH WEST AFRICA: 1♂, Kaoko Otavi, Mar. 1926 (*no name;* SAM); 1♂, Okosongomingo Farm No. 149, 59 km ESE Otjiwarongo, 17 Nov. 1972 (*C.L. Hogue;* LACM); 1♀, Karasburg, 850 m elev., 24 Sept. 1967 (*Ross and Stephen;* CAS).

Subgenus *Metylaeus* Bridwell

Metylaeus Bridwell, 1919:131. Type-species: *Metylaeus cribratus* Bridwell, 1919; original designation.

DIAGNOSIS

Preoccipital carina present; anterior and lateral faces of mesepisternum separated by a carina on lower half; metanotum sharply marginate at sides, usually produced as spiniform process.

DESCRIPTION

(1) Mandible broad, bidentate at apex. (2) Clypeus without preapical depression, with dense to contiguous moderate punctures. (3) Preoccipital carina present. (4) Pronotal collar with anterior carina which extends laterad to posterior lobe. (5) Mesepisternum carinate between anterior and lateral faces in lower half. (6) Lateral, oblique, and transverse propodeal carinae present, strong; basal triangle coarsely areolate. (7) Sulcus of tergum 1 broad, less than half as long as basal face. (8) Tergum 2 with punctiform lateral fovea. (9) Male second and third sterna simple. (10) Male sternum 7 with basal lobule absent or poorly defined, without lateral teeth (Fig. 46). (11) Male gonocoxite broad, blunt, ending slightly beyond level of apex of penis valves, with numerous long, barbed hairs (Fig. 50).

Labral tubercle present in both sexes, not well defined in male; IAD about 1.2 × COD; subantennal sutures about 1.5 × ASD; upper end of female facial fovea ending near inner eye margin; first flagellar segment broader than long, about one-half as long as second segment; scutellar processes present (Figs. 54–55); frontal shield unusually high and short; terminating abruptly a little above level of antennal sockets; dark, slender species with dense to close moderate punctures, usually including first one or two terga.

DISCUSSION

Bridwell (1919) proposed *Metylaeus* as a genus, based in large part on the conspicuous modifications of the scutellum and metanotum. He had available for study both sexes of the type species, but had seen no others. The only other species of which he was aware were two species known from males only: *H. scutispinus* (Alfken) and *H. catalaucoides* (Bridwell) (*H. catalaucoides* was a new name for the improperly associated male of *H. bouyssoui,* a species which Bridwell assumed to belong to his subgenus *Deranchylaeus* of *Hylaeus*); these he knew only from descriptions. Since all of these were known to possess both scutellar and metanotal spines, the presence of such spines was assumed to be characteristic of the new genus. Samples of additional species have negated the significance of these spines as a generic character.

In the females of *H. bouyssoui* and *H. scutispinus* the scutellum is weakly depressed posteromesally, but otherwise is simple. The median area of the metanotum is marked by a sharp oblique carina on each side; the posterior ends of the carinae are joined by a transverse carina, but there are no spines. In females of these species the preoccipital carina is weak, and these are superficially similar to some species of *Deranchylaeus.* The male of *H. scutispinus* has well-developed spines on both scutellum and metanotum and is otherwise similar to *H. cribratus;* the two must be placed in the same group.

Thus, the distinctions between *Metylaeus* and *Deranchylaeus* are less clear-cut than once seemed to be the case. I believe that they are to be treated as related subgenera of *Hylaeus.* Popov (1939) suggested that the Philippine subgenus *Hoploprosopis* ought not be separated from *Metylaeus.* As I have shown elsewhere (Snelling, 1969), the two are readily separable and presumably not at all closely related.

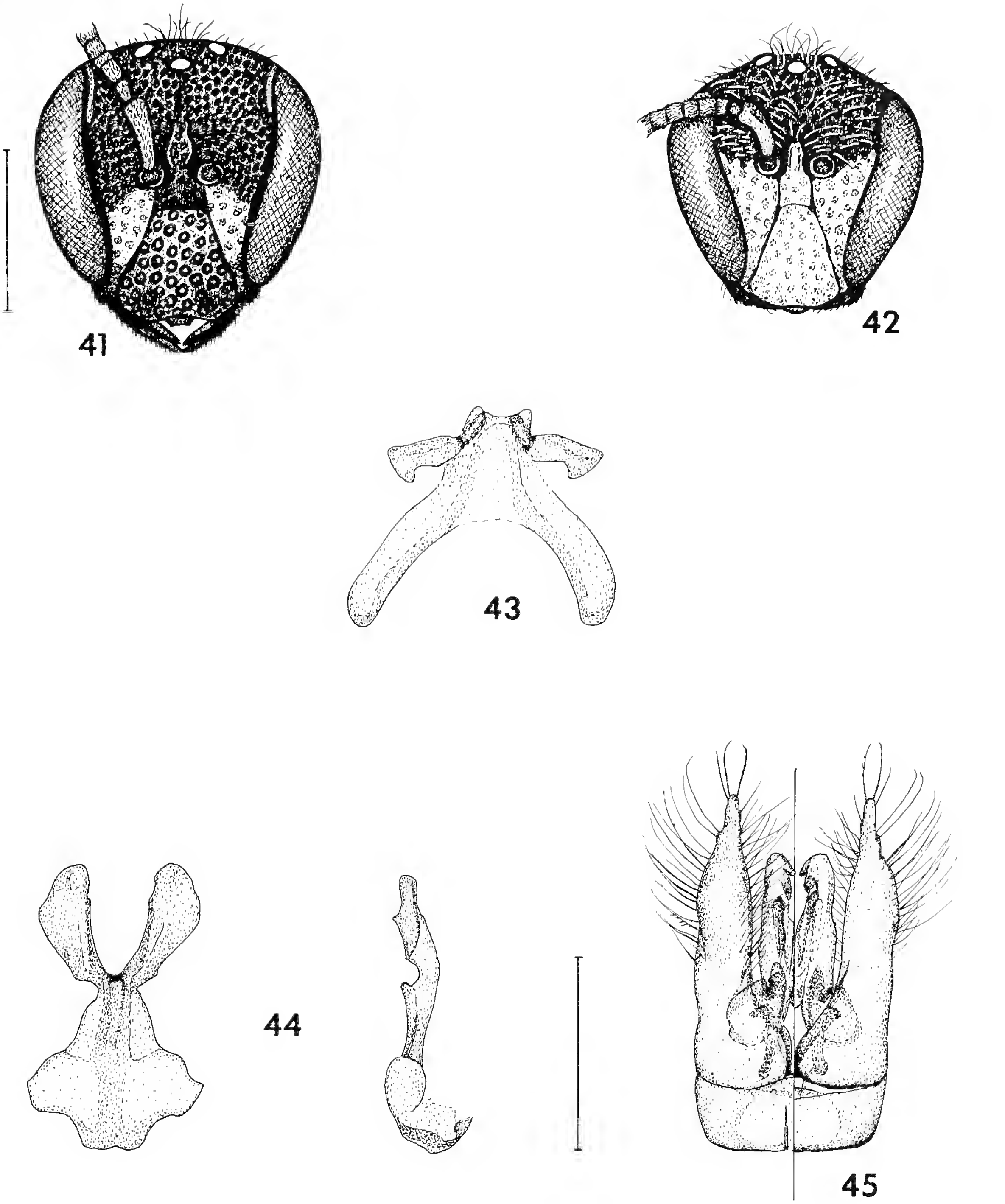
Of the species listed below, *H. spiniger* (Benoist) is known only from Madagascar and is not treated here.

SYNONYMIC LIST OF SPECIES

bouyssoui (Vachal)
cribratus (Bridwell)
  =*catalaucoides* Bridwell, NEW SYNONYMY
  =*rugiceps* Friese, NEW SYNONYMY
  =*semlikiensis* Cockerell, NEW SYNONYMY
gaullei (Vachal)
scutispinus (Alfken)
spiniger (Benoist)

KEY TO SPECIES OF *METYLAEUS*

1. Antenna 12-segmented; female 2
– Antenna 13-segmented; male 5
2. Scutellum simple; metanotum with laterally marginate median area, but no spines 3
– Scutellum and metanotum deeply excavated and with posteriorly directed lateral spines .. *cribratus* (Bridwell)
3. Tergum 1 finely and closely punctate, second densely tessellate and impunctate or nearly so; tergum 2 without apical pubescent fascia; clypeus blackish 4
– First and second terga coarsely and subcontiguously to densely punctate; tergum 2 with complete apical pubescent fascia; clypeus partly ferruginous .... *scutispinus* (Alfken)



Figures 41–45. *H.* (*Deranchylaeus*?) *arnoldi:* **41–42,** frontal view of head of female and male (scale line = 1.00 mm); **43–45,** male sterna 7 and 8 (ventral and lateral views), genitalic capsule (scale line = 0.50 mm). Figures by R.A. DeNicola.

4. Interspaces of tergum 1 slightly shiny, obviously sculptured; second tergum virtually impunctate; first two terga without subdecumbent to suberect hairs .... *bouyssoui* (Vachal)
– Interspaces of tergum 1 smooth, subpolished; second tergum with sparse to scattered minute punctures; first two terga with scattered subdecumbent to suberect hairs, especially laterad .... *gaullei* (Vachal)

5. Scape, flagellum and metabasitarsus black; punctures of tergum 2 much finer than those of first (rarely, punctures

may be very obscure), apical margin not, or weakly, depressed .... *cribratus* (Bridwell)

– Scape and flagellum reddish, metabasitarsus reddish to yellow; tergum 2 nearly as coarsely and closely punctate as first, apical margin sharply depressed .... *scutispinus* (Alfken)

Hylaeus (*Metylaeus*) *bouyssoui* (Vachal)

Figure 53

Prosopis Bouyssoui Vachal, 1899:535. ♀ only. GABON: N'Doro, 15 Sept. and 12 Nov. 1898 (*J. Bouyssou*) (MNHN) [examined].

DIAGNOSIS

Female only: Scutellum and metanotum without sublateral spiniform processes; tergum 1 tessellate and moderately shiny between fine, close punctures, middle impunctate or nearly so. Male unknown.

DESCRIPTION

FEMALE. Measurements. HL 1.56; HW 1.63; TL 5.6, WL 4.3.

Head. Slightly wider than long; HW 1.04 × HL; scape short, SL 0.32 × HL, SL 2.80 × SW. Eyes moderately convergent below, UFW 1.48 × LFW. Clypeus broad, CW 1.05 × CL; BCW 0.55 × CW, 2.20 × ASD, 1.57 × IAD, 1.37 × COD. Clypeal punctures shiny within, moderate, contiguous to subcontiguous, round, shallow, interspaces slightly shiny; supraclypeal area with contiguous, slightly coarser punctures; paraocular areas similar to clypeus; sides of supraclypeal shield moderately flared, margins effaced, disc rugulose, apical width about 0.25 × ASD; punctures of vertex and occiput a little coarser, more regular in shape, shiny within; gena slightly shiny, with moderate to coarse contiguous punctures, shiny within. Fovea ending slightly nearer eye than ocellus.

Thorax. Carina of pronotal collar sharp, disc with dull interspaces between moderate, subcontiguous punctures. Mesoscutum about 1.15× wider than long. Scutellum flat, about 0.34 × length of mesoscutum. Metanotum with median, laterally and posteriorly carinate trapezoidal area, interior of which is irregularly, finely rugulose; lateral areas dull and tessellate near trapezoid, finely and contiguously punctate at extreme side. Mesoscutum dull between moderate, contiguous to subcontiguous punctures; scutellum weakly depressed in middle, more strongly so posteriorly, depressed area with fine to moderate, subcontiguous punctures which become fine and contiguous posteriorly, lateral areas with irregularly spaced, mostly moderate punctures; mesopleuron dull between coarse, contiguous to subcontiguous shallow punctures which are shiny within; metapleuron dull, moderately, contiguously punctate. Side of propodeum slightly shiny, finely, closely and irregularly rugulose; stigmatal and discal areas coarsely rugulose; basal triangle coarsely, quadrately areolate.

Abdomen. Tergum 1 about 1.5× wider than long, disc moderately shiny between fine, subcontiguous to dense punctures, impunctate along midline; pregradulus of tergum 2 moderately shiny between scattered minute punctures, gradulus weakly impressed, disc moderately shiny between very obscure, sparse, minute punctures, margin not depressed in middle.

Pilosity. Propodeum pollinose; first and second terga without apicolateral pubescent fasciae.

Color. Black. A pair of submedian spots on pronotal collar, part of posterior pronotal lobe and basal spot on protibia, yellowish. Antenna and legs brownish, flagellum paler beneath. Wings slightly brownish, veins and stigma dark brown.

TYPE MATERIAL

Described from two females (15 Sept. and 12 Nov. 1898) from N'Doro, GABON, collected by J. Bouyssou. The male described by Vachal is not conspecific. Of the original two females of *P. bouyssoui*, one is in the Paris Museum and bears a red TYPE label and another label, in Vachal's hand: "Bouyssoui/Vach." This specimen is here selected as the lectotype.

DISCUSSION

Because the female does not possess scutellar and metanotal spines, Bridwell (1919) placed *P. bouyssoui* in his subgenus *Deranchylaeus* of *Hylaeus;* the male was recognized to belong to *Metylaeus.* In the original description of the male, Vachal stated that the metanotal spines were triangular. With this distinction between Vachal's male specimen and those which he had described as *M. cribratus,* Bridwell renamed the Vachal male as *M. catalaucoides.*

The female of *H. bouyssoui* is very similar to that of *H. gaullei* but is smaller, the mesoscutum is dull between contiguous to subcontiguous punctures and the first tergum is moderately shiny and distinctly tessellate between fine, close punctures, except along the essentially impunctate midline.

MATERIAL EXAMINED

Only the lectotype has been seen.

Hylaeus (*Metylaeus*) *cribratus* (Bridwell)

Figures 46–47, 51–52

Metylaeus cribratus Bridwell, 1919:131–133. ♂♀. NIGERIA: Ibadan, Aug.–Sept. 1914 (*J.C. Bridwell*) (USNM) [examined].

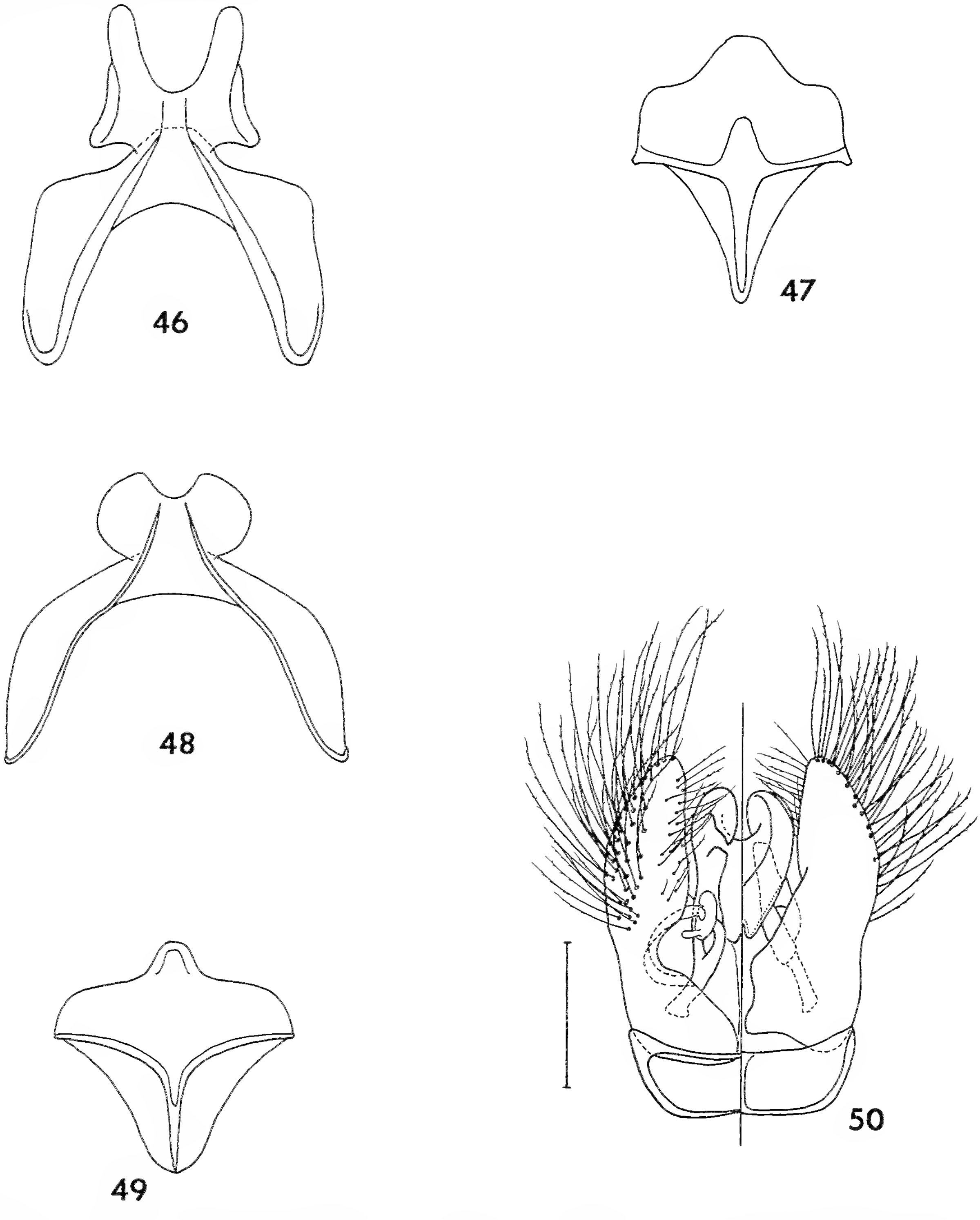
Metylaeus catalaucoides Bridwell, 1919:133. ♂. GABON: N'Doro, 30 Sept. 1898 (*J. Bouyssou*) (MNHN) [examined]. New name for *Prosopis Bouyssoui* Vachal, ♂, not ♀. NEW SYNONYMY.

Prosopis rugiceps Friese, 1921:1105–1106. ♀. ZAIRE: Duma, Ubangi District, 20 Oct. 1910 (*Schubotz*) (type depository unknown). NEW SYNONYMY.

Metylaeus semlikiensis Cockerell, 1936:11. ♀. ZAIRE: Semliki Valley, 16 Aug. 1914 (*J. Bequaert*) (AMNH) [examined]. NEW SYNONYMY.

DISCUSSION

The male which Vachal (1899) described as that of *Prosopis bouyssoui* was correctly recognized by Bridwell (1919) as not



Figures 46–50. Males, *H.* (*Metylaeus*) spp.: **46–47,** sterna 7 and 8, *H. cribratus;* **48–50,** sterna 7 and 8, genitalic capsule *H. scutispinus* (scale line = 0.25 mm).

being conspecific with the female. Accordingly, he renamed the male as *Metylaeus catalaucoides*. The name is based on that of the ant genus *Cataulacus* and is, therefore, misspelled. The erroneous spelling evidently did not originate with Bridwell, for Vachal wrote "fere sicut in Catalauco reticulata Sm. . . . ." The point is moot, however, since this name is a junior synonym of *H. cribratus.*

Vachal's male is from N'Doro and is in the Paris Museum.

It bears a label in Vachal's hand: "Bouyssoui/Vach." Inasmuch as this is the type of *M. catalaucoides,* I have attached to it a red label: "TYPE/*Metylaeus/catalaucoides*/BRIDWELL 1919."

Although no type material of *P. rugiceps* has been examined, nothing in the description would indicate this to be anything other than *H. cribratus;* Friese may not have been aware of Bridwell's species when he described *P. rugiceps.* The specimens from Cameroon and Uganda were identified as *P. rugiceps* by Alfken, who may have seen type material of this name. Cockerell's *M. semlikiensis* is identical to other females from Zaire which form part of a continuous series of variants to typical *H. cribratus.* Cockerell stated otherwise, but there are remnants of a hair band along the margin of the first tergum of the type of *M. semlikiensis.*

MATERIAL EXAMINED

NIGERIA: 9♂♂, 15♀♀, Oloke Meji, Ibadan, Aug.–Sept. 1914 (*J.C. Bridwell;* USNM) (type series of *M. cribratus*); 1♂, 1♀, Lagos, 18 Aug. 1966 (*C.D. Michener;* UKAN). CAMEROON: 1♀, Akoafim, no date (*S.G. Tessmann,* No. 15-31; SAM). GABON: 1♂, N'Doro, 30 Sept. 1898 (*J. Bouyssou;* MNHN) (type of *M. catalaucoides*). ZAIRE: 1♀, Semliki Valley, 16 Aug. 1914 (*J. Bequaert;* AMNH) (type of *M. semlikiensis*); 1♂, 61 mi. E Kenge, 5 Aug. 1957; 1♂, 4♀♀, 18 mi. W Luanza, 1300 m elev., 16 Jan. 1958; 1♂, 39 mi. NE Lusambo, 12 Aug. 1957; 1♂, 2♀♀, Irangi, 900 m elev., Luhoho R., 10 Sept. 1957; 1♀, 39 km S Walikale, 700 m elev., 25 Dec. 1957; 1♀, 33 mi. SW Kamituga, 675 m elev., 17 Aug. 1957 (all *E.S. Ross & R.E. Leech;* CAS). UGANDA: 4♀♀, no further data (MNHU). ANGOLA: 1♂, near Kasai R., July 1931 (*T.D.A. Cockerell;* BMNH).

Hylaeus (*Metylaeus*) *gaullei* (Vachal)

Prosopis Gaullei Vachal, 1899:536. ♀. GABON: Mouny, no further data (MNHN) [examined].

DIAGNOSIS

Female. Scutellum and metanotum without sublateral spines; tergum 1 subpolished, with moderate, irregularly spaced punctures. Male. Unknown.

DESCRIPTION

FEMALE. Measurements. HL 1.80; HW 1.87; WL 5.3; TL 6.6 mm.

Head. Broad, HW 1.03 × HL; scape short, SL 0.26 × HL; SL 2.54 × SW. Eyes moderately convergent below, UFS 1.34 × LFW. Clypeus as broad as long; BCW 0.63 × CW, 2.50 × ASD, 1.36 × IAD, 1.67 × COD. Clypeus weakly depressed on each side of middle, dull between shallow, moderate, subcontiguous to dense punctures which are shinier than interspaces; supraclypeal area with coarse, contiguous punctures; paraocular area similar to clypeus, but punctures mostly subcontiguous and interspaces slightly shiny; supraclypeal shield depressed in middle, with a few obscure moderate to coarse punctures; frons slightly shiny between moderate to coarse, contiguous to subcontiguous deep punctures; vertex and occiput coarsely rugosopunctate, moderately shiny; gena moderately shiny and finely lineolate between moderate to coarse, contiguous to subcontiguous punctures which are shiny within. Fovea ending a little less than halfway between eye and ocellus.

Thorax. Carina of pronotal collar weak at side, slightly depressed in middle, disc moderately shiny between fine to moderate, irregularly spaced punctures. Mesoscutum about 1.3× wider than long. Scutellum flat, about 0.38 × length of mesoscutum. Metanotum weakly convex, about half as long as scutellum. Mesoscutum slightly to moderately shiny between moderate, mostly dense punctures; scutellum moderately shiny, with very irregularly spaced, fine to coarse punctures; metanotum in middle with large, laterally and posteriorly carinate, trapezoidal shiny and irregularly roughened area, lateral areas dull, moderately and contiguously punctate; mesopleuron slightly shiny between shallow, flat-bottomed, moderate to coarse, subcontiguous to dense punctures which are moderately shiny within; metapleuron moderately shiny, coarsely rugosopunctate. Side of propodeum appearing dull because of dense, hoary pubescence, finely rugosopunctate; stigmatal area and disc moderately rugosopunctate.

Metasoma. Tergum 1 about 2.1× wider than long, disc subpolished, nearly impunctate along middle, otherwise with close to sparse, fine punctures; tergum 2 moderately shiny between minute sparse to fine punctures; remaining terga duller, with scattered, obscure, ultraminute punctures.

Pilosity. Pronotal collar with conspicuous, though narrow, transverse fascia; terga 1 and 2 without apicolateral fascia.

Color. Black. Legs, underside of flagellum and tegula brown. Pronotal lobe with posterior yellowish blotch. Wings slightly brownish, veins and stigma medium brown.

TYPE MATERIAL

Described from a single female. The type is in the Paris Museum; there is no type label, but the data are correct, the specimen matches the description and bears a label in Vachal's hand identifying it as *P. Gaullei.* I have no doubt this is the type and have affixed to it a red label: "TYPE? Prosopis/Gaullei/VACHAL 1899." The type is the only specimen examined of this species.

DISCUSSION

The original description is inadequate and Bridwell (1919) assumed *H. gaullei* to be a species of *Deranchylaeus* close to

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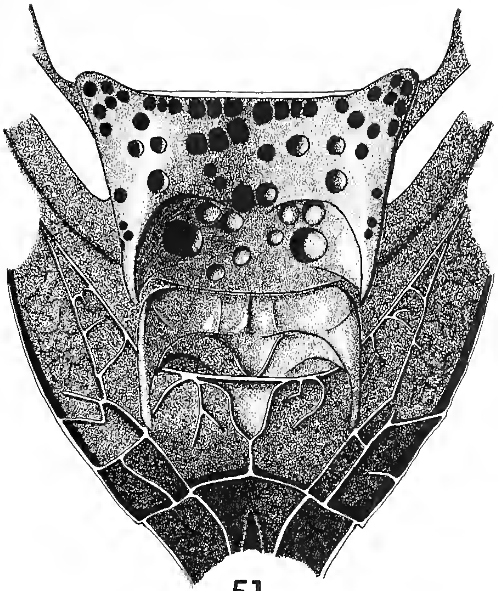
Figures 51-55. *H.* (*Metylaeus*) spp., dorsal view of scutellum, metanotum, and propodeal base: **51-52,** female and male, *H. cribratus;* **53,** female, *H. bouyssoui;* **54-55,** female and male, *H. scutispinus* (scale line = 0.50 mm, 51–52, 54–55 to same scale).



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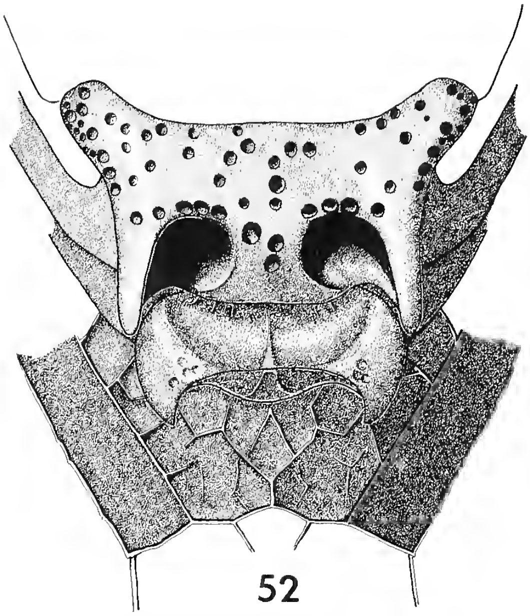

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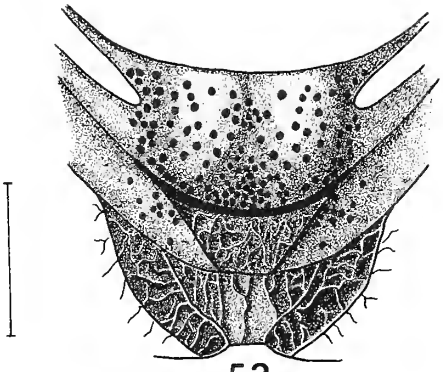

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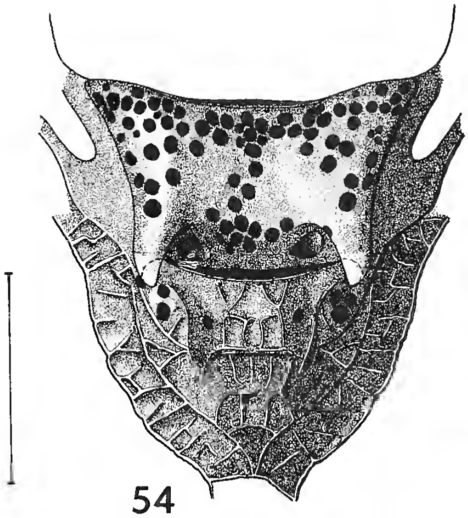

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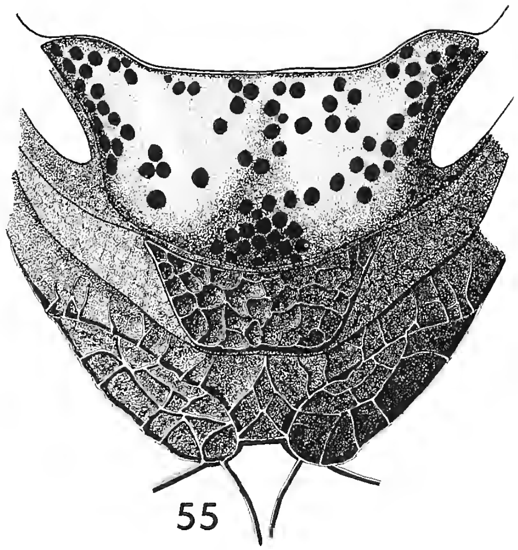

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H. dregei. It is, however, a *Metylaeus* close to *H. bouyssoui.* The larger size, more sparsely punctate mesoscutum and shiny, sparsely punctate first tergum will readily separate *H. gaullei* from *H. bouyssoui.* The lack of scutellar and metanotal spines will differentiate *H. gaullei* from *H. cribratus.*

Hylaeus (*Metylaeus*) *scutispinus* (Alfken)

Figures 48–50, 54–55

Prosopis scutispina Alfken, 1914:195. ♂. ZIMBABWE: Bulawayo, 28 Sept. 1912 (*G. Arnold*) (MNHU) [examined].

DISCUSSION

The female of *H. scutispinus* lacks spines on the scutellum and metanotum, although they are present in the male. Additional features of the female are the ferruginous mandible, labrum, and portions of the clypeus, the sharply and subcontiguously to densely punctate second tergum and the presence of a complete apical pubescent fascia on the second tergum. The male is distinguished by the reddish antenna and by the coarsely and closely punctate second tergum, the apical margin of which is sharply depressed.

MATERIAL EXAMINED

UPPER VOLTA: 13♀♀, 7♂♂, Bobo-Dioulasso, 20 Feb. 1980 (*A. Pauly;* GEMB), on *Guiera senegalensis;* 1♀, Mare-aux-Hippopotames, 3 Oct. 1979 (*A. Pauly;* GEMB); 1♂, Dingasso (near Bobo), 28 Sept. 1979 (*A. Pauly;* GEMB), on *Ziziphus mauritiana;* 1♂, Kougny, 12 Feb. 1980 (*A. Pauly;* GEMB). KENYA: 1♀, Diani Beach, Aug. 1951 (*N.L.H. Krauss;* BMNH); 1♀, Guengere, Pungoue Valley, Mozambique, no date (*no name;* MNHN). BOTSWANA: 1♀, Maun, 930 m elev., 6 Nov. 1976 (*Ross and Stephen;* CAS). SOUTH WEST AFRICA: 1♂, 2♀♀, Kaoko Otavi, Mar. 1926 (*no name;* SAM). ZIMBABWE: 1♂, Bulawayo, 28 Sept. 1912 (*G. Arnold;* MNHU; type of *P. scutispina*); 1♂, Bulawayo, 16 Feb. 1913 (*R.H.R. Stevenson;* SAM).

Nothylaeus Bridwell

Nothylaeus Bridwell, 1919:125–126. Type-species: *Prosopis heraldica* F. Smith, 1853; original designation.

Nothylaeus, sub. *Anylaeus* Bridwell, 1919:129–130. Type-species: *Nothylaeus* (*Anylaeus*) *aberrans* Bridwell, 1919; original designation. NEW SYNONYMY.

DIAGNOSIS

Separable from all known hylaeine genera by the elongate, slender mandible, with acuminate apex and without preapical tooth or with greatly reduced tooth.

DESCRIPTION

(1) Mandible elongate, apex acuminate, preapical tooth absent or greatly reduced. (2) Labral tubercle very broad, covering most of labrum, without median depression. (3) Tentorial pit at or (usually) below midpoint of clypeal length. (4) First flagellar segment of male shorter than, or no longer than, second. (5) Frontal shield present. (6) Lateral and oblique propodeal carinae present, usually entire; propodeal groove broad, shallow. (7) Sulcus of tergum 1 broad, less than one-half as long as basal face. (8) Gradulus of tergum 2 gently arched, slightly deflected laterad; lateral fovea broadly oval. (9) Tergum 3 of male without sublateral pubescent fovea. (10) Male sternum 7 bilobate, each lobe with proximal and distal sublobes, lateral margin serrate or ciliate. (11) Male sternum 8 with apical process short, broad, preapically expanded; dorsal tubercle subapical or apical. (12) Male gonocoxite narrow and elongate, extending much beyond apex of aedeagus.

DISCUSSION

The precise status of *Nothylaeus* is somewhat dubious. Bridwell (1919) proposed *Nothylaeus* as a genus and it has been generally recognized as such, although Cockerell (1936, 1942) seemed to be ambivalent. In originally characterizing *Nothylaeus,* Bridwell stressed the elongate, sharply pointed mandibles of both sexes and the greatly elongated gonocoxal apex of the male.

The elongate gonocoxal apex is not unique to species of *Nothylaeus.* This is a feature that occurs sporadically in some species of African *Hylaeus* and in *Hylaeus* from other parts of the world, as well. These are clear cases of morphological character convergence.

The mandibular structure of both sexes is unique among hylaeine bees. In very nearly all hylaeines, the mandibles of both sexes are short and broad, the outer surface is marked by distinct longitudinal ridges and grooves and the apical margin is truncate to oblique, with one or more preapical teeth. The mandible in *Nothylaeus* is remarkably elongate, at least three times longer than broad at its midlength, there are no distal and dorsal faces, as such, the preapical tooth is absent or greatly reduced and the outer face of the mandible lacks obvious grooves and ridges.

Nothylaeus, as a genus apart from *Hylaeus,* would be more secure if additional supportive features could be found. The robust habitus of *Nothylaeus* species is characteristic, but too elusive to describe adequately. The head is relatively short and broad and many parts of the body are extensively ferruginous, but these features occur widely in *Hylaeus.* However, I am compelled to consider *Nothylaeus* separate from *Hylaeus,* since the mandibular form is so consistent and unique.

No such uncertainty prevails in the case of *Anylaeus,* proposed as a subgenus of *Nothylaeus* by Bridwell (1919). Species assigned to *Anylaeus* differed from those of *Nothylaeus* (s.s.) in having the scutellum and metanotum modified in a manner similar to those of the subgenus *Metylaeus* of *Hylaeus.* This was true for both sexes of the species known to Bridwell at that time. Now, species are known in which the modified thoracic segments occur in the male but not the female. I have here treated *Anylaeus* as a synonym of *Nothylaeus.* The species of *Nothylaeus* will be revised in the second part of this study.

LIST OF INCLUDED SPECIES NAMES

aberrans Bridwell, 1919
abyssinica (Alfken, 1905)
ameliae (Cockerell, 1942)
bevisi (Cockerell, 1917)
binotata (Alfken, 1914)
braunsi (Alfken, 1905)
dentiferella (Strand, 1912)
fortis Cockerell, 1936a
fumata (Strand, 1912)
gigas (Friese, 1911)
haemorrhoa Benoist, 1946*
heraldica (F. Smith, 1853)
isochromus (Cockerell, 1936a)
junodi (Friese, 1911)
libericus Cockerell, 1936a
maculipes Cockerell, 1936a
magretti (Vachal, 1892)
montacuti Cockerell, 1942
neavei (Cockerell, 1942)
nigricans (Friese, 1913)
nyassana (Strand, 1912)
peringueyi Bridwell, 1919
rhodesicus Cockerell, 1942
rubrifacialis (Strand, 1912)
rubriplagiata (Cameron, 1905)
rufipedoides (Strand, 1911)
rufipicta (Strand, 1912)
sansibaribia (Strand, 1912)
simpsoni (Cockerell, 1942)
subfortis Cockerell, 1942
uelleburgensis (Strand, 1912)
ugandicus Cockerell, 1939
umtalicus Cockerell, 1936a
yoruba Bridwell, 1919

Calloprosopis, new genus

Type-species: *Hylaeus magnificus* Cockerell, 1942.

DIAGNOSIS

Body metallic blue in both sexes, female immaculate, male with maculate clypeus; sulcus of first tergum narrow, extending nearly full length of basal face; female with elongate, raised glabrous area at base of metatibia; male with gonobase reduced, not forming cup at base of genital capsule.

DESCRIPTION

(1) Mandible stout, bidentate, apical margin oblique in female, transverse in male. (2) Labral tubercle prominent in both sexes. (3) Tentorial pit at about midlength of clypeus. (4) Pedicel, first and second flagellar segments about equal in length, longer than broad. (5) Frontal shield present. (6) Oblique propodeal carina absent, lateral carina very weak, obvious only near its terminus; basal triangle almost entirely on dorsal face; posterior groove deep and narrow. (7) Sulcus of tergum 1 narrow, deep, extending almost entire length of basal face. (8) Gradulus of tergum 2 broadly convex, pregradulus much longer in middle than at sides; lateral fovea absent, but spiracle in shallow depression. (9) Sternum 3 of male with median, transverse, low swelling. (10) Male sternum 7 transverse, lobes reduced (Fig. 58). (11) Male sternum 8 with elongate distal process, apex transverse, dorsal tubercle absent (Fig. 59). (12) Male genitalia massive, gonocoxite robust, ending at about level of apex of penis valve (Fig. 61).

Integument metallic blue, female without pale marks, male with pale clypeal mark only; scape slender; female metatibia with elongate, glabrous, basal ridge on outer side; male gonobase forming a ring-like flange at base of genital capsule; male volsella elongate, with prominent lateral tubercles.

ETYMOLOGY

The Greek *kallos* (beauty) plus *Prosopis*, an old generic name for *Hylaeus*.

DISCUSSION

This genus closely resembles *Hylaeus*, but differs immediately from all known species of the Ethiopian and South African regions by the metallic blue color. This character, however, does appear in some *Hylaeus* groups in Australia and the Philippine Islands. The presence of what appears to be the basitibial plate in the female and the modifications of the male terminalia are sufficient in my opinion to justify recognition of *Calloprosopis* at generic level. The modifications of the male genital capsule, in particular, are unique among the Hylaeinae. Among all Hylaeinae which I have studied directly, and among those described and illustrated by other workers, the gonobase is large and forms a cup-like base to the genital capsule. In *Calloprosopis* the gonobase, dorsally, projects into an emargination between the gonocoxites; from this area it extends ventrad to form a heavily sclerotized ring. The gonocoxites are heavily sclerotized and are dorsoventrally broadened; they do not extend beyond the apices of the penis valves. The volsellae are heavily sclerotized and the median lobes are elongate, with scattered small tubercles on the outer faces. There is a deep longitudinal groove along the entire length of the penis valves, the apices of which are rather blunt and not as strongly deflected downward as in *Hylaeus*. Sternum 8 of the male is typically hylaeine in appearance but lacks the notch at the base of the apical process which is usually present in *Hylaeus*. Sternum 7, too, is typically hylaeine, but it is much broader than long; the apodemes form a regular arc and the apical process is quite short, with small lobes.

Most of the genitalic features are nothing more than extreme modifications of conditions already present in other

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* Known only from Madagascar.

hylaeines. The structure and orientation of the gonobase are unique, however, and it is largely on this basis that *Calloprosopis* is given generic rank here. A cursory study of various colletid genera in other subfamilies suggests that this peculiarity may be unique within the family.

Calloprosopis magnifica (Cockerell), new combination

Figures 56–61

Hylaeus magnificus Cockerell, 1942:9–10. ♂. KENYA: east foot and slopes, Aberdare Mts., 7000–8500 ft. elev., 24–27 Feb. 1911 (*S.A. Neave*) (BMNH) [examined].

Both sexes are immediately separable from all other known hylaeines in the Ethiopian Region by their metallic color. This species appears to be restricted to high elevations in Kenya.

MATERIAL EXAMINED

KENYA. 1♂, east foot and slopes, Aberdare Mts., 7000–8500 ft. elev., 24–27 Feb. 1911 (*S.A. Neave;* BMNH, cotype); 1♂, 1♀, Mt. Kinganop, 9000 ft. elev., Aberdare Range, cedar forest, 27 Oct. 1934 (*F.W. Edwards;* BMNH); 1♂, Kerita, 2640 m elev., 38 mi. NW Nairobi, 16 Oct. 1957 (*E.S. Ross & R.E. Leech;* CAS).

Psilylaeus, new genus

Type-species: *Psilylaeus sagiops,* new species.

DIAGNOSIS

Frontal shield absent; integument uniformly tessellate, without obvious punctures; propodeum without defined basal triangle; lateral fovea of second tergum broadly oval.

DESCRIPTION

(1) Mandible short, sharply bidentate in male, weakly so in female. (2) Labrum short and broad, male without tubercle, female with elevated median tubercle which is weakly divided in middle. (3) Tentorial pit slightly below midlength of clypeus. (4) Male first flagellar segment transverse, shorter than pedicel, as long as second, each shorter than third. (5) Frontal shield absent. (6) Lateral and oblique propodeal carinae absent. (7) Suleus of tergum 1 about one-half as long as basal face. (8) Gradulus of tergum 2 weakly bowed, concealed. (9) Tergum 3 with round sublateral pubescent fovea, usually hidden under margin of second segment. (10) Male sternum 7 bilobate, basal lobule setose, distal lobule with apically hooked hairs (Fig. 64). (11) Male sternum 8 with apical process broad, setose at margin; dorsal tubercle slightly beyond midlength of apical process (Fig. 65). (12) Male gonocoxite stout, blunt, not reaching level of apex of aedeagus (Fig. 66).

Integument densely tessellate and dull, with sparse to scattered, inconspicuous punctures on thoracic dorsum; front of head dull between fine, contiguous punctures; eyes broadest below midlength; IAD less than COD; frontal shield absent; clypeal margins abruptly divergent in lower one-third; posterior margin of pronotum much below dorsum of mesoscutum, collar virtually absent except at sides; propodeum with long, subhorizontal basal face.

ETYMOLOGY

The generic name combines the Greek *psilos* (bare or smooth) with *Hylaeus* and refers to the virtually impunctate thoracic dorsum, and especially to the smooth propodeum.

DISCUSSION

This genus is known to include only the type species, and is known only from coastal South Africa in the vicinity of Cape Town. The peculiarly smooth integument and unusual propodeal structure are especially characteristic of this small bee. In particular, the sutures which normally demark the propodeal triangle are very weak and largely effaced.

Psilylaeus has been compared with various groups in hylaeines from Australia. In the key by Michener (1965), *Psilylaeus* fails at the last couplet, since it does not agree with either alternative (*Hylaeorhiza* and *Hylaeus*). From *Hylaeorhiza, Psilylaeus* differs in the bilobed, rather than acute, glossa of the male and the outer apical angle of the hind tibia is not obtuse. From *Hylaeus, Psilylaeus* differs (in the key) in the structure of the propodeum. In the more recent key to Australian genera by Houston (1975), *Psilylaeus* will run to *Hylaeus.*

The depressed pronotum, without a well-defined collar, occurs in two Australian subgenera of *Hylaeus: Macrohylaeus* and *Hylaeteron.* The former includes large, metallic species with a long second submarginal cell in the forewing. The known species of *Hylaeteron* are small, robust bees with tridentate female mandibles, sharply reticulate propodeum and exceptionally short subantennal sutures. Both of these subgenera are known only from the Australian area.

Psilylaeus sagiops, new species

Figures 62–66

DIAGNOSIS

Same as generic diagnosis.

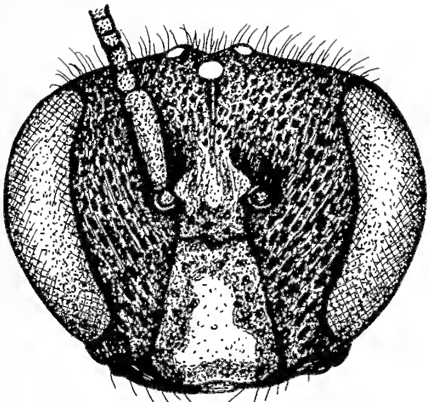
DESCRIPTION

MALE (HOLOTYPE). Measurements. HL 1.12; HW 1.29; SL 0.30; WL 3.50; TL 4.97 mm.

Head. Broad, HW 1.1 × HL; scape short, twice longer than

⟶

Figures 56-61. *Calloprosopis magnifica:* **56-57,** frontal view of head, female and male (scale line = 1.00 mm); **58-61,** male sterna 7 and 8, genital capsule (lateral), genitalic capsule (dorsal and ventral) (scale line = 0.50 mm). Figures 61, 62 by R.A. DeNicola.



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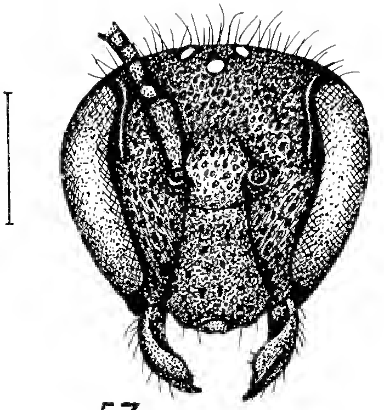

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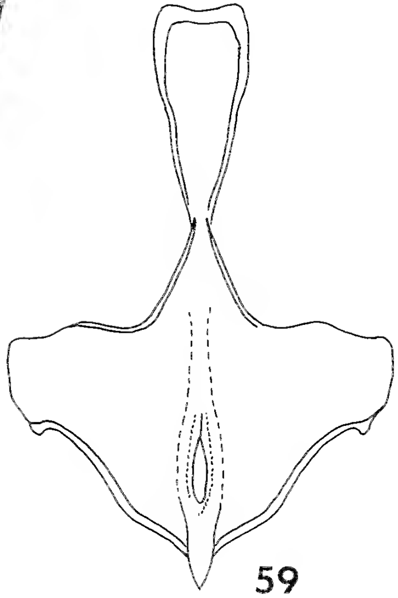

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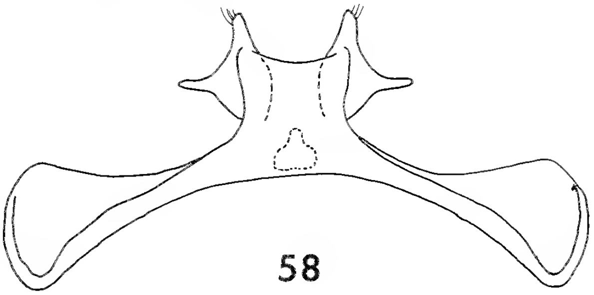

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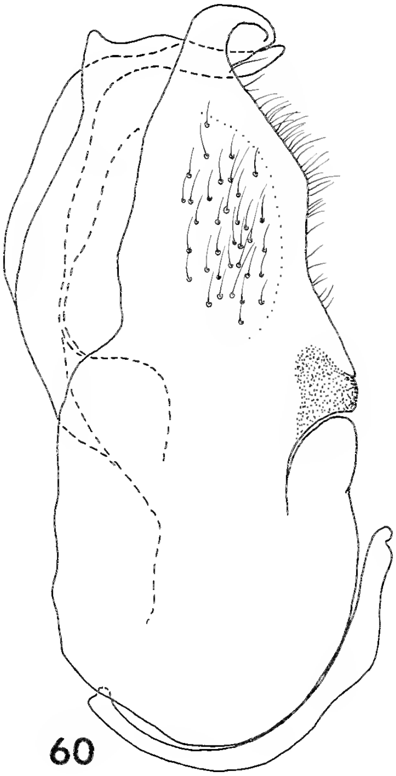

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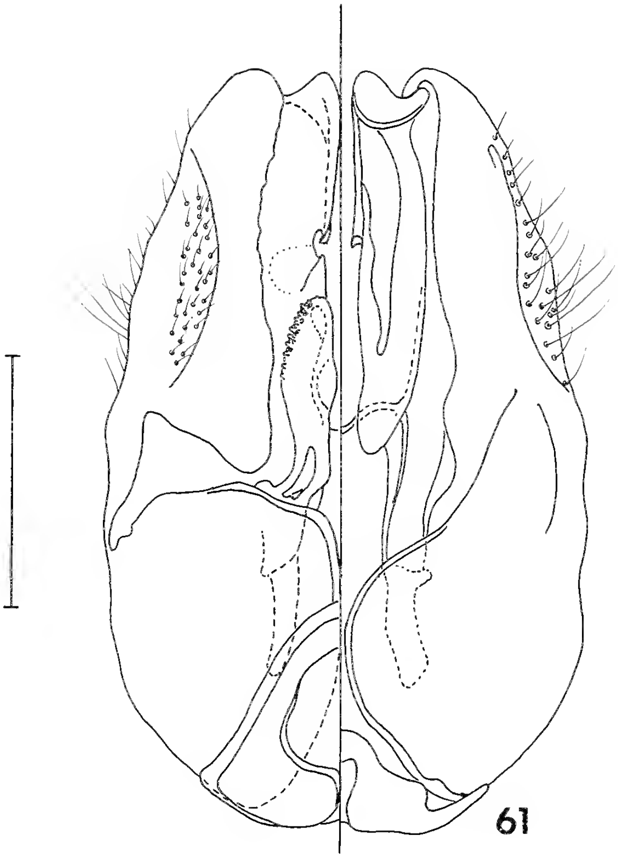

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wide, SL 0.27 × HL. Eyes strongly convergent below, UFW 1.55 × LFW, conspicuously broader below than above in frontal view; in profile, broadest below midpoint, maximum width 0.45 × EL. Clypeus slightly wider at apex than long, epistomal sutures abruptly divergent in lower third; BCW 0.41 × CW × 1. Clypeus and lower half of face slightly shiny, densely tessellate, with scattered obscure shallow punctures; immaculate areas of head duller, densely and finely punctate and tessellate; gena slightly shiny, finely lineolate, with sparse, shallow, fine punctures.

Thorax. Moderately robust, about 1.4× longer than wide. Mesoscutum a little wider than long; in profile, anterior portion convex, rising well above pronotum. Scutellum flat, on same plane as posterior portion of scutum; median length about 0.4 × that of scutum. Postscutellum flattened in profile, sloping away from scutellum, median length less than half that of scutellum. From above, sides of propodeum strongly convergent distad, basal width almost twice apical; in profile, basal face continuous with slope of postscutellum, broadly rounded into, and longer than, posterior face; without carinae or ridges. Slightly shiny, densely tessellate and impunctate; mesopleuron and basal face of propodeum obscurely lineolate; mesopleuron with sparse, fine punctures.

Abdomen. Widest beyond middle; apical width of tergum 1 greater than median length; sternum 3 with a pair of low, shining prominences obliquely directed distad, on either side of midline, highest at about middle; sternum 4 with a pair of broad flattened, shiny callosities; sternum 5 with a similar, but much smaller, pair; apex of sternum 6 broadly rounded. Moderately shiny, finely transversely lineolate; all terga with apical, nonsculptured band; tergum 1 with very fine scattered punctures; tergum 2 more closely punctate, punctures larger; tergum 3 similar to 2.

Terminalia. As described for the genus.

Pilosity. Very sparse; lower half of face with hairs short, stiff; upper half with hairs much longer; scape with a few moderately long hairs; underside of head with scattered long hairs, especially in hypostomal area. Mesoscutum with very short hairs only; scutellum and postscutellum with a few very long hairs at sides; pleura and sides of propodeum with scattered long hairs; propodeum otherwise with sparse, short subappressed hairs. Terga with sparse, short hairs, appressed on discs, longer and partially to fully erect laterad; progressively longer on succeeding segments. Sterna with sparse erect hairs, longest laterad.

Color. Blackish. Mandibles, except ferruginous apices; labrum; clypeus; transverse supraclypeal mark; face between clypeus and eye, extending about halfway upward along inner orbit; narrow line on underside of scape; narrow stripe on sides of pronotal collar; pronotal lobe; apical spot on pro- and mesofemora; basal mark on meso- and metatibia; all light yellowish. Protibia and tarsi, mesotarsi, light ferruginous, apical tarsal segments brownish. Metabasitarsus whitish on basal third, metatarsus otherwise brownish. Tibial spurs whitish. Tegulae brownish. Wings uniformly light brownish, veins and stigma darker.

FEMALE (ALLOTYPE). Measurements. HL 1.05; HW 1.11; SL 0.25; WL 3.30; TL 4.35 mm.

Head. Broad, HW 1.05 × HL. Eyes strongly convergent below, UFW 1.52 × LFW, conspicuously broader below than above; in side view, broadest part below midpoint, and 0.52 × EL. Mandibular apex braod, truncate, obscurely bidentate. Clypeal shape as in male; BCW 0.46 × CW; BCW:COD:CAD:ASD:IAD = 13:10:9:8:10. Scape and flagellum as in male. Frontal line deep, terminating broadly at level of lower margin of antennal sockets. Facial fovea terminating at top of eyes, adjacent to eye margin. Surface sculpture as in male.

Thorax. As in male.

Abdomen. As in male but lacking ventral modifications; apical bands of terga broader.

Pilosity. As described for male but conspicuously shorter.

Color. Blackish. Minute basal spot on mandible; broad longitudinal median stripe on clypeus; narrow stripe along inner orbit, from lower end of eye to lower end of fovea; narrow stripe on pronotal collar on each side, broadly interrupted in middle; pronotal lobe; outer stripe on protibia; basal spot on meso- and metatibia, all pale yellowish. Metatibial spur, tegula, and wings as in male.

TYPE MATERIAL

All from Cape Province, SOUTH AFRICA: Holotype male, Mossel Bay, 11 Oct. 1938 (*R.E. Turner*). Allotype, same locality, 12 Oct. 1938 (*R.E. Turner*). Holotype and allotype in BMNH. Paratypes: 4♂♂, same data as holotype; 2♂♂, 2♀♀, same data as allotype; 1♂, same locality, 1 Oct. 1938 (*R.E. Turner*); 1♀, same locality, Apr. 1933 (*R.E. Turner*); 7♂♂, same locality, Mar.–Apr. 1930 (*R.E. Turner*); 1♂, same locality, 7 Oct. 1941 (*R.E. Turner*); 1♀, same locality, 5 Dec. 1941 (*R.E. Turner*); 6♂♂, same locality, Nov. 1939 (*R.E. Turner*); 1♂, same locality, 12 Jan. 1940 (*R.E. Turner*); 2♂♂, 1♀, same locality, Jan. 1940 (*no name*); 1♀, Cape Town, 1 Apr. 1948 (*no name*); 1♀, Port Elizabeth, no date (*N.L.H. Krauss*); 1♀, Worcester, Jan. 1934 (*R.E. Turner*). Paratypes in BMNH, CORN, LACM, SAM, UKAN, USNM.

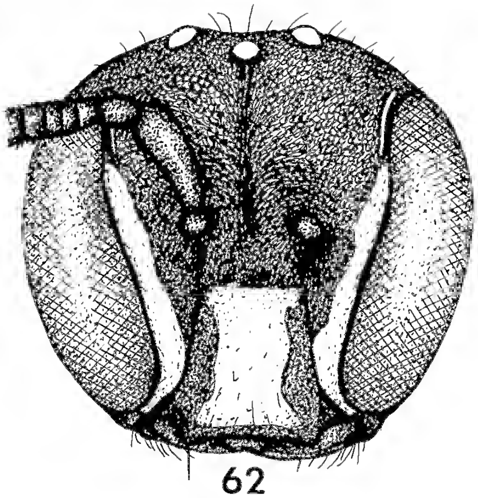
ETYMOLOGY

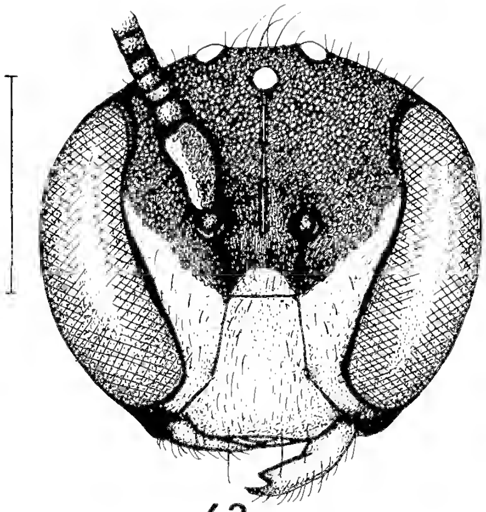
The specific epithet combines the Greek *sagios* (bag) with *ops* (eyes), in allusion to the shape of the lower portion of the eyes.

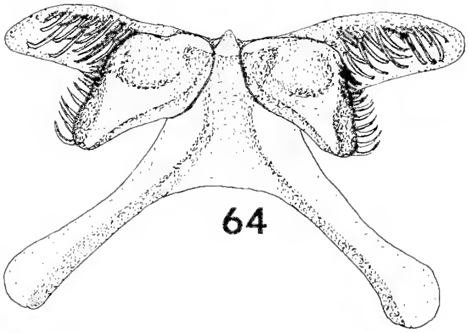
DISCUSSION

Variation is negligible in the limited amount of material studied. The holotype is the largest specimen. The smallest male has a head width of 0.98 mm and a wing length of 2.65 mm, with according allometric variations. Among the males reduction in development of the glabrous processes of the third to fifth sterna is relative to the size of the specimen. Reduction begins with loss of the polished areas on the fifth sternum and some diminution of those of the third and fourth. Still smaller specimens lose next the pair on the fourth sternum, and the smallest male lacks modified areas on all three sterna.

The few females examined are much more uniform. Head


62


63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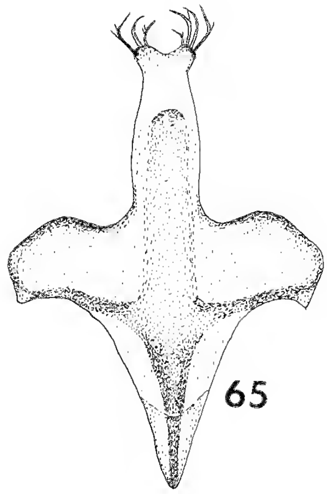
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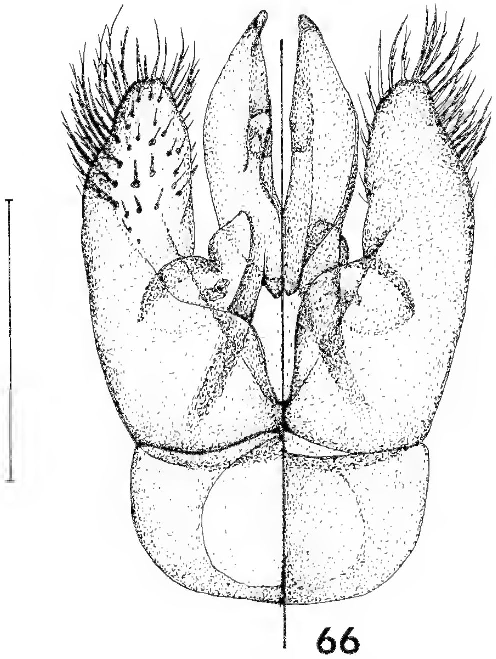
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Figures 62–66. *Psilylaeus sagiops:* **62–63,** frontal view of head, female and male (scale line = 0.50 mm); **64–66,** male sterna 7 and 8, genitalic capsule (scale line = 0.25 mm). Figures by R.A. DeNicola.

width varies from 1.05 to 1.13 mm and wing length from 2.59 to 3.32 mm. The smallest specimen has the head width and head length equal. Smaller specimens tend toward loss of punctation on the mesopleuron and first three terga, but expression of this character is not uniformly correlated with size.

The densely tessellate, impunctate integument, small size, and lack of a defined supraclypeal area will readily separate this species from all other Hylaeinae known from South Africa. The trilineate face marks of the female are reminiscent of the genus *Allodape* in the Anthophoridae.

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This project began in 1968 and has suffered many delays. I must express my deep gratitude to all the curators who have been so patient during the long time I have had material under their care. For the loan of material from their respective institutions, I wish to thank: P.H. Arnaud, Jr. (CAS), G.C. Eickwort (CORN), G.R. Else and I.H.H. Yarrow (BMNH), H.E. Evans (MCZ), M. Favreau and J.G. Rozen, Jr. (AMNH), A.J. Hesse (SAM), the late P.D. Hurd, Jr. and G.I. Stage (USNM), S. Kelner-Pillault (MNHN), C.D. Michener (UKAN), J. Oelkhe (DEI), A. Pauly (GEMB), and E. Pinhey (NMR). A very special gratitude is expressed to the late Embrik Königsmann (MNHU) for locating and making available the critical types of the species described by Alfken, Friese, and Strand.

My thanks, too, to my colleagues at the LACM; J.P. Donahue, C.L. Hogue, and F.S. Truxal, for their advice and comments over the years, both solicited and gratuitous. Some of the illustrations were prepared by R.A. DeNicola, to whom I remain grateful, as always.

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CONTRIBUTIONS IN SCIENCE

REVIEW OF THE LATE PLEISTOCENE AVIFAUNA FROM LAKE MANIX, CENTRAL MOJAVE DESERT, CALIFORNIA

George T. Jefferson

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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REVIEW OF THE LATE PLEISTOCENE AVIFAUNA FROM LAKE MANIX, CENTRAL MOJAVE DESERT, CALIFORNIA

George T. Jefferson[1]

ABSTRACT. Late Pleistocene lacustrine clay, silt, and nearshore sand deposits of Lake Manix, Mojave Desert, California, have yielded 139 specimens of fossil birds, including several articulated partial skeletons. Six extinct and 19 extant taxa are represented. The avifauna includes the first recognized fossil gulls, *Larus oregonus* and *Larus* sp., from Pleistocene terrestrial deposits in the Southwest. *Gavia* cf. *G. arctica* (Arctic Loon), *Phalacrocorax macropus* (extinct cormorant), *Mergus* cf. *M. merganser* (Common Merganser), the extinct chronoclinal subspecies *Fulica americana shufeldti* (Shufeldt's American Coot), and cf. *Actitis* (sandpiper) are new to the Pleistocene record of the region. The avifauna is part of the Rancholabrean Camp Cady Local Fauna, and has most taxa in common with the assemblage from Fossil Lake, Oregon. Habitat preferences of comparative extant taxa and inferred depositional environments indicate extensive reedy marshlands, beach flats, and open water lacustrine conditions.

INTRODUCTION

Since H. Howard's description of the Lake Manix avifauna (Howard, 1955), many additional specimens of fossil birds, including articulated partial skeletons, have doubled the number of taxa known from the site. These additional materials add significantly to an understanding of the late Pleistocene avifauna of the inland Southwest. The first fossil gulls, *Larus oregonus* and *Larus* sp. and other extant and extinct taxa including *Gavia* cf. *G. arctica, Phalacrocorax macropus* (extinct), *Mergus* cf. *M. merganser, Fulica americana* cf. *shufeldti* (extinct), and cf. *Actitis* are new to the Pleistocene record of the region. The Lake Manix avifauna is taxonomically most similar, in the abundance of inland lacustrine forms, to the Wisconsinan age assemblage from Fossil Lake, Oregon. Other comparable late Pleistocene assemblages are known from China Lake, McKittrick, Rancho La Brea, and Carpintaria, California (Table 1). New radiometric dates (Bischoff, pers. comm., 1982) indicate that most of the material from Manix is older than 200 Kyr (thousand years) BP (before present).

J.P. Buwalda of the University of California, Berkeley (UCB), recovered the first bird fossils from Lake Manix during an exploratory expedition in 1913. At that time, he considered the fauna to be early Pleistocene, based on the fragmentary mammalian remains (Buwalda, 1914). L.V. Compton of UCB later published (Compton, 1934) a description of the five specimens collected by Buwalda and first noted similarities with the Fossil Lake avifauna. A relatively large assemblage of birds and mammals was collected in 1952 by H. Winters (1954). The twelve avian taxa from this collection were subsequently described by Howard (1955). The fauna was considered late Pleistocene in age, and no older than Illinoian.

Based on fieldwork performed during the middle 1960's and a review of existing collections, the Rancholabrean age assemblage from Lake Manix was designated the Camp Cady local fauna by G. Jefferson (1968). Initial radiocarbon dating by various institutions indicated the lake beds were Wisconsinan in age (Bassett and Jefferson, 1971).

Fossil vertebrates from Lake Manix are presently housed in five separate institutional collections: the Natural History Museum of Los Angeles County, Vertebrate Paleontology Section (LACM); San Bernardino County Museum, Earth Science Collection (SBCM); University of California, Berkeley, Museum of Paleontology (UCMP); the University of California, Riverside, Earth Sciences Department (UCR); and the United States Geological Survey, Denver, Colorado.

AGE AND STRATIGRAPHY

The Lake Manix avifauna ranges in age from greater than 350 Kyr to about 35 Kyr BP. The stratigraphic section is well dated by C-14 (carbon-14) (Bassett and Jefferson, 1971; Marcus, pers. comm., 1984) and U/Th (uranium-thorium equilibrium) radiometric techniques (Bischoff, pers. comm., 1982), and tephrochronologic correlation (Sarna-Wojcicki, 1980). Most taxa and the majority of specimens fall between 200 and about 300 Kyr BP (Table 2).

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Table 1. Geographic distribution of taxa. Abbreviations: FLO = Fossil Lake, Oregon; CLC = China Lake, California; RLB = Quaternary Rancho La Brea, California; MKC = McKitterick, California; CAC = Carpinteria, California; sf = subfamily; g = genus; s = species; ss = subspecies. Extinct taxon = *. Data from: Fortsch, 1978; Howard, 1946, 1962; Miller, 1925, 1931, 1935; Miller and DeMay, 1942; Stock, 1953.

Lake Manix taxa	FLO	CLC	RLB	MKC	CAC
Gavia cf. *G. arctica*					
Podiceps cf. *P. nigricollis*	s		g	g	
Aechmophorus occidentalis	s	g			
Pelecanus aff. *P. erythrorhynchos*	s				
Phalacrocorax auritus	s	g	g		
*P. macropus**	s				
*Ciconia maltha**			s	s	s
*Phoenicopterus minutus**					
*P. copei**	s				
Cygnus cf. *C. columbianus*	g	g	s	s	s
Branta canadensis	s	g	s	s	
Anas cf. *A. crecca*	s	g	s	s	
A. cf. *A. platyrhynchos*	s	g	s	s	s
Aythya sp.	g	s	g		
Mergus cf. *M. merganser*	s				
Oxyura jamaicensis	s	g		s	
Haliaeetus leucocephalus	s	g	s	s	s
Aquila chrysaetos	s	g	s	s	s
Fulica americana cf. *F. a. shufeldti**	ss	g	s		
cf. *Grus*		g	g	g	
cf. *Actitis*					
Phalaropodinae			sf		
Larus cf. *L. oregonus**	s				
L. sp.	g				
Bubo virginianus	s		s	s	s

Table 2. Stratigraphic/chronologic range of taxa in the Manix Formation. Abbreviations: m TS = meters above base type section, Kyr = approximate thousand years. Stratigraphic occurrence = X. Extinct taxon = *. Data from: Howard, 1955; Jefferson, 1968; Bassett and Jefferson, 1971; Bischoff, pers. comm., 1982.

	m TS 9 11 27 30 36
Taxon	Kyr BP 350+ 300 200 100 20
Gavia cf. *G. arctica*	......X..................
Podiceps cf. *P. nigricollis*	......X--------X ....
Aechmophorus occidentalis	......XX-X-X--X---X--XX
Pelecanus aff. *P. erythrorhynchos*	....XX ....
Phalacrocorax auritus	......X---------X--X---X...
*P. macropus**	...X---------------------X....
*Ciconia maltha**	......X------------------ X...
*Phoenicopterus minutus**	....XX ....
*P. copei**	......X..................
Cygnus cf. *C. columbianus*	......X..................
Branta canadensis	......X---X ....
Anas cf. *A. crecca*	......X..................
A. cf. *A. platyrhynchos*	......X..................
Aythya sp.	......X..................
Mergus cf. *M. merganser*	......X..................
Oxyura jamaicensis	....XX ....
Haliaeetus leucocephalus	......X------------------ X...
Aquila chrysaetos	......X..................
Fulica americana cf. *F. a. schufeldti**	....................X.....
cf. *Grus*	......................X...
cf. *Actitis*	......X..................
Phalaropodinae	......X..................
Larus cf. *L. oregonus**	......X..................
L. sp.	......X--------------------X..
Bubo virginianus	......X..................

Lacustrine, fluvial, and alluvial fan deposits of the Manix Formation (Jefferson, 1968; Jefferson et al., 1982), are well exposed in bluffs along the Mojave River, 32 km (kilometers) east of Barstow, San Bernardino County, California. Here, 39 m (meters) of exposed sediment were deposited in a large freshwater lake that occupied approximately 402 square km, including the present Coyote and Troy playa lake basins and Afton Canyon. The horizontal distribution of laterally equivalent sedimentary facies reflects fluctuations in the depositional system. Fluvial and lacustrine deposits interfinger in a transgressive/regressive sequence in response to Pleistocene climatic changes.

Buwalda (1914) recognized a lower and an upper set of lacustrine deposits within the basin. He attributed their presence to climatic change and/or tectonic activity.

Winters (1954) described eighteen distinct sedimentary units in the stratigraphic section, numbered from the top of the section downward (see columnar section in Jefferson et al., 1982). Following Buwalda (1914) and Blackwelder and Ellsworth (1936), Winters recognized two major, climatically controlled laeustrine phases. He considered the older phase (units 16 through 14) to be Illinoian in age and the younger phase (units 13 through 1) temporally correlative with the Tahoe glaciation. The stratigraphic ranges of avian taxa reported by Howard (1955) are described with reference to Winters' numbered units.

Jefferson (1968) divided the Manix Formation into four members on the basis of lithologically distinctive lacustrine, fluvial, and lateral fluvial and alluvial facies within the basin. The lowest unit, member A, is composed of unfossiliferous alluvial conglomerates (Winters' unit 18). These rocks are poorly exposed in the type stratigraphic section (Winters, 1954; Jefferson, 1968; Jefferson et al., 1982) (located in the NE ¼, SW ¼ of section 10, T 10 N, R 4 E, U.S.G.S. 15 minute Newberry, California Quadrangle, 1955). The basal 11 m of well-exposed deposits in the type section, member B, mainly consists of fluvial sands and gravels (Winters' unit 17). A U/Th date of 350+ Kyr was obtained from a fragment of a small *Equus* sp. humerus located 9 m above the base of these deposits (Bischoff, pers. comm., 1982). The middle 16 m of exposed section, the lower part of member C, is composed primarily of lacustrine silts and clays. The base of member C is estimated to be about 290 Kyr BP. The lower part of member C is approximately equivalent to Buwalda's (1914) lower lake and units 16 through 14 of Winters (1954). The upper 12 m of the Manix Formation, the upper part of member C and member D, consists of lacustrine silts and clays overlain by fluvial sands. These deposits are roughly equivalent to the upper lake beds of Buwalda (1914) and units 13 through 1 of Winters (1954). They range in age from about 200 to 19 Kyr (Bassett and Jefferson, 1971; Sarna-Wojcicki, 1980; Bischoff, pers. comm., 1982; Marcus, pers. comm., 1984).

All but two avian taxa (Table 2) are known from the basal 1 m of member C (Jefferson, 1968), which consists of very nearshore silts and sands, and one half of the recorded taxa (13 of 26) are restricted to this level. This horizon corresponds to unit 16 of Winters (Winters, 1954; Howard, 1955) and to the base of the lower lake of Buwalda (1914) and others (Blackwelder and Ellsworth, 1936).

Generally, the more abundant taxa are longer ranging and exhibit a more continuous stratigraphic record (Table 2 and Table 3). The stratigraphic distribution of all taxa is restricted to lacustrine sedimentary facies. Considering the relatively small sample size for any single taxon, it is probable that observed biostratigraphic ranges within the Lake Manix section are determined by taphonomic factors and do not represent the temporal range of any taxon.

Other avifauna of similar taxonomic composition (Table 1) are Wisconsinan in age. The Manix avifauna shares most taxa with the assemblages from Fossil Lake, Oregon and China Lake, California. Material from Fossil Lake is stratigraphically associated with a C-14 date of 29 Kyr BP (Allison, 1966). A C-14 date of 18 Kyr (Fortsch, 1978) and a U/Th date of 42 Kyr (Davis et al., 1981) are associated with the avifauna from China Lake. The oldest C-14 dates from both McKittrick (Berger and Libby, 1966) and Rancho La Brea (Marcus and Berger, 1984) are about 38 Kyr.

SYSTEMATIC DESCRIPTIONS

Most fossil specimens assigned to extant species are morphologically indistinguishable from the modern birds. The identifications are based primarily on the extensive recent osteological collections at LACM, and all measurements are from LACM specimens, unless otherwise noted.

Table 3. Faunal composition. Abbreviations: Extinct taxon = *.

Taxon	Identified specimens	Relative percentage
Gavia cf. *G. arctica*	1	0.7
Podiceps cf. *P. nigricollis*	4	2.8
Aechmophorus occidentalis	41	29.5
Pelecanus aff. *erythrorhynchos*	12	8.6
Phalacrocorax auritus	15	10.8
*P. macropus**	2	1.4
*Ciconia maltha**	6	4.3
*Phoenicopterus minutus**	14	10.1
*P. copei**	4	2.8
Cygnus cf. *C. columbianus*	3	2.1
Branta canadensis	11	7.9
Anas cf. *A. crecca*	1	0.7
A. cf. *A. platyrhynchos*	2	1.4
Aythya sp.	4	2.8
Mergus cf. *M. merganser*	2	1.4
Oxyura jamaicensis	3	2.1
Haliaeetus leucocephalus	2	1.4
Aquila chrysaetos	2	1.4
Fulica americana cf. *F. a. shufeldti**	1	0.7
cf. *Grus*	1	0.7
cf. *Actitis*	1	0.7
Phalaropodinae	1	0.7
Larus cf. *L. oregonus**	3	2.1
L. sp.	2	1.4
Bubo virginianus	1	0.7
Total	139	99.5

The use of trinominal names for extinct and extant subspecies follows Howard (1946). Subspecific names have been employed by Howard (1946) to distinguish morphologically and/or proportionally distinct fossil forms from modern species of the same size range. She considers the extinct subspecies chronoclinal ancestors to the modern forms. Although the application of subspecific names is noted in the discussions, they are not applied to fossil populations that may be larger or smaller than the modern species or fall within the range of modern subspecies.

Class Aves

Order Gaviiformes

Family Gaviidae

Genus *Gavia* Foster, 1788

Gavia cf. *G. arctica* (Linnaeus, 1758)
(Arctic Loon)

REFERRED MATERIAL. SBCM A 500-1506, left and right angular and dentary.

DISCUSSION. The fragmentary mandible, SBCM A 500-1506, compares favorably with modern specimens of *G. arctica.* It is more slender and not as deep as in *G. immer* (Common Loon). Although incomplete, the dorsal margin of the dentary is straight in lateral view as in *G. arctica,* not concave as in *G. stellata* (Red-throated Loon).

Order Podicipediformes

Family Podicipedidae

Genus *Podiceps* Brehm, 1831

Podiceps cf. *P. nigricollis* Brehm, 1831 (Eared Grebe)

REFERRED MATERIAL. UCR 10555, sternum; UCR 10509 and UCR 10576, distal ends of left humeri; UCR 10556, distal right tibiotarsus.

DISCUSSION. Both distal left humeri, UCR 10509 and 10576, are morphologically indistinguishable from modern specimens of *Podiceps.* The humeri are distinctly smaller than the extinct species *P. parvus* (Shufeldt, 1913) from Fossil Lake, Oregon.

P. nigricollis and *P. auritus* (Horned Grebe) are similar in size and osteologically inseparable. The width of the distal end of the humerus of *P. auritus* is generally larger, but overlaps that of *P. nigricollis.* A sample of seven humeri of *P. auritus* (LACM Ornithology 86335, 86336, 86337, 86339, 86340, and 86341) have a mean width of 7.5 mm (millimeters) and the mean of six *P. nigricollis* (LACM Ornithology 1691, 86329, 86330, 86331, 86332, 86333, and 86334) is 6.9 mm. UCR 10509 and 10576 are closest in size to *P. nigricollis,* measuring 7.2 mm and 6.8 mm in width, respectively.

Genus *Aechmophorus* Coues, 1862

Aechmophorus occidentalis (Lawrence, 1858) Western Grebe

REFERRED MATERIAL. LACM 2457, partial skeleton including left and right femora, tibiotarsi, tarsometartarsi, and other elements (Howard, 1955); LACM 123458, nearly complete postcranial skeleton; UCR 10542, maxilla, mandible, and 4th cervical vertebra; LACM 2466, cervical vertebra (Howard, 1955); LACM 112445, cervical vertebra; UCR 14546, cervical vertebra and first tarsal phalanx; LACM 112459, costal margin of sternum; LACM 112414, synsacrum; LACM 2465, right coracoid (Howard, 1955); UCR 10538 and 10613, right coracoids; UCR 10882, proximal right coracoid; LACM 112401, distal left humerus; UCR 10553, proximal left humerus; LACM 2469, right humerus (Howard, 1955); LACM 123443, proximal left humerus; UCR 14580, 10615, and 10616, right humeri; UCR 10893, proximal right humerus; LACM 1515, fragment humerus; UCR 10612 and 10874, left femora; UCR 10602, distal left femur; LACM 123448, proximal right femur; UCR 10610 and 10611, right femora; UCR 10552, distal right femur; UCR 13955, left tibiotarsus and first tarsal phalanx; UCR 10618, right tibiotarsus; UCR 10617, distal right tibiotarsus; UCR 10554, 10609 and 10769, proximal left tarsometatarsi; LACM 2458, proximal right tarsometatarsus (Howard, 1955); UCR 10767, proximal and distal ends of right tarsometatarsus; UCR 10507, distal right tarsometarsus; UCMP 12859, right tarsometatarsus (Compton, 1934); UCR 10614, proximal tarsometatarsus; LACM 2459, fragment tarsometatarsus (Howard, 1955); UCR 10619, first tarsal phalanx.

DISCUSSION. Miller (1911a) described the extinct subspecies *A. o. lucasi* based on the collections from Fossil Lake, Oregon. Howard (1955:201) described the size of the leg bones of LACM 2457 as falling "in the zone of overlap of the Fossil Lake and Recent specimens, although equal to or greater than the average for *A. o. lucasi.*" Likewise, the skeleton, LACM 123458, is osteologically inseparable from the ranges exhibited by modern specimens of *A. occidentalis* and ancestral *A. o. lucasi.* The femora in LACM 123458 and LACM 2457 are relatively short compared to the type femur (UCMP 12605) for *A. o. lucasi.* The measurements and proportions of the remaining elements, however, are most similar to this extinct subspecies. The complete postcranial skeleton, LACM 123458, is significant in allowing the description of the proportions of limb elements relative to isolated elements. *A. o. lucasi* is only represented by isolated elements from Fossil Lake.

In the forelimb of LACM 123458, the lengths of the coracoid, humerus and ulna (Table 4) are very close to the means of *A. o. lucasi* from Fossil Lake and modern specimens (Howard, 1946). The coracoid falls between the two means, and the humerus and ulna fall on the mean of *A. o. lucasi.*

The femur of the Lake Manix specimen, LACM 123458, measures 42.0 mm in length, which is the same as the smallest of 63 specimens of *A. o. lucasi* and well below the mean of 44.3 mm for eight modern specimens (Howard, 1946). The type of *A. o. lucasi* (Miller, 1911a), a femur (UCMP 12605), measures 48 mm in length. Measurements of femoral length in the Fossil Lake sample are greater than the largest modern specimens and overlap with all but the smallest modern specimens.

The length of the tibiotarsi in LACM 123458, 124 mm measured to the proximal articular surface, falls very near the mean of *A. o. lucasi* reported from Fossil Lake, which is 124.9 mm (Howard, 1946). The total length of this element ranges from 135 to 147 mm in seven modern specimens (Gilbert et al., 1981) compared to 146 mm for LACM 123458. The widths of the proximal and distal ends of the tibiotarsi measure 11.3 mm and 13.3 mm, respectively, compared to a range of 10 to 14 mm for the proximal end of seven modern specimens (Gilbert et al., 1981).

Tarsometatarsal measurements and ratios (Table 4) of LACM 123458 are essentially identical to those for *A. o. lucasi* listed by Howard (1946, 1955). As with the femora from Fossil Lake, tarsometatarsi of *A. o. lucasi* are generally longer than the modern species and heavier-shafted with a narrow proximal end (Howard, 1947).

Where comparable measurements are possible, the size and proportions of isolated skeletal elements from Lake Ma-

Table 4. Measurements for *Aechmophorus occidentalis,* LACM 123458. Means of comparable measurements for Recent specimens are from Howard (1946). Abbreviations: M = mean of Recent specimens; prox. = proximal; dist. = distal; max. = maximum; dia. = diameter; int. = internal; est. = estimated plus or minus 1 mm; intcot. = intercotylar tubercle.

	LACM 123458	M
Coracoid		
Length	44.8	44.3
Humerus		
Length	118.0	116.1
Prox. width	19.4	
Dist. width	11.6	
Mid-shaft max. dia.	6.4	
Radius		
Length	103.4	
Prox. max. dia.	4.8	
Dist. max. dia.	5.4	
Mid-shaft max. dia.	3.3	
Ulna		
Length	107.1	106.1
Prox. width	8.8	
Dist. width	6.0	
Mid-shaft dia.	5.3	
Femur		
Int. length	42.0	44.3
Max. length	46.1	
Width dist. condyles	15.1	
Tibiotarsus		
Length	146 est.	
Length to articular surface	124 est.	119.0
Width prox. articular surface	11.3	
Width dist. condyles	13.3	
Tarsometatarsus		
Length	77.6	74.5
Shaft width	4.2	
Shaft max. depth	7.5	
Prox. width	13.7	
Width intcot.	5.2	
Shaft width/length	5.4%	
Shaft max. depth/length	9.7%	
Prox. width/length	17.6%	
Width intcot./breadth	123.8%	

nix are more similar to LACM 123458 than to *A. occidentalis* and *A. o. lucasi.* Coracoids, UCR 10538 and 10613, are greater than 43 (estimated) and 46.0 mm in length, and fall between the means of the two taxa. Femora UCR 10610, 10611, and 10612, which measure approximately 44 (estimated), 42.6 and 46.6 mm in length, are relatively small. The breadth of the intercotylar tubercle relative to the width of the shaft in tarsometatarsi UCR 10609 and 10767, is 128 and 142 mm (mean 135). This falls below the range for the Recent form (146–170 mm, mean 154) and close to the mean (140) of *A. o. lucasi* (Howard, 1946, 1955).

A. o. lucasi is defined on the basis of a femur larger than the largest Lake Manix specimen. Only one isolated femur from Fossil Lake is as small as those from Lake Manix. LACM 2457 and LACM 123458 have small femora, and although close to *A. o. lucasi* in all other skeletal dimensions, cannot be assigned to the late Pleistocene extinct subspecies from Fossil Lake, Oregon. The assemblage from Fossil Lake is significantly younger than the Lake Manix assemblage which may account for these minor proportional differences.

Order Pelecaniformes

Family Pelecanidae

Genus *Pelecanus* Linnaeus, 1758

Pelecanus aff. *P. erythrorhynchos* Gmelin, 1789 (American White Pelican)

REFERRED MATERIAL. UCR 14724, anterior sternum; UCR 10633, proximal left scapula; LACM 2460, left coracoid (Howard, 1955); UCR 20991, proximal right coracoid; LACM 123445, right humerus; UCR 15669, proximal humerus fragment; LACM 2462, proximal right radius (Howard, 1955); LACM 123447, proximal left carpometacarpus; LACM 2461, distal right femur (Howard, 1955); UCMP 21855, left femur (Compton, 1934); UCMP 12857, first tarsal phalanx left second digit (Compton, 1934); UCMP 12858, first tarsal phalanx, left third digit (Compton, 1934).

DISCUSSION. As noted by Howard (1955) and confirmed by additional specimens, the Lake Manix pelican is morphologically the same, but larger than the extant American White Pelican. No fossils are smaller than the largest modern specimens examined. The complete right humerus, LACM 123445, measures 336 mm in length compared to five modern specimens which range from 284 to 321 mm (Gilbert et al., 1981).

The Lake Manix material apparently represents a robust population of *P. erythrorhynchos.* Although criteria such as size alone have been used previously by others to define fossil avian subspecies or chronoclinal races, I do not concur with the practice. Proportional differences in limb measurements between the modern and fossil specimens cannot be demonstrated on the basis of the small Lake Manix sample.

Family Phalacrocoracidae

Genus *Phalacrocorax* Brisson, 1760

Phalacrocorax auritus (Lesson, 1831) Double-crested Comorant

REFERRED MATERIAL. LACM 123457, nearly complete postcranial skeleton; UCR 10577, premaxilla fragment;

Table 5. Measurements for *Phalacrocorax auritus*, LACM 123457. Abbreviations: M = mean of four large Recent specimens (LACM Ornithology 100734, 100831, 100832, and 101213); prox. = proximal; dist. = distal; dia. = diameter; max. = maximum; est. = estimated plus or minus 1 mm; proc. = process; int. = internal.

	LACM 123457	M
Scapula		
Length	89.2	85.0
Prox. width	18.9	18.0
Humerus		
Length	161.2	154.8
Prox. width	25.0	22.9
Dist. width	17.7	16.6
Mid-shaft dia.	8.8	8.2
Radius		
Length	168.1	160.0
Prox. max. dia.	8.9	8.6
Dist. max. dia.	9.3	9.5
Mid-shaft dia.	4.5	4.6
Ulna		
Length	168 est.	164.5
Prox. width	13.4	12.9
Dist. width	10.0	10.1
Mid-shaft dia.	6.6	6.3
Carpometacarpus		
External length	77.4	74.9
Prox. depth	15.0	13.9
Height proc. metacarpal 1	11.7	11.1
Femur		
Int. length	61.7	57.9
Max. length	64.0	60.4
Dist. width	18.9	16.9
Tibiotarsus		
Length to prox. articular surface	113.7	107.8
Width dist. condyles	14.1	13.1

UCR 10635, left quadrate; UCR 15667, right scapula; UCR 10637, left coracoid; SBCM A 1768-1, distal right coracoid and proximal right femur fragment; UCR 10627, left humerus; UCR 14684, distal right humerus; LACM 2468, distal left ulna; UCR 10557, proximal right carpometacarpus; UCR 10623, distal right carpometacarpus; UCR 14666, proximal and distal ends of tibiotarsus; SBCM A 500-1500, proximal left tarsometatarsus; UCR 10630, distal right tarsometatarsus; UCR 14547, first tarsal phalanx.

DISCUSSION. Lake Manix material compares very favorably with the largest modern specimens of *P. a. albociliatus* (Table 5) from the Pacific coast. Measurements of the principal limb elements of LACM 123457 (Table 5) are distinctly smaller than those given for extinct *P. macropus* (Cope, 1878) (Howard, 1946), and are slightly larger than the largest modern specimens examined or listed by Gilbert et al. (1981). Large size is also evident in all isolated limb elements.

Howard (1932) placed subgeneric value on the ratio of the distance from the anterior intermuscular line to the internal edge of the coracoid compared to the length of the coracoid measured to the internal sternal lip. The subgenus *Phalacrocorax* (*P. auritus, P. carbo,* and *P. olivaceus*) has a ratio of 15 percent, compared to 19–21 percent in the subgenus *Compsohalieus* (*P. pencillatus*) and 21–22 percent in the subgenus *Urile* (*P. pelagicus* and *P. perspicillatus*) (Howard, 1946). *P. macropus* yields a ratio of 17–19 percent. This ratio for LACM 123457 (11.7 mm, 71.9 mm) is 16.3 percent. The isolated left coracoid, UCR 10637, measures 65.2 and 11.0 mm and yields a ratio of 16.9 percent.

Measurements of isolated elements are also larger than the largest *P. auritus* examined, although smaller than *P. macropus.* Width of the distal end of humerus UCR 10627 is 17.5 mm and mid-shaft diameter is 9.8 mm. Distal humerus, UCR 14684 measures 15.6 mm in width. In UCR 14666, the width of the distal end of the tibiotarsus measured across the proximal edge of the supratendinal bridge is 13.1 mm. The proximal end of the specimen is 14.2 mm in width. The left proximal tarsometatarsus, SBCM A 500-1500, measures 14.0 mm in width, 19.1 mm in depth, and has a mid-shaft width of 7.3 mm and depth of 7.1 mm. The ridge supporting the external cotyle in this specimen is thickened and more prominent than in modern specimens.

The Lake Manix material apparently represents a robust population of *P. auritus* larger than the living west coast form (Table 5). No intermediate-sized individuals are present in the sample. Relative limb proportions of LACM 123457 and in modern specimens are essentially identical.

Phalacrocorax macropus Cope, 1878

REFERRED MATERIAL. SBCM A 500-1382, premaxilla; LACM 123442, proximal right humerus.

DISCUSSION. The nearly complete premaxilla, SBCM A 500-1382 (Fig. 1), is damaged along the proximal edge and is missing about 2–3 mm of bone tissue. Its dorsal margin in lateral view is more concave than in *P. auritus.* The specimen is more robust than the premaxilla of either *P. auritus* or *P. pencillatus* relative to its comparatively short length of 62 mm. It measures 16.8 mm in width at the distal margin of the nasal aperture and 13.3 mm in dorsal–ventral height, exceeding the size of both large modern species. These features closely conform to Shufeldt's (1892) description of the upper mandible of *P. macropus* from Fossil Lake, Oregon.

Although the proximal ends of the humeri are not known for *P. macropus,* the size and thickness of the mid-shaft of LACM 123442 support its placement here. The humerus measures 26.1 mm across the proximal end and has a mid-shaft diameter of 10.4 mm. A large modern specimen of *P. auritus* (LACM Ornithology 100734) measures 24.2 mm in proximal width, 16.2 mm across the distal end, and has a mid-shaft diameter of only 8.4 mm. Gilbert et al. (1981) give the range for the proximal width of six modern specimens as 23 to 24 mm. The width of the distal humerus of *P. macropus* ranges from 18.6 to 19.8 mm (Howard, 1946).

Order Ciconiiformes

Family Ciconiidae

Genus *Ciconia* Linnaeus, 1758

Ciconia maltha Miller, 1910

REFERRED MATERIAL. LACM 2463, right humerus (Howard, 1955); UCR 13637, proximal right femur; UCR 14732, proximal right tibiotarsus; UCR 10629, proximal and distal right tarsometatarsus; UCR 10628 and 10759, first tarsal phalanges.

DISCUSSION. All fossil *Ciconia* material from California has been referred to *C. maltha* (Howard, 1942). The Lake Manix specimens are indistinguishable from equivalent elements in the Rancho La Brea sample.

Order Phoenicopteriformes

Family Phoenicopteridae

Genus *Phoenicopterus* Linnaeus, 1758

Phoenicopterus minutus Howard, 1955

REFERRED MATERIAL. LACM 2446, left scapula (Howard, 1955); SBCM A 500-1507, proximal left scapula; UCR 14669, right scapula; LACM 2474, right coracoid fragment and scapula (Howard, 1955); UCR 10578, proximal right coracoid; UCR 10631, left coracoid; UCR 10636, proximal first carpal phalanx; SBCM A 500-1504, proximal left femur; UCR 14544, proximal right femur; LACM 2445 (type specimen), right tibiotarsus and proximal tarsometatarsus (Howard, 1955); LACM 112438, distal left tibiotarsus; LACM 2473, proximal left tarsometatarsus (Howard, 1955); UCR 10875, proximal right tarsometarsus.

DISCUSSION. Howard (1955) described *P. minutus* as a very small flamingo, smaller than extinct *P. stocki* (Miller, 1944) from the Pliocene of Mexico. It differs from *P. stocki*, the larger extinct *P. copei* (Shufeldt, 1892) and the modern *P. chiliensis* (Chilean Flamingo), and *P. ruber* (Greater Flamingo) in minor, but distinctive, morphologic characters. Howard (1955) provisionally referred a left scapula, LACM 2446, and a right coracoid fragment and scapula, LACM 2474, to this taxon. Comparable additional specimens of these elements, SBCM A 500-1507, UCR 14669, 10578, and 10631, now support the assignment of this material to *P. minutus*.

Femora were not previously known for *P. minutus*. SBCM A 500-1504 and UCR 14544 are closely comparable to, but distinctly smaller than, modern species of *Phoenicopterus* as well as the extinct *P. copei* (Shufeldt, 1892). A narrow shallow groove common to all the species of *Phoenicopterus* is present on the lateral margin of the crest in both specimens. The width of SBCM A 1500-1504 is 16.8 mm. The trochanteric ridge visible in this specimen swings medially towards the head of the femur, as in *P. ruber*. UCR 14544, although incomplete and abraded along the dorsal edge of the trochanter, measures 16.1 mm in width.

Figure 1. *Phalacrocorax macropus* premaxilla, SBCM A 500-1382. A, right lateral view. B, dorsal view. Scale bar is 30 mm.

A proximal carpal first phalanx, UCR 10636, although morphologically comparable, is smaller than specimens of *P. ruber* and tentatively referred to *P. minutus*.

Phoenicopterus copei Shufeldt, 1892

REFERRED MATERIAL. LACM 112410, cervical vertebra; LACM 2448, left tarsometatarsus (Howard, 1955); UCR 10879, right tarsometarsus and three associated phalanges; LACM 123440 and UCR 14693, medial first tarsal phalanges.

DISCUSSION. Howard (1955) placed the immature left tarsometatarsus, LACM 2448, in the extinct species *P. copei* based on comparison with measurements of the distal condyles of tibiotarsi from Fossil Lake, Oregon. Tarsometatarsi are not present in the Fossil Lake sample. The widths of the fossil tarsometatarsi are greater than that of modern species of *Phoenicopterus* (Howard, 1946).

Measurements of the right tarsometatarsus, UCR 10879, are very close to LACM 2448, which measures 328 mm in length, 19 mm in width across the proximal articular surface, 12 mm in intercotylar width, and 6.8 mm in height of intercotylar tubercle. UCR 10879 measures 333.6 mm in length, 18.6 mm in width across the proximal articular surface, 12.1 mm in width across the intercotylar tubercle, and the height of the intercotylar tubercle is 6.8 mm (Jefferson, 1968).

The two medial tarsal first phalanges, LACM 123440 and UCR 14693, are large but otherwise comparable to *P. ruber.*

Order Anseriformes

Family Anitidae

Genus *Cygnus* Linnaeus, 1758

Cygnus cf. *C. columbianus* (Ord, 1815) (Whistling Swan)

REFERRED MATERIAL. UCR 10634, scapula; UCR 14725, distal left tibiotarsus; UCR 13953, lateral first tarsal phalanx.

DISCUSSION. The scapula, UCR 10634, is not separable from modern specimens of *C. columbianus.* UCR 14725, a distal left tibiotarsus, measures 18.9 mm in width, which is slightly smaller but otherwise closely comparable to a sample of four modern specimens (LACM Ornithology 86547, 86548, 86552, and 86553 that range from 20.5 to 24.7 mm in width). It is clearly separable from similar-sized specimens of *Branta* where the tendinal groove is distinct and extends to the midshaft. The distal margin of the supra-tendinal bridge is concave in *Cygnus* and straight in *Branta.* The lateral tarsal phalanx, UCR 13953, is morphologically comparable to *C. columbianus* although more slender.

C. buccinator (Trumpeter Swan) and the extinct species *C. paloregonus* (Cope, 1878) are present in the Fossil Lake, Oregon, fauna. Both taxa exceed the dimensions of *C. columbianus,* which is not found at Fossil Lake.

Genus *Branta* Scapoli, 1769

Branta canadensis Linnaeus, 1758 Canada Goose

REFERRED MATERIAL. UCR 10621, maxilla; LACM 123450 and UCR 10622, left scapula; LACM 123449, left coracoid; LACM 112409 and UCR 10625, fragment right coracoid; UCR 10624, right coracoid; UCR 10894, proximal and distal left humerus; UCR 10626, partial right humerus; UCR 10620, distal left ulna; LACM 2464, proximal and distal right femur (Howard, 1955).

DISCUSSION. The Lake Manix specimens are separable into large and small forms that do not overlap in size. The larger specimens (UCR 10621, maxilla; LACM 123450 and UCR 10622, left scapula; LACM 123449, left coracoid; LACM 112409 and UCR 10625, fragment right coracoid; UCR 10624, right coracoid; UCR 10894, proximal and distal left humerus; LACM 2464, proximal and distal right femur) are closely comparable in morphology and size to modern specimens of the largest subspecies of *B. canadensis, B. c. canadensis.*

The relatively small distal left ulna, UCR 10620, is identical in size and morphology to specimens of the Recent *B. c. minima,* smallest subspecies of *B. canadensis.*

Although clearly assignable to Anserini, both ends of the humerus, UCR 10626, are badly damaged. This specimen is tentatively considered a small *B. canadensis* based on an approximate length of 160 mm.

The largest and smallest (nominal) subspecies of *B. canadensis* are also represented at Fossil Lake, Oregon (Howard, 1955). In this respect, the limited Lake Manix sample appears to parallel the Fossil Lake avifauna. However, the material does not warrant subspecific assignment.

Genus *Anas* Linnaeus, 1758

Anas cf. *A. crecca* Linnaeus, 1758 (Green-winged Teal)

REFERRED MATERIAL. LACM 112415, right humerus.

DISCUSSION. Approximately 1 to 2 mm of bone tissue have been abraded from the head and entepicondyle of the right humerus, and the external tuberosity and pectoral attachment are missing. Although the specimen is incomplete, a total length of 56 mm is comparable with the size of *A. crecca.*

Anas cf. *A. platyrhynchos* Linnaeus, 1758 (Mallard)

REFERRED MATERIAL. UCR 10551, partial right humerus; UCR 13956, proximal right humerus.

DISCUSSION. The end of right humerus UCR 10551 proximal to the bicipital crest is missing. The preserved portion is 82 mm in length. A total estimated length of 103–104 mm is slightly larger than the largest modern *A. platyrhynchos* examined.

The proximal humerus, UCR 13956, is inseparable from equivalent elements in the Rancho La Brea sample of *A. platyrhynchos.* It is distinguished from similar-sized small members of the Anserini by a more laterally directed median crest and deeper ligamental furrow.

Genus *Aythya* Boie, 1822

Aythya sp. Greater Scaup or Canvasback

REFERRED MATERIAL. UCR 14545, left coracoid; LACM 2472, right scapula (Howard, 1955); LACM 2475, distal left humerus (Howard, 1955); SBCM AE 873-2, left femur.

DISCUSSION. *A. marila* (Greater Scaup) and *A. valisineria* (Canvasback) are not easily separated osteologically. The lack of diagnostic specimens precludes a specific assignment. Howard (1955) tentatively referred LACM 2472 and 2475 to *A. valisineria.*

Genus *Mergus* Linnaeus, 1758

Mergus cf. *M. merganser* Linneaus, 1758 (Common Merganser)

REFERRED MATERIAL. UCR 10895 and 14581, left coracoids.

DISCUSSION. Of the numerous modern coracoids examined, those of *M. merganser* are generally larger than, but show considerable size overlap with the coracoids of *M. serrator* (Red-breasted Merganser). The fossil coracoids fall within the size range of *M. merganser* and *M. serrator*. However, an excavated area posterior to the brachial tuberosity and antero-ventral to the scapular facet is consistently deeper in *M. merganser* compared to *M. serrator*. Both UCR 10895 and 14581 clearly exhibit this character.

Genus *Oxyura* Bonaparte, 1828

Oxyura jamaicensis (Gmelin, 1789)
Ruddy Duck

REFERRED MATERIAL. LACM 2476, anterior sternum (Howard, 1955); LACM 112433, distal left humerus.

DISCUSSION. Lake Manix specimens are indistinguishable from modern specimens of Ruddy Duck. Although the width (8.8 mm) of the distal left humerus, LACM 112433, is close to that of *Anas crecca*, it is distinguished by having a larger anterior articular ligamental attachment and straighter shaft.

Order Accipitriformes

Family Accipitridae

Genus *Haliaeetus* Savigny, 1809

Haliaeetus leucocephalus Linnaeus, 1758
Bald Eagle

REFERRED MATERIAL. UCR 10638, distal right coracoid; UCR 14739, distal humerus.

DISCUSSION. These specimens compare closely with the Rancho La Brea sample of *H. leucocephalus*. The lateral flange on the posterior margin of the coracoid, UCR 10638, is wide and moderately hooked proximally. This condition is present on a minority of the Rancho La Brea specimens and absent from all available Recent material (Jefferson, 1968). The more laterally positioned scar for *M. coracobrachialis* in UCR 10638 clearly separates it from similar-sized coracoids of the extinct hawk, *Amplibuteo woodwardi* (Miller, 1911b).

Genus *Aquila* Brisson, 1760

Aquila chrysaetos (Linnaeus, 1758)
Golden Eagle

REFERRED MATERIAL. LACM 2470, distal right tibiotarsus (Howard, 1955); UCR 10632, fused first and second tarsal phalanges of left second digit.

DISCUSSION. The Lake Manix specimens are inseparable from the Rancho La Brea sample of *Aquila chrysaetos*. AMNH (American Museum of Natural History) 3467B, a second tarsal phalanx of digit two from Fossil Lake, Oregon, was first assigned to *A. chrysaetos* by Shufeldt (1892). This specimen, which was later referred to *Spizaetus pliogryps* by Howard (1946), is more slender than UCR 10632 and specimens of *A. chrysaetos* from Rancho La Brea. UCR 10632 measures 37.8 mm in length, 14.1 mm in proximal width, and 12.0 mm in proximal dorso-ventral height.

Order Gruiformes

Family Rallidae

Genus *Fulica* Gmelin, 1789

Fulica americana Gmelin, 1789
American Coot
Fulica americana cf. *shufeldti* Brodkorb, 1964

REFERRED MATERIAL. LACM 123446, left ulna.

DISCUSSION. Howard (1946, 1947) considered the relatively small, extinct coot, *F. minor* (Shufeldt, 1892) from Fossil Lake, Oregon, to be an ancestral subspecies (chronocline) of the modern form, *F. americana*, for which she erected subspecies *F. a. minor*. Subsequently Wetmore (1956) elevated "*minor*" to specific level following Shufeldt's original designation. Brodkorb (1964), recognizing that the name *minor* was previously occupied in the genus, renamed the taxon after Shufeldt, calling the form *F. shufeldti*.

The measurements given by Howard (1946) clearly show an overlap in the size of the specimens from Fossil Lake, Oregon, and modern specimens. There is no question that a single species is represented. Following Howard, the extinct form is considered a subspecies of *F. americana*, and is referable to *F. a. shufeldti*.

The ancestral subspecies differs from the modern American Coot in having shorter wings and relatively long legs (Howard, 1946, 1947). Mean length of three Fossil Lake ulnae is 56.9 mm, compared to 61.1 mm for 39 modern specimens (Howard, 1946). The Lake Manix ulna, LACM 123446, measures 56.8 mm.

Genus *Grus* Pallas, 1766

cf. *Grus* sp.
Crane

REFERRED MATERIAL. LACM 2467, fragmentary distal right humerus (Howard, 1955).

DISCUSSION. Howard (1955) questionably assigned this specimen to *Grus*. No additional crane specimens have been recovered.

Order Charadriiformes

Family Scolopacidae

Subfamily Scolopacinae

Genus *Actitis* Illiger, 1811

cf. *Actitis* sp.
(Sandpiper)

REFERRED MATERIAL. LACM 123451, proximal left humerus.

DISCUSSION. Various tribes within the subfamily Scolopacinae cannot be readily separated. LACM 123451 best compares with *Actitis hypoleucos* (Common Sandpiper) in size and approaches the smallest species of *Tringa* (sandpipers and yellowlegs). It differs from humeri of *Phalaropus lobatus* (Red-necked Phalarope, subfamily Phalaropodinae), which are almost identical in size, in having a deeper and more enclosed pneumatic fossa and a more rounded lateral margin of the bicipital crest.

Subfamily Phalaropodinae

Genus and species indet.

REFERRED MATERIAL. LACM 2471, partial left tibiotarsus (Howard, 1955).

DISCUSSION. LACM 2471, a very small, left distal tibiotarsus, was placed within the Phalaropodinae but could not be confidently assigned to the genus *Phalaropus* by Howard (1955). No additional comparable specimens have been recovered.

Family Laridae

Genus *Larus* Linnaeus, 1758

Larus cf. *L. oregonus* Shufeldt, 1892

REFERRED MATERIAL. LACM 123444, associated left humerus, radius, and carpometacarpus; LACM 123802, left first carpal phalanx, digit two.

DISCUSSION. The Lake Manix specimen, LACM 123444 (Fig. 2), represents a robust, medium-sized gull morphologically similar to *L. canus* (Mew Gull) and *L. delawarensis* (Ring-billed Gull). It is larger and more robust than the largest *L. canus* examined, and smaller than *L. delawarensis.* Dimensions of the limb elements differ from the wing of *L. delawarensis* in being shorter and having thicker or stouter mid-shafts. It is most similar to extinct *L. oregonus* from Fossil Lake, Oregon.

The humerus, although slightly smaller, is comparable in robustness to the type of *L. oregonus.* The maximum width of the proximal end of LACM 123444 (the bicipital crest margin shows slight damage) is 16.8 mm, compared to 17.7 mm in the type specimen, AMNH 3494 (measurements from cast). Minimum mid-shaft breadth is 5.8 mm, eompared to 6.6 mm in the type, and the breadth of the shaft immediately distal to the base of the bicipital crest in LACM 123444 is 8.8 mm, versus 9.1 mm.

Howard (1946:186), in describing AMNH 3494, stated that "the depression below the head anconally . . . bounded by the sharp apex of the shaft on one side and the median crest on the other, tends to narrow almost to a point." This condition in LACM 123444 is similar to that in *L. canus.* The depression in *L. delawarensis* is more rounded, intermediate between *L. oregonus* and the wide depression in *L. californicus.* In this character, LACM 123444 is less pointed than AMNH 3494, not as wide or rounded as in *L. delawarensis,* and most similar to the largest specimens of *L. canus,* which exhibit the most rounded condition in this species.

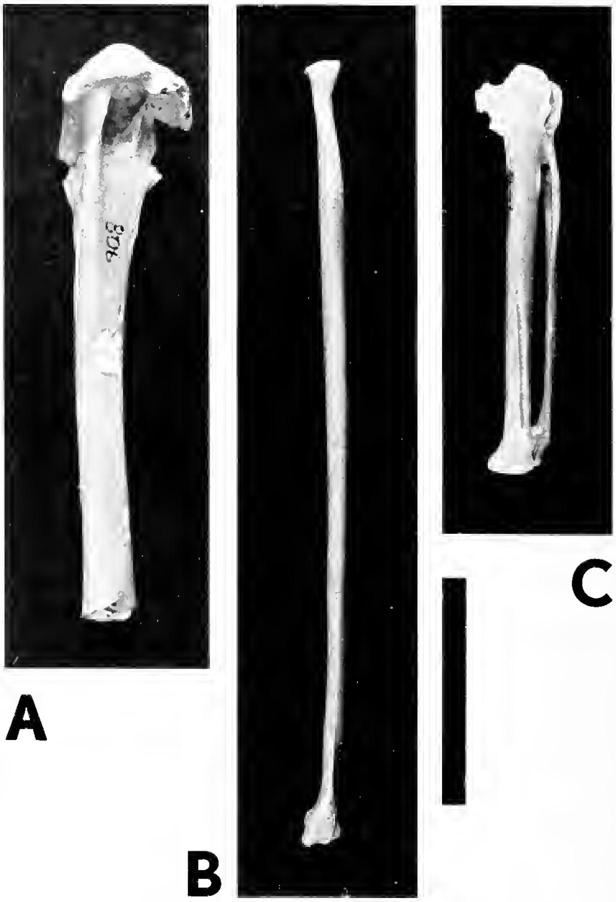

Figure 2. *Larus* cf. *L. oregonus* associated left wing elements, LACM 123444. A, anconal view of humerus. B, anconal view of radius. C, external view of carpometacarpus. Scale bar is 30 mm.

Radii and carpometacarpi of *L. oregonus* are not known from Fossil Lake. The Lake Manix radius, although almost a centimeter shorter than the radii of *L. delawarensis,* measures 102.1 mm in length and is markedly stouter. Maximum thickness of the proximal portion of the shaft is 3.6 mm, much greater than in *L. canus* (LACM Ornithology 87200, 3.2 mm; 87201, 3.2 mm) or *L. delawarensis* (LACM Ornithology 87204, 3.1 mm; 87205, 3.2 mm; 87206, 2.9 mm; 87207, 3.1 mm). The bicipital tubercle is more pronounced and distally elongated in LACM 123444, and the groove bounded by the interosseous crest is longer and deeper in palmar view.

The carpometacarpus is morphologically similar to that of *L. canus* and *L. delawarensis,* but it is shorter and exhibits a considerably thickened main shaft. It measures 53.3 mm in length. LACM 123802, a first carpal phalanx, articulates almost exactly with the carpometacarpus of LACM 123444, and measures 24.8 mm in length.

Larus sp.
Gull

REFERRED MATERIAL. LACM 123803, left proximal radius, coracoid, distal ulna, and proximal and distal carpometacarpus; SBCM A 500-1508, proximal portion of left carpometacarpus; SBCM A 500–1505, distal left carpometacarpus.

DISCUSSION. The specimens represent a large gull of the size of *L. argentatus* (Herring Gull) or *L. occidentalis* (Western Gull), but larger than *L. californicus* (California Gull). Larger specimens of *L. occidentalis* and *L. californicus* exhibit considerable overlap in size with smaller specimens of *L. argentatus*. LACM 123803 and SBCM A 500-1508 fall within this range. However, SBCM A 500-1505 is slightly larger than the largest *L. argentatus* examined. The fossil specimens cannot be distinguished from larger species of the genus *Larus*.

Remains of gulls are extremely rare in Quaternary marine deposits of western North America (Miller, 1924; Brodkorb, 1967). Although abundant and varied at Fossil Lake, Oregon (Howard, 1946), fossil specimens representing the Laridae previously were not known from Pleistocene asphalt or other terrestrial deposits in California (Miller and DeMay, 1942; Howard, pers. comm., 1983). The record from late Pleistocene marine deposits includes a single specimen of *Larus glaucescens* from the upper San Pedro Sand, California (Miller, 1930) and a second specimen from New Port Bay Mesa, California (Howard, 1949). The distribution of *Larus* at Rancho La Brea (Howard, 1936) and in Alaska (Brodkorb, 1967) is restricted to the Holocene. The only known Tertiary specimen is from the Pliocene San Diego Formation of southern California (R. Ceruti, pers. comm., 1983). Although samples are small, taphonomic or preservational biases do not seem to fully account for the very poor representation of gulls at Rancho La Brea or in late Pleistocene coastal marine deposits that yield numerous remains of other, similar-sized avian taxa (Howard, 1949). The inland late Pleistocene record of gulls appears to contrast with their appearance in Holocene coastal communities. These records suggest that a shift in the distribution or population density of gulls may have occurred in response to the disappearance of most inland lacustrine habitats at the end of the Pleistocene.

Order Strigiformes

Family Strigidae

Genus *Bubo* Dumeril, 1806

Bubo virginianus (Gmelin, 1788)
Great Horned Owl

REFERRED MATERIAL. UCR 10514, distal left tibiotarsus.

DISCUSSION. The width of the distal condyles on tibiotarsus UCR 10514 is 13.1 mm, identical to the mean of fifty Rancho La Brea specimens which range from 12.2 to 13.4 mm. A sample of twelve Recent specimens range between 11.9 and 13.4 mm (Howard, pers. comm., 1967). The large extinct owl, *Bubo sinclairi* (Miller, 1911c), overlaps the size of the largest Rancho La Brea specimens, exceeding UCR 10514.

BIOGEOGRAPHY AND PALEOENVIRONMENT

All of the extant species represented in the Lake Manix avifauna are at least seasonally present in southern California. Most taxa are found along the California coast during the winter or are winter visitors on inland lakes, such as the Salton Sea, or along the Colorado River. *Pelecanus* is a summer visitor most common at the Salton Sea. Only *Oxyura* and *Fulica* are wide ranging throughout the year. *Cygnus* is rare in southern California and found in winter on inland lakes or reservoirs to the north (Cogswell and Christman, 1977; Garrett and Dunn, 1981).

All extant, migratory species leave southern California in the spring. They travel northward along the coast or follow inland portions of the north–south Pacific Coast flyway. During Pleistocene pluvial periods, this inland route would have been over the lakes of the Mojave Desert, the lakes east of the Sierra Nevada Mountains including China Lake, the western part of Lake Lahontan, and the lakes of southeastern Oregon, including Fossil Lake (Snyder et al., 1964).

Two-thirds of the extant taxa (9 of 17), represented by 80 percent of the fossil specimens (Table 3), presently prefer, or feed exclusively on, small fish (Cogswell and Christman, 1977): *Gavia arctica, Podiceps nigricollis, Aechmophorus occidentalis, Pelecanus erythrorhynchos, Phalacrocorax auritus, Mergus merganser, Aquila chrysaetos, Haliaeetus leucocephalus,* and *Larus* spp. Abundant fossil remains of the small Tui (Mojave) Chub, *Gila bicolor mojavensis,* are present in the lacustrine deposits (Jefferson, 1968). No other fishes have been reported.

Most of the remaining taxa feed on a variety of water plants and freshwater invertebrates (Cogswell and Christman, 1977): *Cygnus columbianus, Anas crecca, A. platyrhynchos, Oxyura jamaicensis, Fulica americana, Actitis* sp., and *Branta canadensis. Aquila* is mainly a scavenger, and *Bubo virginianus* primarily feeds on small mammals.

The Lake Manix assemblage samples a complex of freshwater lake and lake margin habitats. Judging from food preferences, procurement methods, and nesting habits (Cogswell and Christman, 1977) of the extant forms represented, open water, sandy beach flats, and extensive reedy marshlands must have been persistent lacustrine features. An extensive lacustrine environment is confirmed by lithostratigraphy and reconstructions of the depositional environments (Jefferson, 1968).

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CONTRIBUTIONS IN SCIENCE

FOSSIL PONTOPORIID DOLPHINS (MAMMALIA: CETACEA) FROM THE PACIFIC COAST OF NORTH AMERICA

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FOSSIL PONTOPORIID DOLPHINS (MAMMALIA: CETACEA) FROM THE PACIFIC COAST OF NORTH AMERICA

Lawrence G. Barnes[1]

ABSTRACT. Some remarkably long-snouted fossil marine odontocete cetaceans of late Tertiary age from the eastern margin of the North Pacific Ocean comprise an extinct group classified as the subfamily Parapontoporiinae of the family Pontoporiidae. These fossil dolphins belong in the genus *Parapontoporia* Barnes, 1984, which now includes three known species: latest Miocene *Parapontoporia pacifica* Barnes, 1984, from Baja California, Mexico; latest Miocene *P. wilsoni*, new species, from central California, U.S.A.; and Late Pliocene *P. sternbergi* (Gregory and Kellogg, 1927), from southern California. Analysis of the morphology of these animals indicates that they are closely related to species that have been previously classified in two separate living families of dolphins: the marine Pontoporiidae of the southwest Atlantic Ocean, and the freshwater Lipotidae of China.

The living pontoporiid, the La Plata dolphin or fraciscana, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), lives in shallow water off the Atlantic coast of South America. It is apparently most closely related to two fossil Pliocene marine species, *Pontistes rectifrons* (Bravard, 1884) from Argentina and *Pliopontos littoralis* de Muizon, 1983, from Peru, and together these comprise the nominate subfamily Pontoporiinae of the Pontoporiidae. The name-bearer of the Lipotidae, the beiji or white flag dolphin, *Lipotes vexillifer* Miller, 1918, inhabits Tungting Lake and the Yangtze River (Chang Jiang) in China. This species was traditionally classified in the family Iniidae with the living Amazon dolphin or bouto, *Inia geoffrensis* (de Blainville, 1817), and some fossil taxa, until 1979 when it was placed in the monotypic new family Lipotidae.

The fossil species in the subfamily Parapontoporiinae are intermediate morphologically and zoogeographically, however, between *L. vexillifer* and the species in the subfamily Pontoporiinae, and separate family status for *L. vexillifer* is therefore unwarranted. Based on the new information from the fossil record I recognize, at a new rank and in a new context, a third subfamily in the family Pontoporiidae, the Lipotinae.

INTRODUCTION

Four living genera of odontocetes in the superfamily Platanistoidea contain long-snouted species that are sometimes (although not in every case correctly) referred to as "river dolphins." *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), the franciscana or La Plata dolphin, is a near-shore marine species living in the Atlantic Ocean off the coasts of Brazil, Uruguay, and Argentina. *Inia geoffrensis* (de Blainville, 1817), the bouto or Amazon dolphin, is a freshwater species living in the Amazon, Orinoco, and Madeira River systems of South America. *Lipotes vexillifer* Miller, 1918, the Beiji or white flag dolphin, is a freshwater dolphin inhabiting the Yangtze (Chang Jiang) River system (including Tungting Lake) and the Quiantang River system in China. *Platanista* spp., the susus or Ganges and Indus dolphins of India, Pakistan, Bangladesh, and Nepal are freshwater species.

Each of these four Recent genera has been designated as the type of a separate platanistoid family, although in most published works they have been classified in various subfamilies within the family Platanistidae (e.g., Flower, 1869; Simpson, 1945; Fraser and Purves, 1960). *Pontoporia* Gray, 1846, and *Platanista* Wagler, 1830, have usually been classified in their nominate subfamilies, but following Miller (1918, 1923), most zoologists have joined *Lipotes* Miller, 1918, and *Inia* d'Orbigny, 1834, in the family Iniidae or the subfamily Iniinae, depending on whether the Platanistoidea or Platanistidae was used as the next higher category (see Simpson, 1945; Brownell and Herald, 1972). Some authors have also classified *Pontoporia* within the Delphinidae (Gill, 1872; True, 1908; Miller, 1923; Kellogg, 1928), but they have been in the minority. Zhou, Qian, and Li (1979) recognized substantial differences between *Inia* and *Lipotes* and proposed a separate new family, the Lipotidae. Several fossil species, virtually all of them marine, have been reported to be relatives of various of these, and the systematics of the fossil and Recent Platanistoidea have had a convoluted and confusing history (Kellogg, 1928).

In recent years a larger number of cetologists and paleontologists have realized that the platanistoid dolphins are morphologically diverse and represent more than one family. For example, Kasuya (1973) recognized three extant families (Platanistidae, Iniidae, and Pontoporiidae) and Zhou (1982) recognized four, including the family Lipotidae. Both of these

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authors classified all of these families in the superfamily Platanistoidea, so that the hierarchical relationships among the groups remained virtually unchanged.

The purpose of this paper is to describe, diagnose, and analyze fossils of extremely long-snouted marine dolphins in the genus *Parapontoporia* Barnes, 1984, cetaceans that are morphologically similar to both *Pontoporia* and *Lipotes.* That *Parapontoporia* is morphologically intermediate between the Recent genera *Pontoporia* and *Lipotes* is important to systematics because, as mentioned above, *Pontoporia* and *Platanista* have usually been considered to be more remotely related to *Inia* and *Lipotes* than the latter were to one another.

The fossils that I describe in this study include those of *Parapontoporia pacifica* Barnes, 1984; *P. sternbergi* (Gregory and Kellogg, 1927); and *P. wilsoni,* new species, that were collected from latest Miocene and Late Pliocene sedimentary rock units bordering the eastern North Pacific Ocean in California and Baja California. The type species of *Parapontoporia, P. pacifica,* was based on a fossil from latest Miocene rocks, approximately 6 to 8 million years old, on Isla Cedros, Baja California, Mexico. I have previously demonstrated (Barnes, 1984) that *P. pacifica* is congeneric with *Stenodelphis sternbergi* Gregory and Kellogg, 1927, a species that is known from the Late Pliocene age San Diego Formation in California and one that had needed a new generic allocation for many years (see Barnes, 1973a, 1977). The geographic distribution of these fossils has important biogeographic implications because they are roughly equidistant between the areas occupied by *Lipotes vexillifer* and *Pontoporia blainvillei.* These specimens and taxa were included in a Ph.D. dissertation that I submitted to the University of California at Berkeley (Barnes, 1972), and some were subsequently mentioned in four following publications (Barnes, 1973a, 1977, 1983, 1984). In a subsequent study, Robert L. Brownell, Jr., Edward Mitchell, and I plan to review all fossil and Recent Pontoporiidae of the world and their interrelationships.

MATERIALS AND METHODS

Fossil specimens described in this study are conserved in scientific institutions in the United States as indicated by the following acronyms:

AMNH	American Museum of Natural History, New York, New York.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California.
SDSNH	San Diego Society of Natural History, Natural History Museum, San Diego, California.
UCMP	University of California Museum of Paleontology, Berkeley, California.
UCR	University of California at Riverside, Department of Geological Sciences, Riverside, California.

Precise locality descriptions are not given for some of the specimens. Such information is available to qualified investigators upon request to the appropriate institution.

Comparative specimens of the modern species, *Pontoporia blainvillei, Lipotes vexillifer, Inia geoffrensis,* and *Platanista gangetica,* were studied and used in formulating the descriptions and diagnoses, which are based on cranial characters. Each of the three fossil species of *Parapontoporia* is known by incomplete skulls that do not exhibit entirely overlapping morphology, but enough is known of each species to differentiate all three. The descriptions presented here do not duplicate those already published, but are written in a manner to avoid repetition. Measurements of the skulls were taken following the standardized methods outlined by Perrin (1975). Anatomical terminology for basicranial structures and the middle ear air sinus system follows Fraser and Purves (1960). Most other osteological terms follow Kernan (1918), Kellogg (1927), and Barnes (1978, 1984). All the rendered antomical line drawings with line shading (Figs. 1a, 2a, 3a, 4, 10a, b, 11, 13, 15) were done by J. Patricia Lufkin using orthographic projection. My restorations of *Parapontoporia wilsoni* were derived from these. Specimens were coated for photography with a sublimate of ammonium chloride. My restorations of *P. sternbergi* are based on all available specimens from the San Diego Formation and on the type specimens of the other two species.

Anatomical structures in the illustrations are labeled according to the following abbreviations:

aon—antorbital notch
Bs—basisphenoid bone
ch—cranial hiatus
fc—carotid foramen
fh—hypoglossal foramen
fio—infraorbital foramen
fmx—maxillary foramen
fo—foramen ovale
fp—falcate process of the basioccipital
fpal—palatine foramen
fpmx—premaxillary foramen
Fr—frontal bone
gf—glenoid fossa
jn—jugular notch
Ju—jugal bone
La—lacrimal bone
mc—maxillary crest
me—maxillary eminence
Met—mesethmoid bone
mf—mental foramen
mrg—mesorostral gutter
ms—fossa for middle sinus
Mx—maxillary bone
n—naris
Na—nasal bone
Oc—occipital bone
occ—occipital condyle
Pa—parietal bone
Pal—palatine bone
pop—paroccipital process
Pmx—premaxillary bone
Pt(ll)—pterygoid, lateral lamina
Pt(ml)—pterygoid, medial lamina
pts—fossa for pterygoid sinus

s—mandibular symphysis
Sq—squamosal bone
sqf—squamosal fossa
Vo—vomer bone

Some family group names have been used at various ranks. In cases where I recognize a revised rank, the original author is included in parentheses followed by the author of the emended rank that I recognize. All the variations and synonyms of the family- and genus-group names are listed in the synonymies.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Platanistoidea (Gray, 1863) Simpson, 1945

Family Pontoporiidae (Gill, 1871) Kasuya, 1973

Pontoporiinae Gill, 1871:124 (March, 1871), as a subfamily of Platanistidae; 1872:15, as a subfamily of Delphinidae.
Pontoporiadae Gray, 1871:95, incorrectly formed name, as a monotypic family for *Pontoporia* Gray, 1846.
Stenodelphinae True, 1908:391, as a subfamily of Delphinidae to include *Stenodelphis* d'Orbigny and Gervais, 1847, a junior synonym of *Pontoporia.*
Stenodelphininae. Miller, 1923:40, unjustified emendation of Stenodelphinae.
Pontoporiidae. Kasuya, 1973:28, 61, as a family of Platanistoidea.
Lipotidae Zhou, Qian, and Li, 1979:72, as a monotypic family for *Lipotes.*

DIAGNOSIS OF FAMILY. A family of Platanistoidea that differs from Platanistidae and Iniidae by having skulls with the following unique combination of characters: occipital shield roughly square in posterior view with prominent dorsolateral corners and not narrow dorsally, facial portions of maxillae relatively flat, not steeply inclined posteriorly or laterally, rostral portions of premaxilla and maxilla separated by longitudinal lateral groove, rostrum constricted transversely posterior to end of tooth row, posterior part of alveolar row located at lateral edge of palate and curving upward on side of rostrum at posterior extremity, palate nearly flat posterior to ends of alveolar rows, maxilla bearing a low, non-pneumaticized crest over orbit which is oriented in an anterolateral to posteromedial direction and located medial to margin of maxilla rather than at the margin, fossa for pterygoid sinus having a branch extending dorsally adjacent to anterior wall of each naris, nares of small diameter and curving around anterior wall of braincase rather than being nearly vertical, foramen ovale small, round, distinct from cranial hiatus, located on basisphenoid bone on ventrolateral wall of cranium and confluent with deep sulcus marking course of mandibular division of trigeminal nerve, zygomatic process of squamosal elongate, tapered, inclined anteriorly with large, transversely oriented postglenoid process, and prominent, anteroposteriorly oriented fossa curving around medial and posterior side of glenoid fossa for middle sinus of air sinus system, paroccipital process with fossa on side facing cranial hiatus that held posterior sinus of air sinus system, carotid foramen in basioccipital vestigial, periotic and bulla not firmly attached to braincase by posterior processes and accessory ossicles, teeth comparatively homodont with crowns having a lingual protuberance and roots having a swelling below the enamel line.

INCLUDED SUBFAMILIES. Parapontoporiinae Barnes, 1984; Pontoporiinae (Gill, 1871) Kasuya, 1973; and Lipotinae (Zhou, Qian, and Li, 1979), new rank and new context.

Subfamily Parapontoporiinae Barnes, 1984

Parapontoporiinae Barnes, 1984:6.

EMENDED DIAGNOSIS OF SUBFAMILY. A subfamily of Pontoporiidae differing from Pontoporiinae and resembling Lipotinae by having skull with cranial vertex asymmetrical and offset to left side, vomer exposed between maxillae on palate, spiracular plate on premaxillary surfaces flat, not elevated and convex, posterior terminations of premaxillae not widely separated from anterolateral corners of nasals, squamosal fossa between zygomatic process and braincase deep; resembling Pontoporiinae and differing from Lipotinae by having skull with extremely long, slender rostrum and mandible, very deep lateral groove between rostral parts of maxilla and premaxilla, lateral lamina of pterygoid joined with posterior plates of maxilla and palatine to form extensive bony wall within orbit (but not connecting posteriorly with basisphenoid as in *Pontoporia blainvillei*), tooth crowns small, sharply pointed, with basal lingual bulge, compressed anteroposteriorly and covered with smooth enamel, tooth roots flattened labio-lingually with encircling swelling at gum line; and differing from both Pontoporiinae and Lipotinae by having extreme polydonty, bearing 80 to 82 teeth in each side of each jaw (in contrast to 48 to 61 in *Pontoporia blainvillei* and 32 to 36 in *Lipotes vexillifer*).

INCLUDED GENERA. *Parapontoporia* Barnes, 1984 only.

Parapontoporia Barnes, 1984

Stenodelphis (part). Gregory and Kellogg, 1927.
"*Stenodelphis.*" Barnes, 1973a:37–39; 1977:333–334; Barnes, Howard, Hutchison, and Welton, 1981:56, 57, 61, 64; Deméré, 1981:24–25; de Muizon, 1983:1103.
Stenodelphininae, genus (and species) new. Barnes, 1977: 331.
Parapontoporia Barnes, 1984:6.

DIAGNOSIS OF GENUS. Because the subfamily Parapontoporiinae is at present monotypic, the diagnosis for it and the genus *Parapontoporia* are identical.

TYPE SPECIES. *Parapontoporia pacifica* Barnes, 1984; type by original designation.

INCLUDED SPECIES. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927); *Parapontoporia pacifica* Barnes, 1984; and *Parapontoporia wilsoni,* new species.

Parapontoporia pacifica Barnes, 1984

Figures 1–5, 20a, d

Stenodelphininae, genus and species new (part). Barnes, 1977: 331.

Parapontoporia pacifica Barnes, 1984:7.

EMENDED DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. wilsoni,* new species, and *P. sternbergi* by having skull with dorsal premaxillary surfaces at proximal end of rostrum flat-lying, not tilting medially to form a basin, and by having more elongate fossa for pterygoid sinus in palatine; and differing from *P. sternbergi* by lacking well-defined grooves on the lateral surfaces of dentaries, instead, nutrient foramina on lateral surface of dentary open into only a shallow, elongate depression.

HOLOTYPE. UCR 21244, skull with teeth, lacking the braincase and part of the facial region, mandible lacking right condyle and the post-alveolar section of the left dentary, a probable fifth cervical vertebra, and a first left rib; collected by David P. Whistler, 9–11 August 1965.

TYPE LOCALITY. UCR RV-6505 in weathered badlands exposures southeast of the village of Cedros on Isla Cedros, Baja California, Mexico.

FORMATION AND AGE. From the lower member of the Almejas Formation (Kilmer, 1979), latest Miocene, correlated indirectly with the "Jacalitos" provisional mega-invertebrate stage and the Hemphillian North American land mammal age, and approximately 6 to 8 million years old. The age of the lower member of the Almejas Formation has been discussed by Barnes (1973b, 1977, 1984) and Repenning and Tedford (1977). The Almejas Formation is approximately 800 feet thick and directly overlies the Middle Miocene age Tortuga Formation (Kilmer, 1977, 1979). Fossil invertebrate assemblages from the upper member of the Almejas Formation are similar to those from the Late Pliocene San Diego Formation and are therefore correlative with the "San Joaquin" provisional mega-invertebrate stage and the Blancan North American land mammal age. The vertebrate fossils in the lower member of the Almejas Formation on Isla Cedros are stratigraphically below the invertebrate fossils, in the basal approximately 130 feet of the formation.

The holotype of *Parapontoporia pacifica* was found five feet above the base of the Almejas Formation. Howard (1971) reported seven species of birds, Repenning and Tedford (1977) described walruses and a fur seal, and Barnes (1973b, 1977, 1984) reported 11 species of cetaceans from the lower member of the formation, mostly from horizons above that which produced *P. pacifica.*

The relatively diverse aggregate assemblage of published fossil vertebrate species from the lower member of the Almejas Formation warrants being listed here:

Aves
- *Puffinus tedfordi* Howard, 1971
- *Puffinus* sp.
- *Morus* sp.
- ?*Megapaloelodus opsigonus* Brodkorb, 1961
- *Cerorhinca minor* Howard, 1971
- ?*Endomychura* sp.
- *Mancalla cedrosensis* Howard, 1971

Mammalia
- *Dusignathus santacruzensis* Kellogg, 1927
- *Aivukus cedrosensis* Repenning and Tedford, 1977
- *Thalassoleon mexicanus* Repenning and Tedford, 1977
- cf. *Plesiocetus* sp.
- *Balaenoptera* sp.
- *Parapontoporia pacifica* Barnes, 1984
- *Denebola brachycephala* Barnes, 1984
- *Piscolithax tedfordi* Barnes, 1984
- *Piscolithax boreios* Barnes, 1984
- Phoeoenidae, gen. and sp. undetermined
- *Albireo whistleri* Barnes, 1984
- Delphinoidea, gen. and sp. undetermined
- *Praekogia cedrosensis* Barnes, 1973
- Physeterinae, gen. and sp. undetermined

DESCRIPTION. Skull. The skull (Figs. 1–3) of the holotype and only known specimen of *Parapontoporia pacifica* was described by Barnes (1984) and compared with several specimens of *P. sternbergi* from the younger, Late Pliocene age San Diego Formation. The relatively complete referred specimens of *P. sternbergi* described in the following text confirm that the two species are congeneric. The description of the skull of *P. pacifica* need not be repeated here, but I will summarize some of the main differences between it and the other species of *Parapontoporia.* The holotype of *P. pacifica* does not include the posterior part of the braincase, but it has the most complete rostrum of any known specimen of the genus. No available specimen of *P. sternbergi* has the tip of the rostrum preserved.

Some of the lateral lamina of the pterygoid of *P. pacifica* is preserved, and in company with a small posterior extension of the palatine and a larger projection of the maxilla, produces a thin wall of bone that extends posteriorly within the orbit (Fig. 2). This wall of bone spreads dorsally and partly obscures the foramina and sinuses on the medial wall of the orbit, but it does not appear to have reached posteriorly as far as the basisphenoid as it does in *Pontoporia blainvillei.* This is the only specimen of *Parapontoporia* in which any part of the lateral lamina of the pterygoid is preserved.

The groove on the lateral side of the rostrum that separates the premaxilla from the maxilla is not as deep as in *P. sternbergi.* The groove becomes increasingly wider and shallower distally, and at the anterior end of the rostrum the maxilla is fused to the premaxilla with no visible suture. Both *P. sternbergi* and *P. wilsoni,* new species, have a medial basin formed on the dorsal surface of the proximal part of the rostrum just anterior to the level of the antorbital notches. In *P. pacifica,* there is no such basin because the premaxillae are nearly flat-lying in that area, but both their medial and

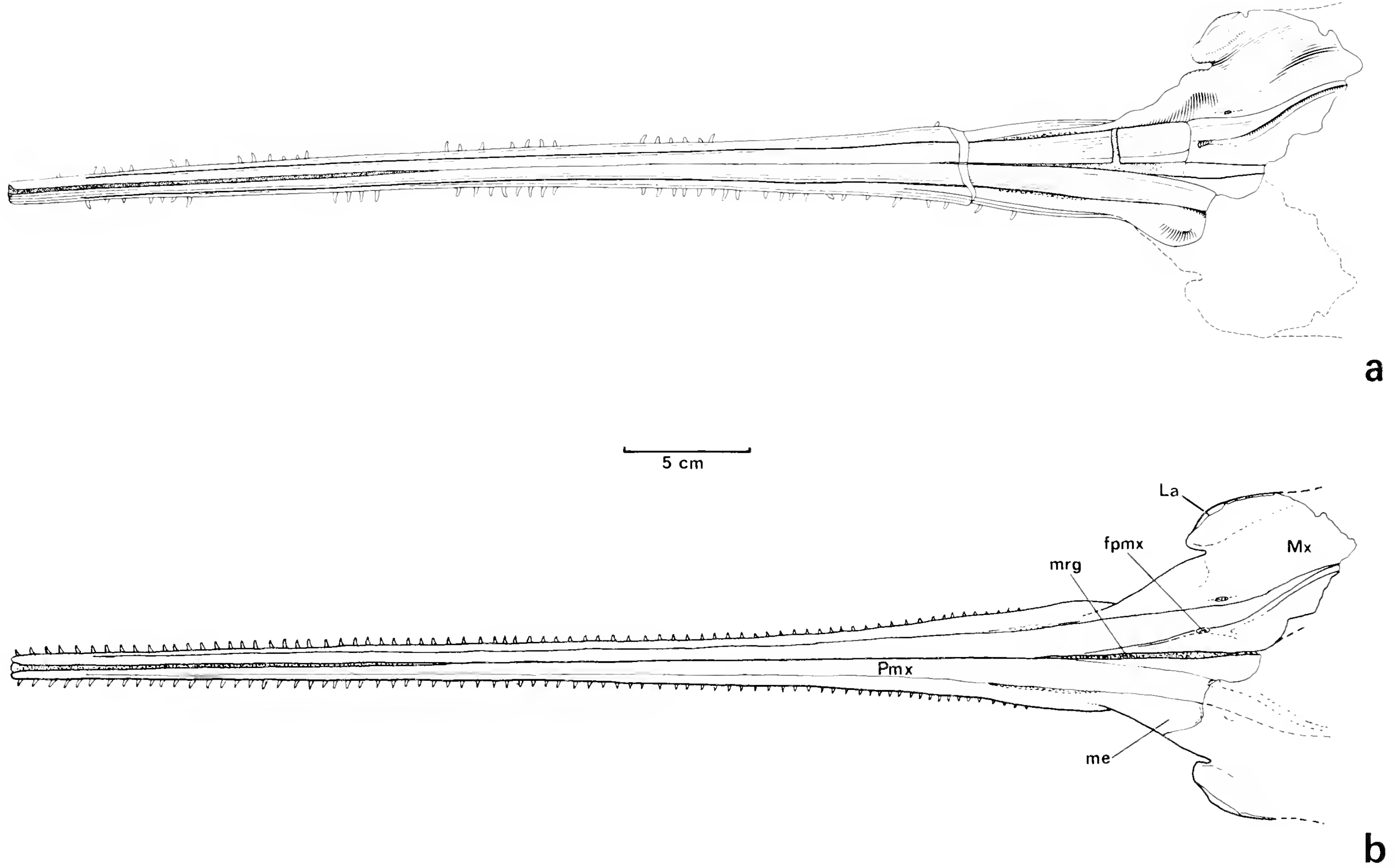

Figure 1. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, dorsal view: **a,** drawing of original specimen; **b,** restoration with structures labeled. Abbreviations used in this and the following illustrations are explained in the section titled Materials and Methods.

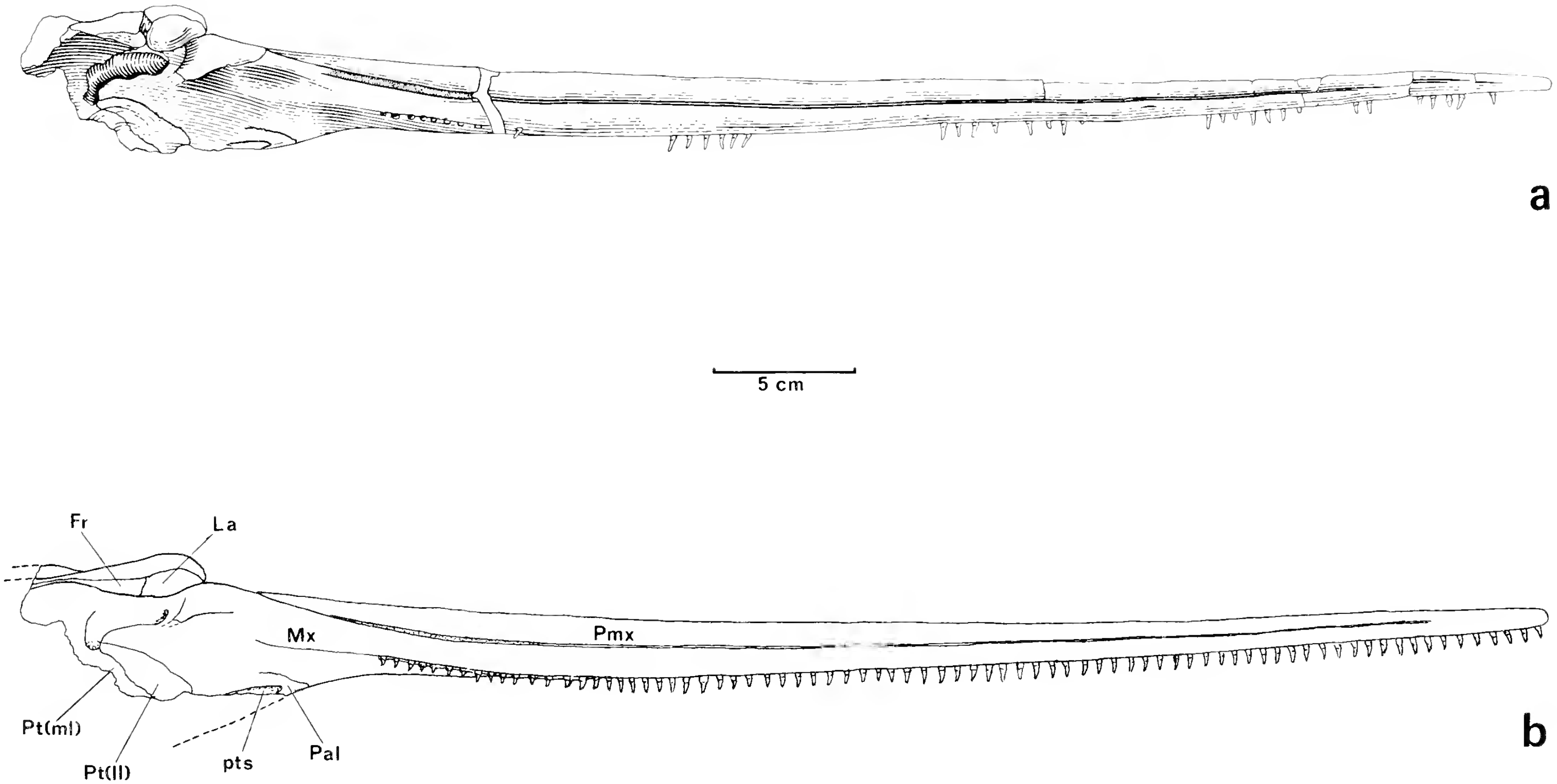

Figure 2. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, right lateral view: **a,** drawing of original specimen; **b,** restoration with structures labeled.

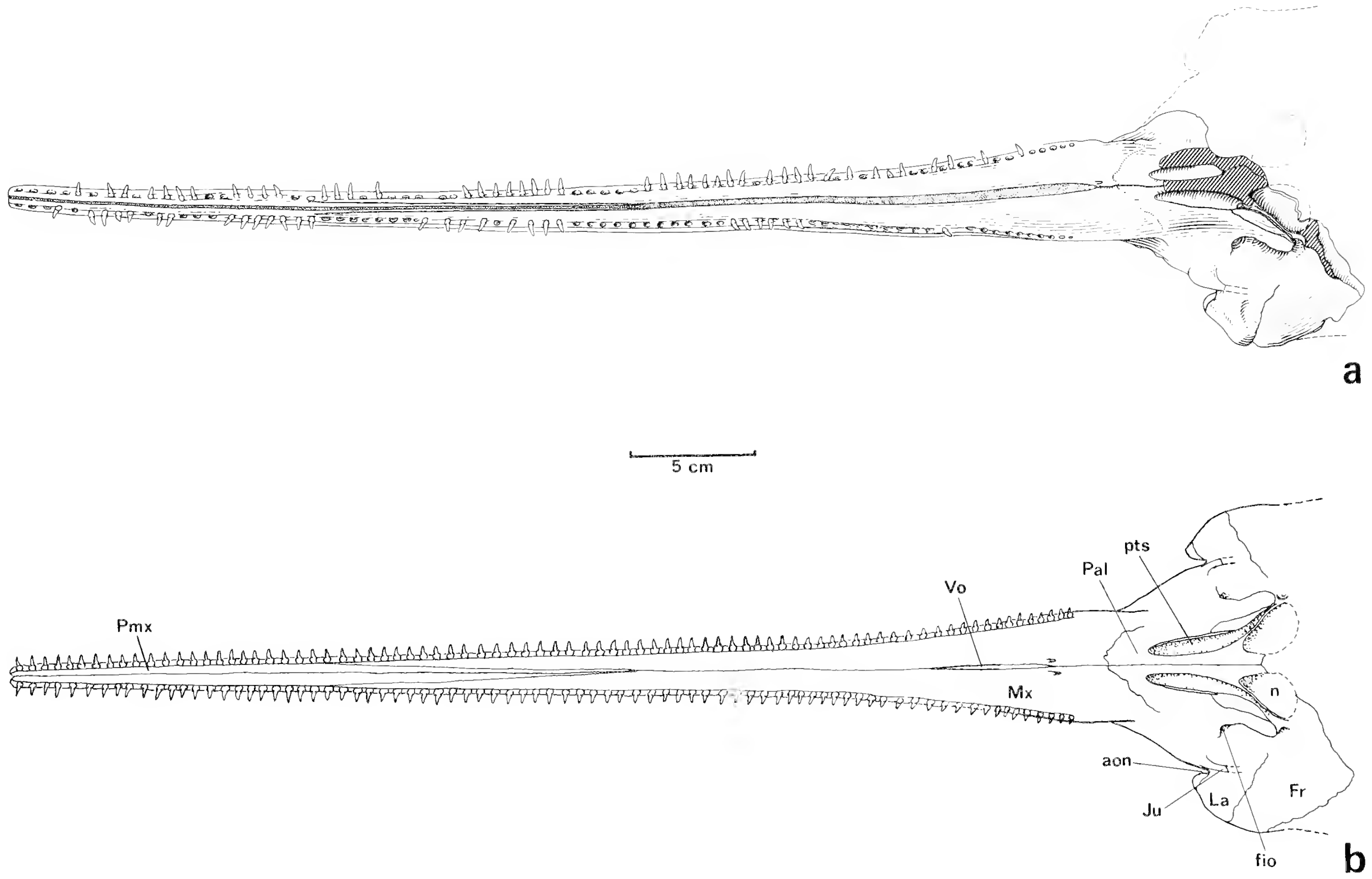

Figure 3. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial skull, ventral view: **a**, drawing of original specimen; **b**, restoration with structures labeled.

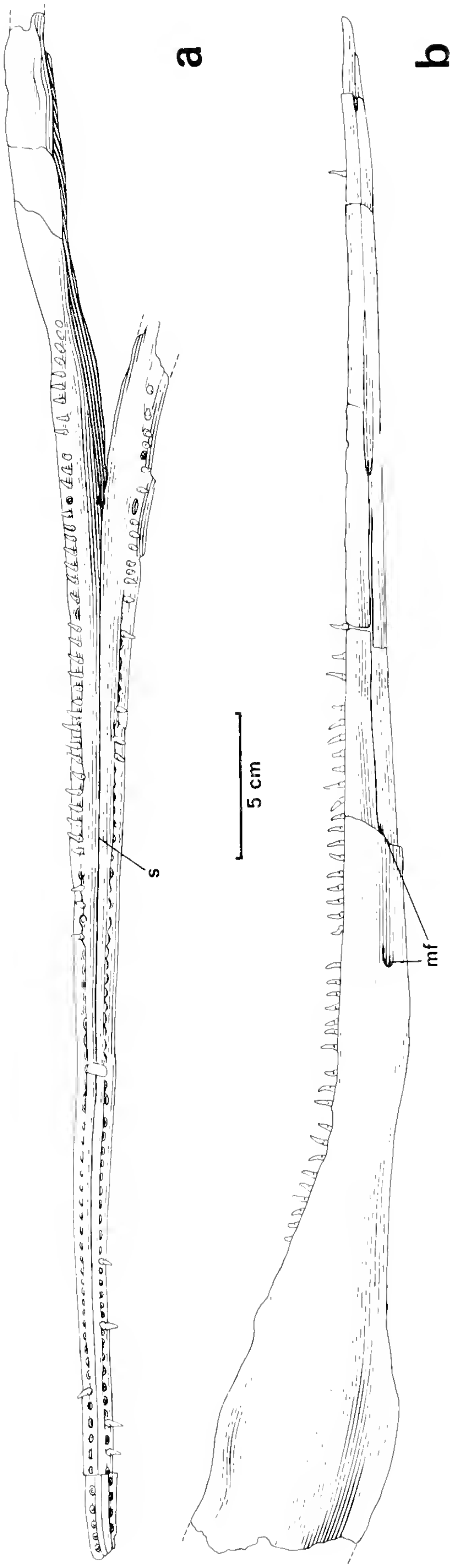

Figure 4. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, partial mandible: **a,** dorsal view; **b,** right lateral view.

lateral margins are very slightly upturned (Figs. 20a–c). At this location there is no narrowing of the premaxillae as in *P. wilsoni,* new species.

The fossae in the palatine bones that held the pterygoid air sinuses are as long anteroposteriorly as in *P. sternbergi,* and nearly twice the length of those in *P. wilsoni,* new species. The rostrum had approximately 80 teeth on each side.

Mandible. The mandible with the holotype of *P. pacifica* (Fig. 4) is the most complete known mandible of any species of *Parapontoporia.* The right and left dentaries each bore alveoli for approximately 82 teeth. The specimen shares characters with the holotype mandible (AMNH 21905) of *P. sternbergi* and is similar in general size and proportions. It has a firmly fused mandibular symphysis marked by a medial groove dorsally and ventrally. The mandible of *P. pacifica* differs from that of *P. sternbergi* by lacking a deep lateral groove (such as is present in Recent *Pontoporia blainvillei*), but has instead only an elongate shallow depression that extends the length of the symphyseal part of each dentary slightly below mid-height on the lateral side (compare Figs. 20d and e).

All bone surface of the mandible is dense and in its tooth-bearing parts the mandible is marked by faint linear striae. Between the alveolar row and the dorsal edge of the lateral groove, the surface of the dentary is bowed outward in cross section. The dorsal surface of each dentary between the midline and the alveolar row is arched transversely.

The ascending ramus has a thin, arched coronoid crest about mid-length, and this culminates posteriorly in an upturned coronoid process (Fig. 4b). Neither *Lipotes vexillifer* nor *Pontoporia blainvillei* has a coronoid crest and in both species the coronoid process projects more posteriorly than dorsally.

Teeth. The teeth of *Parapontoporia pacifica* are like those of *Pontoporia blainvillei* (Figs. 5a–d), but have relatively higher crowns. The smooth enamel crowns curve lingually, have a basal lingual bulge, and are compressed anteroposteriorly. The roots have a swelling encircling them at the gum line and are compressed labio-lingually. The anterior teeth have relatively slender, erect crowns, but progressing posteriorly the crowns are shorter and bend more medially. Because they are more bulbous, the crowns of the posterior teeth are not as compressed anteroposteriorly as are the ones of the more slender anterior teeth.

Cervical vertebra. One isolated vertebra (Fig. 5e), probably a fifth cervical vertebra, was associated with the holotype skull and mandible. This vertebra is greatly compressed anteroposteriorly, has a centrum that is nearly square in outline, a slender neural arch, small diapophyses and parapophyses, and a large transverse foramen that probably did not have a complete bony arch on its lateral side.

This vertebra resembles the fifth cervical of *Lipotes vexillifer* (Miller, 1918:pl. 12, the vertebra that is placed at lower left in the illustration) in having a low, broad neural canal, dorsoventrally expanded transverse foramen, and ventrally directed parapophyses. The resemblance of this vertebra to the fifth cervical of *Pontoporia blainvillei* is not so striking, because in that species (de Carvalho, 1961:fig. 11e) the bone

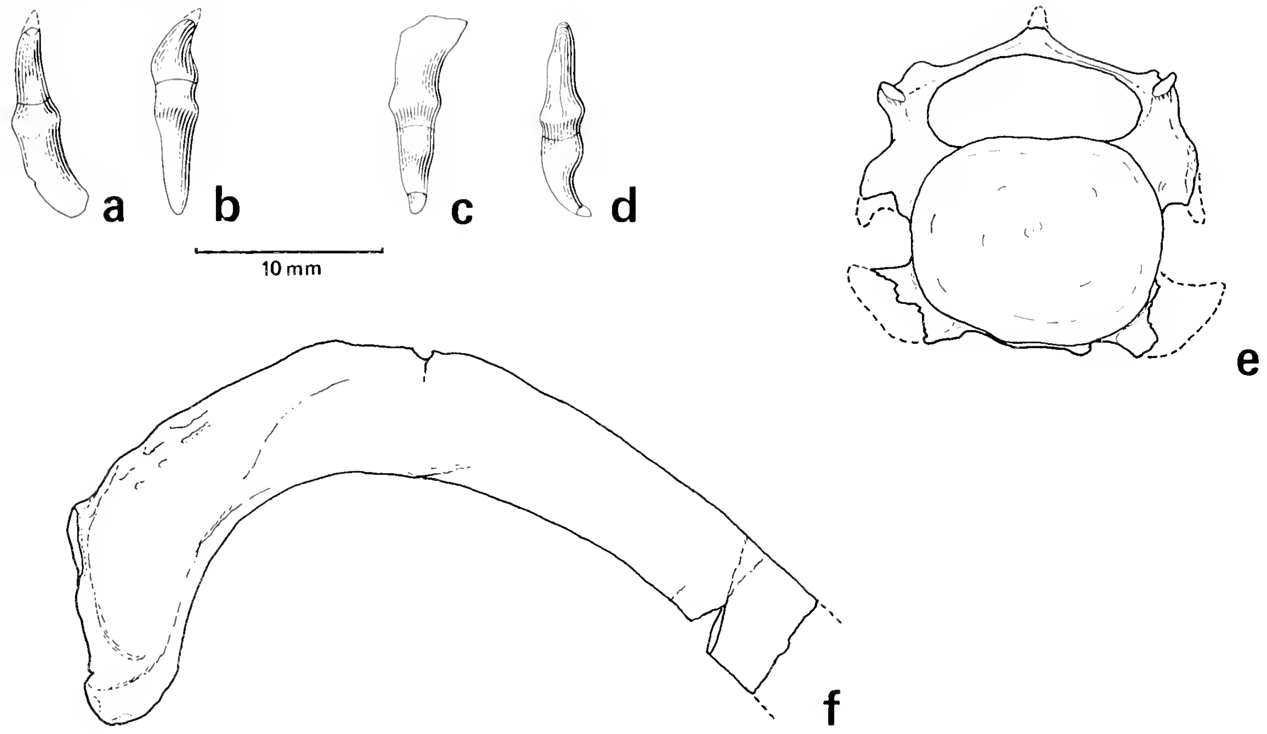

Figure 5. *Parapontoporia pacifica* Barnes, 1984, holotype, UCR 21244, right mandibular tooth: **a,** lingual view; **b,** anterior view; right maxillary tooth: e, lingual view; **d,** anterior view; **e,** cervical vertebra, anterior view; **f,** anterior right rib, anterior view. Scale line is for Figs. a–d only, Figs. e, f natural size.

has relatively larger diapophyses and parapophyses, a higher neural canal, a dorsoventrally compressed transverse foramen, a broader centrum, and no ventral extension of the parapophyses.

Rib. The proximal part of one rib (Fig. 5f), apparently a first left rib, belongs with the holotype. This rib has a large capitulum, a flat tuberculum, a short neck, a wide but anteroposteriorly compressed body, and is strongly curved at its proximal end.

Parapontoporia sternbergi
(Gregory and Kellogg, 1927)

Figures 6–10, 17b, 20c, e, 21b

Stenodelphis sternbergi Gregory and Kellogg, 1927:1.

"*Stenodelphis*" *sternbergi* Gregory and Kellogg, 1927. Barnes, 1973a:37–38; 1977:333–334; Barnes, Howard, Hutchison, and Welton, 1981:56, 57, 61, 64; Deméré, 1981:24–25; de Muizon, 1983:1103.

Parapontoporia sternbergi (Gregory and Kellogg, 1927). Barnes, 1984:6.

EMENDED DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. wilsoni,* new species, by having skull with facial region wider than long, antorbital processes larger, cranial vertex (comprised of frontals and nasals) higher and more compressed transversely, occipital condyles projecting less prominently posteriorly from occipital shield, premaxillary surfaces forming less of a basin at proximal end of rostrum, nares passing more vertically through the skull, temporal fossa compressed anteroposteriorly with its height and length approximately equal, more elongate fossa for pterygoid sinus in palatine, zygomatic process of squamosal more inclined anteriorly, squamosal between postglenoid process and paroccipital process highly compressed anteroposteriorly; and differing from *P. pacifica* by having basin formed on premaxillary surfaces on proximal part of rostrum, shorter fossa for pterygoid sinus in palatine, and deeper groove on rostrum between maxilla and premaxilla, and by having mandible with deep groove on lateral side of each dentary.

HOLOTYPE. AMNH 21905, a section of mandible in the symphyseal area with 24 teeth which have badly eroded crowns, collected by John Reiland. The specimen is not a rostral fragment as was stated by Gregory and Kellogg (1927).

TYPE LOCALITY. India Street at West Walnut, San Diego, San Diego County, California.

REFERRED SPECIMENS FROM THE SAN DIEGO FORMATION. Nearly complete skulls, LACM 6238, SDSNH 22633, 23084; rostra lacking braincases, LACM 26605, SDSNH 25022; cranial vertices, LACM 58902, UCMP 129662, UCMP 129663; cranial vertex associated with rostral fragments, LACM 30464; right squamosal, LACM 26597; partial left maxilla, SDSNH 24794; cranial fragments, LACM

30465; periotics, LACM 58901, LACM 103975, SDSNH 20941, 23058, 23630, 23631, 24734, 25049, UCMP 88581, UCMP 88589, UCMP 129660, UCMP 129661; rostral fragments associated with mandible fragments and teeth, UCMP 88590; premaxillary fragment with teeth, UCMP 88588; rostral fragments, LACM 30432, LACM 30433, LACM 31065; nearly complete mandible, SDSNH 18671; and mandible fragments, LACM 26594, LACM 30463, LACM 30468, LACM 30471 (with teeth), LACM 30472, LACM 30475, LACM 30476, LACM 104004, UCMP 88587.

FORMATION AND AGE. Lower member of the San Diego Formation, Late Pliocene, correlated with the "San Joaquin" provisional mega-invertebrate stage of Addicott (1972) and the Blancan North American land mammal age, and therefore approximately 2 to 4 million years old. The fossil fauna and age of this rock unit have been discussed by Howard (1949), Hertlein and Grant (1954), Barnes (1973a, 1977:332–334), Repenning and Tedford (1977:69–70, fig. 6), and Deméré (1982, 1983).

DESCRIPTION. Skull. The rostrum, mandible, and teeth are the only anatomical parts shared in common between known specimens of *P. pacifica* and *P. sternbergi,* and the braincase and proximal part of the rostrum are the only parts shared in common between specimens of the latter species and *P. wilsoni,* new species. To avoid repetition, I shall emphasize in the following text those characters whereby *P. sternbergi* differs from *P. wilsoni,* new species, and *P. pacifica,* and those parts of the skull that are not known for *P. pacifica.*

The skull of *P. sternbergi* (Figs. 6–8) has a braincase that is somewhat square or boxy in its proportions and it has an extremely long and narrow rostrum. Many of the characters that separate *P. sternbergi* from *P. wilsoni,* new species, are related to the derived state of foreshortening or anteroposterior compression of the braincase of *P. sternbergi* (Fig. 21). This compression is the phenomenon termed telescoping by Miller (1923), whereby the crania of Cetacea have become modified from the condition in generalized mammals so that the bones extend anteroposteriorly past one another. In odontocetes, the predominance of posterior movement of the rostral bones toward the occipital region is typical, and in the more derived states, involved an anteroposterior compression of the braincase as well.

The braincase proportions of *P. sternbergi* are somewhat like those of Recent *Lipotes vexillifer* (Figs. 17b, c), but are different in details, both primitive and derived. The braincase is deep dorsoventrally and has a nearly vertical occipital shield and a wide and fairly flat facial surface that narrows abruptly at the juncture with the rostrum.

On the posterior part of the rostrum, the dorsal surfaces of the premaxillae slope medially toward the mesorostral gutter to form a central basin. At its deepest point, just anterior to the antorbital notches, this basin is approximately 5 mm lower than the adjacent maxillary surfaces (Fig. 20c). Progressing anteriorly from the basin the premaxillae gradually become less tilted. There is a triangular shaped rough area on each premaxilla anterior to the nares. In delphinoids this is the site of attachment of the nasal plug muscle (Lawrence and Schevill, 1956), and a similar situation undoubtedly existed in *P. sternbergi.* The narrow anterior end of this rough area extends into the deepest part of the rostral depression (Fig. 6).

For most of their rostral length the premaxillae are slender, very dense and are separated from the maxillae by a deep longitudinal groove on each side (Fig. 7). There are no obvious maxilla–premaxilla sutures within these grooves. The premaxillae form most of the dorsal surface of the rostrum and roof over the mesorostral gutter, touching (but not fused) for much of their length at the midline. They extend to the extreme anterior tip of the rostrum, and are separated medially there for a short distance to expose the mesorostral gutter. Near the rostral basin the premaxillae become increasingly wider, the grooves between them and the maxillae disappear, and the premaxillae diverge to expose the mesorostral gutter.

At a point approximately 5 mm posterior to the antorbital notches, each premaxilla is perforated by a premaxillary foramen which, as in a common odontocete pattern, is connected to three sulci; anteromedial, posteromedial, and posterolateral. The anteromedial sulcus is partly roofed over by bone and defines the lateral margin of the narrow anterior extension of the rugose area of attachment of the nasal plug muscle (mentioned above). The posterolateral sulcus is deeply incised into the premaxilla. It diverges sharply away from the midline of the skull as it courses toward the lateral margin of the premaxilla, then continues posteriorly in a shallow groove on the maxilla following the edge of the premaxilla. The posteromedial sulcus branches off the posterolateral sulcus just posterior to the premaxillary foramen, but it is very shallow and extends only approximately 15 mm.

Beginning immediately anterior to the nares, the premaxillae become slightly elevated above the surrounding maxillae, and this condition persists to the posterior termination of each premaxilla. These elevated areas around the nares were smooth surfaced in life, but on either side of the available skulls the bone surface is now partly eroded away. When the animal was alive, these slightly elevated premaxillary surfaces, the spiracular plates, supported the premaxillary sacs (which are diverticula of the nasal passages, see Mead, 1975). These plates are asymmetrical. The one on the right side is wider and more elevated on its lateral edge than the one on the left. The left plate tilts more toward its lateral edge, and extends farther posteriorly. Each premaxilla terminates about 5 mm from the corresponding nasal. Extending posteriorly from the posterior end of each premaxilla there is a rough area on the maxilla indicating that at some previous point in the evolutionary history of this lineage of dolphin the premaxilla had extended farther posteriorly adjacent to the nasal as in, for example, the squalodonts.

The mesethmoid septum between the nares is canted to the left as it rises from the skull, and the left naris is slightly larger than the right. The basic construction of the bones surrounding the nares is very similar to that in *Lipotes vexillifer,* and is different from that in *Pliopontos littoralis* and *Pontoporia blainvillei,* in which the spiracular plates are more elevated and the bones around the nares are symmetrical (Fig. 17).

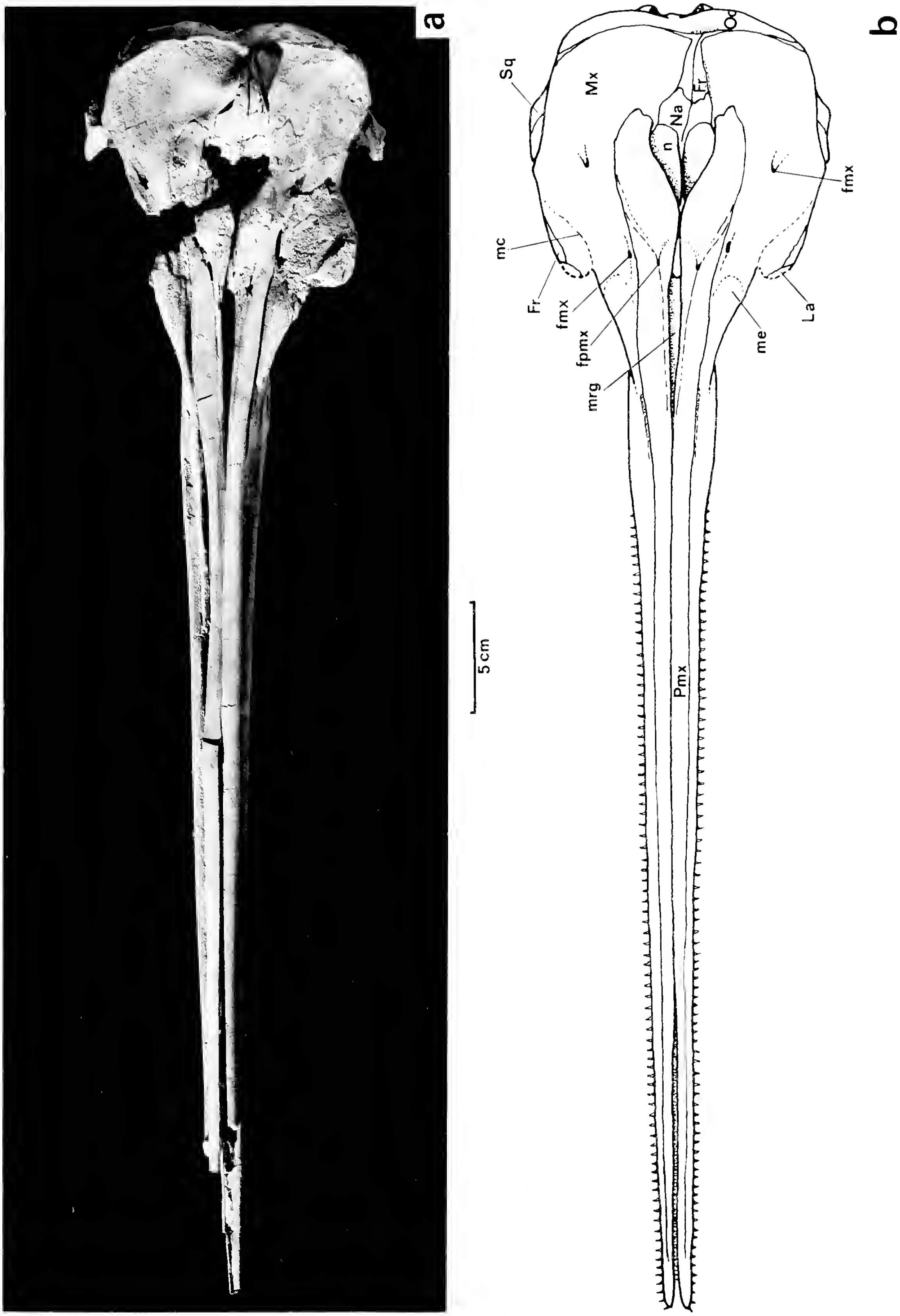

Figure 6. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, dorsal view: **a,** photograph of original specimen; **b,** restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica.*

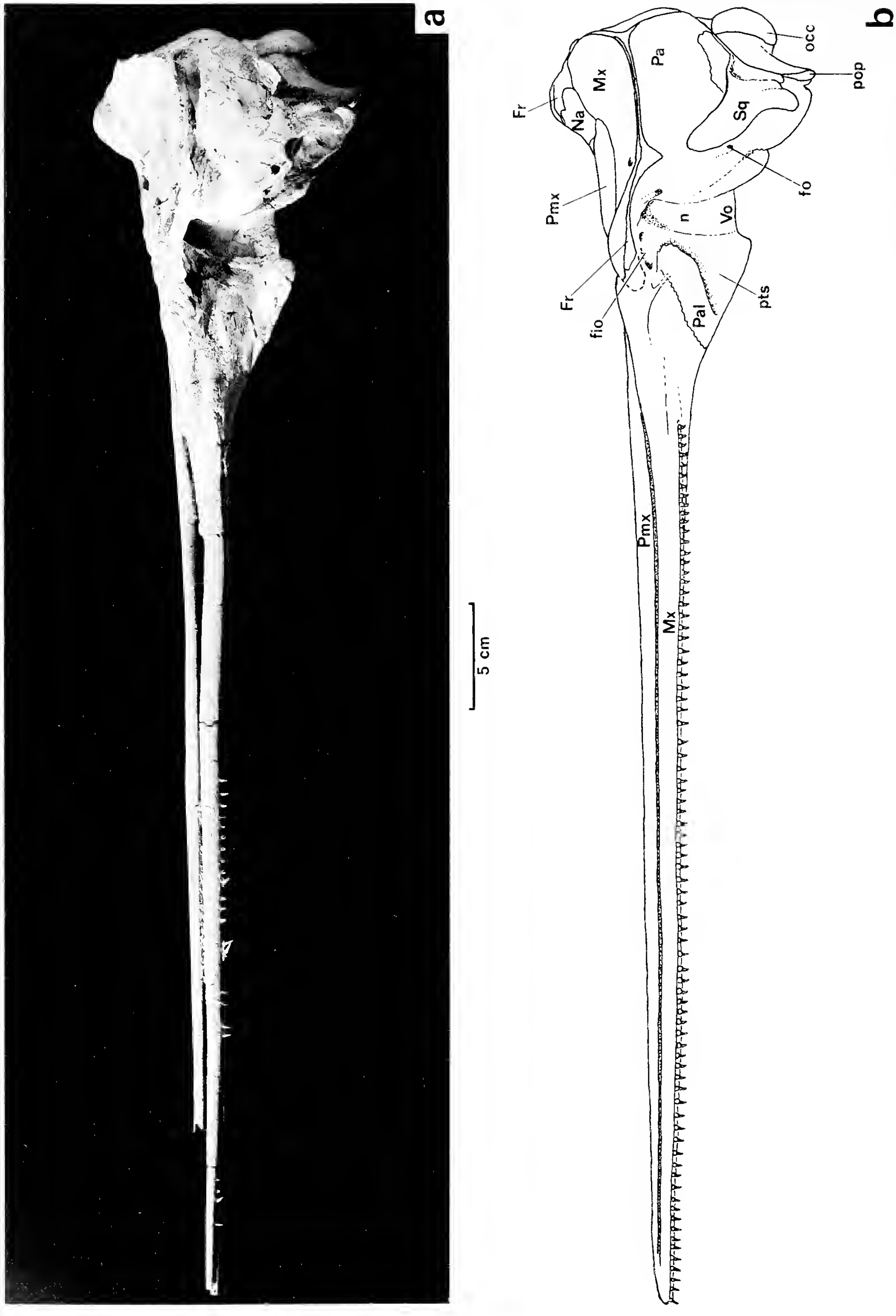

Figure 7. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, left lateral view: **a**, photograph of original specimen; **b**, restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica.*

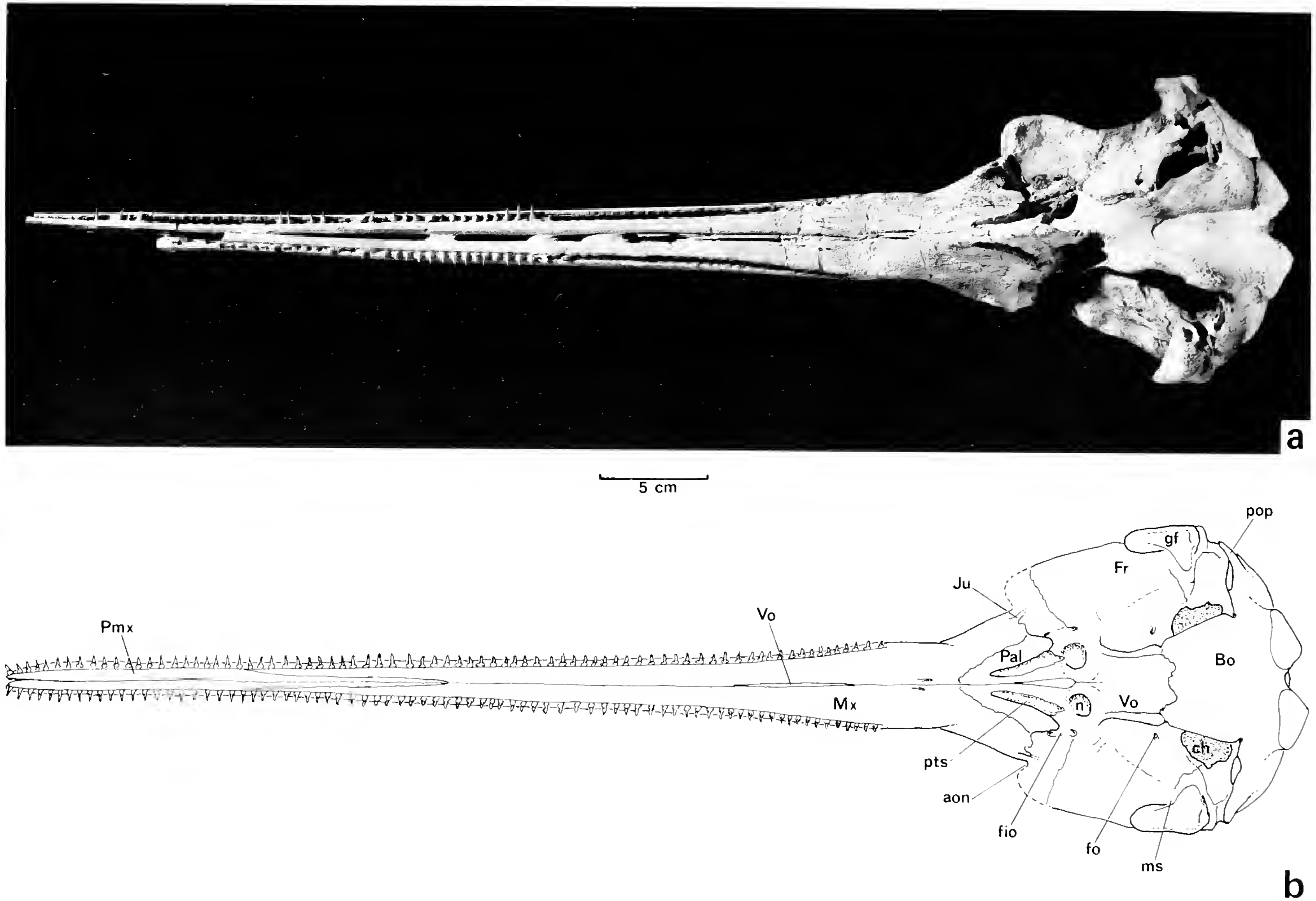

Figure 8. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimen, LACM 6238, skull, ventral view: **a,** photograph of original specimen; **b,** restoration based on all known specimens of the species with extremity of rostrum based on *P. pacifica.*

Table 1. Measurements (in mm) of skulls of *Parapontoporia*. Parentheses indicate estimated measurements. Method follows Perrin (1975).

	P. pacifica	*P. wilsoni*	*P. sternbergi*			
	UCR 21244	UCMP 83790	LACM 6238	LACM 26605	SDSNH 22633	SDSNH 23084
Condylobasal length	—	—	(596+)	—	(605+)	—
Length of rostrum	477	—	(467+)	(341+)	(475+)	—
Width of rostrum at base	(80)	71	69	(64)	(64+)	(61+)
Width of rostrum at midlength	17	—	—	—	—	—
Width of premaxillae at midlength of rostrum	12	—	—	—	—	—
Greatest preorbital width	(126)	104	108	—	—	—
Greatest postorbital width	—	(124)	—	—	120	(118)
Least supraorbital width	(112)	113	—	—	—	—
Greatest width of external nares	—	33	31	—	26	26
Width across zygomatic processes of squamosals	—	138	141	—	(136)	—
Greatest width of premaxillae	—	58	58	—	50	(54)
Greatest parietal width within temporal fossae	—	106	109	—	98	—
Vertical external height of brain case	—	—	94	—	85	—
Internal length of brain case	—	—	94	—	—	—
Length of temporal fossa	—	(73)	—	—	(72)	—
Width of temporal fossa	—	(48)	—	—	41	—
Length of orbit	—	44	—	—	—	—
Length of antorbital process of lacrimal	22	22	—	—	—	—
Length of tooth row	414	—	(398+)	(282+)	(430+)	—

Like the premaxillae, the maxillae are for much of their rostral length composed of dense bone on both their labial and palatal surfaces. The rostrum is constricted transversely at a point approximately 50 mm anterior to the antorbital notches. Both *Lipotes vexillifer* and *Pontoporia blainvillei* have a similar constriction, and it is formed in the following manner. In this area the dense part of the maxilla which is lateral to the tooth row departs from the edge of the premaxilla and extends onto the ventrolateral edge of the rostrum. Posterior to this and anteromedial to the antorbital notches, the porous part of the maxilla is elevated into an eminence that swells dorsally and laterally. The tapered anterior end of this maxillary eminence extends anteriorly forming the lateral edge of the rostrum and passes dorsal to the posterior end of the dense section of the maxilla forming the tooth-bearing part of the rostral margin. This constriction of the margin of the rostrum is typical of all Pontoporiidae (Fig. 17).

The maxillary eminence has pushed the margin of the adjacent premaxilla medially and also constricts the anterior opening of the antorbital notch (Fig. 6). Posteromedial to each maxillary eminence is a single maxillary foramen which is confluent with shallow sulci running posteriorly and anteriorly from it, parallel to the margin of the premaxilla.

All known skulls of *P. sternbergi* have suffered breakage and/or abrasion of the supraorbital area so that details of the antorbital process and maxillary crest are not known for the species. From what is preserved, the species appears to be similar in these structures to *P. pacifica* and *P. wilsoni*, new species, but to have had a more prominent antorbital process. There is an obliquely oriented maxillary crest over the orbit, and the skull SDSNH 22633 has the anterior end of the zygomatic process of the jugal located anteromedial to the antorbital notch (Deméré, 1981:fig. 9) as in the other two species. The same skull, illustrated by Deméré, has the best preserved postorbital process of the frontal of any specimen known of the genus. The process is short and broadly triangular, proportionally shorter and smaller than in *Pontoporia blainvillei*, and not slender with a distal rugosity as in *Lipotes vexillifer*. It apparently did not contact the tip of the zygomatic process of the squamosal (Fig. 7).

The posterior end of each maxilla wraps around the posterior side of each nasal and contacts the elevated frontal on the cranial vertex. In so doing, the maxillae encroach so far medially upon the frontals that just posterior to the cranial vertex only a 2-mm-wide exposure of frontals separates the right maxilla from the left. The cranial vertex is formed of the frontals and nasals and is in the form of an anteroposteriorly elongate, asymmetrical, slightly twisted knob with a cleft at the median suture on its anterior surface. Like the narial region, it is offset to the left side. The median suture between the right and left frontals on the cranial vertex is 13 mm to the left of the midline of the skull, as marked by the septum within the braincase that separated the cerebral hemispheres of the brain. The exposed frontals form the highest point of the vertex just posterior to the nasal bones, and there is a lower area between that point and the occipital crest. This low area posterior to the vertex exists also in other

Pontoporiidae and in Iniidae, and is unlike the condition in species of Delphinidae and Phocoenidae, in which the cranial vertex increases in height continuously from the nares to the occipital crest. Each nasal is thin and wraps around the steeply inclined anterior side of its corresponding frontal. The mesethmoid, forming the posterior walls of the nares, is inclined in the same plane as the nasals, from which it is separated by arcuate sutures.

The occipital shield is oriented almost vertically (Fig. 7), much as in *Lipotes vexillifer.* As in both *Pontoporia blainvillei* and *Lipotes vexillifer,* it is approximately square in posterior view, and adjacent to the temporal fossae its dorsolateral corners are prominent. As in *Pontoporia blainvillei,* the midline of the occipital shield is marked by a prominent median sulcus that extends from the apex of the foramen magnum dorsally to the occipital crest, and is flanked by a large, convex area on each side corresponding to the cerebral hemispheres of the brain. Each convex area is separated from the occipital condyle below it by a prominent oblique sulcus that is not present in *Pontoporia blainvillei.* The occipital condyles are moderately convex and set off prominently from the occipital shield. The dorsal margin of the foramen magnum forms a triangular peak somewhat like that in *Pontoporia blainvillei.* In *Lipotes vexillifer* the foramen magnum is more circular in shape.

The temporal fossa is open posteriorly and curves around the lateral side of the occipital shield. Dorsally, the facial parts of the maxilla and frontal project approximately 8 mm laterally over the posterior part of the temporal fossa. The squamosal fossa, which floors the temporal fossa, forms a deep recess between the cranium and the zygomatic process of the squamosal. Anteriorly the squamosal fossa is floored by only a thin shelf of bone spanning between the zygomatic process and the cranium.

The paroccipital process is located relatively far anteriorly on the braincase and therefore lies beneath the posterior end of the temporal fossa. The paroccipital process terminates ventrally in a flat, rugose surface and is separated medially from the falcate process of the basioccipital by a narrow, deep jugular notch. At the apex of this notch is a relatively large hypoglossal foramen that is nearly 3 mm in diameter.

The zygomatic process of the squamosal is deep and long, and its anterior end is upturned. There is a large, pointed, ventrally directed postglenoid process. The glenoid fossa is canted dorsomedially on the zygomatic process so that the external surface forms a flange which projects ventrolaterally. This ventrally projecting border is deepest anterior to the center of the glenoid fossa and posterior to the point where the zygomatic process turns upward. The glenoid fossa extends medially as a thin shelf which partly underlies a very large fossa for the middle sinus of the middle ear air sinus system. The fossa extends anteriorly along the medial side of the zygomatic process much as in *Lipotes vexillifer* and *Pontoporia blainvillei.* On its lateral surface the zygomatic process of the squamosal is excavated posteriorly by a rugose sternomastoid muscle fossa. The postglenoid process of the squamosal is close to the paroccipital process and there is much wrinkling and compression of the intervening bone, including the muscle fossa, immediately dorsal to the external auditory meatus. Such extreme anteroposterior compression does not exist in this part of the squamosal in *P. wilsoni,* new species.

The cranial hiatus is the opening between the squamosal and the basioccipital in which the periotic lay and through which nerves and blood vessels passed, connecting the ear to the endocranial cavity. This hiatus in *P. sternbergi* is large (Fig. 8), but not relatively as large as in *Pontoporia blainvillei.* There is no indication that there was a large falciform process of the squamosal lateral to the hiatus such as is present in species of Delphinidae. A small falciform process is present in *Pontoporia blainvillei.* Large fossae in the bone around the cranial hiatus of *P. sternbergi* indicate the locations in life of extensive air sinuses. There was a large posterior sinus in the anterior wall of the paroccipital process. A much larger one occurs in the same location in *Pontoporia blainvillei,* and a smaller one exists in *Lipotes vexillifer.* The peribullary sinus in *P. sternbergi* extended laterally dorsal to the posterior process of the periotic, as well as medially where it occupied a large fossa in the lateral side of the falcate process of the basioccipital. The extent of excavation of the falcate process by this fossa is exceptional when compared to most other species of odontocetes, especially *Pontoporia blainvillei,* in which this process is very thick. At the front of this fossa, the very small carotid foramen pierces the basioccipital approximately 5 mm posterior to the suture between the pterygoid and the basioccipital. Lateral to this the basisphenoid bridges between the squamosal and the pterygoid, and bears the foramen ovale which is 4 mm in diameter and located approximately 8 mm anterior to the anterior margin of the cranial hiatus. A deep sulcus, marking the former course of the mandibular division of the trigeminal nerve, leaves the foramen ovale and extends posterodorsally across the basisphenoid (Fig. 8).

The medial lamina of the pterygoid forms a crest that is continuous with, but thicker than, the falcate process of the basioccipital. The posterior end of the vomer covers the ventral surface of the basisphenoid, spreads laterally to within 3 mm of the ventral edge of each pterygoid crest, and stops at the basisphenoid–basioccipital suture. Posteriorly, each falcate process of the basioccipital ends in a curved margin, and between that and the paroccipital process of the exoccipital the hypoglossal foramen lies at the apex of the jugular notch. In *Pontoporia blainvillei* the same foramen lies outside of, and posterior to the notch, rather than within it.

The anterolateral wall of the braincase is very well preserved only in LACM 6238. It is convex and remarkably devoid of foramina, sinuses, and bony processes or crests. The orbit is not as well preserved on any known specimens of *P. sternbergi* as it is on the holotype of *P. wilsoni,* new species, and the description of the latter species should, therefore, be consulted for data on the orbit of *Parapontoporia.*

The vomer forms a deep, narrow keel between the internal nares, and is continuous with the very deep, narrow keel formed by the palatines between the fossae for the pterygoid sinuses (Fig. 20c). These narrow fossae are closely appressed on either side of this very deep and narrow keel at the pos-

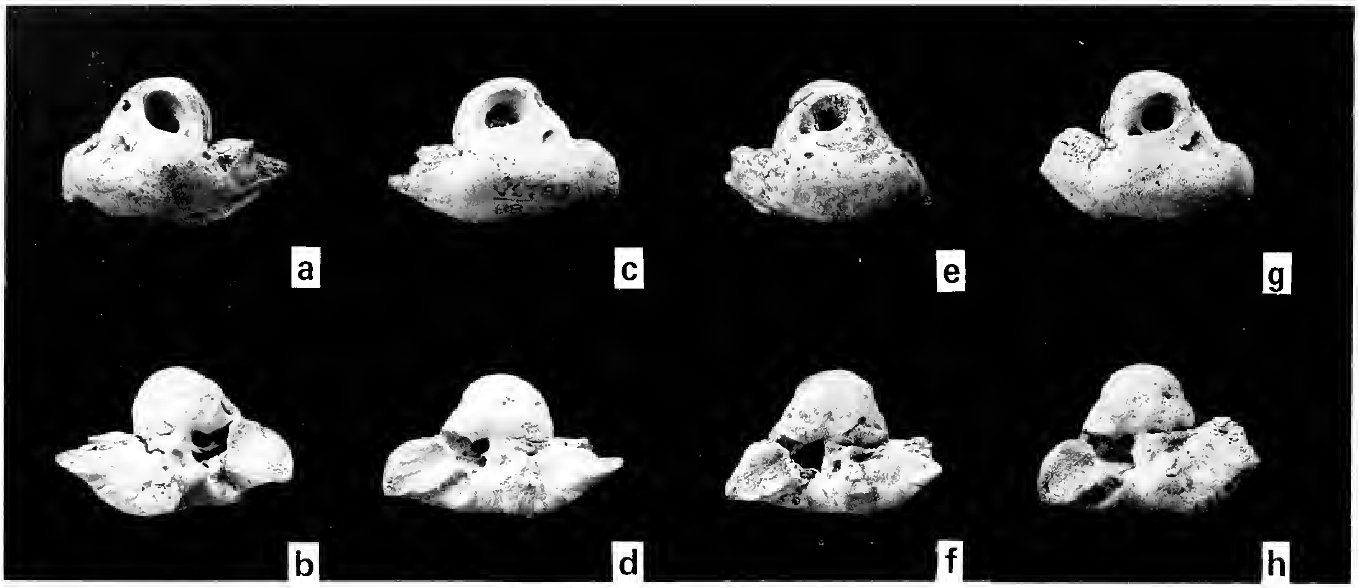

Figure 9. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred periotics from the San Diego Formation: UCMP 88581, right: **a,** cerebral view; **b,** tympanic view; UCMP 88589, left: **c,** cerebral view; **d,** tympanic view; LACM 58901, left: **e,** cerebral view; **f,** tympanic view; LACM 103975, left: **g,** cerebral view; **h,** tympanic view. All natural size.

terior end of the palate, and they extend anteriorly only slightly beyond the level of the antorbital notches. However, they diverge dorsoposteriorly and become enlarged as they ascend into the skull anterior to the nares (Fig. 8b). Such a dorsal expansion of the pterygoid sinus is not common in odontocetes, but does occur also in *Lipotes vexillifer* and *Pontoporia blainvillei.*

The palate is fairly flat for most of its length; not quite as flat as in *Pontoporia blainvillei,* and more deeply fissured medially at the posterior end. Premaxillae appear about midlength on the palate between the maxillae, from which they are separated by elongate sutures. Progressing anteriorly, the premaxillae occupy increasing amounts of the palatal surface so that near the rostral extremity the medial side of the alveolar row is composed entirely of premaxilla (Fig. 8b). The vomer is exposed on the posterior one-fourth of the palate.

On the posterior part of the rostrum the alveolar rows curve slightly dorsally. Here the surface of the maxilla becomes increasingly porous, except for a band of relatively dense bone extending along the dorsal edge of the alveolar row. The alveoli for the teeth are all approximately 2 mm in diameter. The deepest part of the rostrum is at the proximal end ventral to the antorbital notches. Here it is triangular in cross section with a prominent ventral keel. Anterior to this keel are a pair of palatine foramina in each maxilla on either side of the midline. At the deepest part of the keel lie the triangular palatines, wedged between the maxillae.

Periotic. I have previously (Barnes, 1973a:figs. 2a, b) illustrated a periotic (UCMP 57991) from the San Joaquin Formation, a correlative of the San Diego Formation, and identified it as "*Stenodelphis*" *sternbergi.* Periotics like this one have been reported from the San Diego Formation (Barnes, 1973a; Deméré, 1981:fig. 5) and more are described here, but none has ever been found in association with a skull of *P. sternbergi* nor of any other species of *Parapontoporia.*

I now assign seven periotics collected from the San Diego Formation to *P. sternbergi* based upon such resemblances to periotics of *Lipotes vexillifer* as: comparable proportions among the different parts of the periotic, pointed anterior process with a separate rugose process on its medial side, a curved crest that extends along the lateral side of the anterior process from its tip to a tuberosity immediately anterior to the groove for the tympanic membrane, a relatively small, slightly concave and grooved articular surface for the bulla on the posterior process, a deep cleft between the anterior process and the cochlear portion of the periotic, and a relatively small, circular internal acoustic meatus. The periotic of *Lipotes vexillifer* (see Brownell and Herald, 1972:pl. 3, figs. 1–6; Kasuya, 1973:pl. 10, figs. 16–20; Zhou, Qian, and Li, 1979:pl. 3, figs. 1–6) differs from that of *P. sternbergi* by being much larger and by having a relatively larger cochlear portion with more rugosities on its cerebral surface and a more circular internal acoustic meatus.

The periotic of *Pontoporia blainvillei* (see Kasuya, 1973: pl. 9, figs. 17, 20–23) is considerably different from those of both of the above species by being very small and by having relatively smaller anterior and posterior processes, a smaller tuberosity anterior to the groove for the tympanic membrane, a more inflated cerebral surface, a distinctive reticulated, etched pattern on the tympanic side of the cochlear portion, and by lacking a process on the medial side of the anterior process.

The periotics of *P. sternbergi* from the San Diego Formation are variable (Fig. 9) in the shape and degree of infla-

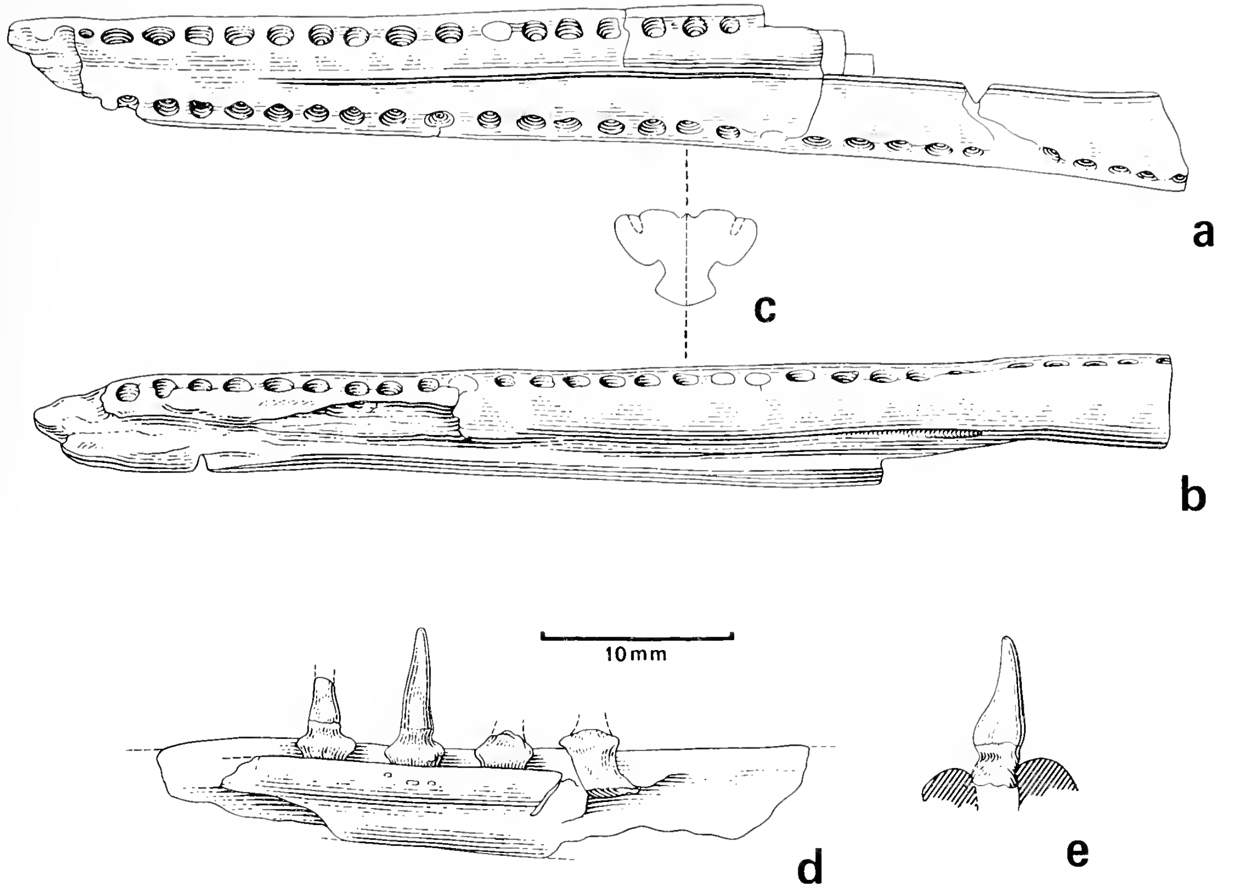

Figure 10. *Parapontoporia sternbergi* (Gregory and Kellogg, 1927), referred specimens from the San Diego Formation: UCMP 88587, mandible fragment: **a,** dorsal view; **b,** left lateral view; **c,** cross section; UCMP 88588, premaxillary fragment with teeth: **d,** lingual view; **e,** posterior view of the complete tooth. Scale line is for Figs. d, e only, Figs. a–c natural size.

tion of the cochlear part and the anterior process, and in the size of the posterior facet for the tympanic bulla.

Mandible. The holotype is a section of a mandible, not a rostrum as it was identified by Gregory and Kellogg (1927). The specimen has no evidence of a vomer or mesorostral gutter which would be present if it were a rostrum, and it is fused at the midline, which is the mandibular symphysis. All skulls of *P. sternbergi,* in a manner typical of odontocetes, exhibit no fusion on the palatal surfaces between the opposite premaxillae or maxillae.

The mandible of *P. sternbergi* is long and slender, and the dentaries are fused for most of their tooth-bearing length by a firm suture. One deep, longitudinal groove extends along the side of each dentary just below mid-height (Fig. 10c). The dorsal margin of this groove projects ventrally so that the opening of the groove is slightly constricted. Anteriorly directed nutrient foramina scattered along the dentary emerge into the upper part of this groove. The groove is less distinct at its posterior end at a point anterior to the end of the symphysis. The ventral surface of the mandible has a broad and flat (or in some specimens a slightly convex) surface and is marked along its midline by a faint groove tracing the position of the mandibular symphysis. The whole surface of the mandible, including the inside of the longitudinal grooves, is composed of dense, striated bone. Along the midline of the dorsal surface of the symphyseal region of the mandible there is a broad, shallow groove with a slight longitudinal ridge that marks the midline and the position of the mandibular symphysis (Figs. 10a, c). There is no median groove in the mandible of *Pontoporia.* Teeth are set 1 to 2 mm apart in circular alveoli separated by septa of cancellous bone. The alveoli are 2 to 3 mm in diameter.

Teeth. The teeth in the holotype mandible fragment (AMNH 21905) are not typical of those in the sample of specimens now available. Some sort of possibly postmortem mechanical or chemical attrition has reduced the crowns of all the teeth in AMNH 21905 to featureless, rounded cores lacking any enamel (Gregory and Kellogg, 1927:fig. 1). The roots of the teeth are more expanded anteroposteriorly, especially at their apices, than those in any other specimen yet recovered from the San Diego Formation. This is the feature which Gregory and Kellogg (1927:3, fig. 3) described as being like a battle-ax. Because the holotype is larger than the other available mandible fragments, I attribute this exceptional root development to extreme old age of the individual.

Upper and lower teeth are similar in morphology. An unworn tooth (Figs. 10d, e) has a crown that is slender, slightly compressed anteroposteriorly, with a nearly straight labial margin and a prominent lingual bulge located proximally near the enamel margin. The enamel is smooth, having no rugosities or crests. No specimen has a complete dentition, but it can be seen in the partial dentitions in the sample available that the more anterior teeth in both the skull and mandible have relatively slender and high crowns, and that progressing posteriorly they are thicker, shorter, and more curved lingually. The anterior teeth are positioned vertically, but the middle and posterior teeth tilt more labially.

The part of the root that is exposed between the bony alveolus and the enamel line of the crown is encircled by a collar which is most prominent anteriorly and posteriorly forming "shoulders" on the root. This condition is preserved on the teeth of the holotype as well. Roots are flattened transversely, particularly so at their apices, which are curved posteriorly (Fig. 10d).

The teeth, or their alveoli, in the nearly complete skull LACM 6238 total at least 77 on each side, and the rostrum was probably at least 20 mm longer when complete. Because the number of teeth in *P. sternbergi* is so close to the known number of 80 to 82 on each side of each jaw in the holotype of *P. pacifica,* I believe that the two species had similar numbers of teeth in both the rostrum and mandible.

***Parapontoporia wilsoni*, new species**

Figures 11–16, 20b, 21a

Stenodelphininae, genus and species new (part): Barnes, 1977: 331.

DIAGNOSIS OF SPECIES. A species of *Parapontoporia* differing from *P. pacifica* by having skull with premaxillae depressed, forming a basin on proximal surface of rostrum anterior to level of antorbital notches; differing from *P. sternbergi* by having facial region longer than wide (antorbital notch to occipital crest versus supraorbital width), deeper basin on proximal surface of rostrum, antorbital process smaller, cranial vertex (comprised of frontals and nasals) lower and less compressed transversely, nares not as vertically oriented in passage through the skull but curving more around anterior wall of braincase, temporal fossa more elongate anteroposteriorly, zygomatic process of squamosal less inclined anteriorly, squamosal between postglenoid process and paroccipital process not as greatly compressed anteroposteriorly; and differing from both *P. sternbergi* and *P. pacifica* by having shorter fossae for pterygoid sinuses on palatines.

HOLOTYPE. UCMP 83790, incomplete skull consisting of the facial portion of the braincase, the posterior part of the rostrum and the basicranium, missing part of basioccipital, supraoccipital, squamosals, pterygoids, parietals, and basisphenoid, collected by John Stanley prior to 1966.

TYPE LOCALITY. UCMP V-6969, in the sea cliff north of Manresa Beach, Santa Cruz County, California.

FORMATION AND AGE. The lower part of the Purisima Formation, latest Miocene, correlated with the "Jacalitos" provisional mega-invertebrate stage of Addicott (1972) and indirectly with the Hemphillian North American land mammal age, and approximately 6 to 8 million years old. The type locality at Manresa Beach is a considerable, but as yet undetermined distance higher stratigraphically than the base of the Purisima Formation and the type locality of the pinniped *Dusignathus santacruzensis* Kellogg, 1927. The age of the lower part of the Purisima Formation has been considered by Cummings, Touring, and Brabb (1962) as correlative with the Jacalitos Formation in the San Joaquin Valley, and by Barnes (1977) and Repenning and Tedford (1977) as also correlative with the lower member of the Almejas Formation on Isla Cedros, Baja California, Mexico.

ETYMOLOGY. The species name honors the late Mr. Leslie E. Wilson, who was a teacher, a collector, and researcher of fossil odontocetes, and a generous benefactor to the University of California Museum of Paleontology. Mr. Wilson helped establish the Remington Kellogg Memorial Fund at the Museum to support student research on fossil marine mammals.

DESCRIPTION. The holotype of *P. wilsoni* (Figs. 11–16) may be compared with the entire cranium and the proximal part of the rostrum of *P. sternbergi,* but only the anterior part of its facial region and the proximal part of its rostrum are directly comparable with the holotype of *P. pacifica.* To avoid the repetition that would arise from describing identical structures known for the two previously described species of *Parapontoporia,* those structures that are not known in the others, or those that serve to differentiate *P. wilsoni* from them, will be emphasized in the following text.

The braincase of *P. wilsoni* is more elongate anteroposteriorly than that of *P. sternbergi* (Fig. 21). In *P. wilsoni* the facial region is relatively longer, the cranial vertex is not so steeply peaked, the nares do not pass so steeply into the skull, the temporal fossa is longer anteroposteriorly, and the posterior part of the squamosal, above the mastoid region and between the glenoid fossa and the paroccipital process, is not so compressed in an anteroposterior plane.

The basin that is located in the center of the proximal part of the rostrum is approximately 8 mm deep; nearly twice as deep as it is in *P. sternbergi.* In *P. pacifica,* there is no such basin (Figs. 20a–c). The premaxillary foramina are located approximately 4 mm farther posterior, relative to the antorbital notches, than they are in *P. sternbergi.* Each foramen has the three typical sulci connected with it (anteromedial, posteromedial, and posterolateral), however, the anterior side of the premaxillary foramen and the proximal part of the anteromedial sulcus are roofed over by bone (Fig. 11), even more so than in *P. sternbergi,* in an unusual manner. The posterolateral sulcus is very deeply incised into the premaxilla and its lateral edge is overhung by a sharp lip of bone. Posterior to this, the posterolateral sulcus curves along the lateral edge of the premaxilla and becomes indistinct opposite the posterior edge of the nares.

The posterior ends of the premaxillae are complete on the holotype of *P. wilsoni,* and confirm the previously given description of this area in *P. sternbergi.* The right spiracular plate is wider than the left, and the posterior end of the left premaxilla extends farther posteriorly than the right. Both premaxillae extend posteriorly closer to the anterolateral corners of the nasals than they do in *P. sternbergi*, and this I interpret as a more primitive character.

The supraorbital region is more complete on the holotype of *P. wilsoni* than it is on any specimens of the other species of *Parapontoporia*, and the antorbital processes and maxillary crests are perfectly preserved. Each antorbital notch is approximately 8 mm deep and, in addition to being partly constricted medially by the maxillary eminence, is partially overlapped laterally by the anterior end of the anteromedially canted maxillary crest on the supraorbital process. The maxillary crests are similar in location, but relatively smaller than those in *Lipotes vexillifer, Pliopontos littoralis,* and *Pontoporia blainvillei.* In *Parapontoporia wilsoni,* the apex of the crest forms an uninterrupted arc from the antorbital process to the postorbital process. Its lateral surface is slightly convex and comprised of maxilla as well as of the frontal and lacrimal above the orbit. In *Pontoporia* this crest is similarly shaped, but is higher, narrower, located closer to the premaxilla, and the lateral surface of the crest is rugose, excavated and slopes more medially, and concomitantly, the frontal and lacrimal are more exposed dorsally. The same crest in *Lipotes vexillifer* is developed into more of a knob.

In *Parapontoporia wilsoni* there is a wide fossa in the maxilla medial to the maxillary crest that extends from the antorbital notch posterolaterally toward the postorbital process. The large posterior maxillary foramen is located medial to this depression where the maxillary surface changes its slope and ascends toward the narial region and the cranial vertex.

Compared with *P. sternbergi, P. wilsoni* has the following primitive characters. The occipital condyles protrude more prominently from the occipital shield (Figs. 13, 14), the posterior part of the temporal fossa is not roofed over as far laterally by the maxilla and frontal, the paroccipital process is not located as far anteriorly on the braincase and therefore is located less beneath the temporal fossa, and the posterior part of the zygomatic process of the squamosal is not compressed against the paroccipital process and therefore the sternomastoid muscle fossa and the intervening bone that is dorsal to the mastoid process is nearly three times the width. The falcate processes of the basioccipital are thinner and are more excavated laterally for the peribullary sinus than in *P. sternbergi.* This is a derived character. On the holotype of *P. wilsoni,* the falcate process is in many places only 1 to 2 mm thick, and in one place it is so thin that, even in its fossilized state, it will transmit light. The zygomatic process of the squamosal is farther from the braincase wall and the intervening squamosal fossa is therefore wider. The shelf of bone anterior to this fossa is small and not upturned as in *P. sternbergi.* The lateral margin of the glenoid fossa forms a more prominent, vertical border (Figs. 15, 16).

The orbit is small and the frontal forms the posterior two-thirds of its roof. The lacrimal is large compared with species of Delphinidae and forms the anterior one-third of the orbital roof (Fig. 16). In *Pontoporia blainvillei* and *Lipotes vexillifer* the lacrimal is larger yet.

The anterior end of the jugal, as is typical of most modern odontocetes, is fused to the lacrimal, extends anteriorly beneath the maxillary eminence on the proximal part of the rostrum and is surrounded dorsally and ventrally by the maxilla. The zygomatic process of the jugal departs from the body of the fused jugal and lacrimal on the anteromedial side of the antorbital notch beneath this eminence. This location of departure of the zygomatic process is similar to that in *Lipotes vexillifer,* but different from that in *Pontoporia blainvillei* in which it is located posterior to the antorbital notch. No known specimen of *Parapontoporia* has a complete jugal.

The optic foramen leaves the braincase beneath a relatively massive strut of bone on the frontal lying posterolateral to the naris. The orbital apertures of the infraorbital foramen complex join to form a large recess in the medial wall of the orbit. These foramina connect dorsally with the maxillary and premaxillary foramina. There is a large but shallow fossa under the anterior part of the supraorbital process indicating that this area held a preorbital lobe of the pterygoid sinus of the middle ear air sinus system.

PHYLOGENETIC RELATIONSHIPS

Before discussing interrelationships of the subfamilies within the family Pontoporiidae, it is important to clarify which previously reputed pontoporiids are not, in my opinion, demonstrably members of the group. *Lonchodelphis occiduus* (Leidy, 1868) is a problematical dolphin from the latest Miocene Purisima Formation in central California. The species was based upon a rostral fragment, and was believed by Allen (1924) to be related to *Pontoporia* after it had been allied first with *Delphinus* by Leidy (1868) and later with *Phocoena* by Jordan and Gilbert (1919). I have (Barnes, 1977:332; 1984:12) pointed out that the specimen is not similar to any specimen of a pontoporiid. No other specimens have ever been assigned to the species and, until a more complete specimen is identified, it should be considered as some unknown type of odontocete. Simpson (1945:101) classified in the Stenodelphininae the Pliocene age Argentinian species, *Pontivaga fischeri* Ameghino, 1891, which was based on a lower jaw fragment. The species cannot be objectively compared with another, contemporaneous pontoporiid from Argentina, *Pontistes rectifrons* Burmeister, 1885, however, which was based on a skull (see Barnes, 1984:11, 12). de Muizon (1983) suggested that the Late Pliocene age Peruvian species, *Pliopontos littoralis* was very closely related to Recent *Pontoporia blainvillei* and might have evolved from *Pontistes rectifrons.* I accept the idea that *Pontoporia, Pontistes,* and *Pliopontos* are related, and *Pontivaga* must be considered as an odontocete of uncertain affinities until a mandible of *Pontistes rectifrons* has been compared with it.

In the classification I propose here, the family Pontoporiidae includes three subfamilies. The nominate subfamily Pontoporiinae includes Recent *Pontoporia blainvillei,* the closely related Pliocene Peruvian *Pliopontos littoralis* de Muizon, 1983, and the Pliocene Argentinian species, *Pontistes rectifrons* Burmeister, 1885. These species all have symmetrical cranial vertices. *Parapontoporia,* the sole genus in the subfamily Parapontoporiinae, has teeth, rostrum, and some cranial characters like *Pontoporia,* but has an asym-

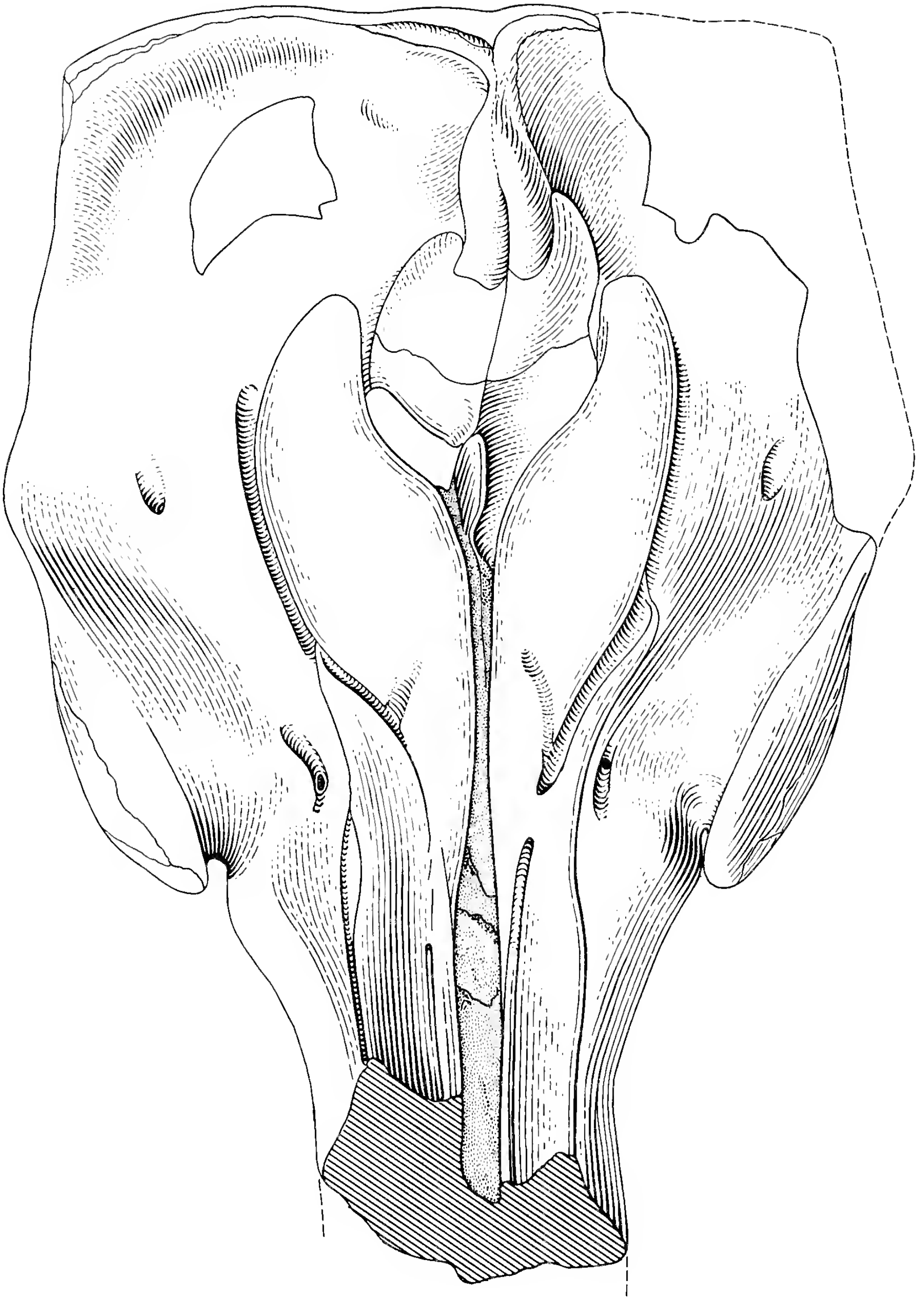

Figure 11. *Parapontoporia wilsoni*, new species, holotype, UCMP 83790, partial skull, dorsal view, natural size.

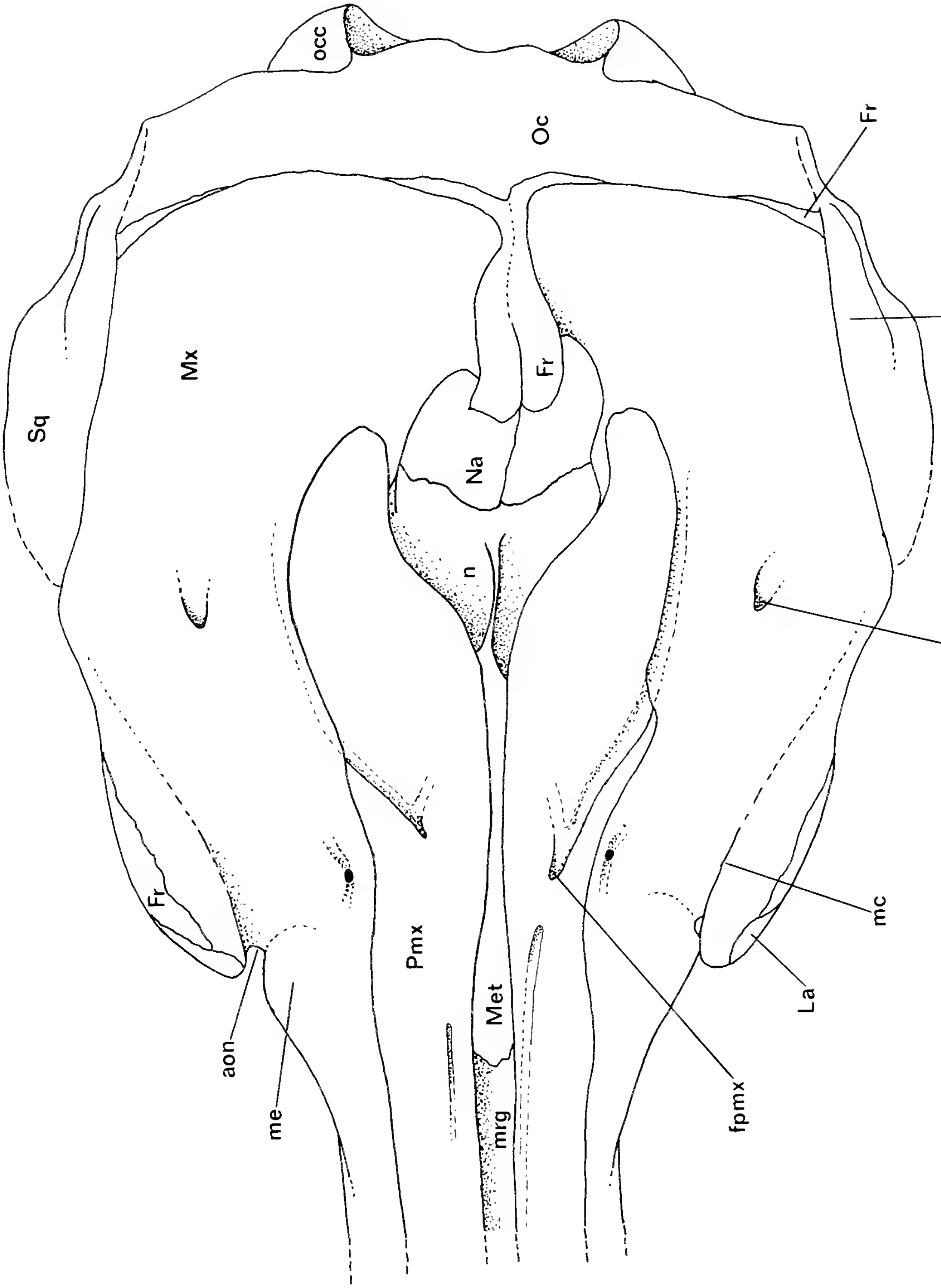

Figure 12. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCMP 83790, dorsal view, natural size.

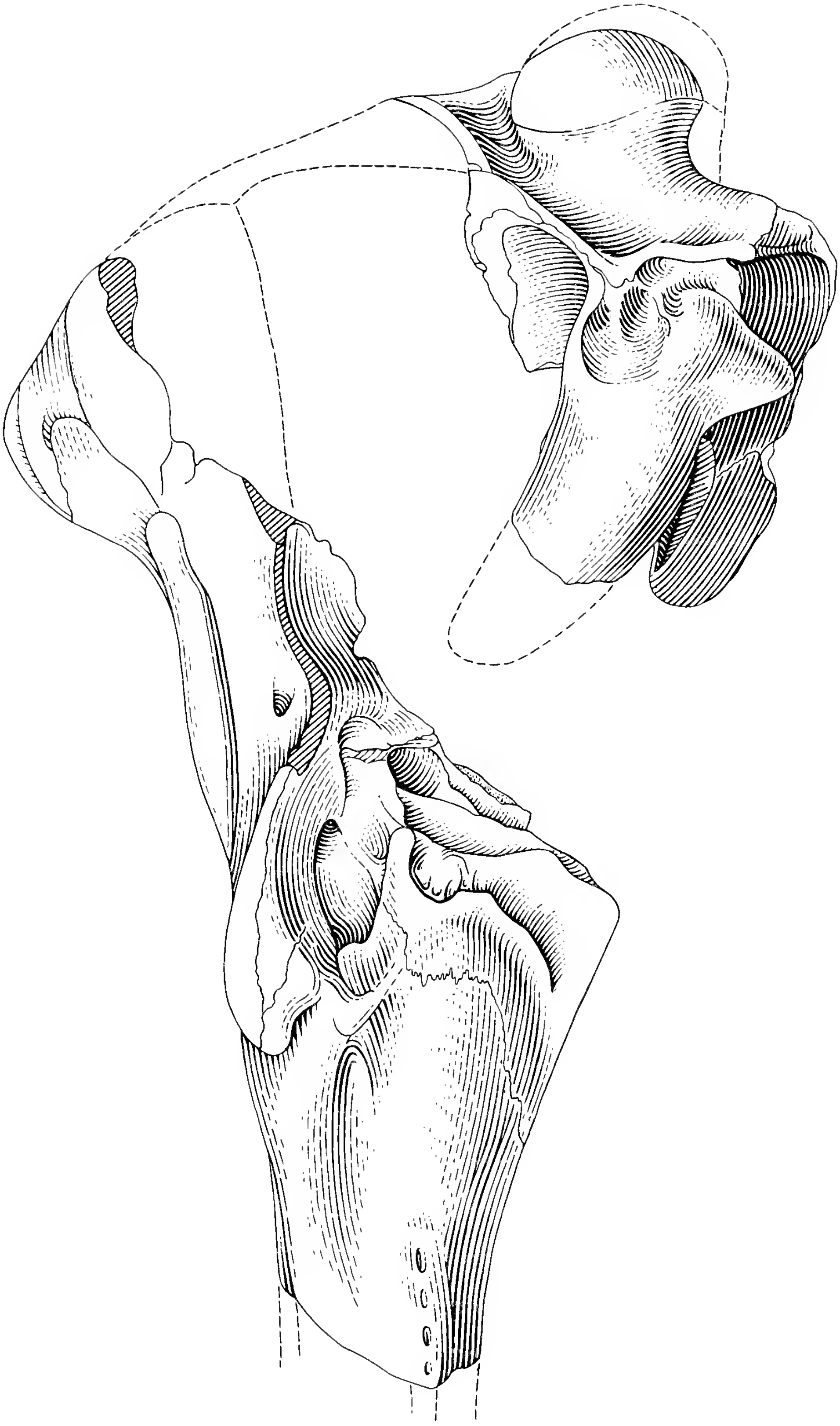

Figure 13. *Parapontoporia wilsoni,* new species, holotype, UCMP 83790, partial skull, left lateral view, natural size.

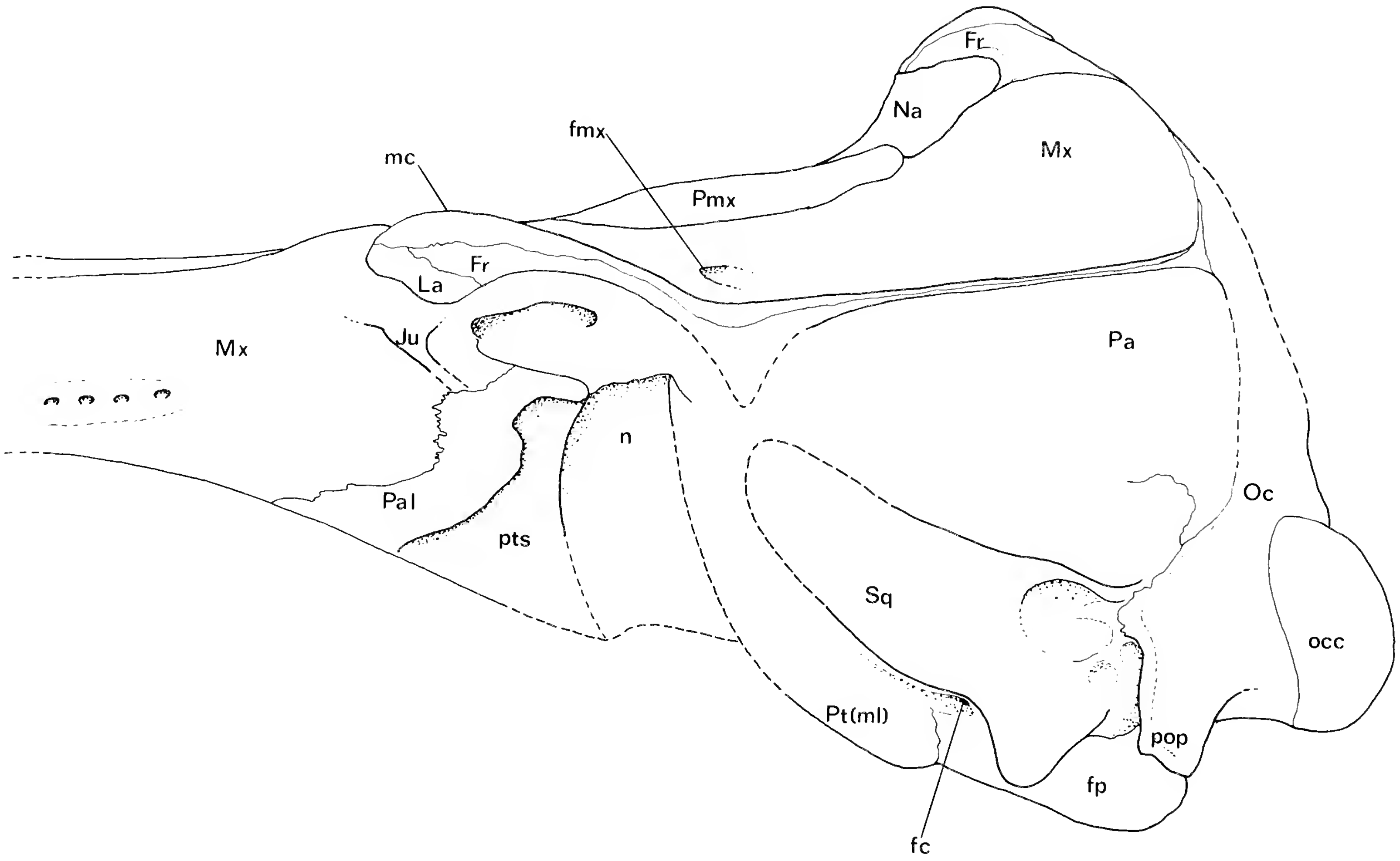

Figure 14. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCMP 83790, left lateral view, natural size.

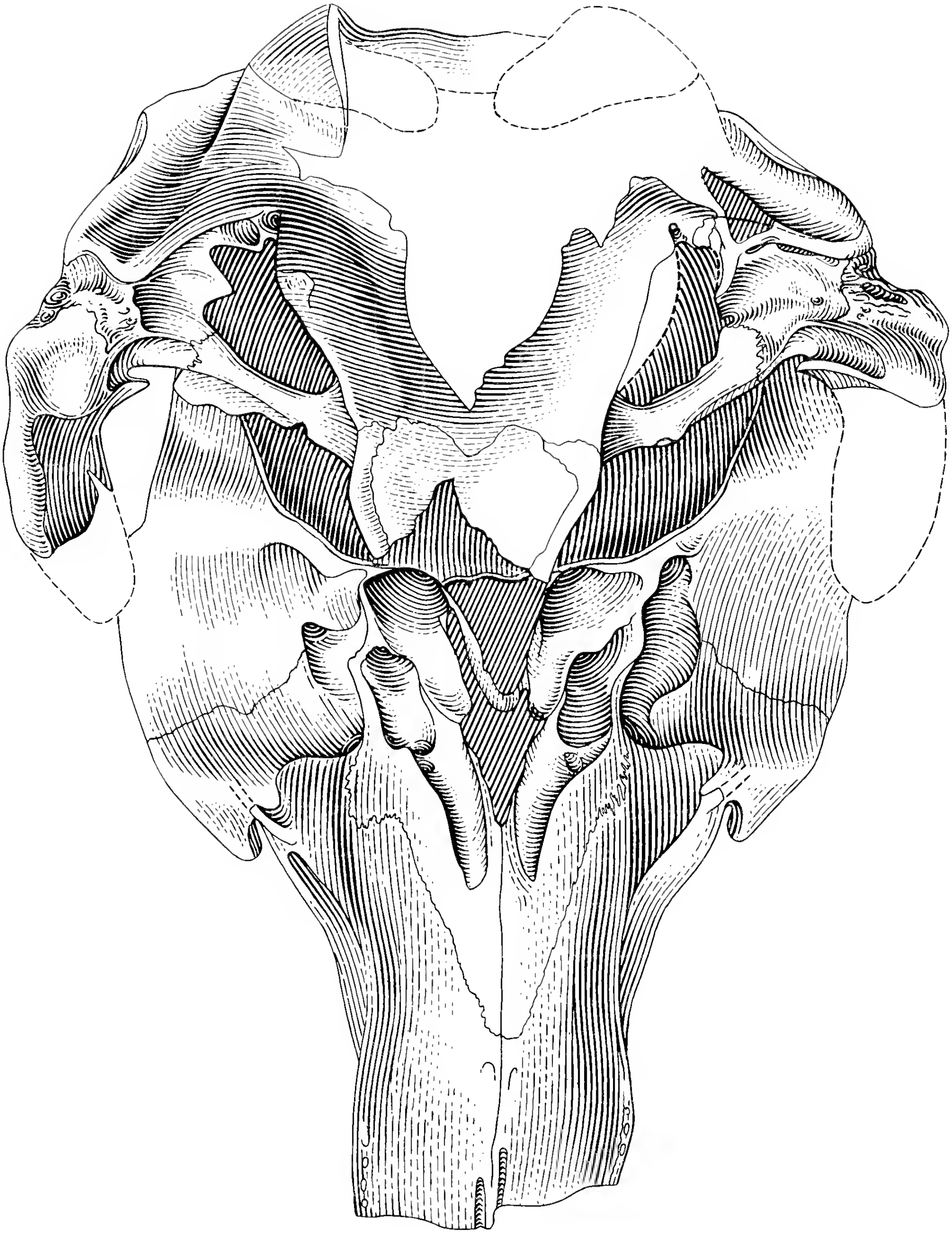

Figure 15. *Parapontoporia wilsoni,* new species, holotype, UCMP 83790, partial skull, ventral view, natural size.

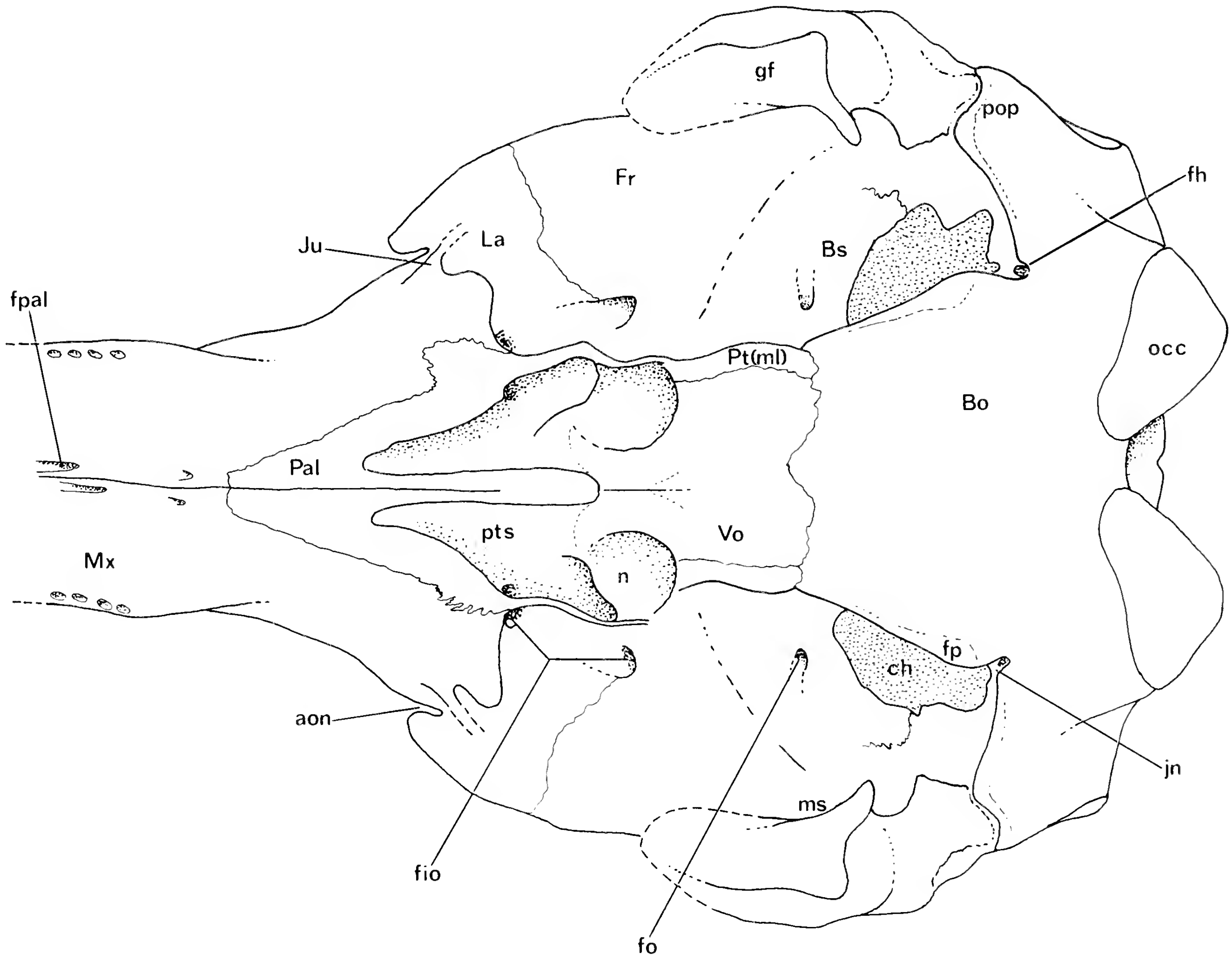

Figure 16. *Parapontoporia wilsoni*, new species, restoration of partial skull based on holotype, UCMP 83790, ventral view, natural size.

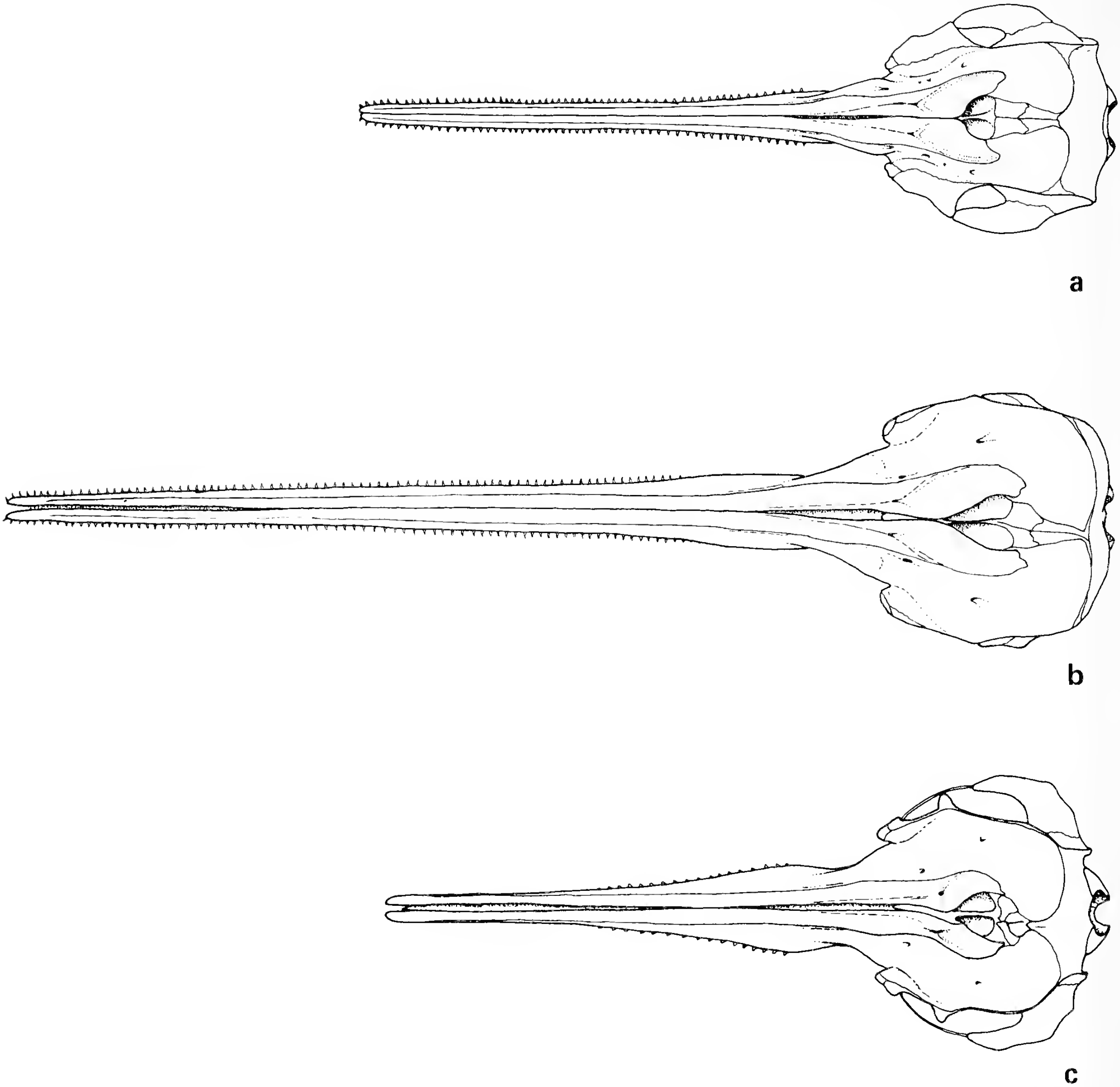

Figure 17. Skulls of Pontoporiidae: **a,** *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844); **b,** *Parapontoporia sternbergi* (Gregory and Kellogg, 1927); **c,** *Lipotes vexillifer* Miller, 1918. (**a** after Flower, 1869:pl. 28, fig. 3; **b** after Fig. 7b, this paper; **c** after Brownell and Herald, 1972:fig. 1.)

metrical cranial vertex and some other derived cranial characters like *Lipotes. Parapontoporia,* therefore, is in many ways intermediate between *Pontoporia* and *Lipotes.* The latter was designated by Zhou, Qian, and Li (1979) as the type genus of a new family, the Lipotidae. To reflect the close relationships and to balance the classification, I recognize the Lipotinae as a third subfamily of Pontoporiidae.

Zhou, Zhou, and Zhao (1984) described a fossil that is possibly Miocene in age as an extinct member of the Lipotidae, calling it *Prolipotes yujiangensis.* All that is known of the species is the holotype mandible fragment, but the specimen does have morphology very similar to the extant *Lipotes vexillifer.* Odontocete mandibles generally have fewer diagnostic characters than do skulls, and as a rule it is unwise to make taxonomic inferences from them. There is nothing in the morphology of *P. yujiangensis,* however, that would preclude a possible relationship between it and *L. vexillifer,* and I provisionally classify both species in the same subfamily.

In summary, the family Pontoporiidae includes three subfamilies: the Pontoporiinae containing *Pontoporia blainvillei* and extinct taxa (*Pontistes rectifrons, Pliopontos littoralis*) that have symmetrical crania, very long rostra, and extreme polydonty; the Parapontoporiinae including species of *Parapontoporia,* which have asymmetrical crania, very long rostra, and extreme polydonty; and the Lipotinae including *Lipotes vexillifer,* which has an asymmetrical cranium, shorter rostrum, and only moderate polydonty (Fig. 17). The fossil *Prolipotes yujiangensis* may belong to the latter subfamily, but no cranial material is known that could confirm this. The family Pontoporiidae is united by a unique suite of shared derived characters as given in the family diagnosis.

The deep grooves on the lateral sides of the dentaries in fossil *Parapontoporia sternbergi* and Recent *Pontoporia blainvillei* are convergent derived characters (autapomorphies). I base this conclusion on two lines of evidence. (1) The most primitive, and chronologically oldest species of the genus *Parapontoporia, P. pacifica,* has no mandibular grooves. Instead it has a shallow longitudinal sulcus on each dentary. Deep mandibular grooves are present, however, in the chronologically youngest species, *P. sternbergi* (Figs. 20d, e). (2) Each dentary of Recent *Pontoporia blainvillei* has only one mental foramen in the mandibular groove, and this enters the groove at its posterior end. In *Parapontoporia* each dentary has four or five foramina that are spaced out along the length of the mandible. This is the case in species of *Parapontoporia* both with and without a mandibular groove, and is the primitive (plesiomorphic) condition among odontocetes.

In *Pontoporia blainvillei,* and apparently also in *Parapontoporia sternbergi,* the nerves and blood vessels emerging from the mental foramina would lie in these grooves, and presumably derive some measure of protection from them. Therefore, the function of the mandibular grooves is the same in both genera, but their origins are separate.

I believe that the unique features of the teeth of *Pontoporia blainvillei* and *Parapontoporia* spp. are shared derived (synapomorphic) characters because even the earliest species of *Parapontoporia, P. pacifica,* has them. The rugose texture of the enamel on the teeth of *Lipotes vexillifer* and *Prolipotes yujiangensis* is probably a primitive character. Many primitive odontocetes have rugose enamel, and this I regard as a carryover from earlier squalodonts and agorophiids. Most modern species have smooth enamel, the derived condition. *Inia geoffrensis,* often classified with *Lipotes vexillifer* in earlier works, has rugose enamel, but the posterior teeth have very large lingual shelves and the dentition is otherwise not very much like that of *Lipotes vexillifer.* Teeth of both *Lipotes vexillifer* and *Prolipotes yujiangensis* have a slightly swollen shoulder on the root, and this is a derived character that is shared with *Pontoporia blainvillei* and *Parapontoporia* spp.

An asymmetrical cranial vertex that is offset to the left side is a convergent derived character that has appeared separately in different groups of odontocetes at different times. Prior to Late Miocene time, representatives of most odontocete families, with the exception of such groups as sperm whales (Physeteridae) and beaked whales (Ziphiidae), had symmetrical cranial vertices and narial regions. *Lipotes vexillifer* and *Parapontoporia* spp. have, among other shared, derived cranial characters, asymmetrical cranial vertices and asymmetrical bones around the external nares. The cranial vertices of *Pontoporia blainvillei* and the fossil species of Pontoporiinae, however, are symmetrical, as well as being lower and more elongate anteroposteriorly than those of *Parapontoporia* spp. or *Lipotes vexillifer.* Because *Pontoporia blainvillei* has asymmetrical nasal diverticula (Schenkken, 1972) and because so many of its other features are derived, I suspect that its cranial symmetry is not primitive, but is a reversal from an earlier asymmetrical condition.

If the above arguments are accepted as valid and *Pontoporia, Parapontoporia,* and *Lipotes* are indeed closely related, then there are at least two possible diagrams that would show their interrelationships, depending on which of the above characters are considered to be shared and derived versus convergent and derived.

In the most parsimonious scheme, and the one that I prefer (Fig. 18), the similar structures of the teeth of *Parapontoporia* and *Pontoporia* are interpreted as shared derived characters (synapomorphies) and the deep mandibular grooves as convergent derived characters (autapomoprhies). The asymmetrical cranial vertex of *Parapontoporia* spp. and *Lipotes vexillifer,* while being a derived character relative to more primitive odontocetes, is the shared primitive character state (symplesiomorphy) for Pontoporiidae, and the symmetrical cranial vertex of *Pontoporia* (and fossil Pontoporiinae) is a unique derived character (autapomorphy), being secondarily symmetrical and a reversal from the asymmetrical condition.

Another possible interpretation of relationships (Fig. 19) is one in which the symmetrical cranial vertex of *Pontoporia blainvillei* is considered to be primitive for the family, and the asymmetrical vertices of *Parapontoporia* spp. and *Lipotes vexillifer* are shared derived characters. This is more consistent with traditional ideas about acquisition of cranial asymmetry in odontocete families, but requires an assumption that in addition to deep mandibular grooves being convergent, as in the first case above, that the unusual *Pontoporia*-like teeth and the very long rostrum are the primitive character state for Pontoporiidae. In that case the lesser tooth count, thick, short rostrum and mandible, and rugose tooth enamel of *Lipotes vexillifer* are derived characters and all of these would then necessarily be interpreted as secondary reversals back to the primitive odontocete condition. In each of the two possible schemes of relationships discussed above, the intermediate position of *Parapontoporia* spp. and the polarity of characters and inferred interrelationships of its included species remain unchanged.

Within the genus *Parapontoporia,* the most primitive species is Late Miocene *P. pacifica,* with no mandibular grooves and no rostral basin (Figs. 20a, d). The approximately contemporaneous species, *P. wilsoni,* however, is more derived and has a very deep rostral basin (apomorphy), but

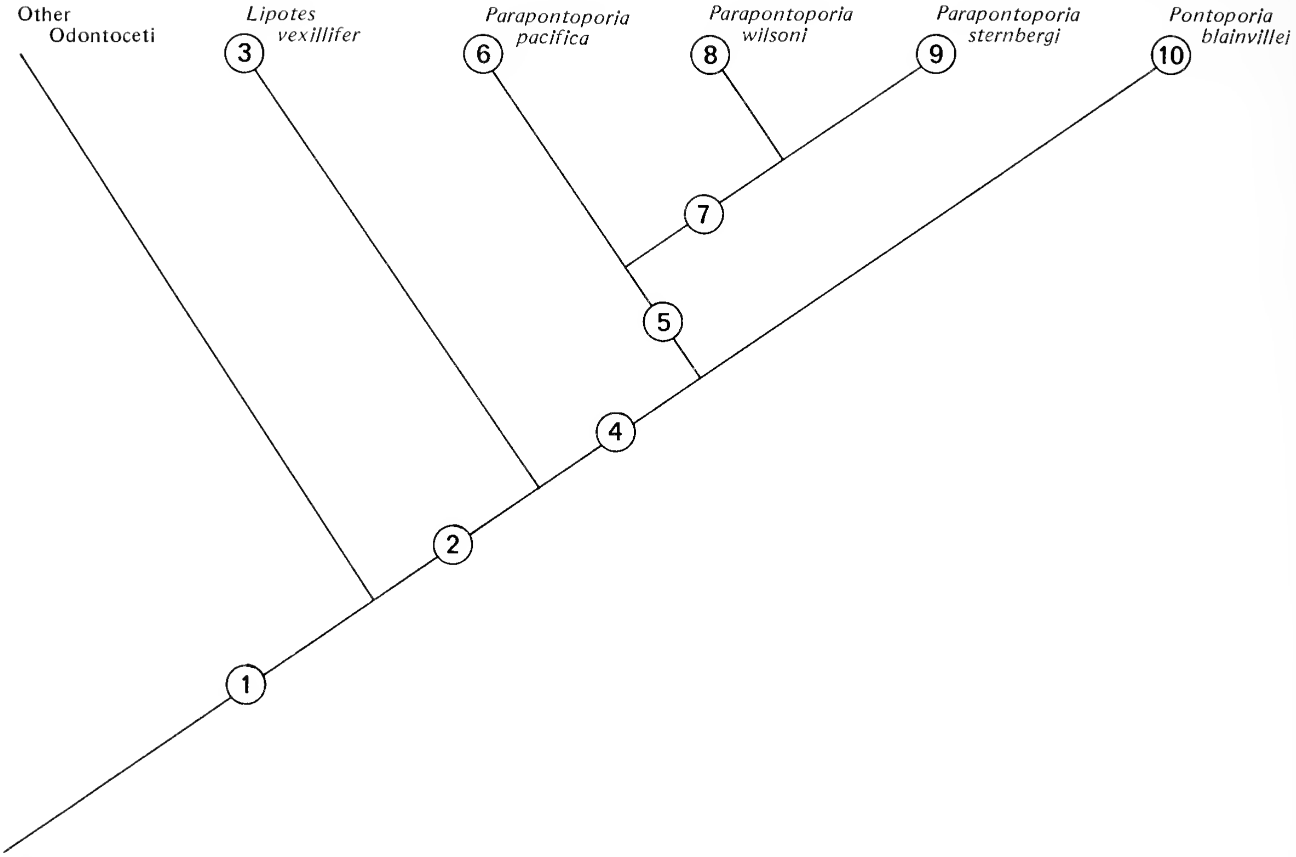

Figure 18. Diagram of the most parsimonious scheme of relationships among taxa of Pontoporiidae, with the fewest implied convergences and evolutionary reversals, but requiring the assumption that the cranial symmetry of *Pontoporia blainvillei* is the result of a secondary reversal from an earlier asymmetrical condition, a contradiction to traditional ideas regarding odontocete evolution. Characters marking the dichotomies are as follows: (1) The primitive state for Odontoceti is a symmetrical cranial vertex. (2) An asymmetrical cranial vertex (apomorphy) is presumed to be the primitive character state of the earliest members of the Pontoporiidae. The family is differentiated from all other groups of Odontoceti, including all other families within the superfamily Platanistoidea, by the shared characters given in the family diagnosis. Interrelationships of the other platanistoid families are insufficiently understood, within the context of the analysis presented here, to be shown separately in this scheme. (3) *Lipotes vexillifer* retains a relatively short, thick rostrum and mandible, and rugose enamel on the teeth as primitive characters (subfamily Lipotinae, presumably including *Prolipotes yujiangensis*, but the species is insufficiently known to include on the diagram). (4) *Parapontoporia* and *Pontoporia* share as synapomorphies: polydonty, *Pontoporia*-like teeth, extremely long rostrum and mandible, and a bony wall in the orbit formed by a posterior extension of the lateral lamina of the pterygoid and, at least in part, also by posterior extensions of the palatine and maxilla. These characters are shared by the subfamilies Parapontoporiinae and Pontoporiinae. (5) Exceptionally long rostrum, extreme polydonty (80–82 teeth in each side of each jaw in contrast with 48–61 in *Pontoporia blainvillei*) are autapomorphies for the genus *Parapontoporia* (subfamily Parapontoporiinae). (6) The most primitive species in the genus. (7) Basin formed on the proximal part of the rostrum; a derived character shared by *P. wilsoni* and *P. sternbergi.* (8) Very deep rostral basin (autapomoprhy), otherwise more primitive than *P. sternbergi,* especially in having a braincase that is less foreshortened anteroposteriorly (less telescoped). (9) Anteroposteriorly compressed (more telescoped) cranium, more vertical narial passages, more elevated and more transversely compressed cranial vertex, and deep mandibular grooves are autapomorphies of *P. sternbergi.* The rostral basin is shallower than in *P. wilsoni,* and in this regard *P. sternbergi* is more primitive. (10) *Pontoporia blainvillei* has the following autapomorphies: vomer not exposed on palate, spiracular plates convex and elevated, posterior premaxillary terminations shortened, shallow squamosal fossa between zygomatic process of squamosal and braincase. Where preserved, these characters are also present in the fossil species, *Pontistes rectifrons* and *Pliopontos littoralis,* but the scope of this study does not include a more detailed analysis of the relationships of the latter species (subfamily Pontoporiinae).

a mandible has not been found and it is not known whether or not it had lateral grooves (Fig. 20b). These two species represent two lines of descent within the genus. The much younger species, the Late Pliocene *P. sternbergi,* has deep mandibular grooves (apomorphy), but only a shallow rostral basin (Figs. 20c, e). Morphologically and temporally it could have evolved from *P. pacifica.* It would have had to have undergone an evolutionary reversal, a shallowing of the rostral basin, to have evolved from *P. wilsoni.* The braincase of *P. sternbergi* is anteroposteriorly compressed (apomorphy) when compared with that of *P. wilsoni* (Fig. 21). Because *P. pacifica* is so primitive, it undoubtedly had an anteroposte-

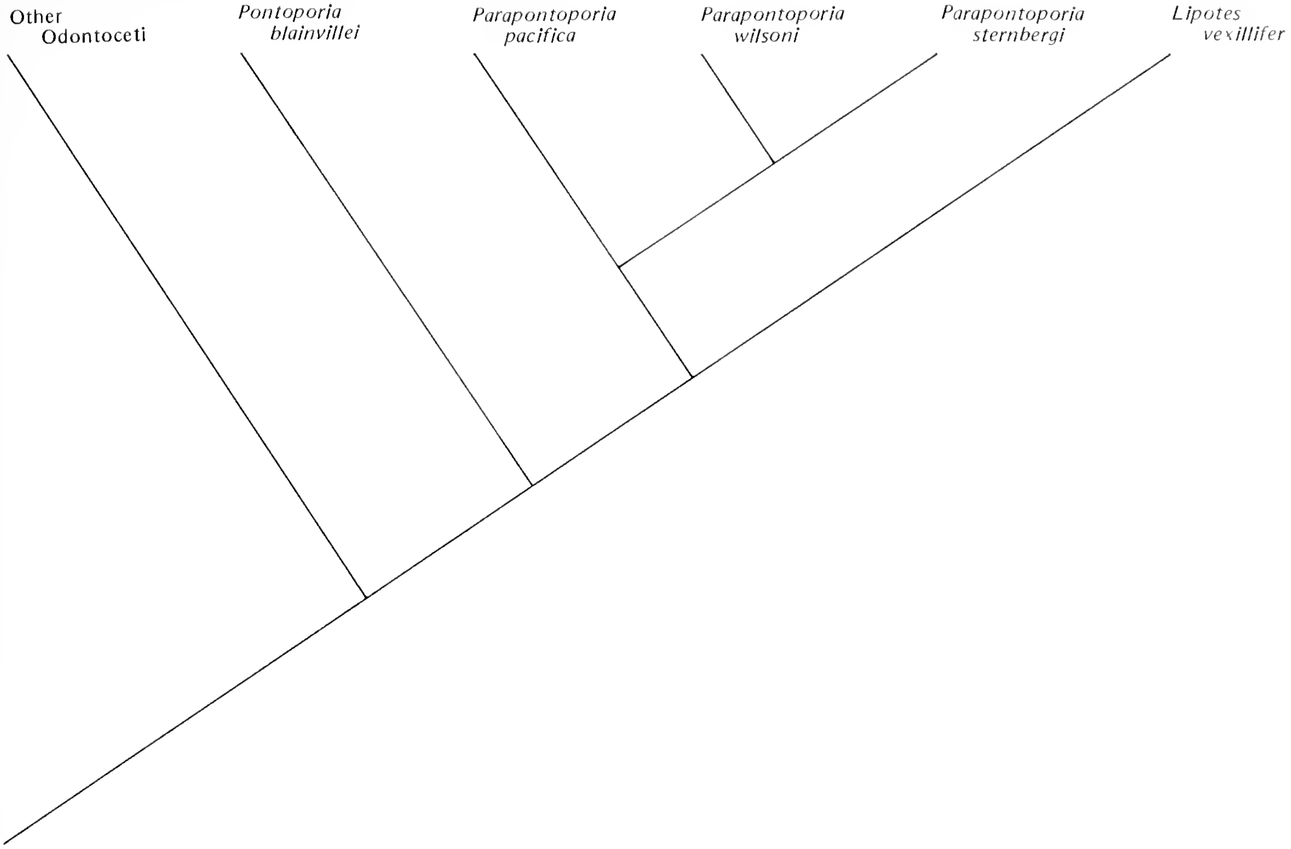

Figure 19. An alternative, less parsimonious interpretation of relationships among taxa of Pontoporiidae. In this scheme the symmetrical cranial vertex of *Pontoporia blainvillei* would be considered as the primitive character state for the family Pontoporiidae, as it is for primitive odontocetes, and the asymmetrical cranial vertices of *Parapontoporia* spp. and *Lipotes vexillifer* would be synapomorphic. This arrangement would suggest, however, that many other characters were the result of convergent evolution of derived states (e.g., long rostra, mandibular grooves, polydonty, and the *Pontoporia*-like teeth in *Pontoporia blainvillei* and *Parapontoporia* spp.) or of evolutionary reversals back to primitive states (e.g., short rostrum, low tooth count, and rugose enamel on teeth of *Lipotes vexillifer*).

riorly elongate braincase with proportions like that of *P. wilsoni,* and if *P. pacifica* were ancestral to *P. sternbergi,* such anteroposterior compression could plausibly have occurred within the lineage in the elapsed time interval of several millions of years.

CLASSIFICATION

Class Mammalia Linnaeus, 1758
  Order Cetacea Brisson, 1762
    Suborder Odontoceti Flower, 1867
      Superfamily Platanistoidea (Gray, 1863) Simpson, 1945
        Family Pontoporiidae (Gill, 1871) Kasuya, 1973
          Subfamily Lipotinae (Zhou, Qian, and Li, 1979), NEW RANK AND CONTEXT
            Prolipotes Zhou, Zhou, and Zhao, 1984
              Prolipotes yujiangensis Zhou, Zhou, and Zhao, 1984. ?Miocene, China
            Lipotes Miller, 1918
              Lipotes vexillifer Miller, 1918. Recent, China
          Subfamily Parapontoporiinae Barnes, 1984
            Parapontoporia Barnes, 1984
              Parapontoporia pacifica Barnes, 1984. Latest Miocene, Baja California
              Parapontoporia wilsoni, NEW SPECIES. Latest Miocene, California
              Parapontoporia sternbergi (Gregory and Kellogg, 1927). Late Pliocene, California
          Subfamily Pontoporiinae (Gill, 1871) Barnes, 1984
            Pontistes Burmeister, 1885
              Pontistes rectifrons (Bravard, 1884). Pliocene, Argentina
            Pliopontos de Muizon, 1983
              Pliopontos littoralis de Muizon, 1983. Early Pliocene, Peru
            Pontoporia Gray, 1846
              Pontoporia blainvillei (Gervais and d'Orbigny, 1844). Recent, Atlantic coast of South America

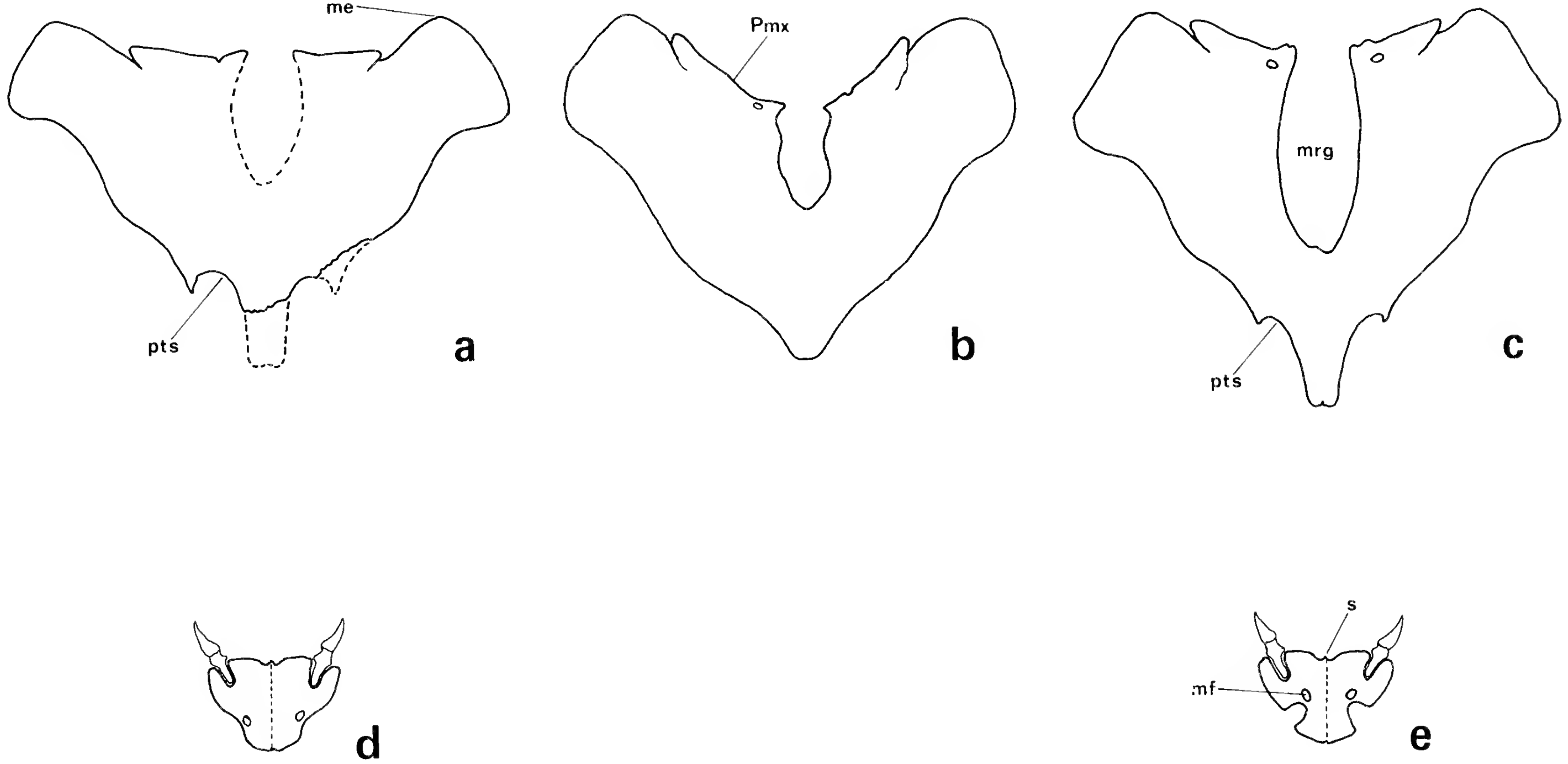

Figure 20. Comparisons of cross sections through the proximal part of the rostrum of **a,** *Parapontoporia pacifica* Barnes, 1984; **b,** *P. wilsoni,* new species; **c,** *P. sternbergi* (Gregory and Kellogg, 1927); and through mandibles at mid-length of the symphyseal area of **d,** *P. pacifica;* and **e,** *P. sternbergi;* all natural size.

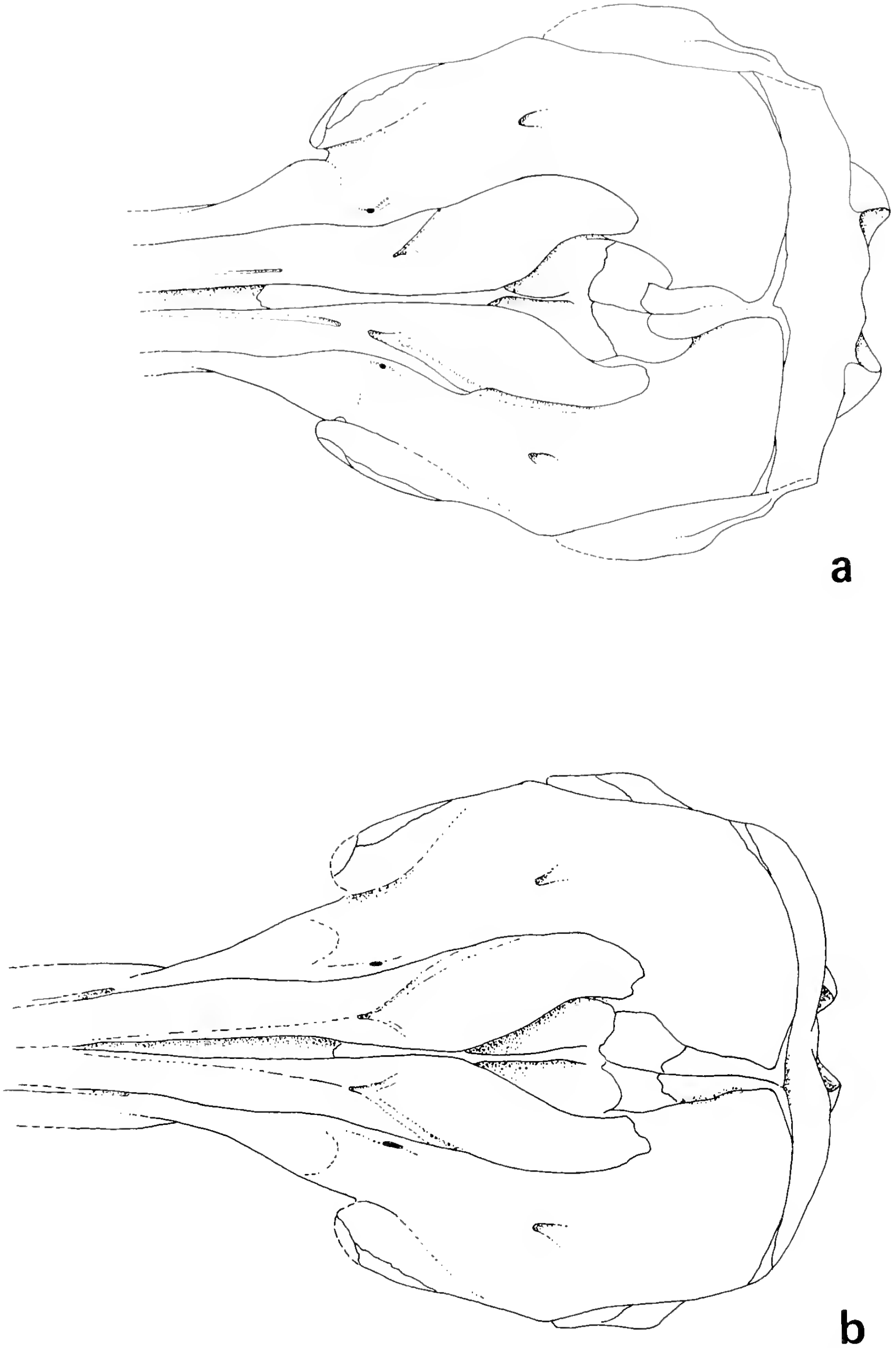

Figure 21. Dorsal views of braincases of two species of *Parapontoporia;* **a**, *P. wilsoni*, new species, based on the holotype; **b**, *P. sternbergi* (Gregory and Kellogg, 1927), based on referred specimens, principally LACM 6238; reduced to the same cranium length.

Use of either of two family group names, Pontoporiidae (or Pontoporiinae) and Stenodelphinae (incorrectly emended to Stenodelphininae), has varied among authors, depending, in some cases, upon their acceptance or rejection of the notion that *Pontoporia* Gray, 1846, is a valid senior synonym of the genus name *Stenodelphis* d'Orbigny and Gervais, 1847. Especially during the early 1900's it was understood by many authors that *Pontoporia* was a preoccupied name, and *Stenodelphis* was the preferred usage. More recently, *Pontoporia* has been confirmed as valid (Hershkovitz, 1961), and in recent literature is the commonly used generic name.

The family group name based upon *Pontoporia*, Pontoporiidae, is available from Gill's (1871) first use of Pontoporiinae as a monotypic subfamily of the Platanistidae. The following year Gill (1872) reclassified the Pontoporiinae as a subfamily in the family Delphinidae. Gray (1871) used the incorrectly formed family name Pontoporiadae, which he classified in the suborder Delphinoidea with the families Iniidae, Delphinidae (including phocoenids), Grampidae, Globicephalidae, Orcadae (*sic*) (these latter three are now classified as synonyms of Delphinidae), and Belugidae (correctly called Monodontidae). True (1908) recognized the genus name *Stenodelphis* instead of *Pontoporia*, and therefore proposed the subfamily Stenodelphinae which he classified in the family Delphinidae. He was followed in this by Miller (1923), Kellogg (1928), and many subsequent authors, including myself (Barnes, 1977), who, however, employed the incorrectly emended form of the name, Stenodelphininae. Simpson (1945) used the same incorrectly formed name, but classified the subfamily with the subfamilies Iniinae and Platanistinae in the family Platanistidae. Rice (1967) recognized the same hierarchy and ranks as did Simpson, but substituted the earlier and correct name, Pontoporiinae. Kasuya (1973) used Gill's name at the family rank, Pontoporiidae, and he classified the family in the superfamily Plantanistoidea, in which he also included the families Iniidae (including *Lipotes*) and Platanistidae. Zhou, Qian, and Li (1979) erected the new monotypic family Lipotidae for *Lipotes*, which had previously been classified in either Iniidae or Iniinae, and Zhou (1982) classified Lipotidae, Iniidae, Pontoporiidae, and Platanistidae as four separate families in the superfamily Platanistoidea.

In summary, each of the living genera, *Pontoporia, Lipotes, Inia,* and *Platanista,* has been the basis for establishment of a family group name. Their ranks in published classifications have varied between subfamily and family, and they have usually been classified in the family Platanistidae or the superfamily Platanistoidea correspondingly. *Pontoporia* has also commonly been classified in Delphinidae, and *Lipotes* and *Inia* have usually been classified together in the family Iniidae or subfamily Iniinae. In my classification *Lipotes* is related to *Pontoporia* and classified in the Pontoporiidae, not the Iniidae. Iniidae and Platanistidae are, therefore, separate families.

CONCLUSIONS

The Parapontoporiinae are an extinct Late Miocene and Pliocene eastern North Pacific subfamily of the dolphin family Pontoporiidae and are represented by one genus, *Parapontoporia* Barnes, 1984. This extremely long-snouted genus is morphologically and zoogeographically intermediate between the living marine franciscana or La Plata dolphin, *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), of the southwest Atlantic and the living freshwater beiji or white flag dolphin, *Lipotes vexillifer* Miller, 1918, of China. The latter two are each placed in separate subfamilies of the Pontoporiidae, called the Pontoporiinae and Lipotinae, respectively. There is a possible fossil relative of *Lipotes* Miller, 1918, *Prolipotes yujiangensis* Zhou, Zhou, and Zhao, 1984, of questionable Miocene age from China. Two South American Pliocene fossil species, *Pontistes rectifrons* (Bravard, 1884) and *Pliopontos littoralis* de Muizon, 1983, are related to *Pontoporia. Lipotes* had previously been classified in the Iniidae, or more recently put in its own monotypic family, Lipotidae.

The genus *Parapontoporia* has been documented previously by several published references to fossils from the latitudes between approximately 27° and 38° north in California and Baja California under such identifications as *Stenodelphis* (or "*Stenodelphis*") *sternbergi* Gregory and Kellogg, 1927. Among these scattered records are at least three species, each of which is characterized and diagnosed in the present study.

The oldest and most primitive of these is *Parapontoporia pacifica* Barnes, 1984, from the latest Miocene age lower member of the Almejas Formation on Isla Cedros, Baja California, and which is between approximately 6 and 8 million years old. An approximately contemporaneous species, *Parapontoporia wilsoni,* new species, from low in the Purisima Formation in central California differs from *P. pacifica* notably by having a deep basin on the proximal surface of the rostrum. A much younger species from the Late Pliocene age lower member of the San Diego Formation at San Diego, California, *P. sternbergi* (Gregory and Kellogg, 1927), is between approximately 2 and 4 million years old. This species does not have as deep a rostral basin as *P. wilsoni* and has a more anteroposteriorly compressed braincase. It also has deep mandibular grooves that are not present in *P. pacifica.* The species is the most abundantly represented of the three, and is the only one known by a complete skull.

At least two schemes of interrelationships are possible between Lipotinae, Parapontoporiinae, and Pontoporiinae, each of which would require the assumption that reversals have occurred in the evolution of certain characters. The most parsimonious hypothesis is that *Lipotes* is the most primitive, that *Pontoporia* is the most derived, and that *Parapontoporia* is intermediate between them. This would indicate that *Pontoporia* had secondarily acquired a symmetrical cranial vertex, that the asymmetrical cranial vertices of *Lipotes* and *Parapontoporia* are a shared primitive character for the family and that the unusual teeth of *Parapontoporia* and *Pontoporia* are shared and derived. In this case the rugose enamel on the teeth and the shorter and thicker rostrum and mandible of *Lipotes* would be primitive characters, and the deep mandibular grooves of living *Pontoporia blainvillei* and the Late Pliocene fossil *Parapontoporia sternbergi* are convergent and derived.

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CONTRIBUTIONS IN SCIENCE

THE GEOLOGY OF THE RÍO BENI: FURTHER EVIDENCE FOR HOLOCENE FLOODING IN AMAZONIA

Kenneth E. Campbell, Jr., Carl David Frailey,
and Jorge Arellano L.

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THE GEOLOGY OF THE RÍO BENI: FURTHER EVIDENCE FOR HOLOCENE FLOODING IN AMAZONIA

Kenneth E. Campbell, Jr.,[1] Carl David Frailey,[2] and
Jorge Arellano L.[3]

ABSTRACT. Quaternary sediments exposed in outcrops along the Río Beni, Bolivia, were deposited in two widely separated depositional realms. The Sierra Realm extends northeastward from the front range of the Andes for 15–30 km, whereas the Monte Realm encompasses all of the northernmost lowlands of Bolivia. In both depositional realms the same stratigraphic sequence occurs: a lower unit of clays with numerous channel-fill deposits at its base, capped by two upper units of clayey silts and fine sands. The sediments of the Sierra Realm were derived from the Bolivian Andes; by all indications they were deposited contemporaneously with those of the Monte Realm. The strata within the Monte Realm are correlated with those to the northwest along the Río Acre and Río Juruá, demonstrating that the deposits cropping out along the lower Río Beni represent the easternmost extension of the Iñapari Formation, a series of Holocene alluvial deposits derived from the Peruvian Andes. The geological deposits of northern Bolivia provide supporting evidence for the hypothesis of large-scale Holocene flooding and deposition in southwestern Amazonia. A catastrophic flood resulting from the sudden draining of glacial Lake Titicaca is proposed to account for some of this flooding and several geological features found in southwestern Amazonia.

RESUMEN. Los sedimentos cuaternarios expuestos en los estratos a lo largo del río Beni, Bolivia, fueron depositados por dos amplias y separadas corrientes deposicionales. La "Corriente de la Sierra" que se extiende al noreste, desde el frente de la Cordillera de los Andes por 15 a 30 kilómetros y la "Corriente del Monte" que abarca la parte septentrional de las tierras bajas de Bolivia. En ambas corrientes deposicionales se presenta la misma secuencia estratigráfica: una unidad inferior de arcillas con numerosos canales basales y dos unidades superiores compuestos por arcillas limosas y arenas finas. Los sedimentos de la Corriente de la Sierra derivan de los Andes bolivianos, por todas las evidencias ellos fueron depositados contemporaneamente a aquellos de la Corriente del Monte. Los estratos de la Corriente del Monte son correlacionados con los descritos para el río Acre y río Juruá al noroeste de Bolivia, de manera que los depósitos que se presentan aguas abajo del río Beni representan la extensión más oriental de la Formación Iñapari, una serie de depósitos aluviales holocénicos derivados de los Andes peruanos. Los depósitos geológicos septentrionales de Bolivia son las evidencias que sustentan la hipótesis de una inundación a gran escala durante el holoceno y la deposición de sedimentos en la Amazonía meridional. Una inundación catastrófica resultante del repentino drenaje del lago glacial Titicaca es propuesto para explicar varios rasgos geológicos encontrados en el sudoeste de la Amazonía.

INTRODUCTION

The Amazon Basin and its neighboring lowlands have yet to receive the in-depth, rigorous geological research warranted a region so important to the South American continent, and indeed, to the world. Occupying an area of over 1,800,000 km^2, these vast lowlands are the subject of only a small number of modern publications that discuss their geological features and sediments (e.g., see citations in Petri and Fúlfaro, 1983). Almost all recent geological research has been directed toward the discovery and exploitation of petroleum resources; without recognized economic importance Quaternary geology has been very neglected. Aside from economics, there are clear reasons for the lack of geological research in Amazonia. The region is quite inaccessible, and river travel is the only means of movement over vast areas. Furthermore, the tropical forest, the largest such forest in the world, provides an almost complete cover of thick vegetation that limits the study of surficial deposits to river cutbanks and well cores. Nevertheless, geological research can and must be carried out in these still remote lands in order that a solid core of geological data is developed upon which future planned developments within the region can be based. This is particularly critical because preliminary data indicate that both

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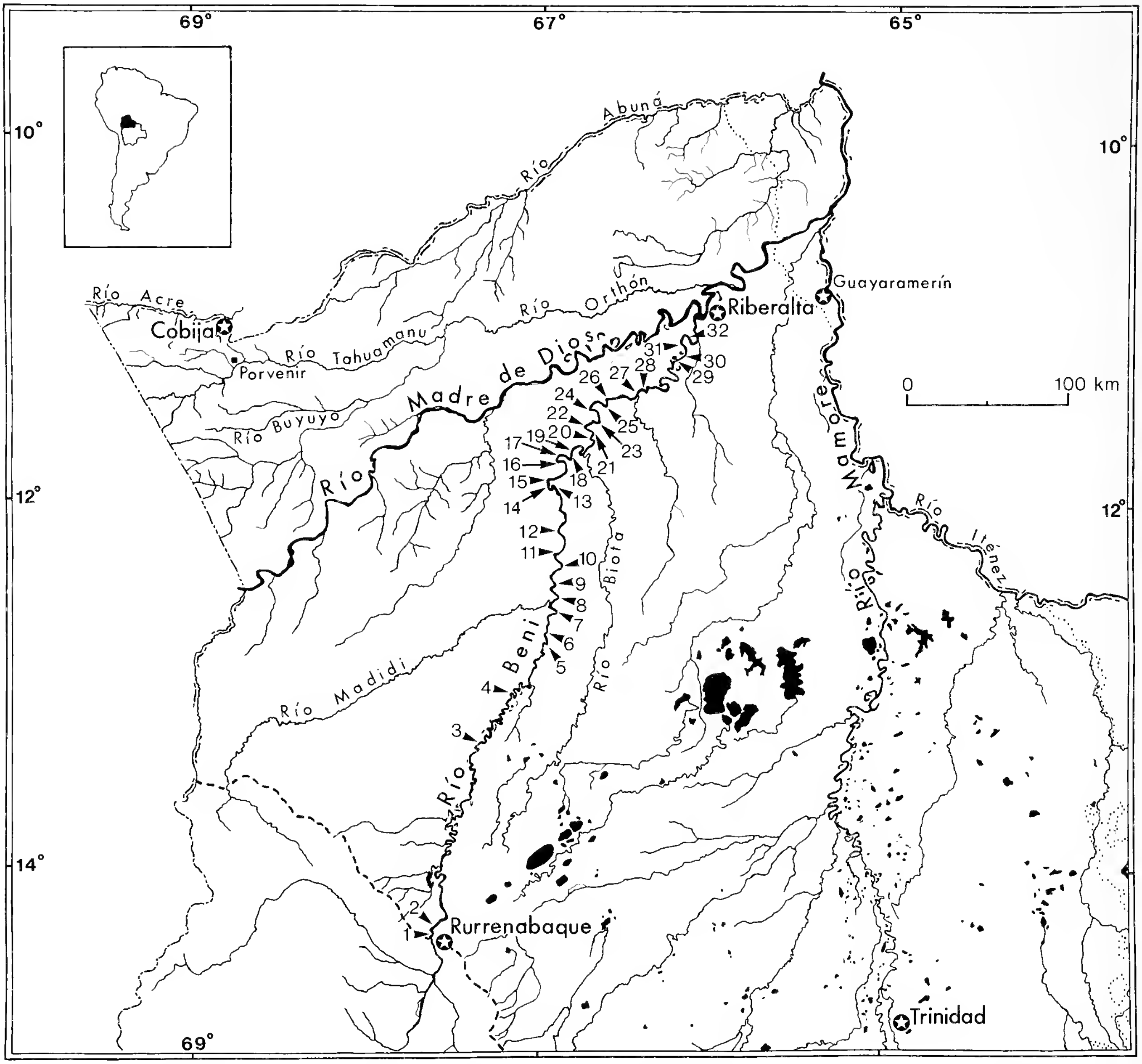

Figure 1. Map of northern Bolivia showing the major outcrops along the Río Beni, with distances in river-km (Servicio de Hidrografia Naval, 1969) from Rurrenabaque: **1.** Buena Vista (11); **2.** Altamarani (17); **3.** San Pablo (227); **4.** San Roque (281); **5.** Santa Catalina (345); **6.** Guayaros (355); **7.** Candelaria (372); **8.** Cavinas (385); **9.** Carmen Alto (395); **10.** Centro Navidad (410); **11.** Barraca Rosario (421); **12.** Fortaleza (437); **13.** Ciudad California (465); **14.** Etea (473); **15.** Florencia (481); **16.** Remanso (496); **17.** Santa Elena (503); **18.** Santa Rosa (510); **19.** Sabacón (515); **20.** Mamorébey (544); **21.** San Manuel (548); **22.** San Martin (557); **23.** Peña Amarilla (569); **24.** Maracaibo (581); **25.** Concepción (595); **26.** San Miguel (601); **27.** Brisa (621); **28.** Barrio Lindo (627); **29.** Palermo (694); **30.** Candelaria (702); **31.** Libertad (720); **32.** Puerto Gonzelo Moreno (728); Riberalta (758). The dashed line (---; lower left) indicates the northeastern limit of the front range of the Andes, while the dotted line (.....; upper and lower right) indicates western limit of Brazilian Shield. Base map: Mapa Geológico de Bolivia, 1978, Yacimientos Petroliferos Fiscales Bolivianos and Servicio Geológico de Bolivia, La Paz.

long-held assumptions (e.g., Abelson, 1983) and newly popular hypotheses (e.g., see papers in Duellman, 1979; Prance, 1982) concerning the late Cenozoic history of Amazonia require reevaluation.

The alluvial deposits covering the vast region of the Amazon Basin and its neighboring lowlands have always been considered to be Pliocene to Pleistocene in age (e.g., Jenks, 1956; Ruegg, 1956; Kummel, 1948; ONERN, 1977; Petri and Fúlfaro, 1983; RADAMBRASIL, 1976, 1977). Recently, however, Campbell and Frailey (1984, in press) have demonstrated that the alluvial deposits cropping out along the Río Acre in southwestern Amazonia and, by correlation, similar deposits cropping out along the upper Río Juruá about 500 km northwest of the Río Acre, are Holocene in age. Alluvial deposits forming three distinct units rest upon deeply weathered Tertiary deposits along both of these rivers. A characteristic basal clay-pebble conglomerate containing reworked Tertiary vertebrate fossils and fossil wood is a widespread, but discontinuous, feature of these Holocene deposits. The deeply weathered Tertiary deposits are indicative of late Pleistocene soil profiles, the upper portions of which were removed prior to the deposition of the Holocene deposits.

To account for this blanket of Holocene sediments occurring over such a broad area, Campbell and Frailey (1984, in press) proposed that massive flooding resulted from the melting of the Andean glaciers at the end of the Pleistocene. They suggested that this flooding scoured the uppermost soil zones developed on Tertiary strata in the region, depositing the clay-pebble conglomerate in its wake. Further, they proposed that this massive early flooding was followed by three distinct cycles of deposition and erosion, the last period of erosion being that which is underway today. Dates of about 5000 yr B.P. and about 2800 yr B.P. were proposed to mark the ends of the first two periods of deposition.

To determine if similar deposits of comparable age and lithology occurred farther to the south, a geological survey crossing the northern lowlands of Bolivia from the front range of the Andes to the Brazilian Shield was executed via the Río Beni in July 1983. We reasoned that if three distinct cycles of Holocene deposition and erosion had occurred over wide areas of the Amazonian lowlands, evidence for these cycles should exist in the alluvial deposits extending eastward from the front range of the Andes. We conducted the survey by means of boat travel from Rurrenabaque, at the base of the front range (Fig. 1), to Riberalta, at the confluence of the Río Beni and Río Madre de Dios. The transect was completed by road between Riberalta and Guayaramerín, the latter a town on the Bolivian–Brazilian border.

The survey was hampered by very unusual heavy rains that fell in eastern Bolivia during the dry season of 1983, a local expression of worldwide climatic anomalies occurring at that time (Philander, 1983a, b; Gill and Rasmusson, 1983). These rains maintained the level of the Río Beni over 2 m higher than what is normal for July, possibly preventing us from observing the contact between the basal Quaternary deposits and the underlying Tertiary strata. In other areas of

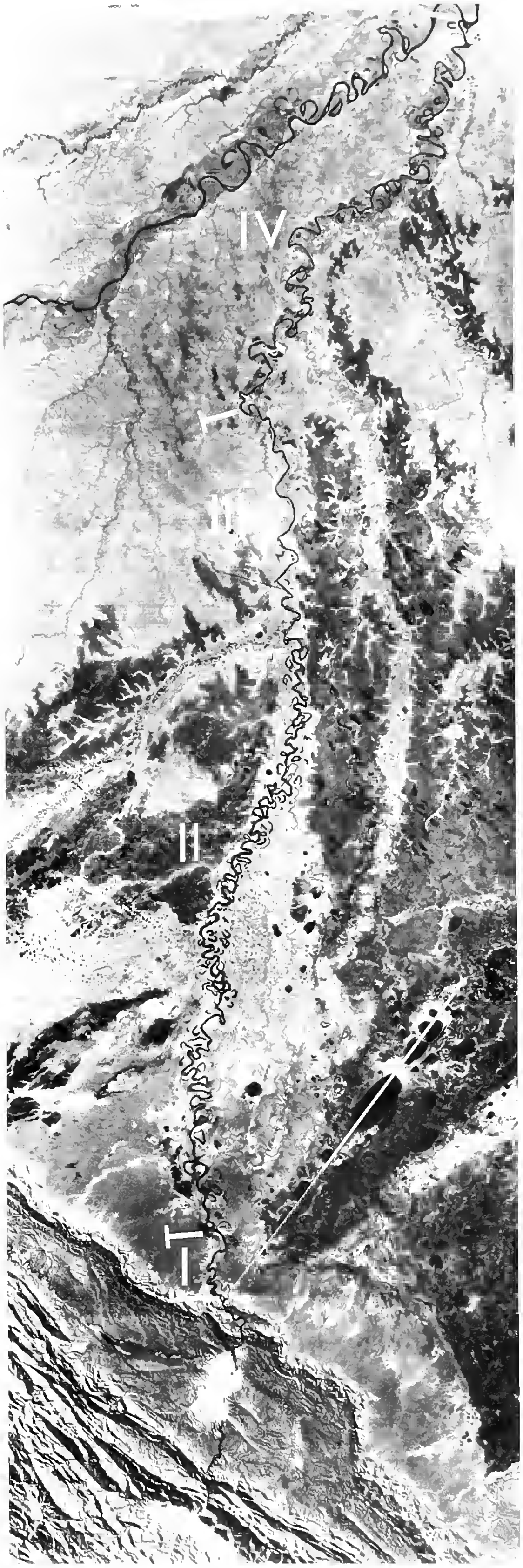

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Figure 2. Satellite photo mosaic showing the course of the Río Beni from the Andes to Riberalta. The four regions of the river discussed in the text are indicated. Northeast of the front range of the Andes the light gray indicates areas slightly higher and better drained than the areas of dark gray to the south. The light gray bands bordering the rivers cutting through areas of dark gray indicate significant natural levees. The white line running through the chain of lakes points directly toward the point of exit of the main channel of the Río Beni from the front range of the Andes.

southwestern Amazonia this contact, if visible at all, is seen only when the rivers are at their lowest level during the dry season. In addition, a newly deposited, deep layer of mud made it very difficult, and in places impossible, to reach the outcrops. All figures of outcrop height are relative to the level of the river at the time we left Rurrenabaque, but unfortunately this level could not be fixed relative to a known datum. The fluctuating level of the river, which rose and fell over 1 m during the course of our trip as the consequence of a single storm, endows all following figures of outcrop height with a degree of error.

GEOLOGY

The eastern lowlands of Bolivia extend through the country from its northern to its southern borders. The Andes flank the lowlands on the west, with the front range in places rising abruptly thousands of meters above the flat, swampy plains. To the east the lowlands are bordered by the low sierras of the Brazilian Shield, and many scattered remnants of the Brazilian Shield stand isolated, surrounded by Quaternary deposits. All of the rivers draining the northern two-thirds of the Bolivian lowlands converge upon the Río Madre de Dios and exit Bolivian territory at its northeastern corner, crossing over the crystalline rocks of the Brazilian Shield. Because the terrain is so flat (e.g., the elevation of Rurrenabaque is 227 m; Cobija, 202 m; Trinidad, 155 m; and Riberalta, 135 m (Instituto Nacional de Estadistica, 1982), the discharge from the rivers draining the eastern cordillera of the Andes cannot be constrained to existing river channels and the lowlands are consequently regularly inundated by seasonal floods. (Note: the Servicio Nacional de Meteorología de Bolivia (in Montes de Oca, 1983) gives the elevations as: Rurrenabaque, 227 m; Cobija, 280 m; Trinidad, 236 m; and Riberalta, 172 m.) The southern one-third of the eastern Bolivian lowlands is, for the most part, an extensive area of swamplands with no external drainage.

The geological deposits cropping out along the Río Beni were formed in two different depositional realms about 180 air-km apart. We consider a depositional realm to be a geographically well-defined area within which deposition of sediments occurred during a specified time, in this case, the Quaternary. The first depositional realm we crossed extends northeastward from the front range of the Andes and is referred to hereafter as the Sierra Realm because of its proximity to the mountains. The second depositional realm encompasses all of the northernmost Bolivian lowlands and is referred to hereafter as the Monte Realm because of its thick cover of tropical forest. The course of the Río Beni east of Rurrenabaque includes about 15 air-km in the Sierra Realm and about 210 air-km in the Monte Realm. The two depositional realms stand out on satellite photographs (Figs. 2, 3) as light gray areas, in contrast to the dark gray of the intervening area which is lower in elevation. The differing shades of gray result from different vegetation types; the lighter grays indicate forests, the darker grays indicate wet savannas or swamplands. The strips of light gray that cross the dark gray areas, and within which lie the river channels, reflect the higher topography of the natural levees bordering the rivers.

In the 180-air-km interval between the two depositional realms only two small outcrops of possible Quaternary deposits were seen. Everywhere else in this interval the banks of the Río Beni are formed exclusively of Recent alluvium with a relatively constant thickness of 2 m. At San Pablo and San Roque (Fig. 1, locs. 3, 4) unstratified, variegated, red, green, and gray clays extended to about 2–3 m above the waterline. These clays are capped by about 1 m of Recent alluvium that forms a flat terrace.

THE SIERRA REALM

The deposits of the Sierra Realm were all derived from the Bolivian Andes immediately to the west. Included are the alluvial fan deposits formed of sediments coming directly off the eastern slopes of the front range and the deposits brought from the valleys of the eastern Andes through the front range by the Río Beni and Río Madidi.

There are only two outcrops along the Río Beni within the Sierra Realm that provide good sections: at Buena Vista and Altamarani, 11 and 17 river-km, respectively, from Rurrenabaque (Fig. 1, locs. 1, 2). The most complete section extends from Altamarani downstream for about 1 km to just above the confluence with the Río Tuihuapa. About 9–10 m thick at its highest, the section consists of three distinct units of unconsolidated alluvial sediments (Fig. 4). The basal unit, Member A, consists of poorly stratified gray, green, and yellow variegated clays about 2 m thick. Channel-fill conglomerates of small pebbles occur in the lower part of this unit. A sharp contact separates these clays from the overlying unit (Member B) of blocky, reddish clayey-silts about 3 m thick, the top of which is marked by two prominent and other smaller dark-gray paleosols. The uppermost unit, Member C, consists of about 4–5 m of fine silts capped by a 20–30-cm-thick layer of black soil.

The same three units occur in the Buena Vista section, but Member C is much thinner, presumably through loss by erosion. In addition, a cobblestone conglomerate passes under Member A at the upriver end of the Buena Vista section. Multiple paleosols are also present at the top of Member B at Buena Vista.

Both the Buena Vista and Altamarani sections occur on the north side of the river, and the terrain extending back from the river's edge is essentially flat. Except for one other outcrop upriver from Buena Vista, also on the north side of the river, the banks of the Río Beni within the Sierra Realm consists of Recent alluvium, about 2 m thick. The third outcrop mentioned did not provide a clear section and was only about 8 m thick. No clastic sediments coarser than sand occur downriver from the Buena Vista section.

For the size of the area drained by the Río Beni and its tributaries, a mountainous region of approximately 67,000 km^2 with peaks up to 7010 m elevation, the quantity of Quaternary river deposits lying east of the front range is remarkably small. Indeed, as can be noted on satellite pho-

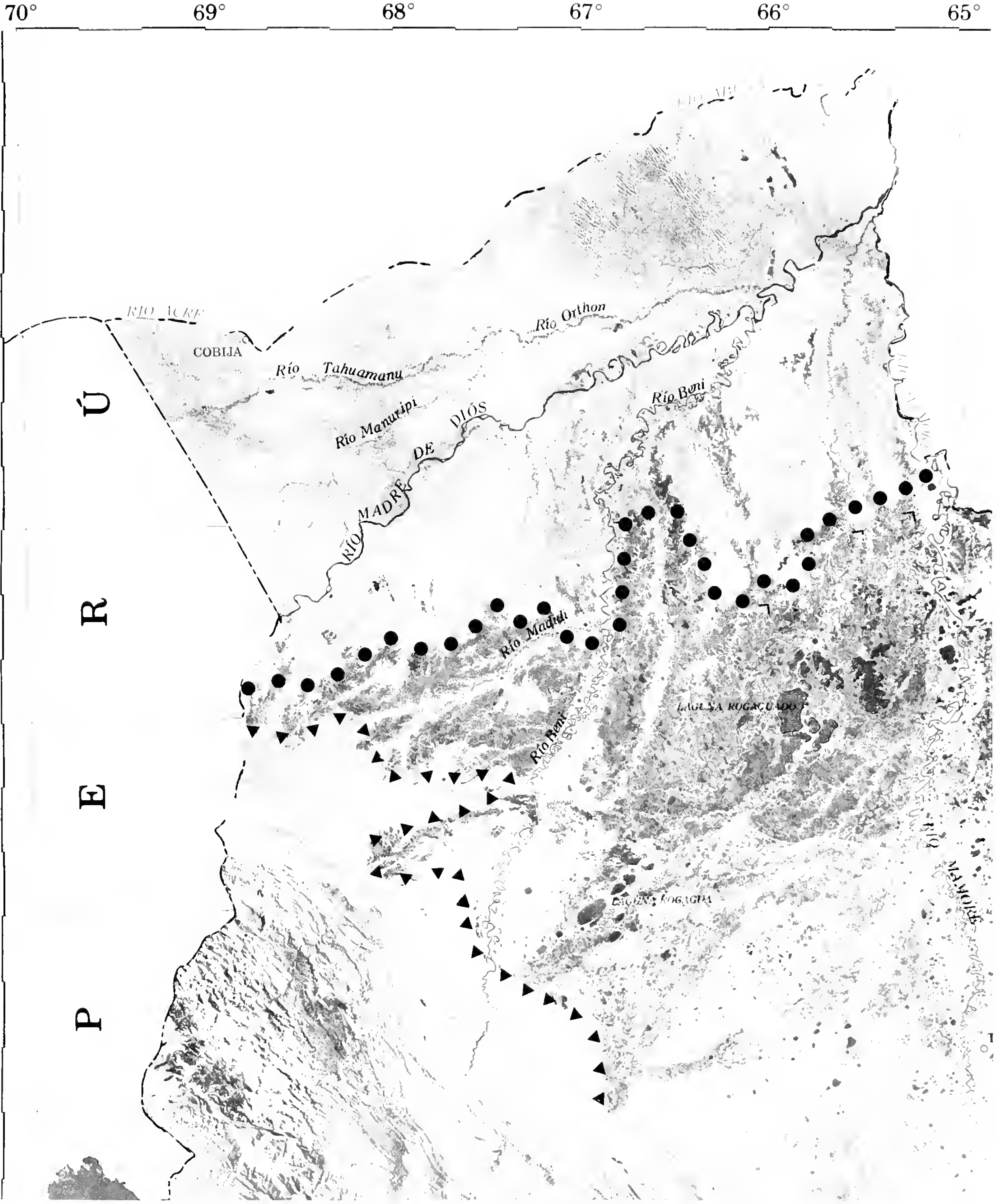

Figure 3. Satellite photo mosaic of northern Bolivia showing the extent of the Sierra and Monte Depositional Realms, the courses of the major rivers, and the linear series of rectangular lakes extending northeastward from Rurrenabaque. The line of dots delimits the southern extent of the Monte Depositional Realm and the line of triangles indicates the eastern limit of the Sierra Depositional Realm. From: Foto-Mosaico Landsat de Bolivia, Edición 1-P.E.B., 1975, Servicio Geológico de Bolivia. Reproduced by permission of the Servicio Geológico de Bolivia.

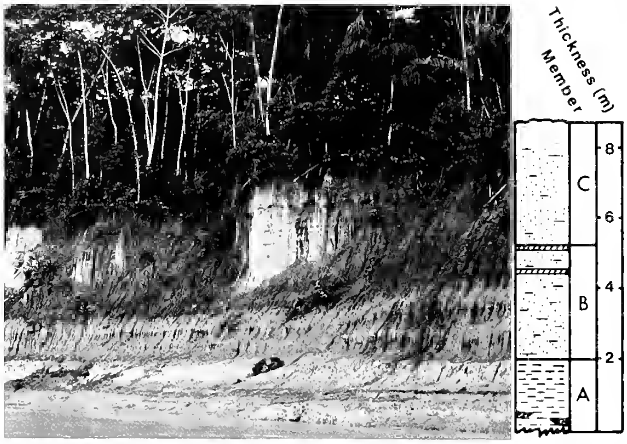

Figure 4. The geological section at Altamarani (Fig. 1, loc. 2) is composed of three units. The lower unit (Member A) of channeled, variably stratified clays is capped by two upper units (Members B and C) of variably stratified, blocky silts, and fine sands. The two dark bands at the top of Member B are prominent paleosols.

tographs (Figs. 2, 3), the eastward extent of the deposits left by the Río Beni at its point of exit from the front range appears to be less than that of the alluvial fan deposits immediately north and south of the river that represent deposition of sediments derived solely from the eastern slopes of the front range. We will return to this absence of expected alluvial deposits later.

THE MONTE REALM

Trending north-northeastward, the Río Beni cuts through the Monte Realm from Santa Catalina (Fig. 1, loc. 5) to its confluence with the Río Madre de Dios at Riberalta. The total areal extent of the Monte Realm is unknown, although from satellite photographs (Fig. 3) it may be inferred to cover approximately 90,000 km^2 in Bolivia. The terrain immediately to the south of the Monte Realm is 15–20 m lower in elevation, flat, swampy, and frequently inundated during the annual rainy season. These areas of lower elevation appear dark on the satellite photos (Figs. 2, 3), in contrast to the lighter color of the better drained Monte Realm.

Outcrops are relatively common along the Río Beni from Santa Catalina to Riberalta, and the geologic sections are all quite similar (see Fig. 1 for major localities). The generalized section (Figs. 5, 6) is composed of three units of unconsolidated alluvial sediments, each similar in lithology to the corresponding unit seen in the Sierra Realm. The basal unit, Member A, consists of about 3–5 m of variably stratified, relatively pure, red, gray, green, and yellow variegated clays. In the lower part of these clays occur many channel-fill deposits composed of fine-grained, well-sorted sands, silts, and clay-ball conglomerates. The size of the multicolored clay balls in the conglomerate range from less than 10 mm to over 250 mm, and they occur both well sorted or poorly sorted, and with or without a silt or sand matrix (Fig. 7a).

Layers of hematite 3–6 cm thick are a distinctive feature of Member A. These occur between the channel deposits in the lower part of the unit and also at the contact with silts and sands of the overlying member. The layers are convoluted in many places (Fig. 8a, b), and represent groundwater deposition of hematite at the contact between differing lithologies.

Members B and C, each about 4–8 m thick, are similar lithologically, being composed of silts and fine sands. In many outcrops the contact between them may be readily distinguished only by sharp color differences (Fig. 5b), but at other localities a distinct disconformity is visible (Figs. 5a, 6). At some outcrops, such as at Ciudad California, channel deposits of sands and clay-ball conglomerates can be seen at the top of Member B. When these channel deposits occur, local layers of hematite may also be present as in Member A, although they are usually much thinner.

The first complete section encountered in the Monte Realm (Santa Catalina, Fig. 5a) differed from those farther down-

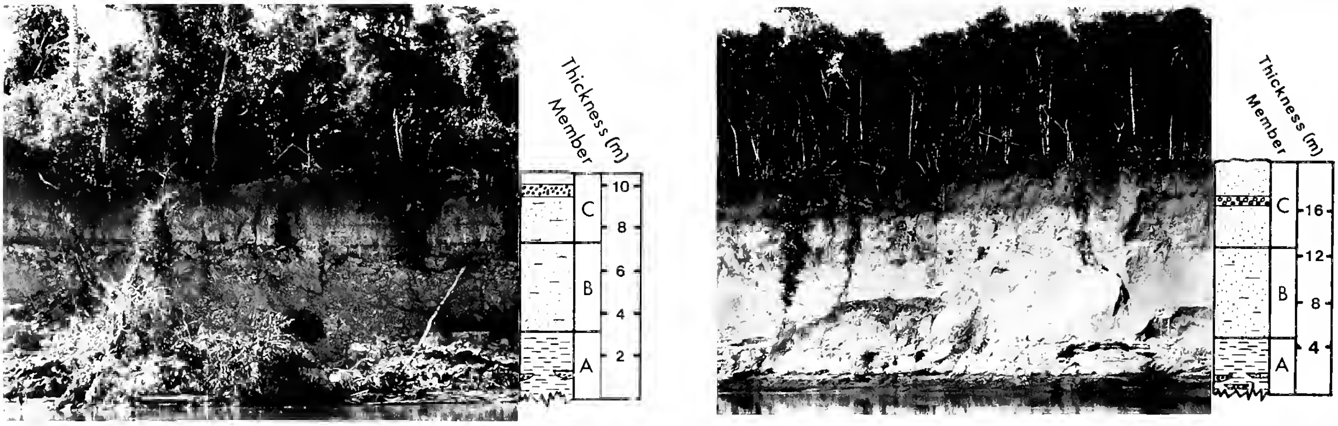

Figure 5. Two geological sections along the Río Beni in the Monte Depositional Realm. **a**(left). Santa Catalina (Fig. 1, loc. 5). **b.** Cavinas (Fig. 1, loc. 8). Both sections show the hematitic concretionary zone in the B zone of the soil profile developed on Member C. The higher clay content of the sediments at Santa Catalina is reflected in the surface texture of the outcrop.

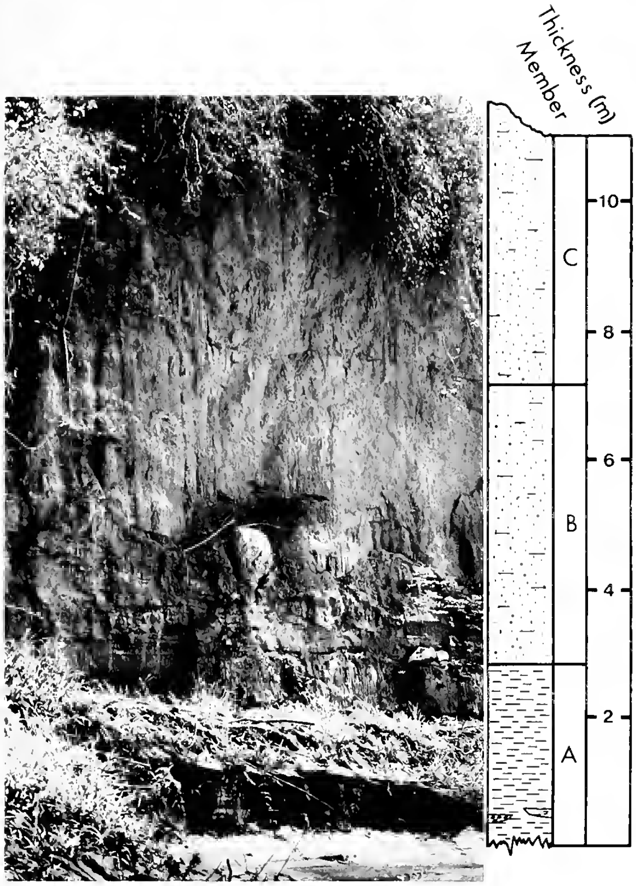

Figure 6. A partial view of the section at San Martin (Fig. 1, loc. 22) clearly shows the two contacts separating the three members of the Iñapari Formation. At this locality the base of Member B shows good stratification.

river (e.g., Cavinas, Fig. 5b) by having a noticeably higher clay content to Members B and C, and by being much thinner. Both of these differences would be expected to occur at the limit of alluvial deposition in what we have come to regard as an environment of deposition similar to a broad delta.

The soil profiles visible in the river cutbanks of the Monte Realm north of its southern limits vary in a consistent, predictable manner with the height of the outcrop, a direct reflection of the length of time the soil has had to develop. The tops of the highest outcrops, here always at an elevation of about 20 m above the level of the river, are taken to represent the original surface formed by the depositional phase prior to the onset of the present cycle of erosion. These outcrops are everywhere characterized by a deep soil profile with a dark red color. Included in this soil profile is a hematitic concretionary zone about 0.5–1 m thick, lying about 2–3 m below the ground surface (Fig. 5b). These hematite deposits differ from the layers of hematite occurring lower in the section at the contacts between different lithologies. Instead of thick, solid layers, the hematite in the soil profiles occurs as agglomerations of small (less than 1 cm diameter) concretions that have in many places grown together. The dark red color of the soil profile was most pronounced at the concretionary zone.

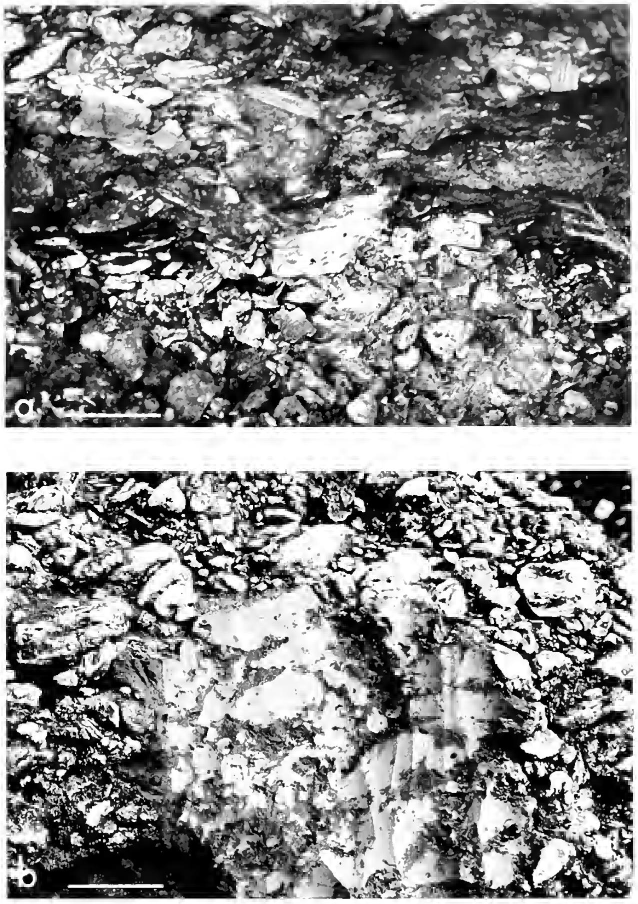

Figure 7. Representative clay-ball conglomerate that occurs in paleochannels within Member B of the Iñapari Formation. **a.** Variably colored clay balls of various sizes with silt and sand matrix; on Río Beni at Ciudad California (Fig. 1, loc. 13). **b.** Unaltered clay balls in well-sorted sand matrix; on Río Acre (Fig. 1), just upstream from the confluence of the Río de los Patos. Scale in each figure equals 10 cm.

This concretionary zone also appears in the thinner sections at the southern limit of the Monte Realm (Fig. 5a), but here it is thinner and does not lie as deep below the surface of the ground. This may reflect the higher clay content of the sediments in this region. Throughout the Monte Realm the A horizon of black humic material of the present soil profile only locally reaches a thickness of more than 15–20 cm.

As in the Sierra Realm, at the major outcrops the terrain extending back from the river's edge usually appears flat, a feature accentuated by the consistent placement of small settlements or villages on these high, isolated reaches of land with river access. The flat tops of the outcrops with incomplete sections indicate rivercut terraces, and within the Monte Realm there are many discontinuous terraces at approximately the same elevations above the river. Two pronounced

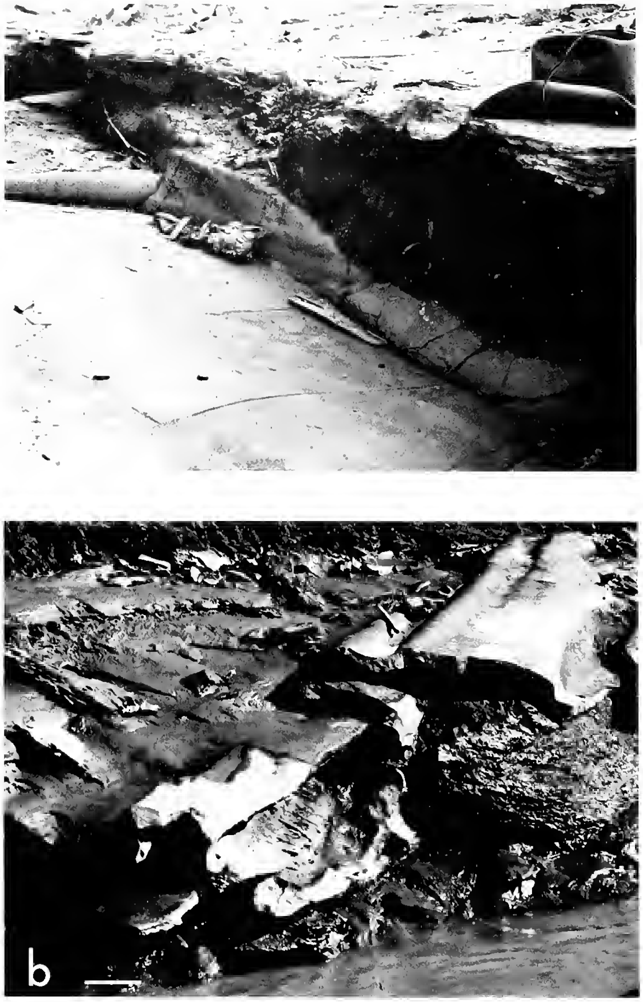

Figure 8. Thick layers of hematite separate Member A of the Iñapari Formation from overlying Member B. In **a,** the hematite layer is shown as it appears in a roadside ditch near the Río Buyuyo (Fig. 1), while in **b** the hematite layer is shown in cross section on the Río Beni near Barraca Rosario (Fig. 1, loc. 11). Note the similarity in surface ribbing and texture. The thickness of the partially mud-covered layer in **b** is 5–6 cm. This hematite layer was observed at almost every outcrop within the Monte Realm where the contact between Members A and B was exposed. Scale equals 15 cm.

terrace levels occurring at several localities along the river are at about 9 and 15 m above the river. In addition to their different elevations, these two terrace levels differ in the soil profiles developed on them. At the 15 m level there is a 1–2 m thick, dark-red soil horizon similar to that seen at the top of the 20 m level, but no hematitic concretionary zone was present. The red color of the B horizon gradually faded into the C horizon and the original colors of the fine silts and sands of Member B or C. The soil profile developed at the 9 m level did not have as dark a red B horizon, nor was it as deep.

The lowest widespread terrace level north of the Río Madidi was at about 3–4 m. This low terrace consisted of an upper 1 m cap of dark silts and sands representing Recent flood deposits and a lower 2–3 m of the variegated red and yellow clays of Member A, into which this terrace had been cut (Fig. 9).

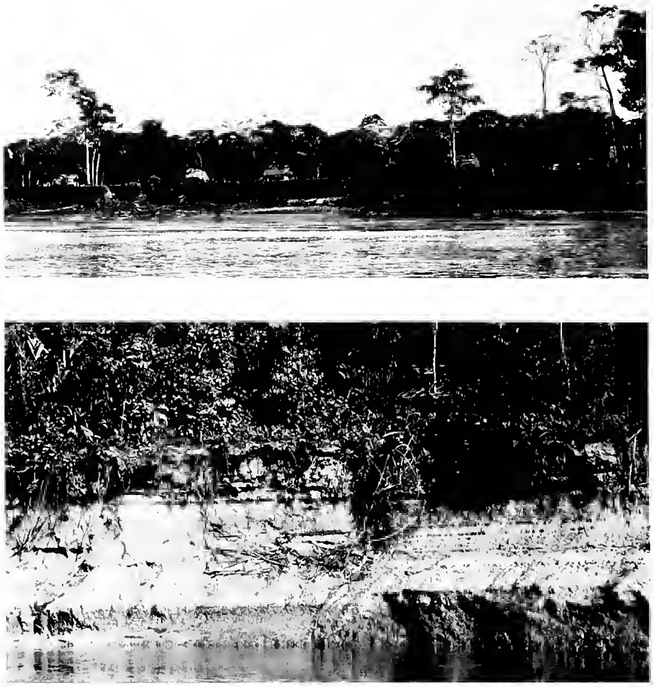

Figure 9. A river terrace at about 3–4 m above the level of the Río Beni. Above, showing cluster of homes on flat terrain; below, showing the 2–3 m of Member A of the Iñapari Formation capped by about 1 m of Recent alluvium. The dark zone at the base of the section reflects the dropping level of the river.

The terrain between Riberalta, on the Río Beni, and Guayaramerín, on the Río Mamore at the border with Brazil, is typical of that of a flat plain dissected by a developing dendritic drainage system. This terrain continues right up to the Río Mamore, but directly across the river loom the northernmost outlying hills of the Sierra dos Parecis, the westernmost range of the Brazilian Shield. Clasts of Shield rocks were found in deposits in Bolivia west of Guayaramerín, but they were not noted in deposits as far west as Riberalta.

CORRELATIONS

The outcrops along the Río Beni can be correlated with those that occur along the Río Acre (Campbell and Frailey, 1984, in press) (Fig. 10). The standard stratigraphic sequence (Fig. 11a), consisting of a basal unit of variably stratified clays with channel-fill deposits of sands and clay-ball conglomerates (Fig. 7b) capped by two thicker units of relatively unstratified, blocky silts and fine sands, is the same along each river. Similarly the three units are separated by disconformities, although along the Río Beni the contact between the upper two units is not always as clear as it is along the Río Acre. Paleochannels occur at the contact between Members B and C in some geologic sections of each river. Un-

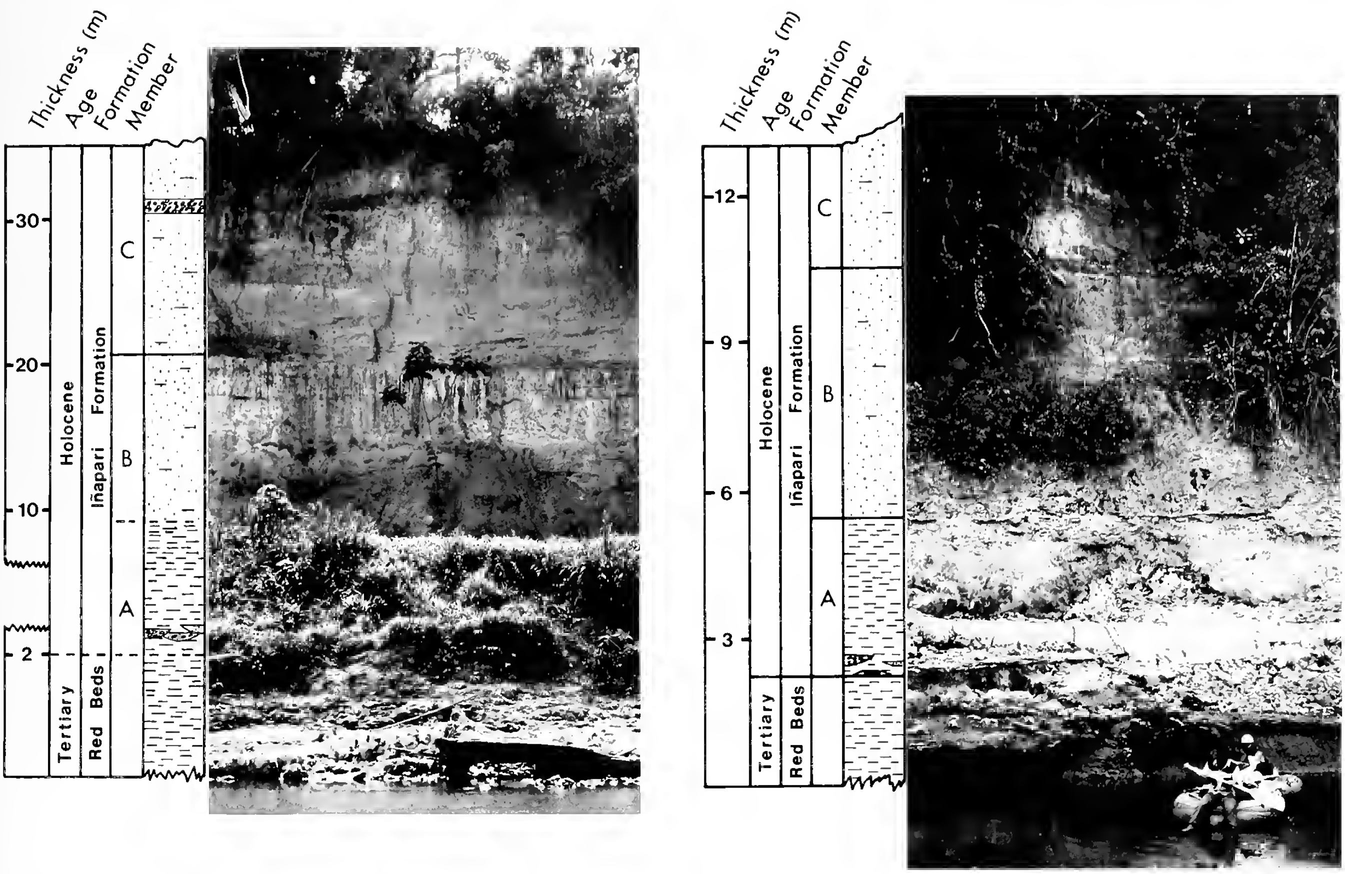

Figure 10. Two geological sections along the Río Acre, demonstrating their similarity to those seen along the Río Beni. **a.** Outcrop at San Lorenzo, about 30 air-km upstream from Iñapari, Peru, showing the various levels of the Iñapari Formation. Tertiary clays are exposed in the foreground. Member A of the Iñapari Formation is covered, but the contact between Members B and C is clear, as is the hematite concretionary zone near the top of Member C. This concretionary zone correlates with that seen in Fig. 5a, b. **b.** Partial section about 50 air-km upstream from Iñapari, Peru. The three members of the Iñapari Formation are clearly seen, as is the contact with the underlying Tertiary strata. The visible layer of hematite occurring at the contact between Members A and B of the Iñapari Formation correlates with that seen in Fig. 8a, b.

fortunately, along the Río Beni the contact between the basal clay unit and the underlying strata could not be seen, so it is not possible to say if the characteristic basal clay-pebble conglomerate occurring along the Río Acre, Río Buyuyo, Río Tahuamanu (Fig. 1), and Río Juruá also occurs along the Río Beni.

The three lithologic units observed along the Río Acre were referred by Campbell and Frailey (1984, in press) to the Iñapari Formation of ONERN (1977). Radiocarbon dates from four samples of wood from Member A of the Iñapari Formation taken at three different localities on the Río Acre ranged from 10,075 ± 150 yr B.P. to 5575 ± 105 yr B.P. (Campbell and Frailey, 1984, in press). We here include the Shiringayoc Formation of ONERN (1977) in the Iñapari Formation. The former was said to occur only along the banks of the rivers, with the latter occurring in broad areas between the rivers in the eastern part of the Departamento de Madre de Dios, Peru, on the frontier with Bolivia. Our field data indicate that the two formations are just one.

The hematite deposits observed along the Río Beni were not noted as a particularly significant feature along the Río Acre at the time of the fieldwork there, primarily because attention was focused on the fossiliferous basal clay-pebble conglomerate. However, these deposits do appear very clearly in field photographs taken at that time. The layered deposits of hematite at the contact between Members A and B of the Iñapari Formation can be seen in Fig. 10b, as well as a similarly prominent layer occurring at the contact between the Holocene and Tertiary strata. A sheet-like layer of hematite was also observed by the senior author in a roadcut leading to a bridge crossing the Río Buyuyo, due south of Porvenir and just east of the border with Peru (Fig. 8a). At this site, the layer of hematite separates the silts of Member B of the Iñapari Formation from the underlying clays of Member A, at the base of which occurs the characteristic clay-pebble conglomerate. The concretionary zone of hematite that occurs in the highest soil profiles along the Río Beni also appears in the complete sections along the Río Acre (Fig. 10a). It may be of interest to note that the nodules of hematite from this concretionary zone were being used as

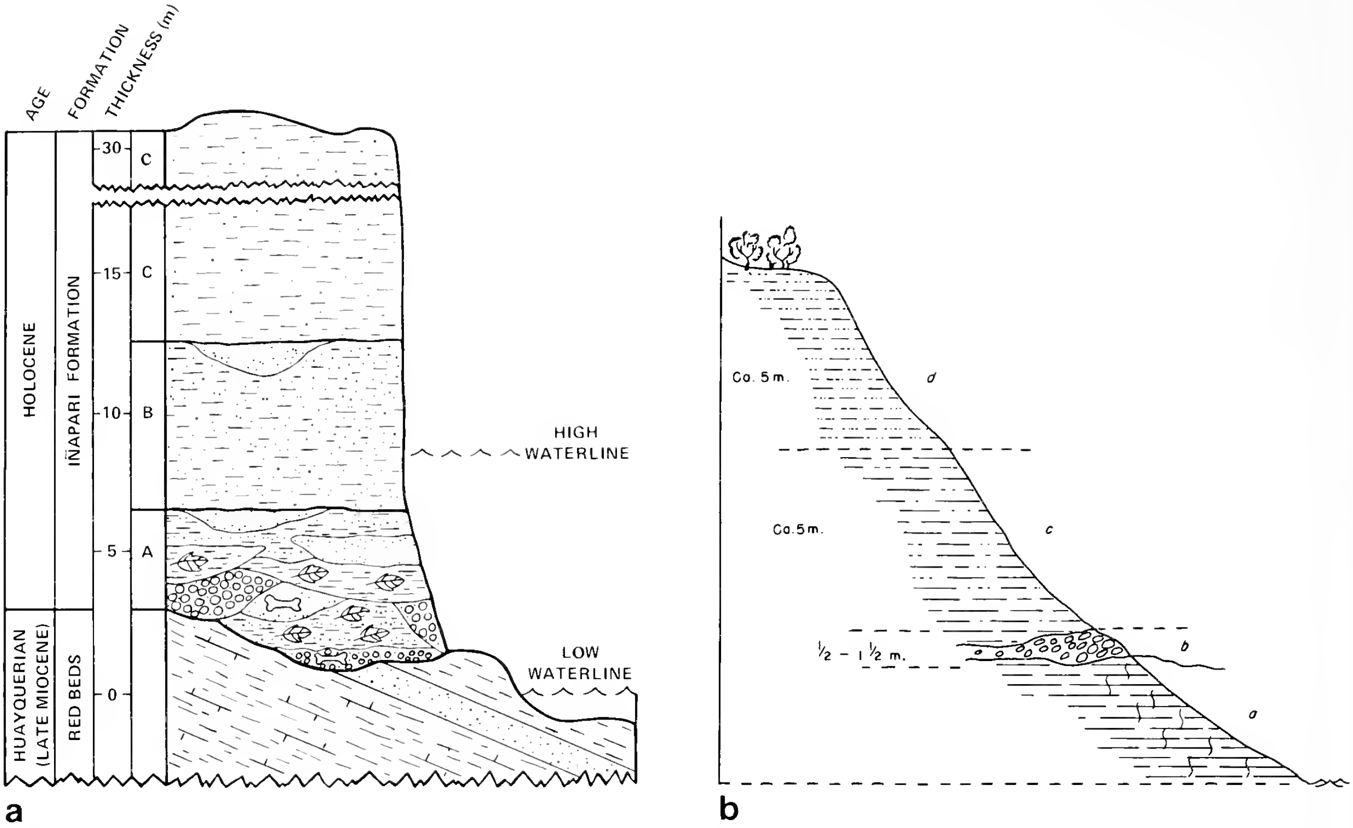

Figure 11. A comparison of the generalized geological sections along the **a** Río Acre and **b** Río Juruá. In **b**, the section at Pedra Preta, "a" represents Tertiary clays; "b" is a "heavy conglomerate" from which came Tertiary fossils; "c" is yellow-greenish clays and silts; and "d" represents buff fine sands and sandy silts. The contact between the different units was not clearly seen, according to the author. **a**, from Campbell and Frailey, 1984; **b**, from Paula Couto, 1978. A series of specific sections for the Río Juruá are presented in Simpson and Paula Couto, 1981.

"gravel" to surface the road running south from Cobija (on the Río Acre) to Porvenir (on the Río Tahuamanu) and the Río Buyuyo. ONERN (1977) states that iron concretions 1–3 cm in thickness occur in the Iñapari Formation (its Shiringayoc Formation).

Campbell and Frailey (1984, in press) correlated the outcrops exposed along the Río Acre with those found along the Río Juruá in western Brazil (Paula Couto, 1978, 1983; Simpson and Paula Couto, 1981) (Fig. 11b). If that correlation is correct and the deposits of the Río Beni correlate with those of the Río Acre, then the deposits of the Río Beni must also correlate with those of the Río Juruá. In that case, all of the Quaternary deposits of the Monte Realm in Bolivia may be referred to the Iñapari Formation. The Iñapari Formation, and the Monte Depositional Realm, must then have a minimum areal coverage extending from its source area somewhere in the Peruvian Andes to the Río Juruá to the northeast, and southeasterly to the Brazilian Shield in eastern Bolivia. Future fieldwork to demonstrate conclusively the broad areal extent of the Iñapari Formation is planned, but for the moment this interpretation is proposed as a working hypothesis.

The widespread deposits of the Monte Realm, i.e., the Iñapari Formation, were almost certainly deposited contemporaneously with those of the Sierra Realm. The stratigraphic and lithologic similarities between the three members of the two deposits also indicate that they must have been formed under very similar circumstances. It is possible that the two depositional realms merge into one in Peruvian territory to the northwest, in which case the deposits of the Sierra Realm will also be referable to the Iñapari Formation. The long distance separating the two depositional realms of the Río Beni, where riverbank outcrops are much lower than those within the depositional realms, indicates that the deposits of the lower Río Beni could not have been derived from the upper reaches of that river.

DRAINAGE SYSTEM ANALYSIS

It is possible to obtain a great deal of information regarding the physiography of northern Bolivia through an analysis of the present drainage system. For this we have used satellite photographs (Figs. 2, 3), a map of the Departamento de La Paz produced from satellite photographs (Instituto Geográphico Militar, 1981), and the only satellite-based topographic map presently available for any part of northern Bolivia (Río

Madre de Dios; Hoja SC 19-16, 1979, Instituto Geográphico Militar, La Paz).

From these sources and field observations it is possible to divide the course of the Río Beni east of the Andes into four regions (Fig. 2). Region I extends from Rurrenabaque through the Sierra Realm, and in it the Río Beni is initially characterized as a braided river and subsequently as an incised, meandering river. The braided portion is a result of the lateral release of water after being channeled through the narrow canyon cut through the front range. Where braided, the river bottom is covered by large cobbles and boulders. Just upriver from Buena Vista the various channels coalesce into one and continue as a single incised channel to a point just downstream from Altamarani, at the eastern limit of the Sierra Realm.

Region II encompasses the river system downriver from the end of Region I to approximately the Río Madidi. In this section the river is characterized as highly meandering, with oxbow lakes, cutoff meanders, and meander scars occurring almost everywhere on both sides of the main channel. The course of the river in the lower half of this section is delimited as a band of light gray cut through the surrounding dark gray (Figs. 2, 3). This color difference is explained by the presence of gallery forests growing on the natural levees formed by the river. The growth of these forests is aided by the slightly higher ground and better drainage afforded the terrain near the main river channel. A similar effect is noted along the Río Madidi and Río Biata, among others, that are also meandering rivers of the highest degree (Figs. 1, 2). The Río Biata can be seen to parallel the Río Beni almost to the front range of the Andes (Figs. 1–3), and evidence from satellite photographs suggests that its channel terminates in cutoff meanders of the Río Beni. During periods of flooding, the Río Biata must share the drainage of water coming through the front range at Rurrenabaque. The Río Beni may have become the main river draining the region because of the additional discharge it receives from the Río Madidi, a factor that may have allowed the Río Beni to deepen its channel at a faster rate than the Río Biata, even though it may have had to cut a longer channel through the Monte Realm.

Region III of the Río Beni extends from approximately the Río Madidi to Ciudad California (Fig. 1, loc. 13). In this region the river channel is incised, with long, straight stretches alternating with broad, gentle curves. The beginning of this section is just downriver from the southern limit of the Monte Realm, and the river is actively downcutting through the loosely consolidated Holocene sediments. It has not yet reached that stage of development where extensive lateral movements of the channel are possible; the channel is still contained within a very narrow valley and there are very few cutoff meanders or oxbow lakes.

In Region IV, from Ciudad California to Riberalta, the Río Beni is a meandering river, with abundant cutoff meanders, oxbow lakes, and meander scars. In contrast to Region II, with its natural levees built up above the surrounding terrain, the meandering river in Region IV is constrained within a narrow valley cut into the deposits of the Monte Realm. The meanders are large and widely spaced initially, but become smaller and more numerous approaching Riberalta, as do the cutoff meanders and oxbow lakes. The valley limits also become more clearly demarcated downstream. On satellite photographs the valley appears as a slightly darker gray, narrow band cutting through the surrounding light gray of the Monte Realm. A similar effect is perhaps more clearly seen for the valley of the larger Río Madre de Dios just to the north (Figs. 2, 3), where prominent scalloping of the valley walls clearly shows how the meandering river is enlarging its valley through lateral erosion.

Outcrops in the Monte Realm occur wherever the river channel curves into the constraining valley wall, undercutting it and forming a cliff. In Region III the outcrops are widely spaced, and all but the two northernmost occur on the eastern side of the river. In Region IV the outcrops are more closely spaced, and in many places alternate from one side of the river to the other as the meanders are deflected from alternate sides of the narrow river valley (Fig. 1). As would be expected, the valley of the Río Beni is broader and its channel more meandering downstream from the confluence of the Río Biata, although its development is clearly not equal to that of the Río Madre de Dios just to the north (Fig. 2).

After the juncture of the Río Beni with the Río Madre de Dios, the enlarged river channel continues its meandering course for a short distance, but gradually the meanders are extended into long curves and then into a relatively straight channel. This reflects the canyonization of the river as it leaves the unconsolidated, fine-grained Holocene sediments of the Amazonian lowlands and begins crossing the hard crystalline rocks of the Brazilian Shield. All the rivers of northern Bolivia drain into Brazil via the Río Madre de Dios, thus the rocks of the Brazilian Shield form the local base level for the entire region.

THE HOLOCENE HISTORY OF SOUTHWESTERN AMAZONIA

The available data are still too few to develop a definitive Holocene history of southwestern Amazonia, but they are sufficiently adequate for us to present our preliminary interpretations. While recognizing that major questions remain and that extensive fieldwork is still to be done, we feel that a picture is emerging.

One of the primary objectives of the geological survey of the Río Beni was to determine if three cycles of Holocene deposition and erosion were detectable in the alluvium deposited by the Río Beni after it exited the front range of the Andes and entered the essentially flat terrain of the eastern lowlands, the region we have termed the Sierra Depositional Realm. As we have described, three different lithologic units do occur in the Sierra Realm, and they are similar in stratigraphic sequence and lithologic composition to the three members of the Iñapari Formation occurring farther downstream in the Monte Depositional Realm and along the Río Acre. The three lithologic units of the two depositional realms are at present correlative only temporally; the deposits are not laterally contiguous anywhere in Bolivia (Fig. 3), and fieldwork in Peru is necessary to resolve their relationship to each other.

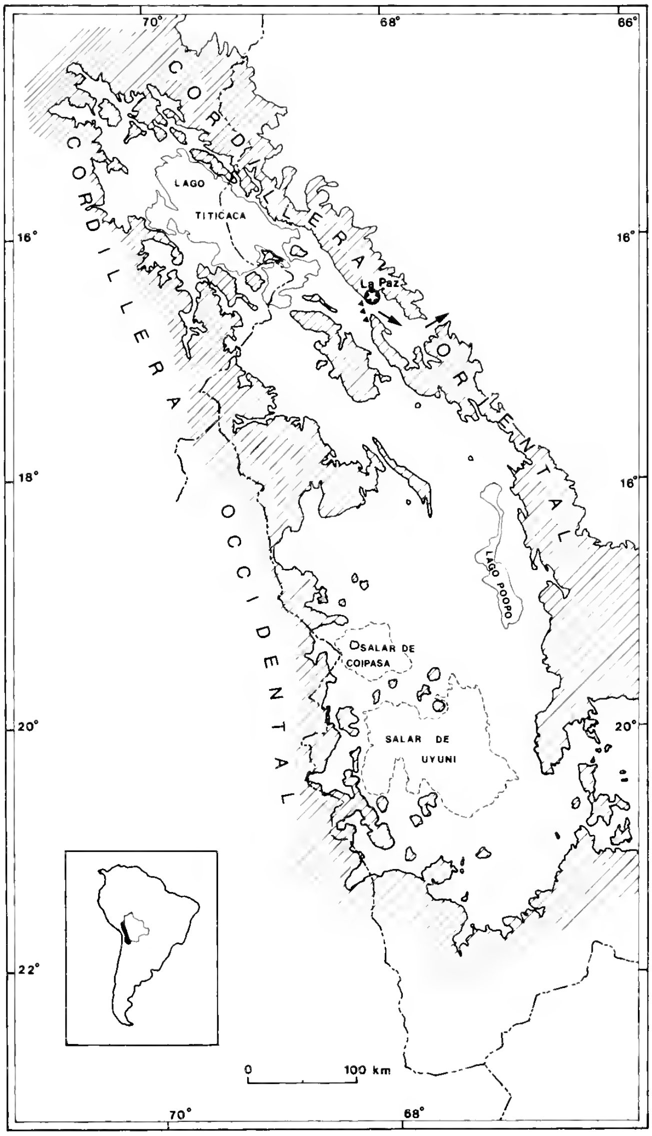

Figure 12. Map of the altiplano of Bolivia and southern Peru. The 4000 m contour line delimits the altiplano, within which lie two large lakes (Lake Titicaca and Lake Poopo) and two large dry salt lakes (Salar de Coipasa and Salar de Uyuni). The hatched area indicates elevations greater than 4000 m within and surrounding the altiplano. The triangles mark the most likely position for an ice dam, and the arrows indicate the direction of flow of the floodwaters out of the altiplano.

As noted earlier, however, the area covered by alluvium deposited by the Río Beni within the Sierra Realm is very small, less even than that immediately to the north and south where alluvium has accumulated from only the eastern slopes of the front range. To account for this lack of extensive alluvial deposits, we propose the occurrence of a catastrophic flood that (1) removed preexisting alluvial deposits from the area immediately east of the exit of the Río Beni from the front range, and (2) cleansed the principal intermontane valleys of the Río Beni of loose alluvium, thereby reducing the quantities of sediments available to form alluvial deposits after the flood. In addition, we propose that this flood (3) formed by scouring the series of depressions now occupied by lakes (Figs. 2, 3) that occur in a straight line northeast of Rurrenabaque, and (4) deposited the characteristic clay-pebble conglomerate that occurs as a basal component of the Holocene Iñapari Formation at least as far north as Cruzeiro do Sul, Brasil, on the Río Juruá.

As the source of the floodwaters, we propose a late Pleistocene lake sited in the Andean altiplano of Bolivia and Peru, the antecedent of Lake Titicaca (Fig. 12). The Andean altiplano is a broad, almost flat region occupying an area of almost 200,000 km^2 between the western and eastern cordilleras of the Andes. Elevations range from about 4000 m at its northern and southern limits to a low point near it center (Salar de Uyuni) of 3660 m. Lohmann (1970:754) referred to the formation of the altiplano peneplain as an "unexplained phenomenon," suggesting that possibly post-Pleistocene lacustrine and fluvial sedimentation redistributed Pleistocene glacial deposits to form the peneplain. He also stated that the altiplano was once continuous across the present La Paz valley, requiring that the erosion of the valley of the Rio de La Paz be a postglacial event. He calculated that approximately 20 km^3 of Quaternary and older material was removed from this valley during the past 10,000 year period, or that material was removed at an annual erosion rate of 2×10^6 m^3/yr (Lohmann, 1970). The mean annual precipitation for La Paz is 439 mm (Montes de Oca, 1983), which is clearly insufficient to account for the erosion required to form the valley. The elevation of the divide separating the altiplano drainage from that of the Río Beni, via the Río de La Paz, is only about 3970 m. The Altiplano has no external drainage, and its only potential outlet would be through the Río de La Paz, if the water were high enough.

The evidence from our preliminary field observations suggests that glacial ice coming out of the Cordillera Real (specifically, the Cordillera de La Paz where elevations reach over 7000 m) covered the eastern half of the altiplano. Reaching a ridge south of La Paz, this glacial ice could have formed a dam behind which collected glacial meltwaters. Alternatively, a glacial ice cap may have formed over the central ridge leading south from Lake Titicaca and the eastern altiplano, meeting the glacial cap coming off the mountains somewhere in the eastern altiplano. The occurrence of a widespread ice cap would help explain the formation of the altiplano peneplain, and topographic features such as numerous streamlined hills resembling rock drumlins suggest that in the eastern part of the altiplano there was ice flow toward the Lake Titicaca basin. This hypothesized glacial ice cover is in contrast to current views (Clapperton, 1983) that hold that during the last glaciation the mountain ice caps terminated in separate piedmont lobes and did not cover the altiplano.

Till deposits documented in the valley of the Río de La Paz to below 3500 m (Dobrovolny, 1956, 1962) indicate that the upper reaches of this valley were filled at various times during the Quaternary with glacial ice prior to the formation of the altiplano peneplain (Lohmann, 1970). Clapperton

(1979) gives a date of 3.27 myr for a till in the Río de La Paz valley that lies at an elevation of about 3900 m. Glaciers in the Cordillera de La Paz now reach elevations as low as 4800 m on the northeast flank of the range, and 5300 m on the southeast flank (Muñoz Reyes, 1977). The size differences of the existing glaciers is a result of the large precipitation differences that exist between the northeast and southeast flank of the mountain range.

The Río de La Paz is eroding headward into the altiplano via its small headwater tributaries, principally the Río Choqueyapu and Río Achocalla. But the upper reaches of the La Paz Valley do not assume the characteristic badland features consistent with headward erosion in a semiarid climate. Rather, the Río Choqueyapu ends headward in large U-shaped glacial valleys, whereas the Río Achocalla is a smaller stream that drains a huge bowl-shaped depression, the Achocalla Valley, with cliff-like rims that in places pose walls with shear drops of hundreds of meters. Except near presently existing stream channels, the bottom of this depression, while generally moderately to steeply sloping, is not eroded into the typical badland topography usually found in regions with poorly indurated Quaternary sediments and semiarid climates. The Río Choqueyapu and the Río Achoealla are clearly underfit streams (fide Dury, 1964), and we find that the Achocalla Valley bears a striking resemblance to the plunge pool of a giant waterfall (see Ahlfeld and Branisa, 1960: fig. 56).

Glacial lakes are known to have occurred in the altiplano, and three have been named (e.g., Ahlfield and Branisa, 1960; Bowman, 1909; Lavenu, 1981; Montes de Oca, 1983; Servant, 1977; Servant and Fontes, 1978). The history of these lakes, however, is not very clear. Lake Ballivián existed in the northern part of the altiplano and is said to have been 50 percent larger than Lake Titicaca, thus covering an area of 12,600 km^2. It left deposits at an elevation of 3850 m. No exact age for this lake has been determined. Lake Minchin existed in the southern part of the altiplano and covered an area of 60,000 km^2 at an elevation of 3760 m. Its period of maximum extension has been put at before 27,500 yr B.P., based on radiocarbon dates of calcareous deposits. Lake Tauca covered an area of 43,000 km^2 at an elevation of 3720 m in the southern altiplano, and is said to have existed from 13,000 to 10,000 yr B.P. Lake Titicaca presently covers about 8400 km^2 at an elevation of 3810 m in the northern part of the altiplano. Clapperton (1983) and Lavenu et al. (1984) report lake levels even higher than 3850 m, with the latter describing newly discovered lake features at an elevation of 3950 m. This is 140 m above the present level of Lake Titicaca and only 20 m less than what would be required for a lake to overflow the lip of the altiplano. Although each of the glacial lakes is said to have existed at different interglacials, is there a possibility that perhaps they represent instead stillstands of a single great lake that covered all of the altiplano?

We propose that just such an extensive glacial lake did form after 14,000 yr B.P. when glacial ice in the Andes receded rapidly (Emiliani et al., 1975; Mercer, 1977). Unless blocked by glacial ice in the western altiplano, this glacial lake may have extended southward to cover an area in excess of 150,000 km^2. As the lake grew in size it overflowed the edge of the glacial ice in the region of La Paz, and the overflowing water began forming the large horseshoe-shaped basin with high, vertical sides which is the Achocalla Valley. At some point the system broke down and a large portion of the remaining lake waters drained catastrophically. Perhaps this resulted from a 200 m uplift of the altiplano northeast of La Paz cited by Lohmann (1970:754) as possibly being contemporaneous in part with the Holocene erosion of the valley of La Paz.

Once the ice dam was breached, the water would have cascaded down the narrow intermontane valley of the Río de La Paz and into the Río Beni, dropping from an elevation of about 4000 m to less than 250 m in a distance of approximately 350 river-km. At several points in the eastern cordilleras the Río Beni flows through very narrow canyons cut transversely through high ridges. These narrow canyons would have restricted the rate of flow, and the water would have formed temporary lakes filling numerous intermontane valleys. The narrow canyon of the front range, which is only about 200 m wide, is just such a constriction. Features visible on satellite photographs, such as what appear to be high plateaus with large, abandoned river channels and possibly giant ripple marks downstream from an anticline composed of Tertiary rocks, suggest that the large valley just west of the front range (Fig. 2, with large white cloud in center) was indeed filled with water. This flooded valley would have maintained great hydraulic pressure on the floodwaters flowing through the narrow canyon of the front range. And because the valley would have served as a giant reservoir, the flow through this canyon onto the lowlands may have continued for some time.

The floodwaters would have emerged onto the flat lowlands as a gigantic, high-pressure stream, much like water passing through a sluice gate in a dam. Carrying away any alluvial deposits in its path, the narrow stream of water scalloped out the chain of rectangular depressions now occupied by lakes that so prominently form a straight line pointing away from the canyon exit (Figs. 1–3). A well-known alternative explanation for this chain of lakes is based on presumed fractures of basement rocks (Montes de Oca, 1983: 152), but it is difficult to see how basement fracturing could be expressed through a surficial cover of Recent alluvium in an area that is regularly inundated by floodwaters and is without recorded seismic activity. Even Laguna Rogaguado (Fig. 3) and the lakes surrounding it, which lie to the northeast of and are in line with the chain of rectangular lakes, may have been formed by the erosive powers of this stream of water.

On satellite photographs there is a strong hint of an alluvial fan of standard shape with its center near the Río Beni and extending northeastward in a large semicircle. A large, dark wedge-shaped slice is removed right of center. It should be noted that although the present course of the main channel of the Río Beni is at an angle to the chain of lakes, the structure of the canyon through the front range is such that a high volume of water would be forced in the direction of

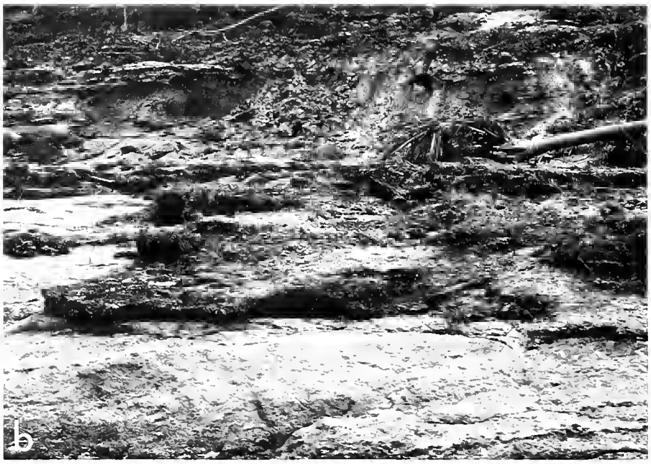

Figure 13. **a.** The partial associated skeleton of a toxodont lies in situ in Tertiary (late Miocene, Huayquerian) clays along the Río Acre. The two lower jaws, a scapula, and several leg bones are visible. **b.** In the foreground, the clay-pebble conglomerate, or Acre Conglomerate Member of the Iñapari Formation, is seen resting on Tertiary clays at a locality on the Río Acre. Channel deposits and stratified clays of Member A of the Iñapari Formation can be seen in the background.

the lakes (Fig. 2). This course is followed today by one of the braided river channels before it turns north-northeastward and joins with the main river channel. After exiting the front range, the floodwaters would have followed a general northward path as a sheet flood, disrupting existing drainage systems.

There is no reason to assume that the pre-Holocene Quaternary drainage system of southwestern Amazonia bore any resemblance to that of the area today. In fact, it may be expected that the pre-Holocene drainage of northern Bolivia flowed due north over the relatively soft Tertiary clays, skirting the western edge of the Brazilian Shield rather than cutting a canyon through its hard crystalline rocks, much like the Ríos Itenez and Mamore do in part today. If such were the case, the later deposition of the Iñapari Formation created a dam, closing off direct northern drainage from Bolivia and forcing the rivers to exit Bolivian territory by crossing over the Brazilian Shield, the course now followed by the Río Madre de Dios before it becomes the Río Madeira and drains into the Río Amazonas. The Iñapari Formation, extending as a blanket over older strata from the Peruvian Andes to the Brazilian Shield, may be effectively covering all evidence of pre-Holocene Quaternary drainage systems.

Racing northward, the sheet flood hypothetically stripped the soil from the surface, exposed the underlying unaltered Tertiary deposits, and deposited the characteristic basal clay-pebble conglomerate of the Iñapari Formation. Prior to the deposition of the Iñapari Formation the general elevation of the region would have been at least 20–35 m lower than today and the terrain was probably even more level than at present. Therefore, it can be assumed that the rivers were at least as easily susceptible to flooding as they are at present, and that any sheet flood could not possibly have been contained in such shallow river valleys.

Of special importance is the probability that in its short-lived passage the sheet flood deposited the characteristic clay-pebble conglomerate with its reworked Tertiary fossil vertebrates and wood that occurs only at the base of the Holocene deposits. Simpson and Paula Couto (1981) and Frailey (1980) remarked on the unusual conditions of the fossil vertebrates in this basal Holocene deposit. Some of the fossils are very water worn, indicating long distance transport, but others cannot have been transported far, or reworked extensively. For example, Simpson and Paula Couto (1981:19) state that ". . . glyptodont scutes may have been worn almost formless but may also occur in large, unworn clusters in which the plates have not been separated at sutures; . . . ." They also reported finding no associated fossil skeletons. Campbell and Frailey (in press) and Frailey (1980) reported on rich fossil localities on the Río Acre where they did find associated vertebrate skeletons, but these were in situ in the Tertiary strata, not part of the clay-pebble conglomerate (Fig. 13a). They were, however, at the same physical level relative to the river channel as the clay-pebble conglomerate (Fig. 13b).

We propose that the Tertiary fossils in the clay-pebble conglomerate were reworked and redeposited near their point of origin by the churning sheet flood, and that the reported differences in wear of the fossils occurred at the time of their primary deposition. In the case of the aforementioned glyptodont scutes, the well-worn, isolated scutes may have undergone long distance transport prior to their fossilization in the Tertiary, while the partial carapaces composed of many scutes were fossilized in the Teriary without being transported far, if at all. Permineralized as a block, the partial carapace was perhaps too strong to be broken up into individual scutes by the passing floodwaters before they were redeposited a short distance from their original site. But at the same time, elements of associated fossil skeletons present in the Tertiary deposits would probably have been dispersed before being redeposited in the clay-pebble conglomerate.

Campbell and Frailey (1984, in press) proposed a flooding mechanism to remove the soil from the Tertiary strata and deposit the clay-pebble conglomerate noted along the Río

Acre and Río Juruá, but at the time they did not have a single catastrophic flood in mind. Instead they proposed that general massive flooding, sparked by rapid melting of Andean glaciers at the end of the Pleistocene (Emiliani et al., 1975) and occurring over a short time period, produced the observed geological features. A single catastrophic flood is a more parsimonious hypothesis to explain the formation of the clay-pebble conglomerate, as well as other geological features in the region. It is necessary, however, to determine where the coarse debris and large bedform features expected from such a flood are located. It is probable that the evidence necessary to document the flood will be found in the mountains rather than in the forested and swampy lowlands where Holocene deposits may be covering all but a few traces of the erosional and depositional features of the flood. The search for such evidence is in progress, but until it is available we recognize the speculative nature of our proposal. Catastrophic flooding of enormous scale resulting from abrupt draining of glacial lakes has been recorded elsewhere (Baker and Nummedal, 1978; Bretz, 1923; Bretz et al., 1956; Malde, 1968), and large-scale catastrophic floods have even been proposed to explain certain geological features on Mars (Baker, 1978).

A hypothesis for the deposition of the three members of the Iñapari Formation was presented by Campbell and Frailey (1984, in press). The hypothesis of a catastrophic flood would modify their interpretation of events slightly in that the fossiliferous basal clay-pebble conglomerate of Member A of the Iñapari Formation is now seen as a unique deposit formed at a specific time prior to the deposition of the remainder of Member A. To recognize this distinction we propose that this unit be named the Acre Conglomerate Member of the Iñapari Formation, after the river where its distinctiveness was first clarified. The type locality is on the south bank of Río Acre, 2 km east of the confluence of Río de Los Patos.

Following the passage of the sheet flood, sediments that formed the Iñapari Formation were washed eastward out of the Peruvian Andes by the meltwaters of the disappearing glaciers. More field data are required to pinpoint the exact source of these sediments. Large-scale seasonal flooding lasting from about 10,000 yr B.P. to about 5000 yr B.P. was proposed by Campbell and Frailey (1984, in press) to account for the highly channeled, variably unstratified and stratified clay deposits of Member A of the Iñapari Formation. This proposal was based in part on the model developed by Kutzbach (1981) to explain early Holocene pluvials in Eurasia.

Rather specific conditions must have existed for the relatively pure clays of Member A of the Iñapari Formation to be deposited over such a broad region. This probability is increased by the fact that Member A in the Sierra Realm is also a channeled clay deposit. It could be expected that the sediment load of rivers entering the Amazonian lowlands had a sizable clay fraction, a feature not unusual for waters draining large areas of recently exposed glacial deposits in high mountains. However, the deposition of clays requires essentially still water. This indicates that inundated areas in the region drained slowly, except in restricted zones where the paleochannels of silts, sands, and clay-ball conglomerates (Fig. 7) indicate fairly weak to strong current flow.

One possible cause of large-scale still water may have been that the preexisting, i.e., pre-Holocene, drainage system was blocked by sediments or otherwise disrupted by debris from the catastrophic sheet flood as described above. This would not be unexpected if, as suggested, the terrain were more flattened than today. Taken together with the increased seasonal precipitation and more rapid and extensive snowpack melt proposed by Campbell and Frailey (1984), an essentially nonexistent drainage system throughout southwestern Amazonia could have accentuated the development of broad, anastomosing rivers with minimal gradients and extensive swamplands susceptible to ready inundation. These conditions would lead to the deposition of widespread clay deposits.

After a change in climate about 5000 yr B.P., and a subsequent period of erosion, Members B and C of the Iñapari Formation were deposited. The lithologic similarity between these two units indicate that they were deposited under similar conditions, and their lithologic differences from Member A, i.e., silts and fine sands instead of clays, indicate that these conditions were different from those that prevailed earlier in the Holocene. The break between the last two periods of deposition was placed at about 2800 yr B.P., under the assumption that the break in deposition represented a significant climatic change that could be expected to correlate with Holocene climatic events recorded elsewhere (Denton and Karlén, 1973; Fairbridge, 1976; Mercer, 1977; Wendland and Bryson, 1974). The worldwide climatic anomalies experienced during 1983 (Philander, 1983a, b; Gill and Rasmusson, 1983) clearly demonstrated how, if not why, such correlations may occur.

The northward drainage of the eastern lowlands of Bolivia must have been completely blocked by the time Member C of the Iñapari Formation was deposited, leaving much of the region south of the Monte Realm waterlogged until drainage was established over the Brazilian Shield. The drainage pattern that has emerged since that time is one of a series of major rivers, often flowing for long distances in roughly parallel courses (Figs. 1, 3), then converging in the northeastern corner of the country and crossing the Brazilian Shield. Secondary drainage follows a classic dendritic pattern, indicating uniformity of substrate and lack of structural control.

The imposition of the drainage system upon the Iñapari Formation can be seen rather clearly in the regions of the Río Beni described earlier. These regions represent different stages of development, or maturity, of the river. Region III is typical of a young river that is actively eroding downward, while Region IV reflects a more mature stage, with a meandering channel developing and occupying a broader valley. A similar effect is reflected in the valley of the Río Madre de Dios, where, of that segment of the river course shown in Fig. 3, the eastern half is far more meandering within a more clearly developed valley than the western half.

The highly meandering nature of Region II of the Río Beni is a result of the Iñapari Formation acting as a local base level for the river, just as the crystalline rocks of the Brazilian

Shield act as the local base level downriver from the confluence of the Río Beni and Río Madre de Dios. The natural levees so prominent in Region II result from deposition of sediment as the river overflowed its low banks during periods of flooding and flowed laterally, unrestrained by valley walls. Such flooding is probably accentuated by the fact that in Region III the river enters into a narrow valley that can only accommodate a portion of the river's discharge during periods of flooding.

The river terraces noted along the Río Beni within the Monte Realm probably resulted from temporary local base levels established and then eroded away in the course of the river over the Brazilian Shield. That terraces of approximately similar height above the river can be found at many localities along the river within the Monte Realm suggests that some of the temporary local base levels lasted for a significant period of time. As one bit of evidence for local control over the formation of these terraces we cite the absence of a comparable series of terraces along the Río Acre. In fact, very few places along the Río Acre upstream from Cobija can be considered as river terraces.

IMPLICATIONS FOR OTHER RESEARCH

Clearly, more documentation of the proposed catastrophic flood and further data regarding the integrity of the Iñapari Formation are required before any definitive statements can be made about the Quaternary history of southwestern Amazonia. Nevertheless, the geological data from the Río Beni reemphasizes the importance of studies of the Quaternary geology of Amazonia to other fields of research as noted by Campbell and Frailey (1984, in press). For example, one important question we can raise is, just how old are the tropical Amazonian forests as we know them? The traditional view is that the forests are millions of years old (e.g., Abelson, 1983). The newly popular hypothesis of "tropical forest refugia," which holds that some areas of forest are very old, having survived intact during the Pleistocene, while surrounding areas of forest were converted to savannas by climatic changes (see papers in Duellman, 1979, and Prance, 1982) is based almost entirely on the distributions of plants and animals. Without supporting geological data, any interpretations of the age of Amazonian ecosystems must be considered speculative.

As another example we may cite the use of the "tropical forest refugia" hypothesis to determine the location of areas of high priority or conservation (Lovejoy, 1982). The Río Acre region is proposed by some (e.g., Brown, 1982) to have been a tropical forest refugium during the Pleistocene, and therefore remained as a stable forest community into the present. But this proposal is untenable given the possibility that the region was swept clear by a passing flood and because the region is covered by the Holocene Iñapari Formation, the youngest deposits of which may be less than two thousand years old. We agree that there is a good probability that tropical forest refugia existed during the Pleistocene, and that these areas should receive priority status regarding conservation. But it is critical for these areas to be delimited first on a geological, not a biological, basis.

In this regard, it is interesting to note that the greatest avian species diversity for any locality in the world, over 500 species, is to be found in the Tambopata Reserve of Peru (Parker, 1982), located just 210 km south of the Río Acre and 150 km southwest of the Río Buyuyo site. Campbell and Frailey (1984, in press) suggested that there is a good probability that this reserve, at an elevation of only 260 m, is resting on surficial deposits of the Iñapari Formation. If so, the high diversity recorded there cannot be a result of long-term environmental stability.

Similarly, studies of such disparate topics ranging from Amazonian biogeography to pedology cannot move forward without a better understanding of the geological history of the region. Unfortunately, a review of a recent important symposium on Amazonia (Donsereau, 1984) held no mention of Quaternary geology, an indication of how the subject is neglected. This can only be to the detriment of all fields of research relating to Amazonia that are, or should be, dependent on a thorough understanding of regional geological history.

Even research into the paleoethnography of Amazonia is incomplete without basic studies of late Quaternary geology. Extensive flooding and depositional events in southwestern Amazonia must have had a dramatic impact on Amerindians in the region. These rather severe environmental changes may explain the absence of early Holocene archaeological sites in Amazonia (Meggers, 1979, 1982), and the fact that few sites in Amazonia with *terra preta* soils are reliably dated beyond about 2000 yr B.P. (Eden et al., 1984). The geological events proposed and described above may also be the basis for some of the myths of Amerindians that speak of periods of great floods (Meggers, 1982). One such myth, said to originate with the "Huni Kui" tribe of the Amahuaca Indians that lived in southwestern Amazonia in the region between the Río Acre and Río Juruá may even be an "eyewitness" account of the catastrophic flood we have proposed:

> In the dim and ancient past beyond recall, when man could still talk with animals, our people had many villages and lived in peace with abundance of everything. They lacked nothing and lived in happiness on the sandy shore of the great river where the water meets the sky.
>
> One day there came a great storm, worse than ever before. It rained day and night. Everything stopped and the people went to their houses. Thunder and lightning came with a terrible wind, destroying the houses.
>
> The sky broke and fell down. The earth went up into the sky. Everything died except some crabs in a hole. No other life remained. The land became sky; the sky, land. Then the sky returned to its place and took the spirits of the dead with it up into the sky. There the spirits lived happily, but on the earth there was nothing but a few crabs. [Lamb, 1974:120–121]

SUMMARY

A geological survey along the Río Beni in northern Bolivia has demonstrated the existence of Quaternary sediments that were deposited in two widely separated depositional realms: the Sierra Realm, with sediments derived from the Bolivian Andes; and the Monte Realm, with sediments derived from the Peruvian Andes. The deposits in the two depositional realms were probably deposited contemporaneously, and the same sequence of deposits occurs in both: a lower unit of channeled, variably stratified clays and two upper units of blocky silts and fine sands.

The sediments of the Monte Realm are referred to the Iñapari Formation of ONERN (1977), a series of alluvial deposits assigned to the Holocene by Campbell and Frailey (1984, in press). The channeled, variably stratified clays of Member A of the Iñapari Formation were deposited from about 10,000 yr B.P. to about 5000 yr B.P. Following a period of erosion, and a change in the environment of deposition, the blocky silts and fine sands of Members B and C of the Iñapari Formation were deposited. A disconformity separating these two members represents a period of erosion, the age of which is put at about 2800 yr B.P. The Iñapari Formation appears to cover at least that part of southwestern Amazonia extending from the Peruvian Andes northeast to the Río Juruá (to Cruzeiro do Sul, Brasil) and southeast to the Brazilian Shield.

The deposition of the Iñapari Formation formed a dam across northern Bolivia, forcing the regional drainage northeastward, over the crystalline rocks of the Brazilian Shield. The imposition of the present drainage system upon the Iñapari Formation is reflected in the varying stages of development of the river valleys in northern Bolivia, with the course of the Río Beni east of the Andes being divisible into four clearly distinct regions.

A catastrophic flood resulting from the sudden draining of glacial Lake Titicaca is proposed to account for (1) the lack of alluvial deposits extending eastward from the front range of the Andes at the point where the Río Beni enters the flat lowlands; (2) the prominent chain of lakes extending northeastward in a straight line from the opening of the Río Beni onto the flat lowlands; and (3) the deposition of the characteristic clay-pebble conglomerate with Tertiary fossil vertebrates and wood, herein named the Acre Conglomerate Member of the Iñapari Formation.

The documentation of Holocene deposits over wide regions of southwestern Amazonia has broad implications for numerous fields of research, including such disparate fields as biogeography, conservation, ecology, hydrology, pedology, and paleoethnography.

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VASCULAR PLANTS OF THE CHANNEL ISLANDS OF SOUTHERN CALIFORNIA AND GUADALUPE ISLAND, BAJA CALIFORNIA, MEXICO

Gary D. Wallace

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MAPS AND TABLES

VASCULAR PLANTS OF THE CHANNEL ISLANDS OF SOUTHERN CALIFORNIA AND GUADALUPE ISLAND, BAJA CALIFORNIA, MEXICO

Gary D. Wallace[1]

ABSTRACT. Vascular plant taxa of the Channel Islands of southern California and Guadalupe Island, Mexico, are treated, to include their distribution among the islands, citation of verified specimens from several herbaria, and a detailed account of earlier synonymous taxa, misidentified specimens, and taxa *incertae sedis* based on herbarium specimens and literature citations. A total of 621 native vascular taxa include 137 endemics and 227 introduced taxa.

RESUMEN. Se tratan los taxa de plantas vasculares de las Channel Islands de California Sur y de la Isla Guadalupe, Mexico, incluyendo sus distribuciones dentro de las islas, citacion verificado de especimenes de diversos herbarios, y una cuenta detallada de sinonimos previos, especimenes mal identificados, y taxa *incertae sedis* basada en especimenes de herbarios y citas de la literatura. Se reporta un total de 621 taxa vasculares indigenos, incluyendo 137 endemicos, y 227 introducidos.

INTRODUCTION

There have been numerous papers over the past century dealing with the plants of the Channel Islands. These were often the results of single visits to a specific island (e.g., Greene, 1887a), summary works primarily based on previously published works (e.g., Brandegee, 1890b; Eastwood, 1941), or works combining these approaches (e.g., Raven, 1963; Thorne, 1967; Foreman, 1967; Philbrick, 1972; Smith, 1976).

The islands treated here and a reference to a treatment of the flora of each are as follows: San Miguel Island (Smith, 1976); Santa Rosa Island (Smith, 1976); Santa Cruz Island (Smith, 1976); Anacapa Islands (Smith, 1976); San Nicolas Island (Foreman, 1967); Santa Barbara Island (Philbrick, 1972); Santa Catalina Island (Thorne, 1967); San Clemente Island (Raven, 1963); Isla Guadalupe (Eastwood, 1929). Each of these deals, almost exclusively, with the flora of a single island or group of islands but none has treated the flora of all of the islands. Foreman (1967), Philbrick (1972), Thorne (1967), Raven (1963), and Eastwood (1929) were among those authors to cite verifiable specimens. Difficulties have arisen over the years in locating specimens upon which earlier and erroneous reports were based, in some cases these have not yet been located. Raven (1963) and Thorne (1967) dismissed these unsubstantiated reports. Philbrick (1972) consistently documented each case of error and misidentification. There was no question as to which reports Philbrick had seen. Philbrick (1972) documented the disposition of persistent errors in the literature. Finally Philbrick (1972) consistently provided citation of specimens which could be available for the monographic and floristic studies of others.

The most recent treatment of the flora of the Channel Islands as a whole was that done by Eastwood (1941). This work was based on herbarium specimens, published reports of collections, and apparently some lists compiled by botanists of specimens they had collected. Eastwood (1941) cited no collections, making confirmation of her insular records difficult. Apparent errors were perpetuated by this work and original determinations were further obscured by the fact that Eastwood occasionally submerged or changed these with no annotation of the specimens she saw. Because of some errors in Eastwood (1941), additional inconsistencies may have been arbitrarily attributed to her list. Some errors attributed to Eastwood's list are undoubtedly the result of her inclusion of data from earlier published and unpublished works. Among major floristic works, Munz and Keck (1959) only occasionally noted specific insular distributions of taxa. Munz (1974) in addition to this was inconsistent in including insular taxa from the northern islands. Smith (1976) gave an effective treatment of the plants of the northern group of islands in his regional flora.

The Channel Islands are an important phytogeographical unit of California. Many of the insular taxa are in need of systematic and evolutionary study as indicated by Raven (1963), Thorne (1967), Philbrick (1972), and Smith (1976). Several taxa reach their northern or southern range limits

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among the Channel Islands and Guadalupe Island, Mexico. The outlier populations may provide important data to assess patterns of variation and evolution. Treatments by Davis (1980) and Philbrick (1980) depict some of the intricacies of evolutionary development found among insular taxa. Knowledge of the occurrence and distribution of the insular plant taxa, as well as the availability of specimens, is vital to workers in these areas.

The high incidence of endemism is apparent in several genera, most notably *Eriogonum* (Polygonaceae), *Dudleya* (Crassulaceae), *Arctostaphylos* (Ericaceae), *Galium* (Rubiaceae), *Malacothrix* (Asteraceae), *Hemizonia* (Asteraceae), *Phacelia* (Hydrophyllaceae), and *Lotus* (Fabaceae). Discussions of the significance, origins, and distributions of the endemic plants on the Channel Islands may be found in Stebbins and Major (1965), Raven (1967, 1977), and Philbrick (1980). General information about the vegetation of the islands may be found in Philbrick and Haller (1977), as well as in the several treatments for specific islands. Westman (1983) discussed the structure of the insular xeric shrublands and compared them to similar mainland sites. Philbrick (1967) and Power (1980) provide introductions and sources for those interested in the diverse aspects of geological, natural and evolutionary history of the Channel Islands.

The Natural History Museum of Los Angeles County has had a long association with the study of the Channel Islands. The combined collections of AHFH, USC, and LAM at LAM contain significant numbers of insular collections of M.B. Dunkle, F.R. Fosberg, and F.H. Elmore as well as numerous specimens collected by R. Moran, B. Trask, I.W. Clokey, and P.J. Rempel among others (herbarium acronyms throughout are as given in Holmgren et al., 1981). One of the most active centers for floristic treatment of the Channel Islands is currently the Santa Barbara Botanic Garden. Dr. Ralph Philbrick and his co-workers have made extensive and intensive collections of the northern islands as well as Santa Barbara Island. Rancho Santa Ana Botanic Garden has been the primary center for the floristic study of Santa Catalina and San Clemente Islands. Dr. Robert F. Thorne has made exhaustive collections on Santa Catalina Island and has made several collection trips to the other islands. The current study of Guadalupe Island, Mexico, is almost exclusively centered at the San Diego Museum of Natural History. Dr. Reid Moran made numerous trips over the years to the island and is the recognized authority on the flora of Guadalupe. Several other institutions have significant insular collections which supported earlier research specialties or interests (AHFH, CAS, CM, DS, F, GH, MO, ND-G, NY, US). The Natural History Museum and the Santa Barbara Museum contain both historical and current specimens, a reflection of sustained interest in the islands.

The objectives of this paper are several. One is to provide a current guide to the floras of each of the islands of this phytogeographically important region. This is done in a manner which clearly distinguishes between those records based upon available herbarium specimens and those based on reports from the literature. Another goal is to present a picture of the floristic relationships among the islands. Finally I wanted to draw the attention of systematists to the insular distributions of native taxa and to the numerous misidentifications and synonymous treatments of those taxa. Their aid in the verification and correction of data in the two appendixes will greatly clarify our knowledge of the insular floras.

This treatment is primarily based on verified herbarium specimens. Specimens cited are deposited in one or more of the following collections: CAS-DS, CM, F, GH, JEPS, LAM (includes AHFH and USC), MO, ND-G, NY, RSA-POM, SBBG, SBM, UC, UCSB, UCSB-SCIR, US, and the Pacific Missile Test Center at Point Mugu, California.

Numerous monographic and floristic publications provided reports of insular plants. These publications are cited in the table of vascular plants only when herbarium specimens could not be found which verified the individual report, or when the report could not be determined to be an error.

Personal communications of the occurrence of taxa on the islands are not included nor are published sightings lacking voucher specimens, reports from unpublished lists, or collections not entered in an herbarium and available for loan.

In most cases, current monographic treatments served as nomenclatural guides. Not all taxonomic judgments made here will meet with approval. Comments including reference to additional monographic treatments will be appreciated. I hope monographers and curators will attempt to verify or deny records known here from literature references citing the specimens upon which the records are based. Appendixes I and II are intended to facilitate this endeavor.

The paper is divided into three major sections, the table of vascular plants, Floristic Relationships, and the appendixes. Floristic Relationships contains Map 1, which shows the spatial relationships among the islands, and two tables. Table 1 lists some features of the islands treated here and gives floristic summaries for each island. Table 2 indicates the numbers of shared endemics and total number of shared native taxa among the islands.

THE VASCULAR PLANTS OF THE CHANNEL ISLANDS OF SOUTHERN CALIFORNIA AND GUADALUPE ISLAND, BAJA CALIFORNIA, MEXICO

The order of inclusion of the major plant groupings is Vascular Cryptogams, followed by the Gymnosperms, Dicotyledons, and Monocotyledons. Families, genera, and species are alphabetically arranged within these groupings. Throughout this paper, the abbreviations of authors' names follow those given by Munz and Keck (1959). In the first column to the right of the name of the taxon there will be one of three abbreviations: NA = native to the islands noted, EN = native and more specifically endemic to islands noted, or IN = introduced. Occasionally a taxon is endemic to the islands treated here and one or a few other of the Mexican islands; in such cases it will be noted as endemic and the additional islands on which the species occurs are given in parentheses after the name of the taxon. The next nine columns correspond to one of each of the islands. A notation in a column opposite the name of a taxon indicates a record of occurrence based on herbarium material. The following abbreviations correspond to the islands to avoid confusion and occur throughout this paper: MI = San Miguel Island, RO = Santa Rosa Island, CR = Santa Cruz Island, AN = Anacapa Islands, NI = San Nicolas Island, BA = Santa Barbara Island, CA = Santa Catalina Island, CL = San Clemente Island, GU = Isla Guadalupe or Guadalupe Island. Citation of specimens and their locations for these records or only location of specimens is noted in Appendix I. Occasionally a number appears in the column; this corresponds to a numerically indexed entry in the Literature Cited section. Most of these reports are neither accepted nor denied but rather are offered for the comment and study of others. Undoubtedly, many of these may be dismissed as the specimens upon which they are based are located and identified or likely herbarium sources are exhausted.

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Vascular Cryptogams										
Selaginellaceae										
Selaginella bigelovii Underw.	NA		RO	CR	AN			CA	CL	
Equisetaceae										
Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & Taylor	NA			CR						
Equisetum laevigatum A. Br.	NA		RO	CR				CA		
Equisetum telmateia Ehrh. var. *braunii* Milde	NA			CR				CA		
Aspidiaceae										
Athyrium felix-femina (L.) Roth var. *sitchensis* Rupr.	NA		31	CR						
Cystopteris fragilis (L.) Bernh.	NA			CR						
Dryopteris arguta (Kaulf.) Watt.	NA		RO	CR	AN			CA	CL	
Polystichum munitum (Kaulf.) Presl. ssp. *munitum*	NA		RO	CR						
Polystichum munitum (Kaulf.) Presl ssp. *solitarium* Maxon	EN									GU
Blechnaceae										
Woodwardia fimbriata Sm. in Rees	NA		RO	CR						
Polypodiaceae										
Polypodium californicum Kaulf.	NA		RO	CR	AN		BA	CA	CL	GU
Polypodium scouleri Hook. & Grev.	NA			CR						GU
Pteridaceae										
Adiantum capillus-veneris L.	NA		RO	CR	AN			CA		
Adiantum jordani C. Muell.	NA		RO	CR	AN			CA	CL	
Adiantum pedatum L. ssp. *aleuticum* (Rupr.) Calder & Taylor	NA			CR						
Aspidotis californica (Hook.) Nutt. ex Copel.	NA			CR				CA		
Cheilanthes clevelandii D.C. Eat.	NA		RO	CR						
Cheilanthes newberryi (D.C. Eat.) Domin	NA								CL	GU
Notholaena californica D.C. Eat.	NA			41				CA		GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Pellaea andromedaefolia (Kaulf.) Fee var. *pubescens* D.C. Eat.	NA		RO	CR	AN			CA	CL	
Pellaea mucronata (D.C. Eat.) D.C. Eat. ssp. *mucronata*	NA		RO	CR	26			CA		GU
Pityrogramma triangularis (Kaulf.) Maxon var. *triangularis*	NA		RO	CR	AN			CA	CL	GU
Pityrogramma triangularis (Kaulf.) Maxon var. *viscosa* (D.C. Eat.) Weath.	NA		RO	CR		NI		CA	CL	
Pteridium aquilinum (L.) Kuhn var. *pubescens* Underw.	NA		RO	CR				CA		
Salviniaceae										
Azolla filiculoides Lam.	NA							CA		
Gymnosperms										
Cupressaceae										
Cupressus guadalupensis Wats. ssp. *guadalupensis*	EN									GU
Cupressus macrocarpa Hartw. ex Gord.	IN			CR	AN			CA		
Juniperus californica Carr.	NA									GU
Pinaceae										
Pinus muricata D. Don	NA		81	CR						
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon	EN									GU
Pinus remorata Mason	NA		RO	CR						
Pinus torreyana Parry ex Carr.	NA		RO							
Dicotyledons										
Aceraceae										
Acer macrophyllum Pursh	NA			CR						
Aizoaceae										
Aptenia cordifolia (L. f.) N.E. Br.	IN				AN			CA		
Carpobrotus aequilaterus (Haw.) N.E. Br.	NA	MI	RO	CR	AN	NI			CL	
Carpobrotus edulis (L.) Bolus	IN					NI				
Malephora crocea (Jacq.) Schwant	IN				AN					
Mesembryanthemum crystallinum L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Mesembryanthemum nodiflorum L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Tetragonia tetragonioides (Pall.) Kuntze	IN	MI	RO	CR	81					
Amaranthaceae										
Amaranthus albus L.	IN	31	RO	CR				CA		
Amaranthus blitoides Wats.	IN	31	RO	CR						
Amaranthus deflexus L.	IN			CR						
Anacardiaceae										
Lithraea molloides (Kell.) Engler	IN							CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Malosma laurina (Nutt. in T. & G.) Nutt. ex Abrams	NA							CA	CL	GU
Rhus integrifolia (Nutt.) Benth. & Hook.	NA	MI	RO	CR	AN			CA	CL	GU
Rhus ovata Wats.	NA			CR				CA		
Schinus molle L.	IN			CR				CA		
Toxicodendron radicans (L.) Kuntze ssp. *diversilobum* (T. & G.) Thorne	NA	MI	RO	CR	AN			CA	CL	
Apocynaceae										
Asclepias fascicularis Dcne. in A. DC.	NA			CR				CA		
Sarcostemma cynanchoides Dcne. ssp. *hartwegii* (Vail) R. Holm	NA							CA		
Vinca major L.	IN			CR				CA		
Araliaceae										
Apiastrum angustifolium Nutt. in T. & G.	NA	MI	RO	CR	AN	NI		CA	CL	
Apium graveolens L.	IN		RO	CR		NI			CL	
Berula erecta (Huds.) Cov.	NA	MI		41	26					
Bowlesia incana R. & P.	IN		RO	CR				CA	CL	
Caucalis microcarpa H. & A.	NA			CR				CA	CL	
Conium maculatum L.	IN			CR		NI		31		
Daucus pusillus Michx.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Foeniculum vulgare Mill.	IN		RO	CR		NI		CA	CL	
Lomatium caruifolium (H. & A.) Coult. & Rose	NA	MI	RO	CR						
Lomatium insulare (Eastw.) Munz	EN					NI			CL	GU
Lomatium utriculatum (Nutt.) Coult. & Rose	NA		RO	CR						
Sanicula arguta Greene ex Coult. & Rose	NA	MI	RO	CR	AN	NI		CA	CL	
Sanicula crassicaulis Poepp. ex DC. var. *crassicaulis*	NA			CR				CA		93
Sanicula hoffmannii (Munz) Bell	NA	MI	RO	CR		NI				
Torilis nodosa (L.) Gaertn.	IN	MI	RO	CR				CA		
Asteraceae										
Achillea millefolium L.	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Achyrachaena mollis Schauer	NA		RO	CR					CL	
Agoseris apargioides (Less.) Greene ssp. *apargioides*	NA		RO							
Agoseris grandiflora (Nutt.) Greene	NA	MI	RO	CR						
Agoseris heterophylla (Nutt.) Greene	NA		RO	CR						GU
Amblyopappus pusillus H. & A.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Ambrosia acanthicarpa Hook.	IN							CA		
Ambrosia camphorata (Greene) Payne	NA									GU
Ambrosia chamissonis (Less.) Greene	NA	MI	RO	CR	AN	NI		CA	CL	
Ambrosia psilostachya DC. var. *californica* (Rydb.) Blake in Tidestr.	NA			41				CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Anthemis cotula L.	IN		5	CR				CA		
Artemisia californica Less.	NA	MI	RO	CR	AN			CA	CL	GU
Artemisia douglasiana Bess. in Hook.	NA		RO	CR				CA		
Artemisia dracunculus L.	NA							CA		
Artemisia nesiotica Raven	EN					NI	BA		CL	
Aster chilensis Nees var. *chilensis*	NA		RO	CR						
Aster exilis Ell.	NA			CR				66		
Aster radulinus Gray	NA		RO	CR						
Baccharis douglasii DC.	NA	MI	RO	CR	26			CA		
Baccharis emoryi Gray	NA							CA		
Baccharis glutinosa Pers.	NA		RO	CR	AN			CA	CL	
Baccharis pilularis DC. ssp. *consanguinea* (DC.) C.B. Wolf	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Baccharis plummerae Gray	NA			CR						
Baeriopsis guadalupensis J.T. Howell	EN									GU
Blennosperma nanum (Hook.) Blake var. *nanum*	NA			CR						
Brickellia californica (T. & G.) Gray	NA			CR	AN			CA		
Centaurea cineraria L.	IN							CA		
Centaurea melitensis L.	IN	MI	RO	CR		NI	BA	CA	CL	GU
Centaurea solstitialis L.	IN		31	CR				CA		
Chaenactis glabriuscula DC. var. *lanosa* (DC.) Hall	NA		RO							
Chrysanthemum coronarium L.	IN			CR		NI		CA		
Chrysanthemum frutescens L.	IN							CA		
Cichorium intybus L.	IN			CR						
Cirsium brevistylum Cronq.	NA			CR						
Cirsium californicum Gray	NA	31	RO	CR				CA		
Cirsium occidentale (Nutt.) Jeps.	NA	MI	RO	CR		NI		CA	CL	
Cirsium ochrocentrum Gray	IN							CA		
Cirsium proteanum J.T. Howell	NA		RO							
Cirsium vulgare (Savi) Ten.	IN							CA		
Cnicus benedictus L.	IN			81						
Conyza bonariensis (L.) Cronq.	IN		81	CR		NI		CA	CL	
Conyza canadensis (L.) Cronq.	IN	MI	RO	CR		NI		CA	CL	
Conyza coulteri Gray	NA		31	CR				CA	CL	
Coreopsis gigantea (Kell.) Hall	NA	MI	RO	CR	AN	NI	BA	CA		GU
Corethrogyne filaginifolia (H. & A.) ssp. *filaginifolia*	NA	MI	RO	CR	AN	NI		CA		
Cotula australis (Sieber ex Spreng.) Hook. f.	IN		RO	CR				CA		
Cotula coronopifolia L.	IN	MI	RO	CR		NI		CA		
Cynara scolymus L.	IN			CR						
Encelia californica Nutt.	NA			CR	AN			CA	CL	
Erigeron foliosus Nutt. var. *foliosus*	NA	MI	RO	CR	AN			CA		
Erigeron foliosus Nutt. var. *stenophyllus* (Nutt.) Gray	NA	MI	31	CR	AN					
Erigeron glaucus Ker	NA	MI	RO	CR	AN					
Erigeron sanctarum Wats.	NA		RO		26					

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Eriophyllum confertiflorum (DC.) Gray var. *confertiflorum*	NA	MI	RO	CR	AN			CA	CL	
Eriophyllum lanatum (Pursh) Forbes var. *grandiflorum* (Gray) Jeps.	NA									GU
Eriophyllum nevinii Gray	EN						BA	CA	CL	
Eriophyllum staechadifolium Lag. var. *artemisiaefolium* (Less.) Macbr.	NA	MI	RO	CR	AN					
Eriophyllum staechadifolium Lag. var. *depressum* Greene	NA	MI	RO	CR	AN					
Evax sparsiflora (Gray) Jeps.	NA		RO	31					CL	
Filago arizonica Gray	NA		66	7				CA	CL	GU
Filago californica Nutt.	NA	MI	RO	CR	AN			CA	CL	GU
Filago gallica L.	IN			CR				CA		
Gnaphalium beneolens A. Davids.	NA	MI	RO	CR		NI		CA	CL	
Gnaphalium bicolor Bioletti	NA	43	RO	CR	AN	NI		CA	CL	GU
Gnaphalium californicum DC.	NA		RO	CR	AN			CA		
Gnaphalium chilense Spreng.	NA	MI	RO	CR	AN	NI		CA		GU
Gnaphalium luteo-album L.	IN	MI	RO	CR		NI		CA	CL	
Gnaphalium microcephalum Nutt.	NA		RO	CR	AN			CA		
Gnaphalium palustre Nutt.	NA			CR				CA	CL	
Gnaphalium purpureum L.	NA		RO	CR	81			CA		
Gnaphalium ramosissimum Nutt.	NA			CR						
Grindelia latifolia Kell.	NA	42	RO	98	AN					
Grindelia robusta Nutt. var. *robusta*	NA			CR		NI		63		
Grindelia stricta DC. ssp. *venulosa* (Jeps.) Keck	NA		RO	31						
Haplopappus canus (Gray) Blake	EN								CL	GU
Haplopappus detonsus (Greene) Raven	EN		RO	CR	AN					
Haplopappus ericoides (Less.) H. & A. ssp. *ericoides*	NA	42								
Haplopappus palmeri Gray ssp. *pachylepis* Hall	NA							CA		
Haplopappus squarrosus H. & A. ssp. *grindelioides* (DC.) Keck	NA	MI	RO	CR				CA		
Haplopappus venetus (HBK.) Blake ssp. *furfuraceus* (Greene) Hall	NA					NI		CA	CL	
Haplopappus venetus (HBK.) Blake ssp. *sedoides* (Greene) Munz	NA	MI	RO	CR	AN					
Haplopappus venetus (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall	NA	MI	RO	CR	AN	NI		CA	CL	
Helenium puberulum DC.	NA							CA		
Helianthus annuus L. ssp. *lenticularis* (Dougl.) Ckll.	NA			CR				CA		
Hemizonia clementina Bdg.	EN				AN	NI	BA	CA	CL	
Hemizonia fasciculata (DC.) T. & G.	NA	42	RO	CR	AN		BA	CA	CL	
Hemizonia fitchii Gray	IN			CR						
Hemizonia frutescens Gray	EN									GU
Hemizonia greeneana Rose ssp. *greeneana*	EN									GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Hemizonia increscens (Hall ex Keck) Tanowitz ssp. *increscens*	NA		RO	CR						
Hemizonia palmeri Rose	EN									GU
Heterotheca grandiflora Nutt.	NA			CR		NI		CA	CL	
Hieraceum argutum Nutt. ssp. *argutum*	NA		RO	CR						
Hypochoeris glabra L.	IN		RO	CR				CA	CL	GU
Jaumea carnosa (Less.) Gray	NA	MI	RO	CR				CA		
Lactuca serriola L.	IN		RO	CR		NI		CA		
Lasthenia californica DC. ex Lindl.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Lasthenia coronaria (Nutt.) Ornduff	NA									GU
Lasthenia glabrata Lindl. ssp. *coulteri* (Gray) Ornduff	NA		RO	31						
Layia glandulosa (Hook.) H. & A. ssp. *glandulosa*	NA			CR						
Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck	NA	MI	RO	CR				CA	CL	GU
Layia platyglossa (F. & M.) Gray ssp. *platyglossa*	NA		RO							
Lepidospartum squamatum (Gray) Gray	NA			CR						
Madia exigua (Sm.) Gray	NA			CR				CA		
Madia gracilis (Sm.) Keck ssp. *gracilis*	NA			CR				CA		
Madia sativa Mol.	IN		5	CR				CA	CL	
Malacothrix clevelandii Gray	NA									GU
Malacothrix coulteri Harv. & Gray var. *cognata* Jeps.	NA		RO	CR						
Malacothrix "B" (see note 1)	EN				20					
Malacothrix foliosa Gray (Los Coronados)	EN								CL	
Malacothrix incana (Nutt.) T. & G.	NA	MI	RO	CR		NI			76	
Malacothrix indecora Greene	EN	MI		CR						
Malacothrix "A" (see note 1)	EN						BA			
Malacothrix "C" (see note 1)	EN					NI				
Malacothrix saxatilis (Nutt.) T. & G. var. *implicata* (Eastw.) Hall	EN	MI	RO	CR	AN	NI				
Malacothrix saxatilis (Nutt.) T. & G. var. *tenuifolia* (Nutt.) Gray	NA							CA		
Malacothrix similis Davis & Raven	NA	18		19						
Malacothrix squalida Greene	EN			CR	AN					
Matricaria matricarioides (Less.) Porter	IN		RO	CR				CA		GU
Micropus californicus F. & M.	NA		RO	CR						
Microseris douglasii (DC.) Sch.-Bip. ssp. *douglasii*	NA	81				NI			CL	
Microseris douglasii (DC.) Sch.-Bip. ssp. *platycarpha* (Gray) Chamb.	NA							CA	CL	
Microseris douglasii (DC.) Sch.-Bip. ssp. *tenella* (Gray) Chamb.	NA	MI	RO	CR						

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Microseris elegans Greene ex Gray	NA	MI	66	CR					CL	
Microseris heterocarpa (Nutt.) Chamb.	NA		RO	CR				CA	CL	GU
Microseris linearifolia (DC.) Sch.-Bip.	NA		RO	CR	AN	NI	72	CA	CL	GU
Pentachaeta lyonii Gray	NA							CA		
Perezia microcephala (DC.) Gray	NA		RO	CR				CA		
Perityle emoryi Torr. in Emory	NA		RO	CR	AN		BA	CA	CL	GU
Perityle incana Gray	EN									GU
Picris echioides L.	IN							CA		
Pluchea odorata (L.) Cass.	NA			CR				CA		
Pluchea sericea (Nutt.) Cov.	NA							CA		
Psilocarphus tenellus Nutt. var. *tenellus*	NA		RO	CR				CA	CL	
Raphinesquia californica Nutt.	NA		RO	CR	AN		BA	CA	CL	
Senecio aphanactis Greene	NA		RO	CR				CA		
Senecio douglasii DC. ssp. *douglasii*	NA			CR				CA	CL	
Senecio lyonii Gray	NA							CA	CL	
Senecio palmeri Gray	EN									GU
Senecio vulgaris L.	IN	MI		CR	AN	NI		CA	CL	
Silybum marianum (L.) Gaertn.	IN		RO	CR			BA	CA		
Solidago californica Nutt.	NA		RO	CR				CA		
Sonchus asper (L.) Hill	IN	MI	RO	CR	AN	NI	BA	CA	CL	
Sonchus oleraceus L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Sonchus tenerrimus L.	IN		31		31	NI	72	CA	CL	GU
Stephanomeria blairii M. & J.	EN								CL	
Stephanomeria cichoriacea Gray	NA		RO	CR						
Stephanomeria diegensis Gottlieb	NA		RO	37				CA	CL	37
Stephanomeria exigua Nutt. ssp. *coronaria* (Greene) Gottlieb	NA	MI	5	CR						
Stephanomeria guadalupensis Bdg.	EN									GU
Stephanomeria virgata Benth. ssp. *virgata*	NA	42	RO	CR				CA	CL	
Stylocline gnaphalioides Nutt.	NA		RO	CR				CA		
Taraxacum laevigatum (Willd.) DC.	IN			CR				CA		
Taraxacum officinale Wiggers	IN			CR				CA		
Thelesperma megapotamicum (Spreng.) Kuntz	NA							CA		
Tragopogon porrifolius L.	IN			CR						
Venegasia carpesioides DC.	NA		RO	CR						
Xanthium spinosum L.	IN	MI	81	CR			BA	CA		
Xanthium strumarium L. var. *canadense* (Mill.) T. & G.	NA			41					CA	
Bataceae										
Batis maritima L.	NA								CL	
Berberidaceae										
Berberis pinnata Lag. ssp. *insularis* Munz	EN		RO	CR	AN					

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Boraginaceae										
Amsinckia intermedia F. & M.	NA	MI	RO	CR	AN		BA	CA	CL	8
Amsinckia menziesii (Lehm.) Nels. & Macbr.	NA			CR				CA		GU
Amsinckia spectabilis F. & M. var. *nicolai* (Jeps.) Jtn. ex Munz	EN	MI				NI			CL	
Amsinckia spectabilis F. & M. var. *spectabilis*	NA	MI	RO	CR	AN	NI	BA		CL	96
Cryptantha clevelandii Greene var. *clevelandii*	NA	MI	RO	CR	AN	NI	BA	CA	CL	28
Cryptantha clevelandii Greene var. *florosa* Jtn.	NA	MI	RO	CR	AN	NI	BA	CA		
Cryptantha foliosa (Greene) Greene	EN									GU
Cryptantha intermedia (Gray) Greene	NA		31	28				CA	CL	
Cryptantha leiocarpa (F. & M.) Greene	NA	42	RO	41						
Cryptantha maritima (Greene) Greene	NA					NI	BA	CA	CL	GU
Cryptantha micromeres (Gray) Greene	NA		RO	CR				CA		
Cryptantha microstachys (Greene ex Gray) Greene	NA							CA		
Cryptantha muricata (H. & A.) Nels. & Macbr. var. *jonesii* (Gray) Jtn.	NA			CR	31					
Cryptantha traskiae Jtn.	EN					NI			CL	
Harpagonella palmeri Gray	NA							CA		GU
Heliotropium curassavicum L. ssp. *oculatum* (Heller) Thorne	NA	MI	RO	CR	AN	NI		CA	CL	
Pectocarya linearis DC. ssp. *ferocula* (Jtn.) Thorne	NA			CR		29		CA	CL	GU
Pectocarya penicellata (H. & A.) A. DC.	NA		31	41	AN			6		50
Pectocarya recurvata Jtn.	NA									GU
Plagiobothrys californicus (Gray) Greene var. *californicus*	NA									GU
Plagiobothrys californicus (Gray) Greene var. *fulvescens* Jtn.	NA	MI	RO	CR	AN			66		
Plagiobothrys californicus (Gray) Greene var. *gracilis* Jtn.	NA	31		CR	AN			CA	CL	
Plagiobothrys canescens Benth.	NA		RO	CR				CA	CL	
Brassicaceae										
Arabis glabra (L.) Bernh.	IN			CR						
Arabis hoffmannii (Munz) Roll.	EN		RO	CR						
Athysanus pusillus (Hook.) Greene	NA			CR				CA		
Brassica geniculata (Desf.) J. Ball	IN	MI	RO	CR		NI		CA	CL	
Brassica kaber (DC.) L.C. Wheeler	IN			CR				CA		
Brassica nigra (L.) Koch in Rohling	IN	81		CR		NI	BA	CA	CL	GU
Brassica rapa L. ssp. *sylvestris* (L.) Janchen	IN	MI	81	CR				CA	CL	40

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Cakile edentula (Bigel.) Hook. var. *edentula*	NA	MI	RO	81		NI				
Cakile maritima Scop. ssp. *maritima*	IN	MI	RO	CR	AN	NI		CA	CL	
Capsella bursa-pastoris (L.) Medic.	IN	MI	RO	CR				CA	CL	GU
Cardamine californica (Nutt.) Greene	NA	MI	RO	CR	81			CA		
Cardamine oligosperma Nutt.	IN			CR						
Cardaria draba (L.) Desv.	IN			CR				31		
Caulanthus inflatus Wats.	IN			CR						
Caulanthus lasiophyllus (H. & A.) Pays.	NA	MI	RO	CR	AN	28	BA	CA	CL	GU
Descurainia pinnata (Walt.) Britt. ssp. *menziesii* (DC.) Detl.	NA		RO	CR	AN			CA	CL	GU
Dithyrea maritima A. Davids.	NA	MI				NI				
Draba cuneifolia Nutt. ex T. & G. var. *integrifolia* Wats.	NA							CA		
Erysimum ammophilum Heller	NA		RO							
Erysimum cheiri (L.) Crantz	IN							CA		
Erysimum insulare Greene	NA	MI	RO		AN					
Erysimum morani Roll.	EN									GU
Hutchinsia procumbens (L.) Desv.	NA	MI	RO	CR	AN	NI	BA			GU
Lepidium lasiocarpum Nutt. ex T. & G. var. *lasiocarpum*	NA	MI	RO	CR	26	NI		CA	CL	GU
Lepidium lasiocarpum Nutt. ex T. & G. var. *latifolium* C.L. Hitchc.	NA									GU
Lepidium latipes Hook.	NA			CR				CA	CL	
Lepidium nitidum Nutt. var. *nitidum*	NA	44	RO	CR	AN	NI	BA	CA	CL	GU
Lepidium oblongum Small	IN	MI		CR	AN	NI		CA	CL	GU
Lepidium virginicum L. var. *pubescens* (Greene) Thell.	NA			41				CA	CL	
Lepidium virginicum L. var. *robinsonii* (Thell.) C.L. Hitchc.	NA			CR		NI				
Lobularia maritima (L.) Desv.	IN					NI		CA		
Nasturtium officinale R. Br.	IN	MI		CR				CA		
Raphanus raphanistrum L.	IN		RO					CA	CL	
Raphanus sativus L.	IN		RO	CR				CA	CL	
Sibara filifolia (Greene) Greene	EN			CR				CA		
Sisymbrium altissimum L.	IN							CA		
Sisymbrium irio L.	IN				AN			CA	CL	GU
Sisymbrium officinale (L.) Scop.	IN		31	CR				CA		
Sisymbrium orientale L.	IN							CA		
Thysanocarpus curvipes Hook. var. *curvipes*	NA			CR						
Thysanocarpus curvipes Hook. var. *elegans* (F. & M.) Rob. in Gray	NA							CA		
Thysanocarpus erectus Wats.	NA									GU
Thysanocarpus laciniatus Nutt. ex T. & G. var. *conchuliferus* (Greene) Jeps.	EN			CR						

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Thysanocarpus laciniatus Nutt. ex T. & G. var. *crenatus* (Nutt.) Brewer	NA		RO	CR						
Thysanocarpus laciniatus Nutt. ex T. & G. var. *laciniatus*	NA			CR				CA	CL	
Thysanocarpus laciniatus Nutt. ex T. & G. var. *ramosus* (Greene) Munz	EN		RO	CR						
Tropidocarpum gracile Hook.	NA							CA	CL	
Cactaceae										
Bergerocactus emoryi (Emgelm.) Britt. & Rose	NA							CA	CL	
Mammillaria blossfeldiana Bodeker var. *shurliana* Gates	NA									GU
Opuntia ficus-indica (L.) Mill.	IN			4	81			CA		
Opuntia littoralis (Engelm.) Ckll. var. *littoralis*	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Opuntia oricola Philbrick	NA	MI	72	4	AN	NI	BA	CA	CL	
Opuntia prolifera Engelm.	NA		RO	CR	AN	NI	BA	CA	CL	GU
Callitrichaceae										
Callitriche longipedunculata Morong	NA								CL	
Callitriche marginata Torr. var. *marginata*	NA							CA	CL	
Campanulaceae										
Githopsis diffusa Gray ssp. *diffusa* (see note 2)	NA			CR						GU
Lobelia erinus L.	IN			CR						
Triodanis biflora (R. & P.) Greene	NA		RO	CR				CA		GU
Capparaceae										
Cleome isomeris Greene	NA		RO	31				CA	CL	
Caprifoliaceae										
Lonicera hispidula (Lindl.) Dougl. ex T. & G. var. *vacillans* Gray	NA	31	5	CR				CA	CL	
Lonicera subspicata H. & A. var. *johnstonii* Keck	NA		98	CR				CA		
Sambucus mexicana Presl ex DC.	NA		RO	CR				CA	CL	
Symphoricarpos mollis Nutt. in T. & G.	NA		RO	CR				CA		
Caryophyllaceae										
Arenaria douglasii Fenzl. ex T. & G.	NA		RO	CR				CA	CL	
Arenaria serpyllifolia L.	IN			CR						
Cardionema ramosissima (Weinm.) Nels. & Macbr.	NA	MI	RO	CR						
Cerastium glomeratum Thuill.	IN	MI	RO	CR				CA	CL	GU
Herniaria cinerea DC.	IN									GU
Polycarpon depressum Nutt.	NA			CR				CA		96
Polycarpon tetraphyllum (L.) L.	IN							85		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Sagina decumbens (Ell.) T. & G. ssp. *occidentalis* (Wats.) Crow	NA	MI	RO	CR				CA		
Silene antirrhina L.	NA	42	RO	CR				CA	CL	GU
Silene gallica L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Silene laciniata Cav. ssp. *major* Hitchc. & Maguire	NA	MI	RO	CR	AN			31	CL	
Silene multinervia Wats.	NA	31	31	CR	31			CA		
Spergula arvensis L.	IN		RO	46				CA		
Spergularia bocconii (Scheele) Foucaud	IN			CR				CA	CL	
Spergularia macrotheca (Hornem.) Heynh. ssp. *macrotheca*	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Spergularia marina (L.) Griseb.	NA		RO	CR				CA	CL	GU
Spergularia villosa (Pers.) Camb.	IN		RO					CA	CL	
Stellaria media (L.) Vill.	IN	MI	RO	CR				CA	CL	
Stellaria nitens Nutt.	NA	31	RO	CR				CA		GU
Chenopodiaceae										
Aphanisma blitoides Nutt. ex Moq. in DC.	NA	28	RO	CR	AN	NI	BA	CA	CL	GU
Atriplex argentea Nutt. ssp. *expansa* (Wats.) Hall & Clem.	NA		RO	CR				CA	CL	
Atriplex barclayana (Benth.) D. Dietr. ssp. *dilitata* (Greene) Hall & Clem.	NA									GU
Atriplex barclayana (Benth.) D. Dietr. ssp. *palmeri* (Wats.) Hall & Clem.	NA									GU
Atriplex californica Moq. in DC.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Atriplex coulteri (Moq.) D. Dietr.	NA	MI	RO	CR	AN	NI		CA	CL	
Atriplex lentiformis (Torr.) Wats. ssp. *breweri* (Wats.) Hall & Clem.	NA	31		CR	AN	31		CA	CL	
Atriplex leucophylla (Moq. in DC.) D. Dietr.	NA	MI	RO	CR	AN	NI		CA	CL	
Atriplex pacifica Nels.	NA			CR	AN	31		CA	CL	
Atriplex patula L. ssp. *hastata* (L.) Hall & Clem.	IN	MI		CR		NI		CA		
Atriplex rosea L.	IN							CA		
Atriplex semibaccata R. Br.	IN	MI	RO	CR	AN	NI	BA	CA	CL	
Atriplex serenana A. Nels. var. *serenana*	NA		46	46				CA		
Atriplex watsonii A. Nels. in Abrams	NA	31	31	CR		NI		CA	CL	
Bassia hyssopifolia (Pall.) Kuntze	NA							CA	CL	
Beta vulgaris L. ssp. *maritima* (L.) Arcang.	IN	MI			AN			CA	CL	
Chenopodium album L.	IN		5	CR						
Chenopodium ambrosioides L. var. *ambrosioides*	IN		RO	CR				CA		
Chenopodium berlandieri Moq. var. *sinuatum* (J. Murr.) H.A. Wahl	NA		RO	CR	AN			CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Chenopodium californicum (Wats.) Wats.	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Chenopodium multifidum L.	IN		RO			NI				
Chenopodium murale L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Monolepis nuttalliana (Schult.) Greene	NA	MI	RO	CR					CL	
Salicornia subterminalis Parish	NA	MI	RO	CR				CA	CL	
Salicornia virginica L.	NA	MI	RO	CR	AN	NI		CA	CL	
Salsola iberica Sennen & Pau	IN			CR		NI		CA	CL	
Suaeda californica Wats.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Cistaceae										
Helianthemum greenei Rob.	EN	68	RO	CR				CA		
Helianthemum scoparium Nutt.	NA		RO	CR				CA		
Convolvulaceae										
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt	EN					NI	BA		CL	
Calystegia macrostegia (Greene) Brummitt ssp. *cyclostegia* (House) Brummitt	NA							CA		
Calystegia macrostegia (Greene) Brummitt ssp. *intermedia* (Abrams) Brummitt	NA							CA		
Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia* (San Martin Isl.)	EN	MI	RO	CR	AN			CA		GU
Calystegia soldanella (L.) R. Br.	NA	MI	RO	CR				58	CL	
Convolvulus arvensis L.	IN		RO	CR				CA		
Convolvulus simulans L.	NA			5				68	CL	
Cressa truxillensis HBK. var. *vallicola* (Heller) Munz	NA	MI	RO	CR				CA	CL	76
Cuscuta californica H. & A.	NA		RO						CL	
Cuscuta ceanothi Behr.	NA			CR						
Cuscuta corymbosa R. & P. var. *grandiflora* Engelm.	NA									GU
Cuscuta occidentalis Millsp.	NA							CA		
Cuscuta salina Engelm. var. *salina*	NA		RO	CR	AN					
Dichondra occidentalis House	NA	MI	RO	CR				CA		
Ipomoea cairica (L.) Sweet	IN							CA		
Ipomoea nil (L.) Roth	IN							CA		
Cornaceae										
Cornus glabrata Benth.	NA							CA		
Crassulaceae										
Crassula aquatica (L.) Schoenl. in Engl. & Prantl	NA							CA		
Crassula erecta (H. & A.) Berger	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Dudleya blochmanae (Eastw.) Moran ssp. *insularis* (Moran) Moran	EN		RO							

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Dudleya caespitosum (Haw.) Britt. & Rose	NA			CR	AN					
Dudleya candelabrum Rose	EN		RO	CR						
Dudleya greenei Rose	EN	MI	RO	CR	AN			CA		
Dudleya guadalupensis Moran	EN									GU
Dudleya hassei (Rose) Moran	EN							CA		
Dudleya nesiotica (Moran) Moran	EN			CR						
Dudleya traskiae (Rose) Moran	EN						BA			
Dudleya virens (Rose) Moran	NA					NI		CA	CL	GU
Crossosomataceae										
Crossosoma californicum Nutt.	NA							CA	CL	GU
Cucurbitaceae										
Cucurbita foetidissima HBK.	NA			CR						
Marah guadalupensis (Wats.) Greene	EN									GU
Marah macrocarpus (Greene) Greene	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Elatinaceae										
Elatine californica Gray	NA							CA		
Ericaceae										
Arbutus menziesii Pursh	NA			CR						
Arctostaphylos catalinae P.V. Wells	EN							CA		
Arctostaphylos confertiflora Eastw.	EN		RO							
Arctostaphylos insularis Greene f. *insularis*	EN			CR						
Arctostaphylos insularis Greene f. *pubescens* (Eastw.) P.V. Wells	EN			CR						
Arctostaphylos tomentosa (Pursh) Lindl. ssp. *insulicola* P.V. Wells	EN		RO	CR						
Arctostaphylos tomentosa (Pursh) Lindl. ssp. *subcordata* (Eastw.) P.V. Wells	EN		RO	CR						
Arctostaphylos viridissima (Eastw.) McMinn	EN			CR						
Comarostaphylis diversifolia (Parry) Greene ssp. *planifolia* (Jeps.) Wallace ex Thorne	NA		RO	CR				CA		
Vaccinium ovatum Pursh	NA		RO	CR						
Xylococcus bicolor Nutt.	NA							CA		
Euphorbiaceae										
Eremocarpus setigerus (Hook.) Benth.	NA		RO	CR				CA	CL	
Euphorbia crenulata Engelm.	NA							CA		
Euphorbia melanadenia Torr.	NA									95
Euphorbia misera Benth.	NA							CA	CL	GU
Euphorbia peplis L.	IN		RO	CR				CA	CL	
Euphorbia pondii Millsp.	NA									GU
Euphorbia serpyllifolia Pers. var. *serpyllifolia*	NA							CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Euphorbia spathulata Lam.	NA							CA	CL	
Ricinus communis L.	IN			41		NI		CA	CL	
Fabaceae										
Acacia decurrens Willd.	IN							CA		
Acacia malanoxylon R. Br.	IN			CR				CA		
Astragalus curtipes Gray	NA	MI	RO							
Astragalus didymocarpus H. & A. ssp. *didymocarpus*	NA	MI	RO	CR	AN			CA	CL	
Astragalus gambelianus Sheld.	NA			CR				CA		
Astragalus miguelensis Greene	EN	MI	RO	CR	AN				CL	
Astragalus nevinii Gray	EN								CL	
Astragalus traskiae Eastw.	EN					NI	BA			
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne	NA		RO	CR	AN			CA		
Astragalus trichopodus (Nutt.) Gray ssp. *trichopodus*	NA							CA		
Coronilla valentina L.	IN							CA		
Cystisus linifolius (L.) Lam.	IN							CA		
Cytisus monspessulanus L.	IN							CA		
Lathyrus laetiflorus Greene ssp. *alefeldii* (White) Brads.	NA							CA		
Lathyrus laetiflorus Greene ssp. *barbarae* (White) C.L. Hitchc.	NA		RO	CR	AN			CA	CL	
Lathyrus tingitanus L.	IN							CA		
Lathyrus vestitus Nutt. ex T. & G. ssp. *vestitus*	NA		RO	CR	81					
Lotus argophyllus (Gray) Greene ssp. *adsurgens* (Dunkle) Raven	EN							CL		
Lotus argophyllus (Gray) Greene ssp. *niveus* (Greene) Munz	EN			CR						
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven	EN					NI	BA	CA	CL	GU
Lotus corniculatus L.	IN			CR				CA		
Lotus grandiflorus (Benth.) Greene var. *grandiflorus*	NA		RO	CR				CA		GU
Lotus hamatus Greene	NA		RO	CR				CA	CL	
Lotus heermannii (Dur. & Hilg.) Greene ssp. *heermannii*	NA							70		
Lotus humistratus Greene	NA			CR				CA		
Lotus micranthus Benth.	NA			CR						
Lotus purshianus (Benth.) Clem. & Clem. ssp. *purshianus*	NA			CR				CA		
Lotus salsuginosus Greene ssp. *salsuginosus*	NA	MI	RO	CR	AN			CA		
Lotus scoparius (Nutt. in T. & G.) Ottley var. *dendroideus* (Greene) Ottley	NA	MI	RO	CR	AN			CA	CL	
Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *scoparius*	NA	MI	RO	CR	AN			CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *traskiae* (Eastw. ex Noddin in Abrams) Raven	EN								CL	
Lotus scoparius (Nutt. in T. & G.) Ottley var. *veatchii* (Greene) Ottley	NA	MI		CR						
Lotus strigosus (Nutt. in T. & G.) Greene ssp. *strigosus*	NA	MI	RO	CR	AN			CA	CL	
Lotus subpinnatus Lag.	NA		RO	CR	AN			CA		
Lupinus agardhianus Heller	NA		RO	CR				CA	CL	
Lupinus albifrons Benth. ssp. *albifrons*	NA	MI	RO	CR	AN	NI		CA		
Lupinus albifrons Benth. var. *douglasii* (J.G. Agardh) C.P. Sm.	NA	MI	RO	CR		NI		31		
Lupinus arboreus Sims	NA	MI	RO	12						
Lupinus bicolor Lindl. ssp. *microphyllus* (Wats.) D. Dunn	NA	MI	RO	CR	AN	NI		CA	CL	GU
Lupinus bicolor Lindl. ssp. *pipersmithii* (Heller) D. Dunn	NA							86		
Lupinus bicolor Lindl. ssp. *tridentatus* (Eastw. ex C.P. Sm.) D. Dunn	NA			CR						
Lupinus bicolor Lindl. ssp. *umbellatus* (Greene) D. Dunn	NA	MI	RO	CR	47			CA	CL	
Lupinus concinnus J.G. Agardh ssp. *concinnus*	NA		31	CR				CA		
Lupinus densiflorus Benth. var. *palustris* (Kell.) C.P. Sm.	NA		RO	CR						
Lupinus guadalupensis Greene	EN								CL	GU
Lupinus hirsutissimus Benth.	NA		RO	CR				CA	CL	
Lupinus latifolius J.G. Agardh ssp. *dudleyi* (C.P. Sm.) Kenney & D. Dunn	NA		91							
Lupinus nanus Dougl. in Benth. ssp. *nanus*	NA			41						
Lupinus niveus Wats.	EN									GU
Lupinus polycarpus Greene	NA		RO							
Lupinus succulentus Dougl. ex Koch	NA	MI	RO	CR	AN			CA	CL	
Lupinus truncatus Nutt. ex H. & A.	NA		RO	CR	AN			CA	CL	
Medicago polymorpha L. var. *brevispina* (Benth.) Heyn.	IN		RO	CR				CA	CL	GU
Medicago polymorpha L. var. *polymorpha*	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Medicago sativa L.	IN	42	RO	CR	AN	NI		CA	CL	
Melilotus alba Medicus	IN			CR		NI		CA	CL	
Melilotus indica (L.) All.	IN	MI	RO	CR	AN	NI		CA	CL	GU
Pickeringia montana Nutt. ssp. *montana*	NA			CR						
Spartium junceum L.	IN					NI		CA		
Trifolium albopurpureum T. & G.	NA		RO	CR		NI		CA		
Trifolium amplectens T. & G. var. *amplectens*	NA	MI	RO	CR	81	28		CA	CL	GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Trifolium amplectens T. & G. var. *truncatum* (Greene) Jeps.	NA	47	RO	CR	AN			CA	33	
Trifolium barbigerum Torr.	NA	MI	RO							
Trifolium ciliolatum Benth.	NA		RO	CR				CA		
Trifolium depauperatum Desv.	NA			CR		NI				
Trifolium fucatum Lindl. var. *gambelii* (Nutt.) Jeps.	NA	MI	RO	CR				CA	CL	
Trifolium gracilentum T. & G.	NA	MI	RO	CR	AN	NI		CA	CL	GU
Trifolium macraei H. & A.	NA		RO	CR				CA		
Trifolium microcephalum Pursh	NA	MI	RO	CR				CA	CL	GU
Trifolium microdon H. & A. var. *pilosum* Eastw.	EN			41		NI		CA		
Trifolium palmeri Wats.	EN					NI	BA	CA	CL	GU
Trifolium repens L.	IN							CA		
Trifolium tridentatum Lindl. var. *aciculare* (Nutt.) McDer.	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Trifolium tridentatum Lindl. var. *tridentatum*	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Trifolium variegatum Nutt. in T. & G.	NA			CR						
Vicia americana Muhl. ex Willd.	NA	MI	RO	CR						
Vicia dasycarpa Ten.	IN					NI		CA		
Vicia exigua Nutt. in T. & G.	NA	42	RO	CR	AN			CA	CL	GU
Vicia hassei Wats.	NA		RO	CR	AN	NI		57	CL	GU
Vicia villosa Roth	IN					NI				
Fagaceae										
Quercus agrifolia Nee var. *agrifolia*	NA		RO	CR						
Quercus chrysolepis Liebm.	NA			CR				CA	CL	
Quercus douglasii H. & A.	NA			CR				CA		
Quercus dumosa Nutt.	NA		RO	CR				CA		
Quercus engelmannii Greene	NA							CA		
Quercus lobata Nee	NA			CR				CA		
Quercus × *macdonaldii* Greene	EN		RO	CR				CA		
Quercus × *morehus* Kell.	EN			CR						
Quercus tomentella Englem.	EN		RO	CR	AN			CA	CL	GU
Quercus wislizenii A. DC. var. *frutescens* Englem.	NA			CR						
Frankeniaceae										
Frankenia grandifolia Cham. & Schlecht. var. *grandifolia*	NA	MI	RO	CR	AN	NI		CA	CL	GU
Garryaceae										
Garrya elliptica Dougl.	NA			CR						
Gentianaceae										
Centaurium davyi (Jeps.) Abrams	NA		RO	CR					CL	
Centaurium exaltatum (Griseb.) W. Wight	NA		5	CR						
Centaurium muhlenbergii (Griseb.) W. Wight	NA			52						

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Centaurium venustum (Gray) Rob.	NA							CA		
Geraniaceae										
Erodium botrys (Cav.) Bertol.	IN		RO	CR					CL	
Erodium cicutarium (L.) L'Her.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Erodium macrophyllum H. & A. var. *californicum* (Greene) Jeps.	NA			CR						
Erodium moschatum (L.) L'Her.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Erodium obtusiplicatum (Maire, Weiller & Wilcz.) J.T. Howell	IN		RO					CA		
Erodium texanum Gray	NA							CA		
Geranium carolinianum L.	IN		RO	CR				CA		
Geranium dissectum L.	IN		RO							
Pelargonium × *hortorum* Bailey	IN		RO	CR		NI		CA		
Pelargonium peltatum (L.) L'Her. ex Ait.	IN					NI				
Hydrophyllaceae										
Emmenanthe penduliflora Benth.	NA			CR				CA	CL	GU
Eriodictyon traskiae Eastw. ssp. *traskiae*	EN							CA		
Eucrypta chrysanthemifolia (Benth.) Greene var. *chrysanthemifolia*	NA	MI	RO	CR	AN			CA	CL	GU
Nemophila menziesii H. & A. ssp. *menziesii*	NA							CA		
Nemophila pedunculata Dougl. ex Benth.	NA	MI	RO	CR		49				
Phacelia cicutaria Greene ssp. *hispida* (Gray) J. Beauchamp ex Thorne	NA		RO	CR	AN			CA	CL	
Phacelia cinerea Eastw. ex Macbr.	EN					NI				
Phacelia distans Benth.	NA	MI	RO	CR	AN		BA	CA	CL	
Phacelia divaricata (Benth.) Gray var. *insularis* (Munz) Munz	EN	MI	RO							
Phacelia floribunda Greene	EN								CL	GU
Phacelia grandiflora (Benth.) Gray	NA		RO	CR				CA		
Phacelia lyonii Gray	EN							CA	CL	
Phacelia phyllomanica Gray	EN									GU
Phacelia ramosissima Dougl. ex Lehm. var. *austrolitoralis* Munz	NA		RO	CR						
Phacelia ramosissima Dougl. ex Lehm. var. *montereyensis* Munz	NA	MI	RO							
Phacelia viscida (Benth.) Torr.	NA	42	RO	CR	AN			CA		
Pholistoma auritum (Lindl.) Lilja ex Lind.	NA			CR			BA	CA	CL	
Pholistoma racemosum (Nutt.) Const.	NA			CR			BA	CA	CL	GU
Juglandaceae										
Juglans californica Wats.	NA							CA		
Lamiaceae										
Lamium amplexicaule L.	IN			CR						

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Lepechinia calycina (Benth.) Epl. in Munz	NA		RO				BA			
Lepechinia fragrans (Greene) Epl.	NA		RO	CR				CA		
Marrubium vulgare L.	IN	MI	RO	CR		NI		CA	CL	
Mentha citrata Ehrh.	IN							CA		
Mentha spicata L.	IN			81				CA		
Nepeta cataria L.	IN							CA		
Pogogyne tenuiflora Gray	EN									GU
Salvia apiana Jeps. var. *apiana*	NA							CA		
Salvia brandegei Munz	NA		RO							
Salvia columbariae Benth. ssp. *columbariae*	NA		RO	CR				CA	CL	
Salvia mellifera Greene	NA		RO	CR	AN			CA		
Satureja douglasii (Benth.) Briq.	NA							CA		
Satureja palmeri (Gray) Briq.	EN									GU
Scutellaria tuberosa Benth. ssp. *australis* Epl.	NA			CR						
Stachys ajugoides Benth.	NA			52						
Stachys bullata Benth.	NA		RO	CR	AN					
Trichostema lanceolatum Benth.	NA							CA		
Linaceae										
Hesperolinon micranthum (Gray) Small	NA							CA		
Loasaceae										
Mentzelia affinis Greene	NA			CR				CA	CL	
Mentzelia micrantha (H. & A.) T. & G.	NA		5	CR				CA	CL	GU
Lythraceae										
Ammannia coccinea Rottb.	NA							CA		
Lythrum californicum T. & G.	NA			CR						
Malvaceae										
Althaea rosea (L.) Cav.	IN							CA		
Eremalche exilis (Gray) Greene	NA			5				CA	CL	
Lavatera assurgentiflora Kell. (see note 3)	EN	MI	RO		31	NI		CA	CL	
Lavatera lindsayi Moran	EN									GU
Lavatera occidentalis Wats.	NA									GU
Malacothamnus clementinus (M. & J.) Kearn.	EN							CL		
Malacothamnus fasciculatus (Nutt.) Greene ssp. *catalinensis* (Eastw.) Thorne	NA							CA		
Malacothamnus fasciculatus (Nutt.) Greene var. *nesioticus* (Rob.) Kearn.	EN			CR						
Malva parviflora L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Malvella leprosa (Ortega) Krapovickas	NA		81					CA	CL	11

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Sidalcea malvaeflora (DC.) Gray ex Benth ssp. *malvaeflora*	NA	MI	RO	CR						
Sphaeralcea palmeri Rose	EN									GU
Sphaeralcea sulphurea Wats.	EN									GU
Moraceae										
Ficus carica L.	IN	MI		CR				CA		
Myrtaceae										
Eucalyptus globulus Labill.	IN		RO	CR	AN	NI		CA		
Nyctaginaceae										
Abronia latifolia Esch.	NA	MI								
Abronia maritima Nutt. ex Wats.	NA	MI	RO	CR	AN	NI		CA	CL	
Abronia umbellata Lam.	NA	MI	RO	CR		NI		CA	CL	
Mirabilis californica Gray var. *californica*	NA		46	CR	AN		BA	CA	CL	
Mirabilis heimerlii (Standl.) Macbr.	EN									GU
Oleaceae										
Hesperelaea palmeri Gray	EN									GU
Olea europaea L.	IN			CR						
Onagraceae										
Camissonia californica (Nutt. ex T. & G.) Raven	NA		RO	CR				CA		
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*	NA	MI	RO	CR		NI	BA		CL	
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *suffruticosa* (Wats.) Raven	NA					NI				
Camissonia guadalupensis (Wats.) Raven ssp. *clementina* (Raven) Raven	EN								CL	
Camissonia guadalupensis (Wats.) Raven ssp. *guadalupensis*	EN									GU
Camissonia hirtella (Greene) Raven	NA			CR						
Camissonia ignota (Jeps.) Raven	NA			CA						
Camissonia intermedia Raven	NA			CR				CA		
Camissonia micrantha (Hornem. ex Spreng.) Raven	NA	MI	RO	CR				CA	CL	
Camissonia robusta Raven	NA	MI		CR				CA	CL	GU
Camissonia strigulosa (F. & M.) Raven	NA	47	RO							
Clarkia davyi (Jeps.) Lewis & Lewis	NA		RO							
Clarkia epilobioides (Nutt.) Nels. & Macbr.	NA		RO	CR	81			CA	CL	
Clarkia prostrata Lewis & Lewis	NA		RO							
Clarkia purpurea (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis	NA		RO	CR				CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Clarkia unguiculata Lindl.	NA		5	CR				CA		
Epilobium canum (Greene) Raven ssp. *canum*	NA	42	RO	CR	AN			CA	CL	
Epilobium ciliatum Raf. ssp. *ciliatum*	NA	MI		CR				CA		
Epilobium foliosum (T. & G.) Suksd.	NA									GU
Gaura sinuata Nutt. ex Ser. in DC.	IN							CA		
Ludwigia peploides (HBK.) Raven ssp. *peploides*	NA			CR						
Oenothera elata HBK. ssp. *hirsutissima* (Gray ex Wats.) Dietrich	NA			CR						
Orobanchaceae										
Orobanche bulbosa G. Beck	NA		RO	CR				CA		
Orobanche californica Cham. & Sehlecht. ssp. *grandis* Heckard	NA		RO							
Orobanche fasciculata Nutt.	NA	81	RO	CR				CA		
Orobanche parishii (Jeps.) Heckard ssp. *brachyloba* Heckard	NA	MI	RO	CR		NI		CA		
Orobanche uniflora L. ssp. *occidentalis* (Greene) Abrams ex Ferris	NA	81		CR						
Oxalidaceae										
Oxalis albicans HBK. ssp. *californica* (Abrams) Eiten	NA			CR				CA		
Oxalis albicans HBK. ssp. *pilosa* (Nutt.) Eiten	NA			CR						
Oxalis corniculata L.	IN			CR				CA		
Oxalis pes-caprae L.	IN							CA	CL	
Papaveraceae										
Dendromecon rigidus Benth. ssp. *harfordii* (Kell.) Raven	EN		RO	CR						
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne	EN							CA	CL	
Eschscholzia californica Cham. var. *californica*	NA	MI	RO	CR				CA		GU
Eschscholzia californica Cham. var. *maritima* (Greene) Jeps.	NA	MI	RO	CR						
Eschscholzia californica Cham. var. *peninsularis* (Greene) Munz	NA			CR				CA		
Eschscholzia elegans Greene	EN									GU
Eschscholzia frutescens (Greene) J.T. Howell	EN									GU
Eschscholzia palmeri Rose	EN									GU
Eschscholzia ramosa (Greene) Greene	NA		RO	CR	26	73	BA	CA	CL	GU
Meconella denticulata Greene	NA			CR						
Papaver californicum Gray	NA			CR						
Papaver somniferum L.	IN							CA		
Platystemon californicus Benth.	NA	MI	RO	CR	AN	NI	BA	CA		GU
Romneya coulteri Harv.	NA							CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Stylomecon heterophylla (Benth.) G. Taylor	NA	MI	RO	CR	AN		BA	CA	CL	
Pittosporaceae										
Sollya heterophylla Lindl.	IN							CA		
Plantaginaceae										
Plantago bigelovii Gray ssp. *californica* (Greene) Bassett	NA	MI	RO							
Plantago coronopus L.	IN							CA		
Plantago erecta Morris ssp. *erecta*	NA	42	RO	CR	AN			CA	CL	
Plantago hirtella HBK. ssp. *galleottiana* (Dcne.) Thorne	NA	42	RO	CR						
Plantago lanceolata L.	IN			CR					CL	
Plantago major L.	IN			CR				CA		
Plantago maritima L. var. *californica* (Fern.) Pilg.	NA		RO							
Plantago ovata Forssk.	IN		RO		AN	NI	BA	CA	CL	GU
Platanaceae										
Platanus racemosa Nutt.	NA			CR				CA		
Plumbaginaceae										
Armeria maritima (Mill.) Willd. ssp. *californica* (Boiss.) G.H.M. Lawr.	NA		RO							
Limonium perezii (Stapf.) F.T. Hubb. ex Bailey	IN							CA	CL	
Limonium sinuatum (L.) Mill.	IN							CA		
Polemoniaceae										
Allophyllum gilioides (Benth.) A. Grant & V. Grant	NA									GU
Allophyllum glutinosum (Benth.) A. Grant & V. Grant	NA							CA		
Eriastrum filifolium (Nutt.) Woot. & Standl.	NA			CR				CA	CL	
Gilia angelensis V. Grant	NA			CR	AN			CA	CL	
Gilia capitata Sims ssp. *abrotanifolia* (Nutt. ex Greene) V. Grant	NA			CR				CA		
Gilia clivorum (Jeps.) V. Grant	NA	MI	RO	CR	AN			CA		
Gilia nevinii Gray	EN		RO	CR	AN	NI	BA	CA	CL	GU
Gilia tenuiflora Benth. ssp. *hoffmannii* (Eastw.) A. Grant & V. Grant	EN		RO							
Linanthus androsaceus (Benth.) Greene ssp. *luteus* (Benth.) Mason	NA	81	5	CR						
Linanthus bicolor (Nutt.) Greene ssp. *bicolor*	NA	42	RO	31				CA	CL	
Linanthus dianthiflorus (Benth.) Greene ssp. *dianthiflorus*	NA			CR				CA		
Linanthus pygmaeus (Brand) J.T. Howell ssp. *pygmaeus*	EN								CL	GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Navarretia atractyloides (Benth.) H. & A.	NA		RO	CR				CA	CL	
Navarretia hamata Greene var. *foliacea* (Greene) Thorne	NA							CA		
Navarretia hamata Greene var. *hamata*	NA			CR				CA	CL	96
Polygalaceae										
Polygala californica Nutt.	NA			CR						
Polygonaceae										
Chorizanthe coriacea Goodm.	NA		RO	CR				CA		
Chorizanthe staticoides Benth. ssp. *staticoides*	NA		5	CR				CA		
Chorizanthe wheeleri Wats.	NA		RO	CR						
Eriogonum arborescens Greene	EN		RO	CR	AN					
Eriogonum cinereum Benth.	NA		RO							
Eriogonum fasciculatum Benth. ssp. *fasciculatum*	NA							CA		
Eriogonum giganteum Wats. ssp. *compactum* (Dunkle) Munz	EN						BA			
Eriogonum giganteum Wats. ssp. *formosum* (K. Bdg.) Raven	EN								CL	
Eriogonum giganteum Wats. ssp. *giganteum* (see note 4)	EN							CA		
Eriogonum grande Greene var. *dunklei* Reveal	EN	MI								
Eriogonum grande Greene ssp. *grande*	NA		RO	CR	AN	NI		CA	CL	
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz	EN	MI	RO	CR	AN					
Eriogonum grande Greene ssp. *timorum* (Reveal) Munz	EN					NI				
Eriogonum zapatoense Moran	EN									GU
Polygonum arenastrum Bor.	IN		RO	CR				CA	CL	
Polygonum argyrocoleon Steud. ex Kunze	IN			CR				CA	CL	
Polygonum aviculare L.	IN		RO	CR				CA	CL	
Pterostegia drymarioides F. & M.	NA	MI	RO	CR	AN		BA	CA	CL	GU
Rumex angiocarpus Murbeck	IN			CR						
Rumex conglomeratus Murr.	IN		RO	CR				CA		
Rumex crispus L.	IN	MI	RO	CR	AN	NI		CA	CL	
Rumex fueginus Phil.	NA	MI		41				31		
Rumex pulcher L.	IN			CR						
Rumex salicifolius Weinm.	NA	MI	RO	CR		NI		CA	CL	
Portulacaceae										
Calandrinia breweri Wats.	NA		RO	CR						
Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr.	NA	MI	RO	CR	AN		BA	CA	CL	GU
Calandrinia maritima Nutt.	NA		RO	CR	AN		BA	CA	CL	GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Calyptridium monandrum Nutt. in T. & G.	NA			52						
Claytonia perfoliata Donn var. *parviflora* (Dougl. ex Hook.) Torr.	NA			CR						
Claytonia perfoliata Donn var. *perfoliata*	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Montia fontana L. ssp. *amporitana* Sennen	NA			CR				31		
Portulaca oleracea L.	IN			CR					CA	
Talinum guadalupense Dudl. in D.S. Jordan	EN								GU	
Primulaceae										
Anagalis arvensis L.	IN	31	RO	CR	AN			CA		93
Anagalis minima (L.) Krause	NA		RO							
Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thomps.	NA		RO	CR	AN			CA	CL	GU
Samolus parviflorus Raf.	NA			CR						
Ranunculaceae										
Clematis lasiantha Nutt. in T. & G.	NA		31	CR						
Clematis ligusticifolia Nutt. in T. & G.	NA		RO	CR				CA		
Delphinium kinkiense Munz	EN								CL	
Delphinium parryi Gray ssp. *parryi*	NA	MI	RO	CR	AN			CA	CL	
Delphinium variegatum T. & G. ssp. *thornei* Munz	EN								CL	
Myosurus minimus L. var. *filiformis* Greene	NA									GU
Ranunculus californicus Benth. ssp. *californicus*	NA	MI	RO	CR						
Ranunculus californicus Benth. var. *cuneatus* Greene	NA	MI	31	CR				31		
Ranunculus hebecarpus H. & H.	NA							CA	GU	
Resedaceae										
Oligomeris linifolia (Vah.) Macbr.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Reseda odorata L.	IN		31					CA		
Rhamnaceae										
Ceanothus arboreus Greene	EN		RO	CR				CA		
Ceanothus crassifolius Torr.	NA									GU
Ceanothus megacarpus Nutt. ssp. *insularis* (Eastw.) Raven	EN	42	RO	CR	AN			CA	CL	
Ceanothus megacarpus Nutt. ssp. *megacarpus*	NA			CR				CA	CL	
Rhamnus californica Esch. ssp. *californica*	NA			CR						
Rhamnus pirifolia Greene	EN	42	RO	CR				CA	CL	GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Rosaceae										
Adenostoma fasciculatum H. & A. var. *fasciculatum*	NA		RO	CR				CA	CL	
Alchemilla occidentalis Nutt.	NA		RO	CR				CA	CL	GU
Cercocarpus betuloides Nutt. ex T. & G. ssp. *betuloides*	NA		31	CR				CA		
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne	NA		RO	CR				CA		
Cercocarpus traskiae Eastw.	EN							CA		
Heteromeles arbutifolia (Ait.) M. Roem.	NA	MI	RO	CR	AN	31		CA	CL	GU
Holodiscus discolor (Pursh) Maxim. ssp. *discolor*	NA			CR				CA		
Lyonothamnus floribundus Gray ssp. *asplenifolius* (Greene) Raven (see note 5)	EN		RO	CR					CL	
Lyonothamnus floribundus Gray ssp. *floribundus*	EN							CA		
Potentilla egedii Wormsk. var. *grandis* (Rydb.) J.T. Howell	NA	MI		CR						
Potentilla glandulosa Lindl. ssp. *glandulosa*	NA							CA		
Prunus lyonii (Eastw.) Sarg.	NA		RO	CR	AN			CA	CL	
Prunus persica (L.) Batsch	IN							CA		
Rosa californica Cham. & Schlecht.	NA		RO	CR				CA		
Rubus procerus P.J. Muell.	IN							CA		
Rubus ursinus Cham. & Schlecht.	NA	MI	RO	CR	26			CA		
Rubiaceae										
Galium angulosum Gray	EN									GU
Galium angustifolium Nutt. ex T. & G. ssp. *angustifolium*	NA							CA		
Galium angustifolium Nutt. ex T. & G. ssp. *foliosum* (Hilend & Howell) Dempst. & Steb.	EN		RO	CR	AN					
Galium aparine L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Galium buxifolium Greene	EN	MI	RO	CR						
Galium californicum H. & A. ssp. *flaccidum* (Greene) Dempst.	NA			CR						
Galium californicum H. & A. ssp. *miguelense* (Greene) Dempst. & Steb.	EN	MI	RO							
Galium catalinense Gray ssp. *acrispum* Dempst.	EN								CL	
Galium catalinense Gray ssp. *catalinense*	EN							CA		
Galium nuttallii Gray ssp. *insulare* Ferris	EN		RO	CR	31			CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Galium porrigens Dempst. var. *porrigens*	NA		RO	CR				22		
Rutaceae										
Ruta chalepensis L.	IN			CR				CA		GU
Salicaceae										
Populus fremontii Wats. ssp. *fremontii*	NA		31	CR				CA		
Populus trichocarpa T. & G.	NA		RO	CR				CA		
Populus × *parryi* Sarg.	NA					NI		CA		
Salix hindsiana Benth. var. *hindsiana*	NA			CR				CA		
Salix laevigata Bebb. var. *laevigata*	NA			CR				CA		
Salix lasiandra Benth. var. *lasiandra*	NA			CR						
Salix lasiolepis Benth. var. *lasiolepis*	NA	MI	RO	CR		NI		CA		
Saururaceae										
Anemopsis californica (Nutt.) H. & A.	NA	31	31	CR		NI		CA	76	
Saxifragaceae										
Heuchera maxima Greene	EN		RO	CR	AN					
Jepsonia malvaefolia (Greene) Small	EN		RO	CR	NI			CA	CL	GU
Lithophragma affine Gray ssp. *mixtum* R.L. Taylor	NA							CA		
Lithophragma cymbalaria T. & G.	NA		RO	CR						
Lithophragma maximum Bacig.	EN								CL	
Ribes malvaceum Sm. in Rees var. *malvaceum*	NA		RO	CR	AN				CL	
Ribes menziesii Pursh var. *menziesii*	NA			CR						
Ribes menziesii Pursh var. *thacherianum* Jeps.	EN			CR						
Ribes sanguineum Pursh	NA									GU
Ribes viburnifolium Gray	NA							CA		
Saxifraga californica Greene	NA		RO	CR						
Scrophulariaceae										
Antirrhinum kelloggii Greene	NA			CR				CA		
Antirrhinum kingii Wats. var. *watsoni* (Vasey & Rose) Munz	NA									GU
Antirrhinum multiflorum Penn.	NA			CR						
Antirrhinum nuttallianum Benth. in DC.	NA	MI	RO	CR	AN			CA	CL	GU
Castilleja affinis H. & A. ssp. *affinis*	NA	42	RO	CR	AN			CA		
Castilleja foliolosa H. & A.	NA							CA		
Castilleja fruticosa Moran	EN									GU
Castilleja grisea Dunkle	EN								CL	
Castilleja guadalupensis Bdg.	EN									GU
Castilleja hololeuca Greene	EN	MI	RO	CR	AN					
Castilleja mollis Penn.	NA	MI	RO							
Collinsia heterophylla Buist ex Grah. ssp. *heterophylla*	NA	31	RO					31	CL	

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Diplacus longiflorus Nutt. ssp. *longiflorus*	NA		RO	CR						
Diplacus parviflorus Greene	EN		RO	CR	AN				CL	
Diplacus puniceus Nutt.	NA							CA		
Galvezia speciosa (Nutt.) Gray	NA						BA	CA	CL	GU
Keckiella cordifolia (Benth.) Straw	NA		RO	CR	AN			CA	CL	
Linaria bipartita Willd.	IN							CA		
Linaria canadensis (L.) Dum.-Cours. var. *texana* (Scheele) Penn.	NA	MI	RO	CR	AN			CA	CL	GU
Mimulus brandegei Penn.	EN			CR						
Mimulus brevipes Benth.	NA			67				CA		
Mimulus cardinalis Dougl. ex Benth.	NA			CR				CA		
Mimulus floribundus Dougl. ex Lindl. var. *floribundus*	NA		RO	41				CA	CL	
Mimulus guttatus Fisch. ex DC. ssp. *guttatus*	NA		RO	CR				CA	CL	
Mimulus guttatus Fisch. ex DC. ssp. *littoralis* Penn.	NA		RO							
Mimulus guttatus Fisch. ex DC. ssp. *micranthus* (Heller) Munz	NA			CR						
Mimulus latifolius Gray	EN									GU
Mimulus nasutus Greene	NA			CR						
Mimulus traskiae Grant in Millsp. & Nutt.	EN							CA		
Orthocarpus attenuatus Gray	NA			81						GU
Orthocarpus densiflorus Benth. var. *densiflorus*	NA	MI	RO	CR		NI				
Orthocarpus purpurascens Benth. var. *pallidus* Keck	NA	MI	RO	CR				CA		
Orthocarpus purpurascens Benth. var. *purpurascens*	NA	MI	RO	CR				CA		8
Scrophularia californica Cham. & Schlecht. ssp. *californica*	NA		RO							
Scrophularia villosa Penn. in Millsp. & Nutt.	EN							CA	CL	GU
Verbascum thapsus L.	IN			CR						
Solanaceae										
Datura wrightii Regel	NA		RO	CR				CA		
Lycium brevipes Benth. var. *brevipes*	NA								CL	
Lycium brevipes Benth. var. *hassei* (Greene) C.L. Hitchc.	EN							CA	CL	
Lycium californicum Nutt.	NA				AN	NI	BA	CA	CL	GU
Lycium fremontii Gray	NA		RO							GU
Lycium verrucosum Eastw.	EN					NI				
Nicotiana attenuata Torr. ex Wats. in King	NA									GU
Nicotiana bigelovii (Torr.) Wats. var. *bigelovii*	NA							CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Nicotiana clevelandii Gray	NA			CR				CA		
Nicotiana glauca Grah.	IN							CA		GU
Petunia parviflora Juss.	NA		RO							
Solanum douglasii Dunal in DC.	NA	MI	RO	CR				CA	CL	GU
Solanum elaeagnifolium Cav.	IN			CR				CA		
Solanum nodiflorum Jacq.	IN					NI			CL	GU
Solanum sarrachoides Sendt. ex Mart.	IN			CR						
Solanum wallacei (Gray) Parish ssp. *clokeyi* (Munz) Thorne	EN		RO	CR						
Solanum wallacei (Gray) Parish ssp. *wallacei*	EN							CA		GU
Tamaricaceae										
Tamarix tetrandra Pallas	IN			CR	AN					
Tropaeolaceae										
Tropaeolum majus L.	IN							CA		
Urticaceae										
Hesperocnide tenella Torr.	NA			CR			BA	CA	CL	GU
Parietaria hespera Hinton	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Soleirolia soleirolii (Req.) Dandy	IN					NI				
Urtica dioica L. ssp. *holoserica* (Nutt.) Thorne	NA			CR	AN			CA		
Urtica urens L.	IN		RO	CR				CA		
Valerianaceae										
Centranthus ruber (L.) DC.	IN			CR				CA		
Verbenaceae										
Lippia nodiflora (L.) Michx. var. *rosea* (D. Don) Munz	IN			CR				CA		
Verbena bracteata Lag. & Rodr.	NA							CA		
Verbena lasiostachys Link	NA	42	81	CR				CA	CL	
Verbena robusta Greene	NA	31	RO	CR				CA		
Violaceae										
Viola pedunculata T. & G. ssp. *pedunculata*	NA		RO	CR				CA	CL	
Viscaceae										
Phoradendron bolleanum (Seem.) Eichler ssp. *densum* (Torr.) Wiens	NA									GU
Vitaceae										
Vitis girdiana Munson	NA							CA		
Monocotyledons										
Arecaceae										
Erythaea edulis (Wendl.) Wats.	EN									GU
Cyperaceae										
Carex barbarae Dewey	NA			CR						

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Carex globosa Boott.	NA		RO	CR				31		
Carex gracilior Mkze.	NA		RO	CR						
Carex montereyensis Mkze.	NA			CR						
Carex pansa Bailey	NA		RO							
Carex praegracilis W. Boott.	NA		RO	CR				CA		
Carex rossii Boott.	NA			81						
Carex senta Boott.	NA			CR						
Carex subbracteata Mkze.	NA		RO	CR						
Carex triquetra Boott.	NA		31	CR				CA		
Carex tumulicola Mkze.	NA		81	CR					CL	
Cyperus alternifolius L.	IN			CR						
Eleocharis macrostachya Britt. in Small	NA		RO	29		NI		CA	CL	
Scirpus americanus Pers. var. *monophyllus* (Presl) Koyama	NA		RO							
Scirpus californicus (C.A. Mey.) Steud.	NA		81	CR						
Scirpus cernuus Vahl. ssp. *californicus* (Torr.) Thorne	NA	MI	RO							
Scirpus microcarpus Presl	NA							CA		
Scirpus olneyi Gray	NA		RO			NI				
Scirpus robustus Pursh	NA							63		
Iridaceae										
Chasmanthe aethiopica (L.) N.E. Br.	IN	MI								
Iris ochroleuca L.	IN					NI				
Sisyrinchium bellum Wats.	NA	MI	RO	CR				CA		
Juncaceae										
Juncus acutus L. var. *sphaerocarpus* Englem.	NA							CA		
Juncus balticus Willd.	NA	MI	RO	CR				CA		
Juncus bufonius L.	NA	MI	RO	CR		NI		CA	CL	GU
Juncus effusus L. var. *bruneus* Engelm.	NA			CR						
Juncus effusus L. var. *pacificus* Fern. & Wieg.	NA		81	CR						
Juncus mexicanus Willd.	NA	MI	RO	CR				CA		
Juncus patens E. Mey.	NA		RO	CR					CL	
Juncus phaeocephalus Engelm. var. *phaeocephalus*	NA		RO							
Juncus textilis Buch.	NA							CA		
Juncus xiphioides E. Mey.	NA		RO	CR				CA		
Luzula subsessilis (Wats.) Buch.	NA	31	RO	CR						
Liliaceae										
Allium lacunosum Wats. var. *lacunosum*	NA		RO	CR						
Allium praecox Bdg.	NA	MI	RO	CR				CA	CL	
Asparagus officinalis L.	IN							CA		
Bloomeria crocea (Torr.) Cov. ssp. *crocea*	NA		RO	CR				CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Brodiaea jolonensis Eastw.	NA	81	RO	CR				CA		
Brodiaea kinkiensis Niehaus	EN								CL	
Calochortus albus Dougl. ex Benth. var. *albus*	NA		RO	CR				CA		
Calochortus catalinae Wats.	NA		RO	CR				CA		
Calochortus luteus Dougl. ex Lindl.	NA			CR				31		
Calochortus splendens Dougl. ex Benth.	NA							CA		
Chlorogalum pomeridianum (DC.) Kunth	NA		RO					CA		
Dichelostemma pulchellum (Salisb.) Heller	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Lilium humboldtii Roezl & Leichtl. ssp. *ocellatum* (Kell.) Thorne	NA		RO	CR						
Triteleia clementina Hoov.	EN								CL	
Triteleia guadalupensis Lenz	EN									GU
Zigadenus fremontii Torr. var. *fremontii*	NA		RO	CR	AN					
Orchidaceae										
Epipactis gigantea Dougl. ex Hook.	NA			CR						
Habenaria elegans (Lindl.) Boland.	NA		RO	CR				CA		
Habenaria unalascensis (Spreng.) Wats.	NA			CR				CA		
Poaceae										
Agrostis diegoensis Vasey	NA		RO	CR				CA	CL	
Agrostis exarata Trin.	NA		RO	CR				CA		
Agrostis semiverticillata (Forsk.) C. Chr.	IN		RO	CR	AN			CA		
Agrostis stolonifera L. var. *major* (Gaudin) Farw.	IN							85		
Ammophila arenaria (L.) Link	IN					NI				
Andropogon glomeratus (Walt.) BSP.	NA			CR						
Aristida adscensionis L. var. *modesta* Hack. in Stuckert	NA		RO	CR		31		CA	CL	GU
Aristida divaricata Humb. & Bonpl. in Willd.	NA			CR						
Arundo donax L.	IN					NI				
Avena barbata Brot.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Avena fatua L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Avena sativa L.	IN		RO	CR				CA	CL	39
Bothriochloa barbinodis (Lag.) Herter	NA		31					CA		
Brachypodium distachyon (L.) Beauv.	IN							CA		
Bromus arizonicus (Shear) Steb.	NA	MI	RO	83	AN	NI	BA	CA	CL	
Bromus carinatus H. & A.	NA	MI	RO	CR	AN	NI		CA	CL	
Bromus diandrus Roth	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Bromus madritensis L.	IN			CR	26					
Bromus maritimus (Piper) Hitchc.	NA	MI	RO	CR	AN	NI		CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Bromus mollis L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Bromus pseudolaevipes Wagnon	NA		RO	CR				CA		
Bromus rubens L.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Bromus stamineus Desv. in Gray	IN			CR						
Bromus sterilis L.	IN							CA		
Bromus tectorum L.	IN									GU
Bromus trinii Desv. in C. Gay	NA	46	RO	CR	AN	NI	BA	CA	CL	GU
Bromus vulgaris (Hook.) Shear	NA	31		5				6		
Calamagrostis rubescens Buckl.	NA			CR						
Cortaderia atacamensis (Phil.) Pilg.	IN			CR				CA		
Crypsis aculeata (L.) Ait.	IN							CA		
Cynodon dactylon (L.) Pers.	IN	31	RO	CR	AN	NI		CA	CL	
Dactylis glomerata L.	IN							CA	CL	
Deschampsia danthonioides (Trin.) Munro in Benth.	NA								CL	
Dissanthelium californicum (Nutt.) Benth.	EN							CA	CL	GU
Distichlis spicata (L.) Greene var. *stolonifera* Beetle	NA	MI	RO	CR	AN	NI		CA	CL	
Echinochloa crus-galli (L.) Beauv. var. *crus-galli*	IN							CA		
Ehrharta calycina Sm.	IN							CA	CL	
Elymus condensatus Presl	NA	MI	RO	CR	AN			CA	CL	
Elymus glaucus Buckl. ssp. *glaucus*	NA		46	CR				CA		
Elymus pacificus Gould	NA	MI	81							
Elymus triticoides Buckl.	NA	MI	RO	CR	AN			CA		
Festuca arundinacea Schreb.	IN							CA		
Gastridium ventricosum (Gouan) Schinz & Thell.	IN		RO	CR				CA	CL	
Hordeum brachyantherum Nevski	NA					33				
Hordeum californicum Covas. & Steb.	NA	MI	RO	CR	AN	NI		CA		
Hordeum depressum (Scribn. & Sm.) Rydb.	NA			CR		33				
Hordeum geniculatum All.	IN		RO	CR				CA	CL	
Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvel.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Hordeum murinum L. ssp. *leporinum* (Link) Arcang.	IN	MI	RO	CR	AN	NI		CA	CL	GU
Hordeum pusillum Nutt.	NA	MI		CR	AN		BA	CA	CL	
Hordeum vulgare L.	IN		RO	CR				CA	CL	
Koeleria pyramidata (Lam.) Beauv.	NA		RO	CR						
Lamarckia aurea (L.) Moench	IN	MI	RO	CR	AN	NI	BA	CA	CL	
Lolium perenne L. ssp. *multiflorum* (Lam.) Husnot	IN			CR		NI		CA	CL	
Lolium perenne L. ssp. *perenne*	IN			CR		NI		CA	CL	
Lolium strictum Presl	IN							CA		
Lolium temulentum L.	IN		RO	CR				CA	CL	
Melica imperfecta Trin.	NA	MI	RO	CR	AN		BA	CA	CL	GU
Monanthochloe littoralis Engelm.	NA	MI	RO	CR				CA		

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Muhlenbergia microsperma (DC.) Kunth	NA		RO	CR	AN		BA	CA	CL	GU
Oryzopsis miliacea (L.) Benth. Hook. ex Aschers. & Schweinf.	IN		RO	CR				CA		
Parapholis incurva (L. f.) C.E. Hubb.	IN	MI	RO	CR		NI	BA	CA	CL	
Paspalum dilitatum Poir. in Lam.	IN							CA		
Paspalum distichum L.	IN			81				CA		
Pennisetum clandestinum Hochst. ex Chiov.	IN	81		CR						
Phalaris aquatica L.	IN							CA		
Phalaris canariensis L.	IN	42		41				CA		
Phalaris caroliniana Walt.	NA			CR		NI	BA	CA	CL	GU
Phalaris lemmonii Vasey	NA		RO					CA	CL	
Phalaris minor Retz.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Phalaris paradoxa L.	IN								CL	
Poa annua L.	IN	MI	RO	CR		31		CA	CL	GU
Poa bolanderi Vasey ssp. *howellii* (Vasey & Scribn.) Keck	NA			CR						
Poa douglasii Nees	NA	MI	RO							
Poa palustris L.	NA							CA		
Poa scabrella (Thurb.) Benth. ex Vasey	NA		RO	CR	AN			CA	CL	GU
Polypogon interruptus HBK.	IN	MI	RO	CR				CA	CL	
Polypogon monspeliensis (L.) Desf.	IN	MI	RO	CR		NI	BA	CA	CL	GU
Schismus arabicus Nees	IN							CA		
Schismus barbatus Thell.	IN			CR						
Scleropoa rigida (L.) Griseb.	IN							CA		
Sitanion jubatum J.G. Sm.	IN							CA		
Sorghum bicolor (L.) Moench	IN							CA		
Sorghum halepense (L.) Pers.	IN							CA		
Stipa cernua Steb. & Love	NA		RO	CR	AN	NI		CA	CL	
Stipa columbiana Macoun var. *nelsoni* (Scribn.) Hitchc.	NA					NI				
Stipa lepida Hitchc.	NA	MI	RO	CR	AN	31	BA	CA	CL	GU
Stipa pulchra Hitchc.	NA	MI	RO	CR	AN	NI	BA	CA	CL	
Triticum aestivum L.	IN								CL	
Triticum cylindricum (Host.) Ces., Pass. & Gib.	IN			CR						
Vulpia bromoides (L.) S.F. Gray	IN	MI	RO	CR	AN	31		CA	CL	GU
Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould	NA	MI	5	5	AN	31		CA	CL	GU
Vulpia myuros (L.) K.C. Gmelin var. *hirsuta* Hack.	IN	MI	RO	CR	AN	NI	BA	CA	CL	GU
Vulpia myuros (L.) K.C. Gmelin var. *myuros*	IN							CA	CL	
Vulpia octoflora (Walt.) Rydb. var. *hirtella* (Piper) Henr.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU

Taxon	Occurrence	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Isla Guadalupe
Potamogetonaceae										
Potamogeton crispus L.	IN							CA		
Potamogeton pectinatus L.	NA		RO	CR				CA		
Ruppia maritima L.	NA		RO	CR				CA	CL	96
Typhaceae										
Typha domingensis Pers.	NA	MI	RO	CR		NI		CA		
Typha latifolia L.	NA					NI		CA	CL	
Zosteraceae										
Phyllospadix scouleri Hook.	NA	66			AN	NI	BA	CA	CL	
Phyllospadix torreyi Wats.	NA	MI	RO	CR	AN	NI	BA	CA	CL	GU
Zostera marina L.	NA		RO	CR	AN			CA		GU

Note 1. Davis (1980) proposed these notations for new taxa he recognizes as a result of his detailed studies of *Malacothrix* on the Channel Islands. They are recognized here since placement into earlier associated taxa would add to the systematic confusion. Dr. Davis is preparing a manuscript treating these taxa (pers. comm.).

Note 2. Morin (Systematic Botany 8(4):436–468. 1983) separates the material from Guadalupe Island to var. *guadalupensis* Morin.

Note 3. A detailed discussion by Philbrick (1980) indicated that this species was native on MI, AN, CA, CL, and possibly native on RO, and NI, but probably cultivated on CR. See also Eastwood (1941).

Note 4. Probably introduced on CR (RSA-POM; SBBG).

Note 5. Probably introduced on CA (Moran 596 LAM!).

FLORISTIC RELATIONSHIPS

The following discussion concerns the distribution of native vascular plant taxa on the islands and the floristic relationships among the various islands. Analysis of dispersal types and patterns as well as evolutionary histories for each taxon would be needed to provide information on the origins of the insular floras and is not in the scope of this work. Introduced taxa are generally distributed among the islands and will not be discussed here further (Table 1). Map 1 shows the spacial relationships among the islands while Table 1 and Table 2 summarize the distributions of the taxa.

Nearly 275 of the taxa native to the islands are found on one or more of the islands of the northern group (San Miguel, Santa Rosa, Santa Cruz, and Anacapa), one or more of the islands of the southern group (San Nicolas, Santa Barbara, Santa Catalina, and San Clemente), and are generally distributed on adjacent mainland areas. Some of these taxa are also native to Guadalupe Island, Mexico.

The northern islands exhibit close floristic affinities. The percentages of native taxa shared among the islands are high. The numbers of shared insular endemies are also high. Thirty-eight of the 58 shared insular endemics occur on the northern islands.

Several groupings of native taxa are worthy of note. The first is native taxa found on the northern islands, generally on the mainland, but absent from the southern islands. The second group consists of taxa found on the southern islands, generally on the mainland, but absent from the northern islands. The third group is composed of taxa which have the southern limits of their ranges on the islands or adjacent mainland areas. The fourth group contains taxa with the northern limits of their ranges on the islands or adjacent mainland areas. There are 39 taxa with mainland ranges which terminate considerably north of their insular occurrences. Twenty-three taxa have mainland ranges which terminate considerably south of their insular occurrence. There are also a few taxa which seem to have insular occurrences which represent westerly extensions of inland ranges.

Taxa which occur on one or more of the islands of the northern group but are absent from the southern islands even though their mainland ranges extend far to the south include the following:

Cystopteris fragilis
Polystichum munitum ssp. *munitum*
Woodwardia fimbriolata
Cheilanthes clevelandii
Pinus torreyana
Acer macrophyllum
Berula erecta
Lomatium utriculatum
Agoseria grandiflora
Aster exilis
Chaenactis glabriuscula var. *lanosa*
Gnaphalium ramosissimum
Lasthenia glabrata ssp. *coulteri*

Layia glandulosa ssp. *glandulosa*
Layia platyglossa ssp. *platyglossa*
Lepidospartum squamatum
Micropus californicus
Stephanomeria cichoriacea
Venegasia carpesioides
Cryptantha muricata var. *jonesii*
Pectocarya penicillata
Plagiobothrys californicus var. *fulvescens*
Erysimum ammophilum
Thysanocarpus curvipes var. *curvipes*
Thysanocarpus laciniatus var. *crenatus*
Cardionema ramosissima
Cuscuta ceanothi
Cuscuta salina
Dudleya caespitosum
Cucurbita foetidissima
Arbutus menziesii
Vaccinium ovatum
Lotus micranthus
Lupinus bicolor ssp. *tridentatus*
Lupinus polycarpus
Trifolium variegatum
Vicia americana
Quercus agrifolia
Quercus wislizenii var. *frutescens*
Centaurium exaltatum
Phacelia ramosissima var. *austrolittoralis*
Salvia brandegei
Stachys bullata
Lythrum californicum
Camissonia hirtella
Camissonia ignota
Camissonia strigulosa
Ludwigia peploides
Oenothera elata ssp. *hirsutissima*
Oxalis albicans ssp. *pilosa*
Meconella denticulata
Papaver californicum
Plantago bigelovii ssp. *californica*
Plantago hirtella var. *galeottiana*
Plantago maritima
Claytonia perfoliata var. *parviflora*
Montia fontana ssp. *amporitana*
Anagallis minima
Rumex fueginus
Samolus parviflora
Clematis lasiantha
Ranunculus californicus var. *californicus*
Rhamnus californica ssp. *californica*
Galium californicum ssp. *flaccidum*
Lithophragma cymbalaria
Saxifraga californica
Diplacus longiflorus
Mimulus nasutus
Petunia parviflora
Carex barbarae
Carex globosa
Carex senta
Scirpus californicus
Scirpus cernuus ssp. *californicus*
Juncus effusus var. *pacificus*
Juncus phaeocephalus
Lilium humboldtii ssp. *ocellatum*
Zigadenus fremontii var. *fremontii*
Epipactis gigantea
Aristida divaricata
Hordeum depressum
Poa bolanderi ssp. *howellii*

Several taxa likewise occur on one or more islands of the southern group but are not known from the northern islands even though their mainland ranges may extend far to the north. These are as follows:

Azolla filiculoides
Malosma laurina
Ambrosia psilostachya var. *californica*
Artemisia dracunculus
Baccharis emoryi
Haplopappus palmeri ssp. *pachylepis*
Helenium puberulum
Malacothrix saxatilis var. *tenuifolia*
Microseris douglasii ssp. *douglasii*
Pluchea sericea
Xanthium strumarium var. *canadense*
Cryptantha intermedia
Cryptantha microstachys
Lepidium virginicum var. *pubescens*
Thysanocarpus curvipes var. *elegans*
Tropidocarpum gracile
Callitriche marginata var. *marginata*
Callitriche longipedunculata
Atriplex serenana var. *serenana*
Bassia hyssopifolia
Convolvulus simulans
Cuscuta occidentalis
Cornus glabrata
Crassula aquatica
Elatine californica
Euphorbia crenulata
Euphorbia serpyllifolia var. *serpyllifolia*
Euphorbia spathulata
Nemophila menziesii ssp. *menziesii*
Juglans californica
Salvia apiana var. *apiana*
Trichostema lanceolatum
Eremalche exilis
Malvella leprosa
Camissonia cheiranthifolia ssp. *suffruticosa*
Allophyllum glutinosum
Navarretia hamata ssp. *foliosa*
Eriogonum fasciculatum ssp. *fasciculatum*
Potentilla glandulosa ssp. *glandulosa*
Galium angustifolium ssp. *angustifolium*
Lithophragma affine ssp. *mixtum*
Castilleja foliolosa

Diplacus puniceus
Mimulus brevipes
Verbena bracteata
Vitis girdiana
Scirpus microcarpus
Juncus acutus var. *sphaerocarpus*
Juncus textilis
Calochortus splendens
Deschampsia danthonioides
Stipa columbiana var. *nelsonii*
Typha latifolia

The ranges of the following taxa have their southern limits on the islands or nearby mainland areas:

Equisetum hyemale ssp. *affine*
Athyrium felix-femina var. *sitchensis*
Adiantum pedatum ssp. *aleuticum*
Pinus muricata
Lomatium caruifolium
Agoseris apargioides ssp. *apargioides*
Aster chilensis
Aster radulinus
Baccharis plummerae
Blennosperma nanum
Cirsium brevistylum
Cirsium proteanum
Erigeron glaucus
Erigeron sanctarum
Eriophyllum staechadifolium var. *artemisiaefolium*
Eriophyllum staechadifolium var. *depressum*
Grindelia latifolia
Grindelia stricta ssp. *venulosa*
Haplopappus squarrosus ssp. *grindelioides*
Haplopappus venetus var. *sedoides*
Hemizonia increscens ssp. *increscens*
Hieraceum argutum
Malacothrix coulteri var. *cognata*
Microseris douglasii ssp. *tenella*
Pentachaeta lyonii
Stephanomeria exigua ssp. *coronaria*
Cryptantha leiocarpa
Erysimum insulare
Silene laciniata ssp. *major*
Calystegia macrostegia ssp. *cyclostegia*
Astragalus curvipes
Lotus grandiflorus var. *grandiflorus*
Lupinus arboreus
Lupinus densiflorus var. *palustris*
Pickeringia montana
Trifolium barbigerum
Garrya elliptica
Erodium macrophyllum var. *californicum*
Phacelia ramosissima var. *montereyensis*
Lepechinia fragrans
Satureja douglasii
Hesperolinon micranthum
Ammannia coccinea
Malacothamnus fasciculatus ssp. *catalinensis*
Sidalcea malvaeflora ssp. *malvaeflora*
Abronia latifolia
Orobanche uniflora ssp. *occidentalis*
Eschscholzia californica var. *maritima*
Plantago maritima
Linanthus androsaceus ssp. *luteus*
Linanthus bicolor ssp. *bicolor*
Chorizanthe wheeleri
Calandrinia breweri
Dodecatheon clevelandii ssp. *insularis*
Ranunculus californicus var. *cuneatus*
Holodiscus discolor ssp. *discolor*
Potentilla egedii var. *grandis*
Salix lasiandra var. *lasiandra*
Ribes malvaceum
Ribes menziesii var. *menziesii*
Antirrhinum multiflorum
Mimulus cardinalis
Mimulus floribundus
Mimulus guttatus ssp. *littoralis*
Mimulus guttatus ssp. *micranthus*
Scrophularia californica ssp. *californica*
Nicotiana bigelovii
Carex gracilior
Carex montereyensis
Carex pansa
Carex subbracteata
Luzula subsessilis
Juncus effusus var. *brunneus*
Allium lacunosum
Calamagrostis rubescens
Koeleria pyramidata
Poa douglasii

The following taxa have the northern limits of their ranges on the islands or nearby mainland:

Notholaena californica
Notholaena newberryi
Rhus ovata
Filago arizonica
Microseris douglasii ssp. *platycarpha*
Stephanomeria diegensis
Lepidium virginicum var. *robinsonii*
Thysanocarpus laciniatus var. *laciniatus*
Bergerocactus emoryi
Opuntia oricola
Opuntia prolifera
Cleome isomeris
Aphanisma blitoides
Atriplex coulteri
Atriplex pacifica
Atriplex watsonii
Xylococcus bicolor
Euphorbia misera

Lathyrus laetiflorus ssp. *alefeldii*
Lotus heermannii
Lupinus agardhianus
Phacelia grandiflora
Lepechinia fragrans
Oxalis albicans ssp. *californicus*
Linanthus dianthiflorus ssp. *dianthiflorus*
Eriogonum cinereum
Oligomeris linifolia
Ceanothus megacarpus ssp. *megacarpus*
Antirrhinum nuttallianum
Orthocarpus purpurascens var. *pallidus*
Lycium californicum
Nicotiana clevelandii
Allium praecox
Lilium humboldtii ssp. *ocellatum*
Monanthochloe littoralis

The following taxa have mainland ranges which terminate considerably north of their insular occurrences:

Polypodium scouleri
Notholaena newberryi
Juniperus californica
Agoseris heterophylla
Coreopsis gigantea
Eriophyllum lanatum var. *grandiflorum*
Gnaphalium purpureum
Lasthenia coronaria
Malacothrix clevelandii
Malacothrix incana
Pectocarya linearis ssp. *ferocula*
Pectocarya recurvata
Plagiobothrys californicus var. *californicus*
Dithyrea maritima
Lepidium lasiocarpum var. *latifolium*
Stellaria nitens
Lupinus albifrons var. *albifrons*
Lupinus albifrons var. *douglasii*
Centaurium davyi
Lepechinia calycina
Camissonia cheiranthifolia ssp. *cheiranthifolia*
Clarkia davyi
Clarkia prostrata
Epilobium foliosum
Armeria maritima
Allophyllum gilioides
Polygala californica
Myosurus minimus var. *filifolius*
Ceanothus crassifolius
Cercocarpus betuloides ssp. *blancheae*
Ribes sanguineum
Castilleja mollis
Orthocarpus attenuatus
Orthocarpus densiflorus ssp. *densiflorus*
Carex tumulicola
Calochortus luteus
Bromus maritimus
Elymus pacificus

The following taxa have mainland ranges which terminate considerably south of their insular ranges:

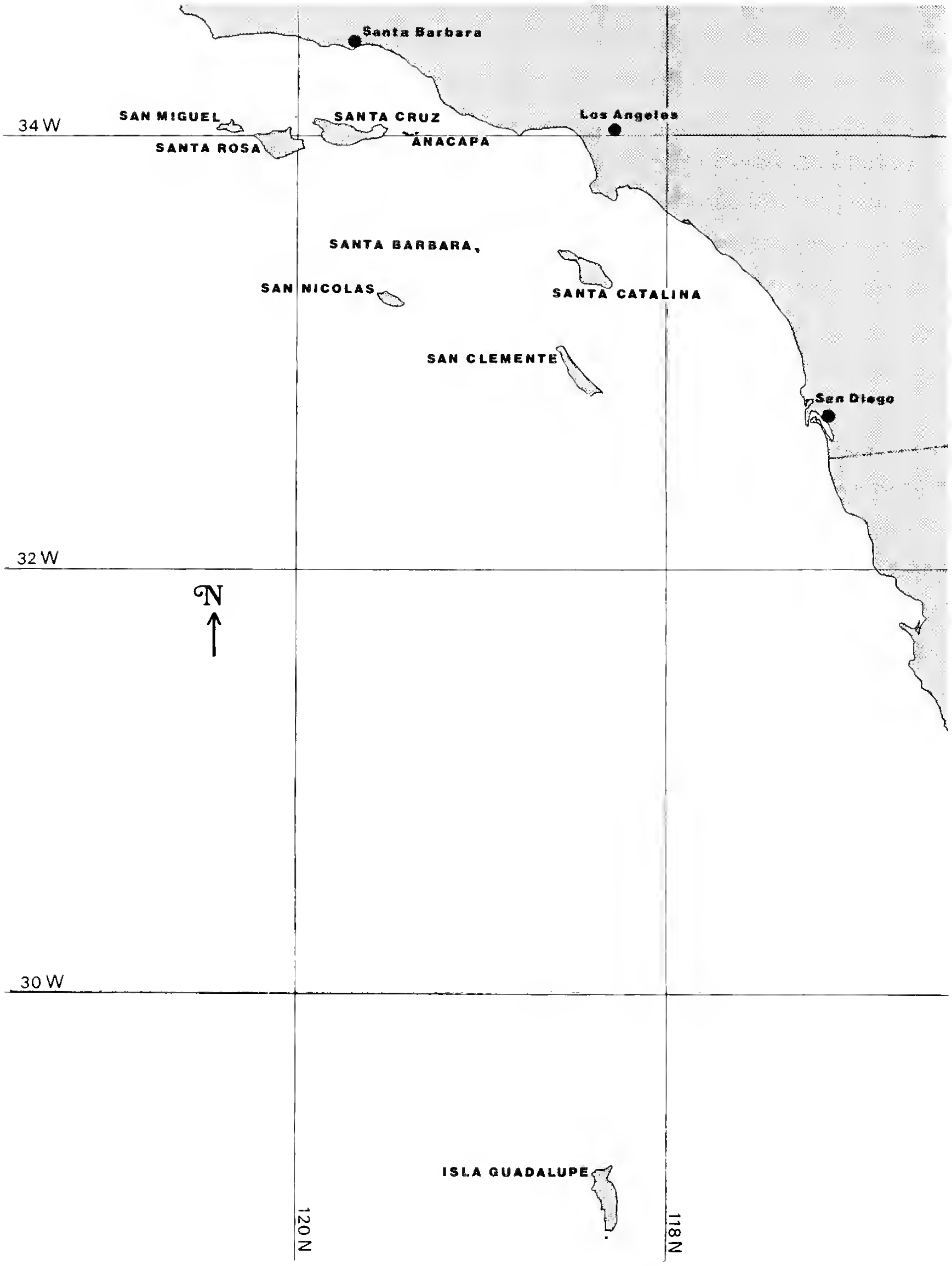
Pityrogramma triangularis var. *viscosa*
Pinus torreyana
Haplopappus venetus ssp. *furfuraceus*
Malacothrix similis
Senecio lyonii
Stephanomeria diegensis
Harpagonella palmeri
Plagiobothrys californicus var. *gracilis*
Atriplex pacifica
Astragalus trichopodus ssp. *lecopsis*
Lotus scoparius var. *veatchii*
Quercus douglasii
Pholistoma racemosum
Salvia brandegei
Mentzelia affinis
Camissonia robusta
Eriogonum grande ssp. *grande*
Calandrinia maritima
Prunus lyonii
Ribes viburnifolium
Galvezia speciosa
Lycium fremontii

Insular occurrences for a few taxa seem to be extensions of generally interior distributions. These include:

Sarcostemma cynanchoides
Thelesperma megapotamicum
Cryptantha maritima
Monolepis nuttalliana
Quercus engelmannii
Erodium texanum
Populus fremontii ssp. *fremontii*
Lycium brevipes var. *brevipes*
Andropogon glomeratus
Poa palustris

The islands of the northern group exhibit closer floristic similarities to one another than do the islands of the southern group. The islands lie close to one another as well as the mainland (Table 1 and Table 2).

Only five taxa, including one endemic, occur on San Miguel Island to the exclusion of the other islands. San Miguel shares 90% of its shared native taxa with Santa Rosa Island and 89% with Santa Cruz Island. San Miguel and Santa Rosa also share alone eight taxa with the mainland and two insular endemics. Though separated from each other, San Miguel and Santa Cruz share alone four taxa with the mainland and one insular endemic. The floristic complement found on San Miguel Island has similarities with that of Santa Rosa Island as well as Santa Cruz Island.



Map 1. Channel Islands of Southern California and Isla Guadalupe, Mexico.

Santa Rosa Island is close to the mainland, and Santa Cruz Island. There are 27 nonendemic native taxa found exclusively on Santa Rosa and the mainland. There are only three unshared endemic taxa on the island, despite its large size, perhaps indicative of less isolation than some of the other islands. There are seven endemics shared exclusively with Santa Cruz Island. There are 31 native taxa restricted to Santa Rosa, Santa Cruz and the mainland. Santa Rosa shares 92% of its shared native taxa with Santa Cruz. The floristic affinities of Santa Rosa Island lie with Santa Cruz Island.

Santa Cruz Island is the largest of the Channel Islands of southern California. Concomitant with its size, ecological diversity, and proximity to the mainland, there are 61 native taxa found exclusively on Santa Cruz and the mainland. This is comparable to 58 such taxa found on Santa Catalina Island to the south. Both islands are at similar distances from the mainland. The fact that 17 of the 19 taxa endemic to more than one of the northern islands occur on Santa Cruz is indicative of the close affinities of Santa Cruz to the other islands of the northern group. A total of 16 taxa are found on the southern islands and Santa Cruz alone of the northern islands.

Table 1. **Features of the Channel Islands of southern California and Isla Guadalupe, Mexico and floristic data for each. Area, and highest altitude, as well as shortest distance to the mainland are given for each island. The numbers of native and introduced taxa are given as are numbers of unshared endemic taxa for each island. The number of insular endemics shared with the other islands dealt with here are also listed for each of the islands.**

Island	Area in km^2	Highest altitude in meters	Distance to mainland in km	Number of native taxa	Number of introduced taxa	Number of unshared insular endemics	Number of shared insular endemics
San Miguel	36	262	42	171	50	1	10
Santa Rosa	218	480	44	370	80	3	35
Santa Cruz	244	660	31	477	137	10	35
Anacapa	3	284	21	166	40	1	18
San Nicolas	57	277	98	114	66	4	13
Santa Barbara	3	193	61	72	29	3	8
Santa Catalina	194	631	32	417	175	8	24
San Clemente	145	589	79	259	83	14	29
Guadalupe	249	1298	253	168	38	35	16

Some of these data are from Philbrick (1967).

Anacapa is a series of small islands forming an eastward extension of Santa Cruz Island. There are only two taxa, including one endemic, that occur on Anacapa Island to the exclusion of the other islands. There are many more taxa on Anacapa than on the more isolated Santa Barbara Island which is of similar size. Anacapa shares 95% of its shared native taxa with Santa Cruz Island and 89% with Santa Rosa Island.

The islands of the southern group are more widely scattered than those of the northern group. The floras are generally more dissimilar among the islands.

San Nicolas Island has two endemic taxa and an additional four taxa restricted to San Nicolas and the mainland. San Nicolas shares about 77% of its shared native taxa with Santa Cruz Island and the same percentage with Santa Catalina Island, although the individual species shared may be different. San Nicolas shares three native taxa exclusively with Santa Cruz and the mainland and only two native taxa exclusively with Santa Catalina and the mainland. San Nicolas shares eight insular endemics exclusively with the southern islands and only one exclusively with the northern islands. The affinities of San Nicolas Island lie equally with the northern and southern islands but the balance seems to favor relationship to the southern islands in light of the high number of shared insular endemics.

Only the three endemic taxa of the 72 native taxa on Santa Barbara Island are not shared by another island. Santa Barbara shares 89% of its shared native taxa with Santa Catalina Island and San Clemente Island and 81% with Santa Cruz Island. Santa Barbara shares six of the endemic taxa exclusive to the southern group of islands.

Santa Catalina Island is the largest island of the southern group. As noted above, there are 58 native taxa exclusive to Santa Catalina and the mainland. Nine of the 16 taxa endemic to more than one island of the southern group are found on Santa Catalina. Santa Catalina shares 86% of its shared native taxa with Santa Cruz Island. There are 37 native taxa common only to Santa Catalina, Santa Cruz, and the mainland. Five taxa are endemic to the northern islands and only Santa Catalina of the southern group. A total of 65 taxa are native to the northern islands and only Santa Catalina Island of the southern group, as well as the mainland. The floristic affinities of Santa Catalina Island lie with the mainland and the Santa Cruz Island area.

There are 14 taxa endemic to San Clemente Island and only five taxa restricted to San Clemente and the mainland. Ten native taxa are exclusively shared by San Clemente and Santa Catalina of the islands, and the mainland. San Clemente shares 87% of its shared native taxa with Santa Catalina and 77% with Santa Cruz Island. San Clemente and Santa Catalina share exclusively three endemic taxa. Twelve taxa are endemic to San Clemente and one or more of the other islands of the southern group. Three endemics are common to the northern islands and San Clemente Island alone of the southern islands. One insular endemic is shared with Islas Los Coronados and three are shared with Guadalupe Island. The floristic affinities of San Clemente Island seem to lie with Santa Catalina Island.

Guadalupe Island is the largest and most isolated of the islands considered here. There are 35 taxa endemic to the island. Twenty-five native taxa are found on Guadalupe and the mainland but are absent from the Channel Islands. Guadalupe shares 88% of its shared native taxa with Santa Catalina, 79% with San Clemente, and 76% with Santa Cruz. Guadalupe Island shares ten endemic taxa with one or more of the Channel Islands. One endemic is shared with Santa Catalina, four nonendemic native taxa are also shared exclusively between these islands and the mainland. Guadalupe shares four endemics with San Clemente and two nonendemics with San Clemente and the mainland only. Guadalupe shares five of the 14 taxa endemic to more than one island of the southern group only. There are clear floristic affinities between Guadalupe Island and the Channel Islands of southern California.

Table 2. Shared native and endemic taxa between island pairs. Number of native taxa, including endemics, shared between island pairs is found in the coordinate box between any two islands in question above the diagonal of dashes. Similarly number of insular endemics shared among any two islands is found below the diagonal of dashes.

	Total number of shared native taxa (including endemics) between island pairs								
	San Miguel	**Santa Rosa**	**Santa Cruz**	**Anacapa**	**San Nicolas**	**Santa Barbara**	**Santa Catalina**	**San Clemente**	**Guadalupe**
Number of shared island endemics between island pairs									
San Miguel	—	150	148	96	69	40	115	91	43
Santa Rosa	10	—	314	147	81	51	237	161	74
Santa Cruz	8	33	—	156	84	56	304	185	82
Anacapa	6	15	16	—	64	54	134	113	54
San Nicolas	3	4	3	3	—	46	84	81	38
Santa Barbara	0	2	2	2	7	—	62	62	40
Santa Catalina	3	14	14	6	7	6	—	209	96
San Clemente	3	11	10	6	10	8	17	—	86
Guadalupe	1	6	6	3	5	4	11	14	—

Many elements of the floras of the Channel Islands of southern California and Guadalupe Island, Mexico, represent surviving populations of mainland taxa. Decreased mainland ranges occasionally create great disjunctions. There are more taxa from northerly distributions surviving on the islands than taxa from predominately southern ranges. This is evident in the above list of taxa which occur on the northern islands, generally on the mainland, but skip the southern islands and the list of taxa with mainland ranges which terminate considerably north of their insular occurrences. Shared insular endemics would seem to indicate stronger floristic affinities between islands than sharing of other native taxa.

San Miguel and Anacapa islands are not very distinctive in their floristic composition from that of Santa Rosa and Santa Cruz islands. The portions of the floras of San Miguel and Anacapa islands that are shared with the mainland or other islands are high. Santa Rosa Island exhibits some floristic divergence from Santa Cruz Island, but is still quite close in its floristic affinities with Santa Cruz. The northern group of islands share high percentages of their native taxa, most have relatively low numbers of unshared endemics, and more shared insular endemics. This seems to portray a more unified floristic region.

The floristic affinities among the southern group of islands are not as pronounced (Table 2). San Nicolas has similar floristic affinities overall with Santa Cruz and Santa Catalina islands but shares more insular endemics with the southern group of islands. Santa Barbara Island shares a higher percentage of its flora than does San Nicolas. Santa Barbara shares a greater percentage of its total native taxa as well as those included which are insular endemics with islands of the southern group. Santa Catalina Island has significant floristic affinity with Santa Cruz Island of the northern group but shares fewer of the endemics restricted to more than one of the southern islands. San Clemente has the most unique floristic elements of the southern islands. It exhibits closest floristic similarity to Santa Catalina Island. All of the islands of the southern group, except Santa Catalina, seem to show greater floristic similarity to other islands of the group than to mainland areas. The greater distances among these islands and to mainland areas, as well as lesser floristic similarities among the islands, indicate that the southern islands are a less cohesive floristic region than the northern islands.

Guadalupe Island, Mexico, has the most unique floristic complement of any of the islands treated here. The relationship of the flora of the island to the Channel Islands of southern California is, however, significant.

APPENDIXES

APPENDIX I. SELECTED EXSICCATAE AND HERBARIA HOUSING INSULAR COLLECTIONS

The citation of herbaria and specimens here provides documentation of the plants of the Channel Islands and Guadalupe Island. Primary consideration is given to the significant insular collections combined at LAM. Most certainly numerous additional specimens are available at RSA-POM and SBBG, institutions considered among the primary centers of insular collections. Specimens from these institutions are cited here as well as from several other herbaria.

The taxa are arranged in the same systematic order found in the table of vascular plants. The islands also are recorded in the same sequence. Each collection citation is followed by the one or more standard herbarium acronyms as given by Holmgren et al. (1981); any not listed in this publication are written out more fully. An exclamation (!) following the acronym indicates collections verified by the author. Acronyms separated by commas indicate duplicate sheets at other institutions. No more than three collections are given for a particular insular record. Herbarium acronyms not following a collection citation and lacking an exclamation (!), indicate herbaria containing specimens which were not specifically verified. Following all three of the collection citations additional herbarium acronyms not accompanied by exclamations, indicate herbaria containing additional collections documenting the insular record. Citations and locations of additional verified specimens will be offered to interested monographers, where possible.

In a very few cases an insular record is given as a literature reference to a particular specimen which I have not yet seen or been able to locate. These are merely for the reader's information, although those considered most reliable were used in the numerical tabulations of the flora.

Vascular Cryptogams

Selaginellaceae
Selaginella bigelovii Underw.
Santa Rosa: Thorne et al. 48854 RSA!; SBBG; SBM.
Santa Cruz: Clokey 4849 LAM!; Raven & Smith 15270 RSA!; Abrams & Wiggins 341 DS!; SBM.
Anacapa: SBBG.
Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Fosberg R96 LAM!; Dunkle 1927 LAM!; CAS; DS; RSA-POM.
San Clemente: Dunkle 7228 LAM!; Elmore 398 AHFH!; Thorne 36120 RSA!; CAS.
Equisetaceae
Equisetum hyemale L. spp. *affine* (Engelm.) Calder & Taylor
Santa Cruz: Hoffmann s.n. Sep. 20, 1930 POM!; SBM.
Equisetum laevigatum A. Br.
Santa Rosa: Thorne et al. 48740 RSA!.
Santa Cruz: Hoffmann s.n. Jul. 1, 1930 LAM!; Raven & Smith 15269 RSA!; Howell 6271 CAS!; SBBG; SBM.
Santa Catalina: Dunkle 1964 LAM!; Fosberg R90 LAM!; Thorne & Everett 34959 RSA!; SBM.
Equisetum telmateia Ehrh. var. *braunii* Milde
Santa Cruz: Clokey 5162 LA!, RSA!; Miller s.n. Jun. 6, 1918 CAS#93549!; SBM.
Santa Catalina: Trask s.n. in Jul. 1900 LAM!; Dunkle 2458 AHFH!; Wolf 3607 RSA!; SBM.
Aspidiaceae
Athyrium felix-femina (L.) Roth var. *sitchensis* Rupr.
Santa Cruz: Clokey 4844 POM!; Munz & Crow 11833 POM!; Wolf 2915 Mar. 27, 1932 RSA!; SBBG; SBM.
Cystopteris fragilis (L.) Bernh.
Santa Cruz: Hoffmann s.n. May 23, 1932 POM!; Hoffmann s.n. May 23, 1932 CAS#194980!; SBM.
Dryopteris arguta (Kaulf.) Watt
Santa Rosa: Dunkle 8429 LAM!; Thorne et al. 48836 RSA!; Munz & Crow 11645 POM!; SBM.
Santa Cruz: Dunkle 8602 LAM!, DS!; Clokey 4844 LAM!; Blakley 3379 RSA!; CAS; SBM.
Anacapa: Blakley 5765 SBBG!.
Santa Catalina: Dunkle 1948 LAM!; Fosberg R85 LAM!; Thorne & Everett 34607 RSA!; DS; SBM.
San Clemente: Munz 6706 POM!.
Polystichum munitum (Kaulf.) Presl ssp. *munitum*
Santa Rosa: SBM.
Santa Cruz: Pierson 11083 RSA!; Munz & Crow 11887 POM!; SBBG; SBM.
Polystichum munitum (Kaulf.) Presl ssp. *solitarium* Maxon
Guadalupe: Anthony 9 NY!; Palmer 102 NY!.
Blechnaceae
Woodwardia fimbriata Sm. in Rees
Santa Rosa: SBM.
Santa Cruz: Clokey 4842 LAM!; Dunkle 8604 LAM!; Balls & Blakley 23741 RSA!; SBM.
Polypodiaceae
Polypodium californicum Kaulf.
Santa Rosa: Thorne et al. 48817 RSA!; SBM.
Santa Cruz: Dunkle 8620 LAM!; SBM.
Anacapa: SBBG; SBM.
Santa Barbara: SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Dunkle 2044 LAM!; Dunkle 2045 LAM!; RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Franceschi s.n. US!; Brandegee s.n. Mar. 23, 1897 US!; Palmer 857 US!.
Polypodium scouleri Hook. & Grev.
Santa Cruz: RSA-POM; SBM.
Guadalupe: Palmer 104 NY!; Moran 6422 RSA!.
Pteridaceae
Adiantum capillus-veneris L.
Santa Rosa: Thorne et al. 48800a RSA!; SBBG; SBM.
Santa Cruz: Pierson 11089 RSA!; Balls & Blakley 23724 RSA!; Williams 42 POM!; SBM.
Anacapa: Hoffmann s.n. May 16, 1929 SBM!; Bond 347 SBM!; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg R94 LAM!; Thorne & Everett 35001 RSA!.
Adiantum jordani C. Muell.
Santa Rosa: Thorne et al. 48990 RSA!; Blakley 3097 RSA!; Dunn, D. 1335 LA!; SBM.
Santa Cruz: Dunkle 8537 LAM!; Clokey 4831 LAM!; Raven & Smith 15177 RSA!; SBM.
Anacapa: SBBG; SBM.
Santa Catalina: Grant s.n. Apr. 20, 1904 LAM!; Fosberg R79 LAM!; Thorne & Everett 34486 RSA!; SBM.
San Clemente: House & Grumbles s.n. Aug. 5, 1913 USC!; Thorne 42967 RSA!; Raven 17694 RSA!; SBBG; DS.
Adiantum pedatum L. ssp. *aleuticum* (Rupr.) Calder & Taylor
Santa Cruz: Clokey 4828 LAM!; Munz & Crow 11839 POM!; Wolf 2912 RSA!; SBBG; SBM.
Aspidotis californica (Hook.) Nutt. ex Copel.
Santa Cruz: Hoffmann 173 SBM!; Clokey 5157 GH!; Munz & Crow 11852 POM!.
Santa Catalina: Trask s.n. in Mar. 1897 LAM!, MO!; Dunkle 1879 AHFH!; Thorne & Everett 34848 RSA!.
Cheilanthes clevelandii D.C. Eat.
Santa Rosa: Dunkle 8512 AHFH!; Spencer 199 US!; Brandegee s.n. in 1888 UC!.
Santa Cruz: Clokey 4838 LAM!; Clokey 5158 LA!, RSA!, UC!; Brandegee s.n. in Apr. 1888 SBM#15936!, UC!.

Cheilanthes newberryi (D.C. Eat.) Domin
San Clemente: Dunkle 7230 LAM!; Trask 326 NY!; DeBuhr & Wallace 709 RSA!.
Guadalupe: Franceschi 39 LAM!, MO!; Moran 18147 SD!; Palmer 105 MO!.
Notholaena californica D.C. Eat.
Santa Catalina: Trask s.n. in 1899 MO!; Blakley 5510 SBBG!.
Guadalupe: Moran 6165 DS!, SD!.
Pellaea andromedaefolia (Kaulf.) Fee var. *pubescens* D.C. Eat.
Santa Rosa: Dunn, N. s.n. LA!; Thorne 48865 RSA!; Raven, Blakley & Ornduff 14968a RSA!; SBM.
Santa Cruz: Wolf 2778 RSA!; Blakley 3301 RSA!; Raven & Smith 15258 RSA!; SBM.
Anacapa: Dunkle 7663 LAM!; SBM.
Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Fosberg R86 LAM!; Wolf 3450 RSA!.
San Clemente: Dunkle 7247 LAM!; Elmore 413 AHFH!; Thorne 42867 RSA!.
Pellaea mucronata (D.C. Eat.) D.C. Eat. ssp. *mucronata*
Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!; Hoffmann 154 POM!; SBM.
Santa Cruz: Clokey 4840 LAM!, NY!, POM!; Hoffmann s.n. LAM!; SBM.
Santa Catalina: Trask s.n. in Jan. 1896 US!; Fosberg R84 LAM!, NY!, US!; Dunkle 1872 AHFH!; Thorne & Everett 34991 RSA!.
Guadalupe: Palmer 100 NY!; Moran 6166 RSA!, SD!; Moran 7838 RSA!, SD!.
Pityrogramma triangularis (Kaulf.) Maxon var. *triangularis*
Santa Rosa: Thorne et al. 48900 RSA!; RSA-POM; SBBG; SBM.
Santa Cruz: SBBG; SBM.
Anacapa: Dunkle 7664 AHFH!; SBBG; SBM.
Santa Catalina: RSA-POM; SBM.
San Clemente: Dunkle 7244 NY!; Thorne 42866 RSA!.
Guadalupe: Mason 1514 CAS!; Moran 7833 DS!, SD!; Palmer 856 NY!, US!.
Pityrogramma triangularis (Kaulf.) Maxon var. *viscosa* (D.C. Eat.) Weath.
Santa Rosa: Hoffmann s.n. Mar. 26, 1927 SBM#507!.
Santa Cruz: Munz & Crow 11544 LA!; Clokey 4824 NY!; Clokey 5152 NY!; SBM.
San Nicolas: Newman 124 Pt. Mugu Nav. Air. Sta.!.
Santa Catalina: Trask s.n. in Mar. 1901 NY!; Rose, Georgia s.n. in 1889 NY!; SBBG.
San Clemente: Trask 328 NY!; Trask 329 NY!; SBBG.
Pteridium aquilinum (L.) Kuhn var. *pubescens* Underw.
Santa Rosa: Dunkle 8511 LAM!, AHFH!, RSA!; Blakley 3177 RSA!; Munz & Crow 11668 POM!; SBM.
Santa Cruz: Dunkle 8603 LAM!, AHFH!, RSA!; Clokey 4835 LAM!; Fosberg 7595 LAM!; SBM.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!; Fosberg S4834 LAM!; Thorne & Thorne 36429 RSA!; SBM.

Salviniaceae
Azolla filiculoides Lam.
Santa Catalina: Thorne 36659 RSA!; Raven 17853 RSA!; Piehl 62522 RSA!; SBBG.

Gymnosperms

Cupressaceae
Cupressus guadalupensis Wats. ssp. *guadalupensis*
Guadalupe: Rempel 758-37 LAM!; Ziezenhenne s.n. in May 1933 AHFH!; Franceschi 3 RSA!; SD.
Cupressus macrocarpa Hartw. ex Gord.
Santa Cruz: SBBG.
Anacapa: SBBG.
Santa Catalina: Parratt 524 LAM!.
Juniperus californica Carr.
Guadalupe: Moran 6454A SD!; Moran 2635A SD!.
Pinaceae
Pinus muricata D. Don
Santa Cruz: Clokey 4850 LAM!, RSA!, POM!; Dunkle 8655 LAM!; Wolf 2844 RSA!.
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Guadalupe: Palmer 90 NY!; Rose 16001 NY!; Howell 8183 RSA!, NY!; CAS.
Pinus remorata Mason
Santa Rosa: Moran 3348 LAM!; Dunkle 8505 LAM!, AHFH!; Thorne et al. 48983 RSA!; SBM.
Santa Cruz: Clokey 4853 LAM!, POM!; Williams 79 POM!; Raven & Smith 15317 RSA!; SBM.
Pinus torreyana Parry ex Carr.
Santa Rosa: Dunkle 8500 LAM!, AHFH!, RSA!; Thorne et al. 48852 RSA!; Abrams & Wiggins 247 RSA!.

Dicotyledons

Aceraceae
Acer macrophyllum Pursh
Santa Cruz: Hoffmann s.n. RSA#5771!; Clokey 4995 POM!; Munz & Crow 11868 POM!; SBBG.
Aizoaceae
Aptenia cordifolia (L. f.) N.E. Br.
Anacapa: SBBG.
Santa Catalina: Thorne 36726 RSA!; Thorne & Everett 33454 RSA!; SBBG.
Carpobrotus aequilaterus (Haw.) N.E. Br.
San Miguel: Dunkle 8413 LAM!, RSA!; Elmore 316 AHFH!; Munz & Norris 11826 POM!; SBBG; SBM.
Santa Rosa: Thorne et al. 48918 RSA!; SBBG; SBM.
Santa Cruz: Sauer & Laughrin 5519 RSA!; SBM.
Anacapa: SBBG; SBM.
San Nicolas: SBBG.
San Clemente: Raven 18045 RSA!.
Carpobrotus edulis (L.) Bolus
San Nicolas: RSA; SBBG.

Malephora crocea (Jacq.) Schwant.
Anacapa: Blakley 2813 SBBG!; Benedict s.n. Apr. 22, 1970 SBBG!.

Mesembryanthemum crystallinum L.
San Miguel: Kanakoff s.n. Apr. 13, 1940 RSA!; SBBG.
Santa Rosa: Dunn, D. 1346 LA!; Thorne et al. 48920 RSA!; Raven, Blakley & Ornduff 14966 RSA!; SBBG; SBM.
Santa Cruz: Ferren 1894 SCIR!; SBBG; SBM.
Anacapa: Dunn, N. s.n. May 14, 1932 LA!; SBBG; SBM.
San Nicolas: Dunkle 8303 LAM!; Raven & Thompson 20704 LA!, RSA!; Foreman & Lloyd 147 RSA!; SBBG; SBM.
Santa Barbara: Thorne 37534 RSA!; SBBG.
Santa Catalina: Dunkle 1755 AHFH!; Fosberg S4713 LAM!; Thorne & Everett 34571 RSA!; SBBG.
San Clemente: Munz 6785 POM!; Raven 18008 RSA!; SBBG.
Guadalupe: Rempel 759-37 LAM!.

Mesembryanthemum nodiflorum L.
San Miguel: Dunkle 8415 LAM!, AHFH!; SBM.
Santa Rosa: Munz & Hoffmann 11724 POM!; SBM.
Santa Cruz: RSA-POM; SBBG.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8303 LAM!, AHFH!; Raven & Thompson 20692 RSA!; Blakley 4131 RSA!; SBM.
Santa Barbara: Dunkle 8147 LAM!; Elmore 310 AHFH!; Bryan, Dr. & Mrs. s.n. LAM!; Thorne 37535 RSA!.
Santa Catalina: Fosberg S4599 LAM!; Dunkle 1812 AHFH!; Thorne & Everett 34646 RSA!; SBM.
San Clemente: Dunkle 8121 LAM!; DeBuhr & Wallace 681 RSA!; Raven 17995 RSA!.
Guadalupe: Moran 13757 SD!; Moran 17384.5 (sic) SD!.

Tetragonia tetragonioides (Pall.) Kuntze
San Miguel: Munz & Crow 11814 POM!; SBM.
Santa Rosa: SBM.
Santa Cruz: Balls & Blakley 23756 RSA!.

Amaranthaceae

Amaranthus albus L.
Santa Rosa: Hoffmann s.n. Jun. 12, 1930 SBM!.
Santa Cruz: Dunkle 8591 LAM!, AHFH!; Dunkle 8644 LAM!, AHFH!; Hoffmann s.n. Jun. 14, 1930 SBM#5109!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4509 LAM!; Dunkle 2004 AHFH!; Trask s.n. in Jun. 1896 US!; Trask s.n. in May 1900 NY!.

Amaranthus blitoides Wats.
Santa Rosa: Hoffmann s.n. Jun. 13, 1930 SBM#7735!.
Santa Cruz: Hoffmann s.n. Jul. 1, 1930 SBM#1845!; RSA-POM; SBBG.

Amaranthus deflexus L.
Santa Cruz: Raven & Smith 15162 RSA!; Junak 616 SCIR!; SBBG.

Anacardiaceae

Lithraea molloides (Kell.) Engler
Santa Catalina: SBBG.

Malosma laurina (Nutt. in T. & G.) Nutt. ex Abrams
Santa Catalina: Trask s.n. in Jun. 1902 LAM!; Fosberg S5373 LAM!, RSA!; Rusby s.n. Aug. 17, 1915 NY!; SBM.
San Clemente: Trask 215 NY; Abrams & Wiggins 393 DS!.
Guadalupe: Rempel 758-37 LAM!.

Rhus integrifolia (Nutt.) Benth. & Hook.
San Miguel: Dunkle 8367 LAM!, AHFH!, RSA!; Voss s.n. Sep. 2, 1930 POM!; SBBG; SBM.
Santa Rosa: Munz & Crow 11643 POM!; Thorne et al. 48853 RSA!; Blakley 3136 RSA!; SBBG; SBM.
Santa Cruz: Fosberg 7625 LAM!, LA!; Dunkle 8595 LAM!, RSA!; Raven & Smith 15215 RSA!; SBBG; SBM.
Anacapa: Dunkle 7632 AHFH!; Elmore 224 AHFH!; SBBG; SBM.
Santa Catalina: Fosberg S4286 LAM!; Elmore 439 AHFH!; Thorne 39380 RSA!; SBBG; SBM.
San Clemente: Dunkle 7239 LAM!; Moran 582 LAM!; DeBuhr & Wallace 721 LAM!; RSA-POM; SBBG.
Guadalupe: Moran 2932 DS!.

Rhus ovata Wats.
Santa Cruz: Fosberg 7686 LAM!, LA!; Thorne & Everett 36782 RSA!; Wolf 2782 RSA!; SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1902 LAM!; Dunkle 1723 AHFH!, POM!; Raven 17803 RSA!; SBBG; SBM.

Schinus molle L.
Santa Cruz: Blakley 3337 RSA!; SBBG.
Santa Catalina: Thorne 36708 RSA!; SBBG.

Toxicodendron radicans (L.) Kuntze ssp. *diversilobum* (T. & G.) Thorne
San Miguel: Dunkle 8417 LAM!, AHFH!, RSA!; SBBG.
Santa Rosa: Thorne et al. 48775 RSA!; Raven, Blakley & Ornduff 14977 RSA!; SBBG; SBM.
Santa Cruz: Fosberg 7709 LAM!, LA!; Elmore 265 AHFH!; RSA-POM; SBM.
Anacapa: Dunkle 7636 LAM!, AHFH!; SBBG.
Santa Catalina: Fosberg S4301 LAM!; Philbrick & Thorne B67-207 RSA!; SBBG.
San Clemente: Munz 1923 POM!; Raven 17732 RSA!; SBBG.

Apocynaceae

Asclepias fascicularis Dcne. in A. DC.
Santa Cruz: Williams 27 POM!; Balls & Blakley 23712 RSA!; SBBG; SBM.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!; Thorne 36678 RSA!; SBBG.

Sarcostemma cynanchoides Dcne. ssp. *hartwegii* (Vail) R. Holm
Santa Catalina: Trask s.n. in Feb. 1897 US!.

Vinca major L.
Santa Cruz: Thorne & Everett 36850 RSA!; SBBG; SBM.
Santa Catalina: Thorne & Everett 33465 RSA!.

Araliaceae

Apiastrum angustifolium Nutt. in T. & G.
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBM.

Santa Cruz: Fosberg 7517 LAM!; Fosberg 7612 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Moran 723 LAM!; SBBG.
San Nicolas: Trask 49 LAM!.
Santa Catalina: Fosberg S4363 LAM!; Dunkle 2073 AHFH!; Fosberg S4717 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Apium graveolens L.
Santa Rosa: Dunkle 8469 LAM!, AHFH!; RSA-POM; SBBG.
Santa Cruz: SBBG.
San Nicolas: Dunkle 8305 LAM!, AHFH!; RSA-POM; SBBG; SBM.
San Clemente: DeBuhr & Wallace 718 LAM!.

Berula erecta (Huds.) Cov.
San Miguel: RSA-POM.

Bowlesia incana R. & P.
Santa Rosa: Munz & Crow 11692 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 2085 LAM!, AHFH!; Fosberg S4320 LAM!; Fosberg S7169 LAM!; RSA-POM; SBBG.
San Clemente: Trask 226 NY!; RSA-POM; SBBG.

Caucalis microcarpa H. & A.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4339 LAM!, MO!; Fosberg S4616 LAM!; Detmers s.n. Apr. 13, 1929 USC!; RSA-POM; SBBG.
San Clemente: RSA-POM.

Conium maculatum L.
Santa Cruz: SBBG; SBM.
San Nicolas: Dunkle 8333 LAM!, AHFH!; Foreman & Smith 184 LA!; RSA-POM; SBBG.

Daucus pusillus Michx.
San Miguel: Dunkle 8400 LAM!; RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8310 LAM!; Dunkle 8354 LAM!; Foreman 230 UC!; RSA-POM; SBBG; SBM.
Santa Barbara: RSA-POM; SBBG.
Santa Catalina: Fosberg S4382 LAM!; Dunkle 1890 AHFH!; Fosberg 4573 LA!, LAM!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7602 LAM!; Dunkle 7300 LAM!; RSA-POM; SBBG.
Guadalupe: Palmer 34 CM!; Moran 6676 SD!.

Foeniculum vulgare Mill.
Santa Rosa: Dunkle 8460 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: Gentry 254 AHFH!; Dunkle 8558 LAM!; RSA-POM; SBBG; SBM.
San Nicolas: RSA-POM; SBBG.
Santa Catalina: Fosberg S5362 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Lomatium caruifolium (H. & A.) Coult. & Rose
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.

Lomatium insulare (Eastw.) Munz
San Nicolas: Trask 51 NY!; Howell 8207 MO!; Foreman & Smith 174 LA!; CAS; DS; RSA-POM; SBBG; SBM.
San Clemente: Evermann s.n. in 1918 CAS#41543!.
Guadalupe: Moran 6474 CAS!, DS!, LA!, RSA!; Carlquist 473 RSA!; Wiggins & Ernst 138 DS!.

Lomatium utriculatum (Nutt.) Coult. & Rose
Santa Rosa: Munz & Crow 11717 LA!; RSA-POM.
Santa Cruz: Fosberg 7527 LAM!; Fosberg 7658 LAM!; RSA-POM.

Sanicula arguta Greene ex Coult. & Rose
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7532 LAM!; Elmore 462 AHFH!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Trask 94 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; Foreman & Smith 197 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Templeton 11387 LAM!; Moran 685 LAM!; Lewis s.n. Mar. 24, 1937 LA!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7236 LAM!; Moran 579 LAM!; RSA-POM; SBBG.

Sanicula crassicaulis Poepp. ex DC.
Santa Cruz: RSA-POM.
Santa Catalina: Trask s.n. in Mar. 1901 NY!; Fosberg S4436 LAM!; Dunkle 2136 LAM!; RSA-POM; SBBG; SBM.

Sanicula hoffmannii (Munz) Bell
San Miguel: RSA-POM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Raven & Smith 15174 CAS!; RSA-POM; SBBG; SBM.
San Nicolas: RSA-POM; SBBG.

Torilis nodosa (L.) Gaertn.
San Miguel: Dunkle 8399 LAM!; RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Davidson, A. in May 1914 LAM!; Fosberg 8125 LAM!; Fosberg S4588 SBM!; RSA-POM; SBBG.

Asteraceae

Achillea millefolium L.
San Miguel: Dunkle 8405 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: Dunn, N. s.n. May 24, 1939 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 5109 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: Ellison s.n. May 12–15, 1929 LA!; SBBG; SBM.
San Nicolas: Trask 72 LAM!; Kanakoff s.n. Apr. 14, 1940 LAM!; RSA-POM; SBM.
Santa Barbara: Dunkle 7420 LAM!; Elmore 308 AHFH!; Bryan, Dr. & Mrs. 3556 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4426 LAM!; Fosberg S7168 LAM!; Dunkle 1754 AHFH!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7292 LAM!, AHFH!; RSA-POM; SBBG.

Achyrachaena mollis Schauer
Santa Rosa: Munz & Crow 11686 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7307 AHFH!; RSA-POM; SBBG.

Agoseris apargioides (Less.) Greene ssp. *apargioides*
Santa Rosa: Dunkle 8499 LAM!, AHFH!; SBM.

Agoseris grandiflora (Nutt.) Greene
San Miguel: SBBG
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Daily 367 SCIR!; SBBG.

Agoseris heterophylla (Nutt.) Greene
Santa Rosa: Hoffmann s.n. Mar. 10, 1932 UC!; RSA-POM; SBM.
Santa Cruz: RSA-POM.
Guadalupe: Greene s.n. Apr. 24, 1885 GH!.

Amblyopappus pusillus H. & A.
San Miguel: Dunkle 8377 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: Dunn, N. s.n. May 14, 1932 LA!; RSA-POM; SBBG.
San Nicolas: Trask s.n. in Apr. 1897 LAM!; Wallace et al. 1621 LAM!; Foreman & Smith 175 LA!; RSA-POM; SBBG.
Santa Barbara: Dunkle 7434 LAM!; Dunkle 8111 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Fosberg S4718 LAM!; Dunkle 1886 AHFH!.
San Clemente: DeBuhr & Wallace 693 LAM!; Dunkle 7268 LAM; RSA-POM; SBBG.
Guadalupe: Anthony 258 RSA!; Carlquist 438 RSA!; Moran 5950 RSA!.

Ambrosia acanthicarpa Hook.
Santa Catalina: RSA-POM.

Ambrosia camphorata (Greene) Payne
Guadalupe: Carlquist 483 RSA!; Moran 6457 RSA!; Greene s.n. Apr. 24, 1885 CAS#381!.

Ambrosia chamissonis (Less.) Greene
San Miguel: Dunkle 8397 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8599 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7609 LAM!; SBBG; SBM.
San Nicolas: Trask 77 LAM!; Trask 10 CAS!; Raven & Thompson 20697 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 1896 AHFH!; Fosberg S4879 LAM!; Fosberg S4922 LAM!; RSA-POM; SBBG.
San Clemente: Dunkle 7286 LAM!, AHFH!; RSA-POM; SBBG.

Ambrosia psilostachya DC. var. *californica* (Rydb.) Blake in Tidest.
Santa Catalina: Trask s.n. in Sep. 1899 NY!; Trask s.n. in Aug. 1902 LAM!; Dunkle 1997 AHFH!; RSA-POM; SBBG.

Anthemis cotula L.
Santa Cruz: Clokey 5113 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 1978 AHFH!; Trask s.n. in Jun. 1896 US!; RSA-POM; SBBG.

Artemisia californica Less.
San Miguel: Dunkle 8409 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: Dunkle 8426 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: Yates s.n. in 1895 LAM!; Dunkle 8538 LAM!, AHFH!; Clokey 5110 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: Hilend 281 USC!; Dunkle 7624 LAM!, AHFH!; Elmore 228 AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 2015 LAM!; Fosberg 7157 LAM!; Ewan 10806 LA!; RSA-POM; SBBG; SBM.
San Clemente: DeBuhr & Wallace 713 LAM!; House & Grumbles s.n. Aug. 5–13, 1930 USC!; Dunkle 7342 LAM!, AHFH!; RSA-POM; SBBG.
Guadalupe: Palmer 48 NY; Moran 6128 SD!.

Artemisia douglasiana Bess. in Hook.
Santa Rosa: Dunkle 8372 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!; Fosberg S5381 LAM!; Dunkle 1998 AHFH!; RSA-POM; SBBG.

Artemisia dracunculus L.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!; Fosberg S5384 LAM!; SBM.

Artemisia nesiotica Raven
San Nicolas: Trask 71 LAM!, MO!; Trask 71a LAM!, MO!; Dunkle 8348 LAM!, AHFH!; RSA-POM; SBBG.
Santa Barbara: Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; Dunkle 8126 LAM!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7276 LAM!, AHFH!; RSA-POM; SBBG.

Aster chilensis Nees var. *chilensis*
Santa Rosa: Hoffmann s.n. Aug. 7, 1930 SBM!.
Santa Cruz: Hoffmann s.n. SBM#10452!; RSA-POM.

Aster exilis Ell.
Santa Cruz: Hoffmann s.n. SBM#10416!; RSA-POM; SBM.

Aster radulinus Gray
Santa Rosa: SBM.
Santa Cruz: RSA-POM; SBBG; SBM.

Baccharis douglasii DC.
San Miguel: SBBG.
Santa Rosa: Dunkle 8503 LAM!, AHFH!; Dunkle 8515 LAM!, AHFH!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Elmore 281 AHFH!; RSA-POM; SBM.
Santa Catalina: Dunkle 1993 LAM!; Williamsen s.n. Aug. 22, 1924 USC!; Fosberg S4744 LAM!; RSA-POM; SBBG; SBM.

Baccharis emoryi Gray
Santa Catalina: Dunkle 2009 AHFH!; Fosberg 7153 LAM!; RSA-POM.

Baccharis glutinosa Pers.
Santa Rosa: Dunkle 8504 AHFH!; RSA-POM; SBBG.
Santa Cruz: Moran 758 LAM!; Dunkle 8629 LAM!, AHFH!; Clokey 5094 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7623 LAM!; SBBG; SBM.
Santa Catalina: Fosberg S4330 LAM!; Fosberg S4797 LAM!; Fosberg S4829 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Baccharis pilularis DC. ssp. *consanguinea* (DC.) C.B. Wolf
San Miguel: Dunkle 8410 AHFH!; SBBG.
Santa Rosa: Dunkle 8461 LAM!, AHFH!; Epling s.n. in Nov. 1938 LA!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 5093 LAM!; Dunkle 8621 LAM!, AHFH!; Elmore 285 AHFH!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7613 LAM!, AHFH!; SBBG; SBM.
San Nicolas: Trask 79 LAM!; Dunkle 8345 LAM!, AHFH!; Foreman & Lloyd 133 LA!; RSA-POM; SBBG; SBM.
Santa Barbara: SBBG.
Santa Catalina: Dunkle 2021 LAM!, AHFH!; Dunkle 2033 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM.

Baccharis plummerae Gray
Santa Cruz: Dunkle 8579 LAM, AHFH!; Wolf 4127 RSA!; Thorne & Everett 36853 RSA!; SBBG; SBM.

Baeriopsis guadalupensis J. T. Howell
Guadalupe: Rempel 759-37 LAM!; Carlquist 468 RSA!; Howell 8327A CAS!.

Blennosperma nanum (Hook.) Blake var. *nanum*
Santa Cruz: SBBG.

Brickelia californica (T. & G.) Gray
Santa Cruz: Yates s.n. in Aug. 1893 LAM!; Dunkle 8543 LAM!; Balls & Blakley 23715 RSA!; SBBG; SBM.
Anacapa: Dunkle 7627 LAM!, AHFH!; Hoffmann s.n. Sep. 22, 1930 POM!; SBBG; SBM.
Santa Catalina: Dunkle 1729 AHFH!, POM!; Dunkle 2022 LAM!, AHFH!; Thorne 35845 RSA!; SBBG.

Centaurea cineraria L.
Santa Catalina: Thorne 36239 RSA!; Thorne & Everett 33443 RSA!; SBBG.

Centaurea melitensis L.
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Clokey 5166 LAM!, RSA!; Williams 9 POM!; Blakley 3449 RSA!; SBBG; SBM.
San Nicolas: Raven & Thompson 20769 RSA!; SBBG.
Santa Barbara: Philbrick & McPherson B68-235 RSA!; Thorne 37492 RSA!; SBBG.
Santa Catalina: Dunkle 1845 AHFH!, POM!; Mosquin 3303 US!; Fosberg S4529 LAM!; SBBG.
San Clemente: Raven 17988 RSA!; SBBG.
Guadalupe: Mason 1521 CAS!; Moran 21168 RSA!.

Centaurea solstitialis L.
Santa Cruz: Dunkle 8546 LAM!, AHFH!, NY!; Hoffmann s.n. Sep. 21, 1930 POM!; Wolf 4169 RSA!; SBBG; SBM.
Santa Catalina: Fosberg 5401 LAM!, NY!, POM!; Thorne 36624 RSA!; SBBG.

Chaenactis glabriuscula DC. var. *lanulosa* (DC.) Hall
Santa Rosa: Munz & Hoffmann 11731 POM!; Blakley 3120 RSA!; Thorne et al. 49038 RSA!; SBM.

Chrysanthemum coronarium L.
Santa Cruz: Dunkle 8622 LAM!, AHFH!.
San Nicolas: RSA-POM.
Santa Catalina: Fosberg S4856!.

Chrysanthemum frutescens L.
Santa Catalina: Millspaugh 4728 F!.

Cichorium intybus L.
Santa Cruz: RSA-POM; SBBG; SBM.

Cirsium brevistylum Cronq.
Santa Cruz: Daily 698 SCIR!.

Cirsium californicum Gray
Santa Rosa: Dunkle 8478 LAM!, AHFH!.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 SBM#11204!.
Santa Catalina: Davidson s.n. in Jun. 1891 LAM!; Trask s.n. in May 1899 US#340043!; Thorne & Everett 35015 RSA!; SBM.

Cirsium occidentale (Nutt.) Jeps.
San Miguel: Hoffmann s.n. Apr. 10, 1930 LAM!; Hoffmann s.n. Jun. 11, 1930 SBM#2758!; Dunkle 8401 LAM!, AHFH!; RSA-POM; SBBG.
Santa Rosa: Hoffmann s.n. Mar. 10, 1932 SBM#12180!; Hoffmann s.n. Jul. 9, 1930 SBM#10519!; Hoffmann s.n. May 5, 1932 SBM!; LA; RSA-POM; SBBG.
Santa Cruz: Hoffmann s.n. Mar. 23, 1929 SBM!; Hoffmann s.n. Jul. 1, 1930 SBM#1603!; RSA-POM; SBBG.
San Nicolas: RSA-POM; SBBG.
Santa Catalina: Fosberg S4440 LAM!; Fosberg S4876 LAM!, SBM; Dunkle 2470 AHFH!; RSA-POM; SBBG.
San Clemente: Dunkle 7227 LAM!, AHFH!; RSA-POM; SBBG.

Cirsium ochrocentrum Gray
Santa Catalina: Eastwood 6510 CAS!, US!.

Cirsium proteanum J.T. Howell
Santa Rosa: Hoffmann s.n. May 10, 1932 SBM#12496!.

Cirsium vulgare (Savi) Ten.
Santa Catalina: Thorne 36627 RSA!; SBBG.

Conyza bonariensis (L.) Cronq.
Santa Cruz: Daily 545 SCIR!; SBM.
San Nicolas: Raven & Thompson 20735 RSA!.
Santa Catalina: Thorne & Propst 37683 RSA!; Thorne 36187 RSA!; SBBG.
San Clemente: Blakley 3653 RSA!; Fosberg & Rainey 55229 RSA!; SBBG.

Conyza canadensis (L.) Cronq.
San Miguel: SBBG.
Santa Rosa: Munz 12810 POM!; Voss s.n. Sep. 4, 1930 POM!; Raven 14978 RSA!; SBM.
Santa Cruz: Hoffmann s.n. Sep. 10, 1931 LAM!; SBM.
San Nicolas: Foreman, Rainey & Evans 77 RSA!; SBBG.
Santa Catalina: Dunkle 2002 AHFH!, POM!; Nuttall 990 POM!; Thorne 36663 RSA!.
San Clemente: Raven 17997 RSA!.

Conyza coulteri Gray
Santa Cruz: Dunkle 8579 NY!; SBBG.
Santa Catalina: Millspaugh 4602 F!; McClatchie s.n. Sep. 8, 1893 NY!; Thorne & Propst 37679 RSA!.
San Clemente: Moran 7156 RSA!; SBBG.
Coreopsis gigantea (Kell.) Hall
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7568 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Ellison s.n. May 12–15, 1929 LA!; Dunkle 7607 LAM!, AHFH!; Moran 743 LAM!; SBBG; SBM.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Dunkle 8360 LAM!, AHFH!; Kanakoff s.n. Apr. 4, 1940 LAM!; RSA-POM; SBBG.
Santa Barbara: Trask in Apr. 1901 LAM!; Dunkle 7444 LAM!, AHFH!; Elmore 297 AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg 7161 LAM!; Wolf 3631 LA!; Moran 628 LAM!; RSA-POM; SBBG.
Guadalupe: Moran 2923 DS!; Palmer 41 CM!.
Corethrogyne filaginifolia (H. & A.) Nutt. ssp. *filaginifolia*
San Miguel: SBM.
Santa Rosa: Dunkle 8458 LAM!, AHFH!; RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Anacapa: Dunkle 7633 LAM!, AHFH!; Elmore 220 AHFH!; RSA-POM; SBM.
San Nicolas: Foreman 162 UC!.
Santa Catalina: Trask s.n. in Oct. 1901 LAM!; Dunkle 2452 AHFH!; Fosberg S5375 LAM!; RSA-POM; SBM.
Cotula australis (Sieber ex Spreng.) Hook. f.
Santa Rosa: RSA-POM; SBBG.
Santa Cruz: Fosberg 7579 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4506 LAM!; RSA-POM; SBBG.
Cotula coronopifolia L.
San Miguel: SBBG.
Santa Rosa: Elmore 198 AHFH!; Dunkle 8436 LAM!, AHFH!; Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBM.
Santa Cruz: Clokey 5114 LAM!; Dunkle 8585 LAM!; RSA-POM; SBBG; SBM.
San Nicolas: Foreman, Evans & Rainey 68 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. Mar. 1901 LAM!; Dunkle 1914 AHFH!; Fosberg S4755 LAM!; RSA-POM; SBBG.
Cynara scolymus L.
Santa Cruz: SBM.
Encelia californica Nutt.
Santa Cruz: Fosberg 7531 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7672 LAM!; SBBG; SBM.
Santa Catalina: Fosberg S4837 LAM!; Fosberg S4290 LAM!; Lewis s.n. May 24, 1937 LA!; SBBG, SBM.
San Clemente: Dunkle 7280 LAM!; Elmore s.n. Nov. 26, 1929 AHFH!; RSA-POM; SBBG.
Erigeron foliosus Nutt. var. *foliosus*
San Miguel: SBBG.
Santa Rosa: Elmore 177 AHFH!; RSA-POM; SBM.
Santa Cruz: Clokey 5089 LAM!; Hoffmann s.n. Jun. 15, 1930 LAM!; RSA-POM; SBM.
Anacapa: Moran 727 LAM!.
Santa Catalina: Fosberg S5361 LAM!; Dunkle 1982 AHFH!; RSA-POM; SBBG.
Erigeron foliosus Nutt. var. *stenophyllus* (Nutt.) Gray
San Miguel: SBBG.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Erigeron glaucus Ker
San Miguel: Dunkle 8375 LAM!; Elmore 315 AHFH!; Elmore 332 AHFH!; RSA-POM; SBBG.
Santa Rosa: Dunkle 8480 LAM!; Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8580 LAM!; Yates s.n. in Aug. 1893 LAM!; Clokey 5091 LAM!, US!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7605 LAM!; Moran 744 LAM!; Dunn, N. s.n. May 14, 1932 LA!; SBBG; SBM.
Erigeron sanctarum Wats.
Santa Rosa: SBM.
Eriophyllum confertiflorum (DC.) Gray var. *confertiflorum*
San Miguel: Dunkle 8420 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: Dunkle 8483 LAM!; Dunn, N. s.n. May 24, 1931 LA!; Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBM.
Anacapa: Dunkle 7637 LAM!; Dunn, N. May 14, 1932 LA!; SBBG; SBM.
Santa Catalina: Fosberg 8104 LA!; Fosberg S4397 LAM!; Dunkle 2163 AHFH!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7345 AHFH!; RSA-POM.
Eriophyllum lanatum (Pursh) Forbes var. *grandiflorum* (Gray) Jeps.
Guadalupe: Palmer s.n. in 1875 GH!.
Eriophyllum nevinii Gray
Santa Barbara: Dunkle 8101 LAM!; Moran 883 AHFH!; Elmore 300 AHFH!; RSA-POM; SBBG.
Santa Catalina: Davidson, A. s.n. LAM!; Dunkle 1969 AHFH!; Fosberg S5609 LAM!; RSA-POM; SBBG; SBM.
San Clemente: DeBuhr & Wallace 705 LAM!; Moran 597 LAM!; Nevin s.n. in Apr. 1885 DS!; RSA-POM; SBBG.
Eriophyllum staechadifolium Lag. var. *artemisiaefolium* (Less.) Macbr.
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: SBBG; SBM.
Anacapa: Moran 734 LAM!; SBBG; SBM.
Eriophyllum staechadifolium Lag. var. *depressum* Greene
San Miguel: RSA-POM.
Santa Rosa: RSA-POM.
Santa Cruz: Clokey 5106 LAM!; Fosberg 7685 LAM!, LA!; Elmore s.n. Apr. 17, 1936 AHFH!; RSA-POM.
Anacapa: Dunkle 7625 LAM!; RSA-POM.
Evax sparsiflora (Gray) Jeps.
Santa Rosa: RSA-POM; SBM.
San Clemente: RSA-POM.

- *Filago arizonica* Gray
  - Santa Catalina: RSA-POM.
  - San Clemente: Dunkle 7317 LAM!; RSA-POM; SBBG.
  - Guadalupe: Palmer 38 CM!; Palmer 37 (in part) NY!.
- *Filago californica* Nutt.
  - San Miguel: SBM.
  - Santa Rosa: RSA-POM; SBBG; SBM.
  - Santa Cruz: Fosberg 7642 LAM!; Hoffmann s.n. Apr. 11, 1931 LAM!; Elmore 443 AHFH!; RSA-POM; SBBG; SBM.
  - Anacapa: SBBG.
  - Santa Catalina: Dunkle 1840 AHFH!; Fosberg S4670 LAM!; Fosberg S4366 LAM!; RSA-POM; SBBG.
  - San Clemente: Dunkle 7312 LAM!; RSA-POM; SBBG.
  - Guadalupe: Palmer 37 CM!, MO!, NY!; Palmer 895 ND-G!; Moran 5662 RSA!.
- *Filago gallica* L.
  - Santa Cruz: Daily 375 SCIR!; SBBG.
  - Santa Catalina: RSA-POM.
- *Gnaphalium beneolens* A. Davids.
  - San Miguel: SBBG.
  - Santa Rosa: Elmore 215 AHFH!; RSA-POM; SBBG; SBM.
  - Santa Cruz: Clokey 5096 LAM!, US!.
  - San Nicolas: SBBG.
  - Santa Catalina: Dunkle 1975 AHFH!.
  - San Clemente: SBBG.
- *Gnaphalium bicolor* Bioletti
  - San Miguel: (Hall 1907: Beck 1903 no herbarium cited).
  - Santa Rosa: RSA-POM; SBBG; SBM.
  - Santa Cruz: Dunkle 8612 LAM!; Elmore s.n. Apr. 18, 1936 USC!; Hoffmann s.n. Apr. 12, 1931 LAM!; RSA-POM; SBBG; SBM.
  - Anacapa: SBBG; SBM.
  - San Nicolas: Dunkle 8358 LAM!, AHFH!; Dunkle 8312 AHFH!; SBBG; SBM.
  - Santa Catalina: Trask s.n. in May 1896 LAM!; DeBuhr 2583 LAM!; Wolf 3429 US!; RSA-POM; SBBG; SBM.
  - San Clemente: Moran 595 LAM!, NY!; Trask in Oct. 1902 US!; Elmore 407 AHFH!; RSA-POM; SBBG.
  - Guadalupe: Moran 13793 RSA!; Moran 18153 RSA!.
- *Gnaphalium californicum* DC.
  - Santa Rosa: SBM.
  - Santa Cruz: Clokey 5223 US!; Ellison s.n. May 12–15, 1929 LA!; SBBG; SBM.
  - Anacapa: SBBG; SBM.
  - Santa Catalina: Fosberg S4449 LAM!, US!; Dunkle 1974 AHFH!; Blake 9853 US!; RSA-POM; SBBG.
- *Gnaphalium chilense* Spreng.
  - San Miguel: Dunkle 8381 LAM!, AHFH!; SBBG; SBM.
  - Santa Rosa: Dunkle 8473 AHFH!; RSA-POM; SBBG; SBM.
  - Santa Cruz: Clokey 5097 LAM!, US!; Dunkle 8588 LAM!; RSA-POM; SBBG; SBM.
  - Anacapa: SBBG; SBM.
  - San Nicolas: Dunkle 8312 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; Foreman 160 US!; RSA-POM; SBBG; SBM.
  - Santa Catalina: Fosberg S4338 LAM!, US!; Fosberg S4622 LAM!; Dunkle 1930 AHFH!; RSA-POM; SBBG; SBM.
  - Guadalupe: Palmer 885 NY!; Moran 6715 RSA!; Moran 17350 RSA!.
- *Gnaphalium luteo-album* L.
  - San Miguel: SBBG.
  - Santa Rosa: RSA-POM; SBBG.
  - Santa Cruz: RSA-POM; SBBG.
  - San Nicolas: RSA-POM; SBBG.
  - Santa Catalina: RSA-POM; SBBG.
  - San Clemente: RSA-POM.
- *Gnaphalium microcephalum* Nutt.
  - Santa Rosa: Dunkle 8459 LAM!, AHFH!; RSA-POM.
  - Santa Cruz: RSA-POM; SBBG; SBM.
  - Anacapa: Dunkle 7620 AHFH!, LAM!.
  - Santa Catalina: RSA-POM.
- *Gnaphalium palustre* Nutt.
  - Santa Cruz: Dunkle 8642 LAM!; RSA-POM; SBBG; SBM.
  - Santa Catalina: Wolf 3598 LAM!, US!; Fosberg S5404 LAM!; Dunkle 1988 AHFH!; RSA-POM; SBBG.
  - San Clemente: RSA-POM.
- *Gnaphalium purpureum* L.
  - Santa Rosa: RSA-POM; SBM.
  - Santa Cruz: Daily 699 SCIR!; SBBG; SBM.
  - Santa Catalina: RSA-POM; SBBG.
- *Gnaphalium ramosissimum* Nutt.
  - Santa Cruz: RSA-POM.
- *Grindelia latifolia* Kell. ssp. *latifolia*
  - Santa Rosa: Dunkle 8451 LAM!; Moran 783 LAM!, NY!; Dunn, N. s.n. May 24, 1931 LA!.
  - Anacapa: Dunkle 7641 LAM!, AHFH!, NY!; Dunkle 7674 LAM!; Kanakoff s.n. Aug. 20, 1940 LAM!; LA.
- *Grindelia robusta* Nutt. var. *robusta*
  - Santa Cruz: RSA-POM.
  - San Nicolas: Wier & Beauchamp s.n. Jun. 29, 1978 UC#1443155!.
  - Santa Catalina: (Millspaugh & Nuttall 1923: Knopf 493 at F).
- *Grindelia stricta* DC. ssp. *venulosa* (Jeps.) Keck
  - Santa Rosa: SBM.
- *Haplopappus canus* (Gray) Blake
  - San Clemente: Trask 292 CAS!; SBM.
  - Guadalupe: Carlquist 455 RSA!; Moran 5971 RSA!.
- *Haplopappus detonsus* (Greene) Raven
  - Santa Rosa: Dunkle 8493 LAM!; RSA-POM; SBM.
  - Santa Cruz: Dunkle 8600 LAM!; Brandegee s.n. in 1896 LAM!; Clokey 5087 LAM!, LA!; RSA-POM; SBM.
  - Anacapa: Dunkle 7614 LAM!; SBM.
- *Haplopappus palmeri* Gray ssp. *pachylepis* Hall
  - Santa Catalina: Trask s.n. in Oct. 1900 LAM!.
- *Haplopappus squarrosus* H. & A. ssp. *grindelioides* (DC.) Keck
  - San Miguel: Munz & Crow 11805 POM!.
  - Santa Rosa: Munz & Crow 11683 POM!.
  - Santa Cruz: Hoffmann 217 POM!; Balls & Blakley 23636 RSA!; Wolf 4150 RSA!; SBM; SCIR.
  - Santa Catalina: Dunkle 2155 AHFH!.
- *Haplopappus venetus* (HBK.) Blake ssp. *furfuraceus* (Greene) Hall
  - San Nicolas: Blakley 4015 SBBG; Foreman 136 UC!.

- Santa Catalina: RSA-POM.
- San Clemente: RSA-POM.

Haplopappus venetus (HBK.) Blake ssp. *sedoides* (Greene) Munz
- San Miguel: Dunkle 8376 LAM!; Dunkle 8416 LAM!; RSA-POM; SBBG.
- Santa Rosa: RSA-POM; SBM.
- Santa Cruz: Mower s.n. Aug. 21, 1966 LA#96251!; RSA-POM; SBM.
- Anacapa: Dunkle 7643 LAM!; Dunkle 8443 LAM!; SBM.

Haplopappus venetus (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall
- San Miguel: SBM.
- Santa Rosa: Hoffmann s.n. Jun. 13, 1930 SBM#2691!; Epling & Erickson s.n. Aug. 8, 1937 LA!.
- Santa Cruz: Hoffmann s.n. Nov. 9, 1930 SBM#10816!; Mower s.n. Aug. 22, 1966 LA#96256!; RSA-POM.
- Anacapa: Dunkle 7676 AHFH!; Elmore 246 AHFH!; Hoffmann s.n. Sep. 22, 1930 SBM#10278!.
- San Nicolas: Wallace et al. 1612 LAM!; Wallace et al. 1615 LAM!; Foreman 215 LA!; RSA-POM; SBBG; SBM.
- Santa Catalina: Dunkle 2024 LAM!; Fosberg S4855 LAM!; Fosberg 7151 LAM!; RSA-POM.
- San Clemente: RSA-POM.

Helenium puberulum DC.
- Santa Catalina: RSA-POM.

Helianthus annuus L. ssp. *lenticularis* (Dougl.) Ckll.
- Santa Cruz: Laughrin 528 SCIR!.
- Santa Catalina: Trask s.n. in Mar. 1901 F!; Nuttall 569 F!.

Hemizonia clementina Bdg.
- Anacapa: Dunkle 7642 LAM!; Hoffmann s.n. Jun. 16, 1930 LAM!; Ellison s.n. May 12–15, 1929 LA!; SBBG; SBM.
- San Nicolas: Trask 80 LAM!; Foreman 214 US!; Raven & Thompson 20773 LA!; RSA-POM; SBBG; SBM.
- Santa Barbara: Dunkle 8113 LAM!; Bryan, Dr. & Mrs. s.n. Jul. 1, 1922 LAM!, US!; Blakley 4799 US!; RSA-POM; SBBG; SBM.
- Santa Catalina: Fosberg S4887 LAM!; Nuttall 195 F!; Eastwood 6492 US!; RSA-POM; SBBG; SBM.
- San Clemente: Dunkle 7277 LAM!; Raven 17836 LA!; Mearns 4046 US!; RSA-POM; SBBG.

Hemizonia fasciculata (DC.) T. & G.
- Santa Rosa: Dunkle 8452 LAM!; SBBG; SBM.
- Santa Cruz: Dunkle 8582 LAM!; Greene s.n. in Jul.–Aug. 1886 US!; RSA-POM; SBBG; SBM.
- Anacapa: Dunkle 7675 LAM!; SBBG.
- Santa Barbara: Dunkle 8137 LAM!; Bryan, Dr. & Mrs. s.n. LAM!; SBBG.
- Santa Catalina: Fosberg S4930 LAM!, NY!; Trask s.n. in May 1898 US!; Dunlavy s.n. May 4, 1934 LA!; RSA-POM; SBBG.
- San Clemente: Trask 195 US!; RSA-POM; SBBG.

Hemizonia fitchii Gray
- Santa Cruz: Nixon 1773 SCIR!; RSA-POM; SBBG.

Hemizonia frutescens Gray
- Guadalupe: Palmer 42 MO!, NY!, CM!.

Hemizonia greeneana Rose ssp. *greeneana*
- Guadalupe: Rempel 758-37 LAM!; Moran 18160 LAM!; Palmer 865 NY!; LA; MO; RSA-POM.

Hemizonia increscens (Hall ex Keck) Tanowitz ssp. *increscens*
- Santa Rosa: Brandegee s.n. in Jun. 1888 US!; SBM.
- Santa Cruz: SBM.

Hemizonia palmeri Rose
- Guadalupe: Moran 17337 MO!; Lindsay 43082 RSA!; Carlquist 470 RSA!.

Heterotheca grandiflora Nutt.
- Santa Cruz: RSA-POM; SBBG.
- San Nicolas: RSA-POM.
- Santa Catalina: Dunkle 1976 LAM!; Fosberg S4302 LAM!; Fosberg 4447 LAM!; RSA-POM; SBBG.
- San Clemente: DeBuhr & Wallace 688 LAM!; RSA-POM; SBBG.

Hieraceum argutum Nutt. ssp. *argutum*
- Santa Rosa: Dunkle 8482 AHFH!; RSA-POM; SBM.
- Santa Cruz: Clokey 5088 LAM!; RSA-POM; SBBG; SBM.

Hypochoeris glabra L.
- Santa Rosa: Thorne et al. 48782 RSA!; Raven, Blakley & Ornduff 14885 RSA!; Munz & Crow 11640 POM!; SBBG; SBM.
- Santa Cruz: Sauer & Hobbs 6029 LA!; Pierson 11031 RSA!; Clokey 5081 POM!; SBBG; SBM.
- Santa Catalina: Thorne 36305 RSA!; SBBG.
- San Clemente: Raven 17693 RSA!; SBBG.
- Guadalupe: Moran 13787 RSA!; Norris, K. S. s.n. May 1, 1951 LA!.

Jaumea carnosa (Less.) Gray
- San Miguel: SBM.
- Santa Rosa: Dunkle 8492 LAM!; Munz & Hoffmann 11726 POM!; SBM.
- Santa Cruz: SBM.
- Santa Catalina: Fosberg S4895 LAM!, POM!; Thorne 45090 RSA!; SBM!.

Lactuca serriola L.
- Santa Rosa: SBM.
- Santa Cruz: Daily 404 SCIR!; SBBG.
- San Nicolas: SBBG.
- Santa Catalina: Thorne 36276 RSA!; SBBG.

Lasthenia californica DC. ex Lindl.
- San Miguel: Munz & Voss 11873 POM!; SBBG; SBM.
- Santa Rosa: Hoffmann s.n. May 10, 1932 POM!; Raven, Blakley & Ornduff 14921 RSA!; Thorne et al. 48859 RSA!; SBBG; SBM.
- Santa Cruz: Fosberg 7523 LAM!; Elmore 468 AHFH!; Raven & Smith 15302 RSA!; SBBG, SBM.
- Anacapa: Dunn, N. s.n. May 14, 1932 LA!; SBBG; SBM.
- San Nicolas: Dunkle 8351 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; SBBG; SBM.
- Santa Barbara: Dunkle 7402 LAM!, AHFH!; Blakley 5695 RSA!; Dunkle 7467 AHFH!; SBBG; SBM.
- Santa Catalina: Dunkle 1742 AHFH!, POM!; Fosberg S4376 LAM!; Wolf 3518 POM!; SBBG; SBM.
- San Clemente: Dunkle 7261 LAM!; Elmore 400 AHFH!; Raven 17193 RSA!; CAS; SBBG.

Guadalupe: Thoburn, Greene & Wing s.n. in Jul. 1897 DS!; Wiggins & Ernst 119 DS!; Greene s.n. in 1885 DS#205127!; RSA-POM.

Lasthenia coronaria (Nutt.) Ornduff

Guadalupe: Anthony s.n. in May–Jun. 1897 UC!.

Lasthenia glabrata Lindl. ssp. *coulteri* (Gray) Ornduff

Santa Rosa: Hoffmann s.n. Apr. 8, 1930 POM!; Raven 14990 RSA!

Layia glandulosa (Hook.) H. & A. ssp. *glandulosa*

Santa Cruz: RSA-POM.

Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck

San Miguel: Youngberg s.n. May 28, 1939 POM!; Munz & Crow 11824 POM!; SBBG; SBM.

Santa Rosa: Dunn, N. May 24, 1931 LA!; Thorne et al. 48858 RSA!; Munz & Crow 11703 POM!; SBBG; SBM.

Santa Cruz: Fosberg 7602 LAM!; Moran 752 LAM!, RSA!; Clokey 5103 NY!; LA; SBBG; SBM.

Santa Catalina: Fosberg S4814 LAM!, NY!; Dunkle 1834 AHFH!; Thorne 35928 RSA!; SBBG; SBM.

San Clemente: Dunkle 7233 LAM!; Thorne 42948 RSA!, NY!; Raven 17331 RSA!; SBBG.

Guadalupe: Anthony 251 US!.

Layia platyglossa (F. & M.) Gray ssp. *platyglossa*

Santa Rosa: Moran 804 LAM!, NY!; Elmore 202 AHFH!; Dunkle 8428 AHFH!; SBM.

Lepidospartium squamatum (Gray) Gray

Santa Cruz: Balls & Blakley 23750 RSA!; SBBG.

Madia exigua (Sm.) Gray

Santa Cruz: Hoffmann s.n. Apr. 10, 1931 LA!; Clokey 5102 POM!; Raven & Smith 15228 RSA!; SBBG; SBM.

Santa Catalina: Davidson A. s.n. Jun. 26, 1891 LAM!; Fosberg S4833 LAM!, POM!; Raven 17812 RSA!; SBBG; SBM.

Madia gracilis (Sm.) Keck ssp. *gracilis*

Santa Cruz: Clokey 5101 LAM!, POM!; Raven & Smith 15178 RSA!; Thorne & Everett 36847 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4427 LAM!; Thorne 36857 RSA!, LA!; Raven 17818 RSA!; SBBG; SBM.

Madia sativa Mol.

Santa Cruz: Dunkle 8578 LAM!, AHFH!; SBBG.

Santa Catalina: Dunkle 2450 AHFH!; Trask s.n. US!; Thorne & Everett 35005 RSA!; SBBG.

San Clemente: Raven 17983 RSA!.

Malacothrix clevelandii Gray

Guadalupe: Palmer 51 NY!, CM!.

Malacothrix coulteri Harv. & Gray var. *cognata* Jeps.

Santa Rosa: Hoffmann 699 POM!; SBM.

Santa Cruz: Fosberg 7535 LAM!; SBM.

Malacothrix foliosa Gray

San Clemente: Trask 213 NY!; Dunkle 7211 LAM!, AHFH!, NY!; Nevin & Lyon s.n. in Apr. 1885 CAS#731!, DS#117575!; RSA-POM; SBBG.

Malacothrix incana (Nutt.) T. & G.

San Miguel: Dunkle 8412 LAM!, MO!, NY!; Elmore 327 AHFH!; Yates s.n. LAM!; SBBG; SBM.

Santa Rosa: Thorne et al. 48912 RSA!; Brandegee s.n. in 1888 GH!; Dunkle 8462 LAM!.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#065169!, NY!.

San Nicolas: Wier & Beauchamp s.n. Jul. 4, 1968 RSA#289130!.

San Clemente: (Raven 1963: Murbarger 189 at UC.)

Malacothrix indecora Greene

San Miguel: SBM.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 NY!, MO!.

Malacothrix "A" (Davis 1980)

Santa Barbara: Dunkle 8105 LAM!; Dunkle 8133 LAM!, NY!; Elmore 370 AHFH!; RSA-POM!.

Malacothrix "C" (Davis 1980)

San Nicolas: Trask s.n. in Apr. 1897 MO!; Foreman, Evans & Rainey 80 UC!; Wier & Beauchamp s.n. Jul. 3, 1978 RSA!.

Malacothrix saxatilis (Nutt.) T. & G. var. *implicata* (Eastw.) Hall

San Miguel: Dunkle 8388 LAM!, NY!; Moran 3439 POM!, NY!; Hoffmann s.n. Apr. 10, 1930 LA!; SBBG; SBM.

Santa Rosa: Dunkle 8433 LAM!; Blakley 3192 RSA!; Dunn, N. s.n. May 24, 1931 LA!; SBBG; SBM.

Santa Cruz: Clokey 5080 NY!; Raven & Smith 15127 RSA!; Eastwood 6416 NY!; SBBG; SBM.

Anacapa: Dunkle 7608 LAM!, NY!; Elmore 248 AHFH!; Ellison s.n. May 12–15, 1929 LA!; SBBG; SBM.

San Nicolas: Trask 65 LAM!, NY!; Trask 64 MO!; Raven & Thompson 20760 RSA!; SBBG; SBM.

Malacothrix saxatilis (Nutt.) T. & G. var. *tenuifolia* (Nutt.) Gray

Santa Catalina: Fosberg S4423 LAM!, NY!; Thorne 36469 RSA!; Nuttall 1010 POM!; SBBG; SBM.

Malacothrix similis Davis & Raven

San Miguel: (Davis 1982: Greene s.n. in Sep. 1886 CAS#734)

Santa Cruz: (Davis & Raven 1962: Brandegee s.n. in 1888 at UC.)

Malacothrix squalida Greene

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 CAS#735!; NY!.

Anacapa: SBBG.

Matricaria matricarioides (Less.) Porter

Santa Rosa: Blakley 3193 RSA!; Thorne et al. 48719 RSA!; SBBG; SBM.

Santa Cruz: Daily 37 SCIR!; SBBG; SBM.

Santa Catalina: Fosberg S4507 LAM!, POM!; Dunkle 2451 AHFH!; SBBG.

Guadalupe: Palmer 47 CM!; Wiggins & Ernst 113 SD!.

Micropus californicus F. & M.

Santa Rosa: Sweet s.n. Apr. 15, 1935 POM!; Thorne et al. 48997B RSA!; SBM.

Santa Cruz: Raven & Smith 15189 RSA!; Blakley 3295 RSA!; Munz & Crow 11515 POM!; SBBG; SBM.

Microseris douglasii (DC.) Seh.-Bip. ssp. *douglasii*

San Nicolas: Raven & Thompson 20767 RSA!.

San Clemente: Thorne 42789 RSA!.

Microseris douglasii (DC.) Sch.-Bip. ssp. *platycarpha* (Gray) Chamb.

Santa Catalina: Thorne 35778 RSA!; Thorne 35935a RSA!; SBBG.

San Clemente: Munz 6739 POM!; Dunkle 7364 AHFH!; Raven 17199 RSA!; SBBG.

Microseris douglasii (DC.) Sch.-Bip. ssp. *tenella* (Gray) Chamb.
San Miguel: SBM.
Santa Rosa: SBM.
Santa Cruz: SBM.

Microseris elegans Greene ex Gray
San Miguel: SBM.
Santa Cruz: SBBG; SBM.
San Clemente: Thorne 42819b RSA!.

Microseris heterocarpa (Nutt.) Chamb.
Santa Rosa: Thorne 48980 RSA!; Raven, Blakley & Ornduff 14908 RSA!; Hoffmann s.n. Mar. 8, 1932 UC!; SBBG.
Santa Cruz: Brandegee s.n. in Apr. 1888 UC!.
Santa Catalina: Brandegee, K. s.n. UC!; Thorne 36347 RSA!, UC!; SBBG.
San Clemente: Trask 235 NY!; Dunkle 7325 AHFH!; Raven 17206 RSA!; SBBG.
Guadalupe: Brandegee s.n. May 20, 1897 UC!; Wiggins & Ernst 206 UC!; Moran 17362 RSA!.

Microseris linearifolia (DC.) Sch.-Bip.
Santa Rosa: Blakley & Smith 3068 RSA!; Hoffmann s.n. in Apr. 1930 CAS#178617!; SBBG; SBM.
Santa Cruz: Blakley 3356 RSA!; Hoffmann s.n. Apr. 11, 1931 LA!; Abrams & Wiggins 50 CAS!; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Trask 66 ND-G#063915!, NY!.
Santa Barbara: (Philbrick 1972: Philbrick & McPherson B68-216)
Santa Catalina: Fosberg S4419 LAM!, NY!; Thorne 35805 RSA!; Dunkle 1823 AHFH!; SBBG.
San Clemente: Dunkle 7296 LAM!, AHFH!; Thorne 42790 RSA!; Raven 17612 RSA!; SBBG.
Guadalupe: Palmer 50 MO!; Anthony 243 MO!; Moran 17361!.

Pentachaeta lyonii Gray
Santa Catalina: Fosberg S5416 LAM!; RSA-POM.

Perezia microcephala (DC.) Gray
Santa Rosa: Dunkle 8424 LAM!; Dunn 1303 LA!; Munz & Crow 11612 POM!; SBBG; SBM.
Santa Cruz: Dunkle 8626 LAM!; Elmore 263 AHFH!; Blakley 3306 RSA!; SBBG; SBM.
Santa Catalina: Fosberg S5380 LAM!; Diehl 258 POM!; Thorne & Everett 34890 RSA!; USC; SBBG; SBM.

Perityle emoryi Torr. in Emory
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8617 LAM!, NY!; Greene s.n. in 1886 NY; Williams 52 POM!; SBBG; SBM.
Anacapa: SBBG; SBM.
Santa Barbara: Dunkle 8104 LAM!, NY!; Thorne 37549 RSA!; Blakley 5626 RSA!; SBBG.
Santa Catalina: Thorne 35754 RSA!; Trask s.n. in Mar. 1899 NY; Dunkle 1954 LAM!, AHFH!; SBBG; SBM.
San Clemente: Dunkle 7335 LAM!; Trask 255 NY!; Raven 17323 RSA!; SBBG.
Guadalupe: Palmer 44 NY!, CM!; Carlquist 439 RSA!; Moran 5628 RSA!.

Perityle incana Gray
Guadalupe: Rempel 758-37 LAM!; Rempel 759-37 LAM!; Palmer 43 CM!; RSA-POM; SBM.

Picris echioides L.
Santa Catalina: Thorne 36450 RSA!; Thorne 36890 RSA!; Thorne 36664 RSA!; SBBG.

Pluchea odorata (L.) Cass.
Santa Cruz: Hoffmann & Cooke s.n. Sep. 20, 1930 POM!; SBBG; SBM.
Santa Catalina: Thorne 36677 RSA!; Dunkle 1993 AHFH!; SBBG.

Pluchea sericea (Nutt.) Cov.
Santa Catalina: Fosberg S4479 LAM!, POM!.

Psilocarphus tenellus Nutt. var. *tenellus*
Santa Rosa: Sweet s.n. Apr. 15, 1935 POM!; Raven 14953 RSA!; Hoffmann s.n. Jun. 15, 1930 LAM!; SBBG; SBM.
Santa Cruz: Blakley 3342 RSA!; Thorne & Everett 36779 RSA!; Raven & Smith 15211 RSA!; SBBG; SBM.
Santa Catalina: Thorne 35987 RSA!.
San Clemente: Thorne 36087 RSA!; Thorne 42974 RSA!; Raven 17664 RSA!.

Rafinesquia californica Nutt.
Santa Rosa: SBM.
Santa Cruz: Brandegee s.n. in 1888 RSA!; SBBG; SBM.
Anacapa: SBBG.
Santa Barbara: Thorne 37511 RSA!; SBBG.
Santa Catalina: Fosberg S4537 LAM!; Dunkle 2149 AHFH!; Thorne & Everett 34888 RSA!; SBBG.
San Clemente: Raven 17608 RSA!; Raven 17244 RSA!; Thorne 42852 RSA!; SBBG.

Senecio aphanactis Greene
Santa Rosa: SBM.
Santa Cruz: Pierson s.n. Mar. 25, 1934 POM!; Wolf 2780 RSA!; Wolf 2805 RSA!; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!.

Senecio douglasii DC. var. *douglasii*
Santa Cruz: Balls & Blakley 23665 RSA!; Balls & Blakley 23633 RSA!; Hoffmann s.n. Jul. 20, 1930 POM!; SBBG; SBM.
Santa Catalina: Nuttall 794 F!.
San Clemente: Dunkle 7227 LAM!.

Senecio lyonii Gray
Santa Catalina: Grant & Wheeler 6134 LAM!, POM!; Thorne 39388 RSA!; Raven 17817 RSA!; SBBG; SBM.
San Clemente: Dunkle 7349 LAM!; Moran 589 LAM!; Raven 17161 RSA!.

Senecio palmeri Gray
Guadalupe: Palmer 49 CM!; Franceschi 10 SBM!.

Senecio vulgaris L.
San Miguel: SBBG.
Santa Cruz: Raven & Smith 15222 RSA!; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Thorne et al. 52350 RSA!.
Santa Catalina: Thorne 36209 RSA!; Thorne, Rollins, Propst & Carolin 36751 RSA!; SBBG.
San Clemente: Raven 17230 RSA!; SBBG.

Silybum marianum (L.) Gaertn.
Santa Rosa: Thorne et al. 48803 RSA!.
Santa Cruz: Dunkle 8539 LAM!, AHFH!; Elmore 264 AHFH!; Clokey 5115 LAM!, POM!; SBBG; SBM.
Santa Barbara: Philbrick & Ricker B69-48 RSA!.
Santa Catalina: Fosberg S4931 LAM!; Thorne & Everett 35047 RSA!; SBBG.

Solidago californica Nutt.
Santa Rosa: Dunkle 8444 LAM!; Epling & Erickson s.n. Aug. 8, 1937 LA!; Voss s.n. Sep. 4, 1930 POM!; SBM.
Santa Cruz: Hoffmann s.n. Sep. 9, 1931 LAM!; Hoffmann s.n. Sep. 20, 1930 POM!; Blakley 23690 RSA!; SBBG; SBM.
Santa Catalina: Dunkle 2001 AHFH!, POM!; Thorne 36703 RSA!; SBBG.

Sonchus asper (L.) Hill
San Miguel: Dunkle 8396 LAM!; Hoffmann s.n. Mar. 25, 1927 SBM#1069!; SBBG.
Santa Rosa: Dunkle 8521 AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Clokey 5079 NY!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Dunkle 8330 AHFH!; Kanakoff s.n. Apr. 12, 1940 LAM!.
Santa Barbara: Bryan, Dr. & Mrs. s.n. LAM!; SBM.
Santa Catalina: Fosberg S4340 LAM!; Fosberg S4620 LAM!; Dunkle 2095 AHFH!; RSA-POM; SBBG.
San Clemente: Dunkle 7209 LAM!, AHFH!; RSA-POM; SBBG.

Sonchus oleraceus L.
San Miguel: Dunkle 8421 LAM!; SBBG; SBM.
Santa Rosa: SBBG; SBM.
Santa Cruz: Dunkle 8589 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7649 AHFH!; SBBG; SBM.
San Nicolas: Dunkle 8306 LAM!, AHFH!, NY!; Foreman, Evans & Rainey 25 LA!; RSA-POM; SBBG.
Santa Barbara: Elmore 304 AHFH!; Dunkle 8131 LAM!, NY!; Dunkle 7450 LAM!, AHFH!, NY!; RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 NY!; Dunkle 2468 AHFH!; Knopf 224 F!; RSA-POM; SBBG.
San Clemente: Trask 353 NY!; RSA-POM; SBBG.
Guadalupe: Palmer 51 NY!; Palmer 871 NY!, US!; Moran 6615 RSA!.

Sonchus tenerrimus L.
San Nicolas: Trask s.n. in Apr. 1900 LAM!; Trask 23 US!; Trask 67 MO!.
Santa Barbara: (Philbrick 1972: Philbrick & McPherson B68-247)
Santa Catalina: Trask s.n. in Mar. 1901 NY!; Millspaugh 4544 F!.
San Clemente: Trask 355 NY!, US!; Trask 356 NY!, US!.
Guadalupe: Palmer 873 NY!, US!; Moran 17416 SD!; Moran 13763 SD!.

Stephanomeria blairii M. & J.
San Clemente: Raven 17310 RSA!; Dunkle 7353 LAM!, AHFH!; House & Grumbles s.n. USC!; SBBG.

Stephanomeria cichoriacea Gray
Santa Rosa: SBM.
Santa Cruz: Hoffmann s.n. Jun. 15, 1930 LAM!; Dunkle 8531 LAM!; Fosberg 7561 LAM!; RSA-POM; SBBG; SBM.

Stephanomeria diegensis Gottlieb
Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!.
Santa Catalina: Piehl 62515 SBBG!; Millspaugh 4534 F!; Fosberg S7147 LAM!
San Clemente: Piehl 631058 SBBG!; Dunkle 7354 LAM!, AHFH!, SBBG!; Raven 18015 SBBG; Abrams & Wiggins 344 CAS!; RSA-POM.

Stephanomeria exigua Nutt. ssp. *coronaria* (Greene) Gottlieb
San Miguel: Greene s.n. in 1886 ND-G#001750!.
Santa Cruz: RSA-POM.

Stephanomeria guadalupensis Bdg.
Guadalupe: Rempel s.n. Jul. 19, 1937 LAM!; Carlquist 457 RSA!; Moran 15119 RSA!.

Stephanomeria virgata Benth. ssp. *virgata*
Santa Rosa: Dunkle 8477 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8625 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Stylocline gnaphalioides Nutt.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg S7684 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Grant 1256 LAM!; Fosberg S4601 LAM!; Dunkle 2145 AHFH!; RSA-POM; SBBG! SBM.

Taraxacum laevigatum (Willd.) DC.
Santa Cruz: RSA-POM.
Santa Catalina: RSA-POM.

Taraxacum officinale Wiggers
Santa Cruz: Daily 610 SCIR!; SBBG.
Santa Catalina: SBBG.

Thelesperma megapotamicum (Spreng.) Kuntze
Santa Catalina: Nuttall 602 F!.

Tragopogon porrifolius L.
Santa Cruz: SBBG; SBM.

Venegasia carpesioides DC.
Santa Rosa: Moran 814 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8608 LAM!; Fosberg 7697 LAM!, LA!; Clokey 5108 LAM!; RSA-POM; SBBG; SBM.

Xanthium spinosum L.
San Miguel: Dunkle 8364 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Daily 148 SCIR!; SBBG.
Santa Barbara: Abrams & Wiggins 39 DS!.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!, NY!; Trask s.n. in Aug. 1897 US!; Fosberg S4547 LAM!; CAS; RSA-POM; SBBG.

Xanthium strumarium L. var. *canadense* (Mill.) T. & G.
Santa Catalina: Dunkle 2437 AHFH!; Fosberg S4897 LAM!; RSA-POM.

Bataceae

Batis maritima L.
San Clemente: Nevin s.n. in 1885 DS#81927!.

Berberidaceae

Berberis pinnata Lag. ssp. *insularis* Munz

Santa Rosa: RSA-POM; SBM.

Santa Cruz: Hoffmann 189 LAM!, LA!; RSA-POM; SBBG; SBM.

Anacapa: Dunkle 7668 LAM!; RSA-POM; SBBG.

Boraginaceae

Amsinckia intermedia F. & M.

San Miguel: Schuyler 21 LAM!; Munz & Norris 11790 POM!, GH!; SBBG; SBM.

Santa Rosa: Moran 779 LAM!; Elmore 212 AHFH!; Thorne et al. 48732 RSA!; SBBG; SBM.

Santa Cruz: Fosberg 7556 LAM!; Fosberg 7520 LAM!; Elmore s.n. Apr. 18, 1936 LAM!; SBBG; SBM.

Anacapa: SBBG; SBM.

Santa Barbara: Dunkle 7461 LAM!, DS!, NY!; Dunkle 8112 LAM!; Thorne 37537 RSA!; SBBG; SBM.

Santa Catalina: Trask s.n. in Apr. 1898 US!; Millspaugh 4700 F!; Templeton 11391 LAM!; CAS; DS; RSA-POM; SBBG; SBM.

San Clemente: Moran 569 LAM!, DS!, GH!, NY!, RSA!; Elmore 427 AHFH!; Trask 248 US!; CAS; SBBG.

Amsinckia menziesii (Lehm.) Nels. & Macbr.

Santa Cruz: Moran 773 LAM!; Raven & Smith 15261 RSA!; SBBG.

Santa Catalina: Dunkle 2060 AHFH!; Wolf 3622 RSA!; SBBG.

Guadalupe: Palmer 69 GH!, MO!, NY!; Moran 6681 RSA!; Howell 8329 CAS!.

Amsinckia spectabilis F. & M. var. *nicolai* (Jeps.) Jtn. ex Munz

San Miguel: Munz & Crow 11789 POM!; SBM.

San Nicolas: Kanakoff s.n. Apr. 22, 1940 LAM!; Trask 58 LAM!; Dunkle 8339 LAM!, RSA!; CAS; US.

San Clemente: Munz 6771 POM!; Thorne 42942 RSA!.

Amsinckia spectabilis F. & M. var. *spectabilis*

San Miguel: Greene s.n. in Sep. 1886 ND-G#042845!; SBBG; SBM.

Santa Rosa: Thorne et al. 49040 RSA!; Munz & Crow 11570 POM!, US!; Raven 14986 RSA!; SBBG; SBM.

Santa Cruz: Webster, Axelrod et al. 84 RSA!; Raven & Smith 15309 RSA!; SBBG; SBM.

Anacapa: SBBG; SBM.

San Nicolas: Kanakoff s.n. Apr. 16, 1940 LAM!; Trask s.n. in Apr. 1897 US!; Trask 59 GH!; CAS.

Santa Barbara: Dunkle 7408 AHFH!.

San Clemente: Raven 17262 RSA!; SBBG.

Cryptantha clevelandii Greene var. *clevelandii*

San Miguel: Schuyler s.n. Apr. 1, 1976 LAM!; Elmore 312 AHFH!; Munz & Crow 11823 POM!; SBBG; SBM.

Santa Rosa: RSA-POM; SBBG; SBM.

Santa Cruz: Clokey 5037 NY!; Clokey 5038 NY!; RSA-POM; SBBG; SBM.

Anacapa: SBBG; SBM.

San Nicolas: RSA-POM.

Santa Barbara: Dunkle 7446 LAM!, AHFH!; Dunkle 7428 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg 10647 LAM!, LA!; Trask s.n. Mar. 1897 NY!; Millspaugh 4606 F!; RSA-POM; SBBG; SBM.

San Clemente: RSA-POM.

Cryptantha clevelandii Greene var. *florosa* Jtn.

San Miguel: Hoffmann s.n. Apr. 10, 1930 LAM!; Youngberg, F. s.n. May 28, 1938 POM#259646!.

Santa Rosa: Hoffmann s.n. Apr. 18, 1929 SBM#5996!; Munz & Crow 11710 POM!.

Santa Cruz: Fosberg 7619 LAM!, LA!; Hoffmann s.n. Jun. 15, 1930 LAM!; Abrams & Wiggins 110 NY!; POM.

Anacapa: Hoffmann s.n. Mar. 16, 1929 SBM!.

San Nicolas: Kanakoff s.n. Apr. 12, 1940 LAM!.

Santa Barbara: Dunkle 7447 LAM!; Dunkle 7428 LAM!.

Santa Catalina: Dunkle 2097 LAM!; Fosberg S4750 LAM!; Hasse 4156 NY!.

Cryptantha foliosa (Greene) Greene

Guadalupe: Greene s.n. Apr. 26, 1885 NY!; Palmer 68 CM!, MO!; Moran 5954 LA!, NY!, RSA!.

Cryptantha intermedia (Gray) Greene

Santa Catalina: Trask s.n. May 1895 MO#2517956!; Trask s.n. in Mar. 1901 US!; Millspaugh 4744 F!; RSA-POM; SBBG.

San Clemente: Dunkle 7260 LAM!, AHFH!; Trask 176 NY!; Trask 277 NY!; RSA-POM; SBBG.

Cryptantha leiocarpa (F. & M.) Greene

Santa Rosa: Raven 14998 UC!.

Cryptantha maritima (Greene) Greene

San Nicolas: Trask 57 LAM!, GH!, NY!; Trask 56 GH!; Dunkle 8353 AHFH!; SBBG.

Santa Barbara: Dunkle 7403 LAM!, NY!; RSA!; Dunkle 8106 AHFH!; Philbrick & Benedict B66-362 RSA!; SBBG.

Santa Catalina: Trask s.n. in Mar. 1900 NY!; Knopf 143 F!; Thorne 35855 RSA!; SBBG.

San Clemente: Trask 221 NY!; Munz 6746 POM!; Raven 17318 RSA!; SBBG.

Guadalupe: Palmer 67 CM!, MO!, NY!; Greene s.n. Apr. 26, 1885 NY; Carlquist 449 RSA!; CAS; DS.

Cryptantha micromeres (Gray) Greene

Santa Rosa: Hoffmann s.n. Apr. 16, 1929 CAS#168340!; SBM.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#001494!; Munz & Crow 11842 POM!; Raven & Smith 15235 RSA!; CAS; SBM.

Santa Catalina: Trask s.n. in Mar. 1901 NY!; Thorne 36872a RSA!.

Cryptantha microstachys (Greene ex Gray) Greene

Santa Catalina: Knopf s.n. Mar. 20–Apr. 10, 1921 F!; Millspaugh 4783 F!.

Cryptantha muricata (H. & A.) Nels. & Macbr. var. *jonesii* (Gray) Jtn.

Santa Cruz: Hoffmann s.n. Apr. 22, 1932 POM#180293!; SBM.

Cryptantha traskiae Jtn.

San Nicolas: Trask s.n. in Apr. 1901 LAM!; Howell 8223 CAS!; Wier & Beauchamp s.n. June 30, 1978 RSA!.

San Clemente: Trask 275 NY!; Raven 17271 RSA!; Pierson 3421 DS!

Harpagonella palmeri Gray
Santa Catalina: Johnson 1437 NY!; Thorne 35873 RSA!; Fosberg S4557 POM!; SBBG.
Guadalupe: Moran 6750 RSA!; Carlquist 463 RSA!.

Heliotropium curassavicum L. ssp. *oculatum* (Heller) Thorne
San Miguel: Elmore 328 AHFH!; SBBG; SBM.
Santa Rosa: Dunkle 8470 LAM!, AHFH!; Thorne et al. 48966 RSA!; SBBG.
Santa Cruz: Dunkle 8593 LAM!; Elmore 277 AHFH!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7611 LAM!; Elmore 222 AHFH!; SBBG; SBM.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; Dunkle 8319 LAM!; RSA-POM; SBBG.
Santa Catalina: Fosberg 7166 LAM!, POM!; Thorne & Everett 34558 RSA!; Wolf 3602 RSA!; SBBG; SBM.
San Clemente: Murbarger 205 UC!.

Pectocarya linearis DC. ssp. *ferocula* (Jtn.) Thorne
Santa Cruz: Fosberg 7623 LAM!; Clokey 5035 NY!; Raven & Smith 15186 RSA!; SBBG; SBM.
Santa Catalina: Fosberg S4404 LAM!, NY, POM!; Grant 913 GH!; Thorne & Everett 34670 RSA!; SBBG; SBM.
San Clemente: Trask 167 NY!; Munz 6690 POM!, GH!; Thorne 36101 RSA!.
Guadalupe: Carlquist 450 RSA!.

Pectocarya penicillata (H. & A.) A. DC.
Anacapa: SBM.

Pectocarya recurvata Jtn.
Guadalupe: Palmer 69a NY!; Anthony 237 GH!; Moran 6594 CAS!.

Plagiobothrys californicus (Gray) Greene var. *californicus*
Guadalupe: Moran 20308 RSA!; Wiggins & Ernst 106 DS!.

Plagiobothrys californicus (Gray) Greene var. *fulvescens* Jtn.
San Miguel: SBM.
Santa Rosa: Munz & Crow 11705 POM!; Munz & Crow 11707 POM!.
Santa Cruz: Fosberg 7681 LAM!, LA!; SBBG; SBM.
Anacapa: SBBG; SBM.

Plagiobothrys californicus (Gray) Greene var. *gracilis* Jtn.
Santa Cruz: RSA-POM; SBM.
Anacapa: SBBG.
Santa Catalina: Fosberg S4379 LAM!; Dunkle 2061 LAM!; Trask s.n. in Mar. 1901 NY!; RSA-POM; SBBG.
San Clemente: RSA-POM.

Plagiobothrys canescens Benth.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Apr. 10, 1931 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg 10648 LAM!, LA!; Grant & Wheeler 6156 LAM!, NY!; Grant & Wheeler 6159 LAM!; RSA-POM; SBBG; SBM.
San Clemente: Trask 210 NY!; RSA-POM.

Brassicaceae

Arabis glabra (L.) Bernh.
Santa Cruz: RSA-POM; SBM.

Arabis hoffmannii (Munz) Rollins
Santa Rosa: SBM.
Santa Cruz: RSA-POM; SBM

Athysanus pusillus (Hook.) Greene
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Fosberg 7630 LAM!; Fosberg 7691 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.

Brassica geniculata (Desf.) J. Ball
San Miguel: SBBG.
Santa Rosa: SBBG.
Santa Cruz: Daily 500 SCIR!; SBBG.
San Nicolas: RSA-POM; SBBG.
Santa Catalina: Fosberg S5378 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Brassica kaber (DC.) L.C. Wheeler
Santa Cruz: SBM.
Santa Catalina: RSA-POM.

Brassica nigra (L.) Koch in Rohling
Santa Cruz: Hoffmann s.n. Jun. 15, 1930 LAM!; SBM.
San Nicolas: RSA-POM.
Santa Barbara: Dunkle 7445 LAM!; SBBG; SBM.
Santa Catalina: Fosberg S4720 LAM!; Dunkle 1918 AHFH!; Fosberg S4730 LAM!; NY; RSA-POM.
San Clemente: Trask 173 US!.
Guadalupe: Palmer 5 NY!.

Brassica rapa L. ssp. *sylvestris* (L.) Janchen
San Miguel: Dunkle 8423 AHFH!; SBM.
Santa Cruz: Hoffmann s.n. Apr. 10, 1930 LAM!; Dunkle 8637 LAM!; RSA-POM; SBM.
Santa Catalina: Detmers s.n. Apr. 14, 1929 USC!; Fosberg S11872 LAM!; RSA-POM.
San Clemente: Raven 17618 RSA!.

Cakile edentula (Bigel.) Hook. var. *edentula*
San Miguel: Dunkle 8389 LAM!, AHFH!; SBBG; SBM.
Santa Rosa: SBM.
San Nicolas: SBBG; SBM.

Cakile maritima Scop. ssp. *maritima*
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBBG.
Santa Cruz: RSA-POM; SBBG.
Anacapa: SBBG.
San Nicolas: Foreman 236 LA!; RSA-POM; SBBG.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Capsella bursa-pastoris (L.) Medic.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8633 AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4615 LAM!; Dunkle 8633 LAM!; Trask s.n. in Mar. 1901 NY!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Guadalupe: Wiggins & Ernst 66 DS!.

Cardamine californica (Nutt.) Greene
San Miguel: SBM.
Santa Rosa: SBM.
Santa Cruz: Fosberg 7583 LAM!; Moran 760 LAM!; Clokey 4944 LAM; RSA-POM; SBM.

Santa Catalina: Trask s.n. in Mar. 1897 LAM!; Thorne & Propst 42483 RSA!.

Cardamine oligosperma Nutt.
Santa Cruz: SBM.

Cardaria draba (L.) Desv.
Santa Cruz: Hoffmann 260 LAM!, LA!; RSA-POM; SBBG; SBM.

Caulanthus inflatus Wats.
Santa Cruz: Elmore 453 AHFH!.

Caulanthus lasiophyllus (H. & A.) Pays.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7702 LAM!; Abrams & Wiggins 169 NY!; RSA-POM; SBBG; SBM.
Anacapa: Moran 724 LAM!; SBBG; SBM.
Santa Barbara: SBBG.
Santa Catalina: Fosberg S4594 LAM!, NY!; Fosberg S4724 LAM!; Dunkle 2084 LAM!; RSA-POM; SBBG; SBM.
San Clemente: Trask 265 NY!; RSA-POM; SBBG.
Guadalupe: Palmer 880 ND-G!; Moran 13777 SD!; Moran 17360 SD!.

Descurainia pinnata (Walt.) Britt. ssp. *menziesii* (DC.) Detl.
Santa Rosa: Hoffmann s.n. May 10, 1932 SBM#12101!.
Santa Cruz: Fosberg 7519 LAM!; Clokey 5987 NY!; Abrams & Wiggins 56 CAS!, DS!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Catalina: Dunkle 2092 AHFH!; Trask s.n. in Mar. 1901 NY!; RSA-POM; SBBG; SBM.
San Clemente: RSA-POM; SBBG.
Guadalupe: Palmer 6 NY!; Moran 5658 DS!.

Dithyrea maritima A. Davids.
San Miguel: SBM.
San Nicolas: Trask 29 NY!, US!; Trask s.n. in Apr. 1897 MO!; Raven & Thompson 20706 LA!; RSA-POM; SBBG.

Draba cunefolia Nutt. ex T. & G. var. *integrifolia* Wats.
Santa Catalina: Trask s.n. in Apr. 1902 LAM!, NY!.

Erysimum ammophilum Heller
Santa Rosa: Munz & Crow 11757 LA!.

Erysimum cheiri (L.) Crantz
Santa Catalina: Thorne & Everett 33447 RSA!.

Erysimum insulare Greene
San Miguel: Dunkle 8384 LAM!; Munz & Norris 11787 LA!; Greene s.n. in Sep. 1886 CAS!; RSA-POM; SBBG; SBM.
Santa Rosa: Moran 797 LAM!; Moran s.n. Apr. 4, 1941 LAM!; Dunkle 8479 AHFH!; RSA-POM; SBBG.
Anacapa: SBBG.

Erysimum moranii Roll.
Guadalupe: Rempel 759-37 LAM!; Moran 15116 RSA!; Moran 18169 RSA!.

Hutchinsia procumbens (L.) Desv.
San Miguel: Dunkle 8403 LAM!, AHFH!; Fosberg S2083 NY!; RSA-POM.
Santa Rosa: Munz & Crow 11754 LA!; RSA-POM.
Santa Cruz: RSA-POM.
Anacapa: SBBG.
San Nicolas: Dunkle 8320 LAM!; Trask 98 NY!; Raven & Thompson 20685 DS!.
Santa Barbara: SBBG.
Guadalupe: Howell 8330 CAS!.

Lepidium lasiocarpum Nutt. ex T. & G. var. *lasiocarpum*
San Miguel: Dunkle 8422 LAM!.
Santa Rosa: RSA-POM.
Santa Cruz: SBBG.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Dunkle 8320a LAM!; Kanakoff s.n. Apr. 13, 1940 LAM!; RSA-POM; SBBG.
Santa Catalina: Millspaugh 4791 F!; Millspaugh 4614 F!.
San Clemente: RSA-POM; SBBG.
Guadalupe: Moran 6718 RSA!; Moran 2889 DS!; Moran 5696 DS!.

Lepidium lasiocarpum Nutt. ex T. & G. var. *latifolium* C. L. Hitchc.
Guadalupe: Palmer 8 NY!; Palmer 841 NY!, US!; Mason 1516 US!.

Lepidium latipes Hook.
Santa Cruz: RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 F!, NY!; Millspaugh 4749 F!.
San Clemente: RSA-POM.

Lepidium nitidum Nutt. var. *nitidum*
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7526 LAM!, LA!; Fosberg 7587 LAM!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Foreman 227 US!; SBM.
Santa Barbara: Dunkle 7413 LAM!; Bryan, Dr. & Mrs. s.n. LAM!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4391 LAM!; Dunkle 2071 AHFH!; Trask s.n. in Mar. 1901 NY!; RSA-POM; SBBG.
San Clemente: Elmore 401 AHFH!; Trask 347 NY!; RSA-POM; SBBG.
Guadalupe: Wiggins & Ernst 110 DS!; Moran 5677 SD!; Moran 12047 SD!.

Lepidium oblongum Small
San Miguel: RSA-POM.
Santa Cruz: RSA-POM.
Anacapa: SBBG.
San Nicolas: Trask 28 GH!; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 NY!.
San Clemente: SBBG.
Guadalupe: Moran 2878 DS!; Palmer 897 GH!, US!; Rose 16006 GH!, NY!, US!.

Lepidium virginicum L. var. *pubescens* (Greene) Thell.
Santa Catalina: Dunkle 2454 AHFH!; RSA-POM; SBBG.
San Clemente: SBBG.

Lepidium virginicum L. var. *robinsonii* (Thell.) C.L. Hitchc.
Santa Cruz: RSA-POM; SBM.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; Dunkle 8320 MO!; RSA-POM; SBBG.

Lobularia maritima (L.) Desv.
San Nicolas: Newman 103 Pacif. Missile Test Center Pt. Mugu!.

Santa Catalina: Fosberg 4483 LAM!; Lister & Powell s.n. Apr. 2, 1928 USC!; Trask s.n. in 1901 NY!; RSA-POM; SBBG.
Nasturtium officinale R. Br.
San Miguel: SBBG.
Santa Cruz: RSA-POM; SBM.
Santa Catalina: Fosberg S4748 LAM!; Dunkle 1925 AHFH!; RSA-POM; SBBG; SBM.
Raphanus raphanistrum L.
Santa Rosa: RSA-POM; SBBG.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Raphanus sativus L.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4663 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Sibara filifolia (Greene) Greene
Santa Cruz: SBM.
Santa Catalina: Trask s.n. in May 1901 LAM!.
Sisymbrium altissimum L.
Santa Catalina: Fosberg 4854 LAM!; Fosberg S5385 LAM!.
Sisymbrium irio L.
Anacapa: SBBG.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Guadalupe: Howell 8276 CAS!.
Sisymbrium officinale (L.) Scop.
Santa Cruz: Daily 336 SCIR!; SBBG; SBM.
Santa Catalina: Fosberg S4465 LAM!; Trask 303 US!, NY!; Trask s.n. in Apr. 1900 NY!.
Sisymbrium orientale L.
Santa Catalina: RSA-POM; SBBG.
Thysanocarpus curvipes Hook. ssp. *curvipes*
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LA!.
Thysanocarpus curvipes Hook. var. *elegans* (F. & M.) Rob. in Gray
Santa Catalina: RSA-POM.
Thysanocarpus erectus Wats.
Guadalupe: Anthony 244 SD!.
Thysanocarpus laciniatus Nutt. ex T. & G. var. *conchuliferus* (Greene) Jeps.
Santa Cruz: Moran 755 LAM!; Williams s.n. Mar. 23, 1941 AHFH!; Munz & Crow 11848 LA!; SBM.
Thysanocarpus laciniatus Nutt. ex T. & G. var. *crenatus* (Nutt.) Brewer
Santa Rosa: SBM.
Santa Cruz: SBM.
Thysanocarpus laciniatus Nutt. ex T. & G. var. *laciniatus*
Santa Cruz: Moran 750 LAM!; Williams s.n. Mar. 23, 1941 AHFH!; Hoffmann s.n. Apr. 10, 1931 LAM!; LA; RSA-POM.
Santa Catalina: Fosberg S4309 LAM!; Dunkle 2123 AHFH!; Detmers s.n. Apr. 13, 1929 USC!.
San Clemente: Dunkle 7308 LAM!, AHFH!.
Thysanocarpus laciniatus Nutt. ex T. & G. var. *ramosus* (Greene) Munz
Santa Rosa: SBM.
Santa Cruz: Fosberg 7626 LAM!, LA!; SBM.
Tropidocarpum gracile Hook.
Santa Catalina: Trask s.n. in 1900 LAM!; Dunkle 2064 AHFH!; SBBG.
San Clemente: RSA-POM.
Cactaceae
Bergerocactus emoryi (Engelm.) Britt. & Rose
Santa Catalina: RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7218 AHFH!; RSA-POM; SBBG; SBM.
Mammillaria blossfeldiana Bodeker var. *shurliana* Gates
Guadalupe: Moran 6708A SD!; Moran 17413 SD!; Moran 15123 SD!.
Opuntia ficus-indica (L.) Mill.
Santa Catalina: Millspaugh 4523 F!.
Opuntia littoralis (Engelm.) Ckll.
San Miguel: SBM.
Santa Rosa: SBM.
Santa Cruz: Elmore 279 AHFH!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: SBBG.
Santa Barbara: Philbrick O-628 SBBG!.
Santa Catalina: Millspaugh 4525 F!.
San Clemente: Blakley 5248 RSA!.
Opuntia oricola Philbriek
San Miguel: SBBG.
Anacapa: Elmore 245 LAM!; SBBG.
San Nicolas: Raven & Thompson 20790 RSA!; SBBG.
Santa Barbara: Blakley 5713 RSA!; SBBG.
Santa Catalina: Fosberg S4892 LAM!, F!.
San Clemente: Elmore 382 LAM!; Dunkle 7217 AHFH!.
Opuntia prolifera Engelm.
Santa Rosa: SBBG.
Santa Cruz: SBBG.
Anacapa: SBBG; SBM.
San Nicolas: SBBG.
Santa Barbara: SBBG.
Santa Catalina: Fosberg S4733 LAM!.
San Clemente: RSA-POM; SBBG.
Guadalupe: Moran 2617 SD!.
Callitrichaceae
Callitriche longipedunculata Morong
San Clemente: Thorne 42802 RSA!.
Callitriche marginata Torr. var. *marginata*
Santa Catalina: Thorne 37697 RSA!; Thorne 36088 RSA!.
San Clemente: Raven 17328 RSA!.
Campanulaceae
Githopsis diffusa Gray ssp. *diffusa*
Santa Cruz: Hoffmann s.n. Apr. 21, 1932 POM!; Hoffmann s.n. May 23, 1932 POM!; Raven & Smith 15236 RSA!.
Guadalupe: Palmer 53 CM!; Moran 27271 SD!. (GU material is *G. diffusa* Gray var. *guadalupensis* Morin (Morin, N. Systematic Botany 8(4):436–468. 1983.)
Lobelia erinus L.
Santa Cruz: SBBG.

Triodanis biflora (R. & P.) Greene

Santa Rosa: SBM.

Santa Cruz: Hoffmann s.n. Jun. 13, 1930 POM!; Raven & Smith 15150 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4811 LAM!; Fosberg 4781 LAM!; Thorne 36334 RSA!.

Guadalupe: Moran 6611 SD!; Moran 6641 SD!; Moran 13810 SD!.

Capparaceae

Cleome isomeris Greene

Santa Rosa: Moran 786 LAM!; Dunkle 8441 LAM!, AHFH!; RSA-POM; SBBG; SBM.

Santa Catalina: Grant 615 LAM!; Trask s.n. in Jul. 1898 US!; Carlson s.n. May 10, 1918 US!; RSA-POM; SBBG; SBM.

San Clemente: SBBG.

Caprifoliaceae

Lonicera hispidula (Lindl.) Dougl. ex T. & G. var. *vacillans* Gray

Santa Cruz: Hoffmann s.n. Jul. 1, 1930 LAM!; Hoffmann s.n. Sep. 10, 1931 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4851 LAM!, NY!; Knopf 139 F!; Trask s.n. in Jun. 1895 US!; LA; RSA-POM; SBBG.

San Clemente: Trask 21 US!; Trask 197 NY!, US!; RSA-POM.

Lonicera subspicata H. & A. var. *johnstonii* Keck

Santa Cruz: RSA-POM; SBBG; SBM.

Santa Catalina: RSA-POM; SBBG.

Sambucus mexicana Presl ex DC.

Santa Rosa: Dunkle 8508 LAM!; RSA-POM; SBM.

Santa Cruz: Hoffmann s.n. Sep. 21, 1930 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4289 LAM!; Dunkle 1984 AHFH!; Detmers s.n. Apr. 14, 1929 USC!; RSA-POM; SBBG; SBM.

San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!; RSA-POM; SBBG.

Symphoricarpos mollis Nutt. in T. & G.

Santa Rosa: SBM.

Santa Cruz: Dunkle 8557 LAM!; Munz & Crow 11550 POM!, LA!; Raven & Smith 15180 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4300 LAM!; Dunkle 2135 LAM!; Detmers s.n. in Spring 1928 USC!; RSA-POM; SBBG.

Caryophyllaceae

Arenaria douglasii Fenzl ex T. & G.

Santa Rosa: RSA-POM; SBM.

Santa Cruz: SBBG; SBM.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4721 LAM!; RSA-POM!.

San Clemente: RSA-POM.

Arenaria serpyllifolia L.

Santa Cruz: RSA-POM.

Cardionema ramosissima (Weinm.) Nels. & Macbr.

San Miguel: SBBG; SBM.

Santa Rosa: Dunkle 8466 LAM!, AHFH!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Fosberg 7670 LAM!, LA!; RSA-POM; SBBG; SBM.

Cerastium glomeratum Thuill.

San Miguel: RSA-POM; SBBG; SBM.

Santa Rosa: RSA-POM; SBM.

Santa Cruz: Fosberg 7669 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: RSA-POM; SBBG.

San Clemente: RSA-POM; SBBG.

Guadalupe: Moran 17304 RSA!.

Herniaria cinerea DC.

Guadalupe: Wiggins & Ernst 195 DS!.

Polycarpon depressum Nutt.

Santa Cruz: SBM.

Santa Catalina: Grant s.n. in Apr. 1901 LAM!; Grant 1023 US!; Trask s.n. in Jun. 1897 US!; SBBG.

Sagina decumbens (Ell.) T. & G. ssp. *occidentalis* (Wats.) Crow

San Miguel: SBM.

Santa Rosa: SBM.

Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Wolf 2909 DS!; Hoffmann s.n. Jun. 15, 1930 CAS#191796!; RSA-POM; SBM.

Santa Catalina: Fosberg S4331 LAM!.

Silene antirrhina L.

Santa Rosa: SBBG; SBM.

Santa Cruz: RSA-POM; SBM.

Santa Catalina: Fosberg S4381 LAM!; Trask s.n. in May 1897 US!; Trask s.n. in Mar. 1898 MO!; NY; RSA-POM; SBBG.

San Clemente: Trask 175 NY!, US!; RSA-POM; SBBG.

Guadalupe: Gander 8999 SD!.

Silene gallica L.

San Miguel: SBBG; SBM.

Santa Rosa: Dunkle 8528 LAM!; Dunn, N. s.n. May 24, 1931 LA!; Dunn, D. 1313 LA!; RSA-POM; SBM.

Santa Cruz: Clokey 4933 LAM!; Clokey 4934 LAM!; Elmore 456 AHFH!; RSA-POM; SBM.

Anacapa: Dunkle 7662 LAM!; SBBG; SBM.

San Nicolas: Trask 25 MO!.

Santa Barbara: Dunkle 7645 LAM!; Dunkle 8143 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Moran 705 LAM!; Dunkle 1827 AHFH!; Detmers s.n. Apr. 13, 1929 USC!; RSA-POM.

San Clemente: Dunkle 7305 LAM!; Dunkle 7259 LAM!; RSA-POM; SBBG.

Guadalupe: Palmer 11 NY!; Palmer 837 NY!; Lindsay 43072 RSA!.

Silene laciniata Cav. ssp. *major* Hitchc. & Maguire

San Miguel: RSA-POM; SBM.

Santa Rosa: Moran 809 LAM!, MO!, NY!; Elmore 206 AHFH!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBM.

Santa Cruz: Clokey 4931 LAM!, NY!; Eastwood 6408 NY!, US!; Johnstone s.n. USC!; RSA-POM; SBM.

Anacapa: Dunkle 7654 LAM!; Elmore 239 AHFH!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG; SBM.

San Clemente: Trask 36 US!.

Silene multinervia Wats.

Santa Cruz: RSA-POM; SBM.

Santa Catalina: Trask s.n. in Mar. 1900 MO!, US!.

Spergula arvensis L.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.

Spergularia bocconii (Scheele) Foucaud
Santa Cruz: RSA-POM; SBBG.
Santa Catalina: Davidson, A. s.n. Jun. 25, 1891 LAM!; Fosberg S4952 LAM!; Wolf 3578 LAM!; RSA-POM.
San Clemente: RSA-POM; SBBG.

Spergularia macrotheca (Hornem.) Heynh. ssp. *macrotheca*
San Miguel: Dunkle 8398 LAM!; RSA-POM; SBM.
Santa Rosa: Dunkle 8484 LAM!; Elmore 189 AHFH!; RSA-POM; SBM.
Santa Cruz: Fosberg 7534 LAM!; Dunkle 8576 LAM!, AHFH!; Elmore s.n. Apr. 17, 1936 USC!; RSA-POM; SBM.
Anacapa: Gustafson s.n. Apr. 9, 1973 LAM!; Johnstone s.n. Jun. 25, 1932 USC!; SBBG; SBM.
San Nicolas: Kanakoff s.n. Apr. 12, 1940 LAM!; Dunkle 8321 LAM!; Raven & Thompson 20691 LA!; RSA-POM; SBM.
Santa Barbara: Dunkle 8110 AHFH!; Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; Dunkle 8130 LAM!; SBBG.
Santa Catalina: Moran 664 LAM!; Fosberg S4466 LAM!; Dunkle 1853 AHFH!; RSA-POM; SBM.
San Clemente: Dunkle 7205 LAM!; Dunkle 7272 LAM!; Elmore s.n. Nov. 25, 1939 AHFH!; RSA-POM; SBBG; SBM.
Guadalupe: Rempel 758-37 LAM!; Moran 6126 RSA!; Moran 17417 RSA!.

Spergularia marina (L.) Griseb.
Santa Rosa: RSA-POM; SBBG.
Santa Cruz: RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4332 LAM!; Dunkle 1737 AHFH!; RSA-POM.
San Clemente: Murbarger 112 UC!.
Guadalupe: Moran 6768 RSA!.

Spergularia villosa (Pers.) Camb.
Santa Rosa: RSA-POM; SBBG.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA.

Stellaria media (L.) Vill.
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 4928 LAM!; Clokey 4929 LAM!; Dunkle 8624 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Moran 706 LAM!; Fosberg S4644 LAM!; Dunkle 2144 AHFH!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Stellaria nitens Nutt.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7575 LAM!; Fosberg 7600 LAM!; Fosberg s.n. Mar. 6, 1932 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 2089 AHFH!; McClatchie s.n. in Sep. 1893 NY!; Trask s.n. in Mar. 1901 NY!.
Guadalupe: Palmer 13 NY!; Moran 18388 SD!; Moran 25386 SD!.

Chenopodiaceae

Aphanisma blitoides Nutt. ex Moq. in DC.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM.
Anacapa: Hoffmann s.n. Mar. 21, 1932 SBM!.
San Nicolas: Trask 21 MO!.
Santa Barbara: Dunkle 7416 LAM!, DS!, NY!; Dunkle 7459 LAM!, AHFH!; RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Trask s.n. in May 1900 NY!; Grant & Wheeler s.n. Apr. 21–26, 1904 DS!; RSA-POM.
San Clemente: Trask s.n. in Apr. 1898 US!; Trask 212 NY!, US!; Blakley 6359 DS!; RSA-POM.
Guadalupe: Moran 5627 CAS!, DS!, RSA!; Moran 5656 DS!, RSA!; Wiggins & Ernst 175 DS!.

Atriplex argentea Nutt. ssp. *expansa* (Wats.) Hall & Clem.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Santa Catalina: RSA-POM; SBM.
San Clemente: RSA-POM; SBBG.

Atriplex barclayana (Benth.) D. Dietr. ssp. *dilitata* (Greene) Hall & Clem.
Guadalupe: Rempel 759-37 Jul. 19, 1937 LAM!.

Atriplex barclayana (Benth.) D. Dietr. ssp. *palmeri* (Wats.) Hall & Clem.
Guadalupe: Greene s.n. in 1885 US!; Palmer 863 US!; Moran 5622 RSA!.

Atriplex californica Moq. in DC.
San Miguel: Dunkle 8370 LAM!, Dunkle 8370 AHFH!; RSA-POM; SBM.
Santa Rosa: Dunkle 8485 LAM!; RSA-POM; SBM.
Santa Cruz: Fosberg 7704 LAM!; Fletcher s.n. LAM!; Clokey 4920 LAM!; RSA-POM; SBM.
Anacapa: Dunkle 7604 LAM!; Dunn, N. s.n. May 14, 1932 LA!; RSA-POM; SBM.
San Nicolas: Dunkle 8317 LAM!; Kanakoff s.n. Apr. 24, 1940 LAM!; Dunkle 8343 LAM!; RSA-POM; SBBG.
Santa Barbara: RSA-POM; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Dunkle 7410 LAM!; Fosberg S4889 LAM!; RSA-POM; SBM.
San Clemente: Dunkle 7275 LAM!; Johnstone s.n. Sep. 5, 1926 USC!; RSA-POM.
Guadalupe: Moran 15126 RSA!.

Atriplex coulteri (Moq.) D. Dietr.
San Miguel: SBBG; SBM.
Santa Rosa: Hoffmann s.n. Jun. 13, 1930 POM!; RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Anacapa: SBM.
San Nicolas: RSA-POM.
Santa Catalina: Fosberg S4648 LAM!; Fosberg S4669 LAM!; Fosberg S4730 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM.

Atriplex lentiformis (Torr.) Wats. ssp. *breweri* (Wats.) Hall & Clem.
Santa Cruz: SBBG; SBM.
Anacapa: Dunkle 7640 LAM!, NY!; RSA-POM; SBBG; SBM.

Santa Catalina: Trask s.n. in Jun. 1897 US!; Trask s.n. in Jun. 1898 US!; Millspaugh 5486 F!.
San Clemente: Trask s.n. Oct. 19, 1902 US!; RSA-POM; SBBG; SBM.

Atriplex leucophylla (Moq. in DC.) D. Dietr.
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM.
Santa Cruz: RSA-POM; SBM.
San Nicolas: Kanakoff s.n. Apr. 13, 1940 LAM!; Dunkle 8340 LAM!; Trask s.n. Apr. 1901 LAM!; RSA-POM; SBM.
Santa Catalina: Fosberg S4894 LAM!; Trask s.n. in Aug. 1902 LAM!; Dunkle 1852 AHFH!; RSA-POM.
San Clemente: Trask s.n. Nov. 22, 1922 US#617893!; RSA-POM.

Atriplex pacifica Nels.
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#015274!, US!.
Anacapa: SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!, US!; Grant & Wheeler s.n. Apr. 21–26, 1904 LAM!; McClatchie s.n. Sep. 13, 1893 NY!; SBBG.
San Clemente: Trask s.n. in May 1901 NY!; Wooton s.n. Apr. 26, 1912 US!; RSA-POM.

Atriplex patula L. ssp. *hastata* (L.) Hall & Clem.
San Miguel: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG.
San Nicolas: SBBG.
Santa Catalina: Dunkle 2440 LAM!, AHFH!; RSA-POM; SBBG.

Atriplex rosea L.
Santa Catalina: RSA-POM.

Atriplex semibaccata R. Br.
San Miguel: Dunkle 8380 AHFH!; Dunkle 8418 LAM!; RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8304 LAM!, AHFH!; Kanakoff s.n. Apr. 13, 1940 LAM!; Dunkle s.n. Nov. 24, 1940 LAM!; RSA-POM; SBM.
Santa Barbara: Dunkle 8123 AHFH!; Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; RSA-POM; SBM.
Santa Catalina: Dunkle 1817 AHFH!; Spalding s.n. in 1925 USC!; Fosberg S4569 LAM!; RSA-POM; SBM.
San Clemente: Elmore 419 LAM!; Dunkle 8123 LAM!; House & Grumbles s.n. Aug. 5–13, 1930 USC!; RSA-POM; SBM.

Atriplex serenana A. Nels. var. *serenana*
Santa Catalina: Moxley s.n. Sep. 19, 1925 USC!; Nuttall 303 F!; Eastwood 6529 US!.

Atriplex watsonii A. Nels. in Abrams
Santa Cruz: Ferren 1907a UCSB!; Ferren 1907b UCSB!.
San Nicolas: Dunkle 8317 AHFH!; Trask s.n. in Apr. 1897 US!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4925 LAM!; Fosberg S4928 NY!; RSA-POM.
San Clemente: Dunkle 7264 LAM!; AHFH!; Dunkle 7274 AHFH!, LAM!; Trask s.n. in Oct. 1902 US!; RSA-POM; SBBG.

Bassia hyssopifolia (Pall.) Kuntze
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM.

Beta vulgaris L. ssp. *maritima* (L.) Arcang.
San Miguel: SBBG.
Anacapa: SBBG.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.

Chenopodium album L.
Santa Cruz: Clokey 4917 LAM!; Howell 6237 CAS!.

Chenopodium ambrosioides L. var. *ambrosioides*
Santa Rosa: Dunkle 8465 LAM!, AHFH!; Dunkle 8514 LAM!, NY!; Dunkle 8527 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8645 LAM!, AHFH!; Clokey 4916 NY!; RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.

Chenopodium berlandieri Moq. var. *sinuatum* (J. Murr.) H.A. Wahl.
Santa Rosa: RSA-POM.
Santa Cruz: Hoffmann s.n. Apr. 10, 1931 LAM!; RSA-POM; SBBG; SBM.
Anacapa: RSA-POM; SBBG.
Santa Catalina: Fosberg S5376 LAM!; Fosberg S4508 LAM!; Dunkle 2005 AHFH!; RSA-POM.

Chenopodium californicum (Wats.) Wats.
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7554 LAM!; Clokey 4915 LAM!; RSA-POM; SBM.
Anacapa: Bond 351 SBM!; SBBG; SBM.
San Nicolas: RSA-POM.
Santa Barbara: Bond 392 SBM!; Dunkle 7453 LAM!; Dunkle 8116 LAM!.
Santa Catalina: Templeton 11382 LAM!; Fosberg S4283 LAM!, SBM!; Lewis s.n. Mar. 24, 1937 LA!; RSA-POM.
San Clemente: Moran 578 LAM!; RSA-POM.

Chenopodium multifidum L.
Santa Rosa: RSA-POM.
San Nicolas: Kanakoff s.n. Apr. 18, 1940 LAM!.

Chenopodium murale L.
San Miguel: Dunkle 8392 AHFH!; RSA-POM; SBM.
Santa Rosa: Dunkle 8468 LAM!, AHFH!; Elmore 178 AHFH!; RSA-POM; SBM.
Santa Cruz: Clokey 4913 LAM!, NY!; Clokey 4914 LAM!, NY!; Dunkle 8592 AHFH!; RSA-POM; SBM.
Anacapa: Dunkle 7610 LAM!; SBBG; SBM.
San Nicolas: Dunkle 8322 LAM!, AHFH!; Trask s.n. in Apr. 1897 US!; RSA-POM.
Santa Barbara: Dunkle 8100 LAM!, NY!; Bond 391 SBM!; Philbrick B68-98 US!; RSA-POM.
Santa Catalina: Trask s.n. in 1900 LAM!, NY!; Fosberg 7162 LAM!; Smith 5071 US!; RSA-POM.
San Clemente: Dunkle 7222 LAM!; Trask 38 US!; Fosberg 55249 US!; RSA-POM.

Guadalupe: Franceschi s.n. in 1893 US!; Rose 16037 NY!, US!; Mason 1520 CAS!; MO.

Monolepis nuttalliana (Schult.) Greene
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: SBM.
San Clemente: RSA-POM; SBBG.

Salicornia subterminalis Parish
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBBG.
Santa Cruz: RSA-POM.
Santa Catalina: Dunkle 1897 AHFH!; Fosberg S4886 LAM!; Fosberg S4888 LAM!; RSA-POM; SBM.
San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!; RSA-POM; SBBG.

Salicornia virginica L.
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM.
Anacapa: Dunkle 7652 LAM!; SBBG.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; Kanakoff s.n. Apr. 19, 1940 LAM!; RSA-POM.
Santa Catalina: Fosberg S4878 LAM!; Fosberg S5426 LAM!; Williamsen s.n. in Aug. 1924 USC!; RSA-POM.
San Clemente: Dunkle 7330 LAM!; Elmore 402 AHFH!; RSA-POM; SBBG.

Salsola iberica Sennen & Pau
Santa Cruz: Dunkle 8653 LAM!; RSA-POM.
San Nicolas: RSA-POM.
Santa Catalina: Fosberg S4967 LAM!.
San Clemente: RSA-POM.

Suaeda californica Wats.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: Munz & Crow 11565 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 4921 LAM!, US!; Clokey 4922 LAM!, US!; Fosberg 7706 LAM!; RSA-POM; SBM.
Anacapa: Dunkle 7602 LAM!; Howell 3811 CAS!; RSA-POM; SBM.
San Nicolas: Trask 19 NY!; Foreman 51 US!; Dunkle 8313 LAM!, AHFH!; RSA-POM; SBM.
Santa Barbara: Philbrick & Benedict B66-417 US!; Dunkle 8114 LAM!, AHFH!; Elmore 302 AHFH!; RSA-POM; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 F!, US!; Fosberg 4913 LAM!; Nuttall 225 F!; RSA-POM; SBM.
San Clemente: Dunkle 7265 LAM!, AHFH!; Trask 36 US!; House & Grumbles s.n. Aug. 5–13, 1930 USC!; RSA-POM; SBBG.
Guadalupe: Moran 13761 LAM!, RSA!; Rempel 758-37 LAM!; Palmer 870 NY!; CAS.

Cistaceae

Helianthemum greenei Rob.
Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!; Dunn, N. s.n. May 24, 1931 LA!.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.

Helianthemum scoparium Nutt.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg 8157 LA!; RSA-POM; SBBG; SBM.

Convolvulaceae

Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
San Nicolas: Dunkle 8344 LAM!, AHFH!; Trask 53 US!; Foreman 211 LA!, US!; RSA-POM; SBBG; SBM.
Santa Barbara: Dunkle 8138 LAM!, AHFH!; Elmore 313 AHFH!; Dunkle 8317 AHFH!; RSA-POM; SBBG; SBM.
San Clemente: Munz 6622 LAM!; Wiggins 11964 DS!; Raven 18030 RSA!; SBBG; US.

Calystegia macrostegia (Greene) Brummitt ssp. *cyclostegia* (House) Brummitt
Santa Catalina: Fosberg 8138 LA!; RSA-POM; SBM.

Calystegia macrostegia (Greene) Brummitt ssp. *intermedia* (Abrams) Brummitt
Santa Catalina: Fosberg S4335 LAM!; Millspaugh 4657 F!; RSA-POM.

Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
San Miguel: Dunkle 8386 LAM!, AHFH!; SBBG; SBM.
Santa Rosa: Dunkle 8457 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 US!; Fosberg 7703 LAM!; Dunkle 8541 AHFH!; LA; RSA-POM; SBBG; SBM.
Anacapa: Moran 720 LAM!; Dunkle 7626 AHFH!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in May 1901 LAM!; Dunkle 1769 AHFH!; Lister & Powell s.n. Apr. 3, 1928 USC!.
Guadalupe: Rempel 759-37 LAM!; Moran 2636 RSA!; Carlquist 471 RSA!.

Calystegia soldanella (L.) R. Br.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG.
Santa Cruz: RSA-POM; SBBG; SBM.
San Clemente: Murbarger 209 UC!.

Convolvulus arvensis L.
Santa Rosa: RSA-POM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 1947 AHFH!; Fosberg S4745 LAM!; RSA-POM; SBBG; SBM.

Convolvulus simulans L.
San Clemente: SBBG.

Cressa truxillensis HBK. var. *vallicola* (Heller) Munz
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBM.
Santa Catalina: Fosberg S4880 LAM!, NY!; Trask s.n. Jun. 1900 NY!; Dunkle 2147 LAM!, AHFH!; RSA-POM; SBBG; SBM.
San Clemente: Trask 184 NY!; RSA-POM; SBBG.

Cuscuta californica H. & A.
Santa Rosa: RSA-POM; SBM.
San Clemente: Trask 187 US!.

Cuscuta ceanothi Behr
Santa Cruz: Clark s.n. Mar. 27, 1980 SCIR!; SBBG.

Cuscuta corymbosa R. & P. var. *grandiflora* Engelm.
Guadalupe: Moran 17420 SD!.
Cuscuta occidentalis Millsp.
Santa Catalina: Nuttall 902 F!; Nuttall 272 F!; RSA-POM; SBBG.
Cuscuta salina Engelm. var. *salina*
Santa Rosa: RSA-POM.
Santa Cruz: RSA-POM; SBBG.
Anacapa: SBBG.
Dichondra occidentalis House
San Miguel: SBBG.
Santa Rosa: Munz & Crow 11574 POM!; Hoffmann s.n. Apr. 18, 1932 POM!; SBM.
Santa Cruz: Wolf 2841 POM!; RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.
Ipomoea cairica (L.) Sweet
Santa Catalina: Spalding s.n. Sep. 19, 1925 USC!.
Ipomoea nil (L.) Roth
Santa Catalina: Millspaugh 4541 F!.
Cornaceae
Cornus glabrata Benth.
Santa Catalina: Trask s.n. in Jun. 1901 LAM!; Dunkle 2032 LAM!; Knopf 126 F!; RSA-POM; SBM.
Crassulaceae
Crassula aquatica (L.) Schoenl. in Engl. & Prantl
Santa Catalina: RSA-POM.
Crassula erecta (H. & A.) Berger
San Miguel: SBBG; SBM.
Santa Rosa: Munz & Crow 11630 LA!; RSA-POM; SBM.
Santa Cruz: Fosberg 7621 LAM!; Fosberg 7643 LAM!; RSA-POM; SBM.
Anacapa: SBBG.
San Nicolas: Newman 100 Pacif. Missile Test Center, Pt. Mugu!; RSA-POM.
Santa Barbara: Dunkle 7411 LAM!; RSA-POM; SBM.
Santa Catalina: Dunkle 2139 LAM!; Templeton 11395 LAM!; RSA-POM; SBM.
San Clemente: Dunkle 7323 LAM!; Moran 568 LAM!; RSA-POM; SBM.
Guadalupe: Carlquist 445 RSA!.
Dudleya blochmanae (Eastw.) Moran ssp. *insularis* (Moran) Moran
Santa Rosa: RSA-POM; SBBG; SBM.
Dudleya caespitosum (Haw.) Britt. & Rose
Santa Cruz: RSA-POM.
Anacapa: SBBG.
Dudleya candelabrum Rose
Santa Rosa: Moran 820 LAM!; SBBG; SBM.
Santa Cruz: Clokey 4949 LAM!; Hoffmann s.n. Apr. 10, 1930 SBM!; Balls & Blakley 23726 RSA!; CAS; SBBG.
Dudleya greenei Rose
San Miguel: Dunkle 8368 LAM!; Moran 3443 NY!; Hoffmann s.n. Jun. 11, 1930 SBM!; RSA-POM; SBBG.
Santa Rosa: Moran 810 LAM!; Moran 821 LAM!; Hoffmann s.n. Jun. 11, 1930 SBM!; RSA-POM; SBBG.
Santa Cruz: Clokey 5358 LAM!, LA!, NY!; Hoffmann s.n. May 14, 1927 SBM#338!; Greene s.n. in Jul.–Aug. 1886 CAS#244!; RSA-POM; SBBG.
Anacapa: Dunkle 7657 LAM!, AHFH!; Hoffmann s.n. Sep. 22, 1930 SBM#10912!.
Santa Catalina: RSA-POM; SBBG.
Dudleya guadalupensis Moran
Guadalupe: Moran 17428 MO!.
Dudleya hassei (Rose) Moran
Santa Catalina: Dunkle 2467 AHFH!; Trask s.n. in Feb. 1896 MO!; McClatchie s.n. 9/6/1893 NY!; RSA-POM; SBBG; SBM.
Dudleya nesiotica (Moran) Moran
Santa Cruz: Moran 3362 CAS!; RSA-POM; SBBG; SBM.
Dudleya traskiae (Rose) Moran
Santa Barbara: Dunkle 8102 LAM!, AHFH!; RSA-POM; SBBG.
Dudleya virens (Rose) Moran
San Nicolas: RSA-POM; SBBG.
Santa Catalina: Fosberg S4502 LAM!, NY!; Dunkle 2466 AHFH!; Fosberg S4890 LAM!; RSA-POM; SBBG.
San Clemente: Trask 165 NY!; RSA-POM; SBBG.
Guadalupe: Moran 6123 SD!; Moran 6131 SD!; Moran 13796 SD!.
Crossosomataceae
Crossosoma californicum Nutt.
Santa Catalina: Trask s.n. in Jun. 1901 LAM!; Dunkle 2862 LAM!, LA!; Thorne 39352 LAM!; RSA-POM; SBBG; SBM.
San Clemente: RSA-POM.
Guadalupe: Moran 6630 RSA!; Moran 15194 RSA!.
Cucurbitaceae
Cucurbita foetidissima HBK.
Santa Cruz: RSA-POM; SBBG; SBM.
Marah guadalupensis (Wats.) Greene
Guadalupe: Anthony 234 LAM!; Palmer 33 CM!; Moran 5974 DS!.
Marah macrocarpus (Greene) Greene
San Miguel: Dunkle 8402 LAM!; RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7622 LAM!, LA!; Fosberg 7584 LAM!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8359 LAM!; SBBG.
Santa Barbara: Dunkle 7439 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBM.
San Clemente: Dunkle 7251 LAM!; Moran 573 LAM!; Elmore 422 AHFH!.
Elatinaceae
Elatine californica Gray
Santa Catalina: Thorne 35898 RSA!; SBBG.
Ericaceae
Arbutus menziesii Pursh
Santa Cruz: Hoffmann 599 LAM!; SBBG; SBM.
Arctostaphylos catalinae P.V. Wells
Santa Catalina: Wallace & Haefs 1412 RSA!; Trask s.n. in Feb. 1900 ND-G#037709!; Fosberg S5398 LAM!, POM!; SBBG; SBM.

Arctostaphylos confertiflora Eastw.
Santa Rosa: Munz & Crow 11587 POM!, LA!; Moran 789 RSA!; Blakley 3168 RSA!; SBM.

Arctostaphylos insularis Greene f. *insularis*
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#037684!, ND-G#037685!, CAS#261!, CAS#261B!.

Arctostaphylos insularis Greene f. *pubescens* (Eastw.) P.V. Wells
Santa Cruz: Fosberg 7588 LAM!, LA!; Hutchinson s.n. Sep. 1, 1928 LAM!; Clokey 5022 LA!; RSA-POM; SBM.

Arctostaphylos tomentosa (Pursh) Lindl. ssp. *insulicola* P.V. Wells
Santa Rosa: Hoffmann 101 Dec. 5, 1920 POM!.
Santa Cruz: Dunkle 8614 (in part) LAM!; Thorne & Everett 36783 RSA!; Raven & Smith 15291 RSA!; SBBG; SBM.

Arctostaphylos tomentosa (Pursh) Lindl. ssp. *subcordata* (Eastw.) P.V. Wells
Santa Rosa: Moran 789 LAM!; Dunkle 8498 LAM!; RSA-POM.
Santa Cruz: Dunkle 8614 (in part) LAM!; Howell 6335 CAS!; Greene s.n. in Jul.–Aug. 1886 ND-G#037697!; RSA-POM; SBBG; SBM.

Arctostaphylos viridissima (Eastw.) McMinn
Santa Cruz: Howell 6368 CAS!; Balls & Blakley 23701 RSA!; Ellison s.n. May 12–15, 1929 LA!; SBBG.

Comarostaphylis diversifolia (Parry) Greene ssp. *planifolia* (Jeps.) Wallace ex Thorne
Santa Rosa: Thorne et al. 48821 RSA!; Thorne et al. 48989 RSA!; Munz & Crow 11662 POM!; SBBG; SBM.
Santa Cruz: Fosberg 7589 LAM!, LA!; Wolf 2827 RSA!; Clokey 5019 LA!; ND-G; SBBG; SBM.
Santa Catalina: Thorne & Everett 35032 RSA!, LA!; Dunkle 1712 POM!; Wallace 1404 RSA!; SBBG.

Vaccinium ovatum Pursh
Santa Rosa: Moran 813 LAM!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Fausett 6 LA!; RSA-POM; SBBG; SBM.

Xylococcus bicolor Nutt.
Santa Catalina: Trask s.n. in Feb. 1900 LAM!; Moran 650 LAM!; Thorne 35969 RSA!; SBBG.

Euphorbiaceae

Eremocarpus setigerus (Hook.) Benth.
Santa Rosa: SBBG.
Santa Cruz: Hoffmann s.n. Aug. 7, 1930 POM!; Balls & Blakley 23652 RSA!; Dunkle 8650 RSA!; SBBG.
Santa Catalina: Fosberg S4949 LAM!; Fosberg S4698 LAM!, POM!; Thorne & Everett 34945 RSA!; SBBG; SBM.
San Clemente: DeBuhr & Wallace 706 LAM!; House & Grumbles s.n. Aug. 5–13, 1930 LAM!; Raven 17676 RSA!; SBBG.

Euphorbia crenulata Engelm.
Santa Catalina: Nuttall 170 F!; Nuttall 236 F!; Millspaugh 4867 F!.

Euphorbia melanadenia Torr.
Guadalupe: (Wheeler 1934: Palmer 783 at F).

Euphorbia misera Benth.
Santa Catalina: Trask s.n. in Oct. 1897 US!; Trask s.n. in Dec. 1900 (scrap) NY!.
San Clemente: Dunkle 7336 LAM!; Blakley 632 RSA!; Thorne 36042 RSA!; SBBG.
Guadalupe: Rempel 759-37 LAM!; Moran 6136 RSA!.

Euphorbia peplis L.
Santa Rosa: Thorne et al. 48883 RSA!.
Santa Cruz: Pierson 11046 RSA!; Daily 522 SCIR!.
Santa Catalina: Fosberg S4530 LAM!; Thorne & Everett 33442 RSA!; Thorne 36697 RSA!.
San Clemente: Dunkle 7216 LAM!.

Euphorbia pondii Millsp.
Guadalupe: Palmer 883 ND-G!; Moran 17353 RSA!; Howell 8331 CAS!.

Euphorbia serpyllifolia Pers. var. *serpyllifolia*
Santa Catalina: Fosberg S4912 LAM!; Thorne & Propst 37685 RSA!; Thorne 36654 RSA!.

Euphorbia spathulata Lam.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Thorne 35774 RSA!; Thorne 39371 RSA!.
San Clemente: Raven 17675 RSA!; SBBG.

Ricinus communis L.
San Nicolas: Wier & Beauchamp s.n. Jul. 4, 1978 RSA!.
Santa Catalina: Thorne & Everett 34875 RSA!; Thorne 39353 RSA!; SBBG.
San Clemente: DeBuhr & Wallace 696 RSA!.

Fabaceae

Acacia decurrens Willd.
Santa Catalina: SBBG.

Acacia melanoxylon R. Br.
Santa Cruz: RSA-POM; SBBG.
Santa Catalina: Lister & Powell s.n. Apr. 1928 LAM!; RSA-POM; SBBG.

Astragalus curtipes Gray
San Miguel: Dunkle 8404 LAM!; Munz & Crow 11828 POM!; SBBG; SBM.
Santa Rosa: Blakley 3127 RSA!; Moran 3337 RSA!; Munz & Crow 11749 POM!; SBBG; SBM.

Astragalus didymocarpus H. & A. var. *didymocarpus*
San Miguel: SBBG; SBM.
Santa Rosa: Moran 799 LAM!, NY!; RSA!; Munz & Crow 11595 POM!, LA!; Raven, Blakley & Ornduff 14913 RSA!; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Sep. 11, 1931 LAM!; Munz & Crow 11890 POM!; Raven & Smith 15303 RSA!; SBBG; SBM.
Anacapa: SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Thorne 36357 RSA!; Thorne & Everett 34601 RSA!.
San Clemente: Trask 206 NY!, DS!.

Astragalus gambelianus Sheld.
Santa Cruz: Raven & Smith 15185 RSA!; SBBG; SBM.
Santa Catalina: Davidson, A. s.n. Jun. 26, 1891 LAM!; Fosberg S4390 LAM!, POM!; Dunkle 2152 LAM!; RSA-POM; SBBG.

Astragalus miguelensis Greene

San Miguel: Dunkle 8372 LAM!; Elmore 319 AHFH!; Voss s.n. Sep. 1, 1930 POM!; CAS; SBBG; SBM.

Santa Rosa: Moran 794 LAM!, RSA!; Thorne et al. 48970 RSA!; Munz & Crow 11560 POM!, LA!; SBBG; SBM.

Santa Cruz: Clokey 4987 POM!; Raven & Smith 15313 RSA!; Webster et al. 97 RSA!; SBBG; SBM.

Anacapa: Dunkle 7606 LAM!, RSA!; Johnstone s.n. Jun. 25, 1932 LAM!; Moran 726 LAM!, RSA!; SBBG; SBM.

San Clemente: Beauchamp 323 LAM!, RSA!; DeBuhr & Wallace 685 RSA!; Thorne 42904 RSA!; SBBG.

Astragalus nevinii Gray

San Clemente: Elmore 395 LAM!; Raven 18007 RSA!; Thorne 35994 RSA!; SBBG.

Astragalus traskiae Eastw.

San Nicolas: Thorne et al. 52358 RSA!; Raven & Thompson 20712 RSA!; Trask s.n. in Apr. 1897 CAS!; LA; SBBG.

Santa Barbara: Dunkle 8127 LAM!, AHFH!; Dunkle 7436 LAM!; Dunkle 8132 AHFH!, RSA!; SBBG.

Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne

Santa Rosa: Thorne et al. 48964 RSA!; SBM.

Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LA!; Williams 56 POM!; Raven & Smith 15292 RSA!; SBBG; SBM.

Anacapa: Ellison s.n. May 12–15, 1929 LA!; SBBG; SBM.

Santa Catalina: Dunkle 1703 LAM!, POM!; Thorne & Everett 34979 RSA!; Jones s.n. May 15, 1903 POM!, MO!.

Astragalus trichopodus (Nutt.) Gray ssp. *trichopodus*

Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Thorne & Everett 34872 RSA!; Fosberg S4431 LAM!; SBBG; SBM.

Coronilla valentina L.

Santa Catalina: SBBG.

Cytisus linifolius (L.) Lam.

Santa Catalina: Eaton s.n. Aug. 2, 1956 LAM!; Thorne 36240 RSA!; Thorne & Everett 33277 RSA!; SBBG.

Cytisus monspessulanus L.

Santa Catalina: Thorne & Everett 34858 RSA!; Thorne 36309 RSA!; Henrickson 13814 RSA!; SBBG.

Lathyrus laetiflorus Greene ssp. *alefeldii* (White) Brads.

Santa Catalina: Fosberg S4806 LAM!, NY!, POM!; Trask s.n. in Apr. 1897 LAM!; Thorne 36205 RSA!; SBBG.

Lathyrus laetiflorus Greene ssp. *barbarae* (White) C.L. Hitchc.

Santa Rosa: Raven 14936 RSA!; Thorne et al. 48993 RSA!; SBBG; SBM.

Santa Cruz: Dunkle 8648 LAM!; Fosberg 7708 LAM!, NY!; SBBG; SBM.

Anacapa: SBBG; SBM.

Santa Catalina: Fosberg S4378 POM!; Thorne 35822 RSA!; Knopf & Johnson 1454 RSA!; SBBG; SBM.

San Clemente: Trask 239 NY!; RSA-POM; SBBG.

Lathyrus tingitanus L.

Santa Catalina: Thorne 36467 RSA!; Thorne & Everett 34862 RSA!; Raven 17765 RSA!; SBBG.

Lathyrus vestitus Nutt. ex T. & G. ssp. *vestitus*

Santa Rosa: Munz & Crow 11578 POM!; Raven, Blakley & Ornduff 15012a RSA!.

Santa Cruz: Munz & Crow 11836 POM!; Thorne & Everett 36827 RSA!; Raven & Smith 15217 RSA!.

Lotus argophyllus (Gray) Greene ssp. *adsurgens* (Dunkle) Raven

San Clemente: Dunkle 7200 LAM!, RSA!; Elmore 410 AHFH!, LAM!.

Lotus argophyllus (Gray) Greene ssp. *niveus* (Greene) Munz

Santa Cruz: Abrams & Wiggins 199 RSA!; Greene s.n. in Jul.–Aug. 1886 CAS#680!; Hoffmann s.n. Sep. 22, 1930 POM!; SBBG; SBM.

Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven

San Nicolas: Trask 42 LAM!; Wallace et al. 1609 LAM!; Foreman, Evans & Rainey 71 LA!; CAS; RSA-POM; SBBG; SBM.

Santa Barbara: Dunkle 7409 LAM!; Moran 825 AHFH!; Kanakoff s.n. in Aug. 1940 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Grant 7162 LAM!, POM!, USC!; Thorne 34900 RSA!; Fosberg 8111 LA!; SBBG; SBM.

San Clemente: Munz 6611 LAM!, POM!; Dunkle 7350 AHFH!; Raven 17149 RSA!; SBBG.

Guadalupe: Howell 8177 MO!, POM!; Moran 5951 LA!, RSA!; Greene s.n. Apr. 19, 1885 CAS#681!.

Lotus corniculatus L.

Santa Cruz: Daily 150 SCIR!.

Santa Catalina: Thorne 36700 RSA!; SBBG.

Lotus grandiflorus (Benth.) Greene var. *grandiflorus*

Santa Rosa: Munz & Crow 11638 POM!; SBM.

Santa Cruz: Thorne & Everett 36751 RSA!; Breedlove 2824 RSA!; SBBG; SBM.

Santa Catalina: Moran 627 LAM!, RSA!; Dunkle 1749 AHFH!, POM; Thorne 35912 RSA!; SBBG.

Guadalupe: Palmer 23 MO!; Greene s.n. in Apr. 1885 ND-G#025788!; Greene s.n. in Apr. 1885 ND-G#025789!.

Lotus hamatus Greene

Santa Rosa: Hoffmann 418 POM!; Hoffmann s.n. Mar. 23, 1929 POM!; SBM.

Santa Cruz: RSA-POM; SBBG; SBM.

Santa Catalina: Davidson s.n. Jun. 26, 1891 LAM!; Dunkle 1841 AHFH!, POM!; Thorne 35843 RSA!; LA; MO; SBBG; SBM.

San Clemente: Raven 17591 RSA!; SBBG.

Lotus heermannii (Dur. & Hilg.) Greene ssp. *heermannii*

Santa Catalina: (Ottley 1923: G.B. Grant 716 no herbarium cited).

Lotus humistratus Greene

Santa Cruz: Pierson, F.W. 11084 RSA!; SBBG.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Trask s.n. in Apr. 1898 US!.

Lotus micranthus Benth.

Santa Cruz: Pierson 7133 RSA!; Wolf 2854 RSA!; SBM.

Lotus purshianus (Benth.) Clem. & Clem. ssp. *purshianus*

Santa Cruz: Weissman 325 DS!; Gorelick s.n. Jun. 28, 1978 RSA!.

Santa Catalina: Fosberg S4386 LAM!, POM!; Thorne & Everett 34074 RSA!; Dunkle 2432 AHFH!; SBBG; SBM.

Lotus salsuginosus Greene ssp. *salsuginosus*

San Miguel: SBBG; SBM.

Santa Rosa: Munz & Crow 11758 POM!, LA!; SBBG; SBM.

Santa Cruz: Fosberg 7647 LAM!; Fosberg 7618 LAM!, LA!; Blakley 3384 RSA!; SBBG; SBM.

Anacapa: SBBG.

Santa Catalina: Fosberg S4415 LAM!, POM!; Fosberg S4422 LAM!; Trask s.n. in Mar. 1896 MO#1864670!; RSA-POM; SBBG.

Lotus scoparius (Nutt. in T. & G.) Ottley var. *dendroideus* (Greene) Ottley

San Miguel: SBBG.

Santa Rosa: Dunkle 8440 LAM!, RSA!; Elmore 196 AHFH!; Munz & Crow 11599 LA!, POM!; SBBG; SBM.

Santa Cruz: Moran 768 LAM!, RSA!; Clokey 5191 LA!, RSA!; Greene s.n. in Jul.–Aug. 1886 CAS#673!, DS#35523!; SBBG; SBM.

Anacapa: Dunkle 7617 LAM!, AHFH!; Gustafson s.n. Apr. 9, 1973 LAM!; Moran 733 LAM!, RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4940 LAM!; Fosberg 8115 LA!, POM!; Heller 8952 NY!; SBBG; SBM.

San Clemente: Wiggins 11956 RSA!; SBBG.

Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *scoparius*

San Miguel: SBBG; SBM.

Santa Rosa: SBBG; SBM.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#025862!.

Anacapa: SBBG.

Santa Catalina: Dunkle 1851 AHFH!; SBBG.

Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *traskiae* (Eastw. ex Noddin in Abrams) Raven

San Clemente: Dunkle 7285 LAM!, RSA!; Elmore s.n. Nov. 26, 1939 AHFH!; Dunkle 7281 LAM!; SBBG.

Lotus scoparius (Nutt. in T. & G.) Ottley var. *veatchii* (Greene) Ottley

San Miguel: Munz & Crow 11780 POM!; Moran 3442 POM!; Greene s.n. in Sep. 1886 CAS#682!; SBM.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#025868!.

Lotus strigosus (Nutt. in T. & G.) Greene ssp. *strigosus*

San Miguel: SBM.

Santa Rosa: Munz & Crow 11633 POM!; Raven, Blakley & Ornduff 14960 RSA!; SBBG; SBM.

Santa Cruz: Wolf 2748 RSA!; Thorne & Everett 36838 RSA!; Raven & Smith 15273 RSA!; SBBG; SBM.

Anacapa: SBBG; SBM.

Santa Catalina: Fosberg S4393 LAM!, POM!; Moran 701 LAM!; Thorne 35871 RSA!; SBBG.

San Clemente: Munz 6750 POM!; Raven 17705 RSA!; Thorne 42798 RSA!; SBBG.

Lotus subpinnatus Lag.

Santa Rosa: Raven 14932 RSA!; SBM.

Santa Cruz: Fosberg 7644 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!; Munz & Crow 11518 POM!, LA!; SBM.

Anacapa: SBM.

Santa Catalina: Trask s.n. in Apr. 1900 LAM!; Fosberg S4465 LAM!; Dunkle 2100 AHFH!; RSA-POM.

Lupinus agardhianus Heller

Santa Rosa: Thorne et al. 48978 RSA!; Munz & Crow 11634 POM!; Hoffmann Apr. 17, 1921 POM!; SBM.

Santa Cruz: Elmore s.n. Apr. 19, 1936 LAM!, AHFH!; Munz & Crow 11511 POM!; Clokey 4976 US!; SBBG; SBM.

Santa Catalina: Fosberg S4413 LAM!, US!; Trask s.n. in May 1897 US!; Dunkle 1835 AHFH!, POM!; LA; SBM.

San Clemente: Thorne 42797 RSA!; Thorne 42947 RSA!; Raven 17706 RSA!; SBBG.

Lupinus albifrons Benth. var. *albifrons*

San Miguel: Dunkle 8387 LAM!; RSA!; SBBG; SBM.

Santa Rosa: Moran 805 LAM!, RSA!; Munz & Crow 11752 LA!, POM!; Raven, Blakley & Ornduff 14958 RSA!; SBBG; SBM.

Santa Cruz: Balls & Blakley 23689 RSA!; Thorne & Everett 36826 RSA!; Webster et al. 73 RSA!; SBBG.

Anacapa: Dunkle 7621 AHFH!; Moran 738 LAM!, RSA!; Hoffmann s.n. Mar. 16, 1929 POM!; SBBG; SBM.

San Nicolas: Trask s.n. in Mar. 1901 LAM!; Kanakoff s.n. Apr. 14, 1940 LAM!; Foreman & Smith 186 LA!; RSA-POM; SBBG; SBM; US.

Santa Catalina: Moran 704 LAM!, RSA!; Eastwood 6472 US!; Thorne 33439 RSA!; LA; MO; SBBG.

Lupinus albifrons Benth. var. *douglasii* (J.G. Agardh) C.P. Sm.

San Miguel: SBBG.

Santa Rosa: Thorne et al. 48969 RSA!; Thorne et al. 48904 RSA!; Thorne et al. 49033 RSA!; SBM.

Santa Cruz: Hoffmann s.n. Mar. 22, 1929 SBM!; Wolf 2770 RSA!; Raven & Smith 15281 RSA!; SBBG; SBM.

San Nicolas: Foreman, Evans & Rainey 28 RSA!; Raven & Thompson 20759 RSA!; Raven & Thompson 20723 RSA!; SBBG.

Lupinus arboreus Sims

San Miguel: Dunkle 8383 LAM!, AHFH!, MO!, RSA!; Blakley 5854 SBBG!; SBM.

Santa Rosa: Moran 796 LAM!, MO!, RSA!; Munz & Crow 11760 LA!, POM!; SBBG.

Lupinus bicolor Lindl. ssp. *microphyllus* (Wats.) D. Dunn

San Miguel: SBBG.

Santa Rosa: Hoffmann s.n. Apr. 16, 1929 POM!; Dunn, N. s.n. May 15, 1932 LA!; Raven, Blakley & Ornduff 14901 RSA!; SBBG.

Santa Cruz: Elmore 446 LAM!, AHFH!; Webster et al. 87 RSA!; Raven & Smith 15137 RSA!; SBBG.

Anacapa: SBBG.

San Nicolas: Trask s.n. in Apr. 1897 US!.

Santa Catalina: Fosberg S4377 LAM!, POM!, US!; Nuttall 169 F!; Dunkle 1801 AHFH!; SBBG.

San Clemente: Moran 592 LAM!, RSA!; Dunkle 7321 AHFH!; SBBG.

Guadalupe: Moran 5959 RSA!; Norris s.n. May 1, 1951 LA!.

Lupinus bicolor Lindl. ssp. *tridentatus* (Eastw. ex C.P. Sm.) D. Dunn

Santa Cruz: Wolf 2747 RSA!.

Lupinus bicolor Lindl. ssp. *umbellatus* (Greene) D. Dunn

San Miguel: Munz & Norris 11775 POM!.

Santa Rosa: Munz & Crow 11592 POM!.

Santa Cruz: Fosberg 7530 LAM!, LA!, POM!; Clokey 4977 NY!, POM!; Fosberg 7657 LAM!; SBBG.
Santa Catalina: Lister & Powell s.n. Apr. 2, 1928 LAM!; Dunkle 1741 POM!.
San Clemente: Dunkle 7319 LAM!; Munz 6742 POM!; Trask 256 US!; SBBG.

Lupinus concinnus J.G. Agardh ssp. *concinnus*
Santa Cruz: Wolf 2802 RSA!; Elmore s.n. Apr. 19, 1936 LAM!; Pierson 11065 RSA!.
Santa Catalina: Merritt s.n. in Aug. 1894 LAM!; Thorne & Everett 34469 RSA!; Thorne 35946 RSA!; SBBG.

Lupinus densiflorus Benth. var. *palustris* (Kell.) C.P. Sm.
Santa Rosa: Hoffmann 729 POM!; Blakley 3189 RSA!; Thorne et al. 48907 RSA!.
Santa Cruz: Sauer et al. 5494 RSA!; Raven & Smith 15311 RSA!; Webster et al. 101 RSA!.

Lupinus guadalupensis Greene
San Clemente: Moran 587 LAM!, MO!, NY!; Beauchamp 262 RSA!; Munz 6741 POM!; SBBG.
Guadalupe: Carlquist 447 RSA!; Greene s.n. Apr. 23, 1885 CAS#702!.

Lupinus hirsutissimus Benth.
Santa Rosa: SBM.
Santa Cruz: Wolf 2727 RSA!; Munz & Crow 11538 POM!; Thorne & Everett 36835 RSA!; SBBG; SBM.
Santa Catalina: Trask s.n. in May 1898 LAM!; Moran 694 LAM!; Dunkle 1936 AHFH!; RSA-POM.
San Clemente: Dunkle 7299 LAM!, AHFH!, RSA!; Trask 255 US!; Raven 17702 RSA!; SBBG.

Lupinus niveus Wats.
Guadalupe: Moran 17348 LAM!; Moran 6475 DS!; Carlquist 474 RSA!.

Lupinus polycarpus Greene
Santa Rosa: SBM.

Lupinus succulentus Dougl. ex Koch
San Miguel: Munz & Voss 11797 POM!; SBBG; SBM.
Santa Rosa: Moran 803 LAM!, RSA!; Thorne et al. 48965 RSA!; Munz & Crow 11716 POM!; SBBG; SBM.
Santa Cruz: Fosberg 7537 LAM!, LA!; Wolf 2812 RSA!; Webster et al. 70 RSA!; SBBG; SBM.
Anacapa: Moran 712 LAM!, RSA!.
Santa Catalina: Fosberg S4414 LAM!; Moran 676 LAM!; Trask s.n. in Apr. 1895 US!; AHFH; RSA-POM; SBBG.
San Clemente: Dunkle 7279 LAM!; Thorne 42906 RSA!; Raven 17677 RSA!; SBBG.

Lupinus truncatus Nutt. ex H. & A.
Santa Rosa: Thorne et al. 48731 RSA!; Raven, Blakley & Ornduff 14973 RSA!; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Jun. 15, 1930 LAM!; Clokey 4975 POM!, US!; Fosberg 7673 LAM!; SBBG; SBM.
Anacapa: Moran 728 LAM!, SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Trask s.n. in May 1897 US!; Moran 692 LAM!, RSA!; SBBG.
San Clemente: Dunkle 7303 LAM!; Moran 588 LAM!, RSA!; Trask 257 US!; SBBG.

Medicago polymorpha L. var. *brevispina* (Benth.) Heyn.
Santa Rosa: SBBG.
Santa Cruz: Dunkle 8573 LAM!; Hoffmann s.n. Jun. 15, 1930 LAM!; Raven & Smith 15144 RSA!; SBBG.
Santa Catalina: Dunkle 1814 AHFH!; Thorne 36901 RSA!; Lister & Powell s.n. Apr. 5, 1928 USC!.
San Clemente: Raven 17131 RSA!.
Guadalupe: Moran 6763 SD!; Moran 6783 RSA!; Wiggins & Ernst 94 DS!.

Medicago polymorpha L. var. *polymorpha*
San Miguel: Munz & Crow 11872 POM!; SBBG.
Santa Rosa: Dunkle 8437 LAM!; Raven, Blakley & Ornduff 14888 RSA!; Thorne et al. 49047 RSA!; SBBG; SBM.
Santa Cruz: Thorne & Everett 36848 RSA!; Balls & Blakley 23737 RSA!; Raven & Smith 15143 RSA!; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Dunkle 8323 LAM!; Raven & Thompson 20709 RSA!; Thorne et al. 52365 RSA!; SBBG.
Santa Barbara: Dunkle 7463 LAM!, AHFH!, RSA!; Thorne 37498 RSA!; SBBG.
Santa Catalina: Fosberg S4321 LAM!; Lister & Powell s.n. USC!; Thorne 35929a RSA!; SBBG.
San Clemente: Dunkle 7327 LAM!; Munz 6691 POM!; Raven 17130 RSA!.
Guadalupe: Moran 2884 DS!; Wiggins & Ernst 93 DS!.

Medicago sativa L.
Santa Rosa: SBBG.
Santa Cruz: Dunkle 8572 LAM!, RSA!; Hoffmann s.n. Jun. 15, 1930 LAM!; SBBG; SBM.
Anacapa: Dunkle 7465 LAM!; SBBG.
San Nicolas: Trask s.n. in Apr. 1901 LAM!.
Santa Catalina: Fosberg S4421 LAM!; Dunkle 1863 AHFH!, POM!; Thorne & Everett 34635 RSA!.
San Clemente: Thorne 42977 RSA!; SBBG.

Melilotus alba Medicus
Santa Cruz: SBBG.
San Nicolas: Foreman, Evans & Rainey 103 LA!; Thorne et al. 52368 RSA!; Raven & Thompson 20738 RSA!; SBBG.
Santa Catalina: Fosberg S4603 LAM!; Thorne 36268 RSA!; SBBG.
San Clemente: Raven 17959 RSA!; SBBG.

Melilotus indica (L.) All.
San Miguel: Dunkle 8391 LAM!, RSA!; SBBG; SBM.
Santa Rosa: Thorne et al. 48810a RSA!; Thorne et al. 49046 RSA!; SBM.
Santa Cruz: Dunkle 8571 LAM!; Williams 44 POM!; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8337 LAM!, RSA!; Kanakoff s.n. Apr. 18, 1940 LAM!; Foreman, Evans & Rainey 88 LA!; SBBG.
Santa Catalina: Fosberg S4322 LAM!; Dunkle 1985 AHFH!; Thorne 35764 RSA!; SBBG.
San Clemente: Raven 17960 RSA!; Raven 17128 RSA!; Blakley 6368 RSA!; SBBG.
Guadalupe: Wiggins & Ernst s.n. DS!.

Pickeringia montana Nutt. ssp. *montana*

Santa Cruz: Hoffmann s.n. May 23, 1932 POM!; SBBG.

Spartium junceum L.

San Nicolas: Newman 109 Pacific Missile Test Center, Pt. Mugu!; Wier & Beauchamp s.n. Jun. 29, 1978 RSA!.

Santa Catalina: Thorne 36907 RSA!; SBBG.

Trifolium albopurpureum T. & G.

Santa Rosa: SBBG; SBM.

Santa Cruz: Hoffmann 213 POM!; Thorne & Everett 36810 RSA!; Raven & Smith 15184 RSA!; SBBG; SBM.

San Nicolas: Trask 37 LAM!, NY!; Thorne et al. 52337 RSA!.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Kennedy 10028 POM!; Thorne & Everett 34603 RSA!.

Trifolium amplectens T. & G. var. *amplectens*

San Miguel: SBM.

Santa Rosa: Raven, Blakley & Ornduff 14896 RSA!; SBBG; SBM.

Santa Cruz: Hoffmann s.n. Sep. 10, 1931 LAM!; Thorne & Everett 36852 RSA!; Raven & Smith 15192 RSA!; SBBG; SBM.

Santa Catalina: Dunkle 2129 AHFH!; Dunkle 1770 AHFH!; Thorne 35986 RSA!; SBBG.

San Clemente: Dunkle 7315 AHFH!; Thorne 36126 RSA!; Raven 17613 RSA!; SBBG.

Guadalupe: Howell 8285 CAS!; Wiggins & Ernst 92 DS!.

Trifolium amplectens T. & G. var. *truncatum* (Greene) Jeps.

San Miguel: Munz & Crow 11830 POM!.

Santa Rosa: Munz & Crow 11711 POM!; Hoffmann s.n. May 10, 1932 POM!; SBM.

Santa Cruz: Fosberg 7528 LAM!, LA!; Munz & Crow 11520 POM!; Pierson 11030 POM!; SBM.

Anacapa: SBBG.

Santa Catalina: Dunkle 1745 AHFH!, POM!; Kennedy s.n. Apr. 21, 1907 LA!, POM!; Dunkle 1770 POM!; SBM.

Trifolium barbigerum Torr.

San Miguel: Munz & Norris 11764 POM!.

Santa Rosa: Hoffmann 711 POM!; Raven 14931 RSA!; SBBG.

Trifolium ciliolatum Benth.

Santa Rosa: SBM.

Santa Cruz: Munz & Crow 11557 POM!; Thorne & Everett 36837 RSA!; Raven & Smith 15188 RSA!; SBBG.

Santa Catalina: Trask s.n. in May 1897 LAM!.

Trifolium depauperatum Desv.

Santa Cruz: Raven & Smith 13239 RSA!.

San Nicolas: Howell 8212 CAS!.

Trifolium fucatum Lindl. var. *gambelii* (Nutt.) Jeps.

San Miguel: Hoffmann 584 POM!; Hoffmann s.n. SBM#11954!; SBBG.

Santa Rosa: Hoffmann 721 POM!; SBM.

Santa Cruz: SBBG; SBM.

Santa Catalina: Gambel s.n. GH!.

San Clemente: Raven 17674 RSA!; SBBG.

Trifolium gracilentum T. & G.

San Miguel: Munz & Norris 11767 POM!; SBM.

Santa Rosa: Munz & Crow 11702 POM!; SBBG; SBM.

Santa Cruz: Fosberg 7679 LAM!; Munz & Crow 11895 POM!; Raven & Smith 15134 RSA!; SBBG; SBM.

Anacapa: SBBG; SBM.

San Nicolas: Trask 35 MO!.

Santa Catalina: Dunkle 2126 AHFH!; Kennedy s.n. Apr. 21, 1907 LA!; Thorne 34604 RSA!; SBBG.

San Clemente: Raven 17200 RSA!; Munz 6692 POM!; Thorne 42793b RSA!; SBBG.

Guadalupe: Howell 8247 POM!; Moran 6599 RSA!; Lindsay s.n. Apr. 12, 1948 RSA!.

Trifolium macraei H. & A.

Santa Rosa: Munz & Crow 11598 POM!, LA!; Raven 14945 RSA!; Hoffmann 686 POM!; SBM.

Santa Cruz: Wolf 2850 RSA!; Hoffmann 212 POM!; Munz & Crow 11510 POM!; SBM.

Santa Catalina: Dunkle 2108 AHFH!; Dunkle 1839 AHFH!, POM!; Fritchey, J.Q.A. 19 MO!.

Trifolium microcephalum Pursh

San Miguel: SBBG; SBM.

Santa Rosa: Blakley 3059 RSA!; Munz & Crow 11632 POM!; Raven, Blakley & Ornduff 14898 RSA!; SBBG; SBM.

Santa Cruz: Fosberg 7648 LAM!, LA!; Clokey 4979 NY!; Elmore 441 AHFH!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4342 LAM!, POM!; Trask s.n. in Mar. 1900 NY!; Thorne 36226 RSA!; SBBG; SBM.

San Clemente: Trask 336 NY!; Munz 6603 POM!; Pierson 3435 RSA!; SBBG.

Guadalupe: Palmer 27 NY!; Howell 8246 NY!; Rose 16036 NY!; RSA-POM.

Trifolium microdon H. & A. var. *pilosum* Eastw.

San Nicolas: Trask s.n. in Apr. 1897 CAS#1179!, US!; Trask 34 MO!.

Santa Catalina: Trask s.n. in May 1897 MO!, US!; Trask s.n. in May 1903 US!.

Trifolium palmeri Wats.

San Nicolas: Trask s.n. in Apr. 1897 US!; Trask 37 MO!.

Santa Barbara: Dunkle 7449 LAM!, AHFH!, RSA!; Dunkle 7415 LAM!; SBBG.

Santa Catalina: Trask s.n. in Mar. 1896 MO!; Trask 334 NY!; Thorne 42793a NY!, DS!; SBBG.

San Clemente: Raven 17648 RSA!; Thorne 42899 MO!; Wooton s.n. Apr. 26, 1912 US!; DS; SBBG.

Guadalupe: Palmer 26 NY!, CM!; Howell 8308 CAS!, NY!; Franceschi 27 RSA!.

Trifolium repens L.

Santa Catalina: Thorne 36699 RSA!.

Trifolium tridentatum Lindl. var. *aciculare* (Nutt.) McDer.

San Miguel: SBM.

Santa Rosa: Munz & Crow 11596 LA!; Moran 798 RSA!; Thorne et al. 48747 RSA!; SBM.

Santa Cruz: Fosberg 7651 LAM!; Hoffmann s.n. LA!; Elmore 465 AHFH!; SBM.

Anacapa: SBBG; SBM.

San Nicolas: Raven & Thompson 20783 RSA!.

Santa Barbara: Dunkle 7442 LAM!, AHFH!; Dunkle 8115 AHFH!; Dunkle 7425 RSA!; SBBG.

Santa Catalina: Dunkle 2112 AHFH!; Trask s.n. in Mar. 1901 LAM!; Thorne & Everett 34485 RSA!.

San Clemente: Dunkle 7288 LAM!, AHFH!, RSA!; Raven 17154 RSA!; Raven 17647 RSA!; SBBG.

Trifolium tridentatum Lindl. var. *tridentatum*

San Miguel: SBBG.

Santa Rosa: Moran 798 LAM!; Munz & Crow 11596 POM!; Munz & Crow 11672 POM!; SBBG.

Santa Cruz: Munz & Crow 11559 POM!; Blakley 3313 RSA!; Raven & Smith 15154 RSA!; SBBG; SBM.

Anacapa: SBBG.

San Nicolas: RSA-POM; SBBG.

Santa Barbara: Dunkle 7425 AHFH!, MO!; Thorne 37500 RSA!; Blakley 5678 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4367 (in part) LAM!; Kennedy s.n. Apr. 21, 1907 LA!, RSA!; Thorne 36867 RSA!; SBBG.

San Clemente: Thorne 36060 RSA!; Thorne 42870 RSA!; SBBG.

Trifolium variegatum Nutt. in T. & G.

Santa Cruz: Hoffmann s.n. Jun. 15, 1930 POM#172011!; SBM.

Vicia americana Muhl. ex Willd.

San Miguel: SBBG; SBM.

Santa Rosa: Munz & Crow 11677 POM!, LA!; Thorne et al. 48765 RSA!; Hoffmann s.n. Apr. 16, 1929 SBM#6195!; SBBG.

Santa Cruz: Raven & Smith 15157 RSA!; Pierson, F.W. 11061 RSA!; SBBG; SBM.

Vicia dasycarpa Ten.

San Nicolas: Foreman, Evans & Rainey 93 LA!; SBBG.

Santa Catalina: Parratt 546 LAM!; Thorne 36498 RSA!; SBBG.

Vicia exigua Nutt. in T. & G.

Santa Rosa: SBM.

Santa Cruz: Brandegee s.n. in 1888 (in part) UC!; Hoffmann s.n. Sep. 21, 1930 POM!; Thorne & Everett 36843 RSA!; SBBG.

Anacapa: SBM.

Santa Catalina: Fosberg 4617 LAM!, POM!, UC!; Dunkle 1767 AHFH!, POM!; Thorne 35954 RSA!; SBBG; SBM.

San Clemente: Raven 17338 RSA!; Raven 17680 RSA!, UC!; SBBG.

Guadalupe: Moran 17478 RSA!, UC!; Newcomb 188 UC!.

Vicia hassei Wats.

Santa Rosa: Moran 782 LAM!, RSA!; Munz & Crow 11614 POM!; SBBG.

Santa Cruz: Munz & Crow 11845 POM!; Pierson 11085 RSA!; Abrams & Wiggins 8 UC!.

Anacapa: [Hoffmann] s.n. Mar. 11, 1928 SBM#4158!.

San Nicolas: Trask 85 MO!, NY!.

San Clemente: Munz 6669 POM!, UC!; Pierson 3442 RSA!; Thorne 42962 RSA!.

Guadalupe: Wiggins & Ernst 200 UC!.

Vicia villosa Roth

San Nicolas: Raven & Thompson 20766 RSA!; SBBG.

Fagaceae

Quercus agrifolia Nee var. *agrifolia*

Santa Rosa: Dunkle 8494 LAM!, AHFH!; Thorne et al. 48771 RSA!; Epling & Erickson s.n. Aug. 8, 1937 LA!; SBM.

Santa Cruz: Fosberg 7628 LAM!; Clokey 4895 LAM!, POM!; Raven & Smith 15205 RSA!; SBM.

Quercus chrysolepis Liebm.

Santa Cruz: Clokey 4897 LAM!; Clokey 4900 LAM!; Hoffmann s.n. Jun. 15, 1930 LAM!; SBBG; SBM.

Santa Catalina: Trask s.n. in Apr. 1900 LAM!; Thorne & Thorne 36420 RSA!; Thorne & Thorne 36430 RSA!.

San Clemente: Dunkle 7361 LAM!, AHFH!, RSA!.

Quercus douglasii H. & A.

Santa Cruz: Thorne & Everett 36774 RSA!; Raven & Smith 15277 RSA!.

Santa Catalina: SBBG.

Quercus dumosa Nutt.

Santa Rosa: Dunkle 8487 LAM!, RSA!; Thorne et al. 48855 RSA!; Munz & Crow 11577 POM!; SBM.

Santa Cruz: Clokey 4896 LAM!, LA!, POM!; Dunkle 8659 LAM!, RSA!; Raven & Smith 15160 RSA!; SBM.

Santa Catalina: Fosberg S4358 LAM!; Grant 6137 LAM!; Moran 707 LAM!, RSA!; SBBG; SBM.

Quercus engelmannii Greene

Santa Catalina: Thorne & Everett 34611 RSA!; Thorne 36864 RSA!.

Quercus lobata Nee

Santa Cruz: Thorne & Everett 36776 RSA!; SBBG.

Santa Catalina: SBBG.

Quercus × *macdonaldii* Greene

Santa Rosa: SBM.

Santa Cruz: Fosberg 7558 LAM!; Hoffmann s.n. Jun. 15, 1930 LAM!; Clokey 5173 LA!, RSA!; SBM.

Santa Catalina: Fosberg S4589 LAM!; Wolf 4230 RSA!; Thorne 36189 RSA!; SBM.

Quercus × *morehus* Kell.

Santa Cruz: Wolf 2759 RSA!; Pierson 11072 RSA!; SBM.

Quercus tomentella Engelm.

Santa Rosa: Dunkle 8507 LAM!; Epling & Erickson s.n. Apr. 8, 1938 LA!; Moran 815 LAM!, RSA!; SBBG; SBM.

Santa Cruz: Fosberg 7594 LAM!; Munz & Crow 11501 LA!, POM!; Raven & Smith 15159 RSA!; SBBG; SBM.

Anacapa: Dunkle 7660 LAM!, AHFH!, RSA!; Moran 714 LAM!, RSA!; SBBG; SBM.

Santa Catalina: Fosberg S5607 LAM!; Raven 17808 LA!; Thorne 35823 RSA!; SBBG.

San Clemente: DeBuhr & Wallace 700 LAM!, RSA!; Dunkle 7357 LAM!, AHFH!; Raven 17720 RSA!; SBBG.

Guadalupe: Moran 18387 LAM!; Moran 13788 LAM!; Walker s.n. Nov. 12, 1938 AHFH!; RSA-POM.

Quercus wislizenii A. DC. var. *frutescens* Engelm.

Santa Cruz: Sauer & Mathias 5676 RSA!; SBM.

Frankeniaceae

Frankenia grandifolia Cham. & Schlecht. var. *grandifolia*

San Miguel: Dunkle 8411 LAM!, RSA!; Dunkle 8382 AHFH!; SBBG; SBM.

Santa Rosa: Dunkle 8430 LAM!; Blakley 3196 RSA!; Munz & Crow 11564 OM!; SBBG; SBM.
Santa Cruz: Clokey 5005 POM!; SBBG; SBM.
Anacapa: Dunkle 7603 LAM!, AHFH!, RSA!; Elmore 250 AHFH!; Dunn, N. s.n. May 14, 1932 LA!; SBBG; SBM.
San Nicolas: Dunkle 8300 LAM!; Kanakoff s.n. Apr. 22, 1940 LAM!; Raven & Thompson 20690 LA!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4471 LAM!; Fosberg S5424 LAM!; Dunkle 1923 AHFH!; RSA-POM; SBBG; SBM.
San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!; Thorne 42912 RSA!; Raven 17183 RSA!; SBBG.
Guadalupe: Moran 6472 RSA!.

Garryaceae

Garrya elliptica Dougl.
Santa Cruz: Williams 55 POM!; Bartholomew & Zadnik 712b RSA!; Beeks 28-4-68-17 RSA!; SBBG.

Gentianaceae

Centaurium davyi (Jeps.) Abrams
Santa Rosa: Elmore 204 AHFH!.
Santa Cruz: Blakley 3296 RSA!; Hoffmann s.n. Jun. 10, 1930 POM!; Clokey 5117 NY!.
San Clemente: Trask 174 US!.

Centaurium exaltatum (Griseb.) W. Wight
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#038921!, US#310252!.

Centaurium muhlenbergii (Griseb.) W. Wight
Santa Cruz: (Jepson 1909–1943: Jepson 12089).

Centaurium venustum (Gray) Rob.
Santa Catalina: Dunkle 1905 AHFH!, POM!; Thorne & Everett 34914 RSA!; Thorne 36354a RSA!; SBBG.

Geraniaceae

Erodium botrys (Cav.) Bertol.
Santa Rosa: Munz & Crow 11636 POM!; SBM.
Santa Cruz: Thorne & Everett 36831 RSA!; Raven & Smith 15172 RSA!.
San Clemente: Thorne 36083 RSA!.

Erodium cicutarium (L.) L'Her.
San Miguel: Dunkle 8378 LAM!, AHFH!; Munz & Crow 11804 POM!; SBBG; SBM.
Santa Rosa: Thorne et al. 48756 RSA!; Dunkle 8464 LAM!; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8338 LAM!, AHFH!; Foreman 228 LA!; Thorne et al. 52370 RSA!; SBBG; SBM.
Santa Barbara: Dunkle 7462 LAM!, AHFH!, RSA!; Dunkle 8134 LAM!; Dunkle 8120 AHFH!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4532 LAM!; Fosberg S4318 LAM!; Thorne & Everett 33459 RSA!.
San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!; Munz 6704 POM!; Raven 17136 RSA!; SBBG.
Guadalupe: Palmer 19 CM!; Wiggins & Ernst 60 DS!.

Erodium macrophyllum H. & A. var. *californicum* (Greene) Jeps.
Santa Cruz: Brandegee s.n. in Apr. 1888 UC!.

Erodium moschatum (L.) L'Her.
San Miguel: SBBG; SBM.
Santa Rosa: Thorne et al. 48738 RSA!; Thorne et al. 49015 RSA!; Raven, Blakley & Ornduff 14881 RSA!; SBBG; SBM.
Santa Cruz: Dunkle 8627 LAM!; Thorne & Everett 36845 RSA!; Webster et al. 88 RSA!; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Kanakoff s.n. Apr. 14, 1940 LAM!; Thorne et al. 52369 RSA!; Raven & Thompson 20781 RSA!; SBBG.
Santa Barbara: Dunkle 7466 LAM!, AHFH!; Thorne 37526 RSA!; Philbrick & McPherson B68-221 RSA!; SBBG.
Santa Catalina: Fosberg S4533 LAM!; Thorne 35748 RSA!; Thorne 42845 RSA!; SBBG.
San Clemente: Dunkle 7306 LAM!, AHFH!; Munz 6665 POM!; Raven 17135 RSA!; SBBG.
Guadalupe: Palmer 20 CM!; Wiggins & Ernst 21 DS!; Norris s.n. May 1, 1951 LA!.

Erodium obtusiplicatum (Maire, Weiller & Wilcz.) J.T. Howell
Santa Rosa: Munz & Crow 11636 LA!, POM!; Thorne et al. 48874b RSA!; Thorne et al. 49008 RSA!.
Santa Catalina: Thorne, Rollins, Propst & Carolin 36750 RSA!; Thorne, Rollins, Propst & Carolin 36757 RSA!.

Erodium texanum Gray
Santa Catalina: Trask s.n. in Mar. 1901 LAM!.

Geranium carolinianum L.
Santa Rosa: SBBG; SBM.
Santa Cruz: SBM.
Santa Catalina: Fosberg S4319 LAM!; Fosberg S4593 LAM!; Fosberg S4627 LAM!; RSA-POM.

Geranium dissectum L.
Santa Rosa: Thorne et al. 48750 RSA!.

Pelargonium × *hortorum* Bailey
Santa Rosa: SBBG.
Santa Cruz: SBBG.
San Nicolas: Wier & Beauchamp s.n. Jun. 30, 1978 RSA#289077!.
Santa Catalina: Thorne 36477 RSA!; SBBG.

Pelargonium peltatum (L.) L'Her. ex Ait.
San Nicolas: Foreman 106 UC!; Wier & Beauchamp s.n. Jun. 30, 1978 RSA!.

Hydrophyllaceae

Emmenanthe penduliflora Benth.
Santa Cruz: Hoffmann s.n. Apr. 22, 1932 POM!; SBM.
Santa Catalina: Fosberg S4694 LAM!; Dunkle 2446 AHFH!; Thorne 35972 RSA!; SBBG.
San Clemente: Dunkle 7302 LAM!, AHFH!, RSA!; Raven 17722 RSA!; SBBG.
Guadalupe: Palmer 73 CM!; Carlquist 448 RSA!; Moran 5962 RSA!.

Eriodictyon traskiae Eastw. ssp. *traskiae*
Santa Catalina: Trask s.n. in Mar. 1902 LAM!; Fosberg S4790 LAM!; Dunkle 1961 AHFH!, POM!; CAS; SBBG.

Eucrypta chrysanthemifolia (Benth.) Greene var. *chrysanthemifolia*

San Miguel: Munz & Norris 11783 POM!; SBBG; SBM.

Santa Rosa: Thorne et al. 48807 RSA!; Blakley & Smith 3082 RSA!; SBBG; SBM.

Santa Cruz: Fosberg 7631 LAM!, LA!; POM!; Munz & Crow 11524 POM!; Wolf 2817 RSA!; SBBG; SBM.

Anacapa: Moran 725 LAM!; SBBG; SBM.

Santa Catalina: Fosberg S4723 LAM!; Fosberg S4412 LAM!; Moran 683 LAM!; RSA-POM; SBBG.

San Clemente: Thorne 36111 RSA!; Raven 17695 RSA!; Raven 17736 RSA!; SBBG.

Guadalupe: Anthony 252 POM!; Moran 5684 RSA!; Howell 8322 POM!.

Nemophila menziesii H. & A. ssp. *menziesii*

Santa Catalina: Moran 681 LAM!, DS!, RSA!; SBBG.

Nemophila pedunculata Dougl. ex Benth.

San Miguel: Hoffmann s.n. Apr. 10, 1930 SBM#9226!, CAS#178505!.

Santa Rosa: Hoffmann s.n. Apr. 17, 1929 SBM#5992!; Hoffmann s.n. Apr. 17, 1929 SBM#5994!; Raven 14934 RSA!; SBBG.

Santa Cruz: Munz & Crow 11539 POM!; Hoffmann s.n. in Mar. 1929 CAS#168319!; SBBG.

San Nicolas: (Howell 1935: Howell 8213 at CAS).

Phacelia cicutaria Greene ssp. *hispida* (Gray) Beauchamp ex Thorne

Santa Rosa: SBM.

Santa Cruz: Fosberg 7538 POM!; Thorne & Everett 36830 RSA!; Raven & Smith 15263 RSA!; SBBG; SBM.

Anacapa: SBBG; SBM.

Santa Catalina: Fosberg S4432 LAM!; Fosberg S4336 LAM!; Trask s.n. in Mar. 1901 ND-G#042100!; RSA-POM; SBBG.

Phacelia cinerea Eastw. ex Macbr.

San Nicolas: Trask s.n. in Apr. 1901 LAM!, ND-G#042098!.

Phacelia distans Benth.

San Miguel: Dunkle 8407 LAM!, AHFH!; Munz & Crow 11813 POM!; Greene s.n. in Sep. 1886 CAS#938!; SBBG; SBM.

Santa Rosa: Dunkle 8476 AHFH!; Moran 795 LAM!, RSA!; Munz & Crow 11753 LA!, POM!; SBBG; SBM.

Santa Cruz: Fosberg 7538 LAM!; Wolf 2794 RSA!; Webster et al. 96 RSA!; SBBG; SBM.

Anacapa: Moran 721 LAM!, RSA!; Howell 3801 RSA!; SBBG; SBM.

Santa Barbara: Dunkle 7460 LAM!; Dunkle 7441 LAM!, AHFH!; Dunkle 8122 LAM!, AHFH!; SBBG.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4598 LAM!; RSA-POM; SBBG.

San Clemente: Thorne 35989 RSA!; Munz 6738 POM!; Raven 17306 RSA!; SBBG.

Phacelia divaricata (Benth.) Gray var. *insularis* (Munz) Munz

San Miguel: Munz & Norris 11829 POM!; Hoffmann s.n. Apr. 20, 1932 POM!; SBBG; SBM.

Santa Rosa: Moran 800 LAM!, RSA!; Munz 11756 POM!; SBBG; SBM.

Phacelia floribunda Greene

San Clemente: Dunkle 7212 LAM!, AHFH!, RSA!; Thorne 36112 RSA!; Raven 17243 RSA!; SBBG; SBM.

Guadalupe: Anthony 242 LAM!; Moran 6712 LA!, RSA!; Moran 5653 RSA!.

Phacelia grandiflora (Benth.) Gray

Santa Rosa: SBM.

Santa Cruz: SBBG; SBM.

Santa Catalina: Raven 17859 RSA!; SBBG.

Phacelia lyonii Gray

Santa Catalina: Davidson, A. s.n. in Jun. 1897 LAM!; Dunkle 2146 LAM!, AHFH!; Fosberg S4749 LAM!; LA; RSA-POM; SBBG.

San Clemente: Moran 682 RSA!; Raven 17690 RSA!; Thorne 36045 RSA!; SBBG.

Phacelia phyllomanica Gray

Guadalupe: Franceschi 43 LAM!, RSA!; Moran 7836 RSA!; Moran 13782 RSA!.

Phacelia ramosissima Dougl. ex Lehm. var. *austrolitoralis* Munz

Santa Rosa: Dunkle 8525 AHFH!; Thorne et al. 48779 RSA!; Thorne et al. 48751 RSA!.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#042054!; Greene s.n. in Jul.–Aug. 1886 ND-G#042053!; Mower s.n. Aug. 22, 1966 LA#96261!; RSA-POM.

Phacelia ramosissima Dougl. ex Lehm. var. *montereyensis* Munz

San Miguel: SBM.

Santa Rosa: Dunkle 8476 LAM!; Dunn, N. s.n. May 15, 1932 LA!; SBM.

Phacelia viscida (Benth.) Torr.

Santa Rosa: Fosberg 7516 LAM!; Fosberg 7638 LAM!; Blakley 3150 RSA!; SBBG.

Santa Cruz: Fosberg 7521 LAM!; Moran 757 LAM!, RSA!; Raven & Smith 15206 RSA!; LA; SBBG; SBM.

Anacapa: SBBG.

Santa Catalina: Trask s.n. in Mar. 1900 NY!; Trask s.n. in Mar. 1901 ND-G#04072!, NY!, US!.

Pholistoma auritum (Lindl.) Lilja ex Lindl.

Santa Cruz: Fosberg 7664 LAM!, LA!, POM!; Elmore s.n. Apr. 18, 1936 AHFH!; Raven & Smith 15153 RSA!; SBBG; SBM.

Santa Barbara: SBBG.

Santa Catalina: Dunkle 2089 LAM!, AHFH!; Moran 684 LAM!, RSA!; Fosberg S4592 LAM!, POM!; SBBG; SBM.

San Clemente: Dunkle 7238 LAM!, AHFH!, RSA!; Thorne 42869 RSA!; Raven 17346 RSA!; SBBG.

Pholistoma racemosum (Nutt.) Const.

Santa Cruz: Fosberg 7667 LAM!, LA!; Elmore s.n. Apr. 18, 1936 USC!; Wolf 2900 RSA!; SBBG; SBM.

Santa Barbara: Dunkle 7443 LAM!, AHFH!; Thorne 37513 RSA!; Blakley 5651 RSA!; SBBG.

Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Grant 3671 LAM!; Millspaugh 4687 F!; LA; RSA-POM; SBBG; SBM.

San Clemente: Dunkle 7219 LAM!, AHFH!; Moran 574 LAM!; Elmore 412 AHFH!; RSA-POM; SBBG.
Guadalupe: Anthony 254 RSA!; Moran 5686 RSA!.

Juglandaceae

Juglans californica Wats.
Santa Catalina: Johnstone s.n. May 20, 1934 USC!; Fosberg S4848 LAM!; Thorne & Everett 34674 RSA!; SBBG.

Lamiaceae

Lamium amplexicaule L.
Santa Cruz: Wolf 2886 RSA!; SBBG; SBM.

Lepechinia calycina (Benth.) Epl. in Munz
Santa Rosa: Moran 790 LAM!, RSA!; SBBG.
Santa Barbara: SBBG.

Lepechinia fragrans (Greene) Epl.
Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!; Thorne et al. 48997 RSA!; Raven 15008 RSA!; SBM.
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 CAS#1140!; Clokey 5044 POM!; Jones s.n. Mar. 25, 1929 POM!, RSA!; LA; SBM.
Santa Catalina: Trask s.n. in May 1901 LAM!; Fosberg S4786 LAM!, POM!; Thorne 36329 LA!, RSA!.

Marrubium vulgare L.
San Miguel: Dunkle 8374 LAM!, AHFH!; SBBG; SBM.
Santa Rosa: SBBG; SBM.
Santa Cruz: Dunkle 8638 LAM!, AHFH!; Clokey 5043 LA!, POM!; SBBG; SBM.
San Nicolas: Newman 114 Pacific Missile Test Center, Pt. Mugu!
Santa Catalina: Thorne & Everett 34428 RSA!; Fosberg S4459 LAM!; Dunkle 1874 AHFH!; SBBG.
San Clemente: DeBuhr & Wallace 711 LAM!; House & Grumbles s.n. Aug. 5–13, 1930 USC!; Elmore 417 AHFH!; RSA-POM; SBBG.

Mentha citrata Ehrh.
Santa Catalina: Thorne 36521 RSA!; Thorne & Everett 34957 RSA!; SBBG.

Mentha spicata L.
Santa Catalina: Thorne 36637 RSA!.

Nepeta cataria L.
Santa Catalina: Millspaugh 4894 F!; Nuttall 831 F!; Pendleton 1391 POM!.

Pogogyne tenuiflora Gray
Guadalupe: Palmer 65 NY!.

Salvia apiana Jeps. var. *apiana*
Santa Catalina: Fosberg S4800 LAM!; Fosberg 4808 LAM!, POM!; Eaton s.n. Jul. 15, 1956 LAM!; SBBG; SBM.

Salvia brandegei Munz
Santa Rosa: Dunkle 8427 LAM!, AHFH!; Epling s.n. Apr. 20, 1940 LA!; Thorne et al. 48929 RSA!; SBBG; SBM.

Salvia columbariae Benth.
Santa Rosa: SBM.
Santa Cruz: SBBG; SBM.
Santa Catalina: Dunkle 1774 AHFH!, POM!; Fosberg S4699 LAM!, POM!; Thorne 35945 RSA!.
San Clemente: Munz 6478 POM!; Thorne 42830 RSA!; Raven 17688 RSA!.

Salvia mellifera Greene
Santa Rosa: SBBG; SBM.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Fosberg 7707 LAM!, POM!; Raven & Smith 15255 RSA!; SBBG; SBM.
Anacapa: Dunkle 7635 LAM!; Moran 736 LAM!, RSA!; SBBG; SBM.
Santa Catalina: Fosberg S4291 LAM!; Fosberg S4805 LAM!; Dunkle 1725 AHFH!, POM!; RSA; SBBG; SBM.

Satureja douglasii (Benth.) Briq.
Santa Catalina: Trask s.n. in Aug. 1902 LAM!; Fosberg S4702 LAM!, POM!; Dunkle 2008 AHFH!, POM!; SBBG.

Satureja palmeri (Gray) Briq.
Guadalupe: Palmer 66 NY!, CM!.

Scutellaria tuberosa Benth. ssp. *australis* Epl.
Santa Cruz: Fosberg 7694 LAM!, LA!; Fosberg 7659 LAM!, LA!; Moran 749 LAM!; RSA-POM; SBBG; SBM.

Stachys bullata Benth.
Santa Rosa: Dunkle 8530 LAM!; Dunn, N. s.n. May 15, 1932 LA!; Munz & Crow 11589 LA!; SBBG; SBM.
Santa Cruz: Hoffmann 218 LA!; Abrams & Wiggins 59 NY!; Eastwood 6414 US!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7659 LAM!; Moran 737 LAM!; SBBG; SBM.

Trichostema lanceolatum Benth.
Santa Catalina: Dunkle 2150 LAM!, AHFH!; Thorne 36707 RSA!; Thorne, Propst & Hoefs 45111 RSA!; SBBG.

Linaceae

Hesperolinon micranthum (Gray) Small
Santa Catalina: RSA-POM; SBBG.

Loasaceae

Mentzelia affinis Greene
Santa Cruz: Fosberg 7536 LAM!, POM!; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!.
San Clemente: SBBG; SBM.

Mentzelia micrantha (H. & A.) T. & G.
Santa Cruz: Clokey 5028 NY!; Clokey 5008 POM!; SBBG; SBM.
Santa Catalina: Dunkle 2465 LAM!; Heller 8954 NY!; Trask s.n. in Mar. 1896 MO!; RSA-POM; SBBG; SBM; US.
San Clemente: Munz 6749 POM!; SBBG.
Guadalupe: Palmer 893 ND-G!, US!; Anthony 259 US!; Wiggins & Ernst 63 US!.

Lythraceae

Ammannia coccinea Rottb.
Santa Catalina: Thorne 36710 RSA!.

Lythrum californicum T. & G.
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#034589!.

Malvaceae

Althaea rosea (L.) Cav.
Santa Catalina: Thorne 36475 RSA!.

Eremalche exilis (Gray) Greene
Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!.
San Clemente: Trask 218 NY!.

Lavatera assurgentiflora Kell.
San Miguel: Greene s.n. in Sep. 1886 MO!, POM!; SBBG.
Santa Rosa: Dunkle 8529 LAM!; Elmore 191 AHFH!; SBBG.
Santa Cruz: RSA-POM.
Anacapa: (Philbrick 1980: Timbrook & Philbrick 652 and 653 at SBBG).
San Nicolas: Wier & Beauchamp s.n. Jul. 4, 1978 RSA!, UC!.
Santa Catalina: Fosberg 7146 LAM!, POM!; Trask s.n. in Mar. 1896 MO!; Moran 625 LAM!, RSA!; SBBG; SBM.
San Clemente: Raven 17303 LA!, RSA!; Blakley 6414 RSA!; Raven 17579 RSA!.

Lavatera linsayi Moran
Guadalupe: Lindsay 1812 DS!; Moran 15118a LAM!; Moran 2630 RSA!.

Lavatera occidentalis Wats.
Guadalupe: Franceschi 12 LAM!; Anthony 247 MO!; Palmer 17 MO!, CM!.

Malacothamnus clementinus (M. & J.) Kearn.
San Clemente: Munz 6684 POM! CAS!, DS!; Thorne 42778 RSA!; Raven 17977 RSA!; SBBG.

Malacothamnus fasciculatus (Nutt.) Greene ssp. *catalinensis* (Eastw.) Thorne
Santa Catalina: Fosberg S5427 LAM!, POM!; Wallace & Haefs 1407 RSA!; Dunkle 1932 LAM!; RSA-POM; SBBG; SBM.

Malacothamnus fasciculatus (Nutt.) Greene var. *nesioticus* (Rob.) Kearn.
Santa Cruz: Hoffmann s.n. Jun. 28, 1930 POM!; Greene s.n. in Jul.–Aug. 1886 CAS#743!; SBBG; SBM.

Malva parviflora L.
San Miguel: Dunkle 8393 LAM!, AHFH!; SBBG; SBM.
Santa Rosa: Thorne et al. 48819 RSA!; Thorne et al. 48879 RSA!; Raven, Blakley & Ornduff 14875 RSA!; SBBG; SBM.
Santa Cruz: Dunkle 8632 LAM!, AHFH!; Hoffman s.n. Apr. 12, 1931 LAM!; Hoffmann s.n. Sep. 21, 1930 POM!; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Kanakoff s.n. Apr. 26, 1940 LAM!; Dunkle 8326 LAM!, AHFH!; Foreman, Evans & Rainey 11 RSA!; SBBG; SBM.
Santa Barbara: Dunkle 8117 LAM!; Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; Thorne 37509 RSA!; SBBG; SBM.
Santa Catalina: Fosberg S4472 LAM!; Fosberg S5434 LAM!; Dunkle 1856 AHFH!; RSA-POM; SBBG.
San Clemente: Dunkle 7293 LAM!; Munz 6784 POM!; Raven 17129 RSA!; SBBG.
Guadalupe: Howell 8261 POM!.

Malvella leprosa (Ortega) Krapovickas
Santa Catalina: Blakley 5378 LAM!, CAS!, RSA!; SBBG.
San Clemente: Trask 258 US!; Munz 6622a POM!; Raven 17956 RSA!, CAS!.
Guadalupe: (Clement 1957: Thoburn, Greene & Wing s.n. in Jun. 1897 at DS).

Sidalcea malvaeflora (DC.) Gray ex Benth. ssp. *malvaeflora*
San Miguel: Munz & Norris 11782 POM!; SBBG; SBM.
Santa Rosa: Moran 780 LAM!, MO!; Elmore 181 AHFH!; Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Raven & Smith 15300 RSA!; Webster et al. 95 RSA!; SBBG.

Sphaeralcea palmeri Rose
Guadalupe: Rempel 759-37 LAM!; Carlquist 469 RSA!; Moran 17332 RSA!.

Sphaeralcea sulphurea Wats.
Guadalupe: Palmer 18 CM!; Franceschi 13 RSA!.

Moraceae

Ficus carica L.
San Miguel: SBBG.
Santa Cruz: SBBG; SCIR.
Santa Catalina: RSA-POM; SBBG.

Myrtaceae

Eucalyptus globulus Labill.
Santa Rosa: SBBG.
Santa Cruz: SBBG.
Anacapa: SBBG.
San Nicolas: Wier & Beauchamp s.n. Jul. 4, 1978 RSA!; SBBG.
Santa Catalina: RSA-POM.

Nyctaginaceae

Abronia latifolia Esch.
San Miguel: Munz & Fosberg 11792 POM!; SBM.

Abronia maritima Nutt. ex Wats.
San Miguel: Dunkle 8390 LAM!, AHFH!, RSA!; Elmore 330 LAM!, AHFH!; Elmore 340 AHFH!; SBBG; SBM.
Santa Rosa: Munz & Crow 11567 POM!; Raven 14997 RSA!; Thorne et al. 49022 RSA!; SBM.
Santa Cruz: Dunkle 8583 LAM!, RSA!; Balls & Blakley 23637 RSA!; Balls & Blakley 23694 RSA!; SBM.
Anacapa: Elmore 243 AHFH!; SBM.
San Nicolas: Dunkle 8342 LAM!, RSA!; Foreman & Lloyd 139 RSA!; Raven & Thompson 20703 RSA!; SBBG.
Santa Catalina: Fosberg S4881 LAM!, POM!; Dunkle 1892 AHFH!, POM!; Moran 675 LAM!, RSA!; SBBG; SBM.
San Clemente: Dunkle 7278 LAM!, AHFH!; Elmore 381 AHFH!; Thorne 42933 RSA!; SBBG.

Abronia umbellata Lam.
San Miguel: Dunkle 8373 LAM!, AHFH!; Elmore 330a AHFH!; Elmore 339 AHFH!; RSA-POM; SBBG; SBM.
Santa Rosa: Dunkle 8490 LAM!; Moran 792 LAM!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
San Nicolas: Trask 23 LAM!; Kanakoff s.n. Apr. 14, 1940 LAM!; Dunkle 8316 LAM!; LA; RSA-POM; SBBG.
Santa Catalina: Thorne 39383 RSA!; Thorne & Everett 34934 RSA!; SBBG.
San Clemente: Dunkle 7266 LAM!; Elmore s.n. Nov. 23, 1939 AHFH!; Raven 17297 RSA!.

Mirabilis californica Gray var. *californica*

Santa Cruz: Clokey 4923 LAM!; Fosberg 7518 LAM!; Howell 6287 US!; RSA-POM; SBBG; SBM.

Anacapa: Dunkle 7671 LAM!, AHFH!, RSA!; SBBG; SBM.

Santa Barbara: Dunkle 7433 LAM!; Dunkle 8107 LAM!; Thorne 37483 RSA!.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!, US!; Moran 669 LAM!; Eastwood 6443 LA!; RSA-POM; SBM.

San Clemente: Dunkle 7234 LAM!; Dunkle 7235 AHFH!, RSA!; Thorne 42871 RSA!; SBBG.

Mirabilis heimerlii (Standl.) Macbr.

Guadalupe: Palmer 886 ND-G!, NY!; Rose 16021 NY!; Carlquist 481 RSA!; LAM.

Oleaceae

Hesperelaea palmeri Gray

Guadalupe: Palmer 81 NY!, CM!.

Olea europaea L.

Santa Cruz: SBBG.

Onagraceae

Camissonia californica (Nutt. ex. T. & G.) Raven

Santa Rosa: SBM.

Santa Cruz: Breedlove 2816 RSA!; Thorne & Everett 36842 RSA!; Raven & Smith 15274 RSA!; SBBG; SBM.

Santa Catalina: Dunkle 1943 AHFH!, POM!.

Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*

San Miguel: Dunkle 8379 LAM!, AHFH!; Dunkle 8414 AHFH!; Elmore 313 AHFH!; RSA-POM; SBBG; SBM.

Santa Rosa: Moran 791 LAM!, RSA!; Dunkle 8467 LAM!, AHFH!; Thorne et al. 49021 RSA!; SBBG; SBM.

Santa Cruz: Raven & Smith 15312 RSA!; Webster et al. 89 RSA!; SBBG; SBM.

San Nicolas: Dunkle 8309 LAM!, AHFH!; Kanakoff s.n. Apr. 18, 1940 LAM!; Foreman, Evans & Rainey 79 LA!, RSA!; SBBG.

Santa Barbara: Hemphill s.n. UC#172325!.

San Clemente: Blakley 5255 RSA!; Raven 17958 RSA!; Raven 17627 RSA!; SBBG.

Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *suffruticosa* (Wats.) Raven

San Nicolas: Trask s.n. in Apr. 1901 LAM!; Raven & Thompson 20761 LA!, RSA!; SBM.

Camissonia guadalupensis (Wats.) Raven ssp. *clementina* (Raven) Raven

San Clemente: Thorne 35991 RSA!; Raven 17125 RSA!, DS!; Raven 186760 RSA!; SBBG.

Camissonia guadalupensis (Wats.) Raven ssp. *guadalupensis*

Guadalupe: Moran & Ernst 6737 DS!.

Camissonia hirtella (Greene) Raven

Santa Cruz: Clokey 5010 POM!.

Camissonia ignota (Jeps.) Raven

Santa Cruz: Hoffmann s.n. Mar. 24, 1929 POM!.

Camissonia intermedia Raven

Santa Cruz: Moran 764 LAM!; Hoffmann s.n. Mar. 25, 1932 POM!; Raven & Smith 15197 RSA!.

Santa Catalina: Trask s.n. in May 1896 F!; Knopf 428 F!; Raven 18171 RSA!.

Camissonia micrantha (Hornem. ex Spreng.) Raven

San Miguel: SBBG; SBM.

Santa Rosa: Munz & Crow 11694 LA!, POM!; Hoffmann s.n. Apr. 16, 1929 POM!; Thorne et al. 49037 RSA!; SBBG; SBM.

Santa Cruz: Jones s.n. Mar. 25, 1929 POM!; Thorne & Everett 36819 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S4315 LAM!; Thorne 36501 RSA!; SBM.

San Clemente: Piehl 62387 RSA!; SBBG.

Camissonia robusta Raven

San Miguel: SBBG.

Santa Cruz: SBBG.

Santa Catalina: Trask s.n. in May 1897 LAM!; Dunkle 1937 AHFH!; Raven 17811 RSA!.

San Clemente: Dunkle 7298 LAM!, AHFH!, RSA!; Munz 6743 POM!; SBBG.

Guadalupe: Copp 151 RSA!; Moran 2891 RSA!; Moran 5661 RSA!.

Camissonia strigulosa (F. & M.) Raven

Santa Rosa: Moran 801 LAM!; Munz & Hoffman 11742 POM!; SBBG; SBM.

Clarkia davyi (Jeps.) Lewis & Lewis

Santa Rosa: Raven 15003 LA!, RSA!; Raven 15007 RSA!; Raven 14955 RSA!; LA; SBBG.

Clarkia epilobioides (Nutt.) Nels. & Macbr.

Santa Rosa: Blakley & Smith 3089 RSA!; Thorne et al. 48773 RSA!; SBBG; SBM.

Santa Cruz: Elmore s.n. Apr. 18, 1936 AHFH!, RSA!, USC!; Munz & Crow 11861 POM!; Raven & Smith 15151 RSA!; SBBG.

Santa Catalina: Haefs 201 MO!; Fosberg 8117 LAM!, POM!; Smith 5965 US!; LA; NY; RSA-POM; SBBG.

San Clemente: Trask 172 US!; Trask s.n. in May 1895 US!; Raven 17710 RSA!; SBBG.

Clarkia prostrata Lewis & Lewis

Santa Rosa: Youngberg s.n. May 29, 1938 POM!; Hoffmann 692 POM!; Hoffmann s.n. Jul. 7, 1930 POM!.

Clarkia purpurea (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis

Santa Rosa: SBM.

Santa Cruz: Sauer et al. 5498 RSA!.

Santa Catalina: Fosberg S4696 LAM!; POM!; Fosberg S4868 LAM!; Haefs & Propst 220 MO!; RSA-POM; SBBG.

Clarkia unguiculata Lindl.

Santa Cruz: SBM.

Santa Catalina: Dunkle 2464 AHFH!.

Epilobium canum (Greene) Raven ssp. *canum*

Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Greene s.n. in Jul.–Aug. 1886 MO!; Hoffmann s.n. Sep. 20, 1930 LA!; RSA-POM; SBBG; SBM.

Anacapa: RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S5419 MO!; Ewan 10804 LA!, MO!; Nuttall 660 MO!; RSA-POM; SBBG.

San Clemente: Trask s.n. in Dec. 1896 MO!; Moran et al. 22691 MO!; RSA-POM; SBBG.

Epilobium ciliatum Raf. ssp. *ciliatum*
San Miguel: Dunkle 8419 LAM!, RSA!.
Santa Cruz: Hoffmann s.n. Sep. 21, 1931 LAM!; Hoffmann s.n. Jul. 1, 1930 POM!; Balls & Blakley 23722 RSA!; SBBG; SBM.
Santa Catalina: Fosberg S5370 LAM!; Trask s.n. in Aug. 1900 LAM!; Thorne 36634 RSA!; SBBG; SBM.
Epilobium foliosum (T. & G.) Suksd.
Guadalupe: Palmer 31 MO!.
Gaura sinuata Nutt. ex Ser. in DC.
Santa Catalina: Thorne 36478 RSA!; SBBG.
Ludwigia peploides (HBK.) Raven ssp. *peploides*
Santa Cruz: Dunkle 8569 LAM!, AHFH!; Balls & Blakley 23680 RSA!.
Oenothera elata HBK. ssp. *hirsutissima* (Gray ex Wats.) Dietrich
Santa Cruz: Stanton s.n. in Nov. 1967 RSA!; Daily 171 SCIR!.
Orobanchaceae
Orobanche bulbosa G. Beck
Santa Rosa: Hoffmann 155 POM!; Thorne et al. 48963 RSA!; Hoffmann s.n. May 9, 1932 POM!; SBM.
Santa Cruz: Hoffmann s.n. Jun. 15, 1930 POM!; SBBG; SBM.
Santa Catalina: Fosberg S4687 LAM!, POM!; Trask s.n. in Apr. 1900 US!; Dunkle 2449 AHFH!; SBBG.
Orobanche californica Cham. & Schlecht. ssp. *grandis* Heckard
Santa Rosa: Hoffmann s.n. Jun. 11, 1930 SBM.
Orobanche fasciculata Nutt.
Santa Rosa: Hoffmann s.n. May 8, 1932 POM!; SBM.
Santa Cruz: Daily 376 SCIR!.
Santa Catalina: Pendleton 1353 POM!; Thorne 36235 RSA!; SBBG.
Orobanche parishii (Jeps.) Heckard ssp. *brachyloba* Heckard
San Miguel: SBBG.
Santa Rosa: Hoffmann s.n. Aug. 9, 1931 SBM!.
Santa Cruz: Daily 530 SCIR!; SBBG.
San Nicolas: Raven & Thompson 20794 RSA!; Wier & Beauchamp s.n. Jun. 31, 1978 RSA!; Wier & Beauchamp s.n. Jul. 1, 1978 RSA!; SBBG.
Santa Catalina: RSA-POM; SBBG.
Orobanche uniflora L. ssp. *occidentalis* (Greene) Abrams ex Ferris
Santa Cruz: Pierson 11088 RSA!; Harvey s.n. Apr. 20, 1936 POM#223655!; SBM.
Oxalidaceae
Oxalis albicans HBK. ssp. *californica* (Abrams) Eiten
Santa Cruz: Dunkle 8544 LAM!, AHFH!; Fosberg 7672 LAM!; Thorne & Everett 36841 RSA!; SBBG; SBM.
Santa Catalina: Fosberg S4586 LAM!, POM!; Trask s.n. in Apr. 1902 LAM!; Dunkle 2866 AHFH!; LA.
Oxalis albicans HBK. ssp. *pilosa* (Nutt.) Eiten
Santa Cruz: SBM.
Oxalis corniculata L.
Santa Cruz: SBM.
Santa Catalina: Thorne 36428 RSA!; Thorne 36331 RSA!; SBBG.
Oxalis pes-caprae L.
Santa Catalina: Fosberg S4523 LAM!; Thorne & Everett 34986 RSA!; SBBG.
San Clemente: Elmore 423 AHFH!.
Papaveraceae
Dendromecon rigida Benth. ssp. *harfordii* (Kell.) Raven
Santa Rosa: Yates s.n. LAM#19889!; Dunkle 8497 LAM!, AHFH!; Harford s.n. in 1873 CAS#2405!; LA; RSA-POM; SBBG.
Santa Cruz: Clokey 4942 LAM!; Fosberg 7605 LAM!, LA!, POM!; Greene s.n. in Jul.–Aug. 1886 CAS#2403!, DS#97726!; SBBG.
Dendromecon rigida Benth. ssp. *rhamnoides* (Greene) Thorne
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4580 LAM!; Moran 613 LAM!; LA; RSA-POM.
San Clemente: Trask s.n. in Jun. 1903 US!.
Eschscholzia californica Cham. var. *californica*
San Miguel: Dunkle 8385 LAM!, AHFH!, NY!; Moran 3447 POM!; Munz & Norris 11772 POM!.
Santa Rosa: Dunkle 8456 LAM!; Elmore 187 AHFH!; Thorne et al. 48873 RSA!; LA; SBM.
Santa Cruz: Fosberg 7640 LAM!; Dunkle 8361 LAM!, AHFH!, RSA!; Greene s.n. in Jul.–Aug. 1886 CAS#299!, US!; LA; SBBG; SBM.
Santa Catalina: Brandegee s.n. May 17–25, 1916 LAM!; Moran 612 LAM!; Fosberg S4954 LAM!; SBBG.
Guadalupe: Greene s.n. Apr. 23, 1885 NY!.
Eschscholzia californica Cham. var. *maritima* (Greene) Jeps.
San Miguel: Yates s.n. LAM#19879!; Elmore 320 AHFH!; Elmore 327 AHFH!; RSA-POM; SBBG.
Santa Rosa: SBBG; SBM.
Santa Cruz: Hoffmann s.n. Sep. 21, 1930 POM!; SBBG; SBM.
Eschscholzia californica Cham. var. *peninsularis* (Greene) Munz
Santa Cruz: Pierson 11066 RSA!; Wolf 2863 RSA!; Wolf 2792 RSA!.
Santa Catalina: Fosberg S4650 LAM!; Millspaugh 4854 F!; Thorne & Everett 34501 RSA!.
Eschscholzia elegans Greene
Guadalupe: Palmer 3 (in part) NY!, (in part) US!, CM!; Greene s.n. Apr. 23, 1885 CAS#288!, NY!; Ernst 273 US!.
Eschscholzia frutescens (Greene) J.T. Howell
Guadalupe: Franceschi s.n. in Jan. 1893 CAS#2654!.
Eschscholzia palmeri Rose
Guadalupe: Rempel 759-37 LAM!; Palmer 889 NY!, US!; Howell 8176 NY!, POM!, US!; Ernst 272 US!.
Eschscholzia ramosa (Greene) Greene
Santa Rosa: SBM.
Santa Cruz: SBBG; SBM.
Santa Barbara: RSA-POM; SBBG.
Santa Catalina: Brandegee, K. s.n. May 17–25, 1916 LAM!; Fosberg S4598 LAM!; Trask 307 NY!, US!; RSA-POM; SBBG.
San Clemente: Dunkle 7213 LAM!, AHFH!; Dunkle 7301 LAM!, AHFH!; Trask 263 NY!, US!; RSA-POM; SBBG.

Guadalupe: Anthony 231 LAM!, POM!; Rose 16032 NY!; Franceschi 20 SBM!; CAS; LA; RSA-POM; US.
Meconella denticulata Greene
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; RSA-POM; SBBG; SBM.
Papaver californicum Gray
Santa Cruz: RSA-POM; SBBG; SBM.
Papaver somniferum L.
Santa Catalina: RSA-POM.
Platystemon californicus Benth.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: Brandegee s.n. in Jun. 1888 CAS#977!; RSA-POM; SBBG; SBM.
Santa Cruz: Moran 765 LAM!; Elmore 458 AHFH!; Fosberg 7555 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Dunkle 8332 LAM!; Kanakoff s.n. LAM!; Trask 26 LAM!; LA; RSA-POM; SBBG; SBM.
Santa Barbara: Dunkle 7400 LAM!; Trask 11 CAS!; Trask s.n. in May 1901 CAS#969!; RSA-POM; SBBG.
Santa Catalina: Brandegee, T.S. s.n. in May 1890 UC!; Trask s.n. in Mar. 1897 CAS#966!.
Guadalupe: Brandegee, T.S. s.n. Mar. 20, 1897 UC!.
Romneya coulteri Harv.
Santa Catalina: RSA-POM; SBBG.
Stylomecon heterophylla (Benth.) G. Taylor
San Miguel: SBBG; SBM.
Santa Rosa: Munz & Crow 11652 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7620 LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Barbara: RSA-POM; SBBG; SBM.
Santa Catalina: RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Pittosporaceae
Sollya heterophylla Lindl.
Santa Catalina: Nuttall 801 F!.
Plantaginaceae
Plantago bigelovii Gray ssp. *californica* (Greene) Bassett
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Plantago coronopus L.
Santa Catalina: Trask 308 US!; Johnson 1758 US!; Fosberg 4671 LAM!, US!, MO!; Davidson, A. s.n. Jun. 26, 1891 LAM!; RSA-POM; SBBG.
Plantago erecta Morris ssp. *erecta*
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7683 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!, US!; Fosberg S4548 LAM!, NY!; Millspaugh 4910 F!; LA; RSA-POM; SBBG.
San Clemente: Dunkle 7324 LAM!, AHFH!; RSA-POM; SBBG.
Plantago hirtella HBK. ssp. *galeottiana* (Dcne.) Thorne
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Plantago lanceolata L.
Santa Cruz: Daily 316 SCIR!.
San Clemente: RSA-POM.
Plantago major L.
Santa Cruz: Dunkle 8590 LAM!, AHFH!; RSA-POM; SBBG.
Santa Catalina: RSA-POM; SBBG.
Plantago maritima L. var. *californica* (Fern.) Pilg.
Santa Rosa: RSA-POM; SBM.
Plantago ovata Forsk.
Santa Rosa: Munz & Crow 11708 LA!; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Trask s.n. in Apr. 1897 CAS#955!; Dunkle 8355 LAM!, AHFH!; Kanakoff s.n. Apr. 12, 1940 LAM!; RSA-POM; SBBG.
Santa Barbara: Dunkle 7430 LAM!, AHFH!; Dunkle 8702 AHFH!; RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM#28733!; Trask s.n. in Mar. 1901 LAM#28734!; Fosberg S4777 LAM!; RSA-POM.
San Clemente: Dunkle 7269 LAM!, AHFH!; Dunkle 7270 LAM!, AHFH!; RSA-POM; SBBG.
Guadalupe: Rempel 758-37 LAM!; Palmer 54 CM!; Palmer 878 ND-G!.
Platanaceae
Platanus racemosa Nutt.
Santa Cruz: RSA-POM; SBBG.
Santa Catalina: RSA-POM.
Plumbaginaceae
Armeria maritima (Mill.) Willd. ssp. *californica* (Boiss.) G.H.M. Lawr.
Santa Rosa: RSA-POM; SBBG; SBM.
Limonium perezii (Stapf.) F.T. Hubb. ex Bailey
Santa Catalina: RSA-POM; SBBG.
San Clemente: SBBG.
Limonium sinuatum (L.) Mill.
Santa Catalina: RSA-POM.
Polemoniaceae
Allophyllum gilioides (Benth.) A. Grant & V. Grant
Guadalupe: Greene s.n. Apr. 26, 1885 UC!; Palmer 77 MO!, NY!; Greene s.n. Apr. 24, 1885 DS!.
Allophyllum glutinosum (Benth.) A. Grant & V. Grant
Santa Catalina: Fosberg S5413 LAM!, NY!; POM!, SBM!, US!; Dunkle 2442 AHFH!; Trask s.n. in Mar. 1897 US!; RSA-POM; SBBG.
Eriastrum filifolium (Nutt.) Woot. & Standl.
Santa Cruz: Greene s.n. in Jul.–Aug. 1886 ND-G#041376!.
Santa Catalina: Trask s.n. in May 1901 LAM!; Thorne 36527 RSA!; SBBG.
San Clemente: Raven 17723 RSA!.
Gilia angelensis V. Grant
Santa Cruz: Fosberg 7674 LAM!, POM!; Elmore 440 LAM!; Raven & Smith 15199 RSA!; CAS; SBBG; SBM.
Anacapa: Blakley 5008 CAS!; SBBG.
Santa Catalina: Moran 697 LAM!, DS!, RSA!; Dunkle 2070 AHFH!; Grant 18438 RSA!; CAS; LA; NY; SBBG; SBM.
San Clemente: SBBG.

Gilia capitata Sims ssp. *abrotanifolia* (Nutt. ex Greene) V. Grant
  Santa Cruz: Fosberg 7700 LAM!, POM!; SBM.
  Santa Catalina: Thorne 36195 RSA!; SBBG.
Gilia clivorum (Jeps.) V. Grant
  San Miguel: Munz & Norris 11763 POM!; SBBG; SBM.
  Santa Rosa: Moran 818 LAM!, RSA!; Munz & Crow 11696 POM!; Raven, Blakley & Ornduff 14907 RSA!; CAS; LA; SBBG; SBM.
  Santa Cruz: Fosberg 7522 LAM!; Breedlove 2818 RSA!; Raven & Smith 15128 RSA!; CAS; SBBG; SBM.
  Anacapa: Moran 722 LAM!; Blakley 4944 CAS!; Blakley 5013 CAS!; SBBG; SBM.
  Santa Catalina: Fosberg S4538 LAM!.
Gilia nevinii Gray
  Santa Rosa: SBBG.
  Santa Cruz: Brandegee s.n. in Apr. 1888 CAS!; SBBG.
  Anacapa: Blakley 4950 CAS!; Blakley 4975 CAS!; SBBG.
  San Nicolas: Trask 53 MO!; Trask 52 NY!; Trask s.n. in Apr. 1897 CAS!.
  Santa Barbara: Dunkle 7429 LAM!; Thorne 37503 RSA!; Moran 830 DS!; SBBG.
  Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!; Fosberg S4496 LAM!; Trask s.n. in Apr. 1900 CAS#473!; RSA-POM; SBBG.
  San Clemente: Dunkle 7320 LAM!; Trask 248 NY!, US!; Raven 17213 RSA!; DS; LA; SBBG.
  Guadalupe: Palmer 78 NY!; Greene s.n. Apr. 25, 1885 CAS#36173!; Moran 17289 RSA!; GH.
Gilia tenuiflora Benth. ssp. *hoffmannii* (Eastw.) A. Grant & V. Grant
  Santa Rosa: Moran 819 LAM!, RSA!; Moran 793 LAM!, RSA!; Munz & Hoffmann 11730 POM!; SBM.
Linanthus androsaceus (Benth.) Greene ssp. *luteus* (Benth.) Mason
  Santa Cruz: SBBG.
Linanthus bicolor (Nutt.) Greene ssp. *bicolor*
  Santa Rosa: Thorne et al. 48860 RSA!.
  Santa Catalina: Dunkle 1795 AHFH!, POM!; Trask s.n. in Mar. 1901 LAM!, NY!; Dunkle 2106 AHFH!.
  San Clemente: Dunkle 7262 LAM!, AHFH!; Munz 6622 POM!; Raven 17226 RSA!; SBBG.
Linanthus dianthiflorus (Benth.) Greene ssp. *dianthiflorus*
  Santa Cruz: Blakley 3310 RSA!; Wolf 2790 RSA!; SBBG; SBM.
  Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Moran 695 LAM!; Dunkle 1740 AHFH!, POM!; SBBG.
Linanthus pygmaeus (Brand) J.T. Howell ssp. *pygmaeus*
  San Clemente: Thorne 36077 RSA!; Raven 17692 RSA!; SBBG.
  Guadalupe: Moran 6644 RSA!; Moran 17388 RSA!; Carlquist 464 RSA!.
Navarretia atractyloides (Benth.) H. & A.
  Santa Rosa: Dunkle 8507 LAM!; Epling & Erickson s.n. Aug. 8, 1937 LA!; SBM.
  Santa Cruz: Dunkle 8559 AHFH!; SBBG; SBM.
  Santa Catalina: Davidson, A. s.n. Jun. 26, 1891 LAM!; Pendleton 1392 POM!; Nuttall s.n. UC!; SBBG.
  San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!.
Navarretia hamata Greene var. *foliacea* (Greene) Thorne
  Santa Catalina: Dunkle 1920 AHFH!, POM!; Fosberg S4674 LAM!; Wolf 3547 LAM!, RSA!; SBM.
Navarretia hamata Greene var. *hamata*
  Santa Cruz: RSA-POM; SBBG.
  Santa Catalina: RSA-POM; SBBG.
  San Clemente: Raven 17724 RSA!; Blakley 3311 RSA!; Clokey 5032 POM!; SBBG.
Polygalaceae
Polygala californica Nutt.
  Santa Cruz: Hoffmann 188 POM!; Raven & Smith 15224 RSA!; SBBG.
Polygonaceae
Chorizanthe coriaceae Goodm.
  Santa Rosa: Munz & Hoffman 11734 POM!; SBM.
  Santa Cruz: SBBG.
  Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!; Thorne & Everett 34600 RSA!.
Chorizanthe staticoides Benth. ssp. *staticoides*
  Santa Cruz: Clokey 4907 LAM!, POM!; Balls & Blakley 23742 RSA!.
  Santa Catalina: Fosberg S4917 LAM!, POM!; Trask s.n. in May 1901 NY!; Trask s.n. in Jun. 1897 US!.
Chorizanthe wheeleri Wats.
  Santa Rosa: Munz & Crow 11679 POM!; Raven, Blakley & Ornduff 15010 RSA!; SBM.
  Santa Cruz: Hoffmann s.n. Apr. 12, 1931 CAS!, LA!, POM!; Munz & Norris 11847 POM!; Raven & Smith 15182 RSA!.
Eriogonum arborescens Greene
  Santa Rosa: Dunkle 8449 LAM!, AHFH!; Dunn, N. s.n. May 15, 1932 LA!; Thorne et al. 49005 RSA!; SBBG.
  Santa Cruz: Yates s.n. in 1893 LAM!; Hutchinson s.n. LAM!; Clokey 4910 LAM!, POM!; LA; RSA-POM; SBBG; SBM.
  Anacapa: Dunkle 7618 LAM!, AHFH!, RSA!; Howell 3791 USC!; Bond 321 SBM!.
Eriogonum cinereum Benth.
  Santa Rosa: RSA-POM.
Eriogonum fasciculatum Benth. ssp. *fasciculatum*
  Santa Catalina: Thorne, Propst & Haefs 45110 RSA!.
Eriogonum giganteum Wats. ssp. *compactum* (Dunkle) Munz
  Santa Barbara: Dunkle 8103 LAM!, AHFH!; Bryan, Dr. & Mrs. s.n. LAM!; Elmore 306 AHFH!; RSA-POM; SBBG; SBM.
Eriogonum giganteum Wats. ssp. *formosum* (K. Bdg.) Raven
  San Clemente: Moran 6843 LA!; Brandegee s.n. Aug. 25, 1894 DS#88608!, DS#88624!; RSA-POM; SBBG.
Eriogonum giganteum Wats. ssp. *giganteum*
  Santa Cruz: RSA-POM; SBBG (probably introduced here).
  Santa Catalina: Davidson, A. s.n. Jun. 26, 1891 LAM!; Grant s.n. Sep. 1, 1906 LAM!; Fosberg S5358 LAM!, SBM!; RSA-POM; SBBG.
Eriogonum grande Greene var. *dunklei* Reveal
  San Miguel: Dunkle 8369 LAM!, AHFH!, DS!; Elmore 325 AHFH!; Elmore 334 AHFH!.

Eriogonum grande Greene ssp. *grande*
Santa Rosa: Hoffmann 133 SBM!.
Santa Cruz: Clokey 4908 LAM!; Greene s.n. in Jul.–Aug. 1886 CAS#336!; Dunkle 8594 LAM!, AHFH!; RSA-POM.
Anacapa: Hoffmann 93 SBM; Dunkle 7612 LAM!, AHFH!; Elmore 232 AHFH!; RSA-POM; SBBG; SBM.
San Nicolas: SBBG.
Santa Catalina: Fosberg 7150 LAM!; Dunkle 2030 LAM!; Davidson, A. s.n. LAM#20543!; RSA-POM.
San Clemente: Dunkle 7290 LAM!, AHFH!; House & Grumbles s.n. Aug. 5–13, 1930 USC!; Johnstone s.n. Sep. 5, 1926 USC!; RSA-POM; SBBG.
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz
San Miguel: Greene s.n. in Sep. 1886 CAS#88643!; RSA-POM; SBBG; SBM.
Santa Rosa: Dunkle 8442 LAM!, AHFH!; Dunn, N. s.n. May 24, 1931 LAM!; Hoffmann 92 SBM!; LA; RSA-POM; SBBG.
Santa Cruz: Hoffmann s.n. SBM#629!; RSA-POM; SBBG.
Anacapa: Hoffmann 85 SBM!; Hoffmann 86 SBM!; Yates s.n. SBM#17301!.
Eriogonum grande Greene ssp. *timorum* (Reveal) Munz
San Nicolas: Moran 3168 LA!; Foreman 213 LA!; Raven & Thompson 20744 LA!; RSA-POM.
Eriogonum zapatoense Moran
Guadalupe: Moran 18170 LAM!, CAS!, RSA!; Rempel 759-37 LAM!.
Polygonum arenastrum Bor.
Santa Rosa: Hoffmann s.n. Apr. 14, 1929 SBM#6286!; Hoffmann s.n. Jun. 12, 1930 SBM#8754!.
Santa Cruz: Hoffmann s.n. Jun. 14, 1930 SBM#5111!; Hoffmann s.n. Sep. 20, 1930 SBM#10306!.
Santa Catalina: Fosberg S5410 LAM!; SBBG.
San Clemente: SBBG.
Polygonum argyrocoleon Steud. ex Kunze
Santa Cruz: Hobbs 78-116 LA!.
Santa Catalina: Fosberg S4461 LAM!; Fosberg S4565 LAM!; Spalding s.n. Sep. 19, 1925 LAM!; RSA-POM; USC.
San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 LAM!.
Polygonum aviculare L.
Santa Rosa: Dunkle 8453 LAM!; Elmore 213 AHFH!; Hoffmann s.n. Jul. 7, 1930 SBM#10398!.
Santa Cruz: Dunkle 8628 LAM!, AHFH!; Hoffmann s.n. SBM#10306!; RSA-POM.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.
Pterostegia drymarioides F. & M.
San Miguel: Hoffmann s.n. SBM#9225!; RSA-POM.
Santa Rosa: Dunn, N. s.n. May 24, 1931 LA!; Hoffmann s.n. SBM#1411!; Hartwell s.n. SBM#14372!; RSA-POM.
Santa Cruz: Clokey 4904 LAM!; Dunkle 8619 LAM!; Fosberg 7620 LAM!, LA!; RSA-POM.
Anacapa: Hoffmann s.n. SBM#5572!; SBBG.
Santa Barbara: Dunkle 7414 LAM!; Bond s.n. SBM#15095!; RSA-POM.
Santa Catalina: Dunkle 2094 AHFH!; Fosberg S4452 (in part) LAM!; Dunkle 1825 AHFH!; RSA-POM.
San Clemente: Moran 576 LAM!; Dunkle 7207 AHFH!, LAM!.
Guadalupe: Palmer 843 ND-G!; Norris s.n. May 1, 1951 LA!.
Rumex angiocarpus Murbeck
Santa Cruz: Hoffmann s.n. Mar. 20, 1932 SBM#11767!; Daily 615 SCIR!.
Rumex conglomeratus Murr.
Santa Rosa: RSA-POM.
Santa Cruz: Daily 542 SCIR!.
Santa Catalina: Fosberg S5369 LAM!; RSA-POM.
Rumex crispus L.
San Miguel: Dunkle 8394 LAM!, AHFH!; Hoffmann s.n. SBM#5001!; RSA-POM.
Santa Rosa: Hoffmann s.n. SBM#6257!; RSA-POM.
Santa Cruz: Dunkle 8586 LAM!; Hoffmann s.n. SBM#6642!; RSA-POM.
Anacapa: Hoffmann s.n. SBM#1788!; SBBG.
San Nicolas: RSA-POM.
Santa Catalina: Dunkle 1919 AHFH!; Trask s.n. in Mar. 1901 LAM!; Fosberg S4965 LAM!; RSA-POM.
San Clemente: Elmore 416 LAM!, AHFH!; RSA-POM.
Rumex fueginus Phil.
San Miguel: Norris s.n. SBM#9265!; RSA-POM.
Rumex pulcher L.
Santa Cruz: Hoffmann s.n. Apr. 11, 1931 LAM!; Hoffmann s.n. SBM#7226!; SBBG.
Rumex salicifolius Weinm.
San Miguel: SBBG.
Santa Rosa: Dunkle 8475 LAM!; Dunkle 8522 LAM!, AHFH!; Hoffmann s.n. SBM#10063!.
Santa Cruz: Clokey 4903 LAM!; Hoffmann s.n. SBM#5213!; RSA-POM.
San Nicolas: Dunkle 8331 LAM!; Raven & Thompson 20729 LA!; RSA-POM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Dunkle 1986 AHFH!; Fosberg S4708 LAM!, SBM!; RSA-POM.
San Clemente: RSA-POM.
Portulacaceae
Calandrinia breweri Wats.
Santa Rosa: SBM.
Santa Cruz: Fosberg 7461 LAM!; RSA-POM; SBM.
Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr.
San Miguel: SBBG.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Anacapa: SBBG; SBM.
Santa Barbara: SBBG.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Palmer 14 CM!; Norris s.n. May 1, 1951 LA#95561!; Moran 6635 RSA!.
Calandrinia maritima Nutt.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.

Anacapa: SBBG.
Santa Barbara: Dunkle 7406 LAM!; Dunkle 7432 LAM!; RSA-POM; SBBG.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; RSA-POM.
San Clemente: RSA-POM; SBBG.
Guadalupe: Carlquist 467 RSA!.

Claytonia perfoliata Donn var. *parviflora* (Dougl. ex Hook.) Torr.
Santa Cruz: RSA-POM; SBBG.

Claytonia perfoliata Donn var. *perfoliata*
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7586 LAM!, LA!; Clokey 4927 LAM!; Clokey 4925 LAM!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: RSA-POM.
Santa Barbara: Dunkle 7457 LAM!, AHFH!; Dunkle 7407 LAM!, AHFH!; SBBG; SBM.
Santa Catalina: Fosberg S4486 LAM!; Fosberg S4435 LAM!; Dunkle 1797 AHFH!; RSA-POM.
San Clemente: Elmore 418 AHFH!; Dunkle 7224 LAM!; RSA-POM.
Guadalupe: Palmer 846 ND-G!; Norris s.n. May 1, 1951 LA#95563!.

Montia fontana L. ssp. *amporitana* Sennen
Santa Cruz: SBM.

Portulaca oleracea L.
Santa Cruz: Hoffman s.n. in 1930 SBM#4187!.
Santa Catalina: RSA-POM.

Talinum guadalupense Dudley in D.S. Jordan
Guadalupe: Rempel 759-37 LAM!; Thoburn, Greene & Wing s.n. in Jul. 1897 DS#140708!; Moran 2635 RSA!.

Primulaceae

Anagallis arvensis L.
Santa Rosa: Elmore 208 LAM!; Dunkle 8454 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Catalina: Fosberg S4433 LAM!; Nuttall 5 NY!; Trask s.n. in 1898 US!; AHFH; USC.

Anagallis minima (L.) Krause
Santa Rosa: SBM.

Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thompson
Santa Rosa: SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Anacapa: Moran 713 LAM!; SBBG; SBM.
Santa Catalina: Moran 604 LAM!; Dunkle 2054 LAM!, AHFH!; Fosberg S4361 LAM!; SBBG; SBM.
San Clemente: Moran 571 LAM!; SBBG; SBM.
Guadalupe: Palmer 55 CM!; Moran 6464 SD!; Moran 21166 SD!.

Samolus parviflorus Raf.
Santa Cruz: Hoffmann s.n. Sep. 10, 1931 LAM!; SBM.

Ranunculaceae

Clematis lasiantha Nutt. in T. & G.
Santa Cruz: Hoffmann 218 POM!; Wolf 2755 RSA!, US!; Raven & Smith 15275a RSA!; CAS; SBBG; SBM.

Clematis ligusticifolia Nutt. in T. & G.
Santa Rosa: Dunkle 8431 LAM!, AHFH!, RSA!; SBBG; SBM.
Santa Cruz: Clokey 4937 LAM!, POM!; Dunkle 8649 LAM!, AHFH!, RSA!; Williams 99 POM!; CAS; SBBG; SBM.
Santa Catalina: Fosberg S5367 LAM!; Dunkle 1990 AHFH!, POM!; Dunkle 1722 AHFH!; SBBG; SBM.

Delphinium kinkiense Munz
San Clemente: Dunkle 7322 LAM!, RSA!; Beauchamp 290 RSA!.

Delphinium parryi Gray ssp. *parryi*
San Miguel: SBM.
Santa Rosa: Hoffmann 129 POM!; Youngberg s.n. May 29, 1938 POM!; Dunn, A.N. & A.M. Martin s.n. May 15, 1932 LA!; SBBG; SBM.
Santa Cruz: Clokey 4936 LAM!; Hoffmann Apr. 10, 1931 LAM!; Breedlove 2861 RSA!; SBBG; SBM.
Anacapa: Moran 714 LAM!, RSA!; SBBG; SBM.
Santa Catalina: Moxley 593 LAM!; Smith, R.J. s.n. May 24, 1934 LAM!; Moran 667 LAM!; LA; RSA-POM; SBBG.
San Clemente: Raven 17820 RSA!.

Delphinium variegatum T. & G. ssp. *thornei* Munz
San Clemente: Raven 17700 LA!; Thorne 42801 RSA!; SBBG.

Myosurus minimus L. var. *filiformis* Greene
Guadalupe: Greene s.n. Apr. 19, 1885 ND-G#018340!.

Ranunculus californicus Benth. var. *californicus*
San Miguel: Schuyler 29 LAM!; Youngberg s.n. May 28, 1938 POM!; SBBG; SBM.
Santa Rosa: Moran 817 LAM!; Dunkle 8488 AHFH!; Thorne et al. 48995 RSA!; LA; SBBG; SBM.
Santa Cruz: Moran 751 LAM!; Fosberg 7690 LAM!; Clokey 5184 NY!, RSA!; LA; SBBG; SBM.

Ranunculus californicus Benth. var. *cuneatus* Greene
San Miguel: Hoffmann s.n. Apr. 19, 1932 POM!; Munz & Norris 11880 POM!; SBM.
Santa Cruz: Wolf 2798 RSA!; SBM.

Ranunculus hebecarpus H. & A.
Santa Catalina: Fosberg S4348 LAM!, POM!; Detmers s.n. Apr. 13, 1929 USC!; SBM.
Guadalupe: Moran 6610 RSA!; Carlquist 443 RSA!.

Resedaceae

Oligomeris linifolia (Vah.) Macbr.
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: SBM.
Anacapa: SBBG.
San Nicolas: Trask s.n. in Apr. 1900 LAM!; Dunkle 8318 LAM!, AHFH!; Raven & Thompson 20741 LA!; RSA-POM; SBBG.
Santa Barbara: Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; RSA-POM; SBBG.
Santa Catalina: Davidson, A. s.n. Jun. 26, 189- LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Guadalupe: Moran 5955 LA!, RSA!; Carlquist 471 RSA!; Palmer 10 CM!.

Reseda odorata L.

Santa Catalina: RSA-POM.

Rhamnaceae

Ceanothus arboreus Greene

Santa Rosa: Munz & Crow 11611 LA!; RSA-POM; SBM.

Santa Cruz: Fosberg 7577 LAM!; Dunkle 8658 LAM!; Moran 747 LAM!; LA; CAS; RSA-POM; SBBG; SBM.

Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Davidson, A. s.n. LAM!; Grant & Wheeler s.n. Apr. 21–26, 1904 LAM!; LA; RSA-POM; SBBG; SBM.

Ceanothus crassifolius Torr.

Guadalupe: Franceschi s.n. UC!; Palmer 22 MO!, NY!.

Ceanothus megacarpus Nutt. ssp. *insularis* (Eastw.) Raven

Santa Rosa: SBBG.

Santa Cruz: Dunkle 8650 LAM!; Fosberg 7559 LAM!; Clokey 5001 DS!, NY!; LA; RSA-POM; SBBG; SBM.

Anacapa: Dunkle 7665 LAM!, AHFH!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4920 LAM!; Trask s.n. in Mar. 1901 NY!; Millspaugh 4590 F!; CAS; RSA-POM; SBBG.

San Clemente: Trask 198 NY!; Blakley 5197 DS!; RSA-POM; SBBG.

Ceanothus megacarpus Nutt. ssp. *megacarpus*

Santa Cruz: SBBG.

Santa Catalina: Dunkle 2038 LAM!; Dunkle 2059 LAM!; Lister & Powell s.n. Apr. 5, 1928 USC!; CAS; DS; RSA-POM; SBBG.

San Clemente: Murbarger 165 UC!.

Rhamnus californica Esch. ssp. *californica*

Santa Cruz: Hoffmann 669 SBM!; RSA-POM.

Rhamnus pirifolia Greene

Santa Rosa: RSA-POM; SBM.

Santa Cruz: Hoffmann s.n. in Jun. 1930 LAM!; Eastwood 6434 GH!; Clokey 4997 DS!, NY!; CAS; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4238 LAM!, NY!; Grant s.n. LAM!; Sargent s.n. Sep. 16, 1874 GH!; AHFH; DS; LA; RSA-POM; SBBG; SBM.

San Clemente: Trask 109 NY!; Moran, Beauchamp & Oberbauer 22682 CAS!; RSA-POM; SBBG.

Guadalupe: Moran 13803 LAM!; Palmer 21 NY!; Moran 12036 RSA!.

Rosaceae

Adenostoma fasciculatum H. & A. var. *fasciculatum*

Santa Rosa: Dunkle 8496 LAM!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Dunkle 8609 LAM!, AHFH!; Dunkle 8657 LAM!, AHFH!; Fausett 20 LA!; RSA-POM; SBBG; SBM.

Santa Catalina: deForest s.n. May 19, 1934 LAM!; Fosberg S4775 LAM!; Fosberg S4562 LAM!; RSA-POM; SBBG.

San Clemente: Dunkle 7347 LAM!, AHFH!; RSA-POM; SBBG.

Alchemilla occidentalis Nutt.

Santa Rosa: RSA-POM; SBBG; SBM.

Santa Cruz: Fosberg 7590 LAM!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4592 LAM!; Fosberg S4341 LAM!; RSA-POM; SBBG.

San Clemente: RSA-POM.

Guadalupe: Palmer 29 CM!; Wiggins & Ernst 34 DS!; Moran 2913 DS!.

Cercocarpus betuloides Nutt. ex T. & G. ssp. *betuloides*

Santa Cruz: Fosberg 7514 LAM!, LA!; Clokey 4957 LA!; SBM.

Santa Catalina: Fosberg S4798 LAM!; Dunkle 1711 AHFH!.

Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C. K. Schneid.) Thorne

Santa Rosa: RSA-POM.

Santa Cruz: Hoffmann 185 LAM!; Yates s.n. in Aug. 1893 LAM!; Fosberg 7627 LAM!, LA!; RSA-POM; SBBG; SBM.

Santa Catalina: Blakley 5478 LAM!; Moran 703 LAM!; Dunkle 2057 LAM!, AHFH!; LA; RSA-POM; SBBG.

Cercocarpus traskiae Eastw.

Santa Catalina: Trask s.n. in Mar. 1897 CAS#141!; Trask s.n. in Apr. 1903 LAM!; Moran 678 LAM!; LA; RSA-POM; SBBG.

Heteromeles arbutifolia (Ait.) M. Roem.

San Miguel: SBBG.

Santa Rosa: Dunkle 8486 LAM!, AHFH!; Elmore 210 AHFH!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Dunkle 8535 LAM!, AHFH!; Elmore 269 AHFH!; Eastwood 6380 MO!; LA; RSA-POM; SBBG; SBM.

Anacapa: Dunkle 7630 LAM!, AHFH!; Johnstone s.n. USC!; RSA-POM; SBBG; SBM.

Santa Catalina: Templeton 11397 LAM!; Fosberg S4445 LAM!; Doushel s.n. Jul. 23, 1915 MO!; LA; RSA-POM; SBBG; SBM.

San Clemente: Dunkle 7337 AHFH!; Elmore 421 AHFH!; DeBuhr & Wallace 701 LAM!; RSA-POM; SBBG; USC.

Guadalupe: Newcomb 184 DS!; Wiggins & Ernst 202 DS!.

Holodiscus discolor (Pursh) Maxim. var. *discolor*

Santa Cruz: Hoffmann 9 POM!; SBBG.

Santa Catalina: Fosberg S5436 LAM!, POM!; Thorne 36905 RSA!; SBBG.

Lyonothamnus floribundus Gray ssp. *asplenifolius* (Greene) Raven

Santa Rosa: Munz & Voss 11569 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Yates s.n. in Aug. 1893 LAM!; Fosberg 7655 LAM!; Dunkle 8611 LAM!; LA; RSA-POM; SBBG; SBM.

San Clemente: Dunkle 7316 LAM!, AHFH!; DeBuhr & Wallace 712 LAM!; RSA-POM; SBBG.

Lyonothamnus floribundus Gray ssp. *floribundus*

Santa Catalina: Trask s.n. in Jun. 1897 LAM!; Fosberg S4686 LAM!; Moran 652 LAM!; LA; RSA-POM; SBBG.

Potentilla egedii Wormsk. var. *grandis* (Rydb.) J.T. Howell

San Miguel: RSA-POM.

Santa Cruz: RSA-POM.

Potentilla glandulosa Lindl. ssp. *glandulosa*

Santa Catalina: RSA-POM.

Prunus lyonii (Eastw.) Sarg.
Santa Rosa: Dunkle 8510 LAM!, AHFH!; Dunn 1326 LA!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Moran 754 LAM!; Dunkle 8556 LAM!, AHFH!; Elmore 271 AHFH!; LA; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7631 LAM!, AHFH!; Moran 732 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Davidson, A. s.n. LAM!; Fosberg S4488 LAM!; Dunkle 1756 AHFH!; LA; RSA-POM; SBBG; SBM.
San Clemente: DeBuhr & Wallace 697 LAM!; Dunkle 7343 LAM!, AHFH!; Dunkle 7243 AHFH!; RSA-POM; SBBG.
Prunus persica (L.) Batsch
Santa Catalina: RSA-POM.
Rosa californica Cham. & Schlecht.
Santa Rosa: Dunkle 8434 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8647 LAM!, AHFH!; Elmore 447 AHFH!; Hoffmann s.n. Jul. 1, 1930 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Davidson, A. s.n. in Jun. 1892 LAM!; Fosberg S4743 LAM!; Dunkle 1946 AHFH!; RSA-POM.
Rubus procerus P.J. Muell.
Santa Catalina: RSA-POM.
Rubus ursinus Cham. & Schlecht.
San Miguel: SBM.
Santa Rosa: Dunkle 8448 AHFH!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4740 LAM!; Davidson, A. s.n. in Jun. 1891 LAM!; Moran 685 LAM!; RSA-POM; SBBG.
Rubiaceae
Galium angulosum Gray
Guadalupe: Palmer 36 MO!, CM!; Moran 18149 MO!; Carlquist 453 RSA!.
Galium angustifolium Nutt. ex T. & G. ssp. *angustifolium*
Santa Catalina: Fosberg S4870 LAM!; Trask s.n. in May 1900 LAM!; Hasse 4135 NY!; LA; RSA-POM; SBBG; SBM.
Galium angustifolium Nutt. ex T. & G. ssp. *foliosum* (Hilend & Howell) Dempst. & Steb.
Santa Rosa: Dunkle 8447 LAM!, AHFH!; RSA-POM; SBM.
Santa Cruz: Hoffmann s.n. Sep. 10, 1931 LAM!; Howell 6196 LA!; Greene s.n. in Jul.–Aug. 1886 NY!; RSA-POM; SBBG; SBM.
Anacapa: Johnstone s.n. Jun. 25, 1932 LAM!; Hoffmann s.n. Jun. 16, 1930 LAM!; Dunkle 7615 LAM!, AHFH!; LA; RSA-POM; SBBG; SBM.
Galium aparine L.
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7668 LAM!, LA!; RSA-POM; SBM.
Anacapa: SBBG; SBM.
San Nicolas: RSA-POM; SBBG.
Santa Barbara: Dunkle 7417 LAM!, AHFH!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4613 LAM!; Fosberg S4311 LAM!; Dunkle 2087 AHFH!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7220 LAM!, AHFH!; Moran 581 LAM!; Dunkle 7311 AHFH!; RSA-POM; SBBG.
Guadalupe: Palmer 35 MO!, NY!; Palmer 850 ND-G!.
Galium buxifolium Greene
San Miguel: Hoffmann s.n. Jun. 11, 1930 LAM!, CAS!; RSA-POM; SBBG; SBM.
Santa Rosa: Moran 807 RSA!.
Santa Cruz: Fosberg 7666 LAM!, LA!; Abrams & Wiggins 74 NY!; Yates s.n. SBM#21111!; CAS; RSA-POM; SBBG.
Galium californicum H. & A. ssp. *flaccidum* (Greene) Dempst.
Santa Cruz: Dunkle 8607 LAM!, AHFH!; Clokey 5145 LA!; Hoffmann 252 LA!; RSA-POM; SBBG; SBM.
Galium californicum H. & A. ssp. *miguelense* (Greene) Demp. & Steb.
San Miguel: SBBG; SBM.
Santa Rosa: Smith 8240 NY!; RSA-POM; SBBG; SBM.
Galium catalinense Gray ssp. *acrispum* Dempst.
San Clemente: Trask 191 NY!; Trask 192 NY!; RSA-POM.
Galium catalinense Gray ssp. *catalinense*
Santa Catalina: Davidson, A. s.n. Jun. 20, 1891 LAM!; Grant & Wheeler s.n. Apr. 21–26, 1904 LAM!, NY!; Beauchamp 376 LAM!; RSA-POM; SBBG.
Galium nuttallii Gray ssp. *insulare* Ferris
Santa Rosa: Moran 807 LAM!, CAS!, DS!, NY!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 5148 LA!, NY!; Clokey 5076 NY!; Howell 6362 NY!; RSA-POM; CAS; DS; SBBG; SBM.
Santa Catalina: Moran 606 LAM!, NY!; Moran 700 LAM!, DS!, NY!; Fosberg S4688 LAM!; RSA-POM; SBBG.
Galium porrigens Dempst. var. *porrigens*
Santa Rosa: Blakley 3055 SBBG!; Blakley 3147 SBBG!.
Santa Cruz: Ferren 1879 SCIR!; RSA-POM.
Rutaceae
Ruta chalepensis L.
Santa Cruz: Daily 623 SCIR!.
Santa Catalina: Millspaugh 4647 F!.
Guadalupe: Moran 12019 SD!.
Salicaceae
Populus fremontii Wats. ssp. *fremontii*
Santa Cruz: SBM.
Santa Catalina: Fosberg S4853 LAM!.
Populus trichocarpa T. & G.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7560 LAM!; Hoffmann s.n. Sep. 8, 1931 LAM!; SBBG; SBM.
Santa Catalina: Fosberg S4830 LAM!; Fosberg S4704 LAM!; Dunkle 1804 AHFH!; SBM.
Populux × *parryi* Sarg.
San Nicolas: Raven & Thompson 20728 DS!.
Santa Catalina: RSA-POM.
Salix hindsiana Benth. var. *hindsiana*
Santa Cruz: RSA-POM.
Santa Catalina: Nuttall 343 F!.

Salix laevigata Bebb. var. *laevigata*
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!; Davidson, A. s.n. LAM#9468!; Dunkle 1730 AHFH!; RSA-POM; SBBG.
Salix lasiandra Benth. var. *lasiandra*
Santa Cruz: RSA-POM; SBM.
Salix lasiolepis Benth. var. *lasiolepis*
San Miguel: SBBG.
Santa Rosa: Dunkle 8516 LAM!, AHFH!, NY!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8636 LAM!, AHFH!; Fosberg 7705 LAM!; Fosberg 7629 LAM!; RSA-POM; SBBG; SBM.
San Nicolas: Blakley 4090 SBBG!; Blakley 4163 SBBG!; Raven & Thompson 20733 DS!; RSA-POM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Fosberg S4553 LAM!; Dunkle 2075 AHFH!; LA; RSA-POM; SBBG.
Saururaceae
Anemopsis californica (Nutt.) H. & A.
Santa Cruz: Clokey 4902 LAM!, NY!; Rowntree s.n. Jun. 15, 1930 SBM!; Abrams & Wiggins 116 CAS!, DS!; RSA-POM; SBBG.
San Nicolas: Trask 98 MO!, NY!, US!.
Santa Catalina: Dunkle 1926 AHFH!; Wolf 3587 US!, DS!; RSA-POM; SBBG.
San Clemente: (Raven 1963: Murbarger 143 at UC).
Saxifragaceae
Heuchera maxima Greene
Santa Rosa: Dunkle 8524 LAM!; Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Clokey 4952 LAM!; Dunkle 8618 LAM!; Greene s.n. in Jul.–Aug. 1886 CAS#23479!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7653 LAM!; Moran 717 LAM!; RSA-POM; SBBG; SBM.
Jepsonia malvaefolia (Greene) Small
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7607 LAM!; Kellogg & Harford s.n. in 1874 CAS#631!; RSA-POM; SBM.
San Nicolas: Howell 8210 CAS!.
Santa Catalina: Dunkle 2019 AHFH!; RSA-POM; SBBG.
San Clemente: Dunkle 7258 LAM!, AHFH!; Dunkle 7356 AHFH!; RSA-POM.
Guadalupe: Palmer s.n. in 1885 GH!; Moran 2917 DS!.
Lithophragma affine Gray ssp. *mixtum* R.L. Taylor
Santa Catalina: Dunkle 2124 LAM!, AHFH!; Moran 682 LAM!; Fosberg S4581 LAM!; RSA-POM.
Lithophragma cymbalaria T. & G.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Moran 746 LAM!; Fosberg 7624 LAM!, LA!; Elmore s.n. Apr. 18, 1936 AHFH!; RSA-POM; SBBG; SBM.
Lithophragma maximum Bacig.
San Clemente: Murbarger 118 UC!.
Ribes malvaceum Sm. in Rees var. *malvaceum*
Santa Rosa: SBM.
Santa Cruz: Hoffmann 190 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7670 LAM!; Dunkle 7669 AHFH!; SBBG; SBM.
San Clemente: Dunkle 7338 LAM!; RSA-POM; SBBG.
Ribes menziesii Pursh var. *menziesii*
Santa Cruz: RSA-POM; SBM.
Ribes menziesii Pursh var. *thacherianum* Jeps.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Elmore s.n. Apr. 18, 1936 AHFH!; RSA-POM; SBBG.
Ribes sanguineum Pursh
Guadalupe: Palmer s.n. in 1875 GH!
Ribes viburnifolium Gray
Santa Catalina: Merritt s.n. in Apr. 1894 LAM!; Fosberg S4774 LAM!; Moran 615 LAM!; RSA-POM; SBBG.
Saxifraga californica Greene
Santa Rosa: SBBG.
Santa Cruz: Moran 761 LAM!; Fosberg 7585 LAM!; Plunkett s.n. Apr. 18, 1936 LA!; RSA-POM; SBBG; SBM.
Scrophulariaceae
Antirrhinum kelloggii Greene
Santa Cruz: Fosberg 7678 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Trask s.n. in Mar. 1897 LAM!; RSA-POM.
Antirrhinum kingii Wats. var. *watsoni* (Vasey & Rose) Munz
Guadalupe: Moran 17408 SD!; Moran 17345 SD!.
Antirrhinum multiflorum Penn.
Santa Cruz: SBM.
Antirrhinum nuttallianum Benth. in DC.
San Miguel: SBM.
Santa Rosa: Epling & Erickson s.n. Aug. 8, 1937 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8605 LAM!, AHFH!; Yates s.n. in Aug. 1893 LAM!; Eastwood 6398 LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Catalina: Trask s.n. in Mar. 1900 LAM!; Dunkle 1903 AHFH!; Fosberg S5391 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.
Guadalupe: Moran 6593 RSA!; Carlquist 451 RSA!.
Castilleja affinis H. & A. var. *affinis*
Santa Rosa: Dunkle 8445 LAM!; Dunn, N. s.n. May 24, 1931 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7698 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!; Fosberg 7634 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7661 LAM!, AHFH!, POM!; Moran 742 LAM!, NY!; Elmore 230 AHFH!; LA; SBBG; SBM.
Santa Catalina: Fosberg S4516 LAM!; Templeton 11389 LAM!; Trask s.n. in Mar. 1901 NY!; LA; RSA-POM; SBBG; SBM.
Castilleja foliolosa H. & A.
Santa Catalina: Davidson, A. s.n. Jun. 25, 1891 LAM!; Beauchamp 349 LAM!; Moran 689 LAM!, NY!; LA; RSA-POM; SBBG.
Castilleja fruticosa Moran
Guadalupe: Rempel 759-37 LAM!; Moran 12068 LAM!; Moran 15733 MO!; RSA-POM.
Castilleja grisea Dunkle
San Clemente: Dunkle 7201 LAM!; Trask 183 NY!; Elmore 411 AHFH!; RSA-POM; SBBG.

Castilleja guadalupensis Bdg.
Guadalupe: Palmer 59 MO!, UC!, CM!.

Castilleja hololeuca Greene
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: Moran 812 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Yates s.n. in Aug. 1893 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Moran 715 LAM!; Dunkle 7622 LAM!, AHFH!; Elmore 226 AHFH!; RSA-POM; SBBG; SBM.

Castilleja mollis Penn.
San Miguel: Schuyler 18 LAM!; Elmore 333 AHFH!; Elmore 341 AHFH!.
Santa Rosa: Munz 11678 POM!, SBM!; Dunkle 8489 AHFH!; Elmore 172 AHFH!; LA; RSA-POM.

Collinsia heterophylla Buist ex Grah. var. *heterophylla*
Santa Rosa: SBBG; SBM.
San Clemente: Dunkle 7295 LAM!, AHFH!; Trask 340 NY!; RSA-POM; SBBG.

Diplacus longiflorus Nutt. ssp. *longiflorus*
Santa Rosa: Sweet s.n. Apr. 15, 1935 POM!.
Santa Cruz: Moran 767 LAM!; Greene s.n. in Jul.–Aug. 1886 ND-G#001718!; Clokey 5206 LA!, NY!, US!; RSA-POM; SBBG; SBM.

Diplacus parviflorus Greene
Santa Rosa: Dunkle 8439 LAM!, AHFH!; Moran 811 LAM!; Elmore 185 AHFH!; LA; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8474 LAM!; Fosberg 7533 LAM!; Fosberg 7599 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Moran 718 LAM!; Dunkle 7616 LAM!; Dunkle 7658 LAM!; RSA-POM; SBBG; SBM.
San Clemente: RSA-POM; SBBG.

Diplacus puniceus Nutt.
Santa Catalina: Davidson, A. s.n. Jun. 26, 1891 LAM!; Fosberg S4353 LAM!; Beauchamp 342 LAM!; LA!; RSA-POM; SBBG.

Galvezia speciosa (Nutt.) Gray
Santa Barbara: Cooper s.n. UC#26766!.
Santa Catalina: Trask s.n. Mar. 1901 LAM!; Fosberg S5415 LAM!; Moran 602 LAM!; RSA-POM; SBBG.
San Clemente: House & Grumbles s.n. USC!; Moran 584 LAM!; Munz 6685 LAM!; RSA-POM; SBBG.
Guadalupe: Rempel 759-37 LAM!; Moran 17423 LAM!, RSA!; Carlquist 454 RSA!.

Keckiella cordifolia (Benth.) Straw
Santa Rosa: Dunkle 8432 LAM!, AHFH!; Moran 787 LAM!; RSA-POM; SBBG.
Santa Cruz: Dunkle 8554 AHFH!; Ellison s.n. May 12–15, 1929 LA!; Mower s.n. Aug. 7, 1966 LA!; RSA-POM; SBBG; SBM.
Anacapa: Dunkle 7656 LAM!, AHFH!.
Santa Catalina: Fosberg S4325 LAM!; Dunkle 1968 LAM!; Herley s.n. Apr. 26, 1932 LA!; RSA-POM; SBBG; SBM.
San Clemente: Dunkle 7287 LAM!, AHFH!; RSA-POM; SBBG.

Linaria bipartita Willd.
Santa Catalina: RSA-POM.

Linaria canadensis (L.) Dum.-Cours. var. *texana* (Scheele) Penn.
San Miguel: RSA-POM.
Santa Rosa: Moran 778 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Moran 753 LAM!; Hoffmann s.n. Jun. 15, 1930 LAM!; Fosberg 7652 LAM!, LA!; RSA-POM; SBBG; SBM.
Anacapa: Moran 731 LAM!; SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Moran 695 LAM!; Templeton 11385 LAM!; RSA-POM; SBBG.
San Clemente: Dunkle 7313 LAM!; Dunkle 7210 AHFH!; RSA-POM; SBBG.
Guadalupe: Moran 17286 RSA!.

Mimulus brandegei Penn.
Santa Cruz: SBM.

Mimulus brevipes Benth.
Santa Catalina: Dunlavy s.n. May 4, 1934 LA!.

Mimulus cardinalis Dougl. ex Benth.
Santa Cruz: Dunkle 8646 LAM!; Dunkle 8542 AHFH!; LA; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4910 LAM!; Fosberg S4846 LAM!; Dunkle 1951 AHFH!; LA; RSA-POM; SBBG.

Mimulus floribundus Dougl. ex Lindl. var. *floribundus*
Santa Rosa: SBM.
Santa Catalina: Fosberg 4845 LAM!, NY!; Dunkle 2434 AHFH!; Trask s.n. in Apr. 1896 MO!; RSA-POM.
San Clemente: Trask 341 US!.

Mimulus guttatus Fisch. ex DC. ssp. *guttatus*
Santa Rosa: Dunkle 8435 LAM!, AHFH!; SBBG; SBM.
Santa Cruz: Fosberg 7645 LAM!; Dunkle 8550 LAM!, AHFH!; Fosberg 7606 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Grant & Wheeler s.n. LAM!; Fosberg 8146 LA!; RSA-POM; SBBG.
San Clemente: Pierson 3741 LA!; RSA-POM; SBBG.

Mimulus guttatus Fisch. ex DC. ssp. *littoralis* Penn.
Santa Rosa: RSA-POM.

Mimulus guttatus Fisch. ex DC. ssp. *micranthus* (Heller) Munz
Santa Cruz: Hoffmann s.n. Mar. 28, 1925 SBM#788!; Hoffmann s.n. May 14, 1927 SBM#8640!.

Mimulus latifolius Gray
Guadalupe: Palmer 58 MO!; Greene s.n. Apr. 22, 1885 ND-G!; Palmer 839 US!.

Mimulus nasutus Greene
Santa Cruz: Hoffmann 179 SBM!.

Mimulus traskiae Grant
Santa Catalina: Trask s.n. in Mar. 1901 LAM!.

Orthocarpus attenuatus Gray
Guadalupe: Moran 13821 LAM!, RSA!.

Orthocarpus densiflorus Benth. var. *densiflorus*
San Miguel: RSA-POM; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7650 LAM!, LA!; Fosberg 7693 LAM!; Elmore 459 AHFH!; RSA-POM; SBBG; SBM.
San Nicolas: Trask 61 MO!.

Orthocarpus purpurascens Benth. var. *pallidus* Keck
San Miguel: RSA-POM.
Santa Rosa: RSA-POM.
Santa Cruz: RSA-POM.

Santa Catalina: Fosberg S4453 LAM!; Fosberg S4938 LAM!; Dunkle 1739 AHFH!.

Orthocarpus purpurascens Benth. var. *purpurascens*

San Miguel: Schuyler 154 LAM!; RSA-POM; SBBG; SBM.

Santa Rosa: RSA-POM; SBBG; SBM.

Santa Cruz: RSA-POM; SBBG; SBM.

Santa Catalina: Dunkle 2166 AHFH!; Moran 657 LAM!.

Guadalupe: (Keck 1927: Brandegee in 1897 at UC).

Scrophularia californica Cham. & Schlecht. ssp. *californica*

Santa Rosa: Hoffmann s.n. Apr. 17, 1929 SBM!.

Scrophularia villosa Penn. in Millsp. & Nutt.

Santa Catalina: Trask s.n. in Mar. 1901 NY!; Grant 1186 US!; Fosberg 8133 LA!; RSA-POM; SBBG.

San Clemente: Trask 230 NY!; Raven 17711 LA!; RSA-POM.

Guadalupe: Moran 8390 RSA!, US!; Moran 5970 RSA!.

Verbascum thapsus L.

Santa Cruz: Dunkle 8555 LAM!, AHFH!; RSA-POM; SBBG.

Solanaceae

Datura wrightii Regel

Santa Rosa: SBM.

Santa Cruz: Dunkle 8570 LAM!, AHFH!; RSA-POM; SBBG; SBM.

Santa Catalina: Fosberg S4928 LAM!; RSA-POM; SBBG.

Lycium brevipes Benth. var. *brevipes*

San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!.

Lycium brevipes Benth. var. *hassei* (Greene) C.L. Hitchc.

Santa Catalina: Davidson, A. s.n. Jun. 25, 1891 LAM!; Hasse 4155 NY!; Trask s.n. in Apr. 1896 US!; RSA-POM.

San Clemente: Trask 331 NY!, US!; Trask 332 GH!, NY!, US!.

Lycium californicum Nutt.

Anacapa: SBBG.

San Nicolas: Trask s.n. in Apr. 1897 US!; Kanakoff s.n. Apr. 27, 1940 LAM!; Foreman 123 US!; RSA-POM; SBBG.

Santa Barbara: Trask s.n. in Apr. 1901 LAM!; Elmore 295 AHFH!; RSA-POM; SBBG.

Santa Catalina: Dunkle 2151 AHFH!; Fosberg S4705 LAM!; Fosberg S4882 LAM!; RSA-POM; SBBG.

San Clemente: Trask 27 US!; Dunkle 7328 LAM!, AHFH!; Elmore 397 AHFH!; RSA-POM; SBBG.

Guadalupe: Lindsay 43081 RSA!; Moran 5631 RSA!.

Lycium fremontii Gray

Santa Rosa: SBM.

Guadalupe: Moran & Ernst 6733 RSA!.

Lycium verrucosum Eastw.

San Nicolas: Trask 60 LAM!; Trask s.n. in Apr. 1897 CAS#720!.

Nicotiana attenuata Torr. ex Wats. in King

Guadalupe: Palmer 64 NY!; Greene s.n. Apr. 25, 1885 CAS#859!.

Nicotiana bigelovii (Torr.) Wats. var. *bigelovii*

Santa Catalina: RSA-POM; SBBG.

Nicotiana clevelandii Gray

Santa Cruz: Hoffmann s.n. Jun. 30, 1930 CAS#176935!; RSA-POM; SBBG; SBM.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!.

Nicotiana glauca Grah.

Santa Catalina: Dunkle 1977 AHFH!; Fosberg S4284 LAM!; Fosberg S4577 LAM!; RSA-POM; SBBG.

Guadalupe: Moran 17327 SD!; Wiggins & Ernst 220 DS!; Moran 2838 DS!.

Petunia parviflora Juss.

Santa Rosa: Dunkle 8430 LAM!; Elmore 170 AHFH!; RSA-POM; SBBG; SBM.

Solanum douglasii Dunal in DC.

San Miguel: RSA-POM; SBBG; SBM.

Santa Rosa: Dunkle 8450 LAM!; Elmore 200 AHFH!; Dunn, D. 1304 LA!; RSA-POM; SBBG; SBM.

Santa Cruz: Dunkle 8623 LAM!; AHFH!; Dunkle 8641 AHFH!; Clokey 5201 LA!; RSA-POM; SBBG; SBM.

Santa Catalina: Moran 688 LAM!; Fosberg 4614 LAM!; Elmore 438 AHFH!; RSA-POM; SBBG.

San Clemente: Dunkle 7225 AHFH!; Elmore 420 AHFH!; House & Grumbles s.n. USC!; RSA-POM; SBBG.

Guadalupe: Moran 6602 NY!, RSA!; Palmer 61 NY!; Palmer 6116 RSA!.

Solanum elaeagnifolium Cav.

Santa Cruz: Laughrin 426 SCIR!.

Santa Catalina: Thorne 36693 RSA!; SBBG.

Solanum nodiflorum Jacq.

San Nicolas: Dunkle 8324 LAM!, AHFH!; RSA-POM; SBBG.

San Clemente: RSA-POM.

Guadalupe: Moran 6448 RSA!; Palmer 60 NY!; Palmer 860 NY!.

Solanum sarrachoides Sendt. ex Mart.

Santa Cruz: RSA-POM.

Solanum wallacei (Gray) Parish ssp. *clokeyi* (Munz) Thorne

Santa Rosa: Moran 777 LAM!; Dunn, D. 1305 LA!; Dunn, N. s.n. May 15, 1932 LA!; SBBG; SBM.

Santa Cruz: Moran 745 LAM!; Elmore 467 AHFH!; Yates 80 LAM!; RSA-POM; SBBG; SBM.

Solanum wallacei (Gray) Parish ssp. *wallacei*

Santa Catalina: Grant & Wheeler s.n. Apr. 21–26, 1904 LAM!; Fosberg S4285 LAM!; Moran 687 LAM!; LA; RSA-POM; SBBG.

Guadalupe: Palmer 62 NY!; Franceschi 15 NY!, SBM!; Moran 18143 SD!.

Tamaricaceae

Tamarix tetrandra Pallas

Santa Cruz: Philbrick B7742 SBBG!.

Anacapa: SBBG.

Tropaeolaceae

Tropaeolum majus L.

Santa Catalina: RSA-POM; SBBG.

Urticaceae

Hesperocnide tenella Torr.

Santa Cruz: Hoffman s.n. SBM#21891!; Hoffman s.n. SBM#11168!; RSA-POM; SBBG.

Santa Barbara: RSA-POM; SBBG.

Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!; Fosberg S4347 LAM!; Fosberg S4487 LAM!; RSA-POM.

San Clemente: Trask 188 NY!; RSA-POM; SBBG.

Guadalupe: Palmer 86 NY!.

Parietaria hespera Hinton.

San Miguel: SBBG.

Santa Rosa: Hoffmann s.n. SBM#6276!; RSA-POM.

Santa Cruz: Fosberg 7682 LAM!; Hoffmann s.n. SBM#1026!; Abrams & Wiggins 26 CAS!; RSA-POM.

Anacapa: Hoffmann s.n. Mar. 16, 1929 SBM#5561!; SBBG.

San Nicolas: Trask s.n. in Apr. 1897 US!.

Santa Barbara: Dunkle 7448 LAM!; Dunkle 7422 LAM!, AHFH!, NY!; Blakley 5624 CAS!; RSA-POM; SBBG.

Santa Catalina: Dunkle 2110 AHFH!; Dunkle 2090 LAM!, AHFH!; Fosberg S4722 LAM!.

San Clemente: Dunkle 7223 LAM!; Dunkle 7219 LAM!; Dunkle 7221 AHFH!; RSA-POM; CAS.

Guadalupe: Anthony 240 LAM!, CAS!; Moran 5687 RSA!, CAS!; Wiggins & Ernst 62 DS!.

Soleirolia soleirolii (Req.) Dandy

San Nicolas: Foreman 120 UC!; RSA-POM; SBBG.

Urtica dioica L. ssp. *holoserica* (Nutt.) Thorne

Santa Cruz: Dunkle 8561 LAM!, AHFH!; Elmore 258 AHFH!; Yates s.n. in Aug. 1893 SBM!; RSA-POM.

Anacapa: Dunkle 7248 LAM!, AHFH!; SBBG.

Santa Catalina: Fosberg S4911 LAM!; Dunkle 1992 AHFH!; RSA-POM.

Urtica urens L.

Santa Rosa: Hoffmann s.n. SBM6277!; RSA-POM; SBBG.

Santa Cruz: Hoffmann s.n. SBM#5416!; Hoffmann s.n. SBM#11856!; RSA-POM.

Santa Catalina: Dunkle 2069 LAM!; Fosberg s.n. Apr. 8, 1931 LAM!; RSA-POM.

Valerianaceae

Centranthus ruber (L.) DC.

Santa Cruz: RSA-POM; SBBG.

Santa Catalina: Fosberg S4418 LAM!; RSA-POM; SBBG.

Verbenaceae

Lippia nodiflora (L.) Michx. var. *rosea* (D. Don) Munz

Santa Cruz: Daily 519 SCIR!.

Santa Catalina: Fosberg S5414 LAM!.

Verbena bracteata Lag. & Rodr.

Santa Catalina: Fosberg S5403 LAM!; RSA-POM; SBBG.

Verbena lasiostachys Link

Santa Cruz: Dunkle 8643 LAM!, AHFH!; Wolf 4160 RSA!; Clokey 5041 POM!.

Santa Catalina: Fosberg S4843 LAM!, POM!.

San Clemente: Munz 6734 POM!; RSA-POM.

Verbena robusta Greene

Santa Rosa: Thorne et al. 48789 RSA!.

Santa Cruz: Dunkle 8548 LAM!, AHFH!; Elmore 291 AHFH!; Thorne 36670 RSA!; SBBG; SBM.

Santa Catalina: Fosberg S5412 LAM!; Fosberg S4606 LAM!; Fosberg S4741 LAM!; RSA-POM; SBBG.

Violaceae

Viola pedunculata T. & G. ssp. *pedunculata*

Santa Rosa: RSA-POM; SBBG; SBM.

Santa Cruz: Fosberg 7689 LAM!, LA!; RSA-POM; SBBG; SBM.

Santa Catalina: Moran 680 LAM!; Fosberg S4455 LAM!; Dunkle 2080 AHFH!; RSA-POM; SBBG.

San Clemente: Dunkle 7326 LAM!, AHFH!; Moran 572 LAM!; RSA-POM; SBBG.

Viscaceae

Phoradendron bolleanum (Seem.) Eichler ssp. *densum* (Torr.) Wiens

Guadalupe: Palmer 85 CM!.

Vitaceae

Vitis girdiana Munson

Santa Catalina: Dunkle 1950 LAM!; Fosberg S4827 LAM!; Knopf & Johnson 1456 DS!; RSA-POM; SBBG.

Monocotyledons

Arecaceae

Erythaea edulis (Wendl.) Wats.

Guadalupe: Franceschi 1 RSA!; Franceschi s.n. 1892 & 1893 US!; Moran 18386 SD!; SBM.

Cyperaceae

Carex barbarae Dewey

Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Balls & Blakley 23621 RSA!; Hoffmann 228 POM!; CAS; SBBG; SBM.

Carex globosa Boott.

Santa Rosa: Thorne et al. 48933 RSA!; SBBG; SBM.

Santa Cruz: Hoffmann s.n. Sep. 9, 1931 LAM!; Clokey 4877 LAM!, NY!; Abrams & Wiggins 143 DS!, POM!, NY; SBBG; SBM; US.

Carex gracilior Mkze.

Santa Rosa: Thorne et al. 48709 RSA!; SBM.

Santa Cruz: Hoffmann s.n. Apr. 12, 1931 POM!; SBM.

Carex montereyensis Mkze.

Santa Cruz: Clokey 4874 LAM!; Williams 36 POM!; SBM.

Carex pansa Bailey

Santa Rosa: Blakley 3198 RSA!; Blakley 3200 RSA!, CAS!; Thorne et al. 49018 RSA!; SBBG; SBM.

Carex praegracilis W. Boott.

Santa Rosa: Munz & Hoffmann 11732 POM!; Hoffmann 718 POM!; Hoffmann s.n. Jun. 13, 1931 RSA!; SBM.

Santa Cruz: Hoffmann s.n. Apr. 13, 1931 RSA!; SBM.

Santa Catalina: Thorne 35902 RSA!, CAS!.

Carex senta Boott.

Santa Cruz: Clokey 4875 LAM!; Williams 44 POM!; Thorne & Everett 36805 RSA!; CAS; SBBG; SBM.

Carex subbracteata Mkze.

Santa Rosa: Hoffmann 717 POM!; Raven, Blakley & Ornduff 14981 RSA!; SBBG.

Santa Cruz: Hoffmann s.n. Dec. 7, 1930 POM!; Hoffmann 214 POM!; Clokey 4874 POM!.

Carex triquetra Boott.
Santa Cruz: SBM.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!, NY!, US!; Dunkle 2140 LAM!; Nuttall 131 NY!, US!; CAS; DS; RSA-POM; SBBG.
Carex tumulicola Mkze.
Santa Rosa: (Smith 1976: Howell 6380 at CAS).
Santa Cruz: Clokey 5971 NY!, UC!.
San Clemente: Raven 18005 CAS!; RSA-POM.
Cyperus alternifolius L.
Santa Cruz: SBM.
Eleocharis macrostachya Britt. in Small
Santa Rosa: Hoffmann s.n. Apr. 8, 1930 SBM!.
San Nicolas: Trask s.n. in 1897 US!; Trask s.n. in Apr. 1901 LAM!; E.Z. Rett & P.C. Orr s.n. in Mar. 1945 SBM#19398!.
Santa Catalina: Trask s.n. in Mar. 1901 LAM!; Trask s.n. in Mar. 1898 US!; Wolf 3597 US!; RSA-POM; SBBG.
San Clemente: RSA-POM.
Scirpus americanus Pers. var. *monophyllus* (Presl) Koyama
Santa Rosa: SBM.
Scirpus californicus (C.A. Mey.) Steud.
Santa Cruz: Dunkle 8581 LAM!, AHFH!; Elmore 293 AHFH!; SBBG; SBM.
Scirpus cernuus Vahl. ssp. *californicus* (Torr.) Thorne
San Miguel: RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Scirpus microcarpus Presl
Santa Catalina: RSA-POM; SBBG.
Scirpus olneyi Gray
Santa Rosa: SBM.
San Nicolas: Dunkle 8329 LAM!, AHFH!; Raven & Thompson 20765 DS!; RSA-POM.
Iridaceae
Chasmanthe aethiopica (L.) N.E. Br.
San Miguel: SBBG.
Iris ochroleuca L.
San Nicolas: SBBG.
Sisyrinchium bellum Wats.
San Miguel: RSA-POM; SBM.
Santa Rosa: Dunkle 8506 AHFH!; RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Santa Catalina: Dunkle 1744 AHFH!; RSA-POM.
Juncaceae
Juncus acutus L. var. *sphaerocarpus* Engelm.
Santa Catalina: Trask s.n. in Aug. 1901 LAM!; Dunkle 1915 AHFH!; Fosberg S4899 LAM!; RSA-POM.
Juncus balticus Willd.
San Miguel: Dunkle 8408 LAM!, AHFH!; SBBG.
Santa Rosa: SBM.
Santa Cruz: SBM.
Santa Catalina: Fosberg S4619 LAM!; Fosberg S4792 LAM!; RSA-POM; SBM.
Juncus bufonius L.
San Miguel: Dunkle 8406 LAM!; RSA-POM; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7636 LAM!; Clokey 4878 LAM!; RSA-POM; SBM.
San Nicolas: RSA-POM.
Santa Catalina: Fosberg S4751 LAM!; Fosberg S4788 LAM!; Wolf 3608 LAM!; RSA-POM; SBM.
San Clemente: RSA-POM.
Guadalupe: Moran 6663 RSA!; Moran 6646 SD!; Moran 17364 SD!.
Juncus effusus L. var. *brunneus* Engelm.
Santa Cruz: SBBG.
Juncus effusus L. var. *pacificus* Fern. & Wieg.
Santa Cruz: RSA-POM.
Juncus mexicanus Willd.
San Miguel: SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Daily 702 SCIR!.
Santa Catalina: Thorne 34967 RSA!; Thorne 37666 RSA!.
Juncus patens E. Mey.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: SBBG; SBM.
San Clemente: RSA-POM.
Juncus phaeocephalus Engelm. var. *phaeocephalus*
Santa Rosa: RSA-POM.
Juncus textilis Buch.
Santa Catalina: RSA-POM.
Juncus xiphioides E. Mey.
Santa Rosa: SBM.
Santa Cruz: SBM.
Santa Catalina: Fosberg S4861 LAM!; Fosberg S5371 LAM!; Fosberg S4861 LAM!; RSA-POM.
Luzula subsessilis (Wats.) Buch.
Santa Rosa: Moran 806 LAM!; RSA-POM; SBBG; SBM.
Santa Cruz: Wolf 2814 US!; RSA-POM; SBBG; SBM.
Liliaceae
Allium lacunosum Wats. var. *lacunosum*
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Brandegee s.n. in 1888 NY!.
Allium praecox Bdg.
San Miguel: SBBG.
Santa Rosa: SBM.
Santa Cruz: Hoffmann s.n. Apr. 11, 1931 LAM!; Hoffmann 261 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Dunkle 1750 AHFH!; Grant & Wheeler s.n. Apr. 23, 1904 LAM!; Fosberg 689 LAM!; RSA-POM; SBBG.
San Clemente: Dunkle 7304 AHFH!; Dunkle 7246 AHFH!; Dunkle 7245 AHFH!; RSA-POM; SBBG.
Asparagus officinalis L.
Santa Catalina: Fosberg S5368 LAM!.
Bloomeria crocea (Torr.) Cov. ssp. *crocea*
Santa Rosa: Dunn, N. s.n. May 15, 1932 LA#21888!; Dunn, N. s.n. May 15, 1932 LA#21891!; Dunn, N. s.n. May 15, 1932 LA#21902!; RSA-POM; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Apr. 11, 1931 LAM!; Clokey 4879 LAM!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG; SBM.
Santa Catalina: Smith, R.J. s.n. May 24, 1934 LAM!; Fosberg S4372 LAM!; Fosberg S4554 LAM!; RSA-POM; SBBG; USC.

Brodiaea jolonensis Eastw.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: SBBG.
Santa Catalina: RSA-POM.

Brodiaea kinkiensis Niehaus
San Clemente: RSA-POM.

Calochortus albus Dougl. ex Benth. var. *albus*
Santa Rosa: Hoffmann s.n. Jun. 6, 1930 LAM!; Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Clokey 4882 LAM!, NY!; Ellison s.n. May 12–15, 1929 LA!; RSA-POM; SBBG.
Santa Catalina: Brown, C. s.n. May 31, 1925 USC!.

Calochortus catalinae Wats.
Santa Rosa: Moran 781 LAM!, NY!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4649 LAM!; Dunkle 1762 AHFH!; Fosberg 8167 NY!; LA; RSA-POM; SBBG.

Calochortus luteus Dougl. ex Lindl.
Santa Cruz: RSA-POM; SBBG; SBM.

Calochortus splendens Dougl. ex Benth.
Santa Catalina: Fosberg S4690 LAM!; Hasse 2753 LAM!; Trask s.n. in Mar. 1896 NY!; RSA-POM.

Chlorogalum pomeridianum (DC.) Kunth
Santa Rosa: RSA-POM; SBM.
Santa Catalina: RSA-POM.

Dichleostemma pulchellum (Salisb.) Heller
San Miguel: RSA-POM; SBM.
Santa Rosa: Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBM.
Santa Cruz: Clokey 4881 LAM!; Fosberg 7633 LAM!, LA!; RSA-POM; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Trask 87 LAM!; Kanakoff s.n. Apr. 12, 1940 LAM!; RSA-POM; SBM.
Santa Barbara: Dunkle 7419 LAM!, AHFH!; RSA-POM; SBM.
Santa Catalina: Fosberg S4632 LAM!; Fosberg S4369 LAM!; Templeton 11398 LAM!; RSA-POM; USC.
San Clemente: Moran 580 LAM!; Dunkle 7304 LAM!; Elmore 391 AHFH!; LA; RSA-POM.
Guadalupe: Moran 6651 SD!; Moran 17415 SD!; Moran 20306 SD!.

Lilium humboldtii Roezl & Leichtl. ssp. *ocellatum* (Kell.) Thorne
Santa Rosa: RSA-POM.
Santa Cruz: Clokey 4885 LAM!; Clokey 4884 LAM!; Hoffmann s.n. Apr. 11, 1930 LAM!; LA; RSA-POM; SBBG; SBM.

Triteleia clementina Hoov.
San Clemente: Dunkle 7283 LAM!, AHFH!; Dunkle 7324 LAM!; Moran 702 LAM!; RSA-POM; SBBG.

Triteleia guadalupensis Lenz
Guadalupe: Moran 12063 RSA!, SD!.

Zigadenus fremontii Torr. var. *fremontii*
Santa Rosa: Munz & Crow 11616 LA!; RSA-POM; SBBG; SBM.
Santa Cruz: Fosberg 7529 LAM!; RSA-POM; SBBG; SBM.
Anacapa: Moran 716 LAM!; SBBG; SBM.

Orchidaceae

Epipactis gigantea Dougl. ex Hook.
Santa Cruz: RSA-POM; SBM.

Habenaria elegans (Lindl.) Boland.
Santa Rosa: Hoffmann s.n. Jun. 13, 1930 CAS#167564!; Rowntree s.n. Jun. 16, 1970 CAS#297877!; SBBG; SBM.
Santa Cruz: Clokey 4886 LAM!; Clokey 4887 LAM!; Hoffmann s.n. Jun. 14, 1930 CAS#176936!; SBBG; SBM.
Santa Catalina: SBBG.

Habenaria unalascensis (Spreng.) Wats.
Santa Cruz: RSA-POM.
Santa Catalina: Fosberg S4495 LAM!; Fosberg S4568 LAM!; Fosberg S4867 LAM!.

Poaceae

Agrostis diegoensis Vasey
Santa Rosa: Brandegee, T.S. 66 US!; RSA-POM; SBBG; SBM.
Santa Cruz: Hoffmann s.n. May 23, 1932 POM#180275!; SBBG; SBM.
Santa Catalina: Fosberg S4729 LAM!; Fosberg S4869 LAM!; Brandegee, T.S. 50 US!; RSA-POM; SBBG.
San Clemente: Abrams & Wiggins 370 DS!, US!.

Agrostis exarata Trin.
Santa Rosa: Hoffmann s.n. Aug. 7, 1930 SBM!; SBM.
Santa Cruz: RSA-POM; SBBG; SBM.
Santa Catalina: Thorne & Thorne 36434 RSA!.

Agrostis semiverticillata (Forsk.) C. Chr.
Santa Rosa: Thorne et al. 48960 RSA!; SBBG; SBM.
Santa Cruz: Dunkle 8553 LAM!, AHFH!, RSA!; Hoffmann s.n. Jun. 28, 1930 LAM!; Dunkle 8635 LAM!, RSA!; SBBG; SBM.
Anacapa: Dunkle 7650 LAM!.
Santa Catalina: Trask s.n. in Mar. 1901 NY!; Thorne 36636 RSA!; Raven 17844 RSA!; SBBG.

Ammophila arenaria (L.) Link
San Nicolas: Foreman 101 UC!; Wier & Beauchamp s.n. Jul. 2, 1978 RSA!.

Andropogon glomeratus (Walt.) BSP.
Santa Cruz: Benedict s.n. Nov. 16, 1969 SBBG.

Aristida adscensionis L. var. *modesta* Hack. in Stuckert
Santa Rosa: SBBG.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!; Thorne & Everett 36806 RSA!; Raven & Smith 15201 RSA!, DS!; SBM.
Santa Catalina: Brandegee 56 US!; Thorne & Thorne 42473 RSA!; Thorne 35942 RSA!.
San Clemente: Abrams & Wiggins 364 DS!, GH!; Raven 17609 RSA!; Raven 17650 RSA!.
Guadalupe: Wiggins & Ernst 215 SD!; Palmer 675 US!.

Aristida divaricata Humb. & Bonpl. in Willd.
Santa Cruz: SBBG.

Arundo donax L.
San Nicolas: Beauchamp s.n. Jul. 1, 1978 RSA!; SBBG.

Avena barbata Brot.
San Miguel: SBBG.
Santa Rosa: Dunkle 8523 LAM!, AHFH!; Dunn, N. s.n. May 15, 1932 LA#11004!; RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8565 LAM!, AHFH!; Clokey 4861 LAM!; Fausett 16 LA!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Kanakoff s.n. LAM!; Foreman & Smith 166 LA!; Thorne et al. 52362 RSA!.
Santa Barbara: RSA-POM.
Santa Catalina: Fosberg S4298 LAM!; Detmers s.n. Apr. 14, 1929 USC!; Thorne 35893 RSA!.
San Clemente: Dunkle 7255 LAM!, AHFH!; Thorne 36145 RSA!; Raven 17290 RSA!.
Guadalupe: Moran 5616 SD!; Palmer 668 ND-G!; Mason 1542 CAS!.
Avena fatua L.
San Miguel: Dunkle 8363 LAM!, AHFH!; SBBG.
Santa Rosa: Thorne et al. 48953 RSA!; SBM.
Santa Cruz: SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Raven & Thompson 20776 DS!; Trask 17 US!.
Santa Barbara: Dunkle 7454 LAM!, AHFH!; Philbrick B6846 RSA!; SBM.
Santa Catalina: Dunkle 1792 AHFH!; Trask s.n. in May 1898 US!; Thorne 33452 RSA!.
San Clemente: Trask 242 US!; Munz 6619 POM!; Raven 17133 RSA!.
Guadalupe: Palmer 94 CM!; Brandegee, T.S. s.n. May 24, 1897 UC!.
Avena sativa L.
Santa Rosa: SBM.
Santa Cruz: SBBG.
Santa Catalina: Fosberg S4425 LAM!; Fosberg S4662 LAM!; Thorne 36274 RSA!.
San Clemente: Raven 17622 RSA!.
Bothriochloa barbinodis (Lag.) Herter
Santa Catalina: McClatchie s.n. Sep. 12, 1893 NY!; Thorne 36196 RSA!; Wolf 4026 RSA!.
Brachypodium distachyon (L.) Beauv.
Santa Catalina: Fosberg S4964 LAM!, RSA!, SBM!; Thorne 36891 RSA!; Raven 17825 LA!, RSA!.
Bromus arizonicus (Shear) Steb.
San Miguel: Hoffmann s.n. Apr. 10, 1930 US!; Beck, R.H. 1 US!.
Santa Rosa: Hoffmann 706 SBM!; Hoffmann 727 SBM!; Hoffmann s.n. Apr. 20, 1929 SBM#7652!, CAS#168467!.
Santa Cruz: (Stebbins, Tobgy & Harlan 1944: Brandegee s.n. in 1888 at UC).
Anacapa: Dunkle 7445 LAM!; SBBG.
San Nicolas: Howell 8226 CAS!, US!.
Santa Barbara: Dunkle 7455 LAM!, AHFH!; Philbrick & Ricker B69-55 US!; Piehl 63132 CAS!; RSA-POM.
Santa Catalina: Fosberg S4646 LAM!; Millspaugh 4632 US!; Brandegee, T.S. 57 US!; RSA-POM.
San Clemente: Trask 357 NY!, US!; RSA-POM.
Bromus carinatus H. & A.
San Miguel: Beck, R.H. 2 US!; Hoffmann 728 SBM!.
Santa Rosa: Hoffmann s.n. Apr. 18, 1929 SBM#7649!; Hoffmann s.n. Jun. 12, 1930 SBM#10181!; Hoffmann s.n. Apr. 8, 1930 US#1535533!; RSA-POM.
Santa Cruz: Hoffmann 262 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!, SBM!; Hoffmann s.n. Mar. 22, 1929 SBM#5454!; RSA-POM.
Anacapa: SBBG; SBM.
San Nicolas: Trask 13 US!; Trask 14 US!; RSA-POM.
Santa Catalina: Fosberg S4608 LAM!; Fosberg S4484 LAM!; Trask s.n. in May 1897 US!; RSA-POM.
San Clemente: RSA-POM.
Bromus diandrus Roth.
San Miguel: Dunkle 8361 LAM!; Bond 405 SBM!; Bond 406 SBM!; SBBG.
Santa Rosa: Hoffmann s.n. Apr. 20, 1929 SBM#7595!; Hoffmann s.n. Apr. 20, 1929 SBM#7648!; RSA-POM.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 SBM#11160!; Clokey 4856 LAM!; Dunkle 8564 LAM!; LA; RSA-POM.
Anacapa: Bond 329 SBM!; Bond 339 SBM!; SBBG.
San Nicolas: Kanakoff s.n. Apr. 16, 1940 LAM!; Blakley 4078 US!; Foreman & Smith 155 LA!; RSA-POM.
Santa Barbara: Dunkle 8139 LAM!; AHFH!; Dunkle 8141 LAM!; AHFH!; RSA-POM.
Santa Catalina: Dunkle 1787 LAM!; Fosberg S4356 LAM!; Detmers s.n. Apr. 14, 1929 LAM!; RSA-POM.
San Clemente: Piehl 62397 US!; RSA-POM.
Guadalupe: Moran 13773 LAM!, RSA!, SD!; Wiggins & Ernst 77 DS!, SD!; Brown, W.W. 31 GH!.
Bromus madritensis L.
Santa Cruz: Fausett 23 LA!; RSA-POM.
Bromus maritimus (Piper) Hitchc.
San Miguel: Hoffmann 681 SBM!; Bond, R. s.n. Apr. 18, 1939 SBM!; Hoffmann s.n. Apr. 10, 1930 SBM#9294!; RSA-POM.
Santa Rosa: Hoffmann 724 SBM!.
Santa Cruz: Yates s.n. in Aug. 1893 SBM#15947!; SBBG.
Anacapa: Dunkle 7634 LAM!; [Hoffmann] s.n. Mar. 11, 1928 SBM#4136!; SBBG.
San Nicolas: Philbrick & Benedict B69-161 US!.
Santa Catalina: Fosberg S4484 SBM!.
Bromus mollis L.
San Miguel: SBBG.
Santa Rosa: Hoffmann 744 SBM!; Dunkle 8520 LAM!; Hoffmann s.n. Apr. 15, 1929 SBM#6278!; RSA-POM.
Santa Cruz: Hoffmann s.n. Jun. 15, 1930 SBM#2304!; Clokey 4855 LAM!, US!; Fausett 17 LA!; RSA-POM.
Anacapa: Hoffmann s.n. Mar. 11, 1928 SBM#4099!; Bond 332 SBM!; SBBG.
San Nicolas: Kanakoff s.n. Apr. 19, 1940 LAM!; Dunkle 8308 LAM!, AHFH!; P.C. Orr & E.Z. Rett s.n. Mar. 26, 1945 SBM#19343!; RSA-POM.
Santa Barbara: RSA-POM.
Santa Catalina: Fosberg S4493 LAM!; Fosberg S4566 LAM!; Dunkle 1916 AHFH!; RSA-POM; USC.
San Clemente: Dunkle 7254 LAM!, AHFH!; Dunkle 7362

AHFH!; E.Z. Rett & P.C. Orr s.n. Apr. 10, 1945 SBM#19338!; RSA-POM.
Guadalupe: Wiggins & Ernst 105 DS!, SD!; Moran 6642 SD!; Moran 2881 DS!.

Bromus pseudolaevipes Wagnon.
Santa Rosa: [no collector, probably Hoffmann] s.n. Jun. 13, 1930 SBM#10180!; [no collector, probably Hoffmann] s.n. Jun. 12, 1930 SBM#10182!; RSA-POM.
Santa Cruz: Hoffmann s.n. Jun. 29, 1930 SBM#10132!, US#1649447!; SBBG.
Santa Catalina: Fosberg S4501 LAM!, SBM!; Trask s.n. in Mar. 1901 NY!; Raven 17772 US!; RSA-POM; SBBG.

Bromus rubens L.
San Miguel: SBBG.
Santa Rosa: Dunkle 8519 LAM!; Hoffmann s.n. May 6, 1932 SBM!; RSA-POM; SBBG.
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 LAM!, SBM!; Dunkle 8639 LAM!, AHFH!; Fausett 18 LA!; RSA-POM; SBBG.
Anacapa: Bond 330 SBM!; SBBG.
San Nicolas: RSA-POM.
Santa Barbara: Dunkle 7423 LAM!, AHFH!; Bond 373 SBM!; Bond 395 SBM!; RSA-POM.
Santa Catalina: Fosberg S4296 LAM!; Dunkle 1778 AHFH!; Dunkle 1917 AHFH!; RSA-POM.
San Clemente: Dunkle 7256 LAM!; RSA-POM.
Guadalupe: Moran 5976 SD!; Wiggins & Ernst 76 DS!; Moran 12026 RSA!, SD!.

Bromus stamineus Desv. in Gray
Santa Cruz: Raven & Smith 15290 RSA!.

Bromus sterilis L.
Santa Catalina: Nuttall 95 F!, US!; Nuttall 562 F!; Nuttall 1219 F!.

Bromus tectorum L.
Guadalupe: Palmer 99 (in part) NY!.

Bromus trinii Desv. in C. Gay
Santa Rosa: [no collector, probably Hoffmann] s.n. Apr. 8, 1930 SBM#10184!.
Santa Cruz: Hoffmann s.n. Apr. 22, 1932 SBM#11947!; Brandegee s.n. in 1888 (in part) UC#121663!.
Anacapa: [no collector, probably Hoffmann] s.n. Mar. 11, 1928 SBM#4091! (in part).
San Nicolas: Trask 1 MO!.
Santa Barbara: Dunkle 7424 LAM!; Piehl 63151 RSA!.
Santa Catalina: Brandegee s.n. Mar. 12, 1890 UC!; Trask s.n. in May 1897 MO!.
San Clemente: Raven 17185 RSA!.
Guadalupe: Palmer 667 NY!, UC!, US!; Palmer 658 US!; Moran 17369 SD!; CSA; DS.

Calamagrostis rubescens Buckl.
Santa Cruz: Blakley & Muller 3726 SCIR!; SBBG.

Cortaderia atacamensis (Phil.) Pilger
Santa Cruz: SBM.
Santa Catalina: RSA-POM.

Crypsis aculeata (L.) Ait.
Santa Catalina: RSA-POM.

Cynodon dactylon (L.) Pers.
Santa Rosa: Dunkle 8474 LAM!; RSA-POM; SBM.
Santa Cruz: Dunkle 8652 LAM!; RSA-POM; SBM.
Anacapa: SBBG.
San Nicolas: Dunkle 8325 LAM!; Trask s.n. in Apr. 1897 NY!; RSA-POM.
Santa Catalina: Fosberg S4439 LAM!; Nuttall 540 US!; RSA-POM.
San Clemente: RSA-POM.

Dactylis glomerata L.
Santa Catalina: RSA-POM.
San Clemente: SBBG.

Deschampsia danthonioides (Trin.) Munro in Benth.
San Clemente: RSA-POM.

Dissanthelium californicum (Nutt.) Benth.
Santa Catalina: Gambel s.n. GH!; MO!.
San Clemente: Trask 324 US!.
Guadalupe: Palmer 96 CM!, MO!, NY!.

Distichlis spicata (L.) Greene var. *stolonifera* Beetle
San Miguel: Dunkle 8366 LAM!; Hoffmann s.n. Apr. 10, 1930 SBM#9367!; Bond 416 SBM!; SBBG.
Santa Rosa: Dunkle 8526 LAM!, AHFH!; Hoffmann s.n. Apr. 14, 1929 SBM!; RSA-POM; SBBG.
Santa Cruz: Dunkle 8587 LAM!, AHFH!; Clokey 4859 LAM!; Elmore 289 AHFH!; RSA-POM; SBBG; SBM.
Anacapa: Bond 353 SBM!; SBBG.
San Nicolas: Dunkle 8314 LAM!, AHFH!; Kanakoff s.n. Apr. 19, 1940 LAM!; Trask s.n. in Apr. 1901 LAM!, US!; LA; RSA-POM; SBM.
Santa Catalina: Trask s.n. in Sep. 1896 US!; Fosberg S4475 LAM!; Fosberg S4871 LAM!, SBM; RSA-POM.
San Clemente: Trask s.n. Oct. 1902 US!; Dunkle 7331 LAM!, AHFH!.

Echinochloa crus-galli (L.) Beauv. var. *crus-galli*
Santa Catalina: Thorne 36427 RSA!.

Ehrharta calycina Sm.
Santa Catalina: Thorne, Rollins, Propst & Carolin 36741 RSA!.
San Clemente: SBBG.

Elymus condensatus Presl
San Miguel: Dunkle 8371 LAM!, AHFH!; RSA-POM; SBM.
Santa Rosa: SBM.
Santa Cruz: Clokey 4867 LAM!; RSA-POM; SBM.
Anacapa: SBBG; SBM.
Santa Catalina: Johnstone s.n. May 20, 1934 USC!; RSA-POM.
San Clemente: Murbarger 59 UC!.

Elymus glaucus Buckl. ssp. *glaucus*
Santa Cruz: Hoffmann 598 US!; RSA-POM; SBM.
Santa Catalina: Fosberg S4610 LAM!; Fosberg S4853 LAM!, NY!; Brandegee 49 US!; RSA-POM.

Elymus pacificus Gould
San Miguel: Bond 419 SBM!.

Elymus triticoides Buckl.
San Miguel: Dunkle 8362 LAM!; Elmore 317 AHFH!; RSA-POM; SBBG.

Santa Rosa: Dunkle 8518 LAM!, AHFH!; Dunn, N. s.n. May 15, 1932 LA!; SBM.
Santa Cruz: Ellison, L. s.n. LA#14864!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
Santa Catalina: Fosberg S4831 LAM!; Trask s.n. in Mar. 1901 NY!; Trask s.n. in May 1898 US!; RSA-POM.

Festuca arundinacea Schreb.
Santa Catalina: RSA-POM.

Gastridium ventricosum (Gouan) Schinz & Thell.
Santa Rosa: SBM.
Santa Cruz: Clokey 4868 LAM!; Clokey 4869 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!, LA!; RSA-POM; SBM.
Santa Catalina: RSA-POM.
San Clemente: Dunkle 7348 LAM!, AHFH!; RSA-POM.

Hordeum californicum Covas & Steb.
San Miguel: Blakley 5837 DS; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM.
Anacapa: SBBG; SBM.
San Nicolas: Trask s.n. in Apr. 1901 LAM!; RSA-POM; SBBG.
Santa Catalina: Fosberg S4945 LAM!; RSA-POM.

Hordeum depressum (Scribn. & Sm.) Rydb.
Santa Cruz: Abrams & Wiggins 125 DS!.

Hordeum geniculatum All.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Clokey 5166 LA!, NY!, RSA!.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.

Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvel.
San Miguel: Dunkle 8365 LAM!, AHFH!; SBM.
Santa Rosa: SBBG; SBM.
Santa Cruz: Clokey 4858 LAM!, NY!; Raven & Smith 15146 CAS!; SBBG; SBM.
Anacapa: SBBG; SBM.
San Nicolas: Trask s.n. in Apr. 1901 NY!; Howell 8211 CAS!; Raven & Thompson 20725 DS!; RSA-POM.
Santa Barbara: Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; Dunkle 8108 LAM!, AHFH!, DS!, NY!; Blakley 5673 DS!; RSA-POM.
Santa Catalina: Dunkle 1906 AHFH!; Knopf 28 F!; Trask s.n. in Mar. 1901 NY!; RSA-POM.
San Clemente: Trask 259 NY!; Mearns 4055 DS!; RSA-POM.
Guadalupe: Palmer 671 F!; Webber & McCoy 11960 DS!; Moran 17386 SD!.

Hordeum murinum L. ssp. *leporinum* (Link) Arcangeli
San Miguel: Dunkle 8365 LAM!, AHFH!; Munz & Crow 11815 LA!; Hoffmann s.n. Apr. 10, 1930 CAS#177736!; SBBG.
Santa Rosa: Dunn, N. s.n. May 15, 1932 LA!; RSA-POM; SBBG.
Santa Cruz: Clokey 4857 LAM!; Fausett 14 LA!; SBBG; SBM.
Anacapa: Blakley 2748 CAS!; SBBG; SBM.
San Nicolas: Kanakoff s.n. Apr. 19, 1940 LAM!; Foreman & Lloyd 132 LA!; SBBG.
Santa Catalina: Fosberg S4295 LAM!; Dunkle 1784 AHFH!; Millspaugh 4660 F!; DS; RSA-POM.
San Clemente: House & Grumbles s.n. Aug. 5–13, 1930 USC!; Dunkle 7271 LAM!; AHFH!; RSA-POM.
Guadalupe: Wiggins & Ernst 12, DS!, SD!; Moran 17321 SD!; Mason 1544 F!.

Hordeum pusillum Nutt.
San Miguel: SBBG.
Santa Cruz: RSA-POM.
Anacapa: SBBG; SBM.
Santa Barbara: RSA-POM.
Santa Catalina: Fosberg S4666 LAM!; Fosberg S4706 LAM!; RSA-POM; SBM.
San Clemente: RSA-POM.

Hordeum vulgare L.
Santa Rosa: SBBG.
Santa Cruz: Raven & Smith 15287 CAS!; SBBG.
Santa Catalina: Fosberg S4567 LAM!; Fosberg S4512 LAM!; RSA-POM.
San Clemente: RSA-POM.

Koeleria pyramidata (Lam.) Beauv.
Santa Rosa: Dunkle 8495 LAM!, AHFH!; RSA-POM; SBM.
Santa Cruz: RSA-POM.

Lamarckia aurea (L.) Moench
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Dunkle 8549 LAM!; RSA-POM; SBBG; SBM.
Anacapa: SBBG.
San Nicolas: Kanakoff s.n. LAM!; RSA-POM.
Santa Barbara: Dunkle 8124 LAM!, AHFH!; Dunkle 7458 LAM!, AHFH!; RSA-POM.
Santa Catalina: Fosberg S4297 LAM!; Fosberg S4660 LAM!; Dunkle 1702 AHFH!; RSA-POM.
San Clemente: Dunkle 7332 LAM!, AHFH!; RSA-POM.

Lolium perenne L. ssp. *multiflorum* (Lam.) Husnot
Santa Cruz: RSA-POM; SBM.
San Nicolas: Foreman, Evans & Rainey 75 LA!; SBBG; SBM.
Santa Catalina: Fosberg S4966 LAM!; RSA-POM; SBBG.
San Clemente: RSA-POM; SBBG.

Lolium perenne L. ssp. *perenne*
Santa Cruz: Dunkle 8634 LAM!; SBBG.
San Nicolas: Foreman 111 UC!.
Santa Catalina: SBBG.
San Clemente: RSA-POM.

Lolium strictum Presl
Santa Catalina: RSA-POM.

Lolium temulentum L.
Santa Rosa: SBM.
Santa Cruz: Hoffmann s.n. Apr. 11, 1931 LAM!; Hoffmann s.n. Apr. 12, 1931 LAM!; SBM.
Santa Catalina: Fosberg S4482 LAM!; Fosberg S4661 LAM!; Brandegee s.n. May 26, 1890 US!; RSA-POM.
San Clemente: Trask 241 US!; RSA-POM.

Melica imperfecta Trin.
San Miguel: Blakley 5839 DS!; RSA-POM; SBBG; SBM.
Santa Rosa: Thorne et al. 48945 RSA!; SBBG; SBM.
Santa Cruz: Fosberg 7609 LAM!, LA!; Clokey 4872 LAM!,

US!; Abrams & Wiggins 15 CAS!, DS!; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
Santa Barbara: Dunkle 7438 LAM!, AHFH!; Piehl 63152a US!; Blakley 5611 DS!; RSA-POM; SBBG.
Santa Catalina: Fosberg S5463 LAM!; Nuttall 350 NY!; Chase 5567 US!; RSA-POM; SBBG; SBM; USC.
San Clemente: House & Grumbles s.n. USC!; Trask 325 US!; Trask 358 US!; RSA-POM; SBBG.
Guadalupe: Moran 13783 SD!, DS!, US!; Wiggins & Ernst 102 DS!, SD!; Moran 13791 RSA!, SD!.

Monanthochloe littoralis Engelm.
San Miguel: Elmore 318 AHFH!.
Santa Rosa: Dunkle 8491 AHFH!; RSA-POM; SBBG.
Santa Cruz: Hoffmann s.n. Mar. 24, 1929 (in part) SBM#5510!.
Santa Catalina: Fosberg S4927 LAM!; Blakley 4729 US!; Pendleton & Reed 1425 US!.

Muhlenbergia microsperma (DC.) Kunth
Santa Rosa: SBM.
Santa Cruz: Fosberg 7635 LAM!; RSA-POM; SBBG; SBM.
Anacapa: SBM.
Santa Barbara: Dunkle 7421 LAM!, AHFH!; Piehl 63155 US!; RSA-POM; SBBG.
Santa Catalina: Trask G12 in Oct. 1896 US!; Trask s.n. in Mar. 1901 US!; Nuttall 323 US!; RSA-POM; SBBG.
San Clemente: Blakley 6325 US!; RSA-POM; SBBG.
Guadalupe: Palmer 656 ND-G!; Palmer 670 ND-G!; Moran 17338 SD!.

Oryzopsis miliacea (L.) Benth. & Hook. ex Aschers. & Schweinf.
Santa Rosa: SBM.
Santa Cruz: Daily 432 SCIR!.
Santa Catalina: RSA-POM; SBBG.

Parapholis incurva (L. f.) C.E. Hubb.
San Miguel: SBBG.
Santa Rosa: Hoffmann s.n. Apr. 9, 1930 US!; RSA-POM; SBBG; SBM.
Santa Cruz: RSA-POM; SBBG.
San Nicolas: Kanakoff s.n. Apr. 14, 1940 LAM!; Foreman 179 US!; Blakley 4008 US!; RSA-POM.
Santa Barbara: Philbrick B69-89 SBBG; Philbrick B69-82 SBBG.
Santa Catalina: Fosberg S4946 LAM!; Dunkle 1908 AHFH!; Brandegee 54 US!; DS; RSA-POM.
San Clemente: Raven 17276 US!; RSA-POM.

Paspalum dilitatum Poir. in Lam.
Santa Catalina: RSA-POM.
Paspalum distichum L.
Santa Catalina: RSA-POM.
Pennisetum clandestinum Hochst. ex Chiov.
Santa Cruz: Cox, W. s.n. Nov. 20, 1975 SCIR#0384!.

Phalaris aquatica L.
Santa Catalina: Blakley 5423 US!; RSA-POM.
Phalaris canariensis L.
Santa Catalina: Fosberg S4474 LAM!.
Phalaris caroliniana Walt.
Santa Cruz: Brandegee s.n. in Jun. 1888 UC!.
San Nicolas: Trask 9 MO!.
Santa Barbara: Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!.
Santa Catalina: Trask s.n. in Mar. 1901 MO!.
San Clemente: RSA-POM.
Guadalupe: Moran 6683 RSA!, SD!; Wiggins & Ernst 125 DS!; Moran 17368 SD!.
Phalaris lemmonii Vasey
Santa Rosa: SBM.
Santa Catalina: Trask s.n. May 1897 MO!; Trask s.n. Mar. 1901 NY!.
San Clemente: Thorne 42957 MO!.
Phalaris minor Retz.
San Miguel: Piehl 6253 DS!; SBBG; SBM.
Santa Rosa: SBM.
Santa Cruz: Hoffmann s.n. Apr. 13, 1931 LAM!; Hoffman s.n. Jun. 15, 1930 SBM#7556!; Raven & Smith 15142 CAS!; RSA-POM.
Anacapa: SBM.
San Nicolas: Raven & Thompson 20792 DS!; RSA-POM.
Santa Barbara: Blakley 5680 CAS!; RSA-POM.
Santa Catalina: Fosberg S4595 LAM!; Wolf 3581 DS!; RSA-POM.
San Clemente: Thorne 42891 MO!; RSA-POM.
Guadalupe: Moran 6789 SD!; Wiggins & Ernst 216 DS!.
Phalaris paradoxa L.
San Clemente: RSA-POM.
Poa annua L.
San Miguel: Hoffmann s.n. Apr. 19, 1932 SBM!.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Moran 6622 RSA!, SD!; Howell 8260 CAS!; Moran 25380 SD!.
Poa bolanderi Vasey ssp. *howellii* (Vasey & Scribn.) Keck
Santa Cruz: Hoffmann s.n. Apr. 12, 1931 SBM#11158!.
Poa douglasii Nees
San Miguel: RSA-POM; SBM.
Santa Rosa: RA-POM; SBM.
Poa palustris L.
Santa Catalina: Trask G-4 in Mar. 1897 MO!.
Poa scabrella (Thurb.) Benth. ex Vasey
Santa Rosa: RSA-POM; SBM.
Santa Cruz: Fosberg 7653 LAM!; Fosberg 7608 LAM!; RSA-POM; SBM.
Anacapa: SBBG; SBM.
Santa Catalina: Fosberg S4521 LAM!; Trask s.n. in Mar. 1901 LAM!, MO!; Fosberg S4653 LAM!; RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Moran 13816 RSA!, SD!.
Polypogon interruptus HBK.
San Miguel: RSA-POM; SBM.
Santa Rosa: Dunkle 8502 LAM!; SBBG; SBM.
Santa Cruz: Clokey 4860 LAM!; Hoffmann 48 LAM!; Dunkle 8551 LAM!; RSA-POM; SBBG; SBM.
Santa Catalina: Fosberg S4511 LAM!; Dunkle 1980

AHFH!; Brandegee s.n. May 13, 1890 UC!; RSA-POM; SBBG.
San Clemente: Murbarger 239 UC!.

Polypogon monspeliensis (L.) Desf.
San Miguel: Dunkle 8395 LAM!; RSA-POM; SBM.
Santa Rosa: Elmore 193 AHFH!; Hoffmann s.n. Apr. 9, 1930 CAS#191780!; RSA-POM; SBM.
Santa Cruz: Dunkle 8552 LAM!; Hoffmann s.n. Jun. 28, 1930 (in part) LAM!; Elmore 267 AHFH!; RSA-POM; SBM.
San Nicolas: Trask s.n. in Mar. 1901 LAM!; Dunkle 8327 LAM!, AHFH!; E.Z. Rett & P.C. Orr s.n. SBM!; DS; LA; RSA-POM.
Santa Barbara: Dunkle 8148 AHFH!; Bryan, Dr. & Mrs. s.n. Jul. 14, 1922 LAM!; RSA-POM.
Santa Catalina: Trask s.n. in May 1901 LAM!; Fosberg S4473 LAM!; Dunkle 1912 AHFH!; RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Rempel 758-37 LAM!; Moran 6604 RSA!, SD!; Moran 17301 SD!.

Schismus arabicus Nees
Santa Catalina: RSA-POM.

Schismus barbatus Thell.
Santa Cruz: Daily 607 SCIR#0814!.

Scleropoa rigida (L.) Griseb.
Santa Catalina: RSA-POM.

Sitanion jubatum J.G. Sm.
Santa Catalina: Nuttall 314 F!.

Sorghum bicolor (L.) Moench
Santa Catalina: RSA-POM.

Sorghum halepense (L.) Pers.
Santa Catalina: Fosberg S4513 LAM!; Dunkle 2464 AHFH!.

Stipa cernua Steb. & Love
Santa Rosa: Hoffmann s.n. CAS!; RSA-POM.
Santa Cruz: Breedlove 2879 DS!; Abrams & Wiggins 216 DS!; RSA-POM.
Anacapa: SBBG.
San Nicolas: SBBG.
Santa Catalina: Fosberg S4308 LAM!; Blakley 5530-A DS!; RSA-POM.
San Clemente: Elmore s.n. Nov. 26, 1939 AHFH!; Blakley 6346 DS!; Piehl 62366 DS!; SBBG.

Stipa columbiana Macoun var. *nelsoni* (Scribn.) Hitchc.
San Nicolas: Trask 11 in Apr. 1897 US#340330!.

Stipa lepida Hitchc.
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Hoffmann s.n. Jun. 14, 1930 LAM!; Fosberg 7610 LAM!, LA!; Brandegee 74 US!; DS; RSA-POM; SBBG; SBM.
Anacapa: SBBG; SBM.
Santa Barbara: Dunkle 8109 LAM!.
Santa Catalina: Fosberg S4609 LAM!; Trask s.n. in Mar. 1901 NY!; Brandegee 59 US!; RSA-POM; SBM.
San Clemente: RSA-POM.
Guadalupe: Wiggins & Ernst 203 DS!, SD!; Moran 6754 RSA!; Wiggins & Ernst 199 DS!.

Stipa pulchra Hitchc.
San Miguel: Blakley 5838 DS!; SBBG; SBM.
Santa Rosa: RSA-POM; SBBG; SBM.
Santa Cruz: Wolf 2772 DS!; Hoffmann s.n. Mar. 23, 1929 CAS#168484!; RSA-POM; SBBG; SBM.
Anaeapa: SBBG; SBM.
San Nicolas: Trask 16 US!; RSA-POM; SBM.
Santa Barbara: Philbrick 68-83 SBBG!; Piehl 631631 CAS!.
Santa Catalina: Dunkle 1780 AHFH!; Dunkle 1786 AHFH!; Knopf 201 US!; RSA-POM; SBM.
San Clemente: Trask 361 US!; Moran 570 LAM!, DS!; Dunkle 7360 AHFH!; Abrams & Wiggins 381 CAS!, DS!; RSA-POM.

Triticum aestivum L.
San Clemente: RSA-POM.

Triticum cylindricum (Host.) Ces., Pass. & Gib.
Santa Cruz: Barbe 1566 RSA!.

Vulpia bromoides (L.) S.F. Gray
San Miguel: Hoffmann s.n. Apr. 20, 1932 SBM#11908!; Hoffmann s.n. Apr. 20, 1932 SBM#11926!; Hoffmann s.n. Jun. 11, 1930 SBM#4991!.
Santa Rosa: Munz & Crow 11657 LA!; Hoffmann s.n. Apr. 16, 1929 SBM#6254!; Hoffmann s.n. Apr. 17, 1929 SBM#6256!; RSA-POM.
Santa Cruz: Hoffmann s.n. Jun. 29, 1930 LAM!, SBM!; Clokey 4871 LAM!, NY!, US!; Abrams & Wiggins 101 DS!, NY!; SBBG; SBM.
Anacapa: Hoffmann s.n. Mar. 16, 1929 CAS#168488!; SBBG; SBM.
Santa Catalina: SBBG.
San Clemente: RSA-POM.
Guadalupe: RSA-POM.

Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould
San Miguel: SBM.
Anacapa: SBBG.
Santa Catalina: Fosberg S4543 LAM!; Fosberg S4728 LAM!, NY!, SBM!; Trask G-22 in Mar. 1898 US!; RSA-POM.
San Clemente: Trask 323 US!; RSA-POM; SBBG.
Guadalupe: Greene 42 in Apr. 1885 US!; Moran 6658 SD!; Wiggins & Ernst 114 DS!.

Vulpia myuros (L.) K.C. Gmelin var. *hirsuta* Hack.
San Miguel: Hoffmann s.n. Apr. 19, 1932 SBM#11890!; SBBG.
Santa Rosa: Hoffmann s.n. May 10, 1932 SBM#12159!; Hoffmann s.n. Mar. 24, 1927 SBM!; Hoffmann s.n. Apr. 18, 1929 SBM#6255!; RSA-POM; SBBG.
Santa Cruz: Clokey 4862 LAM!; Dunkle 8640 LAM!; Brandegee s.n. in 1888 UC!; RSA-POM; SBBG; SBM.
Anacapa: [Hoffmann] s.n. Mar. 11, 1928 SBM#4092!; SBBG; SBM.
San Nicolas: SBBG.
Santa Barbara: Dunkle 8140 LAM!, AHFH!; RSA-POM.
Santa Catalina: Trask G-19 in May 1898 US!; Fosberg S4306 LAM!, NY!; Nuttall 98 NY!, US!; RSA-POM; SBM.

San Clemente: Trask 360 NY!, US!; Dunkle 7257 LAM!, AHFH!; Dunkle 7297 AHFH!; RSA-POM.
Guadalupe: Palmer 672 NY!; Palmer 673 US!; Moran 12387 SD!.

Vulpia myuros (L.) K.C. Gmelin var. *myuros*
Santa Catalina: Brandegee 53 US!; Millspaugh 4667 US!; Millspaugh 4679 US!; RSA-POM.
San Clemente: RSA-POM.

Vulpia octoflora (Walt.) Rydb. var. *hirtella* (Piper) Henr.
San Miguel: Hoffmann s.n. Apr. 20, 1932 SBM#11898!; SBBG.
Santa Rosa: Hoffmann s.n. Apr. 17, 1929 SBM#6262!; RSA-POM; SBM.
Santa Cruz: Hoffmann s.n. Mar. 21, 1932 SBM#11770!; Hoffmann 256 SBM!; Abrams & Wiggins 46 DS!.
Anacapa: SBBG; SBM.
San Nicolas: Howell 8222 CAS!.
Santa Barbara: SBBG.
Santa Catalina: Brandegee 49 US!; Grant 3790 US!; Trask s.n. in Mar. 1901 MO!, NY!, US!; RSA-POM.
San Clemente: RSA-POM; SBBG.
Guadalupe: Palmer 97 NY!; Palmer 637 NY!; Moran 6741 SD!; Howell 8309 CAS!, DS!.

Potamogetonaceae

Potamogeton crispus L.
Santa Catalina: RSA-POM.

Potamogeton pectinatus L.
Santa Rosa: RSA-POM.
Santa Cruz: Clokey 4854 LAM!, LA!; RSA-POM; SBM.
Santa Catalina: RSA-POM.

Ruppia martima L.
Santa Rosa: Hoffmann s.n. Jun. 13, 1930 DS!; Hoffmann s.n. Apr. 28, 1930 CAS!; RSA-POM; SBM.
Santa Cruz: Daily 152 SCIR!.
Santa Catalina: Fosberg S4754 LAM!; Wolf 3591 DS!; RSA-POM; SBM.
San Clemente: RSA-POM.

Typhaceae

Typha domingensis Pers.
San Miguel: SBBG.
Santa Rosa: RSA-POM.
Santa Cruz: SBBG; SBM.
San Nicolas: Blakley 4158 SBBG!.
Santa Catalina: Trask s.n. in Mar. 1897 NY!.

Typha latifolia L.
San Nicolas: RSA-POM; SBBG.
Santa Catalina: Dunkle 2010 LAM!, AHFH!; Fosberg s.n. LAM!; RSA-POM; SBBG.
San Clemente: Raven 18018 RSA!; SBBG.

Zosteraceae

Phyllospadix scouleri Hook.
Anacapa: RSA-POM.
San Nicolas: RSA-POM.
Santa Barbara: RSA-POM.
Santa Catalina: RSA-POM.
San Clemente: RSA-POM.

Phyllospadix torreyi Wats.
San Miguel: SBBG; SBM.
Santa Rosa: RSA-POM; SBM.
Santa Cruz: RSA-POM; SBM.
Anacapa: SBBG.
San Nicolas: RSA-POM.
Santa Barbara: Philbrick & Benedict B70-35 SBBG!.
Santa Catalina: Fosberg S4575 LAM!; Fosberg S4877 LAM!; Fosberg S4757 LAM!; RSA-POM.
San Clemente: RSA-POM.
Guadalupe: Moran 17422 RSA!, SD!; Moran 18156 RSA!.

Zostera marina L.
Santa Rosa: SBM.
Santa Cruz: Dunkle 8568 LAM!; Johnstone s.n. in Dec. 1928 USC!; SBBG; SBM.
Anacapa: Dunkle 7671 LAM!; RSA-POM; SBM.
Santa Catalina: Fosberg S4750 LAM!; RSA-POM.
Guadalupe: Hubbs 19290 LAM!; Moran 7844 SD!.

APPENDIX II. INDEX TO THE DISPOSITION OF SYNONYMS, MISIDENTIFICATIONS, AND TAXA *INCERTAE SEDIS*

It is the intent of this section to indicate the disposition in this paper of taxa known to at least some earlier authors under names not here accepted, not to provide a technical synonymy of all insular taxa. Some of the names given here are indeed synonymous. Many are based on earlier concepts of certain taxa which were more inclusive or fragmented than those currently accepted. Excluded, for some saving of space, are all synonyms recognized in Munz and Keck (1959). It is hoped that readers will find this section useful for locating otherwise obscure reports and specimens upon which they are based. There is a need to document more fully the elimination of records from a flora to avoid interminable speculation as to their origin and fate.

The arrangement of this section is alphabetical by genus and species. First, the combination in question is at the left margin. In most cases, author citations for these names are corrected from its citation, if it was in error. Second, just below and indented is the name of the taxon under which the material or record is included here. Third, again below and indented from the above, a chronological listing of the references using the combination in question. Each entry consists of the authority, date of publication and an abbreviated notation of the insular occurrences to which the name applies. In many cases the specimens, duplicates of the collections, or the specimens upon which these reports most probably are based have been located. In these cases the specimens are cited just preceding the notation of the island. In the case of literature citations, very often subsequent authors simply repeat the citations of earlier workers without seeking out the specimens upon which the record is based.

Occasionally it was not possible to reach a decision as to the disposition of some reports. These are listed as *incertae sedis.* In a few cases a reference documenting the placement of certain taxa is noted following the accepted name used here (e.g., see *Baeria*).

Abronia alba Eastw.
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Eastwood (1898) NI; Davidson and Moxley (1923) NI, CL; Jepson (1925) NI; Hoffmann (1932a) MI, RO; Munz (1935) MI, RO, NI, CL; Eastwood (1941) MI, RO, NI; Gentry (1949) MI, RO, NI, CL; Dunkle (1950) MI, RO, NI, CL.

Abronia alba Eastw. var. *platyphylla* (Standl.) Jeps.
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Hoffmann (1932a) RO; Eastwood (1941) RO.

Abronia alba Eastw. var. *variabilis* Jeps.
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Hoffmann (1932a) RO, CR.

Abronia insularis Standl.
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Eastwood (1941) CL.

Abronia minor Standl.
Abronia umbellata Lam. with introgression from *A. latifolia* Esch. omitted (Tillett, 1967).
Eastwood (1941) RO, CR.

Abronia neurophylla Standl.
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Eastwood (1941) NI.

Abronia umbellata Lam. ssp. *alba* (Eastw.) Munz
Abronia umbellata Lam. with introgression from *A. maritima* Nutt. ex Wats. omitted (Tillett, 1967).
Munz and Keck (1959) MI, RO, NI, CL.

Achillea borealis Bong.
Achillea millefolium L.
Philbrick (1972) BA.

Achillea lanulosa Nutt.
Achillea millefolium L.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, RO, CR, AN, NI, BA, CA, CL; Raven (1963) CL; Foreman (1967) NI.

Achillea millefolium L. *lanulosa* Piper
Achillea millefolium L.
Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL.

Achyrachaena mollis Schauer
omitted as unsubstantiated on CA.
Brandegee (1890a) CA; Brandegee (1890b) CA; Eastwood (1941) CA.

Acrolasia gracilenta Rydb.
Mentzelia affinis Greene
Millspaugh and Nuttall (1923) CA.

Adenostoma fasciculatum H. & A. var. *obtusifolium* Wats.
Adenostoma fasciculatum H. & A. var. *fasciculatum*
Jepson (1909–1943) RO; Eastwood (1941) CR.

Adenostoma fasciculatum H. & A. var. *prostratum* Dunkle
Adenostoma fasciculatum H. & A. var. *fasciculatum*
Dunkle (1941) based on Dunkle 8496 LAM! RO; Dunkle (1950) RO.

Adiantum capillus-veneris L.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Munz (1935) CL.

Adiantum jordani C. Muell.
omitted as column transposition for CA.
Dunkle (1950) p. 293, BA.

Agoseris heterophylla Greene
omitted as unsubstantiated on NI.
Dunkle (1950) NI.
possibly *Malacothrix saxatilis* (Nutt.) T. & G.
Foreman (1967) based on Foreman 134 UC!, misidentified, NI.

Agoseris heterophylla Greene
probably *Agoseris grandiflora* (Nutt.) Greene
Dunkle (1950) MI.

Agropyron repens (L.) Beauv.
incertae sedis
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA; Eastwood (1941) MI, RO, CR, CA; Smith (1976) MI.
Lolium perenne L. ssp. *perenne*
Foreman (1967) based on Foreman 111 UC!, misidentified, NI.

Agrostis canina Bubani
Agrostis diegoensis Vasey
Brandegee (1890a) CA; Brandegee (1890b) CA.

Agrostis exarata Trin.
Agrostis diegoensis Vasey
Eastwood (1941) probably based on Abrams & Wiggins 370 DS!, US!, misidentified; also by Raven (1963) CL.

Agrostis exarata Trin.
Polypogon interruptus HBK.
Brandegee (1890a) probably based on Brandegee s.n. Mar. 13, 1890 UC!, misidentified, CA; Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Agrostis foliosa Vasey
Agrostis diegoensis Vasey
Jepson (1909–1943) RO, CA.

Agrostis microphylla Steud.
Agrostis exarata Trin.
Hoffmann (1932a) probably based on Hoffmann s.n. Aug. 7, 1930 SBM#10765!, misidentified, RO; Smith (1976) RO.

Agrostis scouleri Trin.
Agrostis exarata Trin.
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Eastwood (1941) RO, CR.

Agrostis verticillata Vill.
Agrostis semiverticillatus (Forsk.) Christensen
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) CR; Eastwood (1941) RO, CR, CA.

Allium amplectens Torr. in T. & G.
incertae sedis
Eastwood (1941) CR.

Allium hyalinum Curran
Allium praecox Bdg.
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.

Allium peninsulare Lemmon
Allium praecox Bdg.
Jepson (1909–1943) CA; Eastwood (1941) CA, CL; Munz and Keck (1959) CA, CL; Raven (1963) CL; Thorne (1967) CA; Wiggins (1980) CA, CL.

Allium serratum Wats.
Allium praecox Bdg.
Lyon (1886) CL; Brandegee (1890a) CA; Brandegee (1890b) CA, CL; Millspaugh and Nuttall (1923) CA.

Allocarya acanthocarpa Piper
incertae sedis
Wiggins (1980) GU.

Amaranthus blitoides Wats.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Eastwood (1941) CL.

Amaranthus graecizans L.
Amaranthus albus L.
Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) RO, CR; Eastwood (1941) MI, RO, CR, CA.

Ambrosia californica Rydb.
Ambrosia psilostachya DC. var. *californica* (Rydb.) Blake in Tides.
Eastwood (1941) CR, CA.

Ambrosia chamissonis Less.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Foreman (1967) BA.

Ambrosia psilostachya DC. var. *californica* (Rydb.) Blake in Tides.
omitted as unsubstantiated on RO.
Smith (1976) RO.

Amsinckia catalinensis Suksd.
Amsinckia intermedia F. & M. (Jepson, 1909–1943)
Eastwood (1941) CA.

Amsinckia congesta Suks.
Amsinckia intermedia F. & M. (Jepson, 1909–1943)
Eastwood (1941) CA.

Amsinckia douglasiana A. DC.
incertae sedis
Clokey (1931) CR.
Amsinckia intermedia F. & M.
Millspaugh and Nuttall (1923) based in part on Millspaugh 4616 F!, Millspaugh 4725 F!, Millspaugh 4796 F!, Millspaugh 4890 F!, Nuttall 46 F!, all misidentified, CA.

Amsinckia evermannii Suks.
Amsinckia intermedia F. & M. (Jepson, 1909–1943)
Eastwood (1941) CA, based on Evermann s.n. Mar. 25, 1918 CAS#26982!, CL.

Amsinckia insularis Suks.
Amsinckia intermedia F. & M. (Jepson, 1909–1943)
Eastwood (1941) CA, CL.

Amsinckia intermedia F. & M.
Amsinckia spectabilis F. & M. var. *spectabilis*
Macbride (1917) based on Trask 59 GH!, misidentified, NI.

Amsinckia lycopsoides Lehm.
incertae sedis
Greene (1887a) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Davidson (1896) CA.
Amsinckia spectabilis F. & M. var. *spectabilis*
Greene (1887b) probably based on Greene s.n. in Sep. 1886 ND-G#042845!, misidentified, MI; Yates (1889) MI; Brandegee (1890b) MI.

Amsinckia maritima Eastw.
incertae sedis
Eastwood (1941), MI, CL.
Amsinckia spectabilis F. & M. var. *spectabilis*
Eastwood (1898) based on Trask 59 GH!, misidentified, NI; Eastwood (1941) NI.

Amsinckia microsperma Suks.
Amsinckia spectabilis F. & M. var. *spectabilis* (Jepson, 1909–1943)
Eastwood (1941) CA.

Amsinckia nesophila Suks.
incertae sedis
Eastwood (1941) CA.

Amsinckia sanctinicolai Eastw.
Amsinckia spectabilis F & M. var. *nicolai* (Jeps.) Jtn. ex Munz
Jepson (1909–1943) NI.

Amsinckia spectabilis F. & M.
Amsinckia intermedia F. & M.
Brandegee (1890b, in footnote) CA.

Amsinckia St. Nicolai Eastw.
omitted as unsubstantiated on CR.
Eastwood (1941) CR.

Amsinckia swainiae Suks.
Amsinckia intermedia F. & M. (Jepson, 1909–1943)
Eastwood (1941) CR, CA.

Amsinckia tessellata Gray
incertae sedis
Brandegee (1890a) CA; Davidson (1896) CA.

Amsinckia vernicosa H. & A.
Amsinckia menziesii (Lehm.) Nels. & Macbr.
Watson (1876) based on Palmer 69 GH!, MO!, NY!, misidentified, GU; Eastwood (1929) GU; Dunkle (1950) GU.

Anaphalis margaritacea (L.) Benth. & Hook.
omitted as probable error; also omitted by Hall (1907).
Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA; Eastwood (1941) CA.

Andropogon barbinodis Lag.
Bothriochloa barbinodis (Lag.) Herter
Abrams (1917) CA; Thorne (1967) CA.

- *Andropogon saccharoides* Swartz
  - *Bothriochloa barbinodis* (Lag.) Herter
    - Davidson (1894) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CA.
- *Antennaria margaritacea* Benth. nom. nud. in lit.
  - omitted as probable error.
    - Brandegee (1890a) CA.
- *Aphyllon fasciculata* (Nutt.) T. & G. ex Gray
  - *Orobanche fasciculata* Nutt.
    - Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.
- *Aplopappus canus* (Gray) Blake
  - *Haplopappus canus* (Gray) Blake
    - Munz (1935) CL, GU; Dunkle (1950) CL, GU.
  - *Haplopappus detonsus* (Greene) Raven
    - Munz (1935) RO, CR; Dunkle (1942) AN; Dunkle (1950) RO, CR, AN.
- *Aplopappus ericoides* (Less.) H. & A.
  - *Haplopappus ericoides* (Less.) H. & A. ssp. *ericoides*
    - Greene (1887b) MI; Yates (1889) MI; Brandegee (1890b) MI; Munz (1935) MI.
- *Aplopappus squarrosus* H. & A.
  - *Haplopappus squarrosus* H. & A. ssp. *grindelioides* (DC.) Keck
    - Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.
- *Aplopappus venetus* (HBK.) Blake var. *furfuraceus* (Greene) Munz
  - omitted as column transposition for CA.
    - Dunkle (1950, p. 293) BA.
  - omitted as unsubstantiated on CR.
    - Dunkle (1950) CR.
  - *Haplopappus venetus* (HBK.) Blake ssp. *furfuraceus* (Greene) Hall
    - Munz (1935) CA, CL; Dunkle (1950) CA, CL.
- *Aplopappus venetus* (HBK.) Blake var. *sedoides* (Greene) Munz
  - *Haplopappus venetus* (HBK.) Blake ssp. *sedoides* (Greene) Munz
    - Munz (1935) RO, CR; Dunkle (1950) RO, CR.
- *Aplopappus venetus* (HBK.) Blake var. *vernonioides* (Nutt) Munz
  - omitted as column transposition for CA.
    - Dunkle (1950, p. 293) BA.
  - *Haplopappus venetus* (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall
    - Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, NI, CL.
- *Arabis arcuata* Gray
  - *Arabis hoffmannii* (Munz) Roll.
    - Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.
- *Arctostaphylos* sp.
  - *incertae sedis*
    - Greene (1885) GU; Eastwood (1929) GU.
- *Arctostaphylos andersonii* Gray var. *viridissima* (Eastw.) Jeps.
  - *Arctostaphylos catalinae* P.V. Wells
    - Jepson (1909–1943) CA.
  - *Arctostaphylos confertiflora* Eastw.
    - Jepson (1909–1943) RO.
  - *Arctostaphylos viridissima* (Eastw.) McMinn
    - Jepson (1909–1943) CR.
- *Arctostaphylos crustacea* Eastw.
  - probably *Arctostaphylos tomentosa* (Pursh) Lindl. ssp. *insulicola* P.V. Wells.
    - Munz and Keck (1959) RO, CR.
- *Arctostaphylos diversifolia* Parry
  - *Comarostaphylis diversifolia* (Parry) Greene ssp. *planifolia* (Jeps.) Wallace ex Thorne
    - Brandegee (1888) RO; Yates (1889) RO, CR; Ford (1890) CR; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA; Davidson (1896) CA; Trask (1899) CA; Munz (1935) RO, CR, CA; Dunkle (1950) RO, CR, CA.
- *Arctostaphylos glandulosa* Eastw.
  - *Arctostaphylos tomentosa* (Pursh) Lindl. ssp. *subcordata* (Eastw.) P.V. Wells.
    - Jepson (1909–1943), in references CR.
- *Arctostaphylos insularis* Greene
  - *incertae sedis*
    - Dunkle (1950) CR.
  - *Arctostaphylos catalinae* P.V. Wells
    - Davidson (1896) CA; Munz (1935) CA; Dunkle (1950) CA.
  - *Arctostaphylos confertiflora* Eastw.
    - Munz (1935) based on Munz & Crow 11587 POM!, misidentified, RO; Eastwood (1941) RO; Dunkle (1950) RO; Smith (1976) RO.
- *Arctostaphylos pechoensis* Dudley var. *viridissima* Eastw.
  - *Arctostaphylos catalinae* P.V. Wells
    - Munz and Keck (1959) CA.
  - *Arctostaphylos viridissima* (Eastw.) McMinn
    - Abrams and Ferris (1923–1960) CR; Munz (1935) CR; Eastwood (1941) CR; Munz and Keck (1959) CR.
- *Arctostaphylos pungens* HBK.
  - *Arctostaphylos catalinae* P.V. Wells
    - Brandegee (1890a) CA.
- *Arctostaphylos stanfordiana* Parry
  - *incertae sedis*
    - Yates (1889) CR.
- *Arctostaphylos subcordata* Eastw.
  - *Arctostaphylos catalinae* P.V. Wells
    - Thorne (1967) CA.
  - *Arctostaphylos tomentosa* (Pursh) Lindl. ssp. *subcordata* (Eastw.) P.V. Wells
    - Abrams and Ferris (1923–1960) CR; Munz (1935) RO, CR; Eastwood (1941) CR; Dunkle (1950) RO, CR; Munz and Keck (1959) CR.
- *Arctostaphylos subcordata* Eastw. var. *confertiflora* (Eastw.) Munz
  - *Arctostaphylos confertiflora* Eastw.
    - Munz and Keck (1959) RO.
- *Arctostaphylos tomentosa* (Pursh) Lindl.
  - *incertae sedis*
    - Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Jepson (1909–1943) CR; Hoffmann (1932b) CR; Munz (1935) CR; Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.

Arctostaphylos catalinae P.V. Wells
Lyon (1886) CA; Brandegee (1890b) CA; Munz (1935) CA; Eastwood (1941) CA; Dunkle (1950) CA.
Arctostaphylos tomentosa (Pursh) Lindl. var. *hispida* Hook. nom. nud. pro. syn.
Arctostaphylos tomentosa (Pursh) Lindl. ssp. *insulicola* P.V. Wells
Hoffmann (1932b) based on Hoffmann s.n. Jun. 29, 1930 SBM#5736!, annotated by Eastwood but no such combination found, misidentified, CR.
Artemisia californica Less. f. erecto Dunkle nom. nud. pro. syn.
Artemisia californica Less.
Dunkle (1950) MI, RO, CR, CA.
Artemisia californica Less. f. *flexila* Dunkle nom. nud. pro. syn.
Artemisia californica Less.
Dunkle (1950) MI, RO, CR, CA.
Artemisia californica Less. var. *insularis* (Rydb.) Munz
Artemisia californica Less.
Eastwood (1941) MI, RO, CR, AN, CA; Dunkle (1950) AN.
Artemisia nesiotica Raven
Abrams and Ferris (1923–1960) NI, CL; Howell (1935) NI; Munz (1935) NI, CL; Eastwood (1941) NI, BA, CL; Dunkle (1942) BA; Dunkle (1950) NI, BA, CL.
Artemisia ludoviciana Nutt.
Artemisia douglasiana Bess. in Hook.
Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Ford (1890) CR; Eastwood (1941) RO, CR.
Artemisia vulgaris L.
Artemisia douglasiana Bess. in Hook.
Brandegee (1890b) ref. as same as *A. ludoviciana* of previous lists, RO, CR, CA; Davidson (1896) CA; Millspaugh and Nuttall (1923) CA.
Aspidium sp.
Athyrium felix-femina (L.) Roth var. *sitchensis* Rupr. (ref. Brandegee, 1890b).
Greene (1887a) CR.
Aspidium aculeatum Swartz
Dryopteris arguta (Kaulf.) Watt
Lyon (1886) CA; Brandegee (1890b) CA.
Aspidium munitum Kaulf.
Polystichum munitum (Kaulf.) Presl ssp. *solitarium* Maxon
Watson (1876) GU.
Aspidium rigidum Swartz
Dryopteris arguta (Kaulf.) Watt
Greene (1887a) CR; Brandegee (1888) RO; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA; Trask (1899) CA.
Asplenium filix-foemina Bernh. [sic]
Athyrium felix-femina (L.) Roth. var. *sitchensis* Rupr.
Brandegee (1890b) CR.
Aster foliaceus Lindl.
Aster chilensis Nees var. *chilensis*
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO.

Astragalus antiselli Gray
Astragalus trichopodus (Nutt.) Gray ssp. *trichopodus*
Lyon (1886) CA; Brandegee (1890b) CA.
Astragalus didymocarpus H. & A.
omitted as unsubstantiated on NI; also omitted by Barneby (1964).
Eastwood (1898) NI.
Astragalus douglasii Gray
Astragalus curtipes Gray
Munz (1935) MI; Dunkle (1950) MI.
Astragalus miguelensis Greene
Dunkle (1942) probably based on Elmore 252 AHFH!, misidentified, AN; Dunkle (1950) AN.
Astragalus fastidiosus Greene
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne
Eastwood (1941) CA.
Astragalus leucopsis (T. & G.) Torr.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Eastwood (1941) BA; Dunkle (1942) BA; Gentry (1949) BA; Dunkle (1950) BA.
Astragalus curtipes Gray
Brandegee (1890b) probably based on Greene (1887b), misidentified, MI, see also Barneby (1964) reference for *A. leucopsis* (T. & G.) Torr. var. *brachypus* Greene
Astragalus miguelensis Greene
Gentry (1949) based on Elmore 319 AHFH!, misidentified, MI, based on Elmore 252 AHFH!, misidentified, AN; Dunkle (1950) MI, AN in part.
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne
Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) CR; Brandegee (1890b) RO, CR, CA; Trask (1899) CA; Jepson (1909–1943) CR, CA; Munz (1935) CR, CA; Eastwood (1941) CA; Dunkle (1942) AN; Gentry (1949) CA; Dunkle (1950) RO, CR, AN in part; Munz and Keck (1959) CR, CA; Thorne (1967) CA; Thorne (1969) CA.
Astragalus leucopsis (T. & G.) Torr. var. *brachypus* Greene
probably *Astragalus trichopodus* (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne.
Dunkle (1950) CR.
Astragalus nevinii Gray
omitted as unsubstantiated on CA; also omitted by Barneby (1964).
Davidson and Moxley (1923) CA; Eastwood (1941) CA; Gentry (1949) CA.
Astragalus miguelensis Greene (Barneby, 1964, p. 464)
Jepson (1909–1943) based on Hemphill [at UC], misidentified, AN; Eastwood (1941) AN; Gentry (1949) AN.
Astragalus traskiae Eastw.
Jepson (1909–1943) BA; Eastwood (1941) BA; Dunkle (1942) BA; Gentry (1949) BA; Dunkle (1950) BA.
Astragalus robeartsii Eastw.
incertae sedis
Trask (1904) CL.

Astragalus traskiae Eastw.
omitted as column transposition for CA.
Dunkle (1950, p. 293) BA.
Astragalus miguelensis Greene (Barneby, 1964, p. 462)
Abrams and Ferris (1923–1960) AN.
Astragalus nevinii Gray (Barneby, 1964, p. 462)
Eastwood (1941) CL; Dunkle (1950) CL.

Astragalus trichopodus (Nutt.) Gray var. *gaviotus* (Elmer) Jeps.
Astragalus trichopodus (Nutt.) Gray ssp. *trichopodus*
Jepson (1925) CA.

Astragalus trichopodus (Nutt.) Gray var. *lonchus* (Jones) Barneby
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne
Barneby (1964) CR, AN, CA.

Atriplex bracteosa (Dur. & Hilg.) Wats.
Atriplex serenana A. Nels. var. *serenana*
Hoffmann (1932a) RO.

Atriplex coulteri (Moq.) D. Dietr.
omitted as column transposition for CA.
Dunkle (1950, p. 293) BA.

Atriplex microcarpa (Benth.) D. Dietr.
Atriplex pacifica Nels.
Greene (1887a) based on Greene s.n. in Jul.–Aug. 1886 ND-G#015274!, US!, misidentified, CR.

Atriplex pacifica Nels.
omitted as column transposition for CA.
Dunkle (1950, p. 293) BA.
Atriplex coulteri (Moq.) D. Dietr.
Munz (1935) probably based on Hoffmann s.n. Jun. 13, 1930 POM!, misidentified, RO; Eastwood (1941) RO; Dunkle (1950) RO; Munz and Keck (1959) RO; Smith (1976) RO.

Atriplex palmeri Wats.
Atriplex barclayana (Benth.) D. Dietr. ssp. *palmeri* (Wats.) Hall & Clem.
Watson (1876) GU; Greene (1885) GU; Eastwood (1929) GU.

Atriplex rosea L.
Aphanisma blitoides Nutt. ex Moq. in DC.
Dunkle (1942) based on Dunkle 7459 AHFH!, misidentified, BA; Dunkle (1950) BA.

Atriplex rosei Standl.
Atriplex barclayana (Benth.) D. Dietr. ssp. *dilitata* (Greene) Hall & Clem.
Eastwood (1929) GU.

Atriplex serenana A. Nels. var. *davidsonii* (Standl.) Munz
Atriplex serenana A. Nels. var. *serenana*
Eastwood (1941) RO, CR; Thorne (1967) based on Eastwood 6529 US!, misidentified, CA; Smith (1976) RO.

Atriplex watsonii A. Nels. in Abrams
omitted as column transposition for CA.
Dunkle (1950, p. 293) BA.

Audibertia nivea Benth.
incertae sedis
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Ford (1890) CR.

Audibertia palmeri Gray
Salvia mellifera Greene
Lyon (1886) CA; Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Brandegee (1890b) CR, CA.

Baccharis viminea DC.
Baccharis glutinosa Pers.
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA; Dunkle (1942) AN; Munz and Keck (1959) Channel Islands; Raven (1963) CL.

Baeria aristata Cov.
Lasthenia coronaria (Nutt.) Ornduff
Dunkle (1950) GU.

Baeria chrysostoma F. & M.
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978)
Millspaugh and Nuttall (1923) CA.

Baeria chrysostoma F. & M. var. *gracilis* Hall
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Munz (1935) on the islands; Dunkle (1942) AN; Gentry (1949) CR, CL; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL.

Baeria chrysostoma F. & M. ssp. *hirsutula* (Greene) Ferris
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Munz and Keck (1959) Channel Islands.

Baeria chrysostoma F. & M. var. *palmeri* (Gray) J.T. Howell
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Howell (1942) GU.

Baeria coronaria (Nutt.) Gray
Lasthenia coronaria (Nutt.) Ornduff
Brandegee (1900) GU; Eastwood (1929) GU.

Baeria gracilis Gray
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978)
Brandegee (1888) RO, CR; Yates (1889) RO, CR, AN; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA; Eastwood (1898) NI; Brandegee (1900) GU; Eastwood (1929) GU.

Baeria hirsutula Greene
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Munz (1935) MI, RO, CR; Eastwood (1941) MI, RO, CR, CA; Dunkle (1942) BA; Dunkle (1950) MI, RO, CR, NI, BA, CA.

Baeria macrantha (Gray) Gray
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Munz and Keck (1959) MI, RO.

Baeria palmeri Gray
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Watson (1876) GU; Greene (1885) GU; Vasey and Rose (1890) GU; Eastwood (1929) GU.

Baeria palmeri Gray var. *clementina* Gray
Lasthenia californica DC. ex Lindl. (Johnson and Ornduff, 1978).
Lyon (1886) CA, CL; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) MI, RO, CR, CA, CL; Davidson (1896) CA, CL; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA, CL.

Bahia lanata Nutt. var.
Eriophyllum lanatum (Pursh) Forbes var. *grandiflorum* (Gray) Jeps.
Watson (1876) probably based on Palmer s.n. in 1875 GH!, GU; Eastwood (1929) GU.

Berula angustifolia Koch
Berula erecta (Huds.) Cov.
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Brandegee (1890b) MI, CR; Eastwood (1941) MI, CR.

Bigelovia veneta (HBK.) Gray
Haplopappus venetus (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall
Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Ford (1890) CR; Brandegee (1890b) MI, RO, CR, CA.

Blepharipappus platyglossus (F. & M.) Greene
Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck
Millspaugh and Nuttall (1923) CA.

Bloomeria aurea Kell.
Bloomeria crocea (Torr.) Cov. var. *crocea*
Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA.

Brahea edulis Wendl.
Erythea edulis (Wendl.) Wats.
Watson (1876) GU.

Brassica campestris L.
Brassica rapa L. ssp. *sylvestris* (L.) Janchen
Greene (1885) GU; Greene (1887b) MI; Brandegee (1888) CR; Yates (1889) MI, CR; Brandegee (1890a) CA; Brandegee (1890b) MI, CR, CA; Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Eastwood (1941) MI, CR, CA; Smith (1976) RO, CR.

Brickellia californica (T. & G.) Gray
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Dunkle (1950) CL.

Brodiaea sp.
incertae sedis
Howell (1942) GU.

Brodiaea capitata Benth.
Dichelostemma pulchellum (Salisb.) Heller
Greene (1885) GU; Lyon (1886) CL; Brandegee (1888) RO; Vasey and Rose (1890) GU; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA, CL; Eastwood (1898) NI; Trask (1899) CA; Munz (1935) on the islands; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA, CL; Dunkle (1942) AN; Gentry (1949) CL; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL, GU.

Brodiaea clementina (Hoov.) Munz
Triteleia clementina Hoov.
Munz and Keck (1959) CL.

Brodiaea filifolia Wats.
Brodiaea kinkiensis Niehaus
Munz and Keck (1959) CL.

Brodiaea insularis Greene
Dichelostemma pulchellum Heller
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Eastwood (1929) GU.

Brodiaea laxa (Benth.) Wats.
Triteleia clementina Hoov.
Munz (1935) CL; Dunkle (1950) CL.

Brodiaea lugens Greene
Triteleia guadalupensis Lenz
Brandegee (1900) GU; Eastwood (1929) GU; Munz and Keck (1959) GU; Raven (1963) GU.

Brodiaea minor (Benth.) Wats.
Brodiaea jolonensis Eastw.
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Trask (1899) CA.

Brodiaea pulchella (Salisb.) Greene
Dichelostemma pulchellum (Salisb.) Heller
Foreman (1967) NI.

Brodiaea synandra (Heller) Jeps.
Brodiaea jolonensis Eastw.
Hoffmann (1932a) RO; Munz (1935) RO; Eastwood (1941) RO, CR, CA.

Bromus sp.
incertae sedis
Greene (1887a) CR; Greene (1887b) MI.

Bromus carinatus H. & A.
Bromus maritimus (Piper) Hitchc.
Thorne (1969) based on Fosberg S4484 (LAM!, misidentified, CA.

Bromus carinatus H. & A. var. *hookerianus* (Thurb. in Torr.) Shear
Bromus carinatus H. & A.
Eastwood (1941) MI, RO, CR, NI, CA, CL; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, NI, CA, CL.

Bromus ciliatus L.
possibly *Bromus vulgaris* (Hook.) Shear.
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA.

Bromus hookerianus Thurb. in Torr.

Bromus carinatus H. & A.

Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA, CL; Eastwood (1898) NI, ref. to MI, RO, CR, CA, CL.

Bromus laevipes Shear

omitted as unsubstantiated on AN.

Dunkle (1950) AN.

Bromus pseudolaevipes Wagnon

Hoffmann (1932a) probably based on [Hoffmann] s.n. Jun. 13, 1930 SBM#10180!, misidentified, RO; Eastwood (1941) RO; Hoffmann (1932a) probably based on Hoffmann s.n. Jun. 29, 1930 SBM#10132!, misidentified, CR; Eastwood (1941) CR.

Bromus marginatus Nees in Steud.

Bromus carinatus H. & A.

Hoffmann (1932a) MI, RO, CR, AN; Eastwood (1941) MI, RO, CR; Dunkle (1950) MI, RO, CR, AN, BA; Smith (1976) MI, RO, CR, AN.

Bromus maritimus (Piper) Hitchc.

Thorne (1967) based on Fosberg S4484 LAM!, misidentified, CA.

Bromus maximus Desf.

Bromus diandrus Roth.

McClatchie (1894) CA; Greene (1885) GU.

Bromus orcuttianus Vasey

Bromus pseudolaevipes Wagnon

Jepson (1909–1943) CA; Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Abrams (1917) CA; Eastwood (1941) CA.

Bromus rigidus Roth. ex Reichenb.

Bromus diandrus Roth.

Millspaugh and Nuttall (1923) CA; Clokey (1931) CR; Hoffmann (1932a) RO; Eastwood (1941) MI, RO, CA; Dunkle (1942) AN, BA; Dunkle (1950) MI, RO, BA, CA.

Bromus rigidus Roth ex Reichenb. var. *gussonei* (Parl.) Coss. & Dur.

Bromus diandrus Roth

Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) MI, RO, CR; Eastwood (1941) MI, RO, CR, NI, CA.

Bromus sterilis L.

incertae sedis

Dunkle (1950) GU.

Bromus diandrus Roth.

Eastwood (1929) based in part on Mason 1543 GH!, misidentified, GU.

Bromus rubens L.

Dunkle (1942) possibly based on Bond 373 SBM!, misidentified, BA; also denied by Philbrick (1972).

Bromus tectorum L.

Watson (1876) based on Palmer 99 (in part) NY!.

Bromus trinii Desv. in C. Gay

Watson (1876) based on Palmer 99 (in part) NY!.

Bromus subvelutinus Shear

Bromus carinatus H. & A.

Hoffmann (1932a) based on Hoffmann s.n. Apr. 18, 1929 SBM#7649!, misidentified, RO; Eastwood (1941) RO.

Bromus pseudolaevipes Wagnon

Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Bromus tectorum L.

Bromus sterilis L.

Millspaugh and Nuttall (1923) based in part on Nuttall 95 F!, Nuttall 562 F!, Nuttall 1219 F!, all misidentified, CA; Eastwood (1941) CA.

Bromus virens Buckl.

Bromus carinatus H. & A.

Eastwood (1898) NI.

Bromus vulgaris (Hook.) Shear

Bromus trinii Desv. in C. Gay

Dunkle (1942) based on Dunkle 7242 AHFH!, misidentified, BA; Dunkle (1950) BA.

Buda marina (L.) Dumort.

Spergularia marina (L.) Griesb.

Davidson (1896) CA.

Cakile edentula (Bigel.) Hook. var. *californica* Fern.

Cakile edentula (Bigel.) Hook. var. *edentula*

Hoffmann (1932b) MI, RO; Munz (1935) MI; Munz and Keck (1959) Channel Islands.

Calais linearifolia DC.

Microseris linearifolia (DC.) Sch.-Bip.

Greene (1887a) CR; Yates (1889) CR.

Calamintha palmeri Gray

Satureja palmeri (Gray) Briq.

Watson (1876) based on Palmer 66 NY!, GU; Greene (1885) GU; Vasey and Rose (1890) GU; Eastwood (1929) GU.

Calandrinia caulescens HBK.

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr.

Hoffmann (1932a) MI, RO; Eastwood (1941) MI, RO, CR, CA.

Calandrinia menziesii (Hook.) T. & G.

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr.

Watson (1876) GU; Greene (1885) GU; Greene (1887a) CR; Yates (1889) CR; Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO; Howell (1942) GU.

Calandrinia menziesii (Hook.) T. & G. var. *caulescens* (HBK.) Gray

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr.

Vasey and Rose (1890) GU.

Calochortus sp.

incertae sedis

Greene (1887a) CR.

Calochortus albus Dougl. ex Benth. var. *rubellus* Greene

Calochortus albus Dougl. ex Benth. var. *albus*

Clokey (1931) CR; Eastwood (1941) CR; Dunkle (1950) CR; Smith (1976) CR.

Calochortus kennedyi Porter
Calochortus catalinae Wats.
Lyon (1886) CA.

Calochortus palmeri Wats.
Calochortus catalinae Wats.
Trask (1899) CA; Brandegee (1890b) CA.

Calochortus venustus Benth.
Calochortus catalinae Wats.
Brandegee (1888) CR; Yates (1889) CR.

Calystegia macrostegia (Greene) Brummitt ssp. *cyclostegia* (House) Brummitt
omitted as unsubstantiated on CR; also omitted by Brummitt pers. comm.
Smith (1976) CR.

Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
Foreman (1967) NI; Philbriek (1972) NI, BA, CL.

Camissonia guadalupensis (Wats.) Raven ssp. *guadalupensis*
Camissonia guadalupensis (Wats.) Raven ssp. *clementina* (Raven) Raven
Wiggins (1980) CL.

Caprifolium hispidulum Gray var. *californicum* Greene
Lonicera hispidula (Lindl.) Dougl. ex T. & G. var. *vacillans* Gray
Davidson (1896) CA.

Capriola dactylon (L.) Kuntze
Cynodon dactylon (L.) Pers.
Millspaugh and Nuttall (1923) CA.

Capsella divaricata Walp.
Capsella bursa-pastoris (L.) Medic.
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR.

Cardamine integrifolia (Nutt.) Greene
Cardamine californica Greene
Greene (1887a) CR; Yates (1889) CR.

Cardamine paucisecta Benth.
Cardamine californica Greene
Brandegee (1890b) CR; Millspaugh and Nuttall (1923) CA.

Carex sp.
incertae sedis
Greene (1887a) CR; Brandegee (1890a) CA.

Carex abrupta Mkze.
Carex montereyensis Mkze.
Clokey (1931) based on Clokey 4874 LAM!, misidentified, CR; Eastwood (1941) CR; Munz (1974) CR; Smith (1976) CR.

Carex angustata Boott
incertae sedis
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.

Carex douglasii Boott
incertae sedis
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Eastwood (1941) RO, CR.

Carex glabra Boott
incertae sedis
Eastwood (1941) CR.

Carex praegracilis W. Boott
Carex tumulicola Mkze.
Munz (1935) probably based on Munz 6737 POM!, misidentified, CL.

Carex tumulicola Mkze.
Carex praegracilis W. Boott
Thorne (1967) based on Thorne 35902 RSA!, misidentified, CA; Munz (1974) RO, CR.

Carpobrotus chilensis (Mol.) N.E. Br.
Carpobrotus aequilaterus (Haw.) N.E. Br.
Raven (1963) CL.

Castilleja affinis H. & A. var. *contentiosa* (Macbr.) Bacig.
Castilleja affinis H. & A. ssp. *affinis*
Smith (1976) RO, AN?; omitted since not recognized by L. Heckard (pers. comm.).

Castilleja affinis H. & A. ssp. *insularis* (Eastw.) Munz
Castilleja affinis H. & A. ssp. *affinis*
Munz and Keck (1959) CR; Smith (1976) CR.

Castilleja anacapensis Dunkle
Castilleja affinis H. & A. ssp. *affinis*
Dunkle (1942) based on Dunkle 7639 AHFH!, LAM!, and Dunkle 7661 AHFH!, LAM!, AN; Gentry (1949) AN; Dunkle (1950) AN.

Castilleja foliolosa H. & A.
omitted as unsubstantiated on RO and CR.
Eastwood (1941) CR; Dunkle (1950) RO, CR.
Castilleja guadalupensis Bdg.
Watson (1876) GU; Eastwood (1929) GU; Dunkle (1950) GU.

Castilleja hololeuca Greene
omitted as unsubstantiated on CA and CL.
Jepson (1925) CA, CL.

Castilleja hololeuca Greene var. *grisea* (Dunkle) Munz
Castilleja grisea Dunkle
Munz and Keck (1959) CL.

Castilleja latifolia H. & A.
omitted as unsubstantiated on CR.
Gentry (1949) CR.
Castilleja mollis Penn.
Hoffmann (1932b) RO; Munz (1935) RO; Eastwood (1941) RO; Gentry (1949) RO; Dunkle (1950) RO.

Castilleja latifolia H. & A. ssp. *insularis* Eastw.
Castilleja affinis H. & A. ssp. *affinis*
Eastwood (1941) CR.

Castilleja parviflora Bong.
Castilleja affinis H. & A. ssp. *affinis*
Lyon (1886) CA; Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR, CA.

Castilleja parviflora Bong. var. *californica* (Abrams) Zeile.
Castilleja affinis H. & A. ssp. *affinis*
Hoffmann (1932b) RO, CR.

Castilleja parviflora Bong. var. *douglasii* (Benth.) Jeps.
Castilleja affinis H. & A. ssp. *affinis*
Hoffmann (1932b) RO, CR.

Castilleja sp.
Castilleja grisea Dunkle
Gentry (1949) based on Elmore 384 AHFH!, Elmore 411 LAM!, CL.

Castilleja wightii Elmer
Castilleja affinis H. & A. ssp. *affinis*
Smith (1976) RO?, CR, AN.

Castilleja wightii Elmer ssp. *anacapensis* (Dunkle) Penn.
Castilleja affinis H. & A. ssp. *affinis*
Abrams and Ferris (1923–1960) AN.

Catapodium rigidum (L.) C.E. Hubb.
Scleropoa rigida (L.) Griseb.
Thorne (1967) CA.

Caulanthus lasiophyllus (H. & A.) Pays. var. *inalienum* Rob.
Caulanthus lasiophyllus (H. & A.) Pays.
Dunkle (1942) AN.

Caulanthus lasiophyllus (H. & A.) Pays. var. *rigidum* Rob.
Caulanthus lasiophyllus (H. & A.) Pays.
Dunkle (1942) AN.

Ceanothus arboreus Greene var. *glabra* Jeps.
Ceanothus arboreus Greene
Jepson (1925) RO; Munz (1935) RO; Eastwood (1941) RO.

Ceanothus crassifolius Torr.
Ceanothus megacarpus Nutt. ssp. *insularis* (Eastw.) Raven
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Ford (1890) CR; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA; Jepson (1909–1943) CR; Millspaugh and Nuttall (1923) CA; Dunkle (1950) MI, RO, CR, AN, CA.

Ceanothus crassifolius Torr. var. *planus* Abrams
incertae sedis
Jepson (1925) CR.

Ceanothus cuneatus (Hook.) Nutt.
incertae sedis
Watson (1876) GU; Eastwood (1929) GU; Dunkle (1950) GU.
Ceanothus megacarpus Nutt. ssp. *megacarpus*
Trask (1899) CA in part.

Ceanothus insularis Eastw.
Ceanothus megacarpus Nutt. ssp. *insularis* (Eastw.) Raven
Abrams and Ferris (1923–1960) RO, CR, CA; Eastwood (1941) RO, CR, CA, CL; Munz and Keck (1959) RO, CR, CA.

Ceanothus megacarpus Nutt. var. *pendulus* McMinn
Ceanothus megacarpus Nutt. ssp. *megacarpus*
McMinn (1942) based in part on Parish 10747 DS!, CA.

Ceanothus sorediatus H. & A.
Ceanothus arboreus Greene
Lyon (1886) CA.

Centaurium venustum (Gray) Rob.
Centaurium davyi (Jeps.) Abrams
Gentry (1949) based on Elmore 204 LAM!, misidentified, RO.
Centaurium davyi (Jeps.) Abrams
Clokey (1931) based on Clokey 5117 NY!, misidentified, CR; Eastwood (1941) CR; Gentry (1949) CR.

Centunculus minimus L.
Anagallis minima (L.) Krause
Hoffmann (1932b) RO; Munz (1935) RO; Eastwood (1941) RO; Munz and Keck (1959) RO.

Cerastium viscosum L.
Cerastium glomeratum Thuill.
Hoffmann (1932a) MI, RO, CR; Munz (1935) MI, CL; Eastwood (1941) MI, RO, CR, CA.

Cerasus ilicifolia Nutt. ex H. & A.
Prunus lyonii (Eastw.) Sarg.
Trask (1899) CA.

Cerasus ilicifolia Nutt. ex H. & A. var. *integrifolia*
Prunus lyonii (Eastw.) Sarg.
Trask (1899) CA.

Ceratochloa grandiflora Hook.
Bromus carinatus H. & A. (Raven, 1963).
Lyon (1886) CL.

Cercocarpus betulaefolius Nutt. ex Hook.
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne
Greene (1887a) CR; Yates (1889) CR.

Cercocarpus betuloides Nutt. ex T. & G. var. *alnifolius* (Rydb.) Dunkle
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne
Dunkle (1950) RO, CR, CA.

Cercocarpus betuloides Nutt. ex T. & G. var. *multiflorus* Jeps.
Cercocarpus betuloides Nutt. ex T. & G. ssp. *betuloides*
Hoffmann (1932b) CR; Munz (1935) CR; Eastwood (1941) CR; Dunkle (1950) CR.
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne
Jepson (1909–1943) CA; Jepson (1925) CA; Eastwood (1941) CA; Dunkle (1950) CA.

Cercocarpus betuloides Nutt. ex T. & G. var. *traskiae* (Eastw.) Dunkle
Cercocarpus traskiae Eastw.
Dunkle (1950) CA; Munz and Keck (1959) CA.

Cercocarpus parvifolius Nutt.
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne
Lyon (1886) CA; Brandegee (1890b) CR, CA; Trask (1899) CA.

Cercocarpus traskiae Eastw.
Cercocarpus betuloides Nutt. ex T. & G. ssp. *blancheae* (C.K. Schneid.) Thorne
Munz (1935) probably based on Wolf 2752 RSA!, misidentified, CR.

Cereus sp.
incertae sedis
Yates (1889) AN.

Cereus emoryi Engelm.
Bergerocactus emoryi (Engelm.) Britt. & Rose
Lyon (1886) CL; Brandegee (1890a) CA; Brandegee (1890b) CA, CL; Trask (1899) CA; Trask (1904) CL; Jepson (1909–1943) CA, CL; Jepson (1925) CL; Munz (1935) CA, CL; Eastwood (1941) CA, CL;

Dunkle (1950) CA, CL; Munz and Keck (1959) CA, CL.

Chaenactis tenuifolia Nutt.

Chaenactis glabriscula DC. var. *lanosa* (DC.) Hall

Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Eastwood (1941) RO.

Chaetopappa lyonii (Gray) Keck

Pentachaeta lyonii Gray

Abrams and Ferris (1923–1960) CA; Munz and Keck (1959) CA; Munz (1974) CA.

Cheilanthes californica (Hook.) Mett.

omitted as column transposition for CA.

Dunkle (1950, p. 293) BA.

Aspidotis californica (Hook.) Nutt. ex Copel.

Greene (1887a) CR; Yates (1889) CR; Yates (1890) CR; Brandegee (1890a) CA; Brandegee (1890b) CA; Trask (1899) CA; Millspaugh and Nuttall (1923) CA; Clokey (1931) CR; Hoffmann (1932a) CR; Munz (1935) CR, CA; Dunkle (1940a) CR, CA; Eastwood (1941) CR, CA; Dunkle (1950) CR.

Cheilanthes clevelandii D.C. Eat.

Dunkle (1940a) RO, CR; Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.

Cheilanthes myriophylla Desv.

Cheilanthes clevelandii D.C. Eat.

Brandegee (1888) based on Brandegee s.n. in 1888 UC!, misidentified, RO, based on Brandegee s.n. in Apr. 1888 UC!, misidentified, CR; Yates (1889) CR; Yates (1890) CR; Brandegee (1890b) RO, CR.

Cheilanthes newberryi (D.C. Eat.) Domin

Notholaena newberryi D.C. Eat.

Munz and Keck (1959) CL; Raven (1963) CL.

Cheiranthus asper Cham. & Schlecht.

incertae sedis

Brandegee (1888) RO; Brandegee (1890b) RO.

Chenopodium album L.

Chenopodium murale L.

Watson (1876) based on Palmer s.n. in 1875 NY!, misidentified, GU; Lyon (1886) (possibly according to Raven, 1963), CL; Dunkle (1942) probably based on Dunkle 7610 LAM!, misidentified, AN; Yates (1889) MI.

Chenopodium berlandieri Moq. ssp. *zschakei* (J. Murr.) Zobel.

Chenopodium berlandieri Moq. var. *sinuatum* (J. Murr.) H.A. Wahl

Thorne (1967) CA.

Chorizanthe wheeleri Wats.

omitted as unsubstantiated on CA and CL.

Eastwood (1941) CA, CL.

Cirsium coulteri Harv. & Gray in Gray

Circium proteanum J.T. Howell

Eastwood (1941) RO, CR.

Cirsium occidentale (Nutt.) Jeps. var. *coulteri* (Harv. & Gray in Gray) Jeps.

Cirsium proteanum J.T. Howell

Hoffmann (1932b) RO, CR.

Cirsium proteanum J.T. Howell

omitted as unsubstantiated on CR.

Smith (1976) CR "?."

Cirsium undulatum (Nutt.) Spreng.

Cirsium ochrocentrum Gray

Thorne (1967) based on Eastwood 6510 CAS!, US!, misidentified, CA.

Claytonia perfoliata Donn

incertae sedis

Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR.

Clematis ligusticifolia Nutt. in T. & G.

omitted as unsubstantiated on CL; also omitted by Raven (1963).

Eastwood (1941) CL.

Clematis pauciflora Nutt. in T. & G.

omitted as unsubstantiated on CA and CL; also omitted by Raven (1963).

Eastwood (1941) CA, CL.

probably *Clematis lasiantha* Nutt. in T. & G.

Brandegee (1890b) CR; Eastwood (1941) RO; Smith (1976) based on Howell 6217 CAS!, misidentified, CR.

Cneoridium dumosum (Nutt.) Hook.

Lycium californicum Nutt.

Munz (1974) in part, misidentified, CL.

Cnicus sp.

possibly *Cirsium occidentale* (Nutt.) Jeps.

Greene (1887b) MI.

Cnicus lilacinus Greene

Cirsium occidentale (Nutt.) Jeps.

Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) RO, CR.

Cnicus occidentalis (Nutt.) Gray

Cirsium occidentale (Nutt.) Jeps.

Lyon (1886) CA; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI; Brandegee (1890b) MI, RO, CR, CA; Trask (1904) CL.

Collomia gilioides Benth. var. *glutinosa* Gray

Allophyllum gilioides (Benth.) A. Grant & V. Grant

Watson (1876) based on Palmer 77 MO!, NY!, misidentified, GU; Eastwood (1929) GU.

Comarostaphylis polifolia (HBK.) Zucc.

Comarostaphylis diversifolia (Parry) Greene ssp. *planifolia* (Jeps.) Wallace ex Thorne

Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Convolvulus aridus Greene ssp. *intermedius* Abrams

Calystegia macrostegia (Greene) Brummitt ssp. *intermedia* (Abrams) Brummitt

Munz and Keck (1959) CA.

Convolvulus californicus Choisy

Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*

Lyon (1886) CA; Brandegee (1890b) CA; Davidson (1896) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Convolvulus cyclostegius House
Calystegia macrostegia (Greene) Brummitt ssp. *cyclostegia* (House) Brummitt
Eastwood (1941) CA; Munz and Keck (1959) CA.

Convolvulus macrostegius Greene
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
Lyon (1886) CL; Eastwood (1898) NI; Trask (1904) CL; Jepson (1909–1943) BA, CL; Abrams and Ferris (1923–1960) NI, BA, CL; Jepson (1925) CL; Eastwood (1941) NI, BA, CL; Munz and Keck (1959) NI, BA, CL; Raven (1963) CL.
Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
Greene (1885) GU; Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR, AN; Franceschi (1893) GU; Davidson (1896) CA; Jepson (1909–1943) CR, AN, GU; Abrams and Ferris (1923–1960) CR, AN, GU; Jepson (1925) CR, GU; Eastwood (1929) GU; Eastwood (1941) MI, RO, CR, AN; Howell (1942) GU; Munz and Keck (1959) RO, CR, CA, GU.

Convolvulus occidentalis Gray
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
Brandegee (1890b) CL.
Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
Watson (1876) GU; Lyon (1886) CA; Brandegee (1890b) MI, RO, CR, CA; Trask (1889) CA; Millspaugh and Nuttall (1923) CA.

Convolvulus occidentalis Gray var. *cyclostegius* (House) Jeps.
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
Gentry (1949) based on Elmore 313 AHFH!, misidentified, BA, based on Elmore 396 AHFH!, misidentified, CL.
Calystegia macrostegia (Greene) Brummitt ssp. *cyclostegia* (House) Brummitt
Munz (1935) CA; Gentry (1949) CA; Dunkle (1950) CA.
Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
Gentry (1949) based on Elmore 282 AHFH!, misidentified, CR.

Convolvulus occidentalis Gray var. *macrostegius* Munz
Calystegia macrostegia (Greene) Brummitt ssp. *amplissima* Brummitt
Munz (1935) CL; Dunkle (1942) BA; Dunkle (1950) NI, BA, CL.
Calystegia macrostegia (Greene) Brummitt ssp. *macrostegia*
Munz (1935) CR, CA, GU; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, CA, GU.

Convolvulus sepium L.
Calystegia macrostegia (Greene) Brummitt ssp. *intermedia* (Abrams) Brummitt
Millspaugh and Nuttall (1923) based in part on Millspaugh 4657 F!, misidentified, CA; Eastwood (1941) CA.

Convolvulus soldanella L.
Calystegia soldanella (L.) R. Br.
Lyon (1886) CA; Brandegee (1890a) CA; Millspaugh and Nuttall (1923) CA; Hoffmann (1932b) MI, CR; Eastwood (1941) MI, CR, CA; Raven (1963) CL.

Coreopsis gigantea (Kell.) Hall
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Munz (1935) "all our islands."

Corethrogyne filaginifolia (H. & A.) Nutt. var. *latifolia* Hall
Corethrogyne filaginifolia (H. & A.) Nutt. ssp. *filaginifolia*
Dunkle (1942) AN; Dunkle (1950) AN; Munz and Keck (1959) AN; Munz (1974) AN.

Corethrogyne filaginifolia (H. & A.) Nutt. var. *robusta* Greene
Corethrogyne filaginifolia (H. & A.) Nutt. ssp. *filaginifolia*
Abrams and Ferris (1923–1960) MI, RO, CR; Eastwood (1941) MI, RO, CR; Dunkle (1942) AN; Gentry (1949) based on Elmore 220 AHFH!, misidentified, AN, and MI, RO, CR; Dunkle (1950) MI, RO, CR, AN; Munz and Keck (1959) MI, RO; Munz (1974) MI, RO.

Corethrogyne filaginifolia (H. & A.) Nutt. var. *virgata* (Benth.) Gray
Corethrogyne filaginifolia (H. & A.) Nutt. ssp. *filaginifolia*
Eastwood (1941) MI, RO, CR; Dunkle (1950) MI, RO, CR, CA; Munz and Keck (1959) CA.

Corethrogyne lavendulacea Greene
Corethrogyne filaginifolia (H. & A.) Nutt. ssp. *filaginifolia*
Eastwood (1941) CA.

Cornus glabrata Benth. var. *catalinensis* (Millsp.) Dunkle
Cornus glabrata Benth.
Dunkle (1950) CA.

Cortaderia selloana (Schult.) Asch. & Graebn.
Cortaderia atacamensis (Phil.) Pilg.
Thorne (1967) CA.

Cotyledon sp.
incertae sedis
Franceschi (1893) GU.
Dudleya virens (Rose) Moran
Lyon (1886) CL.

Cotyledon caespitosa Haw.
Dudleya greenei Rose
Lyon (1886) CA; Brandegee (1890b) CR, CA; Davidson (1896) CA; Trask (1899) CA; Millspaugh and Nuttall (1923) CA.

Cotyledon lanceolata (Nutt. ex T. & G.) Benth. & Hook. ex. Wats.
Dudleya greenei Rose
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR, AN; Brandegee (1890b) MI, RO, CR.
Dudleya virens (Rose) Moran
Brandegee (1890a) CA; Brandegee (1890b) CA; Trask (1899) CA.

Cotyledon laxa (Lindl.) Benth. & Hook. ex Wats.
incertae sedis
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Cressa cretica L.
Cressa truxillensis HBK. var. *vallicola* (Heller) Munz
Lyon (1886) CA; Greene (1887b) MI; Yates (1889) MI; Brandegee (1890b) MI, CA; Jepson (1909–1923) MI, CA; Hoffmann (1932b) RO, CR.

Crossostephium insulare Rydb.
Artemisia nesiotica Raven
Davidson and Moxley (1923) NI, CL.

Cryptantha ambigua (Gray) Greene
incertae sedis
Eastwood (1941) MI, CR, CA.

Cryptantha clevelandii Greene var. *hispidissima* Jtn.
Cryptantha clevelandii Greene var. *clevelandii*
Dunkle (1942) AN, BA; Dunkle (1950) MI, RO, CR, BA, CL, GU.

Cryptantha intermedia (Gray) Greene
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Dunkle (1942) BA.
Cryptantha clevelandii Greene var. *florosa* Jtn.
Foreman (1967) based on Kanakoff s.n. Apr. 12, 1940 LAM!, misidentified, NI.

Cryptantha leiocarpa (F. & M.) Greene
Cryptantha clevelandii Greene var. *florosa* Jtn.
Millspaugh and Nuttall (1923) based on Hasse 4156 NY!, misidentified, CA.

Cryptantha ramosissima (Gray) Greene
Cryptantha maritima (Greene) Greene
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Cryptantha torreyana (Gray) Greene
Cryptantha maritima (Greene) Greene
Eastwood (1898) based on Trask 57 LAM!, GH!, NY!, misidentified, NI.

Cryptantha traskiae Jtn.
omitted as unsubstantiated on CA.
Eastwood (1898) CA.
omitted as column transposition for CA.
Dunkle (1950, p. 293) BA.
Cryptantha clevelandii Greene var. *clevelandii*
Dunkle (1942) probably based on Dunkle 7446b AHFH!, misidentified, BA; also noted by Philbrick (1972).

Cupressus macrocarpa Hartw.
Cupressus guadalupensis Wats. ssp. *guadalupensis*
Watson (1876) GU.

Cuscuta californica H. & A.
omitted as unsubstantiated on CR.
Smith (1976) CR.

Cuscuta subinclusa Dur. & Hilg.
Cuscuta ceanothi Behr
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Jepson (1909–1943) CR; Eastwood (1941) CR.

Cytisus canariensis Steud.
Cytisus monspessulans L.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Datura meteloides A. DC.
Datura wrightii Regel
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Jepson (1909–1943) CR; Millspaugh and Nuttall (1923) CA; Hoffmann (1932b) RO; Eastwood (1941) RO, CR, CA; Dunkle (1950) RO, CR, CA; Smith (1976) RO, CR.

Deinandra paniculata (Gray) Davids. & Mox.
Hemizonia increscens (Hall ex Keck) Tanowitz ssp. *increscens*
Davidson and Moxley (1923) RO.

Deinandra wrightii (Gray) Greene
probably *Hemizonia fasciculata* (DC.) T. & G.
Abrams (1917) CA.

Delphinium sp.
probably *Delphinium parryi* Gray ssp. *parryi*
Greene (1887a) CR; Brandegee (1890a) CA.

Delphinium hesperium Gray
Delphinium parryi Gray
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Dendromecon rigidus Benth. var. *harfordii* K. Bdg.
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Jepson (1909–1943) probably misidentified, CA.

Dendromecon arborea Greene
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Dendromecon densifolia Greene
Dendromecon rigidus Benth. ssp. *harfordii* (Kell.) Raven
Eastwood (1941) RO.

Dendromecon flexile Greene
Dendromecon rigidus Benth. ssp. *harfordii* (Kell.) Raven
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Eastwood (1941) CR.
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Davidson (1896) CA; Millspaugh and Nuttall (1923) CA.

Dendromecon harfordii Kell.
Dendromecon rigidus Benth. ssp. *harfordii* (Kell.) Raven
Kellogg (1873) RO; Ford (1890) CR; Munz (1935) Santa Barbara Isl.; Eastwood (1941) RO; Dunkle (1950) RO, CR; Munz and Keck (1959) RO, CR.
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Trask (1899) CA; Davidson and Moxley (1923) CA; Eastwood (1941) CA; Dunkle (1950) CA, CL.

Dendromecon harfordii Kell. var. *rhamnoides* (Greene) Munz
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Munz and Keck (1959) CA, CL.

Dendromecon rhamnoides Greene
Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA, CL.

Dendromecon rigidus Benth. ssp. *rigidus*

Dendromecon rigidus Benth. ssp. *rhamnoides* (Greene) Thorne
Raven (1963) CL.

Dentaria californica Nutt.
Cardamine californica (Nutt.) Greene
Eastwood (1941) MI, RO, CR, CA.

Dentaria integrifolia Nutt. var. *californica* Jeps.
Cardamine californica (Nutt.) Greene
Jepson (1909–1943) CR; Hoffmann (1932b) MI; Smith (1976) all four Channel Islands.

Descurainia pinnata (Walt.) Britt. ssp. *halictorum* (Ckll.) Detl.
Descurainia pinnata (Walt.) Britt. ssp. *menziesii* (DC.) Detl.
Wiggins (1980) probably misidentified, GU.

Dichelostemma capitatum (Benth.) Wood
Dichelostemma pulchellum (Salisb.) Heller
Millspaugh and Nuttall (1923) CA.

Dichondra argentea Willd.
Dichondra occidentalis House
Brandegee (1888) RO; Yates (1889) RO.

Dichondra donelliana Tharp & Johnst.
Dichondra occidentalis House
Tharp and Johnston (1961) based in part on Wolf 2841 POM!, misidentified, CR; Smith (1976) MI, RO, CR.

Dichondra repens Forst.
Dichondra occidentalis House
Brandegee (1890a) CA; Brandegee (1890b) RO, CA; Davidson (1896) CA; Jepson (1909–1943) RO, CA; Hoffmann (1932b) CR; Eastwood (1941) RO, CR, CA.

Diplacus arachnoideus Greene
Diplacus longiflorus Nutt. ssp. *longiflorus*
Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) RO, CR; McMinn (1951) CR.

Diplacus linearis (Benth.) Greene
Diplacus longiflorus Nutt. ssp. *longiflorus*
Eastwood (1941) RO.
Diplacus puniceus Nutt.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Diplacus longiflorus Nutt.
omitted as unsubstantiated on CA.
Gentry (1949) CA.
Diplacus parviflorus Greene
Gentry (1949) probably based on Elmore 185 AHFH!, misidentified, RO.

Diplostephium canum Gray
Haplopappus canus (Gray) Blake
Watson (1876) GU; Brandegee (1890b) GU; Franceschi (1893) GU.
Haplopappus detonus (Greene) Raven
Brandegee (1888) RO; Brandegee (1890b) RO, CR.

Dissanthelium californicum (Nutt.) Benth.
omitted as unsubstantiated on RO and CR.
Eastwood (1941) RO, CR.

Distichlis dentata Rydb.
Distichlis spicata (L.) Greene var. *stolonifera* Beetle
Cockerell (1937) MI.

Distichlis maritima Raf.
Distichlis spicata (L.) Greene var. *stolonifera* Beetle
Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA.

Distichlis stricta (Torr.) Rydb. var. *laxa* (Vasey) Fawcett & West ex Munz
Distichlis spicata (L.) Greene var. *stolonifera* Beetle
Munz (1935) RO, CR, CA, CL; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, NI, CA, CL.

Dithyraea californica Harv. var. *maritima* (A. Davids.) A. Davids. ex Rob. in Gray
Dithyraea maritima A. Davids.
Eastwood (1898) NI; Hoffmann (1932b) MI; Eastwood (1941) MI, NI.

Dithyraea maritima A. Davids.
omitted as unsubstantiated on CA.
Davidson and Moxley (1923) CA.

Dodecatheon clevelandii Greene ssp. *sanctarum* (Greene) Abrams
Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thomps.
Abrams and Ferris (1923–1960) CR, AN, CA, CL.

Dodecatheon hendersoni Gray
Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thomps.
Davidson (1896) CA; Brandegee (1888); RO; Yates (1889) RO; Millspaugh and Nuttall (1923) CA; Munz (1935) RO, CA; Eastwood (1941) CA; Dunkle (1942) AN.

Dodecatheon jeffreyi Moore
Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thomps.
Davidson (1896) CA; Greene (1887a) CR; Yates (1889) CR.

Dodecatheon meadia L.
Dodecatheon clevelandii Greene ssp. *insularis* H.J. Thomps.
Watson (1876) GU; Greene (1885) GU; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA; Franceschi (1893) GU.

Dudleya farinosa (Lindl.) Britt. & Rose
Dudleya greenei Rose
Gentry (1949) based on Elmore 314 LAM!, misidentified, MI.

Dudleya hassei (Rose) Moran
omitted as unsubstantiated on GU.
Moran (1959) GU.

Dudleya virens (Rose) Moran
Dudleya hassei (Rose) Moran
Munz and Keck (1959) CA, in part.

Echeveria albida (Rose) Berger in Engl. & Prantl
Dudleya greenei Rose
Munz (1935) MI; Dunkle (1950) MI.
Dudleya traskiae (Rose) Moran
Munz (1935) BA; Dunkle (1942) BA; Dunkle (1950) BA.
Dudleya virens (Rose) Moran
Munz (1935) CA in part, CL; Dunkle (1950) CA in part, CL, GU.

Echeveria caespitosa (Haw.) DC.
Dudleya caespitosum (Haw.) Britt.
Jepson (1909–1943) CR.

Echeveria greenei (Rose) Berger in Engl. & Prantl
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Dunkle (1942) BA.
omitted as unsubstantiated on GU.
Dunkle (1950) GU.
Echeveria lanceolata Nutt. ex T. & G.
Dudleya virens (Rose) Moran
Jepson (1909–1943) CA.
Echeveria viscida (Wats.) Berger in Engl. & Prantl var. *insulare* (Rose) Jeps.
Dudleya hassei (Rose) Moran
Jepson (1909–1943) CA in part.
Dudleya traskiae (Rose) Moran
Jepson (1909–1943) BA.
Dudleya virens (Rose) Moran
Jepson (1909–1943) CA in part, CL.
Echidocarya californica Gray
Plagiobothrys californicus (Gray) Greene var. *gracilis* Jtn.
Jepson (1909–1943) CR, CA, CL.
Echidocarya californica Gray ssp. *fulvescens* (Jtn.) Abrams
Plagiobothrys californicus (Gray) Greene var. *fulvescens* Jtn.
Abrams and Ferris (1923–1960) RO, AN, CA.
Echinocystis fabacea Naud.
Marah macrocarpus (Greene) Greene
Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR, CA, CL; Hoffmann (1932b) MI, RO, CR, AN; Munz (1935) MI; Dunkle (1942) AN; Dunkle (1950) MI.
Echinocystis guadalupensis (Wats.) Naud.
Marah guadalupensis (Wats.) Greene
Greene (1885) GU; Franceschi (1893) GU; Dunkle (1950) GU.
Marah macrocarpus (Greene) Greene
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Dunkle (1950) MI, RO, CR, AN.
Eleocharis mamillata Lindb. f.
Eleocharis macrostachya Britt. in Small
Munz (1935) RO, CA.
Eleocharis palustris (L.) R. & S.
Eleocharis macrostachya Britt. in Small
Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA; Eastwood (1898) NI, CR; Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) RO; Eastwood (1941) RO, NI, CA; Raven (1963) CL; Thorne (1967) CA.
Elymus multisetus (J.G. Sm.) Jones
Sitanion jubatum J.G. Sm.
Thorne (1967) based on Nuttall 314 F!, misidentified, CA.
Elymus triticoides Buckl. ssp. *multiflorus* Gould
Elymus triticoides Buckl.
Smith (1976) islands.
Epilobium adenocaulon Hausskn.
Epilobium ciliatum Raf. ssp. *ciliatum*
McClatchie (1894) CA; Eastwood (1941) CR; Smith (1976) MI, CR.
Epilobium adenocaulon Hausskn. var. *holosericeum* (Trel.) Munz
Epilobium ciliatum Raf. ssp. *ciliatum*
Thorne (1967) CA.
Epilobium adenocaulon Hausskn. var. *parishii* (Trel.) Munz
Epilobium ciliatum Raf. ssp. *ciliatum*
Smith (1976) CR.
Epilobium californicum Hausskn.
Epilobium ciliatum Raf. ssp. *ciliatum*
Clokey (1931) CR.
Epilobium coloratum Muhl.
Epilobium ciliatum Raf. ssp. *ciliatum*
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR, CA.
Epilobium holosericeum Trel.
Epilobium ciliatum Raf. ssp. *ciliatum*
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Epilobium minutum Lindl. ex Hook.
Epilobium foliosum (T. & G.) Suksd. (Seavey et al., 1977).
Watson (1876) based on Palmer 31 MO! (collection number reported by Seavey, Wright and Raven, 1977 is in error), misidentified, GU; Greene (1885) GU; Eastwood (1929) GU.
Equisetum sp.
incertae sedis
Greene (1887a) CR.
Equisetum funstoni A.A. Eat.
Equisetum laevigatum A. Br.
Hoffmann (1932a) CR; Eastwood (1941) CR, CA; Munz and Keck (1959) CA.
Equisetum hyemale L. var. *californicum* Milde.
Equisetum hyemale L. var. *affine* (Engelm.) A.A. Eat.
Hoffmann (1932a) CR; Munz (1935) CR; Dunkle (1950) CR; Munz and Keck (1959) CR.
Equisetum kansanum J.H. Schaffn.
Equisetum laevigatum A. Br.
Hoffmann (1932a) CR; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA.
Equisetum mexicanum Milde.
probably *Equisetum laevigatum* A. Br.
McClatchie (1894) CA.
Equisetum robustum A. Br.
Equiseteum laevigatum A. Br.
Davidson (1894) CA.
Erigeron foliosus Nutt.
incertae sedis
Lyon (1886) CA; Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR, CA.
Eriodictyon tomentosum Benth.
Eriodictyon traskiae Eastw. ssp. *traskiae*
Lyon (1886) CA; Brandegee (1890b) CA; Abrams and Ferris (1923–1960) CA.
Eriogonum arborescens Greene
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Davidson and Moxley (1923) BA.

Eriogonum giganteum Wats.
Eriogonum giganteum Wats. ssp. *formosum* (K. Bdg.) Raven
Jepson (1925) CL; Munz (1935) CL; Gentry (1949) CL.
introduced on CR.
Jepson (1925) CR; Gentry (1949) CR.

Eriogonum giganteum Wats. var. *compactum* Dunkle
omitted as unsubstantiated on CA.
Dunkle (1950) CA.

Eriogonum giganteum Wats. var. *formosum* K. Bdg.
omitted as unsubstantiated on RO.
Eastwood (1941) RO.

Eriogonum grande Greene
omitted as column transposition for CA.
Dunkle (1950) BA.
omitted as unsubstantiated on MI and BA.
Gentry (1949) MI, BA.

Eriogonum latifolium Sm.
Eriogonum grande Greene ssp. *grande*
Yates (1889) AN.

Eriogonum latifolium Sm. ssp. *grande* (Greene) S. Stokes
Eriogonum grande Greene ssp. *grande*
Davidson and Moxley (1923) CA; Munz and Keck (1959) CR, AN, CA, CL; Raven (1963) CL; Foreman (1967) NI; Thorne (1967) CA.

Eriogonum latifolium Sm. var. *rubescens* (Greene) Munz
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz
Munz and Keck (1959) MI, RO, CR.

Eriogonum molle Greene
Eriogonum zapatoense Moran
Moran (1951) GU.

Eriogonum nudum (Dougl. ex Benth.) S. Stokes
Eriogonum grande Greene ssp. *grande*
Trask (1899) CA; Davidson (1896) CA; Brandegee (1890b) CA, CL; Trask (1904) CL; Abrams (1917) CA; Millspaugh and Nuttall (1923) CA.
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz
Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR.

Eriogonum nudum (Dougl. ex Benth.) S. Stokes var. *grande* Jeps.
Eriogonum grande Greene ssp. *grande*
Jepson (1909–1943) CR; Hoffmann (1932a) RO in part, CR in part, AN; Dunkle (1942) AN.
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz
Jepson (1909–1943) MI, CR in part; Hoffmann (1932a) MI, RO in part, CR in part.

Eriogonum nudum (Dougl. ex Benth.) S. Stokes var. *pauciflorum* Wats.
Eriogonum grande Greene ssp. *grande*
Lyon (1886) CA, CL.

Eriogonum sp.
Eriogonum grande Greene ssp. *formosum* (K. Bdg.) Raven
Lyon (1886) CL.

Eriogonum rubescens Greene
omitted as unsubstantiated on CA and CL.
Eastwood (1941) CA, CL; Gentry (1949) CA, CL.
Eriogonum grande Greene ssp. *rubescens* (Greene) Munz
Greene (1887b) MI; Yates (1889) MI, RO, CR; Eastwood (1941) MI, RO, CR; Gentry (1949) MI, RO, CR.

Eriophyllum sp.
Eriophyllum lanatum (Pursh) Forbes var. *grandiflorum* (Gray) Jeps.
Franceschi (1893) GU.

Eriophyllum staechadifolium Lag.
incertae sedis
Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR.

Eriophyllum staechadifloium Lag. var. *artemisiaefolium* (Less.) Macbr.
omitted as unsubstantiated on CA.
Dunkle (1950) CA.

Eritrichum angustifolium Torr.
Cryptantha maritima (Greene) Greene
Watson (1876) based on Palmer 67 MO!, GU.

Erodium botrys (Cav.) Bertol.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Dunkle (1942) BA.

Erodium brachycarpum (Gordon) Thell.
Erodium obtusiplicatum (Maire, Weiller & Wilcz.) J.T. Howell
Smith (1976) RO.

Erysimum asperum DC.
incertae sedis
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Jepson (1909–1943) CR; Eastwood (1941) RO, CR, CA.
Erysimum insulare Greene
Hoffmann (1932b) based on Hoffmann s.n. SBM#141!, RO, based on SBM#4151!, AN; Eastwood (1941) AN; Dunkle (1942) AN.

Erysimum capitatum (Dougl.) Greene
Erysimum ammophilum Heller
Munz (1935) probably based on Munz & Crow 11757 LA!, misidentified, RO.

Erysimum insulare Greene
omitted as unsubstantiated on NI and CA; also omitted by Foreman (1967).
Eastwood (1941) NI, CA.
Erysimum morani Roll.
Moran (1951) GU.

Eschscholzia sp.
Eschscholzia californica Cham. var. *californica*
Hoffmann (1932b) based on Hoffmann s.n. SBM#12039!, CR.

Eschscholzia californica Cham.
incertae sedis
Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR, CA; Franceschi (1893) GU; Trask (1899) CA.
Eschscholzia californica Cham. var. *californica*
Greene (1885) GU; Gentry (1949) based on Elmore 187 AHFH! RO.

Eschscholzia ramosa Greene
Brandegee (1890b) CL.
Eschscholzia californica Cham. var. *hypecoides* Gray
Eschscholzia elegans Greene
Watson (1876) based on Palmer 3 CM!, NY! in part, US!, GU.
Eschscholzia ramosa Greene
Watson (1876) based on Palmer 3 NY! in part, GU.
Eschscholzia crossophylla Greene
Eschscholzia ramosa Greene
Eastwood (1941) CA.
Eschscholzia elegans Greene
Eschscholzia ramosa Greene
Jepson (1909–1943) CR, BA, CA; Millspaugh and Nuttall (1923) CA; Abrams and Ferris (1932–1960) islands from RO to CL; Hoffmann (1932b) RO, CR; Munz (1935) CR, CA, CL; Eastwood (1941) MI, RO, CR, CA, CL; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL; Munz and Keck (1959) Channel Islands.
Eschscholzia elegans Greene var. *ramosa* Greene
Eschscholzia ramosa Greene
Lyon (1886) CL; Greene (1885) GU; Franceschi (1893) GU.
Eschscholzia glauca Greene
Eschscholzia californica Cham. var. *californica*
Greene (1887a) CR; Yates (1889) RO, CR; Hoffmann (1932b) CR; Eastwood (1941) CR.
Eschscholzia robusta Greene
incertae sedis
Eastwood (1941) RO.
Eschscholzia trichophylla Greene
Eschscholzia ramosa Greene
Eastwood (1941) CR.
Eschscholzia wrigleyana Millsp. & Nutt.
Eschscholzia californica Cham. var. *peninsularis* (Greene) Munz
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Eulobus californicus Nutt. ex T. & G.
Camissonia californica (Nutt. ex T. & G.) Raven
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Trask (1899) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CR, CA.
Eunanus latifolius (Gray) Greene
Mimulus latifolius Gray
Greene (1885) GU.
Euphorbia misera Benth.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Dunkle (1950) BA.
Euryptera insularis (Eastw.) Coult. & Rose
Lomatium insulare (Eastw.) Munz
Davidson and Moxley (1923) NI.
Evax caulescens (Benth.) Gray var. *humilus* Jeps.
Evax sparsiflora (Gray) Jeps.
Hoffmann (1932b) RO; Eastwood (1941) RO, CR.
Festuca bromoides L.
Vulpia bromoides (L.) S.F. Gray
Clokey (1931) CR; Hoffmann (1932a) MI, RO, CR; Eastwood (1941) MI, RO, CR, NI, CA, CL; Raven (1963) CL.
Festuca dertonensis (All.) Asch. & Graebn.
Vulpia bromoides (L.) S.F. Gray
Dunkle (1942) AN; Smith (1976) all four islands.
Festuca megalura Nutt.
Vulpia myuros (L.) K.C. Gmelin var. *hirsuta* Hack
Millspaugh and Nuttall (1923) CA; Clokey (1931) CR; Hoffmann (1932a) MI, RO, CR; Munz (1935) on the islands; Eastwood (1941) MI, RO, CR, CA; Dunkle (1942) AN, BA; Howell (1942) GU; Gentry (1949) MI, RO, CR, CA; Raven (1963) CL; Thorne (1967) CA; Smith (1976) all four islands.
Festuca microstachys Nutt.
Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould
Watson (1876) GU; Greene (1885) GU; Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Eastwood (1941) RO, CR.
Festuca myuros L.
incertae sedis
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Brandegee (1890b) MI, CR.
Vulpia myuros (L.) K.C. Gmelin var. *hirsuta* Hack
Brandegee (1888) based on Brandegee s.n. in 1888 UC#121663!, RO; Yates (1889) RO; Brandegee (1890b) RO; Vasey and Rose (1890) GU; Eastwood (1941) RO.
Vulpia myuros (L.) K.C. Gmelin var. *myuros*
Brandegee (1890a) CA; Jepson (1909–1943) CA; Millspaugh and Nuttall (1923) CA; Abrams and Ferris (1923–1960) CA; Eastwood (1941) CA; Thorne (1967) CA; Thorne (1969) CL.
Festuca octoflora Walt.
Vulpia octoflora (Walt.) Rydb. var. *hirtella* (Piper) Henr.
Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) MI, RO; Munz (1935) MI, RO; Dunkle (1942) AN; Foreman (1967) NI; Thorne (1967) CA; Smith (1976) all four islands.
Festuca octoflora Walt. ssp. *hirtella*
Vulpia octoflora (Walt.) Rydb. var. *hirtella* (Piper) Henr.
Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, NI, CA; Raven (1963) CL.
Festuca pacifica Piper
Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould
Hoffmann (1932a) MI, CR; Eastwood (1941) MI, CR, NI; Gentry (1949) MI, CR, NI; Raven (1963) CL; Smith (1976) AN.
Festuca pratensis Huds.
Festuca arundinacea Schreb.
Thorne (1967) CA.

Festuca reflexa Buckl.

Vulpia microstachys (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould

Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA; Raven (1963) CL; Thorne (1967) CA.

Festuca tenella Willd.

Vulpia octoflora (Walt.) Rydb. var. *hirtella* (Piper) Henr.

Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890a) based in part on Brandegee 49 US!, CA; Brandegee (1890b) CR, CA; Vasey and Rose (1890) based in part on Palmer 674 NY!, GU.

Filago arizonica Gray

Filago californica Nutt.

Vasey and Rose (1890) based on Palmer 895 ND-G!, misidentified, GU; Eastwood (1941) possibly based on Fosberg 7642 LAM!, misidentified, CA; Dunkle (1950) CA.

Foeniculum foeniculum (L.) Karst.

Foeniculum vulgare Mill.

Millspaugh and Nuttall (1923) CA.

Foeniculum officinale All.

Foeniculum vulgare Mill.

Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Frankenia grandiflora Cham. & Schlecht.

Frankenia grandifolia Cham. & Schlecht.

Millspaugh and Nuttall (1923) CA; Dunkle (1942) AN.

Franseria bipinnatifida Nutt.

Ambrosia camphorata (Greene) Payne

Watson (1876) GU.

Ambrosia chamissonis (Less.) Greene

Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Brandegee (1890a) CA; Brandegee (1890b) MI, CR, CA; Hoffmann (1932b) RO, AN; Munz (1935) on the islands; Eastwood (1941) MI, RO, CR, AN, CA, CL; Dunkle (1942) AN.

Franseria bipinnatifida Nutt. var. *dubia* Eastw.

Ambrosia chamissonis (Less.) Greene

Eastwood (1898) NI; Eastwood (1941) NI.

Franseria camphorata Greene

Ambrosia camphorata (Greene) Payne

Greene (1885) based on Greene s.n. Apr. 24, 1885 CAS! GU; Vasey and Rose (1890) GU; Eastwood (1929) GU; Howell (1942) GU.

Franseria chamissonis Less.

Ambrosia chamissonis (Less.) Greene

Greene (1887b) MI; Yates (1889) MI; Brandegee (1890b) MI; Hoffmann (1932b) MI, CR; Munz (1935) MI, CR, CL; Eastwood (1941) MI, CR; Munz and Keck (1959) MI, CR, CL.

Franseria chamissonis Less. ssp. *bipinnatisecta* (Less.) Wiggins & Stockw.

Ambrosia chamissonis (Less.) Greene

Munz and Keck (1959) Channel Islands; Raven (1963) CL.

Franseria chamissonis Less. var. *viscida* Eastw.

Ambrosia chamissonis (Less.) Greene

Eastwood (1898) based on Trask 10 [sic] CAS!; Eastwood (1941) NI.

Gaertneria bipinnatifida Kuntze

Ambrosia chamissonis (Less.) Greene

Millspaugh and Nuttall (1923) CA.

Gaertneria chamissonis Kuntze

Ambrosia chamissonis (Less.) Greene

Davidson and Moxley (1923) MI.

Galium angustifolium Nutt. ex T. & G.

Galium angustifolium Nutt. ex T. & G. ssp. *foliosum* (Hillend & Howell) Dempst. & Steb.

Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR.

Galium angustifolium Nutt. ex T. & G. var. *foliosum* Hillend & Howell

omitted as unsubstantiated on BA; also omitted by Philbrick (1972).

Munz and Keck (1959) BA.

probably *Galium angustifolium* Nutt. ex T. & G. ssp. *angustifolium*

Eastwood (1941) CA.

Galium aparine L. var. *vaillantii* (DC.) Koch

Galium aparine L.

Lyon (1886) CA; Davidson (1896) CA; Brandegee (1890b) RO, CR, CA, CL.

Galium buxifolium Greene

omitted as unsubstantiated on CA.

Davidson (1896) CA.

Galium californicum H. & A.

omitted as unsubstantiated on CL; also omitted by Raven (1963).

Eastwood (1941) CL.

Galium californicum H. & A. ssp. *flaccidum* (Greene) Dempst.

Abrams and Ferris (1923–1960) CR; Eastwood (1941) CR.

Galium californicum H. & A. var. *californicum*

Galium californicum H. & A. ssp. *flaccidum* (Greene) Dempst.

Munz and Keck (1959) CR.

Galium catalinense Gray

Galium buxifolium Greene

Brandegee (1890b) MI, CR; Dunkle (1950) MI, CR.

Galium catalinense Gray ssp. *acrispum* Dempst.

Abrams and Ferris (1923–1960) CL; Dunkle (1950) CL; Munz and Keck (1959) CL.

Galium catalinense Gray var. *catalinense*

Galium catalinense Gray ssp. *acrispum* Dempst.

Raven (1963) CL.

Galium flaccidum Greene

Galium californicum H. & A. ssp. *flaccidum* (Greene) Dempst.

Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) CR.

Galium miguelense Greene
  omitted as unsubstantiated on CA.
    Davidson (1896) CA.
Galium nuttallii Gray
  Galium californicum H. & A. ssp. *miguelense* (Greene) Dempst. & Steb.
    Brandegee (1890b) MI.
Galium nuttallii Gray var. *nuttallii*
  Galium nuttallii gray ssp. *insulare* Ferris
    Thorne (1967) CA.
Galium nuttallii Gray ssp. *ovalifolium* (Dempst.) Dempst. & Steb.
  Gallium porrigens Dempst. var. *porrigens* (accd. Dempster, 1974)
    Munz (1974) CR, CA.
Galium siccatum Wight
  Galium angustifolium Nutt. ex T. & G. ssp. *angustifolium*
    Millspaugh and Nuttall (1923) CA.
  Galium angustifolium Nutt. ex T. & G. ssp. *foliosum* (Hillend & Howell) Dempst. & Steb.
    Eastwood (1941) RO, CR.
Galvezia juncea (Benth.) Ball
  Galvezia speciosa (Nutt.) Gray
    Wiggins (1980) GU.
Gasoul crystallinum (L.) Rothm.
  Mesembryanthemum crystallinum L.
    Smith (1976) MI, RO, CR, AN.
Gasoul nodiflorum (L.) Rothm.
  Mesembryanthemum nodiflorum L.
    Munz (1974) BA, CA; Smith (1976) MI, RO, CR, AN.
Gastridium australe Beauv.
  Gastridium ventricosum (Gouan) Schinz. & Thell.
    Davidson (1894) CA.
Genista linifolia L.
  Cytisus linifolius (L.) Lam.
    Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Gilia achilleifolia Benth. ssp. *achilleifolia*
  omitted as unsubstantiated on CR.
    Munz (1974) CR; Smith (1976) CR.
Gilia achilleifolia Benth. ssp. *multicaulis* (Benth.) V. Grant & A. Grant
  Gilia clivorum (Jeps.) V. Grant
    Smith (1976) RO.
Gilia androsacea (Benth.) Steud.
  Linanthus androsaceus (Benth.) Greene ssp. *luteus* (Benth.) Mason
    Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Eastwood (1941) RO, CR.
Gilia atractyloides (Benth.) Steud. var. *foliaceus* (Greene) Munz
  Navarretia hamata Greene var. *foliacea* (Greene) Thorne
    Munz (1935) CA.
Gilia bicolor (Nutt.) Brand
  Linanthus bicolor (Nutt.) Greene ssp. *bicolor*
    Millspaugh and Nuttall (1923) CA; Munz (1935) CA, CL; Eastwood (1941) RO, CR, CA, CL.
Gilia divaricata Nutt.
  Allophyllum gilioides (Benth.) A. Grant & V. Grant
    Greene (1885) based on Greene s.n. Apr. 24, 1885 DS!, GU.
Gilia gilioides (Benth.) Greene
  omitted as unsubstantiated on CR and CL; also omitted by Raven (1963) on CL.
    Dunkle (1950) CR, CL.
  Allophyllum gilioides (Benth.) A. Grant & V. Grant
    Dunkle (1950) GU.
  Allophyllum glutinosum (Benth.) A. Grant & V. Grant
    Jepson (1909–1943) CA; Munz (1935) CA; Dunkle (1950) CA.
  Gilia nevinii Gray
    Dunkle (1950) BA.
Gilia gilioides (Benth.) Greene var. *glutinosa* (Benth.) Jeps.
  omitted as unsubstantiated on CL; also omitted by Raven (1963).
    Dunkle (1950) CL.
  Allophyllum gilioides (Benth.) A. Grant & V. Grant
    Dunkle (1950) GU.
  Allophyllum glutinosum (Benth.) A. Grant & V. Grant
    Jepson (1909–1943) based on Fosberg 15413 [sic] actually is Fosberg S5413 LAM!, POM! CA; Dunkle (1950) CA.
  Gilia nevinii Gray (Philbrick, 1972)
    Dunkle (1942) BA; Dunkle (1950) BA.
Gilia glutinosa (Benth.) Gray
  Allophyllum glutinosum (Benth.) A. Grant & V. Grant
    Brandegee (1890a) CA; Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Gilia guadalupensis Brand
  probably *Linanthus pygmaeus* (Brand) J.T. Howell ssp. *pygmaeus*
    Eastwood (1929) GU.
Gilia micrantha Steud. ex Benth. in A. DC.
  Linanthus bicolor (Nutt.) Greene ssp. *bicolor*
    Lyon (1886) CL; Greene (1887b) MI; Yates (1889) MI; Brandegee (1890b) MI, CL; Eastwood (1941) MI, CL.
Gilia millefoliata F. & M.
  Gilia clivorum (Jeps.) V. Grant
    Hoffmann (1932b) MI, RO, CR, AN; Munz (1935) MI, RO, CR, AN, CA; Eastwood (1941) MI, RO, CR, AN, CA; Dunkle (1942) AN.
Gilia aff. *multicaulis* Benth.
  Gilia angelensis V. Grant
    Gentry (1949) based on Elmore 440 LAM!, CR (annot. by A. Day).
Gilia multicaulis Benth.
  Gilia angelensis V. Grant
    Lyon (1886) CA; Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR, CA; Millspaugh and Nuttall (1923) CA; Abrams and Ferris (1923–1960) CR; Eastwood (1941) CR, CA; Dunkle (1942) AN.

- *Gilia clivorum* (Jeps.) V. Grant
  - Jepson (1909–1943) RO, CR.
- *Gilia nevinii* Gray
  - Greene (1885) based on Greene s.n. Apr. 25, 1885 CAS!, GU.

Gilia multicaulis Benth. var. *millefolia* Gray
- *Gilia nevinii* Gray
  - Watson (1876) based on Palmer 78 NY!, GU; Jepson (1909–1943) RO, CR, CL based on Munz 6633 POM!, GU based on Anthony 235 GH!.

Gilia multicaulis Benth. var. *nevinii* (Gray) Jeps.
- *Gilia nevinii* Gray
  - Jepson (1925) GU.

Gilia multicaulis Benth. var. *peduncularis* (Eastw.) Jeps.
- *Gilia nevinii* Gray
  - Jepson (1909–1943) CR, CL, GU.

Gilia nevinii Gray
- omitted as unsubstantiated on MI.
  - Eastwood (1941) MI.

Gilia pusilla Benth.
- probably *Linanthus pygmaeus* (Brand) J.T. Howell ssp. *pygmaeus*
  - Greene (1885) GU.

Gilia pusilla Benth. var. *californica* Gray
- probably *Linanthus pygmaeus* (Brand) J.T. Howell ssp. *pygmaeus*
  - Watson (1876) GU; Jepson (1909–1943) GU.

Gilia tenuiflora Benth.
- omitted as unsubstantiated on CA.
  - Eastwood (1941) CA; Dunkle (1950) CA.

Gilia viscidula Gray
- *Navarretia atractyloides* (Benth.) H. & A.
  - Brandegee (1890a) CA; Brandegee (1890b) CA.

Githopsis specularioides Nutt.
- omitted as unsubstantiated on RO and CA.
  - Dunkle (1950) RO, CA.

Githopsis specularioides Nutt. ssp. *candida* Ewan
- *Githopsis diffusa* Gray var. *guadalupensis* Morin
  - Wiggins (1980) GU; (Morin, N. 1983. Syst. Bot. 8(4): 436–468).

Gnaphalium californicum DC.
- omitted as unsubstantiated on CL; also omitted by Raven (1963).
  - Eastwood (1941) CL.

Gnaphalium chilense Spreng.
- *Gnaphalium bicolor* Bioletti
  - Eastwood (1941) probably based on Abrams & Wiggins 375 DS!, misidentified, CL.

Gnaphalium chilense Spreng. var. *confertifolium* Greene
- *Gnaphalium chilense* Spreng.
  - Eastwood (1941) MI, RO.

Gnaphalium decurrens Ives
- *Gnaphalium bicolor* Bioletti
  - Lyon (1886) CL; Brandegee (1890b) CL.
- *Gnaphalium californicum* DC.
  - Brandegee (1890b) RO, CR.

Gnaphalium decurrens Ives var. *californicum* (DC.) Gray
- *Gnaphalium californicum* DC.
  - Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR.

Gnaphalium palustre Nutt.
- *Filago californica* Nutt.
  - Gentry (1949) based on Elmore 443 AHFH!, misidentified, CR.

Gnaphalium sprengelii H. & A.
- *Gnaphalium chilense* Spreng.
  - Watson (1876) GU; Greene (1885) GU; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA; Vasey and Rose (1890) based on Palmer 885 NY!, GU; Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Dunkle (1950) GU.

Gnaphalium wrightii Gray
- *Gnaphalium microcephalum* Nutt.
  - Hoffmann (1932b) CR; Eastwood (1941) CR.

Godetia bottae Spach.
- *Clarkia purpurea* (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis
  - Brandegee (1890a) CA; Brandegee (1890b) CA; Eastwood (1941) CA.

Godetia purpurea (Curt.) G. Don in Sweet
- *Clarkia purpurea* (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis
  - Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.

Godetia quadrivulnera (Dougl. in Lindl.) Spach. var. *tenella* (Cav.) Jeps.
- *Clarkia purpurea* (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis
  - Eastwood (1941) CA.

Godetia tenella (Cav.) Steud.
- *Clarkia purpurea* (Curt.) Nels. & Macbr. ssp. *quadrivulnera* (Dougl. in Lindl.) Lewis & Lewis
  - Lyon (1886) CA; Brandegee (1890b) CA; Trask (1899) CA.

Grindelia glutinosa Dunal
- *Grindelia latifolia* Kell. ssp. *latifolia*
  - Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR.

Grindelia latifolia Kell. ssp. *platyphylla* (Greene) Keck
- *Grindelia latifolia* Keck
  - Smith (1976) AN.

Grindelia perennis A. Nels.
- *incertae sedis*
  - Munz (1935) CA; Eastwood (1941) CA.

Grindelia robusta Nutt. var. *platyphylla* Greene
- *Grindelia latifolia* Kell.
  - Eastwood (1941) RO, AN.

Grindelia rubricaulis DC. var. *platyphylla* (Greene) Steyerm.
- omitted as unsubstantiated on BA.
  - Munz (1935) BA.
- *Grindelia latifolia* Kell.
  - Munz (1935) RO, AN; Dunkle (1950) RO, AN.

Habenaria elegans (Lindl.) Boland. var. *maritima* (Greene) Ames
omitted as unsubstantiated on RO.
Smith (1976) RO.

Habenaria michaeli Greene
Habenaria elegans (Lindl.) Boland.
Hoffmann (1932a) RO; Munz (1935) RO, CR; Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.

Haplopappus canus (Gray) Blake
Haplopappus detonsus (Greene) Raven
Abrams and Ferris (1923–1960) RO, CR; Munz and Keck (1959) RO, CR.

Haplopappus detonsus (Greene) Raven
Haplopappus canus (Gray) Blake
Smith (1976) GU.

Haplopappus squarrosus H. & A. ssp. *squarrosus*
omitted as unsubstantiated on CR.
Smith (1976) CR.

Hazardia cana (Gray) Greene
Haplopappus detonsus (Greene) Raven
Davidson and Moxley (1923) RO, CR; Jepson (1925) RO, CR; Eastwood (1941) RO, CR.

Hazardia detonsa (Greene) Greene
Haplopappus detonsus (Greene) Raven
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Eastwood (1941) RO, CR; Clark (1979) RO, CR.

Hazardia serrata Greene
Haplopappus detonsus (Greene) Raven × *Haplopappus squarrosus* H. & A. ssp. *grindelioides* (DC.) Keck (omitted from text).
Greene (1887a) CR; Yates (1889) RO, CR; Ford (1890) CR; Eastwood (1941) RO, CR.

Hazardia squarrosa (H. & A.) Greene
Haplopappus squarrosus H. & A. ssp. *grindelioides* (DC.) Keck
McClatchie (1894) CA; Millspaugh and Nuttall (1923) CA; Jepson (1925) CR; Eastwood (1941) RO, CR.

Hazardia squarrosa (H. & A.) Greene var. *grindelioides* (DC.) Clark
Haplopappus squarrosus H. & A. ssp. *grindelioides* (DC.) Keck
Clark (1979) MI, RO, CR, AN, CA.

Heleniastrum puberulum (DC.) Kuntze
Helenium puberulum DC.
McClatchie (1894) CA.

Helianthemum scoparium Nutt. var. *vulgare* Jeps.
Helianthemum scoparium Nutt.
Munz and Keck (1959) CA; Thorne (1967) CA; Smith (1976) RO“?,” CR.

Heliotropium chenopodioides Willd.
Heliotropium curassavicum L. ssp. *oculatum* (Heller) Thorne
Millspaugh and Nuttall (1923) CA.

Hemizonia fasciculata (DC.) T. & G. var. *ramosissima* (Benth.) Gray
Hemizonia fasciculata (DC.) T. & G.
Eastwood (1941) BA, CA, CL; Dunkle (1950) BA, CA, CL.

Hemizonia floribunda Gray
Hemizonia clementina Bdg.
Millspaugh and Nuttall (1923) based in part on Nuttall 195 F! and Nuttall 352 F!, misidentified, CA; Eastwood (1941) CA.

Hemizonia paniculata Gray
Hemizonia clementina Bdg.
Millspaugh and Nuttall (1923) based in part on Knopf 148 US! and Smith 5055 US!, misidentified, CA; Eastwood (1941) CA.

Hemizonia paniculata Gray
Hemizonia increscens (Hall ex Keck) Tanowitz spp. *increscens*
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Hoffmann (1932b) CR; Eastwood (1941) RO, CR.

Hemizonia paniculata Gray ssp. *increscens* Hall ex Keck
Hemizonia increscens (Hall ex Keck) Tanowitz ssp. *increscens*
Abrams and Ferris (1923–1960) RO; Smith (1976) RO, CR.

Hemizonia ramosissima Benth.
Hemizonia fasciculata (DC.) T. & G.
Smith (1976) CR.

Hemizonia streetsii Gray
omitted as unsubstantiated on GU.
Wiggins (1980) GU.
Hemizonia clementina Bdg.
Lyon (1886) CA; Davidson (1896) based on Davidson s.n. LAM! CA; Yates (1889) AN; Brandegee (1890b) AN, CA, CL; Eastwood (1898) NI, CA, CL.

Hemizonia wrightii Gray
Hemizonia fasciculata (DC.) T. & G.
Brandegee (1890b) CA; Davidson (1896) CA.

Hesperastragalus didymocarpus (H. & A.) Heller
Astragalus didymocarpus H. & A.
Millspaugh and Nuttall (1923) CA.

Hesperastragalus gambelianus (Sheld.) Heller
Astragalus gambelianus Sheld.
Millspaugh and Nuttall (1923) CA.

Hesperonia californica (Gray) Standl.
Mirabilis californica Gray var. *californica*
Millspaugh and Nuttall (1923) CA.

Hesperonia californica (Gray) Standl. var. *microphylla* Standl.
Mirabilis californica Gray var. *californica*
Eastwood (1941) RO, CR, CA, CL.

Hesperonia cendrosensis Standl.
Mirabilis californica Gray var. *californica*
Jepson (1909–1943) (doubtfully attributable to CL); Davidson and Moxley (1923) CL; Eastwood (1941) CL.

Hesperonia heimerlii Standl.
Mirabilis heimerlii (Standl.) Macbr.
Eastwood (1929) GU.

Hesperonia laevis (Benth.) Standl.
Mirabilis californica Gray var. *californica*
Eastwood (1941) RO; Gentry (1949) CL.

Heuchera sp.
possibly *Jepsonia malvaefolia* (Greene) Small
Watson (1876) based on Palmer s.n. in 1876 GH! sterile; Franceschi (1893) GU; Eastwood (1929) GU.

Heuchera micrantha Dougl.
Heuchera maxima Greene
Clokey (1931) based on Clokey 4952 LAM!, CR.

Heuchera pilosissima F. & M.
Heuchera maxima Greene
Brandegee (1888) RO; Brandegee (1890b) RO, CR.

Hieraceum argutum Nutt.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Eastwood (1941) BA.

Hieraceum grinellii Eastw.
Hieraceum arguta Nutt.
Clokey (1931) CR; Eastwood (1941) CR.

Hirschfeldia incana (L.) Lagr.-Foss.
Brassica geniculata (Desf.) Ball.
Raven (1963) CL; Foreman (1967) NI.

Holodiscus ariaefolius (Sm. in Rees) Greene
Holodiscus discolor (Pursh) Maxim. ssp. *discolor*
Eastwood (1941) CR, CA.

Holodiscus discolor (Pursh) Maxim. var. *franciscanus* (Rydb.) Jeps.
Holodiscus discolor (Pursh) Maxim. ssp. *discolor*
Jepson (1909–1943) CR; Thorne (1967) based on Thorne 36905 RSA! and Fosberg S5436 POM!, CA; Smith (1976) CR.

Hookera minor Britten
Brodiaea jolonensis Eastw.
Millspaugh and Nuttall (1923) CA.

Hordeum glaucum Steud.
Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvel.
Foreman (1967) NI; Smith (1976) all four islands.
Hordeum murinum L. ssp. *leporinum* (Link) Arcang.
Foreman (1967) based on Foreman & Lloyd 132 LA!, misidentified, NI.

Hordeum gussoneanum Parl.
Hordeum geniculatum All.
Hoffmann (1932a) RO; Eastwood (1941) RO.

Hordeum hystrix Roth.
Hordeum geniculatum All.
Thorne (1967) CA.

Hordeum leporinum Link
Hordeum murinum L. ssp. *leporinum* (Link) Arcang.
Foreman (1967) NI; Smith (1976) all four islands.

Hordeum murinum L.
incertae sedis
Greene (1885) GU; Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR, AN; Brandegee (1890b) RO, CR, AN; Hoffmann (1932a) MI; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA.
Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvel.
Vasey and Rose (1890) based on Palmer 671 F!, GU; Dunkle (1942) based on Dunkle 8108 LAM!, AN.
Hordeum murinum L. ssp. *leporinum* (Link) Arcang.
Eastwood (1929) based on Mason 1544 F!, GU.

Hordeum nodosum L.
possibly *Hordeum californicum* Covas & Steb.
Dunkle (1942) AN.
probably *Hordeum geniculatum* All. (Raven 1963).
Lyon (1886) CL; Brandegee (1890b) CL; Millspaugh and Nuttall (1923) CA.

Hordeum stebbinsii Covas
Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvel.
Wiggins (1980) GU.

Hosackia anthylloides (Gray) Millsp. & Nutt.
Lotus grandiflorus (Benth.) Greene var. *grandiflorus*
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Hosackia argophylla Gray
incertae sedis
Brandegee (1890b) CR, CL.
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven
Watson (1876) GU; Brandegee (1890b) CA; Franceschi (1893) GU; Trask (1899) CA.

Hosackia dendroidea (Greene) Abrams
Lotus scoparius (Nutt. in T. & G.) Ottley var. *dendroideus* (Greene) Ottley
Abrams and Ferris (1923–1960) RO, CR, AN, CA.

Hosackia glabra (Vog.) Torr.
Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *scoparius*
Lyon (1886) CA; Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR, CA.

Hosackia nivea (Greene) Wats.
Lotus argophyllus (Gray) Greene ssp. *niveus* (Greene) Munz
Abrams and Ferris (1923–1960) CR.

Hosackia occulta Greene
Lotus grandiflorus (Benth.) Greene var. *grandiflorus*
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Hosackia ornithopus Greene
omitted as unsubstantiated on MI.
Abrams and Ferris (1923–1960) MI.

Hosackia ornithopus Greene ssp. *venusta* (Eastw.) Abrams
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven
Abrams and Ferris (1923–1960) NI, CA.

Hosackia purshiana Benth.
Lotus purshianus (Benth.) Clem. & Clem. var. *purshianus*
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA.

Hosackia wrangeliana (F. & M.) T. & G.
omitted as unsubstantiated on CL.
Eastwood (1941) CL.
Lotus subpinnatus Lag.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA.

Ipomoea hederacea (L.) Jacq.
Ipomoea nil (L.) Roth
Jepson (1909–1943) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA; Thorne (1967) CA.

Isocoma latifolia Greene
Haplopappus venetus (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall
Eastwood (1941) RO, CR.

Isocoma veneta (HBK.) Greene var. *decumbens* (Bdg.) Jeps.
Haplopappus venetus (HBK.) Blake ssp. *vernonioides* (Nutt.) Hall
Hoffmann (1932b) based on Hoffmann s.n. SBM#2091!, misidentified, RO, based on Hoffmann s.n. SBM#10278!, misidentified, AN.

Isomeris arborea Nutt.
Cleome isomeris Greene
Lyon (1886) CA; Brandegee (1888) RO; Yates (1889) RO; Brandagee (1890b) RO, CA; Millspaugh and Nuttall (1923) CA; Munz (1935) CA.

Isomeris arborea Nutt. var. *globosa* Cov.
Cleome isomeris Greene
Jepson (1909–1943) CA, RO; Munz (1935) RO, CA; Eastwood (1941) RO, CR, CA; Dunkle (1950) RO, CR, CA.

Isomeris arborea Nutt. var. *insularis* Jeps.
Cleome isomeris Greene
Jepson (1909–1943) RO, CA; Eastwood (1941) RO, CA; Munz and Keck (1959) RO, CA; Munz (1974) RO, CA; Smith (1976) RO, CA.

Jepsonia neo-nuttalliana Millsp. in Millsp. & Nutt.
Jepsonia malvaefolia (Greene) Small
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Jepsonia parryi (Torr.) Small
Jepsonia malvaefolia (Greene) Small
Jepson (1909–1943) RO, CR, CA, GU; Jepson (1925) RO, CR; Howell (1935) NI; Munz and Keck (1959) Channel Islands; Foreman (1967) NI.

Juncus bufonius L. var. *congestus* Wahlb.
Juncus bufonius L.
Wiggins (1980) GU.

Juncus bufonius L. var. *halophilus* Buch. & Fern.
Juncus bufonius L.
Jepson (1909–1943) CR.

Juncus effusus L.
incertae sedis
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Juncus robustus Wats.
Juncus acutus L. var. *sphaerocarpus* Engelm.
Brandegee (1890a) CA; Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Koeleria cristata (L.) Pers.
omitted as unsubstantiated on CA and CL.
Eastwood (1941) CA, CL.

Koeleria pyramidata (Lam.) Beauv.
Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Munz (1935) RO, CR; Eastwood (1941) RO, CR.

Koeleria macrantha (Ledeb.) Spreng.
Koeleria pyramidata (Lam.) Beauv.
Smith (1976) RO, CR.

Krynitzkia ambigua Gray
incertae sedis
Lyon (1886) CA, CL; Brandegee (1890b) CA, CL.

Krynitzkia foliosa Greene
Cryptantha foliosa (Greene) Greene
Greene (1885) GU; Franceschi (1893) GU; Vasey and Rose (1890) GU.

Krynitzkia intermedia Gray
Cryptantha intermedia (Gray) Greene
Brandegee (1890a) CA; Brandegee (1890b) CA.

Krynitzkia leiocarpa F. & M.
Cryptantha leiocarpa (F. & M.) Greene
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR.

Krynitzkia maritima Greene
Cryptantha maritima (Greene) Greene
Greene (1885) GU; Franceschi (1893) GU; Vasey and Rose (1890) GU.

Krynitzkia micromeres Gray
Cryptantha micromeres (Gray) Greene
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Krynitzkia ramosissima Greene
Cryptantha maritima (Greene) Greene
Lyon (1886) CA; Davidson (1896) CA; Brandegee (1890b) CA.

Lactuca virosa L.
Lactuca serriola L.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CR, CA.

Lastarriaea chilensis Remy
Chorizanthe coriacea Goodm.
Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA; Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) RO, CR; Eastwood (1941) CR, CA.

Lasthenia chrysostoma (F. & M.) Greene
Lasthenia californica DC. ex Lindl. (Johnson & Ornduff 1978)
Raven (1963) CL; Thorne (1967) CA; Philbrick (1972) BA; Smith (1976) all four islands; Wiggins (1980) GU.

Lasthenia hirsutula Greene
Lasthenia californica DC. ex Lindl.
Hoffmann (1932b) MI, RO, CR.

Lasthenia macrantha (Gray) Greene
Lasthenia californica DC. ex Lindl.
Smith (1976) MI, RO.

Lathyrus alefeldii White
omitted as unsubstantiated on RO, CR, and CL.
Abrams and Ferris (1923–1960) CL; Eastwood (1941) RO, CR; Wiggins (1980) CL.

Lathyrus strictus Nutt.
incertae sedis
Hoffmann (1932b) RO; Munz (1935) CA; Dunkle (1950) RO, CR, CA.
Lathyrus laetiflorus Greene ssp. *barbarae* (White) C. L. Hitchc.
Munz (1935) CL; Dunkle (1950) CL.

Lathyrus vestitus Nutt. ex T. & G.
probably *Lathyrus laetiflorus* Greene ssp. *alefeldii* (White) Brads.
Lyon (1886) CA; Brandegee (1890b) CA.
Lathyrus vestitus Nutt. ex T. & G. ssp. *vestitus*
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Lathyrus vestitus Nutt. ex T. & G. ssp. *puberulus* (White ex Greene) C.L. Hitchc.
Lathyrus vestitus Nutt. ex T. & G. ssp. *vestitus*
Smith (1976) FO, CR, AN.

Laurocerasus ilicifolia (Nutt. ex H. & A.) M. Roem.
Prunus lyonii (Eastw.) Sarg.
Millspaugh and Nuttall (1923) CA.

Laurocerasus lyonii (Eastw.) Britt. in Britt. & Shaf.
Prunus lyonii (Eastw.) Sarg.
Abrams (1917) islands; Davidson and Moxley (1923) Channel Islands; Millspaugh and Nuttall (1923) CA.

Lavatera assurgentiflora Kell.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Raven (1967) BA.

Lavatera assurgentiflora Kell. ssp. *glabra* Philbrick in Power
Lavatera assurgentiflora Kell.
Philbrick (1980) CA, CL.

Layia glandulosa (Hook.) H. & A.
Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck
Lyon (1886) CL.

Layia platyglossa (F. & M.) Gray
incertae sedis
Brandegee (1888) RO.
Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck
Gentry (1949) MI, CR based on Elmore 442 AHFH!, CA.
Layia platyglossa (F. & M.) Gray ssp. *platyglossa*
Gentry (1949) based on Elmore 202 AHFH!, RO.

Layia platyglossa (F. & M.) Gray ssp. *platyglossa*
Layia platyglossa (F. & M.) Gray ssp. *campestris* Keck
Abrams and Ferris (1923–1960) CR; Munz and Keck (1959) CR; Smith (1976) CR.

Lepechinia calycina (Benth.) Epl. in Munz var. *wallacei* (Gray) Epl. in Munz
Lepechinia calycina (Benth.) Epl. in Munz
Munz (1935) RO, in part.
Lepechinia fragrans (Greene) Epl.
Munz (1935) RO in part, CR, CA.

Lepidium bipinnatifidum Desv.
Lepidium oblongum Small
Eastwood (1929) GU.

Lepidium dictyotum Gray var. *acutidens* Gray
Lepidium latipes Hook
Hoffmann (1932b) CR; Eastwood (1941) CR, CA, CL.

Lepidium lasiophyllum Nutt.
Lepidium lasiocarpum Nutt. ex T. & G. var. *lasiocarpum*
Brandegee (1888) RO; Yates (1889) RO.

Lepidium medium Greene
Lepidium virginicum L. var. *pubescens* (Greene) Thell.
Millspaugh and Nuttall (1923) CA.

Lepidium menziesii DC.
Lepidium oblongum Small
Watson (1876) GU; Vasey and Rose (1890) based on Palmer 897 GH!, GU.
Lepidium virginicum L. var. *pubescens* (Greene) Thell.
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Lepidium oblongum Small var. *insulare* C.L. Hitchc.
Lepidium oblongum Small
Hitchcock (1945) GU.

Lepidium pubescens Desv.
incertae sedis
Eastwood (1941) AN, NI; Dunkle (1942) AN.
Lepidium oblongum Small
Hitchcock (1936) based on Trask s.n. in Mar. 1901 NY!, misidentified, CA.

Lepidium strictum (Wats.) Rattan
Lepidium virginicum L. var. *pubescens* (Greene) Thell.
Eastwood (1941) NI; Dunkle (1942) AN; Foreman (1967) NI; Smith (1976) AN.

Lepigonum macrothecum F. & M.
Spergularia macrotheca (Hornem.) Heynh. ssp. *macrotheca*
Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, CR; Franceschi (1893) GU.

Leptilon canadensis (L.) Britt. in Britt. & Br.
Conyza canadensis (L.) Cronq.
Millspaugh and Nuttall (1923) CA.

Leptilon linifolium (Willd.) Small
Conyza bonariensis (L.) Cronq.
Millspaugh and Nuttall (1923) CA.

Lepturus incurvatus (L. f.) Trin.
Parapholis incurva (L. f.) C.E. Hubb.
Jepson (1909–1943) based on Brandegee 54 US!, CA.

Lepturus paniculatus Nutt.
Parapholis incurva (L. f.) C.E. Hubb.
Brandegee (1890a) probably based on Brandegee 54 US!, CA; Brandegee (1890b) CA.

Lilium bloomerianum Kell. var. *ocellatum* Kell.
omitted as unsubstantiated on CA.
Eastwood (1941) CA.

Lilium humboldtii Roezl & Leichtl.
Lilium humboldtii Roezl & Leichtl. ssp. *ocellatum* (Kell.) Thorne

Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR.

Lilium humboldtii Roezl & Leichtl. var. *ocellatum* (Kell.) Elwes
omitted as unsubstantiated on CA.
Eastwood (1941) CA.
Lilium humboldtii Roezl & Leichtl. ssp. *ocellatum* (Kell.) Thorne
Jepson (1909–1943) RO; Jepson (1925) RO; Munz (1935) RO, CR; Smith (1976) RO, CR.

Limonium californicum (Boiss.) Heller
probably *Limonium perezii* (Stapf.) F.T. Hubb.
Abrams and Ferris (1923–1960) CL.

Linanthus sp.
incertae sedis
Howell (1942) GU.

Linanthus parviflorus Greene
incertae sedis
Jepson (1909–1943) CR.

Linaria texana Sheele
Linaria canadensis (L.) Dum.-Cours. var. *texana* (Sheele) Penn.
Wiggins (1980) GU.

Lithophragma catalinae Rydb.
Lithophragma affine Gray ssp. *mixtum* R.L. Taylor
Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Lithophragma cymbalaria T. & G.
omitted as unsubstantiated on CA; also omitted by Thorne (1967).
Eastwood (1941) CA.

Lolium multiflorum Lam.
Lolium perenne L. ssp. *multiflorum* (Lam.) Husnot
Raven (1963) CL; Thorne (1967) CA; Foreman (1967) NI.

Lolium temulentum L. var. *arvense* (With.) Bab.
Lolium temulentum L.
Hoffmann (1932a) CR.

Lolium temulentum L. var. *leptochaeton* A. Br.
Lolium temulentum L.
Smith (1976) CR.

Lonicera hispidula (Lindl.) Dougl. ex T. & G. var. *subspicata* (H. & A.) Gray
Lonicera subspicata H. & A. var. *johnstonii* Keck
Ford (1890) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Eastwood (1941) CR.

Lotus argophyllus (Gray) Greene var. *niveus* (Greene) Ottley
Lotus argophyllus (Gray) Greene ssp. *adsurgens* (Dunkle) Raven
Ottley (1923) based on Brandegee s.n. Aug. 25, 1894 CL; Jepson (1925) CL.

Lotus argophyllus (Gray) Greene var. *ornithopus* (Greene) Ottley
omitted as unsubstantiated on CR.
Dunkle (1950) CR.
Lotus argophyllus (Gray) Greene ssp. *adsurgens* (Dunkle) Raven
Munz and Keck (1959) CL.

Lotus dendroideus (Greene) Greene
Lotus scoparius Nutt. in T. & G. var. *dendroideus* (Greene) Ottley
Davidson (1896) CA; Gentry (1949) RO, CR, AN, CA.

Lotus dendroideus (Greene) Greene var. *traskiae* (Eastw. ex Noddin in Abrams) Isely
Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *traskiae* (Eastw. ex Noddin in Abrams) Raven
Isely (1978) CL.

Lotus dendroideus (Greene) Greene var. *veatchii* (Greene) Isely
Lotus scoparius (Nutt. in T. & G.) Ottley var. *veatchii* (Greene) Ottley
Isely (1978) MI.

Lotus eriophorus Greene var. *heermannii* (Dur. & Hilg.) Ottley
Lotus heermannii (Dur. & Hilg.) Greene
Ottley (1923) based on Grant 716 CA.

Lotus grandiflorus (Benth.) Greene var. *mutabilis* Ottley
Lotus grandiflorus (Benth.) Greene var. *grandiflorus*
Clokey (1931) CR.

Lotus micranthus Benth.
probably *Lotus hamatus* Greene
Davidson (1896) CA.

Lotus niveus (Greene) Greene
Lotus argophyllus (Gray) Greene ssp. *adsurgens* (Dunkle) Raven
Gentry (1949) based on Elmore 410 AHFH!, misidentified, CL.
Lotus argophyllus (Gray) Greene ssp. *niveus* (Greene) Munz
Gentry (1949) CR.
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven
Gentry (1949) based on Elmore 409 AHFH!, misidentified, CL.

Lotus scoparius (Nutt. in T. & G.) Ottley var. *dendroideus* (Greene) Ottley
Lotus scoparius (Nutt. in T. & G.) Ottley ssp. *traskiae* (Eastw. ex Noddin in Abrams) Raven
Munz and Keck (1959) CL in part.

Lotus scoparius (Nutt. in T. & G.) Ottley var. *traskiae* (Eastw. ex Noddin in Abrams) Ottley
Lotus scoparius (Nutt. in T. & G.) Ottley var. *dendroideus* (Greene) Ottley
Dunkle (1950) probably based on Dunkle 2056 AHFH!, misidentified, CA.

Lupinus affinis J. G. Agardh
Lupinus succulentus Dougl. ex Koch
Lyon (1886) CL; Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Millspaugh and Nuttall (1923) CA.

Lupinus albifrons Benth.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Eastwood (1941) CL.

Lupinus albifrons Benth. var. *eminens* (Greene) C.P. Sm.
probably *Lupinus albifrons* Benth. ssp. *albifrons*
Hoffmann (1932b) CR; Smith (1976) CR.

Lupinus arboreus Sims
omitted as unsubstantiated on CA.
Eastwood (1941) CA.

Lupinus bicolor Lindl. var. *rostratus* (Eastw.) Jeps.
incertae sedis
Jepson (1909–1943) CR.

Lupinus bicolor Lindl. ssp. *trifidus* (Torr.) C.P. Sm.
omitted as unsubstantiated on CR.
Smith (1976) CR.

Lupinus chamissonis Esch.
incertae sedis
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Eastwood (1941) MI, RO, CR; Smith (1976) MI.

Lupinus clementinus Greene
Lupinus guadalupensis Greene
Davidson and Moxley (1923) CA; Dunkle (1950) CL.

Lupinus concinnus J.G. Agardh var. *agardhianus* (Heller) C.P. Sm.
Lupinus agardhianus Heller
Hoffmann (1932b) RO, CR; Munz (1935) on the islands; Raven (1963) CL.

Lupinus excubitus Jones var. *hallii* (Abrams) C.P. Sm.
Lupinus albifrons Benth. ssp. *albifrons*
Eastwood (1941) NI, CA.

Lupinus gracilis J.G. Agardh
Lupinus agardhianus Heller
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Lupinus micranthus Dougl. in Lindl.
incertae sedis
Brandegee (1888) RO; Brandegee (1890b) RO.
Lupinus bicolor Lindl. ssp. *microphyllus* (Wats.) D. Dunn
Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Eastwood (1898) NI; Millspaugh and Nuttall (1923) CA.

Lupinus microcarpus Sims
incertae sedis
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.

Lupinus microcarpus Sims var. *horizontalis* Jeps.
incertae sedis
Jepson (1909–1943) CR.

Lupinus microcarpus Sims var. *insularis* C.P. Sm.
incertae sedis
Jepson (1909–1943) CR.

Lupinus moranii Dunkle
Lupinus guadalupensis Greene
Dunkle (1943) based on Moran 587 LAM!, MO!, NY!, RSA! CL; Dunkle (1950) CL; Munz and Keck (1959) CL.

Lupinus nanus Dougl. in Benth.
Lupinus guadalupensis Greene
Dunkle (1950) based on Moran 587 LAM!, MO!, NY!, RSA!, misidentified, CL.

Lupinus sparsiflorus Benth.
Lupinus bicolor Lindl. ssp. *microphyllus* (Wats.) D. Dunn
Gentry (1949) based on Elmore 446 AHFH!, misidentified, CR; Smith (1976) CR.

Lupinus sparsiflorus Benth. var. *pondii* (Greene) C.P. Sm.
Lupinus guadalupensis Greene
Wiggins (1980) GU.

Lupinus subvexus C.P. Sm. var. *phoeniceus* C.P. Sm.
incertae sedis
Smith (1976) RO, CR.

Lupinus variicolor Steud.
Lupinus arboreus Sims
Smith (1976) based on Blakley 5104 SBBG! and Blakley 5854 SBBG!, misidentified, MI.

Luzula campestris (L.) DC. var. *congesta* (Thuill.) Meyer
Luzula subsessilis (Wats.) Buch.
Hoffmann (1932a) RO, CR; Munz (1935) RO, CR; Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.

Luzula comosa Meyer
Luzula subsessilis (Wats.) Buch.
Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Eastwood (1941) MI, RO, CR.

Lycium brevipes Benth. var. *hassei* (Greene) C.L. Hitchc.
Lycium verrucosum Eastw.
Jepson (1909–1943) NI.

Lycium californicum Nutt.
omitted as unsubstantiated on MI.
Dunkle (1950) MI.

Lycium richii Gray
Lycium brevipes Benth. var. *hassei* (Greene) C.L. Hitchc.
Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA; Trask (1899) CA; Abrams (1917) CA; Davidson and Moxley (1923) CA; Jepson (1925) CA; Eastwood (1941) CA, CL; Dunkle (1950) CA.

Lycium richii Gray var. *hassei* (Greene) Jtn.
omitted as unsubstantiated on GU.
Dunkle (1950) GU.

Mahonia pinnata (Lag.) Fedde.
Berberis pinnata Lag. ssp. *insularis* Munz
Eastwood (1941) RO, CR.

Malacothrix blairii (M. & J.) Munz
Stephanomeria blairii M. & J.
Abrams and Ferris (1923–1960) CL; Munz (1935) CL; Eastwood (1941) CL; Dunkle (1950) CL; Munz and Keck (1959) CL.

Malacothrix californica DC.
omitted as unsubstantiated on CR and CA.
Munz (1935) CR, CA.

Malacothrix clevelandii Gray
Malacothrix "A" (Davis, 1980)
Gentry (1949) based on Elmore 370 AHFH! BA.
Malacothrix "C" (Davis, 1980)
Foreman (1967) based on Foreman, Evans and Rainey 80 UC! NI.
Malacothrix similis Davis & Raven
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Hall (1907) CR; Abrams and Ferris (1923–1960) CR; Munz (1935) CR; Eastwood (1941) CR; Gentry (1949) CR; Smith (1976) CR.

Malacothrix squalida Greene
Eastwood (1941) AN; Dunkle (1942) AN; Gentry (1949) AN; Smith (1976) AN.

Malacothrix coulteri Harv. & Gray var. *coulteri*
Malacothrix coulteri Harv. & Gray var. *cognata* Jeps.
Williams (1957) RO, CR.

Malacothrix foliosa Gray
incertae sedis
Brandegee (1890b) MI, CR; Jepson (1925) CR.
omitted as column transposition for BA.
Dunkle (1950) CA.
Malacothrix incana (Nutt.) T. & G. var. *incana*
Gentry (1949) based on Elmore 338 AHFH!, misidentified, MI.
probably *Malacothrix indecora* Greene.
Brandegee (1890b) MI, CR; Williams (1957) based on Brandegee s.n. in 1888 at UC, not seen, CR.

Malacothrix foliosa Gray var. *indecora* (Greene) Williams
incertae sedis
Williams (1957) NI.
Malacothrix indecora Greene
Williams (1957) MI, CR.

Malacothrix foliosa Gray var. *squalida* (Greene) Williams
incertae sedis
Williams (1957) MI.
probably *Malacothrix* "A" (Davis, 1980).
Williams (1957) BA.
Malacothrix squalida Greene
Williams (1957) CR.

Malacothrix incana (Nutt.) T. & G. var. *succulenta* (Elmer) Williams
Malacothrix incana (Nutt.) T. & G.
Smith (1976) MI, RO, CR.

Malacothrix indecora Greene
Malacothrix "C" (Davis, 1980)
Eastwood (1898) NI; Jepson (1925) NI.

Malacothrix insularis Greene
incertae sedis
Brandegee (1890b) CR; Eastwood (1941) CR.

Malacothrix insularis Greene var. *squalida* (Greene) Ferris
incertae sedis
Abrams and Ferris (1923–1960) RO.
Malacothrix "A" (Davis, 1980)
Abrams and Ferris (1923–1960) BA.
Malacothrix squalida Greene
Abrams and Ferris (1923–1960) CR, AN.

Malacothrix saxatilis (Nutt.) T. & G.
Malacothrix saxatilis (Nutt.) T. & G. var. *implicata* (Eastw.) Hall
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) MI, RO, CR.
Malacothrix saxatilis (Nutt.) T. & G. var. *tenuifolia* (Nutt.) Gray
Lyon (1886) CA; Brandegee (1890b) CA; Davidson (1896) CA; Jepson (1925) CA.

Malacothrix similis Davis & Raven
Malacothrix squalida Greene (according to Davis pers. comm.).
Smith (1976) AN.

Malacothrix squalida Greene
omitted as unsubstantiated on RO.
Abrams and Ferris (1923–1960) RO; Munz and Keck (1959) RO; Smith (1976) RO.
Malacothrix "A" (Davis, 1980)
Abrams and Ferris (1923–1960) BA; Munz and Keck (1959) BA.
probably *Malacothrix indecora* Greene.
Eastwood (1941) MI.

Malacothrix tenuifolia T. & G.
Malacothrix saxatilis (Nutt.) T. & G. var. *implicata* (Eastw.) Hall
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR, AN.

Malva borealis Wallr.
Malva parviflora L.
Watson (1876) GU; Greene (1885) GU; Lyon (1886) CL; Brandegee (1888) RO; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA, CL; Vasey and Rose (1890) GU; Franceschi (1893) GU; Eastwood (1929) GU.

Malva nicaensis All.
Malva parviflora L.
Smith (1976) CR.

Malva pusilla Sm. in Sowerby
Malva parviflora L.
Eastwood (1898) NI; Eastwood (1941) MI, RO, CR, NI, CA.

Malvastrum exile Gray
Eremalche exilis (Gray) Greene
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Ford (1890) CR; Trask (1904) CL; Eastwood (1941) CR, CL; Thorne (1967) CA.

Malvastrum fasciculatum Greene
Malacothamnus fasciculatus (Nutt.) Greene ssp. *catalinensis* (Eastw.) Thorne
Millspaugh and Nuttall (1923) CA; Dunkle (1950) CA.
Malacothamnus fasciculatus (Nutt.) Greene var. *nesioticus* (Rob.) Kearn.
Dunkle (1950) CR.

Malvastrum thurberi Gray
Malacothamnus fasciculatus (Nutt.) Greene ssp. *catalinensis* (Eastw.) Thorne
Lyon (1886) CA; Brandegee (1890b) CA; Trask (1899) CA.
Malacothamnus fasciculatus (Nutt.) Greene var. *nesioticus* (Rob.) Kearn.
Brandegee (1890b) CR.

Malvastrum thurberi Gray var. *laxiflorum* Gray
Malacothamnus fasciculatus (Nutt.) Greene var. *nesioticus* (Rob.) Kearn.
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR.

Mammillaria goodridgei Scheer in Salm-Dyck
Mammillaria blossfeldiana Boedeker var. *shurliana* Gates
Greene (1885) GU; Vasey and Rose (1890) GU; Howell (1942) GU.

Marah fabacea (Naud.) Greene
Marah macrocarpus (Greene) Greene
Gentry (1949) CL; Smith (1976) RO.

Marah guadalupensis (Wats.) Greene
Marah macrocarpus (Greene) Greene
Abrams and Ferris (1923–1960) NI, CA, CL; Eastwood (1941) MI, RO, CR.

Marah macrocarpus (Greene) Greene var. *major* (S.T. Dunn) Stocking
Marah macrocarpus (Greene) Greene
Munz and Keck (1959) Channel Islands.

Marah major S.T. Dunn
Marah macrocarpus (Greene) Greene
Howell (1935) NI; Eastwood (1941) NI, CA, CL.

Marrubium vulgare L.
omitted as unsubstantiated on BA.
Gentry (1949) BA.

Maruta cotula (L.) DC.
Anthemis cotula L.
Millspaugh and Nuttall (1923) CA.

Meconella oregana Nutt. in T. & G. var. *denticulata* (Greene) Jeps.
Meconella denticulata Greene
Jepson (1909–1943) CR; Munz and Keck (1959) CR.

Medicago apiculata Willd.
Medicago polymorpha L. var. *brevispina* (Benth.) Heyn.
Jepson (1909–1943) CR; Clokey (1931) CR; Hoffmann (1932b) RO, CR; Eastwood (1941) RO, CR, CA, CL.

Medicago denticulata Willd.
Medicago sativa L.
Lyon (1886) CA, CL; Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Brandegee (1890b) MI, CR, CA, CL; Eastwood (1898) NI.

Medicago hispida Gaertn.
Medicago polymorpha L. var. *polymorpha*
Millspaugh and Nuttall (1923) CA; Hoffmann (1932b) RO; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA, CL; Howell (1942) GU; Dunkle (1942) AN, BA; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL.

Megarrhiza californica Torr. in Wats.
Marah macrocarpus (Greene) Greene
Lyon (1886) CA.

Megarrhiza guadalupensis Wats.
Marah guadalupensis (Wats.) Greene
Watson (1876) GU.

Megarrhiza marah Wats.
Marah macrocarpus (Greene) Greene
Lyon (1886) CA.

Melica imperfecta Trin.
omitted as unsubstantiated on NI.
Dunkle (1950) NI.

Melica imperfecta Trin. var. *flexuosa* Boland.
Melica imperfecta Trin.
Hoffmann (1932a) CR; Munz (1935) CR; Eastwood (1941) CR.

Melica imperfecta Trin. var. *minor* Scribn.
Melica imperfecta Trin.
Jepson (1909–1943) CA; Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA.

Melica imperfecta Trin. var. *refracta* Thurb. in Wats.
Melica imperfecta Trin.
Jepson (1909–1943) CR.

Melica torreyana Scribn.
Melica imperfecta Trin.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, CR, CA.

Melilotus parviflorus Desf.
Melilotus indica (L.) All.
Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR, CA.

Mentha piperita L.
Mentha citrata Ehrh.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Mentzelia dispersa Wats.
Mentzelia micrantha Wats.
Watson (1876) GU; Vasey and Rose (1890) based on Palmer 893 ND-G!, GU; Eastwood (1929) GU; Dunkle (1950) GU.

Mentzelia gracilenta T. & G.
Mentzelia affinis Greene
Lyon (1886) CL; Brandegee (1890b) CL; Eastwood (1941) CL.

Mentzelia gracilenta T. & G. var. *eremophila* Jeps.
Mentzelia affinis Greene
Jepson (1909–1943) CA.

Mesembryanthemum aequilaterale Haw.
omitted as unsubstantiated on CA but recently reported by Thorne (pers. comm.).
Millspaugh and Nuttall (1923) CA.
Carpobrotus aequilaterus (Haw.) N.E. Br.
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1890b) MI, CR; Jepson (1909–1943) MI, CR; Hoffmann (1932a) RO.

Mesembryanthemum chilense Mol.
Carpobrotus aequilaterus (Haw.) N.E. Br.
Munz (1935) MI; Eastwood (1941) MI, RO, CR, CA; Dunkle (1942) AN; Gentry (1949) MI.

Mesembryanthemum cordifolium L. f.
Aptenia cordifolia (L. f.) N.E. Br.
Munz and Keck (1959) CA.

Mesembryanthemum edule L.
Carpobrotus edulis (L.) Bolus
Foreman (1967) NI.

Micrampelis macrocarpa (Greene) Greene
Marah macrocarpus (Greene) Greene
Millspaugh and Nuttall (1923) CA.

Micropus californicus F. & M.

Filago californica Nutt.

Watson (1876) based on Palmer 37 CM!, NY!, misidentified, GU; Eastwood (1929) GU; Dunkle (1950) GU.

Microseris anomala Wats.

Microseris linearifolia (DC.) Sch.-Bip. (Chambers, 1955).

Brandegee (1888) CR; Yates (1889) CR; Eastwood (1941) CR.

Microseris aphantocarpha (Gray) Sch.-Bip.

Microseris douglasii (DC.) Sch.-Bip. ssp. *platycarpa* (Gray) Chamb.

Eastwood (1941) CA, CL.

Microseris lindleyi (DC.) Gray

omitted as unsubstantiated on MI.

Dunkle (1950) MI.

Microseris heterocarpa (Nutt.) Chamb.

Lyon (1886) CL; Brandegee (1888) RO, CR; Brandegee (1890a) CA; Brandegee (1890b) RO, CR, CA, CL; Brandegee (1900) GU; Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Munz (1935) on the islands; Eastwood (1941) RO, CR, CA, CL; Dunkle (1950) RO, CA, CL, GU.

Microseris lindleyi (DC.) Gray var. *clevelandii* (Greene) Hall

omitted as unsubstantiated on AN.

Dunkle (1950) AN.

Microseris heterocarpa (Nutt.) Chamb. (Chambers, 1955)

Dunkle (1950) CR, GU.

Microseris linearifolia (DC.) Sch.-Bip.

omitted as unsubstantiated on MI.

Dunkle (1950) MI.

Microsteris traskiae (Eastw. ex Milliken) Davids. & Mox.

Allophyllum glutinosum (Benth.) A. Grant & V. Grant

Davidson and Moxley (1923) CA.

Mimulus douglasii Gray

Mimulus traskiae Grant in Millsp. & Nutt.

Davidson and Moxley (1923) based on Trask s.n. in Mar. 1901 LAM! CA.

Mimulus flemingii Munz

Diplacus parviflorus Greene

Abrams and Ferris (1923–1960) RO, CR, AN; Munz (1935) RO, CR; Dunkle (1942) AN; Dunkle (1950) RO, CR, AN, CL; Munz and Keck (1959) RO, CR, AN, CL; Raven (1963) CL; Munz (1974) RO, CR, AN, CL.

Mimulus glutinosus Wendl.

incertae sedis

Brandegee (1890b) RO, CR.

Diplacus puniceus Nutt.

Brandegee (1890a) CA; Brandegee (1890b) CA; Trask (1899) CA.

Mimulus glutinosus Wendl. var. *puniceus* (Nutt.) Gray

Diplacus puniceus Nutt.

Lyon (1886) CA.

Mimulus guttatus Fisch. ex DC. var. *depauperatus* (Gray) Grant

Mimulus guttatus Fisch. ex DC. ssp. *guttatus*

Gentry (1949) based on Elmore 257 AHFH!, misidentified, CR.

Mimulus latifolius Gray

Mimulus brandegei Penn.

Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Jepson (1925) CR; Munz (1935) CR; Eastwood (1941) CR; Dunkle (1950) CR.

Mimulus longiflorus (Nutt.) Grant

Diplacus longiflorus Nutt. ssp. *longiflorus*

Munz (1935) CR; Dunkle (1950) RO, CR.

Mimulus longiflorus (Nutt.) Grant var. *linearis* (Benth.) Grant

Diplacus longiflorus Nutt. ssp. *longiflorus*

Dunkle (1950) CR.

Diplacus puniceus Nutt.

Dunkle (1950) CA.

Mimulus luteus L.

Mimulus guttatus Fisch. ex DC. ssp. *guttatus*

Lyon (1886) CA; Brandegee (1888) RO, CR; Yates (1889) CR; Brandegee (1890b) RO, CR, CA; Trask (1899) CA.

Mimulus moschatus Dougl.

incertae sedis

Eastwood (1941) RO, CR.

Mimulus nasutus Greene

probably *Mimulus guttatus* Fisch. ex DC. ssp. *guttatus*

Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR.

Mimulus puniceus (Nutt.) Steud.

Diplacus puniceus Nutt.

Davidson (1896) CA; Abrams and Ferris (1923–1960) CA; Munz (1935) CA; Dunkle (1950) CA; Munz and Keck (1959) CA; Thorne (1967) CA; Munz (1974) CA; Wiggins (1980) CA.

Mirabilis californica Gray

Mirabilis heimerlii (Standl.) Macbr.

Greene (1885) GU.

Mirabilis laevis (Benth.) Curran

Mirabilis californica Gray var. *californica*

Hoffmann (1932a) RO; Munz (1935) CR, CA; Dunkle (1942) AN, BA; Dunkle (1950) RO, CR, BA, CA; Munz and Keck (1959) CR, CA; Raven (1963) CL; Thorne (1967) CA; Philbrick (1972) BA.

Mirabilis heimerlii (Standl.) Macbr.

Franceschi (1893) GU; Moran (1951) GU.

Mirabilis laevis (Benth.) Curran var. *cedrosensis* (Standl.) Munz

Mirabilis californica Gray var. *californica*

Munz (1935) CL; Dunkle (1950) CL; Munz and Keck (1959) CL.

Mirabilis laevis (Benth.) Curran var. *cordifolia* Dunkle

Mirabilis californica Gray var. *californica*

Dunkle (1941) based on Dunkle 7234 LAM! CL; Dunkle (1950) CL; Munz and Keck (1959) CL.

Monardella lanceolata Gray

incertae sedis

Lyon (1886) CA; Brandegee (1890b) CA.

- *Montia perfoliata* (Donn) Howell
  - *Claytonia perfoliata* Donn var. *perfoliata*
    - Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Hoffmann (1932a) MI; Munz (1935) the islands; Eastwood (1941) MI, RO, CR, CA; Dunkle (1942) AN, BA; Howell (1942) GU; Gentry (1949) CL; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL, GU; Raven (1963) CL; Smith (1976) MI, RO, CR, AN; Wiggins (1980) GU.
- *Montia perfoliata* (Donn) Howell var. *parviflora* (Dougl. ex Hook.) Jeps.
  - *Claytonia perfoliata* Donn var. *parviflora* (Dougl. ex Hook.) Torr.
    - Hoffmann (1932a) CR; Eastwood (1941) CR; Smith (1976) CR.
- *Muhlenbergia debilis* (HBK.) Kunth
  - *Muhlenbergia microsperma* (DC.) Kunth
    - Watson (1876) GU; Greene (1885) GU; Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Vasey and Rose (1890) based on Palmer 656 ND-G! and Palmer 670 ND-G! GU; Franceschi (1893) GU.
- *Muhlenbergia gracilis* (HBK.) Kunth
  - *Muhlenbergia microsperma* (DC.) Kunth
    - Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA.
- *Munzothamnus blairii* (M. & J.) Raven
  - *Stephanomeria blairii* M. & J.
    - Raven (1963) CL; Thorne (1969) CL; Munz (1974) CL.
- *Myosurus lepturas* (Gray) Howell var. *filiformis* (Greene) Abrams
  - *Myosurus minimus* L. var. *filiformis* Greene
    - Abrams and Ferris (1923–1960) GU.
- *Nasturtium aquaticum* Tragus
  - *Nasturtium officinale* R. Br.
    - Greene (1887a) CR; Yates (1889) CR.
- *Navarretia filifolium* (Nutt.) Kuntze
  - *Eriastrum filifolium* (Nutt.) Woot. & Standl.
    - Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA.
- *Navarretia viscidula* Benth.
  - *Navarretia atractyloides* (Benth.) H. & A.
    - Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
- *Nemophila aurita* Lindl.
  - *Pholistoma racemosum* (Nutt.) Const.
    - Watson (1876) GU.
- *Nemophila erodiifolia* Millsp. in Millsp. & Nutt.
  - *Pholistoma racemosum* (Nutt.) Const.
    - Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
- *Nemophila parviflora* Dougl. ex Benth.
  - probably *Nemophila pedunculata* Dougl. ex Benth.
    - Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.
  - *Nemophila pedunculata* Dougl. ex Benth.
    - Hoffmann (1932b) based on Hoffmann s.n. Apr. 10, 1930 SBM#9226!, misidentified, MI, based on Hoffmann s.n. Apr. 17, 1929 SBM#5992!, SBM#5993! and SBM#5994!, misidentified, RO; Eastwood (1941) MI, RO.
- *Nemophila racemosa* Nutt. ex Gray
  - omitted as unsubstantiated on NI; also omitted by Foreman (1967).
    - Dunkle (1950) NI.
- *Neomammillaria goodridgei* (Scheer) Britt. & Rose
  - *Mammillaria blossfeldiana* Boedecker var. *shurliana* Gates
    - Eastwood (1929) GU.
- *Nesothamnus incanus* (Gray) Rydb.
  - *Perityle incana* Gray
    - Howell (1942) GU.
- *Nicotiana bigelovii* (Torr.) Wats.
  - *Nicotiana attenuata* Torr. ex Wats. in King
    - Watson (1876) based on Palmer 64 NY!, misidentified, GU.
- *Nicotiana clevelandii* Gray
  - *incertae sedis*
    - Brandegee (1890a) CA; Eastwood (1941) CA.
- *Nicotiana petuniaeflora* Greene
  - *Nicotiana attenuata* Torr. ex Wats. in King
    - Greene (1885) based on Greene s.n. Apr. 25, 1885 CAS#859! GU; Eastwood (1929) GU.
- *Notholaena californica* D.C. Eat.
  - omitted as unsubstantiated on RO.
    - Eastwood (1941) RO.
  - *Aspidotis californica* (Hook.) Nutt. ex Copel.
    - Eastwood (1941) CR, CA.
- *Notholaena candida* (Mart. & Gal.) Hook.
  - *Notholaena californica* (D.C. Eat.) (A. Smith pers. comm.).
    - Greene (1887a) CR; Yates (1889) CR; Yates (1890) CR; Dunkle (1940a) CR.
- *Notholaena newberryi* D.C. Eat.
  - omitted as unsubstantiated on CR.
    - Eastwood (1941) CR.
  - *Cheilanthes newberryi* (D.C. Eat.) Domin (A. Smith pers. comm.).
    - Watson (1876) GU; Greene (1885) GU; Lyon (1886) CL; Brandegee (1890b) CL, GU; Vasey and Rose (1890) GU; Franceschi (1893) GU; Abrams and Ferris (1923–1960) CL, GU; Eastwood (1929) GU; Dunkle (1940a) CL; Eastwood (1941) CL; Howell (1942) GU; Dunkle (1950) CL, GU; Wiggins (1980) GU.
- *Oenothera biennis* L. var. *hirsutissima* Gray ex Wats.
  - *Oenothera elata* HBK. ssp. *hirsutissima* (Gray ex Wats.) Dietrich
    - Brandegee (1890b) CR.
- *Oenothera bistorta* Nutt. in T. & G.
  - *incertae sedis*
    - Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR, CA; Eastwood (1941) MI, RO, CR, CA.
- *Oenothera cheiranthifolia* Hornem. ex Spreng.

omitted as unsubstantiated on CA.
Eastwood (1941) CA; Gentry (1949) CA.
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR; Hoffmann (1932b) RO; Munz (1935) MI, RO, BA; Eastwood (1941) MI, RO, CR, NI; Dunkle (1942) BA; Gentry (1949) MI, RO, CR, NI, BA; Dunkle (1950) MI, RO, CR, NI, BA; Munz and Keck (1959) MI, RO; Raven (1963) CL.

Oenothera cheiranthifolia Hornem. ex Spreng. var. *nitida* (Greene) Munz
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*
Jepson (1909–1943) MI; Abrams and Ferris (1923–1960) MI; Hoffmann (1932b) RO; Munz (1935) MI, RO; Dunkle (1950) RO, CR; Munz and Keck (1959) MI.

Oenothera contorta Dougl. in Hook. var. *epilobioides* (Greene) Munz
Camissonia strigulosa (F. & M.) Raven
Hoffmann (1932b) MI; Eastwood (1941) MI, RO.

Oenothera contorta Dougl. in Hook. var. *strigulosa* (F. & M.) Munz
Camissonia strigulosa (F. & M.) Raven
Hoffmann (1932b) RO; Munz (1935) RO; Dunkle (1950) RO; Munz and Keck (1959) RO.

Oenothera dentata Cav.
Camissonia strigulosa (F. & M.) Raven
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO.

Oenothera guadalupensis Wats.
Camissonia guadalupensis (Wats.) Raven ssp. *clementina* (Raven) Raven
Abrams and Ferris (1923–1960) CL; Munz (1935) CL; Eastwood (1941) CL; Dunkle (1950) CL; Munz and Keck (1959) CL.
Camissonia guadalupensis (Wats.) Raven ssp. *guadalupensis*
Watson (1876) GU; Abrams and Ferris (1923–1960) GU; Eastwood (1929) GU; Dunkle (1950) GU; Munz and Keck (1959) GU.

Oenothera guadalupensis Wats. ssp. *clementina* Raven
Camissonia guadalupensis (Wats.) Raven ssp. *clementina* (Raven) Raven
Raven (1963) CL.

Oenothera hirta Link. var. *jonesii* H. Lev.
Camissonia micrantha (Hornem. ex Spreng.) Raven
Clokey (1931) CR.

Oenothera hookeri T. & G.
omitted as unsubstantiated on RO and CA.
Eastwood (1941) RO, CA.
Oenothera elata HBK. ssp. *hirsutissima* (Gray ex Wats.) Dietrich
Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) CR.

Oenothera leptocarpa Greene
Camissonia californica (Nutt. ex T. & G.) Raven
Hoffmann (1932b) RO; Thorne (1967) CA.

Oenothera micrantha Hornem. ex Spreng.
Camissonia micrantha (Hornem. ex Spreng.) Raven
Lyon (1886) CA; Brandegee (1890b) CA; Trask (1899) CA; Hoffmann (1932b) MI, RO, CR; Eastwood (1941) MI, RO, CR, CA, CL; Munz and Keck (1959) Channel Islands; Raven (1963) CL; Thorne (1967) CA.
Camissonia robusta Raven
Moran (1951) based on Moran 2891 RSA! cited by Raven (1969) GU.

Oenothera micrantha Hornem. ex Spreng. var. *jonesii* (H. Lev.) Munz
Camissonia hirtella (Greene) Raven
Munz and Keck (1959) Channel Islands.

Oenothera nitida Greene
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*
Greene (1887b) MI; Yates (1889) MI; Eastwood (1941) MI, RO.

Oenothera spiralis Hook. var. *nitida* (Greene) Jeps.
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *cheiranthifolia*
Jepson (1925) MI.

Oenothera strigulosa (F. & M.) T. & G.
Camissonia strigulosa (F. & M.) Raven
Eastwood (1941) RO.

Oenothera viridescens Hook.
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raim. in Engl. & Prantl ssp. *suffruticosa* (Wats.) Raven
Eastwood (1898) NI.

Oligomeris glaucescens Camb.
Oligomeris linifolia (Vah.) Macbr.
Eastwood (1898) NI; Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, RO, CR, NI, CA, CL.

Opuntia cholla Weber
Opuntia prolifera Engelm.
Wiggins (1980) AN.

Opuntia engelmannii Salm-Dyck. in Engelm.
Opuntia littoralis (Engelm.) Ckll. var. *littoralis*
Lyon (1886) CA.

Opuntia engelmannii Salm-Dyck. in Engelm. var. *littoralis* Engelm.
Opuntia littoralis (Engelm.) Ckll. var. *littoralis*
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR, AN; Brandegee (1890b) MI, RO, CR, CA; Eastwood (1898) NI; Trask (1899) CA; Trask (1904) CL.

Opuntia megacantha Salm-Dyck.
Opuntia ficus-indica (L.) Mill.
Millspaugh and Nuttall (1923) based on Millspaugh 4523 F!, misidentified CA; Jepson (1909–1943) CA.

Opuntia megacarpa Griff.
probably *Opuntia ficus-indica* (L.) Mill.
Eastwood (1941) CA.

Opuntia occidentalis Engelm. & Bigel.

Opuntia littoralis (Engelm.) Ckll. var. *littoralis*

Millspaugh and Nuttall (1923) CA; Davidson and Moxley (1923) CA; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA, CL.

Opuntia phaecantha Engelm. in Gray var. *discata* (Griffiths) Benson & Walkington

incertae sedis

Thorne (1967) CA.

Orobanche californica Cham. & Schlecht.

probably *Orobanche parishii* (Jeps.) Heckard ssp. *brachyloba* Heckard.

Thorne (1967) CA.

Orobanche fasciculata Nutt. var. *franciscana* Achey

Orobanche fasciculata Nutt.

Thorne (1967) CA; Smith (1976) MI, RO.

Orobanche grayana G. Beck

possibly *Orobanche californica* Cham. & Schlecht. ssp. *grandis* Heckard

Hoffmann (1932b) RO; Eastwood (1941) RO.

Orobanche uniflora L. var. *minuta* (Suksd.) Achey

Orobanche uniflora L. ssp. *occidentalis* (Greene) Abrams ex Ferris

Munz and Keck (1959) CR.

Orobanche uniflora L. var. *sedi* (Suksd.) Achey

Orobanche fasciculata Nutt.

Munz (1935) based on Hoffmann s.n. May 8, 1932 POM!, misidentified, RO.

Orobanche uniflora L. ssp. *occidentalis* (Greene) Abrams ex Ferris

Eastwood (1941) CR.

Orthocarpus purpurascens Benth.

incertae sedis

Brandegee (1890a) CA; Brandegee (1890b) CA; Trask (1904) CA; Gentry (1949) MI, CR in part, CA; Dunkle (1950) MI, CR, CA.

Orthocarpus densiflorus Benth. var. *densiflorus*

Eastwood (1898) based on Trask 61 MO!, misidentified, NI; Eastwood (1941) NI; Gentry (1949) based on Elmore 460 AHFH!, misidentified, CR; Dunkle (1950) NI.

Orthocarpus purpurascens Benth. var. *pallidus* Keck

Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Gentry (1949) RO; Dunkle (1950) RO.

Oxalis californica (Abrams) Knuth

Oxalis albicans HBK. ssp. *californicus* (Abrams) Eiten

Abrams and Ferris (1923–1960) CA; Munz and Keck (1959) CR, CA.

Oxalis pilosa Nutt.

Oxalis albicans HBK. ssp. *pilosa* (Nutt.) Eiten

Munz (1935) CR; Eastwood (1941) CR; Munz and Keck (1959) CR.

Oxalis wrightii Gray

Oxalis albicans HBK. ssp. *pilosa* (Nutt.) Eiten

Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.

Parietaria debilis Forst. f.

Parietaria hespera Hinton

Watson (1876) GU; Greene (1885) GU; Lyon (1886) CA, CL; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Vasey and Rose (1890) GU; Brandegee (1890b) RO, CR, CA, CL; Jepson (1909–1943) CR; Millspaugh and Nuttall (1923) CA.

Parietaria floridana Nutt.

Parietaria hespera Hinton

Eastwood (1929) GU; Howell (1935) NI; Munz (1935) RO, CR, CL; Eastwood (1941) RO, CR, NI, CA, CL; Dunkle (1942) AN; Howell (1942) GU; Raven (1963) CL; Thorne (1967) CA.

Soleirolia soleirolii (Req.) Dandy

Foreman (1967) based on Foreman 120 UC!, misidentified, NI.

Parietaria hespera Hinton var. *californica* Hinton

Parietaria hespera Hinton

Smith (1976) RO, CR, AN.

Pelargonium sp.

Pelargonium peltatum (L.) L'Her. ex Ait.

Foreman (1967) based on Foreman 106 UC! NI.

Pellaea mucronata (D.C. Eat.) D.C. Eat.

omitted as column transposition for CA.

Dunkle (1950) BA.

omitted as unsubstantiated on CL; also omitted by Raven (1963).

Dunkle (1950) CL.

Penstemon cordifolius Benth.

Keckiella cordifolia (Benth.) Straw

Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Ford (1890) CR; Brandegee (1890b) RO, CR, CA; Trask (1899) CA; Trask (1904) CL; Millspaugh and Nuttall (1923) CA; Munz (1935) RO, CR, CA, CL; Eastwood (1941) RO, CR, CA, CL; Dunkle (1942) AN; Raven (1963) CL; Thorne (1967) CA; Smith (1976) RO, CR, AN.

Perityle emoryi Torr. in Emory

omitted as unsubstantiated on MI.

Dunkle (1950) MI.

Perityle fitchii Torr.

Perityle emoryi Torr. in Emory

Lyon (1886) CL; Greene (1887a) CR; Yates (1889) CR.

Perityle grayi Rose

Perityle emoryi Torr. in Emory

Vasey and Rose (1890) GU; Eastwood (1929) GU; Howell (1942) GU.

Petromecon frutescens Greene

Eschscholzia frutescens (Greene) J.T. Howell

Eastwood (1929) GU.

Petromecon palmeri (Rose) Greene

Eschscholzia palmeri Rose

Eastwood (1929) GU.

Peucedanum sp.

incertae sedis

Greene (1887a) CR.

Peucedanum caruifolium (H. & A.) T. & G.
Lomatium caruifolium (H. & A.) Coult. & Rose
Brandegee (1888) RO, CR; Yates (1889) RO, CR; Brandegee (1890b) RO, CR.

Phaca fastidia Kell.
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne
Millspaugh and Nuttall (1923) CA.

Phaca leucopsis T. & G.
Astragalus trichopodus (Nutt.) Gray ssp. *leucopsis* (T. & G.) Thorne
Millspaugh & Nuttall (1923) CA.

Phacelia douglasii Torr.
Pholistoma racemosum (Nutt.) Const.
Yates (1889) CR; Jepson (1909–1943) CA.

Phacelia hispida Gray
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Eastwood (1941) BA.

Phacelia insularis Munz
omitted as unsubstantiated on CR.
Dunkle (1950) CR.

Phacelia parryi Torr.
Phacelia viscida (Benth.) Torr.
Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) CR.

Phacelia phyllomanica Gray
Phacelia floribunda Greene
Lyon (1886) CL; Eastwood (1941) CL; Dunkle (1950) CL.

Phacelia ramosissima Dougl. ex Lehm.
incertae sedis
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO, CR.

Phacelia ramosissima Dougl. ex Lehm. var. *cinerea* (Eastw. ex Macbr.) Jeps.
Phacelia cinerea Eastw. ex Macbr.
Jepson (1925) NI.

Phacelia suffrutescens Parry
Phacelia ramosissima Dougl. ex Lehm. var. *austrolittoralis* Munz
Greene (1887a) based on Greene s.n. in Jul.–Aug. 1886 ND-G#042054!, misidentified, CR; Yates (1889) CR; Eastwood (1941) CR.

Phacelia tanacetifolia Benth.
Phacelia cicutaria Greene ssp. *bispida* (Gray) J. Beauchamp ex Thorne
Munz (1974) probably based on Fosberg 7538 POM!, misidentified, CR; Smith (1976) CR.

Phalaris bulbosa L.
Phalaris minor Retz.
Hoffmann (1932a) based on Hoffmann s.n. Jun. 15, 1930 SBM#7556!, misidentified, CR; Eastwood (1941) CR.

Phalaris canariensis L.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Lyon (1886) CL.
Phalaris caroliniana Walt.
Eastwood (1898) based on Trask 9 MO! (annotated by Anderson, 1959), misidentified, NI.

Phalaris intermedia Bosc. ex Poir. in Lam.
possibly *Phalaris caroliniana* Walt.
Brandegee (1900) GU.
Phalaris caroliniana Walt.
Brandegee (1888) based on Brandegee s.n. in Jun., 1888 UC!, misidentified, CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.

Phalaris minor Retz.
Phalaris caroliniana Walt.
Foreman (1967) based in part on Trask 9 MO! annotated by Anderson (1959), misidentified, NI.

Philibertia hirtella (Gray) Parish
Sarcostemma cynanchoides Dcne. ssp. *hartwegii* (Vail) R. Holm.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Phoradendron bolleanum (Seem.) Eichler
Phoradendron bolleanum (Seem.) Eichler ssp. *densum* (Torr.) Wiens
Watson (1876) based on Palmer 85 CM! GU.

Phoradendron guadalupensis Trelease
Phoradendron bolleanum (Seem.) Eichler ssp. *densum* (Torr.) Wiens
Eastwood (1929) GU.

Photinia arbutifolia (Ait.) Lindl. var. *macrocarpa* Munz
Heteromeles arbutifolia (Ait.) R. Roem.
Eastwood (1941) CA; Gentry (1949) CA, CL; Dunkle (1950) CR, CA, CL; Munz and Keck (1959) CA, CL.

Pinus insignis Dougl. ex Loud.
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Watson (1876) based on Palmer 90 NY! GU.

Pinus insignis Dougl. ex Loud. var. *binata* Engelm. in Wats.
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Greene (1885) GU; Brandegee (1890b) GU; Franceschi (1893) GU.
Pinus remorata Mason
Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR; Abrams and Ferris (1923–1960) RO, CR.

Pinus radiata D. Don
incertae sedis
Jepson (1925) RO, CR; Gentry (1949) CR.
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Jepson (1925) GU; Howell (1942) GU.

Pinus radiata D. Don f. *binata* (Engelm. in Wats.) J.T. Howell
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Howell (1942) based in part on Howell 8183 NY! GU.
Pinus radiata D. Don f. *guadalupensis* J.T. Howell
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Howell (1942) based in part on Howell 8267 CAS! GU.
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Pinus remorata Mason
Abrams and Ferris (1923–1960) RO; Wiggins (1980) RO.
Pinus remorata Mason
Pinus radiata D. Don var. *binata* (Engelm. in Wats.) Lemmon
Wiggins (1980) GU.
Pityrogramma triangularis (Kaulf.) Maxon
omitted as column transposition for CA; also omitted by Philbrick (1972).
Dunkle (1950, p. 293) BA.
Pityrogramma triangularis (Kaulf.) Maxon var. *semipallida* J.T. Howell
incertae sedis
Smith (1976) RO, CR.
Pityrogramma triangularis (Kaulf.) Maxon var. *viscosa* (D.C. Eat.) Weath.
probably *Pityrogramma triangularis* (Kaulf.) Maxon.
Dunkle (1950) GU; Wiggins (1980) GU.
Pityrogramma viscosa (D.C. Eat.) Maxon
omitted as column transposition for CA; also omitted by Philbrick (1972).
Dunkle (1950, p. 293) BA.
Pityrogramma triangularis (Kaulf.) Maxon var. *viscosa* (D.C. Eat.) Weath.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CR, CA, CL; Dunkle (1950) RO, CR, CL.
Plagiobothrys arizonicus (Gray) Greene ex Gray
Plagiobothrys canescens Benth.
Brandegee (1890b) CA; Davidson (1896) CA; Millspaugh and Nuttall (1923) CA.
Plagiobothrys arizonicus (Gray) Greene ex Gray var. *catalinensis* Gray
Plagiobothrys canescens Benth.
Lyon (1886) CA; Davidson (1896) CA; Jepson (1909–1943) CA, CL; Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA; Munz and Keck (1959) CA, CL.
Plagiobothrys californicus (Gray) Greene
incertae sedis
Greene (1887a) CR; Yates (1889) CR.
Plagiobothrys californicus (Gray) Greene var. *californicus*
Plagiobothrys californicus (Gray) Greene var. *fulvescens* Jtn.
Munz and Keck (1959) probably based on Munz & Crow 11705 POM!, misidentified, RO; Smith (1976) RO.
Plagiobothrys californicus (Gray) Greene var. *gracilis* Jtn.
Plagiobothrys californicus (Gray) Greene var. *californicus*
Raven (1963) GU.
Plagiobothrys canescens Benth. var. *catalinensis* (Gray) Jeps.
Plagiobothrys canescens Benth.
Jepson (1925) CA.
Plagiobothrys cooperi Gray
Plagiobothrys californicus (Gray) Greene var. *gracilis* Jtn.
Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA.
Plagiobothrys tenellus (Nutt.) Gray
omitted as unsubstantiated on RO and erroneously attributed to Munz and Keck (1959).
Smith (1976) RO.
Plantago bigelovii Gray
Plantago erecta Morris ssp. *erecta*
Millspaugh and Nuttall (1923) based in part on Millspaugh 4910 F!, and Nuttall 1215 F!, misidentified, CA; Eastwood (1941) CA.
Plantago coronopus L. ssp. *commutata* (Guss.) Pilg.
Plantago coronopus L.
Abrams and Ferris (1923–1960) CA.
Plantago dura Morris
Plantago erecta Morris ssp. *erecta*
Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Plantago fastigiata Morris
Plantago ovata Forsk.
Thorne (1969) CL.
Plantago heterophylla Nutt.
Plantago bigelovii Gray ssp. *californica* (Greene) Bassett
Munz (1935) MI, RO; Eastwood (1941) MI, RO.
Plantago hookeriana F. & M. var. *californica* (Greene) Poe.
Plantago erecta Morris ssp. *erecta*
Munz (1935) RO, CA, CL; Dunkle (1942) AN; Munz and Keck (1959) Santa Barbara Islands.
Plantago insularis Eastw.
Plantago ovata Forsk.
Eastwood (1898) NI; Trask (1904) CL; Millspaugh and Nuttall (1923) CA; Abrams and Ferris (1923–1960) Islands; Eastwood (1941) NI, CA, CL; Dunkle (1942) AN, BA; Howell (1942) GU; Dunkle (1950) NI, BA, CA, CL; Munz and Keck (1959) Santa Barbara Islands; Raven (1963) CL; Foreman (1967) NI; Thorne (1967) CA; Munz (1974) Channel Islands; Smith (1976) RO, CR "?," AN.
Plantago insularis Eastw. var. *insularis*
Plantago ovata Forsk.
Wiggins (1980) GU.
Plantago maritima L.
omitted as unsubstantiated on BA; also omitted by Philbrick (1972).
Dunkle (1942) BA.
Plantago coronopus L.
Brandegee (1890a) CA.

Plantago maritima L. var. *californica* (Fern.) Pilg.

Hoffmann (1932b) RO; Munz (1935) RO; Eastwood (1941) RO.

Plantago obversa Morris

Plantago erecta Morris ssp. *erecta*

Davidson and Moxley (1923) CA.

Plantago patagonica Jacq.

Plantago erecta Morris ssp. *erecta*

Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR, CA.

Plantago ovata Forsk.

Watson (1876) based on Palmer 54 MO!, misidentified, GU; Greene (1885) GU; Lyon (1886) CL; Vasey and Rose (1890) based on Palmer 878 ND-G!, misidentified, GU; Brandegee (1890b) CL; Eastwood (1929) GU.

Plantago speciosa Morris

Plantago erecta Morris ssp. *erecta*

Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) AN, CA.

Platystemon aculeolatus Greene

Platystemon californicus Benth.

Jepson (1909–1943) based on type of Trask s.n. in May 1901 CAS#969! BA.

Platystemon californicus Benth.

omitted as unsubstantiated on CL; also omitted by Raven (1963).

Brandegee (1890b) CL.

Platystemon californicus Benth. var. *ciliatus* Dunkle

Platystemon californicus Benth.

Dunkle (1940b) based on Dunkle 7400 LAM! BA; Dunkle (1942) BA; Dunkle (1950) BA; Munz (1974) BA.

Platystemon californicus Benth. var. *nutans* Bdg.

Platystemon californicus Benth.

Jepson (1909–1943) CR; Jepson (1925) CR; Dunkle (1950) RO, CR; Munz (1974) RO, CR.

Platystemon californicus Benth. var. *ornithopus* (Greene) Munz

Platystemon californicus Benth.

Dunkle (1950) MI, RO, CR, NI; Munz (1974) MI, RO, NI.

Platystemon cernuus Greene

Platystemon californicus Benth.

Jepson (1909–1943) based on type of Trask s.n. on Mar. 1897 CAS#966!, CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Platystemon hispidulus Greene

Platystemon californicus Benth.

Jepson (1909–1943) based on type of Trask s.n. in Apr. 1897 CAS#958!, NI; Davidson and Moxley (1923) NI, CA; Eastwood (1941) NI, CA.

Platystemon setosus Greene

Platystemon californicus Benth.

Jepson (1909–1943) based on type of Trask 11 in May 1902 CAS#971!, BA; Eastwood (1941) BA.

Platystigma californicum Benth. & Hook. in Brew. & Wats.

Meconella denticulata Greene

Brandegee (1890b) CR.

Platystigma denticulatum (Greene) Greene

Meconella denticulata Greene

Greene (1887a) CR; Yates (1889) CR.

Pluchea camphorata (L.) DC.

Pluchea odorata (L.) Cass.

Millspaugh and Nuttall (1923) CA; Abrams and Ferris (1923–1960) CA; Hoffmann (1932b) CR; Munz (1935) CR, CA; Eastwood (1941) CR, CA.

Pluchea purpurascens (Sw.) DC.

Pluchea odorata (L.) Cass. (Gillis, 1977).

Thorne (1967) CA; Smith (1976) CR.

Poa nevadensis Vasey ex Scribn.

incertae sedis

Eastwood (1941) CR.

Poa steriantha Trin. (perhaps erroneous combination)

possibly *Poa scabrella* (Thurb.) Benth. ex Vasey.

Yates (1889) CR.

Polygonum aviculare L. var. *littorale* (Link) Koch

Polygonum aviculare L.

Hoffmann (1932a) CR; Eastwood (1941) RO, CR, CA.

Polygonum coccineum Muhl.

omitted as unsubstantiated on CA.

Thorne (1967) CA.

Polygonum ramosissimum Michx.

incertae sedis

Hoffmann (1932a) CR; Eastwood (1941) CR.

Polypodium californicum Kaulf. var. *kaulfussii* D.C. Eat.

Polypodium californicum Kaulf.

Munz (1935) on islands; Dunkle (1940a) RO, CR, CA; Eastwood (1941) RO, CR, CA, CL; Dunkle (1942) AN, BA; Dunkle (1950) AN, BA, CA; Smith (1976) AN.

Polypodium scouleri Hook. & Grev.

omitted as column transposition for CA; also omitted by Philbrick (1972).

Dunkle (1950, p. 293) BA.

omitted as unsubstantiated on CA; also omitted by Millspaugh and Nuttall (1923).

Brandegee (1890a) CA; Brandegee (1890b) CA.

omitted as unsubstantiated on CL; also omitted by Raven (1963).

Dunkle (1950) CL.

Polypodium vulgare L. var. *hesperium* (Maxon) Nels. & Macbr.

probably *Polypodium californicum* Kaulf.

Dunkle (1942) AN; Dunkle (1950) AN.

Polypodium vulgare L. var. *kaulfussii* (D.C. Eat.) Fern.

Polypodium californicum Kaulf.

Hoffmann (1932a) RO, CR.

Polystichum munitum (Kaulf.) Presl

Polystichum munitum (Kaulf.) Presl ssp. *solitarium* Maxon (D.H. Wagner pers. comm.).

Watson (1876) based on Palmer 102 NY! GU; Eastwood

(1929) GU; Dunkle (1950) GU; Raven (1963) GU; Smith (1976) GU; Wagner (1979) GU.

Populus fremontii Wats.

Populus × *parryi* Sarg.

Foreman (1967) based on Raven & Thompson 20728 DS!, misidentified, NI.

Populus fremontii Wats. var. *wislizenii* Wats.

Populus fremontii Wats. ssp. *fremontii*

Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.

Potamogeton foliosus Raf.

omitted as unsubstantiated on CA.

Thorne (1967) CA.

Potentilla anserina L.

Potentilla egedii Wormsk. var. *grandis* (Rydb.) J.T. Howell

Greene (1887b) MI; Yates (1889) MI; Eastwood (1941) MI; Dunkle (1950) CR.

Prunus ilicifolia (Nutt. ex H. & A.) Walp.

Prunus lyonii (Eastw.) Sarg.

Lyon (1886) CA; Brandegee (1890b) RO, CR, CA; Jepson (1925) Santa Barbara Islands; Eastwood (1941) CA, CL; Dunkle (1950) RO, CR, CA, CL; Munz and Keck (1959) CA, CL; Munz (1974) CA, CL; Smith (1976) RO; Wiggins (1980) CA, CL.

Prunus ilicifolia (Nutt. ex H. & A.) Walp. ssp. *lyonii* (Eastw.) Raven

Prunus lyonii (Eastw.) Sarg.

Raven (1963) CL; Thorne (1967) CA; Smith (1976) RO, CR, AN.

Prunus ilicifolia (Nutt. ex H. & A.) var. *occidentalis* (Lyon) Bdg.

Prunus lyonii (Eastw.) Sarg.

Brandegee (1888) RO, CR.

Prunus occidentalis Lyon

Prunus lyonii (Eastw.) Sarg.

Lyon (1886) CA; Greene (1887a) CR; Yates (1889) RO, CR; Ford (1890) CR; Davidson (1896) CA.

Pteris aquilina L.

Pteridium aquilinum (L.) Kuhn var. *pubescens* Underw.

Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Yates (1890) RO, CR; Brandegee (1890b) RO, CR.

Quercus chrysolepis Liebm.

Quercus tomentella Engelm.

Watson (1876) GU.

Quercus dumosa Nutt. var. *macdonaldii* (Greene) Jeps.

Quercus × *macdonaldii* Greene

Jepson (1925) CR, CA.

Quercus dumosa Nutt. f. *myrtifolia* (Willd.) Trel.

Quercus dumosa Nutt.

Clokey (1931) CR.

Quercus lobata Nee

omitted as unsubstantiated on RO.

Brandegee (1888) RO.

Quercus × *morehus* Kell.

omitted as unsubstantiated on CA; also omitted by Millspaugh and Nuttall (1923).

Davidson (1896) CA.

Quercus oblongifolia Torr.

incertae sedis

Brandegee (1890b) RO, CR, CA; Eastwood (1941) RO, CR.

Ranunculus californicus Benth.

incertae sedis

Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) MI, RO, CR.

Ranunculus deppei Nutt. in T. & G.

Ranunculus californicus Benth. ssp. *californicus*

Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR.

Rhamnus catalinae A. Davids.

Rhamnus pirifolia Greene

Davidson and Moxley (1923) based on T. Payne 2344 LAM! CA; Eastwood (1941) CA.

Rhamnus crocea Nutt. in T. & G.

Rhamnus pirifolia Greene

Watson (1876) GU; Lyon (1886) CA; Brandegee (1890b) MI, CR, CA; Trask (1899) CA; Trask (1904) CL; Eastwood (1929) GU.

Rhamnus crocea Nutt. in T. & G. var. *insularis* (Greene) Sarg.

omitted as unsubstantiated on BA; also omitted by Philbrick (1972).

Munz (1935) ambiguous implication perhaps a collective term for the Santa Barbara Islands, BA.

Rhamnus pirifolia Greene

Jepson (1909–1943) CR, CA; Hoffmann (1932b) RO; Munz (1935) CA; Dunkle (1950) MI, RO, CR, CA, CL.

Rhamnus crocea Nutt. in T. & G. ssp. *pirifolia* (Greene) C.B. Wolf

Rhamnus pirifolia Greene

Abrams and Ferris (1923–1960) RO, CR, CA, CL, GU; Munz and Keck (1959) Channel Islands.

Rhamnus insularis Greene

Rhamnus pirifolia Greene

Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Ford (1890) CR; Eastwood (1941) CR.

Rhamnus insulus Kell.

Rhamnus pirifolia Greene

Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, RO, CR, CA, CL.

Rhus diversiloba T. & G.

Toxicodendron radicans (L.) Kuntze ssp. *diversilobum* (T. & G.) Thorne

Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, RO, CR; Brandegee (1890b) MI, RO, CR, CA; Trask (1899) CA; Eastwood (1941) MI, RO, CR, CA; Dunkle (1942) AN; Dunkle (1950) MI, RO, CR, AN, CA, CL.

Rhus integrifolia (Nutt.) Benth. & Hook.

omitted as column transposition for CA; also omitted by Philbrick (1972).

Dunkle (1950, p. 293) BA.

Rhus laurina Nutt. in T. & G.
omitted as unsubstantiated on RO and CR.
Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.
Malosma laurina (Nutt. in T. & G.) Nutt. ex Abrams
Watson (1876) GU; Greene (1885) GU; Lyon (1886) CA; Brandegee (1890b) CA; Franceschi (1893) GU; Davidson (1896) CA; Trask (1899) CA; Jepson (1909–1943) CA; Eastwood (1929) GU; Munz (1935) CA; Eastwood (1941) CA, CL; Dunkle (1950) CA, CL; Munz (1974) CA.

Rhus ovata Wats.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Lyon (1886) CL.

Ribes malvaceum Sm. in Rees
omitted as unsubstantiated on CA.
Eastwood (1941) CA.

Ribes malvaceum Sm. in Rees var. *clementinum* Dunkle
Ribes malvaceum Sm. in Rees var. *malvaceum*
Dunkle (1943) based on Dunkle 7338 LAM! CL; Dunkle (1950) CL.

Ribes menziesii Pursh
incertae sedis
Brandegee (1888) CR; Brandegee (1890b) CR; Munz (1974) CR.

Ribes sanguineum Pursh
probably *Ribes malvaceum* Sm. in Rees var. *malvaceum*
Brandegee (1890b) CR.

Ribes sanguineum Pursh var. *malvaceum* (Sm. in Rees) Loud.
Ribes malvaceum Sm. in Rees var. *malvaceum*
Brandegee (1888) CR; Yates (1889) CR; Ford (1890) CR.

Ribes subvestitum H. & A.
omitted as unsubstantiated on CA.
Eastwood (1941) CA.
Ribes menziesii Pursh var. *thacherianum* Jeps.
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Eastwood (1941) CR.

Ribes thacherianum (Jeps.) Munz
Ribes menziesii Pursh var. *thacherianum* Jeps.
Munz and Keck (1959) CR; Munz (1974) CR; Smith (1976) CR.

Ribes viburniflorum Gray
Ribes viburnifolium Gray
Trask (1899) typographical error CA.

Rosa gratissima Greene
Rosa californica Cham. & Schlecht.
Gentry (1949) CR.

Rubus vitifolius Cham. & Schlecht.
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Eastwood (1941) CL.
Rubus ursinus Cham. & Schlecht.
Millspaugh and Nuttall (1923) CA; Munz (1935) RO, CR, CA; Eastwood (1941) MI, RO, CR; Dunkle (1942) AN; Dunkle (1950) RO, CR, CA.

Rumex acetosella L.
Rumex angiocarpus Murbeck
Hoffmann (1932a) based on Hoffmann s.n. Mar. 20, 1932 SBM#11767!, misidentified, CR; Eastwood (1941) CR.

Ruta graveolens L.
Ruta chalepensis L.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.

Sagina apetala Ard.
Sagina decumbens (Ell.) T. & G. ssp. *occidentalis* (Wats.) Crow
Crow (1978) based on Abrams & Wiggins 81 DS#209805!, misidentified (petals present, capsules longer than sepals, leaf bases not ciliate), CR.

Sagina occidentalis Wats.
Sagina decumbens (Ell.) T. & G. ssp. *occidentalis* (Wats.) Crow
Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR, CA; Millspaugh and Nuttall (1923) CA; Hoffmann (1932a) MI; Eastwood (1941) MI, RO, CR, CA; Munz (1974) CR.

Salicornia sp.
incertae sedis
Greene (1887b) MI.

Salicornia bigelovii Torr.
probably *Salicornia virginica* L.
Eastwood (1941) MI.

Salicornia subterminalis Parish
Salicornia virginica L.
Dunkle (1942) based on Dunkle 7652 LAM!, misidentified, AN; Gentry (1949) based on Elmore 402 AHFH!, misidentified, CL.

Salix argophylla Nutt.
incertae sedis
Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CR, CA.

Salix goodingii Ball
incertae sedis
Eastwood (1941) CR.

Salix laevigata Bebb.
incertae sedis
Brandegee (1888) RO.

Salix lasiolepis Benth. var. *bigelovii* (Torr.) Bebb.
Salix lasiolepis Benth.
Smith (1976) RO.

Salix lasiolepis Benth. var. *bracelinae* Ball
Salix lasiolepis Benth.
Foreman (1967) based on Raven & Thompson 20733 DS!, misidentified, NI.

Salix longifolia Muhl.
incertae sedis
Greene (1887a) CR; Yates (1889) CR; Ford (1890) CR; Brandegee (1890b) CR.

Salsola kali L.
Salsola iberica Sennen & Pau
Foreman (1967) NI.

Salsola pestifera A. Nels.
Salsola iberica Sennen & Pau
Thorne (1967) CA.

Salvia apiana Jeps.
omitted as unsubstantiated on CR.
Eastwood (1941) CR.

Salvia brandegei Munz
omitted as unsubstantiated on AN.
Dunkle (1942) AN.

Salvia leucophylla Greene
incertae sedis
Eastwood (1941) CR.

Salvia mellifera Greene
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Munz (1935) CL; Dunkle (1950) CL.

Salvia mellifera Greene var. *jonesii* Munz
omitted as unsubstantiated on MI and AN.
Eastwood (1941) (perhaps a misinterpretation of San Miguel Mt. in San Diego Co. cited by Munz 1935) MI; Dunkle (1942) AN; Dunkle (1950) CR.

Salvia palmeri (Gray) Greene
probably *Salvia mellifera* Greene.
Eastwood (1941) CR.

Sambucus caerulea Raf.
Sambucus mexicana Presl ex DC.
Millspaugh and Nuttall (1923) CA.

Sambucus glauca Nutt. in T. & G.
Sambucus mexicana Presl ex DC.
Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR, CA; Trask (1899) CA; Trask (1904) CL.

Samolus floribundus HBK.
Samolus parviflorus Raf.
Jepson (1909–1943) CR; Abrams and Ferris (1923–1960) CR.

Samolus valerandi L.
Samolus parviflorus Raf.
Brandegee (1890b) CR.

Samolus valerandi L. var. *americanus* Gray
Samolus parviflorus Raf.
Greene (1887a) CR; Yates (1889) CR; Eastwood (1941) CR.

Sanicula bipinnatifida Dougl. ex Hook.
Sanicula arguta Greene ex Coult. & Rose
Lyon (1886) CL; Brandegee (1890b) CL; Davidson (1896) CL.

Sanicula laciniata H. & A.
Sanicula arguta Greene ex Coult. & Rose
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Millspaugh and Nuttall (1923) CA.

Sanicula menziesii H. & A.
Sanicula arguta Greene ex Coult. & Rose
Eastwood (1898) NI.

Saxifraga malvaefolia Greene
Jepsonia malvaefolia (Greene) Small
Greene (1887a) CR; Yates (1889) CR.

Saxifraga parryi Torr.
Jepsonia malvaefolia (Greene) Small
Brandegee (1890b) CR.

Saxifraga reflexa Hook.
incertae sedis
Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR.

Scandix pecten-veneris L.
Daucus pusillus Miehx.
Foreman (1967) based on Foreman 230 UC!, misidentified, NI.

Scirpus pungens Vahl.
Scirpus americanus Pers. var. *monophyllus* (Presl) Koyama
Brandegee (1888) RO; Yates (1889) RO; Brandegee (1890b) RO; Eastwood (1941) RO.

Scirpus riparius Spreng.
omitted as unsubstantiated on CR.
Yates (1889) CR; Eastwood (1941) CR.
Scirpus cernuus Vahl. ssp. *californicus* (Torr.) Thorne
Greene (1887b) MI; Yates (1889) CR; Brandegee (1890b) MI; Eastwood (1941) MI, RO, CR.

Scrophularia californica Cham. & Schlecht.
Scrophularia villosa Penn. in Millsp. & Nutt.
Lyon (1886) CA; Brandegee (1890b) CA; Trask (1899) CA.

Scrophularia californica Cham. & Schlecht. var. *catalinae* Jeps.
omitted as unsubstantiated on MI and AN.
Dunkle (1942) AN; Dunkle (1950) MI, AN.
Scrophularia villosa Penn. in Millsp. & Nutt.
Munz (1935) CA, CL; Dunkle (1950) CA, CL.

Scutellaria tuberosa Benth. var. *similis* Jeps.
Scutellaria tuberosa Benth. ssp. *australis* Epl.
Smith (1976) CR.

Secale cereale L.
Elymus glaucus Buckl. ssp. *glaucus*
Thorne (1967) based on Fosberg S4555 LAM!, misidentified, CA.

Selaginella rupestris (L.) Spring.
Selaginella bigelovii Underw.
Lyon (1886) CA; Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890b) CR, CA.

Senecio lyonii Gray
omitted as unsubstantiated on CR, BA, and GU.
Eastwood (1941) CR; Gentry (1949) CR, BA; also omitted by Philbrick (1972); Dunkle (1950) GU.

Sida hederacea (Dougl.) Torr.
Malvella leprosa (Ortega) Krapovickas
Munz (1935) CL; Raven (1963) CL; Thorne (1967) CA.

Sida leprosa (Ortega) K. Schum. var. *hederacea* (Dougl.) K. Schum.
Malvella leprosa (Ortega) Krapovickas
Clement (1957) GU; Smith (1976) RO.

Sidalcea malvaeflora (DC.) Gray ex Benth.
omitted as unsubstantiated on CA.
Eastwood (1941) CA; Gentry (1949) CA.

- *Silene conoidea* L.
  - *Silene multinervia* Wats.
    - Brandegee (1888) CR; Yates (1889) CR; Brandegee (1890a) CA.
- *Silene quinquevulnera* L.
  - *Silene multinervia* Wats.
    - Greene (1887a) CR; Yates (1889) CR.
- *Sisymbrium canescens* Nutt.
  - *Descurainia pinnata* (Walt.) Britt. ssp. *menziesii* (DC.) Detl.
    - Watson (1876) GU; Greene (1885) GU; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Eastwood (1929) GU.
- *Sisymbrium pinnatum* (Walt.) Greene
  - *Descurainea pinnata* (Walt.) Britt. ssp. *menziesii* (DC.) Detl.
    - Greene (1887a) CR; Yates (1889) CR; Jepson (1909–1943) CR; Hoffmann (1932b) RO.
- *Sisymbrium reflexum* Nutt.
  - *Caulanthus lasiophyllus* (H. & A.) Pays.
    - Watson (1876) GU; Greene (1885) GU; Lyon (1886) CL; Brandegee (1888) RO; Yates (1889) RO; Vasey and Rose (1890) GU; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA, CL.
- *Solanum calvum* Bitter
  - *Solanum nodiflorum* Jacq.
    - Eastwood (1929) based in part on Palmer 60 in part NY! GU.
- *Solanum nigrum* L.
  - probably *Solanum douglasii* Dunal in DC.
    - Lyon (1886) CA; Brandegee (1890b) MI, RO, CR, CA.
  - possibly *Solanum nodiflorum* Jacq.
    - Franceschi (1893) GU.
  - *Solanum nodiflorum* Jacq.
    - Watson (1876) based on Palmer 60 in part NY! GU; Vasey and Rose (1890) based on Palmer 860 NY! GU.
- *Solanum nigrum* L. var. *douglasii* (Dunal in DC.) Gray
  - *Solanum douglasii* Dunal in DC.
    - Watson (1876) based on Palmer 61 NY! GU; Brandegee (1888) RO.
- *Solanum profundeincisum* Bitter
  - *Solanum douglasii* Dunal in DC.
    - Eastwood (1929) based in part on Palmer 61 NY! GU.
- *Solanum villosum* (L.) Mill.
  - *Solanum douglasii* Dunal in DC.
    - Gentry (1949) based on Elmore 200 AHFH! RO, based on Elmore 420 AHFH! CL.
- *Solanum wallacei* (Gray) Parish
  - *Solanum wallacei* (Gray) Parish ssp. *clokeyi* (Munz) Thorne
    - Eastwood (1941) RO, CR.
  - *Solanum wallacei* (Gray) Parish ssp. *wallacei*
    - Wiggins (1980) CA, GU.
- *Solanum xantii* Gray
  - *Solanum wallacei* (Gray) Parish ssp. *clokeyi* (Munz) Thorne
    - Munz (1935) RO; Munz and Keck (1959) RO, CR; Smith (1976) RO, CR.
  - *Solanum wallacei* (Gray) Parish ssp. *wallacei*
    - Watson (1876) based on Palmer 62 NY!, misidentified, GU.
- *Solanum xantii* Gray var. *wallacei* Gray
  - *Solanum wallacei* (Gray) Parish ssp. *clokeyi* (Munz) Thorne
    - Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR.
  - *Solanum wallacei* (Gray) Parish ssp. *wallacei*
    - Greene (1885) GU; Franceschi (1893) based on Franceschi 15 SBM! GU.
- *Sollya fusiformis* Briq.
  - *Sollya heterophylla* Lindl.
    - Thorne (1967) CA.
- *Sonchus tenerrimus* L.
  - *Sonchus asper* (L.) Hill
    - Hoffmann (1932b) based on Hoffmann s.n. Mar. 25, 1932 SBM#1069!, misidentified, MI.
- *Sophia pinnata* (Walt.) Howell
  - *Descurainia pinnata* (Walt.) Britt. ssp. *menziesii* (DC.) Detl.
    - Millspaugh and Nuttall (1923) CA.
- *Spergularia biflora* (R. & P.) F. & M.
  - omitted as unsubstantiated on MI.
    - Dunkle (1950) MI.
- *Spergularia perfoliata* (L.) DC.
  - *incertae sedis*
    - Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR; Eastwood (1941) CR.
- *Spergularia marina* (L.) Griseb.
  - omitted as column transposition for CA.
    - Dunkle (1950, p. 293) BA.
- *Spergularia rubra* (L.) J. & C. Presl
  - *Spergularia bocconei* (Scheele) Foucaud
    - Eastwood (1941) CL.
- *Sphaeralcea fasciculata* (Nutt.) Arthur var. *laxiflora* (Gray) Jeps.
  - *Malacothamnus fasciculatus* (Nutt.) Greene ssp. *catalinensis* (Eastw.) Thorne
    - Jepson (1909–1943) CA.
- *Sphaerostigma bistortum* (Nutt. ex T. & G.) Walp.
  - *Camissonia robusta* Raven
    - Millspaugh and Nuttall (1923) CA.
- *Sphaerostigma micranthum* (Hornem. ex Spreng.) Walp.
  - *Camissonia micrantha* (Hornem. ex Spreng.) Raven
    - Millspaugh and Nuttall (1923) CA.
- *Statice arctica* Blake var. *vulgaris* Blake
  - *Armeria maritima* (Mill.) Willd. ssp. *californica* (Boiss.) G.H.M. Lawr.
    - Munz (1935) RO; Dunkle (1950) RO.
- *Stellaria nitens* Nutt.
  - omitted as unsubstantiated on CL; also omitted by Raven (1963).
    - Dunkle (1950) CL.
- *Stephanomeria elata* Nutt.
  - *Stephanomeria virgata* Benth. ssp. *virgata*
    - Greene (1887a) CR; Yates (1889) CR.
- *Stephanomeria paniculata* Nutt.
  - *Stephanomeria virgata* Benth. ssp. *virgata*
    - Lyon (1886) CA; Brandegee (1890b) CA; Eastwood (1941) CA.

Stephanomeria tomentosa Greene
Stephanomeria virgata Benth. ssp. *virgata* (Gottlieb, 1972).
Greene (1887a) CR; Yates (1889) CR; Jepson (1925) CR; Munz (1935) CR; Eastwood (1941) RO, CR; Dunkle (1950) RO, CR.

Stephanomeria virgata Benth. var. *tomentosa* (Greene) Munz
Stephanomeria virgata Benth. ssp. *virgata*
Munz and Keck (1959) CR; Smith (1976) RO "?," CR.

Stipa sp.
incertae sedis
Greene (1887a) CR.

Stipa andersonii (Vasey) Bdg.
Stipa lepida Hitchc.
Brandegee (1890b) RO, CR.

Stipa lepida Hitchc. var. *andersonii* (Vasey) Hitchc.
Stipa lepida Hitchc.
Millspaugh and Nuttall (1923) CA; Munz (1935) RO; Eastwood (1941) RO, CA.

Stipa robusta (Vasey) Scribn.
incertae sedis
Eastwood (1898) NI.

Stipa vaseyi Scribn.
probably *Stipa columbiana* Macoun var. *nelsoni* (Scribn.) Hitchc.
Jepson (1909–1943) probably based on Trask 11 US!, misidentified, NI; Davidson and Moxley (1923) NI; Abrams and Ferris (1932–1960) NI.

Stipa viridula Trin.
incertae sedis
Brandegee (1888) CR; Yates (1889) CR.

Stylophyllum hassei Rose
Dudleya hassei (Rose) Moran
Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Abrams (1917) CA; Abrams and Ferris (1923–1960) CA; Eastwood (1941) CA.

Suaeda sp.
probably *Suaeda californica* Wats.
Eastwood (1898) NI.

Suaeda californica Wats. var. *pubescens* Jeps.
Suaeda californica Wats.
Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL; Smith (1976) RO, CR.

Suaeda californica Wats. var. *taxifolia* (Standl.) Munz
Suaeda californica Wats.
Smith (1976) RO, CR.

Suaeda fruticosa (L.) Forsk.
Suaeda californica Wats.
Howell (1942) based on Howell 8189 CAS!, misidentified, GU.

Suaeda taxifolia Standl.
Suaeda californica Wats.
Gentry (1949) based on Elmore 302 AHFH! BA.

Suaeda torreyana Wats.
probably *Suaeda californica* Wats.
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) MI, CR; Brandegee (1890a) CA; Brandegee (1890b) MI, RO, CR, CA; Eastwood (1941) MI, RO, CR, CA; Dunkle (1950) MI, RO, CR, BA, CA.

Symphoricarpos albus (L.) Blake var. *mollis* (Nutt. in T. & G.) Keck
Symphoricarpos mollis Nutt. in T. & G.
Munz (1935) CR, CA.

Syrmatium ornithopum (Greene) Greene
omitted as unsubstantiated on CR.
Eastwood (1941) CR.
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven
Abrams (1917) NI, BA, CA, CL, GU; Millspaugh and Nuttall (1923) CA; Eastwood (1941) NI, BA, CA, CL.

Syrmatium patens Greene
Lotus scoparius (Nutt. in T. & G.) Ottley var. *veatchii* (Greene) Ottley
Greene (1887a) CR; Greene (1887b) MI; Eastwood (1941) MI.

Syrmatium traskiae Eastw. ex Noddin in Abrams
probably *Lotus scoparius* (Nutt. ex T. & G.) Ottley var. *dendroideus* (Greene) Ottley
Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CA.
Lotus scoparium (Nutt. ex T. & G.) Ottley ssp. *traskiae* (Eastw. ex Noddin in Abrams) Raven
Abrams (1917) CL; Davidson and Moxley (1923) CL; Eastwood (1941) CL.

Syrmatium venustum (Eastw.) Davids. & Mox.
Lotus argophyllus (Gray) Greene ssp. *ornithopus* (Greene) Raven
Davidson and Moxley (1923) NI.

Taraxacum officinale Wiggers
omitted as unsubstantiated on CL; also omitted by Raven (1963).
Eastwood (1941) CL.

Taraxacum taraxacum (L.) Karst.
Taraxacum officinale Wiggers
Millspaugh and Nuttall (1923) CA.

Tellima affinis (Gray) Gray
Lithophragma affine Gray ssp. *mixtum* R.L. Taylor
Brandegee (1890a) CA; Brandegee (1890b) CA.

Tetragonia expansa Murr.
Tetragonia tetragonioides (Pall.) Kuntze
Hoffmann (1932a) MI, RO; Munz (1935) MI; Eastwood (1941) MI, RO.

Thalesia fasciculata (Nutt.) Britt.
Orobanche fasciculata Nutt.
Millspaugh and Nuttall (1923) CA.

Thelesperma gracile (Torr.) Gray
Thelesperma megapotamicum (Spreng.) Kuntze
Millspaugh and Nuttall (1923) based in part on Nuttall 602 F! CA; Eastwood (1941) CA.

Thelypodium laciniatum (Hook.) Endl.
probably *Caulanthus lasiophyllus* (H. & A.) Pays.
Brandegee (1890a) CA; Brandegee (1890b) CA; Yates (1889) CR.

Thelypodium lasiophyllum (H. & A.) Greene
Caulanthus lasiophyllus (H. & A.) Pays.
Greene (1887a) CR; Greene (1887b) MI; Yates (1889) MI, CR; Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Hoffmann (1932b) MI, RO; Eastwood (1941) MI, RO, CR, AN, CA, CL; Thorne (1967) CA; Philbrick (1972) BA; Smith (1976) MI, RO, CR, AN.
Thelypodium lasiophyllum (H. & A.) Greene var. *inalienum* Rob.
Caulanthus lasiophyllus (H. & A.) Pays.
Smith (1976) AN.
Thysanocarpus conchuliferus Greene
omitted as unsubstantiated on CA.
Eastwood (1941) CA.
Thysanocarpus laciniatus Nutt. ex T. & G. var. *ramosus* (Greene) Munz
omitted as unsubstantiated on CA.
Dunkle (1950) CA.
Tillaea angustifolia Nutt. in T. & G.
Crassula erecta (H. & A.) Berger
Brandegee (1890a) CA; Brandegee (1890b) CA; Davidson (1896) CA; Millspaugh and Nuttall (1923) CA.
Tillaea erecta H. & A.
Crassula erecta (H. & A.) Berger
Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU; Hoffmann (1932b) MI; Howell (1935) NI; Eastwood (1941) MI, RO, CR, NI, CA; Dunkle (1942) BA; Howell (1942) GU; Dunkle (1950) MI, RO, CR, AN, NI, BA, CA, CL, GU.
Tillaea leptopetala Benth.
Crassula erecta (H. & A.) Berger
Vasey and Rose (1890) GU.
Tillaea minima Miers ex H. & A. in Hook.
Crassula erecta (H. & A.) Berger
Watson (1876) GU; Greene (1885) GU; Lyon (1886) CA; Greene (1887a) CR; Brandegee (1888) RO; Yates (1889) RO, CR; Brandegee (1890b) RO, CR, CA.
Tissa macrotheca (Hornem.) Britt.
Spergularia macrotheca (Hornem.) Heynh. ssp. *macrotheca*
Vasey and Rose (1890) GU; Brandegee (1890b) MI, RO, CR, CA, CL; Millspaugh and Nuttall (1923) CA; Eastwood (1929) GU.
Tissa pallida Greene ex Britt.
Spergularia macrotheca (Hornem.) Heynh. ssp. *macrotheca*
Vasey and Rose (1890) GU; Eastwood (1929) GU.
Tissa salina (J. & C. Presl) Britt.
Spergularia marina (L.) Griseb.
Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA; Davidson and Moxley (1923) CA.
Tithymalus leptocerus (Engelm.) Millsp. in Millsp. & Nutt.
Euphorbia crenulata Engelm.
Millspaugh and Nuttall (1923) based on Millspaugh 4867 F!, Nuttall 170 F!, Nuttall 236 F! CA.
Toxicodendron diversilobum (T. & G.) Greene
Toxicondendron radicans (L.) Kuntze ssp. *diversilobum* (T. & G.) Thorne
Millspaugh and Nuttall (1923) CA; Gentry (1949) MI, RO, CR, CA; Raven (1963) CL; Smith (1976) apparently all four Channel Islands.
Trichosterigma miserum (Benth.) Kl. & Gke.
Euphorbia misera Benth.
Davidson and Moxley (1923) CA; Millspaugh and Nuttall (1923) CA.
Trifolium amplectens T. & G.
incertae sedis
Greene (1887a) CR; Brandegee (1890a) CA; Brandegee (1890b) CR, CA; Davidson (1896) CA; Trask (1899) CA; Jepson (1909–1943) CR, CA; Dunkle (1950) MI, RO, CR, NI, CA, CL, GU.
Trifolium dichotomum H. & A.
Trifolium albopurpureum T. & G.
Eastwood (1898) based on Trask 37 LAM!, NY! NI; Foreman (1967) based in part on Trask 37 LAM!, NY! NI.
Trifolium fucatum Lindl. var. *flavulum* Jeps.
Trifolium fucatum Lindl. var. *gambelii* (Nutt.) Jeps.
Hoffmann (1932b) MI; Munz (1935) MI; Eastwood (1941) MI, RO, CR.
Trifolium gracilentum T. & G.
Trifolium palmeri Wats.
Dunkle (1950) probably based on Dunkle 7415 LAM! and Dunkle 7449 AHFH!, misidentified, BA.
Trifolium gracilentum T. & G. var. *inconspicuum* Fern.
Trifolium gracilentum T. & G.
Hoffmann (1932b) MI, RO; Eastwood (1941) MI, RO; Dunkle (1950) RO, CR.
Trifolium gracilentum T. & G. var. *palmeri* McDer.
omitted as unsubstantiated on CR.
Dunkle (1950) CR.
Trifolium microdon H. & A.
Trifolium tridentatum Lindl. var. *aciculare* (Nutt.) McDer.
Dunkle (1942) probably based on Dunkle 7425 LAM!, misidentified, BA; Dunkle (1950) BA.
Trifolium stenophyllum Nutt.
incertae sedis
Eastwood (1898) NI; Eastwood (1941) NI; Dunkle (1950) NI.
Trifolium stenophyllum Nutt.
Trifolium amplectens T. & G. var. *truncatum* (Greene) Jeps.
Nuttall (1848) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, RO, CR, CA, CL; Dunkle (1950) MI, RO, CR, CA, CL.
Trifolium depauperatum Desv.
Howell (1935) based on Howell 8212 CAS!, misidentified, NI.
Trifolium tridentatum Lindl.
incertae sedis
Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Yates (1889) CR; Brandegee (1890a)

CA; Brandegee (1890b) MI, RO; Trask (1899) CA; Trask (1904) CL; Jepson (1909–1943) CR, CA.

Trisetum barbatum Steud.
Bromus trinii Desv.
Brandegee (1888) based on Brandegee s.n. in 1888 UC! CR; Yates (1889) CR; Brandegee (1890b) CR; Vasey and Rose (1890) based in part on Palmer 658 US!, and Palmer 667 US!, UC! GU; Eastwood (1941) CR.

Triteleia lugens Greene
Triteleia guadalupensis Lenz
Moran (1951) GU.

Tropidocarpum dubium A. Davids.
Tropidocarpum gracile Hook.
Eastwood (1941) CL.

Typha sp.
incertae sedis
Hoffmann (1932a) RO.

Typha angustifolia L.
Typha domingensis Pers.
Jepson (1909–1943) CR; Millspaugh and Nuttall (1923) CA; Eastwood (1941) RO, CR, CA; Foreman (1967) based on Blakley 4158 SBBG!, misidentified, NI.

Typha domingensis Pers.
Typha latifolia L.
Raven (1963) based on Raven 18018 RSA!, misidentified, CL.

Urtica gracilis Ait. var. *holoserica* (Nutt.) Jeps.
Urtica dioica L. ssp. *holoserica* (Nutt.) Thorne
Munz (1935) CR, CA; Dunkle (1942) AN.

Urtica holoserica Nutt.
Urtica dioica L. ssp. *holoserica* (Nutt.) Thorne
Lyon (1886) CA; Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR, CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR, CA; Gentry (1949) CR, CA; Munz and Keck (1959) CR, CA; Munz (1974) CR, CA; Smith (1976) CR.

Uva-ursi pungens (HBK.) Abrams
Arctostaphylos catalinae P.V. Wells
Millspaugh and Nuttall (1923) CA.

Uva-ursi tomentosa (Pursh) Abrams
Arctostaphylos catalinae P.V. Wells
Millspaugh and Nuttall (1923) CA.

Verbena prostrata R. Br. in Ait.
incertae sedis
Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1890b) CA; Millspaugh and Nuttall (1923) CA.

Verbena robusta Greene
Verbena lasiostachys Link
Jepson (1909–1943) CL; Eastwood (1941) CL; Gentry (1949) CL.

Vicia americana Muhl. ex Willd. var. *linearis* Wats.
incertae sedis
Jepson (1909–1943) CA; Eastwood (1941) CA.
Vicia hassei Wats.
Jepson (1909–1943) based on Munz 6669 POM!, UC! CL.

Vicia californicus Greene
Vicia americana Muhl. ex Willd.
Hoffmann (1932b) based on Hoffmann s.n. Apr. 16, 1929 SBM#6195! RO.

Vicia exigua Nutt. in T. & G.
omitted as unsubstantiated on NI; also omitted by Foreman (1967).
Dunkle (1950) NI.

Vicia exigua Nutt. in T. & G. var. *hassei* (Wats.) Jeps.
Vicia hassei Wats.
Wiggins (1980) GU.

Vinca minor L.
Sollya heterophylla Lindl.
Millspaugh and Nuttall (1923) based on Nuttall 801 F!, misidentified, CA.

Vitis californica Benth.
Vitis girdiana Munson
Brandegee (1890a) CA; Brandegee (1890b) CA.

Vulpia megalura (Nutt.) Rydb.
Vulpia myuros (L.) K.C. Gmelin var. *hirsuta* Hack.
Philbrick (1972) BA.

Woodwardia radicans (L.) Sm.
Woodwardia fimbriata Sm. in Rees
Greene (1887a) CR; Yates (1889) CR; Yates (1890) CR; Brandegee (1890b) CR; Hoffmann (1932a) RO.

Xanthium canadense Mill.
Xanthium strumarium L. var. *canadense* (Mill.) T. & G.
Greene (1887a) CR; Yates (1889) CR; Brandegee (1890b) CR.

Xanthium pennsylvanicum Wallr.
omitted as unsubstantiated on MI and BA.
Eastwood (1941) MI, BA.
Xanthium strumarium L. var. *canadense* (Mill.) T. & G.
Millspaugh and Nuttall (1923) CA; Eastwood (1941) CR.

Xanthoxalis californica Abrams
Oxalis albicans HBK. ssp. *californica* (Abrams) Eiten
Millspaugh and Nuttall (1923) CA.

Zannichellia palustris L.
Ruppia maritima L.
Munz (1935) based on Wolf 3591 DS!, misidentified, CA; Eastwood (1941) CA.

Zauschneria californica Presl
Epilobium canum (Greene) Raven ssp. *canum*
Lyon (1886) CA; Greene (1887a) CR; Greene (1887b) MI; Brandegee (1888) RO; Brandegee (1890b) MI, RO, CR, CA; Trask (1899) CA; Millspaugh and Nuttall (1923) CA; Eastwood (1941) MI, CR, CA; Dunkle (1950) RO, CA, CL; Munz and Keck (1959) Santa Barbara Islands.

Zauschneria californica Presl ssp. *angustifolia* Keck
Epilobium canum (Greene) Raven ssp. *canum*
Abrams and Ferris (1923–1960) CA; Dunkle (1950) CA; Munz and Keck (1959) CA.

Zauschneria californica Presl ssp. *californica*
Epilobium canum (Greene) Raven ssp. *canum*
Thorne (1967) CA; Smith (1976) MI, RO, CR, AN.

Zauschneria californica Presl ssp. *mexicana* (Presl) Raven
  Epilobium canum (Greene) Raven ssp. *canum*
    Raven (1963) CL; Thorne (1967) CA; Smith (1976) CR.
Zauschneria californicum Presl var. *villosa* (Greene) Jeps.
  Epilobium canum (Greene) Raven ssp. *canum*
    Jepson (1909–1943) RO, CR, CA, CL; Abrams and Ferris (1923–1960) RO, CR, CL; Munz (1935) RO, CR, CL; Gentry (1949) RO, CR, CA, CL; Dunkle (1950) RO, CR, CA, CL.
Zauschneria cana Greene
  Epilobium canum (Greene) Raven ssp. *canum*
    Yates (1889) CR; Jepson (1909–1943) CR, AN; Abrams and Ferris (1923–1960) CR, CA; Davidson and Moxley (1923) CR, AN; Munz (1935) CR, CA; Eastwood (1941) CR, AN, CA; Dunkle (1942) AN; Dunkle (1950) RO, CR, CA; Munz and Keck (1959) CR, AN, CA; Thorne (1967) CA; Munz (1974) CR, AN, CA; Smith (1976) CR, AN.
Zauschneria villosa Greene
  Epilobium canum (Greene) Raven ssp. *canum*
    Greene (1887a) CR; Yates (1889) CR; Davidson and Moxley (1923) RO, CL; Eastwood (1941) RO, CR, CA, CL.
Zostera marina L. var. *latifolia* Morong
  Zostera marina L.
    Smith (1976) Channel Islands.

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RUGOSE CORALS (COELENTERATA, ANTHOZOA) FROM THE LOWER PERMIAN MCCLOUD LIMESTONE AT TOMBSTONE MOUNTAIN, NORTHERN CALIFORNIA

Edward C. Wilson

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RUGOSE CORALS (COELENTERATA, ANTHOZOA) FROM THE LOWER PERMIAN MCCLOUD LIMESTONE AT TOMBSTONE MOUNTAIN, NORTHERN CALIFORNIA

Edward C. Wilson[1]

ABSTRACT. A rugose coral faunule consisting of one solitary and three massive species occurs in an Upper Wolfcampian Series stratum of the McCloud Limestone at Tombstone Mountain, Shasta County, California. It is the youngest coral fauna in the formation and has species in common with older parts of the formation and with Lower Permian formations of Oregon and Spitsbergen. *Wexolina tombstonensis* n. gen., n. sp. is a very large solitary coral. *Kleopatrina* (*K.*) *svalbardense* Fedorowski was described from the Lower Permian (Sakmarian) Treskelodden Formation of Spitsbergen. *Langenheimia klamathensis* Wilson ranges lower in the formation elsewhere. *Petalaxis occidentalis* (Merriam) was described from the Lower Permian Coyote Butte Formation of Oregon. Coarsely clastic sediments, algae, and the corals indicate a high-energy, shallow-water, warm, marine paleoenvironment.

INTRODUCTION

Skinner and Wilde (1965) zoned the Lower Permian McCloud Limestone of northern California into informal fusulinid Zones A to H. Zones A to G are Wolfcampian and Zone H is Leonardian (Skinner and Wilde, 1965; Wilde, 1971). Wilson (1982) described the corals of the formation from Zones A to F. This paper reports the corals from Zone G.

STRATIGRAPHY

A section was measured and intensively collected in the McCloud Limestone at Tombstone Mountain, Shasta County, California (Fig. 1). It is 1765 ft. (538 m) thick and consists of a lower Zone A part overlain unconformably by Zone G and Zone H rocks (Fig. 2). The Zone A rocks have a small faunule of poorly preserved solitary and fasciculate rugose corals and tabulate corals (loc. 6178). The Zone G rocks contain the coral faunule reported in this paper (locs. 6181–6183). The Zone H rocks have only rare, poorly preserved, fasciculate (?) corals (*Heritschioides*?).

The corals occur in beds cropping out between 865 and 880 ft. (264 and 267 m) above the base of the section. The locality is within Zone G of Skinner and Wilde (1965) which they considered to be Late Wolfcampian and correlative with the Coyote Butte Formation of central Oregon on the basis of six shared fusulinid species.

The corals, except for *Wexolina tombstonensis* n. gen., n. sp., which presently is unknown outside the type locality, have noteworthy stratigraphic ranges and geographic distributions. *Kleopatrina* (*K.*) *svalbardense* Fedorowski, 1980, was described from the Lower Permian (Sakmarian) Treskelodden Formation of southern Spitsbergen. Its presence in northern California suggests a correlation between the two areas despite the intervening distance. The single specimen of *Langenheimia klamathensis* Wilson, 1982, was originally described from Zone F in the formation farther south. Its occurrence in Zone G at Tombstone Mountain establishes the first stratigraphic range for the species (Fig. 3). *Petalaxis occidentalis* (Merriam, 1942), erected for specimens from the Lower Permian Coyote Butte Formation of central Oregon, establishes a correlation of that formation with the McCloud Limestone using corals. This corroborates Skinner and Wilde's (1965) fusulinid correlation.

Figure 3 incorporates ranges of the Zone G coral genera into those from Zones A to F of the McCloud Limestone previously reported by Wilson (1982).

Assignment of the McCloud Limestone coral faunas to the Durhaminid Coral Province by Wilson (1982) is reinforced by the discovery of *Kleopatrina* (*K.*) *svalbardense,* a species previously known only from the Lower Permian of Spitsbergen, also part of the Durhaminid Coral Province. *Wexolina* and *Langenheimia,* although presently unknown outside the McCloud Limestone, must be considered members of the same province because of this association. *Petalaxis,* widespread in the Durhaminid Coral Province, also occurs in the westernmost Tethys Coral Province of Japan and possibly China (Sando, 1983).

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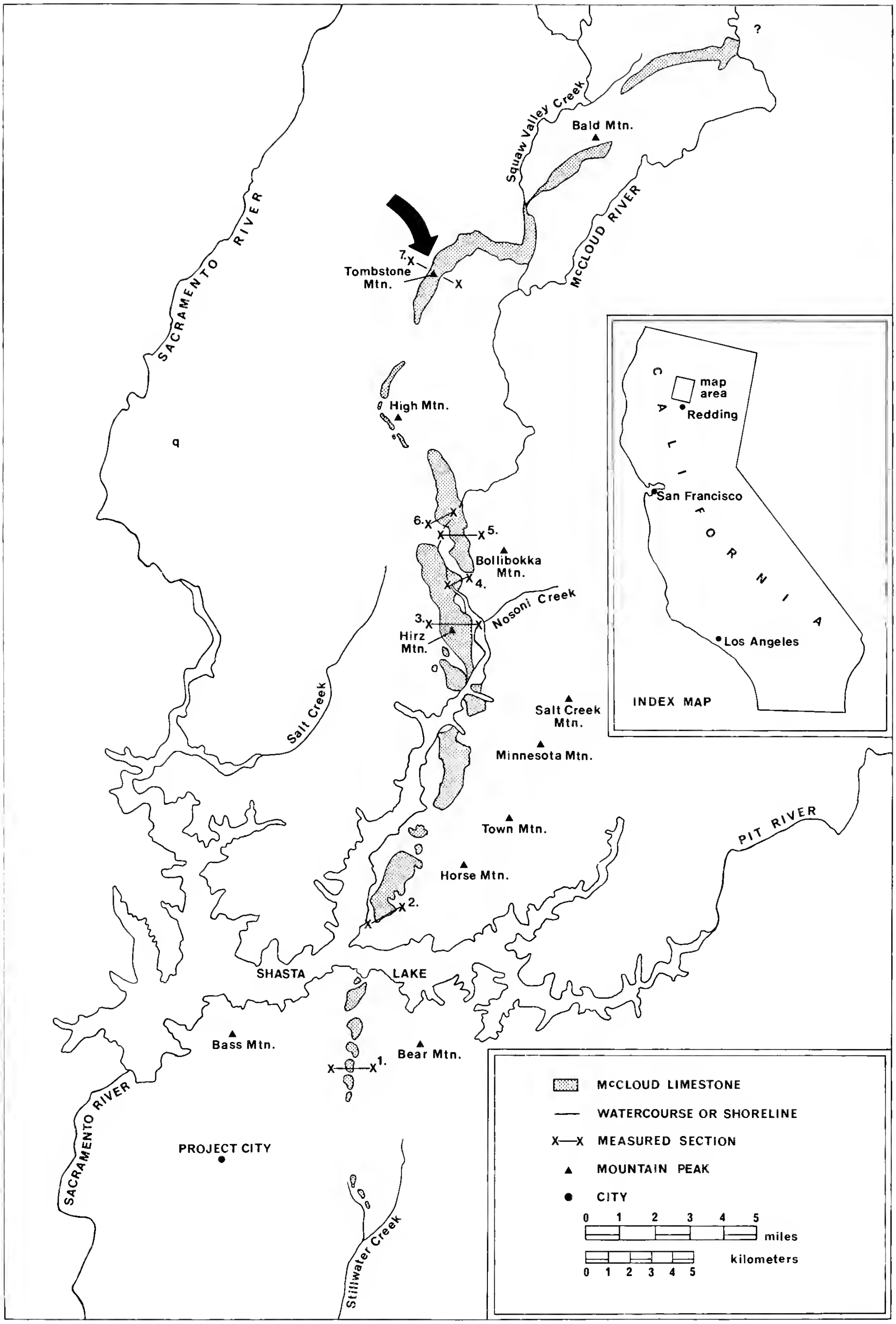


Figure 1. McCloud Limestone exposures in Shasta County, California, showing locations of new measured section (7) at Tombstone Mountain and other sections (1–6) from which corals previously were described by Wilson (1982).

PALEOECOLOGY

The beds containing the corals described here, as well as the whole of fusulinid Zone G at Tombstone Mountain, is a coarse conglomerate with limestone clasts derived from all the older McCloud Limestone fusulinid zones (Skinner and Wilde, 1965). The corals described here occur in the matrix, where the four species were found together. Reworked corals in some of the clasts may be distinguished from the corals in the matrix by careful examination although similar rock colors and styolitic resorption makes this difficult in places. The conglomerate indicates uplift of the older parts of the McCloud Limestone and redeposition in a shallow, wave- and current-affected, high-energy environment.

The presence of only cerioid colonial corals may represent a response to turbulent water, in which massive shape is more competent than a fasciculate shape. Similarly, the gigantic size of the single solitary coral species may represent adaptation to strong wave action. The cerioid corals did not grow to a very large size, perhaps because of rapid deposition. I saw none with a diameter greater than 0.5 m and most were a fraction of that. Coralla of the four species apparently lived as a community among the cobbles and in the intervening sandy stretches but generally not touching. Some were overturned prior to burial.

Random collecting of the cerioid coralla produced 40 specimens, 27 of which are *Petalaxis occidentalis,* seven *Kleopatrina* (*K.*) *svalbardense,* and six *Langenheimia klamathensis.* The first species clearly dominates numerically and its presence elsewhere may indicate a comparable shallow-water, high-energy environment. Intensive collecting yielded only seven coralla of *Wexolina tombstonensis,* although I saw a few others that could not be collected.

A few algal stromatolites indicate a paleoenvironment in the euphotic zone. Sando (1980) considered algal–coral associations in Mississippian rocks to indicate a depositional depth of less than 50 m. Wells (1957) considered colonial rugose corals indicative of well-oxygenated, gently circulating, marine water with annual temperature minima of 16° to 21°C. Most paleogeographic maps place the Permian equator on the west coast of North America somewhere in California or Baja California, suggesting a tropical environment for the present site of the McCloud Limestone.

An earlier statement that "the McCloud Limestone was deposited in clear, shallow, warm marine water with full access to the open seas" (Wilson, 1982) is supported by the paleoenvironmental evidence discussed above.

SYSTEMATIC PALEONTOLOGY

Morphological terminology is from Easton (1944) and Hill (1981). Because I consider present family-level systematics of most Permian rugose corals to be highly provisional, I have not used them. The genera are separated into solitary and cerioid groups, and the cerioid corals are arranged alphabetically.

Locality and type numbers refer to the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section (acronym LACMIP) locality register and type catalogues. All specimens are deposited in LACMIP.

SOLITARY CORALS

Genus *Wexolina* new genus

DIAGNOSIS. Corallum solitary, large; calyx deep, steep-walled, inverted cone-shaped; septa numerous, reaching from corallite wall far into tabularium, thin in dissepimentarium, dilate in tabularium in neanic stages, becoming thin in counter quadrants in ephebic stages; cardinal septum short; cardinal fossula closed, high on wall of calyx; dissepimentarium wide, normal; tabellae of two zones, axial and periaxial; axial tabellae concave *upwards* to cytose; periaxial tabellae generally horizontal.

TYPE SPECIES. *Wexolina tombstonensis* n. sp.

DISCUSSION. In transverse section, *Wexolina* somewhat resembles *Bothrophyllum* Trautschold, 1879, *Pseudotimania* Dobrolyubova and Kabakovich, 1948, and *Timania* Stuckenberg, 1895. It may be distinguished from *Bothrophyllum* by its closed cardinal fossula and counter septum of normal length. It may be distinguished from *Pseudotimania* by its counter septum of normal length. It may be distinguished from *Timania* by its counter septum of normal length and absence of alar fossulae. In addition, none of these genera has the deep, inverted cone-shaped calyx formed by two zones of tabellae that characterizes *Wexolina.*

Until neanic stages are known for *Wexolina,* familial relationships cannot be established.

ETYMOLOGY. The genus is named for Mr. John Bonnett Wexo.

Wexolina tombstonensis new species

Figures 4, 5a–f

DIAGNOSIS. Because *Wexolina* is monotypic, the diagnoses of the genus and of the type species are identical.

EXTERNAL DESCRIPTION. Corallites solitary, cylindrical in ephebic stages, with apical angles of 40° in late neanic stages (2.5 to 4 cm diameters), apparently slightly curved with no abrupt angles, very large diameters to 10.3 cm, lengths unknown but apparently large; epitheca with annual (?) constrictions 1.5 cm apart, a few minor constrictions between, and fine growth lines; calices very deep (6 cm), sides sloping very steeply (50° to 70°) downwards and inwards, lacking central flat floor, cardinal fossulae prominent, located more than half-way up calyx sides; axial boss absent.

TRANVERSE SECTION DESCRIPTION. Corallites circular, 10.3 cm maximum diameter; septa of 2 orders, 84 to 88 each at maturity, all extending to corallite wall; major septa thin in dissepimentarium, highly dilate in cardinal quadrants in tabularium, thin to dilate in counter quadrants in tabularium, adaxially attenuate, some sinuous, some lengthened far into tabularium (amplexoid?), 30 to 40 mm long in adult stages (corallite diameters 10 cm), with shortened cardinal septum (24 mm long in holotype); minor septa thin, very short, confined to outer 2 to 3 rows of dissepiments in adult stages, not seen in earlier stages (abraded corallites);

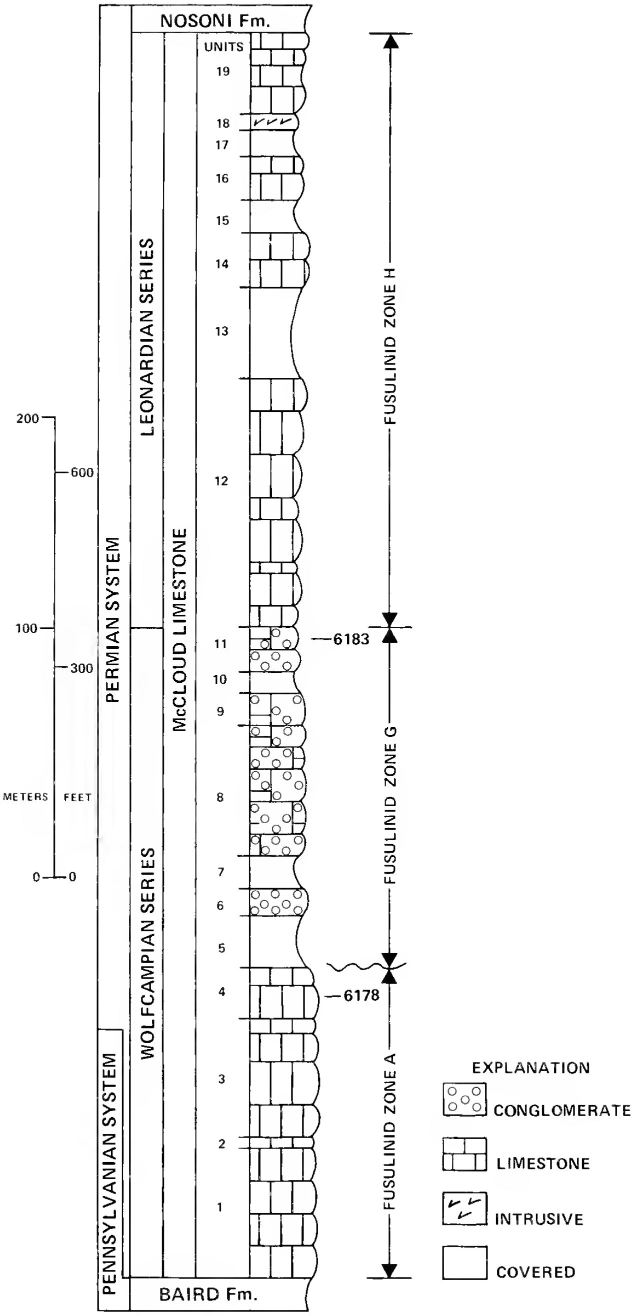


Figure 2. Columnar section of the McCloud Limestone at Tombstone Mountain, Shasta County, California. Locality numbers at right of column show position of the only two coral faunas in the section. Fauna of the higher locality is the subject of this paper. Lower locality is mentioned in "Stratigraphy" section.

septal microstructure of fibers at right angle to sinuous dark, center line; cardinal fossula closed, with neighboring several pairs of septa arched around adaxial end, 32 mm deep in holotype; tabularium filled with chaotic pattern of sections of tabellae and attenuate septal ends; dissepimentarium wide, width 15 to 20 mm in adult stages, not observed in younger stages (abraded), lacking inner wall at tabularium interface; dissepiments in 12 to 20 ranks in adult stage, regular peripherally, herringbone, angular, or straight adaxially; corallite wall very thin, width 0.1 to 0.2 mm.

LONGITUDINAL SECTION DESCRIPTION. Dissepimentarium in adult stage (diameter 95 mm) of 19 to 22 ranks of steeply dipping dissepiments of very mixed sized: generally small and globose near wall, becoming larger and more elongate adaxially; tabellae of two zones, axial and periaxial; axial tabellae of 10 to 12 ranks each side of approximate center of corallite (not indicated structurally), very variable, most near center concave *upwards,* most near sides steeply dipping downwards and *inwards;* periaxial tabellae in 1 to 2 ranks, generally flat and horizontal, some cystose.

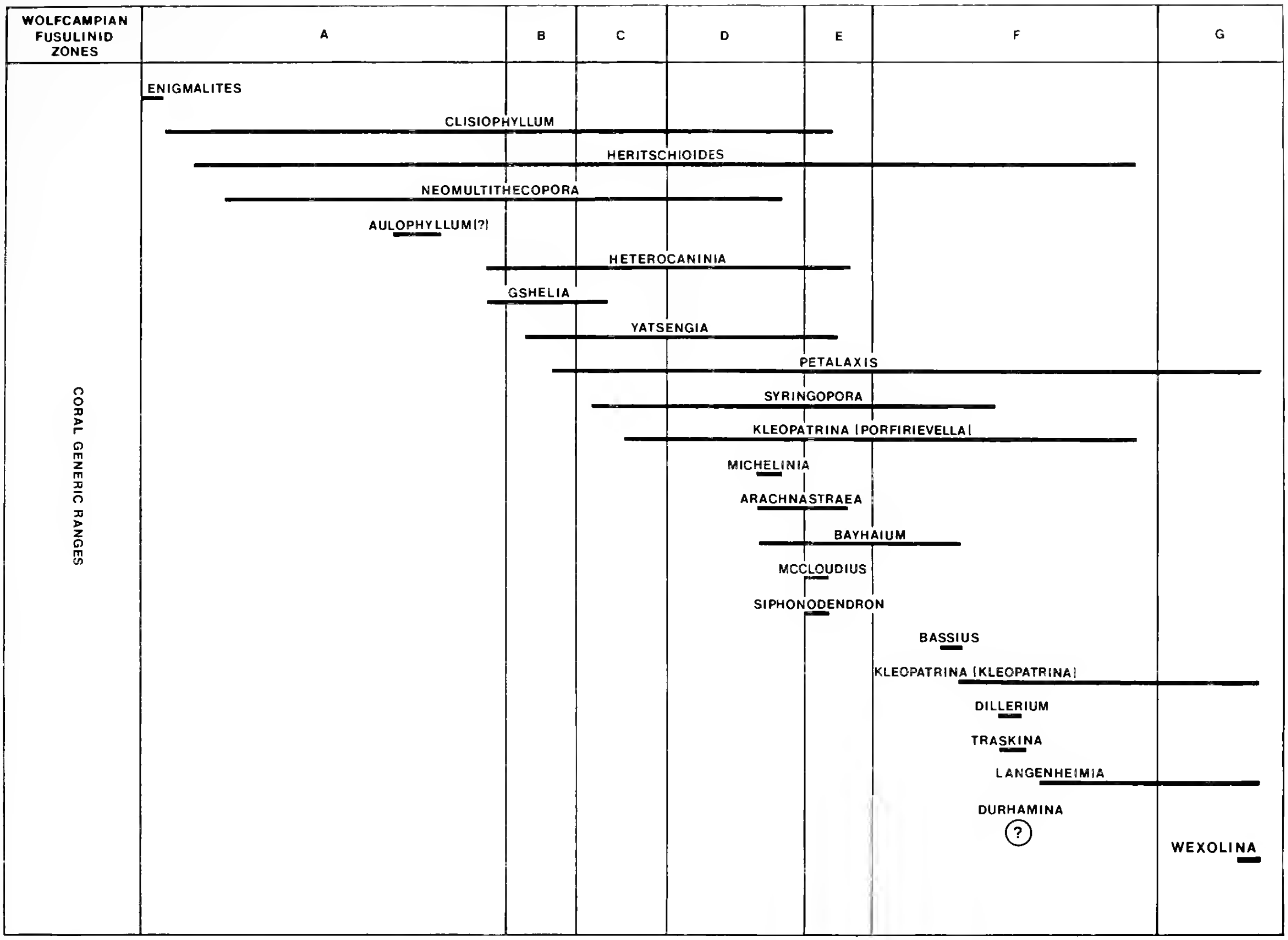
DOCUMENTATION. LACMIP holotype 7170, LACMIP paratypes 7171–7176. Ten thin sections and 41 polished sections from eight coralla from LACMIP localities 6181 (paratypes 7172–7174), 6182 (holotype 7170, paratype 7171), and 6183 (paratypes 7175–7176) were studied. These three localities are on strike within the same bed.

DISCUSSION. Most of the type specimens of this solitary coral are preserved with the dissepimentaria mostly or wholly removed by pre-burial abrasion. The calicular area of the holotype is an exception but even it is progressively abraded apically. The holotype has a dissepimentarium one-third the diameter of the tabularium. Following is a list of sections made of coralla from the type series, giving type designations, corallite diameters, and septal numbers: holotype 7170, 10.3 cm—88 septa, 9.7 cm—84 septa; paratype 7171, 6.0 cm—68 septa, 4.0 cm—60 septa, 2.2 cm—51 septa, 1.6 cm—32 septa; paratype 7172, 3.5 cm—55 septa; paratype 7173, 5.2 cm—64 septa; paratype 7174, 5.0 cm—67 septa, 3.5 cm—52 septa; paratype 7175, 2.7 cm—49 septa, 2.4 cm—39 septa, 2.0 cm—37 septa; paratype 7176, 6.4 cm—80 septa, 5.7 cm—87 septa.

Unfortunately, the early ontogenic stages are unrepresented below 1.5 cm diameter eroded apices (probably originally approximately 2.5 cm with dissepimentaria), although a special search was made for small specimens. For this reason, the genus and species cannot be assigned with certainty to family.

The cyathopsid (?) of Wilson (1982:19, fig. 9f) was collected from the McCloud Limestone at Potter Ridge, about 30 km south of Tombstone Mountain, where it occurs 38 m below *Langenheimia klamathensis.* Specimens of the cyathopsid (?) are very poorly preserved, but figure 9f of Wilson (1982) shows a corallite of similar large size to *Wexolina tombstonensis,* somewhat more abundant septa (90), similar sinuous septa protruding into the calyx, and a very similar closed cardinal fossula with a short cardinal septum. Without better preserved specimens it is impossible to tell if the cyathopsid (?) is referable to *Wexolina,* but these characters suggest that it may be.

W. tombstonensis occurs in a conglomeratic unit at Tombstone Mountain and is associated with abundant specimens of three species (in three genera) of cerioid rugose corals. These factors indicate that the environment of deposition, and perhaps the living environment, was a very high energy one. The preservation in the holotype of the calyx, the most



ⓘ Stratigraphic position uncertain but within Zone E or F

Figure 3. Stratigraphic ranges of coral genera in the McCloud Limestone in relation to Wolfcampian Series fusulinid zones of Skinner and Wilde (1965). Zone G coral genera extensions reported in this study are added to previous ranges reported by Wilson (1982).

delicate part of the corallum, and the absence of the apical parts beyond 10 cm below, where the corallum is badly eroded, suggest that this corallum may have continued to live and grow even after its apical parts were destroyed. Perhaps coralla for this species lay loose on the substrate of such a high energy environment that only the youngest parts nearest the polyp remained intact. The highly dilate septa of the tabularium may represent an adaption of a dense central core resistant to erosion.

ETYMOLOGY. The species is named for Tombstone Mountain.

CERIOID CORALS

Kleopatrina (*Kleopatrina*) *svalbardense* Fedorowski, 1980

Figures 6a–d

Kleopatrina (*Kleopatrina*) *svalbardense* Fedorowski, 1980: 21, pl. 4, figs. 1a–1d, 2, 3a–3b.

EXTERNAL DESCRIPTION. Corallum cerioid, hemispheroidal, maximum observed diameter 14 cm; calyx not observed; corallites parallel.

TRANSVERSE SECTION DESCRIPTION. Corallites 4 to 7 sided, 8 to 11 mm wide at greatest diameter; septa of 2 orders, 12 to 22 each, straight to slightly sinuous, rarely lonsdaleoid; major septa generally touching axial structure, especially cardinal and counter septa, 2.3 to 4 mm long, somewhat dilate in tabularium or thin throughout; minor septa well developed, 1 to 2 mm long, generally crossing dissepimentarium, extending into tabularium as nubs in some; dissepimentarium generally regular, width 1.6 to 2.7 mm; dissepiments concentric, herringbone, pseudoherringbone, or lonsdaleoid (uncommon); axial structure clisiophylloid, circular to subcircular, rather small, 1 to 2 mm diameter, formed of straight to slightly sinuous, somewhat thickened medial plate connected to cardinal and counter septa, with radiating straight to slightly sinuous septal lamellae touching axial ends of many septa, connected by 2 to 4 axial tabellae; corallite wall 0.1 to 0.2 mm wide.

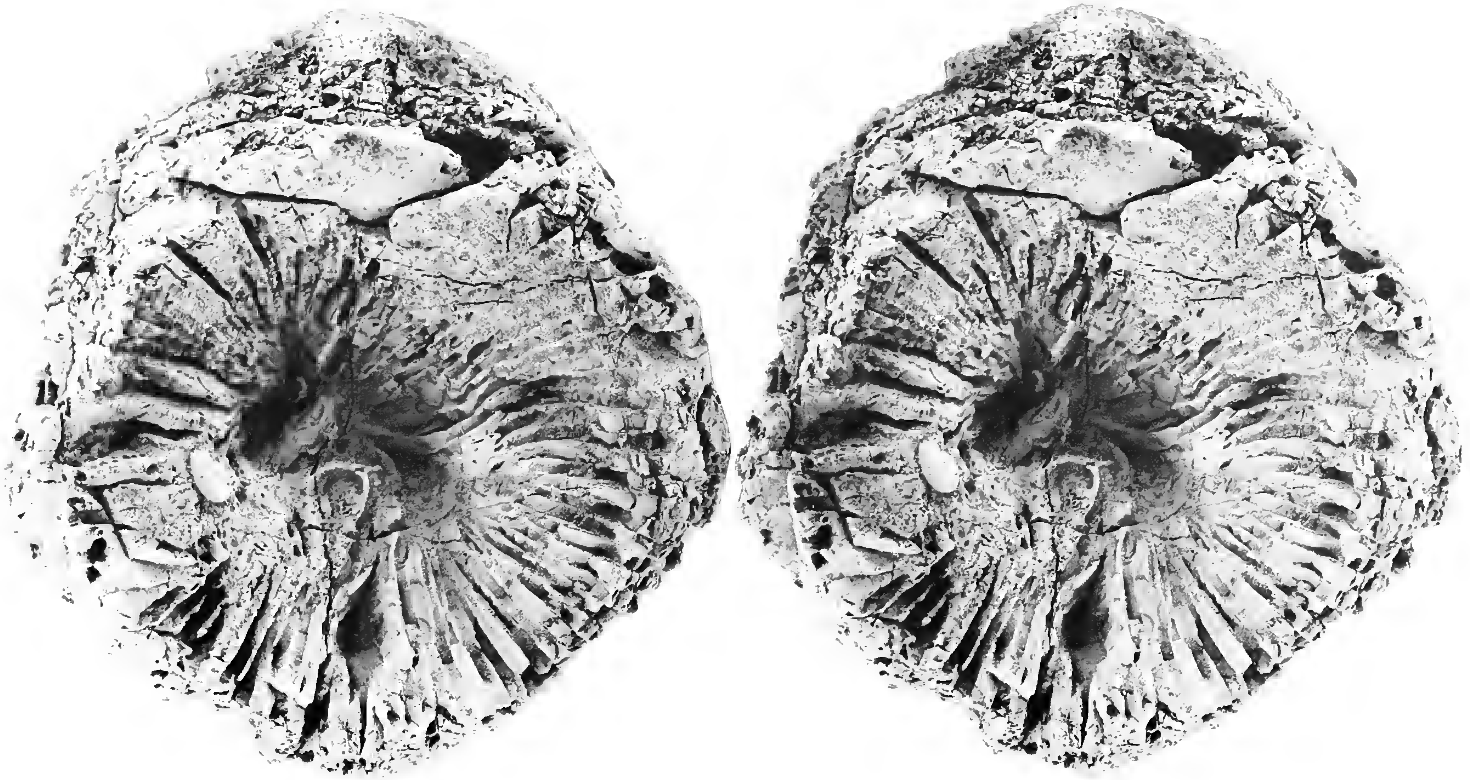


Figure 4. *Wexolina tombstonensis* n. gen., n. sp. LACMIP holotype 7170. Stereophoto of calyx. Cardinal fossula is near lower edge. Gastropod on left is *Naticopsis* sp. ×1.

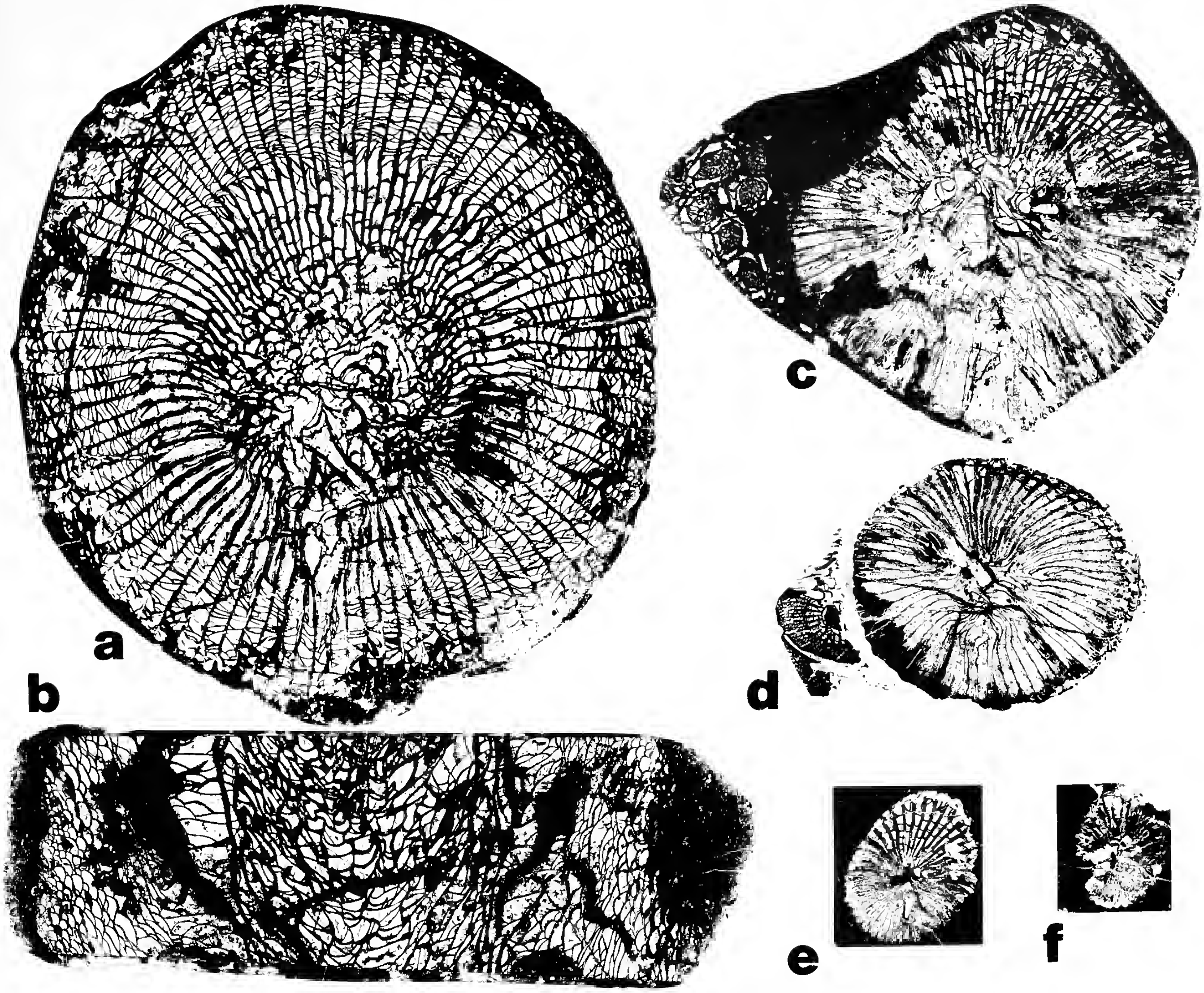


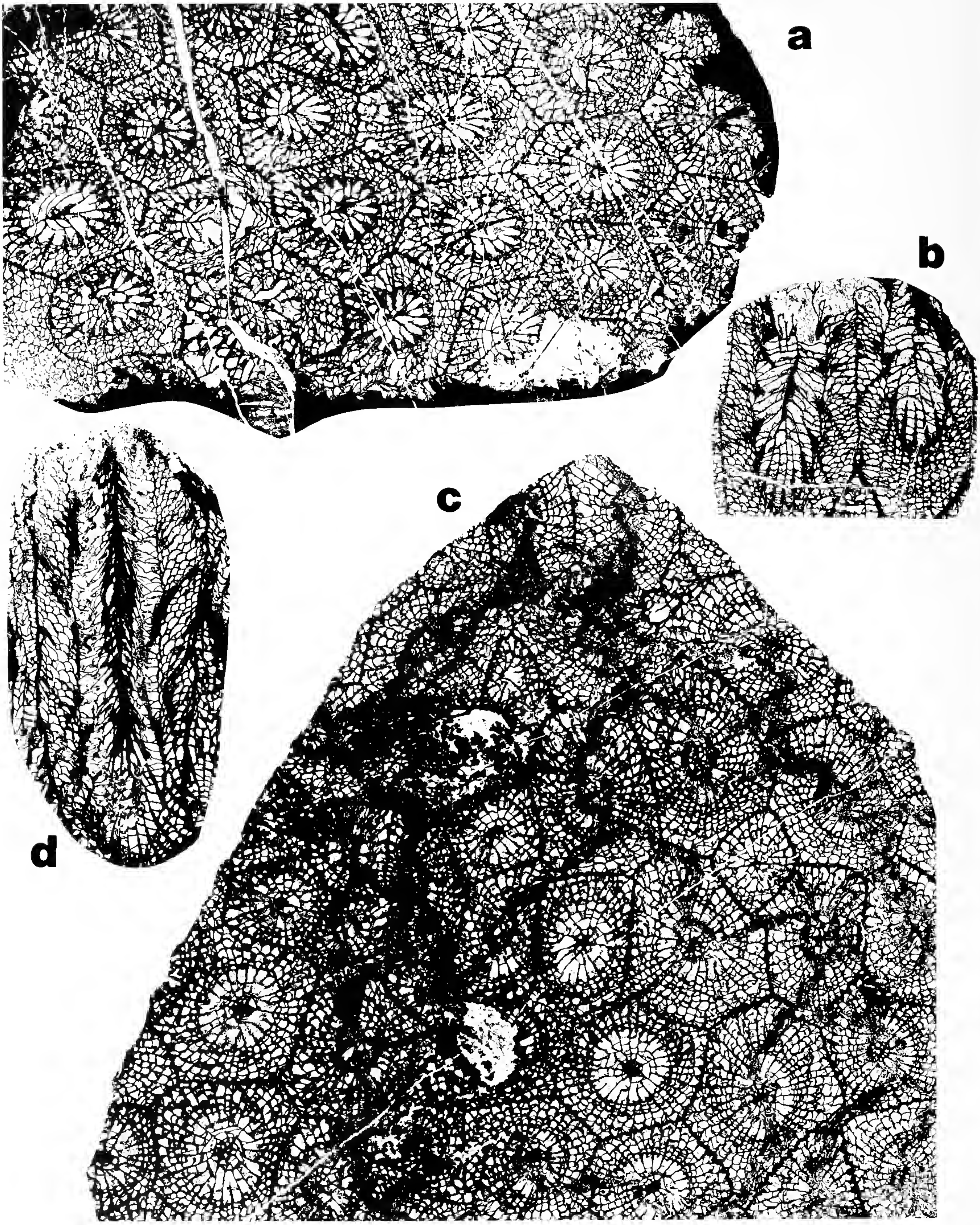
Figure 5. *Wexolina tombstonensis* n. gen., n. sp. **a, b,** LACMIP holotype 7170, transverse and longitudinal sections. **c-f,** transverse sections, paratypes 7176 (c), 7171 (d–f). Partial transverse sections of *Petalaxis occidentalis* left of 5c and *Langenheimia klamathensis* left of 5d. ×1.

LONGITUDINAL SECTION DESCRIPTION. Dissepimentarium of 3 to 7 steeply to gently dipping ranks of medium sized cystose (a few are elongate) dissepiments; tabellae of 2 zones, axial and periaxial; periaxial tabellae generally gently dipping in and up to axial tabellae, rarely flat, some cystose, 15 to 22 per cm; axial tabellae in 1 to 3 ranks, large to small, elongate to cystose, steeply sloping inwards and up to medial plate, 15 to 23 per cm; some corallites lack axial tabellae in places and have gently sloping tabulae instead.

DOCUMENTATION. LACMIP hypotype 7177–7178. Three thin sections and 30 polished sections from hypotype 7177 from LACMIP locality 6181, three thin sections and 17 polished sections from one additional corallum from the same locality, five thin sections and 53 polished sections from two coralla from LACMIP locality 6182, two thin sections and 23 polished sections from hypotype 7178 from LACMIP locality 6183, and 31 polished sections from two coralla from the same locality were studied.

DISCUSSION. This coral previously was known only from the Lower Permian (Sakmarian) Treskelodden Formation of southern Spitsbergen. Its occurrence in the Upper Wolfcampian of the McCloud Limestone provides an apparent biostratigraphic correlation between the two formations despite their great geographic separation.

Seven McCloud Limestone specimens are the basis for the above description. Their characters fall within the range of those of the type specimens from Spitsbergen, although some coralla from the former occurrence have corallites a little smaller in average diameters. The chief character distinguishing this species from others in the genus is the nearly universal


a
b
c
d

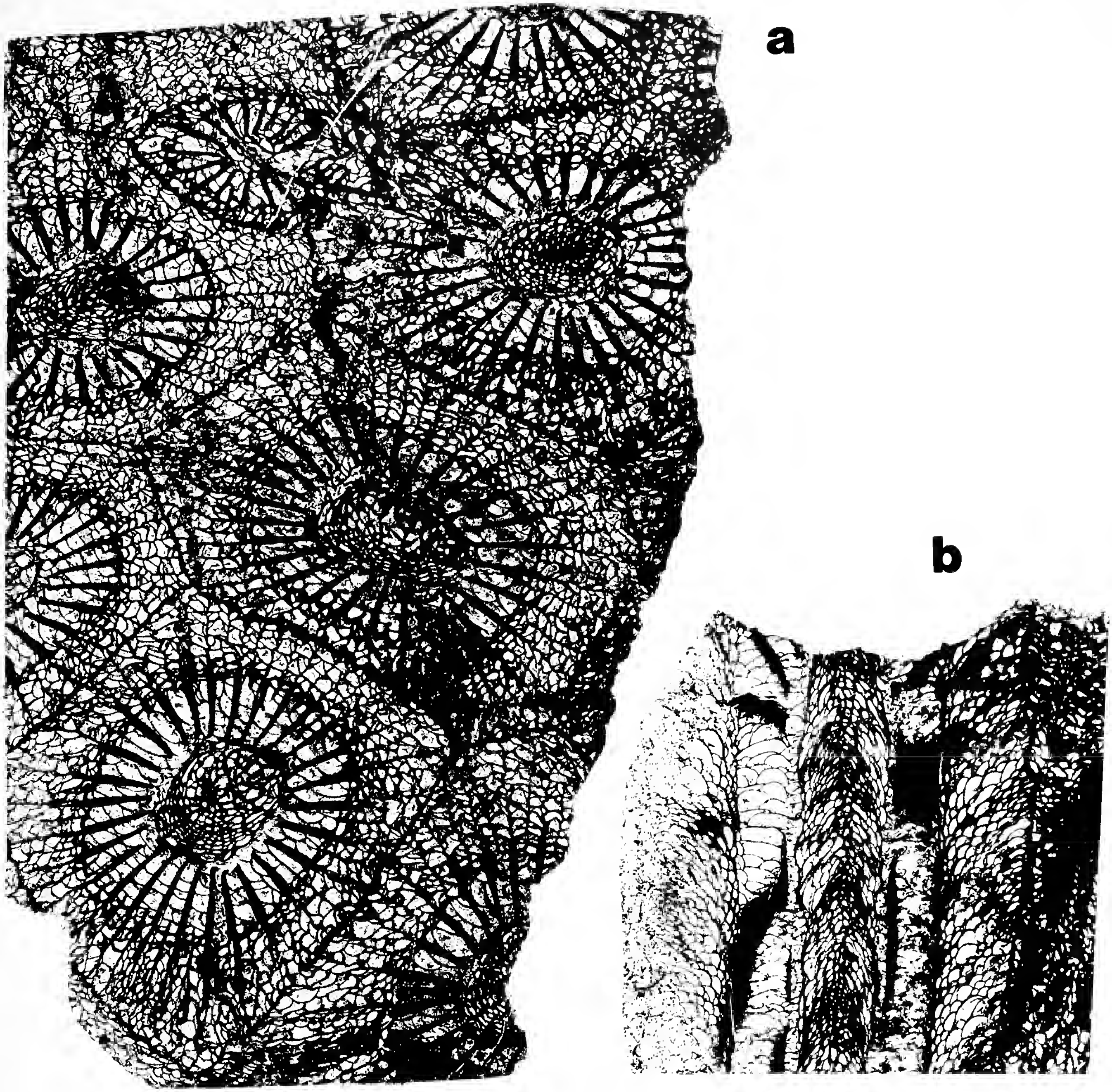


Figure 7. *Langenheimia klamathensis* Wilson, 1982. LACMIP hypotype 7179, transverse (a) and longitudinal (b) sections. ×3.

connection of the cardinal and counter septa to the complex axial structure, which also is touched by other major septa, giving it a distinct arachnoid appearance. The very short septal-like structures on the external wall between major and minor septa mentioned by Fedorowski (1980:21) can be seen in some corallites of the McCloud Limestone specimens.

Langenheimia klamathensis Wilson, 1982

Figures 7a–b

Langenheimia klamathensis Wilson, 1982:65, figs. 37f, 38a–b.

←

Figure 6. *Kleopatrina svalbardense* Fedorowski, 1980. **a, b,** LACMIP hypotype 7177, transverse (a) and longitudinal (b) sections; **c, d,** LACMIP hypotype 7178, transverse (c) and longitudinal (d) sections. ×3.

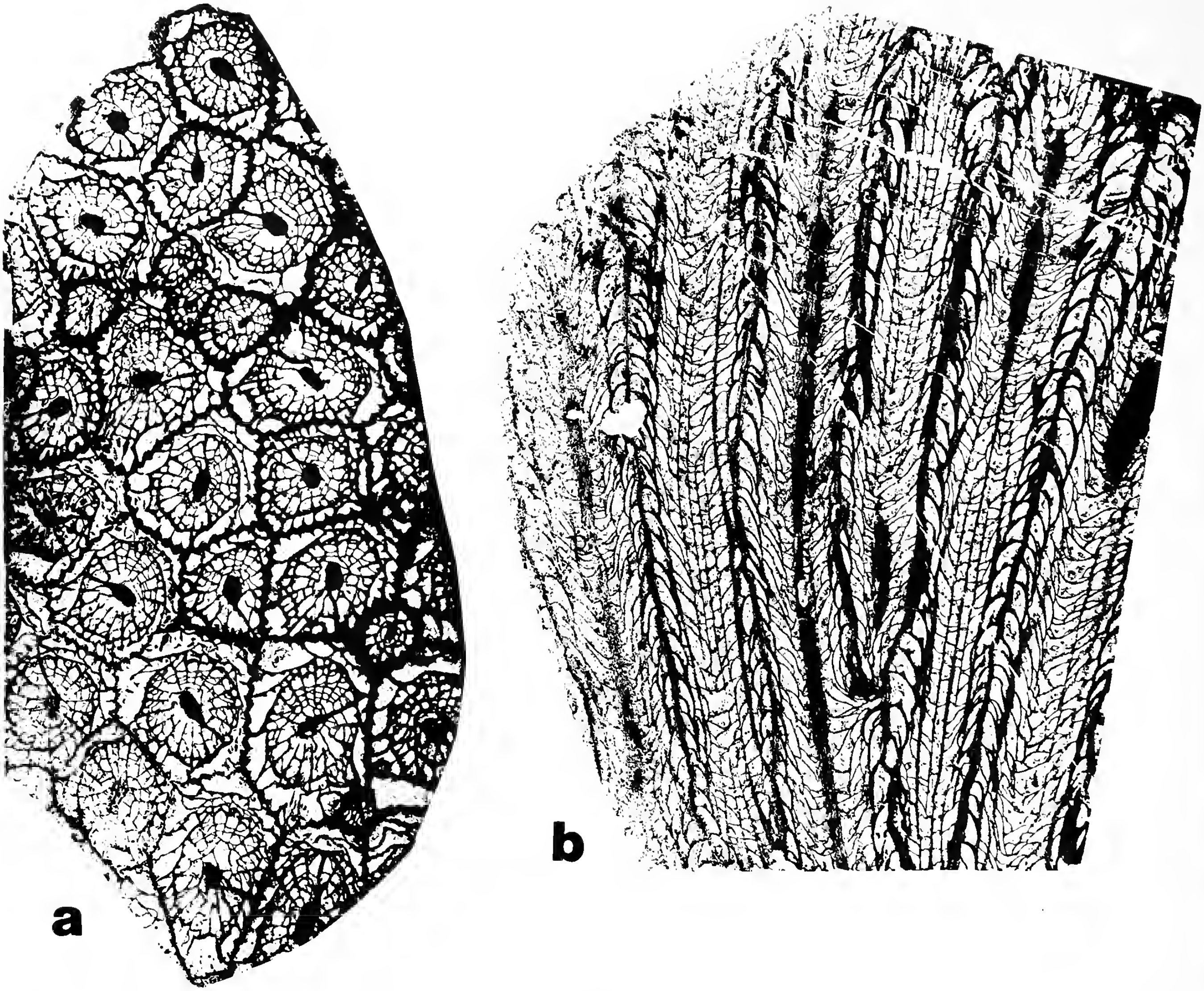


Figure 8. *Petalaxis occidentalis* (Merriam, 1942). LACMIP hypotype 7180, transverse (a) and longitudinal (b) sections. ×3.

DESCRIPTION. The Tombstone Mountain specimens referred to this species are so similar morphologically to the type specimens from lower in the formation described by Wilson (1982) that the original description will accommodate them and is not repeated here.

DOCUMENTATION. LACMIP hypotype 7179. Four thin sections and 16 polished sections from the hypotype from LACMIP locality 6181, two thin sections and 10 thin sections from one additional corallum from the same locality, and three thin sections and 20 polished sections from four coralla from LACMIP locality 6182 were studied.

DISCUSSION. Occurrence of this species in fusulinid Zone G at Tombstone Mountain extends its range upward in the formation from the type locality in fusulinid Zone F at Potter Ridge, about 30 km south of Tombstone Mountain. This highly distinctive species is known only from these two localities.

Petalaxis occidentalis (Merriam, 1942)

Figures 8a–b

Lithostrotion (*Lithostrotionella*) *occidentalis* Merriam, 1942: 377, pl. 56, figs. 2, 4, 7, 8, 11.

Petalaxis occidentalis (Merriam). Sando, 1983:32, pl. 20, figs. 1, 2.

DESCRIPTION. The Tombstone Mountain specimens referred to this species are so similar morphologically to the type specimens described by Merriam (1942) that the original description will accommodate them and need not be repeated here.

DOCUMENTATION. LACMIP hypotype 7180. Two thin sections and 24 polished sections from the hypotype from LACMIP locality 6181, four thin sections and 21 polished sections from two additional coralla from the same locality, two thin sections and 26 polished sections from 7 coralla from LACMIP locality 6182, and four thin sections and 60 polished sections from 17 coralla from LACMIP 6183 were studied.

DISCUSSION. This is the first report of *Petalaxis occidentalis* outside the type locality in the Coyote Butte Formation of central Oregon. Its presenee in fusulinid Zone G at Tombstone Mountain reinforces Skinner and Wilde's (1965: 13) correlation of their Zone G of the McCloud Limestone with the Coyote Butte Formation on the basis of six species of fusulinids common to both.

LOCALITIES

The following localities are entered in the LACMIP locality register. They are located in the McCloud Limestone, fusulinid Zone G, Upper Wolfcampian, on Tombstone Mountain, Shasta County, California, in the northwest ¼ of the southwest ¼ of the southeast ¼ of section 19, township 37 north, range 3 west, Mt. Diablo Meridian and Base Line, as shown on the U.S. Geological Survey 15 minute topographic quadrangle of Dunsmuir, California (1954, scale 1:62,500).

6181. South along strike from the base of LACMIP locality 6183 and east of the southern edge of the southeastern peak. Conglomeratic limestone with large solitary corals and abundant cerioid corals.

6182. Ten feet (3.05 m) stratigraphically higher, down the dip slope from LACMIP locality 6181. Conglomeratic gray limestone with enormous solitary corals and cerioid corals.

6183. This locality is 865 to 880 ft. (263.6 to 268 m) above the base of a measured section that begins on the west face of the mountain at the exposed base of the McCloud Limestone west of the northern peak, offsets from that peak to the southwest peak, and extends eastward over the southeast peak and along an east-trending ridge to the base of the overlying Nosoni Formation. Limestone, medium gray, weathers same, conglomeratic, thin-bedded, with abundant cerioid corals (some overturned), large solitary corals, fusulinids.

ACKNOWLEDGMENTS

I am grateful to Peter T. Gavin, Phillip G. Owen, and Eric Scott for field assistance in 1982, 1983, and 1984 on the arduous trips to Tombstone Mountain. Mr. John B. Wexo generously financed the 1984 field trip. The Natural History Museum of Los Angeles County and its Foundation supported this study in many ways. Dr. Winfield Henn of the Shasta–Trinity National Forest provided collecting permits. Photographs were prepared by Mr. Richard Meier and figures are by Miss Mary Butler. Preparation of specimens was done by me using facilities at LACMIP.

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3 October 1985

CONTRIBUTIONS IN SCIENCE

THE LATE MIOCENE DOLPHIN *PITHANODELPHIS* ABEL, 1905 (CETACEA: KENTRIODONTIDAE) FROM CALIFORNIA

Lawrence G. Barnes

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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THE LATE MIOCENE DOLPHIN *PITHANODELPHIS* ABEL, 1905 (CETACEA: KENTRIODONTIDAE) FROM CALIFORNIA

Lawrence G. Barnes[1]

ABSTRACT. Fossil species of the unusual and relatively highly derived kentriodontid dolphin genus *Pithanodelphis* Abel, 1905, are now known from rocks bordering both the North Atlantic and the North Pacific Ocean basins. The type species of this genus, Late Miocene *Pithanodelphis cornutus* (du Bus, 1872), is known from the Antwerp Basin in Belgium. A skull illustrated by Abel in 1905 is here designated as the lectotype of this species. An approximately contemporaneous species, *Pithanodelphis nasalis,* new species, differs from *P. cornutus* by having a different suite of derived and primitive cranial characters and it is one of the most abundant fossil cetaceans in the Late Miocene age Monterey and Modelo formations in southern California.

Bones around the nares and cranial vertex of species of *Pithanodelphis* are asymmetrical, but in a unique manner that is totally unlike the condition in species of modern Delphinidae and other Odontoceti which possess cranial asymmetry. The nasal bones are very large. In recognition of these derived characters, *Pithanodelphis* is classified in a new subfamily of Kentriodontidae, the Pithanodelphinae. Apparently *Pithanodelphis nasalis* was able to produce sounds used for echolocation, lived in moderately deep water offshore over the continental shelf, and had a heterogeneous diet comprised mostly of small fishes. Adult individuals attained a body length of approximately 200 cm. The vertebral column is similar to those of the Middle Miocene fossil kentriodontine dolphin, *Delphinodon dividum* True, 1912b, and the extant bottlenosed dolphin, *Tursiops truncatus* Montagu, 1821.

INTRODUCTION

Recent studies have shown that during Miocene time an extinct group of dolphins, the family Kentriodontidae, which was first recognized from fossils found in deposits around the North Atlantic Ocean, also had an equally significant history in the North Pacific Ocean (Barnes, 1977, 1978; Barnes and Mitchell, 1984). Five kentriodontid genera are now known to have had species that lived in both ocean basins, and one of these is the genus *Pithanodelphis* Abel, 1905. The type species of the genus is *P. cornutus* (du Bus, 1872), which is known only from specimens found in Late Miocene sediments in the Antwerp Basin in Belgium. I have previously (Barnes, 1977) recognized the genus *Pithanodelphis* from the approximately correlative Monterey Formation in southern California, and classified the genus in the nominate kentriodontid subfamily Kentriodontinae (Barnes, 1978).

The fossils from California represent a new species that I described in a Ph.D. dissertation (Barnes, 1972). This species is known by several skulls and some postcranial bones, most of which are from a vertically and laterally restricted stratigraphic section of the Monterey Formation in the San Joaquin Hills in Orange County, California, near the southern limit of the topographic and depositional feature known as the Los Angeles Basin (Woodford et al., 1954). Some of the fossils were discovered in naturally formed outcrops, but most were discovered in 1969 as a result of earth-moving for construction of an extensive commercial/manufacturing complex for North American Rockwell Land Corporation near Aliso Creek in the Laguna Niguel district, part of which later became the offices of the United States General Services Administration. This site has been discussed by Domning (1978), Howard (1978), and Barnes, Raschke, and McLeod (in press). One additional specimen that I refer to this species is from the correlative Upper Member of the Modelo Formation that is exposed 84 km to the north of Laguna Niguel in the Santa Monica Mountains, Los Angeles County, California. The purpose of this paper is to diagnose these fossils as a new species and to describe the available sample of specimens.

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METHODS AND MATERIALS

In this study, the closest comparisons are made between the new species and two other kentriodontids. I refer the reader to descriptions and illustrations of specimens of *Kentriodon pernix* Kellogg, 1927, provided by Kellogg (1927, 1928), Barnes (1978, including other species of kentriodontids), and Barnes and Mitchell (1984), and of *Delphinodon dividum* True, 1912b, provided by True (1912b), Barwick (1939), and Barnes (1978). I have also made comparisons with various living odontocete taxa. Systematics and ranges of these are provided by Hershkovitz (1966) and Rice (1984).

Measurements of skulls and the mandible were made following the methods outlined by Perrin (1975). In the tables of measurements, a number in parentheses following the description of a parameter refers to the same measurement of Perrin. Anatomical terminology is derived from Kellogg (1927), Fraser and Purves (1960), Kasuya (1973), Barnes (1978, 1984), and Barnes and Mitchell (1984). The repository of specimens, the Natural History Museum of Los Angeles County, Los Angeles, California, is abbreviated LACM. Precise locality descriptions may be provided to qualified investigators upon request.

In the illustrations, bones and other anatomical structures are labeled according to the following abbreviations:

aon—antorbital notch
Bo—basioccipital bone
Bs—basisphenoid bone
ch—cranial hiatus
eam—external acoustic meatus
fio—ventral apertures, infraorbital foramen
fmx—maxillary foramen
fop—optic foramen
fpal—palatine foramen
fpmx—premaxillary foramen
Fr—frontal bone
gf—glenoid fossa
Ju—jugal bone
La—lacrimal bone
Met—mesethmoid bone
mrg—mesorostral gutter
ms—middle sinus
Mx—maxillary bone
n—naris
Na—nasal bone
Oc—occipital bone
occ—occipital condyle
Pa—parietal bone
Pal—palatine bone
Pmx—premaxillary bone
pop—paroccipital process
Pt—pterygoid bone
Pt(ll)—lateral lamina of pterygoid
Pt(ml)—medial lamina of pterygoid
pts—fossa for pterygoid sinus
sq—squamosal bone
sqf—squamosal fossa
Vo—vomer bone

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Suborder Odontoceti Flower, 1867

Superfamily Delphinoidea (Gray, 1821) Flower, 1864

Family Kentriodontidae (Slijper, 1936) Barnes, 1978

Kentriodontinae Slijper, 1936:556; as a subfamily of the family Delphinidae.
Kentriodontidae. Slijper, 1958:label in fig. 36; emended rank without explanation in text.
Kentriodontidae. Barnes, 1978:3; emended rank, as a family of the superfamily Delphinoidea.

EMENDED DIAGNOSIS OF FAMILY. A family in the superfamily Delphinoidea differing from Albireonidae, Monodontidae, Delphinidae, and Phocoenidae by having skulls with small pterygoid sinus in pterygoid hamulus; differing from Monodontidae, Delphinidae, and Phocoenidae by lacking excavation in exoccipital for posterior sinus and in lateral side of basioccipital for peribullary and/or pterygoid sinus, by having symmetrical posterior ends of premaxillae which contact nasals on both right and left sides, and by having symmetrical cranial vertex (except in case of kentriodontids with asymmetrical vertex, which have midline between nasals twisted to right instead of to left); differing from Delphinidae and Phocoenidae by lacking anterior sinus and lacking large posterodorsal extension of antorbital lobe of pterygoid sinus between frontal and maxilla; differing from Albireonidae and Phocoenidae by lacking premaxillary eminences and having instead, wide, flat, and elevated spiracular plates on premaxillae on either side of external nares; differing from Monodontidae and Delphinidae by having symmetrical mesethmoid and external nares, equal areas of vertex covered by right and left nasals, and by having right and left spiracular plates approximately equal in size; and differing from Albireonidae by having mesorostral gutter open dorsally.

INCLUDED SUBFAMILIES. Kampholophinae Barnes, 1978; Kentriodontinae (Slijper, 1936) Barnes, 1978; Lophocetinae Barnes, 1978; and Pithanodelphinae, new subfamily.

Subfamily Pithanodelphinae, new subfamily

DIAGNOSIS OF SUBFAMILY. A subfamily of Kentriodontidae differing from Kampholophinae, Lophocetinae, and Kentriodontinae by having skulls with asymmetrical cranial vertex in which midline between nasals bends toward right side posteriorly, right maxilla encroaches farther than left toward midline posteriorly, right spiracular plate is slightly wider than left, and right nasal is higher than left, posterior end of premaxilla extending as slender projection between nasal and maxilla rather than wide, abruptly terminating and with elevated posterolateral corner, nasal bone much larger and very convex, olfactory fontanelle present in posterior wall of each naris; differing further from Kampholophinae and Kentriodontinae by having periotic with narrower, more transversely compressed anterior process; and differing further from Kentriodontinae by lacking obliquely oriented sulcus on anterolateral surface of nasal bone within upper part of naris.

TYPE AND ONLY INCLUDED GENUS. *Pithanodelphis* Abel, 1905, Late Miocene, Belgium and California.

Pithanodelphis Abel, 1905

Phocaenopsis Huxley, 1859, part. du Bus, 1872:500.

Pithanodelphis Abel, 1905:142; for *Phocaenopsis cornutus* du Bus, 1872, only.

EMENDED DIAGNOSIS OF GENUS. The same as for the subfamily until other genera are assigned to the subfamily.

TYPE SPECIES. *Pithanodelphis cornutus* (du Bus, 1872).

INCLUDED SPECIES. *Pithanodelphis cornutus* (du Bus, 1872); and *Pithanodelphis nasalis,* new species.

***Pithanodelphis nasalis,* new species**

Figures 1–14

aff. *Pithanodelphis* Abel, 1905. Barnes, 1977:328 (table 4).

DIAGNOSIS OF SPECIES. A species of *Pithanodelphis* differing from *P. cornutus* by having skull with more prominent lambdoidal and occipital crests, occipital shield smaller and not as convex, temporal fossa curving farther around margin of occipital shield, nasal relatively larger, zygomatic process of squamosal smaller with more tapered anterior end.

HOLOTYPE. LACM 30093, a nearly complete skull, dorsoventrally crushed, lacking much of the basicranium, bearing 23 whole or incomplete teeth in place, with 16 loose teeth, right and left tympanic bullae, left periotic, malleus, incus, and stapes; right and left dentaries with 11 whole or partial teeth in place, collected by W. Earl Calhoun and Michael K. Hammer in 1969.

TYPE LOCALITY. LACM locality 5077, Laguna Niguel district, San Joaquin Hills, Orange County, California.

PARATYPES. LACM 26635, an undistorted but badly shattered incomplete skull lacking anterior end of the rostrum and basicranium, bearing five whole or partial teeth in place, and one fragment of the extremity of the rostrum, collected at LACM locality 5069 by W. Earl Calhoun in 1969. LACM 29087, two fragments of a skull (the dorsolateral corner of the braincase and the left squamosal), partial vertebral column and ribs, collected at LACM locality 5082 by Marion J. Bohreer and W. Earl Calhoun in 1969.

REFERRED SPECIMENS FROM THE MONTEREY FORMATION. LACM 31186, right side of rostrum collected at LACM locality 5071 by Marion J. Bohreer in 1969; LACM 122670, left periotic collected by Michael D. Quarles, 8 November 1982, and LACM 123872, skull, collected by David P. Whistler and L.G. Barnes, 31 May 1975, both from LACM locality 6902; LACM 123873, skull collected at LACM locality 1101 by Michael K. Hammer.

FORMATION AND AGE. The holotype, paratypes, and referred specimens listed above are all from rocks that have been identified as the upper part of the Monterey Formation (Vedder, Yerkes, and Schoellhamer, 1957; Fife, 1974), correlated with the "Margaritan" provisional mega-invertebrate stage of Addicott (1972), with the Mohnian foraminiferal stage, and indirectly with the later part of the Clarendonian North American land mammal age, and are of Late Miocene age, approximately 10 to 11 million years old (Barnes, 1977; Repenning and Tedford, 1977; Howard, 1978). This part of the Monterey Formation has yielded a diverse fossil vertebrate assemblage (Barnes, Raschke, and McLeod, in press), including the bird fossils that were described by Howard (1976, 1978), the sirenian fossils reported by Domning (1978), and a fairly diverse cetacean assemblage reported by Barnes (1977). Stratigraphically lower within the Monterey Formation in the same district of Orange County vertebrate fossils, including birds (Howard, 1966, 1968) and cetaceans (Barnes, 1978), have been reported that have closer affinities with Middle Miocene assemblages in California, especially with the Sharktooth Hill Local Fauna in central California. These older assemblages in the Monterey Formation have been correlated indirectly with the earlier part of the Clarendonian land mammal age (Howard, 1978:24).

In the upper part of the Monterey Formation in Laguna Niguel, *Pithanodelphis nasalis* is associated with the gannet, *Morus lompocanus* (Miller, 1925); the booby, ?*Miosula media* Miller, 1925; the sea cow, *Dusisiren jordani* (Kellogg, 1925a); and the pinnipeds, *Pithanotaria starri* Kellogg, 1925b, and *Imagotaria downsi* Mitchell, 1968, all of which were originally based on specimens from the Late Miocene age diatomites of the Sisquoc Formation near Lompoc, Santa Barbara County, California. This association further reinforces the age yielded by the correlations given above (see also Repenning and Tedford, 1977).

Because the holotype and paratypes of *Pithanodelphis nasalis* were exposed during a construction project as mentioned in the introduction, they were collected in a salvage situation and the precise stratigraphic relationships between them were not recorded. The holotype, LACM 30093, was collected from a fine-grained yellow siltstone bed that was approximately 6 to 8 inches thick and was exposed within a section of otherwise fairly uniformly bedded white diatomite 140 m north of the excavation for the foundation of the main North American Rockwell building. The paratype skull, LACM 26635, was found in a loose, coarse-grained, bed of gray sand uncovered near the northeast corner of the same building. Because the strata in this immediate area generally dip toward the north, the bed that yielded the paratype skull was probably stratigraphically lower in the Monterey Formation than the one that yielded the holotype, but was probably no more than 10 m lower.

The paratype partial skeleton, LACM 29087, was collected from a coarse sand bed within bedded diatomite at the northwest corner of the building, and its stratigraphic position was therefore probably also lower than the holotype. The vertebral column of the paratype was bisected in the thoracic area by machinery that was cutting a trench, and Bohreer and Calhoun independently collected opposite ends of the skeleton. After later conversations with both men I was convinced that only one individual fossil skeleton was involved.

Another partial skull, LACM 123872, and an isolated periotic, LACM 122670, referred to the species were both collected near the base of a very coarse, ca. 3-m-thick bed of yellow sand exposed in a road cut 400 m northwest of the main building site. The sand bed that yielded these fossils has subsequently been observed in the field to lie stratigraphically above the diatomite that produced the holotype, and it is the highest part of the Monterey Formation that is exposed in the vicinity (Barnes, Raschke, and McLeod, in press).

The referred skull, LACM 123873, is from another nearby site, LACM 1101, the same locality that yielded the partial skeleton of an otariid pinniped (LACM 1404) that was identified by Downs (1955) as cf. *Allodesmus kernensis* Kellogg, 1922. This specimen is actually an imagotariine otariid, possibly *Imagotaria downsi* or a closely related species. *I. downsi* is known from such Late Miocene (Clarendonian age) formations in California as the Towsley, Sisquoc, and Santa Margarita (Repenning and Tedford, 1977). The locality (LACM 1101) is 1.4 km from the other Laguna Niguel sites mentioned above that yielded *Pithanodelphis nasalis,* and is separated from them by the wide valley that was formed by Aliso Creek and, thus, no direct stratigraphic correlation is possible. The site is, however, in a well-bedded diatomite very much like that which yielded the holotype skull, and this diatomite is overlain by a coarse yellow sand bed like that which produced the referred specimens of *P. nasalis* at LACM locality 6902. The strata are undoubtedly correlative, and I therefore conclude that all the specimens from these Laguna Niguel localities were collected within the uppermost few tens of meters of the Monterey Formation.

REFERRED SPECIMEN FROM THE MODELO FORMATION. LACM 15196, incomplete skull and jaws with some associated postcranial bones collected from LACM locality 1230, Studio City, Los Angeles County, California, by Terry and Michael Pohl about 1955.

FORMATION AND AGE. Upper Member of the Modelo Formation, Late Miocene age, correlated with the upper part of the Monterey Formation in the San Joaquin Hills (Woodford et al., 1954:fig. 2). The locality is within outcrops of diatomaceous shale that have been mapped as the Upper Member of the Modelo Formation of Late Miocene age (Hoots, 1931). A nearby outcrop of the same rock unit produced the fossil bird, *Sula pohli* Howard, 1958.

ETYMOLOGY. The species name, *nasalis,* is derived from Latin, *nasus,* for nose, and is in reference to the exceptionally large nasal bones of this species.

DESCRIPTION. Skull. The description and reconstructions (Figs. 3, 5, 8) of the skull of *Pithanodelphis nasalis* are composites, being based on all the available skulls. The holotype is the most complete known skull, but unfortunately it is also the most distorted, the braincase being flattened with the basicranium being pushed to the left side. The paratype skull, LACM 26635, although badly shattered, was not distorted by sediment compaction and exhibits the original proportions of the braincase, thus providing information on the undistorted facial surface and true cranium height. Information on the structure of the zygomatic process, rostrum, and palate was obtained mostly from the holotype (LACM 30093). Both the paratype and holotype yielded data on the squamosal and pterygoid regions. Both of these skulls confirmed the confident identification of the paratype partial skeleton, which includes two skull fragments. The referred skull, LACM 15196, from the Modelo Formation, is the only one with the occipital condyles intact. My restoration of the shape of the pterygoid hamulus and its contained fossa for an air sinus is tenuous. The holotype is crushed obliquely in this area, but it preserves the shapes of the pterygoid–palatine suture, the posterior opening of the sinus and the semicircular notch in the lateral lamina of the pterygoid, and shows that the anterior part of the pterygoid sinus is virtually the same width as the posterior part, and that the hamulus is continuously floored by thin bone. The paratype and holotype skulls both show the relationships between the pterygoid and palatine, and the exposure of the vomer between the pterygoid hamuli.

The sample of skulls includes a range of sizes, with the holotype near the mean (Table 1). The paratype skull, LACM 26635, is the largest and has osteological characters indicative of advanced maturity: its crests, tuberosities and nasal bones are prominent.

Characters that indicate that the small skull referred to the species, LACM 123872, is from a juvenile individual are: small size, short postorbital process of the frontal, incompletely formed vomer on the palate between the pterygoids and a cleft between the frontals on the cranial vertex.

Pithanodelphis nasalis has skull proportions like the living freshwater South American stenine delphinids in the genus *Sotalia* Gray, 1866. The facial surface is roughly square, the rostrum is narrow and of medium length with a broad base, and the braincase is highly vaulted with prominent corners, widely flaring zygomatic processes, and a high vertex.

The premaxillae occupy most of the dorsal rostral surface, have dense surface structure, and on the holotype extend only 7 mm anteriorly beyond the maxillae. They are not fused medially but are closely appressed over the midline of the mesorostral gutter at rostral midlength. The rostral part of each premaxilla is transversely convex, becoming flat-lying posteriorly and nearly vertically oriented at the anterior end. The mid-part of each premaxilla is depressed around the premaxillary foramen, but the medial edge next to the mesorostral gutter is elevated. The premaxillary foramina are situated slightly anterior to the location of the antorbital notches and approximately equidistant between the medial and lateral premaxillary margins. A faint anteromedial sulcus extends anteriorly from each premaxillary foramen and converges toward the medial margin, intersecting it at a point nearly one-third of the distance to the anterior end of the rostrum. Medial to this faint groove, the surface of the premaxilla is rugose, and this marks the area of attachment of the nasal plug muscle (Lawrence and Schevill, 1956).

A deeper posterolateral sulcus extends posteriorly from each premaxillary foramen, toward the lateral margin of the premaxilla, reaching it at a point over the middle of the orbit. There is only a very faint posteromedial sulcus. Adjacent to the lateral narial margins the spiracular plates are broad, elevated, and convex. The posterior terminations of the premaxillae narrow abruptly and have a slender posterior projection that is constricted between the maxillae and the swollen nasals. This thin projection is only 1 to 2 mm wide and extends about half the remaining distance posteriorly to the occipital crest between the maxilla and nasal.

On the anterior part of the rostrum the lateral surface of the maxilla has a porous texture and presents a nearly vertical surface adjacent to the alveolar row. The maxilla is thicker posteriorly where it forms a squared margin of the rostrum anterior to the antorbital notch and has only a narrow dorsal surface exposure adjacent to the premaxilla. There are three anterior maxillary foramina around the antorbital notches and above the anterior part of the orbit, and one larger posterior maxillary foramen over the posterior part of the orbit. Two or three small foramina exit from the maxillary–premaxillary suture anterior to the antorbital notch.

On the antorbital process the dorsal surface of the maxilla is thin but rugose. Elsewhere on the facial surface the maxilla is smooth, and its margins are elevated medially adjacent to the nasal and posteriorly along the occipital crest. The posteromedial corner of each maxilla extends around the posterior side of the corresponding nasal bone to encroach on the frontal where it is exposed at the cranial vertex. On all of the skulls, the left maxilla does not extend medially as far as does the right one. On the surface of each maxilla is a low, crescent-shaped ridge extending from the area of the posterolateral side of the nasal toward the temporal fossa. Such ridges undoubtedly mark the attachment of one or more of the layers of the nasal musculature (see Mead, 1975), and are most pronounced on the most mature skull (LACM 26635).

The external nares are narrow anteriorly, wide posteriorly, pass vertically into the skull and are separated by a relatively high, thin mesethmoid septum. The right and left narial passages are equal in size and shape. A circular olfactory foramen, approximately 5 mm in diameter in LACM 26635, is located in the center of the posterior wall of each naris. These foramina are the vestiges of a more primitive condition in which the olfactory lobe of the brain had a major connection with the nasal passages. In some primitive fossil odontocetes (e.g., *Zarhachis* Cope, 1868; *Squalodon* Grateloup, 1840; *Argyrocetus* Lydekker, 1894; *Eurhinodelphis* du Bus, 1867) the mesethmoid and ectethmoid bones are distinct and divide the primitively single olfactory fontanelle into two apertures. In Recent delphinids the mesethmoid and ectethmoids are fused into one solid plate and only tiny perforations remain in some individuals and taxa to represent the olfactory foramina (see Kellogg, 1928:199–202). *Pithanodelphis nasalis* demonstrates an intermediate condition in which the mesethmoid and ectethmoids are fused but the olfactory foramina are still relatively large.

There is no prominent suture between the mesethmoid and nasal bones, and the posterior walls of the narial passages merge smoothly with the vertical anterior surfaces of the very bulbous nasals. A large, basin-like depression is on the midline of the anterodorsal surfaces of the nasals. The nasals are separated posteriorly by two vertical, median wedges of the frontals. The frontals are also exposed on the vertex behind the nasals, where they extend as wedges between the nasals and the maxillae, and between the maxillae and the supraoccipital. The nasal bones are proportionally larger than in any other known delphinoid species. On all specimens the left nasal is slightly lower and wider than the right. The suture separating the two nasals bends to the right of the midline of the braincase posteriorly, and the posterior ends of the nasals, therefore, are shifted slightly to the right side of the skull. In derived living odontocetes with asymmetrical cranial vertices, the displacement of the nasal bones is always to the left.

The occipital shield has an unusual conformation for a delphinoid (Fig. 10). The occipital condyles, preserved only on LACM 15196, are separated by a notch ventrally and are relatively small for the skull size (Fig. 8). The occipital crest and the laterally located lambdoidal crests are large and flare posteriorly to outline the occipital shield, which is inclined anterodorsally, has a generally convex surface, and bears a sulcus dorsal to the foramen magnum. The temporal fossae wrap posteriorly around the occipital shield to such an extent that there is no more than a 50 to 60 mm distance between the right and left lamboidal crests across the posterior surface of the cranium (Fig. 10). The exoccipital is thin, vertically oriented, and flares anterolaterally where it is appressed to the posterior surface of the squamosal. On no specimen is the paroccipital process complete. The posterior side of the right maxilla protrudes farther posteriorly and therefore pushes the occipital shield further posteriorly than does the left maxilla.

The ventral surface of the rostrum is slightly up-curved anteriorly and the palatal surface is generally flat except where it becomes slightly convex posteriorly near the palatine bones. The extent of palatal exposure of the vomer between the maxillae varies in the sample. On the holotype it is about 35 mm long, but on the referred skull LACM 123872 it is 50 mm long. At the anterior end of the exposed vomer the premaxillae appear on the palate medial to the maxillae. They increase in width anteriorly, so that within a distance of 55 mm, the maxillae are entirely excluded from between the alveolar rows.

The largest teeth are in the middle part of the tooth row, where the alveoli are about 5 mm in diameter, and the anterior and posterior ones are progressively smaller. The alveoli are circular with the bone around them raised and rugose. At the anterior rostral extremity, the alveolar rows are very close together. They gradually diverge posteriorly until they are 52 to 55 mm apart at their posterior ends. In specimens with complete tooth rows, the number of upper teeth on each side varies from 27 to 30. In the available

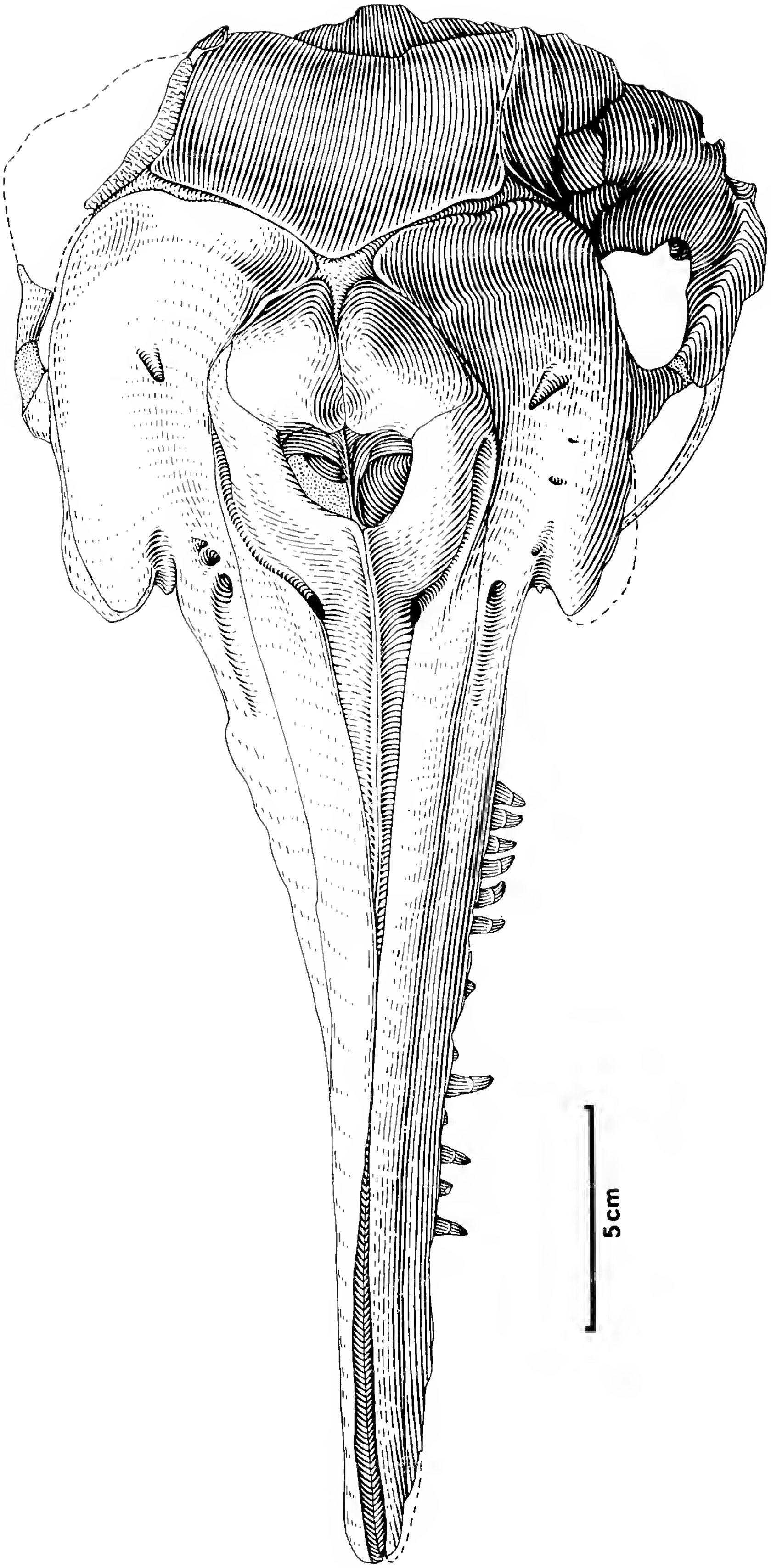


Figure 1. *Pithanodelphis nasalis*, new species, holotype, skull, LACM 30093, LACM locality 5077, dorsal view.

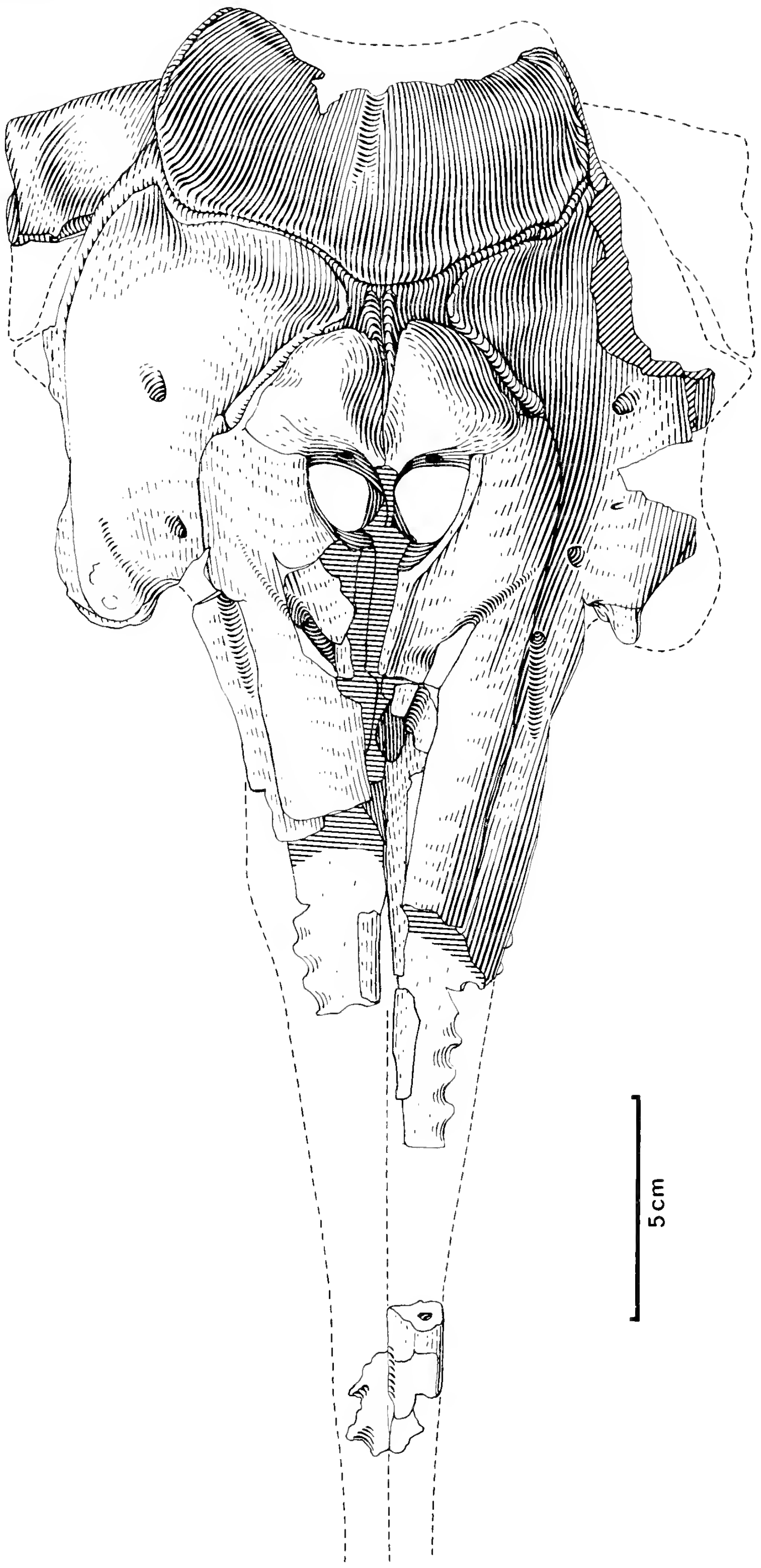


Figure 2. *Pithanodelphis nasalis,* new species, paratype, skull LACM 26635, LACM locality 5069, dorsal view.

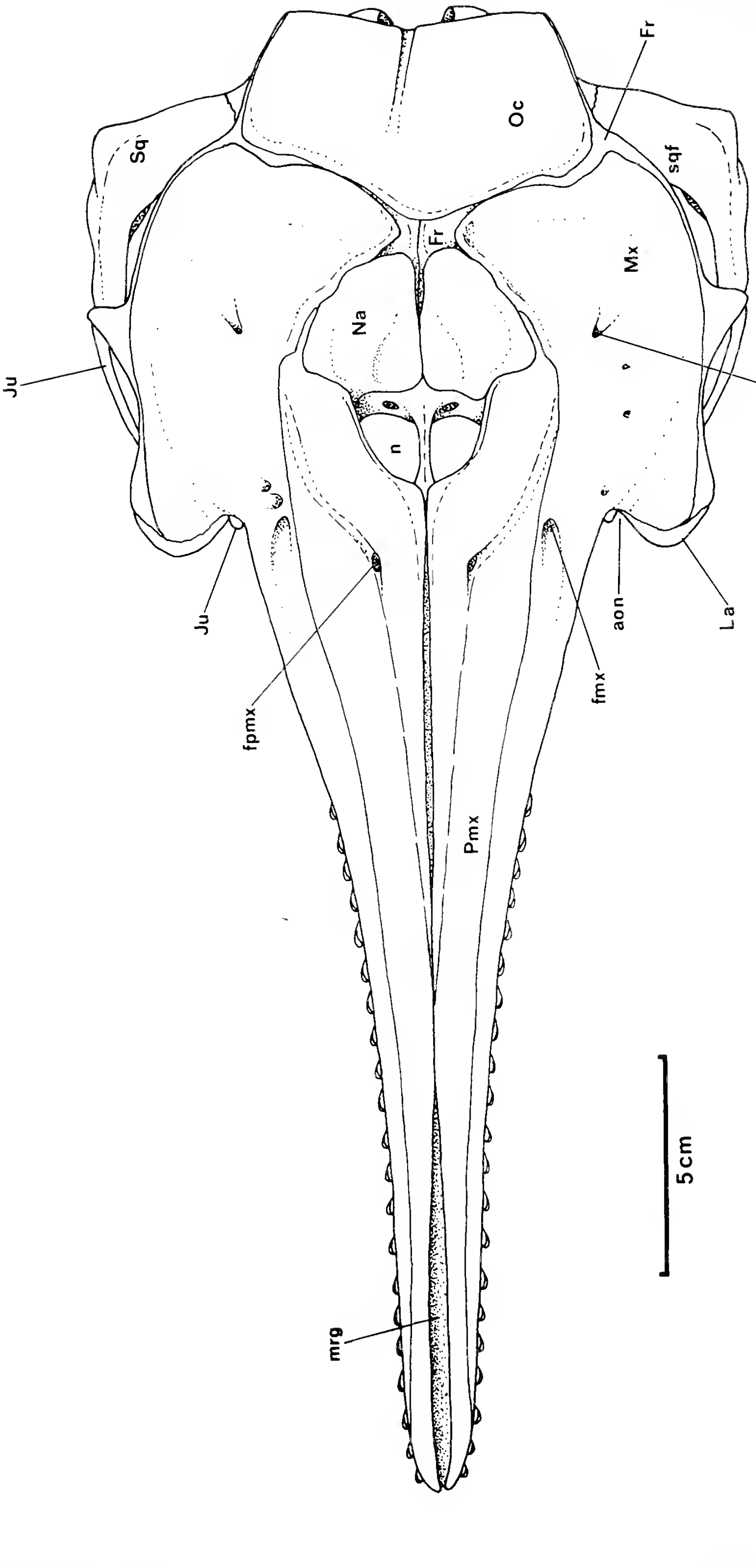


Figure 3. *Pithanodelphis nasalis,* new species, composite reconstruction of skull, dorsal view, based on available specimens; for explanation of abbreviations see Methods and Materials.

sample, the posterior part of the dentition is variable in the following ways. The alveolar row stops at variable distances from the antorbital notch, and this accounts for the above-mentioned variation in the tooth count. In the holotype, LACM 30093, the posteriormost alveoli are significantly smaller than in the paratype, LACM 26635, and in the referred skull, LACM 123872. Some of the specimens show crowding of the posterior teeth, so that in some cases two adjacent alveoli merge.

A palatine foramen in each maxilla near the exposed vomer is confluent with a groove that extends anteriorly and converges on the midline. A larger, less well defined groove on each maxilla originates at the maxillary–palatine suture and extends anteriorly to converge on the midline of the palate. The palatine bones, marked by arc-shaped sutures, extend anteriorly on the palate to a point varying between 14 and 19 mm anterior to the level of the antorbital notches. The maxillae extend posteriorly between the palatines at the midline, between the pterygoid sinus fossae. On the paratype skull (LACM 26635) the vomer descends between the palatines to form a thin, deep keel that extends posteriorly between the nares. The palatines form the sides and roof of the fossae for the pterygoid sinuses, which are shallow, triangular, and pointed anteriorly. Parts of the thin, non-porous pterygoid bone which floored the sinuses are preserved on the holotype skull (LACM 29087). In this area, the bone is very crushed but I can discern a hamular process and a semicircular notch in the lateral lamina of the pterygoid.

The vomer forms a very thin keel separating the nares and it underlies the basisphenoid bone as a thin horizontal plate, extending posteriorly as far as the cranial hiatus. Posterior to this point the basioccipital crest is broken away on all specimens.

Within the orbit there are several foramina. A foramen, elliptical in outline, pierces the lateral wall of the narial passage in the paratype (LACM 26635) and connects with the orbit. The infraorbital foramen is in a position typical of species of Recent Delphinidae—medial to the antorbital notch and near the margin of the pterygoid; but it is smaller, simpler, and not surrounded by struts of bone. The orbital aperture of the foramen is 4 mm in diameter and connects with a branch extending anteriorly within the rostrum to emerge as the premaxillary foramen. Lateral to this, but still confluent with the infraorbital foramen, a smaller foramen connects to the anterior maxillary foramina, and posteriorly another branch leads to the posterior maxillary foramen. A shallow fossa is excavated in the ventral surface of the frontal anterior to, and separated from, the tract of the optic nerve by a thin, elevated crest. This fossa was undoubtedly the location of a small preorbital lobe of the pterygoid air sinus. The sinus did not extend dorsally between the frontal and the maxilla as it does in phocoenids, and, to a lesser extent, in some Recent species of Delphinidae. Another fossa in the frontal bone, posterior to the tract for the optic nerve, marks the site of a postorbital lobe of the pterygoid air sinus (Fraser and Purves, 1960).

The orbit is relatively smaller than in a delphinid such as the Recent common dolphin, *Delphinus delphis* Linnaeus, 1758, but it is still relatively large for a kentriodontid. The antorbital process of the frontal is prominent. The lacrimal bone comprises the anteroventral surface of the antorbital process and its anterolateral part is very thick, but it becomes thin and narrow medially. The lacrimal is wedged into a shallow depression in the ventral surface of the maxilla medial to the antorbital notch. The jugal is fused to the anterior edge of the lacrimal and protrudes into the middle of the antorbital notch, thereby forming a small eminence. This eminence is particularly well preserved on the right side of the holotype (LACM 30093). Such an eminence is unusual for a delphinoid, but a similar one occurs in some species of Recent beaked whales (family Ziphiidae).

The left jugal of the holotype is entirely preserved and appears to retain its approximate original curvature. It measures approximately 80 mm in curvilinear length, is slender and round in cross section anteriorly, and is flattened transversely in its posterior part where it contacts the zygomatic process of the squamosal. It articulates with the squamosal on a small, anteriorly directed process on the ventral margin of the zygomatic process that is in a position similar to that in *Delphinus delphis.*

The temporal fossa is very large, elongate and expanded dorsoventrally. Its anterior part is overhung by the frontal and maxilla. The postorbital process of the frontal is large, tapered, and extends posteroventrally to contact the end of the zygomatic process of the squamosal. Within the posterior part of the temporal fossa the surface of the parietal protrudes laterally. The zygomatic process of the squamosal is large, deep dorsoventrally, and approximately 55 mm long, measuring from the suture with the exoccipital to the anterior extremity. It does not diverge at an angle from the braincase as in most living species of Delphininae, but, more like the monodontids, has its long axis parallel to the midline of the skull. Because the zygomatic process is set far laterally on the cranium, there is a wide squamosal fossa between that process and the lateral wall of the braincase. This squamosal fossa forms a broad and concave floor of the temporal fossa and has a thin and upturned anterior margin.

Distinctive characters of the zygomatic process of *P. nasalis* are its narrow dorsal edge and prominent and square posterolateral corner lateral to the paroccipital process. The latter serves to buttress the glenoid fossa in the area posterior to the nearly vertical postglenoid process. The fossa for the middle air sinus, medial to the glenoid fossa, is partly underhung by a thin, medial extension of the glenoid articular surface for the mandible. A sharp, anteromedially directed crest of bone separates this fossa from the cranial hiatus (which held the ear bones). The homologous crest in most other species of dolphins is developed into the elongate styliform process that descends from the skull, but no indication of such a process is present on any skull of *P. nasalis.* A small foramen (approximately 1 mm in diameter and which can be probed with a needle to a depth of several mm) enters the squamosal dorsal to the position of the external acoustic meatus. The foramen is present on the paratype and holotype of *P. nasalis,* and apparently is characteristic of this species, although its homology and function are unknown. Posterior

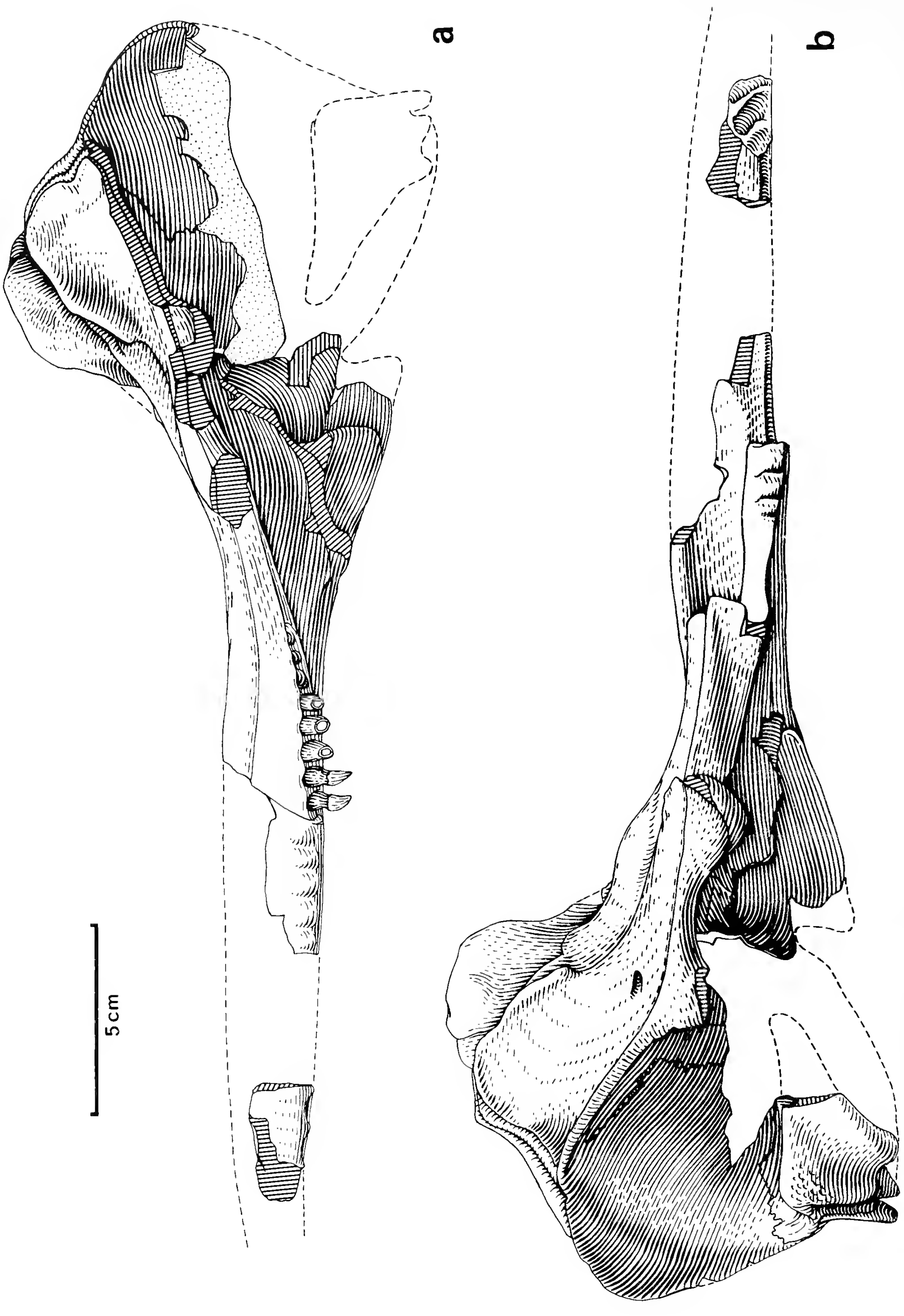


Figure 4. *Pithanodelphis nasalis*, new species, paratype skull, LACM 26635, LACM locality 5069; **a**, left lateral view; **b**, right lateral view.

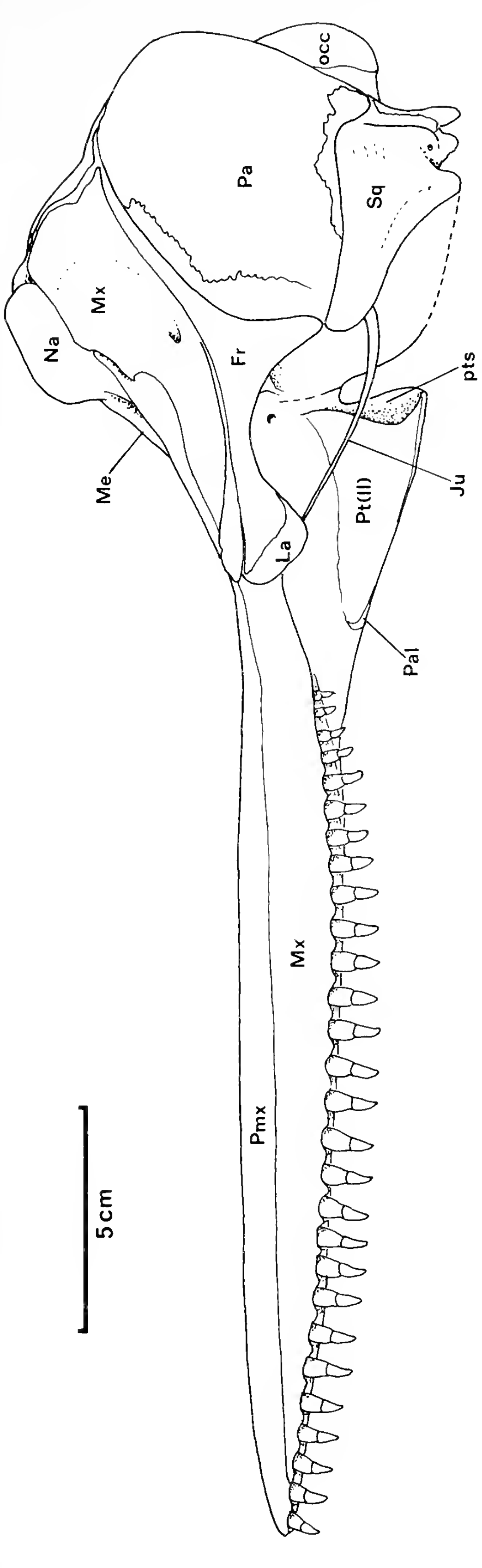


Figure 5. *Pithanodelphis nasalis*, composite restoration of skull based on available specimens, left lateral view; for explanation of abbreviations see Methods and Materials.

to the glenoid fossa, on the ventral surface of the squamosal, the location of the external acoustic meatus is marked by a broad groove that is oriented transversely. A ventrally projecting part of the squamosal forms the posterior wall of this groove, and is itself separated from the exoccipital by a fissure.

Some ontogenetic changes can be noted within the available sample of skulls. Aside from obvious size increase these include: relative enlargement of the nasal bones and corresponding deepening of the depression between them anteriorly, fusion of the lateral margins of the premaxillae to the maxillae in the area of the spiracular plates around the nares, increase in prominence of the occipital and lambdoidal crests, and increase in thickness of the lateral part of the maxilla anterior to the antorbital notch.

Periotic. One of the two known periotics of *P. nasalis* is the left one from the holotype (LACM 30093). The other (LACM 122670) was found isolated. The cochlear portion of the holotype periotic is crushed in its ventral and medial sections, but the bone is otherwise intact. The periotic of *P. nasalis* is notable by its compact appearance, i.e., the cochlear portion is not prominent, the anterior and posterior processes are small and do not project prominently from the bone, and the whole periotic is somewhat flattened dorsoventrally. In general proportions, absolute size, and relative positions of structures, the periotics of *P. nasalis* somewhat resemble those of an earlier, problematic fossil odontocete, *Lamprolithax simulans* Kellogg, 1931, a species that is known only by isolated periotics from the Middle Miocene age Sharktooth Hill Bonebed in California. These two species show differences of at least generic magnitude, however, and *P. nasalis* has a relatively smaller cochlear portion with a smaller internal acoustic meatus. In *P. nasalis* the cochlear portion is not tilted so much anteriorly and does not have as prominent a crease where it meets the medial surface of the anterior process, the cerebral surface of the periotic lateral to the cochlear portion is smoother and flatter, and the extremity of the anterior process bends dorsally rather than ventrally. Specimens of *L. simulans* (see Kellogg, 1931:figs. 119, 120) have a sinuous, elevated cerebral surface lateral to the cochlear portion, a more distinct and circular fossa for the head of the malleus, and an articular facet for the tympanic bulla which is three-sided, flattened posteriorly, and has an extremity which bends more laterally than posteriorly. In contrast, the periotic of *P. nasalis* has a four-sided posterior articular surface (produced by acquisition of a corner on the lateral edge) and the extremity of the posterior process points posteriorly.

Unusual features of the *P. nasalis* periotic are an eminence on the cochlear portion between the *fenestra rotunda* and the cerebral orifice of *aquaeductus cochleae,* a prominent crest on the posteromedial margin of the internal acoustic meatus, the small size of the meatus, and the small, pointed anterior process. The latter two characters, and the orientation of the meatus, being twisted anteromedially, are similar to the periotic of the holotype of the lophocetine kentriodontid *Lophocetus calvertensis* (Harlan, 1842) (see Barnes, 1978:fig. 1k),

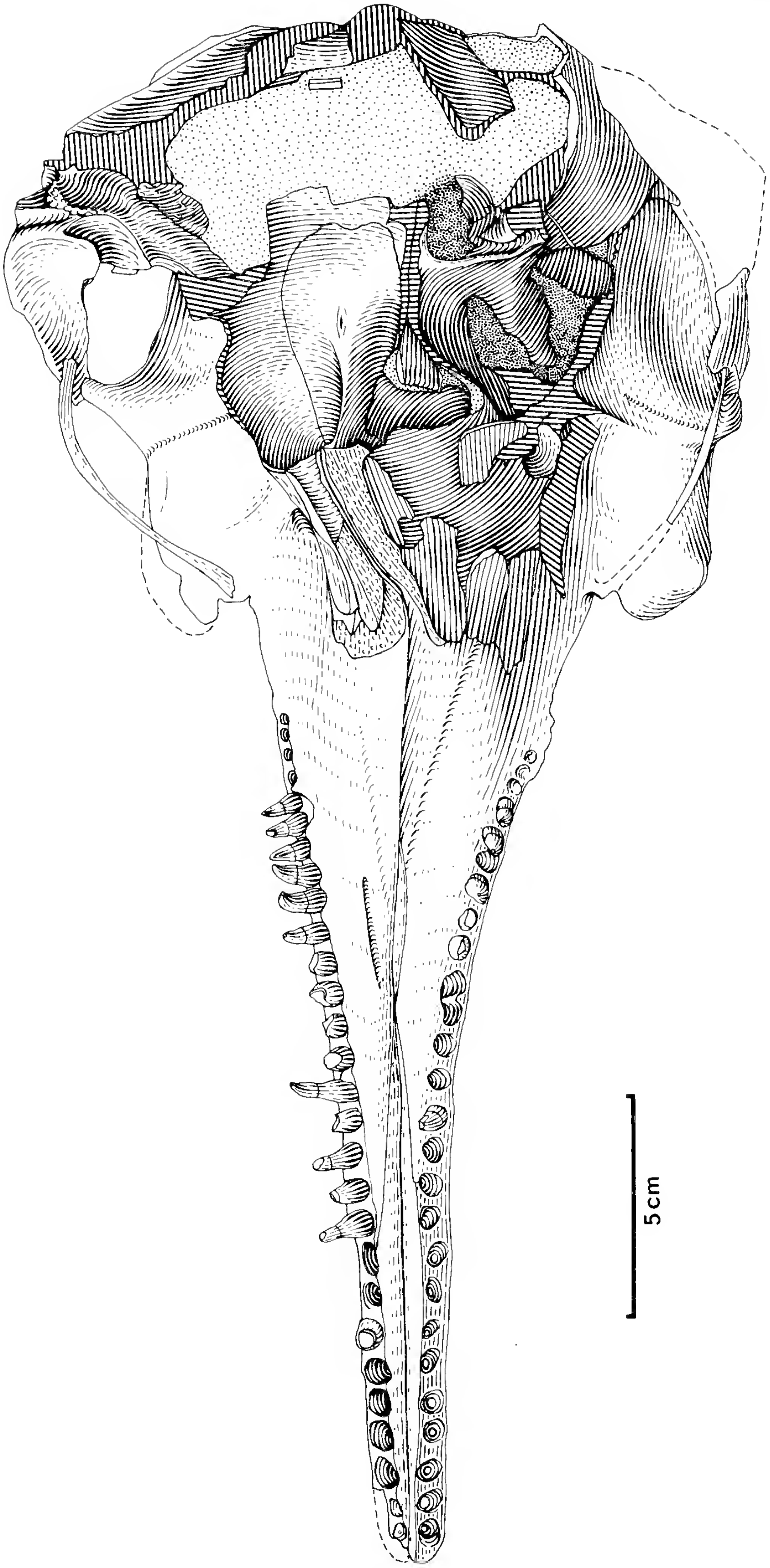


Figure 6. *Pithanodelphis nasalis*, new species, holotype, skull, LACM 30093, LACM locality 5077, ventral view.

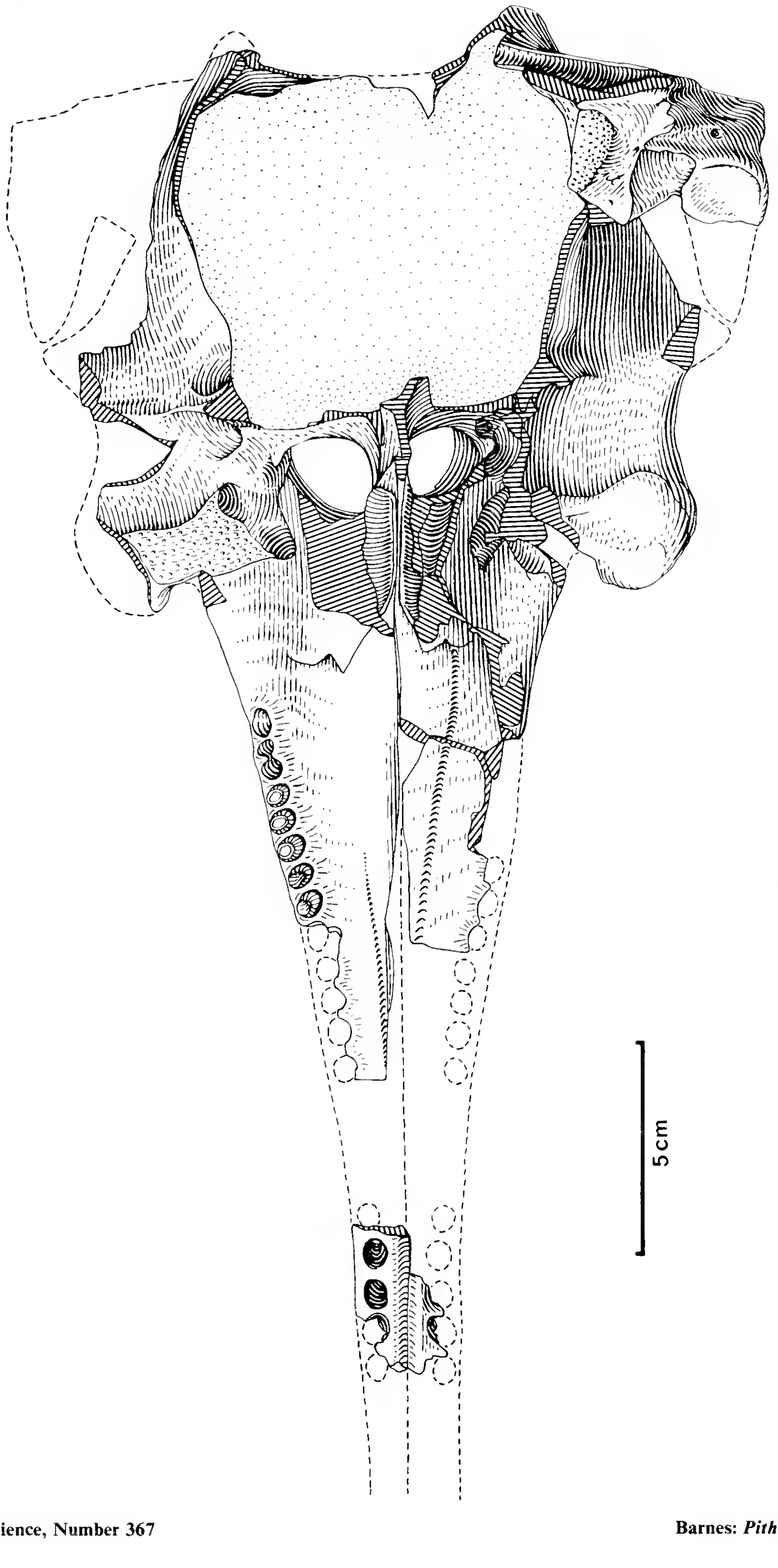


Figure 7. *Pithanodelphis nasalis*, new species, paratype, skull, LACM 26635, LACM locality 5069, ventral view.

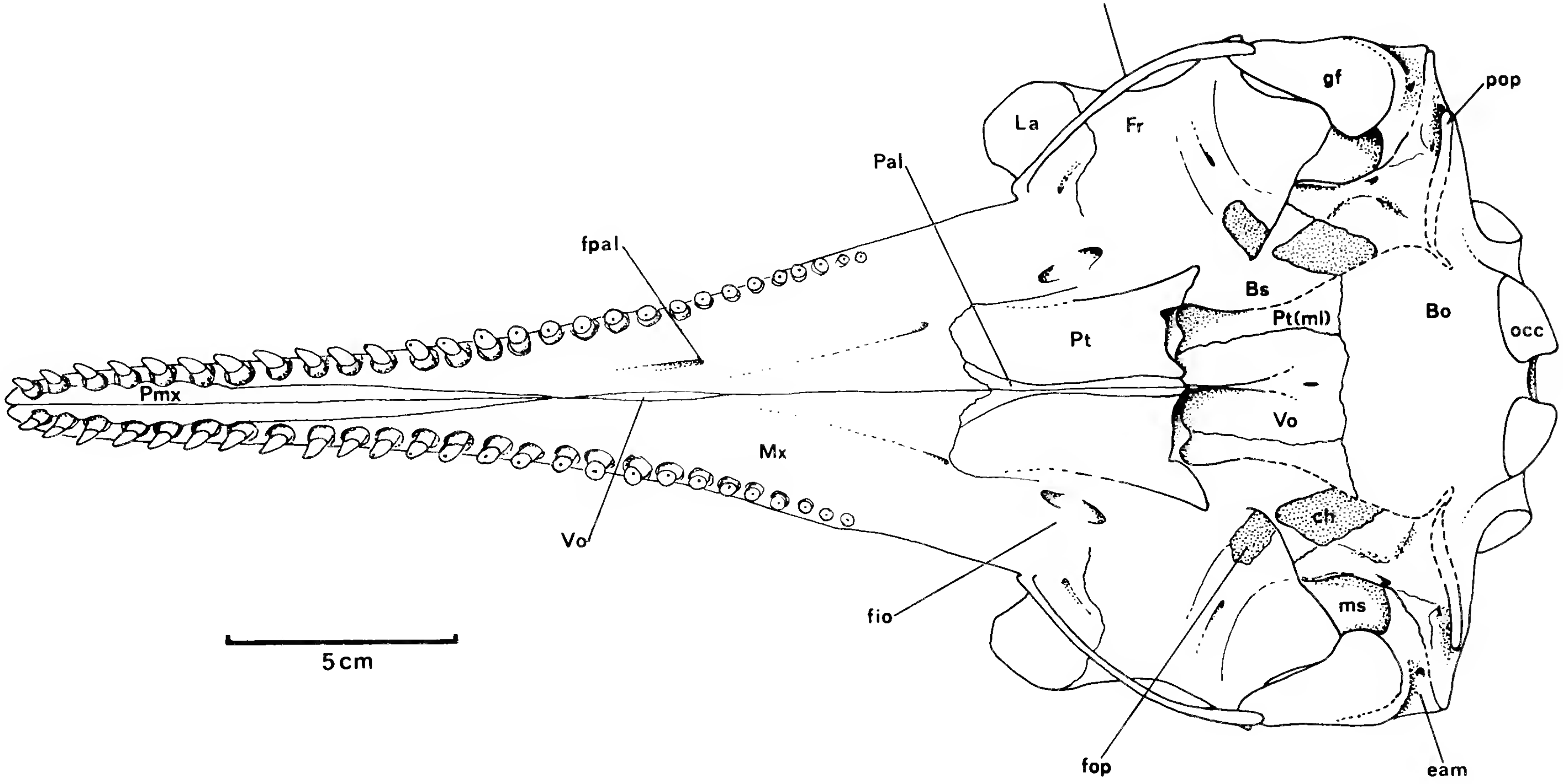


Figure 8. *Pithanodelphis nasalis,* new species, composite reconstruction of skull based on available specimens, ventral view; for explanation of abbreviations see Methods and Materials.

and might indicate some type of evolutionary relationship between *Pithanodelphis* and *Lophocetus* Cope, 1867.

Tympanic bulla. Both tympanic bullae preserved with the holotype are crushed and incomplete. The involucrum is wide and massive compared with living dolphins in the genera *Delphinus* Linnaeus, 1758, or *Stenella* Gray, 1866, and, in its proportions, more resembles those of living porpoises in the genera *Phocoena* Cuvier, 1817, or *Phocoenoides* Andrews, 1911. On the ventral surface of the bulla the posterior end of the involucrum is large and bulbous, the longitudinal groove is broad and shallow, and a transverse constriction separates the anterior and posterior parts. The anterior lip of the bulla is rounded and there is no elongate styliform process at the aperture of the auditory tube (eustachian tube in part). The sigmoid process is bulbous and the posterior process has an elongate projection posterior to the articular facet for the periotic.

Ossicles. The malleus, incus, and stapes (Figs. 11e–f) were found in the matrix near the left periotic and bulla of the holotype of *Pithanodelphis nasalis.* Ossicles are rarely found and described for fossil cetaceans, but fortunately, the same elements have been described for the holotype of *Kentriodon pernix* (see Kellogg, 1927:28–31, figs. 8–20), and the two species may be compared. The anterior process of the malleus, which in life was fused to the bulla, is incomplete (Fig. 11f), and might have been as large as in *K. pernix.* Compared with *K. pernix,* the tubercle on the malleus of *P. nasalis* is longer and the oblique groove cited by Kellogg is deeper. This groove leads to a foramen (*fovea lateralis*) for the *chorda tympani* nerve that transects the bone from the juncture of the two facets for the incus to the opposite (ventral) side.

The *crus breve* was broken off of the incus. The *crus longum* is shorter and wider than that of *K. pernix,* and the body of the bone has wider articular facets for the malleus. The facet for articulation with the stapes protrudes farther from the side of the *crus longum* than in *K. pernix.*

The stapes of *P. nasalis* differs from that of *K. pernix* by having a larger foramen (intercrural aperture), a wider head, a more uniformly oval-shaped footplate, a smaller scar for insertion of the stapedius muscle, and a more elongate facet for the incus which is not set so obliquely on the bone.

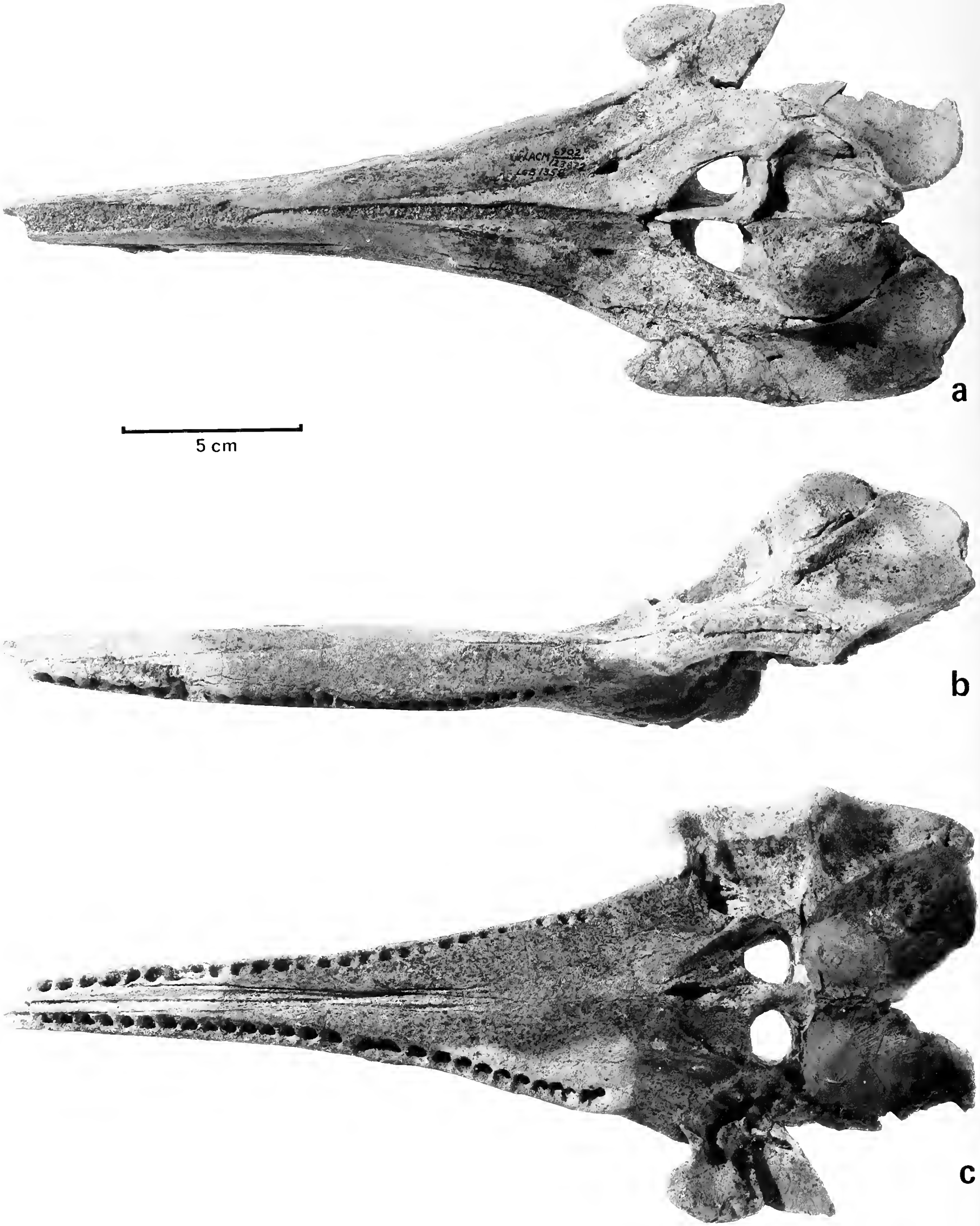
The ossicles have been described for a more distantly related, but contemporaneous fossil delphinoid, the primitive phocoenid, *Salumiphocaena stocktoni* (Wilson, 1973) (see Barnes, 1977, 1984, 1985). That species has a malleus with a wider anterior process and a shorter tubercle, and an incus with a very reduced *crus breve* (Wilson, 1973:figs. 8a–d). Based on comparisons of the ossicles of the three species, *Pithanodelphis nasalis, Kentriodon pernix,* and *Salumiphocaena stocktoni,* the former is the most primitive and the latter is the most derived.

Mandible. Some oblique displacement of the right and left dentaries shows that although the two sides were joined by an extensive, rugose symphysis, they were not ankylosed. The symphysis amounts to 40 percent of the length of the mandible. The holotype bears alveoli for 22 teeth in the left dentary, and 21 in the right, of which eight were posterior to the symphysis in the left dentary and seven in the right.

Table 1. Measurements (in mm) of skulls of *Pithanodelphis nasalis,* new species. Parentheses indicate estimated measurements.

	LACM 30093 Holotype	LACM 26635 Paratype	LACM 123872
Length of rostrum (2)	216	—	185
Width of rostrum at base (3)	78.5	87.5	73
Width of rostrum at midlength (5)	28	—	26
Width of premaxillae at midlength of rostrum (6)	17	—	17
Greatest preorbital width (10)	(127)	(145)	(115)
Greatest postorbital width (11)	(145)	(156)	(115)
Least supraorbital width (12)	125	(138)	112
Greatest width of external nares (13)	33	37.5	33
Greatest width across zygomatic processes of squamosals (14)	(146)	166	—
Greatest width of premaxillae (15)	64.5	80	68
Greatest parietal width, within temporal fossae (16)	79	99	—
Length of temporal fossa (19)	(85)	(82.5)	—
Width of temporal fossa (20)	(65)	68.5	—
Length of orbit (25)	(45)	47	—
Length of antorbital process of lacrimal (26)	20	21	15.5
Length of tooth row (32)	188	—	168
Number of teeth—left tooth row (33)	28	—	30
Number of teeth—right tooth row (34)	26	—	30

The tooth-bearing portion of each dentary is broad dorsally, narrowly keeled ventrally, and bears two or three mental foramina spaced along its lateral surface. The mandible is slender and slightly up-turned anteriorly, and has a deeper, somewhat keeled profile in the posterior symphyseal region. Posterior to the alveolar rows the dentary expands dorsally and ventrally and the bone in this part is thin and more delicate. The posterior end of the coronoid process is directed posteriorly and is separated by a concave mandibular notch from the condyle. A slightly elevated coronoid crest 45 mm posterior to the end of the alveolar row is turned slightly laterally. The angle of the mandible extends farther posteriorly than does the coronoid process, but not farther than the condyle. The condyle has a lateral buttress, is excavated medially, and, when viewed posteriorly, has a vertical medial margin and a convex lateral margin. On the medial surface of the dentary, the anterior margin of the large mandibular foramen extends to about the midlength of the post-symphyseal portion. The opening of this foramen (the mandibular fossa) extends nearly from the dorsal to the ventral margin of the inner surface of the dentary.


LACM 6902/23872
a
5 cm
b
c

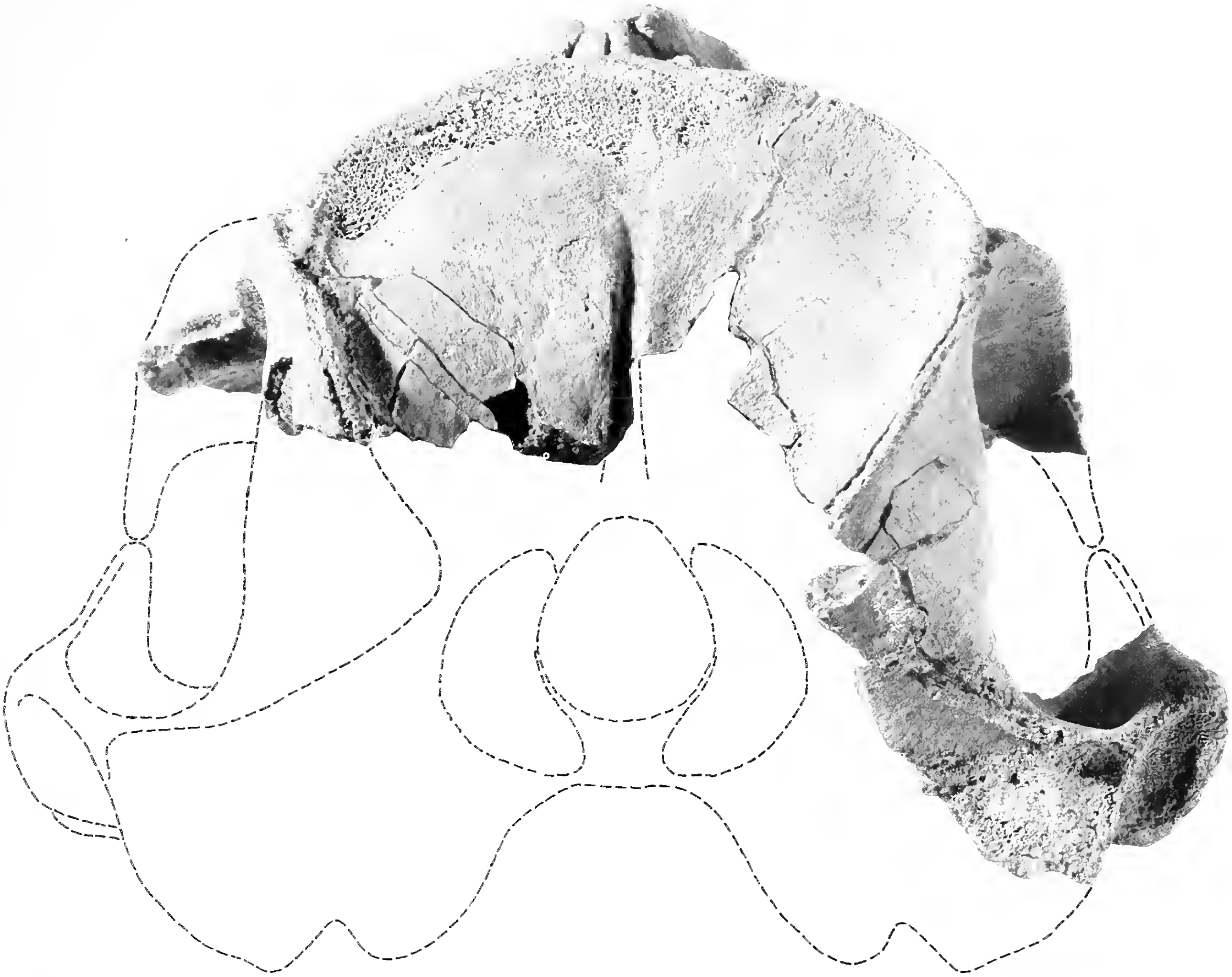


Figure 10. *Pithanodelphis nasalis,* new species, paratype, LACM 26635, LACM locality 5069, posterior view, missing parts indicated by dashed outline, natural size.

In the symphyseal portion of the mandible, the alveolar rows are nearly parallel. They begin to diverge abruptly at the posterior end of the symphysis. Interalveolar septa are comprised of cancellous bone and are recessed between prominent labial and lingual borders of the alveolar row. Except for the posteriormost one or two, all of the alveoli are about 4 or 5 mm in diameter and are directed dorsolaterally.

The mandible of *Kentriodon pernix* differs from that of *P. nasalis* by being more slender and more elongate, having a relatively shorter symphysis, a larger mandibular fossa and nearly twice as many teeth. The only known mandible of *Delphinodon dividum,* that of the holotype, is incomplete, missing its anterior end. Compared with *P. nasalis,* it appears to have had a shorter symphysis and it has a higher, less posteriorly projecting coronoid process, a larger mandibular fossa, and more teeth in that part of each dentary which is posterior to the symphysis.

Teeth. The dental formula on each side in *P. nasalis* is 26–30/21–22. The teeth in the middle parts of both the maxillae and dentaries are approximately 15 mm to 20 mm long, and the anterior and posterior ones are shorter. Each tooth has a smooth, conical, enamel-covered crown that is curved lingually at the apex. Teeth in the anterior and middle parts of the alveolar row have nearly vertical crowns; the more posterior ones have crowns that are shorter and more curved lingually. All crowns bear a proximal lingual bulge that is most prominent on the posterior teeth. The roots taper proximally, bend posteriorly and are bulbous below the gum line (due to added outer layers of cement). No tooth in any of

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Figure 9. *Pithanodelphis nasalis,* new species, referred specimen, skull, LACM 123872, LACM locality 6902; **a**, dorsal view; **b**, left lateral view; **c**, ventral view.

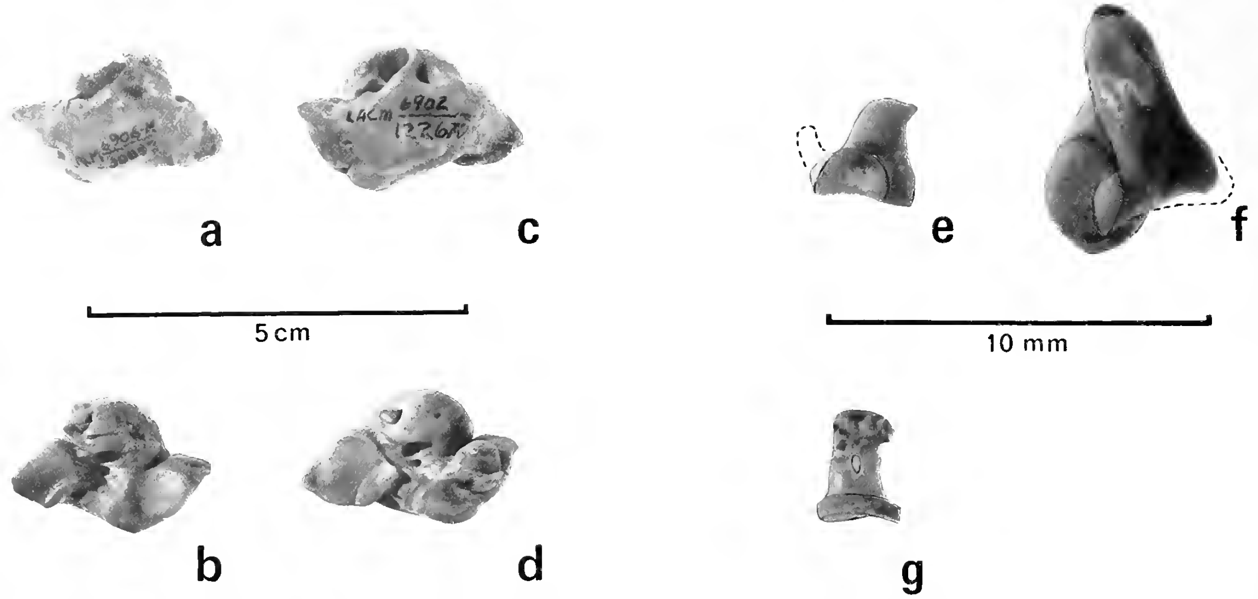

Figure 11. *Pithanodelphis nasalis,* new species, left periotics and ossicles: holotype periotic, LACM 30093, LACM locality 5077; **a,** cerebral or dorsal view; **b,** tympanic or ventral view; referred periotic, LACM 122670, LACM locality 6902; **c,** cerebral or dorsal view; **d,** tympanic or ventral view; holotype ossicles, LACM 30093, LACM locality 5077; **e,** malleus, dorsomedial view; **f,** incus, ventral view; **g,** stapes, posterior view; **a-d,** natural size, **e-g,** ×5.

the skulls shows an open pulp cavity, indicating that the large skulls are all of adults. There is no anteriorly directed, tusk-like premaxillary tooth as in *Kentriodon pernix* (see Kellogg, 1927:pls. 2, 4, 5; Barnes and Mitchell, 1984:fig. 14a).

Vertebrae. The vertebral column of the paratype skeleton (LACM 29087) is not complete, but includes the seventh cervical, the first through sixth thoracic, the last three lumbar, and 25 caudal vertebrae. Apparently there were at least one and possibly two or three additional terminal caudal vertebrae that were not preserved. An unknown number of thoracic and lumbar vertebrae were lost when the skeleton was exposed by a trenching machine.

The spinous processes and the non-rib-bearing transverse processes of these vertebrae are moderately elongate and flat. They are not significantly expanded distally, as is the case in some fossil and living odontocetes (see the unrelated, Recent *Pontoporia blainvillei* (Gervais and d'Orbigny, 1844), for example). The pedicles of the neural arches tilt anteriorly and are positioned anteriorly on the centra. The pedicles of the lumbar and anterior caudal vertebrae are thinner and flatter than those of the thoracic vertebrae. The transverse processes on the thoracic vertebrae are knob-like distally and have shallow foveae for attachment of ribs. At least as far posteriorly in the body as the sixth thoracic vertebra, the capitulae and tuberculae of the ribs were widely separated, judging by the distance between their respective foveae on the vertebrae. The transverse processes of the posterior lumbar and anterior caudal vertebrae are positioned at mid-height on the centra. Starting at the seventh caudal and continuing posteriorly, each vertebra has a vertebrarterial canal on each side, located posterior to the middle of the centrum. Caudals seven through twelve retain spinous and transverse processes, and in each of these vertebrae the canal pierces the transverse process and is positioned ventral to the posterior edge of the pedicle of the neural arch. After the twelfth caudal, the vertebrae lack spinous and transverse processes, and become progressively more rectangular in shape posteriorly. The eighteenth caudal vertebra is significantly more expanded transversely than the one immediately before it, and has rounded anterior and posterior ends of its centrum. These features indicate that this vertebra was the point of caudal flexion at the anterior margin of the caudal fluke. The vertebrae posterior to this one are expanded transversely. Including the estimated number of missing terminal caudal vertebrae, at least nine vertebrae were originally included within the fluke.

Partial vertebral columns have been described for only two other species of Kentriodontidae; the type specimens of *Kentriodon pernix* (see Kellogg, 1927) and of *Delphinodon dividum* (see True, 1912b). The vertebrae of *Pithanodelphis nasalis* differ from those of *K. pernix* by having spinous processes that are higher and narrower and centra that are more compressed anteroposteriorly and more expanded dorsoventrally. The vertebrae of *Delphinodon dividum* are much more like those of *P. nasalis* in both size and shape. Compared with *P. nasalis,* the spinous processes of *D. dividum* are slightly narrower anteroposteriorly and, in the anterior thoracic region, these processes of *D. dividum* are more nearly vertical and in the anterior caudal region they tilt more anteriorly. The centra of the anterior thoracic vertebrae of *D. dividum* are slightly more compressed anteroposteriorly. Based on these comparisons, the vertebral column of *Pithanodelphis nasalis* is more derived than that of *Kentriodon pernix* and more primitive than that of *Delphinodon dividum.*

At least on the basis of vertebral structure, the living del-

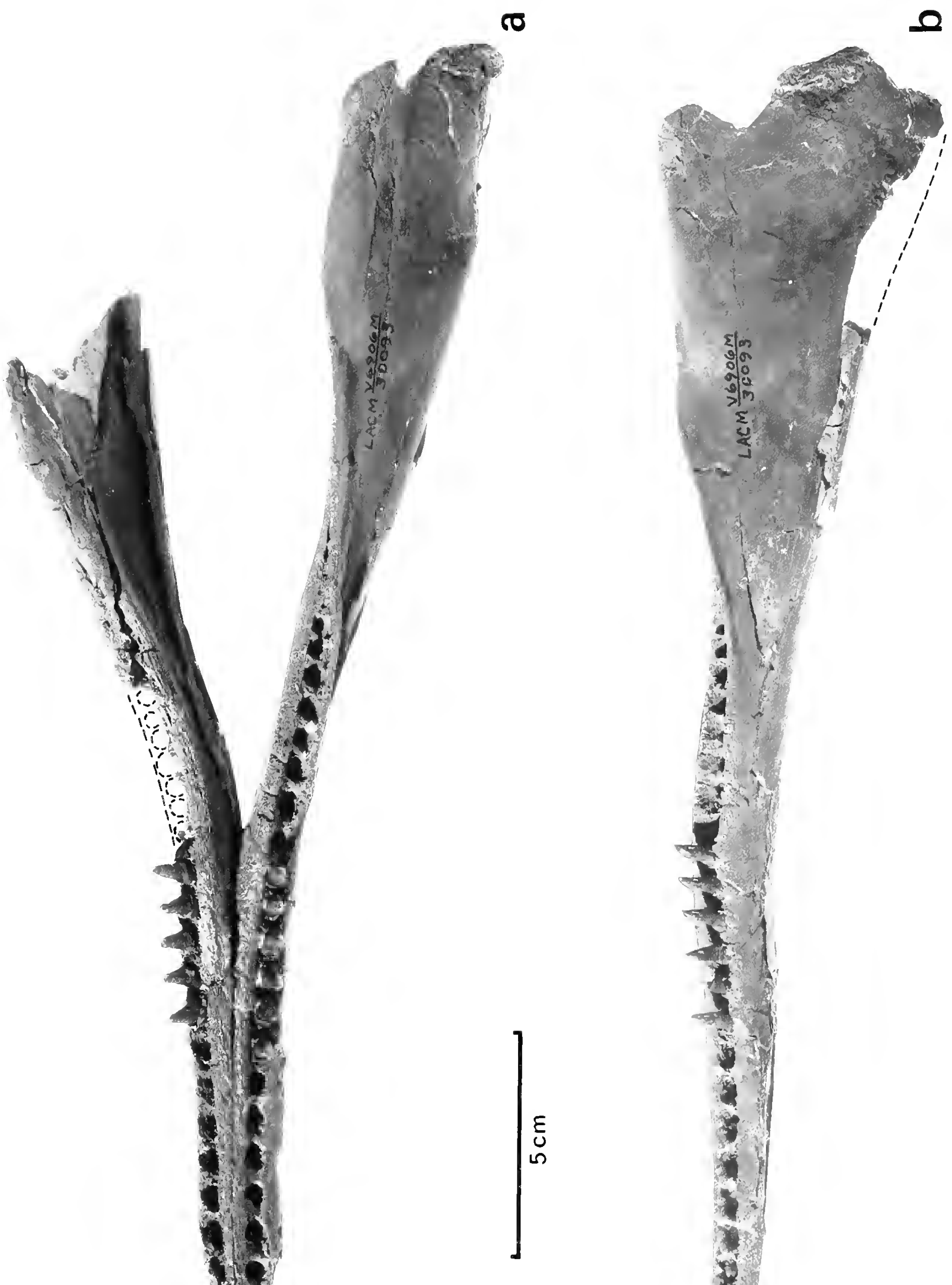

Figure 12. *Pithanodelphis nasalis,* new species, holotype, mandible, LACM 30093, LACM locality 5077; **a,** dorsal view; **b,** lateral view of left dentary.

Table 2. Measurements (in mm) of the holotype mandible, LACM 30093, of *Pithanodelphis nasalis*, new species.

Total length of dentary (38)	(298)
Length of tooth row (37)	(170)
Length of symphysis	(120)
Height at coronoid process (39)	66
Length of mandibular fossa (40)	94
Number of teeth—left tooth row (35)	22
Number of teeth—right tooth row (36)	22

phinid species in the genera *Sotalia* and *Sousa* Gray, 1866, are more primitive than *Pithanodelphis nasalis* in having fewer vertebrae, longer centra, and wide, short spinous and transverse processes. The same is true of otherwise relatively derived living species of delphinids such as the pilot whales, *Globicephala* spp.; false killer whales, *Pseudorca crassidens* Owen, 1846; and killer whales, *Orcinus orca* Linnaeus, 1758.

In vertebral shape and proportions, a close living analog of *P. nasalis* is the bottlenosed dolphin, *Tursiops truncatus* Montagu, 1821. Although it is a larger animal, it is useful for interpreting the vertebrae of the fossil. The paratype of *P. nasalis* probably had 26 to 28 caudal vertebrae and individuals of *T. truncatus* have from 26 to 29 (Nishiwaki, 1963). Both species have approximately nine of these caudal vertebrae within the flukes. In *T. truncatus,* the anteriormost caudal vertebra that bears a vertebrarterial canal is the tenth rather than the seventh as in *P. nasalis.* Caudals amount to 36 percent of the vertebral column in *T. truncatus,* and I presume they comprised approximately the same percentage in *P. nasalis* and that the remainder of the vertebrae in the lumbar, thoracic, and cervical regions of the two species are approximately proportional. Based on the measurements of adult skeletons of *T. truncatus,* I calculated that the vertebral column of the paratype of *Pithanodelphis nasalis* (LACM 29087) was approximately 155 cm long. Estimating that it had a skull the length of that with the holotype (LACM 30093), and adding another cm for flesh covering the tip of the rostrum, the probable total body length of the paratype of *P. nasalis* in life was approximately 192 cm. As evidenced by the large paratype skull, LACM 26635, some individuals attained a larger size, and probably reached a total body length of approximately 200 cm.

DISCUSSION

The Late Miocene species *Phocaenopsis cornutus* was first briefly described by du Bus (1872:500), based on two fragmentary skulls from deposits in the Antwerp Basin, Belgium. The genus to which he referred his species, however, *Phocaenopsis* Huxley, 1859, was originally based only on an isolated humerus from New Zealand which Huxley thought was Pleistocene in age. Fordyce (1981) has subsequently shown that the type species of *Phocaenopsis, P. mantelli,* is Early Miocene in age and that it belongs either in the family Rhabdosteidae (=Eurhinodelphidae) or Squalodontidae. du Bus (1872:499) had also assigned another fossil species, *Phocaenopsis scheynensis* du Bus, 1872, to the same genus, but both of these generic assignments were without sound basis because of the non-comparable nature of the type materials.

Abel (1905:133) transferred *Phocaenopsis scheynensis* to the genus *Acrodelphis* Abel, 1899, and (1905:142) *Phocaenopsis cornutus* to the new genus *Pithanodelphis* Abel, 1905. Abel (1905:140–45, figs. 24–25) identified one of the two skulls described by du Bus as the "original de *Phocaenopsis cornutus,* du Bus." This is the specimen that I now designate as the lectotype of the species. Abel's illustrations of the dorsal and right lateral views of the skull and the accompanying text demonstrate the distinctive characters of the species. du Bus had mentioned no other referred bones of this species, but Abel (1905:figs. 26–27) illustrated fused atlas and axis vertebrae that he referred to the species, and in the diagnosis (p. 143) stated that the atlas and axis were nearly always fused, separate only in one example. In my opinion, Abel's referral of those cervical vertebrae to *Pithanodelphis cornutus* is unfounded, because there are no demonstrated associations with skulls.

The genus *Pithanodelphis* remained monotypic until the present study, and no additional specimens have been referred to the type species. Abel originally classified it in the subfamily Delphininae of the family Delphinidae. True (1912b:192) retained *Pithanodelphis cornutus* in the family Delphinidae and compared it with his new fossil species, *Delphinodon dividum.* Winge (1921) did not contest the familial assignment of *Pithanodelphis,* but did observe that the large medial extensions of the posterior ends of the maxillae behind the cranial vertex was an unusual character when compared with living species in the Delphinidae. (This condition is characteristic of all kentriodontids.) Kellogg (1927) named *Kentriodon pernix* as a new genus and species of delphinid and compared it with *D. dividum.* When Slijper (1936) named the Kentriodontinae as an extinct subfamily of the Delphinidae, he included within it *Kentriodon* and *Delphinodon* and excluded *Pithanodelphis.* Simpson (1945) did not recognize the Kentriodontinae, nor any other extinct or living subfamilies of Delphinidae, but he did list *Delphinodon, Kentriodon,* and *Pithanodelphis* among the extinct genera of the family. I recognized the Kentriodontidae as a separate family (Barnes, 1978:25–26), and classified *Pithanodelphis, Kentriodon, Delphinodon,* and other genera in the nominate subfamily, Kentriodontinae. As a result of the present study, I now recognize substantial numbers of unique, derived features of *Pithanodelphis* that warrant its classification within a separate, new subfamily, the Pithanodelphinae.

I had previously characterized (Barnes, 1978) the family Kentriodontidae, in part, as lacking asymmetry of the cranial vertex, such as exists in all species of Delphinidae (sensu stricto). *Pithanodelphis nasalis* and *P. cornutus* are, however, kentriodontids that do, in fact, have asymmetrical cranial vertices, but the extent of this asymmetry and the ways in which the bones had become modified from the primitive pattern are different from species in the Delphinidae. Among the species of Delphinidae, the pattern of asymmetry and the relationships of the bones that comprise the cranial vertex are very uniform (Barnes, 1978:3), and the unique type of cranial asymmetry of species of *Pithanodelphis* differs in the following ways. The posterior ends of the premaxillae are the same length instead of the right one being longer. Both premaxillae contact the nasals instead of only one. The posterior end of the right premaxilla adjacent to the nares is only 2 to 4 mm wider than the left instead of being approximately twice as wide. The nasal bones are high and peaked, forming the highest part of the cranial vertex, not low and hemispherical and forming the anterior side of the vertex. The spiracular plates are of equal height, rather than the left being more elevated than the right. The area of the cranial vertex that is occupied by the right and left nasals is equal, rather than the left nasal being smaller. The suture between the two nasal bones twists to the right posteriorly, rather than to the left. The mesethmoid septum between the nares lies on the midline of the skull, instead of being offset to the left side. The nares are equal in diameter, rather than the right being larger.

In *Pithanodelphis,* as in species of Delphinidae, the posterior end of the right maxilla extends farther toward the midline than does the left, and the shapes of the right and left halves of the occipital crest are different. *Pithanodelphis* has additional unique, derived characters that differentiate it from Delphinidae: the left nasal bone is lower than the right, a very slender posterior extension of each premaxilla is compressed between the maxilla and the nasal, and the exposed area of the frontals behind the nasals has a shape with five points.

The cranial asymmetry of *Pithanodelphis* is, therefore, of a different nature than that which is found within the Delphinidae and such asymmetry was probably acquired independently in the two groups from different ancestors that had symmetrical cranial vertices. An as yet unnamed, contemporaneous species of true delphinid, which has an asymmetrical cranial vertex of the type seen in living delphinids, has been found in the same part of the Monterey Formation as *Pithanodelphis nasalis* (see Barnes, 1977). The presence of cranial asymmetry, as well as the well-developed spiracular plates around the nares in *Pithanodelphis,* suggest the presence in life of some type of specialized musculature and nasal passage diverticulae. In living odontocetes such structures have been implicated in production of sound that is used in echolocation (see Mead, 1975).

The retention of a fairly large olfactory fontanelle, as in *Pithanodelphis nasalis,* is primitive and is a relatively uncommon occurrence among other species of fossil odontocetes known after Middle Miocene time. Other primitive cranial characters of the species are the large, laterally placed zygomatic process of the squamosal, the long and tapered postorbital process of the frontal, the exceptionally large temporal fossa and the relatively small fossa for the pterygoid sinus in the pterygoid hamulus. The relatively small size of the paroccipital process is a derived character.

Pithanodelphis might have evolved from some taxon within the subfamily Kentriodontinae because, in addition to the family characteristics, it shares with the earlier Middle Miocene species of *Delphinodon* and *Kentriodon* the following characters: wide facial region, intermediate length rostrum with premaxilla extending only a short distance anteriorly beyond the maxilla, elongate postorbital process of the frontal, transversely compressed and otherwise similarly shaped zygomatic process of the squamosal, deep squamosal fossa between the zygomatic process and the braincase, similar distribution of air sinuses, and similar sizes and positions of the basioccipital crests and cranial hiatus. *Pithanodelphis nasalis* more specifically shares with *D. dividum:* a slightly arched rostrum, similar tooth count, small paroccipital process, convex lateral margin of the maxilla over the temporal fossa, zygomatic process of the squamosal with tapered anterior end and projecting posterolateral corner, and similar structure and proportions of vertebrae. Teeth without accessory denticles, and the unusually large nasal bones of *P. nasalis* are derived characters compared with *D. dividum.*

Species in the genus *Lophocetus* also have relatively large nasal bones, but these are shaped differently than those of *Pithanodelphis,* being not significantly higher than the maxillae, and more compressed transversely by them. The periotics of both *Lophocetus calvertensis* (see Barnes, 1978:fig. 1k) and *Pithanodelphis nasalis* share an oddly tapered anterior process, a wide lateral portion and a relatively large internal acoustic meatus that is tilted anteriorly on the cochlear portion. It may be that the contemporaneous Late Miocene species of *Pithanodelphis* and *Lophocetus* had closely related Middle Miocene ancestors within the subfamily Kentriodontinae, such as the derived kentriodontine genus *Delphinodon,* and evolved in divergent ways.

Pithanodelphis nasalis and *P. cornutus* are the only species assigned to the genus *Pithanodelphis.* Each species has a different combination of primitive and derived characters. My interpretation of the polarity of these characters is based on the anatomy of much more primitive Odontoceti such as species in the families Agorophiidae, Squalodontidae and in the kentriodontid subfamily Kampholophinae. The more derived characters of *P. cornutus* include its reduced cranial crests and more rounded, convex occipital shield. The derived characters of *P. nasalis* include its larger nasal bones and smaller, more tapered zygomatic processes of the squamosals.

There are very few previously named fossil odontocetes of Late Miocene age from the North Pacific realm (Barnes, 1977), and most are known only by one specimen. In the existing fossil cetacean collections of this age that have been obtained from southern California deposits, however, *Pithanodelphis nasalis* is the most abundant odontocete species and is now represented by seven specimens that are mentioned in this study. This is also the largest published sample of skulls of any kentriodontid species. Such a relatively good sample could, of course, be attributed to a collecting bias, but six of the seven specimens came from a relatively small geographic area in Orange County and from a restricted stratigraphic interval in the Monterey Formation from which virtually all noticeable vertebrate fossils, ranging from single bones to complete skeletons, were collected and prepared. The only specimen of *P. nasalis* recorded in this study that is not from the Monterey Formation in Orange County is from the Modelo Formation in the Santa Monica Mountains of Los Angeles

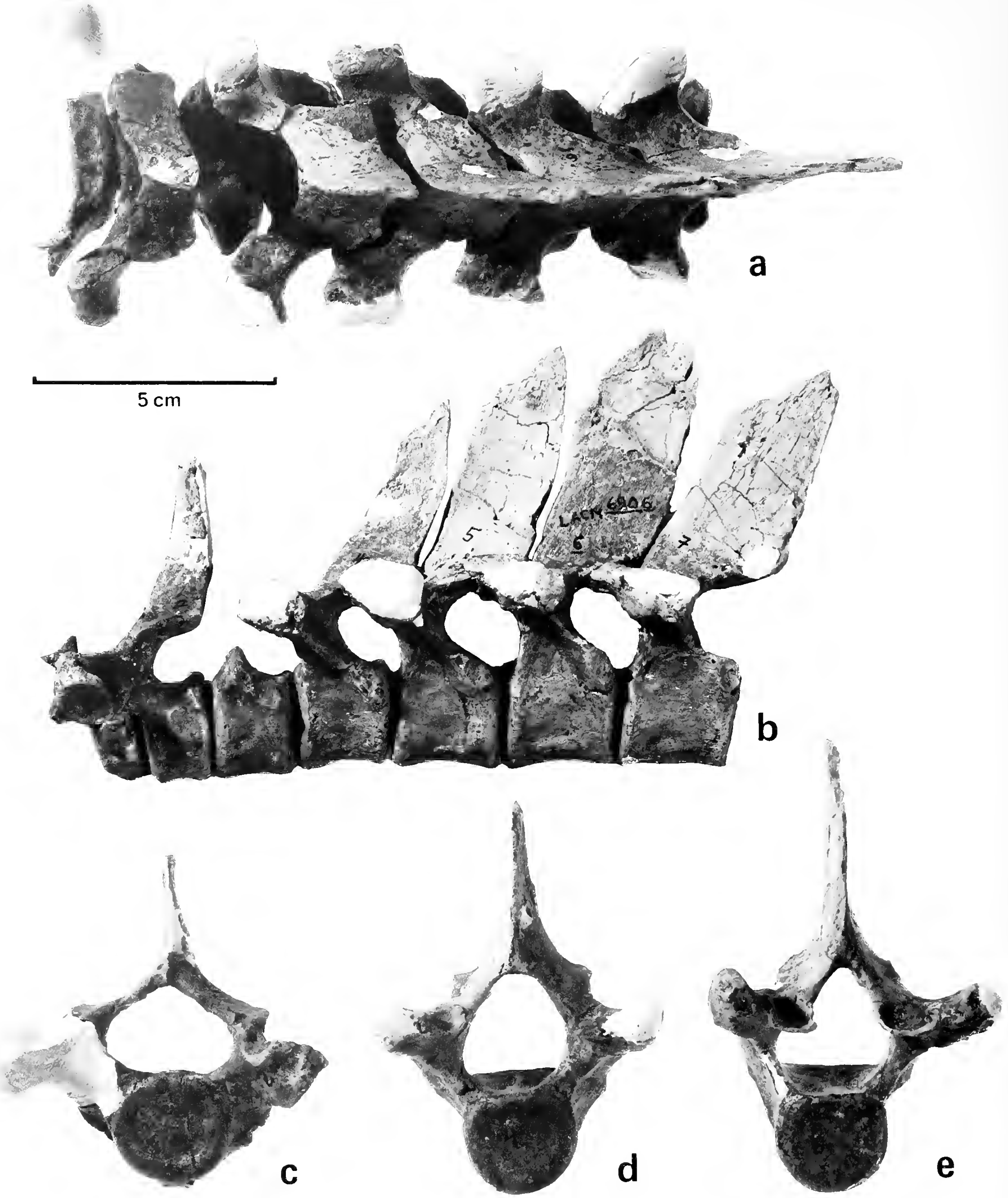

Figure 13. *Pithanodelphis nasalis,* new species, paratype, LACM 29087, LACM locality 5082, cervical and thoracic vertebrae; cervical vertebra 7 through thoracic vertebra 6; **a,** dorsal view; **b,** left lateral view; anterior views of individual vertebrae; **c,** first thoracic; **d,** third thoracic; **e,** sixth thoracic. All to the same scale.

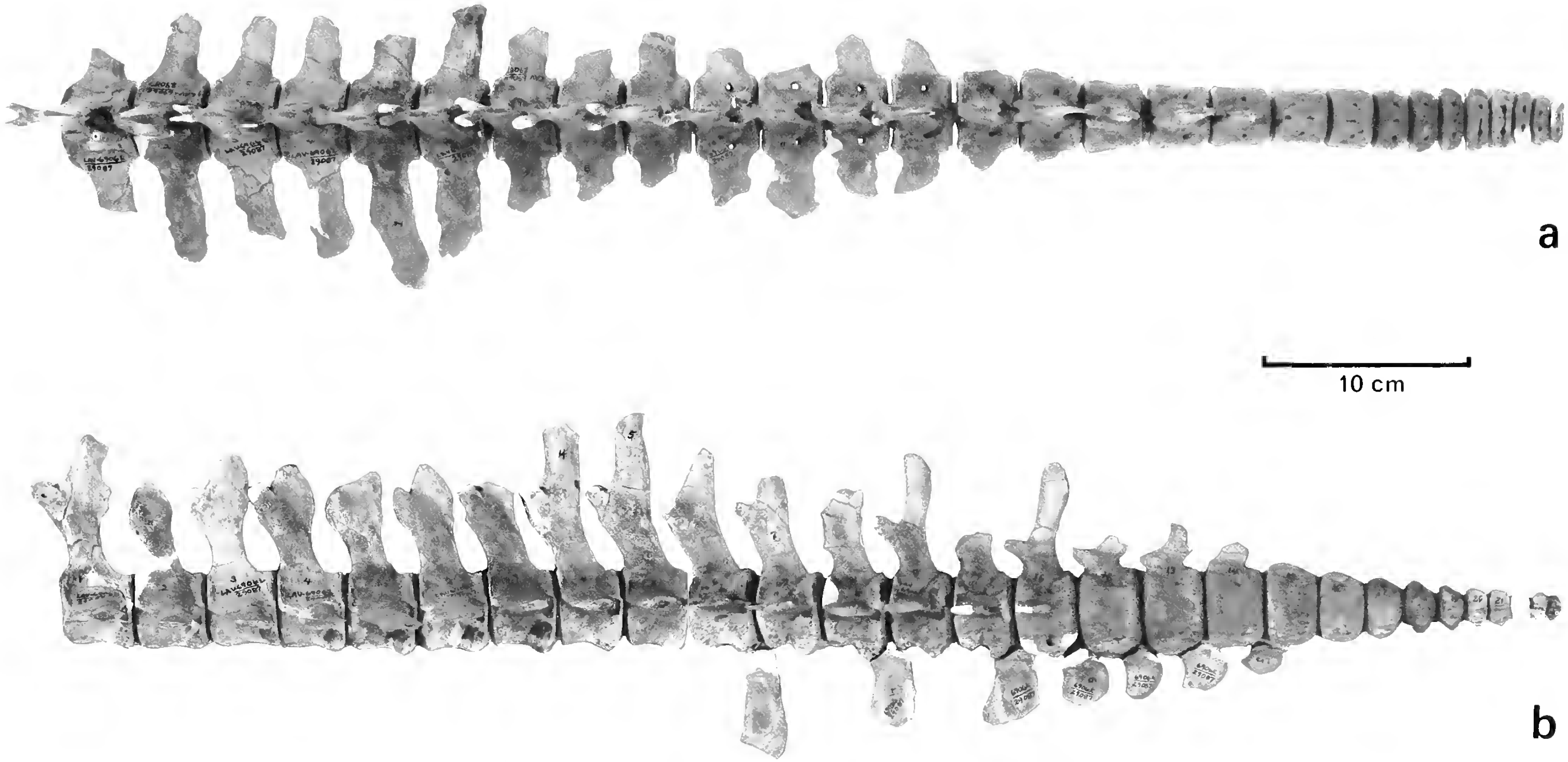

Figure 14. *Pithanodelphis nasalis,* new species, paratype, LACM 29087, lumbar and caudal vertebrae and chevron bones, LACM locality 5082; **a,** dorsal view; **b,** left lateral view.

County. This formation has been correlated with the Monterey Formation in Orange County (Woodford et al., 1954: fig. 2) and because both rock units were deposited in the same marine basin, the Los Angeles Basin, all the specimens may therefore be regarded as part of the same faunal aggregate.

Furthermore, the relatively restricted source of the specimens from the Monterey Formation reinforces the conclusions based on morphological similarities that the specimens attributed to *P. nasalis* represent one species. The sample of skulls presents a range of size, but a consistency of morphology. Within the sample of skulls of *P. nasalis* the variability (in the positions of the premaxillary and maxillary foramina, in the size and shape of the nasals and the antorbital and postorbital processes, and in the size and anterior extent of the fossae for the pterygoid sinuses) is commensurate with that in the small sample of three skulls of the Atlantic kentriodontid, *Kentriodon pernix,* from the Calvert Formation (Barnes and Mitchell, 1984).

Pithanodelphis nasalis was a contemporary of the earliest known delphinid (sensu stricto; see Barnes, 1977:330), which was recovered from the same part of the Monterey Formation at Laguna Niguel. The earliest known phocoenid, *Salumiphocaena stocktoni* (Wilson, 1973), and two other kentriodontids, *Lophocetus repenningi* Barnes, 1978 and *Liolithax* sp. (see Barnes, 1978), are also known from correlative rock units in California.

Another contemporaneous odontocete, the small dolphin *Delphinavus newhalli* Lull, 1914, was collected from the Monterey Formation near Santa Maria, Santa Barbara County, California. It has been classified in the family Delphinidae by Lull (1914) and Simpson (1945), but objectively considered, the present state of preservation and preparation of the holotype and only known specimen preclude its assignment to any particular family (Barnes, 1977:329). *Delphinavus newhalli* is a much more derived species than *Pithanodelphis nasalis.* In contrast with *P. nasalis,* it has 40 upper teeth instead of 26 to 30, a more slender mandible with a symphysis approximately one-fourth as long, an edentulous anterior tip of the premaxilla that does not extend beyond the end of the maxilla, and a shorter, thicker zygomatic process of the squamosal that has a more dorsoventrally expanded anterior end.

Hesperocetus californicus True, 1912a, is another contemporaneous dolphin, and is even more problematic. It is known only by a fragment of mandible that was found in the San Pablo Formation in the San Francisco Bay area of California (see Barnes, 1977). It differs from *P. nasalis* by being larger, and by having a thicker mandible with much larger teeth that have rugose, rather than smooth, enamel.

Several lines of evidence suggest that *Pithanodelphis nasalis* was an offshore species that lived in deep water over the continental shelf. Diatomaceous sediments are usually considered to have been deposited in deeper waters over the continental shelves (cf. Calvert, 1966), and all the known fossil ocurrences of *P. nasalis* have been found either in such sediments or in lenses of coarser clastic sediment that are enclosed within diatomites. Furthermore, both the San Joaquin Hills and Santa Monica Mountains occurrences of *P. nasalis* are at sites that, in Late Miocene time, were many miles out in the marine basin from the inferred ancient shorelines (Woodford et al., 1954). Most of the specimens consist of parts of associated or articulated skeletons or are otherwise relatively unabraded, indicating that they were not transported great distances before their final deposition. Some cetacean carcasses in the modern oceans have been known to drift great distances prior to sinking to the sea floor (Schäfer, 1972:20–21) and it is possible, of course, that the *Pithanodelphis nasalis* fossils represent carcasses that were not buried near the same environment in which they lived. It is undoubtedly significant, however, that all the known specimens have been found in the sedimentary context described above.

Pithanodelphis nasalis had an overall adult body length of approximately 200 cm. The vertebral column has proportions very much like the living bottlenosed dolphin, *Tursiops truncatus.* Its rostrum and teeth are also like that species and other small living delphinids, and by analogy, its diet was probably generalized, consisting mostly of small pelagic fish and some squid (Rice, 1984:479). Such a diet would also be consistent with the inference that *P. nasalis* was an offshore species. *Pithanodelphis nasalis* was also a generalized animal in its postcranial, mandibular, and dental morphology. Its cranial asymmetry, moderate development of fossae for air sinuses, and large mandibular fossa suggest that it was capable of echolocating. The orbits are relatively large compared with *Kentriodon pernix,* indicating that *P. nasalis* had large eyes. The teeth are large and deeply rooted. The largest teeth are in the middle of the tooth row, and all teeth have a considerable accretion of cementum on their roots. The large temporal fossa indicates that there was strong temporal musculature, which, in conjunction with the large teeth, long, firmly ankylosed mandibular symphysis and large postglenoid process, suggests that *P. nasalis* could effect a strong grasp with its jaws.

CLASSIFICATION

The classification presented below reflects the changes in knowledge of the family Kentriodontidae subsequent to my 1978 publication and includes the taxa that were discussed by Barnes and Mitchell (1984). Within genera, the more primitive species are listed first, and in general, I follow this arrangement throughout the classification. Certain aspects of the anatomy of *Leptodelphis stavropolitanus* Kirpichnikov, 1954, *Sarmatodelphis moldavicus* Kirpichnikov, 1954, and *Microphocaena podolica* Kudrin and Tatarinov, 1965, are poorly known, and it is difficult to assign these genera to established subfamilies. The new subfamily Pithanodelphinae reflects the very derived characters of *Pithanodelphis,* including the asymmetry of the cranial vertex, which is not known among other species of Kentriodontidae and which was acquired in a manner unlike that in other families within the superfamily Delphinoidea. *Oligodelphis azerbajdzanicus* was classified by Mchedlidze (1976) as a species of Delphinidae, but appears to belong in the Kentriodontidae, and should therefore be re-evaluated in detail.

Class Mammalia Linnaeus, 1758
  Order Cetacea Brisson, 1762
    Suborder Odontoceti Flower, 1867
      Superfamily Delphinoidea (Gray, 1821) Flower, 1864
        Family Kentriodontidae (Slijper, 1936) Barnes, 1978
          Subfamily Kampholophinae Barnes, 1978
            Kampholophos Rensberger, 1969
              Kampholophos serrulus Rensberger, 1969. Middle Miocene, California, U.S.A.
            Liolithax Kellogg, 1931
              Liolithax pappus (Kellogg, 1955) Barnes, 1978. Middle Miocene, Maryland, U.S.A.
              Liolithax kernensis Kellogg, 1931. Middle and Late Miocene, California, U.S.A.
              Liolithax sp. Barnes, 1978. Late Miocene, California, U.S.A.
          Subfamily Kentriodontinae Slijper, 1936
            Kentriodon Kellogg, 1927
              aff. *Kentriodon.* Barnes and Mitchell, 1984. Early Middle Miocene, California, U.S.A.
              Kentriodon pernix Kellogg, 1927. Middle Miocene, Maryland, U.S.A.
              Kentriodon obscurus (Kellogg, 1931) Barnes and Mitchell, 1984. Middle Miocene, California, U.S.A.
            Delphinodon Leidy, 1869 (in part)
              aff. *Delphinodon dividum* True, 1912b. Barnes and Mitchell, 1984. Late Early and/or Early Middle Miocene, Japan; California, U.S.A.
              Delphinodon dividum True, 1912b. Middle Miocene, Maryland and Virginia, U.S.A.
          Subfamily Lophocetinae Barnes, 1978
            Lophocetus Cope, 1868
              Lophocetus repenningi Barnes, 1978. Late Miocene, California, U.S.A.
              Lophocetus calvertensis (Harlan, 1842) Cope, 1868. Late Miocene, Maryland, U.S.A.
          Subfamily Pithanodelphinae, new subfamily
            Pithanodelphis Abel, 1905
              ***Pithanodelphis nasalis,* new species.** Late Miocene, California, U.S.A.
              Pithanodelphis cornutus (du Bus, 1872) Abel, 1905. Late Miocene, Belgium
          Kentriodontidae, *incertae sedis:*
            Oligodelphis Mchedlidze and Aslanova *in* Mchedlidze, 1976
              Oligodelphis azerbajdzanicus Mchedlidze and Aslanova *in* Mchedlidze, 1976. Late Oligocene, Azerbaidzhan S.S.R., U.S.S.R.
            Sarmatodelphis Kirpichnikov, 1954
              Sarmatodelphis moldavicus Kirpichnikov, 1954. Late Miocene, Moldavian S.S.R., U.S.S.R.
            Leptodelphis Kirpichnikov, 1954
              Leptodelphis stravropolitanus Kirpichnikov, 1954. Late Miocene, Stavropol, Russian S.F.S.R., U.S.S.R.
            Microphocaena Kudrin and Tatarinov, 1965
              Microphocaena podolica Kudrin and Tatarinov, 1965. Late Miocene, Ukrainian S.S.R., U.S.S.R.

CONCLUSIONS

Pithanodelphis nasalis is a new species of small fossil dolphin classified in the new subfamily Pithanodelphinae of the extinct delphinoid family Kentriodontidae. The species is known by fossil skulls and postcranial bones from the Monterey and Modelo formations at about 33°30′ and 34°05′ north latitudes, respectively, in the Los Angeles Basin in southern California, U.S.A. Its abundance in collections suggests that this dolphin was the most abundant odontocete cetacean inhabiting the North Pacific Ocean off the coast of southern California at approximately 10 to 11 million years ago. The fossil material is sufficient to confidently differentiate *P. nasalis* from previously named, contemporaneous small odontocetes from California: *Hesperocetus californicus* True, 1912a; *Delphinavus newhalli* Lull, 1914; *Salumiphocaena stocktoni* (Wilson, 1973); and *Lophocetus repenningi* Barnes, 1978.

Pithanodelphis nasalis and *P. cornutus* (du Bus, 1872), an approximately contemporaneous fossil species that was found in the Antwerp Basin in Belgium, are the only species presently assigned to the genus and to the subfamily Pithanodelphinae. *Pithanodelphis* might have evolved from some taxon within the subfamily Kentriodontinae. *Pithanodelphis nasalis* is similar to two well-known Middle Miocene Atlantic kentriodontines, *Kentriodon pernix* Kellogg, 1927, and *Delphinodon dividum* True, 1912b. Its vertebral structure is more derived than that of the former, more primitive than that of the latter, and its cranial structure is more derived than both. Species of *Pithanodelphis* differ notably from all other delphinoids by having extremely large, convex nasal bones that comprise the highest part of the cranial vertex.

Pithanodelphis nasalis and *P. cornutus* are the only species of Kentriodontidae that are known to have had cranial asymmetry. The manner in which this asymmetry was expressed is different, however, from species in the other families of the superfamily Delphinoidea; the Monodontidae, Phocoenidae, and Delphinidae; and this feature is, therefore, a convergent derived character. Asymmetry was possibly acquired separately in each of the modern delphinoid families (and in other odontocete families as well).

The presence of cranial asymmetry and other derived characters of *Pithanodelphis nasalis,* such as spiracular plates on the premaxillae, moderate development of fossae for air sinuses in the basicranium, and large mandibular fossae, suggest that the species could echolocate. It has a rostrum of moderate length and a homodont dentition comprised of conical-crowned teeth. Like most small Recent delphinids with such features, it probably had a generalized diet consisting mostly of small fishes and occasional squid. The morphology of its vertebral column is relatively primitive and, in conformation and numbers of vertebrae, is approximately analogous to that of the living bottlenosed dolphin, *Tursiops truncatus*. *Pithanodelphis nasalis* was a smaller animal, however, with an overall body length at maturity of approximately 200 cm. The nature of the sedimentary deposits that yielded the fossils and the preservation of the bones indicate that the usual habitat of the species was probably offshore in deep water over the continental shelf.

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CONTRIBUTIONS IN SCIENCE

EVOLUTIONARY RELATIONSHIPS OF THE ATHERINOPSINAE (PISCES: ATHERINIDAE)

Brian N. White

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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EVOLUTIONARY RELATIONSHIPS OF THE ATHERINOPSINAE (PISCES: ATHERINIDAE)

Brian N. White[1]

ABSTRACT. The Atherinopsinae, a subfamily of the silverside fish family Atherinidae, is cladistically diagnosed on the basis of five synapomorphies: 1) Baudelot's ligament ossified, 2) proximal end of fourth ceratobranchial with moderate toothplates, 3) palatine with medial bony shelf, 4) ventral projection of nasal bone contacting lachrymal, and 5) lateral ethmoid with ventral bony knob. Two tribes are recognized. The Atherinopsini is restricted to the Pacific shores of North America and includes four genera: *Atherinops, Atherinopsis, Colpichthys,* and *Leuresthes.* Its members share three derived character states: 1) supraoccipital process trifid, 2) leading edge of vomer with paired dorsal projections, and 3) expanded hypophyses formed by bifurcation of haemal spines. The Basilichthyini is distributed throughout the temperate marine and fresh waters of South America and includes two genera: *Basilichthys* and *Odontesthes.* It is characterized by three synapomorphies: 1) basioccipital fenestrated, 2) extrascapular composed of two bony elements, and 3) haemal arches expanded to form broad hypophyses. Within the northern tribe, *Leuresthes* is most closely related to *Atherinopsis* whereas *Atherinops* is considered to be most closely related to *Colpichthys.* The tropical subfamily Menidiinae is considered to be the sister group of the Atherinopsinae.

INTRODUCTION

After more than a century of effort, the evolutionary relationships of the silverside family Atherinidae have not been adequately resolved. This study attempts to answer several questions concerned with the evolutionary history of the Atherinopsinae, an American subfamily. First, is the Atherinopsinae (*sensu* Schultz, 1948) monophyletic? If so, what is its sister group? Another question involves internal relationships of the subfamily: is the Atherinopsinae composed of phylogenetically distinct North and South American lineages? The biogeographic history of the Atherinopsinae will be considered in a separate contribution.

The New World atherinids have long been considered a monophyletic group. The Atherinopsinae of Jordan and Hubbs (1919) included almost all American silversides. In a later revision, Schultz (1948:42) redefined the Atherinopsinae and restricted the subfamily "to that group of genera now known from the Americas that have the premaxillary dilated or broadened posteriorly and extending opposite or into five or more of the broadened hypophyses of the haemal arches, these specialized hypophyses mostly interconnecting with one another by flattish, broadened, spine-like bony processes opposite the tapering part of the air bladder." This definition is based on a derived character having systematic importance at the level of the New World atherinids and excludes from the Atherinopsinae many genera included in the subfamily by Jordan and Hubbs (1919), which Schultz accommodated by the formation of a new subfamily, the Menidiinae.

Only seven of the eight genera included in the Atherinopsinae by Schultz (1948) are still recognized: *Atherinops* (Steindachner, 1876), *Atherinopsis* (Girard, 1854), *Austromenidia* (Hubbs, 1918), *Basilichthys* (Girard, 1854), *Colpichthys* (Hubbs, 1918), *Leuresthes* (Jordan and Gilbert, 1880), and *Odontesthes* (Evermann and Kendall, 1906). *Hubbsiella* (Breder, 1936) was synonymized with *Leuresthes* by Moffatt and Thomson (1975). The validity of some other atherinopsine genera, e.g. *Colpichthys* and *Atherinopsis,* have been called into question (Todd, 1976).

Schultz (1948) did not consider the Menidiinae and Atherinopsinae to be sister groups. Instead, he allied the Atherinopsinae with the Old World subfamily Atherininae because a small number of atherinine species have haemal modifications similar to those of some of the atherinopsine fishes. He did admit, however, that this similarity may be due to parallel evolution and have no bearing on the phylogenetic relationships of the two subfamilies. Jordan and Hubbs (1919) proposed that the New World silversides (the Atherinopsinae and Menidiinae of Schultz, 1948) and the Old World Atherininae formed a monophyletic group.

Patten (1978) believed the Atherinopsinae of Jordan and Hubbs (1919) to be monophyletic but did not consider this assemblage to be related closely to the Atherininae. He also questioned the division of the American atherinids into two subfamilies, charging that Schultz (1948) used primitive characters to define the Menidiinae.

The differing opinions of Patten (1978), Schultz (1948), and Jordan and Hubbs (1919) raise questions about the evo-

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lutionary relationships of the American silversides which are the basis for this study. Their resolution requires that the New World silversides be viewed in a wider phylogenetic context and that the Atherinopsinae be compared with outgroup species chosen from as many other teleostean taxa as possible.

METHODS AND MATERIALS

The methods of Willi Hennig (1966) are used herein to assess evolutionary relationships. Known commonly as cladistics, phylogenetic systematics, or cladism, this approach groups organisms solely on the basis of shared derived character states, or synapomorphies. Similarity due to the shared possession of primitive or plesiomorphic character states is discounted as uninformative and excluded from analysis.

Grouping organisms according to patterns of common ancestry demands that all taxonomic groups be monophyletic. Put another way, all members of a taxonomic group must share a common ancestor and all the descendants of that ancestor must be included in the group. Synapomorphic character states are used to diagnose taxonomic groups. The hierarchic arrangement of synapomorphic character states on a cladogram serves to define the evolutionary relationships between different groups.

Synapomorphic character states were determined by outgroup analysis (Lundberg, 1972; Watrous and Wheeler, 1981). Outgroups were chosen primarily, but not exclusively, from within the Atherinomorpha (Rosen and Parenti, 1981). In outgroup analysis, character states restricted to the ingroup are considered to be derived whereas states occurring in both the ingroup and outgroup are assessed as being primitive.

In some cases, character states that are suspected of being derived have limited occurrence among outgroup taxa and must therefore be evaluated more critically. In such instances, it is necessary to consider if it is more parsimonious to assume that the character state in question was independently derived in the ingroup and outgroup or whether it is derived for a larger group and only retained by a small number of otherwise distantly related descendants. The assumption that requires the fewest number of evolutionary steps, the sum total of all gains and losses necessary to explain the observed distribution of the character state, is accepted.

Arguments based on parsimony require a reasonable knowledge of the overall relationship of the ingroup to related lineages. For the purposes of this study, a recent phylogeny proposed for the Atherinomorpha (White et al., 1984; Collette, 1984) (Fig. 1) and the ideas of Patten (1978) concerning the relationships of the Atherinidae (Fig. 2) were used to settle questions of parsimony. In one case, the ontogeny of a character was used to polarize a transformation series between three states.

At least two male and two female specimens of every atherinopsine genus, except *Basilichthys,* were cleared and counterstained (Dingerkus and Uhler, 1977) to facilitate observation of bone and cartilage. Only a single, male specimen of *Basilichthys* was cleared and stained because of material constraints. Osteological character states judged to be phylogenetically informative were examined further in a number of partially dissected alcohol specimens. Material from numerous outgroups was cleared and counterstained or dissected as well.

The original description of every generic synonym is referenced in the synonymies presented in the discussion section.

The preserved materials used in this study were furnished by the following institutions: Natural History Museum of Los Angeles County (LACM), Academy of Natural Sciences of Philadelphia (ANSP), California Academy of Sciences (CAS), National Museum of Natural History (USNM), University of Arizona (UA), University of California at Los Angeles (UCLA), and University of Florida (UF). The acronym SU refers to collections of Stanford University now housed at CAS. A list of species examined is provided below. Following each catalog number, in parentheses, are the total number of specimens examined with the number of cleared and stained preparations, if any, denoted by an asterisk.

Order Atheriniformes

Family Atherinidae

Subfamily Atherinopsinae

Atherinops affinis. LACM: 346(1), 347(1), 1808(1), 1809(1), 1984(1), 1995(1), 2619(1), 6609-1(1), 6612-2(1), 6615-2(1), 6616-1(1), 6635-2(1), 6683-1(1), 7990(1), 8823-8(1), 8909-2(1), 8947-13(1), 9280-2(1), 9281-1(1), 9297-1(1), 9380-2(1), 9439-2(1), 9592-3(1), 22075(1), 20125(1*), 22304(1), 22306(1), 30706-1(1), 31699-5(1), 32068-5(1), 32084-14(1), 32085-14(1), 32086-10(2,1*), 32184-14(9,1*), 32697-1(1), 32704-2(1), 33080-1(3), 33138-1(1), 33541-1(1), 35153-10(1), 35794-1(1), 35815-1(1), 37013-1(4), 37552-5(1), 37575-7(2,1*), 38545-2(1), 38548-1(1*), 82622-5(1), W48-34(1), W49-157(1), W50-144(1), W55-20(15), W55-90(1*), W56-253(1), W63-59(1), W63-63(1), W68-43(21,2*).

Atherinopsis californiensis. LACM: 348(2,1*), 3896(1), 6735-2(1), 7936(3), 9283-1(1), 9439(3,1*), 20024(2), 20025(3,2*), 20120(1), 22300(1), 22302(1), 22795(1), 23227(1), 24066(1), 30636-6(1), 31306-2(6,3*), 31583-4(6,1*), 31807-6(3), 31864-1(1), 31940-1(1), 32043-8(1), 32044-8(1), 32056-13(3), 32059-12(1), 32704-2(1*), 32925-3(3), 32944-1(5), 33076-1(1), 34093-1(1), 37609-5(2), 42663-4(2*), W49-4(1), W49-143(2), W58-377(42,1*), W67-151(1), W67-152(1).

Basilichthys archaeus. USNM: 128536(2), 77530(1).

Basilichthys australis. LACM: 42705-1(1*); CAS: SU22735(2); USNM: 84326(4).

Basilichthys semotilus. CAS: 45193(1), 45194(2), SU23227(2).

Colpichthys regis. LACM: 7153(13,1*), 35728-1(10), 35730-1(10,4*), 39570-4(1*), W49-130(3), W50-190(2), W51-15(10), W55-12(9,3*), W55-30(4).

Leuresthes sardina. LACM: 1523(1*), 9295(1*), 35728-7(4), W49-121(1*), W50-18*(2,1*), W51-258(1).

Leuresthes tenuis. LACM: 1786(2), 1810(2), 4382(1), 4402(1), 6615(1), 6635-3(1), 6735-1(1), 8946-8(1), 9280-1(1),

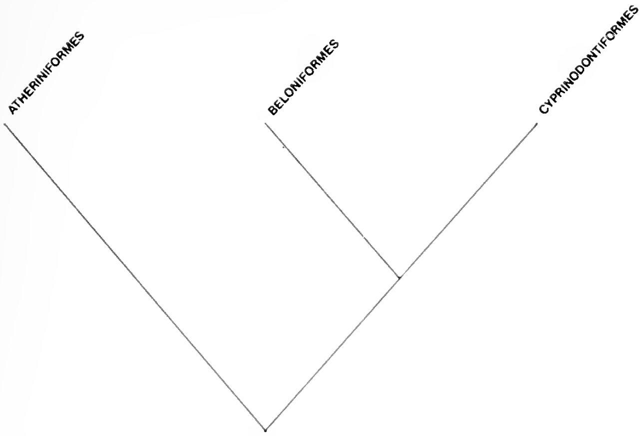

Figure 1. Relationships of the Atherinomorpha (White et al., 1984; Collette, 1984).

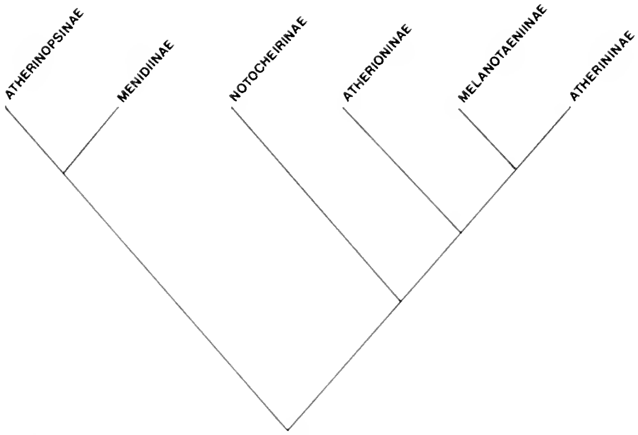

Figure 2. Relationships of the subfamilies of the Atherinidae (Patten, 1978).

9453-1(1), 9592-2(1*), 20123(2), 20131(3,2*), 22307(2), 22879(1), 24070(2), 31306-3(2), 31757-7(1), 31759-22(2,1*), 32056-12(1), 32597-1(4,2*), 32946-1(1), 32947-1(2), 33077-1(1), 33078-1(2), 33079-1(2), 33080-1(1*), 33139(1), 33487-1(2), 37690-1(2), 38457-1(2,1*), W51-66(28,2*), W55-115(2), W57-152(2), W66-62(3), W67-149A(1), W68-43(2), 015-SO-08MA-01(4*), 024-RB-08-MA-01(4*), 024-SO-08-MA-01(5*), 024-SO-22-MA-01(4*).

Odontesthes argentinense. USNM: 148502(4).

Odontesthes bonariensis. CAS: SU52812(4*).

Odontesthes brevianalis. USNM: 84338(1).

Odontesthes hatcheri. CAS: 12699(1), 42586(2).

Odontesthes incisus. CAS: SU31601(3); USNM: 163378(5).

Odontesthes mauleanum. CAS: 44702(2), 45201(2), SU12691(2); USNM: 77296(1), 84334(3).

Odontesthes nigricans. USNM: 77299(4), 88714(2), 103782(1).

Odontesthes perugiae. CAS: 11730(1).

Odontesthes regia. LACM: 20094(1), 42696-1(138,3*); CAS: SU6072(1), SU9285(2), 11905(2), 45171(1), 45172(2), 45173(1), 45174(3); USNM: 77633(4), 77644(1).

Odontesthes smitti. USNM: 256719(10).

Undescribed species from Gulf of California. UCLA: W78-11(4).

Subfamily Menidiinae

Archomenidia sallei. LACM: 43459-1(4).

Chirostoma grandocule. UCLA: W2-54(4).

Chirostoma labarcae. UA: 66-108-7(6).

Chirostoma sphyraena. UA: 66-128-1(2).

Coleotropis blackburni. LACM: 8335(2).

Eurystole eriarcha. LACM: 1562(1*), 9044-16(4), 31784-5(2*).

Hubbesia gilberti. LACM: 8964-2(1), 22328(7).

Labidesthes sicculus. LACM: 8965-1(2).

Melaniris chagresi. LACM: 9132-1(1*), 9148-9(1), 9167-10(7).

Melanorhinus cyanellus. LACM: 20129(1), 35486-5(1*).

Membras martinica. LACM: 8975-1(1); ANSP: 125238(5); UF: 35105(10).

Menidia beryllina. LACM: 8964-2(10).

Menidia peninsulae. LACM: 8962-2(2*).

Nectarges nepenthe. LACM: 20101(2*), 20103(1).

Poblana sp. LACM: 32616-1(4).

Xenatherina sp. LACM: 43458-1(4).

Xenomelaniris brasiliensis. ANSP: 120027(8).

Subfamily Notocheirinae

Iso rhothophilus. CAS: 46621(4).

Subfamily Atherioninae

Atherion elymus. LACM: W65-31(2).

Subfamily Melanotaeniinae

Pseudomugil signifer. LACM: 34988-3(2).

Subfamily Atherininae

Atherina breviceps. LACM: 42651-1(1*), 42695-1(4,1*).

Atherinomorus ogilbyi. LACM: 37481-1(13).

Atherinomorus pinguis. LACM: 31299-20(7).

Hypoatherina harringtonensis. LACM: 5833(2*).

Hypoatherina panatela. LACM: 42472-3(6).

Order Beloniformes

Family Belonidae

Pseudotylosurus angusticeps. LACM: 41470-8(2).

Family Exocoetidae

Cypselurus opisthopus. LACM: 30455-1(3).

Exocoetus monocirrhus. LACM: 30473-5(4).

Family Hemirhamphidae

Hyporhamphus unifasciatus. LACM: 6949-2(4).

Family Scomberesocidae

Cololabis saira. LACM: 34083-1(3).
Scomberesox saurus. LACM: 11223-1(4).
Strongylura timucu. LACM: 5875(8).

Order Cyprinodontiformes

Family Anablepidae

Anableps dowi. LACM: 42632-16(6*).
Oxyzygonectes dowi. LACM: 4876(3).

Family Cyprinodontidae

Belonesox belizanus. LACM: 42632-15(1).
Cyprinodon variegatus. LACM: 1309(5), 1310(4).
Floridichthys carpio. LACM: 1311(3).

Family Fundulidae

Fundulus diaphanus. LACM: 39823-1(4*).

Family Goodeidae

Goodea sp. LACM: 32615-1(2).
Xenotoca variata. LACM: 151(3).

Family Poecillidae

Poecilia sphenops complex. LACM: 9191-21(3).

Family Profundulidae

Profundulus guatemalensis. LACM: 1969-47(4).

Family Rivulidae

Rivulus isthmensis. LACM: 2779(3).

RESULTS

In all of the atherinopsine fishes examined, Baudelot's ligament is ossified at its point of attachment to the base of the skull such that two thin, sharp spines are directed posteroventrally from the basioccipital (Fig. 3). As in most other teleost fishes, the unossified portion of this ligament has a point of attachment on the cleithrum. The placement, size, and shape of these paired ossifications are constant throughout the Atherinopsinae. Baudelot's ligament is not ossified in any of the other atheriniform species examined except *Iso rhothophilus.* Species of the marine genus *Iso* are very deep bodied and their overall appearance is quite different from that of the Atherinopsinae. This dissimilarity carries over to the ossification of Baudelot's ligament, as the orientation of the ossification on the base of the skull of *I. rhothophilus* does not resemble that characteristic of the Atherinopsinae.

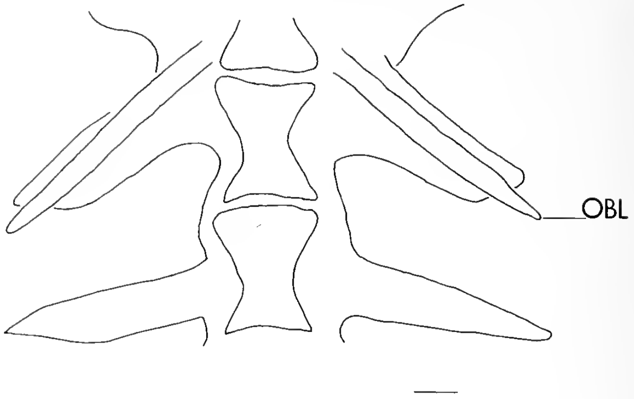

Figure 3. Ventral view of first two vertebrae and base of skull: *Colpichthys regis.* OBL = ossified Baudelot's ligament. Scale equals 1 mm.

In *I. rhothophilus,* the spines are placed higher on the skull and are more laterally directed than in the atherinopsine fishes. Therefore, the condition observed in *I. rhothophilus* is considered to be independently derived and not homologous with the atherinopsine condition. Baudelot's ligament is ossified in each of the belonid, hemirhamphid, and scomberesocid species examined, but not in the exocoetids. In the halfbeaks and sauries, the ossified ligaments form flat, swordlike processes quite different from the cylindrical ossifications typical of the Atherinopsinae. In the needlefishes, the ossified portion of each ligament is much stouter than in the Atherinopsinae. For these reasons, the beloniform pattern is not considered to be homologous with the atherinopsine pattern.

A second derived character state shared by the atherinopsine fishes is found in the branchial basket: there are no enlarged toothplates on the proximal end of the fourth ceratobranchial, but instead, there is a series of paired toothplates running the length of the fourth ceratobranchial (Fig. 4a). In almost all atherinopsine species, these toothplates are relatively narrow and do not contact their partners on the dorsal midline of the fourth ceratobranchial. However, in *Colpichthys regis* and in an undescribed atherinopsine collected in the Gulf of California by Dr. Boyd Walker, these paired toothplates are expanded so that they contact their partners on the dorsal surface of the fourth ceratobranchial. The typical atheriniform condition is seen in *Menidia* (Fig. 4b) in which an enlarged toothplate occurs on the proximal end of the fourth ceratobranchial.

A third characteristic of the Atherinopsinae is found on the palatine bone. In every atherinopsine species examined, there is an ossified shelf on the medial side of the head of the palatine bone. This shelf serves to brace the palatine against the mesethmoid. It was not seen outside the Atherinopsinae. *Nectarges* and *Atherinomorus* (Fig. 5) were chosen to illustrate the primitive atherinomorph condition of this character. Ontogenetic stages of the palatine bone were observed in cleared and stained larval specimens of *Leuresthes tenuis.* The medial bony shelf appears after the head of the palatine has developed the hammerlike shape shared by the Atherinopsinae and Menidiinae.

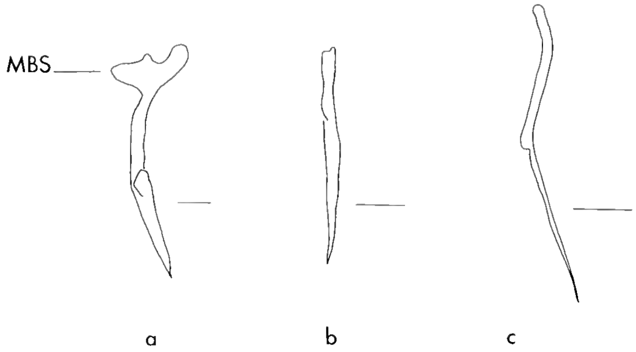

Figure 5. Posterior view of right palatine bone: a) *Leuresthes tenuis,* b) *Nectarges nepenthe,* c) *Atherinomorus pinguis.* MBS = medial bony shelf. Scale equals 1 mm.

A fourth derived feature of the Atherinopsinae concerns the state of the nasal bone. The atherinopsine nasal bone has a ventral projection (Fig. 6a) that makes contact with the anterodorsal corner of the lachrymal bone. In other atherinomorphs, this projection is lacking and connection between the nasal and lachrymal bones is accomplished via an extension of the anterior tip of the nasal sensory canal (Fig. 6b). In most atherinopsines, the ventral nasal projection is well developed but in the California and Gulf grunions, reduction of the projection seems to have accompanied enlargement of the lachrymal bone.

A fifth derived character state of the atherinopsine fishes involves the lateral ethmoid. In the Atherinopsinae, there is on the ventral surface of the lateral ethmoid a bony knob (Fig. 7a) that abuts the posterior edge of the palatine. This knob apparently provides additional support for the palatine and presumably strengthens the entire snout. There is considerable variation in this feature within the Atherinopsinae, although it was well developed in all specimens examined. It is most strongly developed in *Atherinops affinis* and least developed in some specimens of *Atherinopsis californiensis* (Fig. 7b). It was not encountered in any of the non-atherinopsine species available for comparison.

Several synapomorphic osteological features occur in the North American Atherinopsinae. The supraoccipital process of most of the North American atherinopsines is trifid (Fig. 8a). In some specimens of *Leuresthes tenuis* the supraoccipital process is bifid, but in *L. sardina* and the other North American species the supraoccipital is strongly trifid. A trifid supraoccipital process has been reported in several halfbeak species (Collette, 1966). However, this contrasts with the bifid condition of the supraoccipital process (Fig. 8b) of nearly all other atherinomorphs (Rosen, 1964). A bifid supraoccipital process is considered here to be the primitive silverside condition.

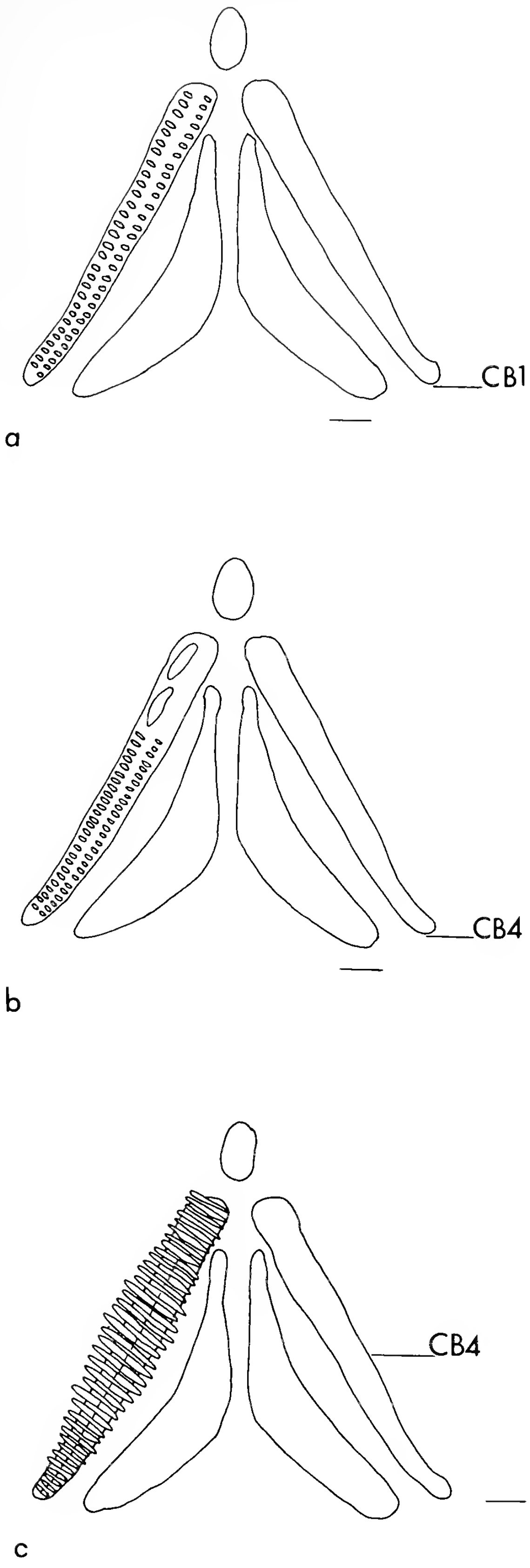

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Figure 4. Dorsal view of fourth ceratobranchial dentition in the Atherinidae: a) *Atherinops affinis,* b) *Menidia peninsulae,* c) *Colpichthys regis.* CB4 = fourth ceratobranchial. Scale equals 1 mm.

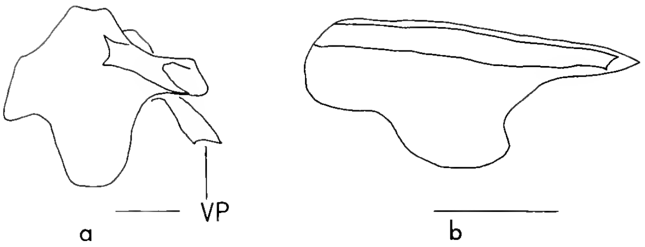

Figure 6. Medial view of right nasal bones: a) *Atherinopsis californiensis,* b) *Melanorhinus cyanellus.* VP = ventral process. Scale equals 1 mm.

Another derived character state shared by the North American genera occurs on the vomer. In the northern atherinopsines, a dorsal lip on the anterior edge of the vomer has a pair of bony projections (Fig. 9) that contact the mesethmoid. In other atherinids, there is either a single projection, as in *Menidia,* or there is none at all, as in *Iso* (Patten, 1978). Presumably, these projections help brace the mesethmoid. The mesethmoid is a point of attachment for ligaments running to the palatine and maxillary bones and it is reasonable to conclude that the additional support it receives from these paired vomerine processes serves to strengthen the snout and jaws of the atherinopsines of the northeastern Pacific.

One unique modification of the North American atherinopsines involves the development of the haemal funnel into which the swimbladder extends. The ontogeny of the broad, haemal hypophyses begins with a cartilaginous haemal arch. A groove develops on the ventral surface of the simple haemal spines that deepens as ossification proceeds. The spines finally bifurcate, with each half expanding to form a rectangular bony plate (Fig. 10a). Extending from the ventral surface of each of these plates is a long, spinelike projection that curves medially to meet its fellow from the opposite side (Fig. 11a) (Schultz, 1948; Clothier, 1951). These spines do not fuse, but form a second funnel ventral to the one formed by the rectangular plates above them. It is into this second funnel that the posterior end of the swimbladder projects. This unusual modification of the anterior haemal arches leaves them without a haemal spine and, in this way, the North American atherinopsines differ from most other teleosts. A similar condition is known to occur, however, in one other atherinid, the atherinine species *Atherinason hepsetoides* (Patten, 1978). Specimens of *A. hepsetoides* were not available for examination, but evidence presented by Patten (1978) suggests that *A. hepsetoides* is distantly related to the North American Atherinopsinae. Furthermore, none of the closest relatives of *A. hepsetoides* has developed a similar condition. I conclude that the haemal modifications of *A. hepsetoides* and of the North American atherinopsines are independently derived.

The form of the haemal arches is remarkably similar in all of the northern atherinopsines except for the undescribed species from the Gulf of California, which lacks these haemal modifications. The body cavity of this species is truncate and the swimbladder does not extend into the region of the caudal vertebrae.

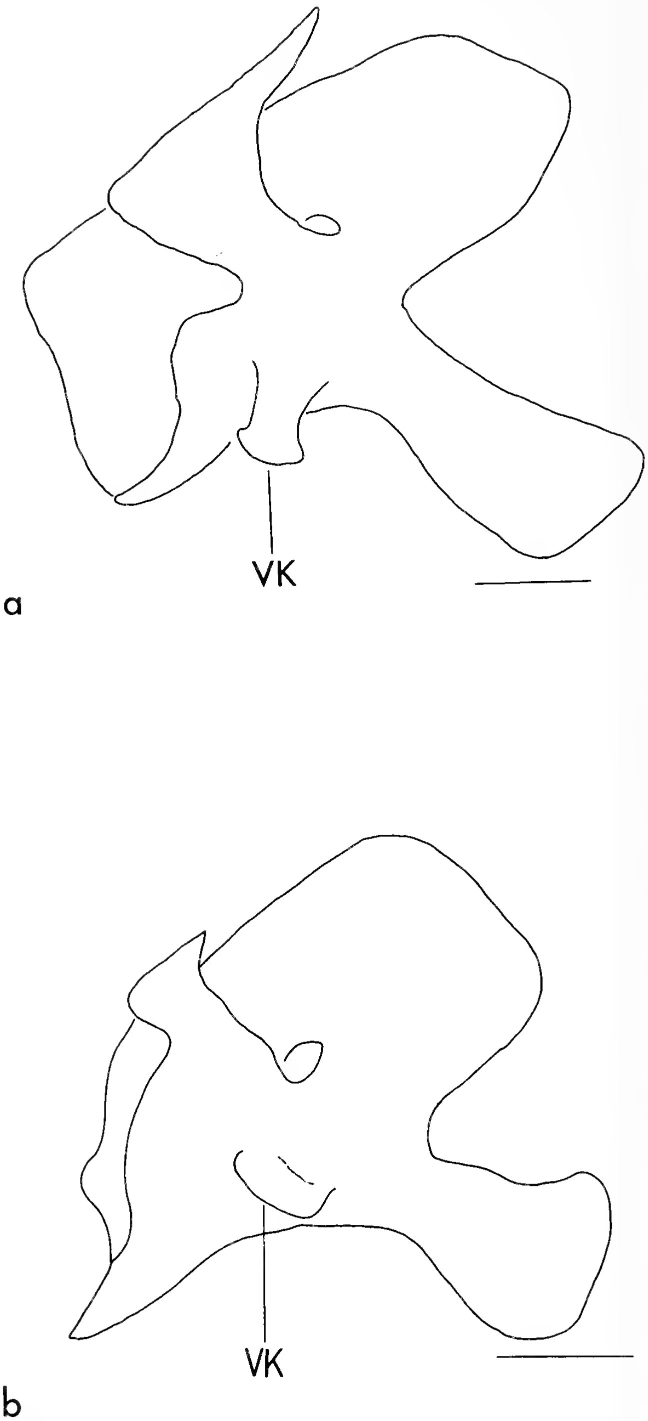

Figure 7. Ventral view of right lateral ethmoid, anterior edge to right: a) *Atherinops affinis,* b) *Atherinopsis californiensis.* VK = ventral knob. Scale equals 1 mm.

The haemal modifications of the southern species are in stark contrast with those of their northern counterparts. The development of their hypophyses could not be observed because no larval material was available but the hypophyses

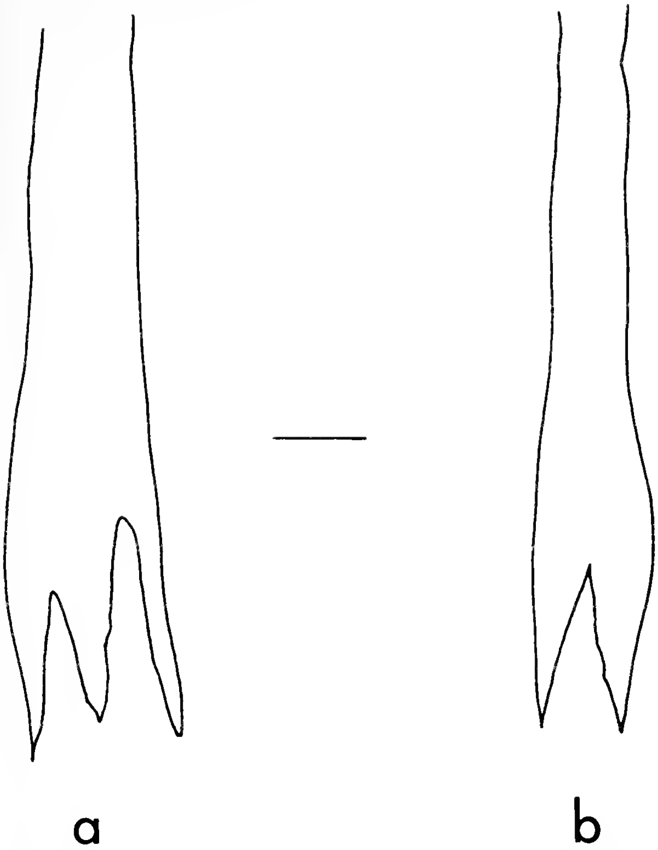

Figure 8. Dorsal view of supraoccipital process: a) *Atherinopsis californiensis,* b) *Menidia peninsulae.* Scale equals 1 mm.

of the South American atherinopsines cannot be derived from haemal spines, as they are in the North American atherinopsines, because the haemal spines of the adult fishes are intact. It appears that the haemal funnel occurring in the southern species (Fig. 10b) develops from an expansion of the haemal canals themselves instead of a bifurcation of the haemal spines. There is only a single haemal funnel in the southern atherinopsines, with the swimbladder extending into the expanded lumens of a series of haemal arches that each have a well-developed spine (Fig. 11b). The hypophyses of the South American atherinopsines are furrowed delicately and fenestrated in the same manner as the basioccipital bone (Fig. 12). In some species, the hypophyses are quite complex, as shown in Figure 10b, or they are simple. In *Basilichthys australis,* for example, the hypophyses appear to be nothing more than a simple flaring of the walls of the haemal canals. A similar condition occurs in the atherinine species *Atherina boyeri,* but it is not considered to be homologous with the South American atherinopsine condition because other evidence indicates that the Atherininae is distantly related to the Atherinopsinae (Patten, 1978). In two South American species, *Odontesthes incisus* and *O. nigricans,* the swimbladder is not posteriorly extended and the haemal arches are unmodified.

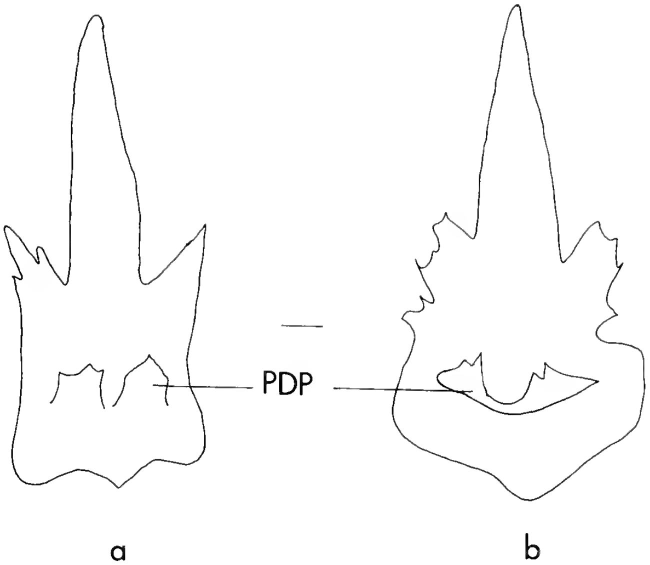

Figure 9. Dorsal view of vomer: a) *Atherinopsis californiensis,* b) *Atherinops affinis.* PDP = paired dorsal processes. Scale equals 1 mm.

Two other derived character states are shared by the South American atherinopsines. First, in all of the southern species examined, the posterior portion of the basioccipital bone is sculpted by a series of irregularly spaced foramina (Fig. 12). Within the Atherinomorpha, this feature is found only in the South American atherinopsines.

Another derived feature of the South American atherinopsines involves the extrascapular bone. In most of the southern atherinopsine species, the extrascapular is composed of two bony elements (Fig. 13b, c), one oriented horizontally and the other vertically. Both elements bear sensory canals. In the North American atherinopsines, both sensory canals are accommodated by a single bone (Fig. 13a). In most atherinomorphs, the extrascapular bone is absent, but in some genera, e.g. *Menidia,* it is fused with the posttemporal (Patten, 1978). Even though these two bones are fused in *Menidia,* the direct communication between the two sensory canals suggests that the single extrascapular bone of the North American species is the ancestral condition for the subfamily. This is not surprising, because in most fishes, the extrascapular is composed of a single element (Weitzman, 1962; Mead and Bradbury, 1963; Springer, 1968; Zehren, 1979). There is some variation in the form of the extrascapular bone in the South American atherinopsines. In *Basilichthys semotilus,* for example, the extrascapular bone resembles the North American atherinopsine condition. This is not true of the other species of *Basilichthys* examined. In three specimens, two separate elements occurred. In one specimen, only one element was present; the anterior vertical element was absent on both sides. In another specimen having only one element, the posterior horizontal elements were absent. In three other specimens, both elements are present and united to form a single bone. Because the development of two extrascapular elements is widespread among the South American atherinopsine genera, it is considered to be a derived feature uniting

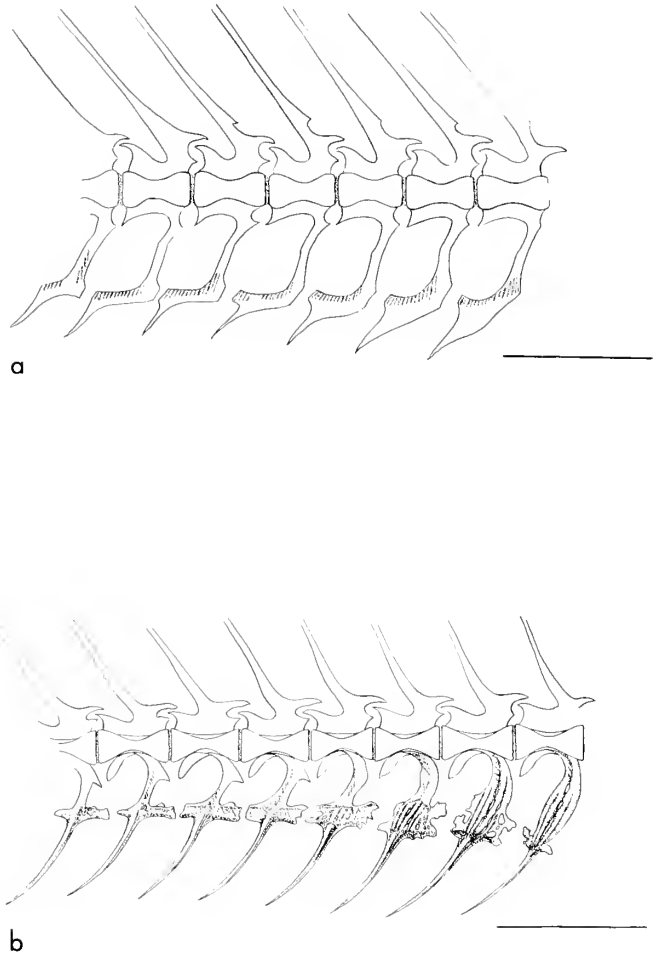

Figure 10. Lateral view of haemal hypophyses: a) *Atherinops affinis,* b) *Odontesthes regia.* Scale equals 1 mm.

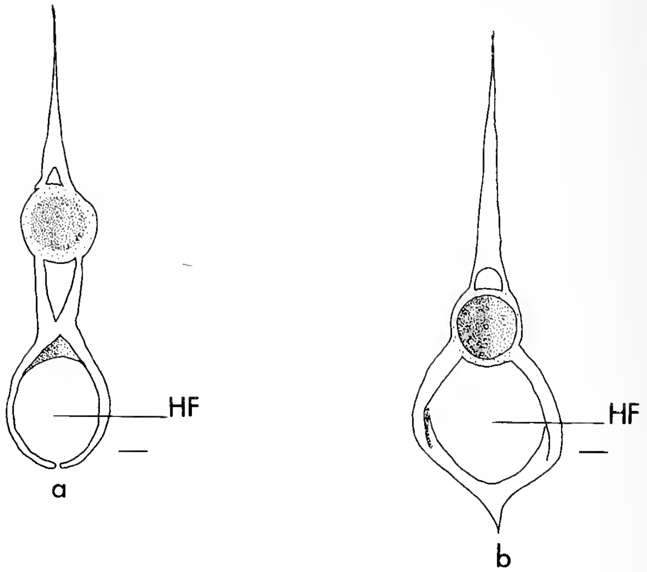

Figure 11. Anterior view of caudal vertebra: a) *Atherinops affinis,* b) *Odontesthes regia.* HF = haemal funnel. Scale equals 1 mm.

them in a monophyletic group. The variation noted in *Basilichthys semotilus* and *Odontesthes incisus* is assumed to be secondarily derived.

The menidiine fishes share several derived character states. The parapophyses on the first vertebra are directed anteriorly, and are blunt distally (Fig. 14). The first parapophyses of most other atherinomorphs are pointed and directed posteriorly. In some cyprinodontiforms, notably *Fundulus diaphanus,* the parapophyses of the first few vertebrae project forward and in others, such as *Anableps dowi,* the parapophyses on most or all of the vertebrae are anteriorly directed. In these cases though, the parapophyses are pointed and not blunt as in the menidiines. Furthermore, only the menidiine fishes have just the parapophyses on the first vertebra modified. There is variation in this feature within the Menidiinae. In none of the menidiine genera examined, except *Chirostoma,* are the parapophyses on the first vertebra pointed and directed posteriorly, as in the atherinopsine fishes. Inspection of juvenile specimens shows this to be a modification of the typical menidiine pattern as the parapophyses on the first vertebra of the smaller individuals are directed anteriorly and are blunt.

In the Menidiinae and Atherinopsinae, the supraoccipital canal extends over the frontal and pterotic bones. In both subfamilies, three pores occur in the pterotic portion of the canal. However, the two American subfamilies differ in the number of pores that occur in the frontal portion of the canal. The atherinopsine fishes have five frontal pores whereas the menidiines usually have only four. When the supraorbital pores are numbered according to the system of Gosline (1949), the atherinopsine total is seven (Fig. 15a) and the menidiine total is six (Fig. 15b). There is some variation in the number of supraorbital pores in the Menidiinae. The Mexican freshwater genus *Poblana* resembles the atherinopsine fishes in having seven supraorbital pores. In *Labidesthes sicculus,* the supraorbital canal lacks a bony roof so that no pores are evident on the top of the head. This is true of the Old World atherinid subfamilies as well. Parenti (1981) concluded that it is primitive for the cyprinodontiform fishes to have seven supraorbital pores and this is assumed to be the case in the New World atherinids as well. There is great variation in the number of supraorbital pores in the Beloniformes. In some species, the cranial pores are miniscule and very numerous, numbering up to 123 in the continuous supraorbital-postorbital-temporal canal of *Scomberesox saurus* (Parin and Astakhov, 1982). In others, a pattern similar to the one seen in the Atherinopsinae occurs. No beloniform species examined during the course of this study was found to have the reduced number of supraorbital pores characteristic of the Menidiinae.

Another derived menidiine character state involves the enlarged toothplates present on the proximal end of the fourth ceratobranchial (Fig. 4b). In all menidiine species examined, these toothplates are fused to the ceratobranchial and cannot

Figure 12. Lateral view of neurocranium: *Odontesthes regia.* B = basioccipital. Open space blackened. Scale equals 1 mm.

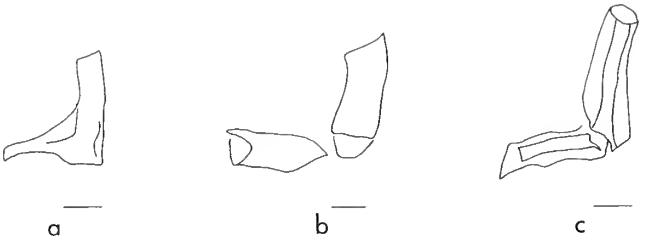

Figure 13. Lateral view of right extrascapular bone: a) *Atherinops affinis,* b) *Odontesthes regia,* c) *Basilichthys australis.* Scale equals 1 mm.

be dislodged from the branchial basket. In no other atheriniform for which information is available are the toothplates attached in this manner (Patten, 1978). In the Cyprinodontiformes, a series of teeth extends posteriorly along the dorsal surface of the fourth ceratobranchial between the paired toothplates that are arrayed along its right and left hand sides. This does not resemble the menidiine pattern. Proximal toothplates are absent in the Beloniformes.

Two unique osteological characters appear in both the Atherinopsinae and Menidiinae. First, in both these subfamilies, there is a modification of the pectoral girdle involving the scapula and cleithrum. These two bones are connected in the atherinopsine and menidiine fishes by a series of small, bony buttresses. These buttresses resemble small foramina in lateral view but are in fact bony struts passing between the cleithrum and scapula. Some specimens have many struts and others have few, but their shape, size and placement are constant in the two subfamilies. The buttresses are always elliptical in cross section and placed high along the dorsolateral surface of the cleithrum in a horizontal or nearly horizontal arrangement. In *Atherinomorus,* the only other genus in which bony struts were found to pass between the scapula and cleithrum, the struts were vertically arranged along the anterior edge of the cleithrum and are considered to be independently derived.

Another modification shared by the Atherinopsinae and Menidiinae involves the palatine bone. In the fishes belonging to these subfamilies, the head of the palatine is either straight or shaped like a hammer. In Figure 16, the range of variation exhibited by the palatine bone in New World atherinids and the atherinomorphs as a whole is illustrated. In *Leuresthes* (Fig. 16a), and all other atherinopsines, the head of the palatine is shaped like a hammer. This is true of many menidiines also, although in some, such as *Nectarges* (Fig. 16b), the palatine head is just bluntly rounded. During the course of this study, the more typical atherinomorph condition (Parenti, 1981), shown in the tapering, pointed palatine of the Old World atherinid *Atherinomorus* (Fig. 16c) was not encountered in any menidiine or atherinopsine species examined.

The two grunion species share several derived character states. First, neither *Leuresthes tenuis* nor *L. sardina* have strongly developed teeth in the jaws as adults. It has been reported that minute teeth do occur in these fishes (Moffatt and Thomson, 1975) and that it is necessary to examine dried skeletal material to observe them. No teeth were seen in any of the cleared and stained or alcohol preserved specimens examined in the course of this study. There is variation in the dentition of the other atherinids. In *Atherinopsis californiensis,* the jaw teeth are arranged in several rows, whereas only a single row of teeth is found on the jaws of *Atherinops affinis.* However, no other atherinid species are known to have the weak dentition characteristic of the grunions. In fact, most atherinomorphs have well-developed teeth in the jaws.

A suite of derived traits is associated with the reproductive biology of the grunions. Both *Leuresthes tenuis* and *L. sardina* are lunar spawners that fertilize and bury their eggs at the surf line on sandy beaches during the extreme high tides of spring and early summer. The embryos develop in the sand for approximately two weeks, when high tides again reach the nests and initiate hatching (Walker, 1952). Though a few other fishes are known to spawn on a lunar cycle, e.g. *Menidia menidia,* the remarkable reproductive habits of the grunions are a well-known specialization. The eggs of both grunion species lack filaments. All other atherinopsine eggs known have filaments as do the eggs of most atherinomorphs (Rosen and Parenti, 1981; Collette, 1984).

The shape of the vomer in the California and Gulf grunions is unusual (Fig. 17a). In both *Leuresthes tenuis* and *L. sardina,* the leading edge of the vomer is emarginate and the lateral condyles are reduced greatly. This contrasts with the form of the vomer in the other atherinopsines and menidiines, where the lateral condyles are well developed and the

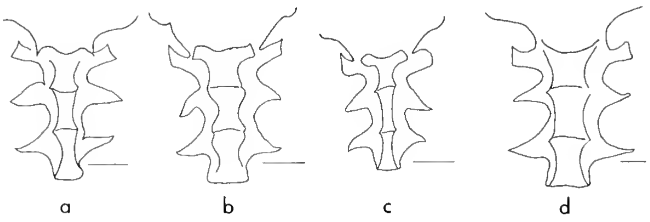

Figure 14. Ventral view of anterior vertebrae and base of skull: a) *Menidia peninsulae,* b) *Nectarges nepenthe,* c) *Melaniris chagresi,* d) *Chirostoma labarcae.* Scale equals 1 mm.

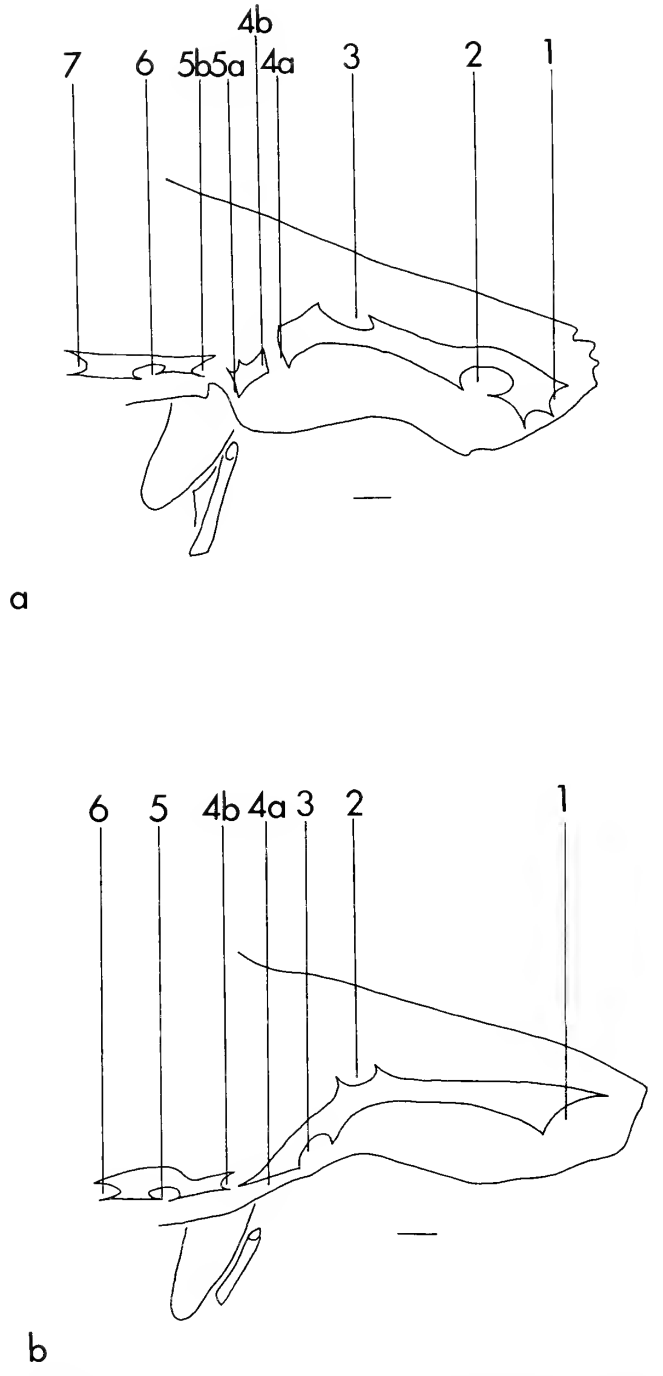

Figure 15. Supraorbital pore pattern: a) *Atherinops affinis,* b) *Melanorhinus cyanellus.* Pores numbered according to the system of Gosline (1949). Scale equals 1 mm.

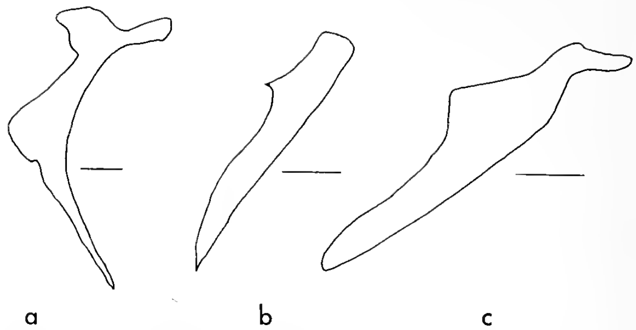

Figure 16. Lateral view of right palatine: a) *Leuresthes tenuis,* b) *Nectarges nepenthe,* c) *Atherinomorus pinguis.* Scale equals 1 mm.

leading edge has a strong median process (Fig. 17b). In overall size, the vomer of the two grunions is reduced in comparison with those of other atheriniforms.

The dorsal process on the premaxilla of *L. tenuis* and *L. sardina* is long and slender and placed near the symphysis of the upper jaw (Fig. 18a). The jaws are greatly protractile in grunions and are not bound to the snout by a frenum as in *Basilichthys, Atherinops* or *Atherinopsis.* A similar condition is developed in *Odontesthes* (Fig. 18b), but in this South American genus, the dorsal process is placed farther back along the shaft of the premaxilla, suggesting that the dorsal processes of the northern and southern genera were independently derived.

Consideration of the other derived character states described here suggests that the evolution of jaw mobility in the Atherinopsinae involves the independent development of slender, premaxillary dorsal processes and the loss of the frenum to the upper jaw in the North American grunions and the South American genus *Odontesthes.*

Atherinopsis californiensis shares with *Leuresthes tenuis* and *L. sardina* another modification of the ethmoid region. In these three species, the lateral ethmoid has a pointed, bony strut that runs along the lateral edge of the parasphenoid (Fig. 19). This bony strut was not observed in any of the other atherinid species examined. It is lacking in the beloniform and cyprinodontiform fishes as well.

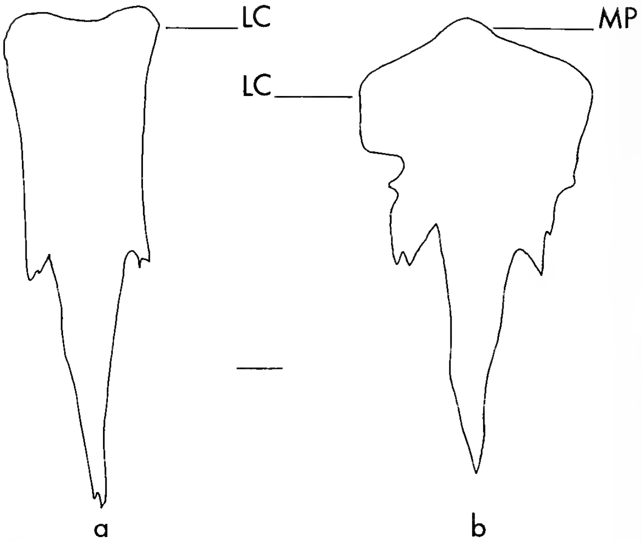

Figure 17. Ventral view of vomer: a) *Leuresthes tenuis,* b) *Atherinops affinis.* LC = lateral condyle, MP = median process. Scale equals 1 mm.

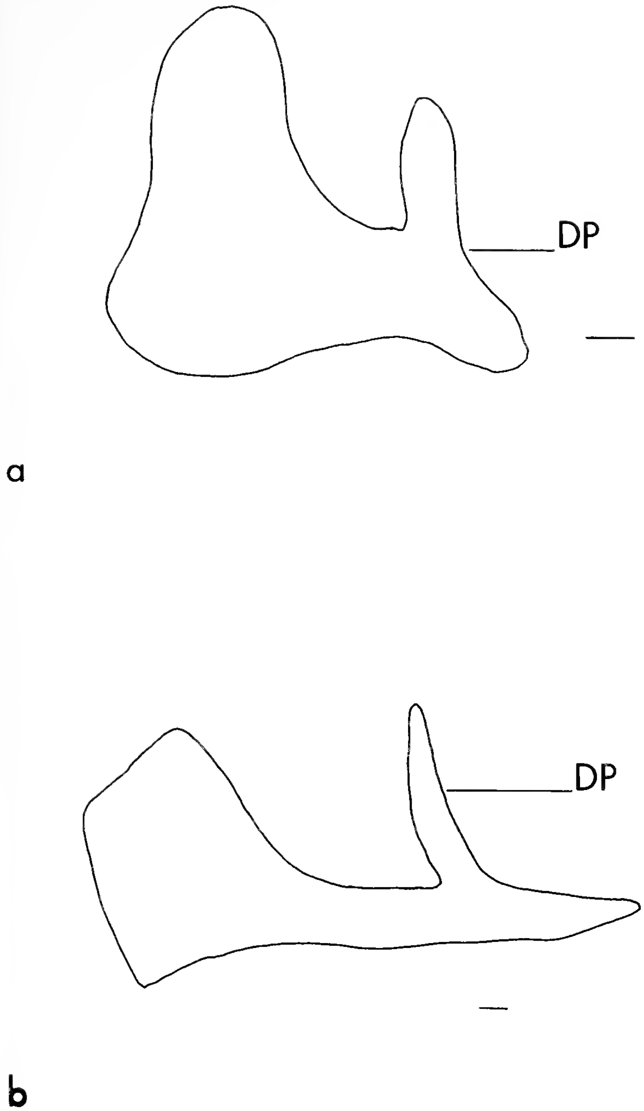

Figure 18. Lateral view of right premaxillary bone: a) *Leuresthes tenuis,* b) *Odontesthes regia.* DP = dorsal process. Scale equals 1 mm.

Another derived feature that *Atherinopsis californiensis, Leuresthes tenuis,* and *L. sardina* have in common involves the shape of the third epibranchial (Fig. 20a). The proximal arm of the third epibranchial of these three fishes is twisted about its long axis. Not only is the proximal arm of the third epibranchial crooked, but it is noticeably thinner in *Atherinopsis californiensis, Leuresthes tenuis,* and *L. sardina* than it is in the other atherinopsines and menidiines, in which the proximal arm of the third epibranchial is stout and uncontorted (Fig. 20b).

A single derived character state distinguishes *Atherinopsis californiensis* from all other atherinomorphs. In *A. californiensis,* there is a small pocket on the anterior tip of the ventral process of the maxilla formed by a bony ledge projecting from its ventral surface (Fig. 23a).

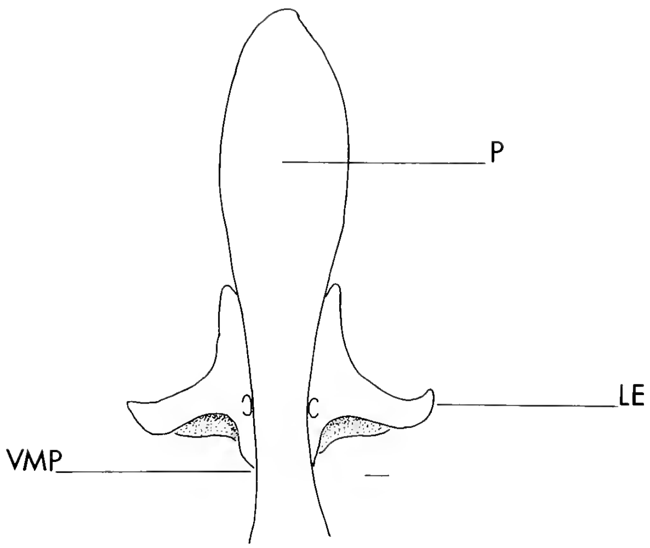

Figure 19. Ventral view of parasphenoid and lateral ethmoids: *Atherinopsis californiensis.* P = parasphenoid, MP = median process, LE = lateral ethmoid. Scale equals 1 mm.

Two unique osteological features are shared by *Atherinops affinis, Colpichthys regis,* and the undescribed atherinopsine species from the Gulf of California. In these fishes, the anterior edge of the quadrate is angled forward (Fig. 21b). This feature is most apparent in dissected specimens because the quadrate is held in position by the flesh that is digested away in cleared and stained specimens. It can, of course, be observed in cleared specimens, but mobility of the suspensorium, of which the quadrate is a part, makes interpretation of the exact orientation of the quadrate more difficult. In none of the other atherinomorph genera examined was a similar positioning of the quadrate observed. It is typical within the Atherinomorpha for the anterior edge of the quadrate to have a vertical orientation (Fig. 21a).

The bicuspid teeth shared by *Atherinops affinis, Colpichthys regis,* and the undescribed species are unlike those of any other atherinid (Schultz, 1948). In *Atherinops affinis,*

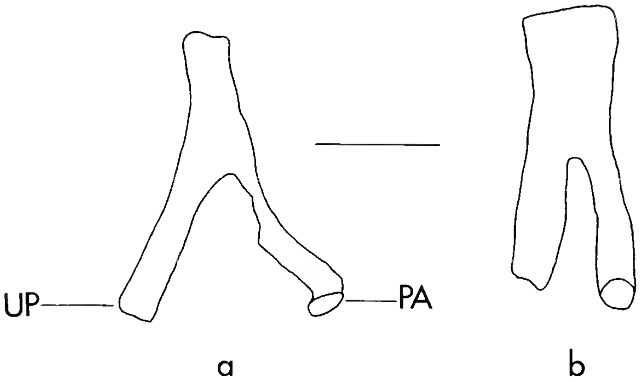

Figure 20. Left epibranchial: a) *Atherinopsis californiensis,* b) *Atherinops affinis.* PA = proximal arm, UP = uncinate process. Scale equals 1 mm.

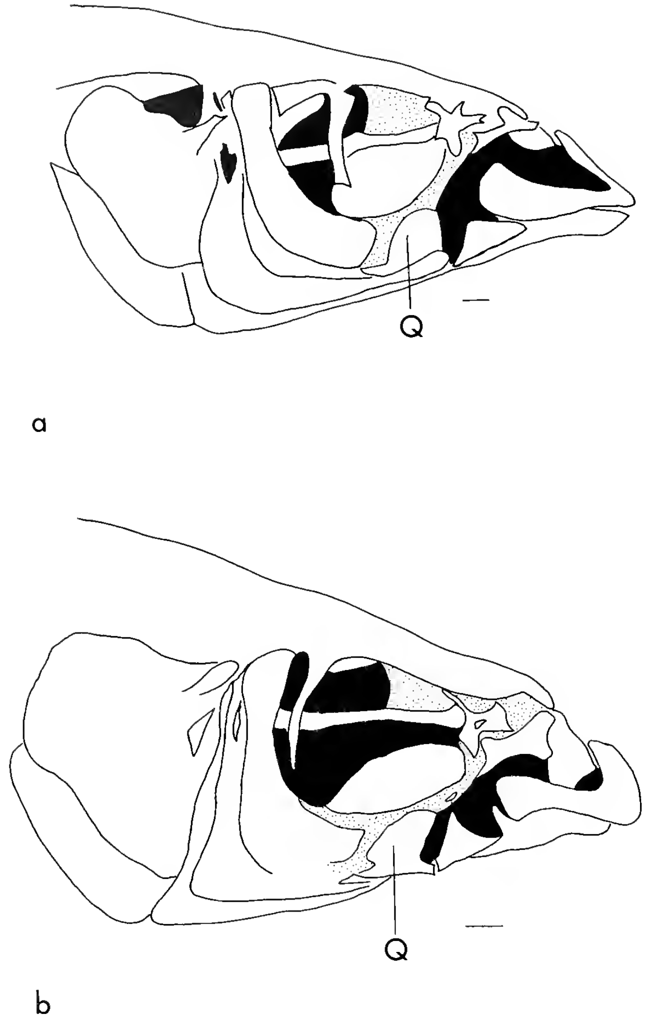

Figure 21. Orientation of the quadrate: a) *Odontesthes regia,* b) *Atherinops affinis.* Q = quadrate. Cartilage stippled, open space blackened. Scale equals 1 mm.

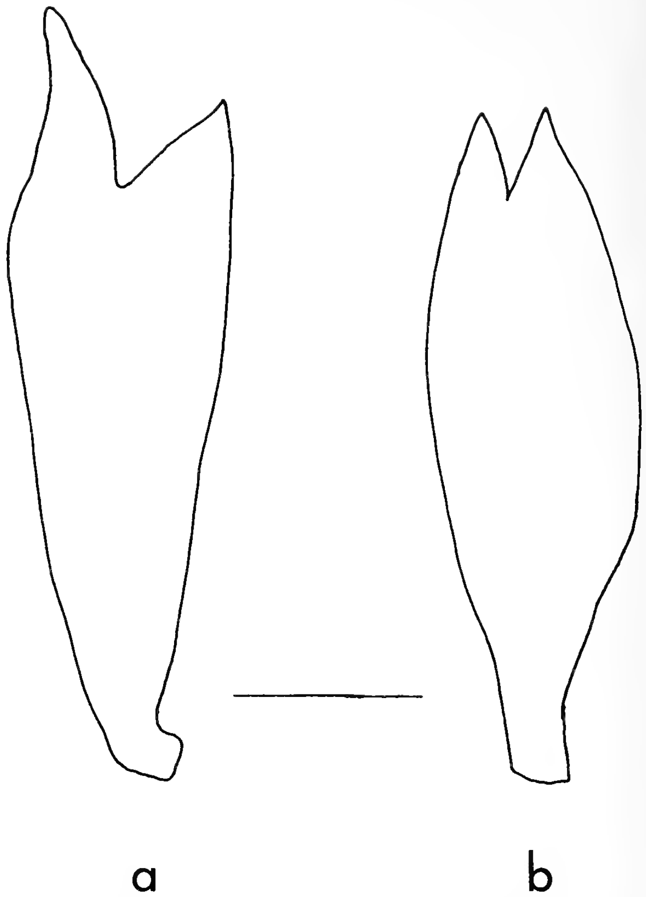

Figure 22. Jaw teeth: a) *Colpichthys regis,* b) *Atherinops affinis.* Scale equals 0.1 mm.

the cusps on each tooth are of equal size (Fig. 22b). In *Colpichthys regis* and the undescribed species, the cusps are unequal (Fig. 22a). Bicuspid and even tricuspid teeth are known to occur in some cyprinodontiform fishes (Parenti, 1981) and in the Hemirhamphidae as well.

Colpichthys regis and the undescribed atherinopsine from the Gulf of California have in common several special features involving the dorsal process of the maxilla and the dentition of the branchial basket. There is a notch in the dorsal process of the maxilla of both of these Gulf of California atherinopsines (Fig. 23b). This notch was not seen in any other atherinomorph species. Also shared by *C. regis* and the undescribed species is the modification of the fourth ceratobranchial toothplates described above. The toothplates are wide and meet on the dorsal midline of the fourth ceratobranchial (Fig. 4c). Another unique feature seen in these two species involves the teeth on the third pharyngobranchial elements. These upper pharyngeal bones are covered with long hairlike teeth that apparently serve to strain fine sand particles.

A single derived feature distinguishes *Atherinops* from all other atherinomorph species: the fold of skin connecting the distal ends of the premaxillary and maxillary bones is frilled (Fig. 24).

Several unique character states occur in the South American atherinopsines. In the fishes assigned to the genus *Basilichthys,* the ventral process of the maxilla has a rounded projection on its dorsal surface that was not seen in any other atherinomorph species examined (Fig. 23c).

Every species of *Odontesthes* or *Austromenidia* examined lacks a mesethmoid. The Atherinomorpha is defined, in part, on the presence of a disclike mesethmoid. Therefore, loss of the mesethmoid is considered to be a derived character state shared by these two genera.

Another derived feature shared by *Odontesthes* and *Austromenidia* involves the opercle. In every species examined, except *O. incisus,* the opercle has on its anterodorsal corner a complex array of foramina of varying sizes (Fig. 25). This condition appears to be unique within the Atherinomorpha. The absence of these foramina in *O. incisus* is judged to be a secondary loss for two reasons. First, the occurrence of

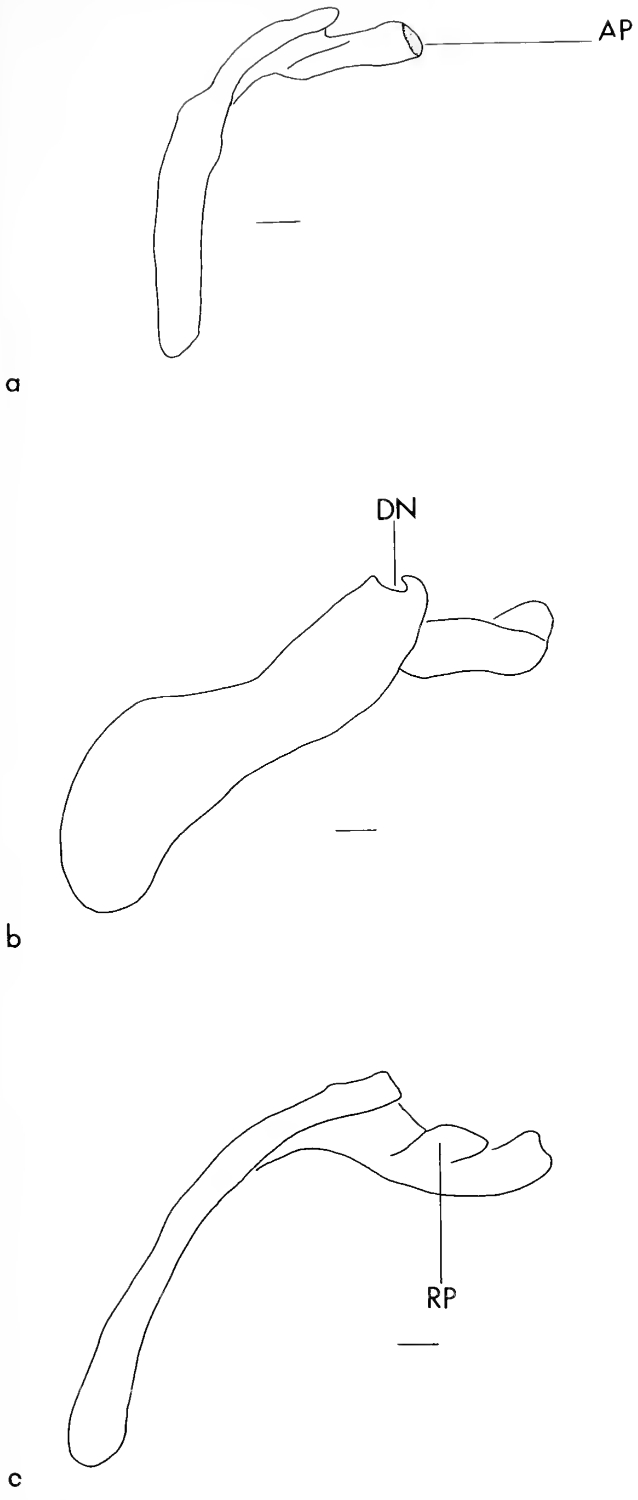

Figure 23. Lateral view of right maxilla: a) *Atherinopsis californiensis,* b) *Colpichthys regis,* c) *Basilichthys australis.* AP = anterior pocket, DN = dorsal notch, RP = rounded process. Scale equals 1 mm.

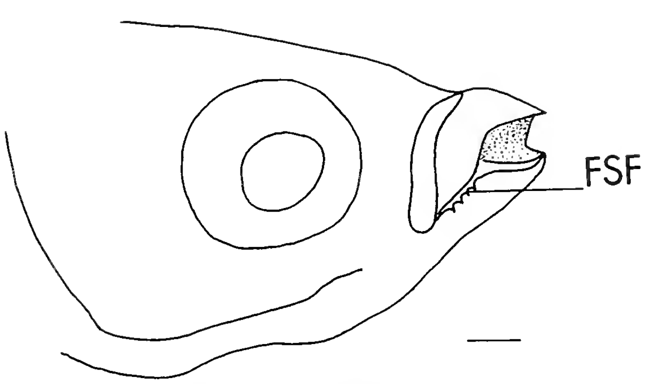

Figure 24. Lateral view of head: *Atherinops affinis.* FSF = frilled skin fold. Scale equals 1 mm.

these foramina is widespread among the other species in these genera and second, the assumption that the foramina have been lost in *O. incisus* is congruent with the other two derived character states described above.

DISCUSSION

The synapomorphic character states described in the previous section support a phylogeny of the New World atherinids (Fig. 26). Five derived character states (Node A) support the hypothesis that the Atherinopsinae (*sensu* Schultz, 1948) is monophyletic: 1) Baudelot's ligament ossified, 2) proximal end of the fourth ceratobranchial without enlarged toothplates, 3) palatine head with medial bony shelf, 4) ventral projection of nasal bone contacting lachrymal, and 5) lateral ethmoid with ventral bony knob.

The Menidiinae is proposed as the sister group of the Atherinopsinae because they share seven synapomorphies: 1) scapula and cleithrum connected by small bony struts, 2) palatine head hammer shaped, 3) premaxilla with small anterior joint and broad alveolar arm, 4) premaxilla connected to the coronoid by a short ligmanent 5) premaxilla free from maxilla ventrally, 6) ethmomaxillary ligament attached to palatine, and 7) posttemporal bone with flat anterior spine extending into posttemporal fossa of skull (Patten, 1978).

Three derived character states support the contention that the Menidiinae (*sensu* Schultz, 1948) is monophyletic: 1) parapophyses on the first vertebra directed anteriorly and blunt distally, 2) number of supraorbital canal pores reduced to four, and 3) toothplates fused to proximal end of fourth ceratobranchial.

The internal relationships of the Atherinopsinae are clarified by 18 derived character states. Three synapomorphies characterize a South American assemblage (Node B): 1) basioccipital fenestrated, 2) extrascapular composed of two bony elements, and 3) haemal arches expanded to form broad hypophyses. A North American lineage (Node C) is defined by three osteological modifications: 1) supraoccipital process trifid, 2) a pair of dorsal projections on leading edge of vomer, and 3) bifurcation of haemal spines forming expanded hypophyses. Within the northern line one group composed of the species of *Atherinops* and *Colpichthys* (Node D) is char-

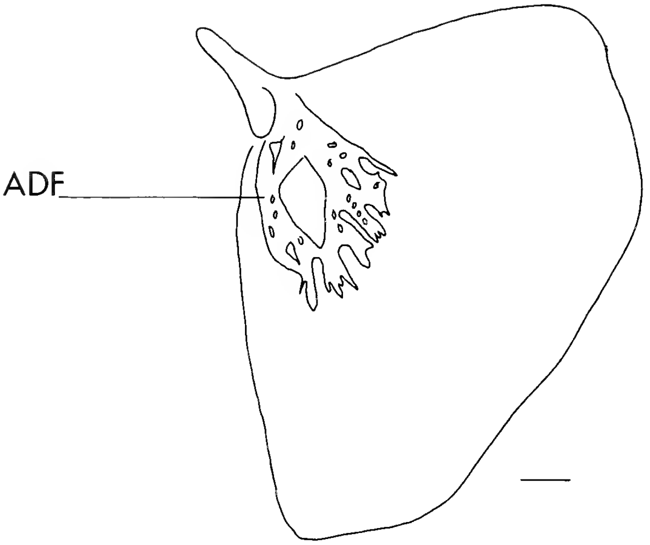

Figure 25. Medial view of right opercle: *Odontesthes regia.* ADF = anterodorsal fenestration. Scale equals 1 mm.

acterized by two derived features: 1) leading edge of quadrate angled anteriorly, not vertical, and 2) teeth bicuspid. *Atherinopsis* and *Leuresthes* comprise a second lineage (Node E) defined by two synapomorphies: 1) medial edge of lateral ethmoid produced to form a spinelike projection contacting lateral edge of parasphenoid, and 2) proximal arm of third epibranchial contorted.

Colpichthys regis and the undescribed Gulf of California species are proposed sister species sharing three derived character states: 1) dorsal process of maxilla notched, 2) teeth on third pharyngobranchial long, hairlike, and 3) paired toothplates on fourth ceratobranchial wide, gap between partners much reduced. *Atherinops* can be diagnosed by the frilled skin fold running between the distal ends of the maxilla and premaxilla.

Two South American atherinopsine groups are recognized on the basis of four synapomorphies. One assemblage, comprising the genus *Basilichthys,* is characterized by one osteological modification: ventral maxillary process with rounded projection on dorsal surface. The second assemblage, which includes all other South American atherinopsines, is defined by three derived character states: 1) mesethmoid lacking, 2) anterodorsal corner of opercle fenestrated, and 3) dorsal process of premaxilla thin and spinelike, mouth protractile.

The evolutionary relationships illustrated in Figure 26 suggest a change in the taxonomy of the Atherinopsinae. The North and South American assemblages deserve tribal status and names are proposed here for each group. The name proposed for the northern tribe, the Atherinopsini, is taken from *Atherinopsis* (Girard, 1854). The name proposed for the southern tribe, the Basilichthyini, is taken from *Basilichthys* (Girard, 1854). Both names are based on the first genus described in the tribe. None of the North American genera currently recognized need be synonymized to afford sister groups equal taxonomic rank. Four northern genera are recognized: *Atherinops, Atherinopsis, Colpichthys,* and *Leuresthes.* Included in *Colpichthys,* is the undescribed species from the Gulf of California. Two genera are recognized in the Basilichthyini: *Basilichthys* and *Odontesthes. Austromenidia* is a junior synonym of *Odontesthes.*

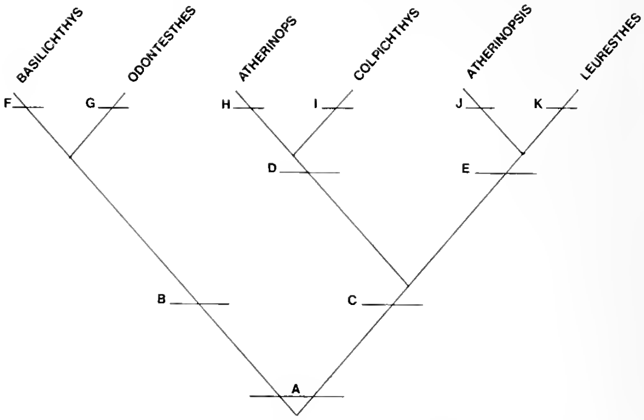

Figure 26. Generic relationships of the Atherinopsinae. Node A. Baudelot's ligament ossified, proximal end of fourth ceratobranchial with moderate toothplates, palatine head with medial bony shelf, ventral projection of nasal bone contacting lachrymal, lateral ethmoid with ventral bony knob. Node B. Basioccipital fenestrated, extrascapular composed of two bony elements, haemal arches expanded to form broad hypophyses. Node C. Supraoccipital process trifid, paired dorsal projections on leading edge of vomer, bifurcation of haemal spines forming expanded hypophyses. Node D. Anterior edge of quadrate angled forward, teeth bicuspid. Node E. Lateral ethmoid with medial process contacting parasphenoid, proximal arm of third epibranchial contorted. Node F. Maxilla ventral process with rounded projection. Node G. Anterodorsal corner of opercle fenestrated, mesethmoid lacking, mouth protractile. Node H. Skin fold running from corner of mouth to maxilla frilled. Node I. Dorsal process of maxilla notched, teeth on third pharyngobranchial hairlike, toothplates on fourth ceratobranchial expanded. Node J. Ventral process of maxilla with anterior pocket. Node K. Beach spawning habits, mouth protractile, vomer reduced, dentition reduced or lacking on jaws.

Schultz (1948) was correct in his conclusion that the Atherinopsinae and Menidiinae are distinct evolutionary assemblages. The Atherinopsinae is diagnosed cladistically by five characters; the Menidiinae by three. However, his contention that the Atherinopsinae is most closely related to an Old World subfamily, the Atherininae, is not supported by this study.

The evidence presented here supports instead the hypothesis that the Atherinopsinae and Menidiinae "represent a lineage far removed from the ancestry of Atherininae" (Patten, 1978:99), do not form a monophyletic group, and contribute two congruent, synapomorphic character states to the definition of the New World line.

Apparently, similar osteological modifications have evolved more than once in the New World atherinids. For instance, in both the Basilichthyini and Atherinopsini, the swimbladder extends into a modified haemal funnel. Independent evolution of this character is suggested by the fact that the morphology of the haemal funnel is quite different in the two atherinopsine tribes. It is problematical whether the posterior extension of the swimbladder in the northern and southern tribes evolved independently. It could be that elongation of the swimbladder occurred only once in the evolution of the Atherinopsinae and that it is a derived character state shared by all members of the subfamily. On the other hand, posterior extension of the swimbladder and the haemal funnel in the two tribes suggests that extension of the swimbladder and modification of the haemal arches are correlated because expanded haemal arches only occur in those species that have the swimbladder elongated. It seems reasonable to assume that if extension occurred only once in the Atherinopsinae, then the haemal modification in the northern and southern species would be identical. This argument is offered in support of the existence of separate North and South American tribes within the Atherinopsinae, but since its truthfulness cannot be objectively tested, posterior extension of the swimbladder is excluded from the diagnoses of the Atherinopsini and Basilichthyini.

It is interesting to note that in the atherinid subfamily most distantly related to the Atherinopsinae, the Atherininae, the swimbladder extends into modified haemal arches in several species. Some atherinine species, e.g. *Atherina boyeri,* approach the Basilichthyini in this regard. One species, *Atherinason hepsetoides,* resembles quite closely the Atherinopsini. However, the haemal arches of the Notocheirinae, Atherioninae, and Melanotaeniinae are unmodified and it has been concluded that primitively the haemal arches are unspecialized in the Atherininae (Patten, 1978). It is apparent that the similarities seen in the haemal arches of the Atherinopsinae and some atherinine species were derived independently and are nonhomologous.

The premaxilla of the two North American grunion species and the fishes of the South American genus *Odontesthes* seem to have had independent origins as well. The premaxillae of *Basilichthys, Atherinops, Atherinopsis,* and *Colpichthys* have broadly based, triangular dorsal processes and the upper jaws are not protrusile. The phylogenetic information discussed above suggests that these are the most primitive taxa in the Atherinopsinae and therefore, it is concluded that the condition of their upper jaws is the ancestral state for the subfamily. The upper jaws of *Odontesthes, Leuresthes tenuis,* and *L. sardina,* on the other hand, are protrusile and the premaxilla in these fishes has a long, slender dorsal process. However, as has already been mentioned, the placement of the elongate dorsal process in the northern and southern species is different and jaw protrusion is considered on the grounds of parsimony to have evolved more than once. Within the Atherinidae, there is a good deal of variation in the form of the premaxillary dorsal process. The premaxillae of the Atherinopsinae and Menidiinae are unique in that they have only a small anterior joint (Patten, 1978). Therefore, it would be unwise to compare jaw protrusion in the other subfamilies with those of the New World atherinids because the morphology of the upper jaws is different. However, it is interesting that jaw protrusion has evolved several times in the family (Patten, 1978) and that the genetic background of these fishes allows for the development of analogous solutions to the problem of jaw mobility.

Similar situations have been documented in other taxonomic groups. In plethodontid salamanders, it has been demonstrated that morphological specializations associated with the tongue, limbs, and digits have evolved separately on several occasions (Wake and Lynch, 1976; Larson et al., 1981). The independent evolution of similar traits has also been noted in the foot structure of gekkonine and diplodactyline geckos (Russell, 1979) and in the adaptive ecology of leptodactyline frogs (Martin, 1970).

Many systematists have studied parallel evolution and several formal definitions have been proposed. According to Simpson (1961:78), "Parallelism is the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry." Mayr (1969:202) defined parallelisms as "similarities resulting from joint possession of independently acquired phenotypic characteristics produced by a shared genotype inherited from a common ancestor." Hecht and Edwards (1976:654) stated that in parallel evolution "the character is present in the ancestral form but a common derived state has been independently evolved in each descendant form." Nelson (1978:123) proposed that "parallelism can be defined as the presence in two monophyletic taxa of a common character state which has been derived through identical successive character state changes from a dissimilar state present in the most recent common ancestor of both taxa."

The independent development of an association between the swimbladder and the haemal funnel in the Basilichthyini and Atherinopsini fits all of these definitions but the last. To meet the requirements of Nelson's definition, the haemal modifications of the Basilichthyini and Atherinopsini would have to develop in exactly the same manner and be identical in all respects. However, if this were true, it would be difficult to recognize that the northern and southern condition were independently derived. In fact, they would probably be viewed as a single derived character state shared by both tribes, definitive for the subfamily, but uninformative about its internal relationships.

It has been suggested that "the concept of parallelism be omitted from systematic studies" and "the term convergence be applied to all cases of nonhomologous character similarities" (Eldredge and Cracraft, 1980:74). In the case of the atherinopsine fishes, the haemal modifications of the Basilichthyini and Atherinopsini clearly are nonhomologous, but the development of a haemal funnel is a striking similarity that presumably evolved from the primitive condition held by their immediate common ancestor. I believe it misleading to call this an example of convergent evolution because the haemal morphology of the two tribes is divergent. However, the Atherinopsini and Basilichthyini evolved comparable haemal specializations that have the same function from a genotype inherited from their most recent common ancestor. This developmental potential passed on by the ancestral atherinopsine was expressed differently in its two descendant lineages, but they evolved in similar directions nonetheless, probably because of some unknown genetic or epigenetic constraints. In this sense, parallel evolution has occurred in the Atherinopsinae and, questions of process aside, I find the definitions of Simpson (1961) and Mayr (1969) are meaningful and useful.

KEY TO THE GENERA OF ATHERINOPSINE FISHES

1a. Supraoccipital process trifid (Fig. 8a) (sometimes bifid in *Leuresthes tenuis*); vomer with paired dorsal projections (Fig. 9); air bladder extending into haemal funnel composed of modified haemal spines (Figs. 10a, 11a); extrascapular composed of single bony element (Fig. 13a); basioccipital not fenestrated. Atherinopsini 2

1b. Supraoccipital process bifid (Fig. 8b); vomer without paired dorsal projections; air bladder extending into haemal funnel composed of modified haemal arches (Fig. 10b, 11b); extrascapular composed of two bony elements (Fig. 13b, c) (a single element in *Basilichthys semotilus* and some *Odontesthes incisus*); basioccipital fenestrated (Fig. 12). Basilichthyini 5

2a. Jaw teeth bicuspid (Fig. 22); leading edge of quadrate angled anteriorly (Fig. 21b); proximal arm of third epibranchial straight not contorted (Fig. 20b); lateral ethmoid without medial process contacting parasphenoid 3

2b. Jaw teeth unicuspid; leading edge of quadrate vertical (Fig. 21a); proximal arm of third epibranchial crooked, contorted (Fig. 20a); lateral ethmoid with medial process contacting parasphenoid (Fig. 19) 4

3a. Ventral process of premaxillary with bony pocket on anterior tip (Fig. 23a); vomer not reduced; jaws not protractile; jaw teeth not reduced . . . . *Atherinopsis*

3b. Ventral process of premaxillary without bony pocket on anterior tip; vomer reduced; jaws greatly protractile; jaw teeth minute or absent . . . . *Leuresthes*

4a. Tooth cusps equal in length (Fig. 22b); skin fold between corner of mouth and maxilla frilled (Fig. 24); dorsal process of maxilla without notch; toothplates on fourth ceratobranchial not expanded (Fig. 4a) . . . . *Atherinops*

4b. Tooth cusps unequal in length (Fig. 22a); skin fold between corner of mouth and maxilla not frilled; dorsal process of maxilla with notch (Fig. 23b); toothplates on fourth ceratobranchial expanded (Fig. 4c) . . . . *Colpichthys*

5a. Mesethmoid absent, mouth protractile; anterodorsal corner of opercle fenestrated (Fig. 25) (except in *Odontesthes incisus*); ventral process of maxilla without rounded projection on dorsal surface . . . . *Odontesthes*

5b. Mesethmoid present; mouth not protractile; anterodorsal corner of opercle not fenestrated; ventral process of maxilla with rounded projection on dorsal surface (Fig. 23c) . . . . *Basilichthys*

CLASSIFICATION AND SYSTEMATIC ACCOUNTS

Subfamily Atherinopsinae
Tribe Atherinopsini
Genus *Atherinops* Steindachner, 1876
Genus *Atherinopsis* Girard, 1854
Genus *Colpichthys* Hubbs, 1918
Genus *Leuresthes*
Jordan and Gilbert, 1880
Tribe Basilichthyini
Genus *Odontesthes*
Evermann and Kendall, 1906
Genus *Basilichthys* Girard, 1854

Subfamily Atherinopsinae Fowler, 1904

DIAGNOSIS. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob.

COMPOSITION. Six genera: *Atherinops* Steindachner, 1876; *Atherinopsis* Girard, 1854; *Basilichthys* Girard, 1854; *Colpichthys* Hubbs, 1918; *Leuresthes* Jordan and Gilbert, 1880; *Odontesthes* Evermann and Kendall, 1906.

DISTRIBUTION. West coast of North America from Vancouver Island to the Gulf of California in marine waters. Temperate South America in fresh and marine waters.

Tribe Atherinopsini Fowler

DIAGNOSIS. Supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel developed from bifurcated haemal spines.

COMPOSITION. Four genera: *Atherinops* Steindachner, 1876; *Atherinopsis* Girard, 1854; *Colpichthys* Hubbs, 1918; *Leuresthes* Jordan and Gilbert, 1880.

DISTRIBUTION. Marine waters of western North America from Vancouver Island into the Gulf of California.

Genus *Atherinops* Steindachner

Atherinops Steindachner, 1876:89 (type species *Atherinopsis affinis* Ayres, by monotypy).

DIAGNOSIS. Atherinopsines with fold of skin running from corner of mouth to distal end of maxilla frilled.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel comprised of modified haemal spines; jaw teeth bicuspid; anterior edge of quadrate angled forward.

COMPOSITION. One species, the type.

DISTRIBUTION. Outer coast and islands of Oregon, California, and Baja California.

Genus *Atherinopsis* Girard

Atherinopsis Girard, 1854:134 (type species *Atherinopsis californiensis* Girard, by monotypy).

DIAGNOSIS. Atherinopsines with pocket on anterior tip of ventral process of maxilla.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel comprised of modified haemal spines; proximal arm of the third epibranchial contorted; lateral ethmoid with medial process contacting parasphenoid.

COMPOSITION. One species, the type.

DISTRIBUTION. Outer coasts and islands of North America from Vancouver Island to Baja California.

Genus *Colpichthys* Hubbs

Colpichthys Hubbs, 1918:67 (type species *Atherinops regis* Jenkins and Evermann, by original designation).

DIAGNOSIS. Atherinopsines with notch in dorsal process of maxillary bone; toothplates on fourth ceratobranchial expanded; teeth on third pharyngobranchial hairlike.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel composed of modified haemal spines; jaw teeth bicuspid; anterior edge of quadrate angled anteriorly.

COMPOSITION. Two species: *C. regis* and a new species from Gulf of California.

DISTRIBUTION. Gulf of California.

Genus *Leuresthes* Jordan and Gilbert

Leuresthes Jordan and Gilbert, 1880:29 (type species *Atherinopsis tenuis* Ayres, by monotypy).

Hubbsiella Breder, 1936:6, figs. 2–4 (type species *Menidia clara* Evermann and Jenkins, by monotypy).

DIAGNOSIS. Atherinopsines with beach spawning habits; jaw teeth reduced or absent; mouth greatly protractile; vomer reduced.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; supraoccipital process trifid; vomer with paired dorsal projections; haemal funnel composed of modified haemal spines; proximal arm of third epibranchial contorted; lateral ethmoid with medial process contacting parasphenoid.

COMPOSITION. Two species: *L. sardina* and *L. tenuis.*

DISTRIBUTION. Outer coasts and islands of California, Baja California, and the Gulf of California.

Tribe Basilichthyini, New

DIAGNOSIS. Basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Two genera: *Basilichthys* Girard, 1854; *Odontesthes* Evermann and Kendall, 1906.

DISTRIBUTION. Temperate South America in marine and fresh waters including high Andean streams.

Genus *Basilichthys* Girard

Basilichthys Girard, 1854:198 (type species *Atherina microlepidota* Jenyns, by subsequent designation of Jordan, 1919).

Protistius Cope, 1874:66 (type species *Protistius semotilus* Cope, by monotypy).

Gastropterus Cope, 1878:700 (type species *Gastropterus archaeus* Cope, by monotypy).

Pisciregia Abbott, 1899:342 (type species *Pisciregia beardsleei* Abbott, by monotypy).

DIAGNOSIS. Atherinopsines with rounded projection on ventral process of maxilla.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Approximately 6 species; generic revision needed.

DISTRIBUTION. Marine and fresh waters of Peru and Chile.

Genus *Odontesthes* Evermann and Kendall

Odontesthes Evermann and Kendall, 1906:94, fig. 3 (type species *Odontesthes perugiae* Evermann and Kendall, by subsequent designation of Jordan and Hubbs, 1919).

Kronia Ribeiro, 1915:9 (type species *Kronia iguapensis* Ribeiro, by monotypy).

Pseudothyrina Ribeiro, 1915:11 (type species *Pseudothyrina iheringi* Ribeiro, by monotypy).

Austromenidia Hubbs, 1918:307 (type species *Basilichthys regillus* Abbott, by original designation).

Cauque Eigenmann, 1928:56 (type species *Chirostoma mauleanus* Steindachner, by original designation).

Patagonina Eigenmann, 1928:56, 60 (type species *Patagonia hatcheri* Eigenmann, by monotypy).

Patagonia Eigenmann, 1928:56 (l.c. in footnote, *lapsus pro Patagonina,* takes same type).

? *Austroatherina* Marrero, 1950, not seen, after de Buen 1953 (type species *Atherina incisa* Jenyns).

Yaci de Buen, 1953:51, figs. 31, 32, 33 (type species *Yaci retropinnis* de Buen, by monotypy).

DIAGNOSIS. Atherinopsines with mesethmoid lacking, mouth protractile, anterodorsal corner of opercle fenestrated.

DESCRIPTION. Baudelot's ligament ossified; proximal end of fourth ceratobranchial with moderate toothplates; palatine head with medial bony shelf; ventral projection of nasal bone contacting lachrymal; lateral ethmoid with ventral bony knob; basioccipital ridged and fenestrated; extrascapular composed of two bony elements; haemal funnel developed from expanded haemal canals.

COMPOSITION. Approximately 10 species; generic revision needed.

DISTRIBUTION. Temperate South America in marine and fresh waters from Peru to southern Brazil. Also Malvinas and Juan Fernandez Islands.

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CONTRIBUTIONS IN SCIENCE

A REVIEW OF THE GENERA OF CLEPTOPARASITIC BEES OF THE TRIBE ERICROCINI (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling and Robert W. Brooks

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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A REVIEW OF THE GENERA OF CLEPTOPARASITIC BEES OF THE TRIBE ERICROCINI (HYMENOPTERA: ANTHOPHORIDAE)

Roy R. Snelling[1] and Robert W. Brooks[2]

ABSTRACT. The genera comprising the New World bee tribe Ericrocini are reviewed. Each genus is separated by a key, is described, its included species-group names listed, and pertinent morphological features illustrated. Nine genera are recognized: *Mesoplia* (=*Melissa*) and its new subgenus *Eumelissa* (type species, *Melissa decorata* F. Smith), *Hopliphora* (=*Eurytis* = *Oxynedys* = *Cyphomelissa*), *Mesonychium* (=*Epiclopus*), *Ericrocis*, *Abromelissa* (new genus; type species, *Melissa lendliana* Friese), *Aglaomelissa* (new genus; type species, *Melissa duckei* Friese), *Ctenioschelus* (=*Melissoda*), *Mesocheira*, and *Acanthopus*.

A cladistic analysis of the Ericrocini is included.

Known hosts are listed in a table.

INTRODUCTION

The Ericrocini are a New World tribe of cleptoparasitic bees largely centered in the Amazonian Basin. So far as known, all hosts are within the related tribe Centridini. Despite their attractive appearance, these moderate- to large-sized bees have received scant attention from taxonomists, probably due largely to their rarity in collections.

HISTORICAL RESUME

The first ericrocine genus to be described was *Acanthopus*, proposed by Klug (1807) for a single South American species. Lepeletier and Serville (1825) described *Mesonychium* (monobasic) and *Mesocheira* (three species). *Ctenioschelus* was described by Romand (1840) for a single, bizarre species and in 1841 Lepeletier described *Melissoda* (later shown to be isogenotypic with *Ctenioschelus* through synonymy), *Mesoplia* and *Hopliphora*. Shuckard (1840) named *Ischnocera*, with no included species, but it has long been recognized as an obvious synonym of *Ctenioschelus*.

F. Smith (1854) added two new genera, *Eurytis* (monobasic), and *Melissa* (four species). All these genera were placed in his subfamily Denudatae, together with such genera as *Melecta*, *Thalestria*, and *Liogaster*. He recognized *Eurytis*, *Melissa* (=*Mesoplia*), *Mesocheira*, *Ctenioschelus* (=*Melissoda* = *Ischnocera*) and *Acanthopus*. The one Nearctic genus, *Ericrocis*, was described by Cresson (1887) for a single species.

Ashmead (1899) assigned these bees to the family Nomadidae, recognizing the genera *Ericrocis*, *Eurytis* (=*Hopliphora*), *Melissa*, *Mesocheira*, *Mesonychium*, and *Acanthopus* (=*Ctenioschelus*). A few years later, Schrottky (1902) produced his key to the Brazilian genera of Nomadidae, recognizing *Melissa*, *Eurytis*, *Mesocheira*, *Ctenioschelus*, and *Acanthopus*, to which he added two new genera: *Cyphomelissa* and *Oxynedes*.

For the next 40 years, Schrottky's generic concepts were more or less followed by Cockerell, Ducke, and Friese, the principal describers of Neotropical bees during that time. Generic limits were flexible and considerable confusion existed regarding the application of the names *Melissa*, *Mesonychium*, and *Mesoplia*. These three names were very inconsistently used, but in general *Melissa* was used to contain most species in preference to *Mesoplia*, and *Mesonychium* fell heir to those species which seemed not to be *Mesoplia*.

The Nearctic genus, *Ericrocis*, was included in the Melectinae by Linsley (1939) who noted, however, its uniqueness and commented that it is "perhaps . . . an offshoot from some group like *Epicharis*, which Grutte considers to be ancestral to *Acanthopus* and *Rathymus*." As Linsley noted, Cockerell and Atkins (1902) had earlier emphasized the unusual features of *Ericrocis* and related genera, and suggested that a separate subfamily might be appropriate for these bees.

When Michener (1944) reorganized the higher classification of the bees, he placed *Ericrocis*, and such similar genera as *Acanthopus*, *Mesocheira*, and *Ctenioschelus*, in the tribe Ericrocini, near the Centridini. He clearly set forth the dif-

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ferences between the Ericrocini and such cleptoparasitoid groups as Melectini, Epeolini, and Nomadini.

The last author to deal with the group, more or less as a whole, was Moure (1946). The geographic scope of this work was limited to Brazil, but since nearly all the genera occur there, the treatment was nearly complete. Moure recognized, and separated in a key, *Ctenioschelus, Mesonychium, Mesoplia, Hopliphora, Cyphomelissa, Acanthopus,* and *Oxynedis* (a misspelling of *Oxynedys*). Under Moure's concepts, *Mesoplia* included *Melissa,* and *Epiclopus* fell into *Mesonychium.*

TERMINOLOGY

In general, the morphological terminology follows that established by Michener (1944), Michener and Fraser (1978), and Winston (1979). A few terms used here necessitate explanation. The *interantennal distance* is the shortest distance between the inner margins of the antennal sockets. The *antennal socket diameter* is the maximum transverse distance across the antennal socket, from inner margin to outer margin. The *antennocular distance* is the shortest distance between the outer margin of the antennal socket and the inner eye margin.

As in most bees, the short anterior face of the mesepisternum and the much longer lateral face meet in a curved surface. Sometimes, this juncture is marked by a raised carina, the *anterior mesepisternal carina* (amc, Fig. 70). In most ericrocines that possess this carina, it is thin, translucent, and lamelliform. Ventrally, the anterior mesepisternal carina usually is confluent with a carina that bounds the posterior portion of the procoxal cavity; this is the *acetabular carina* (acc, Fig. 70) (Bohart and Menke, 1976). In a few ericrocines (e.g., *Acanthopus*), there is a low, rounded, shiny ridge which begins in front of the metacoxa and extends for a short distance onto the lateral face of the mesepisternum, the *sternopleural ridge* (spr, Fig. 70). In most genera, the mesepisternum slopes abruptly toward the coxal cavity, but there is no definite shiny ridge. The *supraspiracular ridge* originates dorsolaterally on the propodeum and extends posteriorly, above the propodeal spiracle. The ridge is said to be *strong* if it terminates in a blunt tooth or projection, *weak* if it becomes evanescent apicad.

Male genital structures are somewhat confusing. The gonostylus is, in dorsal view, short, broad and more or less flattened. In some genera the gonostylus is simply a very broad, somewhat flattened structure, bearing diagnostic gonostylar setae, but with little, if any, dorsal lobe. Dorsal lobes are present in such genera as *Mesoplia, Abromelissa,* and *Acanthopus;* they may be present or absent in *Hopliphora.* When present, the dorsal lobe is usually narrow, thin, lightly sclerotized and always setose (Fig. 22). A second, much shorter and broader, lobe may also be present immediately above the base of the longer lobe.

In some genera there is a distinctive, heavily sclerotized plate along the inner, basal portion of the gonostylus. No similar structure is known within the Centridini or Rhathymini. For want of a better term this structure is here called the *inner* apical sclerotization of the gonocoxite.

SYSTEMATICS

Although there are parasitic bee species in other families, the greatest diversity, in numbers of genera and of species, is within the Anthophoridae. One subfamily, the Nomadinae, is exclusively parasitic and includes the majority of the species in such large genera as *Nomada, Hypochrotaenia,* and *Epeolus.* The few remaining parasitoid groups are mostly in the Anthophorinae: Melectini, Rhathymini, and Ericrocini.

The most conspicuous difference between these three tribes, as a group, and the worldwide Nomadinae is that females of Nomadinae, with some exceptions (especially in the Old World), possess a distinct, usually beveled, prepygidial fimbria or brush on the distal portion of the fifth abdominal tergum. Most Nomadinae females, and often the males as well, have a conspicuous, sharply defined, pygidial plate that is commonly about one-half as broad at the base as the width of the sixth tergum. Females of the Nomadinae (except *Hexepeolus*) have only five exposed metasomal sterna (six exposed sterna in cleptoparasitic Anthophorinae) and the legs are commonly spiculate or tuberculate. In both sexes the second abscissa of vein M+Cu of the hind wings is usually at least twice as long as the (usually) transverse cu-v; in those groups in which the second abscissa is not twice as long as cu-v, the labrum is conspicuously longer than broad. The apical portions of the wings are not papillate, as they are in the Ericrocini.

The Melectini are a worldwide group that includes the genera *Melecta* and *Thyreus* and a few smaller genera. *Melecta* is a Holarctic genus that appears to be limited to northern temperate regions and *Thyreus* is an exclusively Old World genus that is primarily southern, reaching South Africa and Australia. The hosts are mostly within the related pollen-gathering tribe Anthophorini, from which the Melectini are presumed to be derived.

Characteristics by which the Melectini differ from the Ericrocini are: the marginal cell barely, or not at all, exceeds the last submarginal cell; the mesotibial spur is not modified; the male gonostyli are slender and elongate; the mesobasitarsus is more or less rounded in cross section and is without a cariniform ridge along the posterior margin, whereas, in the Ericrocini they are laterally flattened, with a cariniform ridge (except *Acanthopus* and *Hopliphora*); the labrum is about as long as broad (except *Zacosmia*) and has a distinct basal bulla on either side; and, the meso- and metatibiae of the females are provided with coarse, spine-like setae.

The Rhathymini are exclusively Neotropical; there are fewer than half a dozen species, all placed in the genus *Rhathymus.* Known hosts are species of Centridini. The Rhathymini are, like the Ericrocini, presumed to be derived from the Centridini and the two groups have many shared character states, e.g., the general pattern of the wing venation, the lack of spine-like setae on the meso- and metatibiae of the females, the configuration of the scutellum and of the face, as well as other features. Rhathymini differ from Ericrocini in the presence of basal bullae on the labrum, the wings are hairy, the papillae are smaller and have hairs, the mesotibial spur is unmodified, and the body is without appressed, metallic scale-like hairs.

Tribe Ericrocini

Ericrocini Cockerell and Atkins, 1902:46. Michener, 1944: 288; 1954:145.

Ctenioschelini Michener, 1965:10. NEW SYNONYMY.

Medium-sized to large, robust bees, often with distinct patterns of white and iridescent blue, green or purple reflective scales and/or hairs, especially on abdomen.

Head conspicuously narrower than thorax, which is broader than long or deep; labrum broader than long, with transverse preapical ridge or median tubercle; clypeus about twice wider than long, apical margin broadly concave; lateral angle confluent with inner eye margin or nearly so. Malar space virtually absent. Mandible simple or with a single preapical tooth; posterior angle below middle of lower end of eye. Postflabellum present. Maxillary palpus with 1–4 segments. Antenna short, except in male *Ctenioschelus;* scape robust, shorter than combined lengths of first three flagellar segments; first flagellar segment short, little, if any, longer than broad (except male *Ctenioschelus*).

Pronotum short, collar closely appressed to front of mesoseutum; scutellum usually bituberculate. Three submarginal cells present in forewing; marginal cell considerably exceeding third submarginal cell; distal part of wings strongly papillate, basal part sparsely hairy; jugal lobe of hindwing no more than one-third as long as vannal lobe; second abscissa of M+Cu sometimes absent, always shorter than oblique cu-v and less than one-half as long as M. Mesotibial spur bifid or multidentate at apex; tarsal claws with large inner basal lobe or tooth; tarsal arolia absent (except *Ctenioschelus*).

Female pygidial plate often poorly defined; prepygidial fimbria absent; female sternum 6 with longitudinal median carina. Male tergum 7 bilobate or bidentate at apex; gonostylus squamiform in dorsal view.

The tribal name Ericrocini was first proposed by Cockerell and Atkins (1902) to include the Nearctic genus *Ericrocis.* Ctenioschelini was first introduced by Michener (1965). Even though *Ctenioschelus* is an older generic name than *Ericrocis,* the Law of Priority applies to tribal names and Ericrocini thus remains the correct name for this group.

DISCUSSION

The affinities of the Ericrocini have been obscure, though they have been presumed to be derived from the Centridini which are their hosts, perhaps via the same stock from which *Epicharis* is derived.

CLADISTIC ANALYSIS

The proboscis is considered to be directed downward so that it has anterior and posterior surfaces, thus Figures 70 and 72 show the posterior surface of the labiomaxillary complex.

The cladogram was made with aid of the computer program PAUP (Swofford, 1984). *Caenonomada,* which is undoubtedly the centridine genus with the most ancestral traits, was considered as the outgroup using ordered, unweighted character (i.e., 0 = primitive, 1 = derived, 2 or more = more derived characters of a transformation series). Polarity decisions were also decided considering "primitive" anthophorids such as Exomalopsini and in some cases short-tongued bees. Variables which exhibit two or more characters within a taxon were scored as the most primitive character found in that taxon. For example in variable 33 not all species of *Mesonychium* have flattened setae, on their meso- or metadistitarsus, so the absence of these setae, which is a plesiomorphy, was used for *Mesonychium* in the cladistic analysis. The reasoning is that the plesiomorphic, rather than the apomorphic, character will best show the relationships to other taxa. Therefore the characters of the most primitive members would be more useful in elucidating cladogenesis.

Table 1 is a list of 67 variables relevant to the Ericrocini, Rhathymini, and Centridini. Polarities of variables were ascertained by consideration of the Centridini, from which the ericrocine bees were presumably derived. Table 2 gives the raw data. The Centridini are solitary, nest-making bees. Before 1944 the Centridini had often also included exomalopsine bees, but since Michener (1944), the Centridini has included only *Centris* and *Epicharis.* Snelling (1984) elevated *Ptilotopus,* previously a subgenus of *Centris,* to generic standing. For purposes of outgroup comparisons we are including a fourth genus *Caenonomada,* in the Centridini. *Caenonomada* is the most "primitive" centridine bee, having previously been placed in the Exomalopsini (Michener and Moure, 1957). The reasons for this transfer will be given in a subsequent paper. The Centridini may be paraphyletic. *Centris, Epicharis,* and *Ptilotopus* share some apomorphies with the Ericrocini, which are not shared with *Caenonomada,* such as fusion of gonostylus with apex of gonocoxite, loss of arolia, the elongate, narrowed flabellum which has a cobblestone-like posterior surface, profile of the scutellum vertical to overhanging the metanotum, profile of the metanotum more or less vertical, the elongate mesocoxae, the stigma not extending into the marginal cell and not wider than the prestigma (measured to the costal margin of the wing), and alar papillae large and not ending in hairs [except *Epicharis* (*Epicharoides*) and *E.* (*Epicharitides*) which have alar papillae small and ending in hairs]. Therefore *Caenonomada* may be the sister group to the rest of the Centridini and Ericrocini. For purposes of this study we consider Centridini paraphyletic.

The Rhathymini are shown as the sister group to Ericrocini (Fig. 78a) or as the sister group to Ericrocini plus Centridini (Fig. 78b). *Rhathymus* shares with *Caenonomada* and/or *Epicharis* plesiomorphic hairy wings, small alar papillae ending in hairs, a hairy propodeal triangle, presence of arolia, presence of basal bullae on labrum, and unmodified mesotibial spurs, all of which are not shared with Ericrocini. The many common synapomorphies of the Rhathymini and Ericrocini could be convergences somewhat reminiscent of convergences between ericrocine and nomadine or melectine

Table 1. List of variables. Apomorphies are discussed first under each character (plesiomorphies are in brackets; their symbols for Table 2 are 0).

1. Labrum with preapical ridge or tubercle (1). [Labrum simple.] This ridge is not found in Centridini and is an obvious apomorphy of Ericrocini.

2. First flagellar segment of female differentiated, longer than others and shorter to longer than scape (1). [First flagellar segment of female not differentiated, more or less similar in length and shape to following segments.] A non-differentiated first flagellar segment is a plesiomorphy for bees in general and is typical of sphecoid wasps, short-tongued, and exomalopsine bees. Primitive centridine bees possibly had a slightly differentiated first flagellar segment as seen in *Caenonomada*. The highly derived centridines have a very long first flagellar segment. If such Centridini are ancestral to Ericrocini, their undifferentiated first flagellar segment is apomorphic. If Centridini is monophyletic (*sensu* Hennig), i.e., the sister group to Ericrocini, the ericrocine first flagellar segment would be primitive.

3. Inner eye margins divergent above (1). [Inner eye margins more or less parallel.] In nearly all Ericrocini and in all Centridini the inner eye margins are more or less parallel. The divergent eye margins apparently have appeared twice, once in *Ericrocis* and once in the *Mesonychium* group.

4. Male flagellar segments greatly elongated, flagellum longer than body (1). [Male flagellar segments normal, length of a segment about equal to width.] The bizarre greatly elongated flagellum of *Ctenioschelus*, reminiscent of long-horned beetles, is an obvious apomorphy.

5. Mandible of female simple, without subapical tooth (pollex) on upper margin (1). [Mandible of female with subapical tooth on upper margin.] Typically bees have toothed mandibles; loss of this tooth is derived.

6. Paraglossa two-thirds as long as prementum or longer (1). [Paraglossa less than two-thirds as long as prementum.] Short paraglossae are found in short-tongued and exomalopsine bees and are considered ancestral. Centridini as well as ericrocine bees have short paraglossae except the *Hopliphora* group.

7. Stipes without comb (1). [Stipes with comb.] Most non-parasitic long-tongued bees have stipital combs. Almost all parasitic anthophorids have lost the comb but have retained the preapical concavity which housed the comb of bristles. The presence of the comb is a plesiomorphy and its loss an apomorphy associated with parasitic habits.

8. Lower end of anterior conjunctival thickening [=suspensory thickening of Winston (1979)] near basal third of prementum (1). [Lower end of anterior conjunctival thickening near base of prementum.] Colletid and andrenid bees have the lower end of the anterior conjunctival thickening near the basal third of the prementum. This is the primitive character for Apoidea, whereas halictids and nearly all long-tongued bees have the lower end of the anterior conjunctival thickening near the base of the prementum. *Acanthopus* has presumably reverted (for Apoidea) to the ancestral condition which is an apomorphy for Ericrocini.

9. First segment of labial palpus less than twice as long as second (1). [First segment of labial palpus at least twice as long as second.] Short-tongued bees have the first and second labial palpal segments nearly the same length. The evolutionary trend has been toward a shortening of the second segment and/or lengthening of the first segment either of which is derived for Apoidea. In the Ericrocini and Centridini the comparatively short first segment of the labial palpus is found only in *Acanthopus* and is an apomorphy as is the apomorphy of character 8.

10. Mentum appearing Y-shaped because of deep apical emargination (Fig. 73) (1). Mentum appearing U-shaped because of deeper emargination (Fig. 71) (2). [Mentum with little if any apical emargination.] The mentum of most long-tongued bees is long, narrow and apically with little or no emargination. The deep apical emargination of the mentum of the Ericrocini is characteristic for this tribe (Fig. 73) and *Nomada* (Nomadinae) although in *Mesoplia* the emargination is not strong (Fig. 76). *Acanthopus* has the most derived mentum in that it is so deeply divided that it appears U-shaped.

11. Lorum basally divided such that the loral apron is separate sclerites held together by membrane (1). [Lorum V-shaped.] The lorum in Centridini as well as other anthophorids is V- or Y-shaped (Fig. 73). *Acanthopus* has a uniquely apomorphic lorum, basally divided such that the loral apron (Michener, 1985) is two sclerites held mediobasally by membrane and is fused to the cardines (Fig. 71).

12. Postflabellum present (1). [Postflabellum absent.] The postflabellum (Michener and Brooks, 1984) is unique to the ericrocine bees and is an obvious apomorphy.

13. Forewing tips (and sometimes marginal cell) infuscated with rest of wing clear (1). [Forewing tips concolorous with rest of wing, clear or infuscated.] Infuscated wing tips have appeared convergently many times in the Apoidea. The primitive condition of a concolorous wing, whether infuscated or clear, is found in most bees including the Centridini and most Ericrocini. Only the *Ctenioschelus* group and some *Mesoplia* have infuscated wing tips although they are variable in *Ctenioschelus* since the Middle American populations have less distinctive infuscation than the Brazilian ones.

14. Maxillary palpus with three or four segments (1). Maxillary palpus with one or two segments (2). Maxillary palpus absent or represented by a small bump fused to stipes (3). [Maxillary palpus with five or six segments.] The maxillary palpus primitively has six segments as seen in most bees including *Caenonomada*. Other centridines have five segments. The evolutionary direction in the ericrocines has been reduction and sometimes fusion of segments, culminating in complete loss of the palpus in *Acanthopus*.

15. Metasomal integument with metallic reflection (1). [Metasomal integument without metallic reflection.] Note that this statement refers to the color of the *integument*, not the metallic body hairs. The plesiomorphic condition is found in most Centridini [*Centris* s. str., some *C.* (*Paracentris*), and *C.* (*Wagenknechtia*) have metallic terga] and almost all Ericrocini where the integument is black to red-brown with no metallic reflections. Only *Abromelissa* has the apomorphic metasomal integumental color which is metallic blue.

16. Vestiture metallic in color (1). [Vestiture non-metallic.] The primitive condition is found in Centridini and *Ericrocis*. All other ericrocines have metallic vestiture.

17. Profile of scutellum vertical or at least at strong angle to scutum (1). Profile of scutellum overhanging metanotum (2). [Profile of

scutellum with posterior part more or less horizontal to a 45° angle.] Most of the short-tongued and exomalopsine bees have the primitive type of scutellum as does *Caenonomada.* The ericrocines, like the rest of the centridines, have an apomorphic scutellum whose profile is vertical and additionally overhangs the metanotum in *Mesoplia, Abromelissa,* and the *Ctenioschelus* group.

18. Profile of metanotum vertical (1). [Profile of metanotum slanting, more or less at a 45° angle.] Most short-tongued bees, all exomalopsine bees and *Caenonomada* have the plesiomorphic type of metanotum which slants. All the rest of the centridines and ericrocines have an apomorphic, more or less vertical metanotum.

19. Propodeal triangle hairless (1). [Propodeal triangle hairy.] A propodeal triangle with hair is found in all Centridini. The Ericrocini have a hairless propodeal triangle which is presumably an apomorphy, although many other bee groups possess this character.

20. Propodeum in profile with horizontal basal zone short, less than one-third as long as declivous surface (1). Propodeum in profile entirely declivous (2). [Propodeum in profile with horizontal basal zone long, about two-thirds as long as declivous surface.] Most "primitive" anthophorids and *Caenonomada* have a propodeum with a long horizontal basal zone. The evolutionary trend has been a shortening of this zone.

21. Jugal lobe shortened, one-third to one-half as long as vannal lobe measured from wing base (1). Jugal lobe short, one-fourth to less than one-third as long as vannal lobe (2). Jugal lobe very short, less than one-fourth as long as vannal lobe (3). [Jugal lobe long, apex much nearer vannal incision than wing base.] The evolutionary direction has been a shortening of the jugal lobe from a plesiomorphic long lobe of about three-fourths the length of the vannal lobe (as in *Caenonomada*) to a smaller one.

22. Hindwing with second abscissa of M+Cu almost absent to half the length of the crossvein cu-v (1). [Hindwing with second abscissa of M+Cu about equal in length to crossvein cu-v, second abscissa of M+Cu 0.75 to less than 1.50 times as long as crossvein cu-v.] In the Centridini the second abscissa of the M+Cu is about equal to the length of vein cu-v. The evolutionary trend in the Ericrocini has been toward a shortening of the second abscissa of the M+Cu which has culminated in its near to complete absence.

23. Hindwing with second abscissa of M+Cu considerably shorter than M (1). [Hindwing with second abscissa of M+Cu about as long as vein M.] This character is correlated with the previous character because as the second abscissa of M+Cu shortens (which is primitively almost equal in length to vein M as seen in short-tongued and exomalopsine bees), vein M will obviously be lengthened.

24. Hindwing with crossvein cu-v slanted toward wing base from second abscissa of M+Cu (1). [Hindwing with crossvein cu-v perpendicular to slanted apically to wing tip from second abscissa of M+Cu.] The hindwing of short-tongued bees generally has vein cu-v perpendicular to or slanted apically to wing tip from the second abscissa of vein M+Cu. Generally in the derived anthophorids this crossvein has become slanted toward wing base from the second abscissa of M+Cu.

25. Stigma not or scarcely extending into marginal cell, not wider than prestigma measured to costal margin of wing (1). [Stigma slender, posterior margin angulate at base of vein R, extending into marginal cell but oblique and straight there, not or little wider than prestigma.] *Caenonomada* has a moderately large stigma that extends into the marginal cell. A slendering of the stigma and its decreasing extension into the marginal cell is the derived condition. *Caenonomada* has a stigma intermediate between most exomalopsines and the rest of the centridines.

26. Stigma about as long as prestigma (1). Stigma shorter than prestigma, absent to nearly absent (2). [Stigma longer than prestigma.] The plesiomorphic long stigma as seen in *Caenonomada* has apomorphically decreased in length until it is nearly absent in the other Centridini, but it has decreased in length somewhat less in the Ericrocini.

27. Wings bare or with small patches of hair (1). [Wings hairy throughout or at least over large areas.] Hairy wings are found in the Exomalopsini, Melitomini, Eucerini, *Caenonomada,* and *Epicharis.* The Ericrocini have lost the hair.

28. Alar papillae large, not ending in hairs (1). [Alar papillae small and ending in hairs.] "Primitive" anthophorids, *Caenonomada,* and two subgenera of *Epicharis* (*Epicharoides* and *Epicharitides*) have alar papillae that end in hairs. In the other Centridini and the Ericrocini the papillae have become larger and have lost the small apical hairs.

29. First recurrent vein distad to interstitial, or nearly so with 1st transverse cubital vein (1). [First recurrent vein intersecting distal half of posterior margin of submarginal cell 2.] The first recurrent vein intersects the distal half of the posterior margin of submarginal cell 2 in all Centridini. The interstitial first recurrent and 1st transverse cubital veins in Ericrocini is an apomorphy. The polarity of this character is reversed for the Apoidea since exomalopsine, melitomine, and eucerine bees have the first recurrent and 1st transverse cubital interstitial.

30. First recurrent vein (as well as second) intersecting submarginal cell 3 (1). [First recurrent vein basad to interstitial with 1st transverse cubital vein.] In almost all apoids the first recurrent vein intersects submarginal cell 2 or is interstitial with the vein shared by submarginal cells 2 and 3. It is extremely rare to find the first and second recurrent veins entering submarginal cell 3. This is an obvious apomorphy and unique to *Acanthopus* among the ericrocine-centridine bees.

31. Marginal cell short, length less than 1.2 the distance from apex of marginal cell to wing tip (1). Marginal cell very short, length less than 0.7 the distance from apex of marginal cell to wing tip or marginal cell very long, length 1.8 the distance from apex of marginal cell to wing tip (2). [Marginal cell long, length 1.2–1.45 the distance from apex of marginal cell to wing tip.] Primitively the marginal is long, longer than the distance from the apex of the marginal cell to the wing tip. This plesiomorphy is seen in exomalopsine bees as well as *Epicharis* and *Caenonomada.* This Y-shaped variable consists of an apomorphic shortening in the Ericrocini starting from a long marginal cell, but in *Acanthopus* the evolutionary direction apparently changed to a lengthening of the marginal cell.

32. Mesobasitarsus laterally compressed, posterior margin carinate (1). [Mesobasitarsus somewhat round in cross section to slightly compressed, posterior margin not carinate.] The posterior margin of the mesobasitarsus is commonly compressed and carinate, terminating in a blunt tooth or spur that extends beyond the end of the segment. Its presence, found in most ericrocines, is an apomorphy since the Centridini lack it.

Table 1. Continued.

33. Meso- and/or metadistitarsi with flattened setae (1). [Meso- and/or metadistitarsi normal, without flattened setae.] The dark flattened setae of the meso- and/or metadistitarsi have presumably arisen twice in the Ericrocini. *Ericrocis* and most *Mesonychium* have this apomorphy not found in the Centridini.

34. Metadistitarsus five times longer than wide (1). [Metadistitarsus at most four times longer than wide.] The greatly elongated metadistitarsus of *Acanthopus* is unique in the Ericrocini and Centridini.

35. Arolia absent (1). [Arolia present, small.] The primitive centridine *Caenonomada* has small arolia. Arolia have been lost in all other centridines and ericrocines except in *Aglaomelissa* and *Ctenioschelus* in which they are small. The loss of arolia is certainly an apomorphy since almost all bees and sphecoid wasps have arolia. If the cladogram is correct it is very unlikely that the presence of arolia in *Aglaomelissa* and *Ctenioschelus* is independently derived since the arolium is a complex structure, composed of many parts, all of which are present in these two as in other aroliate bees. Moreover, it would be improbable if their presence requires five independent losses of arolia in the other Ericrocini. We believe that, assuming the accuracy of the cladogram, the origin of arolia in *Aglaomelissa* and *Ctenioschelus* is best explained as a reversion due to reactivation of genes that were suppressed during much of centridine and ericrocine evolution.

36. Mesotibial spur modified with several apical teeth (1). [Mesotibial spur normal, apically simple.] The modified mesotibial spur of the Ericrocini is an obvious apomorphy which the Centridini do not possess.

37. Females with tooth of tarsal claw a flattened basal lobe (1). [Female with tooth of tarsal claw not a flattened basal lobe.] The modified tooth becoming a flattened lobe is an apomorphy of Ericrocini which has convergently appeared at least three times in the Anthophoridae. Almost all non-parasitic bees have the plesiomorphic toothed claw, whereas all Ericrocini, Rhathymini, Melectini, and almost all Nomadinae have the tooth a flattened basal lobe.

38. Strigilar malus without teeth (1). [Strigilar malus with teeth.] Primitively the strigilar malus has teeth as found in many short-tongued bees. The loss of the teeth has occurred twice in the Ericrocini, once in the *Mesonychium* group and again in *Aglaomelissa*. This character may be of little phylogenetic significance since it is so variable throughout the Anthophoridae but it further unites the *Mesonychium* group and may prove valuable for future studies.

39. Scopa absent (1). [Scopa present.] All non-parasitic female bees have scopae [except Hylaeinae (Colletidae)]. The loss of the scopa is an obvious apomorphy seen in the Ericrocini and to varying degrees in all parasitic bees.

40. Anterior mesepisternal carina present (1). [Anterior mesepisternal carina absent.] The junction of the short anterior face and the long lateral face of the mesepisternum is rounded in Centridini. The apomorphic state has apparently appeared twice, once in *Acanthopus* and again in the *Ctenioschelus* group though lacking in *Ctenioschelus*.

41. Sternopleural ridge present (1). [Sternopleural ridge absent.] The presence of the sternopleural ridge is an apomorphy found only in the *Hopliphora* group.

42. Supraspiracular ridge well developed, terminating abruptly in a blunt tooth-like process (1). [Supraspiracular ridge weak to absent.] The supraspiracular ridge is not developed in Centridini and many ericrocines. It is developed in the *Mesonychium* and *Ctenioschelus* groups (except *Aglaomelissa*).

43. Scutellum bilobed (1). Scutellum bilobed and projecting over propodeum (2). [Scutellum not projecting over propodeum, simple.] In Centridini as in most non-parasitic anthophorids the scutellum is not modified. The scutellum is commonly modified in most parasitic anthophorids and all Ericrocini. The modification in ericrocine bees is the presence of two rounded lobes which are further modified in the *Ctenioschelus* group (except *Aglaomelissa*) as dorsoventrally flattened plate-like eminences extending over the vertical metanotum and propodeum.

44. Midcoxal length 1.00–1.35 length of distance from summit of coxa to hind wing base (1). Midcoxal length at least 1.36 length of distance from summit of coxa to hind wing base (2). [Midcoxal length 0.85–0.99 length of distance from summit of coxa to hind wing base.] In many parasitic anthophorine bees the midcoxa has become elongated as well as more exposed and hence is a further derivation as seen in most ericrocines (except the reversion found in the *Mesonychium* group) and centridines (except *Caenonomada*).

45. Hind basitarsus of female with distal process, not provided with a pencillus (1). [Hind basitarsus of female with distal process ending in a pencillus.] Almost all non-parasitic anthophorid bees have a pencillus. The loss of the pencillus in almost all parasitic bees is an apomorphy.

46. Basitibial plate absent or only represented by a carina (1). [Basitibial plate of female present, well developed.] The basitibial plate present in female Centridini has been lost in the Ericrocini as well as most other parasitic bees and is an apomorphy.

47. Basitibial plate of male incomplete, represented by a scale or series of tubercles (1). Basitibial plate absent or only represented by a carina (2). [Basitibial plate of male present, well developed.] Male Centridini have well-developed basitibial plates (except *Centris*). The loss of these plates in male Ericrocini is an apomorphy.

48. Dorsum of metasomal tergum 1 subangulate in profile (Fig. 77) (1). [Dorsum of metasomal tergum 1 rounded in profile (Fig. 76).] Usually, the vertical and horizontal faces of the first metasomal tergum, as viewed in profile, meet in a distinctly rounded angle, the junction, however, may be so narrowly and abruptly rounded as to appear angulate. This is an obvious apomorphy of the *Ctenioschelus* group.

49. Prepygidial and pygidial fimbriae absent (1). [Prepygidial and pygidial fimbriae present.] The Centridini as well as all non-parasitic anthophorine bees have prepygidial and pygidial fimbriae. The loss of these fimbriae in the Ericrocini is derived.

50. Metasomal terga with patches of appressed white hair (1). [Metasomal terga, without patches of appressed white hair.] The Centridini have the metasoma with long, erect to suberect hair and/or entirely covered with appressed hair or virtually all bare. Most ericrocines have patches of white hair either laterally on the terga or in various patterns, but this apparently has been reversed in the *Hopliphora* group and *Abromelissa*. This apomorphy has arisen many times in other parasitic anthophorids.

Table 1. Continued.

51. Metasomal sternum 3 of male with dense lateral patch of white hair (1). [Metasomal sternum 3 of male simple, without dense lateral patch of white hair.] The Centridini lack the dense lateral patch of white hair on metasomal sternum 3. All Ericrocini have this apomorphy except the *Hopliphora* and *Mesonychium* groups.

52. Metasomal sterna 4 and/or 5 of male with dense apical band of long curved hair (1). [Metasomal sterna 4 and 5 of male simple without apical band of long curved hair.] *Caenonomada, Epicharis,* and the Ericrocini (except *Mesoplia* and *Mesonychium*) share the apomorphy of an apical band of long curved hair on metasomal sterna 4 and/or 5. "Primitive" anthophorids such as Exomalopsini, Melitomini, and Eucerini lack bands.

53. Metasomal sternum 5 (and sometimes 4) on basal half of disc with felt-like pad of dense hair (1). [Metasomal sternum 5 and 4 simple, without felt-like pad of dense hair.] The presence of a felt-like pad of short pubescence on metasomal sternum 5 (and sometimes 4) which Centridini lacks is an obvious apomorphy found in all Ericrocini except the *Mesonychium* group.

54. Male metasomal sternum 4 concealed (1). [Male metasomal sternum 4 normal, not concealed.] Because the margins of the fourth metasomal sternum may be broadly incurved, each segment may be largely hidden under the preceding segment. This apomorphy is found scattered throughout the Ericrocini.

55. Male metasomal sternum 5 concealed (1). [Male metasomal sternum 5 normal, not concealed.] See discussion for character 54.

56. Female metasomal sterna 2–5 longitudinally carinate medially (1). [Female metasomal sterna 2–5, not carinate medially.] Female ericrocines usually have metasomal sterna 2–5 uniformly flat as in most bees. *Mesocheira* is the only genus which has the unique apomorphy of sterna 2–5 carinate medially.

57. Female metasomal sternum 6 with longitudinal median carina (1). [Female metasomal sternum 6 longitudinally simple without median carina.] All Ericrocini have this unique apomorphy which the Centridini as well as other non-parasitic anthophorids lack.

58. Sixth metasomal sternum of male medioapically flat, not convex, usually entire or emarginate, rarely pointed (1). [Sixth metasomal sternum of male bluntly pointed medioapically, strongly convex.] The sixth metasomal sternum of male medioapically pointed and convex is seen in all exomalopsine, melitomine, eucerine, and centridine bees.

59. Sternal apodemes of some metasomal sterna without dorsal processes (1). [Sternal apodemes of metasomal sterna with dorsal processes.] Centridini have metasomal sternal apodemes with dorsal processes. This condition is commonly found among the non-parasitic Anthophoridae. All Ericrocini have lost the dorsal processes except *Ericrocis.* This loss is an apomorphy.

60. Eighth metasomal sternum of male without or with greatly reduced spiculum (1). [Eighth metasomal sternum of male with spiculum.] Most anthophorid bees have a spiculum as found in the Centridini. An obvious apomorphy is loss or great reduction of the spiculum as seen in the Ericrocini except *Abromelissa.*

61. Spatha short, weakly developed (1). Spatha absent (2). [Spatha present, well developed.] Centridini except *Epicharis* have a well to weakly developed spatha. The presence of a spatha is presumably a plesiomorphy since it is commonly found among "primitive" anthophorids. Apparently the loss of the spatha in Ericrocini is an apomorphy.

62. Eighth metasomal sternum of male without apical process (1). [Eighth metasomal sternum of male with apical process.] Many short-tongued bees, the "primitive" anthophorid and Centridini have a well-developed apical process which may be variously modified. The reduction of this apical process such that the disc of the eighth sternum is broader than long is an apomorphy typical of Ericrocini.

63. Eighth metasomal sternum of male a broad plate (1). [Eighth metasomal sternum of male short, transverse, sometimes with one or two long apical processes.] For discussion see variable 62.

64. Penis valve without basolateral lobe (1). [Penis valve with basolateral lobe.] The penis valves of centridine bees have basolateral lobes. The presence of these lobes is an apomorphy though a weak one since it has apparently appeared three times, being a character of *Ericrocis, Aglaomelissa,* and the *Hopliphora* group.

65. Gonostylus of male greatly reduced to absent, if present then represented only by a membranous, flat, circular to slit-like area (1). [Gonostylus of male an elongate appendage.] The presence of a gonostylus as an elongate appendage often incurved apically distad of the penis valves is common in the "primitive" anthophorids and the Centridini. Recognition of the gonostylus is often aided by the long setae which all anthophorid bees have on their gonostyli, as well as the reduced sclerotization of the gonostylus. The most primitive condition is articulation to the apex of the gonocoxite as it is in *Caenonomada.* In the other centridines and ericrocines it is fused to the apex of the gonocoxite and is very narrow, round in cross section and more elongate. The reduction or absence of the gonostylus is a weak apomorphy since it has disappeared in three separate ericrocine groups.

66. Mesopleuron with knob-like process (1). [Mesopleuron without knob-like process.] The knob-like process on the mesopleuron of *Rhathymus* is an obvious autoapomorphy.

67. Apical margin of metasomal sternum 5 laterally with notch (1) (Fig. 76). [Apical margin of metasomal sternum 5 laterally simple.] This unique autoapomorphy is found only in *Mesocheira.*

bees. Figure 78b necessitates 11 convergences between the two tribes, which is possible considering there are 12 convergences [characters 7, 17, 18, 20(2), 21(2), 37, 39, 45–47, 49, 58, and 59] between the melectine and the ericrocine-rhathymine bees. Nevertheless, the male terminalia of Ericrocini and Rhathymini are similar and in conjunction with the numerous apparent synapomorphies shared by the two tribes, we prefer Figure 78a. The cladogram of Figure 78a eliminates all 11 convergences of Figure 78b and so is 11 steps shorter.

Unique characters for taxa were obvious apomorphies, whereas other polarity decisions encompassed centridine

Table 2. Matrix of characters listed in Table 1. Variables 1–67 are represented by the columns from left to right. Variables which are not constant are indicated by both characters which appear in the genus, i.e., ⦶.

CAENONOM	0000000000000000000120110000000000000000000000000001000000001000000
RHATHYMU	01001010100003001102301110002000000101000⦶001201⦶010000000100001010
MESOPLIA	110000100101⦶101211221111111201100111010001⦶11201110101011112110000
HOPLIPHO	1100011001010101111221111111201100111010101111201001100011112111⦶00
MESONYCH	11100010010102011112211111112011⦶01111100110112011⦶0010011112110100
ABROMELI	1110000001010111211231111111201100111110011011201001000011102110000
ERICROCI	1110001001010100111221111111202110111010001211201111100011012111100
AGLAOMEL	0100101001011201211231111111201000011111001111211111100011112111000
CTENIOSC	1101101001011201211231111111201000011010012111211111100011112110000
MESOCHEI	0100101001011201211231111111201100111011012111211111101111112110001
ACANTHOP	1100111112110301111221111111210001111011101111201001101011112111000

outgroup comparisons or centridine-exomalopsine outgroup comparisons or comparisons against short-tongued bees, with the variables of the ericrocine bees. The long first flagellar segment of the Centridini, which is a derived feature for the family Anthophoridae, is considered here as a plesiomorphy, the somewhat non-differentiated first flagellar segment of the ericrocines being the apomorphous character.

Table 1 includes notes on the distribution of characters of the variables and the bases for our judgments of polarity (evolutionary direction). Discussion is frequently abbreviated but is sufficient to suggest reasons for our decisions.

DISCUSSION

Linsley (1939) suggested that *Ericrocis* may have arisen from *Centris* (=*Hemisia*) or *Epicharis.* Michener (1944) stated that Melectini, Ericrocini, and the Rhathymini may have had a common origin with *Anthophora* but later he (Michener, 1974) separated the melectine and rhathymine-ericrocine lineages in his dendrogram, indicating common origins of the Anthophorini with the former and Centridini with the latter. Our work supports Michener's latter hypothesis and is more or less in agreement with Rozen's larval work (1969). Rozen states that the larvae of melectines, ericrocines, and rhathymines share an apomorphy not found in centridine or anthophorine larvae, i.e., they lack galeae. But as he points out, this may not indicate a common origin for these parasitic bees since galeae have been lost in many unrelated groups of bees and loss characters are often convergent. Rozen further states that the Melectini share a plesiomorphy with the Anthophorini not shared with the Ericrocini and Rhathymini; i.e., the maxillary palpus is preapical in position. The Ericrocini and Rhathymini have maxillary palpi which are apical as well as greatly elongated labiomaxillary regions. These apomorphies support the contention that the Ericrocini and Rhathymini are sister groups. On the other hand the strongly denticulate atrial wall and spinous primary tracheal opening of the ericrocines (not found in rhathymines) is similar to the spiracular structure of *Epicharis* and anthophorines and therefore could suggest a separate origin for the Rhathymini. We believe that the rhathymine-ericrocine clade is monophyletic (*sensu* Hennig) since it has 10 adult and two larval synapomorphies. It is unlikely that all of the apomorphies are convergent and have appeared *de novo* in each tribe. We have presented, however, other characters which do not support this hypothesis.

We have recognized several lineages within the Ericrocini: (a) *Ericrocis* group (*Ericrocis*), (b) *Hopliphora* group (*Hopliphora* and *Acanthopus*), (c) *Mesoplia* group (*Mesoplia*), (d) *Mesonychium* group (*Mesonychium* and *Abromelissa*), and (e) *Ctenioschelus* group (*Ctenioschelus, Aglaomelissa,* and *Mesocheira*). Here and below the numbers in parentheses represent variables as numbered in Table 1. The most "primitive" lineage is presumably *Ericrocis* since it lacks metallic setae (16) and integumental coloration (15) and has metasomal sternal apodemes (59) like Centridini. This is not fully convincing since the loss of metallic coloration could be a reversion in *Ericrocis* rather than a plesiomorphy shared with Centridini. Metallic hair has arisen three times at least in the Anthophorinae, in *Amegilla* (Anthophorini), in *Thyreus* (Melectini) as well as in the Ericrocini. Many *Thyreus* have non-metallic white appressed vestiture like *Ericrocis* and a polarity decision of whether that type of vestiture is primitive or derived will probably be similarly uncertain.

Acanthopus has the most derived mouthparts and legs of any ericrocine and two unique apomorphies in the forewing, making its relationship to the rest of the Ericrocini obscure. Nevertheless, it shares three strong apomorphies with *Hopliphora,* i.e., relatively long paraglossae (6), presence of the sternopleural ridge (41) and the absence of tergal patches of white appressed hair (50). *Hopliphora* and *Acanthopus* are the largest ericrocines and both have large centridine hosts. Lack of apomorphies for *Hopliphora* suggests that it is possibly a paraphyletic group from which *Acanthopus* evolved. We have no problem in recognizing paraphyletic taxa since we find it unnecessary that classifications and cladograms be redundant, especially when more than one cladogram is equally plausible (or parsimonious).

The *Mesoplia, Mesonychium,* and *Ctenioschelus* groups have three apomorphies, a well-developed scutellum which overhangs the metanotum (43) (reverted to a less developed state in *Mesonychium*), metasomal sternum 3 of male with dense lateral patch of white hair (51) (which is reversed in the *Mesonychium* group), and penis valve with basolateral lobe (64) (lost in *Aglaomelissa*). In view of the reversals, one must admit that the three characters are not very convincing.

Mesoplia is quite distinctive, having elongate segments in the maxillary palpus (14), the male has lost the apical bands of long curved hair on metasomal sterna 4 and 5 (52) and has a broadly emarginate sternum 5 such that it is concealed under sternum 4 (55).

The *Mesonychium* and *Ctenioschelus* groups share a reduction of the number of maxillary palpal segments to one or two (14) (reduced to three in *Abromelissa*), a reduction of the length of the jugal lobe to less than one-fourth the distance between the vannal incision and wing base (21) (reduced to between one-third and one-fourth this distance in *Mesonychium*), and presence of the supraspiracular ridge (42).

The *Mesonychium* group is characterized by five strong apomorphies. The inner eye margins are divergent above (3), the strigilar malus lacks teeth (38), the midcoxa is short (44), metasomal sternum 3 lacks a dense lateral patch of white hair (51), and sterna 4 and 5 lack dense felt-like pads of pubescence (53) which ancestrally cover the basal halves of their discs. It is interesting also that *Abromelissa* is the only ericrocine genus with metallic integument (15). The *Mesonychium* group, although it includes Amazonian species, is largely peripheral to the distribution of other ericrocine genera. *Mesonychium* is one of the largest genera in the tribe, with about half a dozen species in Chile and temperate Argentina. Also limited to Chile is its possible derivative, *Abromelissa*, so *Mesonychium* may be paraphyletic.

The *Ctenioschelus* group is distinguished by several derived characters: the subapical mandibular tooth is lost (5), the forewing tips are infuscated (13), and tergum 1 has a relatively sharply angulate profile (48) (Fig. 76). Other noteworthy characters which are found in two of the three genera are the presence of arolia (35) (except *Mesocheira*), the apically simple labrum (1), the presence of an anterior mesepisternal carina (40) (except *Ctenioschelus*), and the projection of the scutellar lobes over the propodeum (43) (except *Aglaomelissa*). There is also a trend toward the development of the occipital margin into a sharp ridge or flange, or a flange-like carina across the entire pronotum, and of strongly developed acetabular carinae with the procoxae deeply recessed. The *Ctenioschelus* group is centered in Amazonia but *Mesocheira* ranges from central Mexico to Paraguay. *Ctenioschelus* and *Aglaomelissa* are primarily South American, but both range north to Costa Rica.

KEY TO GENERA OF ERICROCINI

1a. Second and third submarginal cells of forewing each receiving a recurrent vein; metatarsus without dense fringe of long, dark plumose hairs 2

b. Third submarginal cell large, receiving both recurrent veins; metatarsus very long, with dense brush of long, dark, plumose hairs .... *Acanthopus*

2a. Juncture of basal and discal surfaces of tergum 1 slightly humped and subangulate in middle (Fig. 77); mesobasitarsus without distal, flattened, spine-like projection on posterior margin (Fig. 49); mandible simple 3

b. Juncture of basal and discal surfaces of tergum 1 evenly rounded, never appearing subangulate (Fig. 76); mesobasitarsus almost always with distal, flattened process on posterior margin, often continued basad as a raised, cariniform ridge (Fig. 1); mandible usually with single preapical tooth 5

3a. Scutellum bituberculate, the processes stout, subconical and suberect; forewing dusky with apex darker 4

b. Scutellum bituberculate, the processes flat and plate-like, directed caudad; forewing dusky, with an apical cloud in marginal cell in addition to that at wing apex .... *Mesocheira*

4a. Pronotum carinate between collar and lobe; mesepisternum with lamelliform ridge between anterior and lateral surfaces; male antenna normal, not extending much beyond tegula .... *Aglaomelissa*

b. Pronotum not carinate between collar and lobe, end of collar clearly defined; mesepisternum abruptly rounded between anterior and lateral surfaces; male flagellar segments greatly elongate, flagellum extending well beyond apex of abdomen .... *Ctenioschelus*

5a. Meso- and metadistitarsi with a cluster of appressed, short flattened setae on each side (Fig. 28) (setae reduced in some *Mesonychium* in which antennocular distance is greater than antennal socket diameter and third submarginal cell is distinctly narrowed anteriorly); inner eye margins divergent above; male gonostylus without dorsal lobe (Figs. 33, 38) 6

b. Meso- and metadistitarsi with normal setae and hairs, without flattened setae (Fig. 2); inner eye margins various, but usually not divergent above; male gonostylus with dorsal lobe (Figs. 7, 22, 43) (except some *Hopliphora*) 7

6a. Abdominal scales contrasting black and white (may be somewhat tawny); labrum with erect preapical median tubercle; scutellum without raised, mammiform tubercles ....*Ericrocis*

b. Abdominal scales or hairs iridescent blue or green, with or without contrasting whitish hairs; labrum with transverse preapical ridge; scutellum usually with a pair of mammiform tubercles .... *Mesonychium*

7a. Abdominal integument blackish, usually more or less covered with blue or green-reflective, appressed, scale-like hairs, but if not, mesepisternal hairs are black; tegula rectangular or elliptical but not abruptly narrowed anteriorly (Figs. 61, 63, 64) 8

b. Abdominal integument shiny metallic blue, with sparse erect blackish hairs; hairs of thorax whitish; tegula abruptly narrower in anterior one-third (Fig. 66) ....*Abromelissa*

8a. Tegula oval, outer margin evenly curved (Fig. 61); abdomen usually appearing black, without patterns of appressed pale pubescence .... *Hopliphora*

b. Tegula, from above, approximately elliptical, often with outer margin somewhat sinuate in part and with posterior margin oblique or truncate; abdomen bright iridescent bluish or greenish, often with conspicuous patches of white or yellowish pubescence .... *Mesoplia*

Ericrocis Group

Although the body is richly marked with conspicuous patterns of blackish and white to tawny pubescence, the complete lack of metallic-reflective hairs or scales is diagnostic for this group. Other characteristics of the *Ericrocis* group are: inner eye margins divergent above (shared with *Mesonychium* group); meso- and metadistitarsi with flattened setae (shared with some *Mesonychium*); sternal apodemes of some metasomal sterna without dorsal processes (unique within the Ericrocini).

(A) Inner eye margins divergent above. (B) Ocellocular distance greater than diameter of anterior ocellus. (C) Mandible with preapical tooth. (D) Maxillary palpus two-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia short, less than half as long as velum, finely serrate on inner margin. (G) Mesobasitarsus usually compressed and more or less sharply carinate along posterior margin; distal process usually present. (H) Meso- and metadistitarsi with lateral patch of short, flattened setae on each side (Fig. 28). (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing about 0.80 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex or with two stout teeth. (M) Gonostylus without dorsal lobe.

The one genus included in this group, *Ericrocis,* is restricted to the Nearctic Region.

Genus *Ericrocis* Cresson

Figures 34–38, 60, 72–74

Ericrocis Cresson, 1887:131, 134. Type species: ? *Crocisa lata* Cresson, 1878 (monobasic).

DIAGNOSIS

Abdominal color black, with conspicuous pattern of appressed, plumose white to somewhat tawny hairs; labrum with a median preapical tubercle; dorsal face of scutellum without tubercles.

DESCRIPTION

(1) Head much broader than long; inner eye margins essentially straight, strongly divergent above; occipital margin nearly flat, slightly elevated above ocelli. (2) Maxillary palpus two-segmented, first segment distinctly longer than second. (3) Labrum with median preapical tubercle; apical margin subtruncate. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance slightly greater than diameter of anterior ocellus. (6) Occipital margin subangulate. (7) Antenna short in both sexes; minimum length of first flagellar segment about equal to maximum width and shorter than second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum deeply impressed, more weakly so distad; parapsidal lines in broad, shallow impressions. (10) Dorsal face of scutellum broadly impressed along midline, broadly convex on either side. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge evanescent distad.

(13) Tegula (Fig. 65) rectangular, narrowed anteriorly, outer margin somewhat sinuate. (14) Second submarginal cell narrower on M than first or third; 1st m-cu interstitial with 1st r-m; 2nd m-cu a little basad of 2nd r-m.

(15) Mesotibial spur slender, parallel-sided, apex bispinose, outer spine often obsolete, intercalary denticles present. (16) Metatrochanter rounded ventrally; metatibial spurs normal; metadistitarsus about 2.5 times longer than wide.

(17) Female sixth tergum with weakly defined pygidial plate, apex narrowly rounded. (18) Male fourth sternum broadly concave along apical margin, with a distal fringe of long, dark plumose hairs, their apices broadly reflexed. (19) Male fifth sternum broadly and more shallowly concave along apical margin, with or without distal fringe. (20) Male seventh sternum (Fig. 34) transverse, evenly rounded or with short, truncate projection. (21) Male eighth sternum (Fig. 35) short, bilobate at apex. (22) Male gonostylus short, thick, truncate; dorsal lobe absent; inner apical sclerotization of gonocoxite poorly defined. (23) Penis valve abruptly deflected ventrad; basolateral lobe absent (Fig. 38).

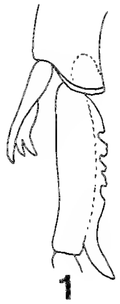
DISCUSSION

This Nearctic genus is, in many respects similar to the South American genus *Mesonychium,* with which it shares the presence of a cluster of short, flattened setae on either side of the meso- and metadistitarsi, a feature unique to these two genera. Unlike *Mesonychium* and all other ericrocine genera, *Ericrocis* lacks metallic hairs or scales. Instead, there are richly marked patterns of black and white and (sometimes) tawny pubescence. *Ericrocis* includes two species: *E. lata* (Cresson) and *E. pintada* Snelling and Zavortink. The genus was revised by Snelling and Zavortink (1985).

It should be noted that the figures of the labiomaxillary complex cited by Winston (1979: fig. 44) as those of *Mesocheira bicolor* appear, instead, to be based on *Ericrocis lata.* Michener and Fraser (1978) figure mandibles purported to

⟶

Figures 1-7. *Mesoplia* (*M.*) *azurea.* **1,** female mesobasitarsus, pilosity omitted; **2,** metadistitarsus, lateral view; **3,** male sternum 7; **4,** male sternum 8; **5-7,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm (Figs. 3–7 only).



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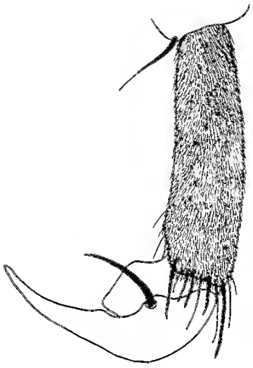

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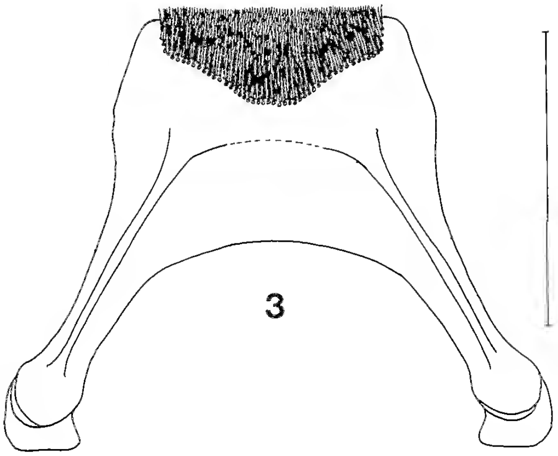

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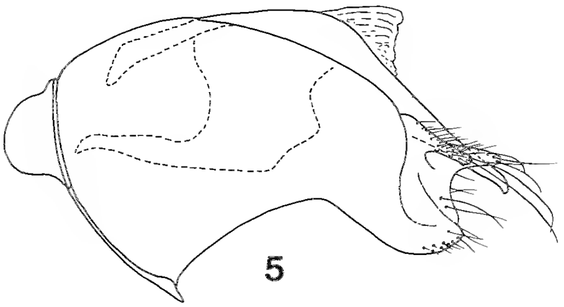

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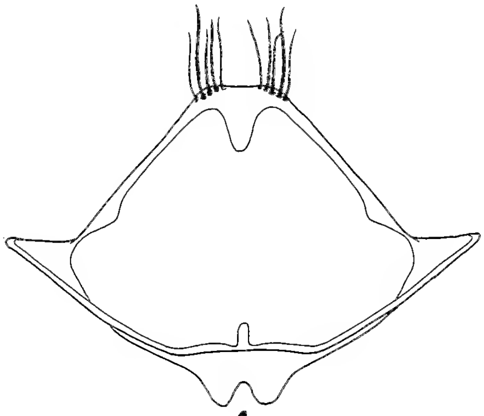

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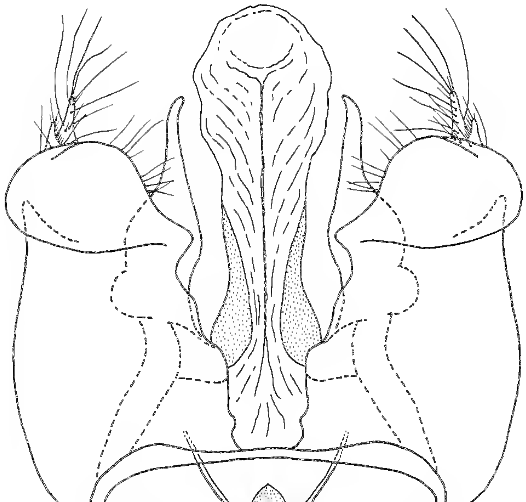

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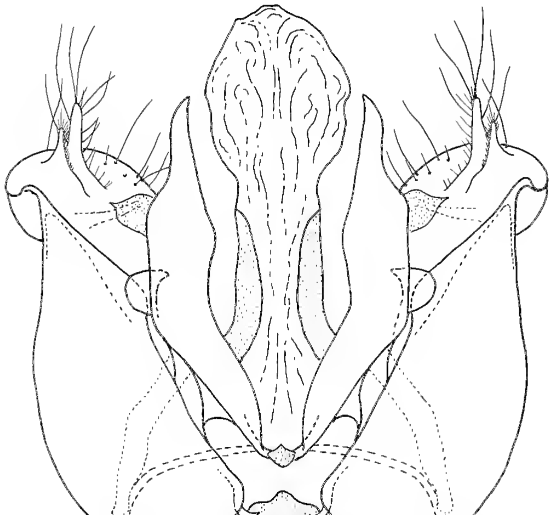

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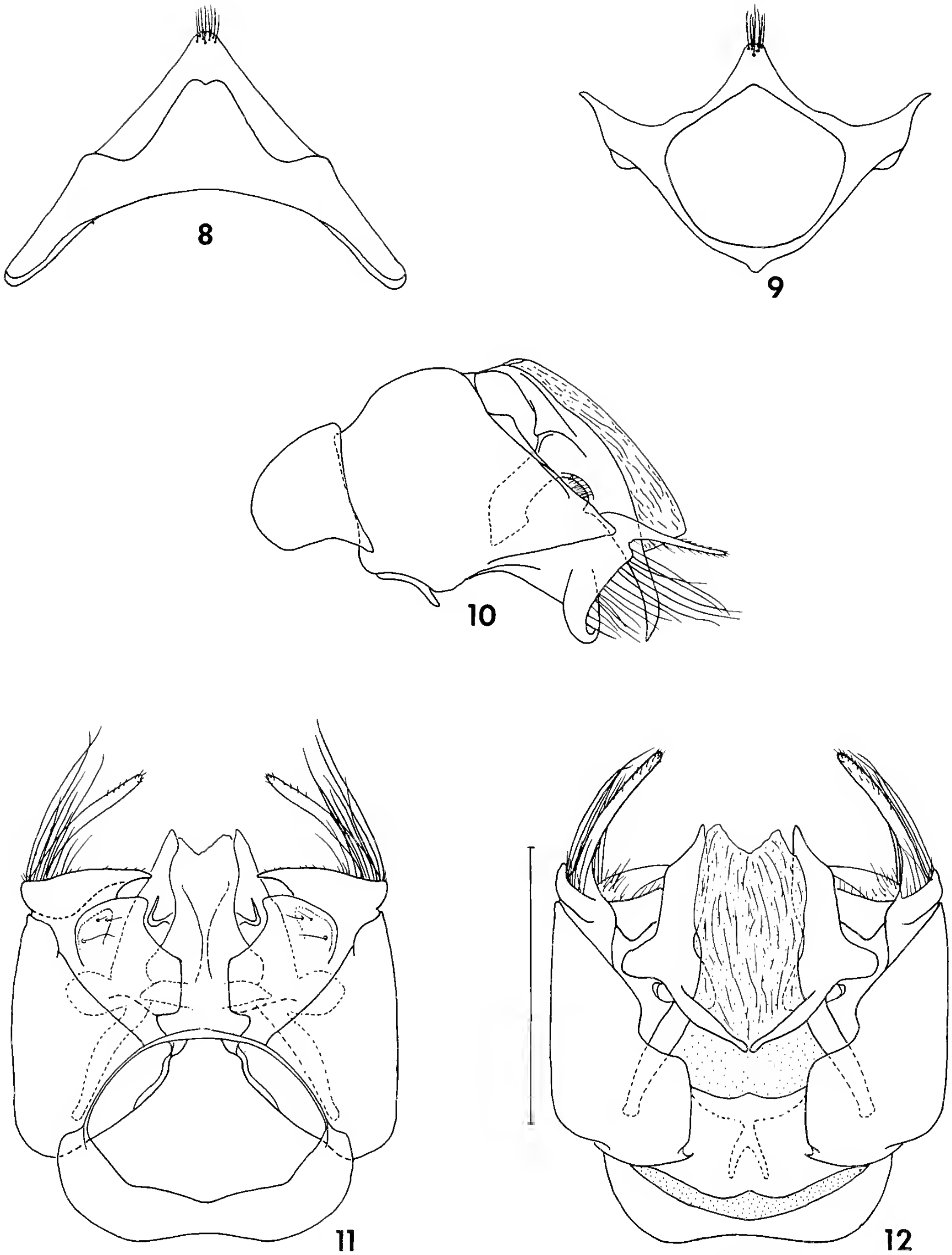


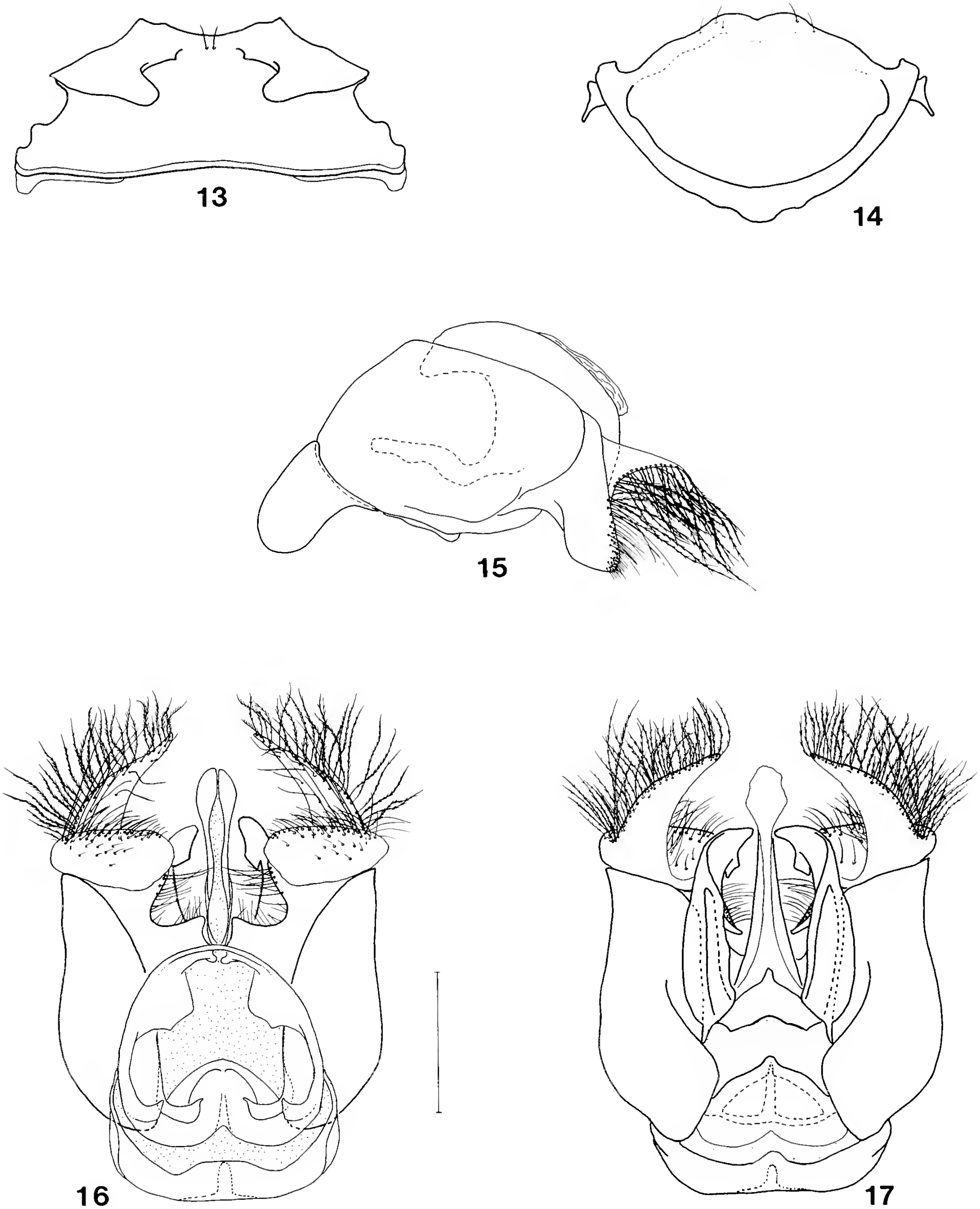
Figures 8-12. *Mesoplia* (*Eumelissa*) *decorata,* male. **8,** sternum 7; **9,** sternum 8; **10-12,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

be those of *E. lata* (Fig. 16); since the mandible of *E. lata* possesses a distinct preapical tooth (wholly lacking in the figure), the mandible figured is not that of *E. lata.* Also, they stated that the tooth of the pollex is absent (p. 477); it is present as the preapical tooth.

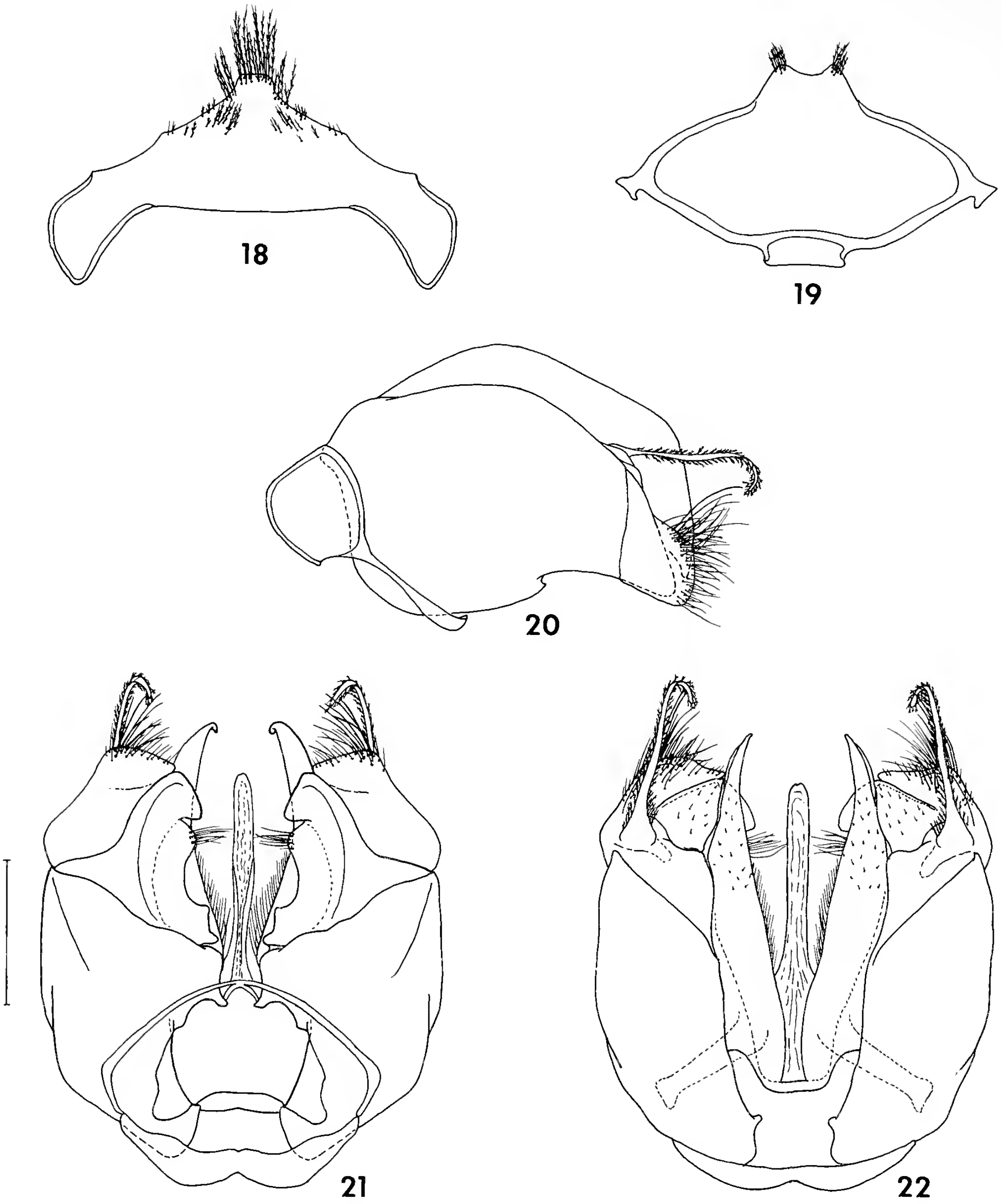
Hosts for *Ericrocis* are not known but, based on distribution, will almost certainly prove to be species of *Centris,* subgenus *Paracentris,* and possibly subgenus *Acritocentris.*

INCLUDED NAMES

arizonensis Baker, 1906 (*Ericrocis*)
lata (Cresson, 1878) (? *Crocisa*)



Figures 13-17. *Acanthopus palmatus,* male. **13,** sternum 7; **14,** sternum 8; **15-17,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.



Figures 18–22. *Hopliphora velutina,* male. **18,** sternum 7; **19,** sternum 8; **20–22,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

melectoides Baker, 1906 (*Ericrocis*)
pintada Snelling and Zavortink, 1985 (*Ericrocis*)
rossi Linsley, 1939 (*Ericrocis*)
rugosa Fox, 1893 (*Ericrocis*)

Hopliphora Group

The two genera that comprise this group are characterized by the lack of tergal patches or bands of appressed pale hairs, the presence of a sternopleural ridge (weak in some *Hopliphora*), and the relatively long paraglossa (at least two-thirds as long as the prementum).

(A) Inner eye margins slightly convergent above. (B) Ocellocular distance equal to diameter of anterior ocellus. (C) Mandible with or without preapical tooth. (D) Maxillary palpus absent or three-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia slender, shorter than velum, without teeth. (G) Mesobasitarsus compressed and carinate along posterior margin; distal process present, or not compressed and without distal process. (H) Meso- and metadistitarsi without lateral patches of short, flattened setae. (I) Metatarsus with or without posterior fringe. (J) Marginal cell of forewing about 0.75–1.8 times distance from its apex to wing tip; third submarginal cell usually more or less triangular. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bidentate at apex. (M) Male gonostylus with or without dorsal lobe.

The group is represented by the two South American genera *Hopliphora* and *Acanthopus.*

Genus *Hopliphora* Lepeletier

Figures 18–27, 61

Hopliphora Lepeletier, 1841:458. Type species: *Mesocheira velutina* Lepeletier and Serville, 1825 (monobasic).

Eurytis F. Smith, 1854:279. Type species: *Eurytis funereus* F. Smith, 1854 (monobasic).

Oxynedys Schrottky, 1902:491. Type species: (*Oxynedys beroni* Schrottky, 1902) = *Mesocheira velutina* Lepeletier and Serville, 1825 (monobasic and original designation).

Cyphomelissa Schrottky, 1902:493. Type species: (*Cyphomelissa pernigra* Schrottky, 1902) = *Melissa diabolica* Friese, 1900 (monobasic and original designation). NEW SYNONYMY.

Oxynedis: Moure, 1946:18, 27, 31 (lapsus).

DIAGNOSIS

Third submarginal cell receiving second recurrent vein only.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, slightly convergent above; occipital margin distinctly elevated above ocelli. (2) First segment of maxillary palpus distinctly shorter than second or third. (3) Labrum with transverse preapical ridge; apical margin convex to concave. (4) Interantennal distance distinctly greater than antennal socket diameter; antennocular distance distinctly less than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment less than width at apex and less, usually distinctly so, than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum broadly and deeply impressed on anterior three-fourths, less strongly so toward posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum broadly impressed along midline and with a pair of suberect to erect blunt to subacute tubercles. (11) Anterior mesepisternal carina and acetabular carina absent; sternopleural ridge present, but often weak. (12) Supraspiracular ridge strong, terminating in stout, tooth-like process well above, and slightly behind, spiracle.

(13) Tegula (Fig. 63) oval, outer margin evenly curved. (14) Second submarginal cell, on M, as wide as, or wider than, first; third submarginal cell not at all narrowed, or greatly narrowed, anteriorly; 1st m-cu distinctly basad of 1st r-m; 2nd m-cu at, or a little beyond, middle of third submarginal cell; marginal cell 0.75 times as long as distance from its apex to wing tip.

(15) Mesotibial spur robust and very broad at apex (slender and parallel-sided in one species), outer distal tooth often indistinguishable from prominent intercalary teeth. (16) Metatrochanter rounded beneath; metatibia with two normal spurs; metadistitarsus 2.5–3.5 times longer than wide.

(17) Female sixth tergum with well-defined, sharply marginate pygidial plate, apex acute and reflexed, or narrowly rounded and flat. (18) Male fourth sternum with distal margins straight or broadly emarginate, with distal fringe of more or less prostrate long, dark, plumose hairs. (19) Male fifth sternum either fully exposed and with straight apical margin or hidden and with deeply emarginate margin, with or without distal fringe. (20) Male seventh sternum with margin angularly (Fig. 18) or broadly (Fig. 23) produced. (21) Male eighth sternum variously produced. (22) Male gonostylus short, thick, blunt; dorsal lobe present (Fig. 22) or absent (Fig. 27); inner apical sclerotized portion of gonocoxite distinct. (23) Penis valve evenly curved ventrad; basolateral lobe obsolete (Figs. 22–27).

DISCUSSION

Those species in which the third submarginal cell is triangular, or even petiolate, have traditionally been placed in the separate genus *Cyphomelissa.* However, species assigned to *Hopliphora* have the third submarginal cell so strongly narrowed anteriorly that the difference becomes one of degree only. It is not enough, in our opinion, to place these two groups of species in separate genera.

Superficially, some species of *Mesonychium* look much like small *Hopliphora* and were included in *Cyphomelissa* by Schrottky (1902). The following names are applicable to *Hopliphora* as we understand the genus.

INCLUDED NAMES

beroni (Schrottky, 1902) (*Oxynedys*)
commata (Moure, 1958) (*Cyphomelissa*)
diabolica (Friese, 1900) (*Melissa*)
funereus (F. Smith, 1854) (*Eurytis*)
iheringi (Schrottky, 1902) (*Acanthopus*)
magnifica (Moure, 1958) (*Cyphomelissa*)
pernigra (Schrottky, 1902) (*Cyphomelissa*)
superba (Ducke, 1902) (*Melissa*)
velutina (Lepeletier and Serville, 1825) (*Mesocheira*)

Genus *Acanthopus* Klug

Figures 13–17, 62, 70, 71

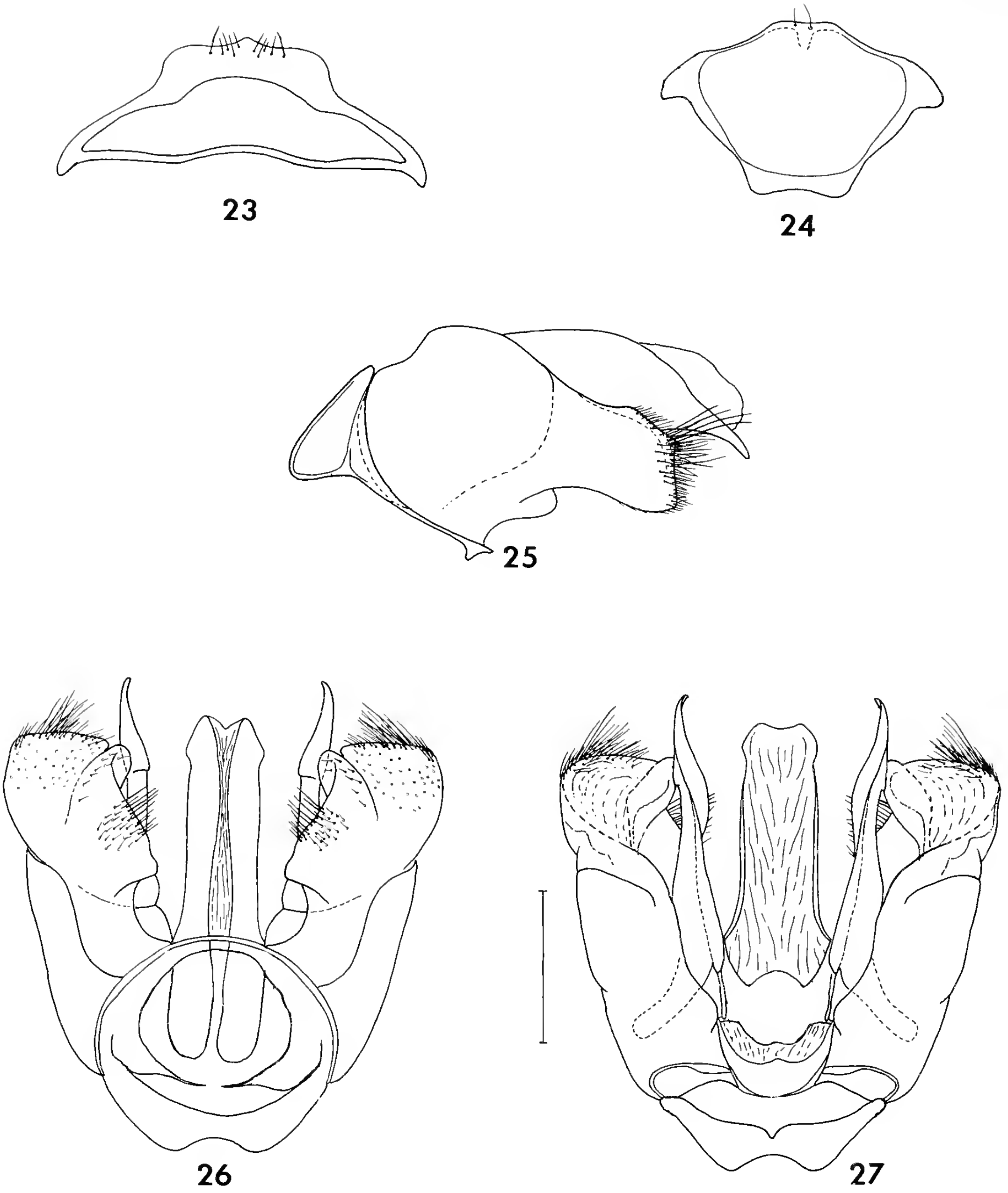
Acanthopus Klug, 1807:199, 226. Type species: (*Apis splendida* Fabricius, 1793) = *Apis palmata* Olivier, 1789 (monobasic).

DIAGNOSIS

Third submarginal cell receiving both recurrent veins.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, distinctly convergent above; occipital

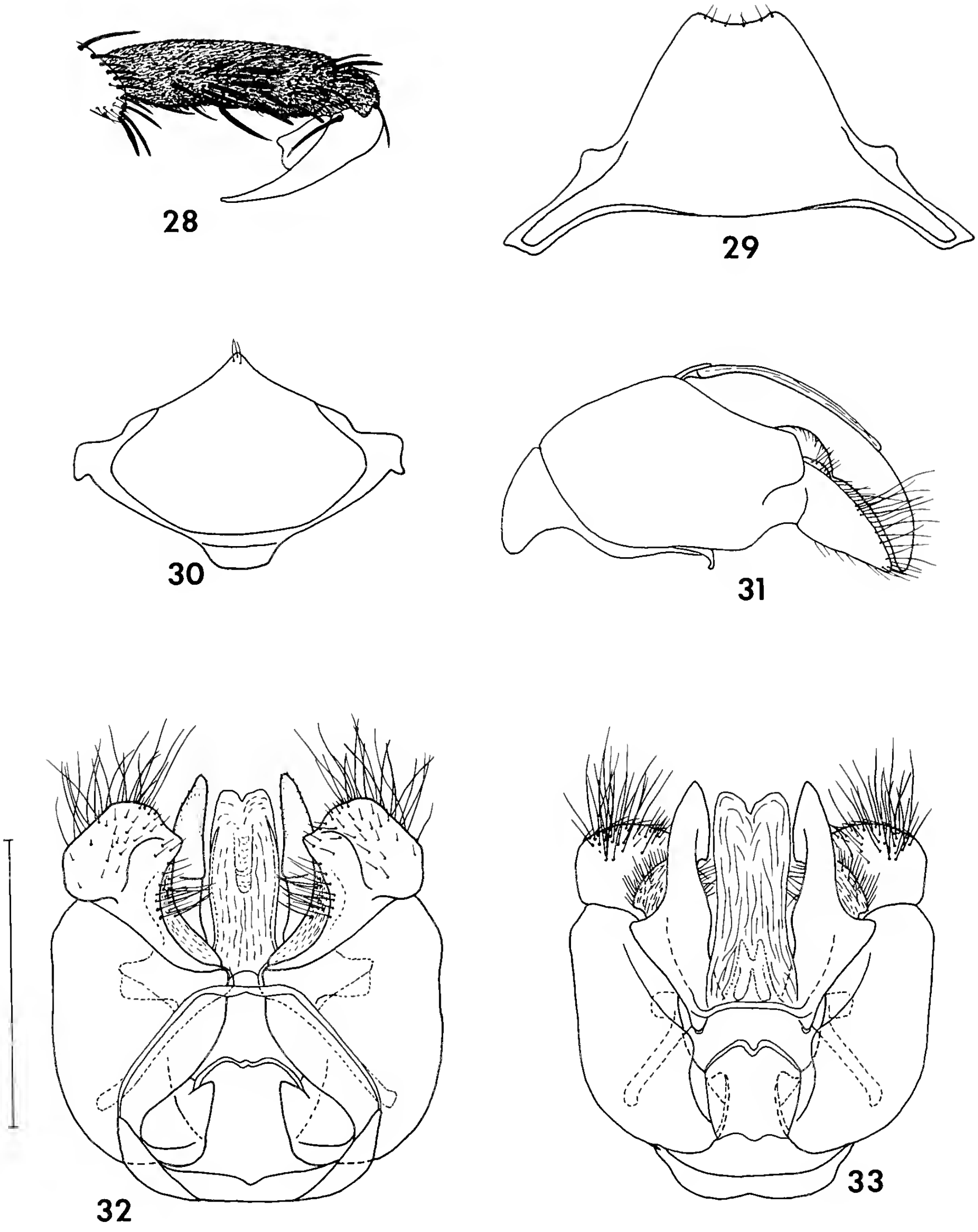


Figures 23–27. *Hopliphora superba,* male. **23,** sternum 7; **24,** sternum 8; **25–27,** genital capsule, lateral, ventral, and dorsal view. Scale line = 1.00 mm.

margin broadly convex and distinctly elevated above ocelli. (2) Maxillary palpus absent. (3) Labrum with narrow, short transverse preapical ridge; distal margin weakly, broadly convex. (4) Interantennal distance less than antennal socket diameter. (5) Ocelloccipital distance about three times diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment greater than apical width and greater than length of second or third segments on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum deeply impressed for entire length; parapsidal lines not impressed. (10) Dorsal face of scutellum deeply impressed in middle, with a pair of erect, conical tubercles. (11) Anterior mesepisternal carina present; acetabular carina obsolete in middle; sternopleural ridge present. (12) Supraspiracular ridge weak, evanescent distad.

(13) Tegula (Fig. 62) elliptical, outer margin evenly curved, posterior margin oblique. (14) Second submarginal cell about

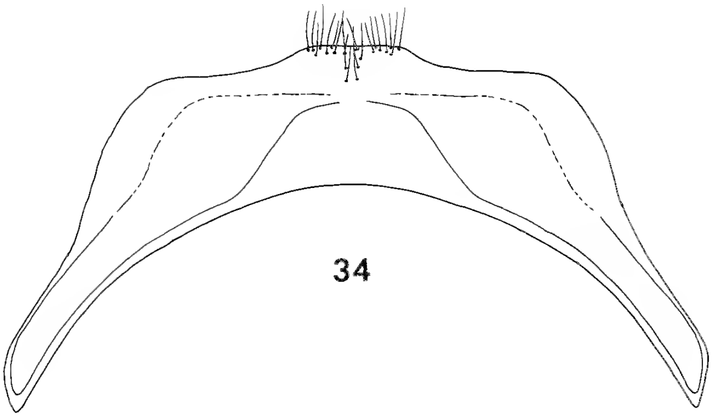


Figures 28–33. *Mesonychium coerulescens.* **28,** metadistitarsus, lateral view; **29,** male sternum 7; **30,** male sternum 8; **31–33,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm (Figs. 29–33 only).

as broad as long; third submarginal cell on M longer than first or second, receiving 1st and 2nd m-cu, latter near midlength; marginal cell 1.8 times as long as distance from its apex to wing tip.

(15) Mesotibial spur wide, outer spine much longer than inner, surface between strongly oblique and with three long, widely spaced intercalary teeth. (16) Metatrochanter rounded beneath; metatibial spurs normal, outer spur strongly curved at tip; metadistitarsus about six times longer than wide.

(17) Female sixth tergum with short, subtruncate pygidial plate. (18) Male fourth sternum deeply, subangularly incised and with a prostrate fringe of long hairs. (19) Male fifth sternum largely hidden, posterior margin deeply incised and with distal fringe of prostrate hairs. (20) Male seventh sternum (Fig. 13) with posterior margin broadly and somewhat irregularly produced, apically acuminate. (21) Male eighth sternum (Fig. 14) moderately produced, apex weakly emarginate. (22) Male gonostylus short, broad, thickly digitiform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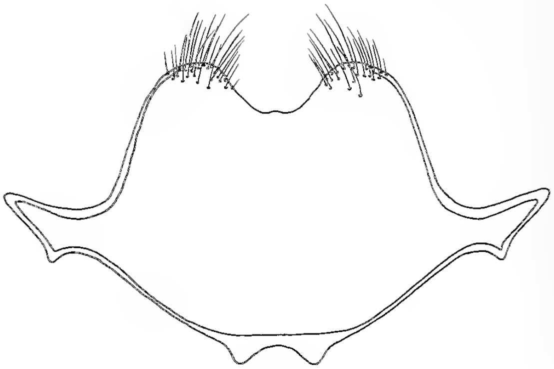
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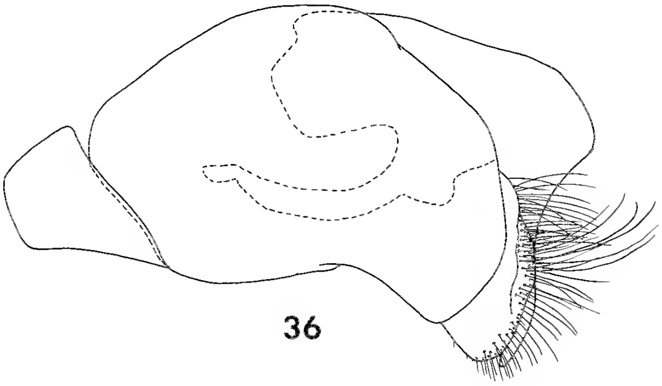
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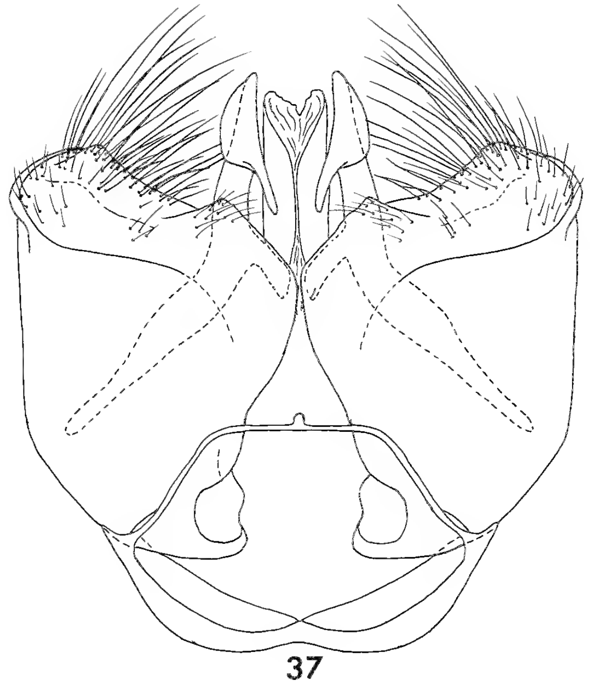
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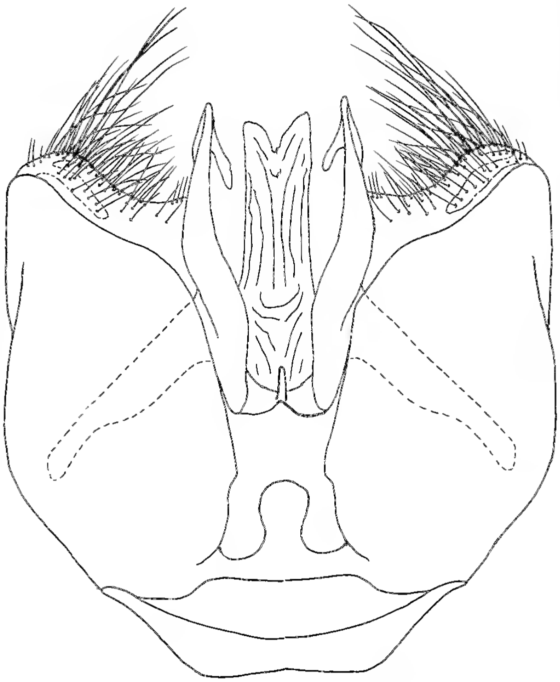
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Table 3. Known or suspected hosts of Ctenioschelini.

Parasitoid	Host	Authority
Mesoplia dugesi	*Centris anomala* Snelling	Snelling, 1984[1]
Mesoplia rufipes	*Centris carrikeri* Cockerell	Rozen, 1969
	Centris inermis Friese (as *C. segregata* Crawford)	Coville et al., 1983
	Epicharis albofasciata F. Smith	Rozen, 1969
Mesonychium gayi	*Centris chilensis* Spinola	Wagenknecht, 1974
	Centris cineraria F. Smith	Wagenknecht, 1974
	Centris nigerrima Spinola	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Mesonychium jenseni	*Centris autrani* Vachal	Wagenknecht, 1974
Mesonychium wagenknechti	*Centris chilensis* Spinola	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Abromelissa lendliana	*Centris cineraria* F. Smith	Wagenknecht, 1974
	Centris nigerrima Spinola	Wagenknecht, 1974
	Centris orellanai Ruiz	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Aglaomelissa duckei	*Centris carrikeri* Cockerell	NEW RECORD[2]
Acanthopus palmatus (as *A. splendidus urichi*)	*Ptilotopus derasus* (Lepeletier)	Rozen, 1969

[1] Suspected host—observed at nest site.

[2] Suspected host—observed at nest site (J.G. Rozen, Jr., personal communication).

in profile; dorsal lobe long, slender; inner apical sclerotization of gonocoxite small but distinct. (23) Penis valve abruptly deflected ventrad; basolateral lobe absent (Fig. 17).

DISCUSSION

The unusual wing venation (elongate marginal cell and second submarginal cell receiving both recurrent veins) and the conspicuous peculiar fringes on the metatarsi will immediately separate *Acanthopus* from other genera of ericrocines.

There is apparently but a single species, ranging from Trinidad and the Guianas to Brazil. The one known host is a species of *Ptilotopus* (Table 3).

INCLUDED NAMES

excellens Schrottky, 1902 (*Acanthopus*)
jheringi Friese, 1904 (*Acanthopus*)
palmata (Olivier, 1789) (*Apis*)
splendida (Fabricius, 1793) (*Apis*)
urichi Cockerell, 1926 (*Acanthopus*)

Mesoplia Group

Diagnostic for this group are the elongate segments of the maxillary palpus, the male lacks felt-like pads of pubescence along the apical margins of metasomal sterna 4 and 5 (shared with the *Mesonychium* group), and male sternum 5 is broadly emarginate and largely concealed under sternum 4. The inner eye margins are approximately parallel, rather than divergent above as in the *Mesonychium* group.

(A) Inner eye margins weakly to distinctly divergent above. (B) Ocellocular distance less than, equal to, or greater than diameter of anterior ocellus. (C) Mandible with adnate preapical tooth. (D) Maxillary palpus three- or four-segmented. (E) Hypostomal carina moderately high, lamelliform. (F) Malus of protibia short to long, usually with one or two teeth along inner margin. (G) Mesobasitarsus compressed and carinate along posterior margin; distal process present. (H) Meso- and metadistitarsi without lateral patches of short, flattened setae. (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 0.90–0.94 distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex. (M) Male gonostylus with dorsal lobe.

Only the genus *Mesoplia* is included in this group which ranges from the southwestern United States (Arizona) to Argentina.

Genus *Mesoplia* Lepeletier

Figures 1–12, 63, 64, 75

Mesoplia Lepeletier, 1841:457. Type species: *Mesocheira azurea* Lepeletier and Serville, 1825 (monobasic).

←

Figures 34-38. *Ericrocis lata,* male. **34,** sternum 7; **35,** sternum 8; **36-38,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

Melissa F. Smith, 1854:279. Type species: *Mesocheira azurea* Lepeletier and Serville, 1825 (designation of Sandhouse, 1943:570).

DIAGNOSIS

Same as description for *Mesoplia* group.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, subparallel to divergent above; occipital margin nearly straight to low-convex, slightly, or not at all, elevated above ocelli. (2) Maxillary palpus, except first segment, slender and elongate, segments more or less fused but recognizable. (3) Labrum with transverse preapical ridge; apical margin subtruncate. (4) Interantennal distance greater than antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance equal to, or greater than, diameter of anterior ocellus. (6) Occipital margin rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment less than apical width and distinctly less than length of second segment on same side.

(8) Pronotum with or without carina between collar and front of posterior lobe. (9) Midline of mesoscutum impressed for most of its length; parapsidal lines weakly, or not, impressed. (10) Dorsal face of scutellum impressed along midline, with suberect to erect mammiform tubercle on each side. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge weak, terminating well before spiracle.

(13) Tegula shape as in Figures 60 and 61, narrowed in front, outer margin more or less sinuate. (14) First submarginal cell, on M, as wide as, or wider than, second or third; second and third submarginal cells narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu at, or a little distad of, middle of third submarginal cell.

(15) Mesotibial spur usually moderately broadened distad and with one or more distinct intercalary teeth, but may be parallel-sided for entire length. (16) Metatrochanter rounded beneath; metatibial spurs of female normal; of male, normal or with two very short, stout spurs or with a single short, stout spur; metadistitarsus two and one-half to three times longer than wide.

(17) Female sixth tergum with well-defined pygidial plate, apex narrowly to broadly rounded. (18) Male fourth sternum weakly to strongly concave along apical margin, with or without distal fringe of long, plumose hairs. (19) Male fifth sternum hidden, distal margin deeply incurved and usually with distal fringe of long, plumose hairs. (20) Male seventh sternum either (a) quadrately produced distad and with dense patch of dark, bristle-like setae (Fig. 3) or (b) with posterior margin more or less triangular, apex acute, truncate or bilobed, and with scattered normal setae (Fig. 8). (21) Male eighth sternum with small apical process which may be acute, truncate or bilobate (Figs. 4, 9). (22) Male gonostylus short, broad, thick and deflected ventrad (Figs. 5–7) or short, broad, thin and curved mesad above the inner apical sclerotization of the gonocoxite (Figs. 10–12). (23) Penis valves evenly curved, or abruptly deflected, ventrad; basolateral lobe distinct.

DISCUSSION

Mesoplia includes a dozen or so species ranging from southern Arizona in the United States southward to northern Argentina. The genus is apparently absent from Chile and most of the species occur in the Amazonian region of South America.

We have herein divided *Mesoplia* into two subgenera. The males of the two subgenera are especially different in details of the genitalia and associated sterna and these segregates may be better regarded as distinct genera. However, the magnitude of differences in the males is not reflected in the females. Until all of the species of *Mesoplia* in the broad sense can be critically examined, we believe that generic separation of the two segregates recognized here would be premature.

Known and suspected hosts are all species of *Centris* and *Epicharis* (Table 3).

Subgenus *Mesoplia*

Figures 1–7, 60

DIAGNOSIS

MALE. With a single metatibial spur or with two very short, stout spurs, the longer not extending beyond basal one-third of metabasitarsus; metafemur often with robust basal tooth-like projection ventrally; metatibia with inner, distal patch of black hairs. Female: pygidium broad, densely covered with appressed iridescent scales; dorsal surface of metacoxa angulate or carinate at juncture with anterior face.

DESCRIPTION

(24) Ocellocular distance equal to, or (usually) greater than, diameter of anterior ocellus. (25) Pronotum with or without low carina from collar to front of posterior lobe. (26) Dorsal face of metacoxa sharply subangulate or carinate where it meets anterior and posterior faces. (27) Metafemur of male with or without stout, tooth-like basoventral projection. (28) Metatibia of male with inner, distal hair patch and with one or two apical spurs; if with two apical spurs, both short and stout, neither extending beyond basal one-third of metabasitarsus. (29) Tegula shape as in Figure 60. (30) Female pygidium broad, apex broadly rounded, disc covered with appressed metallic scales. (31) Male seventh sternum (Fig. 3) quadrately produced and with distal patch of short, dense, stout, black setae. (32) Male gonostylus short, broad, thick, deflected ventrad (Fig. 5); dorsal lobe short, broad. (33) Basolateral process of penis valve relatively stout (Fig. 7).

DISCUSSION

This subgenus, with species ranging from the southwestern United States to Argentina, includes two distinctive species groups. In both sexes of the *M. azurea* group (*sensu* Moure, 1960a, b) there is a low carina extending laterad from the pronotal collar to the front of the posterior lobe. In the males, the metafemur has a stout, basal projection on the ventral surface and there is a single metatibial spur.

The *M. bifrons* group (*sensu* Moure, 1960a, b) includes species that do not possess a carina between the pronotal collar and the posterior lobe. Males do not have a basoventral projection on the metafemur and there are two short, stout metatibial spurs.

In the following list, names marked by an asterisk (*) belong to the *M. azurea* group and those marked with a dagger (†) belong to the *M. bifrons* group; group placement is uncertain for those names that are unmarked.

INCLUDED NAMES

**azurea* (Lepeletier and Serville, 1825) (*Mesocheira*)
†bifrons (Fabricius, 1804) (*Melecta*)
chalybea (Friese, 1912) (*Melissa*)
chiruana (Holmberg, 1885) (*Melissa*)
**dugesi* (Cockerell, 1917) (*Mesonychium*)
**guatemalensis* Cockerell, 1912 (*Mesoplia*)
**imperialis* (Ashmead, 1900) (*Melissa*)
†imperialis (Friese, 1912) (*Melissa*) PREOCCUPIED
†imperatrix (Friese, 1913) (*Melissa*)
†insignis (F. Smith, 1879) (*Melissa*)
itaitubina (Ducke, 1902) (*Melissa*)
maculata (Friese, 1900) (*Melissa*)
ornata (Spinola, 1841) (*Mesocheira*)
†pilicrus (Friese, 1902) (*Melissa*)
pretiosa (Friese, 1912) (*Melissa*)
†regalis (F. Smith, 1854) (*Melissa*)
**rufipes* (Perty, 1833) (*Crocisa*)
simillima Schrottky, 1920 (*Mesoplia*)

Eumelissa, new subgenus

Figures 8–12, 61

DIAGNOSIS

MALE. Metatibial spurs normal, inner spur extending to, or beyond, midlength of metabasitarsus; metafemur without basal tooth; metatibia without inner, distal seta patch. Female: pygidium narrow, shiny, surface bare; metacoxa rounded above, neither carinate nor angulate at juncture with anterior face.

DESCRIPTION

(24) Ocellocular distance equal to, or less than, diameter of anterior ocellus. (25) Pronotum without carina between collar and front of posterior lobe. (26) Metacoxa abruptly rounded between dorsal and lateral faces, not angulate or subcarinate. (27) Metafemur of male without basal tooth or projection. (28) Metatibia of male without inner, distal patch of setae and with two normal apical spurs, the longer extending to, or beyond, midlength of metabasitarsus. (29) Tegula (Fig. 61) elliptical, narrowed behind. (30) Female pygidium completely marginate, narrow, apex narrowly rounded, disc bare and shiny. (31) Female sixth sternum weakly carinate along midline. (32) Male seventh sternum (Fig. 8) with apical margin somewhat triangularly produced in middle, apex acute, truncate or bilobate, with a few short, simple setae. (33) Gonostylus of male short, broad, curved mesad over inner plate (Fig. 11); dorsal lobe elongate. (34) Basolateral process of penis valve relatively slender (Fig. 12)

TYPE SPECIES

Melissa decorata F. Smith, 1854.

ETYMOLOGY

Greek prefix *eu-* (beautiful) plus *melissa* (bee).

DISCUSSION

Males of this subgenus are easily recognized by the unmodified metafemur and metatibia, as well as by the genitalia and associated structures. Both sexes share the unmodified metacoxa, the dorsal surface of which is distinctly rounded into the anterior and posterior surfaces, rather than carinate or sharply subangulate as in species of *Mesoplia* s. str. Females otherwise are very similar to those of the nominate subgenus but differ in the narrow, shiny pygidial plate which is devoid of the dense covering of metallic scales characteristic of that subgenus.

The included species are all South American, but we have seen both sexes of a possibly undescribed species from Costa Rica. Moure (1960b) included *Melissa duckei* Friese with this group of species, but in our opinion this species is not congeneric and is the type species for the genus *Aglaomelissa*, described below.

INCLUDED NAMES

albogutta (Ducke, 1905) (*Melissa*)
albopunctata Moure, 1967 (*Mesoplia*)
decorata (F. Smith, 1854) (*Melissa*)
friesei (Ducke, 1902) (*Melissa*)
guedesii (Ducke, 1902) (*Mesocheira*)

Mesonychium Group

Diagnostic characteristics of this group are inner eye margins divergent above (shared with *Ericrocis* group); strigilar malus without teeth (shared with *Aglaomelissa* in the *Ctenioschelus* group); the mesocoxa is less than 1.35 times the distance from the summit of the coxa to the base of the hind wing; metasomal sternum 3 of the male is without a dense lateral patch of white hair; and, male sterna 4 and 5 are without felt-like pads of pubescence along the apical margins. Metallic, scale-like hairs are present in *Mesonychium*, but absent in *Abromelissa*, in which the metasomal integument is metallic bluish, a unique apomorphy within the Ericrocini.

(A) Inner eye margins divergent above, often strongly so. (B) Ocellocular distance greater than diameter of anterior ocellus. (C) Mandible with preapical tooth. (D) Maxillary palpus one- or two-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia short, one-half or less length of velum, inner margin simple. (G) Mesobasitarsus usually compressed and more or less sharply carinate along posterior margin; distal process usually present. (H) Meso- and metadistitarsi with lateral patch of short, flattened setae on each side (Fig. 28) (except *Abromelissa* and a few *Mesonychium*). (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 0.60–0.94 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex or with two stout teeth. (M) Gonostylus without dorsal lobe.

The two included genera, *Mesonychium* and *Abromelissa* are confined to South America.

Genus *Mesonychium* Lepeletier and Serville

Figures 28–33, 65

Mesonychium Lepeletier and Serville, 1825:107. Type species: *Mesonychium coerulescens* Lepeletier and Serville, 1825 (monobasic).

Epiclopus Spinola, 1851:183. Type species: *Epiclopus gayi* Spinola, 1851 (monobasic).

DIAGNOSIS

Abdomen with appressed metallic scales or hairs; labrum with transverse preapical ridge which may be divided in middle; scutellum usually bituberculate.

DESCRIPTION

(1) Head much broader than long; inner eye margins straight, moderately to strongly divergent above; occipital margin little, if any, elevated above ocelli. (2) Maxillary palpus consisting of a single short, spindle-shaped segment. (3) Apical margin of labrum subtruncate; preapical transverse ridge (sometimes interrupted in middle) present. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded to subangulate. (7) Antenna short in both sexes; minimum length of first flagellar segment distinctly less than, to about equal to, apical width and much shorter than, to as long as, length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed for nearly its entire length; parapsidal lines weakly impressed, if at all. (10) Dorsal face of scutellum broadly, often weakly, impressed along midline; with a pair of erect, mammiform tubercles or (one species) no tubercles. (11) Anterior mesepisternal carina, acetabular carina, and sternopleural ridge absent. (12) Supraspiracular ridge weak to moderately strong, terminating in a stout tooth or projection above spiracle. (13) Tegula (Fig. 64) elliptical, outer margin evenly curved. (14) Second submarginal cell, on M, wider than, or equal to, first and wider than third; third submarginal cell narrowed anteriorly, sometimes triangular or petiolate; 1st m-cu basad of, or interstitial with, 1st r-m; 2nd m-cu distinctly basad of 2nd r-m.

(15) Mesotibial spur long, slender, parallel-sided, outer distal tooth obsolete. (16) Metatrochanter rounded beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide.

(17) Female sixth tergum with short, distinct pygidial plate, apex narrowly rounded to subtruncate. (18) Male fourth sternum usually concealed under third, its apical margin broadly, deeply incurved. (19) Male fifth sternum exposed, apical margin broadly, shallowly incurved or subtruncate. (20) Male seventh sternum (Fig. 29) more or less produced in middle, subtruncate to bilobate at apex. (21) Male eighth sternum (Fig. 30) with apical margin little produced. (22) Male gonostylus short and broad in dorsal view, stoutly digitiform in lateral view; dorsal lobe absent; inner apical sclerotization of gonocoxite usually well defined. (23) Penis valve weakly curved ventrad; basolateral lobe prominent (Fig. 33).

DISCUSSION

Mesonychium has never been adequately distinguished from *Mesoplia* by previous workers. Although species in the two genera are often somewhat similar in appearance, the two are distinct. Most species of *Mesonychium*, for example, possess very distinct patches of flattened setae on the meso- and metadistitarsi, which are lacking in *Mesoplia*. Male gonostyli lack dorsal lobes in species of *Mesonychium* and in both sexes of this genus the inner eye margins are moderately to strongly divergent above. *Mesonychium* is similar to the Nearctic genus *Ericrocis*, from which it is easily separated by the presence of metallic blue or green hairs and/or scales on various areas of the body.

Mesonychium appears to be an exclusively South American genus with species in Peru and Brazil south to Argentina and Chile. Within the genus there are two principal groups. The first of these includes the generotype and a few other species in which the meso- and metadistitarsi bear a cluster of short, flattened setae on each side and the pubescence of the head and body are generally dark. In a few species in this group the pubescence of the thoracic dorsum is very short and sparse. Species assigned to the *M. coerulescens* group include: *M. asteria* (F. Smith), *M. garleppi* (Schrottky), *M. jenseni* (Friese), *M. littoreum* Moure, *M. viridescens* (Friese), and *M. viridis* (Friese).

A second group of species lacks the distitarsal setae and in most the thorax and first two abdominal segments are densely clothed with long, erect white hairs; at least one species is dark haired. The species of this second group include those previously assigned to *Epiclopus*, but this group is so diverse in its morphological features that use of that name, even as a subgenus, would not be appropriate at this time. The following species belong to this group: *M. gayi* (Spinola), *M. wagenknechti* Ruiz, and an undescribed Peruvian species.

Although *M. lendlianum* (Friese) has traditionally been associated with such other Chilean species as *M. gayi*, which it resembles, it is anomalous in *Mesonychium*, and is the sole representative of the new genus *Abromelissa*, described below.

INCLUDED NAMES

albescens (Friese, 1921) (*Melissa)*
andina (Friese, 1925) (*Melissa*)
asteria (F. Smith, 1854) (*Mesocheira*)

coerulescens Lepeletier and Serville, 1825 (*Mesonychium*)
chilensis (F. Smith, 1854) (*Melecta*)
garleppi (Schrottky, 1910) (*Cyphomelissa*)
gayi (Spinola, 1851) (*Epiclopus*)
jenseni (Friese, 1906) (*Melissa*)
littoreum Moure, 1944 (*Mesonychium*)
porteri (Herbst, 1917) (*Melissa*)
violacea (Friese, 1900) (*Melissa*)
viridescens (Friese, 1930) (*Melissa*)
viridis (Friese, 1900) (*Melissa*)
wagenknechti Ruiz, 1938 [*Mesonychium* (*Epiclopus*)]

Abromelissa, new genus

Figures 39–43, 66

DIAGNOSIS

Separable from all other ericrocine genera by the metallic blue integument of the abdominal terga, without appressed metallic-reflective scales or hairs; further separable from *Mesonychium* and *Ericrocis* by the presence of a long cylindrical dorsal lobe on the male gonostylus, and in both sexes by the broader than long abdomen.

DESCRIPTION

(1) Head much broader than long; inner eye margin straight, moderately divergent above; ocelli on top of preocciput. (2) Maxillary palp three-segmented, first segment very short, second more than twice longer than first and about 1.5 times longer than third. (3) Apical margin of labrum subtruncate; preapical transverse ridge present and entire. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment greater than apical width and greater than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed almost to posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum barely impressed along midline and without mammiform tubercles, but with a pair of sublateral, short, erect spines at margin of declivity. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge strong, ending in a stout, blunt projection above spiracle.

(13) Tegula pyriform (Fig. 66). (14) Second submarginal cell, on M, wider than either first or third; third submarginal cell narrower on Rs than on M; 1st m-cu interstitial with 1st r-m; 2nd m-cu much basad of 2nd r-m.

(15) Mesotibial spur long, slender, parallel-sided, outer distal tooth obsolete. (16) Metatrochanter rounded beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide and without lateral patch of short, flattened setae.

(17) Female sixth tergum with short, distinct pygidial plate, apex narrowly rounded. (18) Male fourth sternum exposed, its apical margin transverse and with a dense fringe of decumbent, long, dark hairs. (19) Male fifth sternum normally visible only at extreme sides, its apical margin broadly and shallowly incurved and partially concealed under fourth. (20) Male seventh sternum (Fig. 39) with well-developed distal lobe, weakly trilobate. (21) Male eighth sternum (Fig. 40) with apical margin moderately produced. (22) Male gonostylus (Fig. 43) with dorsal, elongate, cylindrical lobe; inner apical sclerotization of gonocoxite short, broad and concave on dorsal face (Fig. 42), stout and subtruncate in lateral view (Fig. 41). (23) Penis valve strongly curved ventrad; basolateral lobe prominent.

TYPE SPECIES

Melissa (*Epiclopus*) *lendliana* Friese, 1910.

ETYMOLOGY

Combines Greek *habros* (graceful or pretty) with *melissa* (bee).

DISCUSSION

This genus includes only the type species, found in Argentina (Provinces of Neuquen and Valdivia) and Chile (Provinces of Aconcagua, Coquimbo, Valparaiso, Santiago, Ñuble, Curico, and Aisen). *Melissa friesei* Herbst, 1918 (not *M. friesei* Ducke, 1902) and *Mesonychium frieseanum* Ruiz, 1938, are synonyms of *A. lendliana* (NEW SYNONYMIES). The one species of *Abromelissa* superficially resembles two Chilean species of *Mesonychium*, *M. gayi* and *M. wagenknechti*, since the hairs of the thorax and first tergum are long, erect and pale, and there are no short, appressed, metallic-reflective scales on the body. From both of these, however, it differs in the dark metallic blue color of the tergal integument, a feature which appears to be unique within the tribe.

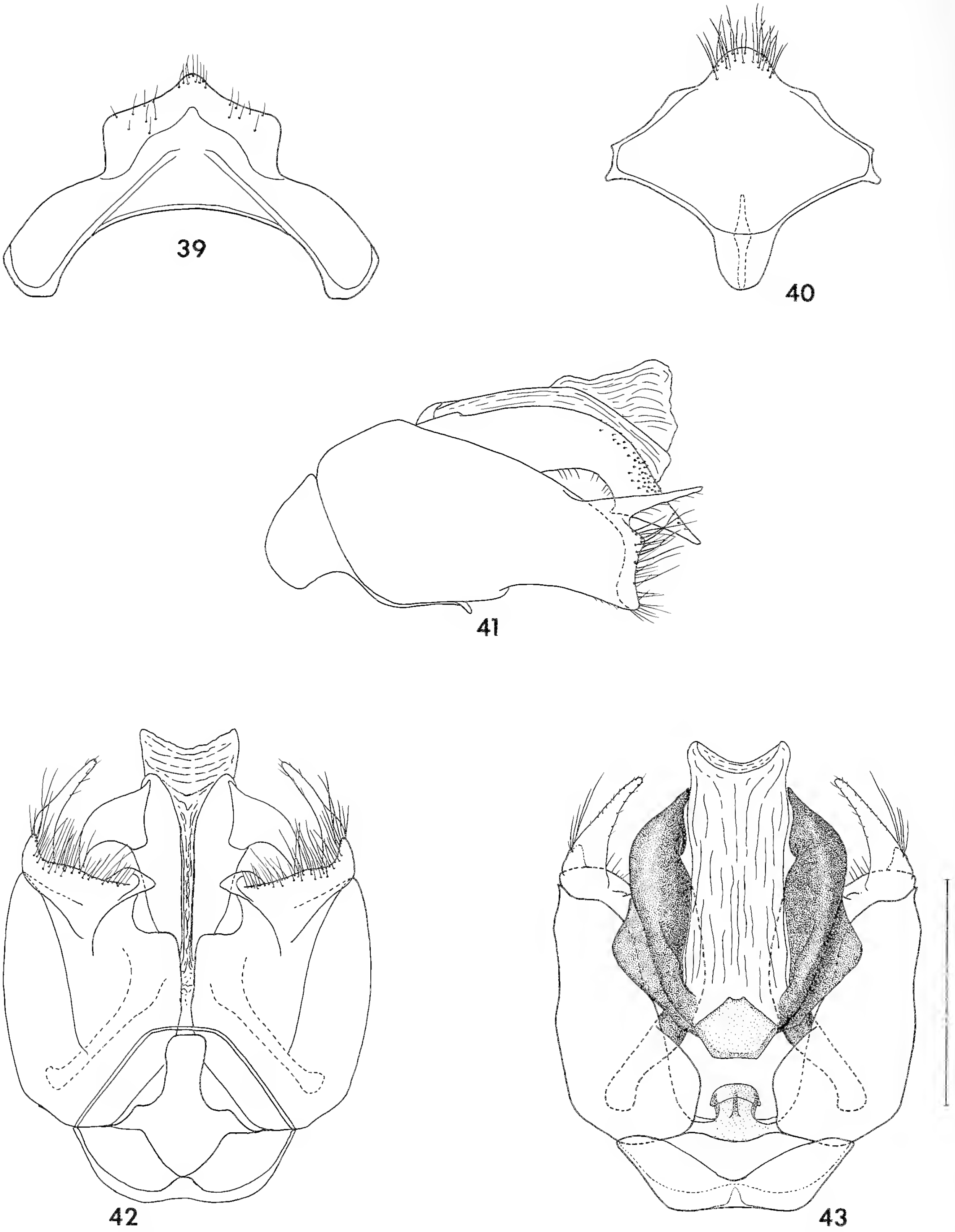
In addition to the characteristics described above, there are a few other features of *Abromelissa* that are distinctive within the *Mesonychium* group. The surface of the mesoscutum is smooth and shiny between subcontiguous coarse punctures and sparse giant punctures, and the scutellum is coarsely rugosopunctate and foveolate on the dorsal face. Although the mesobasitarsus is without a ridge along its posterior margin, an inconspicuous distal process is present. The male pygidial plate is narrowly translucent at its apex and is weakly bilobate.

The known hosts are all species of *Centris* in the subgenera *Paracentris* and *Wagenknechtia* (Table 3).

Ctenioschelus Group

Several unique apomorphies define the *Ctenioschelus* group: the preapical tooth is lost; the forewing tips are infuscated; metasomal tergum 7 is subangulate in profile (Fig. 76). Arolia are present (except in *Mesocheira*) and an anterior mesepisternal carina is present (except in *Ctenioschelus*).

(A) Inner eye margins subparallel or weakly convergent above. (B) Ocellocular distance less than diameter of anterior ocellus. (C) Mandible without preapical tooth, sometimes fused with stipes. (D) Maxillary palpus consisting of one short segment. (E) Hypostomal carina high, lamelliform. (F) Malus



Figures 39-43. *Abromelissa lendlianum,* male. **39,** sternum 7; **40,** sternum 8; **41-43,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

of protibia short (0.25 or less length of velum), stout, simple. (G) Mesobasitarsus neither compressed nor carinate along posterior margin; distal process absent. (H) Meso- and metadistitarsi without lateral patches of short, flattened setae. (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 1.0–1.2 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum slightly elevated and subangulate. (L) Male seventh tergum bidentate, teeth well separated. (M) Male gonostylus absent or, if present, without dorsal lobe.

The three genera, *Aglaomelissa, Ctenioschelus,* and *Mesocheira* occur in Central and South America.

Aglaomelissa, new genus

Figures 44–48, 67

DIAGNOSIS

Separable from *Ctenioschelus* and *Mesocheira* by the following combination of characteristics: male antenna short; anterior mesepisternal carina present; scutellar prominences mammiform; marginal cell of forewing without apical cloud.

DESCRIPTION

(1) Head a little broader than long; inner eye margins straight, slightly convergent above; occipital margin elevated above ocelli. (2) Maxillary palpal segment short, broad, lightly sclerotized and fused to stipes. (3) Labrum without preapical tubercle or transverse ridge; apical margin slightly produced and truncate. (4) Interantennal distance slightly greater than antennal socket diameter; antennocular distance about equal to one-half antennal socket diameter. (5) Ocelloccipital distance about two times diameter of anterior ocellus. (6) Occipital margin subcarinate. (7) Antenna short in both sexes; minimum length of first flagellar segment less than greatest width and distinctly less than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed almost to posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum broadly impressed in middle and with a pair of suberect mammiform tubercles. (11) Anterior mesepisternal carina sharp, lamelliform and confluent with acetabular carina, or nearly so; sternopleural ridge absent. (12) Supraspiracular ridge evanescent where its distal portion turns ventrad.

(13) Tegula (Fig. 67) elliptical, outer margin narrowed anteriorly. (14) Submarginal cells about equally long on M, third much narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu distinctly basad of 2nd r-m; marginal cell about as long as distance from apex to wing tip.

(15) Mesotibial spur stout, apex broad, with 1–3 elongate intercalary teeth. (16) Metatrochanter compressed and subangular below; outer metatibial spur short, stout, strongly curved at apex; metadistitarsus about twice longer than wide.

(17) Female sixth tergum with well-defined, narrow pygidial plate, apex subacute. (18) Male fourth sternum broadly incurved and with distal fringe of long, plumose, prostrate hairs. (19) Male fifth sternum more shallowly incurved and with shorter distal fringe. (20) Male seventh sternum (Fig. 44) with median lobe on apical margin. (21) Male eighth sternum (Fig. 45) with apical margin produced, emarginate, and narrowly truncate in middle. (22) Male gonostylus absent (Figs. 46, 47) inner apical sclerotization of gonocoxite distinct. (23) Penis valve evenly curved ventrad; basolateral lobe absent.

TYPE SPECIES

Melissa (*Mesocheira*) *duckei* Friese, 1906.

ETYMOLOGY

Greek, *aglaos* (splendid or beautiful) plus *melissa* (bee, also an old generic name in this tribe).

DISCUSSION

Although this genus is related to *Ctenioschelus* and *Mesocheira,* it is easily separated from both. Males of *Ctenioschelus* have extraordinarily long antennae, and both sexes of that genus lack pronotal, anterior mesepisternal, and acetabular carinae. In *Mesocheira* the processes of the dorsal face of the scutellum are flattened and plate-like, extending over the base of the abdomen.

The only species of *Aglaomelissa* is known from a few specimens from Costa Rica, Panama, Trinidad, Colombia, and Venezuela.

Although Moure (1960b) included *A. duckei* in his *Mesoplia decorata* group, this bee is clearly not a *Mesoplia.* Particularly indicative of its relationship to *Ctenioschelus* and *Mesocheira* are the presence of the anterior mesepisternal carina and the subangulate profile of the first metasomal tergum.

The suspected host is a species of *Centris* (Table 3).

Genus *Ctenioschelus* Romand

Figures 49–54, 68

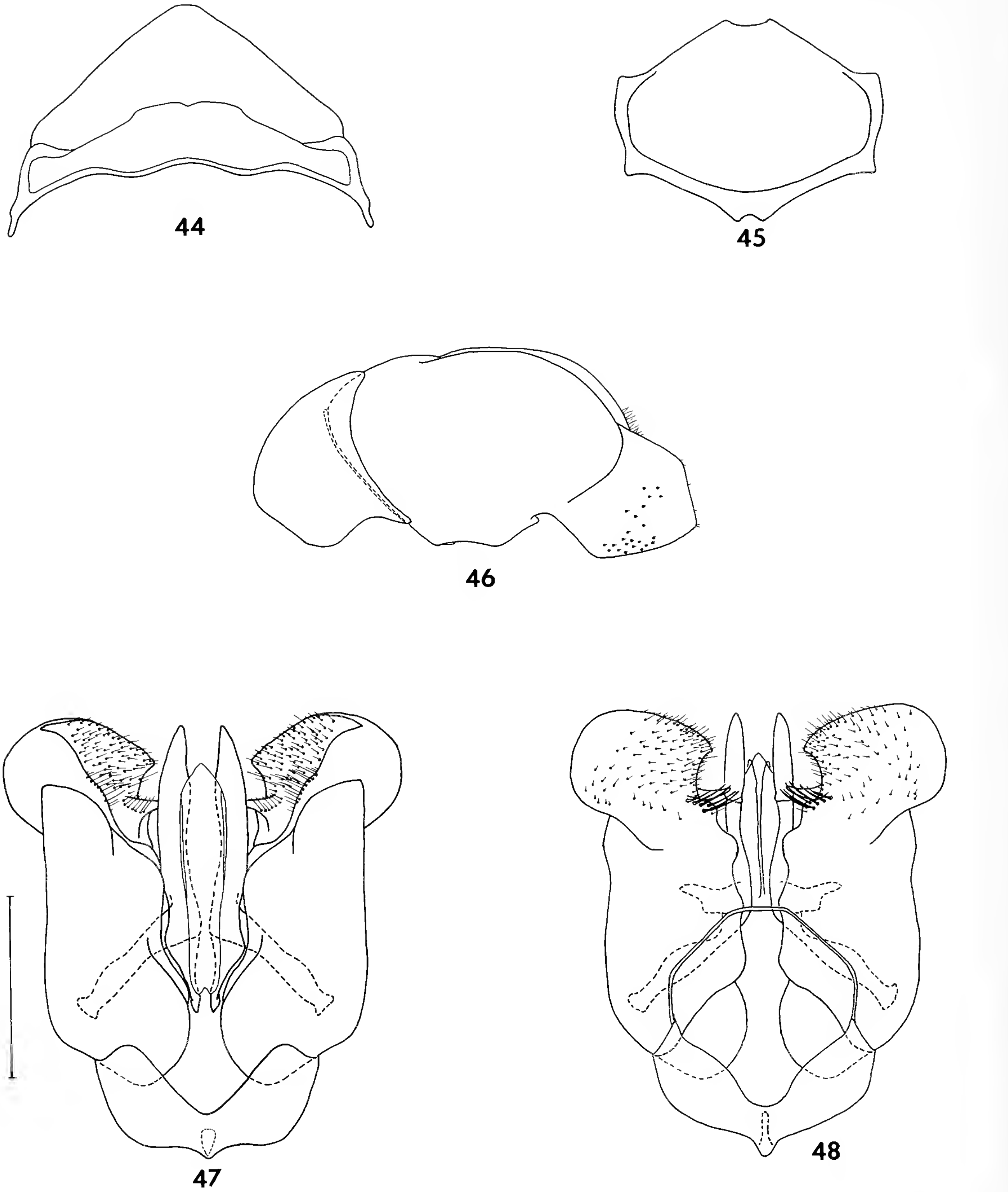
Ctenioschelus Romand, 1840:336. Type species: *Acanthopus goryi* Romand, 1840 (monobasic).

Ischnocera Shuckard, 1840:166. No included species.

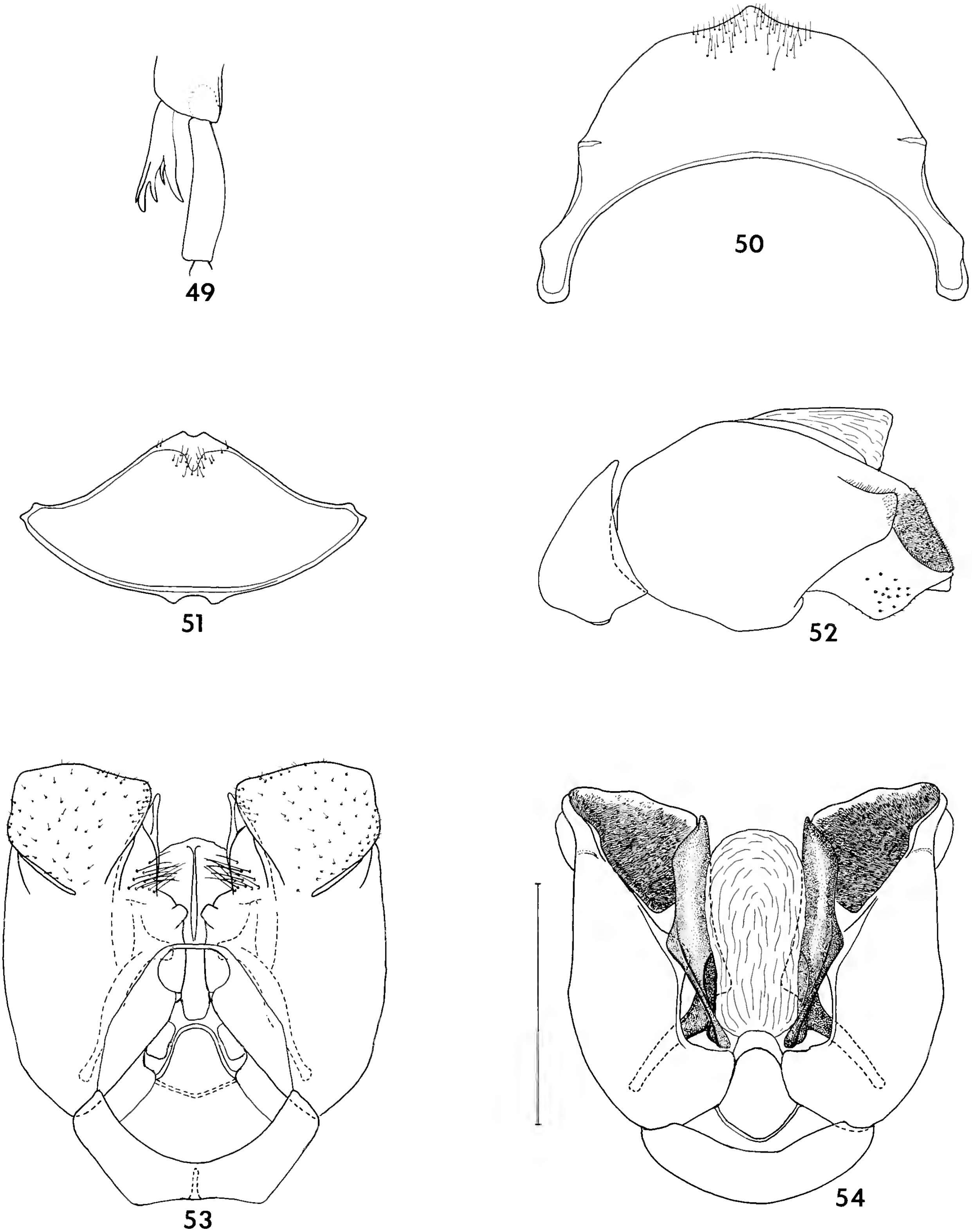
Melissoda Lepeletier, 1841:508. Type species: (*Melissoda latreillei* Lepeletier, 1841) = *Acanthopus goryi* Romand, 1840 (monobasic).

DIAGNOSIS

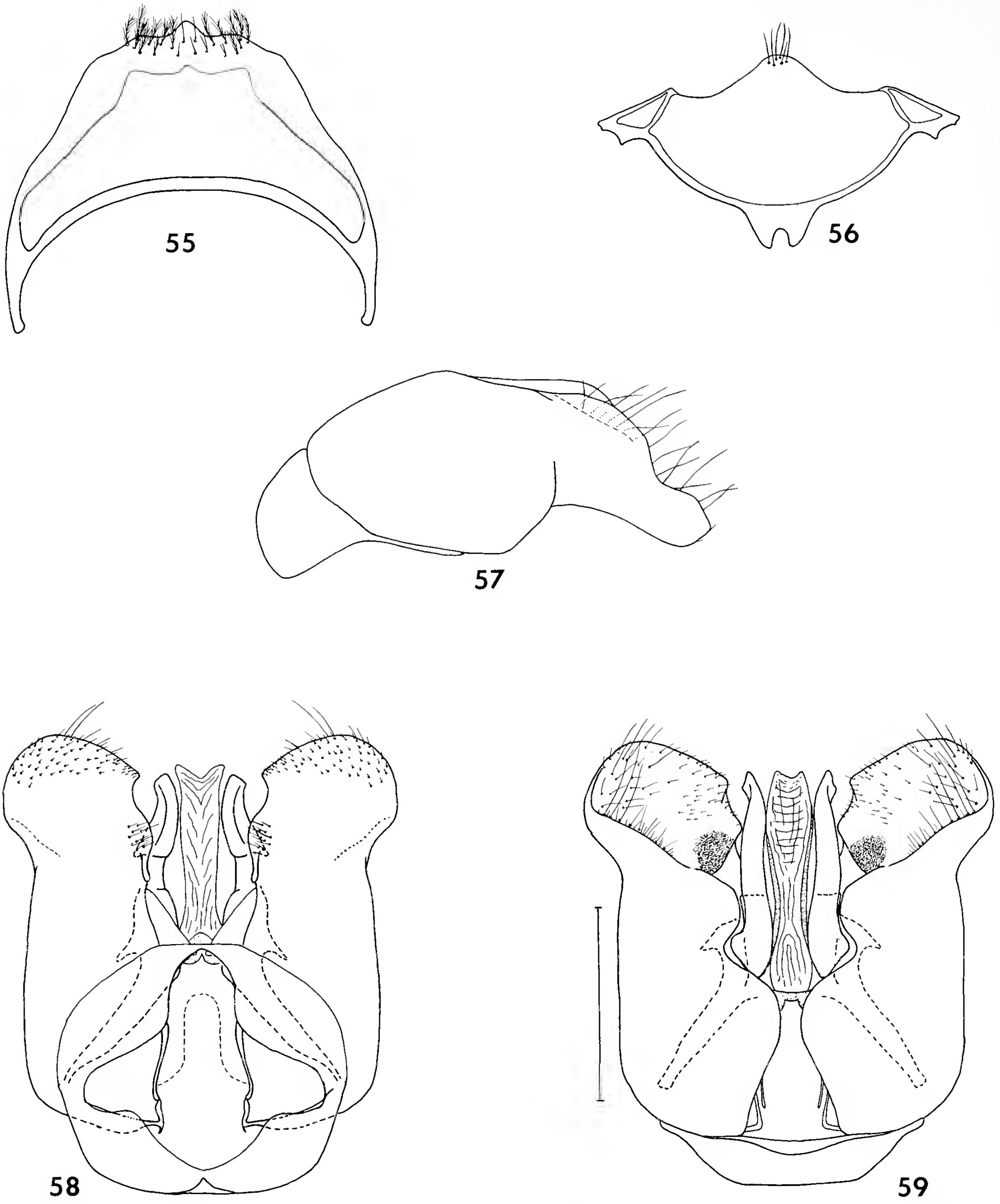
Male immediately separable from all other ericrocine genera by the greatly elongate flagellum reaching beyond apex of abdomen. Additional features characteristic of both sexes: no anterior mesepisternal carina; scutellar tubercles prostrate, mammiform, and extended over propodeum; meso-



Figures 44–48. *Aglaomelissa duckei,* male. **44,** sternum 7; **45,** sternum 8; **46–48,** genital capsule, lateral, dorsal, and ventral views. Scale line = 1.00 mm.



Figures 49-54. *Ctenioschelus goryi.* **49,** female mesobasitarsus, pilosity omitted; **50,** male sternum 7; **51,** male sternum 8; **52-54,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

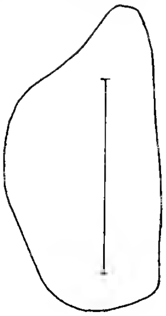


Figures 55-59. *Mesocheira bicolor,* male. 55, sternum 7; 56, sternum 8; 57-59, genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

basitarsus without posterior carina or distal process; juncture of basal and discal faces of first tergum elevated and angulate.

DESCRIPTION

(1) Head a little broader than long; inner eye margins essentially straight, convergent above; occipital margin little elevated above ocelli. (2) Maxillary palpal segment short, flattened. (3) Labrum impressed along midline and with weak transverse preapical ridge; apical margin broadly rounded, subtruncate in middle. (4) Interantennal distance less than antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance more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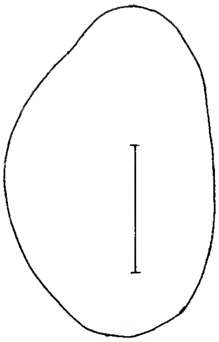
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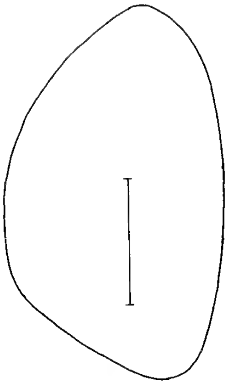
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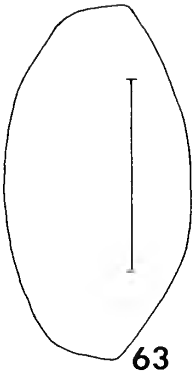
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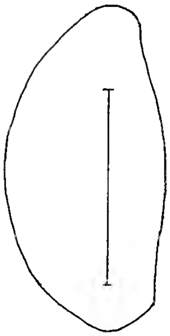
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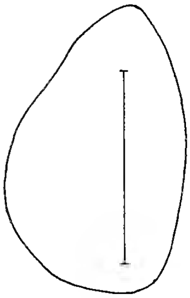
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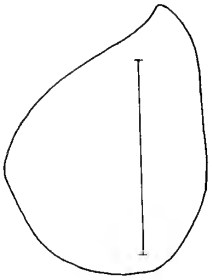
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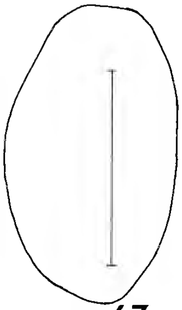
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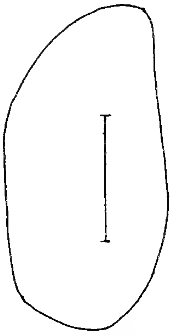
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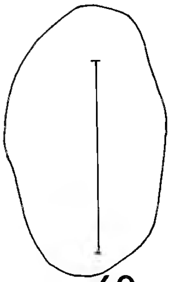
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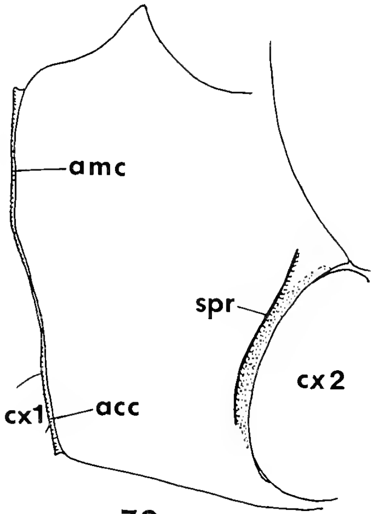

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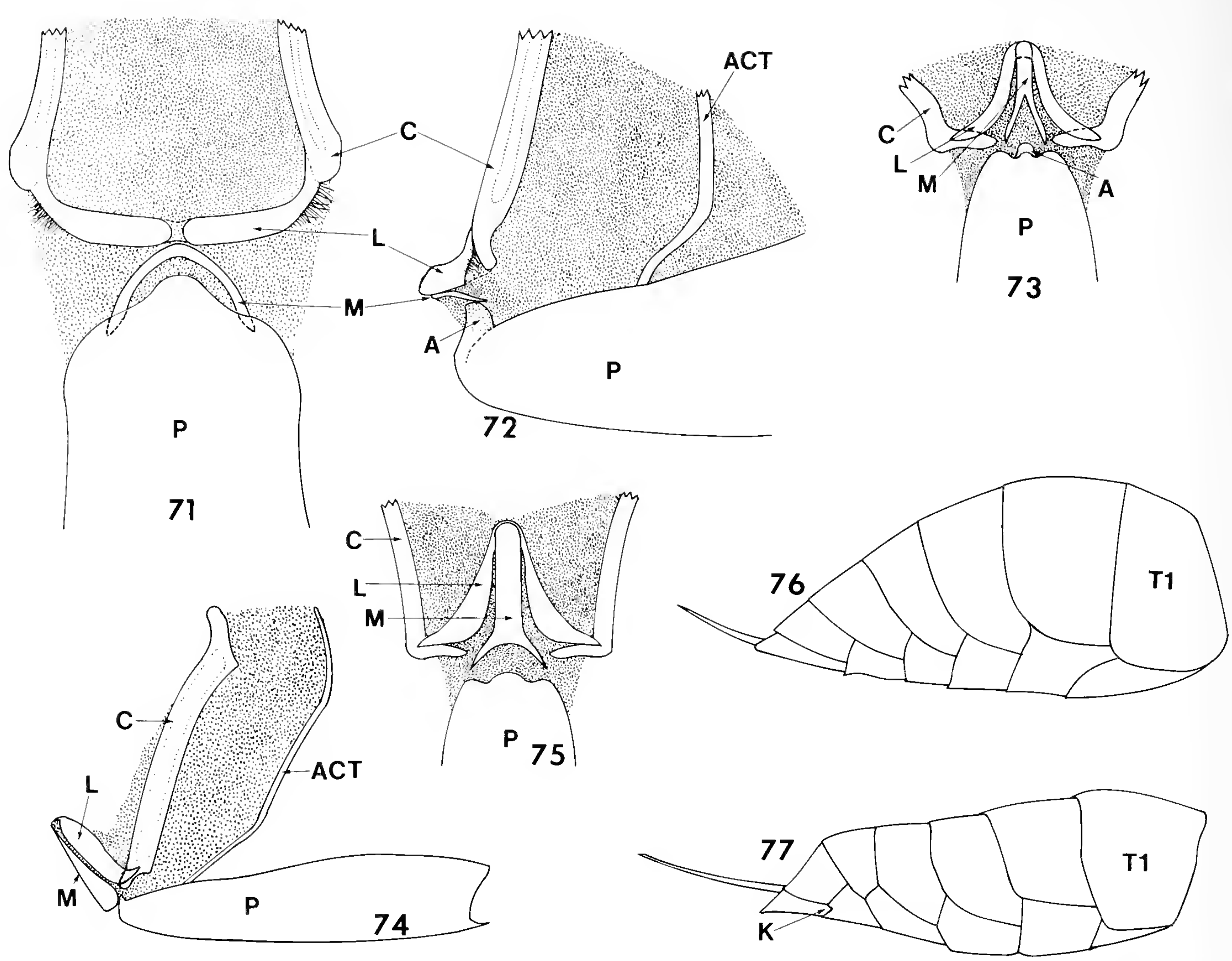
Figures 60–69. Dorsal view of left tegula of: **60,** *Ericrocis lata;* **61,** *Hopliphora velutina;* **62,** *Acanthopus palmatus;* **63,** *Mesoplia* (*M.*) *rufipes;* **64,** *M.* (*Eumelissa*) *decorata;* **65,** *Mesonychium coerulescens;* **66,** *Abromelissa lendliana;* **67,** *Aglaomelissa duckei;* **68,** *Ctenioschelus goryi;* **69,** *Mesocheira bicolor;* scale line = 1.0 mm. **70,** diagrammatic mesopleuron, illustrating positions of: anterior mesepisternal carina (amc); acetabular carina (acc); mesocoxa (cx 2); procoxa (cx 1); sternopleural ridge (spr). Precoxal depression stippled.

than twice diameter of anterior ocellus. (6) Occipital margin subangulate. (7) Antenna short in female, flagellum longer than body length in male; minimum length of female first flagellar segment less than width and about one-half as long as second segment; minimum length of male first flagellar distinctly greater than width and less than one-third as long as second on same side; middle segments of male flagellum about seven times longer than wide.

(8) Pronotal collar prominent on each side, no carina between collar and posterior lobe. (9) Midline of mesoscutum



Figures 71-77. *Acanthopus palmatus,* female: **71-72,** Posterior and side view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. *Ericrocis lata,* female: **73-74,** posterior and side view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. **75,** side view of metasoma, spiracles omitted. *Mesoplia imperatrix,* male: **76,** posterior view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. *Mesocheira bicolor,* female: **77,** side view of metasoma, spiracles omitted, arrow indicates character 67. Abbreviations are A, basal apodeme of prementum; ACT, anterior conjunctival thickening [=suspensory thickening of Winston (1979)]; C, cardo; K, notch of metasomal sternum 5; L, lorum; M, mentum; P, prementum; T1, first metasomal tergum. Dotted areas represent the membranous surface of the labiomaxillary tube extending toward its attachment to the head.

not impressed; parapsidal lines weakly impressed. (10) Dorsal face of scutellum impressed along midline; lateral processes nearly prostrate, dorsally convex, projecting over concave vertical face, metanotum, and propodeum. (11) Anterior mesepisternal carina, acetabular carina, and sternopleural ridge absent. (12) Supraspiracular ridge prominent, shelf-like, not curved ventrad behind spiracle.

(13) Tegula subrectangular, outer margin sinuate (Fig. 68). (14) First submarginal cell, on M, narrower than second or third; third submarginal cell much narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu distinctly basad of 2nd r-m; wing tip infuscated.

(15) Mesotibial spur broad at apex, with two or three long intercalary teeth. (16) Metatrochanter compressed and angulate ventrally; metatibial spurs normal; metadistitarsus about three times longer than wide.

(17) Female sixth tergum with short, poorly defined, narrowly truncate pygidial plate. (18) Male fourth sternum broadly emarginate, distal portion bare and transparent, but largely hidden by long brush of hairs arising near midlength. (19) Male fifth sternum similar but transparent margin narrower, more fully concealed by preapical fringe. (20) Male seventh sternum (Fig. 50) rounded distad, subangulate in middle. (21) Male eighth sternum (Fig. 51) produced along apical margin, with small median emargination. (22) Male gonostylus almost absent, situated beneath much enlarged

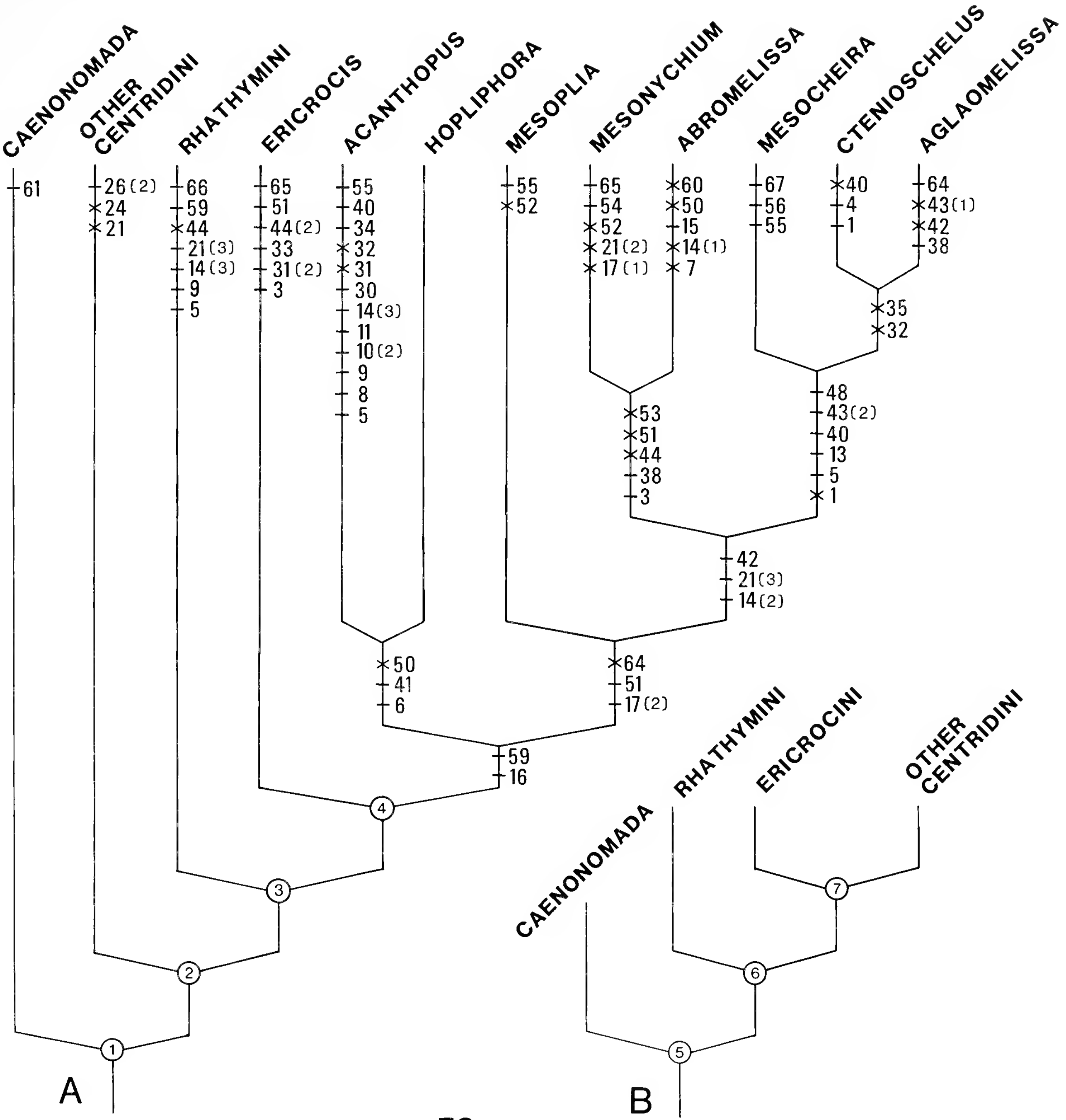


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Figure 78. A. Cladogram showing the generic relationships of the Ericrocini and its sister group the Rhathymini which are shown derived from the Centridini. *Caenonomada* has other apomorphies which have not been given. A bar indicates an apomorphy, an X a reversal. Synapomorphies which root both trees are 20, 23, 24, 52. Synapomorphies of the centridine-rhathymine-ericrocine lineage (internode 1–2) are the derived characters of variables 17, 18, 20(2), 25, 26, 44, 47(2). When there is more than one derived character composing a variable the relevant one is indicated in parentheses. Synapomorphies of the rhathymine-ericrocine lineage (internode 2–3) are 2, 7, 14, 21(2), 29, 37, 39, 46, 49, 64. Synapomorphies of the Ericrocini (internode 3–4) are 1, 10, 12, 19, 22, 27, 28, 31, 32, 35, 36, 45, 50, 53, 57, 58, 60, 61(2), 62. B. Alternative cladogram showing relationships of the tribes. Synapomorphies of rhathymine-centridine-ericrocine bees (internode 5–6) are 17, 18, 20(2), 25, 26, 47(2). Synapomorphies of Rhathymini are 2, 5, 7, 14(3), 21(3), 29, 37, 39, 45 (character is not constant), 46, 49, 58, 59, 64, 66. Synapomorphies of centridine-ericrocine bees (internode 6–7) are 27 (character is not constant), 28, 31 (character is not constant), 44. Synapomorphies for Centridini (excluding *Caenonomada*) are 21 (reversion), 24 (reversion), 26(2). Synapomorphies of the Ericrocini are 1, 2, 7, 10, 12, 14, 19, 21(2), 22, 27–29, 31, 32, 35–37, 39, 43, 45–47, 49, 50, 57–60, 61(2), 62–64.

concave and densely setose inner apical sclerotization of gonocoxite (Fig. 54). (23) Penis valve evenly curved ventrad; basolateral lobe weak (Fig. 54).

DISCUSSION

The bizarrely slender and elongate antennae are immediately distinctive for *Ctenioschelus* males. Females resemble those of *Mesoplia* but are readily separable by the subangulate profile of the first tergum. The one species is apparently not common and ranges from Costa Rica to Brazil. Brazilian specimens have their forewing tips more heavily infuscate than do the Peruvian to Central American populations. Its host is unknown.

INCLUDED NAMES

goryi (Romand, 1840) (*Acanthopus*)
latreillei (Lepeletier, 1841) (*Melissoda*)

Genus *Mesocheira* Lepeletier and Serville

Figures 55–59, 69, 76

Mesocheira Lepeletier and Serville, 1825:106. Type species: (*Mesocheira bicolor* Lepeletier and Serville, 1825) = *Melecta bicolor* Fabricius, 1804 (designation of Taschenberg, 1883).
Mesochira Schulz, 1906:257 (lapsus).

DIAGNOSIS

Scutellar processes prostrate and shelf-like, extending over base of abdomen; anterior mesepisternal carina present; marginal cell of forewing with apical cloud.

DESCRIPTION

(1) Head a little broader than long; inner eye margins essentially straight, weakly convergent above; occipital margin not elevated above ocelli. (2) Maxillary palpal segment short, button-like. (3) Labrum impressed along midline, without preapical ridge or tubercle; apical margin transverse or slightly concave. (4) Interantennal distance about equal to antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance almost twice diameter of anterior ocellus. (6) Occipital margin reflexed and cariniform. (7) Antenna short in both sexes; minimum length of first flagellar segment about one-half maximum width and less than one-half length of second segment on same side.

(8) Side of pronotal collar raised and subcarinate, with high lamelliform carina from collar to front of posterior lobe. (9) Midline and parapsidal lines of mesoscutum weakly impressed. (10) Dorsal face of scutellum narrowly impressed along midline; lateral processes flat, shelf-like, extending over base of abdomen. (11) Anterior mesepisternal carina lamelliform, confluent below with acetabular carina; sternopleural ridge absent. (12) Supraspiracular ridge prominent, curved ventrad for a short distance behind spiracle.

(13) Tegula subrectangular, outer margin sinuate (Fig. 69). (14) First submarginal cell, on M, narrower than second or third; third submarginal cell strongly narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu virtually interstitial with 2nd r-m; wing clear, with apical infuscation in marginal cell and at wing tip.

(15) Mesotibial spur stout, weakly broadened distad, with one or two long, acute intercalary teeth. (16) Metatrochanter compressed and subangulate beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide.

(17) Female sixth tergum with well-defined, acute pygidial plate. (18) Male fourth sternum with sharp, median, longitudinal carina on basal one-half, distal margin nearly straight. (19) Male fifth sternum hidden under fourth, apical margin deeply concave. (20) Male seventh sternum (Fig. 55) with apical margin strongly produced, subtruncate and with median triangular projection. (21) Male eighth sternum (Fig. 56) with medioapical portion produced, often irregular in shape. (22) Male gonostylus almost absent, reduced to a mere slit only visible from apicodorsal aspect (Fig. 59); inner apical sclerotization of gonocoxite nearly absent. (23) Penis valves evenly curved ventrad; basolateral lobe moderately produced.

DISCUSSION

The plate-like, posteriorly directed mesoscutellar processes will separate both sexes of *Mesocheira* from all other ericrocine genera. There appears to be but a single species that ranges from Mexico to Brazil and Paraguay. Although hosts are unknown, the relatively small size suggests species of the subgenera *Hemisiella* and *Heterocentris* of *Centris*. The senior author has taken females at a nest site of *C.* (*Hemisiella*) *nitida* F. Smith in Mexico.

The figures of the labiomaxillary complex of the mouthparts, illustrated (fig. 44) by Winston (1979) as those of *Mesocheira bicolor*, are not of that bee. They appear to be based on *Ericrocis lata*.

INCLUDED NAMES

bicolor (Fabricius, 1804) (*Melecta*)
bilamellosa (Cockerell, 1949) (*Exaerete*)
elizabethae Cockerell, 1910b (*Mesocheira*)
melanura (Cockerell, 1949) (*Exaerete*)
pulchella Holmberg, 1887 (*Mesocheira*)
sericea Guérin-Méneville, 1846 (*Mesocheira*)

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CONTRIBUTIONS IN SCIENCE

THE STATUS OF *SMILODON* IN NORTH AND SOUTH AMERICA

Annalisa Berta

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THE STATUS OF *SMILODON* IN NORTH AND SOUTH AMERICA

Annalisa Berta[1]

ABSTRACT. South American representatives of the sabercat genus *Smilodon* (Felidae, Machairondontinae, Smilodontini) are referred to a single species, *Smilodon populator* Lund, 1842, from Pleistocene (?Uquian, Ensenadan–Lujanian) localities in Argentina, Bolivia, Brazil, Ecuador, Peru, and Uruguay. North American *Smilodon* from Pleistocene (late Irvingtonian–Rancholabrean) deposits are also assigned to *S. populator.* Diagnostic characters of *S. populator* include: large size; skull with broad muzzle; upper canines strongly recurved; upper canines and cheek teeth with finely serrated anterior and posterior margins; P^4 with very reduced protocone; mandible usually with single, large mental foramen; mandibular flange greatly reduced. Variation was noted in several characters; smaller size, triangular occiput, and P_3 were more common among middle Pleistocene (Ensenadan and Irvingtonian) samples of *S. populator.* During the late Pleistocene, South American populations displayed a larger mean size than their North American contemporaries.

Smilodon gracilis (Cope, 1880) is a more primitive related form known from the late Pliocene (Blancan) through the middle Pleistocene (Irvingtonian) of North America. The derived species *S. populator,* apparently evolved in North America during the middle Pleistocene (late Irvingtonian) and spread into South America. As in North America, *Smilodon* became extinct in the southern continent at the end of the late Pleistocene (Rancholabrean and Lujanian, respectively).

INTRODUCTION

Although *Smilodon* has been known from the Pleistocene of North and South America since the early part of the 19th century, no previous studies have critically compared samples from the two continents. Such comparisons are essential to an understanding of the phylogenetic interrelationships of this sabercat and they also serve to strengthen existing biostratigraphic correlations between the Americas during the Pleistocene. The present contribution is an evaluation of the status of *Smilodon* in North and South America with emphasis upon its South American record of occurrence.

ORGANIZATION AND METHODS

In addition to citations of the original publications of F. Ameghino and P.W. Lund, cross-references to compilations of their publications are given. The *Obras Completas y Correspondencia de Florentino Ameghino* edited by A.J. Torcelli consists of 24 volumes published between 1913 and 1926. The *Memorias sobre a paleontologia Brasileira Revistas e comentadas por Carlos de Paula Couto* is a single volume of Lund's work published in 1950. These compilations include reproductions of most of the work of F. Ameghino and P.W. Lund, and have had wider distribution than many of the original publications.

The chronology and usage of South American late Cenozoic Land Mammal Ages follows that proposed by Patterson and Pascual (1972). From oldest to youngest, the Uquian, Ensenadan, and Lujanian Land Mammal Ages are presently included within the Pleistocene, with the Uquian straddling the boundary between the Pliocene and Pleistocene. Correlation of North and South American late Cenozoic Land Mammal Ages follows Marshall et al. (1982) and suggests the following correlations: Lujanian with late Rancholabrean, Ensenadan with early and middle Rancholabrean and middle and late Irvingtonian, and Uquian with late Blancan and early Irvingtonian.

Metrical data presented in this study should be interpreted with caution. The scope of this analysis necessitated the use of measurements published by others, although care was taken to eliminate those that were not directly comparable with the system of measuration utilized here and described by Merriam and Stock (1932). Samples were often very small; this was especially true for South American late Pleistocene populations which unlike their North American contemporaries were not homogeneous with respect to locality and in some cases possibly age. Statistics were computed through the use of the BMDP (Dixon and Brown, 1979) programs.

The following institutions are referred to in the text: AMNH, American Museum of Natural History, New York, New York; BM(NH), British Museum (Natural History), London, England; FMNH, Field Museum of Natural History, Chicago, Illinois; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata, Mar del Plata, Argentina; MNHN, Museum National d'Histoire Naturelle, Paris, France; ROM, Royal Ontario Mu-

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seum, Toronto, Ontario, Canada; UZM L, Peter W. Lund Collection, Universitets Zoologiske Museum, Copenhagen, Denmark.

HISTORICAL REVIEW

The discovery of sabercats in South America was first announced by Lund (1842) and was based on material recovered from late Pleistocene–Holocene cave faunas of Lagoa Santa in eastern Brazil. *Smilodon* and a single species, *S. populator,* were named from isolated teeth and associated metapodials. Earlier, Lund (1839a) erroneously referred some of this material to *Hyaena neogaea.* Since at the time of the original designation *Hyaena neogaea* was insufficiently defined and no type material was designated, this species is regarded as a *nomen nudum* following Paula Couto (1955).

Subsequently, additional sabercats of Pleistocene age were discovered in Argentina, Bolivia, Ecuador, and Peru. Most of these specimens were attributed to *Smilodon,* although a few were described as new genera and subgenera [i.e. *Smilodon* (*Prosmilodon*) Rusconi, 1929; *Smilodontidion* Kraglievich, 1948].

Méndez-Alzola (1941) provided the most detailed description of South American sabercats and referred the Argentine material to *S. bonaeriensis.* Paula Couto (1955) reviewed the literature and, on the basis of Brazilian material, distinguished at the subspecific level the South American *S. populator populator* from the North American *S. populator californicus.* Churcher (1967) examined some Argentine material and added supplementary information about the South American species which he referred to *S. neogaeus.* Hoffstetter (1952) contributed to our knowledge of *Smilodon* from Ecuador, while Churcher (written comm., 1981) is describing an excellent sample from the Talara tar seeps of Peru.

At present two species of *Smilodon* are recognized. The small, slender *S. gracilis* is recorded from late Pliocene–middle Pleistocene (late Blancan–late Irvingtonian) localities in North America (Berta, in press). The large, robust, and more derived *S. populator* (synonyms include *S. floridanus* Leidy, 1889, *S. californicus* Bovard, 1907, and *S. fatalis* sensu Slaughter, 1963) is recorded from middle–late Pleistocene (late Irvingtonian–Rancholabrean) localities in North and South America. Various authors (e.g. Webb, 1974b; Robertson, 1976) have suggested interrelationships between North and South American *Smilodon,* but until now such proposals have been based on comparisons made from the literature rather than firsthand study of collections.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Sabercats have been recorded from Argentina (Buenos Aires, and Mar del Plata and environs), Bolivia (Tarija, Ñuapua), Brazil (Lagoa Santa Caves), Ecuador (La Carolina, Punin), Peru (Talara), and Uruguay (Fig. 1). The oldest record, *Smilodontidion riggii* (Kraglievich, 1948), was reported from the Chapadmalal Formation near Mar del Plata, Argentina, and assigned a Chapadmalalan (late Pliocene) age. However, according to G. Scaglia (pers. comm., 1981; Churcher, 1977: 255) this material was not collected in situ but rather from landslide deposits at the base of a cliff that are more likely Ensenadan in age.

The Uquian record of sabercats is based on material collected from the Vorohue Formation at Mar del Plata and Miramar, Argentina. According to J.L. Kraglievich's (1952) chronological subdivisions, this rock unit encompasses the Vorohuean subage, an intermediate subdivision between the Uquian and Ensenadan Land Mammal Ages, regarded by Pascual et al. (1966) as indistinguishable from the Uquian. Scaglia (pers. comm., 1981), however, questions the validity of this record and interprets this material as having been derived from Ensenadan-age deposits.

Discounting these questionable records, *Smilodon* is well documented from deposits that range in age from Ensenadan–Lujanian. Argentine localities assigned an Ensenadan age are listed by Méndez-Alzola (1941). Outside of Argentina, sabercats have been recovered from middle and late Pleistocene deposits of Tarija and Ñuapua, Bolivia (Boule and Thévenin, 1920; Hoffstetter, 1963, 1968). Known collections of these faunas come from various stratigraphic levels (MacFadden et al., 1983) and are Ensenadan and possibly Lujanian in age. Lujanian age deposits that have yielded abundant *Smilodon* include Buenos Aires, and Mar del Plata and environs (Méndez-Alzola, 1941); Talara, Peru (Churcher, written comm., 1981); La Carolina and Punin, Ecuador (Hoffstetter, 1952); and various sites in Uruguay (Mones and Francis, 1973). *Smilodon* apparently became extinct in South America during the late Pleistocene; the Lujanian–Holocene Lagoa Santa Caves of Brazil represent its latest known occurrence.

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Family Felidae Gray, 1821

Subfamily Machairodontinae Gill, 1872

Tribe Smilodontini Kurtén, 1963

Genus *Smilodon* Lund, 1842

Hyaena Lund, 1839a:94 (not *Hyaena* Brisson, 1762).
Felis Lund, 1839c:271 (not *Felis* Linnaeus, 1758).
Munifelis Muñiz, 1845 (fide F. Ameghino, 1889:333).
Felis (*Trucifelis*) Leidy, 1868:175.
Trucifelis Leidy, 1869:366.
Machaerodus Lydekker, 1884:33.
Drepanodon Leidy, 1889:14.
Machairodus Leidy, 1889:14.
Machaerodus Winge, 1895:3, 13 (not *Machairodus* Kaup, 1833).
Smilodontopsis Brown, 1908:188.
Prosmilodon Rusconi, 1929:5 (as a subgenus of *Smilodon*).
Smilodontidion J.L. Kraglievich, 1948:6.

TYPE SPECIES. *Smilodon populator* Lund, 1842.

INCLUDED SPECIES. Type species and *S. gracilis* (Cope, 1880).

EMENDED DIAGNOSIS. Differs from all other machairodont genera but shares with *Megantereon* the following derived characters: glenoid process enlarged; prominent postorbital process; well-developed supraoccipital crest; upper canines elongate, compressed and recurved; upper and lower incisors enlarged; P2/2 lost; long postcanine diastema; P3/3 reduced; P^4 protocone reduced; lower canines reduced; and limbs and feet short and stocky. More derived than *Megantereon* in having incisors enlarged and procumbent; upper canines longer and more robust; P^4 ectoparastyle enlarged; and mandibular flange reduced.

KNOWN DISTRIBUTION. ?Uquian. Ensenadan–Lujanian (middle–late Pleistocene) of South America and Irvingtonian–Rancholabrean (middle–late Pleistocene) of North America.

Smilodon populator Lund, 1842b

Figures 2–4

Felis cultridens Bravard, 1828:143, table III, figs. 10–13; Blainville, 1864, II (Des *Felis,* Chap. 3:141).

Hyaena neogaea Lund, 1839a:94; 1839b:224, 232; 1840a: 265; 1840b:312; 1842a:12; Burmeister, 1864:123; 1879: 106; Paula Couto, 1940:24; 1945:253.

Felis protopanther Lund, 1839c:207; 1840a:293, pl. XXVI, figs. 10–11; Burmeister, 1879:106; H. Gervais and F. Ameghino, 1880: (Obras II:532).

Munifelis bonaerensis Muñiz, 1845.

Machaerodus neogaeus (Lund) Pictet, 1853:221; Burmeister, 1864:123; 1867:183; 1879:106; Lydekker, 1885:47; Winge, 1895:3, 13, 80, 82; Spillman, 1931:53; 1938:373.

Felis smilodon Desmarest, 1853:150, 152, 221, 223; 1860: 61; Blainville, 1855, pl. XX; Paula Couto, 1940:24; 1945: 253.

Smilodon blainvillii Desmarest, 1860:61.

Felis (*Trucifelis*) *fatalis* Leidy, 1868:175.

Trucifelis fatalis Leidy, 1869.

Machaerodus necator P. Gervais, 1878:1361 (*nomen nudum*).

Machaerodus cf. *M. neogaeus* Branca, 1883:137–147, pl. XIX.

Machaerodus fatalis Lydekker, 1884:333.

Smilodon ensenadensis F. Ameghino, 1888:6 (Obras V:473); 1898:195 (Obras XII:628); Paula Couto, 1945:253, 255.

Drepanodon or *Machaerodus floridanus* Leidy, 1889:14.

Machaerodus ensenadensis F. Ameghino, 1889:339 (Obras XII:849, pl. IV, fig. 18); Bosca, 1923:182.

Smilodon floridanus Adams, 1896:433.

Smilodon crucians F. Ameghino, 1904:123 (Obras XV:201); 1909:122 (Obras XVII:610); J.L. Kraglievich, 1947:4, fig. 1.

Smilodon bonaerensis F. Ameghino, 1907:39, fig. 3 (Obras XVII:11, fig. 3); Rusconi, 1931:3, 4, 6, 8, figs. 1, 2, 4, 6, 7; Méndez-Alzola, 1941:10.

Smilodon californicus Bovard, 1907:155.

Smilodontopsis troglodytes Brown, 1908:188.

Smilodontopsis conardi Brown, 1908:190.

Figure 1. Distribution of *Smilodon populator* in South America. Symbols: ●, Lujanian; ■, Ensenadan; ○, ?Uquian.

Smilodon nebraskensis Matthew, 1918:228.

Smilodon neogaeus ensenadensis Boule and Thévenin, 1920: 235, pl. XXVI, figs. 1–5.

Smilodon (*Prosmilodon*) *ensenadensis* Rusconi, 1929:5; 1936: 206.

Smilodon (*Trucifelis*) *californicus* Merriam and Stock, 1932: 16.

Smilodon (*Trucifelis*) *fatalis* Merriam and Stock, 1932:16.

Smilodon (*Trucifelis*) *floridanus* Merriam and Stock, 1932: 16.

Smilodon (*Trucifelis*) *nebraskensis* Merriam and Stock, 1932: 16.

Smilodon (*Trucifelis*) *californicus brevipes* Merriam and Stock, 1932:161.

Smilodon neogaeus Paula Couto, 1940:24–27; 1945:253, 255–256, 261, note 38; 1950:58–59, note 18, 366, note 433, 538; 1953:96, 99; Churcher, 1967:245.

Smilodon necator Paula Couto, 1940:24; 1945:253.

Smilodon (*Prosmilodon*) *ensenadensis ferox* J.L. Kraglievich, 1947:5.

Smilodon (*Prosmilodon*) *ensenadensis minor* J.L. Kraglievich, 1948:11; Rusconi, 1929:5; 1931:14.

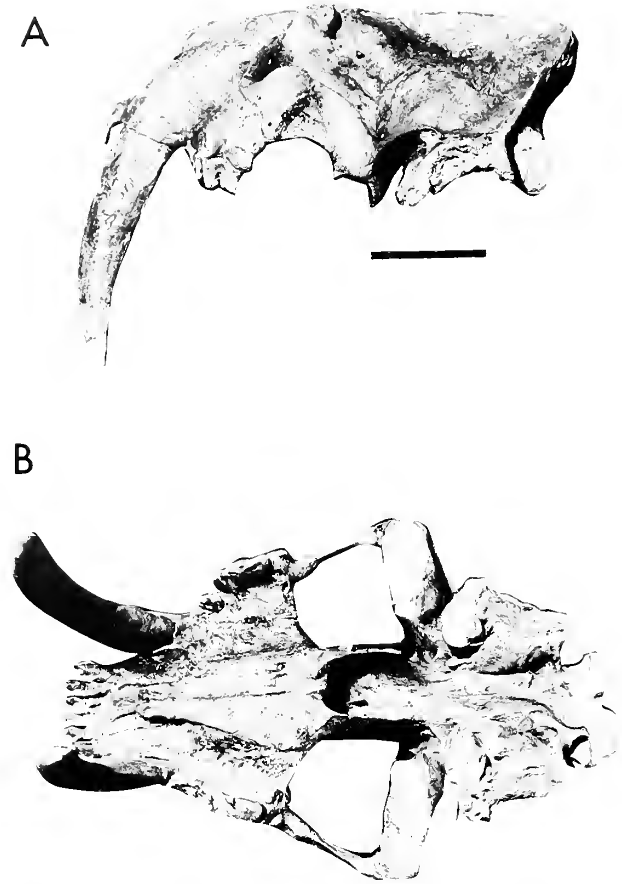


Figure 2. *Smilodon populator,* MACN 46, from near Lujan, Buenos Aires Province, Argentina. Lateral (A) and ventral (B) views of skull. Scale = 10 cm.

Smilodontidion riggii J.L. Kraglievich, 1948:6, figs. 3, 5–6, 8–9; Pascual et al., 1966:59.

Smilodon sp. Spillman, 1948:261; Hoffstetter, 1949:8; Hoffstetter, 1952:165, figs. 39, 40, pl. V, fig. 8, pl. VI, figs. 1–8.

Smilodon populator populator Paula Couto, 1955:11, fig. 10.

Smilodon trinitensis Slaughter, 1960:487.

Smilodon fatalis Slaughter, 1963:74.

SYNTYPES. UZM L specimens, right I^2, I^3, fragmentary right C^1, left metacarpals, II, IV, and right metacarpal V; from Lagoa Santa Caves, Brazil.

Type of *S. bonaerensis.* MACN 46, a nearly complete skeleton, from Luján, Buenos Aires Province, Argentina.

Type of *S. crucians.* MACN 1460, right ramus with I$_3$–M$_1$; from Tarija, Bolivia.

Type of *S. (Prosmilodon) ensenadensis ferox.* MACN 1457, anterior portion of right ramus with symphyseal region, C root, and P$_{3-4}$ alveoli; from Tarija, Bolivia.

Type of *S. (P.) ensenadensis minor.* MACN 16693, occipital portion of skull; MACN 16692, right cuboid; MACN 16689, right and left humeri; MACN 16695, proximal and distal portions of left femur; MACN 16697, proximal portion of right radius; MACN 16691, proximal portion of right tibia; MACN 16690, left astragalus; right calcaneum; and MACN 16694, right metatarsal III. Probably all of the same individual; from Punta Hermengo, Miramar Province, Argentina.

Type of *Smilodontidion riggii.* MACN 6802, patella, proximal phalanges III, IV, V, femur, tibia, astragalus, calcaneum, metatarsal IV, fibula, and ischium; from Chapadmalal Formation, Buenos Aires Province, Argentina.

EMENDED DIAGNOSIS. Differs from *Smilodon gracilis* in having large, robust skull with broad muzzle, upper canines strongly recurved, upper canines and cheek teeth with finely serrated anterior and posterior margins, P^4 with very reduced protocone, mandible usually with a single, large mental foramen, and mandibular flange greatly reduced.

SOUTH AMERICAN DISTRIBUTION. Ensenadan–Lujanian, Bolivia; Lujanian, Brazil; Lujanian, Ecuador; ?Uquian, Ensenadan–Lujanian, Argentina; Lujanian, Peru; and Lujanian, Uruguay.

SOUTH AMERICAN MATERIAL STUDIED. See Appendix 1.

DESCRIPTION

Smilodon populator is best known in North America from the late Pleistocene tar pits of Rancho La Brea, California (Merriam and Stock, 1932). The South American record of this sabercat is described herein using the Rancho La Brea sample as the standard of comparison.

SKULL. Cranial measurements are listed in Appendix 2A. South American individuals are characterized by development of very large, robustly proportioned skulls. As seen in dorsal view, the reduced nasals display deeply notched anterior ends and the muzzle is short and broad. The well inflated postorbital processes are characterized by a marked convexity of their posterior border. The zygomata are deep and widely arched (Fig. 2A). The sagittal crest rises prominently behind the slightly convex frontal region. In ventral view (Fig. 2B), the auditory bullae are slightly inflated and comparatively longer than in the Rancho La Brea sample. The enlarged mastoid process is closely appressed to the postglenoid process.

Some variation is apparent in the shape of the occiput (Fig. 3A, B). Most specimens examined show development of a rounded, convex occiput with a strong vertical keel on the basioccipital—the typical condition in *S. populator* as noted by Merriam and Stock (1932:32). However, several specimens including MACN 8682 display narrower, more triangular occiputs with less distinct vertical keels. Slaughter (1963) noted that triangular occiputs were characteristically developed among North American pre-Wisconsinan (late Irvingtonian and early Rancholabrean) *Smilodon* which he referred to *S. fatalis.* While it is generally true that most specimens that display a triangular occiput are Ensenadan or Irvingtonian in age, several Lujanian and Rancholabrean specimens (e.g. MACN 8661, Fig. 3A) also exemplify this condition. It is also possible that the shape of the occiput may represent sexual dimorphism or age variation as it was ob-

Figure 3. *Smilodon populator,* occipital views of skull showing extremes in variation. A, MACN 8661 from Olivos, Buenos Aires Province, Argentina; B, MACN 8682 from P. Piedras, Buenos Aires Province, Argentina. Scale = 10 cm.

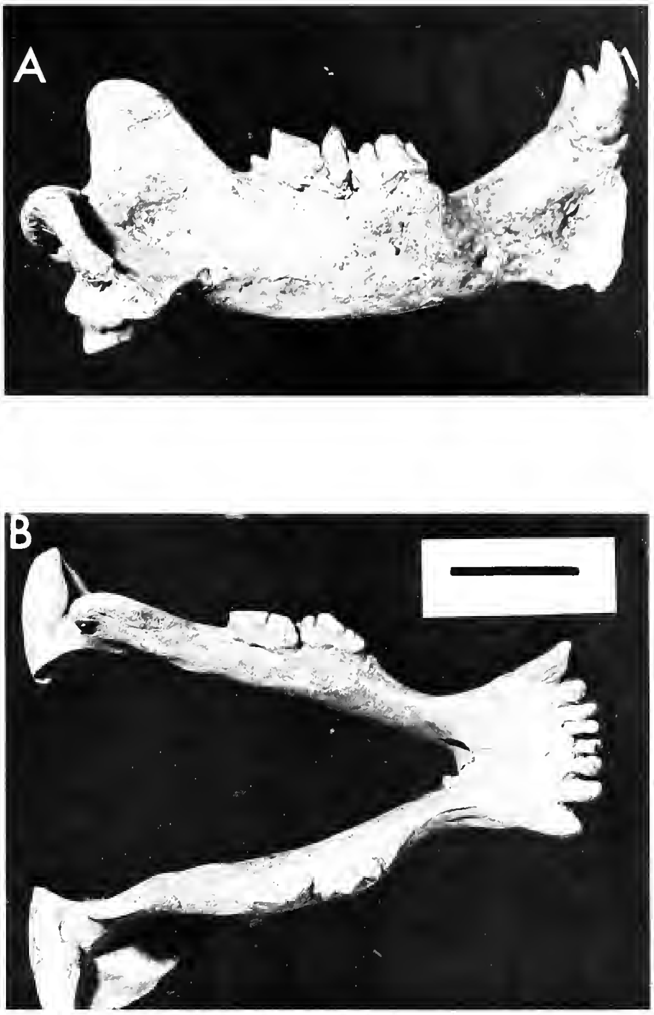


Figure 4. *Smilodon populator,* MACN 46, from near Lujan, Buenos Aires Province, Argentina. Lateral (A) and occlusal (B) views of mandible. Scale = 5 cm.

served that those specimens that exhibit a narrower, more triangular occiput usually possess well-developed sagittal crests and often typify subadult individuals.

UPPER DENTITION. Appendix 2B lists upper tooth dimensions. Upper incisors are large, sharp and procumbent. I^1 is comprised of lingual and labial cusps positioned on either side of the V-shaped notch encircling the principal cusp. I^2 is similar in morphology, with the lingual ridge extending further anteriorly. The caniniform I^3 consists of a principal cusp and small basal cusp positioned on a circular serrate ridge on the lingual tooth margin. The strongly developed posterolateral ridge is serrated in unworn specimens.

The long, slender canine is strongly recurved and fine enamel serrations are developed on the anterior and posterior margins. Although few sabers are preserved in entirety, the canine is longer than in Rancho La Brea specimens (Fig. 2). Paula Couto (1955, table 1) lists canine length for a specimen from Brazil as approximately 277.5 mm compared with a range of measurement for this tooth among the Rancho La Brea sample of 200–262 mm (Merriam and Stock, 1932:48).

P^3 is relatively small and variable in morphology. It is double-rooted and consists of a principal cusp flanked by anterior and posterior cusps. Occasionally, a second posterior cusp develops, as in ROM 2116 and MLP 10-2. A strong anterolingual cingulum is usually present. In MACN 46, however, the anterior and posterior cusps are small, and the anterolingual cingulum is absent. The orientation of P^3 varies from a linear to oblique position behind the canine.

The small ectoparastyle and parastyle of the upper carnassial form the anterior blade of the tooth. The metacone is always anteroposteriorly longer than the paracone. The protocone is usually very reduced or absent although a separate protoconal root is usually present. The occasional presence of the protocone was noted in Rancho La Brea *Smilodon* by Merriam and Stock (1932:48) and confirmed in this study. Unworn specimens characteristically show development of serrations along the cutting edge. M^1 is a very reduced, double-rooted tooth with a transversely elongated crown comprised of a principal cusp, the parametacone, and a small protocone. The tooth is oriented at nearly right angles to the anteroposterior axis of P^4.

MANDIBLE. The horizontal ramus is anteroposteriorly short and robust (Fig. 4A, B, Appendix 2A). The anterior face of the massive symphysis is concave and pitted by foramina. The flange is very reduced ventrally in comparison with *Smilodon gracilis,* although its anterior margin is usually thick and laterally flared. The diastema between the C and P_4 is comparatively shorter among most of the South American sample although its length is variable, a feature apparently related to age (Merriam and Stock, 1932, pl. 4). Usually a single, large mental foramen is positioned below the diastema near the ventral border of the ramus although double foramina occasionally occur in the Californian and Talaran populations (Churcher, 1984; this study). The coronoid process is greatly reduced. Among several South American specimens (e.g. MACN 46 and MACN 18057) the prominent angular process swings laterally farther away from the deeply excavated masseteric fossa than in most Rancholabrean specimens (Fig. 4).

LOWER DENTITION. Appendix 2B lists lower tooth dimensions. Lower incisors are broad, recurved, and set in a transverse line. The small I_1 bears a prominent V-shaped notch encircling the principal cusp and a lingual ridge which terminates in a basal cusp. I_2 is similar in morphology, with serrations present on the lingual ridge. The caniniform I_3 exhibits a prominent serrate lingual ridge. The lower canine has in addition to the lingual ridge a prominent posterior ridge, slightly labial to the midline of the tooth; both ridges are serrated.

P_3, commonly present in Ensenadan and Irvingtonian specimens, is extremely variable in morphology (CV for length = 23.4). In MACN 6270, P_3 is single-rooted and comprised of a single principal cusp followed by a small posterior cusp. In another specimen, ROM 5100, the alveolus for this tooth indicates that it was double-rooted. Loss of P_3 is more common among Lujanian and Rancholabrean specimens. As noted by Merriam and Stock (1932:51), this tooth is present in only 6% of the La Brea sample (N = 678).

P_4 is double-rooted and comprised of a principal cusp flanked by a relatively small anterior cusp and two progressively smaller posterior cusps. The second posterior cusp is occasionally positioned on a strong lingual cingulum. The crown of this tooth and M_1 are inclined posteriorly.

M_1 usually possesses a small anterior cingulum in front of the paraconid. Presence of this cusp among North American specimens was previously noted (Bovard, 1907). The paraconid blade is noticeably shorter anteroposteriorly than the protoconid and both are serrated. Most specimens show slight development of a basal posterior cingulum behind the protoconid.

DISCUSSION

The known South American samples of sabercats are all referred to *Smilodon populator.* As previously mentioned, *Smilodon* was established by Lund (1842b) who described a single species, *S. populator,* from the Lagoa Santa Caves, Brazil. Muñiz (1845) described a sabercat skeleton collected from near Luján, Argentina, under the name *Munifelis bonaerensis.* However, his generic name is invalid since it was published in a newspaper (La Gaceta Mercantil), which does not satisfy the publication requirement established by the International Code of Zoological Nomenclature. Later authors (Ameghino, 1907; Rusconi, 1931; Méndez-Alzola, 1941) incorrectly referred to sabercats under the name *Smilodon bonaerensis.* Burmeister (1867) applied the name *Machaerodus bonaerensis* to the Argentine material, although he later acknowledged that *S. bonaerensis* was probably conspecific with *S. neogaeus* (Lund, 1839a).

Ameghino (1888:6) described *Smilodon ensenadensis* (=*Machaerodus ensenadensis*) based on an upper canine recovered from Ensenadan deposits in Ensenada, Argentina. Rusconi (1929) listed small sabercats from the Ensenadan of Argentina under the subgenus *Smilodon* (*Prosmilodon*). L. Kraglievich (1934) followed Rusconi's usage of *Prosmilodon.* In 1947 J.L. Kraglievich formally diagnosed *Smilodon* (*Prosmilodon*) on the basis of its small size and presence of P_3. The variable presence of this tooth among smilodontines has been previously discussed. Presence or absence of this tooth generally can be used to distinguish Ensenadan or Irvingtonian *S. populator* from Lujanian or Rancholabrean forms of this species.

A right ramus (MACN 1457) collected from Tarija, Bolivia, and originally described and figured by Ameghino (1902) as *Machaerodus ensenadensis,* was referred by Kraglievich (1947) to *Smilodon* (*Prosmilodon*) *ensenadensis ferox.* This subspecies was distinguished from *S. bonaerensis* on the basis of its smaller size, lack of serrations on the upper canine, and presence of a double-rooted P_3. Examination of the type and referred material indicates that the upper canine is heavily worn along both the anterior and posterior margins, obliterating serrations had they been present. A second subspecies, *Smilodon* (*Prosmilodon*) *ensenadensis minor,* was distinguished by J.L. Kraglievich (1948) on the basis of its

Table 1A. ANCOVA for length of lower canine of *Smilodon populator* adjusted for length and width of P_4 as a test for significant differences based on locality and age. * = $P \leq 0.05$, ** = $P < 0.01$. Abbreviations = AP = anteroposterior length, T = transverse width.

Souce of variation	Sum of squares	Degrees of freedom	Mean square	F-value	Regression coefficient
Locality	0.06274	1	0.06274	0.04	
Age	37.41456	1	37.41456	23.32**	
Locality/age	29.88608	1	29.88608	18.63**	
AP, P_4	6.25910	1	6.25910	3.90*	0.23330
T, P_4	0.00007	1	0.00007	0.00	−0.00183
AP & T, P_4	12.34655	2	6.17328	3.85*	
Error	75.41120	47	1.60449		

smaller size and more robust postcranium. Examination of the type indicates that it falls within the limits of variation shown by *Smilodon*. The subgenus *Smilodon* (*Prosmilodon*) is here referred to *Smilodon*.

Smilodon crucians was recognized by Ameghino (1904) on the basis of its small size, shallow ramus, and long postcanine diastema. These characters are attributable to ontogenetic variation (see Merriam and Stock, 1932, pl. 4, fig. 10) and indicate that *S. crucians* represents a juvenile individual. As expected, the high coefficient of variation value for postcanine diastema length among both North and South American sabercats (see Appendix 2A) further weakens its use as a taxonomic character. Examination of the holotype of *S. crucians* (MACN 1460) revealed the presence of serrations on the lower canine and cheek teeth, which supports synonymy of this species with *S. populator*.

A new genus of sabercat, *Smilodontidion*, was proposed by J.L. Kraglievich (1948) on the basis of limb elements collected from near Chapadmalal, Argentina. This genus was distinguished by its smaller size and slightly different morphology, regarded here as the result of both individual and age variation. The incomplete fusion of epiphyses on the femur and tibia indicates that this specimen represents a young adult. I agree with Churcher (1967) that *Smilodontidion* should be synonymized with *Smilodon*.

Table 1B. Adjusted group means for length of lower canine of *Smilodon populator*. Abbreviations: N = sample size, as in Table 1A.

	North America		South America	
Age	Rancholabrean	Irvingtonian	Lujanian	Ensenadan
AP, C	14.81744	13.80000	17.81667	11.43333
N	43	4	3	3

The results of systematic reevaluation of North American *Smilodon* are summarized in the following discussion (see also Berta, in press). The oldest name for a North American *Smilodon* is *Felis* (*Trucifelis*) *fatalis* proposed by Leidy (1868). The type, a fragmentary maxilla containing P^4 from Hardin County, Texas, redescribed and illustrated by Leidy (1869) is judged too incomplete to provide specific diagnosis. Later, Leidy (1889) described a fragmentary skull lacking teeth as a new species of the European genus *Machairodus*, *M. floridanus*. This species has been referred to *Smilodon* by all later workers. Bovard (1907) proposed the species of *Smilodon californicus* separating it from *S. floridanus* by the latter's shorter muzzle, more posterior position of the posterior nares and possibly by ridges on the palate. The sample from Rancho La Brea consisting of thousands of individuals was more fully described by Merriam and Stock (1932) who proposed certain differences in the mastoid region to distinguish the two species. Kurtén's (1965) study of Florida sabercats led him to synonymize *S. floridanus* with *S. fatalis* and maintain *S. californicus* as distinct. Webb (1974b) in his evaluation of additional Florida material strengthened the case for synonymy of *S. californicus* with *S. floridanus* using broad overlap of cranial, mandibular, and tooth measurements.

More recently, Kurtén and Anderson (1980) recognized a single derived species, *Smilodon fatalis* and considered "the numerous North American taxa of sabertooths (with the exception of *S. gracilis*) to have, at most, subspecific standing." Churcher (1984) followed Slaughter (1963) in assigning to *Smilodon fatalis* the following species: *Smilodontopsis conardi* Brown, 1908; *Smilodontopsis troglodytes* Brown, 1908; *Smilodon nebraskensis* Matthew, 1918; and *Smilodon trinitensis* Slaughter (1960).

The genus *Smilodontopsis* proposed by Brown (1908) was founded on specimens from the Conard Fissure, Arkansas, and distinguished from *Smilodon* by the possession of an entepicondylar foramen on the humerus. Two species, *S. troglodytes* and *S. conardi* were described on differences in the morphology of the upper carnassial. *Smilodon nebraskensis* was based on a lower jaw from Nebraska and distinguished from *S. californicus* by its "decidedly shorter postcanine diastema" (Matthew, 1918), a character of suspect taxonomic value. *Smilodon trinitensis* was founded by Slaughter (1960) on a lower jaw from the Trinity River, at Dallas, Texas. It was distinguished from previously described species by its large cheek teeth, relative to mandibular measurements and the absence of P_3. As noted previously, P_3 is more commonly present in middle Pleistocene samples and is extremely variable in morphology.

The taxonomic confusion surrounding North American *Smilodon* brought out in the preceding discussion suggested as the next step, critical evaluation of the status of *S. floridanus* and *S. fatalis* (sensu Slaughter, 1963). As shown in this study, all of the characters diagnostic of North American *S. floridanus* also typify South American *S. populator*. Among the most useful of these characters are: large, robust skull with broad muzzle, upper canines strongly recurved, upper canines and cheek teeth with finely serrated margins, P^4 with

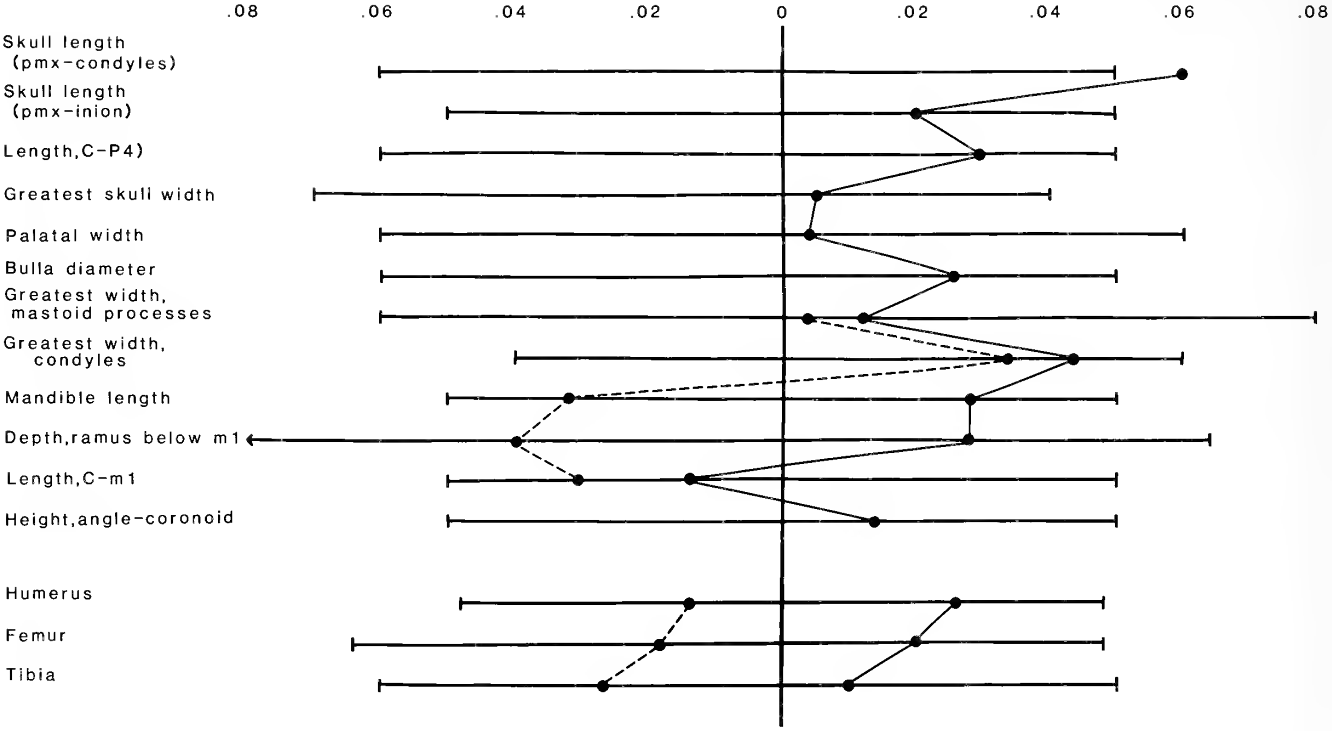


Figure 5. Ratio diagram of cranial, mandibular, tooth, and limb measurements (see Appendix 2) of South American *Smilodon populator* (solid line, Lujanian sample; dashed line, Ensenadan sample) compared with North American *Smilodon populator* (Rancho La Brea sample; Merriam and Stock, 1932) as the standard. A log difference scale is provided and horizontal bars show the observed range of variation of the standard.

very reduced protocone, mandible usually with a single, large mental foramen, and mandibular flange greatly reduced.

A ratio diagram (Fig. 5 see Appendix 2 for sample statistics; for the method see Simpson, 1941) illustrates the differences between mean measurements of South American *S. populator* and the Rancho La Brea sample, the standard of comparison. Two sets of data are compared: (1) skull and mandible dimensions and (2) forelimb and hindlimb lengths from both North and South American middle and late Pleistocene samples. South American specimens of *S. populator* from late Pleistocene (Lujanian) localities are on the average larger for nearly every dimension studied than North American Rancho La Brea individuals, an observation noted previously by Paula Couto (1955) and Kurtén (1965). However, nearly all of the South American specimens fall within the observed range of variation for the Rancho La Brea sample.

Although sample sizes are small, mandibular dimensions of middle Pleistocene (Ensenadan) *S. populator* average smaller than either Lujanian or Rancholabrean specimens. Mean values of lower tooth dimensions for South American *S. populator* from Ensenadan localities approximate those of North American Irvingtonian individuals with several exceptions. Among Ensenadan individuals P_3 averages larger whereas P_4 and M_1 average smaller than corresponding teeth in Irvingtonian specimens (Appendix 2B).

While most limb elements are short and stocky in smilodontines, this is not true for the femur of *S. populator* which is proportionately longer and not nearly as robust as in most large felids (Gonyea, 1976, table 4, fig. 6). Analysis of limb lengths (Appendix 2C, Fig. 5) suggest that the principal fore- and hindlimb elements (humerus, femur, and tibia) average longer among Lujanian *S. populator* than the same elements among Rancholabrean individuals. Proportions of the hindlimb of Ensenadan *S. populator* are much the same as the Rancholabrean population except for their smaller size.

Slaughter (1963) used five characters to diagnose *S. fatalis.* Each of these characters is listed below and then reconsidered in light of reexamination of both North and South American specimens.

(1) Total skull length less than any specimen of *S. californicus* (=*S. floridanus*). Following Merriam and Stock (1932), Slaughter (1963, table 3) lists the smallest skull from Rancho La Brea as 256.4 mm. Although the present study substantiates this claim, six skulls ranging between 259.5 and 273.0 mm increase the previously known North American sample of "small" *S. populator* individuals.

(2) Occiput narrow and triangular, not rounded above. As previously discussed, occiput shape is variable. North and South American populations of middle and late Pleistocene *S. populator* contain specimens which exhibit narrow, tri-

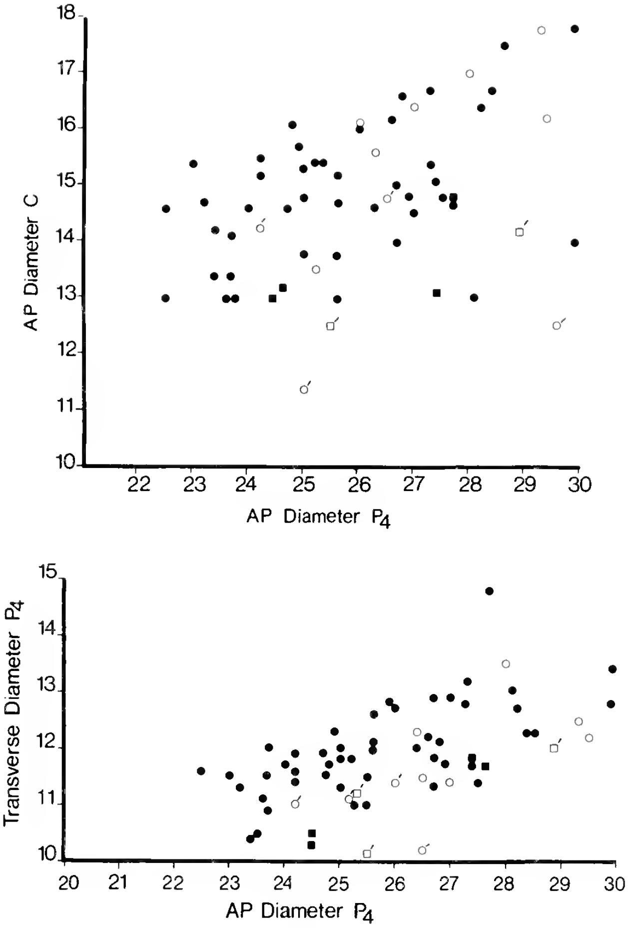
angular occiputs although they are more common among middle Pleistocene individuals.

(3) Basioccipital lacking well-developed keel. This was the most variable character observed. Although it is often associated with a more triangular occiput, just as many individuals with a rounded occiput display an indistinct, flattened keel.

(4) Inferior canine much reduced with anteroposterior diameter less than 54% of the same measurement of P^4.

(5) P^4 thin, having a transverse diameter less than 43% of the anteroposterior diameter. In his figures 1 and 2 Slaughter showed a difference between North American *Smilodon californicus* material of late Pleistocene (Wisconsin) age from California and Florida and a smaller group of all middle Pleistocene (pre-Wisconsin) material which he referred to *Smilodon fatalis*. Figure 6 presented here repeats Slaughter's bivariate plots with the addition of South American *Smilodon populator*. When these data are added the ranges of the various measurements overlap and strengthen the case for synonymy of North American *Smilodon* species with South American *Smilodon populator*.

Slaughter's dental characters (length of lower canine adjusted for length and width of P$_4$) were further evaluated in an analysis of covariance (ANCOVA) for *Smilodon populator* collected from (1) different localities (North vs. South America) and (2) different ages (middle vs. late Pleistocene) (Table 1A and B). Mean length of canine for *S. populator* differed only in age within the South American sample which led to the significant interaction term (Table 1B). However, for the characters evaluated sample sizes for middle Pleistocene *Smilodon* are very small (N = 4, North America; N = 3, South America). When age is eliminated as a factor and P$_4$ length is adjusted for width, using a pooled late Pleistocene sample there is no significant difference in adjusted means between North and South American *S. populator* (adjusted group means for length of P$_4$; North American samples = 39.74772, South American samples = 41.48333). The results of analysis of covariance using Slaughter's dental characters do not support recognition of more than one *Smilodon* species; both North and South American samples are referred to *S. populator*.



Figures 6A, 6B. **Fig. 6A.** Bivariate plot of canine length versus P$_4$ length for *Smilodon populator* and *Smilodon fatalis* (sensu Slaughter, 1963). Plot gives comparison of *S. populator* from North America (data from Merriam and Stock, 1932 and this study; ●, Rancholabrean) and South America (data from this study; ○, Lujanian, ♂ Ensenadan, and *Smilodon fatalis* from North America (data from Slaughter, 1963; ■, Rancholabrean, □ Irvingtonian). **Fig. 6B.** Bivariate plot of P$_4$ width versus length for *Smilodon populator* and *Smilodon fatalis* (sensu Slaughter, 1963). Comparison and symbols as above.

The practice of recognizing a species solely on the basis of size is questioned here for several reasons. Earlier work (Slaughter, 1963; Webb, 1974b) has shown that size overlap in a number of cranial and tooth measurements for *Smilodon* is too great to permit species discrimination. Size variation has been previously identified among wide-ranging large carnivores; the spotted hyena (*Crocuta crocuta*) (Kurtén, 1957) and the puma (*Felis concolor*) (Kurtén, 1973). Strong sexual dimorphism in the puma was demonstrated for all skull and tooth measurements studied (condylobasal length, zygomatic width, C length, P^4 length, and M$_1$ length). The results of comparison of these variances in a standardized local population of North American *Felis concolor* statistically adjusted for 35°N latitude (Kurtén, 1973; table 2) and in the combined North and South American *Smilodon populator* are given in Table 2. Statistically significant differences were observed between these variances for only two dimensions, condylobasal length and zygomatic width. If one assumes a similar pattern of variation among other large cats then greater importance can be attached to the fact that all other dimensions (C, P^4, and M$_1$ lengths) do not show any statistically significant differences between samples. The data indicate that for these tooth dimensions, variation in *S. populator* can be accounted for simply as the result of sexual dimorphism. Kurtén was able to distinguish sexual variation from individual and latitudinal variation in the puma. In the present study comparisons were made on the basis of total variability within *S. populator* since I could not partition the variances associated with either sex or latitude. Based on Kurtén's data,

Table 2. Variation in *Felis concolor*[1] and *Smilodon populator* from North and South America. Abbreviations: N = sample size; s^2 = variance; F = F ratio; P = probability; 1 = data from Kurtén, 1973, table 2.

Character	N	Taxon	s^2	F	P
Condylobasal length	116	*F. concolor*	163.890	1.928	~0.02
	28	*S. populator*	316.008		
Zygomatic width	118	*F. concolor*	115.313	8.170	~0.001
	30	*S. populator*	14.113		
C length	144	*F. concolor*	1.507	1.435	~0.2
	37	*S. populator*	2.164		
P^4 length	141	*F. concolor*	0.649	1.200	~0.5
	31	*S. populator*	0.79		
M_1 length	143	*F. concolor*	0.268	1.06	~0.5
	42	*S. populator*	0.252		

undoubtedly, both individual and latitudinal variation are important aspects to the observed variation in *Smilodon*. However, the fact that the comparable variation in tooth dimensions in North and South American *Smilodon* can be accounted for solely by sexual dimorphism without consideration of these other parameters, further strengthens the argument for recognition of *Smilodon populator* as a single wide-ranging species.

PHYLOGENETIC RELATIONSHIPS AND ZOOGEOGRAPHIC PATTERNS

Judging from the oldest stratigraphic record, sabercats of the genus *Smilodon* originated in North America during the late Cenozoic. *S. gracilis* (Cope, 1880), the sister taxon of the more derived *S. populator*, is well represented from the late Blancan through Irvingtonian of Florida. This species is also known from the type locality at Port Kennedy Cave in Pennsylvania and with less certainty from the Palm Springs Formation, Vallecito Creek, California (Kurtén and Anderson, 1980; Berta, in press). The following characters distinguish *S. gracilis* from *S. populator*: canines only slightly recurved; canines and cheek teeth with very finely serrated margins; P^4 with well-developed protocone; mandible with two mental foramina and an enlarged flange (Berta, in press).

The earliest record of *S. populator* is from the Irvingtonian of Arkansas, California, and Nebraska. During the late Pleistocene *S. populator* extended its range throughout the United States, Central America, and into South America. In South America, this species has been recorded from Argentina, Bolivia, Brazil, Peru, and Uruguay. The extension of *S. populator* into South America is not so surprising when one considers the equally wide range of such present-day species as the lion, *Felis leo* and the puma, *Felis concolor*.

The end of the Pleistocene marked the extinction of *Smilodon* in both North and South America. As was true for large canids the extinction of sabercats can be related to extinction of their large, thick-skinned herbivorous prey which included ground sloths, glyptodonts, proboscideans, horses, notoungulates, and litopterns. While supporting this interpretation of *Smilodon* prey, Akersten (1985) added that the "canine shear-bite" of this species would have been just as effective on smaller thin-skinned prey. However, it should be stressed, as elaborated by Rosenzweig (1966), that larger carnivores generally take larger prey. It seems likely that the extinction of sabercats can be related in part to their specialized hunting and feeding strategy and resultant social behavior which was dependent on a large herbivore megafauna, so reduced in number and diversity at the present time.

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APPENDIX 1.
SOUTH AMERICAN MATERIAL STUDIED

ARGENTINA

MACN Specimens: 46, nearly complete skeleton (type of *S. bonaerensis*); 997, incomplete skull; 1107 humerus; 2354, right ramus with I_{1-3}, C, left tibia; 2838, humerus; 5010, right ramus; 5109, right femur; 5273, skull, right ramus, proximal femur, tibia, ulna; 5822, fragmentary skull (juvenile); 6205, left ramus with C root and P_4–M_1; 6210, right ramus with P_3–M_1; 6234, tibia; 8661, posterior portion of skull; 8682, posterior portion of skull; 8707, right femur; 9446, distal right humerus; 9650, right humerus; 10037, proximal femur; 10485, tibia; 10502, proximal humerus; 10523, radius; 10861, ulna; 11554, right ramus with I_3, C alveolus, P_4–M_1; 12011, rostral fragment; 12393, fragmentary lower I; 12445, C_1; 12474, C fragment; 12532, ramus with M_{1-2}; 12846, skull fragment; 13606, C^1; 13922, occipital fragment; 14165, left maxillary fragment with P^{3-4}; 13206, M_1; 16693, occipital portion of skull; 16692, ulna; 16689, right and left humeri; 16695, proximal and distal portions of left femur; 16697, proximal right radius; 16691, proximal right tibia; 16690, left astragalus; 16694, right metatarsal III; [12846–16694 are probably all from the same individual, the type of *S.* (*P.*) *ensenadensis minor;*] 17448, fragmentary C^1, incomplete skull; 18026, right maxillary fragment with P^4; 18051, symphyseal portion of mandible; 18057, skull and mandibles.

MLP Specimens: 10-1, skull and mandibles; 10-2, incomplete skull and mandibles; 10-10, right ramus; 10-13, left humerus; 10-14, left humerus; 10-20, left ulna; 10-22, right radius; 10-23, right radius; 10-33, left tibia; 10-35, left tibia; 10-37, incomplete right scapula; 10-44, pelvis, sacrum, and lumbar vertebrae; 10-47, axis; 10-48, thoracic and lumbar vertebrae, sacrum, pelvis, right femur.

MMP Specimens: 5M, left femur; 21-S, posterior portion of skull;

34-S, left hindlimb (distal tibia and fibula, astragalus, calcaneum, mesocuneiform, ectocuneiform, cuboid, navicular, metatarsal II–V, proximal phalanges and digits I–V, medial phalanges and digits II–V; ungual phalanges I–IV, sesamoids); 227-S, proximal femur; 465-S, left femur; 495-S (a–f), left and right tibiae, distal epiphysis of femur, astragalus, cervical vertebrae V–VI; 652-S, humerus; 765-M (a–g), phalanges; 768-M, M_1, left P_4; 796-M (a–w), portion of skull, vertebrae (atlas, lumbar, sacrum), pelvis, hindlimb (distal femur, fibula, tibia, left and right astragalus, right and left calcaneum, ectocuneiform, cuboid, navicular, right and left metatarsals II, III, IV, V); 1311-M, incomplete skull with right maxillary, parietal and occipital regions partly restored.

AMNH Specimens: 11101, skull and mandible with nearly complete skeleton; 11103, vertebrae and skeletal fragments; 11104, pelvis; 11105, left femur; 11106, right calcaneum.

FMNH Specimens: P 14294, complete mandible and partial skeleton including: atlas, cervical and thoracic vertebrae, ribs, sternumbrae, humeri, left scapula, ulna, radius, scapholunar, unciform, magnum, metacarpal I, proximal, medial and ungual phalanges, pelvis, femora, tibiae, astragali, left metatarsal II, right metatarsals III, IV and V, and patella; P 14271, skull and mandible (partially restored) and partial skeleton including: atlas, cervical, thoracic, and lumbar vertebrae, sacrum, ribs, left humerus, left and right metacarpal II, right metacarpals II and V, left scapholunar, proximal phalanges, pelvis, right fibula, patella, left astragalus and calcaneum; P 14279, left maxillary fragment with P^{3-4}.

BOLIVIA

MACN Specimens: 1455, left premaxillary and maxillary fragment with I^{2-3}, C; 1457, anterior portion of right ramus with C, P_3 alveolus, P_4 (type of *S.* (*P.*) *ensenadensis ferox*); 1459, distal left humerus; 1460, right ramus with I_3–M_1, right and left humerus, left tibia, manus (type of *S. crucians*).

BRAZIL

UZM L Specimens: right I^2, I^3, fragmentary right C^1, left metacarpal II and IV, right metacarpal V (type of *S. neogaeus*); left distal metacarpal II, phalanges (hindfoot), C^1, right ramus with incisor alveoli, C root, P_4–M_1 (text and figures *in* Paula Couto, 1955); Winge (1895: 13) lists additional cranial and postcranial material housed in the UZM collections.

BM(NH) Specimens: 18972, left P^{3-4} associated with skull figured by Blainville (1855), left femur (diaphysis), right humerus, right ulna, right distal tibia, right astragalus, phalanx, cervical vertebrae, and right calcaneum, all probably from the same individual.

MNHN, right side of skull with I^{1-3}, P^4–M^1, left C, and fragmentary ramus with complete dentition (text and figures *in* Blainville, 1855).

ECUADOR

EPN Specimens: V.1507, nearly complete skull; V.1903, cervical vertebrae; V.2990, anterior portion of right scapula; V.1902, proximal right radius; V.1899, left magnum; V.1891, right patella; V.1894, right tibia; V.1895, right tibia; V.1896, proximal right tibia; V.1212, right cuboid; V.1893, left metatarsal III; V.1182, right C^1; V.1185, fragment of left maxillary with P^{3-4}; V.1186, maxillary fragment with right I^{1-2}, left I^{1-3}; V.1187, fragment of right maxillary with P^4; V.1193, right I^3; V.1197, fragmentary right I^3; V.1195, left I^2; V.1183, mandible with left I_{2-3}, P_4–M_1 and right I_{2-3}, C, P_4–M_1; V.1184, right ramus with P_3 alveolus; V.1191, left dP_4 in fragmentary mandible; V.718, fragment of scapula; V.1188, right humerus; V.1189, left scapholunar; V.1190, left metacarpal IV and V, right metacarpal V; V.1206, left metacarpal III; V.1203–04, phalanx I, digit I (forefoot); V.1292, patella; V.1180, left "perone"; V.1198–1202, phalanges (text and figures *in* Hoffstetter, 1952).

PERU

The extensive Talaran collection of *S. populator* is currently being described by C.S. Churcher (written comm., 1981).

Appendix 2A–C. Measurements and statistics for *Smilodon populator* from North and South America. Abbreviations: a, approximate measurement; AP, greatest anteroposterior dimension; CV, coefficient of variation; N, sample size; OR, observed range of variation; SE, standard error; T, greatest transverse dimension; $\bar{x}$, mean; 1, measurements following Méndez-Alzola, 1941; Hoffstetter, 1952; Churcher, 1967 and this report; 2, measurements following Merriam and Stock, 1932; 3, measurements following Slaughter, 1963 and this report.

2A. Cranial and mandibular measurements

	South America[1]								North America[2]			
	Ensenadan				Lujanian				Rancholabrean			
	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV
1. Length, premaxillary–condyle	—	— —		—	3	358.6 ± 3.18	355.0–365.0	1.54	25	308.6 ± 0.958	271.4–344.1	7.77
2. Length, premaxillary–inion	—	— —		—	4	352.3 ± 10.46	335.0–353.0	5.93	25	336.0 ± 1.000	292.7–377.9	7.45
3. Length, C^1–P^4	1	110 —		—	3	121.2 ± 0.186	121.1–121.6	0.264	24	112.1 ± 0.330	97.0–126.3	7.08
4. Greatest width, zygomatic arches	—	— —		—	6	211.8 ± 5.49	191.0–225.0	0.634	24	208.8 ± 0.626	182.9–240.1	7.20
5. Palatal width at P^4	—	— —		—	4	128.6 ± 5.06	117.0–140.0	7.86	24	127.5 ± 0.298	114.7–135.4	5.62
6. A–P diameter, auditory bulla	—	— —		—	4	60.3 ± 2.89	53.7–67.8	9.59	24	54.2 ± 0.224	46.7–63.9	9.93
7. Greatest width, mastoid processes	3	136.9 ± 3.89	132.0–144.6	4.92	9	138.9 ± 3.71	114.4–147.6	8.01	24	134.6 ± 0.431	122.0–154.3	7.71
8. Greatest width, condyles	3	70.2 ± 3.02	66.1–76.0	7.33	10	71.7 ± 1.33	66.1–78.1	5.86	25	65.0 ± 0.154	57.6–72.3	5.94
9. Length, symphysis–condyle	2	194.5 —	183.0–206.0	—	9	224.3 ± 5.00	198.0–242.8	6.63	25	209.5 ± 0.632	178.3–230.0	7.55
10. Length, diastema (C_1–P_3)	3	54.7 ± 3.78	50.1–62.0	11.65	3	68.1 ± 39.32	64.7–70.0	4.37	25	61.7 ± 0.314	46.3–71.8	12.72
11. Depth, ramus below M_1	3	36.8 ± 2.31	32.7–40.7	10.88	8	43.0 ± 15.21	40.0–49.0	7.81	25	40.3 ± 0.110	36.0–45.6	6.84
12. Mandibular toothrow length	2	50.5 —	48.0–53.0	—	3	52.7 ± 2.05	48.0–57.0	6.59	25	54.1 ± 0.123	48.3–60.9	5.72
13. Height, angle–coronoid	1	48.5 —		—	6	71.0 ± 3.60	61.1–84.2	12.43	25	68.9 ± 0.207	60.3–76.3	7.53

2B. Upper and lower tooth measurements

		South America[1]								North America							
		Ensenadan				Lujanian				Irvingtonian[3]				Rancholabrean[2]			
		N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV
C	AP	2	42.5 —	42.0–43.0	—	13	44.6 ± 1.240	37.6–51.3	10.6					24	42.1 ± 0.537	36.0–46.1	6.25
	T	2	19.1 —	18.8–19.3	—	13	21.5 ± 0.103	20.3–24.0	6.27					24	20.6 ± 0.374	18.0–22.9	8.89
P^3	AP	—	— —	—	—	9	17.2 ± 0.616	13.7–20.5	10.74					17	17.1 ± 0.329	15.0–19.7	7.94
	T	—	— —	—	—	9	9.4 ± 0.321	8.4–11.5	10.24					17	9.3 ± 0.150	8.4–10.6	6.66
P^4	AP	—	— —	—	—	9	40.5 ± 1.43	38.4–44.4	10.61	1	37.2 —			22	40.1 ± 0.538	33.4–46.0	6.29
	T	—	— —	—	—	9	15.4 ± 0.258	14.2–16.4	5.03	1	15.6 —			22	16.5 ± 0.329	14.2–19.9	9.36
M^1	AP	—	— —	—	—	4	5.7 ± 0.286	5.0–6.2	10.05								
	T	—	— —	—	—	4	13.4 ± 0.314	12.7–13.9	4.69								
C	AP	3	14.2 ± 0.38	13.5–14.8	4.58	9	16.6 ± 1.05	15.6–17.8	24.13	3	14.2 ± 0.087	14.1–14.4	1.07	22	14.7 ± 0.231	13.0–16.6	7.40
	T	2	10.1 —	10.0–10.1	—	9	11.2 ± 0.179	10.0–12.3	4.80	3	9.1 ± 0.284	8.5–9.6	6.24	22	10.6 ± 0.413	9.7–12.2	19.22
P_3	AP	2	12.0 —	11.4–12.5	—	1	6.0 —	—	—	4	8.7 ± 1.02	5.7–10.1	23.40	2	6.2 ± —	5.7–7.0	—
	T	2	7.4 —	7.3–7.5	—	1	6.0 —	—	—	4	6.3 ± 0.450	5.0–7.0	14.52	2	8.1 ± —	6.5–9.6	—
P_4	AP	4	25.5 ± 0.50	24.2–26.5	3.94	10	27.7 ± 0.426	26.3–29.7	4.87	3	26.1 ± 1.47	24.0–28.9	9.72	25	24.6 ± 0.273	22.5–26.8	5.55
	T	4	10.9 ± 0.256	10.2–11.4	4.70	9	12.3 ± 0.206	11.5–13.5	5.08	3	11.1 ± 0.550	10.1–12.0	8.59	23	11.9 ± 0.173	10.9–12.8	6.97
M_1	AP	3	26.3 ± 1.63	24.5–29.5	10.73	10	28.3 ± 0.445	25.7–30.0	4.98	4	28.1 ± 0.564	27.0–29.5	4.01	25	28.7 ± 0.338	25.9–32.1	5.89
	T	3	13.9 ± 0.874	12.2–15.0	10.89	10	13.3 ± 0.137	13.0–14.2	3.26	4	13.1 ± 0.147	12.2–15.0	9.88	25	14.3 ± 0.236	12.8–16.1	8.28

2C. Limb length measurements

	South America[1]								North America[2]			
	Ensenadan				Lujanian				Rancholabrean			
	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV	N	$\bar{x}$ ± SE	OR	CV
Humerus	2	334.0 —	316.0–352.0	—	6	365.4 ± 10.50	340.5–395.0	7.04	10	344.9 ± 7.80	309.0–385.0	7.13
Radius	1	225.0 —	—	—	5	275.7 ± 8.06	249.7–294.8	6.54	10	265.7 ± 6.84	235.0–295.0	8.14
Metacarpal III	1	95.0 —	—	—	3	95.4 ± 1.10	94.3–97.6	2.00	737	— —	83.0–107.8	—
Femur	4	352.8 ± 2.81	347.0–360.0	1.59	4	384.0 ± 9.17	365.0–408.0	4.78	10	367.7 ± 9.80	317.0–408.0	8.43
Tibia	7	251.4 ± 7.86	220.0–282.6	8.27	5	280.4 ± 4.21	272.5–294.2	3.36	10	273.6 ± 8.10	239.0–305.0	9.31
Metatarsal III	1	98.5 —	—	—	4	98.0 ± 0.595	94.7–99.1	1.21	766	—	85.5–111.5	—

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CONTRIBUTIONS IN SCIENCE

A NEW RECORD OF GIANT SHORT-FACED BEAR, *ARCTODUS SIMUS*, FROM WESTERN NORTH AMERICA WITH A RE-EVALUATION OF ITS PALEOBIOLOGY

Steven D. Emslie and Nicholas J. Czaplewski

Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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A NEW RECORD OF GIANT SHORT-FACED BEAR, *ARCTODUS SIMUS*, FROM WESTERN NORTH AMERICA WITH A RE-EVALUATION OF ITS PALEOBIOLOGY

Steven D. Emslie[1] and Nicholas J. Czaplewski[2]

ABSTRACT. Remains of the extinct giant short-faced bear, *Arctodus simus,* from Labor-of-Love Cave in Nevada constitute the first record of this species in eastern Nevada. The skeleton was found in association with black bear remains, *Ursus americanus,* eroding from a gravel lens in silt sediments along the banks of a stream flowing through the cave. The deposits are probably late Pleistocene in age. The *Arctodus* remains are from a small adult and represent one of the most complete skeletons recovered of this species. Association of cranial with postcranial bones allowed us to determine proportions and ratios of limb elements in a single individual. The hypothesis that *A. simus* was a highly predaceous cursorial carnivore is examined. We prefer to believe that this animal was largely herbivorous, based upon comparative studies of the skull and functional morphology of the jaw in living *Tremarctos ornatus,* and upon the non-cursorial features in the limbs of *A. simus.*

INTRODUCTION

The recovery of a partial skeleton of the giant short-faced bear, *Arctodus simus,* and the black bear, *Ursus americanus,* from a cave in east-central Nevada, represent the first records of these bears from eastern Nevada; *U. americanus* currently occurs in western Nevada (Hall, 1946). The cave and the bear remains were originally discovered by members of a local speleological society in Ely, Nevada, who named the cave "Labor-of-Love Cave." Other mammals represented at this cave include *Ursus* cf. *arctos* and *Ovis canadensis.*

The cave is located at the base of a limestone cliff on the east side of the Schell Creek Range, White Pine County, Nevada. The east-facing entrance is at an elevation of 2050 m. The cave extends over 137 m into the mountain along a fault plane and consists of one main passage. Currently, a small stream flows the entire length of the cave and emerges at the base of a talus slope 30 m below the cave entrance. Air and water temperatures in the cave remain constant year-round at 10°C.

Postcranial material from Labor-of-Love Cave includes the first associated limb elements of *A. simus* on which relative proportions can be determined. This analysis, together with earlier studies on the living spectacled bear, *Tremarctos ornatus,* an animal similar in structure to *A. simus,* allows a re-evaluation of the paleobiology of the latter species.

We conclude that *A. simus* was not necessarily adapted for a cursorial, predaceous life-style, nor could it have attained its large size by strict carnivory. Based on skull and jaw architecture, tooth morphology and wear, and limb structure, *A. simus* was probably largely herbivorous, but retained bone-crushing capabilities and may have been an opportunistic predator and scavenger.

SITE LOCATION

Two concentrated bone deposits (BC-1, BC-2) were found in two pools of water along the stream edge, and located approximately 10 m apart at the rear of the cave (Fig. 1a). Diversion of stream flow through fissures in the limestone bedrock maintains these pools as quiet backwater areas.

In summer 1982, under an emergency permit from the U.S. Forest Service, one of us (SDE) collected and preserved bones from the two pools before they were washed away by fluctuations in stream flow or stolen by vandals. The permit was authorized under the aegis of the Natural History Museum of Los Angeles County (LACM) where the specimens are now housed. Bones in the cave were photographed, mapped, and collected over a period of three days. Spatial orientation of bones was mapped (Figs. 1b, 2) by triangulation, using two or three large aluminum nails, placed in the substrate at each bone concentration. Each bone was then carefully removed, wrapped in aluminum foil to avoid contamination, assigned a field number, and packed in a labeled box prior to removal from the cave. Excavations in cave strata were not initiated, and are planned for future investigations. Consequently, no detailed analyses of cave sediments have been completed. The material was transported

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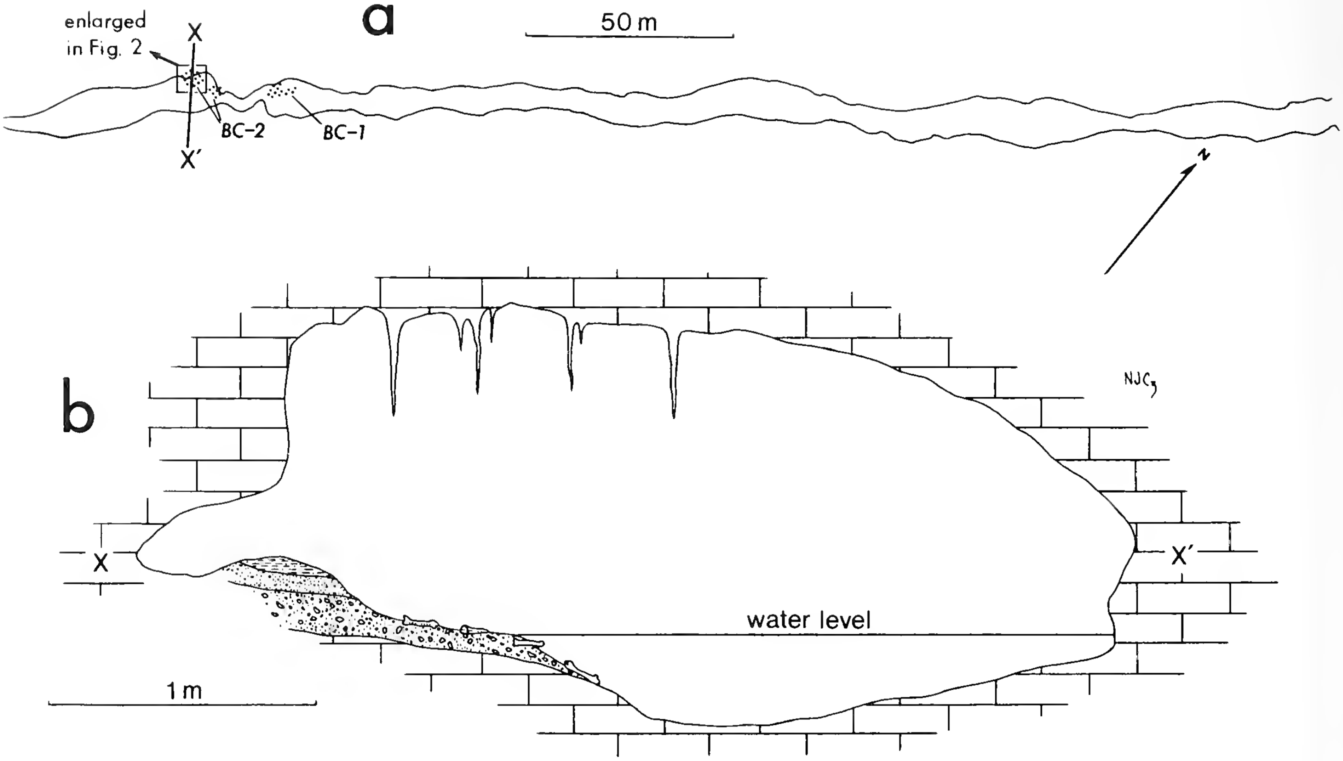


Figure 1. Plan view (a) and cross section (b) of Labor-of-Love Cave showing the locations of Bone Concentrations (BC) #1 and #2 and the gravel lens from which the bones at BC-2 were eroding.

to the George C. Page Museum of LACM for curation and transferred to LACM for permanent storage. The bones were identified using comparative collections of Pleistocene and Recent mammals in the museum. Other fossil remains of *A. simus* at the American Museum of Natural History, New York, and Recent remains of *Ursus arctos* and *U. americanus* at the U.S. National Museum, Washington, D.C., were also examined.

All vertebrate fossils recovered from the cave are identified below, but only the remains of *A. simus* are discussed in detail in this paper.

SYSTEMATIC PALEONTOLOGY

Order Carnivora

Family Ursidae

Genus *Ursus* Linnaeus, 1758

Ursus americanus Pallas, 1780

(Black Bear)

REFERRED MATERIAL. LACM 122435, several skull fragments including maxillae and premaxillae, both lower jaws, atlas, axis, one thoracic and three other vertebral fragments, both scapulae, humeri, ulnae, radii, a right tibia, metacarpal II (right and left), III (right), IV (right and left), and V (right and left), metatarsal III (right) and IV (right), and ten rib fragments; LACM 123780, left tibia; LACM 123783, diaphyses of right and left humeri; LACM 123786, right M_1.

DISCUSSION. LACM 122435 was recovered from BC-1 and represents an immature individual, approximately 3–4 years old at times of death based on epiphyseal fusion of long bones. LACM 123780 was also found in BC-1 but represents another individual. LACM 123783 and 123786 were found eroding from the gravel lens at BC-2, in direct association with bones of *A. simus* (Fig. 2b, c). A minimum of three *U. americanus* individuals are represented.

Ursus cf. *U. arctos* Linnaeus, 1758

(Grizzly Bear)

REFERRED MATERIAL. LACM 123782, diaphysis of left tibia.

DISCUSSION. This tibia, found at BC-1, compares well in size and morphology to that of a modern Kodiak bear (Fig. 3). It is more robust, with a shaft flared at both proximal and distal ends, and has a more sharply ridged shaft than in other bear species. These characters are lacking in late Pleis-

Table 1. Measurements of the right mandible (LACM 122434) of *Arctodus simus* from Labor-of-Love Cave, Nevada.

Length, anterior base of C_1 to condylar process	253.0 mm
Depth of mandible at P_3	56.5 mm
Depth of mandible at coronoid process	ca. 112–113 mm
Alveolus length, C_1–M_3	154.0 mm
Alveolus length, P_1–M_3	120.5 mm
Alveolus length, P_2–M_3	111.0 mm
Alveolus length, P_3–M_3	98.2 mm
Alveolus length, P_4–M_3	87.0 mm
Alveolus length, M_1–M_3	74.5 mm
Alveolus length, M_2–M_3	44.2 mm
C_1, anterior–posterior length	28.0 mm
greatest width	19.7 mm
M_1, anterior–posterior length	30.2 mm
trigonid length	19.8 mm
trigonid width	12.8 mm
talonid width	17.2 mm
M_2, anterior–posterior length	28.0 mm
trigonid width	20.1 mm
talonid width	18.3 mm
M_3, anterior–posterior length	18.7 mm
greatest width	14.5 mm

tocene remains of *A. simus* and *U. americanus* from Labor-of-Love Cave and Rancho La Brea, and from modern *U. americanus.*

Genus *Arctodus* Leidy, 1854

Arctodus simus (Cope) 1879

(Giant Short-faced Bear)

REFERRED MATERIAL. LACM 123781, proximal left femur; LACM 122434, numerous skull fragments including premaxillae and maxillae, both lower jaws (see Tables 1, 2; Figs. 4, 5), humeri, radii, ulnae, femora, and tibiae, atlas, right metacarpal III, right metatarsal V, fibula fragment, phalanx, and one rib fragment.

DISCUSSION. LACM 123781 was recovered from BC-1 and is from an immature individual as it lacks the proximal epiphysis. LACM 122434 was recovered from BC-2 and represents one adult individual. A minimum of two *A. simus* individuals are represented.

Order Artiodactyla

REFERRED MATERIAL. LACM 123784, fragmented humerus.

Table 2. Measurements of teeth (right maxilla) of *Arctodus simus* (LACM 122434) from Labor-of-Love Cave, Nevada.

Alveolus length, C^1–M^2	137.6 mm
Alveolus length, P^1–M^2	100.1 mm
Alveolus length, P^2–M^2	93.0 mm
Alveolus length, P^3–M^2	87.3 mm
Alveolus length, P^4–M^2	78.7 mm
Alveolus length, M^1–M^2	56.3 mm
C^1, anterior–posterior length	27.9 mm
greatest width	17.9 mm
P^4, anterior–posterior length	20.8 mm
greatest width	14.7 mm
M^1, anterior–posterior length	24.1 mm
greatest width	23.8 mm
M^2, anterior–posterior length	35.0 mm
greatest width	21.7 mm

DISCUSSION. This specimen, recovered from BC-2, is too fragmented for positive identification beyond order, but is from a deer-sized animal. Its position in the pool at time of discovery is shown in Figure 2a.

Family Bovidae

Genus *Ovis* Linnaeus, 1758

Ovis canadensis Shaw, 1804

(Bighorn Sheep)

REFERRED MATERIAL. LACM 123785, left M^3.
DISCUSSION. Recovered from BC-1.

GEOLOGIC HISTORY AND TAPHONOMY

Exact geologic age of the fossils is not known; two bones, an ulna of *U. americanus* from BC-1 and a humerus of *A. simus* from BC-2, were submitted to Beta Analytic, Coral Gables, Florida, for radiocarbon dating. Dates on collagen of 4160 ± 180 years B.P. were obtained for the ulna of *U. americanus* and 5320 ± 120 years B.P. for the humerus of *A. simus* (Murray Tamers, pers. comm.). The unusually young date for *A. simus* is inconsistent with other fossil records of this species. Error in the dates may be due to low amounts of carbon obtained from the bone or to contaminants in the water within the cave. All previous finds of *A. simus* are older than 12,650 ± 350 years B.P. (Kurtén and Anderson, 1980) and are associated with faunas characteristic of the Pleistocene (Irvingtonian and Rancholabrean Land Mammal Ages). Based on the number and diversity of complete speleothems we believe that Labor-of-Love Cave has been sealed since at least the close of the Pleistocene, or approximately 12,000 years B.P., and that the above C14 ages do not reflect the true ages of this material.

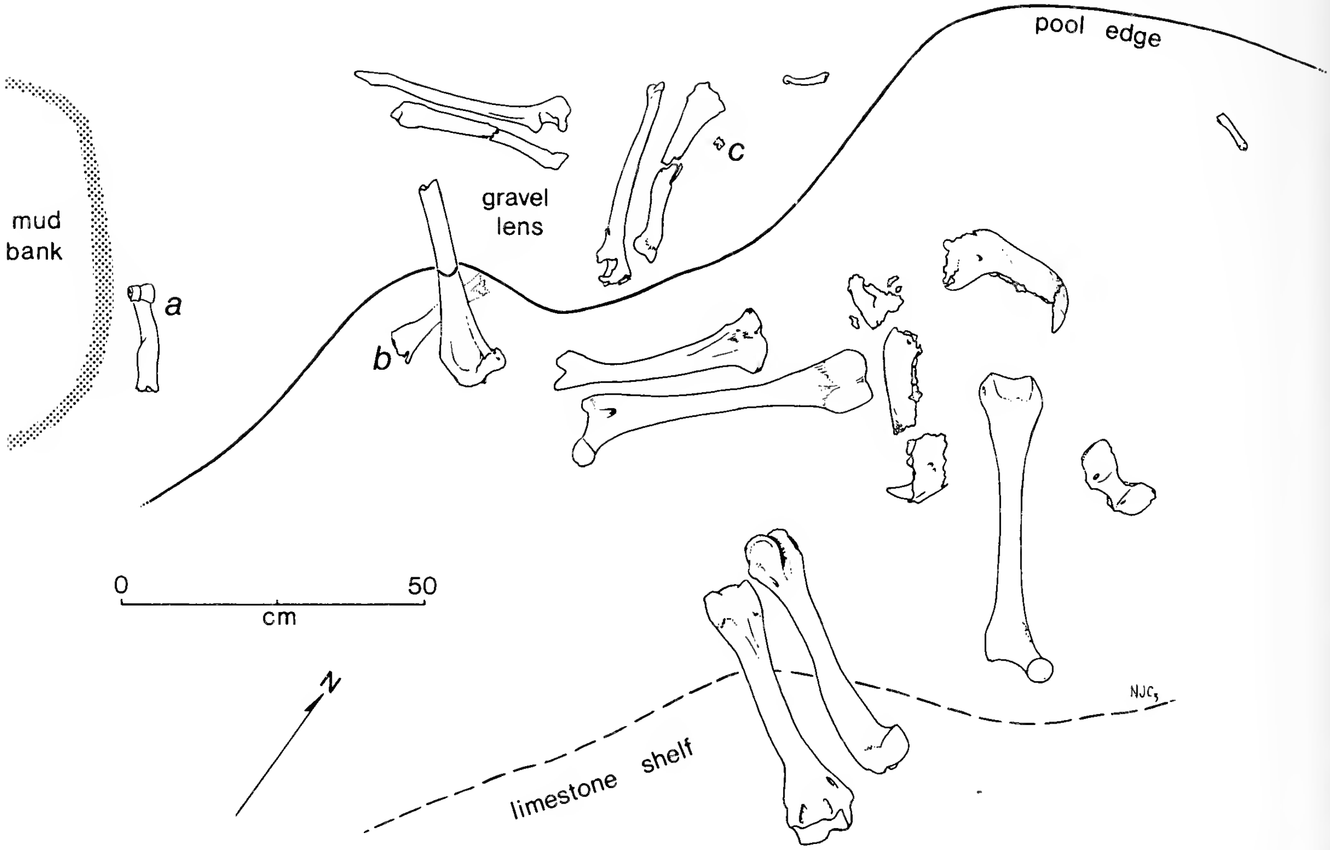


Figure 2. Plan view of the bones at BC-2. All bones shown are from one skeleton of *Arctodus simus* except (a) Artiodactyla humerus, (b) *Ursus americanus* humerus, and (c) *U. americanus* right M_1.

Labor-of-Love Cave developed within mountains formed primarily of uplifted Dunderberg Shale and limestone of middle to late Cambrian age (Hose and Blake, 1976). The cave follows a fault plane through the limestone. Examination of speleothems, flowstone, and stratified silt deposits indicates the cave has undergone alternate periods of filling from perhaps several entrances, erosion of these sediments, and pronounced changes in cave environment. Hanging flowstone shelves were observed throughout the cave at heights where water and/or sediments once existed, between 0.5 and 1.5 m above current levels. Several stalagmites undercut by erosion are now tilted, and clay sediments still cling to the walls of the cave near the roof.

All bones at BC-1 were lying submerged at the bottom of the pool or partially buried in silt in the bottom. Bones at BC-2 were lying at the bottom of the pool, and on the surface of a gravel lens at the pool edge (Fig. 2). Undisturbed deposits nearby show this gravel lens is overlain by a 20-cm-thick layer of sandy silt, followed by a 25–30-cm-thick layer of fine silt (Fig. 1b). Bones exposed on the gravel lens included nearly articulated pairs of radii and ulnae and a partially buried tibia of *A. simus* (Fig. 6b), and the molar and a left humerus of *U. americanus.* The close association and articulation of the remains of *A. simus* suggest the gravel lens is the site of primary deposition of these bones (Fig. 2).

Fine, densely packed laminar cross-bedded deposits are still present in the rear of the cave (Fig. 6c) indicating that deposition and erosion of sediments has been occurring over a long period of time. We believe that the bear skeletons have eroded from the deposits relatively recently, based on their completeness and close association at each bone concentration. Some bones were found where originally deposited, in the gravel lens at BC-2. Those bones which were eroded from these sediments probably were transported only a short distance (<5 m) before being redeposited as found. Both bear skeletons had fragmented skulls (possibly caused by the pressure of overlying sediments) and corresponding skeletal elements preserved at each pool. Possible carnivore tooth marks on the bone suggest the bear carcasses had been scavenged prior to burial. The absence of pelves or complete scapulae may support this conclusion as these elements are usually the first to be destroyed during carnivore feeding (Hill, 1980;

Binford, 1981). Most of the ribs, vertebrae, and phalanges from these skeletons were not recovered, presumably having been washed downstream or redeposited in gravel bars. These elements were found by Voorhies (1969) to be most susceptible to fluvial transportation in experiments with Recent mammal carcasses.

The relative completeness of the black bear skeleton from BC-1 and the short-faced bear skeleton from BC-2 suggests that these animals died in the cave, perhaps during a period of winter hibernation. Bones of other animals found in the cave also display breakage and tooth marks, and may represent food items transported to the cave by carnivores.

PALEOECOLOGY

Detailed information on the paleoecology of eastern Nevada during the late Pleistocene is available from recent studies in Smith Creek Canyon, Snake Range, which is located 75 km northeast of Labor-of-Love Cave. The elevation of the entrance to this canyon is 1710 m and the area is similar in topography and environment to the area of Labor-of-Love Cave. Studies of the paleoecology at Smith Creek Canyon can, therefore, be useful in reconstructing the habitat available to *A. simus* in eastern Nevada during the late Pleistocene.

Analysis of packrat middens from three caves in Smith Creek Canyon provided Thompson (1979) with specific information on the vegetation of this area during the late Wisconsinan and early Holocene. His results indicated that many plants occurred in the canyon during the Pleistocene that are found only at higher elevations today. These plants included bristlecone pine (*Pinus longaeva*), fern-bush (*Chamaebatiaria millefolium*), gooseberry currant (*Ribes montigenum*), cliff-bush (*Jamesia americana*), and bush oceanspray (*Holodiscus microphyllus*). Spruce (*Picea*) and fir (*Abies*) were absent from the samples. Thompson (1979) postulated that the period 12–13,000 years B.P. was characterized by greater effective moisture than today with conditions changing to those of the present by 10,500 years B.P.

Thompson (1979), Thompson and Mead (1982), and Mead et al. (1982) have shown that much of the Great Basin during the late Pleistocene consisted of pluvial lakes. Above lake level, valleys were dominated by sagebrush (*Artemisia tridentata*) cover, similar to the area today. Alpine glaciers extended down to 2800 m in elevation in the Snake Range, 75 km northeast of Labor-of-Love Cave. Vertebrates recovered from the Snake Range, Smith Creek Cave (dated at ≥12,000 years B.P.) and packrat middens from Smith Creek Canyon, include species now restricted to higher elevations or higher latitudes. These include *Ochotona princeps, Spermophilus richardsonii, Thomomys talpoides, Phenacomys intermedius,* and *Mustela vison.* One undescribed bone identified as *Ursus* sp. from Smith Creek Cave is a questionable identification (Miller, 1979).

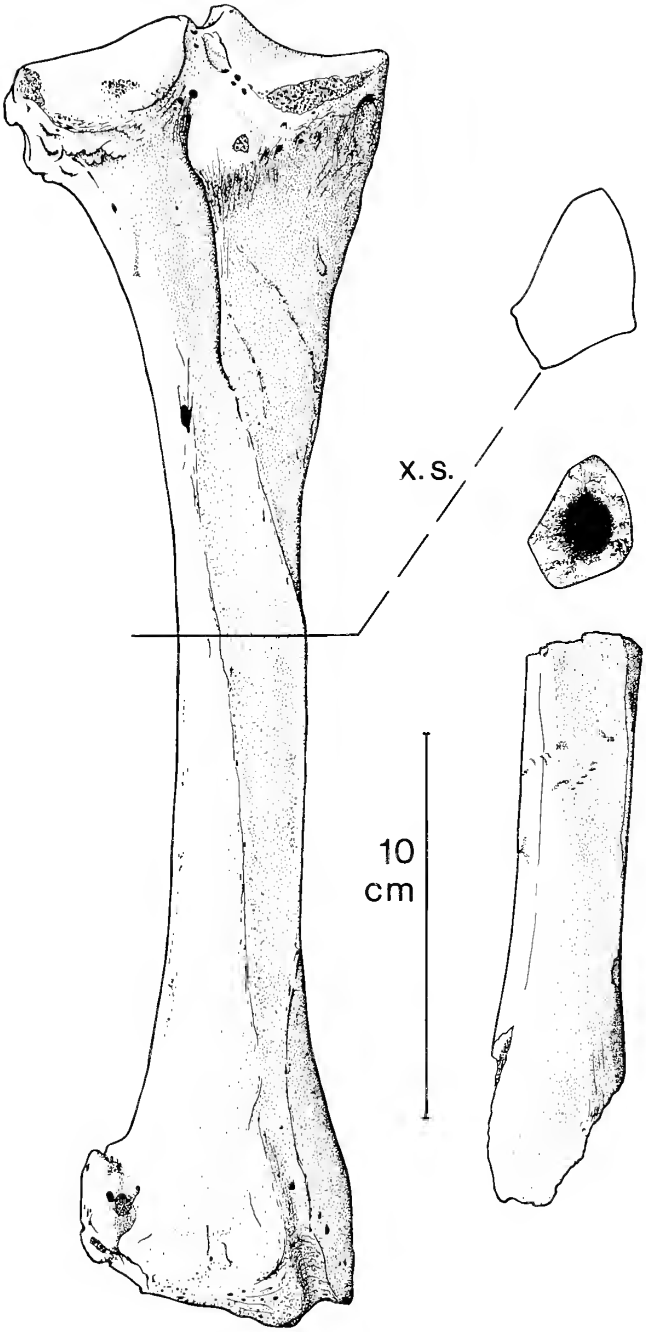


Figure 3. The partial left tibia (LACM 123782) of *Ursus* cf. *arctos* found at BC-1 compared to a tibia of Recent *U. arctos middendorfi.* Note the characteristic flaring of the shaft at the proximal and distal ends, and the distinct ridges in *U. arctos* and the fossil specimen.

In summary, the late Pleistocene habitat of eastern Nevada probably consisted of pluvial lakes and open, sagebrush-covered flats in the valley bottoms. Mountain ranges surrounding the valleys bore alpine glaciers above 2800 m with subalpine to alpine faunal and floral elements in the canyons and valley

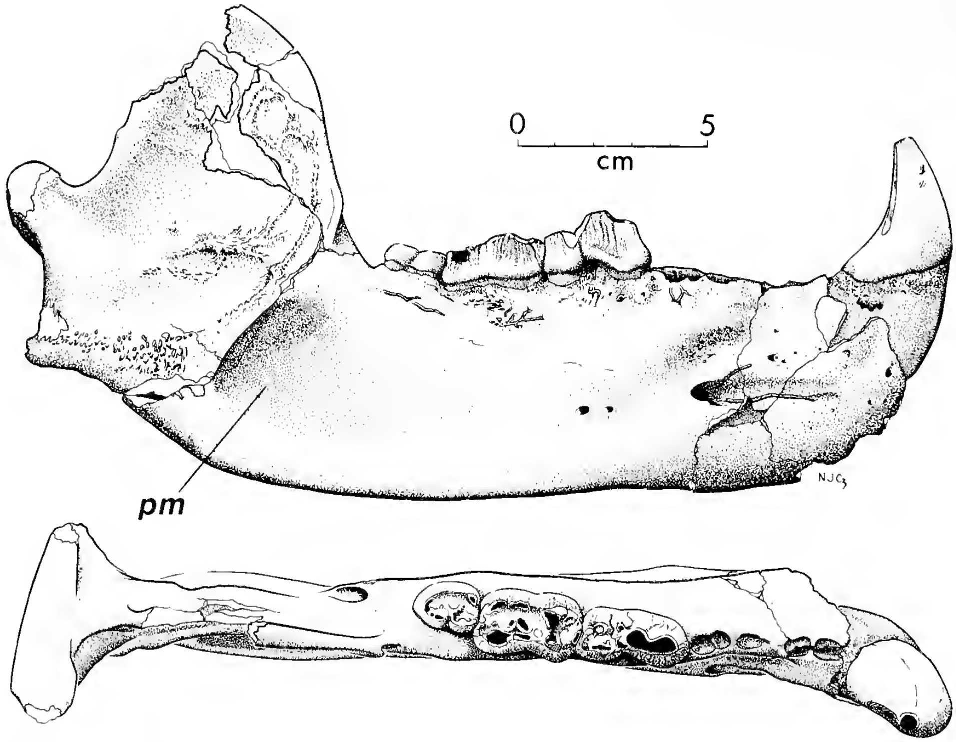


Figure 4. The right mandible (LACM 122434) of *Arctodus simus* from Labor-of-Love Cave showing the premasseteric fossa (pm) characteristic of the subfamily Tremarctinae. The position of this specimen in the pool at time of discovery is shown in Figure 2.

edges. Open forests of bristlecone pine and other conifers extended to the valley edge.

DISCUSSION

Arctodus simus remains have been reported from fossil localities throughout North America, particularly western North America (Kurtén and Anderson, 1980). Other Pleistocene records not reported by Kurtén and Anderson include several elements of a large *A. simus* from northern Utah (Nelson and Madsen, 1983), a fragmentary partial skeleton from Duck Flat, Washoe County, Nevada (D.R. Tuohy, in litt.), numerous cranial and postcranial elements from Natural Trap Cave, Big Horn County, Wyoming (L.D. Martin, pers. comm.), an isolated tooth from Adair County, Oklahoma (Puckette, 1976), a cranium, five vertebrae, and partial pelvis from Hot Springs Mammoth Site, Fall River County, South Dakota (L. Agenbroad, pers. comm.), and a skull, femur, and ten vertebrae from Cueva Quebrada, Val Verde County, Texas (Lundelius, 1984). Isolated material from Rancho La Brea has permitted a composite construction of the complete skeleton of *A. simus.* An unpublished record of this species from American Falls, Idaho, consists also of a relatively complete skeleton, but the postcranial elements are fragmented and incomplete (Jon Becker, pers. comm.) and are not useful for proportional analyses. A nearly complete skeleton from Fulton County, Indiana, is currently under analysis by William Turnbull and associates (pers. comm.). Consequently, the material from Labor-of-Love Cave constitutes one of the most complete skeletons from one individual recovered in North America. This provides more accurate proportional data on limbs, with which to evaluate the paleobiology of *A. simus.*

PALEOBIOLOGY

Kurtén (1967), in his singular monograph on *Arctodus* bears, stated that *A. simus* had cursorial adaptations, and was probably a highly predaceous carnivore. His conclusion was based primarily on the long limbs, slender leg elements, and "felid-like" characters of the skull of *A. simus* when compared to other ursids. However, we contend that this species may have been largely herbivorous based upon characteristics in the skull, limbs, and body size. In addition, anatomic and functional morphologic comparisons with the living spectacled bear, *Tremarctos ornatus,* add support to our argument. Finally, sympatric records of Pleistocene bears suggest that *Arctodus* and *Ursus* species used different feeding strategies.

SKULL

Kurtén (1967) described the skull of *A. simus* as having several felid-like characteristics such as a shortened face, large rostral breadth, high vaulted calvarium, and similar orientation of the zygomatic arches, and he used these convergent features to advance his hypothesis that *A. simus* was an active carnivore. However, these skull features may be related to large body size and reduction of premolars in bears, and a comparison to felids is inappropriate. In addition, the same features are present in the skull of *Tremarctos ornatus,* the only living relative of *Arctodus* (Davis, 1955). The South American spectacled bear (*T. ornatus*) is primarily herbivorous, feeding on bromeliads, leaves, tree bark and fruits, berries, and cactus fruits and pulp, and only occasionally eats carrion; reports of these bears killing prey are uncertain (Peyton, 1980).

One important similarity in the jaw of *Tremarctos* and *Arctodus* is the presence of a premasseteric fossa (Fig. 4). In a detailed examination of the structure of the dentary and related muscles in *T. ornatus,* Davis (1955) concluded this fossa has one of two functions: it is either a depression accommodating a small cheek pouch formed in the oral vestibule (as in the mandrill, *Papio maimon*), or it reflects modeling in jaw architecture to allow a larger zygomaticomandibularis muscle. This muscle, which is important in allowing lateral grinding motions of the jaw and aids in elevating the mandible, is large in herbivorous animals and small in carnivorous animals (Davis, 1964). Since the size of the premasseteric fossa is far too small to be a useful cheek pouch for the size and food requirements of *T. ornatus,* it is probably related more to the jaw mechanics to accommodate a large zygomaticomandibularis muscle (Davis, 1955). Davis (1955:43) also points out that "a functional pouch occurs elsewhere only in social animals that compete for food (primates), or in animals that forage for food and retreat to a safe place to masticate it (rodents). Bears fall into neither of these categories." In regards to the fossa itself, Davis (p. 44) states that it does not interfere with the trajectory systems of the skull and "is situated in tissue that contributes little or nothing to the internal support of the mandible." A similar function for the premasseteric fossa can be projected for *A. simus,* because its jaw architecture is very similar to the closely related *T. ornatus.* Although morphologic associations between fossil and living animals should be made with caution, we believe the close affinities of these two bears permit reliable comparisons.

The teeth of *A. simus* also suggest a largely herbivorous diet. Kurtén (1967) suggested that *A. simus* was predaceous based primarily on the high-crowned nature of the first lower molar, and the relatively large size of the canines. He noted that the protoconid and paraconid in the first molar form a carnassial shear with the paracone and metacone of the upper fourth premolar. He additionally referred to the trenchant shape of the first lower molar. Such a carnassial shape is characteristic of many carnivorous fissipeds, but we believe it is not developed in *A. simus.* Instead, with moderate wear, the protoconid and paraconid apices of the first molar are worn to a relatively flat, blunt loph. While the M_1 of *Arctodus* is high-crowned, it is no more trenchant than that of other bears and, like *U. arctos,* it wears flat. Moreover, the only apparent shear facet is worn into the labial surface of the tooth in the indentation between the talonid and trigonid where the paracone of M^1 occludes, not along the labial sides of the paraconid and protoconid (Fig. 4). This small shear facet would be relatively inefficient for slicing flesh. The trigonid of M_1 is tall and conical, somewhat reminiscent of the bone-crushing posterior premolars of hyaenas. The talonid forms an offset, small crushing platform that is confluent with those of the posterior molars. Perhaps the offset nature of this tooth functions in crushing plants and bone. The M_2 is extremely broad relative to its length (Table 1) and forms, with the third molar, a large crushing platform as in omnivorous bears. Although cusps of canids and felids can wear flat, particularly in aged animals, the general trend in most highly predaceous carnivores is to maintain a sharp, shearing blade on the carnassials. Except in very young specimens, all of the material of *A. simus* that we have observed (including that at the Los Angeles County Museum of Natural History and the American Museum of Natural History) have flattened cusps. In summary, these characters of the teeth indicate to us that *A. simus* may have been omnivorous or primarily herbivorous, but had bone-crushing capabilities.

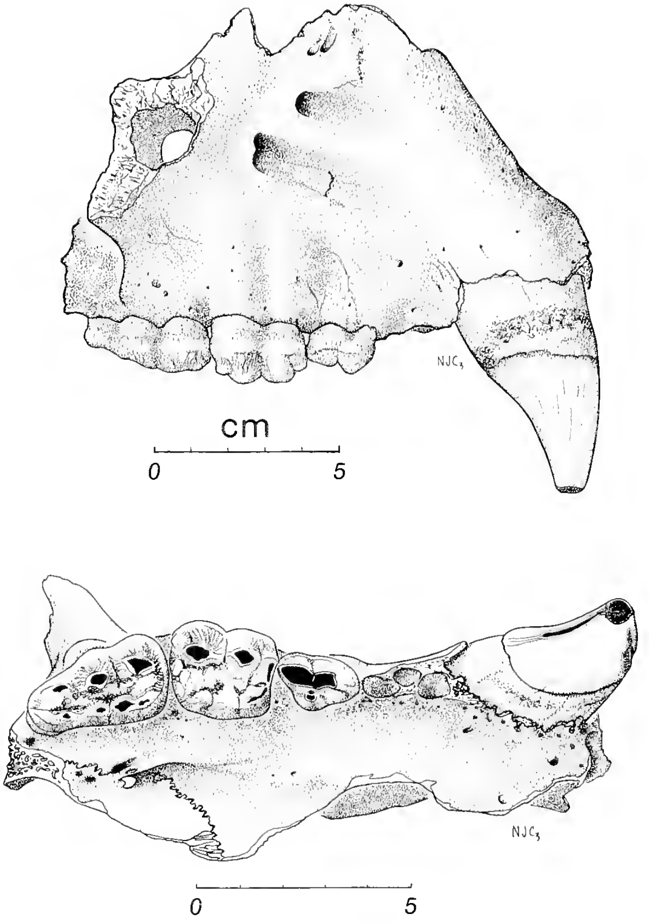
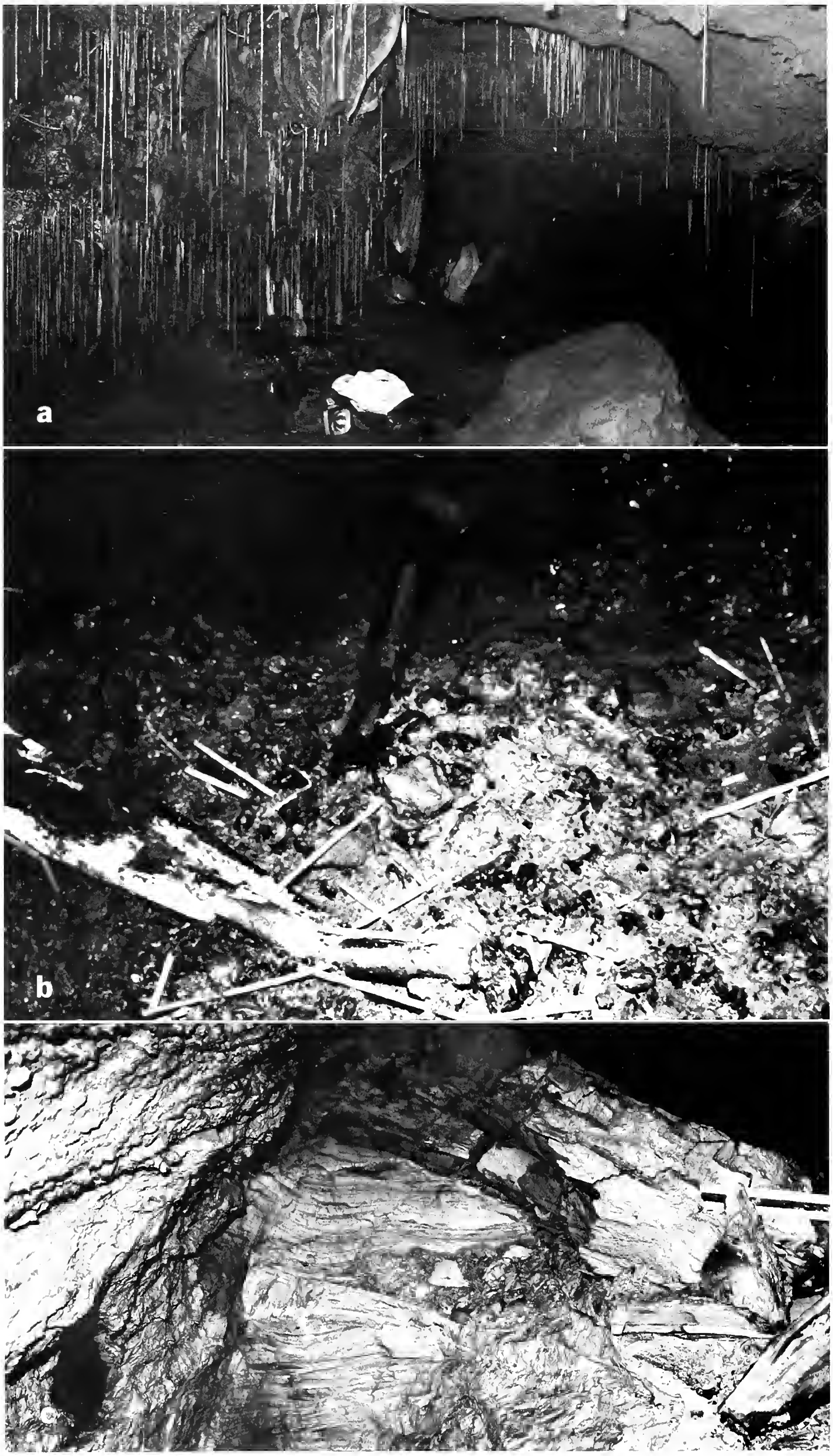


Figure 5. The right maxilla (LACM 122434) of *Arctodus simus* from BC-2. Its position in the pool at time of discovery is shown in Figure 2.

Tremarctos ornatus, like *A. simus,* has shorter dentaries and an overall shorter face when compared to *Ursus arctos* (Davis, 1955) and is rarely predaceous, as already noted. Although the polar bear, an obligate carnivore, has carnassials that are no more sectorial than those of other living


a
b
c

bears, they do have tall, pointed cusps in the unworn condition, and the teeth show a trend towards homodonty (DeMaster and Stirling, 1981), indicating possible convergence with carnivorous pinnipeds. Additionally, the lack of sectorial teeth in the polar bear may simply reflect its relatively late (mid-Pleistocene) derivation from bunodont *U. arctos* (Kurtén, 1964). Moreover, while no one would argue that felids are not highly predaceous with teeth adapted to a carnivorous diet, such dental morphology does not necessarily mandate carnivory; *Felis planiceps* of southeast Asia seems to prefer fruit (Goodwin, 1954). Consequently, Kurtén's suggestion that *A. simus* was highly predaceous based on skull structure and teeth cannot be substantiated.

LIMB PROPORTIONS

The major value of the *A. simus* postcranial material from Labor-of-Love Cave is that it provides an opportunity to examine relative limb proportions from a single individual. Table 3 provides measurements of the limb elements of the partial skeleton of *A. simus* from BC-2. Length proportions of limb elements are compared to similar proportions for several species of *Tremarctos, Arctodus,* and *Ursus* (Table 4). Kurtén's proportions for the fore- and hindlimb elements were determined using composite material from several fossil specimens. He found little variation in limb proportions within *A. simus,* though considerable size variation within the taxon was noted. Our calculations (Table 4) indicate that the limb proportions of *A. simus* are lower than those given by Kurtén (1967) but still evince considerable divergence from other bear taxa; forelimb proportions do not overlap with Recent bears or fossil *Tremarctos,* and hindlimb proportions overlap only slightly with *U. arctos.* This divergence can be attributed, as Kurtén concluded, to the relatively longer limbs of *A. simus* compared to other bears.

The strongest evidence for cursorial adaptation in *A. simus* offered by Kurtén (1967) was its relatively long slender legs. The humerus and femur are longer than the radius and tibia, respectively. Hildebrand (1982) discusses skeletal and other adaptations which increase speed in cursorial animals, including an increase in limb length. However, the lengthening of limbs in cursorial animals usually takes place in the distal limb segments, not the proximal as in *A. simus.* Longer proximal limb elements are a feature of digging animals, such as the badger, and of mediportal and graviportal animals, such as bears (Davis, 1964). *A. simus,* however, lacks other characteristics of a digging life-style such as a long olecranon on the ulna and long claws. Other non-cursorial characteristics of bears include plantigrade feet (which is noted for *A. simus* by Kurtén) and a stride with no or scarcely any unsupported intervals (Hildebrand, 1982).

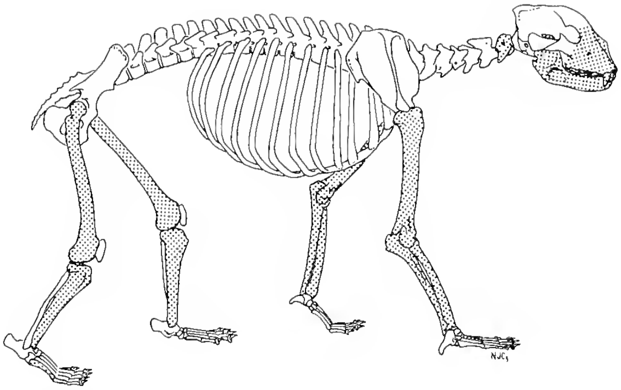


Figure 7. Skeleton of *A. simus* with shaded bones indicating elements recovered from the adult individual represented at BC-2.

If *A. simus* was largely herbivorous and not a highly predaceous, cursorial carnivore, another explanation for its long limbs is needed. An interesting comparison can be made with the maned wolf, *Chrysocyon brachyurus,* of South America. This fox inhabits open, tall-grass prairies (Nowak and Paradiso, 1983), has extremely long and slender limbs relative to body size (as in *A. simus*), is not especially swift nor does it take swift prey (Hildebrand, 1954), and runs with a loping gait (John Eisenberg, pers. comm.). The long limbs may be an adaptation for increased vision over tall ground cover in an open habitat (Nowak and Paradiso, 1983). A similar interpretation may be applied to *A. simus* in the Great Basin, where its former habitat is known, but the habitat for this species throughout its range in the Pleistocene of North America is largely unknown. It is equally possible that the longer limbs of *A. simus* were used in tearing and pulling down vegetation, including shrubs and small trees, in order to feed on leaves, fruits or bark.

BODY SIZE

The body size attained by *A. simus* may also be an indication of herbivory. Body size is limited by many factors, including specialization to specific habitats and diet (Eisenberg, 1981). In terrestrial mammals, herbivores usually have a larger biomass and greater numerical density than carnivores. This trend is caused by a more restricted energy base available to carnivores according to Eisenberg (1981) who also discusses the average size of recent mammalian genera (using head and body length) in relation to niche specialization. Table 5 summarizes these data in comparison to *A. simus.* This table indicates that Recent terrestrial carnivores are limited to a maximum size by their diet, and that omnivory has allowed

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Figure 6. The gravel and silt deposits at BC-2. (a) The gravel lens containing the remains of *A. simus* (LACM 122434) extends from the mound of sediments in the right foreground to the kneeling figure. The stream and pool containing bones are to the right; water is flowing in the direction of the figure, toward the cave entrance. (b) An articulated radius and ulna, and a partly buried tibia of *A. simus* eroding from the gravel lens as shown in Figure 2. (c) Finely laminated and cross-bedded sediments just upstream of BC-2 are all that remain of deposits that once nearly filled the cave.

Table 3. Measurements (in mm) of limb bones of *Arctodus simus* (LACM 122434) from Labor-of-Love Cave. Breadth reflects the greatest lateral-medial breadth, and depth reflects the greatest anterior-posterior depth at each point of measurement.

Element	Total length	Proximal breadth	Proximal depth	Transverse diameter prox. head	Least breadth shaft	Least depth shaft	Distal breadth	Distal depth
Left ulna	375	28.8	65.2	—	—	—	—	—
Left radius	355	—	37.9	—	26.2	17.1	—	26.0
Right humerus	454	79.5	—	97.7	35.3	33.9	—	62.8
Right femur	490	124.0	58.0	62.7	39.6	30.4	99.0	56.2
Right tibia	352	90.0	81.7	—	31.2	34.0	63.6	40.5
Right V metatarsal	85	22.5	23.3	—	11.7	10.5	18.3	15.3
Right III metacarpal	—	17.5	31.1	—	13.5	13.1	—	—

bears to attain larger average sizes. The largest living bear is the Kodiak Bear, *U. a. middendorfi*, with a mean biomass of approximately 300 kg (Eisenberg, 1981: Appendix 2), although individual bears may be as large as 700 kg (Novak and Paradiso, 1983). It should be pointed out that the giant panda (*Ailuropoda melanoleuca*), a herbivore, reaches a biomass of approximately 182 kg and a head and body length of 1200–1300 mm, indicating an herbivorous diet does not necessarily result in a large body size.

In comparing measurements of *A. simus* (as estimated by Kurtén, 1967), to Eisenberg's data (Table 5) and our own, it is apparent that this species exceeded the modern limitations for a terrestrial carnivore. Only two Recent skeletons of *U. arctos* (USNM 216206 and USNM 199252, Alaskan males) equal or exceed the size of *A. simus* from Labor-of-Love Cave, which we believe to be a small adult, perhaps a female, compared to other finds. A recent record of *A. simus* from Utah, representing the largest known individual of this species, was estimated by Nelson and Madsen (1983) to have been 25–30% larger than all previous records, and to have weighed between 620–660 kg. This estimate is over four times the average size of the largest terrestrial carnivore (*Panthera*) today. These measurements place *A. simus* well within the size range of modern (and Pleistocene) terrestrial frugivore/omnivores and herbivore/grazers as presented by Eisenberg. If we accept Kurtén's interpretation of *A. simus* as having been primarily carnivorous, then this animal was atypical in size. It is more logical to assume that *A. simus* reached its

Table 4. Comparison of relative proportions of limb segments of *Arctodus simus, Tremarctos floridanus, T. ornatus, Ursus arctos,* and *U. americanus* using greatest length for each element, in mm.

	Arctodus simus				*T. floridanus*[2]				
	Male[1]	Female[1]	Hay Springs[1]	Labor-of-Love Cave	Male	Female	*T. ornatus*[2]	*U. arctos*	*U. americanus*
$\frac{\text{Radius}}{\text{Humerus}} \times 100$									
N	1/2	5/6	—	1/1	3/3	2/3	4/4	9/9	5/5
x̄	87.6	85.6	—	78.2	83.0	83.8	84.3	88.4	90.3
Range	—	—	—	—	—	—	82.8–86.0	83.0–95.0	85.5–97.9
$\frac{\text{Tibia}}{\text{Femur}} \times 100$									
N	—	7/7	1/1	1/1	3/3	7/7	4/4	9/9	5/5
x̄	—	74.5	74.8	71.4	73.4	74.0	79.5	73.5	77.0
Range	—	—	—	—	—	—	74.8–81.7	70.4–75.1	74.8–78.4

[1] Data from Kurtén (1967); we were unable to repeat his calculation of the male R/H ratio from his Table 27 and have changed this value according to data he provides in Tables 10 and 11. However, because these ratios are based on non-associated elements from different localities, their accuracy is questionable.
[2] Data from Kurtén (1966).

great size by being primarily omnivorous or herbivorous. We have demonstrated here that the hypothesis for herbivory is equally plausible to one of carnivory, but neither hypothesis can be rejected with an analysis of functional morphology. We prefer to believe that *A. simus* was primarily herbivorous, as *T. ornatus*, but also may have been an opportunistic predator and scavenger with bone-crushing capabilities.

SYMPATRY OF PLEISTOCENE BEARS

The remains at BC-2 indicate a co-occurrence of *A. simus* and *U. americanus* in this area of Nevada. Sympatric records of these two bears are not unusual and have been documented at several Pleistocene localities including Rancho La Brea and McKittrick (Merriam and Stock, 1925; Schultz, 1938). However, associations of *A. simus* and *U. arctos* are rare and have occurred only at Little Box Elder Cave in Wyoming and Fairbanks II in Alaska (Kurtén and Anderson, 1974, 1980). Kurtén and Anderson (1980) speculate that invading *U. arctos* in the late Wisconsinan may have played a role in the extinction of *A. simus* through competition. However, this scenario is at odds with Kurtén's earlier suggestions that *A. simus* was a highly predaceous carnivore. If we accept Kurtén's interpretations it seems unlikely that the larger and more powerful *A. simus* could be out-competed by the smaller and less powerful *U. arctos*. Finally, apparent sympatry of *U. americanus* and *A. simus* during the late Pleistocene is more likely if the former species was omnivorous, as it is today, and the latter species was largely herbivorous. In this situation, the invasion of a third species, *U. arctos*, which can be primarily carnivorous in parts of its range today (Nowak and Paradiso, 1983), may have allowed a sympatric relationship between these three species. If further investigations in Labor-of-Love Cave provide more positive evidence for an association of *A. simus* and *U. arctos* there, valuable insights on the interspecific relationship of these species may be gained.

ACKNOWLEDGMENTS

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Table 5. Comparisons of the macroniche, average length, and weight of Recent mammalian genera (after Eisenberg, 1981) to the proposed niche, length (estimated by Kurtén, 1967) and weight (estimated by Kurtén, 1967 and Nelson and Madsen, 1983) of *Arctodus simus*.

Taxon	Niche	[1]Average head and body length (mm)	[2]Range of average weights (kg)
Equus	Terrestrial herbivore/ grazer	1508	166–260
A. simus	Terrestrial herbivore/ omnivore	1432	270–660
Ursus	Terrestrial frugivore/ omnivore	817	77–300
Panthera	Terrestrial carnivore	718	39–151

[1] Average head and body length for Recent mammalian genera was derived by Eisenberg (1981, Table 43, p. 265) by summing the mean values for the two extreme size-classes in a genus.

[2] Range of weights for Recent mammalian genera was taken from weights of all species within a genus as presented by Eisenberg (1981, Appendix 2).

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