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A DEFINITION AND CLASSIFICATION
OF THE
TRIBE STIRIINI (LEPIDOPTERA: NOCTUIDAE)

By CHARLES L. HOGUE



Los Angeles County Museum • Exposition Park • Los Angeles 7, Calif.

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DAVID K. CALDWELL

Editor

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A DEFINITION AND CLASSIFICATION
OF THE
TRIBE STIRIINI (LEPIDOPTERA: NOCTUIDAE)¹

By CHARLES L. HOGUE²

INTRODUCTION

The Stirini are a structurally uniform but superficially diverse tribe of noctuid moths found only in the New World, chiefly in central and northern Mexico and the southwestern United States. As in most higher noctuid taxa, the tribe's constituents are poorly known and, prior to the present work, virtually unstudied with regard to phylogenetic relationships. The primary purpose of this study, therefore, has been to study the phylogenetic relationships in order to define the tribe and to bring its internal classification into order.

I have conformed in my presentation, as well as in my actual procedure of study, to the taxonomic principle that higher categories are to a large degree subjective and constructed on the basis of personal and practical reasons but are primarily and ideally based on some real phenomenon of organisms, in this case, their phylogenetic relationships (Simpson, 1961: see especially pp. 108-109). Hence, I have attempted to elucidate and infer phylogenetic relationships separate from, and prior to, the assembling and dividing of the various groups into taxa and ranks and assigning names. This has the desired effects of keeping phylogenetic logic and conclusion clear (Arnett, 1961:107) and making them most available for future scrutiny and improvement as more information becomes available. And it further satisfies, I hope, a need in systematics expressed by Michener (1957:173) ". . . for all systematists to publish with their works full statements of the type of relationships and other considerations behind their classifications."

This study is based entirely on the morphology of the adult moths. Specimens of all the known species were studied and all but the rarest were personally dissected. Dissections were mostly of the genitalia, but at least one specimen of almost every species was dissected in full and mounted on slides so that the entire endo- and exoskeleton could be studied in detail.

Unfortunately, several species of dubious taxonomic status are still unknown either as females, or more critically, as males. These are the females of "*Antaplagia*" *prepontendyta* Dyar, "*Lythrodes*" *arivaca* Barnes, *Plagiomimicus astigmatosus* Dyar, "*Stiria*" *iticys* Dyar and *Xanthiria primulina* Druce, and the males of *Plagiomimicus chalcospilans* Dyar, *P. raglena* Dyar, *P. unicum* Barnes and Benjamin, *Cirrhophanus hyperion* Dyar and *C. hoffmanni* Hogue, new species.

¹Work completed while the writer was a graduate student, Department of Zoology, University of California, Los Angeles, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Acknowledgment is due my colleagues, W. A. Powder and S. Ramalingam, for numerous, miscellaneous helps, and to the following persons for putting at my disposal their personal collections or collections in their care: C. F. Harbison, San Diego Museum of Natural History; R. Leuschner, Los Angeles, California; L. M. Martin, Los Angeles County Museum; B. Mather, Jackson, Mississippi; P. T. Riherd, Mercedes, Texas; F. H. Rindge, American Museum of Natural History; F. P. Sala, Burbank, California; and Mr. and Mrs. L. A. Willahan, Los Angeles, California.

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The photographs are the work of R. J. Pence, of the University of California, Los Angeles.

TAXONOMIC HISTORY

When Grote (1874) originally described the genera *Stiria* and *Stibadium* he remarked on their close relationship. In his *List of the Noctuidae of North America* in the same publication he suggested a further relationship of these genera by placing them next to his earlier described *Plagiomimicus*. This treatment was the first trace of the tribe Stiriini. *Basilodes* and *Cirrhophanus* had already been described by other authors but Grote failed to see their affinities with the above genera and placed them in seemingly arbitrary positions quite apart from the others. His arrangement of these genera in his later *Check List of the Noctuidae of America, North of Mexico, Part I* (1875) was approximately the same.

Between the time of the above lists and Grote's *New Check List of North American Moths* (1882a), several new forms became known which Grote related to *Stiria*, *Stibadium* and *Plagiomimicus*. He grouped these in the "New List" under a formal name, "Stiriinae." In addition to the three genera just mentioned, this group included the genera *Polenta* (synonymized by Grote with *Plagiomimicus*), *Fala* and *Acopa*. Although this was the first formal declaration of the taxonomic group which is the subject of this study, Grote

(1882b) implied the existence and position of the group in another paper published in the same year when he stated, "The following genera [*Antaplaga*, *Plagiomimicus*, *Polenta*, *Stiria*, and *Stibadium*] seem to fall in between *Heliothis* and *Plusia*." In the "New List," Grote still excluded *Basilodes*, which he put in the "Calpinae," and *Cirrhophanus*, which he put with *Antaplaga dimidiata* under the "Heliothinae." These three groups and the "Plusiinae," however, were contiguous in the list, indicating that Grote thought they were somewhat related.

In the same year that Grote published his "New List," Smith (1881-1882) devoted a paragraph to the stiriine genera in his *Synopsis of the North American Genera of the Noctuidae* (pp. 30, 35). He considered *Stiria*, *Stibadium*, *Plagiomimicus* and *Basilodes* generically indistinct. For the first time in the literature, *Basilodes* was united with the other stiriine genera but no statement of a formal grouping was made. In his *Synopsis of the North American Heliothinae*, also published in the same year (Smith, 1882), Smith's treatment of *Antaplaga* was identical to that of Grote in the "New List." Both placed the genus immediately between *Pippona* and *Grotella*.

The identity of the nominal species *Polenta tepperi* and *Plagiomimicus richii* proved to be a source of consternation to Grote for some time. At first, since some specimens he had, which were identified as *tepperi*, possessed the typical foretibial claw and facies of *Plagiomimicus*, he included *tepperi* in that genus and synonymized *Polenta* with it. The lack of a foretibial claw on the type of *tepperi* (which he had then not seen), however, puzzled him. He questioned the statement of the original describer of the species, Morrison, and its curator, Smith, to that effect (Grote, 1883a:75) and wanted the character state verified (Grote, 1882b:75-76). Later, on the insistence of Smith (1883:229) that the claw was in fact absent (it was, but because it had broken off), and a personal superficial examination of the type, Grote described the new species *richii* from his specimens with the fore claw (Grote, 1886). He then excluded *Polenta tepperi* from *Plagiomimicus* and the "Stiriinae" and replaced it with his new *richii* (Grote, 1886; 1890:69). He followed this treatment until Smith (1893:263-264) stated his error of observation and corrected the situation by synonymizing *richii* with *tepperi*.

In his publications following the "New List" Grote continued to revise and expand the "Stiriinae." To the group, in his discussion *On the North American Calpinae to Heliothinae* (Grote, 1883a), were added the genera *Basilodes*, *Chamaeclea*, *Cirrhophanus*, and *Neumoegenia* which were new or formerly excluded. *Cirrhophanus* was only provisionally included for Grote thought that it might be distantly related to *Gortyna*, a non-stiriine genus. Two further genera, *Hypsoropha* and *Plusiodonta*, were added, without explanation, in his *Introduction to a Study of the North American Noctuidae*, published also in 1883 (Grote, 1883b). In both of these papers, Grote continued to allude to the possible affinities of the Stiriinae with the Plusiinae because of similarities in wing shape and metallic coloring.

Grote continued to follow essentially the same classification in his later

lists and discussions (Grote, 1890a; 1895), oscillating in his placement of *Cirrhophanus* with the Stiriinae and with the Heliothinae. He excluded some genera included earlier, such as *Hypsoropha* and *Plusiodonta*, and added some species to *Basilodes* which are now placed in the closely allied genus *Chalco-pasta*. He mentioned the exclusively American distribution of the group in a paper comparing the noctuid fauna of Europe and North America (Grote, 1890b:69). It is notable that his former group names were given formal tribal status there and in his "Revised List" (Grote, 1890). Thus, for the first time, the tribe Stiriini was formally declared.

The genera of the Stiriini have been variously treated by other workers. Smith's (1891:52-53; 1893:261-266; 1903:48) and Dyar's (1903:183, 196-197) lists and catalogues generally followed Grote's arrangement. Dyar segregated *Antaplaga* more than Smith but still put it near other heliothidine genera. This genus was then already becoming an ill-defined catch-all for unrelated forms.

Hampson (1910) treated all of the then known Stiriini in volume 9 of his *Catalogue of the Lepidoptera Phalaenae in the British Museum*. He completely destroyed all semblance of a natural group with his arrangements, especially in the phylogeny of the Acronyctinae, the subfamily in which he placed the stiriine forms. The diagram, by his own careful explanation, was not intended as a true phylogeny, but it did attempt to show general phylogenetic relationships. On the diagram, the Stiriini were widely dispersed among various foreign and American genera. This situation was obviously due to Hampson's customary reliance on artificial characters. He described a number of new genera and species which clarified the taxonomy of the tribe in some respects.

Barnes and McDunnough (1917:70-73) and McDunnough (1938:99-100) abandoned Hampson's artificial classification in their check lists and generally grouped the stiriine genera naturally as did Grote.

Draudt's (1919-1939) generic arrangement in volume 7 of Seitz's *Macrolepidoptera of the World* was identical to that of Hampson except in the addition of the numerous new species described since Hampson.

The most recent treatment of the tribe by Forbes (1954:169, 251-252) was restricted to the species occurring in northeastern United States. His definition of the tribe was, therefore, somewhat incomplete but accurate as far as it went. The genera he included are all good Stiriini except *Stiriodes*. Forbes was the first since Grote to treat the group formally as a tribe.

GEOGRAPHICAL DISTRIBUTION

The Stiriini have been only sparsely collected. The larger museums of the United States have the majority of the known material, but the overall amount is small compared to that for most other noctuid groups. While many of the common species of the southwestern United States are represented, primarily collected by O. C. Poling in the early 1900's, the Mexican species are known

from few localities and are represented by very few specimens, for some of these, uniques or only one sex being known. The locality data from these specimens reflects better the activities of collectors than the ranges of the moths. Few noctuid collectors have been active in Mexico in recent years. Most material dates back to the late 19th and early 20th centuries and is mainly from two sources: (1) the sporadic collections for the Godman-Salvin, *Biologia Centrali-Americana* project studied by Druce and (2) miscellaneous accumulations sent to the United States National Museum by Roberto Müller and William Schaus and studied by Dyar.

Because of the paucity of material, only a few broad, tentative generalizations about the distribution of the Stiriini can be made. The tribe appears to be entirely Central and North American. No known noctuids from the Old World or South America can be included in it. The center of distribution, where most of the species occur, seems to be central and northern Mexico and the southwestern United States. The collections from the northeastern and midwestern United States are mostly sporadic and of only a few species. There is very little material from extreme southern Mexico and other Central American countries.

Except for a few from central Mexico and northeastern United States, all of the collections are from arid or semiarid areas. The tribe thus seems to be generally adapted to dry climates and edaphic conditions and is probably associated with xerophytic plant types. This may explain the significance of certain stiriine structures such as the foretibial "claw" and frontal protuberance. The corneous, heavy appearance of these structures suggests that they are fossorial adaptations for digging through either a pupal cell wall or the overlying soil, through which the adult moth must pass when emerging from its underground pupation site. These materials may be expected to be quite compact and hard in arid regions. As far as I know, however, there are no recorded observations or experiments to demonstrate such a function for these structures. The frontal protuberance, and foretibial "claws" also tend to occur in many other unrelated noctuids of arid regions.

ECOLOGY

There is even less information available on the ecology of the Stiriini than about their geographical distribution. No life histories have been fully elucidated and other kinds of ecological data are almost completely unrecorded. According to the literature, only six per cent of the species have even been reared so that at least their food plants, larvae and pupae are known.

Superficial descriptions of larvae and pupae and listings of host plants have been recorded for the following species: *Plagiomimicus expallidus* (Crumb, 1956:211), *P. pityochromus* (Crumb, 1956:211), *P. spumosus* (Murtfeldt, 1894; Comstock, 1946; Crumb, 1956:210), *Cirrhophanus triangulifer* (Jones, 1937; Crumb, 1956:212), *Basilodes chrysopsis* (Crumb, 1956:213) and *B. pepita* (Dyar, 1921; Crumb, 1956:213).

From such incomplete information it would be dangerous to make any generalizations. However, a few consistencies are apparent from the data which at least are worthy of note. They may possibly indicate some broad tendencies, since the species listed above belong to diverse genera.

The larvae of all the species just noted feed on plants of the family Compositae, especially the flower heads of ambrosias. This constancy in food preferences, as far as demonstrated, lends support to the validity of the tribe as a phyletic unit. Furthermore, this association may explain the cryptic colors of the larvae and adults of some species. Jones (1937) reports finding a specimen of *Cirrhophanus triangulifer* ". . . sitting by day in the flower-head of *Bidens involucrata*, the golden yellow-brown of its wings matching closely the color of the flower." He noted also that the flower-feeding larvae matched the flower-heads closely in color. A similar association is known for other noctuid species, especially diurnal ones.

The larva of *Plagiomimicus spumosos* feeds on sunflowers. But instead of feeding on the surface of the flower-head it burrows into the interior and is not cryptically colored but pale and unmarked like borers in general (Comstock, 1946). Likewise, the adult is not colored like the flower and probably does not rest among its petals during the day.

Similarities in the morphology of the larvae of the few stiriine species of which he had specimens led Crumb (1956) to group them into a single taxon, "Amphipyridae, group 5." He included four other genera in this group which may be related to the Stiriini.

The larva of *Cirrhophanus triangulifer* and *Plagiomimicus spumosos* are known to form an extra hard, underground pupation cell. The foretibial "claw" and frontal protuberance of these species might be modifications for penetrating the walls of these cells during emergence. (See remarks on these structures under "Geographical distribution," section immediately above).

The dates on specimen labels generally indicate the seasonal occurrence of the adults. By far the majority of species have been collected in the fall or late summer, a lesser number in the spring, and a few in both, indicating bivoltinism. Mid-summer and mid-winter thus seem to be poor times for collecting Stiriini. The adult flight periods probably correspond to the flowering seasons of the host plants.

A REPRESENTATIVE SPECIES: *BASILODES RUGIFRONS*

Most of the characteristic attributes of the Stiriini are only generally and vaguely describable in words. To convey the nature of these attributes more fully and accurately, I have illustrated many of them. The illustrations, however, are restricted to genitalic and surface features since these were the only ones universally available and of the greatest taxonomic importance. Therefore, I feel it is necessary to illustrate in some detail at least one species, *Basilodes rugifrons* (Grote).

The following discussion and illustrations (Figs. 2-5) are not intended to be morphologically comprehensive since many details are not treated, such as head sutures, axillary sclerites, etc. But they will serve as a basic depiction of stiriine structure and also as an explanation of the terminology used in the remainder of this paper. As nearly as possible, the structures are described in the same sequence as they are in the formal taxonomic descriptions.

Head (Figs. 2a; 3a, b). The most unusual feature of the head and a characteristic stiriine feature is the protruding, heavily sclerotized *frontal protuberance* (fp). It is composed of two parts, a *peripheral ring* (pr) and a ventral *secondary prominence* (secp). Below the frontal protuberance, the *infraclypeal plate* or *clypeal shelf* (csf) runs transversely across the head. In a cleared specimen the *ocular diaphragm* (od), which is perforated by an oval orifice, can be seen below the surface of the large, hemispherical *eye* (e). Each of the paired *ocelli* (oc) is situated immediately above the eye and behind the enlarged *scape* (scp) of the *antenna* (ant). On the ventral surface of the head the most conspicuous structures comprise the mouthparts and consist of the long *proboscis* (prob) and the three segmented, paired *labial palpi* (lp). Other less conspicuous elements of the mouthparts are the minute paired, 2-4 segmented *maxillary palpi* (mxp) and the paired *pilifers* (pf). The *anterior tentorial arms* (ata) traverse the head internally.

The *cervical sclerite* (cs) lies in the cervical membrane and connects the head with the propleuron.

Prothorax (Figs. 2a; 3a). The prothorax is much smaller than the other thoracic segments. Its simple *pleura* (p) unite dorsad with the flat, small *notum* (n) from which the large rectangulo-conical *patagia* (pt) arise. Cephaloventrad the pleura connect broadly with the *sternum* (s). Most of the morphological sternum is no longer evident externally in the Lepidoptera but is believed to be represented internally by a flat, emarginate lamella, the *lamella of the discrimen* (ld). The latter is supposedly formed by medial migration and invagination of the two lateral halves of the primitive pre-lepidopteran sternum (Weber, 1928). The same condition prevails in the meso- and metathorax.

The *parapatagia* (ppt) are weak straplike sclerotizations behind the patagia and above the large cephalically displaced *mesothoracic spiracle* (sp).

Mesothorax (Figs. 2a, b; 3a). The mesothorax is the largest and most complex of the three thoracic segments. Its pleuron is composed of several sclerites, the largest of which is the anterior episternum. The latter is incom-

pletely subdivided into a dorsal *anepisternum* (aneps) and a ventral *katépisternum* (keps) by the *anepisternal cleft* (anepsc). An unsclerotized area of the anepisternum, the *basalar cleft* (bcl), lies just below the *basalare* (ba). The *preepisternum* (peps) lies immediately cephalad of the katépisternum.

Caudad of the large episternum is the V-shaped epimeron. The anterior arm of the V is termed the *anterior epimeron* (aepm) and the posterior arm, the *posterior epimeron* (pepm). A large *subalare* (sa) resides in the membrane between the tips of the arms of the V.

The *pleural suture* (pls) runs a devious course between the episternum and epimeron. It is straight and clearly visible ventrad but makes a curve caudad at the level of the anepisternal cleft and disappears beneath a strong overfold of the dorsal end of the anterior epimeron. Dorsally the pleural suture is lost in a complex of structures of doubtful morphological interpretation. The most conspicuous of these are the *pleural wing process* (pwp) and the *tegular arm* (tega), the latter providing a base for the *tegula* (teg). Internally, the pleural suture is represented by the *pleural ridge* (plr).

The ventral margin of the largest sclerite of the thorax, the *mesoscutum* (sc), is complexly modified. The modifications are associated with the intricate articular system at the bases of the wings and include the *suralare* (sra), *scutal ridge* (sr), *scutal incision* (si), *adnotale* (ad), and *posterior notal wing process* (pnp). The deep *scuto-scutellar suture* (sss), marked internally by the *scuto-scutellar ridge* (ssr), separates the *scutellum* (scl) from the *scutum* (sc). The externally reduced *postnotum* (pn) is hidden beneath the scutellum and is obvious only internally, laterad as the *lateropostnotum* (lpn) and mesad as the dorsal half of the *phragma* (ph).

As in the prothorax, the sternum is mostly internal and in the form of a lamella, the *lamella of the discrimen* (ld), which is very large and entire, *i.e.*, bridging completely with the furca. Another element of the sternum, the *spina* (spi), deeply invades the interior of the mesothorax cephalad of the lamella. Externally the spina is indicated by a deep pit in the mesosternum just anterior to a small V-shaped sclerite, the *spinasternum* (sst). The tip of the spina bears a cephalically projecting, flat horn, the *horn of the spina* (hs).

Behind the lamella and medially connected with it is a strong invagination, the *furca* (f). The furca connects laterad with the dorsal end of the posterior epimeron by means of a *furcal bridge* (fb). The *phragma* (ph) is very large and occupies much of the interior of the metathorax.

Metathorax (Figs. 2a; 3a). The metathorax is smaller than the mesothorax but has most of the same elements. A large, rectangular, undivided *episternum* (eps) occupies the anterior third of its pleuron. The *basalare* (ba) is a rounded sclerite partially set off from the dorsal part of the episternum. The *epimeron* (epm) is partially membranous caudad and complexly modified internally to form part of the tympanal complex which will be discussed separately below. The *subalare* (sa) resides in the membrane dorsad of the epimeron.

In contrast to the condition in the mesothorax, the *pleural suture* (pls)

runs a straight path dorsoventrad between the episternum and epimeron. It runs dorsad into the *pleural wing process* (pwp). A small simple *tegular arm* (tega) resides in a notch between the pleural wing process and the basalare, but it bears no tegula.

The *scutum* (sc) is constricted dorsomesad by the infringement of the mesoscutellum but is well developed laterad. The ventral margin of the scutum is modified like that of the mesothorax into a *suralare* (sra), *scutal incision* (si), *adnotale* (ad), and *posterior notal wing process*. (pnp). There is no definite scutal ridge. The *scutal suture* (ss) marks the presence of an apodeme, the scutal phragma, which is a part of the tympanal complex to be discussed below. Behind the scutum, and separated from it by the *scuto-scutellar suture* (sss), is the elongate *scutellum* (scl).

Again, as in the pro- and mesothorax, the *lamella of the discrimen* (ld) represents most of the morphological sternum. It is similar in shape to that of the mesothorax but smaller and does not bridge completely with the complex, large *furca* (f).

Legs (Figs. 2a; 3a; 4c). The foreleg of *B. rugifrons*, like that of all Stiriini, is very much stouter and shorter as a whole than in most noctuids. This is especially true of the tibial segment. The tibia characteristically bears an apical "claw" composed of a seta. Some other noctuids have a similarly appearing "claw" but it is usually morphologically a spine. The tibia also bears an *epiphysis* (epi).

The mid- and hindlegs are more normal than the foreleg. Their coxae are longitudinally divided by a *coxal suture* (cxs) into an anterior *eucoxa* (euc) and posterior *meron* (m). The tibiae of both bear *spurs*: one pair subapically on the posterior face on the midleg; one pair subapically, and another pair about a third from the end, on the posterior face on the hindleg.

All three legs have five tarsal segments each (1-5) which bear *plantar bristles* (prbr) on their plantar surfaces. These bristles are arranged roughly in three longitudinal rows. The *ungues* (ung), or tarsal claws (not to be confused with tibial "claws") are located at the tips of the last tarsal segments.

Of unknown function and taxonomic significance are fairly large, well-defined *sensilla* (sens) located subapically on the outer surfaces of the foretibiae. These, and other smaller sensilla, occur in fairly constant position on all the legs in the Stiriini. Their presence in noctuids has not been reported in the literature, to my knowledge.

Wings (Fig. 4b). The shape and venation of the wings are typical for most trifold noctuids. A single *areole* (ar), a secondary cell formed by the fusion of R_3 and R_4 , is present. The *frenulum* (fr) of the hindwing is formed by very long bristles: the male has several fused ones and the female three separate ones.

The wing pattern is not illustrated here (see Holland, 1903: plate XXVIII, figure 5, for a colored photograph of this species' upper wing pattern). It is somewhat modified from the primitive noctuidiform pattern but some of the elements are still evident. The AM and PM lines traverse the wing

faintly in their primitive positions. They are joined caudad by a dark area to form a roughly hexagonal spot on the inner margin. The median shade is absent; the distal lines are obscured by a dark area spreading in a short distance along the outer margin. The orbicular spot and apical patch are completely absent but the reniform spot is represented by a small, round dot. For better examples of the full noctuiform pattern on the forewing in the Stiriini, see the figures of various units in the genus *Plagiomimicus* (e.g., Figs. 7-9).

The hindwing is patternless and evenly white above. The pale lower surfaces of both fore- and hindwings are similar and also without pattern.

Tympanal complex (Figs. 2a; 3a, c). Elements from both the metathorax and the abdomen enter into the tympanal complex. The metathoracic elements are intricate derivations mainly from the metepimeron and to a lesser extent, metascutum. From the metepimeron come the four *pockets* (I, II, III, IV), the largest and most ventral of which is IV. Overlying the pockets is the transparent thin *anterior tendon plate* (atp). Between the semicircle formed by the pockets is the thin, taut *tympanal membrane* (t) which is separated indistinctly from the *conjunctiva* (cj) by the slightly sclerotized, nodular *epaulette* (ep). The *alula*, a broad posterior flap of the wing base bordered by the *axillary cord* (ax), overlies the entire complex externally. Ventrad and caudad of pocket IV is the *posterior tendon plate* (ptp); this structure is reduced to a narrow strip in the Stiriini; it is typically a large, convex, hat-shaped sclerotization in other trifold Noctuidae. The *scutal phragma* (scph), an elongate apodeme of the scutum, also enters into the tympanal complex. It is also characteristically reduced in the Stiriini.

The abdominal elements of the tympanal complex are the earlike *hood* (h), inclosing the first abdominal spiracle, and the *countertympanic cavities* (ctc). Where the countertympanic cavities from the two sides adjoin, the median *countertympanic septum* (cts) is formed. The opening of the countertympanic cavities to the exterior is termed the *countertympanic orifice* (co).

Abdomen (Fig. 4d). The abdomen has eight complete annular segments (I-VIII), each consisting of a strongly arched and well sclerotized *tergite* (T) and *sternite* (S) which are connected laterad by a broad pleural membrane. The tergite and sternite of VIII are modified slightly and associated with the genitalia in both sexes. They will be considered with those structures below. TI is quite small and partially unsclerotized. SI and SII are fused into a single plate to the sides of which are deep invaginations, the *abdominal furcae* (abf). The cephalolateral corners of the other basal sternites may also be slightly invaginated as *secondary abdominal furcae* (sabf). A strongly sclerotized, narrow trough, the *tergopleural groove* (tpg), extends from the cephaloventral corners of TII under TI into the countertympanic cavities. The elements entering into the tympanal complex have already been mentioned. The first seven pleural membranes have large, central spiracles (sp).

Vestiture (Fig. 4a). The body vestiture of *B. rugifrons* is typical of the Stiriini. That of the head is deep, close and composed of medium, spatulate, evenly colored scales. That of the thorax is very dense, deep, spreading and

generally composed of long spatulate scales with dentate tips. The individual scales are darker colored distad except for the extreme tips which are a sharply contrasting white. Together the scales give the thorax a rough, irrorate appearance.

The thoracic vestiture is well tufted, *tegular* (tegt), *patagial* (ptt), *posterior mesoscutal* (pmesosct) and *metascutal* (metasct) tufts being present. The last is composed of hairlike, white scales. The abdomen is untufted except for a slight, transverse first *abdominal tuft* (It). The rest is generally clothed with dense, imbricated, normal, self-colored scales. The vestiture of the ventral side of the thorax and legs is typical of most noctuids, being generally scanty and composed of linear scales basad on the legs and on the body, and dense, imbricated, medium, spatulate scales distad on the legs.

Male genitalia (Figs. 5a-e). Abdominal segment VIII, because of its proximity to the genitalia and because its tergite and sternite have special patterns of sclerotization, is usually considered with the genitalia. In *B. rugifrons* the *tergal sclerotization* (VIIT) is V-shaped and the *sternal sclerotization* (VIIS) U-shaped.

The genitalia proper are joined to VIII by a long, loose intersegmental membrane and are composed of many varied elements of great taxonomic value. The dorsal *tegumen* (tg) is united laterad on each side with the ventral *vinculum* (vin) by a small, incompletely separated, slightly sigmoid sclerite, the *pleurite* (pl) (homologous with pleurite of Forbes ?); the whole complex forms an oval ring through the center of which passes the intromittant organ, the phallus. The phallus is composed of a strongly sclerotized, cylindrical *aedeagus* (ae) in which the inverted *vesica* (ves) normally lies. The latter is everted and inflated during copulation and bends at a right angle (dextrad) to the aedeagus. It has many long slender spines, the *cornuti* (cn) of the *primary group* (pg), on its ventral surface. A short, secondary row of small cornuti, the *secondary group* (sg), is situated in the angle of the vesica. The phallus is supported in the membrane between the tegumen and vinculum by a ventral, shield-shaped *juxta* (jx) and a dorsal pair of twin, seculate sclerites, together termed the *anellus* (anel).

Articulating with the dorsal *neck of the tegumen* (ntg) is the *uncus* (un) which bears numerous short setae. The former is limited in extent cephalad generally by the furcation of the lateral portions of the tegumen and caudad by the base of the uncus. The ventral end of the vinculum is enlarged cephalad and folded inward to form the *saccus* (sac).

The rectum also passes through the ring formed by the tegumen and vinculum and protrudes caudad as the *tuba analis* (ta). The sclerotizations in the latter, termed the *scaphium* (sca) (dorsal) and *subscaphium* (ssca) (ventral) are weakly developed in the Stiriini.

Articulating with the vinculum and juxta on either side are a pair of large, flat, clasping structures, the *valves* (val). Each valve has a complicated inner structure with several elements. The homologies of these elements are not yet known; therefore I use a noncommittal descriptive terminology here,

dividing the inner surface of the valve into three basic areas: (1) a narrow, dorsobasal *costa* (cos), a ventrobasal *sacculus* which is broken into a *basal division* (bsl) bearing a *basal lobe* (blbsl), and a *distal division* (dsl) bearing both a weak *basal lobe* (bldsl) and a spinelike *distal lobe* (dldsl) and (3) a distal, undifferentiated area bearing a row of stout setae, the *corona* (cor) at its margin.

Female genitalia (Figs 5f-g). Most of the components of the female genitalia of *B. rugifrons* are typical of only the most advanced stiriine types. The *ovipositor lobes* (ovlb) are pointed, well sclerotized, convex and elongate. Each of the pleura of segment VIII has a large, median, elongate, V-shaped unsclerotized area. The ventral margins of the pleura are deeply folded under ("strongly deflexed") cephalad, arch laterad around the depressed *lamella postvaginalis* (lpv) and connect with the *lamella antevaginalis* (lav). These structures are associated with each other and with the *ostium bursae* (ob) or mouth of the long, narrow *ductus bursae* (dbu) and, when viewed ventrally, appear as an integral, structural complex which, for convenience, is here termed the "sterno-ostial concavity." This area is characteristically ovoid in *B. rugifrons*.

The ductus bursae is ribbed and heavily sclerotized and expands into the large, saclike *corpus bursae* (crpbu). The sclerotization and ribbing of the ductus bursae continues onto the posterior third and posterior *lobe* of the corpus bursae. Leaving the apex of the lobe is a fine membranous duct, the *ductus seminalis* (dsm). The *postapophysis* (pap) and *antapophysis* (aap) are long apodemes running cephalad from the ovipositor lobes and VIII, respectively. They serve as places of attachment for the muscles which retract the genitalia.

ANALYSIS OF RELATIONSHIPS

Since there are no known fossil Stiriini, I have had to infer the tribe's internal phylogenetic relationships entirely from the available attributes of the modern forms. Unfortunately, these attributes consist only of the adult integumentary anatomy and scant bits of ecological and geographical information. On this basis, only a rough, general idea of the internal relationships of the tribe's members can be formulated, but one which is sufficient to serve as a foundation for a preliminary definition and classification.

The general procedure of phylogenetic analysis which I used is based on the traditional comparative method and will not be detailed here, being abundantly discussed and exemplified elsewhere (Cain and Harrison, 1958, in part; 1960; Simpson, 1961:Chap. 3; Ross, 1956).

A statistical (so called "objective" or "quantitative") treatment was attempted experimentally, however. The method tried was designed mostly after that employed by Hardwick (1958:20-25) and partially after that of Michener and Sokal (1957). Many such methods are now being developed for use in taxonomy (see Sokal, 1961, and papers listed by him). They may be very useful in *indicating* patterns of similarity and dissimilarity but cannot be regarded as absolute measuring devices or indicators of true phylogenetic relationships in any sense. I found them unsatisfactory in the present study for the following reasons (see also the criticisms of Inger, 1958:370-373):

a. It was impossible to be truly objective in deciding what were unit characters and in breaking them into classes. As I gained experience with the group, I tended to vary in my evaluation of these factors.

b. Characters did not break down into an equal number of states³ so that their comparison directly was invalid because characters having few states would carry more grouping weight than characters having many. Furthermore, and most importantly, it seemed fundamentally inconsistent with generally accepted theory on the varying rates and processes of evolution to consider taxa equivalent and measurable in any mathematical sense.

c. In trying to be objective, I had to leave out much useful phylogenetic information such as obviously degenerate character states, primitive states, adaptive characters, etc. An attempt has been made by Cain and Harrison (1960) to integrate such data into statistical measurements of affinities (leading to a natural but not necessarily phyletic classification), but it seems futile to go to such efforts in view of the dubious foundation.

d. The resulting arrangements were illogical in places, certain forms being unduly approximated on the basis of a large number of adaptive or spurious character states in common (*e.g.*, size, cryptic colors, valve lobe shapes, shapes of frontal protuberances, etc.), while more important but fewer characters (particularly the sterno-ostial complexities of segment VIII of the

³The term "state" (= "character state") is used throughout this paper to mean a particular condition or single variant of a varying quality of a structure, *ie.*, a "character." To clarify with an example: *red* may be a state of the character *color*.

female) received too little emphasis and allowed obviously related forms to be too greatly separated. These results may be due to the nature of the material, perhaps always coming about in compact, geologically recent groups in which adaptive traits are numerous and diverse and basic characters are few and stable (Noctuidae, Lepidoptera, Chiroptera, birds?).

Results of the analysis

There are 100 stiriine species recognized in this study. This is such a large number from the standpoint of phylogenetic manipulation and so many are poorly known that I decided early to leave their detailed phylogeny and systematics to later studies and to work only on higher levels.

The species may be grouped on two levels. The first (lower) is composed of groups whose included forms are so extremely similar that they are undoubtedly very close relatives, taxonomically perhaps superspecies or species groups (as I call them in my classification), or even elements of polytypic species. My judgment is entirely empirical at this level but probably reliable in producing truly monophyletic units. Several isolated species which are not similar enough to any other to form a combined unit are treated as units of their own on the same level as the others.

Thirty-one such units were formed; they are listed with their constituent forms in Table 1. Four of these are composed of a single species, each of which is known from only one sex and so divergent from the other units or poorly known that its relationships are obscure. These are the "atypical" species mentioned in the section on the definition of the tribe. They were excluded from the phylogenetic treatment but are given summary treatment in the classification.

The above units may be further grouped into broader, roughly equivalent, monophyletic groups or phyletic units of a higher level. There are seven such units which are listed with their constituents in Table 1.

Commensurate with the general principle followed in this presentation that all classification should follow phyletic inferences, phylogenetic terminology is used exclusively in the discussion that follows. In this respect, I call the lower level, close groups of forms "primary phyletic units" (listed by Roman numerals) and the higher level groups of these, "major phyletic lines" (listed by Arabic numerals). For reference and clarity, however, I give the later applied taxa names in parentheses following citation of a phyletic unit.

The immediate phylogenetic relationships of the primary phyletic units are first discussed. Then the major phyletic lines of the tribe, represented by monophyletic groups of primary phyletic units, are treated likewise after a few remarks on the value of certain characters. Both are summarized at the end in the form of phylogenetic diagram (Fig. 1).

Relationships of the primary phyletic units. Units I-X are only a generally similar group. There is much variation in the shape of the frontal protuberance, position and shape of the valve lobe, shapes of the female ovipositor lobes, bursae copulatrix, etc. Most structures of the male and female genitalia

as well as the almost universally similar noctuiform wing pattern, however, indicate unity. With the possible exception of units IX (*Plagiomimicus psamathochromus* and *argyropolius*) and X (*P. phalaenoides*), which may form a small derivative group of their own on the basis of the double-lobed, distal sacculus division, all the units form a diverse, but probably monophyletic major phyletic line (1).

There are several character states possessed by unit I (see character complexes, A-D, next section, for basis) which indicate that it is the most primitive of this line, indeed the most primitive stiriine unit of all. Not only the other units of this line but probably also all subsequent major phyletic lines stem from moths most like those of unit I.

Unit II (*P. laodamia*) is very similar to unit I and probably only a recent derivative of it. The few main different character states are obviously only slightly modified versions of their more primitive counterparts in unit I or are of little significance: (1) the pointed, upcurved ovipositor lobe still shows strong striae and is partially unsclerotized and flat like that of unit I; (2) the distally displaced valve lobe is still quite similar in shape to the central lobe of unit I and resides on an only slightly more angular and broader valve whose other features, e.g., well developed corona, small finger-like basal sacculus division lobe, are the same; (3) the single, conoidal lobe of the bursa copulatrix, instead of two secondary lobes, is hardly significant since comparable differences occur sporadically throughout the tribe.

Units III-V (*P. spumosus* and allies, *P. pityochromus* and allies, and *P. tepperi*, respectively) are all independent but more extreme derivatives of I. Their morphologies are equally diverse (V is somewhat more peculiar) so it is impossible to infer the order of their derivation.

In spite of the somewhat extreme and diverse natures of units III and IV they grade together almost completely through primitive unit I. The grades are so numerous that only the best defined will be mentioned:

1. Between I and III: The single valve lobe of I shows a gradual lengthening and increasing curvature and migration basad through many of the members of III. The sequence begins with a very short lobe similar to that of *ochoa* (unit I) in *P. jalada*, proceeds through the slightly longer, more curved and basally displaced lobes of *manti*, *corozona*, *astigmatosus* and *dimidiatus* and ends with a very long, curved basal lobe in *spumosus*. A progressive broadening of the valve, reduction in the number and stoutness of the coronal setae and decreasing length of the basal sacculus division parallel the behavior of the lobe.

2. Between I and IV: The spinelike valve lobe of unit I shows a sequence of increasing spine shape and migration distad through the species of IV. The lobe of *expallidus* is most like that of I, being short, rounded and situated fairly near the base of the distal sacculus division. The lobe of *pityochromus* is more spinelike and distal, and that of *concinus* is quite spinelike and located far distad.

In many of its character states, the single species of unit V is peculiar.

The combination of states, noctuiform forewing pattern, simple VIII segment in the female genitalia, and the single median lobe of the male valve seems to place it best near the foregoing units, I, III and IV. However, most of its states are so strongly modified from those of the latter two units that the species is not detectably a derivative of either of them and even somewhat uncertainly of primitive unit I. For the present, I tentatively consider this unit equivalent with III and IV as independent derivatives of the ultimately primitive line represented by I.

I am even more dubious about the status of units VI (*P. hutsoni* and *olivalis*), VII (*P. hachita* and allies) and especially VIII (*P. alessaea*). The first two have many characters in common, e.g., circular unsclerotized areas in VIII pleura in the female; similar, simple ostial regions in the female genitalia; elongate valves with a small, broad, distal lobe in the male genitalia, etc., but their facies vaguely and inscrutably dissent throwing doubt on the homology of these characters. VIII is even more distinct: the valve lobe is set far distad, almost off the edge of the valve and is a strong spine; the wing pattern is completely absent, and the secondary group of cornuti on the vesica is absent, a few enlarged spicules on the sinistral inflation being present instead. Considering the general level of organization of the female genitalia, i.e., of the most primitive type (see next section) and the equally diverse other peculiar character states, I tentatively place these units in a roughly equivalent status as derivatives of the main ancestral stem of major phyletic line 1.

Units IX (*P. argyropoliis* and *psamathochromus*) and X (*P. phalaenoides*) are very similar. The latter unit has a few slightly peculiar features, e.g., (1) oblong, doubly narrowed valve instead of a broad valve with a strongly angled or produced distoventral corner, (2) distal lobe of the distal sacculus division rounded and with minute denticles at the tip instead of spinelike and (3) very few cornuti. These states are clearly variations of their more generalized counterparts in unit IX. Because of the type of female genitalia (most primitive type; see next section), I place them near the rest of the units of major phyletic line 1, but consider them of special derivative status because of the double lobed distal sacculus division. This condition is prophetic of the bilobed condition of most of the higher Stiriini. Therefore, I consider units IX and X as representative of the section of the ancestral stock of line 1 which gave rise to the rest of the tribe. This special position prompts me to consider these units as a second (2) major phyletic line.

XI (*Chrysoecia scira* and allies), XII (*C. dela* and allies, subspecies ?) and XIII (*Gorgora morga*) superficially appear to be very different units. In fact, they are so different at first inspection that the latest classification prior to the present one put them in three widely separated genera. The last unit, containing the single peculiar species *Gorgora morga* was even placed in a different subfamily, the Acontiinae.

The nearly identical female genitalia of these units, however, indubitably unite them as major phyletic line 3. Other subtle but probably significant similarities are also present: (1) the zigzags in the courses of the PM lines of

XI and XII (see especially *scira* and *atrolinea* where these lines are well developed) are almost identical; (2) the orbicular spot has a tendency in all (especially XIII) to enlarge rectangularly; (3) the thoracic vestiture is "hairy"; (4) the lunules of the forewing are usually marked; (5) the cornuti of the male vesica are diminutive centrally (not so in *scira*, however), etc.

Although XI may be somewhat more primitive than the other units of this line in the better developed noctuiform wing pattern, most features are equally diverse so the units are best considered equally divergent.

Unit XIV (*Chichimeca*) is distinct from all other units by its preponderance of degenerate character states, e.g., (1) the tiny distal sacculus division lobe (this is quite similar to a parallel degenerate state in unit XXI of major phyletic line 5, but is so withdrawn that its homology with other distal sacculus lobes is indeterminable); (2) the sclerotization and ribbing of the posterior region and lobe of the corpus bursae is obsolete and (3) the wing pattern is completely absent. Therefore, I consider this unit as an autonomous major phyletic line, 4.

Units XV-XXI (*Cirrhophanus*) are another diverse, large group like major phyletic line 1 but their unity and intragroup arrangement is much clearer because of numerous, fairly continuous intergradations. This group comprises major phyletic line 5.

The most probable primitive unit is XV (*C. chryseochilus*) which still retains a fairly complete noctuiform wing pattern. This pattern is disrupted by a secondary pattern of longitudinal streaks (mainly from darkened wing veins), which is characteristic for most other members of the group, especially in the most immediate derivative, unit XVI (*C. triangulifer* and allies).

One species in the latter unit, *C. triangulifer*, shows a character state which especially relates it to units VII-XXI apart from other general similarities. This character is a multiple foretibial "claw." The claw, as it exists in this species, is a compact series of two or three, entirely separate, small setae which appear topologically to have arisen by a division of the usual, single large seta. In this condition, these setae resemble a commonly occurring anomaly (duplication) in the chaetotaxy of mosquitoes (and probably in most insects) which may take part likewise in their evolution and differentiation (Belkin, 1952: 129). Further evolution appears to have been for these separate setae to fuse into a heavy unit, as it is found in the remaining units, thus producing a condition superficially similar to the original one. However, the fundamental, multiple construction remains to reveal the mode of derivation and indicates the derivative status of the units possessing it.

The next five units, XVII (*C. plesioglaucus* and *comstocki*), XVIII (*C. papago* and *miaiphona*), XIX (*C. hoffmanni*), XX (*C. discistrigus*) and XXI (*C. compositus* and *hyperion*), are grouped mainly because of the common, multiple foretibial claw (this condition not personally confirmed for *C. hyperion*) but there are other features which suggest monophyly also: (1) XVIII, XIX and XX have the streaked forewing pattern, (2) there is a sequence of gradual loss of the primitive ovipositor lobe striae and elongation

and curving of the lobes themselves through the units, and (3) all have lost the basal lobe of the distal sacculus division. I have not analyzed the comparative morphology of these units thoroughly, however (this awaits the discovery of more material, especially critically in rare species like *C. hyperion* and *hoffmanni*), and therefore consider them equally derivative for the present.

Unit XVII has a very distinctive wing pattern which hardly looks like anything in related units. The structure of the female genitalia and especially the thoracic vestiture, however, indubitably relate it to unit XVI. These characters have virtually identical states in the two units in all respects, even as to color of the thoracic vestiture. The very different wing colors appear to be adaptive. There is one field observation (Jones, 1937; see "Ecology") that the yellow-orange color and streaked wing pattern typical of unit XVI has a cryptic function: It camouflages the adults which have the habit of resting on similarly colored flowers. It is possible that the wing color and pattern of XVII also have a comparable, specialized cryptic function, but camouflage these moths to differently colored flowers. Even by themselves, the beautiful wings of these moths are very suggestive of a brightly colored flower. Therefore, the very different colors involved may be easily explained by the strong selective forces and simple genetic basis which have been demonstrated as involved in comparable situations in other moths (Ford, 1955:188).

The annectant features of the single species of unit XXII (*Cuahtemoca chalcocraspedon*) are sufficient to make it a major phyletic line (6). The reasoning for this is appropriate to the next section and is discussed there in more detail under phyletic line 6.

Major phyletic line 7 is composed of units whose great similarity suggests relatively recent divergence. The line, however, divides into two sections primarily on the basis of two types of valve lobes. In the first section, containing units XXIV (*Chalcopasta territans* and allies) and XXV (*C. chalcotoxa* and allies), the distal sacculus division bears a single, basal fingerlike lobe (secondarily absent from two species in XXV). In the second section, containing units XXVI (*Basilodes chrysopis* and allies) and XXVII (*B. rugifrons* and allies), the lobe is located far distad and is spinelike.

Though marked, this dichotomy is not strong considering the topology of these states. Each lobe, when present without the other, is extremely similar in shape and place of origin to a counterpart in the double lobed condition in unit XXIII (*C. ellica*) and other lower Stirriini. It appears, therefore, that the latter is an inclusive condition immediately primitive to the two former mutually contradictory and derivative, single lobed conditions.

Though primitive in this important respect, other character states indicate that unit XXIII has probably diverged from its ancestors. Most conspicuous among these is the field of gold color (a cryptic specialization?) covering much of the noctuiform pattern of the forewing. This state and other similarities relate this unit to unit XXIV. The latter is a derivative of the former as indicated by the distal sacculus lobe condition just described and the more extensive gold on the forewing.

Unit XXV contains three species, two of which have very peculiar male genitalia. In these the valves are oddly shaped and the lobes are altogether absent (a probable degenerate condition), although a ventrally directed spur (remnant of distal lobe ?) is developed from the distal end of the sacculus. The latter is absent from one side in one species. These peculiar states and others, *e.g.*, fusiform corpus bursae and tubular, coiled phallus vesica, separate these species from unit XXIV. However, the third species of unit XXV (*C. acantha*) has normal genitalia and otherwise is similar to unit XXIV (especially to *C. restricta*) and connects the two units.

The two remaining stiriine units, XXVI (*Basilodes chrysopis* and allies) and XXVII (*B. rugifrons* and allies) are extremely similar. The latter has a somewhat peculiar wing pattern but this is obviously a simplified version of the former's primitive noctuiform type: AM and PM lines traverse the same paths in detail (note particularly the sharp angles of the AM line basad, and of the PM line distad, at vein 1A). The area between these lines is brown in *B. chrysopis* of unit XXVI and remains so only in the inner area in most species of unit XXVII forming a characteristic hexagonal or square macula. A tiny dark dot in the reniform of these two forewing types further reveals the relationship.

Relationships of the major phyletic lines. As a basis for the discussion of the relationships themselves, a few preliminary remarks are necessary regarding the value of certain stiriine characters to higher intratribal phylogeny.

Most morphological characters of the Stiriini show either such great uniformity or extremely diverse variation that they offer no clues to an inference of major phylogenetic trends or relationships. There are relatively few conservatively varying characters showing fairly consistent correlation and patterns of parallel variation throughout the tribe as a whole so that they can be taken to reflect a picture of overall evolutionary history. In the main, I have found only the following characters and character complexes (A-D) to have application in this respect.

(A) Forewing pattern. This, the most frequently used discriminating character complex in the Lepidoptera, is usually considered of dubious phyletic value because it is so subject to homoplasy and extreme variation resulting from relatively minor genetic alterations. I find, on the contrary, that the forewing pattern can be of great usefulness, at least in the Stiriini, in determining relationships if carefully analyzed. In the first place, although independently derived states of this character may come to resemble each other superficially, their usual great complexity never permits them to do so in every minute detail. Close inspection almost always reveals fundamental differences. In the second place, regardless of the degree of specialization attained by some states, primitive elements usually persist to reveal true relationships.

The generalized noctuid pattern (noctuiform) has been worked out in detail. AM and PM transverse lines, apical patch, and orbicular and reniform spots are all very stable elements of the noctuiform pattern. They show considerable qualitative variation but their presence together is quite constant in

most Noctuidae. The presence of these states may therefore be considered primitive for the Stiriini.

The noctuiform forewing pattern is rather fully expressed in several units. The genus *Plagiomimicus* is characterized by it, even though a few primary phyletic units show considerable modification from the noctuiform condition: (1) unit VII (*hachita* and allies) has lost the reniform and orbicular spots and apical patch but retains the transverse lines; (2) VIII (*alesaea*) has lost all traces of any noctuiform elements, an obvious degeneration; (3) the pattern of VI (*olivalis* and *hutsoni*) is very much diffused and the spots are missing but the basic transverse line pattern is still manifest.

The noctuiform pattern is retained in a few units of each major phyletic line suggesting that they are relicts of the primitive stock of their respective lines: (1) XXII (*Cuahtemoca chalcocraspedon*). This unit has, in addition, a tarnished, metallic luster prophetic of the brilliant gold of still higher units, especially XXIII-XXV (*Chalcopasta*). (2) XV (*Cirrhophanus chryseochilus*). The pattern of this unit is similar to that of XXII but is disrupted by a secondary, lined or streaked pattern which is further modified in its derivative units in the same genus. (3) XXIII-XXV, especially XXIV (*Chalcopasta ellica*). These still show vestiges of the noctuiform pattern in spite of an extensive influx of brilliant gold. (4) XVI-XVII. The well developed noctuiform pattern of unit XXVI (*Basilodes chrysopsis* and allies) is probably closest to that of its own ancestors and those of its closest relatives, units XXIII-XXVII (*Chalcopasta* and *Basilodes*). Some variants (*B. pepita*, *chrysopsis*) show somewhat bronzy lusters or limited, diffuse, golden areas slightly more brilliant than the tarnished luster of unit XXII (*Cuahtemoca*) and inclined towards the obviously highly specialized condition in unit XXIV (*C. territans* and allies) where brilliant metallic gold is the predominant wing color masking most of the noctuiform elements.

(B) Male genitalia. The taxonomic value of this complex of structures in the Lepidoptera has been abundantly discussed elsewhere. Unfortunately, many opinions are based on speculations of the functional significance of the various elements and not on experimental evidence. For this reason, they should be taken with reservation. The recent studies of Callahan (1958) and Callahan and Chapin (1960) should help to remove some of these speculations. These authors have admirably demonstrated the mechanism of the phallus and bursa copulatrix in a few unrelated species from which some reliable conclusions can be drawn regarding variations in these structures. For example, there is obviously a very definite correlation between the shapes of the phallus vesica and the bursa copulatrix as well evidenced by their intimate interposition during copulation. One would expect these characters to vary rather conservatively, therefore, since major variations in one would require major concordant variations in the other—statistically unlikely—to retain reproductive success.

Like most stiriine structures, the male genitalia are either too constant (e.g., shape of vesica, distribution of cornuti) or sporadic (shape of uncus,

shape of basal sacculus division lobe) in variation to be of much general phylogenetic significance. I have found only three characters with states of value in this regard: (1) presence or absence and shape of lobes of distal sacculus division, (2) length of tegumen neck and (3) presence or absence, number and shape of coronal setae.

The interpretation of the first of these is complicated by the dubious homologies of the various states. Various fingerlike and spinelike lobes occur on the distal division of the sacculus, but their positions are varied and inconsistent within groups. Thus it is impossible to trace fully the changes that have occurred. Only in the higher Stiriini where their detailed shape and place of origin are constant, and in certain other groups where the various states grade together, are the lobes of undoubtedly homology.

Probably, a single, fingerlike lobe of the type found in unit I (*Plagiomimicus ochoa* and *resolutus*) of the first major phyletic line is the most primitive. It greatly resembles in shape and position the lobe of related *Nocloa* and allies and to a great extent many Heliothidini and Oncocnemedini (these two tribes may be fairly closely related to the Stiriini). The single lobe in the other units of the same line probably corresponds to it even though it varies in shape and position a great deal.

A second lobe was subsequently acquired (morphological source unknown) by higher Stiriini and persisted with the former as an intermediate primitive state from which several unlobed degenerations subsequently occurred.

The length of the tegumen neck shows a trend of variation generally paralleling that of other characters (to be discussed) and in this respect is probably phylogenetically significant. In units I-X (*Plagiomimicus*) the neck is extremely short and erect like the condition in most related noctuids. This state therefore appears to be primitive. Increasing length and recumbence, especially well expressed in units XV (*Cirrhophanus chryseochilus*), XXII (*Cuahtemoca*) and XXVI-XXVII (*Basilodes*), is a derivative trend.

A final male genitalic character showing one probable primitive state concerns the presence or absence, number, shape and distribution of the coronal setae of the valve. The Acronyctinae normally have a well developed, even row of stout coronal setae along the entire distal edge of the valve. On the basis of prevalence, this state would appear to be primitive for the subfamily and likewise for the included Stiriini.

(C) Female genitalia. In inferring the relationships of the major phyletic lines I have placed the greatest reliance on characters of the female genitalia, especially those of the pleura, sterno-ostial region, *i.e.*, ventral pleural margins and sternum of segment VIII, and the ostial lamellae. Lesser reliance was placed on characters of the ovipositor lobes. The several elements of this structural complex coordinately show a sequence of increasing complexity in the lines from one to the other. This sequence is so logical topologically and completely intergrading that it is likely a valid indicator of the actual evolutionary progression of the tribe.

Basically, the sequence is as given below. A few units of each line may show parallel, secondary modifications, of course, *e.g.*, declining ventral margin of VIII pleuron, pointed ovipositor lobes, but most units, especially the more primitive ones, exemplify the sequence stages well.

In the simplest, initial condition in line 1 (Fig. 7k), the pleura of abdominal segment VIII are completely and evenly sclerotized and confluent with the sternal region, their ventral margins not being defined. No special, complex sterno-ostial concavity is present, therefore. The lamella postvaginalis is not a discrete sclerite. The latter is represented only by an extended sternal area, which, with the 1. antevaginalis, forms a simple ring around the ostium bursae.

In line 2, obviously secondarily modified lamellae (forming a sclerotized chamber, Fig. 14k) obscure the arrangement to some degree, but there are essentially no changes, the separation of this line being based on male genitalic characters (see below).

Line 3 exhibits the first logical step towards greater complexity in these structures (Fig. 16k). An elongate median area in each of the pleura of VIII becomes unsclerotized (strong striae still remain to suggest an intermediate stage in a desclerotization process). Still, no special, complex sterno-ostial concavity is present but the ventral margins of the pleura become sharply defined though remaining undeflexed and partially contiguous. The lamella postvaginalis becomes a vaguely defined sclerite separate from the rest of the sternum (now largely membranous) and fills the space between the cephalically diverging ventral pleural margins. The lamellae now are proper sclerites but still ring the ostium bursae simply.

Plagiomimicus resolutus of unit I of major phyletic line 1 shows an inclination towards the above condition, more so than any other member of the line.

The pleura of VIII themselves are essentially unchanged in line 4 (*Chichimeca*) but their ventral margins become slightly deflexed (underfolded), entirely separated, and divergent cephalad (Fig. 19k). The lamella postvaginalis enlarges and fills the area between the diverging margins of VIII. The lamella antevaginalis is reduced but forms a slightly bowed ring around the ostium bursae with the 1. postvaginalis. Thus, an ill-defined sterno-ostial concavity is formed.

In line 5 (*Cirrhophanus*) greater complexity appears (Fig. 21k). The pleura of VIII themselves are still essentially unchanged with large, elongate, unsclerotized areas containing striae (these are lost secondarily in some units of this line) but their ventral margins separate even more and become more deeply deflexed (or secondarily strongly declining). The sternum of VIII becomes a depressed, oval area, as viewed ventrally, with a well defined, oval lamella postvaginalis situated between the pleural margins and the lamella antevaginalis forming a bowed ring around the ostium bursae with the 1. postvaginalis.

The sterno-ostial concavity may be considered well developed in the preceding line but not so completely as in the most advanced stiriine lines, 6 (*Cuahtemoca*) and 7 (*Chalcopasta* and *Basilodes*). Here, these structures reach

their ultimate modification (Figs. 26k, 30k). The ventral margins of the pleura are well separated and greatly deflexed and curve out around a well defined, variously shaped (usually transverse, semilunar or ligulate, with an eroded posterior margin) lamella postvaginalis. The latter forms a strongly bowed ring around the ostium bursae with the lamella antevaginalis. The unsclerotized areas of VIII pleura remain but usually completely lose their striae (weakly manifest in some).

Changes in two other characters of the female genitalia generally parallel this sequence. One concerns a very minute and sometimes obscure feature, *i.e.*, striae on the ovipositor lobes and in the unsclerotized areas of VIII. The other concerns the shape of the ovipositor lobes.

The ovipositor lobes are blunt, short and flat, and have well developed striae in line 1, which has a simple sterno-ostial region. They remain generally so in the lines with slightly more complicated ostial regions and completely sclerotized VIII pleura, but become pointed, long and convex and without striae in the most derivative units although these may be retained in some cases (*e.g.*, unit XVI of line 5). There is an intermediate phase wherein the lobes are only slightly convex and the striae are reduced in number and strength (units XXII, *Cuahtemoca chalcocraspedon*, and XV, *Cirrhophanus chryseochilus*). These units also show similar weak striae in the unsclerotized area of the VIII pleura, indicating the transitional phase between the condition where an unsclerotized area is present with strong striae and with blunt lobes, and the condition where an unsclerotized area and pointed lobes are present but no striae remain in the former.

The flat, blunt lobes are topologically (and functionally ?, see next paragraph) closer to the general noctuid type, *i.e.*, soft membranous pads, than the pointed lobes, and therefore probably are more primitive.

I might speculate on the function of the heavily sclerotized, pointed lobes. Their shape and rigidity suggests that they are used by the female moth to insert eggs in some confined space, perhaps between flower petals (the known larvae are flower feeders) or in the soil or bark crevices for protection against rigorous desert conditions (most species range in arid regions). If such is the case, this state is to be considered a derivative specialization since most noctuids deposit their eggs in general open situations.

(D) A final obscure, but probably phylogenetically significant structure, the scutal phragma, shows a trend in the same direction as those discussed above. In line 1, this structure is somewhat keel-shaped, projecting moderately into the thoracic cavity. This is closer to the type found in most noctuids (a very strongly keeled and strongly projecting apodeme) than to the type in the more advanced Stiriini (a barely projecting low ridge); therefore, it is likely to be primitive.

In light of the foregoing considerations, the phylogenetic relationships of the major phyletic lines of the Stiriini appear to be as follows:

The most primitive major phyletic line is number 1 (most of the genus *Plagiomimicus*) as indicated by its preponderance of primitive states: (1) well

developed noctuiform forewing pattern, (2) very short, erect tegumen neck, (3) well developed corona, (4) moderately keeled scutal phragma, (5) simple sterno-ostial region, (6) completely sclerotized VIII pleura which are confluent with the sternum, and (7) flat, blunt ovipositor lobes with well developed striae.

Only one primary phyletic unit of this line, however, possesses all of these states: I (*P. ochoa* and *resolutus*). The remaining units are independent derivatives not on the main line of tribal evolution and show various special modifications of all these primitive states, except those in segment VIII of the female genitalia. Subsequent major lines probably stemmed from moths most like those of unit I.

Major phyletic line number 2 is distinct from 1 only in one significant feature, a double, instead of a single lobed distal sacculus division. This feature could be an independent acquisition but in view of the great similarity in shape and position of these lobes with those of the many remaining higher Stiriini in which they are double (especially units XVI: *Cirrhophanus dyari* and allies and XII: *Chrysoecia dela* and allies), it appears that this line represents the section of line 1 which gave rise to all the more derivative major lines.

As indicated by the only slightly more complex female genitalia and similar double lobed, distal sacculus division, major phyletic line 3 (*Chrysoecia* and *Gorgora*) is the closest relative and a derivative of line 2. The noctuiform pattern and most other primitive states are strongly modified in all the members of this line. No unit therefore can be considered relictual.

As mentioned in the preceding section, major line 4 (unit XIV: *Chichimeca*) is distinctive and degenerate in most character states. The female genitalia, however, are of a type most similar to that of line 3 but slightly more complex. The line, therefore, appears to be the closest derivative of that line.

Major phyletic line 5 is large and diversified, most units being rather specially modified. However, there are two units (XV and XVI) exhibiting several other primitive states whose level of female genitalic complexity (see above) situates them as immediate derivatives of line 4 and primitive to the remaining Stiriini.

The wing pattern and shape of the single species of line 6 (*Cuahtemoca chalcocraspedon*) is strikingly similar (even to scattered blue scales) to that of one species (*ochoa*) of the most primitive stiriine unit, unit I. The female and male genitalia of this line, however, are quite advanced and of the type found in line 7 (*Chalcopasta* and *Basilodes*). Furthermore, the forewing is perfused with tarnished gold of a shade similar to one species in unit XXVII (*Basilodes pepita*). The gold resides in the basal and distal sectors and reniform and orbicular spots almost exactly like the brilliant gold of unit XXIII (*Chalcopasta ellica*).

The line, therefore, may be considered an annectant relict representing closely the ancestral stock derived very early from line 5 which gave rise to the remaining, most advanced line 7.

Units XXIII-XXVII (*Chalcopasta* and *Basilodes*) of line 7 are without

question the most highly advanced Stiriini. This is indicated mainly by the complex female genitalia which represent the derivative extreme of the sequence of variation in these structures. In addition, the tegumen neck is quite long (not so extreme in *Chalcopasta* except in primitive *ellica*) or very long and arched and the ovipositor lobes are completely without any trace of striae (except in *ellica*). The noctuiform forewing pattern and corona are still fairly well developed in most species, however. The former shows at least partially from beneath the secondarily acquired gold masking colors.

DEFINITION OF THE TRIBE

Description of Adults

General. Facies robust. Size small to medium large. Colors predominantly brown, grey-brown, orange-yellow and brownish-yellow, a few forms white and metallic gold. Integument moderately sclerotized in most, darkly pigmented in some. Sexes similar, female slightly larger than male.

Head. Size medium. Frons with large, heavily sclerotized protuberance of varied but basically characteristic shape and composition, *i.e.*, raised outer, circular or ovate ring with a secondary central, subcentral or ventral conical or broad elevation; a few atypical but easily derivable types, *e.g.*, deep smooth crater without any central elevation, rectangular, rough plateau without central depression, or transverse trough with lower external node. Clypeal shelf strong, prominent. Proboscis fully developed, apex unmodified except for normal sense organs. Labial palpus moderately long, approaching or moderately exceeding frons and slightly upcurved; apical segment short to very short (nearly spherical), penultimate segment and basal segments usually subequal, former rarely somewhat longer or shorter than latter. Eye large, globoid and naked, without lashes. Ocelli present. Antenna simple, filiform or slight serrate, sparingly ciliate. Cervical sclerite with propleural arm very short.

Thorax. Large, cuboid. Lamella of prodiscrimen shallowly to moderately emarginate; parapatagia weakly sclerotized. Mesoscutum and mesoscutellum strongly convex; lateropostnotum moderately projecting internally; horn of spina well developed. Other sclerites and sutures typical of most Acronyctinae, very constant in shape and position.

Legs. Foreleg short; tibia very short and stout, shorter than or subequal to first tarsal segment, bearing strong, heavily sclerotized apical "claw" composed of a spinelike or shovel-shaped, single, stout seta or several apically fused setae; "claw" bearing apex of tibia often produced and strongly angled. Rest of foreleg and mid- and hindlegs moderate in length; tarsi with numerous sharp plantar bristles (rarely blunt tipped), arranged roughly in three rows, lateral tarsal bristles usually short; unguis small. No "spines" on mid- and hindtibiae; spurs well developed, normal.

Wings. Forewing elongate, triangular; apex acute to nearly a right angle, tornus obtuse, latter sometimes with small fringe tooth, both sharp or smoothly rounded; margins straight or slightly convex, outer margin entire, crenulate in some. Pattern and colors varied, basic noctuiform elements primitively present but suppressed or totally obscured in cryptic and degenerate, derived forms; when former, PM line sharply angled distad beneath apical patch, projecting through ST line; AM line oblique, straight or slightly angled over cell Cu; dashes absent; orbicular and reniform usually fairly well developed; subreniform and claviform absent; median shade always reduced and displaced distad. Hindwing normal in shape; pattern lacking except for faint exterior line, varied in color, usually white, brown or fuscous. Frenulum of female with three free

setae, of male with several fused setae. Venation of both wings of normal trifold type.

Tympanal complex. Generally simple. Epaulette weak, nodular. Pockets all present: I and II nearly vertical, strong, with broad orifices; III weak in some, varying in position from close to IV to close to II; IV large, with small to large orifice. Bügel absent. Anterior tendon plate large. Posterior tendon plate greatly reduced, a narrow strip. Scutal phragma also greatly reduced, a long, low or slightly lobed, hanging flap. Countertympanic cavities moderate in size, ovoid. Hood small, undivided, inclosing spiracle I. Alula small.

Abdomen. Short, stout at base, strongly tapering caudad. Abdominal furca moderately deep, slightly hooked at tip. Small accessory abdominal furcae developed in other basal segments. Sternites and tergites well sclerotized and arched. Brushes absent.

Vestiture. Generally rough. No special hair pencils, scale patches, etc. (except in male, a short, transverse patch of linear scales in base of U-shaped sternal sclerotization of abdominal segment VIII). Head, including palpi, with dense, deep, close and pure vestiture, composed of small to medium, spatulate, dentate, evenly-colored scales. Dorsum of thorax with dense, deep, spreading and pure or mixed vestiture, composed of elongate spatulate or linear, self-colored or distally dark scales (except for white tips); with following tufts: rounded or transverse patagial; spreading and often strongly erect regular; slight anterior mesoscutal in some; strong posterior mesoscutal, sometimes lateral mesoscutal and other small extra mesoscutal tufts present; loose spreading metascutal; all tufts poorly developed in many. Venter of thorax with scanty, shallow, loose and mixed vestiture, composed of medium spatulate and very long linear scales and hairlike linear scales. Legs with dense, deep, compact and mixed vestiture composed of linear, elongate and medium spatulate scales basad and dense, shallow, imbricated scales distad. Abdomen with shallow, rich, imbricated and pure vestiture, composed of evenly colored normal scales; untufted except for slight, transverse tuft on TI.

Male genitalia. Tegumen broad or somewhat narrow, unlobed, with short erect to long curved neck. Uncus simple, cylindrical or medially swollen, straight or slightly undulate, sharply pointed apically. Vinculum equal to or shorter than tegumen, attached to latter laterad by small sigmoidally-shaped flaps (pleurites ? of Forbes); saccus short, stout or elongate, sometimes with small, anterior nipple. Valves symmetrical, simple, generally oblong in shape, parallel-sided, some with convex lower margin. Corona well developed and simple to weak or almost obsolete. Costa often broadly expanded. Sacculus divided into basal and distal divisions; basal division bearing a basal lobe, latter a low mound to a long fingerlike lobe; distal division bearing basal setose verrucae or a weak to well defined, fingerlike lobe and/or a distal spinelike or fingerlike lobe. Phallus with aedeagus well sclerotized; caecum small; vesica simple, ovoid to pear-shaped, moderately inflated and bent acutely dextrad on inflation, slight sinistral inflation in some as well; vesica armed with numerous (few in some) distal, basally-directed, long to short cornuti, usually a sec-

ondary row or patch of spinelets or denticles in crotch of angled vesica; vesica densely spiculate on side opposite cornuti. Anellus divided, with triangular, crescent-shaped or ovoid, paired, fused, approximated or moderately separated sclerites. Juxta subquadrate, kite- or shield-shaped with elongate, median rounded ridge. Tuba analis long; scaphium and subscaphium weak. VIII tergal sclerotization V- or U-shaped, arms sometimes fused and swollen caudad; sternal sclerotization U-shaped, inclosing transverse patch of long, linear scales.

Female genitalia. Ovipositor lobe partially or completely sclerotized, of two intergrading types; one thin, short, flat, and blunt, the other rigid, elongate and convex with pointed, straight or slightly upcurved tips, longitudinal striae well developed in former type, reduced or absent in latter. Postapophysis and antapophysis long, usually slender, stocky in some, subequal in length, former slightly longer than latter. Segment VIII varied, of three main intergrading types: (1) pleuron evenly sclerotized and confluent with sternum, ventral margin not defined; no special, complex sterno-ostial concavity, to (2) pleuron with large, elongate, curved, median unsclerotized area containing distinct striae, ventral margin defined evenly along entire length, not deflected, contiguous mesad or caudad with opposite margin; no special, complex sterno-ostial concavity, to (3) pleuron with a large, variously shaped, median unsclerotized area with or without striae, ventral margin defined along entire length, moderately to strongly deflexed cephalad and (with opposite margin) inclosing a depressed lamella postvaginalis and associated with it and l. antevaginalis to form a generally oval, special, complex sterno-ostial concavity. Lamella postvaginalis not defined to well defined, ligulate to circular in shape; l. antevaginalis ligulate; both lamellae usually forming a simple or bowed ring around ostium or rarely specially sclerotized and fused into a chamber. Ductus bursae moderately long, broad, usually well sclerotized and ribbed cephalad, membranous caudad, often with a quadrangular sclerotized plate in crotch of corpus bursae lobe. Corpus bursae large, a simple, ellipsoid or cudgel-shaped sac except for simple or lobulate ventral or lateral (sinistrad) posterior lobe; lobe and posterior third usually strongly ribbed and sclerotized like the ductus, remainder membranous; no signa; ductus seminalis leaving apex or outer corner of lobe.

Diagnosis

The Stiriini are defined and diagnosed in full, of course, only by the combination of all the character states listed above. There are, however, a few fairly unique and constant features which could be used as "key characters." These are (1) the extremely short, stout foretibia, (2) the single, strong, apical tibial "claw" composed of a single stout seta or several apically fused setae, (3) the frontal protuberance composed of a peripheral ring around a subcentral or ventral secondary prominence, (4) the sharply right-angled phallus, the vesica of which has a distal group of cornuti on one side and small, secondary basal group in the angle, (5) the simple bursa copulatrix with posterior third ribbed

and sclerotized like the ductus, (6) the generally rigid, well sclerotized ovipositor lobes, and (7) the rough vestiture and prominent and often erect tegular and posterior dorsal thoracic tufts. Usually several of these states occur in all species of the Stiriini and all are combined in most species.

Integrity and affinities

It is highly probable that the species included in the Stiriini (Table I), as here defined, form a natural monophyletic unit. The large number of similar and completely intergrading character states shown by its components is alone strong evidence of monophyly. The unit is so compact that it should perhaps be considered a lower taxonomic category than a tribe, possibly a supergenus or subtribe. However, the tribal status is best retained until the Noctuidae are better studied as a whole, and such categories become more meaningful taxonomically. Tribes as such are at least handy working units for comprehensive studies though not always equivalent.

The phylogenetic position of the Stiriini within the trifold noctuids (Pantehinae, Acronyctinae, Amphipyrynae, Agrotinae, Hadeninae, Cuculliinae) is uncertain. The various subfamilies in this group are presently defined on rather artificial characters, their comparative anatomy and basic relationships remaining uninvestigated. The subfamilies to which the stiriine genera are presently assigned by Forbes (1954), Acronyctinae, and McDunnough (1938), Amphipyrynae, particularly are of dubious integrity since they are largely defined by negative, superficial character states (*e.g.*, lack of mid- and hind-tibial spines, hairless and unlashd eyes). It appears certain, at least, that the tribe is a relatively specialized (fossorial? foretibial "claws" and frontal protuberance) and secondarily simplified (reduced scutal phragma, reduced posterior tendon plate and simple tympanum) phyletic unit but I can give only an opinion as to its primitive relatives based on only a few indications and by no means a comprehensive survey of the trifids.

The Stiriini seem to be derived from a generalized agrotine stock undergoing loss of mid- and hindtibial spines, reduction of foretibial "claws," scutal phragma and posterior tendon plate, and acquisition of a frontal protuberance and other specific, specialized features (wing pattern, valve lobes, ovipositor lobes, etc.). The derivation was either direct or, more likely, through intermediate phases possibly represented by the generally similar *Heliothidini* or *Oncocnemedini* which have less simplified (usually), spined mid- and hindtibiae, multiple foretibial "claws," fully developed scutal phragma and posterior tendon plate. Both of these groups have multiple foretibial "claws" which could be a primitive condition giving rise to the single stiriine "claw" through loss of all but the functionally most important terminal one and the male genitalia are simple like those of the Stiriini (valve usually with a single, simple median lobe). Furthermore, many of the *Oncocnemedini* have a phallus vesica which is angled and has cornuti much like the Stiriini.

In spite of the compactness of the tribe, there are a few atypical forms which are impossible to classify comfortably within it. Only the males of these

are known. They may be remotely primitive or derivative Stiriini or homoplastically similar species belonging to other phyletic units. I have considered them tentatively as the former since their few available character states and those of the tribe occur in similar combinations even though they are not individually identical. These species and their most conspicuous, atypical character states are the following:

1. *prepontendyta* Dyar, 1914 (*Antaplaga*). Valve broad at base, sacculus and costa very narrow, with wide membrane between. Lateral tarsal setae heavy, with blunt tips.

2. *primulina* Druce, 1889 (*Metoponia*). Frontal protuberance poorly developed, only a slight, smooth bulge on the frons.

3. *iticys* Dyar, 1914 (*Stiria*). Lobe of distal division of the sacculus (basal ?, distal ? lobe) very short, heavy and spatulate. Frontal protuberance a circular plateau with higher, rough, central elevation and dorsal, semicircular ridge.

4. *arivaca* Barnes, 1907 (*Lythrodos*). This species has stiriine characteristics as far as I can determine but it is known from only a single, holotype male which I have not been able to study in enough detail to venture anything but a guess as to its proper intratribal position (see "Classification").

There is a moderately large array of other noctuid species which show some attributes of the Stiriini. These species may represent Stiriini still more atypical than the above or may be the tribe's closest and possibly primitive relatives. They are here excluded from the tribe for lacking one or more of the most characteristic stiriine states, or for having some outstandingly non-stiriine state. For example, all forms were excluded which did not have a foretibial "claw" composed of a single, stout seta or several apically fused setae, or did have unmodified soft, padlike female ovipositor lobes. These non-stiriine character states are always associated (correlated?) with other such states which further suggests a separate integrity.

All of the species and genera mentioned in the next three paragraphs share some basic character states with the Stiriini, the most significant probably being the greatly reduced posterior tendon plate and scutal phragma. Each, however, is similar to the Stiriini in only a few character states: general stiriine facies; presence of a frontal protuberance, and foretibial "claw" (when present, morphologically a spine not a single seta or group of fused setae); simple tympanum; long, numerous cornuti on vesica of phallus, etc. The possible relationships of these forms to the Stiriini have been implied in the arrangements of various authors but have yet to be studied and elucidated fully. This whole complex of generally similar forms may constitute a phyletic group of many tribes of which the Stiriini are but one.

The genera *Nocloa* Smith, 1906, *Lythrodos* Smith, 1903, *Oslaria* Dyar, 1904, *Redingtonia* Barnes and McDunnough, 1912, *Chalcamistis* Dyar, 1916, *Ruacodes* Hampson, 1906, *Argyrhoda* Hampson, 1910, *Paramiana* Barnes and Benjamin, 1924, *Phaioecia* Dyar, 1911, and *Euamiana* Barnes and Benjamin, 1927 (and others?), include very similar species and undoubtedly should be lumped into one genus. Tarsal segments 2-4 of the short, "clawless" foreleg

are very short (nearly spherical), the foretarsal ungues are very much larger and heavier than those of the mid- and hindlegs, the phallus is straight (vesica not angled), with long, slender cornuti and the valve has a single, median lobe and a diffuse corona. "*Stibadium*" *murisca* Schaus, 1921, also belongs with these genera.

As mentioned parenthetically above, several species have a foretibial "claw" similar to that of the Stiriini. However, this "claw" is morphologically a spine (no basal alveolus) rather than a seta or group of fused setae. Therefore, the resemblance is due to homoplasy rather than homology. Other similarities are present which are probably also homoplastic. These species and their features somewhat resembling those of the Stiriini are as follows: *Fala ptychophora* Grote, 1875, frontal protuberance, female bursa copulatrix and male valve; "*Antaplaga*" *koebeli* Riley, 1893, frontal protuberance and thoracic tufting; "*Tarache*" *pyralina* Schaus, 1904, frontal protuberance, forewing pattern and wing shape; *Rolua monetifera* Dyar, 1915, and "*Xanthothrix*" *stigmatogon* Dyar, 1921 (belongs in the genus *Rolua*), and *Narthecephora pulvera* Smith, 1900, male genitalia.

Other species and genera generally similar to the Stiriini and possibly not too distantly related to them are *Tristyla alboplagiata* Smith, 1893, *Heminoctoa mirabilis* (Neumoegen, 1884), *Chamaeclea* Grote, 1883, *Azenia* Grote, 1882, *Satrapodes* Hampson, 1910, *Neumoegenia* Grote, 1882, *Ogdontia* Butler, 1891, and *Stiriodes* Hampson, 1910. None of these have an armed foretibia, however, and most have a frontal protuberance of a different type than that of the Stiriini. *Stiriodes* was included in the Stiriini by Forbes (1954) but, although the genus has something of a stiriine facies, it is abundantly distinct structurally.

Species which at some time have been erroneously included in stiriine genera in important publications are given below:

1. *aliaga* Barnes, 1905, in *Stiria* originally. It was transferred to *Nocloa* by Hampson (1910:254) where it may be left pending further study.

2. *crenulosum* Dyar, 1909, in *Stibadium* originally and by Hampson (1910:528) and Draudt (1919-1939:294). The generic status of this species is as yet undefined. It is very close to "*Stibadium*" *navium* (number 11 below).

3. *duplicatus* Smith, 1891, in *Cirrhophanus* originally and by Smith (1893:261), Dyar (1903:196), and Hampson (1910:202, questionably). This species was placed in the new genus *Phaioecia* by Dyar (1911). It is very close to *Nocloa aliaga* (number 1 above).

4. *grisescens* Barnes and McDunnough, 1910, in *Antaplaga* originally. This species is close to the genotype of *Grotella* and probably belongs in that genus.

5. *koebeli* Riley, 1893, in *Antaplaga* originally and by Dyar (1903); in *Chalcopasta* by Hampson (1910:222), Draudt (1919-1939:308) and McDunnough (1938:101). The generic status of this species is as yet undefined.

6. *melanocrypta* Dyar, 1912, in *Antaplaga* originally and by Draudt

(1919-1939:325). This species is very close to the genotype of *Grotella* and undoubtedly belongs in that genus.

7. *mina* Schaus, 1894, in *Basilodes* originally and by Druce (1889:503). It was transferred to the new genus *Satrapodes* by Hampson (1910:217) and should be left there pending further study.

8. *mirabilis* Neumoegan, 1884, in *Basilodes* originally and by Smith (1893:262), Dyar (1903:196) and Hampson (1910:208, questionably). It was segregated into the new genus *Heminocloa* by Barnes and Benjamin (1924:165-166) and is best retained there pending further study.

9. *murisca* Schaus, 1921, in *Stibadium* originally and by Draudt (1919-1939:293). It belongs with *Nocloa* and related genera (see above) in an as yet undefined generic position.

10. *nanata* Neumoegan, 1884, in *Stiria* originally and by Smith (1893:262) and Dyar (1903:197). It was transferred to *Nocloa* by Hampson (1910:255) and should be left there pending further study.

11. *navium* Harvey, 1875 (*Telesilla*), in *Stibadium* by Smith (1893:263), Dyar (1913:197), Hampson (1910:109), Draudt (1919-1939:294), and McDunnough (1938:99). It belongs with *crenulosum* in an as yet undefined generic position.

12. *philobia* Druce, 1889 (*Zatrephes*), in *Basilodes* by Hampson (1910:207) and Draudt (1919-1939:304). The taxonomic position of this species is undefined; it should be returned to *Zatrephes* pending further study.

13. *pyralina* Schaus, 1904 (*Tarache*), in *Antaplaga* by Hampson (1910:385) and Draudt (1919-1939:324). The generic status of this species is as yet undefined.

14. *pyronea* Druce, 1895 (*Grotella*), in *Antaplaga* by Hampson (1910:389) and Draudt (1919-1939:325). This species is very close to the genotype of *Grotella*, and undoubtedly belongs in that genus where it was placed originally.

15. *viridescens* Schaus, 1914, in *Stibadium* originally. It was transferred to *Oslaria* by Hampson (1910:257) and should be left there pending further study.

16. *viridifera* Grote, 1882 (*Zothea*), in *Plagiomimicus* by Smith (1891:53; 1893:264) and Dyar (1903:197). It belongs with *viridescens* Schaus (see above) in the genus *Oslaria*.

The affinities of *albigutta*, *fastigiata* and *tristriga*, described near the genus *Basilodes* by Herrich-Schaeffer (1868, Zoologisch-mineralogischer verein, Regensburg, Correspondenz-blatt 22:181) from Cuba and known only from the types until recently were in doubt. I am informed by E. L. Todd (personal communication) that they are erebines.

In the original description of her new plusiine genus *Plusiophaes*, Prout (1921:123-124) stated that the genus is probably distantly related to *Chalcopasta*. Her opinion undoubtedly derived from the fact that both genera possess similarly shaped, partly metallic gold forewings. Probably this same similarity

caused several true species of *Chalcopasta* to be originally described in the genus *Plusia*, a genus related to *Plusiophaes*. Grote's inclination to relate the Stiriini to the Plusiinae was undoubtedly prompted by these same similarities. Neither *Plusia*, *Plusiophaes*, nor any of the Plusiinae are actually closely related to *Chalcopasta*, the similarities being due without question to convergence. The convergence is strikingly great between some species, e.g., *Phytometra stenochrysis* Warren of Japan (Plusiinae) and *Chalcopasta sinuata* (Stiriini).

CLASSIFICATION

Introduction

Based on the phylogenetic inferences developed in the preceding section, which I believe are in best accord with present information, I am proposing the following classification of the Stiriini. The classification should be considered preliminary in view of the incompleteness of the phylogenetic inferences necessitated by the restricted data. It awaits further improvement when more attributes than only the adult skeletal morphology become available, *e.g.*, early stages, life histories, geographical distribution, etc.

I have made the classification particularly conservative by expanding the limits of genera both to emphasize relationships and to preserve nomenclatorial usage as much as possible without greatly affecting the approximate equivalence of taxa. Accordingly, I have recognized very few genera, proposed only two new genera (these were absolutely necessary) and refrained from applying formal names to the 31 species groups. The genera roughly correspond to the major phyletic lines. The species groups all equal the primary phyletic units.

As has been mentioned repeatedly in this paper, the Stiriini are basically a very compact and uniform series of intergrading forms. What variation there is, is very diverse and inconsistent, there being but few moderately conservative characters and many annectant situations. The latter strongly suggests recency of origin of the tribe and, possibly, hybridization.

Partly as a result of these characteristics and partly as a result of my extreme conservatism in recognizing genera, I have found it exceedingly difficult to characterize the tribe's higher categories (genera) though relatively easy to characterize its lower categories (species groups). This is a common situation with natural classifications, and a difficulty which I believe has retarded the natural classification of the Noctuidae in general. This family is outstandingly a basically uniform, superficially diverse group also. Unfortunately, superficial characters form the basis of most classifications to date.

Diagnoses and key

For the sake of expediency and ease of reference, I have expanded the following phylogenetic key to include the diagnoses of the genera and species groups. As far as possible, easily observed features of both males and females are given, the most diagnostic being first. Exceptions are common, but if the whole set of character states is utilized fairly good discrimination is ensured.

1. *Female genitalia*: Pleuron of abdominal segment VIII completely and evenly sclerotized *or* with a large indistinct but definitely oval unsclerotized area; ventral margin not defined (at least not cephalad) so that pleuron and sternum confluent. *Male genitalia*: Tegumen neck usually very short and erect. *General*: Pattern noctuiform, at least transverse lines present, never any metallic or iridescent colors, wing veins never darkened to produce a streaked pattern. Genus 1: *PLAGIOMIMICUS*. 2

Female genitalia: Pleuron of abdominal segment VIII with a median, elongate unsclerotized area; ventral margin entirely defined, separating pleuron from sternum. *Male genitalia:* Tegumen neck usually moderate or very long. *General:* Pattern varied, if noctuiform, then generally brassy or brilliant metallic gold or with areas of such color, wing veins sometimes darkened to produce a streaked pattern. 10

- 2. (1) *Female genitalia:* Pleuron of abdominal segment VIII completely and evenly sclerotized. *Male genitalia:* Distal sacculus division with two lobes or a single long, or moderately long, spikelike, or straplike basal lobe or a single strong, narrow, spinelike distal lobe. 3

Female genitalia: Pleuron of abdominal segment VIII with a large, oval unsclerotized area. *Male genitalia:* Distal sacculus division with a single, short, poorly developed, broad spinelike lobe set far distad. 8

- 3. (2) *Male genitalia:* Distal sacculus division with a single lobe. *Female genitalia:* Ostial lamellae not specially modified into a large, purse-shaped chamber or if so modified, then mouth of chamber wider than width of chamber. *General:* Forewing color varied, never with fine, brownish-gold AM and PM lines, reniform and orbicular usually strong. 4

Male genitalia: Distal sacculus division with two lobes. *Female genitalia:* Ostial lamellae modified into a large, purse-shaped chamber with mouth narrower than width of chamber (one exception, *phalaenoides*, not so modified but with forewing as follows). *General:* Forewing color light, even, silvery-grey with fine, brownish-gold transverse lines, reniform and orbicular obsolescent. 9

- 4. (3) *Female genitalia:* Ovipositor lobe with well defined striae. *Male genitalia:* Corona strong, along entire distal valve margin. 5

Female genitalia: Ovipositor lobe without striae. *Male genitalia:* Corona weak, never along entire distal valve margin, usually restricted to distodorsal tip, often curving obliquely onto inner valve surface. 6

- 5. (4) *Female genitalia:* Ovipositor lobe straight, flat and blunt. Lobe of corpus bursae with two secondary, smaller lobes. *Male genitalia:* Distal sacculus division with lobe erect, set basad. Phallus vesica slightly irregular, inflated on anterior side distad. *General:* Angulation of PM line beneath apical patch not extreme, reaching only to middle of patch.
 Species group I: *P. ochoa* & *resolutus*

Female genitalia: Ovipositor lobe curving dorsad, slightly convex and pointed. Lobe of corpus bursae simple, conoidal. *Male genitalia:* Distal sacculus division with lobe reclinate, set far distad. Phallus vesica smooth-

- ly pear-shaped, not inflated secondarily. *General*: Angulation of PM line beneath apical patch extreme, reaching to, or past, far edge of patch, almost touching outer margin. Species group II: *P. laodamia*
6. (4) *General*: Forewing multicolored, markings distinct and well developed. 7
General: Forewing white, self-colored, markings entirely absent
. Species group VIII: *P. alesaea*
7. (6) (Note three alternatives.) *General*: Frontal protuberance an oval ring with a broad lower elevation. Wing color usually predominantly brown. Orbicular spot not markedly dark. *Male genitalia*: Distal sacculus division with a basal, fingerlike, or straplike lobe, lobe sometimes quite long and curving mesad. Uncus gradually curving. Costa well expanded. Basal sacculus division very short, rectangular. Saccus slender, tapered. *Female genitalia*: Ductus bursae entirely membranous except for distinct ostial lamellae which may be modified into a chamber. Setae of ovipositor lobe long. Postapophysis and antapophysis subequal.
. Species group III: *P. spumosus* & allies
General: Frontal protuberance a circular, smooth-bottomed cup with no secondary prominence. Wing color predominantly brown. Orbicular spot markedly dark. *Male genitalia*: Distal sacculus division with a heavy spine-like lobe usually set toward distal edge of valve. Uncus undulate. Costa barely expanded. Basal sacculus division short, rectangular. Saccus slender, tapered. *Female genitalia*: Ductus bursae entirely membranous, no sclerotized chambers. Setae of ovipositor lobe long. Postapophysis and antapophysis subequal. . . . Species group IV: *P. pityochromus* & allies
General: Frontal protuberance an inverted, heart-shaped ring with lower lip produced into a conical prominence. Wing color light, with olive-green markings. Orbicular spot obsolete. *Male genitalia*: Distal sacculus division with a thin, spikelike lobe set near edge of valve. Uncus gradually curved. Costa expanded obliquely. Basal sacculus division very broad, triangular. Saccus stout, cylindrical. *Female genitalia*: Ductus bursae very heavily sclerotized and confluent with lamellae to form a bowl-shaped chamber. Setae of ovipositor lobe minute. Postapophysis almost one-third longer than antapophysis. Species group V: *P. tepperi*
8. (2) *General*: Forewing with broad, diffuse, fuliginous green AM and PM lines. ST line an indistinct, continuous shade. Integument darkly pigmented. *Female genitalia*: Ovipositor lobe elongate, bluntly pointed.
. Species group VI: *P. olivalis* & *hutsoni*
General: Forewing with well defined, thin, black AM and PM lines. ST line broken into a row of dots or absent. Integument normally pigmented.

Female genitalia: Ovipositor lobe triangular, sharply pointed.
 Species group VII: *P. hachita* & allies

9. (3) *Male genitalia:* Distoventral corner of valve produced or strongly angled. Distal lobe of distal sacculus division pointed, without minute denticles. Costa expanded obliquely. Cornuti of phallus vesica numerous (at least more than twenty). *Female genitalia:* Lamellae modified into a large, purse-shaped chamber with a narrowed mouth.
 Species group IX: *P. argyropolius* & *psamathochromus*

Male genitalia: Distoventral corner of valve not produced nor strongly angled. Distal lobe of distal sacculus division with minute denticles on rounded tip. Costa moderately expanded, not oblique. Cornuti of phallus vesica very few (less than five). *Female genitalia:* Lamellae not modified into a narrow-mouthed, purse-shaped chamber, instead, an indistinct, small chamber with a wide mouth present.
 Species group X: *P. phalaenoides*

10. (1) *Female genitalia:* Ventral margins of VIII pleura entirely and evenly defined, convex and contiguous mesad or caudad, not deflexed. Pleural unsclerotized area curved and with strong striae. *General:* A low, semi-circular ridge below frontal protuberance (above clypeal shelf). *Male genitalia:* Cornuti of phallus vesica diminutive in center of primary group (except *C. scira*). 11

Female genitalia: Ventral margins of VIII pleuron unevenly defined cephalad, approximate caudad, not contiguous. Pleural unsclerotized area curved or V-shaped, usually without striae. *General:* Never a semicircular ridge below frontal protuberance. *Male genitalia:* Cornuti of phallus vesica subequal or varying in size longitudinally, not toward center of group. 13

11. (10) *General:* Forewing predominantly orange or multicolored, discoidal macula white when present. Transverse lines usually strong, at least PM weakly evident. Plantar bristles sharply pointed. *Male genitalia:* Valve oblong, tip broad. Distal sacculus division with two separate full lobes. Corona of several slender setae Genus 2: *CHRYSOECIA* 12

General: Forewing predominantly black with a large, quadrate, orange discoidal macula. Transverse lines not at all evident, masked by black color. Plantar bristles with rounded tips. *Male genitalia:* Valve triangular, tip pointed. Distal sacculus division with a single, bifurcated lobe. Corona of two very stout setae.
 Genus 3: *GORGORA*; Species group XIII: *G. morga*

12. (11) *General*: Forewing multicolored, white in distal and basal sectors, median sector predominantly brown with scattered blue scales; transverse lines somewhat indistinct. Cup of frontal protuberance generally round. *Male genitalia*: Lobe of basal sacculus division a short, thin, irregular finger or a broad, short peak. Basal lobe of distal sacculus division weak, arising some distance from distal lobe. Secondary group of cornuti of phallus vesica a row of many, short, subequal denticles. Species group XI: *C. scira* & allies
- General*: Forewing bicolored, ground color orange, zigzag transverse lines usually strong, rarely obsolescent; no blue scales. Cup of frontal protuberance a transverse trough. *Male genitalia*: Lobe of basal sacculus division a long, curved, broad finger. Basal lobe of distal sacculus division strong, arising close to distal lobe. Secondary group of cornuti of phallus vesica reduced to a few unequal, fairly long spines. Species group XII: *C. dela* & allies
13. (10) *General*: Forewing pattern entirely absent, self-colored, usually sooty white, if orange, fringe concolorous. Forewing elongate. *Male genitalia*: Costa greatly expanded. Distal sacculus division with a single, tiny, spike-like lobe. *Female genitalia*: Greatly attenuated. Sclerotization and ribbing of ductus and corpus bursae obsolescent. Genus 4: *CHICHIMECA*; Species group XV: *C. thoracica* & allies
- General*: Forewing pattern present, if self-colored, fringe contrasting dark. Forewing shape varied, not elongate. *Male genitalia*: Costa not greatly expanded, usually hardly expanded at all. Distal sacculus division almost always with a strong, spinelike lobe. *Female genitalia*: Not attenuated, usually quite compact. Sclerotization and ribbing of ductus and corpus bursae strong. 14
14. (13) *General*: Forewing never with brilliant metallic or brassy gold colors; pattern usually streaked, *i.e.*, with darkened veins and streaks between veins. *Female genitalia*: Ventral margin of VIII abdominal pleuron moderately deflexed or declining. Striae in unsclerotized area of VIII pleuron well defined, weak or absent. Striae of ovipositor lobe almost always present. Genus 5: *CIRRHOPHANUS* 15
- General*: Forewing with brilliant metallic or brassy gold areas *or* if dull colored then streaks not present. *Female genitalia*: Ventral margin of VIII abdominal pleuron greatly deflexed or declining. Striae in unsclerotized area of VIII pleuron and on ovipositor lobe usually absent (rarely weak). 21
15. (14) *General*: Foretibial "claw" a simple seta or group of three entirely separate setae. Forewing pattern streaked; streaks in cell Cu forming a

- trident (base distad). *Male genitalia*: Distal sacculus division with two lobes, or with one, weakly sclerotized, fingerlike lobe 16
- General*: Foretibial "claw" composed of several, apically-fused setae. Forewing streaked or not, but streaks in cell Cu never forming a trident.
- Male genitalia*: Distal sacculus division with a single spinelike, heavily sclerotized lobe. 17
16. (15) *Male genitalia*: Distal sacculus division with a single, long, basal fingerlike lobe. Tegumen neck very long. Phallus vesica with an appendicular lobe. *General*: Forewing ground color dark purplish basad, marginal sector lighter, brownish yellow. *Female genitalia*: Ovipositor lobe convex, well sclerotized, sagittate. Species group XV: *C. chryseochilus*
- Male genitalia*: Distal sacculus division with two lobes. Tegumen neck short. Phallus vesica without any appendicular lobes. *General*: Forewing ground color orange, marginal sector lighter, but not brownish-yellow. *Female genitalia*: Ovipositor lobe flat, partially unsclerotized, broad and blunt. Species group XVI: *C. triangulifer* & allies
17. (15) *General*: Forewing with a purplish iridescent cast. *Male genitalia*: Distal sacculus division with lobe very heavy, long, and set at far distal edge of valve. *Female genitalia*: Sterno-ostial concavity triangular. Ovipositor lobe short, pointed, curved upward, with strong striae.
- Species group XVII: *C. plesioglaucus* & *comstocki*
- General*: Forewing generally dull orange-yellow or brownish-white. *Male genitalia*: Distal sacculus division with small lobe set in from distal edge of valve. *Female genitalia*: Sterno-ostial concavity subquadrate or flask-shaped. Ovipositor lobe not with above combination of character states. 18
18. (17) *General*: Forewing ground color dull orange, streaked with definite, though diffuse, transverse lines. Fringe concolorous with wing. *Female genitalia*: Ovipositor lobe straight, flat, blunt, without striae. *Male genitalia*: Secondary group of cornuti of phallus vesica present, a long curved row of sharp, equal spinelets.
- Species group XVIII: *C. papago* & *miaiphona*
- General*: Forewing ground color pale white or yellowish, with streaks but no definite transverse lines, instead a diffuse stain in discoidal area or forewing ground color orange, self-colored. Fringe marked, not entirely concolorous with wing. *Female genitalia*: Ovipositor lobe curved, pointed, striae weak or absent. *Male genitalia*: Discrete secondary group of cornuti of phallus vesica absent although a separate group of scattered, curved-tipped spicules may be present. 19

19. (18) *General*: Forewing with terminal line distinct. *Female genitalia*: Ovipositor lobe elongate. Ductus bursae sclerotized and ribbed for less than one-half its length. Species group XIX: *C. hoffmanni*
- General*: Forewing with terminal line absent. *Female genitalia*: Ovipositor lobe short, triangular. Ductus bursae sclerotized and ribbed well over one-half its length. 20
20. (19) *General*: Forewing streaked, fringe light, interrupted by extensions of streaks. *Female genitalia*: Ductus bursae short, much shorter than corpus. Corpus bursae ellipsoid, with sclerotization and ribbing normal; lobe and ductus seminalis posterior. Dorsal edge of ovipositor lobe curved, striae absent or very weak. *Male genitalia*: Distal sacculus division lobe reclinate. Cornuti of phallus vesica in one continuous group.
. Species group XX: *C. discistrigus*
- General*: Forewing not streaked, fringe evenly dark. *Female genitalia*: Ductus bursae very long, about as long as corpus. Corpus bursae ovate, transverse, without sclerotization and ribbing; lobe and ductus seminalis directed at right angle to ductus bursae. Dorsal edge of ovipositor lobe nearly straight; striae distinct. *Male genitalia*: Distal sacculus division lobe erect. Cornuti of phallus vesica in two widely separated groups.
. Species group XXI: *C. compositus*
21. (14) *General*: Forewing with brassy-gold restricted to marginal and basal sectors and to reniform and orbicular; scattered blue scales along costal area. *Male genitalia*: Distal sacculus division with two lobes of about equal length, set close together.
. Genus 6: *CUAHTEMOCA*; Species group XXII: *C. chalcocraspedon*
- General*: Forewing with brassy gold color general or brilliant metallic gold in distal and basal sectors and in reniform and orbicular or generally dull colored. *Male genitalia*: Distal sacculus division with no lobes, one lobe or two lobes, if latter then set far apart or unequal in length. 22
22. (21) *General*: Forewing with brilliant metallic gold over much of wing in well defined fields. No black dot in reniform. Outer margin entire. *Male genitalia*: Distal sacculus division with no lobes or with well developed, basal, fingerlike lobe; an erect, distal, spinelike lobe absent altogether or reduced and set well on valve close to basal lobe. Corona weak or absent. *Female genitalia*: Ventral margin of VIII pleuron strongly declining or deflexed. Genus 7: *CHALCOPASTA*. 23
- General*: Forewing without brilliant metallic gold; brassy or yellow gold may be present but if so then generally distributed over entire wing or in diffuse areas. A black dot evident in reniform. Outer margin crenulate. *Male genitalia*: Distal sacculus division with well developed, distal, spine-

like lobe; basal lobe usually absent or represented at most by small, setose verrucae, if well developed then set far from distal lobe and the latter then set far to edge of valve. *Female genitalia*: Ventral margins of VIII pleuron always strongly deflexed. Genus 8. *BASILODES* 25

23. (22) *General*: Median sector of forewing brown, only basal and distal sectors gold, both reniform and orbicular filled with gold. *Male genitalia*: Distal sacculus division with two lobes. Tegumen neck quite long, arched. *Female genitalia*: Ovipositor lobe straight, saggitate, with blunt tips. Unsclerotized area of VIII pleuron with weak striae Species group XXIII: *C. ellica*

General: Median sector of forewing always gold; gold may extend over most of wing but not in reniform. *Male genitalia*: Distal sacculus division with single, erect, fingerlike lobe or without erect lobe. Tegumen neck short. *Female genitalia*: Ovipositor lobe angled dorsad, acuminate, with sharp tips. Unsclerotized area of VIII pleuron without striae. 24

24. (23) *General*: Gold masking most of forewing pattern, always entirely covering distal third of wing. *Male genitalia*: Distal sacculus division with single, basal, erect, fingerlike lobe. Phallus vesica pear-shaped, swollen end basad. *Female genitalia*: Corpus bursae ellipsoid-oblong, lobe normal. Species group XXIV: *C. territans* & allies

General: Gold restricted to oblique median area of forewing, weak or absent in distal third. *Male genitalia*: Distal sacculus division with a basal, fingerlike, lobe or without lobe, if former then phallus vesica swollen distad, if latter then a distal spur pointing ventrad on valve and phallus vesica tubular and coiled. *Female genitalia*: Corpus bursae ellipsoid-oblong or fusiform, if former then lobe displaced cephalad. Species group XXV: *C. chalcotoxa* & allies

25. (22) *General*: Frontal protuberance an oval to heart-shaped hollow cup with ventral portion slightly convex. Forewing coloring bronzy or with some yellow gold, no fringe tooth at tornus. *Male genitalia*: Phallus vesica elongate, secondary group of cornuti absent. *Female genitalia*: Ventral margins of VIII pleura close together, distance about equal to the width of the ventral sclerotized half of the neighboring pleuron. Species group XXVI: *B. chrysopis* & allies

General: Frontal protuberance a heart-shaped ring with a subcentral truncate, conical secondary prominence. Forewing coloring never metallic gold; usually yellow and with a large hexagonal or quadrate macula mesad in inner area, small fringe tooth at tornus. *Male genitalia*: Phallus vesica pear-shaped, secondary group of cornuti present. *Female genitalia*: Ventral margins of VIII pleura widely separated, distance about twice the width of the ventral sclerotized half of the neighboring pleuron. Species group XXVII: *B. rugifrons* & allies

Genus 1: *PLAGIOMIMICUS*

- 1873, *Plagiomimicus* Grote. Buffalo Soc. Nat. Sci., B. 1:182. Type species: *P. pityochromus* Grote, 1873; Albany, Alabama; monobasic.
- 1874, *Stibadium* Grote. Buffalo Soc. Nat. Sci., B. 2:74. Type species: *S. spumosum* Grote, 1874; Kansas; monobasic. Synonymy of Smith, 1882. Brooklyn Ent. Soc., B. 5:30, 35.
- 1875, *Polenta* Morrison. Boston Soc. Nat. Hist., Proc. 18:124. Type species: *Schinia tepperi* Morrison, 1875; Texas; monobasic. Synonymy of Grote, 1880. Brooklyn Ent. Soc., B. 3:38.
- 1877, *Antaplaga* Grote. Canad. Ent. 9:70-71. Type species: *A. dimidiata* Grote, 1877; Colorado; monobasic. NEW SYNONYMY.
- 1918, *Neophaeus* Dyar. U. S. Natl. Mus., Proc. 54:350. Type species: *N. chalcospilans* Dyar, 1918; Mexico; monobasic. NEW SYNONYMY.

Remarks

This large and perhaps unwieldy genus includes two major phyletic lines, 1 and 2. Possibly some of its diverse species groups are worthy of generic separation, most likely those of line 2, but in keeping with my policy of extreme conservatism in this preliminary study, I prefer to recognize a single broad genus. This also obviates the necessity of proposing several new generic names which might suffer synonymy when the group is studied more extensively.

The genus is very difficult to characterize as a whole because of its diverse constituents. The description below is only very generally applicable except for the female genitalic structures, primarily those of segment VIII which are the most constant and diagnostic. The single lobe of the distal sacculus division of the valve is extremely variable in position and shape throughout the genus but fairly constant in species groups. A double lobe is the only defining character state separating the species groups on the second major phyletic line. This state may have special significance, however, in representing a major evolutionary step.

Forbes (1954:171), in his key to the acronyctine genera, erroneously ascribes two "spines" (setal "claws") to the foretibia of the genus "*Plagiomimicus*" (including only two species, *pityochromus* and *concinus*).

Description

General. A diverse genus. Typically medium in size and robustness, a few fairly large and small forms. Dull colored, usually brown. Frontal protuberance quite varied in shape, usually an oval ring with a broad, rough ventral elevation, a few odd types. Foretibial "claw" a single massive seta, often flattened and curved. Forewing pattern typically noctuiform, dull colored, brown, some lighter colors: yellow, white. Thoracic vestiture of hair-like to spatulate, dentate scales; stiriine tufts present in most, poorly developed in some.

Male genitalia. Tegumen usually broad, narrow in some, neck short to very short, erect. Uncus short to moderately long, gradually curving, straight or gradually undulate. Saccus elongate. Valve variously shaped, usually oblong, ventral margin strongly convex in some; costa usually well expanded; basal sacculus division short, with broad, short lobe; distal division with single lobe, varied in shape and position; corona usually well developed, sometimes diffuse. Phallus vesica swollen, often expanded somewhat sinistrad as well as dextrad; cornuti well developed, numerous, moderately long, secondary group often with fairly long spinelets. Anellus sclerites crescent-shaped to triangular. Juxta subquadrate to shield-shaped. VIII tergal and sternal sclerotizations varied, former usually V-shaped, latter U-shaped.

Female genitalia. Ovipositor lobe varied in shape and degree of sclerotization, from flat, partially sclerotized with striae to elongate, convex, heavily sclerotized and sharply pointed types, without striae. VIII pleuron evenly sclerotized (sometimes with small, irregular, unsclerotized areas), confluent with sternum, ventral margin not defined; no special, complex sterno-ostial concavity present. Lamella postvaginalis confluent with sternum, not a discrete sclerite, rarely fused with 1. antevaginalis (and sometimes ductus bursae also) to form a specially shaped, heavily sclerotized chamber. Corpus bursae fusiform to cudgel-shaped; posterior lobe usually well sclerotized and ribbed; sclerotized plate in crotch of lobe usually well developed and defined.

Species group I: *P. ochoa* and *resolutus*

Figure 6

Description

General. Size medium, expanse about 30mm. Frontal protuberance simple, an elongate to oval, rough surfaced plateau (slightly hollowed in *ochoa*). Foretibial "claw" broad and heavy, arising from moderately projecting, straight extension of tibial apex. Forewing apex acute, sharp, tornus moderately sharp; pattern noctuiform, ground color brown, markings darker brown, angulation of PM line beneath apical patch sharply acute, scattered blue scales in costal and inner areas. Hindwing brown, exterior line distinct. Scutal phragma moderately projecting. Thoracic vestiture of mixed linear and spatulate scales; tufts normal.

Male genitalia. Tegumen broad, slightly bulbous dorsad in *ochoa*, neck very short and erect. Uncus moderately long, cylindrical, curving sharply basad, more gradually distad; setae especially dense and erect dorsad. Saccus elongate, rectangular, rapidly narrowed cephalad. Valve oblong, distal half slightly narrowed; costa moderately expanded; basal sacculus division moderately long, ending rather abruptly, lobe a narrow, short finger; distal division with single, fingerlike lobe arising mesad; corona a single row of several, bristlelike, equal setae running along entire distal edge of valve. Phallus vesica slightly irregular, inflated cephalodistad; cornuti numerous, moderately long and heavy distad, shorter and thinner basad, secondary group a long row of

short, cuspidate denticles, an irregular sclerotized area between patches; aedeagus somewhat angled. Anellus sclerites triangular. Juxta subquadrate. VIII tergal sclerotization V-shaped, arms and base narrow, former weak caudad; sternal sclerotization U-shaped.

Female genitalia. Ovipositor lobe of primitive, broad, flat, blunt type, striae distinct. Postapophysis almost twice as long as antapophysis, both slender. VIII pleuron with slight unsclerotized area centrally (striae faintly showing here in *ochoa*), ventral margin vaguely defined in *resolutus*. Sternum slightly unsclerotized caudad, jutting cephalad. Corpus bursae ellipsoid; posterior lobe with two short secondary lobes, sclerotization and ribbing moderately strong; sclerotized plate in crotch of first secondary lobe, a second plate also in crotch of second lobe.

Remarks

This group is quite distinct from the others in the genus in having the ovipositor lobes of the primitive type. Several other character states are also primitive and set the group apart (see "Phylogenetic analysis"). It may be advisable therefore to recognize the group as a separate genus but since there are only two species and there is general resemblance to the other *Plagiomimicus*, I choose not to follow this course.

Included species

1. *resolutus* Dyar, 1909. Ent. Soc. Wash., Proc. 11:26 (*Plagiomimicus*).
2. *ochoa* Barnes, 1904. Canad. Ent. 36:241-242 (*Stibadium*).
=*dollii* Smith, 1908. N. Y. Acad. Sci., Ann. 18:118-119 (*Plagiomimicus*).
Synonymy of Barnes and McDunnough, 1917. Check List Lepid. Boreal Amer. p. 70.

Species group II: *P. laodamia*

Figure 7

Description

General. Size medium large, expanse about 40mm. Frontal protuberance oval to heart-shaped, depressed dorsad and with broad lower elevation. Foretibial "claw" broad, flat, arising from moderately produced, straight tibial apex. Forewing apex acute, slightly sharp, tornus moderately sharp; pattern noctuid-form, ground color medium brown, markings darker brown, medium shade not distinct, PM angulation beneath apical patch extreme, nearly reaching outer margin. Hindwing brown, exterior line distinct, offset distad. Thoracic vestiture mainly of linear dentate scales; anterior mesoscutal tuft developed in addition to other normal tufts.

Male genitalia. Tegumen broad, neck very short, erect. Uncus very short, stout, narrowed apically, curving sharply basad, setae long and dense dorsad. Saccus elongate, narrowed gradually cephalad. Valve elongate, rectangular, distal half slightly narrowed; costa moderately expanded; basal sacculus division broad, moderately long, lobe narrow, prominent; distal division with

single spinelike lobe arising far distad, near edge of valve; corona a row of several stout, equal setae running along entire distal edge of valve. Phallus vesica normal, cornuti numerous, long, stout, closely bunched; secondary group a row of subequal, short denticles (longer sinistrad). Anellus sclerites crescent-shaped, fused cephalad. Juxta kite-shaped. VIII tergal sclerotization U-shaped, nearly circular, arms and base broad; sternal sclerotization U-shaped, arms not expanded.

Female genitalia. Ovipositor lobe slightly convex, pointed, and curved dorsad; striae distinct. Postapophysis about one-third longer than antapophysis, latter slightly sinuate. VIII pleuron completely sclerotized and confluent with sternum. Lamellae jutting slightly cephalad, forming a simple ring around ostium bursae. Corpus bursae cudgel-shaped, somewhat truncate cephalad; posterior lobe conoidal, sclerotization and ribbing strong; plate in crotch of lobe well developed.

Included species

3. *laodamia* Druce, 1890. Zool. Soc. London, Proc. p. 520 (*Plusiodes*). The figure of this species is incorrectly labeled as *laverna* by Draudt (1919-1939:pl. 43, row a, fourth from left).

Species group III. *P. spumosus* and allies

Figure 8

Description

General. Size medium to medium-small, expanse about 23-35mm. Frontal protuberance an oval ring with a broad, moderately prominent lower elevation. Foretibial "claw" flat, arising from strongly produced, straight tibial apex. Forewing apex strongly acute, to nearly a right angle, sharp, costal and outer margins moderately to slightly convex, tornus rounded to sharp; pattern varied but basically noctuiform, ground color brown, markings of darker shade (some special patterns and colors: yellow submarginal sector in *aureolus*, nearly all white in *dimidiatus*, crescent-shaped and oval, silver maculae in *olvello*, powdery suffusion in *hilli*), apical patch prominent in most, reniform and orbicular obsolescent in some, PM angulation beneath apical patch barely obtuse to sharply acute. Hindwing white or brown, markings obsolescent. Thoracic vestiture varied, usually of long, spatulate, dentate scales, some with mixed types; tufts normal.

Male genitalia. Tegumen broad, neck very short, erect. Uncus moderately long to long, cylindrical, slightly swollen subapically in most, gradually curving. Saccus quite elongate, narrowed gradually cephalad, with rounded point. Valve oblong and slightly narrowed distad or broad, with straight dorsal and convex ventral margins; costa greatly expanded; basal sacculus division broad, swollen and very short, ending abruptly, lobe very broad and short; distal division with single lobe, short and spikelike to very long and curving mesad, always arising about the center, sometimes a tiny secondary lobe present basad in addition; corona of slender setae at dorsal tip of valve, sometimes running

obliquely onto inner surface. Phallus vesica normal, expanded sinistrad in some; cornuti numerous, varied in shape: moderately long and slender or stout and subequal in some, long, stout distad and shorter basad in others, secondary group a row of spinelets, latter shorter dextrad, quite long and angled sinistrad. Anellus sclerites oval, widely separated or triangular or crescent-shaped and approximated. Juxta subquadrate to shield-shaped. VIII tergal sclerotization narrowly V-shaped in most, arms weak or fused into a heavy convexity in *hilli*; sternal sclerotization U-shaped.

Female genitalia. Ovipositor lobe convex, varied in shape: apex pointed, usually abruptly narrowed subapically, evenly and heavily sclerotized, without striae, often with long setae (nearly reaching tip of lobe). Postapophysis slightly longer than antapophysis and often much heavier. VIII pleuron completely sclerotized (a very slight medial unsclerotized area in some, never containing striae) and confluent with sternum. Sternum membranous caudad producing an indefinite lamella postvaginalis, latter jutting cephalad and continuous laterad with I. antevaginalis to form a wide, simple ring around ostium, sometimes slightly enlarged to form an indefinite, squarish chamber or sclerotized and fused into a purse-shaped, wide-mouthed chamber. Corpus bursae cudgel-shaped or oblong, slightly curved in some; posterior lobe broad, sclerotization and ribbing strong in most, almost absent in some (those with oblong corpora); plate in crotch of lobe well developed.

Remarks

This is the largest species group in the genus and the tribe. It contains *dimidiatus*, the genotype of *Antaplaga*, which formerly formed the nucleus for this conglomerate genus in spite of its obvious distinctive appearance (mentioned by various authors, e.g., Barnes and Benjamin, 1924:170). Should anyone feel that this species group should have generic status of its own, the nominal genus *Stibadium* is available for it and carries a meaningful usage established by the McDunnough check list (1938).

This group has been related to the next in the phylogeny section and could be combined with it to form a separate genus. Species group V (*P. tepperi*) may be included also to form a genus *Plagiomimicus* which would be more compact than the present and perhaps more useful.

One new species, *bajae*, is described herein (see appendix).

Included species

4. *jalada* Schaus, 1898. N. Y. Ent. Soc., J. 6:144 (*Stibadium*).
5. *aureolus* Edwards, 1882. Papilio 2:126-127 (*Stibadium*).
6. *bajae* Hogue, new species. (See appendix).
7. *olyello* Barnes, 1907. Canad. Ent. 39:94-95 (*Stibadium*).
8. *raglena* Dyar, 1912. U. S. Natl. Mus., Proc. 42:68 (*Stibadium*).
9. *unicus* Barnes and Benjamin, 1926. Insec. Incit. Mens. 14:4-5 (*Stibadium*).

10. *chalcospilans* Dyar, 1918. U. S. Natl. Mus., Proc. 54:350 (*Neophaeus*).
11. *laverna* Druce, 1898. Biol. Cent. Amer., Heter. 2:496-497; 3: pl. 95, fig. 22 (*Thalpochares*).
12. *manti* Barnes, 1904. Canad. Ent. 36:243 (*Stibadium*).
13. *dimidiatus* Grote, 1877. Canad. Ent. 9:71 (*Antaplaga*).
14. *corozona* Schaus, 1898. N. Y. Ent. Soc., J. 6:144 (*Stibadium*).
15. *astigmatosus* Dyar, 1921. Insec. Incit. Mens. 9:42 (*Stibadium*).
16. *curiosus* Neumoegan, 1883. Papilio 3:141-142 (*Stibadium*).
17. *spumosus* Grote, 1874. Buffalo Soc. Nat. Sci., B. 2:74 (*Stibadium*).
18. *mavina* Barnes and McDunnough, 1910. Canad. Ent. 42:250-251 (*Stibadium*). I suspect that this species was based on a faded or aberrant specimen of the preceding and should be synonymized with it. I have not examined the types, however, so leave a formal determination of synonymy to future students.
19. *hilli* Barnes and Benjamin, 1923. Contrib. Nat. Hist. Lepid. N. Amer. 5:83-84 (*Stiria*).
= *caliente* Hill, 1923. So. Calif. Acad. Sci., B. 22:17; fig. (*Antaplaga*).
Synonymy of Hill, 1923. *Ibid.* p. 19.

Species group IV: *P. pityochromus* and allies

Figure 9

Description

General. Size medium to medium-small, expanse about 25-33 mm. Frontal protuberance a circular, smooth-bottomed prominent cup with no secondary prominence. Foretibial "claw" shovel-shaped, arising from strongly produced, strongly angled tibial apex. Forewing apex acute, moderately sharp, tornus rounded; pattern noctuiform, ground color medium to light brown, transverse lines light, apical patch prominent, orbicular markedly dark (absent in *expallidus*). Hindwing white to brown. Thoracic vestiture of spatulate scales; tufts normal.

Male genitalia. Tegumen moderately broad, neck very short and erect. Uncus moderately long, swollen mesad, undulate; setae fairly numerous, longer ventrad. Saccus elongate, narrowed cephalad with a rounded point. Valve oblong, apex rounded; costa little expanded; basal sacculus division moderately broad, ending somewhat abruptly, lobe short; distal division with a single, moderately long, curved, spinelike lobe set far distad near edge of valve (except in *concinus* where it is more basal as in preceding unit); corona of few, slender setae, restricted to dorsal apex of valve or normal. Phallus vesica normal; cornuti numerous, subequal, moderately long and stout, secondary group a patch of fairly long, stout spinelets. Anellus sclerites widely separated, crescent-shaped. Juxta broadly kite-shaped. VIII tergal sclerotization triangular, heavily sclerotized and convex caudad; sternal sclerotization U-shaped, arms broadened caudad.

Female genitalia. Ovipositor lobe convex, evenly and strongly sclerotized, apex pointed, usually abruptly narrowed subapically, without striae, with long setae (about reaching tip of lobe). Postapophysis slightly longer and heavier than antapophysis, both usually slender (stout in *expallidus*). VIII pleuron completely sclerotized (small irregular unsclerotized areas in some, containing no striae) and confluent with sternum. Sternum unsclerotized caudad, producing an indefinite lamella postvaginalis, latter jutting cephalad and connecting with l. antevaginalis to form a wide, simple ring around ostium or enlarged to form a squarish, indefinite chamber. Corpus bursae cudgel-shaped, curved; posterior lobe with two secondary lobes, sclerotization and ribbing strong; sclerotized plate in crotch of first lobe well developed.

Remarks

As mentioned above, this group is not sharply differentiated from the preceding. At present it corresponds approximately (*concinus* added) to the genus *Plagiomimicus* in the restricted sense of previous authors (Draudt, 1919-1939:313; McDunnough, 1939:99-100).

Included species

20. *expallidus* Grote, 1882. Papilio 2:185 (*Plagiomimicus*).

21. *triplagiatus* Smith, 1890. Ent. Amer. 6:139 (*Plagiomimicus*).

22. *pityochromus* Grote, 1873. Buffalo Soc. Nat. Sci., B. 1:182 (*Plagiomimicus*).

= *medius* Morrison, 1875. Boston Soc. Nat. Hist., Proc. 18:123-124 (*Schinia*). Synonymy of Grote, 1882. New Check List N. Amer. Moths p. 35. This name applies to specimens with a split reniform. There may be at least a subspecific difference involved but it awaits determination.

23. *concinus* Dyar, 1909. Ent. Soc. Wash., Proc. 11:23 (*Stibadium*).

Species group V: *P. tepperi*

Figure 10

Description

General. Size somewhat varied, generally small, expanse about 23-28 mm. Frontal protuberance an inverted, heart-shaped ring with lower lip produced into a conical prominence. Foretibial "claw" tiny, arising from unproduced tibial apex. Forewing apex acute, sharp, outer margin shallowly undulate, tornus rounded; pattern noctuiform, ground color olive green, lines white, apical patch prominent, reniform rudimentary, orbicular absent. Hindwing white to brown, markings obsolescent. Thoracic vestiture of spatulate scales; tufts normal.

Male genitalia. Tegumen very broad, neck very short, erect. Uncus short, stout, gradually curving; setae short, erect and longer dorsad. Saccus stout, elongate, cylindrical, rounded cephalad. Valve very short, almost rhomboid; costa expanded obliquely; basal sacculus division very broad, triangular, end-

ing abruptly, lobe a short, straight finger; distal division with a single, long, thin, spinelike lobe, set near edge of valve; no discrete corona. Phallus vesica small; cornuti stout, shorter basad, secondary group absent. Anellus sclerites crescent-shaped. Juxta rectangular. VIII tergal sclerotization bracket-shaped; sternal sclerotization of two parallel, separated strips, weakly connected cephalad.

Female genitalia. Ovipositor lobe convex, evenly and heavily sclerotized, acuminate, setae short. Postapophysis almost a third longer than antapophysis and much heavier. VIII pleuron completely sclerotized and confluent with sternum. Sternum slightly unsclerotized caudad. Ductus bursae very heavily sclerotized and confluent with lamellae to form a bowl-shaped chamber. Corpus bursae very narrow caudad, gradually swollen cephalad; posterior lobe with weak secondary lobes; sclerotization and ribbing strong.

Remarks

As mentioned in the phylogeny section, this species group (one species, *tepperi*) deviates somewhat from the two preceding groups. It might, therefore, be considered as an autonomous genus to which the name *Polenta* may be applied (as has been done by most recent authors).

Included species

24. *tepperi* Morrison, 1875. Acad. Nat. Sci. Philadelphia, Proc. pp. 68-69 (*Schinia*).

= *richii* Grote, 1886. Canad. Ent. 18:99-100 (*Plagiomimicus*). This synonymy is discussed in detail in the section on taxonomic history.

Species group VI: *P. hutsoni* and *olivalis*

Figure 11

Description

General. Size medium small or small, expanse about 20 or 30mm. Frontal protuberance an inverted heart-shaped ring with lower lip produced into a conical prominence. Legs slender, foretibial "claw" moderately strong, arising from strongly projecting, straight tibial apex. Forewing apex acute, rounded, tornus rounded; pattern as follows: median and submarginal sectors white, suffuse, fuliginous, brownish-green transverse lines, reniform and orbicular absent, apical patch obsolete. Hindwing brownish-black, markings obsolete. Thoracic vestiture hairy (*olivalis*), or of short spatulate scales (*hutsoni*); tufts poorly developed in both.

Male genitalia. Tegumen moderately broad, neck short. Uncus moderately long, cylindrical, tip slightly narrowed, straight; setae short and sparse. Saccus elongate or stout. Valve oblong; costa small; basal sacculus division short, ending diffusely, lobe a broad, low mound; distal division with a single, short, stout spine, set far distad; corona diffuse, weak. Phallus vesica slightly inflated sinistrad; cornuti moderately long (*olivalis*) or very short (*hutsoni*) and subequal, secondary group a short row of spinelets on a convex, sclerotized

plate. Anellus sclerites separated, U-shaped. Juxta shield-shaped. VIII tergal sclerotization of parallel, entirely separate strips; sternal sclerotization a nearly complete circle, broad caudad, narrow cephalad.

Female genitalia. Ovipositor lobe convex, evenly and heavily sclerotized, elongate, bluntly pointed. Postapophysis and antapophysis slender, subequal. VIII segment very short, pleuron with large, central, oval, unsclerotized area, confluent with sternum. Sternum unsclerotized caudad to form an ill-defined, chevron-shaped lamella postvaginalis; I. antevaginalis ligulate, lamellae not jutting cephalad, flush with segment. Ductus bursae completely membranous. Corpus bursae cudgel-shaped; posterior lobe simple, sclerotization and ribbing very weak, essentially absent in *hutsoni*.

Included species

25. *hutsoni* Smith, 1907. Amer. Ent. Soc., Trans. 33:140 (*Stibadium*).
= *fuliginosus* Smith, 1907. Amer. Ent. Soc., Trans. 33:140-141 (*Stibadium*).
Synonymy of Barnes and McDunnough, 1916. Contrib. Nat. Hist. Lepid. N. Amer. 3:168. I have seen the types of these nominal species and agree with this synonymy.

26. *olivalis* Barnes and McDunnough, 1916. Contrib. Nat. Hist. Lepid. N. Amer. 3:12-13, pl. 3, fig. 8 (*Stiria*).

Species group VII: *P. hachita* and allies

Figure 12

Description

General. Size medium-small, expanse about 25-28mm. Frontal protuberance a moderately deep, circular, smooth cup with prominent lower lip. Foretibial "claw" shovel-shaped, arising from a strongly projecting, slightly angled tibial apex. Forewing apex acute, rounded, tornus rounded; pattern as follows: broad white median sector between well defined, black AM and PM lines, outer and basal sectors white also or contrasting yellow, ST line broken into a row of small dots (absent in *biundulalis*). Thoracic vestiture of linear scales; tufts poorly developed.

Male genitalia. Tegumen moderately broad, neck short. Uncus moderately long, slightly swollen mesad, straight to undulate; setae short. Saccus elongate, pointed cephalad. Valve oblong, costa small; basal sacculus division short, ending diffusely, lobe only a broad, flat mound; distal division with a single, short, stout spine, set far distad; corona diffuse, weak. Phallus vesica slightly inflated sinistrad; cornuti numerous, moderately long and subequal, secondary group a row of long spinelets. Anellus sclerites crescent-shaped, fused or separated. Juxta shield-shaped. VIII tergal sclerotizations two entirely separate, parallel strips; sternal sclerotization U-shaped, arms very broad caudad.

Female genitalia. Ovipositor lobe convex, evenly and heavily sclerotized, triangular, sharply pointed. Postapophysis and antapophysis subequal, stout.

VIII very short, pleuron with large, central, oval, unsclerotized area, confluent with sternum. Lamellae as in preceding species group. Ductus bursae completely membranous. Corpus bursae cudgel-shaped; posterior lobe simple; sclerotization and ribbing very weak.

Included species

27. *hachita* Barnes, 1904. Canad. Ent. 36:241 (*Antaplaga*).
28. *sexseriatus* Grote, 1881. Papilio 1:155 (*Grotella*).
29. *biundulalis* Zeller, 1872. Zool. Bot. Ges. Wien, Verhandl. 22:502-503, taf. III, figs. 14a-14c (*Sedenia*).

Species group VIII: *P. alesaea*

Figure 13

Description

General. Size small, expanse about 23mm. Frontal protuberance an oval or heart-shaped ring inclosing a low, subcentral, truncate, secondary prominence. Foretibial "claw" quite heavy and long, arising from strongly projecting, straight tibial apex. Forewing short, shape nearly deltoid; pattern completely absent, self-colored, white. Hindwing patternless and white also. Thoracic vestiture of spatulate scales; tufts poorly developed (? my specimens rubbed).

Male genitalia. Tegumen moderately broad, neck short. Uncus short, stout, swollen mesad; setae dense, longer and erect dorsad. Saccus elongate, pointed cephalad. Valve oblong; costa small; basal sacculus division moderately broad, ending diffusely, lobe a short pommel; distal division with a single, long, sharp, stout spine set very far distad and extending off the valve margin; corona weak. Phallus vesica slightly inflated sinistrad; cornuti few, distal ones very short and stout, set on a curved, sclerotized plate, basal ones slightly longer and finer, free from plate, secondary group absent, a few enlarged spicules in a row on sinistral inflation instead. Anellus sclerites crescent-shaped, separated. Juxta broadly shield-shaped.

Female genitalia. Ovipositor lobe convex, acuminate, strongly and evenly sclerotized. Postapophysis about one-quarter longer than antapophysis, both slender. VIII pleuron completely sclerotized, confluent with sternum. Sternum unsclerotized caudad and jutting cephalad as a semicircular plate (lamella postvaginalis) to form a flat, simple chamber with the l. antevaginalis. Corpus bursae oblong; lobe simple, sclerotization and ribbing strong and extending over one-third of the entire corpus.

Remarks

The single species in this group was undoubtedly placed originally in the genus *Antaplaga* because of the lack of any wing pattern in common with several species formerly included in that genus but segregated in the present study as the genus *Chichimeca*. There is definitely no close relationship between

alesaea and species of *Chichimeca*, the similarity in wing ornamentation having arisen undoubtedly by parallel degeneration and loss of pattern frequently seen in noctuids.

Included species

30. *alesaea* Dyar, 1918. U. S. Natl. Mus., Proc. 54:350 (*Antapлага*).

Species group IX: *P. psamathochromus* and *argyropolius*

Figure 14

Description

General. Size medium, expanse about 30-33mm. Frontal protuberance an oval ring with a broad, low, ventral elevation. Foretibial "claw" strong and flat, arising from strongly produced, straight tibial apex. Forewing apex acute, sharp, tornus moderately sharp; pattern noctuiform but simplified: color light silvery-grey or powdery grey-brown, when former, AM and PM lines fine, brownish-gold (*argyropolius*), when latter, generally like most species in group III (*psamathochromus*), orbicular and reniform obsolescent in both. Hindwing pale, markings obsolete. Thoracic vestiture primarily of linear scales; tufts poorly developed.

Male genitalia. Tegumen unusually narrow, ventral arms long, neck short. Uncus short, fusiform; setae numerous, longer and erect dorsad. Saccus very long, rounded cephalad. Valve rhomboid-oblong, distoventral corner produced or strongly angled; costa expanded moderately obliquely; basal sacculus division short, swollen, deltoid, nearly confluent with distal division, lobe a short, broad or narrow finger; distal division with two lobes: basal irregular, finger-like, distal a strong, curved spine; corona weak. Phallus vesica normal; cornuti numerous, moderately long distad, shorter basad (latter extending far basad over ventral surface in *psamathochromus*), secondary group a short row of several spinelets, these longer and curved sinistrad in *argyropolius*, subequal in *psamathochromus*. Anellus sclerites long, approximated cephalad. Juxta subquadrate, shield-shaped. VIII tergal sclerotization U-shaped, base very broad; sternal sclerotization U-shaped, arms broad.

Female genitalia. Ovipositor lobe convex, evenly and heavily sclerotized, sagittate. Postapophysis about one-fifth longer than antapophysis, both very slender. VIII pleuron completely sclerotized, confluent with sternum (ventral margin faintly defined caudad in *psamathochromus*). Lamellae specially sclerotized and fused into a purse-shaped, narrow-mouthed chamber. Corpus bursae oblong or cudgel-shaped; lobe simple, sclerotized plate in crotch of lobe extensive, extending onto lobe considerably; sclerotization and ribbing moderately strong.

Remarks

This species group and the next are related and distinct from the others in the genus *Plagiomimicus* in possessing a double lobe on the distal sacculus

division of the male valve. The special phyletic significance of this state has already been discussed and may be sufficient to warrant the separation of this group as a separate genus.

Included species

31. *psamathochromus* Dyar, 1909. Ent. Soc. Wash., Proc. 11:22-23 (*Stibadium*).

32. *argyropolius* Dyar, 1914. U. S. Natl. Mus., Proc. 47:376 (*Stiria*).

Species group X: *P. phalaenoides*

Figure 15

Description

General. Size medium, expanse about 28mm. Frontal protuberance an ovoid ring with a subcentral, broad, truncate lower elevation. Foretibial "claw" moderately heavy and shovel-shaped, arising from strongly projecting, straight tibial apex. Forewing almost identical in all respects to that of *argyropolius* in preceding group but markings a little darker. Hindwing pale, markings obsolete. Thoracic vestiture of mixed linear and spatulate scales; tufts poorly developed.

Male genitalia. Tegumen moderately broad, ventral arms long, neck moderately long. Uncus short and stout; setae numerous, longer and erect dorsad. Saccus elongate, rounded cephalad. Valve oblong, angular, twice narrowed, once mesad, once again distad, apex rounded, acuminate; costa moderately expanded; basal sacculus division inflated, deltoid, somewhat confluent with distal division, lobe a short, broad finger; distal division with two lobes, both fingerlike, basal broader, distal with minute denticles apically; corona diffuse. Phallus vesica cylindrical, slightly expanded sinistrad; cornuti very few (2-5) and short, secondary group a patch of several unequal denticles arising from sclerotized plate, latter extending distad nearly to primary group. Anellus sclerites ovoid, separated. Juxta shield-shaped, VIII tergal sclerotization nearly circular, broad cephalad; sternal sclerotization broadly U-shaped, arms expanded.

Female genitalia. Ovipositor lobe convex, evenly and heavily sclerotized, short, acuminate. Postapophysis nearly twice as long as antapophysis. VIII pleuron completely sclerotized, confluent with sternum. Sternum unsclerotized caudad, lamellae not modified into a large, narrow-mouthed, purse-shaped chamber, instead, an indistinct, small chamber with a wide mouth present. Corpus bursae elongate, cudgel-shaped; lobe simple, sclerotized plate in crotch well developed; sclerotization and ribbing moderately strong but somewhat restricted in area.

Included species

33. *phalaenoides* Dyar, 1918. Insec. Incit. Mens. 6:133-134 (*Stiria*).

Genus 2: *CHRYSOECIA*

1910, *Chrysoecia* Hampson. Catalogue Lepid. Phalaenae Brit. Mus. 9:182.

Type species: *Anthoecia scira* Druce, 1889; Ruicon, Guerrero, Mexico; monobasic.

Remarks

Hampson originally erected this genus to include the single species *scira*. I have enlarged the genus to include two of the three primary phyletic units of major phyletic line 3, excluding the primary phyletic unit represented by one species, *Gorgora morga* (unit XIII) which I treat as generically distinct (see below). The two species groups (units XI and XII) of this genus are superficially very different but have female genitalia of the same type.

Description

General. Medium-small in size. Frontal protuberance of two types: (1) a shallow, round cup with slightly produced ventral lip or (2) a transverse trough with a ventral, external, median node, a low, semicircular ridge below both types on the frons. Foretibial "claw" a single seta. Forewing pattern of two types (see descriptions below), PM line always strongly zigzagged, reniform and orbicular (especially latter) with a tendency to enlarge and square out, lunules usually marked. Thoracic vestiture usually somewhat hairy with poorly developed tufts.

Male genitalia. Tegumen normal in breadth or somewhat narrowed, neck short and erect or moderately long. Uncus usually moderately long and cylindrical. Valve oblong, usually slightly curved; costa moderately expanded; basal sacculus division broad, often with a fairly long, fingerlike lobe (may be reduced); distal division always with two lobes: basal lobe fingerlike and often weak, distal lobe spinelike; coronal setae slender. Phallus vesica normal, slightly angular; cornuti often diminutive in center of primary group, secondary group a row of denticles or a very few (2-5), unequal spines.

Female genitalia. Uniform. Ovipositor lobe of primitive, blunt flat type, striae distinct. VIII pleuron with large, elongate, median, unsclerotized area containing distinct striae, ventral margin defined evenly along entire length, contiguous or approximate with opposite margin. Sternum membranous or sclerotized. Lamellae ill-defined, much as in preceding genus, forming a simple ring around the ostium bursae. No special, complex sterno-ostial concavity present. Ductus bursae membranous or heavily sclerotized and confluent with lamellae. Corpus bursae ellipsoid or elongate; lobe simple; sclerotization and ribbing strong.

Species group XI: *C. scira* and allies

Figure 16

Description

General. Size medium-small, expanse about 25-30mm. Frontal protuberance a shallow, small round cup, with ventral lip slightly produced externally,

a low, semicircular ridge below this on frons. Foretibial "claw" moderately strong, arising from slightly produced tibial apex. Forewing apex rounded, tornus rounded and margins moderately convex; pattern and coloring complex: AM and PM lines zigzagged and dark, orbicular and reniform obsolescent, center of former greatly expanded in some, scattered blue scales through median sector and costal area, outer and basal areas white. Hindwing fuscous, lighter basad, markings obsolescent. Thoracic vestiture of linear to moderately spatulate scales; tufting usually poorly developed, small, lateral and anterior mesoscutal tufts developed in *scira*.

Male genitalia. Tegumen slender, ventral arms somewhat long, neck moderately long. Uncus moderately long to long, cylindrical. Saccus triangular to oblong. Valve oblong, straight or slightly upcurved; costa moderately expanded; basal sacculus division broad, ending diffusely, lobe a short, thin finger or broad, short peak; distal division with weak basal lobe, distal lobe a sharp, moderately long spine arising near edge of valve; coronal setae slender. Phallus vesica slightly angular; cornuti several, moderately long and stout in *scira*, more numerous, moderately long and stout only peripherad (diminutive centrad) in all others, secondary group a row of short, subequal denticles. Anellus sclerites crescent-shaped to ovate. Juxta shield-shaped. VIII tergal sclerotization V-shaped; sternal sclerotization U-shaped, arms slightly expanded.

Female genitalia. Postapophysis slightly longer than antapophysis. Ventral margins of VIII pleura contiguous mesad. Lamella postvaginalis vaguely triangular, jutting cephalad slightly with ligulate l. antevaginalis. Ductus bursae membranous caudad, becoming abruptly sclerotized and ribbed about halfway. Corpus bursae ellipsoid; lobe simple; sclerotization and ribbing strong.

Included species

34. *scira* Druce, 1889. Biol. Cent. Amer., Heter. 1:301; 3: pl. 28, fig. 5 (*Anthoecia*).

=*benjamini* Hill, 1924. So. Calif. Acad. Sci., B. 23:158 (*Chamoclea*, sic) [*Chamaeclea*]. NEW SYNONYMY. The Arizona specimens of this species given this name by Hill may be subspecifically distinct from *scira* but I do not regard them worthy of such recognition.

35. *gladiola* Barnes, 1907. Canad. Ent. 39:67 (*Chamaeclea*, sic) [*Chamaeclea*].

36. *requies* Dyar, 1909. Ent. Soc. Wash., Proc. 11:21-22 (*Centrartha*, sic) [*Centrarthra*].

Species group XII: *C. atrolinea* and allies

Figure 17

Description

General. Size medium-small, expanse about 28mm. Frontal protuberance a transverse, shallow trough with a ventral, external node, a low, semi-circular ridge below this on frons. Foretibial "claw" moderately strong, flattened, arising from slightly produced tibial apex. Forewing apex rounded, tornus mod-

erately sharp; pattern varied with regard to presence or absence of elements but extremely constant in position and color: ground color orange-yellow, markings black, thin zigzagging lines, median shade complete, lunules marked. Hindwing fuscous. Thoracic vestiture hairy; tufts poorly developed.

Male genitalia. Tegumen moderately broad, neck short, erect. Uncus moderately long, sharply curved basad, swollen distad. Saccus elongate, rounded cephalad. Valve oblong, slightly upcurved; costa expanded somewhat obliquely; basal sacculus division broad, somewhat inflated, ending diffusely, lobe a long, curved finger; distal division lobes about equal, in length, directed at right angles, basal lobe fingerlike, distal lobe spinelike; coronal setae slender, few. Phallus vesica normal; cornuti moderately long, stout peripherad, short and thin centrad, secondary group of a few, unequal, fairly long spines. Anellus sclerites triangular, approximate cephalad. Juxta subquadrate. VIII tergal sclerotization V-shaped; sternal sclerotization U-shaped.

Female genitalia. Postapophysis almost one-third longer than antapophysis. Ventral margins of VIII approximate caudad. Ill-defined lamella postvaginalis filling entire space between ventral VIII margins. Ductus bursae heavily sclerotized and fused with lamellae. Corpus bursae elongate; lobe simple; sclerotization and ribbing strong.

Included species

37. *atrolinea* Barnes and McDunnough, 1912. Contrib. Nat. Hist. Lepid. N. Amer. 1:25, pl. 1, fig. 3 (*Antaplaga*).

38. *dela* Druce, 1894. Ann. Mag. Nat. Hist., Ser. 6, 13:361 (*Acontia*).

39. *stigmata* Dyar, 1912. U. S. Natl. Mus., Proc. 42:67 (*Antaplaga*).

40. *hemicrocea* Dyar, 1912. U. S. Natl. Mus., Proc. 42:67-68 (*Antaplaga*).

These four species are considered by Draudt (1919-1939:324) as two species, *dela* and *atrolinea* with *stigmata* and *hemicrocea* as forms of *dela*. He mentions, however, that even *atrolinea* may be nothing more than a northern form of *dela*. I tend to concur with the latter view although there is some possibility that *hemicrocea*, which is the most distinctive in wing pattern, may actually constitute a separate species. These forms need further study to determine their proper status.

Genus 3: *GORGORA*

1914, *Gorgora* Dyar. U. S. Natl. Mus., Proc. 47:377. Type species: *G. morga* Dyar, 1914; Mexico City, Mexico; monobasic.

Remarks

There is only a single species group containing one species in this genus but it is so distinct from the other members of major phyletic line 3 on the basis of the male genitalia that I choose to recognize its original generic status even though the female genitalia do not deviate from the type typical of the line.

Dyar described this genus originally in the subfamily Erastriinae (Acon-

tiinae) possibly by reason of its gaudy colors. It has now been shifted to an entirely different subfamily removing an enigma for the acontiine specialists.

Description

See description of species group below.

Species group XIII: *G. morga*

Figure 18

Description

General. Size medium, expanse about 32mm. Frontal protuberance a simple, rough oblong plateau slightly hollowed dorsad, a low semicircular ridge below this on frons. Foretibial "claw" moderately stout, arising from slightly produced tibial apex; plantar bristles long with rounded tips. Forewing shape somewhat elongate, margins somewhat convex, apex and tornus rounded; pattern unique: ground color shining black with a large quadrangular, orange discal spot, marginal area orange, lunules black. Hindwing fuscous. Thoracic vestiture hairy, orange; tufts poorly developed.

Male genitalia. Tegumen broad, ventral arms moderately long, neck very short and erect. Uncus moderately long, gradually curving, slightly swollen subapically; setae numerous, moderately long. Valve triangular-oblong; costa moderately expanded; basal sacculus division very broad, ending diffusely, lobe a short pommel; distal division with a single, unequally forked, heavily sclerotized lobe, arising mesad; corona represented by two, very short, stout apical setae. Phallus vesica normal; cornuti moderately long, stout peripheral, diminutive centrad, secondary patch a curved row of short spinelets. Anellus sclerites crescent-shaped. Juxta subquadrate. VIII tergal sclerotization V-shaped; sternal sclerotization square.

Female genitalia. (Described from photograph of holotype.) Ovipositor lobe of primitive, flat, blunt type, striae distinct. Postapophysis almost one-fourth longer than antapophysis. VIII pleuron with an elongate, median unsclerotized area containing distinct striae, ventral margin defined but not deflected, contiguous mesad with opposite margin. No special, complex sterno-ostial concavity present. Lamellae not determinable from photograph. Corpus bursae elongate; lobe simple; sclerotization and ribbing strong.

Included species

41. *morga* Dyar, 1914. U. S. Natl. Mus., Proc. 47:378 (*Gorgora*).

Genus 4: **CHICHIMECA** Hogue, new genus

Type species: *Eulithosia thoracica* Edwards, 1884; Arizona.

Remarks

The peculiar degenerate nature and fairly numerous species of the single primary phyletic unit XIV of the fourth major phyletic line make it desirable

to recognize it as a distinct genus. No other name being available, I propose the new genus *Chichimeca*.

The genus is made up of several species formerly placed in the nominal genus *Antaplaga*. The general appearance of these was responsible largely for a few *Grotella* species and *Plagiomimicus alesaea* being lumped into this genus. All have similar facies and self-colored, white (rarely yellow-orange) wings but, of course, are distinct structurally.

Description

See description of species group below.

Species group XIV: *C. thoracica* and allies

Figure 19

Description

General. Size medium-small to small, expanse about 22-32mm. Frontal protuberance a circular to oval ring inclosing a subcentral, truncate secondary prominence. Foretibial "claw" quite stout, shovel-shaped, arising from moderately produced, straight tibial apex. Forewing shape elongate, all margins moderately convex, apex acute, tornus broadly rounded; pattern absent, self-colored, sooty white to yellow-orange. Hindwing varied in color, usually like forewing, pattern obsolete. Thoracic vestiture somewhat hairy, tufts poorly developed.

Male genitalia. Tegumen moderately broad, neck short and erect. Uncus moderately long, cylindrical, slightly swollen mesad or subapically, slightly undulate; setae sparse and short. Saccus oblong, nipped cephalad. Valve oblong, slightly curved; costa greatly expanded; basal sacculus division short, lobe pommel-shaped; distal division with a single, small spikelike lobe arising mesad; corona weak, usually running obliquely onto inner surface of valve. Phallus vesica normal; cornuti numerous, short, spiculate, secondary group a short row of spinelets. Anellus sclerites crescent-shaped, fused. Juxta shield-shaped. VIII tergal sclerotization narrowly U-shaped; sternal sclerotization U-shaped, arms broad.

Female genitalia. Attenuated. Ovipositor lobe of primitive flat, blunt type, striae distinct. Postapophysis about one-fifth longer than antapophysis, both very slender and attenuated. VIII pleuron with an elongate, median, unsclerotized area containing distinct striae, ventral margin defined and slightly deflected, approximate with opposite margin caudad, diverging out around lamella postvaginalis and associated with it and l. antevaginalis to form an ill-defined sterno-ostial concavity. Lamella postvaginalis elongate, oval; l. antevaginalis weak, ligulate, bowed cephalad. Ductus bursae entirely membranous. Corpus bursae elongate, constricted gradually mesad; lobe simple, pointed; sclerotization and ribbing obsolescent.

Remarks

The species in this group are quite uniform. Several nominal species

among the smaller white forms (numbers 44-51) may be synonymized upon further study.

Included species

42. *thoracica* Edwards, 1884. Papilio 4:44 (*Eulithosia*).
43. *spretata* Draudt, 1927 in Seitz. Macrolepid. World 7:325, pl. 47, row a (*Antaplagia*).
44. *subfumosa* Dyar, 1909. Ent. Soc. Wash., Proc. 11:25-26 (*Antaplagia*).
45. *anaemica* Draudt, 1927 in Seitz. Macrolepid. World 7:324, pl. 46, row k (*Antaplagia*). Originally described as a new form of *subfumosa*. Its exact status in this difficult group awaits further study.
46. *salacon* Druce, 1895. Ann. Mag. Nat. Hist., Ser. 6, 16:39 (*Grotella*).
47. *simplicia* Dyar, 1926. Insec. Incit. Mens. 14:185 (*Antaplagia*).
48. *dulcita* Schaus, 1898. N. Y. Ent. Soc., J. 6:144 (*Grotella*).
49. *pseudovarra* Dyar, 1926. Insec. Incit. Mens. 14:184 (*Antaplagia*).
50. *varrara* Dyar, 1918. U. S. Natl. Mus., Proc. 54:350 (*Antaplagia*).
51. *muricolor* Dyar, 1926. Insec. Incit. Mens. 14:184 (*Antaplagia*).

Genus 5. *CIRRHOPHANUS*

- 1812, *Cirrhophanus* Grote. Canad. Ent. 4:187. Type species: *C. triangulifer* Grote, 1872; Missouri ?; monobasic.
- 1884, *Eulithosia* Edwards. Papilio 4:43. Type species: *E. composita* Edwards, 1884; Arizona; selection of Hampson, 1910. Catalogue Lepid. Phalaenae Brit. Mus. 9:384. NEW SYNONYMY.
- 1910, *Hoplolythra* Hampson. Catalogue Lepid. Phalaenae Brit. Mus. 9:214. Type species: *Lythrodus discistriga* Smith, 1903; syntypes: Walter's Station, California, Southern Arizona; monobasic. NEW SYNONYMY.
- 1918, *Pumora* Dyar. U. S. Natl. Mus., Proc. 54:348. Type species: *P. hyperion* Dyar, 1918; Cuernavaca, Mexico; monobasic. NEW SYNONYMY.

Remarks

This genus, comprising major phyletic line 5, is, like *Plagiomimicus*, another large and somewhat unwieldy assemblage of primary phyletic units. There is greater uniformity of structure here, however. The female genitalia are consistently similar, the special sterno-ostial concavity always being present as a rounded depression between well defined and moderately deflexed or declining ventral margins of the VIII abdominal pleura. The latter have a large V-shaped unsclerotized median area sometimes containing striae. The ovipositor lobe is generally of the typical primitive, flat, blunt type but a few secondary, relatively minor modifications of this occur. The wing pattern is characteristically streaked and orange is a frequent ground color.

Most of the atypical members of this genus have in common a multiple foretibial "claw," which immediately classes them as derivative. Simplified wing

pattern and small size are other more conspicuous, derivative features. Some of these atypical forms have had separate generic status formerly, e.g., *Pumora* (unit XXI) and *Hoplolythra* (unit XX). These may prove to be valid with future study. For the present, however, I choose to recognize a large, encompassing genus to emphasize similarities rather than dissimilarities.

Description

General. A large and varied genus. Size small to medium-large. Frontal protuberance usually an oval to reniform ring with lower lip mesally produced into a conical, secondary prominence or an inverted, heart-shaped ring with a central, truncate, secondary prominence (*chryseochilus* only). Foretibial "claw" a single seta, a group of two or three separate setae or a multiple group of fused setae. Forewing shape fairly constant, angles slightly rounded, tornus often sharply angled; pattern varied but usually with streaks due to darkened veins and lines between veins (streaks in cell Cu often forming a trident, three pronged figure, with base distad); colors varied but usually orange or yellowish-orange with darker orange or brown markings. Hindwing varied in color (may be bicolored: black and orange), markings obsolete. Thoracic vestiture quite varied, almost always of spatulate or broad scales; tufts strong, the normal stiriine tufts present plus additional mesoscutal tufts in some.

Male genitalia. Tegumen broad, neck short to very long. Uncus usually fairly long and curving. Valve usually rhomboid-oblong or simply oblong; costa expanded variously; basal sacculus division moderately long, lobe usually short but may be quite long; distal division with at least one lobe which is usually distal and spinelike but sometimes two lobes present which are close together (even on common plate); corona always weak. Phallus vesica normal, simple (with small appendicular lobe in *chryseochilus*); cornuti varied, primary group usually of numerous, long spines, secondary group usually present and composed of short spinelets.

Female genitalia. Ovipositor lobe varied, usually pointed and with striae, not markedly modified from primitive stiriine flat, blunt type. VIII pleuron with an elongate, median unsclerotized area (containing weak striae in some), ventral margin defined and moderately deflexed or declining cephalad, approximate caudad with opposite margin and curving or diverging cephalad around lamella postvaginalis and associated with it and I. antevaginalis to form a special, complex sterno-ostial concavity, latter usually circular or subquadrate in shape. Lamella postvaginalis round or somewhat reduced and ill-defined; I. antevaginalis ligulate, bowed. Corpus bursae very varied in shape (see descriptions of species groups); sclerotization and ribbing almost always strong.

Species group XV: *C. chryseochilus*

Figure 20

Description

General. Size medium, expanse about 33mm. Frontal protuberance an inverted, heart-shaped ring inclosing a subcentral, truncate secondary promi-

nence, latter barely exceeding height of ring. Foretibial "claw" a single, shovel-shaped seta arising from moderately produced tibial apex. Forewing apex acute, sharp, tornus sharp; pattern complex, basically noctuiform: ground color purplish-brown basad, veins dark producing streaked pattern, streaks in cell Cu forming a trident, marginal sector brownish-yellow, AM line obsolescent, PM line strong. Hindwing brown, markings absent. Thoracic vestiture mixed, mostly of linear scales; tufts normal.

Male genitalia. Tegumen broad, ventral arms short, neck very long. Uncus long, cylindrical, gradually curving. Saccus oblong. Valve oblong, slightly up-curved; basal sacculus division moderately long, lobe short; distal division with a single, long, basal, fingerlike lobe; corona weak. Phallus vesica with an appendicular lobe; cornuti few, moderately long, secondary group a patch of spinelets. Anellus sclerites triangular. Juxta rectangular. VIII tergal sclerotization V-shaped; sternal sclerotization U-shaped, arms broad.

Female genitalia. Ovipositor lobe convex, well sclerotized, sagittate, striae obsolescent. Postapophysis about one-fourth longer than antapophysis, both slender, latter somewhat spatulate. VIII pleuron with a large, V-shaped, median unsclerotized area containing weak striae, ventral margin moderately deflexed, curved. Sterno-ostial concavity ovoid. Lamella postvaginalis cleoid; I. antevaginalis ligulate. Corpus bursae ellipsoid; lobe simple; sclerotization and ribbing strong but restricted to extreme posterior end.

Included species

52. *chryseochilus* Dyar, 1909. Ent. Soc. Wash., Proc. 11:25 (*Basilodes*).

Species group XVI: *C. triangulifer* and allies

Figure 21

Description

General. Size medium to medium large, expanse about 34-50mm. Frontal protuberance a transverse, oval shallow cup with ventral lip mesally produced into a conical prominence. Foretibial "claw" a moderately strong, single seta or a few (2-3), small, separate setae (*triangulifer*) arising from slightly produced tibial apex. Forewing apex acute, rounded, tornus rounded; pattern complex: ground color yellow-orange, generally like preceding group but noctuiform elements more modified; transverse line orange, irregular, confused by longitudinal streaks, etc.; streaks in cell Cu forming a trident (base distad). Hindwing fuscous to yellow, sometimes only basal area fuscous; pattern obsolete. Thoracic vestiture of mixed scale types; strongly and complexly tufted: in addition to normal stiriine tufts anterior, dorsolateral and lateral mesoscutal tufts developed.

Male genitalia. Tegumen varied, moderately broad to fairly narrow, ventral arms and neck moderately long to short. Uncus of medium length, cylindrical and straight; setae numerous, slightly longer dorsad. Saccus elongate to stout, bluntly pointed cephalad. Valve oblong to rhomboid-oblong; costa ex-

panded obliquely; basal sacculus division moderately long, broader basad, ending diffusely, lobe a short peak or a very long, straight finger; distal division with two close lobes (on single plate in *triangulifer*), basal lobe fingerlike or lobulate, distal lobe spinelike with broad base; corona well developed. Phallus vesica normal; cornuti numerous, subequal, moderately long and stout, secondary group a curved patch of spinelets. Anellus sclerites crescent-shaped, separate. Juxta subquadrate. VIII tergal sclerotizations V- or U-shaped, tips of arms expanded; sternal sclerotization U-shaped, arms expanded.

Female genitalia. Ovipositor lobe of primitive, flat, blunt type, striae distinct. Postapophysis slightly longer than antapophysis. VIII pleuron with an elongate, median unsclerotized area (containing weak striae only in *dyari*); ventral margin moderately deflexed, curved. Sterno-ostial concavity round. Lamella postvaginalis round; I. antevaginalis ligulate. Corpus bursae varied in shape: usually tubular and curved (*dyari* and closest species), bulbous (*triangulifer*), lobe deflected laterad (*nigrifer*); sclerotization and ribbing strong.

Included species

53. *dyari* Cockerell, 1899. Canad. Ent. 31:288 (*Cirrophanus*, sic).

54. *dubifer* Dyar, 1907. N. Y. Ent. Soc., J. 15:109 (*Cirrhophanus*).

This species may prove to be indistinct from the preceding.

55. *nigrifer* Dyar, 1907. N. Y. Ent. Soc., J. 15:108 (*Cirrhophanus*).

56. *magnifer* Dyar, 1907. N. Y. Ent. Soc., J. 15:108 (*Cirrhophanus*).

57. *triangulifer* Grote, 1872. Canad. Ent. 4:187 (*Cirrhophanus*).

=*pretiosus* Morrison, 1875. Boston Soc. Nat. Hist., Proc. 18:122-123 (*Chariclea*). Synonymy of Grote, 1875. Check List Noctuidae Amer. N. of Mexico, pt. I, p. 12.

Species group XVII: *C. plesioglaucus* and *comstocki*

Figure 22

Description

General. Size medium, expanse about 32mm. Frontal protuberance a reniform ring with lower lip produced mesad into a conical prominence. Foretibial "claw" of multiple fused setae, arising from unproduced tibial apex. Forewing shape somewhat elongate, nearly elliptical; pattern unique: ground color with iridescent purpurescent cast, dark bronzy in distal sector (a wide, diffuse, white, median sector in *comstocki*), a few short, longitudinal, dark streaks. Hindwing fuscous. Thoracic vestiture exactly as in preceding group, even to coloration.

Male genitalia. Tegumen narrow, neck long and curved. Uncus short, cylindrical, tapering, straight; setae sparse and short. Saccus ellipsoid, stout. Valve rhomboid-oblong, a sharp angle dorsobasad; costa barely expanded; basal sacculus division long, nearly confluent with distal division, lobe a low peak; distal division produced distad into a strong, long, spinelike lobe; corona

absent. Phallus vesica normal; cornuti stout, short, heavier distad and on distinct sclerotized plate, weaker basad, secondary group a patch of sharp denticles. Anellus sclerites crescent-shaped. Juxta kite-shaped. VIII tergal sclerotization square with open end; sternal sclerotization broadly U-shaped, arms expanded.

Female genitalia. Ovipositor lobe slightly modified from primitive flat, blunt type: slightly pointed and upcurved, striae distinct. Postapophysis slightly longer than antapophysis. Pleuron with a V-shaped unsclerotized median area (no striae), ventral margin moderately deflexed. Sterno-ostial concavity subtriangular. Lamellae indistinct. Corpus bursae oblong; lobe simple; sclerotization and ribbing strong.

Included species

58. *plesioglaucus* Dyar, 1912. U. S. Natl. Mus., Proc. 42:68 (*Antaplaga*).

59. *comstocki* Hill, 1924. So. Calif. Acad. Sci., B. 23:184, pl. 3, fig. 6 (*Chamoclea*, sic) [*Chamaeclea*]. This species is very close to the preceding and considered synonymous with it or as a subspecies by some authors. I consider it a distinct species here and leave the determination of its proper status to future studies.

Species group XVIII: *C. papago* and *miaiphona*

Figure 23

Description

General. Size medium, expanse about 28-35mm. Frontal protuberance large, an inverted heart-shaped ring with lower lip produced mesad into a conical prominence. Foretibial "claw" of multiple fused setae, arising from unproduced tibial apex. Forewing apex acute, rounded, tornus rounded; pattern fairly simple: ground color yellow-orange with diffuse reddish or orange transverse lines, veins streaked, streak through cell Cu simple, not like a trident. Thoracic vestiture hairy; tufts poorly developed.

Male genitalia. Tegumen moderately broad, neck short. Uncus moderately long, convex, straight; setae numerous, short, subequal. Saccus ellipsoid, pointed. Valve rhomboid-oblong; costa expanded obliquely; basal sacculus division moderately long, ending diffusely, lobe a short peak; distal division with single broad, short spinelike lobe; corona weak, somewhat diffuse. Phallus vesica inflated sinistrad; cornuti subequal, short and stout, secondary group a long, curved row of sharp, equal spinelets. Anellus sclerites crescent-shaped. Juxta rectangular. VIII tergal sclerotization square, tips of arms expanded; sternal sclerotization U-shaped.

Female genitalia. Ovipositor lobe of primitive, blunt, flat type, striae absent. Postapophysis slightly longer than antapophysis. Pleuron with an elongate median unsclerotized area (no striae), ventral margin moderately deflexed, nearly parallel with opposite margin. Sterno-ostial concavity subquadrate. Lamella postvaginalis weak, rectangular. Corpus bursae oblong; lobe simple; sclerotization and ribbing strong.

Included species

60. *papago* Barnes, 1907. Canad. Ent. 39:95-96 (*Cirrhophanus*).

61. *miaiphona* Dyar, 1912. U. S. Natl. Mus., Proc. 42:69-70 (*Cirrhophanus*).

Species group XIX. *C. hoffmanni*

There is only a single known specimen of this species (62.), a female. It is a new species and described in the appendix.

Species group XX: *C. discistrigus*

Figure 24

Description

General. Size medium-small, expanse about 25-30mm. Frontal protuberance small, a reniform ring with lower lip produced mesad into a conical prominence. Foretibial "claw" small, of multiple fused setae arising from unproduced tibial apex. Forewing apex acute, rounded, tornus very slightly toothed; pattern vaguely similar to preceding unit: ground color brownish-yellow, streaked by darker veins, streaks intense and broadened distad especially on fringe, diffuse brownish-orange stain in discoidal and basal areas. Hindwing orange, markings obsolete. Thoracic vestiture entirely of spatulate scales; tufts normal, small anterior mesoscutal tufts developed.

Male genitalia. Tegumen medium, neck long and curved. Uncus moderately long, cylindrical, swollen mesad. Saccus short, pointed. Valve rhomboid-oblong, costa moderately expanded; basal sacculus division moderately long, ending in a sharp corner, lobe pommel-shaped; distal division distally produced into a short, sharp spine; corona weak. Phallus vesica normal; cornuti short and stout distad, changing to broad, uncinat spicules basad, discrete secondary group absent. Anellus sclerites crescent-shaped, fused. Juxta elongate, shield-shaped. VIII tergal sclerotization U-shaped, angles sharply produced; sternal sclerotization U-shaped, arms expanded.

Female genitalia. Ovipositor lobe short, pointed, nearly deltoid, upcurved, tip strongly sclerotized, partially unsclerotized basad, with weak striae. Postapophysis slightly longer than antapophysis, both stout. VIII pleuron with a V-shaped, median unsclerotized area (no striae), ventral margin moderately deflexed, nearly parallel with opposite margin. Sterno-ostial concavity ovoid. Lamella postvaginalis weakly defined, chevron-shaped; l. antevaginalis ligulate. Ductus bursae sclerotized and ribbed (especially on side toward corpus lobe). Corpus bursae ellipsoid, curved; lobe simple; sclerotization and ribbing strong.

Remarks

Hampson erected the genus *Hoplolythra* for this species and as indicated by the derivation of the name and placement of the species, he agreed with Smith, the original describer, on a relationship to *Lythrodes*. Both taxa do have similarly streaked forewings but are abundantly distinct structurally.

Included species

63. *discistrigus* Smith, 1903. Amer. Ent. Soc., Trans. 29:207 (*Lythrodus*).

Species group XXI: *C. compositus* and *hyperion*

Figure 25

Description

General. Size small, expanse about 20-25mm. Frontal protuberance a reniform to heart-shaped ring with lower lip produced mesad into a conical prominence. Foretibial "claw" of multiple fused setae (? *hyperion*), arising from unproduced tibial apex. Forewing apex acute, rounded; pattern of two types: (1) self-colored, yellow-orange, fringe brown (*compositus*), (2) bi-colored, median sector yellow, distal and basal sectors chocolate-brown (*hyperion*). Hindwing fuscous to yellow-orange, markings obsolete. Thoracic vestiture of mixed, linear and spatulate scales; tufts poorly developed.

Male genitalia (unknown for *hyperion*). Tegumen narrow, neck moderately long. Uncus moderately long, cylindrical, tapered, curved; setae sparse and tiny. Saccus rhomboid. Valve ellipsoid-elongate; costa moderately expanded; basal sacculus division moderately long, ending diffusely, lobe a broad, low mound; distal division with small, pointed, erect lobe; corona obsolete. Phallus vesica elongate; cornuti moderately long, equal, few and restricted to a small patch at far distal end, secondary group absent from normal position, a loose patch of broad, uncinat spicules located basad instead. Anellus sclerites triangular, nearly fused. Juxta rectangular. VIII tergal sclerotization V-shaped; sternal sclerotization round.

Female genitalia. Ovipositor lobe broad, pie-shaped with slightly up-curved tip, striae distinct. Postapophysis about one-third longer than antapophysis, both quite short. Pleuron with elongate, median unsclerotized area (no striae), ventral margin moderately deflected. Sterno-ostial concavity subquadrate, small. Lamella postvaginalis subquadrate; l. antevaginalis ligulate, well defined. Ductus bursae very long and slender, well sclerotized and ribbed, especially on lobe side. Corpus bursae ovate and transverse; lobe not defined; ductus seminalis at tip directed at right angle to ductus bursae; corpus entirely membranous.

Remarks

Since *hyperion* is a rare species and known only from females, I have not been able to study it completely to definitely substantiate its placement in this group. The female genitalia are virtually identical to those of *compositus* as far as I can determine. The type of genitalia is peculiar (very long ductus bursae and transverse corpus bursae) so it would appear improbable that the similarity is spurious.

Included species

64. *compositus* Edwards, 1884. Papilio 4:44 (*Eulithosia*).

65. *hyperion* Dyar, 1918. U. S. Natl. Mus., Proc. 54:348 (*Pumora*).

Genus 6: **CUAHTEMOCA** Hogue, new genusType species: *Chalcopasta chalcocraspedon* Dyar, 1913; Zacualpan, Mexico.*Remarks*

The single species and species group of major phyletic line 6 is worthy of generic distinction on the basis of its relictual, annectant status. No other name being available, I propose the new genus *Cuahtemoca*.

Description

See the description of the single species group below.

Species group XXII: *C. chalcocraspedon*

Figure 26

Description

General. Size medium, expanse about 30-35 mm. Frontal protuberance a heart-shaped ring inclosing a ventral, conical prominence. Foretibial "claw" rounded, a single seta arising from slightly produced tibial apex. Forewing apex acute, sharp, tornus sharp, outer margin slightly concave below apex; pattern noctuiform: ground color brown in median sector, brassy gold in marginal and basal sectors and in reniform and orbicular, scattered blue scales along costal area. Hindwing grey-brown, exterior line evident. Thoracic vestiture entirely of spatulate, dentate scales; tufts normal, anterior mesoscutal tuft developed.

Male genitalia. Tegumen moderately broad, neck long. Uncus moderately long, cylindrical, straight; setae moderately dense, longer dorsad. Saccus short, pointed. Valve rhomboid-oblong, apex rounded; costa slightly expanded; basal sacculus division long, confluent with distal division, lobe a short point; distal division with two close lobes: basal long, fingerlike, distal shorter, sclerotized, spinelike. Phallus vesica normal; cornuti very numerous, long and equal, secondary group absent. Anellus sclerites crescent-shaped, separated. Juxta shield-shaped. VIII tergal sclerotization U-shaped, base and tips of arms expanded; sternal sclerotization nearly circular.

Female genitalia. Ovipositor lobe sagittate, evenly sclerotized, points blunt, striae obsolescent. Postapophysis slightly longer than antapophysis, both slender. VIII pleuron with an elongate, unsclerotized median area containing obsolescent striae, ventral margin defined, moderately deflexed cephalad, arching cephalad; with opposite margin inclosing a depressed lamella postvaginalis and associated with it and 1. antevaginalis to form a special, complex, oval sterno-ostial concavity. Lamellae ligulate, bowed. Ductus bursae short, membranous. Corpus bursae elongate, curved, slightly swollen mesad; lobe simple, ventral; sclerotization and ribbing moderately strong.

Included species

66. *chalcocraspedon* Dyar, 1913. U. S. Natl. Mus., Proc. 44:297 (*Chalcopasta*).

Genus 7: *CHALCOPASTA*

- 1910, *Chalcopasta* Hampson. Catalogue Lepid. Phalaenae Brit. Mus. 9:218. Type species: *Basilodes territans* Edwards, 1884; Arizona; by original designation.
- 1912, *Rodriguesia* Dyar. Ent. Soc. Wash., Proc. 14:61. Type species: *Deva ornata* Ottolengui, 1898; Hot Springs, New Mexico; monobasic (= *Chalcopasta howardi* Edwards, 1877; Prescott, Arizona; synonymy of Barnes and McDunnough, 1916. Contrib. Lepid. N. Amer. 3:167-168).

Remarks

As discussed in the phylogeny section, major phyletic line 7 divides into two main sections primarily on the basis of the development of the lobes of the distal sacculus division: (1) a basal, fingerlike lobe or (2) a distal, spinelike lobe. The genus *Chalcopasta*, as here defined, stands for the first section. One unit, XXIII (*C. ellica*), has both lobes developed but since the distal lobe is reduced and the wings have areas of brilliant gold and other character states resemble more those of the first section, this unit is placed with them.

With regard to the identity of *Deva ornata* Ottolengui, 1898, Barnes and McDunnough (1916:167-168) state: "We have carefully examined the type in the National Museum and find that in maculation, squamation, and structure it is an exact match of *Chalcopasta howardi* with the exception of the palpi which are strongly upturned and entirely different to those of *howardi*. Although we could find no trace of glue or shellac we strongly incline to the opinion that the head has been neatly glued on the specimen in question, as we cannot believe that two species could resemble each other so exactly in every detail except the palpi. It would be necessary for the specimen to be relaxed to prove our contention and we must leave this to one of the curators of the museum." I am informed by J. G. Franclemont (personal communication), a recent curator at the National Museum, that this specimen has been relaxed and the head found in fact to be glued on. Dyar's erection of the genus on the basis of the long palpi was, therefore, erroneous. The otherwise detailed resemblance to *howardi* and others of the genus *Chalcopasta* requires the sinking of *Rodriguesia* under *Chalcopasta*.

Description

General. Size medium to medium-large; facies robust. Frontal protuberance a circular to oval ring inclosing a subcentral or central, conical prominence. Foretibial "claw" flattened and shovel-shaped, arising from strongly produced and sometimes slightly angled tibial apex. Forewing apex acute, sharp, tornus rounded, outer margin entire, undulate slightly in some; basic, brown noctuiform pattern overrun by discrete fields of brilliant metallic gold. Thoracic vestiture of varied scale types; tufts normal, tegular tufts often strongly erect.

Male genitalia. Tegumen moderately broad, neck long and arched to short and straight. Uncus moderately long to long, cylindrical and straight; setae

numerous and short. Valve oblong, apex rounded; costa barely expanded; basal sacculus division long, ending diffusely, lobe only a low mound; distal division normally with one basal, erect, fingerlike lobe but may also have a short, distal spinelike lobe or no lobes present at all, when latter, a spur at distal end pointing ventrad; coronal setae slender and restricted to dorsodistal margin of valve, or absent altogether. Phallus vesica usually normal in shape but may be swollen distad or tubular and coiled once; cornuti numerous, varied in shape. Anellus sclerites crescent-shaped or scutate. Juxta rectangular or shield-shaped. VIII tergal sclerotization narrowly V-shaped; sternal sclerotization U-shaped or circular.

Female genitalia. Ovipositor lobe varied, sagittate to acuminate, always heavy and well sclerotized, weak striae rarely present, usually striae absent. Postapophysis subequal to or slightly longer than antapophysis. VIII pleuron with an elongate, median, unsclerotized area without striae (weak striae in *ellica*), ventral margin defined, moderately deflexed or strongly declining cephalad, diverging or curving out cephalad; with opposite margin inclosing a depressed lamella postvaginalis and associated with it and l. antevaginalis to form a special, complex sterno-ostial concavity. Lamella postvaginalis oval to ligulate; l. antevaginalis ligulate, bowed. Corpus bursae quite varied in shape: usually ellipsoid-oblong, sometimes cudgel-shaped or fusiform; lobe normal or displaced laterad (one species: *restricta*); sclerotization and ribbing strong.

Species group XXIII: *C. ellica*

Figure 27

Description

General. Size medium, expanse about 30mm. Frontal protuberance a rough, heart-shaped plateau with no discrete secondary prominence. Foretibial "claw" heavy, shovel-shaped, arising from strongly produced, straight tibial apex. Forewing apex acute, sharp, tornus rounded, costal margin very straight; pattern basically noctuiform, irrorated brown but extensively overrun in distal and basal areas by brilliant metallic gold, reniform and orbicular (and sometimes area between) also filled with this color. Hindwing brown, pattern obsolete. Thoracic vestiture of linear scales; tufts normal but somewhat poorly developed.

Male genitalia (described from photograph). Tegumen moderately broad, neck long, arched. Uncus moderately long, cylindrical, slightly tapering, straight; setae numerous, short. Valve oblong, apex rounded; costa barely expanded; distal sacculus division with two lobes: basal erect, fingerlike, distal short, broad, spinelike; coronal setae slender. Juxta shield-shaped. States of other characters not determinable from photograph.

Female genitalia. Ovipositor lobe bluntly pointed, striae weakly developed. Postapophysis about one-fourth longer than antapophysis. VIII pleuron with an elongate median unsclerotized area containing weak striae. Sterno-ostial concavity deltoid. Lamella postvaginalis rectangular; l. antevaginalis

ligulate. Ductus bursae membranous, becoming abruptly sclerotized and ribbed about halfway. Corpus bursae cudgel-shaped; lobe simple; sclerotization and ribbing strong.

Included species

67. *ellica* Dyar, 1915. Insec. Incit. Mens. 3:80 (*Chalcopasta*). This species is incorrectly labeled as *fulgens* by Draudt (1919-1939. pl. 44, row k).

Species group XXIV: *C. territans* and allies

Figure 28

Description

General. Size medium to medium-large, expanse about 28-40mm.; very robust facies. Frontal protuberance a circular to oval ring inclosing a sub-central, conical prominence. Foretibial "claw" strong, flattened, arising from strongly produced tibial apex. Forewing apex acute, sharp, tornus rounded, outer margin slightly concave beneath apex; basic noctuiform pattern as in preceding group but even more extensively overrun by gold; reniform, apical patch, costal area, anterior end of PM line and basal area still exposed. Hindwing white to fuscous; pattern obsolete. Thoracic vestiture of spatulate, dentate scales, tufts normal, very well developed, tegular strongly erect.

Male genitalia. Tegumen moderately broad, neck short. Uncus long, cylindrical, straight; setae short, numerous. Valve oblong, apex rounded, slightly upcurved; costa moderately expanded; distal sacculus division with a single, erect, basal, fingerlike lobe; coronal setae slender. Phallus vesica sometimes expanded sinistrad; cornuti very numerous, short, stout, spiculate basad, longer and spinelike distad, secondary group a patch of sharp spinelets. Anellus sclerites crescent-shaped. Juxta rectangular. VIII tergal sclerotization narrowly V-shaped, tips of arms expanded; sternal sclerotization U-shaped.

Female genitalia. Ovipositor lobe small, acuminate, pointed, convex and heavily sclerotized (no striae). Postapophysis and antapophysis subequal, both fairly stout. VIII pleural unsclerotized area V-shaped, no striae. Sterno-ostial concavity oval to flask-shaped. Lamella postvaginalis oval to ligulate, posterior margin eroded; l. antevaginalis ligulate, bowed. Ductus bursae short, mostly membranous. Corpus bursae ellipsoid-oblong; lobe simple, ventral; sclerotization and ribbing strong.

Included species

The first seven species are difficult to separate on the basis of wing pattern. I suspect that there are actually fewer valid species.

68. *territans* Edwards, 1884. Papilio 4:45 (*Basilodes*).

= *arizona* French, 1889. Canad. Ent. 21:161 (*Plusia*). Synonymy of (?) Barnes and McDunnough, 1917. Check List Lepid. Boreal Amer., p. 71.

69. *anopis* Dyar, 1918. U. S. Natl. Mus., Proc. 54:348-349 (*Chalcopasta*).

70. *arianda* Druce, 1889. Biol. Cent. Amer., Heter. 1:329, pl. 30, fig. 11 (*Plusia*).
71. *chalcophanis* Dyar, 1918. U. S. Natl. Mus., Proc. 54:348 (*Chalcopasta*).
72. *pterochalcea* Dyar, 1909. Ent. Soc. Wash., Proc. 11:24-25 (*Basilodes*).
73. *riandana* Dyar, 1912. U. S. Natl. Mus., Proc. 42:69 (*Chalcopasta*).
74. *howardi* Edwards, 1877. Pacific Coast Lepid., No. 25, p. 1 (*Plusia*).
= *ornata* Ottolengui, 1898. Canad. Ent. 30:106-107, pl. 5, fig. 1 (*Deva* ?). See remarks under genus for synonymy.
75. *fulgens* Barnes and McDunnough, 1912. Contrib. Nat. Hist. Lepid. N. Amer. 1:25-26 (*Chalcopasta*). Figured in an earlier number in the same volume of the same series, 1(4):pl. 25, fig. 3. This species is incorrectly labelled as *ellica* by Draudt (1919-1939:pl. 44, row k).
76. *sinuata* Hampson, 1918. Nov. Zool. 25:152-153 (*Chalcopasta*).
77. *restricta* Hampson, 1918. Nov. Zool. 25:152-153 (*Chalcopasta*).

Species group XXV. *C. chalcotoxa* and allies

Figure 29

Description

General. Size medium, expanse about 27-30mm. Frontal protuberance a circular ring inclosing a central, conical prominence. Foretibial "claw" shovel-shaped, arising from moderately produced tibial apex. Forewing apex acute, sharp, tornus rounded; pattern basically noctuiform: ground color irrorated, dark brown, extensive oblique inroad (not as extensive as in two preceding species groups) of brilliant metallic gold in median sector (also in marginal sector in *acantha*), otherwise as preceding species group. Thoracic vestiture as in preceding species group.

Male genitalia. Of two types: (1) Like preceding unit except for phallus vesica which is swollen distad; cornuti of short spines displaced dorsad (*acantha*), (2) Peculiar. Tegumen narrow, neck short. Uncus long, slender, cylindrical, tapering and arched; setae sparse and short. Valve oblong, angular, wider distad; costa not expanded; distal sacculus division normal but without lobe as in preceding unit, instead produced distoventrad as a spurlike lobe (reduced on one valve in *acema*); corona absent. Phallus vesica tubular, coiled once; cornuti moderately long or long, secondary group absent. Anellus sclerites slender, crescent-shaped. Juxta elongate, rectangular. VIII tergal sclerotization narrowly V-shaped; sternal sclerotization circular, nearly solid in some (not *acantha*), only a subcentral, membranous area, a few small, lanceolate scales on posterior margin of latter (visible only in slide preparations).

Female genitalia. Generally the same as in preceding species group, but with two main peculiarities: (1) lobe of corpus bursae displaced cephalad so corner from which ductus seminalis leaves almost at middle (*acantha*), (2) corpus bursae fusiform (*acema* and *chalcotoxa*).

Included species

78. *acantha* Druce, 1889. Biol. Cent. Amer., Heter. 1:329; 3:pl. 30, fig. 13 (*Plusia*).

79. *chalcotoxa* Dyar, 1909. Ent. Soc. Wash., Proc. 11:25 (*Basilodes*).

80. *acema* Druce, 1889. Biol. Cent. Amer., Heter. 1:330; 3:pl. 30, fig. 14 (*Plusia*).

The last two species tend to intergrade and may actually constitute a single varied species.

Genus 8: *BASILODES*

1852, *Basilodes* Guenée. Hist. Nat. Ins. Spec. Gen. Lepid. Noc. II 6:358. Type species: *B. pepita* Guenée, 1852; Florida; monobasic.

1869, *Deobriga* Walker. Char. Undes. Lepid. Heter., p. 41. Type species: *D. chrysopasa* Walker, 1869; locality unknown; monobasic (= *Basilodes pepita* Guenée, 1852; Florida; synonymy of Hampson, 1910. Catalogue Lepid. Phalaenae Brit. Mus. 9:207).

1874, *Stiria* Grote. Buffalo Soc. Nat. Sci., B. 2:73. Type species: *S. rugifrons* Grote, 1874; Kansas, Colorado Territory; monobasic. Synonymy of Smith, 1882. Brooklyn Ent. Soc., B. 5:30, 35.

Remarks

As mentioned under the preceding genus, major phyletic line number 7 divides into two main sections on the basis of many features, principally the expression of either a basal or distal lobe on the distal sacculus division of the male valve. The dichotomy of brilliant, gold or dull-colored forewing is also important. The genus *Chalcopasta* represents the first section, the present genus *Basilodes* represents the second.

Basilodes antedates *Stiria* and is therefore the appropriate name for the genus. The tribe, however, retains the name Stiriini since according to the International Code of Zoological Nomenclature suprageneric names are based on priority and are not affected by synonymy.

One new species, *B. inquinatus*, is described herein (see appendix).

Description

General. A very compact, structurally uniform genus. Size medium to medium-large. Frontal protuberance varied, of two main types: (1) an oval to heart-shaped, shallow cup with a slightly convex ventral portion, (2) a heart-shaped ring inclosing a subcentral, truncate, low, conical prominence. Foretibial "claw" strong, setiform or shovel-shaped, arising from strongly produced tibial apex. Forewing apex acute, sharp, tornus rounded or sharp, often with slight fringe tooth; outer margin crenulate, general outline often somewhat sinuate and convex mesad; pattern primitively noctuiform, often with diffuse areas or general hue of brassy or yellow gold color, derived patterns varied but mostly of type similar to that in species group XXVII: ground color

yellow, transverse lines, reniform and orbicular weak, a large hexagonal or square macula mesad in inner area, a small dot in reniform. Thoracic vestiture very rough, of spatulate scales; tufts normal and heavy, tegular tufts erect.

Male genitalia. Tegumen moderately broad, somewhat inflated ventrad in some, neck long and arched. Uncus moderately long, cylindrical, swollen mesad or not, straight or slightly curved; setae dense and moderately long. Saccus varied, usually rectangular, pointed or nipped cephalad. Valve oblong, apex rounded; costa barely expanded; basal sacculus division long, ending diffusely, lobe a low mound; distal division with a strong, curved, distal, spine-like lobe and weakly developed basal setose verrucae, rarely developed into a lobe; corona fully developed. Phallus vesica varied, of two types: (1) elongate, without secondary group of cornuti, (2) normally pear-shaped with secondary group of cornuti; primary group of cornuti varied in length and stoutness but always quite numerous. Anellus sclerites seculate. Juxta rectangular or kite-shaped. VIII tergal sclerotization circular, sternal sclerotization U-shaped or circular.

Female genitalia. Ovipositor lobe heavily sclerotized and rigid; deltoid to saggitate in outline. Postapophysis somewhat larger than antapophysis, both moderately strong. VIII pleuron with a V-shaped, median unsclerotized area, ventral margin strongly deflexed and arching; with opposite margin inclosing a depressed lamella postvaginalis and associated with it and I. antevaginalis to form a special, complex sterno-ostial concavity. Lamella postvaginalis ligulate or crescent-shaped, eroded caudad; I. antevaginalis ligulate, bowed. Corpus bursae elongate, slightly curved and swollen mesad; lobe simple, ventral; sclerotization and ribbing moderate to very strong.

Species group XXVI: *B. chrysopis* and allies

Figure 30

Description

General. Size medium to medium-large, expanse about 30-40mm. Very robust facies. Frontal protuberance an oval to heart-shaped, shallow cup with slightly convex ventral portion. Foretibial "claw" moderately heavy, arising from strongly produced, straight tibial apex. Forewing apex acute, sharp, tornus rounded, outer margin crenulate, general outline somewhat sinuate; pattern noctuiform: ground color brassy or yellow-gold, brown median sector in most *chrysopis*, a small, eccentric, dark dot in reniform. Thoracic vestiture of spatulate, dentate scales; tufts normal, heavy.

Male genitalia. Tegumen moderately broad, inflated ventrad in *inquinatus* resulting in short vincular arms, neck long and arched. Uncus moderately long, cylindrical, swollen mesad, straight; setae dense, long, equal. Saccus rectangular, pointed or nipped cephalad. Valve rhomboid-oblong, apex rounded; costa barely expanded; distal sacculus division with strong, curved, distal spinelike lobe, sometimes also a weak (large in *pepita*), irregular basal lobe. Phallus vesica elongate; cornuti short to long, longer distad, secondary group absent.

Anellus sclerites seculate, approximate. Juxta rectangular. VIII tergal sclerotization V-shaped, tips of arms expanded; sternal sclerotization U-shaped to circular.

Female genitalia. Ovipositor lobe elongate to broadly sagittate, heavily sclerotized (no striae). Postapophysis somewhat longer than antapophysis. VIII pleuron with V-shaped unsclerotized area. Sterno-ostial concavity round, width about equal the width of sclerotized, ventral half of neighboring pleuron. Lamella postvaginalis semilunar; l. antevaginalis ligulate, bowed. Corpus bursae somewhat constricted at base of lobe; sclerotization and ribbing very strong.

Included species

81. *chrysopsis* Grote, 1881. Papilio 1:154-155 (*Basilodes*). This is an extremely variable species, having many intergrading forms. I think the following is one of these forms and, therefore, synonymize it with the present species.

= *catharops* Dyar, 1911. Ent. Soc. Wash., Proc. 13:64 (*Basilodes*).

NEW SYNONYMY.

82. *inquinatus* Hogue, new species. (See appendix).

83. *auratus* Schaus, 1911. Ann. Mag. Nat. Hist., Ser. 8, 7:47 (*Basilodes*).

84. *pepita* Guenée, 1852. Hist. Nat. Ins. Spec. Gen., Lepid. Noc. II 6:358; Noc. pl. 12, fig. 1 (*Basilodes*).

= *chrysopasa* Walker, 1869. Char. Undes. Lepid. Heter. pp. 41-42 (*Deobriga*). Synonymy of Hampson, 1910. Catalogue Lepid. Phalaenae Brit. Mus. 9:207.

Species group XXVII: *B. rugifrons* and allies

Figures 2-5

Description

General. Size medium to medium large, expanse about 28-40mm. Very robust. Frontal protuberance a heart-shaped ring inclosing a subcentral, truncate, conical prominence. Foretibial "claw" usually strong, shovel-shaped, arising from fairly strongly produced tibial apex. Forewing apex acute, sharp, tornus sharp with moderate fringe tooth, outer margin crenulate, general outline undulate; pattern: usually, ground color yellow, a hexagonal or quadrate brown macula halfway along the inner margin, a brown area spreading in from outer margin, PM and AM lines weak, brown, reniform and orbicular obsolescent, a small dot in former; this pattern modified strongly in a few: (1) all dark brown, markings barely showing, small silver discal spots (*dysnoa*), (2) wide suffused median sector, pattern generally obscure (*tachymora*). Thoracic vestiture of spatulate scales; tufts normal, heavy.

Male genitalia. Scarcely different from preceding species group. Uncus tending to be more curved; corona weaker. Phallus vesica of normal shape, not elongate; secondary group of cornuti present, a short row of spinelets. Juxta kite-shaped.

Female genitalia. Ovipositor lobe deltoid to saggitate, heavily sclerotized, convex. Postapophysis somewhat longer than antapophysis, both moderately strong. VIII pleuron with a V-shaped unsclerotized area. Sterno-ostial concavity oval, width about twice the width of sclerotized ventral half of neighboring pleuron. Lamella postvaginalis crescent-shaped; 1. antevaginalis ligulate. Corpus bursae normal; sclerotization and ribbing moderately strong.

Included species

85. *dysnoa* Dyar, 1912. U. S. Natl. Mus., Proc. 42:69 (*Chalcopasta*).

=*biforis* Draudt, 1926, in Seitz. Macrolepid. World 7:308, pl. 44, row 1 (*Chalcopasta*). Originally described as an aberration of *dysnoa* and considered as no more than a synonym by various authors but the synonymy needs re-examination.

86. *consuelus* Strecker, 1900. Lepid. Rhop. Heter., Suppl. 3, p. 34 (*Stiria*).

The next six species are very similar and several may be synonymized upon future study.

87. *rugifrons* Grote, 1874. Buffalo Soc. Nat. Sci., B. 2:73 (*Stiria*).

88. *ruficeps* Draudt, 1927, in Seitz. Macrolepid. World 7:310, pl. 45, row b (*Stiria*).

89. *colimae* Draudt, 1927, in Seitz. Macrolepid. World 7:310, pl. 45, row b (*Stiria*). There is question as to the identity of this species. Apparently the type material was never labelled as such and its repository is unknown. Judging from the figure accompanying the original description, I guess that this species may be at most a variation or subspecies of the preceding species. However, I leave the problem to future studies.

90. *intermixtus* Dyar, 1918. U. S. Natl. Mus., Proc. 54:349 (*Stiria*).

91. *ischune* Dyar, 1912. U. S. Natl. Mus., Proc. 42:70 (*Stiria*).

92. *mouris* Dyar, 1912. U. S. Natl. Mus., Proc. 42:70 (*Stiria*).

93. *sisaya* Dyar, 1912. U. S. Natl. Mus., Proc. 42:70 (*Stiria*).

94. *tachymora* Dyar, 1914. U. S. Natl. Mus., Proc. 47:375 (*Stiria*).

95. *dyari* Hill, 1924. So. Calif. Acad. Sci., B. 23:183-184, pl. 3, fig. 3 (*Stiria*).

96. *sulphureus* Neumoegan, 1882. Papilio 2:135 (*Stiria*).

=*demaculatus* Strand, 1916. Arch. Naturges. 81:165 (*Stiria*). Described originally as an aberration of *sulphurea* and considered as such by various authors.

GENERIC STATUS UNDETERMINED

97. *prepontendyta* Dyar, 1914. U. S. Natl. Mus., Proc. 47:375 (*Antaplaga*).

98. *primulina* Druce, 1889. Biol. Cent. Amer., Heter. 1:303; 3:pl. 28, fig. 10 (*Metoponia*). Hampson has given this species autonomous generic

standing (*Xanthiria* Hampson, 1910. Catalogue Lepid. Phalaenae Brit. Mus. 9:244-245). It would seem best to retain this combination until the species is better known and further studied.

99. *iticys* Dyar, 1914. U. S. Natl. Mus., Proc. 47:375-376 (*Stiria*).

100. *arivaca* Barnes, 1907. Canad. Ent. 39:66-67 (*Lythrodes*). The streaked forewing pattern is similar to certain members of the genus *Cirrhophanus* but a relationship is yet to be determined on a structural basis.

TABLE I
SUMMARY OF CLASSIFICATION AND COMPOSITION OF
PHYLETIC UNITS

GENERA	MAJOR PHYLETIC LINES	PRIMARY PHYLETIC UNITS— SPECIES GROUPS	SPECIES		
1. <i>Plagiomimicus</i> Grote, 1873	1	I.	1. <i>resolutus</i> Dyar, 1909 2. <i>ochoa</i> (Barnes, 1904)		
		II.	3. <i>laodamia</i> (Druce, 1890)		
		III.	4. <i>jalada</i> (Schaus, 1898) 5. <i>aureolus</i> (Edwards, 1882) 6. <i>bajae</i> Hogue, new species 7. <i>olvello</i> (Barnes, 1907) 8. <i>raglena</i> (Dyar, 1912) 9. <i>unicus</i> (B. & Benj., 1926) 10. <i>chalcospilans</i> (Dyar, 1918) 11. <i>laverna</i> (Druce, 1898) 12. <i>manti</i> (Barnes, 1904) 13. <i>dimidiatus</i> (Grote, 1877) 14. <i>corazona</i> (Schaus, 1898) 15. <i>astigmatosus</i> (Dyar, 1921) 16. <i>curiosus</i> (Neum., 1883) 17. <i>spumosus</i> (Grote, 1874) 18. <i>mavina</i> (B. & McD., 1910) 19. <i>hilli</i> (B. & Benj., 1923)		
		IV.	20. <i>expallidus</i> Grote, 1882 21. <i>triplagiatus</i> Smith, 1890 22. <i>pityochromus</i> Grote, 1873 23. <i>concinus</i> (Dyar, 1909)		
		V.	24. <i>tepperi</i> (Morrison, 1875)		
		VI.	25. <i>hutsoni</i> (Smith, 1907) 26. <i>olivalis</i> (B. & McD., 1916)		
		VII.	27. <i>haclita</i> (Barnes, 1904) 28. <i>sexseriatus</i> (Grote, 1881) 29. <i>biundulalis</i> (Zeller, 1872)		
		VIII.	30. <i>alesaea</i> (Dyar, 1918)		
			2	IX.	31. <i>psamathochromus</i> (Dyar, 1909) 32. <i>argyropoliis</i> (Dyar, 1914)
				X.	33. <i>phalaenoides</i> (Dyar, 1918)

TABLE I (continued)

GENERA	MAJOR PHYLETIC LINES	PRIMARY PHYLETIC UNITS— SPECIES GROUPS	SPECIES
2. <i>Chrysoecia</i> Hampson, 1910	3	XI.	34. <i>scira</i> (Druce, 1889) 35. <i>gladiola</i> (Barnes, 1907) 36. <i>requies</i> (Dyar, 1909)
		XII.	37. <i>atrolinea</i> (B. & McD., 1912) 38. <i>dela</i> (Druce, 1894) 39. <i>stigmatorosa</i> (Dyar, 1912) 40. <i>hemicrocea</i> (Dyar, 1912)
3. <i>Gorgora</i> Dyar, 1914		XIII.	41. <i>morga</i> Dyar, 1914
4. <i>Chichimeca</i> new genus	4	XIV.	42. <i>thoracica</i> (Edwards, 1884) 43. <i>spretta</i> (Draudt, 1927) 44. <i>subfumosa</i> (Dyar, 1909) 45. <i>anaemica</i> (Draudt, 1927) 46. <i>salacon</i> (Druce, 1895) 47. <i>simplicia</i> (Dyar, 1926) 48. <i>dulcita</i> (Schaus, 1898) 49. <i>pseudovarria</i> (Dyar, 1926) 50. <i>varrara</i> (Dyar, 1918) 51. <i>muricolor</i> (Dyar, 1926)
5. <i>Cirrhophanus</i> Grote, 1872	5	XV.	52. <i>chryseochilus</i> (Dyar, 1909)
		XVI.	53. <i>dyari</i> Cockerell, 1899 54. <i>dubifer</i> Dyar, 1907 55. <i>nigrifer</i> Dyar, 1907 56. <i>magnifer</i> Dyar, 1907 57. <i>triangulifer</i> Grote, 1872
		XVII.	58. <i>plesioglaucus</i> (Dyar, 1912) 59. <i>comstocki</i> (Hill, 1924)
		XVIII.	60. <i>papago</i> Barnes, 1907 61. <i>miaiphona</i> Dyar, 1912
		XIX.	62. <i>hoffmanni</i> Hogue, new species
		XX.	63. <i>discistrigus</i> (Smith, 1903)
		XXI.	64. <i>compositus</i> (Edwards, 1884) 65. <i>hyperion</i> (Dyar, 1918)
6. <i>Cuahtemoca</i> new genus	6	XXII.	66. <i>chalcocraspedon</i> (Dyar, 1913)

TABLE I (continued)

GENERA	MAJOR PHYLETIC LINES	PRIMARY PHYLETIC UNITS— SPECIES GROUPS	SPECIES
7. <i>Chalcopasta</i> Hampson, 1910	7	XXIII.	67. <i>ellica</i> Dyar, 1915
		XXIV.	68. <i>territans</i> (Edwards, 1884) 69. <i>anopis</i> Dyar, 1918 70. <i>arianda</i> (Druce, 1889) 71. <i>chalcophanis</i> Dyar, 1918 72. <i>pterochalcea</i> (Dyar, 1909) 73. <i>riandana</i> Dyar, 1912 74. <i>howardi</i> (Edwards, 1877) 75. <i>fulgens</i> B. & McD., 1912 76. <i>sinuata</i> Hampson, 1918 77. <i>restricta</i> Hampson, 1918
		XXV.	78. <i>acantha</i> (Druce, 1889) 79. <i>chalcotoxa</i> (Dyar, 1909) 80. <i>acema</i> (Druce, 1889)
8. <i>Basilodes</i> Guenée, 1852		XXVI.	81. <i>chrysopis</i> Grote, 1881 82. <i>inquinatus</i> Hogue, new species 83. <i>auratus</i> Schaus, 1911 84. <i>pepita</i> Guenée, 1852
		XXVII.	85. <i>dysnoa</i> (Dyar, 1912) 86. <i>consuelus</i> (Strecker, 1900) 87. <i>rugifrons</i> (Grote, 1874) 88. <i>ruficeps</i> (Draudt, 1927) 89. <i>colimae</i> (Draudt, 1927) 90. <i>intermixtus</i> (Dyar, 1918) 91. <i>ischune</i> (Dyar, 1912) 92. <i>mouris</i> (Dyar, 1912) 93. <i>sisaya</i> (Dyar, 1912) 94. <i>tachymora</i> (Dyar, 1914) 95. <i>dyari</i> (Hill, 1924) 96. <i>sulphureus</i> (Neumoegan, 1882)
Generic Status Undetermined (<i>Xanthiria</i> Hampson, 1910)		XXVIII.	97. <i>prepontendyta</i> Dyar, 1914
		XXIX.	98. <i>primulina</i> Druce, 1889
		XXX.	99. <i>iticyes</i> Dyar, 1914
		XXXI.	100. <i>arivaca</i> Barnes, 1907

APPENDIX: DESCRIPTIONS OF NEW SPECIES

6: **Plagiomimicus bajae** Hogue, new species

Figures 31b-c, 32a-e, k

Description

Adult male. Size medium-small, forewing length 13.5-14 mm. Upper surface of forewing with mixed medium grey-brown, brown and white scales; scales predominantly brown in center of wing forming a large, oblique, pear-shaped macula (apex directed toward apex of wing); macula bounded immediately distad by a thin, white PM line bounded cephalad (along costal area) and basad by light scales; marginal sector of mixed light and dark scales giving a finely irrorated, grey-brown shade generally blending with fringe; orbicular and reniform and other markings entirely absent. Upper surface of hindwing predominantly white, grading to grey-brown distad and blending with fringe; exterior line faint. Lower surface of forewing dirty, grey brown, slightly lighter toward distal and costal margins. Lower surface of hindwing evenly, dirty white. Vestiture of head (including palps) and thorax of spatulate scales, light basad, becoming dark distad with white tips; a few white scales on antenna, especially at base. Abdomen evenly, dirty light-brown. Frontal protuberance an oval ring inclosing a fairly broad, truncate, ventral prominence, latter slightly exceeding height of ring.

Adult female. Identical to male except for slightly larger size; forewing length 15 mm.

Male genitalia. Generally like other members of species group III (*P. spumosus* and allies). Tegumen neck very short, stout and erect. Uncus moderately long, strongly curved basad, cylindrical. Ventral margin of valve slightly inflexed before tip, dorsal margin straight. Lobe of distal sacculus division a moderately upcurved, sharp spine with a smaller accessory lobe basad. Corona entirely at distal apex of valve, not curving obliquely onto inner surface, composed of seven or eight setae. Phallus vesica inflated slightly sinistrad; primary cornuti subequal, normal in number and distribution for species group.

Female genitalia. Ovipositor lobe short, evenly sagittate, not abruptly narrowed before tip. Postapophysis considerably stouter than antapophysis. Corpus bursae elongate, straight, nearly tubular, slightly swollen cephalad. Sclerotized plate in crotch of lobe very well defined, triangular; sclerotization and ribbing of lobe and ductus bursae very weak.

Diagnosis

Bajae is immediately separable from its nearest relatives in the *P. spumosus* species group, *aureolus* and *olvello*, by the large, pear-shaped, dark-brown macula in the center of the forewing which is lacking in the other species. *Aureolus* also has a straighter uncus and the dorsal margin of its valve is more curved than in *bajae*. Both *aureolus* and *olvello* have the phallus vesica expanded sinistrad giving the whole phallus a "hammer" shape. This is not so in

bajae which is more like the majority of other *Plagionimicus* in having only a very slightly, sinistrally expanded vesica. Furthermore, both of the former species have a much longer distal sacculus division lobe than *bajae*.

The female genitalia of *bajae* do not have good distinctive features but are generally unlike *aureolus* in having a more distinct plate in the crotch of the lobe of the bursa copulatrix and unlike *olvello* in having a straighter corpus bursae.

Remarks

P. bajae occurs only a short distance across the California border in Baja California (note record at Rosarito). The species, to my knowledge, has not been taken by collectors in southern California but it probably occurs in this area.

Material

Holotype. Male; Punta Prieta, Baja California, Mexico; March 27, 1935 (V. H. dos Passos); with genitalia slide No. CLH 610420-3 [Amer. Mus. Nat. Hist.]. *Allotype*. Female; Rosarito, Baja California, Mexico; March 28, 1935 (V. H. dos Passos); with genitalia slide No. CLH 610427-8 and right foreleg slide No. CLH 610512-27 [Amer. Mus. Nat. Hist.]. *Paratypes*. 1 male; Catavina, Baja California, Mexico; March 4, 1935 (V. H. dos Passos) [Amer. Mus. Nat. Hist.]. 1 male; 7 mi. N. Catavina, 114° 40'- 29° 45', Baja California, Mexico; April 3, 1933 (C. F. Harbison) [San Diego Mus. Nat. Hist.].

62: *Cirrhophanus hoffmanni* Hogue, new species

Figures 31a, 32f

Description

Adult male. Unknown.

Adult female. Size medium, forewing length 14 mm. Upper surface of forewing with white ground color, markings dark-brown as a diffuse smudge over discal region and darker brown streaks along veins and between veins distad; terminal line distinct, dark brown. Posterior third of wing white; fringe double, both rows of grey-brown tipped, spatulate scales, inner row alternating dark and light. Upper surface of hindwing fuscous, markings obsolete; fringe double also: inner fringe light rust, outer white with a few grey scales. Lower surface of forewing dark brown, paling to yellow-brown along costal margin; veins showing as slightly darker lines. Lower surface of hindwing dark brown across anterior third and around outer margin, grading to white basad. Vestiture of head white on vertex and basal segment of antenna; grey-brown around frontal protuberance; antenna orange-brown, dorsal scales white. Thoracic vestiture somewhat rubbed on specimen so tufts not clear but scales all white. Foreleg grey-brown scaled, mid-leg the same cephalad, rest white like hindleg. Frontal protuberance a reniform ring with ventral lip produced strongly as a

conical prominence. Foretibial "claw" of multiple, fused setae situated on a moderately produced, straight tibial apex.

Female genitalia. Ovipositor lobe elongate, well sclerotized, tip pointed and slightly upturned. Postapophysis slightly longer than antapophysis. Sternostial concavity decidedly flask-shaped. Lamella postvaginalis semi-lunar; 1. antevaginalis ligulate, bowed. Ductus bursae short, membranous, becoming abruptly sclerotized and ribbed just beyond middle. Corpus bursae ellipsoid, slightly curved, lobe simple; sclerotization and ribbing strong.

Diagnosis

Hoffmanni is abundantly distinct from its nearest relatives, *discistrigus*, *miaiphona* and *papago*. Superficially, it may be distinguished from the first by its considerably greater size and fuscous, instead of yellow, hindwing. The diffuse, brown, discal smudge and streaks of brown between the veins distad on the forewing separate it easily from the latter two species, both of which have fairly well defined transverse lines and no other color except the ground color, between the veins distad.

Differences in the female genitalia are also well defined. The ovipositor lobe of *hoffmanni* is considerably longer and better sclerotized than that of any of the other species. The ventral margins of VIII pleuron are considerably more approximate caudad and curved (to form a decidedly flask-shaped sterno-ostial concavity) than those of the other species in which they tend to be straight and parallel (to form a subquadrate or oval sterno-ostial concavity).

Remarks

Hoffmanni is an addition to a hitherto undefined group in the genus *Cirrhophanus* which has the unique stiriine character state of multiple, fused setae in the foretibial "claw." On the basis of several characters, it appears to be somewhat intermediate in phylogenetic position between *papago-miaiphona* and *discistrigus*.

The single known specimen appears at first glance to have rubbed forewings. The light, posterior third of the wings, however, is seen under magnification to be nearly fully scaled.

Even though there is but a single specimen of this species available for study, its distinctiveness is so great that I feel justified in describing it as a new entity. The species comes from Mexico, a poorly known region from the standpoint of its insect fauna, and one which probably holds numerous other undescribed noctuid species. I name the species for C. C. Hoffmann whose Mexican collections in the American Museum of Natural History have made it possible for me to study in detail some of the rarest stiriine species.

Material

Holotype. Female; Balsas, Guerrero, Mexico; September, 1933 (C. C. Hoffmann); with genitalia slide No. CLH 610413-8 and right foreleg slide No. CLH 610512-31 [Amer. Mus. Nat. Hist.].

82: **Basilodes inquinatus** Hogue, new species

Figures 31d-e, 32f-j, m

Basilodes pepita in part of Draudt, 1927, in Seitz. Macrolepid. World 7:304, pl. 44, row f.

Description

Adult male. Size medium-large, forewing length 16-18 mm. Upper surface of forewing generally dirty, brassy gold; markings dark brown; orbicular and reniform distinct, centered with brassy gold, latter also with a small, eccentric dark dot; inner margin at base with an area of elongate, semi-erect, brown scales extending almost to AM line; AM line excurved to center of cell Cu, then incurved at about a right angle, to vein 1A, then excurved again obtusely to inner margin; PM line excurved under apical patch, then incurved acutely and continuing almost straight to inner margin (only a very slight, distal deflection at vein 1A); apical patch evident only as a shade at angle of PM line; median shade diffusely evident caudad near AM line and on costal margin above orbicular; ST line very weak; fringe grey-brown. Upper surface of hindwing dark brown; exterior line faintly evident; fringe of mixed light and brown scales. Lower surfaces of forewing and hindwing similar, light brown, forewing somewhat darker centrally with reniform and PM line faintly showing through; hindwing with exterior line evident. Vestiture of head of small, brownish-white scales on sides of vertex and on scape and pedicel of antenna, darker basad and laterad of frontal protuberance; antenna orange-brown, darker basad on dorsal side, dorsal scales small and white; palpal scales dark brown; thoracic scale tufts of very long, spatulate scales which are light brown basad, darker brown distad and tipped with white; patagial scales shorter and lighter; pleura and venter of thorax with long, light-yellow-brown, hairlike scales, legs with mixed light and dark brown scales. Abdomen brown, slightly darker dorsad, tuft of TI white. Frontal protuberance moderately prominent, a round to inverted, heart-shaped ring with a broad, rough lower convexity.

Adult female. Identical to male except for slightly larger size; forewing length 18-20 mm.

Male genitalia. Tegumen neck very long. Uncus cylindrical, quite long and straight, not swollen mesad, with numerous, decumbent, moderately long setae. Vinculum quite short. Saccus rectangular with small anterior nipple. Corona well developed, extending across entire tip of valve (of 13-14 setae in holotype); basal sacculus division elongate with slight basal lobe; distal division with slight basal lobe set with short setae and distal, upcurved, spinelike lobe set almost at edge of valve. Phallus vesica elongate, nearly twice as long as aedeagus, cornuti long and slender, longer distad.

Female genitalia. Ovipositor lobe very long (almost as long as postapophysis), tips rounded. Ventral margin of VIII pleuron greatly deflexed (but not so much as in *pepita*). Sterno-ostial concavity elongate.

Diagnosis

Of the species in the *Basilodes chrysopsis* species group, *inquinatus* superficially looks most like *pepita*. The forewing patterns of these two species are very similar but there are constant differences in my material. The posterior, distal deflection of the PM line at vein 1A is much stronger in *pepita* than in *inquinatus*, the angle of the incurving PM line in cell Cu is much sharper in *inquinatus* than in *pepita* and the median shade of *pepita* is the more distinct. The most obvious difference is the general appearance of the ground color. It is a much more clean and brilliant brassy gold in *pepita* than in *inquinatus* which is quite dirty and dull. *Pepita* is also slightly larger and more robust than *inquinatus*.

Inquinatus can be distinguished at present from *auratus* only by the complete, rather than divided reniform, lighter and more golden general coloring and longer female ovipositor lobe. Unfortunately, *auratus*, being known from only a single female specimen, cannot be diagnosed more fully.

Several character states in the male and female genitalia clearly separate *inquinatus* from the other members of its species group. The females have a slightly rounded tip to the ovipositor lobe; this is sharply pointed in *pepita*. The ventral margins of VIII pleura of both *pepita* and *chrysopsis* are greatly deflected, less so in *inquinatus*. With regard to the male genitalia, the uncus of *pepita* and *chrysopsis* is swollen mesad and has somewhat erect setae while the uncus of *inquinatus* is perfectly cylindrical and has recumbent setae. The vesica cornuti of *inquinatus* are quite long while those of *chrysopsis* are proportionately less than half as long and considerably stouter; those of *pepita* are even shorter and stouter. The basal lobe of the distal sacculus division of *pepita* is much better developed than in either of the two other species.

The frontal protuberances of both *pepita* and *chrysopsis* are rather prominent, smooth bottomed, oval cups which are slightly shallower ventrad than dorsad. *Inquinatus* differs from both in this character in having a round or heart-shaped, moderately prominent plateau with a shallow depression rising to a broad, rough mound midventrally.

Remarks

Draudt (1919-1939:304) records *pepita* from Mexico but he must have been referring to specimens of *inquinatus* in the U. S. Natl. Mus. This is shown by his figure (pl. 44, row f, fifth from the left) which is definitely of *inquinatus*. As far as I know, true *pepita* does not occur in Mexico.

Material

Holotype. Male; Tehuacán, Puebla, Mexico; September 11, 1932 (C. C. Hoffmann); with genitalia slide No. CLH 610407-7 [Amer. Mus. Nat. Hist.]. *Allotype*. Female; Zacualpan, Mexico, Mexico; September, 1914 (C. C. Hoffmann) [Amer. Mus. Nat. Hist.]. *Paratypes*. 1 male; Tehuacán, Puebla, Mexico; September, 1937 (C. C. Hoffmann) [Amer. Mus. Nat. Hist.]. 1 male; Tehuacán, Puebla, Mexico; September 10 [U. S. Natl. Mus.]. 1 female; Tehuacán,

Puebla, Mexico; September, 1908 (R. Müller; 1730); with genitalia slide No. CLH 610420-7 and right foreleg slide No. CLH 610512-54 [U. S. Natl. Mus.], 1 female; Tehuacán, Puebla, Mexico; September, 1911 (C. C. Hoffmann) [Amer. Mus. Nat. Hist.].

SUMMARY

1. The Stiriini are a structurally uniform but superficially diverse tribe of noctuid moths found only in the New World, chiefly in central and northern Mexico and the southwestern United States. The tribe's internal phylogenetic relationships were determined from a comparative study of the adult integumentary anatomy and serve as a basis for a definition and classification.

2. Historically, the Stiriini have not been treated as a taxonomic unit before the present work. A few investigators, such as A. R. Grote, who originally designated the tribe, J. B. Smith, M. Draudt, W. T. M. Forbes, *et al.*, have given some attention to the tribe's constituents.

3. There is only scanty information available regarding the tribe's ecology and geographical distribution. Most forms range in arid and semiarid regions. The few known larvae are exclusively feeders on Compositae.

4. The entire integumentary anatomy of one species, *Basilodes rugifrons*, is described and illustrated in some detail.

5. The phylogenetic relationships of the 100 species are reconstructed within the limits of the restricted data. An "objective," statistical method was first attempted but found to be inadequate and invalid. The traditional comparative method was finally utilized.

6. Twenty-seven "primary phyletic units" (groups of very close species) and seven "major phyletic lines" (higher groups of primary phyletic units representing major evolutionary stages) are recognized. The former are given species group status; the latter roughly correspond to the eight genera recognized. These genera are *Plagiomimicus*, *Chrysoecia*, *Gorgora*, *Chichimeca*, *Cirrhophanus*, *Cuahtemoca*, *Chalcopasta* and *Basilodes*.

7. Each species group and genus is described and diagnosed in an expanded, phylogenetic key. The important taxonomic features of a typical member of each species group is illustrated. An annotated, bibliographic listing of the species included in each species group is given.

8. Two new genera, *Chichimeca* and *Cuahtemoca*, and three new species, *Plagiomimicus bajae*, *Cirrhophanus hoffmanni* and *Basilodes inquinatus*, are described.

9. The tribe is formally defined and diagnosed and its external affinities and integrity are briefly discussed.

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ILLUSTRATIONS

NOTE ON THE ILLUSTRATIONS

The illustrations are all original and, with two exceptions, based on direct observation of personally prepared specimens. The drawings of the female genitalia of *Gorgora morga* and male genitalia of *Chalcopasta ellica* were based on photographs. Most are direct reproductions of the actual aspect of the specimens but some were reconstructed (especially those of thoracic tufts) to improve symmetry and accuracy. For the genitalia I used a microprojector for sketching outlines and proportions directly on the final drawing paper. Details were checked with a compound microscope and the final drawings made freehand. All lines were made with a Hunt, No. 102 point and stipples with a No. 1 Koh-I-Noor, Rapidograph. The drawings are reduced approximately 2.8 times.

To facilitate comparison, the figures of the species groups (6-30) are arranged and lettered (a-k) uniformly as follows: (a) oblique, frontal view of denuded head to show frontal protuberance; (b) oblique, posterior view of thorax and head to show vestiture; (c) dorsal view of right wings to show pattern; (d) inner view of right foreleg; (e) segment VIII of the male, opened and flattened to show patterns of tergal (to right) and sternal (to left) sclerotization (scale patch in base of sternal sclerotization omitted); (f) lateral view of left side of tegumen, vinculum, uncus, etc., of male genitalia; (g) inner view of right valve; (h) ventral view of phallus (vesica fully inflated); (i) ventral view of juxta; (j) dorsal view of anellus; (k) ventral view of female genitalia (VIII and ovipositor lobes spread flat). The parts of the male genitalia are shown at the same scale (see scale below valve) except segment VIII.

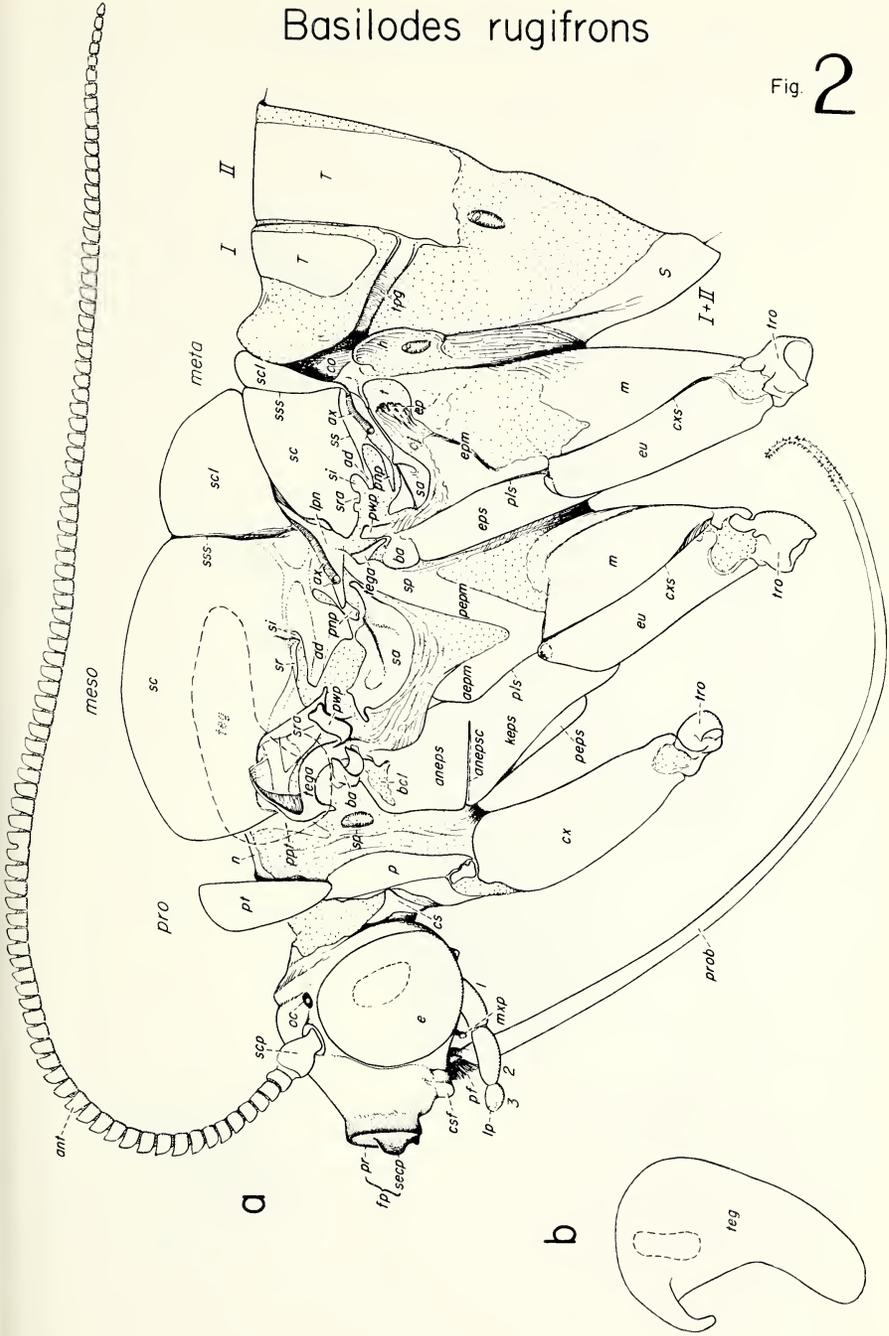
LIST OF ABBREVIATIONS USED IN ILLUSTRATIONS

aap	antapophysis	h	hood
abf	abdominal furca	hs	horn of the spina
ad	adnotale	jx	juxta
ae	aedeagus	keps	katapisternum
aepm	anterior epimeron	lav	lamella antevaginalis
anel	anellus	ld	lamella of the discrimen
aneps	anepisternum	lp	labial palpus
anepscl	anepisternal cleft	lpn	lateropostnotum
ant	antenna	lpv	lamella postvaginalis
ar	areole	m	meron
ata	anterior tentorial arm	metasc	metascutal tuft
atp	anterior tendon plate	mxp	maxillary palpus
ax	axillary cord	n	notum
ba	basalare	ntg	neck of the tegumen
bcl	basalar cleft	ob	ostium bursae
blbsl	basal lobe of basal sacculus division	oc	ocellus
bldsl	basal lobe of distal sacculus division	od	ocular diaphragm
bsl	basal sacculus division	ovlb	ovipositor lobe
cae	caecum	p	pleuron
cj	conjunctiva	pap	postapophysis
cn	cornuti	pepm	posterior epimeron
co	countertympanic orifice	peps	preepisternum
cor	corona	pf	pilifer
cos	costa	pg	primary group of cornuti
crpbu	corpus bursae	ph	phragma
cs	cervical sclerite	pl	pleurite
csf	clypeal shelf	plr	pleural ridge
ctc	countertympanic cavities	pls	pleural suture
cts	countertympanic septum	pmesosct	posterior mesoscutal tuft
cx	forecoxa	pn	postnotum
cxs	coxal suture	pnp	posterior notal wing process
dbu	ductus bursae	ppt	parapatagium
dldsl	distal lobe of distal sacculus division	pr	peripheral ridge
dsl	distal sacculus division	prbr	plantar bristles
dsm	ductus seminalis	prob	proboscis
e	eye	pt	patagium
ep	epaulette	ptp	posterior tendon plate
epi	epiphysis	ptt	patagial tuft
epm	epimeron	pwp	pleural wing process
eps	episternum	s	sternum
euc	eucoxa	S	abdominal sternite
f	furca	sa	subalare
fb	furcal bridge	sabf	secondary abdominal furca
fp	frontal protuberance	sac	saccus
fr	frenulum	sc	scutum

sca	scaphium	teg	tegula
scl	scutellum	tega	tegular arm
scp	scape	tegt	tegular tuft
scph	scutal phragma	tg	tegumen
secp	secondary prominence	tpg	tergopleural groove
sg	secondary group of cornuti	tro	trochanter
si	scutal incision		
sp	spiracle	un	uncus
spi	spina	ung	ungues
sr	scutal ridge		
sra	suralare	val	valve
ss	scutal suture	ves	vesica
ssca	subscaphium	vin	vinculum
ssr	scuto-scutellar ridge		
sss	scuto-scutellar suture	It	abdominal tuft
sst	spinasternum		
t	tympanal membrane	VIIIS	VIII sternal sclerotization
T	abdominal tergite		
ta	tuba analis	VIIIT	VIII tergal sclerotization

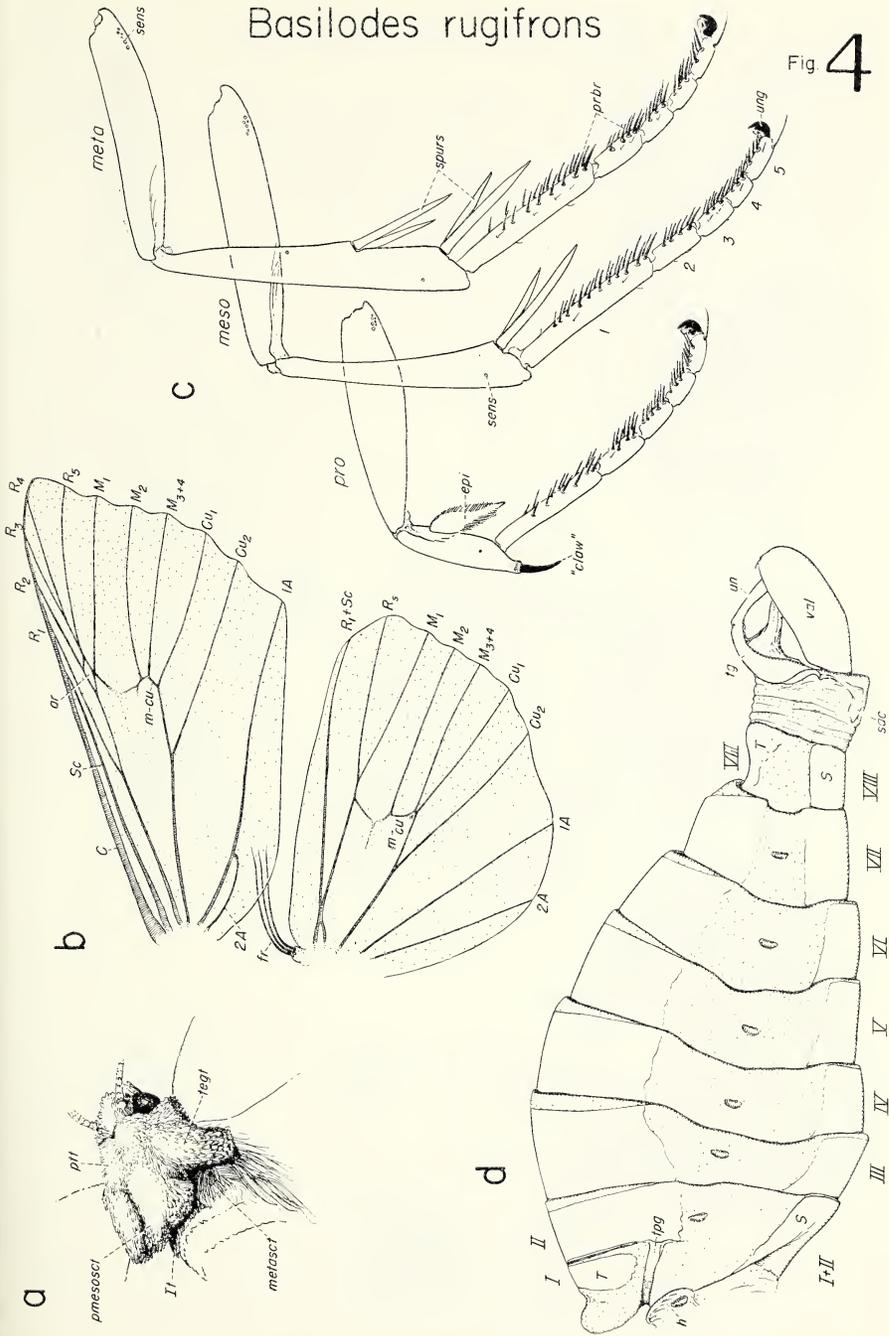
Basilodes rugifrons

Fig 2



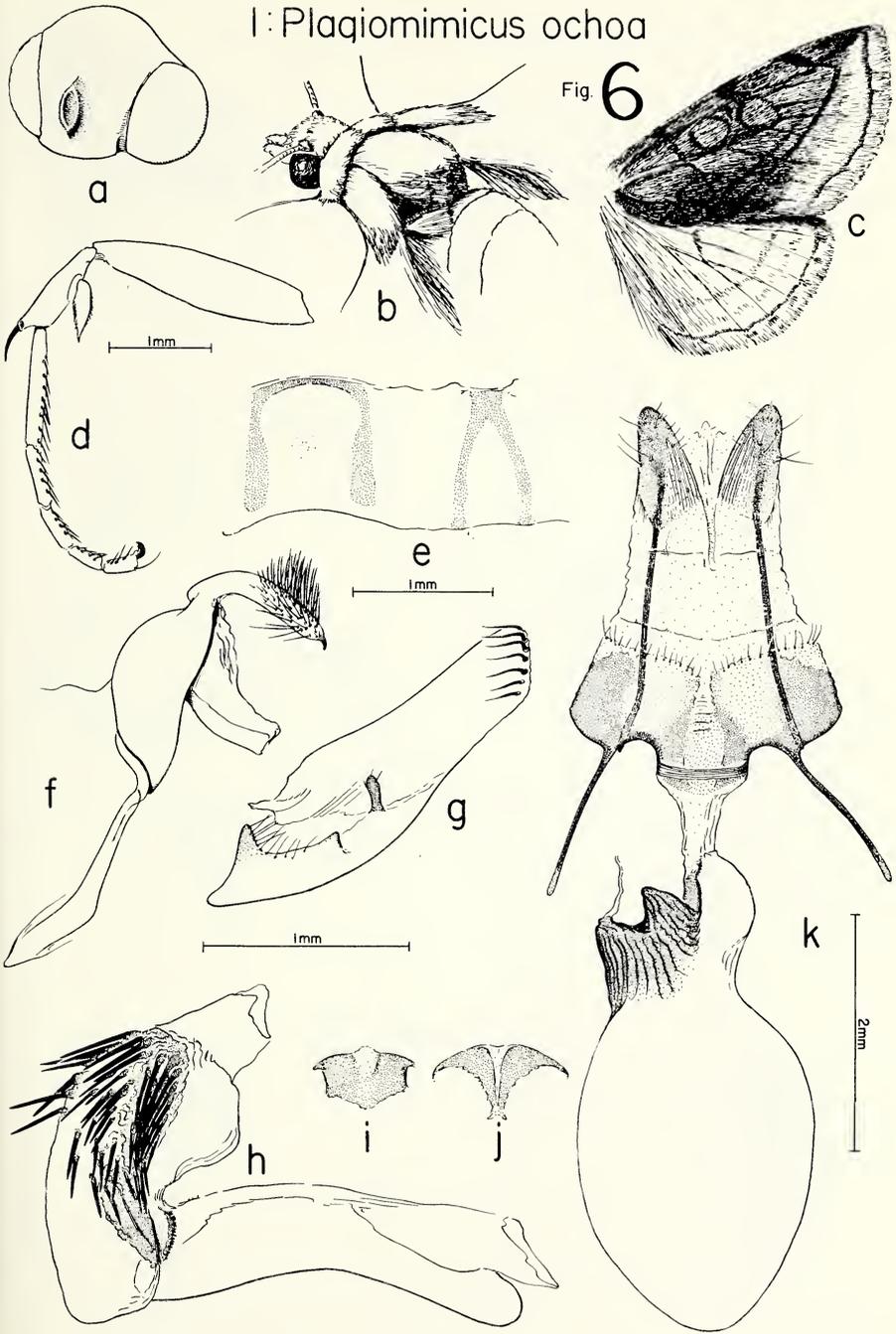
Basilodes rugifrons

Fig 4



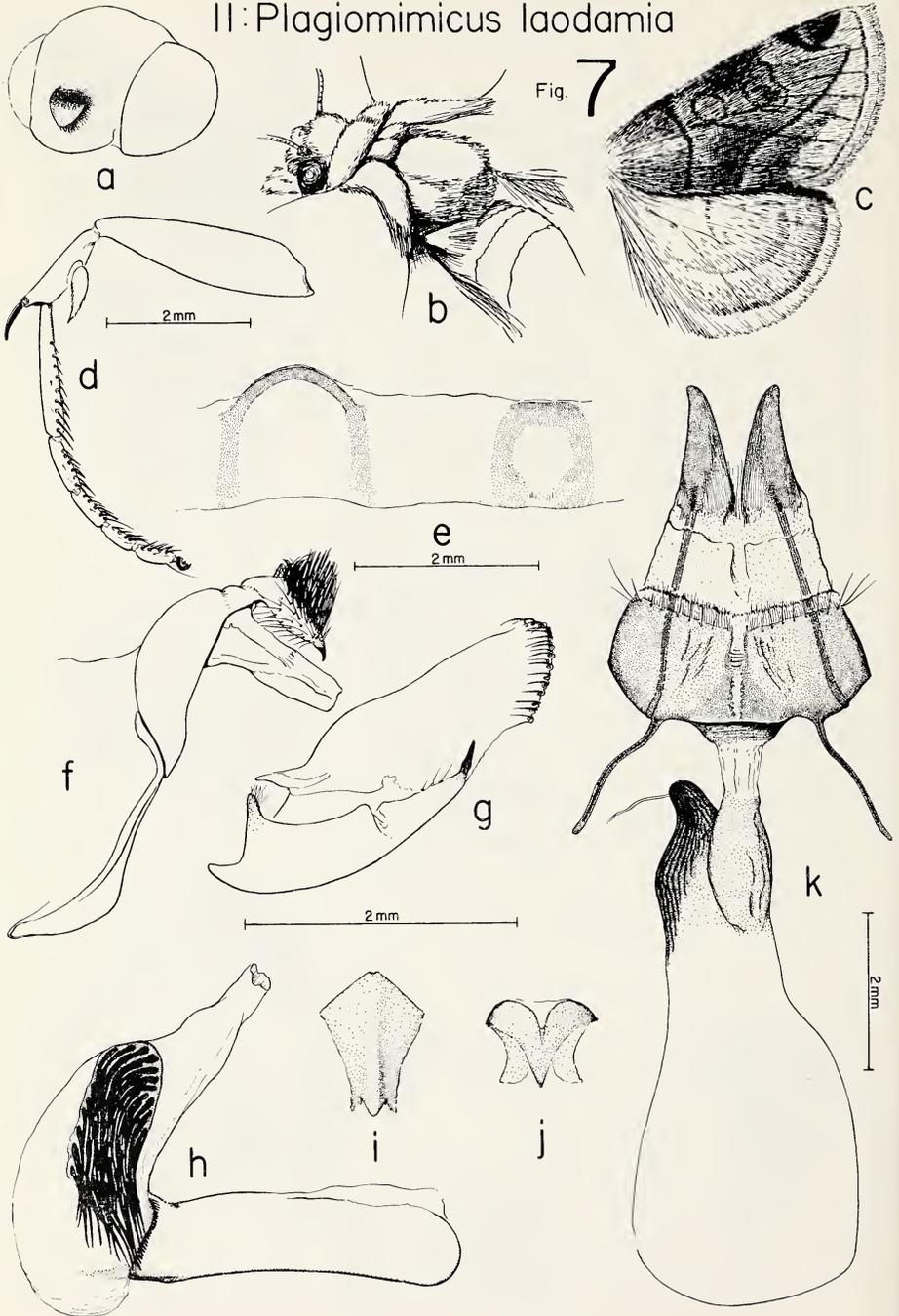
I: *Plagiomimicus ochoa*

Fig. 6



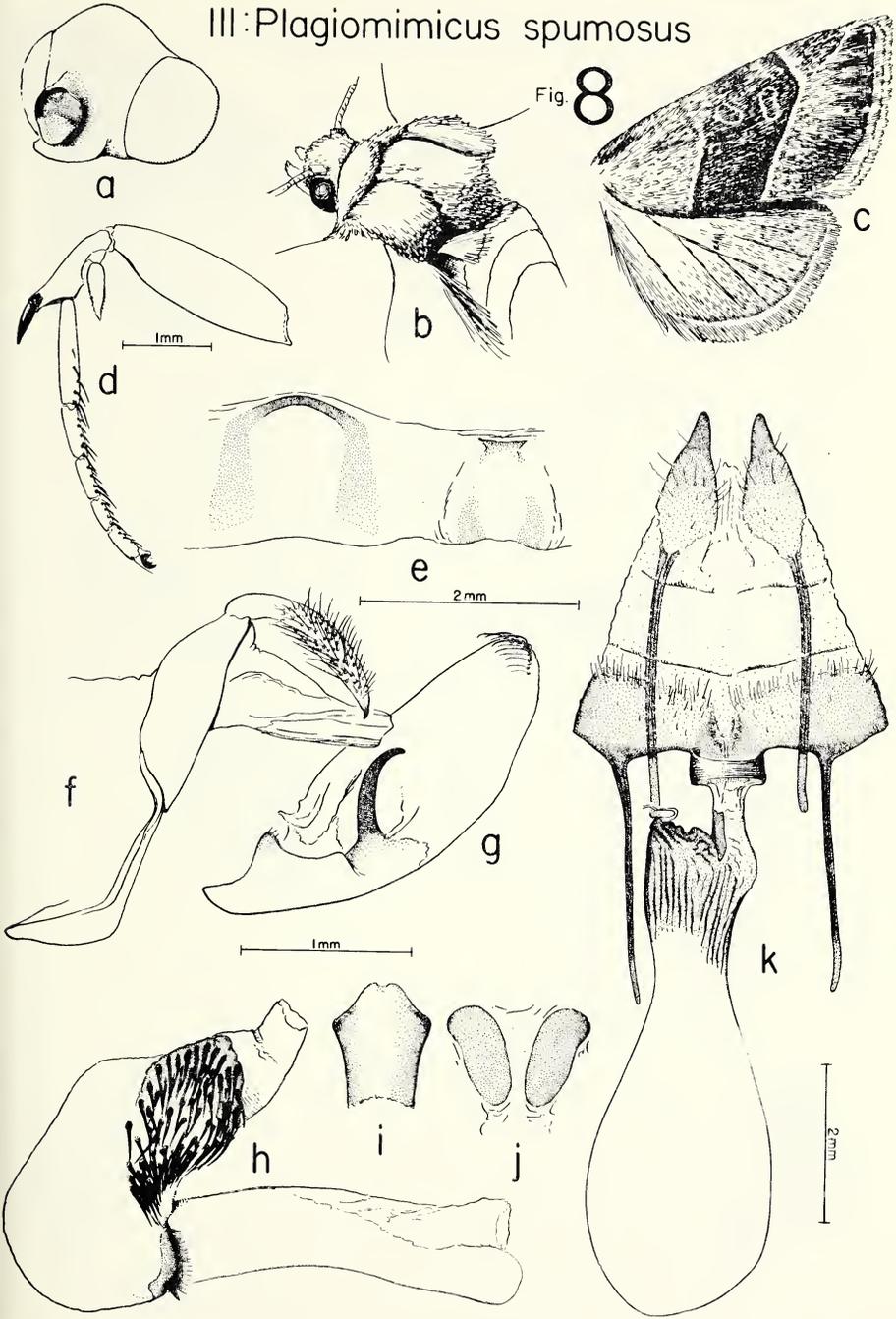
II: *Plagiomimicus laodamia*

Fig. 7



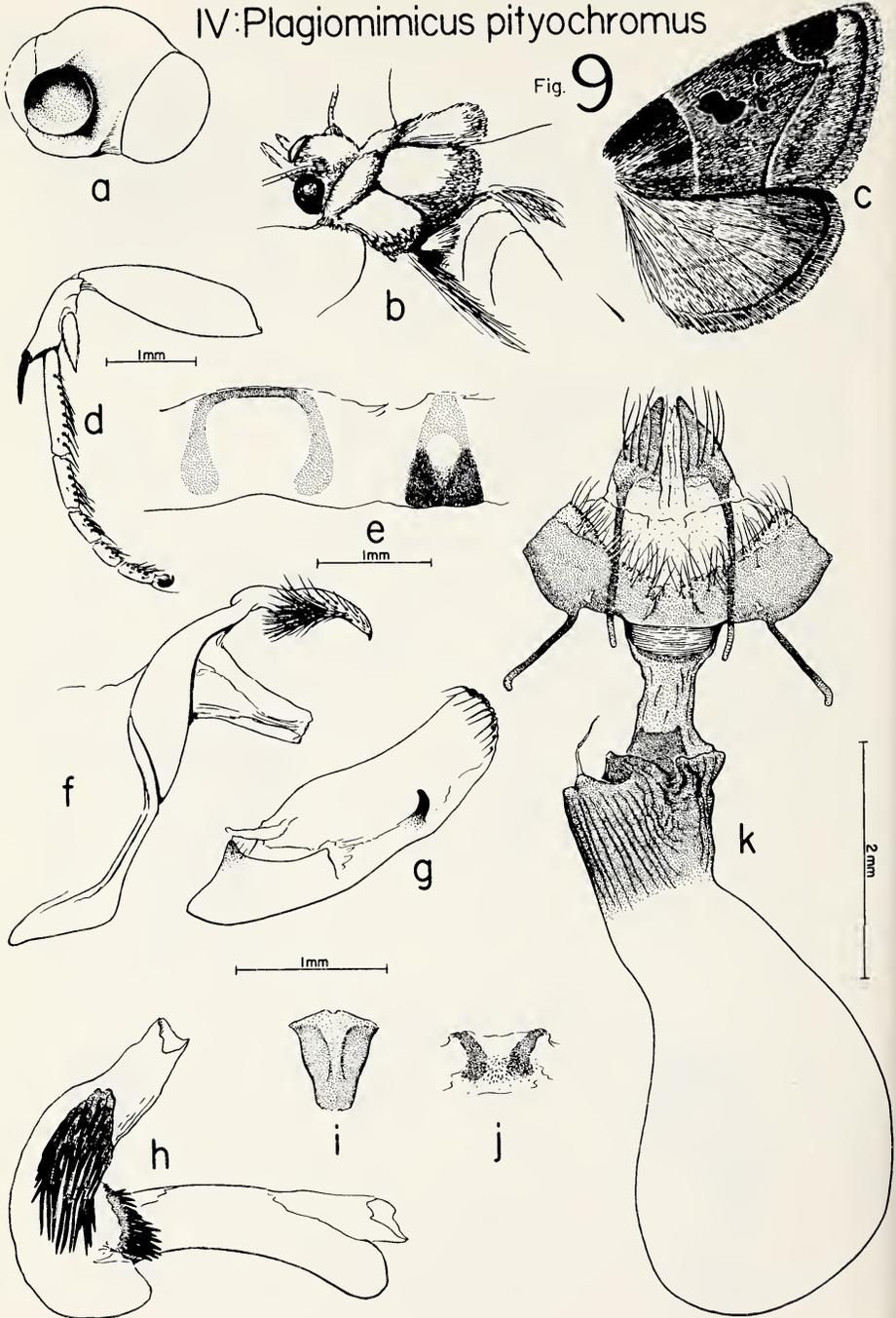
III: *Plagiomimicus spumososus*

Fig 8



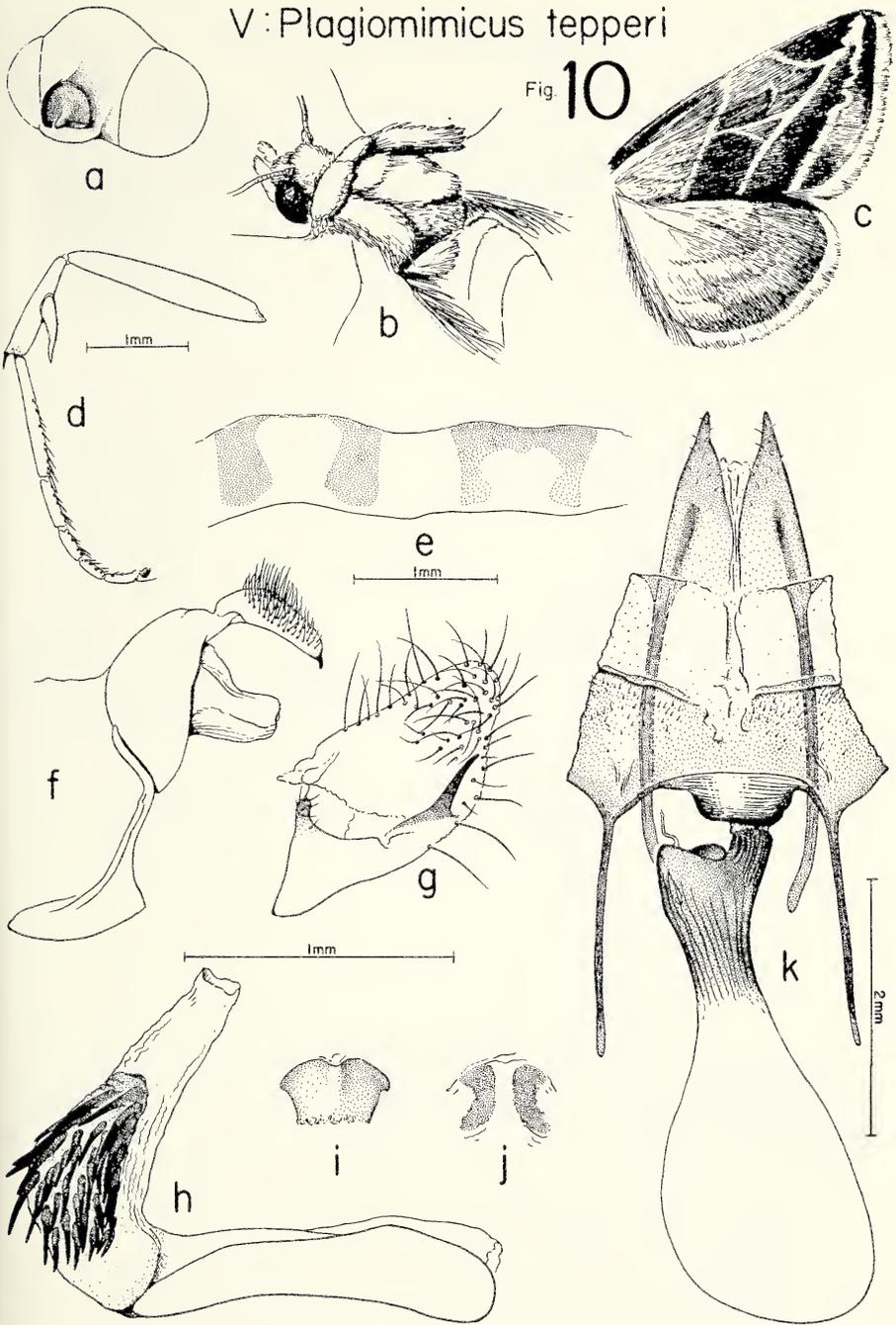
IV: *Plagiomimicus pityochromus*

Fig. 9



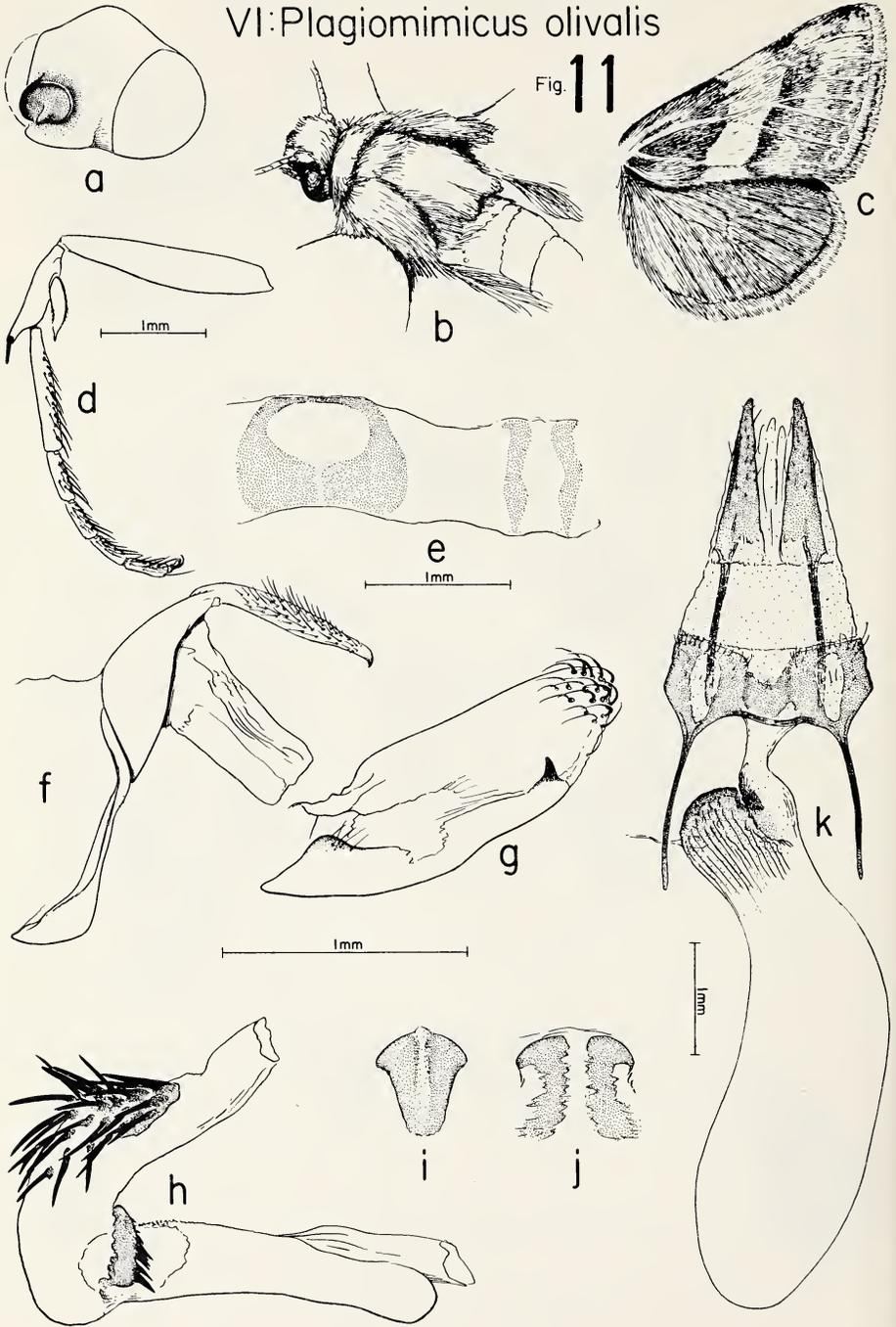
V: *Plagiomimicus tepperi*

Fig. 10



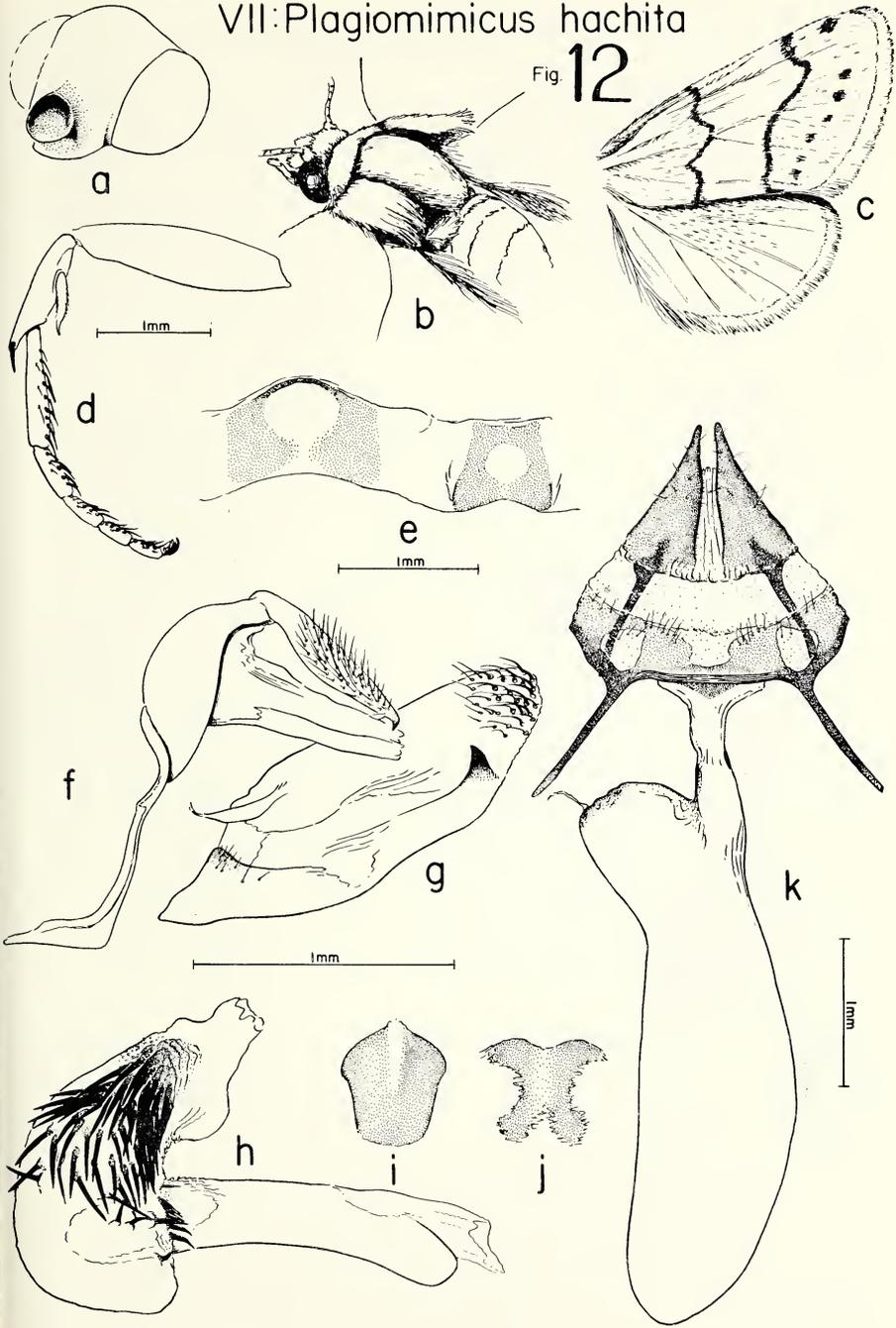
VI: *Plagiomimicus olivalis*

Fig. 11



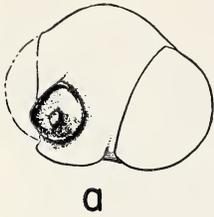
VII: *Plagiomimicus hachita*

Fig 12



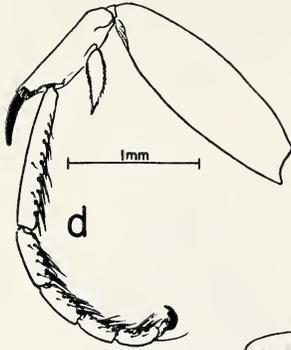
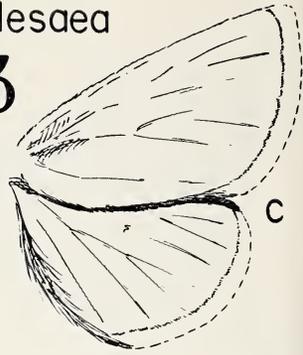
VIII: *Plagiomimicus alesaea*

Fig. 13



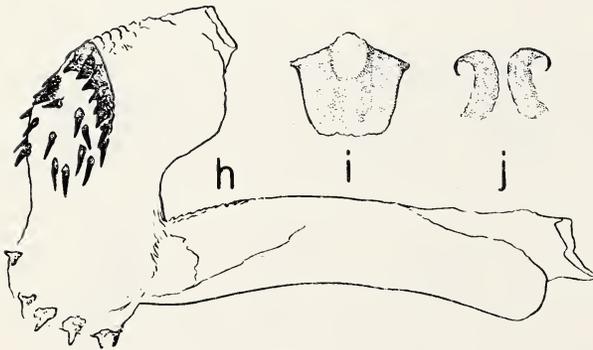
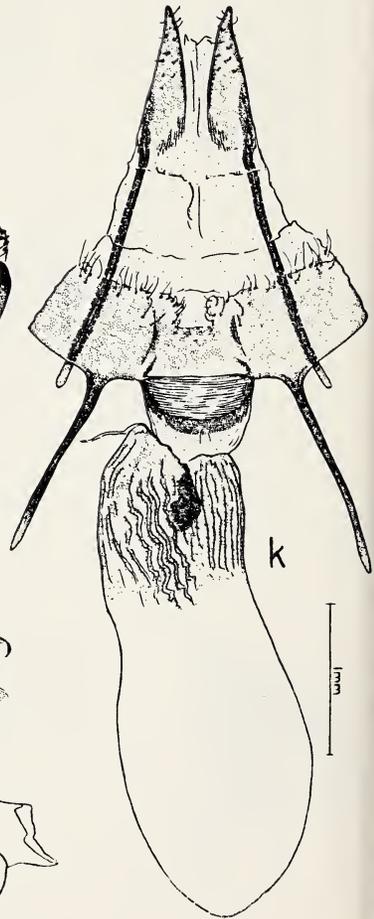
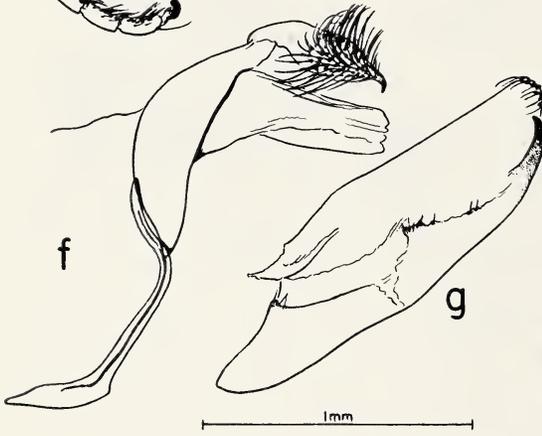
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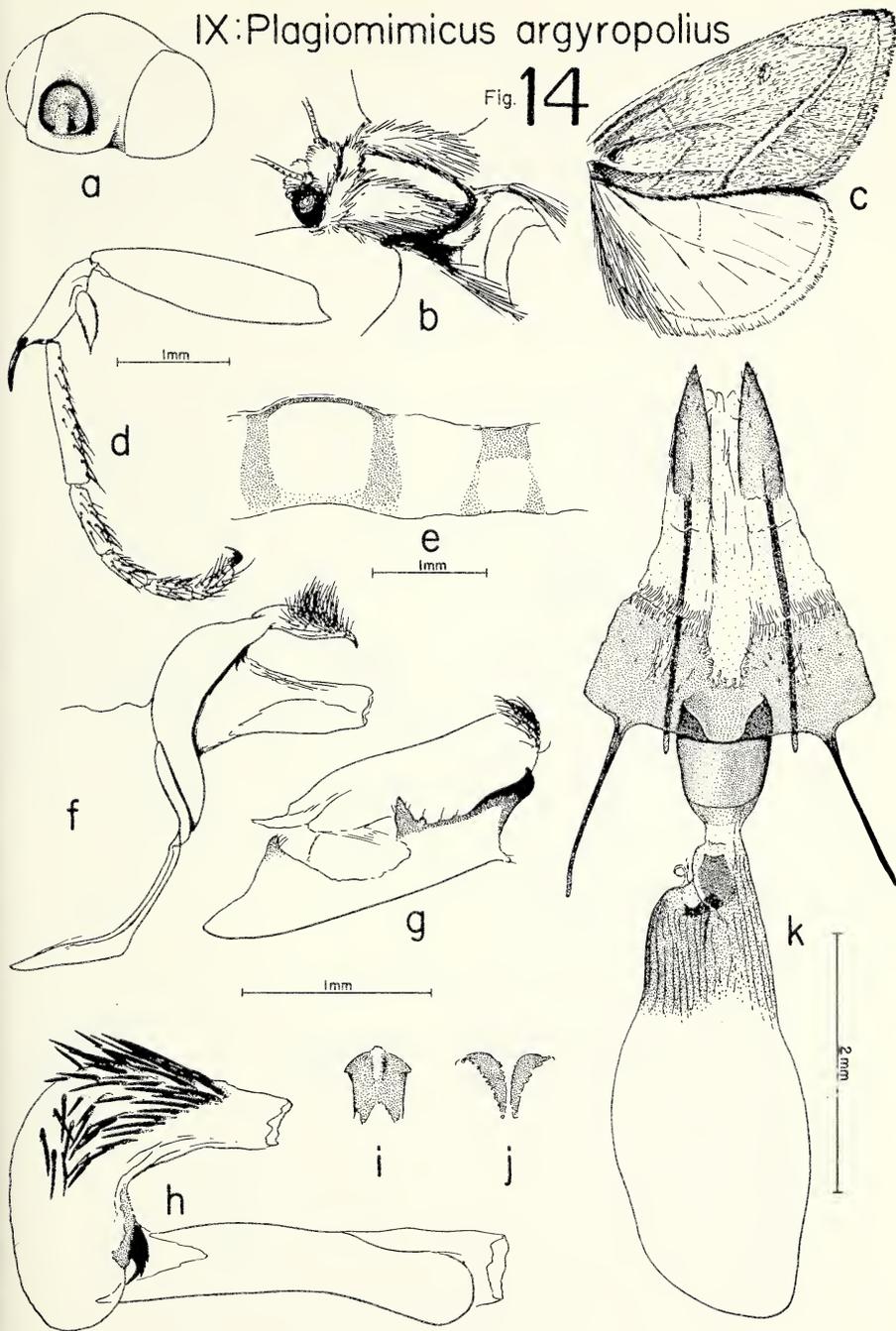
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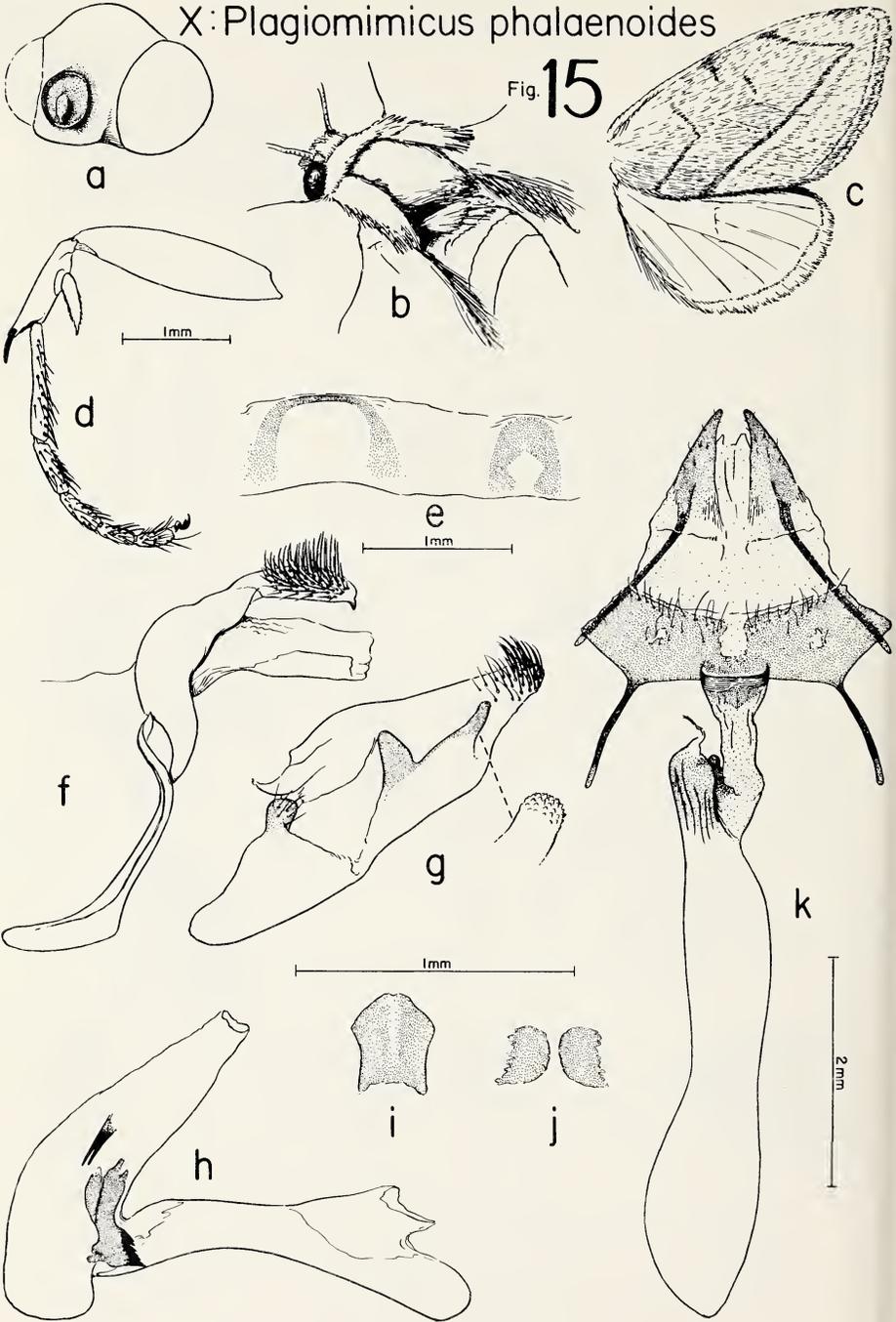
IX: *Plagiomimicus argyropolius*

Fig. 14



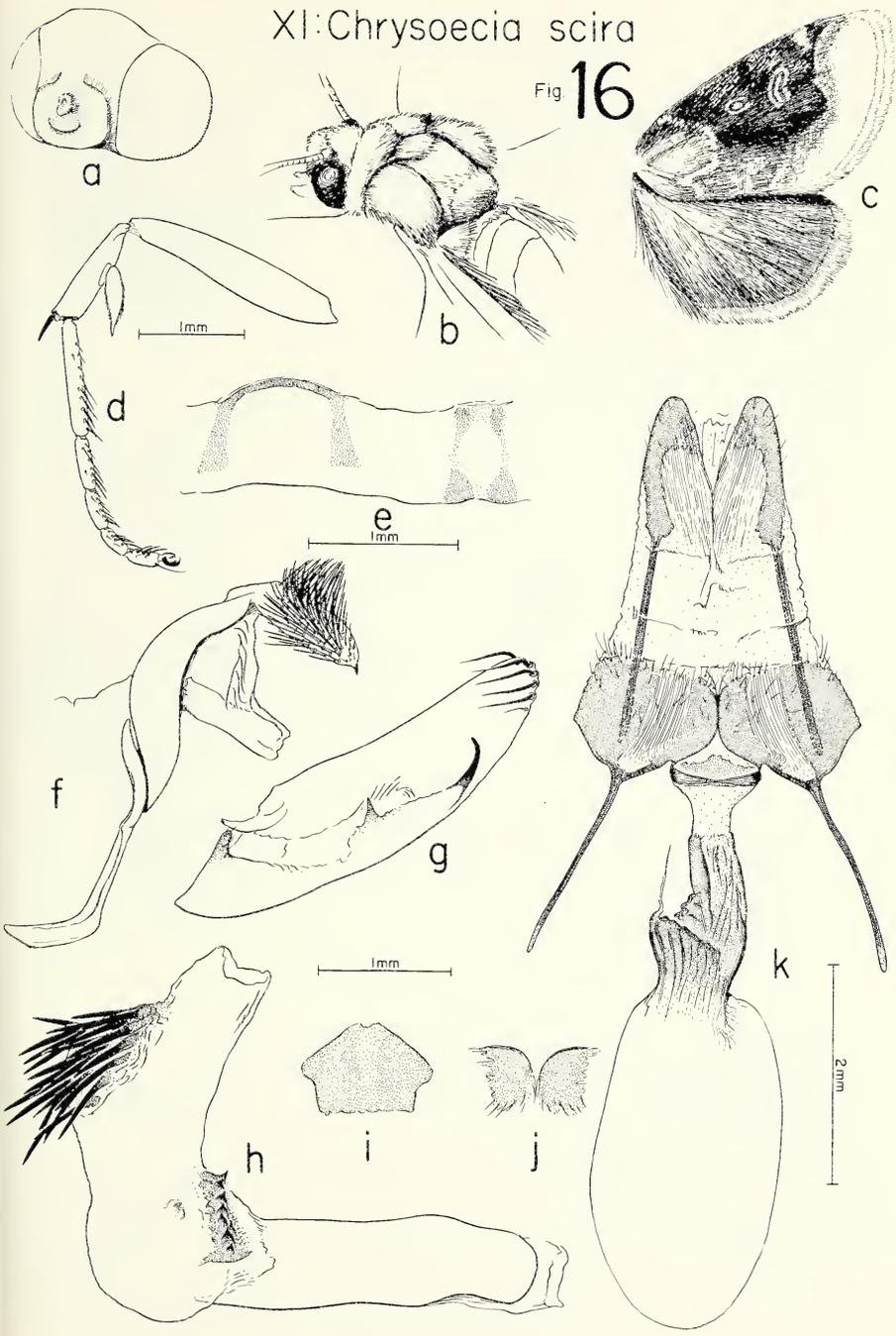
X: *Plagiomimicus phalaenoides*

Fig. 15



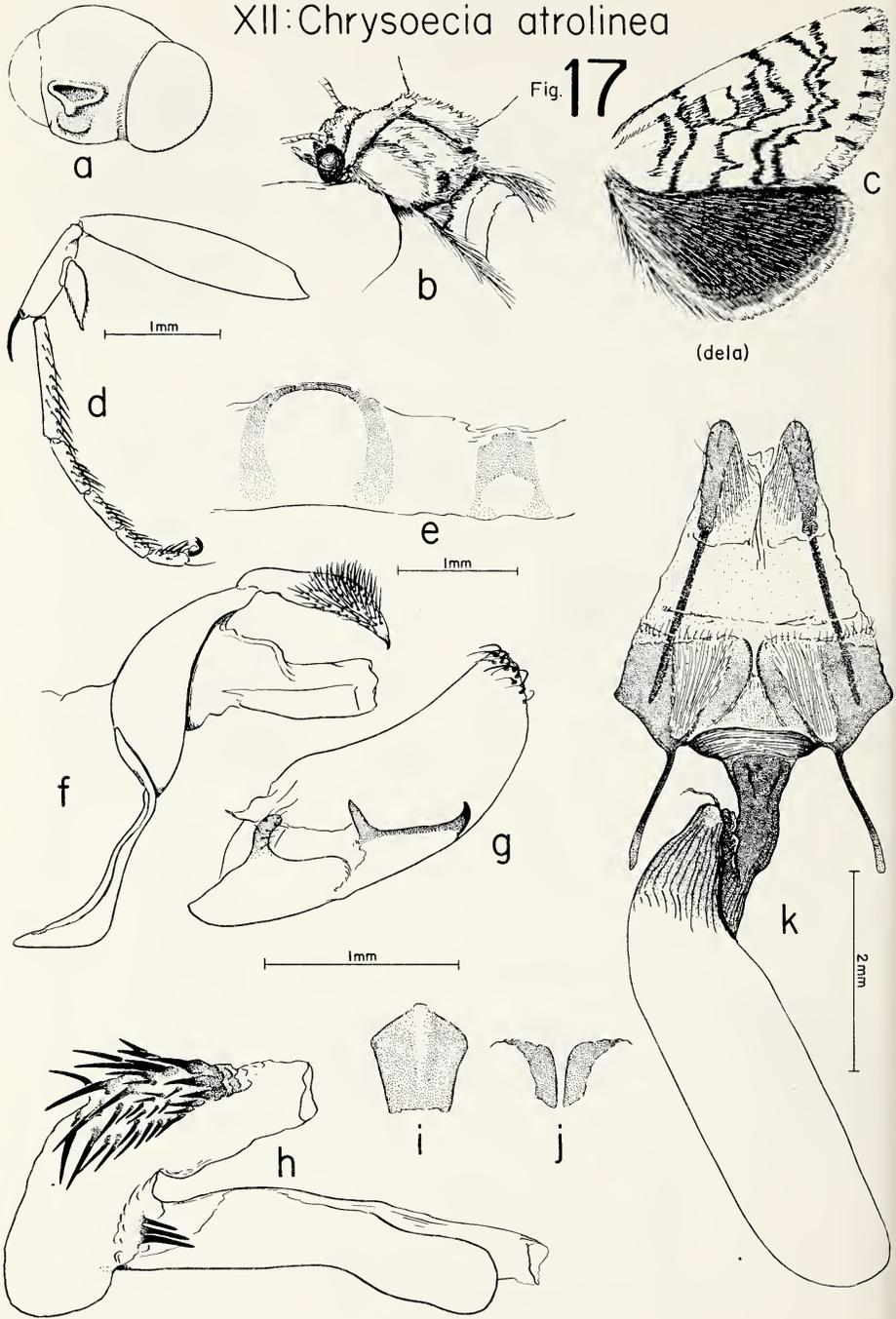
XI: *Chrysoecia scira*

Fig. 16



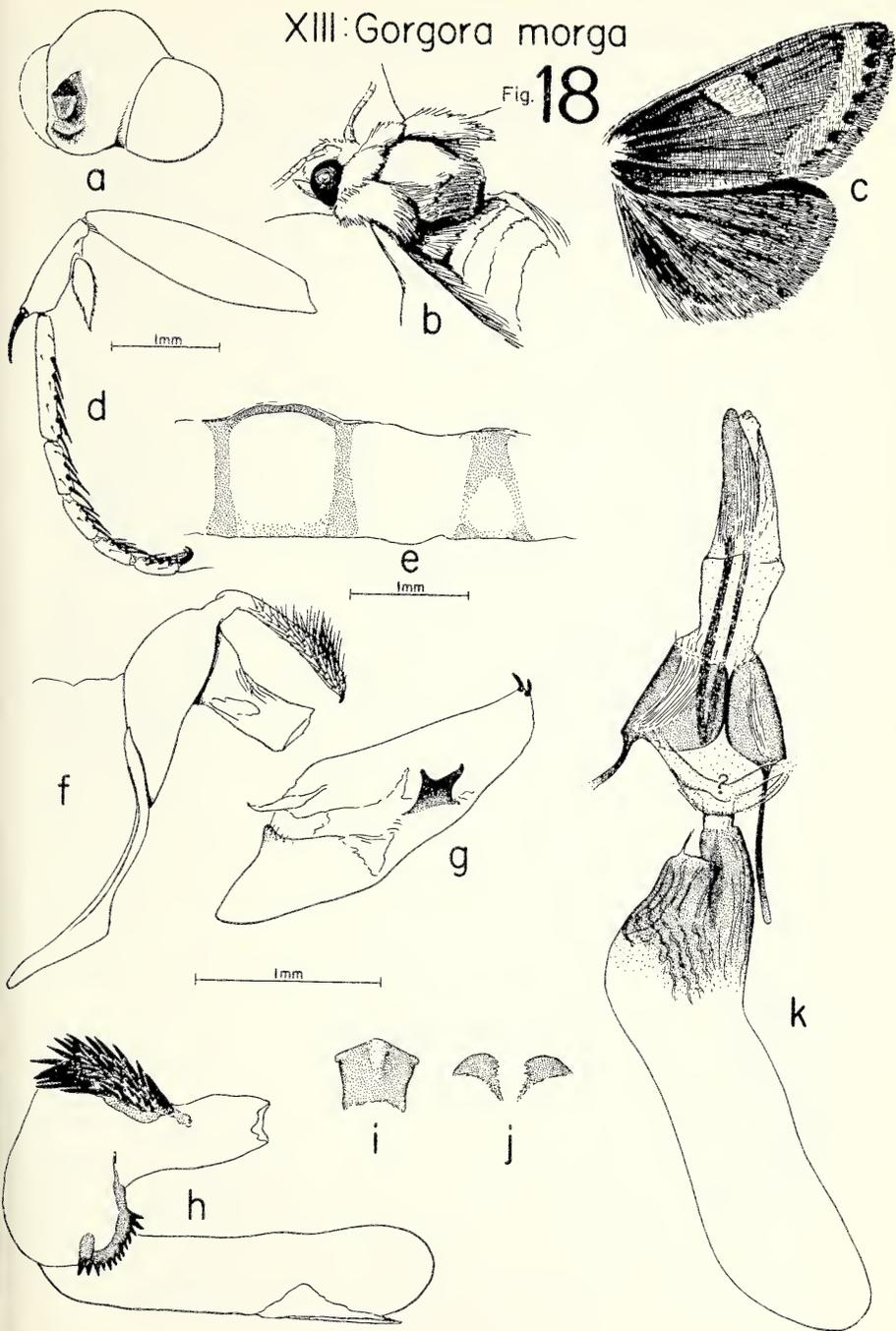
XII: *Chrysoecia atrolinea*

Fig. 17



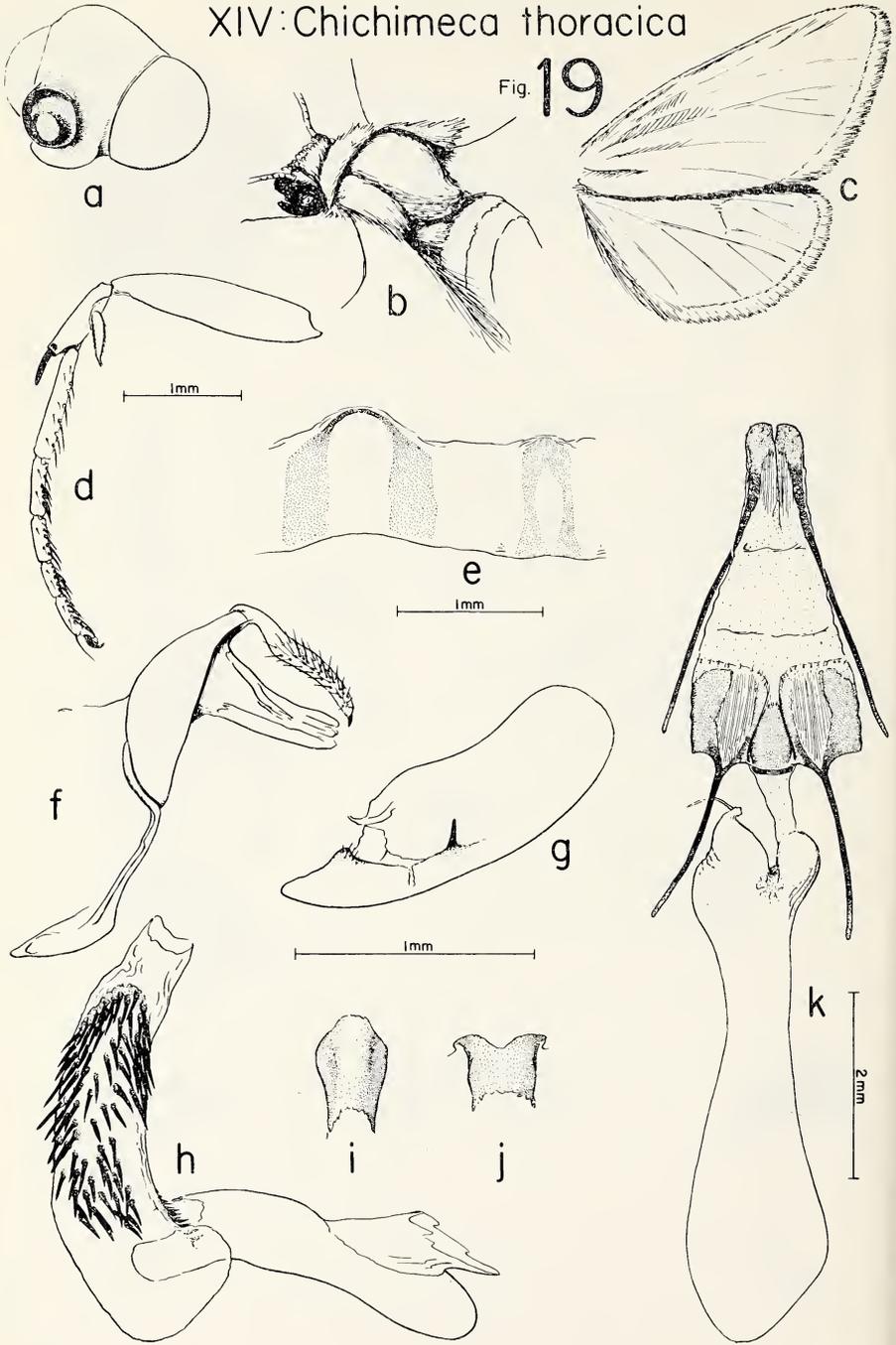
XIII: *Gorgora morga*

Fig. 18



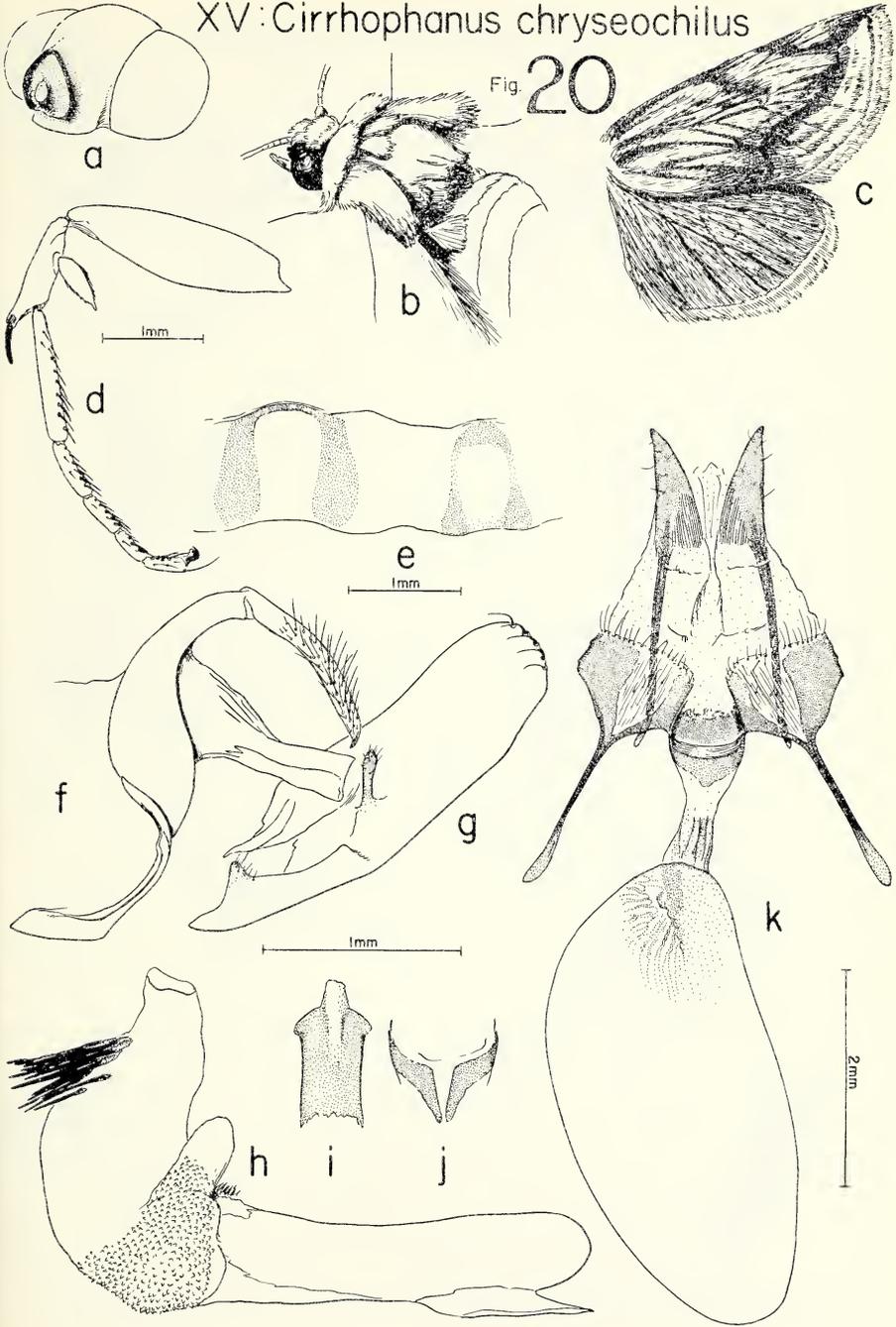
XIV: Chichimeca thoracica

Fig. 19



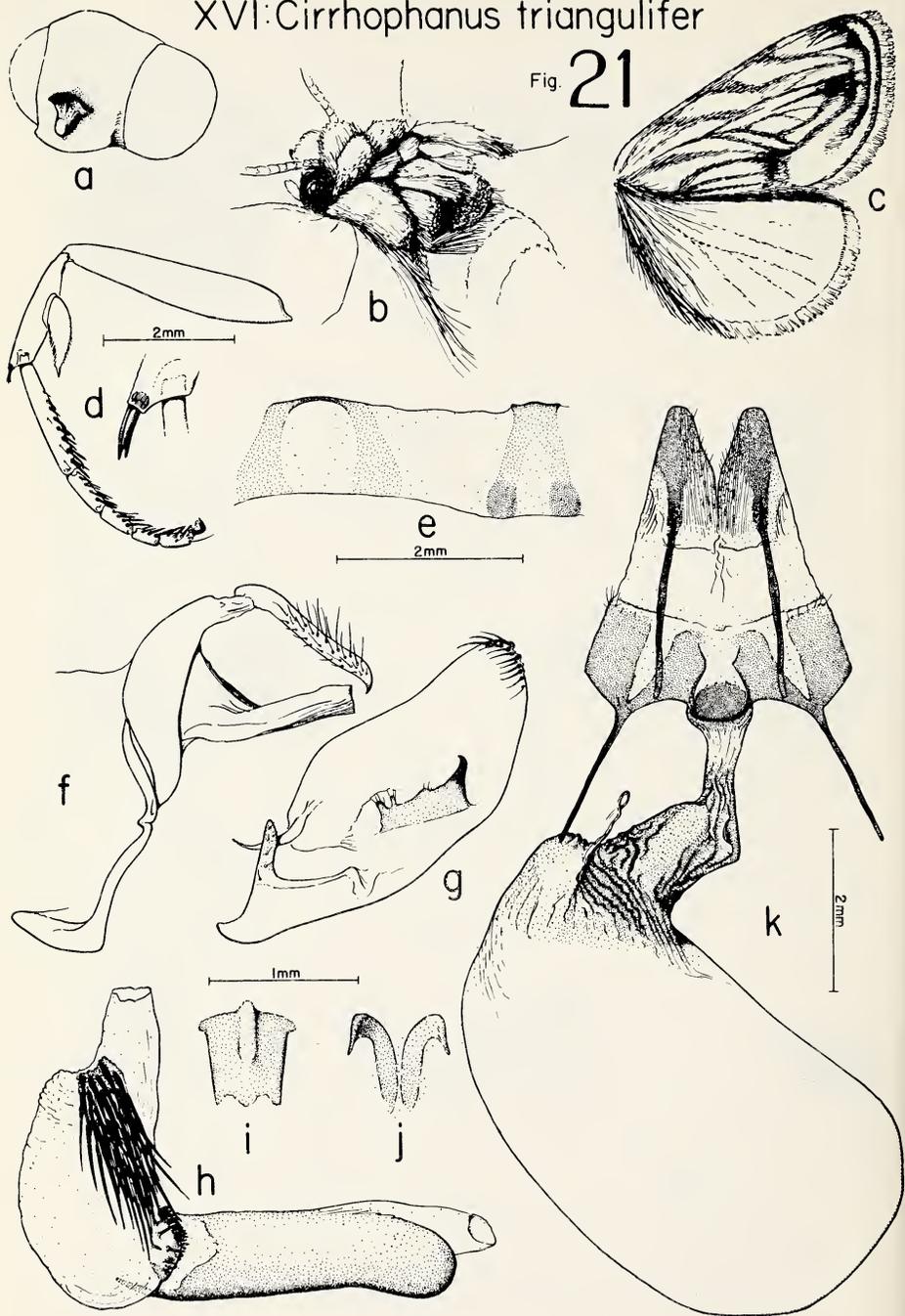
XV: *Cirrhophanus chryseochilus*

Fig. 20



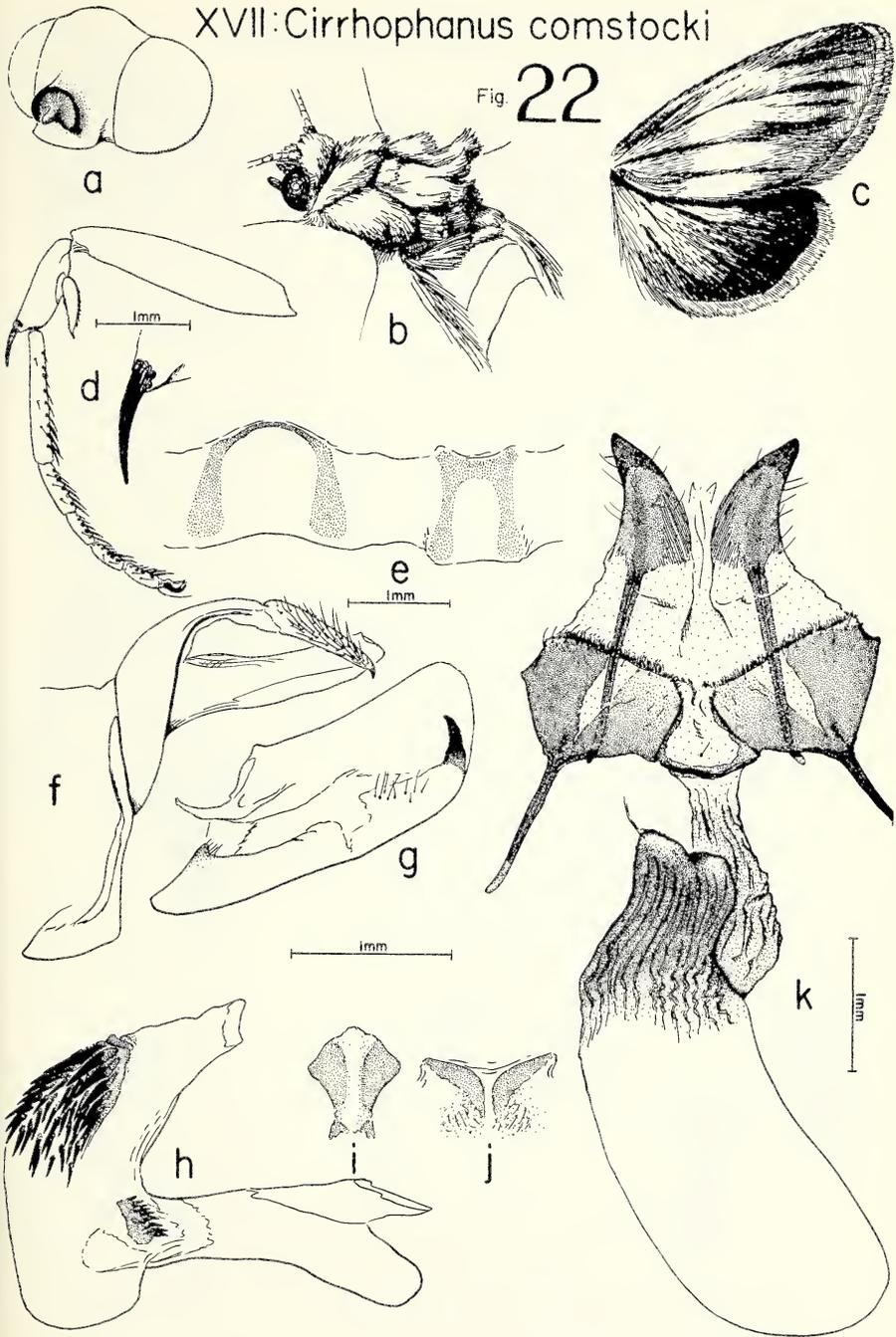
XVI: *Cirrhophanus triangulifer*

Fig. 21



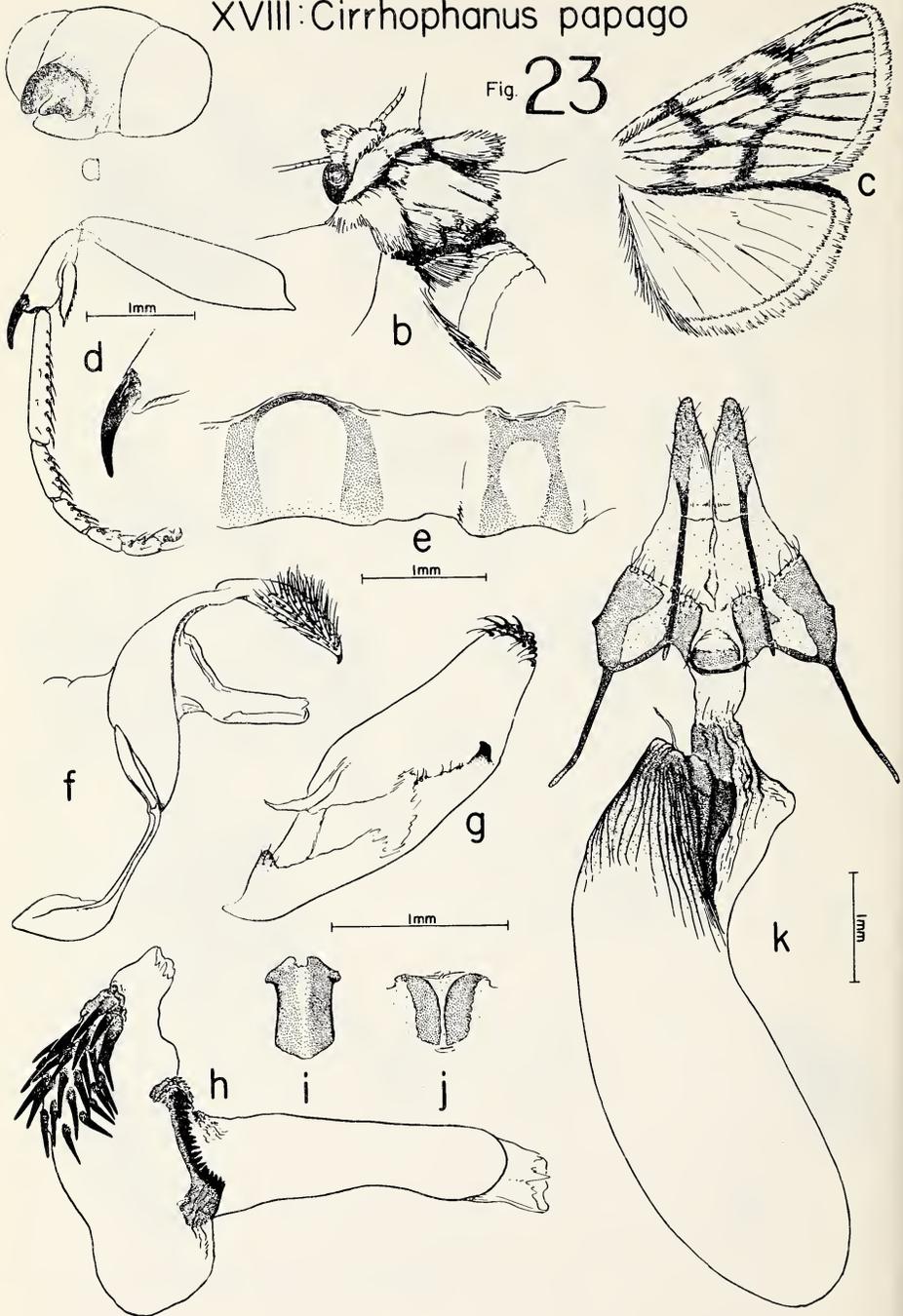
XVII: *Cirrhophanus comstocki*

Fig. 22



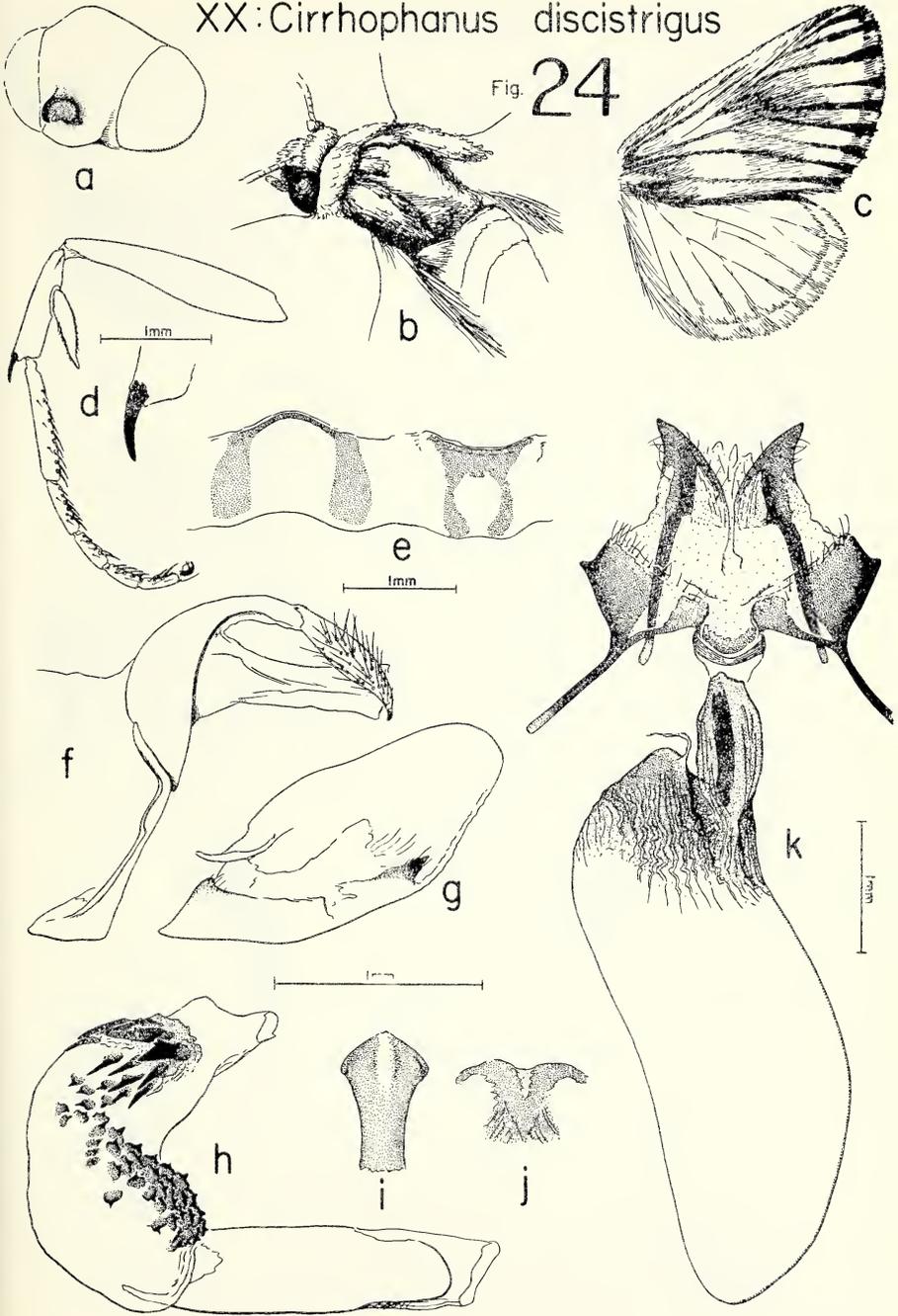
XVIII: *Cirrhophanus papago*

Fig. 23



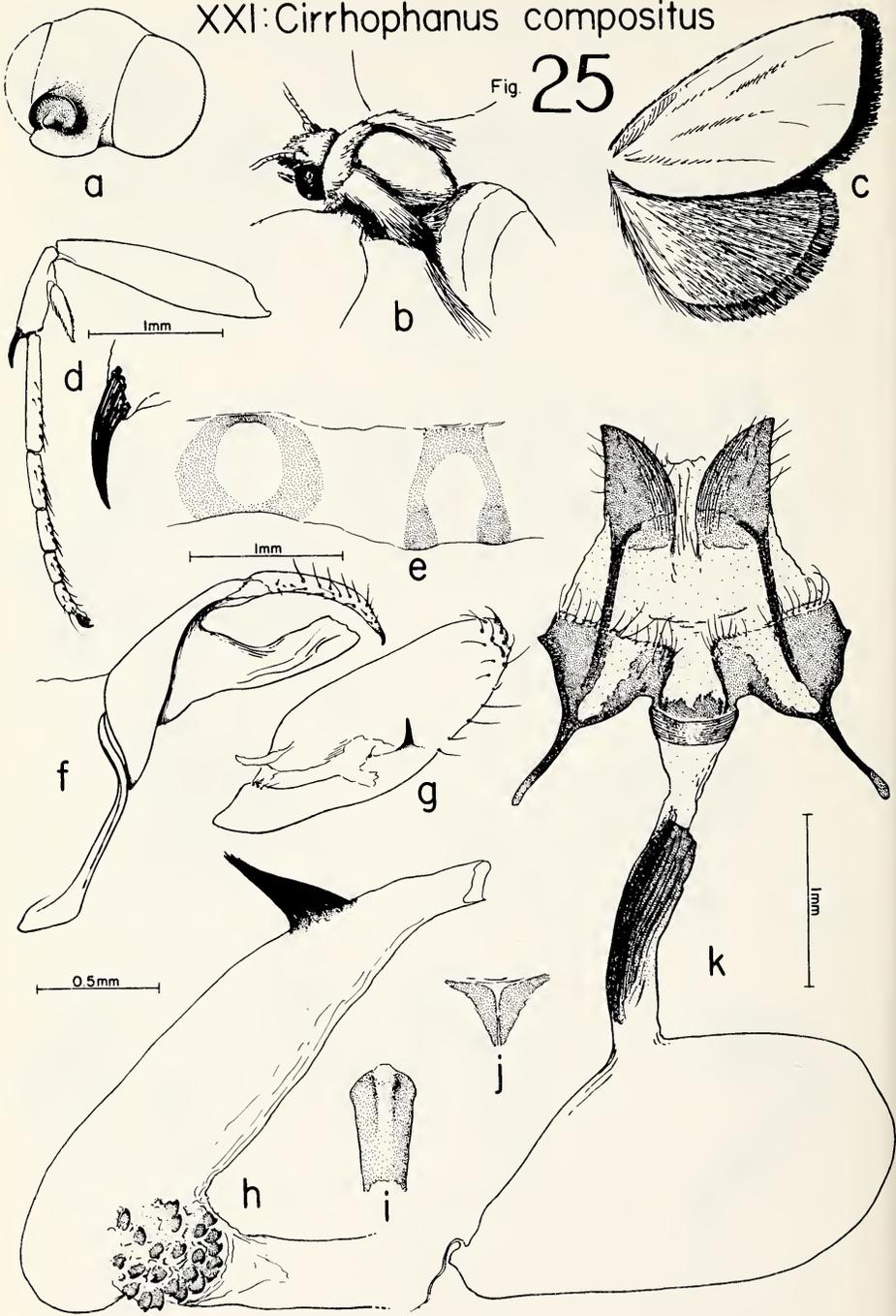
XX: *Cirrhophanus discistrigus*

Fig. 24



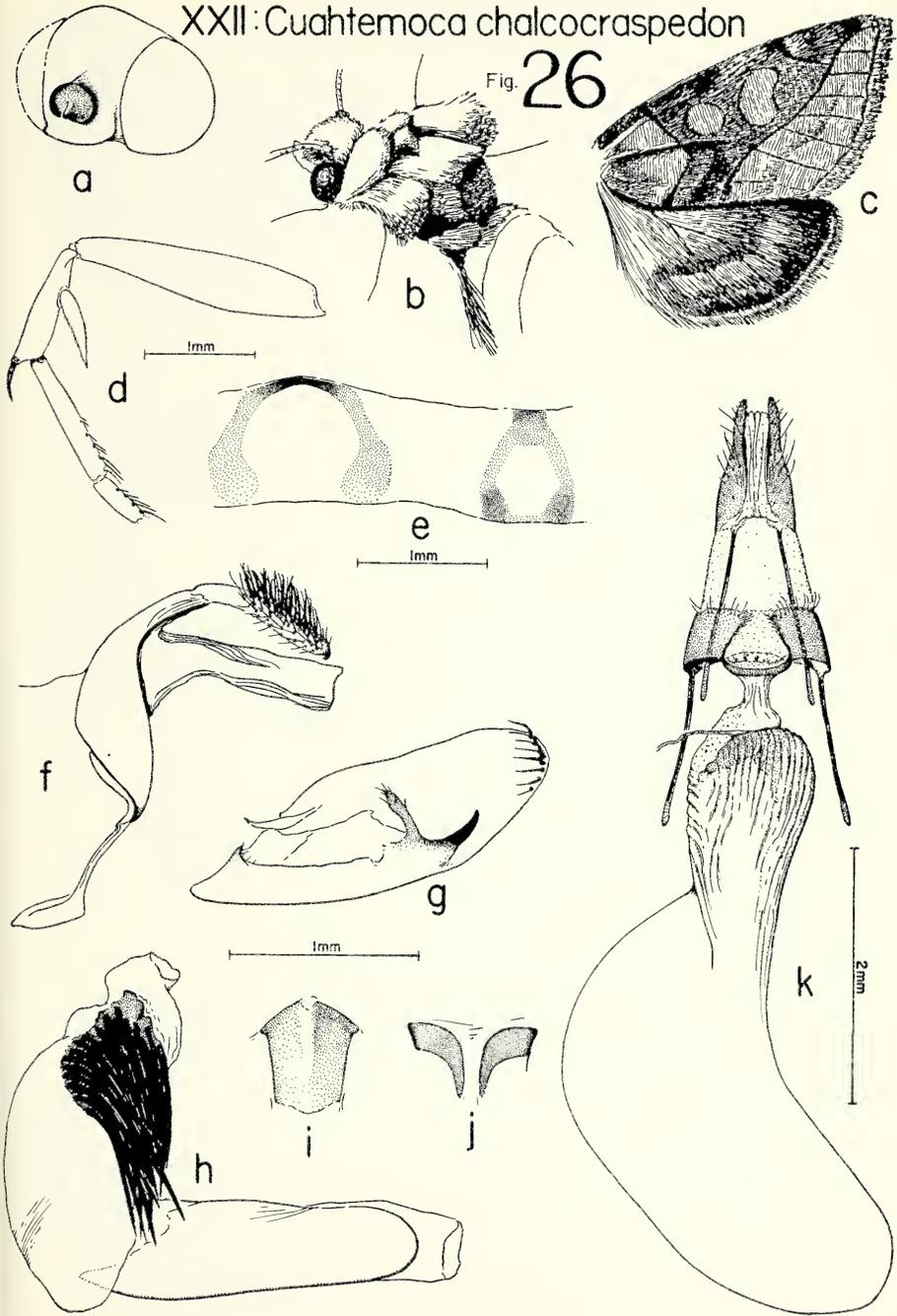
XXI: *Cirrhophanus compositus*

Fig. 25



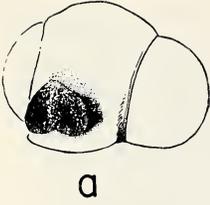
XXII: *Cuahtemoca chalcocraspedon*

Fig. 26

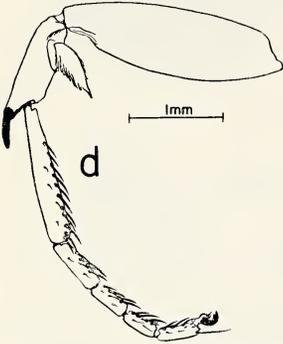
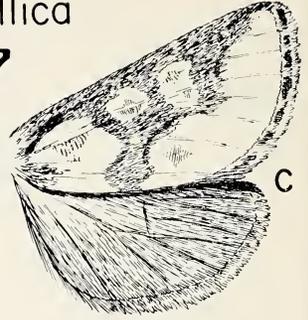


XXIII: Chalcopasta ellica

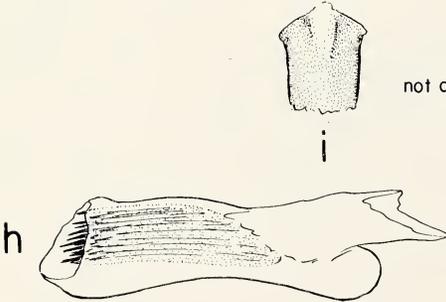
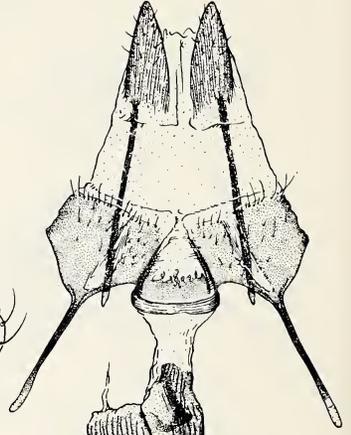
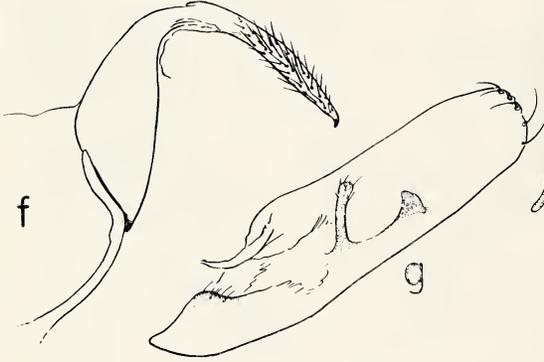
Fig. 27



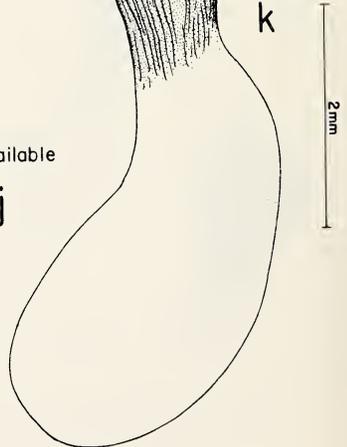
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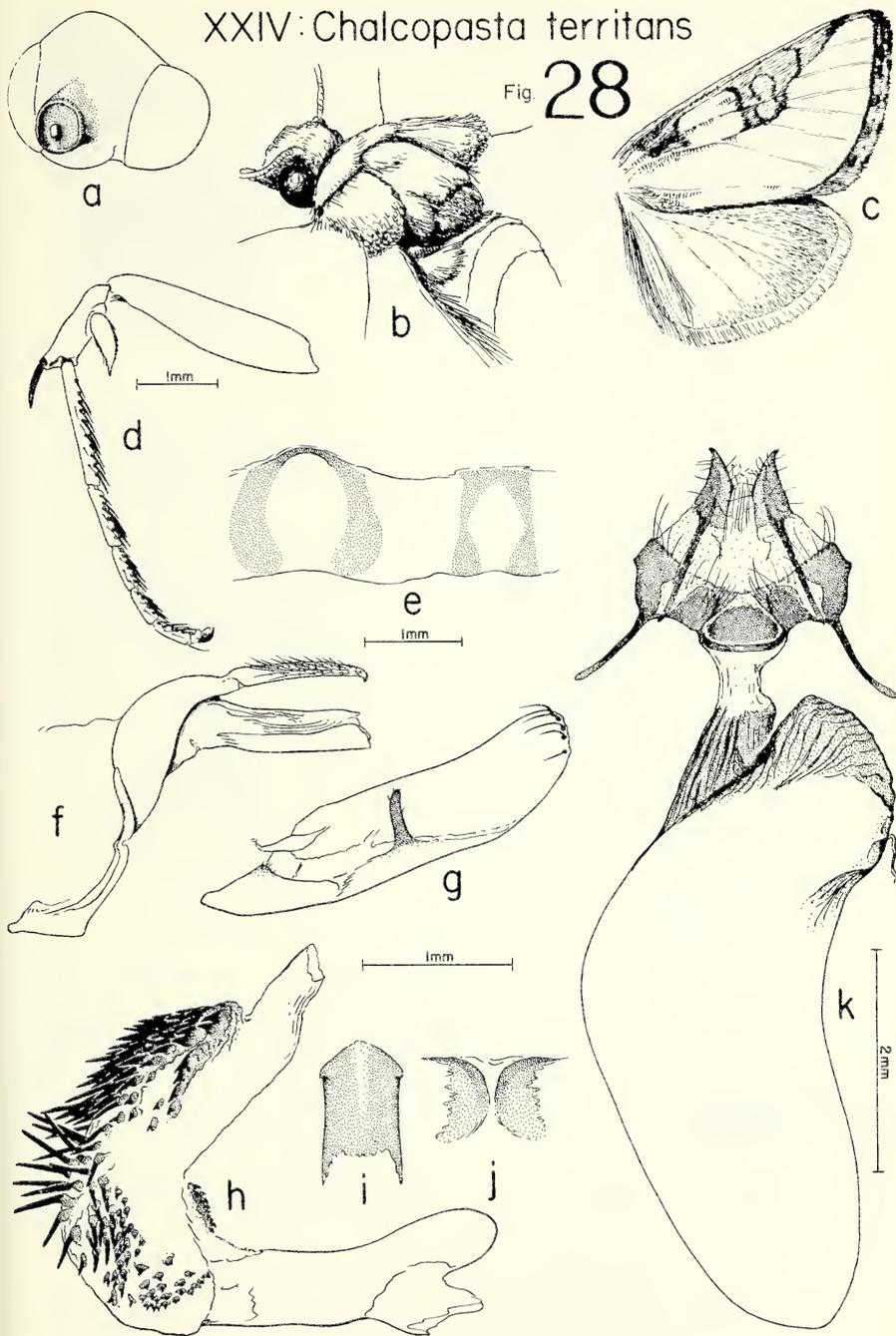


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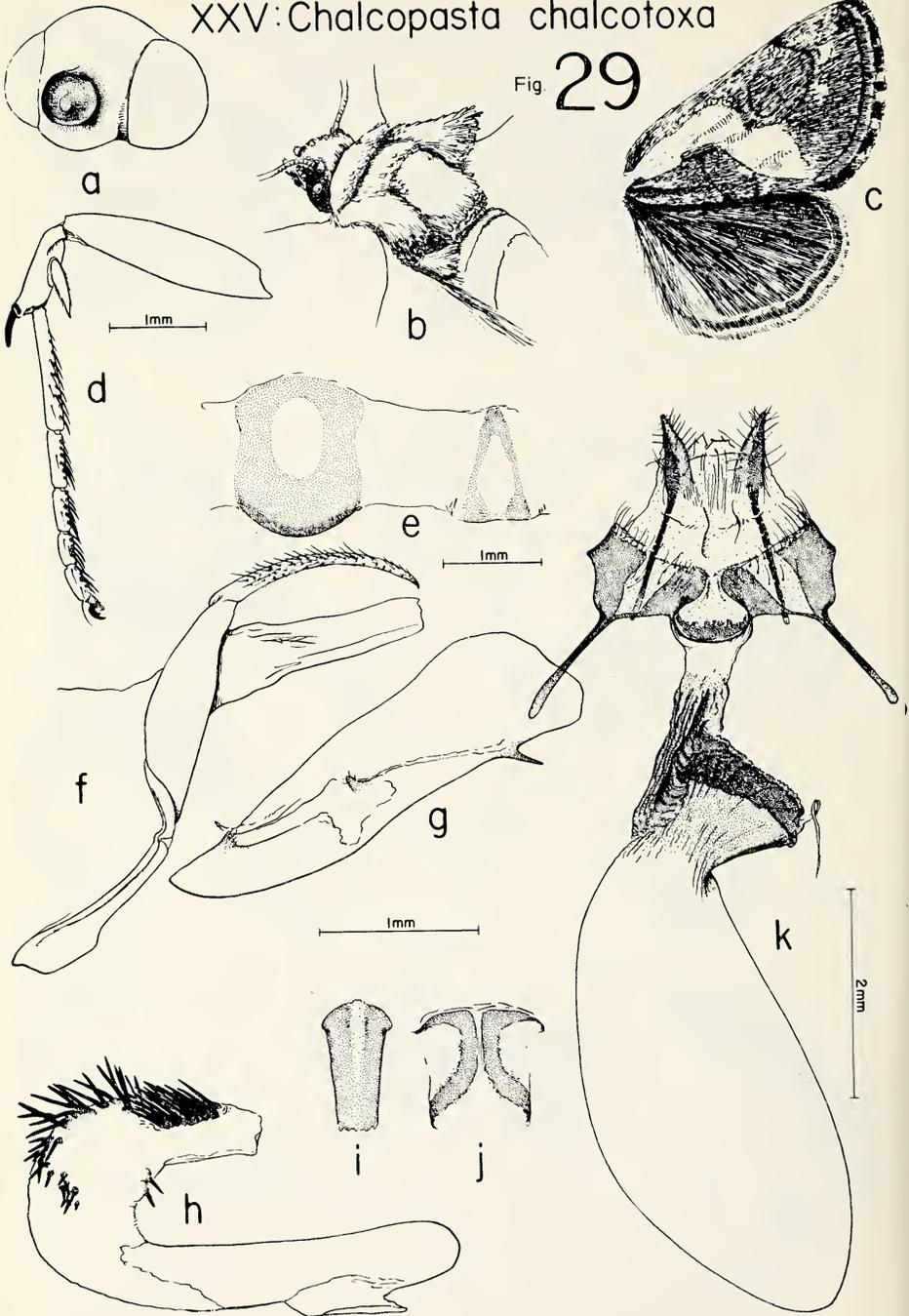
XXIV: *Chalcopasta territans*

Fig. 28



XXV: *Chalcopasta chalcotoxa*

Fig 29



XXVI: *Basilodes chrysopsis*

Fig. 30

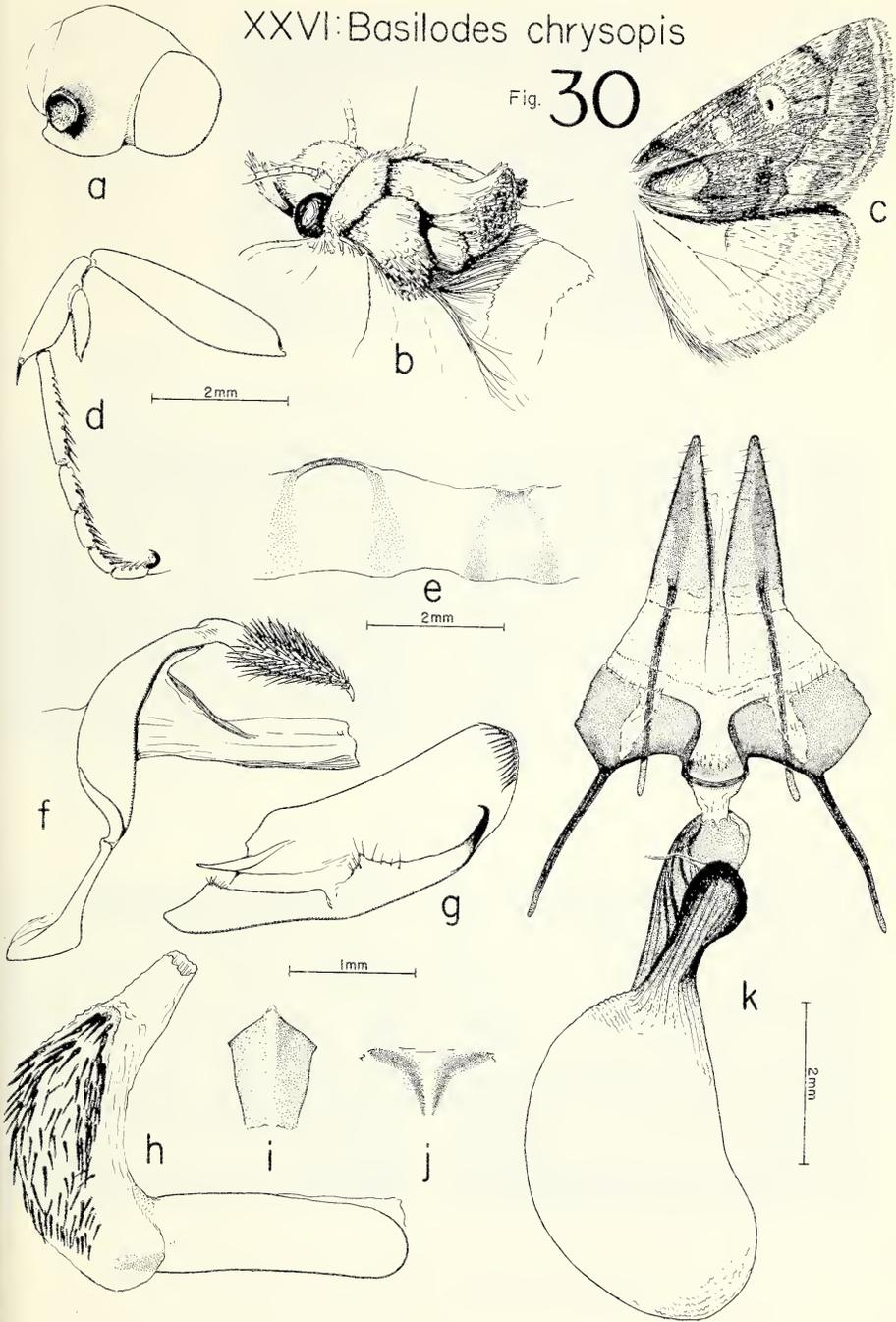
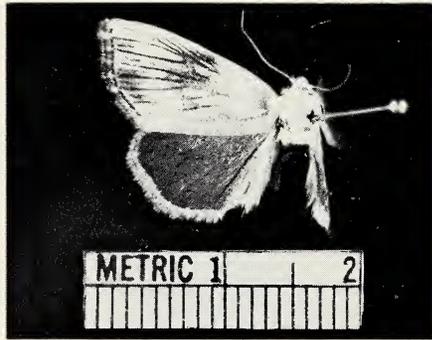
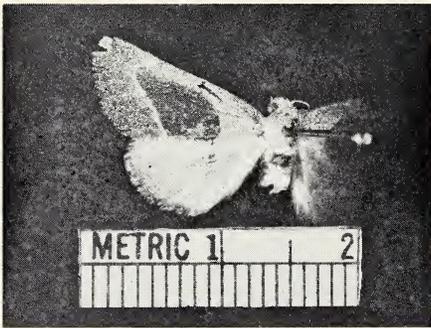


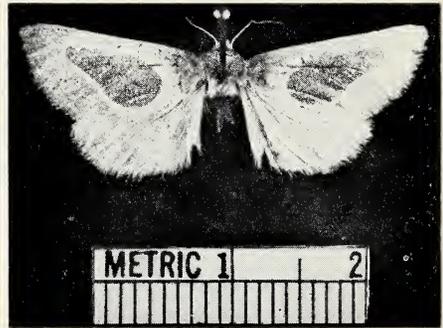
Fig. 31



a

Cirrhophanus hoffmanni

b



c

Plagiomimicus baja

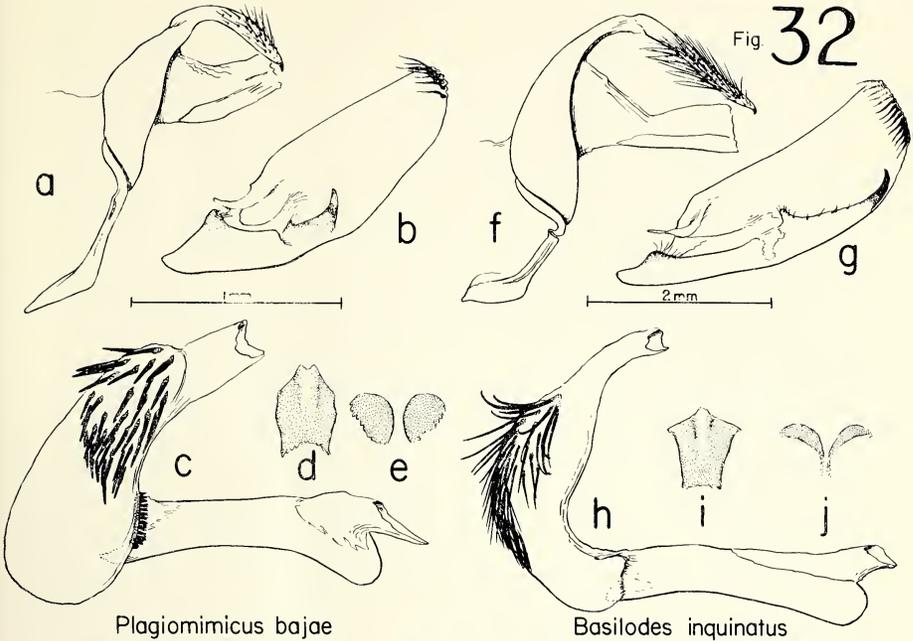
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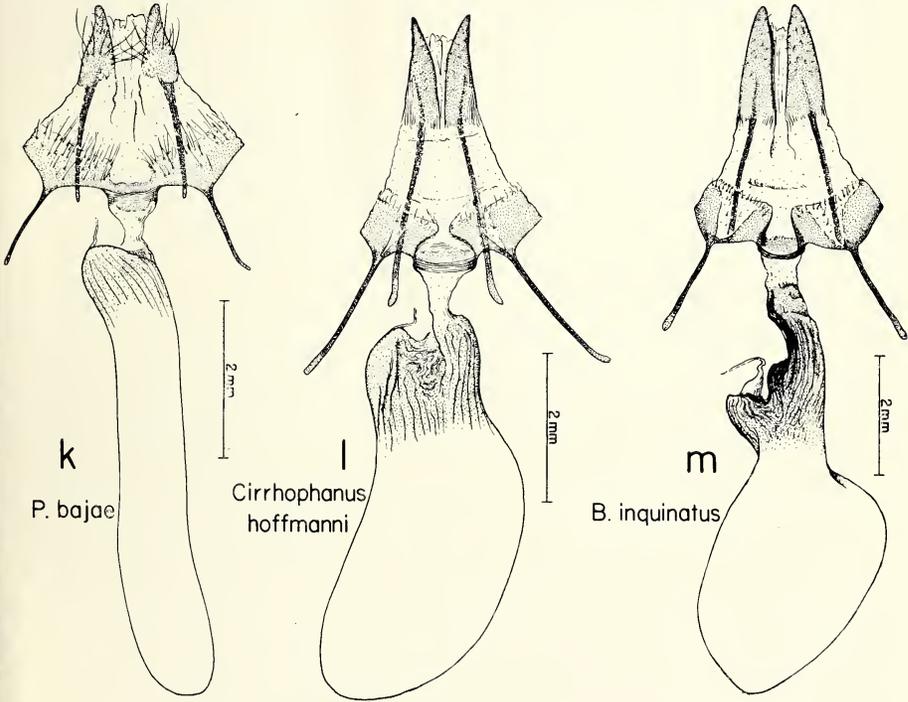
Basilodes inquinatus

Fig. 32



Plagiomimicus bajae

Basilodes inquinatus



P. bajae

Cirrhophanus hoffmanni

B. inquinatus



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CONTRIBUTIONS IN SCIENCE

NUMBER 65

MARCH 18, 1963

A NEW COSTA RICAN SALAMANDER (GENUS *OEDIPINA*)
WITH A RE-EXAMINATION OF *O. COLLARIS*
AND *O. SERPENS*

By ARDEN H. BRAME, JR.



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DAVID K. CALDWELL

Editor

A NEW COSTA RICAN SALAMANDER (GENUS *OEDIPINA*)
WITH A RE-EXAMINATION OF *O. COLLARIS*
AND *O. SERPENS*

By ARDEN H. BRAME, JR.¹

ABSTRACT: The plethodontid salamander, *Oedipina collaris*, is redescribed and shown to be a valid form with *O. serpens* relegated to the position of a junior synonym under *collaris*. A new species, *Oedipina poelzi*, is described from the Cordillera Central of Costa Rica. Its relationships are shown to be with *O. collaris*.

The discovery of an undescribed long legged and strikingly colored *Oedipina* from the vicinity of El Angel Waterfall in north-central Costa Rica provided the impetus for study of this complex genus. The present paper is concerned with the description of the new form and consideration of the validity of *Oedipina collaris* and *O. serpens*.

In 1907, Stejneger described an elongate salamander, *Spelerpes collaris* (= *Oedipina collaris*), from a single very large adult. Stejneger's original description is inadequate because several additional related forms are now known which approach most of the characters in his description. It is necessary, therefore, to rediagnose and redescribe the holotype, mentioning important characters not covered by Stejneger.

Oedipina collaris (Stejneger, 1907)

Figure 1A

1907. *Spelerpes collaris* Stejneger, Proc. U. S. Natl. Mus., 32(1538): 465-6.
1924. *Oedipus collaris* Dunn, Zool. Ser., Field Mus. Nat. Hist., 12: 99.
1944. *Oedipina collaris* Taylor, Univ. Kansas Sci. Bull. 30, Pt. I (12): 226.
1949. *Oedipina serpens* Taylor, Univ. Kansas Sci. Bull. 33, Pt. I (6): 286-8.

Holotype: USNM 37350, adult male, from Topaz Mine, Nicaragua, "90 miles N. W. of Bluefields, and 50 miles back in direct line from the coast"; elevation 400 feet (120 meters).

Referred Material: KUMNH 23815, adult male (holotype of *O. serpens*) from Morehouse Finca, 5 miles southwest of Turrialba, Provincia de Cartago, Costa Rica; and MCZ 9831, adult male, from La Loma, on the trail from Chiriquito to Boquete, Provincia de Bocas del Toro, western Panama.

Diagnosis: *Oedipina collaris* is the largest species in the genus both in length (57.7 to 71.9 mm. snout-vent length) and in bulk. In addition, it is distinguished from all other species of *Oedipina* by the following combination of characters: long snout that becomes progressively narrower toward the tip ("sharp"), (see Fig. 1A, and Table 2); large numbers of maxillary (80 to 98) and dentary teeth (85 to 110); extremely long and robust limbs (in proportion

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to snout-vent length) with only 9 to 10 costal folds remaining uncovered when limbs are appressed to sides of trunk; 19 costal grooves per side; eyes small in proportion to head width (1.7 to 2.0 mm. at head width of 6.3 to 7.9 mm.); color drab lead-black over entire body (Panamanian specimen with lateral thin grayish stripes).

Description of Holotype: Adult male, snout very long (see Fig. 1A, and Table 2), narrowing progressively towards the tip ("sharp"); small well defined mental gland at tip of chin; nostril small, labial protuberances strongly defined; canthus rostralis not strongly arched. Snout-vent length 9.1 times head width. Vomerine teeth 8 left, 14 right, extending about one mm. past the lateral border of the internal nares; maxillary teeth 42-41. Two premaxillary teeth piercing lip. Tail missing. Limbs long, allowing 10 costal folds to remain uncovered when appressed to sides of trunk; snout-vent length 5.8 times right hind limb. Webbing of hands and feet extensive but tips of middle three toes free, webbing very thick causing toes to appear nearly united; digits flattened. Fingers in order of decreasing length: 3, 4, 2, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements In Millimeters: Head width 7.9; anterior rim of orbit to snout 4.4; anterior rim of orbit to external nares 3.6; horizontal orbital diameter 2.0; interorbital distance 2.8; distance between vomerine teeth and premaxillary teeth 2.9; distance between parasphenoid teeth and premaxillary teeth 3.7; internal choanae (nares) to premaxillary teeth 2.6; distance separating internal choanae 2.3; snout to posterior angle of vent 71.9; axilla-groin length 45.2; hind limb length 12.4; width of right foot 4.

Coloration In Alcohol: Lead black on all body surfaces except for pale white areas at the edge of the gular fold and semi-lunar pale white marks at the insertion of the legs, bend of the elbow and of the knee; the side of the head shows some indications of being pale.

Remarks: Taylor (1949) described *Oedipina serpens* from a single Costa Rican specimen. He discussed differences of this specimen from *O. collaris* and presented a table (p. 288) contrasting the two species. This table indicates that a number of characters separate them, but from recent examination of both holotypes it is evident that Taylor did not examine the holotype of *collaris*, but relied wholly upon Stejneger's description and Dunn's (1926) additional notes.

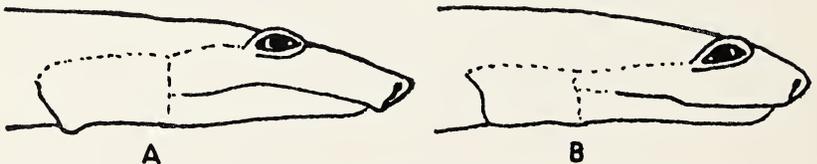


Fig. 1. A. Lateral view of the head and snout of the holotype (USNM 37350) of *Oedipina collaris* (Stejneger, 1907), an adult male.

B. Lateral view of the head and snout of the holotype (LACM 1722) of *Oedipina poelzi*, an adult male.

Some of the characters used by Taylor (1949) in his table are discussed below. Taylor lists *Oedipina collaris* as having a sharp snout and *Oedipina serpens* as having a blunt truncate snout; here he relies on Dunn's (1926) terminology where Dunn used sharp merely to indicate a progressive narrowing of the snout towards the tip, but Taylor apparently ignores Stejneger's (1907) statement (truncate snout) used for the same specimen. Indeed, both specimens may be said to have "sharp" snouts with truncate tips.

Taylor's head width measurement for *O. serpens* is considerably larger (8.8 mm.) than mine (7.7 mm.) and my head width for *O. collaris* (which is just 1.9 mm. snout-vent length longer than *serpens*) is 7.9 mm. Therefore, the snout-vent length is 9.1 times the head width in both holotypes, not 7.5 times for *collaris* and 8.4 times for *serpens* as Taylor reports. In addition, *O. collaris* has 8 left and 14 right vomerine teeth (not 9 per side as first reported by Dunn and later by Taylor who apparently followed Dunn); I counted 16 left and 17 right vomerine teeth on *O. serpens* which is higher than Taylor's 15 per side. Numbers of vomerine teeth are more variable than maxillary teeth as can be seen in Table 1.

I counted 10 costal folds between the appressed limbs of *O. collaris* and $9\frac{1}{2}$ between the appressed limbs of *O. serpens*, whereas Taylor mentioned 11 (again apparently *vide* Dunn, 1926) versus 9 respectively. Of the other characters which are either of a highly variable or subjective nature, only slight differences in the shape of the feet seem worth mentioning and it may be pointed out here that foot shape and its associated webbing are quite variable in the genus *Oedipina*. *O. collaris* has a slightly broader foot 4.0 mm. versus 3.6 mm. for *O. serpens* and the feet are more flattened in *collaris*, characters not worthy of taxonomic consideration in this genus. The comparative measurements of *O. collaris* and *O. serpens* given in Tables 1 and 2 indicate that there is only one species involved, and this is further strengthened by the high degree of similarity in coloration, both specimens being uniformly lead black. It is apparent that *Oedipina serpens* is a junior synonym of *Oedipina collaris*.

A third specimen of *O. collaris* from Panama differs primarily in being smaller (57.7 mm. snout-vent length) and in having a lateral stripe similar to the species of *Oedipina* being described below. Dunn (1926. 431-32) reported the specimen in life to be black above and below with a gray band on each side between insertions of the legs; snout lighter, tinged with brown; tail with many white flecks on sides.

Range: (See map, Fig. 2), *Oedipina collaris* is represented by three specimens from the Caribbean drainage of three different countries: central-eastern Nicaragua, northeastern Costa Rica and west-northwestern Panama from 400 to 2000 feet (120 to 610 meters) elevation.

A university of Southern California field team, working in Costa Rica in the spring and summer of 1959, collected a brightly colored *Oedipina* from the vicinity of El Angel Waterfall and from former Costa Rican President Mario Echandi's Finca. Due to the large size, robust shape, and long limbs of these organisms, it was immediately evident that they were either *O. collaris*

or *O. serpens* (= *O. collaris*) or representatives of an undescribed related species. Examination of the holotypes of the above indicates that the new material represents a distinct form, and I take great pleasure in naming it for my

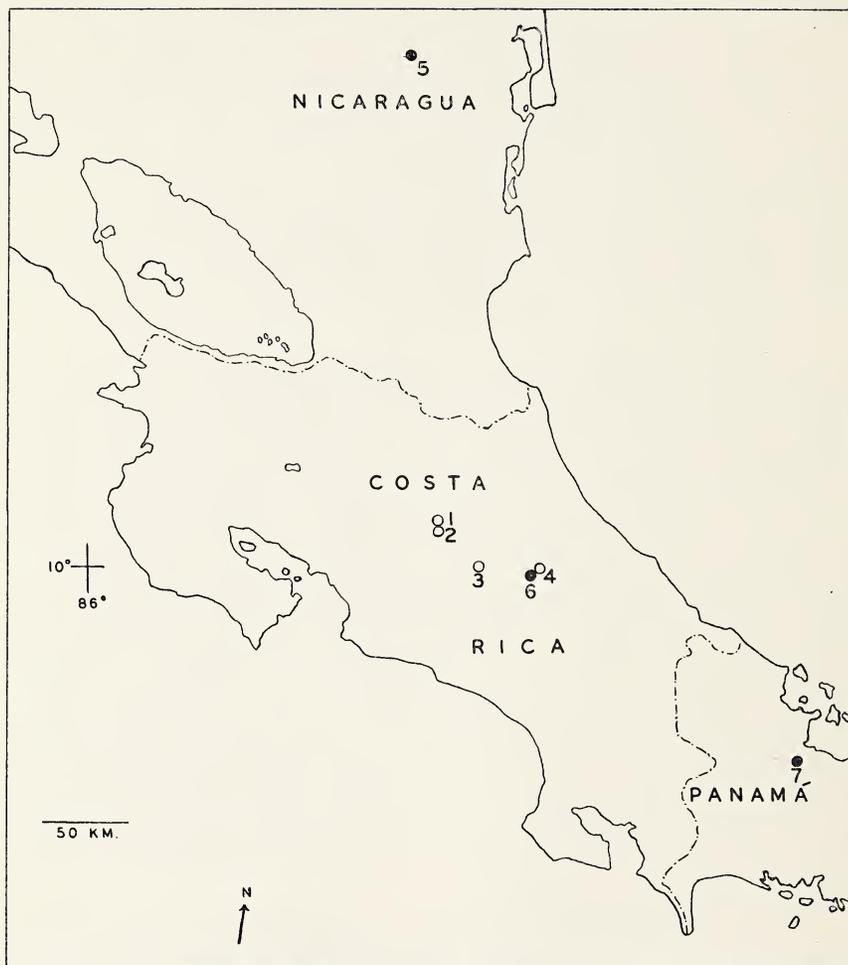


Fig. 2. Map showing ranges of *Oedipina poelzi*, open circles: 1 and 2 indicating area of type locality, vicinity of El Angel Waterfall; 3 indicating the area of Cascajal de Las Nubes; and 4 indicating the locality along the road to Peralta, 6.2 miles from the Rio Reventazon Bridge, from Turrialba. Range for *Oedipina collaris*, closed circles: 5 indicating type locality, 90 miles northwest of Bluefields, Nicaragua; 6 indicating Morehouse Finca, 5 miles southwest of Turrialba, Costa Rica; and 7 indicating La Loma, on the trail from Chiriquito to Boquete, Panama.

German friend, Friedrich Pölz, of Radbruch, Über Winsen, who has greatly aided me in my herpetological endeavours:

***Oedipina poelzi*, NEW SPECIES**

Figures 1B, and 3

Holotype: LACM 1772, adult male, from the area of the stone quarry in the vicinity of El Angel Waterfall (former American Cinchona Plantation and Isla Bonita of Taylor, 1952.), 3.8 miles by road south of Cariblanco (5 miles north of Vara Blanca), along the Vara Blanca-Puerto Viejo Road, Provincia de Heredia-Provincia de Alajuela boundary, Costa Rica; elevation 5000 feet (1520 meters); collected by Arnold G. Kluge, Robert J. Lavenberg, and the author at 1:00 P.M., April 3, 1959.

Paratypes: (41 specimens total), CRE 74.1-7, CRE 75.2-5, and CRE 76.1 (12 specimens) same data as for holotype; CRE 304.1-2, same locality as holotype, collected by John L. Mohr, Thomas R. Pray, and Jay M. Savage, February 1, 1960; LACM 1723-6 same locality as holotype, collected by James Kezer, June 2, 1962; UF 10456-8, from the area of the type locality, collected by Archie Carr, December 2, 1956; UMMZ 123674, from the type locality, collected by Charles F. Walker, William Bussing, and David B. Wake, August 8, 1961; UMMZ 119528-30, UMMZ 123665-73, near the holotype locality, 12 to 14.1 miles north of Vara Blanca from 4400 to 5100 feet (1340 to 1555 meters) elevation on the east slope of Volcan Poas, Provincia de Alajuela, collected by Priscella and Andrew Starrett and Thomas M. Uzzell, Jr., August 6, 1957; UMMZ 119527, along the road to Peralta, 6.2 miles north of the Rio Reventazon Bridge (from Turrialba), Provincia de Cartago, about 3000 feet (915 meters) elevation, collected by Priscella and Andrew Starrett and Thomas M. Uzzell, Jr., August 3, 1957; CRE 174.1-6, from the finca of Mario Echandi, Cascajal de Las Nubes, Provincia de San Jose, collected by Arnold G. Kluge, Alfonso Jimenez, John de Abate, and the author, between 1:00 and 4:00 P.M., June 1, 1959.

Diagnosis: *Oedipina poelzi* is distinguished from its closest relative, *Oedipina collaris*, by its short, broad, blunt snout, with short interorbital distance (1.7 to 2.1 mm. in large adults versus 3.0 to 3.7 mm. in *collaris*); short distance between anterior rim of orbit and external nares (1.8 to 2.1 mm. in large adults versus 2.7 to 2.9 mm. in *collaris*); (See Table 2 for additional comparative head measurements and Fig. 1 for head shape comparisons); its fewer numbers of maxillary teeth (42 to 70 total with mean of 53 in 29 adults versus 80 to 98 in *collaris*); its smaller size (snout-vent length of large adults from 45.1 to 63.6 mm. with mean of 55.6 mm. in 29 specimens versus 57.7 to 71.6 mm. in *collaris*); right foot moderately large (2.1 to 2.4 mm. in width in large adults versus 2.7 to 4.0 in *collaris*); and in its striking dorsal and lateral coloration, consisting of a dorsolateral band of medium to dark brown and a thin lateral stripe of cream or yellowish white contrasted sharply with the deep-black venter (see Fig. 3).



Fig. 3. Lateral view of the holotype (LACM 1722) of *Oedipina poelzi*, an adult male.

The combination of long limbs (hind limbs 6.7 to 10.0 mm., mean of 8.4 mm., in 29 adults over 45 mm. snout-vent length); moderate numbers of costal grooves (19 per side, in all but one individual with 18, in 42 specimens); wide head (5.1 to 6.7 mm., mean 6.1 mm., in 29 adults over 45 mm. standard length); moderate numbers of maxillary teeth, and unique coloration will distinguish *Oedipina poelzi* from all other forms in the genus.

Description Of Holotype: Adult male, snout short (see Fig. 1B) and blunt, truncate at tip; small well defined mental hedonic gland at tip of chin; nostril small, labial protuberances well developed; canthus rostralis moderately arched. Snout-vent length 9.1 times head width, and 5.9 times snout-gular fold length; vomine teeth 10 left, 16 right, extending just past the lateral posterior border of the internal nares. Maxillary teeth 25-29, extending posteriorly three-fourths distance of eyeball. Two premaxillary teeth piercing lip. Postorbital groove distinct, extending posteriorly from eye as small depression for 2.4 mm., sharply proceeding ventrally and extending across gular area parallel to and 2.0 mm. anterior to gular fold. Tail laterally compressed with no basal constriction; 1.4 times snout-vent length. Postiliac gland evident as pale spot. Limbs long, $9\frac{1}{2}$ costal folds remaining uncovered when appressed to sides of trunk; snout-vent length 7.4 times right fore limb, and 6.5 times right hind limb. Fingers and toes long and linear, semiconical in shape, not very flattened; thin webbing of hands and feet extensive but tips of middle three toes free; toes 1 and 5 fused to 2 and 4 respectively. Fingers in order of decreasing length: 3, 4, 2, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements In Millimeters: Head width 6.4; snout-gular fold (head length) 9.8; head depth at posterior angle of jaw 3.6; eyelid length 2.9; eyelid width 1.3; anterior rim of orbit to snout 2.8; anterior rim of orbit to external nares 2.1; horizontal orbital diameter 1.9; interorbital distance 1.8; distance between vomerine teeth and premaxillary teeth 3.0; internal choanae (nares) to premaxillary teeth 1.8; distance separating external nares 2.0; snout to fore limb 15.0; snout projection beyond mandible .9; snout to posterior angle of vent 58.1; snout to anterior angle of vent 55.8; axilla-groin length 36.7; fore limb length 7.9; hind limb length 9.0; width of right hand 1.2; width of right foot 2.0; tail length 80.8; tail depth at base 3.7; tail width at base 3.3.

Coloration In Life: Medium dark brown dorsally forming a broad band that passes well on to the tail, and becomes much lighter there; an indistinct thin white stripe laterally stopping abruptly at the dense black ground color below the mid lateral area and on the venter; tail coloring less uniform with brown patches overlying the dark black ground color; limbs mostly of black ground color with a few small brown patches above; a few whitish guanophores laterally on tail and fewer on venter of tail, many tiny guanophores on tail dorsally; numerous small guanophores on trunk venter, with larger ones on gular area; eyes orange-brassy; upper lip light white; head with diffuse brown patches overlying the black color; a dark ring of pigment around the cloacal slit. In alcohol, the dorsal brown band and lateral white stripes barely evident, but guanophores still clearly discernible, (see Fig. 3).

TABLE 1. Data on *Oedipina collaris* and *O. poelzi*

		Snout-Vent Length	Axilla-Groin Length	Head Width	Hind Limb Length	Coastal Folds Between Appressed Limbs	Snout-Gular Fold Length	Maxillary Teeth	Vomerine Teeth	Tail Length
<i>O. collaris</i>										
USNM 37350	♂	71.9	45.2	7.9	12.4	10	—	83	22	—
KUMNH 23815	♂	70.0	45.2	7.7	13.6	9½	11.9	98	33	130.2
MCZ 9832	♂	57.7	36.0	6.3	10.7	9	9.9	80	22	155.2
<i>O. poelzi</i>										
UMMZ 123668	♂	62.9	41.8	6.4	9.7	10	10.0	60	26	106.2
UMMZ 123666	♂	61.3	38.7	6.5	9.5	9	10.1	62	23	87.0
UMMZ 123671	♂	59.2	37.9	6.7	10.0	10	9.3	52	24	117.2
UF 10456	♂	58.7	37.4	6.1	9.2	10½	9.9	61	22	—
CRE 304.1	♂	58.5	37.6	6.4	9.2	10	9.9	67	28	121.8
CRE 74.5	♂	58.1	37.1	6.2	9.0	10	9.2	49	15	—
LACM 1722	♂	58.1	36.7	6.4	9.0	9½	9.8	54	26	80.8
UF 10458	♂	55.7	35.3	5.8	8.9	10½	9.2	53	21	108.8
CRE 174.1	♂	55.6	36.5	6.0	7.8	11	8.4	44	16	92.3
CRE 75.2	♂	55.1	34.2	6.5	8.8	9	9.4	54	25	—
CRE 174.2	♂	49.3	31.3	5.7	7.4	9½	8.5	44	19	110.4
CRE 174.4	♂	44.7	29.2	5.4	6.4	10	7.3	41	18	85.8
CRE 174.5	♂	41.5	27.5	4.9	6.3	10½	6.9	38	15	74.0
CRE 174.6	♂	40.8	26.1	4.9	6.1	10	6.3	33	14	54.3
CRE 74.3	♂	63.6	41.7	6.6	8.9	10½	10.1	63	21	106.9
UMMZ 123673	♀	61.7	39.5	6.3	9.0	10	10.2	70	26	97.7
UMMZ 123674	♀	61.2	39.4	6.2	8.3	10½	9.0	54	31	118.1
UF 10457	♀	61.0	41.0	6.5	8.2	11½	8.8	54	23	117.8
CRE 75.3	♀	60.0	39.5	6.6	8.8	11	9.7	51	24	98.3
CRE 74.4	♀	59.4	38.9	6.3	8.5	11	9.4	61	29	119.9
UMMZ 119527	♀	58.5	37.9	6.5	10.0	10½	9.2	70	34	100.6
UMMZ 123670	♀	55.7	37.4	6.2	8.1	10½	8.7	54	26	92.2
CRE 174.3	♀	55.6	36.9	6.0	7.2	10½	8.2	42	15	68.7
UMMZ 123669	♀	54.5	36.0	6.3	8.3	10	8.4	46	19	100.2
CRE 74.2	♀	53.5	34.3	6.2	8.0	11	9.1	55	22	96.7
UMMZ 123672	♀	52.9	34.5	5.7	8.0	10	8.6	49	21	96.3
CRE 74.1	♀	49.1	30.8	5.8	7.6	10½	8.3	53	21	58.0
UMMZ 123665	♀	48.9	31.4	5.3	7.7	10	8.0	51	25	67.7
UMMZ 123667	♀	47.3	29.8	5.7	7.8	9	7.3	42	26	89.8
UMMZ 119529	♀	45.7	29.4	5.1	7.2	10	7.7	42	22	66.8
CRE 74.7	♀	45.1	28.0	5.4	6.7	9½	7.7	44	22	70.9
CRE 75.4	♀	45.1	28.3	5.6	7.4	10	7.4	45	22	73.4
LACM 1723	♀	42.3	26.2	5.0	7.1	9	7.8	42	22	65.0
LACM 1724	♀	38.0	23.7	4.6	6.3	9	6.6	43	18	50.1
LACM 1725	♀	37.2	22.9	4.8	6.3	9	7.2	44	21	53.8
LACM 1726	♀	36.4	21.8	4.7	6.3	8½	6.7	41	23	50.8
UMMZ 119528	♀	35.1	22.1	4.3	5.9	9	6.2	40	17	—
CRE 304.2	♀	33.8	20.7	4.3	5.8	9½	6.2	38	21	32.0
CRE 76.1	♀	32.6	19.7	4.4	6.3	9	6.2	42	18	—
CRE 75.5	♀	30.2	18.3	4.3	5.3	9	5.5	29	15	—
CRE 74.6	♀	29.2	17.0	4.1	5.0	9	5.6	34	17	25.8
UMMZ 119530	♀	24.4	14.6	3.6	4.4	9	4.7	23	—	21.4

Variation: Tables 1 and 2 present the important comparative measurements and data for the holotype and 41 paratypes. The dorsal color varies from medium light orange-brown to very dark brown with some individuals showing medium or yellow brown bands; the amount of brown patching on the head and tail is variable. Males have slightly longer limbs and more definite truncation of the snout.

Habitat: On April 3, 1959, the holotype and 12 of the paratypes were collected on both sides of the large El Angel Waterfall, beside the stream just north of the fall under logs and stones. Most individuals were taken from moss and lichen mats covering the road cuts near the falls where water seepage was constant. Also collected at the type locality were one snake, *Rhadinaea serperastr*, several frogs of the genus *Eleutherodactylus*, and three other salamanders; 3 *Chiropetrotriton abscondens*, 1 *Bolitoglossa subpalmata*, and 2 *Oedipina syndactyla?*.

TABLE 2. Head and Foot Data on *Oedipina collaris* and *O. poelzi*

		Interorbital Distance	Anterior Rim of Orbit to Snout	Anterior Rim of Orbit to Nares	Vomerine Teeth to Premaxillary Teeth	Internal Choanae to Premaxillary Teeth	Distance Between Internal Choanae	Width of Right Foot
<i>O. collaris</i>								
USNM 37350	♂	2.8	4.4	3.6	2.9	2.6	2.3	4.0
KUMNH 23815	♂	2.9	4.6	3.7	2.8	2.5	2.4	3.6
MCZ 9832	♂	2.4	3.8	3.0	2.7	2.4	2.0	2.7
<i>O. poelzi</i>								
CRE 74.3	♀	2.0	2.7	2.1	1.9	1.6	1.6	2.2
CRE 75.3	♀	1.8	2.8	1.9	1.8	1.7	1.7	2.4
CRE 304.1	♂	2.1	2.9	2.1	2.0	1.8	1.8	2.2
LACM 1722	♂	1.8	2.8	2.1	2.1	1.8	1.8	2.2
CRE 75.2	♂	1.7	2.7	1.8	2.1	1.9	1.7	2.1

Relationships: Similarity of body form, long limbs, bulk and great length, link *Oedipina poelzi* more closely to *O. collaris* than to any other member of the genus. Important differences in snout length and shape (Fig. 1) and coloration serve as significant distinguishing characters. *Oedipina poelzi* differs from the long robust-limbed *O. elongatus*, *O. parvipes*, and *O. complex* by having more costal grooves (19 per side in *poelzi* versus 17 per side) and from the short slender-limbed species, by having longer legs and wider heads.

Range: *Oedipina poelzi* is known presently only from the slopes of the Cordillera Central, north of the cities of Heredia, San Jose, and Turrialba, in north central Costa Rica from 3000 feet to 5100 feet (915 meters to 1555 meters). (See map, Fig. 2).

ACKNOWLEDGMENTS AND ABBREVIATIONS

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A NEW TOADFISH OF THE GENUS *PORICHTHYS*
FROM CARIBBEAN PANAMA

By DAVID K. CALDWELL and MELBA C. CALDWELL

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DAVID K. CALDWELL

Editor

A NEW TOADFISH OF THE GENUS *PORICHTHYS*
FROM CARIBBEAN PANAMA

By DAVID K. CALDWELL¹ and MELBA C. CALDWELL²

ABSTRACT: A new species of toadfish, *Porichthys pauciradiatus*, is described from Caribbean Panama in Caledonia Bay. Its relationship to other recorded forms in this genus is discussed.

In April, 1939, the Allan Hancock Foundation research vessel VELERO III, under the direction of Captain Hancock, made a short cruise to the southern Caribbean sea. Details of this cruise were given by Garth (1945), and a list of the fishes collected is now in press (Caldwell and Caldwell, *In Press*). In preparing the list of fishes, we found seven specimens from Panama which represent an undescribed species of the genus *Porichthys*, family Batrachoididae. This form may now be known as:

***Porichthys pauciradiatus*, NEW SPECIES**

Figures 1-3.

Diagnosis: A species of *Porichthys*, as discussed by Hubbs and Schultz (1939), distinguished by a low number (27-28) of anal fin-rays and a correspondingly low number (29-31) of dorsal fin-rays.

Description: Dorsal II-29 (II-29 to 31)³; anal 28 (27 in four, 28 in two); pectorals 14-14 (14-14 to 15-15); pelvics I, 2 (I, 2).

Palatine teeth caninelike, slightly curved backward, about 6 to 10 in the single series on each side, the anteriormost teeth strongest; vomerine canine teeth 1 or 2 at each outer angle of bone, teeth strong, slightly curved backward; premaxillary teeth finely caninelike; mandibular teeth biserial anteriorly, with the inner row continued backward as strong canines. Peritoneum dark. The pattern of pigmentation (consisting primarily of 8 dorsal saddles) is shown in the figures accompanying this paper and these should be considered as part of the description. The fins were colorless.

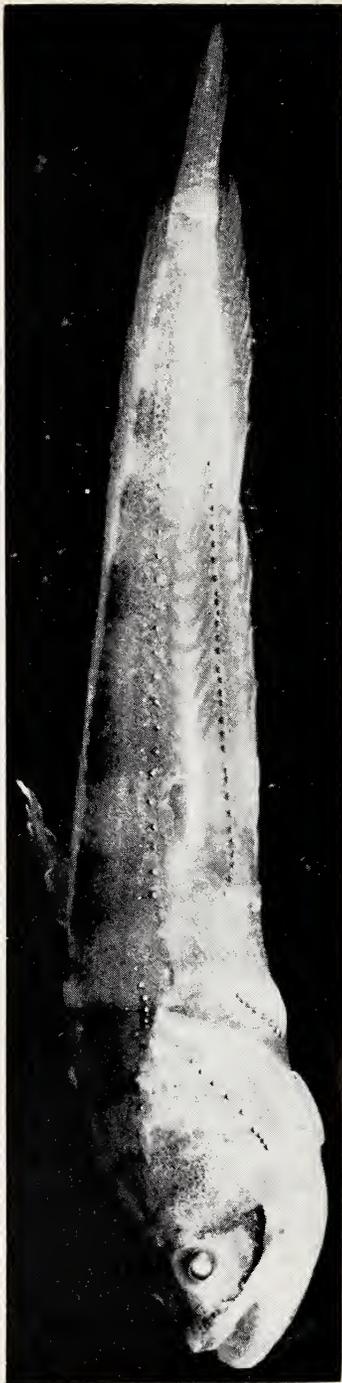
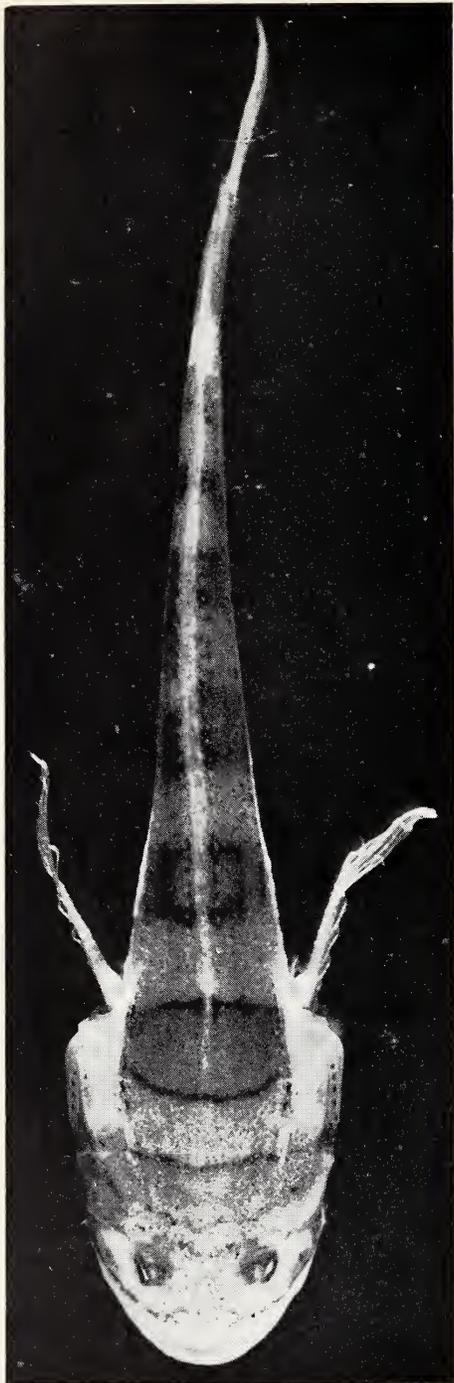
Measurements in thousandths of the standard length for the holotype and (in parentheses) for three of the paratypes 18.5 to 34.5 mm. in standard length: Greatest body depth, 186 (190-207); distance from tip of snout to origin of soft dorsal fin, 354 (341-368); distance from tip of snout to origin of spinous dorsal fin, 289 (277-292); distance from tip of chin to anus, 410 (385-436); length of head, 307 (286-335); interorbital width, 59 (46-50); length of orbit, 44 (55-62); length of upper jaw, 165 (152-176); length of

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³Counts in parentheses are for the six paratypes.

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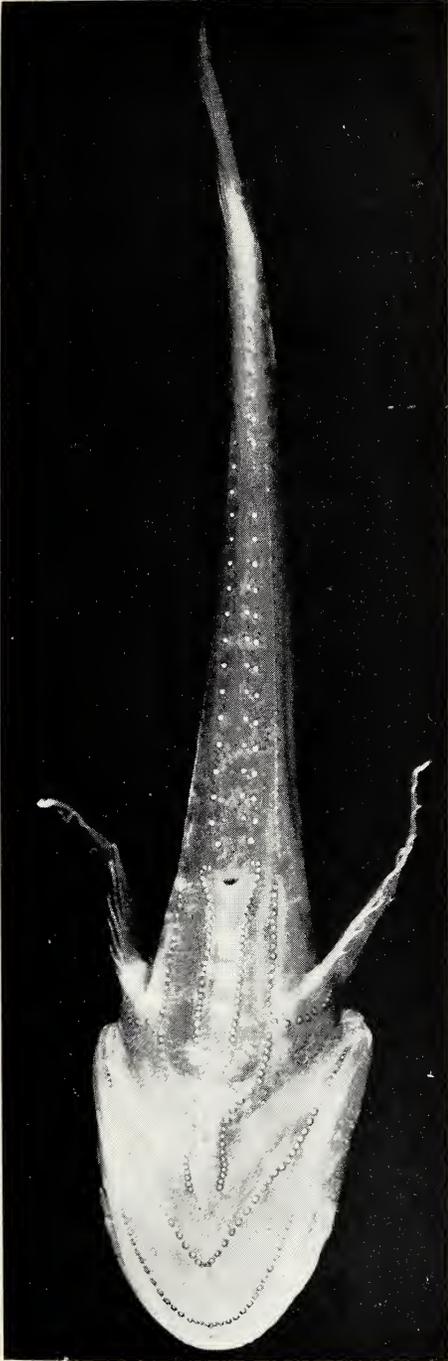


Fig. 1. *Porichthys pauciradiatus*, new species. Dorsal view of the holotype, 33.9 mm. standard length, AHF 3037. (Photograph by Armando Solis, Los Angeles County Museum).

Fig. 2. *Porichthys pauciradiatus*, new species. Lateral view of the holotype, 33.9 mm. standard length, AHF 3037. The tip of the right pectoral fin should not be misinterpreted as being an extended anterior part of the dorsal fin. There is no such extension. (Photograph by Armando Solis).

Fig. 3. *Porichthys pauciradiatus*, new species. Ventral view of the holotype, 33.9 mm. standard length, AHF 3037. (Photograph by Armando Solis).

snout, 50 (47-62); distance from tip of lower jaw to anteriormost point of the V-shaped forward extension of the branchiostegal row of photophores, 84 (70-95).

Holotype: University of Southern California, Allan Hancock Foundation fish collection (AHF) 3037, 33.9 mm. in standard length, dredged at VELERO III station A 7-39, April 4, 1939, in Caledonia Bay, Panama ($8^{\circ} 53' 03''$ N, $77^{\circ} 41' 20''$ W). Depth one to five fathoms, hard sand bottom.

Paratypes: AHF 2766, six specimens, 18.4 to 34.3 mm. standard length, collected with the holotype.

Relationships: From all of the described forms of the genera *Porichthys* and *Nautopaedium*, as recognized by Hubbs and Schultz (1939), *P. pauciradiatus* differs in its low number of anal fin rays. Its average number of dorsal fin-rays is correspondingly low. In the event that *P. nautopaedium* Jordan and Bollman (1890: 171) is proved valid, *P. pauciradiatus* differs from it as well in having fewer dorsal and anal fin-rays. Hubbs and Schultz (1939: 486), although placing *P. nautopaedium* in the synonymy of *P. margaritatus*, did so with hesitancy. For reasons noted below, we also feel that *P. nautopaedium* may be valid.

Hubbs and Schultz (p. 484) listed three small specimens of a *Porichthys* from Cape San Lucas, Baja California, Mexico, that were in such poor condition that they did not assign them a specific name. The three specimens were characterized by their low dorsal and anal fin-ray counts. Hubbs and Schultz felt (1) that their material either was true *P. margaritatus*, in which case the name *P. nautopaedium* would have to be assigned to the group they called *P. margaritatus*, (2) that their specimens were aberrant *P. notatus* or a subspecies of it, or (3) that they represented an undescribed species. Inasmuch as Richardson (1844: 67) gave a count of only 26 anal fin-rays and 34 dorsal fin-rays (33 in his figure) in his original description of *P. margaritatus* from the Gulf of Fonseca in Pacific Central America, we think that the *Porichthys* "species" of Hubbs and Schultz should bear the name *P. margaritatus*, as they suggested, and that their *P. margaritatus* should be assigned the alternative name of *P. nautopaedium*, which those writers also suggested. Our discovery of a series of well-preserved specimens of an unidentified species with a low anal and dorsal fin-ray count shows (1) that Richardson was probably not in error in listing only 26 anal fin-rays for his *P. margaritatus*, and (2) that the *Porichthys* "species" of Hubbs and Schultz probably were not aberrant in their possession of low anal and dorsal fin-ray counts.

We think that *P. pauciradiatus* is nearer the *Porichthys* "species" of Hubbs and Schultz, discussed above, than to any other member of the genus. It is conceivable that additional material of both populations—from the Caribbean side of Central America at Caledonia Bay, Panama, and from the Pacific side at Cape San Lucas, Baja California—may indicate that they are only subspecifically distinct. At present, the primary differences seem to be the number of

dorsal saddles (8 in *P. pauciradiatus*, 6 in *Porichthys* "species") and the fact that *P. pauciradiatus* apparently has an incomplete row of pleural photophores while *Porichthys* "species," according to Hubbs and Schultz (p. 484) seems to have a complete or nearly complete row. From *P. margaritatus*, as described by Richardson, *P. pauciradiatus* differs in possessing fewer pectoral fin-rays (14 to 15 in *P. pauciradiatus*, 16 in *P. margaritatus*) and fewer dorsal fin-rays (29 to 31 in *P. pauciradiatus*, 33 or 34 in *P. margaritatus*).

In its V-shaped branchiostegal row of photophores, *P. pauciradiatus* further differs from *Nautopaedium porosissimum*, *Porichthys myriaster* and *P. greeni*—see Hubbs and Schultz (1939: fig. 57).

P. pauciradiatus also differs from *P. greeni* in having its dorsal and anal fins free from the caudal.

In addition, *P. pauciradiatus* differs further from *P. analis*, *P. margaritatus* (as recognized by Hubbs and Schultz) and perhaps from *Porichthys* "species" of Hubbs and Schultz in having its pleural row of photophores apparently ending abruptly above the end of the second third of the anal fin base (see discussion above).

We compared our material with similar-sized specimens of all of the species recognized by Hubbs and Schultz, with the exception of their *Porichthys* "species," and find that none have the color pattern of *P. pauciradiatus* (see Figs. 1-3). In no case were the dorsal saddles of the other forms as distinct as they were in *P. pauciradiatus*, nor did they appear to be as sharply outlined with dark pigment.

Remarks: our specimens were small, and their premaxillary and palatine teeth were directed backward. We found the same condition in small specimens of *Nautopaedium porosissimum* that we examined. On the basis of this, and like Hubbs and Schultz (1939: 489), we question the validity of *Nautopaedium* as a distinct genus based solely on the angle of direction of these teeth. However, presuming that *Nautopaedium* continues to be recognized as a valid genus, and that our small specimens are correctly assigned to the genus *Porichthys*, *P. pauciradiatus* is the first representative of its genus in the Atlantic. According to Hubbs and Schultz (1939: 473), the other species in the genus *Porichthys* are confined to the eastern Pacific.

Derivation of New Name: From the Latin *pauci*, meaning few, and *radiatus*, meaning rayed; in reference to the reduced number of dorsal and anal fin-rays characteristic of the new species.

Comparative Material Examined: Each lot of material contained at least one specimen of a size comparable to our specimens of *P. pauciradiatus*.

Porichthys myriaster Hubbs and Schultz

Three specimens, University of California, Los Angeles, fish collection (UCLA), W 51-129, from Corona del Mar, Orange County, California.

Porichthys analis Hubbs and Schultz

Twelve specimens, UCLA, W 50-191, from near San Felipe, Baja California (Gulf of California), Mexico.

Porichthys notatus Girard

Five specimens, California Academy of Sciences (CAS) 19905, from San Pablo Bay, Marin County, California.

Porichthys margaritatus Richardson (of Hubbs and Schultz)—may be *P. nautopaedium* Jordan and Bollman

Two specimens, CAS 6857, from La Libertad, Ecuador.

Porichthys greeni Gilbert and Starks

Thirteen specimens, Stanford University Natural History Museum (SU) 6485 (type), and SU 6512 (paratypes) from Panama Reef, Panama.

Nautopaedium porosissimum (Valenciennes)

Five specimens, United States National Museum 83833, from 34° 35' 30" N, 75° 45' 30" W, off North Carolina.

Acknowledgments: We wish to thank John S. Garth and Jay M. Savage of the University of Southern California for bringing to our attention the Caribbean collection which contained the new species and for placing it at our disposal. For arranging the use of comparative material housed in the collections of their respective institutions, we are indebted to the following: Boyd W. Walker and Wayne Baldwin, University of California, Los Angeles; William I. Follett, California Academy of Sciences; Leonard P. Schultz, United States National Museum; George S. Myers, Stanford University Natural History Museum.

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MARINE SHORE FISHES FROM NEAR PUERTO LIMÓN,
CARIBBEAN COSTA RICA

By DAVID K. CALDWELL



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DAVID K. CALDWELL

Editor

MARINE SHORE FISHES FROM NEAR PUERTO LIMÓN, CARIBBEAN COSTA RICA

By DAVID K. CALDWELL¹

ABSTRACT: Sixty-three species of marine shore fishes, collected from a coralline tidepool habitat, are listed from Caribbean Costa Rica in the vicinity of Puerto Limón. Most of the specimens represent the first records of the species from Costa Rica, and five species (*Coryphopterus dicrus*, *C. glaucofraenum*, *Lythrypnus nesiotus*, *Enneanectes boehlkei* and *Parophidion schmidti*) constitute major range extensions into the southwestern Caribbean from the north.

INTRODUCTION

Recently the Los Angeles County Museum (LACM) acquired a significant collection of marine shore fishes from two localities near Puerto Limón, Caribbean Costa Rica. Shore fishes from this region, and especially ones collected in a coralline tidepool habitat, are scarce in research collections and consequently some of the specimens represent major range extensions into the southwestern Caribbean from the north. Although known from other localities in the southwestern Caribbean, most of the species recorded are listed from Costa Rica for the first time.

This and an earlier report (Caldwell, Ogren and Giovannoli, 1959, and papers cited therein) summarize the majority of records of marine shore fishes from Caribbean Costa Rica. I wish here to correct two printer's errors which unfortunately appeared in the earlier paper after galley proof had been read: On page 23, the specimens from UF 5726 and UF 5848 belong to the species *Caranx latus*; on page 24, the specimens from UF 5784 belong to the species *Pomadasyς crocro*.

Where possible, I have followed the phylogenetic arrangement of families used by Briggs (1958). Detailed references to the literature used in determining southern Caribbean marine shore fishes were included by Caldwell and Caldwell (*In press*). Therefore, only those references which stimulated particular comment on certain of the present material have been cited herein. The number of specimens follows the catalog number, then the range of lengths (unless otherwise stated, lengths are standard length), and the station number.

ECOLOGICAL NOTES

The collections were made with the use of rotenone by William A. Bussing and John R. Paxton. Mr. Bussing kindly made his field notes available

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to me for inclusion here. He described the general shoreline in the region of the two collections as being composed of eroded coral limestone which sometimes formed barrier reefs 100 to 200 yards from the main shore. He noted that tide pools one to five feet in depth were often formed by these reefs, and that the pools usually were isolated at low tide. Brain and finger coral were found living in the pools and it was noted that at the time of the collections there was a heavy growth of brown branched algae, and many green and red forms as well. Turtle grass also was usually present. The water temperature at the time of the collections was 27° C. The tide ranged from high to low. Mr. Bussing further stated that a great deal of rubbish and sewage entered the water between the towns of Piuta and Puerto Limón. Both localities are in Limón Province, Caribbean Costa Rica. Pertinent specific data not common to the two collections were recorded as follows:

Station CR 126.

May 22, 1962. Two kilometers north of Puerto Limón at the town of Piuta. The bottom consisted primarily of dead coral and coral sand. Collections were made in enclosed tide pools up to 75 feet from shore in water depths up to five feet.

Station CR 127.

May 23, 1962. One and one-half kilometers north of Puerto Limón at the town of Piuta. The bottom consisted primarily of sand and mud. Collections were made about 100 yards from shore in water depths up to ten feet.

ANNOTATED LIST OF SPECIES

MORINGUIDAE

Moringua sp.

LACM 2519, 113, about 55 to about 330 mm. total length, CR 126; LACM 2523, 17, about 55 to about 305 mm. total length, CR 127.

MURAENIDAE

Echidna catenata (Bloch)

LACM 2510, 5, about 195 to about 400 mm. total length, CR 126.

Enchelycore nigricans (Bonnaterre)

LACM 2517, 24, about 195 to about 405 mm. total length, CR 126.

Gymnothorax albimentis (Evermann and Marsh)

LACM 2491, 1, about 68 mm. total length, CR 126; LACM 2529, 2, about 60 and about 68 mm. total length, CR 127.

Gymnothorax funebris Ranzani

LACM 2516, 5, about 127 to about 553 mm. total length, CR 126; LACM 2526, 2, about 213 and about 475 mm. total length, CR 127.

Gymnothorax moringa (Cuvier)

LACM 2481, 10, about 117 to about 217 mm. total length, CR 126; LACM 2527, 8, about 64 to about 305 mm. total length, CR 127.

Gymnothorax vicinus (Castelnaud)

LACM 2518, 8, about 195 to about 224 mm. total length, CR 126.

Gymnothorax virescens Poey

LACM 2496, 5, about 158 to about 177 mm. total length, CR 126; LACM 2524, 21, about 60 to about 305 mm. total length, CR 127.

Muraena miliaris (Kaup)

LACM 2525, 2, about 218 and about 231 mm. total length, CR 127.

ECHELIDAE

Chilorhinus svensoni Lütken

LACM 2503, 6, 45.6 to 75.3 mm., CR 126; LACM 2530, 2, 50.0 and 60.0 mm., CR 127.

OPHICHTHIDAE

Ahlia egmontis (Jordan)

LACM 2487, 1, about 345 mm. total length, CR 126.

Myrophis punctatus Lütken

LACM 2475, 4, about 65 to about 70 mm. total length, CR 126; LACM 2528, 1, about 55 mm. total length, CR 127.

BELONIDAE

Strongylura marina (Walbaum)

LACM 2488, 1, about 45.7 mm. (snout badly damaged), CR 126.

HOLOCENTRIDAE

Holocentrus ascensionis (Osbeck)

LACM 2513, 12, 48.7 to 87.4 mm., CR 126; LACM 2538, 16, 50.6 to 87.8 mm., CR 127.

Holocentrus vexillarius Poey

LACM 2514, 31, 33.6 to 88.9 mm., CR 126; LACM 2535, 22, 31.5 to 106.7 mm., CR 127.

Plectrypops retrospinis (Guichenot)

LACM 2570, 1, 35.6 mm., CR 127.

SERRANIDAE

Mycteroperca bonaci (Poey)

LACM 2565, 1, 22.2 mm., CR 127.

Rypticus saponaceus saponaceus (Bloch and Schneider)

LACM 2490, 2, 118.3 and 128.9 mm., CR 126; LACM 2563, 2, 74.7 and 82.6 mm., CR 127.

Rypticus subbifrenatus Gill

LACM 2478, 15, 27.5 to 53.8 mm., CR 126; LACM 2562, 8, 24.6 to 54.1 mm., CR 127.

Serranus flaviventris (Cuvier)

LACM 2552, 4, 30.0 to 39.4 mm., CR 127.

APOGONIDAE

Apogon maculatus (Poey)

LACM 2508, 7, 27.0 to 60.1 mm., CR 126; LACM 2572, 14, 27.1 to 62.7 mm., CR 127.

Apogon pigmentarius (Poey)

LACM 2556, 13, 26.4 to 45.4 mm., CR 127.

CARANGIDAE

Caranx latus Agassiz

LACM 2493, 1, 47.8 mm., CR 126.

LUTJANIDAE

Lutjanus apodus (Walbaum)

LACM 2472, 10, 20.0 to 28.2 mm., CR 126; LACM 2515, 2, 100.4 and 159.0 mm., CR 126; LACM 2571, 1, 20.6 mm., CR 127; LACM 2531, 8, 68.5 to 178.2 mm., CR 127.

Lutjanus synagris (Linnaeus)

LACM 2497, 1, 24.3 mm., CR 126; LACM 2542, 1, 134.9 mm., CR 127.

POMADASYIDAE

Haemulon macrostomum Günther

LACM 2504, 10, 30.0 to 93.4 mm., CR 126.

LEIOGNATHIDAE

Eucinostomus argenteus Baird and Girard

LACM 2485, 6, 17.0 to 31.2 mm., CR 126; LACM 2566, 1, 47.4 mm., CR 127.

Eucinostomus pseudogula Poey

LACM 2477, 1, 28.1 mm., CR 126.

CHAETODONTIDAE

Chaetodon capistratus Linnaeus

LACM 2498, 3, 20.4 to 27.6 mm., CR 126; LACM 2548, 2, 18.6 and 21.3 mm., CR 127.

Chaetodon ocellatus Bloch

LACM 2474, 1, 30.1 mm., CR 126; LACM 2554, 1, 65.8 mm., CR 127.

Chaetodon striatus Linnaeus

LACM 2494, 2, 21.5 and 23.7 mm., CR 126.

Pomacanthus paru (Bloch)

LACM 2473, 1, 40.4 mm , CR 126.

POMACENTRIDAE

Abudefduf saxatilis (Linnaeus)

LACM 2501, 5, 19.7 to 31.6 mm., CR 126; LACM 2546, 18, 11.9 to 36.1 mm., CR 127; LACM 2534, 19, 79.0 to 112.8 mm., CR 127.

Abudefduf taurus (Müller and Troschel)

LACM 2500, 9, 20.6 to 35.4 mm., CR 126; LACM 2520, 12, 80.8 to 137.5 mm., CR 126; LACM 2551, 1, 26.3 mm., CR 127; LACM 2533, 1, 132.7 mm., CR 127.

Eupomacentrus fuscus (Cuvier)

LACM 2522, 263, 15.1 to 68.6 mm., CR 126; LACM 2537, 105, 19.0 to 68.7 mm., CR 127.

Eupomacentrus leucostictus (Müller and Troschel)

LACM 2486, 12, 44.9 to 58.1 mm., CR 126; LACM 2543, 6, 47.8 to 63.8 mm., CR 127.

Eupomacentrus variabilis (Castelnau)

LACM 2484, 5, 28.2 to 42.5 mm., CR 126; LACM 2575, 7, 37.6 to 49.4 mm., CR 127.

LABRIDAE

Halichoeres bivittata (Bloch)

LACM 2479, 17, 32.4 to 85.8 mm., CR 126; LACM 2545, 5, 25.1 to 82.4 mm., CR 127.

Halichoeres kirschi (Jordan and Evermann)

LACM 2506, 40, 16.9 to 85.3 mm., CR 126; LACM 2544, 5, 17.1 to 50.3 mm., CR 127.

Thalassoma bifasciatum (Bloch)

LACM 2476, 1, 15.6 mm., CR 126; LACM 2569, 6, 26.9 to 58.4 mm., CR 127.

SCARIDAE

Scarus croicensis Bloch

LACM 2559, 8, 39.4 to 84.0 mm., CR 127.

Sparisoma rubripinnis (Valenciennes)

LACM 2502, 33, 12.9 to 52.9 mm., CR 126; LACM 2541, 30, 18.9 to 102.6 mm., CR 127.

ACANTHURIDAE

Acanthurus bahianus Castelnau

LACM 2489, 70, 26.0 to 47.8 mm., CR 126; LACM 2574, 18, 28.0 to 63.0 mm., CR 127.

Some of the smaller individuals were tentatively assigned to this species on the basis of general appearance in body form and color pattern. These specimens were not yet fully transformed, and still showed many larval characteristics of the acronurus, or pelagic, sea stage. On the basis of vertical fin-ray counts, the small specimens must either be assigned to this species or to *A. chirurgus*.

Acanthurus chirurgus (Bloch)

LACM 2507, 9, 33.0 to 45.5 mm., CR 126.

Acanthurus coeruleus Bloch and Schneider

LACM 2492, 1, 32.4 mm., CR 126; LACM 2547, 1, 31.1 mm., CR 127.

GOBIIDAE

Bathygobius soporator (Valenciennes)

LACM 2512, 36, 23.5 to 64.4 mm., CR 126; LACM 2553, 19, 21.8 to 63.8 mm., CR 127.

Coryphopterus dicrus Böhlke and Robins

LACM 2480, 9, 16.0 to 32.1 mm., CR 126; LACM 2549, 31, 15.3 to 31.0 mm., CR 127.

According to range data included by Böhlke and Robins (1960a: 114), in describing this species, the present specimens serve to extend the range of *C. dicrus* into the southwestern Caribbean from south Florida, the Bahamas, off Yucatan in the Gulf of Mexico, Puerto Rico and the Virgin Islands.

Coryphopterus glaucofraenum Gill

LACM 2550, 4, 28.4 to 37.6 mm., CR 127.

According to range data given by Böhlke and Robins (1960b: 110), this species has not previously been reported from the southwestern Caribbean. Caldwell (*In press*) also reported this species from this region, from Panama.

Gobionellus boleosoma (Jordan and Gilbert)

LACM 2567, 1, 23.7 mm., CR 127.

Lythrypnus nesiotus Böhlke and Robins

LACM 2560, 1, 13.9 mm., CR 127.

The pigmentation in alcohol of this specimen was much like that given by Böhlke and Robins (1960a: 83) in their original description of this species. However, the pigmentation differed from their description and illustration in that the membranes of the innermost ventral fin-rays had numerous small scattered melanophores. In addition, the soft dorsal and caudal fins had numerous spots (Fig. 1), many times larger than those of the

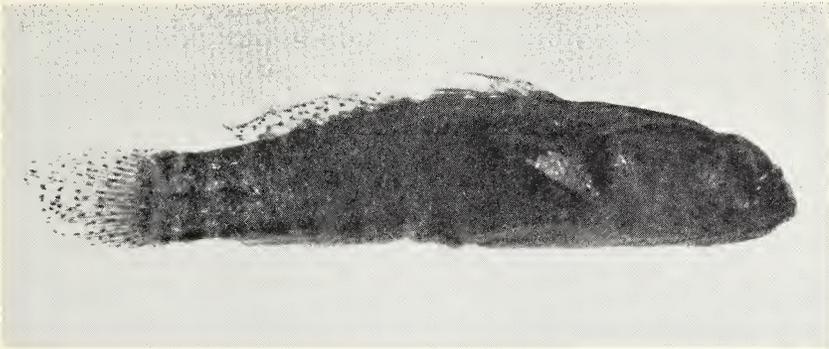


Fig. 1. *Lythrypnus nesiotes*, 13.9 mm., from near Puerto Limón, Caribbean Costa Rica.

anal fin and interspaced with small scattered melanophores, which tended to form irregular rows.

This specimen constitutes a significant range extension into the southwestern Caribbean from the Bahamas, Haiti, Puerto Rico and the Virgin Islands (*vide* Böhlke and Robins, 1960a: 84).

BLENNIIDAE

Entomacrodus textilis (Quoy and Gaimard)

LACM 2557, 10, 28.2 to 49.6 mm., CR 127.

Ophioblennius atlanticus macclurei Silvester

LACM 2483, 28, 35.1 to 46.1 mm., CR 126; LACM 2540, 85, 35.9 to 67.7 mm., CR 127.



Fig. 2. *Enneanectes boehlkei*, 21.7 mm., from near Puerto Limón, Caribbean Costa Rica.

TRIPTERYGIIDAE

Enneanectes boehlkei Rosenblatt

LACM 2561, 2, 21.7 and 26.9 mm., CR 127.

While the background color of the larger of these specimens appeared to be close to that described and illustrated by Rosenblatt (1960: 7 and fig. 1), the background of the smaller example was much lighter, so that the lateral bars stood out sharply (Fig. 2). In other respects, these specimens satisfactorily fit Rosenblatt's original description of this species.

The specimens constitute a significant range extension into the southwestern Caribbean from Florida, the Bahamas, Puerto Rico and Martinique (*vide* Rosenblatt, 1960: 9).

CLINIDAE

Labrisomus nuchipinnis (Quoy and Gaimard)

LACM 2482, 28, 37.3 to 103.6 mm., CR 126; LACM 2568, 5, 66.0 to 110.9 mm., CR 127.

Paralinius nigripinnis (Steindachner)

LACM 2505, 8, 8.9 to 38.0 mm., CR 126; LACM 2573, 1, 31.8 mm., CR 127.

BROTULIDAE

Ogilbia sp.

LACM 2499, 10, 37.5 to 46.8 mm., CR 126; LACM 2564, 16, 31.2 to 41.8 mm., CR 127.

OPHIDIIDAE

Parophidion schmidti (Woods and Kanazawa)

LACM 2578, 3, 58.9 to 72.4 mm., CR 126.

The presence of this species in the southwestern Caribbean constitutes a significant range extension from Bermuda and the Bahamas (Böhlke and Robins, 1959: 51) and Jamaica (Robins and Böhlke, 1959: 9).

SPHYRAENIDAE

Sphyraena barracuda (Walbaum)

LACM 2558, 1, 63.9 mm., CR 127.

MUGILIDAE

Mugil curema Valenciennes

LACM 2511, 5, 31.2 to 40.4 mm., CR 126; LACM 2532, 6, 144.9 to 202.8 mm., CR 127.

ATHERINIDAE

Atherinomorous stipes (Müller and Troschel)

LACM 2509, 2, 53.9 and 59.3 mm., CR 126; LACM 2539, 106, 30.5 to 70.2 mm., CR 127.

SCORPAENIDAE

Scorpaena plumieri Bloch

LACM 2521, 9, 73.5 to 135.0 mm., CR 126; LACM 2536, 3, 61.1 to about 165 mm., CR 127.

BOTHIDAE

Bothus lunatus (Linnaeus)

LACM 2495, 1, 34.6 mm., CR 126.

CANTHIGASTERIDAE

Canthigaster rostratus (Bloch)

LACM 2555, 1, 17.6 mm., CR 127.

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A COLLECTION OF REPTILES AND AMPHIBIANS FROM THE
HIGHLAND FAUNAL ASSEMBLAGE OF WESTERN MEXICO

By ROY W. McDIARMID



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DAVID K. CALDWELL

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A COLLECTION OF REPTILES AND AMPHIBIANS FROM THE HIGHLAND FAUNAL ASSEMBLAGE OF WESTERN MEXICO

By ROY W. McDIARMID¹

ABSTRACT: Data taken from 21 species of reptiles and amphibians from western Mexico indicate the herpetofauna to be part of the highland faunal assemblage. Elements of the assemblage are assigned to three separate faunal groups: (1) the coastal lowlands; (2) the foothills of the Sierra Madre Occidental and the western border of the Mexican Plateau; (3) the Mexican Plateau. *Hyla smaragdina* is reported for the first time in Nayarit and *Rana sinaloae* is new to the fauna of Jalisco.

During the past 20 years a number of herpetofaunal studies have been conducted in western Mexico. Most of these studies were reports on amphibians and reptiles from miscellaneous localities. A few workers have approached the faunal studies in this region from an ecologic and geographic aspect. The first such study, by Bogert and Oliver (1945), was on the herpetofauna of Sonora. These authors analyzed the faunal elements from a geographic viewpoint and commented on the transition of various species from the tropical plant formations of the south to the temperate desert regions in the northern part of the state. Duellman (1958) presented a preliminary analysis of the herpetofauna of Colima. Zweifel (1960) discussed the herpetofauna of the Tres Mariás Islands with reference to its derivation from the mainland fauna. Duellman (1961) gave a full account of the species of reptiles and amphibians inhabiting the state of Michoacán. In his presentation he gave a brief description of the natural landscape of the area and analyzed the various species assemblages of the major faunistic groups.

In February and August of 1957 Dr. T. H. Lewis, while conducting research on the medicinal effects on the peyote cactus (*Lophophora*), made a collection of 189 amphibians and reptiles representing 29 species from the states of Nayarit and Jalisco. The greater portion of this collection (that reported herein) was made in a remote part of the Sierra de Los Huicholes along the Nayarit-Jalisco border (Fig. 1). The material was presented to the University of Southern California for study and is deposited in the Los Angeles County Museum (LACM). In the following species account the first number(s) in parentheses are the field number(s), the second number(s) are the LACM museum catalog number(s).

The species taken by Dr. Lewis and discussed in this paper are members of the highland faunal assemblage, according to Duellman (1961). The report adds to existing ideas concerning the highland faunal assemblage and substantiates present ideas concerning the distribution and relationships of various herpetofaunal elements in western Mexico.

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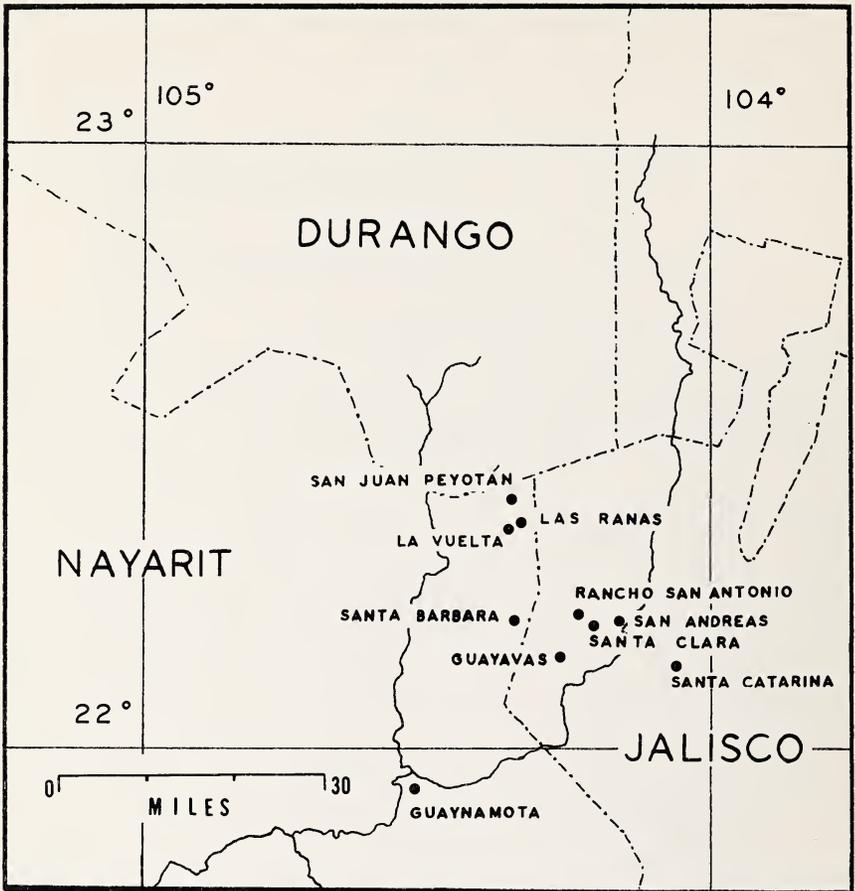


Fig. 1. Map of the Sierra de Los Huicholes along the Nayarit-Jalisco border showing localities at which amphibians and reptiles were collected and key geographic landmarks.

ACKNOWLEDGMENTS

I wish to extend my appreciation to Dr. T. H. Lewis for the privilege of reporting on the collection and for providing valuable information on the specimens and the study area. I also thank Mr. Anthony Gaudin for his exact drawings of the tadpole of *Hyla smaragdina*. I especially extend my appreciation to Dr. Jay M. Savage for his aid in identification of the specimens and for his valuable criticisms of the manuscript.

PHYSIOGRAPHY AND VEGETATION

The entire region, which includes the Sierra de Los Huicholes, is located on the Pacific side of the western edge of the Mexican Plateau. The area is extremely broken in topography with deep barrancas and steep trails. As a result of the irregular terrain the presence of various vegetational elements depends on the elevation and slope.

The vegetation is composed of elements from the oak-woodland and tropical deciduous forest plant associations (Leopold, 1950). The oak-woodland association forms a narrow belt on the western slope of the Sierra Madre Occidental dominated by deciduous oaks and harsh bunch grasses (Fig. 2).

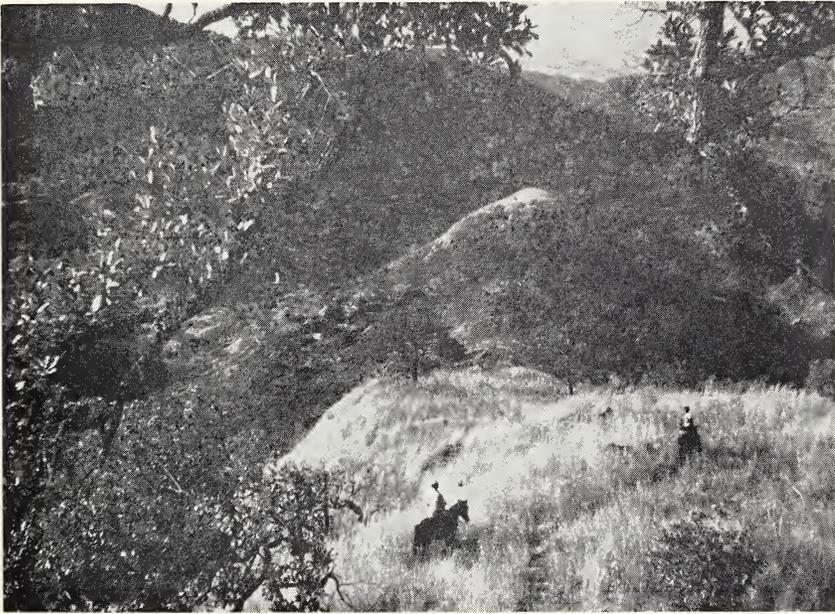


Fig. 2. Oak-woodland association characteristic of the Sierra de Los Huicholes near La Vuelta.

The elements from the tropical deciduous forest are characteristic of the higher elevations of the Pacific Coastal Plain, and are abundant along the larger rivers and streams of western Mexico.

Some of the common plants of this mixed plant formation are *Acacia*, *Pithecolobium*, *Ficus*, *Bursera*, *Bombax*, *Haematoxylon*, and the epiphyte, *Tillandsia*. At somewhat higher elevations, various oaks are dominant, among them *Quercus conspersa* and *Quercus magnoliaefolia*. Pines are found only at the highest elevations in the area.

SPECIES ACCOUNT

SALIENTIA

Bufo marinus (Linnaeus)

Three specimens (215-217; LACM 1797) of this large ubiquitous toad were collected at La Vuelta, Nayarit on August 20, 1957. *Bufo marinus* is abundant throughout Nayarit and coastal western Mexico from southern Sonora to Guatemala.

Bufo mazatlanensis Taylor

Bufo mazatlanensis was collected at two localities in Nayarit. Two adults (22, 249; LACM 1798) and two juveniles (235, 236; LACM 1799) were taken at La Vuelta on August 26, 1957. Cranial crests are not well developed on the juvenile specimens, which measure 21 mm. snout-vent length respectively. A series of nine young toads (240-248; LACM 1800) was obtained on August 10 and 11, 1957, at Las Ranas. The young toads measure from 23 mm. to 33 mm. snout-vent length.

In western Mexico *Bufo mazatlanensis* ranges from northern Sonora southward to northern Jalisco.

Bufo occidentalis Camerano

Two adults (218, 219; LACM 1801), measuring 66 mm. and 64 mm. snout-vent length respectively, were collected on August 20, 1957, at La Vuelta, Nayarit. Six days later two additional toads (253, 254; LACM 1802) were collected at the same locality. They measure 55 mm. and 73 mm. snout-vent length.

The presence of *Bufo occidentalis* near La Vuelta agrees with the study by Duellman (1961) in which he found this toad to be nearly restricted to the pine-oak association above 900 meters in Michoacán. *Bufo occidentalis* is found along the foothills in western Mexico from Sinaloa southward to Tehuantepec.

Eleutherodactylus augusti cactorum Taylor

An adult male (211; LACM 1803) was collected in Santa Barbara, Nayarit, on August 14, 1957. The frog measures 49.5 mm. snout-vent length and agrees with Zweifel's (1956) ratios of measurement and the color pattern of his specimen. *Eleutherodactylus augusti cactorum* ranges along the foothills of the Pacific coast from southern Arizona to the Isthmus of Tehuantepec.

Eleutherodactylus occidentalis Taylor

One specimen (29; LACM 1804), measuring 28 mm. snout-vent length, was secured in San Juan Peyotán, Nayarit, on February 7, 1957. This frog was collected in the same pond with *Eleutherodactylus rugulosus vocalis*.

Eleutherodactylus occidentalis ranges along the western edge of the Mexican plateau from southern Sinaloa to Colima.

Eleutherodactylus rugulosus vocalis Taylor

A series of specimens, ten juveniles (24-33; LACM 1805) and one adult (21; LACM 1806), is referred to this subspecies. All the specimens were col-

lected in a pond in a dry river bed at the bottom of a deep barranca near La Vuelta, Nayarit, on February 7, 1957. The juveniles vary in length from 21 mm. to 36 mm. The adult measures approximately 51 mm. snout-vent length. The nose of this specimen is badly defaced and exact measurements are impossible to determine. Dorsal color of the juveniles in life ranged from dark gray through greenish to brick red. Ventral surface of the hind legs was sulfur yellow.

Eleutherodactylus rugulosus vocalis, as reported by Duellman (1958, 1961), occurs in the foothills of the Sierra Madre Occidental from central Sinaloa southward into Michoacán.

Hyla smaragdina Taylor

On August 21, 1957, five tadpoles and one metamorphosing frog were collected in a swift running stream in a deep barranca near Santa Barbara, Nayarit. All the larvae were adherent to rocks in the stream. Upon examination, the larvae were found to be similar to the tadpoles of the southern Mexican frog *Hyla sumichrasti* figured and described by Starrett (1960), and different from all other larvae of the genus. The tadpoles differ from *sumichrasti* in the following significant characteristics: (1) more depressed body; (2) shorter tail in proportion to body; (3) more elongate and robust spiracle tube located lower on the body; (4) a shorter third row of anterior denticles; and, (5) all six posterior denticle rows of equal length (in *sumichrasti* only the first three are of equal length and the others are shorter). On the basis of these differences the tadpoles from Santa Barbara are assigned to *Hyla smaragdina*, a close relative of *Hyla sumichrasti* from western Mexico. Scrutiny of the metamorphosing froglet reveals striking similarities with *Hyla smaragdina* figured by Taylor (1940) in significant characteristics and confirms the identification.

Description of Tadpole: Six specimens (259; LACM 1807), (Figs. 3-4).

Body elongate and tapering; greatest depth about one-third of length from tip of snout to anal opening and two-thirds of greatest width; tail length one and one-half times as long as body; tail musculature not quite reaching the slightly rounded tip; dorsal tail fin not extending onto body. Eyes dorsal; interorbital distance about one-third of body width; nostrils much closer to eyes than to snout. Spiracle sinistral, forming a tube opening two-thirds of way back on body and two-thirds of depth from dorsal surface; anal tube long, dextral. Dorsal color on body consisting of scattered brown pigment occasionally forming small blotches; belly light; tail musculature exhibiting brown reticulations; blotches of brown pigment on dorsal tail fin, fewer on posterior half of ventral tail fin.

Mouth large, ventrally located; nearly equal to width of body; lips wide, completely bordered by papillae surrounding mouth. Denticle rows 3/6; anterior (upper) two rows about equal in length, third row slightly shorter; denticles of innermost row heaviest; posterior rows complete, all six of about equal

length; denticles heaviest on innermost row decreasing row by row posteriorly; larger specimens show a rudimentary seventh row. Beaks well developed and serrated; lighter triangle in center of anterior beak.

Hyla smaragdina ranges along the Pacific slope of the Sierra Madre Occidental from Morelos northward to Nayarit. The new locality, the first record for Nayarit, extends the known range of the species northward about 200 miles. This species probably occurs along the western slope of the mountains in Sinaloa and Durango.

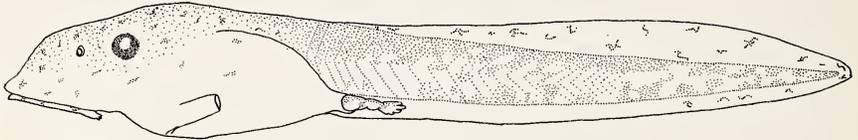


Fig. 3. Lateral view of a tadpole of *Hyla smaragdina*.

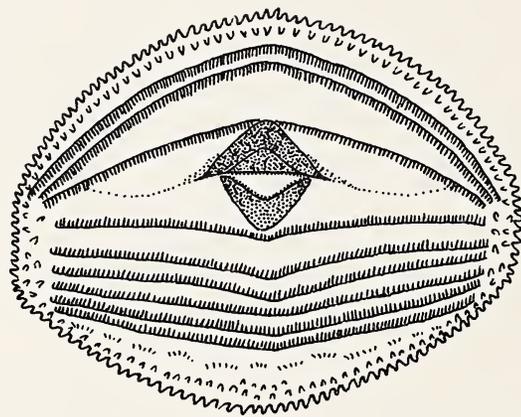


Fig. 4. Mouthparts of a tadpole of *Hyla smaragdina*.

Phyllomedusa dacnicolor Cope

A series of 34 tadpoles (LACM 1808) was collected on different days in August in a slow meandering stream in San Juan Peyotán, Nayarit. The larvae were at various stages of development. One larva has four legs apparent but there is no indication of tail reduction; another larva has two legs; 24 larvae measure about 46 mm. total length; the remaining eight vary in size from 13 to 31 mm. total length. No adults were collected in the area. In coloration and morphology, these tadpoles agree with the description given by Taylor (1942). The anus is dextral; the spiracle is sinistral; the denticle formula is 2/3.

Phyllomedusa dacnicolor is found from southern Sonora southward to Chiapas along the Pacific slope in western Mexico.

Rana pipiens Schreber

Three specimens (23, 225, 227; LACM 1809) of this wide-ranging frog were collected in La Vuelta, Nayarit. They measure from 45 to 50 mm. snout-vent length.

Rana sinaloae Zweifel

Four specimens (222-224, 226; LACM 1810) of this ranid were taken on August 19, and 20 in La Vuelta, Nayarit. The measurements are as follows: snout-vent lengths 50, 41, 45.2, 37 mm.; head widths 17, 14.2, 16.7, 13.9 mm.; head lengths 18, 14.3, 15.8, 13.9 mm.; tibia lengths 28.1, 21.3, 24.1, 21 mm.; tympanum diameters 3.9, 3.1, 4, 3.4 mm. respectively. The tibia length/snout-vent length ratios are 0.562, 0.519, 0.533, and 0.567, respectively. The tympanum diameter/head width ratios are 0.229, 0.214, 0.239, and 0.244, respectively.

Another specimen (256; LACM 1811) was secured on August 22 in Guayavas. This represents the first record of *Rana sinaloae* in Jalisco. Pertinent data for the specimen are: snout-vent length 32.9 mm.; head width 12 mm.; head length 11.9 mm.; tibia length 17.9 mm.; tympanum diameter 2.9 mm. The tibia length/snout-vent length ratio is 0.544. The tympanum diameter/head width ratio is 0.242.

The ratios of tibia length/snout-vent length are slightly higher than that of the holotype (Zweifel, 1954). The highest ratio is about equal to the ratio of the Colima specimen reported by Duellman (1958). The tympanum diameter/head width ratios are higher than that of the type as given by Zweifel and very close to the ratio for the specimen from Colima.

The type locality of *Rana sinaloae* is 14 miles by road southwest of El Batel, Sinaloa at an elevation of 4200 feet. Another individual was collected on the same day 10 miles by road northeast of El Batel at 6400 feet (Zweifel, 1954). Duellman (1958) reports a specimen of *Rana sinaloae* from Pueblo Juarez, Colima at about 1500 feet. Smith (1959) reports a series of seven young *Rana sinaloae* from 18.8 miles northwest of Ahuacatlan, Nayarit. Additional specimens have been collected by me at the type locality in 1960 and again in 1962. The specimens reported in this paper from Nayarit and Jalisco fill in the 175 mile gap between the type locality and the locality reported by Smith in Nayarit.

From the material available it appears that *Rana sinaloae* ranges along the Pacific slopes of the Sierra Madre Occidental from southern Sinaloa to Colima (Fig. 5).

TESTUDINATA

Kinosternon integrum LeConte

A female (201; LACM 1812) of this turtle was collected in a small creek in San Juan Peyotán, Nayarit on August 10, 1957. The specimen measures 116.4 mm. carapace length and 78.9 mm. plastron length. A male *Kinosternon integrum* (213; LACM 1813) was collected near San Juan Peyotán, Nayarit

on August 27, 1957, and measures 164.1 mm. carapace length and 107 mm. plastron length. *Kinosternon integrum* is found in western Mexico from Sonora to Guerrero and eastward to Veracruz.

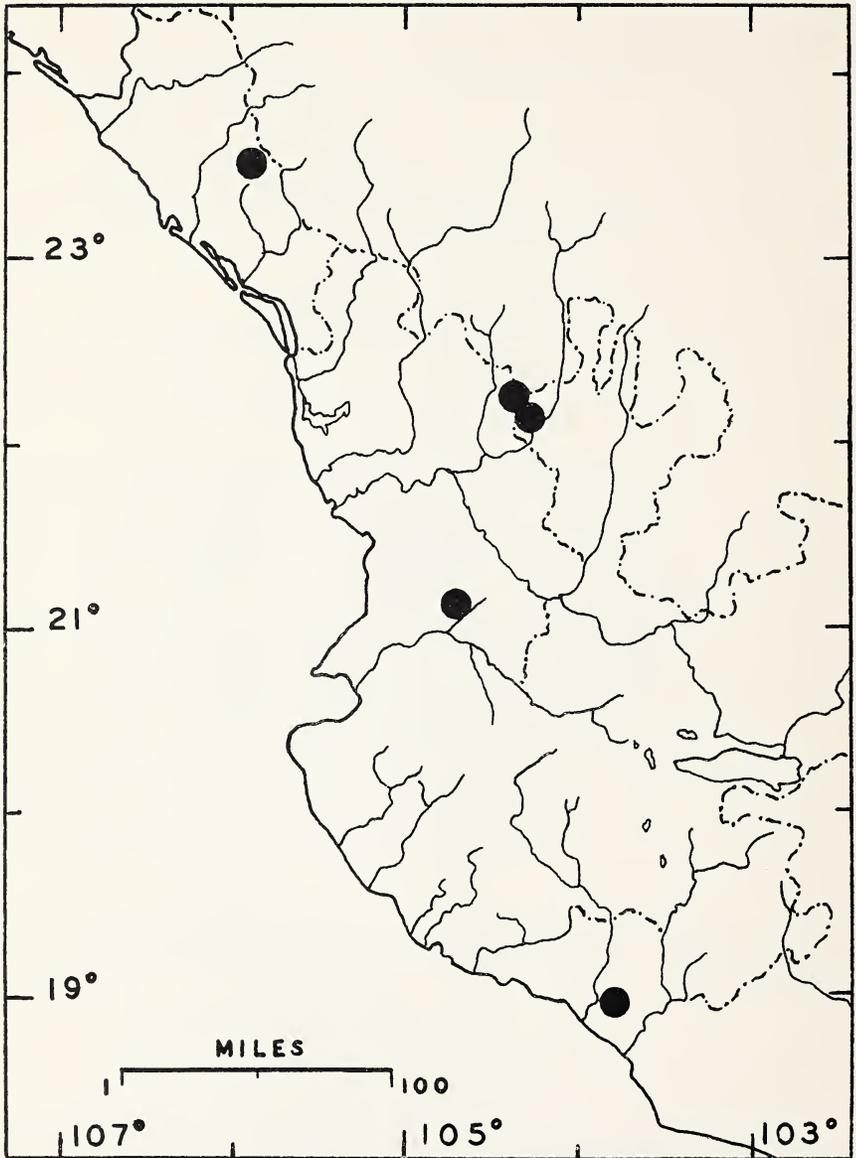


Fig. 5. Map showing the known range of *Rana sinaloae* in western Mexico. Dots indicate localities at which specimens have been collected.

SAURIA

Anolis nebulosus (Wiegmann)

On August 22, 1957, two specimens (220, 221; LACM 1814) of this anole were collected at Guayavas, Jalisco. On August 26 another specimen (257; LACM 1815) was taken at the same locality. The three specimens are females with snout-vent lengths of 40.5, 42.1, 38.8 mm. respectively. *Anolis nebulosus* ranges from Sinaloa to Michoacán.

Phrynosoma orbiculare (Linnaeus)

Two specimens of this lizard were collected in Jalisco. The first (232; LACM 1816) was taken on August 22, 1957, at Guayavas. The specimen, a female, measures 60.8 mm. snout-vent length; 34.5 mm. tail length; 16 mm. head width; 15.4 mm. head length. There are 27 spines on the lateral fringe and 35 femoral pores.

The second specimen (233; LACM 1817) was collected on August 21, 1957 at Santa Clara. This male measures 74 mm. snout-vent length; 56 mm. tail length; 17 mm. head width; 17.8 mm. head length. There are 26 spines on the lateral fringe and 39 femoral pores.

Horowitz (1955) divided *Phrynosoma orbiculare* into five subspecies, *bradti*, *durangoensis*, *cortezi*, *orbiculare* and *orientale*, on the basis of variation in: (1) ratios of total length/snout-vent length; (2) ratios of head width/head length; (3) ratios of occipital horn length/snout-vent length; (4) number of femoral pores; (5) number of spines in the lateral fringe. As presented by Horowitz, the variation expressed by the values for occipital horn length/snout-vent length shows such a great degree of overlap that I consider the ratios of no significance in separating the populations. Examination of the remaining data presented by Horowitz (1955, page 215, Table 1) indicates extensive overlap in the characters which he utilized to distinguish the five subspecies. I am unable to assign the Jalisco specimens to any of the subspecies recognized by Horowitz. Because of the overlap in the range of the variation of characters in the populations recognized by Horowitz, the division of the population into five subspecies is considered unjustified.

Davis (1953) described *Phrynosoma orbiculare alticola* from Morelos, on the basis of comparison with specimens of *Phrynosoma o. orbiculare*. Horowitz's material indicates that the characters of the specimens referred to *alticola* are within the range of variation of *orbiculare*. Under these circumstances *alticola* does not seem to be a valid race.

On the basis of available data in the literature and the studied specimens, it is impossible to segregate *Phrynosoma orbiculare* into recognizable populations. Rather than recognize distinct subspecific populations, it is more reasonable to consider the species as being highly variable and exhibiting minor differences from population to population, and attribute these differences to clinal variation. These conclusions are in accord with the findings of Smith and Lafe (1945).

Phrynosoma orbiculare is known in western Mexico from the Sierra Madre Occidental of Chihuahua, Durango, Jalisco and Zacatecas.

Sceloporus clarkii boulengeri Stejneger

A single male (212; LACM 1818) measuring 109 mm. snout-vent length, was collected on August 14, 1957, at Santa Barbara, Nayarit. The known range of *Sceloporus clarkii boulengeri* is southern Sonora southward to Jalisco.

Sceloporus dugesii dugesii Bocourt

On August 26, 1957, a single specimen (255; LACM 1819) of this *Sceloporus* was collected at La Vuelta, Nayarit. The specimen is a male measuring 46.8 mm. snout-vent length. There is a narrow black nuchal collar, with a posterior light edge passing onto the shoulder; a dark line runs from the eye through the ear to the collar, bordered on both sides by a narrow white line. The dorsal coloration in preservative is blue gray. The specimen agrees in other respects with the diagnosis given by Smith (1939).

The new locality extends the known range of *Sceloporus dugesii dugesii* about 75 miles to the north. The range of the lizard extends from Nayarit to Colima.

Urosaurus bicarinatus tuberculatus Schmidt

Seven specimens of this lizard (8-14) were collected in the Sierra de Los Huicholes south of San Juan Peyotán, Nayarit on February 8, 1957. The specimens were reported by Zweifel (1959c).

Cnemidophorus costatus huico Zweifel

Seven specimens were collected at La Vuelta, Nayarit. Three of these specimens (18-20) were collected on February 8, 1957. The other four (228-231) were taken on August 19, 1957. The seven specimens were reported by Zweifel (1959a).

Heloderma horridum horridum Wiegmann

A beaded lizard was collected on the evening of August 26, 1957 on a trail a few miles south of San Juan Peyotán, Nayarit. The specimen (209; LACM 1820) is a male and measures 293 mm. snout-vent length. Large insect larvae were found in the stomach.

Another male (210; LACM 1821), measuring 315 mm. snout-vent length, was collected on a cool rainy evening in heavy grass above Santa Barbara, Nayarit on August 14, 1957. The stomach of this lizard contained 23 eggs similar in dimensions to quail eggs. The eggs were ruptured and the shells were packed together in a telescopic fashion.

Heloderma horridum horridum is found in western Mexico from central Sinaloa southward to the Isthmus of Tehuantepec.

SERPENTES

Coniophanes lateritius lateritius Cope

A single female (200; LACM 1822) of this seemingly rare snake was collected on August 20, 1957, near Santa Clara, Jalisco. Pertinent data for the

specimen are: 243 mm. snout-vent length; 153 mm. tail length; 136 ventrals; 93 caudals; 19 scales at mid-body; 7 supralabials and 8 infralabials on each side. A black collar extends 8 scale rows posteriorly from the parietals and is bordered posteriorly by a narrow white edge. There are light spots on the head and labial region and dark spots on the throat. The black collar fails to reach the ventrals by one scale row.

The specimen agrees in color and scale counts with the specimen from Puerta Vallarta, Jalisco, described and figured by Smith and Grant (1958) and is similar in color and pattern to the individual from near San Blas, Nayarit, reported by Zweifel (1959c) and again by Wellman (1959). The specimen reported here represents the sixth specimen of this race reported in the literature. Smith and Grant suggest that the type locality of Guadalajara was incorrect and the specimen probably came from a more humid area closer to the coast. Zweifel (1959b) concurs with Smith and Grant. Tanner and Robison (1960) report a specimen from an upland habitat near Magdalena, Jalisco. Duellman (1961) indicates that the subspecies inhabits a broad-leaf forest in the foothills of Michoacán. The latter two records together with the record here reported verifies Guadalajara as the actual type locality, inasmuch as Guadalajara is situated in the same plant formation and at about the same elevation as these localities. *Coniophanes lateritius lateritius* is found in various habitats from central Nayarit southward to Michoacán.

Pituophis deppei deppei Duméril

A large female (214; LACM 1823) was collected on August 21, 1957 at Santa Clara, Jalisco. Pertinent data for the snake are: 1143 mm. total length; 150 mm. tail length; 231 ventrals; 57 caudals; 31 body blotches; 10 caudal blotches; dorsal interspaces 4 to 4½ scales in length.

Pituophis deppei deppei ranges from Chihuahua and southern Coahuila southward on the western slopes of the Sierra Madre Occidental and on the Central Plateau to the Valley of Mexico, southeastern Puebla and adjacent Veracruz.

Thamnophis dorsalis (Baird and Girard)

Three specimens of garter snakes were collected in the study area. A female (250; LACM 1824) was collected on August 20, 1957, at Rancho San Antonio, Jalisco. A second female (251; LACM 1825) was taken at the same locality on August 23, 1957. A third specimen (252; LACM 1826), a male, was collected at Guayavas, Jalisco on August 22. Pertinent data for these snakes are: total lengths 555, 727, 885 mm.; tail lengths 165, 197, 245 mm.; ventrals 158, 159, 158; caudals 91, 79, 91; supralabials 8, 8, 8, respectively.

The color patterns of the three specimens are the same as that described by Milstead (1953) for the subspecies *Thamnophis dorsalis cyclides*. However, the scale characteristics are intermediate between *T. dorsalis dorsalis* and *T. dorsalis cyclides*. These specimens appear to be members of an intermediate population. The intergrading population was discussed by Milstead and

ranges in a wide belt just south of the Tropic of Cancer in southern Sinaloa, Durango and Tamaulipas and in northern Nayarit, Jalisco, Zacatecas and San Luis Potosí.

DISCUSSION

The present report adds to our knowledge of 21 species from a remote part of the Sierra de Los Huicholes along the Nayarit-Jalisco border in western Mexico. It becomes evident that the herpetofauna of the region is a composite of elements from three herpetofaunal groups: (1) the coastal lowlands; (2) the foothills of the Sierra Madre Occidental and the western border of the Mexican Plateau; (3) the Mexican Plateau.

Components of the herpetofauna derived from the coastal lowlands are: *Bufo marinus*, *Bufo mazatlanensis*, *Phyllomedusa dacnicolor*, *Anolis nebulosus*; *Sceloporus clarkii boulengeri*, *Urosaurus bicarinatus tuberculatus*, *Cnemidophorus costatus huico*, *Heloderma horridum horridum*, and possibly *Coniophanes lateritius lateritius*.

Elements from the Mexican Plateau found in the area are: *Phrynosoma orbiculare*, *Pituophis deppei deppei*, and *Thamnophis dorsalis*.

Species which are characteristic of the foothills of the Sierra Madre Occidental and the western part of the Mexican Plateau are: *Bufo occidentalis*, *Eleutherodactylus augusti cactorum*, *Eleutherodactylus occidentalis*, *Rana sinaloae*, and *Sceloporus dugesii dugesii*. *Hyla smaragdina* and *Eleutherodactylus rugulosus vocalis* are species associated with riparian habitats in the area.

Two species, *Rana pipiens* and *Kinosternon integrum*, are widely distributed in both the lowlands and the foothills of the Sierra Madre Occidental.

The highland faunal assemblage described in this paper is a distinct composite of elements from three major faunal groups. Species characteristic of the highland faunal assemblage range in the foothills and along the western edge of the Mexican Plateau from Sinaloa southward to Colima and Michoacán.

Two of the species are state records. *Hyla smaragdina* is new to the fauna of Nayarit, and *Rana sinaloae* is reported for the first time in Jalisco.

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THE SALAMANDERS OF SOUTH AMERICA

By ARDEN H. BRAME, JR.
and
DAVID B. WAKE



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THE SALAMANDERS OF SOUTH AMERICA

By ARDEN H. BRAME, JR.¹

and

DAVID B. WAKE²

ABSTRACT: A resumé of all previous work on South American salamanders, including an historical taxonomic survey, is given. All recognizable taxa are described or redescribed. Two genera (*Bolitoglossa* and *Oedipina*) and 18 species of plethodontid salamanders occur in South America. *Bolitoglossa sima*, previously synonymized with *B. altamazonica*, is recognized, and *Oedipus paraensis* is shown to be a synonym of *B. altamazonica*. Six new forms are described, five from Colombia (*Bolitoglossa pandi*, *B. capitana*, and *B. nicefori* from the Cordillera Oriental; *B. valleculla* from the Cordillera Central; and *B. savagei* from the Sierra Santa Marta) and one from Ecuador (*Bolitoglossa chica* from the 1,000 foot level northwest of Quito, Ecuador). Evolutionary relationships are discussed and a hypothesis concerning the origin of Latin American salamander genera of the family Plethodontidae is presented with special emphasis upon the entry into South America.

INTRODUCTION

South American salamanders are the classical exception to the idea that salamanders are an exclusively north-temperate group, for only in the neotropics do they penetrate south of the equator. Biologists have always been intrigued with organisms living under novel or unusual conditions, or in unexpected regions, and it is surprising that South American salamanders virtually have been ignored for so long. When we initiated this study we were under the impression, along with most herpetologists, that the South American salamander fauna was small and insignificant. As we began to accumulate the widely scattered preserved material we discovered that the fauna, to the contrary, was varied and of considerable systematic and biogeographic importance. We have had the unique opportunity of examining and directly comparing virtually all specimens collected from the South American continent, and can now present a comprehensive review of the South American salamander fauna, its evolutionary relationships, and its origins.

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HISTORICAL REVIEW

Fifteen names have been proposed for South American salamanders. In the following list are indicated authors, dates, and type localities for all names based on South American material, and Panamanian forms found later to occur in South America.

Spelerpes adspersus Peters, 1863; Bogotá (Departamento de Cundina-marca), Colombia

- Oedipus altamazonicus* Cope, 1874, Nauta (Departamento de Loreto), Peru
Spelerpes (Oedipus) parvipes Peters, 1879; Laceres (Cáceres?), (Departamento de Antioquia), Colombia
Spelerpes peruvianus Boulenger, 1883; Moyabamba (Departamento de San Martín), Peru
Spelerpes palmatus Werner, 1897; Cordillera, Ecuador
Geotriton andicola Posada Arango, 1909; Colombia
Spelerpes simus Vaillant, 1911; Ecuador
Oedipus complex Dunn, 1924; Las Cascadas, near Gamboa, Canal Zone, Panama
Oedipus paraensis Unterstein, 1930; Pará (Estado do Pará), Brazil
Eladinea estheri Miranda Ribeiro, 1937; Belém (Estado do Pará), Brazil
Bolitoglossa borburata Trapido, 1942; Río Borburata, Estado de Carabobo, Venezuela
Bolitoglossa phalarosoma Wake and Brame, 1962; Medellín, Departamento de Antioquia, Colombia
Magnadigita hypacra Brame and Wake, 1962; Páramo Frontino, Departamento de Antioquia, Colombia
Bolitoglossa biseriata Tanner, 1962; Río Tuira at mouth of Paya tributary, Provincia de Darién, Panamá
Bolitoglossa orestes Brame and Wake, 1962; Culata, Estado de Mérida, Venezuela

At the time of Dunn's monograph of the Plethodontidae (1926), the latest review of the South American forms, seven species had been described from South America. Dunn synonymized *peruvianus*, *palmatus*, and *simus* with *altamazonicus*, and *andicola* with *adpersus*. He placed all recognized species (*adpersus*, *altamazonicus*, and *parvipes*) in the genus *Oedipus*.

Upon re-examination of the holotype of *peruvianus* and comparison with other Amazonian species, Parker (1939) concluded that *peruvianus* and *altamazonicus* were distinct species, and in the same paper he suggested that *Eladinea estheri* was a synonym of *altamazonicus*.

Taylor (1944) reviewed the generic status of Central and South American salamanders and referred *adpersa* to the genus *Magnadigita* (with a query), *parvipes* to the genus *Oedipina*, *borburata* to *Bolitoglossa*, and tentatively placed *altamazonica*, *peruviana*, and *paraensis* in *Bolitoglossa*. Taylor considered the validity of the genus *Eladinea* to be in question.

In 1944, Dunn, on the basis of newly collected material, removed *andicola* from the synonymy of *adpersa*, but placed both in the preoccupied genus *Oedipus*.

Myers and Carvalho (1945) pointed out similarities between *estheri*, *altamazonica*, and *paraensis*, but stated that certain identification of *estheri*, even to genus, was premature.

Wake and Brame (1962) showed that *andicola* was a synonym of *adpersa*.

Brame and Wake (1962b) reexamined the type of *palmata* and concluded that it was a species distinct from *altamazonica*. Finally, Wake and Brame (1963) demonstrated the invalidity of the genus *Magnadigita* and assigned all nominal members of that genus to *Bolitoglossa*. At the present time two genera, *Bolitoglossa* and *Oedipina*, are recognized in South America.

In 1875, Jiménez de la Espada described *Urotropis platensis* from a single specimen that he believed had been collected near Montevideo, Uruguay. The species was shown to be a member of the genus *Ensatina* by Dunn (1923) and has been discussed by Myers and Carvalho (1945) and by Stebbins (1949). It is now generally accepted that *platensis* was based on California salamanders that somehow reached Spain by way of Uruguay.

MATERIALS AND METHODS

Materials for the present study have been obtained from the major collections of the world, and number 671 specimens. All material was thoroughly examined and measurements were taken in the following manner, unless otherwise stated. Standard length is measured from the tip of the snout to the posterior edge of the vent. Head width is measured at the broadest point. Snout-gular fold distance is measured from the tip of the snout to the gular fold on the mid line. Limb length is measured from the axilla or groin to the tip of the longest digit of the straightened limb. All measurements were made by the senior author with the same vernier calipers and are in millimeters. Limb length is expressed in terms of limb interval units. Limb interval refers to the number of costal folds between the tips of the longest digits of the fore and hind limbs when the limbs are appressed to the sides of the trunk. All maxillary, premaxillary, and vomerine teeth have been counted and counts are based on totals of ankylosed teeth per individual. Dentary teeth have not been counted because the specimen must be mutilated in order to obtain accurate counts, and because numbers of dentary teeth have not proved to be taxonomically significant in *Bolitoglossa*. The parasphenoid tooth patch has not been counted for the same reasons. Data is presented in the following manner: measurement (number of adults examined: smallest adult—mean—largest adult); teeth (number of adults examined: lowest number—mean—highest number). Color descriptions are based on alcoholic material, unless otherwise stated.

Museum numbers of all material examined are presented under each species. Certain species occur in Central as well as South America; only specimens from South America are listed under material examined, but the range of each species is clearly stated.

GENUS *OEDIPINA*

SPECIES ACCOUNT

Two closely related species of *Oedipina* occur in South America. Both are known also from southern Central America. Only four individuals of the genus have been collected from Colombia and Ecuador (Fig. 21).

Oedipina parvipes (Peters, 1879)

Figure 1

Spelerpes (Oedipus) parvipes Peters, 1879. Monatsb. Königl. Preufs. Akad. Wissens., Berlin, 1879: 778.

Holotype—ZMB 9518; from Laceres (Cáceres), Cenia (on the Cauca River), Departamento de Antioquia, Colombia.

Material Examined—BM 1914.5.21.90, Peña Lisa, Condoto, Departamento de Choco, Colombia; and holotype.

Diagnosis—A medium sized species (maximum: 57.7 standard length) distinguished from *O. elongatus* by its less robust habitus and less contrasting light and dark coloration; from *O. complex* by its long and pointed snout, small eyes, 0-19 maxillary teeth that do not extend past the internal nares posteriorly, and 9-19 vomerine teeth arranged in series and never patched; from all species of *Oedipina* except *elongatus* and *complex* by 17 rather than 19 costal grooves.

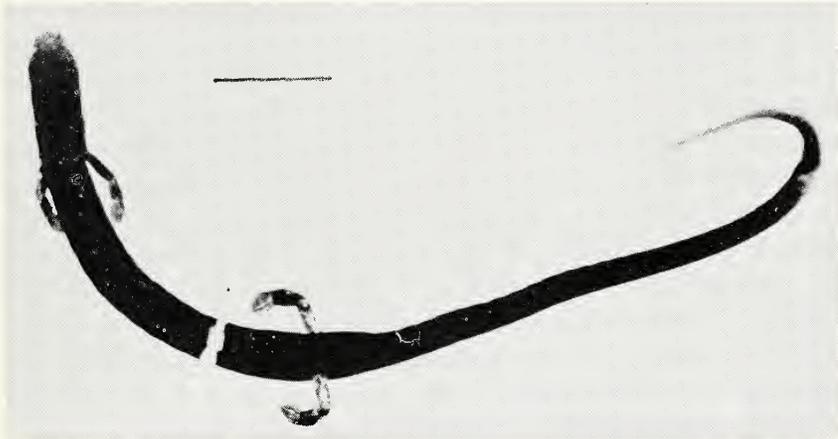


Fig. 1. *Oedipina parvipes* BM 1914.5.21.90, Peña Lisa, Colombia. Male. Line equals 1 cm.

Remarks.—No information concerning the holotype has been available since the original description. Brame recently examined the holotype and it is worthwhile to present the following data. Counts and measurements: premaxillary teeth 2, maxillary teeth 19, vomerine teeth 15, costal grooves 17, limb interval $8\frac{1}{2}$, standard length 40.4, axilla-groin length 27.9, head width 3.9, snout-gular fold length 6.3, tail length 48.7, hind limb length 7.3. Maxillary teeth do not extend past the level of the internal choanae. The holotype is in poor condition and head shape and eye size are impossible to determine due to desiccation. Dunn (1926) translated the color description by Peters (1879) as follows: "black, upperside of head mainly white, gular fold white, sides of belly and tail sprinkled with white; on the upper arm, on the elbow, and on the base of the thigh, a white spot."

Important counts and measurements of the other Colombian specimen (a male) are: premaxillary teeth 2, maxillary teeth 2, vomerine teeth 9, costal grooves 17, limb interval $7\frac{1}{2}$, standard length 47.5, axilla-groin length 31.0, head width 4.4, snout-gular fold length 7.7, tail length 78.1, hind limb length 9.2.

The holotype has more teeth than any of forty other members of the species examined by us. The other Colombian specimen resembles Panamanian *parvipes* in having low numbers of maxillary teeth, an elongate and narrowly tipped snout, and relatively small eyes. The two Colombian specimens are much darker than individuals from the Canal Zone which are light brown dorsally and gray to white ventrally. Dark *parvipes* are known from far western Panamá.

Range—Western Panamá to southwestern Colombia.

Oedipina complex (Dunn, 1924)

Figure 2

Oedipina complex Dunn, 1924. Occ. Papers Boston Soc. Nat. Hist., 5: 94.

Holotype—MCZ 9408; a young male from Las Cascadas, near Gamboa, Canal Zone, Panamá.

Material Examined—Medem field number 641 (to be deposited in USNM), just above sea level near the Penal Colony on Isla Gorgona, 25 miles west of the mainland, Departamento de Cauca, Colombia; BM 1901.3.29.115, Paramba, 800 meters (2500 feet), Provincia de Imbabura, Ecuador.

Diagnosis—A small species (maximum: 45.6 standard length) distinguished from *O. elongatus* by its less robust habitus, presence of maxillary teeth, and less contrasting light and dark coloration; from *O. parvipes* by short and rounded to blunt-tipped snout, large eyes, 13-45 maxillary teeth that extend beyond the internal choanae posteriorly, and 13-32 vomerine teeth arranged either in patches or series; from all *Oedipina* except *elongatus* and *parvipes* by 17 (rarely 18) rather than 19 costal grooves.



Fig. 2. *Oedipina complex* USNM, Isla Gorgona, Colombia. Female. Line equals 1 cm.

Remarks—The two specimens reported here represent the first records of the species from South America. It is of value, therefore to present the following information concerning them.

Medem 641. Female. Counts and measurements: premaxillary teeth 3, maxillary teeth 13, vomerine teeth 16, costal grooves 18, limb interval $8\frac{1}{2}$, standard length 32.4, axilla-groin length 20.2, head width 3.6, snout-gular fold length 5.4, tail length 33.0, hind limb length 5.9. Coloration: black laterally and gray ventrally with a light brown band dorsally from the neck onto the tail; white blotches on last $\frac{1}{2}$ of tail; head with a large white patch between the eyes and posteriorly onto neck, some white spots on snout; dorsum of proximal portions of fore and hind limbs whitish.

BM 1901.3.29.115. Male. Counts and measurements: no premaxillary teeth, maxillary teeth 17, vomerine teeth 32, costal grooves 17, limb interval 9, standard length 45.6, axilla-groin length 29.3, head width 4.9, snout-gular fold length 7.5, tail length 79.2, hind limb length 8.2. Coloration: dark brown dorsally and laterally, gray-brown ventrally; head with large white patch from anterior edge of eyes to level of gular fold, white coloration on snout; dorsum of proximal portions of fore and hind limbs whitish.

The Ecuadorian specimen (BM 1901.3.29.115) was examined by Dunn (1926) who called it *parvipes*. We think the specimen is a very large *complex* based on the following points: 1) The snout is somewhat intermediate between the pointed snout of typical *parvipes* and the blunt snout of typical *complex*. It resembles *complex* more than *parvipes*, however. 2) Although the holotype of *parvipes* has more maxillary teeth (19) than this individual (17), these numbers are more typical of *complex* than of *parvipes*. 3) The number of vomerine teeth (32) is higher than the highest number we have seen in either *complex* (28) or *parvipes* (19), but is closer to the number normally found in *complex*. 4) The vomerine teeth are in a patch. Patched vomerine teeth are occasionally found in large *complex*, but the teeth are in single rows in all *parvipes*. 5) It is larger (by 2.5 mm. standard length) than the largest *complex* but well within the known size range of *parvipes*. 6) The foot is less syndactylous than that of *parvipes* and is shorter with broader digits. The foot closely resembles that of *complex* but is proportionately larger. 7) Both *complex* and *parvipes* in South America have similar coloration consisting of a dark ground color with a large whitish patch on the head and often some scattered whitish coloration on the tail.

The Colombian specimen closely resembles Panamanian *complex* in all features, but has one more costal groove than is normally found. This specimen and a single individual of *Bolitoglossa biseriata* also collected on Isla Gorgona are the only insular records of salamanders south of Isla Tigre, an island close to the mainland in the Golfo de Fonseca, Provincia de Valle, Honduras.

Range—Western Panamá thru western Colombia to northern Ecuador.

GENUS *BOLITOGLOSSA*

Representatives of 16 species of *Bolitoglossa* have been found in South America (Figs. 22, 23, 24). These species appear to form four species groups, three of which are characterized below. The fourth contains nine apparently rather closely related species, but the group is diverse and it is impossible to define its limits at the present time. The definable species groups are:

The *phalarosoma* Group

One species: *Bolitoglossa phalarosoma*.

Moderate size (3 individuals: 46.8, 55.8, 58.2 standard length); head very narrow in relation to standard length (standard length 7.4, 7.6, 8.0 times head width, respectively); eyes moderate; snout moderate, not shortened; moderate numbers of maxillary teeth (30, 51, 43); limbs short (limb interval 4-4½); hands and feet flattened, completely webbed; ground color solid black with a few large white spots in two dorsolateral series over shoulders.

The *altamazonica* Group

Four species: *Bolitoglossa altamazonica*, *Bolitoglossa chica*, *Bolitoglossa peruviana*, *Bolitoglossa sima*.

Small size (adult means: 40.3, 39.5, 39.7, 43.0 standard length, respectively); head of moderately narrow width in relation to standard length (standard length 6.2-7.3 times head width); eyes moderate; snout not greatly shortened; low to moderate numbers of maxillary teeth but considerable interspecific variation (adult means: 15, 2, 37, 34, respectively); limbs short (limb interval 2-5); hands and feet flattened, completely or almost completely webbed; variable coloration with solid or mottled dorsal color, usually no banding or spotting dorsally.

The *palmata* Group

Two species: *Bolitoglossa orestes*, *Bolitoglossa palmata*.

Small to moderate size (adult means: 40.0, 47.2 standard length, respectively); head of moderate to moderately narrow width (standard length 6.0-7.1 times head width); eyes very large; snout very noticeably shortened; relatively low to moderate numbers of maxillary teeth (adult means: 20 and 39 respectively); limbs short (limb interval 3-5½); hands and feet characteristic with sharply demarcated, moderately robust digits that are flattened but thickened and rounded at tips, and are joined by thin web extending almost to tips.

The nine remaining species (*adpersa*, *biseriata*, *borburata*, *capitana*, *hypracra*, *nicefori*, *pandi*, *savagei*, and *vallecula*) are, for convenience, included in the *adpersa* group.

Bolitoglossa phalarosoma Wake and Brame, 1962

Figure 3

Oedipus platydactylus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Bolitoglossa phalarosoma Wake and Brame, 1962. Contrib. Sci. Los Angeles Co. Mus., 49: 1.

Holotype—BM 97.11.12.22; an adult female from Medellín, 1538 meters (5048 feet), Departamento de Antioquia, Colombia.

Material Examined—BM 97.11.12.21, same data as holotype (paratype); MLaS 6, "Antioquia," Colombia, and holotype.

Diagnosis—A medium-sized species (3 individuals: 46.8, 55.8, 58.2 standard length) with moderate numbers of maxillary teeth (30, 51, 43, respectively) distinguished from all other South American species by its very narrow head (standard length 7.4-8.0 times head width), flattened and completely webbed hands and feet, and distinctive coloration (ground color solid black with a few large white patches in two dorsolateral series along the sides of the head and over the shoulders).



Fig. 3. *Bolitoglossa phalarosoma* BM 97.11.12.22, Medellín, Colombia. Female. Holotype.

Remarks—Detailed information concerning this species is to be found in the original description (Wake and Brame, 1962).

Range—Known only from Departamento de Antioquia, Colombia (Fig. 23).

Bolitoglossa altamazonica (Cope, 1874)
Figures 4 and 20D

Oedipus altamazonicus Cope, 1874. Proc. Acad. Nat. Sci. Philadelphia, 1874: 120.

Oedipus paraensis Unterstein, 1930. Zool. Anz., 87: 270.

Eladinea estheri Miranda Ribeiro, 1937. O Campo, 8(87): 42-46.

Bolitoglossa altamazonica Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 219.

Syntypes—ANSP or USNM (3 specimens); now lost or destroyed, from Nauta, Departamento de Loreto, Peru.

Material Examined—PERU, DEPARTAMENTO DE LORETO: USNM 85119, Iquitos, 117 meters (386 feet); MCZ 5124, Río Pacaya or Río Ucayali; BM 1913.7.28.29-30 (2 specimens), Río Pacaya; ZSZMH 3090, between Iquitos and Leticia; AMNH 43569, Royaboya, 150 meters (495 feet), collected by H. Bassler. DEPARTAMENTO DE CUZCO: CNHM 78394, Cosñipata, 830 meters (2600 feet), collected by Kalinowski. BRAZIL, ESTADO DO PARÁ: CAS 65003, Belém, collected by the Hopkins-Branner Expedition. BOLIVIA, DEPARTAMENTO DE COCHABAMBA: AMNH 3746, "Cochabamba," collected by Miller and Boyle. COLOMBIA, DEPARTAMENTO DE META: MLaS 3, Acacias, 700 meters (2300 feet), collected by Nicéforo María. DEPARTAMENTO DE BOYACA: MCZ 24921, Muzo, 1240 meters (3980 feet), collected by Nicéforo María.

Diagnosis—A small (10: 30.6-40.3-48.0) member of the *altamazonica* group with low numbers of maxillary teeth (10: 11-15-26) distinguished from *chica* by more maxillary teeth; from *sima* by a narrower head, fewer maxillary teeth (Fig. 7), and emarginated, less fully webbed and smaller hands and feet; from *peruviana* by fewer maxillary teeth.

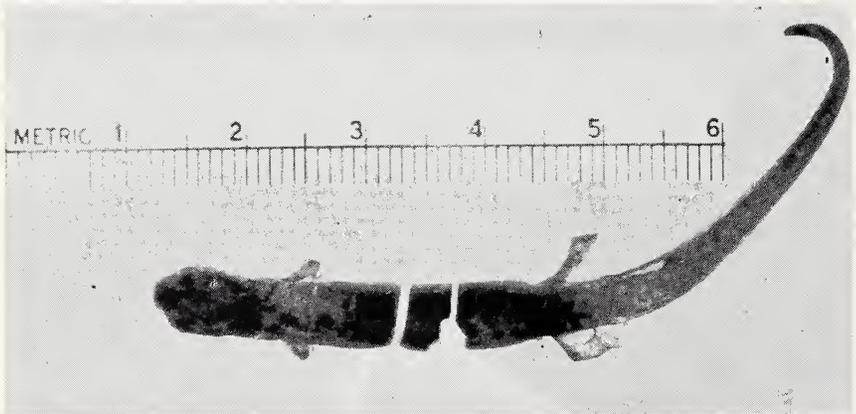


Fig. 4. *Bolitoglossa altamazonica* BM 1913.7.28.30, Río Pacaya, Peru. Female.

Remarks—Pertinent counts and measurements of the examined material are presented in Table 1. In addition to the material examined three specimens (MNRJ) are known from Benjamin Constant, 110 meters (363 feet), on the Río Javary near the Peruvian border, Estado do Amazonas, Brazil (Myers and Carvalho, 1945), four newly hatched specimens (cotypes of *Eladinea estheri*, in MNRJ and MP) are known from Utinga, near Belém, Estado do Pará, Brazil (Miranda Ribeiro, 1937), and a single individual (holotype of *Oedipus paraensis*, deposited in ZMB but now lost or destroyed) was collected at Santa Isabel, near Belém, Estado do Pará, Brazil (Unterstein, 1930). Darlington (1957) states that Dunn wrote him informing him of a salamander (uniden-

tified) collected at about 200 meters in northern Bolivia. Parker (1939) mentions a single individual, that he calls *altamazonica*, collected in the Utinga forest, near Belém, Estado do Pará, Brazil. We have been unsuccessful in attempts to locate the last two specimens in museums.

The series examined by us is rather variable in coloration. Most individuals are darker dorsally and laterally than ventrally, but some have light dorsal streaking and mottling. Others are uniformly dark-colored dorsally. Patches or spots of light color are absent with the exception of light-colored areas around the nasolabial grooves, and, in one specimen (USNM 85110), on the snout. Ventral melanophore networks are reticulate, punctate, or intermediate. One specimen (MLaS 3) has some small guanophores scattered sparsely on its ventral surfaces. Most specimens are in poor conditions due to poor initial preservation or long term preservation and many are badly faded. Two specimens (BM 1913.7.28.29-30) are greenish due to preservation in a copper container. The ground color of the most recently collected individual (MLaS 3) is a dark blackish-brown.

The question of the validity of *Eladinea estheri* has been discussed by Parker (1939) and Myers and Carvalho (1945). The types are hatchlings and do not differ noticeably from hatchlings of other *Bolitoglossa*. Oviparity of the species led Miranda Ribeiro (1937) to establish the new genus on the false premise that all Central and South American salamanders were ovoviviparous. All *Bolitoglossa* for which we have information are, on the contrary, oviparous. There are no other characters and there is no recourse but to place the name in the synonymy of *altamazonica*.

Unterstein (1930) described *Oedipus paraensis* from a single specimen collected near Belém, Brazil. The holotype is now lost. We have examined a specimen from Belém and find it to be identical with Peruvian material, and Parker (1939), who had Peruvian *altamazonica* for comparison, examined a salamander from Belém and called it *altamazonica*. Because the holotype is lost, because no information is contained in the original description that would distinguish *paraensis* from *altamazonica*, because *altamazonica* is known from the vicinity of Belém, and since all extant museum specimens from the area are assignable to a single species we refer the name to the synonymy of *altamazonica*.

Considerable variation is seen in the series of *altamazonica* examined by us (Table 1), and we are not certain that all are members of the same species. We have reservations, in particular, about assignment of the Colombian and Bolivian specimens. A Colombian specimen (MCZ 24921) is the only member of the species known to have been collected above 1000 meters in elevation. It is also from the Magdalena drainage, while all others are from the Amazonian drainage. Our *altamazonica* may be composite, but final solution of the problem must await the collection of additional material.

Range—North-central Colombia through eastern Peru to central Bolivia; through Amazonian Brazil to Belém (Fig. 22).

Bolitoglossa chica, NEW SPECIES

Figures 5, 20E, and 26

Holotype—JAP 4366; an adult female from the grounds of the Hotel Zaracay, 2 km. E. of Santo Domingo, 670 meters (2200 feet), Provincia de Pichincha, Ecuador, collected on June 15, 1962, by Robert K. Mullen and Peter D. Spoecker.

Paratype—EPN 2411, an adult male from the lower part of the Río Bolaniguas, a southern affluent of Río Guañabamba in the Río Esmeraldas system, at about 0° 15' N. Latitude and 79° 06' W. Longitude (250-400 meters), Provincia de Pichincha, Ecuador, collected in August, 1956, by Manuel Olalla.

Diagnosis—A small (2 individuals: 38.7, 40.3 standard length) member of the *amazonica* group distinguished from all other members of the group by very few or no maxillary teeth (0, 4, respectively); from *colonnea* by absence of an interorbital dermal ridge.

Description of the holotype—Adult female, snout of moderate length, broad and truncate, slightly rounded at tip; nostril small, labial protuberances of nasolabial groove moderate; canthus rostralis indistinct, gently rounded. Standard length 6.6 times head width; standard length 4.3 times snout-gular fold length. Relatively deep, distinct groove below eye extends full length of eye opening, does not communicate with lip. Eye relatively small, only slightly protuberant. Poorly defined postorbital groove extends posteriorly from eye as irregular, indistinct depression for 1.8 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as indistinct depression parallel to and 3.2 mm. anterior to gular fold. Vomerine teeth 16, in slightly curved series that extend to medial border of internal nares. No maxillary teeth. No premaxillary teeth. Relatively robust tail 0.84 times standard length; round with no lateral compression; marked basal constriction. Post-iliac gland not evident. Limbs short and slender; limb interval 3; standard length 5.4 times right fore limb; standard length 5.0 times right hind limb. Webbing of hands and feet nearly complete; digits fairly broad and well defined; triangular and broadly rounded tips of digits free of web, but total webbed area very extensive (Fig. 20E). Longest finger and longest toe more pointed than others. No sub-terminal pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 5.9; snout to gular fold (head length) 9.0; head depth at posterior angle of jaw 2.9; eyelid length 2.2; eyelid width 1.2; anterior rim of orbit to snout 2.9; horizontal orbital diameter 1.7; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.4; snout to fore limb 10.8; distance separating internal nares 1.9; distance separating external nares 2.3; snout projection beyond mandible 0.5; snout to posterior angle of vent (standard length) 38.7; snout to anterior angle of vent 35.4; axilla to groin 21.1; tail length 32.0; tail width at base 3.5; tail depth at base 3.6; fore limb length 7.2; hind limb length 7.7; width of right hand 2.9; width of right foot 3.4.



Fig. 5. *Bolitoglossa chica*. JAP 4366, Santo Domingo, Ecuador. Female. Holotype.

Coloration in alcohol: light gray-brown dorsally, light gray laterally and ventrally. Light ground color of entire organism covered with even punctuation of small melanophores that form some isolated reticula. Eyelid edges dark black. Sparsely scattered large guanophores on ventral surfaces of head, trunk, tail, and limbs. Uniformly cream-colored in life.

Variation—Pertinent counts and measurements of the only paratype are found in Table 1. The paratype is an adult male, and is a little larger than the holotype. It has a slightly narrower but more truncate snout. It is slightly less robust than the holotype and has a proportionately longer tail. The paratype has some small maxillary teeth (4) and has more vomerine teeth (31) than the holotype. The vomerine teeth are in series that extend to the lateral borders of the internal nares or beyond, and the series become patched laterally.

Coloration of the paratype has been altered both by preservation and by rather extensive growths of what appears to be a fungus. The skin of the dorsal and lateral surfaces is partially disintegrated in spots, and these spots are lighter in coloration than surrounding areas. Hair-like hyphae protrude from the infested areas. Dorsal and lateral surfaces appear dark brown, ventral surfaces light brown. Melanophores are in reticula over most of the organism, but are punctate in some scattered areas. Large guanophores are sparsely scattered over ventral surfaces, as in the holotype.

Remarks—The species is known from but two individuals. The greatly reduced numbers of maxillary teeth appear to be highly significant. *Bolitoglossa colonea* of southern Central America also has greatly reduced numbers of maxillary teeth, but differs markedly from *chica* in having a large interorbital dermal ridge and a shorter, more truncate snout.

The holotype was captured on a broad-leafed fern at night during a moderately heavy rain.

The name *chica* is derived from the Spanish word *chica* (small).

Range—Northeastern Ecuador (Fig. 22).

Bolitoglossa peruviana (Boulenger, 1883)

Figure 6

Spelerpes peruviana Boulenger, 1883. Ann. Mag. Nat. Hist., Ser. 5, 12: 165.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Oedipus peruvianus Parker, 1939. Mem. Mus. Roy. d' Hist. Nat. Belgique, Ser. 12, 2: 87-89.

Bolitoglossa peruviana Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 219.

Holotype—BM 1946.9.6.17; an adult female from Moyobamba, 854 meters (2800 feet), Departamento de San Martín, Peru, collected by A. H. Roff in 1874.

Material Examined—JAP 6773, slightly above Río Paute 2 km. NNE. Mendez, circa 2000 meters (6560 feet), Provincia de Santiago—Moruma, Ecuador, collected by Peter D. Spoecker on August 9, 1962; and holotype.

Diagnosis—A small (2 individuals: 37.0, 42.3 standard length) member of the *altamazonica* group with moderate numbers of maxillary teeth (36, 37, respectively) distinguished from *altamazonica* and *chica* by many more maxillary teeth; from *sima* by small hands and feet (standard length 11.6-13.7 times foot width, versus 9.2-10.6 in *sima*) that are less completely webbed.

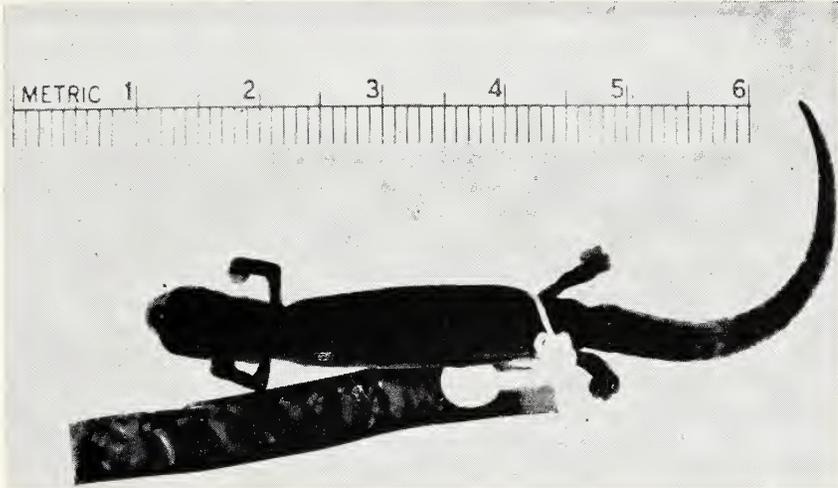


Fig. 6. *Bolitoglossa peruviana* JAP 6773, Mendez, Ecuador. Female.

Remarks—Pertinent counts and measurements of the material examined are found in Table 1. Parker (1939) examined the holotype of *peruviana* and compared it with *altamazonica*. He concluded that it was a member of a distinct species that differed from *altamazonica* in having more vomerine and maxillary teeth, vomerine teeth that extended past the lateral edges of the choanae and were only narrowly separated from the parasphenoid tooth patch, a divided parasphenoid tooth patch, and in unspecified details of coloration. Brame recently reexamined the type of *peruviana* and we concur with the conclusions of Parker. The type has 37 maxillary teeth while an individual of *altamazonica* of the same size and sex has but 19, and the maximum in *altamazonica* is 26. The type has 30 vomerine teeth while the individual of *altamazonica* of the same size and sex has but 9, and the maximum for *altamazonica* is 21. The vomerine teeth of certain *altamazonica* (MLaS 3) extend beyond the lateral borders of the choanae and that character does not separate the two species. Distance between parasphenoid and vomerine teeth, and separation or non-separation of the parasphenoid tooth patch are characters that are rather variable in *Bolitoglossa*, and are not of taxonomic significance. The holotype is now very light in coloration and is obviously faded. Boulenger (1883) described the color as "light brownish above, with ill-defined brown longitudinal lines; a tri-

angular spot, base forward on the crown; lower surfaces and hind limbs brown, with slight lighter variegations." The color as described by Boulenger does not seem to differ greatly from that of some *altamazonica*.

The recently collected Ecuadorian specimen is tentatively assigned to *peruviana* on the basis of similarity of proportions, similarity of hands and feet, and high numbers of maxillary teeth (36). Several differences exist between this specimen and the type of *peruviana*, and we have some reservations about assignment of the specimen. Only 13 vomerine teeth are found and they extend to the medial edge of the choanae. The snout is proportionately somewhat shorter than that of the type. Ground color of the entire organism is solid dark blackish with blackish-brown dorsolateral streaks on either side from the back of the head, over the shoulders, and onto the trunk. The ventral surfaces are sprinkled with small white guanophores. White pigment is present on the snout, and a large white spot lies between the eyes. The only other member of the *altamazonica* group that approaches *peruviana* in numbers of maxillary teeth is *sima* from which the specimen differs markedly in its dark coloration, its ventral guanophores, its noticeably smaller and less fully webbed hands and feet, and its shorter snout. The individual was collected under a banana log in a plantation. Both it and the type of *peruviana* are from the Amazonian drainage.

Peracca (1904) mentions a specimen from Ecuador which he assigned to *peruviana*. The specimen, in the Torino Museum, is unavailable for study. Since no definite locality information or description is given, its taxonomic assignment must remain in doubt.

Range—North-central Peru to southeastern Ecuador (Fig. 22).

Bolitoglossa sima (Vaillant, 1911)

Figures 8 and 20F

Spelerpes simus Vaillant, 1911. Miss. Geogr. Amer. Sud., 9(2): 58.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Holotype—MHNP 06-284; an adult female from "Equateur" collected by Dr. Rivet.

Material Examined—USNM 20591, Plaza de Oro, Provincia de Esmeraldas, Ecuador; USNM 22453, Ecuador or Colombia; JAP 2993-5, 1 km. N. Cachavi, 20 meters (66 feet), Provincia de Esmeraldas, Ecuador, collected by James A. Peters, Dec. 3, 1958; and holotype.

Diagnosis—A medium-sized (4: 36.7-43.0-45.9) member of the *altamazonica* group with moderate numbers of maxillary teeth (4: 28-34-44) distinguished from other members of the group by its extensively webbed hands and feet (Fig. 20F) and distinctive coloration (light dorsal ground color mottled with several shades of brown); distinguished further from *altamazonica* and *chica* by higher numbers of maxillary teeth; from *altamazonica* and *peruviana* by larger hands and feet (standard length 9.2-10.6 times foot width, versus 11.0-13.3 in *altamazonica* and 11.6-13.7 in *peruviana*).

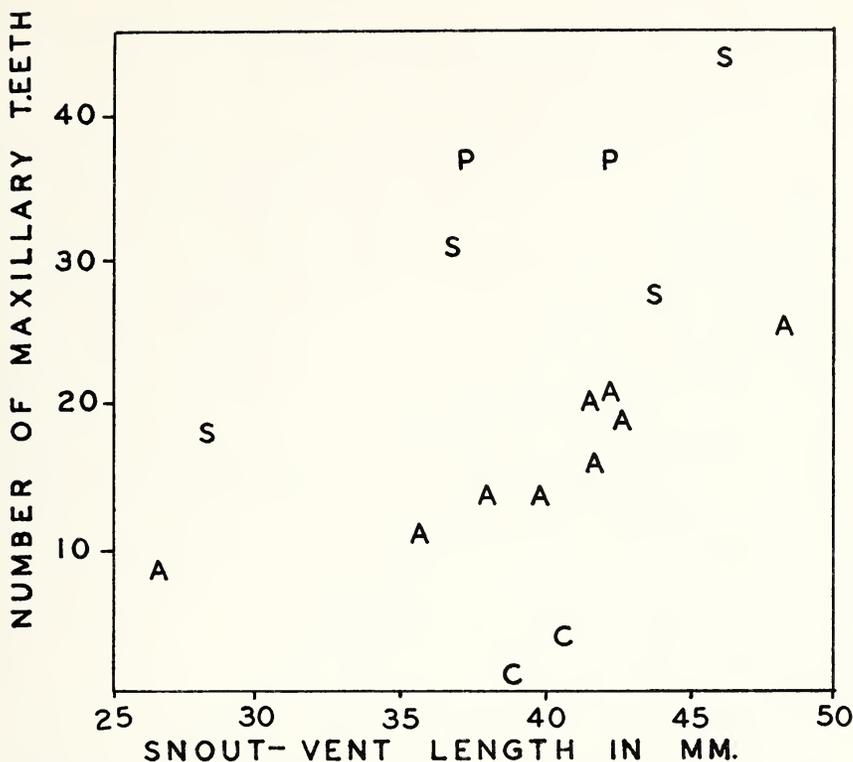


Fig. 7. *Bolitoglossa altamazonica* Group. Variation in maxillary teeth. A, *altamazonica*; C, *chica*; P, *peruviana*; S, *sima*.

Remarks—Vaillant (1911) described *sima* from a single Ecuadorian specimen. His description was obviously inadequate and Dunn (1926) placed the name in the synonymy of *altamazonica* without examining the type, stating that the description was poor and that the figure resembled *altamazonica*. We have examined the type and additional recently collected material and find that they are representatives of a distinct species. Pertinent counts and measurements of examined material are found in Table 1. USNM 22453 is in very poor condition and accurate measurements and tooth counts are not possible.

Some of the information given by Vaillant (1911) is in error and the description is inadequate in other ways. The following account is based on our examination of the holotype. Counts and measurements: 1 premaxillary tooth; maxillary teeth 24 (plus several that have been knocked out), vomerine teeth 20 (in single rows), costal grooves 13, limb interval $3\frac{1}{2}$, standard length 45.7, axilla-groin length 26.0, head width 6.9, snout-gular fold length 10.9, tail length 49.0, hind limb length 9.8. Maxillary teeth extend to the front of the eye on the left side and to the center of the eye on the right. The vomerine series extend to the lateral edge of the internal nares on both sides. Webbing of

the hands and feet is very extensive. The specimen is now faded but it appears that the ground color was originally light, with mottling of darker color dorsally.

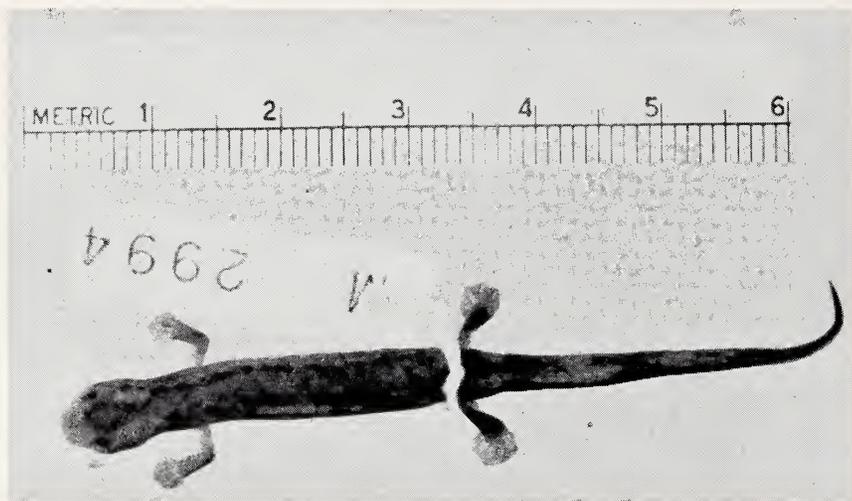


Fig. 8. *Bolitoglossa sima* JAP 2994, Cachavi, Ecuador. Male.

B. sima is a moderately robust species with a head of moderate width (standard length 6.2-6.6 times head width) and fairly short limbs (limb interval 3-4). The snout is of moderate length and width, and is flattened and truncate anteriorly. The eyes are of moderate size. Maxillary teeth increase steadily with size (Fig. 7), the largest specimen (45.9 standard length) having the highest numbers of teeth (44). Maxillary teeth extend posteriorly to a point between the front and center of the eye. Vomerine teeth are in a single series in three individuals, and are slightly patched laterally in two (USNM 20591, JAP 2993). The vomerine series extend to the medial border of the choanae in most. The tail is virtually round in cross-section with little lateral compression. Webbing of the hands and feet is complete and is more extensive than in any other South American *Bolitoglossa*. The digits are very flattened and indistinct. Tips of the longest digits project as small obtuse angles from the pad-like webbing (Fig. 20F). Size of hands and feet is greater in *sima* than in other members of the *altamazonica* group. All six specimens are similar in coloration, and are generally brownish, lighter ventrally than dorsally. The dorsal surfaces are mottled with several shades of from very light to very dark brown with no determinable pattern. Enlarged brown dorsal glandules are evident on the head and body. The top of the head is dark brown. All ventral surfaces are uniformly covered with tiny punctate melanophores.

Some information is available concerning the habitat of *sima*. The following information was provided by James A. Peters. Three salamanders col-

lected by him were found in the nesting bases of the stems of giant elephant ear plants, which catch and hold water. All were taken in plants that were shaded either by trees or by other elephant ear plants. The plants grow in large clumps, 10-15 feet in diameter, and the salamanders were in the innermost plants, well down toward the base of the stem. The general area was dense wet forest, but the actual collection locality was a grassy field, cleared for cattle grazing, with scattered trees left for shade. Elephant ear plants grow in the shade. No salamanders were found in the same plants growing in the forest proper.

Dunn (1926: 398) indicated on his map that USNM 20591 was from southern Ecuador in the Amazonian drainage. Information accompanying the specimen states that it is from Plaza de Oro, a locality in northwestern Ecuador in the Pacific drainage. The newly collected material is from the Pacific drainage, also in northwestern Ecuador not far from Plaza de Oro. Unfortunately specific information is not available concerning collection of the type.

Range—Northwestern Ecuador near the Colombian border, and perhaps into Colombia (Fig. 22).

TABLE 1. Data on *Bolitoglossa altamazonica* group

	Sex	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa altamazonica</i>										
MCZ 24921	♂	42.0	23.3	6.3	9.1	9.3	4	39.9	21	20
CNHM 78394	♂	41.6	22.7	6.2	9.9	9.6	4	36.7	16	13
ZSMH 3090	♂	30.6	15.5	4.9	6.4	7.1	2	31.0	—	15
MLaS 3	♀	48.0	27.5	6.7	9.2	10.2	4½	28.2	26	21
BM 1913.7.28.29	♀	42.5	24.8	5.8	8.9	8.9	4	43.0	19	9
AMNH 3746	♀	43.6	24.3	6.8	10.2	10.2	2	—	—	16
AMNH 43569	♀	41.3	21.9	5.7	9.8	9.7	3	—	20	17
MCZ 5124	♀	39.8	22.5	5.7	9.0	8.7	4	44.5	14	13
BM 1913. 7.28.30	♀	37.9	20.9	5.6	7.8	7.9	5	37.8	14	12
CAS 65003	♀	35.6	20.4	5.7	8.2	8.0	3½	34.0	11	14
USNM 85119	♀	26.7	13.2	4.8	6.3	6.8	4	23.3	9	14
<i>Bolitoglossa sima</i>										
JAP 2994	♂	36.7	19.6	5.9	8.8	8.8	3	32.6	31	10
USNM 20591	♀	45.9	24.3	7.0	10.2	11.2	3	37.3	44	18
MNHN 3302	♀	45.7	26.0	6.9	9.8	10.9	3½	49.0	32	20
JAP 2993	♀	43.7	24.9	6.8	9.8	9.8	4	41.6	28	22
JAP 2995	♀	28.2	14.3	5.0	6.1	7.0	—	22.4	18	9
<i>Bolitoglossa peruviana</i>										
BM RR 1946.9.6.17	♀	42.3	24.0	5.9	6.7	9.6	3½	36.9	37	30
JAP 6773	♀	37.0	22.1	5.8	8.4	8.0	4	34.2	36	13
<i>Bolitoglossa chica</i>										
EPN 2411	♂	40.3	21.9	6.3	8.7	9.2	3½	41.8	4	31
JAP 4366	♀	38.7	21.1	5.9	7.7	9.0	3	32.0	0	16

Bolitoglossa orestes Brame and Wake, 1962

Figure 9

Oedipus adpersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Bolitoglossa orestes Brame and Wake, 1962. Copeia, 1962: 171.

Holotype—BM 1905.5.31.103; an adult female from Culata, 3000 meters (9810 feet), Cordillera de Mérida, Estado de Mérida, Venezuela, presented by W. F. H. Rosenberg.

Material Examined—VENEZUELA, ESTADO DE MÉRIDA: BM 1905.5-31.95-102, same data as holotype; LM 4506, NMB 2671, and AMNH 10557-60, Culata, collected by Rosenberg; MCZ 2605, Culata, collected by Briceño; CM 10086, Mérida, collected by Rosenberg; BM 1904.6.30.18, Mérida; AMNH 10555-56, Chama, 2000 meters (6540 feet), collected by Rosenberg; BM 1905.5.31.105-107, 108 (2 specimens), Fugueros, 3500 meters (11450 feet), (Estado de Mérida ?); NMW 9179: 1-4 and 9181: 1-4 (total 8 specimens), Culata and Chama, collected by Rosenberg; and holotype. Material examined is the type series.

Diagnosis—A small (9 males: 31.4-37.7-39.7; 13 females: 30.3-42.2-46.9) member of the *palmata* group with low numbers of maxillary teeth (25: 7-20-30) distinguished from *palmata* by its smaller adult size, small numbers of vomerine teeth (7-15), and great abundance of tiny guanophores ventrally.



Fig. 9. *Bolitoglossa orestes* BM 1905.5.31.101, Culata, Venezuela. Female.

Remarks—Detailed information concerning this species is to be found in the original description (Brame and Wake, 1962 b).

Range—Cordillera de Mérida, western Venezuela (Fig. 23).

Bolitoglossa palmata (Werner, 1897)

Figure 10

Spelerpes palmatus Werner, 1897. Zool. Anz. 20: 266.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Bolitoglossa palmata Brame and Wake, 1962. Copeia, 1962: 173.

Lectotype—ZIUW q43; a juvenile from "Cordillera," Ecuador, collected by M. Wagler.

Material Examined—CM 13118, between Baeza and Archidona, 2000 meters (6540 feet), Cordillera de Guacamayo, Provincia de Napo-Pastaza, Ecuador, collected by Philip W. Hershkovitz; UMMZ 84735 (3 specimens), same date as above; and lectotype.

Diagnosis—A medium-sized (1 male: 35.6; 3 females: 49.4-50.8-53.3) member of the *palmata* group with moderate numbers of maxillary teeth (4: 24-39-47) distinguished from *orestes* by its larger adult size, larger numbers of vomerine teeth (14-23) and distinctive coloration (uniform light brown dorsally and laterally with a sharply demarcated dark brown venter).

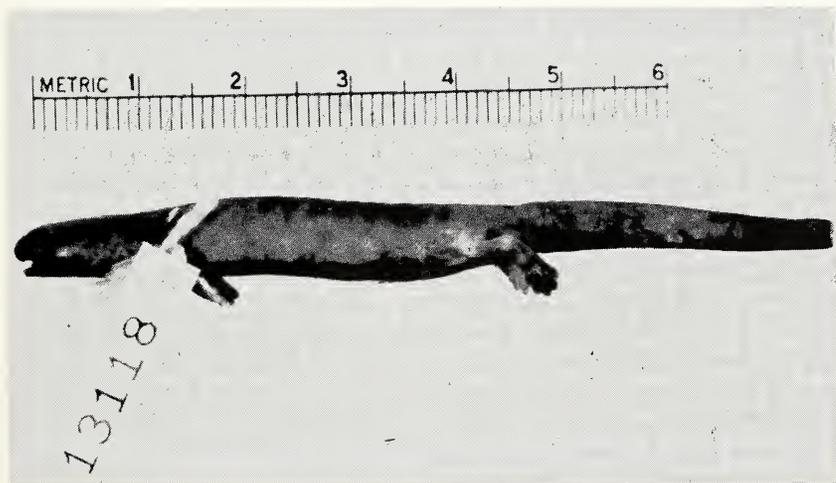


Fig. 10. *Bolitoglossa palmata* CM 13118, between Baeza and Archidona, Ecuador. Female.

Remarks—The authors have recently redescribed this species and detailed information is found in our publication (Brame and Wake, 1962 b).

Range—Cordillera de Guacamayo, central Ecuador (Amazonian drainage) (Fig. 22).

Bolitoglossa hypacra (Brame and Wake, 1962)

Figure 11

Magnadigita hypacra Brame and Wake, 1962. Proc. Biol. Soc. Washington, 75: 71.

Holotype—USNM 131481; an adult female from Páramo Frontino, 3610 meters (11850 feet), Departamento de Antioquia, Colombia, collected by M. A. Carriker, Jr.

Material Examined—Holotype. The species is known only from the holotype.

Diagnosis—A medium-sized species (62.8 standard length) with high numbers of maxillary teeth (48) distinguished from *biseriata*, *borburata*, *capitana*, *nicefori*, *savagei*, and *vallecula* by less webbing and distinctive coloration (coarse dorsal speckling of yellow-buff on dark brown ground color, and large yellow spots scattered sparsely on lateral and ventral brown ground color); from *subpalmata* by larger size, fewer maxillary and vomerine teeth, and coloration; from *cerroensis* by more maxillary and vomerine teeth; from *marmorea* by fewer vomerine teeth, smaller head, hands, and feet, shorter limbs, and coloration.

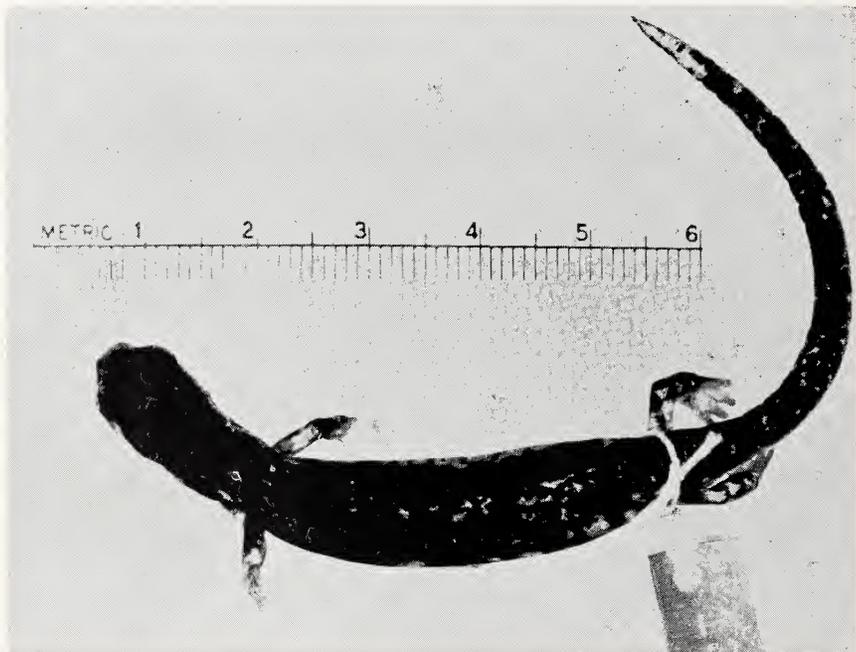


Fig. 11. *Bolitoglossa hypacra* USNM 131481, Páramo Frontino, Colombia. Female. Holotype.

Remarks—Detailed information concerning this species is to be found in the original description (Brame and Wake, 1962 a).

Range—Cordillera Occidental, northwestern Colombia (Fig. 23).

***Bolitoglossa valleculea*, NEW SPECIES**

Figures 12, 20A, and 26

Oedipus adspersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Holotype—MLaS 8a; an adult female from Yarumal, 2300 meters (7550 feet), Departamento de Antioquia, Colombia, collected in January, 1962, by Hermano Nicéforo María.

Paratypes—COLOMBIA, DEPARTAMENTO DE ANTIOQUIA: MLaS 8b-8h (7 specimens), same data as holotype; MLaS 5, 5a, 5b, La Ceja, 2217 meters (7270 feet); MLaS 9, San Pedro, 2700 meters (8850 feet); MLaS 10, 10a, 10b, 6 km. toward Rionegro from Retiro, 2300 meters (7540 feet); AMNH 39445-7, Santa Rosa de Osos, 2640 meters (8660 feet); AMNH 14027, "Andes"; MCZ 8163, "Quindío" (probably from Sonson region, 2545 meters [8350 feet]). Apparently all were collected by Hermano Nicéforo María, and information supplemental to that accompanying the AMNH and MCZ specimens was provided by him.

Diagnosis—A medium-sized species (12 males: 37.6-44.9-51.9; 8 females: 44.6 -51.9-58.7) with high numbers of maxillary teeth (16: 28-44-61) distinguished from *biseriata*, *borburata*, *capitana*, *nicefori*, *pandi*, and *savagei* by less fully webbed hands and feet (Fig. 20); from *adspersa* by more maxillary teeth relative to size (Fig. 14) and presence of red or yellow pigmentation on the ventral surfaces of trunk and tail; from *hypacra* by its smaller size and ventral coloration.

Description of the holotype—Adult female, snout of moderate length and width, truncate; nostril small, labial protuberances of nasolabial groove moderate; canthus rostralis of moderate length, angular, marked by dark pigment. Standard length 6.8 times head width; standard length 4.6 times snout-gular fold length. Distinct groove below eye extends almost full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, moderately protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 2.8 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as well defined groove parallel to and 2.8 mm. anterior to gular fold. Vomerine teeth 20, in curved series that extend about to lateral borders of internal nares. Maxillary teeth 53, extending posteriorly to point about two-thirds through eye. Four premaxillary teeth, none piercing lip. Dentary teeth 72. Tail slender, 0.92 times standard length; moderately compressed laterally; moderately constricted at base. Post-iliac gland not evident. Limbs relatively robust, of moderate length; limb interval $2\frac{1}{2}$; standard length 5.3 times right fore limb; standard length 5.0

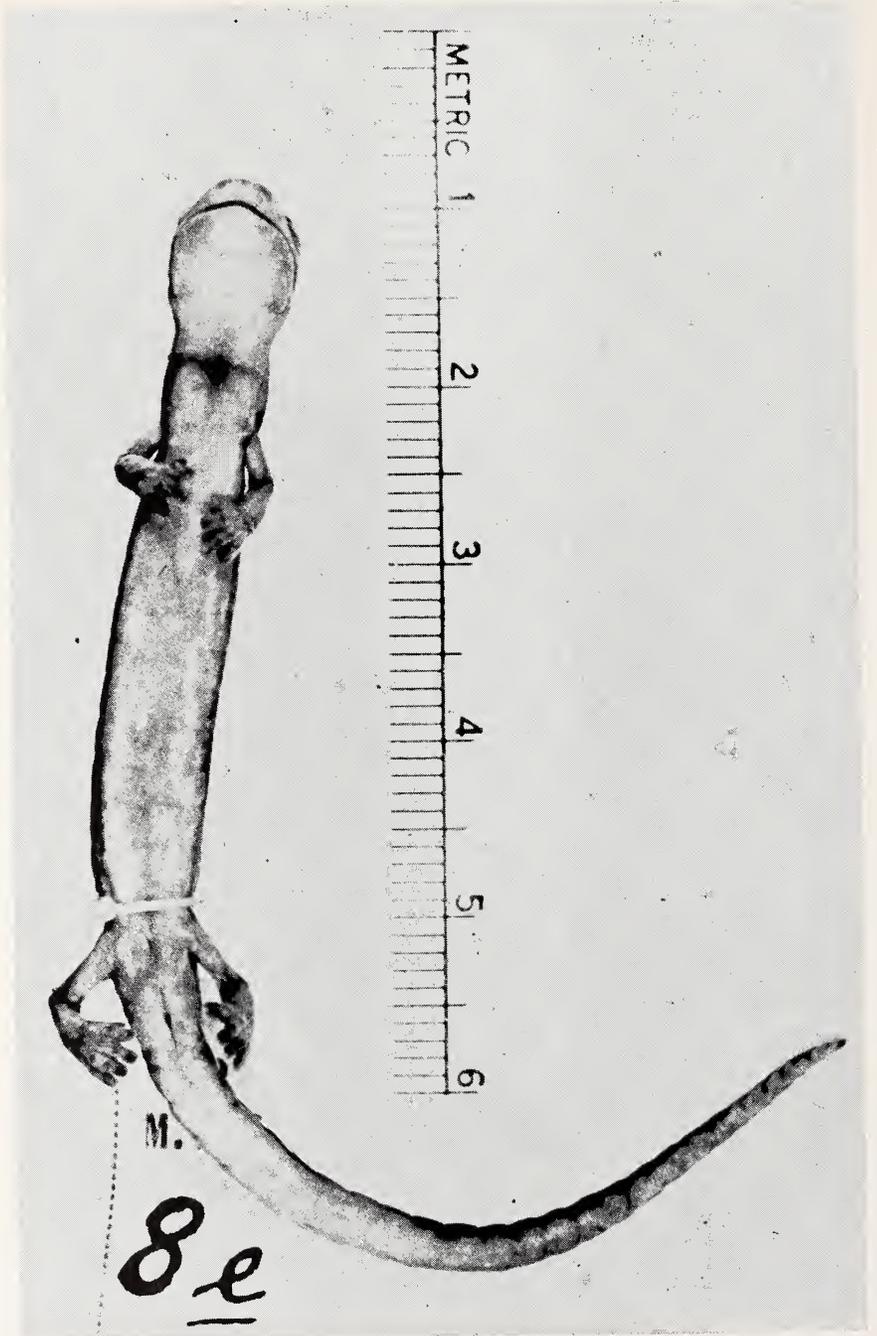


Fig. 12. *Bolitoglossa valleculea* MLaS 8e, Yarumal, Colombia. Male.

times right hind limb. Webbing of hand and foot not complete; tips of digits broadly rounded, free from web; 2 phalanges of toes 2, 3, and 4, 1½ phalanges of finger 3, and terminal phalanx of fingers 2 and 4 and toe 5 free from web. Pronounced subterminal pads present on fingers and toes. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 7.9; snout to gular fold (head length) 11.8; head depth at posterior angle of jaw 4.7; eyelid length 3.8; eyelid width 1.9; anterior rim of orbit to snout 3.3; horizontal orbital diameter 2.5; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.7; snout to fore limb 15.6; distance separating internal nares 2.0; distance separating external nares 2.4; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 54.1; snout to anterior angle of vent 49.7; axilla to groin 28.8; tail length 50.0; tail width at base 3.2; tail depth at base 3.9; fore limb length 10.3; hind limb length 10.9; width of right hand 4.8; width of right foot 5.6.

Coloration: dorsal ground color of entire organism mottled dark brown as a result of varying concentrations of melanophores scattered on a light background. Center of back with many small and indistinct yellowish areas showing through melanophore network. Two distinct but discontinuous black lines extend on either side of the body from area over shoulders posteriorly along dorso-lateral portion of trunk and onto lateral portions of tail. A less distinct dark line extends from the canthus rostralis to behind eye and along lateral borders of trunk to insertion of hind limbs. Ground color of ventral surfaces yellowish with scattered grayish-brown suffusions that are comprised of punctate and reticulate melanophore patterns; much of ventral surface unmarked by melanophores and appears clear yellowish.

Variation—Pertinent counts and measurements of the type series are listed in Table 2. Sexual dimorphism is noted in regard to size and limb length. The 12 males average 44.9 standard length with a limb interval of from 1 to 2½ (mean 2); 8 females average 51.9 standard length with a limb interval of from 2½ to 4 (mean 3). Maxillary teeth increase in number with increasing size (Fig. 14).

Webbing of the hands and feet of the series is similar to that of the type, but some variation is seen. MLaS 5b has much more webbing than other *vallecula* but the webbing of all fingers and toes is obviously incomplete. Other individuals may have slightly more or less webbing than the type. Subterminal pads are evident in well-preserved individuals. The hands and feet of *adpersa* and *vallecula* are similar, but those of *vallecula* are less fully webbed with a few exceptions. In general, the amount of webbing is intermediate between the amounts in *hypacra* and *savagei*, and resembles that in *adpersa*.

Considerable variation is seen in head width with some evidence of sexual dimorphism. Males have broader heads (standard length 5.7-7.0 times head width, mean 6.4) than females (standard length 6.4-7.3 times head width, mean 6.9). MLaS 5b, a male, has a noticeably broader head and a broader and more

truncate snout than other *vallecula*. This specimen is the most aberrant of the type series in webbing and coloration as well.

TABLE 2. Data on *Bolitoglossa vallecula*

		Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa vallecula</i>										
MLaS 8e	♂	51.9	28.0	7.4	12.2	11.3	2½	51.5	45	18
MLaS 10	♂	49.7	26.6	7.9	11.8	11.0	2	56.4	54	24
MLaS 8g	♂	49.2	24.5	7.6	12.6	11.2	1	61.0	40	21
MLaS 8b	♂	47.9	24.4	7.2	11.8	11.0	1½	52.0	38	14
MLaS 8f	♂	45.7	24.6	7.3	11.0	11.1	2	44.2	41	24
MLaS 10a	♂	45.0	23.9	7.2	11.2	9.7	2	51.2	45	17
AMNH 39447	♂	44.2	23.8	6.5	11.8	10.0	2	46.6	45	18
MLaS 5b	♂	43.6	23.9	7.7	10.8	10.9	2	40.1	47	22
MCZ 8163	♂	42.3	22.6	6.7	12.0	10.2	1½	—	40	19
MLaS 5	♂	41.3	21.7	6.7	10.2	10.2	2	41.7	47	17
MLaS 5a	♂	40.7	20.1	6.3	9.8	10.7	2	43.7	47	17
AMNH 39445	♂	37.6	20.7	6.4	9.5	9.2	2	—	36	16
MLaS 8c	♀	58.7	32.1	8.1	12.2	11.2	3	61.2	47	22
AMNH 14027	♀	56.1	32.1	8.2	11.8	11.3	4	—	61	20
MLaS 9	♀	55.8	31.1	8.1	12.0	11.8	2½	57.3	47	18
MLaS 8a	♀	54.1	28.8	7.9	10.9	11.8	2½	50.0	53	20
MLaS 8h	♀	49.3	26.8	7.1	11.0	10.7	3	47.5	28	14
MLaS 10b	♀	49.2	27.3	7.7	11.0	10.9	2½	47.7	50	26
AMNH 39446	♀	47.5	27.2	6.7	11.1	11.3	2½	—	46	19
MLaS 8d	♀	44.6	24.2	6.8	11.0	10.0	2½	43.1	31	17

Although most paratypes resemble the holotype in general color pattern, some variation is evident. Fifteen individuals are lighter middorsally than laterally. Four exceptions, MLaS 5b, MLaS 8c, MLaS 10, and MLaS 10a, have dense melanophore networks dorsally and laterally and appear almost solid black when viewed from above. Dark lateral sides are present in all of the specimens. In those with light color dorsally the aspect is of a light striated wash. One (MLaS 8b) has extensive amounts of light, bright yellowish dorsally. The venter of the trunk of all individuals has at least some yellowish white coloration. The entire venter of some is light, most have light as the dominant color, but some are relatively dark with light areas that are sharply demarcated from the dark background. According to the collector, Nicéforo María, the light ventral surfaces of specimens from San Pedro and Retiro (MLaS 9, 10a, 10b) were red in life. In preservative MLaS 10b is salmon pink and the others are light pink. It seems likely that the other *vallecula* also had reddish ventral coloration that has faded in preservation. Light ventral color appears to be due to the absence of melanophores and presence of reddish and yellowish chromato-

phores. The throat is usually rather light, with many small lightly pigmented areas. Several are very dark ventrally (MCZ 8163, MLaS 8d, MLaS 5b). The venter of the tail is light-colored in contrast to the darker lateral portion in all 17 individuals that have tails. Light ventral tail coloration is dominant in 15 of the 17. In some the venter of the tail is almost entirely light colored.

Remarks—The salamanders from San Pedro and Retiro were collected in bromeliads at some distance from the ground. The salamanders from Yarumal were on the ground under stones and heaps of decaying vegetation.

There is some doubt concerning the locality data accompanying AMNH 14027. The catalogue lists the locality as "Andes, Colombia" but a note for this number states "label says Yarumal." It is probable that Andes refers to the mountains in a very general way and not to the Colombian city of the same name. The type locality of *vallecula* is Yarumal, and it is likely that this specimen was collected there also.

The name *vallecula* is an allusion to the habitat of the species on the lower slopes and valleys of the Cordillera Central, northwestern Colombia.

Range—Cordillera Central, northwestern Colombia (Fig. 23).

***Bolitoglossa savagei*, NEW SPECIES**

Figures 13 and 20B

Oedipus adpersus (part) Ruthven, 1922. Univ. Michigan Mus. Zool. Misc. Publ., 8: 49.

Oedipus adpersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 393.

Holotype—UMMZ 54595; an adult female from Cerro San Lorenzo, 1400-2100 meters (4500-7000 feet), Sierra Nevada de Santa Marta, Departamento de Magdalena, Colombia, collected in 1913.

Paratypes—COLOMBIA DEPARTAMENTO DE MAGDALENA, Sierra Nevada de Santa Marta: UMMZ 48213; UMMZ 48195; San Miguel, 1800-2100 meters (4500-7000 feet); UMMZ 45615-20, 45622-26, 45628-30, Cerro San Lorenzo, 1400-2100 meters (4500-7000 feet); UMMZ 63334, La Cumbre, 2140 meters (7000 feet); UMMZ 63335 (22 specimens) La Popa, 1525 meters (5000 feet) on Cerro San Lorenzo; UMMZ 54592-93, Quebrada Viernes Santo, east slope Cerro San Lorenzo, 1500-1800 meters (5000-6000 feet); CNHM 1815; USNM 36693-7000, Río Frío, 1000 meters (3280 feet); ANSP 19723-4, San Lorenzo Trail, Hacienda Cincinnati, 1830 meters (6000 feet); MCZ 3894-95, Cerro San Lorenzo.

Referred Material—ZMB 25918, Mérida, Estado de Mérida, Venezuela.

Diagnosis—A medium-sized species (20 males: 36.4-44.1-51.7; 11 females: 38.2-48.8-55.1) with high numbers of maxillary teeth (31: 23-48-79) distinguished from *biseriata*, *borburata*, *capitana*, *nicefori*, and *pandi* by incompletely webbed hands and feet; from *adpersa* by more fully webbed hands and feet

and more maxillary teeth (Fig. 14); from *vallecula* by more fully webbed hands and feet and less light pigmentation ventrally; from *hypacra* by more fully webbed hands and feet, shorter limbs, and coloration.



Fig. 13. *Bolitoglossa savagei* UMMZ 45615, Cerro San Lorenzo, Colombia. Female.

Description of the holotype—Adult female, snout of moderate length, broadly rounded; nostril small, labial protuberances of nasolabial groove small; canthus rostralis of moderate length, rounded. Standard length 6.1 times head width; standard length 4.4 times snout-gular fold length. Shallow groove below eye extends almost full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, only slightly protuberant. Poorly defined postorbital groove extends posteriorly from eye as shallow depression for 2.4 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as indefinite depression parallel to and 3.4 mm. anterior to gular fold. Vomerine teeth 33, in long curved series that extend beyond lateral borders of internal nares. Maxillary teeth 79, extending posteriorly to point about three-fourths through eye. Three maxillary teeth, none piercing lip. Tail of moderate size, 0.97 times snout-vent length; virtually round in cross section with little lateral compression; moderately constricted at base. Post-iliac gland not evident. Limbs of moderate length; limb interval 3; standard length 4.5 times right fore limb; standard length 4.5 times right hind limb. Webbing of hands and feet not complete; tips of digits knob-like, free from web; terminal phalanx of finger 3 and toes 3 and 4 free from web; web forms pad-like surface from which project the small rounded knobs of the digit tips.

Subterminal pads pronounced. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 5, 2, 1.

Measurements: head width 8.9; snout to gular fold (head length) 12.3; head depth at posterior angle of jaw 4.5; eyelid length 3.7; eyelid width 2.2; anterior rim of orbit to snout 3.6; horizontal orbital diameter 2.8; interorbital distance 2.5; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to fore limb 15.2; distance separating internal nares 2.0; distance separating external nares 2.4; snout projection beyond mandible 0.7; snout to posterior angle of vent (standard length) 54.5; snout to anterior angle of vent 51.4; axilla to groin 33.3; tail length 53.0; tail width at base 4.6; tail depth at base 4.7; fore limb length 12.0; hind limb length 12.2; width of right hand 4.9; width of right foot 6.0.

Coloration: dorsum and venter of head and trunk light brown with markings of medium dark brown. Dorsal ground color almost uniform light brown with a few irregularly placed darker markings; ground color of lateral and ventral surfaces of trunk darker. Tail mottled light and dark brown dorsally and laterally; light yellowish ventrally. Limbs mottled light and dark brown. Throat uniform brown with some light spots.

Variation—Pertinent counts and measurements of the type series are listed in Table 3. Sexual dimorphism is noted in regard to size and limb length. The 19 males average 43.7 standard length with a limb interval of from 2 to 3; 11 females average 48.8 standard length with a limb interval of from 3 to 4. Maxillary teeth are numerous and increase in number with increasing size (Fig. 14). *B. valleculea* and *savagei* have similar numbers of maxillary teeth, and both have more than *adpersa*. Vomerine teeth are numerous and range from 13 to 33 in adults. Vomerine teeth are in long curved series; slight lateral patching is present only in a few individuals. Head width is variable and some sexual dimorphism is indicated. Males over 42 standard length have slightly broader heads on the average (standard length 6.0-6.7 times head width, mean 6.3) than do females (standard length 6.1-7.1 times head width, mean 6.5).

Webbing of hands and feet is slightly variable in the series. The webbing in the holotype is less well-developed than in the majority of the series. Two phalanges of the longest digits are free from webbing in the least webbed individuals, but most are more fully webbed. The typical foot, viewed ventrally, is a large rounded pad from which project rounded knob-like digital tips containing but one phalanx. The most frequently encountered foot type is illustrated (Fig. 20B).

Coloration is rather variable. Of 55 specimens 28 have a definite longitudinal band dorsally with the light color usually sharply set off from the darker lateral color. Of the 28, some are striated with light and dark, others are predominantly dark streaked with light, and still others are predominantly light streaked with dark. A few are almost uniformly light dorsally. Nine of the remaining 17 specimens have light mottling on a dark background dorsally, and 8 are almost uniformly dark brownish-gray. The venter of the trunk is brown-

ish and is a little lighter than the sides. Ventral melanophores are arranged in a dense, poorly defined reticulum. The venter is mottled with light markings of variable size and shape, and some moderate size guanophores are present. Tails are present in 47 individuals. In 21 the tail is almost uniform light yellowish ventrally, and in the remainder the tail is mottled with light yellow and dark brown. Only two or three approach uniform dark brown ventral coloration.

TABLE 3. Data on *Bolitoglossa savagei*

<i>Bolitoglossa savagei</i>	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
ZMB 25918	51.7	30.1	7.9	12.8	12.2	2	41.4	63	—
USNM 36696	50.6	28.0	7.7	11.0	11.3	3	—	50	23
UMMZ 45623	49.2	27.2	7.4	11.2	11.4	2½	—	65	20
UMMZ 45618	46.4	24.5	7.4	11.0	10.8	2	48.2	57	28
USNM 36694	46.2	24.9	6.9	10.6	9.6	3	49.3	41	16
UMMZ 63335	46.1	23.9	7.8	11.2	10.8	2	45.7	64	31
UMMZ 63335	46.0	23.4	7.4	11.2	10.8	2	44.8	61	27
UMMZ 45616	46.0	25.3	7.3	11.6	11.0	2½	44.7	49	22
UMMZ 45619	45.6	25.3	6.8	10.3	10.2	2	43.7	51	22
UMMZ 63335	44.9	23.9	7.6	11.2	11.0	2	40.0	51	31
USNM 33693	44.4	24.4	7.3	11.2	10.2	3	51.7	31	17
USNM 36698	44.1	23.8	7.3	10.6	10.5	2½	—	39	23
USNM 36695	43.4	24.5	6.6	10.2	9.8	3	50.9	52	21
MCZ 3894	42.0	23.4	6.7	10.0	9.9	2½	40.3	35	22
UMMZ 54593	40.9	21.3	7.1	10.8	9.3	2	42.2	40	21
UMMZ 63335	40.6	21.4	6.7	10.4	10.2	2	39.1	24	29
UMMZ 63335	40.0	21.9	6.5	9.0	9.9	2½	35.8	29	29
UMMZ 63335	39.3	26.0	6.6	9.2	9.8	2½	41.2	34	13
USNM 33697	38.4	21.7	6.2	9.2	8.9	3	41.6	23	16
UMMZ 45628	36.4	19.6	6.3	8.9	9.2	3	35.5	41	22
CNHM 1815	55.1	34.9	8.6	11.2	11.2	4	59.2	61	22
UMMZ 54595	54.5	33.3	8.9	12.2	12.3	3	53.0	79	33
UMMZ 48195	52.9	30.2	8.5	11.8	12.0	4	—	62	—
UMMZ 63335	51.8	28.9	8.0	11.2	11.8	3½	49.2	55	22
UMMZ 45617	50.9	29.6	7.2	10.8	10.2	4	—	50	24
MCZ 3895	50.7	28.6	7.9	11.5	11.2	3	47.2	43	19
UMMZ 45615	48.7	27.9	7.4	11.2	11.4	3	42.4	61	22
UMMZ 45620	47.3	25.7	7.1	11.0	10.8	3	49.0	42	25
UMMZ 45622	43.7	22.1	7.2	10.8	10.2	3	40.0	51	19
UMMZ 36699	43.2	23.9	6.4	9.7	9.5	3	44.0	31	15
UMMZ 45625	38.2	21.0	6.6	9.9	9.2	3	34.0	47	26
UMMZ 63335	36.7	19.6	6.1	8.3	8.7	2	30.2	24	21
USNM 36700	33.8	17.2	6.0	8.2	8.2	3	27.1	19	15
UMMZ 63335	33.4	17.6	6.1	8.2	8.6	2½	30.2	21	21
UMMZ 63335	30.6	16.6	5.7	7.6	7.8	2½	30.3	21	22
UMMZ 63335	21.4	10.7	4.2	5.0	5.2	3	17.1	0	7

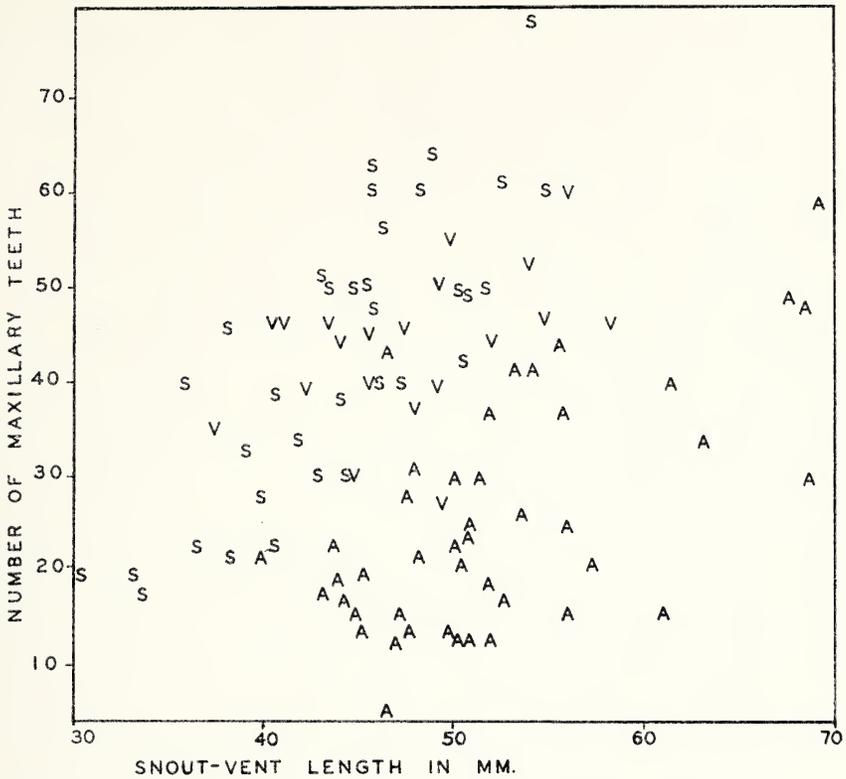


Fig. 14. Variation in maxillary teeth. A, *Bolitoglossa adspersa*; S, *B. savagei*; V, *B. valleculea*.

Remarks—A single specimen (ZMB 25918) from Mérida, Venezuela, agrees with the type series of *savagei* in all basic characters. The webbing of the hands and feet, similarity in habitus, and high maxillary tooth counts indicate the specimen is assignable to *savagei* or is a member of a population closely related to *savagei*. The individual is dark brown mottled with various shades of dark color. Pertinent counts and measurements for the specimen are included in Table 3.

Information concerning the habitat of *savagei* has been published by Ruthven (1922). The species apparently is limited to heavily forested regions and is, according to Ruthven, a "bromeliadiculous" form. He restricts the term bromeliadiculous to forms which breed in bromeliads or occur principally in bromeliads. Although principally found in bromeliads in trees and on the ground, specimens were occasionally found in decaying logs and stumps or under decaying leaves.

Ruthven (1922) states "this is a viviparous species;" but comments no further and offers no evidence for the statement. We have examined reproduc-

tive tracts of a number of adult females and, although the oviducts of some were enlarged, we found no evidence of development proceeding in the oviducts. Very large ova were seen in the ovaries of some, but not in the oviducts. Peters (1863) reported finding developing ova 3 mm. in diameter in both oviducts of *Spelerpes adspersus* (= *Bolitoglossa adspersa*) and stated that the species bears living young. Ruthven referred his material to *adspersa* and may have followed Peters in calling the species viviparous. Nicéforo María (1958) reported discovery of the eggs of *adspersa* at Dintel, Colombia (20 miles NW. of Bogotá), demonstrating that the species is oviparous. We have not seen the salamanders that were collected with the eggs and we have not examined *adspersa* from the Dintel area, but the locality is close to other *adspersa* localities in the Bogotá region and is at an elevation (2650 meters) similar to that at which *adspersa* is found. The only other species known from localities near Dintel is *Bolitoglossa capitana*, a species well-known to Nicéforo María (his *Bolitoglossa andicola*). Posada Arango (1909) reported that *Geotriton andicola* (= *Bolitoglossa adspersa*) was an ovoviviparous form, but he offered no proof for his statement.

To the best of our knowledge ovoviviparity or viviparity in Central and South American plethodontid salamanders has never been proven. On the contrary, all species for which we have reliable information are oviparous. Literature references to ovoviviparity and viviparity in these salamanders apparently are based on the unproven statements of Peters (1863), Posada Arango (1909), and Ruthven (1922).

Jay M. Savage initiated a study of South American salamanders some years ago but abandoned the project. He called our attention to the presence of representatives of this species in various museums and pointed out the value of a systematic review of the South American salamanders. It is with pleasure that we name this species after him, in appreciation for his encouragement and invaluable advice.

Range—Sierra Nevada de Santa Marta, northern Colombia, and Cordillera de Mérida, western Venezuela (Fig. 23).

Bolitoglossa borburata Trapido, 1942

Figure 15

Bolitoglossa borburata Trapido, 1942. Bol. Soc. Venezolana Cien. Nat., 8. 297.
Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Holotype—USNM 115509; an adult female from Valle del Río Borburata, Estado de Carabobo, Venezuela, at 1200 meters (3900 feet) collected by P. Anduze.

Material Examined—VENEZUELA, ESTADO DE ARAGUA: UMMZ 113870 (7 specimens), UMMZ S-1608 (cleared and stained), Rancho Grande, 1090 meters (3575 feet); UMMZ 113871, Choroni-Maracay Road;

UMMZ 113872 (2 specimens), mountain crest above Choroní. ESTADO DE CARABOBO: BM 1920.1.20.3726, Río San Esteban; and holotype.

Diagnosis—A medium-sized species (4 males: 38.0-44.6-47.9; 7 females: 45.9-54.8-62.9) with high numbers of maxillary teeth (11: 49-57-71) distinguished from *adspersa*, *hypacra*, *savagei*, and *valleculela* by its more fully, almost completely webbed hands and feet; from *nicefori* by its markedly narrower head; from *biseriata* by absence of very light coloration ventrally; from *pandi* by more maxillary teeth in individuals of similar size, absence of cream-colored ventral spots, and gray-brown rather than reddish-gray ventral and lateral ground color; from *capitana* by smaller adult size and absence of uniform lead-black coloration; from *lignicolor* by smaller size and more maxillary teeth (21 *lignicolor*: 23-35-60).

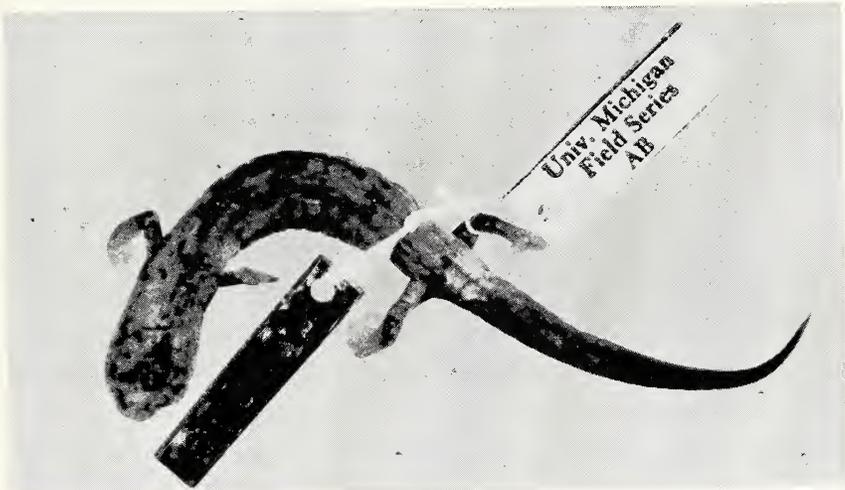


Fig. 15. *Bolitoglossa borburata* UMMZ 113871, Rancho Grande, Venezuela. Female.

Remarks—Pertinent counts and measurements of the material examined are listed in Table 5. *B. borburata* is a moderately robust form with a relatively broad, sub-truncate snout and fairly short limbs (limb interval 3-4). It is very closely related to *savagei* which it resembles in numbers of maxillary and vomerine teeth, and in proportions. Apparently *borburata* is a larger species than *savagei*; 4 of the 7 females are larger than the largest *savagei* and only one *savagei* exceeds the female average. The eyes are slightly larger and more protuberant than those of *savagei*. In addition *borburata* has more fully webbed feet and differs in details of coloration.

Sexual dimorphism is evident only in regard to size. The 4 males average 44.6 standard length; the 7 females average 54.8. Head width is slightly variable (standard length 5.9-6.7 times head width in individuals over 45.0 standard length). Vomerine teeth are in single long series in all individuals and teeth extend to the lateral borders of the internal nares or beyond.

Webbing of hands and feet is virtually complete in *borburata*. The webbed pad is very extensive, but the tips of all digits extend from the pad. The digits are distally flattened and lack subterminal pads. Characters associated with webbing distinguish *savagei* from *borburata*. The digits of *savagei* are more discrete and cylindrical, less flattened, and less webbed than those of *borburata* and have well-developed subterminal pads. The digits of *savagei* are more robust than those of *borburata* and, when viewed ventrally, project from the pad as distinct, shortened, blunt-tipped nubbins. Viewed ventrally, the hands and feet of *borburata* have extensive pads from which the digits extend smoothly as broadly rounded to slightly pointed projections.

Coloration of *borburata* is similar in pattern to *savagei* but the two species are distinct in details. Seven of the 11 *borburata*, including the 5 largest individuals, are longitudinally streaked or banded with light coloration that overlies the dark ground color and is distinct from the darker lateral ground color. The holotype is also light dorsally. In the 4 remaining individuals the dorsal ground color is dark, with extensive mottling of irregular light patches that overlie the ground color. Ventral surfaces of the throat and trunk are gray-brown (lighter than the lateral surfaces in 9, darker in 2). Ventral melanophore networks are reticulate in 10, punctate in 1. Seven specimens have tails and the venters of all are darker than the trunk venters. One specimen (BM 1920.1.20.3726) has light yellowish spots (probably originally whitish) on the tail venter overlying the ground coloration. Tails of *savagei* and *vallecula* usually have light ventral ground color in contrast to the situation in *borburata*.

Range—Central highlands, northern Venezuela (Fig. 23).

Bolitoglossa biseriata Tanner, 1962

Figure 16

Bolitoglossa biseriata Tanner, 1962. *Herpetologica* 18: 18.

Holotype—UU 3847; from Río Tuira at mouth of Paya tributary, Provincia de Darién, Panamá, collected by P. Galindo.

Material Examined—USNM 145656, Lower Río Calima, Departamento de Valle, Colombia, collected by I. Cabrera; USNM 145657, prison camp on Isla Gorgona, Departamento de Cauca, Colombia, collected by F. Medem; and holotype.

Diagnosis—A relatively small species (7: 33.0-41.1-48.7) with moderate numbers of maxillary teeth (7: 15-31-54) distinguished from all South American species by its characteristic color pattern (extensive light coloration dorsally and ventrally, very dark laterally); further distinguished from *adspersa*, *hypacra*, *savagei*, and *vallecula* by its completely webbed hands and feet with very flattened digits.

Remarks—Tanner (1962) described *biseriata* from a single Panamanian specimen collected near the Colombian border. Two recently collected Colombian

individuals are assignable to *biseriata*. Pertinent counts and measurements are listed in Table 5. In addition we have examined uncatalogued Panamanian material in CNHM.

The holotype is a juvenile and the low numbers of maxillary (15) and vomerine (11) teeth are not typical of adults. The feet are poorly preserved and the color is badly faded.

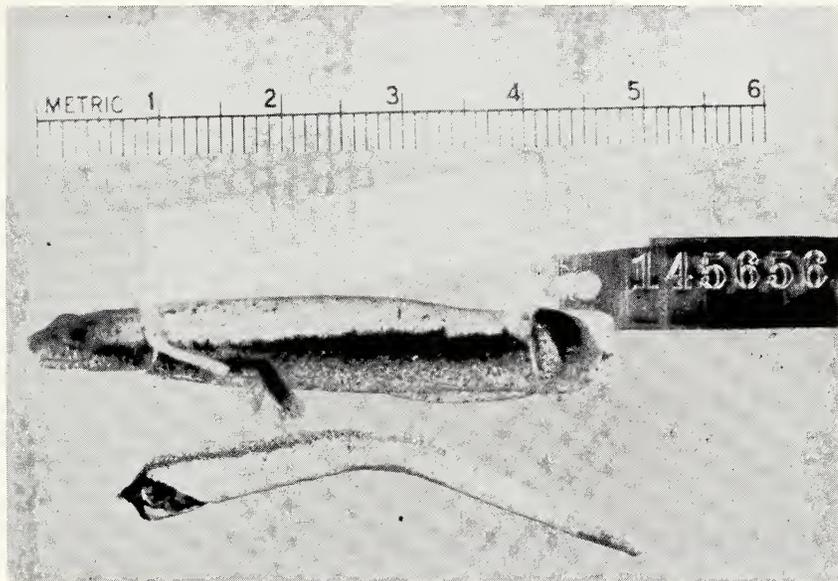


Fig. 16. *Bolitoglossa biseriata* USNM 145656, lower Río Calima, Colombia. Female.

B. biseriata is a relatively slender form with a relatively broad truncate snout and limbs of moderate length. Adults have moderate numbers of maxillary (maximum 54) and vomerine (maximum 28) teeth. Vomerine teeth are in series that are patched laterally and extend about to the center of the internal nares. Maxillary teeth extend to a point about three-fourths through the eye. Standard length is from 6.1 to 6.8 times head width. The moderate sized eyes are moderately protuberant. Dorsal surfaces of the head, trunk, and tail are sprinkled with many enlarged, evenly spaced, pigmented glandules.

Webbing of hands and feet is complete and the digits are very flattened and indistinct. The longest digits extend from the extensively webbed pad as small triangular points; other digits are indistinct. Hands and feet of the material examined are broader than those illustrated by Tanner (1962) and webbing is more extensive.

Coloration of the species is distinctive. Coloration of the largest specimen (USNM 145656) is well preserved, and is described in detail. A strongly biseriata pattern is present with extensive light coloration dorsally and ventrally, and

dark color laterally. The dorsum of the trunk and tail is strikingly pigmented with pink-beige to cream. Reddish-brown color is present on top of the head, and a few blackish markings are present on the dorsal portion of the trunk. A broad blackish stripe extends from the eyes and jaws posteriorly along the sides of the trunk and onto the tail where it narrows to a pin-stripe and becomes indefinite. The stripe is speckled with tiny punctate guanophores. Ventral surfaces of the head, trunk, and tail are cream-colored as a result of a dense guanophore reticulum. Scattered punctate melanophores are present ventrally, and they coalesce occasionally to form small, irregularly shaped dark brown spots. Limbs are dark blackish dorsally, cream ventrally. The tail is almost entirely cream-colored. The borders of the mouth are variegated with black, brown, and cream, with scattered tiny punctate guanophores. The iris is gray with numerous punctate melanophores.

The other Colombian specimen (USNM 145657) has the same general pattern as that described above but has less cream coloration and slightly more dark lateral and ventral coloration. The individual has a broad light dorsal band that is tan medially and yellowish-cream laterally. The head and limbs are light dorsally. The color pattern is strongly biseriata.

Extensive light coloration is present dorsally and ventrally in the holotype, with darker coloration laterally.

The holotype was collected in the leaf axils of a *Heliconia* (Tanner, 1962) and the Isla Gorgona specimen was found on a leaf of a broad-leafed shrub. No additional ecologic data are available. Apparently *biseriata* is a lowland, arboreal species.

Range—Central Panamá to southwestern coastal Colombia and Isla Gorgona (Fig. 23).

Bolitoglossa adspersa (Peters, 1863)

Figure 17

Spelerpes (Oedipus) adspersus Peters, 1863. Monatsb. Königl. Preuss Akad. Wissens., Berlin, 1863: 468.

Geotriton andicola Posada Arango, 1909. Estudios Científicos: 125.

?*Magnadigita adspersa* Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 210.

Bolitoglossa adspersa Nicéforo María, 1958. Bol. Inst. La Salle, 45(198): 10.

Syntypes—ZMB 4916 (4 specimens); from Bogotá, 2500 meters (7150 feet), Departamento de Cundinamarca, Colombia.

Material Examined—COLOMBIA, DEPARTAMENTO DE CUNDINAMARCA: ZMB 4915 (4 specimens), ZMB 4932 (5 specimens), ZMB 4933 (3 specimens), ZMB 5141 (2 specimens), ZMB 8937 (3 specimens), all with same data as syntypes; CNHM 81901–2, Arrayan, 3100 meters (10000 feet); CNHM 81903–4, Cruz Verde, 3300 meters (10900 feet); CNHM 81905–8, Monserrate-Arrayan, collected by Nicéforo María; ZSZMH 1824, Bogotá, collected by Franz Werner; SM 29627, Bogotá, collected by Nicéforo María; NMB 3046–8, Bogotá, collected by Fuhrmann; MNHN 7815, Bogotá; ANSP

24101-11, Aguadita, 2550 meters (8400 feet); UMMZ 57485, 89424 (13 specimens), 78297 (5 specimens), 57486, Bogotá and vicinity, collected by Nicéforo María; AMNH 6829-35, 10324, 10326-45, 10247-9, 18355-438, Bogotá, collected by Nicéforo María and Apolinar María; MCZ 9083-152, Bogotá, collected by Nicéforo María; MCZ 7220-4, Bogotá; MCZ 20939, Fusagasuga, 1746 meters (5800 feet), collected by Bequaert; BM 1919.3.6.38-47, BM 65.6.12.19-20, Bogotá; MLaS 2, 2a, 2b, above San Miguel, 2800 meters (9200 feet), collected by Nicéforo María; MVZ 62953-93, E. Bogotá, 2650 meters (8700 feet), collected by Stebbins and Hendrickson; ICNB (no number), 2 specimens, Páramo de Palacio, 3 km. south Lagunas de Siecha, 3600-3650 meters (11900-12050 feet), collected by Jorge Hernández C.; ICNB (no number), 13 specimens, Cerro Monserrate, 3000 meters (9900 feet), collected by Jorge Hernández and Fred Medem; ICNB (no number), 9 specimens, Páramo Cruz Verde, 3100 meters (10200 feet), collected by Leopold Richter and E. R. Dunn; ICNB (no number), 1 specimen, below Salto Tequendama bordering Sabana de Bogotá, 2250 meters (7400 feet), collected by E. R. Dunn and Armando Dugand; ICNB (no number), 39 specimens, Cerro Monserrate-Arrayan, 2900 meters (9600 feet), collected by Hernando Osorno Mesa and E. R. Dunn; LACM 1745-76, Cerro Monserrate, 3240 meters (10700 feet), collected by Fred Medem; and syntypes. DEPARTAMENTO DE SANTANDER: AMNH 20382-408, mountains near Muzo.

Diagnosis—A medium-sized species (20 males: 43.1-49.9-69.1; 22 females: 43.9-54.7-68.4) with moderate numbers of maxillary teeth (43: 6-27-60) distinguished from *biseriata*, *borburata*, *capitana*, *nicefori*, and *pandi* by less webbing of hands and feet and strongly demarcated digits, and distinctive coloration (pale gold spots, flecks, and bars dorsolaterally on a deep blackish-brown to black ground color); from *savagei* and *vallecula* by fewer maxillary teeth (Fig. 14) and coloration; from *hypacra* by more webbing of hands and feet and coloration.



Fig. 17. *Bolitoglossa adspersa* LACM 1745, Cerro Monserrate, Colombia. Male. Line equals 1 cm.

Remarks—Pertinent counts and measurements of *adspersa* from various parts of its range are included in Table 4. *B. adspersa* is a moderately robust form with a moderate to relatively narrow head. Considerable variation is seen in regard to many characters of the species. Some evidence of sexual dimorphism

is seen; 20 males average 49.9 standard length with a limb interval of $1\frac{1}{2}$ to 4 (mean $2\frac{1}{2}$), and 22 females average 54.7 standard length with a limb interval of 2 to 5 (mean $3\frac{1}{2}$). Limbs of males are noticeably longer than those of females. Heads of males tend to be broader than those of females; standard length is 6.1 to 6.9 (mean 6.4) times head width in 20 adult males, 6.3 to 7.5 (mean 6.7) in 21 adult females. Most *adpersa* have low numbers of maxillary teeth as adults (6-32). Several populations have higher numbers; individuals from Páramo de Palacio have up to 43 teeth, from Aguadita up to 45, and from San Miguel up to 60. In general maxillary teeth increase in number with increasing size of individuals, but the correlation is not absolute (Fig. 14). Some large individuals have few teeth (ICNB, Monserrate-Arrayan, no number, 31 teeth at 68.0 standard length) while much smaller individuals from different regions have many more teeth (ANSP 24105, 44 teeth at 46.4 standard length). Considerable variation occurs in some local populations (*e. g.* Aguadita) and male individuals of similar size (46.4 and 45.2 standard length) from the same population may have markedly different numbers of teeth (44 and 21 respectively). Vomerine teeth are in curved series that extend to about the center of the internal nares. Numbers of vomerine teeth increase, in general, with increasing size of individuals. The range of vomerine teeth in adults over 45 standard length is 12 to 35 (mean 21).

Webbing of hands and feet is somewhat variable. This variation has been illustrated by Taylor (1944: 201, Fig. 2B; 224, Fig. 3) and Wake and Brame (1963: Fig. 1). More webbing is present than in *vallecula* and some individuals have as much webbing as certain *savagei*. In general digits are robust and well defined, with very pronounced subdigital pads. The digits are not flattened distally. The terminal phalanx of fingers 2 and 4 and of toes 2 and 5, the terminal and about one-half of the penultimate phalanx of finger 3 and toe 4, and the terminal and penultimate phalanges of toe 3 are free from webbing in most individuals. Specimens with slightly more or slightly less webbing are commonly encountered.

Coloration of 3 individuals of *adpersa* has been described in some detail from live material by Stebbins and Hendrickson (1959). Most individuals examined by us have a dark brown, blackish-brown, or black dorsal and lateral ground color, with a lighter grayish-brown ventral ground color. The dorso-lateral surfaces of almost all *adpersa* are marked with many irregularly-shaped spots, flecks, streaks, and bars, all longitudinally oriented. In preservation these appear tan or yellowish to silverish, but in living salamanders they are metallic pale gold and rusty according to Stebbins and Hendrickson. A few guanophores are present ventrally, especially on the ventrolateral portions of the trunk and on the throat. The ventral melanophore network is a dense reticulum. The lower eyelid is whitish in most specimens. Only slight deviation from the above color description is encountered. Some individuals from Páramo de Palacio appear almost solid black dorsally, perhaps due to preservation. An individual from San Miguel (MLaS 2) has a poorly defined dorsal band that is a little lighter than the ground color.

TABLE 4. Data on *Bolitoglossa adspersa*

		Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa adspersa</i>										
MLaS 2	♂	69.1	36.3	10.6	17.2	14.5	2	55.2	60	24
ICNB Tequendama	♂	63.0	33.2	9.1	14.3	13.0	1½	—	35	28
ANSP 24101	♂	55.7	31.7	9.0	15.0	12.2	2	53.5	45	29
ANSP 24102	♂	53.4	29.0	8.2	13.8	11.7	2	50.1	42	35
CNHM 81902	♂	51.9	27.3	7.7	12.1	11.2	3	36.1	20	21
ANSP 24106	♂	51.9	26.9	8.2	14.2	12.2	2½	45.2	38	21
ICNB Palacio	♂	50.7	24.7	8.2	14.0	12.8	2	47.8	26	25
MVZ 62991	♂	50.5	28.3	7.8	11.3	11.5	3½	45.4	25	23
ANSP 24104	♂	48.1	26.2	7.6	11.0	10.7	3	40.6	23	14
MVZ 62978	♂	47.9	24.4	7.4	10.4	12.1	2½	34.8	32	26
ANSP 24110	♂	47.2	25.0	7.1	12.0	11.1	1½	—	17	19
MVZ 62954	♂	46.8	26.6	7.5	10.8	10.8	3	38.8	14	12
ANSP 24105	♂	46.4	24.7	7.6	11.2	10.9	2½	48.8	44	25
CNHM 81901	♂	46.4	24.6	7.1	11.0	10.0	2½	37.3	6	14
ANSP 24109	♂	45.2	24.7	7.0	10.8	10.2	2	38.8	21	21
MVZ 62964	♂	45.1	24.1	7.1	10.6	10.2	3	26.1	15	24
ANSP 24107	♂	44.9	24.9	7.1	10.2	10.2	3	30.9	17	15
MVZ 62989	♂	44.3	23.9	6.8	9.4	10.0	4	34.2	18	17
ANSP 24108	♂	43.7	23.9	6.8	10.2	9.8	2½	34.8	24	20
AMNH 20390	♂	43.1	23.7	6.8	10.8	10.0	3	27.2	19	14
MLaS 2b	♀	68.4	38.2	10.5	16.0	13.6	3½	56.2	49	17
ICNB Mons.-Arrayan	♀	68.0	38.0	9.3	12.2	13.2	3½	55.2	31	23
MLaS 2a	♀	67.7	34.0	10.7	16.2	14.3	2	56.0	50	30
ICNB Palacio	♀	61.6	33.4	9.3	13.0	14.6	4	—	41	27
CNHM 81907	♀	61.0	36.7	8.9	13.2	12.2	4½	37.0	17	18
CNHM 81908	♀	57.0	31.7	8.2	12.6	11.3	4	49.0	22	21
AMNH 20392	♀	56.1	33.3	8.1	11.8	12.0	4	—	17	21
MVZ 62990	♀	55.9	31.0	8.0	12.1	12.1	4	—	26	13
ANSP 24111	♀	55.7	32.6	8.3	11.8	12.0	4	—	38	20
ICNB Palacio	♀	54.2	29.8	8.4	13.0	12.2	3½	45.8	41	23
ANSP 24103	♀	53.6	30.2	8.0	11.0	11.0	4	43.8	27	27
CNHM 81906	♀	52.8	29.0	8.1	12.3	10.8	3	41.0	18	22
MVZ 62977	♀	51.8	29.2	6.9	10.4	10.9	5	—	14	25
MVZ 62992	♀	50.7	27.6	7.4	10.4	11.7	4½	43.8	14	16
MNHN 7815	♀	50.4	29.7	—	10.3	10.8	3	—	22	17
AMNH 20398	♀	50.1	29.7	7.4	10.8	11.0	4	—	14	17
AMNH 20387	♀	50.0	28.4	7.8	11.0	11.3	4	—	24	17
ICNB Palacio	♀	50.0	28.0	7.7	11.2	11.2	3	44.2	31	20
MVZ 62993	♀	49.7	26.1	7.7	11.2	11.7	4	37.9	15	20
AMNH 20396	♀	47.6	25.7	7.5	10.4	11.2	4	—	15	20
AMNH 20388	♀	47.4	26.4	7.5	10.7	10.7	3½	34.0	29	18
AMNH 20383	♀	43.8	24.3	7.0	10.2	9.8	2½	—	20	18
CNHM 81903	♀	39.9	22.3	6.6	9.7	9.3	4	27.0	23	14

Individuals from San Miguel are the most aberrant of the material examined. They are very large with especially large hands and feet and very high numbers of maxillary teeth. They also have much longer limbs than other *adspersa*. In other characters they closely resemble typical *adspersa*. The San Miguel material may represent a distinct species, but because of proximity of locality and similarity in most characters, we assign it to *adspersa*.

Dunn (1944) assigned the material from San Miguel, Aguadita, and Tequendama Falls to *Oedipus andicola*. We have examined many *adspersa* and are unable to distinguish the material from these localities from "typical" *adspersa*. Dunn said the material differed from *adspersa* in being larger (males to 70 standard length, versus males to 53, females to 70 in *adspersa*), in being uniform above or with a broad light dorsal band, and in having limb intervals of 2 (versus 4 to 5 in *adspersa*). The size character will partially separate the material from *adspersa*, but examination of Table 4 shows that sharp breaks are seen only with males, and many Aguadita specimens are similar in size to *adspersa* from other areas. The other characters are of no value, and final determination of the systematic status of this material must await collection of additional specimens from the critical intermediate regions. We consider the material to be representative of a considerably variable species (*adspersa*).

The status of *Geotriton andicola* (= *adspersa*) has recently been discussed (Wake and Brame, 1962). We have since examined additional material and remain convinced that the description of Posada Arango (1909) fits that of *adspersa* more closely than any other Colombian salamander. Should the material from San Miguel prove to be representative of a species distinct from *adspersa*, the name *andicola* may be available for it.

According to Dunn (1944), Stebbins and Hendrickson (1959), and information accompanying some of the specimens, *adspersa* is a ground-dweller usually found at relatively high elevations in very moist situations. Stebbins and Hendrickson describe the habitat of their material in some detail.

The species is apparently oviparous (Nicéforo María, 1958; see also comments concerning habits of *Bolitoglossa savagei*) despite reports of viviparity and ovoviviparity by Peters (1863) and Posada Arango (1909).

Material of *adspersa* from certain localities near Bogotá mentioned by Dunn (1944) and Werner (1900) has been unavailable for study. All localities were in the Departamento de Cundinamarca. Nicéforo María informs us that some of the collection of the Instituto de La Salle was destroyed in rioting in 1948. Possibly some of the material mentioned by Dunn was lost at that time.

Range—Cordillera Oriental, central Colombia (Fig. 23).

***Bolitoglossa nicefori* NEW SPECIES**

Figures 18 and 26

Bolitoglossa adspersa (part) Nicéforo María, 1958. Bol. Inst. La Salle, 45(198): 12.

Holotype—MLaS 4; an adult male from 14 km. N. San Gil, 1500 meters (4900 feet), Departamento de Santander, Colombia, collected by Hermano Nicéforo María. The species is known only from the holotype.

Diagnosis—A medium-sized species (46.8 standard length) with moderate numbers of maxillary teeth (37) distinguished from all South American species by its exceptionally wide head (standard length 5.4 times head width); distinguished further from *adspersa*, *hypacra*, *savagei*, and *vallecula* by its more fully webbed hands and feet and coloration (ground color lead black with some gray-white indistinct markings); from *capitana* by its smaller size; from *biseriata* and *pandi* by its extensive dark coloration.

Description of the holotype—Adult male, snout of moderate length, broad and truncate; nostril small, labial protuberances of nasolabial groove pronounced, white tipped; canthus rostralis indistinct. Mental hedonic gland faintly indicated. Head broad; standard length 5.4 times head width; standard length 3.8 times snout-gular fold length. Deep groove below eye extends full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, moderately protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 2.5 mm., sharply proceeds ventrally at level of posterior end of mandible and extends across gular area as poorly defined depression parallel to and 3.8 mm. anterior to gular fold. Vomerine teeth 29, in irregular slightly patched series extending to lateral borders of internal nares. Maxillary teeth 37, extending posteriorly to point about three-fourths diameter of eye. Three premaxillary teeth, piercing lip. Testes bilobed, unpigmented. Trunk moderately robust. Tail 0.91 times standard length; robust and almost round in cross-section, tapering rapidly to tip. Post-iliac gland pronounced, light gray. Moderately robust limbs of moderate length; limb interval 3; standard length 4.3 times right fore limb; standard length 4.3 times right hind limb. Hands and feet small; standard length 10.9 times right foot. Webbing of hands and feet extensive; slightly more than terminal phalanges of finger and toe 3 free from webbing; webbing of other digits virtually complete, but extreme tips protrude. Digits only moderately flattened, with rounded points at tips. Subterminal pads slightly developed. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 8.7; snout to gular fold (head length) 12.2; head depth at posterior angle of jaw 4.2; eyelid length 3.2; eyelid width 1.9; anterior rim of orbit to snout 4.0; horizontal orbital diameter 2.6; interorbital distance 2.9; distance between vomerine teeth and parasphenoid tooth patch 0.3; snout to fore limb 16.3; distance separating internal nares 2.2; distance separating external nares 2.6; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 46.8; snout to anterior angle of vent 43.7; axilla to groin 23.9; tail length 42.6; tail width at base 4.7; tail depth at base 4.7; fore limb length 10.9; hind limb length 10.9; width of right hand 3.4; width of right foot 4.3.



Fig. 18. *Bolitoglossa nicefori* MLaS 4, San Gil, Colombia. Female. Holotype.

Coloration in alcohol: dorsal ground color of head, trunk, tail, and limbs lead black with suffused faded gray-white spots of irregular size concentrated between and behind the eyes on the head, just lateral to the midline on either side of the trunk, and in heavy concentrations on the tail and proximal limb surfaces. Ground color of ventral surfaces slightly lighter than that of dorsal surfaces, gray-black. Low concentration of faded moderate-sized guanophores on all ventral surfaces.

Remarks—The single example of *nicefori* was collected about 80 cm. above the ground in a bromeliad on a coffee plantation at moderate elevations. Its proportionately very broad head and its extensively, but not fully, webbed hands and feet distinguish it from *savagei*, which occurs to the north, and *adspersa*, which occurs to the south. It has been confused with *adspersa*, but apparently occurs at much lower elevations and in different habitats than *adspersa*. The foot of *nicefori* has been illustrated by Wake and Brame (1963).

We have named the species in honor of Hermano Nicéforo María, who, through efforts on our behalf, has made this study of South American salamanders possible.

Range—Cordillera Oriental, north central Colombia (Fig. 23).

***Bolitoglossa capitana*, NEW SPECIES**

Figures 19 and 26

Bolitoglossa andicola Nicéforo María, 1958. Bol. Inst. La Salle, 45(198): 11.

Holotype—MLaS 1a; an adult female from Hacienda La Victoria between Albán and Sasaima, 1780 meters (5840 feet), in the Cordillera Oriental about 50 km. NW. Bogotá, Departamento de Cundinamarca, Colombia, collected by Hermano Nicéforo María.

Paratypes—MLaS 1, MLaS 1b, same data as holotype; CNHM 132986, W. Albán, Departamento de Cundinamarca, Colombia, collected by Nicéforo María.

Diagnosis—A large species (4: 64.4-79.2-85.5) with large numbers of maxillary teeth (4: 57-72-87) distinguished from *adspersa*, *hypacra*, *savagei*, and *vallecula* by its large size, almost fully webbed hands and feet, and uniform lead black dorsolateral coloration; from *biseriata*, *borburata*, and *pandi* by its size and coloration; from *nicefori* by its size, relatively narrower head, and more maxillary and vomerine teeth.

Description of the holotype—Adult female, snout of moderate length, blunt tipped; nostrils moderately small, labial protuberances moderate; canthus rostralis arched, moderately well defined. Standard length 6.7 times head width; standard length 5.1 times snout-gular fold length. Well defined groove below eye follows curvature of eye, does not extend full length of eye opening, does not communicate with lip. Eye of moderate size, moderately protuberant. Upper eyelids very large. Moderately well defined postorbital groove extends

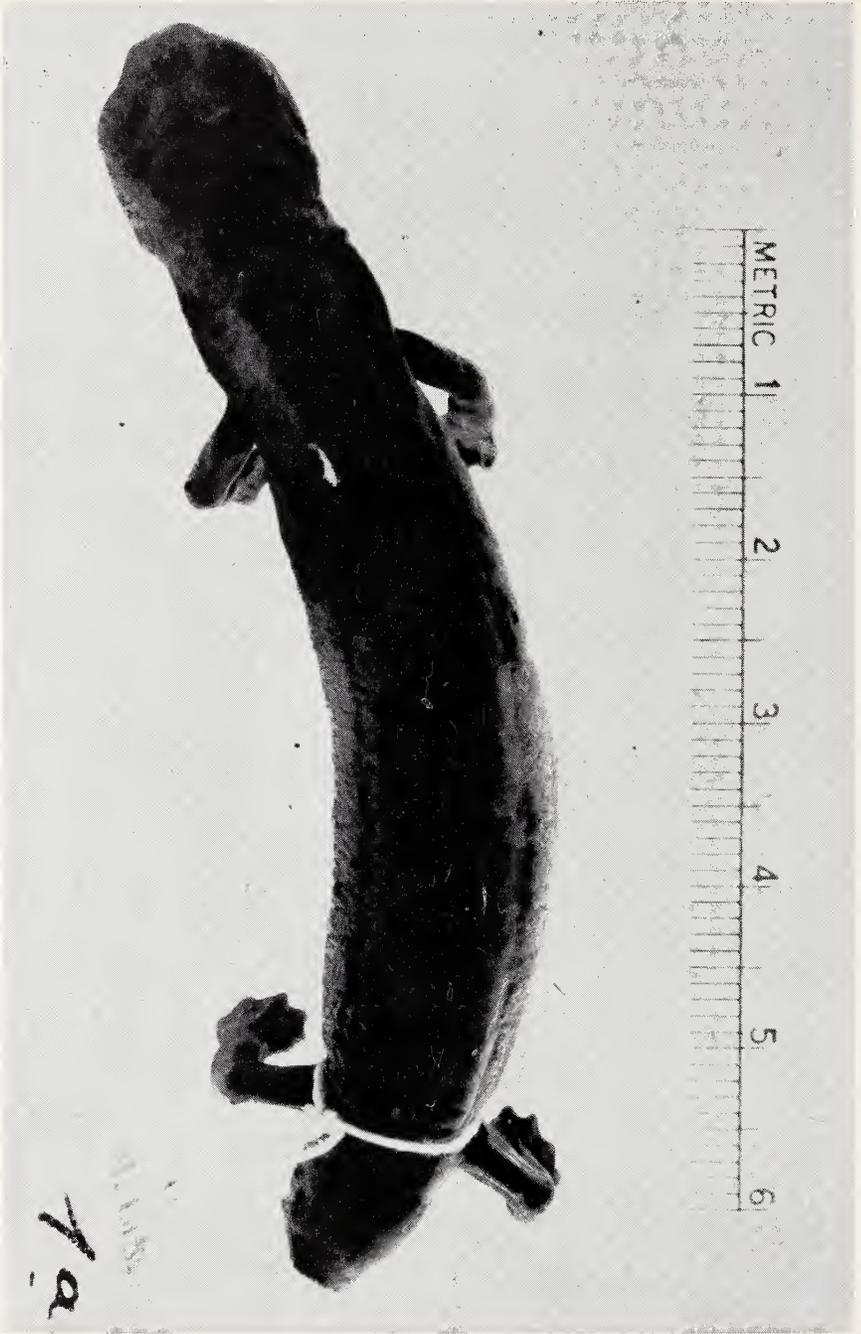


Fig. 19. *Bolitoglossa capitata* MLaS 1a, Hacienda La Victoria, Colombia. Female. Holotype.

posteriorly from eye as small depression for 4.4 mm., sharply proceeds ventrally at level of posterior end of mandible and extends across gular area parallel to and 5.8 mm. anterior to gular fold. Vomerine teeth 31, in series extending well beyond lateral border of internal nares. Maxillary teeth 80, extending posteriorly nearly to posterior border of eyeball. Premaxillary teeth 7, not piercing lip. Robust tail constricted at base, slightly compressed laterally. Post-iliac spot large and clearly discernible. Robust limbs of moderate length; limb interval 4; standard length 5.3 times right fore limb, 4.8 times right hind limb. Webbing of hands and feet extensive and thickened; virtually complete but web emarginate between all digits. Digits moderately flattened; not well defined except at tips. Tips of all digits rounded points that extend from webbing. Small, poorly defined subterminal pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 12.3; snout to gular fold (head length) 16.2; head depth at posterior angle of jaw 5.4; eyelid length 5.0; eyelid width 3.1; anterior rim of orbit to snout 4.8; horizontal orbital diameter 3.3; interorbital distance 3.3; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to fore limb 22.4; distance separating internal nares 3.0; distance separating external nares 4.2; snout projection beyond mandible 1.1; snout to posterior angle of vent (standard length) 82.3; snout to anterior angle of vent 76.4; axilla to groin 45.5; tail length 57.5; tail width at base 6.8; tail depth at base 7.2; fore limb length 15.5; hind limb length 17.0; width of right hand 5.7; width of right foot 7.2.

Coloration in alcohol: ground color of dorsal and lateral surfaces of head, trunk, and tail uniform lead black; venter gray-black, palms of hands and feet, lower edge of lower eyelids, and labial protuberances whitish. Limbs uniform lead black dorsally and ventrally. Post-iliac spots large, light, and well defined.

Variation—Pertinent counts and measurements of the type series are listed in Table 5. The single male is considerably smaller (64.4 standard length) than the three females (82.3-85.5 standard length). In *Bolitoglossa* females are normally larger than males. Heads are relatively narrow (standard length 6.7-7.4 times head width). Limbs of all are relatively short (limb interval 3-4). *B. capitana* has more maxillary teeth (mean 72) than other South American species and vomerine teeth are numerous (4: 28-33-37). Vomerine teeth are in long curved series that extend beyond the lateral edges of the internal nares. No significant variation in webbing of hands and feet or in coloration from that described for the holotype is discernible. All have virtually fully webbed hands and feet, and all are colored a uniformly dark black.

Remarks—Nícéforo María (1958) presented a photograph of MLaS 1a (then numbered MLS 119). The foot of the holotype has been illustrated by Wake and Brame (1963).

The name *capitana* was derived from the Latin, *capitaneus* (chief in size), and refers to the fact that the species is the largest known to occur in South America.

Range—Cordillera Oriental, central Colombia (Fig. 23).

Bolitoglossa pandi, NEW SPECIES

Figure 20C

Holotype—ZSZMH 2858; an adult female from Pandi, 1300 meters (4260 feet), Departamento de Cundinamarca, Colombia, collected by Wilhelm Fritsche, September 19, 1913. The species is known only from the holotype.

Diagnosis—A medium-sized species (50.4 standard length) with moderate numbers of maxillary teeth (39) distinguished from *hypacra*, *savagei*, and *vallecula* by its extensively webbed hands and feet and distinctive coloration (solid dark reddish-gray dorsally with cream spots ventrally); from *adpersa* by extensive webbing of hands and feet and presence of prefrontal bones; from

TABLE 5. Data on *Bolitoglossa biseriata*, *B. pandi*, *B. nicefori*, *B. capitana*, and *B. borburata*

		Snout - Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa biseriata</i>										
USNM 145657	♂	36.7	21.9	6.0	8.4	8.8	4	29.2	33	24
USNM 145656	♂	48.7	27.3	7.2	10.2	11.2	3	45.2	54	28
<i>Bolitoglossa pandi</i>										
ZSZMH 2858	♀	50.4	28.6	7.8	11.0	10.3	2	—	39	20
<i>Bolitoglossa nicefori</i>										
MLaS 4	♀	46.8	23.7	8.7	10.9	12.2	3	42.6	37	25
<i>Bolitoglossa capitana</i>										
MLaS 1b	♂	64.4	35.7	9.6	13.4	13.9	3	53.2	57	28
CNHM 132986	♂	85.5	49.1	11.5	18.3	17.3	3½	—	62	37
MLaS 1	♂	84.4	47.2	12.5	18.4	16.8	4	70.8	87	34
MLaS 1a	♂	82.3	45.5	12.3	17.0	16.2	3½	57.5	80	31
<i>Bolitoglossa borburata</i>										
UMMZ 113870	♂	47.9	26.5	7.2	10.3	10.7	3	46.9	49	21
UMMZ 113870	♂	47.6	26.4	7.9	11.2	11.3	3	42.4	57	22
UMMZ 113872	♂	45.0	24.1	7.7	11.1	11.0	3	40.8	49	23
UMMZ 122386	♂	41.4	23.1	7.6	10.4	9.9	—	—	37	18
UMMZ 113870	♂	38.0	21.3	6.7	9.2	10.0	3	—	53	19
UMMZ 113872	♂	62.9	35.2	9.8	13.7	14.0	3½	56.0	64	33
UMMZ 113870	♂	58.0	32.4	9.2	13.8	13.2	3	49.0	61	22
UMMZ 113870	♂	56.3	31.4	9.3	13.2	13.2	4	37.2	61	23
USNM 115509	♂	56.2	29.8	8.4	11.7	13.1	—	—	71	23
UMMZ 113871	♂	54.0	28.7	8.7	13.0	12.3	4	38.5	63	32
BM 1920.1.20.3726	♂	50.5	27.7	8.2	10.7	11.5	4	43.8	50	20
UMMZ 113870	♂	45.9	23.9	7.6	10.3	11.1	3	—	52	33
UMMZ 113870	♂	33.2	17.5	5.6	7.9	8.2	3	—	31	18

biseriata by slightly less webbing and absence of a biseriata color pattern; from *capitana* by smaller size and reddish-gray rather than black ground color; from *nicefori* by narrower head and coloration.

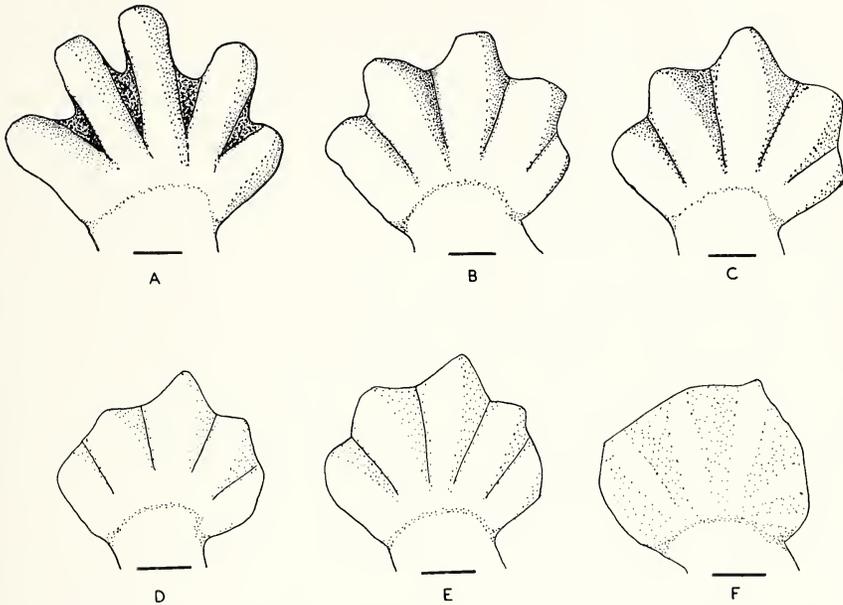


Fig. 20. Left Hind Feet. Outlines drawn through use of microprojector. Line equals 1 mm. A. *Bolitoglossa valleculea* MLaS 8e, Yarumal, Colombia. Male. B. *B. savagei* UMMZ 45618, Cerro San Lorenzo, Colombia. Male. C. *B. pandi* ZSZMH 2858, Pandi, Colombia. Female. Holotype. D. *B. altamazonica* CNHM 78394, Cosñipata, Peru. Male. E. *B. chica* EPN 2411, lower Río Bolaniguas, Ecuador. Male. F. *B. sima* JAP 2994, Cachavi, Ecuador. Female.

Description of the holotype—Adult female, head badly mutilated, snout moderately long and somewhat truncate. Skin removed from entire head region, except eyelids. Groove below eye following curvature of eye. Eye and eyelid moderate in size. Standard length 6.5 times head width; standard length 4.9 times snout-gular fold length. Vomerine teeth 20, in curved series extending beyond lateral borders of internal nares. Maxillary teeth 39, extending slightly beyond center of eye. Two premaxillary teeth. Moderate-sized, well defined prefrontals present on either side of skull. Prevomers appressed to each other posteriorly, where anterior prevomerine tooth series meet; bones separate anteriorly to encircle internasal glandular region, fail to meet again anteriorly. Processes of prevomer form posterior margin of internal nares and extend lateral to lateral border of nares; bear vomerine teeth. Premaxillae fused; frontal processes long, extending posterior to point slightly beyond orbital margin; processes slightly dilated posteriorly. Nasals moderate for genus, trianguli-

lar with most acute angle posterior in position. Trunk vertebrae lack basiphysal accessory processes. Trunk distended by presence of enlarged ova and greatly enlarged oviducts. Tail very short, regenerated. Post-iliac gland evident, grayish-white. Limb length moderate; limb interval about $2\frac{1}{2}$; standard length 4.9 times right fore limb; standard length 4.6 times right hind limb. Webbing of hands and feet extensive with terminal phalanx of longest finger and toe relatively free from webbing (Fig. 20C). Digit tips rounded with borders sloping proximally to meet sloping border of adjacent digit at point approximately corresponding with the articulation of the terminal and penultimate phalanges of digits involved. Web formed primarily by fusion of expanded lateral borders of digits, but since lateral borders start expanding near tip, webbing extends almost to tip of all toes. Digits moderately discrete, somewhat flattened. Subterminal pads small, poorly developed. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 7.8; snout to gular fold (head length) 10.3; head depth at posterior angle of jaw 4.5; eyelid length 3.3; eyelid width 1.8; anterior rim of orbit to snout 3.2; horizontal orbital diameter 2.3; interorbital distance 2.8; distance between vomerine teeth and parasphenoid tooth patch 0.4; snout to fore limb 14.9; distance separating internal nares 1.9; snout to posterior angle of vent (standard length) 50.4; snout to anterior angle of vent 46.9; axilla to groin 28.6; fore limb length 10.3; hind limb length 11.0; width of right hand 3.7; width of right foot 4.8.

Coloration in alcohol: ground color of eyelids, dorsum of trunk and tail, and dorsal and proximal portions of limbs a solid but somewhat muted reddish-gray with a slight bluish cast. Small and indistinct unpigmented area near base of tail only modification of dorsal ground color. Ground color lightens ventrolaterally and ventrally. Large irregularly shaped pigmented areas ventrally on trunk, limbs, and tail, and on the small piece of intact throat skin at lateral edge of gular fold. Cream-colored ventral pigment due to presence of numerous chromatophores (possibly guanophores) that are concentrated primarily in the ventrolateral regions but are present over most of the venter, often occurring as individual cells. Cream chromatophores virtually absent dorsally, present only in small concentration above insertion of left fore limb. Hands and feet with some irregular unpigmented areas dorsally, essentially unpigmented ventrally.

Remarks—The holotype is in a very poor state of preservation. We hesitate describing the species from this single individual and have done so only because of its readily discernible distinctiveness. The specimen has been in the Hamburg Museum since 1913 catalogued under the name "*Spelerpes adspersus*." Because it was thought that the specimen was simply an example of that relatively common species, someone was allowed to dissect the head, probably to study the musculature. Surprisingly, color is remarkably well preserved.

The name *pandi* is derived from the name of the type locality. Fred Medem and J. R. Tamsitt have told us that the city of Pandi is in a relatively

dry region where one would ordinarily not expect to find *Bolitoglossa*. We were also told that it is hazardous to collect in the region due to unsettled political conditions, and our efforts to obtain additional material have failed.

Range—Cordillera Oriental, Central Colombia (Fig. 23).

DISCUSSION OF EVOLUTIONARY RELATIONSHIPS

Generic Relationships

Genus *Oedipina*

The genus *Oedipina* ranges from Guatemala to Ecuador and includes about 12 species.

Oedipina is represented in South America by two species, both known from Panamá, and it is likely that the genus is a relative newcomer to South America. The two species are found only in the lowlands of western Colombia and Ecuador. The genus as a whole has a much more limited South American distribution than *Bolitoglossa*. Both species, *complex* and *parvipes*, are members of the primitive section of the genus. They are fairly closely related to each other, and to the larger *elongatus* of Central America. The senior author is presently studying this genus and will discuss its relationships at a later date.

Genus *Bolitoglossa*

The genus *Bolitoglossa* ranges from southern Mexico to Brazil and Bolivia and includes about 50 species.

Bolitoglossa is represented in South America by 16 species, only one of which (*biseriata*) is known from Panamá. The genus is widely distributed in South America, and is known from very high elevations to sea level in both Atlantic and Pacific drainages.

The *Bolitoglossa* of South America fall into four groups. Three have been delimited earlier in this paper: the *phalarosoma*, *altamazonica*, and *palmata* groups. The fourth is something of a catchall and is not easily delimited, but all of its members show evidence of relationship. Definition of the fourth group is not attempted at this time, but, for convenience, it is called the *adspersa* group in the following account.

The *phalarosoma* group contains a single very distinctive species, *phalarosoma*. The combination of very narrow head, slender habitus, distinctive coloration, and fully webbed hands and feet separate it from all other South American species. Its relationships are obscure. Wake and Brame (1962) stated that it was probably related to *alvaradoi*, a Costa Rican species that resembles *phalarosoma* in coloration and in webbing of hands and feet. We have since examined additional examples of *alvaradoi* and, although small individuals resemble *phalarosoma* in coloration, habitus, and webbing of hands and feet, we are impressed by the many differences that separate the two species. In addition to the larger size, wider head, more maxillary teeth, and

more extensive light coloration of *alvaradoi* mentioned in our earlier paper, *alvaradoi* possesses well-developed basipophyseal accessory processes on the trunk vertebrae. These processes are absent in *phalarosoma*. The affinities of *alvaradoi* appear to be with *lignicolor* and its allies, but it also may be related to *phalarosoma*.

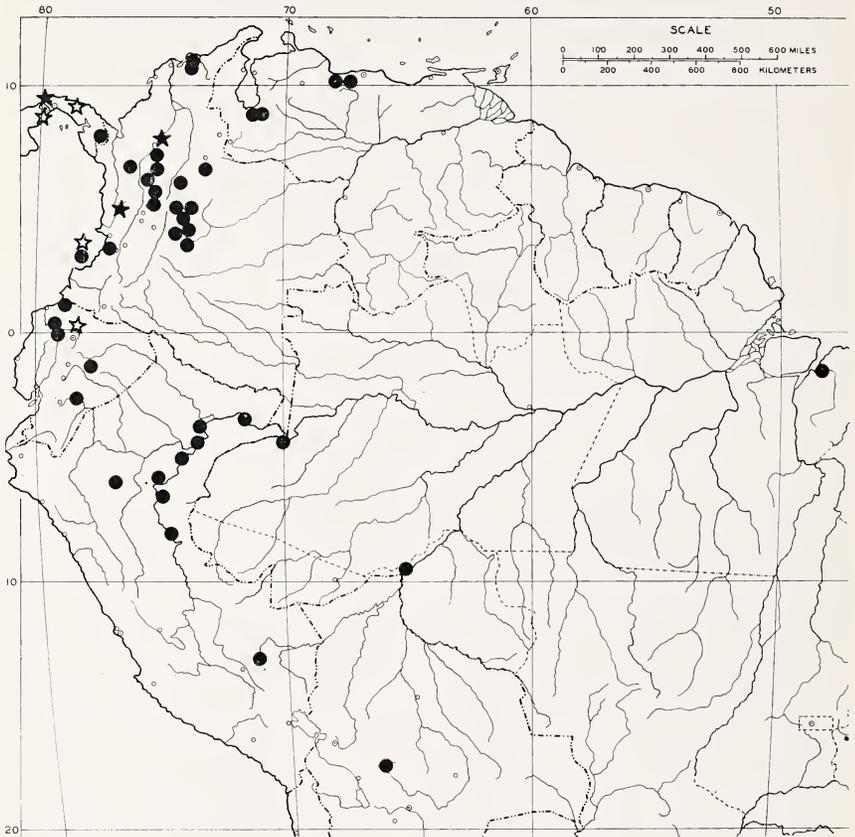


Fig. 21. Distribution of *Bolitoglossa* and *Oedipina* in South America. • *Bolitoglossa*; ★ *Oedipina* complex; ☆ *Oedipina parvipes*.

Several Central American species may be related to *phalarosoma*; these include *arborescendens*, *flaviventris*, and *platydactyla*. The unique holotype of *arborescendens* has a broader head, longer limbs, and more maxillary teeth than *phalarosoma*. The lighter belly and larger size of *flaviventris* separate it from *phalarosoma*. *B. platydactyla* is a much larger species with lighter coloration and slightly less webbing of hands and feet. Both *flaviventris* and *platydactyla* have basipophyseal accessory processes on their trunk vertebrae; no infor-

mation is available concerning *arborescandens*. *B. arborescandens* and *phalarosoma* resemble each other in slender habitus and webbing of hands and feet. The single *arborescandens* is solid dark-colored dorsally, but one specimen of *phalarosoma* is colored similarly. *B. flaviventris* and *platydactyla* are slender species with relatively narrow heads, and both have about the same numbers of maxillary teeth as *phalarosoma*. The color pattern of *flaviventris* is more similar to that of *phalarosoma* than is that of *platydactyla*. Hands and feet of *flaviventris* are extensively webbed, but are shaped a little differently than those of *phalarosoma*.



Fig. 22. Distribution of southern species of *Bolitoglossa* in South America.

We believe placement of *phalarosoma* in a separate species group is justifiable. Its relationships seem to be with Central American rather than South American salamanders, but we cannot name the closest relative.

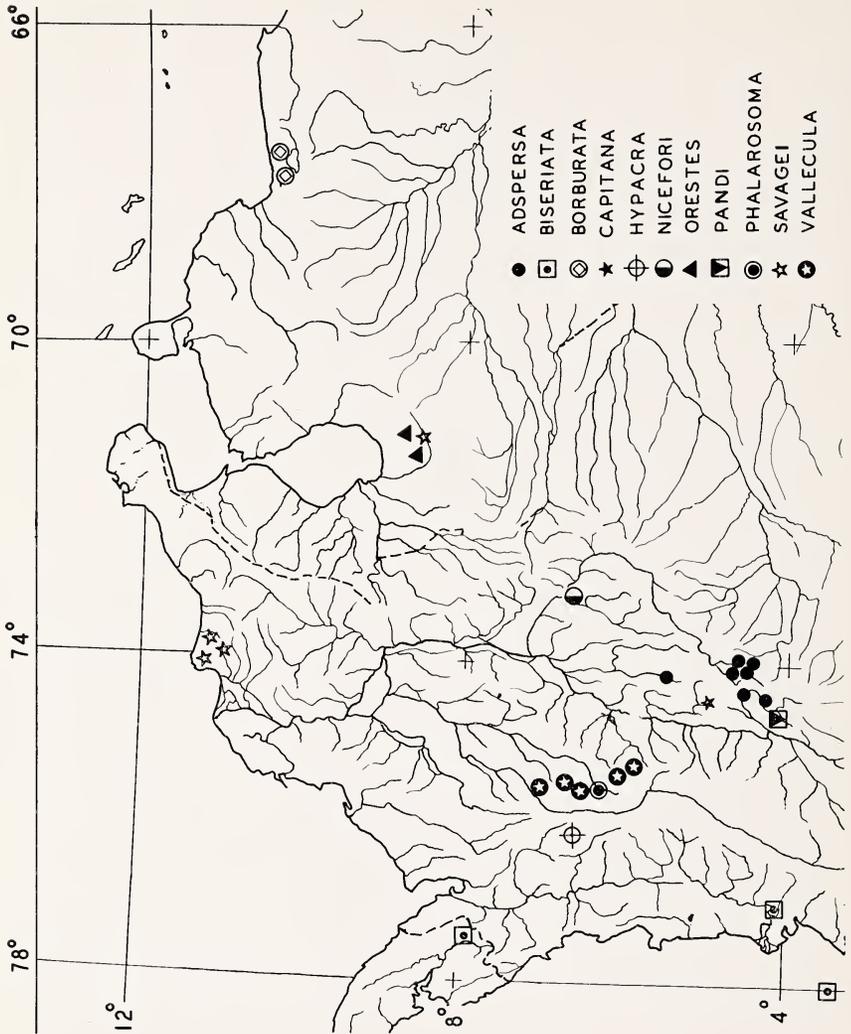


Fig. 23. Distribution of northern species of *Bolitoglossa* in South America.

The *altamazonica* group contains four species: *altamazonica*, *chica*, *peruviana*, and *sima*. The group may be related to *colonnea* of Central America, to *biseriata* of Panamá and Colombia, or to the *palmata* group.

The highly specialized *colonnea* resembles members of the *altamazonica* group in body proportions and in shape and extent of webbing of hands and feet, but differs in having a pronounced dermal interorbital ridge and a broader, shorter, and much more truncate snout. Few or no maxillary teeth are present in *colonnea*, as in *chica*. Prefrontal bones are absent in *colonnea*, but present

in *sima*; no information is available concerning the other species of the group.

Relationship of *biseriata* to the *altamazonica* group is indicated by similarity of hand and foot shape, extent of webbing, limb length, and size. The head of *biseriata* is slightly broader and it has more maxillary teeth than the *altamazonica* group. Coloration of *biseriata* is very different than that of any of the *altamazonica* group. *B. biseriata* appears to be closer to members of the *adpersa* group than to the *altamazonica* group.

The *palmata* group differs markedly from the *altamazonica* group in hand and foot shape, type of webbing, and in having a noticeably shorter snout. Snouts of the *altamazonica* group are shortened, but not as greatly as those of the *palmata* group. The *palmata* group also has shorter limbs and tends to have more maxillary teeth. Both groups are relatively small and have relatively narrow heads.

B. sima and *altamazonica* are closely related. They resemble each other in numbers and arrangement of vomerine teeth, ventral coloration, and shape of hands and feet. *B. sima* has more maxillary teeth, a slightly broader head, and relatively larger hands and feet (standard length 9.2-10.6 times right foot, mean 9.7; versus 11.1-13.3, mean 12.0 in *altamazonica*) than *altamazonica*.

The relationship of *chica* to *peruviana* is similar to that of *sima* to *altamazonica*. In both instances one is a Pacific species (*chica*, *sima*) and one is an Amazonian species (*peruviana*, *altamazonica*). *B. chica* and *peruviana* resemble each other in size, proportions, shape and webbing of hands and feet, and numbers and arrangement of vomerine teeth. *B. peruviana* has many more maxillary teeth, however, and has somewhat smaller hands and feet (standard length 11.6-13.7 times right foot; versus 10.1-11.4 in *chica*). Apparently *peruviana* is darker-colored than *chica*.

B. chica resembles *sima* and *altamazonica* in general proportions, but differs in having fewer maxillary teeth, less fully webbed hands and feet, and lighter coloration. Its hands and feet are smaller than those of *sima*, but larger than those of *altamazonica*.

B. peruviana and *sima* resemble each other in most body proportions and in numbers of maxillary teeth. The head of *peruviana* is somewhat broader, and its hands and feet are smaller and less fully webbed than those of *sima*.

B. peruviana and *altamazonica* are similar in proportions, including head width and size of hands and feet, and apparently in coloration, but *peruviana* has more maxillary teeth and somewhat more fully webbed hands and feet.

In conclusion, the most generalized member of the *altamazonica* group may be *sima* which is the largest species and has the longest limbs, largest hands and feet, and the broadest head of the group. It also has relatively high numbers of maxillary teeth. The hands and feet of *sima* are more fully webbed than those of the other species, however, and the mottled color pattern may be specialized. The entire group is highly specialized, and is one of the more advanced groups of *Bolitoglossa*. A dendrogram illustrating the relationships within the *altamazonica* group is presented (Fig. 24).

The relationships of the *palmata* group have been discussed previously (Brame and Wake, 1962 b). The combination of greatly shortened snout and very distinctive, nearly fully webbed hands and feet separate the two species (*palmata* and *orestes*) from all other *Bolitoglossa*. The relationships of the group may be either with the *adspersa* group, or with the *altamazonica* group. The hands and feet are more similar to fully webbed members of the *adspersa* group (e.g. *pandi*) than to any member of the *altamazonica* group, but do not resemble any other species closely. Both *orestes* and *adspersa* lack prefrontal bones, but we have so little information concerning presence or absence in other forms that it is difficult to relate species on that basis alone. All other South American species for which we have information (*borburata*, *pandi*, *savagei*, *sima*) have prefrontal bones. Size and general habitus of the *palmata* group may relate it to the *altamazonica* group. *B. palmata* and *orestes* are very closely related to each other, and are not obviously closely related to any other species.

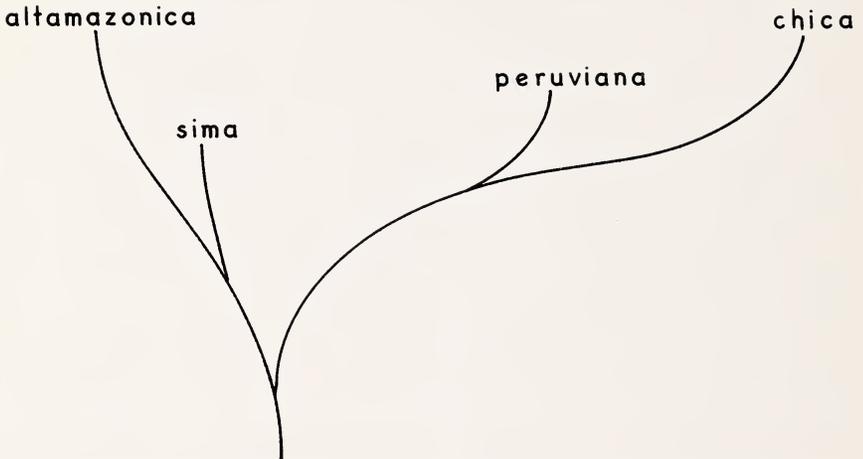


Fig. 24. Dendrogram illustrating relationships within the *Bolitoglossa altamazonica* group.

The *adspersa* group contains nine species: *adspersa*, *biseriata*, *borburata*, *capitana*, *hypacra*, *nicefori*, *pandi*, *savagei*, and *vallecula*. We cannot define the group at this time, but are convinced that all members are more closely related to other members of the group than to other South American salamanders. Certain species (*adspersa*, *borburata*, *savagei*, *vallecula*) are very closely related; the others are on the fringes of this core group.

One highland species, *hypacra*, is clearly related to southern Central American highland forms (*cerroensis*, *marmorea*, *subpalmata*). All have very little webbing, moderate numbers of teeth, and fairly similar proportions. We have previously discussed the relationship of *hypacra* to these Central American species (Brame and Wake, 1962 a). Apparently *hypacra* is the most gen-

eralized and primitive of the South American species. It has long limbs, relatively high numbers of teeth, and less webbing than any other South American species. It may be relatively close to *vallecula*, a somewhat smaller species with shorter limbs and only slightly more webbing of hands and feet.

A series of related species (*adpersa*, *borburata*, *savagei*, and *vallecula*) may have arisen from the same ancestral stock that gave rise to *hypacra* and its relatives. All are similar in size and proportions, including head width, and all have similar numbers of vomerine teeth that are similarly arranged. Several trends are evident in this series. Very little webbing is present in *vallecula*, but webbing increases in amount in *adpersa* and *savagei*, and reaches a maximum in the nearly fully webbed *borburata*. Maxillary teeth increase in number from the relatively low numbers of *adpersa* (mean 27) to the increasingly higher numbers of *vallecula* (44), *savagei* (48), and *borburata* (57). Limb length varies from relatively long in *vallecula* to moderate in *savagei* and *borburata* to relatively short in *adpersa*. A tendency for light dorsal banding is best developed in *borburata*, least developed in *adpersa*, and intermediate in development in *vallecula* and *savagei*. On the basis of relatively long limbs and very little webbing of hands and feet, we think *vallecula* is the most primitive of the series. The advanced end is not determined. *B. borburata* has specialized coloration and extensive webbing, but *adpersa* has reduced numbers of maxillary teeth (presumably advanced) and lacks prefrontal bones. *B. borburata* has high numbers of maxillary teeth (presumably primitive) and has well-developed prefrontal bones. Prefrontals are present in *savagei* as well, and appear to be present in two partially dissected *vallecula*. Our ideas concerning relationships of these four species may be clarified by the accompanying dendrogram (Fig. 25).

The relationship of *vallecula* to *savagei* is close. Both are very similar in size, proportions, and numbers of maxillary teeth, but limbs of *vallecula* appear to be slightly longer and its hands and feet are less fully webbed than those of *savagei*. There is a tendency for light ventral pigmentation in both, but the tendency is stronger in *vallecula* than in *savagei*.

B. savagei and *borburata* are also closely related. The two species resemble each other in most characters but differ in amount of webbing of hands and feet, and in coloration. *B. borburata* has almost fully webbed hands and feet, while those of *savagei* have less webbing. *B. borburata* has flattened digits with pointed tips, but *savagei* has more robust, rounded digits with rounded to more or less truncate tips.

B. borburata is much closer to *savagei* than to *vallecula*. *B. vallecula* is a little smaller, has slightly longer limbs, and has somewhat fewer maxillary teeth than *borburata*. Light ventral pigmentation, universally present in *vallecula*, is not found in *borburata*, and *borburata* has far more extensively webbed hands and feet.

As is evident from the accompanying graph (Fig. 14), *adpersa* has fewer maxillary teeth than either *vallecula* or *savagei*. The hands and feet of *adpersa*

are somewhat intermediate in amount of webbing between *savagei* and *vallecula*. The color pattern of *adspersa* is very different from that of the other three species of the series. *B. adspersa* may be an offshoot from the main line that gave rise to *vallecula*, *savagei*, and *borburata*.

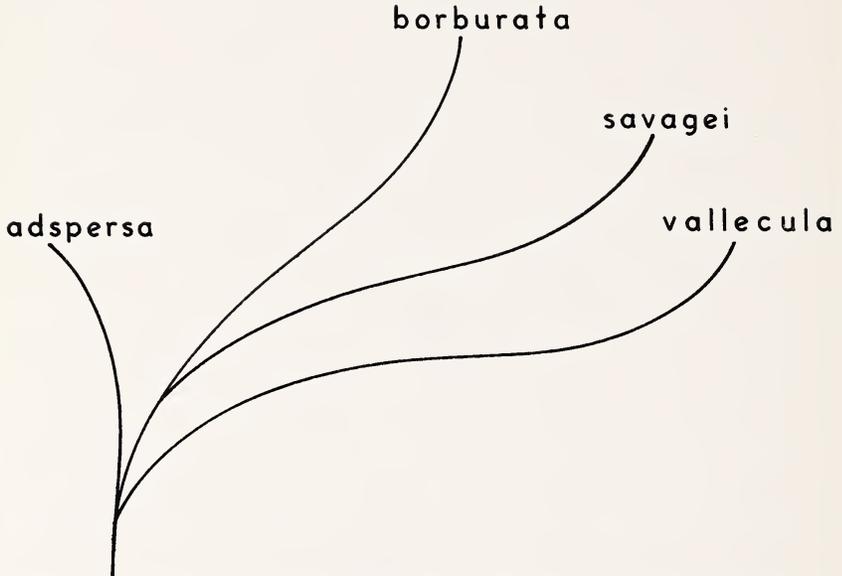


Fig. 25. Dendrogram illustrating relationships of four species of the *Bolitoglossa adspersa* group.

Within the series of four closely related species discussed above, the presumed gap, based on webbing, separating the old generic groupings (*Magnadigita* and *Bolitoglossa*) of Taylor (1944) has been bridged. According to the characters proposed by Taylor it would be necessary to place *vallecula* in *Magnadigita*, and *borburata* in *Bolitoglossa*. *B. adspersa* and *savagei* are intermediates, however, and the sequence of closely related forms, *vallecula* to *savagei* to *borburata*, very nicely joins the two webbing types.

We once stated that *borburata* was closely related to *lignicolor* of Panamá and Costa Rica (Brame and Wake, 1962 b). Although the two may be related we are no longer as convinced of close relationship as we were earlier. The two species resemble each other in a general way in regard to coloration. Both have prefrontal bones and extensively webbed hands and feet. There are, however, numerous differences. *B. lignicolor* is much larger and has far fewer maxillary teeth than *borburata*. The hands and feet of both are extensively webbed but are otherwise not similar. The digits of *lignicolor* are thick and heavy, and are joined by a thin web, but the entire foot of *borburata* is thin and flattened. Enlarged dermal glandules are present dorsally in *lignicolor*, but such glandules appear to be absent in *borburata*. Osteological differences also separate the two

species. The vomers of the two species are not similar. Well-developed basiphyseal accessory processes are present on the trunk vertebrae of *lignicolor*, but are only faintly indicated in *borburata*. *B. lignicolor* appears to be more closely related to *alvaradoi*, *yucatanana*, and possibly *striatula* than to *borburata*.

The relationships of *biseriata* are not clearly defined. Tanner (1962) was handicapped by having only a single immature specimen with which to work. He thought the species was close to the *rufescens* group and compared it with *rufescens*, *occidentalis*, *colonnea*, *palustris*, *yucatanana*, and *striatula*. We have seen more material and suggest that the species is, instead, related to South American forms. It is a larger species than *rufescens* and *occidentalis* and has many more maxillary teeth than either of these species or than *colonnea*. It is possible that *biseriata* may be related to *striatula*. *B. striatula* resembles *biseriata* in having flattened, fully webbed hands and feet, moderate numbers of maxillary teeth, moderate numbers of vomerine teeth in series that are patched laterally, enlarged dorsal glandules, and extensive light pigmentation. *B. striatula* is a larger species, however, and differs greatly from *biseriata* in color pattern and details of coloration.

It is possible that *biseriata* is related to *vallecula*, *savagei*, and *borburata*. All have similar proportions, and *biseriata* is only a little smaller and has but slightly fewer maxillary teeth than the others. Trends toward light-colored wash-like dorsal bands, light pigmented ventral surfaces of trunk and tail, and increasing amounts of webbing of hands and feet have been noted earlier. It can be argued that all three trends reach a culmination in *biseriata*, but other characters dictate against such a relationship. The coloration of *biseriata* differs markedly from that of the other species, and the very flattened, fully webbed hands and feet bear no resemblance to those of *vallecula* and *savagei*.

In its tendency for reduced size, slightly reduced numbers of maxillary teeth, and its very flattened, fully webbed hands and feet, *biseriata* resembles the *altamazonica* group. It is possible that *biseriata* is on the borders of both the *adpersa* and *altamazonica* groups, forming a link between them.

The relationships of the three remaining members of the *adpersa* group, *capitana*, *nicefori*, and *pandi*, are enigmatic. *B. nicefori* is fairly close to *adpersa*, but differs in having a broader head, and more fully webbed and differently shaped hands and feet. The color pattern of the single *nicefori* differs from that of any seen in *adpersa*. Only a single aberrant specimen of *vallecula* (MLaS 5a) has hands and feet that resemble those of *nicefori*. *B. nicefori* has a much broader head than any other South American salamander, and again the only specimen that even approaches it in this character is the single *vallecula* mentioned above. We suggest that the relationships of *nicefori* lie with *adpersa*, and possibly with *vallecula*.

The relationships of *pandi* are with other members of the *adpersa* group, but we cannot name its closest relative. It resembles the group as a whole in size, general proportions, and numbers of teeth, but its coloration is different than that seen in any other member of the group, and it has more fully webbed

hands and feet than *adspersa*, *hypacra*, *savagei*, and *vallecula*. The hands and feet of *pandi* are shaped differently than those of *nicefori* and *borburata*, and it is much smaller than *capitana* and has far fewer teeth. All *adspersa* skeletons (7) examined by us lack prefrontal bones, but well-developed prefrontals are present in *pandi*.

The relationships of the large *capitana* are rather puzzling. In gross structure it resembles *robusta*, a large Central American species with uniform dark blackish coloration, many maxillary and vomerine teeth, and robust limbs of moderate length. Both lack basipophyseal accessory processes on the trunk vertebrae. *B. robusta*, however, is considerably larger than *capitana*, has a proportionately broader head, and has as little webbing as any member of the genus. *B. capitana* has nearly fully webbed hands and feet. *B. capitana* resembles *schmidti* of Honduras in size, webbing, and habitus, but *schmidti* has a broader head, fewer maxillary teeth, and has a color pattern of mottled black on gray. *B. adspersa* and *capitana* may be related. Proportions are similar in the species, but *capitana* has more maxillary teeth than any other South American species, while *adspersa* has fewer than any other member of its group. The hands and feet of *adspersa* have less webbing than those of *capitana*. Although we do not know its closest relative, *capitana* may be close to the ancestral stock that gave rise to the *adspersa* group. The main argument against this idea is the extensive webbing of the hands and feet found in *capitana*. Support for the idea is found in the generalized characters of *capitana* (size, numbers of teeth, coloration) and its resemblance to *robusta*, a generalized species that may be close to the ancestral stock of the *adspersa* group.

To summarize, four species groups of *Bolitoglossa* occur in South America. The relatively primitive *adspersa* group contains the presumably primitive *hypacra*, near the ancestral stock, and a series of closely related species, *adspersa*, *borburata*, *savagei*, and *vallecula*. Three species, *capitana*, *nicefori*, and *pandi*, are related to this series, but the relationship is not clear. *B. biseriata* is located on the borders of this group. Only two, the relatively advanced *biseriata* and *borburata*, are lowland forms; the remainder occur at moderate to high elevations.

Four specialized lowland species, *altamazonica*, *chica*, *peruviana*, and *sima*, comprise the *altamazonica* group. This advanced group may be linked with the *adspersa* group through *biseriata*.

Two specialized highland species, *palmata* and *orestes*, represent the *palmata* group. The affinities of this group may be with either the *adspersa* or the *altamazonica* group, or with both.

Set apart from all other South American species is the slender Colombian form, *phalarosoma*, whose affinities are with Central American species.

Origin of the South American Salamander Fauna

Salamanders occur predominantly in the Northern Hemisphere, and in tropical regions they have been successful only in the Americas, where an extensive radiation has taken place in the family Plethodontidae. Fossil records

of salamanders are totally lacking in Central and South America, but it seems evident that plethodontids have had northern origins and are to be considered members of the Old Northern Herpetofaunal Element (Dunn, 1931; Savage, 1960). Savage (1960) has discussed the historical and present association of this element with the Arcto-Tertiary Geoflora (for general discussion of geoflora development see Axelrod, 1960). The family Plethodontidae in North America today is associated primarily with derivatives of the Arcto-Tertiary Geoflora. The specialized neotropical plethodontid genera are separated from the North American genera by the semi-arid to desert regions of northern Mexico and southwestern United States. While the neotropical genera are associated in part with relicts and disjuncts of the Arcto-Tertiary Geoflora, it is significant that many species of these genera are closely associated with derivatives of the Neotropical-Tertiary Geoflora. Since the neotropical salamander genera have obvious northern affinities it is of interest to attempt an estimation of the date at which entrance into the neotropical region occurred and at which the association with Neotropical-Tertiary Geofloral elements began.

Dunn (1926) believed migration of salamanders southward took place in late Miocene to Pliocene, but he did not elaborate on this statement. Martin and Harrell (1957), in an attempt to explain the disjunct occurrence of certain identical and/or paired-species of trees and shrubs in eastern United States and the Mexican highlands, concluded that disjunctions occurred in pre-Pliocene rather than Pleistocene times, and they cited plethodontid distribution as a portion of their indirect evidence. Martin and Harrell stated that a continuous forest corridor is necessary for plethodontid dispersal, and, since the genera of neotropical plethodontids are in their opinion morphologically diverse, they concluded that entrance into the neotropical region and separation from the northern representatives of the family antedated the Pleistocene and was probably pre-Pliocene.

Axelrod (1960) reviewed the development of the major Tertiary geofloral patterns. At the beginning of Tertiary the Neotropical-Tertiary Geoflora formed a world-wide broad tropical belt that extended as far north as southwest Alaska on the West Coast of North America, and possibly to Nova Scotia on the East. The Arcto-Tertiary Geoflora formed a broad belt of temperate coniferous and deciduous hardwood forests north of this region. In the region where the two major geofloras met there was a mixing of elements resulting in the formation of what Axelrod calls a broad "ecotone." This "ecotone" formed in Middle Cretaceous, and probably extended southward along low mountains into Mexico during Cretaceous and early Eocene. Axelrod explains that high mountains were not required for southward migration because climatic zonation was weaker than today. Because the high latitudes were climatically mild, the tropics were probably cooler than today (in order to maintain the normal heat budget of the earth), and this effect facilitated southward movement of warm-temperate types along low mountains. The disjuncts discussed by Martin and Harrell (1957) could have moved south at this time. Today these Arcto-

Tertiary disjuncts in Mexico live with warm temperate to subtropic plants, and this relation is typical of the ancient Arcto-Tertiary-Neotropical-Tertiary "ecotone." The northern borders of the tropics began to shift toward the equator in early Tertiary as a result of a general cooling trend. At this same time the Madro-Tertiary Geoflora developed *in situ* in western and southwestern United States and northern Mexico, in response to a general Tertiary drying trend. This geoflora expanded steadily from late Eocene and Oligocene through Miocene and Pliocene, and resulted in the present-day semiarid woodland, chaparral, thorn forest, arid scrub, desert grassland, and desert vegetation of southwestern North America. Axelrod thinks the disjunctions of Arcto-Tertiary plants developed during Eocene, and predate development of the intervening dry zone. He finds no evidence of a humid temperate forest in the intervening area during Pleistocene.

Because of the findings concerning geofloral distributional patterns it has been necessary to reconsider the statements of Dunn (1926) and Martin and Harrell (1957) concerning plethodontid distribution. We suggest that plethodontids were primitively associated with elements of the Arcto-Tertiary Geoflora, and in early Tertiary, when the "ecotone" between the Arcto-Tertiary and Neotropical-Tertiary Geofloras was far north, may have entered the "ecotone" along with their Arcto-Tertiary associates, both plant and animal. It is possible that the entire neotropical group of plethodontids was derived from a common ancestral stock, and thus it is likely that only a single group of plethodontids adapted to the ecotonal situation, the majority remaining in the region occupied by Arcto-Tertiary Geofloral derivatives. As the tropical border shifted southward in Oligocene and Miocene in response to the cooling and drying trends, the "ecotone" and its associated salamander fauna also shifted southward, especially at higher elevations. In early Tertiary the Madro-Tertiary Geoflora was developing in the increasingly arid southwestern United States and northern Mexico from Upper Cretaceous and Paleocene subtropical floras and was rapidly expanding in those areas (Axelrod, 1960). Madro-Tertiary elements continued their development during Oligocene and Miocene and expanded in the area between the northern border of the tropics and the main Arcto-Tertiary Geofloral region which had also shifted somewhat to the south. The final result of long-range Tertiary climatic trends was that the plethodontids were effectively separated by the arid region into two major groups: the northern group which continued a close association with Arcto-Tertiary Geofloral elements (and formed portions of the Eastern American and Western American Complexes of the Old Northern Faunal Element of Savage, 1960), and the neotropical group which was associated with the ancient "ecotone," and located to the south below the arid region that was the site of the Madro-Tertiary Geofloral expansion. The neotropical plethodontids are an excellent example of the Central American Complex of the Old Northern Faunal Element of Savage (1960).

An extensive Tertiary radiation took place in the neotropical plethodontids

and a number of species were able to move out of the ecotonal situation and adapt to areas occupied by Neotropical-Tertiary Geofloral derivatives in subtropical and tropical regions. Once this important change took place the plethodontids were able to spread southward rapidly. There is evidence that this ecological shift has occurred more than once. Today seven recognized genera and over 100 species of plethodontids occur in the neotropical region in a variety of forest habitats, from lowlands to high páramo, and from the northern limits of humid forest in northeastern Mexico south to central Bolivia and east to the mouth of the Amazon.

In this paper we are primarily concerned with entrance of plethodontids into South America, and it is necessary to consider very briefly the problem of land connections between Central and South America. Olsson (1932, 1942, 1956) has reviewed the geological history of Tertiary northeastern South America. He indicates that folding and uplift of the Andes began at the close of Cretaceous, and, as a compensation to this uplift, downfolding to the west resulted in the formation of the Bolivar geosyncline in the region of the present-day Golfo de Urabá and Río Atrato Valley in northwestern Colombia. Although the region is not well-known geologically, marine Tertiary deposits are found in northwestern Colombia commencing with upper Eocene and extending through Oligocene, Miocene, and probably into Pliocene. This indicates that South America was effectively separated from lower Central America for most of Tertiary by a narrow marine barrier, the flooded geosyncline or Bolivar portal. Geosynclines in Panamá, Costa Rica and Nicaragua also served as marine barriers during portions of Tertiary, and an archipelago existed in southern Central America with the islands separated by relatively narrow marine passages.

Nygren (1950) and Durham and Allison (1960) think the Bolivar geosyncline was drained earlier than Pliocene, probably in late Miocene. Nygren, who has studied sedimentation in the Bolivar geosyncline area in Colombia, believes that the seaway was open from Upper Eocene to middle Miocene, and that cross geosynclinal highs were probably above sea level for transitory periods during this time. Nygren states that the portal was closed in late Miocene and should have been no obstacle for migration of land faunas since that time.

The data of Simpson (1940, 1950, 1953) are in conflict with those of the geologists and paleontologists cited above in respect to dating of the closure of the Bolivar portal. Simpson, on the basis of fossil and recent mammal distribution, thinks South America was isolated from early Paleocene to late Pliocene. A few North American mammals entered South America and some South American mammals entered North America in late Miocene, but according to Simpson (1953) these may have utilized an island chain in moving north and south because so few groups migrated. Many North American mammals appear in South America for the first time in Chapadmalan faunas, and many South American mammals appear in North America for the first time in Blancan faunas. The evidence is strong for approximate equivalence of Blan-

can and Chapadmalan, and Blancan is considered by various authorities to be latest Pliocene to earliest Pleistocene.

Despite some controversy concerning dating of closure of the Bolivar portal, marine and terrestrial paleontological and geological evidence indicates that the portal was drained sometime from late Miocene to Pliocene and a complete and passable land bridge was formed by the time of the Blancan and Chapadmalan faunas.

Weeks (1947) and Olsson (1932) discuss several periods of major orogenic activity during Tertiary in South America. The Andes apparently were raised and lowered several times during Tertiary, but there is no evidence that the Tertiary Andes were ever as high as they are presently. Weeks states that the Andes were raised to their present conformation in a final major uplift during Pleistocene, but according to Nygren (1950) the high peaks of the Cordillera Occidental were raised in middle Miocene, with only slight changes in elevation during Pleistocene. The uplifts initiated in Miocene evidently persisted through Pliocene and Pleistocene and continue to today. Weeks (1947) mentions indication of glaciation during Pleistocene in the higher mountains and in Patagonia.

Two genera of plethodontids, *Bolitoglossa* and *Oedipina*, occur today in South America. Both entered South America from lower Central America to the northwest, and it seems apparent that several invasions took place. The time of the first invasion is not clear, but it probably occurred following closure of the Bolivar portal in Plio-Pleistocene. This idea was apparently first clearly stated, but not elaborated, by Dunn (1931) who thought the portal closure occurred toward the end of Miocene. The first group may have entered by island hopping, however, before a continuous land bridge was established. Both genera demonstrate fair amounts of vagility as shown by their relatively extensive ranges and by the fact that both have been able to reach the ancient Isla Gorgona across a 25 mile marine barrier.

Forerunners of the *altamazonica* group of *Bolitoglossa* may have been the first to arrive in South America. The group is now the most widely distributed in South America, and has penetrated much farther south than other groups. Today it is peripheral in distribution, and occurs south of other South American species (Fig. 23). These points indicate that the group has probably been in South America for a relatively long time. In addition the group is well adapted to lowland tropical forests and the first invaders would be expected to be lowland species, since there is no evidence that high mountains ever existed across the Bolivar portal area. An additional feature indicating the relative age of the group is that it is not clearly related to any Central American species, a reflection of long separation. Today paired-species are found on either side of the Andes, possibly indicating that restriction of genetic interchange across the mountains is relatively recent.

A second invasion may have been accomplished by ancestors of the *pal-mata* group of *Bolitoglossa*. We think the invasion of this group was relatively

early because the group is highly specialized, has no close Central American relatives, and now occupies a peripheral highland position. The *palmata* group ancestors probably entered South America by a discontinuous highland route, almost certainly following the isthmian connection. The *palmata* group is adapted to a cool highland environment. It may have entered South America during an early glacial period when a relatively small depression of the mean annual temperature would have shifted the subtropical and lower montane forests to lower elevations than today and provided a temporary continuous corridor of favorable environment. It should be remembered, however, that the group shows some relationships to the *adspersa* group and may have evolved from the latter in South America.

Multiple invasions probably occurred from late Pliocene through Pleistocene, with both highland and lowland species involved. Certain members of the *adspersa* group of *Bolitoglossa* (e.g., *hypacra*) are obviously closely related to Central American species. Despite the fact that *hypacra* is relatively primitive its entrance into South America appears to have been rather recent because it is closely related to Panamanian and Costa Rican highland species, it is located in the highland region closest to Panamá, and it is not known elsewhere in South America. Other members of the *adspersa* group may have originated in South America from an ancestor that entered from Central America by a discontinuous highland route. The ancestor of the series *vallecula-savagei-borburata* appears to have been close to that that gave rise to *hypacra*. This common ancestor has given rise to the relatively primitive, slightly webbed species occurring at moderately high elevations (*vallecula*), to a species with more webbing occurring at moderate elevations (*savagei*), and to a specialized, fully webbed species of relatively low elevations (*borburata*).

The entrance of the two species of *Oedipina* and of the *phalarosoma* group of *Bolitoglossa* appears to have been recent. Both species of *Oedipina* are known from Panamá, and *B. phalarosoma* has Central American rather than South American relatives and is located in a northern Colombian lowland situation. All probably entered recently by humid lowland routes.

Recent movements may have been both into and out of South America. Some species (e.g. *B. biseriata*) that evolved in South America may have moved northward. *B. biseriata* is related to highland species of the *adspersa* group and upon entering the lowlands it may have moved back north into Panamá. Movement may have been in either direction, however, depending on the source of the ancestral forms.

The presence of only *Oedipina* and *Bolitoglossa* in South America is not surprising. These are the only genera known from Panamá, and two additional genera known from Costa Rica (*Chiropterotriton*, *Parvimolge*) are not known from tropical lowland localities and could have entered South America only during long cool periods which probably did not exist in this area. Of the seven neotropical plethodontid genera only *Bolitoglossa* and *Oedipina* have had notable success in tropical lowland forests.

KEY TO THE SALAMANDERS OF SOUTH AMERICA

- 1a. Costal grooves 17 to 22; body elongate; sublingual fold present
 *Oedipina* 2
- 2a. Snout blunt and short; maxillary teeth extending posteriorly past level
 of internal choanae; eye large *O. complex*
- 2b. Snout long and pointed; maxillary teeth not extending posteriorly past
 level of internal choanae; eye small *O. parvipes*
- 1b. Costal grooves always 13; body short and robust; sublingual fold absent . .
 *Bolitoglossa* 3
- 3a. Limbs very long in females with only 2 costal folds separating appressed
 limbs; hands and feet nearly webless *B. hypacra*
- 3b. Limbs of females relatively short with from 2½ to 5 costal folds separating
 appressed limbs; hands and feet with moderate to complete webbing 4
- 4a. Snout noticeably shortened 5
- 5a. Vomerine teeth few (7 to 15); many tiny guanophores ventrally; size
 small (less than 46.9) *B. orestes*
- 5b. Vomerine teeth moderate (14 to 23); no guanophores ventrally; size
 moderate (to 53.3) *B. palmata*
- 4b. Snout moderate to long 6
- 6a. Head very broad (standard length 5.4 times head width); feet with
 only outer digits completely involved in web, with middle digit relatively
 free *B. nicefori*
- 6b. Head moderately broad to narrow (standard length 5.7 to 8.0 times
 head width); feet never with only outer digits completely involved in
 web 7
- 7a. Large (to 85.5 standard length); body robust; color solid lead black
 *B. capitana*
- 7b. Medium to small (standard length not over 70); color rarely solid lead
 black 8
- 8a. Number of maxillary teeth very low (0 to 4 in two specimens)
 *B. chica*
- 8b. Number of maxillary teeth moderate to high (11 to 87) 9
- 9a. Head very narrow (standard length 7.4 to 8.0 times head width); dorsum
 with large white patches in shoulder region *B. phalarosoma*
- 9b. Head moderate to broad (standard length 5.7 to 7.6 times head width);
 dorsum without large white patches in shoulder region 10
- 10a. Biseriate color pattern with black lateral bands, buff dorsal band and
 whitish ventral band; hands and feet fully webbed *B. biseriata*
- 10b. Color pattern not strongly biseriate; hands and feet variously webbed
 11
- 11a. Tails usually with sharply defined reddish, yellowish, or white ventral
 stripe, or stripe broken into patches; hands and feet moderately webbed;
 rounded semitruncate terminal phalanges, or terminal phalanges with

- small rounded nubbins at tips 12
- 12a. Hands and feet moderately webbed; terminal phalanges rounded, semitruncate *B. valleculea*
- 12b. Hands and feet nearly completely webbed; terminal phalanges tipped with small round nubbins *B. savagei*
- 11b. Tails uniform or spotted ventrally, never with sharply defined yellow ventral stripe; hands and feet moderately to fully webbed, never with nubbin-tipped phalanges 13
- 13a. Dorsal color dark brown to black, with rusty-gold longitudinally oriented dashes, streaks, or spots; hands and feet moderately webbed *B. adspersa*
- 13b. Dorsal color patterns uniform black or brown, or with dorsal band of tan, or with mottled brown, never with rusty-gold longitudinally oriented dashes, streaks, or spots; hands and feet almost fully webbed 14
- 14a. Usually light buff dorsal band with black lateral bands and gray venter; adults with high numbers of maxillary teeth (37 to 71) *B. borburata*
- 14b. Dorsal band never present; color of dorsum either uniform black or brown or mottled brown; adults with small or moderate numbers of maxillary teeth (11 to 44) 15
- 15a. Adults with low numbers of maxillary teeth (11 to 26) *B. altamazonica*
- 15b. Adults with moderate numbers of maxillary teeth (28 to 44) . . . 16
- 16a. Large cream spots ventrally on trunk and tail *B. pandi*
- 16b. Coloration either solid dark or light ventrally 17
- 17a. Large fully webbed feet (standard length 9.2 to 10.6 times foot width); dorsum mottled brown *B. sima*
- 17b. Small nearly fully webbed feet (standard length 11.6 to 13.7 times foot width); dorsum of uniform coloration *B. peruviana*

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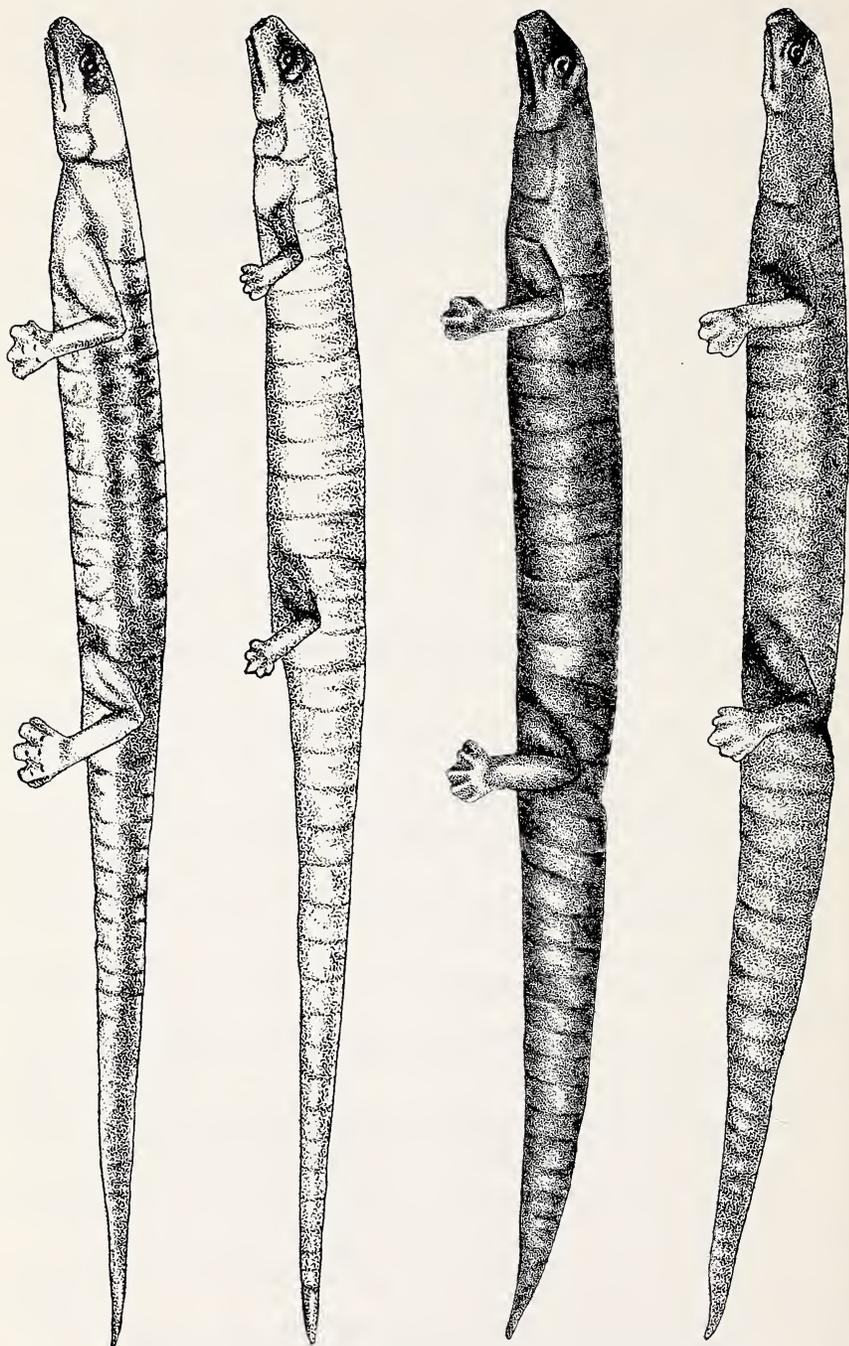


Fig. 26. Left to right. *Bolitoglossa valleculea* MLAs 8a, Yarumal, Colombia, female, holotype, 54.1 mm standard length; *Bolitoglossa chica* JAP 4366, Santo Domingo, Ecuador, female holotype, 38.7 mm standard length; *Bolitoglossa capitana* MLAs 1a, Hacienda La Victoria, Colombia, female, holotype, 82.3 mm standard length; *Bolitoglossa nicefori* MLAs 4, San Gil, Colombia, female, holotype, 46.8 mm standard length.

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By Melba C. Caldwell
David H. Brown
and
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DAVID K. CALDWELL

Editor

INTERGENERIC BEHAVIOR BY A CAPTIVE PACIFIC PILOT WHALE

By Melba C. Caldwell¹

David H. Brown²

and

David K. Caldwell³

ABSTRACT: Intergeneric behavior is described in which a captive male Pacific pilot whale, *Globicephala scammoni* Cope, attended a dead female Pacific striped dolphin, *Lagenorhynchus obliquidens* Gill, which had lived with him for three years. The same pilot whale had acted in a similar manner with a female of his own species which died after sharing his tank for over a year; but did not do so with another female pilot whale which died after an association of only about ten days.

It was thought that primarily the behavior had a sexual basis, but that elements of epimeletic (care-giving) behavior were involved in which length of time of association was a major factor as a stimulus.

Intergeneric behavior has been reported for captive cetaceans of the family Delphinidae on three occasions. Norris and Prescott (1961: 294) noted that on two successive days a freshly-captured adult male Dall porpoise, *Phocoenoides dalli* (True), was supported by two female striped dolphins, *Lagenorhynchus obliquidens* Gill, when it injured itself by running into the wall of the tank. Essapian (1962: 215) reported that a male Atlantic bottlenose dolphin, *Tursiops truncatus* (Montagu), supported a dead female common dolphin, *Delphinus delphis* Linnaeus, with which it had been closely associated in life. Brown (1962: 62) discussed possible homosexual behavior between living captive female individuals of *L. obliquidens* and the Pacific pilot whale, *Globicephala scammoni* Cope. Various genera of the Delphinidae often associate closely in nature (see Brown and Norris, 1956; Norris and Prescott, 1961), and intergeneric behavior in the wild also should be expected.

We now report another instance of intergeneric behavior in a captive environment.

On March 28, 1962, the whale tank at Marineland of the Pacific oceanarium, near Los Angeles, California, contained three Pacific pilot whales (*G. scammoni*) and three striped dolphins (*L. obliquidens*). On this day, an interesting case of intergeneric behavior was observed. All of the captives were highly trained and several of the animals had been living together for over three years.

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These two species, both Delphinidae, are often found closely associated in nature (Brown, 1960; Norris and Prescott, 1961) and live well together in captivity.

Observation windows at three levels afforded good underwater vision of the entire tank. In addition, the animals could be observed from a fourth level, above the surface.

The pilot whales in the tank were a large male (about 3500 pounds, 18 feet in length), a large female (about 1500 pounds, 15 feet in length), and a smaller female (about 1200 pounds, 12 feet in length). Respectively they were known as *Bimbo*, *Bubbles* and *Squirt*.

On the above date, at 11:00 a.m., we were notified that the large male pilot whale was carrying a dead striped dolphin (*Debbie*) around in the whale tank. The behavior had been noted shortly after 9:00 a.m.

At 10:10 a.m., when notes were first made, the male was resting near the bottom of the tank at a point near the main inlet pipe below his usual resting area near the surface. He was holding the dead dolphin in his mouth by one of its tail flukes (Fig. 1A and 5) with the body resting between his pectoral fins. The male's eyes were open to approximately twice normal size, giving him a "startled" expression (Fig. 2A). After an exceptionally long interval of about 10 minutes, he rose to the surface carrying the dead animal with him. His next dive also was clocked and again the underwater interval was 10 minutes.

At 11:20 a.m. the personnel of Marineland made an attempt to retrieve the dolphin. A diver entered the tank with a spear gun. Although it could not be seen from our vantage point, other observers stated that the two female pilot whales in the tank initially assumed a position between the descending diver and the male pilot whale.

Having entered the tank, the diver knelt waiting behind one of the large water inlet pipes, and when the male pilot whale approached, succeeded in spearing the dead dolphin and quickly passed the line to other personnel on the top deck. Upon pulling on the line, they succeeded in drawing the dolphin to the surface, but the whale forcibly retrieved the body in his mouth before it could be removed from the tank. In lunging for the dolphin, the male pilot whale struck the heavy stainless steel gate in the upper part of the tank that seals the flumeway into which the personnel were attempting to maneuver the dead animal. In his excitement, the whale damaged the gate and inflicted a large abrasion on his left side about two feet long and one foot wide. At the same time, he scraped the leading edge of his dorsal fin. The diver, not having time to leave the tank, was, in the confusion, also struck a glancing blow. However, he escaped injury, and it generally was believed by onlookers that the blow was not deliberate on the part of the whale.

The pilot whale snapped the $\frac{1}{4}$ -inch nylon line, bent the harpoon sharply, and returned to the bottom of the tank with the dolphin. After about 10 minutes, he surfaced to breathe carrying it with him (Fig. 3A). On surfacing he again commenced to carry the dolphin, once by grasping the still-embedded

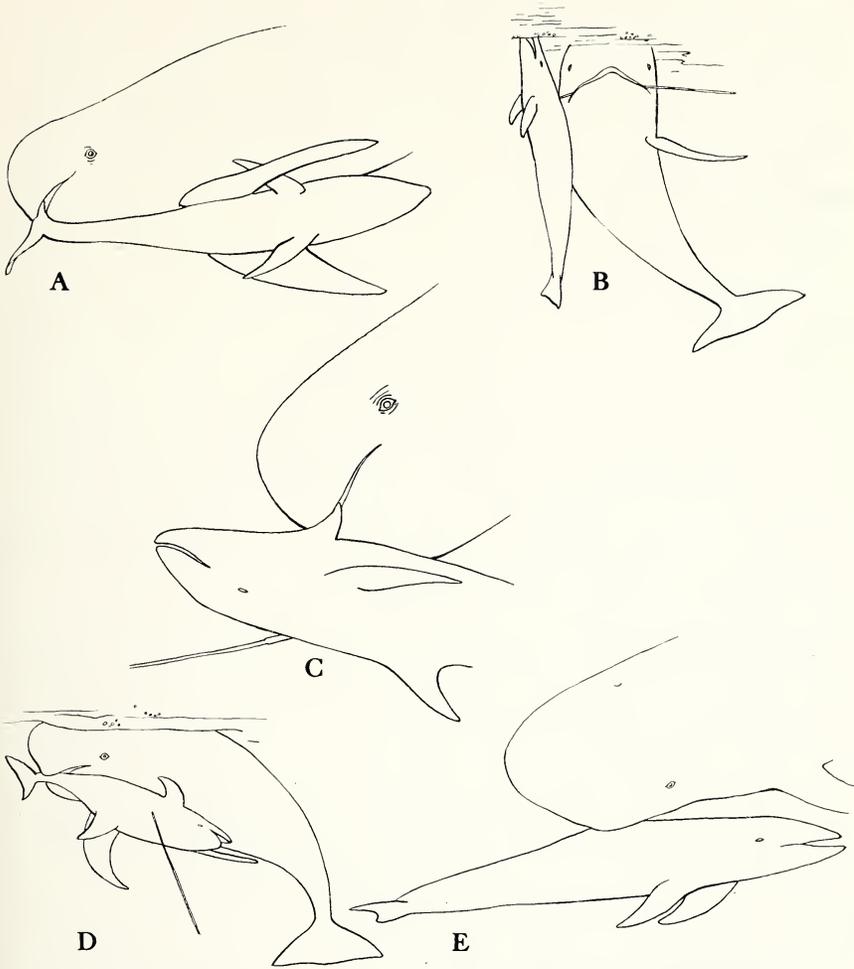


Fig. 1. Interspecific behavior by a captive male *Globicephala scammoni* toward a dead female *Lagenorhynchus obliquidens*. Line drawings, indicating various methods of carrying carcass, prepared from photographs. A: By means of the tail flukes. B: By means of an embedded harpoon. C: By means of a pectoral flipper. D: By means of the caudal peduncle. E: By means of the dorsal fin.

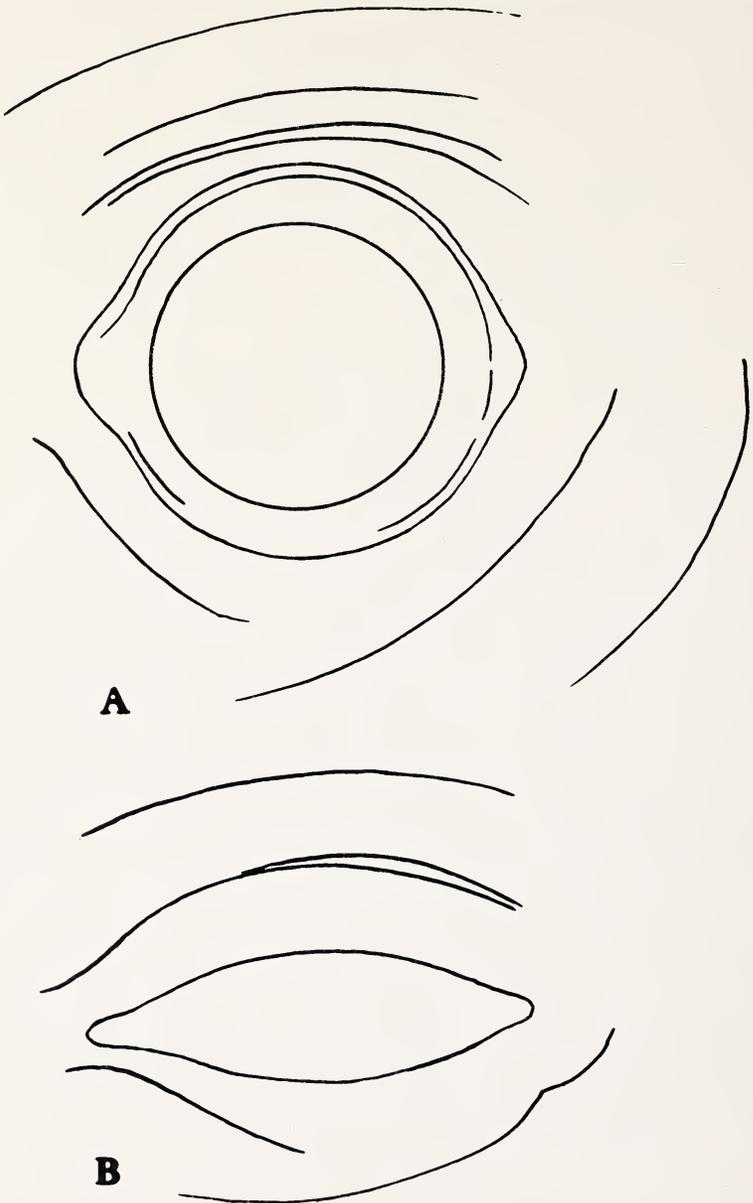


Fig. 2. Line drawings, prepared from photographs, of the eye of a captive male *Globicephala scammoni*. A: Size of eye opening when initially carrying carcass of dead female *Lagenorhynchus obliquidens*. B: Size of eye opening after carrying carcass for several hours. B is the usual state of the eye opening for this animal.

harpoon in his mouth (Fig. 1B). During this period, after an attempt was made to snare the dead animal at the surface, the pilot whale then began dropping the dolphin before he surfaced for air (Fig. 3B). Upon recovery, he always took it in his mouth very gently, usually by the pectoral flipper (Fig. 1C and 6). On two occasions he made unsuccessful attempts to take it by the snout. He also made fruitless efforts to grasp the body. On several occasions he took the caudal peduncle in his mouth and succeeded in carrying the dolphin (Fig. 1D). Once he carried the body by the dorsal fin (Fig. 1E).

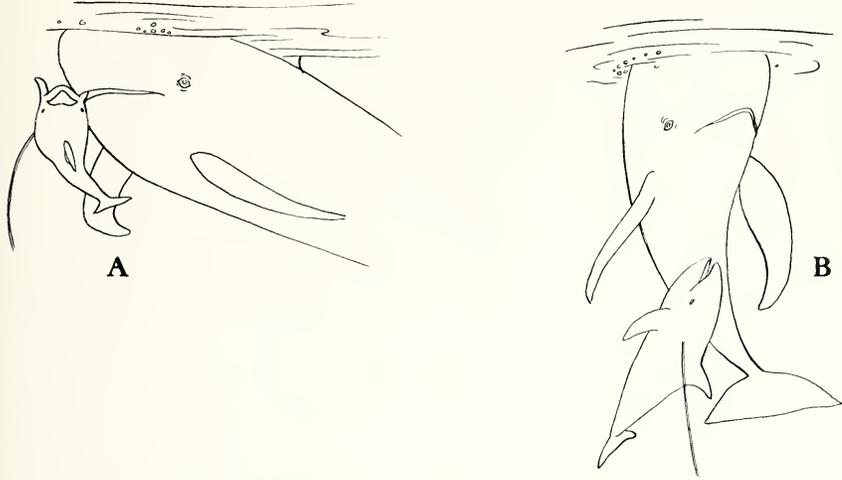


Fig. 3. Interspecific behavior by a captive male *Globicephala scammoni* toward a dead female *Lagenorhynchus obliquidens*. Line drawings prepared from photographs. A: Initially carrying carcass to surface when rising to breathe. B: Leaving carcass below when rising to breathe (after attendants had attempted to remove carcass from above).

At 12:00 noon, the management decided to continue the scheduled whale performance. Both large whales refused to feed. The smaller female pilot whale and the remaining dolphins performed as usual. The male pilot whale was now surfacing every half to two minutes, as opposed to the ten-minute period noted above.

When approached by a diver, the male pilot whale avoided him by circling the tank carrying the dolphin in his mouth, but he usually remained in the area of the inlet pipe. Once, when the pilot whale surfaced for air, the dead animal was suctioned toward the outlet pipe in the center of the tank; the pilot whale quickly retrieved the body and returned to the inlet pipe.

At 12:40 p.m., the divers again harpooned the dolphin, this time using a $\frac{3}{8}$ -inch nylon line. The dead animal was drawn to the surface once more. Again the large pilot whale seized the body before it could be removed from the tank, easily snapping the extremely strong line in the process.

At 12:50 p.m., the male pilot whale began leaving the dolphin for two or three seconds longer than necessary to breathe. Also, he left the body on the bottom and did not attempt to carry it toward the surface. The smaller female pilot whale approached the body but left when the large male returned. The other striped dolphins in the tank also approached the dead animal, but quickly swam away on the male's return. The male pilot whale now frequently rubbed his cephalic melon against the dead body, and also left the dolphin to rub his melon on the inlet pipe. By this time his eye had closed to a normal attitude (Fig. 2B). During this period he also rubbed his body slowly against the dead animal.

Both larger pilot whales refused to perform for the 1:30 p.m. show, but the small female whale and the surviving dolphins performed as usual. At 1:45 p.m., the male pilot whale attempted to lift the body with his pectoral flippers, but did not succeed.

From a small boat held in position above the dead animal, Marineland personnel lowered a modified swordfish harpoon into the water near the dead body of the dolphin. The pilot whale tried to push the harpoon away with his head. However, after several attempts, while the male whale surfaced to breathe the dolphin was harpooned, brought to the surface, and quickly removed from the tank. The pilot whale made a great flurry to recapture it, and this time failed. The time of removal was 2:00 p.m.

The male pilot whale gave several shrill cries immediately after this that could be heard clearly at the first level of viewing windows below the surface.

Members of the Lockheed Aircraft Corporation staff lowered a hydrophone into the tank at about 11:00 a.m., but reported no unusual vocalizations during the behavioral sequence prior to these calls. Unfortunately, the final cries were not recorded.

At 2:15 p.m., the male pilot whale seemed completely normal. He was resting at or near the surface with his eyes half closed in his normal attitude. However, both he and the larger female whale again refused to perform at the 3:30 p.m. show, but both readily took food from the attendant's hand.

The following day they both performed as usual, and, other than the abrasions sustained by the male whale, no ill effects were noted from the experience.

On March 8, 1960, the same male pilot whale had carried a dead female pilot whale at the surface for about four hours (Brown, 1962: 62). The two animals had lived together since January, 1959. The male whale was said to have effected intromission with the dead animal several times, and the behavior discussed above also may have had a sexual connotation although no attempts at intromission were observed by the numerous onlookers.

On another occasion, a female pilot whale died in the same male pilot whale's tank and he ignored the body. The period of their exposure to each other had been only 10 days. McBride (1940: 26) reported a case wherein two male *Tursiops truncatus* that had been contained in a tank together for a long time were separated for a period of three weeks. When brought back together,

McBride stated, "No doubt could exist that the two recognized each other. . . ." They played together in a frenzied fashion for several hours and were inseparable for several days thereafter and neither paid any attention to a female in the tank with them. These observations seem to indicate that individual recognition and attachment may then well play a major role in cetacean behavior which involves more than one individual. This is probably true for any cooperative behavior by cetaceans.

The behavior detailed above is especially significant because it was shown by a male, for whom incidents of long-term aiding behavior are less frequently reported than for females. The behavior also was constantly performed for a minimum of four hours until forcibly terminated. Again, the interaction was between different genera, the important factor probably being apparent affection for a recognized individual.

The great variety of responses made to a situation also is significant. There was no stereotyped method of carrying the dolphin, and both the area of the body held at the time, and the position assumed either at the surface or at the bottom of the tank varied with circumstances. The gentle handling of the body was particularly striking and showed the most careful deliberation. The deep scratches on the flukes and flippers (Fig. 4) of the dead animal were made when the pilot whale successfully retrieved the dolphin from the men attempting to remove it from the tank, and are evidence for the forceful efforts he was exerting in retaining possession of the body.

The wideness of the eye opening was important in that it gave an indication of the emotional state of the animal. Best and Taylor (1955: 836) suggested that emotional manifestations in man and various animals are sympatho-adrenal effects, and that a startled expression is due to the involuntary action under emotional stress of Mueller's orbital muscle, which retracts the upper eyelid. The wideness of the eye, coupled with the refusal of the pilot whale to feed after an abstinence of some 22 hours, despite strong conditioning to do so, together with persistence of the behavior in the face of injury, rules out likelihood of play.

The striped dolphin involved in the sequence with the male pilot whale was captured on August 28, 1958, and after introduction into the circular tank some three months later, had adapted well to the captive environment and with the exception of a five-day period of partial inappetence in January, 1961, had demonstrated no signs of abnormal behavior or symptoms of disease. Some eight weeks prior to her death, a swelling of the mammaries had been observed, together with a generalized edema of the entire posterior ventral region. The animal's feeding behavior remained normal in spite of a gradual increase in abdominal size. The progressive swelling, together with a marked tendency to avoid the more rigorous play behavior of her companions, indicated a possible pregnancy—a contention further supported by the considerable reproductive activity noted in the striped dolphin colony during the spring and autumn of 1960.

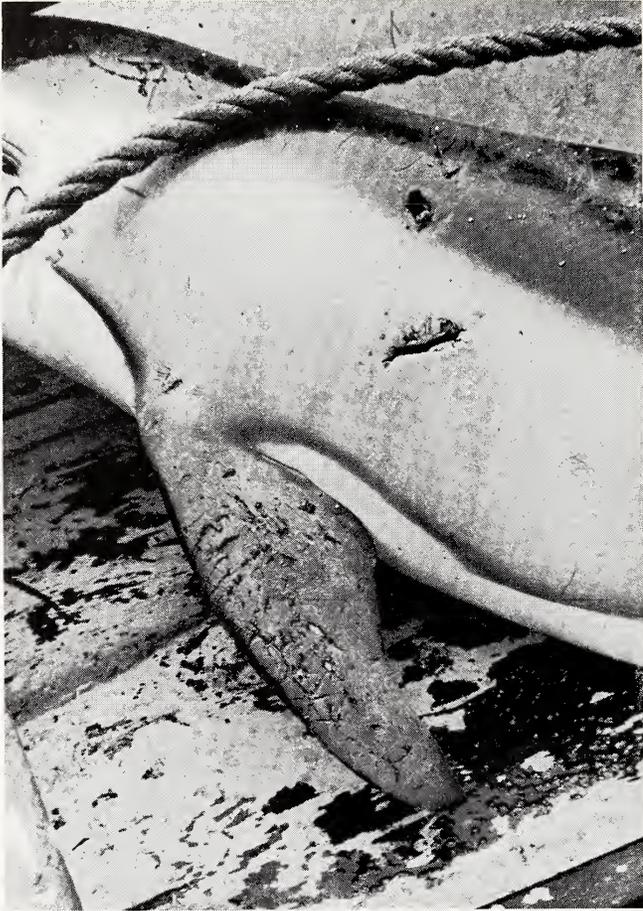


Fig. 4. Left pectoral flipper of dead *Lagenorhynchus obliquidens* showing deep lacerations, caused by teeth of captive male *Globicephala scammoni*, made when attempts were made to remove the dead animal from the pilot whale. The hole in the side of the body was caused by the harpoon used to retrieve the dead animal.

After death and subsequent removal from the tank, the dolphin was necropsied by veterinary pathologists of the Los Angeles County Livestock Department. Gross examination revealed a large tumor-like tissue in the right lung. However, subsequent histologic studies showed this not to be neoplastic. An extensive abscess was found throughout the posterior ventral abdominal wall. This, however, appeared secondary to the lesions found in the lung.

Some months before, the animal had been observed to fall and strike her body on a metal platform, after leaping clear of the water at a feeding performance. While at the time a cursory examination of the dolphin failed to

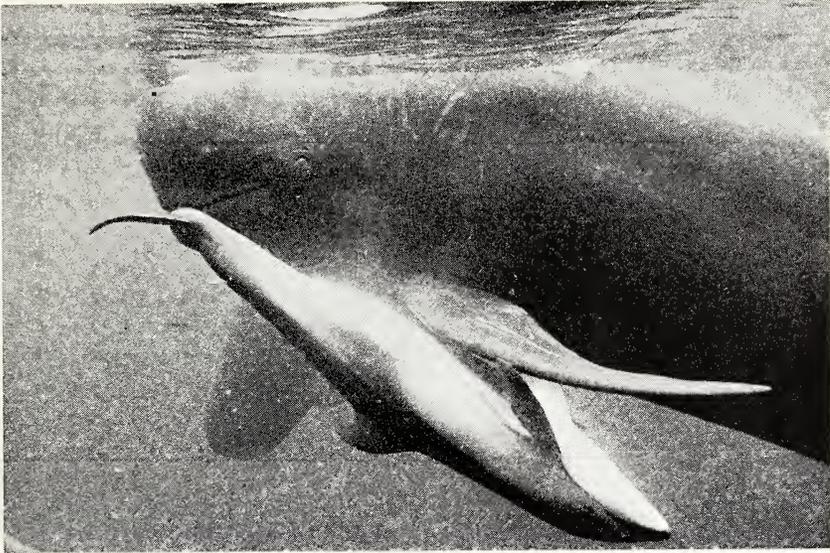


Fig. 5. Captive male *Globicephala scammoni* carrying dead *Lagenorhynchus obliquidens* by tail fluke. Photograph by Cliff Brown, Marineland of the Pacific.

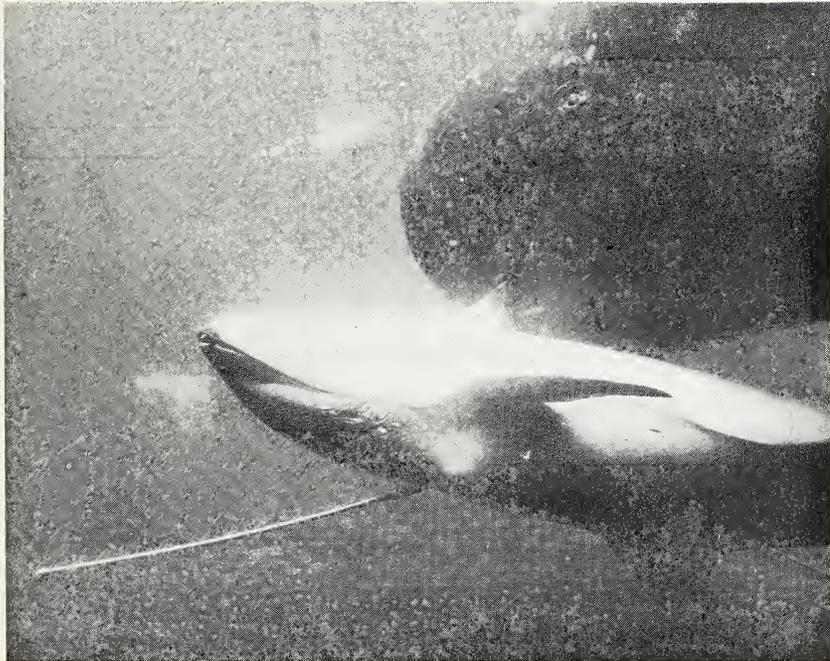


Fig. 6. Captive male *Globicephala scammoni* carrying dead *Lagenorhynchus obliquidens* by pectoral flipper. Photograph by Cliff Brown, Marineland of the Pacific.

detect injury, it is conceivable the impact of the fall resulted in trauma, which initiated and eventually ended in toxemia and the pathologic condition described.

Many still and motion picture photographs were made during the demonstration of the pilot whale's behavior and these are on permanent file with us. However, for clarity, line drawings for the most part were used in this paper. These drawings were prepared from certain of the photographs by Mary V. Butler of the Los Angeles County Museum.

We would like to thank the Los Angeles County Livestock Department, and particularly Drs. Rankin W. McIntyre and C. A. Delli Quadri for the skillful post-mortem examination of the striped dolphin.

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By JAY M. SAVAGE



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DAVID K. CALDWELL

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STUDIES ON THE LIZARD FAMILY XANTUSIIDAE

IV. THE GENERA

By JAY M. SAVAGE¹

ABSTRACT: The genera of the night lizards, family Xantusiidae, are characterized on the basis of osteological, external morphological and other features. The family is re-defined. Two subfamilies Cricosaurinae and Xantusiinae, the former a new taxon for *Cricosaura* of Cuba, are described. Three genera are placed in the second subfamily, *Klauberina*, *Lepidophyma* and *Xantusia*. The nominal genus *Gaigeia* is placed in the synonymy of *Lepidophyma*. Distribution and systematic position of all species in the family are considered.

The night lizards, family Xantusiidae, form a small group of peculiar, secretive American species. Superficially these lizards resemble the Old World lacertids, family Lacertidae, in general habitus but closer scrutiny of their structure appears to ally them with the circumtropical geckos, family Gekkonidae. The group has, as far as known, a disjunct distribution in North America and the West Indies. One genus is found in the southwestern United States, Baja California and extreme northern Sonora, Mexico; another is restricted to the Channel Islands off southern California; a third ranges from northern and central Mexico south through Central America to Panamá; and a monotypic genus inhabits a portion of Cuba. All known species have retiring habits and are probably most active at night. They are found during the day in rocky or limestone crevices, under debris in desert areas or under trash littering the floor of humid forests. At least six species of xantusiids bear living young and four of these forms are definitely placental lizards. The life histories of the other members of the family are unknown. Recently, one species of the group, *Xantusia vigilis*, has been utilized for experimental research particularly with regard to hormonal characteristics, sex cycles and color changes (Atsatt, 1939; Caswell, 1950; Bartholomew, 1950, 1953; and Miller, 1952).

The family has considerable attraction for the systematic biologist because it is a small, clearly defined unit in which the species and genera have not been adequately treated, its position within the suborder Sauria is not satisfactorily determined, the distributional pattern is curious, the ecologic preferences of the species are, while poorly known, suggestively linked with certain morphologic modifications, the known life histories of member forms are peculiar and the group is beginning to have some value as experimental animals. Each of these factors emphasizes the fruitful field of study offered by these creatures and the desirability of a modern systematic analysis of the family as a prelude to other types of investigations.

My interest in the xantusiids dates from 1947 when I was a freshman at Stanford University. At that time Professor George S. Myers, Curator of

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Zoological Collections in the Stanford Natural History Museum, turned over to me for identification a collection of reptiles from Baja California, Mexico. Included in this material were the first known mid-peninsular representatives of the night lizard, *Xantusia vigilis*, which were subsequently described as a new subspecies (Savage, 1952). While working out the status of these Mexican night lizards it became obvious that the family Xantusiidae offered a neatly circumscribed group for evolutionary study. It was also apparent that such an analysis besides furnishing meaningful data on the xantusiids might provide a possible springboard for later research on the major classification of the lizards. For these reasons I have, since 1947, been accumulating materials and data toward a complete systematic revision of the family Xantusiidae. The present paper may be considered as a major step towards completion of the work.

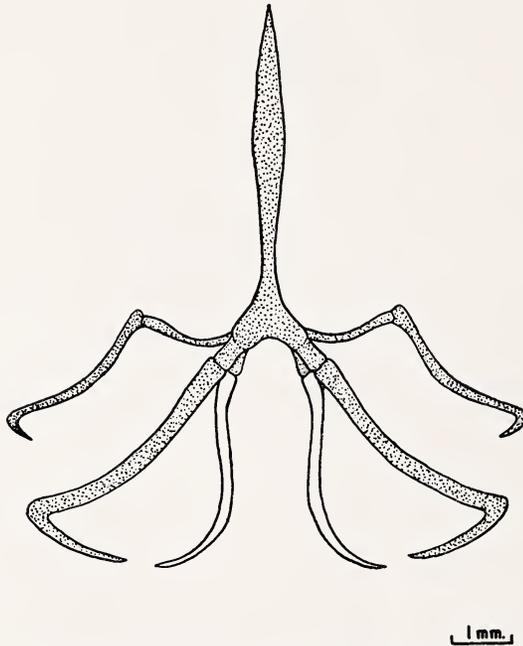


Fig. 1. Ventral view of hyoid apparatus of *Xantusia arizonae* (JMS 317).

MATERIALS, AND ACKNOWLEDGMENTS

The preserved materials upon which this report is based have come from all the major herpetological collections in the United States. Examples of all recognized species have been examined in detail. Osteological observations are taken from dry prepared skeletons, cleared and stained specimens and radiographs. The bulk of the skeletal material and radiographs are in the osteological collections at the University of Southern California (JMS, USC)

and the Los Angeles County Museum (LACM). Osteological material examined includes: 2 *Cricosaura*, 6 *Klauberina*, 3 *Xantusia henshawi*, 1 *Xantusia arizonae*, 20 *Xantusia vigilis*, 8 *Lepidophyma flavimaculatum*, 1 *Lepidophyma micropholis*, and 2 *Lepidophyma gaigeae*. The series of *Xantusia vigilis* has been used as a point of reference to verify possible differences subject to individual variation. Detailed analysis of the skeletal morphology of the family is reserved for a future paper.

I should like to acknowledge my indebtedness to those persons and institutions which have contributed to the completion of this study: Mr. Charles M. Bogert, American Museum of Natural History; Dr. Rolf L. Bolin, Hopkins Marine Station; Dr. Bayard H. Brattstrom, Orange County State College; Sr. Antenor L. de Carvalho, Museu Nacional do Brasil; Dr. Doris M. Cochran, United States National Museum; Dr. Richard E. Etheridge, San Diego State College; the late Professor Gordon F. Ferris, Stanford University; Dr. Norman E. Hartweg, University of Michigan; Dr. Max K. Hecht and Mrs. Bessie M. Hecht, Queens College; Dr. Robert F. Inger, Chicago Natural History Museum; Dr. Laurence M. Klauber, San Diego Natural History Society; Mr. Arnold G. Kluge, University of Southern California; Mr. Arthur Loveridge, Harvard University; Dr. Samuel B. McDowell, Rutgers University; Dr. Malcolm R. Miller, University of California, San Francisco; Mr. Benjamin Shreve, Harvard University; Dr. Hobart M. Smith, University of Illinois; the late Miss Margaret H. Storey, Stanford University; Dr. Edward H. Taylor, University of Kansas; Dr. Fred S. Truxal, Los Angeles County Museum; Mr. Jerome B. Tulecke, University of Kansas; Mr. David B. Wake, University of Southern California; Dr. Charles F. Walker, University of Michigan; Dr. Heinz Wer-muth, Stuttgart; and Dr. Ernest E. Williams, Harvard University.

I should especially like to thank Dr. George S. Myers of Stanford University, who first encouraged my interest in xantusiid lizards. Portions of the study were carried out while I was a student under his direction at Stanford.

The osteological illustrations were prepared by Russell Cangialosi. The figures of external characteristics were drawn by Anthony J. Gaudin of the University of Southern California.

The investigation was completed at the University of Southern California and was supported in part by a U.S. Public Health Service research grant A-3549 from the Institute of Arthritis and Metabolic Diseases.

DEFINITION OF FAMILY FAMILY XANTUSIIDAE BAIRD, 1859

Premaxillary single; nasals paired; frontals paired or fused into a single element; parietal foramen present or absent; lachrymal partially or completely fused with prefrontal; jugal well-developed, bounding the posterior limit of orbit; postfrontal and postorbital fused into a single element; supratemporal fossa completely closed by squamosal and postfronto-orbital arches which lie adjacent to parietal and frontal; tabulare reduced to a narrow element; pre-

vomer single; palatines in contact with one another anteriorly but widely separated for most of length; ectochoanal cartilages greatly expanded to underlie palatine, prevomer and fenestra exochoanalis; pterygoids not meeting one another; epipterygoids fitting into notch in pterygoid, closely attached to parietal, not connected to parietal by a ligament; simple osteoderms present on head of only one or two species; 14-15 scleric ossicles; teeth pleurodont, simple in some forms, triconodont in others, 7-8 present on premaxillary, 9-15 on maxillaries and 12-18 on dentaries; no teeth on palate. Lower jaw composed of three bones: dentary, coronoid and angular. No Mecklian groove. Hyoid apparatus (Fig. 1) with two complete arches and a third nearly complete arch; epibranchial of third arch not continuous with ceratobranchial, connected to exoccipital by a ligament. Vertebrae procoelous, condyle of each centrum not expanded, capped by a small intercentrum; intervertebral canals very large; 26-29 presacral vertebrae, mode 28; three cervical vertebrae; all caudal vertebrae except basal four or five split into two halves by a septum which divides transverse processes and centra; first two autonomy centra with peculiar "butterfly" shaped transverse processes (Fig. 2); chevron bones attached to intercentral region of caudal vertebrae. Interclavicle cruciform; clavicles dilated, perforate or hook-shaped; emarginate scapulocoracoid and non-emarginate primary coracoid fenestrae present; no parasternum or parasternal ribs; no hypoischium. Basal tarsalia fused into a single element; intermedium present; phalangeal formula of hand 2-3-4-5-3 or 2-3-4-4-3; phalangeal formula of foot 2-3-4-5-4.



Fig. 2. Diagrammatic representation of caudal vertebrae in Xantusiidae. Arrow indicates first autonomy vertebra. Detail of vertebrae below indicates autonomy septa and fracture planes. Diagram follows system of R. E. Etheridge.

Tongue rather elongate, covered with transverse plicae on posterior half and anteriorly by scale-like papillae which gradually grade into villous papillae; slightly notched at tip, attached to floor of mouth except distally; glottis located some distance back of end of tongue; tongue not retractible into a sheath. Soft palate formed of two broad flaps which extend posterior to pterygoid and overlap on their median edges. Lungs paired. Pupil vertical; no movable eyelids; tympanum exposed. Head covered by enlarged scales, arranged in regular series; dorsal scales granular or flattened, never imbricate; ventrals are enlarged rectangular plates. Femoral pores always present in males, and in females of some species. Four limbs, pentadactyle; digits all directed forward.

All species in which the life history is known are viviparous with a placental connection between parent and offspring. Known forms secretive, probably all nocturnal.

DISCUSSION OF SYSTEMATIC CHARACTERS

SQUAMATION (Figs. 3-4): There has been considerable confusion in the past concerning the status and relationships of several genera and species of Xantusiidae due to the absence of a standardized terminology for the squamation of these lizards. In order to analyze the scutellational differences and similarities between members of the family properly it has been necessary to revise completely the existing terminology employed for the scales of these animals. The accompanying list forms a system of scale nomenclature applicable to all known xantusiids. Its chief merits lie in the fact that the named elements in different forms are probably homologous and are at least positionally analogous.

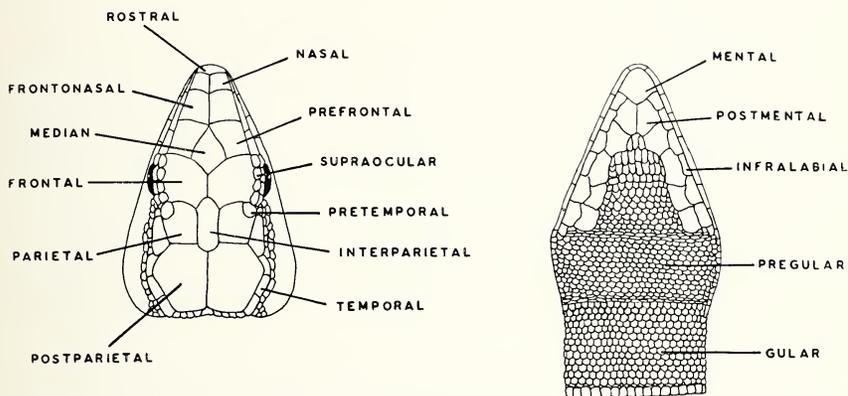


Fig. 3. Dorsal and ventral views of head of hypothetical night lizard, to indicate terminology of scales.

UPPER SURFACE OF HEAD

Rostral — plate at tip of snout, bordering lip.

Nasals — the scales in which the nostrils are at least partially pierced; extending from supralabials up and over the snout to meet one another on the mid-line of head; in contact with rostral along their anterior margin.

Frontonasals — one or a pair of scales separating nasals from prefrontals.

Prefrontals — scales separating the frontonasals from the frontals and the enlarged median, or both.

Median — a large azygous scale meeting prefrontals anteriorly and the frontal or frontals posteriorly. In the older literature this scale has been called a median prefrontal and a frontal.

Frontals — a scale or pair of scales lying between the eyes and in contact with the prefrontals and/or the median anteriorly and the interparietal posteriorly. Usually called frontoparietals in previous work on the xantusiids.

Parietals — a pair of scales in contact with posterior margin of frontal and separating the temporals from the interparietal.

Interparietal — a single large median scale in which the parietal eye is pierced.

Postparietals — a pair of large plates in contact with the interparietal along its posterior margin and separating it from the nuchal scales.

Supraoculars — scales above the orbit forming a distinct series continuous with the ocular ring.

Pretemporals — a pair of scales separating the supraoculars from contact with the parietal or interparietal.

Temporals — a series of enlarged scales or granules bordering the lateral edge of the postparietals, parietals or interparietal, and pretemporals, and separating these scales from the pretympanic scales; sometimes divided into upper and lower segments.

SIDE OF HEAD

Postnasals — the scales just posterior to nasal and separating it from anterior loreal; nostril always pierced partially in the postnasal.

Loreals — usually an anterior and a posterior loreal which separate the prefrontals and median from supralabials; bordered anteriorly by the postnasal and posteriorly by the loreolabials or the loreolabials and the upper preoculars.

Loreolabials — one to several large scales that separate the loreals from the preoculars and from the supralabials below the orbit.

Ocular Ring — scales bordering the orbit anteriorly, below and posteriorly, continuous with supraoculars if they are present, may be divided into pre-, sub- and postoculars.

Tunics — scales on the tunic of skin that covers the margins of the brille of the eye.

Pretympanics — scales covering the sides of the head between the postoculars and the ear-opening and below the temporals.

Auriculars — a row of modified scales bordering the anterior margin of the ear-opening.

Supralabials — enlarged scales bordering the upper lip.

UNDER SIDE OF HEAD AND NECK

Mental — the enlarged scale at symphysis of lower jaw.

Infralabials — scales bordering the lower lip.

Postmentals — a series of large scales posterior to the mental and separating the infralabials from the pregular scales. These scales are fused with the infralabials in *Lepidophyma*.

Pregulars — all the small scales on the throat anterior to the gular fold.

May be divided into the anterior preular scales, lying anterior to the first preular fold and posterior preulars, lying posterior to the first preular fold.

Gulars — the scales lying on the gular fold.

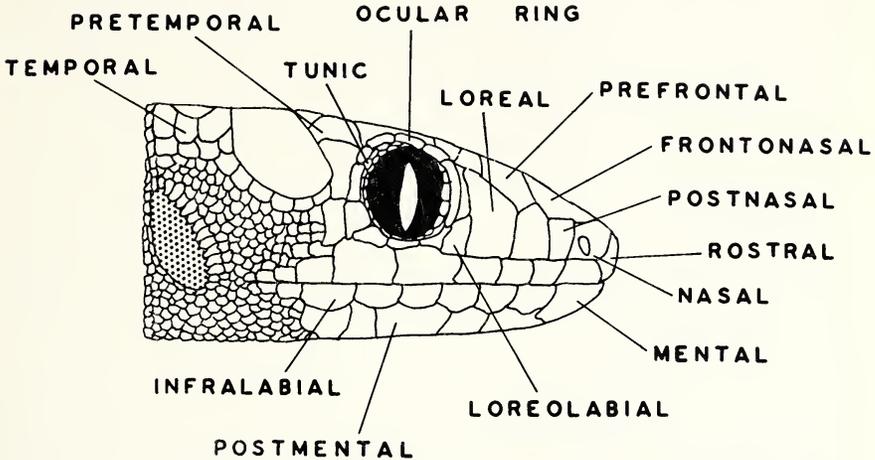


Fig. 4. Lateral view of head of hypothetical night lizard, to indicate terminology of scales.

BODY, LIMBS AND TAIL

Dorsals — scales on back and sides of neck and body.

Ventrals — enlarged rectangular plates on ventral side of body between the gular fold and the preanal region.

Preanals — the enlarged scales just anterior to anus.

Radials — scales along the anterior surface of the forearm.

Femorals — scales along the anterior surface of upper leg.

Tibials — scales on upper surface of lower leg.

Lamellae — scales on the under surface of the fingers and toes.

Caudals — rectangular scales arranged in whorls around the tail.

OSTEOLOGY: The bony structure of the family will be discussed in detail in a future paper and only those characteristics of fundamental significance in delimiting the major groups are indicated in the present summary. Terminology generally follows Romer (1956).

Since systematic herpetology has depended rather heavily upon external features for the recognition of biological units in reptiles it is interesting to note the strong correlation between modifications in the skeleton and the external structures. Perhaps the best region for such a comparison is the head. In *Cricosaura*, for example, the form with the simplest pattern of head shields (one frontal, no median or parietals and an enlarged interparietal), the roof of the cranium is also simplified by the coossification of the frontals and parietals into two simple elements. The genera with paired frontal and parietal

bones have a much more complex arrangement of the head scales. Further, the only group without enlarged, platelike temporals (*Xantusia*) has the underlying bones of that region (postfronto-orbital, squamosal and tabulare) greatly reduced. In *Cricosaura*, where the temporals are moderately large plates, the underlying bones are somewhat expanded. *Klauberina* and *Lepidophyma* have the temporals extremely well-developed and these plates are underlain by very expanded postfronto-orbitals, squamosals and tabulares. *Lepidophyma*, the only genus with the frontals expanded to close the orbit completely above and having the outer margin of frontals even and not concave, has the supraoculars greatly reduced so that they are represented by a thin, fleshy ridge just above the eye.

In the genera with well-developed supraoculars the frontals do not completely roof over the orbit above and their outer margins are deeply concave. Also the restriction of the prefrontals to the side of head in *Lepidophyma* and their presence on top of the cranium of other genera is correlated with the supraocular character.

These points show that there is a considerable degree of agreement between the evidence of osteology and scutellation in the head region of xantusiids so far as differences and similarities between genera are concerned. Other osteological features do not appear to be as closely associated with external appearances in these lizards.

LIFE HISTORY AND ECOLOGY: All species of xantusiids in which the life history is known are viviparous and have a definite placental connection between the parent and offspring. Unfortunately we have no information on this aspect of the natural history of *Cricosaura typica*. Placentation has been described in detail for only one species, *Xantusia vigilis* (Heimlich and Heimlich, 1950:5). Placentae are also present in other forms of *Xantusia*. In addition, Dr. Malcolm R. Miller, of the Department of Anatomy, University of California has examined my material of *Klauberina*, *Xantusia* and *Lepidophyma* and is of the opinion that placentae are also formed in these species groups.

The sex cycle has been worked out in detail for *Xantusia vigilis* by Dr. Miller (1948, 1951) but unfortunately there are no comparable studies on any other xantusiid species. It is interesting to note that Miller concludes that the sex cycle approaches most closely that of the geckos *Hoplodactylus* and *Platydictylus* for female and male *X. vigilis*, respectively. Some of the points of apparent similarity between *Hoplodactylus* and *Xantusia* females may be due to the fact that both are viviparous groups. The xantusiids also appear to have some resemblance to the lacertids in their sexual cycles.

The number of young produced by these lizards also appears to be generic or specific in nature. *Klauberina* has from four to nine offspring, *Xantusia* one to three and *Lepidophyma flavimaculatum* about six. It seems probable that other members of the genus *Lepidophyma* also have about this number, according to Dr. Miller.

Miller (1951) has presented the only general life history study of any xantusiid, based upon his work on *Xantusia vigilis*.

The food habits of *Klauberina* and *Xantusia* have been discussed by Brattstrom (1952), Knowlton (1949) and Schwenkmeyer (1949). *Klauberina* apparently consumes a high percentage of plant food, as might be suspected from its triconodont, shearing dentition. *Xantusia* is essentially insectivorous and of course has simple teeth. The food habits of *Cricosaura* and *Lepidophyma* are not known in any detail. Superficial examination of stomach contents leads me to suggest that they are primarily insectivores. Neither genus has strongly triconodont teeth, although the teeth are weakly triconodont in *Lepidophyma*.

The habitats of the various forms are also characteristic. *Cricosaura* has been taken on only a few occasions, each time under rocks at Cabo Cruz, Oriente Province, Cuba, or under forest litter in the same general vicinity. *Klauberina* may be found under trash or any cover on the Channel Islands of California. *Xantusia henshawi* and *Xantusia arizonae* are found primarily under granite flakes in heavily bouldered areas, the former in extreme southern California and adjacent Baja California, Mexico, and the latter in north and central Arizona. While most readily captured from beneath exfoliated granite flakes, these two forms probably inhabit any rock crevices or cracks in this habitat and I have taken them under trash piles near boulders. *Xantusia vigilis* is found most abundantly under litter in the higher arid regions of southern California, southern Nevada and extreme southwestern Utah, and the dry regions of Baja California, Mexico. They are particularly common under yucca and agave debris in the driest areas but have been taken under fallen pine logs and rarely under granite flakes in regions not inhabited by either *X. henshawi* or *X. arizonae*. *Lepidophyma gageae* has been taken only in limestone crevices in the limestone region of Hidalgo and San Luis Potosi, Mexico. The other members of the genus *Lepidophyma* are from wooded areas and are usually found under debris on the forest floor.

The family as a whole is made up of rather retiring, secretive lizards that are probably most active at night.

INFRAFAMILIAL UNITS IN THE XANTUSIIDAE

The following natural key will serve to distinguish between the subfamilies and genera recognized. Each alternative of the key has two parallel sections, the first giving a synopsis of external features and the second of osteological differences.

A NATURAL KEY TO THE RECENT SUBFAMILIES AND GENERA OF XANTUSIID LIZARDS

- 1a. Two frontonasal scales; a single frontal; no parietals; pretympansics large flattened scales; a single anterior postmental; anterior pregulars flattened, plate-like scales. Nasal bones completely separated from one another by

nasal process of premaxillary, which reaches frontal; frontal single, parietal single; squamosal separated from parietal; no epipterygoid process on prootic; anterior palate of incompletely neochoanate type, with fenestra vomeronasalis externa completely surrounded by prevomer; sternum with a definite posterior projection; clavicles hook-shaped without closed foramina; phalangeal formula of hand 2-3-4-4-3. (CRICOSAURINAE)
 *CRICOSAURA*

1b. One frontonasal scale; two frontals; two parietals; pretympansics not flattened or rectangular, round; a pair of anterior postmentals or postmentals fused with infralabials; anterior pregulars not flattened or plate-like, rounded. Nasal bones contacting one another for most of length, premaxillary not reaching to frontals; two frontals; two parietals; squamosal contacting parietal; an epipterygoid process from prootic; anterior palate of paleochoanate type, fenestra vomeronasalis externa bordered by prevomer and maxillary; sternum without a posterior projection; clavicles perforate, with large, completely closed foramina; phalangeal formula of hand 2-3-4-5-3. (XANTUSIINAE)

2a. Nostrils pierced in suture between nasal, postnasal, rostral and first supralabial; supraoculars well-developed; postmentals and infralabials distinct; gulars enlarged into plates which are much larger than pregulars; scales on back and sides essentially homogenous in size and shape; radials and femorals enlarged into plates; caudal scales arranged in whorls of equal sized scales. Orbit not completely roofed over above by frontal; prefrontal extending onto top of head to separate anterior portion of frontal from orbit; postfronto-orbital not expanded medially, gradually decreasing in width posteriorly.

3a. No pretemporals; temporal series of three or four enlarged plates; two rows of supraoculars; ventrals in 16 longitudinal rows; caudals faintly keeled. Jugal, postfronto-orbital and squamosal expanded; ectopterygoid and palatine in contact or narrowly separated from one another; teeth triconodont, mandibular teeth lying internal to maxillary teeth when mouth closed.
 *KLAUBERINA*

3b. Pretemporals present; temporal series of five to seven slightly enlarged granules; one row of supraoculars; ventrals in 12-14 longitudinal rows; caudals smooth. Jugal, postfronto-orbital and squamosal reduced, very narrow; ectopterygoid and palatine widely separated from one another; teeth simple, mandibular teeth interdigitating with maxillary teeth when mouth closed.
 *XANTUSIA*

2b. Nostrils pierced in suture between nasal and postnasal, separated from rostral and usually separated from first supralabial; supraoculars reduced to a fleshy ridge projecting from side of frontal above eye; postmentals and

infralabials fused to form a single series; gulars small, same size as pre-gulars; scales on back and sides a heterogeneous mixture of granules and enlarged scales; radials and femorals not enlarged, same sizes as other scales on limbs; caudals arranged in whorls of large and small scales. Orbit completely roofed over above by frontal, outer margins of frontal even, not concave; prefrontal restricted to side of head, not separating anterior portion of frontal from upper margin of orbit; postfronto-orbital expanded medially, not gradually decreasing in width posteriorly.
 *LEPIDOPHYMA*

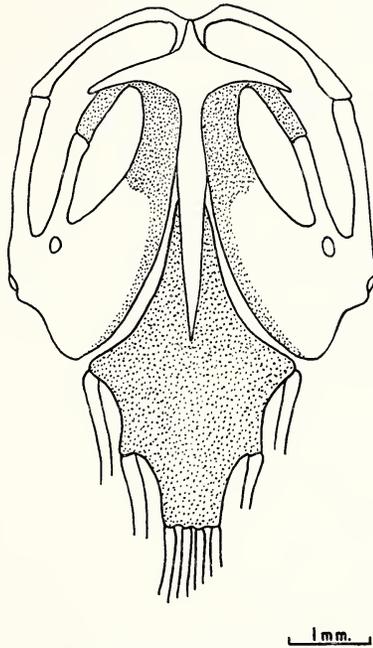


Fig. 5. Ventral view of pectoral girdle of *Cricosaura* (JMS 315).

DESCRIPTIONS

Subfamily CRICOSAURINAE, new subfamily

DEFINITION: Two frontonasal scales, a single frontal; no parietals; pre-tympanics large, flattened scales; a single anterior postmental; anterior pre-gulars flattened, plate-like scales; nasals completely separated from one another by nasal process of premaxillary that reaches to frontal; frontal single; parietal single; squamosal separated from parietal; no epipterygoid process from prootic; anterior palate of incompletely neochoanate type, fenestra vomeronasalis externa completely surrounded by prevomer; sternum

with a definite posterior projection; clavicles hook-shaped without closed foramen; phalangeal formula of hand 2-3-4-4-3.

A single monotypic genus is placed in this subfamily.

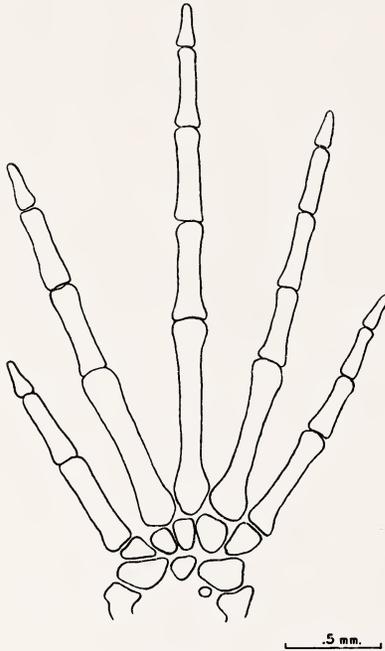


Fig. 6. Dorsal view of skeleton of right manus in *Cricosaura* (JMS 315).

Genus *CRICOSAURA* Gundlach and Peters, 1863

Figures 5-9

1863. *Cricosaura* Gundlach and Peters, p. 362, in Peters (generic type *Cricosaura typica* Gundlach and Peters, 1863, by monotypy).

1890. *Cricolepis* Boulenger, p. 83 (substitute name for *Cricosaura*, therefore takes same type).

DEFINITION: No median; pretemporals present; three enlarged temporals; two rows of supraoculars; nostril pierced in nasal-postnasal suture; postmentals and infralabials distinct; gulars enlarged rectangular scales, about same size as anterior pregulars; dorsal scales flattened, almost quadrangular, homogeneous in size except for two or three reduced rows in middle of back; ventrals in eight longitudinal rows; radials and femorals enlarged into small plates; caudal scales smooth, with two rows of small dorsal scales for each row of larger ventral scales.

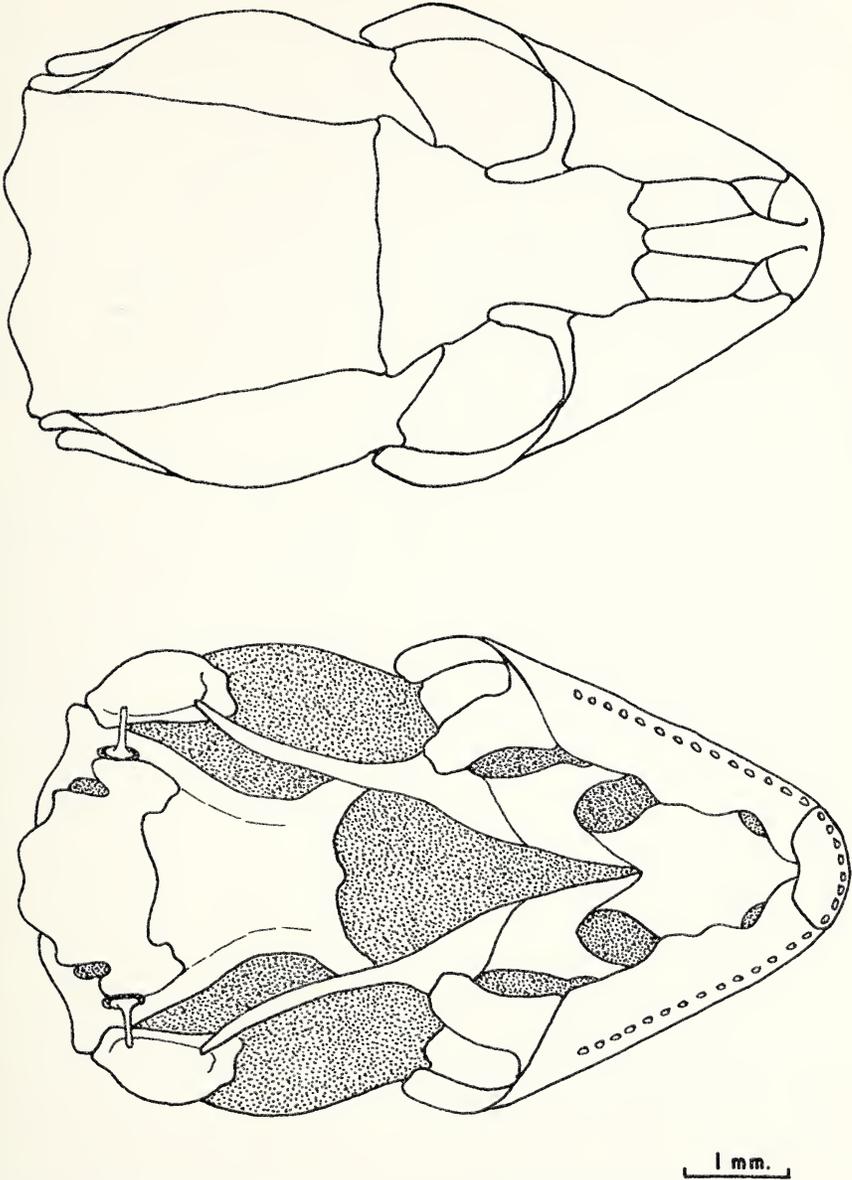


Fig. 7. Dorsal and ventral views of skull of *Cricosaura* (JMS 315).

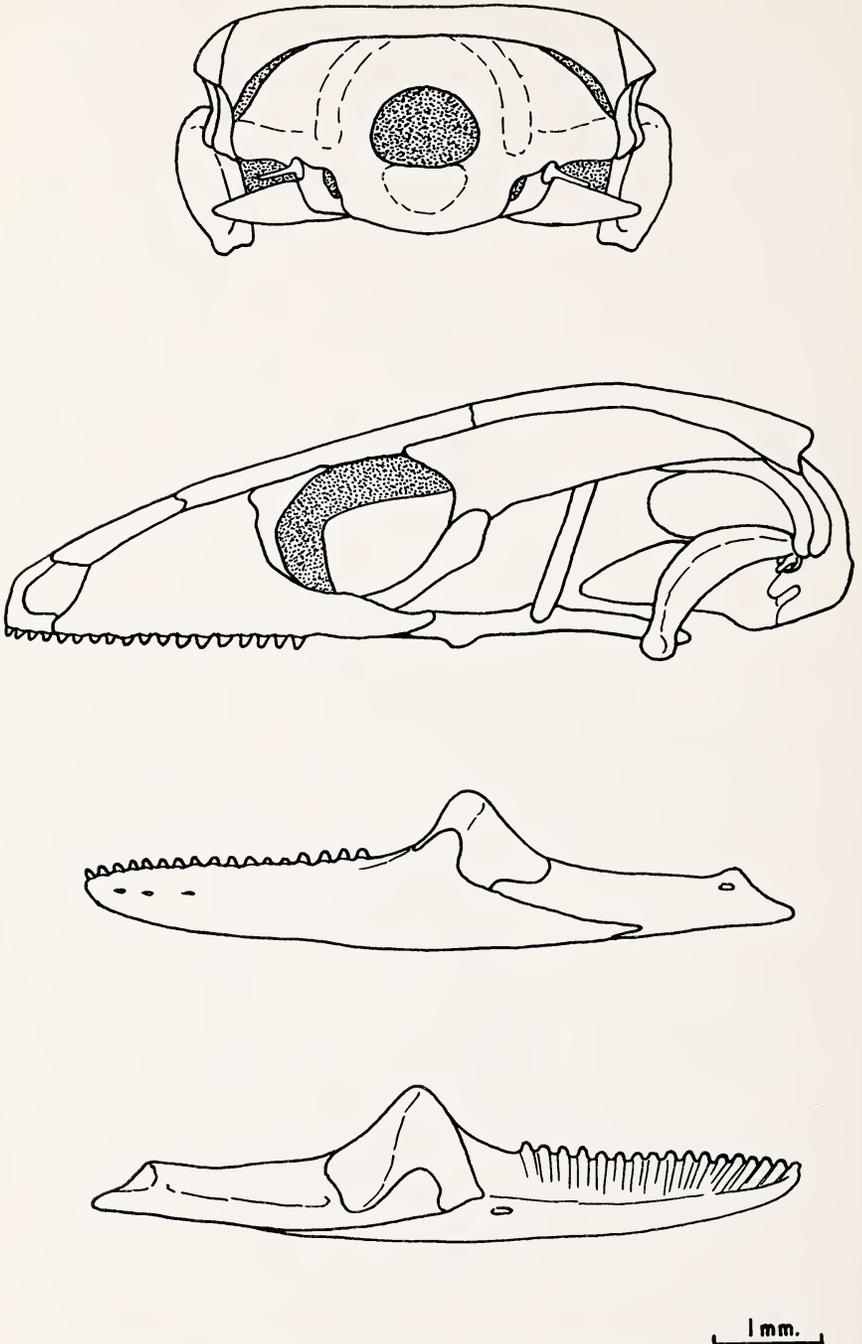


Fig. 8. Lateral and posterior views of skull of *Cricosaura* (JMS 315).

Cranium without osteoderms; no parietal foramen; prefrontal extending onto top of cranium; jugal narrow, postfronto-orbital slightly expanded medially; ectopterygoid and palatine widely separated; teeth on both jaws simple, interdigitating with one another when mouth closed.

RANGE: Known only from the Cabo Cruz region, Oriente Province, Cuba.

This genus contains but a single known species.

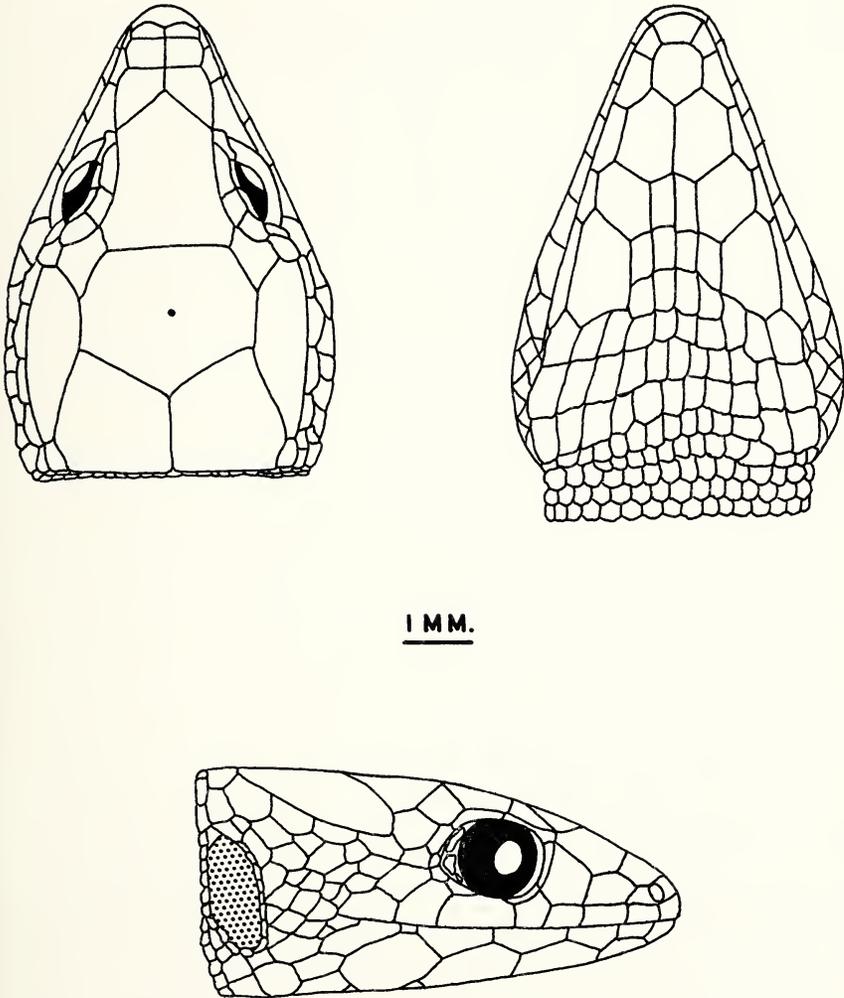


Fig. 9. Arrangements of head scales in *Cricosaura*; dorsal, ventral and lateral views (USC 1653).

Subfamily XANTUSIINAE Baird, 1859

DEFINITION: One frontonasal scale; two frontals; two parietals; pretympans granular; anterior postmentals paired or fused to infralabials; anterior pregulars granular; nasals contacting one another for most of their length; premaxillary not reaching frontals; frontals paired; parietals paired; squamosal touching parietal; an epiptyergoid process from prootic; anterior palate of paleochoanate type, fenestra vomeronasalis externa bordered by prevomer and maxillary; sternum without posterior projection; clavicles perforate; phalangeal formula of hand 2-3-4-5-3.

Genus *KLAUBERINA* Savage, 1957

Figures 10-13

1957. *Klauberina* Savage, p. 83 (generic type *Xantusia riversiana* Cope, 1883, by original designation).

DEFINITION: A large median; no pretemporals; temporal series of enlarged plates; two rows of supraoculars; nostril pierced at juncture between nasal, postnasal, rostral and first supralabial; postmentals and infralabials distinct; gulars enlarged rectangular plates much larger than pregulars; dorsal scales granular, essentially homogeneous in size and shape; ventrals in 16 longitudinal rows; radials and femorals forming enlarged plates; caudal scales faintly keeled, arranged in whorls of scales all of same size.

Cranium covered by osteoderms; frontals not roofing over orbit, outer margins concave in outline; a parietal foramen sometimes roofed over by osteoderms; prefrontal extending onto top of head; jugal moderate; postfronto-orbital not expanded medially, gradually decreasing in width from anterior to posterior; ectopterygoid and palatine nearly in contact with one another; teeth on both jaws strongly triconodont, with all cusps in a single median row, mandibular teeth lying internal to maxillary teeth when mouth closed.

RANGE: Known only from San Clemente, San Nicholas and Santa Barbara Islands in the Channel Island group off the coast of southern California.

A single species is included in this genus, which is most closely related to *Xantusia* Baird, 1859.

Genus *XANTUSIA* Baird, 1859

Figures 14-18

1859. *Xantusia* Baird, p. 255 (generic type *Xantusia vigilis* Baird, 1859, by monotypy).

1895. *Amoebopsis* Cope, p. 758 (generic type, *Xantusia gilberti* Van Denburgh, 1895 = *Xantusia vigilis* Baird, 1859, by monotypy).

1895. *Zablepsis* Cope, p. 758 (generic type, *Xantusia henshawi* Stejneger, 1893, by monotypy).

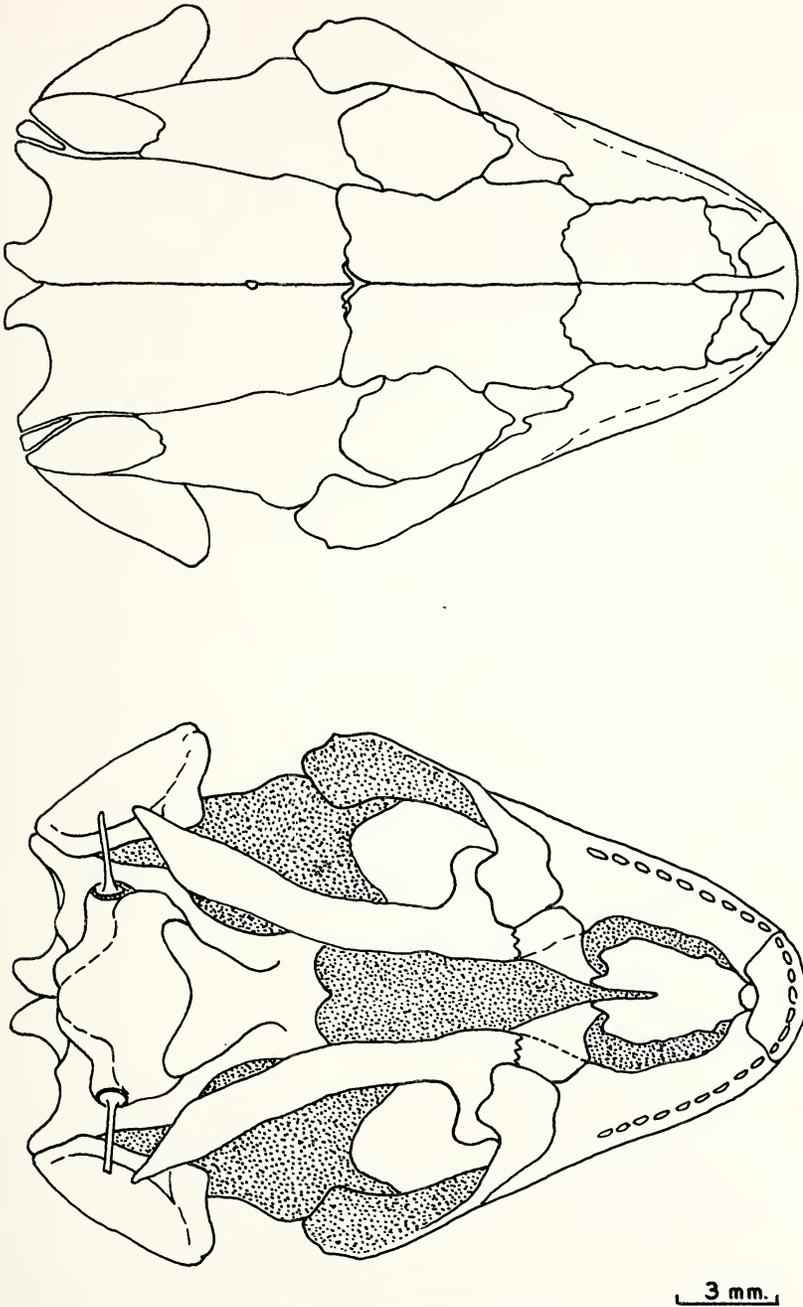
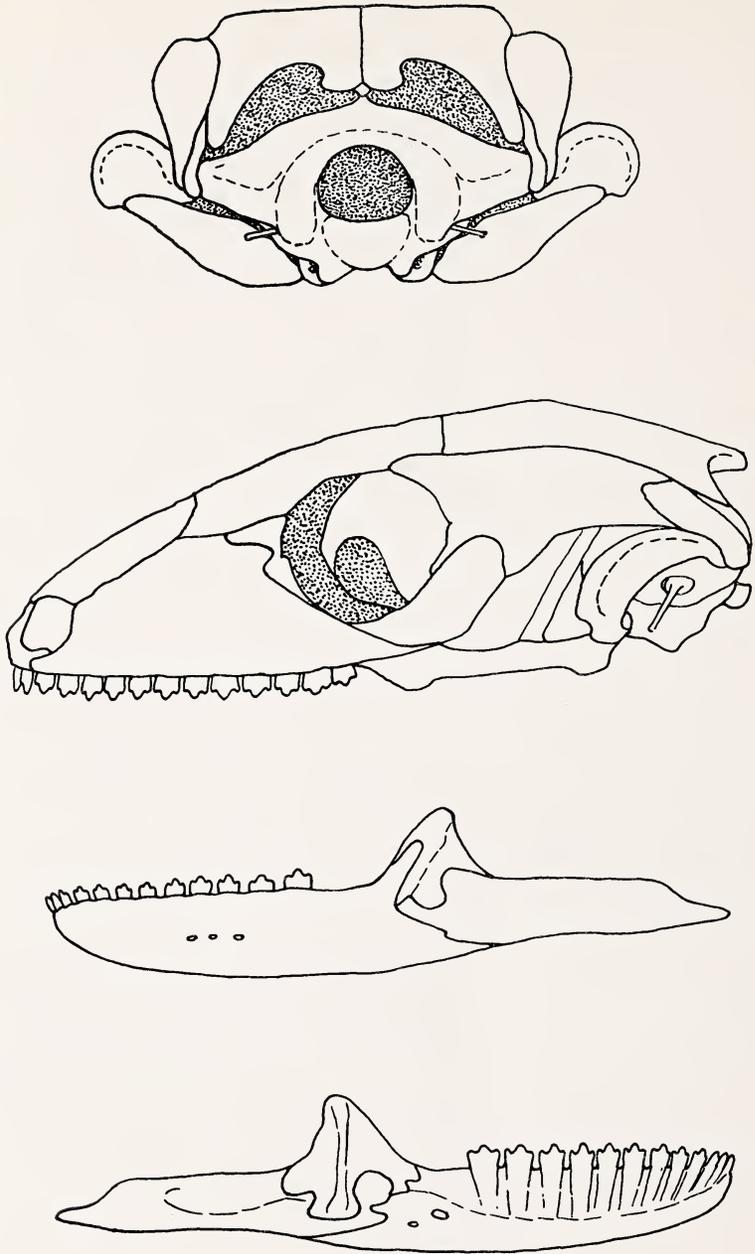
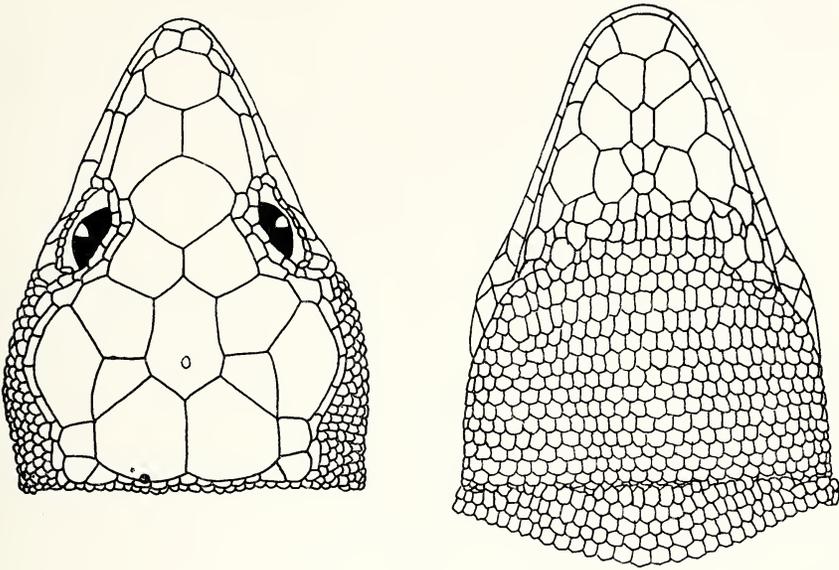


Fig. 10. Dorsal and ventral views of the skull of *Klauberina* (JMS 311).



3 mm.

Fig. 11. Lateral and posterior views of skull of *Klauberina* (JMS 311).



2 MM.

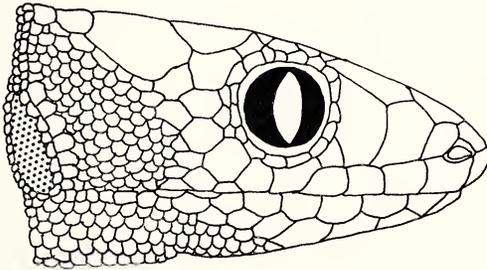


Fig. 12. Arrangement of head scales in *Klauberina*; dorsal, ventral and lateral views (LACM 11355).

DEFINITION: A large median; pretemporals present; temporal series of small scales; one row of supraoculars; nostrils pierced at juncture between nasal, postnasal, rostral and first supralabial; postmentals and infralabials distinct, gulars enlarged plates, much larger than anterior pregulars; dorsal scales granular, essentially homogeneous in size and shape; ventrals in 12-14 longitudinal rows; radials and femorals forming large plates; caudal scales smooth, not arranged in alternating whorls of large and small scales.

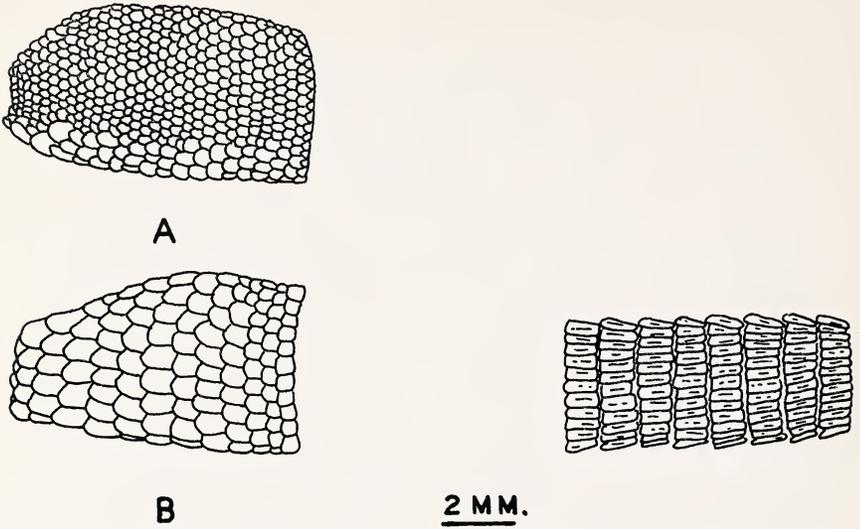
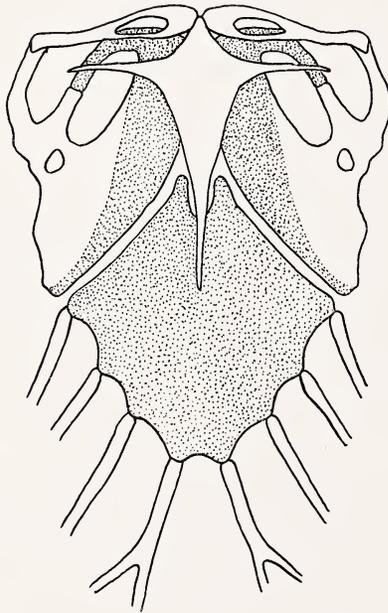


Fig. 13. Scutellation in *Klauberina*: femoral region (left) A. dorsal, B. anterior; lateral view of tail (right). (LACM 11355).



1 mm.

Fig. 14. Ventral view of pectoral girdle of *Xantusia henshawi* (JMS 316).

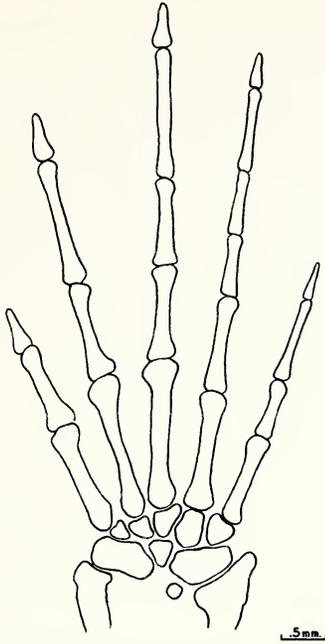


Fig. 15. Dorsal view of skeleton of right manus in *Xantusia arizonae* (JMS 317).

Cranium without osteoderms (except possibly in old *X. henshawi*); frontals not roofing over orbits, outer margins concave in outline; parietal foramen present; prefrontal extending onto top of head; jugal very narrow; postfronto-orbital not expanded medially, gradually decreasing in width from anterior to posterior; ectopterygoid and palatine widely separated from one another; teeth on both jaws simple, interdigitating with one another when mouth is closed.

RANGE: Found from extreme southern Utah, southern Nevada, northwestern and central Arizona south and west through southern California to tip of Baja California, Mexico; also found in the inner coast ranges of central California north to San Benito County and in extreme northwestern Sonora, Mexico.

The three species referred to the genus are *henshawi*, *arizonae* and *vigilis*.

NOTES ON *XANTUSIA*: Brattstrom (1953:374) has recently listed *X. vigilis* as fossil in the La Brea tar pits in Los Angeles, Los Angeles County, California. He points out that the species must have had formerly a wider range because the nearest locality records are from 25 miles away across mountain ranges. However, examination of Brattstrom's specimens, fragments of the jaws, reveal them to be totally unlike the skeleton of any living

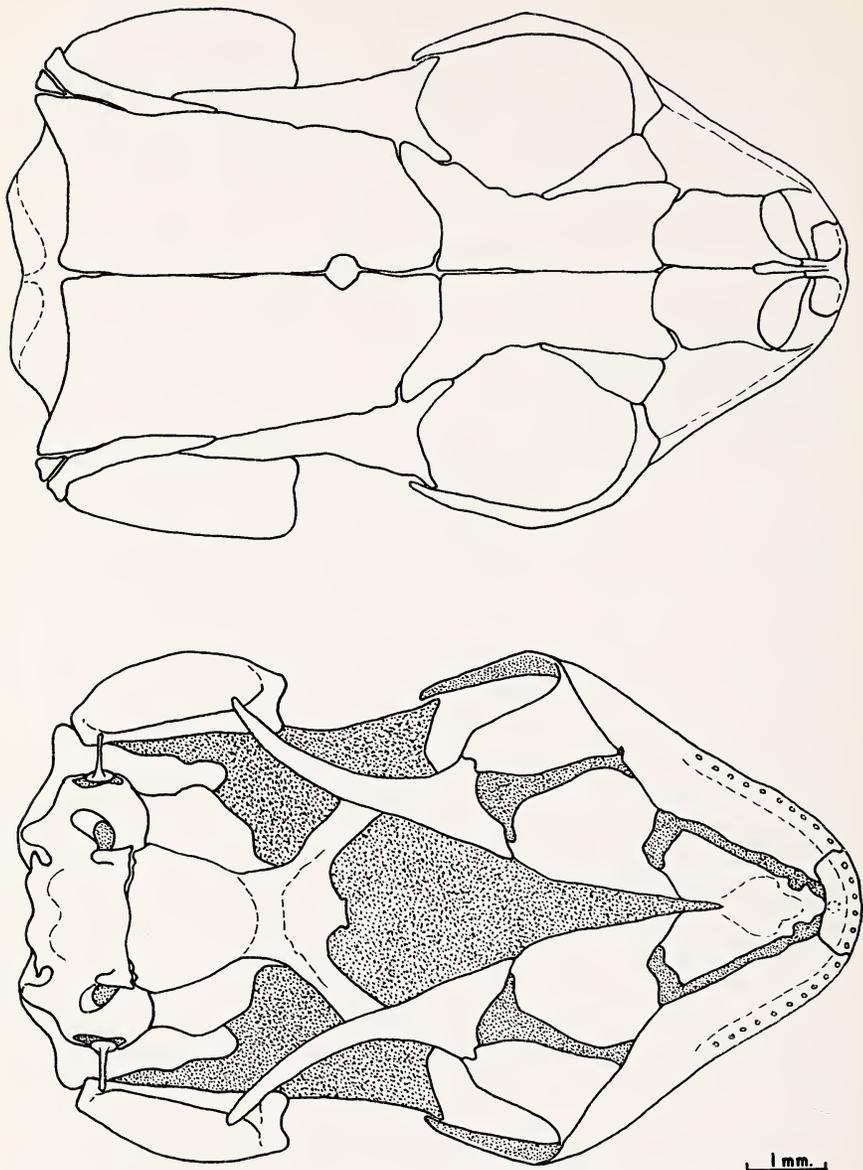


Fig. 16. Dorsal and ventral views of skull of *Xantusia vigilis* (JMS 313).

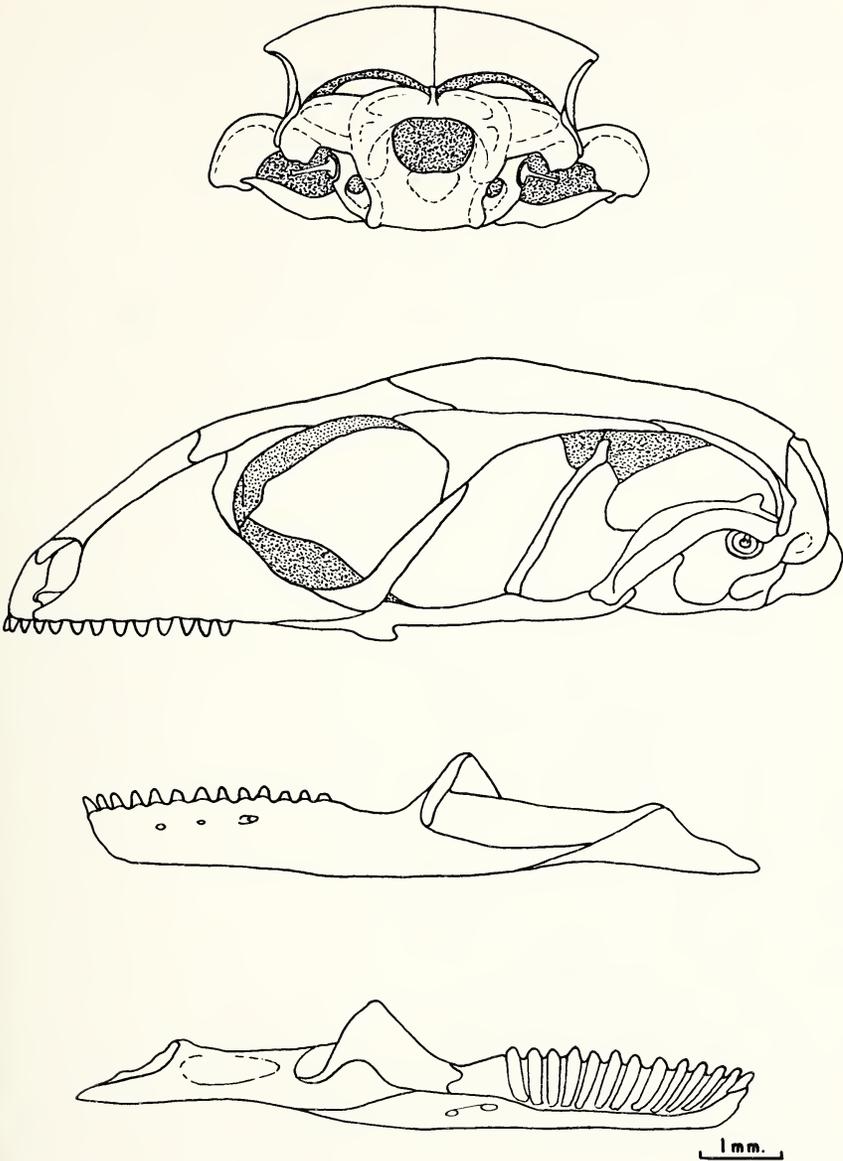


Fig. 17. Lateral and posterior views of skull of *Xantusia vigilis* (JMS 313).

Xantusia. Closer scrutiny indicates that they belong to some member of the family Iguanidae, probably the genus *Uta*. Brattstrom's statement that all xantusiids have tricuspid teeth, and his remarks propoing to establish that tricuspid teeth are present in *Xantusia vigilis*, are in error, as proved by examination of his material and the osteological work done in preparation of this paper. Hecht (1956) mentions the proper allocation of this specimen based on my re-examination of the La Brea jaw fragments.

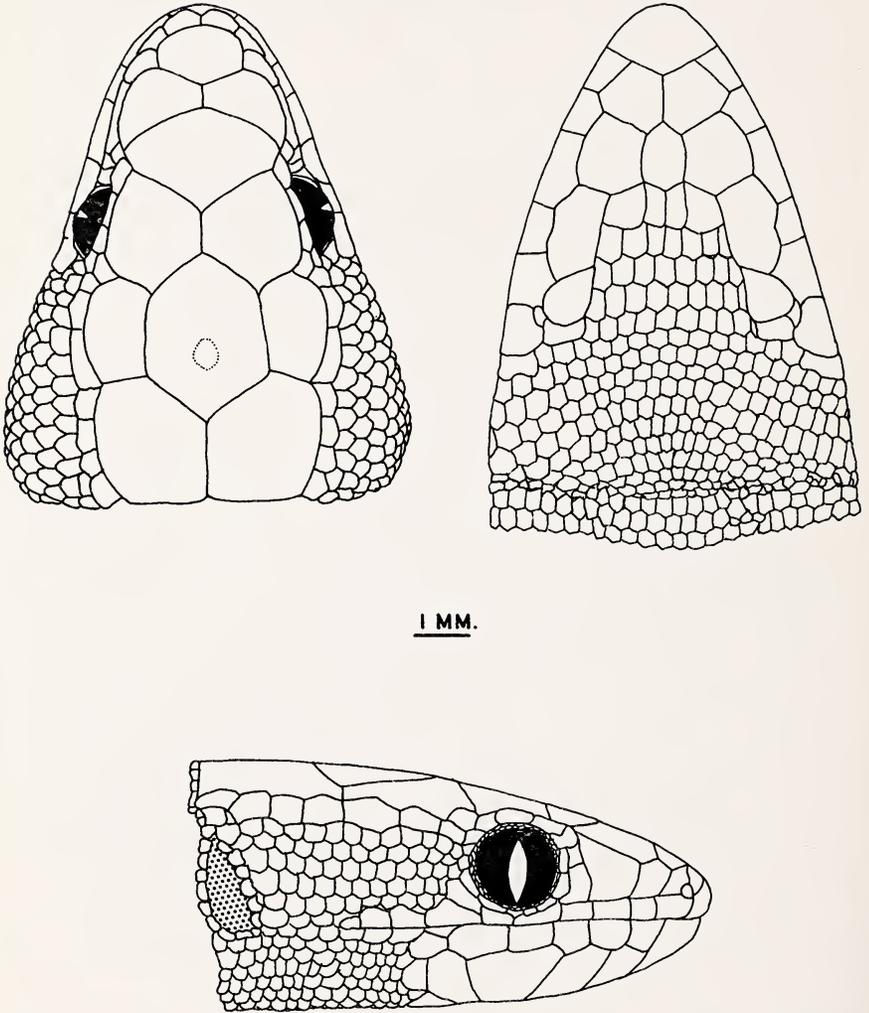
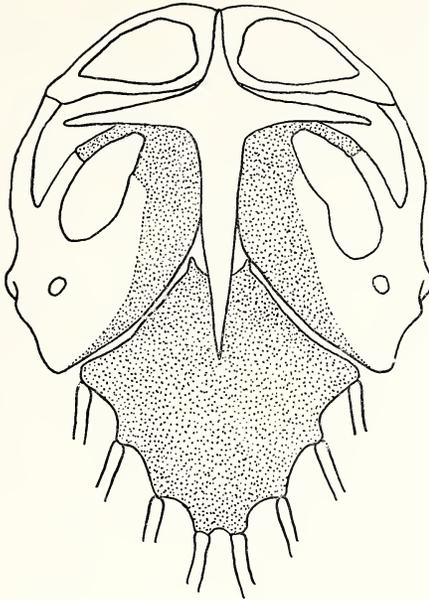


Fig. 18. Arrangement of head scales in *Xantusia vigilis*; dorsal, ventral and lateral (USC-AAS 59-228).



1 mm.

Fig. 19. Ventral view of pectoral girdle of *Lepidophyma gaigeae* (JMS 318).

Genus *LEPIDOPHYMA* Auguste Duméril, 1851

Figures 19-23

1851. *Lepidophyma* Auguste Duméril (in Duméril and Duméril), p. 137 (generic type *Lepidophyma flavimaculatum* A. Duméril, 1851, by monotypy).

1863. *Poriodogaster* A. Smith (in Gray), p. 154 (generic type, *Poriodogaster grayii* A. Smith, 1863 = *Lepidophyma flavimaculatum* A. Duméril, 1851, by monotypy).

1878. *Akleistops* Müller, p. 390 (generic type, *Akleistops guatemalensis* Müller, 1878 = *Lepidophyma flavimaculatum* Duméril, 1851, by monotypy).

1939. *Gaigeia* Hobart M. Smith, p. 24 (generic type, *Lepidophyma gaigeae* Mosauer, 1936, by monotypy).

1953. *Impensodens* Langebartel, p. 102 (generic type, *Impensodens arizelogyphus* Langebartel, 1953, by monotypy).

DEFINITION: A median sometimes present; a pretemporal; temporal series of enlarged plates; supraoculars reduced to a narrow fleshy ridge above the eye; nostril pierced in nasal-postnasal suture; postmentals and infralabials fused to form a single series; gulars not enlarged, same size as pregulars; dorsal scales a mixture of heterogeneous granules of various sizes or of granules and enlarged tuberculate scales; ventrals in 8-10 longitudinal rows; radials and femorals same size as other scales on limbs, not enlarged into plates; most caudal scales with a definite keel, arranged in whorls of alternating large and small scales.

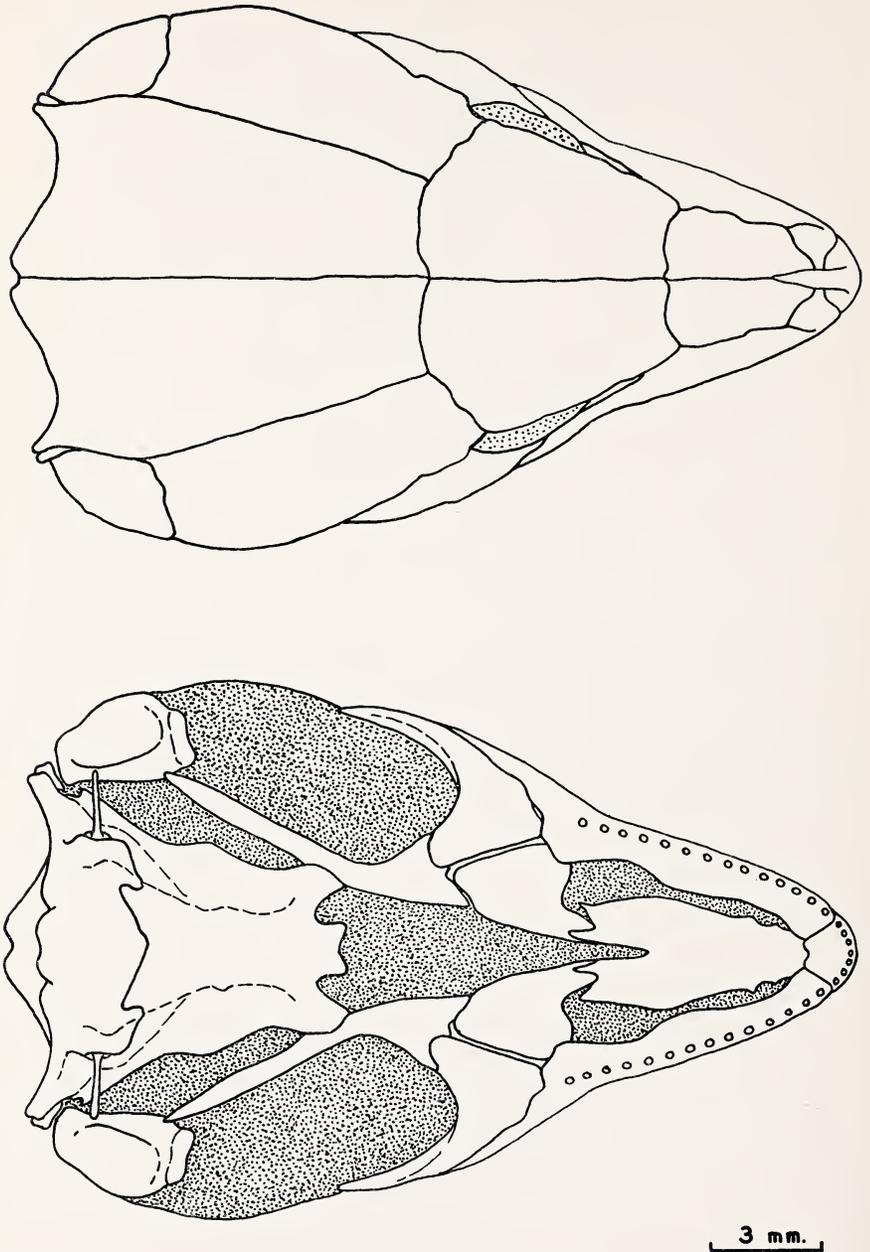


Fig. 20. Dorsal and ventral views of skull of *Lepidophyma flavimaculatum* (JMS 319).

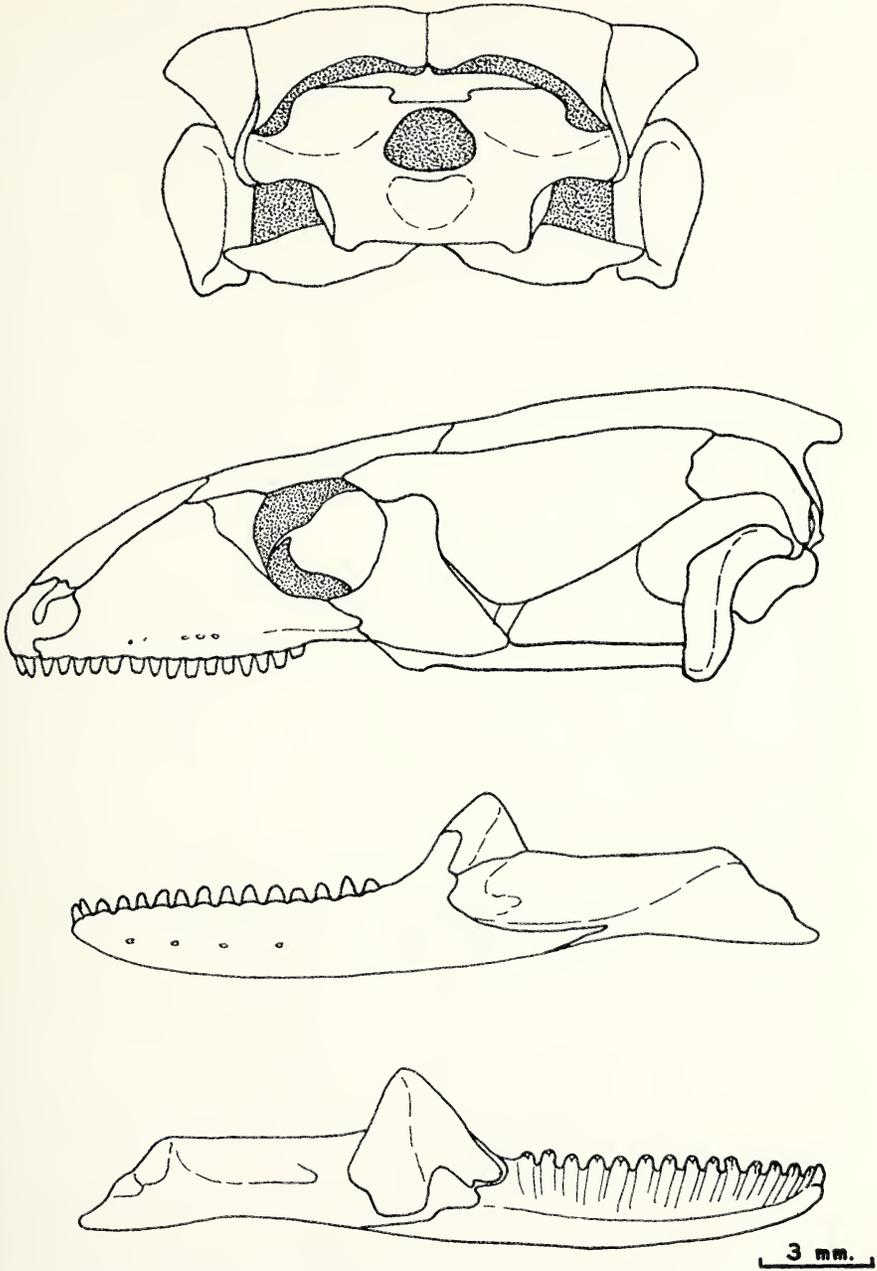


Fig. 21. Lateral and posterior views of skull of *Lepidophyma flavimaculatum* (JMS 319).

Cranium without evidence of osteoderms; frontals roofing over orbits, outer margins straight, never concave; no parietal foramen; prefrontal excluded from upper surface of skull; jugal greatly expanded; postfronto-orbital greatly expanded, widest medially; ectopterygoid and palatine meeting or narrowly separated; teeth on both jaws weakly tricondont with anterior and posterior cusps on inner surface of teeth, when mouth is closed the teeth interdigitate or the mandibular teeth lie internal to maxillary teeth.

RANGE: Central and eastern Mexico from Tamaulipas south, and from Guerrero, on the west Mexican coast, through Central America to Panamá.

NOTES ON *LEPIDOPHYMA*: The genus *Lepidophyma* was first introduced to science by Auguste Duméril (in Duméril and Duméril, 1851:137), who described a new genus and species, *Lepidophyma flavimaculatum*, from Petén Province, Guatemala. He redescribed the species the next year (1852: 412, pl. 17) and presented an excellent colored plate of it.

Gray (1863:154) published the manuscript name *Poriodogaster grayii* A. Smith for a specimen of this genus of unknown provenance but thought by Gray to be from Baja California, Mexico.

Peters (1874:307) reported a specimen of *Poriodogaster* from Panamá for the first definite locality for this nominal form.

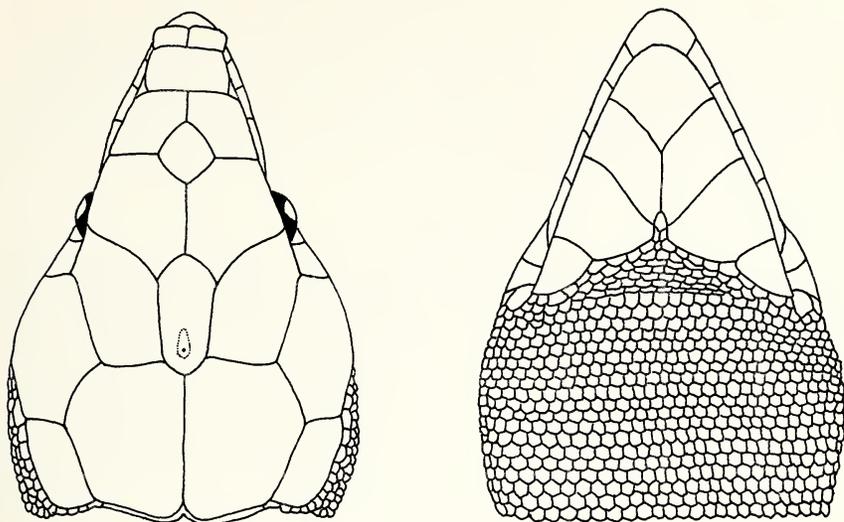
Bocourt (1876:307) described a new *Lepidophyma*, *L. smithii*, from Tehuantepec (probably the isthmus not the town), Mexico and Guatemala. He also concluded that *Poriodogaster grayii* was a synonym of *L. flavimaculatum* A. Duméril.

In one of the classic works on American herpetology, Bocourt (in Duméril, Bocourt and Mocquard, 1878:306-313) described and illustrated in some detail both *Lepidophyma flavimaculatum* (pl. 20F) and *Lepidophyma smithii* (pl. 20F and 20G).

In the same year Müller (1878:390) inadvertently proposed a new genus and species, both of which are synonymous with *Lepidophyma flavimaculatum*. Müller had an example of this night lizard from Guatemala which he thought was a new form when it was first received in Basel. He gave it the manuscript name *Akleistops guatemalensis*. In his paper he refers this example to *Lepidophyma* but is uncertain as to whether the specimen was representative of *L. flavimaculatum*, *L. smithii* or *L. grayii*. In passing, he mentions his own manuscript name and therefore unintentionally proposes a new generic and specific name for his animal.

Barbour (1924:10) described a new subspecies, *obscurum*, of *L. flavimaculatum* from Panamá. His form is based entirely upon differences in coloration between Panamá and Guatemala members of the species.

Mosauer (1936:3) gives the description of an entirely new kind of *Lepidophyma* taken in the limestone region of Hidalgo, Mexico. This form, *L. gaigeae*, differed radically from either of the two previously recognized forms in being without the numerous enlarged, tuberculate scales on body and tail that characterize both *L. flavimaculatum* and *L. smithii*.



10 MM.

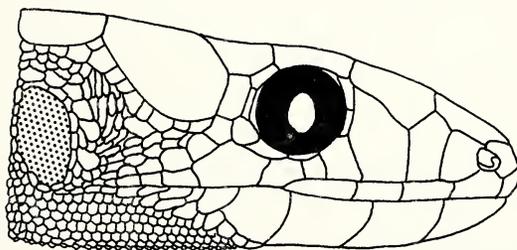
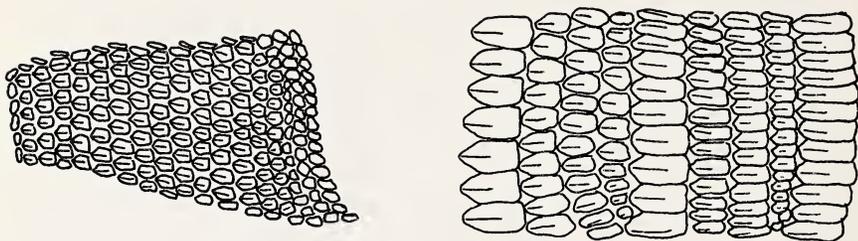


Fig. 22. Arrangement of head scales in *Lepidophyma flavimaculatum*; dorsal, ventral and lateral (USC-CR 178).

Hobart M. Smith (1939:24) was so struck by the marked differences between *L. gaigeae* and the other known forms that he proposed a new genus, *Gaigeia*, for Mosauer's species. The only difference given by Smith to separate the two nominal groups rested on the degree of enlargement and differentiation of the tuberculate dorsal scales.

In that same year Taylor (1939:131) described a new species of *Lepidophyma* from high forests in Hidalgo, Mexico. This lizard, *L. sylvaticum*, is nearly intermediate between *L. flavimaculatum* and *Gaigeia gaigeae* in squamation. The new form has tubercles on the sides and back as in the former species, but they are not lined up to form definite vertical rows and resemble the latter form to some degree.



2 MM.

Fig. 23. Scutellation in *Lepidophyma*: anterior surface of femoral region (left), lateral view of tail (right).

Hobart M. Smith (1942:349) described two new species of *Gaigeia* from Oaxaca, Mexico. One, *G. dontomasi*, is very similar to *G. gaigeae*, while the other, *G. radula*, resembles Taylor's *sylvaticum*. Smith neatly solves the problem of where to place the two latter forms by including them within the limits of *Gaigeia* simply because they do not have the lateral tubercles arranged in vertical rows. Smith also described two new subspecies of *Lepidophyma smithii* in this same paper. One form, *L. smithii tehuanae*, is from Oaxaca, Mexico; the second is from Querétaro, Mexico, and is named *L. smithii occulor*.

Subsequent workers have accepted Smith's arrangement of two genera, *Lepidophyma* with two species, and *Gaigeia* with four.

Walker (1955) described a new race, *Lepidophyma flavimaculatum tenebrarum* from northwest Tamaulipas, Mexico, and concluded that the recognized races of *flavimaculatum* and *smithii* are representative of a single species. In addition he described a new cave-dwelling species *Lepidophyma micropholis*, also from Tamaulipas. This form is clearly allied to *L. flavimaculatum* although distinctive in details of lepidosis.

Taylor (1955) described three new species of *Lepidophyma* from Costa Rica, *reticulatum*, *anomalum* and *ophiophthalmum*. All are members of the *L. flavimaculatum* group. He subsequently (1956) placed *anomalum* in the synonymy of *L. flavimaculatum obscurum*.

Neither *reticulatum* or *ophiophthalmum* may be separated from *Lepidophyma flavimaculatum* on the basis of the original descriptions, since all

characters of the two forms fall within the range of variation of the later species. Examination of topotypic material of the nominal Costa Rican taxa reveals no features inconsistent with their reference to *L. flavimaculatum*. Presently no attempt is made to determine the possible subspecific allocation of Taylor's names since Mr. Jerome B. Tulecke, University of Kansas, is undertaking a review of *Lepidophyma*.

Werler and Shannon (1957) reported on a new species, *Lepidophyma tuxtlae*, from Volcán San Martín, Veracruz, Mexico, which differed from *L. flavimaculatum* primarily in the arrangement of the paravertebral scale rows. This form may be tentatively regarded as a race of *L. flavimaculatum*.

Lepidophyma pajapanensis (Werler, 1957) from Volcán San Martín Pajapan, Veracruz, Mexico, is also related to *L. flavimaculatum* and may be a valid taxon, allied to *L. micropholis*.

The lizards included in the genus *Gaigeia* by Smith (1942) appear to form two distinct species groups. One of these contains *Gaigeia gaigeae* and *Gaigeia dontomasi* which differ markedly in lateral scutellation from *Lepidophyma flavimaculatum*. However, the divergences in dorsal squamation present in these forms are bridged in the second group placed by Smith in *Gaigeia*. The two species, *Gaigeia radula* and *Gaigeia sylvatica* are intermediate in scutellation between the extremes. The former species is most like *Gaigeia gaigeae* but has enlarged tuberculate scales, while *G. sylvatica* is very similar to *Lepidophyma flavimaculatum* except that the lateral tubercles are not arranged in vertical rows. The two supposed genera are practically identical in their skeletons (see osteological section). These facts force me to the conclusion that only one genus is involved. Naturally the group takes the older name *Lepidophyma*.

The characteristics of the dorsal scales appear to have undergone a gradual change from a rather simple heterogeneous pattern of granules and enlarged scales to a pattern of granules and enlarged, keeled, tuberculate scales. Differences in these features do not seem to warrant generic recognition.

Genus *PALAEOXANTUSIA* Hecht, 1956

1956. *Palaeoxantusia* Hecht, p. 4 (generic type *Palaeoxantusia fera* Hecht, 1956, by monotypy).

DEFINITION: A genus of night-lizards based on fragmentary lower jaws (Hecht, 1956, 1959), characterized by: 1) 13 conical teeth; 2) a distinct mandibular depression and groove for the adductor mandibulae externus superficialis. The following key will serve to distinguish the genera of the family on the basis of mandibular features:

- 1a. Teeth conical
- 2a. A distinct mandibular depression and groove along outer posterior margin of dentary *PALAEOXANTUSIA*

- 2b. No distinct mandibular depression or groove along outer posterior margin of dentary.
 - 3a. 17-18 mandibular teeth *CRICOSAURA*
 - 3b. 12-16 mandibular teeth *XANTUSIA*
- 1b. Teeth triconodont
 - 4a. Cusps on teeth in a single median row *KLAUBERINA*
 - 4b. Anterior and posterior cusps on inner surface of teeth, not in line with median cusp *LEPIDOPHYMA*

Paleoxantusia is intermediate to *Klauberina* and *Xantusia* in the characteristics of the mandible and may represent the ancestral stock from which *Xantusia* developed. A single species, *P. fera* is recognized.

RANGE: Known only from Middle Eocene deposits from Sublette County, Wyoming.

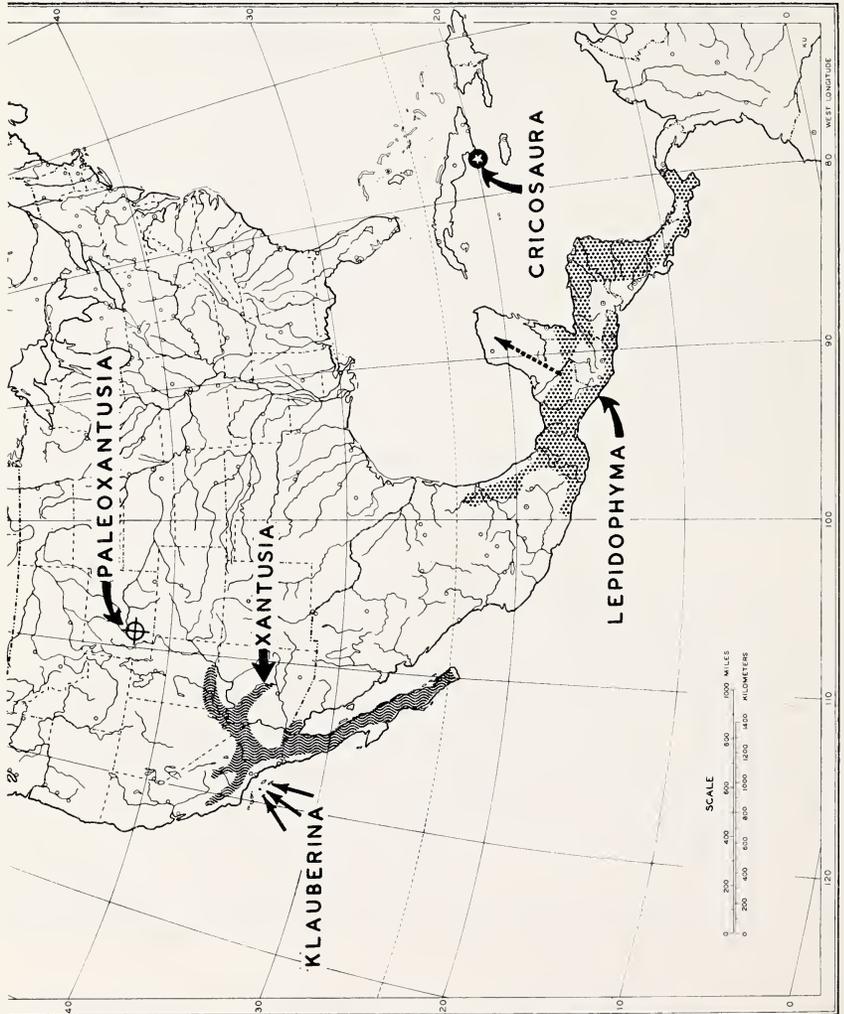


Fig. 24. Distribution of the genera of night lizards, family Xantusiidae. The arrow in the Yucatan Peninsula indicates the site for the fossil species of *Lepidophyma*.

SUMMARY CLASSIFICATION

As a result of the systematic revision of the family Xantusiidae the classification presented below has been adopted in this report. For details on the osteology, external morphology, habits, and distribution of the various genera included in the family see the appropriate sections in the main body of this paper.

Order SAURIA Macartney, 1802.

Suborder GEKKOTA Latreille, 1825.

Family XANTUSIIDAE Baird, 1859.

Subfamily CRICOSAURINAE, new subfamily.

Genus *CRICOSAURA* Gundlach and Peters, 1863.

Cricosaura typica Gundlach and Peters, 1863.

Subfamily XANTUSIINAE Baird, 1859.

Genus *KLAUBERINA* Savage, 1957.

Klauberina riversiana riversiana (Cope, 1883).

Klauberina riversiana reticulata (Hobart M. Smith, 1946).

*Genus *PALEOXANTUSIA* Hecht, 1956.

**Paleoxantusia fera* Hecht, 1956.

Genus *XANTUSIA* Baird, 1859.

Xantusia henshawi Stejneger, 1893.

Xantusia arizonae Klauber, 1931.

Xantusia vigilis vigilis Baird, 1859.

Xantusia vigilis gilberti Van Denburgh, 1895.

Xantusia vigilis utahensis Tanner, 1957.

Xantusia vigilis wigginsi Savage, 1952.

Genus *LEPIDOPHYMA* Auguste Duméril, 1851.

Lepidophyma gaigeae Mosauer, 1936.

Lepidophyma dontomasi (Hobart M. Smith, 1942).

Lepidophyma sylvaticum Taylor, 1939.

Lepidophyma radula (Hobart M. Smith, 1942).

Lepidophyma flavimaculatum flavimaculatum

A. Duméril, 1851.

Lepidophyma flavimaculatum obscurum Barbour, 1924.

Lepidophyma flavimaculatum occulor

Hobart M. Smith, 1942.

Lepidophyma flavimaculatum smithii Bocourt, 1876.

Lepidophyma flavimaculatum tehuanae

Hobart M. Smith, 1942.

Lepidophyma flavimaculatum tenebrarum

Walker, 1955.

Lepidophyma flavimaculatum tuxtlae

Werler and Shannon, 1957.

Lepidophyma micropholis Walker, 1955.

Lepidophyma pajapanensis Werler, 1957.

**Lepidophyma arizeloglyphus* (Langebartel, 1953).

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THE MACHRIS BRAZILIAN EXPEDITION

BOTANY: *LYTHRACEAE*

By A. LOURTEIG¹

ABSTRACT: Two new species, *Diplusodon astictus* and *D. caesariatus*, are described from Brazil. Species of the genus *Cuphea* collected in Brazil are discussed.

The specimens of *Lythraceae* received from the Los Angeles County Museum were collected by Dr. E. Yale Dawson and my determinations already have been listed by him (Dawson, 1962:6). The present paper reviews some of these determinations.

Two species of *Cuphea* were collected. *C. polymorpha* St. Hilaire is, to my knowledge, the first record for the State of Goiás. The species occurs in Paraguay and in Brazil (States of São Paulo, Rio de Janeiro and Minas Gerães).

C. fuchsiifolia St. Hilaire and *C. Gardneri* Koehne are known primarily from the type collections, but the latter also from a specimen of Schwacke destroyed in Berlin and of which I have seen no duplicates. Both species are very closely related. Whether they should be considered as subspecies of one species or as two distinct species is difficult to say at present; much more material from different localities is needed. The specimen collected by Yale Dawson (14428) which I annotated as *C. fuchsiifolia* St. Hil. shows a pubescence of the leaves that would not match exactly either of the two species, and that of the stem approaches *C. Gardneri*. The size and shape of the calyx, characters to

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Fig. 1. *Diplusodon astictus*: a, branch, x $\frac{1}{2}$; a', detail of an inflorescence, x 1; b, leaf, lower surface, x 1.5; b', the same, detail of the apex, x 6; c, flower without corolla, x 3; d, anther, x 6; e, calyx with fruit, x 3. From the type and isotype.

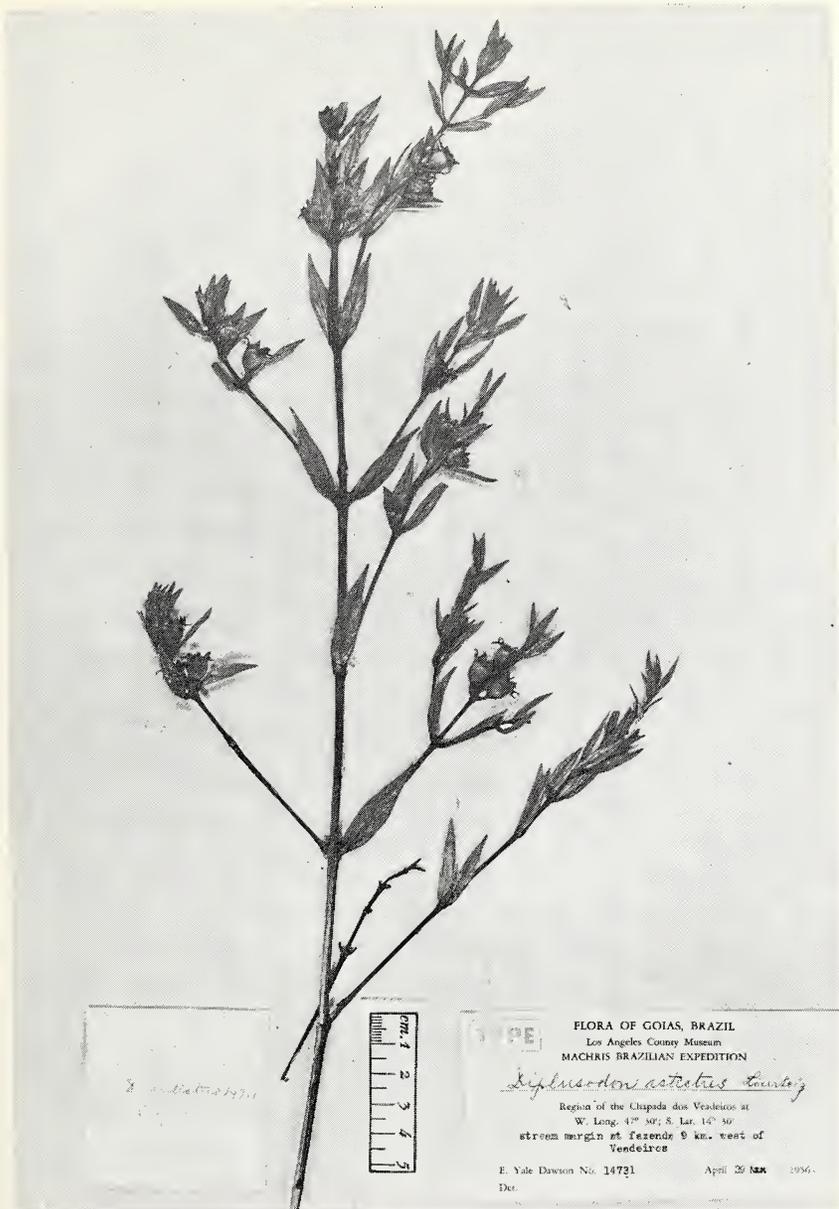


Fig. 2. *Diplusodon astictus* Lourteig. The type specimen.

which Koehne assigns importance for keying out the two species, would lead us to *C. fuchsiiifolia*. However, the shape of the leaves and the general facies of the specimen have led me to file it under *C. Gardneri* Koehne.

Nine specimens of *Diplusodon* were collected. Seven of these were already recorded for Goiás, but in several instances only on the evidence of the type collection. One specimen has not been listed because I did not recognize it. It was necessary for me to revise some other collections that were not represented in Paris in order to establish the correct names. The specimen annotated by me (*In Dawson, 1962:6*) as *D. incanus* proved, after comparison with the types of that species and its allies, to be a new species.

***Diplusodon astictus*² Lourt., n. sp.**

Figures 1 and 2

Sectio 1. Subuninerves. Series 2.

Fruticulus glaberrimus (alt. ignota), laxe ramosus, ramis decussatis. Internodia longa, usque ad 7 cm. Folia caulina internodiis breviora, in ramulis longiora, sessilia, lanceolata (25-40 x 4-9 mm), acuta vel acutiuscula, coriacea, subrigida, epunctata, nervo medio fusco, valde prominente, 1 vel 2 paribus nervorum lateralium prominulis vel parum conspicuis, marginibus subrevolutis.

Flores in ramulis multi, decussati, pedunculati (± 2 mm). Bracteolae oblongae, 1-nerviae, subacutae, tubo calycino subaequales. Calyx subcoriaceus, urceolato-campanulatus (± 8 mm); lobi dimidium tubi aequantes, triangulares acuti, acuminati; appendices lobis paullo breviores, curvato-reflexae. Petala roseo-violacea ? (± 14 x 7 mm), oblongo-subspathulata. Stamina 12, lobos subaequantia v. paullo superantia. Ovarium subglobosum. Ovula 25. Stylus calycem duplo superans.

Habitu *D. punctato* Pohl simili; foliis punctis carentibus et appendicibus calycinis bene evolutis differt.

Typus: BRAZIL, Goiás, region of the Chapada dos Veadeiros at W. Long.

²From the Greek, *αστικτός*, epunctate.

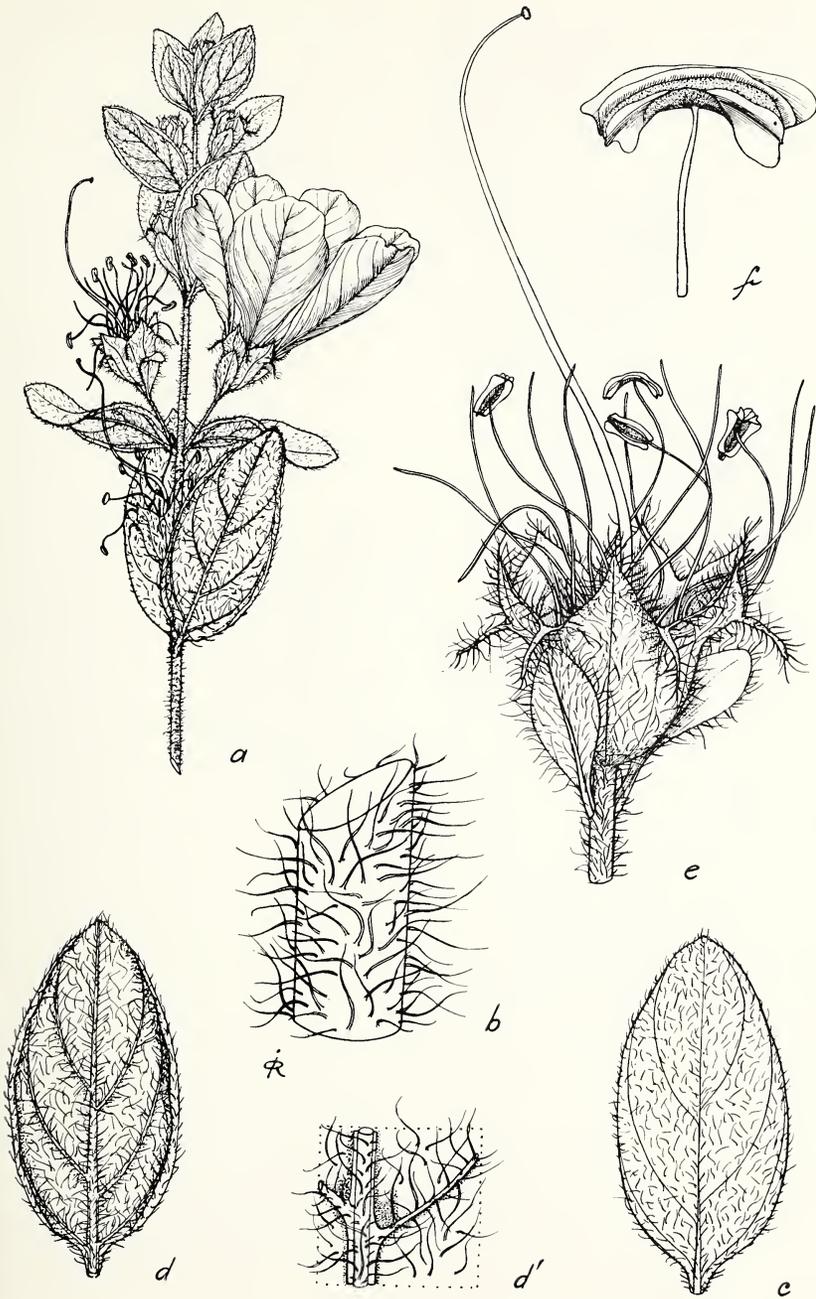


Fig. 3. *Diplusodon caesariatus*: a, apex of a branch, x 1.5; b, detail of the stem, x 10; c, leaf, upper surface, x 3; d, the same, lower surface; d', detail of d, x 6; e, flower without corolla, x 4; f, anther. From the type.



Fig. 4. *Diplusodon caesariatus* Lourteig. The type specimen.

47° 30'; S. Lat. 14° 30', stream margin of fazenda 9 Km west of Veadeiros, leg. E. Yale Dawson (14731) 29 IV 1956, U.S. Isotypus, P.

Very near to *D. punctatus* Pohl which it resembles in its habit. It differs in the absence of punctations and in the presence of appendices on the calyx.

***Diplusodon caesariatus*³ Lourt., n. sp.**

Figures 3 and 4

Sectio 2. Penninerves. Series 4.

Frutex 3 m altus, ramosissimus, dense foliatus, omnibus partibus incanovilloso-hirtellis. Ramuli subteretes minute hirtelli. Internodia usque 3 cm. longa vel brevissima. Folia internodiis longiora, ovato-oblonga vel elliptica (15-26 x 6-15 mm), subacuta, margine subrevoluta, penninervia, utroque latere costae 2 v. 3 paribus, nervorum supra impressis, subtus prominulis, subsessilia; pagina inferiore villosa-hirtella pilis secus nervos longioribus superiore pilis sparsis atque brevioribus.

Flores decussati; pedunculus hirtellus (3-4 mm); bracteolae ca. apicem insertae, tubo calycino aequilongae v. paullo minores, obovato-ellipticae, l-nerviae, basi attenuatae, pubescentia ei calycis simillima. Calyx (5-6 mm) campanulatus, villosus; lobi acuti, ciliati, tubi ½-⅓ aequilongi, erectiusculi; appendices lobis aequilongae v. subaequilongae, patulae vel ± reflexae. Petala roseo-violacea, obovata vel suborbicularia (15-17 x 10-12 mm). Stamina 16, lobos duplo superantia. Ovarium obovoideum vel subglobosum, complanatum. Ovula 22-26. Stylus 2½-3½-plo calycem superantia. Stigmata crassa.

Species *D. incano* Gardner simillima, magnitudine foliorum, florumque, praetera pubescentia (hirsuta) et magnitudine bracteolarum differt. Affinis *D. humili* Koehne et *D. pulchellae* Koehne (Ser. 7) est; differt appendicibus calycinis et longitudine bracteolarum.

Typus: BRAZIL, Goias, region of the Chapada dos Veadeiros at W. Long. 47° 30'; S. Lat. 14° 30', in gallery forest area along road 19-19½ Km north of São João da Aliança, leg. Yale Dawson (14397) 19 IV 1956, P.

³From the Latin, *caesariatus*, covered with long hairs.

Following Koehne's key (*Pflanzenreich* 188, 190) we are led to *D. incanus* Gardner which agrees with the new species in its main characters, but differs in that its leaves and flowers are much smaller; the pubescence is also different. The new species is related to *D. humilis* Koehne and *D. pulchella* Koehne especially in its pubescence; it differs in the appendices of the calyx which are equal or nearly equal in length to the calyx lobes, and in the relative size of the bracteolae.

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FOSSIL BIRDS FROM THE ANZA-BORREGO DESERT

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By Hildegard Howard



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FOSSIL BIRDS FROM THE ANZA-BORREGO DESERT

By Hildegard Howard¹

ABSTRACT: Avian remains from the Vallecito Creek fauna indicate the presence of at least 28 species, including grebes, geese, ducks, raptors, quail, turkey, rail, coot, kildeer, woodpecker and perching birds. At least ten extinct forms occur, six of which are here described as new; on the basis of relative number of extinct species, the fauna is seemingly younger than the Rexroad or Hagerman Lake faunas, but older than late Pleistocene faunas typified by the Rancho La Brea.

The avian fossils here to be discussed were collected with a much larger representation of mammals, and a few reptiles, in the Vallecito Creek valley of the Anza-Borrego desert, San Diego County, California. Field parties, directed by Dr. Theodore Downs, of the Los Angeles County Museum, have been engaged in collecting and mapping this area, under grants from the National Science Foundation, since 1958 (nos. G 5035 and G 11360). Preliminary reports of the results of the work appeared as abstracts of papers presented at meetings of the Geological Society of America (Downs, 1957, and Downs and Woodard, 1961). In the latter, such mammalian genera as *Megalonyx*, *Stegomastodon*, *Tremarctos*, *Equus* (*Plesippus*), and *Tanupolama* are tentatively recorded, and the authors conclude that the fauna is deposited in the Upper Palm Spring formation, which they consider to be of middle Pleistocene age. One other paper concerning the collections from Vallecito Creek describes a new species of pocket gopher, genus *Geomys* (White and Downs, 1961).

Unlike the abundant horse, camel and gopher, whose remains were widely and profusely distributed throughout the many collecting sites in the Vallecito Creek area, no avian species is represented by more than eleven bones, and the entire avian collection was recovered from only 25 separate collecting sites. The bird remains are poorly preserved, and seem to represent a fortuitous sampling of the avifauna of the area. Approximately 100 bones are sufficiently diagnostic to merit mention.

The more than three hundred collecting sites within the Vallecito Creek area have each been given individual Los Angeles County Museum Vertebrate Paleontology locality numbers. Where locality numbers are indicated in the following pages, it will be understood that reference is to these sites. A detailed account of the stratigraphic and geographic position of localities in the area is in preparation by Downs and Woodard. The twenty-five avian localities are to be found within the boundaries mapped on the United States Geological Survey (1959) Arroyo Tapiado and Agua Caliente Springs quadrangles of California, and in particular in Township 14 south, Range 7 and 8 east, and sections 14, 15, 23, 24, 25, 30, 32, and 36.

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Specimen numbers in the text refer to the catalogued collections in vertebrate paleontology at the Los Angeles County Museum.

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Photographs were made by George Brauer; retouching and art work by Mary Butler.

DESCRIPTION OF THE AVIFAUNA

The identifiable avian remains in the Vallecito Creek fauna represent nine orders, and at least thirteen families and twenty-eight species. About half of the species are represented by only one or two bone fragments from one or two collecting sites. No species can be said to be characteristic of the area. At best four or five sites seem to be the limit of occurrence of any one form.

Of the nine orders, the Anseriformes is most abundant (28 bones, 7 species, 10 sites), the Passeriformes a close second (26 bones, at least 6 species, 7 sites); next the Falconiformes (15 bones, 4 species, 5 sites) and Gruiformes and Galliformes (13 and 12 bones respectively, and 2 species and 5 sites each), followed by the Strigiformes and Podicipediformes (4 bones, 2 species each, the owls from 3 sites, the grebes from 2), Charadriiformes (2 bones, 1 species, 1 site), and Piciformes (1 bone). Suggestion of association of skeletal elements occurs in only a few species; in two of these several pedal phalanges are associated with tarsometatarsus.

Forty-seven bones are believed to represent ten extinct species, of which six are newly described. Twenty-nine specimens cannot be distinguished from those of existing species and are assigned, at least tentatively, to nine species. Thirty bones can be only loosely assigned within a family or order; these represent at least another nine species and may include additional extinct forms, especially among the Passeriformes. Nearly 30 fragments are unidentified.

The avifauna, as identified, is listed below; extinct forms are starred.

LIST OF BIRDS IN THE VALLECITO CREEK FAUNA

Podicipediformes—Grebes

*Podiceps caspicus***Podiceps*, sp.

Anseriformes—Ducks and Geese

Anser*, sp.Brantadorna downsi*, new genus and species*Anas acuta* ?*Anas clypeata***Bucephala fossilis*, new species*Melanitta perspicillata* ?**Oxyura bessomi*, new species

Falconiformes—Diurnal Birds of Prey

**Teratornis incredibilis*

Hawk, sp.

Aquila chrysaetos ?**Neophrontops vallecitoensis*, new species

Galliformes—Fowl

*Lophortyx gambeli***Agriocharis anza*, new species

Gruiformes—Rails and Cranes

Rallus limicola ?*Fulica americana* ?**Fulica hesterna*, new species

Charadriiformes—Shorebirds

Charadrius vociferus

Strigiformes—Owls

**Asio*, sp.

Strigidae, sp.

Piciformes—Woodpeckers

Picinae, sp.

Passeriformes—Perching Birds

Corvidae, sp.

Fringillidae, sp.

Passeriformes, sps. (4 or more sps.)

PODICIPEDIFORMES

Podiceps caspicus

A distal end of humerus (no. 2791) from locality 1433 resembles this element in *Podiceps* as distinguished from that of *Podilymbus* in having a narrower, more shallow impression of the brachialis anticus muscle. Other characters fall within the range of variation of *Podiceps caspicus*, and the fossil is, therefore, assigned to this existing species. A proximal end of tarso-metatarsus (no. 2879) from the same locality is also so assigned. It is im-

mediately distinguishable from that of *Podilymbus podiceps* by its slenderness, and in this respect resembles *Podiceps caspicus*. The fossil is slightly narrower proximally than in *Podiceps auritus*, and the small ridge extending distally from below the hypotarsus is also narrower than in the latter species.

Podiceps, sp.

A nearly complete left tarsometatarsus (no. 2854) and a distal half of the same element of the right side (no. 2853), both from locality 1606 and probably belonging to the same individual, are distinct from specimens of Recent species compared. In length the complete bone falls between Recent specimens of *Podiceps grisegena* and *Aechmophorus occidentalis*. It closely approximates the size of three complete tarsometatarsi from the San Diego Pliocene. The San Diego grebe was originally assigned to *Podiceps parvus* (Howard, 1949: 183-185) on the basis of size of tibiotarsus, carpometacarpus, humerus and proximal end of tarsometatarsus. All of these bones are smaller than Recent specimens of *P. grisegena* but larger than those of *P. auritus*, as is also true of the type tarsometatarsus of *P. parvus* and associated coracoids and carpometacarpus from Fossil Lake, Oregon, Pleistocene. The complete tarsometatarsi now available from San Diego are found to be 8-11 mm. longer than the type of *P. parvus*, and actually longer than this element in *P. grisegena*, although more slender. It is suggested, therefore, that the San Diego grebe, although similar in body size to *P. parvus*, was a longer-legged bird, probably of a different species.

The Vallecito tarsometatarsi may belong to this same San Diego species; certainly they resemble the San Diego specimens in general size and proportions more closely than any others examined, although the complete bone (no. 2854) is 1.3 mm. longer. Possible distinctive characters are noted in the intercotylar area, and the hypotarsus in no. 2854, but these may be due to the fact that the bone had undergone considerable crushing. It is considered unwise to establish the rather poor Vallecito material as the type of a new species at least until the San Diego collection can be thoroughly reviewed.

ANSERIFORMES

The excellent work by Woolfenden (1961) on the postcranial skeleton of this order has been of immeasurable assistance in studying the anseriform bones found in the Vallecito Creek fauna. At the same time, it has served as a guide in pointing out the limitations to specific identification within the group. Great variation may be encountered in this order, even within a genus, and certain elements have little diagnostic value. Without a large series of Recent material for comparison, definite identification of the fragmentary fossil specimens presented a real problem. It is safe to assert, however, that at least seven anseriform species are represented, all but one in the subfamily Anatinae (as recognized by Delacour, 1954: 17). Apparently four tribes of the latter subfamily are represented.

Anser (Chen) sp.
Plate III, fig. C.

The only avian bone from locality 1514 is a proximal end of right humerus (no. 2783), lacking the bicipital portion. It belonged to a large goose of about the size of *Branta canadensis interior*, or *B. c. canadensis*, but with characters more suggestive of those of the smaller *Anser (Chen) hyperboreus*. The prominent ridge extending up the shaft towards the head is more external in position than in available Recent specimens of *Anser albifrons*, but a similarly placed ridge is found among specimens of *A. hyperboreus* and *Branta canadensis*. A distinct line beneath the humeral head, marking the proximal border of the attachment of the head of the triceps muscle, is recorded by Wolfenden (op. cit.: 9) as most often found in humeri of the genus *Branta*. Such a line, however, occurs as well in some Recent specimens of *A. hyperboreus* (LACM no. Bi 1437). The proximal end of the fossil humerus curves so that the head is bent slightly anconally, a character also suggestive of some specimens of *A. hyperboreus*; the anconal border of the head is evenly rounded and does not overhang the shaft or the capital groove, again more like *A. hyperboreus* than *Branta canadensis*. The head is relatively thicker, measured from anconal to palmar surfaces, than in either of these species.

Because of the great range of variation encountered in Recent skeletons of geese, and the incompleteness of the fossil specimen, I consider it unwise to establish a distinct species on the basis of this specimen although the combination of large size with characters noted above suggests that the species represented is no longer existent. Comparisons with previously described species of extinct geese are not wholly satisfactory since only two species, *Eremochen russelli*, from the Pliocene of Oregon, and *Branta propinqua*, from the Pleistocene of Oregon, are represented by the humerus. The element in *Eremochen*, as described by Brodkorb (1961: 174) has a more prominent head, and more distally located external tuberosity; also the distal border of the humeral head on the anconal side projects markedly towards the internal side and overhangs the capital groove.

Branta propinqua was smaller even than *Branta nigricans*, whereas the Vallecito Creek humerus represents a very large goose. *Anser pressus* from the Idaho Pliocene, and *Branta esmeralda* of the Nevada Miocene, though larger than *B. propinqua*, were probably of smaller size than the fossil at hand. *Presbychen abavus* from the California Miocene and *Branta dickeyi* from the California Pleistocene and Oregon Pliocene (?) are at the opposite extreme in size, and exceed even *Branta canadensis canadensis*. *Branta hypsibata* from the Oregon Pleistocene is only questionably valid as a species (Howard, 1946: 167) since the type tarsometatarsus rather closely resembles slender specimens of *Anser hyperboreus*. Even if valid, it would seem to have been a smaller, more slender bird than the one from Vallecito Creek.

Branta howardae from the California Pliocene is based on so small a fragment of carpometacarpus of such unusual character that it is doubtful that

other parts of the skeleton can with certainty be ascribed to the species unless found associated with a similar carpometacarpus. The size of the type of *B. howardae* appears to be suitable for the species represented by the Vallecito Creek humerus.

Measurements of Vallecito Creek humerus no. 2783: breadth across head and external tuberosity, 23.5 mm.; thickness of head (from palmar to anconal sides), 13.0 mm.; ratio of thickness of head to breadth across head and external tuberosity, 55.7 per cent.

An incomplete coracoid (no. 3717), from locality 1360, also represents a large goose. Whether it is of the same species as the humerus cannot be determined. Only a portion of the lower end is preserved and there are no dependable diagnostic characters.

Brantadorna, NEW GENUS

Type species: Brantadorna downsi.

Generic diagnosis: Humerus with shaft relatively shallow, but bearing acute ridge anconally, directed toward external tuberosity and joining with line for attachment of head of triceps muscle slightly mediad to external tuberosity; external tuberosity prominent; attachment of latissimus dorsi anterioris muscle well external to shaft ridge and paralleling it; head (as seen in palmar view) forming abrupt, obtuse angle with capital groove. Coracoid with furcular facet completely undercut and area below deeply depressed, but without foramina; furcular facet apparently lacking a notch; glenoid facet visible when bone viewed dorsally, furcular facet less visible, facing more internally; neck (in external view) almost flat.

Brantadorna downsi, NEW SPECIES

Plate I, figs. G–I

Type: Proximal end of right humerus lacking bicipital area and internal tuberosity; L.A. Co. Mus. no. 3911. Collected by Harley Garbani, Dec. 28, 1958.

Locality: L.A. Co. Mus. loc. no. 1323; Mesquite Oasis. Arroyo Tapiado quad. (1959); California coordinates: 2,008, 985-274,496.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene; Upper Palm Spring formation.

Paratype: Proximal half of right coracoid, L.A. Co. Mus. no. 3910, collected with type at type locality.

Diagnosis: Characters of species the same as for genus, and, in addition: humerus with head bending anconally; proximal contour of head broad and low; pectoral attachment on external tuberosity facing slightly externally; coracoid with glenoid facet slightly depressed and contour abruptly flared above scapular facet.

Referred material: Fragment of distal end of humerus from type locality,

possibly from the same bone as the type proximal end; too poorly preserved to contribute information.

Measurements: Humerus: breadth across head and external tuberosity, 16.2 mm.; thickness of head (from anconal to palmar sides), 8.4 mm.; length pectoral scar on external tuberosity, 6.9 mm.; distance from external border of attachment of head of triceps muscle to medial edge of pectoral attachment on external tuberosity, 2.9 mm.; distance from median crest to shaft ridge, 7.2 mm. (although the median crest itself is not present, its distalmost edge has left an impression in the matrix). Coracoid: distance from procoracoid to head, 16.0 mm.; breadth across furcular facet, 9.1 mm.; breadth below furcular facet, 8.5 mm.; height (proximo-distally) glenoid facet, 7.9 mm.; breadth glenoid facet, 6.4 mm.

Discussion: While the prominence and acuteness of the shaft ridge, the obtuseness of the angle between the head and capital groove, and the position of the attachment of the latissimus dorsi anterioris muscle of the humerus are suggestive of conditions noted in *Branta*, the broad, low head and shallow shaft are ducklike; the external position of the shaft ridge, and the abruptness of the angle between the head and capital groove are more typical of *Tadorna*; the prominence of the external tuberosity is also tadorne in degree, between the ducks and geese. The least breadth of the area between the shaft ridge and pectoral scar is only 40 per cent of the distance from the medial crest to the shaft ridge; in *Branta* and *Anser* it is over 50 per cent, in *Tadorna* 36-38 per cent. In the deep depression of the furcular canal of the coracoid, with strong undercutting of the furcular facet, *Brantadorna* most nearly resembles the smaller, Gadwall duck, *Anas strepera*. However, the rotation of this area is typically ducklike in the latter species, whereas it is more gooselike in *Brantadorna*.

As members of the tribe Tadornini have been observed (Woolfenden, *op. cit.*) to combine characters of both Anserinae and Anatinae, and some tadorne genera have marked anserine characters, I recommend the referral of *Brantadorna* to the Tadornini. The generic name is selected to denote the dual character of the form; the species name, *downsi*, is chosen in honor of Dr. Theodore Downs.

In a study now under way on fossil *Anabernicula* from several localities, I have become convinced that this genus, too, is tadorne. Comparison of *Brantadorna* with *Anabernicula* reveals the following distinctions in *Brantadorna*: head of humerus forming obtuse rather than right angle with capital groove, shaft ridge more acute, attachment of latissimus dorsi anterioris muscle more externally placed and more nearly parallel to shaft; coracoid more undercut below furcular facet, and furcular facet lacking notch. In all of these characters, *Brantadorna* is more gooselike than is *Anabernicula*.

Anas acuta ?

A distal three-quarters of carpometacarpus with fragment of process of metacarpal 1, and a complete wing phalanx (digit 2, phalanx 1) found together



A



B



C



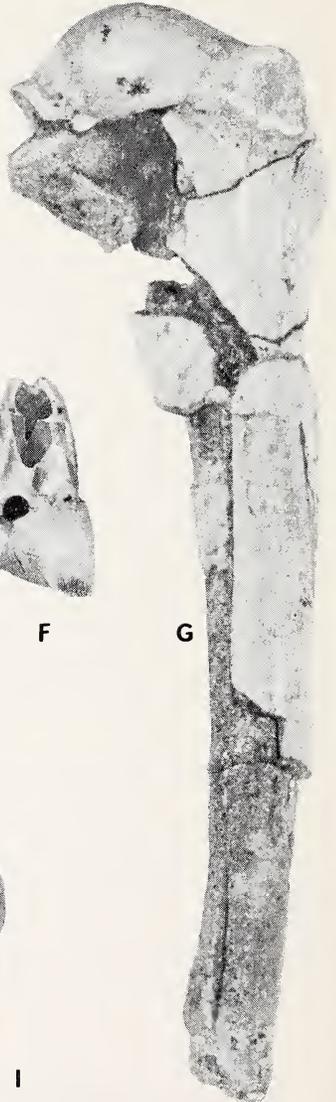
D



E



F



G



H



I

Plate I. A-C, *Bucephala fossilis*, n. sp., A and B, type carpometacarpus, internal and external views, C, paratype humerus, anconal view; D, E, *Oxyura bessomi*, n. sp., type carpometacarpus, internal and external views; F, *Fulica hesterna*, n. sp., type tibiotarsus, anterior view; G-I, *Brantadorna downsi*, n. sp., G, type humerus, anconal view, H and I, paratype coracoid, internal and dorsal views. All figs. x 2.

at locality 1759, and bearing catalog number 2868, resemble the Pintail Duck, *Anas acuta* in size and such characters as are observable. The diagnostic trochlear end of the carpometacarpus is lacking.

Anas clypeata

A proximal end of carpometacarpus (no. 2789) from locality 1114, cannot be distinguished from Recent specimens of the Shoveller Duck, *Anas clypeata*. A proximal end of humerus (no. 2871) from locality 1249, also resembles specimens of this living species except that the external edge of the shaft anconally tends to be slightly more angular, and in this one respect is closer to the Gadwall, *Anas strepera*.

A proximal end of ulna (no. 2784, locality unknown), and an articular end of scapula (no. 4966 from loc. 1433) have the general characters and size suitable for this species. For these latter, undiagnostic elements, the assignment is made tentatively.

***Bucephala fossilis*, NEW SPECIES**

Plate I, figs. A-C

Type: Proximal end of carpometacarpus, L. A. Co. Mus. no. 2787. H. G. Garbani, collector, October 17, 1959.

Locality: L.A. Co. Mus. loc. no. 1430, Arroyo Tapiado. Arroyo Tapiado quad. (1959); California coordinates: 2,012,400-279,400.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene; Upper Palm Spring formation.

Paratype: Proximal portion of left humerus, L.A. Co. Mus. no. 2885, lacking bicipital area and internal tuberosity; from type locality; John White, collector, June 29, 1961.

Diagnosis: Carpometacarpus similar to that of *Bucephala albeola* in general conformation, and particularly in prominence of diagonal ridge on external surface of head. Distinguished from *B. albeola* by more proximally upturned process of metacarpal 1, with inferior border (as viewed externally) slanting upward directly from facet for digit 1; in *B. albeola* process jutting forward rather than upward.

Humerus distinguished from that of *B. albeola* by more prominent angularity of shaft anconally, with more marked depression between apex of shaft and pneumatic fossa; attachment of supraspinatus muscle, beneath pneumatic fossa, markedly raised; pectoral attachment on external tuberosity shorter and less tilted palmad.

Referred material: One proximal end and one fragment of carpometacarpus from the type locality, nos. 2886, 2887, resembling, the type insofar as characters are preserved; proximal fragments of ulna and scapula, and a manubrial fragment of sternum (all no. 4966 from locality 1433), tentatively referred. Ulna with deep humero-ulnar depression suggestive of the condition

found in the ulna of *Melanitta perspicillata*, but element much smaller than in that existing species; scapula with less extended acromion (laterally) than in *B. albeola*; manubrium of sternum similar to that of *B. albeola* in contour of ventral lips of coracoidal sulci and V-shaped connection of sulci, without spine, but notch in dorsal manubrial area much more pronounced; large, centrally placed dorsal pneumatic foramen 4.6 mm. posterior to center of dorsal notch.

Measurements of type and paratype: Carpometacarpus, breadth carpal trochlea, 3.8 mm.; greatest depth proximal end through process of metacarpal 1, 9.1 mm.; height process of metacarpal 1, 5.7 mm.; depth immediately below facet for digit 1, 3.8 mm. Humerus, breadth across head and external tuberosity, 10.0 mm.; depth head, 4.7 mm.; length pectoral scar on external tuberosity, 4.1 mm. Measurements of referred specimens.—Carpometacarpus no. 2886, breadth carpal trochlea, 3.5 mm.; greatest depth proximal end, 8.2 mm.; height process metacarpal 1, 5.2 mm.; depth immediately below facet for digit 1, 3.5 mm.; scapula no. 4966, greatest breadth proximally, 6.8 mm.; breadth posterior to acromion through glenoid facet, 5.8 mm., distance from coracoidal tuberosity to acromion, 5.5 mm., height glenoid facet through coracoidal tuberosity, 4.5 mm., breadth shaft posterior to facet, 3.6 mm.; ulna no. 4966, breadth proximal end, 6.7 mm., depth proximal end, 5.8 mm.; sternum no. 4966, breadth across ventral lips of coracoidal sulci in central manubrial area, 12.1 mm., breadth across dorsal manubrial notch, 6.9 mm.

Discussion: One other fossil species in North America has been referred to the genus *Bucephala*, namely *B. ossivalis* from the Pliocene of Bone Valley, Florida, described from a coracoid. *B. fossilis* cannot be directly compared with this species, as no coracoid referable to the genus has yet appeared in the Vallecito Creek material. However, comparisons of size relative to *B. albeola* and *B. clangula* appear to justify distinction. *B. ossivalis* is said to be larger than *B. albeola* and smaller than *B. clangula* (Brodkorb, 1955:19). Brodkorb's measurements of the type coracoid of *B. ossivalis* are from 10 to 17 per cent greater than comparable maximum measurements on available specimens of *B. albeola* in the Recent skeleton collection of the Los Angeles County Museum, and from 7 per cent smaller to within range of specimens of *B. clangula*. On the other hand, *B. fossilis* falls within the range of size of *B. albeola* in one or more measurements of each element with the exception of the tentatively referred ulna, and is from 12 to 21 per cent smaller than *B. clangula*. The ulna referred to *B. fossilis* is 1 per cent deeper and 8 per cent broader in proximal end than the maximum of *B. albeola* and from 10 to 11 per cent smaller than in *B. clangula*.

Added evidence suggesting distinction of the two fossil species lies in the reduced extent of the acromion on the scapula tentatively referred to *B. fossilis*, resulting in a short span from the coracoidal articulation to the acromion. This suggests a relatively short procoracoid on the coracoid, in contrast to the description of a well developed procoracoid for *B. ossivalis* (Brodkorb, *op. cit.*). These comparisons coupled with the apparent discrepancy in age, as well

as space, for the two occurrences justifies the naming of the separate species from Vallecito Creek.

Melanitta perspicillata ?

A left scapula (no. 2878) from locality 1758, resembles Recent specimens of the Surf Scoter in its heaviness, its relatively straight internal margin, and blunt acromion. The scapula is, however, an undependable element on which to base identification. A fragment of glenoid facet of coracoid was found with the scapula and may belong to the same species. Fragments of ulna, radius and sternum were found at the same locality and possibly represent the same species, but are too fragmentary for identification.

***Oxyura bessomi*, NEW SPECIES**

Plate I, figs. D-E

Type: Left carpometacarpus lacking only metacarpal 3 and portion of distal contour. L.A. Co. Mus. no. 2785; collected Dec. 2, 1958 by Leonard C. Bessom, for whom the species is named.

Locality: L.A. Co. Mus. loc. no. 1304, south side of Vallecito Creek, Arroyo Tapiado quad. (1959), California coordinates: 2,011,500-269,150; separated from major portion of Vallecito Creek type section by faulting.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene, Upper Palm Spring formation.

Diagnosis: Carpometacarpus with posterior contour of external crest of trochlea receding abruptly below articular facet, providing a concave outline that faintly rims, but reveals fossa at base of trochlea when viewed externally; rimming of fossa discernible as faint ridge without lobe when fossa viewed posteriorly; posterior rim of internal crest slightly deflected medially; attachment of metacarpal 3 almost merging with base of internal crest of trochlea, and proximal symphysis short; external surface, proximally, having deep groove running posteriorly from ligamental attachment to external crest of trochlea; area proximal to ligamental attachment low, and proximal contour of external crest broadly rounded; marked longitudinal ridge below ligamental attachment abruptly delimiting metacarpal 1; otherwise external surface flat; process of metacarpal 1 well defined and directed more forward than upward.

Referred material: Distal end of left ulna, no. 2784, from type locality; proximal end of left carpometacarpus lacking process of metacarpal 1, no. 2888, from locality 1430; nearly complete left coracoid, no. 2535, from loc. 1114; and proximal end of right coracoid, no. 4966, from locality 1433.

The shaft of the ulna is relatively deeper than in the existing species of *Oxyura*, and the intermuscular line running up from the carpal tuberosity is more sharply delineated than in most Recent specimens compared. The ulna, however, is not a dependable element for diagnosis, and the characters tend to vary. The referred coracoids have the deep furcular facet, reduced brachial tuberosity, and absence of deep excavation under the facet, characteristic of this element in *Oxyura*. They differ from specimens of *O. jamaicensis* and *O.*

ferruginea in greater depression of shaft below the furcular facet; thin, more angular ventro-internal margin of shaft; more inwardly curved procoracoid with greater excavation of shaft adjacent thereto; smoothly notched furcular facet; relatively wider shaft below procoracoid.

The referred carpometacarpus differs slightly from the type and is closer to the existing species in having a shorter external longitudinal ridge, a slightly higher proximal contour of the external crest as it rims the carpal fossa; on the other hand, the internal trochlear crest is more medially deflected than in the type, thus still farther deviated from the condition found in the existing species.

Measurements: Type carpometacarpus, length to facet for digit 3, 33.6 mm.; height process metacarpal 1 (proximo-distally), 4.9 mm.; depth head from tip of process of metacarpal 1 to posterior edge of internal crest of trochlea, 8.3 mm.; breadth carpal trochlea, 3.5 mm.; height distal symphysis, 4.5 mm. Coracoid no. 2535, length to middle of sternal end, 37.2 mm.; breadth furcular facet, 4.85 mm.; breadth below furcular facet, 5.1 mm.; distance from distal edge of scapular facet to head, 10.8 mm.

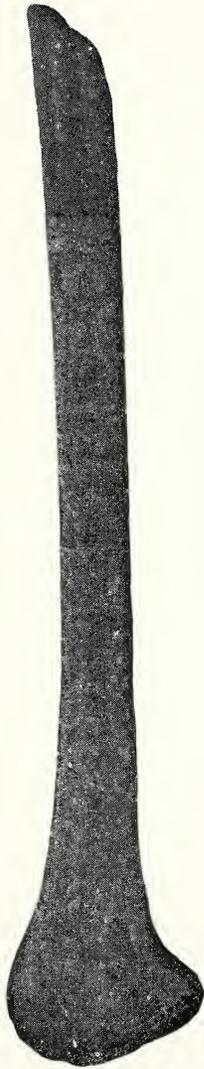
Discussion: A concave posterior contour of external crest of the trochlea occurs in both the aythyine and the oxyurine ducks, but the abruptness of the outline as it recedes below the articular facet, and the faint ridge rimming the fossa are characteristic of *Oxyura*. The high attachment of metacarpal 3 with reference to the carpal trochlea, and consequent thickness of the neck immediately below the trochlea, also separate the fossil from the aythyine ducks, and show relationship to *Oxyura*. Compared with Recent specimens of *Oxyura jamaicensis* and *O. ferruginea*, the entire bone is stockier, there is less evidence of a lobe on the external rim of the carpal trochlea below the articular facet, the internal crest is more medially deflected posteriorly, the proximal contour of the external trochlear crest is more broadly rounded and lower with respect to the proximal contour of the internal crest, and the process of metacarpal 1 is more clearly defined and juts out from the digital facet at a more abrupt angle. In each of these characters, *O. ferruginea* is slightly closer to the fossil than is *O. jamaicensis*. In neither existing species is the external longitudinal ridge clearly defined, although a shorter ridge or scar occurs in some specimens; the flatness of the external surface adjacent to the location of the ridge is observed in one or two Recent specimens.

On the basis of the characters of the type carpometacarpus, one is tempted to assign this fossil species to a distinct genus. The variations noted in the referred carpometacarpus, however, narrow the differences from existing species of *Oxyura* in most respects. Also, if, as I believe, the coracoids are correctly referred to *O. bessomi*, resemblance to *Oxyura* is marked.

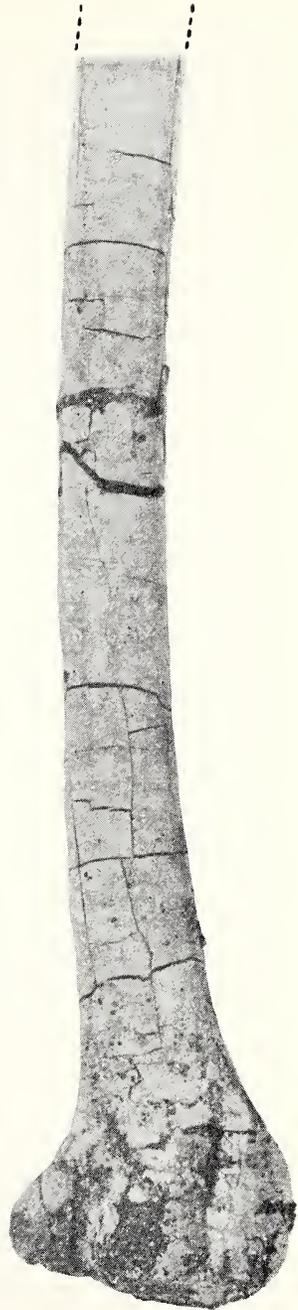
Plate II. A and C, *Teratornis incredibilis*, distal portion of radius, palmar and anconal views; B, *Teratornis merriami*, maximum-sized specimen of radius from Rancho La Brea, palmar view. All figs. x 1.



A



B



C

FALCONIFORMES
Teratornis incredibilis
 Plate II

A distal end of a radius with part of the shaft (no. 3803), from locality 1318, is assigned to *Teratornis incredibilis*, known heretofore only from the type cuneiform (Howard, 1952:51) found in Smith Creek Cave, Nevada, of late Pleistocene age. Assignment of the radius to this species is based on its general resemblance to that of *Teratornis merriami* and its tremendous size. Generic characters, as contrasted to the condor, genus *Gymnogyps*, are: shaft thick and angular externally; distal end markedly flared and thickened internally, expansion and thickening extending for greater distance proximally than in *Gymnogyps*; external expansion more pointed than internal and not extending so far proximally.

Size alone is sufficient to distinguish this bone from that of *Teratornis merriami*. There are, however, the following qualitative characters that define the species *T. incredibilis* in spite of the fact that the surface contours of the Vallecito radius are somewhat eroded: distal contour straighter; ligamental prominence extending more proximally, and more markedly set off from shaft in palmar view (the bone is crushed here, but crushing cannot wholly account for the abrupt drop from the prominence to the shaft); shaft immediately above distal end (palmar view) flat (see ratio in table of measurements); tendinal groove (anconal face) adjacent to ligamental prominence deeper than in *T. merriami* and extending farther proximally; groove adjacent and external to this, narrower than in *T. merriami*.

MEASUREMENTS OF RADIUS

	<i>T. incredibilis</i>	<i>T. merriami</i> (maximum)
Breadth distal end	37.3 mm.	26.7 mm.
Depth distal end (internally)	14.6 mm.	11.1 mm.
Depth distal end (externally)	11.1 mm.	8.2 mm.
Breadth shaft above distal end	17.0 mm.	11.0 mm.
Depth shaft above distal end	12.0 mm.	9.3 mm.
Ratio depth to breadth shaft	70.6 %	84.6 %

Hawk, sp.

A proximal tip of humerus (no. 3804) from locality 1319 represents a hawk of about the size of *Buteo swainsoni*. It is distinguished from the humerus of falcons or caracara by the very moderate excavation of the capital groove, with no undercutting of either the head or the proximal surface of the median crest. The specimen is too incomplete to attempt to establish its relationship among the hawks.

Aquila chrysaetos?

Two incomplete pedal phalanges, phalanx 1, digit 1 and phalanx 2, digit 2, (both no. 2779) from locality 1614, are similar in contour to those of the Golden Eagle, *Aquila chrysaetos*, and seem to fall within the size range of that species.

Neophrontops vallecitoensis, NEW SPECIES

Plate III, fig. B.

Type: Distal half to two-thirds of left tarsometatarsus, badly broken in matrix, but pieced together in laboratory; with associated fragment of metatarsal 1, and 8 pedal phalanges; L.A. Co. Mus. no. 2866; collected by J. A. White and H. J. Garbani, Jan. 23, 1963.

Locality: L.A. Co. Mus. loc. no. 1299, Arroyo Hueso. Arroyo Tapiado quad. (1959); California coordinates 2,010,230-281,102.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene; Upper Palm Spring formation.

Paratype: Distal end of right tarsometatarsus, L.A. Co. Mus. no. 3769, from locality 1356, Arroyo Tapiado; collected by Kay Murphy, March, 1959.

Diagnosis: Closely resembling tarsometatarsi of *Neophrontops americanus* Miller but larger. Compared with broadest Rancho La Brea specimen (L.A. Co. Mus. no. E2061), both type and paratype with distal trochleae deeper anteroposteriorly, and facet for metatarsal 1 more elevated; shaft of type deeper anteroposteriorly but relatively more slender in lateral dimension, and more abruptly sloping from a high angle nearly centrally located on anterior surface of shaft (this portion of shaft missing in paratype).

Discussion: Of 96 measurable specimens of *N. americanus* in the L.A. County Museum collections from Rancho La Brea, none equals the type of *N. vallecitoensis* in either breadth of distal end or depth of shaft, and only one specimen equals the slightly smaller paratype in breadth of distal end. In the entire Rancho La Brea series, only three or four specimens have the facet for metatarsal 1 relatively as elevated when taken in proportion to breadth of distal end. The ratio of depth of trochleae to breadth of distal end is exceeded in the Rancho La Brea series, but actual depth of trochleae is not equalled. The shape of the shaft as described for the type is not duplicated in the *N. americanus* series. Although length cannot be measured for *Neophrontops vallecitoensis*, comparison of the type with specimens of *N. americanus* (using the greatest depth of shaft as point of reference) indicates that the Vallecito Creek bone must have been at least 115 mm. in length if not more. Greatest length for *N. americanus* (see Howard, 1932, p. 80) is 97.2 mm. Other measurements for both type and paratype are shown below.

Metatarsal 1 of *N. americanus* is not available for comparison. The Vallecito Creek fragment of distal end of this element differs from that of hawks and eagles, and more closely resembles that of the old world type of vultures in the presence of two nearly equal, narrow tendinal grooves; in the more strictly predatory hawks and eagles, in which the foot is a strong grasping tool,

the medial groove is greatly enlarged at the expense of the more lateral one. In comparison with the few pedal phalanges in the Rancho La Brea collection thought to represent *N. americanus*, the Vallecito Creek phalanges are straighter (less bowed anteriorly) as well as larger.

Measurements of Type and Paratype of *Neophrontops vallecitoensis*
compared with maximum for *N. americanus*

	<i>Neophrontops vallecitoensis</i>		<i>N. americanus</i>
	Type	Paratype	
Tarsometatarsus			
Breadth dist. end	19.6 ap.mm.	17.4 mm.	17.5 mm.
Greatest depth shaft	9.4	—	8.0
Depth first trochlea	10.1	8.5	8.3
Depth mid. trochlea	—	7.7	7.6
Depth 3rd trochlea	9.8	9.0	8.8
Distance from prox. edge facet for M1 to dist. end 1st trochlea	23.5	20.1	19.3
Metatarsal 1			
Breadth distal end	8.1		
Pedal phalanges (length)			
D1, Ph 1	25.1		
D2, Ph 2	20.1		
D3, Ph 2	17.6		
D4, Ph 4	13.5		

Two other species of *Neophrontops* are recorded in the fossil record, *N. dakotensis* from the South Dakota Pliocene, and *N. vetustus* from the Nebraska Miocene. Each is described from a humerus of lesser size than that of *N. americanus*.

GALLIFORMES

Lophortyx gambeli

Of eight quail bones from four localities, only one can be assigned with assurance. A proximal end of right humerus (no. 2881) from locality 1703 agrees in size with both *Lophortyx gambeli* and *L. californicus*, but the area below the head is more depressed than in the latter species and is bordered externally by a ridge continuing distally from the external tuberosity as in *L. gambeli*; the ridge is absent in Recent specimens of *L. californicus*, *Callipepla squamata* and *Oreortyx pictus*. A proximal end of right tarsometatarsus no. 2880 from locality 1114 resembles in size and general contours tarsometatarsi of Recent *L. californicus* and *L. gambeli*. As the hypotarsus is incomplete in the fossil, its height is uncertain; approximate measurements suggest that it was short as in *L. gambeli*.

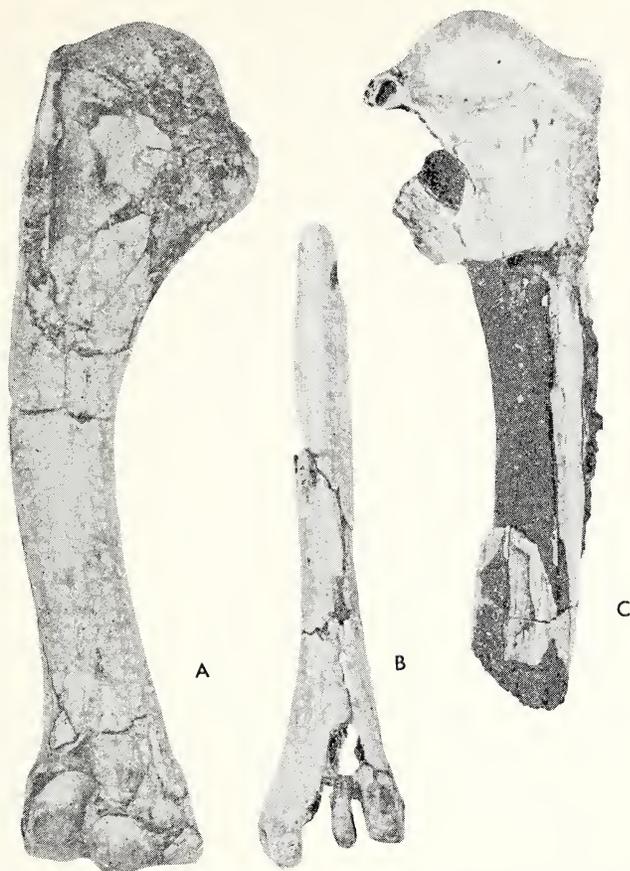


Plate III. A, *Agriocharis anza*, n. sp., type humerus, palmar view; B, *Neophrontops vallecitoensis*, n. sp., type tarsometatarsus, anterior view; C, *Anser*, sp., proximal end of humerus no. 2783, anconal view. All x 1.

Quail, sp.

A proximal end of femur (no. 2880) from locality 1114, seems to differ from both species of *Lophortyx* in the extent of the trochanter, being seemingly raised above the iliac facet for a greater distance posteriorly. Two other fragments of femur, and a humeral head from locality 1114, a fragment of anterior face of tarsometatarsus from locality 1433, and a distal end of tarsometatarsus from locality 1615, are identified as quail, but are too fragmentary for detailed assignment.

***Agriocharis anza*, NEW SPECIES**

Plate III, fig. A

Type: Right humerus, nearly complete, but with internal tuberosity and

area immediately below head anconally, abraded and crushed; L.A. Co. Mus. no. 3753; collected by James Garbani, March 1, 1959.

Locality: L.A. Co. Mus. locality no. 1358; Arroyo Tapiado. Arroyo Tapiado quad. (1959); California coordinates: 2,019,000-271,094.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene. Upper Palm Spring formation.

Paratypes: Proximal fragment of left humerus, and fragments of sternum, sacrum and ulna, collected with the type humerus at locality 1358, and bearing the same catalogue number as the type.

Diagnosis: Humerus similar to that of *Agriocharis ocellata* in relatively straight-sided, blunt external condyle, lacking medial bend and pointed tip characteristic of *Meleagris gallopavo*; attachment of pronator brevis deeply incised and set so as to be clearly visible when bone is viewed from palmar side; attachment of anterior articular ligament slightly convex and facing slightly distally and medially; brachial depression deep; muscle attachment below pneumatic fossa markedly depressed at medio-distal edge. Sternum similar to that of *Agriocharis* as distinguished from *Meleagris* in abrupt angle formed at junction of dorsal manubrial area with dorsal lip of coracoidal sulcus, and seemingly lesser anterior protrusion of dorsal lip; triangular space between right and left sides of sulcus narrow and shallow.

Measurements of type: length, 112.4 mm.; breadth of distal end, 24.0 mm., approximately; breadth of proximal end 30.3 mm. approximately; breadth of shaft, 14.3 mm., depth of shaft, 8.5 mm.

Discussion: Direct comparisons of the Vallecito Creek humerus have been possible with Recent specimens of *Agriocharis ocellata* and *Meleagris gallopavo* and Pleistocene specimens of *Meleagris crassipes* from Mexico and *Parapavo californicus* from California. The sternum has been compared with two Recent specimens each of *M. gallopavo* and *A. ocellata* and a series of twenty Pleistocene specimens of *Parapavo californicus* from Rancho La Brea. *Meleagris crassipes* and *Parapavo californicus* agree with *M. gallopavo* in the curved, pointed tip of the external condyle of the humerus and hence are distinguished from *Agriocharis anza*. In the palmar visibility of the attachment of the pronator brevis, *A. anza* most closely resembles *A. ocellata*, but the attachment is even more visible than in the Recent species because of the medial slant of the adjacent attachment of the anterior articular ligament; the latter attachment faces more directly palmar in all other species compared. The marked depression of the brachial area is not duplicated in any of the other species; possibly this depression is partly due to the crushing of the bone. The notably broad, flat humeral shaft in *A. anza* may also be the result of crushing. In the fragment of sternum the lateral border of the dorsal part of the manubrium is preserved on the left side, and shows a much more abrupt angle, with respect to the dorsal lip of the coracoidal sulcus than in *M. gallopavo* or *P. californicus*. The narrow shallow triangular area between the sulci, however, more closely resembles the condition in *Parapavo* than in either Recent species.

Six other species of fossil turkeys have been previously described, all assigned to the genus *Meleagris*. *Agriocharis* does, however, appear in the fossil record, without specific designation; Wetmore (1924: 8) recorded a fragment of spurred tarsometatarsus from the Arizona Pliocene and assigned it to this genus on the basis of the distance of the spur core from the distal end. The early authors, Cope, Marsh, and Shufeldt, did not consider *Agriocharis* when describing their species of fossil turkeys. For the Pleistocene species *Meleagris superba* Cope, *M. celer* Marsh and *M. richmondi* Shufeldt, and the Oligocene *M. antiqua* Marsh, therefore, some possibility of wrong generic diagnosis exists. I believe, however, that the Vallecito Creek bird is properly distinct from these species. *M. superba* is known from many elements, and was a much larger bird than *Agriocharis anza*, the humerus ranging in size from 147 mm. to 159.5 mm. From Shufeldt's (1913: 25-35 and 1915: 66-67) reviews of Marsh's material, I strongly suspect that *M. celer* should be synonymized with *M. superba*. Only three bones (leg elements) were ascribed to *M. celer* by Marsh (1872: 261) and they occurred in the same New Jersey Pleistocene deposit as those of *M. superba*. The range in size of *M. superba*, were the *M. celer* bones so assigned, would not be disproportionate in view of what is known of sex variation in present-day meleagrids.

M. richmondi from the Pleistocene of Alameda County, California, is based on a single worn fragment of anterior part of sternum. Shufeldt's (1915: 67) type description indicates merely that the specimen has meleagrid characters but is the size of a grouse. If the illustration (*op. cit.*, pl. 2, fig. 19) is truly of natural size as indicated, the specimen falls within the minimum size range of sterna of *Parapavo californicus*, and could, therefore, be of an appropriate size for *A. anza* as well. The illustration, however, shows one notable distinguishing character, namely the marked anterior extension of the dorsal lip of the sulcus beyond the ventral lip; this condition is found in *Parapavo californicus* and to a lesser extent in *Meleagris gallopavo*, but not in *Agriocharis ocellata*. The small fragment of sternum of *A. anza* is worn so that it is difficult to determine this character, but measurements indicate less forward thrust of the dorsal area than in *M. richmondi*.

The type of *Meleagris antiqua* is a fragment of distal end of humerus. Aside from the fact that there is little likelihood of identity of species with so great an age discrepancy as exists between Oligocene *M. antiqua* and Pleistocene *M. anza*, the illustration of *M. antiqua* as presented in Shufeldt's (1913: pl. 3) review of Marsh's species (Marsh, himself did not illustrate the species) clearly shows distinct differences from *A. anza*. In fact I believe that Shufeldt was correct in doubting the validity of the assignment of *M. antiqua* to the Meleagridae. The illustration shows the entepicondyle to be large and nearly on a level distally with the condyles, a character suggestive of the Cracidae rather than the Meleagridae. Furthermore, the line delimiting the proximal border of the internal condyle is cracid in character; in meleagrids this border is more rounded and ball-like.

GRUIFORMES

Rallus limicola ?

A fragment of manubrial end of sternum (no. 2867) from locality 1114 resembles this part of the skeleton in existing *Rallus limicola* but is slightly broader across the coracoidal sulci than available comparative material at either the Los Angeles County Museum or the University of California Museum of Vertebrate Zoology. Other measurements fall within the range in size of Recent specimens. It should be noted that *R. limicola* has been recorded from the western Pleistocene at McKittrick, California (Miller, 1925: 320) and Fossil Lake, Oregon (Howard, 1946: 182); in the latter locality, the specimens are said to represent "a larger than average bird of that species."

The only previously described fossil rail to which the present fragment might be assigned is *Rallus prenticei* from the Rexroad fauna of Kansas; *R. phillipsi* from Wikieup, Arizona, was presumably larger. A measurement of the sternal facet on the illustration of the coracoid assigned to *R. prenticei* (Wetmore, 1944: 101) suggests a breadth across the coracoidal sulci of the sternum of that species of at least 9.8 mm. Considerable size range would be required to include the Vallecito Creek specimen in this species, but it is not beyond possibility.

Measurements of fossil sternum no. 2867: Breadth across coracoidal sulci, 8.7 mm., breadth across dorsal manubrial notch, 4.5, breadth of anterior border of carina at base, 2.0 mm.; the same measurements in the maximum available specimen of *R. limicola are*, 8.5 mm., 4.7 mm., and 2.2 mm. respectively.

Fulica americana ?

Five sites yielded coot bones. Distal ends of tibiotarsus were collected at locs. 1299, 1433 and 1430 (2 specimens). At locality 1433, the tibiotarsus was associated with a distal end of tarsometatarsus and five pedal phalanges; another distal end of tarsometatarsus came from locality 1114, and an incomplete coracoid from locality 1606.

The two tibiotarsi from locality 1430, the tarsometatarsus from locality 1114, and the coracoid appear to be indistinguishable from corresponding elements of the existing *Fulica americana*, except that in the one tibiotarsus in which the supratendinal bridge is complete, it is found to be deeper (proximo-distally) than the maximum for *Fulica americana*; its position, however, is the same as that found in *F. americana* rather than that of the type of the new species described below. These four specimens are allocated to the existing species, but in view of the fact that the elements from localities 1299 and 1433 warrant description as an extinct species, the possibility that a single, variable ancestral form could be represented must not be overlooked. The allocation is therefore made tentatively.

***Fulica hesterna* NEW SPECIES**

Plate I, fig. F

Type: Distal end of left tibiotarsus, lacking posterior contours of both condyles; L.A. Co. Mus. no. 2873; collected by T. Downs, Oct. 17, 1959.

Locality: L.A. Co. Mus. loc. no. 1433, Arroyo Tapiado. Arroyo Tapiado quad. (1959); California coordinates: 2,012,112,600-279,550.

Fauna: Vallecito Creek.

Age and formation: Middle Pleistocene; Upper Palm Spring formation.

Paratype: Distal end of tarsometatarsus; also L.A. Co. Mus. no. 2873, from the type locality; collected by T. Downs, Oct. 17, 1959.

Diagnosis: Type similar to tibiotarsi of *Fulica*, as distinguished from those of *Rallus* or *Gallinula*, in general contours; internal condyle, in particular, thrust farther laterally, and small foramen present on external side of shaft above condyle (absent in *Rallus*). Distinguished from *F. americana* by more vertical position of supratendinal bridge, achieved by less posterior tilting of proximal border, particularly at external side.

Paratype tarsometatarsus distinguished from tarsometatarsi of *F. americana* by more evenly balanced position of external and internal trochleae with respect to the middle trochlea; internal trochlea only 24 per cent higher above distal end than external trochlea (as contrasted with 50-60 per cent in *F. americana*), and set more laterally, less posteriorly on the shaft than in the existing species.

Referred material: Distal end of tibiotarsus no. 2875 from locality 1299 and five pedal phalanges associated with the paratype tarsometatarsus from locality 1433.

Owing to fragmentation, the position of the supratendinal bridge is less clearly defined in the referred tibiotarsus than in the type, but appears to have the same vertical position. Both tibiotarsi are noteworthy in that the supratendinal bridge is deep proximo-distally, equalling the maximum found in the existing *F. americana*.

Only one of the pedal phalanges is complete (digit 2, phalanx 1); no distinction from the phalanx of *F. americana* is observable, and the length falls within the range of that species. Assignment is based on the association of the phalanges with the paratype tarsometatarsus.

Discussion: Two other fossil coots have been recorded, *Fulica minor* from the Pleistocene of Fossil Lake, Oregon, and *F. infelix* from the Pliocene of Juntura, Oregon. As stated in a previous paper (Howard, 1946: 182-183), the large collection of coot bones from Fossil Lake constitutes a series overlapping in size *F. americana*, but tending to smaller average length of wing bones and greater average length of leg bones. On this basis, it was contended that the trinomial, *F. americana minor*, more correctly expresses the relationship of the fossil to the Recent form. A series of coot tibiotarsi and tarsometatarsi from Fossil Lake, loaned by the American Museum of Natural History, was re-examined for this study. As previously noted, no qualitative differences from *F. americana* were observed. Even the breadth of the distal end of tibiotarsus does not reflect the size difference found in length of that element. *F. hesterna* is therefore, distinguished from *F. (a.) minor* by the same characters enumerated in the description above.

The typical character of the more vertical supratendinal bridge of *F.*

hesterna distinguishes it, as well, from *F. infelix*. This distinction seemed apparent from the illustration of the type of the latter species (Brodkorb, 1961: 182) and was further confirmed by Brodkorb in correspondence. Furthermore, the groove for the peroneus profundus, which is said to be shallow in *F. infelix*, is well marked in *F. hesterna*, with well developed bordering ridges.

MEASUREMENTS OF COOT BONES

	<i>F. hesterna</i>		<i>F. minor</i>	<i>F. infelix</i>	<i>F. americana</i>	
	no. 2873	no. 2875			min.	max.
Tibiotarsus						
Breadth distal end	8.3	8.4	7.8-9.1	7.6	7.7-9.3	
Proximo-distal depth of supratendinal bridge	2.5	2.5	1.8-2.5	1.9	1.9-2.5	
Tarsometatarsus						
Breadth across distal trochleae	8.7	...	8.0-10.0	...	8.1-9.4	
Height internal condyle above distal end	3.0		3.3-4.3	...	3.5-3.8	
Height external condyle above distal end	2.3		1.3-2.0		1.5-1.7	
Ratio of external condyle distance, to internal condyle distance (from distal end)	76.0%		39%-47%	...	39%-48%	

CHARADRIIFORMES

Charadrius vociferus

A proximal end of left humerus and proximal end of right carpometacarpus, both no. 2870 from locality 1114, resemble Recent specimens of the Killdeer, *Charadrius vociferus*. Diagnostic characters of these elements that distinguish *C. vociferus* from *Eupoda montana* are as follows: humerus with sharp external ridge on shaft running straight to head, not curving medially as in *Eupoda*; greater excavation of shaft below head; and shorter external tuberosity. Carpometacarpus with stout process of metacarpal 1, and distal edge of process forming right angle with area of pollical facet; process more slender and more upturned (proximally) in *Eupoda*.

STRIGIFORMES

Asio, sp.

A fragment of distal end of femur (no. 2855) from locality 1297, and two pedal phalanges (no. 2780) from locality 1449, agree in general size with Recent specimens of Long-eared Owl, *Asio otus*. Only the posterior contours of the femur are preserved, and even in this region the bone is cracked away in places, leaving only a cast of the contour. The specimen resembles the femur of *Asio o. wilsonianus*, more than that of any other living owl compared, in the

shape and position of the muscle attachment above the external condyle, the triangular shape of the area above this same condyle and the extension of the fibular groove around onto the distal surface of the bone; this groove is even more marked, however, in the fossil form than in the specimens of the Recent species at hand. The fossil also differs from the Recent specimens of *A.o. wilsonianus* in less excavation of the popliteal area, straighter rise of the shaft from the internal condyle, and more broadly rounded contour of external condyle.

It is probable that the owl represented by this femur was specifically distinct from the living *Asio otus*. I do not consider it wise, however, to name it, using so fragmentary a specimen as type.

The pedal phalanges represent phalanx 1 of digit 3, and either phalanx 3 of the same digit or phalanx 2 of digit 2. The conformation of these phalanges is not identical to any specimens in the Recent collection and the species represented is probably now extinct. In shape of the proximal articular surface of phalanx 1, digit 3, resemblance is closest to Recent specimens of the genus *Strix*, but the element is smaller than in *S. varia* or *S. occidentalis* and agrees more closely in size with *Asio wilsonianus*. A prominent ridge occurs nearly centrally on the proximal surface, with equal depressions on each side; the position of the ridge is similar in some specimens of *Strix*, but in others one side is more depressed.

Because of the general agreement in size, the femur and the phalanges are here recorded together under *Asio*. The possibility that the phalanges belonged to a separate species referable to *Strix* should not be disregarded.

Strigidae, sp.

A fragment of tip of upper mandible (no. 3865), from locality 1114, can be assigned to the Strigidae, as contrasted with the Tytonidae, on the basis of the presence of a ridge bordering the outer contour, ventrally, with a slight groove between this ridge and the tomium. It is impossible to assign the specimen further, except to indicate that in size it is close to *Strix varia*, and is, therefore, presumably of a larger species than that represented by the femur and phalanges just discussed.

PICIFORMES

Picinae, sp.

A single distal half of radius (no. 2869) from locality 1333, represents the woodpeckers. In size the specimen agrees closely with radii of Recent *Colaptes cafer*, but I make no attempt to identify this very undiagnostic element even to genus.

PASSERIFORMES

Skeletal characters of the multitudinous members of this order are difficult to distinguish. Study of the osteology of the group is a specialty in itself, and one that requires extensive collections of Recent comparative material. No

detailed identifications of the more than twenty passerine bones from Vallecito Creek are attempted. Six or more species appear to be represented.

Corvidae, sp.

A shaft of carpometacarpus (no. 2534) and fragment of distal end of tibiotarsus (no. 2876), both from locality 1114, agree in general with comparable elements of the crow, *Corvus brachyrhynchos*, although the carpometacarpal shaft is heavier than recent specimens at hand. Another shaft of carpometacarpus and fragment of wing phalanx (both no. 2890) from the same locality possibly belonged to the same individual. All specimens are too incomplete to provide reliable evidence as to the identity of the species represented.

Passeriformes, sps.

Twenty other isolated bones of passeriforms are present in the collection, taken from localities 1114, 1250, 1323, 1437, 1461 and 1615. These include 9 humeri, 3 carpometacarpi, 2 femora, 4 tibiotarsi, 1 tarsometatarsus and 1 wing phalanx; they appear to represent at least four species. Two consolidated masses containing passerine bones also occur (localities 1461 and 1249) and may represent owl pellets. In one of the "pellets" (from locality 1249), fragments of upper and lower mandible are notable, and suggest a fringillid with broad, short bill.

SUGGESTIONS CONCERNING EVOLUTION AND DISTRIBUTION

Unlike mammals, in which skull characters and dentition play an important taxonomic role among Recent as well as fossil forms, classification of living avian species rarely makes use of detailed conformation of skeletal parts. The avian paleontologist must make his own comparisons, and decisions regarding the significance of skeletal characters of the groups with which he works and the parts of the skeleton represented in fossil form. Few published osteological analyses of families or orders of living birds have been presented in sufficient detail to serve fully the needs of the paleontologist. Those, such as Woolfenden's (1961) on the Order Anseriformes, that do present detailed studies, serve to emphasize that no one element of the bird skeleton is unfailingly diagnostic, and furthermore, that groups that may be distinguishable by one element may be strikingly similar in others.

The fragments representing the fossil avifauna of Vallecito Creek have but little to contribute as evidence of evolution within any of the individual groups involved, but that little is worth considering. *Fulica hesterna* seems the most likely possibility of an actual ancestral form leading to existing populations, particularly if, as suggested above, all the coot bones found (including those tentatively assigned to the living *Fulica americana*) belong to a single species with a wide range of variation, from which existing *F. americana* could have been derived. This possibility is intriguing in view of the fact that slight

differences noted in coot bones in the late Pleistocene (resulting in the description of *Fulica minor*) are entirely a matter of proportion, and include no qualitative differences such as noted for *F. hesterna*.

The overlapping in some characters suggests the possibility that the vulture, *Neophrontops vallecitoensis*, might have been the forerunner of the late Pleistocene *N. americanus*, abundantly represented at Rancho La Brea. The turkey, *Agriocharis anza*, on the other hand, seems to bear no direct relationship to the abundant *Parapavo californicus* of California's late Pleistocene, but rather to indicate a former more northerly distribution for the genus *Agriocharis*, which is today limited to Mexico and Central America. This is not to say that *A. anza* should be interpreted as ancestral to the living *A. ocellata*. The occurrence of *Teratornis incredibilis* widens the geologic record of this extinct family of giant vultures although it contributes nothing to our knowledge of its evolution. That the same species is also recorded in the late Pleistocene negates the possibility of ancestral relationship of *T. incredibilis* to *T. merriami*.

I should not care to venture detailed suggestions as to the evolutionary implications of most of the extinct Anseriformes herein reported. As Woolfenden (*op. cit.*) has shown, this is a complicated group with many overlapping characters even among existing forms. The fossil fragments here ascribed to extinct species, while indicating generic position, and distinction from living species, are far too limited to provide evidence of an evolutionary nature as regards related existing species. The addition of *Brantadorna* to the fossil record is, however, significant. Combined with the previously described, and rather widely distributed *Anabernicula*, the new genus suggests that the strange, "gooselike" tadornine ducks may have formed an important part of the North American avifauna in past time although no living descendants remain on this continent today.

ECOLOGIC CONSIDERATIONS

Roughly 50 per cent of the avian representation from Vallecito Creek, both as to species and number of specimens, indicates an aquatic habitat. The assemblage contrasts, however, with that from Manix Lake (about 125 miles to the north, in San Bernardino County, California), deposited under lacustrine conditions, where the avifauna is over 90 per cent aquatic and includes several species of waders.

The presence of turkey and quail at Vallecito Creek suggests brushy areas. If the two consolidated masses of passerine bones represent owl pellets, as seems likely, roosting or nesting sites, probably in trees, must have been nearby. More detailed ecologic conditions might be revealed were the passerine bones to be specifically identified.

STRATIGRAPHIC OCCURRENCE

The type section of the bone-bearing deposits of Vallecito Creek is an area of approximately seven square miles extent, representing roughly 3600 feet in

thickness of deposits, in which stratigraphy can be traced. Nineteen of the twenty-five avian sites occur within this section and are somewhat generally distributed both horizontally and vertically. The other six are nearby, but separated from the type section by faulting. When the geologic study of the deposits is completed, it is anticipated that these outlying sites may be stratigraphically related to those in the type section. At present this has been done only in a general way.

Dr. Downs has kindly supplied information so far assembled as to the stratigraphic relationship of the avian sites. In order of stratigraphic occurrence, from top to bottom of the type section, these sites and their contained avifaunas are listed below. Outside the type section the relative positions of the sites can be only approximated. Loc. 1360 (containing 1 goose bone) in the third fault block southeast, is near the top of the formation at the approximate level of loc. 1759 of the type section; loc. 1758 (containing 2 specimens of *Melanitta perspicillata?*, and 3 unidentified duck bones), and loc. 1358 (containing the type material of the new species, *Agriocharis anza* and 4 unidentified bones) occur at the approximate level of loc. 1297 of the type section; loc. 1606 (containing 2 bones of an extinct species assigned as *Podiceps* sp., and 1 bone of *Fulica americana?*) and loc. 1356 (containing 1 specimen referred to *Neophrontops vallecitoensis*, n. sp.) are at the approximate level of loc. 1249 of the type section. These four localities are near the middle of the formation, 1758 and 1606 in the first fault block southeast of the type section, 1358 and 1356 in the second. One locality that occurs south of Vallecito Creek from the other deposits, and separated from them by a fault, cannot be even tentatively positioned. This is locality no. 1304 in which the type specimen and referred ulna of *Oxyura bessomi* occurred.

There is no notable change in avifauna to be observed in contrasting lowermost and uppermost levels, unless the concentration of passeriform bones in the upper levels is significant. Two passerine bones were found at the lowermost level. Otherwise all passerine bones occurred in the upper half of the deposit. Only two localities, 1114 and 1433, contained enough avian species to be considered faunal assemblages. These bear no outstanding differences although water birds predominate in the latter, passerines in the former.

COMPARISON WITH OTHER FOSSIL AVIFAUNAS

Distinction of the Vallecito Creek avifauna from the late Pleistocene assemblages is marked by the absence of any of the well-known extinct species which characterize California's asphalt deposits. The presence of related species of *Neophrontops* and *Teratornis* as well as turkey, quail, and golden eagle (?), suggest that ecologically many of the Rancho La Brea species could be expected to occur if the faunas had been contemporaneous. Other than the Recent species represented, only one species, *Teratornis incredibilis*, is recorded elsewhere. This species was originally described from Smith Creek Cave, Nevada, of late Pleistocene age. It would seem, however, that the species was not

COLLECTING SITES IN THE TYPE SECTION, WITH CONTAINED AVIFAUNAS
 Arranged in relative stratigraphic position from topmost locality (1323) to
 lowermost (1437). Thickness of sediments between vertically
 separated localities is not reflected²

Loc. no.	Avifauna	No. of bones	Loc. no.	Avifauna	No. of bones
1323	<i>*Brantadorna downsi</i> , n. sp.	3			
	Passeriformes, sp.	1			
	Unidentified	1			
1759	<i>Anas acuta</i> ?	2			
1250	Passeriformes, sp.	2			
1114	<i>Anas clypeata</i>	1	1333	Picinae, sp.	1
	<i>*Oxyura bessomi</i> , n. sp.	1			
	<i>Lophortyx gambeli</i> ?	4			
	<i>Rallus limicola</i> ?	1			
	<i>Fulica americana</i> ?	1			
	<i>Charadrius vociferus</i>	2			
	Strigidae, sp.	1			
	Corvidae, sp.	4			
	Passeriformes, sps.	10			
	Unidentified	8			
1461	Passeriformes, sps.	5			
1297	<i>*Asio</i> , sp.	1			
1615	Quail, sp.	1			
	Passeriformes, sp.	1			
1249	<i>Anas clypeata</i> ?	1			
	Fringillidae, sp.	1			
	(in owl pellet ?)	(indiv.)			
1433	<i>Podiceps caspicus</i>	2	1299	<i>*Fulica hesterna</i> , n. sp.	1
	<i>Anas clypeata</i> ?	1		<i>*Neophrontops valle-</i>	
	<i>*Bucephala fossilis</i> , n. sp.	3		<i>citoensis</i> , n. sp.	10
	<i>*Oxyura bessomi</i> n. sp.	1			
	Quail, sp.	1			
	<i>*Fulica hesterna</i> , n. sp.	7			
	Unidentified	5			
1430	<i>*Bucephala fossilis</i> , n. sp.	4			
	<i>*Oxyura bessomi</i> , n. sp.	1			
	<i>Fulica americana</i> ?	2			
	Unidentified	5			
1319	Hawk, sp.	1			
1703	<i>Lophortyx gambeli</i>	1			
1318	<i>*Teratornis incredibilis</i>	1			
1614	<i>Aquila chrysaëtos</i> ?	2			
1514	<i>*Anser</i> , sp.	1			
1449	<i>*Asio</i> , sp.	2			
1437	Passeriformes, sp.	2			

²Localities placed in adjacent columns occur at the same level in the type section.

abundantly represented in the late Pleistocene, for, despite its gigantic size, it is recorded from a single carpal bone in the Nevada cave collection, a collection which totals over 600 bones of birds. I do not believe that this one species can be considered a marker for late Pleistocene, balanced against weightier evidence to the contrary as shown in comparisons of total faunas.

Downs (1957) suggests that the mammalian genera found at Vallecito Creek indicate probable correlation of this fauna with that of the Curtis Ranch of Arizona, and the Bautista and Irvingtonian of California. Unfortunately the birds do not lend themselves to similar correlation. In the first place avian fossils are very rare in the faunas noted. But of greater importance is the fact that avian genera, as now recognized, are less bound by epochal limitations than are mammalian genera, and, therefore, cannot be depended upon as markers. *Neophrontops*, for example, represented in the Vallecito Creek avifauna, was first named from the late Pleistocene, and is also recorded from lower Pliocene and middle Miocene. Many Recent genera, also, are recorded at least into the Miocene.

In a broad way, the percentage of extinct species to total species count assists in correlating fossil avifaunas. Brodkorb (1955: 31) and I (Howard, 1955: 205), independently, noted that mid-Pliocene avifaunas are found to contain only extinct species, and that comparison of late Pleistocene with Plio-Pleistocene avifaunas shows a difference in per cent of extinct species composing them. However, our percentage figures did not agree, demonstrating that these calculations can be taken only as suggestions of relative age, and, at least in the present state of knowledge, cannot be used as definite age indicators. Where faunas are poorly preserved and incompletely represented, allowances must be made both for the original author's interpretation of fragmentary material, and the reviewing author's interpretation of tentative recordings. The Vallecito Creek avifauna, for example, is composed of at least twenty-eight species, but only sixteen can be listed (even tentatively) by specific name. Another three can be generically assigned, and seemingly represent extinct forms. Nine species can be identified only to family or order. The bones of these latter species are either so fragmentary that their identity cannot be determined, or they belong to the Order Passeriformes, a group in which identification of species is difficult even among Recent forms, and has not been attempted here. At best, judgment as to percentage of extinct forms can be based only on the sixteen specifically identified and the three generically assigned species, which, of course, represent an incomplete fauna. Of these nineteen species, ten are considered to be extinct, nine are possibly still existing.

A similar break-down of species, and generic listings for eight other avifaunas was made for comparison with Vallecito Creek. A graph was prepared (Fig. 1) to show the per cent of extinct species to total count of forms for which reasonable identification could be made. As the documentation of passerine birds varies greatly depending on preservation of material and the author's willingness to attempt identification, I felt that a more accurate com-

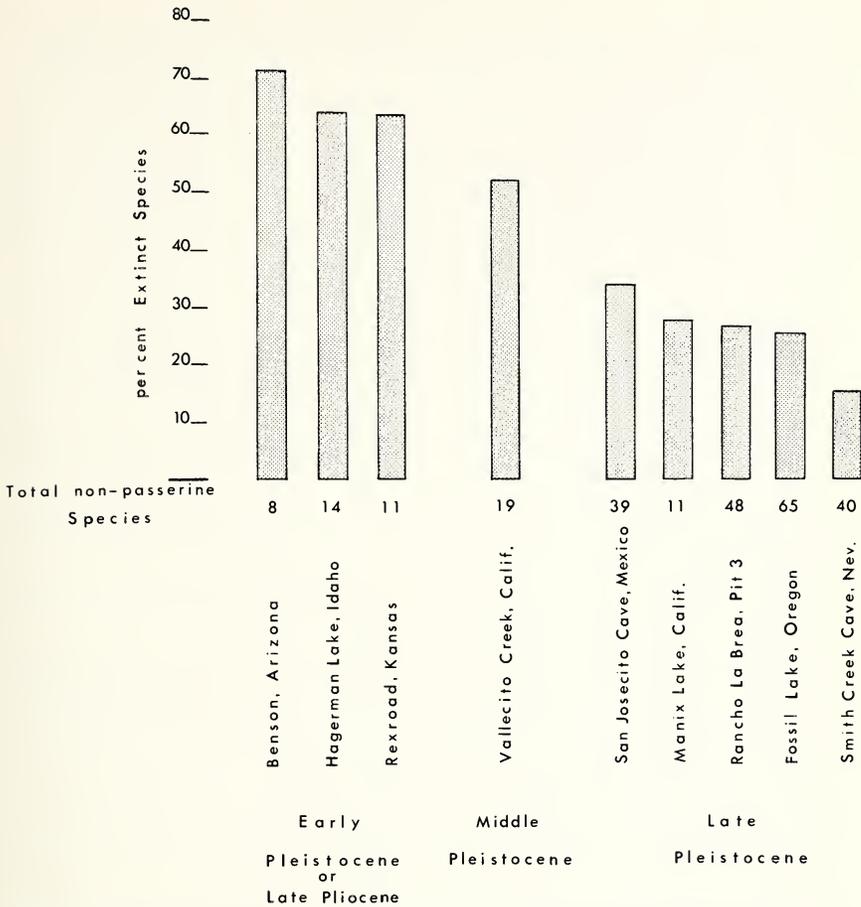


Figure 1. Graph illustrating per cent of extinct species relative to total non-passerine representation in the Vallecito Creek avifauna compared with other avifaunas of Pleistocene or late Pliocene age. Figures were compiled from listings by the following authors: Smith Creek Cave, Howard, 1952; Fossil Lake, Howard, 1946; Rancho La Brea Pit 3, Howard, 1962; Manix Lake, Howard, 1955; San Josecito Cave, L. Miller, 1943; Rexroad, Wetmore, 1944, Tordoff, 1959; Hagerman Lake, Wetmore, 1933 and 1956, A. Miller, 1948, and Brodkorb, 1958; Benson, Wetmore, 1924.

parison could be obtained by omitting this group in the calculations. Lacking adequate avifaunas for the Curtis Ranch, Bautista or Irvingtonian faunas to which Downs refers, three others, not too far removed in age, though presumably older, were used for comparison, as well as five from late Pleistocene.

Although the actual percentages here calculated differ from those that Brodkorb (*op. cit*) listed for some of the same sites, the resulting geochronologic grouping is approximately the same for most of the faunas. The Rancho

La Brea figure is affected by use here of the avifauna from a single deposit, Pit 3, which is radiocarbon dated at approximately 14,500 years BP. A comparative analysis of avifaunas of thirteen La Brea pits (Howard, 1962) indicates that other pits may have been in operation before or after Pit 3.

Even though this method of correlation is inexact, the comparisons shown do suggest that the Vallecito Creek fauna assumes an intermediate position relative to the typical late Pleistocene assemblages and those of early Pleistocene-late Pliocene age. The birds, therefore, strengthen Down's contention of possible mid-Pleistocene age.

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A NEW CHAETODONT FISH, *HOLACANTHUS LIMBAUGHI*,
FROM THE EASTERN PACIFIC

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By WAYNE J. BALDWIN



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A NEW CHAETODONT FISH, *HOLACANTHUS LIMBAUGHI*,
FROM THE EASTERN PACIFIC

By WAYNE J. BALDWIN¹

ABSTRACT: A new species of chaetodont fish, *Holacanthus limbaughi*, is described from Clipperton Island. Its relationship to other eastern Pacific members of the genus is discussed.

During the fall of 1956 and summer of 1958 the author was a member of two exploratory expeditions to Clipperton Island (Lat. 10° 18' N, Long. 109° 13' W), a remote coral atoll located approximately 600 miles due west of Costa Rica. These expeditions, organized and directed by personnel from the Scripps Institution of Oceanography, La Jolla, California, allowed us four weeks total elapsed time on the island. Among other duties, the author was responsible for collecting fishes and with the generous assistance of other expedition members 30 collections were made. It is believed that the inshore ichthyofauna is reasonably well collected. These collections are now being studied and will later be reported as a unit, but some new species will be reported earlier.

Holacanthus limbaughi, new species

Figure 1

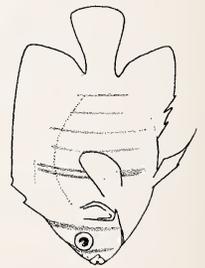
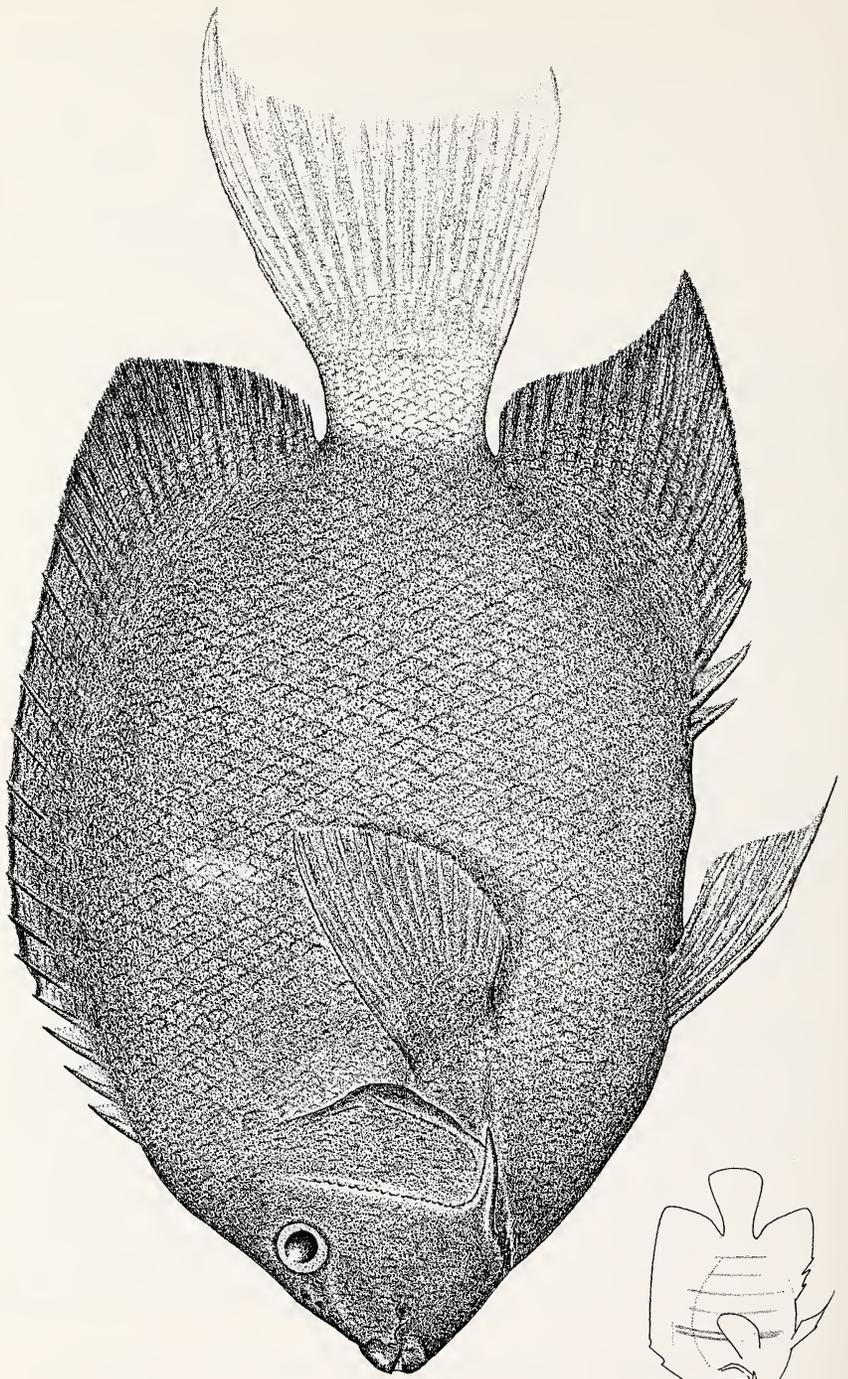
Holotype: U.S. National Museum number 178998, adult male, 171.4 mm. standard length. Collected on the northwest shore of Clipperton Island with explosives by Conrad Limbaugh, Wayne J. Baldwin, and party, 22 to 29 October, 1956.

Paratypes: Clipperton Island; UCLA 56-236, 2, (176.1-214.5 mm.) taken with the holotype, UCLA 58-287, 3, (70.5-96.6 mm.), UCLA 58-289, 1, (198.6 mm.), LACM 3308, 1, (187.2 mm.) taken with the holotype, LACM 3309, 1, (200.0 mm.), LACM 3307, 1, (79.0 mm.).

Of eleven specimens of a new *Holacanthus* collected at Clipperton Island, six paratypes and one 24.0 mm. juvenile were deposited in the fish collection of the University of California, Los Angeles, California (UCLA). The holotype was deposited in the United States National Museum, the remaining three paratypes went to the Los Angeles County Museum, Los Angeles, California (LACM).

H. limbaughi appears to be fairly common close to shore in waters 20 to 30 feet in depth and deeper as noted by several expedition members while diving immediately outside the reef "breaker line." Eight specimens, including the holotype, were collected with explosives in areas a short distance from shore, two specimens were speared, and one juvenile was captured in a hand net while diving.

¹Department of Zoology, University of California, Los Angeles, California.



Diagnosis: A *Holacanthus* distinguished by the following combination of characters: uniform dark brown color, one light oval spot below spinous dorsal, light brown caudal fin lacking a narrow black margin, caudal fin concave with the upper caudal rays prolonged, rounded soft dorsal, moderately pointed anal.

Counts and Measurements: The values for the holotype are given first, the range of values for the nine paratypes are shown in parentheses. Measurements are expressed in thousandths of standard length and all proportions are straight line measurements made with needle-point dividers. All counts and measurements follow Hubbs and Lagler (1958) except for those explained below.

Body depth—depth of body at origin of anal fin; *interorbital width*—width of bony interorbital over center of eyes; *length of orbit*—horizontal distance through center of eye; *upper and lower caudal lobe*—distance from base of upper and lower caudal rays to their extremities; *longitudinal scale rows*—number of diagonal scale rows from upper end of operculum to center base of caudal fin; *scales above the lateral line*—number of scales between lateral line and base of sixth dorsal spine; *gill rakers*—total number of gill rakers on lower limb of first gill arch.

Body depth 583 (524-601); head length 272 (262-321); snout length 115 (103-130); interorbital width 096 (096-109); length of orbit 064 (058-121); preopercular spine length 085 (056-109); length maxillary 071 (069-092); depth caudal peduncle 149 (143-154); snout to base of dorsal 329 (324-390); snout to base of anal 624 (620-658); snout to base of pectoral 277 (254-321); snout to base of pelvics 379 (350-404); length first dorsal spine 064 (057-095); length seventh dorsal spine 090 (086-135); length of 14th. dorsal spine 125 (120-180); length first anal spine 067 (054-119); length second anal spine 087 (083-163); length third anal spine 105 (098-177); length dorsal fin 793 (737-805); length anal fin 514 (422-492); length pectoral fin 275 (261-305); length pelvic fin 293 (213-300); length upper caudal lobe 353 (250-340); length lower caudal lobe 280 (220-278); length middle caudal rays 250 (234-269).

Dorsal XIV, 17 (XIV, 17-18); anal III, 18 (III, 17-18); pectoral 18 (17-18); longitudinal scale rows 47 (45-48); scales above lateral line 7 (6-9); scales below lateral line 25 (26-27); gill rakers 12 (11-12); dorsal ray number at termination point of lateral line 11 (9-13).

Description: Body oblong, compressed, its greatest depth midway between snout and base of caudal, 1.8 (1.7-1.9) in standard length. Head profile unevenly convex with a slight indentation over eyes, head 3.7 (3.2-3.8) in stand-

Figure 1. *Holacanthus limbaughi*, Holotype, USNM 178998. 171.4 mm. standard length, from Clipperton Island.

Figure 2. Diagrammatic representation of barred pattern of juvenile *Holacanthus limbaughi*, UCLA 58-370, 24.0 mm. standard length, from Clipperton Island. See text for full color description.

ard length. Bony interorbital evenly convex, its width slightly less than length of snout, 3.0 in head. A distinct shallow preorbital groove anterior to eye, running forward immediately below nostrils. Nostrils nearly equal in size, posterior opening occasionally the larger. Preorbital bone with two to four prominent spines on free margin. Free margin of preoperculum moderately dentate, 21 (20 to 30) serrae above preopercular spine, usually with one or two small spines below. Interopercal with one to three prominent spines on ventral margin. Operculum entire or with a few weak serrae on lower edge. Teeth long, narrow, pointed, in brushlike series. Caudal peduncle 1.8 (1.7-2.1) in head. Margin of spinous dorsal continuous with margin of soft dorsal, the spines gradually increasing in length posteriorly, last dorsal spine 2.2 (2.0-2.5) in head. Soft dorsal not notably produced, usually rounded. Anal spines strong with the third longest, slightly less than last dorsal spine in length. Soft anal pointed to rounded posteriorly, moderately produced in larger individuals. Four specimens in the 70 to 90 mm. range have the dorsal and anal evenly rounded, the anal not produced. Caudal convex in small individuals becoming notably concave to slightly truncate in large specimens and with the upper caudal lobe produced. Pectorals equal to length of head. Pelvics elongate, reaching to past anus and occasionally to base of anal. Dorsal, anal, and caudal fins wholly covered with small irregular, ctenoid scales except for membranes between first three dorsal spines and between anal spines. Pectoral and pelvic fins scaled only on the rays. Smaller specimens have only the base of pectorals scaled. Scales on body rough, ctenoid, moderately large with numerous small accessory scales. Scales on head small, closely packed. Lateral line strongly arched, terminating below posterior half of soft dorsal, may be quite indistinct in large specimens.

Coloration in Alcohol: Body uniform dark brown. One light, oval spot on side of body equal to diameter of eye located one snout length below seventh or eighth dorsal spine, may be indistinct or completely lacking. Dorsal and anal dark brown as rest of body except for membranes between anterior dorsal spines and between anal spines being somewhat lighter. Both dorsal and anal with a narrow black margin at tips of rays becoming broader posteriorly. Caudal dusky to light brown, becoming darker with increase in size. Caudal fin color gradually grades into the darker body on the caudal peduncle without a sharp demarcation. Pectoral and pelvic fins about same color as body, pectorals lighter in smaller specimens.

Freshly Preserved Coloration: Body dark brown but with a purplish cast in sunlight. The oval spot below the spinous dorsal more pronounced, may appear light gray. Membranes between anterior dorsal spines and anal spines brownish orange, gradually grading into the darker brown posteriorly. The narrow margin at edge of dorsal and anal bright blue, wider and more pronounced posteriorly. The caudal fin is light gray to light brown with the tips of the rays slightly darker.

Comparison: Members of the genus *Holancanthus* as defined by Fraser-

Brunner (1933) have large scales (less than 50 in longitudinal series), incomplete lateral line, hind edge of the preopercular bone covered with skin, large interopercal, and about nine rows of scales on the cheek. Three species of *Holacanthus* have been described since the revision of the subfamily Pomacanthinae by Fraser-Brunner (1933). These include *H. africanus* Cadenat 1950, *H. xanthotis* Fraser-Brunner 1950, and *H. armitagei* (Smith) 1955. No new species that correspond to *H. limbaughi* have come to light since the revision by Fraser-Brunner (1933).

Two previously described members of the genus are known from the eastern Pacific Ocean, *H. passer* Valenciennes and *H. clarionensis* Gilbert. Counts and proportions of *H. limbaughi* are in close proximity to those of *H. passer* and *H. clarionensis* but reliable diagnostic characters remain in the degree of prolongation of the dorsal and anal fins, caudal fin shape, and coloration. The dorsal and anal fins of *H. limbaughi* and *H. clarionensis* are narrowly rounded with at most a sharply pointed anal in the former species, while *H. passer* has the dorsal and anal notably prolonged often reaching to the tip of the caudal fin. The caudal fin of *H. limbaughi* is notably concave with the upper lobe distinctly elongate as opposed to the slightly truncate caudal of *H. clarionensis* and the evenly convex caudal fin of *H. passer*, both lacking the prolongation of the upper caudal lobe.

Unlike the majority of species within the family Chaetodontidae, *H. limbaughi* is quite drab in color, being overall dark brown except for the lighter caudal fin and light oval spot below the spinous dorsal. In life *H. clarionensis* is bright orange with the posterior half of the body olive brown, bright orange caudal and the pectoral and pelvic fins yellow. *H. passer* is overall dark purple with a white bar across mid-body below the spinous dorsal, caudal, pectoral, and pelvic fins yellow. The light caudal fin of *H. limbaughi* gradually grades into the dark body of the caudal peduncle without a sharp demarcation and without a narrow black margin at its tip as in *H. passer* and *H. clarionensis*.

Remarks: One 24.0 mm. juvenile, UCLA 58-370, differs from the holotype by its shorter head, larger eye, broader interorbital, evenly convex caudal fin, and with the dorsal, anal, pectoral, and pelvic fins being somewhat longer. It is similar in body color but with the dorsal, anal, and pelvic fins somewhat darker. There are seven narrow vertical crossbars on head and body (Fig. 2). Two bars on the head run vertically past the anterior and posterior margin of eye with the anterior bar on each side of the head joining over the eyes. The five remaining bars on the body are evenly spaced beginning below the seventh dorsal spine and ending at the termination point of lateral line below the soft dorsal. The bar located below the seventh dorsal spine is widest with its central portion light gray and corresponds in position to the light oval spot below the spinous dorsal of the holotype. This barred pattern, as shown by Fraser-Brunner (1933), is quite similar to the barred phase of both *H. passer* and *H. clarionensis* in specimens of a comparable size.

Derivation of name: This species is named for the late Conrad Limbaugh

who was instrumental in collecting the specimens and was in charge of the Clipperton Island shore parties.

Acknowledgments: The author wishes to thank the members of the 1956 and 1958 Clipperton Island shore parties for their generous assistance in collecting many of the specimens and especially to Mr. John Wintersteen and Dr. Ernst S. Reese, then graduate students in the Department of Zoology, University of California. Thanks are due to the personnel aboard the research vessel *Spencer F. Baird* for their kind cooperation in handling and transporting equipment and supplies to and from the island. The author wishes to thank Dr. Boyd W. Walker for his helpful suggestions and for reading the manuscript.

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A NEW SPECIES OF *ACMAEA* (ARCHAEOGASTROPODA)
FROM THE PLEISTOCENE OF SAN NICOLAS ISLAND,
CALIFORNIA

By JERE H. LIPPS

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A NEW SPECIES OF *ACMAEA* (ARCHAEOGASTROPODA)
FROM THE PLEISTOCENE OF SAN NICOLAS ISLAND,
CALIFORNIA

By JERE H. LIPPS¹

ABSTRACT: A new species, *Acmaea mitchelli* which possesses shell sculpture of imbricate ribs, is described from Pleistocene marine terrace deposits on San Nicolas Island, California. It is compared with and differentiated from similar species of *Acmaea* from California. Evidence suggests that the new species lived on rocks in the high intertidal zone somewhat above mean tide level. The new *Acmaea* may be related to *A. limatula*.

Collections of invertebrates made by members of the Los Angeles County Museum, the U.S. Geological Survey, and myself include over 200 specimens of a new species of *Acmaea* from six localities (Fig. 1) in Pleistocene marine terrace deposits on San Nicolas Island, Ventura County, California. These collections suggest that a large population of this new species co-existed with other species of *Acmaea* on the island during the Pleistocene. On this basis and the distinct morphology of the specimens, the description of this *Acmaea* is presented herein.

References to the Los Angeles County Museum Section of Vertebrate Paleontology are hereafter abbreviated as LACM VP, those to the Section of Invertebrate Paleontology as LACM IP, those to the U.S. Geological Survey as USGS, and those to the invertebrate paleontology collections, Department of Geology, University of California, Los Angeles as UCLA.

SYSTEMATIC DESCRIPTION

Class GASTROPODA Cuvier, 1797
Order ARCHAEOGASTROPODA Thiele, 1925
Suborder PATELLINA von Ihering, 1876
Family ACMAEIDAE Carpenter, 1857
Genus *Acmaea* Eschscholtz, 1833
Acmaea mitchelli new species
Fig. 2, a-d; Fig. 3, a-kk; Fig. 4, a-kk

Acmaea n. sp. Vedder in Vedder and Norris, 1963, U.S. Geol. Survey Prof. Paper 369, table 4, p. 40.

Diagnosis: Apex in anterior half of shell; sculpture of evenly radiating ribs; ribs narrow, imbricate with nodes which may be hollow ventrally; internal color white with an even brown marginal band.

¹Department of Geology, University of California, Los Angeles.

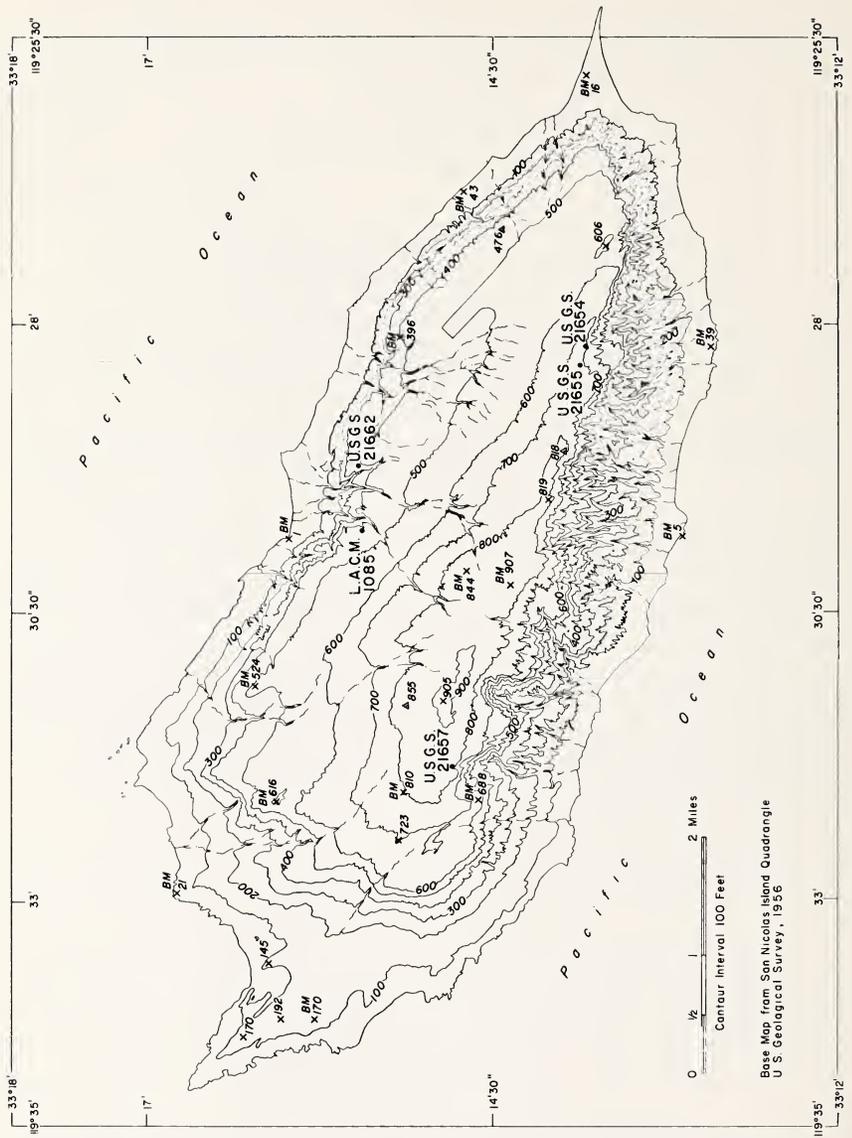


Figure 1. Map of San Nicolas Island, Ventura County, California, showing the type locality (LACM VP 1085) of *Acmaea mitchelli* Lipps, new species, and other localities from which specimens of *A. mitchelli* have been collected.

Description: Shell an open cone, medium in size for the genus, bilaterally symmetrical, thicker in apical region. Outline elliptical. Apex acute, inflected

anteriorly so that it projects slightly beyond the surface of the anterior end-face. Anterior end-face straight in profile. Posterior and lateral faces convex outward. Sculpture of ribs radiating from the apex with one to three ribs intercalated between the primary ribs. Ribs prominent, narrow, rounded, imbricate, straight on anterior and posterior end-faces, curved posteriorly on lateral faces, increasing in height and width near margin of shell. Imbrications on ribs form nodes which may be hollow ventrally. Ribs intercalated between primary ribs slightly narrower and less prominent. Spacing of ribs nearly uniform with interspaces narrower than width of adjacent ribs. Growth lines conspicuous. Color brownish gray externally. Margin of shell arched dorsally along lateral edges, crenulate due to expression of ribbing. Aperture elliptical. Internal color white except for an even brown marginal band extending dorsally from margin for about one-third of interior of shell. Brown band semi-glossy. White area next to brown band glossy. Apical area dull. Internal surface faintly reflects the external ribbing.

Holotype: No. 1126 LACM IP collections. Length 28.0 mm.; width 20.6 mm.; height 10.9 mm.; distance from apex to anterior margin of shell 7.3 mm. Collected by Edward D. Mitchell, Jr., April 16, 1960, at LACM VP Locality 1085.

Paratypes: Thirty-six figured paratypes nos. 1127-1 to 1127-36 and 46 unfigured paratypes nos. 1127-37 to 1127-82, LACM IP collections. Twenty-five unfigured paratypes nos. 12155, 12155 a-x, Type Collection, Department of Paleontology, California Academy of Sciences. Twenty-five unfigured paratypes no. 34970, UCLA. All paratypes were collected by Jere H. Lipps and Edward D. Mitchell, Jr., April, 1960 from LACM VP Locality 1085.

Etymology: This species is named for Edward D. Mitchell, Jr., Vertebrate Paleontology Section, Los Angeles County Museum, who found the holotype and many of the paratypes, in recognition of his studies of the paleontology of the California Channel Islands.

Type locality and occurrence: LACM VP Locality 1085, San Nicolas Island, Ventura County, California (same as USGS Locality 21666): at the head of a small gully which joins the second western tributary to Mineral Creek (the most westerly of three deep canyons which empty into the sea just west of Coney Point). The locality is 5775 feet north and 3500 feet east of 33°14' 30" N., 119°30'30" E.; San Nicolas Island Quadrangle (ed. 1943, reprinted 1952). Altitude about 425 feet above sea level. See Figure 1.

In addition to the type locality, *Acmaea mitchelli* was found at USGS Localities 21654, 21655, 21657, and 21662 (J. G. Vedder, written communication; and personal collections). The type locality and USGS Locality 21662 are on the northern side of the island; the remainder are on the southern side in terrace deposits at higher elevations (see Fig. 1).

Age: Kanakoff (*in* Howard, 1955:137) considered the molluscan assemblage from LACM VP Locality 1085 to correspond to the cold water fauna of the Lower Pleistocene deposits on the mainland. Vedder and Norris (1963:

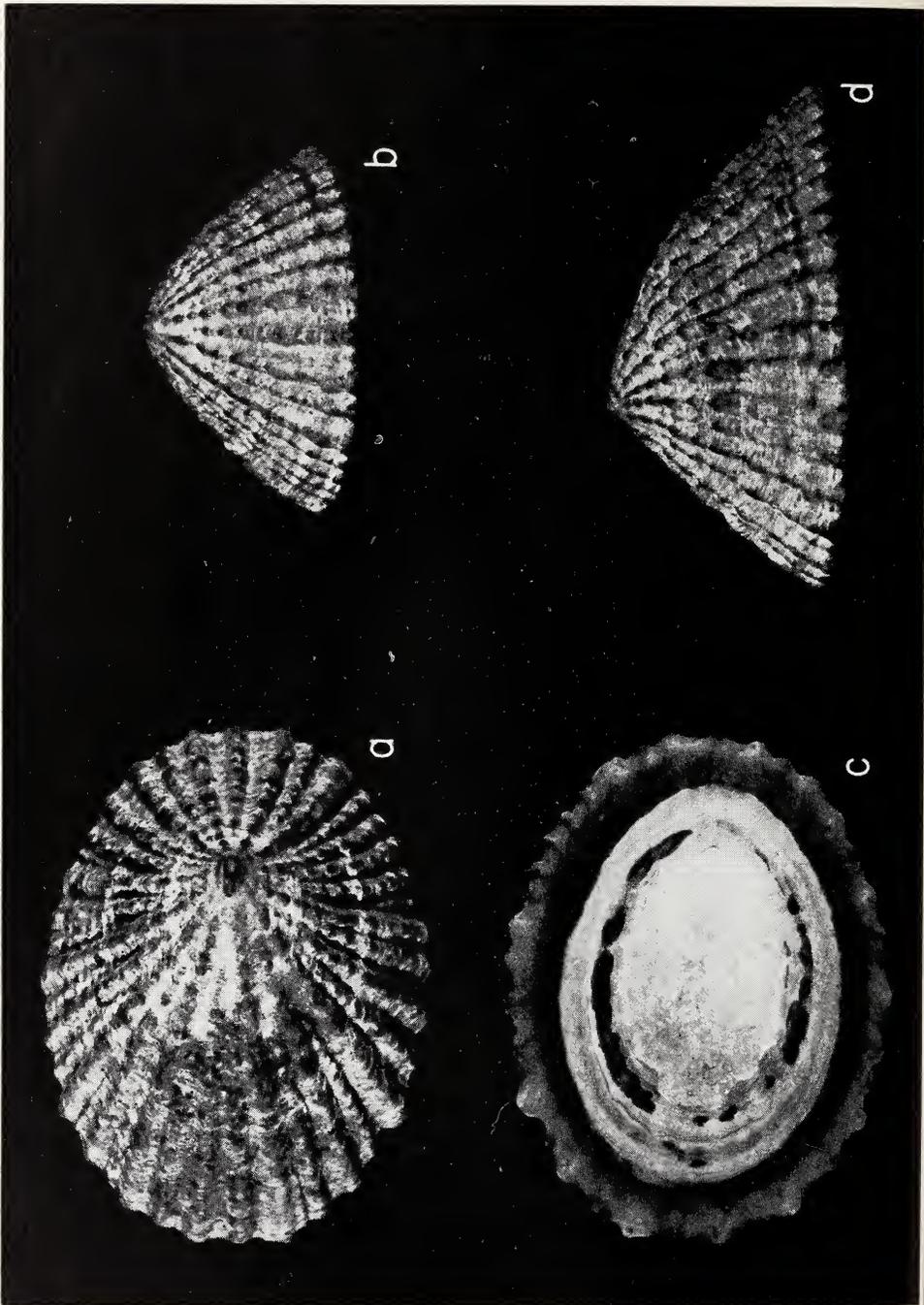


Figure 2. *Acmaea mitchelli* Lipps, new species. Holotype LACM IP 1126. Dorsal (a), anterior (b), ventral (c), and left lateral (d) views of the shell. Approximately $2\frac{1}{2}$ times natural size. Locality LACM VP 1085, Pleistocene marine terrace deposit, San Nicolas Island, Ventura County, California.

52-53) have tentatively dated the terraces as Late Pleistocene on the basis of geomorphic and faunal evidence.

Variation: Shell characters within one species of *Acmaea* may be extremely variable due to response to ecologic stresses, and the specimens of *A. mitchelli* thus show many variations (see Figs. 3 and 4). Individuals of *A. mitchelli* with a smaller periphery may be flattened, whereas those with a larger periphery have a relatively higher spire. The shell perimeter is commonly elliptical or oval, but in smaller specimens may be nearly circular, and in some specimens may be irregular and no longer bilaterally symmetrical. The apex is situated in the anterior half of the shell and its position ranges from sub-central to distinctly anterior. The anterior end-face is commonly flat in profile, but may be convex in differing degrees. Some individuals have more widely spaced and fewer ribs than the holotype. The margin of the shell is often thicker than the rest of the shell, resulting in constriction of the aperture. One paratype (LACM IP no. 1127-2; dorsal and ventral views in Figs. 3-c; 4-c) shows distortion of the right-lateral face with incomplete development there of the ribs. These features may have been due to the animal living next to a hard surface. The ornamentation of the individual ribs and the pattern of internal coloration vary only slightly. The internal marginal brown band varies in width and intensity of coloration, but this in part may be due to preservation.

SIMILAR SPECIES OF CALIFORNIA *Acmaea*

Seven species of *Acmaea*, which also occur in California, are herein illustrated for comparison with *A. mitchelli* and their similarities and distinctive characters noted. Reference to the original description of each species is also given.

Acmaea conus Test Figures 5 (g-h); 6 (g-h)

Test, A. R. (G.), 1945, *Nautilus*, 58: 92-96.

Acmaea conus differs from *A. mitchelli* in its roughly rounded ribs which are irregularly spaced and commonly branched. Internally, *A. conus* has a dark apical spot not found in *A. mitchelli*.

Acmaea digitalis Eschscholtz Figures 5 (a-c); 6 (a-c)

Eschscholtz, F. in Rathke, M. H., 1833, *Zoologischer Atlas*, 5:20, pl. 23, figs. 7-8, Berlin.

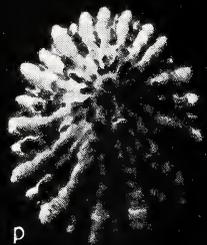
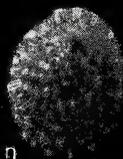
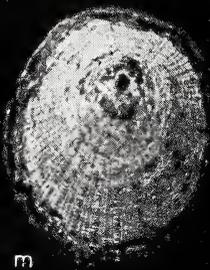
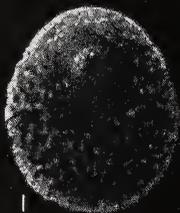
This species is very similar to *A. mitchelli* in shell form. Ribs of *A. digitalis* are spaced widely, rarely intercalated, and neither imbricated nor very pronounced. The apex of *A. digitalis* is normally far anterior on the shell and it is recurved. *A. digitalis* has a characteristic dark apical spot and variable marginal coloration not found in *A. mitchelli*.



Figure 3. *Acmaea mitchelli* Lipps, new species. Dorsal view of the holotype (a), LACM IP 1126, and 36 paratypes (b-kk), LACM IP 1127-1 to 1127-36. Natural size. Locality LACM VP 1085, Pleistocene marine terrace deposit, San Nicolas Island, Ventura County, California.



Figure 4. *Acmaea mitchelli* Lipps, new species. Ventral view of the holotype (a), LACM IP 1126, and 36 paratypes (b-kk), LACM IP 1127-1 to 1127-36. Natural size. Locality LACM VP 1085, Pleistocene marine terrace deposit, San Nicolas Island, Ventura County, California.



Acmaea funiculata (Carpenter)

Figures 5 (d-f); 6 (d-f)

Carpenter, P. P., 1864, Rept. British Assoc. Adv. Sci., 1863: 612, 650.

This *Acmaea* differs from *A. mitchelli* in having a relatively higher spire, sculpture consisting of thin, irregularly spaced ribs radiating from the apex, and a shell which is white in color, externally and internally.

Acmaea limatula Carpenter

Figures 5 (l-n); 6 (l-n)

Carpenter, P. P., 1864, Rept. British Assoc. Adv. Sci., 1863: 540.

A. limatula generally has a lower and rounder shell than does *A. mitchelli*, and the sculpture consists of from two to five finely imbricate ribs between more pronounced ribs. These pronounced ribs closely resemble the imbricated ribs of the new species. Internally, *A. limatula* has a dark apical spot.

Acmaea limatula morchii Dall

Figures 5 (i-k); 6 (i-k)

Dall, W. H., 1878, Proc. U.S. Natl. Mus., 1: 47.

This subspecies shows a close resemblance to *A. mitchelli*, as their shells have a similar shape, the same relative shell height, constricted aperture, and imbricate ribs with nodes which have concave hollows on their ventral sides. *A. limatula morchii* differs from *A. mitchelli* in having less prominent radial ribs, fine intermediate ribs between the principal ones, the nodes of the ribs are more concave on the ventral side, and there is a dark apical spot internally.

Acmaea pelta Eschscholtz

Figures 5 (r-t); 6 (r-t)

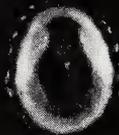
Eschscholtz, F., in Rathke, M. H., 1833, Zoologischer Atlas, 5:19, Berlin.

This species displays a varied external color pattern of bands or checkerboards. The anterior end is commonly more narrow than the posterior end and the faces of the shell are usually planar. Ribs, when present, are heavy

Figure 5. Dorsal view of similar species of California *Acmaea*. All illustrations approximately natural size. a-c. *A. digitalis* Eschscholtz from Laguna Beach, Calif., UCLA hypotypes: a. no. 35295; b. no. 35296; c. no. 35297. d-f. *A. funiculata* (Carpenter) from Catalina Island, Calif., at 30-40 fathoms. UCLA hypotypes: d. no. 35298; e. no. 35299; f. no. 35300. g-h. *A. conus* Test from mouth of Santa Ynez Canyon, Calif. LACM IP hypotypes: g. no. 1128-1; h. no. 1128-2. i-k. *A. limatula morchii* Dall. UCLA hypotypes: i. no. 35301; j. no. 35302; k. no. 35303. l-n. *A. limatula* Carpenter from Morro Bay, Calif. UCLA hypotypes: l. no. 35304; m. no. 35305; n. no. 35306. o-q. *A. scabra* (Gould) from San Pedro, Calif. UCLA hypotypes: o. no. 35307; p. no. 35308; q. no. 35309. r-t. *A. pelta* Eschscholtz from San Francisco Bay, Calif. UCLA hypotypes: r. no. 35310; s. no. 35311; t. no. 35312.



a



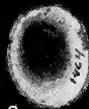
b



c



d



e



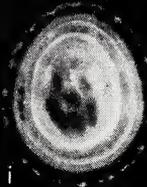
f



g



h



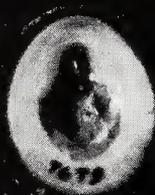
i



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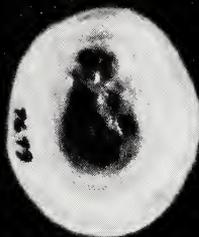


k

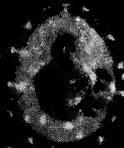


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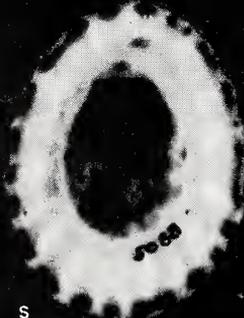
p



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t

and broad, nonspinose, and widely spaced. A dark internal coloration is commonly present posterior to the apex on the inside of the shell. With the exception of a somewhat narrowed anterior end in some specimens, *A. mitchelli* has none of the above characters.

Acmaea scabra (Gould)

Figures 5 (o-q); 6 (o-q)

Gould, A. A., 1846, Proc. Boston Soc. Nat. Hist., 2:152.

The shells of *A. scabra* have very heavy ribs with nodes, or more rarely spines. The ribs are generally fewer in number, broader, not imbricate, and more widely spaced than those of *A. mitchelli*. Commonly, *A. scabra* has a markedly scalloped marginal outline whereas *A. mitchelli* does not. The internal coloration of *A. scabra* differs considerably, generally consisting of scattered brown markings or a dark apical spot, or more rarely only a regular marginal band as in *A. mitchelli*.

PALEOECOLOGY OF *Acmaea mitchelli*

Test (1946) stated that it is possible to determine the ecologic niche of a species of *Acmaea* by means of certain adaptive features of the shells. The following characteristics, which Test (1945; 1946) stated are adaptations to an ecologic niche, are displayed by the shells of *A. mitchelli*: 1) the restriction of the aperture in many specimens, an adaptation to prevent dessication in limpets subject to exposure; 2) a thick, heavy shell and prominent sculpture, which serve to withstand the impact of ocean waves on the animal; 3) an irregular margin caused by conformation to the substrate where the animal lived; and 4) a relatively high spire, which Test (1945) attributed to exposure or other unfavorable conditions, but which Shotwell (1950) considered a result of growth. These shell features suggest that in life *A. mitchelli* was subject to long periods of exposure and wave action.

Acmaea mitchelli is found associated with molluscan species (see Vedder and Norris, 1963, table 4) representing the "exposed rocky shore association: *Mytilus californianus*-*Littorina planaxis* community" of Valentine

Figure 6. Ventral view of similar species of California *Acmaea*. All illustrations approximately natural size. a-c. *A. digitalis* Eschscholtz from Laguna Beach, Calif. UCLA hypotypes: a. no. 35295; b. 35296; c. no. 35297. d-f. *A. funiculata* (Carpenter) from Catalina Island, Calif. at 30-40 fathoms. UCLA hypotypes: d. no. 35298; e. no. 35299; f. no. 35300. g-h. *A. conus* Test from mouth of Santa Ynez Canyon, Calif. LACM IP hypotypes: g. no. 1128-1; h. no. 1128-2. i-k. *A. limatula morchii* Dall. UCLA hypotypes: i. no. 35301; j. no. 35302; k. no. 35303. l-n. *A. limatula* Carpenter from Morro Bay, Calif. UCLA hypotypes: l. no. 35304; m. no. 35305; n. no. 35306. o-q. *A. scabra* (Gould) from San Pedro, Calif. UCLA hypotypes: o. no. 35307; p. no. 35308; q. no. 35309. r-t. *A. pelta* Eschscholtz from San Francisco Bay, Calif. UCLA hypotypes: r. no. 35310; s. no. 35311; t. no. 35312.

(1961). *A. mitchelli* occurs most abundantly nearer the paleo-shoreline (see Vedder and Norris, 1963, pl. 2), as inferred from field relations of the sediments and the terrace platform, than the paired valves of pelecypods and remains of other animals indicative of the mid-intertidal zone of Valentine (1961: fig. 2). Many well-preserved shells of *A. mitchelli* were found in close association with articulated foot bones of the extinct flightless goose *Chendytes milleri* Howard, which Miller (1960) interpreted as having been deposited in the high intertidal zone.

These interpretations and observations suggest that *A. mitchelli* occupied an ecologic niche in the high intertidal zone probably somewhat above the average mean tidal level where wave impact and exposure were important factors affecting marine life.

Many specimens of *A. mitchelli* have distorted or irregular margins (see Figs. 3 and 4). Such features occur in Recent limpets living on rocks in the high intertidal, which regularly return to the same spot after foraging short distances for food, as does *A. scabra* (see Hewatt, 1940). Thus, it may be inferred that *A. mitchelli* likewise returned consistently to the same spot after foraging for food, and that it also lived on rocks (many are present in the deposit and were undoubtedly available during the Pleistocene).

Acmaea mitchelli may have competed with *A. digitalis* and *A. scabra*, with which it is associated in the Pleistocene deposits, and which today occupy a position in the high intertidal zone. The other modern occupant of this zone, *A. conus*, is not known to occur in the Pleistocene sediments of San Nicolas Island.

PHYLETIC RELATIONSHIPS

True phyletic relationships of species of *Acmaea* are difficult to establish positively on the basis of shell morphology and should properly be based on certain characteristics of the radular ribbon (Test, 1946). Lacking the radular ribbon, the paleontologist can, at best, only suggest possible relationships.

Shell characters of *A. mitchelli* are most like those found in the closely related group of *A. scabra*, *A. digitalis* and *A. limatula*. Of this group, *A. limatula* and its varieties have shell sculpture (supposedly a conservative character) similar to that of *A. mitchelli* and this similarity may indicate a phyletic relationship.

ACKNOWLEDGMENTS

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A REVIEW OF THE FISHES OF THE GENUS
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By JOHN E. FITCH



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Editor

A REVIEW OF THE FISHES OF THE GENUS *PLEURONICHTHYS*

By JOHN E. FITCH¹

ABSTRACT: The genus *Pleuronichthys* is confined to the north Pacific. Five of the six species, *coenosus*, *decurrrens*, *verticalis*, *ritteri*, and *ocellatus*, inhabit American coastal waters, and *cornutus* lives along Asiatic shores. All members of this specialized genus, commonly called turbot, are characterized by having the dorsal fin originating on the blind side.

In this review, more than 5,700 individuals were examined and identified. A key was constructed for distinguishing the species, and variations and relationships are discussed.

Each species is illustrated with a photograph and its distinguishing characters, color, geographic distribution, maximum size, food, and synonymy are outlined. In addition, various life-history aspects are discussed where information was available.

The hornyhead and Asiatic turbot (*verticalis* and *cornutus*) appear to be the most highly specialized, and the C-O turbot (*coenosus*), the most primitive.

In the eastern north Pacific, flatfishes of the genus *Pleuronichthys* (turbot) are relatively unexploited and probably represent one of California's most abundant shallow-water bottomfish resources. They are small fishes, seldom exceeding a foot in length or a pound in weight, yet they are tasty and firm of flesh. Only during the past decade have they been marketed in any quantity, and then primarily for mink food (Best, 1959).

One reason such low tonnages have been harvested probably lies in the fact that most turbot inhabit shallow water within three miles of shore, where commercial trawling is prohibited by law. Because of their relatively small sizes and small mouths, few are either fished for or hooked by sport fishermen.

Because our expanding human population has reached the point where we can no longer afford to waste protein resources by under-harvesting them, it was deemed advisable to learn as much as possible about the turbot in our waters. Immediately a major obstacle, proper species identification, presented itself. To overcome this obstacle, I undertook the present study, which includes all the turbot of the world.

MATERIAL AND METHODS

Since 1955, when I first became interested in the genus *Pleuronichthys*, I have, with assistance from my co-workers, examined, identified, and measured over 5,700 individuals. Most of these were weighed, and their sexes were

¹Research Associate, Los Angeles County Museum; Research Director, California State Fisheries Laboratory, Terminal Island. This is an expanded version of a thesis originally submitted in June 1963 in partial fulfillment of the requirements for the degree of Master of Arts in Zoology at the University of California, Los Angeles.

TABLE 2
Vertebral Counts for the Species of *Pleuronichthys*

Species	Precaudal Vertebrae					Caudal Vertebrae							Total Vertebrae					
	12	13	14	15		22	23	24	25	26	34	35	36	37	38	39	40	41
<i>ritteri</i>	24	1				5	19	1			4	20	1					
<i>ocellatus</i>	24	1				10	15				9	16						
<i>coenostus</i>	1	24						7	16	2				7	17	1		
<i>verticalis</i>		25					17	7	1				17	7	1			
<i>cornutus</i>	11	14					4	16	5				11	13	1			
<i>decurrens</i>			23	2				1	13	11					1	12	11	1

TABLE 3
Gill Raker Counts for the Species of *Pleuronichthys*

Species	Total Gill Rakers									
	8	9	10	11	12	13	14	15	16	17
<i>cornutus</i>	5	14	6							
<i>verticalis</i>		1	11	13						
<i>decurrens</i>		2	10	12	1					
<i>ocellatus</i>			4	6	11	3	1			
<i>coenosus</i>				2	6	9	7	1		
<i>ritteri</i>					1	5	11	6	1	1

determined. In addition, numerous biological and ecological observations have been made on Californian members of the group, and 314 specimens (50 *ritteri*, 58 *coenosus*, 50 *decurrens*, 54 *verticalis*, 52 *ocellatus*, and 50 *cornutus*) were selected for use in evaluating the various species (Tables 1-4). I have examined material from throughout the known geographic ranges of the six species involved, except for *decurrens* and *coenosus*. I did not see any *decurrens* or *coenosus* from the northernmost limits of their range.

All measurements were made on the ocular side and generally follow the standardized methods of Hubbs and Lagler (1958). *Body height* involves the greatest straight-line distance between the ventral and dorsal contours exclusive of the fin rays. *Head length* was measured from the tip of the upper jaw to the posterior extremity of the bony operculum. The *interorbital ridge length* was measured in a straight line from the anterior edge or tip of the anteriormost protuberance or spine to the posterior edge or tip of the posteriormost (3rd) protuberance or spine.

Fin ray, gill raker, and pored scale counts were made with the aid of a binocular dissecting scope at low power. Generally, if the dorsal fin ray count was high, the anal ray count on the same fish also would tend to be high, regardless of fish length. This was true for all six species. The scales of *Pleuronichthys* are covered to various depths by integument, and because of this, are probably one of the least accurate (and thus least reliable) of the counts that can be made.

Vertebral counts were made either by skeletonizing fresh material or by X-raying preserved material. Both methods yield satisfactory and accurate results.

The synonymy of each species is limited to those references which are of value in understanding its taxonomy, systematics, distribution, or ecology.

SYSTEMATIC ACCOUNT

Norman (1934) distinguishes *Pleuronichthys* from other genera in subfamily Pleuronectinae by the small mouth (maxillary on ocular and blind sides less than $\frac{1}{3}$ head); by the small, acute jaw teeth, better developed on the blind side; by the thick lips with transverse plicae; by the dorsal origin

TABLE 4
 Ranges of Selected Measurements (Per Mille of Standard Length)
 for the Species of *Pleuromichthys*

Measurement	<i>cornuttus</i>	<i>verticalis</i>	<i>decurrens</i>	<i>coenostus</i>	<i>ocellatus</i>	<i>ritteri</i>
Standard length (mm)	71-199(25) ‡	168-294(25) ‡	154-226(25) ‡	156-242(25) ‡	35-184(25) ‡	157-225(25) ‡
Total length	1260-1296(24)	1232-1292(24)	1242-1298(25)	1233-1319(25)	1230-1308(25)	1275-1325(24)
Head length	215-250(24)	221-272(25)	242-279(25)	226-272(25)	221-272(25)	214-241(24)
Bony upper orbit*	072-091(25)	068-097(25)	083-104(25)	080-098(25)	085-109(25)	063-081(25)
Maxillary length	046-060(23)	051-067(24)	056-070(25)	057-071(25)	050-065(23)	050-066(25)
Interorbital ridge length †	073-103(23)	073-100(25)	076-097(25)	077-100(25)	085-106(24)	058-077(24)
Head width at mid-orbit	075-097(25)	076-102(25)	086-105(25)	077-105(24)	078-098(25)	065-081(24)
Snout to anal fin insert	298-338(10)	349-393(5)	368-398(5)	321-338(2)	330-386(21)	340-413(15)
Snout to pectoral insert	222-252(10)	250-291(5)	258-279(5)	236-252(2)	233-274(22)	234-262(15)
Snout to pelvic insert	219-267(10)	262-295(5)	258-277(5)	245-252(2)	248-304(22)	242-286(15)
Body height	483-556(23)	451-528(25)	524-590(25)	479-527(24)	475-586(25)	505-570(24)
Caudal peduncle height	112-135(23)	107-132(25)	110-128(25)	112-142(25)	114-146(25)	099-128(25)
Pectoral fin length	122-148(24)	123-156(25)	141-182(25)	147-180(25)	122-170(23)	120-167(25)
Pelvic fin length	077-102(24)	069-097(25)	088-115(25)	076-105(25)	087-120(24)	077-100(25)

* horizontal axis

† first to third protuberance

‡ number of specimens measured appears in parens.

being on the blind side; and by the supratemporal branch of the lateral line with a long posterior prolongation. In the several hundred specimens that I examined critically, these generic characters held true without exception.

Fossil Record

Jordan and Gilbert (1920) described several fossil flatfishes from the California Miocene (Lompoc), including *Zororhombus veliger*. David (1943) designated Jordan's *Zororhombus* as a subgenus within *Pleuronichthys*. She based her opinion upon published records and one "fine specimen" in the California Institute of Technology collection (now in the Los Angeles County Museum collection). The characters she used to distinguish the subgenus *Zororhombus* (larger number of precaudal vertebrae, larger mouth, and deeper body than for any living species) are of such magnitude they cast doubt upon the validity of placing Jordan's *veliger* in the genus *Pleuronichthys*. None of the living species of *Pleuronichthys* has more than 26 caudal vertebrae (Table 2), *veliger* has 29. Similarly, no living *Pleuronichthys* has fewer than 12 precaudal vertebrae, *veliger* has 11. David (1943) states for *veliger*, "mouth 2 in head on ocular side," yet Norman (1934) characterizes the genus *Pleuronichthys* with the statement, "maxillary on ocular side less than $\frac{1}{3}$ head," which agrees with the information I obtained by measuring these characters on 150 specimens representing the six known living species (Table 4).

My examination of over 10,000 fossil otoliths (mostly in the Los Angeles County Museum collections) from one Eocene, four Pliocene, and eleven Pleistocene deposits of southern California has failed to turn up a single otolith of *Pleuronichthys*.² Species that are now associated with turbot ecologically are in profusion among these deposits, but there are no turbot. *Pleuronichthys* otoliths (sagittae) resemble rice grains in size and shape, and it would be impossible to overlook or fail to recognize them. Many tiny otoliths, 1 or 2 mm. in greatest dimension, from gobies, *Lepidogobius lepidus*, and sanddabs, *Citharichthys stigmaeus*, are among the screenings, so the larger *Pleuronichthys* otoliths, if they were present, would also be retained.

Based upon a few otoliths from a Californian deposit (Rose Canyon, San Diego county), flatfishes were present in the north Pacific during the Eocene. Several authors (Gilbert, 1910; Jordan and Gilbert, 1919 and 1920; Jordan, 1924) described fossil flatfishes from diatomaceous Miocene deposits of southern California, but none of these is congeneric with any flatfish living off our coast today. There is no fossil evidence to indicate when, in geologic time, *Pleuronichthys* evolved or entered the north Pacific fauna.

Pleuronichthys

The genus *Pleuronichthys* was described by Girard in 1858, with *coenosus* as the type species. It is closely related to *Hypsopsetta* but differs in numerous

²Since this manuscript went to press, an otolith of *Pleuronichthys* (cf. *ritteri*) was unearthed in the Playa del Rey formation, a Pleistocene deposit (Los Angeles Museum of Invertebrate Paleontology site 59).

characters. Three of the most obvious differences are that *Pleuronichthys* has the dorsal originating on the blind side (median line in *Hypsopsetta*), has either spines or protuberances on the interorbital ridge or around the eyes (head of *Hypsopsetta* is smooth), and has transverse plicae on the thickened lips (no plicae in *Hypsopsetta*).

Within the genus *Pleuronichthys* a number of characters are relatively constant for all members. The scales are cycloid. The lower pharyngeals each have one or two rows of slender, acute teeth. The pelvic fin of the blind side is inserted a little anterior to and farther from the median line than that of the ocular side. The lateral line tubules are not greatly branched. There are 34 to 41 vertebrae, 12 to 15 precaudal plus 22 to 26 caudal. Dorsal rays number 62 to 83; anal rays, 43 to 62; pectoral rays 9 to 14; and caudal rays 10 + 9 or 19 (10 + 10 in one of 58 *coenosus*). The gill rakers are short and weak, ranging from 8 to 17 in number. The head is of about average length, making up between 22 and 27 percent of standard length. Either partially- or fully-ambicolorated individuals have been noted among all species except *ocellatus*. Ambicoloration is rare except in *decurrans*, in which 21 of 899 specimens showed the character to some degree.

There are six species of *Pleuronichthys* in the north Pacific, five American and one Asiatic.

Variation

In *Pleuronichthys*, there is so little interspecific variation (Tables 1 to 4) that meristic characters and proportional measurements seldom will serve to distinguish a particular species from more than one of the remaining five. Once the left eye has migrated to the right side of the fish, and a demersal existence is commenced, no body proportion changes significantly (Table 4). Meristic characters show considerable uniformity for any given species within its entire geographic range (Tables 1, 2, 3). This apparent lack of variation does not preclude positive specific identification, however.

Within any species, greatest variation concerns color patterns, yet volumes have been written about the color-changing capabilities of flatfishes subjected to different substrate patterns. In all species, there is a tendency for brown or black spots on the ocular side at midbody and along the dorsal and ventral body contours. In *ocellatus* and *verticalis*, the midbody spot may be ocellated in white. The black spots of *ocellatus* and *ritteri* have been used as diagnostic characters by numerous workers, yet they frequently are entirely lacking. Similarly, the typically profuse reddish-brown spots of *cornutus* may be large, small, or missing. In the Gulf of California, *verticalis* is brightly mottled and marked in various shades of brown. Such colorful specimens are the exception in *verticalis* from the outer coast, but in each large catch of them, a few specimens display coloration typical of those in the Gulf.

The lateral line has a long, posteriorly extending supratemporal branch in all species. This "accessory lateral line" seldom terminates at the base of the same dorsal ray on both the blind and ocular side. In *coenosus*, *ritteri*, and

ocellatus, a short anterior extension always branches off near its origin. This anterior extension sometimes contains only three or four scales but usually it has more than 15. The other three species are supposed to lack an anterior accessory lateral line; however, such a branch occurs as often as 10 percent of the time in *verticalis* and *decurrens*, and it was noted in 50 percent of the *cornutus* I examined.

Some sexual differences have been noted. The pelvic fins of the males often extend past the anal opening, while those of the females seldom reach the anus. Females grow at a slightly more rapid rate than do males and attain greater maximum lengths, thus most large turbot are females.

When checking meristic characters, 50 individuals apparently will include nearly all extremes. This is amply illustrated by dorsal ray counts for *coenosus*. On 50 specimens, I tallied 66 to 77 dorsal rays; Townsend (1936) counted 65 to 78 in 62 *coenosus* from Washington, near the northern end of their range. The literature failed to reveal any other dorsal ray counts for *coenosus* that were lower than 66 or higher than 75, regardless of where, within the species' range, (Baja California to Alaska) they were taken. A similar situation was encountered with *decurrens*.

The fewest dorsal rays noted for any species of *Pleuronichthys* was 62 (*ritteri* and *ocellatus*), while the most was 83 (*cornutus*), a total spread of only 22 rays (Table 1). Four of the six species have dorsal ray counts that range over 13 or 14 numbers of the 22-ray spread noted for the genus (*ocellatus* have 62 to 74, *verticalis* have 66 to 79, *decurrens* have 67 to 79, and *cornutus* have 70 to 83). Dorsal ray counts for the other two species range through 9 to 12 numbers.

Relationships

Norman (1934) indicates *Pleuronichthys* is closely related to *Hypsopsetta*, and points out numerous characters by which the two genera differ. Most salient of these are the dorsal fin insertion on the blind side in *Pleuronichthys* (in *Hypsopsetta* it originates on the median line of the head), and the high interorbital ridge in *Pleuronichthys*, generally provided with bony spines or protuberances (*Hypsopsetta* has a low interorbital, lacking in spines or prominences).

In *P. verticalis* and *P. cornutus* the interorbital ridge attains its greatest development, terminating both anteriorly and posteriorly in a sharp, projecting spine. Near its anterior end in these two species there is also a spine which rises vertically from the ridge, being higher and sharper in *verticalis*. The ridges of *ritteri*, *ocellatus*, and *coenosus* are about equal in their development. In these three, there are slightly raised, round bony protuberances at the anterior and posterior ends of the ridge, and a small bony lump on the dorsal surface of the ridge near its anterior end. *P. decurrens* is intermediate between the spiny ridged *verticalis-cornutus* complex and the *ritteri-ocellatus-coenosus* group. In addition, *decurrens* often has several raised bony prominences around the posterior margin of the upper orbit.

The dorsal fin also shows variation in its origin on the blind side. In five species (*verticalis*, *cornutus*, *ritteri*, *ocellatus*, and *coenosus*), it originates on about a level with the snout, well above the lower corner of the mouth. In *decurrens*, except for completely ambicolored individuals where it originates on a level with the snout, the dorsal fin originates much lower on the blind side, usually opposite and level with the lower corner of the mouth.

Two other features showing specialization within *Pleuronichthys* are the dentition on the ocular side of the jaw and the development of the supra-temporal branch of the lateral line.

In four species (*decurrens*, *ritteri*, *ocellatus*, and *coenosus*), there is a single row of small, blunt teeth in the lower jaw on the ocular side. This side of the lower jaw of *verticalis* and *cornutus* is without teeth.

Finally, in all species of *Pleuronichthys* there is a supratemporal branch of the lateral line with a well developed posterior prolongation. However, three species (*ritteri*, *ocellatus*, and *coenosus*) also have a short anterior prolongation. In *verticalis* and *decurrens* there rarely is an indication of an anterior prolongation of the supratemporal lateral line branch, while in *cornutus* it was noted on about half of 57 specimens checked.

When all these characters are considered, a pattern of relationship materializes.

Species	Dorsal origin	Interorbital ridge development	Lower jaw teeth ocular side	Anterior accessory lateral line
<i>verticalis</i>	high	strong	absent	absent
<i>cornutus</i>	"	"	"	" (mostly)
<i>decurrens</i>	low	intermed.	present	"
<i>ritteri</i>	high	weak	"	present
<i>ocellatus</i>	"	"	"	"
<i>coenosus</i>	"	"	"	"

Thus, *verticalis* and *cornutus* form a specialization complex at one level, while *ritteri*, *ocellatus*, and *coenosus* group naturally at the other extreme (Fig. 1). Because of the stronger interorbital ridge spine development in *verticalis*, I believe it earns the distinction of being the most highly specialized of the *Pleuronichthys*, while *coenosus* with the lowest and flattest interorbital ridge is the least specialized. *P. decurrens*, because of its intermediate ridge development and lower dorsal fin origin, is placed between the two complexes mentioned above. The lines in Figure 1 are meant to show relationship because of common characters, they should not be construed as depicting evolution of the various species in time.

SPECIES IDENTIFICATION

Only two previous works have covered all species of *Pleuronichthys* (Starks and Thompson, 1910; Norman, 1934); however, neither of these provided sufficient information to make it possible to identify all material at hand.

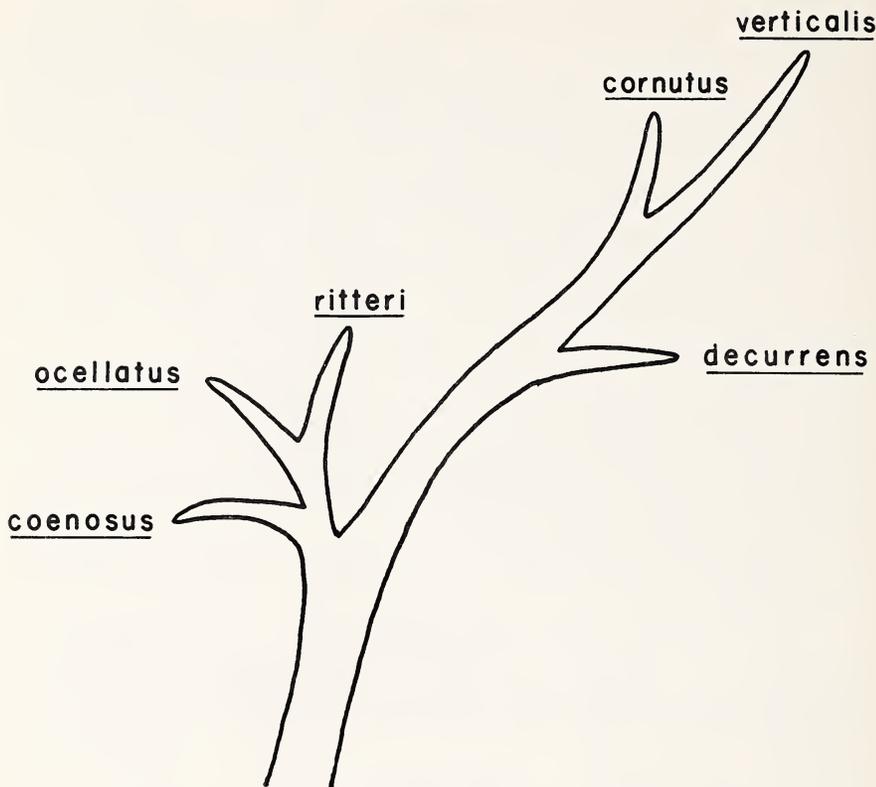


Figure 1. Probable relationships of the species of *Pleuronichthys*.

Starks and Thompson described *P. nephelus* as new, and Norman accepted this species. It is here shown to be conspecific with *P. coenosus*. Former reviewers relied heavily upon lateral line scale counts, yet lateral line scales are the most difficult of all the meristic characters to distinguish because they are deeply covered by integument and masked by innumerable small accessory scales. To obtain an accurate pored scale count, it is almost necessary to remove all other scales above and below the lateral line—a meticulous and time-consuming task that can be accomplished only on fresh material with the aid of a dissecting scope.

Gill raker and fin ray counts have been relied upon in the past as key characters when they actually are not definitive for any given species. I found overlapping counts for five of the six species at six different numbers (27 percent of the total range, Table 1) for dorsal fin rays, and at four different numbers (20 percent of the total range, Table 1) for anal fin rays. Similarly, four of the six species have overlapping gill raker counts for 30 percent of their range (Table 3).

Finally the black spots often used to key out *ritteri* and *ocellatus* are not always present; however, in their absence, other characters as used in the following key are perfectly valid.

Key to Species of *Pleuronichthys*

1. No teeth on ocular side of jaws; interorbital ridge terminating posteriorly in a sharp backward projecting spine **2**
 A single row of minute jaw teeth on ocular side of mandible; interorbital ridge never terminating posteriorly with a sharp, backward projecting spine (occasionally a slightly raised bony tubercle may be present) **3**
2. Ocular side of body and fins plain colored, mottled, or marbled, never covered with small brown spots; several white flecks or spots along dorsal and ventral body margins; anal fin rays 44-51; snout to anal fin insertion 34.9 to 39.3 percent of standard length *verticalis* (p. 15)
 Ocular side of body and fins uniformly covered with small brown spots; never with white streaks or spots along dorsal and ventral body margins; anal fin rays 52 to 62; snout to anal fin insertion 29.8 to 33.8 percent of standard length *cornutus* (p. 18)
3. Origin of dorsal fin opposite (level with) lower corner of mouth on blind side; supratemporal branch of lateral line with a posterior prolongation only (2 of 50 specimens had short anterior branches also); precaudal vertebrae 14 or 15 *decurrens* (p. 20)
 Origin of dorsal fin well above lower corner of mouth on blind side, usually about on level of snout; supratemporal branch of lateral line always with anterior as well as posterior prolongations; precaudal vertebrae 12 or 13 **4**
4. Caudal peduncle narrow, 4.4 to 5.6 into body height; bony orbit of upper eye relatively small, 6.3 to 8.1 percent of standard length, 6.6 to 8.8 times into body height; ocular side of body usually with a solid black blotch (no white border) on the fish's mid-line at $\frac{1}{2}$ its standard length *ritteri* (p. 23)
 Caudal peduncle wider, 3.8 to 4.4 into body height; bony orbit of upper eye larger, 8.1 to 10.9 percent of standard length, 4.7 to 6.4 times into body height; if a black blotch is present on center of ocular side of body (*ocellatus*), it is encircled with white **5**
5. Ocular side of body almost always with a large black blotch bordered with white on fish's mid-line at $\frac{1}{2}$ its standard length; total vertebrae 34 or 35 *ocellatus* (p. 26)
 Ocular side of body plain, without distinguishing black blotches or spots; total vertebrae 37 to 39 *coenosus* (p. 28)

Field Recognition

The six species of *Pleuronichthys* can be determined at a glance if one is thoroughly familiar with all of them. In freshly caught specimens, color and "texture" differences are sufficient to distinguish the various species, but these differences are usually relative.

P. decurrens and *ritteri* have basically dark green shades on their ocular sides, generally distinguishing them from the other four species, which have brown tones predominating. The distinct "pebbly" appearance of *decurrens*, caused by slightly depressed scales, separates it from *ritteri*, and the other species. In addition, the numerous high, bony protuberances along the interorbital ridge and posterior rim of the orbit (much more rugose and numerous than any other species), and the dorsal origin opposite the lower corner of the mouth on the blind side, will rule out all other turbot.

The other basically "green colored" turbot, *ritteri*, lacks the characters mentioned above for *decurrens*. The black blotch on *ritteri*'s mid-body and two others just inside the dorsal and ventral body contours about a head length anterior to the last fin rays, when they are present (perhaps 50 percent of the time), will furnish positive identifying characters. If these black blotches are not present, or even if they are, the diamond-shaped body, narrow caudal peduncle, and thinness of the fish, while relative characters, are excellent for substantiating identity.

The scales of all *Pleuronichthys* are covered by integument, but some more-so than others. One of the "smoothest" turbot is *verticalis*, and its smoothness plus its yellowish-brown body flecked with irregular white spots along the dorsal and ventral contours are sufficient to distinguish it. Other easily observed characters are the overhanging sharp spine on the posterior end of the interorbital ridge (sometimes broken or damaged), and the lack of jaw teeth on the ocular side.

The basic body color of *coenosus* (brownish-green) coupled with its "highlighted" scalation (the body scales on its ocular side are more heavily outlined by pigment than are the scales on other turbot), and the typical (if present) caudal pattern (a dusky C-shaped ring partially surrounding a dark circular blotch), will positively identify this species. Other helpful characters include numerous dusky blotches on an otherwise white blind side in most adults, a generally oval body outline, a relatively broad, flat caudal peduncle, and a relatively smooth, low, bony interorbital ridge.

The gulf turbot, *ocellatus*, typically is uniformly light brown, and almost all specimens have a large circular black spot bordered with white at midbody on the ocular side. These two characters will usually distinguish *ocellatus* at a glance; however, it is also helpful to know that *ocellatus* has a relatively wide caudal peduncle, slight bony protuberances on the interorbital ridge, and black spots on the body contours about where they are found on *ritteri*. *P. ocellatus* and *verticalis* are the only two *Pleuronichthys* in the Gulf of California.

The only other turbot, *cornutus*, is the easiest of all to distinguish if it has its typical pattern of brownish spots evenly covering the entire ocular side of the body and fins. In some, the spots are minute, and in others they appear to be mostly lacking; however, additional support toward positive identification may be obtained from the overhanging sharp spine on the posterior end of the interorbital ridge and the lack of jaw teeth on the ocular side. Finally, this is the only member of the genus inhabiting waters on the Asiatic side of the Pacific.

Hornyhead turbot, *Pleuronichthys verticalis* Jordan and Gilbert, 1881

Differential Diagnosis: May be distinguished from all other species of *Pleuronichthys*, except *cornutus*, by the lack of jaw teeth on the ocular side and by the sharp, backward-projecting spine on the posterior end of the interorbital ridge. It can be distinguished from *cornutus* by its plain-colored body and fins (*cornutus* is uniformly covered with brown spots), by its lower anal fin ray count (44 to 51 compared with 52 to 62 for *cornutus*), by its greater distance between snout and anal fin insertion (34.9 to 39.3 percent of standard length compared with 29.8 to 33.8 percent for *cornutus*), and by its extremely fleshy lips.

Additional Distinguishing Characters: Dorsal rays 66 to 75; anal rays 44 to 51; pectoral rays 10 to 12; total gill rakers 9 to 11; pored lateral line scales 88 to 103; total vertebrae 36 to 38, precaudal vertebrae 13, caudal vertebrae 23 to 25; anterior branch of accessory dorsal lateral line absent on 88 percent of specimens; posterior branch of accessory lateral line reaches base of dorsal ray 29 to 48 on ocular side, lips more fleshy than for any other member of the genus.

Color: When fresh, body on ocular side is yellowish-brown with whitish flecks and spots along dorsal and ventral contours. Various intensities of the general body color give an overall appearance of marbling, particularly among Gulf of California specimens which are especially brightly marbled. Many specimens have a brownish-white rosette-like blotch at midbody on the ocular side. Almost all have small, irregular, white "streaks" along their dorsal and ventral contours.

Distribution: Pt. Reyes, California, south to Magdalena Bay, Baja California, and in the northern Gulf of California.

Spawning: Females were encountered every month of the year with enlarged (ripe) gonads containing transparent eggs. During April, May, and June many males were encountered from which milt would run when pressure was applied over the gonads. Budd (1940) was unable to obtain fertilized eggs of *verticalis* in plankton tows at Monterey until late April but they were found from then until late August. None was taken during late fall and winter, however.

Eggs: According to Budd (1940) the pelagic eggs are spherical with a diameter of 1.07 (1.03-1.11) mm. The thin membrane appears slightly trans-

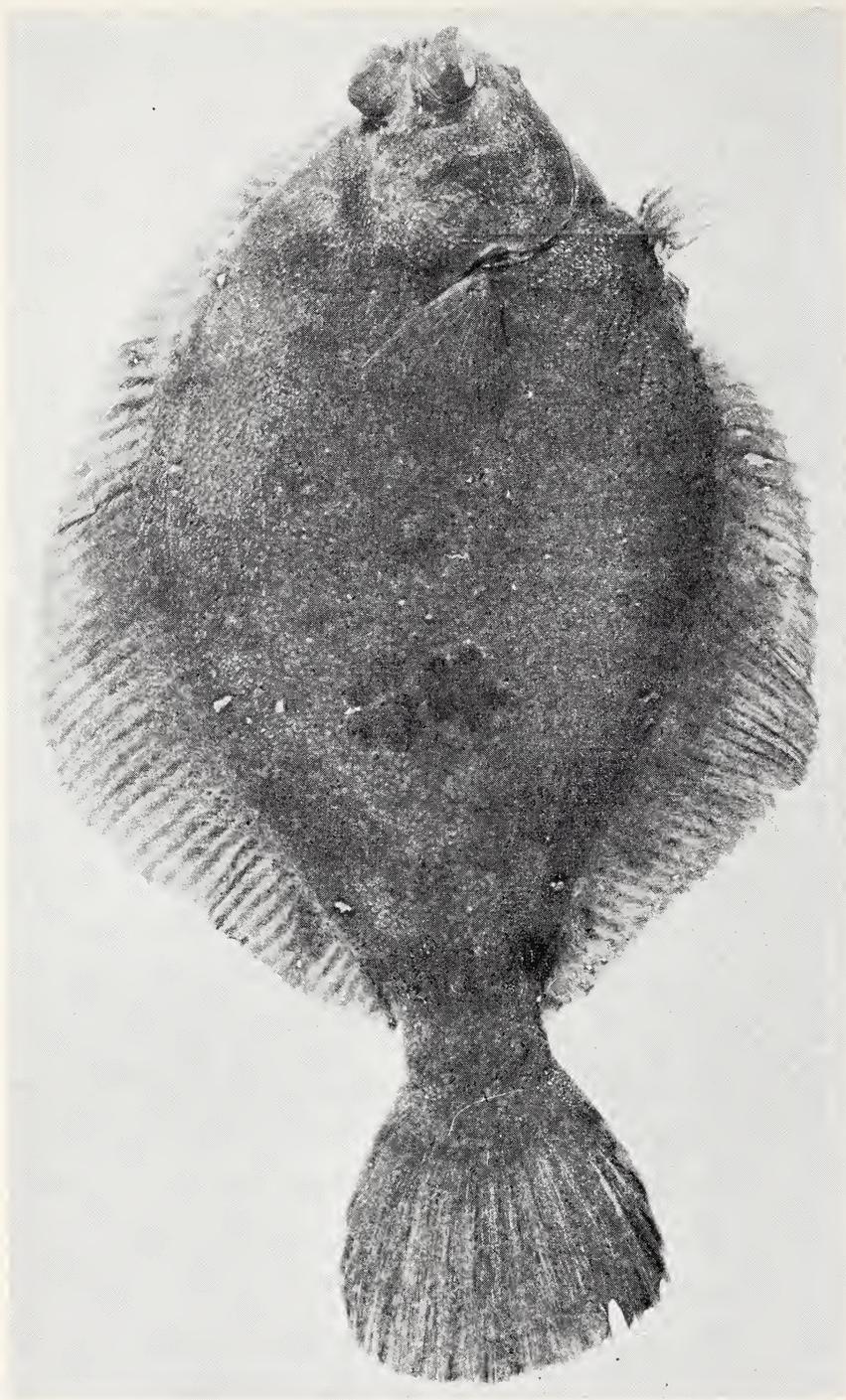


Figure 2. Hornyhead turbot, *Pleuronichthys verticalis*, 203 mm.s.l., 256 mm.t.l., collected at Cape Colnett, Baja California, January 9, 1959. Photograph by Jack W. Schott.

lucent because of a hexagonal pattern extending through the entire thickness of it. The yolk is perfectly clear and transparent. Hatching was estimated to occur about 4 days after fertilization.

Larvae: Newly hatched larvae measure about 3.16 mm. in standard length and are hampered in their movements by a buoyant yolk sac (Budd, 1940). There is no indication of a mouth and the yolk sac extends to the rectum, about the mid-point of the body. The body is well covered with amber chromatophores and sparsely sprinkled with melanophores. By six days the larva measures about 3.35 mm. and has well-formed, functional jaws. Budd did not carry *verticalis* larvae past six days.

Maximum Size: The largest encountered (of 3,774) was 295 mm. standard length (365 mm. total) and weighed 835 grams. It was a ripe female trawled in 6½ fathoms off Oceanside on April 22, 1957. No larger specimen appears to be noted in the literature.

Food: Of 12 stomachs examined, three were empty, two contained clam siphons alone, two contained polychaet worms alone, and five contained a preponderance of clam parts (mostly siphons) and small amounts of polychaet worms.

Depth Distribution: Specimens were trawled at all depths from 5 to 102 fathoms, but most were taken between 25 and 50 fathoms.

Sex Ratios: Of 2,590 individuals sexed, 530 (20 percent) were males. At the height of spawning in the late spring nearly equal number of males and females are captured in trawling operations. At other times the catch is predominantly females; usually the largest individuals are exclusively females.

Material Examined: In all, I examined and identified 3,774 specimens of *verticalis*: 3,139 were from Californian waters; 621 were from the outer coast of Baja California; and 14 were from the upper Gulf of California.

Synonymy:

Pleuronichthys verticalis: Jordan and Gilbert, Proc., U.S. Natl. Mus., 3, 1880: 49-50 (type descr., outside Golden Gate); Jordan and Gilbert, Proc. U.S. Natl. Mus., 4, 1881:68-69 (ecol., size, food, life hist., Monterey, San Francisco); Jordan and Jouy, Proc. U.S. Natl. Mus., 4, 1881:1 (Mont., S. F.); Jordan and Evermann, Bull. U.S. Natl. Mus., 47(3) 1898:2604, 2637-2638 (anat., color, tax., syn., distrib.); Starks and Morris, Univ. of Calif. Publ. Zool., 3, 1907:243-244 (tax., S. Francisco to S. Diego); Gilbert, Proc. U.S. Natl. Mus., 48, 1915:378 (localities); Hubbs, Univ. Calif. Publ. Zool., 16, 1916:168 (size, color, S. Fran.); Starks, Calif. Fish and Game, 4, 1918:171 (tax., anat., color, distrib., fig.); Higgins, Calif. Fish and Game, 5, 1919:157 (records); Fowler, Proc. Acad. Nat. Sci. Phila., 75, 1923:297 (So. Calif. localities); Fowler, Copeia 120, 1923:79 (Long Beach aquarium); Ulrey and Greeley, Bull. So. Calif. Acad. Sci., 28(1) 1928:32 (So. Calif. coast); Ulrey, J. Pan-Pac. Res. Inst., 4(4) 1929:5 (So. Calif.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish., 1930:225 (Calif. coast); Walford, Calif. Div. Fish and Game, Fish Bull. 28, 1931:154 (common name, tax., anat., color, size, distrib., fig.); Croker, Calif. Div. Fish and Game, Fish Bull. 40, 1933:90 (with netted mackerel); Norman, Monograph of flatfishes, 1, 1934:317, 321-322 (tax., syn., anat., color, size, distrib., fig.); Phillips, Calif. Fish and Game, 21, 1935:142-143 (netted Monterey); Barnhart, Marine fishes So. Calif., 1936:28-29 (tax., anat., color, size, distrib., fig.);

Kumada and Hiyama, Marine fishes Pac. Coast Mex., 1937:50 (diagnosis, misprinted "*verticalis*," fig.); McCully, Calif. Fish and Game, 35(1) 1939:13 (field key); Roedel, Calif. Div. Fish and Game, Fish Bull. 68, 1948: 12, 24, 138 (common name, characters, relationship, use, gear, distrib., fig.); Clothier, Calif. Div. Fish and Game, Fish Bull. 79, 1950:44-45 (vert. characters, Newport Beach to Gaviota); Cannon, How to Fish Pac. Coast, 1953:226-227 (names, descript., color, size, range, fishing methods, fig.); Roedel, Calif. Dept. Fish and Game, Fish Bull. 91, 1953:69 (common name, range, descr., use, size, color, fig.); Berdegue, Sect. Mar. Mex., 1956:315 (fig., tax., descr., color, distrib., use); Miller, Calif. Dept. Fish and Game, Field Guide 1, 1959:26-27 (characters, illus. key, distrib.).

Asiatic turbot, *Pleuronichthys cornutus* (Temminck and Schlegel, 1846)

Differential Diagnosis: May be distinguished from all other species of *Pleuronichthys* except *verticalis* by the lack of jaw teeth on the ocular side and by the sharp, backward-projecting spine on the posterior end of the inter-orbital ridge. It can be distinguished from *verticalis* by its uniformly brown-spotted body and fins on the ocular side (*verticalis* has no such brown spots), by its higher anal fin ray count (52 to 62 compared with 44 to 51 for *verticalis*), and by its shorter distance between snout and anal fin insertion (29.8 to 33.8 percent of standard length compared with 34.9 to 39.3 percent for *verticalis*).

Additional Distinguishing Characters: Dorsal rays 70 to 83; anal rays 52 to 62; pectoral rays 10 to 12; total gill rakers 8 to 10; pored lateral line scales 92 to 105 (98 to 110 by Norman, 1934; 93 to 118 by Okada, 1955); total vertebrae 36 to 38, precaudal vertebrae 12 or 13, caudal vertebrae 23 to 25; anterior branch of accessory lateral line present on nearly 50 percent of the specimens; posterior branch of accessory lateral line reaching base of dorsal ray 38 to 53 on ocular side.

Color: When fresh, greyish-brown to reddish-brown on ocular side, covered with brownish spots which may be from pinhead to eye-diameter size. Smaller spots profusely sprinkled over dorsal and anal fins.

Distribution: Coasts of China, Japan, Korea, and Formosa.

Spawning: Fall and winter according to Okada (1955).

Maximum Size: Fowler (1933) gives 305 mm. total length.

Food: Small worms and crustaceans (Okada, 1955).

Depth Distribution: Trawled to depths of 125 fathoms (Jordan and Starks, 1904).

Material Examined: I examined 57 specimens of *cornutus*, 6 from the Stanford University collection and 51 from the University of Michigan collection. These had been taken from off China, Japan, and Korea.

Synonymy:

Platessa cornuta: Temminck and Schlegel, Faun. Jap., Poiss., 1846: 179 (type descr., fig., Nagasaki); Bleeker, Verh. Batav. Gen. 26, 1854:121 (Japan); Boeseman, Zool. Meded., 28, 1947:145-146 (color, localities, characters, tax., Spec. 1336 designated as Temminck and Schlegel's type).

Heteroprosopon cornutus: Bleeker, Compt. Rend. Ac. Sci. Amst., 1862; 8 (Nagasaki).

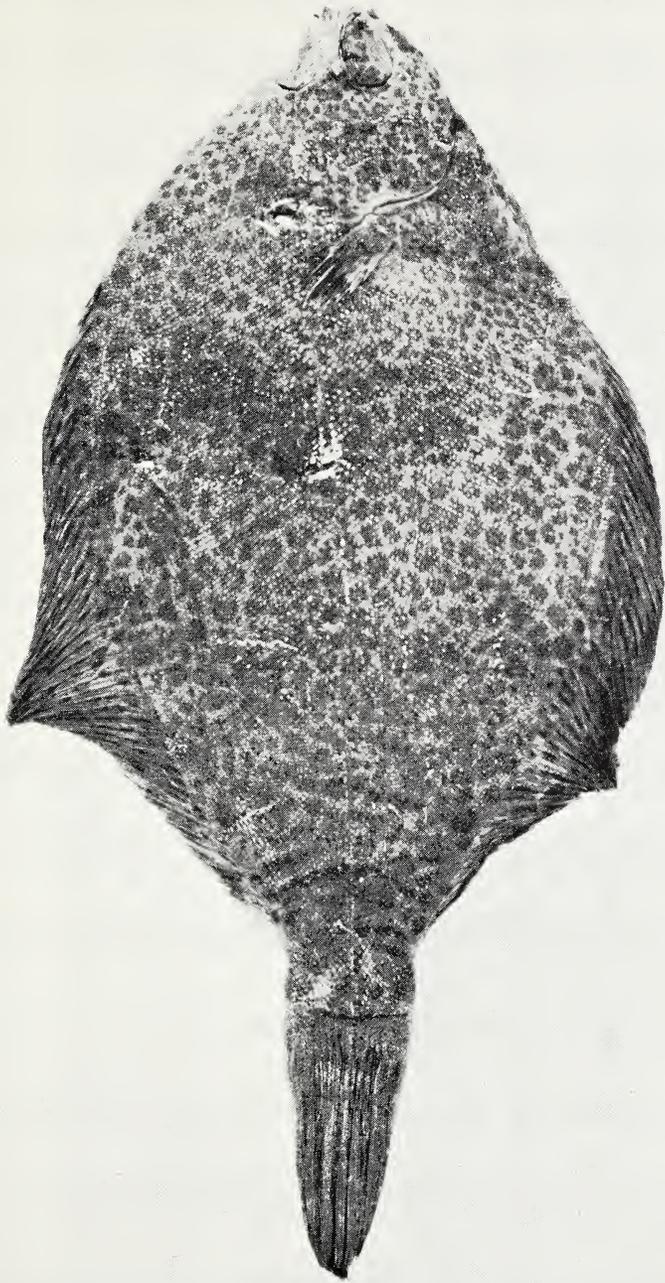


Figure 3. Asiatic turbot, *Pleuronichthys cornuttus*, 108 mm.s.l., 138 mm.t.l., collected at Hong Kong, China, November 10, 1936 (SU 32779). Photograph by Jack W. Schott.

Parophrys cornuta: Günther, Cat. Fish, 4, 1862:455 (listed, copied); Günther, Shore fishes, Challenger, 1880:70 (Kobel); Namiye, Class. Cat., 1881:110 (Tokyo); Ishikawa and Matsuura, Prel. Cat., 1897:24 (Yeshigo); Otaki, J. Bur. Fish., 1897:7, 90 (fig., Japan).

Pleuronichthys cornutus: Steindachner, Reise Aurora, 1896:217 (Kobe); Jordan and Evermann, Bull. U.S. Natl. Mus., 47(3), 1898:2637 (key, Japan); Jordan and Snyder, Proc. U.S. Natl. Mus., 23, 1901:769, (listed, common Japan); Jordan and Starks, Bull. U.S. Fish Comm., 22, 1902 (1904):623 (Suruga Bay 65-125 fms.); Jordan and Starks, Proc. U.S. Natl. Mus., 31 (1484) 1907:200-202 (tax., syn., vernacular names, habitat, characters, color, distrib.); Starks and Thompson, Proc. U.S. Natl. Mus., 38 (1744) 1910:277-287 (tax., rel., characters, key, distrib.); Jordan and Metz, Mem. Carnegie Mus., 6(2) 1913:60 (listed, Fusan); Jordan, Tanaka, and Snyder, J. Coll. Sci., Tokyo, 33(1) 1913:325 (listed, distrib.); Jordan and Thompson, Mem. Carnegie Mus. 6(4), 1914:309 (listed, Misaki); Hubbs, Proc. U.S. Natl. Mus., 48 (2082) 1915:475-476 (syn., characters, variation, measurements, localities); Jordan and Hubbs, Mem. Carnegie Mus., 10, 1925:298 (common name, records, characters); Oshima, Jap. J. Zool., Trans. Abstr., 1(5) 1927:194; Mori, J. Pan-Pac. Res. Inst., 3(3) 1928: 3-8 (Korea); Schmidt, Bull. Acad. Sci. U.S.S.R., 1931:119 (listed); Schmidt, Transl. Pac. Comm. Acad. Sci. U.S.S.R., 2, 1931:126 (size, Nagasaki); Norman, Monograph of flatfishes, 1, 1934:318-321 (tax., syn., key, descr., color, distrib.); Fowler, Hong Kong Nat., 4(2) 1933:169-170 (tax., syn., characters, color, size, distr.); Okada, Fishes of Japan, 1955:384-385 (vernacular names, descr., color, size, habits, distrib., spawning, food, "figure is misprinted sinistral").

Curlfin turbot, *Pleuronichthys decurrens* Jordan and Gilbert, 1881

Differential Diagnosis: May be distinguished from all other species of *Pleuronichthys* by its dorsal fin origin being opposite (level with) lower corner of mouth on blind side (for all other species the dorsal originates on blind side well above lower corner of mouth, usually on a level with snout) and its higher precaudal vertebral count (14 to 15 in *decurrens*, 12 to 13 for all others).

Additional Distinguishing Characters: Dorsal rays 67 to 79; anal rays 45 to 53; pectoral rays 10 to 14; total gill rakers 9 to 12; pored lateral line scales 82 to 96; total vertebrae 38 to 41, precaudal vertebrae 14 to 15, caudal vertebrae 24 to 26; anterior branch of accessory lateral line absent in 96 percent of specimens; posterior branch of accessory lateral line reaches base of dorsal ray 38 to 56 on ocular side; single row of minute teeth in mandible on ocular side; two or three bony protuberances along posterior bony rim of upper eye; skin on ocular side "pebbly" in appearance because of slightly depressed scales; numerous fine brown spots over dorsal and anal rays and membranes on ocular side.

Color: When fresh, deep olive-green on ocular side of body and fins. Dorsal and anal fins uniformly speckled with brownish spots. Specimens frequently seen with blind side either completely brown except for head (ambicolored) or half-brown.

Distribution: Alaska south to San Quintin, Baja California.

Spawning: Transparent eggs have been noted in their ovaries from Novem-

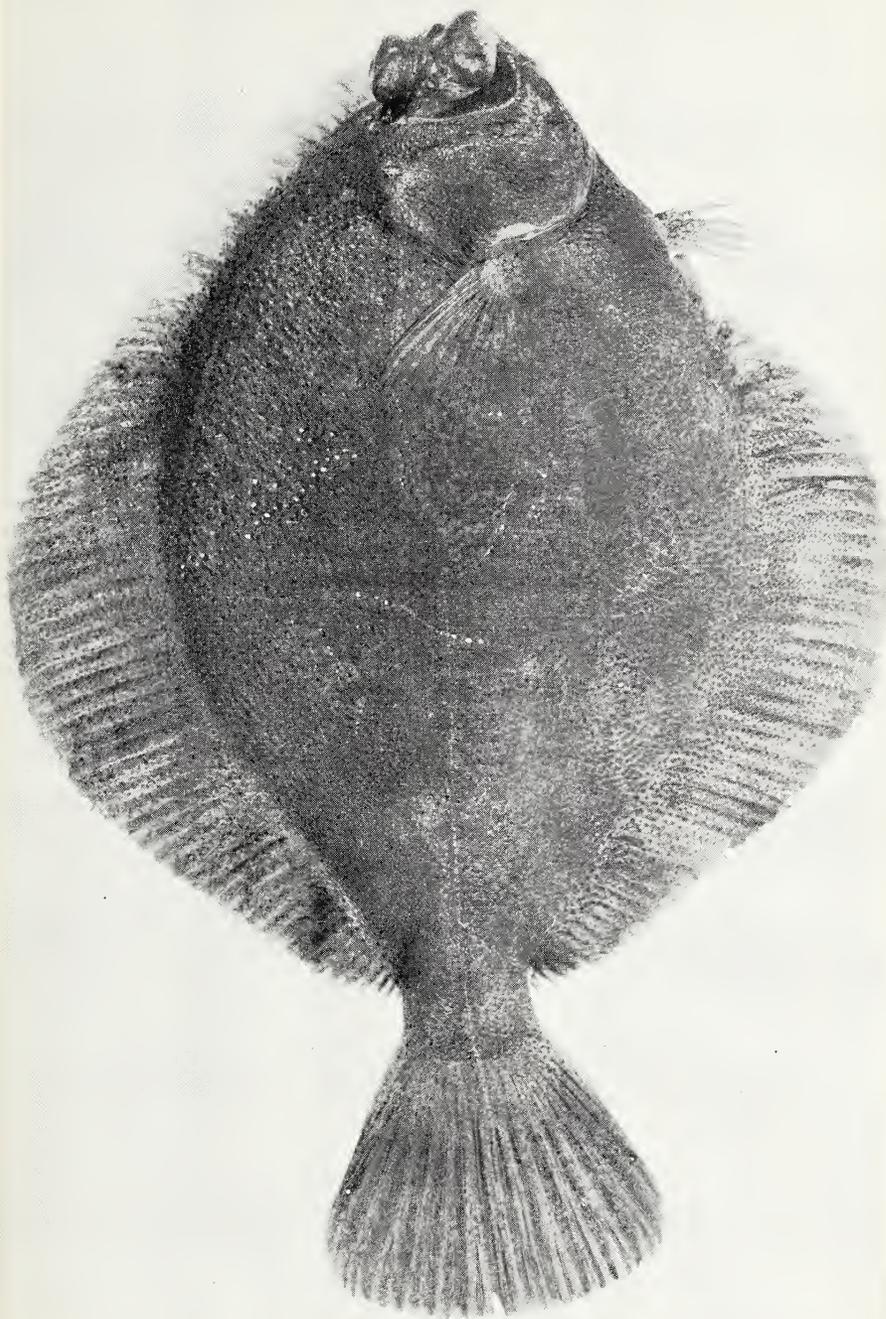


Figure 4. Curlfin turbot, *Pleuronichthys decurrens*, 171 mm.s.l., 222 mm.t.l. collected off Seal Beach, California, November 13, 1956. Photograph by Jack W. Schott.

ber through June; however, according to Budd (1940) their spawning season corresponds closely to that of *verticalis*, roughly late April through August.

Eggs: The pelagic eggs have a specific gravity about equal to that of sea water, are spherical, and average 1.44 (1.31-1.50) mm. in diameter, being considerably larger than *verticalis* eggs. Each egg is enclosed in a thin membrane which appears slightly translucent because of a hexagonal pattern throughout its thickness. The yolk is clear and transparent and contains no oil globule (Budd, 1940). Hatching was estimated to occur in slightly less than 7 days (160 hours) after fertilization.

Larvae: Newly hatched larvae measure about 3.88 mm. in standard length. They may be distinguished from larvae of *verticalis* by a more evenly rounded head and by the fact the dorsal fin fold never displays a sharp supra-cephalic crest. The general body melanophores are more numerous than in *verticalis* but the rectum is less heavily pigmented. Four days after hatching the larva measures 4.35 mm. in standard length and the jaws are functional (Budd, 1940). Budd was unable to carry larvae of *decurrens* past 11 days; they were slightly longer than 4.75 mm. standard length at that time.

Maximum Size: The largest encountered (of 899 measured) was 363 mm. total length, weighing 774 grams. It was a female trawled off Santa Rosa Island on June 13, 1961, in 70 to 80 fathoms. No record could be found in the literature of any that were larger.

Food: Twelve stomachs were examined and two of these were empty. Of the remainder, six contained polychaet worms, three contained nudibranchs or tectibranchs, and one was filled with crustacean (crab?) eggs and brittle star fragments.

Depth Distribution: Seldom trawled in depths shallower than 10 fathoms. Gilbert (1895) states *decurrens* was taken at depths of 21 to 191 fathoms (misquoted by Clemens and Wilby, 1962, as 21 to 291 fms.); none seems to have been taken below 102 fathoms south of Pt. Conception, however.

Sex Ratio: Of 693 individuals sexed, 170 (24 percent) were males. This ratio did not seem to differ greatly during the height of the spawning season. The largest individuals are exclusively females.

Material Examined: In all, 899 specimens of *decurrens* were examined and identified. One of these was from off Coos Bay, Oregon; 882 were from Californian waters; and 16 were from off Baja California as far south as San Quintin.

Synonymy:

Pleuronichthys decurrens: Jordan and Gilbert, Proc. U.S. Natl. Mus., 4, 1881: 68-69 (type descr., ecol., food, size, life hist., Monterey and San Francisco north); Jordan and Jouy, Proc. U.S. Natl. Mus., 4, 1881:2 (Monterey and San Francisco); Gilbert, Rept. U.S. Comm. Fish., 19, 1895:473 (*Albatross* collections 21 to 191 fms.); Jordan and Evermann, Bull. U.S. Natl. Mus., 47(3) 1898:2637-2638 (anat., tax., color, size, syn., Monterey north mostly deep water); Garman, Mem. Mus. Comp. Zool. Harvard, 24, 1899:398 (off Calif. coast); Jordan and Evermann, Bull. U.S. Natl. Mus., 47(4) 1900:3310 (San Francisco, fig. 926); Starks and Morris,

Univ. Calif. Publ. Zool., 3, 1907:244 (tax., S. Barb. Isls. to S. Francisco); Starks and Thompson, Proc. U.S. Natl. Mus., 38(1744) 1910:277-279 (tax., anat., color, size, San Pedro to S. Francisco); Snyder, Proc. U.S. Natl. Mus., 44, 1913:458-459 (size, color, young at 10-15 fms., Mont. Bay); Gilbert, Proc. U.S. Natl. Mus., 48, 1915:378 (S. Nicolas Isl. 31-32 fm.); Starks, Calif. Fish and Game, 4, 1918:164, 170 (tax., anat., not uncommon in deep water); Higgins, Calif. Fish and Game, 6, 1920:87-88 (Huntington Beach); Ulrey and Greeley, Bull. So. Calif. Acad. Sci., 28(1) 1928:32 (S. F. to S. Barb. Isls.); Ulrey, J. Pan-Pac. Res. Inst., 4(4) 1929:5 (So. Calif.); Jordan, Evermann, and Clark, Rept. U.S. Comm. Fish., 1930:225 (Mont. north); Walford, Calif. Div. Fish and Game, Fish Bull. 28, 1931:3, 18, 153 (common name, tax., anat., color, size, range, fig.); Schultz, Hart, and Gunderson, Copeia, 1932(2):67-68 (Zaikof Bay and Wrangell, Alaska); Norman, Monograph of flatfishes, 1, 1934:317-319 (tax., syn., anat., color, size, distrib., fig.); Phillips, Calif. Fish and Game, 21, 1935:142-143, 148 (netted Mont. Bay); Barnhart, Marine fishes of So. Calif., 1936:28-30 (tax., anat., color, size, distrib., fig.); Schultz, Univ. Wash. Publ. Biol., 2(4) 1936:158 (tax., distrib.); Schultz and DeLacy, Mid-Pac. Mag., 49(1) 1936:67 (syn., refs., Alaska to S. Barb. Isls.); Townsend, Rept. Int. Fish. Comm., 11, 1936:8-10 (vert. characters); Budd, Calif. Div. Fish and Game, Fish Bull. 56, 1940:27-32 (spawning, eggs and larvae figured, Monterey); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, 68, 1946:319-320 (name, characters, size, records, range, fig.); Roedel, Calif. Div. Fish and Game, Fish Bull. 68, 1948:12, 24, 139 (common name, characters, use, fishery, distrib., fig.); McCully, Calif. Fish and Game, 35(1) 1949:13 (field key); Clothier, Calif. Div. Fish and Game, Fish Bull. 79, 1950:25-27, 45 (vert. characters, Eureka, Crescent City); Cannon, How to Fish Pac. Coast, 1953:226-227 (names, characters, size, color, range, fishing tackle, fig.); Roedel, Calif. Dept. Fish and Game, Fish Bull. 91, 1953:68 (common name, distrib., characters, fig.); Wilimovsky, Stan. Ich. Bull., 4(5) 1954:283 (listed, southeast Alaska); Best, Calif. Fish and Game, 45(1) 1959:5-18 (fishery); Miller, Calif. Dept. Fish and Game, Field Guide 1, 1959:26-27 (characters, distrib., illust. key); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, (second edit.), 68, 1961:191-192 (common name, tax., characters, size, Brit. Col. records, distrib.).

Paralichthys californicus: Herz, [not *P. californicus* of Ayres] Sci. Guide Element. Schools, 6(3) 1941:37-38 (field characters, size, distrib., fig.).

Pleuronichthys coenosus: Lockington, Proc. U.S. Natl. Mus. 2, 1879: 72, 97-100 (key; in part, excluding specimen "4"; descr., meas., counts, possibly identical with *Pleuronectes quadrituberculatus* Pallas, if so, to be called *Pleuronichthys quadrituberculatus*); Jordan and Gilbert, Proc. U.S. Natl. Mus., 3, 1880:50 (in part, includes *Pleuronichthys coenosus* Lockington, except his spec. 4; probably identical with *Pleuronectes quadrituberculatus* Pallas).

Pleuronectes quadrituberculatus: Lockington, Proc. U.S. Natl. Mus., 2, 1879:99 (*Pleuronichthys coenosus* possibly a synonym); Jordan and Gilbert, Proc. U.S. Natl. Mus., 3, 1880:50 (synonym of *Pleuronichthys quadrituberculatus*).

Pleuronichthys quadrituberculatus: Lockington, Proc. U.S. Natl. Mus., 2, 1879: 99 (*Pleuronichthys coenosus* possibly a synonym); Jordan and Gilbert, Proc. U.S. Natl. Mus., 3, 1880:50 (*Pleuronichthys coenosus* Lockington a synonym, in part; *Pleuronectes quadrituberculatus* Pallas a synonym; characters, measurements, localities of capture).

Spotted turbot, *Pleuronichthys ritteri* Starks and Morris, 1907

Differential Diagnosis: May be distinguished from all other species of *Pleuronichthys* except *ocellatus* and *verticalis* by its low vertebral count (34 to 36 total vertebrae for *ritteri*, 37 to 41 for all others except *ocellatus* and

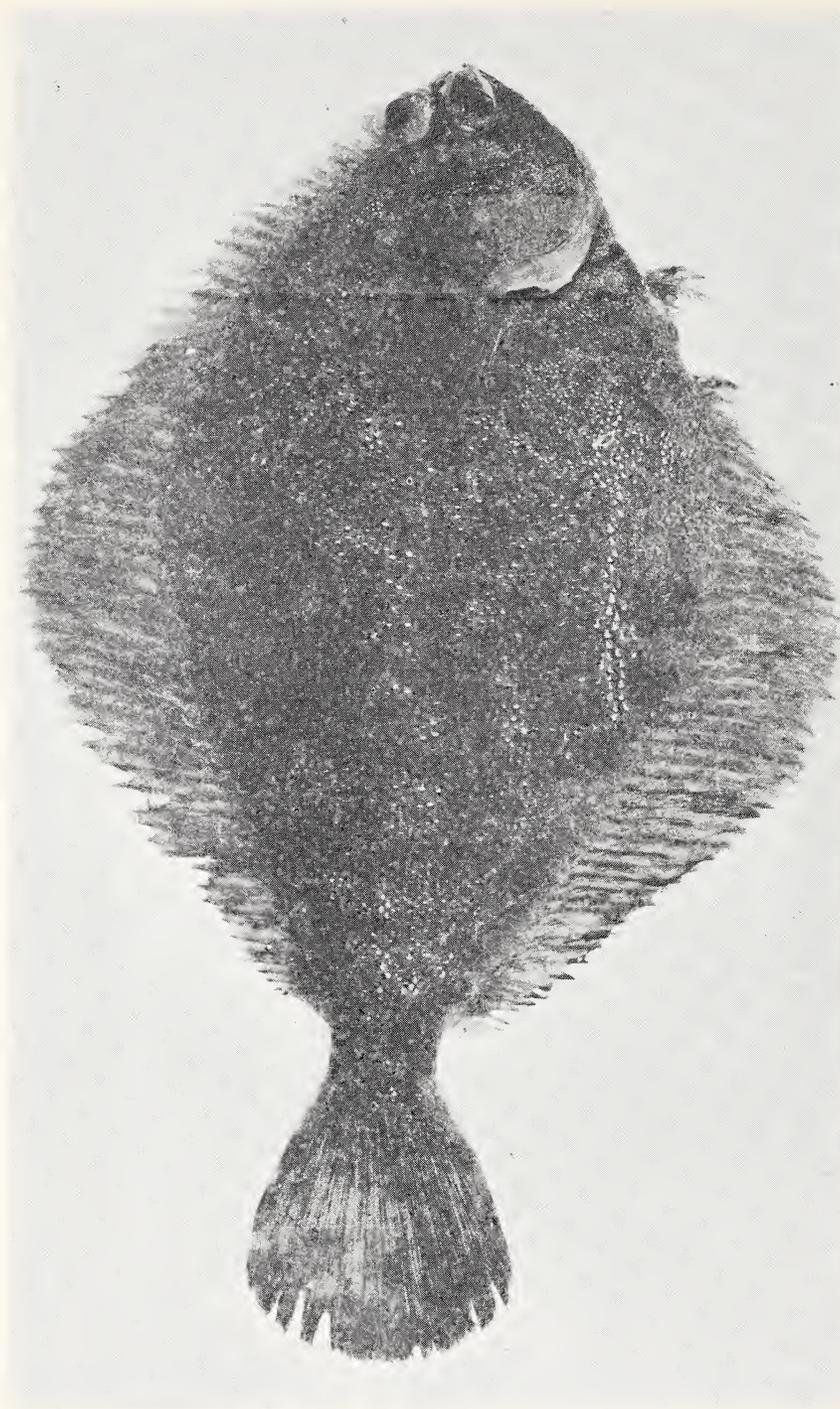


Figure 5. Spotted turbot, *Pleuronichthys ritteri*, 226 mm.s.l., 284 mm.t.l., collected at Belmont Shore, California, November 7, 1956. Photograph by Jack W. Schott.

verticalis). Differs from *verticalis* by having a single row of minute teeth in ocular side of lower jaw (*verticalis* has none), and from *ocellatus* by having a smaller bony upper orbit (6.3 to 8.1 percent of standard length compared with 8.5 to 10.9 percent for *ocellatus*), by having a shorter interorbital ridge measured from the first to third protuberance (5.8 to 7.7 percent of standard length compared with 8.5 to 10.6 percent for *ocellatus*), and by the usually present solid black blotch centrally located on the ocular side (in *ocellatus* this centrally-located blotch is bordered with white).

Additional Distinguishing Characters: Dorsal rays 62 to 70; anal rays 43 to 49; pectoral rays 9 to 11; total gill rakers 12 to 17; pored lateral line scales 83 to 98; total vertebrae 34 to 36, precaudal vertebrae 12 to 13, caudal vertebrae 22 to 24; anterior branch of accessory dorsal lateral line present on all specimens; posterior branch of accessory dorsal lateral line reaches base of dorsal ray 29 to 39.

Color: When fresh, dull greyish-green on ocular side of body. A dark blotch frequently present at approximate mid-body, exclusive of caudal, sometimes a smaller blotch a head length behind this. Other dark blotches sometimes along dorsal and ventral body contours, near bases of both dorsal and anal fin rays, one head length in advance of posteriormost rays.

Distribution: Santa Barbara, California, south to Magdalena Bay, Baja California.

Spawning: Ripe females in spawning condition were noted in trawl catches from November through April. Observations are too scanty for drawing conclusions during other months.

Maximum Size: The largest of 1,416 specimens measured and weighed was 295 mm. total length. This individual, a ripe female taken in March 1957, near Long Beach, California, weighed slightly less than a 328-gram *ritteri* that was 10 mm. shorter.

Food: Five of 28 stomachs examined were empty and two others contained amorphous material. Of those with food, 12 contained only polychaete worms, 2 contained only clam parts, and 7 had primarily polychaetes (more than 50 percent by volume) plus other animal matter in them (6 of the 7 had clam siphon tips, and 2 of the 7 contained amphipods).

Depth Distribution: Adult *ritteri* have been caught in water as shallow as 1½ fathoms and as deep as 25. Most, however, are captured in 10 fathoms or less.

Sex Ratios: Twenty-five percent (358) of 1,410 specimens sexed were males.

Material Examined: In all, I examined and identified 1,416 specimens of *ritteri*: 939 from Californian waters, and 477 from off Baja California as far south as Magdalena Bay.

Synonymy:

Pleuronichthys ritteri: Starks and Morris, Univ. Calif. Publ. Zool., 3, 1907:243-244 (type descr., type loc. San Diego, cotypes S. D. and S. Pedro, fig.); Starks and

Thompson, Proc. U.S. Natl. Mus., 38 (1744) 1910:277-287 (tax., anat., color, size, S. Pedro south); Metz, Ann. Rept. Laguna Mar. Lab., 1, 1912:60 (common near Newport); Gilbert, Proc. U.S. Natl. Mus., 48, 1915:378 (off San Diego 25 fms.); Hubbs, Univ. Calif. Publ. Zool., 16, 1916:169 (size, color, San Pedro, La Jolla); Starks, Calif. Fish and Game, 4, 1918:165, 172-173 (tax., anat., color, size, distrib., fig.); Fowler, Proc. Acad. Nat. Sci. Phila., 75, 1923:297 (La Jolla); Ulrey and Greeley, Bull. So. Calif. Acad. Sci., 28(1) 1928:32 (records); Ulrey, J. Pan-Pac. Res. Inst., 4(4) 1929:5 (So. Calif.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish., 1930:225 (San Diego Bay); Walford, Calif. Div. Fish and Game, Fish Bull. 28, 1931:18 (common name, distrib.); Norman, Monograph of flatfishes 1, 1934:318, 324-325 (tax., syn., rel., anat., color, size, distrib., fig.); Barnhart, Marine fishes southern Calif., 1936:28, 30 (tax., anat., color, size, localities, fig.); Roedel, Calif. Div. Fish and Game, Fish Bull. 68, 1948:12, 24 (common name, characters); McCully, Calif. Fish and Game, 35(1):1949:13 (field key); Clothier, Calif. Div. Fish and Game, Fish Bull. 79, 1950:25-27, 45 (vert. characters, San Diego); Cannon, How to Fish Pac. Coast, 1953:228-229 (names, characters, size, color, range, fishing tackle, fig.); Roedel, Calif. Dept. Fish and Game, Fish Bull. 91, 1953:69 (common name, range, characters); Berdegue, Sect. Mar. Mexico, 1956: 315 (listed, Baja California); Miller, Calif. Dept. Fish and Game, Field Guide 1, 1959:26-27 (characters, distrib., illus. key).

Gulf turbot, *Pleuronichthys ocellatus* Starks and Thompson, 1910

Differential Diagnosis: May be distinguished from all species of *Pleuronichthys* except *ritteri* by its low vertebral (total) count (*ocellatus* has 34 or 35 total vertebrae whereas all others except *ritteri* have 36 to 41 vertebrae). May be distinguished from *ritteri* by its larger bony upper orbit (8.5 to 10.9 percent of standard length in *ocellatus*, 6.3 to 8.1 in *ritteri*), by its longer interorbital ridge measured from the first to third protuberance (8.5 to 10.6 percent of standard length in *ocellatus*, 5.8 to 7.7 percent in *ritteri*, and by the usually present, white-bordered black blotch, centrally located on the ocular side (*ritteri* may have a centrally-located black blotch but it is never bordered with white).

Additional Distinguishing Characters: Dorsal rays 62 to 74; anal rays 44 to 53; pectoral rays 10 to 12; total gill rakers 10 to 14; pored lateral line scales 84 to 90; total vertebrae 34 to 35, precaudal vertebrae 12 to 13, caudal vertebrae 22 to 23; anterior branch of accessory dorsal lateral line present on all specimens; posterior branch of accessory dorsal lateral line reaches base of dorsal ray 33 to 44.

Color: When fresh, uniform light brown or yellowish-brown on ocular side. A dark blotch ringed with white is usually present at approximate mid-body, excluding caudal fin, on eyed side. A dark blotch on the body near both the dorsal and anal fin ray bases about a head length in advance of their posteriormost rays.

Distribution: Upper half of Gulf of California, from about Concepcion Bay and Guaymas, northward.

Spawning: Females were ripe and apparently capable of spawning from November through March. Observations were too scanty to be useful during other months.

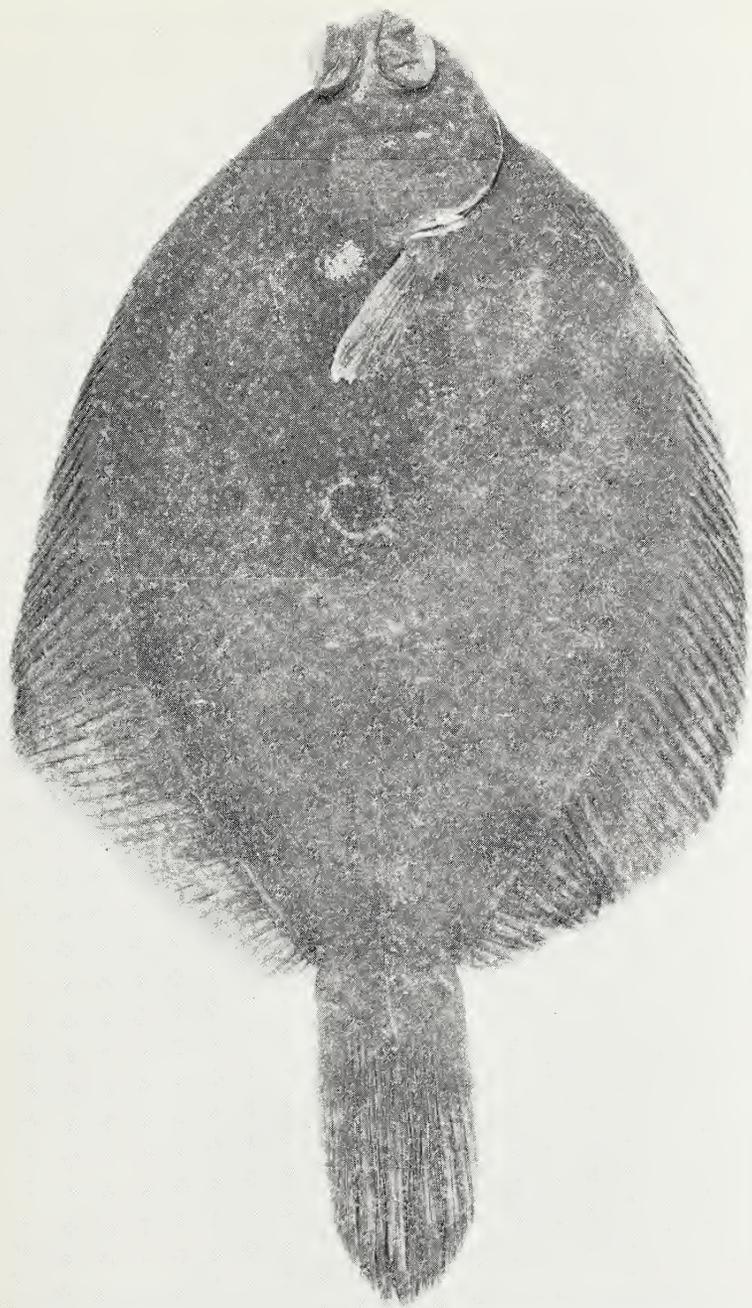


Figure 6. Gulf turbot, *Pleuronichthys ocellatus*, 113 mm.s.l., 142 mm.t.l., collected off San Luis Gonzaga, Baja California, February, 1960. Photograph by Jack W. Schott.

Maximum Size: The largest *ocellatus* encountered was a male 184 mm. standard length (239 mm. total) weighing 170 grams. It was caught in a gill net in 5 fathoms off San Francisquito, Gulf of California.

Food: One of 10 stomachs examined was empty. Six of the remaining 9 contained polychaet worms, amphipods, and clam siphon tips and the other 3 contained clam siphon tips exclusively.

Depth Distribution: Captured in water 3 feet deep near shore and trawled in 73 fathoms, well offshore.

Sex Ratios: Half of 16 specimens checked for sex were males.

Material Examined: I examined and identified 191 specimens of *ocellatus*, all from the Gulf of California, Concepcion Bay north to San Felipe and Guaymas north to Pt. Peñasco. Included in the material examined were the holotype (USNM 74605) and eight paratypes (SU 198 and 5369).

Synonymy:

Pleuronichthys ocellatus: Starks and Thompson, Proc. U.S. Natl. Mus., 38 (1744) 1910:277-287 (type descr., tax., syn., characters, color, Gulf of Calif. deep water, fig.); Norman, Monograph of flatfishes, 1, 1934:318, 325:326 (tax., syn., key, descr., characters, color, fig.); Breder, Bull. Bing. Oceanogr. Coll., 2(3) 1936:4 (misprint "Gonzago" Bay, Conception Bay); Fowler, Monogr., Acad. Nat. Sci. Phila., 6, 1944:495 (listed, Gulf of California); Berdegue, Sect. Mar. Mex., 1956:315 (listed).

C-O turbot, *Pleuronichthys coenosus* Girard, 1856

Differential Diagnosis: May be distinguished from *verticalis* and *cornutus* by having teeth in its lower jaw on the ocular side (*verticalis* and *cornutus* have none) and by its lack of a sharp projecting spine on the posterior end of the interorbital ridge. It can be distinguished from *decurrens* by having an anterior branch to the dorsal accessory lateral line and by its more dorsally inserted dorsal fin (level with snout in *coenosus*, opposite lower corner of mouth in *decurrens*). Distinguished from *ritteri* and *ocellatus* by its greater number of total vertebrae (37 to 39 in *coenosus*, compared with 34 to 36 in *ritteri* and *ocellatus*).

P. nephelus (Starks and Thompson, 1910) was placed in synonymy of *P. coenosus* by Hubbs (1928) who said he could, "find no grounds for the separation of the nominal Puget Sound species *P. nephelus*." I was unable to distinguish the type material of *nephelus* from *coenosus* either by fin ray counts or by scale counts, characters used by Starks and Thompson to differentiate *nephelus*. Furthermore, all other characters I investigated on *nephelus* fitted comfortably within the ranges of variation determined for *coenosus* (Tables 2-4).

Additional Distinguishing Characters: Dorsal rays 66 to 77; anal rays 46 to 55; pectoral rays 9 to 12; total gill rakers 11 to 15; pored lateral line scales 77 to 92; total vertebrae 37 to 39, precaudal vertebrae 12 to 13, caudal vertebrae 24 to 26; anterior branch of accessory dorsal lateral line always present; posterior branch of accessory dorsal lateral line reaches base of rays 29 to 44 on ocular side; adults nearly all with dusky blotches on blind side of body.

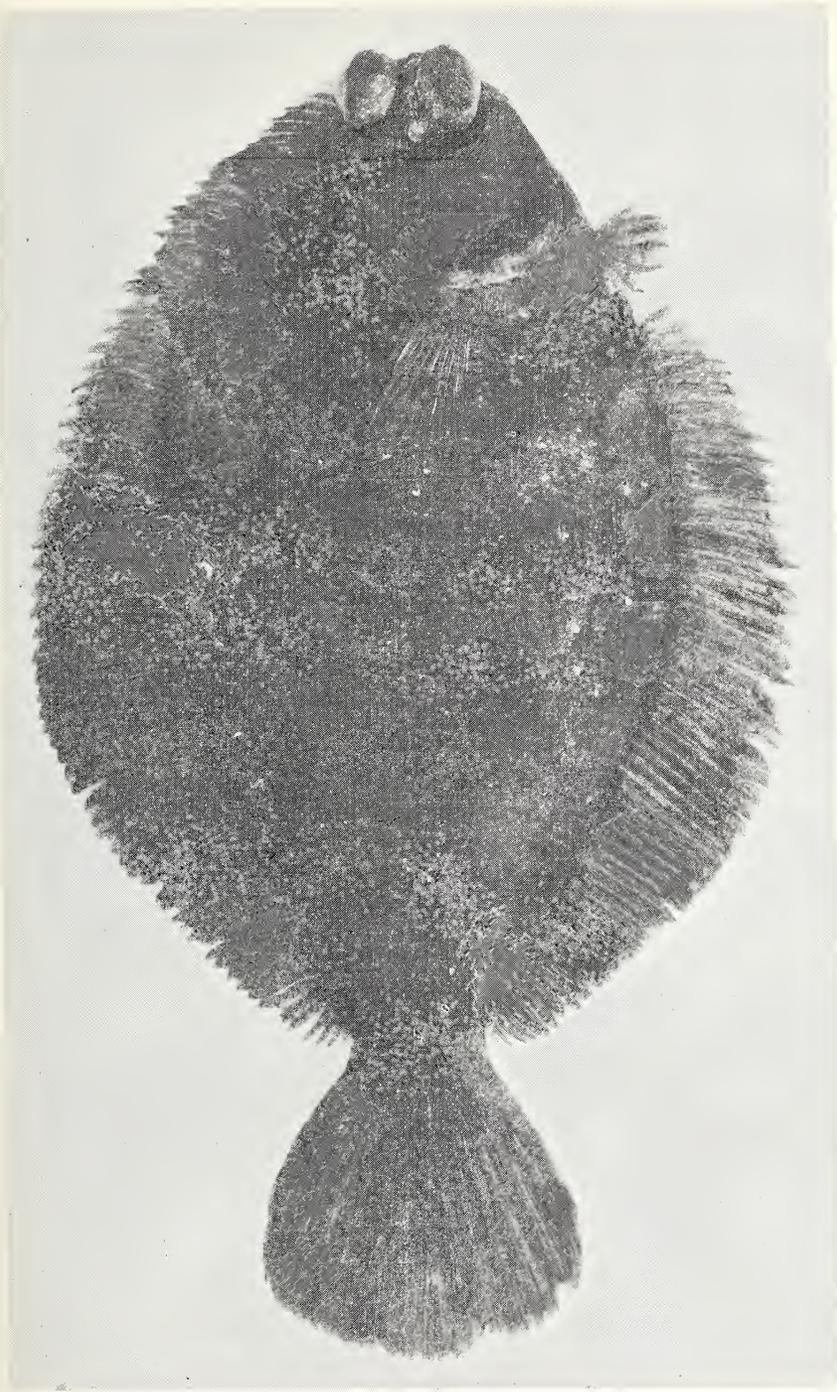


Figure 7. C-O turbot, *Pleuronichthys coenosus*, 210 mm.s.l., 270 mm.t.l., collected off Seal Beach, California, November 13, 1956. Photograph by Jack W. Schott.

Color: When fresh, body and fins brownish-green, occasionally a brownish or yellowish-brown blotch at center of body on ocular side. Various intensities of basic colors give marbled appearance to body and fins. Caudal often marked with central dusky blotch partially encircled anteriorly with a dusky C-shaped bar, especially easy to see on live (aquarium) fish. Blind side often with dusky blotches in adults.

Distribution: Alaska south to Cape Colnett, Baja California

Spawning: Females with transparent eggs in their ovaries have been taken during every month of the year; however, most spawning appears to take place from about May through September. Budd (1940) found their fertilized eggs in plankton tows made off Monterey during November and April.

Eggs: Their eggs closely resemble those of *verticalis* and *decurrens* in all respects except size, being 1.88 mm. in average diameter (Budd, 1940). Hatching was estimated to occur 12 days (280 hours) after fertilization.

Larvae: The greatly increased length of the incubation period has a marked effect on the larva which is large, well-developed, extremely active, and able to swim about at will immediately after hatching (Budd, 1940). It is comparable in its degree of organization to the week-old larva of *verticalis*. A newly hatched *coenosus* larva was 5.54 mm. in standard length, had a well-formed head, and large, functional jaws. The entire body is heavily pigmented as is the rectum. Budd was unable to carry *coenosus* larvae beyond eight days, during which time they changed very little.

Maximum Size: The largest *coenosus* encountered among 585 measured was 333 mm. total length. It was trawled in 10 fathoms in Santa Monica Bay on May 10, 1961. A slightly smaller individual, at 431 grams, was the heaviest noted.

Food: Two of 10 stomachs examined were empty, 5 contained polychaet worms (1 exclusively), 5 contained clam parts, particularly siphons (1 exclusively), 1 contained the remains of a two-inch rockfish, *Sebastes* sp., 1 an amphipod, and 1 had several nudibranchs and tectibranchs in it.

Depth Distribution: Seldom encountered in water shallower than 5 fathoms and seldom deeper than 30. I was able to find a single record of *coenosus* from 35 fathoms, but none deeper.

Sex Ratios: Forty percent (188) of 470 specimens sexed were males. Individuals were examined during every month of the year but there were no noticeable differences in this ratio. Females tended to be somewhat larger than males.

Material Examined: In all, 585 specimens of *coenosus* were examined and identified. Six of these, the holotype (USNM 74606) and 7 paratypes (SU 21414) of *nepheus* (= *coenosus*), were from San Juan Island, Puget Sound; 486 were from California waters; and 90 were from off Baja California, as far south as Cape Colnett.

Synonymy:

Pleuronichthys coenosus: Girard, Proc. Acad. Nat. Sci. Phila., 7, 1854:139

(type descr., San Francisco); Jordan and Gilbert, Proc. U.S. Natl. Mus., 3, 1880:50 (key characters, Santa "Catilina" Isl., San Luis Obispo); Smith, List fishes San Diego, Calif., 1880:no page ("*caenosus*" common San Diego); Jordan and Gilbert, Proc. U.S. Natl. Mus., 4:1881:68 (ecol., food, life-hist., size, San Diego-north); Jordan and Jouy, Proc. U.S. Natl. Mus., 4 1881:2 (Santa Catalina Isl., Wilmington, San Diego, Monterey, San Francisco); Eigenmann, Proc. U.S. Natl. Mus., 15, 1892:128-131, 174-176 (life-hist., egg, syn., abundant San Diego Bay); Jordan and Evermann, Bull. U.S. Natl. Mus., 47(3) 1898:2637-2639 (tax., anat., color, syn., San Diego north); Starks and Morris, Univ. Calif. Publ. Zool., 3, 1907:243 (Calif. distrib.); Starks and Thompson, Proc. U.S. Natl. Mus., 38 (1744) 1910:277-287 (tax., anat., color, size, key characters, San Francisco to San Pedro); Hubbs, Univ. Calif. Publ. Zool., 16, 1916:169 (La Jolla); Starks, Calif. Fish and Game, 4, 1918:171-173 (tax., anat., color, fig., size, common entire Calif. coast); Fowler, Proc. Acad. Nat. Sci. Phila., 75, 1923:288 (Pt. Firmin); Hubbs Jour. Pan-Pac. Res. Inst., 3(3) 1928:16 (listed, Oregon, Wash., *P. nephelus* a synonym); Ulrey and Greeley, Bull. So. Calif. Acad. Sci., 28(1) 1928:31 (San Diego north); Ulrey, J. Pan-Pac. Res. Inst. 4(4) 1929:5 (So. Calif.); Jordan, Evermann, and Clark, Rep. U.S. Comm. Fish., 1930:225 (San Diego north); Walford, Calif. Div. Fish and Game, Fish Bull. 28, 1931:18 (tax., Calif. distrib.); Norman, Monogr. of flatfishes, 1, 1934:317-326 (tax., key, synon., anat., color, size, fig., Calif. coast); Barnhart, Marine fishes southern Calif., 1936:28-30 (tax., anat., color, size, fig., So. Calif. north); Schultz, Univ. Wash., Publ. Biol. 2(4) 1936:158 (tax., common San Diego north); Schultz and DeLacy, Mid-Pac. Mag., 49(1) 1936:67-68 (syn., refs., Wash. records, Alaska to San Diego); Schultz and DeLacy, Mid-Pac. Mag., 49(3) 1936:212 (refs., *P. nephelus* a synonym); Townsend, Rept. Int. Fish. Comm., 11, 1936:9-10 (vert. characters); Budd, Calif. Div. Fish and Game, Fish Bull. 56, 1940:33-37 (spawning, eggs and larvae figured, Monterey); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, 68, 1946:320-321 (characters, size, Brit. Col. records, fishery, range, fig.); Roedel, Calif. Div. Fish and Game, Fish Bull. 68, 1948:12, 24 (common name, distrib., characters); McCully Calif. Fish and Game, 35(1) 1949:13 (field key); Clothier, Calif. Div. Fish and Game, Fish Bull. 79, 1950:25, 26, 27, 45 (vert. key and characters, Santa Barbara, Gaviota); Cannon, How to Fish Pac. Coast, 1953:226-228 (names, characters, size, color, range, fishing tackle, fig.); Roedel, Calif. Dept. Fish and Game, Fish Bull. 91, 1953:69 (common name, distrib., characters); Wilimovsky, Stan. Ich. Bull., 4(5) 1954:283 (listed, southeast Alaska); Miller, Calif. Dept. Fish and Game, Field Guide 1, 1959:26-27 (characters, distrib., illus. key); Clemens and Wilby, Bull. Fish. Res. Bd. Canada, rev. edit., 68:1961:192-193 (common name, tax., characters, size, Brit. Col. records, distrib.).

Pleuronichthys nephelus: Starks and Thompson, Proc. U.S. Natl. Mus., 38 (1744) 1910:277-287 (type descr., key, fig., Puget Sound); Kincaid, Wash. Dept. Fish., 1919:51 (characters, color, size, Puget Sound); Hubbs, J. Pan-Pac. Res. Inst., 3(3) 1928:16 (synonym of *P. coenosus*); Norman, Monogr. of flatfishes, 1, 1934:317-326 (tax., key, anat., color, size, fig., Puget Sound); Schultz and DeLacy, Mid-Pac. Mag., 49(3) 1936:212 (synonym of *P. coenosus*).

Parophrys coenosa: Günther, Cat. fishes Brit. Mus., 4, 1862:456 (synon., copied descr.).

Pleuronectes quadrituberculatus: Jordan and Gilbert, Proc. U.S. Natl. Mus., 3, 1880:50 (synonym of *Pleuronichthys quadrituberculatus*).

ACKNOWLEDGMENTS

It would be difficult to find enough space to mention all the people who should be thanked for having assisted me since I started working on this

group of fishes in 1955. A number of individuals were especially helpful and I should like to express my appreciation to these persons by name.

Elbert H. Ahlstrom, U.S. Bureau of Commercial Fisheries, La Jolla, furnished information regarding use of the caudal complex for identifying pleuronectids; W. I. Follett, California Academy of Sciences, San Francisco, assisted with synonymies for the Californian species; Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, loaned me specimens of *ocellatus*; Robert R. Miller, University of Michigan loaned me specimens of *cornutus*; George S. Myers, Stanford University (SU), loaned me paratypes of *ocellatus* and *nephelus*, and specimens of the Asiatic *cornutus*; Leonard P. Schultz, U.S. National Museum (USNM), loaned me X-rays of the holotypes of *ocellatus* and *cornutus*; and Boyd W. Walker, University of California, Los Angeles, loaned me specimens of *ocellatus* and offered much-needed advice and criticism during various stages of my research; John Bollinger and Keith Radford, Scripps Institution of Oceanography, X-rayed numerous specimens of *cornutus*, *ocellatus*, and "*nephelus*" for me.

In addition, numerous associates at California State Fisheries Laboratory were always willing to lend a hand: John L. Baxter, Leo Pinkas, and Parke H. Young assisted greatly in collecting and processing material; Jack W. Schott took all of the photographs of *Pleuronichthys*; Mrs. P. Patricia Powell checked a number of my references for accuracy; and Mrs. Loretta Morris typed the manuscript and put it into presentable form.

To all of these, as well as any others I have inadvertently omitted, I offer my heartfelt thanks.

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NUMBER 77

DECEMBER 30, 1963

A NEW POECILIID FISH, *PHALLICHTHYS TICO*,

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C2L868

FROM COSTA RICA

By WILLIAM A. BUSSING



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Editor

A NEW POECILIID FISH, *PHALLICHTHYS TICO*,
FROM COSTA RICA

By WILLIAM A. BUSSING¹

ABSTRACT: A new poeciliid fish, *Phallichthys tico*, is described from near Tilarán, Provincia de Guanacaste, Costa Rica. Its ecology, and relationships to other species of the genus are discussed. Certain characters of the new species necessitate expansion of the genus.

During the course of fieldwork on the ichthyofauna of Costa Rica in the summer of 1961, an undescribed fish of the family Poeciliidae was collected in a swamp near Tilarán, Provincia de Guanacaste. Subsequently, in 1962, a large series of the new form was collected while I was carrying out an intensive ecologic analysis of the fishes of the Río Puerto Viejo, Provincia de Heredia, Costa Rica. The characteristics of the new species indicate a close relationship to *Phallichthys amates* and *Phallichthys fairweatheri*, also of Middle America. It differs significantly from the previously known members of the genus, particularly in the gonopodial suspensorium and its inclusion in *Phallichthys* requires expansion of the generic limits to a considerable degree.

Phallichthys tico, new species

Figures 1-3.

Holotype: LACM 2780; a male 17.4 mm. standard length collected by W. A. Bussing in the Río Puerto Viejo 5.5 kilometers downstream from junction with the Río Sarapiquí and 6.5 kilometers SE of the Pueblo of Puerto Viejo, Sarapiquí drainage, Provincia de Heredia, Costa Rica, on June 14, 1962.

Paratypes: LACM 2781; 20 males 12.4 to 17.6 mm. standard length and 92 juveniles and females 9.0 to 22.1 mm. standard length, same data as the holotype. UMMZ 180304; 3 males 13.7 to 14.6 mm. standard length and 3 females 17.5 to 19.2 mm. standard length, same data as the holotype. LACM 2782; 12 males 12.1 to 17.7 mm. standard length and 18 juveniles and females 7.8 to 32.9 mm. standard length collected by W. A. Bussing and Salvador Jiménez C. in a swamp 200 feet from the Río San Luís, 9 kilometers NNE of Tilarán, Arenal drainage, Provincia de Guanacaste, Costa Rica, on August 21, 1961.

The type specimens are deposited in the Los Angeles County Museum (LACM), the University of Michigan Museum of Zoology (UMMZ), the University of Miami Ichthyological Museum and the American Museum of Natural History.

Diagnosis: This diminutive *Phallichthys* is immediately distinguished from the other two known species of the genus by the presence of a prominent black blotch on the posterior quarter of the dorsal fin in both sexes. Other outstanding

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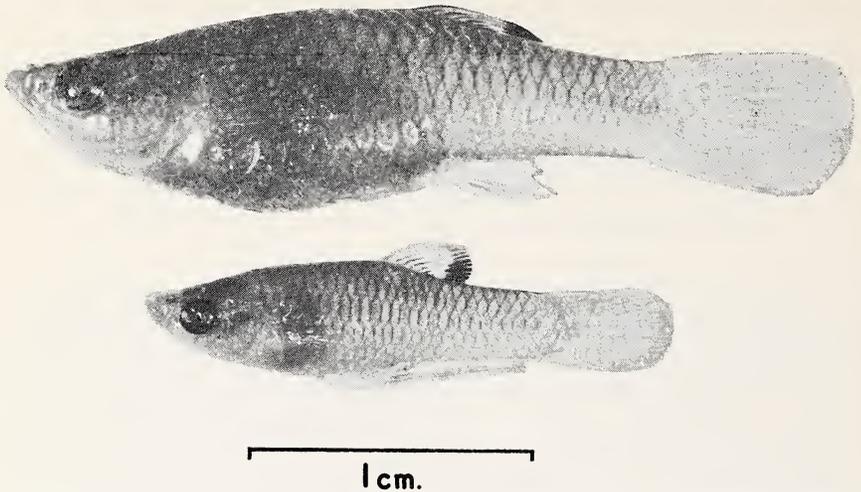


Figure 1. Adult pair of *Phallichthys tico*, n. sp., female above, male below. Photograph by the author.

differences follow for which counts and measurements (expressed in percent of SL) are given, first for *P. tico*, followed by those for *P. fairweatheri* and *P. amates*, respectively, in parentheses. Standard length, largest male collected 17.7 mm. (30 mm., 40 mm.); largest female 32.9 (44 mm., 56 mm.). Depth of adult males 25-30 (39-41, 33-41); adult females 28-34 (37-40, 37-40). Depressed length of dorsal fin of males 24-28 (33-38, 30-47); females 20-25 (29-33, 27-37). Total gill rakers on first arch 10-12 (20-25, 20-22). Ray 4p of gonopodium with symmetrical serrae on both right and left halves (serrae on both halves but unsymmetrical, serrae on right half only). Large distal uncini on gonapophysis I (small proximal uncini present, usually no uncini present but occasionally distal uncini). Membranous knob on end of gonopodium (no such knob, no such knob).

General Description: General appearance robust but not deep-bodied. Predorsal profile of female very slightly convex; male profile more strongly convex. Greatest depth of female slightly more than male but deep part of body extended farther anteriorly giving a considerably deeper aspect to the female. Body contours of both sexes gently rounded. Mouth opening dorsally.

Dorsal originates at highest point on body in both sexes. Dorsal origin slightly in advance of anal origin in females, in males origin of dorsal fin slightly behind origin of gonopodium. Dorsal fin rounded in both sexes. In females anal fin truncate or very slightly rounded. Short pelvic fins of females not quite reaching origin of anal fin. Second and third pelvic fin rays of males elongated and extending beyond origin of anal fin. Gill rakers 10-12 on first gill arch, upper 8-9 widely spaced and of moderate length, lower 2-4 greatly reduced. Dorsal rays usually 8, seldom 7 or 9; anal rays 10, seldom 9; pectoral

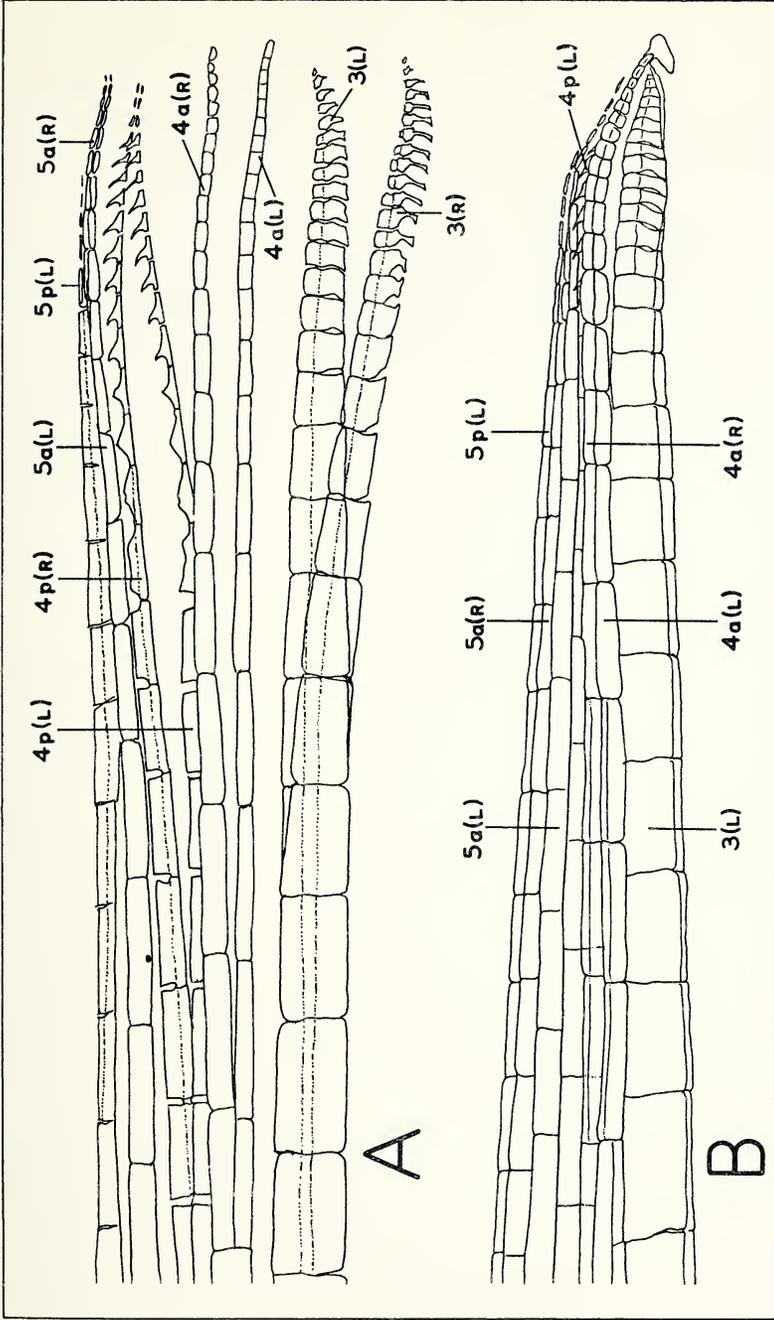


Figure 2. Gonopodium of *Phallichthys tico*, n. sp. A. Partial dissection to reveal symmetry of gonopodium. B. Natural orientation of gonopodium showing membranous knob and crest.

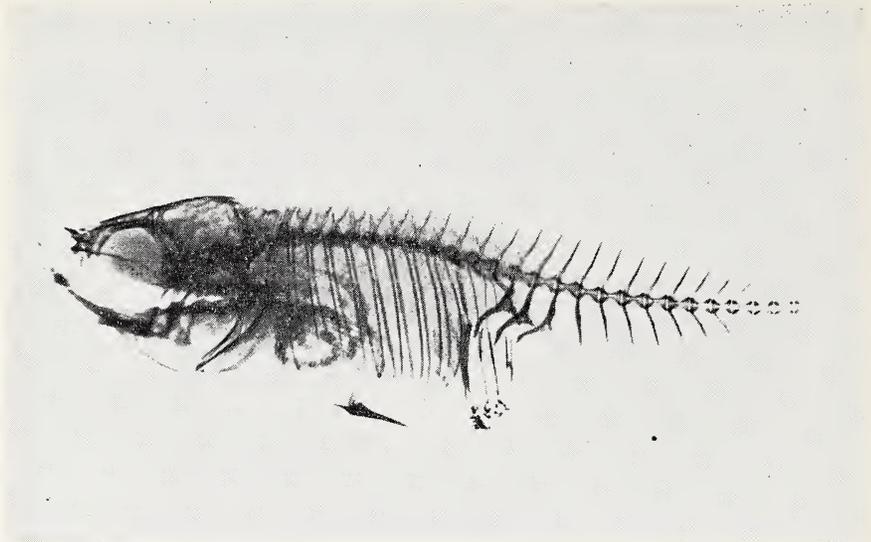


Figure 3. Radiograph of an adult male of *Phallichthys tico*, n. sp., (LACM 2781) to show gonopodial suspensorium.

rays 11, occasionally 10 or 12; pelvic rays 6; principal caudal rays 13, occasionally 12 or 14. Scales in lateral series 26 or 27. Vertebrae usually 29, occasionally 30 including urostyle.

Measurements: Body measurements were made according to the methods described in Rosen and Bailey (1959) and recorded in Tables 1 and 2 for ready comparison with tables of measurements for *P. amates* and *P. fairweatheri* in Rosen and Bailey. The small collection made near Tilarán contains several females (largest 32.9 mm. SL) larger than any taken from the Río Puerto Viejo (largest 22.1 mm. SL). The only proportional difference between these two populations is the deeper body of the female specimens from Tilarán, the result of an advanced state of pregnancy in the latter females.

Gonopodium: Gonopodium of mature males consists of rays 3, 4 and 5 of anal fin forming a shallow trough open to the left. Ray 3 deep and compressed. Last 10-12 segments on ray 3(r) forming long thin spines which curve to the left and form the bottom of the trough. Corresponding segments on ray 3 (l) not produced into spines.

Right and left halves of ray 4 symmetrical. Ray 4a slender, tapering gradually to tip. Ray 4p also slender but last 11 segments modified into slender retrorse serrae, 2 or 3 tiny segments without serrae at very tip of ray 4p.

Ray 5 symmetrical and composed of anterior and posterior halves which together form a V-shaped groove on the posterior surface of the gonopodium. Rays slender and tapering gradually to tip, terminal segments of ray 5a extending farther than end of ray 5p. Right and left halves of rays 6 to 10 sym-

metrical; rays 6, 7 and 8 constricted near middle of ray and split into anterior and posterior elements distally; rays 9 and 10 split only into right and left halves.

Ray 4a forms tip of gonopodium from which hangs a membranous knob shaped like the head of a bird. A subterminal membranous crest on anterior margin of ray 3 similar to, but much smaller than that found in the genus *Xenophallus*.

Gonapophysis I curved forward, a pair of long, slender uncini arise near center of gonapophysis and curve sharply downward. Uncini of gonapophysis II straight, of moderate length and projecting posteroventrally. Gonapophysis III lacks uncini.

Gonactinost 1 free, gonactinosts 2, 3 and 4 fused into an expanded plate, lateral wings produced along entire length of gonactinost 4. Gonactinosts 5, 6, 7, 8 and 9 free and slender, interdigitating with gonapophyses; gonactinost 10 reduced, one-third the length of other gonactinosts. Lateral wing-like processes midway along gonactinost 9 in mature males.

Dentition: Two rows of teeth present in each jaw, those of the premaxillary and dentary alike in structure. Teeth of the outer row sharp-pointed, long, slender and incurved, attached on the outside surface of the tooth-bearing bone. Inner series about one half the length of the outer series. Teeth of both series gradually reduced in length toward edge of jaws.

Coloration: Ground color in life tan overlaid by a reticular pattern formed by dermal melanophores under the scales. Scales at first appear edged in black but on close examination it is seen that the reticular pattern showing through the scales actually edges the scale pocket which encloses each scale. Pectoral, ventral, anal and caudal fins clear, a fleeting iridescent blue often seen on the dorsal and anal fins of both sexes in life, as in *P. amates pittieri*. Interradial membrane between distal part of other dorsal rays slightly pigmented. Base of dorsal fin also pigmented in some specimens. One or two small superficial irregular blotches above anus in females. A series of obscure thin vertical bands along the body sometimes present on immature specimens.

Relationships: *Phallichthys tico* forms a natural group with the other members of the genus on the basis of the robust or deep body; long, thin gonopodium showing few specializations such as hooks, claws and serrae; the modification of rays 6 and 7 of the anal fin in mature males; the pigment patches occurring above the anus of the female and the general agreement in most other characters.

Important differences exist however, which necessitate expansion of the genus *Phallichthys*. The following discussion points out however, that some of these differences can be correlated with variation occurring in other species of *Phallichthys* and in other genera. The long distal uncini on gonapophysis I arise about midway along the gonapophysis in *P. tico* but show no great departure from the condition of the proximal uncini in *P. fairweatheri*. In addition a cleared and stained male specimen of *P. amates pittieri* from the Río

Puerto Viejo has long distal uncini on gonapophysis I, indicating that this character varies in different populations of the same species. The fact that *P. tico* has paired rather than unilateral development of serrae on ray 4p is not significant since this feature is known to vary (Bailey, *in litt.*) within the genus *Poeciliopsis*. A few minute serrae are sometimes found on ray 4p(r) in dextral species (*P. fairweatheri*) and on ray 4p(l) in members of the Río Puerto Viejo population of *P. pittieri* (a sinistral species).

Other differences show possible relationships or examples of parallelism with other genera. The broadly expanded primary gonactinostal complex is similar to that of other genera (i.e. *Carlhubbsia* and *Poeciliopsis*). The entire gonopodial suspensorium, with the exception of the long ligastyle, and the gonopodium is strikingly similar to that found in some members of the genus *Poeciliopsis* (see Alvarez and Aguilar, 1957) but the new species is distinct in body depth and other characters. *P. tico* like *P. fairweatheri* has a long liga-

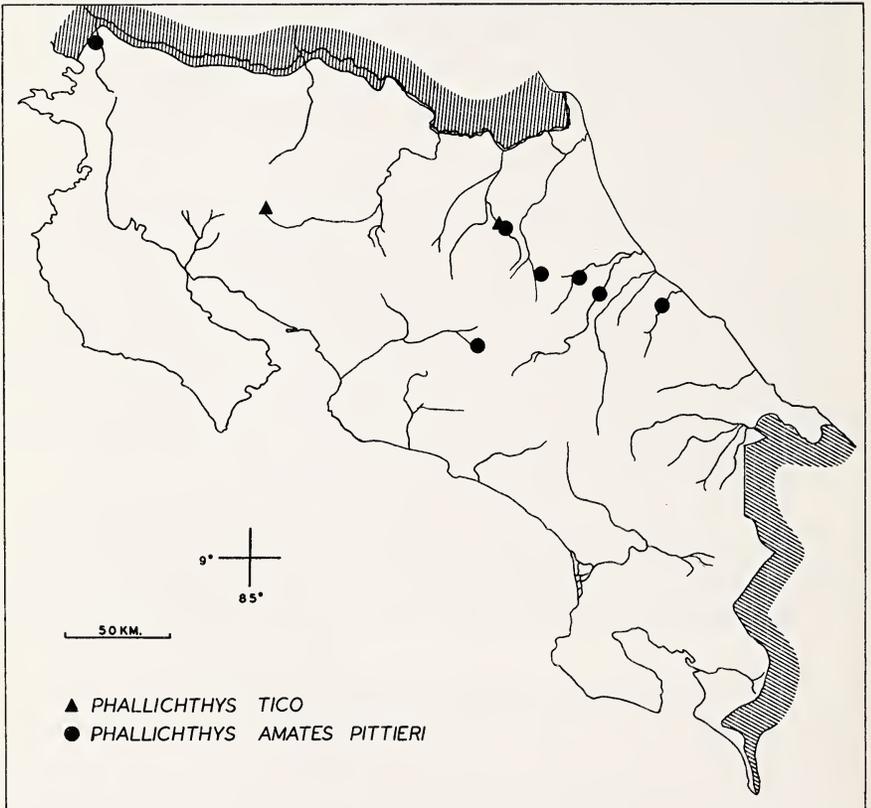


Figure 4. República de Costa Rica showing distribution by collection localities of *Phallichthys tico*, n. sp., and *Phallichthys amates pittieri*.



Figure 5. Type locality, backwater of the Río Puerto Viejo, Costa Rica. Photograph by the author.

style which apparently correlates with the short primary gonactinostal complex rather than for a deep body as suggested by Rosen and Bailey (1959).

Phallichthys may be expanded to include the following: body moderately deep (25-30% of SL) to deep (33-41% of SL); dorsal and ventral margins of body angular or not angular; ray 4p of gonopodium with row of unpaired distal serrae on either right or left half of ray or with paired symmetrical or unsymmetrical distal serrae; uncini of first gonapophysis, if present, either short and emerging near base of vertebra or long and located distally; primary gonactinostal complex either narrow or widely expanded.

P. tico shows evidence of being the most specialized member of the genus, although its exact relationships to the other two species are not obvious. *P. tico* is basically similar to previous described *Phallichthys* but shows some affinity to other poeciliid genera, especially *Poeciliopsis*.

Range: The species is known only from Costa Rica in two localities about 110 kilometers apart: the Río Puerto Viejo and a swamp near the Río San Luís. Both rivers ultimately connect with the Río San Juan which flows into the Caribbean. The known range will surely be expanded through further collecting and it is likely that the poorly known rivers on the Atlantic slope of Nicaragua will yield specimens of this species as well as *P. amates*. *P. tico* is sympatric in part of its range with *P. amates pittieri* (Fig. 4).

Habitat and Ecology: The type locality is in a small (ca. 200 sq. m.) backwater pool which was formerly part of the main river channel of the Río Puerto Viejo. It is now connected to the main river at only one point and be-

comes almost isolated during the dry season. During high waters the area may be under 3 meters of water and the pool becomes a part of the main stream. The topography of the pool changes little although the bottom is composed of over 6 meters of soft mud which is continually emitting gases of decomposition. Thick grasses line the indistinct shoreline on all sides (Fig. 5). The average water depth is less than 0.5 meter but deeper holes are present. As one leaves the main river there is a sharp change from clear to highly turbid water of a milky brown color. A rich plankton population was present as opposed to the relatively poor plankton content of the main river. No higher aquatic plants were present but a large quantity of brown algal scum floated at the surface as did patches of the "oily" material characteristic of stagnant pools. A partial chemical and physical analysis of water taken 5 cm. below the surface at 11:00 A.M. November 21, 1962, follows: temperature 30°C.; pH 6.4; reserve pH 7.3; oxygen 1.9 ppm; free carbon dioxide 24.0 ppm; bicarbonate alkalinity 115.5 ppm; hardness 109.0 ppm; chloride 5.3 ppm. The analysis was made when the water was low and the pool well isolated. The difference between the pH and the reserve pH (pH after water sample agitated for 2 minutes) indicates that the acid condition was due largely to dissolved carbon dioxide and is borne out by the high carbon dioxide analysis. The bicarbonate alkalinity is also increased due to the high carbon dioxide content. In contrast, a typical analysis of the main river water shows it to be clearer, soft, of neutral pH and high in oxygen, and it appears to consist principally of rain water with very few dissolved mineral substances. The conditions of the isolated backwater are unique along this river which has very few shallow protected shores that would provide *P. tico* a suitable habitat. Other species inhabiting the inner reaches of the pool are *Phallichthys amates pittieri*, *Mollienisia sphenops*, *Rhoadsia eigenmanni* and *Cichlasoma friedrichstahli*.

The Tilarán habitat is a shallow, clear-water swamp extending over several hectares. *P. tico* is found in the deeper (0.3 meter) sections where it retreats into dense grass clumps when approached. The temperature was 24°C. during the early morning; no chemical measurements were taken. *Brachyrhaphis episcopi* and *Rivulus isthmensis* also inhabit these swampy pools. Specimens were collected with dip net and rotenone.

Individuals of the new species stay close to shore at all times; they frequent shallow mud shores or hover in small aggregations of 20 to 30 individuals a few centimeters below the surface near grassy shores. They are very easily frightened and disappear into vegetation at the slightest disturbance. Seining was not feasible at either locality and all specimens were taken either with a hand dip net plunged very rapidly beneath them or with rotenone.

Although the fish is usually found in midwater, it frequently browses on the bottom in shallow water. Food consists principally of plant material (one-celled green and brown algae and diatoms); but protozoans are also taken. Small crustaceans were not detected in analyses of the digestive tract although they were plentiful at the Puerto Viejo habitat. In an aquarium *P. tico* remains

TABLE I
Body measurements of 10 male specimens of *Phallichthys tico* expressed in thousandths of standard length.

Measurement	LACM		Holotype		LACM 2781		LACM 2781			
	2781	2781	LACM 2780	LACM 2781	2781	2781	2781	2781		
Standard length (mm)	17.6	17.5	17.4	17.1	17.0	16.8	15.5	15.5	14.0	13.7
Body, greatest depth	289	285	298	269	294	255	283	258	285	284
Caudal peduncle, least depth	164	171	183	163	176	154	180	161	178	175
Dorsal origin to snout tip	539	542	528	573	529	470	554	503	535	540
Anal origin to mandibular symphysis	568	565	557	538	552	476	580	496	571	540
Dorsal origin to caudal base	482	474	465	467	482	422	483	438	478	452
Anal origin to caudal base	505	485	522	479	517	446	483	464	528	510
Head length	301	297	298	304	300	267	309	277	307	291
Head width	193	194	195	198	188	160	193	174	192	182
Snout length	90	91	97	105	94	83	96	83	92	87
Orbit length	96	102	109	111	100	101	109	96	107	109
Postorbital length of head	136	125	137	128	129	113	141	116	128	131
Interorbital, bony width	136	142	143	140	129	113	148	116	128	109
Mouth, over-all width	119	114	114	122	117	107	129	96	107	102
Dorsal fin, depressed length	255	257	264	251	270	244	270	245	271	262
Anal fin, depressed length	392	417	408	444	411	375	451	406	457	437
Caudal fin length	318	331	321	315	323	285	341	290	328	313
Pectoral fin length	210	228	224	216	211	196	212	193	214	211
Pelvic fin length	181	182	183	175	194	178	187	161	185	145

TABLE 2
Body measurements of 10 female specimens of *Phallichthys tico* expressed in thousandths of standard length.

Measurement	LACM 2782					LACM 2781				
	Standard length (mm)	32.9	28.1	23.1	22.1	21.4	20.4	20.2	19.0	18.8
Body, greatest depth	343	306	320	303	285	294	297	289	292	282
Caudal peduncle, least depth	161	163	164	167	168	166	173	168	170	158
Dorsal origin to snout tip	589	572	571	579	584	602	594	594	585	587
Anal origin to mandibular symphysis	671	647	623	642	626	647	638	657	632	621
Dorsal origin to caudal base	431	448	458	447	439	441	445	447	452	457
Anal origin to caudal base	395	398	432	416	411	416	425	431	425	423
Head length	264	281	294	289	289	294	297	294	303	305
Head width	200	199	203	208	210	215	212	215	212	192
Snout length	91	88	90	99	98	107	94	105	101	96
Orbit length	75	78	82	95	93	98	99	94	101	101
Postorbital length of head	115	131	134	117	126	127	133	136	127	141
Interorbital, bony width	136	138	151	153	149	156	153	157	154	146
Mouth, over-all width	103	106	116	126	121	132	123	126	111	107
Dorsal fin, depressed length	224	231	238	244	242	250	257	247	244	248
Anal fin, depressed length	203	220	225	235	224	235	237	236	223	220
Caudal fin length	249	277	303	316	322	328	326	331	319	316
Pectoral fin length	197	181	216	230	224	235	217	215	223	209
Pelvic fin length	136	142	147	162	168	171	168	163	159	152

hidden in the area of densest vegetation at the surface or the bottom, and ventures into midwater only when undisturbed. It readily accepts *Tubifex* worms and prepared dry foods.

The species is named *tico* in honor of the República de Costa Rica, the only country from which the species is known.

Acknowledgments: I wish to thank the government of Costa Rica and the U.S. State Department for making my stay in Costa Rica possible. I am grateful to the University of Costa Rica which afforded me excellent laboratory facilities, equipment and assistance; to Leslie R. and Lydia Holdridge who generously offered the use of their home at Finca La Selva and provided transportation by dugout to the finca and on many of my collecting trips; to Jay M. Savage for his many helpful suggestions and for reviewing the manuscript; to Donn E. Rosen, Reeve M. Bailey and Luis R. Rivas for their advice concerning the relationships of the species and for reviewing the manuscript and to my wife, Myrna López de Bussing, Salvador Jiménez C., Alexis Obando and Rafael Chavarría S. who assisted in the collecting.

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THE CHRONOLOGIC AND GEOGRAPHIC RANGE
OF DESMOSTYLIANS

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By EDW. D. MITCHELL, JR.
AND
CHARLES A. REPENNING



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THE CHRONOLOGIC AND GEOGRAPHIC RANGE OF DESMOSTYLIANS¹

By EDW. D. MITCHELL, JR.²

AND

CHARLES A. REPENNING³

ABSTRACT: This study attempts to summarize the scattered literature on desmostylian ranges, and in addition presents new data for early, middle, and late Miocene records of *Desmostylus* and a late Miocene record of *Paleoparadoxia*. Based on new data and a literature review, we believe the following ranges are valid: *Desmostylus* ranges from early Miocene, or possibly late Oligocene, to late Miocene; *Paleoparadoxia* ranges from early to late Miocene; *Cornwallius* is confined to the early Miocene; and *Vanderhoofius* is confined to the middle Miocene. Both *Desmostylus* and *Paleoparadoxia* are circum-North Pacific in distribution, whereas *Cornwallius* and *Vanderhoofius* are restricted to the eastern North Pacific. More than one desmostylian genus may be found in the same bed, and in the late Miocene of California both sirenians and desmostylians occur together.

INTRODUCTION

Desmostylians were heavily built, quadrupedal, amphibious mammals, apparently confined to the shores of the North Pacific basin largely during the Miocene Epoch. Fossils of desmostylians are found from the southern islands of Japan northward to Sakhalin, Kamchatka, and Alaska, thence southward to British Columbia, Washington, Oregon, California, and Baja California. Their bones and teeth are usually found in littoral marine deposits.

Marsh (1888), in the original description of the genus *Desmostylus*, included it in the Sirenia, and desmostylians have been most commonly so grouped since then. However, others have suggested relationships with multituberculates (Abel, 1922), proboscidians (Osborn, 1902), and perissodactyls (particularly tapirs; Ijiri and Kamei, 1961). Reinhart (1953) separated the Desmostylia from the Sirenia by raising the group to ordinal status, and related the Desmostylia to both sirenians and proboscidians through a hypothetical Paleocene paenungulate ancestor (Reinhart, 1959).

Since V. L. VanderHoof (1937) monographed desmostylians, it has been generally thought that "the stratigraphic range of *Desmostylus* appears to be strictly limited to Temblor and Briones time; that is, upper Middle Miocene and lower Upper Miocene" (VanderHoof, 1937: 195). This belief in the restricted range of *Desmostylus* (in the eastern North Pacific) still persists

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despite Remington Kellogg's statement, six years before VanderHoof's publication, that *Desmostylus* is "found in formations varying in age from lower to upper Miocene" (Kellogg, 1931: 226). Although Kellogg cited localities in San Luis Obispo and Orange Counties, California, he provided no additional details for early Miocene records (1931: 224).

It is our intent in this paper to give complete data documenting examples of early, middle, and late Miocene records of *Desmostylus* in the eastern North Pacific and to summarize the geographic and chronologic ranges of all other desmostylians now known to us. In addition, we present data on a new record of *Paleoparadoxia* from the late Miocene of California, and on the association of desmostylians and sirenians in central California.

In compiling our summary of records, we have used the following cheek tooth characters in the identification of desmostylian genera:

Desmostylus: Columns of cheek teeth closely appressed, usually polygonal in cross section, cingulum absent, enamel base not swollen, column height about three times diameter of column.

Cornwallius: Columns of cheek teeth not closely appressed, circular in cross section, cingulum may be present but never surrounds entire tooth, enamel base may be swollen, column height about one to two diameters of column.

Paleoparadoxia: Columns of cheek teeth may or may not be appressed, polygonal or circular in cross section, cingulum may be present and may surround entire tooth, enamel base swollen, column height forms about half of crown height.

Vanderhoofius: Cheek teeth of *Vanderhoofius* are unknown.

We regard *Kronokotherium* Pronina (1957) from Kamchatka and *Desmostylella* Nagao (1937) from Japan as synonyms of *Desmostylus*, and follow VanderHoof (1937:191-192) and Reinhart (1959:66) in not considering *Neodesmostylus* a desmostylian.

We have attempted to treat all desmostylian records here by a uniform set of standards so that the relative age of the occurrences can be seen. The boundaries of epochs used are those of Weaver, *et al.* (1944) for marine metazoans, except that the Miocene-Pliocene boundary is placed at the top of the Neroly Stage. This usage does not agree with epochal boundaries used by Weaver, *et al.* (1944) for foraminiferal stages, with those used by Wood, *et al.* (1941) for North American mammalian ages, or with the epochal correlations customarily employed in Japan. This will explain our seeming departures from some previous age assignments. We have had to rely entirely upon the statements of Japanese workers as to the age of Japanese desmostylian records.

Correlation between marine metazoan stages of western North America, foraminiferal stages of the same area, mammalian ages of North America, European Miocene and Pliocene stages, and Japanese formational correlations (most commonly correlated with European stages, but sometimes with North

American stages), and the epochal assignments arbitrarily used with them are indicated in Table 1. No single chronology along the western side of the North Pacific is in wide use. The stages shown on Table 1 for the Japan area represent a composite of names proposed by Takai (1939), Makiyama (1940), and Tai (1959), with correlations made by these authors and by Asano (1958), Hatai (1960), Watanabe (1953), Yabe (1959), and Ijiri and Kamei (1961). In the following discussion we try to clearly specify whether we are referring to a formation or a stage.

Table 1 also shows the range in time of occurrences of desmostylian and sirenian fossils in the North Pacific basin. Insofar as possible the fossil occurrences have been placed on the chart on the basis of evidence of age independent of any significance that might be given to the desmostylian and sirenian fossils. For the most part this evidence has been based on either foraminifera or molluscs and echinoids. A few records were also associated with land mammals.

The following abbreviations are used in the text: UCMP—Museum of Paleontology, University of California, Berkeley; USGS—United States Geological Survey; and USNM—United States National Museum.

DESMOSTYLIAN RANGES

Genus **DESMOSTYLUS** Marsh, 1888

CALIFORNIA—Teeth of *Desmostylus* are moderately common fossils in rocks of middle Miocene age in California (the Temblor Stage of Weaver, *et al.*, 1944). It is not the object of this report to place all discoveries on record but only to document one record of unquestioned age and identity for each stage in which one or more records are known. Because early, middle, and late Miocene records are known from one area in California (the Cuyama Valley area of San Luis Obispo and Santa Barbara Counties), these are given here, although records from other areas might be equally appropriate. Our California teeth all fall within the range of variability of *D. hesperus*, as V. L. VanderHoof (1937) interpreted the species.

Early Miocene

Material: USNM 22922 and USNM 22923: Two incomplete cheek teeth (Fig. 1).

Collector: John G. Vedder, 1960.

Locality: USGS vertebrate locality (Menlo Park register) M1028: In bed of stream midway along a northwest-trending reach of a small drainage in the Caliente Range, San Luis Obispo County, California, 4.3 miles northwest of the town of New Cuyama, Santa Barbara County, California. The locality is 1.05 miles east of the west edge and 0.25 mile south of the north edge of the Cuyama Ranch 7.5-minute U.S. Army quadrangle, 1943 edition.

Formation and Age: Painted Rock Sandstone Member of the Vaqueros Formation (terminology of Hill, Carlson, and Dibblee, 1958), early Miocene:

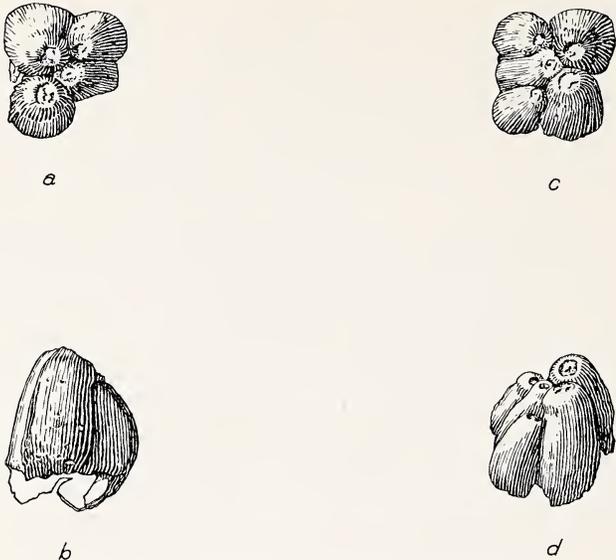


Figure 1. *Desmostylus*, cf. *D. hesperus*, occlusal (a) and side (b) views of cheek-tooth USNM 22922; and occlusal (c) and side (d) views of cheektooth USNM 22923; both from early Miocene of Cuyama Valley area, California. One-half natural size.

Vaqueros Stage of Weaver *et al.* (1944), Saucesian Stage of Kleinpell (1934), and Arikareean Age of Wood, *et al.* (1941).

Remarks: Vedder described the occurrence as being in a coquinoid bed containing barnacle fragments and *Lyropecten miguelsenis* (Arnold). In the same area stratigraphically higher beds contain a large fauna from which Vedder reported *Turritella inezana altacorona* Loel and Corey, *Rapana vaquerosensis* (Arnold), and "*Crassatella*" *granti* (Wiedey). Underlying and overlying strata contain Saucesian foraminifera according to Hill, Carlson, and Dibblee (1958:2987). Beds containing the same marine fauna farther east in the Caliente Range are interbedded with continental sediments containing a mammalian fauna assigned to the Arikareean Age by Repenning and Vedder (1961). The molluscan faunal associations above and below the *Desmostylus* teeth suggest an early Miocene age (Vaqueros Stage) in the West Coast standard chronology.

Middle Miocene

Material: USNM 22925: An incomplete cheek tooth (Fig. 2).

Collector: John G. Vedder, 1961.

Locality: USGS vertebrate locality (Menlo Park register) M1030: 5.2 miles southwest of town of New Cuyama, on the south side of Cuyama Valley, Santa Barbara County, California. This is 0.2 mile west of the east edge and



a



b

Figure 2. *Desmostylus*, cf. *D. hesperus*, occlusal (a) and side (b) views of cheek-tooth USNM 22925 from the middle Miocene of Cuyama Valley area, California. One-half natural size.

6.9 miles south of the north edge of the McPherson Peak 15-minute U.S. Army quadrangle, 1943 edition.

Formation and Age: Lower part of the type section of the Branch Canyon Formation (terminology of Hill, Carlson, and Dibblee, 1958) middle Miocene: Temblor Stage of Weaver, *et al.* (1944); Relizian Stage of Kleinpell (1934); Hemingfordian or Barstovian Age of Wood, *et al.* (1941).

Remarks: According to Vedder, the *Desmostylus* remains were associated with very poorly preserved echinoids that may be referred to *Vaquerosella andersoni* (Twitchell). Vedder further stated that beds in the same stratigraphic position in the same area contain *Aequipecten* cf. *A. andersoni* (Arnold) and *Amusium lomdocensis* (Arnold)?, and that beds several feet below the *Desmostylus* locality contain *Turritella ocoyana* Conrad, "*Trophon*" *kernensis* Anderson, *Ficus (Trophosycon) ocoyana* (Conrad)?, *Bruclarkia* cf. *B. oregonensis* (Conrad), "*Phos*" *dumbleanus* Anderson (in Hanna), *Oliva californica* Anderson, and *Scaphander* cf. *S. jugularis* (Conrad). The underlying shaly strata contain Relizian foraminifera according to Hill, Carlson, and Dibblee (1958:2992), and to the north, in the eastern Caliente Range, strata with a similar marine molluscan fauna are interbedded with continental beds containing mammalian faunas of both Hemingfordian and Barstovian Ages (Repenning and Vedder, 1961). The combined molluscan fauna associated with or below the *Desmostylus* occurrence suggests a middle Miocene age in the West Coast standard chronology. *Desmostylus* is a common fossil in beds of the Temblor Stage in many parts of California.

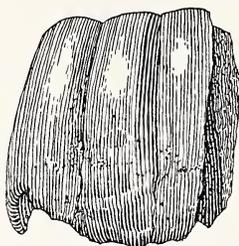
Late Miocene

Material: USNM 22924: An incomplete cheek tooth (Fig. 3).

Collector: John G. Vedder, 1961.



a



b

Figure 3. *Desmostylus*, cf. *D. hesperus*, occlusal (a) and side (b) views of cheek-tooth USNM 22924 from the late Miocene of Cuyama Valley area, California. One-half natural size.

Locality: USGS vertebrate locality (Menlo Park register) M1029: On the south side of Cuyama Valley, along northeast limb of anticlinal valley east of Branch Canyon, 4.7 miles south southwest of the town of New Cuyama, Santa Barbara County, California. This is 1.5 miles east of west edge and 0.8 mile north of south edge of Cuyama Ranch 7.5-minute U.S. Army quadrangle, 1943 edition; 0.29 mile east southeast of the termination of the road as shown on this map.

Formation and Age: In the highest part of the Branch Canyon Formation (terminology of Hill, Carlson, and Dibblee, 1958) near the type section, late Miocene: Cierbo or Neroly Stage of Weaver, *et al.* (1944); Barstovian or Clarendonian Age of Wood, *et al.* (1941).

Remarks: According to Vedder the *Desmostylus* remains were associated with abundant echinoids which Richard C. Allison, of the University of California, has identified as almost all *Astrodapsis cuyamanus* Kew, with the possibility of another form being represented by a small specimen. Stratigraphically above the *Desmostylus* locality are beds with a molluscan fauna from which Vedder reported *Turritella carrisaensis* Anderson and Martin. Coquinoid beds underlying the *Desmostylus* locality contain abundant echinoids which Eaton, Grant, and Allen (1941) assigned to the lower Neroly and Cierbo Stages. Several tens of feet below the locality Vedder reported the occurrence of a fauna which contains *Astraea* cf. *A. raymondi* (Clark), *Agasoma sinuata*

(Gabb), "*Trophon*" cf. "*T.*" *carisaensis* (Anderson), "*Trophon*" *gillulyi* Grant and Eaton, *Lyropecten crassicardo* (Conrad), *Lyropecten estrellanus* (Conrad), and *Aequipecten* cf. *A. pabloensis* (Conrad). These mollusks suggest a late Miocene age in the West Coast standard chronology. Repenning has collected sirenian remains from this unit. Sirenians are common in the late Miocene of California, but are apparently unknown in earlier deposits. On the north side of Cuyama Valley in the eastern Caliente Range, strata containing a meager fauna including a few of these mollusks are interbedded with continental beds containing a mammalian fauna assigned a Barstovian Age by Repenning and Vedder (1961). However, this marine molluscan fauna is also found interbedded with strata containing mammals that have been assigned a Clarendonian Age in other parts of California (see Savage, 1955:15) so that the correlation of this record of *Desmostylus* to the sequence of North American mammalian ages is not certain.

The correlation of these beds with the Cierbo and lower Neroly Stages by Eaton, Grant, and Allen would suggest an occurrence of *Desmostylus* somewhat younger than the youngest record cited by VanderHoof, which he referred to the Briones Stage. However, more recent consideration of the "Briones" record cited by VanderHoof (1937:197, UCMP locality V-3108) has led C. A. Hall to believe that the locality is in rocks "more probably assignable to the Cierbo formation" and that "the range of *Desmostylus* might be extended to the upper Upper Miocene" (Hall, 1958:23, 50).

Desmostylus teeth seen by Repenning in private collections have been collected from the Felton local fauna near Santa Cruz, California (UCMP locality V-5555) and were found in association with primitive *Hipparion* horses (of probable early Clarendonian Age) and two teeth of cf. *Paleoparadoxia* now in the Museum of Paleontology at the University of California (UCMP 45274 and 63981). Also associated in the same beds in the area of Santa Cruz are many specimens of the sirenian *Halianassa vanderhoofi* Reinhart. Vanderhoof (1941) compared this sea cow with European forms of Tortonian age. The association with *Hipparion* would tend to favor a younger age, perhaps Sarmatian. According to recent stratigraphic studies by Joseph C. Clark, of Stanford University, marine mollusks and echinoids of late Miocene age are found within the same unit and about 40 feet above VanderHoof's sea cow locality, although other specimens of sea cows are found throughout the unit and the horse and *Desmostylus* teeth also seem to be scattered throughout the unit. Overlying strata contain a Pliocene marine mollusk fauna.

In summary, *Desmostylus* records in California indicate a range from the Vaqueros Stage of the early Miocene to the Cierbo or Neroly Stage of the late Miocene.

OREGON—The only records of *Desmostylus* from Oregon are from the Astoria Formation, principally in the vicinity of Newport. As has been known for years (see VanderHoof, 1937:202), they are associated with marine mollusks of the Temblor Stage. Recently Douglas Emlong of Gleneden Beach,

Oregon, found part of a skull of the rhinoceros *Aphelops* associated with *Desmostylus* remains in the Astoria Formation about 4 miles north of Newport, making possible an estimate of the age in North American land mammal terms. The rhinoceros represents a Hemingfordian to Barstovian stage of evolution within the Rhinocerotidae. The specimen is now in Mr. Emlong's private museum.

WASHINGTON—The only record of *Desmostylus* from the state of Washington seems to be that cited by Kellogg (1931:226) from the "upper Miocene Montesano formation" near the town of Vesta in Grays Harbor County. According to Howard D. Gower of the U.S. Geological Survey, the brief locality and lithologic description given by Kellogg indicates that the specimen came from the upper part of the Astoria Formation, which may be equivalent to the basal conglomeratic part of the Montesano Formation to the north (personal communication, 1963). Recent studies by Warren O. Addicott, also of the U.S. Geological Survey, indicate that the molluscan fauna at this locality is late Miocene in age (personal communication, 1963).

WESTERN NORTH PACIFIC—*Desmostylus* records are abundant in the Miocene on the Asiatic side of the North Pacific basin. The genus is known from Kamchatka (as *Kronokotherium*, Pronina, 1957), Sakhalin, Hokkaido, and Honshu (see detailed summaries of Yabe, 1959; Hatai, 1960; and Ijiri and Kamei, 1961). These records range throughout the Miocene although only two records of late Miocene age are cited by Ijiri and Kamei (1961:16, table 1), both from Honshu. The oldest records of *Desmostylus* appear to be from southern Sakhalin and Hokkaido, where associated foraminifera indicate a correlation with the Zemorrian Stage according to Asano (1958:45, 47). This age assignment is reviewed by Yabe (1959) and indicates a correlation with either the earlier part of the Vaqueros Stage or the Blakeley Stage, as these correlations are currently understood. By the definition of the Miocene used here, this is most likely earliest Miocene but could be of latest Oligocene age; it appears to be older than the earlier Miocene record from the Caliente Range described here.

ATLANTIC OCEAN—Stenzel and Turner (1944) listed "*Desmostylus*" in a Miocene fauna near Burkeville, Texas, and referred to it as a "sea cow." Floyd, Miller, and Berry (1958) mentioned "sea cow" also, but this was based on the statement of Stenzel and Turner (1944) and not on new material (personal communication, W. B. N. Berry, 1963). We have been unable to verify this record.

Genus **CORNWALLIUS** Hay, 1923

The holotype of *Cornwallius sookensis* was found in the Sooke Formation of Vancouver Island, British Columbia (Cornwall, 1922). In all, three teeth (Cornwall, 1922; Clark and Arnold, 1923) and the temporal bone (Hay, 1923:107) of *Cornwallius* are known from the Sooke Formation, which is considered to be of early Miocene age (Weaver *et al.*, 1944:597). This is the

only record of *Cornwallius* which is datable on independent evidence with any degree of accuracy.

Teeth called *Cornwallius sookensis* have also been found near San Telmo Point in Baja California, Mexico (VanderHoof, 1942). The *Cornwallius*-bearing rocks at the Baja California locality were referred to the San Gregorio Formation by Durham (1950) and were considered lowest Miocene in the standard West Coast chronology by Durham and Allison (1960:56) on the basis of the *Cornwallius* teeth. No other control is available to date this record.

Byers (1959:289) stated that "Vertebrate-fossil remains, chiefly teeth, have been found . . . on the north side of Unalaska [Island, Alaska]. These teeth were identified by G. Edward Lewis . . . as those of *Cornwallius* sp., a marine mammal of early Miocene age." Drewes, *et al.* (1961:606) further commented on these bones and teeth: the "most significant specimen is a low-crowned cheek-tooth fragment with typical desmostylid cusps. The fragments probably are referable to a single animal of the genus *Cornwallius*, which is generally indicative of an early Miocene age, although identification as *Desmostylus* is possible."

MacNeil, *et al.* (1961: fig. 1) listed "*Cornwallius*-bearing beds on Unalaska" at the bottom of the Miocene in their correlation chart on the basis of Byers' (1959) statement. Little control for this age assignment is available other than the *Cornwallius* remains; they were associated with *Mya* sp. cf. *M. grewingki* Makiyama, a species which probably indicates a correlation to the Blakeley Stage according to F. S. MacNeil of the U.S. Geological Survey.

Insofar as we have interpreted published material from Japan, the genus has never been found on the western side of the North Pacific; all citations to *Cornwallius* from the western Pacific appear to be referable to either *Desmostylus* or *Paleoparadoxia*. However, Fuyuji Takai (of Tokyo University) left two photographs with Donald E. Savage (of the University of California) of a specimen collected near Nagoya, Honshu that appears to be referable to *Cornwallius*.

Genus **VANDERHOOFIUS** Reinhart, 1959

Only two specimens of *Vanderhoofius coalingensis* were listed by Reinhart (1959). One (mandible UCMP 39989) is the holotype and the other (mandible UCMP 39990) is the paratype; both are from UCMP locality V-4854 southwest of Coalinga, California. They were found in direct association with abundant teeth of *Desmostylus hesperus*. Reinhart gave the formation as "Upper member of Temblor sandstone." The associated molluscan fauna indicates a Temblor Stage assignment.

Genus **PALEOPARADOXIA** Reinhart, 1959

The type specimen of *Paleoparadoxia tabatai* is from Aikawa on the island of Sado, Japan, from near the base of the Turusi beds probably of middle Miocene age (Tokunaga, 1939). Ijiri and Kamei (1961:16) tabulated three Japanese records of *Paleoparadoxia*, all from Honshu (the island of Sado is

off the west coast of Honshu). These are shown in their list as being from early, middle, and late Miocene localities.

A complete skeleton of *Paleoparadoxia tabatai* was found in the Miocene Yamanouchi Formation at Inkyoyama, Izumimachi, Toki City, Gifu Prefecture, Honshu (Ijiri and Kamei, 1961:26). This skeleton was found stratigraphically "near" the holotype of *Desmostylus japonicus* from Togari, Kani-gun, Gifu Prefecture, even though the two localities are about 3 km. apart (Yabe, 1959:49). The most important point here is that in a "broad sense the Izumi skeleton of *Cornwallius*? [= *Paleoparadoxia* of Ijiri and Kamei] and the Togari skull of *Desmostylus japonicus* . . . are from the same, Togari beds . . ." (Yabe, 1959:49).

Reinhart (1959) listed only two referred specimens from North America (mandible UCMP 40862 and tooth UCMP 32076). He stated (1959:97) that the "type specimen from Japan and U.C.M.P. no. 32076 were found in a littoral formation of middle Miocene age." The tooth (UCMP 32076) is from UCMP locality V-3301 (not V-3801 as stated by Reinhart), which Vander-Hoof (1937:201) considered to be "Temblor" in age. The exact locality and age of the mandible (UCMP 40862) is unknown. It is reported to be from the area of Santa Cruz, California, and Reinhart suggested that it is from the Santa Margarita Formation of late Miocene age. Two isolated teeth of *Paleoparadoxia* from the Santa Margarita Formation of the Santa Cruz area are in the collection of the Museum of Paleontology of the University of California. Because they represent the first definite record of this family in the late Miocene of the eastern North Pacific Ocean, their occurrence is described here.

Material: UCMP 45274, a complete tooth, and UCMP 63981, an incomplete tooth (Fig. 4).

Collectors: UCMP 45274 was collected by Eleanor and Gladys Pavey of Watsonville, California, in about 1952. UCMP 63981 was collected by T. E. McCaw of Santa Cruz, California, in about 1950 and was given to J. C. Clark of Stanford University who, in turn, donated it to the Museum of Paleontology of the University of California.

Localities: The two specimens were collected from different localities, about 2,000 feet apart, from the same formation. UCMP 45274 was collected from UCMP locality V-5555, a sand pit generally known as the Graham sand pit, which is located on the south side of Bean Creek one mile northwest of Camp Evers junction in Scotts Valley along the Lockhart Gulch Road, Santa Cruz County, California. UCMP 63981 was collected from UCMP locality V-4004, a sand pit formerly known as the Pacific Coast Aggregates Company sand pit and currently as the Santa Cruz Aggregates sand pit, which is located on the north side of Bean Creek and about 2,000 feet north-northwest of the Graham pit.

Formation and Age: The Santa Margarita Formation, latest Miocene: Neroly Stage of Weaver *et al.* (1944); Clarendonian Age of Wood *et al.* (1941); Mohnian or Delmontian Stage of Kleinpell (1934).

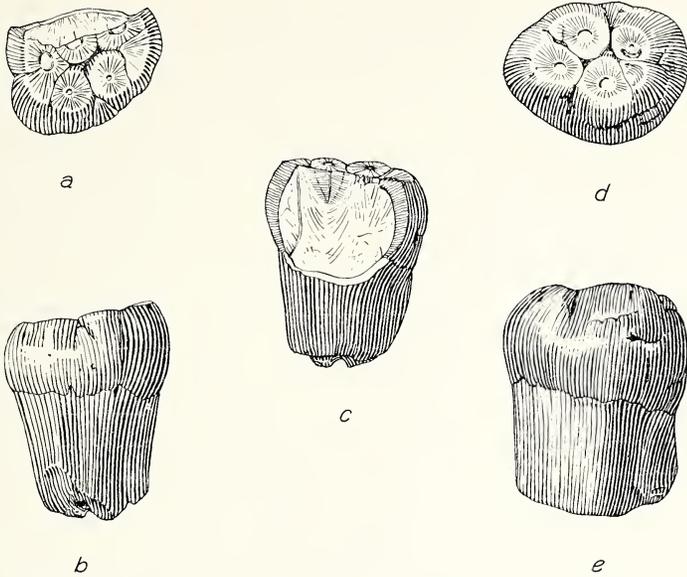


Figure 4. *Paleoparadoxia* sp., occlusal (a) and side (b, c) views of cheektooth UCMP 63981; and occlusal (d) and side (e) views of cheektooth UCMP 45274: both from late Miocene of Santa Cruz area, California. Natural size.

Remarks: Joseph C. Clark of Stanford University is currently engaged in a detailed study of the geology of the area which includes these localities. The following remarks are based largely upon his preliminary conclusions. In the Bean Creek area the Santa Margarita Formation contains scattered and in many cases wave-rounded teeth and bone fragments of sharks, birds, several land mammals including a primitive *Hipparion*, and marine mammals including *Desmostylus*, *Paleoparadoxia*, the sirenian *Halianassa*, cetaceans, and pinnipeds. Most of these fossils have been collected by private collectors during or following quarrying and screening of the unconsolidated sand that makes up the formation. For the most part there is no stratigraphic control of the occurrence of the vertebrate fossils in the formation. However, sirenian remains, seen in place at several localities by Repenning, occur as low as 15 feet above the base and as high as 40 feet below the top of the formation. The formation varies in thickness but at the localities here discussed is about 280 feet thick. There is no reason to think that the other mammalian remains are not scattered throughout the formation as are the sirenians.

The little deformed Santa Margarita Formation rests with angular unconformity on folded and faulted marine beds containing foraminifera which indicate an early Luisian age. Clark has made several collections from the echinoid bed 40 to 60 feet below the top of the Santa Margarita. Provisional identification of these specimens includes *Lyropecten estrellanus* (Conrad)

and *Astrodapsis spatiosus* Kew. The invertebrates are suggestive of a very late Miocene age (Neroly Stage). The siliceous mudstone unit conformably overlying the Santa Margarita Formation contains a meagre invertebrate fauna that is similar to the fauna of the lower part of the Purisima Formation of Pliocene age. Preliminary study thus suggests that the *Paleoparadoxia* and *Desmostylus* remains from the Santa Cruz area are of the latest Miocene age and occur very close to the Miocene-Pliocene boundary. The associated *Hipparion* indicates a Clarendonian age and the foraminifera in the underlying unit suggests that the Santa Margarita is younger than early Luisian age.

NORTH PACIFIC DESMOSTYLIAN AND SIRENIAN DISTRIBUTION

Sirenians are found in the Eocene of the Caribbean, and apparently have continuously occupied the Caribbean since then. Throughout much of the Eocene the Central American seaway provided free access between the Caribbean and the Pacific, as indicated by the similarity of marine invertebrate faunas and the endemism of the isolated South American nonmarine mammal fauna. There seems to be no reason to think that Caribbean sirenians did not also enter the Pacific basin, although no records of such entry are published. The paucity of records may be explained by the scarcity of marine Tertiary deposits on the Pacific side of Central America. F. H. Kilmer of the University of California, Santa Barbara, is presently working on a sirenian from the Miocene of Baja California that is presumably older than the late Miocene sirenians discussed below.

Kellogg (1925) described *Halianassa* (= *Metaxytherium*) *jordani* from diatomite deposits near Lompoc, California, which were mapped as Sisquoc Formation by Dibblee (1950: pl. 1). Kellogg stated that the sirenian was found at least 1,100 feet above the base of the diatomite and that it was "Sarmatian, or Upper Miocene" in age (1925:60). According to Dibblee, the lower 1,000 feet of the Sisquoc Formation is assignable to the Delmontian Stage, the remainder to early and perhaps middle Pliocene (1950:44). Other late Tertiary sirenians are known from western North America. Reinhart described a specimen (*Halianassa* sp.) from Baja California that was found in rocks "of early Pliocene age, but could be as old as middle Miocene" (1959:45). VanderHoof (1941) commented on a sea cow (*Halianassa vanderhoofi* Reinhart, 1959) from near Santa Cruz, California, and suggested that it was Tortonian in age. We favor a younger age for this record (see *Remarks* under Late Miocene record of *Desmostylus*). Reinhart (1959:44) reported that "the oldest sirenian reported from the Pacific coast of Central America is an Oligocene form from Chiapas, Mexico . . ." Müllered (1932), who described the rib fragments upon which this record is based, stated that they were Oligocene in age. It may or may not be sirenian, but it does not appear to have lived in the Pacific basin because the marine Tertiary rocks of Chiapas were deposited by Caribbean waters northeast of the Sierra Madres according to J. W. Durham, of the University of California.

TABLE 1—CHRONOLOGIC RANGE OF DESMOSTYLIANS AND SIRENIANS IN THE NORTH PACIFIC OCEAN

BASIC CHRONOLOGY		EAST PACIFIC CHRONOLOGIES				WEST PACIFIC CHRONOLOGY						
EUROPEAN STAGES	ARBITRARY EPOCH DIVISIONS	PACIFIC COAST NORTH AMERICAN MICROFAUNAL STAGES ¹		PACIFIC COAST NORTH AMERICAN MAMMALIAN AGES ²		MEXICO	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS	
		WHEELERIAN	SAN JOAQUIN	BLANCAN (in part)	NORTH AMERICAN MAMMALIAN AGES ²							KAMCHATKA
ASTIAN	PLIOCENE	EARLY MIOCENE	LATE MIOCENE	WHEELERIAN	SAN JOAQUIN	BLANCAN (in part)	MEXICO	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS
PLAISANCIAN		EARLY MIOCENE	LATE MIOCENE	VENTURIAN	ETCHEGOIN	HEMPHILLIAN						
PONTIAN	MIOCENE	DEL MONTIAN	MOHNIAN	REPETTIAN	JACALITOS	CLARENDONIAN	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS	
SARMATIAN		DEL MONTIAN	MOHNIAN	REPETTIAN	JACALITOS	CLARENDONIAN						WEST PACIFIC (JAPAN) STAGES
TORTONIAN	MIOCENE	SAUCESIAN	LUISIAN	DEL MONTIAN	NEROLY	BARSTOVIAN	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS	
HELVETIAN		SAUCESIAN	LUISIAN	NEROLY	BARSTOVIAN	WEST PACIFIC (JAPAN) STAGES						WEST PACIFIC RECORDS
BURDIGALIAN	EARLY	ZEMORRIAN	RELIZIAN	REPETTIAN	C IERBO	HEMINGFORDIAN	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS	
AQUITANIAN		ZEMORRIAN	RELIZIAN	C IERBO	HEMINGFORDIAN	WEST PACIFIC (JAPAN) STAGES						WEST PACIFIC RECORDS
CHATTIAN	LATE OLIocene	REFUGIAN	VAQUEROS	BLAKELEY	BRIONES	WHITNEYAN	UNITED STATES	CANADA	ALASKA	WEST PACIFIC (JAPAN) STAGES	WEST PACIFIC RECORDS	
CHATTIAN	REFUGIAN	VAQUEROS	BLAKELEY	BRIONES	WHITNEYAN	WEST PACIFIC (JAPAN) STAGES						WEST PACIFIC RECORDS
<div style="display: flex; justify-content: space-between;"> <div style="width: 30%;"> <p> Desmostylus</p> <p> Cornwallius</p> <p> Paleoparadoxia</p> <p> Sirentian</p> </div> <div style="width: 60%; text-align: right;"> <p><i>Dashed where record uncertain</i></p> </div> </div>												

¹Weaver, et al., 1944
²Wood, et al., 1941

TABLE 1
 Chronologic Range of Desmostylians and Sirenians in the North Pacific Ocean.

Northward, then, along the eastern shore of the North Pacific Ocean, there are few or no records of sirenians until they appear in late Miocene deposits in California. This is at the time when Olsson (1932) reported the beginning of endemism in the Pacific invertebrates of northern Peru, which until then had been clearly similar to Caribbean faunas of Trinidad. As has been discussed, the late Miocene contains the last of the records of desmostylians in the North Pacific basin.

SUMMARY AND CONCLUSIONS

In this paper we have followed recent usage among marine mollusk stratigraphers in arbitrarily selecting the top of the Neroly Stage and the middle of the Blakeley Stage as the limits of the Miocene Series on the west coast of North America. We have attempted to consider all pertinent desmostylian records in this chronologic framework. The generic assignment of some of these records is based on our interpretation of the taxonomic significance of tooth characters. Review of pertinent literature and documentation of new occurrences indicate that the following ranges are valid:

1. *Desmostylus* is circum-North Pacific in distribution; in the Japan area published records indicate that it could range in age from equivalents of the late Blakeley Stage (early Miocene) to equivalents of the Neroly Stage (late Miocene), and in North America it ranges in time from the Vaqueros Stage to the Neroly Stage. A record from the Vaqueros Stage is documented from Cuyama Valley, California, and late Miocene records are discussed or documented from Cuyama Valley and Santa Cruz, California, and from Grays Harbor County, Washington.
2. *Paleoparadoxia* is also circum-North Pacific in distribution; following Japanese workers, we now regard all previous records termed *Cornwallius* from the western North Pacific as representing *Paleoparadoxia*. The genus appears to have an early to late Miocene range in the western Pacific, and a middle to late Miocene range in the eastern Pacific. Late Miocene records are documented from near Santa Cruz, California.
3. *Cornwallius* is known only from a few fossils from early Miocene rocks in the eastern North Pacific. The genus evidently ranges from Alaska to Baja California in the eastern Pacific. Desmostylians referred to the genus *Cornwallius* from the western North Pacific are more probably referable to other genera.
4. *Vanderhoofius* is known only from the middle Miocene of California.

Based upon published records, sirenians do not appear in the eastern Pacific until the late Miocene. In the Santa Cruz and Cuyama Valley areas of California fossils of both desmostylians and sirenians have been found in the same beds. Sirenians have been found in eastern North Pacific Pliocene deposits.

ACKNOWLEDGMENTS

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MORPHOLOGICAL DATA ON TWO SIBLING SPECIES
OF SMALL HONEY-GUIDES

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By HERBERT FRIEDMANN



Los Angeles County Museum • Exposition Park • Los Angeles 7, Calif.

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MORPHOLOGICAL DATA ON TWO SIBLING SPECIES OF SMALL HONEY-GUIDES

By HERBERT FRIEDMANN¹

ABSTRACT: Trunk skeletons of two sibling species of *Indicator* reveal that in *exilis* the posterior sternal notches are deeper, the coracoids and clavicles proportionately slightly longer, and the entire rib "basket" laterally broader than in *pumilio*. These differences substantiate the distinctness of the two species but seem unlikely to have any value as isolating mechanisms.

It has been known to all students of African birds that a number of species of the genus *Indicator* are very similar in plumage coloration and differ chiefly in size. Chapin's discovery (1958) of the smallest of the group, *I. pumilio*, served to call further attention to the situation, and a few years later (1962) he published a useful review and commentary on *I. pumilio*, *I. exilis*, *I. willcocksii*, and *I. meliphilus*. He could, actually, have included *I. minor* as well, as the size difference between it and the largest race of *exilis* and of *meliphilus* is quite small. Aside from the discovery of *pumilio*, the most important clarification was the elucidation of the status of *willcocksii* as a species distinct from, and sympatric with, *exilis*.

One cannot help but wonder at the delicacy of the isolating mechanisms required to keep apart such closely similar organisms as *exilis*, *willcocksii* and *pumilio*, and, on the other hand, one cannot refrain from searching for possible additional differences between them. It is with the latter aspect of the situation that I here put on record some new morphological data.

Through the generosity of Dr. Chapin I have recently been given alcoholic bodies of a female *exilis* and of a female *pumilio*. The soft parts revealed nothing, but the cleaned trunk skeletons did show some differences; greater differences, in fact, than I had anticipated in two such very similar species. The accompanying sketches, kindly made for me by Mary Butler, staff illustrator of the Los Angeles County Museum, illustrate the points of difference.

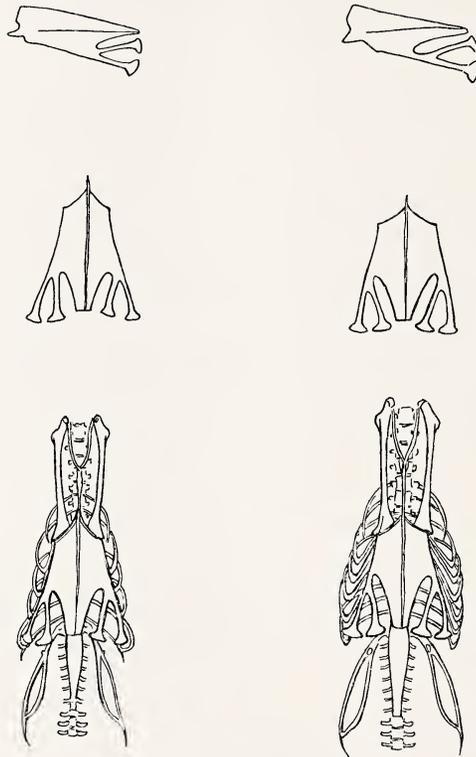
I. pumilio, besides being slightly smaller, as was already known from the original description, has the sternal notches, between the processus lateralis posterior and the processus intermedius and the metasternum somewhat shallower, less deeply incised, than in *I. exilis*. The coracoids and the clavicles are slightly shorter in *pumilio* than in *exilis* relative to the length of the sternum, and the entire body, as shown by the lateral curvature of the rib structure, is definitely more compressed in *pumilio* than in *exilis*. The two agree in the degree of development of the sternal keel, as indeed do all the African species of *Indicator*. The Himalayan *I. xanthonotus* has a lesser, more depressed keel,

¹Director, Los Angeles County Museum.

approaching that of *Melichneutes*, as I have shown elsewhere (Friedmann, 1955, pp. 11-12). Both *exilis* and *pumilio* agree very closely in the configuration and dimensions of their synsacral elements. In the illustration the species are drawn to the same size to emphasize the differences mentioned above.

It would have been particularly pertinent and appropriate to include comparisons with the body skeleton of *I. willcocksii*, but no museum seems to have any preserved anatomical material of that species.

While the differences here pointed out are real, if minor, they are obviously not such as could conceivably play any role as isolating mechanisms in the lives of the birds. They are of interest in suggesting that in the process of speciation in the small species of *Indicator* the already existing plumage mode was relatively unaffected while small internal changes were developed. What enabled these slightly divergent species to remain distinct must have been ethological rather than morphological characters. The smaller, stubbier bill



Left figures *Indicator pumilio*; right figures *Indicator exilis pachyrhynchus*.

Top row, sternum, lateral view.

Middle row, sternum, ventral view.

Bottom row, body skeleton, ventral view.

of *pumilio* and the absence of dark malar streaks in its adult plumage may, of course, be more apparent to the birds than to human observers. The relative importance of ethological characters seems always to be greater in sibling species than in morphologically diverse ones. Yet Chapin found *I. pumilio* and *I. exilis pachyrhynchus* in the same localities, even coming to feed on the exposed comb at the same wild beehives. In his experience at Tshibati, he found both species to be silent, so it was not possible to distinguish them by sound, and he found it difficult to tell them apart in life with a field glass, since the dusky malar stripe of adult *exilis* is lacking in the young of that species causing them to resemble adult or young *pumilio*. He noted little, if any, difference in behavior between the two.

Furthermore, as Chapin has pointed out, it seems most unlikely that *pumilio* would, or has a chance to, interbreed with *willcocksii*, as the former is a highland species and the latter a lowland one, although Prigogine secured examples of the latter at Kamituga, showing that it ranges eastward to the base of the mountains in the Kivu district, as well as to the Semliki Valley, a little farther north.

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EVIDENCE OF AESTIVATING LUNGFISH FROM THE
SANGRE DE CRISTO FORMATION, LOWER PERMIAN
OF NORTHERN NEW MEXICO

By PETER PAUL VAUGHN



Los Angeles County Museum • Exposition Park • Los Angeles 7, Calif.

EVIDENCE OF AESTIVATING LUNGFISH FROM THE SANGRE DE CRISTO FORMATION, LOWER PERMIAN OF NORTHERN NEW MEXICO¹

By PETER PAUL VAUGHN²

ABSTRACT: Cylinders that resemble the natural casts of lungfish burrows known from the lower Permian of Texas have been found high in the Sangre de Cristo formation of northern New Mexico. This is the first evidence for the existence of lungfish in the late Paleozoic of the Four Corners area, and it provides an excellent indication of conditions of seasonal drought. The Sangre de Cristo burrows were probably formed earlier in the Permian than were those in Texas. This fits in with other evidence to indicate that arid conditions of the early Permian of western North America set in earlier in the Four Corners area than in the Midcontinent.

INTRODUCTION

One of the most interesting paleontological discoveries in recent years was announced by Romer and Olson (1954), when they described natural casts of lungfish burrows found in lower Permian sediments of northcentral Texas. These burrows were found at two localities in the Clear Fork group, one in the Arroyo formation and one in the overlying Vale formation.

Tooth plates from the burrows in the Vale formation indicate that the burrows were made by the lungfish *Gnathorhiza dikeloda*. The similarity of the burrows in both formations indicate that they were probably made by the same species, but this is not certain; no tooth plates have been recovered from the Arroyo burrows, and the only species of lungfish known from the Arroyo is *G. serrata*—both species are known from the Vale. However, as Romer and Olson (1954:5) point out, "lungfish remains are exceedingly rare in the Arroyo; only four or five occurrences have been reported, and these have consisted of single teeth. It may well be that *G. dikeloda* was in existence during the Arroyo times, but that it found suitable habitat in few localities in the areas which are now exposed. With increasing aridity during the Vale, the number of habitats and the chance of discovery probably were greatly increased." At both the Arroyo and Vale localities, lungfish remains are found in only a small fraction of the burrows, but this is only to be expected for, as Romer and Olson (1954:5) say, probably "most of the fishes which occupied them survived to the return of the waters and swam away." Remains

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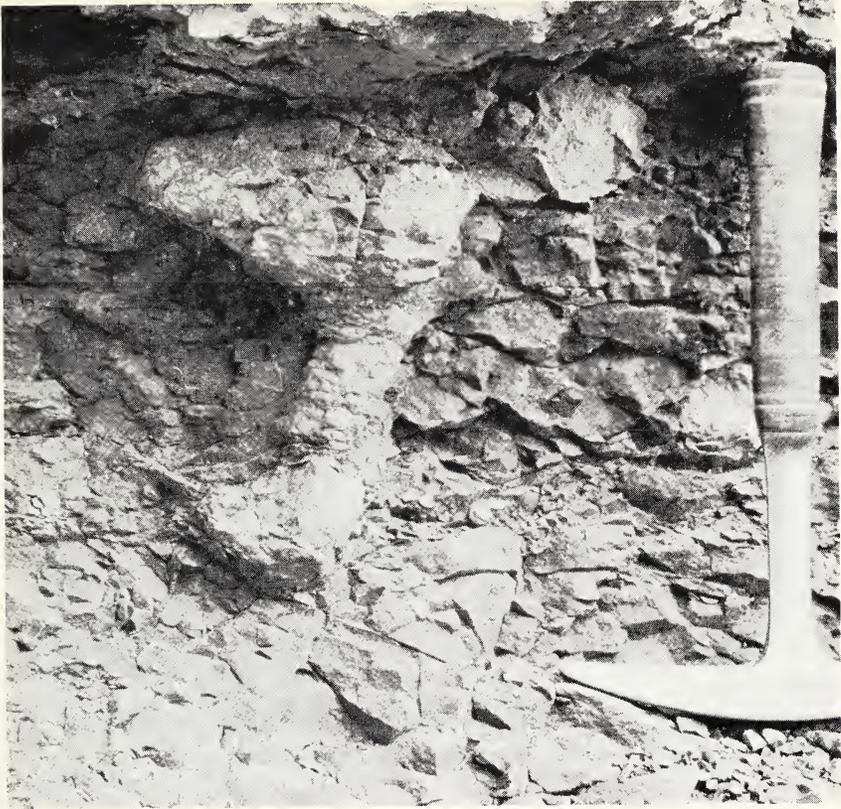


Figure 1. A natural cast of a lungfish burrow in the Sangre de Cristo formation. The surrounding matrix has been partially removed. The upper, dilated end of the cylinder is not as distinct from the surrounding matrix as are the middle and lower parts. The hammer is 32 cm. long.

of other animals besides lungfish are found in some of the burrows; these include small palaeoniscoid fishes and the small amphibian *Lysorophus*. This is probably due, as Romer and Olson (1954:5) explain, to these animals' "presence . . . in the returning waters before the burrows had been filled by sediments!"

Besides the obvious and important fact that we now know with certainty that lungfish were aestivating at least as long ago as the early Permian, this discovery sheds light on other areas too. It supports Olson's (1958) evidence for increasing aridity during the time of deposition of the Clear Fork group, and it highlights an interesting ecological succession. The sediments and fauna of the underlying Wichita group indicate somewhat moister conditions (Romer, 1958). The Wichita fauna includes the lungfish genus *Sagenodus*,

for which there is no evidence of aestivation and whose tooth plates resemble, in a general way, those of the living, non-aestivating Australian lungfish, *Neoceratodus*. The succession, *Sagenodus* to *Gnathorhiza*, would seem to be, as Romer and Olson (1954) believe, a genuine ecological replacement in response to decreasing moisture. There is no reason to believe that this is a phylogenetic succession; both *Sagenodus* and *Gnathorhiza* are known from the Pennsylvanian (Romer and Smith, 1934). Romer and Olson feel that the evidence of an aestivating habit for *Gnathorhiza* reinforces their earlier ideas of relationship of this genus to the living, aestivating African and South American lungfish, *Protopterus* and *Lepidosiren*. In addition to the insights into early lungfish habits and relationships afforded by this discovery, we now have an excellent fossil indicator of past conditions of seasonal drought and, further, we have a new means whereby the presence of lungfish can be established for horizons and geographic areas from which they have been previously unknown.

BURROWS IN THE SANGRE DE CRISTO FORMATION

To date, no remains of lungfish of any kind have been reported from Pennsylvanian or Permian sediments west of northcentral Texas, despite the fairly extensive list of other vertebrates found in lower Permian sediments of the Four Corners area.

In the summer of 1963, a field party from the University of California, Los Angeles, found objects in the Sangre de Cristo formation of northern New Mexico that resemble the natural casts of the Texas lungfish burrows so closely that they must surely represent the work of similar fish. The locality lies alongside the Pecos River in San Miguel County, shortly south of the village of Pueblo, almost immediately on the east side of the bridge where New Mexico State Highway 3 crosses the river. The burrows occur in sediments at the base of a cliff on the north side of the road. This locality may be reached by driving south through the town of Ribera from U.S. Highway 84-85. The Pecos River has exposed a large swath of the Sangre de Cristo formation in this region, permitting a gradual ascent of the formation through a horizontal distance of about ten miles from Northwest to Southeast (see geologic map by Bachman and Dane, 1962). The burrows occur less than a mile northwest of the contact of the Sangre de Cristo formation with the overlying Meseta Blanca Sandstone member of the Yeso formation, that is to say, the burrows occur near the top of the Sangre de Cristo formation. Remains of amphibians, reptiles and plants were found lower in the section in this region; these will be described at a later time.

The burrows, or, rather, the casts of burrows, occur in a red, silty mudstone beneath a stream channel lens that consists of fine conglomerates and shales. As in a specimen from the Vale formation at hand, the mudstone is cut at acute angles by parting planes with gently undulating surfaces. There are many burrows, packed closely together as in the Texas occurrences, with

distances of from three to twelve inches between them. Most of the burrows are vertical, but some are on slight slants, and in a few the lower ends are bent toward the horizontal. The burrows reach upward to the bottom of the stream channel lens. Typically, the upper end of a burrow is dilated and poorly defined, and the lower end is somewhat swollen; the cross section is circular, or nearly so. As in the specimens from Texas, the cylinders are composed of a harder material than the surrounding matrix and are easily divided horizontally into "checkers" of varying thickness. The cylinders are slightly lighter in color than the surrounding matrix and contain fewer and smaller reduction spheres. Usually, there is a greenish-gray central core that may have a diameter as much as one-third that of the whole cylinder; this core runs almost to the lower end of the cylinder. The cylinder shown in the photograph (Fig. 1) is about 23 cm. long and is about 4.5 cm. in diameter halfway down its length; some are larger, with diameters as great as 6.5 cm. About ten to fifteen yards to the South of the photographed burrow, cylinders can still be made out at the same level, but they are less distinct from the surrounding matrix, and the overlying stream channel sediments are finer.

No bones or traces of bones have been found in the burrows, even though several dozen cylinders were taken apart. But, it must be remembered that even in the Texas occurrences most of the cylinders are empty. One possible explanation of the difference would be that conditions at the Sangre de Cristo locality were not favorable for the preservation of bone, but a much more likely explanation is that the Sangre de Cristo lungfish were more successful in survival to the return of the waters—at least at this locality and in the season represented. Smith (1931:180) says of the living African lungfish, *Protopterus aethiopicus*, that "Estivating fish are known to survive for 18 months and estimates based upon metabolism indicate that they may survive much longer periods." In view of such hardiness, we may suspect that the Texas fossils represent calamities: perhaps the fish in their burrows were covered too rapidly by sediments in the returning waters, and many were not able to emerge; or perhaps the waters were delayed in returning—by a prolonged dry season or by a change in stream pattern—and the percentage of mortality was thereby increased. The burrows in New Mexico are too similar to those in Texas not to be attributed to the work of lungfish. That no skeletal parts of lungfish have as yet been found anywhere in the upper Paleozoic of New Mexico does not seem to be strong evidence that these fish were not there when it is remembered that remains of lungfish are exceedingly rare even in the Arroyo formation of Texas.

In none of the Texas cylinders has an upper termination been definitely made out, but the greatest lengths known are, at the Arroyo locality, 28 cm., and at the Vale locality, 45 cm. Some of the Sangre de Cristo burrows equal in length the longest reported from the Arroyo, but none even approach the length of the longest from the Vale. Comparison of sizes is most conveniently made on the basis of diameter. The Texas cylinders range from about 5.5 to

10 cm. in diameter. The Sangre de Cristo cylinders range in diameter from about 4.5 to 6.5 cm., and it would seem from this that they are definitely smaller than those from Texas. There are also some differences in orientation and shape. The cylinders in Texas are all vertical, whereas some of the Sangre de Cristo cylinders are slightly slanted and in some the lower portion is bent toward the horizontal. Also, the Sangre de Cristo cylinders are usually swollen at their lower ends, whereas, according to Romer and Olson (1954:6) although some of the Texas "burrows may be somewhat narrower in their upper portions; they are, however, essentially cylinders rather than 'flasks.'" Actually, the Sangre de Cristo burrows are more like those of living lungfish than are those from Texas. Possibly, the smaller size of the burrows from New Mexico as compared with those from Texas is indicative of an earlier, more primitive stage of development.

AGE OF THE SANGRE DE CRISTO BURROWS

The Sangre de Cristo formation was deposited in the zeugogeosyncline between the late Paleozoic San Luis-Uncompahgre highland to the West and the late Paleozoic Front Range and Sierra Grande uplifts to the East (see Hills, 1963). Brill (1952:827) says, "In the zeugogeosyncline, where faunal evidence is lacking, the Virgil-Wolfcamp contact is drawn arbitrarily in the Sangre de Cristo formation. The upper Sangre de Cristo formation in the southern part of the trough is equivalent to the Abo formation, which is Wolfcampian. In the Pecos region [near the burrow locality], the Sangre de Cristo formation is underlain by Virgil rocks and overlain by the Yeso formation of Leonardian age." This determination of a Wolfcampian (earliest Permian) age for the upper part of the Sangre de Cristo formation receives corroboration from Baars' (1962) correlation of the Meseta Blanca Sandstone member of the Yeso formation with the De Chelly Sandstone, of Leonardian age. From this stratigraphic evidence, the New Mexico burrows, which lie near the top of the Sangre de Cristo formation, would seem to be Wolfcampian in age.

The Texas burrows are in the Clear Fork group, which is Leonardian (later early Permian) in age (see Dunbar, *et. al.*, 1960), and they are, thus, younger than the burrows in New Mexico. The horizon of the Sangre de Cristo burrows is equivalent to some horizon in the Wichita group of Texas, which is Wolfcampian in age. There is no sign of aestivating lungfish in the Wichita group, and, as noted earlier, Wichita conditions would seem to have been generally moister than Clear Fork conditions. The evidence of aestivating lungfish, and the consequent indication of conditions of seasonal drought, in the Wolfcampian of New Mexico would therefore fit in nicely with other evidence, presented elsewhere, for an earlier onset of arid conditions in the Four Corners area than in northcentral Texas (see Romer, 1960; Vaughn, *In press*).

ADDITIONAL PALEOGEOGRAPHIC CONSIDERATIONS

As far as it is known, the early Permian vertebrate fauna of New Mexico, and of the Four Corners area in general, is basically like that of the Mid-continent, but there are differences, mostly at the specific level but some at the generic level, and there are differences in relative abundance of groups (Romer, 1960). Recent study of faunas from southeastern Utah (Vaughn, 1962; *In press*) has shown that some of the supposed differences do not really exist, but significant contrasts remain, due probably, as Romer (1960) thinks, to differences in climate and to the presence of some kind of barrier, possibly a seaway. The evidence for the presence of lungfish in the early Permian of New Mexico is not surprising, but it does add to the picture of the basic similarity of Four Corners and Midcontinent faunas.

It must be noted that the Sangre de Cristo burrows occur on the eastern side of the late Paleozoic San Luis-Uncompahgre highland and Pedernal massif, whereas the classic lower Permian vertebrate localities in New Mexico lie on the western side, in the Abo and Cutler formations. There is no evidence of lungfish from the Abo and Cutler formations, but this is not sufficient reason to assume that they did not occur in those areas of deposition. As a matter of fact, the site of the Sangre de Cristo burrows lay not far to the East of a fairly wide "pass" between the San Luis-Uncompahgre highland and the Pedernal massif (see Hills, 1963: fig. 5); it would be presumptuous without much more data to assume that this "pass" was high enough throughout the early Permian to prevent the passage of lungfish westward. As shown by the scarcity of their remains in the Arroyo formation of Texas, preservation of lungfish seems to have been a rare event, and preservation of their burrows must have required exceptional conditions.

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THE ROLE OF OLFACTION IN FOOD LOCATION BY
THE TURKEY VULTURE (*CATHARTES AURA*)

By KENNETH E. STAGER



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THE ROLE OF OLFACTION IN FOOD LOCATION BY THE TURKEY VULTURE (*CATHARTES AURA*)¹

By KENNETH E. STAGER²

ABSTRACT: An experimental approach to the problem of the olfactory ability of the turkey vulture, correlated with morphological studies, has provided evidence of a well-developed sense of smell in this species.

Information is presented concerning the ethology of cathartine vultures. The flight, food-locating habits, agonistic and predatory behavior of the five cathartine vultures are compared. The king vulture (*Sarcoramphus*) of tropical America, although its behavior is poorly known, appears, on the basis of present ethological and morphological data, also to utilize olfaction in its location of food. The need for a detailed study of the food-locating habits of *Sarcoramphus* is thus indicated. There is no evidence, either ethological or morphological, to indicate that olfaction plays more than a minor role, if any, in food location by *Coragyps*, *Gymnogyps*, and *Vultur*. There likewise are no data to indicate that the Old World vultures employ any sense other than vision in the location of food.

INTRODUCTION

The subject of olfactory ability in vultures has been commented upon since the time of Aristotle and Pliny ((Soudek, 1927) and debated pro and con by zoologists in general and by ornithologists in particular since 1826 (Audubon, 1826).

The degree of olfactory acuity possessed by any particular group of animals is a most difficult subject to investigate. Compared with our knowledge of the visual and auditory senses of animals, we know practically nothing with respect to the sense of olfaction. The subjective nature of olfaction makes it one of the most difficult of the senses to measure in terms of degree or nervous response.

Compared with the demonstrated macrosmatism of certain insects and mammals, it can be safely stated that the Class Aves on the whole is microsomatic, but to accept the belief that birds are anosmatic is comparable to arguing that the Class Mammalia is incapable of flight, thus ignoring the highly specialized mammalian Order Chiroptera.

The question of olfactory ability among vultures, or the lack thereof, has been complicated by the tendency of early investigators to apply a too generalized interpretation to their findings, both for and against, and their failure to realize that they were dealing with two entirely different kinds of vultures. In the past there has been a tendency for investigators of the be-

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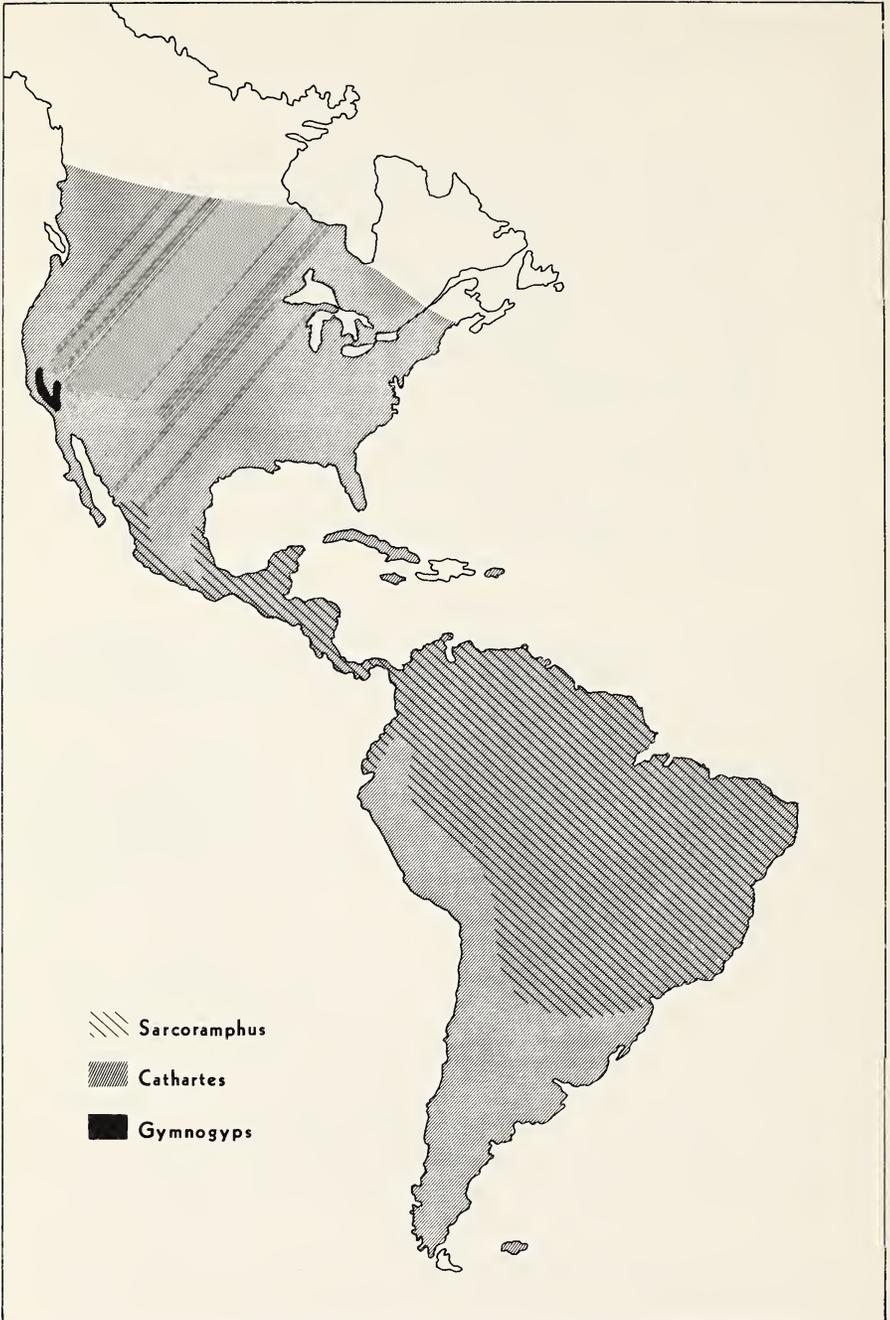


Figure 1. Geographical distribution of *Cathartes*, *Gymnogyps*, and *Sarcoramphus*.



Figure 2. Geographical distribution of *Coragyps* and *Vultur*.

havior of aegyptine vultures of the Old World to include the cathartine vultures of the New World in their conclusions. The inverse mistake has been made by students of cathartine vulture behavior in the interpretation of their data. The resultant confusion has greatly delayed the solution of the entire problem.

The purpose of this study is to place the problem of olfaction in vultures in its correct perspective and to consider morphological and behavioral evidence to determine if there are, within the family Cathartidae, certain genera that possess and utilize a well-developed sense of smell.

A. THE CATHARTINE VULTURES

The Suborder Cathartae includes but one living family, the Cathartidae, although it contains two monotypic extinct families, the Teratornithidae and the Neocathartidae. The living family Cathartidae, commonly referred to as the New World vultures and sometimes known as the pseudo-vultures, resembles superficially the true vultures, or Old World vultures of the Suborder Falcones. The differences between the two groups, however, are profound. The internal structure of the two involves differences not only in the skeletal framework, but also in the musculature and other portions of the soft anatomy as well. As pointed out by Friedmann (1950:6), the general resemblance is adaptive, as both groups perform the same service as scavengers in the niche they inhabit.

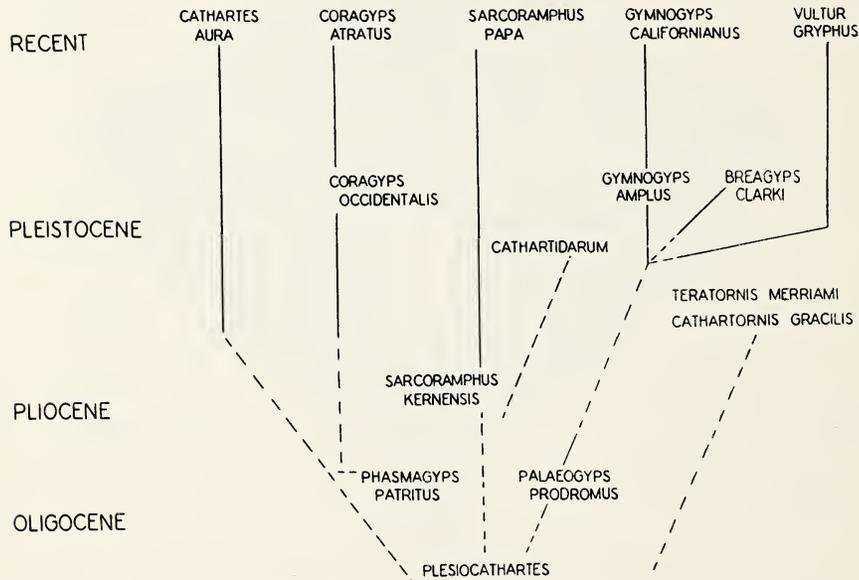


Figure 3. Phylogenetic tree showing possible relationships of cathartine vultures. After Fisher, 1944.

The family Cathartidae is restricted to North and South America and certain adjacent islands. The family comprises five living genera: the turkey vulture (*Cathartes*); the black vulture (*Coragyps*); the king or royal vulture (*Sarcoramphus*); the Andean condor (*Vultur*); and the nearly extinct California condor (*Gymnogyps*). All references in this work to the genus *Cathartes* refer to the species *Cathartes aura* and do not include the small, and little-known, yellow-headed vulture *Cathartes burrovianus*.

B. PALEONTOLOGICAL RECORD

The earliest known representative of the cathartine line in North America is *Neocathartes*, a long-legged vulture of the Upper Eocene (Wetmore, 1956). At the same time a similar vulture (*Plesiocathartes*) appeared in France. *Plesiocathartes* was indistinguishable from the cathartids and continued into the Lower Oligocene. During this time the family Cathartidae was becoming established in North America, being represented by two genera, *Paleogyps* and *Phasmagyps*. There is an absence of records of Miocene vultures throughout the world, but according to Howard (1950:12), the cathartine vultures are restricted to the New World from the Pliocene on. All cathartine genera of the Pliocene and Pleistocene are represented by living forms today except for the large condor-like vulture, *Breagyps*, which is known only from the late Pleistocene of California and Nevada. Ancestral relationships of the Cathartidae are best shown by Fisher (1944:294), who presented them in the form of a phylogenetic tree (Fig. 3). The rise and decline of cathartine species in North America is well shown by Miller (1942:212), in his diagram indicating abundance and the geologic history of the family (Fig. 4).

C. HISTORICAL REVIEW

The literature pertaining to olfaction in birds is relatively sparse before 1834. References to the sense of smell in vultures consist chiefly of scattered notes relative to the remarkable powers of scent possessed by all vultures.

In 1826, however, John James Audubon, appearing before the Natural History Society of Edinburgh, read his classic paper (Audubon, 1826) entitled: "Account of the Habits of the Turkey Buzzard (*Vultur aura*), particularly with the view of exploding the opinion generally entertained of its extraordinary power of smelling." Audubon was of the firm opinion that vultures lacked a sense of smell and that they relied solely upon remarkable vision as a means of locating their food. To substantiate his argument, Audubon conducted a number of poorly contrived experiments which in reality tended to test the visual acuity of vultures rather than their possible olfactory ability.

The experiments of Audubon (1826) were supposedly conducted with the turkey vulture, but a critical examination of his remarks reveals that he was concerned chiefly with the actions of the black vulture (*Coragyps*), rather than the turkey vulture. The aggressive behavior of the birds used in

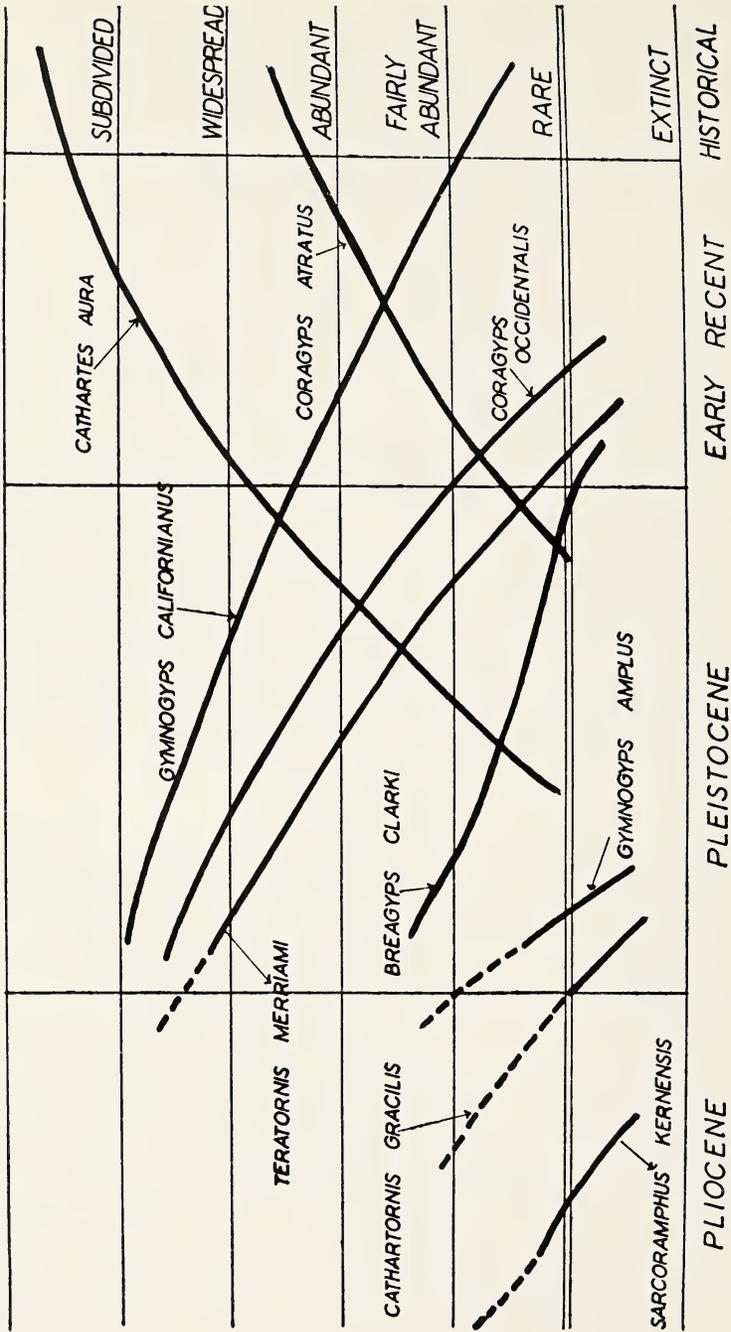


Figure 4. Diagram showing abundance and geologic history of cathartine vultures. After Miller, 1942.

his experiments are typical of *Coragyps*, and in sharp contrast to the shyness so characteristic of *Cathartes*. Although Audubon believed that his experiments had conclusively settled the question of olfaction in vultures, he was soon to learn that his paper had initiated an argument among ornithologists—an argument that is still alive today. As criticism of the Audubon experiments mounted, a friend of Audubon, John Bachman, came to his rescue. Bachman (1834) repeated the experiments of Audubon in the presence of a learned group of citizens. These observers then signed a document to the effect that they had witnessed the tests and were thoroughly convinced that the vulture lacked a sense of smell and was attracted to its prey entirely by vision. The Bachman experiments also failed to quiet the critics of Audubon, the most vigorous of whom was a Mr. Charles Waterton (1830; 1832; 1833; 1834; and 1870). In his efforts to discredit Audubon, however, Waterton made several misleading statements and presented arguments as confusing as those of his opponents.

Since Audubon's time there has accumulated a rather extensive amount of literature on the olfactory ability of birds in general and vultures in particular. Most of the early literature is anecdotal, being sight observations of vultures in the wild, supported at best with simple uncontrolled tests.

Gurney (1922) was the first student of avian olfaction to indicate that the cathartine vultures of the New World were unrelated to the aegyptine vultures of the Old World and that the two groups should be studied independently. There are numerous observations on the lack of olfactory ability among the vultures of the Old World (Adams, 1858; Chapman, 1921; Dresser, 1875; Hadfield, 1875; Hill, 1905; Hunter, 1883; Hutton, 1837; Kirk, 1864; Lilford, 1893; Macgillivray, 1837; Meinertzhagen, 1959; Soudek, 1927; and Stewart, 1959). It is interesting to note, however, that all of these references pertain to casual or accidental observations on the behavior of Old World vultures and do not involve any controlled experimentation.

A review of the literature concerned with observations on the behavior of cathartine vultures reveals that, in spite of the negative findings of Audubon (1826) and Bachman (1834), the observations are singularly balanced in the affirmative for a sense of smell, especially as they apply to observations on the turkey vulture (*Cathartes aura*). Observations indicative of a sense of smell and worthy of mention are those of Bent (1937); Bishop (1921); Dickey and van Rossem (1938); Earl (1929); Forbush (1927); Gill (1904); Gosse (1847); Grinnell (1913); Hall (1925); Hopkins (1887); Howell (1932); Lewis (1928); Rhoads (1883); Sayles (1887); Schomburgk (1839); Sells (1837); Taylor (1923); and Williams (1922). Observers who were of the opinion that cathartine vultures lacked a sense of smell are as follows: Audubon (1826); Bachman (1834); Barrows (1887); Bedichek (1960); Housse (1949); Hoxie (1887); Lehmann (1940); and Leighton (1928).

Charles Darwin (1841), while in Valparaiso, Chile, during the cruise of H.M.S. *Beagle*, made a crude olfactory experiment with captive Andean condors (*Vultur gryphus*) that left him believing that this species lacked a

sense of smell. At the same time, however, he stated his belief that the turkey vulture has a sense of smell.

Various observers have presented ideas for the purpose of explaining the ability of turkey vultures to find hidden baits by means other than a sense of smell. One hypothesis widely quoted in the literature and attributed to Darlington (1930) suggests that the turkey vulture locates hidden food by hearing the buzzing of flies and other necrophagous insects, and that they may then observe the concentration of these insects about a hidden item of food and thereby detect its location. The hypothesis should be attributed to Taber (1928) rather than to Darlington, however, as it was he who first proposed it. Taber also expressed the opinion that the turkey vulture may observe the movements of carrion-eating mice and ground squirrels to and from a hidden carcass and, "having perceived these signs, the vulture through long experience *knows* [my italics] that this means food." Here, too, is an interesting hypothesis, but with no evidence to support it. Lehmann (1940) was of the opinion that turkey vultures sit about watching the movements of domestic dogs in the forested areas. The dogs, with their keen sense of smell, locate the hidden carrion and thus disclose its location to the keen-eyed vultures.

Not willing to accept the senses of smell, vision or hearing as the means whereby the turkey vulture locates its hidden food, Beck (1920) proposed the presence of a fourth sense that he termed the occult sense, or food-finding sense. Beck never quite describes this food-finding power but sums up his discussion of this illusive fourth sense by stating:

Unfortunately, research on these occult senses is difficult—often impossible. Theories have to be based upon analogies and chance observations. Under these conditions chance observation must assume a somewhat greater significance than ordinarily is placed upon it.

Another hypothesis is that proposed by McKechnie (1923) in which he suggested that the true purpose of well-developed olfactory tracts in soaring birds, such as the turkey vulture and the albatross, may be for the purpose of detecting the direction and quality of air currents rather than for the detection of food. McKechnie offered no evidence to support this idea but suggested the need for experiments to determine the validity of the hypothesis.

An olfactory experiment performed by Hill (1905) is of interest because of the rather startling results obtained and the wholly unwarranted conclusions given. Placing a domestic turkey in an enclosure, the investigator first subjected it to the fumes of carbide and water, followed by carbon bisulphide and then a sponge soaked in chloroform. His final test was to place a saucer filled with hot dilute sulphuric acid in the enclosure with the turkey. To the saucer of acid he then added one ounce of potassium cyanide. The reaction resulting in prussic acid became so violent that the experimenter considered the neighborhood unsafe. The turkey became violently ill and died. From this test the author concluded that birds cannot smell.

During the 136 years that have elapsed since Audubon stirred up the controversy over the presence or absence of a sense of smell in New World vultures, it is most surprising to find that very little actual study has been made of the behavior of the turkey vulture and the role played by olfaction in its economy. Beebe (1909) conducted experiments with captive turkey and black vultures in the New York Zoological Gardens. Negative responses were obtained from the black vultures, but the turkey vultures readily located the hidden but odoriferous bait. The experiment was not repeated, nor was it properly controlled.

Strong (1911) attempted some simple experiments to test the olfactory acuity of the turkey vulture, using meat wrapped in paper. His results were negative, and he believed that the conditions of his experiments did not warrant the conclusion that the meat was not smelled by the turkey vulture.

In Panama, Chapman (1929) conducted a number of experiments with non-captive turkey vultures and obtained very positive responses showing olfactory prowess. He failed to carry his tests to a desired conclusion, however; and he never had an opportunity to resume the tests.

Coles (1938), in an unpublished doctoral thesis, gave a good review of earlier experimentation with the turkey vulture, and then described the experimentation he undertook to further test the olfactory acuity of this species. Using captive turkey vultures, Coles contrived a number of different tests that he hoped might settle the question of olfaction. His first test consisted of placing leather hoods over the heads of the captive birds to prevent vision but still allow freedom of the nostrils and mouth. After being conditioned without food for thirty-six hours, the birds were introduced into a pen containing a pan of decomposed meat. The birds never succeeded in locating the meat or subsequent samples of strong chemicals. Instead of acting normally, the hooded birds crouched with heads down or walked in ever-decreasing smaller circles. From this behavior the writer decided that the test techniques were too foreign to the normal environmental conditions of the vulture to be of value and the experiment was terminated.

The second experiment consisted of placing two crocks of fresh water in the cage with the vultures after the birds had been fed heavily salted food and denied drinking water for forty-eight hours. One crock was treated with concentrated ammonia that, according to the author, filled the entire room with strong fumes. With this condition prevailing, the vultures were still expected to be able to distinguish, through olfaction, the crock that was free of ammonia. Negative results were reported for this experiment, as the birds showed no discrimination and drank readily from the ammonia filled crock.

The third experiment performed by Coles was of a multiple-choice type. The captive vultures were conditioned to eat out of three metal containers, each of which had a removable metal collar that hid the contents from view. The vultures soon learned to open the containers and obtain the food contained therein. The test was accomplished by placing food in one of the three con-

tainers, placing the containers in the experimental pen and then introducing the hungry vultures. Coles found that the vultures would investigate each container, but opened only the one containing the hidden food. Trials of this type were repeated a sufficient number of times to provide valid data regarding the possession of a sense of smell by turkey vultures.

The fourth experiment performed by Coles was designed to test olfactory sense perception within a given area. For this test, a 6-foot square, wooden frame was placed on the floor of the vulture cage. The frame was covered with paper, with poultry wire above the paper so that the vultures could walk upon it without breaking through the paper. A pan of meat could then be placed under the frame at any point of the 36-square-foot grid. It was hoped by the investigator that the vultures would be able to detect the exact point on the grid where the meat pan had been hidden. Only negative results were obtained as the vultures were unable to locate the pan.

The latter experiment described above was the last of the series performed by Coles, and from the results of all of his tests he concluded that the turkey vulture possesses a sense of smell, but that it is of limited use and secondary to the well-developed sense of vision possessed by the species.

Owre and Northington (1961) have recently published on a series of controlled feeding experiments performed by them on captive turkey vultures in Florida. Two captive birds were used in the feeding trials. Each of the vultures was presented with leaf-filled pans, one of which contained meat concealed from view. The pans were presented to the birds in the open, concealed from direct view behind screens, or concealed in boxes with single openings. In each of the experiments, pans containing food were selected first a significant number of times. Evidence of olfactory acuity is thus believed afforded. Owre and Northington concluded that the interpretation of their results suggests that smell may be of a degree of importance varying with the situation confronting the birds. They also found that the vultures showed a preference for freshly-killed chicks over other types of fresh and decaying food.

The literature bearing upon the sense of smell and olfactory organs of birds in general is too exhaustive to treat in this survey, and is best summarized in a few key papers: Raspail (1899); Strong (1911); Gurney (1922); Soudek (1927); Ishihara (1932); Technau (1936); Walter (1943); and Pumphrey (1948).

D. EARLY PERSONAL OBSERVATIONS

My observations on food location by turkey vultures began in the summer of 1935. While conducting field work in the lower Colorado River valley of eastern Riverside County, California, an opportunity presented itself which enabled me to conduct a simple experiment involving the turkey vultures of that desert area. On this occasion the skinned carcass of a badger (*Taxidea taxus*) was carefully concealed in the heart of a thick-foliaged creosote bush (*Larrea*) on the flat desert floor, one mile west of the river valley proper. The

carcass was securely wrapped in newspapers and placed in the bush just after dawn. A close watch was kept on the bait site throughout the day. In the afternoon of the second day a lone turkey vulture was observed circling in the area where the bait was concealed. A gentle wind was blowing from the west and the vulture sailed around the bait site in decreasing circles until a landing was made approximately thirty feet up-wind of the bait-containing bush. The vulture walked back and forth in the up-wind area for several moments, launched itself into the air again and resumed circling the bait site. After completing a series of low-level circles about the bush, the vulture once more landed on the ground, some thirty feet from the bait, but on this occasion the landing was made directly down-wind of the bush. After a short inspection of the area, the vulture walked directly up-wind toward the bait and, with its beak, pulled the paper-wrapped carcass from the center of the creosote bush. The paper was torn from the carcass with little effort and feeding on the badger commenced. This experiment was only partially controlled, in that the package was partially visible from a point above and to the side of the bush. Visual stimulus cannot, therefore, be ruled out completely, but the actions of the vulture appeared to be based on an olfactory cue.

The second opportunity to observe the food-locator mechanism of turkey vultures was afforded me during the winter of 1946-47. During this period I was engaged in field activities in the tropical hill country of southern Sinaloa, Mexico. Base of operations was the small village of Copala, situated approximately sixty miles east of the seaport city of Mazatlan, on the Mazatlan-Durango highway. The town of Copala harbored a population of domestic pigs which more or less roamed at large. During my stay in Copala, I witnessed the outbreak of a devastating epizootic among the pig population that killed approximately 90 percent of all the pigs in the village. The putrifying carcasses of pigs were encountered everywhere in the vicinity of Copala and the stench was most unpleasant.

Black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) were always to be found in the area in normal numbers, but with the outbreak of the epizootic among the pigs, the concentration of vultures increased to several hundred. The ratio of black vultures to turkey vultures was approximately ten to one.

During this period of vulture concentration in the Copala area I had occasion to set a number of steel traps for the collection of small carnivores. The first set was made in a dark cavity under a debris-covered log in the bottom of a dry stream course. The bait, consisting of several skinned bird bodies, was placed far back in the dark cavity, completely out of sight when viewed from any angle. On the morning of the second day an adult turkey vulture was found caught in the steel trap which had been set in the entrance to the bait cavity. Even though caught in the trap, the bird had devoured the bait. To explain this behavior on the grounds that it was vision that had led the vulture to the bait is far too simple an approach. While it is true that no con-

clusions could be made on the basis of this one incident, the behavior of other turkey vultures on subsequent days gave ample evidence that a sense other than vision was being utilized in food location.

A supply of fresh fish was obtained from the seacoast and ground into a thick, oily paste for use as bait for further carnivore trapping. The fish paste was allowed to age for a period of days and during that time blow flies managed to get to it to deposit eggs, with a subsequent hatching of larvae. As a result the fish paste became putrified and developed an odor so foul that it was difficult to work near it. The decomposed mass took on the consistency of cream with a grayish-brown color.

A number of steel traps were baited with this foul-smelling paste. This was accomplished by smearing a small amount on the rock surface at the back of a cairn of rocks, piled so as to compel the animal to step into the steel trap at the entrance before it could reach the bait. The paste was of ground color and invisible when viewed from directly in front of the rock cavity. Although invisible, the fish paste gave off a decidedly putrid odor that could be detected even by the human nose at a distance of several yards. In an attempt to prevent the traps from being sprung by turkey vultures, all sets were made at night.

During the following days, fourteen turkey vultures were captured in steel traps as they attempted to reach the hidden bait. Although the black vulture (*Coragyps*) outnumbered the turkey vultures approximately ten to one in the trapping area, not one specimen of *Coragyps* was caught by the steel trap sets. Black vultures would be found congregated around the trapped turkey vulture, but were apparently attracted to the site by the flapping of the turkey vulture in its attempt to free itself from the steel trap.

On one occasion a trap set was made in a heavily shaded ravine filled with tropical plant growth. A complete canopy of tree branches shielded the trap area, making it difficult to see even close by at the ground level. The putrid fish paste was smeared at the back of a dark rock cavity as in previous sets. On the following day an adult turkey vulture was found securely caught by the foot. The vegetation was so dense that the vulture could only reach the bait by walking to it from several yards down the ravine. Nothing was visible from above; the set was made at night, and yet the bird had had no difficulty finding the bait even though it could not fly to the site. From these observations it became evident that the subject of olfaction in cathartine vultures would be worthy of further investigation, at least with regard to the turkey vulture *Cathartes*.

My early observations on the food-locating behavior of the turkey vulture, supported by a detailed survey of the literature pertaining to food location by vultures, indicated the need for a careful re-examination of this interesting problem. The paths of investigation I followed and the techniques I used are set forth in the following pages.

E. METHODS

1. Study Area

The study area for this research includes both the Old World and the New. The major portion of the controlled field experimentation has been conducted in Ventura County, California, but additional experimentation and extensive comparative ethology of vultures has been conducted in southeastern California; the States of Sonora and Sinaloa of western Mexico; central Goias, Brazil; the Bolivian Chaco of eastern Bolivia; central India in the State of Madhya Pradesh; and the Myitkyina area of northern Burma.

The major study area in Ventura County, California, was the 1200-acre Cerro Viejo ranch located five miles north of Santa Susana. Cerro Viejo ranch consisted of varied terrain—small open valleys flanked by gently rolling grass covered hills in some portions, which were in contrast to the steep canyons and broken ridges of the higher elevations. The south slopes of the higher hills were covered with *Artemesia*. Dense chaparral (primarily *Sumac* and *Ceanothus*) covered the north exposures. The canyon bottoms were filled with scattered stands of live oak (*Quercus*) and cottonwood (*Populus*). One high pasture area, known as Eagle Nest, was covered with grass and scattered groves of black walnut (*Juglans*).

From April until October the entire area was patrolled by a small population of turkey vultures, estimated at fourteen. The varied terrain of Cerro Viejo ranch proved ideal for experimentation with the forced air unit, the concealed bait chambers and the decoy replacement techniques which are described in detail in this section.

The second major study area in Ventura County was located on the property of the Rancho Sespe in the bottom lands of the Santa Clara river, three miles east of the town of Santa Paula, and approximately nineteen miles west of the Cerro Viejo study area. In this latter area the river bottom land consisted of pasture with stands of cottonwood (*Populus*) and willow (*Salix*) with scattered windbreak rows of *Eucalyptus*. Ethyl mercaptan tests were conducted in this area. The river bottom land of this study area was the feeding area of a colony of turkey vultures numbering approximately thirty, with a known nocturnal roost two miles to the northwest of the test site.

2. Forced Air Unit (Fig. 5)

A four-bladed exhaust fan with a 20-inch diameter was mounted in a horizontal position atop an enclosed frame 30 inches by 30 inches by 45 inches. The fan was driven by a quarter horse-power motor attached directly below. Fitted to the circular lip of the exhaust fan housing was a 7-foot circular stack 18 inches in diameter. A baffle placed in the top portion of the circular stack aided in the upward draft of air above the top of the tower. On one side of the base frame, and near the bottom, there was a hinged door 18 inches high and 24 inches wide. The door consisted of a frame covered with fine mesh window screen and equipped with a spring catch. The door also served as the main air



Figure 5. Forced air unit, showing auxiliary bait chamber attached.

intake vent of the unit. Canisters of odorous baits were placed in the bottom of the chamber and the odors sucked upwards through the powerful fan. Electric power was supplied to the unit from a portable gasoline-driven 1500-watt generator. This unit was generally placed at least 100 yards from the fan unit and connected to it by a heavy-duty rubber insulated cord. The fan unit was completely portable, breaking down into three sub-units. In order to accommodate large baits the size of small deer (*Odocoileus*), bobcats (*Lynx*), dogs and cats, a supplementary chamber 30 inches wide by 48 inches long by 22 inches tall was adapted for attachment to the air-intake door side of the base frame. An air-intake screen the same dimensions as those of the hinged door described above was fitted to the end of the bait chamber at the end opposite the base frame door. The entire chamber was collapsible by means of slotted joints. The top of the chamber overhung the walls 3 inches on all sides.

3. Portable Hidden Bait Chambers

A number of chambers of several sizes were used. The largest and most used unit consisted of a breakdown chamber 5 feet long by 3 feet wide by 10 inches high. The sides and ends were made of perforated pressed fiber board $\frac{3}{8}$ inch thick with perforations one inch apart. The chamber was bottomless with a folding top of unperforated fiber board 6 feet wide and 7 feet long, thus allowing a 6-inch overhang all around. The sides and ends were connected by tongue and groove joints with retaining pins to permit breakdown for easy transport.

A large number of smaller chambers consisting of heavy cardboard packing boxes with perforations on their sides were also used. These small units averaged approximately 2 cubic feet and were used for hidden baits placed in tree foliage, hollow cavities of tree trunks and large, dense-foliaged bushes.

4. Mounted Decoy Deer—Fresh Deer Carcass Replacement

A mounted specimen of a yearling female mule deer (*Odocoileus hemionus*) was employed as a visual decoy in conjunction with substituted fresh carcasses of road-killed yearling female deer supplied by the California Department of Fish and Game.

5. Ethyl Mercaptan—Compressed Air Unit

A dispensing device for ethyl mercaptan (Fig. 6) consisted of using a high pressure compressed air cylinder with a capacity of 90 cubic feet, or 2,000 pounds pressure. The cylinder contained dry (SCUBA type) air and was placed on its side in a wooden cradle for support. A standard oxygen pressure regulator was attached to the cylinder outlet so that the flow of air could be held to a minimum amount. To cut the flow of air to a still smaller quantity, a low pressure gas petcock was attached to the outlet of the regulator. A two-foot length of quarter-inch polyethylene tubing led from the petcock to a two-



Figure 6. Ethyl mercaptan dispensing device, showing compressed air tank attached.

hole rubber stopper in the mouth of a one-gallon canister of ethyl mercaptan. An outlet tube from the second hole of the stopper allowed the highly volatile mercaptan to be dispensed on predetermined wind currents. The air pressure applied to the mercaptan canister helped to force the mercaptan fumes onto the prevailing wind. The unit was compact, completely portable, and could be set up and concealed in vegetation with little effort. It was readily put into operation by attaching the two-way rubber stopper unit to the mercaptan canister and regulating the air flow through the system.

Ethyl mercaptan ($\text{CH}_3\text{CH}_2\text{SH}$), a thioalcohol, is one of a large group of highly volatile organosulfur compounds. It is used as a fuel gas odorant, especially for liquefied petroleum gases. Because of the highly volatile quality and dangerously low flash point (below 0°F .) of ethyl mercaptan, it was thought unwise to dispense it by means of the forced air unit. The gas would have had to pass the electric motor and this would probably have resulted in an explosion within the unit.

6. Hidden Baits—Central India

Tests were conducted with aegyptine vultures in the State of Madhya Pradesh, central India. Baits consisting of large quantities of fresh animal meat were placed on an elevated wooden platform and concealed with thick layers of thatch straw.

7. Anatomical Studies

In order to obtain comparative reproductions of avian brains for illustrating the size of their respective olfactory bulbs, a technique was developed for taking latex rubber casts of cranial cavities. The process consisted of flowing successive coats of liquid latex into the clean cranial cavity. An average of six coats of latex was laid down within the cavity and care was taken to insure that the latex filled all areas in the anterior portion of the brain chamber. Prior to introduction of the latex, care was taken to block off all small foramina with lacquer cement. The cavity was then coated with a wash of medical green soap to prevent bonding of the latex with the walls of the cavity. After the final coat of rubber had dried, the cast was allowed to cure for several days before removal. The thin cast was then collapsed from the walls and withdrawn through the foramen magnum. Powdered talc was dusted into the hollow cast and worked between the exterior surface of the cast and the cranial walls during the removal operation to prevent binding. Once removed, the cast immediately resumed its original shape, thus showing the conformation of the brain and the presence and size of the olfactory bulbs. The thin latex casts were then carefully filled with plaster of Paris, so as to preserve their shape and facilitate handling.

Latex casts were made of all the recent genera of cathartine vultures, namely *Cathartes*, *Coragyps*, *Sarcoramphus*, *Gymnogyps* and *Vultur*, as well as fossil forms from the Pleistocene deposits of Rancho La Brea. Pleistocene

species included are: *Cathartes aura*, *Coragyps occidentalis*, *Gymnogyps amplus*, *Breagyps clarki* and the giant vulture *Teratornis merriami*. Similar casts were obtained of Old World vultures of the following genera: *Sarcogyps*, *Neophron*, *Pseudogyps*, *Torgos*, *Aegypius*, *Trigonoceps*, *Gyps*, *Necrosyrtes*, *Gypohierax* and *Gypaëtus*.

Dissections of the olfactory tracts of *Cathartes aura*, *Coragyps atratus*, *Sarcoramphus papa*, and *Gymnogyps californianus* (partial) were made from material preserved in 70 per cent ethyl alcohol.

Complete olfactory tracts of a number of species of cathartine and aegyipiine vultures were obtained fresh and fixed for sectioning in Heidenhains "Susa" solution. Fixed material was stored in 70 per cent ethyl alcohol. After decalcifying, sectioning and mounting, the serial sections of the olfactory tracts were alternately stained with silver nitrate and Masson's Trichrome (Foote-Goldner modification). Species whose olfactory tracts were fixed, sectioned and stained were: *Cathartes aura*, *Coragyps atratus*, *Sarcoramphus papa*, *Gymnogyps californianus*, *Sarcogyps calvus* and *Columba livia*.

FIELD EXPERIMENTATION TO DETERMINE THE ROLE OF OLFACTION IN FOOD LOCATION BY THE TURKEY VULTURE (*Cathartes aura*)

There has been relatively little serious experimentation on the olfactory acuity of birds in general. Aside from the work already commented upon involving both cathartine and aegyipiine vultures, it is of interest to note that many of the bird species selected for use in olfactory experimentation by physiologists have been those species known to show little or no development of olfactory epithelium. This has been particularly true in the use of the domestic pigeon (*Columba livia*). Numerous physiologists (Banjandarow and Larin, 1935; Walter, 1943; Calvin, 1957; and Michelsen, 1959) have conducted laboratory experiments directed towards eliciting a conditioned reflex on an olfactory stimulus in the domestic pigeon, yet a histological examination of the upper respiratory tract of this species shows it to be quite devoid of any well developed olfactory epithelia. Walter (1943:1) states:

. . . it is of no importance to physiologists to deal with anatomical data. If the olfactory organ were not developed at all, we could hardly expect a sense of smell to exist. But on the other hand the occurrence of the anatomical substratum does not in the least ensure the presence of sensory perception.

The findings in the present study indicate strongly that the sensory physiologist in particular will do well to consider neuroanatomical and neurohistological evidence in choosing his experimental species.

The reason that pigeons have figured so predominantly in physiological experiments is probably attributable to the fact that the species is readily obtainable. Pigeons are available for the taking, while more suitable species such as the turkey vulture (*Cathartes aura*), the kiwi (*Apteryx*) and procellariiform

birds such as the albatross, shearwater and petrel require more effort to obtain and maintain.

The purpose of my research was to obtain evidence to support the premise that the turkey vulture (*Cathartes aura*) has a well-developed sense of smell and employs this sense to a high degree as an integral part of its foodlocator mechanism. The possession of such a mechanism would help account for the species being the most successful of all cathartine vultures in the New World today. To obtain this evidence I followed three paths: (1) experimentation with non-captive turkey vultures; (2) comparative morphological studies of cathartine vulture olfactory tracts; and (3) comparative behavior studies of cathartine vultures.

Field experimentation by earlier workers with non-captive turkey vultures has been justly criticized for the poor manner in which the tests were contrived. Because of lack of proper controls, the possibility of a visual stimulus was not ruled out in tests that were designed to test olfaction alone.

A. FORCED AIR UNIT

In order to avoid the mistakes made by these earlier workers, it was considered necessary to develop a device capable of dispensing the odors of fresh and decomposing animal tissue, yet one completely eliminating all visual clues. The forced air unit (see "Methods" for description of unit) was designed to fill this need. The experiments set forth here were considered controlled experiments in the sense that all visual stimuli concerned with the bait material were eliminated. The machine itself was visible to the turkey vultures and it was not operated without bait for any definite period of time.

Considerable care and study were given to the problem of proper terrain selection, in order that the device could be employed under optimum conditions. The basic idea underlying these experiments was to place animal tissue odors upon air currents of known direction and dependability. If these requirements could be met and a subsequent pattern of attraction of *Cathartes* to the dispensing site could be established, it would be safe to conclude that the stimulus that brought the vultures to the site was olfactory rather than visual.

Precautions employed to rule out all visual stimuli were as follows:

1. The forced air unit was set up at test sites under cover of total darkness.
2. All baits were placed in the blower at night to rule out any possibility of molestation by nocturnal carnivores.
3. The power generator was fueled and tested at time of bait placement in order to limit to a minimum servicing activity after daylight.
4. The unit was placed in operation by 8 A.M. each day, although the first vultures were often not observed on the wing until approximately 10 A.M. Pre-flight operation of the unit insured the dispersal of all insects, due to the very strong exhaust force of the fan unit.

5. At the end of each day's run, all baits were removed from the unit to prevent disturbance by carnivores.

6. The observation point was located at least 200 yards from the generator unit and 275 yards from the blower unit proper. Check of proper functioning of both units was visual with the aid of a tripod-mounted 25-power spotting scope. A small cloth streamer opposite the exhaust of the gasoline engine generator indicated operation of this unit, while a small piece of paper placed on the intake screen of the forced air unit indicated suction. If the fan unit ceased operating, the paper would immediately fall off.

The Cerro Viejo ranch area (see "Study Area,") was selected for the forced air tests because of ideal terrain to be found there. A maze of deep canyons and sharp ridges on the north portion of the ranch made it possible to select canyons where wind direction was steady up-canyon as the south ridges warmed and thermal up-draft caused the air masses to move in a definite pattern.

Air dispersal patterns from the forced air unit were checked at a number of canyon sites prior to actual tests by placement of small fumigating smoke bombs in the unit and observing the smoke pattern from the circular tower. Burning, oil-soaked rags and leaves were also employed. Continuous check on wind direction during actual odor dispersal tests was made with the aid of a simple hand-made weather vane located at the site and visible from the observation point.

Turkey vultures were not abundant on the Cerro Viejo ranch, but this condition proved to be an advantage rather than a detriment. The study area was regularly patrolled by an estimated four vultures, although as many as fourteen were observed in the immediate vicinity on one occasion. The few birds that worked up into the canyon country where the test sites were located were solitary birds that consistently cruised the ridge lines at low elevations or swept down through the maze of canyons, often only a few feet above the ground. Vultures flying in this manner were the targets of the experiment, for it was thought that knowing the directional dispersal of the odors from the forced air unit it would be possible to predict the exact direction of approach of a vulture if it were receiving an olfactory stimulus from the unit. Conversely, any vulture passing up-wind of the unit would not be influenced in any manner and would cruise on out of the area.

When all was in readiness, the unit was set up in a deep canyon, fifty yards below the confluence of two smaller canyons. All controls previously described were observed and the unit was baited at 4 A.M. on June 1. The bait consisted of the bodies of nine ground squirrels (*Citellus beecheyi*) collected the previous day.

The unit was put in operation at 8 A.M., with the wind freshening and blowing steadily up-canyon by 9:30 A.M. No vultures were observed in any sector throughout the morning. The unit was shut down for refueling at 12

noon and began operating again at 12:15 P.M. A vulture sighting was made at 1:48 P.M. when a single individual crossed the canyon a quarter of a mile below the unit (up-wind).

At 4:30 P.M. a lone vulture was observed coming down the right-hand canyon within fifty feet of the canyon floor and directly towards the unit. The bird was quartering back and forth on a one hundred foot front. It passed over the unit at an elevation of approximately fifty feet, wheeled sharply and began to circle tightly, directly above the tower. The vulture made seven complete circles above the unit and then began to swing in wider circles, completing a total of three. At this point it once again closed the diameter of its circles, decreased its altitude and swept around the unit for five complete circles at an elevation approximately five feet above the top of the tower. On the sixth circle it swooped low below the level of the top of the tower to a point where it had to resort to wing beats, with the tips of its wings almost touching the ground. It appeared as though it was about to land, but instead continued to circle at tower level for an additional four complete circles. The vulture then increased its elevation and widened the diameter of its circles. After a total of six more passes above the tower it sailed over the ridge line to the southeast and was gone. The bird had approached the unit on one of the two specifically predicted olfactory routes available to it and had evidenced a very positive interest in the test site proper. The behavior of this vulture indicated that it was responding solely to an olfactory response, as all visual stimuli related to baits were absent.

The unit was moved that night to a new location in a large canyon approximately one mile to the southeast of the first site. Installation was made in a small grove of pepper trees (*Schinus*) and the unit was baited at 4 A.M. the following day with the same bait used the previous day, plus the body of a bobcat (*Lynx felis*).

The unit was set in operation at 8 A.M. on June 2, although a dense ground fog masked the entire area until 9 A.M. The first vulture in the area was not sighted until 10:10 A.M. The bird was crossing the ridge lines at right angles and as it crossed the head of the canyon occupied by the forced air unit it swung into a circling flight, executing three rising spirals and then continued off across the higher ridges to the north. At 10:40 A.M. a vulture was noted in the same area at the head of the canyon but at a lower elevation and moving directly down-canyon towards the unit. The bird held a steady course towards the pepper tree grove and did not quarter to the right or left as the vulture had done on the previous day. It passed directly over the unit at an elevation of approximately fifty feet, pulled into a steep climb and turned back on its course in a tight circle of approximately one hundred feet in diameter. This action was followed by a series of eight slow circles directly over the unit. On the ninth turn it set a course to the southwest and glided on out over the large valley below. As on the previous day, the response had been from the exact predicted route of approach. No additional vultures were observed in the area during the remainder of the day. The unit was shut down at 5 P.M., the bait

boxed up and removed by truck to the headquarters area of the ranch. On June 3, 1960, the same bait was placed in the unit at the pepper tree site at 4 A.M. and the unit operated throughout the day, with no vulture activity observed in the entire Cerro Viejo area.

Under cover of darkness on June 3, 1960, the forced air unit was disassembled and moved to the high meadow area known as Eagle Nest on the upper slopes of the Santa Susana Mountains. Installation was made in a scattering of black walnut trees (*Juglans*). The large lateral bait chamber (see "Methods") was attached.

At 4:30 A.M. on June 4, 1960, one half of a mule deer (*Odocoileus*) carcass was placed in the large lateral bait chamber along with the bodies of twelve ground squirrels. A densely-leaved branch of black walnut was cut and placed in front of the intake vent of the lateral bait chamber to further safeguard against any visual stimuli. A dense fog cover began dissipating by 7:45 A.M.

No vultures were observed in the area until 2:10 P.M. when a solitary bird was noted 200 yards to the northwest approaching directly towards the unit from down-wind in the predetermined approach zone. The vulture circled the blower eight consecutive times and then drifted back on the down-wind corridor. Facing up-wind it rode the air current slowly for approximately three minutes and then closed slowly on the blower once again at an elevation of approximately 75 feet. Another series of five 50-foot wide circles were completed directly above the unit, after which the bird drifted down the slopes toward the main valley to the south. The vulture had circled directly above the stack for a total of twelve minutes.

During the period of July 18 to 24, 1960, inclusive, the experiments were repeated at all three of the previously-used test sites, with results similar to those described for the first series being obtained at all three sites. A total of nine approaches were made during this period.

B. PORTABLE HIDDEN BAIT CHAMBERS

A number of experiments employing the use of various types of animal baits concealed in perforated cardboard cartons (see "Methods") were carried out at selected sites at Cerro Viejo ranch between August 24 and 30, 1959, as well as at other selected localities. Baits consisting of decomposing fish, shellfish (*Haliotis*), ground squirrels (*Citellus*), kangaroo rats (*Dipodomys*), domestic cat, and snakes (*Pituophis*) were used. The same control procedures for placement of baits were employed in these tests as had been used with the forced air unit.

Prior to daylight on August 24, 1959, a perforated box containing approximately thirty-five decomposing fish was placed on a horizontal limb of a large oak tree, well within the dense canopy of foliage. The tree was situated at the base of the west slope of a large north-south canyon. Immediately behind the tree the hillside was cut by a small but steep ravine which led to the top of the slope. No vulture activity was noted in the immediate area of the

baited oak tree until 3:30 P.M. At this time five turkey vultures were observed circling at the head of the small ravine directly to the west of the oak tree site. The birds were repeatedly observed to swoop down the ravine directly toward the oak tree, then pull out in a steep climb directly above the tree and return to their original position above the head of the ravine. This activity was continued for thirty-five minutes, during which time the number of vultures increased to a total of nine birds. A fence line with wooden posts ran along the top of the ridge at right angles to the ravine in question. The three fence posts opposite the head of the ravine were occupied by resting vultures, while the remainder executed the swooping action over the bait-laden tree. None of the nine vultures made any attempt to enter the dark interior of the tree, and after the lapse of thirty-five minutes the birds sailed off towards the large valley to the south. Following the departure of the vultures I made an examination of the immediate area of the baited tree. I could smell the bait while standing under the canopy of the tree, but it was barely discernible a few feet from the edge of the tree. I then climbed to the head of the ravine behind the tree to a point next to the fence posts previously occupied by the vultures. From this point the odor of the decomposing fish was extremely strong, although the bait site was 200 yards below. A steady current of air could be felt blowing up the ravine from the direction of the tree to the fence line on the ridge. A smoke bomb ignited at the bottom of the ravine in close proximity to the bait site sent a column of smoke directly up the ravine past the fence posts at the ridge. From the pattern of the smoke column it was evident why the vultures had concentrated at this point.

The large hidden bait chamber (see "Methods") was utilized at various sites at Cerro Viejo ranch. The first trial was made in a small stand of live oak trees (*Quercus agrifolia*) in a pasture to the south of the ranch headquarters. The chamber was set up several days prior to the introduction of bait. The same control procedures were followed as previously described, with bait placed in the unit prior to daylight. Bait consisted of a domestic cat and five ground squirrels (*Citellus*). The bait was completely invisible inside the chamber, which stood in the deep shade of the oak grove. The pasture was bordered on the south side by a very steep hillside densely covered with chaparral. The hillside with a north exposure was masked in shadow in the late afternoon, and consequently was subjected to an up-draft on its slopes toward the warm exposed ridge. The grove of oak trees was situated close to the foot of this slope.

At 4 P.M. of the day following the introduction of the bait to the chamber a single turkey vulture was observed circling above the group of trees. Its circling pattern carried it to the ridge of the steep hill, directly to the south of the oak trees harboring the bait chamber. As the vulture neared the ridge line, it turned sharply and swooped down towards the oak trees. When directly above the trees it rose in a steep climb and circled back to the ridge line with a behavior much resembling that of the vultures previously commented upon in connection with the box of fish in the oak tree. This circling and diving pat-

tern was executed for approximately ten minutes, at which time the lone vulture changed to a series of close-to-the-ground circles about the grove of oak trees. The circles were approximately ten feet off the ground and the bird had to resort frequently to wing flapping to maintain air speed. From this low angle of flight it was possible for the vulture to see the bait chamber under the oaks. The bird did not land, however, and after four complete turns around the bait chamber, it sailed out over the pasture to the north and was lost to view.

The large bait chamber was next set up in the pepper tree grove mentioned in earlier experiments (see "Forced Air Unit"). All control procedures were observed and the chamber was baited with a hind quarter of fresh mule deer and several freshly killed ground squirrels. No vulture activity about the bait site was observed until approximately 2 P.M. of the first day. At this time a lone vulture came down the canyon towards the pepper tree grove on a down-wind course. It circled the clump of pepper trees for three turns and then landed in an open portion of the canyon bottom, down-wind from the bait chamber concealed in a dense portion of the pepper tree grove. The bird stood motionless for several minutes facing directly up-wind towards the bait chamber, located some 75 yards distant. After five minutes the bird gave a few quick wing beats, lifted itself into the air, and sailed over the pepper trees and on down the canyon, up-wind of the test site.

Various other baits were used in the small-sized bait chambers (see "Methods") with varying success. A perforated box, containing a number of decomposing abalone (*Haliotis*) and the bodies of approximately two dozen kangaroo rats (*Dipodomys*), was securely hidden in a dense growth of thorn-apple (*Datura*), but it attracted no vultures. A single four-foot long gopher snake (*Pituophis*), found dead on the highway and placed in the hollow cavity of a tree, attracted two turkey vultures. The dead snake had in this instance been placed in a burlap sack and dropped into the dark cavity of a large half-dead cottonwood tree (*Populus*). The two vultures were observed to circle the tree repeatedly before landing in the dead branches of the tree top. From here they again took flight and continued circling the tree. The two birds next landed on the ground, down-wind from the tree, and walked to within fifty feet of the hollow trunk. Taking wing once again, they resumed their circling of this tree and landed in the upper branches a second time. After perching in the top of the tree for several moments they, again, took wing and left the area.

C. MOUNTED DECOY DEER—FRESH DEER CARCASS REPLACEMENT

The mounted decoy mule deer (see "Methods") was placed in a pasture overgrown with wild mustard (*Brassica campestris*). Placement was made before dawn and care was taken to make the decoy resemble as closely as possible the carcass of a dead deer. Mule deer (*Odocoileus hemionius*) were abundant at Cerro Viejo ranch and, therefore, a normal source of food for the turkey vulture. The decoy was not a crudely prepared specimen, but had

been mounted by modern taxidermy methods and therefore resembled the actual animal in every detail. Care was taken not to disturb the vegetation about the decoy, and although it lay on its side among the mustard as though dead, it was plainly visible to any vulture passing over the pasture. A central observation point 50 yards to the west afforded a full view of the pasture as well as the low hills on both sides and the entire sky above. During the next five days (August 25 to 29, 1959), repeated sightings of vultures were made over the pasture area. The vultures were obviously aware of the decoy as they frequently passed over it at a normal hunting elevation of 100 to 200 feet. Observation of the site by me and by assistants was continuous throughout the daylight hours of the five-day period. We employed ordinary vision, 6-power binoculars and a 25-power spotting telescope. At no time during this period were any vultures observed closer to the decoy than in the normal searching passes over the pasture as previously described. At the end of the five-day period the decoy was removed and the test was terminated.

On July 18, 1960, the following season, the experiment was repeated, but with modifications. On this date the same mounted decoy was placed at the head of a pasture adjacent to the one used as the test site in 1959. Placement of the decoy was again made before daylight and all precautions were taken not to disturb the vegetation about the decoy. During the subsequent three days, turkey vultures were repeatedly seen to pass over the decoy (which was in plain view from the air above). Observation of the site was made from the same location used in 1959. On no occasion, however, did a single vulture descend to the decoy during the three-day period. Both the 1959 and 1960 sites were in the open and sufficiently far from any object or animal that might have deterred the relatively shy turkey vulture from investigating the decoy. During the pre-dawn hours of the fourth day, the mounted decoy was carefully removed and the fresh carcass of a road-killed mule deer, furnished by the California Department of Fish and Game, was substituted at the exact spot previously occupied by the mounted decoy. The carcass had been selected as to size and sex, so as to resemble very closely that of the mounted decoy. Considerable care was taken to insure that the head of the fresh specimen was turned downward in the same manner as that of the decoy. To the human observer the two decoys appeared to be one and the same. Several vultures passed over the pasture during the day, but none descended to the fresh deer. The bait was left in place during the night and was examined before dawn to insure that it was still in the same position and had not been disturbed by carnivores during the night.

At 10:55 A.M. a vulture was observed circling above the decoy site, and by 11:05 A.M. the first vulture had been joined by two others. The circling, however, was not directly above the carcass, but was some 100 yards to the north at a point where the pasture pinched off into a small canyon. At 11:20 A.M. the three circling vultures were joined by a fourth bird. The offset circling continued much in the same manner as before, but was closer to the

ground (35 feet). At 11:25 one vulture left the circle and drifted directly towards the carcass. When directly above the decoy the vulture turned sharply upward and back on its course toward the other circling birds 100 yards away. A second bird repeated the flight pattern and soon all four vultures were making the direct pass over the carcass, turning sharply upward and back to the circling area. At 11:36 one of the four vultures made directly for the carcass as before, but instead of turning back on its course it circled close above the carcass and on the second turn landed beside the deer. Within two minutes all four vultures were on the ground and pulling at the decomposing deer carcass. An immediate check of wind direction at the decoy site verified the fact that the offset circling area in the mouth of the small ravine at the head of the pasture was in the down-wind zone of the decoy. A similar experiment was repeated during the 1960 season at a different site, with the same results. The turkey vultures did not land and examine the mounted decoy, but readily came to the fresh carcass after flying a verification pattern in the down-wind zone (Fig. 7).

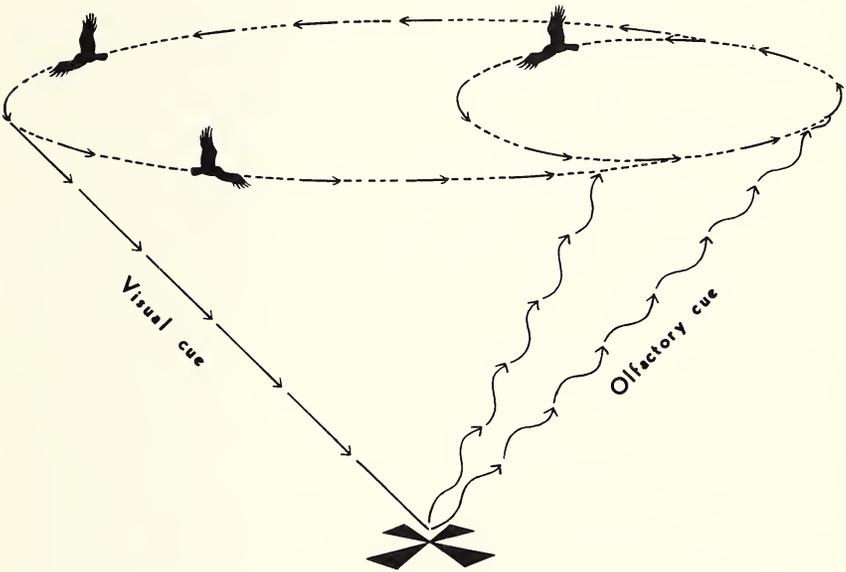


Figure 7. Diagram showing verification flight pattern of the turkey vulture (*Cathartes aura*).

D. ETHYL MERCAPTAN—COMPRESSED AIR UNIT

The decision to conduct field tests with ethyl mercaptan ($\text{CH}_3\text{CH}_2\text{SH}$) as an olfactory attractant for turkey vultures came as a result of conversations with field engineers of the Union Oil Company of California.

According to Mr. Ralph Openshaw, a retired engineer of the company,

his organization had used turkey vultures to aid in locating leaks in large natural gas lines. During the period of 1938-1939, the company was troubled by a number of hard-to-find leaks in a 12-inch natural gas line that extended from Orcutt Hill, California, northward for 42 miles to the town of Avila, California. It was suggested to them by a company engineer in Texas that an effective way of locating line leaks in rough terrain was to introduce a heavy concentration of ethyl mercaptan into the line and then patrol the route and observe the concentrations of turkey vultures circling or sitting on the ground at definite points along the line. According to Mr. Openshaw, this procedure was most successful. A high concentration of ethyl mercaptan was introduced into the forty-two miles of gas line and a traverse of the route was made. At several points along the line, turkey vultures were observed either circling or sitting on the ground. At those locations the odor of the ethyl mercaptan was very pronounced and examination of the line revealed the leaks. As a result of using this procedure, the field engineers of the Union Oil Company have long ago recognized the turkey vulture as possessing a well-developed sense of smell.

The first trials using ethyl mercaptan as an attractant for turkey vultures were made at the head of the Gulf of California in Sonora, Mexico, between January 10 and 14, 1961. The test area was just north of the gulf town of Puerto Peñasco. Careful observation just before the tests had shown that a winter population of approximately twenty turkey vultures roosted in a lone tree on the desert floor some ten miles due north of the town. The birds daily took flight at approximately 9:30 A.M. and flew due south to the town and the beaches of the Gulf of California. The prevailing wind on the desert flat north of the town was from west to east and blew steadily each day from approximately 9 A.M. on. Three test sites were selected at varying distances north of the town. All were to the west (up-wind) of the flight line of the vultures from their roost to feeding grounds in and around the town.

On January 10, 1961 at 9:30 A.M. an 8-ounce container of ethyl mercaptan was uncapped and placed in a bush some 500 yards west of the established flight line. The fresh morning breeze carried the volatile fumes due east so that they intersected the line of flight at a right angle. A 25-power spotting scope was set up 200 yards to the west of the mercaptan site and on the same east-west line. The bush containing the mercaptan was visible in the foreground and any vulture passing the point of intersection with the fumes was visible in the field of the scope. The first vultures (three birds) flying south to Puerto Peñasco were noted at 9:48 A.M. Two minutes later their line of flight brought them abreast of the mercaptan-laden wind and they swung abruptly into a circling flight approximately 200 feet above the ground. The three birds circled tightly at this point for five minutes before one of the three began quartering up-wind towards the mercaptan site. Decreasing its elevation to approximately 100 feet, the vulture passed directly over the bush containing the mercaptan. From this point it continued on to the west and was

lost to view. Attention was then directed back to the intersection point where the remaining two vultures had been circling. Five vultures were observed circling tightly at approximately 200 feet elevation, but it was impossible to determine whether the original two birds were among these five. After approximately six minutes the birds spiraled upwards and then flex-glided on southward toward Puerto Peñasco. At 11:15 A.M., a single vulture was observed moving on the south-bound line toward Puerto Peñasco, and as it passed into the field of the focused spotting scope, it also swung in a tight circle at the point of intersection with the mercaptan fumes. Directly behind it came two more birds that joined the circling flight of the first vulture. The three vultures were joined by an additional four birds and the group of seven soared slowly up-wind toward the mercaptan site. When a short distance down-wind of the mercaptan, the vultures again began their circling action for a period of three minutes. The circling was within 100 feet of the ground at this point. At the end of the three-minute period the group of vultures drifted on southward toward Puerto Peñasco.

On January 11, 1961, a similar site was established six miles north of Puerto Peñasco and the mercaptan was uncapped at 9 A.M. The first vulture sighting was made at 10 A.M. when four vultures were noted heading south on the same line as the previous day. As the lead vulture sailed into the field of the spotting scope, it wheeled sharply and began a tight circling action down-wind of the mercaptan fumes. The three other birds immediately joined the lead bird and all four circled tightly within the telescope field for approximately eight minutes, gradually working up-wind toward the mercaptan site. When directly over the bush holding the mercaptan, the birds began to fly in widening circles and then moved out of the area in three directions. At 10:30 A.M., three additional south-bound vultures crossed the fume-dispersal line and again all three birds began a tight circle in the area covered by the spotting scope. The vultures circled steadily at point of intersection for ten minutes and then moved on south toward Puerto Peñasco without closing on the mercaptan site as the previous group of vultures had done.

A third test site, five miles north of Puerto Peñasco, was used on January 14, 1961. In contrast to the previous two tests, the mercaptan was poured into an open pan rather than being retained in an uncapped bottle. The pan was placed in a dense bush at 9:45 A.M. but no vultures were observed moving south until approximately 10:30 A.M. At this time, six vultures, strung out in an irregular column, were observed moving south along the north-south tract to Puerto Peñasco. At a considerable distance behind the group of the first six came an additional three birds. As the first of the six birds came into the down-wind zone of the mercaptan, it swung into a tight circle as on the previous test days. The remaining five birds individually took up the tight circling as they arrived opposite the mercaptan. A short time later the second group of three birds also joined those already circling, making a total of nine birds circling close together approximately 150 feet above the ground and

directly down-wind of the mercaptan. The group of nine turkey vultures continued to circle the same spot for a period of approximately five minutes. All were visible in the field of the prefocused spotting scope. At the end of five minutes two of the vultures landed on the ground and stood motionless and facing up-wind toward the mercaptan site while the seventh bird moved on south toward Puerto Peñasco. The six other birds passed directly over the mercaptan and then drifted off slowly toward the south. The two vultures continued to stand motionless on the open ground down-wind of the mercaptan for a full six minutes. They then rose into the air once more with several rapid flaps of their wings. Several more tight circles were executed and the two birds then moved south toward the beach without closing on the mercaptan. The experiments in the Puerto Peñasco area were terminated at this time.

It was of interest to note that flies, especially green blow flies (Family *Calliphoridae*), were attracted to the mercaptan containers as long as they were closed and giving off only a limited amount of odor. However, as soon as the containers were uncapped or the mercaptan was poured into an open pan, all flies disappeared. The mercaptan apparently acted as an attractant in low concentrations, but became a repellent in heavy concentration.

Following the field trials with ethyl mercaptan in Sonora, a more sophisticated mercaptan-dispensing unit was devised (see "Methods").

On September 6, 1961, the compressed air unit described above was put into action on the upper brush-covered slopes on the north side of the Santa Clara River Valley, directly to the north of the Rancho Sespe site (see "Study Area"). Ground fog enveloped the entire area at the time of installation. The compressed air flow through the mercaptan canister was initiated at 8 A.M. The fog dissipated from the valley at approximately 9 A.M. A steady breeze was blowing up the slopes from the valley floor, thus carrying the mercaptan fumes toward the ridges to the north. Any vulture receiving an olfactory stimulus from the mercaptan would have to be foraging along the ridges to the north. At 9:15, eight turkey vultures were sighted foraging over the floor of the valley to the south and up-wind of the unit. No response was expected or received from these birds. The unit operated throughout the morning and continued observation of the ridges to the north disclosed no vultures in the down-wind area. In the valley below, however, numerous vultures were observed throughout the morning. The compressed air unit was securely hidden in a dense stand of live oak, but the mercaptan fumes were easily detected by the human nose in the down-wind zone several hundred yards from the site. By mid-afternoon it was obvious that the concentration of vulture activity was on the valley floor and up-wind of the dispensing site. The unit was shut down and dismantled at 3:30 P.M.

On September 7, 1961, the unit was installed on the floor of the Santa Clara River valley in the area where the vulture activity had been noted the previous day and directly below the previous dispensing site on the slope to the north. The unit was placed under a small willow tree (*Salix*) and further

camouflaged with several large tumbleweeds (*Salsola*). The mercaptan flow was initiated at 8:30 A.M., although the entire valley was enveloped in a dense ground fog. By 9:20 A.M. the fog had begun to lift and visibility was approximately one-half mile. A steady breeze began to blow up the valley from the west. At 9:45 the fog had completely disappeared, leaving the entire valley in sunlight. At 10:25 twenty-four turkey vultures were observed spiraling up from their known roosting trees (see "Study Area") two miles to the northwest. After gaining altitude the flock of vultures scattered in several directions with many of the group moving up the valley toward the mercaptan site. At 11:08 A.M. two vultures were observed circling directly down-wind of the unit at an elevation of 200 feet. These vultures were joined by a third at 11:10 and all three birds continued to circle in the down-wind zone. The circling was frequently interrupted by the birds facing into the wind and gliding slowly up-wind towards the dispensing site, only to swing about upon reaching the willow bush containing the dispenser and return to the down-wind circling area, approximately 200 yards from the dispenser. From 11:30 on throughout the remainder of the day there was a continuous circling and quartering with from two to twelve vultures in the pattern. At 11:46, one bird from a circling group of seven glided slowly up-wind towards the willow bush. The bird was cruising at ten feet above the ground, and upon reaching the dispenser site went into a tight, low-level circling flight, frequently resorting to wing flapping in order to maintain air speed. After two minutes of circling the bird returned down-wind to the circling group of vultures that now numbered nine birds. At 12:40 P.M., vultures began landing on an earthen dike 150 yards from the dispenser, but exactly in line with the flow of mercaptan fumes. The birds stood motionless on the dike, but all were facing directly into the wind. The wind held steady from the west and numbers of vultures continued to circle or face into the wind, quartering back and forth on a 50-yard front. The number of birds on the ground varied from two to five, with arrivals and departures from the circling group in the air above. Vultures remained continuously in the down-wind air zone and on the ground until the experiment was terminated at 4 P.M.

On September 9, 1961, the unit was operated as on the previous day. Dispensing of mercaptan began at 8:15 A.M., with the fog burning off at 9:10 A.M. Vultures began circling directly down-wind of the unit at 9:30 A.M., and behavior was similar to that of the previous day. The largest number circling and on the ground down-wind of the dispenser at any one time was fourteen. At 1:30 P.M., the number of birds had dropped to two and examination of the unit showed that the tank of air had been exhausted. A fresh tank of air was quickly substituted and by 2:15 the number of circling birds was back to ten. Frequent sorties would be made towards the dispenser site as on the previous day, but the most used air position appeared to be 150 to 200 yards down-wind. Immediately down-wind of the dispenser the mercaptan fumes were overpowering to the human nose to the point of being nauseating. Two hundred yards down-wind, however, the fumes were very strong, but not so

overwhelming and with a different odor. This difference of odor of the same substance at varying distances is in accord with the observations of Kinross (1930:116) who states:

. . . the odors of many substances change so much with dilution that a strong solution and a weak solution seem to have nothing in common; indole, which in strength smells like a sewer, when very dilute had the fragrance of narcissus.

The attractant quality of the ethyl mercaptan kept vultures circling and standing on the ground down-wind of the dispenser the remainder of the afternoon until the experiment was terminated at 4:30 P.M.

Operation of the compressed air unit was resumed on September 10, 1961, but a change in weather resulted in a cloud overcast with strong, gusty and erratic winds in the valley. Fewer vultures were noted in the air and these birds showed little interest in the mercaptan, as the fumes were swirled in all directions. The limited supply of mercaptan was exhausted by midday and the experiment was terminated. The two previous days, however, had provided adequate data, coupled with the observations already described from the Puerto Peñasco area, to show a definite olfactory response by the turkey vulture to an ethyl mercaptan stimulus.

E. HIDDEN BAIT TESTS—CENTRAL INDIA

During the period of February through March of 1959, while participating in a Los Angeles County Museum expedition to central India, I was afforded an excellent opportunity to observe the habits of a number of species of aegyptiine vultures. Opportunities were also afforded to conduct field experiments on the olfactory acuity of this subfamily of birds.

The main base camp of the expedition, located in the Balaghat Forest District of the state of Madhya Pradesh, was the scene of considerable skinning and preparation of large specimens of mammals, such as tigers, leopards, and large ruminants. Activity of this nature in India soon draws a large concentration of vultures, ready to feed on any discarded carcasses. Because carcasses were continually present, the concentration of vultures remained in the immediate vicinity of the camp, ever alert to swarm upon a carcass when the latter was dragged into an open area for them. During the waiting periods, the giant Sal trees about the camp were heavy with them, both day and night. The vulture population about the camp area numbered approximately 150 individuals of three species. The Indian white-backed vulture (*Pseudogyps benghalensis*) made up approximately 95 per cent of the group, with 3 per cent being *Neophron percnopterus* and the remaining 2 per cent, *Sarcogyps calvus*. The latter two species did not roost in the immediate camp area, but were always on the periphery of activity during daylight hours.

In order to perform a controlled test designed to detect possible olfactory acuity, the skinners were requested to set aside over 200 pounds of muscle during the fleshing out of a large tiger specimen. A site was selected in a near-

by open, dry paddy field. An elevated platform in the center of the paddy field enabled the bait to be placed off the ground out of reach of jackals and pariah dogs.

At 10:00 P.M. that night, with the help of two assistants, I placed the mass of muscle atop the platform and security covered it with a thick, ten-inch layer of thatching straw. By putting the bait in place under the cover of darkness, there was no possibility of observation by the diurnal vultures.

During the subsequent days the large concealed bait developed an overpowering odor, discernible at a considerable distance—even by the relatively weak olfactory equipment of man. Each night the thatch straw cover was checked to insure that it had not become dislodged to disclose the bait to the keen-eyed vultures. Vultures swarmed the area during the daylight hours of each day, but never once did any of the three species show the slightest indication that they had detected the location of such a desirable food item. On the night preceding the twelfth day the thatch was removed so as to disclose the bait. The following morning a large king vulture (*Sarcogyps calvus*) immediately located the remains of the bait, alighted on the platform and began to devour the remains of the tiger meat.

F. FLY ATTRACTANT TESTS

During the course of field studies with turkey vultures at Cerro Viejo ranch it was thought advisable to devise an experiment that would attract large numbers of flies in order to test the hypothesis of Taber (1928) and Darlington (1930), both of whom believed that the turkey vulture locates hidden carrion by observing concentrations of necrophagous insects rather than by a sense of smell.

The hypothesis is an interesting one, but hardly tenable in the light of the findings presented in this report. Experimentation with hidden baits in Central India showed that, although the bait site was black with flies and other necrophagous insects, the vultures were unable to detect the presence of the carrion. It is reasonable to assume that the aegyptine vultures of the Old World, which are apparently completely dependent upon vision for the location of food, would be attracted readily to baits by the presence of necrophagous insects if these insects served as a visual indicator of food. I have also had considerable experience with kills made by tigers and leopards in India and Burma, and observation has shown that these large carnivores drag their prey under cover of brush or trees. Although the carcasses are covered with flies and the air above is thick with insects, the vultures seldom if ever detect the presence of the kill. Experimental use of the forced air unit in this study has shown that the turkey vulture readily responds to an olfactory stimulus from a site that is free of necrophagous insects. The absence of insects about the forced air unit during operation was due to the very strong exhaust qualities of the machine. There is no evidence to support the proposal of Darlington (1930) that

the turkey vulture may possess an auditory sense attuned to the sound of buzzing insects.

For a fly attractant, a twenty-four-hour-old mixture of casein, brown sugar and water in equal parts, as suggested by Dethier (1947:2), proved effective for this purpose when placed in the mouth of an abandoned ground squirrel burrow. The baited burrow was located in the center of an open pasture and kept under observation for a period of five days. Large numbers of flies were attracted to the site, but no interest was indicated by turkey vultures, although the vultures periodically passed over the pasture on hunting flights during the five-day test period.

COMPARATIVE FOOD-LOCATION BEHAVIOR OF CATHARTINE VULTURES

As pointed out by Fisher (1944:272), the New World vultures of the family Cathartidae form a heterogeneous group of large birds limited in range to the Americas. In addition to morphological differences, they differ decidedly in their behavior. In order to understand the differences as well as the similarities among the five cathartine genera, I shall compare them on the basis of flight, food-locating habits, and agonistic and predatory behavior. This is pertinent to the present inquiry as these differences are reflected in food location behavior, and must, therefore, be properly evaluated.

A. FLIGHT

The detailed mechanics of cathartine flight were ably discussed by Fisher (1946:549-553). The flight of Old World vultures has been studied in detail by a number of persons, with the best general account being presented by Hankin (1913). On the other hand, the mannerisms of cathartine flight have been reported by relatively few persons. A recent publication by Cone (1962) presented a detailed study of soaring flight in land birds, especially vultures.

The giant condors *Vultur* and *Gymnogyps* are both excellent soaring vultures, and although they are relatively clumsy on the ground and often resort to considerable wing flapping at take-off, once airborne they soar and sail with a minimum of wing motion. A great many observations pertaining to the flight of *Gymnogyps* have been recorded by Koford (1953), but detailed accounts of the flight of *Vultur* are lacking. According to Koford (1953:41):

The outstanding characteristic of the flight of condors is high stability in soaring. Frequently even an experienced observer mistakes a distant transport plane for a condor or a condor for a plane. It is probable that condors can soar for more than one hour at a time without flapping.

With regard to altitude, Koford (1953:46) stated that:

In general, condors do not soar as high or as low over the ground as turkey vultures in the same locality. On days of light breezes condors rise higher than on days of strong winds. . . . Over high ridges and peaks near roosting areas it is rare to see a condor more than 500 feet above the ground. Over lower hills near feeding areas, where condors circle in rising columns of air in order to gain altitude for long glides, they rise to an estimated 3000 feet. . . . In areas where condors are actively searching for food they usually soar less than 500 feet above ground except when arriving and departing. Doubtless there is an optimum altitude for searching for food. Great height would not favor the detection of carcasses as small as those of ground squirrels.

For take-off on level ground, *Gymnogyps* must run into the wind for 25 to 40 feet, but if the wind is strong, take-off can be effected by merely extending the wings while facing into the wind. From the brief discussions of the flight of *Vultur* by other authors, Fisher (1946:553) obtained the impression that its flight is similar to that of *Gymnogyps*. Along the Peruvian coast, Murphy (1936:276) found that *Vultur* “. . . is given to soaring just above the brinks of sea cliffs and in the same relative position over seaward ridges of coastal hills.” This type of flight is similar to that recorded by Grinnell (1933:164) for *Cathartes* along the coast of northern California.

The black vulture *Coragyps* is also a soaring vulture but much less so than the large condors. *Coragyps* circles more, alternately flapping and soaring. It possesses a broad soaring wing but, according to Fisher (1946:552), the shortness of the wing decreases the lifting surface, making frequent flapping necessary. Howell (1924:128) states that the black vulture is always distinguishable from the turkey vulture by its habit of alternately flapping and sailing. It is necessary for *Coragyps* to take two or three hops on the ground before springing into the air. Even so, it becomes air-borne more rapidly than *Cathartes*. Compared to the other four cathartine genera, *Coragyps* is a relatively sedentary vulture, spending most of its active hours around the habitation of man, ever ready to scavenge bits of food. It rarely resorts to long flights unless food is scarce.

Very little published information is available concerning the flight of *Sarcoramphus*. Dickey and van Rossem (1938:99-102) observed king vultures in El Salvador and reported that these vultures “. . . were seldom observed soaring overhead, but from the hilltops we could look down on them circling about and just skimming the tree tops of the jungle.” They (p. 100) also observed that:

King vultures may be fairly common in a locality and still not be particularly noticeable. Although occasionally to be seen soaring at high altitudes, they are essentially inhabitants of the forest and spend a great deal of time at rest in such cover.

My own experience with *Sarcoramphus* in Brazil agrees essentially with that of Dickey and van Rossem. I have frequently observed king vultures soaring in small circles high above dense forested areas, but my most frequent en-

counters with them have been in dense gallery or continuous primary forest (Stager, 1961:9). In attempting to get within shotgun range of *Sarcoramphus*, I have found that they will repeatedly fly with relative ease from the crown of one giant rain forest tree to another without going above the forest canopy. They descend to the floor of dense forest apparently with little effort, as I have flushed them from such locations on two occasions. Their flight through forested areas is rather labored and audible, however, as it requires continuous flapping of the wings. As far as I am able to determine, *Sarcoramphus* is the only cathartine vulture that can be described as a forest dweller. The king vulture apparently has no forest-dwelling counterpart among the aegyptine vultures of the Old World. The palm nut vulture *Gypohierax* of Africa frequents peripheral areas of forests along river courses (Chapin, 1932:521), but apparently does not penetrate deep within the forest as does *Sarcoramphus* in tropical America.

It is interesting to note that Slud (1960:89) did not observe *Sarcoramphus* within the forest on any occasion, but frequently saw it circling in the air above. His observations were made during a year-long stay in the heavy wet forest of northeastern Costa Rica.

The flight of *Cathartes* differs decidedly from that of the other four cathartine genera. Fisher (1946:552) stated: "Use of the wing in *Cathartes* in most respects holds an intermediate position between *Coragyps* and *Gymnogyps*. It flaps more than does the Condor but less than the black vulture." In a strong wind *Cathartes* can take off by extending the wings and facing into the wind. In the absence of wind, *Cathartes* is slower than *Coragyps* on take-off from level ground. Fisher (1946:553) noted that *Cathartes* needs a longer take-off run than *Coragyps* and flapping flight appears to be more difficult for it than for the latter species. Sprunt (1937:383) commented on the large numbers of turkey vultures killed by automobiles on the roads of the southeastern United States as the birds attempt to rise into the air from the carcasses of automobile-killed animals on the highways. Sprunt attributes the large number of casualties to the inability of *Cathartes* to make a rapid take-off in the path of the oncoming auto. It would be interesting to compare the ability of *Coragyps* to escape the oncoming car with that of *Cathartes*. Sprunt (1937) made no mention of *Coragyps*, however, so it must be assumed that this feeding on roads is confined mostly to *Cathartes* in his area.

Off the ground, however, *Cathartes* is a superb flyer. The soaring flight of the turkey vulture is not as stable as that of *Gymnogyps* and *Coragyps*, as it tends to wobble and tip from side to side. In calm weather it soars with greater facility than any of the other cathartines. It can spiral upward at a very rapid rate and often climbs to considerable heights. Observers often attribute too much importance to the circling soaring flight of turkey vultures in connection with feeding activities. This type of flight is primarily used in gaining altitude. The vulture catches a rising thermal, spirals rapidly upwards, and then flex-glides on a straight course for great distances.

Contrary to the popular opinion that *Cathartes* is a high-altitude hunter, it is basically a very low-level forager. In its searching flight it skims over crest lines of hills and sails down canyons, often only a few feet above the surface of the ground. It is frequently observed sailing swiftly below tree-top level through broken stands of vegetation, then banking sharply to swoop back on its course, apparently to reinforce an olfactory or visual cue. If it loses air speed close to the ground it will resort to wing flapping until speed is regained. *Cathartes* is highly adept at wind-facing and can remain within a relatively small area of air space for long periods of time. In wind-facing it does not hang motionless in one spot, but will quarter back and forth on a relatively small front with much tilting from side to side. Over level ground it commonly flies a low-level searching course, frequently resorting to upward swoops to regain altitude. With necessary altitude regained it will then side-slip downward with a rush, often skimming just above the surface of the ground. In this low-level type of flight it has no peer among the other cathartine vultures.

B. FOOD LOCATING HABITS

The California Condor feeds primarily on large animals that are generally in open areas, and therefore easily located by visual means. Koford (1953:62), from his extensive observations, suggested that *Gymnogyps* may observe the actions of *Cathartes* and ravens (*Corvus corax*) and thereby learn the location of a carcass. Koford also noted that condors will readily join a circling condor group, indicating that each condor is aware of the activities of other condors as each goes about its own search for food. This action is in agreement with the observations made by Stewart (1959:56) on Old World vultures in Spain. In areas where condors feed on ground squirrels (*Citellus*), Koford (1953:62) frequently saw condors fly straight to a group of turkey vultures, either in the air or on the ground. Koford (1953:55) reported that a stuffed doe deer (*Odocoileus*) decoy placed near another carcass on two occasions failed to attract turkey vultures and ravens feeding nearby, or condors flying overhead. This action is in accord with my experimentation with *Cathartes*. Koford (1953:55) concluded that the favorite food species of *Gymnogyps* in order of preference were: cattle, sheep, deer, ground squirrels and horses. He also estimated that these five species provided 95 per cent of the condor's diet. With the exception of the ground squirrel, all of the above species are large and obvious and easily located by visual means. Koford (1953:56) points out that:

. . . condors alight, walk, and take off in a laborious manner, but they excel in flying long distances. Their specializations fit them for eating carcasses which are large enough to feed them for a day or more at the expense of only one landing and one take-off. It would be wasteful from the standpoint of derivable energy, for a condor to descend to the ground in order to feed on a single small carcass.

Koford (1963:62) concluded that if *Gymnogyps* possesses a sense of smell, it is normally of little importance in finding food.

The food-locating habits of *Vultur* are essentially the same as those of *Gymnogyps*, but with certain notable exceptions. The Andean condor feeds on the large and obvious mammal carcasses occurring on the high wind-swept paramos of the Andes. It is also known to descend to sea level along the coasts of Peru and northern Chile where it feeds on the carcasses of fish, cetaceans, and pinnipeds. Unlike *Gymnogyps*, the Andean condor is known to attack and kill animals the size of a calf (Wiggins, 1945:168). According to Murphy (1936:908) the Andean condor feeds upon the fresh eggs of the guano cormorant (*Phalacrocorax bougainvillii*) on the rookery islands off the coast of Peru. As in the case of *Gymnogyps*, the Andean condor can only afford to expend energy feeding on small items of food if this type of food is present in sufficient quantity to justify a landing and take-off. In a large sea bird colony this condition would be amply met. Murphy (1925:189) presents conclusive evidence that *Vultur* also feeds upon live diving petrels (*Pelecanoides garnotii*) secured from the mouths of their nesting burrows.

The habits of *Sarcoramphus* are the least known of all the cathartine vultures. The king vulture finds a large portion of its food on the floor of tropical forests but is occasionally known to join the two smaller species, *Cathartes* and *Coragyps*, at a carcass at the margin of forested areas. Most observers of *Sarcoramphus* agree that this large vulture seldom if ever ventures out on the open savanna or upon denuded mountainsides to feed (Lehmann, 1940:459). The method employed by the king vulture to locate food has puzzled its observers for a long period of time. Pinto (1936:49) pointed out that the king vulture comes to food in the forest with rapidity and in a direct line, although he questions the ability of the bird to locate food by visual means because of the low-level approach it makes through the trees. Pinto was reluctant to attribute the food location to olfaction because of the distances from which it comes to food. Lehmann (1940:459) was of the opinion that the king vulture forages through the dense forest in search of kills made by jaguar (*Felis onca*). Dickey and van Rossem (1938:100) were of the belief that the king vulture arrives at a carcass after it has been discovered by *Cathartes* or *Coragyps*. They also noted that king vultures often showed up at the side of a carcass long after it had been reduced to only skin and a few bones by the smaller species of vultures. Wetmore (1957:22) found it watching *Cathartes* closely within secondary forest growth near the beach on Coiba Island, Panama.

The black vulture (*Coragyps*) obtains a large portion of its food by general scavenging around the habitations of man. In some areas, *Coragyps* forages out from communal roosts and resorts to soaring high above the countryside. Bent (1937:37) stated:

When a black vulture flying and circling at great height becomes aware of a carcass lying far below it, the bird at first circles down but soon drops with great swiftness with legs hanging and,

at times, wings flapping furiously. Such actions of descent from a height immediately attract the attention of other vultures on the ground or roosting in trees and they at once follow up the clue. One such action, even a mistaken one, can quickly collect a flock of vultures.

In August of 1953, I made extensive observations on the feeding habits of both *Coragyps* and *Cathartes* in southeastern Sonora, Mexico, and found that there appeared to be a definite food-finding relationship between the two genera. *Cathartes* was observed on the wing earlier in the day than *Coragyps*, but as the countryside warmed and thermals began to rise, the black vultures, by flapping and gliding, would spiral upwards to considerable heights. From these points of vantage they might easily watch the actions of the low-flying *Cathartes* as the latter quartered back and forth over the dense arid tropical forest below. If a turkey vulture turned back or began circling at a given point, the black vultures would come streaming to the site from all directions. My observations have frequently indicated that although *Cathartes* is the first to discover or arrive at a source of food, it is generally driven from the food by the hordes of black vultures. It is safe to assume that as the high circling *Coragyps* observe the movements of the low-flying *Cathartes*, they likewise would be quick to react to the stimulus of one of their own number dropping downward towards a turkey vulture or to a carcass that the plummeting bird had discovered on its own.

It is a well-established fact that *Coragyps* will attack and kill live animals as large as young pigs and lambs and remove the eyes of new-born calves and cows in a weakened condition (Bent, 1937:35). McIlhenny (1939:472) described in detail the mass attacks of *Coragyps* on skunks (*Mephitis*) and opossums (*Didelphis*) foraging in open fields during daylight hours. Figgins (1923:666) found *Coragyps* taking live young herons from the nest. Live food of this type was in all the open and easily located by visual means. To date there is no evidence to indicate that *Coragyps* employs olfaction in food location.

Food location by the turkey vulture forms the basis of this research and detailed information found elsewhere in this paper will not be repeated here, except as a general comparison of behavior. *Cathartes* is the most widely distributed vulture in the Americas (Figs. 3 and 4) and forages over a great variety of terrain. For the most part it is solitary in its widespread and continuous search for food. Communal roosting is of common occurrence throughout its range, but numbers of individuals at the roost are fewer than is recorded for the roost of *Coragyps*. The turkey vulture is migratory in the northern portion of its range where the bulk of the population withdraws southward in October, to return in March. The wide-ranging *Cathartes* has been found foraging at 10,000 feet elevation in the Sierra Nevada mountains of California (Emlen, 1931:83).

Solitary individuals are to be found sailing over the remotest desert areas of the western United States and Mexico, as well as over the bleak wastes at the

extreme tip of South America (Peters, 1931:190). The low-level searching flight of the turkey vulture allows the bird to take advantage of small items of food. The low-level traverse also places the vulture in a position to receive and respond to olfactory stimuli. *Cathartes* is known to have excellent eyesight, and vision may well be its most important sense; but, as demonstrated in the field experiment section of this paper, olfaction plays a most important role in the food-finding economy of the species. Even in the case of large and obvious items of food, the turkey vulture, under controlled field conditions, has repeatedly demonstrated the need for obtaining a reinforcing olfactory cue before alighting for final investigation and actual feeding. *Coragyps* will drop with great rapidity upon a large suspect item and investigate afterward. The final and sometimes lengthy, close circling flight of *Cathartes* about a large carcass prior to landing, has often been interpreted by observers as extreme caution and timidity on the part of the vulture (Bent, 1937:23). My own observations, however, indicate that olfactory cues are necessary releasing components for feeding behavior. The procedure is reversed when the primary cue is olfactory and the potential food source is hidden from view. The low-flying vulture closes on the odor source and locates the object of its search by the combined senses of olfaction and vision.

The turkey vulture will readily feed upon the large and obvious carcasses, but a large percentage of its diet consists of small items. Pearson (1942:87) stated: "The black vulture seems to pay but little attention to the small carcasses that form a large part of the food of the turkey vulture." Snakes, lizards, small mammals, birds and fish are readily taken as food. Bent (1937:20) mentioned that they will eat grasshoppers and even stranded tadpoles. Observations indicate that *Cathartes* shows a preference for food that is relatively fresh rather than putrid. If food is in short supply in a given area, the turkey vulture will feed on carrion that is well advanced in putrefaction. The tests of Owre and Northington (1961:204) indicated that their captive *Cathartes* showed a decided preference for recently-dead, newly hatched chicks, rather than for putrefied carrion.

My field observations have also shown that *Cathartes* will readily pass over choice items of food, both obvious and hidden. This action can be attributed to lack of hunger and is generally indicated by the vulture's mode of flight. When the vulture is not hungry, its flight is at higher elevations and on a set course. The low-level, quartering flight that carries the bird close over ridge lines and down through ravines or through broken stands of vegetation, indicates that the daily quota of food has not yet been attained. Various observers have suggested that for the most part the other four genera of cathartine vultures observe the food-locating actions of *Cathartes* and are directed to much of their food in this manner. My own observations in Sonora, Mexico, indicate a possible relationship of this sort between *Coragyps* and *Cathartes*. Schomburgk (1839:255) considered *Cathartes* to be a "scout" for *Sarcoramphus*. In areas where condors feed on ground squirrels, Koford (1953:62) has on many

occasions observed *Gymnogyps* flying toward turkey vultures as they circled or sat on the ground. Although Murphy (1925) mentioned both *Vultur* and *Cathartes* as being common on the guano islands off the coast of Peru, he gives no indication that there is any relationship between these two genera of the sort mentioned for the other members of the family Cathartidae.

C. AGONISTIC AND PREDATORY BEHAVIOR

The five genera of cathartine vultures differ so decidedly in their agonistic and predatory behavior that a comparison of these types of relationships is important in achieving an understanding of the behavior of the family as a whole.

Although equally large in size, the two condors differ remarkably as to aggressive behavior. There appear to be no records of *Gymnogyps* attacking live animals, although *Vultur* is known to kill both mammals and birds. In captivity, the California condor is a docile species, but Lehmann (1940:458) reported that some captive Andean condors are savage and pugnacious.

Sarcoramphus is not known to be aggressive or to kill live prey, but *Coragyps* has a well-documented reputation for attacking live animals. The turkey vulture is a very timid species in its contacts with live animals. Reports of predation on live animals by *Cathartes* should be evaluated with extreme care, as it is quite likely that they are based on misidentification. Hamilton (1941:254) reported the killing of young pigs by *Cathartes*, but his information was hearsay and the description of the action of the birds involved fits that of *Coragyps*. Owre and Northington (1961:204) reported that when live chicks were released in the compartments occupied by captive turkey vultures, the latter immediately retreated, although they had had a great deal of experience in feeding on dead chicks. Owre and Northington (1961) also noted that on one occasion when a turkey vulture started to feed on a dying chick, it dropped it and moved away in haste when the chick suddenly moved. Bent (1937:20) commented on the wariness of *Cathartes* when preparing to feed on young pigs killed on the road by automobiles. The vulture would walk carefully about the dead pig, apparently ready to beat a hurried retreat if the pig should move. Murphy (1936:837) stated that the turkey vulture is the enemy of the blue-footed booby (*Sula nebouxii*) but presents no proof that the vulture actually preys on the species. Murphy (1936:907) implicated the turkey vulture in the destruction of cormorant eggs with the statement: ". . . great destruction of guanay eggs had been wrought by gulls, turkey vultures and condors." Referring to destruction of the eggs of the Inca tern (*Larosterna inca*), Murphy (1936:1145) stated: ". . . the vultures are inveterate nest-robbers and quickly gobble up eggs left within sight or within easy reach." It may be that the turkey vultures of the Peruvian guano islands have developed a taste for bird eggs, but from personal experience I would expect the species to be present in the guano islands mainly for the purpose of feeding on the dead birds that normally accumulate in sea bird colonies.

Further study might well show that the turkey vulture has been implicated in the descriptions of the depredations made by Andean condors, solely upon the basis of its being present in the area along with the condors.

Numerous observers have commented upon the agonistic behavior of Old World vultures. One of the best and most recent papers on the subject is that by Petrides (1959:104) concerning the competition for food between five species of African vultures.

Among the cathartine vultures, the smaller species (*Coragyps* and *Cathartes*) appear to give way to the larger species, but mostly in deference to their size rather than because of any aggressive behavior on the part of the larger vultures. Dickey and van Rossem (1938:101), reporting the relationship of *Coragyps* to *Sarcoramphus*, stated that ". . . once they do arrive there is no doubt that the smaller species keep their distance." Among the two smaller genera, *Cathartes* will readily give way to the aggressive *Coragyps*. Although the turkey vulture most frequently discovers or arrives at a food site ahead of the black vulture, the former will soon be crowded aside by the swarming masses of *Coragyps*. Bent (1937:36) stated: "The black vultures are often obliged to share their feasts with turkey vultures . . ." My observations, however, have repeatedly shown that the opposite is true and it is most frequently the turkey vulture that is forced to share its food with the black vulture.

A COMPARATIVE ANALYSIS OF THE OLFATORY MORPHOLOGY OF CATHARTINE AND AEGYPIINE VULTURES

As early as 1837, Richard Owen (1837:35), the eminent British anatomist, called attention to the well-developed olfactory tract of the turkey vulture and concluded with the statement:

The above notes show that the turkey vulture has a well-developed organ of smell, but whether he finds his prey by that sense alone or in what degree it assists, anatomy is not so well calculated to explain as experiment.

One hundred years later, Technau (1936:570), in his excellent paper on the nasal glands of birds, again called attention to the highly-developed olfactory tract of the turkey vulture and pointed out that it must, indeed, be functional and utilized by the bird.

Very recently, Bang (1960:547) stated the problem very clearly when she said:

It seems curious that the large olfactory organs of certain species have so often been pointed out by anatomists, yet most olfactory learning studies have been done on feebly equipped birds such as pigeons and have tended to keep alive in textbooks the idea that the chemical sense in birds is minimal or lacking. The maze type and conditioned reflex studies on microsmatic forms and the succession of uncontrolled field-tests initiated by those of Audubon have kept dust from settling on the question, but have proved nothing about birds with superior receptors.

Portmann (1961:47), in reviewing the problem of olfaction in birds, pointed out the unsettled state of current knowledge on the subject and urges a re-examination of the whole problem. He indicates that the morphological facts are strong evidence against the simple conclusion that birds are anosmatic. He believes that the development of the olfactory part of the nasal cavity, and the well-marked variation in the proportion of the olfactory bulb of the brain support an opposite view.

In order to re-emphasize the high degree of development of the olfactory chambers of the turkey vulture and to draw comparisons between it and the other four genera of cathartine vultures, I have divided the comparison into four categories as follows: (1) External Nares, (2) Posterior or Olfactory Chamber, (3) Microanatomy of the Olfactory Chamber, and (4) Comparative Size of the Olfactory Bulbs.

A reference index as to the relative size of the cathartine vultures is as follows:

Gymnogyps and *Vultur*—very large, with a wing measurement of more than 760 mm.

Sarcoramphus—large and robust, with a wing measurement of 480 to 525 mm.

Coragyps—medium size and heavily built, with a wing measurement of 409 to 464 mm.

Cathartes—medium size to rather small, lightly built, with a wing measurement of 450 to 485 mm.

A. EXTERNAL NARES

The external nares are perforate in all five genera of cathartine vultures, but differ decidedly in their respective sizes (Fig. 8). Measurements made on museum specimens reveal that, in order of nostril size, *Cathartes* possesses the largest nostril (10.8 mm. x 3.8 mm.) which occupies the entire nasal fossa. The nostril of *Gymnogyps* is the next in size (9.5 mm. x 3.8 mm.). In relation to the size of the head, however, the nasal opening is quite small. In *Coragyps* the small opening (7.9 mm. x 2.3 mm.) occupies only the posterior half of the nasal fossa and is narrowly acuminate anteriorly. The nasal openings in *Sarcoramphus* (7.5 mm. x 2.7 mm.) are partially obstructed by the fleshy protuberances of the cere. Although *Vultur* is one of the two largest vultures, it possesses the smallest nostril openings of all (7.2 mm. x 3.2 mm.).

It is of interest that the largest nostril openings occur in *Cathartes*, the genus showing the highest degree of olfactory chamber development. To what degree the large nares assist in olfaction is not known. All five genera possess a wide secondary choana, and, as pointed out by Portmann (1961:47), “. . . choanal smell is probably a fact in many birds and particularly in groups where the external nasal openings are small or even closed.”

The anterior respiratory conchae of the five genera of the family Cathar-

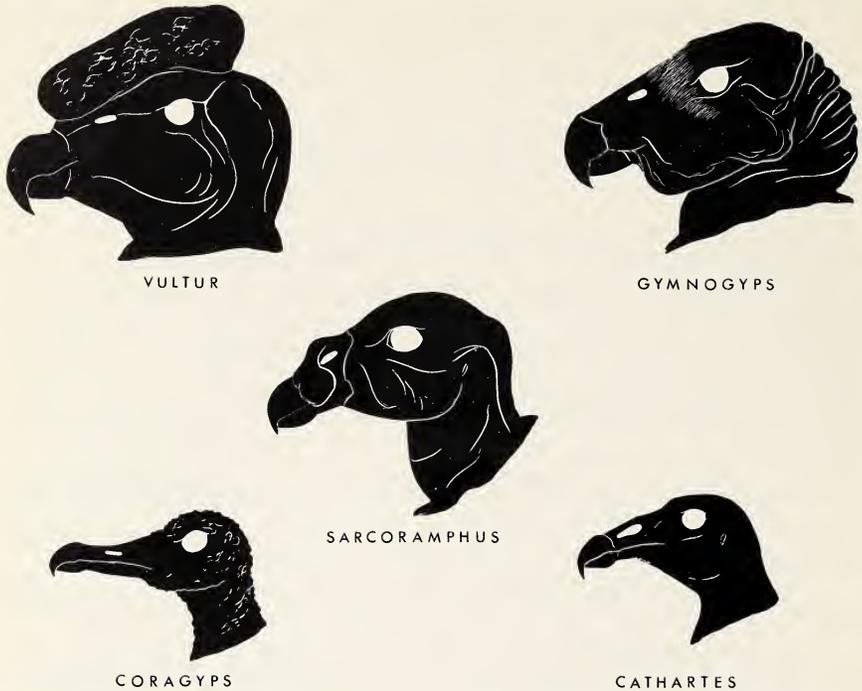


Figure 8. Lateral view of the heads of *Cathartes*, *Coragyps*, *Sarcoramphus*, *Gymnogyps*, and *Vultur*, showing the relative size of the external nares.

tidae appear to vary with each genus. In *Cathartes* and *Sarcoramphus*, the anterior concha is tilted from the horizontal to an almost vertical position. This condition is especially evident in *Sarcoramphus*, where the anterior end of the concha opens in a horizontal position towards the external nares, while the main axis of the structure turns directly downwards to open into the secondary choana (Fig. 9).

In *Coragyps*, the anterior concha is well developed and lies on a horizontal axis (Fig. 10). The area of anterior concha in the single specimen of *Gymnogyps* available was so damaged that I cannot present a proper description of the structure. I have not had an opportunity to examine the respiratory tract of the Andean condor (*Vultur*) so I am unable to make a statement regarding the structure in this genus.

B. POSTERIOR OR OLFACATORY CHAMBER

The paired olfactory chambers in cathartine vultures are cul-de-sacs enclosed on three sides, as pointed out by Bang (1960:549). The olfactory tubercle is situated on the latero-ventral side of each chamber and its degree of development varies according to the genus of vulture.

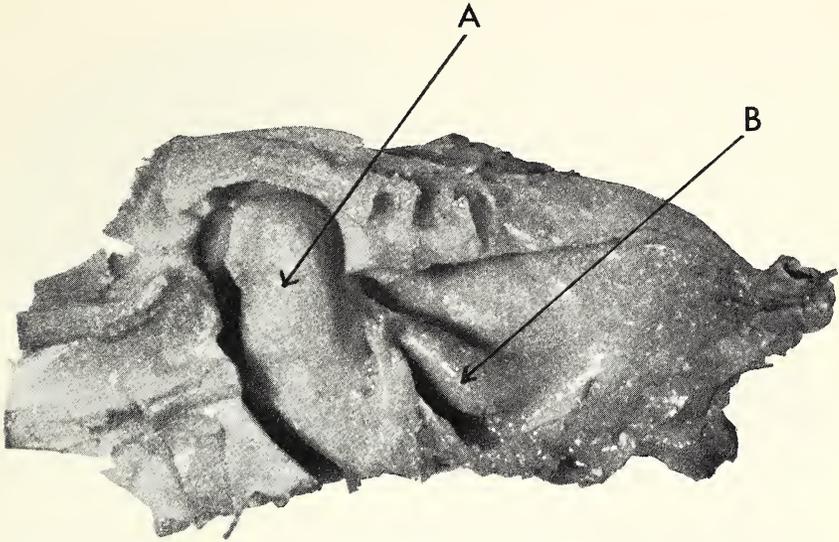


Figure 9. Dissection of olfactory chamber of the king vulture (*Sarcoramphus papa*), showing right anterior concha (a) and olfactory tubercle (b).

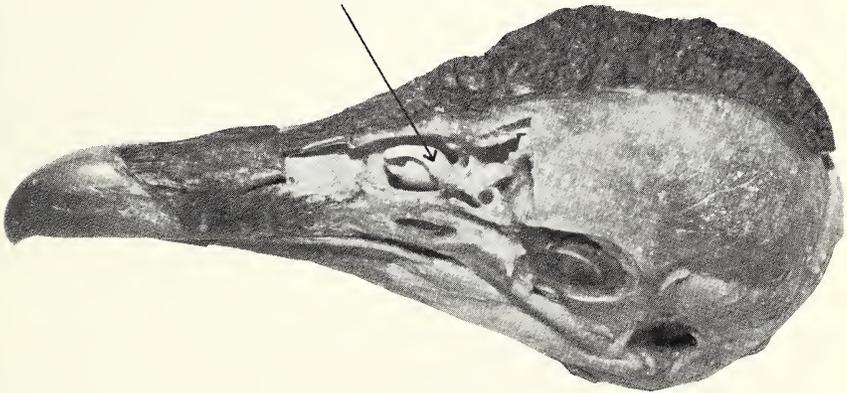


Figure 10. Dissection of anterior respiratory chamber of the black vulture (*Coragyps atratus*) showing left anterior concha.

Olfactory chambers of all genera of New World vultures were examined, with the exception of the genus *Vultur* for which no anatomical specimens were available. The highest degree of development within the family Cathartidae appears to occur in the genus *Cathartes*. In this vulture the tubercle is in the form of a large concha, scrolled two and one-half times (Fig. 11). The

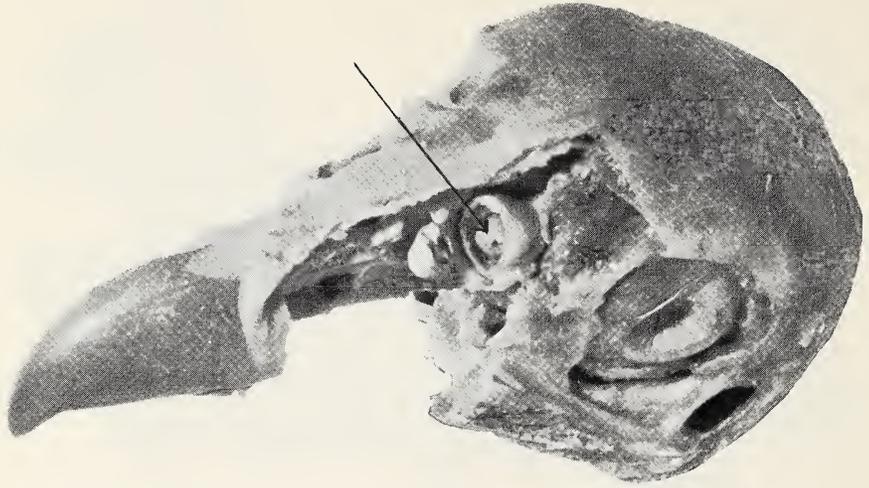


Figure 11. Dissection of olfactory chamber of the turkey vulture (*Cathartes aura*), showing a cross section through the left olfactory concha.

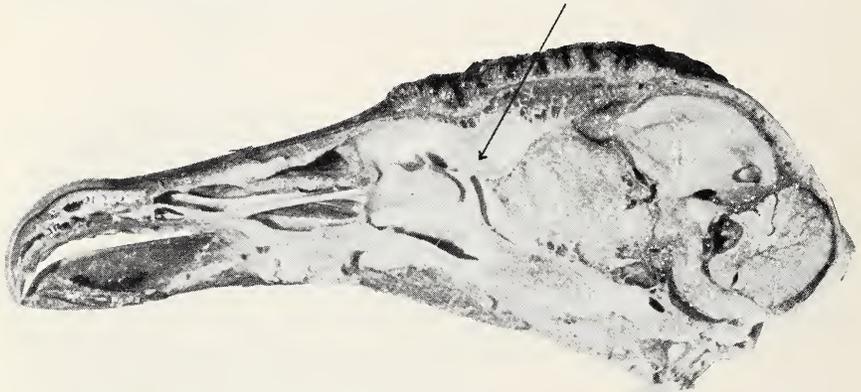


Figure 12. Dissection of olfactory chamber of the black vulture (*Coragyps atratus*), showing right olfactory tubercle (right median sagittal view).

concha fills the olfactory chamber and measures 14 mm. in length by 9 mm. high. In cross section the scrolled concha is 8 mm. in diameter.

In *Gymnogyps* there is evidence of a beginning of a concha, as the olfactory tubercle is in the form of a thin lip, 15 mm. long. The lip extends out from the lateral wall and is 4 mm. wide at its greatest width. In *Sarcoramphus* the tubercle is somewhat "S" shaped, with a length of 8 mm. (Fig. 12). There is no evidence of a lip formation as in *Gymnogyps*. The tubercle in *Coragyps* is the smallest of all the cathartine vultures examined. It is oval in shape, with a length of only 6 mm. (Fig. 12).

C. MICROANATOMY OF THE OLFACTORY CHAMBER

Portmann (1961:44) stated that the olfactory tubercle or concha is the only region of the nasal cavity that is covered with true olfactory epithelium, but Bang (1960:549) presented evidence to show that, not only is the tubercle or concha of the olfactory chamber of the turkey vulture innervated by branches of the olfactory nerve, but that strong branches of the olfactory nerve also lie along the roof, posterior and ventro-lateral walls and upper portion of the septum nasi of the olfactory chamber.

The olfactory chamber areas of four of the five genera of cathartine vultures were fixed and sectioned for microscopic examination (see "Methods"). The only genus for which material was not available was the Andean condor (*Vultur*).

Cross sections through the olfactory tubercle or concha area of *Cathartes* shows what appears to be a thick layer of olfactory epithelium on both surfaces of the large and much scrolled conchae (Fig. 13). The lining of the olfactory chamber appears to have a lining of epithelial cells identical in appearance to those of the conchae.

The surfaces of the concha appear to consist of an outer layer of epithelium comprised of olfactory and sustentacular cells. The sub-layer that I in-



Figure 13. Photomicrograph of olfactory epithelium of the turkey vulture (*Cathartes aura*).

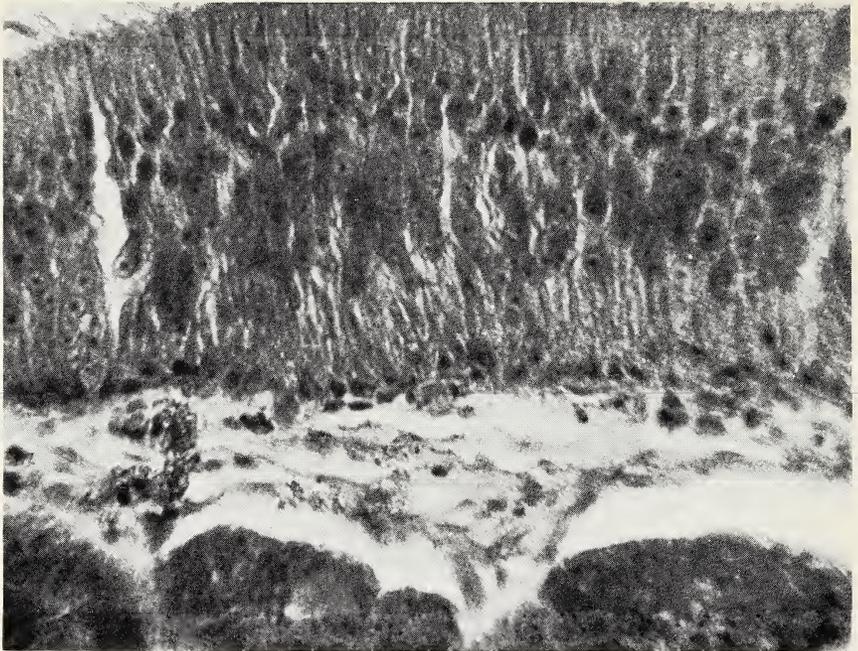


Figure 14. Photomicrograph of olfactory epithelium of the king vulture (*Sarcoramphus papa*).

terpret to be the tunica propria appears to contain a large concentration of Bowman's and mucous glands. The cell layers lining the walls of the olfactory chamber appear to be of a similar arrangement.

Examination of cross sections through a similar area in the olfactory tract of *Sarcoramphus* reveals a similar arrangement of cells on the surface of the olfactory tubercle as well as on the lining of the lateral wall of the chamber above the tubercle (Fig. 14). In *Sarcoramphus* there appears to be a great reduction in the number of Bowman's and mucous glands of the tunica propria, as compared to the large numbers of those glands present in *Cathartes*. It can be postulated that *Sarcoramphus*, living in the humid forests of the American tropics does not require the large number of glands to keep the olfactory epithelium moist as does *Cathartes* which ranges into extremely arid regions.

A cross section through the olfactory tubercle of *Coragyps* discloses an arrangement of cells somewhat resembling that described for *Sarcoramphus*. However, the layer of olfactory epithelium (Fig. 15) is not as thick as that observed in the preceding two genera, nor are the sustentacular cells as compact. The walls of the olfactory chamber show a lining of cells similar in appearance to those described for the olfactory tubercle.



Figure 15. Photomicrograph of olfactory epithelium of the black vulture (*Coragyps atratus*).

The olfactory tract material obtained from the California condor (*Gymnogyps*) unfortunately had been frozen before I received it. The freezing of the specimen caused a general rupturing of the epithelial layer, due to formation of ice crystals within the cells. Consequently, it is not possible to make a statement with regard to the arrangement of the epithelial cells in this genus.

Examination of a cross section through the olfactory chamber of the Old World vulture *Sarcogyps* fails to show an epithelial development comparable to the cellular arrangement observed in the cathartine vultures. Sections through the olfactory tract of the domestic pigeon (*Columba livia*) likewise show no appreciable development of an olfactory epithelium.

D. OLFACTORY BULB

Latex rubber endocranial casts (see "Methods") of the five recent genera of cathartine vultures provide an excellent index to the size of the olfactory bulb. Although *Cathartes* is the smallest cathartine vulture, it possesses an olfactory bulb far surpassing in size that of any of the other New World vultures, including the large condors.

When viewed dorsally (Fig. 16), the general configuration of the brain of *Cathartes* differs from that of the other four genera in the reduction of mass in the latero-anterior area of the cerebral hemispheres. This reduction of mass

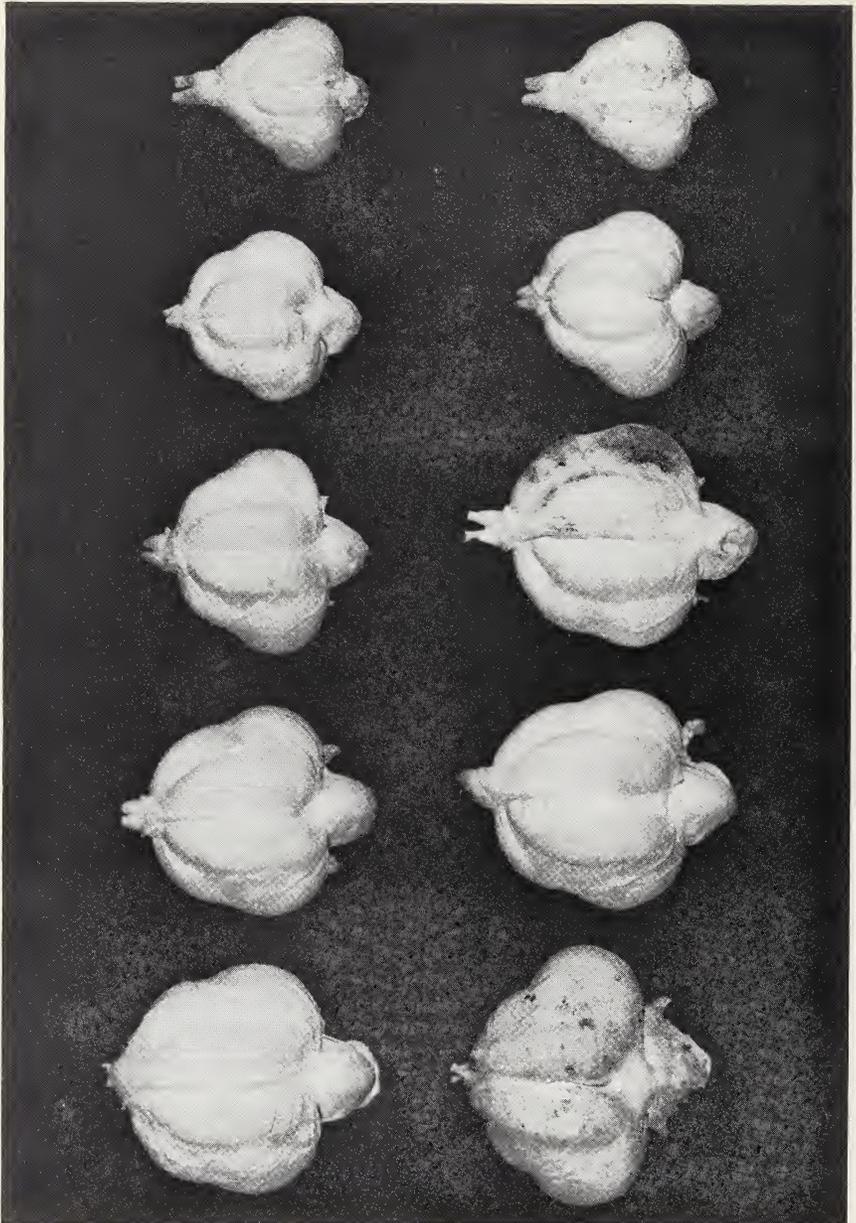


Figure 16. Endocranial casts of recent and Pleistocene cathartine vultures. Dorsal view, upper row, left to right (Recent): *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*. Bottom row, left to right (Pleistocene): *Teratornis*, *Gymnogyps*, *Breagyps*, *Coragyps*, and *Cathartes*.

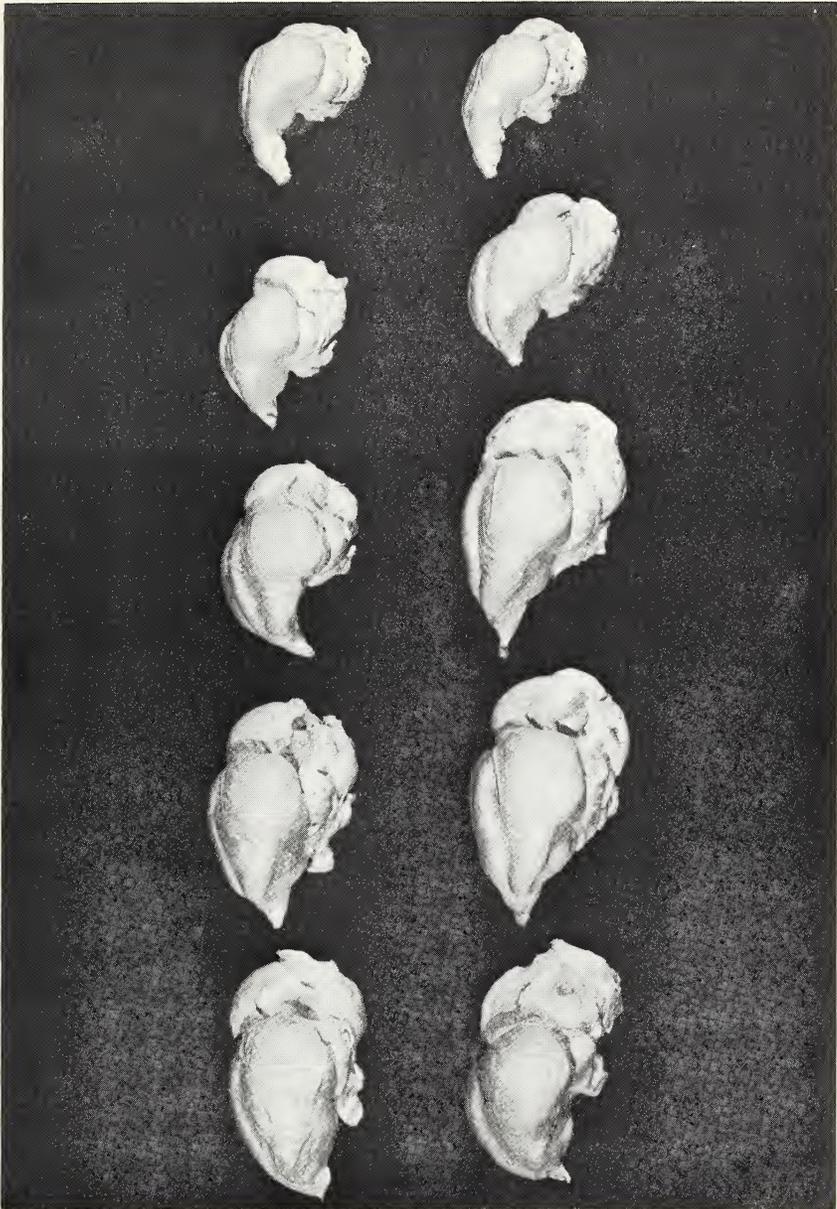


Figure 17. Endocranial casts of recent and Pleistocene cathartine vultures. Lateral view, upper row, left to right (Recent): *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*. Bottom row, left to right (Pleistocene): *Teratornis*, *Gymnogyps*, *Bregyps*, *Coragyps*, and *Cathartes*.

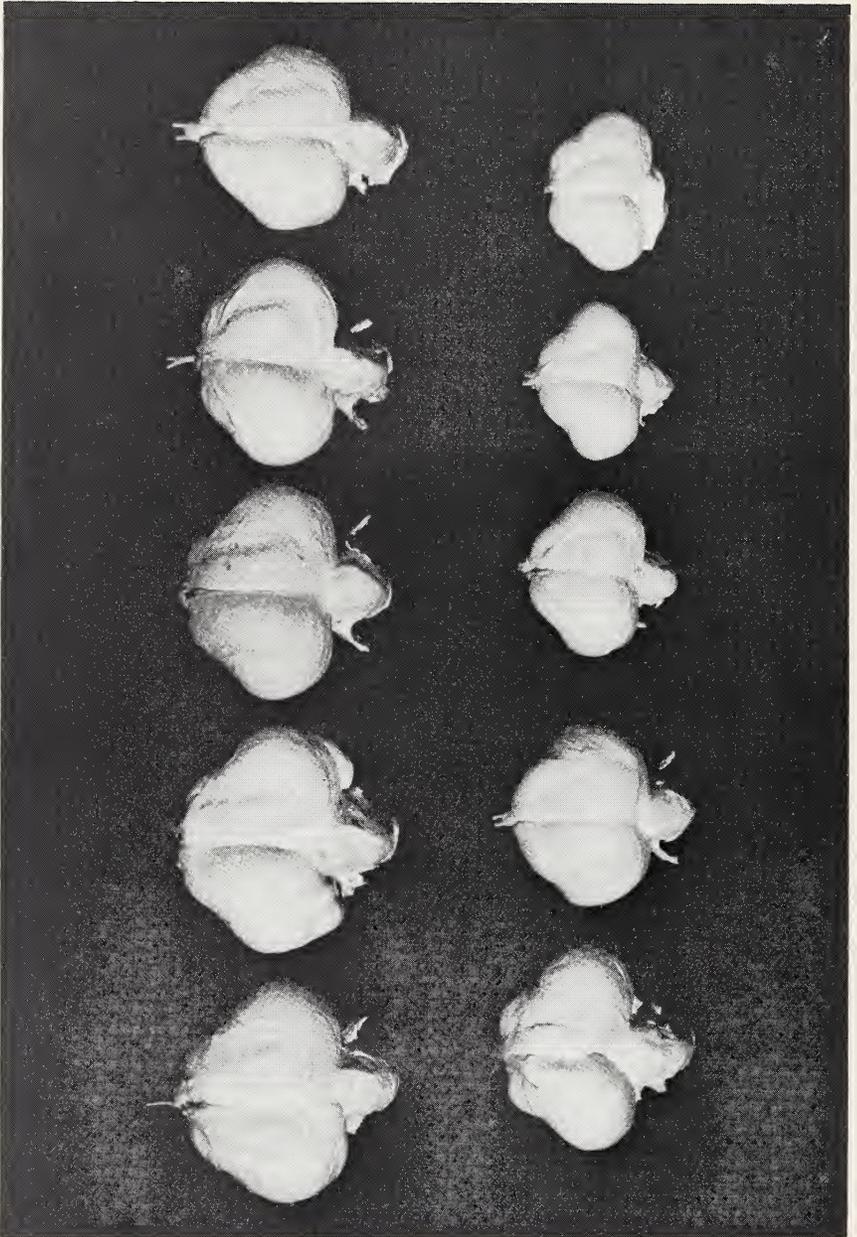


Figure 18. Endocranial casts of the recent aegyptine vultures. Dorsal view, upper row, left to right: *Torgos*, *Trigonoceps*, *Aegyptius*, *Sarcogyps*, and *Gyps*. Bottom row, left to right: *Pseudogyps*, *Gypaetus*, *Necrosyrtes*, *Gypohierax*, and *Neophron*.

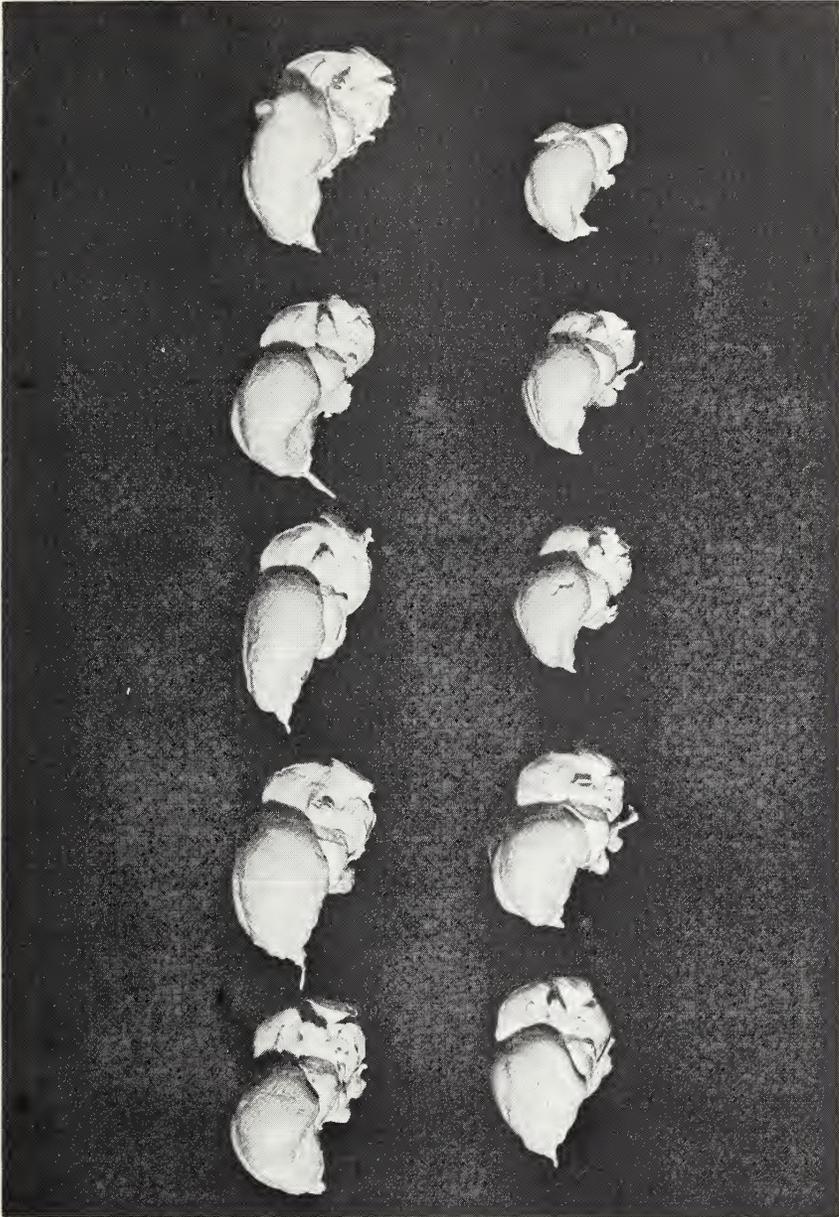


Figure 19. Endocranial casts of the recent aegyptine vultures. Lateral view, upper row, left to right: *Aegyptius*, *Torgos*, *Gyps*, *Sarcogyps*, and *Trigonoceps*. Bottom row, left to right: *Gypaëtus*, *Pseudogyps*, *Necrosyrtes*, *Gypohierax*, and *Neophron*.

in the forward area gives it a unique triangular shape, accentuated by the forward extension of the large olfactory bulbs.

The next largest olfactory bulb is found in the king vulture (*Sarcoramphus*). In gross size, the brain of *Sarcoramphus* is larger than that of the two smaller vultures *Cathartes* and *Coragyps*, but is smaller than the brain of either *Gymnogyps* or *Vultur*.

In lateral view (Fig. 17), the endocranial casts of *Vultur*, *Gymnogyps* and *Coragyps* bear a striking resemblance in general outline, while that of *Sarcoramphus* resembles the profile of *Cathartes* except for the greater size of the olfactory bulb in the latter genus.

It would appear to be of some significance that the largest olfactory bulb occurs in the genus *Cathartes*, the cathartine vulture demonstrating the greatest olfactory prowess in food-location.

Due to the unique mode of preservation of Pleistocene fossils in the asphalt deposits of Rancho La Brea, California, crania of all species of cathartine vultures entrapped there are available for use in the preparation of endocranial casts. Casts were prepared of *Breagyps clarki*, *Gymnogyps amplus*, *Coragyps occidentalis*, and *Cathartes aura* (Figs. 16 and 17). An endocranial cast was also obtained of the giant vulture-like *Teratornis merriami*.

Casts of the brains of the vultures of the Pleistocene period, when compared with casts of present-day forms, permit a postulation as to the possible olfactory abilities of these ancient birds.

The olfactory bulb of *Cathartes aura* of the Pleistocene equals in size that of the present-day *Cathartes*. There appear to be no appreciable morphological differences between the two birds. The cast of the Pleistocene *Cathartes* is slightly smaller than the brain of the present-day form, but this may well be individual variation. Based upon a comparison of size of the olfactory bulbs of the two forms, it can be stated with assurance that the turkey vulture of the Pleistocene probably had an olfactory acuity equalling that of the turkey vulture today. The species is sparsely represented in the Rancho La Brea deposits and this fact has been interpreted by some workers as indicating that the species was uncommon in the area during the Pleistocene. Viewed from an ethological standpoint, however, it may well be that the shy *Cathartes* did not join the other species of vultures at the great asphalt entrapment feasts, and thereby escaped the fate of the other species of vultures that are represented so abundantly at Rancho La Brea.

Coragyps occidentalis, the progenitor of *Coragyps atratus*, although somewhat larger than the latter, possessed an olfactory bulb equally small. The olfactory bulb of *Gymnogyps amplus* is similar in size to that of the present-day *Gymnogyps* (Fig. 16). The giant vulture *Teratornis merriami* was apparently dependent upon vision for food location, as the endocranial cast reveals a very small olfactory bulb (Fig. 16).

The endocranial casts of the ten aegyptine vulture genera (Figs. 18 and 19) have small olfactory bulbs as compared with those of the Cathartidae.

SUMMARY AND CONCLUSIONS

The historical background of the long-debated question of olfaction in birds, especially as it applies to New World vultures, is reviewed.

Field experiments, free of all visual food stimuli, conducted with the turkey vulture (*Cathartes aura*), are reported in detail.

Odors from fresh and decomposing animal tissue baits, placed on predetermined air currents by means of a forced air unit, elicited positive olfactory responses from turkey vultures. Turkey vultures were also able to detect the presence of concealed animal baits placed in bait chambers at various sites.

Experiments employing a visual decoy in the form of a mounted deer carcass failed to draw turkey vultures to the site. When the decoy was replaced with a fresh deer carcass of identical size and appearance, there was a rapid response from the turkey vultures in the area. Assembly at the carcass and feeding did not begin, however, until the vultures had obtained an olfactory cue from the potential food site. The dispensing of ethyl mercaptan on predetermined air currents elicited strong olfactory responses from large numbers of turkey vultures at test sites in Mexico and California. The hypothesis of Taber (1928) and Darlington (1930) which proposes that turkey vultures locate hidden food by observing the activities of necrophagous insects was found to be untenable as a result of the above-mentioned experiments, coupled with fly attractant tests in California and hidden bait experiments with aegyptine vultures in central India.

All previous references in the literature indicate a marked difference in behavior between the five genera of New World vultures, and an examination of these behavioral differences and similarities have contributed towards a clearer understanding of vulture food-locating behavior.

A comparative analysis of the mode of flight of the five genera of cathartine vultures shows that the turkey vulture (*Cathartes*) is capable of, and utilizes, a low-level searching flight that brings it close to the ground and in range of low-lying olfactory cues. The high-altitude soaring and circling habits of *Coragyps* and *Gymnogyps* enable these genera to locate food by visual means and also to locate food indirectly by observing the actions of low-flying *Cathartes* below. The ability of the turkey vulture to locate food sources by olfaction enables it to forage over a greater variety of terrain types than permitted the other cathartine genera. *Coragyps* will readily drop upon a suspect item of food without prior inspection, but *Cathartes* circles the potential food source until an olfactory cue has been obtained, even though the carcass is large and obvious.

Although *Cathartes* is the smallest of the five cathartine genera, it possesses the largest external nares. The anterior respiratory conchae are similarly arranged as to the angle at which they tilt downward towards the secondary choana. Only *Cathartes* possesses a large, much scrolled olfactory conchae in the olfactory chamber. Microscopic examination of the sectioned material

from the olfactory chamber of *Cathartes* shows what appears to be a highly developed olfactory epithelium, not only on both surfaces of the scrolled conchae, but on the walls of the chamber as well. Examination of sectioned material from the olfactory chamber of *Sarcoramphus* shows an arrangement of olfactory epithelium very similar in appearance to that found in *Cathartes*. The tunica propria of *Cathartes* contains large numbers of Bowman's and mucous glands in contrast to the small number present in the tunica propria of *Sarcoramphus*. It can be postulated that *Sarcoramphus*, living in the humid forests of tropical America, does not require the large number of glands to keep the olfactory epithelium moist as does *Cathartes* which ranges into extremely arid regions. The layer of olfactory epithelium present in *Coragyps* is not as thick as that observed in *Cathartes* or *Sarcoramphus*, nor are the sustentacular cells as compact. Examination of a cross section through the olfactory chamber of the Old World vulture *Sarcogyps* fails to show an epithelial development comparable to the cellular arrangement present in cathartine vultures.

A comparison of endocranial casts of cathartine vultures shows that although the brain of *Cathartes* is the smallest of the five genera, it possesses the largest olfactory bulb. The second largest olfactory bulb occurs in *Sarcoramphus*. On the basis of the size of the olfactory bulbs of fossil vultures, as demonstrated by endocranial casts, it can be postulated that among the cathartine genera of the Pleistocene period, *Cathartes* possessed olfactory equipment closely resembling that of the present-day turkey vulture, while *Coragyps*, *Breagyps*, and *Gymnogyps* of the Pleistocene lacked the needed morphological structures, as do their descendents today. Examination of endocranial casts of all recent genera of aegyipiine vultures reveals that all possess a very small olfactory bulb, similar in size to the bulbs found in the other members of the suborder Falcones.

From the evidence at hand it can be concluded that among the cathartine vultures, the turkey vulture (*Cathartes aura*) possesses and utilizes a well-developed olfactory food-locating mechanism. The king vulture (*Sarcoramphus*) of tropical America, although its behavior is little known, appears on the basis of present ethological and morphological data, also to utilize olfaction in its location of food. The need for a detailed study of the food-locating habits of *Sarcoramphus* is thus indicated. There is no evidence, either ethological or morphological, to indicate that olfaction plays more than a minor, if any, role in food location by *Coragyps*, *Gymnogyps* and *Vultur*. There likewise were no data to indicate that the Old World vultures employ any sense other than vision in the location of food.

Finally, it can be said that the turkey vulture appears to be the most successful of all cathartine vultures in the New World today, and that this success can be attributed largely to its demonstrated olfactory acuity. Olfaction, assisted by a specialized type of foraging flight, enables the turkey vulture to seek and locate food in a greater variety of terrain types than are available to the other members of the family Cathartidae.

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THE FISH FAUNA OF THE PLAYA DEL REY LOCALITY,
A SOUTHERN CALIFORNIA MARINE PLEISTOCENE DEPOSIT

By JOHN E. FITCH



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THE FISH FAUNA OF THE PLAYA DEL REY LOCALITY, A SOUTHERN CALIFORNIA MARINE PLEISTOCENE DEPOSIT¹

By JOHN E. FITCH²

ABSTRACT: An assortment of fish remains excavated since 1935 from the Playa del Rey deposit, Los Angeles County, California, contained nearly 2,000 recognizable items. Elasmobranchs were represented by teeth, vertebrae, stings, and body spines; teleosts by otoliths, pharyngeal teeth, vertebrae, and other bony parts. Most of the 47 species identified from these remains still inhabit quiet coastal waters adjacent to Los Angeles County; however, a few no longer are constituents of the local fauna, but can be found living in warm tropical waters several hundred miles to the south. Thus, the fish remains from this formation typify a shallow-water, sandy or sandy-mud habitat at a time when local ocean temperatures were several degrees warmer than they are today.

Southern California is blessed with numerous Pleistocene outcroppings containing rich fossil assemblages. Mollusks were described from some of these more than a century ago (Conrad, 1855), and in the ensuing 105 years, at least 90 other authors contributed additional information on this group (Valentine, 1961). On the other hand, published information on southern California's Pleistocene fish fauna is limited to a single paper (Kanakoff, 1956).

PLAYA DEL REY LOCALITY (*Palos Verdes Sand*)

The Playa del Rey or "Lincoln Avenue deposit" was first brought to public attention in 1937 when Willett recorded a mixed molluscan fauna containing 296 species. These had been screened and sorted from several tons of fossiliferous material during 1935 and 1936. In addition to mollusks, this deposit contained remains of at least 28 species of crustaceans, 3 echinoderms, 1 bryozoan, 2 marine mammals, and "a goodly representation of fish material. . ." (Willett, 1937).

The habitat apparently was a fine-grained silty sand, typical of a quiet-water embayment 10 to 12 fathoms deep (Willett, 1937; Valentine, 1961). Among the mollusks reported by Willett, 261 live in the same latitude today, while 19 are found only farther to the south, many being confined to Mexican waters. A deep-water or northern fauna was also mixed in, but these remains, because of their worn appearance and rarity, were believed to be detrital, having washed in from adjacent areas.

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TABLE 1
List of Fish Remains Found in the Playa del Rey (Pleistocene) Deposit

Scientific name	Common name	Type and number of remains found				
		teeth	otoliths	vertebrae	stings	other
ELASMOBRANCHS						
<i>Notorynchus maculatus</i>	sevendill shark	4				
<i>Alopias vulpinus</i>	thresher shark	2				
<i>Carcharodon carcharias</i>	great white shark	6		4		
<i>Isurus glaucus</i>	bonito shark	2				
<i>Carcharhinus</i> spp.	carcharhinid sharks	26				
<i>Galeorhinus zyopterus</i>	soupin shark	15				
<i>Scoliodon longurio</i>	sharpnose shark	1				
<i>Sphyrna</i> spp.	hammerhead sharks	3		17		
<i>Squatina californica</i>	angel shark	10		8		
<i>Raja</i> spp.	skates			8		3†
<i>Urolophus halleri</i>	round stingray				164	
<i>Myliobatis californicus</i>	bat ray	205				
	unidentified sharks	3				
TELEOSTS						
<i>Engraulis mordax</i>	northern anchovy				68	
<i>Merluccius productus</i>	hake				24	
<i>Paralichthys californicus</i>	California halibut				1	
<i>Citharichthys sordidus</i>	Pacific sanddab				29	
<i>Citharichthys stigmaeus</i>	speckled sanddab				238	

TABLE 1 (continued)

Scientific name	Common name	Type and number of remains found				
		teeth	otoliths	vertebrae	stings	other
<i>Citharichthys</i> spp.	sanddabs		23			
<i>Lypsetta jordani</i>	slender sole		1			
<i>Pleuronichthys ritteri</i>	spotted turbot		1			
<i>Parophrys vetulus</i>	English sole		1			
<i>Leuresthes tenuis</i>	grunion		6			
<i>Atherinopsis californiensis</i>	jacksmelt		3			
<i>Atherinops affinis</i>	topsmelt		1			
<i>Sphyraena argentea</i>	California barracuda		1			
<i>Anisotremus davidsoni</i>	sargo		1			
<i>Micropogon ectenes</i>	berrugato		2			
<i>Umbrina roncadore</i>	yellowfin croaker		13			
<i>Genyonemus lineatus</i>	white croaker		217			
<i>Roncadore stearnsi</i>	spotfin croaker		19			
<i>Menticirrhus undulatus</i>	California corbina		1			
<i>Cynoscion nobilis</i>	white seabass		5			
<i>Cynoscion reticulatus</i>	striped corvina		4			
<i>Seriplus politus</i>	queenfish		275			
<i>Phanerodon furcatus</i>	white seaperch		9			
<i>Cymatogaster aggregata</i>	shiner perch		6			
<i>Pimelometopon pulchrum</i>	California sheephead					7†
<i>Sebastes paucispinis</i>	bocaccio		6			
<i>Sebastes jordani</i>	shortbelly rockfish		2			
<i>Sebastes aurora</i>	aurora rockfish		1			

TABLE 1 (continued)

Scientific name	Common name	Type and number of remains found				
		teeth	otoliths	vertebrae	stings	other
<i>Sebastodes diploproa</i>	splitnose rockfish		1			
<i>Sebastodes rhodochloris</i>	swordspine rockfish		1			
<i>Sebastodes</i> spp.	rockfishes		13			
<i>Chitonotus pugetensis</i>	roughback sculpin		1			
<i>Lepidogobius lepidus</i>	bay goby		1			
<i>Porichthys notatus</i>	plainfin midshipman		161			
<i>Porichthys myriaster</i>	specklefin midshipman		15			
<i>Otophidium taylori</i>	spotted cusk-eel		83			
<i>Otophidium scrippsae</i>	basketweave cusk-eel		140			
<i>Lepophidium negropinna</i>	giant cusk-eel		2			
	unidentifiable teleosts		33	25		7**

†spines from skate "wings"

‡pharyngeal bone (1) and teeth (6)

**pharyngeal bone (1) and assorted fin and vertebral spines (6)

Although Willett reported that some 700 specimens of fish remains were saved, Kanakoff (1956) listed only 380 items representing 21 species. This was all of the fish material from the "Lincoln Avenue deposit" still in the Los Angeles County Museum at that time. Apparently many of the items mentioned by Willett had been misplaced in the ensuing 20 years.

Because this site was rich in fish remains, and still could be excavated, many additional pounds of fossiliferous matrix were screened in 1963 to obtain many of the items reported herein. To make this report as complete as possible, I reexamined the specimens listed by Kanakoff for LACMIP 59, and incorporated them with the abundant material obtained since 1956. Thus, my paper lists all of the fish remains from the Playa del Rey presently preserved in Los Angeles County Museum (Table 1).

THE FISH FAUNA

Teleost remains were represented by 1,409 otoliths and otolith fragments, 2 pharyngeal bones, 6 pharyngeal teeth, 25 vertebrae, and 6 miscellaneous spines and similar structures. In addition, there were 276 teeth, 37 vertebrae, 164 stings, and 3 miscellaneous items from sharks, skates, and rays. I was able to determine names for all but 34 of the 1,409 otoliths, and for the pharyngeal teeth, as well as all but three of the elasmobranch remains.

Croaker (family Sciaenidae) otoliths, with 535 individuals in seven genera and eight species, were the most abundant of these structures. Six teleost fish families were represented by only a single species each, and in four of these (Sphyraenidae, Pomadasyidae, Gobiidae, and Cottidae) there was but a single otolith. A pharyngeal bone and teeth were from sheephead, *Pimelometopon pulchrum*. The various unidentified teleost vertebrae and other assorted bones probably came from some of the same species that left otoliths. The unidentified otoliths were too fragmental or too badly worn to assign names; they too probably were from the same species as those identified.

The elasmobranch remains were from at least 12 species belonging to 12 genera in 8 families. Plate-like jaw teeth of bat rays, *Myliobatis californicus*, and stings (caudal spines) of either this species or of round stingrays, *Urolophus halleri*, comprised over 75 per cent of the 480 elasmobranch remains.

SYSTEMATIC ACCOUNT

Hexanchidae—cow sharks

Notorynchus maculatus Ayres—sevengill shark

On rare occasions young individuals are taken off southern California, particularly in Santa Monica Bay. Their usual range is from about northern British Columbia to Monterey Bay. Specimens exceeding 8 or 9 feet are seldom seen, but they are reported to attain 15 feet. They are usually captured near the bottom in water 50 to 600 feet deep.

Four sevengill shark teeth (Figure 1) were screened from this deposit. These are extremely difficult to distinguish from sixgill shark teeth (*Hexanchus* sp.), but the serrations on sevengill teeth are slightly larger.

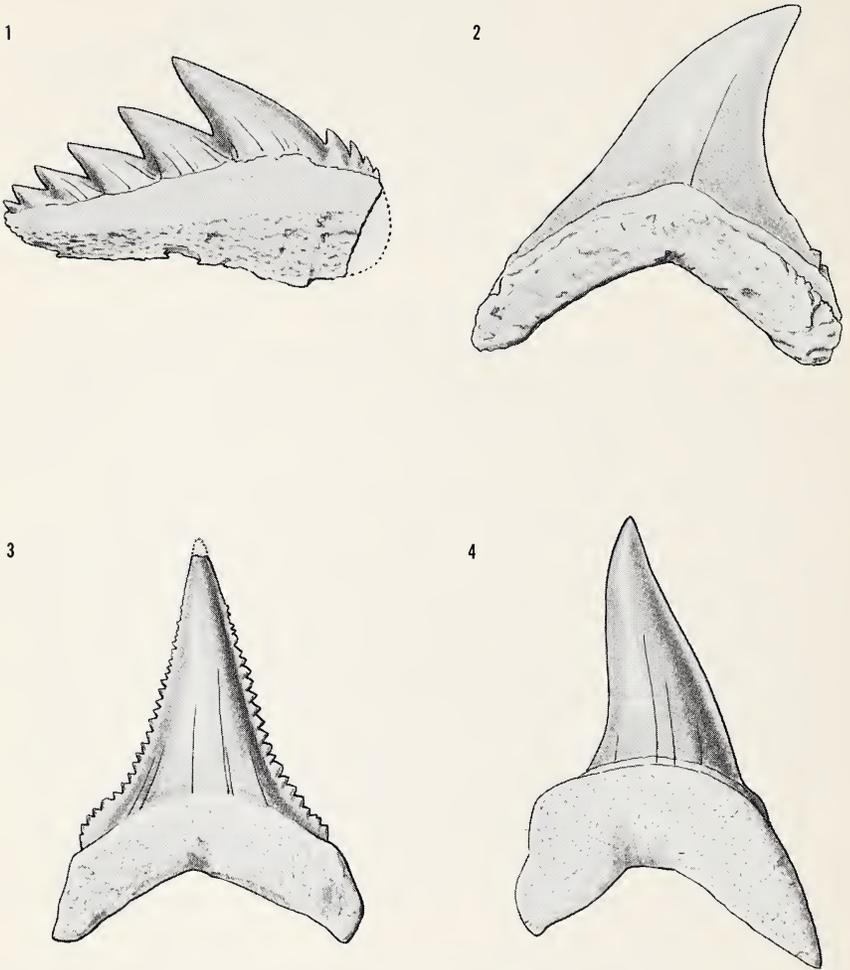


Figure 1. Lower right lateral tooth of sevengill shark, *Notorynchus maculatus* (width of base to break 20.5 mm, LACMIP 59).

Figure 2. Upper left lateral tooth of thresher shark, *Alopias vulpinus* (width of base 5.8 mm, LACMIP 59).

Figure 3. Lower right anterior tooth of great white shark, *Carcharodon carcharias* (width of base 19.4 mm, LACMIP 59).

Figure 4. Lower left lateral tooth of bonito shark, *Isurus glaucus* (width of base 17.7 mm, LACMIP 59).

*Lamnidae—mackerel sharks**Alopias vulpinus* (Bonnaterre)—thresher shark

Thresher sharks are known from temperate and tropical waters of all world seas. On our coast, this species ranges from Vancouver Island, British Columbia, well into Mexican waters. They are also fairly abundant on the high-seas, usually at or near the surface. The individuals most likely to visit shallow waters near shore are young. An 18-foot specimen is the largest known from our coast, but most are shorter than 8 feet, with the tail making up about half the length. Two thresher shark teeth (Figure 2) were found in this deposit.

Carcharodon carcharias (Linnaeus)—great white shark

This shark also inhabits all world seas, and has been captured on numerous occasions along our coast between Washington and Ensenada, Baja California. The modern-day record of 35 feet may be an unreliable estimate; most Californian specimens are shorter than 12 feet. This species probably is responsible for most of California's shark attacks, usually made in relatively shallow water near shore. Six teeth (Figure 3) and four vertebrae were found in this deposit.

Isurus glaucus (Müller and Henle)—bonito shark

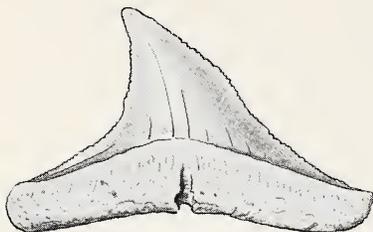
Our bonito shark is possibly identical to its Atlantic relative, but on the Pacific coast it ranges only from about Monterey Bay to the vicinity of Magdalena Bay, Baja California. It or a similar species occurs well offshore, where it is captured on longline gear. Bonito sharks are abundant in our waters, but seldom exceed 8 feet; however, they may attain lengths of 13 feet. They usually are found at or near the surface over fairly deep water. Two of the shark teeth were from this species (Figure 4).

*Carcharhinidae—requiem sharks**Carcharhinus* spp.—carcharhinid sharks of several species

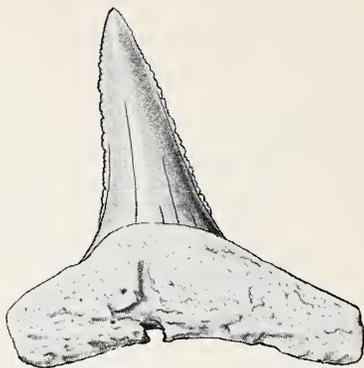
These are typically tropical sharks along the Pacific coast, yet at least four species have been captured off southern California at one time or another. While rare in our waters, all become abundant in more tropical waters, especially around offshore islands and land masses, although a few are pelagic forms. Identical or similar species are known from most world seas. Some species probably reach 15 feet, while others may never exceed 5. In our area, they usually are captured near the bottom close to shore.

Considerable confusion exists regarding speciation within this genus, mainly because intraspecific variation is not fully understood. Their teeth appear distinguishable at the species level, but because of general confusion among taxonomists as to which species are valid, it seems wise not to try placing names on the 26 *Carcharhinus* teeth (Figures 5 and 6) found in this deposit.

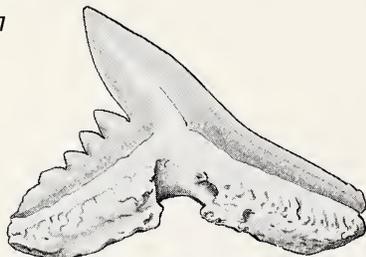
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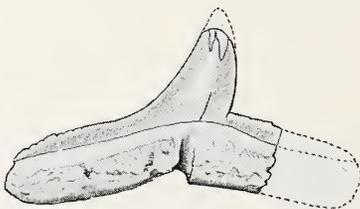


Figure 5. Upper right lateral tooth of *Carcharhinus* sp. (width of base 17.6 mm, LACMIP 59). When fresh, the margins of this tooth were finely but evenly serrate.

Figure 6. Lower left lateral tooth of *Carcharhinus* sp. (width of base 13.7 mm, LACMIP 59). When fresh, the margins of this tooth were finely but evenly serrate.

Figure 7. Lower left lateral tooth of soupfin shark, *Galeorhinus zyopterus* (width of base 6.6 mm, LACMIP 59).

Figure 8. Lower right lateral tooth of sharpnose shark, *Scoliodon longurio* (width of base to break 5.8 mm, LACMIP 59). The shoulders of this tooth were finely serrate when fresh.

Galeorhinus zyopterus Jordan and Gilbert—soupfin shark

Soupfin sharks are abundant between northern British Columbia and Abreojos Point, Baja California. The males typically inhabit waters in the southern part of this range, while females prefer the northern. This small species seldom exceeds 6 feet. They usually are found at or near the bottom in several hundred feet of water, but sometimes are in quite shallow areas. There were 15 soupfin shark teeth in this deposit (Figure 7). In the report by Kana-koff (1956), I mistakenly identified these as leopard shark, *Triakis semi-fasciata*, teeth.

Scoliodon longurio (Jordan and Gilbert)—Pacific sharpnose shark

This small, tropical species has been seen once or twice in recent years off southern California, occurring as far north as Long Beach. Adults are usually extremely abundant from about Magdalena Bay, Baja California, to Peru. Some individuals may reach 3½ feet, but most do not exceed 2 or 3. They usually inhabit quiet waters near shore, where they can be caught at or near the bottom. One tooth (Figure 8) was recovered from the Playa del Rey deposit.

Sphyrnidae—hammerhead sharks*Sphyrna* spp.—hammerhead sharks, species undetermined

Three species of these tropical sharks have been recorded from our waters in modern times. The largest hammerheads may reach 15 feet, although individuals exceeding 8 feet are rare. During summer months of warmwater years, hammerheads are fairly abundant off California to about Santa Bar-

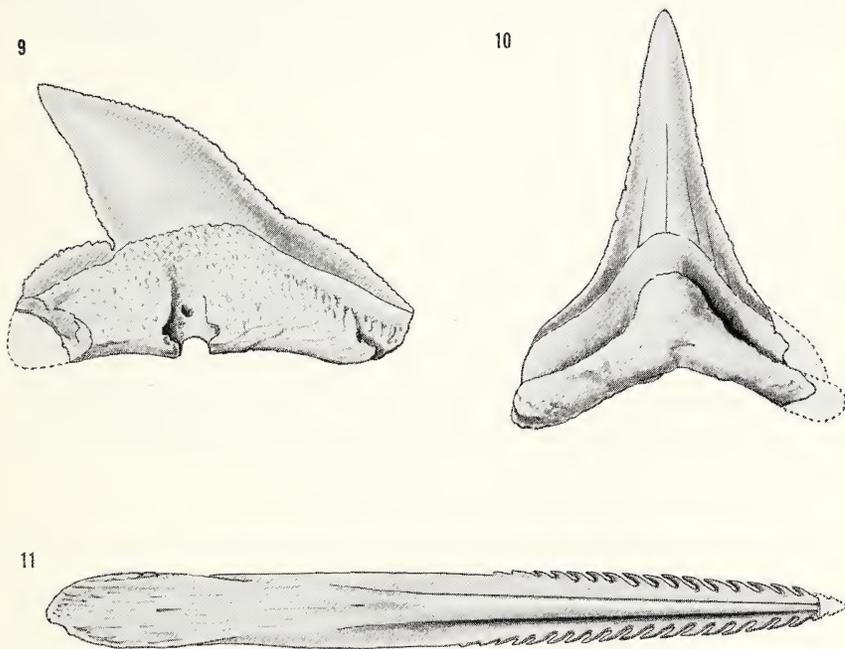


Figure 9. Upper left lateral tooth of hammerhead shark, *Sphyrna* sp. (width of base to break 12.8 mm, LACMIP 59). The margins of this tooth were finely but evenly serrate when fresh.

Figure 10. Lower anterior tooth of angel shark, *Squatina californica* (width of base 4.7 mm, LACMIP 59).

Figure 11. Caudal "sting" of round stingray, *Urolophus halleri* (length of sting to break 32.8 mm, LACMIP 59).

bara. They usually are found at or near the surface over the continental shelf, sometimes entering quiet waters near shore and sometimes staying many miles offshore. Our present (inadequate) knowledge of their dentition, precludes placing specific names on the 3 teeth (Figure 9) and 17 vertebrae from this deposit that were definitely from hammerheads.

Squatinidae—angel sharks

Squatina californica Ayres—Pacific angel shark

Angel sharks are reported in the literature from Alaska, but not from British Columbia. Most of our recent records place this species within the area bounded by Oregon and Magdalena Bay. They also are found in the northern Gulf of California. Although they are said to reach 5 feet, the largest of several hundred examined during the past 20 years was slightly shorter than 4 feet and weighed 31 pounds. They usually abound on sandy bottoms from just outside the surf zone to depths of several hundred feet. They were represented in this deposit by 10 teeth (Figure 10) and 8 vertebrae.

Rajidae—skates

Raja spp.—skates of various species

Six species of skates are known from Californian waters and several additional species are known from off Mexico. Skates usually live on the bottom in water deeper than 50 feet, but occasional young individuals are captured in shallow water near shore. Some attain 6 to 8 feet, but most species apparently are shorter than 2. They are especially abundant on sandy-mud or firm-mud bottoms. Some species have large spines scattered over their upper surfaces, and the adult males of most species have numerous, strong, curved spines near the tips of their "wings." There were 8 skate vertebrae in this deposit, and 3 spines from skate "wings." At present, I cannot tell if these remains represent more than one species, but they appear to be from at least two.

Dasyatidae—stingrays

Urolophus halleri Cooper—round stingray

Round stingrays have been captured at Humboldt Bay, California, but are unusual north of Point Conception. They are most common from about Ventura to Panama, often being extremely abundant during the summer in shallow bays, estuaries, sloughs, and along the outer coast. They are especially fond of areas where the bottom is sandy or sandy-mud. Of several thousand examined during the past 20 years, the largest was 22 inches long. All of the 164 stings (Figure 11) found in this deposit have been assigned to this species, although some may have been from other stingrays. They were believed to be *Urolophus* mainly because they were too small for adult bat rays (*Myliobatis*) or diamond stingrays (*Dasyatis*), and also because *Urolophus* occurs in our

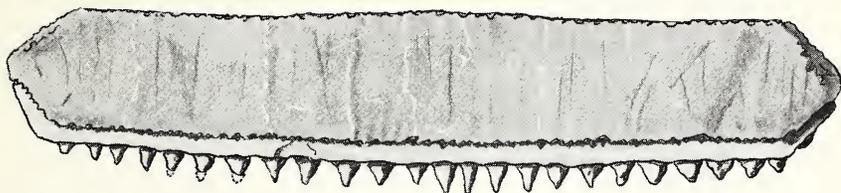
waters in such profusion today, compared with other stingrays. While not absolute, these criteria do seem of sufficient strength to warrant this identification.

Myliobatidae—eagle rays

Myliobatis californicus Gill—bat ray

Bat rays are abundant between southern Oregon and Magdalena Bay, Baja California, and also are found in the upper Gulf of California. They attain widths slightly over 4 feet and weights to 209 pounds. They usually inhabit shallow, quiet embayments, but also abound offshore in depths to at

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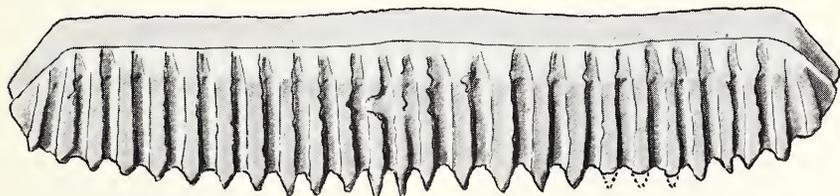


Figure 12. Median tooth of bat ray, *Myliobatis californicus*: a. upper "crushing" surface, b. under side (greatest width 32.0 mm, LACMIP 59).

least 200 feet. Bat rays wreak considerable havoc among shallow-water bivalves, and are especially fond of young oysters, crushing the shells of these and other mollusks with their heavy, plate-like teeth, 205 of which were found in this deposit (Figure 12).

Unidentifiable sharks

Three shark teeth screened from the Playa del Rey deposit were so badly worn they could not be identified, even to family, but probably do not represent additional species.

*Engraulidae—anchovies**Engraulis mordax* Girard—northern anchovy

Northern anchovies are small schooling fishes that range throughout most of the area between the north end of Vancouver Island and Magdalena Bay. At times they are found 100 miles or more offshore, but most “observed” schools are near shore, sometimes in the surf zone and in the innermost channels of harbors, back bays, and estuaries. They are usually at or near the

13



Figure 13. Right sagitta of northern anchovy, *Engraulis mordax* (length 4.1 mm, LACMIP 59). Left, outer face; right, inner face.

surface but many are found in the stomachs of bottom-living predators caught in 600 to 800 feet of water. Most of the 68 anchovy otoliths (Figure 13) in the Playa del Rey deposit were in poor condition, more from deterioration than from wear and tear such as would have occurred if they had settled out in an active surf area.

*Merlucciidae—hakes**Merluccius productus* (Ayers)—Pacific hake

Pacific hake range from the Gulf of Alaska to Cedros Island, and offshore for 350 miles or more. During some periods, hake are caught in shallow water near shore, but mainly they inhabit areas near the bottom fairly well offshore. They seem to prefer living above sandy or sandy-mud bottoms,

14



Figure 14 Left sagitta of hake, *Merluccius productus* (length 8.8 mm, LACMIP 59). Left, outer face; right, inner face.

sometimes to depths of nearly 500 fathoms but they are caught mostly in 20 to 100 fathoms. Hake otoliths (Figure 14) are quite thin and delicate, and most of the 24 in this deposit were badly deteriorated.

*Bothidae—left-eyed flounders**Paralichthys californicus* (Ayers)—California halibut

During extensive periods when coastal waters are warm, California halibut are caught far north of their typical range. Thus they have been caught

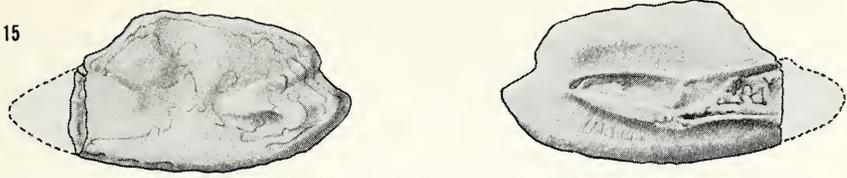


Figure 15. Left sagitta of California halibut, *Paralichthys californicus* (length to break, 7.0 mm, LACMIP 59). Left, outer face; right, inner face.

off the Klamath River, California, but are not common north of San Francisco, ranging from there to Magdalena Bay. They prefer sandy or sandy-mud bottoms in water shallower than about 25 fathoms. There was a single California halibut otolith (Figure 15) in this deposit.

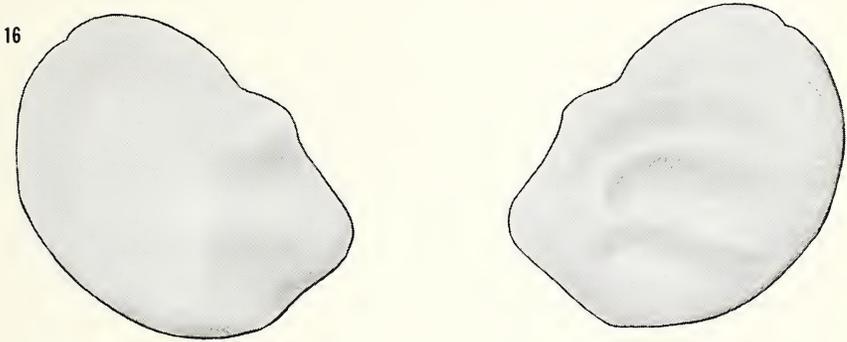


Figure 16. Right sagitta of Pacific sanddab, *Citharichthys sordidus* (length 5.8 mm, LACMIP 59). Left, outer face; right, inner face.

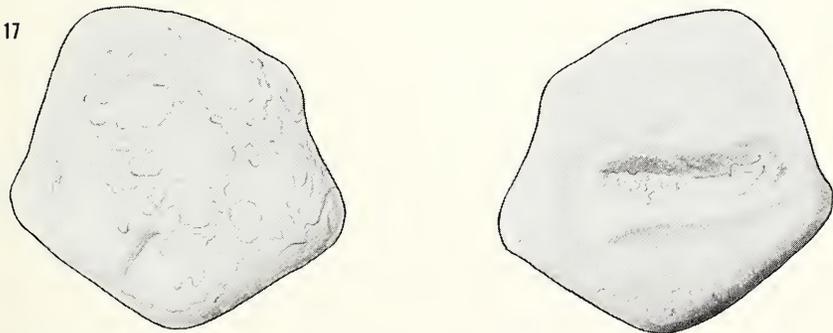


Figure 17. Right sagitta of speckled sanddab, *Citharichthys stigmaeus* (length 2.4 mm, LACMIP 59). Left, outer face; right, inner face.

Citharichthys sordidus (Girard)—Pacific sanddab

Pacific sanddabs range from about southern Alaska to Magdalena Bay. They are most abundant in 20 to 50 fathoms, but occur both shallower and deeper. They prefer sandy or sandy-mud bottoms, living directly on the substrate. An extremely large individual might reach 12 inches. Twenty-nine of the otoliths belonged to this species (Figure 16).

Citharichthys stigmaeus Jordan and Gilbert—speckled sanddab

Trawling with a fine-meshed net has revealed that speckled sanddabs are one of the most abundant bottom-living species inhabiting California's shallow coastal waters. They occur profusely from about Vancouver Island to Magdalena Bay, usually in 5 to 25 fathoms, occasionally as deep as 70 fathoms and rarely in 100. They live mostly on a sandy or firm sandy-mud substrate, and adults seldom are 5 inches long. In all, 238 of their otoliths (Figure 17) were identified from this deposit.

Citharichthys spp.—sanddabs

Twenty-three otoliths were unquestionably from sanddabs, but they were so badly worn or fragmented I was unable to assign specific names. They probably were from either speckled or Pacific sanddabs, but some may have been from *C. xanthostigma* Gilbert (longfin sanddab), the third and only other species inhabiting our waters at present.

Pleuronectidae—righteyed flounders*Lyopsetta exilis* (Jordan and Gilbert)—slender sole

Slender soles are almost as abundant in deeper waters (70 to 100 fathoms) as speckled sanddabs are in shallow areas. They have been captured all the way from Alaska to Cedros Island, typically on sandy-mud or muddy bottoms, occasionally as shallow as about 30 fathoms. Although large individuals may reach lengths of 12 inches, they are slender and thin, and seldom weigh more than a few grams. A single slender sole otolith (Figure 18) was found.

Pleuronichthys cf. *ritteri* Starks and Morris—spotted turbot

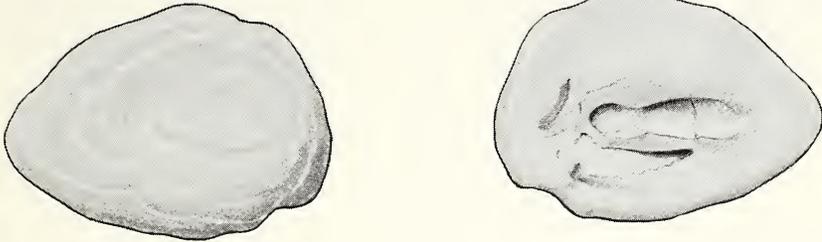
Spotted turbot are captured in relatively shallow water (1½ to 25 fathoms, but mostly less than 10) over sandy-mud or muddy bottoms from about Santa Barbara to Magdalena Bay. Four species of *Pleuronichthys* inhabit our waters and the otoliths of all are quite similar, but the single turbot otolith in this deposit (Figure 19) seemed to fit *P. ritteri* best.

Parophrys vetulus Girard—English sole

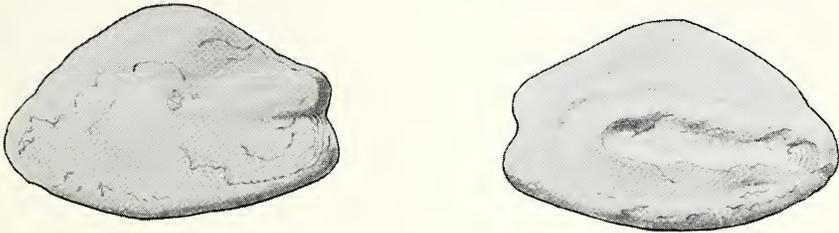
Off southern California, English soles are usually caught in 10 to 70 fathoms of water, moving inshore and offshore with changing seasons. The species ranges throughout the continental shelf area between about Alaska

and Cedros Island. They prefer sandy-mud or muddy bottoms, where they feed upon small mollusks, brittle starfish, polychaete worms, and other invertebrate organisms inhabiting these substrates. A single English sole otolith (Figure 20) was identified.

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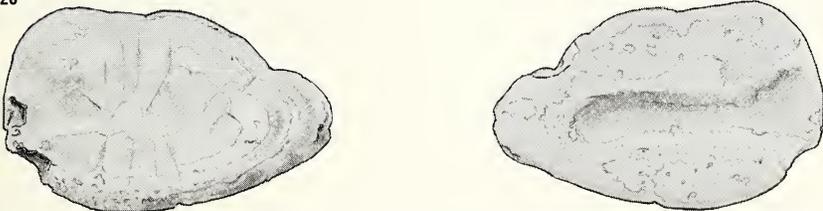
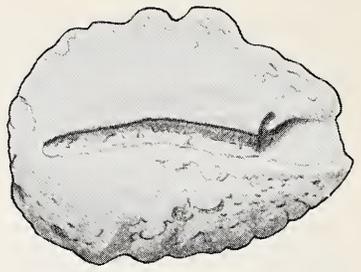


Figure 18. Left sagitta of slender sole, *Lyopsetta exilis* (length 3.5 mm, LACMIP 59). Left, outer face; right, inner face.

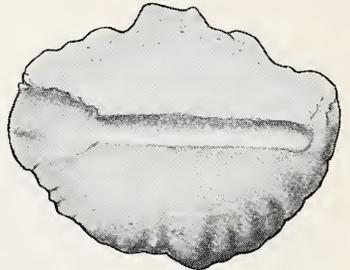
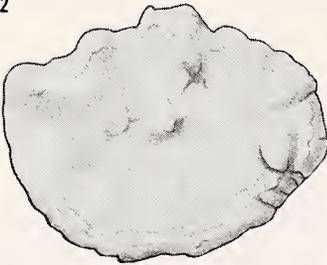
Figure 19. Left sagitta of turbot, *Pleuronichthys cf. ritteri* (length 3.2 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 20. Right sagitta of English sole, *Parophrys vetulus* (length 6.0 mm, LACMIP 59). Left, outer face; right, inner face.

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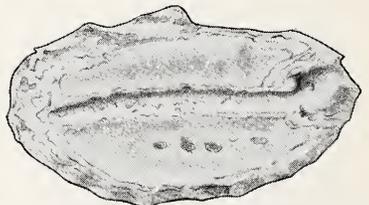
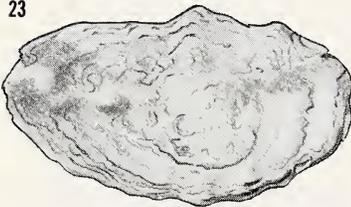


Figure 21. Left sagitta of grunion, *Leuresthes tenuis* (length 2.9 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 22. Right sagitta of topsmelt, *Atherinops affinis* (length 3.5 mm, LACMIP 59). left, outer face; right, inner face.

Figure 23. Left sagitta of jacksmelt, *Atherinopsis californiensis* (length 5.3 mm, LACMIP 59). Left, outer face; right, inner face.

*Atherinidae—silversides**Leuresthes tenuis* (Ayres)—California grunion

California grunion range as far north as Monterey Bay and south nearly to Magdalena Bay, but they are not often seen north of Point Conception. They are most often found in loose schools or aggregations within a short distance of shore in water 15 to 40 feet deep. At spawning, adults seek out sandy beaches where eggs are deposited intertidally beneath the sand. Considerable spawning also takes place along firm sandy-mud shorelines of most coastal embayments. A large adult might be 8 inches long. There were six grunion otoliths (Figure 21) in this deposit.

Atherinopsis californiensis Girard—jacksmelt

Jacksmelt are found between Oregon and Santa Maria Bay, Baja California. They prefer murky water over sandy bottoms, but are not restricted to such areas. They typically form loose schools or aggregations close to the surface in water 5 to 100 feet deep. Oftentimes they move into quiet waters of back bays and harbors. Three of the otoliths were from jacksmelt (Figure 23).

Atherinops affinis (Ayres)—topsmelt

Four subspecies of topsmelt inhabit almost every marine habitat known between northern Oregon and Magdalena Bay. They often school or aggregate with jacksmelt. They usually are found at or near the surface, seldom any great distance offshore, where the bottom is sandy or sandy-mud. Many are seen in sloughs, back bays, and harbors, and many others inhabit offshore kelp beds. A single otolith was from a topsmelt (Figure 22).

*Sphyraenidae—barracudas**Sphyraena argentea* Girard—California barracuda

During some warmwater years, barracuda wander great distances north of their usual haunts, thus they have been reported from Alaskan waters on a few occasions. Typically they are found nearshore in fairly large schools between about Point Conception and Magdalena Bay. Young fish frequently "invade" quiet waters of back bays and harbors. Individuals weighing more than 10 pounds (18 is probably a top weight) are almost exclusively females. A broken otolith (Figure 24) was unquestionably from a fairly large, adult barracuda.



Figure 24. Left sagitta of California barracuda, *Sphyraena argentea* (length to break 10.7 mm, LACMIP 59). Left, outer face; right, inner face.

*Pomadasyidae—grunts**Anisotremus davidsoni* (Steindachner)—sargo

The sargo's distribution is usually reported as Point Conception south to Cape San Lucas and in the Gulf of California; however, there is some question as to whether they actually occur south of Magdalena Bay and in the lower Gulf. They usually inhabit shallow-water areas, where they aggregate around

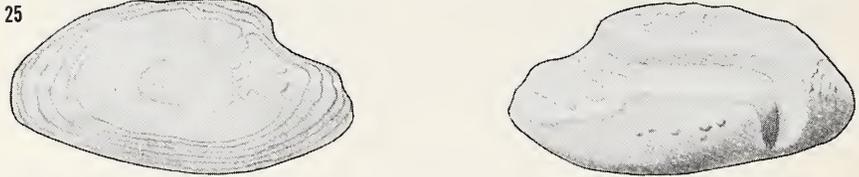


Figure 25. Right sagitta of sargo, *Anisotremus davidsoni* (length 9.8 mm, LACMIP 59). Left, outer face; right, inner face.

pier pilings, rocky outcroppings, and similar objects. Frequently small schools are observed moving over sandy bottoms along the open coast. There was a single sargo otolith in this deposit (Figure 25).

*Sciaenidae—croakers**Micropogon ectenes* Jordan and Gilbert—berrugato

This southern species hasn't been taken within several hundred miles of California during man's tenure here. They usually are fairly abundant in Magdalena Bay, throughout the Gulf of California, and south perhaps to Panama. They prefer shallow embayments and similar habitat where the water is relatively quiet, and the bottom is firm sandy-mud. Both berrugato otoliths in this deposit were from adult specimens (Figure 26).

Umbrina roncador Jordan and Gilbert—yellowfin croaker

Yellowfin croakers are found in shallow water from about Point Conception south to Magdalena Bay. They usually live close to the bottom where the substrate is sand, sandy-mud, or firm mud. They seldom travel any great distance outside the surf zone, but often enter back bays and estuaries, sometimes in fairly dense aggregations. The 13 yellowfin croaker otoliths were from juveniles and adults alike (Figure 27).

Genyonemus lineatus (Ayres)—white croaker

This gregarious species is so abundant in shallow water over most of its usual range (San Francisco to Magdalena Bay), and takes bait so readily, it usually is considered a nuisance and has many derogatory names applied to it by sportfishermen. During some years, they travel considerable distances north of their usual haunts, and thus have been reported from Vancouver Island on rare occasions. Most of the time they "hang out" on sandy, sandy-

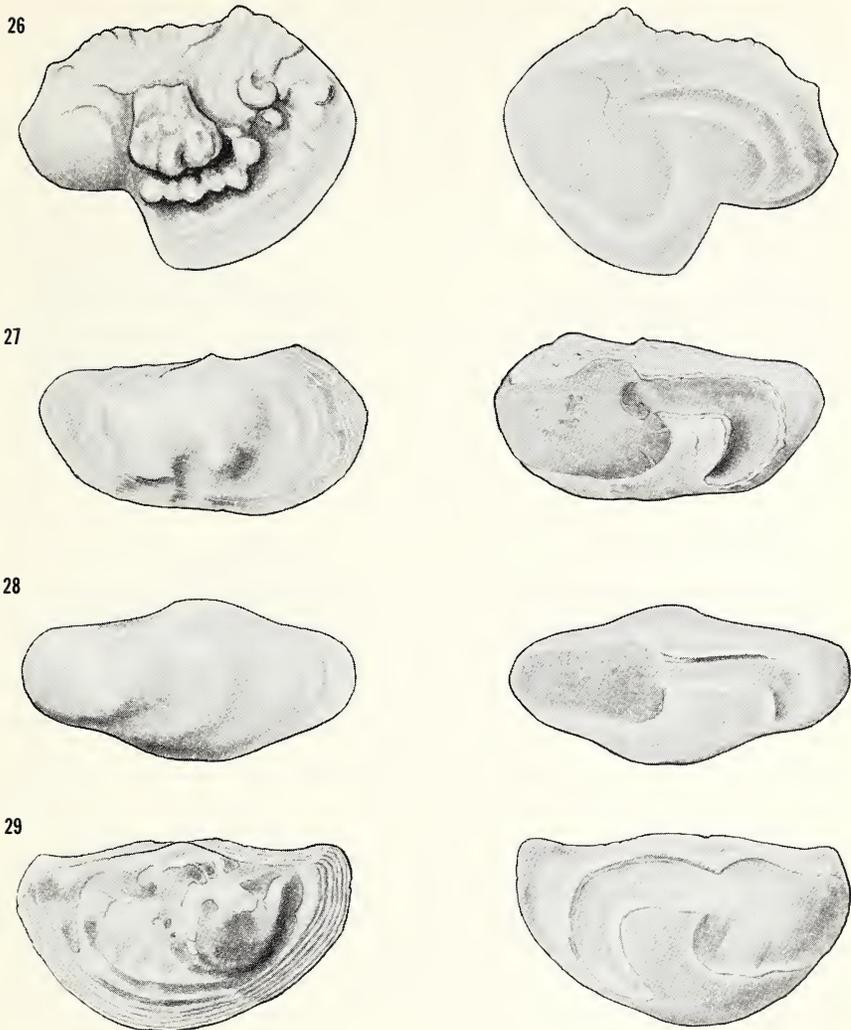


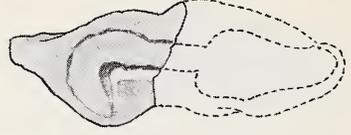
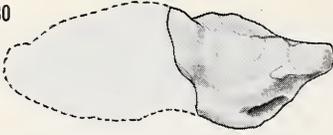
Figure 26. Right sagitta of berrugato, *Micropogon ectenes* (length 20.5 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 27. Right sagitta of yellowfin croaker, *Umbrina roncadior* (length 12.4 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 28. Right sagitta of white croaker, *Genyonemus lineatus* (length 8.5 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 29. Left sagitta of spotfin croaker, *Roncadior stearnsi* (length 12.2 mm, LACMIP 59). Left, outer face; right, inner face.

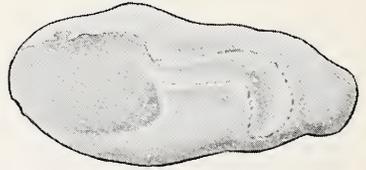
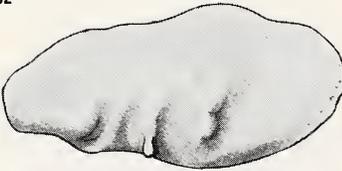
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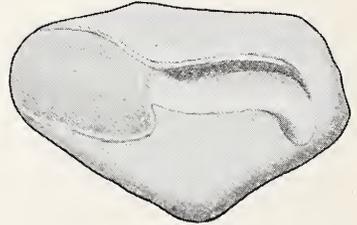
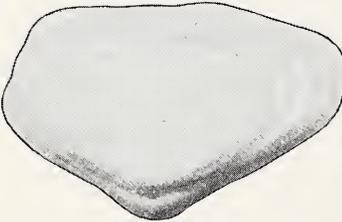


Figure 30. Left sagitta of California corbina, *Menticirrhus undulatus* (length to break 3.8 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 31. Right sagitta of white seabass, *Cynoscion nobilis* (length 21.5 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 32. Right sagitta of striped corvina, *Cynoscion reticulatus* (length 9.2 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 33. Right sagitta of queenfish, *Seriphus politus* (length 7.6 mm, LACMIP 59). Left, outer face; right, inner face.

mud, or firm mud bottoms. They sometimes are caught in shallow bays and estuaries, but are equally at home in 100 fathoms. The 217 white croaker otoliths (Figure 28) were from about equal numbers of juveniles and adults.

Roncador stearnsi (Steindachner)—spotfin croaker

These desirable sport fishes are known from about Point Conception to San Juanico Bay, Baja California, where they live along beaches and in bays over bottoms varying from coarse sand to heavy mud. They seldom are caught in depths greater than 10 fathoms. The 19 spotfin croaker otoliths (Figure 29) were from juveniles as well as large adults.

Menticirrhus undulatus (Girard)—California corbina

California corbinas have been reported from Point Conception to San Juanico Bay; however, a species in the upper Gulf of California is very similar and may be identical. They live along the bottom and have been noted in water from a few inches to about 45 feet deep. They prefer coarse sand or sandy-mud, especially where sand crabs (*Emerita*) abound. A broken otolith was unquestionably from an adult corbina (Figure 30).

Cynoscion nobilis (Ayres)—white seabass

This choice game fish rarely is found north of San Francisco, but during a recent warmwater period a few individuals were caught at Juneau, Alaska. To the south, they abound along sandy beaches and off rocky headlands at least to Magdalena Bay, and fair numbers also occur in the northern Gulf of California. Young fish are usually in shallower water than adults, often being abundant in bays and estuaries. The five white seabass otoliths were from fairly large adults (Figure 31). Very large adults may weigh as much as 70 pounds.

Cynoscion reticulatus (Günther)—striped corvina

This southern species has not been reported north of Santa Maria Bay, Baja California, in modern times. It ranges from there to Panama, and is especially common throughout the Gulf of California. They prefer sandy-mud or firm-mud bottoms of embayments and quiet offshore waters. Numerous individuals are captured by shrimp trawlers operating in 5 to 30 fathoms, and many are caught by sport gear in a few feet of water near the surf zone. The four striped corvina otoliths were all from young fish (Figure 32). The largest adult I have seen, weighed just under 5 pounds.

Seriphus politus Ayres—queenfish

Queenfish have been captured from Yaquina Bay, Oregon, to San Juanico Bay, but they are not common north of Point Conception. They are a gregarious species, and are extremely abundant throughout much of their range, where they prefer relatively quiet waters. They often inhabit coastal bays and

sloughs, living throughout the water column, particularly where the bottom is sandy or firm sandy-mud. Their otoliths were among the most numerous in this deposit; the 275 I found represented all sizes of fish from the smallest juveniles to the largest adults (Figure 33). Large adults seldom exceed a foot in length.

Embiotocidae—surfperches

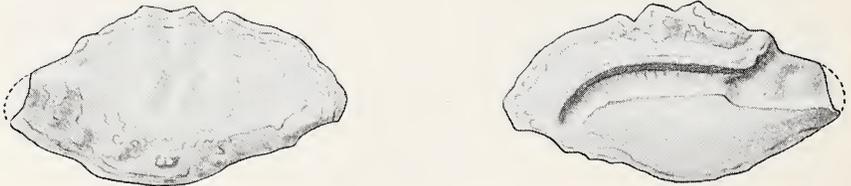
Phanerodon furcatus Girard—white seaperch

This species seldom takes a hook, but is commonly netted between about San Francisco (rarely to Vancouver Island) and Point Cabras, Baja California. They are relatively small schooling fishes, and usually live throughout the water column, but are commonest just off the bottom. Their favorite substrate is coarse sand or cobbles, but they also are found in bays over mud bottoms and in kelp beds among rocks. Judging from their present numerical abundance I anticipated finding more than the nine white seaperch fossil otoliths. (Figure 34).

Cymatogaster aggregata Gibbons—shiner perch

Shiner perch literally infest much of their range (Port Wrangel, Alaska, to Santo Tomas Point, Baja California). They prefer calm water with smooth

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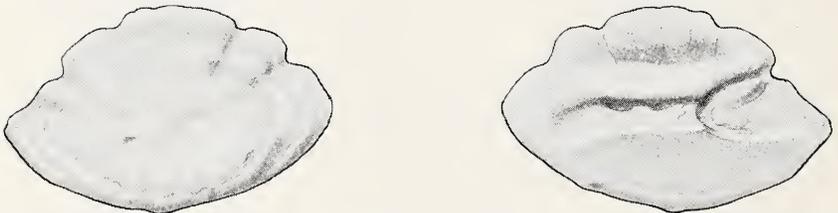


Figure 34. Left sagitta of white seaperch, *Phanerodon furcatus* (length 9.0 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 35. Left sagitta of shiner perch, *Cymatogaster aggregata* (length 5.0 mm, LACMIP 59). Left, outer face; right, inner face.

bottoms, where "swarms" of them mingle with other small fishes around pier and wharf pilings, over eel grass beds, and throughout the waters between. They have been trawled from 400 feet of water, but are most abundant shallower than 50 feet. A large individual would be around 5 inches long. Only six of the otoliths were from shiner perch (Figure 35).

Labridae—wrasses

Pimelometopon pulchrum (Ayres)—California sheephead

Sheephead seldom wander very far from a rocky substrate. They have been caught in Monterey Bay a few times, but are usually found from Point Conception to Cape San Lucas and throughout the Gulf of California. They usually live at or near the bottom in water 20 to 100 feet deep, but may go either shallower or deeper. Large males sometimes will weigh just over 30 pounds (at about 3 feet), but most individuals weigh less than 20. Sheephead were represented by one pharyngeal bone from a juvenile and six assorted teeth.

Scorpaenidae—rockfishes

Sebastes paucispinis (Ayres)—bocaccio

Except in the young stages, bocaccio are considered a deep-water species (65 to 175 fathoms) off southern California. Schools of juveniles, however, often move inshore where quantities are caught from piers, docks, and similar structures. Adults have been caught from Queen Charlotte Sound to San Carlos, Baja California. They occur over broken (rocky) as well as smooth bottoms, and are especially numerous over firm sandy-mud where trawlers capture considerable tonnages each year. Six of the rockfish otoliths apparently were from bocaccio, mostly small individuals (Figure 36). Large adults may be 3 feet long and weigh 15 pounds.

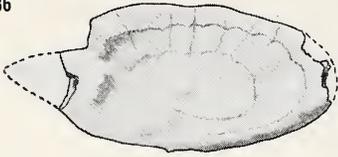
Sebastes jordani Gilbert—shortbelly rockfish

This small rockfish has been taken throughout the area between Washington and Ensenada, Baja California. Sometimes they show up in water 10 to 15 fathoms deep, especially when young, but usually they stay in deeper water, perhaps to 150 fathoms. They prefer living slightly above the bottom over smooth sandy-mud substrates. Two of the otoliths were from this species (Figure 37).

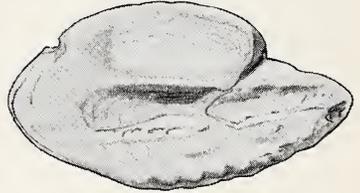
Sebastes aurora (Gilbert)—aurora rockfish

Aurora rockfish are not often seen off southern California, even though they are known from the Columbia River to San Diego. They seldom are caught shallower than 50 fathoms, and range into 275 fathoms. They are caught at or near the bottom over a variety of substrates, but seem to prefer rocky habitat. A single otolith was from this species (Figure 38).

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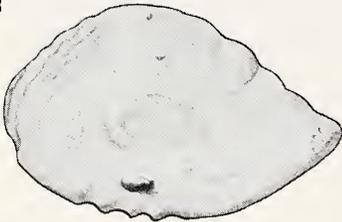


Figure 36. Left sagitta of bocaccio, *Sebastodes paucispinis* (length of fragment 7.3 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 37. Left sagitta of shortbelly rockfish, *Sebastodes jordani* (length 6.4 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 38. Right sagitta of aurora rockfish, *Sebastodes aurora* (length 6.3 mm, LACMIP 59). Left, outer face; right, inner face.

Sebastodes diploproa (Gilbert)—splitnose rockfish

These are among the commoner rockfish in fairly deep water (usually 100 to 250 fathoms) between Vancouver Island and the Coronado Islands, Baja California. They prefer living on or just above a smooth sandy-mud or firm mud bottom, but occasional catches are made over rocky substrates.

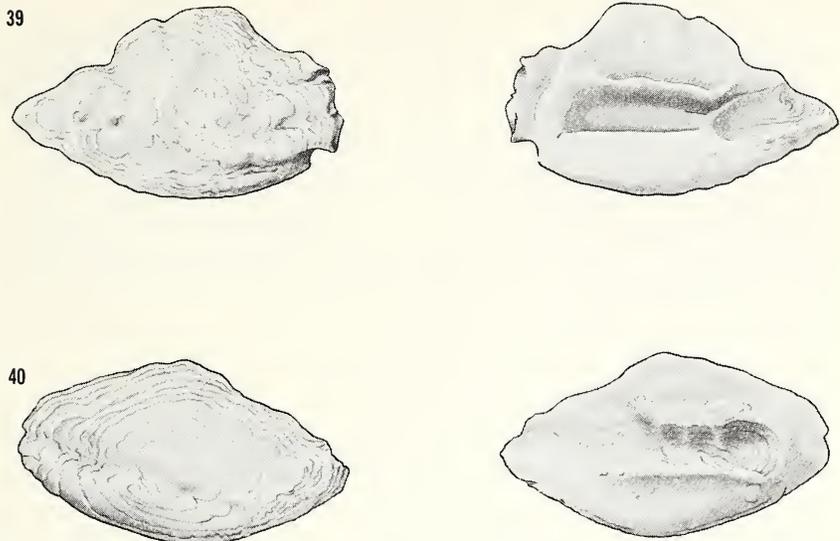


Figure 39. Left sagitta of splitnose rockfish, *Sebastes diploproa* (length 12.9 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 40. Right sagitta of swordspine rockfish, *Sebastes rhodochloris* (length 7.0 mm, LACMIP 59). Left, outer face; right, inner face.

They never attain very large sizes (16 inches maximum) and are of little commercial value except for mink food. One otolith was from a large splitnose rockfish (Figure 39).

Sebastes cf. rhodochloris (Jordan and Gilbert)—swordspine rockfish

Two of the rockfish otoliths (Figure 40) seemed to identify with this small species, which occurs between about San Francisco and Guadalupe Island, Baja California. They prefer depths of 50 to 70 fathoms, but have been taken in 120, usually over rocky substrate.

Sebastes spp.—various species of rockfish

Thirteen rockfish otoliths were so badly fragmented or worn they could not be identified to species. Some of the smaller ones seemed to be from bocaccio, but others could have come from any of the 50 rockfish species known in our waters.

Cottidae—sculpins

Chitonotus pugetensis (Steindachner)—roughback sculpin

These small fishes (adults may reach 5 or 6 inches) are fairly abundant on sandy or sandy-mud bottoms in 20 to 60 fathoms between northern British

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Figure 41. Right sagitta of roughback sculpin, *Chitonotus pugetensis* (length 3.0 mm, LACMIP 59). Left, outer face; right, inner face.

Columbia and Santa Maria Bay, Baja California. Occasional individuals may be taken in water as shallow as 5 to 10 fathoms. There was one roughback sculpin otolith in this deposit (Figure 41).

Gobiidae—gobies

Lepidogobius lepidus (Girard)—bay goby

As the common name implies, this small goby (adults reach 4 or 5 inches) is most at home in the sheltered waters of bays, sloughs, and harbors where they sometimes are taken in the subtidal area. Occasionally, they are trawled

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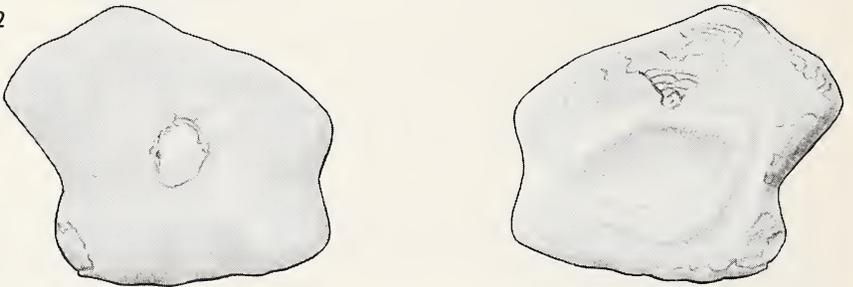


Figure 42. Left sagitta of bay goby, *Lepidogobius lepidus* (length 2.7 mm, LACMIP 59). Left, outer face; right, inner face.

in fair numbers from depths as great as 40 to 50 fathoms. Their usual range is from northern Vancouver Island to Ensenada. One otolith was from a bay goby (Figure 42).

Batrachoididae—toadfishes

Porichthys notatus Girard—plainfin midshipman

Plainfin midshipmen are among the half-dozen most abundant species in trawl catches made in intermediate depths (50 to 120 fathoms). In some localities between southeastern Alaska and Cedros Island, they seasonally move into the intertidal zone. On the other hand, they have also been trawled from 200 fathoms. They prefer firm mud or muddy bottoms during much of the year, seeking out rocky habitat for spawning. Most of the 161 otoliths from this species (Figure 43) were from young individuals.

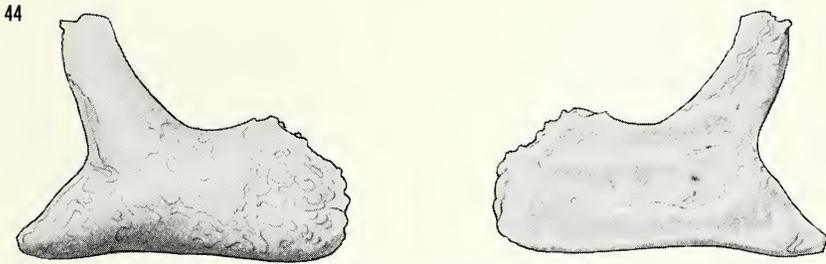
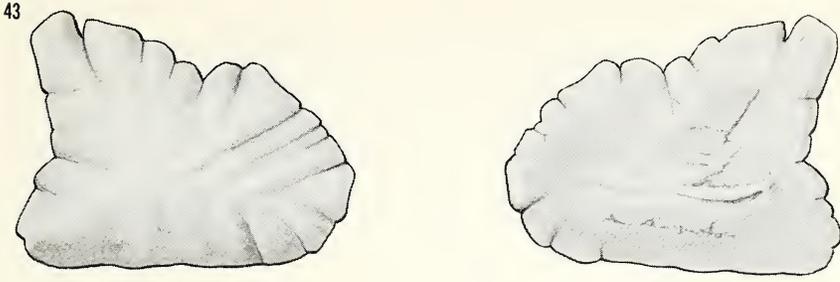


Figure 43. Left sagitta of plainfin midshipman, *Porichthys notatus* (length 6.3 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 44. Left sagitta of specklefin midshipman, *Porichthys myriaster* (length 9.2 mm, LACMIP 59). Left, outer face; right, inner face.

Porichthys myriaster Hubbs and Schultz—specklefin midshipman

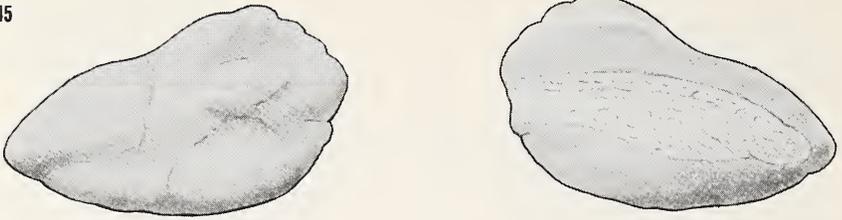
Specklefin midshipmen are neither as abundant as *P. notatus* nor so wide-ranging, being known from about Point Conception to Magdalena Bay. They often seek out rocky intertidal areas for spawning, but at other times move into depths of 50 fathoms or so. Their habits and habitat preferences are similar to those of *P. notatus*. Only 15 of the otoliths were from specklefin midshipmen (Figure 44).

Ophidiidae—cusk-eels

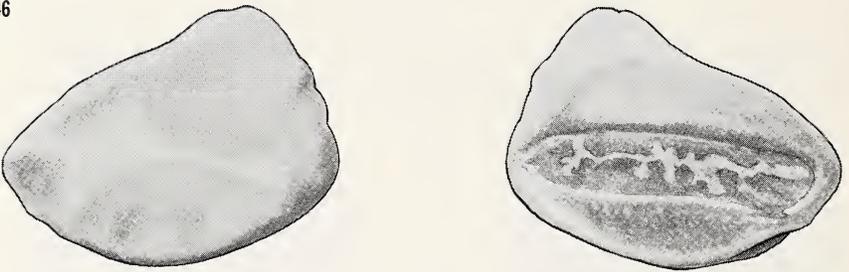
Otophidium taylori (Girard)—spotted cusk-eel

Spotted cusk-eels have been caught from about Humboldt Bay, California, to San Cristobal Bay, Baja California. They are fairly abundant throughout this range (in from 10 to at least 130 fathoms), but because of their secretive habits they are not often caught. They often are found in association with rocks, particularly where they form loose jumbles intermixed with sandy-

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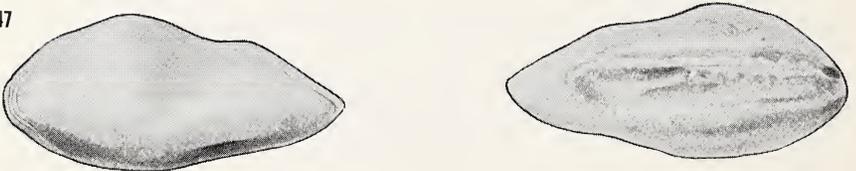


Figure 45. Right sagitta of spotted cusk-eel, *Otophidium taylori* (length 7.6 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 46. Right sagitta of basketweave cusk-eel, *Otophidium scrippsae* (length 7.8 mm, LACMIP 59). Left, outer face; right, inner face.

Figure 47. Left sagitta of giant cusk-eel, *Lepophidium negropinna* (length 12.3 mm, LACMIP 59). Left, outer face; right, inner face.

mud or mud. They hide among these rocks during the daytime, moving into the open at night. When startled, cusk-eels will burrow rapidly tail-first into the substrate. There were 83 otoliths from this species (Figure 45).

Otophidium scrippsae Hubbs—basketweave cusk-eel

This species has habits similar to those of *O. taylori*, but seems to live in shallower water (intertidal to 20 fathoms) over a more restricted range (Point Conception south to Turtle Bay, Baja California). Their otoliths were more abundant (140 were found) than those of *O. taylori* in this deposit (Figure 46).

Lepophidium negropinna Hildebrand and Barton—giant cusk-eel

This species has not been recorded north of Cedros Island during modern times. It ranges from there throughout the Gulf of California to Talara, Peru. Their habits are probably similar to those of *Otophidium*, because specimens can be trawled over relatively smooth, firm bottoms. Two of the otoliths were from this species (Figure 47), both from fairly large individuals (perhaps 15 to 18 inches long).

Unidentifiable Teleost Remains

Thirty-three otoliths were too badly worn or fragmented to classify with any certainty. I doubt if any of these represented species not enumerated above. Other unidentifiable remains included 25 assorted vertebrae (mostly small), and a half-dozen broken-off neural spines and/or fin spines. A single badly-eroded pharyngeal bone also could not be identified, although it appeared to be from an embiotocid perch.

DISCUSSION

The city of Los Angeles has been conducting a surveillance of its Hyperion sewer outfall in Santa Monica Bay since 1957, and 32 of the 35 teleosts discussed above have been common constituents of their trawl catches. The other three (striped corvina, berrugato, and giant cusk-eel) are southern species, and haven't been taken within several hundred miles of California within modern times (Figure 48).

Only the longnose shark among the elasmobranchs has not been caught as far north as Playa del Rey during modern times. All of the others are fairly abundant in Santa Monica Bay, but some are not found there every year. Hammerheads and carcharhinid sharks are "southerners" and only appear during warmwater years, while the sevengill is a "northerner" and shows up most frequently when the bay waters are cold (Figure 49).

Thus, all forms identified in the Playa del Rey formation are still extant, and most can be captured in relatively shallow water adjacent to the site of this deposit.

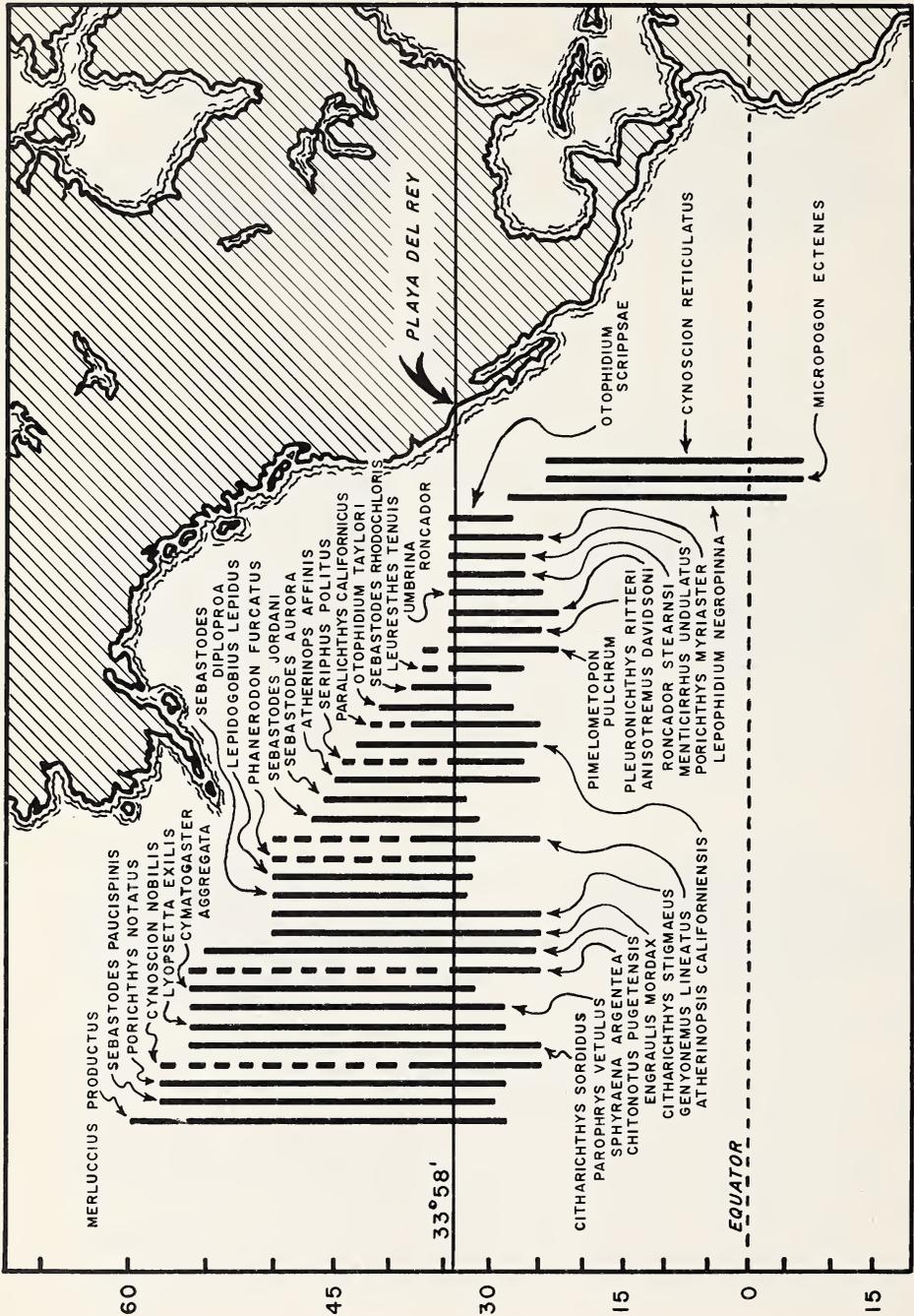


Figure 48. Present-day geographic distributions of the 36 species of teleost fishes identified from the Playa del Rey deposit (LACMIP 59, lat. 33° 58' N.). Solid lines depict usual latitudinal distribution broken lines represent infrequent movement or migrations.

It is extremely gratifying to find the fish fauna so compatible with the various invertebrate faunas described by Willett (1937). My findings are in no way at odds with Valentine's (1961) statement that the habitat appears to have been a fine-grained silty sand, typical of a quiet-water embayment 10 to 12 fathoms deep.

The few "northern" fish remains (rockfishes, hake, English sole, and slender sole) were mostly badly worn, broken, and uncommon, as were the few northern mollusks that Willett found. Not many of the typical shallow-water and "southern" forms showed such signs of wear and tear. In fact, most of the otoliths were in such excellent shape that I wondered if they had not resulted from a catastrophic die-off, perhaps from an extensive red-tide condition.

If they had been the partially digested remnants of meals eaten by predatory fishes, marine mammals, and birds, most of the otoliths would have shown some signs of erosion on their inner (concave) faces, as well as margins and outer faces. Such was not the case. I examined many of the otoliths from younger fishes to see if their margins would show annuli (growth zones) that would offer a clue as to the season of the year during which death had occurred, but was not able to come up with enough concrete information to hazard a guess.

The presence of southern forms among both elasmobranchs and teleosts, bears out the contention that this deposit was laid down when local ocean temperatures were several degrees warmer than they are today. When such oceanic warming does take place, there is a tendency for anomalies to occur among the various vertebrate and invertebrate faunas (Radovich, 1961). During these times prolific and extensive dinoflagellate blooms (red-tide) often are noted, sometimes in every month of the year. The killing power of such blooms has been amply demonstrated in Florida (Gunter *et al.*, 1948) and California (Reish, 1963) during the past two decades. There is no reason to believe that such phenomena did not occur during the Pleistocene also, or that their effects were any less damaging to marine animal aggregations or communities than they are today.

ACKNOWLEDGMENTS

Many people either helped make this study possible or helped make my work easier. George P. Kanakoff, Curator of Invertebrate Paleontology, Los Angeles County Museum, deserves special consideration because he, more than anyone else, recognized fossil fish otoliths for what they were, and saw to it they were saved whenever encountered. His wife, Ruthe P. Kanakoff, devoted much time helping gather field samples and searching out otoliths. Shelton P. Applegate, Associate Curator of Vertebrate Paleontology, Los Angeles County Museum, checked my identifications of the various shark remains, and in several instances furnished specific names for items I had not been able to iden-

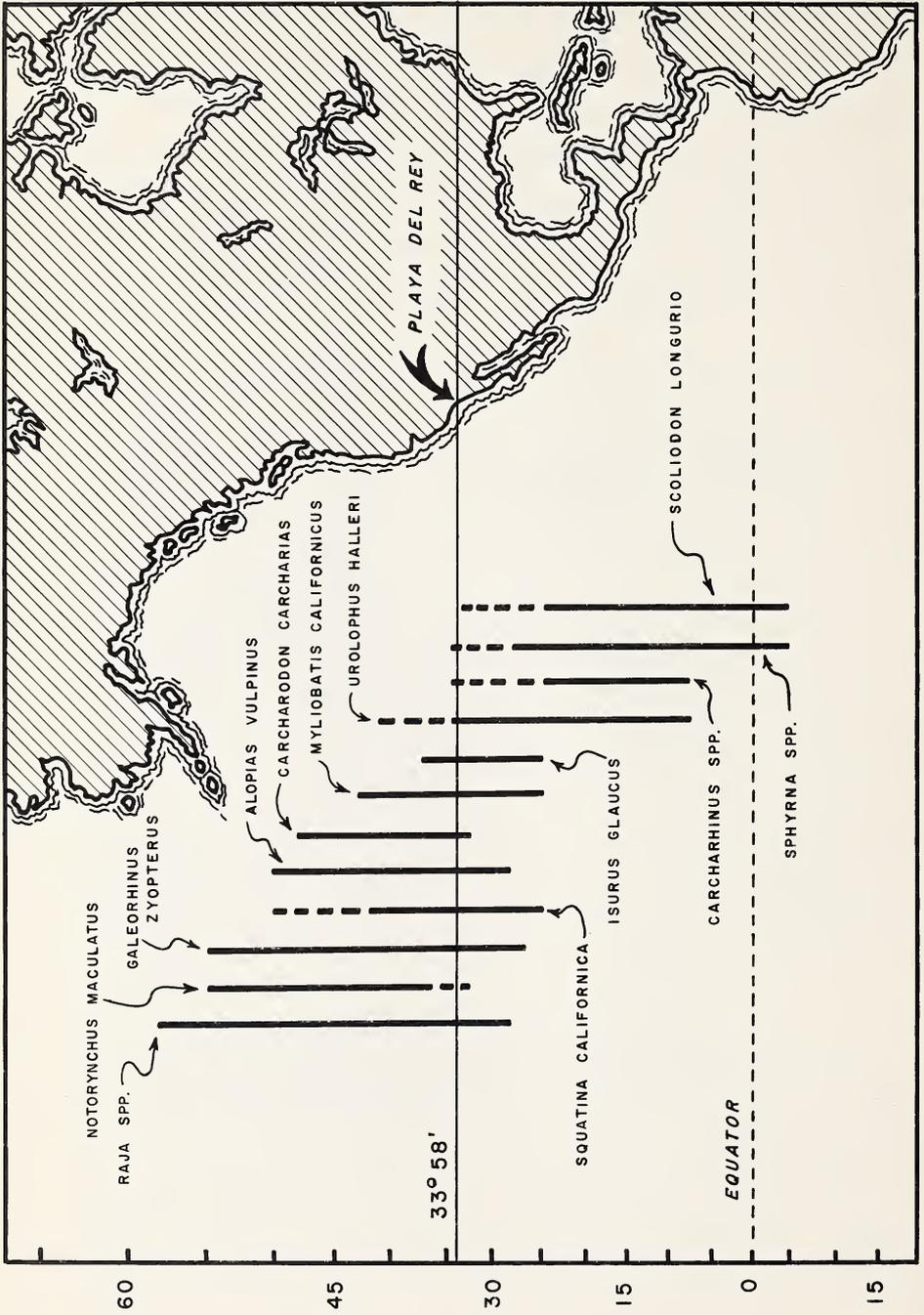


Figure 49. Present-day geographic distributions of the elasmobranchs identified from the Playa del Rey deposit (LACMIP 59; lat. 33° 58' N.). Solid lines depict usual latitudinal distribution, broken lines represent infrequent movements or migrations.

tify. John L. Baxter, California State Fisheries Laboratory, reviewed my manuscript and offered many helpful suggestions for improving it.

Many student assistants and volunteers worked long hours at the Museum separating identifiable material in various Pleistocene and Pliocene screenings. Without their labors, very few otoliths would have been on hand and my study could not have been so comprehensive. For this alone, each of these individuals deserves to be thanked by name, and if I forget anyone I hope I will be forgiven. In alphabetical order they were: John E. Fitch, Jr., Elizabeth Henderson, Charlene Hopka, Jean Hopkins, Camilla Ingram, Esther James, Elsa Kops, Pat La Follett, Jules Levin, Louis Marinkovich, David Marshall, Patricia Mears, Rita Miller, Peter Oringer, Mary Pedersen, Sherry Parkhurst, Joan Troesch, Robert Rashkin, Roger Reimer, James Smith, Wilma Webster, Barbara Weeks, and Adie Wing.

Gerhard Bakker, Assistant Professor, Los Angeles City College, made all of the drawings of otoliths, teeth, and other fossil structures, and Walter Thomsen, Redondo Beach, produced the two fish distribution maps from some hazy sketches I furnished him. Mrs. Loretta Morris, San Pedro, typed the manuscript and all its revisions for me.

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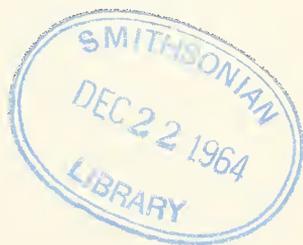
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A NEW SWIFT FROM MT. MOROTO, UGANDA

By HERBERT FRIEDMANN



A NEW SWIFT FROM MT. MOROTO, UGANDA¹

By HERBERT FRIEDMANN²

ABSTRACT. A new race of *Apus pallidus* from Mt. Moroto, northeastern Uganda, is described and named *A. p. kapnodes*. The relationships of *A. niansae* with the *A. pallidus* group are discussed with the conclusion that until fuller data are available the two should be treated as species.

Among a collection of over 4,000 birds from Kenya and Uganda brought back by the Knudsen-Machris 1963 expedition of the Los Angeles County Museum are eleven specimens of a swift from Mt. Moroto, which prove to represent a hitherto unknown race. The expedition had as its primary objectives the collecting of a group of elephants, of chimpanzees, and other large mammals for the Museum's exhibition galleries, but made large collections of other animals as well. In anticipation of a complete report on the entire, very extensive collection, this bird is described and named at this time.

Apus pallidus kapnodes, NEW SUBSPECIES

Type: adult male, collected on Mt. Moroto, Uganda, at an altitude of 8,500 feet, May 13, 1963, Los Angeles County Museum no. 39899, by the Knudsen-Machris Expedition. The subspecific name is a Greek adjective signifying dark color.

Characters: similar to *A. pallidus somalicus* (Clarke), but much darker above and below, and larger. The head and body, except for the whitish chin and throat are Chaetura Black in *kapnodes*, as compared with Hair Brown in four examples of topotypical *somalicus* from former British Somaliland. (Capitalized color terms are those of Ridgway, 1912.) The wing length of the present series of *kapnodes* measures from 151 to 158 mm. (average 154.2 mm.) in eight males, 151 to 160 mm. (average 156 mm.) in three females; in *somalicus* the wing length of two males is 145 and 148 mm., of two females 147 and 153 mm. In the original description of *somalicus* the wing length was given as 152-156 mm., but the four specimens examined, including one from Bihendula, the type locality, are much smaller. The colors of the soft parts of *kapnodes* were recorded on the labels as: iris dark brown, bill black, feet purplish gray.

In his study of the relations of all the species of the genus *Apus*, Lack (1956:55) mentioned a specimen of a dark form of *pallidus* from Maroto

¹Cost of publication of this paper was borne by Mr. Maurice A. Machris.

²Director, Los Angeles County Museum.

(= Moroto), Uganda, taken in January, and one from British Somaliland in June, as being darker than *pallidus*, a little darker than *brehmorum*, but not quite so dark as one example of *illyricus*. The mention of a dark bird from British Somaliland, the home of typical *somalicus*, raises a question as to the extent of individual variation in that race, but the four specimens from there seen in the present study are so uniformly paler than the Moroto birds that the distinctness of the latter population seems well established.

There is one as yet unresolved problem to be discussed, namely the relationships of *niansae* with the *pallidus* group. Chapin (1939:455f.) considered *somalicus* a synonym of *niansae*, but his conclusions have not been generally followed by subsequent students of these birds. Three specimens of *niansae* have been available to me in the present study, and they are distinct from both *kapnodes* and *somalicus* in being larger, with wings over 170 mm. in length. In color they are close to *kapnodes*, but even slightly darker on the underparts, especially the under wing coverts. White (1953:77) advocated considering *Apus somalicus* a race of *niansae*, and not of *pallidus*, but it is not wholly clear that the two are completely allopatric in their breeding areas, so they are here kept as different species. More recently Lack (1956:54) supported White's decision that *niansae* and *somalicus* were conspecific, but concluded that there were two reasonable ways of treating the evidence, one being to treat *somalicus* and *niansae* as races of *pallidus*, and the other to consider *niansae* and *somalicus* a species apart from *pallidus*. Inasmuch as he had insufficient data to make a firm decision, Lack listed them as *A. pallidus* ? *niansae*, and *A. pallidus* ? *somalicus*. It would seem that eventually, when our knowledge of their respective allopatry or sympatry is more definite, it may be possible to determine if they are one specific group, but until then it is better to be conservative and to keep *niansae* as a species characterized chiefly by its larger size.

Range: Known only from Mt. Moroto, northeastern Uganda, between 5,000 and 8,500 feet. Mackworth-Praed and Grant (1957:780f.) give the range of *somalicus* as British Somaliland to central Kenya, without mention of actual Kenyan localities. They do not mention Uganda at all, so Mt. Moroto would appear to be a western extension of range for the species. In neither his 1922 nor his 1932 paper did van Someren record the species, and it is also absent from Jackson's 1938 work on the birds of Kenya and Uganda. Meinertzhagen (1937:756) collected one specimen at Nanyuki, Kenya, which is the only Kenya record I have been able to find. If there are other examples known from northern and central Kenya they should be examined as they may turn out to be *kapnodes* and not typical *somalicus*, or even more probably, *niansae*.

For the loan of comparative material of *somalicus* from British Somaliland, I am indebted to the American Museum of Natural History.

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By HERBERT FRIEDMANN AND KENNETH E. STAGER



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DAVID K. CALDWELL

Editor

RESULTS OF THE 1964 CHENEY TANGANYIKAN
EXPEDITION.
ORNITHOLOGY

By HERBERT FRIEDMANN¹ AND KENNETH E. STAGER²

ABSTRACT: The 1964 Cheney Tanganyikan Expedition collected 123 species and subspecies of birds, the majority, and the most interesting and important, of which came from two isolated, forested mountain areas, the Uluguru Mountains and the Ukaguru Mountains. Prior to the work of this expedition the avifauna of the Ukagurus was practically unknown, as only 7 kinds of birds had been taken there by one itinerant naturalist. The present list records 43 species from that area. A history of the ornithological exploration of the Ulugurus and a complete list of the birds definitely recorded from there, 165 in number, of which 9 are new records at this point, are given, plus 47 others, the specimens of which have not been examined by a professional ornithologist, as well as a report on the Cheney specimens. The Cheney Expedition also collected a few birds in the lowlands east of Lake Manyara and near Babati. These are listed in the present annotated catalog as well.

The 1964 Cheney Tanganyikan Expedition of the Los Angeles County Museum worked primarily in two isolated mountain areas, one of which, the Ukaguru Mountains, was practically unknown zoologically, and the other, the Ulugurus, was looked upon as a promising region for further investigation, as it was the home of several endemic species of birds.

The expedition departed from Nairobi, Kenya, on January 2, 1964. It traveled south to Arusha and then east to Moshi. The party moved directly to the Uluguru Mountains by way of Dodoma (Fig. 1). Camp was established at Bunduki, at an elevation of 5,018 feet, in the Ulugurus, on January 6, 1964, and the expedition collected in and around that spot until January 15, when camp was moved to Mandege, elevation 5,300 feet, in the Ukaguru Mountains (Fig. 2). Field work in the Mandege area commenced on January 17, and continued through January 22. From Mandege, the expedition retraced its route toward Arusha by way of Dodoma, stopping for three days at Babati (January 24-26 inclusive) and then proceeded north to the Lake Manyara area. Arriving in the Lake Manyara area on January 2, the expedition left the Dodoma-Arusha road at Kwa ku chinga, and moved westward toward Lake Manyara. Field work there was terminated on January 29, and the expedition departed for Nairobi on January 30, arriving there on January 31, 1964.

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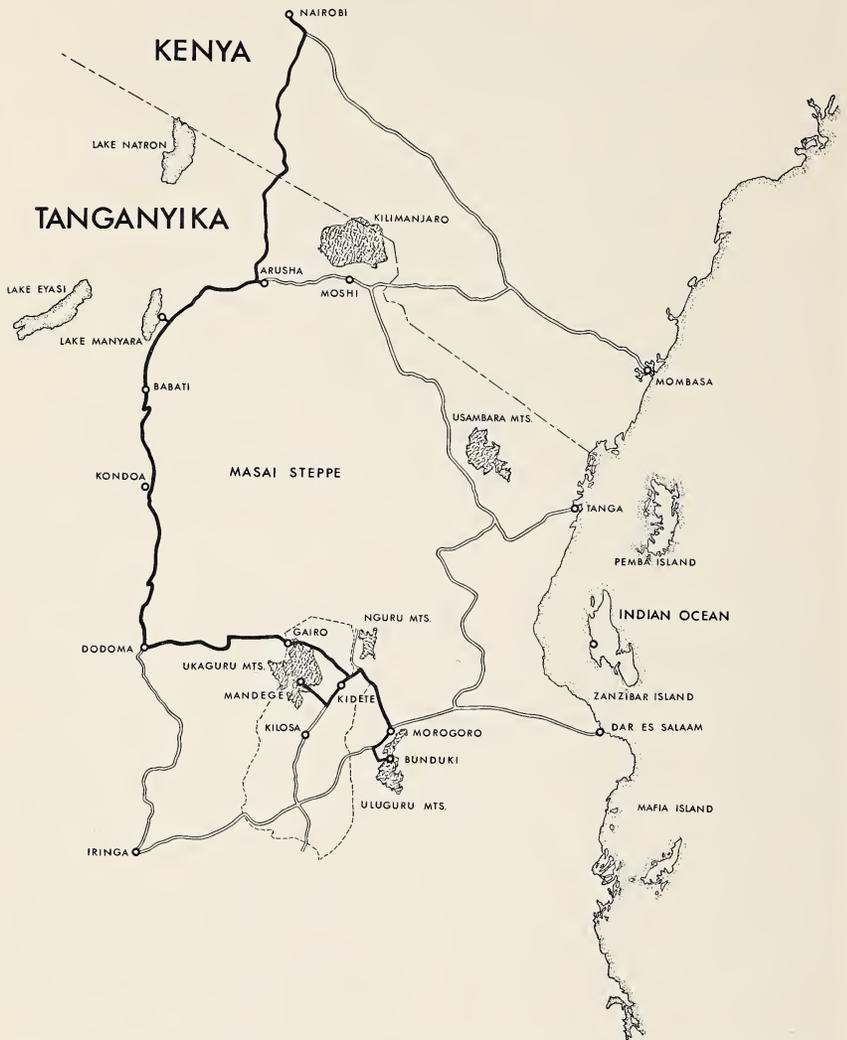


Figure 1. Map showing location of the Uluguru and Ukaguru Mountains. Heavy black line indicates route taken by expedition.

Expedition personnel consisted of William J. Cheney, sponsor; Kenneth E. Stager, ornithologist; Julian McKeand, professional white hunter and his African staff of twelve men. Two trained specimen preparators from the Coryndon Museum of Nairobi were provided by Mr. John G. Williams.

While the specimens of greatest scientific interest in the present collection are those obtained in the two mountain ranges, the expedition made every effort to collect lowland birds in other areas, particularly on the east side of Lake Manyara and near Babati. The following annotated catalog contains all the birds obtained; in most cases the lowland forms call for only slight comment.

For arranging the loan of specimens needed for comparative purposes in the course of the recent study, grateful acknowledgments are due to M. A. Traylor, of the Chicago Natural History Museum, and to R. A. Paynter, of the Museum of Comparative Zoology, Harvard University. A few puzzling specimens were taken to the United States National Museum by the senior author and were compared with material there. Mrs. B. P. Hall, of the British Museum (Natural History), kindly supplied information about specimens in that institution, collected by Fuggles-Couchman and by Swynnerton. Mr. J. F. Pollard, Regional Forest Officer at Morogoro, Tanganyika, kindly sent for our use a copy of an unpublished forestry report on the Ukaguru Mountains. During its work in Tanganyika, the expedition was given much appreciated assistance and advice by Mr. John G. Williams, ornithologist of the Coryndon Museum, Nairobi, Father J. V. Doorne of the Catholic Mission at Bunduki, and Mr. A. J. Mence, Chief Game Warden, Game Division, Tanganyika, at Dar es Salaam. The maps illustrating the present report were drawn by Mrs. Dorothy Kresch of the Los Angeles County Museum's division of exhibitions.

The main acknowledgment the Museum has to make in this connection is, however, to the generous sponsors of the expedition, Mr. William J. Cheney, and his mother, Mrs. Eva F. Cheney, who made possible the results which have enriched the Museum and have contributed to the advancement of our knowledge of the zoology of a fascinating part of the continent of Africa. The Cheneys not only assumed the cost of the expedition but also provided the funds for the publication of this report on its work.

The way in which joint reports, such as this, come to be written often reverses the relative importance of the contributions of the authors. The junior author made the collection, supplied the field notes and the photographs. The senior author is responsible for the identifications, systematic notes, the historical introduction, and the compiled lists of the birds of the Uluguru and Ukaguru Mountains. Each author read and approved the parts written by the other.

A very few specimens of birds from the Uluguru Mountains reached European museums in the last decade of the nineteenth century, collected by Stuhlmann, who sent them to the museum of Berlin, but no special report was ever made on them. Some of them, involving 14 species, were mentioned in various of Reichenow's publications (1889, 1894, 1895, 1900-1905). Stuhl-

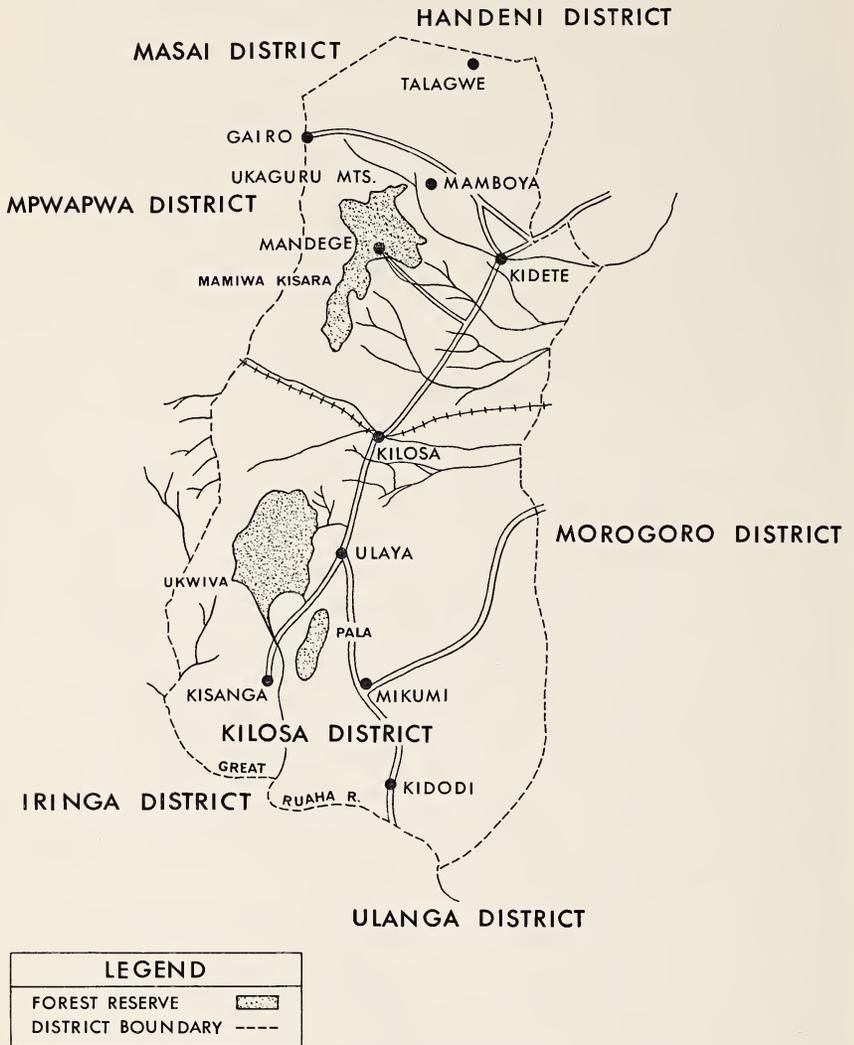


Figure 2. Map showing location of Mandege in the Kilosa forest district.



Figure 3. Uluguru Mountains, showing remnant cap of indigenous mountain forest. Near Bunduki, 1964.

mann seems to have collected chiefly, if not only, in the eastern portion of the Ulugurus. The only explicit locality of his there, known to us, is Mhonda, mentioned as the source of one of his specimens, by Reichenow (1889).

The next person to have collected and observed birds in these mountains was Ludwig Schuster. Schuster's data and specimens were gathered in 1913, but were not published by him until 1926. He mentioned some 14 kinds of birds from the Uluguru Mountains, but as his paper was a general survey of all his work in many parts of Tanganyika it is quite possible that in some cases of wide ranging species he may have had Uluguru records but saw no particular need to mention them. Schuster's collecting localities in the Ulugurus included Bunduki, where the Cheney expedition worked, and also Nyandiduma, Mamba, in the western part of the range, and Mseru at the eastern end.

Arthur Loveridge visited the Uluguru Mountains at least as early as November, 1918, when he found a nest of a paradise flycatcher there, which he reported on some years later (1922:846). C. M. F. Swynnerton collected some birds in the Ulugurus in June, 1920, but the only published information on what he obtained is the mere mention by Sclater and Moreau (1933:198, fn.) of an example of a shrike, *Chlorophoneus nigrifrons*, taken by him there. However, through the kind cooperation of Mrs. B. P. Hall, we have learned that the British Museum received 69 specimens of 37 species of Uluguru birds from Mr. Swynnerton.

Serious ornithological exploration of this mountain range may be said to have begun as recently as 1921 and 1922. During those two years Salimu bin Asmani (or Salimu Asumani), a trained native collector employed by Arthur Loveridge, made the first sizable Uluguru collections, chiefly around the village of Bagilo, which was his home. These birds, representing 98 species, are now



Figure 4. Uluguru Mountains, showing encroachment of human cultivation on the mountain forest. The stands of *Eucalyptus* and conifers in the foreground are experimental plantings at the forestry station, Bunduki, 1964.

largely in the Museum of Comparative Zoology at Harvard University, where they came as part of the large Loveridge East African collection, which was reported on as a whole by Friedmann and Loveridge (1937). Some years earlier a selected number of Uluguru specimens had been given by Loveridge to the late Lord Rothschild's museum at Tring, and a few of them were published on by Hartert (1922, 1923). These specimens are now in the American Museum of Natural History, in New York.

In 1926 Loveridge made a further, extensive collection in both the Ulugurus and the Usambaras, with particular attention to the reptiles and amphibians of the two ranges, whose faunal affinities he wished to study. The Uluguru and the Usambara Mountains are separated by over 120 miles of low, hot, acacia-dotted grasslands, while the Nguru Mountains form a connecting area between them. The report on the cold-blooded terrestrial vertebrates by Barbour and Loveridge (1928) revealed that both the Usambaras and the Ulugurus included in their faunas many species of reptiles and amphibians common to the West African forests. This was more noticeably the case in the Usambaras; the Ulugurus were found to support numerous forms with obvious



Figure 5. Ukaguru Mountains. View is to the south from Mandege. Plantings on the lower slopes are introduced tree species on forestry service experimental plots.

links with the fauna of the Nyika Plateau of Nyasaland to the southwest. Included in the introduction to the report are useful ecological notes on the Uluguru collecting localities, but Loveridge and his assistant, Salimu, did not work at Bunduki, the area where the Cheney expedition made its collection. Although his primary objective was to study the cold-blooded terrestrial vertebrate fauna, Loveridge was able to assemble a very important, large and most interesting collection of 77 species of birds, which was reported on by

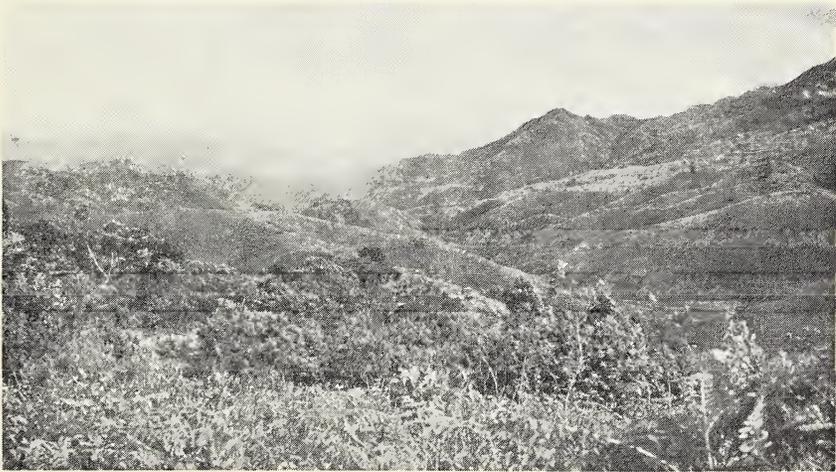


Figure 6. Ukaguru Mountains, looking southeast along the Jakulu river valley from Mandege. Foothills in the background are covered with poor *Brachystegia* forest.

Friedmann (1927, 1928). During the course of the field work on this trip, Loveridge and his assistant, Salimu, collected a number of new birds, the most surprising of which was a very distinct new species of large bush-shrike, subsequently named *Malaconotus alius*. In the early 1950's, a sisal planter near Morogoro, Mr. Th. Andersen, made occasional collecting trips into the nearby Ulugurus and supplied a few specimens of the new bush-shrike and other birds to the museums of Nairobi, Copenhagen, Hamburg, Bremen, and New York, but no report has ever been made on his birds.

In 1937, R. E. Moreau spent some time in the Kibungu forest, elevation 900 feet, at the eastern foot of the Ulugurus, and also in the Kinole forest in the northern part of the range, where he discovered a most remarkable, wholly unexpected, new genus and species of warbler, *Scepomycter winifredi*. In the middle 1940's, Moreau sent his collector, Charles Abdallah, to get additional specimens of this most intriguing new find, in which he was successful. J. G. Williams of the Coryndon Museum, Nairobi, also paid short visits to these mountains to collect specimens of the endemic birds for his institution.

The Uluguru Mountains achieved something of a reputation as a promising source of novelties and rarities as a result of these finds. When, in 1963, Mr. William J. Cheney, a generous friend of the Los Angeles County Museum, proposed to sponsor a collecting trip to eastern Africa for the Museum, the Uluguru Mountains, site of the most distinct recent discoveries in tropical East African ornithology, was suggested as a worthwhile area for further work. Although his own personal interest was more in big game hunting, and the Ulugurus were not known to be a particularly good place for that, Mr. Cheney graciously consented to the idea of going there, and of making the expedition primarily ornithological. From the very beginning, he had intended to collect as many birds as possible, as he had invited his friend, K. E. Stager, the Museum's senior curator of birds, to accompany him.

While the present report deals particularly with the birds brought back by the Cheney expedition, it includes also a summary-compilation of the results of all earlier collections as far as the data were available to us. This is given as a mere listing of the presently known avifauna of the Uluguru Mountains. That of the Ukagurus, based on the present collection and the handful of species obtained by Fuggles-Couchman, is, of course, much less complete. The absence from the latter list of many of the birds present in the Ulugurus cannot be interpreted as definite evidence that they do not occur in the Ukagurus, except as in such cases as *Apalis flavigularis*, where we know that the race *griseiceps* occurs in the Ukagurus and *uluguru* in the range from which it derives its name, and *Pycnonotus tephrolaemus*, which is represented in the Ulugurus by the race *neumanni* and in the Ukagurus by *chlorigulus*.

The only mention in print of any birds from the Ukaguru Mountains is in Fuggles-Couchman's account (1939) of birds collected or observed by him during a six year sojourn in the Eastern Province of Tanganyika. During the course of this residence he visited both the Ulugurus and the Ukagurus, as well

as the Ngurus and the Usagaras. Fuggles-Couchman mentioned only six birds from the Ukagurus, but Mrs. B. P. Hall has informed us of a seventh, of which a specimen was sent by him from there to the British Museum. His list of Ukaguru birds, which constituted all that was known prior to the Cheney expedition's work, is as follows:

Tauraco livingstonii cabanisi
Viridibucco simplex
Pycnonotus tephrolaemus chlorigulus
Aleonax adustus roehli
Batis capensis mixta
Laniarius fülleborni
Cinnyris moreaui

Of these, Fuggles-Couchman's specimen of *Aleonax adustus roehli* was probably the basis of the only mention of the Ukaguru Mountains in Mackworth-Praed and Grant (1957:167). His example of *Tauraco livingstonii cabanisi* was similarly the basis for Moreau's (1958:95) listing of this locality for that bird.

Fuggles-Couchman has given a convenient description of the whole area, based in part on the Tanganyika government's Land Development Survey's report for 1929-1930. From it we may extract the following, "... The province contains three important ranges of mountains, the island group of Uluguru and Nguru and the ranges of the Ukaguru and Usagara, which form one long range running along the western boundary of Kilosa District ...

"The Uluguru and Nguru Mountains are the highest ranges in the province, the Uluguru reaching 9000 feet. Both ranges have extensive areas of temperate rain-forest on them ... Small areas of tropical forest exist at the eastern foot of the Ulugurus in the upper reaches of the Ruvu River ... The Ukaguru, Usagara, and Uvidunda Mountains are somewhat similar, but do not contain such large areas of rain-forest, much of what there is appearing to be of secondary growth. Below is the similar long grass country found on the Ulugurus ... The rainfall decreases from the coastal belt inland, becoming as low as 39.2 inches at Morogoro, at 1600 feet, while at the eastern foot of the Ulugurus it rises to 56 inches."

To the above we may add some further data, on the Ukaguru Mountains, extracted and summarized from an unpublished, typewritten report on the mountain forests of the Kilosa District, submitted to the Ministry of Lands and Surveys, Forest Division, at Morogoro, by J. McCarthy in 1963. The area involves part of a large mountain chain to the north and west of Kilosa Township, which levels off to the north-east where it flattens out into the Dodoma Plateau, while forming the high ridge of the Kilombero Escarpment to the south and west. Between these points is the Usagara area, which is roughly separated into two main mountain masses by the intersecting valleys of the

Mdukwe and Mkondoa Rivers. To the north is the Ukaguru mass, containing the forest reserves of Talagwe, Mamboya, Ikwamba, Uponera, Mamboto, and Mamiwa Kisara. The first two are isolated peaks and are essentially outliers of the main Ukagurus. To the south is the Rubeho mass, containing the Ukwiva Forest Reserve. The total area comprises some 235 square miles of which nearly 175 square miles form the Ukwiva Forest Reserve. The altitude of the Ukagurus ranges from 4000 to 7000 feet with a general average of 6500 feet, but the rise is impressive because of the fact that the range rises from a low plateau of not more than 1000 feet. Up to about 4000 feet the vegetation is largely poor *Brachystegia* woodland flora, but above that altitude it is generally montane rain forest, or more accurately, mist belt forest, as it does not have the lush, luxuriant growth of lowland primary rain forest. The forest canopy is rarely closed completely, but the density of the lower trees and shrubs allows little light to penetrate to the ground. Tree growth in this forest is usually poor with heights between 30 and 60 feet in most cases. On the moister slopes the forest is largely composed of *Albizia* trees, while on the drier parts trees of the genera *Myrica* and *Macaranga* are dominant. On the very steepest slopes on the higher reaches of the mountain streams the Ukindu palm, *Phoenix reclinata*, is common, while in the lower valleys the most numerous tree is *Newtonia buchanani*.

The upper reaches of the Ukaguru forests harbor a variety of game mammals, particularly elephants, buffaloes, pigs, and baboons; also leopards, monkeys, occasional lions (in the drier foothills), rock rabbits, tree rats and squirrels.

At Mandege, where records of rainfall have been kept, the annual precipitation varies between 55 and 80 inches, with an average of 60 inches, as compared with a rainfall of 30 to 50 inches in the Rubeho Mountains to the south-east. On the whole the precipitation in the Ukagurus appears to be fairly similar to that in the Uluguru, and the general aspect of the montane forest in the two groups of mountains is similar.

This may be seen from the photographs illustrating this paper; figures 3 and 4 show the Uluguru, figures 5 and 6 the Ukaguru.

In the following lists of the birds of the Uluguru and of the Ukaguru Mountains, respectively, the linear order and the nomenclature follows that of Mackworth-Praed and Grant (1955, 1957), except in the case of families subsequently revised in the continuation of the check-list of birds of the world, commenced by the late J. L. Peters, and in the case of recent descriptions of new forms. In the Uluguru list there are some birds, recorded in the literature as being from that mountain mass, which are lowland species that probably were collected only at the base of the mountains. The order and nomenclature of these lists is also used in the annotated catalog of the present collection. In those species where some differences of opinion or some doubts seem justified, these are expressed in the text. It seems better to handle matters in this manner for ready reference.

a. Birds recorded from the Uluguru Mountains.

Phalacrocorax africanus africanus
Scopus umbretta bannermani
Falco tinnunculus tanganyikae
Francolinus hildebrandti hildebrandti
Coturnix coturnix africana
Numida mitrata reichenowi
Guttera pucherani
Sarothrura rufa
Sarothrura elegans
Tringa hypoleucos
Columba arquatrix arquatrix
Turturaena delegorguei sharpei
Streptopelia semitorquata semitorquata
Tympanistria tympanistria fraseri
Aplopelia larvata larvata
Treron australis brevicera
Cuculus solitarius solitarius
Cerococcyx montanus patulus
Ceuthmochares aereus australis
Tauraco livingstonii cabanisi
Megaceryle maxima maxima
Alcedo semitorquata
Halcyon albiventris orientalis
Halcyon chelicuti chelicuti
Melittophagus pusillus meridionalis
Bycanistes bucinator
Bycanistes brevis
Glaucidium capense scheffleri
Colius striatus cinerascens
Apaloderma narina narina
Heterotrogon vittatum vittatum
Lybius torquatus irroratus
Buccanodon leucotis leucogrammicum
Buccanodon olivaceum olivaceum
Viridibucco leucomystax
Pogoniulus bilineatus bilineatus
Trachyphonus erythrocephalus erythrocephalus
Campethera cailliautii cailliautii
Campethera abingoni abingoni
Dendropicos fuscescens hartlaubii
Mesopicos griseocephalus kilimensis
Smithornis capensis medianus

Motacilla clara torrentium
Anthus lineiventris
Turdoides jardinei kirki
Malacocincla rufipennis distans
Alcippe abyssinica stierlingi
Pycnonotus barbatus micrus
Pycnonotus masukensis roehli
Pycnonotus virens zombensis
Pycnonotus tephrolaemus neumanni
Pycnonotus milanjensis striifacies
Phyllastrephus cerviniventris
Phyllastrephus debilis rabai
Phyllastrephus fischeri placidus
Nicator gularis
Suaheliornis kretschmeri kretschmeri
Muscicapa striata neumanni
Alseonax adjustus fülleborni
Alseonax cinereus cinereolus
Dioptrornis fischeri nyikensis
Chloropeta natalensis
Chloropeta similis
Chloropetella holochlora
Batis capensis mixta
Platysteira peltata peltata
Trochocercus cyanomelas bivittatus
Trochocercus albonotatus albonotatus
Tchitrea suahelica suahelica
Turdus abyssinicus nyikae
Zoothera gurneyi otomitra
Neocossyphus rufus rufus
Cercomela familiaris falkensteini
Thamnolaea cinnamomeiventris subrufipennis
Saxicola torquata promiscua
Cossypha heuglini heuglini
Cossypha natalensis
Cossypha caffra iolaema
Modulatrix stictigula stictigula
Déssornis anomala grottei
Sheppardia sharpei sharpei
Alethe fülleborni usambarae
Pogonocichla stellata orientalis
Sathrocercus mariae usambarae
Seicercus ruficapillus minullus
Seicercus umbrovirens fuggles-couchmani

Calamonastes simplex undosus
Schoenicola brevisrostris alexinae
Apalis flavigularis uluguru
Apalis melanocephala moschi
Apalis caniceps tenerrima
Apalis chariessa
Apalis porphyrolaema
Apalis bamendae chapini
Artisornis metopias
Scepomycter winifredae
Camaroptera brachyura fuggles-couchmani
Cisticola woosnami schusteri
Cisticola cantans pictipennis
Cisticola erythroptis sylvia
Cisticola natalensis valida
Cisticola brachyptera isabellina
Prinia subflava tenella
Melocichla mentalis orientalis
Hirundo angolensis angolensis
Hirundo daurica emini
Hirundo abyssinica unitatis
Ptyonoprogne fuligula rufigula
Psaldiprocne holomelaena holomelaena
Psaldiprocne orientalis orientalis
Campephaga sulphurata
Campephaga quiscalina münzerni
Coracina caesia pura
Dicrurus ludwigii ludwigii
Dryoscopus cubla nairobiensis
Tchagra minuta reichenowi
Tchagra senegala orientalis
Laniarius ferrugineus sublacteus
Laniarius fülleborni ulugurensis
Laniarius funebris funebris
Telophorus nigrifrons nigrifrons
Telophorus quadricolor nigricauda
Malaconotus alius
Oriolus oriolus oriolus
Oriolus chlorocephalus amani
Lamprocolius chalybeus sycobius
Onychognathus walleri walleri
Onychognathus morio rüppellii
Onychognathus tenuirostris theresae

Stilbopsar kenricki kenricki
Zosterops senegalensis stierlingi
Zosterops winifredae
Nectarinia famosa cupreonitens
Cinnyris venustus falkensteini
Cinnyris loveridgei
Cyanomitra olivacea alfredi
Anthreptes collaris elachior
Anthreptes neglectus
Amblyospiza albifrons montana
Ploceus bertrandi
Ploceus ocularius suahelicus
Ploceus subaureus aureoflavus
Ploceus bicolor kersteni
Quelea erythropus
Quelea quelea aethiopica
Euplectes hordeacea hordeacea
Euplectes gierowii friederichseni
Euplectes nigroventris
Euplectes capensis crassirostris
Euplectes ardens ardens
Spermestes nigriceps nigriceps
Pirenestes minor
Pirenestes frommi
Cryptospiza reichenovii australis
Cryptospiza salvadorii kilimensis
Mandingoa nitidula chubbi
Lagonosticta rubricata haematocephala
Coccopygia melanotis kilimensis
Estrilda astrild cavendishi
Vidua funerea nigerrima
Vidua macroura
Linurgus olivaceus kilimensis
Carduelis citrinelloides hypostictus
Emberiza orientalis orientalis
Emberiza flaviventris flaviventris

To the above we may add the following species from a list kindly sent us by Mr. Th. Andersen of the birds his native collectors obtained for him in the Ulugurus. These are mentioned here rather than in the main list because as far as we know the specimens have not been examined by an experienced ornithologist. Mr. Andersen's list contained a few additional species whose identifications seemed open to question, and which it seemed better to leave out until they could be examined carefully.

Anas sparsa
Milvus migrans parasitus
Lophoaelus occipitalis
Cuncuma vocifer
Accipiter melanoleucus
Accipiter badius subsp.
Accipiter tachiro sparsimfasciatus
Gallinula chloropus meredionalis
Charadrius hiaticula tundrae
Charadrius squatarola
Rostratula benghalensis
Capella gallinago
Tringa nebularia
Turtur afer
Cuculus poliocephalus subsp.
Cuculus clamosus
Clamator glandarius
Chrysococcyx caprius
Chrysococcyx klaas
Gallirex porphyreolophus chlorochlamys
Gymnoschizorhis personata leopoldi
Merops boehmi
Upupa africana
Caprimulgus europaeus subsp.
Caprimulgus fossii
Semeiophorus vexillarius
Pogoniulus pusillus affinis
Indicator exilis exilis
Apus apus subsp.
Anthus trivialis trivialis
Argya rubiginosa heuglini
Pycnonotus importunus subsp.
Phyllastrephus flavostriatus (kungwensis?)
Platysteira peltata peltata
Tchitreia viridis ferreti
Apalis murina subsp.
Tchagra australis minor
Malaconotus blanchoti blanchoti
Oriolus oriolus oriolus
Oriolus auratus notatus
Cinnyris shelleyi hofmarnni
Anthreptes longuemarei orientalis
Anthreptes rectirostris tephrolaema
Amauresthes fringilloides

Hypargus niveoguttatus
Estrilda subflava clarkei
Stegamura paradisaea

b. Birds recorded from the Ukaguru Mountains

Turturoena delegorguei sharpei
Aplopelia larvata larvata
Cuculus poliocephalus poliocephalus
Cuculus solitarius solitarius (no specimen records)
Cercococcyx montanus patulus
Tauraco livingstonii cabanisi
Heterotrogon vittatum vittatum
Viridibucco simplex
Viridibucco leucomystax
Dendropicops fuscescens hartlaubii
Motacilla clara torrentium (no specimen records)
Pseudoalcippe abyssinicus stierlingi
Pycnonotus barbatus micrus
Pycnonotus masukensis roehli
Pycnonotus tephrolaemus chlorigulus
Pycnonotus milanjensis striifacies
Phyllastrephus fischeri placidus
Alseonax adustus roehli
Dioptrornis fisheri nyikensis
Batis capensis mixta
Trochocercus albonotatus albonotatus
Geokichla gurneyi raineyi
Cossypha caffra iolaema
Modulatrix stictigula stictigula
Alethe fulleborni usambarae
Pogonocichla stellata orientalis
Sylvia atricapilla
Sylvia borin
Sathrocercus mariae usambarae
Phylloscopus trochilus acredula
Apalis flavigularis griseiceps
Scepomycter winifredae (no specimen records)
Psalidoprocne holomelaena holomelaena (no specimen records)
Laniarius fülleborni uluguruensis
Chlorophoneus nigrifrons
Corvultur albicollis
Zosterops senegalensis stierlingi
Cinnyris mediocris moreaui
Cyanomitra olivacea alfredi

Anthreptes collaris elachior
Cryptospiza reichenovii australis
Coccygia melanotis kilimensis
Carduelis citrinelloides hypostictus

As already mentioned, present knowledge of the bird life of the Ukaguru Mountains is too incomplete to permit an analysis of the similarities and differences it reveals with respect to that of the Uluguru Mountains. The following few examples may be mentioned, as they seem significant.

Alseonax adustus: represented in the Ulugurus by the race *fülleborni*; in the Ukagurus by the race *roehli*.

Pycnonotus tephrolaemus: represented in the Ulugurus by the race *neumanni*; in the Ukagurus by the race *chlorigulus*.

Apalis flavigularis: represented in the Ulugurus by the race *uluguru*; in the Ukagurus by the race *griseiceps*.

Scepomycter winifredi: known definitely only from the Ulugurus; sight record only from the Ukagurus.

Cinnyris loveridgei: known from the Ulugurus, not from the Ukagurus.

Cinnyris mediocris moreaui: known from the Ukagurus, not from the Ulugurus.

ANNOTATED LIST OF SPECIMENS

FAMILY SCOPIDAE

Scopus umbretta bannermani C. H. B. Grant

One male was collected at Bunduki, Uluguru Mountains, on January 14. The hammerkop had not been recorded previously from this mountain mass, although it is known from numerous Tanganyikan localities. The above specimen was the only individual of this species observed at Bunduki.

FAMILY SAGITTARIIDAE

Sagittarius serpentarius (J. F. Miller)

One adult female was collected on the east side of Lake Manyara, on January 28. It weighed 8 pounds and was in very abraded plumage and was in an active stage of replacement of the body feathers. Its crop contained one snake, one lizard, one frog, and seven grasshoppers. On January 28 another specimen, an adult male, was taken.

FAMILY ACCIPITRIDAE

Necrosyrtes monachus pileatus (Burchell)

The hooded vulture is represented in the collection by one male taken on the east side of Lake Manyara, on January 28. It had the testes slightly enlarged.

Milvus migrans parasitus (Daudin)

An adult female yellow-billed kite was collected 5 miles north of Morogoro on January 5. The bird was feeding in the center of the road when it was hit and killed by one of the expedition's vehicles.

Aquila rapax rapax (Temminck)

The tawny eagle was found along the eastern side of Lake Manyara where two males were collected on January 28 and 29. One of them was noted as having the gonads slightly enlarged. The northern race *raptor* is less rufescent in all plumage stages than in nominate *rapax*, but the difference is not invariable. Tanganyikan specimens are of the southern race *rapax* while the southern and central Kenya birds are intermediate but nearer to the typical form than to *raptor*.

Melierax gabar (Daudin)

A male with somewhat enlarged gonads was collected on the east side of Lake Manyara on January 29. This is probably the commonest of the small hawks of eastern Africa, and occurs in two color phases—a pale gray bird, such as the present specimen, and a black plumaged one.

FAMILY FALCONIDAE

Polihierax semitorquatus castanotus (Heuglin)

One male was collected on the east side of Lake Manyara, on January 28.

FAMILY PHASIANIDAE

Francolinus sephaena grantii Hartlaub

One male of this francolin was taken on January 28 on the east side of Lake Manyara. This is one of the common birds of the East African plains country.

Pternistes leucoscepus infuscatus Cabanis

Two specimens, one of each sex, were obtained on January 28, on the east side of Lake Manyara. The conclusions of Hall (1963:129) have been accepted as a guide in studying and identifying these birds subspecifically.

FAMILY NUMIDIDAE

Numida mitrata reichenowi Ogilvie-Grant

Two males of the East African helmeted guinea fowl were collected on January 13, 2 miles east of Mlali, at the west foot of the Uluguru Mountains.

The allocation of these specimens to the race *reichenowi* is a matter of conforming to recent usage. It is not yet settled whether the proposed race *uhehensis* Reichenow, may prove to be separable. In an earlier comment on

Uluguru guinea fowl, Friedmann (1928:76) referred examples from that mountain range to *uhehensis* because they all had short, bluntly pyramidal bony helmets, whereas specimens of typical *reichenowi* had the helmet much longer. The present examples agree in this respect with the three Uluguru birds discussed in the 1928 paper, and the uniformity of the two series argues for further consideration of the validity of *uhehensis*. Unfortunately, no pertinent material from elsewhere in its supposed range has been available for study. It may be noted that van Someren (1922:25) considered that a specimen from Makindo, Tanganyika, might be of that race.

FAMILY OTIDIDAE

Eupodotis senegalensis canicollis (Reichenow)

A male with slightly enlarged testes was collected on the east side of Lake Manyara, on January 28.

FAMILY CHARADRIIDAE

Hoplopterus armatus (Burchell)

On January 28, an adult female blacksmith plover was collected on the east side of Lake Manyara.

FAMILY SCOLOPACIDAE

Tringa hypoleucos Linnaeus

One example of this European migrant, a female, was collected at Bunduki, Uluguru Mountains, on January 14. The specimen was secured from a mist net set over the stream that flows through Bunduki.

FAMILY GLAREOLIDAE

Glareola pratincola fülleborni Neumann

Two specimens, one male, one female, were obtained on January 28, on the east side of Lake Manyara. The species was abundant on the mud flats along the shore of Lake Manyara.

FAMILY PTEROCLIDAE

Eremialector decoratus loveridgei Friedmann

Two females, taken on the east side of Lake Manyara, on January 27, agree with the characters of this race, originally described from Dodoma, farther south in Tanganyika. The species was relatively abundant and encountered singly or in pairs.

FAMILY COLUMBIDAE

Cuculus poliocephalus poliocephalus Latham

One adult male and one immature male were taken at Bunduki, Uluguru Mountains, January 7 and 14. The immature specimen has the bill dusky, not

yellow as in the adult, has the mantle and abdomen paler, the breast more barred with terminal whitish transverse tips on the feathers, and the upper wing coverts more streaked with whitish.

Olive pigeons were common about Bunduki and frequented the tops of the tall *Eucalyptus* that had been introduced in the area.

Turturoena delegorguei sharpei Salvadori

One female was obtained at Mandege, Ukaguru Mountains, on January 22. An earlier record from the Ulugurus is one from Bagilo (Friedmann, 1928). The Mandege specimen was secured by mist net in heavy secondary forest growth.

Streptopelia decipiens perspicillata Fischer and Reichenow

One adult male of this pigeon was taken on January 27, on the east side of Lake Manyara where it was found to be a common species.

Streptopelia capicola tropica Reichenow

One adult male was taken on the east side of Lake Manyara, January 27. A common species in this area.

Stigmatopelia senegalensis aequatorialis (Erlanger)

One female was collected on January 26, on the east side of Lake Manyara, 60 miles south of Arusha. A common species of the plains country.

Aplopelia larvata larvata Temminck and Knip

One female was collected at Mandege, Ukaguru Mountains, January 20. This dove was previously known from two localities in the Ulugurus; Bagilo and Nyange.

This lemon dove was netted in dense secondary forest, but escaped and flew to the base of a nearby tree where it sought refuge underground in an earthen hole. The bird was then captured by hand from this dark hole.

FAMILY CUCULIDAE

Cuculus poliocephalus poliocephalus Latham

A single specimen, a female taken at Mandege, Ukaguru Mountains, January 21, 1964, presents some unusual features. It is small, wing 140 mm., tail 125; culmen from cere 17.5 mm., and is unusually rufescent, the forehead, crown, occiput, back, and upper wing coverts being bright rufous barred with black with faint greenish gloss, while the rump and upper tail coverts are more uniformly dark rufescent, almost bay, with subdued blackish bars. It is considerably darker on the posterior upper parts than comparable examples from India.

The subspecific identification is based on the small size of the specimen which agrees thereby with nominate *poliocephalus* rather than with *rochii*. This is in line with the findings of Grant and Mackworth-Praed (1936:131-133) and of Moreau and Moreau (1937:163-164), who found the Indian bird to be a more frequent visitor to eastern Africa than the Madagascan race. Other Tanganyikan records for this cuckoo range from late November to nearly the middle of April, with the majority in March and April.

Cuculus solitarius solitarius Stephens

At Bunduki, Uluguru Mountains, two males and one female were collected January 7 to 9, 1964. The female had a much enlarged ovary and was nearly in breeding condition; one male had the testes only slightly swollen; of the other no observations were noted. The two males weighed 75 grams each. Fuggles-Couchman (1939:82) noted that the red-chested cuckoo usually did not begin calling at lower levels in Tanganyika until the middle of November but that he heard it in "full song" on October 9 at 5,500 feet in the Ulugurus. The condition of the present January female suggests a prolonged breeding season in the Ulugurus.

In January, 1964, cuckoos of this species called continuously throughout the day in the forests of both the Ulugurus and the Ukagurus.

Cercococcyx montanus patulus Friedmann

Two males, with slightly enlarged testes, were collected at Mandege, Ukaguru Mountains, January 18 and 20. Both had fairly abraded remiges, the terminal portions being especially frayed. This cuckoo was previously known from the Uluguru Mountains, where the type was collected at Bagilo. The range of *patulus*, now known to include the Ukagurus, extends from the Usambara, Uluguru, and Ukaguru Mountains to south Angoniland, southwest of Lake Nyasa. It is not known from the Ngurus, but may well be found to occur there as well.

The fact that the adult plumage of *montanus* resembles that of the immature stage of the other species of the genus, *mechowi* and *olivinus*, suggests that the present species may be closer to the original *Cercococcyx* stock and that the two western species developed from it.

Both of the above specimens were collected by listening to their loud calls and thereby locating the birds in the tops of forest trees.

Chrysococcyx klaas klaas Stephens

One adult male, with gonads slightly enlarged, was taken 5 miles south of Babati, northern Tanganyika, on January 25.

Ceuthmochares aereus australis Sharpe

One male was collected at Bunduki, Uluguru Mountains, on January 10; testes slightly enlarged. Previously recorded from the Ulugurus from Mkaraji

by Friedmann and Loveridge (1937), and from the thickets around the foothills of that area by Fuggles-Couchman (1939:83).

The above specimen was collected in dense primary forest on the hills above Bunduki.

FAMILY MUSOPHAGIDAE

Tauraco livingstonii cabanisi (Reichenow)

Three males and two females were collected at Bunduki, Uluguru Mountains, January 7-12. Weights were recorded of 260 grams for one male and 270 grams for one female. This colorful bird is apparently common in the Uluguru forests, where it has been recorded from Bagilo, Nyange, and Nyingwa, as well as now from Bunduki.

In his study of the Musophagidae, Moreau (1958:95) mentioned a specimen of the present species from the Ukagurus. We are informed by Mrs. B. P. Hall that a specimen was collected there by Fuggles-Couchman, and was sent by him to the British Museum. This is probably the same individual.

Livingstone's turacos were equally common in the Uluguru and Uka-gurus. They were calling loudly in both mountain ranges, but no specimens were secured at Mandege. At Bunduki, turacos could be isolated in small clumps of forest trees, where they could be collected with ease. In the Ukagurus the forest was more uniformly continuous, making it more difficult to obtain examples of these wary birds.

Gymnoschizorhis personata leopoldi (Shelley)

One male with somewhat enlarged testes was collected on the east side of Lake Manyara on January 29. Mackworth-Praed and Grant (1957:538) wrote that the breeding season of this Tanganyikan race of the bare-faced go-away-bird, is from September to December. The gonadal condition of the present specimen suggests a later terminal date.

A common species in the scattered Acacia forests east of Lake Manyara.

FAMILY CORACIIDAE

Coracias caudatus caudatus Linnaeus

One adult male, with small testes, was collected on January 28, on the east side of Lake Manyara. This roller is a common bird in the open country of eastern Africa and occurred abundantly in the Lake Manyara area.

FAMILY ALCEDINIDAE

Megaceryle maxima maxima (Pallas)

One adult male and one subadult female were collected on January 7, at Bunduki, Uluguru Mountains. These appear to be the first records of this large kingfisher from that mountain range.

At least three of these large kingfishers were found working the trout-stocked stream at Bunduki and were looked upon with great disfavor by the members of the Uluguru trout fishing club, whose club house is located there.

Alcedo semitorquata Swainson

An adult female, taken at Bunduki, January 13, is the first record for the half-collared kingfisher from the Uluguru Mountains. According to Jackson (1938:561) this is a rare bird in Kenya and it may also be uncommon in Tanganyika.

The single specimen of this species secured at Bunduki was taken in a mist net placed across the stream. No other half-collared kingfishers were observed in the area.

Halcyon albiventris orientalis Peters

Two examples, one of each sex, collected at Bunduki on January 7 and 8, add the brown-hooded kingfisher to the known avifauna of the Uluguru Mountains. The female is in very abraded plumage, the ends of many of the feathers being worn and frayed. It may have been a bird that had completed its breeding and had not yet begun to enter the post-nuptial molt. The species has been found nesting in November in the coastal belt of northern Tanganyika.

Halcyon chelicuti chelicuti (Stanley)

On January 28, an adult male was collected east of Lake Manyara. The striped kingfisher is a wide-spread, common bird throughout most of eastern Africa.

FAMILY BUCEROTIDAE

Bycanistes brevis Friedmann

A male, taken at Bunduki, Uluguru Mountains, on January 11, agrees in its small dimensions with topotypical *brevis*. In the years since describing *brevis* as a southern, smaller race of *B. "cristatus"* all the additional material personally examined by the senior author has borne out the distinctness of the two populations, but students of African birds, working chiefly with the material in the British Museum, have equally consistently written as though the species could not be split into geographic races. The present use of a binomial is a concession to current nomenclatural usage, but the matter still seems worthy of reexamination with adequate material. It may be mentioned that van Someren (1932:287) found that his series supported the recognition of a larger, northern, and a smaller, southern race of this hornbill.

Hornbills were noted as uncommon in the Bunduki area during our brief stay there. The large silvery-cheeked hornbills were the only species observed and in each instance they were noted singly and late in the day. They seemed to be feeding below Bunduki, as each bird would appear from down the valley, alight on the tops of certain tall, solitary trees at Bunduki and then fly

on up the mountain to the dense stand of forest. The above listed specimen weighed 1275 grams.

Tockus erythrorhynchus erythrorhynchus (Temminck)

One adult male was obtained on the east side of Lake Manyara on January 26. This species and *Tockus deckeni* were both common in the savanna country around Lake Manyara.

Tockus deckeni (Cabanis)

One adult male was collected on the east side of Lake Manyara on January 28.

Field studies are badly needed to elucidate the nature of the isolating mechanisms that operate between this species, *jacksoni*, and *erythrorhynchus* in the areas where all three are sympatric. It may be recalled that at one time several not uninformed writers considered *jacksoni* merely the young of *deckeni*. This is mentioned merely to emphasize the similarity in habits and in habitat of the two, but there is no longer any doubt as to their distinctness (see Friedmann, 1930:420-425, for fuller discussion).

FAMILY PHOENICULIDAE

Phoeniculus purpureus marwitzi (Reichenow)

One adult male of this kakelaar was collected east of Lake Manyara on January 27. A common species in the Lake Manyara area.

FAMILY STRIGIDAE

Asio capensis capensis (A. Smith)

Two specimens, one of each sex, were taken on January 29 east of Lake Manyara. The male is slightly paler than the female. The marsh owl is widely distributed, but local in its occurrence in much of eastern and southern Africa. In Tanganyika it has been recorded only a small number of times, and apparently chiefly in the interior. Moreau and Moreau (1937:170) cited one specimen from the Pangani River, 10 miles east of Korogwe, about 50 miles inland, as the most eastern Tanganyikan record.

Three birds were flushed from the tall savanna grass and two were collected.

Glaucidium perlatum (Vieillot)

An adult female of this small owl was taken east of Lake Manyara, on January 27, where the species was noted as common in the large, densely foliated *Acacias*.

FAMILY CAPRIMULGIDAE

Caprimulgus fossii clarus Reichenow

One female was obtained 5 miles south of Babati on January 24.

It may be noted that *clarus* is here considered as a race of *fossii*, as sug-

gested by Friedmann (1930:309-312), by Bowen (1931:40-43) and by Chapin (1939:427), and not as a race of *Scotornis climacurus* as suggested by Grant and Mackworth-Praed (1937:18-20). Chapin has pointed out that *C. fossii* and *Scotornis* occur side by side along the middle Congo River, and that the two must therefore be looked upon as species even though one race of *fossii*, *apatelius*, does seem to be intermediate between *C. f. clarus* and *S. climacurus*. In view of the difficulty of taxonomic placement reflected in these divergent treatments it would seem advisable to cease recognizing *Scotornis* as generically distinct from *Caprimulgus*, and the two species should be restudied both in the field and the museum to evaluate their distinctness and the nature of their relationship.

Nightjars were common on the Babati-Dodoma road at night, where the above specimen was hit by one of the expedition vehicles.

FAMILY COLIIDAE

Colius striatus cinerascens Neumann

One male, three females and one unsexed bird were collected at Bunduki, Uluguru Mountains, January 7-8. One of the females was in full breeding condition, having a large egg, partially shelled, in the oviduct; the male showed some gonadal enlargement also. The speckled mousebird appears not to have been recorded before from the Ulugurus, but its presence there was to be expected in view of its very widespread range. The present series agrees with *cinerascens* in having the upper back unbarred and in having dusky, blackish throats. On geographic grounds *cinerascens* is the race that might have been expected to inhabit the unforested parts of the Ulugurus. No comparative material has been available to test the distinctness of *cinerascens* from *kikuyuensis*, or to test whether the race may be separated convincingly from *affinis*. In an earlier study, it was concluded (Friedmann, 1930, p. 321) that *cinerascens* was a synonym of *affinis*.

Colies were common in the marginal vegetation surrounding the native cultivations on the hillsides about Bunduki. They were usually observed in pairs, but small groups of four to five birds were sometimes encountered.

FAMILY TROGONIDAE

Heterotrogon vittatum vittatum (Shelley)

One adult male was collected at Mandege, Ukaguru Mountains, on January 17. Its presence in the Ukagurus is in keeping with its occurrence in the Ulugurus, where a good series was obtained in 1926 by Loveridge at Bagilo, Nyange, Nyingwa, and Viture (Friedmann, 1928:81).

Trogons were not observed in the Bunduki area of the Ulugurus during our stay there. The above specimen was the only trogon observed or heard in the Ukagurus.

FAMILY CAPITONIDAE

Tricholaema lacrymosum lacrymosum Cabanis

One female was collected 5 miles south of Babati on January 25. It had a somewhat enlarged ovary and would probably have come into breeding condition by the end of the month. No material of *T. l. narokensis* Jackson has been available for comparison but it is not likely that that race, whose validity is doubtful at best, extends from Doiyo Narok to the acacia savannahs around Babati.

Virdibucco leucomystax (Sharpe)

One female of this little barbet was collected at Mandege, Ukaguru Mountains, on January 19. The use of the binomial nomenclature used here is in agreement with Mackworth-Praed and Grant (1957:723). Recently Goodwin (1964:212-213) concluded that *leucomystax* and *simplex* are not as closely related as they might seem to be at first glance. He pointed out that the two are at least partly sympatric, that their vocalisms are said to be different, and that although both have a similar olive coloration they differ in the pattern of their head markings and also in size. Goodwin suggested that *leucomystax* and *coryphaeus* are actually much more closely related and may form one superspecies. It may be noted that Fuggles-Couchman (1939:88) identified his Ukaguru bird as *V. simplex*. Loveridge (in Friedmann and Loveridge, 1937:181) collected two examples of *leucomystax* in the Uluguru Mountains. The total present data thus reveal that *leucomystax* occurs in both areas, while *simplex* has been recorded only from the Ukagurus. It will be of interest to see if it is present in the Ulugurus as well.

FAMILY PICIDAE

Dendropicos fuscescens hartlaubii Malherbe

Four examples of the little cardinal woodpecker were obtained as follows: Bunduki, Uluguru Mountains, one male, two females, January 6-13; Mandege, Ukaguru Mountains, one female, January 21. The Mandege specimen has the top of the head and the dorsal bars darker, blacker, than the Bunduki birds and is very slightly larger; wing 88 mm. as compared with 85 mm. in Bunduki females.

Thripias namaquus namaquus (Lichtenstein)

One male was collected east of Lake Manyara on January 27.

FAMILY ALAUDIDAE

Mirafrja javanica marginata Hawker

Two males of the singing bush-lark were taken east of Lake Manyara, on January 27 and 28. They agree in size and in coloration with a series from subcoastal Kenya. The nomenclature used here is in accordance with the

usage proposed by Peters (*in* Mayr and Greenway, 1960:4), wherein the group of races formerly considered as a species "*cantillans*" are united with *javanica*.

Singing bush-larks were noted as common in the Lake Manyara area and were encountered daily.

Mirafra rufocinnamomea torrida Shelley

A male in breeding condition was shot east of Lake Manyara on January 29. This lark occurs from the Marsabit plains in Kenya, southward to at least Ugogo and central Tanganyika at altitudes of from 2,000 to 5,500 feet.

Flappet larks were common in the Lake Manyara area and the loud cracking sound made during flight could be heard throughout the day.

FAMILY MOTACILLIDAE

Motacilla clara torrentium Ticehurst

One male and two females were obtained at Bunduki, Uluguru Mountains, January 9, 10, 14. The male is generally darker slate gray above than the females and also lacks the broad white margins on the inner secondaries and also lacks the whitish spot below the ear-coverts found in the present two females. These differences are probably purely individual as they are not regularly characteristic of male birds. The present specimens constitute the first records for the mountain wagtail from the Uluguru Mountains. The common name, mountain wagtail, is not wholly appropriate, as this species is not restricted to the highlands. However, its preference for rapidly flowing streams does often cause it to live in the hills as it is there that the brooks are more apt to be rapid in their movements.

Although no specimens were secured in the Ukagurus, the species was observed along stream courses at Mandege on several occasions.

FAMILY TIMALIIDAE

Alcippe abyssinica stierlingi (Reichenow)

One male was taken at Bunduki, Uluguru Mountains, January 6; five females were collected at Mandege, Ukaguru Mountains, January 18 to 21. The Bunduki specimen had the gonads somewhat enlarged. It is generally agreed that Hartert's proposed race *uluguru* is not distinct (Friedmann, 1928; Moreau, 1940).

All of the above specimens were secured in mist nets set in heavy forest. The species is equally abundant in both the Uluguru and Ukaguru mountains, although only one specimen was taken in the former area.

FAMILY PYCNOTIDAE

Pycnonotus barbatus micrus Oberholser

Five examples of this wide-ranging bulbul were obtained; two males, one female, at Bunduki, Uluguru Mountains, July 10-12; one male, two miles east

of Mlali, west foot of the Uluguru Mountains, January 13; one male, Mandege, Ukaguru Mountains, January 20. All are in fairly worn plumage. This species was not obtained in the Uluguru range by Loveridge in his 1926 visit, although he did collect it in the Usambaras. One cannot put down the suspicion that he met with it in the Ulugurus as well, but by then he may have made no effort to collect it because of its general ubiquity. Schuster (1926:733) not only recorded it there, but even found a nest at Mamba, in the western part of the range, on December 30, 1913.

Yellow-vented bulbuls occur abundantly in the Uluguru Mountains in peripheral vegetation bordering native cultivations. The species did not appear to be as common in the Mandege area, but this may be due to the more forested nature there.

Pycnonotus tephrolaemus chlorigulus (Reichenow)

One male and two females of this relatively local bulbul were collected at Mandege, Ukaguru Mountains, on January 18 and 20. They agree with *chlorigulus* in having whitish upper and lower eyelids and in having a conspicuous olive green patch on the throat attenuating laterally to a narrow band connecting with the olive green of the mantle. The presence of *chlorigulus* in the Ukaguru Mountains is of interest, as the race in the Ulugurus is *neumanni*, and it might have been expected that the same race would be found to inhabit both of these relatively adjacent mountainous areas. It is true that Mackworth-Praed and Grant (1955:138) stated the range of *chlorigulus* as extending from the Nguru Mountains to eastern Dodoma, Kilosa, and Iringa, which fairly well encompasses the Ukagurus, but until now it was not known which race, if any, inhabited that particular area.

Fuggles-Couchman (1939:93) obtained a specimen of the bulbul on July 30, at Vingwele, in the Ukagurus, where he frequently heard it in the forest.

The mountain greenbul was rather uncommon in the forest of the Mandege area as only three specimens were obtained. All were secured by mist nets set in heavy forest.

Pycnonotus milanjensis striifacies (Reichenow and Neumann)

Four males and three females were collected at Bunduki, Uluguru Mountains, January 6 to 12; two females were taken at Mandege, Ukaguru Mountains, January 18. The specimens from the two mountain ranges are alike in dimensions and in coloration. One of the Bunduki males is immature and is duskier, less yellowish, more greenish, below than are the adults. Judging by the present series and by the fact that Loveridge (*in* Friedmann, 1928:90) also obtained a number of specimens at two localities in the Ulugurus (Bagilo and Nyingwa), it appears that this species is common in that mountain range. Rand (1958:185) noted that Uluguru birds agree closely with others from Kilimanjaro in being slightly more golden than Usambara, Chyulu, and Mt. Meru examples. The present series agrees with his findings.

Bulbuls of this species are equally abundant in the forests of both the Uluguru and the Ukagurus as shown by the large series collected. Next to *Pycnonotus masukensis*, this species was the commonest bulbul caught in the mist nets. Many were captured, and large numbers of them were liberated.

Pycnonotus masukensis roehlii (Reichenow)

A good series of this greenbul was collected in both the Uluguru and the Ukaguru Mountains. In the former area 6 males and 6 females were obtained at Bunduki, January 6 to 14; in the latter region, at Mandege, 7 males were taken, January 18 to 22. The subspecies *roehlii* is characterized by the grayish tinge on the sides of the head and the breast, the gray throat, and the circumocular ring of gray.

Although obscure in habits, this bulbul was by far the most frequently-taken bird in the mist nets set in the forests of the Uluguru and the Ukagurus. Large numbers of netted birds were liberated.

Pycnonotus virens zombensis (Shelley)

Two specimens, both males, were taken at Bunduki, Uluguru Mountains, January 9 and 10. This form was previously known from Vituri and Nyange in the same mountain area, so it appears that it is a common, widely distributed species there. Rand (*in* Mayr and Greenway, 1960:252) gave the distribution of this race as extending, “. . . north into southern Tanganyika Territory (to foothills of Uluguru Mountains and Mafia Island) . . .” The bird actually occurs well up in the Uluguru, far beyond the “foothills.”

The Little Greenbul was not met with in the Ukagurus and was relatively uncommon at Bunduki in the Uluguru, compared to the preceding two species.

Phyllastrephus fischeri placidus (Shelley)

Fischer's greenbul was collected in both the Uluguru and the Ukaguru ranges; at Bunduki, in the former area, one male was obtained on January 8; at Mandege, in the latter range, one male and two females were collected on January 18 and 20. The race *placidus* is a bird of the higher country from the Marsabit area of northern Kenya south to Nyasaland.

FAMILY MUSCICAPIDAE

Muscicapa striata neumanni Poche

Two males were obtained, one two miles east of Mlali, west foot of the Uluguru Mountains, January 13, and one east of Lake Manyara, January 27. The former is slightly darker above and may possibly be typical *striata*, but the difference is also within the range of individual variation.

Aleonax adustus fülleborni (Reichenow)

A series of five males and three females was obtained at Bunduki, Uluguru Mountains, January 6 to 14. Several of the birds showed signs of

gonadal enlargement. Fuggles-Couchman (1939:94) recorded the species (race *roehli*) from the Ukaguru Mountains, where he obtained a specimen at Vingwele, at 5,000 feet, on June 23. The use of the subspecific name *fülleborni* for the Uluguru population follows that advocated by Mackworth-Praed and Grant (1955). It may be mentioned, however, that in earlier studies (Friedmann, 1928:84; Moreau, 1940:458) it was concluded that the name *subadustus* was the proper allocation.

Dusky flycatchers appeared to be common in the Bunduki area, as specimens were obtained in a variety of plant associations. Some were secured relatively high in forest trees and others from near the forest floor by means of mist nets.

Aleonax cinereus cinereolus (Finsch and Hartlaub)

One female, not in breeding condition, was collected at Bunduki, Uluguru Mountains, on January 6. It was in somewhat abraded plumage.

Bradornis microrhynchus Reichenow

Two males of this common flycatcher were collected east of Lake Manyara on January 27.

Dioptrornis fischeri nyikensis (Shelley)

A good series, collected in both the Uluguru and the Ukaguru ranges, consists of the following specimens: four males and one female, one young male, Bunduki, January 6 to 14; three males and one female, Mandege, January 19 to 22. Chapin (1953:611) stated that *nyikensis* begins to intergrade with nominate *fischeri* in the Mbulu district of Tanganyika, some distance to the north of where the present specimens were taken. The Uluguru and Ukaguru birds show no signs of such intermediacy. The nominate race is characterized by a greater development of the white circumocular area, and is somewhat deeper slate gray on the upperparts. Moreau (1940:458) noted that this flycatcher occurs on most of the suitable mountain groups of central and norther Tanganyika, but appears to be absent from the Usambaras and the South Pare Mountains. Schuster (1926:712) found it common at Bunduki, where he obtained 6 specimens in March, 1913.

An abundant and obvious species at both Bunduki and Mandege. These flycatchers were very active during the early morning hours and readily responded to "squeaking" decoy calls. They frequented the trees and were seldom encountered in nets placed at ground level.

Melaenornis pammelaina tropicalis (Cabanis)

One male of this black flycatcher was collected 5 miles south of Babati, on January 25.

Chloropeta natalensis massaica Fischer and Reichenow

One female was collected at Bunduki, Uluguru Mountains, January 8. The

single specimen was secured by mist net set in the dense river-bottom vegetation along the stream course at Bunduki.

Batis capensis mixta (Shelley)

Specimens collected were as follows: Bunduki, Uluguru Mountains, two adult males, one juvenal male, one adult female, January 11, 12, 1964; Mandege, 5,300 feet, Ukaguru Mountains, six adult males, four adult females, January 18-22, 1964. The examples from the two mountain ranges are alike in coloration and in size of bill and wing. One of the males from Bunduki had the testes slightly enlarged, about 1.5 mm. in length. Fuggles-Couchman (1939:94) recorded this bird from the Ukagurus, where he found it common and collected one at Masenge, at 6,000 feet on October 5. The need for further study with ample material from the various Tanganyikan mountain "islands" is indicated by the findings of Moreau (1940:458) who noted that specimens from the Ulugurus and from Kilimanjaro had longer tails, 35 to 37 mm., while those from the Usambara, Handeni, and Nguru Mountains had tails measuring 30 to 32 mm.

Before realizing the importance of measuring the tail length in the present series all but two pairs of the birds, one pair from the Ulugurus and one from the Ukagurus, were sent on loan to W. J. Lawson of the Durban Museum. The specimens retained here show tail lengths of 34 and 37.2 mm. in the Uluguru examples and 32.7 and 33 mm. in those from the Ukagurus. These figures indicate that the Ukaguru birds agree with those from the Usambara, Handeni, and Nguru Mountains rather than with the Uluguru and Kilimanjaro birds. The birds from all the Tanganyikan highland forests should be measured and all the data brought together before attempting to map these potential races.

These small flycatchers occur commonly in the heavy forests of the Ulugurus and Ukagurus and all of the above specimens were secured close to the forest floor by means of mist nets. It was interesting to note that when the species became entangled in a mist net it was most frequently both a male and a female and the two birds would generally be within six inches of one another. Whether this was due to a male pursuing a female, or that the pair was moving through the forest in close proximity to one another, can only be speculated upon.

Batis molitor molitor (Hahn and Küster)

One male was collected on the east side of Lake Manyara, 60 miles south of Arusha, on January 26. It had the testes somewhat enlarged, measuring nearly 2 mm. in length. In assigning this specimen to the nominate race we are following the decision of Mackworth-Praed and Grant (1955:226), who considered *puella* a synonym. However, Chapin (1953:664-665) recognized *puella*, although admitting that there is a band of gradual intergradation with nominate *molitor*, and he gave the range of *molitor* as extending northward from South Africa to Nyasaland and the southwestern side of Lake Tanganyika,

and that of *puella* as encompassing northern Tanganyika to Kenya north to Barsaloi, thus leaving our portion of Tanganyika untreated.

Trochocercus albonotatus albonotatus Sharpe

Three females of this flycatcher were collected at Bunduki, Uluguru Mountains, January 10, and at Mandege, Ukaguru Mountains, January 19. One of the specimens is subadult and has the throat dark gray, not black as in the other two. In an earlier report on Loveridge's 1926 Uluguru collection (Friedmann, 1928:85) a series of this species was referred to Grote's subspecies *subcaeruleus* because of close agreement with the supposed characters of that race. In view of subsequent opinion as to the nonvalidity of *subcaeruleus*, the Uluguru population is considered the same as typical *albonotatus*. Chapin (1953:696) found that *subcaeruleus* was a little more bluish gray on the upperparts, but that the difference was slight. He did, however, consider the race might be recognized and that it would be found to occupy the entire Nyasa area as well as the type locality, Mlalo, Usambara.

These small crested flycatchers were only encountered in mist nets set in heavy forest and were not otherwise observed.

Tchitrea suahelica suahelica (Reichenow)

At Bunduki, Uluguru Mountains, a series of five males and four females was collected January 6 to 11. The birds were in breeding condition, with much enlarged gonads, except for one female which was in very abraded plumage and may have been through breeding. The others, to judge by their fresher plumage, probably were about to begin to breed. This species was previously known from Tawa, Mamba, and Vituri, in the Ulugurus. Schuster (1926:713) found a nest at Mamba, on December 30, 1913.

An abundant and obvious species in the forest of the Ulugurus. These attractive flycatchers were nesting in the Bunduki area during the expedition's stay there. A pair of birds were observed incubating eggs in a nest placed in a giant clump of bamboo that overhung the stream near our camp. The species was very aggressive and would respond immediately to a squeaking decoy call.

FAMILY TURDIDAE

Turdus abyssinicus nyikae Reichenow

One male, testes slightly enlarged, was collected at Bunduki, Uluguru Mountains, January 11. The bird shows signs of feather replacement in the wings. In considering this specimen as *nyikae*, we are following Mackworth-Praed and Grant (1955:332), who concluded that *T. o. uluguru* was not distinct, but we may register a suspicion that further study with adequate comparative material may reinstate *uluguru* as a valid race. Moreau (1940:459) used the latter subspecific designation.

The olive thrush may be fairly common in the Ulugurus, but mist nets yielded only a single specimen. The species was not met with in the Ukaguru Mountains, but it is quite possible that it occurs there.

Zoothera gurneyi otomitra (Reichenow)

One female, taken at Mandege, Ukaguru Mountains, on January 21, adds the Ukagurus to the localities in which this ground-thrush is known to occur. It was previously recorded from the Ulugurus, the Usambaras, and north-eastern Tanganyika generally, wherever suitable forests are found. The specimen is in much abraded plumage.

The single specimen was flushed from the forest floor in dense mist forest. No other individuals were observed.

Saxicola torquata promiscua Hartert

One male, testes slightly enlarged, was taken at Bunduki, Uluguru Mountains, January 12. Schuster (1926:740) reported the species abundant in the Ulugurus in 1913.

Cossypha caffra iolaema Reichenow

One adult male, one subadult male, two juvenal females, were taken at Bunduki, Uluguru Mountains, January 6 to 9; one adult male at Mandege, Ukaguru Mountains, January 20. The subadult bird is largely in adult plumage but still has some of the dusky scallop-margined feathers of immaturity on the breast and upper abdomen and also still has the pale buffy streaked feathers on the forehead, sides of face, and on the entire occiput. One of the juvenal birds could hardly have left the nest more than 10 days before it was collected, as its tail feathers are only about half grown. The Kenya robin-chat was recorded from the Ulugurus by Schuster (1926:740-741).

Robin-chats were common in thickets and secondary forest growth along trails and about native cultivations. They were very inquisitive and readily responded to squeaking decoy calls.

Modulatrix stictigula stictigula (Reichenow)

Four specimens of this species, still rare in collections, were obtained: two males and one female at Bunduki, Uluguru Mountains, January 8, 13, 14, and one male at Mandege, Ukaguru Mountains, January 21. The species is apparently restricted to mountain forests of Tanganyika, the nominate race being known from the Usambara, Uluguru, Ukaguru, Uzungwe, and Ukinga ranges, while a smaller and darker race *pressa* is recorded from the Nkuku Forest on Mt. Rungwe in southwestern Tanganyika. The Ukaguru bird agrees in all respects with its Uluguru counterparts. Moreau (1940:456) found Uluguru birds to be intermediate in size and in color between typical *stictigula* of the Usambaras and *pressa*, but felt they should not be designated by a different name as they formed part of a cline of progressively darker and smaller birds from north to south.

The presence of this thrush in both the Ulugurus and the Ukagurus was detected only with the use of mist nets set in heavy forest. Total netting time

in both mountain ranges yielded only the above four specimens, which indicates that the species was not very numerous.

Alethe fülleborni usambarae Reichenow

Two males of this shrike-like thrush were taken, one at Bunduki, Uluguru Mountains, January 14, and one at Mandege, Ukaguru Mountains, January 21. Both had the testes slightly enlarged. Their wings measured 106 and 108 mm. respectively, very slightly longer than Reichenow's type, 103 mm. This bird continues to be very rarely collected, and hence additional specimens are always welcome.

A shy species, and, as with the other forest thrushes, it was only detected by the use of mist nets set in dense forest at ground level.

Pogonocichla stellata orientalis (Fischer and Reichenow)

A surprising series of 24 specimens of this rather elusive denizen of the forest floor was obtained within a fortnight's collecting in the Uluguru and the Ukaguru Mountains. Such a result could only be accomplished with the use of mist nets, as the white-starred bush-robin is ordinarily not too easy to approach. The present series contains 5 juvenal, 4 immature, and 15 birds in adult plumage. Their localities and dates are as follows: Bunduki, Uluguru Mountains, 3 juvenal males, 2 juvenal females, one immature male, 5 adult males, 4 adult females, January 6 to 14; Mandege, Ukaguru Mountains, 3 immature males, 2 adult males, 4 adult females, January 18 to 22. Three specimens were marked as having the gonads somewhat enlarged.

This species is of unusual interest in that it shows geographical, racial, differences in either having, or skipping, the immature plumage. The present subspecies has this intermediate plumage well developed, but the race *guttifer*, of the highlands of northeastern Tanganyika as far east as Mt. Kilimanjaro, is said not to have this stage but to molt directly from the juvenal into the adult plumage.

Considering the number of local races of this woodland bird in the forest "islands" of East Africa, it is remarkable, as Moreau (1951:397) has already pointed out, that *orientalis* has as extensive a range as it does, encompassing isolated forests from as far south as Namuli in Mozambique, Kungwe near the southeastern corner of Lake Tanganyika, and the Uluguru and Ukaguru Mountains in central Tanganyika.

Although shy, the white-starred bush-robin proved to be an abundant species in both the Ulugurus and the Ukagurus. As mentioned above, the use of mist nets yielded large numbers of these attractive birds—so many in fact that large numbers were liberated. Although the species is abundant on the forest floor, it also forages through the crown of the forest. Specimens collected from the tree tops were located only by the sharp eyes of Nandi hunters. Often it required considerable patience on the part of these men to point out the presence of this bird in the forest crown.

FAMILY SYLVIIDAE

Sylvia atricapilla atricapilla (Linnaeus)

The blackcap is a winter visitor from Europe and is very common in much of eastern Africa during the northern winter season: two males were collected at Mandege, Ukaguru Mountains, on January 19 and 22.

Sylvia borin (Boddaert)

One female of the European garden warbler, a common winter visitor to eastern Africa, was collected at Mandege, Ukaguru Mountains, on January 21.

Sathrocercus mariaae usambarae (Reichenow)

Six specimens of this forest warbler were collected: at Bunduki, Uluguru Mountains, January 6 to 14, four females; at Mandege, Ukaguru Mountains, January 18 and 19, one adult male and one immature female. The young bird differs from the others in having a yellowish wash on the abdomen. Two of the birds were noted as having small ovaries. The Mandege adult and one of those from Bunduki have narrow blackish pectoral streaks, the young bird has them also but less dusky in tone; the other three show little trace of them.

Although frequently heard in deep forest at both Bunduki and Mandege, the forest warbler was seldom seen. The species was readily trapped in mist nets set on the forest floor, however.

Phylloscopus trochilus acredula (Linnaeus)

One male was collected on January 21 at Mandege, Ukaguru Mountains. This Palearctic winter visitor is said (Mackworth-Praed and Grant, 1955:384) to reach only as far south as the Sudan and Ethiopia during the northern winter. The present specimen has the underparts as white as *acredula*. It has faint yellow streaks on the breast, but has the wing formula of *trochilus* and not of *collybita*.

Apalis flavigularis griseiceps Reichenow and Neumann

Three males and two females were collected at Mandege, Ukaguru Mountains, January 18 to 21. One of the birds was noted as showing slight gonadal enlargement. This subspecies ranges from the Chyulu Hills of southeastern Kenya to northeastern and south-central Tanganyika, and is now recorded for the first time from the Ukagurus. It is remarkable that in the not too distant Ulugurus there is a different race characterized by having a much darker forehead, crown, and occiput and by having the abdominal yellow deeper and more extensive, extending anteriorly to the dusky pectoral band.

An exceedingly common species in the forests of both the Ulugurus and the Ukagurus, occurring in the crown of the forest as well as close to the forest floor. Large numbers were caught in mist nets in the latter area, and released.

Apalis flavigularis uluguru Neumann

This race, restricted to the Uluguru Mountains, is represented in the present collection by two males and two females collected at Bunduki, January 6 to 14, where it was numerous.

Apalis flavida golzi (Fischer and Reichenow)

On January 25, 5 miles south of Babati, one female of this warbler was collected.

Artisornis metopias (Reichenow)

Two examples of each sex were taken at Bunduki, Uluguru Mountains, on January 6 to 12. The females are slightly smaller than the males. In the Usambaras the breeding season of this warbler is said to be in January, and it would be expected that in the Ulugurus it would be about the same. However, there are no indications of the gonadal condition on the labels of the present specimens.

Hall and Moreau (1962:341) give good reasons for submerging the genus *Artisornis* in *Orthotomus*. The two make very similar stitched nests, and the species *metopias* is remarkably similar in structure and in coloration to the Asiatic *O. sepium*. The only deterrant to making this change is that the nest of the second African species, *moreaui*, has yet to be discovered. If it also is a stitched structure, the case would seem definite. If it is not, and since *moreaui* and *metopias* seem related, it may be necessary to retain *Artisornis* for them.

The use of a binomial for the present specimens is a matter of conforming to the nomenclature of Mackworth-Praed and Grant (1955). However, it may be pointed out that in an earlier study (Friedmann, 1928:478) the Uluguru birds, separated as a race *altus*, were found to be characterized by having the middle of the throat washed with reddish brown, the sides and flanks browner, less grayish, than typical "ruficeps" of the Usambaras. Moreau (1940:461) found *altus* to be a valid, recognizable subspecies. The present specimens agree with the characters of *altus*, but no comparative material has been available for study.

Red-capped forest warblers, although shy and secretive, appeared not to be too rare in the Bunduki area of the Ulugurus. The species was encountered in the tall grass and vegetation in the dense forest. All four specimens were secured with mist nets, set in the vegetation described. The species was not noted in the Ukagurus but it may occur there as it has been recorded from the Nguru Hills.

Scepomycter winifredi (Moreau)

This relatively recently discovered monotypic genus of warbler is known only from the Uluguru Mountains. At Bunduki, on January 10, 11, and 14, four examples, three males and one female, were obtained. These were in breeding condition, a fact that concurs with the statement of Williams (1951:

469) to the effect that the breeding season of this bird begins in October and continues until February or March.

Although previously recorded from only the Uluguru Mountains, a warbler of this species was definitely observed at Mandege on January 17, 1964. The bird was observed at very close range in heavy forest, but due to circumstances could not be collected at that time. A subsequent search for the bird at the same spot failed to disclose the species, nor were any other individuals observed or collected during the expedition's short stay at Mandege.

At Bunduki, all four specimens were secured by mist nets set in dense forest. An analysis of the contents of the stomachs of three of the four specimens showed them to be filled with insect material as follows: Orthoptera (Acrididoidea, Blattoidea); Hemiptera (Heteroptera); Coleoptera (Carabidae, Tenebrionidae or Alleculidae, Curculionidae); Hymenoptera (Formicidae). The most abundant insects of the above listed orders were weevils (Curculionidae).

Cisticola chiniana fischeri Reichenow

Three examples from northern Tanganyika are attributable to this race; one male from 5 miles south of Babati, January 25, and two males, east side of Lake Manyara, January 26. The rattling *Cisticola* appeared to be a common bird in the low savannah country about Lake Manyara.

Cisticola cantans pictipennis Madarasz

One male was taken at Bunduki, Uluguru Mountains, January 11; a female at Mandege, Ukaguru Mountains, January 21. This appears to be a southern extension of the range of this race, hitherto not recorded south of northern Tanganyika, around Arusha and the Usambara Mountains.

Cisticola galactotes nyansae Neumann

One male was taken at Babati, northern Tanganyika, on January 25. The specimen was mist netted in a grassy patch in the heart of the town.

Prinia subflava tenella (Cabanis)

One male was collected 2 miles east of Mlali, at the west foot of the Uluguru Mountains, on January 13. This is one of the common, widespread warblers of eastern Africa.

FAMILY HIRUNDINIDAE

Hirundo angolensis angolensis Bocage

One immature male, one adult female and two immature females, collected at Bunduki, January 7 to 11, extend the known range of this swallow to the Uluguru Mountains. Angola swallows were abundant about Bunduki and several were observed with nests at the buildings of the Catholic mission school there.

Psalidoprocne holomelaena holomelaena (Sundevall)

One female, in breeding condition, was taken at Bunduki, Uluguru Mountains, on January 11. This black swallow is apparently common in the Ulugurus, where it has been recorded from Bagilo, and Nyange as well as from Bunduki. In referring this specimen to the nominate race, we are following the decision of Mackworth-Præd and Grant (1955:554) in considering *massaica* as a synonym. In an earlier report (Friedmann, 1928:84) the latter name, then currently recognized, was used for Uluguru specimens.

Black rough-winged swallows were observed flying in and out of holes in the bank of a road cut at Mandege, in the Ukagurus, between January 17 and 22, 1964.

FAMILY LANIIDAE

Eurocephalus anguitemens rüppelli Bonaparte

One male, with enlarged testes, was collected on the east side of Lake Manyara, on January 28. The bird shows evidence of ecdysis, especially in the wings.

Lanius cabanisi Hartert

Two females of the long-tailed fiscal were collected on the east side of Lake Manyara, on January 29. The species was common in this area and observed daily.

Urolestes melanoleucus aequatorialis Reichenow

On the east side of Lake Manyara, January 26 to 28, two males and two females of this magpie-shrike were collected.

Most authors who have had occasion to discuss the plumages of this bird write that the sexes are alike. However, the present two females differ markedly from the males in having the lateral feathers of the lower breast and the abdomen broadly edged with white; in one of the specimens these white edgings are much broader and encompass the entire outer webs of these feathers. Shelley (1912:233) seems to be one of the few writers who have noted a similar sexual plumage dimorphism in this species.

Laniarius fülleborni ulugurensis Rand

A good series of the sooty bush-shrike was collected, as follows: Bunduki, Uluguru Mountains, January 8 to 12, two males, one female; Mandege, Ukaguru Mountains, January 19 to 21, four males, two females. Fuggles-Couchman (1939:98) had already recorded this shrike from the Ukagurus, where he collected a male in breeding condition on December 15 at 5,500 feet. Rand (1957:49) described the population of the Ulugurus as a new subspecies *ulugurensis*, on the basis of their grayer, more of a dark slate, color than the birds of the Usambara Mountains (*usambaricus*) and suggested that Nguru Mountain birds might also be *ulugurensis*. The present series indicates that the birds of the Ukagurus agree with those of the Ulugurus, but the former

are very slightly grayer than the latter. We cannot help but wonder if the species may not have been subdivided into too many races on slight characters. The females are paler, more grayish than the males from the same localities, a fact which makes one wonder at the distinctness of *usambaricus*, the type of which is a male, and *ulugurensis*, based on a female specimen. In this connection it may be noted that Diesselhorst (1961) concluded that *ulugurensis* should be considered the same as typical *filleborni*.

In both the Ulugurus and the Ukagurus, the sooty bush-shrike was a common species of heavy forest and the dense thickets of secondary plant growth on the periphery of human habitations. It is an inquisitive species and was often decoyed into view by "squeaking."

Laniarius aethiopicus sublacteus (Cassin)

Two specimens, one male taken at Bunduki, Uluguru Mountains, January 10 and one female collected 2 miles east of Mlali, west foot of the Ulugurus, January 13, are referred to this subspecies on geographical grounds, but with some reservations. According to Jackson (1938:1213) and to Mackworth-Praed and Grant (1955:613) *sublacteus* should have the wings plain black with no white on the middle, upper coverts or on the inner secondaries. Both present specimens have some white, more extensive in the Mlali than in the Bunduki bird, and they may therefore be considered intermediates between *sublacteus* and *major*. Jackson's description admits some occasional white on the scapulars in *sublacteus*, so it appears that there is some variability in this character. The present race had been recorded previously from Nyange, in the Uluguru Mountains (Friedmann, 1928:87).

Dryoscopus cubla nairobiensis Rand

At Bunduki, Uluguru Mountains, January 6 to 10, two males and two females of the puff-back shrike were collected. One of the birds was noted as having slightly enlarged gonads.

Chlorophoneus nigrifrons (Reichenow)

Two of the various color phases of the black-fronted bush-shrike were collected; at Bunduki, Uluguru Mountains, January 6 to 12, three males in the slightly orange-yellow breasted phase and one female in the buff breasted plumage; at Mandege, Ukaguru Mountains, January 19 to 21, three males and one female in the buff breasted phase.

One of the yellow breasted males has faint dusky transverse bars on the throat, breast and upper abdomen, and lacks the orange or apricot tinge found on the other two; it may be subadult. The females of the buff-breasted phase are somewhat dusker below than the males and one of them also has the faint transverse bars.

Chapin (1947:53-64; 1954:36) summarized the geographic occurrence of the four color phases of this bird; black-breasted males are known only in the

Usambaras and on Mt. Namuli in Mozambique; red-breasted birds of both sexes are recorded from Kenya, from Mt. Kilimanjaro, and from the Katanga south to the Transvaal; yellow-breasted examples are known from Kenya and Tanganyika; and buff-breasted birds from Mt. Kenya, Teita, and Tanganyika. The species is restricted everywhere in its range to highland forests. Sclater and Moreau (1933:198-201, pl. 6) figured in color three of the phases of this shrike. From a footnote to their account (p. 198) we learn that C. M. F. Swynerton collected one ("*münzerni*") in the Uluguru, the only published reference to his having worked in that mountain mass. In a later paper, Moreau and Southern (1958:310) concluded that the Uluguru population, completely isolated on all sides, has developed no distinctive characters of its own.

Without exception, all specimens of the black-fronted bush-shrike collected in the Uluguru and Ukaguru Mountains were secured from the crown of the forest, rather than from the lower levels of tree growth.

Malaconotus alius Friedmann

This large black-capped bush-shrike, wholly restricted to the Uluguru Mountains, was sought for diligently but not obtained by the expedition, although one example, an adult male, taken on May 20, 1952, by Th. Andersen, was acquired for the collection. It must be a bird of low numerical status and very local in its distribution to have evaded the search made for it. Hall and Moreau (1962:347) concluded that the area it inhabits is probably less than 100 square miles, but they suggested that it might occur in some of the small patches of woodlands on the mountains immediately to the west of the Ulugurus. So far no one has found it there.

FAMILY CORVIDAE

Corvultur albicollis (Latham)

What appeared to be a "family group" of five white-necked ravens was seen at Mandege, Ukaguru Mountains, on January 20, and four of the birds were collected; an adult male, an immature male, and two immature females. The adult was in an active phase of molt as it has several new remiges and rectrices only partly grown. The immature birds, fully grown in size, have well marked grayish diagonal areas on either side of the breast extending postero-ventrally from the lateral ends of the white nuchal collar, and also have some similar grayish feathers immediately behind the white collar giving it a "frayed" look.

FAMILY ZOSTEROPIDAE

Zosterops senegalensis stierlingi Reichenow

A series of this widely distributed white-eye was collected in both the Uluguru and the Ukaguru Mountains. At Bunduki, one male and four females were taken, January 7 to 10; at Mandege, three males and two females were obtained January 18-19. The present nomenclatural usage for these specimens is based on the findings of Moreau's exhaustive study (1957) which differs in

many points from the listing in Mackworth-Praed and Grant (1955). Moreau concluded that the whole of the *Zosterops* inhabiting southern tropical Africa belong to the same species, *senegalensis*, and that the racial name *stierlingi* may be retained for the more richly pigmented birds of the highlands of Tanganyika and Nyasaland. He pointed out (p. 368) the possibility of some hybridization of *stierlingi* with *flavilateralis* at Kibungo, 700 feet, eastern foot of the Uluguru, as some of the lowland birds there show convergence toward the forest-edge birds of the higher mountains. He also stated (p. 405) that the birds, "... some yellower and some greener (usually called *anderssoni* and *stierlingi*) of Nyasaland and south-western Tanganyika (north to Uluguru and Usambara) form a special case, and that local color trends are traceable through the highlands southward from Iringa."

In the absence of anything comparable to the material studied by Moreau, his conclusions are followed here. It may be pointed out, however, that the Ukaguru specimens are brighter yellow below, and very slightly darker above, than the Uluguru birds. The Ukaguru birds also have more yellow on the forehead than the Uluguru examples, but the latter are variable in this respect, the extremes variants ranging from birds with no well defined frontal yellow to others with almost as much yellow as in the Ukaguru birds. Without Moreau's large study as a source of background information against which to view these two series of specimens, it would have seemed valid to consider them as representing two races, but in the light of his statement about localized color trends, it seems advisable to call them all the same, and to be content merely to mention their observable differences.

FAMILY NECTARINIIDAE

Cinnyris mediocris moreaui W. L. Sclater

At Mandege, Ukaguru Mountains, January 18 to 21, ten adult males, one immature male, and one adult female were obtained. The female and the immature male are alike in coloration but the latter is larger and has a much longer bill, agreeing in this respect with the ten adults. Two of the adult males have metallic green upper tail coverts; in all the others these feathers are bright violet blue. Mackworth-Praed and Grant (1955:785) wrote that the female has a "metallic greenish grey wash on head and mantle." This is not found in our present example of this sex or in the immature male, both of which have the head and entire upperparts dark olive green. Two of the adult males were noted as having the testes slightly enlarged.

This sunbird had been recorded previously from Vingwele in the Ukagurus, and also from the Uvidundas by Fuggles-Couchman (1939:102).

Cinnyris loveridgei Hartert

Loveridge's sunbird is wholly restricted to the Uluguru Mountains, where it occurs at elevations of about 2,500 to 7,500 feet in the forest. At Bunduki, January 7 to 14, a series of ten adult males, four adult females and one im-

mature male were collected. One of the females may have been wrongly sexed as it has a few metallic green feathers on the crown, wings, mantle, and throat. The fact that fifteen specimens could be collected in a week suggests that the bird is common where it occurs.

Cinnyris venustus falkensteini Fischer and Reichenow

One immature male, collected at Bunduki, Uluguru Mountains, on January 14, was in the process of acquiring the purplish feathering on the throat and breast, but elsewhere it is in juvenal plumage.

Cyanomitra olivacea alfredi Vincent

This race of the olive sunbird was obtained in both the Ulugurus and the Ukagurus. In the former range, at Bunduki, January 6 to 14, three males and four females were collected; at Mandege, in the Ukagurus, January 18 to 21, five males, one female and one unsexed bird were taken. The specimens from the two mountain masses are alike. Besides the above specimens, one other male was taken at Mandege. It agrees fairly well with the others in dimensions and in dorsal coloration, but differs markedly below. The chin and throat are pale yellow and the center of the abdomen also has some blotches of still paler yellow among the olive green feathers of the breast, sides, and flanks. The feathers of these areas are much greener, less grayish than in all the other examples of *alfredi*, and this individual has two further points of difference: it lacks the yellow tufts on the sides of the chest and it has a faint suggestion of a pale orange spot at the postero-median part of the throat. It was taken to the United States National Museum for further comparison, and there were found two examples of the nominate race from southern Mozambique that agreed with it in having the touch of orange-red on the middle of the lower throat, and that also had considerable yellow on the throat and middle of the abdomen, although not as much yellow as in the Mandege bird. However, two males of *C. o. cephalis* from Gabon proved to be just as yellow on the underparts and also lacked the yellow pectoral tufts. It seems therefore that the Mandege bird belongs with this species, and may represent a little known plumage phase. It certainly does not approximate any other species in its characters.

Anthreptes collaris elachior Mearns

At Bunduki, Uluguru Mountains, January 8, one adult male was collected, another was taken at Mandege, in the Ukagurus, January 19. Both birds had the testes somewhat enlarged. The Uluguru example has a slightly longer bill, but the difference is only 2 mm. Otherwise the two are similar.

FAMILY PLOCEIDAE

Bubalornis albirostris intermedius (Cabanis)

One adult male red-billed buffalo-weaver was collected on the east side of Lake Manyara on January 28. It had the gonads slightly enlarged, about 2 mm. in length.

Histurgops ruficauda Reichenow

One male with large gonads and one female of this weaver were collected on January 28, east of Lake Manyara. Several nesting colonies of this large weaver were observed in clumps of acacias on the undulating ground close to the east shore of Lake Manyara. Each tree held from fifteen to twenty nests.

Passer griseus griseus (Vieillot)

One adult male gray-headed sparrow was collected at Babati, on January 26, where it was a common species about the village.

Amblyospiza albifrons montana van Someren

At Bunduki, Uluguru Mountains, two specimens were collected on January 8. One is a female, the other is marked as a male but is in the streaked plumage of the female and is thus probably immature. It is slightly darker above and the ventral, especially the pectoral, streaks are darker and heavier than in the female.

Both of the above specimens were taken simultaneously in a mist net set in the tall grass at the edge of the river. These individuals were the only two birds of this species seen in the Bunduki area.

Ploceus bertrandi (Shelley)

Two adult males were collected at Bunduki, Uluguru Mountains, on January 8 and 10, respectively. Also obtained there was a female, which appears to have been a young bird, and which represents a plumage that has not been described in the literature. It has a shorter bill, culmen 15 mm. (18 mm. in adult males), the mandible horn color, the maxilla black, and has no black on the head, the forehead, crown, occiput, sides of face olive green like the back, but has a well defined yellow collar conterminous latero-ventrally with the yellow of the throat and breast, entire underparts from chin to under tail coverts yellowish with a faint orange tinge on the breast. The wings, tail, back and rump are like those areas in the adult males.

Ploceus ocularis suahelicus Neumann

Four males, one female of the spectacled weaver were collected at Bunduki, Uluguru Mountains, January 6 to 9; one marked as a male, but female by plumage, was taken 2 miles east of Mlali, at the west foot of the Ulugurus, on January 13. Two of the males had enlarged gonads.

Quelea cardinalis rhodesiae Grant and Mackworth-Praed

Three males and two females of the cardinal quelea were obtained on the east side of Lake Manyara on January 29. The red coloration in the three males extends well down on the breast, and does not extend posteriorly from the hind crown to the occiput, making it obvious that these birds are *cardinalis* and not *erythropros*.

A common species about Lake Manyara where it was found travelling in mixed flocks with *Quelea quelea*. A mist net set in the tall savannah grass caught over one hundred individuals from one fast flying flock, much to the consternation of the Nandi trapper tending the net. The above series and those of *Quelea quelea* were obtained from this flock.

Quelea quelea aethiopica (Sundevall)

On the east side of Lake Manyara, on January 29, six specimens of this common weaver were collected, three of each sex. The males were all noted as having somewhat enlarged testes.

Euplectes gierowii friederichseni Fischer and Reichenow

One female of this weaver was collected 2 miles east of Mlali, at the west foot of the Uluguru Mountains, on January 13. This appears to be the first record for this species from the Ulugurus; it probably does not ascend very far into the mountains but is a denizen of the lower foothills only.

Euplectes orix nigrifrons (Böhm)

At Babati on January 25 and 26, four males of this bishop bird were obtained. This is a wide-ranging inhabitant of much of eastern Africa from Uganda and Kenya to Nyasaland and Mozambique.

Euplectes capensis crassirostris (Ogilvie-Grant)

One male was taken at Bunduki, Uluguru Mountains, January 10. It is in the "off season" plumage. The species had previously been recorded from the Ulugurus, under the racial name *zambesiensis*, which is now considered a synonym of *crassirostris* (Moreau, 1962:69).

Euplectes axillaris zanzibaricus (Shelley)

Three males and one female of this species were collected at Babati on January 25 and 26 where they were found to be abundant in the tall grass about the village.

Spermestes nigriceps nigriceps Cassin

At Bunduki, Uluguru Mountains, one male and two females of this mannikin were collected on January 6. This species was common about Bunduki and the above specimens were secured with mist nets set in the tall grass at the river's edge.

Cryptospiza reichenovii australis Shelley

At Bunduki, Uluguru Mountains, two males and three females were collected January 7 to 14; at Mandege, Ukaguru Mountains, five males and three females were taken January 19 to 22. This species of crimson-wing had been

known from other localities in the Ulugurus. The series from the Ukagurus are like the birds of the Ulugurus in every respect. A very common species along the roads and trails at both Bunduki and Mandege.

Lagonosticta rubricata haematocephala Neumann

One male of this common little fire-finch was collected 2 miles east of Mlali, western foot of the Uluguru Mountains, on January 13.

Coccygia melanotis kilimensis Sharpe

At Bunduki, Uluguru Mountains, four males and one female yellow-bellied waxbills were collected, January 6 to 8; at Mandege, Ukaguru Mountains, two additional males were obtained on January 18 and 19. The specimens from the two mountain areas are alike. These small waxbills were very common in secondary growth on the periphery of forest clearings and along trails.

Granatina ianthinogaster ianthinogaster (Reichenow)

One adult male was collected 5 miles south of Babati, on January 25. The purple grenadier is a common bird in the low country from central Kenya to southern Tanganyika.

FAMILY FRINGILLIDAE

Carduelis citrinelloides hypostictus (Reichenow)

Two males and two females of this citril were collected at Bunduki, Uluguru Mountains, January 6 to 12; one male was taken at Mandege, Ukaguru Mountains, January 19. The species appeared to be common in both mountain areas.

FAMILY EMBERIZIDAE

Emberiza orientalis orientalis (Shelley)

At Bunduki, Uluguru Mountains, one male three-streaked bunting was collected on January 8. It was in breeding condition with very large testes. A few additional individuals were observed, but the species did not appear to be common in the Bunduki area, nor was it met with in the Ukaguru Mountains.

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MAMMALS COLLECTED BY THE LOS ANGELES COUNTY

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VENEZUELA, 1958

By BERNARD B. BUTTERWORTH AND ANDREW STARRETT



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By BERNARD B. BUTTERWORTH¹ AND ANDREW STARRETT²

ABSTRACT: Fifteen species belonging to six orders of mammals, collected in northeastern Venezuela by a Los Angeles County Museum expedition in 1958, are recorded along with pertinent measurements and reproductive information where available. *Phyllostomus elongatus* is reported from Venezuela for the first time.

INTRODUCTION

In the summer of 1958, the Los Angeles County Museum sent an expedition, consisting of Stephen C. Bromley, Arnold S. Menke, and the senior author, to northeastern Venezuela to make general collections of animals. A small number of mammals was collected, chiefly in two localities: (1) in the State of Monagas, on Highway 8, the main highway from Maturín to Barrancas, about 42 kilometers southeast of Maturín; and (2) in the Territorio Federal Delta Amacuro, approximately 140 kilometers northeast of Barrancas.

The camp at the first locality was situated between the Río Guanipa and the Río Tigre, in an area of grasslands interrupted by dense jungles of palms and philodendrons which followed the rivers and their tributary streams. Some tall grasses bordered cultivated areas. Much of the flat open grassland was under water due to the seasonal rains, and what was not actually submerged was marked with many large puddles of standing water. During the time the expedition was located in this area, from June 14 to July 15, it rained for at least a part of each day.

The second locality, which was accessible only by boat or helicopter, was on the Caño Mariusa, one of the many interconnected rivers (caños), 100 to 150 yards wide, which flow from the Río Orinoco and drain northeastward into the Atlantic Ocean. Deep, impenetrable jungle extended to the edges of the caños and prohibited entrance to the shores except in rare instances. The jungle was many-storied with large trees which had buttress and adventitious roots, and penetration was impossible because of the dense vegetation, swamps and mosquitoes. Tides occurred in the caños, along which great masses of water hyacinth flowed continuously toward the ocean. Collecting in this area was done mainly by motorboat. During the expedition's stay at Caño Mariusa, from July 17 to August 14, it rained frequently.

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Several species of aquatic mammals were seen, but not collected, in the Orinoco and in the vicinity of the second campsite. Manatees were observed in the Orinoco during the trip by boat from Barrancas to Caño Mariusa. Unidentified porpoises, possibly of more than one species, were seen on several occasions, both in the Orinoco and in the caños. One was shot but not recovered. On August 7, in the middle of the afternoon, the senior author watched three large otters playing in the water near the edge of one of the caños. They avoided capture, but the combination of the large size of these animals and their diurnal activity suggests that they may have been *Pteronura* (see Cabrera and Yepes, 1940:156-157).

In the accounts which follow, all measurements are in millimeters. Those listed, unless otherwise specified, are the standard external measurements: total length, tail length, hind foot length and height of ear from notch, in that order. The specimens listed are now in the collections of the Los Angeles County Museum.

ACCOUNTS OF SPECIES

MARSUPIALIA

Didelphis marsupialis marsupialis Linnaeus

Specimens—One adult female with pouch young, 42 kilometers southeast Maturín, July 12.

Measurements—864, 460, 59, 58

Although several individuals were seen around the Monagas locality, only one specimen was captured. It was caught, still alive, in a Schuyler Rat Killer baited with bananas and set at the edge of a dense forest at the base of a thick mass of vegetation. The marsupium of the animal contained twelve young, which averaged 77 millimeters, total length.

CHIROPTERA

Rhynchonycteris naso (Wied)

Specimens—Eleven (five in alcohol), nine adults and two juveniles. 140 kilometers northeast Barrancas, July 22 to August 3.

Measurements—Forearm (two adult males, four adult females): 35.3, 35.5, 34.2, 34.5, 35.3, 38.0.

These bats were shot, during the day, from the bark of trees which projected out over the water along Caño Mariusa and other streams. Four of the six adult females collected were gravid. One of these, which had been fluid-preserved, contained an embryo which measured 14.0 millimeters crown-rump length, and a second had a near-term female fetus (furred dorsally, but without fur on the venter) with a 15.0 millimeter forearm. Of the two non-gravid

females, one had a young male, forearm 22.9 millimeters, clinging to its venter, and the other had a slightly enlarged uterus but showed no mammary development. The one fluid-preserved adult male had descended testes which measured 2.9 by 4.3 millimeters, and which, upon sectioning, showed mature spermatozoa in the seminiferous tubules. The young male, which was clinging to the adult female, had inguinal testes which measured 1.0 by 1.8 millimeters and showed early meiotic activity but had no mature spermatozoa in the seminiferous tubules.

Saccopteryx bilineata (Temminck)

Specimens—One subadult male. 60 kilometers southeast Maturín, July 1.

Measurements—Forearm: 40.5. Cranial: condylobasal length, 15.8; zygomatic width, 10.0; postorbital constriction, 3.2; length of upper tooth row C-M³, 7.0. This bat was captured in flight with an insect net at dusk.

Noctilio labialis minor Osgood

Specimens—Five: one, 42 kilometers southeast Maturín, June 18; four, 140 kilometers northeast Barrancas, August 4 and 5.

Measurements—Forearm: two adult males, 57.9, 60.0. Cranial (one adult male, three adult females): greatest length, 20.7, 20.0, 19.4, 19.5; condylobasal length, 19.5, 18.7, 18.4, 18.4; zygomatic width, 15.5, 15.1, 14.7, 14.4; postorbital constriction, 5.8, 5.4, 5.6, 5.8; length of upper tooth row C-M³, 8.0, 7.7, 7.7, 7.8; width across canines at cingula, 7.1, 6.9, 6.2, 6.1.

The first specimen was shot at 7:30 p.m. as it flew around a large tree in a grassy meadow with a number of other large bats. The other four were taken in a mist net at Caño Mariusa on two successive nights. The males had a characteristic strong musky odor which was not noted about the females. Three of the specimens are brown phase, the other two red; all have the light mid-dorsal line at least evident. These bats were heavily infested with batflies.

Carollia perspicillata perspicillata (Linnaeus)

Specimens—Two. 42 kilometers southeast Maturín, July 11.

Measurements—Cranial (one adult male, one adult female): condylobasal length, 20.3, 20.4; interorbital constriction, 5.3, 5.5; length of upper tooth row C-M³, 7.5, 7.5.

These two specimens were smoked out of a hollow tree along with the *Phyllostomus* mentioned below.

Phyllostomus elongatus (E. Geoffroy)

Specimens—One male. 42 kilometers southeast Maturín, July 11.

Measurements—95, 30, 18, 30. Forearm (dried skin): 64.0; metacarpal III, 60.0; first phalanx of digit III, 17.5; second phalanx of digit III, 32.0. Tragus (fresh) 10.0; height of noseleaf (fresh), 20.0 (lancet, 17.0). Cranial: greatest length, 30.1; condylobasal length, 26.5; zygomatic width, 16.9; postorbital

constriction, 5.5; mastoid breadth, 14.7; breadth of braincase, 11.3; length of upper tooth row C-M³, 11.3; width across canines at cingula, 8.2; greatest width across upper molars, 11.5; length of mandible, 20.1; length of mandibular tooth row C-M₃, 12.7.

This specimen, smoked out of a hollow tree along with the two *Carollia* mentioned above, marks the first record for this species for Venezuela, although the locality falls within the range (based on known specimens) given by Cabrera (1957:67): "From Ecuador and Dutch Guiana to Mato Grosso and the south of Peru." The measurements from this specimen fall generally within the ranges of those published for this species from Ecuador (one specimen: Sanborn, 1936), Brasil (four specimens: Vieira, 1942), and Surinam (Husson, 1962). Karl F. Koopman, who kindly compared the specimen with others of the genus in the collections of the Chicago Natural History Museum and verified the identification, wrote that it agreed well with a series of *P. elongatus* from Peru (personal communication).

***Rhogeosia tumida riparia* Goodwin**

Specimens—One subadult male, skin without skull. 60 kilometers southeast Maturín, July 1.

Measurements—Forearm: 26.6.

This specimen was caught in flight with an insect net at dusk. The identification of the skin was made by George G. Goodwin, who kindly compared it with series of specimens of this genus at the American Museum of Natural History.

PRIMATES

***Cebus nigrivittatus castaneus* (I. Geoffroy)**

Specimens—One adult male, skin without skull. 140 kilometers northeast Barrancas, July 25.

Measurements—794, 434, 124, 40.

This monkey was shot from a tall tree where it was feeding on fruit along with several other individuals, in deep jungle area off Caño Mariusa. *Cebus* were more secretive than the red howlers and were not seen in the open at any time.

***Alouatta seniculus straminea* (Humboldt)**

Specimens—Three. 170 kilometers northeast Barrancas, August 5.

Measurements—(adult male, adult female, nursing juvenile male) 1260, 640, 160, 45; 1080, 590, 135, 39; 420, 225, 68, 28. Cranial (adult male and adult female): greatest length of skull, 105, 88; condylobasal length, 115, 85; zygomatic breadth, 83, 68; mastoidal width of braincase, 42, 40; greatest width across maxillary tooth row, 26, 22; length of maxillary tooth row C-M³, 45, 37; cranial breadth, 59, 53; width of hyoid bone, 57, 27; depth of hyoid bone, 53, 27. Approximate weights: adult male, 20 pounds; adult female, 13 pounds.

These three red howlers represent a family group. A fourth member of the group, a second half-grown young, escaped. The adults were shot, out of a tree 15 to 20 feet tall, in a dense jungle off Caño Mariusa. The young animal was taken alive and subsequently died.

Red howlers were seen on several occasions along the Orinoco and caños, usually in groups of two to five animals.

CARNIVORA

Felis onca Linnaeus

Specimens—One female, skin without skull. State of Bolivar, about 20 kilometers northeast Upata, near La Grulla, no date.

Skin was purchased from nationals who had shot it.

RODENTIA

Calomys laucha Olfers

Specimens—Thirteen (five in alcohol), five adult males, four adult females and four juveniles. 42 kilometers southeast Maturín, June 21 to July 9.

Measurements—Cranial (four adult males and two adult females): condylobasilar length, 18, 17, 16, 15, 17, 17; greatest length of skull, 22, 20, 21, 18, 21, 20; mastoidal width of braincase, 10, 11, 10, 10, 10, 10; greatest width across maxillary tooth row, 2.5, 3.0, 2.5, 3.0, 2.5, 2.5; length of maxillary molar tooth row, 4.0, 4.0, 3.5, 3.0, 4.0, 3.0; zygomatic breadth, 12, 12, 12, 10, 11, 11; cranial breadth, 10, 8, 10, 9, 10, 10. All adults were in an active reproductive condition, the males had descended scrotal testes averaging 10 by 4 millimeters and all adult females were pregnant.

These specimens represent the first record for the genus from Venezuela (see Butterworth, 1960, and Hershkovitz, 1962:142ff., for further details). Hershkovitz (*loc. cit.*) refers these specimens to *C.I. laucha*.

Rattus norvegicus (Berkenhout)

Specimens—Four: three, 42 kilometers southeast Maturín, June 17 to July 15; one, on houseboat, 140 kilometers northeast Barrancas, August 9.

Measurements—(two adult males, two adult females) 310, 347, 351, 360; 155, 190, 192, 195; 38, 35, 35, 38; 23, 22, 22, 21. Cranial (one adult male): condylobasilar length, 34; greatest length of skull, 39; mastoidal width of braincase, 14; greatest width across maxillary tooth row, 5; length of maxillary molar tooth row, 7; zygomatic breadth, 17; cranial breadth, 13.

One female was pregnant, containing five embryos.

Dasyprocta rubrata flavescens Thomas

Specimens—One juvenile male. 60 kilometers southeast Maturín, June 25.

Measurements—377, 11, 73, 33.

This juvenile, only a few days old, was collected by nationals on the edge of a forest near the Río Tigre. The fur is generally dark with a reddish tinge. The long rump hairs are orange-buff at their bases, gradually deepening in color to mahogany terminally. The nape and the upper surfaces of the feet are black. We have identified the specimen, as accurately as possible from published descriptions and without comparison with other specimens, following Tate (1935) in the use of the species designation *rubrata* for this form. Cabrera (1961:585) considers this name to be synonymous with *D. aguti cayana* (Lacepede).

Hydrochoerus hydrochaeris (Linnaeus)

Specimens—Two incomplete skulls. 42 kilometers southeast Maturín, June 26.

These two skulls were found in a meadow cut by numerous streams. Two living animals were observed along the bank of Caño Mariusa, and one was found dead in the same caño. On geographical grounds, these specimens probably represent the nominal subspecies, *H. h. hydrochaeris* (Linn.) (Cabrera, 1961:583).

ARTIODACTYLA

Odocoileus virginianus gymnotis (Wiegmann)

Specimens—One. 42 kilometers southeast Maturín, June 26.

A seven point buck was butchered by nationals in the camp area. No measurements were taken on this animal. A live animal was seen at the edge of a dense jungle, 60 kilometers southeast of Maturín.

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