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NOTES ON THE *CHAMAELEO BITAENIATUS* COMPLEX

By A. S. Rand[1]

The lizards known as *Chamaeleo bitaeniatus* have long been considered a series of morphologically differentiated populations of a single widespread and quite variable species. This idea was first proposed by Tornier in 1896 and was accepted by Loveridge in his 1957 check list.

Examination of the collections in the Museum of Comparative Zoology and of the recent literature suggests that the situation is somewhat more complicated. Two of the forms considered as geographical races occurring in Kenya have been collected at the same locality without indication of intergradation. A similar situation is reported by Witte, 1941, and Laurent, 1952, for the mountains east of the African great lakes where two other "subspecies" occur together in the same area, though largely separated ecologically.

On the basis of the present study, six species are recognized: *C. rudis*, *C. bitaeniatus*, *C. ellioti*, *C. höhnelii*, *C. schubotzi*, and *C. kinetensis*. Three races of *C. rudis* are recognized: *C. r. rudis*, *C. r. schoutedeni* and *C. r. sternfeldi*, the latter described in this paper.

The *Chamaeleo bitaeniatus* complex is a group of medium-sized chameleons from the highland regions of East Africa, occurring both in the mountain forests and the highland savannas and ranging from the Abyssinian plateau in the north to the vicinity of Lake Nyasa in the south, and from the mountains west of the Rift in the Belgian Congo to the Chulu hills in Kenya. No members of the group are known from the mountains in easternmost Tanganyika, e.g., the Usambaras and the Ulugurus. The group is characterized by having the body scalation at least somewhat heterogeneous, by lacking (in both sexes) annulated horns, occipital lobes, tarsal spurs, axillary pockets and dorsal fins. All species possess a ventral, a gular, and a dorsal crest, formed in each case by a single row of enlarged scales, and they all show some indication of one or two rows of enlarged plates along the sides of the body. What evidence is available suggests that all give birth to live young.

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PREVIOUS WORK

Four revisions of this species complex have been attempted since Fischer first described *bitaeniatus* in 1884. No two of the revisers have come to the same conclusions, and I have yet a fifth arrangement to suggest.

Tornier, 1896, grouped the four species described to that date as races of *bitaeniatus*. He pointed out the closeness of relationships and concluded that each represented a segment of a morphological series. He used the dorsal and ventral crests, the body scalation, the shape of the casque, and the rostral projection as the characters on which to arrange the species. His series ran: *ellioti* — *bitaeniatus* — *leikipiensis* — *höhnelii.*

Sternfeld, in two papers in 1912, regarded the five described forms as races and named four additional ones. These nine forms he arranged in three morphological series, each descended from a stem form which he postulated as being close to *ellioti.* One line included *graueri, rudis* and *schubotzi,* the second *bitaeniatus, leikipiensis, höhnelii,* and *bergeri,* and the last only *tornieri.* In addition to the characters employed by Tornier, he used head and body proportions and the arrangement as well as the size of the various crests. He believed that intergrades connected all these forms.

Parker, 1932, apparently accepting as subspecies all the forms recognized by Sternfeld but omitting *C. bequaerti* Witte, 1922, divided the series into four groups. The first included *bitaeniatus, ellioti, graueri* and *tornieri,* the second, *rudis,* the third, *leikipiensis, höhnelii* and *bergeri,* and the fourth, *schubotzi.* He stated that the second group intergraded with the first through *graueri,* the third intergraded with the first through *leikipiensis-bitaeniatus,* and the fourth was distinct, combining some of the characters of group three with others of group two, but without intergradation. The characters cited are those used by Sternfeld.

Loveridge, 1957, in his East African check list, recognized six subspecies of *bitaeniatus: bitaeniatus, ellioti* (including as synonyms *graueri, tornieri* and *bequaerti*), *rudis* (including *burgeoni*), *schubotzi, höhnelii* (including *leikipiensis* and *bergeri*), and *altaeelgonis.* He also mentioned, in a footnote, *C. b. kinetensis* of Schmidt, 1943, as an intermediate between *bitaeniatus* and *ellioti,* and *C. b. schoutedeni* Laurent (1952) without comment. No discussion or documentation of these assignments was attempted in the check list.

Both Witte and Laurent have discussed sections of this group in relation to the forms in the mountains of the eastern Belgian Congo, and their conclusions are discussed under the appropriate forms.

These classifications differ primarily in the degree of splitting and in the places where the splits are made. The arrangement offered here differs basically from the others in that, on the ground of arguments from sympatry and character displacement, I have attempted to show that these divisions are of specific rather than subspecific value.

MATERIAL

This revision was based primarily on the large collection of chameleons in the Museum of Comparative Zoology (MCZ). Critical specimens were also borrowed from the American Museum of Natural History (AMNH), Chicago Natural History Museum (CNHM), California Academy of Sciences (CAS), British Museum (Natural History) (BMNH), and the Genoa, Berlin, Paris and Coryndon museums.

ACKNOWLEDGMENTS

I would like to thank the curators of the various museums cited above for their kindness in allowing me to examine specimens in their care. I would also like to thank Dr. E. E. Williams for his advice and assistance throughout.

CHARACTERS USED

The nine characters used in this paper are, with two exceptions, those used by Sternfeld. These two exceptions are the throat grooves in *ellioti* and the number of scales between junction of the canthal ridges and the upper labials, the latter a character used by Laurent, 1952, to define *C. rudis schoutedeni*. I have arranged the characters in the order of their apparent taxonomic usefulness.

1. *Parietal crest* (formed by the parietal bone). The shape of the parietal crest seen in profile varies considerably in these forms. In *höhnelii* it is high, rising steeply from the top of the head, and is strongly curved; in the other forms the crest rises considerably less steeply and is almost straight in outline. In dorsal view, the parietal crest is of nearly uniform width throughout its length, except in the *C. rudis sternfeldi* from

Kilimanjaro and Mt. Meru, where it widens posteriorly into a knob.

2. *Rostral projection.* In all specimens of *höhnelii* there is a scale-covered upward projection on the end of the snout (formed by the dorsal projections of the maxillary bones). There is considerable variation in the length of this projection and in the amount of lateral compression. This variation does not seem to be correlated with age, sex, or locality. A small rostral projection is present in some specimens of *C. rudis rudis,* but it differs from that of *höhnelii* in being very small, dorsoventrally compressed, and directed anteriorly.

3. *Ventral crests.* A row of enlarged scales is present along the ventral midline in all these forms. It may extend from the gular region to the vent as in most specimens; in *ellioti* it usually extends onto the base of the tail for a greater or lesser distance. This is also true for occasional specimens of *rudis* and *bitaeniatus* but not for *höhnelii.* In all forms the length of the scales forming the gular crest is greatest anteriorly and least posteriorly. This characteristic is strongly marked in *höhnelii,* which has a very long gular crest and a moderate pectoral crest. In the other forms, the gular crest is not as long and the difference between gular and pectoral crests is not nearly as marked. In *höhnelii* and some specimens of *C. rudis rudis* the longest scale in the gular crest measures between ⅓ and more than ½ the vertical diameter of the orbit; in all the other forms the longest scale is at most about ⅓ this distance. In *rudis* and *schubotzi* the ventral crest is very difficult to distinguish from the rest of the body scales on the posterior part of the belly. In many specimens of *C. r. schoutedeni* the gular crest is also very short. The crest is formed of scales that are either uniform in size or long and conical alternating with short ones. Usually the alternation of long and short scales occurs in animals with long crests and in those parts of the crest where the scales are longest.

4. *Body scalation.* The scales on the body, legs and tail of all these forms are somewhat heterogeneous. This characteristic is least marked in *ellioti,* well marked in *bitaeniatus, höhnelii* and *rudis,* and extremely well marked in *schubotzi.* In all the forms there is a tendency for one or two rows of large plates to be present along the side, the upper row running from the crest on the temporal arch back over the hind leg and sometimes continued on to the tail, and the lower row running from the axilla back to the hind leg. These may be absent in *ellioti,* or the upper one may be weakly developed. In *höhnelii, bitaeniatus* and *rudis*

the upper row is almost always present, although it may be interrupted and a lower row of plates slightly smaller in size may be present. In *schubotzi*, two rows of very large plates are present, the lower row as large or slightly larger than the upper; the diameter of the largest of these plates is greater than the length of the eye opening when the eye is closed. In all the other forms the plates are smaller or, rarely, equal.

5. *Throat grooves.* In the populations of *ellioti* from Kenya and eastern and northern Uganda, there are present on each side of the throat one or two long, sharply defined, longitudinal grooves, usually lined with black pigment. In the *ellioti* populations from farther south, these grooves are more numerous (up to four main ones), more branched, and not lined with black. This transition seems to be a gradual one, and the southern populations are scarcely distinguishable from the other species on the basis of this character.

6. *Shape of head. C. höhnelii, ellioti* and *bitaeniatus* have long, narrow heads, *rudis* and *schubotzi* short, broad heads. This difference can be expressed by comparing the greatest width of the head measured between temporal ridges with the length of the head measured from the tip of the snout to the end of the parietal crest. In *höhnelii* the head is more than twice as long as wide; in *ellioti* and *bitaeniatus* it is twice to slightly more than twice as long as wide; in *rudis* and *schubotzi* it is less than twice as long as wide (one specimen of *rudis* is just twice as long as wide). *C. ellioti* shows some geographical variation in this. The differences are even more striking in the palatal view of prepared skulls. The shape of the head is paralleled by the shape of the body, *höhnelii, ellioti* and *bitaeniatus* usually having laterally compressed, deep bodies, and *rudis* and *schubotzi* having squat, thick bodies. However, since body shape depends to such an extent on fixation, I have been unable to measure it convincingly.

7. *Pattern.* This is an extremely difficult character to use in distinguishing animals that are as variable as chameleons and on which I have so little information about color in life. All these remarks concern preserved specimens. Most specimens of *ellioti* (almost all those in which the body color is dark) have a ventral crest of a contrasting light color. My specimens of *bitaeniatus* are all light in color, as is their ventral crest. However, Fischer's (1884) description of *bitaeniatus* mentions a light, contrasting, ventral crest. Specimens of *rudis* and *höhnelii*, most of which are dark, have the ventral crest the same

color as the body. The two specimens of *schubotzi* are light, probably as a result of fading in alcohol.

Almost all my specimens of *ellioti* have a marked light-colored, lateral line; this is also indicated in the *bitaeniatus* and was mentioned by Fischer (1884). This line is lacking in *rudis* and *höhnelii.*

8. *Dorsal crest.* A dorsal crest, present in all forms, differs in the degree of development and in the relative size of the scales composing it. Usually, the crest is composed of units of three or four scales increasing in size posteriorly. The difference between the first and last scales in a series may be very great, as it is in *höhnelii,* or very slight, as it is in some specimens of *ellioti.* The other forms seem to be intermediate in this respect, and a great deal of individual variation is evident, particularly in *rudis.*

Key to the forms of the C. BITAENIATUS group.[1]

1. Parietal crest very high, strongly arched; a rostral projection present; gular crest long (longest scale ⅓ to more than ½ the vertical diameter of the orbit); belly crest short .... *C. höhnelii*
   Parietal crest profile low to moderate, almost straight; no rostral projection; gular crest variable; belly crest short to moderate 2
2. Head less than twice as long as broad[2]; scalation heterogeneous; body squat in appearance 4
   Head about twice as long as broad or longer; scalation more or less heterogeneous; body laterally compressed 3
3. Scalation weakly heterogeneous; 1 or 2 well-marked throat grooves usually present; particularly in north of range (northern Uganda and the Sudan), these grooves frequently containing black pigment .... *C. ellioti*
   Scalation much more strongly heterogeneous; 1 or 2 lateral rows of enlarged plates present; many shallow grooves on the throat .... *C. bitaeniatus*
4. Scalation very strongly heterogeneous; 2 rows of very large plates (greatest diameter longer than aperture of closed eye) .... *C. schubotzi*
   Scalation not so strongly heterogeneous; 1 or 2 rows of large plates (greatest diameter not longer than aperture of closed eye) 5
5. Parietal crest widening posteriorly, frequently forming a knob .... *C. r. sternfeldi*
   Parietal crest not widening posteriorly 6
6. Junction of canthal ridges separated from labials by 1 or 2 scales; gular crest very short .... *C. r. schoutedeni*

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[1] Omitting *C. kinetensis.*

[2] In very young individuals the head is proportionately broader.

Junction of canthal ridges separated from labials by 3 or 4 scales; gular crest moderate to long . . . . *C. r. rudis*

CHAMAELEO HÖHNELII Steindachner

1891 *Chamaeleon höhnelii* Steindachner, Sitzb. Akad. Wiss. Wien, 100, Abt. 1: 309, pl. 1, figs. 1-1a. Laikipia, 6000 ft., Kenya Colony.

1891 *Chamaeleon leikipiensis* Steindachner, Sitzb. Akad. Wiss. Wien, 100, Abt. 1: 311, pl. 1, figs. 2-2a. Laikipia, 6000 ft., Kenya Colony.

1912 *Chamaeleon bitaeniatus bergeri* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 252. Sergoit, north of Eldama Ravine Station, Kenya Colony (erroneously given as ''Sirgoi, südlich von Ravine'' in the original description).

1935 *Chamaeleon bitaeniatus altaeelgonis* Loveridge, Bull. Mus. Comp. Zool., 79: 15. Kaburomi, 10,500 ft., Mount Elgon, Uganda.

1957 *Chamaeleo bitaeniatus höhnelii:* Loveridge, Bull. Mus. Comp. Zool., 117(2): 201.

1957 *Chamaeleo bitaeniatus altaeelgonis:* Loveridge, Bull. Mus. Comp. Zool., 117(2): 201-2.

Description. The parietal crest, in profile, rises steeply and then curves sharply downwards, so that the highest point is anterior of the posterior end of the crest. The profiles vary from a condition with a very steep anterior border and a sharp curvature (so that the profile is almost square) to one in which the rise and fall is much more gentle. The crest is always higher and more strongly curved than in any other species. It is uniform in width.

The crests alongside the parietal crest rise from the posterior end of the supraorbital crest and curve medially and posteriorly to run parallel to the parietal crest for a short distance. They may, but usually do not, join this crest. They are usually distinct but may be weak.

A short rostral projection, usually somewhat laterally flattened, is always present. It projects dorsally from the tip of the snout and is scale covered. There is considerable variation in size and lateral flattening in this projection, apparently uncorrelated with sex or age. A rostral projection occurs in both hatchlings and well developed embryos.

The dorsal crest is strongly developed. It is made up of groups of three to five scales. Within each group the scales increase in size posteriorly, with the last two much larger than those preceding them and the very last two or more times larger than the one in front of it.

The gular crest is long, the longest scales a half to more than a half the vertical diameter of the orbit. The crest on the belly is much shorter, and in some cases the scales composing it are only slightly larger than the surrounding belly scales; it is not continued on the tail. The long conical gular-crest scales usually alternate with small scales that may be either single or paired.

The scalation is strongly heterogeneous on the body, the upper surfaces of the legs and the tail, the large scales being strongly convex. The largest scales, separated by small scales, are arranged in a row running from the neck back of the temporal arch to above the hind legs, sometimes continuing a short distance on the tail. A second series of enlarged scales, which are separated by small scales and which are smaller than those in the upper row but larger than the enlarged scales between the two rows, is usually present below the upper row.

There are many small, shallow grooves on the throat. The head is considerably longer than broad. The body usually appears somewhat laterally compressed. In alcohol the specimens appear uniformly dark.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

Four names have been applied to this species. Three of these appear to be based on individual variation. Sternfeld, 1912b, proposed *bergeri* for those specimens in which the nasal projection, the high casque, and the gular crest were most exaggerated: he used *leikipiensis* Steindachner, 1891, for those in which these characters were least well developed. and restricted *höhnelii* to those that were intermediate in these characters. The examination of several large series in the Museum of Comparative Zoology shows no correlation of variation in these characters with sex, size, or geography. *Bergeri* and *leikipiensis* are therefore considered direct synonyms of *höhnelii.*

The fourth name, *altaeelgonis*, was proposed for a population occurring at high altitudes on Mt. Elgon and differing from the population at lower altitudes on this same mountain only in size. Until we know more about the phenotypic effects of altitude on the growth of these reptiles, and about the populations living at high altitudes on other mountains, it seems best to consider this also a synonym of *höhnelii.*

Material examined. **Kenya.** Njoro, Rift Valley Prov., *ca.* 7,500 ft.: MCZ 61179, CNHM 58267-76, 79068-90. Molo, Mau Plateau, 9,000 ft.: MCZ 34994, CNHM 2295, 6425-29. Mt. Kenya: MCZ 29457-58, CNHM 2299, 2304. Nani Moru Track, Mt. Kenya, 10,000 ft.: MCZ 57198. Kenia Forest (= Mt. Kenya?): MCZ 11489. Hills west of Mt. Kenya: MCZ 7839. Voi: CNHM 2307-08. Lagari: CNHM 1845. Kijaba: CNHM 2281. Lukenya: CNHM 2288-89. Lukenya Hills, Athi Plains: CNHM 2292-93. Four mi. W. of Nyeri, 1,660 m.: CAS 86010. Wambugu: MCZ 29469-88(50). Nakuru: MCZ 13360. Loita Plains, Mau Escarpment, S. Masai Reserve, 7,000 ft.: MCZ 17992. Lengetia, Mau Narok, 9,000 ft.: MCZ 62230. Fort Hall: MCZ 29459-68. S. Kinangop Plateau, 10,000 ft.: MCZ 47251-52. Elgonyi, S. Mt. Elgon, 7,000 ft.: MCZ 41800. Kabete, nr. Nairobi: MCZ 31384-85.

Uganda. Budadiri, Mt. Elgon, 4,000 ft.: MCZ 41796-99. Butandiga, west Mt. Elgon, 6,000 ft.: MCZ 41771-95(25). Sipi, west Mt. Elgon, 6,500 ft.: MCZ 41751-69(52). Kuburomi, west Mt. Elgon, 10,500 ft.: MCZ 40274-300. Bulambuli, west Mt. Elgon: MCZ 41770. Madangi, west Mt. Elgon, 11,000 ft.: MCZ 41801-02.

CHAMAELEO BITAENIATUS Fischer

1884 *Chamaeleo bitaeniatus* Fischer, Jahrb. Hamburg. Wiss. Anst., 1: 23, pl. ii, figs. 7a-b. Lake Naivasha, Kenya Colony.

1887 *Chamaeleo bivittatus* (lapsus: *nomen nudum*) F. Müller, Verh. Naturf. Ges. Basel, 8: 294. Witu, Kenya Colony.

1957 *Chamaeleo bitaeniatus bitaeniatus:* Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest in profile is low and straight, or nearly so, rising gradually, posteriorly, so that the highest point is at or near the posterior end. The crest is frequently slightly curved so that in profile the posterior part is parallel to the mouth opening. The parietal crest is approximately uniform in width.

The crests on each side of the parietal crest are nearly straight and run from between the orbits back to parallel the parietal crest on each side for almost half its length. Anteriorly they usually extend laterally to meet the supraorbital crest, frequently above the eye and occasionally behind the orbit. Posteriorly they usually do not join the parietal crest, but are separated from it. These crests are usually distinct, but occasionally they may be obscured by other projections in this area.

There are no rostral projections.

The dorsal crest is moderate in size and composed of groups of 2-5 scales, increasing strongly posteriorly within each group.

Usually the first and second scales of each group do not have the conical, laterally compressed shape of the larger, more posterior ones. Ordinarily the last scale in each group is markedly larger than the one just before it.

Ventral and gular crests are moderately developed, the gular crest being longer but not strikingly so. The largest scales in the gular crest are frequently anteroposteriorly flattened and rarely separated by small scales. Occasionally a continuation of the ventral crest onto the tail is indicated.

The body scalation is markedly heterogeneous, always with an upper row of large plates (which are the largest scales on the body) and almost always with a lower row of large plates. The plates in the upper row are very numerous and frequently in contact. They are never strongly convex.

There are numerous shallow grooves on the side of the throat. The head is narrow, more than twice as long as wide.

The preserved specimens are usually light in color, with indications of light lateral lines following the rows of enlarged plates. The ventral crest is light in color but not markedly lighter than the body, although Fischer (1884) comments that the type had a light ventral line. Preserved specimens usually appear laterally compressed.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

C. bitaeniatus Fischer, 1884, was the first name applied to any of these chameleons. Since that time, only one other name has been used for this species, *C. bivittatus* Müller, 1887. This name appears in a catalogue of the herpetological collections of the Basel Museum, with only a collector and a locality following it. A *nomen nudum*, it is apparently a lapsus for *bitaeniatus*.

Since Tornier (1896), *C. bitaeniatus*, as a binomial, has been used frequently to apply to chameleons in this group. As discussed under *ellioti*, Loveridge in 1942 and in the 1957 check list included specimens of *C. ellioti* under *C. b. bitaeniatus*. As discussed under *C. rudis*, Hellmich, 1956, referred to specimens of that species from southern Tanganyika as *C. b. bitaeniatus*.

C. kinetensis Schmidt, 1943, which may belong here, is discussed below.

Material examined. **Kenya.** Subukia, Nakuru Dist., Rift Valley Prov., 7,000 ft.: CNHM 58266, 79105. Lukenya Hills, Athi Plains: CNHM 2287, 2290, 2291, 2294(2). Lukenya: CNHM 2282-83, 2297. Kijabe: CNHM 2285-86. Kedong Valley: CAS 66018. Athi River, 1,500 m.: CAS 85751. Bukori, S. foot of Mt.

Elgon: MCZ 41715-21. Loita Plains, Mau Escarpment, S. Masai Reserve, 7,000 ft.: MCZ 17995-97. Plains N. of Mt. Kenya: MCZ 8184. Hills W. of Mt. Kenya: MCZ 58228. Plains by Guaso Nyiro: MCZ 7838. Mtito Andei: MCZ 29906. Near Meru River: MCZ 7837. Laikipia: MCZ 8183. Lake Naivasha, Coryndon, Chulu Hills: MCZ 29453.

Tanganyika. Longido West: MCZ 13561.

Ethiopia. Addis Ababa: Genova CE 27995. Between Sancurar and Amarr (Boran): Genova CE 28815. Between Badditu and Oime: Genova CE 28816.

Somalia? Coronna: Genova CE 2888(2).

CHAMAELEO ELLIOTI Günther

1895 *Chamaeleon ellioti* Günther, Ann. Mag. Nat. Hist., (6) 15: 524, pl. xxi, fig. A. Kavirondo, 3900-4000 ft. and foot of Mt. Ruwenzori 5-6000 ft. Restricted by Loveridge to Bugoye, east foot of Ruwenzori Mountains, Uganda.

1922 *Chamaeleon bequaerti* Witte, Revue Zool. Bot. Afr., 10: 69, pl. ii, fig. 1. Beni, Kivu Dist., Belgian Congo.

1942 *Chamaeleo bitaeniatus ellioti:* Loveridge, Bull. Mus. Comp. Zool., 91: 365.

1942 *Chamaeleo bitaeniatus bitaeniatus:* Loveridge, Bull. Mus. Comp. Zool., 91: 364-5.

1957 *Chamaeleo bitaeniatus ellioti* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

1957 *Chamaeleo bitaeniatus bitaeniatus* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest is like that of *C. bitaeniatus.* The crests lateral to the parietal crest are like those in *bitaeniatus*, except that they usually join the supraorbital crest over the eye anteriorly, and posteriorly they usually curve medially to meet the parietal crest.

There is no rostral projection.

The dorsal crest is quite low. It is formed of groups of 2-5 scales that increase in size posteriorly, though without the great differentiation typical of other species, particularly *höhnelii.*

The gular crest is low and quite uniform; the largest scales are usually laterally compressed triangles, not alternating with small scales. The ventral crest is distinct, slightly lower than the gular crest, and usually continued a short distance on the tail.

The body scalation is much more homogeneous than in *bitaeniatus.* An upper row of enlarged scales is frequently present, but the scales are really quite small, never much larger than surrounding large scales and not in contact; a lower row of somewhat enlarged scales is sometimes present.

Particularly in the northern populations, one or two deep, black-lined grooves are present on the side of the throat.

The head is at least twice as long as broad. There is some geographical variation in this character, the specimens from southwest Uganda and the Congo having narrower heads than do those from Kenya.

In alcohol this species is usually dark, with a clear light lateral line and with the ventral crest lighter than the belly.

Preserved specimens are usually laterally compressed.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

The oldest name for this species is *elliotí*, and Günther's description and figure clearly show the black-lined grooves along the throat, characteristic of the northeastern populations of this species.

C. bequaerti is well described by Witte, 1922, from Beni, Congo, and his figure shows clearly black-lined throat grooves. In his concluding paragraph, Witte writes that Boulenger examined the type and considered it intermediate between *C. senegalensis* and *C. ellioti* and very close to the latter. Witte does not discuss the differences which led him to separate *bequaerti* from *ellioti*, and there is nothing in the description nor in a single paratype from Beni (now in the Museum of Comparative Zoology) that serves to distinguish them. It seems advisable to consider them synonymous.

Loveridge, 1942, on the basis of specimens collected in Uganda, recognized *ellioti* as distinct from *bitaeniatus*. He writes, ". . . one can separate *ellioti* by its longer gular-ventral and dorsal crests, the latter being brick red or dried-blood red (orange in typical *bitaeniatus*)." These are colors in life. My examination of these specimens from Uganda assigned by Loveridge to *bitaeniatus* show them to agree with *ellioti* in scalation and in possession of throat grooves, and to differ in these characters from typical *bitaeniatus* from Kenya. They are therefore referred by me to *ellioti*. The differences in color noted by Loveridge are not visible on preserved specimens, and while such color differences represent significant intraspecific variation in *ellioti*, they do not reflect the specific difference between *ellioti* and *bitaeniatus*.

Material examined. **Kenya.** Kitale, 6,000 ft.: MCZ 53968. Kericho: MCZ 52196-97. Yala River: MCZ 18361-62. Kaimosi, Kakamega: MCZ 41722-50.

Uganda. Behungi Escarpment, Kigezi Dist.: CNHM 9866-69. Kisolo, Lake Mutanda, Virunga volcanoes, 6,000 ft., Kigezi Dist.: CNHM 9870-71, 9873, 9875-76, 9878, 9880-82. Mushongero, Lake Mutanda, 5,924 ft.: MCZ 47214-15. Kibale Forest, Toro: MCZ 47191-99. Mabira Forest, nr. Jinja: MCZ 31184-85. Mubango, Mabira Forest: MCZ 47178-90. Entebbe: MCZ 31161-83. Nyakabande, Kigezi Dist., 6,925 ft.: MCZ 47212-13. Mihunga, Ruwenzori Mts., 6,000 ft.: MCZ 47210-11. Bugoye, Ruwenzori Mts.: MCZ 47201-09. Mt. Ruwenzori, 6,000 ft.: CNHM 1844(2). Lukungu Mts., W. Mt. Elgon: MCZ 41621-22. Kampala: MCZ 7258(3). Bundibugyo, Bwamba Region: MCZ 47200. Fort Portal: AMNH 49915.

Rwanda. Kisenyi, N. shore of Lake Kivu, 1,460 m.: CNHM 12782, MCZ 24838-42(8). Kiranga, nr. Kisenyi: MCZ 47216-50(67). Lake Kivu: MCZ 37143.

Congo. Beni, Semliki Valley: MCZ 43029, CNHM 12762. Mambawanga Hill, 40 mi. W. of Beni: CNHM 12806. Rutshuru, Kivu Dist.: MCZ 24829-32, CNHM 12832. Ruwenzori Mts., 3,000 m.: CAS 85987. Tshibati (Lwiro), 32 mi. N. of Bukavu, 1,950 m.: CAS 85763-67. Lulenga, N. of Lake Kivu, 6,000 ft.: MCZ 24843-60.

Tanganyika. Kabare, Bukoba: MCZ 18722-23. Rungwe [loc. questioned]: AMNH 47361-71.

Sudan. Kipia, Imatong Mts. 8,700 ft.; MCZ 45267.

CHAMAELEO RUDIS RUDIS Boulenger

1906 *Chamaeleon rudis* Boulenger, Ann. Mag. Nat. Hist., (7) 18: 473. Ruwenzori Mountains above 10,000 ft., Uganda.

1912 *Chamaeleon bitaeniatus graueri* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 250. Rugege and Bugoie Forests, Ninagongo, 2500-3000 m. and Ruwenzori, *ca.* 25000 m.

1912 *Chamaeleon bitaeniatus tornieri* Sternfeld, Sitzb. Ges. Naturf. Freunde, Berlin, 1912: 383, pl. xvii, fig. 35. Lendu Plateau, Ituri Dist., Belgian Congo.

1933 *Chamaeleon burgeoni* Witte, Revue Zool. Bot. Afr., 24: 120. Mombasa, near Lubero, Kivu Dist., Belgian Congo.

1957 *Chamaeleon bitaeniatus rudis:* Loveridge, Bull. Mus. Comp. Zool., 117: 201.

1957 *Chamaeleon bitaeniatus ellioti* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest profile is like that of *bitaeniatus,* except that in one specimen from Kenya assigned to *C. rudis* the crest is very high, although straight.

The crests lateral to the parietal crest are like those in *höhnelii,* except that they sometimes do not meet the supraorbital crests. There are three to four scales between junction of canthal ridges and the supralabials.

In most specimens there is no rostral projection. In some specimens of *C. rudis rudis* from the Lake Kivu area, the junction of the canthal ridges projects slightly forward to form a small dorsoventrally flattened projection.

The gular crest varies from very long in some specimens of *C. rudis rudis* from the Ruwenzori Mountains to moderately short in others. The large scales are conical, frequently alternating with small ones. The ventral crest is shorter than the gular crest, frequently almost indistinguishable, and very occasionally continued a short distance on the tail.

The body scalation is usually moderately heterogeneous, with an upper row of enlarged scales usually present and the lower row sometimes present. The enlarged scales, not much greater than other large scales, are strongly convex.

There are many small, shallow, throat grooves. The head is broad, less than twice as long as wide. The preserved specimens show little or no lateral flattening of the body. In alcohol the specimens are usually uniformly dark.

The dorsal crest is variably enlarged and made up of groups of scales composed of 1 to 3 small scales, one medium-sized laterally compressed scale and, finally, one large laterally compressed scale.

Discussion. Four names have been proposed for the broad-headed chameleons living in the Ruwenzori Mountains and the mountains south to Lake Kivu. The oldest of these is *C. rudis* Boulenger, 1906, who distinguished it from *bitaeniatus* on its "coarser scaling and in the much larger scales forming the gular and ventral crest, the longest of these on the throat, measuring half the diameter of the orbit." Sternfeld, 1912, described *graueri,* distinguishing it from *rudis* on the basis of its having the gular crest scales less enlarged. He apparently did not realize that this name was preoccupied by *C. graueri* Steindachner, 1911, a synonym of *C. johnstoni.*

Mr. Battersby has kindly made a detailed comparison of the type of *rudis* with a cotype of *graueri.* He reports (letter of April 24, 1959) that the longest scales are "a little smaller than size of the eye opening or about ½ to ¼ the orbital ring'' in the type of *rudis* and ''about ⅔ of eye opening or ⅕ of orbital ring'' in the cotype of *graueri*. He also lists several other scale characters in which these two differ. He also says that though these characters are difficult to define, he feels a ''sense'' of difference. Though the subjective impression of an experienced systematist is often more reliable than many objective measurements, I feel that, since all the characters he mentions show considerable individual variation in other populations, *graueri* should be considered for the present conspecific with *rudis*.

Loveridge, 1957, regarded *graueri* as a synonym of *ellioti*. *C. graueri,* with its heterogeneous scales and broad head, even if not identical with *rudis,* as here believed, is certainly much closer to it than to *ellioti*.

Sternfeld, 1912b, described *C. tornieri* as like *ellioti* in habitus but differing from it in having a short, broad head. Since I have been unable to examine the type, my assignment of this form is based on his description and figures and is only tentative. It is included here because of his emphasis on its short, broad head. However, he quotes field color notes as ''Kehlfalten grünblau oder blau.'' It is possible that this refers to grooves on the throat that occur in *C. ellioti* but not in *C. rudis;* however, these, if present, are not evident in the photograph published with the original description.

Witte, 1933, described *C. burgeoni* from the mountains north of Lake Kivu as close to *rudis* and differing from it only in the presence of small lateral protuberances on the end of the snout. In 1941, he considered it conspecific with *bitaeniatus* and himself questioned its distinctness from what he called *C. b. graueri* (= *rudis*). His hesitancy in giving it subspecific status is understandable since at every locality where he collected *burgeoni* he also took *rudis*. Laurent, 1952, when he described *schoutedeni* from further south, apparently re-examined Witte's material and decided that *burgeoni* was indistinguishable from the other broad-headed chameleons (*graueri* = *rudis*) occurring with it. He pointed out the closeness of relationship between *rudis* in the Ruwenzori, the population near Lake Kivu (for which the name *burgeoni* is available since *graueri* Sternfeld 1912 is preoccupied by *C. graueri* of Steindachner, 1911), and his new *schoutedeni*. He was somewhat dubious about the validity of *burgeoni*.

I can find no consistent differences between the MCZ specimens from the Ruwenzori Mts. and those from near Lake Kivu, and I consider *C. burgeoni* a synonym of *C. rudis rudis*. However, there are specimens from the Kivu area which do have a small nasal protuberance not seen elsewhere and some specimens from the Ruwenzori Mountains have gular crests longer than any that occur outside that area.

Material examined. **Uganda.** Kisolo, Lake Mutanda, Virunga volcanoes, Kigezi Dist.: CNHM 9872, 9874, 9877, 9879. W. slope Mt. Ruwenzori, 12,400 ft.: AMNH 47433.

Rwanda. N. slope of Mt. Karisimbi, 11,000 ft.: AMNH 47442. Lukumi, Mt. Karisimbi, 12,000 ft.: AMNH 47445.

Congo. Ruwenzori Mts., west slope of Stanley Group, 3,300 m.: CAS 85720-22. Tembwe: MCZ 42895. Kabara, Kivu volcanoes, 11,000 ft.: MCZ 42348-49. Kabara, S.W. Mikeno, 10,600 ft.: MCZ 24827. Ruero, S.W. slope of Mt. Mikeno, 9,000 ft.: AMNH 47444. Mt. Ninagongo (= Mt. Niragongo), 9,200 ft.: MCZ 29826. Karambi, E. of Rutshuru, 6,000 ft.: MCZ 24828.

CHAMAELEO RUDIS SCHOUTEDENI Laurent

1952 *Chamaeleo bitaeniatus schoutedeni* Laurent, Rev. Zool. Bot. Afr., 46: Kabumbe Valley, 2400 meters, Kabobo Mountain, Albertville Terr., Tanganyika Prov., Belgian Congo.

Description. Like *C. rudis rudis* but differing from it in having 1 to 2 scales between the junction of the canthal ridges and the supralabials rather than 3 to 4, and in having, in most specimens, very short gular and ventral crests.

Discussion. Laurent, 1952, proposed the name *C. bitaeniatus schoutedeni* for the broad-headed chameleons that he found on Kabobo Mountain. He pointed out their close relationship to the broad-headed forms farther north and distinguished his new form on the basis that it possessed one or two scales between the junction of the canthal ridges and the supralabials rather than the three or four in the typical subspecies, and that the majority of the specimens of *schoutedeni* had a very much reduced gular, and ventral crests. The only two specimens I have seen from Mt. Kabobo certainly conform to Laurent's description and are different from the *C. rudis* from farther north.

Material examined. **Congo.** MCZ 59160-61: River Kabumbe, 2350-2400 m., Mt. Kabobo, Albertville Terr.

CHAMAELEO RUDIS STERNFELDI subsp. nov.

Type: MCZ 56173 ♂, Laikinae, Mt. Meru; Arusha dist.; Northern Prov., Tanganyika Terr., 7,500 ft. alt., August, 1957. Collected by C. J. P. Ionides.

Paratypes: MCZ 56165-72, 56174-75, 2 ♂ 7 ♀, 1 skeleton: same data as type. MCZ 44526: Mt. Meru east at 9,000 ft., B. Cooper, 1938. Berlin 17550 (one of the cotypes of *schubotzi*): Kilimanjaro. Paris 23*103: Kilimanjaro.

Diagnosis. A chameleon of the *C. rudis* group, differing from all the known forms in having the parietal crest always swollen posteriorly and forming in some individuals a distinct knob. Body scalation moderately heterogeneous; 3 to 4 scales between the junction of the canthal ridges and the labials; gular and ventral crests short.

Description. Body stocky; head short and broad, i.e., distance from tip of snout to end of parietal crest less than twice greatest width measured between temporal ridges in type and twelve paratypes (slightly greater in one paratype with extremely developed parietal crest); parietal crest swollen posteriorly (strongly in type and eight paratypes, weakly in four paratypes and not swollen in one paratype). Parietal crest in profile moderate and almost straight. No rostral projection. Ventral crests weak and composed of subequal scales, longest on the throat (longest ¼ vertical diameter of eye or less) where they are cone shaped and occasionally the most anterior ones alternate with small scales; posteriorly the scales are shorter and anteroposteriorly flattened, very indistinct on posterior belly; crest not continued on to tail.

Dorsal crest weakly developed in type and most paratypes (slightly stronger in three paratypes), composed of scales in groups of three anteriorly and four posteriorly, increasing posteriorly in size within the group though only moderately.

Scalation heterogeneous; sides of body and tail and upper surfaces of limbs covered with irregularly-sized, convex, small scales interspersed with larger convex scales. In the type the largest of these form a row running from the neck just behind the temporal crests to the base of the tail; a second row of scales slightly smaller than these runs from just behind and above the shoulder to just in front of the hind leg. The row is much less distinct and more irregular. The upper row is at least indicated in all specimens; the lower row is present in five paratypes and absent in five; in no specimen is the largest scale as large as the length of the closed eye opening. The sides of the throat show no indication of well marked grooves. No definite pattern is discernible in any of these specimens.

Chamaeleo rudis sternfeldi subsp. n.

Measurements of type and paratypes in mm.

Specimen	*Sex*	*Snout-vent length*	*Head length*	*Head width*
Laikinoi, Mt. Meru				
MCZ 56165	Female with eggs	84	23	13
MCZ 56166	Female with eggs	80	23	13
MCZ 56167	Skeleton			
MCZ 56168	Male	75	23	13
MCZ 56169	Female with eggs	68	20	11
MCZ 56170	Female with eggs	77	21	11
MCZ 56171	Female with eggs	82	23	11
MCZ 56173, *Type*	Male	81	24	14
MCZ 56174	Female with eggs	73	21	11
MCZ 56175	Male	62	21	12
Mt. Meru east				
MCZ 44526	?	72	20	11
Mt. Kilimanjaro				
Berlin 17750	?	48	17	9
Paris 23 * 103	?	79	22	12

CHAMAELEO RUDIS subspecies

There are seven specimens of *C. rudis* which do not fit the classification given above. Three of these are from Embagai, Tanganyika. Like *C. rudis schoutedeni,* they have a very weakly developed gular crest, but the canthals are more widely separated from the labials than in typical *schoutedeni.*

A specimen is known from the Loita Plains on the Mau Escarpment in Kenya. At this same locality, both *C. bitaeniatus* and *C. höhnelii* were collected. This specimen differs from others in that the parietal crest rises more steeply posteriorly.

A single specimen from Gilo in the southern Sudan is most like *C. r. rudis,* but geographically widely separated. More material is necessary to determine its true relationships.

Two specimens from Litembo east of Lake Nyasa, which Hellmich, 1956, described under the name *C. b. bitaeniatus,* have not been examined but from his description seem to be *C. rudis.*

Material examined. **Sudan.** Gilo, 6,000 ft.: CNHM 47600.

Kenya. Loita Plains, Mau Escarpment, S. Masai Reservation, 7,000 ft.: MCZ 17994.

Tanganyika. Embagai, above Ngaruka: BM(NH) 1938.1.16. 18-20.

CHAMAELEO KINETENSIS Schmidt

1943 *Chamaeleo bitaeniatus kinetensis* Schmidt, Field Mus. Nat. Hist., Zool., Ser., 24: 336. Mount Kineti, Imatong Mountains, Anglo-Egyptian Sudan. Altitude 10,458 ft.

Discussion. Schmidt, 1943, proposed the name *C. bitaeniatus kinetensis* for a single specimen from Mt. Kineti in the Sudan, which he felt was "allied to *Chamaeleo bitaeniatus ellioti* from which it is distinguished primarily by its smaller size and less uniform dorsal crest." I have examined this specimen and find that it lacks the throat grooves found in the single specimen of *ellioti* I have seen from this area. In most respects it resembles *bitaeniatus*, but the body scalation is more homogeneous than in any other *bitaeniatus* and no more heterogeneous than many *ellioti*. I cannot with confidence assign it to any of the species recognized here, nor am I convinced that it represents an additional full species. I suspect that it is an aberrant *C. bitaeniatus*, but whether an aberrant individual or a representative of an aberrant population I cannot tell. Until further material is available, it seems best to suspend judgment and provisionally recognize *C. kinetensis* as a full species.

Material examined. **Sudan.** Mt. Kineti, Imatong Mts.: CNHM 34483, Type.

CHAMAELEO SCHUBOTZI Sternfeld

1912 *Chamaeleon bitaeniatus schubotzi* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 252. Mt. Kenya, 1400 ft., Kenya Colony (restricted by Parker, 1932).

1932 *Chamaeleon bitaeniatus schubotzi:* Parker, Journ. Linn. Soc. London, Zool., 38: 227.

1957 *Chamaeleo bitaeniatus schubotzi:* Loveridge, Bull. Mus. Comp. Zool., 117: 201.

Description. The parietal crest is like that of *bitaeniatus* in profile. It is not swollen posteriorly.

The crests lateral to the parietal crest arise from the supraorbital crests behind the orbits and curve posteromedially to meet the parietal crest, much as in *höhnelii*.

There is no rostral projection.

The gular crest is moderately low; the long scales are sometimes separated by small, paired scales. The ventral crest is slightly shorter than the gular crest and not continued on the tail.

The body scalation is very heterogeneous, more so than in any other species. There are two lateral rows of enlarged plates, the largest greater than the length of the closed eye.

The dorsal crest is made up of groups of scales, usually two to four small granules followed by two or three enlarged scales that increase in size posteriorly.

There are many shallow throat grooves. The head is broad, less than twice as long as broad. The preserved specimens show no lateral flattening of the body. In alcohol, the specimens show no lateral or ventral stripes.

Discussion. C. schubotzi was described by Sternfeld on the basis of three specimens, with dubious localities. Parker (1932) later assigned a specimen from Mt. Kenya to this species and restricted the type locality to Mt. Kenya. I have examined two of Sternfeld's specimens, an adult labeled Mt. Kenya and a juvenile labeled Mt. Kilimanjaro, as well as Parker's specimen. The Berlin specimen labeled no. 15409, from Kenya, collected by Kolb, and Parker's specimen agree with Sternfeld's description of *schubotzi.* The juvenile, however, does not. It does match other specimens from Mt. Kilimanjaro described here as *C. rudis sternfeldi.* (For this reason it seems advisable to select the larger Berlin specimen no. 15409, from Mt. Kenya, as the lectotype of *C. schubotzi* Sternfeld.) These broad-headed specimens with extremely heterogeneous scales seem related to *rudis* and to be geographical representatives of it. However, the morphological difference between *schubotzi* and *rudis* is greater than that between any two populations of *rudis.* For this reason it seems best to recognize *schubotzi* as a full species.

Material examined. **Kenya.** Mt. Kenya: Berlin 15409, Type. Mt. Kenya, 14,000 ft.: BM(NH) 1932.5.2.110.

DISCUSSION OF RELATIONSHIPS

Two forms have been collected commonly in the highlands of Kenya. One, *höhnelii,* is an animal of the higher mountains. It has a nasal projection, a very high casque and a very long gular crest. In each of these characteristics it shows much individual variation that does not seem correlated with sex, age, or with geographical distribution. A population occurs at very high altitudes on Mt. Elgon which differs in smaller size from the typical *höhnelii* lower down on the mountain.

Occurring on many of these same mountains, but apparently at lower altitudes and not so closely associated with the mountain forest, is a form, *bitaeniatus,* lacking the specializations of *höhnelii* and having very heterogeneous scalation, in which the large scales are flat or very weakly convex. *Bitaeniatus* and *höhnelii* occur in the same general area, and though they are apparently separated altitudinally, there are several collections containing both from the same localities (Loita Plains, Mau Escarpment; Lukenya; Lukenya Hills; Kijabe; hills west of Mt. Kenya). Since they seem to be, at least to some extent, sympatric, and since I have been unable to find any indications of intergradation even in the locality from which we have both forms, I feel *höhnelii* can no longer be considered a subspecies of *bitaeniatus* but must be called *Chamaeleo höhnelii*. *C. bitaeniatus* also occurs on Longido West in northern Tanganyika and in the mountains of Ethiopia and Somali Republic.

As one proceeds west in Kenya toward Lake Victoria, *bitaeniatus* is abruptly replaced by another form, *ellioti*, also with a head about twice as long as broad, with one or two distinct grooves (usually lined with black) on the sides of the throat, and with much less heterogeneous scalation. These two, *ellioti* and *bitaeniatus*, seem to have the same habitat preferences and to replace each other geographically; there is as yet no evidence of sympatry, though their ranges interdigitate to some extent. These have been considered subspecies, and I would continue this assignment except for the pattern of geographical variation in *ellioti*. *Ellioti* and *bitaeniatus* are very similar in body shape and in ornamentation and apparently in color in life, except for the differences in degree of heterogeneity of scalation and the striking black throat grooves in *ellioti*. These throat grooves are very distinct and usually black in the populations of *ellioti* from east of Lake Victoria and in those from northern Uganda across to the Ruwenzori Mountains and in one specimen from the Imatong Mountains. However, as one goes south in Uganda on the west side of the lake, the grooves become more numerous and less distinct (due to branching), and much less frequently lined with black, until in the mountains around Lake Kivu and those west of Lake Tanganyika, they are quite indistinct. The populations from the latter areas are almost indistinguishable from *bitaeniatus* on the basis of this character. This change is a rather gradual one and can be validly interpreted as what Brown and Wilson, 1956, have called "character displacement." This throat grooving is, I believe, a species-recognition character and one that has been acquired by *ellioti* in the eastern part of its range to enable the chameleons themselves to distinguish their own species from the similarly proportioned and closely related *bitaeniatus* where these two taxa occur together. In areas a long distance from the zone of contact, there would be no selection for this character, and consequently one would expect it to be less well marked.

The evidence for *bitaeniatus* and *ellioti* demonstrates that they are most different where they are closest together and thus are, in all probability, species. However, this character displacement involves only *ellioti* and I have been unable to recognize any tendency to character modification in *bitaeniatus*.

The two forms may replace each other geographically because they are too similar ecologically to coexist. Evidence on this point is almost nonexistent, however, and we can say only that both seem to be animals associated with cultivation and savanna conditions rather than mountain rain forest, and even this is based on very little evidence as far as *bitaeniatus* is concerned.

C. ellioti is the only member of this group occurring in most of the lowlands of Uganda, but in the mountains that edge the west side of the Rift Valley it is replaced by yet another series of populations.

These mountain forms, the *rudis* group, are closely associated with the mountain forest and consist of a series of more or less isolated populations from the Ruwenzori on the north, south to the mountains east of Lake Nyasa with outliers on Mt. Kilimanjaro, Mt. Meru, at Embagi in northern Tanganyika, and single specimens assigned to this species are known from the Mau Escarpment in Kenya and from Gilo in the Sudan. All these agree in being squat chameleons with short, broad, heads and heterogeneous scalation.

In three of these areas, Mt. Ruwenzori, the mountains north of Kivu, and the mountains west of Lake Tanganyika, *ellioti* comes into contact with *rudis*. There is little evidence of the exact situation on Ruwenzori. In the mountains north of Lake Kivu, Witte records both forms from a large number of his collecting stations, with *ellioti* absent from the highest ones and *rudis* absent from the lowest ones, but with a broad zone of overlap. Laurent's account of the situation in these mountains shows similar distributional relationships, but he also notes that there is a marked ecological difference between the two, *ellioti* being an animal of the open, dryer areas, and *rudis* associated with the mountain forest. He notes that *ellioti* reaches high altitudes where the forest has been cut for cultivation. This situation probably is duplicated in the other mountain areas as well.

The extensive interdigitation of ranges, if not actual overlap, seems to me to make maintenance of two non-reproductively isolated lizard populations without any indication of intergradation highly improbable. The situation appears to parallel that of *bitaeniatus* and *höhnelii*, and I believe *ellioti* must be considered specifically distinct from the mountain forms.

It is interesting to note that the *ellioti* populations that occur in close proximity to the short-headed mountain forms have a head that is noticeably narrower than those *ellioti* which are sympatric with long-headed *bitaeniatus*. I believe that in chameleons, head and body shape can be a very important species recognition character and that this cline can be interpreted as another case of character displacement, on the same grounds that the geographical variation in throat grooves was so interpreted. This adds further weight to the opinion that *ellioti* is specifically distinct from *rudis*. These two clines, one in head shape, the other in throat grooving, are roughly parallel in that direction, but they do not run concordantly. In head shape, the area of most rapid change is in central Uganda between the Kenya populations and those of the Ruwenzori Mountains and southwestern Uganda. In throat grooving, the area of most rapid change is in southwestern Uganda between the populations of the Ruwenzori Mountains and north central Uganda and the populations of the area north of Lake Kivu.

C. rudis has been collected in numbers in four areas: the Ruwenzori Mountains; the mountains north of Lake Kivu; Mt. Kabobo; and Mt. Kilimanjaro and Mt. Meru. The population in each of these areas shows some peculiarity. In the Ruwenzori Mountains (*C. r. rudis*), some individuals have very long gular crests; in the Kivu area (also referred to *C. r. rudis*), some individuals have a small rostral protuberance; in the Mt. Kabobo area (*C. r. schoutedeni*), most individuals have the gular crest very reduced and the junction of the canthal ridges narrowly separated from the labials; on Mt. Kilimanjaro and Mt. Meru (*C. r. sternfeldi*), most individuals have the posterior end of the parietal crest much swollen.

I have also seen small samples, 1 to 3 specimens, from several other localities: Gilo, southern Anglo-Egyptian Sudan; Embagi, northern Tanganyika; and the Loita Plains, Mau Escarpment, Kenya. Hellmich (1956) describes two specimens from Litembo, Tanganyika, west of Lake Nyasa. None of these specimens match clearly the populations from the four areas mentioned above. This is primarily because they lack the peculiarities that characterize these populations. Additional specimens might tie them to one or another of the better known populations but it seems equally probable that additional specimens would disclose characters that would distinguish them.

The pattern of geographical distribution and variation in *rudis* contrasts with that in *ellioti.* In *ellioti* the range is continuous, or nearly so, over most of the area where it occurs, and the geographical variation observed is more or less clinal in nature. In *rudis,* which is restricted to mountain forest, the distribution is apparently widely disjunct, and almost every one of the isolated populations shows some morphological peculiarity that distinguishes it from the rest of the species.

The remaining well defined species, *schubotzi,* is rather peculiar in several respects. It is known only from the top of Mt. Kenya, where it apparently lives in the alpine meadows above the range of *C. höhnelii.* It is a small chunky species, with a broad head and extremely heterogeneous lateral scalation, with the much enlarged plates strongly convex. It appears to be most closely related to *rudis,* but well-differentiated from it.

There is a single small specimen known from Mt. Kineti in the Imatong Mountains of the Anglo-Egyptian Sudan which Schmidt (1943) described as *C. kinetensis.* This specimen is most like *C. bitaeniatus* but has less heterogeneous scales and is, in this character, like *ellioti* which is known from the Imatong Mountains. With no more evidence than this single specimen, Schmidt's name cannot be assigned definitely to any known species and consequently is conserved.

All of these chameleons form a closely related complex. On the basis of the proportion and scale characters used here it is possible to distinguish several species. However, on these characters I cannot propose any definitive system of relationships among the species. I suspect that *ellioti* and *bitaeniatus* are closely related and that *höhnelii* is also related to *bitaeniatus,* while *rudis* and *schubotzi* are closely related to each other and a little more distantly to the other three. *C. kinetensis* seems also close to *bitaeniatus* and *ellioti.* This arrangement is based more on shape and proportions than scale characters and is only one of several groupings that could be proposed. Interspecific relationships in the genus *Chamaeleo* as a whole are poorly understood at present and it may well be necessary to consider characters in addition to the currently used externals before they are well understood.

Until the relationships are understood, any discussion of the origin of the species must be tentative at best. I can only speculate that the barriers which in the past isolated populations of the ancestral "*bitaeniatus*" were ecological rather than physical in nature. Even today the various species seem to be restricted to certain types of habitat. The differentiation in the population of *C. rudis* on different mountains demonstrates the reduced gene flow between populations separated by unfavorable habitat and suggests one possible means of speciation. These populations of *rudis* seem most easily interpreted as relics of a period when the rainfall was higher and the forest which is now restricted to the mountains was much more extensive. This period of more widespread forest may equate with the last pluvial period in the Pleistocene of East Africa as has been suggested by Moreau, 1952. The decreasing rainfall which followed the pluvial maxima must have resulted in a retreat of the forests from the lower elevations to their present positions on the higher mountains. This fragmentation of the forests must also have meant a fragmentation of the population of chameleons living in them. Such a break-up of *rudis* into isolated populations, each subject to slightly different conditions and consequently different selection pressures, would have produced the differentiation discussed in this paper.

The origin of the several species undoubtedly lies further in the past than does the origin of the races of *rudis*. It seems quite possible that this speciation was also associated with the ecological changes of a complex sort which must have been associated with the Pleistocene climatic changes in East Africa.

SUMMARY

The chameleons of the *bitaeniatus* group are a closely related complex of forms in East Africa. Though most of the forms were originally described as species, they have in recent years been considered races of a single species. A re-examination of the material shows that apparently at least five and possibly six species are involved. One species was known from the very high altitudes of Mt. Kenya (*C. schubotzi*), two species from the lower elevations in the highlands (*C. bitaeniatus* in Kenya, Somali Republic, Ethiopia and extreme northern Tanganyika, and *C. ellioti* in Ruanda, Uganda, Anglo-Egyptian Sudan and extreme western Kenya), another (*C. rudis*) above *C. ellioti* in the mountains west of Lake Victoria and on Mt. Kilimanjaro and Mt. Meru. Each of these forms has a different geographical

range and in most places only a single taxon occurs. However, sympatry has been demonstrated between *höhnelii* and *bitaeniatus* and between *rudis* and *ellioti*. *C. bitaeniatus* and *ellioti* are not demonstrated to be sympatric but they show character displacement, becoming more different, where their ranges approach one another.

Two of these species show marked geographical variation. *C. ellioti* shows climatic variation apparently associated with character displacement. *C. rudis* occurs on separated mountains in isolated forest populations, three of which are recognized as different subspecies.

A single specimen from Anglo-Egyptian Sudan does not fit any of the other species and the name, *C. kinetensis*, proposed for it by Schmidt (1943) is retained.

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MORPHOLOGY, PALEOECOLOGY, AND PHYLOGENY OF THE PERMO-PENNSYLVANIAN AMPHIBIAN *DIPLOCERASPIS*

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CAMBRIDGE, MASS., U.S.A.
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No. 2 *Morphology, Paleoecology, and Phylogeny of the Permo-Pennsylvanian Amphibian* DIPLOCERASPIS[1]

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INTRODUCTION

The Permo-Carboniferous lepospondylous amphibian, *Diplocaulus*, has long attracted paleontological interest because of the remarkable horn-like extensions of the posterior lateral corners of the skull. Several earlier Carboniferous (Westphalian) amphibians, *Keraterpeton*, *Batrachiderpeton*, and *Diceratosaurus*, possess "horns," though very much shorter ones, and have been thought to include the ancestry of *Diplocaulus*. In 1952 A. S. Romer described, from the Permo-Carboniferous of the Appalachian region, an amphibian which bears "long horns" similar to those of *Diplocaulus*. Although the amount of material was small and the skulls were fragmentary, it sufficed to distinguish a new genus, *Diploceraspis*. Romer suggested that this amphibian represented an evolutionary lineage paralleling *Diplocaulus* in adaptation, and was derived from a different Westphalian "horned" type than the latter. Because of similarly sculptured neural arches he tentatively related *Diploceraspis* to the "short-horned" *Diceratosaurus*.

Douthitt (1917) devoted a monograph to *Diplocaulus* and to interpretation of that unusually adapted skull. Whatever selective factors directed the evolution of this adaptation, similar ones must have acted on the *Diploceraspis* lineage. A comparative study of both genera elucidates the adaptation and assists in clarifying the phyletic relation of both to more primitive, "short-horned" types. Unfortunately, the specimens available to Romer were inadequate for such a study. During the summers of 1954-57, however, field parties from Lafayette College collected a large quantity of *Diploceraspis* material. Availability of these specimens permits a much more detailed and complete description of *Diploceraspis* and a more thorough comparison with *Diplocaulus* and with the possible ancestral types from Westphalian rocks.

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Grants from the Society of Sigma Xi, the American Academy of Arts and Sciences, the Geological Society of America, and the National Science Foundation (N.S.F. G 2156) supported the field work and provided assistance in the preparation of the fossils. Study of the *Diploceraspis* material and preparation of portions of this paper were undertaken during sabbatical leave granted by Lafayette College.

Dr. Herbert Barghusen served as field assistant and was responsible for the discovery of locality 7-55 which yielded the

greater portion of the *Diploceraspis* specimens, including a complete skull. Mr. Wilson Piatt conducted most of the preparation as an undergraduate research assistant.

Dr. Donald Baird loaned me a series of latex casts of *Diceratosaurus* and *Ptyonius* specimens from the Westphalian vertebrate locality at Linton, Ohio. I should like, also, to acknowledge the courtesy of the staff of the American Museum of Natural History (AMNH), of the Museum of Comparative Zoology (MCZ), and of the Carnegie Museum (CM) in making specimens of *Diplocaulus* and *Diploceraspis* available for comparative study.

THE MATERIALS AND THEIR STRATIGRAPHIC OCCURRENCE

The original *Diploceraspis* specimens described by Romer (1952) were collected by parties from Carnegie Museum (Burke, 1935). Most of these came from localities within the Dunkard group (very late Stephanian or early Autunian), but a few were found in a Conemaugh (early Stephanian) locality. Romer placed all the Dunkard *Diploceraspis* in a single species, *D. burkei*, but separated the Conemaugh *Diploceraspis* as *D. conemaughensis* (see discussion below). The Carnegie collections include vertebrae, a clavicle, other fragmentary clavicular or interclavicular specimens, several incomplete skulls, and several "horns" and other fragmentary skull material.

The new material, described in some detail below, includes several hundred vertebrae, numerous complete as well as fragmentary clavicles, several interclavicles, some ribs and limb fragments that may belong to *Diploceraspis*, a hundred or more "horn" fragments, several partial lower jaws, several incomplete skulls of various sizes, and a single nearly perfect skull. No articulated skeletal material has yet been found. All specimens occurred in limestone and/or in limy shale intimately associated with limestone. Table 1 gives a list of Dunkard *Diploceraspis* localities and a summary of specimens from each. Nearly all *Diploceraspis* localities, old and new, occur near the center of the northern portion of the Dunkard basin — southern Marshall and northern Wetzel counties in West Virginia, southwestern Greene County in Pennsylvania, and northeastern Monroe County in Ohio. A second, small concentration appears in the center of the southern portion of the basin — Wood County, West Virginia. Of the thirty-one *Diploceraspis* localities, one occurs in the upper part of the Conemaugh group; two in the lower part of the Washington Formation, the basal unit of the Dunkard group; three

Table 1. SUMMARY OF *DIPLOCERASPIS* LOCALITIES

Locality-Carnegie (Moran 1952)	Material	Location	Stratigraphic Position
1	Vertebrae and skull fragments of *D. conemaughensis*	Soho St. Quarry, Pittsburgh, Penna.	Conemaugh gr. Forty feet below Pittsburgh coal
6	Vertebra	Adams Township, Monroe Co., Ohio	Lower Washington Fm.
7	Skull fragments	Sand Hill Dist., Marshall Co., W. Va	Lower Washington Fm.
13	Vertebrae	Proctor Dist., Wetzel Co., W. Va.	Lower Greene Fm.
14	Vertebra, clavicle	Liberty Dist., Marshall Co., W. Va.	Lower Greene Fm.
16	Clavicle	Tucker Dist., Wirt Co., W. Va.	Middle Greene Fm.
18	? Vertebrae	Clay Dist., Marshall Co., W. Va.	Middle Greene Fm.
20	Clavicle, vertebrae	Clay Dist., Marshall Co., W. Va.	Middle Greene Fm.
21	? Vertebrae	Liberty Dist., Marshall Co., W. Va.	Middle Greene Fm.
23	? Vertebrae	Proctor Dist., Wetzel Co., W. Va.	Middle Greene Fm.
24	? Vertebrae	Springhill Township, Greene Co., Penna.	Middle Greene Fm.
26	Partial skulls, vertebrae	Liberty Dist., Marshall Co., W. Va.	Upper Greene Fm.
27	Vertebrae	Meade Dist., Marshall Co., W. Va.	Upper Greene Fm.
28	Vertebrae	Battelle Dist., Monongalia Co., W. Va.	Upper Greene Fm.

Locality-Carnegie (Moran 1952)	Material	Location	Stratigraphic Position
29	? Vertebrae	Franklin Dist., Marshall Co., W. Va.	Upper Greene Fm.
30	? Vertebrae	Franklin Dist., Marshall Co., W. Va.	Upper Greene Fm.
L	Vertebrae	Tucker Dist., Wirt Co., W. Va.	Upper Greene Fm.
35	Skull fragments, vertebra	Proctor Dist., Wetzel Co., W. Va.	Upper Greene Fm.
36	Skull fragments (horns)	Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
37	Vertebra	Proctor Dist., Wetzel Co., W. Va.	Upper Greene Fm.
Locality-Lafayette			
5-55	Vertebra, clavicle	Limestone, elevation 1360′, 0.5 mi. E. of intersection of W. Va. 89 and U.S. 250 in cut on W. Va. Rt. 89, 80°32′ 37″W, 39°52′ 15″N	Middle Greene Fm.
6-55	Skull and mandible fragments, vertebrae, clavicles and interclavicles	Lime sandstone and congl., elevation 1352′, 0.2-0.3 mi. N of north boundary of Sherrard on W. Va. Rt. 88, Union Dist., Marshall Co., 80°40′ 57″W, 39°59′ 34″N	Middle Greene Fm.
7-55	Complete skull, partial skulls, skull fragments, partial mandibles, vertebrae, ribs, clavicles, interclavicles.	Limestone, elevation 1282′, 1.5 mi. N of north boundary of Sherrard on W. Va. Rt. 88 Union Dist., Marshall Co., 80°41′ 35″W, 40°0′ 22″N	Middle Greene Fm.

TABLE 1. SUMMARY OF *DIPLOCERASPIS* LOCALITIES (*Cont.*)

Locality-Lafayette	Material	Location	Stratigraphic Position
9-55	Vertebrae	Limestone, elevation 1060′, 0.7 mi. E of Bristoria on Holbrook Road, 80°23′ 23″N, 39°51′ 52″N, Richhill Township, Greene Co., Penna.	Lower Greene Fm.
13-55	Vertebra, clavicle	Locality 28 of Moran. Corrected elevation 1385′, 80° 24″ W, 39°39′ 36″ N, Battelle Dist., Monongalia Co., W. Va.	Upper Greene Fm.
15-55	Vertebrae	Limestone and limy shale, elevation 1330′, ridge crest west of Uniontown on W. Va. Rt. 7, 80°34′23″W, 39°38′ N, Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
17-55	Partial skull	Limestone and limy shale, elevation 1240′, on east side of hill east of Knob Fork, W. Va. Rt. 7, 80°31′ 52″W, 39°38′ 47″N, Center Dist., Wetzel Co., W. Va.	Middle Greene Fm.
18-55	Skull fragments, vertebrae	Limestone, elevation 1085′, road running SE to Wayne Ridge from W. Va. Rt. 2 just north of Kent, 80°50′ 40″W, 39°46′ 25″N, Franklin Dist., Marshall Co., W. Va.	Middle Greene Fm.

Locality- Lafayette	Material	Location	Stratigraphic Position
21-55	Vertebrae	Limestone and limy shale, elevation 1195′, Great House Hill Road north of W. Va. Rt. 7, ½ mi. east of Wileyville, 80°38′ 57″W, 39° 37′ 23″N, Center Dist., Wetzel Co., W. Va.	Upper Greene Fm.
22-55	Skull fragments, partial mandibles, vertebrae, interclavicles, clavicles	Limestone and shaley ls., elevation 1050′, Brock Ridge Road north of W. Va. Rt. 7, about 1 mi. west of Wileyville, 80°42′ 7″W, 39° 37′ 30″N, Proctor Dist., Wetzel Co., W. Va.	Middle Greene Fm.
1-56	Vertebrae	Limestone and limy shale, elevation 960′, 2.0-1.75 mi. west of Murphytown on U.S. Rt. 50, 81°27′ 40″W, 39°14′ 30″N to 81°28′30″W, 39°14′ 45″N, Clay Dist., Wood Co., W. Va.	Middle Greene Fm.
2-56	Skull fragments, vertebrae, clavicle	Limestone, elevation 960′, Montgomery Hill east of Murphytown on U.S. Rt. 50, 81°24′ 50″W, 39°14′ 40″ N, Clay Dist., Wood Co., W. Va.	Middle Greene Fm.
4-56	Skull fragment (horn)	Limestone, elevation 1060′, Limestone Hill on Gates Road 0.4 mi. west of U.S. 21 (Probably Moran's localities L and 31), 81°32′ 20″W, 39°2′ 53″N, Steele Dist., Wood Co., W. Va.	Upper Greene Fm.

in the lower part of the Greene Formation, the upper unit of the Dunkard group; fourteen in the middle Greene; and eleven in the upper Greene. The upper Conemaugh is generally regarded as mid-Stephanian (early Virgilian) age. The Dunkard may bridge the Stephanian-Autunian boundary; the vertebrates of the middle Greene suggest early Autunian. A complete discussion of Dunkard stratigraphy and vertebrate occurrences will be published separately.

MORPHOLOGY

Introduction

Diploceraspis, quite plainly, is a lepospondyl and, just as clearly, belongs to the order Nectridea. Romer (1945) recognized three families: Lepterpetontidae, Urocordylidae, and Keraterpetontidae. The latter group includes a poorly understood form, *Scincosaurus*, the three "short-horned" forms, *Diceratosaurus*, *Keraterpeton*, and *Batrachiderpeton*, and the "long-horned" *Diplocaulus* (Figs. 12, 13). *Diploceraspis* appears to belong to this group, and comparisons here emphasize these genera but refer to the urocordylids as well.

Diceratosaurus was most completely described by Jaekel (1903) with later notes by Moodie (1916) and Romer (1930); Watson (1913) described *Batrachiderpeton;* Steen (1938) restudied *Urocordylus*, *Scincosaurus*, and *Keraterpeton;* and Douthitt (1917) gave the most complete discussion of *Diplocaulus*. Olson (1951) analysed relative growth in *Diplocaulus*. In addition to this published work, I have examined the *Diceratosaurus* material displayed in a superb series of casts prepared by Dr. Donald Baird, Princeton University, and also studied the *Diplocaulus* skulls in the collection of the American Museum of Natural History.

Skull

General form. The observer's initial impression of a *Diploceraspis* skull (Figs. 1, 2, 3) is of a flattened, short-faced form, like that of *Diceratosaurus* or *Keraterpeton*, on to which have been grafted two flat "horns," albeit unusually slender ones, from a *Diplocaulus*. In *Diplocaulus* the line of horn and face forms a broad, continuous curve or, in other terms, the face is wide so that the horns and face form a single, crescentic unit. In *Diploceraspis*, on the contrary, the line of horn is quite straight, and it meets the curved line of the face with a relatively sharp break (a concave curve) at the posterior end of the orbits. The *Diploceraspis* face, therefore, is relatively long and narrow compared to that of *Diplocaulus* (Fig. 13).

The fragmentary condition of most skull material makes precise size comparisons difficult. Specimen MCZ 3009, the complete *D. burkei* skull, is 55.7 mm. long, from snout tip to occipital border along the midline, and appears to be the largest *Diploceraspis* in the collections (Table 2). This is about half the length of a large *Diplocaulus*. The smallest *D. burkei* skull is represented by a fragmentary jugal, MCZ 3015, which is about one-third the breadth of the similar element in MCZ 3009. A still smaller skull (CM 8544), with a jugal about half the width of that in MCZ 3015, was assigned by Romer to *D. conemaughensis*. Other *D. conemaughensis* appear to overlap *D. burkei* in size.

As indicated, the horns appear narrower and straighter than those in *Diplocaulus*, but it is very difficult to measure this apparent difference because of the lack of any inflection between face and horn in the latter genus. The horns taper evenly and gradually toward the tips — in some individuals (MCZ 3032) the taper is so very gradual that the distal end of the horn is extremely long and narrow (Fig. 6). In some this portion is gently curved. The horn tips are recurved posteromedially to a varying degree and are serrate along their anterolateral edges. The internal space within the horn constricts distally so that near the tips the horns are, for practical purposes, solid bone. The horn tips were subject to abnormal growth, since in specimen MCZ 3009 (Fig. 6) the right horn tip recurves anterolaterally rather than posteromedially.

The small skull, CM 8551, described and illustrated by Romer (1952), shows a much greater angle between horns than the two new ones, MCZ 3009 and MCZ 3012, which also show both sides of the skull. MCZ 3009 is approximately 75 per cent larger than CM 8551, MCZ 3012 30 per cent larger. Three fragmentary specimens, MCZ 3013, MCZ 3010, and MCZ 3019, the first about 50 per cent smaller than CM 8551, the second about the same size, and the third about 30 per cent larger, show intermediate angles. A postparietal, about the same size as that of MCZ 3009, indicates a similar horn angle. The angle, therefore, shows individual variation but seems to decrease with size, in contrast to *Diplocaulus* in which it increases (Olson, 1951). When size is considered, the angle between the horns is rather small — distinctly less so than in *Diplocaulus magnicornis* and about the same as in *Diplocaulus*

TABLE 2A

DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Explanation of measurements. Based on Olson's study of *Diplocaulus* (1951). Measurements not used by Olson are starred.

Sk_l = Distance from tip of snout at premaxillary suture to posterior margin at postparietal suture.

Skw_1 = Distance between posterolateral corner of tabulars.

Skw_2 = Distance between lateral ends of occipital condyles.

Pi-Fr = Distance from anterior margin of pineal opening to frontal-parietal suture at junction of suture between parietals.

I_{p_l} = Distance from anterior termination of suture between postparietals at point of intersection of more posterior postparietal-parietal suture to posterior termination of the suture between the postparietals.

Pa_l = Distance along suture between parietals from frontal suture to anterior parietal-postparietal suture.

Fr_l = Length of frontal along midline.

$O\text{-}S_l$ = Distance along midline from anterior edge of orbits to snout tip.

Io_w = Minimum distance between orbits.

$^*Eo_w$ = Maximum distance between lateral margins of orbits.

O_w = Greatest orbital width perpendicular to midline.

O_l = Greatest orbital length parallel to midline.

Pmx_l = Distance from posterior termination of suture between premaxillae to intersection of this suture with tip of snout.

Nar_w = Distance between medial borders of nares.

Po_l = Distance from midpoint of postfrontal-postorbital suture to posterior corner of postorbital.

Pa_w = Distance perpendicular to midline from suture between parietals to junction of parietal, squamosal, and tabular.

Ip_w = Distance perpendicular to midline from posterior termination of suture between parietals to greatest lateral extent of postparietal.

Sq_w = Distance from midline of skull to lateral point of squamosal.

$^*J_w$ = Distance from midline of skull to lateral point of jugal.

St_l = Distance from junction of parietal, postparietal, and tabular to tip of horn.

$^*H_w$ = Distance from posterior termination of suture between postparietals to posterolateral corner of quadratojugal.

$^*Sq_b$ = Greatest width of squamosal on ventral surface, perpendicular to lateral border of horn.

$^*T_l$ = Length from tip of horn to lateral end of otic notch.

$^*Ot_l$ = Distance from lateral end of pterygoid-exoccipital suture to lateral end of otic notch.

$^*Ot_w$ = Width across otic notch from posterolateral end of quadratojugal-squamosal suture to opisthotic, perpendicular to posterior border of horn.

$^*C_l$ = Length of centrum on ventral midline.

$^*C_w$ = Width of centrum across posterior face.

*V_h = Height of vertebra from ventral points of centrum to top of neural spine.
*NS_h = Height of neural spine above level of zygapophyses.
*Tr_w = Width between tips of transverse processes.
*HS_d = Distance from posteroventral edge of centrum to ventral edge of haemal arch.

TABLE 2B

DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Tabulation of measured skulls. See Table 2A for explanation of measurements. Dimensions in millimeters.

	MCZ 3009	CM 8548	MCZ 3010	MCZ 3013	MCZ 3018	MCZ 3019	MCZ 3012
Sk_l	55.7						
Skw_1	191.8	116 ±					117.0
Skw_2	20.0		14.2?				
Pi-Fr	5.7						
I_{p_l}	11.9			6.0	5.8		
Pa_l	13.1						
Fr_l	21.0	17.0					
$O\text{-}S_l$	11.8	9.0					
Io_w	11.2	8.5 ±					
Eo_w	30.0						
O_w	8.4						
O_l	11.8						
Pmx_l	8.0						
Nar_w	11.5	10.0 ±					
Po_l	7.2						
Pa_w	37.3			19.7	23.7 ±		
Ip_w	36.8			22.6	31.3 ±	28.4	
Sq_w	70.2			39.7			
J_w	25.0			17.3			
St_l	84.9						
H_w	36.8			23.9			

SPECIMEN	Sq_b	T_l	Ot_l	Ot_w
MCZ 3009	13.9	83.7	32.7	17.8
CM 8544	3.2	11.2 ±	8.2 ±	6.6 ±
MCZ 3032		90?		
MCZ 3010	8.3	48.6	19.8 ±	17.5 ±
MCZ 3026	8.1			
MCZ 3013	6.8	28.5	17.4	10.7
MCZ 3016	7.0 ±			

TABLE 2B *(Cont.)*

SPECIMEN	Sq_b	T_l	Ot_l	Ot_w
MCZ 3033	7.9			
	6.1			
	5.3			
	8.0			
	8.4			
	4.0			
MCZ 3018	8.3		17.5	
MCZ 3017		71.6		
	7.5 ±	49.5 ±		
	7.1	51.4		
MCZ 3019			19.0	13.0 ±
MCZ 3012		53.0 ±		

TABLE 2C
DIMENSIONS OF *DIPLOCERASPIS* SPECIMENS

Tabulation of measured vertebrae. See Table 2A for explanation of measurements. Dimensions in millimeters.

Specimen	Region	C_l	C_w	V_h	NS_h	Tr_w	HS_d
MCZ 3020	"Atlas"	5.0	3.2	—	—	7.9	—
		6.0	4.0	8.7	5.2	9.0	—
		5.6	3.5	—	—	8.2	—
		5.6	—	8.3	5.3	8.7	—
		5.5	3.8	—	—	8.8	—
MCZ 3029	"Atlas"	—	—	—	—	9.4	—
		5.7	3.8	—	—	9.4	—
MCZ 3030	"Axis"	5.2	4.1	7.8	5.0	10.4	—
MCZ 3024	"Axis"	4.9	3.2	7.7	4.6	—	—
		5.9	3.4	7.8	4.8	8.0 ±	—
		3.2	1.9	5.5	3.1	—	—
		6.0	3.9	9.4	5.7	9.2	—
MCZ 3003	"Dorsal"	8.5	3.4	7.7	4.0	10.4	—
MCZ 3027	"Dorsal"	9.1	4.5	—	—	11.4	—
		7.7	4.9	9.3	5.0	—	—
		8.5	4.3	—	—	13.2	—
		7.5	3.8	8.7	4.7	—	—
		8.7	3.4	7.8	—	—	—
		10.9	—	—	—	—	—
		8.5	3.0	8.3	4.0	—	—
		9.0	3.0	8.7	4.6	—	—
		10.3	—	7.9	4.6	—	—
		9.1	—	8.4	3.7	—	—
		7.8	3.0	6.9	3.9	—	—
		7.3	—	6.8	—	—	—
		8.4	—	8.8	3.3	—	—

TABLE 2C (*Cont.*)

Specimen	Region	C_l	C_w	V_h	NS_h	Tr_w	HS_d
MCZ 3005	"Dorsal"	12.0±	—	—	—	13.2	—
		10.0	—	8.9	—	—	—
MCZ 3023	"Dorsal"	10.0	4.8	9.8	4.7	14.0±	—
		10.0	4.0	9.5	4.5	—	—
		12.1	—	—	—	—	—
		11.2	4.1	9.4	—	14.2	—
		9.5	3.8	9.3	4.8	—	—
		7.6	3.8	8.9	5.3	—	—
		8.7	3.2	8.1	4.0	—	—
		9.4	3.9	7.3	3.5	8.9	—
		9.5	—	8.8	4.3	—	—
		10.7	5.7	12.4	6.7	14.0±	—
		13.3	5.0	12.1	6.2	—	—
		5.0	2.9	—	—	—	—
MCZ 3033	"Dorsal"	6.6	3.1	8.4	4.7	—	—
		11.4	4.3	9.3	4.0	—	—
		8.0	—	8.2	—	—	—
		9.7	3.8	9.1	4.2	10.7	—
		9.1	4.7	10.5	5.6	13.6	—
		8.4	3.6	8.9	4.5	—	—
		7.3	—	7.8	—	—	—
		5.2	2.3	5.8	—	—	—
		8.0	3.5	8.9	3.6	8.4	—
		8.5	3.4	9.0	4.3	10.2	—
		8.9	4.0	9.4	4.5	—	—
		9.4	4.1	9.8	5.0	—	—
		8.2	3.4	6.1	—	10.1	—
		8.9	3.7	9.1	5.0	13.6	—
		6.9	2.9	8.6	5.0	8.8	—
		5.9	3.7	7.8	3.9	10.6	—
		5.7	1.7	4.1	1.7	—	—
		9.9	3.2	7.7	—	—	—
		8.0	2.9	6.9	3.4	—	—
MCZ 3006	"Sacral"	8.8	3.2	7.0	—	—	8.7
MCZ 3007	"Caudal"	12.5	3.3	8.2	3.8	—	13.4
MCZ 3021	"Sacral"	9.9	3.4	6.4	3.5	—	10.7
	"Sacral"	8.0	2.5	4.8	2.0	—	8.0
	Ant. Caudal ?	8.2	1.9	4.8	2.6	—	8.0
MCZ 3008	Ant. Caudal ?	2.3	—	1.07	—	—	2.4
MCZ 3028	Caudal	9.0	—	5.8	—	—	9.6
		9.3	1.4	4.3	1.7	—	6.4
		10.4	—	6.3	2.6	—	10.2

TABLE 2C (*Cont.*)

Specimen	Region	C_l	C_w	V_h	NS_h	Tr_w	HS_d
MCZ 3032	Caudal	13.9	3.8	7.7	—	—	13.8
		11.0	3.8	7.4	—	—	12.7
		9.2	2.2	4.8	2.1	—	7.7
		9.2	1.9	5.1	2.1	—	7.8
		10.2	2.3	4.4	1.5	—	7.3

brevirostris (Fig. 13). Since *Diplocaulus* horns are curved backward, the angle decreases distally. In consequence, *Diploceraspis* horns angulate more sharply proximally than those of *Diplocaulus brevirostris* but less so distally. The posteromedial border of the horn is inflected anteriorly near the midline before it turns medially to the nearly straight, transverse, occipital border. In consequence, the posterior edge of the postparietal displays a very flat S-curve, convex backward distally, concave backward proximally. The acuity of these curves varies from individual to individual.

The position and character of orbits and external nares reflect the length and the narrowness of the *Diploceraspis* face. The ratio of the interorbital width to the breadth of skull at the anterior end of orbits is 0.39 in *Diploceraspis,* as compared with 0.19 in *Diplocaulus,* and the orbits are elongated anteroposteriorly as compared with *Diplocaulus.* The nares open on the anteroventral border of the skull as in *Diplocaulus,* but extend further upward and backward onto the dorsal surface.

As described by Romer, the skull surface is sculptured by small pits, differing from those of *Diplocaulus* only in size. These pits are roughly circular, although those adjacent to some of the sutures are elongated parallel to the suture line. In a very small specimen of *Diploceraspis burkei* (MCZ 3015, a fragmentary squamosal) they range from 0.2 to 0.3 mm. in diameter. On the squamosal of the larger specimen, MCZ 3013, they average about 0.4 mm., and on the squamosal of the still larger one, MCZ 3009, about 0.6-0.7 mm. In the smallest *Diploceraspis conemaughensis,* CM 8544, the pits are approximately 0.1 mm. in diameter. This specimen is about half the size of MCZ 3015. In other *D. conemaughensis,* they are similar in size to those of comparable *D. burkei* specimens. The lateral line system is described in a subsequent paragraph.

The palatal aspect of the skull is generally similar to that of *Diplocaulus.* The quadrate articulates with the lower jaw far forward — approximately on a line with the posterior border of

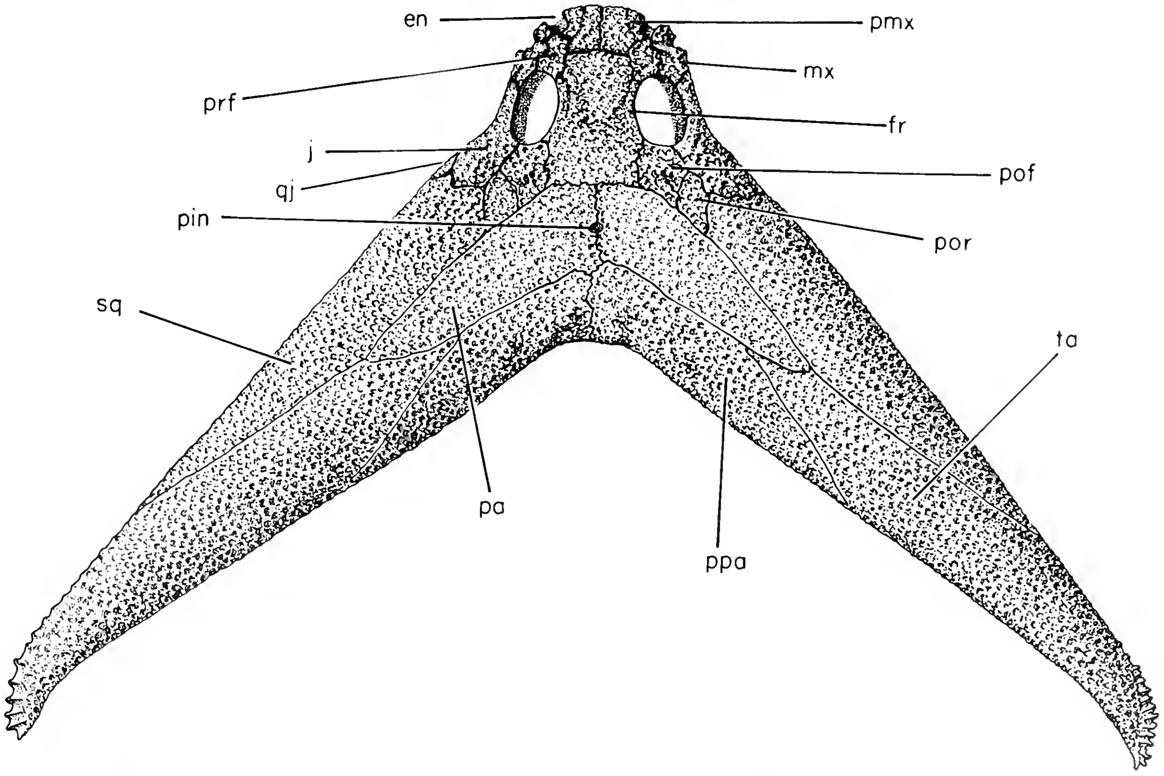

FIG. 1. *Diploceraspis* skull, reconstructed dorsal view. Approximate enlargement, x 0.8. Abbreviations: *en*, external naris; *fr*, frontal; *j*, jugal; *mx*, maxilla; *pa*, parietal; *pin*, pineal; *pmx*, premaxilla; *pof*, postfrontal; *por*, postorbital; *ppa*, postparietal; *prf*, prefrontal; *qj*, quadratojugal; *sq*, squamosal; *ta*, tabular.

the frontal, midway between the occipital condyles and the front of the skull. The interpterygoid vacuities are very large; the subtemporal fossae are relatively small but extend posteriad a considerable distance (Fig. 4). The otic notches, like those of *Diplocaulus,* have rotated completely onto the ventral surface and form elongate, ellipsoidal openings under the proximal portion of each horn. The internal nares are surrounded almost completely by the vomers and palatines; the maxilla and premaxilla are nearly excluded from the narial border. The ventrolateral border of the skull turns sharply upward in front of the quadrate so that the depth of the skull at the front end of the quadratojugal is about twice that at the anterior end of the jugal. In consequence, the ventral border of the lower jaw lies in line with the ventral border of the quadratojugal, and the jaw is approximately as deep as the facial region of the skull. *Diploceraspis* lacks the ventral flange of the quadratojugal which in *Diplocaulus* extends markedly below the ventral surface of the horn.

Corresponding to the relative narrowness of the *Diploceraspis* face, the arch of marginal and palatal teeth is narrow rather than broadly rounded as it is in *Diplocaulus.* The row of vomerine teeth lies immediately posterior to the premaxillary teeth and, therefore, in front of the anterior margin of internal nares rather than behind as in *Diplocaulus.* The tooth row is relatively short, even more so than that of *Diplocaulus.* The marginal row comprises 14 or 15 teeth on each side and terminates along a transverse line just behind the posterior border of the internal nares. The palatal row extends somewhat more posteriad, to a point near the posterior border of the orbits, and consists of 17 or 18 teeth on each side. The arch of the lower jaw is correspondingly short and narrow and includes 11 teeth on either side. The teeth, both marginal and palatal, are sharply to squatly conical; the tips are invariably sharp and, on a few teeth, are slightly recurved. A few, two or three, coronoid teeth, similar to the marginal teeth, are present just inside the anterior end of the lower jaw. The palatal teeth are, typically, adpressed, so much so that some are flattened transversely. The marginal teeth, though not adpressed, are closely spaced. Their bases are overgrown by ridges of bone and the teeth thus fused firmly to the marginal and palatal bones. The teeth are relatively larger and less closely spaced than in *Diplocaulus.*

The lateral line canals are well developed over the face and snout (Fig. 3). The anterior commissure is apparently represented

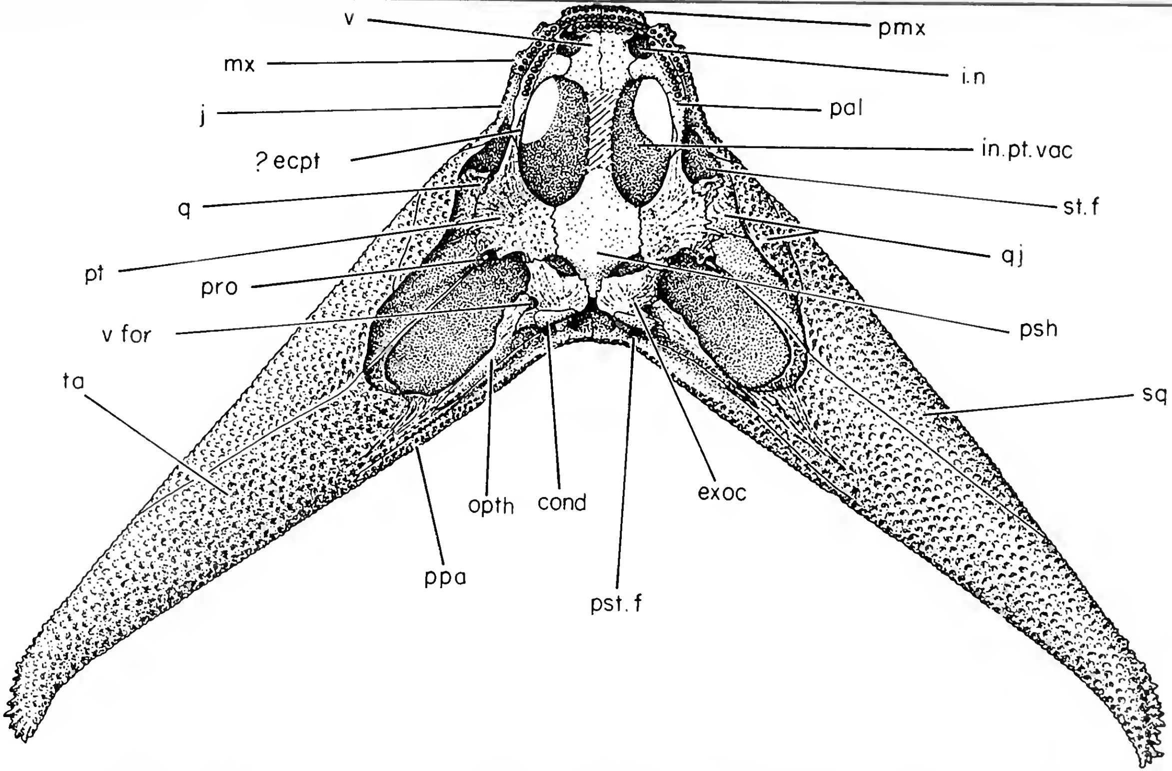

FIG. 2. *Diploceraspis* skull, reconstructed palatal view. Approximate enlargement, x 0.8. Number of teeth shown is incorrect: vomer bears 6 rather than 5, palatine 11 rather than 9. Abbreviations: *cond*, condyle; *ecpt*, ectopterygoid; *exoc*, exoccipital; *i.n*, internal naris; *in.pt.vac*, interpterygoid vacuity; *opth*, opisthotic; *pal*, palatine; *pro*, prootic; *psh*, parasphenoid; *pst.f*, posttemporal fenestra; *pt*, pterygoid; *q*, quadrate; *st.f*, subtemporal fossa; *v*, vomer; *v.for*, vagus foramen; (See caption, Figure 1 for other abbreviations.)

by a deeply sculptured, transverse groove across the anterior surface of the premaxillae. The supraorbital canals, which originate anteromediad to the external nares, pass back and outward to and across the posterior border of the nares. From the nares they continue laterad for a short distance and then curve posteromedially in front and just medial to the orbits. They parallel the medial border of the orbits and terminate near their posterior margin.

The infraorbital canals originate on the maxillae near the narial openings, turn dorsomediad to approach an antorbital commissure with the supraorbital, and curve below the orbits to terminate along the posterolateral face of the jugal. The postfrontal, postorbital, squamosal, and postparietal bear enlarged pits with raised rims which may represent other portions of the lateral line system. On the mandible both oral and mandibular canals are present; the former, rather indistinct, extends along the dentary, parallel and just ventral to the mouth border, and ends near the coronoid process; the mandibular follows the dentary-splenial and dentary-angular sutures to about the midpoint of the mandible, turns ventrad, and disappears.

Skull roof. A complete skull is known from only one specimen, MCZ 3009. In consequence, the description of orbital and preorbital elements is limited to the characteristics of that individual although an incomplete, badly crushed specimen, MCZ 3025, and an eroded, partial skull, CM 8548, check on some of the interpretation (Fig. 1).

In accordance with the unusual form of the skull, the bones of the face are relatively small and somewhat atypic in their relationships. The premaxilla consists of a horizontal, subrectangular plate on the dorsal surface and a short vertical flange that forms the anterior edge of the face, contacts the maxilla below the external naris, and bears seven or eight teeth. The dorsal (horizontal) portion angulates sharply with the anterior part to mark the boundary of the flattened skull roof. In the absence of nasals (see discussion below), the premaxillae contact the prefrontals behind the nares. This relationship is unique among the Keraterpetontidae, but a somewhat similar pattern occurs in *Urocordylus* where the prefrontals extend forward between nares and nasals to contact the premaxillae. Because of the absence of the nasals the premaxillae contact the frontals — a condition approached in *Batrachiderpeton* which has tiny nasals, and duplicated in *Diplocaulus* which also lacks nasals.

Like the premaxilla, the maxilla consists of two sharply angulated elements, a horizontal, subrectangular dorsal plate and a

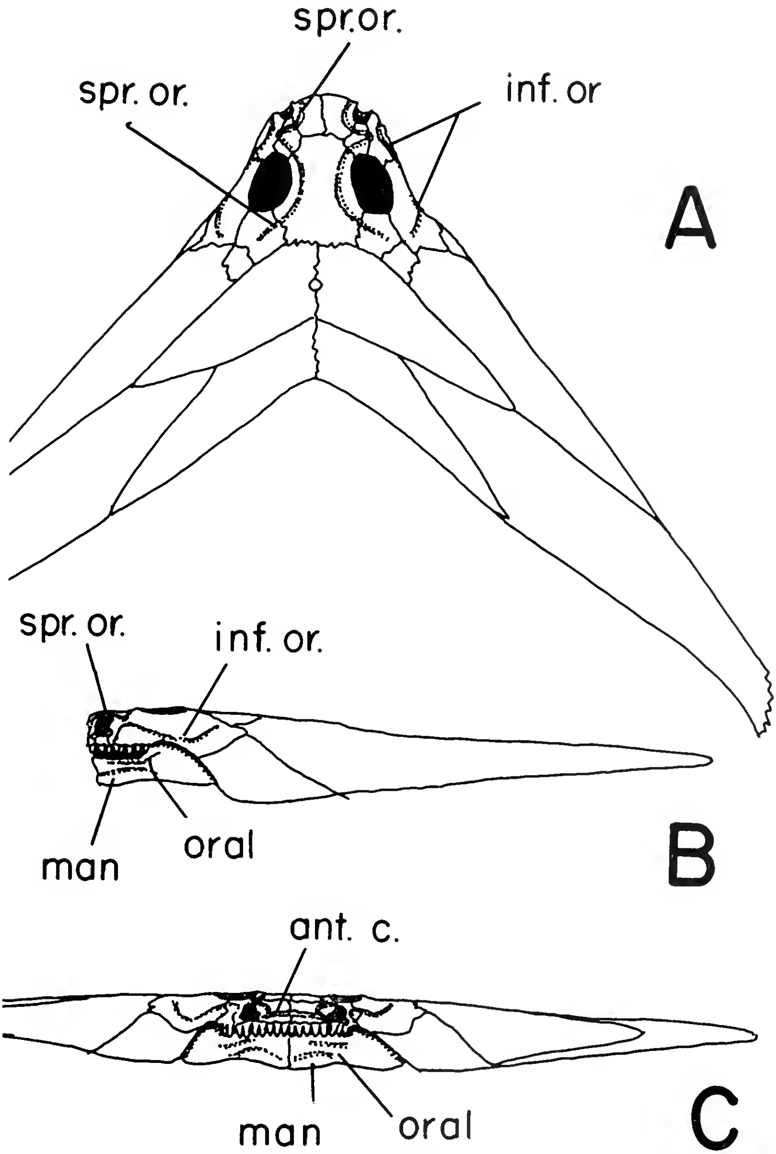

FIG. 3. *Diploceraspis* skull and mandible, reconstructed. *A,* dorsal; *B,* lateral; *C,* frontal view. Approximate enlargement x 0.67. The dotted lines indicate the position of the lateral line canals. Abbreviations: *ant.c,* anterior commissure; *inf.or,* infraorbital canal; *man,* mandibular canal; *oral,* oral canal; *spr.or,* supraorbital canal.

vertical, descending process that bears seven or eight teeth. The horizontal and vertical portions are rather sharply separated by a difference in sculpture and by a deep V-shaped notch that receives the anterior end of the jugal. No suture can be distinguished between the two portions in MCZ 3009, but the possibility remains that the maxilla as described here includes a fused lacrimal bone (see discussion below). The dorsal portion of bone forms the anterolateral border of the orbit and is bounded medially by the prefrontal. The latter relationship occurs also in *Diplocaulus* although in that genus the lacrimal is also present.

The frontals of *Diploceraspis* are fused, at least in the three specimens in which they are known, into a single interorbital plate like those in *Diplocaulus* and *Urocordylus*. I have not been able to detect any trace of midline suture on either dorsal or ventral surface, and the sculpture shows no trace of a dual origin for this element. The anterior contact of premaxillae and frontal was discussed above. As in *Diplocaulus,* the frontal forms most of the medial border of the orbits and separates the pre- and postfrontals, whereas in the other nectrideans these elements contact each other, albeit narrowly, and separate the frontal from the orbits. Watson ascribed this condition in *Diplocaulus* to the dorsomedial shift of the eyes in a very flat skull; presumably the explanation would hold here as well.

A single element lies between the premaxilla, maxilla, and frontal on each side. The immediate question is which of three bones, prefrontal, lacrimal or nasal, is represented here. The bone is vaguely diamond-shaped, forms the posterior border of the external naris, contacts the premaxilla anteromedially and the frontal posteromedially, continues laterad as the anterior border of the orbit, and lies against the maxilla between orbit and naris. It is crossed by a lateral line groove from the maxillary contact, posterior to the corner of the naris, to the frontal suture.

An interpretation of this bone as the nasal seems to me most improbable. In general in the amphibians, the nasals lie side by side along the midline of the snout. The questionable elements in *Diploceraspis* are separated by the premaxillae and frontal. Furthermore, these bones also form the anterior border of the orbits and contact the maxilla — atypic characteristics for the tetrapod nasal. Finally, in other amphibians, the supraorbital lateral line canal passed directly from the premaxilla onto the nasal, but, as indicated, in *Diploceraspis* this canal passes laterad from the premaxilla along the posterior margin of the external naris and continues laterad for a short distance over the maxilla (or the lacrimal fused to the maxilla) before it turns in and back to cross the bone here described.

The choice then lies between lacrimal, prefrontal or an element formed by fusion of the two. No trace of a suture occurs on either the external or internal surface of the bone; nor does the pattern of surficial pitting show a discontinuity. If this bone was formed by fusion of prefrontal and lacrimal there seems no good reason for the lateral shift of the supraorbital canal to the maxilla. Although the possibility of fusion cannot be totally rejected, it too appears improbable.

The topographic relationships of the bone are such that it might be either the prefrontal which established a maxillary contact with loss of the lacrimal or the lacrimal which has acquired premaxillary and frontal contacts with the loss of the prefrontal. No trace of a groove or tube for the lacrimal duct can be identified, but, since the presence of this structure in other nectrideans has not been confirmed, its absence in *Diploceraspis* may not be significant. The course of the supraorbital lateral line canal is more instructive, however. In other amphibians this canal typically originates on the premaxilla and passes posterolaterad across the nasal. On the nasal it bends sharply laterad, curves across the lacrimal and then swings posteromediad onto the prefrontal and finally onto the frontal. In those forms in which the prefrontal separates nasal and lacrimal, the outward curve may be confined to the prefrontal and the canal lies entirely medial to the lacrimal. In others the canal passes directly from nasal to frontal — here again medial to the lacrimal. In any case the supraorbital lateral line canal crosses or is medial to the lacrimal; it never lies lateral to the lacrimal on the maxilla; but it may be laterad, it may cross, or lie mediad of the prefrontal.

As already described, this canal in *Diploceraspis* crosses the posterior end of the naris in front of this questionable bone, curves across the maxilla laterad to it and then turns mediad across it just in front of the orbit. If the bone is the lacrimal then the position of the supraorbital canal is unique. If the bone is the prefrontal then the supraorbital canal lies in a normal position. In consequence I interpret this element to be the prefrontal.

Two questions concerning the bones of the snout still remain. Is the nasal fused to the premaxilla (or prefrontal)? Is the lacrimal fused to the maxilla? As to the former question, no trace of a transverse suture or of a change in dermal sculpture appears in the skulls studied. If fusion occurred, it happened early in development, and since the nasals are absent in the similar *Diplocaulus*, their disappearance here is not unexpected. The problem of lacrimal-maxilla fusion is not so easily settled. Although no complete suture appears, the dorsal portion of the maxilla shows partial separation from the ventral, tooth-bearing part, and bears quite different dermal sculpture. Furthermore, the position of the supraorbital lateral line on this medial portion is very similar to its pattern on the lacrimal in other amphibians. The jugal reaches forward to touch this dorsal element and, indeed, separates it in part from the ventral portion. This element also forms a short part of the anterolateral border of the orbit. If this is the lacrimal, then prefrontal-lacrimal-maxilla-jugal pattern is precisely like that in *Keraterpeton* and quite distinct from that in *Batrachiderpeton* and *Diplocaulus*. In these latter genera, the jugal fails to reach the lacrimal; the lacrimal excludes the prefrontal from the naris and is excluded from the orbit. It differs also from that in *Diceratosaurus, Urocordylus,* and *Scincosaurus* but only in that the jugal fails to reach so far anteriad, a condition probably related to the relative lateroventral position of the orbits in these genera. I conclude from this that the lacrimal is present, is partially fused with the maxilla, and has essentially normal relationships to the other bones of the snout.

The jugal consists of two rather distinct parts, a slender anterior ramus along the lateral border of the orbit and a broader posterior plate. The anterior ramus contacts, as indicated above, the maxilla and the lacrimal and also supports the palatine. The ventral border, forming the upper edge of the mouth is somewhat emarginate (Fig. 4). This anteriad extension of the jugal occurs also in *Diplocaulus, Keraterpeton,* and, to a lesser extent, in *Batrachiderpeton*. In these forms, however, the maxilla reaches posteriad for a considerable distance below the anterior ramus, separating it from the mouth. The shape and relationships of the posterior portion are, on the other hand, fairly typical for the nectrideans and differ only because of posteriad shift of the postorbital, described in the next paragraph.

The pattern of the postorbital and postfrontal bones is unusual and is duplicated only in *Diplocaulus*. A relatively large pentameral bone forms the posterior border of the orbit and extends between the medial elements of the skull table, the frontal and parietal, and the anterior lateral element of the cheek, the jugal. A smaller, squarish bone lies posterolaterad to the element just described. This second bone is bounded anterolaterally by the jugal, posterolaterally by the squamosal and posteromedially by the parietal.

The larger, anterior bone shows the essential relationships of the postfrontal in more normal amphibians. Among the other nectrideans the postfrontal-prefrontal contact is typically quite slender, and the two bones in a similar position in *Diplocaulus* are completely separated by the frontal. The lateral contact with the jugal is unusual but is inevitable if the postorbital is lost or "pulled" backward out of the orbit. There is consequently no positive evidence that this bone is the postorbital, and if the smaller element behind it is postorbital (see below), then it must be postfrontal. If the posterior element is the supratemporal, unlikely as that seems, then the identification remains doubtful.

The posterior of these bones in *Diplocaulus* has been termed, variously, squamosal (Case, 1911, p. 86), supratemporal (Williston, 1909), and postorbital (Douthitt, 1917, p. 6; Watson, 1913, p. 960). The topographic relationships of the bone in *Diploceraspis* as well as in *Diplocaulus*, suggest that the latter interpretation is most reasonable. In the typical, "unspecialized," amphibian skull, the supratemporal has broad contacts with parietal, squamosal, and tabular. It also touches the postparietal posteriorly in some and the postfrontal and/or postorbital anteriorly. In no example does the supratemporal contact the jugal. Defined broadly, the supratemporal lies between the squamosal and the parietal and postparietal. The questionable element here does not touch either tabular or postparietal; it does contact the jugal, and, like the postorbital of other amphibians, is bounded laterally by the jugal and squamosal bones and medially by the postfrontal and parietal. The only difference in relationship of this bone from the typical postorbital is the loss of contact with the orbital border. Watson pointed out in 1913 that the postorbital in *Batrachiderpeton* had been carried backward (or the orbit forward) so that the orbital border was much narrowed. In *Urocordylus* the postorbital is also nearly excluded from the orbit and the supratemporal occupies the typical position (Steen, 1938, p. 209). All evidence therefore indicates that this is the postorbital in *Diploceraspis* as well as in *Diplocaulus*.

The remaining elements of the cheek region, the quadratojugal and squamosal, reflect in their size and form the development of "horns." The quadratojugal is roughly trapezoidal, extends along the lateral margin of the skull from the posterior corner of the mouth to a point some distance behind the quadrate, and curves onto ventral and dorsal surfaces of the skull. It joins the jugal anteriorly and anteromedially. A ramus extends medioventrally to contact, in anterior-posterior sequence, the quadrate, pterygoid, and the ventral ramus of squamosal and to floor the subtemporal fossa (Figs. 2, 4). A large foramen pierces this ramus just laterad of the quadrate. The ventrolateral edge of the quadratojugal forms a continuous line with the squamosal unlike the distinct ventral flange observed in *Diplocaulus*. It also differs from *Diplocaulus* in sharing a pterygoid contact with the squamosal — and thus retains the typical amphibian condition.

The squamosal is a very large triangular bone that forms most of the anterolateral edge of the "horn." The dorsal portion contacts the quadratojugal and postorbital anteriorly, the parietal anteromedially, and the tabular posteromedially. The lateral border curves broadly to the ventral surface and extends some distance posteromedially to contact the tabular again near the midline of the horn, medially to form the lateral border of the otic notch (which is ventral in *Diploceraspis*), and anteromedially to join the quadratojugal (Fig. 2). All of these surfaces are sculptured. In this respect it differs from the *Diplocaulus* squamosal which has much of its ventral surface smooth. It also differs in its relation to the otic notch, for in *Diplocaulus* an anteromediad process of the tabular excludes it from the otic notch. The internal surface of the dorsal plate of the squamosal gives rise to a flange that extends anteroventrally along the internal ramus of the quadratojugal to a broad suture with the pterygoid (Fig. 4). An internal flange extending to the pterygoid occurs also in *Batrachiderpeton* and *Diplocaulus,* and probably, in *Diceratosaurus.* In all, the relationship of the squamosal to the other elements of the skull is normal in spite of the unusual form of the bone. This form results, inevitably, from the forward shift of the quadrate and the development of a "horn" at the dorsal posterolateral corner of the skull.

Of the bones in the temporal series, the inter- and supratemporals and the tabular, only a single element occurs in *Diploceraspis.* This is the principal element of the "horn" and is generally of extremely elongate, trapezoidal form. This bone contacts the squamosal anterolaterally, the parietal anteriorly, and the postparietal anteromedially. It curves onto the ventral surface both anterolaterally and posteromedially so that the distal end of the bone forms a hollow, flattened cylinder. The characteristic sculpture covers the dorsal and ventral surfaces. This cylinder continues posterolaterally into the recurved tips of the horn. Anterolaterally the ventral plate contacts the ventral plate of the squamosal; it also forms the posterior border of the otic notch, makes contact with the opisthotic behind the notch and forms an anteromedial juncture with the postparietal.

The bone occupying this position in *Diplocaulus* has been considered by most authorities to be the tabular (Douthitt, 1917, p. 7, and others). Olson (1951, pp. 90-91), however, has argued that it is, rather, the supratemporal. In consequence a brief discussion is necessary here. In the nectridean *Urocordylus,* two temporal elements are present. The anterior of these is a small, slender bone between the squamosal and parietal which makes a short anterior contact with the postorbital and a somewhat wider contact with the posteriad temporal bones. The posterior element forms the posterior corner of the skull table and the medial border of the otic notch, contacts the parietal and postparietal medially, and the squamosal laterally, and, presumably, joins the opisthotic ventrally. These are the typical relations of the supratemporal (anterior element) and tabular (posterior element) in the Amphibia and are so regarded by Steen (1938, p. 207).

Among the other nectrideans, only a single temporal element has been identified, that with the typical relations to squamosal, postparietal, skull table, and opisthotic characteristic of the tabular. The only difference in *Diplocaulus* (and *Diploceraspis*) is the great enlargment of the bone to form the "horn." It is difficult to understand why the supratemporal would assume the position of the tabular and lose its normal relationship to the postorbital, parietal, and squamosal. In consequence, Olson's interpretation is rejected.

Like the squamosal of the cheek region and the tabular of the temporal, the medial bones of the skull roof, the parietal and postparietal, show marked modification in shape and size to form the posteromedial portion of the "horns." They resemble quite closely the homologous elements in *Diplocaulus.* The parietals are narrow, elongate, triangular bones. A moderately large opening appears near the midpoint of the interparietal suture. The flared dorsal end of the epipterygoid is fused to the underside of the parietal (Fig. 4).

The postparietals are, similarly, narrow, elongate triangular bones. They are bordered by the parietals anteriorly and anterolaterally and by the tabular posterolaterally. Each curves a short distance onto the occipital surface and descends to the exoccipital and opisthotic by two short rami separated by a large opening, presumably the posttemporal fossa (see discussion in next section). They also form the dorsal border of the foramen magnum.

Occipital surface. The occipital plate is formed by three elements on either side (Fig. 5). The postparietal bone which covers the dorsal border is described above. The exocciptal bone is relatively large and comprises the condyle, a ventral plate, and two vertical processes, one of which extends directly upward to contact the postparietal and the other of which extends up and out to a rather long juncture with the opisthotic. These two rami are separated by a notch that forms the lower edge of a large oval opening into the skull. The ventral plate is also notched for the inner edge of a foramen immediately in front of the occipital condyle. It contacts the opisthotic again in front of the foramen and continues forward to a junction with the exoccipital ramus of the pterygoid. The length of this suture is somewhat variable from specimen to specimen, but, in all, a rather large ovoid gap is left between pterygoid and parasphenoid contacts. The anteromedial corner of the ventral plate is joined in complex suture with the parasphenoid. Behind this point the margin is free and the two exoccipitals fail to touch along the midline. The base of the occipital condyles lies at the junction of the dorsal rami and the ventral plate. The condylar surfaces are wide, shallow, and fairly flat, rather like 110° segments of a cylinder with its axis nearly perpendicular to the midline. They show very slight transverse curvature and face somewhat mediad so that the head could have been turned only a very short distance sideways.

The inner face of the exoccipital is quite complex. A narrow, horizontal plate forms a shelf along the medial and anteromedial sides of the base of the ascending (postparietal) ramus. The narrow groove between this shelf and the ventral plate is lined with a thin sheet of granulose bone. This sheet may represent the bony cap of the basioccipital cartilage whose presence is suggested by the midline gap between the exoccipitals. If I am correct in this interpretation then the groove and the shelf above represent the basioccipital contact of the exoccipital. Another feature of the inner surface is a strong ridge arising from the opisthotic border just behind the small foramen described above. This extends anteromedially and continues up the anterolateral side of the postparietal ramus. A deep groove lies posterior to the ridge and extends as a fossa into the condylar base. A much shallower groove anterior to the lateral end of the ridge continues laterally into the foramen. The overall shape of the exoccipital and its relationship to the pterygoid, parasphenoid, and postparietal are similar to those of *Diplocaulus* (Douthitt, 1917, p. 12). Although Douthitt did not report an unossified gap between pterygoid and parasphenoid contacts, it does occur in some *Diplocaulus* specimens. The condyles in *Diplocaulus* curve further ventrally, face more directly posteriad, and are more strongly curved.

The opisthotic is a wedge-shaped bone with a broad medial "head" and a tapering paroccipital process extending laterally. The "head" contacts the exoccipital and extends above that bone on the occipital surface to the postparietal. The dorsal border of the opisthotic is formed by the postparietal, but a slender tongue of the tabular reaches medially from the lateral end of the paroccipital along its dorsal internal border. The "head" of the opisthotic is strongly concave internally and bears a thin, circular sheet of granulose bone. The free, anteroventral border of the opisthotic forms the posterior edge of the otic notch. Although Douthitt reports the exoccipital and opisthotic as fused in *Diplocaulus*, sutures can be distinguished in many specimens of that genus. The character of the opisthotic "head" could not be distinguished in the specimens of *Diplocaulus* available for study, but it appears to bear a rough, "unfinished" inner surface. Like *Diplocaulus* and unlike the other genera (*Urocordylus*, *Scincosaurus*, and *Batrachiderpeton)* in which the character is known, the opisthotic lacks a pterygoid contact.

The openings in the occipital surfaces just described are difficult to interpret. Douthitt (1917, p. 12) described the rather similar occipital structure of *Diplocaulus* and suggested that the small foramina in front of the condyles on the ventral surface served for passage of the vagus but did not offer any interpretation of the larger openings above the condyles. Similar, small precondylar openings occur in *Diceratosaurus*, but none of the available specimens show the occipital area above the condyle. Watson in his description of *Batrachiderpeton* (1913, p. 952) indicated that a foramen above the condyle was the exit of the glossopharyngeal and vagus nerves and that a smaller opening on the ventral surface of the opisthotic just in front of the condyles was the fenestra ovalis. This area has not been described in the other nectrideans.

The upper opening in *Diploceraspis* and *Diplocaulus* is bordered by the postparietal, the paroccipital process of the opisthotic, and the exoccipital. In other amphibians, the rhachitomes for example, this is the position of the posttemporal fenestra. I see no reason to consider it otherwise in *Diploceraspis*. Since Watson did not discuss the relation of the upper opening to the bony elements of the occiput in *Batrachiderpeton*, no conclusion can be offered here on that genus. The foramen for the vagus (and associated nerves) in the amphibians pierces the occipital surface obliquely above the condyle, and is directed posterolaterally rather than directly to the rear. It opens along the suture between the opisthotic and exoccipital somewhat posterior to the fenestra ovalis. If one rotates the ventrolateral portions of this typical occiput under and forward with a corresponding rotation of the otic notch and the quadrate, the opisthotic forms the ventral edge of the occiput, lateral to the condyles, and the ventrolateral portion of exoccipital-opisthotic contact would come to lie on the ventral (palatal) surface of the skull. The otic notch would then be in front of the opisthotic rather than below and outside it, and the fenestra ovalis and vagus foramen would open ventrolaterally rather than posterolaterally. This is precisely the condition in *Diploceraspis* and *Diplocaulus*. Douthitt's conclusion that the ventral precondylar foramen of *Diplocaulus* was the vagus nerve opening is thus substantiated by the morphology of the *Diploceraspis* occiput.

Palate — Basicranium. The palate of *Diploceraspis* (Figs. 2, 4, 5) shows many of the features typical of other specialized amphibians with flattened skulls (Watson, 1951, pp. 46-49) — reduction of the basioccipital and basisphenoid, development of large interpterygoid vacuities, a corresponding reduction of the palatal ramus of the pterygoid, shift of the quadrate anteriad of the occipital condyles, development and lengthening of a parasphenoid-pterygoid suture, and the appearance of pterygoid-exoccipital and parasphenoid-exoccipital contacts. In these characteristics *Diploceraspis* parallels *Diplocaulus* and departs from the pattern of the less modified nectrideans. On the other hand, they are anticipated in some genera, for example *Diceratosaurus*, so that they represent a logical continuation of a trend.

The vomers, separated by an indistinct midline suture, form the medioanterior portion of the palatal complex. Each bone is roughly quadrangular, lying against the premaxilla anteriorly, forming the medial border of the internal naris, contacting the palatine laterally, forming the anteromedial border of the interpterygoid vacuity, and joining the parasphenoid posteriorly. Each vomer bears a row of six teeth along its anterior border. These lie in line with and continue the arc of the palatine teeth.

The palatine is a delicate triradiate bone. Its anterolateral border is braced against the maxilla, and it extends a narrow tooth-bearing process forward along the latter bone almost excluding it from the border of the internal naris. A rather broader but short process extends medially behind the internal naris to make a loose contact with the vomer. The base of this process bears an internal

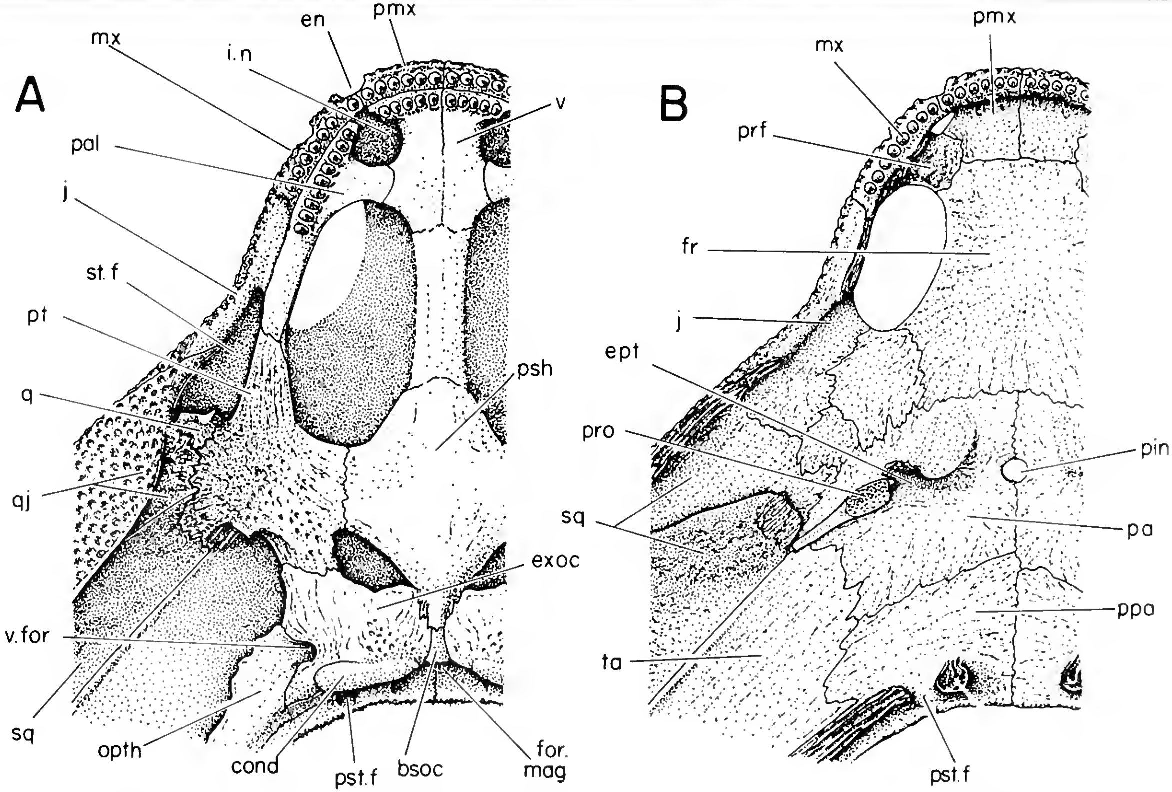

FIG. 4. *Diploceraspis* skull, reconstructed palatal details. Approximate enlargement x 1.5. *A*, Palatal elements in place. *B*, Palatal elements removed to show undersurface of skull roof. Abbreviations: *bsoc*, basioccipital; *ept*, epipterygoid; *for.mag*, foramen magnum. For other abbreviations see captions, Figures 1 and 2. Number of teeth shown incorrectly: vomer bears 6 rather than 5; palatine 11 rather than 9.

facet that braces the bone dorsally against the prefrontal. The third process extends posteriorly to contact the pterygoid — this portion is also braced dorsally by an extensive suture with the jugal. The eleven or twelve teeth lie in an arcuate row just inside the maxillary contact. The vomerine and pterygoid rami form the anterior and anterolateral borders of the interpterygoid vacuity; the pterygoid ramus also forms a short segment of the border of the subtemporal fossa.

The ectopterygoids have not been definitely identified but may be represented by a short, tiny splinter of bone at the palatine-pterygoid suture.

The pterygoid is a moderately large bone vaguely quadriradiate in ventral aspect. The palatine ramus is a narrow tongue of bone joined in a complex, jagged suture with the palatine. The short, wide, lateral ramus contacts the quadrate, quadratojugal, and squamosal successively in a continuous, jagged suture. The posterior ramus forms a contact with the exoccipital, and the medial ramus with the parasphenoid. The internal, dorsal, surface of the pterygoid bears a ridge-like ascending process that extends from the posteromedial corner of the palatine ramus to the posterolateral corner of the lateral ramus. This process abuts anteromedially against the epipterygoid (see below) in a complex suture and continues posterolaterad in contact with the prootic (and possibly the parietal as well) to or near the squamosal-tabular end of that element. The posteromedial face of this ridge is deeply concave — a concavity which is accentuated by a parallel ridge which lies just mediad of the base of the ascending process. The ridge is also modified by a deep notch just behind the epipterygoid contact. The ventral, external, surface of the pterygoid is marked by a short flange projecting posteriad between the lateral and exoccipital rami into the otic notch. This flange is variously developed in *Diploceraspis*, extends as a continuation of the lower surface of the lateral ramus and roofs a shallow groove that runs anterolaterad along the posterior border of the exoccipital ramus. The exoccipital contact is fairly short and is probably separated in all *Diploceraspis* from the pterygoid-parasphenoid and the exoccipital-parasphenoid contacts by a moderately large vacuity. It differs significantly from the pterygoid of *Diplocaulus* only in the presence of a quadratojugal contact.

The parasphenoid comprises a posterior, moderately thick, diamond-shaped plate, which contacts the pterygoids and exoccipitals on either side and forms the posteromedial borders of the interpterygoid vacuities, and a narrow, thin, anterior ramus,

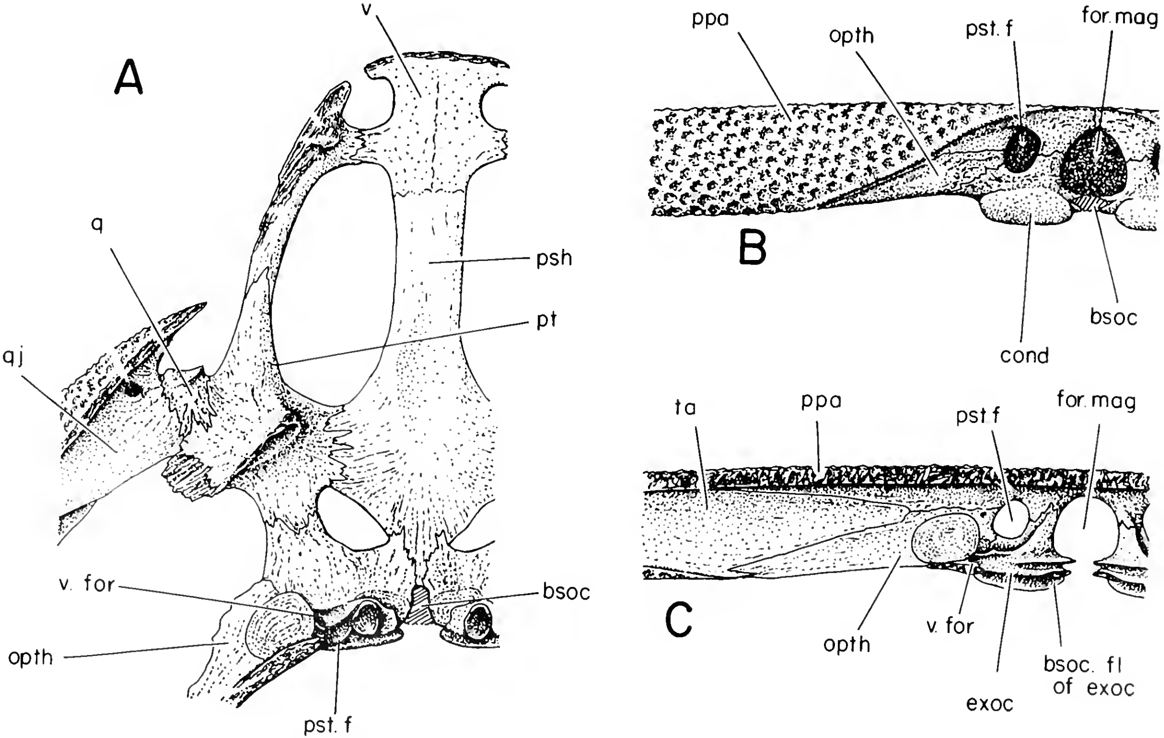

FIG. 5. *Diploceraspis* skull, reconstructed palatal and occipital details. Approximate enlargement, x 1.5. *A*, Dorsal (internal) view of palatal elements. *B*, Posterior view of occiput. *C*, *Anterior* (internal) view of occiput. Abbreviation: *bsoc. fl. of exoc*, basioccipital flange of exoccipital. For other abbreviations see captions, Figures 1, 2, and 4.

which extends forward between the vacuities to the vomers. The posterior tip of parasphenoid extends a short distance backwards between the exoccipitals and may represent an ossified portion of the basisphenoid.

The quadrate is a small element, lying entirely on the ventral surface, and is triangular shaped, with apex posteriad, in ventral aspect. The medial leg of the triangle forms a complex suture with the pterygoid, the lateral leg with the quadratojugal. The base of the triangle forms a trochlear condyle facing anteroventrad. The inner (dorsal) surface is likewise triangular but it extends posteriad as a thin sheet of bone over the quadratojugal and pterygoid to approach the squamosal.

The epipterygoid is apparently represented by a short process that extends from the ascending process of the pterygoid to the parietal, and then spreads as a horizontal sheet anterolaterad over the inner surface of the latter bone. Since in all specimens, some seven or eight partial skulls, this sheet is fused to the parietal, some question of identity remains, and it may be interpreted as a descending process of the parietal. In all specimens, however, the anterolateral borders of the sheet form a sharp margin and define a layer of bone distinct from the parietal. Moreover, the position of this element is lateral to the ascending ramus of the pterygoid, and the vertical process extends a considerable distance down along the lateral side of this pterygoid ramus — the proper position for the epipterygoid. Posteromedially it touches the small element here interpreted as an ossified portion of the prootic as does the epipterygoid in other, more "normal" amphibians. Between the prootic and epipterygoid is a distinct notch, presumably for the passage of branches of the trigeminal. In summary, this bone possesses the proper topographic relationships for the epipterygoid and varies from that bone in other amphibians only in its extensive dorsal fusion with the parietal. In the very flat shallow skull of *Diploceraspis* some bracing of palate against skull roof would seem essential, and the modification of epipterygoid for this function seems reasonable. Douthitt (1917, pp. 11-12) found a similar element in *Diplocaulus*.

FIG. 6. Variation in *Diploceraspis* skulls. All enlarged, x 0.7. *A*, MCZ 3010, dorsal view; left horn, left postparietal, right horn including exoccipital, pterygoid, and quadrate. *B*, CM 8544, *Diploceraspis conemaughensis*, ventral view; left horn including portions of exoccipital and pterygoid. *C*, CM 8548, ventral view; left horn and portion of face, details poorly preserved. *D*, MCZ 3013, dorsal view; left horn including pterygoid. *E*, MCZ 3032, probably

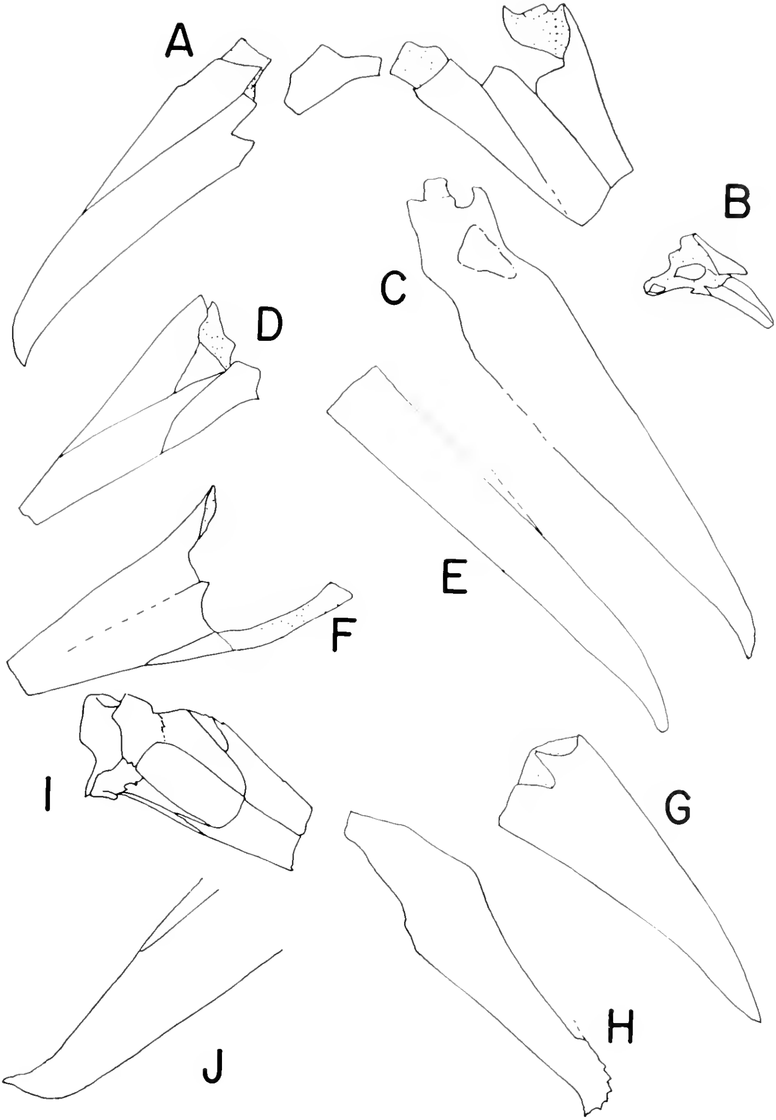

FIGURE 6

ventral view of the left tabular. *F,* MCZ 3026, ventral view; right horn. *G,* MCZ 3017a, dorsal view; right horn. *H,* MCZ 3017b, dorsal view; right tabular and portion of squamosal. *I,* MCZ 3019, ventral view; left horn including exoccipital, partial pterygoid, epipterygoid, and prootic. *J,* MCZ 3009, dorsal view; tip of left horn of complete skull.

On one side of specimen MCZ 3009 and in the partial skull, MCZ 3019, a small spoon-shaped bone lies against the inner surface of the parietal, posteromedial to the ascending ramus of the pterygoid (Fig. 4). The "bowl" of the "spoon" is covered by a thin sheet of granulose bone similar to that on opisthotic and exoccipital described above and faces posteroventrad. The anterior tip of the "bowl" touches the epipterygoid; the anteroventral edge of the "bowl" and of the "handle" articulate with a facet on the ascending process of the pterygoid; the posterodorsal edge of the bone fits in a facet on the under surface of the parietal; and the "handle" of the "spoon" extends out and back to approach, if not actually touch, the squamosal and tabular. If the element, here interpreted as the epipterygoid, is correctly identified, then the bone just described must be an ossification in the chondrocranium — certainly it has the expected relationships for the prootic. The only alternative interpretation is that of epipterygoid, and its position, posteromedial to the pterygoid, does not support this hypothesis. The apparent absence of this element in most *Diploceraspis* skulls may be due to accidents of preservation and preparation as well as variation in ossification from individual to individual. In most *Diploceraspis* specimens the otic notch and interior of the skull were filled with fish scales and fragments of bone. Since the prootic element is rather delicate, loosely attached, and of the same size as the fragments in this bone "hash," it could be easily removed inadvertently during preparation — I know this to be true of one specimen.

Mandible

The general modification of skull form in *Diploceraspis* conditioned the shape and character of the mandible. Although no intact mandible has yet been recovered, a number of fragmentary specimens (MCZ 3011, MCZ 3014, MCZ 3006, MCZ 3004 and MCZ 3031) provide adequate information for a reconstruction (Fig. 7). The mandibular arch is short and broad, like that of *Diplocaulus*, but the posterior "legs" of the arch are subparallel rather than divergent. It bears a short tooth row, typically 12 teeth on either side. Three or four coronoid teeth are also present. The jaw is relatively deep and bears a relatively high coronoid process. The retroarticular process is also well developed. It lies in line with the ventral edge of the jaw and the circular facet for muscle insertion faces ventrolaterad. In these three features the *Diploceraspis* departs markedly from the pattern of *Diplocaulus*.

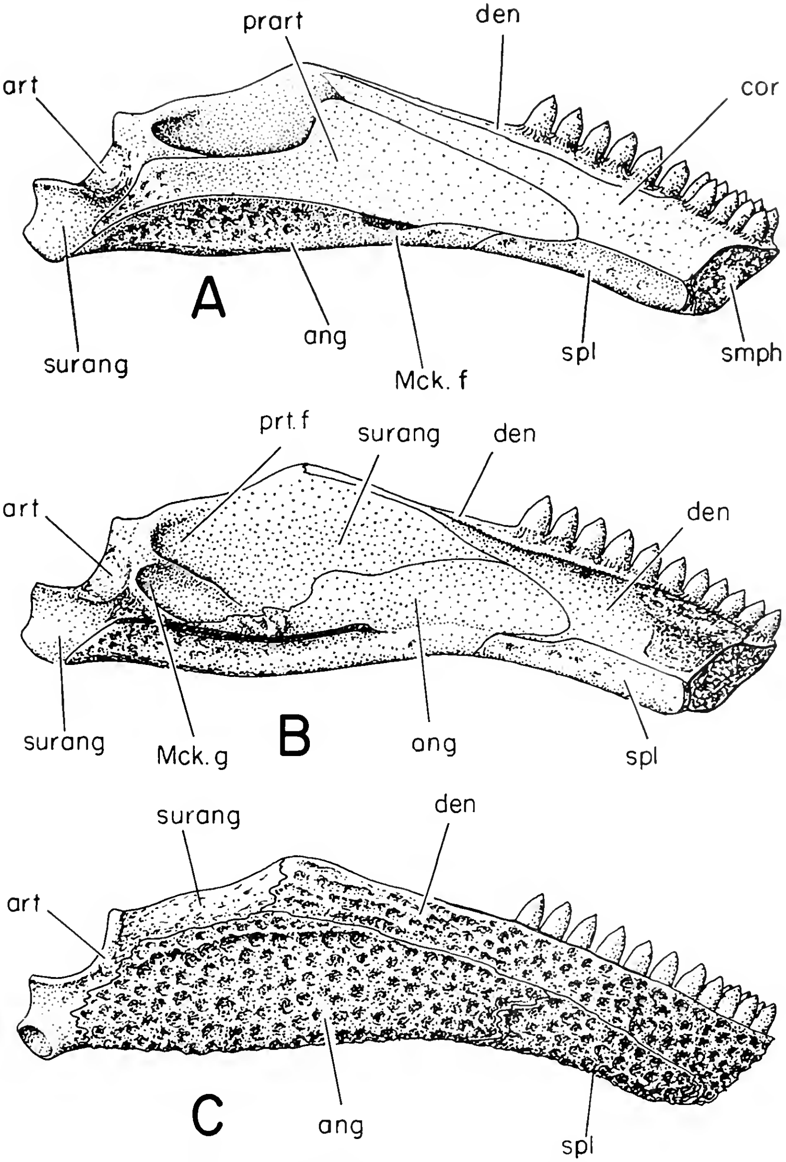

FIG. 7. *Diploceraspis,* reconstructed mandible. Approximate enlargement x 2.3. *A,* Medial view, all elements in place. *B,* Medial view, inner elements removed. *C,* Lateral view. Abbreviations: *ang,* angular; *art,* articular; *cor,* coronoid; *den,* dentary; *Mck.f,* Meckelian fenestra; *Mck. g,* Meckelian groove; *prart,* prearticular; *prt. f,* prearticular fossa; *smph,* symphysis; *spl,* splenial; *surang,* surangular.

The prearticular fossa is relatively short but otherwise normal. Some specimens show a distinct bony node at the bottom of the fossa, presumably a muscle attachment. The articular fossa is double faceted to receive the trochlear condyle of the quadrate and is very low on the jaw — so low that it is below the level of the tooth row as well as the coronoid process. The lateral facet faces posterodorsally, the medial posteromedially. The articulation, therefore, differs radically from that of *Diplocaulus* which faces posteromedially. The inner surface of the jaw is pierced near its ventral margin by a large Meckelian foramen, between the angular and prearticular. I have been unable to distinguish an anterior Meckelian foramen. The inner surface of the surangular bears a deep groove for the Meckelian cartilage. This apparently continued forward, sheathed laterally and ventrally by the angular and medially by the prearticular, to end in a sheet of granulose bone near the anterior end of the dentary. The symphysis is broad but not tightly sutured, for all the jaws observed have separated at this point. The external surface of the mandible is finely pitted; the lateral line canals are described in the preceding section (p. 50).

The articular is presumably represented by the articular fossa, but no suture separates it from the surangular. The latter bone has a very small lateral exposure, forming the dorsal border of the jaw behind the coronoid process and the retroarticular process, but it spreads broadly over the inner surface of the angular, inside the prearticular fossa. Douthitt (1917, p. 15) did not distinguish the surangular from articular in *Diplocaulus;* if most of what he called articular is surangular then the general relationship is the same even though the surangular has a much more extensive lateral exposure.

The *Diploceraspis* angular, conversely, has a broad lateral exposure and a relatively narrow medial one — much narrower than that of *Diplocaulus*. The *Diploceraspis* jaw also differs from that of *Diplocaulus* in the presence of one instead of two splenial elements. The splenial extends halfway up the outer surface of the jaw but has only a very narrow flange exposed on the inner surface. This reverses the condition observed in *Diplocaulus*. In *Diplocaulus* the splenial enters into the symphysis, but it fails to do so in *Diploceraspis*.

The dentary is relatively long, reaching back to the summit of the coronoid process, but is quite shallow. The coronoid consists of a long, narrow posterior arm extending anteriad along the inner margin of the dentary from the coronoid process, and of a broad sheet of bone over the inner surface of the jaw below the tooth row. The prearticular, similarly, comprises a slender posterior ramus that reaches back between the surangular and angular to the base of the retroarticular process and a deeper anterior portion that covers the inner face of the jaw in front of the prearticular fossa and below the coronoid process. Comparison with *Diplocaulus* is difficult because the coronoid has not been distinguished in that genus. Douthitt suggested, however, that the coronoid was represented by a narrow splint of bone paralleling the inner border of the tooth row. If he is correct, *Diplocaulus* differs in this respect from *Diploceraspis*, which has a large coronoid spread broadly over the anteromedial surface of the jaw.

Axial Skeleton

As indicated by Romer (1952, p. 71), *Diploceraspis* vertebrae are characterized by strong sculpture along the crest of the neural spine and by a pattern of fine, vermiculate lines on the centra (Fig. 9). They agree with *Diplocaulus* in the latter characteristic but differ in the former, for the spine in *Diplocaulus* bears a distinctive pit on an otherwise unornamented crest.[2] The sculpture is somewhat like that of *Diceratosaurus*, but unlike the latter genus the dorsal ends of the spine are not strongly expanded, and the sculpture consists of elongate pits and anastamosing ridges rather than circular pits. The vertebrae are of lepospondylous type consisting of a coossified centrum and neural arch. The centra are amphicoelous — the cross-section is shaped like an hourglass. Since no articulated skeletons are known, the number of vertebrae is indeterminate.

The anterior, "atlas," vertebra (Fig. 8A) bears a pair of nearly flat glenoid cavities to receive the occipital condyles. A short spine juts forward between these glenoid facets. The neural arch extends well anteriad above facets and spine to cover the top and sides of the neural canal where it passes into the foramen magnum. No transverse processes are present; presumably no ribs were borne. The ventral surface of the centrum bears an indistinct median keel anteriorly that terminates in the interglenoid spine. The neural spine extends posteriad, above the postzygapophyses, to fit into a zygantrum on the succeeding, "axis," vertebra. Accessory apophyses above the postzygapophyses also extend posteriad to embrace the sides of the neural arch of the "axis." The neural

[2] A few *Diplocaulus* arches show a fine sculpture not very different from that of some *Diploceraspis*.

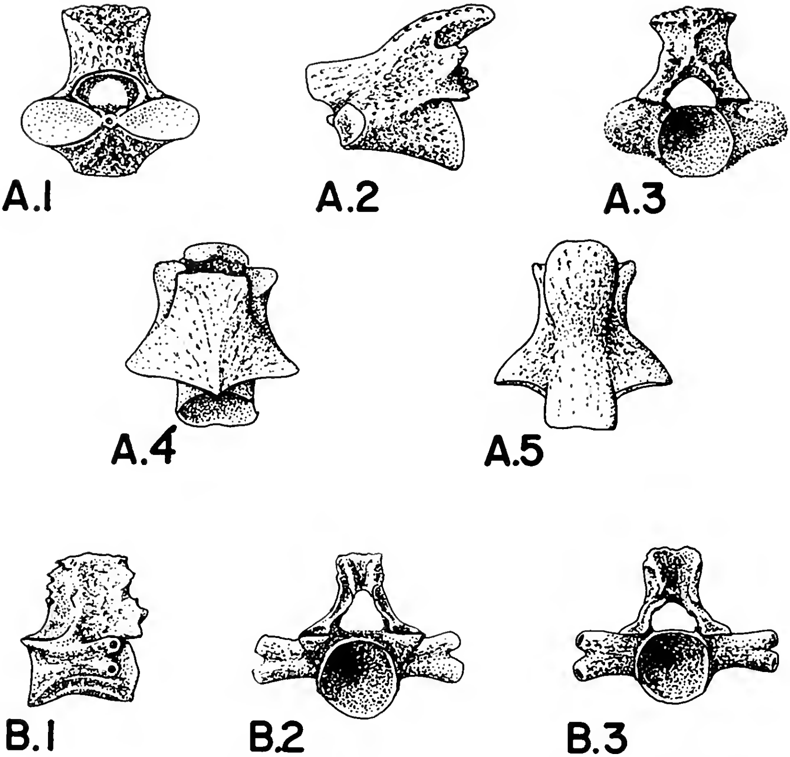

FIG. 8. *Diploceraspis,* "atlas" and "axis" vertebrae. Approximate enlargement, x 2.3. *A,* "Atlas." *A.1,* Anterior view; *A.2,* lateral view, anterior to left; *A.3,* posterior view; *A.4,* ventral view, anterior up; *A.5,* dorsal view, anterior up; *B,* "Axis." *B.1,* Lateral view, anterior to left; *B.2,* anterior view; *B.3,* posterior view.

spine is far more strongly developed than in *Diplocaulus* and the zygapophyses face ventrally rather than posteroventrally. Otherwise, the "atlas" agrees with that of *Diplocaulus;* it has not been described in the other nectrideans.

The "axis" (Fig. 8B) is distinguished from the remaining vertebrae by the presence of an anterior zygantrum (for the zygosphene of atlas) in the place of a zygosphene. This centrum is also relatively short (its length is only about 2/3 the height of the vertebra) as compared with the thoracic vertebrae (which are longer than high). The transverse processes extend posterolaterally to

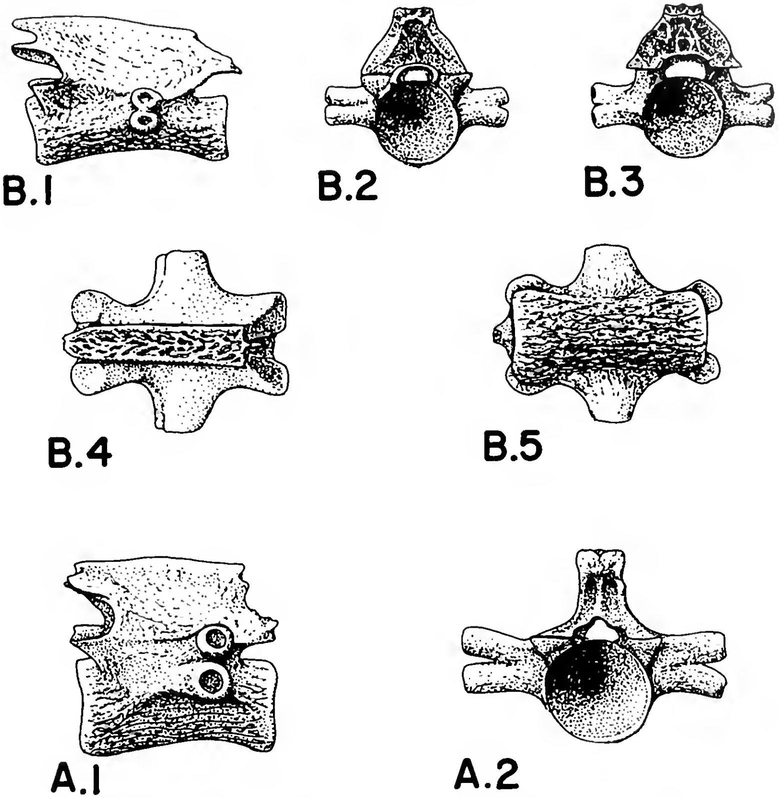

FIG. 9. *Diploceraspis,* "trunk" vertebrae. Approximate enlargement, x 2.3. *A,* Anterior "trunk" vertebra. *A.1,* Lateral view, anterior to left; *A.2,* anterior view. *B,* Posterior "trunk" vertebra. *B.1,* Lateral view, anterior to left; *B.2,* anterior view; *B.3,* posterior view; *B.4,* dorsal view, anterior to left; *B.5,* ventral view, anterior to left.

separate, near their distal ends, into distinct dia- and parapophyses. As in *Diplocaulus,* these processes are both borne on the centrum, and the articular facets lie one above the other.

The thoracic vertebrae vary considerably in character, probably as a consequence of individual as well as regional differences (Fig. 11). The anterior thoracics, on analogy with *Diplocaulus,* should be relatively short and high. Figure 9A shows a vertebra of this type; Figure 9B is of a longer, lower vertebra that is, presumably, a posterior thoracic. All the anterior thoracic vertebrae and the majority of the posterior bear both dia- and parapophyses; a few, perhaps 10 per cent, of the latter have a single transverse process on either side. The diapophysis and parapophysis typically coalesce at their bases; in some they separate only near their distal ends; in others they are distinct to the point of basal coalescence. The articular ends of these processes are typically round or slightly flattened. Each one has a central canal that opens terminally in the center of the articular facet. As in the "axis," the articular facets lie one above the other. The basal portion of the diapophysis lies at the upper border of the centrum and is connected by ridges to the zygapophyses. The basal portion of the parapophysis lies near or slightly above the middle of the centrum and extends in low ridges, a long anterior and a short posterior, along the sides of the centrum.

The articular surfaces of the zygapophyses are horizontal or nearly so. They are complemented by complex articulations between the neural arches and spines. The anterior tip of the neural spine forms a zygosphene that fits onto the posterior end of the neural spine of the preceding vertebra. The ventral surfaces of the zygosphene, directed laterally as well as ventrally, extend posteroventrad to the posterior end of the prezygapophyses. These surfaces are embraced by zygantra extending the sides of the neural arch of the preceding vertebra. The posterior end of arch and spine, of course, bears complementary hollows and projections. As a consequence of the horizontal position of the zygapophyses and the presence of accessory articulations on the neural arch and spine, vertical bending of the backbone must have been very limited. The articulations above the zygapophyses on the neural arch also must have had limited lateral bending — but to a much lesser extent. The medial edges of the prezygapophyses are connected by a sheet of bone that roofs the anterior end of the neural canal. This "roof" fits into a recess between the postzygapophyses of the preceding vertebra and provides a continuous dorsal shield over the spinal cord. No such structure is observed in *Diplocaulus.*

In *Diplocaulus*, the seventeenth (Case, 1911, p. 88) or eighteenth (Douthitt, 1917, p. 18) vertebra has an unusual form. The neural arch and centrum have the typical elongate character of the immediately preceding thoracics, but the neural spine is relatively low. The centrum, like that of the three or four preceding vertebrae, bears a strong, undivided transverse process with a single broad articular facet. The posterior ventral surface of the centrum, however, bears a pair of heavy spines. These are directed strongly posteriad to extend behind the end of the centrum, and, in some if not all individuals, join ventrally to form a distinct haemal arch. The posterior tip of the arch fits against or into the end of the haemal arch of the succeeding vertebra. Both Case and Douthitt interpret this to be the sacral vertebra.

Romer (1952, p. 71) described a somewhat similar *Diploceraspis* vertebra with the two posteroventral spines although these did not join to form an arch (CM 8555). Another vertebra (MCZ 3006) of this type appears in the new collection. At least five other vertebrae (MCZ 3021) of otherwise similar character show fusion of these spines (Fig. 10A) to form a strong haemal arch projecting posteriad as in *Diplocaulus*. Romer interpreted this vertebra as the anterior caudal — in the absence of an articulated skeleton neither alternative can be rejected.

A few *Diploceraspis* caudal vertebrae bear short transverse processes or articular facets for caudal ribs (Fig. 10B). Two specimens, one large, the other very small, have short, distinct, undivided transverse processes, and relatively high neural arches and deep haemal arches. These arches are unusually robust and are somewhat swollen laterally. The haemal spines bear deep anterior recesses. The presence of rib articulations suggest that these represent anterior caudal vertebrae. The recess in the haemal spine appears of proper size to receive the posteriorly directed spine of the "sacral" vertebra. The first caudal vertebra of *Diplocaulus*, as described by Case, also has expanded arches and is the last to bear a transverse process. In consequence, I interpret these atypical vertebrae to be the anterior ones of the caudal series.

The remaining caudal vertebrae show great variation (Fig. 10C) — presumably, primarily regional differentiation. Relatively large, flat vertebrae with large neural and haemal arches probably represent anterior caudals because of their similarity to the anterior caudals of *Diplocaulus*. Occurrence of two specimens with indistinct rib facets suggests that the second caudal may also have borne a short rib. The zygantrum and zygosphene are weakly developed, and the zygapophyses relatively small. In some at least the tips of the haemal arches may have been in contact. In several, the sides of the arches bear shallow, vertical grooves. The posterior caudals are long and slender. Both arches and spines are low, and the vertebrae are nearly quadrangular in cross-section. The zygapophyses are very weak or undeveloped. No specimens with unroofed neural and haemal canals have been recognized, but otherwise they resemble the caudal vertebrae of *Diplocaulus*.

Only a few ribs are known in association with *Diploceraspis* material. These are, of course, double-headed, one head above the other, and fairly straight. In the absence of articulated specimens, an estimate of their length relative to body size is impossible

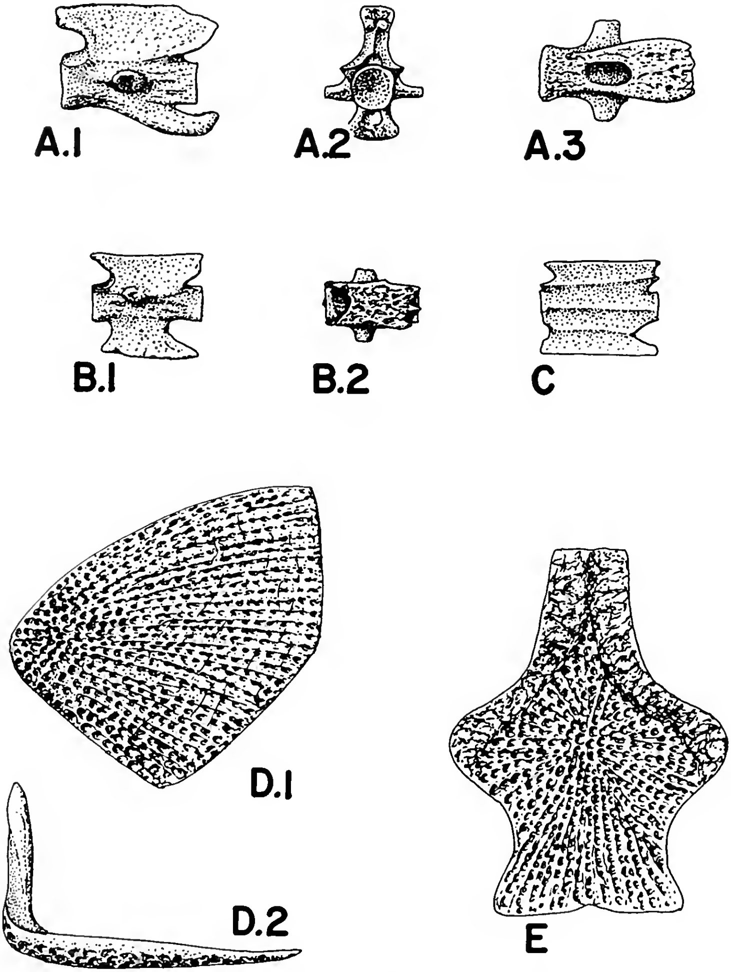

FIG. 10. *Diploceraspis,* caudal vertebrae and pectoral girdle. Approximate enlargement, x 2.3. *A,* First caudal. *A.1,* Lateral view, anterior to left; *A.2,* anterior view; *A.3,* ventral view, anterior to left. *B,* Anterior caudal. *B.1,* Lateral view, anterior to left; *B.2,* ventral view, anterior to right. *C,* Posterior caudal, lateral view, anterior to right. *D,* Right clavicle. *D.1,* Ventral view, anterior up; D.2, anterior view. E, Interclavicle, ventral view.

though one must expect that, like those of *Diplocaulus,* they were long.

I have already described the remarkable similarities in the axial skeleton of *Diploceraspis* and *Diplocaulus.* In the presence of both dia- and parapophyses and in the sculpture of the centra, they stand distinct from the other nectrideans. Unfortunately, the vertebrae of *Batrachiderpeton* are unknown. The vertebrae of *Urocordylus, Scincosaurus, Keraterpeton* and *Diceratosaurus* all possess accessory articulations above and/or below the zygapophyses, but these differ in detail from those of *Diploceraspis.* In all, the ribs are either single-headed or, if double-headed, the capitulum articulates with a facet on the centrum rather than on a long parapophysis. In none do the centra show the complex sculpture of fine lines and pits. A single, suggestive exception occurs in two *Diceratosaurus* vertebrae associated with MCZ 2331. One of these, seemingly an "atlas," shows traces of vermiculate sculpture on the centrum, widespread glenoid cavities, an anteriad extension of the neural arch and a posterior zygosphene. The neural spine is vertical rather than sloping strongly to the rear as

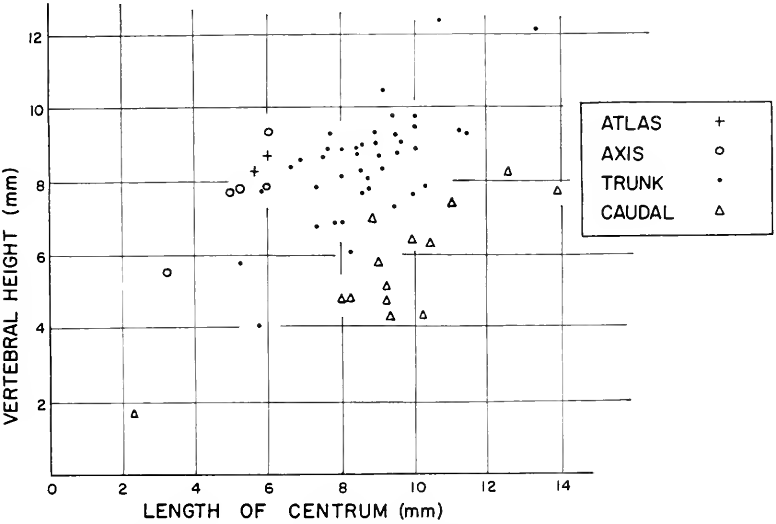

FIG. 11. *Diploceraspis* vertebrae, scatter diagram of length versus height. Length was measured along midline of ventral surface of centrum. Height was measured from the ventral edge of the posterior end of the centrum to the highest point of the neural spine.

in *Diploceraspis.* The second, an "axis," has both posterior and anterior zygantra and a strong, apparently double transverse process. The centrum, unfortunately, is not exposed.

Appendicular Skeleton

Only two appendicular elements, clavicle and interclavicle, can be assigned with certainty to *Diploceraspis* (Fig. 10D, E). Other recognizable bones from the pectoral and pelvic girdles and limbs are rare in the present collection, and none of the better preserved ones belong to *Diploceraspis.* From analogy with *Diplocaulus* one would expect the limbs to be small, weak, and poorly ossified. The absence of identifiable remains provides support — if only by negative evidence — for this presumption.

The clavicle, described by Romer (1952, p. 70), is of typical nectridean form. The ventral plate is triangular to subrectangular in shape and is finely sculptured on its external (ventral) surface. The sculpture consists of medium to large circular or elongated pits on the lateral corner and smaller pits arranged in rows radiating from the lateral corner toward the midline. Individual variation in sculpture pattern is rather large. The ascending process is a slender rod extending directly upward from the lateral angle of the triangle. The sides of the process are striated vertically.

The interclavicle is roughly pentameral. A fairly slender process extends anteriad above the anteromedial edges of the clavicles. This process expands behind the posteromedial edges of the clavicles to form short, broad, lateral processes. Posteriad to these processes the interclavicle is constricted and extends some distance posteriad. The sides of this portion are straight and parallel in some specimens; in others, the posterolateral corners flare laterally. The posterior border is straight. The central and posterior portions of the ventral surface are covered by fine pits, circular anteromedially, radially elongate toward the edges of the bone. The anterior margins and anterior process are striated ventrally to receive the dorsal surface of the clavicles. The shape resembles that of *Diplocaulus.*

Growth and Development

Although available specimens show a wide range of size, their fragmentary character makes precise comparison of growth changes impossible. The small *Diploceraspis conemaughensis* specimen, CM 8544, has well developed horns, apparently much larger than those of *Diplocaulus* in the same size range. This precocious development is reflected in Figure 14 as shown in tabular length; the large *D. burkei,* MCZ 3009, has relatively longer horns than a *Diplocaulus* twice its size, and the tabulars of MCZ 3009 are twice as long as those of *Diplocaulus* of the same size. In both *Diplocaulus* and *Diploceraspis,* growth rates at the posterolateral corners of the skull were far greater than the "normal" nectrideans and accelerated late in development. *Diploceraspis,* however, shows a markedly different growth rate than *Diplocaulus* in spite of the overall similarity; the allometry of horn on skull size is distinct in the two genera.

The direction of horn growth shows a similar difference. The angulation of the horns decreases in *Diploceraspis* with growth, shows negative allometry, and demonstrates acceleration of posteriad growth relative to laterad in late stages. *Diplocaulus* skulls, however, show positive allometry with acceleration of laterad growth in late stages.

Comparative Discussion and Summary

Table 3 summarizes the morphology of *Diploceraspis* as well as comparative features of other nectrideans. *Diplocerapsis* and *Diplocaulus* are close in general form and many details but differ in other details, particularly in the topography and proportions of the "face-snout" region and in the character of jaws and tooth row. The keraterpetontids show unity in skull topography and proportions with the exception of characteristics related to flattening of the skull and enlargement of the horns. *Urocordylus* differs importantly in skull characteristics. Comparison of early growth stages indicates that the divergence is related to developmental rates since an immature *Urocordylus* differs very little in skull form from an immature keraterpetontid.

FUNCTION AND ADAPTATION

General

As already indicated (p. 60), flattening of skull and body and accompanying skeletal modifications are common trends in amphibian evolution. Watson (1951, pp. 53-78) has analyzed the functional significance of these modifications, and presumably his interpretations hold in large part for *Diploceraspis* and *Diplocaulus.* These two nectrideans, however, differ from the others in the presence of horns, in the extreme anteriad shift of the jaw articulation, and in ventral rotation of the occipital surface.

TABLE 3

COMPARATIVE MORPHOLOGY OF KERATERPETONTIDS

CHARACTER	DIPLOCERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	UROCORDYLUS	SCINCOSAURUS
Skull form	flattened, cornuate	flattened, cornuate	slightly flattened, short horns	slightly flattened	slightly flattened, short horns	deep, no horns	slightly flattened, no horns(?)
Snout/Skull proportions	short	short or very short	short	short	short	long	short
Premaxilla	enlarged, contact frontals	enlarged, contact frontals	small, no frontal contact	small, no frontal contact	enlarged, nearly contact frontals	small, no frontal contact	small, no frontal contact
Nasals	absent or fused	absent or fused	large	large	small	large, elongate	large
Lacrimals	fused to maxillae laterad of prefrontals or absent; contact orbit	anteriad of prefontals; do not contact orbit	probably laterad of prefontals; contact orbit	laterad of prefontals; contact orbit	anteriad of prefontals; do not contact orbit	laterad of prefontals; contact orbit	laterad of prefontals, contact orbit
Prefontals	contact nares	do not contact nares	contact nares	contact nares	do not contact nares	contact nares	contact nares
Orbital position	dorsal, moderately separated	dorsal, close	dorsolateral, separated	dorsolateral, separated	dorsolateral, separated	dorsolateral, moderately separated	dorsolateral, separated
Frontals	long, single	long, single	short, paired	short, paired	short, paired	long, single	short, paired
Prefontal-Postfrontal contact	no	no	yes	yes	yes	yes	yes, broad

Postorbital	does not touch orbit	does not touch orbit	contacts orbit	contacts orbit	contacts orbit	very narrow contact with orbit	?
Maxilla	does not touch orbit if dorsal part is prefontal	does not touch orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit	contacts orbit
Jugal	borders mouth	does not border mouth	*ibid.*	*ibid.*	*ibid.*	*ibid.*	*ibid.*
Quadratojugal	no flange; pterygoid contact	flange; no pterygoid contact	no flange;?	no flange;?	possibly flanged;?	no flange;?	no flange
Squamosal	internal flange to quadrate	internal flange to quadrate	internal flange to quadrate	?	internal flange to quadrate	?	?
Length of skull table	long	long	long	long	long	short	long
Width of skull table	very wide	very wide	moderate	moderate	wide	narrow	moderate
Parietals and postparietals	elongated laterally	elongated laterally	narrow	narrow	narrow	very narrow	moderate
Tabular	large, cornuate	large, cornuate	small, cornuate	small, cornuate	moderate, cornuate	small, slightly cornuate	?not cornuate
Otic notch	faces ventrad	faces ventrad	?ventro-posteriad	?	?ventro-posteriad	?	ventro-posteriad
Exoccipital	contacts pterygoid and parasphenoid	contacts pterygoid and parasphenoid	contacts pterygoid and parasphenoid	?	separated from pterygoid and parasphenoid by basisphenoid	?	separated from pterygoid and parasphenoid by basisphenoid

TABLE 3 (*Cont.*)

CHARACTER	DIPLOCERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	UROCORDYLUS	SCINCOSAURUS
Basioccipital	unossified	?unossified	? small	?	small	?	small
Pterygoid articulation	sutured to parasphenoids	sutured to parasphenoids	sutured to parasphenoids	?	movable, to basisphenoid	movable, to basisphenoid	movable, to basisphenoid
Teeth	small, short	small, short	small, short	small, short	small, short	small, short	?
Marginal tooth row	short	short	short	short	short	long	?
Palatal teeth	arch anteriad of the internal nares	arch posteriad of the internal nares	double arch, both anteriad and posteriad of internal nares	?arch anteriad of the internal nares	arch posteriad of the internal nares, shagreen teeth on pterygoid	?	?
Interpterygoid vacuities	very large	very large	small	?	none	?	small
Quadrate	anteriad position	anteriad position	slightly anteriad	slightly anteriad	slightly anteriad	posteriad	slightly anteriad
Epipterygoid	braced against skull roof	braced against skull roof	?	?	?	?	?
Mandible form	short, deep, sides subparallel	short, shallow sides diverge	short, deep, sides subparallel	?	short, deep, sides diverge	long, deep, sides subparallel	?
Retroarticular process	present	absent	?	?	absent	?	?
Coronoid process	well developed	low	well developed	?	low	?	?

Articular facets	double, postero-dorsal as well as posteromedial	posteromedial	?dorsomedial	?	dorsomedial	?	?
Angular	broad lateral exposure	narrow lateral exposure	?	?	narrow lateral exposure	?	?
Splenial	single, not in symphysis, narrow inner flange	double, in symphysis, narrow outer flange	?	?	single, in symphysis, narrow outer flange	?	?
Neural spine form	large, moderately expanded; that of atlas large	large, moderately expanded; none on atlas	large, strongly expanded	?	?	moderate	?
Neural spine "ornamentation"	small, anastamosing pits and ridges	single large pit	small, circular pits	"Corrugated"	?		?
Neural arch "ornamentation"	none	none	none	?	?	distal vertical grooves	?
Accessory articulations	zygantra-zygosphene on neural spine	zygantra-zygosphene on neural spine	?zygantra-zygosphene on spine	?zygantra-zygosphene on neural arch	?	zygantra-zygosphene on neural arch	?none
Transverse processes	thoracic double	thoracic double	?single except possibly double on "axis"	? single	?	single	single

TABLE 3 (*Cont.*)

CHARACTER	DIPLOCERASPIS	DIPLOCAULUS	DICERATOSAURUS	KERATERPETON	BATRACHIDERPETON	UROCORDYLUS	SCINCOSAURUS
Ribs	double headed	double headed	double in anterior, single in posterior thoracic	double headed in anterior thoracic; not known otherwise	?	double headed	double headed
Centra	fine, vermiculate "ornamentation"	fine, vermiculate "ornamentation"	no ornamentation except possibly on "atlas"	no ornamentation	?	no ornamentation	?
Clavicle	ventral plate triangular, sculptured; dorsal rod slender	*ibid.*	*ibid.*	?	more quadrangular	–	?
Interclavicle	pentameral, sculptured	*ibid.*	*ibid.*	?	*ibid.*	–	?

Rather major functional and adaptive differences presumably underlie this morphological divergence even though the overall pattern is similar.

A flattened body in amphibians correlates, apparently without exception, with a fully aquatic, bottom-living habit. Lateral line canals are also a positive index of aquatic life. The limbs typically are small; fish-like movements of trunk and tail provide the primary means of locomotion. The flattening is associated in some, but not all types, with a bottom-feeding habit; it presumably affords greater stability on the substrate and provides concealment on muddy bottoms or in shallow pools. In some amphibians it is associated with another hallmark of aquatic life, large external gills. In *Diplocaulus* and *Diploceraspis* the massive skull with large horns presumably ballasted the animal and held it to the bottom. The detailed structural adaptations of *Diploceraspis* are imposed upon these general trends.

Locomotion

Although the limbs, the scapula, cleithrum, and coracoid from the shoulder girdle, and the entire pelvic girdle are unknown in *Diploceraspis,* their absence implies small size and incomplete ossification. If functional at all the limbs could not have provided very effective or rapid propulsion. Body and tail movements must have furnished the primary locomotive power.

Among recent vertebrates, accessory vertebral articulations typically indicate extreme flexibility of the spine. Although the movement between individual vertebrae is limited, this limitation provides positive control of movement and permits load distribution along a sinusoid curve. Accessory articulations are well developed in the eel-like nectrideans and imply an eel-like swimming motion. In *Diploceraspis* (and *Diplocaulus* as well) the broad flat body would prevent such an activity, but lateral sinuous motions on the substrate with the legs, the ends of the ribs, and perhaps, the horns, acting as holdfasts would be possible. Romer (1945, p. 159) suggested that up-and-down undulation like that of a skate was possible for *Diplocaulus*. As Douthitt (1917, p. 28) pointed out, however, the zygosphene articulations would prevent vertical bending movements as would the horizontal zygapophyses and the articulation between the tips of the haemal arches. Since the horns extend far posteriad of the occipital condyles, vertical movement of the head while on or near the substrate was very limited. Finally the position of the rib heads, one directly above the other, would eliminate vertical movement of the ribs.

On the other hand, the articulation of the ribs with the transverse processes facilitated horizontal movement. The robust ribs may indicate strong intercostal musculature as well as reinforcement of the broad flat trunk. The low vertebral arches imply the shallowness of the long median muscles of the back. The only definite indications of muscle scars on the vertebrae are sharp ridges on the anterior and posterior borders of the transverse processes, a suggestion of strong intertransversarii. Presumably the other segmental muscles of the vertebrae were weak, or, at best, moderately developed.

The low occiput, neural arches, and spines provide very poor angles of insertion for the occipital musculature. The condyles, however, indicate some vertical movement of the head, counterbalanced perhaps by the weight of the horns behind the condyles The sharp ridge bounding the laterodorsal edges of the occiput probably reflects the insertion of the surficial cervical musculature. The deeper occipital musculature may have inserted broadly over the surface of opisthotic and on the occipital flange of the postparietal. The lateral bending force of the occipital musculature must have been rather great but since the head could not move laterally on the "atlas," the movement must have been taken up in the trunk.

The caudal vertebrae are strongly compressed in the vertical plane and lack ribs. The tail in consequence was vertically flattened and, by analogy with *Diplocaulus*, very long. The accessory neural spine and haemal arch articulations of the anterior caudals restricted vertical movement; the horizontal zygapophyses would allow extreme lateral bending. The tail, like the trunk, must have moved principally in a sinuous lateral pattern. The slenderness of the tail suggests that it was not the principal driver in locomotion but that it provided a slow glide along the bottom as the animal hunted or fed.

To summarize, the intervertebral articulations and the shallowness of the median epaxial musculature indicates very slight vertical movement though the head could be tilted on the "atlas." The stout transverse processes, the heavy ribs, the position of the rib heads, the intervertebral articulations, and the inferred character of the lateral epaxial and intercostal musculature imply vigorous lateral bending. The limbs, presumably short and weak, the rib ends, and the horns could have served as holdfasts in a sinuous motion along the lake floor. The vertically flattened tail probably supplemented this mode of locomotion and provided a weak but adequate force for a slow glide over the substrate. The active tail may have also distracted predators from the vulnerable trunk.

Feeding

The generalized character of the amphibian teeth and jaws as well as the lack of detail on feeding adaptations in Recent forms hinders interpretation of food and feeding habits in fossils. The small, short teeth suggest that the prey was rather small and/or inactive. The sharp, unbroken tips of these teeth argue against food species with heavy shells or carapaces, but the strong basal support of the teeth in the dentary, maxilla, and premaxilla and the bracing of the palatine against the prefrontal suggest that some crushing action was necessary. The relatively broad, short jaws imply a scooping action rather than a direct strike—this also accords with the general clumsy body form and awkward locomotion. The row of palatal teeth just inside and parallel to the marginal row probably assisted with seizure and crushing of small prey. The absence of teeth from the inner areas of the palate again suggests small or inactive prey, for there was apparently no need to hold objects once they were inside the marginal tooth row.

Jaw structure, mechanics, and musculature accord with Watson's generalizations (1951, pp. 53-78) on the flattened amphibians. With the lower border of the mandible resting on the substrate, the skull was tilted up and back to open the mouth. To permit the motion, the jaw articulation was anterior of the occipital condyles. Because the mandible is essentially fixed in position, the depressor mandibulae muscles would pull the occipital border of the skull down and forward and thus assist the occipital musculature in tilting the skull. The considerable development of the retroarticular processes implies that this action was of considerable importance. Their ventrolateral direction implies that the depressors originated from the lateroposterior bones of the otic border. The horns, behind the fulcrum of the occipital condyles, served to counterweight the skull and reduce the muscular effort necessary to tilt it. Since the undersurface of the horns slopes upward behind the quadratojugals, they could move down through perhaps a 12° arc without being forced into the substrate. With the skull tilted back so that the undersurface of the horns lay on the substrate, the mouth would open through a distance slightly greater than the depth of the lower jaw, and produce a gape of four or five millimeters in a large *Diploceraspis*.

The depressor mandibulae muscles, in tilting the skull, placed major stresses on the mandible. The concave arch of the ventral borders of the mandibular rami, the thick ventral portions of the angular and splenial and the complex suture between these elements may have served as adaptations to these stresses.

The jaws were closed, of course, by action of the mandibular adductors which in *Diploceraspis* served to tilt the skull down and forward. Because of the shallowness of the skull, these muscles were limited in length or forced into an unfavorable angle of insertion. The extension of the subtemporal fossae far posteriad of the quadrate demonstrates that a large mass, perhaps the greater part, of the adductor system took origin in this area. The quadrate is braced strongly laterodorsally by the quadratojugal, and posterodorsally by the internal flanges of the quadratojugal and squamosal. These supports indicate a strong postero- and laterodorsal pull of adductors, but the absence of direct dorsal bracing implies that few muscle fibers ran directly upward to the undersurface of the jugal. The quadrate is supported mediodorsally by the epipterygoid against the skull roof, medially by the parasphenoid and medioposteriorly by the exoccipitals. This medial bracing provided support against stresses induced by the pterygoid adductors. The lateral facing facet of the quadrate trochlear condyle also indicates a strong median pull.

All of these muscles must have had rather acute angles of insertion on the mandible, particularly those attached to the somewhat elevated coronoid processes. The rugosity near the posterior end of the floor of the adductor fossae suggests that a portion of the posterior adductors inserted by a tendon in this region; the tendon presumably passed over a pulley-like groove on the posterior margin of the fossa. The shallowness and delicacy of the skull forward of the subtemporal fenestra and the lack of a pulley structure along the anterior border of the fenestra imply that the anterior adductors were weak or absent. The mechanical system of the *Diploceraspis* jaw appears to be of the type described by Olson (1961) as "Kinetic Inertial" although the muscle pattern is quite different from other amphibians with this type of jaw action. Adduction of the upper jaw downward onto the lower was rapid, but took its power mostly from the inertia of the moving skull.

The small gape of the mouth, the small teeth, and the marginal position of the palatal teeth coincide in the implication of small prey species. The sharp tips on the teeth argue against a herbivorous habit and suggest rather the necessity of grasping and holding some small active creature. The indication of rapid jaw action again suggests an elusive prey. The lack of great power in jaw musculature and the delicacy of the teeth would have prevented crushing of heavily armored forms, but the jaws and teeth are sufficiently braced to break up thin valves or carapaces.

RESPIRATION

The nares form the only direct evidence of respiratory structure in *Diploceraspis,* but the body and head form, the probable environment, and the locomotor adaptations suggest respiratory requirements and limit structural possibilities. So far as known, *Diploceraspis* inhabited shallow, warm lakes and ponds (see PALEOECOLOGY). The low oxygen concentration in such environments requires of modern aquatic amphibians: 1) intermittent air breathing, 2) large external gills, or 3) some other specialized mechanism of respiration. In cool, swift water even large forms such as *Cryptobranchus* and *Megalobatrachus* obtain adequate respiration through the buccopharyngeal membranes and the highly vascularized skin (Noble, 1931, p. 468).

The much flattened body of *Diploceraspis* provided a large surface area for gas exchange. Some respiration through the skin seems reasonably probable—the elaborate ornamentation of skull, shoulder girdle, and neural spines may reflect, in some fashion, vascularization of the skin. In view of the large, heavy skull and weak locomotion of *Diploceraspis,* repeated trips to the surface for air seem improbable. In very shallow water, tilting the head up and back would bring the end of the snout to the surface; the position of the nares on the anterior surface of the snout is consistent with such action; but this would only work in an inch or two of water.

Several authors, e.g. Williston (1909) and Douthitt (1917, pp. 31-32), suggested that *Diplocaulus* had external gills and that these were positioned beneath the horns. The same suggestion would presumably hold for *Diploceraspis.* Two separate but related problems enter here: whether external gills were present and what their position might have been. No direct evidence for a branchial system occurs in either *Diplocaulus* or *Diploceraspis;* the gill bars, if present, must have been cartilaginous. The Williston-Douthitt hypothesis then rests on the probable need of these forms for external gills and the presence of such gills in some aquatic amphibians. If present, the gills must have been directed up and out above the horns or down and beneath them. The upper end of the shoulder girdle probably lay very close to the posterior margin of the skull and, if, as is highly probable, the lateral tips of the opisthotic marked the width of the "neck," there would be no passageway for external gills above the horns.

The shift of the jaw articulation anteriad and of the otic area ventroanteriad suggests that the pharyngeal region underlay the posterior of the skull. This constitutes a further argument against a dorsal position for the external gills and supports the Williston-Douthitt view. Douthitt recognized that gills in this position would be abraided against the bottom and pointed out that the ventral flange of the *Diplocaulus* quadratojugal formed a protective "pocket." *Diploceraspis* lacks the flange and the pocket; in either form, as the head tilted back to open the mouth, the horns would have forced the gills into the bottom sediment. The arrangement appears quite inefficient if functional at all, and I reject as improbable the suggestion that *Diploceraspis* possessed external gills.

Again, the anteriad location of the quadrate, and ventroanteriad position of the otic notch suggest that the pharynx lay completely beneath the skull rather than largely posteriad to it. The laterodorsal portions of hyobranchial skeleton, so far as developed, should thus have been beneath the otic notches—would, in fact, have supported the ventral wall of the pharynx beneath these notches. The great size and wide extension of the otic notches beneath the horns thus indicate the presence of a pair of very extensive though shallow pharyngobranchial pouches. The precise structure of these pouches is indeterminable. In some Recent larval frogs (Noble, 1931, p. 160) an "opercular" flap covers the branchial area so that the gills on the arches become "internal." In the urodeles the gills are lost prior to the fusion of the operculum to the throat, and the gills are never "internal." In the large form *Cryptobranchus*, a spiracular opening remains after fusion of the operculum; this serves for escape of water brought in during the bucco-pharyngeal respiration.

The pharyngeal pouches of *Diplocerasips* (and *Diplocaulus*) may, therefore, have housed gills (either primarily or secondarily internal) or consisted simply of highly vascularized tissue. The location of the vagus foramina, directed laterally on the ventral surface of the exoccipitals, may reflect the peculiar position of the branchial arches. One cannot determine the nature of the respiratory movements with any probability, but tilting of the head to open the mouth would compress the pharyngeal pouches and expel water. As the head tilted forward to close the mouth the pouches would expand and draw in water through the nares. The pharyngeal pouches, with or without gills, would greatly increase the respiratory surface, permit survival in low oxygen environments, and protect the respiratory membranes from damage and clogging by the sediment on which the animal moved.

DEFENSE

In many modern amphibians behavior supplements or largely supplants morphological features as protection against predators. In others, poison glands in the skin make the animal unpalatable or even dangerous. The morphologic analysis of defensive mechanisms in fossil forms may miss entirely if such types of protection operated. In *Diploceraspis* certain features of body form appear to be protective, but I cannot claim that this was their primary function or that they were the primary means of defense.

The body shape and habitus of *Diploceraspis* probably concealed the animal against the bottom; one might expect associated adaptations in skin pigment and texture. Since the body was quite flat (a large *Diploceraspis* probably had a trunk-head length of 25 cm., a trunk width of 5 to 7 cm. and a thickness of 2 cm.), attacks would of necessity be made from above, and few potential predators had sufficient mouth gape to pick the animal off the bottom. The head was well protected against dorsal attack by the heavy dermal bone; the neural spines, transverse processes and heavy ribs provided some protection for the trunk. The tail may have distracted enemies from the trunk though the only evidence for this is the relative paucity of caudal vertebrae in the collection.

If, as suggested, the lateral body musculature was powerful, the horns may have served as an effective—even deadly—deterrent. Vigorous contraction of the lateral musculature would have pulled the horns to or even well over the trunk. The pointed and serrate horn tips when driven into the head or gill slits of a shark might well have discouraged further attack. The horns would also prevent a large predator, amphibian or fish, from swallowing even a small *Diplocerasips* whole.

SENSORY ADAPTATIONS

Sensory adaptations in *Diploceraspis* are reasonably obvious. The orbits as in most flattened, bottom animals opened directly upward, and the eyes must have projected above the dorsal surface. Drawn downward into the skull for protection, they probably bulged through the interpterygoid vacuities into the roof of the mouth. The nares show no special adaptation for olfactory function. The otic capsule is poorly ossified and the stapes is unknown. If the "otic notches" housed pharyngeal pouches (p. 88) and the depressor mandibulae originated on the lateroposterior edges of the notches (p. 85), no room would be left for a tympanic membrane and the "spiracular" opening may have been closed or reduced to a narrow slit. Since any external ear structure would have been pressed against the bottom muds, the need for or value of such a structure is doubtful, and its absence expected *a priori.*

If the otic system was degenerate, the lateral line system was clearly functional. In some Recent newts with optic and olfactory nerves cut, the lateral line organs function as direction and disstance perceptors during feeding (Noble, 1931, p. 417). The strong development of the anterior commissure on the premaxillae, the supraorbital canals over the snout, the infraorbital canals across the maxillae and jugals, and the canals of the mandible suggest a similar function in *Diplocerasрsis*. Since the eyes, from their dorsal position, could provide little information on the substrate area ahead of the snout, the lateral line organs may have provided the chief sensory clues in feeding.

The Horn Problem

Much intellectual effort including my own has been expended on interpretation of the horns of *Diplocaulus* and *Diploceraspis.* Williston (1909) and Douthitt (1917, p. 32) suggested that they functioned in *Diplocaulus* to protect the external gills. Douthitt further argued that they counterbalanced the large head but concluded despairingly that head size was itself inadaptive and possibly a result of metabolic derangement, as postulated by Case (1911, p. 90). Olson (1951) suggested functions in locomotion and protection.

This peculiar modification of skull presents two separate though related problems. To begin, the horns are *not* excrescences on the posterolateral corners of the skull but are rather extensions of the posterotemporal region. The bones of this region, the parietals, postparietals, tabulars and squamosals accelerated in growth around and above the otic notch so that the notch was enlarged and rolled onto the ventral surface. As growth continued the extreme posterolateral corner of the temporal region accelerated relative to the otic-supraotic region and the tabular portion of "horn" developed. The horn thus comprises three regions: the proximal infratemporal, the otic, and the distal tabular. I have already ascribed respiratory adaptations to the modified otic area so that in growth at least the horns served initially for support and protection of the pharyngeal pouches. The extension of the infratemporal region (below the squamosal) provided added space for the temporal musculature. The tabular portion of the horn surely served several functions: to counterweight the head, to aid in crawling, to defend the animal against predators, and to ballast and stabilize it on the bottom. The rather marked increase in horn development at the 80 mm. skull length stage in *Diplocaulus* implies that one or all of these functions became critical at about this size and may indicate the time of shift to total bottom living habit. The tabular enlarged at an earlier stage in *Diploceraspis*, but the acceleration of posteriad growth of the horns may have resulted from a comparable functional shift.

The ultimate direction in horn development and function was probably given by three factors:

1. The extreme flattening of the body and skull which reduced the power of cervical and temporal musculature.
2. The necessity of tilting the head to open the mouth.
3. The expansion of the pharyngeal region and the consequent enlargement of the posterior parts of the skull, above the pharynx.

The resultant large, shallow, skull required post-occipital counterweights; the other horn functions are undoubtedly significant but not necessary for existence.[3]

PRESERVATION AND PALEOECOLOGY

Occurrence

All *Diploceraspis* material has been found in pond or lake deposits defined by massive or laminated gray limestones, clayey limestones, marlstones, and limy shales. Several localities, e.g. 6-55, are lime-pebble or lime-cobble conglomerates. Skull fragments, scales, and teeth of paleoniscids, lungfish, and crossopterygians are typically abundant in the association. Pleuracanthid teeth and spines are also common. Vertebrae of *Lysorophus* and

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[3] Primary adaptive significance is not necessarily of initial phylogenetic significance but may have developed late in the evolutionary history. The presence of tabular horns may in fact have been *sine qua non* for the initiation of the respiratory modifications and the adoption of this particular mode of life. The animal was a functional whole and dissection of different adaptations obscures the totality of a small amphibian highly adapted to the bottom environment of a shallow lake.

Megamolgophis occur at some localities. *Eryops* and other labyrinthodont amphibian material appear at a few places. *Edaphosaurus* is a fairly common associate—at locality 7-55 a partial, articulated skeleton occurred in the same stratum as the abundant *Diploceraspis* specimens. Only one other reptile has been found in a *Diploceraspis* locality (Romer, 1952, p. 105), and even a highly fossiliferous reptile locality like 24-55 has yielded no trace of *Diploceraspis.* Coprolites are common at some localities; these have a characteristic spiral twist, contain bone fragments, and are presumably pleuracanthid feces.

Diploceraspis skulls are typically broken along a plane of structural weakness near the anterior edge of the parietals, and the horns are commonly separated. Even isolated skull elements from anteriad of the break are extraordinarily rare. The halves of the mandible are invariably separated and commonly show additional damage. In spite of breakage, however, the skull fragments preserve delicate structures, including portions of the palate and the horn tips and show no indication of violent rolling or abrasion. The vertebrae are well preserved including the long slender transverse processes, but caudal vertebrae are disproportionately rare. Ribs are extremely rare; clavicles and interclavicles moderately abundant; and pelvic elements and limb bones are not definitely known.

The other vertebrate material occurring with *Diploceraspis* shows similar preservation—entirely disarticulated but with no evidence of abrasion. A wide variety of sizes and shapes occurs on the same bedding surface with no clear evidence of sorting. In some cases, individual beds consist predominately of bone; the internal cavities of most *Diploceraspis* skulls are filled with fish scales and teeth.

Environment of Preservation

The vertebrate associations, fish and aquatic amphibians, and the lithology indicate burial in lakes and ponds. The clastic lime beds appear to be desiccation conglomerates. No clear evidence exists for strong wave or current action; the lack of abrasion and the preservation of delicate structures indicate otherwise. Warm temperatures and abundant algae presumably account for the deposition of calcium carbonate. Burrowing organisms—except possibly for the lysorophids—are unknown, but the irregular distribution of the fossils, across as well as on the depositional surfaces, implies some reworking.

If wave or current action was not responsible for disarticulation and fragmentation of the *Diploceraspis*, then predators and/or scavengers must have broken and dragged the bodies apart. Horns are obviously inedible and dangerous to an animal that swallowed them. The vertebrae are equally inedible and the shallowness of the back musculature and the prominent neural and transverse spines would make the trunk vertebrae unattractive to all but small scavengers. The tail, however, somewhat less "bony" and well muscled, would probably provide a meal for a moderate sized shark or even an *Eryops*. The lateral trunk area, the limbs, and the face would be equally appetizing. In all, the preservation suggests scavenging or predation by a form capable of breaking and swallowing the small bones, and sufficiently small to reject vertebrae and horns. The pleuracanthid sharks are obvious candidates; *Diploceraspis* bone fragments occur in what appear to be pleuracanthid coprolites. Smaller scavengers cleaned the flesh from vertebrae and skull. The filling of scales in skull cavities demonstrates that the flesh had been removed before burial.

Most *Diploceraspis* localities produce only a few specimens. These presumably represent the typical environments of life and burial: sedimentation rather rapid, population sparse to dense, mortality low to moderate, and environment of preservation unfavorable. A few localities, the bone beds, present special problems. The abundance of fossils here implies action by one or all of four factors: slow sedimentation, dense population, catastrophic mortality, and a favorable environment for preservation. Most of these bone concentrations occur at the transition from limestone to laminated limy shale. The transition itself implies changes in rate of sedimentation, kind of sedimentation, and/or in pH. Any one of these changes might have induced temporary, slow sedimentation or a population increase or catastrophic mortality or a favorable environment of preservation. The data at hand do not provide a unique solution.

Life Environment

The evidence cited above indicates that the present occurrence of *Diploceraspis* corresponds with the life environment. Although burrowing organisms may have mixed the vertebrates, it seems likely that the faunal associations represent a biocoenosis. The physical environment then was lacustrine and warm. The association of a swamp-lake border herbivore, *Edaphosaurus*, suggests shallow water, but the presence of sharks and fish several feet in length demonstrates depths of several feet, at least during high water. The lysorophids and lungfish from the Texas Permian occur in seasonal ponds with evidence of aestivation; their presence here suggests seasonally stagnate, warm and turbid environments.

Diploceraspis is not known from river channel deposits, from floodplain claystones nor from non-carbonate lacustrine shales and siltstones. These lithologies have been searched with some determination but little success: a small reptile skeleton, a *Megamolgophis* vertebra, several *Edaphosaurus* fragments, an eryopsid intercentrum, and perhaps a dozen pleuracanthid teeth. The absence of *Diploceraspis* might well be an accident since the total collection is so small and these lithologies are extremely difficult to search in road cut outcrops. The implication remains, however, that *Diploceraspis* was largely limited to marly lakes and ponds, although one can only speculate on the limiting factors.

Probable predators include the pleuracanthid sharks, *Eryops*, crossopterygians, and for small individuals, *Megamolgophis* and some of the paleoniscids. Selective preservation limits knowledge of potential food species. Ostracods, small gastropods, *Spirorbis*, and estherids are locally abundant and would be "bite-size" for *Diploceraspis*. Since the accumulation of specimens in the *Diploceraspis* bone beds may represent a number of years mortality—or a few minutes—estimates of population density are meaningless. The rarity of small individuals, even fragments, implies low mortality rates after the larval period, but differential preservation may have altered relative abundance significantly.

PHYLOGENY AND EVOLUTIONARY PATTERN

Introduction

The lack of information on function and adaptation among keraterpetontids as well as the incomplete record hinders interpretation of phylogeny and evolution. Small scale similarities and differences in skulls and vertebrae may represent stable characters evolved early in the radiation of the group and thus may serve to unite genera in phyletic lines and to distinguish between parallel lineages. Or they may represent adaptive parallels and divergences developed late in the evolutionary history of the various lineages.

The time sequence is also somewhat troublesome. *Batrachiderpeton* occurs near the base of the Westphalian series; *Keraterpeton* in slightly higher beds, and *Diceratosaurus* at the top of the series. *Diplocaulus* appears in lower Stephanian rocks; *Diploceraspis* near the middle of the Stephanian series. If both long-horned forms derived from *Diceratosaurus*, the transformation of skull occurred in a remarkably short period of time. If they evolved from *Batrachiderpeton* or a contemporary, they left no record for the remainder of the Westphalian.

RELATIONSHIP OF *Diploceraspis burkei* AND *D. conemaughensis*

Romer (1952, p. 73), comparing very limited suites of the Conemaugh and Dunkard *Diploceraspis*, concluded that they probably represented distinct species and named them, respectively, *D. conemaughensis* and *D. burkei.* He stated that *D. conemaughensis* differed from *D. burkei* "by smaller size, somewhat lesser 'horn' attenuation, and a lesser degree of curvature and spinesence at the 'horn' tip." He also suggested that the punctate sculpture was finer. No additional *D. conemaughensis* have been found, but the extensive suite of *D. burkei* specimens makes further comparison desirable.

All *D. conemaughensis* specimens are smaller than the largest *D. burkei;* one is smaller than any *D. burkei* yet collected. With the exception of this very small individual, however, the *D. conemaughensis* lie within the size range of *D. burkei.* Because of the lack of a definite adult stage and the small number in the *D. conemaughensis* sample, one cannot now conclude that *D. conemaughensis* averaged smaller in size.

The degree of horn attenuation in *Diploceraspis burkei* increases with total size and also varies considerably among individuals of similar size. The apparent stubbiness of the horn in *D. conemaughensis,* therefore, reflects the size of specimens rather than implying specific difference. Curvature and spinescence of the horn tips vary considerably between individuals of *D. burkei* and may also increase with size. The pitting of external bone is also in the *D. burkei* size range. These characters cannot serve to define *D. conemaughensis.*

The apparent size difference may be real. Certainly, the difference in age, mid-Stephanian against very late Stephanian-early Autunian would imply the existence of morphologically distinct groups. Consequently, I believe it best to retain the name of *D. conemaughensis* with the recognition that additional collecting may show it to be a synonym of *D. burkei.*

Romer pointed out that *D. conemaughensis* indicates precocious development of the horns in this lineage. If the *D. conemaughensis* specimens represent a population of relatively small individuals, the other known differences represent allometric development in the larger individuals of *D. burkei*. By this token, *D. conemaughensis* represents the ancestral population for *D. burkei* or is so close to it as to make no difference.

RELATIONSHIP OF *Diploceraspis* AND *Diplocaulus*

Romer (1952, pp. 67-72) emphasized that *Diploceraspis* differed from *Diplocaulus* in spite of their superficial similarity and argued that they represented distinct though parallel evolutionary lines. Although the current study demonstrates additional similarities, it also shows marked dissimilarities between the two genera. In general, the similarities (other than the basic nectridean pattern) concern flattening of the skull and body and development of horns. These include:

1. Dorsal position of orbits.
2. Loss of prefrontal-postfrontal contact.
3. Separation of maxilla from border of orbit.
4. Lateral expansion of squamosal, tabular, parietal and postparietal.
5. Ventral position of otic notch.
6. Loss of basisphenoid and basioccipital.
7. Development of large interpterygoid vacuities.
8. Sutural junctions of pterygoid to exoccipital and parasphenoid and of latter to exoccipital.
9. Anterior position of quadrate.
10. Brace of pterygoid against parietal by epipterygoid.
11. Presence of long, double, transverse processes on vertebrae.

Most of these characteristics developed in other amphibian evolutionary lineages with flattening of the skull; they indicate little about phylogeny.

The reduction (or fusion) of the nasals, the fusion of the frontals and the shift of the postorbital away from the orbital border in *Diploceraspis* and *Diplocaulus* may also relate to change in skull shape though the adaptive significance is not apparent. The vermiculate pattern on the centra similarly lacks apparent functional importance. These three characteristics, therefore, are the only "non-adaptive" or "conservative" characteristics that cannot be found in the other keraterpetontids.

The apparent adaptive differences between the two genera lie primarily in these characteristics of the jaws and teeth in *Diploceraspis:*

1. The presence of the jugal on the border of the mouth.

2. The absence of a ventral flange on the quadratojugal.
3. The arch of palatal teeth anteriad of the internal nares.
4. The relatively greater size of the teeth.
5. The greater depth of the mandible and the presence of a coronoid process.
6. The presence of a retroarticular process.
7. The dorsal direction of the articular facets.
8. The wide lateral exposure of the angular.
9. The single splenial with wide lateral and narrow medial flanges.

The differences in the snout, i.e. the position of the lacrimals laterad of the prefrontals and nasal contact of the prefrontals in *Diploceraspis*, lack apparent adaptive meaning as do the large neural spine on the "atlas," the fine pitting on the neural spines, the contact of the quadratojugal with the pterygoid, and the exclusion of the squamosal from the otic notch. These at least counterbalance the "nonadaptive" similarities cited; since they occur in spite of overall parallelism in adaptation, they probably have greater significance.

Finally, the development of the horns apparently differs radically in *Diploceraspis* and *Diplocaulus*. As described in a preceding section, the horn of *Diploceraspis* shows a strong laterad growth gradient in early development succeeded by a strong posteriad gradient; horn development in *Diplocaulus* begins with posteriad extension and concludes with laterad.

I conclude from this analysis that the two "long-horned" nectrideans evolved their horns in parallel from a common "short-horned" or hornless ancestor. The great similarity of the two implies common ancestry; the difference in details of skull and vertebrae and in the form of teeth and jaws indicates a period of separate evolution prior to their appearance. The difference in development of horns suggests that the two lineages separated prior to the evolution of elongate horns.

Phylogeny of the Keraterpetontids

The keraterpetontids (summary in Table 3), taken in the broad sense, comprise three rather distinct morphologic groups. The oldest, and in many ways the most primitive group, includes *Batrachiderpeton*. This form, in spite of the relatively large horns, shows primitive characters in palate and basicranium. No interpterygoid vacuities are present; the pterygoid articulation with the basicranium is movable; the basisphenoid and basipterygoid are well ossified; and the exoccipital lacks pterygoid and parasphenoid contacts. The jaw articulations lie in line with the occipital condyles.

The group also includes *Scincosaurus*. Its morphology and relationships are not well known, but it, alone among the keraterpetontids, appears to lack horns. As in *Batrachiderpeton*, the

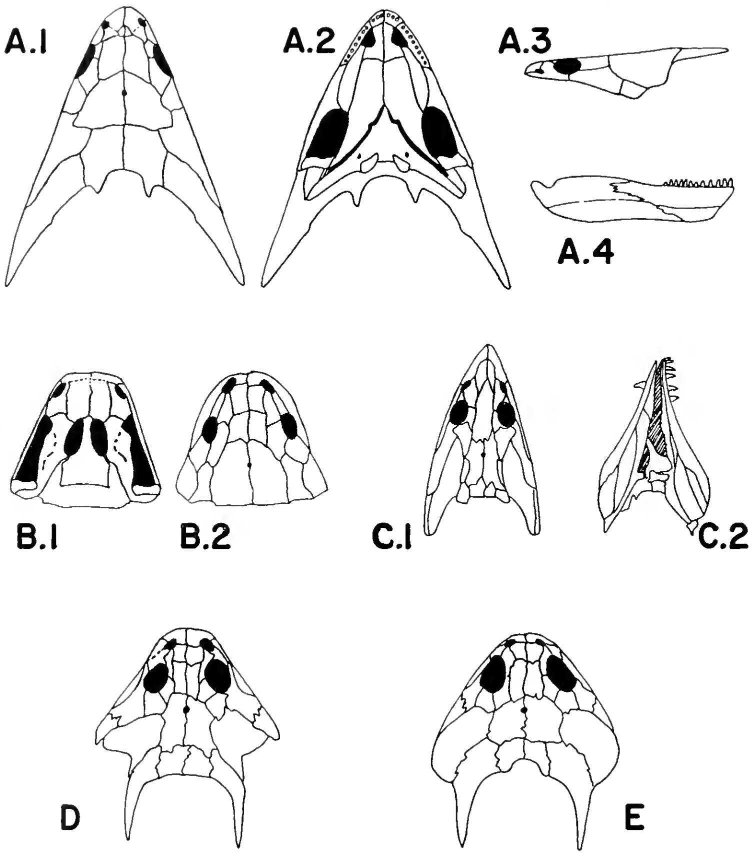

FIG. 12. The nectridean skull. *A, Batrachiderpeton*, after Watson, 1913. *A.1*, Dorsal reconstruction, approximately x 0.5. *A.2*, Palatal reconstruction, approximately x 0.5. *A.3*, Lateral view, approximately x 0.4. *A.4*, Mandible, approximately x 0.8. *B, Scincosaurus*, approximately x 2.4, after Steen, 1938. *B.1*, Palatal reconstruction; *B.2*, dorsal reconstruction. *C, Urocordylus*, approximately x 0.45, after Steen, 1938. *C.1*, Dorsal reconstruction; *C.2*, ventral view. *D. Keraterpeton*, dorsal reconstruction, approximately x 0.8, after Steen, 1938. *E, Diceratosaurus*, AMNH 6856, dorsal view, approximately x 0.8.

basisphenoid and basipterygoid are well ossified; the exoccipital is limited to the posterior border of the skull, and the pterygoid has a movable contact with the basicranium. Small interpterygoid vacuities are present, however, and the jaw articulations lie slightly ahead of the condyles.

Keraterpeton and *Diceratosaurus* form a second group marked by short horns, a reduced basicranium (basisphenoid and basioccipital), sutural junctures between pterygoid, parasphenoid, and exoccipital, and moderately large interpterygoid vacuities. The

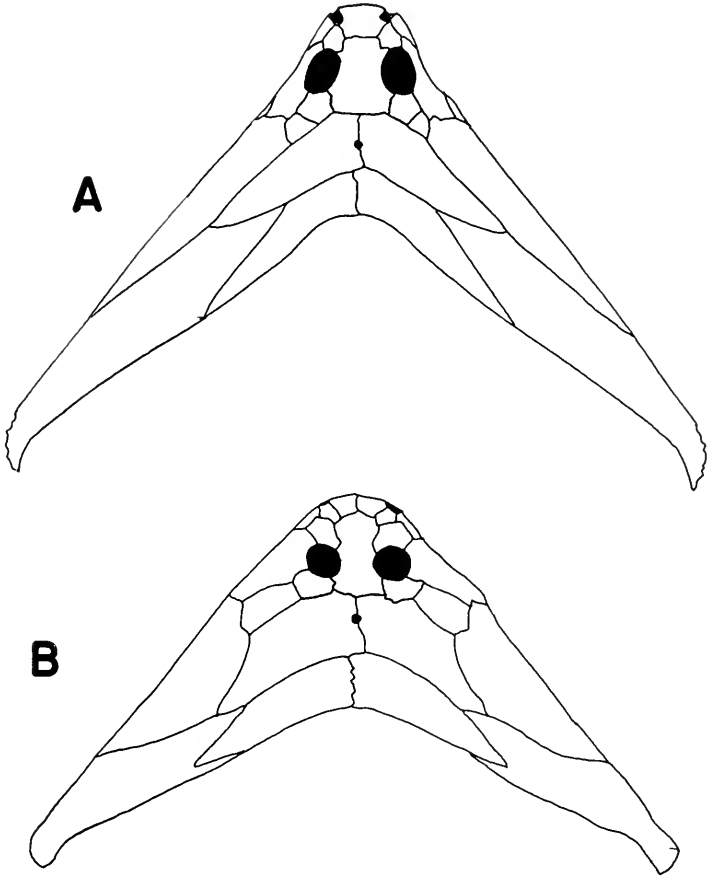

Fig. 13. The nectridean skull. *A, Diploceraspis,* dorsal reconstruction, approximately x 0.5. *B, Diplocaulus,* dorsal view, Chicago Natural History Museum CNHM-UC 636, approximately x 0.25, after Olson, 1951.

jaw articulation is some distance in front of the condyles. They differ significantly only in ornamentation of the neural spines and in excavation of the posterior border of the postparietals near the median line in *Diceratosaurus*.

Diplocaulus and *Diploceraspis* make up a third group. They differ from those in the second by extreme development of the horns, by a further anteriad shift of the articulars, by the extreme flattening of the skull, and by the great size of interpterygoid vacuities. The differences between the two genera were discussed in the preceding section.

These morphologic grades are not necessarily evolutionary or taxonomic units. The evidence is against the unity of the third group, and the phyletic lineages probably crosscut all groups. *Scincosaurus* occupies an isolated position. Though it might have been derived from *Batrachiderpeton* by reversal of the trend in horn evolution, the only positive evidence is to the contrary. The arrangement of snout elements in *Scincosaurus,* i.e., the lateral position of the lacrimal and its contact with the orbit, represents the primitive nectridean condition. The arrangement in *Batrachiderpeton* of the lacrimal anteriad of the prefrontal and excluded from the orbit occurs only in *Diplocaulus* among the other nectrideans. *Scincosaurus* retains the primitive basicranial-palatal characteristics lost in the *Keraterpeton* group and so cannot have been derived from there. It is too late in time to be the ancestor of *Keraterpeton,* although it may represent a conservative lineage retaining some of the characters of that ancestor.

Batrachiderpeton, in palate and basicranium, would form an ideal ancestor for the remaining keraterpetontids. Although the horns are slightly larger and diverge more than those of *Keraterpeton* and *Diceratosaurus,* this would not seem to disqualify them as ancestors. The arrangement of bones in the snout is troublesome, however. Evolution would, necessarily, have had to reverse the modified (?specialized) position of the lacrimal in *Batrachiderpeton.* On the other hand, this character connects *Batrachiderpeton* to *Diplocaulus.* The two also resemble each other and differ from the *Keraterpeton* group and *Diploceraspis* in the lack of a coronoid process on the mandible and in the arch of the vomerine teeth posteriad of the internal nares. Watson suggested (1913) that *Diplocaulus* evolved from *Batrachiderpeton,* and I see nothing in the current comparisons to contradict his conclusion.

Keraterpeton and *Diceratosaurus* are nearly contemporaneous in middle and late Westphalian time. Their differences, so far as known, are comparable to those in closely related contemporaneous genera (and therefore slightly divergent lineages) or to successive genera in a single lineage. No decision seems possible on present evidence. Their ancestry must be in a population similar to the early Westphalian *Batrachiderpeton* but distinguished

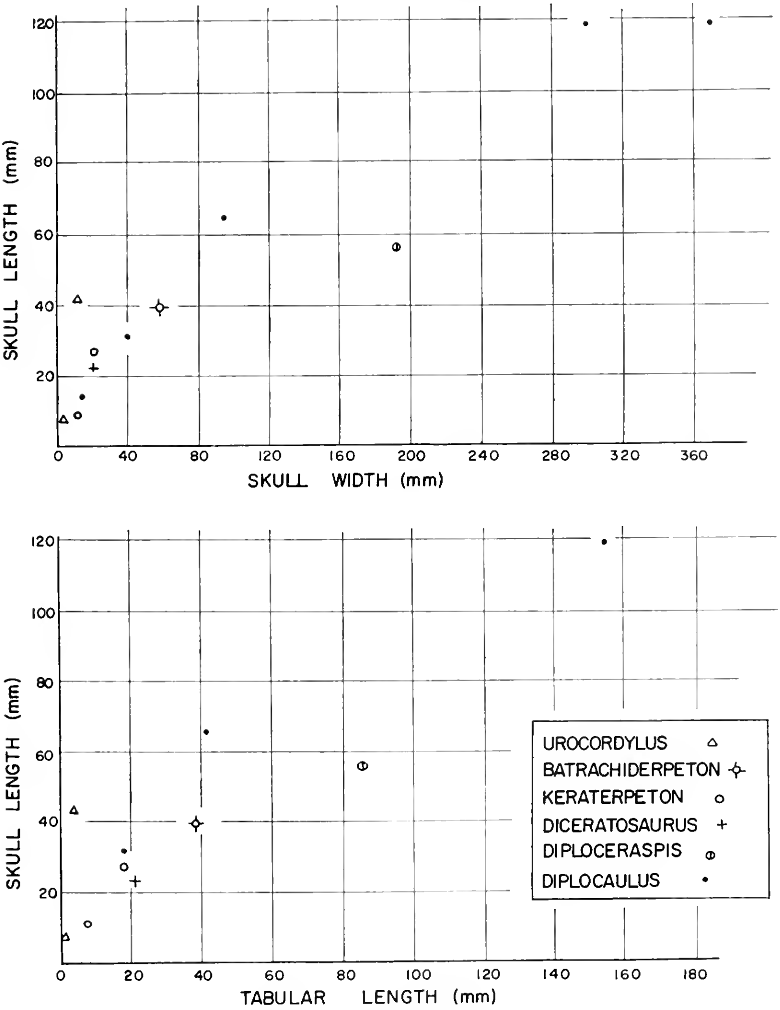

Fig. 14. Nectridean skull proportions. Upper graph shows skull length plotted against skull width; lower graph shows skull length against tabular length. See Table 2 for definition of measurements.

by retention of the primitive position of the lacrimal.

Diploceraspis, as demonstrated above, parallels *Diplocaulus* rather than lying in or near its lineage. As *Diplocaulus* and *Batrachiderpeton* are united by character of snout, supplemented by similarities in jaw and palatal tooth row, so *Diploceraspis* and *Diceratosaurus* are also united. They share the primitive lateral position of the lacrimal. The palatal tooth row of *Diceratosaurus* is double, but the principal series, like that of *Diploceraspis*, curves anteriad of the internal nares. The two have similar high coronoid processes. Finally, the sculpture of the neural spines is very similar. I concur then with Romer (1952, pp. 71-72) that *Diploceraspis* evolved from a *Diceratosaurus* population.

Figure 15 summarizes the phyletic scheme just discussed. As reconstructed, it includes eight distinct morphologic-phyletic units (three lineages and four grades of morphologic specialization) only five of which are known from fossils. Only one of these units comprises as many as two genera although a wider knowledge of Carboniferous amphibians would probably fill out some of the

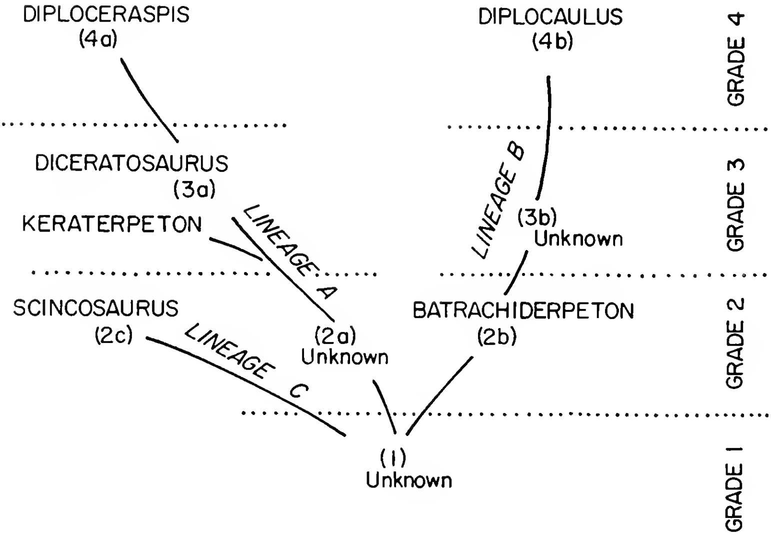

Fig. 15. Phylogeny of the keraterpetontids. Note that three genera postulated in interpretation are not known from the fossil record. The stratigraphic sequence of forms in Lineages A and B accords with the inferred phylogenetic sequence. The "grades" are morphological levels indicating the approach to the specialized condition in *Diploceraspis* and *Diplocaulus*.

groups. The taxonomic arrangement should reflect this phyletic pattern, but several alternatives exist.

Romer (1945, p. 591) includes the horned genera then known, as well as *Scincosaurus*, in a single family, the Keraterpetontidae. Logically, *Diploceraspis* would fall here also. Although some paleontologists (e.g. Case, 1946, p. 351) regard *Diplocaulus* as sufficiently distinct to be placed in a separate family, this would require recognition of a superfamily with at least two and possibly four families for the five well known genera. If *Batrachiderpeton* is placed with *Diplocaulus* in this separate family as it has been by many workers (e.g. Case, 1946, p. 351), the vertical splitting of lineages would approach absurdity. *Batrachiderpeton* differs from the probable ancestor of *Diceratosaurus* (Unit 2a in Fig. 15) by only a single character, the position of the lacrimal, hardly more than a specific difference in a tightly knit genus. But the suggested arrangement would set it in a separate family.

All in all, I believe it best to retain the taxonomic scale suggested by Romer, to regard these six genera as members of a single family and to use subfamilial ranks to indicate phylogeny. Again, extreme vertical or horizontal classifications are possible, but the most reasonable compromise seems to be the recognition of a "primitive" horizontal subfamily, Batrachiderpetontinae, which would include the hypothetical ancestors of the entire family (Unit 1), *Batrachiderpeton* (Unit 2b), the postulated ancestor of *Diceratosaurus* (Unit 2a), and *Scinosaurus* as *incertae sedis*. A vertical subfamily, Keraterpetontinae would include *Diploceraspis* (4a) as well as *Diceratosaurus* and *Keraterpeton* (3a). A second vertical subfamily, Diplocaulinae, would be formed for *Diplocaulus* (4b) and the as yet undiscovered genus (3b) linking it to *Batrachiderpeton*. The arrangement of subfamilies and their diagnostic characteristics would be:

Family Keraterpetontidae Romer 1945

Nectrideans with slightly or strongly flattened skull, tabular "horns," short snout, jaw articulation anteriad of occipital condyles, short tooth row, and some type of accessory articulations between vertebrae.

Subfamily Batrachiderpetontinae

Skull moderately flattened; horns absent, short, or of moderate length; jaw articulation about on line with or just ahead of condyles; paired frontals; interpterygoid vacuities small or absent; basioccipital and basisphenoid ossified; movable pterygoid-basisphenoid articulation;

no sutural contact between exoccipitals, pterygoids, and parasphenoids.
Batrachiderpeton, ? Scincosaurus.

Subfamily Keraterpetontinae.

Skull moderately to strongly flattened; horns short to long; jaw articulation far anteriad of condyles; interpterygoid vacuities moderate to large; frontal paired or single; basioccipital and basisphenoid reduced or unossified; sutural junction of pterygoid with parasphenoid; sutural junctions of exoccipital with pterygoid and parasphenoid; lacrimal laterad of prefrontal and bordering orbit; arch of vomerine teeth anteriad of internal nares; well developed coronoid process; neural spines of vertebrae pitted or corrugated.
Keraterpeton, Diceratosaurus, Diploceraspis.

Subfamily Diplocaulinae

Skull moderately to strongly flattened; horns short to long; jaw articulation far anteriad of condyles; interpterygoid vacuities moderate to large; frontal paired or single; basioccipital and basisphenoid reduced or unossified; sutural junction of pterygoid with parasphenoid; sutural junctions of exoccipital with pterygoid and parasphenoid; lacrimal anteriad of prefrontal and separated from orbit; arch of vomerine teeth posteriad of internal nares; coronoid process absent from mandible; neural spines smooth except for single large pit.
Diplocaulus.

ADAPTATION AND EVOLUTION OF *DIPLOCERASPIS*

Watson (1951, pp. 41-49, 66-76, 89-90) described the typical evolutionary sequence in the flattening of the amphibian skull and discussed the adaptive significance of this change. Among the labyrinthodonts, the modification is associated with a fully aquatic habit, but even the brachyopids which most resemble *Diploceraspis* are much larger and presumably fed on moderate sized vertebrates as do crocodiles now. In the latter the flattened form is an adaptation to concealment and locomotion in shallow water not for bottom feeding.

The morphology of *Diploceraspis* and *Diplocaulus* strongly suggests bottom-feeding adaptations and thus the parallel with the labyrinthodonts is primarily structural not functional. In this circumstance, some morphologic divergence, i.e. the development of horns, the rotation of the pharyngeal region, the extreme anteriad position of the jaw articulation, and the strength of vertebrae and ribs, is to be expected. Preceding sections of this paper describe the functional importance of these characteristics; their evolutionary origin requires explanation.

The character and proportions of snout, jaws, and teeth remain similar (Table 3) in all keraterpetontids. The *Batrachiderpeton-Diplocaulus* lineage has more extensive development of teeth on the inner portions of the palate, and these animals may have taken larger and/or more active prey, e.g. large worms, that could not be engulfed in a single bite. If this interpretation is correct, the initial divergence of the two lineages would be related to differences in feeding between two otherwise similar populations.

The structure of the primitive keraterpetontids implies more active locomotion than that of *Diploceraspis* and *Diplocaulus,* and these forms may have sought food above the bottom, at the surface, or even on land. The incipient flattening of skull and body suggests, however, that the bottom-feeding habit was already primary.

Batrachiderpeton shows slight differentiation of tabular and suprapharyngeal portions of the horns; in *Diceratosaurus* the difference is marked and the ventrad rotation of the otic surface has begun. The tabular horns of these early keraterpetontids may have had some function in defense though their position proximal to the upper end of the cleithrum must have limited their mobility and usefulness. Since the pharynx lay largely behind rather than beneath the skull roof, they may have served a largely passive function in support and protection of the pharyngeal region, in particular of an opercular flap.

The throat and shoulder region of the primitive genera provide sufficient space for egress of external gills though no branchial arches have been observed. The coal swamp and pond deposits from which these forms come probably had low partial oxygen pressures and external gills would be useful though perhaps not necessary. The development of the suprapharyngeal horn in *Diceratosaurus* indicates some development of pharyngeal pouches leading on to *Diploceraspsis.* The parallel development of these pouches in *Diplocaulus* would tend to demonstrate an antecedent structure in their common ancestor — possibly external gills plus a protective flap, internal gills in pharyngeal pouches, or simply vascularized pharyngeal pouches. Present morphological evidence does not discriminate between these alternatives.

The changes between the short- and long-horned types represent completion of the adaptation to bottom feeding in shallow ponds. The trends of flattening, horn development, modification of the palate, and shift of the jaw articulation were carried to their adaptive extremes. Whatever the function of the horn in the primitive forms, its further modification is related to a complex of apparently inseparable functions. The suprapharyngeal portion enlarged to cover and support the pharyngeal pouches, but this enlargement was functionally possible only if the tabular portion extended to counterbalance the added weight. The total weight of skull was valuable in holding the animal on the substrate but was tolerable in locomotion only if the animal remained on the bottom. Continuous bottom life was possible only to an animal with a modified respiratory system, i.e. with pharyngeal pouches. The horns counter-weighted the skull in opening the mouth, but because they limited the amount of tilting and thus the mouth gape, only animals that ate small organisms would be viable.

The initial feeding adaptations in teeth, jaw and snout, therefore, preconditioned the evolutionary history of the keraterpetontids. Whether the horn structure was pre-adaptive remains uncertain; the presence of the horn, however, was necessary for the particular evolutionary path that developed. If *Diceratosaurus* is the direct ancestor of *Diploceraspsis,* the evolutionary shift was rapid — between the late Westphalian and middle Stephanian — but nearly all the unique structural features of *Diploceraspsis* are foreshadowed in *Diceratosaurus* and might involve a very few genetic changes as these affected growth gradients and fields.

SUMMARY

New specimens of the nectridean amphibian, *Diploceraspsis,* from the Dunkard group, late Pennsylvanian-early Permian of Ohio, Pennsylvania, and West Virginia, provide additional morphologic information. The skull is broad and flat with a short snout, upward facing eyes, elongate tabular horns, and ornamentation of closely spaced circular pits. The jaw articulation lies far forward of the occipital surface. The basicranium is reduced, and extensive sutures join the pterygoid, parasphenoid, and exoccipital. The vertebrae are characterized by sculptured centra and neural processes. The ribs are long, straight, and double-headed. The clavicles comprise a triangular, sculptured ventral plate and a slender, rod-like ascending process. The interclavicle is relatively large, pentameral, and sculptured. The trunk, like

the skull, is broad and flat; the tail is slender and compressed in the vertical plane. *Diploceraspis* shows major similarities to *Diplocaulus* as well as significant minor differences. The features of these two "long-horned" forms are anticipated in varying degrees by the earlier "short-horned" nectrideans, the keraterpetontids.

The form and occurrence of *Diploceraspis* indicate a shallow lacustrine habitat. They crawled on the bottom and were probably very weak swimmers. They fed on small invertebrates collected from the substrate. The enlarged otic area presumably covered large pharyngeal pouches that served for respiration in low oxygen environments. The horns counterbalanced the weight of the skull over the condyles, ballasted the animals to the bottom, supported and shielded the pharyngeal pouches, and assisted in defense.

Diploceraspis evolved in parallel to *Diplocaulus*. *Diceratosaurus* is the probable ancestor of the former, *Batrachiderpeton* of the latter. The common ancestor of these horned amphibians was slightly antecedent to and little different from *Batrachiderpeton*. The early keraterpetontids were probably active swimmers and possibly partly terrestrial; the "long-horned" types evolved in adaptation to a completely aquatic, bottom-feeding life with its stringencies and possibilities.

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A REVIEW OF THE NORTH AMERICAN TERTIARY SCIURIDAE

By

Craig C. Black

Carnegie Museum
Pittsburgh, Pa.

With Twenty-Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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No. 3. *A Review of the North American Tertiary Sciuridae*

By

CRAIG C. BLACK

CONTENTS

INTRODUCTION

The family Sciuridae is one of the more cosmopolitan of rodent families, its members occurring in Eurasia, Africa, and North and South America. Tree squirrels, chipmunks, flying squirrels, and a variety of ground squirrels-prairie dogs, marmots, susliks, etc. constitute the family, which is generally divided into two subfamilies: the Petauristinae for the flying squirrels, and the Sciurinae including all other forms. The earliest members are found in the Middle Oligocene of North America and in the Phosphorites (possibly Stampian) of France.

Oligocene and Miocene sciurids have frequently been assigned to the genus *Sciurus*. Such assignments have not been made in the belief that these middle Tertiary species were necessarily referable to *Sciurus* in the strict sense, but rather because the dentition of most members of the family is so conservative that differences between forms are subtle and difficult to detect. Also, much of the material is so fragmentary that its true affinities can only be determined by comparative study of the entire family, living and extinct, a procedure too time consuming to be undertaken in the course of most faunal studies. In Europe, particularly, sciurid specimens have usually been assigned to *Sciurus*, with little or no attention being paid to possible ground squirrel affinities. In North America, on the other hand, specimens referred to most groups of living sciurids have been described, but with the exception of Bryant's work (1945) no attempt has been made to trace the evolution of these groups.

The present study reviews the North American Tertiary members of the family in an endeavor to trace the interrelationships of the known forms. A great deal of sciurid material has been found in various collections which had not previously been studied or even mentioned in the literature. These specimens together with those previously described have provided a much better understanding of the history of the family. Certain generic groups appear to have originated in North America and some of these appear to have been restricted to this continent throughout their history. In the first category are *Marmota,* probably *Eutamias* and possibly *Citellus;* in the second are: *Cynomys, Tamias, Ammospermophilus* and *Tamiasciurus.* As regards *Citellus,* however, such European species as *Sciurus feignouxi, Sciurus bredai,* and possibly *Sciurus costatus* resemble spermophiles more closely than they do *Sciurus, S. feignouxi* in particular being very reminiscent of *Miospermophilus.* It is possible, therefore, that the spermophiles had their origin in Eurasia and that the present diversity of ground squirrels in North America is the result of a secondary radiation after immigration. The place of origin of the family and of *Sciurus* itself is unknown.

An adequate understanding of the evolution and distribution of the family can hardly be reached until the Old World Tertiary squirrels have also been studied. Nevertheless, a review of the North American Tertiary representatives should not only serve to elucidate the relationships of these forms but should also supply a basis for an understanding of the record for the family in Europe.

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A draft of this paper was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University.

PREVIOUS STUDIES

For the most part, work on fossil squirrels has consisted of brief treatments of specimens as members of faunas without any serious attempts to arrive at an outline of sciurid evolution. Exceptions to this rule are papers by Bryant (1945) and Wilson (1960); Downs (1956) has briefly discussed many of the known fossil sciurids in connection with a description of *Arctomyoides oregonensis*.

Marsh (1871) was the first to describe a fossil sciurid from the North American Tertiary, placing it in the genus *Arctomys* (=*Marmota*). Cope in 1873 described *Paramys relictus,* which he assigned to *Sciurus* in 1874. With this species, now placed in *Prosciurus,* began the confusion of prosciurines with true squirrels, a confusion that has persisted to the present day. In 1879 and 1881, Cope described two species of *Sciurus, S. ballovianus* and *S. vortmani* from the John Day, both of which are true sciurids. Between 1881 and 1930 the only additions to our knowledge of the North American Sciuridae were Douglass' (1903) account of *Palaearctomys,* the first extinct genus of North American squirrel to be described, Kellogg's (1910) discussion of the Thousand Creek sciurids, Matthew's (1924) brief discussion of *Sciurus aberti* from the Snake Creek, and the description of *Otospermophilus gidleyi* by Merriam, Stock, and Moody (1925). Matthew in 1903 described a specimen from Pipestone Springs as *Sciurus (Prosciurus) vetustus*. In 1910 he raised *Prosciurus* to full generic rank and placed it in the family Ischyromyidae. In this genus he placed Cope's *S. vortmani* and *S. relictus,* leaving only *S. ballovianus* in the Sciuridae. Wood (1937) pointed out that *S. vortmani* was a true sciurid. Since 1937, there has been little confusion as to the proper generic assignment of material either to *Prosciurus* or *Sciurus* but uncertainty still exists as to the position of *Prosciurus* in relation to squirrel evolution, and this will be discussed later (p. 230).

During the 1930's a considerable amount of new material was described, principally by Gazin (1930, 1932) and by Wilson (1936, 1937a) from the Tertiary of the Great Basin. Gazin's contributions included, for the first time, descriptions of fossil spermophiles based on skull material. The first fossil chipmunk was described by Hall (1930) from the late Miocene Barstow Formation.

Matthew (Matthew and Mook, 1933) described a nearly perfect skull from the Deep River Formation, naming it *Sciurus angusticeps,* and took that opportunity to point out that he believed it to be impossible to trace squirrel subgenera into the Tertiary. In particular, he criticized the assignment by Merriam, Stock, and

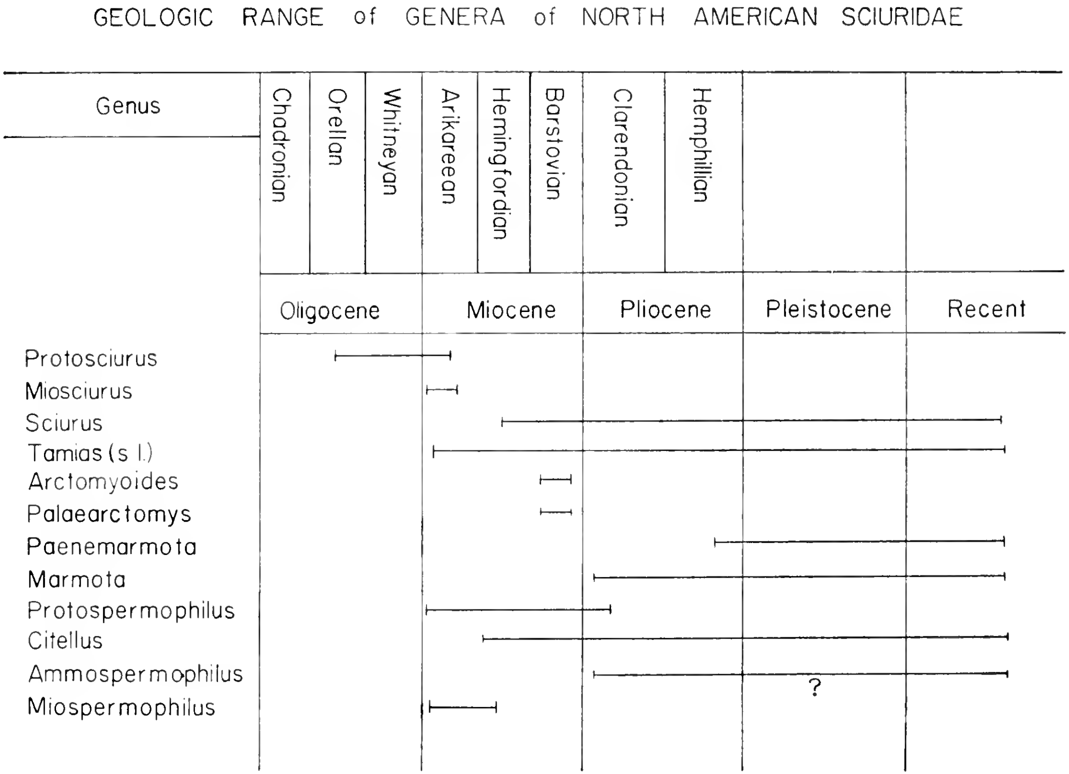
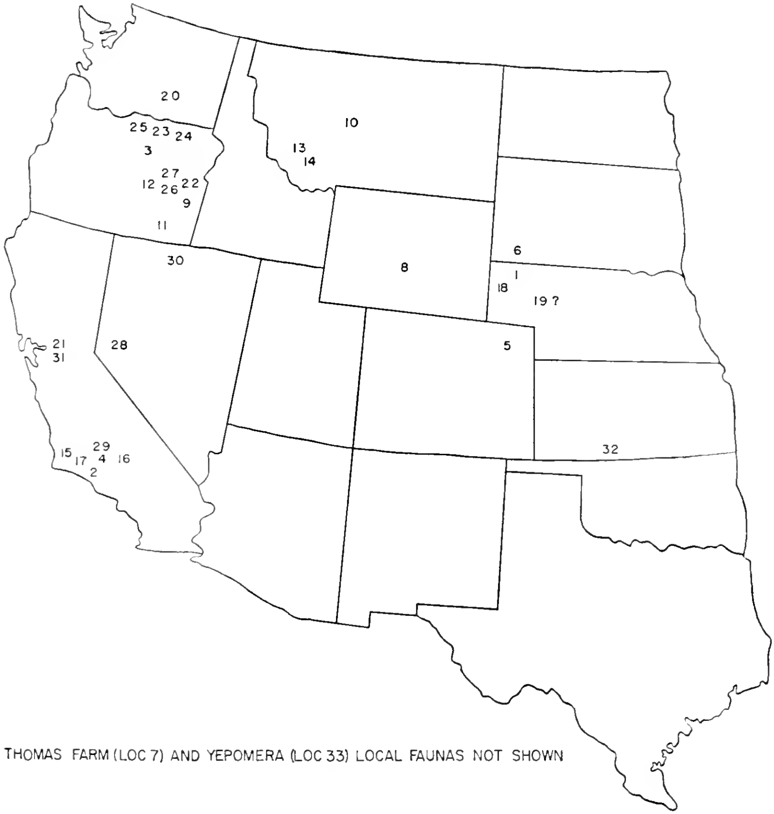


FIGURE 1. Geologic range of all genera of North American sciurids with a pre-Pleistocene fossil record.

Moody (1925) of a mandible from the Rattlesnake to the subgenus *Otospermophilus*, stating that when subgeneric identification could not be made on the basis of a good skull he failed to see how it could be done on a partial ramus.

By the late thirties, a fairly large body of material had been accumulated, including tree squirrels, ground squirrels, chipmunks, and marmots. Bryant (1945), in a work devoted principally to the classification of North American Recent sciurids on the basis of their osteology and myology, discussed for the first time all the known North American fossil squirrels. The broad outlines of sciurid evolution were clarified here and a considerable degree of order brought out of previous uncertainty. However, Bryant



THOMAS FARM (LOC 7) AND YEPOMERA (LOC 33) LOCAL FAUNAS NOT SHOWN

Figure 2. Geographic distribution of localities from which Tertiary squirrels are known in North America.

did not examine all the pertinent fossil material and his approach, weighted towards the side of Recent species, led to certain misconceptions in his phylogenies. Recently, Wilson (1960) discussed the problems of sciurid evolution in some detail. His discussion of the European material that he was able to examine is especially valuable and he points out for the first time the resemblance of several European late Oligocene and Miocene species to the ground squirrels.

The geologic range of North American sciurids is shown in Figure 1.

The geographic distribution of the material examined for this study is shown in Figure 2. Each locality is represented numerically on the map, with the age of the fauna and the species occurring at that locality listed below.

Oligocene	
Orellan	
1. Meng Ranch, Nebraska	*Protosciurus mengi*
Whitneyan	
2. Las Posas Hills, California	Sciurid indet.
Miocene	
Arikareean	
3. John Day Basin, Oregon	*Miosciurus ballovianus* *Protosciurus condoni* *Protosciurus rachelae* Sciurid indet. (some flying squirrel features) *Protospermophilus vortmani*
4. Tecuya Canyon, California	*Protosciurus tecuyensis*
5. Martin Canyon Quarry A, Colorado	*Miospermophilus bryanti* *Tamias* sp. *Protospermophilus* sp.
6. Wounded Knee local fauna, South Dakota	*Tamias* sp.
7. Thomas Farm l.f., Florida	*Tamias* sp.
Hemingfordian	
8. Split Rock l.f., Wyoming	*Miospermophilus wyomingensis* *Protospermophilus kelloggi* *Tamias* sp.

9. Skull Spring l.f., Oregon	*Protospermophilus malheurensis* *Citellus (Otospermophilus) tephrus*
10. Deep River l.f., Montana	*Protospermophilus angusticeps*
11. Beatty Buttes l.f., Oregon	*Sciurus* sp.
Barstovian	
12. Mascall, Oregon	*Protospermophilus oregonensis*
13. Flint Creek l.f., Montana	*Citellus (O.) primitivus*
14. Lower Madison Valley l.f., Montana	*Citellus (O.) primitivus* *Palaearctomys montanus* *Arctomyoides arctomyoides*
15. Quatal Canyon l.f., California	*Protospermophilus quatalensis*
16. Barstow, California	*Tamias* sp.
liocene	
Clarendonian	
17. Cuyama l.f., California	*Protospermophilus quatalensis*
18. Upper Snake Creek, Nebraska	*Citellus (O.) matthewi*
19. Loup Fork, Nebraska (exact age unknown)	*Citellus (Citellus?)* sp. *Marmota vetus*
20. Ellensburg Beds, Washington	*Citellus (O.) wilsoni*
21. Ingram Creek, California	*Citellus (O.)* sp.
22. Juntura, Oregon	*Ammospermophilus?*
Hemphillian	
23. McKay Reservoir l.f., Oregon	*Citellus (O.) shotwelli* *Citellus (O.) wilsoni* *Citellus (C.) mckayensis*
24. Westend Blowout l.f., Oregon	*Citellus (O.) shotwelli*
25. Arlington Beds, Oregon	*Citellus (O.) wilsoni* *Citellus (O.) shotwelli*

26. Drewsey, Oregon	*Citellus (O.) shotwelli*
27. Rattlesnake, Oregon	*Citellus (O.) gidleyi*
28. Smiths Valley, Nevada	*Citellus (O.) argonautus*
29. Kern River, California	*Citellus (O.) argonautus*
30. Thousand Creek, Nevada	*Citellus (O.) argonautus* *Marmota nevadensis* *Marmota minor*
31. Schell Ranch, California	*Citellus (O.) argonautus*
32. Clark Co., Kansas	*Citellus (O.) fricki*
33. Yepomera l.f., Mexico	*Citellus (O.) pattersoni* *Citellus matachicensis* *Paenemarmota*

METHODS

All measurements are in millimeters and were taken using an ocular micrometer, except those of the skulls and limb bones which were taken with a dial caliper. When two transverse measurements are given for the cheek teeth the first is that across the trigonid, the second across the talonid. Measurements of the teeth were taken across the occlusal surface unless otherwise noted.

The terminology employed throughout is that generally used in the literature dealing with squirrels. The terminology used for the cheek teeth is illustrated in Figure 3.

Tooth structure within the North American Sciuridae falls into two rather distinct categories. M^1-M^2 are subquadrate with expanded protocones, indistinct metaconules and low complete lophs in the tree squirrels, while in the ground squirrels M^1-M^2 are generally triangular with large metaconules, high lophs, and constricted to incomplete metalophs. M_1-M_2 are transversely rectangular to square in the tree squirrels and chipmunks, and they are rhomboidal with narrower lingual than buccal margins in the ground squirrels and marmots. In the first category the posterolophids are low and entoconids generally distinct while in the second the posterolophids are elevated and the entoconids submerged within them.

These two basic types of dentition show various modifications in the North American members of the family but most fossil specimens are easily assignable to one of these groups. Both types

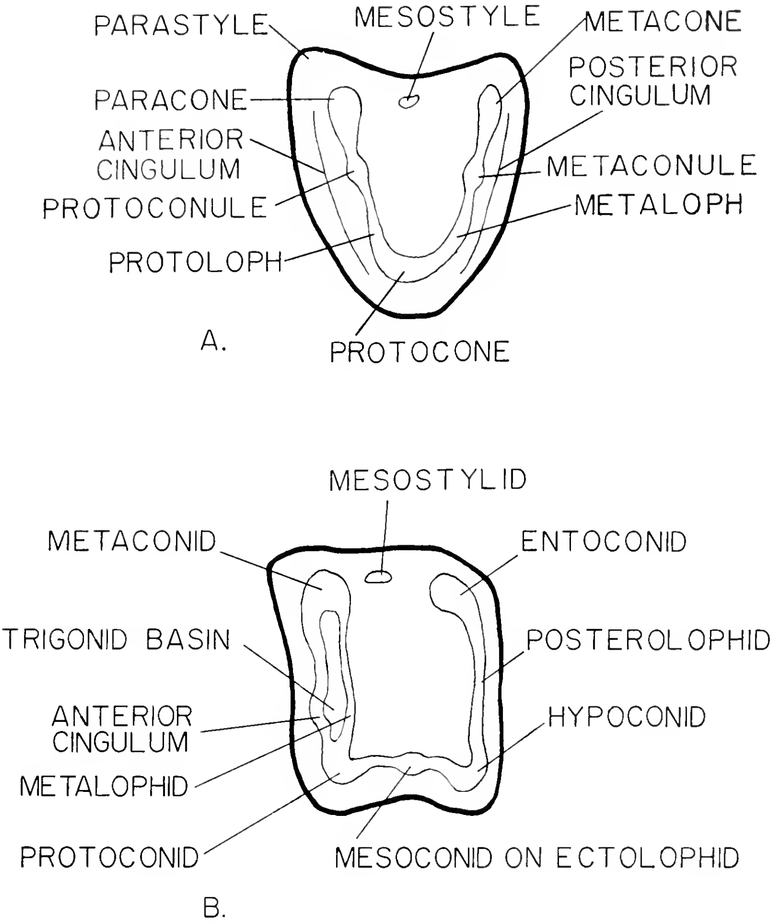


Figure 3. Terminology used to describe occlusal patterns of squirrel cheek teeth. 3a, Upper. 3b, Lower.

are strongly correlated with the two very distinct dietary preferences of the two squirrel groups. The low-crowned heavier dentition of the tree squirrels reflects the primary crushing function of the dentition while the higher-crowned, sharper-lophed dentition of the ground squirrels reflects the greater shearing or cutting action necessitated by the herbaceous diet of this group.

Thanks to the collections of Carnegie Museum and the Museum of Comparative Zoology, specimens of all species of North American Recent Sciuridae have been available for study.

Wood, *et al.* (MS.) has been followed for correlation and terminology of North American deposits.

The following abbreviations are used:

A.C.	Amherst College
A.M.N.H.	American Museum of Natural History
C.M.	Carnegie Museum
C.N.H.M.	Chicago Natural History Museum
F:A.M.	Frick Collections American Museum of Natural History
F.G.S.	Florida Geological Survey
K.U.	University of Kansas Museum of Natural History
L.A.C.M. (C.I.T.)	Los Angeles County Museum (California Institute of Technology Collection)
M.C.Z.	Museum of Comparative Zoology, Harvard University
S.D.S.M.	South Dakota School of Mines and Technology
U.C.M.P.	University of California Museum of Paleontology
U.F.	University of Florida
U.M.M.P.	University of Michigan Museum of Paleontology
U.O.M.N.H.	University of Oregon Museum of Natural History
U.S.N.M.	United States National Museum
U.W.	University of Wyoming
Y.P.M.	Peabody Museum of Natural History, Yale University
a-p	anteroposterior
tr.	transverse
approx.	approximately

CLASSIFICATION

The generally accepted suprageneric classification of squirrels was set forth by Pocock (1923) on the basis of a detailed study of the baculum and glans penis in the family. He recognized six subfamilies within the Sciuridae and separated the flying squirrels as a distinct family. Simpson (1945) accepted Pocock's groupings but reduced his subfamilies to tribal rank and included the flying squirrels in the Sciuridae as a subfamily. Bryant (1945) did not employ formal taxonomic categories above the genus in his classification of Nearctic squirrels, placing related genera in informal divisions and sections, but his classification agreed in most respects with Simpson's modification of Pocock, differing only in that he did not recognize *Tamiasciurus* as tribally distinct from *Sciurus*, and in recognizing *Ammospermophilus* as a distinct genus. Moore (1959), the latest author to revise the Sciurinae, adds two new tribes, Ratufini and Protoxerini, to those admitted by Simpson and transfers *Sciurotamias* from the Callosciurini to the Tamiasciurini.

The classification proposed here differs in two respects from Moore's. First, the chipmunks, *Tamias* and *Eutamias*, are raised to tribal rank and, second, *Tamiasciurus* is included in the tribe Sciurini with *Sciurotamias* returned to the Callosciurini.

Suborder Protrogomorpha
  Family Sciuridae Gray, 1821
    Subfamily Sciurinae Baird, 1857
      Tribe Tamiini new form (Tamiina Moore 1959)
        Tamias, Eutamias

      Tribe Sciurini Burmeister, 1854
        Sciurus, Miosciurus, Protosciurus,
        Tamiasciurus, Reithrosciurus,
        Guerlinguetus, Microsciurus,
        Syntheosciurus, Sciurillus

      Tribe Ratufini Moore, 1959
        Ratufa

      Tribe Protoxerini Moore, 1959
        Protoxerus, Epixerus, Heliosciurus

      Tribe Funambulini Simpson, 1945
        Funambulus, Funisciurus, Paraxerus,
        Myosciurus

      Tribe Callosciurini Simpson, 1945
        Callosciurus, Sundasciurus, Glyphotes,
        Nannosciurus, Dremomys, Lariscus,
        Menetes, Rhinosciurus, Hyosciurus,
        Prosciurillus, Rubrisciurus,
        Exilisciurus, Sciurotamias

      Tribe Marmotini Simpson, 1945
        Citellus, Ammospermophilus, Cynomys
        Marmota, Protospermophilus,
        Miospermophilus, Palaearctomys,
        Arctomyoides, Paenemarmota,
        Paracitellus (?)

Tribe Xerini Simpson, 1945
Xerus, Atlantoxerus, Spermopholopsis
Subfamily Petauristinae Simpson, 1945
Petaurista, Eupetaurus, Sciuropterus,
Glaucomys, Eoglaucomys, Hylopetes,
Aeretes, Trogopterus, Belomys,
Pteromyscus, Petaurillus, Iomys

The tribes Ratufini, Protoxerini, Funambulini, and Callosciurini are retained but I may state that the included genera seem to me to be more closely related to each other and to those of the Sciurini than they are to the Marmotini or to the Xerini. It seems rather unlikely that each group was independently derived from the Tamiini. Unfortunately, there is no paleontological evidence on which to base a tree squirrel phylogeny and I have not had the opportunity to examine representatives of all the Recent genera.

In the following pages I stress the intermediate position of *Tamias* and *Eutamias* between the ground squirrels and the tree squirrels. This is reflected in the skeleton, dentition, and habit. Chipmunks appear to have been a distinct stock since at least the late Oligocene, as have the Marmotini and the Sciurini. Both Bryant (1945) and Moore (1959) recognized that the chipmunks were a distinct group, differing from the marmots, on the one hand, and the spermophiles, on the other, in many cranial and skeletal characters. Bryant set them off as a section within his Terrestrial Squirrel and Chipmunk Division while Moore placed them in a separate subtribe, Tamiina, of the Marmotini. However, I feel that they differ from the marmots and spermophiles as greatly as they do from the tree squirrels and are fully entitled to tribal status.

The tribe Sciurini, as here recognized, includes the European and American tree squirrels plus the North American red squirrel, *Tamiasciurus*. Placement of *Tamiasciurus* in the Sciurini is contrary to majority opinion regarding its relationships. (For a resumé of the taxonomic history of the genus see Moore 1959, pp. 183-184.) Bryant (1945, p. 383) is one of the few recent authorities who has placed *Sciurus* and *Tamiasciurus* together; in most classifications *Tamiasciurus* is given tribal to subfamilial rank, the basis for which is the absence of an os genitale. Layne (1952, 1954) has shown, however, that some individuals do possess vestigial bacula and baubella. The conclusion he reached, namely that reduction of the os genitale is a specialization, is, I believe, valid. Moore (1959, p. 183) concurs but still argues for separate tribal status for *Tamiasciurus*. He emphasizes two skull characters, the presence of three transbullar septa and a high squamosal, that he believes distinguish *Tamiasciurus* from *Sciurus*. However, as he himself points out, some individuals of the Persian tree squirrel *Sciurus (Tenes) anomalus* have three septa, but because this condition is variable in *Tenes* and also because it has a low squamosal, he believes it to be distinct tribally from *Tamiasciurus*. However, the variability in the number of septa in this subgenus of *Sciurus* could argue just as well in the opposite direction. Also, in twenty-six specimens of *Tamiasciurus* examined in the mammal collection of the Museum of Comparative Zoology at Harvard, three showed only two septa, and the third septum was variably developed in the other twenty-three skulls. Perhaps *Tenes* is in the process of acquiring a third transbullar septum, as *Tamiasciurus* may have done in the past; if this is so, the presence of three septa in *Tamiasciurus* need not bar it from close relationship to *Sciurus*. The presence of a low squamosal (a squamosal extending up the side of the skull less than half the distance between the posterior zygomatic root and the postorbital notch) in the Sciurini is a character that is extremely hard to evaluate. What the adaptive significance of this may be is unknown, and a similar uncertainty applies to most of the characters Moore has used. He has set out to find skull characters which would separate groups within the Sciurinae, and, having found a series of characters, he has then defined tribal and subtribal units in terms of them with little or no regard to the relative weight to be given to each character. This is in general the practice followed in keys, which, while allowing for ready identification of individual specimens, all too often obscure actual relationships. However, Moore has managed to convey relationships and natural groupings in most instances, particularly as regards his recognition of the independent origins of the pygmy squirrel groups, but his use of the tribe Tamiasciurini does, I believe, obscure the relationships of this genus. In the majority of its characters *Tamiasciurus* closely resembles *Sciurus*, and its true relationships are, I believe, with that genus.

Moore (1959, p. 183) grouped *Sciurotamias* with *Tamiasciurus* in the tribe Tamiasciurini, again because of the fact that *Sciurotamias* possesses three transbullar septa. He states, however, that in many other skull characters these two genera are quite dissimilar and that this grouping is only tentative. *Sciurotamias* appears to me to be much more closely related to the oriental tree squirrels of the tribe Callosciurini than it is to *Sciurus* and *Tamiasciurus*, and I have placed it in the Callosciurini.

The flying squirrels present serious problems. That they are more closely related to each other than they are to various groups of tree squirrels is, I believe, highly unlikely. *Glaucomys, Sciuropterus, Eoglaucomys* and *Hylopetes* are probably much more closely related to *Sciurus*, and certainly much more closely related to each other, than any of them are to the highly specialized Asian flying squirrels. That the flying squirrels are descended from tree squirrels seems obvious and there is certainly nothing in their morphology that would argue against such derivation. The *Glaucomys* group differs from *Sciurus* in the possession of gliding membranes, in somewhat longer limbs in relation to vertebral column length, and in the wide valley separating the entoconid and metaconid on M_1-M_2. The other forms are generally more specialized, especially in their dentition. From a tree squirrel structural and behavioral base, independent evolution of more than one gliding stock could have occurred. The true relationships of the flying squirrels might best be illustrated by placing some of them in the tribe Sciurini and some in the tribe Callosciurini, possibly as distinct subtribes. However, decision must await a full study of the various Asian genera of flying squirrels and, pending this, I retain the currently recognized subfamily.

The subordinal position of the Sciuridae has been considerably debated in the last decade. Simpson (1945) grouped the squirrels with the Aplodontoidea, Geomyoidea, and Castoroidea in the suborder Sciuromorpha. Wood (1955) removed the Geomyoidea and Castoroidea, split the Aplodontoidea into two superfamilies (Ischyromyoidea and Aplodontoidea transferring the Eomyidae to the Myomorpha) and retained the Sciuroidea within this suborder. Lavocat (1956a), in reviewing recent concepts of rodent classification, suggested that the Sciuridae be placed by themselves in the Sciuromorpha and that the term Protrogomorpha be revived to include the Ischyromyoidea and Aplodontoidea. More recently Wood has proposed (1959), as Lavocat suggested, that either the Sciuromorpha be limited to the Sciuridae and that the Ischyromyoidea and Aplodontoidea be placed in the suborder Protrogomorpha or that the suborder Sciuromorpha be dropped and the Sciuridae remain unallocated to a suborder. Simpson (1959, p. 260) has suggested that all rodents should be either grouped in two suborders, the Caviomorpha and a second suborder for all other rodents, or that no suborders be used in the group and that the classification of the order be extended only to the superfamilial level. Wood (1962, p. 250), in his excellent review of the Paramyidae, follows his earlier (1959) classification and states, "It seems much more appropriate to use the suborder for collections of families large enough to need two levels of superfamilial coordination and to omit suborders for rodents of unknown superfamilial relationship."

I would agree with this statement; however, after a study of the Oligocene and early Miocene squirrels of North America, I believe the Sciuridae should be grouped with Wood's Ischyromyoidea and Aplodontoidea in the suborder Protrogomorpha. As pointed out in detail below, the primitive condition of the zygomasseteric complex in the genera *Protosciurus* and *Miosciurus* bridges the gap between the protrogomorph condition and the fully developed sciuromorph type. In all respects other than zygomasseteric structure, the Sciuridae are much closer to the paramyid evolutionary level than are the Mylagaulidae or Aplodontidae, families which have been placed in the Protrogomorpha because of their primitive zygomasseteric structure. Lavocat (1956a, p. 53) argues that the Sciuridae are only primitive in their dentition while their zygomasseteric complex is specialized. However, they are no more specialized in this respect than the Aplodontoidea are in their dentition. Since early members of both groups can be traced into the Ischyromyoidea, and intermediate stages of zygomasseteric and tooth development are known, it appears much more natural to group the Ischyromyoidea, Aplodontoidea, and Sciuridae together in one suborder. If the Sciuridae were to be considered a separate subordinal group because their zygomasseteric complex is now specialized, the Aplodontoidea should also be given separate subordinal rank because of their dental specializations. This type of fragmentation of natural, closely related groups merely obscures their relationships, however, and I would strongly urge their continued association in one suborder.

Use of the subordinal term Protrogomorpha rather than the older Sciuromorpha for this assemblage is preferable. The sciuromorph type of zygomasseteric structure has been independently evolved in various rodent families, some of which are certainly more closely related to the typical myomorph families than they are to the Aplodontoidea, Ischyromyoidea and Sciuridae, and is thus not diagnostic of a natural group. The suborder Sciuromorpha of Brandt (1855) has changed so completely in recent years that it bears little resemblance to the original. Such families as the Geomyidae, Heteromyidae, and Castoridae, while possessing a sciuromorph type of zygomasseteric structure, are no longer believed to be closely related to the Sciuridae. The Geomyidae and Heteromyidae appear to be myomorphs (see Wilson 1949b) and undoubtedly had an origin within the Paramyidae independent of that of the Sciuridae. The Castoridae were also probably independently evolved from the Paramyidae (Wood, 1955). Since nomenclatural priority is not obligatory in dealing with categories higher than the superfamily, I believe that the use of the subordinal term Protrogomorpha to include the Ischyromyoidea, Aplodontoidea and Sciuridae better expresses our present knowledge of relationships.

SYSTEMATIC REVIEW

Family SCIURIDAE Gray, 1821

Dental formula: I^1_1, C^0_0, P^{1-2}_1, M^3_3. Cheek teeth little advanced over those of the Paramyidae; upper molars triangular to subquadrate with paracone, metacone, protocone as major cusps; no hypocone. M^1-M^2 four crested with conules variably present; posterior cingulum of M^3 enlarged; lower molars rectangular to rhomboidal; entoconids distinct or suppressed in posterolophids; trigonid basins small; masseter coming to extend above infraorbital foramen and onto rostrum with the formation of a flat plate on the anterior surface of the zygoma; infraorbital foramen oval to slit-like.

Range. Middle Oligocene to Recent, North America. Phosphorites to Recent, Europe. Miocene to Recent, Africa and Asia. Recent, South America.

Subfamily SCIURINAE Baird, 1857

The Sciurinae are defined as comprising that group of sciurids lacking gliding membranes.

Range. Middle Oligocene to Recent in North America.

Tribe TAMIINI new rank (Tamiina Moore 1959)

Limbs intermediate in proportion between Marmotini and Sciurini; three sacral vertebrae; skull moderately convex; infraorbital foramen oval, no infraorbital canal; diastema long; diastemal part of mandible drops only slightly anterior to P_4; upper molars subquadrate; metaconules small; metalophs only slightly constricted at protocones; entoconids incorporated into posterolophids; posterointernal corner of M_1-M_2 angular; M_1-M_2 not compressed anteroposteriorly.

Range. Early Miocene to Recent in North America.

TAMIAS Illiger

Type species. Sciurus striatus Linnaeus

Except on characters of the baculum and upper dentitions which show the presence or absence of P^3, it is impossible to distinguish *Eutamias* from *Tamias*. None of the material described below, therefore, can be placed in one genus of chipmunk rather than the other with any certainty. The material is much too fragmentary to warrant erection of a new genus and has consequently been placed in *Tamias* as a purely arbitrary assignment. However, this has not been done with any belief that these specimens truly represent species of the Recent genus.

TAMIAS sp.

Plate 1, figure 1

Referred specimens. S.D.S.M. Nos. 58100-26 LP^4, 58100-25 $RM^{1 \text{ or } 2}$, 58100-29 $RM^{1 \text{ or } 2}$, 58100-31 $RM^{1 \text{ or } 2}$, 58100-28 LM^3, 58100-32 LdP^4, 58100-3 RP_4, 58100-2 $LM_{1 \text{ or } 2}$.

Horizon and locality. Sharps formation, Lower Arikareean, early Miocene. Wounded Knee local fauna, Pennington County, South Dakota.

Description. The deciduous fourth upper premolar is triangular in outline with a narrow protocone and expanded anterior cingulum. The lophs are complete, rather high, and each shows the presence of a conule. The mesostyle is large; the posterior cingulum reduced. P^4 is worn and somewhat broken along its buccal margin. In outline the tooth is nearly rectangular due to a large protocone and small anterior cingulum. The protoloph is complete and shows no sign of a protoconule; the metaloph is partially constricted and bears a prominent metaconule. The mesostyle and posterior cingulum are small. There are three teeth that are either first or second upper molars. One, S.D.S.M. No. 58100-25, appears to be somewhat squarer in outline than the other two but this is at least partially due to its increased stage of wear. S.D.S.M. No. 58100-31 differs from the other two in having a distinct protoconule and metaconule. All three teeth are otherwise similar in crown pattern. The protocone does not occupy the entire lingual margin but is larger than in the Recent species. As a result the teeth are more nearly square than they are in living forms. This squareness is also contributed to by a rather expanded and angular protocone-posterior cingulum crest. The lophs are complete, relatively low, and show no signs of conules in Nos. 58100-25 and 58100-29. The mesostyle is well developed. M^3 is only slightly larger than M^1 or M^2 and is triangular in outline. It is not greatly expanded posteriorly. There is a faint indication of a metaloph remnant passing from the base of the protocone into the central basin. The protoloph is low, and no mesostyle is present. The protoconid and metaconid of P_4 are very closely appressed and there is no indication either of an anteroconid or of a trigonid basin. The buccal valley is very broad and shallow. The entoconid is submerged in the high posterolophid. The mesostylid is large. $M_{1\text{ or }2}$ is as long as it is wide. There is no trace of an anteroconid. The entoconid is distinct and the entoconid corner angular. A large mesoconid fills the broad shallow buccal valley. Although the tooth is worn, the posterolophid does not appear to have been high.

Discussion. The eight teeth in this collection and the other isolated teeth assigned below to the Tamiini resemble those of *Tamias ateles* Hall more closely than they do any other sciurid teeth from the North American Tertiary. In fact it is quite remarkable how little difference exists between these early Miocene forms and those from the Barstow and Tonopah. The upper molars agree with those from the Martin Canyon Quarry A in Colorado and the Barstow material in being rather square in outline and in having low lophs with no indication of protoconules. Large mesostyles are present in the upper molars of the Wounded Knee specimens and on those from Barstow. The partial constriction of the metaloph and development of a metaconule are not seen until the Barstovian *Tamias ateles* stage is reached with the exception of one tooth in the Wounded Knee fauna, S.D.S.M. No. 58100-31. The lower molars also are extremely similar for all the Miocene specimens known. The rather low posterolophid of the South Dakota *Tamias* specimens is an ideal starting point for the development of the higher posterolophids seen in the later forms.

TAMIAS sp.
Plate 1, figure 2

Sciurus sp. B Wilson, 1960, p. 63.

Referred specimens. K.U. No. 10170 $LM^{1 \text{ or } 2}$, 10171 RM^3, 10172 $RM_{1 \text{ or } 2}$.

Horizon and locality. Pawnee Creek Formation, Upper Arikareean, early Miocene. Martin Canyon Quarry A, NW ¼, Section 27, T.11N., R.53W., Logan County, Colorado.

Description. The first or second upper molar is square with a rather small protocone situated in the middle of the lingual border and a small cusp-like expansion at the junction of the posterior cingulum with the protocone. There is no indication of a mesostyle and there is no large parastyle at the buccal termination of the anterior cingulum. The lophs are low and there is no indication of either a protoconule or metaconule. M^3 is well worn. It is triangular in occlusal outline with no marked posterointernal expansion. The lower molar, although larger and somewhat more compressed anteroposteriorly, resembles that from the Lower Hemingfordian Split Rock local fauna. There is a strong anteroconid on the anterior cingulum. The trigonid basin is extremely small and opens into the talonid basin with only a weak metalophid present. The posterolophid is high with the entoconid submerged within it. The buccal valley is deep and tapers internally. There is no trace of a mesoconid and the ectolophid is weak. A small mesostylid is present.

Discussion. These *Tamias* specimens from Colorado differ from the Wounded Knee specimens but agree with all other Miocene chipmunks in lacking the mesoconid and could easily have been ancestral to the later forms. Likewise, they could have been derived from the older Wounded Knee population through a loss of the mesoconid and elevation of the posterolophid.

TAMIAS sp.
Plate 1, figure 3

Black, 1963, p. 487.

Referred specimens. F.G.S. V-6021, $LM^{1 \text{ or } 2}$, F.G.S. V-6020, RP_4, U.F. No. 3873, a fragment of left mandible with M_1 and F.G.S. No. V-5951, RM_3.

Horizon and locality. Arikareean, early Miocene. Thomas Farm, Gilchrist County, Florida.

Description. The following description is quoted from Black, 1963 (pp. 487-488). "The upper molar is unworn and shows a high, somewhat compressed protocone. The anterior cingulum is broad and joins the protocone at its base, well below the level of the protoloph. Buccally, the anterior cingulum bears a small parastyle. The protoloph and metaloph are low and complete, merging with the protocone about halfway down its buccal slope. A small metaconule is present in the metaloph. The posterior cingulum is narrow but expands slightly where it joins the protocone. A small mesostyle is present at the base of the paracone.

"The diastema of the mandible is long in relation to overall size and the diastemal depression shallow. P_4 has a trapezoidal shape with the protoconid and metaconid separated by a narrow notch. There is no indication of an anterior cingulum or anteroconid. The posterolophid is somewhat elevated and passes in a gentle curve from the hypoconid to the entoconid with the entoconid submerged within the posterolophid. There is no mesostylid present. The ectolophid is low and weak and bears no trace of a mesoconid. M_1 is square in outline with an angular entoconid corner. A small anteroconid is present on the anterior cingulum. The metalophid is complete and the small trigonid basin completely enclosed. The posterolophid is low. The entoconid is submerged in the posterolophid. The ectolophid is low and weak and the buccal valley is shallow. No mesostylid is present. The M_3 is extremely elongate, more so than in any other sciurid and it is quite possible that this is not a chipmunk M_3 and should not be associated with the other material described here. However, the tooth bears no resemblance to that of the prosciurines and on the basis of size alone it is here tentatively referred to *Tamias*. Most of the enamel on the tooth is missing and the crown pattern obliterated."

Discussion. These specimens represent the only Tertiary record for the family east of the Mississippi. Future work at Thomas Farm will undoubtedly bring to light more material of this species but, until then, little can be said about the relationships of this sciurid. The material available, with the exception of M_3, agrees well with the chipmunks known from the Miocene of South Dakota, Wyoming, and Colorado, and it probably belongs with this group. In size, this population is closer to the Split Rock *Tamias* than to the earlier South Dakota and Colorado populations.

TAMIAS sp.
Plate 2, figure 1

Referred specimen. U.W. No. 1434 $LM_{1 \text{ or } 2}$.

Horizon and locality. Split Rock Formation, early Hemingfordian, middle Miocene. NW ¼, Section 36, T.29N., R.90W., Fremont County, Wyoming.

Description. The molar is square in occlusal outline and smaller than that of *Tamias ateles* Hall. There is a large anteroconid closing the trigonid basin anteriorly but the basin is open posteriorly as the metalophid is incomplete. The buccal valley is deep and there is no mesoconid present. The entoconid is submerged in the high posterolophid. There is no mesostylid.

Discussion. This is one of the smallest sciurids known from the North American Tertiary. It resembles the other specimens herein described as members of the Tamiini in all respects and is closer in size to the Thomas Farm chipmunks than to the other Miocene forms.

TAMIAS ATELES (Hall)
Plate 2, figure 2

Eutamias ateles Hall, 1930, p. 314; Wilson, 1942, p. 104.
Tamias (Neotamias) ateles Bryant, 1945, p. 358.

Type. U.C.M.P. No. 28521, RM^1-M^3.

Hypodigm. Type and U.C.M.P. Nos. 28522 RM^1, 28523 RM_3, L.A.C.M. (C.I.T.) No. 5236a $RM_{1 \text{ or } 2}$, No. 5236b $LM_{1 \text{ or } 2}$, No. 5236c $LM^{1 \text{ or } 2}$.

Horizon and locality. Barstovian, late Miocene to Clarendonian, early Pliocene. Eleven miles N.E. of Hinkley, San Bernardino County, California. Also C.I.T. Loc. No. 172, 9 miles N. of Tonopah, Nevada.

Emended diagnosis. Teeth small; protoconules absent; protolophs not constricted at junction with protocone; metaconules present; mesostyles large; posterointernal part of M_3 large; talonid basin enclosed by high narrow posterolophid and lingual lophid; entoconid not distinct; no mesoconid.

Description. M^1 and M^2 are rather square in occlusal outline, more so than in Recent *Tamias,* due to the greater expansion of the lingual end of the posterior cingulum. The anterior cingula are moderately enlarged but there is no prominent parastyle. The lophs are low and resemble those of living *Tamias* in absence of a protoconule, presence of a metaconule, and partial constriction of the metaloph at the protocone. The mesostyles are large, whereas in Recent species they are small and indistinct, blending into the posterior base of the protocone. M_3 differs from its counterpart in Recent species only in the retention of a vestigial metaconule. In outline, the tooth is broadly triangular with little or no constriction of the posteroexternal portion.

Discussion. As has already been discussed, *Eutamias ateles* is extremely similar to the early Miocene forms known from the Great Plains and could have easily evolved from the Colorado population. Although slightly larger, *T. ateles* is also nearly identical to the Recent *Tamias striatus* and *Eutamias minimus*. The slight constriction of the metaloph and the absence of the mesoconid agree well with these species. However, *T. ateles* agrees almost equally well with other living species and it is certainly much too early in time to be conspecific with any of the Recent forms.

Measurements of *Tamias* sp.

		Wounded Knee l.f.	Martin Canyon l.f.	Thomas Farm l.f.	Split Rock l.f.	Barstow	Tonopah
dP^4	a-p	1.3					
	tr.	1.4					
P^4	a-p	1.3					
	tr.	1.5					
$M^{1 \text{ or } 2}$							
	a-p	1.3, 1.4, 1.3	1.7	1.3		1.3, 1.4, 1.5	1.4
	tr.	1.6, 1.7	1.9	1.5		1.6, 1.6, 1.7	1.6
M^3	a-p	1.5	1.7			1.6	
	tr.	1.6	1.7			1.6	
P_4	a-p	1.4		1.2			
	tr.	1.2–1.4		1.0–1.2			
$M_{1 \text{ or } 2}$							
	a-p	1.3	1.7	1.2	1.2		1.4, 1.5
	tr.	1.3–1.4	1.6–1.7	1.2–1.2	1.1–1.1		1.5–1.6, 1.5–1.5
M_3	a-p			1.8			
				1.4–1.3			

Tribe SCIURINI Burmeister, 1854

Limbs long, slender; distal ends of radius and ulna, and tibia and fibula slender; three sacral vertebrae; skull roof convex, more so than in the Marmotini (except in *Protosciurus* and *Miosciurus*); zygomatic plate inclined at 60° or more in relation to basicranial axis; skull broad interorbitally; diastema short and diastemal part of mandible drops steeply anterior to P_4 (except in *Miosciurus*); anterior end of mandible below level of alveolar border; upper molars quadrate with protocone occupying most of lingual border; metaconules small to absent; lophs low; entoconids generally large and distinct; posterolophids low.

Range. Middle Oligocene to Recent in North America.

MIOSCIURUS n. gen.

Type species. Sciurus ballovianus Cope.

Diagnosis. Size small; skull narrow, skull roof flat; cranium deeper than in *Protosciurus;* zygomatic plate triangular, facing anterolaterally, bounded by distinct anterior and dorsal ridges; diastema short, very shallow; mental foramen high on side of jaw; masseteric fossa ending below M_1; teeth low crowned; lophs low on upper molars; conules absent; entoconids and anteroconids distinct.

Range. Early Miocene, John Day Basin, Oregon.

Miosciurus resembles *Protosciurus* and *Sciurus* in possessing low-crowned cheek teeth, large protocones, low lophs on the upper molars and square lower molars with distinct entoconids. However, it is easily distinguished from *Sciurus* by the absence of a well-developed sciuromorph masseteric complex. The masseter is restricted to the anterior and lateral portions of the zygomatic arch and had not yet migrated forward beyond the infraorbital foramen onto the rostrum. In keeping with the primitive condition of the zygomatic plate, the masseteric fossa ends below M_1 not yet having migrated forward under P_4. *Miosciurus* is distinguished from *Protosciurus* by its smaller size, relatively deeper cranium in relation to skull width, shallow diastemal depression and more superior position of the mental foramen. In general, the lower molars tend to be somewhat shorter in relation to their width than they do in *Protosciurus* and the posterior cingulum-protocone union is not as expanded as in that genus. As will be discussed later, it appears likely that *Miosciurus* is close to the point of the ground squirrel divergence.

MIOSCIURUS BALLOVIANUS (Cope)

Plate 2, figure 3

Sciurus ballovianus Cope, 1881, p. 177.

Type. A.M.N.H. No. 6901, incomplete skull, both mandibles, and the head of the right humerus.

Hypodigm. Type only.

Horizon and locality. Diceratherium Beds, John Day Formation, early Miocene. John Day Basin, Oregon.

Diagnosis. As for genus.

Description. The rostrum is short and was probably somewhat deeper than long. Bryant (1945, p. 345) states that it is narrow but this is apparent only and undoubtedly due to displacement of the right premaxilla towards the midline. It must in fact have been rather broad in relation to the overall size of the skull. The frontal projections of the premaxillae are broad, as in *Sciurus* and *Tamias.* A major portion of both the frontals and parietals is missing, exposing casts of the olfactory lobes and the cerebrum. A thin rim of bone is left along the upper border of the orbits with the postorbital process preserved on the left side; it is long and slender, tapering to a thin point and is directed outward, backward and downward. The interorbital distance is relatively great, as in tree squirrels, and the skull roof is flat.

In the construction of the zygomatic plate *Miosciurus ballovianus* resembles some species of *Protosciurus.* The plate is triangularly shaped, bordered by rather well-developed ridges, and faces downward, forward, and outward. It lies lateral and dorsal to the infraorbital foramen but does not expand beyond it onto the rostrum. The masseteric tubercle is small and lies at the lateroventral margin of the oval infraorbital foramen. The infraorbital foramen is situated a short distance anterior to P^3; it is more ovate than is indicated by Bryant's description. The zygomatic notch would appear to have been opposite P^4-M^1 although this is difficult to determine since these teeth are missing on the right side and the alveoli are broken. There is no indication that any part of the masseter spread onto the premaxilla, and there is no trace of a pouch muscle pit behind the incisors. The palate is much too broken and distorted to provide any information.

Both mandibles lack the coronoid, condyle, and angle. The diastema is short and the diastemal depression shallow with the mental foramen lying near its dorsal border just anterior to P_4. The masseteric fossa is rounded and ends below the posterior end of M_1. The ascending ramus arises opposite the middle of M_3.

The upper incisors are oval in cross section and are wider and not as deep as those of the living sciurids. Of the upper cheek teeth only the left M^1 and right M^2 are preserved; the alveoli show that P^3 was present. Both molars are subquadrate with enlarged protocones, but these are not as broad as in *Protosciurus* and *Sciurus*. The protocones are sharper cusps and the posterior cingulum is not expanded at the protocone as in those genera. Protolophs and metalophs are complete, directed somewhat anteriorly, and show no indication of conules. The anterior cingulum is large and rises to a high parastyle; the posterior cingulum is much smaller and fuses with the posterior slope of the metacone before reaching the buccal margin. The mesostyles are large.

The lower incisors are not as compressed as in the Recent squirrels, and are somewhat more convex buccally. The molars increase in size from M_1 to M_3. The trigonids are much higher than the talonids. M_1 and M_2 are rather square with large entoconids and rounded entoconid corners. The anteroconid of M_1 is large and only slightly constricted at its union with the protoconid. On M_2, however, there is a furrow between the anteroconid and protoconid on the buccal face of the tooth and the anteroconid-protoconid union is greatly constricted. The metalophid is complete on both M_1 and M_2 although stronger on M_1, and the trigonid basins are small. The buccal valleys are broad and dammed by weak ectolophids. The hypoconids are somewhat larger than the protoconids. M_3 is similar in most details except that the hypoconid is much larger than on the other molars. The tooth has the typical, rather elongate sciurid shape, and there is an expanded, blade-like posterolophid.

Discussion. *Miosciurus ballovianus* appears to stand in an intermediate position between the chipmunks, on the one hand, and the tree squirrels, on the other. It resembles tree squirrels in: (1) low-crowned, rather heavy dentition; (2) low protolophs and metalophs; and (3) absence of metaconules. *M. ballovianus* resembles chipmunks in: (1) deep cranium; and (2) slight drop of mandible anterior to P_4. In several characters such as the slightly constricted and sharp protocone, the elevated posterolophid, and the partially submerged entoconid, it is intermediate between these two groups but somewhat more chipmunk-like than tree squirrel-like.

This combination of characters leads me to believe that *M. ballovianus* is not far removed from the point of tree squirrel-ground squirrel divergence and that most of the characters seen in this species were present in the ancestor of these two groups.

The shallow diastemal depression, primitive masseteric complex, slightly constricted protocone, and the condition of the entoconid are all characters which were probably present in the ancestral population. However, the deep cranium and complete absence of metaconules would rule out *M. ballovianus* as the ancestor for both tree squirrels and ground squirrels. It does not appear to have left any descendants but it cannot be far removed from the major point of divergence in sciurid evolution.

Measurements

Interorbital width	approx.	7.5
Depth of diastema at mental foramen		3.1
Depth of mandible below M$_1$		4.2
Length of diastema	approx.	2.7

	a-p	tr.
RI^1	1.6	1.0
LI^1	1.6	1.0
LM^1	1.5	1.7
RM^2	1.5	1.7
RI$_1$	0.9	1.8
LI$_1$	0.9	1.8
LM$_1$	1.5	--- -1.5
LM$_2$	1.6	1.6-1.6
LM$_3$	1.8	1.7-1.5
RM$_1$	1.5	1.5-1.5

PROTOSCIURUS n. gen.

Type species. Protosciurus condoni n. sp.

Diagnosis. Skull roof flat; cranium broad, shallow; masseter restricted to masseteric tubercle and lateral margin of zygoma, not passing over the infraorbital foramen onto the rostrum; masseteric fossa ending below M$_1$; diastema short; diastemal depression deep; mental foramen considerably below level of diastema; cheek teeth low crowned; lophs on upper molars low; conules reduced or absent; entoconids large on lower molars; buccal valley wide, shallow.

Range. Middle Oligocene of Nebraska, late Oligocene or early Miocene of Oregon, early Miocene of California.

Discussion. Protosciurus condoni, the type species, is based on an excellent skull that affords a good understanding of the genus. The mid-Oligocene *P. mengi* may confidently be grouped with it, but the remaining species are placed here primarily as a matter of convenience pending better knowledge of them. They agree with *P. condoni* in having cheek teeth of tree squirrel type combined with at least some indication that the zygomasseteric structure had not yet attained the complete sciuromorph condition. It is possible that certain of the European Oligocene and early Miocene forms should be included with this group. However, until all the European material can be adequately reviewed, I restrict *Protosciurus* to the North American forms.

Protosciurus condoni[1] n. sp.
Plates 3, 4

Type. U.O.M.N.H. F-5171, nearly complete skull lacking only the zygomatic arches and rostrum anterior to the incisive foramina and the right mandible lacking the incisor and angle.

Hypodigm. Type only.

Horizon and locality. John Day Formation, Oregon. (The specimen was collected by Condon in 1870 and no further locality data were given.) Late Oligocene or, more probably, early Miocene.

Diagnosis. Largest species of genus; masseteric fossa deep, ending below middle of M_1 with no muscle scar anterior to it; deep pit for insertion of *M. temporalis* behind M_3; protoconules minute on M^1-M^2, metaconules present; M_{1-2} not as long in relation to width as in *P. tecuyensis;* no mesoconids.

Description. The skull is extremely flat dorsally, curving only slightly from a point above the posterior root of the zygoma to the occiput. It is broad interorbitally with no supraorbital notch, shallow at the orbits, and little inflated in the cranium. The rostrum is broad but not deep. The origin of the postorbital process is broad and the process itself is drawn out to a fine point. The lyre-shaped temporal ridges are very weak, originating at the posterior end of the postorbital processes and meeting in a rather stout sagittal crest some little distance in front of the occiput.

The nasals are slender posteriorly, where they project well behind the premaxillary-frontal suture. The premaxillae are broadly expanded at their suture with the frontals and almost exclude the maxillae from the dorsal surface of the rostrum. The premaxillary-maxillary suture on the side of the rostrum is vertical. There is no indication of any swelling of the premaxillae

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[1] Named for the late Professor Thomas Condon in recognition of his pioneering work in the John Day Basin.

lateral to the incisors such as is seen in the protospermophiles. Unfortunately, the extent of the participation of the maxillae in the formation of the anterior root of the zygoma cannot be determined. There is no indication that the masseter had expanded anterior to the infraorbital foramen; it appears to have been confined to the zygomatic root lateral to the infraorbital foramen and to the masseteric tubercle. The portion of the zygomatic plate preserved does not exhibit the anterolateral torsion seen in *Miosciurus*. The zygomatic notch is opposite the posterior end of P_4. The masseteric tubercle is large and lies below and lateral to the infraorbital foramen. The infraorbital foramen opens just anterior to, and slightly above P^3. It is ovate, expanded at the bottom and compressed at the top. The canal is moderately long.

As in *Marmota* and *Sciurus*, the tooth rows are parallel and the palate is broad. The posterior palatine foramen lies opposite the anterior end of M^3 and just behind the maxillary-palatine suture rather than on it. The internal narial opening is broad and does not pinch in posteriorly as in the spermophiles. The pterygoid fossa is narrow but very deep and is bounded laterally by a well-defined ectopterygoid ridge, which, although partially broken in this specimen, was clearly higher and stouter than in Recent squirrels. The pterygoid plate is broad and probably extended back to the bulla.

The ventral wing of the alisphenoid is in contact with the palatine and the pterygoid with a single foramen, the fused buccinator and masticatory, lying in the center of the wing. The alisphenoid turns upwards and slightly backwards just behind the foramen ovale. There is no sharp notch formed between the alisphenoid and bulla as is seen in *Cedromus*. The foramen ovale lies immediately behind the pterygoid fossa with a foramen medial to the foramen ovale for a vein connecting the internal maxillary veins. There appear to be two foramina situated posterior and medial to the foramen ovale, one of which may be the foramen lacerum medium and the other the eustachian canal. The dorsal wing of the alisphenoid cannot be traced with any certainty but it does not appear to pass as far dorsally in the posterior wall of the orbit as it does in modern squirrels.

The exact limits of the bones within the orbit cannot be seen on this specimen. The sphenopalatine foramen would appear to be bounded above by the frontal, anteriorly and below by the maxilla and posteriorly by the orbital process of the palatine. A small sphenofrontal foramen is present as in *Sciurus*. The posterior wall of the orbit is flat rather than gently rounded and the internal limit of the orbit narrows to a very deep groove. The large optic foramen opens into this narrow area and just below and behind the optic foramen the sphenoidal fissure opens into the orbit.

The squamosal forms a greater part of the posterior wall of the orbit than it does in *Sciurus* or *Marmota,* passing over the optic foramen and almost reaching the medial wall. Dorsally the squamosal almost reaches the postorbital notch. Immediately behind the posterior zygomatic root, a distinct postglenoid foramen is present.

The lateral margins of the basioccipital are prominently raised, buttressing the bullae medially, and these ridges are carried forward on the basisphenoid to just behind and medial to the foramen ovale. The basioccipital is quite broad and extends forward to meet the basisphenoid well behind the foramen ovale as in *Sciurus* and *Marmota,* but in contrast to *Paramys* (Wood, 1962, p. 17) where the suture lies at the posterior margin of the foramen. There is no prominent median heel on the basioccipital but there is a wide, shallow arch running forward along the midline of the bone. The foramen lacerum posterius is large, more so than in Recent sciurids, and lies between the petrosal and basioccipital at the posteromedian angle of the bulla. Just posterior to the foramen lacerum posterius a single hypoglossal foramen passes through the basioccipital. The bullae are compressed laterally and hence appear more elongate than in Recent forms; two and a half transbullar septa are present. The occiput is broad and shallow, sloping only slightly posteriorly. The paroccipital processes are broken but appear to have been large. Just above them the occiput is more deeply concave than in the modern forms. The foramen magnum and condyle are as in *Sciurus.*

The mandible is heavy with a deep and relatively short diastema. The mental foramen lies below the diastemal level and only a short distance anterior to P_4. The masseteric fossa is deep and set off by heavy ridges above and below; it extends forward to the back of M_1 with no indication of a scar anterior to this point. The condyle is elongate anteroposteriorly and faces upward and slightly outward. The coronoid process rises from a broad base and curves upward and backward, but the dorsal border does not become horizontal as it does in *Citellus.* Immediately behind M_3 and internal to the ascending ramus there is a deep pit for the insertion of *M. temporalis,* which suggests a much greater development of this muscle especially of its medial part in *Protosciurus,* than in Recent forms. This, together with the deep pterygoid fossa, accords with the fact that the masseter complex was not yet fully developed into the sciuromorph type. With the exception of this pit and the posterior position of the masseteric fossa the mandible closely resembles that of *Sciurus carolinensis.*

P^3 is a stout peg. P^4, although somewhat smaller than M^1-M^2, is completely molariform, resembling M^1-M^2 in all details. These three teeth are all broad internally with a large protocone and expanded protocone-posterior cingulum crest within which a small cusp is evident. The anterior cingulum is large but there is no well developed parastyle. The lophs are low, complete, and show small protoconules and metaconules. The buccal border is preserved only on the left M^2. Here a small mesostyle is present at the base of the paracone. M^3 is the largest tooth in the series with a greatly expanded metacone. There is no sharp indentation between protocone and metacone; the posterior cingulum passes evenly posterointernally from the protocone to the metacone.

P_4 is badly broken, but it would appear that the protoconid and metaconid were closely appressed; it is impossible to determine whether or not an anteroconid was present. M_1 and M_2 are nearly square in outline. The four principal cusps are large, and there are well developed anterior cingula and mesostylids present, but there is no sign of a mesoconid. The buccal valleys are broad, rather shallow, and slope from the talonid basin to the buccal margin. The entoconid corners are angular and the posterolophids low. M_3 is the largest tooth of the series. It displays a prominent anteroconid, a mesostylid, an expanded entoconid, and a very large hypoconid. The posterior half of the tooth is almost as wide as the anterior half, a condition generally true for Recent tree squirrels and chipmunks but not for other members of the family.

Discussion. P. condoni, while decidedly primitive, is certainly a tree squirrel and an almost ideal ancestor for the later tree squirrels. With an increase in depth of the cranium, a greater flexure of the basicranial axis (probably in conjunction with increased arboreal activity), further perfection of the zygomasseteric structure, and minor changes in the dentition, *P. condoni* could readily be transformed into *Sciurus.* However, due to the scarcity of tree squirrels in the fossil record this transition cannot be documented at present, but it probably took place through a stage such as is represented by *P. rachelae* also from the John Day. *P. condoni* is clearly distinct from *Cedromus* or *Prosciurus* but unfortunately tells us little about the possible paramyid ancestry of the family. As stated elsewhere (p. 230), I do not believe *Cedromus* to be a sciurid or to have had any direct connection with the ancestry of the family.

Measurements

Interorbital width at supraorbital notch	23.0
Interorbital width at postorbital notch	19.0
Depth rostrum anterior to masseteric tubercle	16.2
Depth cranium behind M^3	19.4
Depth cranium at anterior end of bullae	19.2
Width across occiput	30.5
Length of diastema	9.9
Length of mandible, anterior tip to condyle	47.1
Alveolar length P^3-M^3	15.8
Alveolar length P_4-M_3	14.9

PROTOSCIURUS MENGI[1] n. sp.

Plate 5, figure 1

Type. U.M.M.P. No. 39559, portion of left horizontal ramus with P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Lower Orellan, Middle Oligocene. A. Meng Ranch, S.12, T.33N., R.54W., northwest of Crawford, Sioux County, Nebraska.

Diagnosis. Smaller than *P. condoni;* M_{1-2} not as long in relation to width as in *P. tecuyensis;* mesoconids strong.

Description. The masseteric fossa appears to have terminated below M_1 but the mandible is too badly broken to be absolutely certain of this. The origin of the ascending ramus is at the posterior border of M_2. There is a pit behind M_3 for the insertion of part of *M. temporalis.*

The teeth increase in size from P_4 to M_3. Strong entoconids, mesostylids and mesoconids are present on all the teeth. The anteroconid is a distinct cusp on P_4 but blends progressively into the anterior cingulum on M_1-M_3. The trigonid is considerably higher than the talonid. The metalophid is progressively weaker from P_4-M_3 and the trigonid basin is small on all teeth. The entoconid is large and distinct but partially incorporated in the posterolophid which is higher than in *Sciurus* or *Protosciurus condoni.* The entoconid corner is very slightly rounded. The mesoconid slopes buccally on all the teeth leaving little or no shelf area in the buccal valley. The enamel of the talonid basin is finely wrinkled on all teeth.

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[1] Named for A. Meng on whose ranch the specimen was collected.

Discussion. P. mengi is the oldest known sciurid. It resembles Recent tree squirrels in many respects and seems certainly to belong with that group of sciurids. However, its dentition differs from that of *Sciurus* in the following characters: (1) The teeth are not as wide as those of *Sciurus;* (2) the posterolophid is somewhat higher thus submerging more of the entoconid within it; (3) the trigonid is higher; and (4) the metalophid is weaker. *P. mengi* agrees with *P. condoni* as regards the first of these characters but differs from *P. condoni* as regards the other three. *P. mengi* bears some resemblance to *Sciurus* sp. (Stehlin and Schaub, 1951, p. 198, fig. 295 A) from the upper Stampian. However, the trigonid basin and entoconid are smaller in *P. mengi* and the metalophid is not as strong.

As one would expect, the characters seen in *P. mengi* are neither those of a typical tree squirrel nor ground squirrel but are intermediate between these two groups in most respects. With an increased development of the posterolophid and incorporation of the entoconid within it, *P. mengi* could easily have given rise to the small chipmunk-like sciurids of the early Miocene and through this stage to the *Miospermophilus* ground squirrels. Likewise, *P. mengi* is very probably close to the ancestry of *P. condoni* and possibly other members of the genus.

Measurements

Alveolar length P_4-M_3	11.4

PROTOSCIURUS TECUYENSIS (Bryant)

Plate 5, figure 2

Sciurid sp. Stock, 1920, p. 272.
Sciurus tecuyensis Bryant, 1945, p. 341.

Type. U.C.M.P. No. 23611, partial right mandible with M_1-M_2.

Hypodigm. Type only.

Horizon and locality. Lower Arikareean, early Miocene. East side Tecuya Canyon, about 35 miles south of Bakersfield, Kern County, California.

Emended diagnosis. Jaw heavy; masseteric crests prominent; masseteric fossa ending below hypoconid of M_1 with small scar anterior to it below protoconid of M_1; molars as long or longer than wide; anteroconid large; mesostylid distinct, set off from entoconid.

Description. The jaw is very heavy, about as in *Protosciurus condoni,* and more so than in *P. mengi.* The masseteric fossa and crests are correspondingly deep and prominent. M_1 and M_2 are essentially identical in structure, M_2 being somewhat the larger. The large entoconids are set off from the mesostylids by sharp grooves. The anteroconids are better defined and the mesoconids relatively a little smaller than in *P. mengi*. There is no shelf at the base of the mesoconid and the buccal valleys are shallow. The most striking character is the anteroposterior elongation of the molars.

Discussion. In most respects *P. tecuyensis* is similar to *P. condoni* of the John Day. It differs from the latter in the greater length of the molars in relation to their width. At present no descendants of *P. tecuyensis* can be recognized.

Measurements

Depth below anterior end M_1	9.0
Alveolar length P_4-M_3	13.4

PROTOSCIURUS RACHELAE[1] n. sp.

Plate 6

Type. A.M.N.H. No. 7241, a partial left maxilla and premaxilla with I, M^1-M^3.

Hypodigm. Type and U.O.M.N.H. No. F-5039, a fragment of right mandible with M_1-M_3.

Horizon and locality. John Day Formation, probably early Miocene, exact horizon not recorded. John Day Basin, Oregon.

Diagnosis. Smaller than *P. condoni* and *P. tecuyensis;* lophs of M^1-M^2 very low; conules absent; M_1-M_2 wider in relation to length than in *P. condoni, P. mengi,* or *P. tecuyensis;* no mesoconid; posterolophid low.

Description. Only that part of the premaxilla surrounding the anterior end of the incisor and bordering the incisive foramen is preserved. There is no pit in the premaxilla posterior to the incisor for the insertion of a dorsal cheek pouch muscle. The relationship of the infraorbital foramen to the zygomatic plate is clearly demonstrated in that section of the maxilla that is preserved. The infraorbital foramen opens just anterior to and slightly above P^3 and the canal is moderately long as in *P. condoni*. However, the foramen is much more compressed in *P. rachelae* and is a vertical slit. This greater compression is probably due to a

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[1] Named for Rachel H. Nichols whose work at the American Museum on the behalf of paleontologists throughout the world will always be remembered.

somewhat more extensive zygomatic plate lateral to the infraorbital foramen in *P. rachelae.* The masseteric tubercle is large and lies at the ventrolateral corner of the infraorbital foramen. The zygomatic plate is restricted to that part of the maxilla that forms the anterior root of the zygomatic arch lateral to the infraorbital foramen. The plate probably passed above the infraorbital foramen but this portion of the arch is not preserved. The zygomatic plate is concave and faces anterolaterally more so than in *P. condoni* and the plate area appears to be relatively larger in *P. rachelae* than in *P. condoni.* The zygomatic notch is opposite the posterior half of P^4.

P^3 and P^4 are represented only by their roots. M^1-M^3 are low crowned, increase in size from front to back, and have low, rounded, complete lophs. M^1 and M^2 are subquadrate with expanded protocones. There is no indication of either protoconules or metaconules. The anterior cingulum is only moderately expanded and lacks a large, steep parastyle. The incisor is not greatly compressed; it is flattened internally and gently rounded externally. The enamel extends one-third of the way down the external surface but does not overlap onto the internal surface.

Too little of the mandible is preserved to be sure of the extent of the masseteric fossa but it would appear to have terminated below the center of M_1. The molars are quadrate and increase in size from M_1 to M_3. They are moderately worn but all details of the crown pattern are readily discernible. M_1 and M_2 are nearly identical in shape and pattern, with M_2 being slightly larger. They are wider than long and on each the entoconid is distinct and the entoconid corner angular. The trigonid is only slightly higher than the talonid and the trigonid basin is extremely small. The metalophid, although worn, appears to have been complete. The posterolophid is low. A small mesostylid is present. The buccal valley is shallow and shows no trace of a mesoconid. There is little or no development of an anteroconid. M_3 is expanded posteriorly with an enlarged hypoconid and an entoconid that is almost completely submerged in the posterolophid.

Discussion. *P. rachelae* is smaller than *P. condoni* and differs from it in several other respects. The zygomatic plate appears to be somewhat more fully developed in *P. rachelae,* approaching the condition seen in *Miosciurus ballovianus. P. rachelae* also resembles *M. ballovianus* in the absence of conules in the lophs of M^1-M^2. However, the low, rounded lophs and broad protocones of *P. rachelae* tend to ally it with *Protosciurus* rather than *Miosciurus. P. rachelae* resembles *P. mengi* in many details of the lower dentition but differs from it in having much lower trigonids, distinct entoconids, and somewhat lower, more rounded cusps.

There is nothing that would exclude *P. rachelae* from the ancestry of later tree squirrels and several characters seen in the species suggest this. These are: (1) the shape of M^1-M^2 which are wider than long; (2) the low rounded protolophs and metalophs; (3) the absence of conules; (4) the broad protocones; (5) the low trigonids and posterolophids; (6) the distinct entoconids; and (7) the angular entoconid corners of M_1-M_2. *P. rachelae* represents an advance over *P. condoni* toward the tree squirrel condition, and quite probably stands in direct ancestry to later tree squirrels.

Measurements of the cheek teeth of the species of *Protosciurus*

		P. condoni	*P. mengi*	*P. tecuyensis*	*P. rachelae*
P^3	a-p	1.5			
	tr.	1.9			
P^4	a-p	3.2			
	tr.	3.6			
M^1	a-p	3.4			1.9
	tr.	3.8			2.4
M^2	a-p	3.6, 3.6			2.0
	tr.	4.0, 4.0			2.6
M^3	a-p	4.2, 4.2			2.3
	tr.	4.0, 4.0			2.3
P_4	a-p	3.2	2.5		
	tr.		2.2-2.5		
M_1	a-p	3.3	2.5	3.1	2.2
	tr.	3.4-3.4	2.7-2.8	2.8-3.1	2.3-2.5
M_2	a-p	3.6	2.8	3.4	2.4
	tr.	3.8-3.8	3.0-3.1	3.1-3.2	2.7-2.7
M_3	a-p	4.4	3.2		2.6
	tr.	3.8-3.4	3.0-2.6		2.5-2.1

SCIURUS sp.

Sciurus sp. Wallace, 1946, p. 123.

Referred material. L.A.C.M. (C.I.T.) Nos. 3076 and 3078, both specimens are right maxillary fragments with M^2-M^3. In L.A.C.M. (C.I.T.) No. 3076 the right M^2-M^3 are preserved along with the alveoli of P^3-M^1, a portion of the palate, part of the zygomatic plate, and the masseteric tubercle and infraorbital foramen.

Horizon and locality. Hemingfordian, Middle Miocene, Beatty

Butte Tuffs exposed on E. side of Beatty Butte, 24 miles SW. of Blitzen, Oregon.

Description. The infraorbital foramen is lateral to and only slightly above the masseteric tubercle. It is compressed but the long axis is more nearly horizontal than vertical. The masseteric tubercle is low and situated just anterior to the alveolus for P^3. The zygomatic plate does not appear to be as fully developed as in Recent sciurids, judging from the inclination of the infraorbital foramen. It faces downward and forward and does not rise as steeply towards the superior surface of the rostrum as it does in Recent forms. This incomplete development is also reflected in the more horizontal position of the infraorbital foramen which has not yet been compressed into a vertical slit by the upward expansion of the masseter.

The second upper molar is quadrate in outline with a broad protocone and low lophs without conules. The anterior cingulum is relatively narrow and the parastyle low. There is a very large mesostyle on the buccal margin of the tooth. M^3 is triangular with a broad protocone and expanded posterior cingulum which passes diagonally from the protocone to the postero-buccal corner of the tooth. The paracone is high and the protoloph drops abruptly away from it to the protocone. The anterior cingulum and parastyle are small.

Discussion. These specimens clearly indicate the presence of *Sciurus* in this late Hemingfordian fauna but the material is much too fragmentary to indicate any precise relationship to modern species. It does, however, appear to be fully as advanced as the Recent forms, and, in the dentition, resembles *S. carolinensis* more than any other species.

GENUS AND SPECIES INDETERMINATE

Plate 7, figure 1

Referred specimen. Y.P.M. No. 13602, a right mandible with I, P_4-M_3, lacking the ascending ramus and angle.

Horizon and locality. Arikareean, early Miocene. John Day Valley, Oregon.

Description. The mandible is slender and shallow with a long diastema and shallow diastemal depression. The mental foramen lies somewhat below the diastemal level midway between P_4 and the anterior extremity. The masseteric fossa extends forward under the posterior half of P_4 and is sharply pointed anteriorly. That part of the area of insertion of *M. temporalis* behind M_3 is a well defined pit with an elevated ridge along the medial side.

P_4 is trapezoidal with closely appressed protoconid and metaconid. These cusps are separated by a narrow but deep notch. The ectolophid is low and bears a large mesoconid, which fills the shallow buccal valley. The posterolophid is curved and the entoconid submerged within it. There is a notch between the end of the posterolophid and the metaconid and no indication of a mesostylid. M_1 and M_2 are compressed anteroposteriorly and relatively wide. The trigonid basins are very small and completely enclosed. There is no indication of an anteroconid on either tooth. The ectolophids are low and the buccal valleys shallow. The posterolophids are low and pass almost directly transversely across the teeth to end in distinct entoconids. There is a deep notch between the entoconids and the prominent mesostylids. M_3 is triangular with a moderately expanded hypoconid and a posterolophid that is slightly constricted at the entoconid. There is a distinct notch between the entoconid and the small mesostylid.

Discussion. This specimen has an extremely advanced masseteric structure which is quite in contrast to that seen in the other John Day sciurids. The dentition is closer to that of *Protosciurus* and *Sciurus* than to that of other squirrels. M_1-M_2 are, however, somewhat wider in relation to their length than they are in *Protosciurus* and *Sciurus* and the notch between the entoconid and mesostylid is more prominent than in either of those genera. In this respect the specimen is somewhat reminiscent of *Glaucomys*.

Measurements

Depth at mental foramen		5.22
Depth below M_1		6.53
Alveolar length P_4-M_3		8.22
Occlusal length P_4-M_3		8.02
	a-p	tr.
P_4	1.75	1.50-1.85
M_1	1.85	2.20-2.35
M_2	2.00	2.50-2.50
M_3	2.30	2.40-2.05

TRIBE MARMOTINI Simpson 1945

Limbs relatively short, stout; distal ends of radius and ulna, and tibia and fibula broad; three to four sacral vertebrae; skull roof flat to moderately convex; zygomatic plate inclined at 50°

or less in relation to basicranial axis; skull relatively narrow interorbitally; diastema long, diastemal depression shallow; anterior end of mandible at or above level of alveolar border; upper molars triangular to subquadrate; metaconules usually well developed; entoconids indistinct and incorporated in posterolophids (except in *Arctomyoides* and *Protospermophilus*); lingual portion of lower molars generally more greatly compressed anteroposteriorly than buccal portion.

Range. Early Miocene to Recent in North America.

PALAEARCTOMYS Douglass

Type species. Palaearctomys montanus Douglass.

Diagnosis. Rostrum broad, deeper than in *Marmota*; zygomatic plate failing to reach dorsal surface of rostrum; infraorbital foramen slit-like; masseteric tubercle small, set well below infraorbital foramen; zygomatic arch slender; palate broad; postpalatal vacuities present just above internal nares; postorbital processes large, with no posterior curvature; diastemal region of mandible extremely heavy; molars small in relation to size of skull; upper incisors grooved, lower incisors with many fine longitudinal striations.

Range. Probably late Miocene (Barstovian).

PALAEARCTOMYS MONTANUS Douglass

Plates 8, 9

Palaearctomys montanus Douglass, 1903, p. 183.
Palaearctomys macrorhinus Douglass, 1903, p. 184.

Type. C.M. No. 740, poorly preserved skull without dentition, basicranium, most of occiput, nearly complete right and left mandibles, and a few skeletal elements.

Type of synonym. C.M. No. 733, well preserved skull lacking the nasals, left zygomatic arch, occipital region and basicranium, and RP^4, M$^{2-3}$, LM$^{1-3}$

Hypodigm. The types only.

Horizon and locality. Lower Madison Valley Formation, probably Barstovian, late Miocene. Gallatin County, Montana.

Diagnosis. As for the genus.

Douglass (1903) described two species of *Palaearctomys*, both based on skulls from the Lower Madison Valley. One specimen, C.M. No. 733, was in excellent condition while the other, C.M. No. 740, was badly broken. The latter was made the type of *P.*

montanus. This skull was reconstructed using an excessive amount of plaster and a Recent marmot skull as a model. The reconstruction thus resembled the Recent *Marmota monax* in most respects. This condition was quite in contrast to that displayed in the uncrushed skull. Consequently, the well preserved skull was made the type of *P. macrorhinus* and from the description of each species (Douglass, 1903, pp. 182–186) little comparison was made between the two. Bryant (1945) discussed both species but again made no real comparison of the two except as noted in his diagnosis.

It is quite obvious that these two skulls belong to the same species, once due allowance has been made for the plaster in the type skull. Measurements of all areas where the original bone has not been distorted, such as length of palate and depth of rostrum, are nearly identical for the two skulls. Also, the postpalatine vacuities occur in both specimens and are unknown in any other sciurid. The material is therefore considered to represent one species, *Palaearctomys montanus.*

Description. The skull is heavy and although of approximately the size of that of *Marmota monax* is considerably deeper through the rostrum and orbital region. As in *Marmota*, the skull roof is flat, the postorbital processes large, and the skull narrow behind the postorbital processes. The sagittal crest is prominent, especially in C.M. No. 740 where the temporal ridges are fused opposite the squamosal root of the zygomatic arch. The zygomatic arch is expanded posteriorly, although not to the extent seen in *Marmota*, and the jugal is somewhat twisted so that it does not lie in the vertical plane, although not as much so as in the ground squirrels. The arch is extremely thin and there is no well defined fossa marking the origin of the posterior part of the *M. masseter lateralis* as there is in *Marmota*. The nasofrontal sutures, and the premaxillary-frontal sutures form a straight line across the roof of the skull parallel to the anterior edge of the orbit. This is quite in contrast to the condition in *Marmota* where the nasals extend posteriorly well beyond the premaxillary-frontal sutures. The extent of premaxillary-frontal contact is also greater in *Palaearctomys* than in *Marmota*. The nasals expand as they pass anteriorly; they do not extend anteriorly in advance of the incisors. The premaxillary-maxillary suture passes anteriorly to the dorsal lip of the zygomatic plate and then descends in a straight line down the rostrum and across the palate to the incisive foramen. The *M. masseter lateralis* appears to have been limited to the maxilla. The zygomatic plate does not reach the dorsal surface of the rostrum but terminates at the level of the incisor alveolus. There is a slight depression in the maxilla just below its dorsal extension. The lateral edges of the anterior zygomatic roots do not overhang the plate area as they do in *Marmota.* The infraorbital foramen is a vertical slit set rather high on the side of the rostrum; the canal is short. The zygomatic notch is opposite the contact between P^4-M^1. The masseteric tubercle is extremely small, lying just anterior to P^3 and well below the infraorbital foramen; a low, rugose ridge runs from it to the base of the infraorbital foramen. The palate is broad and the tooth rows nearly parallel. The palatine-maxillary suture extends forward to the level of the middle of M^1, where, in contrast to the condition in *Marmota,* it is transverse. Beginning opposite M^3 and extending back below the internal nares there are two large postpalatal fossae that appear to lie completely within the palatines. These fossae resemble those occurring in geomyids; however, they do not appear to have foramina at their anterior ends, as do those of *Geomys.* Near the posterior border of the lateral wall of each fossa there is a rather large opening. These openings may be due to breakage but they could also be foramina. What function the fossae may have served is unknown; comparable structures are not known in any other sciurid, fossil or Recent. The internal nares open much farther posteriorly than in *Marmota,* due to the presence of these fossae. The buccinator and masticatory foramina are fused. The paroccipital processes are stout and stand well away from the bullae.

The mandibles are extremely heavy and deep, much more so than in *Marmota* or in *Arctomyoides.* The diastemal area in particular is short, very deep and greatly swollen lateral to and above the incisor. The anterior tip of the mandible lies about on the level of the alveolar border. The dorsal surface of the mandible drops steeply anterior to P_4 and then curves upward to the rim of the incisor alveolus. The mental foramen lies about two-thirds of the way up the side of the mandible and midway between the incisor and P_4. The ventral masseteric crest is strong. The ascending ramus rises opposite the anterior end of M_3; its anterior border forms a continuous slope. The condyle is broad and lower than in *Marmota.*

Judging from the size of the alveolus, P^3 was rather small, as are all of the cheek teeth in relation to skull size. P^4 is incomplete, lacking the anterior cingulum and much of the protoloph. The protocone appears to have been broad. The posterior cingulum is small, the metaloph low and complete, with the metaconule completely subordinated within it. A large mesostyle is present. M^1-M^2 are subquadrate in outline with expanded protocones. The protolophs and metalophs are low, complete, and there is no metaconule. The anterior cingula are only moderately expanded and the parastyles are small, both notable differences from *Marmota*. The mesostyles are large. M^3 is triangular in outline with only a slight expansion of the posterobuccal portion of the tooth. The upper incisor is extremely heavy and almost triangular in outline. There is one well marked groove on the anterior face as well as innumerable fine longitudinal striations.

The known lower cheek teeth are all so worn that some of the pattern has been obliterated. P_4 is smaller than M_1 and is trapezoidal in outline. The protoconid and metaconid are set close together but there is a distinct deep notch between them; anteriorly, they are united by a small anteroconid. The ectolophid is low and bears a mesoconid. The posterolophid is low and terminates in a distinct entoconid. A narrow notch separates the entoconid from the large mesostylid. M_1-M_2 are rectangular in outline. They are wider than long and the buccal and lingual widths are equal. There is no trace of an anteroconid, a mesoconid, or a mesostylid on any of the molars. The metalophid was evidently incomplete on all and the trigonid not greatly elevated above the talonid. The posterolophid on M_1-M_2 is low and passes slightly diagonally from the hypoconid to the distinct entoconid. The buccal valleys are broad and shallow. M_3 is triangular in outline with greatly enlarged hypoconid and posterolophid. The lower incisors are very compressed and flattened both medially and laterally. They are much larger than in Recent species of *Marmota*. They are not distinctly grooved as are the upper incisors but the enamel bears many fine longitudinal striations.

Discussion. *Palaearctomys* resembles *Marmota* in a general way and is certainly closer phylogenetically to it than to other sciurids. Nevertheless, it differs in a great many characters, the most striking of which are the small size of the cheek teeth and large size of the incisors in relation to skull size. The presence of postpalatal fossae is also unique in this genus. This would indicate a rather early separation of the *Palaearctomys* line. There appears to be no close relationship between *Palaearctomys* and *Arctomyoides* or *Paenemarmota*. These three genera probably represent as many offshoots within the Marmotini, none of which has left any descendants.

Measurements

	C.M. No. 740	No. 733
Depth of rostrum (taken just anterior to dorsal termination of zygomatic plate)	24.0	23.9
Width of rostrum	21.2	22.2
Length of palate (posterior edge of incisors to internal narial opening)	46.4 (approx.)	44.7
Interorbital width (behind postorbital processes)	20.8	20.0
Length mandible (anterior tip of incisor to condyle)	70.5	—
Length of diastema	16.8	—
Depth of mandible at mental foramen	12.7	—
Depth of mandible under M$_1$	17.7	—
Alveolar length P^3-M^3	—	15.4
Alveolar length P$_4$-M$_3$	15.1	—

	C.M. No. 733			C.M. No. 740	
	a-p	tr.		a-p	tr.
RP^4	3.30	3.60	RI$_1$	7.20	3.30
RM^2	3.80	4.30	RP$_4$	3.30	3.00-3.30
RM^3	4.30	4.10	RM$_1$	3.40	3.80-3.80
LM^1	3.50	4.10	RM$_2$	3.60	4.30-4.20
LM^2	3.80	4.30	LI$_1$	7.20	3.30
LM^3	4.20	4.10	LP$_4$	3.40	3.00-3.30
			LM$_1$	3.30	3.80-3.80
			LM$_2$	3.60	4.30- —
			LM$_3$	4.20	4.20-3.70

ARCTOMYOIDES Bryant

Type species. Sciurus arctomyoides Douglass.

Diagnosis. Diastemal depression shallow and long, dropping gently from P$_4$; superior border of masseteric fossa nearly reaching alveolar border; upper incisor with distinct median longitudinal groove; lophs on M^1 complete, low; protocone, anterior cingulum broad; M^1 subquadrate; M$_1$-M$_2$ nearly square in outline, entoconids large, ectolophids weak, metalophids incomplete.

Range. Late Miocene (Barstovian).

ARCTOMYOIDES ARCTOMYOIDES (Douglass)
Plate 7, figure 2

Sciurus arctomyoides Douglass, 1903, p. 181.
Arctomyoides arctomyoides Bryant, 1945, p. 361.

Type. C.M. No. 741 incomplete premaxillae and partial right maxilla with right and left I^1 dP^3-dP^4 and M^1, RI_1, nearly complete left mandible with dP_4-M_3, incomplete I_1.

Hypodigm. Type only.

Horizon and locality. Late Miocene, Lower Madison Valley Formation near Logan, Gallatin County, Montana.

Diagnosis. As for genus.

Description. The upper incisors are not greatly compressed and their anterior faces bear many fine longitudinal striations and a single median groove. The deciduous third premolar is a very small peg-like tooth that fits against the anterointernal portion of dP^4. The anterior cingulum and parastyle of dP^4 are large, making the tooth much longer buccally than lingually. The protocone occupies most of the lingual border. The protoloph is low, complete, without conules, and passes directly across the tooth. The metaloph is low and passes anteromedially to the protocone; it is only partially constricted at the protocone and lacks a distinct metaconule. The mesostyle is well developed and the posterior cingulum small. M^1 is nearly quadrangular in outline. The protocone is very broad and there is a small cuspule at the junction between protocone and posterior cingulum. The lophs are low and without conules. The anterior cingulum is broad and the parastyle high but not as well developed as on dP^4. The mesostyle is large.

The horizontal ramus of the mandible is massively built beneath the cheek teeth, more slenderly in the symphysial region. The diastemal portion of the mandible is long and shallow, sloping gently away from dP_4. The mental foramen lies near the center of the lateral surface of the symphysial region beneath the midpoint of the diastema. The masseteric fossa is deep and lies high on the side of the mandible with its superior border almost merging with the alveolar border. It is gently rounded anteriorly, terminating below the anterior end of M_1. Bryant (1945, p. 362) states that the dorsal surface of the condylar process is in the same plane as the alveolar border, but this is not the case. The ascending ramus has been crushed and forced somewhat downward and the condyle itself is missing; with proper restoration the process would actually be well above the alveolar border. The anterior border of the coronoid process merges with the alveolar border opposite the protoconid of M_2.

The lower incisors are greatly compressed and have many fine longitudinal striations on their anterior faces; the incisors taper considerably toward their tips, due to the extreme youth of the specimen. dP_4 is much longer than wide and is considerably smaller than M_1. The protoconid and metaconid are widely separated and joined anteriorly by a heavy, short, anterior cingulum. The metalophid is weak but does close off the trigonid basin posteriorly. The posterolophid curves gently from the hypoconid to the distinct entoconid. The ectolophid is partially elevated and set close to the buccal margin. Neither mesostylid nor mesoconid is distinct. M_1 and M_2 are essentially identical in structure, except that the anterior cingulum joins the protoconid at a somewhat greater angle on M_1, the trigonid basin being thus slightly more rounded on M_1. On both teeth the metalophid is weak; the protoconid and hypoconid are of equal size and are joined by an elevated ectolophid bearing a prominent mesoconid; the posterolophid is curved, ending in a large entoconid; a large mesostylid is present. M_3 is not much larger than M_2 but differs from that tooth in having a greatly expanded hypoconid and a crenulated posterolophid that curves much more sharply from the hypoconid to the metaconid; entoconid and mesostylid are lost to view among the crenulations.

Discussion. Douglass assigned this species to *Sciurus,* stating (1903, p. 182) "the teeth are intermediate between those of *Sciurus* and *Arctomys,* rather more resembling some species of the former." Bryant placed the species in a new genus, *Arctomyoides,* observing that it was closer to *Marmota* than to *Sciurus* (he mistook dP^4 for P^4 but recognized the presence of dP_4) in many characters of the dentition. These included (1945, p. 362) "enlarged parastyles, protocones of P^4-M^1 small and teeth consequently triangular in occlusal outline, protolophs and metalophs convergent toward the protocones rather than parallel, ectolophids elevated and situated well in from the margins of the molars, talonid basins deep and longer than wide, posterolophids crescentic, diastemal portion of mandibular ramus long and shallow and its anterodorsal border as high as the alveolar border, and the dorsal surface of the condyloid process is level with the mandibular tooth row." Certain of these characters do not indicate as close a relationship to *Marmota* as Bryant believed. The parastyle on M^1 is enlarged but no more so than in the protospermophiles and not as much so as in *Marmota*. It is high on dP^4 but it is generally much higher on dP^4 than on P^4 in all groups of sciurids. The protocone on M^1 is actually nearly as wide as the lingual margin of the tooth making the tooth subquadrate rather than triangular. The protolophs and metalophs are no more convergent than in *Sciurus niger* or *S. carolinensis*. The ectolophids are more elevated and set further in than in *Sciurus* but they do not approach the condition seen in *Marmota vetus, Marmota minor,* or Recent marmots. The talonid basins are more as in *Marmota* as regards depth, but in *Marmota* they are wider than long, just the reverse of what is seen in *Arctomyoides*. The posterolophids are somewhat curved, more so than in *Sciurus* but less so than in *Marmota*. The mandible differs from both *Sciurus* and *Marmota* in its construction. Other differences between *Arctomyoides* and *Marmota* were noted by Bryant and include the presence of large mesoconids and entoconids.

It seems evident that *Arctomyoides* possesses a suite of characters that sets it apart from both *Sciurus* and *Marmota*. In fact it is just as close to *Protospermophilus* as to either of them, particularly in the structure of dP^4-M^1. On the evidence, I believe that *Arctomyoides* was probably an early offshoot from the line leading to *Marmota* from *Protospermophilus*. *Arctomyoides* evolved certain specializations of its own, such as the increased length of the molars, the high position of the masseteric fossa on the side of the jaw, and a long, shallow diastema, and independently acquired such marmot specializations as the increased prominence of the ectolophid.

Measurements

Diastemal length	13.0
Depth below P_4	11.0
Depth below M_1	11.8
Alveolar length dP_4-M_3	15.5

	a-p	tr.		a-p	tr.
dP^3	1.20	1.20	dP_4	3.30	2.50-3.10
dP^4	3.40	3.20	M_1	4.00	4.00-4.10
M^1	3.90	4.40	M_2	4.20	4.40-4.40
I	2.30	3.80	M_3	4.30	4.40-3.80
			I	4.00	2.00

PAENEMARMOTA Hibbard and Schultz

Type species. Paenemarmota barbouri Hibbard and Schultz

Emended diagnosis. "A ground squirrel (Tribe Marmotini) belonging in the "Terrestrial Squirrel Section" of Bryant (1945, p. 372); larger than all other known ground squirrels. Lower teeth with base of incisor well behind M_3, rather than beneath (incisor crosses beneath M_{2-3} and its base forms a slight swelling on the external surface of the ascending ramus slightly beneath alveolar plane); P_4 larger than M_1 and progressively molariform; all four cheek teeth with rugose talonid basins and basin trench along ectolophid and metalophid margins of basin and individually varying in extent along posterolophid margin of basin; protoconid larger than in *Marmota* and about as high as parametaconid in unworn teeth; mesoconid present or absent on the ectolophid of M_3 and P_4, and lower incisor with longitudinal striations. Upper teeth with P^4 as large as, or larger than M_1; metaconule well developed on P^4 and absent or only slightly developed on molars; posterior cingulum prominent across width of tooth because of broad posterior valley; M^3 with well-developed metaloph that is more or less parallel to protoloph and separated from protocone in unworn teeth; M^3 also with broad posterior valley with or without a rugose floor but lacking the pronounced posterior lobe of some modern ground squirrels; P^3 with anterior cingulum and double-cusped "protoloph" followed by a distinct valley and loph-like posterior cingulum; upper incisor striated. Masseteric tubercle very prominent; palate more concave (upward) than in *Marmota* and most ground squirrels; cheek pouch rudimentary; lower jaw massive; and masseteric fossa variable in form but without pronounced dorsal crest of *Marmota*." (Repenning, 1962, p. 543.)

Range. Hemphillian of Mexico and early Pleistocene of Nebraska, Kansas, Texas and Arizona.

PAENEMARMOTA BARBOURI Hibbard and Schultz

Type. K.U. No. 6994, a nearly complete left ramus with incisor, P_4-M_3.

Horizon and locality. Early Pleistocene, Rexroad Formation. S.34, T.34S., R.30W., Meade County, Kansas, Locality No. 22.

Diagnosis. As for genus.

Discussion. This genus has recently been reviewed by Charles

A. Repenning (1962) and has not been examined by me. From the published descriptions and illustrations (Hibbard and Schultz, 1948; Repenning, 1962), *Paenemarmota* would appear to be a highly specialized offshoot of the true *Marmota* stock. The genus appears to have little in common with *Palaearctomys* or *Arctomyoides*. It does resemble *Marmota nevadensis* in certain respects, however, particularly in the rugose talonid basins and overall size and shape of the dentition. P_4 of *M. nevadensis* is not as large as that of *Paenemarmota*, however.

Repenning believes *Paenemarmota* to be possibly more closely related to *Citellus* than to *Marmota* although he states that sufficient fossil evidence is not available at present to be certain of exact relationships. From his descriptions and illustrations, *Paenemarmota* would appear to me to have been derived from the *Marmota* lineage probably just shortly after the marmots arose from the protospermophiles. The enlarged P^4_4, the presence of mesoconids in the Pliocene material, the general shape of the teeth, and the absence of mesostylids with the resulting rather broad gap between the entoconid and metaconid all tend to ally *Paenemarmota* with *Marmota*. The differences in the heaviness of the dorsal border of the masseteric fossa and the presence of the basin trench of the talonid would not contradict this relationship. Both dorsal and ventral masseteric crests vary widely in prominence in samples of *Marmota monax* and, while the dorsal crest is not prominent in *Paenemarmota*, I would not consider this character of equal weight in determining relationships with some dental and other mandibular characters. The presence of the basin trench is dependent upon the development of ridges or cuspules in the talonid basin and can be found in both the spermophile and marmot groups. On the evidence available, I would favor a closer relationship to *Marmota* than to *Citellus* for *Paenemarmota*.

MARMOTA Frisch

Type species. Mus marmota Linnaeus.

The genus *Marmota* is very poorly represented in the fossil record with only three pre-Pleistocene records known at present. Marmots first appear in the early Pliocene of Nebraska and can be traced through the Pliocene. However, the lineages of modern species cannot be traced back into the Pliocene with any degree of accuracy. *M. vetus* of the Clarendonian and *M. minor* of the Hemphillian are both much smaller than the Recent species but show the enlargement of P_4, the narrow lingual borders of M_1-M_2.

and the reduced M^3_3 characteristic of all modern forms. *M. nevadensis* from the Hemphillian is not closely related to either *M. vetus* or *M. minor* and certainly was not ancestral to Recent species of the genus. Nevertheless, it is even further removed from *Palaearctomys* and *Arctomyoides* and is therefore retained in *Marmota* for the present.

Range. Early Pliocene to Recent in North America.

MARMOTA NEVADENSIS (Kellogg)
Plate 10

Arctomys nevadensis Kellogg, 1910, p. 422.
Marmota nevadensis Wilson, 1937b, p. 34; Bryant, 1945, p. 363.

Type. U.C.M.P. No. 12506, the anterior portion of a left mandible with broken incisor, P_4-M_1.

Hypodigm. Type of U.C.M.P. No. 12544, RI_1, RP_4, and half of LP_4.

Horizon and locality. Hemphillian, late Pliocene. Locality 1105 near Thousand Creek, Humboldt County, Nevada.

Emended diagnosis. Ramus larger and more massive than in any other species of *Marmota;* P_4 not molariform, as long as but narrower than M_1; talonid basins of P_4-M_1 with complex cuspules and/or low ridges.

Description. The jaw is extremely robust and especially heavy below M_1. In contrast to *Palaearctomys,* the anterior portion of the diastemal area is not swollen, and the diastemal depression is shallow anterior to P_4. The mental foramen lies just anterior to P_4 and about two-thirds of the way down the ramus. The poorly marked anterior termination of the masseteric fossa lies below the anterior end of M_1.

The incisor is not as strongly recurved as that of *Palaearctomys,* is moderately compressed and bears many prominent longitudinal grooves. P_4 is about as long as M_1 but neither as wide nor as molariform. The protoconid and metaconid are closely appressed and there is a strong anterior cingulum between these cusps about halfway down the anterior face of the tooth; an anteroconid is lacking. The trigonid basin is small and the trigonid is elevated well above the talonid basin. The ectolophid is a high crest set far in from the buccal margin. A small mesostylid at the base of the metaconid is partially set off from the posterolophid by a shallow notch. The posterolophid curves in a smooth arc through the entoconid which is completely submerged within it. The posterolophid is crenulated and steeply elevated above the deep talonid basin. Within the basin are six cuspules arranged in pairs and running postero-buccally from the mesostylid. M_1 is rhomboidal in outline. The trigonid pit is completely enclosed and set high above the talonid basin. As on P_4, the strong anterior cingulum bears no anteroconid. The ectolophid and posterolophid are high. Three ridges running from the lingual border into and fusing within the talonid basin correspond serially to the cuspules on P_4. The mesostylid is small but distinct, and set off from the posterolophid by a shallow depression.

Discussion. Bryant (1945, p. 363) considered *Marmota nevadensis* to be intermediate between *Arctomyoides* and the Recent *Marmota.* This appears to me not to be the case. *M. nevadensis* differs markedly from Recent species of *Marmota* in such characters as its much more massive mandible and the accessory talonid cuspules. *M. nevadensis,* nevertheless, does appear to be closer to the true marmot line of descent than do either *Arctomyoides* or *Palaearctomys*, although certainly not ancestral to any Recent species of *Marmota. M. nevadensis,* while showing some resemblance to *Paenemarmota,* especially in the possession of ridges and tubercles in the talonid basins of P_4-M_1 (a point of resemblance to *Cynomys* also), nevertheless, differs quite markedly in having much more strongly developed trigonid lophids with enclosed trigonid pits, and in the smaller size of P_4 in relation to M_1. Finally, *M. nevadensis* is quite different from *M. vetus* and from the descendant species, *M. minor* (also from the Thousand Creek fauna), a form which certainly does appear to be on the main evolutionary line leading to Recent *Marmota. M. nevadensis* probably diverged from the main line of marmot development sometime in the late Miocene or early Pliocene.

Measurements

Length of diastema		20.6
Depth of mandible below mental foramen	approx.	14.5
Depth of mandible below P_4	approx.	20.0

Type		a-p	tr.
U.C.M.P. No. 12506	LP_4	7.00	5.00-6.30
" "	LM_1	6.40	6.60-7.00
U.C.M.P. No. 12544	RI_1	6.80	4.50
" "	RP_4	6.90	5.60-6.80

MARMOTA VETUS (Marsh)

Plate 11, figure 1

Arctomys vetus Marsh, 1871, p. 121.

Palaearctomys vetus Matthew, 1909, p. 116; Bryant, 1945, p. 360.

Type. Y.P.M. No. 10323, a left ramus lacking the angle and anterior portion of the diastema.

Hypodigm. Type only.

Horizon and locality. Miocene or Pliocene, "Loup Fork Beds" northern Nebraska; "in the Pliocene beds, on the Loup Fork in northern Nebraska" (Marsh, 1871, p. 121).

Diagnosis. Smallest known species of *Marmota*; ectolophids strong on P_4-M_3; M_1-M_2 compressed anteroposteriorly; P_4 elongate; metalophid complete on M_1, not on M_2-M_3; single median groove on lower incisor.

Description. The dorsal surface of the mandible drops steeply anterior to P_4 and the diastemal depression is deep. The mental foramen lies just anterior to P_4 and approximately one-third of the way down the side of the diastema. The masseteric fossa ends bluntly below the anterior end of M_1. It is deeply concave with a strong inferior and a weak superior ridge. The alveolus of the incisor terminates just below the coronoid process in a distinct rounded knob. The condylar process is long and inclined more backward than upward.

P_4 is nearly as long as M_1. However, it is not molariform and is much narrower than the molars. The protoconid and metaconid are rather closely appressed with only a shallow valley separating them anteriorly. A prominent ridge passes down the anterior face of the protoconid but does not join the metaconid. The posterolophid is elevated and the entoconid is completely incorporated within it. Lingually, there is a distinct notch between the metaconid and posterolophid with no indication of a mesostylid. The ectolophid is high and thick on all the cheek teeth but there is no sign of a mesoconid on any of them. M_1-M_2 are compressed anteroposteriorly, with M_1 being somewhat smaller. The talonid basin is quite deep on both and is rimmed by high ectolophids and posterolophids. The metalophid is complete on M_1 but not on M_2. Small mesostylids are barely distinguishable on the slopes of the metaconids, which are themselves separated by slight notches from the posterolophids. On M_3, the metalophid is still weaker than on M_2 and passes into the talonid basin. The posterior half of M_3 is expanded considerably with a greatly enlarged hypoconid and a heavy, steep posterolophid that passes almost without interruption into the metaconid slope.

Discussion. Marmota vetus is obviously closely related to the true marmots. Matthew placed it in *Palaearctomys* and Bryant followed suit. Neither author examined the type specimen. *M. vetus* differs from *Palaearctomys* in the larger size of P_4-M_3 relative to overall size, the greater anteroposterior compression of M_1-M_2, and the complete submergence of the entoconid within the posterolophid. *M. vetus* resembles *Marmota monax* and *M. flaviventris* in nearly all respects except size, a character which offers no drawbacks in evolving the Recent marmots from *M. vetus* through *M. minor.*

M. vetus resembles *Protospermophilus oregonensis* in some respects and it may have evolved from the protospermophile ground squirrels. The diastema is longer in *P. oregonensis* but the mandible resembles that of *M. vetus* in all other characters. There are several differences in the dentition between these species, particularly the presence of large entoconids and mesoconids in *P. oregonensis*. However, the general shape of the lower cheek teeth is similar in the two forms and the lingual compression of M_1-M_2 is also suggestive of possible relationship. Most of the early spermophiles while having rounded posterointernal corners on M_1-M_2 lack this lingual compression of the teeth. However, enough is not known at present about the spermophiles and early marmots to rule out a spermophile ancestry for *Marmota.*

Measurements

Length of mandible	approx. 38.0
Length of diastema	approx. 6.8
Depth of mandible below mental foramen	approx. 6.2
Depth of mandible below M_1	9.2
Alveolar length P_4-M_3	14.0

MARMOTA MINOR (Kellogg)

Plate 11, figure 2

Arctomys minor Kellogg, 1910, p. 425.
Marmota minor Wilson, 1937b, p. 34; Bryant, 1945, p. 363.

Type. U.C.M.P. No. 12538, maxillary and mandibular fragments with LP^3-P^4, RM^2-M^3, LM_2-M_3, RP_4, RM_1-M_2, upper and lower incisors, and various skeletal fragments.

Hypodigm. Type only.

Horizon and locality. Hemphillian, middle Pliocene. Locality No. 1083 at Thousand Creek, Humboldt County, Nevada.

Emended diagnosis. Larger than *Marmota vetus,* smaller than Recent species; cheek teeth mesodont; P^3 relatively large; metaconules prominent; metalophs slightly constricted; P_4 longer than M_1-M_2, almost as wide; metalophids on M_1-M_3 less reduced than in Recent species, more reduced than in *M. vetus;* posterolophids relatively low.

Description. The mandible, so far as revealed by the fragments preserved, appears to have been of almost the same proportions as that of *Marmota monax.* It is not swollen through the masseteric fossa nor in the diastemal region. The diastemal depression does not drop as abruptly anterior to P_4 as in the Recent species.

P^3 is relatively large, circular in outline, with a high central crest and expanded anterior and posterior shelf areas that are ringed by sharp cingula. P^4 is triangular in outline. The anterior cingulum is expanded and there is a large tricuspate parastylar area. The protocone is a high, pointed cusp; the anterior cingulum joins it near the base while the small posterior cingulum rises almost to the apex. The high and steep protoloph and metaloph pass directly across the tooth to the protocone. The metaconule is large and distinct, and the metaloph is constricted at the protocone. A small mesostyle is present. M^2 is essentially identical in structure except that the anterior cingulum and parastyle are not as expanded. The anterior portion of M^3 resembles that of M^2, being moderately large and the protoloph high and steep. Posteriorly, the buccal half of the posterior cingulum is expanded. From the low metaconule, crests pass to the protocone and to the posterior cingular expansion, and there is a large mesostyle with a short crest passing internally from it.

P_4 is elongate and trapezoidal in outline. The trigonid is narrower and somewhat more elevated than the talonid. There is a strong anterior cingulum well down on the anterior face of the tooth. This encloses a deep trigonid pit bounded posteriorly by the strong metalophid. There is no anteroconid, mesostylid, or mesoconid. The posterolophid is a high and sharp crest, terminating abruptly at the entoconid corner and constricted at its union with the hypoconid. The trigonid basin is open lingually between the entoconid corner and the metaconid but is closed buccally by a low ectolophid. M_1 and M_2 are essentially identical, differing only in the slightly greater development of the metalophid on M_1, which joins the metaconid well down on its slope, isolating a small trigonid pit. On M_2 the metalophid passes into the talonid basin leaving the trigonid basin open posteriorly. M_1-M_2 are compressed anteroposteriorly with rounded entoconid corners and no distinct entoconid. The posterolophids are high and sharp passing through the entoconid area to the lingual margins. They fail to join the metaconids, thus leaving the talonid basin open on the lingual margin. The buccal valleys are wide and closed internally by low ectolophids. M_3, with the exception of its somewhat expanded hypoconid-posterolophid area, is identical with M_1-M_2.

The upper incisors are shallowly grooved and well rounded laterally. The ungrooved lower incisors are very finely striated.

The right and left humeri are represented by the distal segments below the deltoid crests. They agree in most respects with those of *M. monax* but the ectepicondylar process does not appear to have been as expanded as in *M. monax*. A partial right ulna is present which does not differ from that of *M. monax*. The partial right and left radii of *M. minor* are also extremely similar to those of *M. monax* but differ from those of the Recent species in being relatively broader through the distal third of the shaft. A partial left tibia in the collection does not appear to differ from that of *M. monax*. The calcaneum, metatarsals, and phalanges are similar to those of *M. monax*.

Discussion. Marmota minor is structurally intermediate between *M. vetus* and the Recent species. The proportions of M_1-M_2 in *M. minor* have changed from those of *M. vetus* with the length of M_1 equalling that of M_2 in the later species and with M_1 and M_2 becoming wider in relation to their length in *M. minor*. As regards the lower dentition of *M. minor*, it is more advanced than in *M. vetus*, less so than in the Recent forms in the following characters: (1) P_4 longer than M_1-M_2; (2) metalophid of M_1-M_3 reduced; (3) posterior portion of M_3 reduced; (4) diastemal depression deep anterior to P_4. What is known of the skeleton is scarcely distinguishable from that of *M. monax*, but not enough postcranial material is yet known for the species to determine the extent of fossorial adaptation at this stage in marmot evolution. Subsequent marmot evolution involved a general increase in size, an enlargement of P_4, reduction of the posterior portion of M_3, a further anteroposterior compression of M_1-M_2, and probably further fossorial specialization.

Measurements of the cheek teeth
of *Marmota vetus, M. minor,* and *M. monax.*[1]

		M. vetus	*M. minor*		*M. monax*
P^3	a-p		3.0		2.8
	tr.		3.0		3.1
P^4	a-p		4.2		4.6
	tr.		4.4		4.9
M^1	a-p				4.6
	tr.				5.2
M^2	a-p		3.8		4.7
	tr.		4.5		5.6
M^3	a-p		4.4		5.7
	tr.		4.5		5.6
P_4	a-p	3.0	4.0		4.8
	tr.	2.4-3.0	3.4-4.1		4.0-4.7
M_1	a-p	3.1	3.5		4.2
	tr.	3.6-3.6	4.3-3.9		5.0-5.3
M_2	a-p	3.5	3.5	3.5	4.6
	tr.	3.9-3.8	4.5-4.2	4.5-4.2	5.7-5.5
M_3	a-p	4.0	4.2		6.1
	tr.	4.0-3.4	4.6-4.0		6.3-5.5

PROTOSPERMOPHILUS Gazin

Type species. Citellus (Protospermophilus) quatalensis Gazin.

Emended diagnosis. Skull slightly convex; cranium moderately expanded; dorsal limit of zygomatic plate terminating on side of rostrum; masseteric tubercles small; notches in ventral border of zygomatic plate opposite either M_1 or line of contact between P_4 and M_1; masseteric fossa deeply concave, ending below M_1; generally a small pit anterior to masseteric fossa for separate slip of masseter; cheek teeth low crowned but robust; protoconules absent or subordinated in protolophs, metaconules distinct; protocone-posterior cingulum union expanded; entoconid a distinct cusp; entoconid corner angular.

Range. Early Miocene to early Pliocene of western North America.

The genus *Protospermophilus* first appears in the early Miocene of the Great Basin and Great Plains areas and persists through

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[1] The measurements given for *M. monax* represent the mean measurements taken from a sample of 20 specimens.

to the early Pliocene of the Mohave-Sonoran region. Judging from the scattered occurrences previously recorded and the new forms described below, it appears to have been widespread over much of western North America during this time, about as *Citellus* is today. *Protospermophilus* probably formed a separate evolutionary line that, despite its name, had nothing to do with the modern spermophiles after the late Oligocene. There is a strong possibility, however, that the marmots may have evolved from this group sometime in the mid-Miocene.

Structurally, *Protospermophilus* possesses a combination of features that tend to set it off from other sciurids. It shares the development of cheek pouches, the shallow diastema, and slight convexity of the skull with *Citellus*, but in combination with these characters are the robust rostrum, deep incisors, and heavy, crushing dentition, which are more characteristic of *Sciurus*. The dentition is at least superficially somewhat like that of *Sciurus*, with robust, crushing teeth rather than the more lophodont type of dentition seen in *Citellus*, *Cynomys*, and to a lesser degree in *Marmota*.

PROTOSPERMOPHILUS VORTMANI (Cope)

Plate 12, figure 1

Sciurus vortmani Cope, 1879, p. 1.
Prosciurus vortmani Matthew, 1909, p. 107.
Sciurus vortmani Bryant, 1945, p. 343.

Type. A.M.N.H. No. 6960, a left mandible lacking the anterior portion of the jaw, coronoid, condyle, and angle.

Hypodigm. Type and U.C.M.P. No. 39000, right mandible lacking anterior tip of jaw, ascending ramus, angle and M_2-M_3.

Horizon and locality. Diceratherium Beds, John Day Formation, early Miocene. John Day Basin, Oregon.

Diagnosis. Smallest species of genus; mandible short, relatively stout; diastema heavier than in *Miospermophilus;* no crescentic scar anterior to masseteric fossa; entoconids small; postero-lingual corners slightly rounded; no ectostylid or mesoconid; lingual margin elevated into ridge; no distinct mesostylid.

Description. The jaw is of approximately the same size and proportions as that of *Protospermophilus angusticeps* except that it is not quite as robust nor as deep. The diastemal depression is shallow. The masseteric fossa is deep, rounded anteriorly, and terminates below the anterior half of M_1. Both upper and lower borders are marked by well developed ridges. The coronoid process arises at the posterior end of M_2. The mental foramen lies just anterior to P_4 and about halfway down the side of the diastema. U.C.M.P. No. 39000 is somewhat smaller than the type but it is certainly within the normal range of variation.

The incisor is extremely compressed. Its buccal margin is convex rather than flat as is generally the case in *Sciurus*. The cheek teeth increase in size from P_4 to M_3. The anterior portion of the premolar is damaged on the type but preserved on U.C.M.P. No. 39000. The protoconid and metaconid are not as closely appressed as in the later species of the genus. A small anteroconid is present on P_4 but absent on M_1 where the anterior cingulum is small. There is no indication of a mesoconid or ectostylid on P_4-M_3. The ectolophid is not deeply recessed and the buccal valley is consequently shallow. M_1 and M_2 are rhomboidal with small entoconids and somewhat rounded postero-lingual borders. There is a small mesostylid on M_1-M_2. The lingual border of M_3 tapers gradually from the metaconid to the hypoconid, giving the crown a triangular outline.

Discussion. Protospermophilus vortmani is quite far removed from other sciurids known from the early Miocene with the possible exception of the material from Martin Canyon Quarry A in northeastern Colorado. The dentition is closer to that of *Miospermophilus* than to any other contemporary form, but, even here, there are important differences, such as the presence of a low posterolophid and of a distinct entoconid in *P. vortmani*. Also, the structure of the mandible is quite different, that of *P. vortmani* being much heavier, especially through the diastemal area. *P. vortmani* is closely related to *P. kelloggi* of the early Hemingfordian and probably also to the few specimens from Quarry A. It seems quite likley that *P. vortmani* is close to the point of origin of the genus, which probably arose sometime in the late Oligocene.

Measurements

A.M.N.H. No. 6960

Alveolar length P_4-M_3		10.4
Depth below M_1		approx. 8.5
	a-p	tr.
P_4	2.40	2.10-2.50
M_1	2.40	— -2.80
M_2	2.50	— —
M_3	2.80	2.90-2.20

U.C.M.P. No. 39000		
Alveolar length P_4-M_3		10.2
Depth below M_1		8.2
	a-p	tr.
P_4	2.20	2.00-2.20
M_1	2.30	2.40-2.60

PROTOSPERMOPHILUS sp.

Plate 12, figure 2

Sciurus sp. A Wilson, 1960, p. 62.

Referred specimens. K.U. Nos. 10163 LdP^4, 10164 LdP^4, 10165 RM$^{1 \text{ or } 2}$, 10166 RM$^{1 \text{ or } 2}$, 10167 LI$_1$, 10168 RM$_{1 \text{ or } 2}$, 10169 LM$_3$.

Horizon and locality. Pawnee Creek Formation, Arikareean early Miocene. Martin Canyon Quarry A, NW1/4, S.27, T.11N., R.53W., Logan County, Colorado.

Description. The deciduous upper premolars are triangular in occlusal outline due to the presence of a large parastyle. They closely resemble the deciduous premolars of *P. kelloggi* although the protoloph and metaloph are not as high. They also differ from those of *P. kelloggi* in having a small loph running lingually for a short distance from the large mesostyle. The upper first and/or second molars are quadrate with a large protocone and a small bulbous expansion at the point where the posterior cingulum joins the protocone. This is characteristic of all later members of the genus. The protoloph and metaloph are lower than in later forms and there is only a faint indication of the metaconule. The mesostyle is small.

The lower incisor is compressed and bears many fine striations on its anterior face. In this respect it is similar to the lower incisors of *Miospermophilus*, as well as to the later species of *Protospermophilus*. It is flattened medially and conxex laterally. M$_{1 \text{ or } 2}$ is much wider than long and the talonid basin is faintly rugose, characters which are again generally typical for *Protospermophilus*. The entoconid is a distinct cusp connected through a low, uninterrupted posterolophid to the hypoconid. The entoconid is separated from the mesostylid by a shallow notch. Whether an anteroconid was present cannot be determined due to the advanced stage of wear but, if present, it was small. The buccal valley is shallow and the ectolophid poorly developed. The entoconid and posterolophid of M$_3$ are enlarged as in *P. kelloggi*. There is a large mesoconid that fills the buccal valley.

Discussion. This material from northeastern Colorado, although suggestive of *Protospermophilus,* is too incomplete for specific determination. It is similar to *P. kelloggi* in many ways, especially in the structure of the lower molars and in the structure of the lingual portion of the first and second upper molars. It differs from other species of *Protospermophilus* in the very low lophs of the upper molars. However, upper teeth are unknown for *P. vortmani* so that comparisons can not be made with the only other early Miocene species of the genus. However, it is to be expected that the lophs would be low in the early members of the genus since this was undoubtedly the condition in the ancestral members of the family. Although the material is too poor for a definite statement, I feel it is highly likely that this population will prove to be ancestral to *P. kelloggi* when further specimens are available.

Measurements

		a-p	tr.
K.U. No. 10163	dP^4	2.50	2.30
K.U. No. 10164	dP^4	2.30	2.25
K.U. No. 10165	M$^{1 \text{ or } 2.}$	2.40	2.80
K.U. No. 10166	M$^{1 \text{ or } 2.}$	2.40	2.80
K.U. No. 10167	I$_1$	4.25	2.00
K.U. No. 10168	M$_{1 \text{ or } 2.}$	2.50	3.00-3.00
K.U. No. 10169	M$_3$	3.50	3.40-2.90

PROTOSPERMOPHILUS KELLOGGI[1] n. sp.

Figures 4, 5

Type. A.C. No. 11830 RM$_{1 \text{ or } 2}$.

Hypodigm. Type and U.W. No. 1415 LdP^4, A.C. No. 10581 RdP^4, C.N.H.M. PM2183 RdP^4, A.C. Nos. 11828 RP^4, 10566 LP^4, 10567 LP^4 and RP^4, C.N.H.M. PM2184 LP^4, PM2185 three RP^4, PM2186 LP^4, PM2200 RP^4, PM2201 RP^4, PM2202 RP^4, U.W. No. 1426 RP^4, A.C. Nos. 10573 LM$^{1 \text{ or } 2}$, 10574 two LM$^{1 \text{ or } 2}$, 10575 LM$^{1 \text{ or } 2}$, 10576 RM$^{1 \text{ or } 2}$, 10577 two RM$^{1 \text{ or } 2}$, and two LM$^{1 \text{ or } 2}$, 10578 LM$^{1 \text{ or } 2}$, 10579 RM$^{1 \text{ or } 2}$ and LM$^{1 \text{ or } 2}$, 10583 RM$^{1 \text{ or } 2}$, 11287 RM$^{1 \text{ or } 2}$ and LM$^{1 \text{ or } 2}$, 11289 two LM$^{1 \text{ or } 2}$ and RM$^{1 \text{ or } 2}$, 11290 LM$^{1 \text{ or } 2}$, 10572 two LM$^{1 \text{ or } 2}$ and two RM$^{1 \text{ or } 2}$, 10580 RM$^{1 \text{ or } 2}$ and two LM$^{1 \text{ or } 2}$, C.N.H.M. PM2206 four LM$^{1 \text{ or } 2}$, PM2207 six RM$^{1 \text{ or } 2}$, PM2187 LM$^{1 \text{ or } 2}$, U.W. Nos. 1419 LM$^{1 \text{ or } 2}$, 1420 LM$^{1 \text{ or } 2}$,

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[1] Named for Rufus B. Kellogg founder of the Kellogg Fellowship at Amherst College.

1421 RM$^{1\text{ or }2}$, 1422 LM$^{1\text{ or }2}$, 1423 eight RM$^{1\text{ or }2}$, 1428 four LM$^{1\text{ or }2}$, 1435 RM$^{1\text{ or }2}$, A.C. No. 10568 LM^3, 10569 LM^3, 10570 LM^3, 10571 LM^3, 11829 RM^3, 11288 two LM^3, C.N.H.M. PM2188 RM^3, PM2189 LM^3, PM2208 RM^3, PM2209 LM^3, U.W. Nos. 1424 RM^3, 1425 RM^3, A.C. Nos. 10586 LdP$_4$, 10585 LdP$_4$, U.W. No. 1429 LdP$_4$, A.C. Nos. 10582 two RP$_4$, 10585 LP$_4$ and two RP$_4$, C.N.H.M. PM2190 RP$_4$, PM2191 RP$_4$, PM2192 RP$_4$, PM2193 LP$_4$, PM2203 RP$_4$, U.W. Nos. 1416 RP$_4$, 1430 two RP$_4$, A.C. Nos. 10590 two RM$_{1\text{ or }2}$, 11831 RM$_{1\text{ or }2}$, 11832 LM$_{1\text{ or }2}$ and RM$_{1\text{ or }2}$, 10589 LM$_{1\text{ or }2}$ and RM$_{1\text{ or }2}$, 11292 LM$_{1\text{ or }2}$ and three RM$_{1\text{ or }2}$, 11830 RM$_{1\text{ or }2}$, 11835 LM$_{1\text{ or }2}$, C.N.H.M. PM2194 LM$_{1\text{ or }2}$, PM2195 RM$_{1\text{ or }2}$, PM2196 LM$_{1\text{ or }2}$, PM2197 LM$_{1\text{ or }2}$, PM2210 RM$_{1\text{ or }2}$, U.W. Nos. 1417 LM$_{1\text{ or }2}$, 1418 LM$_{1\text{ or }2}$, 1431 five RM$_{1\text{ or }2}$, 1432 six LM$_{1\text{ or }2}$, 1433 two RM$_{1\text{ or }2}$, A.C. Nos. 11291 two LM$_3$, 11833 two RM$_3$, 10588 RM$_3$ and three LM$_3$, 10584 LM$_3$ and two RM$_3$, C.N.H.M. PM2198 RM$_3$, PM2199 RM$_3$, PM2204 LM$_3$, PM2205 LM$_3$, PM2211 RM$_3$, PM2212 two LM$_3$, U.W. No. 1427 LM$_3$.

Horizon and locality. Split Rock Formation, early Hemingfordian Middle Miocene. Seven miles northwest of Three Forks, Wyoming, south of U.S. 287, S.36, T.29N., R.90W., Fremont County, Wyoming.

Diagnosis. Larger than *Protospermophilus vortmani,* smaller than *P. angusticeps;* dentition not as heavy as in *P. angusticeps, malheurensis,* and *quatalensis;* anterior cingulum small on P^4; indentation slight between protocone and posterior cingulum on M^1-M^2; metaconule generally present on M^3; ectolophid prominent; mesoconid present; entoconid large and distinct; metalophid weak.

Description. The cheek teeth increase in size from P$^4_4$-M$^3_3$. The anterior cingulum of P^4 is very small and subject to obliteration by wear. On dP^4, however, the anterior cingulum and parastyle are well developed. The anterior cingulum of the molars is wide and carries a large parastyle. The protoloph is complete on all cheek teeth and shows only a faint trace of a protoconule on a few of the first and second molars. The metaloph is constricted and the metaconule large on P^4-M^2. On M^3 the metaconule is variably developed but usually present. A faint indentation of the protocone occurs on some of the molars at the point where the posterior cingulum joins it. The mesostyle is small but present on all teeth.

The protoconid and metaconid of P$_4$ are practically fused into one cusp. There is no indication of a trigonid basin, nor of an anteroconid. The hypoconid and entoconid are large and connected by an elevated posterolophid. The mesostylid is small. The ectolophid is set well back from the buccal margin. The deciduous premolars differ primarily in being more cuspate, a strong anteroconid being present together with a large mesostylid and mesoconid.

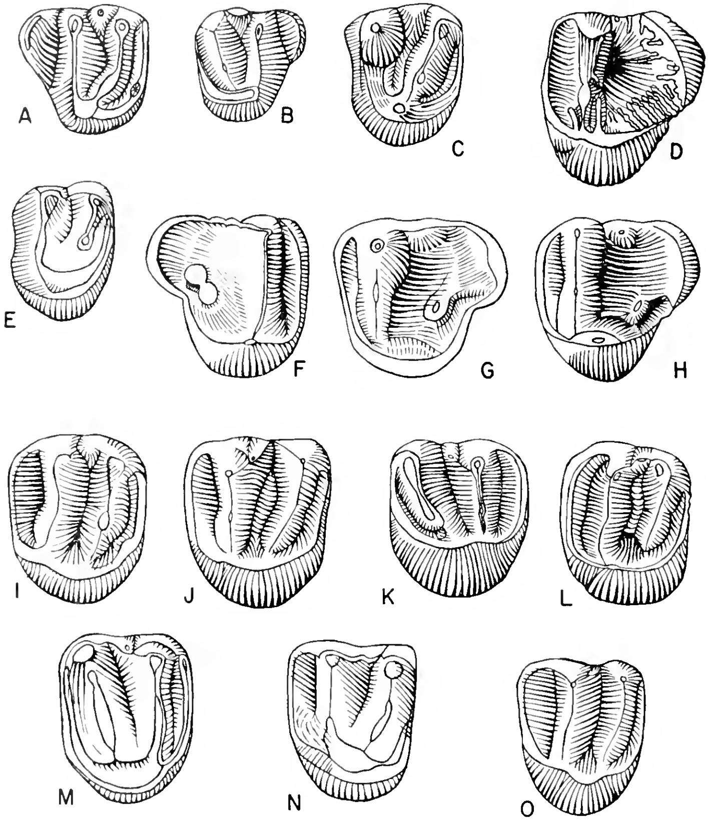

Figure 4. Upper teeth of *Protospermophilus kelloggi* n. sp., x10. *A,* U. W. No. 1415, LdP^4. *B,* C.N.H.M. PM2183, RdP^4. *C,* A.C. No. 10566, LP^4. *D,* A.C. No. 10568, LM^3. *E,* A.C. No. 10567, LP^4. *F,* A.C. No. 10569, RM^3. *G,* A.C. No. 10570, LM^3. *H,* A.C. No. 10571, LM^3. *I,* U.W. No. 1419, $LM^{1\text{ or }2}$. *J,* C.N.H.M. PM2187, $LM^{1\text{ or }2}$. *K,* A.C. No. 11287, $RM^{1\text{ or }2}$. *L,* U.W. No. 1420, $LM^{1\text{ or }2}$. *M,* U.W. No. 1421, $RM^{1\text{ or }2}$. *N,* A.C. No. 10573, $LM^{1\text{ or }2}$. *O,* A.C. No. 10572, $LM^{1\text{ or }2}$. (Anterior end to left except for *B, F, K,* and *M.*)

The first molars are rather square with a greater length in proportion to their width than is the case for the second molars which are more greatly compressed anteroposteriorly. Except for these differences in shape, the first and second lower molars are identical. The anterior cingulum bears little trace of an anteroconid. The trigonid basin is usually open into and not much higher than the talonid basin. The ectolophid is set well back and the mesoconid is either absent or small. The posterolophid is

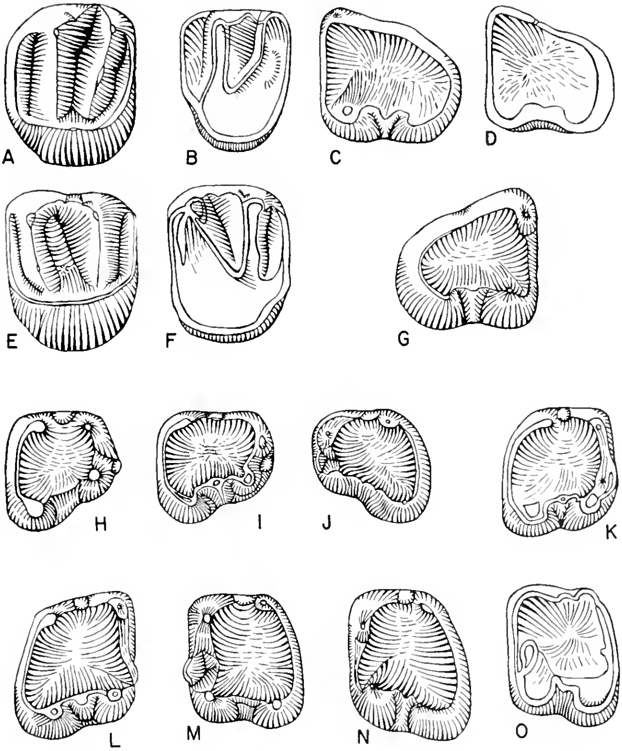

Figure 5. Upper and lower teeth of *Protospermophilus kelloggi* n. sp., x10. *A*, A.C. No. 10578, $LM^{1 \text{ or } 2}$. *B*, U.W. No. 1422, $LM^{1 \text{ or } 2}$. *C*, A.C. No. 10584, LM_3. *D*, U.W. No. 1427, LM_3. *E*, A.C. No. 10583, $RM^{1 \text{ or } 2}$. *F*, U.W. No. 1435, $RM^{1 \text{ or } 2}$. *G*, A.C. No. 11833, RM_3. *H*, A.C. No. 10582, RP_4. *I*, C.N.H.M. PM2190, RP_4. *J*, U.W. No. 1429, LdP_4. *K*, Type, A.C. No. 11830, $RM_{1 \text{ or } 2}$. *L*, A.C. No. 11831, $RM_{1 \text{ or } 2}$. *M*, U.W. No. 1418, $LM_{1 \text{ or } 2}$. *N*, U.W. No. 1417, $LM_{1 \text{ or } 2}$. *O*, A.C. No. 11832, $LM_{1 \text{ or } 2}$. (Anterior end to left except for *E, F, G, H, I, K*, and *L*.)

elevated and crescentic in shape, joining the hypoconid to the large entoconid. The mesostylid is generally small. M_3 resembles the first and second molars except that the hypoconid and posterolophid are greatly expanded, making the tooth longer than wide. The entoconid remains a distinct cusp within this expansion, giving the posterointernal corner of the tooth an angular appearance.

Discussion. P. kelloggi was probably descended from the protospermophile population of Quarry A but too little is known of the Quarry A species to document this change at present. *P. kelloggi* was almost certainly ancestral to *P. angusticeps* of the Deep River, the larger size and greater robustness of the dentition of *P. angusticeps* being the only differences between the two species. There are also some resemblances between *P. kelloggi* and *P. oregonensis* and the latter was either evolved from *P. kelloggi* or *P. angusticeps.*

Measurements

		N	M	S	V	SR
dP^4	a-p	2	2.19			
	tr.	2	2.19			
P^4	a-p	6	1.96	.09	4.64	1.96 ± .27
	tr.	6	2.40	.05	1.95	2.40 ± .15
$M^{1 \text{ and } 2}$	a-p	48	2.35	.13	5.36	2.35 ± .39
	tr.	48	2.88	.13	5.20	2.88 ± .45
M^3	a-p	13	2.82	.10	3.65	2.82 ± .30
	tr.	13	2.81	.16	5.52	2.81 ± .48
dP_4	a-p	3	2.18			
	tr.	3	2.02			
P_4	a-p	13	2.17	.09	4.15	2.17 ± .27
	tr.	13	7.69	.10	5.91	1.69 ± .30
$M_{1 \text{ and } 2}$	a-p	51	2.29	.11	4.80	2.29 ± .33
	tr.	51	2.58	.23	8.90	2.58 ± .69
M_3	a-p	18	2.79	.15	5.37	2.79 ± .45
	tr.	18	2.63	.13	4.94	2.63 ± .39

Protospermophilus angusticeps (Matthew)

Plate 13, figure 1

Sciurus angusticeps Matthew, *in* Matthew and Mook, 1933, p. 4.
Protospermophilus angusticeps Bryant, 1945, p. 349; Black, 1961b, p. 5.

Type. A.M.N.H. No. 21336, a well preserved skull.

Hypodigm. Type and A.M.N.H. No. 21331, a left maxilla with

P^4-M^3 and a partial right mandible with P_4-M_3; Y.P.M. Nos. 14029, a partial left maxilla with M^3, 14030 a partial left maxilla with M^1-M^2, 14031 a partial left mandible with M_1-M_3, 14032 a partial left mandible with M_1-M_3, 14033 a partial left mandible with M_1-M_2, and 14034 a partial left mandible with M_1.

Horizon and locality. Deep River Formation, Upper Hemingfordian, late Middle Miocene. In the vicinity of Fort Logan, Montana.

Diagnosis. Larger than *Protospermophilus quatalensis,* about equal in size to *P. malheurensis;* skull profile more convex and cranium deeper than in either; rostrum shallower but broader than in *P. malheurensis;* ridges on premaxillae lateral to incisors not prominent; teeth larger, more robust than in *P. kelloggi* or *P. malheurensis;* mandible deeper than in *P. quatalensis;* talonid basins rugose when unworn.

Description. In lateral view the skull roof is gently convex from the tip of the snout, resembling that of *Citellus* in general contour and size. There is a slight concavity at the level of the orbits breaking the outline, but this is not as pronounced as in *Cynomys.* In dorsal view the skull is constricted between the orbits. The cranium is only moderately inflated, lacking almost entirely the inflation medial to and below the posterior zygomatic root. The postorbital bar is missing. The zygomatic arch, although crushed, does not appear to have been as greatly bowed outward as in *Cynomys* and *Citellus,* being more nearly parallel as in *Sciurus.* However, it was apparently somewhat twisted, so that the original medial surface faced upward as it does in the Recent *Cynomys* and *Citellus.* The temporal ridges are extremely weak and fail to meet the occiput.

The contact between the nasals, premaxillae and frontals forms an almost straight line across the dorsal surface just in front of the orbits. The nasals are slender and the premaxillae greatly expanded at this contact. However, anteriorly the nasals form the complete dorsal surface of the rostrum in contrast to the condition seen in *Protospermophilus quatalensis.* The maxillae are excluded from the dorsal surface due to the expansion of the premaxillae. Laterally, there are no prominent ridges on the premaxillae marking the course of the upper incisors. At the level of the superior margin of the infraorbital foramen the premaxillary-maxillary sutures bend posteriorly for a short distance and then turn ventrally. When they reach the ventral surface, they turn anteriorly to join the incisive foramina. There are small pits anterior to the incisive foramen and just posterior to the incisors that appear to indicate the presence of cheek pouches. The masseteric fossae extend forward onto the premaxillae, and the dorsal margins of the fossae are marked by slightly raised ridges lateral to the incisors. The zygomatic notch is opposite the contact between P^4 and M^1. The masseteric tubercle is rather small and situated almost directly below the infraorbital foramen. The infraorbital foramen is vertical and compressed to a narrow slit.

The exact relationships of the tooth rows can not be determined, but they would appear to have converged slightly posteriorly. The pterygoid plates are missing and the size of the pterygoid fossa can not be ascertained. It is also impossible to gain any information concerning the orbital or basicranial foramina. The bullae are small, with their long axis directed anteroposteriorly, and somewhat compressed laterally. There are two transbullar septa. The occipital surface is vertical with a median ridge flanked by narrow depressions running vertically from the top of the skull to the foramen magnum. The foramen magnum is vaguely triangular in outline due to its expanded superior border. The occipital condyles lie at the inferior corners of this triangle and do not expand up the lateral margins.

The diastema, ascending ramus, and angle are not preserved on the five specimens referable to this species. Anteriorly, the masseteric fossa is pointed, with a small crescent-shaped depression at its termination below the anterior end of M_1. This depression undoubtedly received a separate slip of the masseter which was beginning its migration onto the rostrum above. The fossa is deep with prominent ridges above and below. From what little is left of the diastemal area, it would appear that the mandible sloped downward gently from P_4, as in *P. vortmani*, rather than dropping off abruptly as in *Protosciurus* and *Sciurus*. The jaws are more robust than those of *Miospermophilus*.

The upper dentition, although not high crowned, is extremely heavy and robust. The upper incisors are strongly recurved and the enamel on their anterior face is finely wrinkled. There is also one shallow groove running down the middle to the anterior face. P^3 is represented only by large alveoli. P^4 is much smaller than the molars but is similar to them in pattern. The protocone is broad and elevated above the lophs and cingula. The anterior cingulum is narrow and bears only a small parastyle at its buccal end. The protoloph passes straight across the tooth to the protocone, while the metaloph joins the protocone at a distinct angle and is constricted at this union. There is no indication of a protoconule, and the metaconule is small. The posterior cingulum is wide lingually but narrows rapidly and fails to reach the buccal margin. M^1 and M^2 are identical in pattern, varying only slightly in their occlusal outlines, M^2 being somewhat wider in relation to its length. The anterior cingula are broad and carry high parastyles on their buccal margins. The lophs are heavy with little indication of conules, and the metaloph is constricted at its junction with the protocone. There is an expansion at the posterointernal corner of the teeth where the posterior cingulum joins the protocone. However, the indentation at this point is not as strong as that present in *P. malheurensis* and *P. quatalensis*. There is a distinct mesostyle on all three molars. M^3 is slightly larger than M^2, due to the expansion of the posterior half of the tooth; this section is sharply constricted and set off from the protocone. There is no indication of a metaconule such as is sometimes found in *P. kelloggi.*

The lower dentition gives the same impression of heaviness as does the upper, and when unworn, the talonid basins are rather rugose, the rugosity disappearing rapidly with wear. The cheek teeth increase in size from P_4 to M_3. The only lower fourth premolar preserved is well worn with most of the pattern consequently obliterated. The protoconid and metaconid are closely appressed and there is no trace of an anteroconid. M_1 is generally somewhat squarer in occlusal outline than is M_2, which is considerably wider than long. On both teeth the trigonid basins are not greatly elevated above the talonids, from which they are isolated by a short metalophid that merges into the base of the high metaconid. The trigonid basins are bounded anteriorly by distinct, bulbous cingula. In all cases the entoconids are distinct cusps and are joined to the hypoconids through uninterrupted posterolophids. The ectolophids are set well back from the buccal margins and generally bear rather large mesoconids. The mesostylids are prominent and are set off from the entoconids by shallow valleys. M_3 varies considerably in occlusal outline with wear. When unworn, the posterointernal area is expanded, giving the tooth a somewhat rectangular appearance. As wear proceeds, the outline becomes more and more triangular through a reduction of the width of the posterior half of the tooth. There is no distinct trigonid basin on M_3 nor is there any indication of an anteroconid.

Discussion. The crushing dentition of *P. angusticeps* is as advanced as any known in the genus, comparable to that of *P. quatalensis* and surpassing that of *P. malheurensis*. The same is also true for the zygomasseteric structure, which is as advanced in *P. angusticeps* as in later species. *P. angusticeps* could not have given rise to *P. malheurensis* because of the great discrepancy in the size of the teeth in relation to overall skull size in the latter. It is highly unlikely that *P. angusticeps* was ancestral to *P. quatalensis* for the same reason. There are some resemblances between *P. angusticeps* and *P. oregonensis* of the Great Basin, however, and the later species was probably descended from a Great Plains species, very possibly *P. angusticeps*. There are no members of the genus known after the Middle Miocene in the Great Plains and it is probable that as the region became more arid and the grasslands expanded a large share of the food supply for the group was removed, with the subsequent extinction of *Protospermophilus* in this area.

Measurements

A.M.N.H. No. 21336

Length of skull	59.3
Depth of rostrum at anterior end of zygomatic plate	14.5
Width of rostrum at anterior end of zygomatic plate	12.2
Width of skull at postorbital notch	approx. 13.5
Width of skull behind posterior zygomatic root	approx. 23.0
Length of palate	27.5
Alveolar length P^3-M^3	approx. 12.0

A.M.N.H. No. 21331

Alveolar length P^3-M^3	approx. 10.8
Depth of mandible below M_1	8.1

		N	M
P^4	a-p	3	2.30
	tr.	3	2.90
M^1	a-p	4	2.60
	tr.	4	3.20
M^2	a-p	3	2.70
	tr.	3	3.33
M^3	a-p	2	2.80
	tr.	2	2.95

P_4	a-p	1	2.20
	tr.	1	2.00-2.30
M_1	a-p	5	2.54
	tr.	5	2.74-3.02
M_2	a-p	4	2.82
	tr.	4	3.08-3.15
M_3	a-p	3	3.00
	tr.	3	2.93-2.60

PROTOSPERMOPHILUS OREGONENSIS (Downs)

Plate 13, figure 2; Plate 14, figure 1

Arctomyoides oregonensis Downs, 1956, p. 217.

Type. U.C.M.P. No. 39093 left mandibular ramus without coronoid and condylar processes.

Hypodigm. Type and U.C.M.P. No. 40241 left P_4.

Horizon and locality. Late Hemingfordian or early Barstovian, middle to late Miocene. SE ¼ of NE ¼, S. 15, T.12S., R.25E., Wheeler County, Oregon.

Emended diagnosis. Largest species of genus; length of diastema in relation to alveolar length greater than in other protospermophiles; ectolophid moderately developed; mesoconid large; large anteroconid on M_1-M_2; anteroposterior compression of M_1-M_2 greater than in any other species of the genus.

Description. The mandibular ramus is shallow and thin in relation to its overall length. The diastema is long, dropping gently from P_4, and the diastemal depression is shallow. The mental foramen lies just below the diastemal level midway between P_4 and the incisor. The masseteric fossa ends below the anterior root of M_1 and is rounded anteriorly. The jaw is crushed in this region but the fossa was evidently deeply concave. The angle is not twisted medially but lies in the vertical plane of the ramus. The ascending ramus rises steeply opposite hypoconid of M_2.

The incisor is greatly compressed and flattened both laterally and medially. P_4-M_3 are only moderately worn, and the talonid basins are all rugose. The protoconid and metaconid are closely appressed on P_4 with a minute anteroconid present on the protoconid slope. The ectolophid is moderately strong and bears a small mesoconid. The posterolophid is low and passes almost straight across P_4 to the entoconid. A small mesostylid is present lingually. The molars are nearly identical in structure. They increase in size from M_1 to M_3 with M_3 having a greatly expanded hypoconid and heavy expanded posterolophid. Strong anteroconids, moderately developed ectolophids, and mesoconids are present on M_1-M_3. The trigonid basin is enclosed on M_1-M_2 by a heavy metalophid. On M_3 the trigonid basin is open with the metalophid passing into the talonid basin. Small mesostylids are present on M_1-M_2 but absent on M_3. The posterolophids on M_1-M_2 are low and curve anteriorly to the entoconids. The teeth are consequently much narrower lingually than buccally.

Discussion. Downs (1956, pp. 217-222) in discussing the relationships of *Protospermophilus oregonensis* believed that it showed a greater resemblance to *Arctomyoides arctomyoides* than to any other Miocene sciurid. At that time he was able to examine *Palaearctomys "macrorhinus"* which he assumed from Bryant's (1945) earlier work was closely related, possibly congeneric with *Arctomyoides,* but he did not examine *Arctomyoides arctomyoides.* As I have pointed out above (p. 153) *Arctomyoides* is probably only distantly related to *Palaearctomys. Protospermophilus oregonensis* differs from *Arctomyoides arctomyoides* in the following characters: mandible more slender, relatively longer diastema, different position and extent of masseteric fossa (a character which Downs [*op. cit.,* p. 221] pointed out), entirely different proportions of P_4-M_3, presence of strong anteroconids and metalophids on M_1-M_2, and small mesostylids. It is clear that *Protospermophilus oregonensis* is not closely related to *Arctomyoides.*

The characters which distinguish *P. oregonensis* from *Arctomyoides* are precisely those found in the protospermophile group of Tertiary sciurids. *P. oregonensis* is particularly close to *P. angusticeps* from the Deep River, and although larger could certainly have evolved from that species. *P. oregonensis* differs from *P. quatalensis* in its larger and more slender mandible and larger cheek teeth.

P. oregonensis does bear certain resemblances to the earliest known species of *Marmota, M. vetus* (Marsh). These include: general compressed shape of P_4-M_3, strong metalophids on M_1-M_2, well developed ectolophids on P_4-M_3, and the position and shape of the masseteric fossa. *P. oregonensis* differs from *M. vetus* in possession of mesoconids and in its much lower crowned teeth. *P. oregonensis* differs considerably from *Palaearctomys montanus* particularly in the greater anteroposterior compression of M_1-M_2 in *P. oregonensis.* The resemblances between the protospermophiles in general and *P. oregonensis* in particular and such early marmots as *Marmota vetus* and *M. minor* are discussed more fully above (p. 163).

Measurements

U.C.M.P. No. 39093

Length of diastema	10.4
Depth of mandible at mental foramen	6.5
Depth of mandible below M_1	8.7
Alveolar length P_4-M_3	12.5

	a-p	tr.
I_1	3.70	1.60
P_4	2.60	2.30-2.60
M_1	2.90	3.00-3.20
M_2	3.10	3.50-3.50
M_3	3.60	3.50-3.00

U.C.M.P. No. 40241

	a-p	tr.
P_4	2.50	2.30-2.60

PROTOSPERMOPHILUS MALHEURENSIS (Gazin)

Plate 13, figure 3; Plate 14, figure 2

Sciurus malheurensis Gazin, 1932, p. 56.
Protospermophilus malheurensis: Bryant, 1945, p. 347.

Type. L.A.C.M. (C.I.T.) No. 129, a skull lacking the region posterior to the postorbital bar, the nasals, incisors, RP^3, and LP^3-M^1.

Hypodigm. Type and L.A.C.M. (C.I.T.) No. 333, a poorly preserved skull without dentition and rostrum, L.A.C.M. (C.I.T.) Nos. 3077A LM^1, and 3077B RM^1.

Horizon and locality. Late Hemingfordian, late Middle Miocene. 28 miles S. of Harper and 3 mi. NW. of Skull Spring, Malheur County, Oregon. L.A.C.M. (C.I.T.) Nos. 3077A and 3077B from Beatty Butte local fauna, Oregon.

Emended diagnosis. Rostrum deep; skull roof flat; lateral incisor ridges intermediate in development between *P. angusticeps* and *P. quatalensis;* pits posterior to upper incisors deep; cheek teeth small in relation to size of skull.

Description. Of the two skulls, the type, although not as complete, is by far the better preserved. The upper profile is flatter than that of *P. angusticeps,* particularly from the postorbital bar to the occiput. The interorbital width is approximately the same in the two species. The rostrum is narrow and quite deep. The frontal-nasal and frontal-premaxillary sutures are as in *P. angusticeps,* as is the almost total exclusion of the maxillae from the dorsal surface of the skull. The rostral ridges lateral to the incisors are more pronounced than in *P. angusticeps,* but are not as greatly developed as in *P. quatalensis.* In contrast to the condition in *P. angusticeps,* the premaxillary-maxillary suture passes straight down the side of the rostrum until it reaches the palate, where it turns forward to the incisive foramen. The pits just behind the incisors are deep. The masseteric tubercles are low and drawn out from the ventral border of the infraorbital foramen back towards P^3. The infraorbital foramen is slit-like. The zygomatic plate is not appreciably different in area and shape from that of *P. angusticeps.*

Little can be learned concerning the basicranial region due to the poor preservation of L.A.C.M. (C.I.T.) No. 333. It would appear that the pterygoid fossa was relatively large and deep. The ectopterygoid ridge is strong and the lateral pterygoid plate evidently reached the bullae. These are of the same size and shape as those of *P. angusticeps* and also have two septa. The occiput slants slightly posteriorly as in some species of *Citellus,* and has a median ridge flanked by narrow depressions as in *P. angusticeps.* The foramen magnum is ovate and lacks the somewhat expanded superior margin seen in *P. angusticeps.* The condyles differ from those of *P. angusticeps* in being more greatly expanded lateral to the foramen magnum.

In relation to the size of the skull, the teeth are small. The anterior cingulum on P^4 is small with no parastyle, while on M^1-M^3 it is large and carries a high parastyle. The protoloph on P^4-M^3 is complete, passes directly across to the protocone, and shows no trace of a protoconule. The metaloph on P^4-M^2 is constricted at its junction with the protocone, passes obliquely across to the protocone, and shows a distinct metaconule. A large metaconule is also present on M^3. There is a small mesostyle on all the teeth. On P^4-M^2 the posterior cingulum fails to reach the buccal margin and, lingually, joins the protocone at a right angle. At this junction there is a slight expansion marked by a shallow groove on the protocone. The posterior cingulum on M^3 bends sharply buccally from the protocone and then expands posteriorly.

Discussion. There is no record of *Protospermophilus* in the Great Basin between the early Miocene and the late Middle Miocene so that it is difficult to trace the descent of *P. malheurensis.* However, it was probably descended from *P. vortmani* but, as only lower teeth and jaws are known for the latter and upper teeth and skulls for the former, there is no way to determine how great the change between these forms may have been. It is probable that *P. malheurensis* gave rise to *P. quatalensis* of the Barstovian and early Clarendonian.

Measurements

L.A.C.M. (C.I.T.) No. 129

Depth of rostrum at anterior end of zygomatic plate	14.5
Width of rostrum at anterior end of zygomatic plate	11.5
Length of palate	29.0
Width of palate at M^1	8.2
Alveolar length P^3-M^3	10.5

	a-p	tr.
I^1	4.30	2.40
P^4	2.00	2.40
M^1	2.40	2.70
M^2	2.40	2.80
M^3	2.50	2.70

PROTOSPERMOPHILUS QUATALENSIS (Gazin)

Plate 13, figure 4; Plate 15

Citellus (Protospermophilus) quatalensis Gazin, 1930, p. 64.
Protospermophilus quatalensis: Bryant, 1945, p. 350.
Sciurus venturus Bryant, 1945, pp. 345-346.

Type. L.A.C.M. (C.I.T.) No. 30, a partial skull with LP^3-M^2 and RP^4-M^1, and partial right and left mandibles with RM_1-M_2 and LP_4-M_1.

Type of synonym. U.C.M.P. No. 34450, a partial left ramus with M_1-M_3.

Hypodigm. Types and L.A.C.M. (C.I.T.) Nos. 31 a partial left mandible with P_4-M_2, and 32 a partial left mandible with P_4-M_3.

Horizon and locality. Upper Barstovian, late Miocene. Quatal Canyon, 8 mi. E. of Cuyama Valley, Ventura County, California. U.C.M.P. No. 34450, Clarendonian, early Pliocene, N. side of Apache Canyon, 8 mi. NE of Cuyama Valley, S.2, T.8N., R.23W., Ventura County, California.

Emended diagnosis. Size of *P. malheurensis;* rostrum broad, short, relatively shallow; premaxillae with dorsal expansion to tip of snout; ridges lateral to incisors heavy; mandibles shallow below P_4-M_3; cheek teeth small in relation to skull size; notch between protocone and posterior cingulum deep on M^1; lingual border of P^4-M^2 straight due to well developed cusp-like expansion at lingual end of posterior cingulum; ectolophids weak; no mesostylid on lower molars.

Discussion. Bryant (*op. cit.*, p. 346) described a mandible from the early Pliocene Cuyama fauna as a new species of *Sciurus, S. venturus.* He did not compare it with *Protospermophilus quatalensis* but it appears almost identical to that species. The mandible is somewhat heavier and deeper but the low, heavy posterolophids, almost complete submergence of the entoconid, and the heavy dentition all indicate relationship with *Protospermophilus* rather than *Sciurus.*

Description. The skull roof is crushed, and missing behind the orbits with the premaxillae riding over the nasals. The lateral and ventral relationships of the premaxillae and maxillae have not been distorted. Also the dorsal position of the premaxillae appears to be true with a greater expansion onto the top of the rostrum than is known in any other North American sciurid. The ridges on the premaxillae lateral to the incisors are extremely heavy and are confluent with the dorsal edge of the masseteric fossa. The premaxillary-maxillary suture passes straight down the side of the rostrum to the level of the infraorbital foramen where it bends posteriorly towards the masseteric tubercle; it then bends anteriorly to the incisive foramen. The cheek-pouch muscle pits posterior to the incisors are approximately as in *P. malheurensis.* The masseteric fossa terminates anterodorsally on the premaxilla just anterior to the premaxillary-maxillary suture. There is a large, shallow concavity marking the dorsal half of the fossa. The infraorbital foramen lies above the masseteric tubercle, and is rather small and compressed. The masseteric tubercle is large, and there is a well developed muscle scar medial to it which passes anteriorly to the premaxillary-maxillary suture. The notch in the zygomatic plate is opposite the middle of M^1.

The jaw is shallow below the cheek teeth, more so in the Quatal Canyon material than in the Clarendonian specimen, and is unlike any other species of *Protospermophilus* in which the jaw is known. The masseteric fossa is consequently compressed and more acutely angled anteriorly. The small crescentic scar anterior to the main area of the masseteric fossa lies below P_4. The diastema is very shallow and broad and the mental foramen lies just anterior to P_4 almost on the dorsal surface of the diastema.

The upper incisors are strongly recurved and show many fine striations on their anterior faces. P^3 is a minute peg, although on the right side, where it is missing, the alveolus is large. The upper cheek teeth are all nearly square in outline although this was probably not the case of M^3 which is absent on both sides. The lingual border of P^4-M^2 is flat with a large bulbous expansion posterior to the protocone at the point where the posterior cingulum joins the protocone. There is a marked cleft at this point on M^1 but this is not present on P^4 and M^2. The anterior cingulum is rather small on P^4 carrying a small parastyle which would be lost with wear; on M^1-M^2 the anterior cingulum is larger with a high parastyle. The protoloph is complete on P^4-M^2 with no trace of a protoconule; the metaloph is constricted on these teeth and shows a large metaconule. The posterior cingulum is short and displays the large lingual expansion mentioned above. A small mesostyle is present on P^4-M^2.

The lower incisors also show many fine striations on their anterior faces. They are not as deep nor as compressed as in *Sciurus* or *Citellus*, resembling more those of *Marmota*. The lower cheek teeth are small but robust. They all display rather rugose talonid basins. P_4 is much smaller than M_1-M_3. The protoconid and metaconid are distinct but closely appressed. There is no trace of an anteroconid. The posterolophid is continuous, heavy, and of medium height with the entoconid almost completely blended into it. The buccal valley is deep and is dammed internally by a large mesoconid. The ectolophid is weak and the mesostylid absent. M_1 and M_2 are identical in pattern, differing only in size. They both have strong anteroconids, open trigonid basins, weak ectolophids, deep buccal valleys, strong mesoconids, no mesostylids, and wide, heavy posterolophids. (Bryant, *op. cit.*, p. 350, states that mesostylids are present but I can find no trace of them.) M_3 agrees in pattern with the first two molars except that the hypoconid and posterolophid are greatly expanded posteriorly.

Discussion. *P. quatalensis* is the last protospermophile known. There seems to be little doubt but that it was descended from *P. malheurensis*. In the small size of its teeth in relation to skull size it reflects the condition seen in that species and stands in contrast to that of the Great Plains species. It differs from *P. malheurensis* primarily in the structure of the rostrum which is more heavily built than in its ancestor. Part of this massiveness is due to the enlarged incisors and the consequent lateral expansion of the premaxillae. This condition could have been easily reached from that in *P. malheurensis* with the depth of the rostrum decreasing as the premaxillae expanded laterally to accomodate the incisors. The dorsal expansion of the premaxillae onto the top of the rostrum would tend to strengthen the incisor alveoli allowing for greater strain to be placed on them. Only minor changes in the dentition would be necessary to bring *P. malheurensis* to the level of *P. quatalensis.*

Measurements

L.A.C.M. (C.I.T.) No. 30		
Length of diastema		6.5
Depth of mandible below mental foramen		6.4
Depth of mandible below M$_1$		7.0
Alveolar length P^3-M^3		10.3
Alveolar length P$_4$-M$_3$		10.2
	a-p	tr.
LP^4	2.30	2.50
LM^1	2.50	2.70
LM^2	2.60	——
RP^4	2.30	2.50
LI$_1$	3.40	1.90
LP$_4$	2.20	1.80-2.10
LM$_1$	2.40	2.40-2.60
RM$_1$	2.40	2.40-2.50
RM$_2$	2.70	2.70-2.70
L.A.C.M. (C.I.T.) No. 31		
Alveolar length P$_4$-M$_3$		10.5
	a-p	tr.
P$_4$	2.00	1.50-2.00
M$_1$	2.50	2.40-2.70
M$_2$	2.70	2.90-3.00
L.A.C.M. (C.I.T.) No. 32		
Alveolar length P$_4$-M$_3$		10.6
	a-p	tr.
M$_1$	2.50	2.60-2.80
M$_2$	2.80	3.00-3.10
M$_3$	3.20	3.00-2.70
U.C.M.P. No. 34550		
	a-p	tr.
M$_1$	2.60	2.70-2.90
M$_2$	2.70	3.10-3.10
M$_3$	3.20	3.10-2.90

Miospermophilus n.gen.

Type species. Palaearctomys? bryanti Wilson.

Diagnosis. Size small; cheek teeth low crowned; protoconules subordinated in protolophs; metaconule small; metaloph slightly constricted at the protocone; protocone partially constricted, not occupying all of the lingual border on M^1-M^2; lower molars rhomboidal, inner half narrower than outer half; posterolophids low; entoconids small; ectolophids set well in from buccal margin; diastema fairly long, diastemal depression shallow; masseteric fossa ending below posterior half of P_4.

Range. Late Arikareean of northeastern Colorado to early Hemingfordian of central Wyoming.

Miospermophilus bryanti (Wilson)

Plate 16

Sciurus sp. Galbreath, 1953, p. 98.
Palaearctomys? bryanti Wilson, 1960, p. 57.

Type. K.U. No. 10149, a complete right mandible.

Hypodigm. K.U. Nos. 9290, partial right mandible with P_4, M_2-M_3, 10156 RdP^4, 10155 LP^4, 10157 two L$M^{1\text{ or }2}$ and R$M^{1\text{ or }2}$, 10158 R$M^{1\text{ or }2}$, 10159 L$M^{1\text{ or }2}$, 10160 LM^3, 10161 upper incisors, 10162 lower incisors, 10150 LP_4, 10151 RP_4, 10152 LM_2, 10153 RM_2, 10154 LM_3.

Horizon and locality. Pawnee Creek Formation, late Arikareean, early Miocene. Martin Canyon Quarry A, NW. 1/4, S. 27, T.11N., R.53W., Logan County, Colorado.

Diagnosis. Smaller than *M. wyomingensis;* diastemal region of mandible long; diastemal depression shallow; metaloph not as constricted as in that species; lophs low; metaconules small; protocone large; entoconid not completely submerged in posterolophid.

Description. The mandible agrees in most respects with that of *Citellus variegatus.* The diastemal region is long and slender as in *Citellus* and not as massive as that of *Marmota.* The diastemal depression is shallow and the superior border of the mandible curves gently downward from the anterior end of P_4. In *Protosciurus* and *Palaearctomys,* the border drops steeply anterior to P_4. The masseteric fossa ends below the posterior end of P_4 and is somewhat rounded. The coronoid process is long, sharply pointed, and curves backward, its dorsal border paralleling the condylar process, as in spermophiles. In marmots and tree squirrels it is generally shorter, not as slender, and does not curve as far backwards. The articular face of the condyle shows a tendency toward the lateral expansion seen in *Citellus* and *Marmota*, but not in *Sciurus*. The angle is rather blunt and only slightly twisted medially.

The deciduous fourth upper premolar is smaller than P^4. The anterior cingulum is greatly expanded but lies well below the level of the protoloph. The protocone is high and rather sharp, the lophs joining it well down on its external face. The protoloph is low, unconstricted, and shows no sign of a protoconule; the metaloph is constricted and the metaconule is distinct. The posterior cingulum is very small. Buccally, there is a large mesostyle uniting the paracone and metacone. P^4 is quite different from its deciduous predecessor. The anterior cingulum is much narrower and lower, there is no mesostyle, the lophs are sharper and steeper, and the metaconule is only slightly developed.

On M^{1-2} the anterior cingulum is moderately expanded and bears a large parastyle; the posterior cingulum is small. There is a faint metaconule in the metaloph, which is slightly constricted at the protocone; there is no distinct protoconule and the protoloph is unconstricted. A small mesostyle is present. The anterior cingulum is smaller on M^3 than on M^{1-2} and lacks a parastyle. The protoloph is low and complete. There is no trace of a metaconule or of a mesostyle. The posteroexternal portion of M^3 is expanded as in *Citellus*. The upper incisors are extremely compressed and have many fine, interwoven striations running longitudinally on their anterior faces.

The lower dentition is low crowned and rather lightly built. The protoconid and metaconid are closely appressed on P_4 with no trace of an anteroconid. The posterolophid forms a gentle curve from the large hypoconid through an indistinct entoconid to the metaconid. The ectolophid is weak, set well in from the buccal margin, and shows no trace of a mesoconid or ectostylid. M_1 is rather more quadrate than M_2, the anterior and posterior halves of the tooth being more nearly equal in width. The trigonid basin is small, enclosed, and raised only slightly above the level of the talonid basin on M_1 and M_2. The protoconid and hypoconid are of equal size on these teeth. The entoconid is small on both; the posterolophid is somewhat elevated and curves gently through the entoconid. The mesostylid is small and there is no mesoconid or ectostylid. The ectolophid is set well back from the buccal margin. M_3 is the largest cheek tooth, with a large, expanded hypoconid and a posterolophid in which the entoconid is completely subordinated. A small mesoconid is present on the rather weak ectolophid. The lower incisor is extremely compressed, rounded lingually, and has many very fine striations running longitudinally.

Discussion. Wilson (1960), in his discussion of *M. bryanti*, pointed out its many resemblances to the chipmunks but concluded that it was probably more closely allied to *Arctomyoides* and *Palaearctomys*, both of which were placed in close relationship to *Marmota* by Bryant (1945). After a careful examination of the specimens, this suggested relationship seems highly dubious to me. *Arctomyoides* appears to be a highly specialized offshoot of the marmot line and *Palaearctomys*, although somewhat closer to *Marmota*, also possesses certain characters that distinguish it from that genus and from *Miospermophilus*. Wilson (1960, pp. 61-62) opposes assignment of *M. bryanti* to the chipmunks on three counts: "(1) *P. ? bryanti* differs from *Eutamias* and *Tamias* in a number of morphological details, such as heaviness of lower jaw and relatively short anteroposterior diameters of molars M^{1-2}_{1-2}; (2) chipmunks may not in themselves be a natural group (White, 1953, p. 560); (3) characters most strongly suggesting assignment of *P. ? bryanti* to chipmunks would also suggest chipmunk affinities for several of the European Miocene species and it is hardly likely that these all are chipmunks."

The lower jaw while heavier and deeper than in the modern species of chipmunks is still much more slender than any other sciurid mandible known from the North American Oligocene or Miocene, and this could easily be interpreted as a hold-over from the ancestral paramyine condition. If the specimen is an early spermophile, these morphological differences from, as well as the resemblances to, chipmunks are easily explainable (especially if, as discussed later, p. 234, the spermophiles were descended from a chipmunk-like sciurid). The greater anteroposterior compression of the molars agrees well with the interpretation of this form as an early spermophile. Wilson's second point seems hardly applicable in this instance. Whether or not chipmunks are a natural group, *M. bryanti* does resemble them in many details, and, or so it seems to me, assignment to this group rather than to the marmots would have been more acceptable on the characters available. Wilson's third objection to a chipmunk relationship for this species is perfectly valid; in view of their habitat preferences and their sparse representation in the North American Tertiary, you would not expect a large number of chipmunks in the European record. However, this similarity of *M. bryanti* to European species argues more convincingly for a spermophile relationship than for a marmot relationship. It seems much more likely to me that these European species represent ground squirrels, which are abundantly represented in the North American Tertiary and which are so abundant today.

As Wilson points out there are several features found in *M. bryanti* which are more advanced than they are in *Arctomyoides* or *Palaearctomys*. These include: greater compression and fine striation of the incisor, and less elongation of M_3. These are characters which one would certainly expect in an early spermophile. He emphasizes the small size of the dentition in relationship to jaw size in *M. bryanti* and *Palaearctomys*. The ratio of jaw length to alveolus length in *M. bryanti* is approximately 4.2; in *Palaearctomys* it is 4.4; and in *C. (Otospermophilus) variegatus* and *beechyi* it ranges from 4.0-4.2. *M. bryanti* is, therefore, just as close to the true spermophiles in this respect as it is to *Palaearctomys*. Finally, the fine longitudinal striations on the incisors appear to be an extremely variable character occurring in several sciurid lines, including the true spermophiles.

There are many characters which argue for considering this species to be a true spermophile, in addition to those already mentioned: (1) the metaloph on M^{1-2} is slightly constricted; (2) the protocone is not greatly expanded anteroposteriorly; (3) the lower molars are narrower internally than externally with the entoconid displaced anteriorly; (4) the entoconid is relatively small and a part of the curving posterolophid; and (5) the diastema is relatively long and the diastemal depression shallow. The characters in common between *M. bryanti* and the chipmunks indicate, I believe, that the ground squirrels evolved from chipmunk-like sciurids, probably in the late Oligocene.

Miospermophilus bryanti is close to the point of chipmunk-ground squirrel divergence as its many resemblances to both groups attest. *M. wyomingensis* was undoubtedly descended from *M. bryanti*.

Measurements

K.U. No. 10149

Length of mandible	31.0
Length of diastema	6.3
Depth of mandible below P_4	6.0
Alveolar length P_4-M_3	7.4

		K.U. 10149	K.U. 9290	Various teeth (from Wilson, 1960)	
I_1	a-p	2.50	2.70	2.60	2.00 (young)
	tr.	1.20	1.30	1.30	1.10
P_4	a-p	1.30	1.40	1.25	1.40
	tr.	—-1.40	1.10-1.50	1.30	1.40
M_1	a-p	1.60	—		
	tr.	1.70-1.80	—		
M_2	a-p	1.70	1.70	1.80	1.80
	tr.	2.00-2.00	2.00-2.00	2.00	2.00
M_3	a-p	2.00	2.00	2.00	2.00
	tr.	2.00-1.60	2.00-1.60	2.00	2.00

		Various teeth (from Wilson, 1960)		
I^1	a-p	3.10	2.70	2.80
	tr.	1.40	1.25	1.40
dP^4	a-p	1.30		
	tr.	1.40		
P^4	a-p	1.40	1.50	
	tr.	1.70	1.80	
M^1	a-p	approx. 1.50	approx. 1.60	
	tr.	2.00	2.00	
M^2	a-p	1.70	1.75	
	tr.	2.20	2.20	
M^3	a-p	2.20		
	tr.	2.10		

MIOSPERMOPHILUS WYOMINGENSIS n. sp.

Figure 6

Type. A.C. No. 10898 LM$_{1 \text{ or } 2}$.

Hypodigm. C.N.H.M. PM2171 RdP^4, PM2183 RdP^4, A.C. Nos. 10895 RP^4, 10899 two LP^4, 10563 LP^4, C.N.H.M. PM2168 LP^4, PM2169 LP^4, U.W. No. 1409 LP^4, A.C. Nos. 10563 LM$^{1 \text{ or } 2}$, 10896 RM$^{1 \text{ or } 2}$, 10897 RM$^{1 \text{ or } 2}$, 10564 LM$^{1 \text{ or } 2}$, C.N.H.M. PM2170 RM$^{1 \text{ or } 2}$, PM2172 LM$^{1 \text{ or } 2}$, PM2173 RM$^{1 \text{ or } 2}$, U.W. Nos. 1407 RM$^{1 \text{ or } 2}$, 1408 RM$^{1 \text{ or } 2}$, 1411 LM$^{1 \text{ or } 2}$, C.N.H.M. PM2174 LM^3, U.W. Nos. 1410 RM^3, 1412 RM^3, C.N.H.M. PM2178 LdP$_4$, PM2179 LdP$_4$, PM2213 RP$_4$, PM2175 LP$_4$, A.C. Nos. 10565 two RM$_{1 \text{ or } 2}$, 11286 LM$_{1 \text{ or } 2}$, C.N.H.M. PM2176 LM$_{1 \text{ or } 2}$, PM2177 LM$_{1 \text{ or } 2}$, U.W. Nos. 1413 LM$_{1 \text{ or } 2}$, 1414 RM$_{1 \text{ or } 2}$, C.N.H.M. PM2180 LM$_3$, PM2181 LM$_3$, PM2182 RM$_3$.

Horizon and locality. Split Rock Formation, early Hemingfordian, Middle Miocene. Seven miles northwest of Three Forks Wyoming, south of U.S. 287, S. 36, T.29N., R.90W., Fremont County, Wyoming.

Diagnosis. Larger than *M. bryanti;* lophs higher and sharper; protocone not filling lingual margin; metaconules very distinct; metaloph greatly constricted; entoconid incorporated in posterolophid; entoconid region angulate; posterointernal part of M_3 partially expanded.

Description. The subquadrate P^4 is smaller than the molars. The protoloph and metaloph converge towards the protocone where the metaloph is sharply constricted. The anterior cingulum is small, bending abruptly posteriorly to join the protocone. The posterior cingulum terminates below the metacone, not passing to the buccal side of the tooth, and rises gradually to join the protocone without a sharp bend. The protoconule is not visible as a separate component of the protoloph. The mesostyle is small.

The deciduous fourth upper premolars are slightly smaller than the permanent teeth. The anterior cingulum is restricted to the buccal half of the tooth and is a small flat shelf. The posterior cingulum is very small and rises gently to join the protocone. The metaloph is constricted at its junction with the protocone and the metaconule is distinct.

It is impossible to separate upper first and second molars, and the description given here applies to both. The teeth are generally triangular to subquadrate in outline. There is no indication of any division of the protocone into two cusps. The lophs and cusps are relatively sharp and the trigon is V-shaped. The metaconules are generally distinct cusps. The protoloph joins the protocone at a right angle to the anteroposterior axis of the tooth while the metaloph passes slightly anteriorly to join the protocone. The metaloph is usually constricted at the protocone. The anterior cingulum is moderately developed and somewhat higher than the posterior cingulum. The anterior cingulum changes direction abruptly at the protocone, joining it at a right angle while the posterior cingulum rises to the protocone in a gentle curve. There is usually a small mesostyle on all the teeth.

The third upper molars are approximately as long as they are wide and are triangular in occlusal outline. The paracone is the highest cusp with the protocone and metacone about equal in height. The protocone is swollen and fills the lingual portion of the tooth with the posterior cingulum bending sharply posteriorly and buccally. The anterior cingulum is well developed, rising steeply to join the paracone, and it is lower than the protoloph. The metacone is swollen and occupies the whole posterointernal corner of the tooth. There is no mesostyle.

The length of the fourth lower premolars is approximately equal to their posterior width. The occlusal outline is trapezoidal with the trigonid much narrower than the talonid due to the

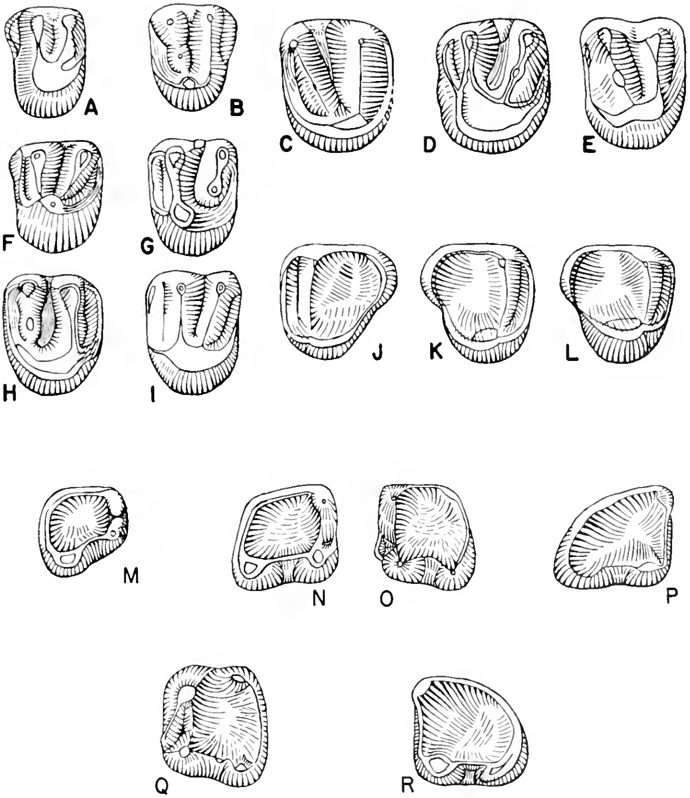

Figure 6. Upper and lower teeth of *Miospermophilus wyomingensis* n. sp., x10. *A,* C.N.H.M. PM2168, LP^4. *B,* A.C. No. 10895, RP^4. *C,* A.C. No. 10896, RM$^{1 \text{ or } 2}$. *D,* C.N.H.M. PM2172, LM$^{1 \text{ or } 2}$. *E,* A.C. No. 10897, RM$^{1 \text{ or } 2}$. *F,* U.W. No. 1409, LP^4. *G,* C.N.H.M. PM2169, LP^4. *H,* C.N.H.M. PM2173, RM$^{1 \text{ or } 2}$. *I,* U.W. No. 1411, LM$^{1 \text{ or } 2}$. *J,* C.N.H.M. PM2174, LM^3. *K,* U.W. No. 1412, RM^3. *L,* U.W. No. 1410, RM^3. *M,* C.N.H.M. PM2213, RP$_4$. *N.* U.W. No. 1414, RM$_{1 \text{ or } 2}$. *O,* U.W. No. 1413, LM$_{1 \text{ or } 2}$. *P,* C.N.H.M. PM2182, RM$_3$. *Q,* Type, A.C. No. 10898, LM$_{1 \text{ or } 2}$. *R,* C.N.H.M. PM2180, LM$_3$. (Anterior end to left except for *B, C, H, K, L, M, N,* and *P.*)

close apposition of the protoconid and metaconid. There is no indication of a complete metalophid and a narrow valley separates the protoconid and metaconid anteriorly. The metaconid is the highest cusp with the protoconid and hypoconid of almost equal height. The entoconid is rather indistinct, being nearly completely incorporated within the posterolophid. There is a short lingual arm from the entoconid to the metaconid. The posterolophid is low and curves gently to the entoconid.

The first and second lower molars are almost identical in structure, with M_1 somewhat squarer in occlusal outline than M_2. The metaconid is the highest cusp with the protoconid and hypoconid much lower and of equal size. The metalophid is generally incomplete, failing to close off the small trigonid basin posteriorly. The anterior cingulum is short and straight, usually without an anteroconid. Mesostylids and mesoconids are variable in their degrees of expression. The entoconid is generally incorporated within the posterolophid, although in some specimens it is present as a distinct cusp. The posterolophid is high and curves sharply at the entoconid angle. The ectolophid is well developed.

M_3 is longer than wide, with the talonid basin greatly enlarged The entoconid is completely incorporated in the swollen posterolophid, which is expanded posteriorly. The anterior cingulum is strong and lacks all trace of an anteroconid. In the absence of a metalophid, the trigonid basin is completely open posteriorly.

Discussion. Miospermophilus wyomingensis is closely related to *M. bryanti* and very probably descended from it. Relationships of *M. wyomingensis* to later Miocene spermophiles are uncertain at present, due primarily to the rather poor material known for the rest of the Miocene. The genus *Citellus,* however, probably evolved from *Miospermophilus,* either directly from *M. wyomingensis,* or, more probably from an as yet unknown species of the genus.

Measurements

		N	M
dP^4	a-p	2	1.48
	tr.	2	2.03
P^4	a-p	7	1.55
	tr.	7	2.00
$M^{1 \text{ and } 2}$	a-p	10	1.85
	tr.	10	2.20
M^3	a-p	3	2.04
	tr.	3	2.06

dP$_4$	a-p	2	1.48
	tr.	2	2.04
M$_{1 \text{ and } 2}$	a-p	8	1.88
	tr.	8	1.90
M$_3$	a-p	3	2.10
	tr.	3	2.00

Citellus Oken

Type species. Mus citellus Linnaeus.

Ground squirrels of the genus *Citellus* are rather common elements of most later Tertiary faunas, particularly throughout the Pliocene of the Great Basin and Mohave-Sonoran areas. However, many of these occurrences are limited to isolated teeth or fragments of mandibles and maxillae with dentitions. Because of the generalized nature of the early ground squirrel dentition, this fragmentary material can tell us very little about the relationships of most of the forms involved, except in a very broad sense, and it is not until the Hemphillian that any definite lineages can be traced leading toward the modern forms. Throughout the Miocene and early Pliocene all ground squirrels are at an otospermophile level of evolution. By the late Pliocene some populations had begun evolving towards the more highly specialized condition seen in the subgenera *Citellus* and *Ictidomys*, but the greatest change in these lines seems to have been a late Pliocene and Pleistocene phenomenon.

Recent ground squirrels can be separated into two groups on dental characters but the recognition of subgenera within these two broad groupings is extremely difficult on this basis alone. The two broad groups are: (1) the more generalized spermophiles of the subgenera *Otospermophilus*, *Callospermophilus*, *Poliocitellus*, and *Xerospermophilus*, and (2) the more specialized *Citellus* and *Ictidomys*. In the first, the dentition is low crowned, with low trigonids, low lophs on the upper molars, and long and sometimes complete metalophs on M$^{1-2}$; in the second, the dentition is high crowned with high trigonids and lophs, and short metalophs on M$^{1-2}$. The Tertiary ground squirrels all fall into the first category, with the exception of *C. (Citellus) mckayensis* from the Hemphillian of Oregon and a mandible of unknown age (perhaps early Pliocene) from Nebraska. Due to the fragmentary nature of this material and the generalized aspect of the dentitions, I have assigned most of it to the subgenus *Otospermophilus*, the least specialized of Recent ground squirrel subgenera.

Range. Middle Miocene to Recent in North America.

CITELLUS (OTOSPERMOPHILUS) TEPHRUS (Gazin)

Plate 17

Sciurus tephrus Gazin, 1932, p. 59.
Citellus ridgwayi Gazin, 1932, p. 61; Bryant, 1945, p. 354.
Protospermophilus tephrus Bryant, 1945, p. 349.

Type. L.A.C.M. (C.I.T.) No. 332, a partial skull lacking zygomatic arches, posterior part of cranium and left cheek teeth.

Type of synonym. L.A.C.M. (C.I.T.) No. 334, facial region of skull.

Hypodigm. Types and L.A.C.M. (C.I.T.) No. 335, poorly preserved skull lacking basicranium and occiput.

Horizon and locality. Late Hemingfordian, late Middle Miocene. Twenty-eight miles south of Harper and approximately three miles northwest of Skull Spring, Malheur County, Oregon.

Emended diagnosis. Size small; rostrum deep, narrow; zygomatic plate extending only two-thirds of way up rostrum; cheek-pouch muscle pit shallow; infraorbital foramen compressed, slit-like; protocones narrowed; large mesostyles set close to metacones.

In his original description of the sciurids from Skull Springs, Gazin (1932) recognized three forms: *Sciurus malheurensis*, *Sciurus tephrus* and *Citellus ridgwayi*. Bryant (1945) transferred *S. malheurensis* and *S. tephrus* to *Protospermophilus* and left *Citellus ridgwayi* as previously placed by Gazin. It is quite obvious that the skull referred to *Protospermophilus tephrus* represents a true spermophile as do the two skulls assigned to *Citellus ridgwayi*. All three skulls have been distorted considerably through crushing. In the case of the two skulls originally assigned to *Citellus ridgwayi*, this crushing flattened the skulls, particularly in the rostral region, making them appear broad and shallow. In the case of L.A.C.M. (C.I.T.) No. 332 the crushing compressed the skull laterally making it appear much narrower and deeper than it actually was. When these distortions are taken into account, it is clear that only one form is represented. Measurements of the length of the diastema and length of the tooth rows and the patterns of the cheek teeth are essentially identical. Hence, these three skulls are all here referred to *Citellus tephrus*.

Description. The skull is small and rather delicate with a long rostrum which is much deeper than it is broad. The ridges lateral to the incisors are moderately prominent and merge with the dorsal projection of the masseteric fossa. The plate itself is expanded but passes only two-thirds of the way up the side of the rostrum. The infraorbital foramen is compressed into a vertical slit lying immediately above the enlarged masseteric tubercle and only slightly anterior to P^3. The skull is rather broad interorbitally, as is best shown in L.A.C.M. (C.I.T.) No. 335. The palate is broad and the tooth rows nearly parallel.

P^3 is small, simple, and peg-like. The other cheek teeth on the type are rather worn but most of the pattern is discernible. P^4 is much smaller than the other teeth and has a narrow protocone and anterior cingulum. The protoloph on P^4-M^2 is complete and the metaloph only slightly constricted. There is no indication of a protoconule, and the metaconule, while present, is weak on the three teeth. There is a large mesostyle set close to the base of the metacone on M^1 and M^2; on P^4 it is small. The anterior cingula of M^1 and M^2 are not expanded and there is no elevated parastyle. M^3 is as wide as it is long and has neither metaconule nor mesostyle. The posterior cingulum is greatly expanded and is deeply notched at its junction with the protocone.

Discussion. Bryant (1945, pp. 348-349) placed this species in the genus *Protospermophilus* on the basis of its zygomasseteric structure. However, the incomplete development of the zygomatic plate merely represents an evolutionary stage through which most sciurid lines passed at one time or another. The characteristic features of the protospermophiles are not primarily in this structural complex but in the heavier build of the jaws and dentition. *Citellus* (*Otospermophilus*) *tephrus* does not have the heavy lophs and massive cusps of the protospermophiles but is much closer in these characters to the conditions seen in *C. (Otospermophilus) beechyi.* It is smaller than any other Tertiary spermophile, with the exception of *Miospermophilus.*

M. wyomingensis is too advanced to have been ancestral to *C. tephrus.* The lophs of the former species are higher and the metaloph constricted, conditions not seen in *C. tephrus.* However, *M. bryanti* had not acquired these specializations and could have been ancestral to *C. tephrus. C. tephrus* could have given rise to later members of the *Otospermophilus* group although transitional forms are not at present known. It resembles the Barstovian *C. (Otospermophilus) primitivus* in many respects and could have been ancestral to that species.

Measurements

	No. 332	No. 334	No. 335
Length of palate	19.7	21.1	20.5
Alveolar length P^3-M^3	7.8	8.2	8.1

	No. 332		No. 334		No. 335	
	a-p	tr.	a-p	tr.	a-p	tr.
RP⁴	1.40	1.90	1.60	2.10	....	....
RM¹	1.80	2.20	1.90	2.40	1.80	2.30
RM²	1.90	2.30	2.00	2.50	2.00	2.40
RM³	2.20	2.20	2.20	2.20	2.10	2.20
LP⁴	...	..	1.60	2.10	..	....
LM²	....	....	....	....	2.00	2.50
LM³	....	....	....	...	2.20	2.20

CITELLUS (OTOSPERMOPHILUS) PRIMITIVUS Bryant

Plate 18, figure 1

Sciurus sp. Douglass, 1903, pp. 153 and 181.
Citellus primitivus Bryant, 1945, p. 352.
Citellus (Otospermophilus) primitivus: Black, 1961a, p. 72.

Type. C.M. No. 746, right mandible with P_4-M_3 lacking angle, condyle, and coronoid.

Hypodigm. Type and C.M. No. 727 a badly crushed and damaged skull and jaws.

Horizon and locality. Upper Barstovian, late Miocene. Type from Madison Valley Formation, Gallatin County, Montana. C. M. No. 727 from 1 mile S. of New Chicago, Granite County, Montana.

Emended diagnosis. Zygomatic plate almost completely sciuromorph; mandible about the size of *Citellus (Otospermophilus) variegatus;* masseteric crest heavy; masseteric fossa deeply concave, pointed anteriorly, ending below anterior roots of M_1; prominent pit posterior to M_3 for medial part of *M. temporalis;* diastemal depression shallow; dentition small in relation to jaw size.

Description. The zygomatic plate is well developed, extending dorsally close to the top of the rostrum, and the maxillary border of the anterior zygomatic root is concave, overhanging the plate area. The cheek-pouch muscle pits are small. There appear to be three transbullar septa. The mandible is slender and the diastema is long with a shallow diastemal depression. The mental foramen is situated slightly below the diastemal surface and midway along its length. The masseteric fossa is deep and limited above and below by heavy ridges. Anteriorly it is pointed, ending below the anterior root of M_1. There is a thin bony ridge continuous with the inner alveolar border which passes backwards to unite with the ascending ramus and which encloses a prominent pit delimiting the area of insertion of the medial part of *M. temporalis.*

P^3 was evidently a small peg, and P^4 is not preserved. M^1-M^2

are low crowned, triangular in outline, with wide anterior cingula, relatively high parastyles and somewhat constricted protocones. The protolophs pass directly across the teeth and the metalophs join the protocone obliquely. Both crests are low and the metaconules small. The metaloph is partially constricted on both M^1-M^2. The mesostyles are large. The posteroexternal portion of M^3 is considerably expanded and there is a faint metaconule present.

P_4-M_3 are low crowned, and M_1-M_2 are rhomboidal in outline with M_2 somewhat more compressed anteroposteriorly than M_1. The protoconid and metaconid of P_4 are so closely appressed that they almost appear to represent one cusp. There is no trace of a trigonid basin on P_4. The posterolophid is low and curves gently through the entoconid corner. There is no distinct entoconid on P_4 and the mesostylid is small. On M_1-M_2 the entoconids are not completely incorporated within the posterolophids. The posterolophids are low and the entoconid corners slightly curved. Distinct mesostylids and mesoconids are present on both teeth. The metalophid on M_1 is weak but does cut off a small trigonid basin while on M_2 the metalophid is not complete and the trigonid basin is open posteriorly. M_3 is similar to M_1-M_2 except that the hypoconid and posterolophid are enlarged.

Discussion. Citellus (O.) primitivus was probably descended from *Citellus (O.) tephrus* of the Hemingfordian. It is more advanced than that species in having large parastyles on M^1-M^2, and a somewhat greater constriction of the metaloph at the protocone. The lophs in both species are very low, however, more so than in the Pliocene otospermophiles, and the metaconcules are small. *Citellus (O.) primitivus* has a more fully developed zygomatic plate and is larger than *C. (O.) tephrus* but these changes are to be expected during the course of ground squirrel evolution and they could have easily evolved from the condition in *C. (O.) tephrus.*

Later species of *Citellus (Otospermophilus)* cannot be traced back to *C. (O.) primitivus* but this is due primarily to the fragmentary nature of so much of the spermophile material. *Citellus (O.) primitivus* was undoubtedly in the main line of spermophile evolution as Bryant (1945) suggested.

Measurements

C.M. No. 746 Type.

Alveolar length P_4-M_3	10.0
Depth below P_4	8.8

	a-p	tr.
I_1	3.70	1.70
P_4	2.00	2.10 —
M_1	2.10	2.30-2.50
M_2	2.30	2.70-2.70
M_3	2.70	2.70-2.20

C.M. No. 727

Alveolar length P^3-M^3	10.0
Alveolar length P_4-M_3	9.8

	a-p	**tr.**
M^1	2.20	....
M^2	2.30	....
M^3	2.60	2.60
P_4	2.00	1.60-2.00
M_1	2.10	2.30-2.40
M_2	2.40	2.60-2.60
M_3	2.70	2.70-2.20

CITELLUS (OTOSPERMOPHILUS) MATTHEWI[1] n. sp.

Plate 18, figure 2

Sciurus cf. *aberti* Matthew, 1924, p. 84; Bryant, 1945, p. 346.

Type. A.M.N.H. No. 17578, partial right mandible with I, P_4 M_3.

Hypodigm. Type only.

Horizon and locality. Quarry No. 1 Upper Snake Creek Beds. Probably Clarendonian, early Pliocene. Approximately 20 miles S. of Agate, Sioux County, Nebraska. The specimen was collected by an American Museum of Natural History party in 1918. Matthew (1924, p. 63) states, "In 1918 Mr. Thomson's principal collecting was from quarries in *Aphelops* draw." It is quite probable therefore that Quarry No. 1 was located in *Aphelops* draw. A jaw of *Aelurodon haydenianus validus* Matthew and Cook was also obtained from Quarry No. 1 (Matthew, 1924, p. 100). This would appear to date Quarry No. 1 and on this basis I place the age of *Citellus (Otospermophilus) matthewi* as Clarendonian.

Diagnosis. Jaw heavy, deep; masseteric fossa rounded anteriorly below hypoconid of P_4; cheek teeth wider buccally than lingually; high crowned; entoconid corner rounded; posterolophids high; trigonid basins small; no mesoconids or anteroconids; posterior half of M_3 much narrower than anterior half; incisor not greatly compressed.

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[1] Named for the late Dr. W. D. Matthew

Description. The jaw is heavy, more so than in most spermophiles, but in general shape it is very close to that of the Recent *Citellus (Otospermophilus) variegatus.* It is deep below P_4 and also through the posterior portion of the diastema about as in *Sciurus.* The disastema, however, would appear to have been longer in relation to tooth length than in *Sciurus,* and does not drop as abruptly anterior to P_4 as in the tree squirrels. The mental foramen is placed well forward of P_4 and towards the diastemal surface. The masseteric fossa is rounded anteriorly, ending below the posterior half of P_4. It is not deeply concave and its upper border is not well defined.

The cheek teeth increase in size from P_4 to M_3 and, with the exception of P_4, are longer buccally than lingually. There is no indication of an anteroconid on P_4, in which the small trigonid basin opens toward the anterior face of the tooth. The basin is extremely shallow and would be obliterated with little wear, following which the high protoconid and metaconid would appear to be fused into a continuous ridge. The trigonid is much higher than the talonid on P_4. There is no trace of a mesoconid or of a mesostylid. The talonid basin is deep and completely enclosed by the high posterolophid, ectolophid and trigonid. There is no indication of a distinct entoconid and the entoconid corner is rounded. M_1 and M_2 are essentially identical in structure. The trigonid basin is only slightly higher than the talonid basin, with which it is confluent due to the incomplete nature of the metalophid. Anteriorly, the trigonid basin is enclosed by a complete anterior cingulum, which shows no trace of an anteroconid. The buccal valley is deep and becomes broader as it passes internally. The ectolophid and posterolophid are high and the talonid deeply basined. The entoconid corner is rounded with the entoconid submerged in the posterolophid. The mesostylid is also almost completely submerged in the lingual lophid. There is no mesoconid. The protoconid is larger than the hypoconid on both teeth. M_3 is wider than long and much wider anteriorly than across the hypoconid-entoconid. The metalophid is incomplete. The posterolophid and ectolophid are high and the hypoconid and posterior cingulum expanded. The lower incisor is not as greatly compressed as in most sciurids and is moderately convex laterally. The anterior face is rounded, and the enamel extends about halfway down the lateral side of the tooth.

Discussion. Citellus (Otospermophilus) matthewi is typically spermophile-like in its dentition; it is thus rather difficult to understand why Matthew (1924, p. 84) referred it to the living

S. aberti. Bryant (1945, p. 346) followed Matthew in this determination, not having examined the specimen himself. *Citellus (O.) matthewi* has a deeper and heavier jaw than the living spermophiles and the dentition is also heavier and large. Nevertheless, the high posterolophids of M_1-M_2, the complete incorporation of the entoconids in the posterolophids, the rounded entoconid corner, and the shallow diastemal depression clearly indicate ground squirrel affinities. It seems quite obvious that this species was a true spermophile somewhat larger in overall dimensions than the living *Citellus (Otospermophilus) variegatus* but similar to it.

Measurements

Depth below P_4		9.2
Alveolar length P_4-M_3		12.5
	a-p	tr.
I_1	3.40	2.00
P_4	2.60	2.30-2.60
M_1	2.80	3.10-3.10
M_2	3.00	3.40-3.30
M_3	3.50	3.60-3.00

CITELLUS (OTOSPERMOPHILUS) SHOTWELLI[1] n. sp.

Plate 19; Plate 20, figure 1

Citellus sp. Wilson, 1937b, p. 33.

Type. U.O.M.N.H. F-3596 fragmentary skull with RP^3-M^3, LP^4-M^2, right and left mandibles, and partial skeleton.

Hypodigm. Type and U.O.M.N.H. F-7964 left mandible with P_4-M_3, F-7965 left mandible with P_4-M_3, F-7966 right mandible with P_4-M_2, F-7969 left mandible with M_1-M_2, L.A.C.M. (C.I.T.) Nos. 5243 right mandible with M_2-M_3 and 5239 partial left mandible with M_1-M_2.

Horizon and locality. Hemphillian, Pliocene. Type from east bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon. U.O.M.N.H. F-7964, F-7965, F-7966, F-7969 all from the late Hemphillian Westend Blowout local fauna, Oregon; L.A.C.M. (C.I.T.) No. 5243 from the late Hemphillian Arlington beds, Oregon, and L.A.C.M. (C.I.T.) No. 5239 from Hemphillian deposits near Drewsey, Oregon.

Diagnosis. M^1-M^2, M_1-M_2 compressed, much wider than long;

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[1] Named for Dr. J. Arnold Shotwell.

P^4 much smaller than M^{1-3}; paracones and metacones set close together; entoconids distinct on M_1-M_2; posterolophids low, buccal valleys of P_4-M_3 narrow, curving posteriorly; metalophids generally complete on M_2.

Description. The preserved portions of the skull are much too fragmentary to provide any information. The mandible is deep below the alveolar border and is moderately heavy. The diastema is long and the diastemal depression shallow. The masseteric fossa terminates broadly under the hypoconid of P_4. It is deeply concave and the dorsal and ventral borders are heavy. The condyle lies slightly above the alveolar border, and the long axis is directed transversely.

P^3 is a simple, sharply conical peg. The subtriangular P^4-M^2 have narrow protocones and their anterior cingula do not reach the lingual borders. The anterior cingulum on P^4 is narrow and there is no indication of a parastyle, whereas on M^1-M^2 the cingulum is wider and the parastyle is prominent. The lophs are high, the metaconules large, and the metalophs incomplete, except at extreme stages of wear on P^4-M^2. Mesostyles are very small and set at the base of the paracone slopes. The paracones and metacones are close together with only a narrow valley between them. The posterior cingula are narrow and not greatly expanded toward the protocones. On M^3, the posterior cingulum bends sharply posteriorly from the protocone and the posteroexternal portion of M^3 is expanded. The parastyle is not as well developed on M^3 as it is on M^1-M^2.

P_4 is trapezoidal, M_1-M_3 rhomboidal, and M_1-$_2$ much wider than long. The protoconid and metaconid of P_4 are closely appressed with only a shallow notch separating them that is quickly obliterated by wear. There is neither anteroconid, nor mesostylid nor mesoconid on P_4. The posterolophid is low and passes straight across P_4 to the lingual margin, where it curves anteriorly to end at the small entoconid. The ectolophid is low and the buccal valley deep and narrow. The trigonid on M_1-M_3 is only slightly higher than the talonid. The metalophid is short and lies progressively farther down the metaconid slope from M_1 to M_3. In the Arlington specimen, L.A.C.M. (C.I.T.) No. 5243, the trigonid of M_2-$_3$ is higher than in the type and Westend Blowout material, and the metalophid on M_2 is complete. The posterolophid is low and terminates in a small but distinct entoconid. The buccal valley is narrow and deep and swings posteriorly as it passes internally. Small mesostylids are present on M_1-M_3. In L.A.C.M. (C.I.T.) No. 5239 the entoconid of M_1-$_2$ is not as distinct and the posterolophid is rather blade-like at the entoconid corner. The incisor has a rounded lateral face and is only moderately compressed.

The skeletal elements preserved include right and left radius and ulna, distal end of the left tibia, right calcaneum, and part of the right hind foot. The radius and ulna are longer and considerably broader distally than those of *C. (Otospermophilus) variegatus*. This is particularly true for the distal end of the radius. The distal end of the tibia, however, agrees almost perfectly in size with that of the living species. The calcaneum is rather more heavily built and the metatarsals somewhat longer than in the Recent forms.

Discussion. All of the material here referred to *C. (Otospermophilus) shotwelli* differs from *C. (O.) wilsoni* in having M^1-M^2 and M_1-M_2 wider than long, and from *C. (O.) gidleyi* in larger size. The specimens from McKay Reservoir, Westend Blowout, Drewsey, and the Arlington beds resemble each other more closely than they do any other Pliocene population of spermophile and the differences between the samples from these localities are primarily those of size. Among contemporaneous forms *C. (O.) shotwelli* is closest to *C. (O.) gidleyi* and these two species quite probably had a common ancestry in the early Pliocene. *C. (Otospermophilus) shotwelli*, particularly the Westend sample, is closer to the Recent *C. (Otospermophilus) beechyi* than to any other Recent otospermophile and would appear to be in the phyletic line leading to the Recent species.

Measurements

	F-3596	F-7964	F-7965	F-7966
Length of mandible	41.0	....	....	....
Length of diastema	9.5	....	....	....
Depth of mandible below P_4	8.5	8.3		7.5
Alveolar length P_4-M_3	11.1	10.8	10.6	11.0

	F-3596	
	a-p	tr.
P^4	2.30	2.80
	2.30	2.80

M^1	2.60	3.30
	2.60	3.30
M^2	2.60	3.20
	2.60	3.30
M^3	3.20	3.20

		F-3596	F-7964	F-7965	F-7966
I_1	a-p	2.90			
	tr.	1.60			
P_4	a-p	2.30	2.40	2.20	2.30
	tr.	2.00-2.60	2.00-2.50	1.90-2.40	2.00-2.50
M_1	a-p	2.40	2.40	2.30	2.50
	tr.	3.00-3.20	2.60-2.80	2.80-2.90	3.00-3.00
M_2	a-p	2.60	2.50	2.50	2.70
	tr.	3.30-3.30	3.00-3.10	3.20-3.20	3.30-3.20
M_3	a-p	3.20	3.20	3.10	
	tr.	3.40-3.00	3.20-2.90	3.20-2.90	

		F-7969	L.A.C.M. (C.I.T.) 5239	L.A.C.M. (C.I.T.) 5243
M_1	a-p	2.40	2.50	
	tr.	2.90-3.00	2.90-3.10	
M_2	a-p	2.60	2.70	2.70
	tr.	3.20-3.20	3.30-3.30	3.50-3.50
M_3	a-p			3.50
	tr.			3.70-3.00

Citellus (Otospermophilus) gidleyi

(Merriam, Stock and Moody)

Plate 20, figure 2

Otospermophilus gidleyi Merriam, Stock and Moody, 1925, p. 68.
Citellus (Otospermophilus) gidleyi: Bryant, 1945, p. 353.

Type. U.C.M.P. No. 26793, incomplete horizontal ramus of left mandible with P_4-M_3.

Hypodigm. Type only.

Horizon and locality. Hemphillian, Middle Pliocene. About 5½ miles west of Dayville, Grant County, Oregon.

Emended diagnosis. Smaller than Recent species of *Citellus (Otospermophilus)*; posterolophid low; lingual notch shallow; trigonid basins enclosed posteriorly by complete metalophid; mesostylid present on M_1-M_2; small ectostylids on M_1-M_3.

Description. The mandibular ramus is deep in relation to overall size, and the diastemal depression is shallow. The masseteric fossa is rounded anteriorly and more deeply concave than in Recent species. The protoconid and metaconid are closely appressed on P_4, the anterior half of the tooth being thus much narrower than the posterior. The posterolophid is low and there is no mesostylid or ectostylid. M_1 and M_2 are compressed anteroposteriorly. The posterolophids curve gently to the entoconid corner and terminate in small but distinct entoconids. The mesostylids are set off from both the entoconids and metaconids by shallow notches. The buccal valleys constrict internally. The protoconids and hypoconids are of equal size. The metalophids are complete and the trigonid basins are enclosed as small pits. The hypoconid and posterolophid of M_3 are moderately expanded and there is no mesostylid; in all other respects this tooth resembles M_1 and M_2.

Discussion. As has been pointed out (see p. 204), *C. (Otospermophilus) gidleyi* resembles *C. (Otospermophilus) shotwelli* in almost all respects. It is a decidedly smaller species, however. The similarity of the two would suggest a common ancestry probably in the late Clarendonian. No descendants of *C. (O.) gidleyi* are known.

Measurements

Depth of mandible below P_4		8.6
Alveolar length P_4-M_3		8.4
	a-p	tr.
I_1	1.50	2.80
P_4	1.80	1.40-2.20
M_1	1.80	2.20-2.20
M_2	2.00	2.50-2.50
M_3	2.50	2.50-2.20

CITELLUS (OTOSPERMOPHILUS) ARGONAUTUS Stirton and Goeriz

Otospermophilus argonautus Stirton and Goeriz, 1942, p. 462.
Citellus sp. Kellogg, 1910, p. 427; Bryant, 1945, p. 356.
Citellus? species Wilson, 1936, p. 19; Bryant, 1945, p. 358.
Citellus sp. Wilson, 1937a, p. 14; Bryant, 1945, p. 356.

Type. U.C.M.P. No. 34281, part of right lower jaw with P_4 and partial M_1.

Hypodigm. Type and U.C.M.P. No. 34280, left ramus without dentition, L.A.C.M. (C.I.T.) Nos. 1794 a partial left ramus with M_2, 1795 a right ramus without dentition, 1965 a partial right ramus with P_4-M_2, 5240 RI^1 and LI_1, 5241 a partial right ramus without dentition and U.C.M.P. No. 12570 a worn RM_1.

Horizon and locality. Hemphillian, Middle Pliocene. Type from Charles E. Schell ranch, site 1 in andesitic tuff, 5 miles west of Knights Ferry, Stanislaus County, California, U.C. Loc. V. 3813. L.A.C.M. (C.I.T.) Nos. 1794 and 1795 from Smiths Valley local fauna, Lyon County, Nevada; L.A.C.M. (C.I.T.) Nos. 1965, 5240, and 5241 from Kern River local fauna, Kern County, California; and U.C.M.P. No. 12570 from Thousand Creek local fauna, Humboldt County, Nevada.

Emended diagnosis. Smaller than *Citellus (Otospermophilus) shotwelli* and *wilsoni,* near size of *C. (O.) gidleyi;* M_1-M_2 not as greatly compressed anteroposteriorly as in *C. (O.) gidleyi;* ectolophids heavy, set well in from buccal margin; mandible heavier than in *C. (O.) gidleyi.*

Description. The diastemal depression is shallow, and the diastema only moderately long. The main area of the masseteric fossa terminates under the anterior end of M_1, but a broad scar extends forward beyond it to a point under P_4.

The protoconid and metaconid of P_4 are closely appressed with a shallow groove between them on the anterior face. The buccal valley is deep and narrow. The ectolophid is strong with no indication of a mesoconid. The posterolophid curves through the entoconid corner with no indication of a distinct entoconid. There is no mesostylid. On M_1-M_2 the anterior cingulum and metalophid are strong and enclose a small trigonid basin. The ectolophid is prominently developed and the buccal valley narrow and deep.

Discussion. Although represented in four different faunas in California and Nevada, *Citellus (O.) argonautus* is still known from only the most fragmentary material. However, the low-crowned cheek teeth and low trigonids clearly indicate that this species is an otospermophile. It is a smaller species than *C. (O.) shotwelli* and *wilsoni. C. (O.) argonautus* differs from *C. (O.) gidleyi* in the greater suppression of the entoconid within the posterolophid and the squarer outline of M_1-M_2. *C. (O.) argonautus* may have been ancestral to *C. (O.) bensoni* of the early Pleistocene but the material available is inadequate to be certain of this relationship.

Measurements

Type U.C.M.P. No. 34281

	a-p	tr.
P_4	2.10	1.80-2.20
M_1	....	2.40- ...

L.A.C.M. (C.I.T.) No. 1965

Alveolar length P_4-M_3	8.8
Depth of mandible below P_4	5.6

	a-p	tr.
P_4	1.70	1.40-1.90
M_1	1.70	....- ...
M_2	2.10	....-2.40

L.A.C.M. (C.I.T.) No. 1794

	a-p	tr.
M_2	2.10	..-2.50

U.C.M.P. No. 12570

	a-p	tr.
M_1	2.10	2.00-2.20

CITELLUS (OTOSPERMOPHILUS) WILSONI Shotwell

Plate 21

Citellus (Otospermophilus) wilsoni Shotwell, 1956, p. 728.

Type. U.O.M.N.H. F-4097, right mandible lacking incisor, condyle, coronoid, and anterior tip of jaw.

Hypodigm. Type and U.C.M.P. No. 55611, a nearly complete skull, U.O.M.N.H. F-3634 left maxillary fragment with M^1, F-3635 left maxilla with P^4-M^3, F-3636 right maxillary fragment with P^4-M^1, F-3612 fragment of right mandible, F-3628 fragment of right mandible with P_4-M_1, F-3629 fragment of right mandible with M_1-M_2, F-3494 fragment of right mandible, F-2658 fragment of left mandible, F-4085 fragment of left mandible with P_4 and M_2, F-4098 fragment of left mandible, L.A.C.M. (C.I.T.) Nos. 5246, a partial skull, 5244 a right mandible with P_4-M_3 and 5245 an edentulous left mandible and several isolated teeth and foot bones.

Horizon and locality. U.C.M.P. No. 55611 Clarendonian; Ellensburg, Washington. Type and U.O.M.N.H. F-3634, F-3635, F-3636, F-3612, F-3628, F-3629, F-3494, F-2658, F-4085, F-4098 Hemphillian; east bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon. L.A.C.M. (C.I.T.) Nos. 5244-5246 (data from Dr. T. Downs), Hemphillian; Loc. 375 near common corner of Sections 29, 30, 31, and 32, T.3N., R.22E., about 5 miles SE, of Arlington, Gilliam County, Oregon.

Emended diagnosis. Near size of *Citellus (O.) shotwelli;* molars rhomboidal in outline, not as greatly compressed anteroposteriorly as in *C. (O.) shotwelli;* metaloph incomplete, metaconule large on P^4-M^2; entoconid completely incorporated within posterolophid; metalophid progressively shorter from M_1-M_3, leaving trigonid basin open into talonid basin on M_2-M_3; ectolophids high, set well in from buccal margins on P_4-M_3.

Description. The skull resembles that of *C. (O.) variegatus* in most respects. The infraorbital foramen is nearly triangular, compressed dorsally and broad ventrally. The masseteric tubercle is large and lies at the ventrolateral corner of the infraorbital foramen. The zygomatic plate and masseteric fossa are completely sciuromorph and the notch in the zygomatic plate is opposite the middle of M^1. The mandible is moderately heavy and deep, the diastemal depression shallow, and the masseteric fossa ends broadly below the hypoconid of P_4.

P^4-M^2 are subtriangular in outline with narrow protocones but with broad posterior cingulum-protocone connections. The anterior cingulum is low and short, merging into the protocone well down on the anterior face on P^4. On M^1-M^2 the anterior cingula are broader, bear large parastyles, and do not pass to the lingual borders. The posterior cingulum rises to the top of the protocone on P^4-M^2. On all three teeth the lophs are low, the metaconules large and the metalophs incomplete. The paracones and metacones are widely separated. Small mesostyles are present on P^4-M^2. There is a small metaconule on M^3, which is joined to the base of the protocone by a low loph. The posteroexternal portion of M^3 is expanded and there is a shallow notch between it and the posterior slope of the protocone.

P_4 is trapezoidal in outline. A deep notch, partially blocked anteriorly by a small anteroconid, divides the protoconid and metaconid for about one-third of the distance down the crown. The ectolophid is high and narrow, the buccal valley is broad, and the posterolophid is constricted at the hypoconid and terminates internally at the entoconid, leaving a notch between the entoconid and metaconid. M_1-M_2 are not greatly compressed anteroposteriorly but the degree of anteroposterior compression of M_3, which is no longer than wide, is especially notable. The position of the metalophid shifts from M_1 to M_3. On M_1 it is complete and closes off the small trigonid basin, on M_2 it passes to the base of the metaconid slope, and on M_3 it passes into the talonid basin. The posterolophids are high and pass through the entoconid areas to small mesostylids. The ectolophids on M_1-M_3 are high, narrow ridges set well in from the buccal margins, and the buccal valleys are broad and deep.

Discussion. Citellus (Otospermophilus) wilsoni differs markedly from *C. (O.) shotwelli* and *C. (O.) gidleyi* in possessing upper and lower molars which show very little anteroposterior compression. In this respect *C. (O.) wilsoni* agrees with the Recent *C. (O.) variegatus* and differs from *C. (O.) beechyi.* The Clarendonian skull, here referred to *C. (O.) wilsoni,* also shows a close resemblance to *C. (O.) variegatus* as well as to other Recent species of the subgenus. By the early Pliocene most features of the skull and dentition, characteristic of modern species of *Otospermophilus,* have appeared and two distinct phyletic lines, culminating in two living species, can be recognized. The changes which took place between the early Pliocene and the present in the *C. (O.) wilsoni* to *C. (O.) variegatus* line are, as far as can be told from the material available, extremely small and consist of a slight increase in size, a slight elevation of the protoloph and metaloph, expansion of the anterior cingulum on M^1-M^2, loss of the mesostyle, and slight elevation of the ectolophid and posterolophid on M_1-M_2. All these changes are ones of degree and, as stated above, are rather trivial. However, taken together and considerng the age of the material, I believe these Pliocene forms should be considered as distinct from the Recent species.

Measurements

U.C.M.P. No. 55611

Length of skull	50.8
Width of rostrum at anterior end of zygomatic plate	11.5
Depth of rostrum at anterior end of zygomatic plate	9.8
Width of skull at supraorbital notch	12.9
Width of skull at postorbital notch	14.3
Length of diastema	13.3
Alveolar length P^3-M^3	10.2

	a-p	tr.
I^1	3.35	1.70
	3.35	1.70
P^4	2.00	2.50
	2.00	2.50

M^1	2.40	2.80
	2.30	2.90
M^2	2.40	3.10
	2.40	3.10
M^3	2.70	2.90
	2.70	2.90

U.O.M.N.H. Nos.	F-4097	F-4085
Length of diastema	—	8.5
Depth of mandible below P_4	8.3	7.8
Alveolar length P_4-M_3	11.2	approx. 11.5
P_4 a-p	2.30	2.30
tr.	1.90-2.50	1.90-2.40
M_1 a-p	2.40	
tr.	2.60-2.90	
M_2 a-p	2.70	2.80
tr.	3.00-3.00	3.20-3.20
M_3 a-p	3.20	
tr.	3.20-2.80	

U.O.M.N.H. No. F-3635

Alveolar length P^3-M^3		11.8
	a-p	tr.
P^4	2.40	2.50
M^1	2.50	3.10
M^2	2.70	3.20
M^3	3.10	3.10

L.A.C.M. (C.I.T.) No. 5246

Width of skull at supraorbital notch		12.5
Width of skull at postorbital notch		16.3
Alveolar length P^3-M^3		11.3
	a-p	tr.
I^1	3.20	1.70
P^3	1.20	1.40
P^4	2.20	2.80
M^1	2.50	3.40
M^2	2.60	3.50
M^3	2.60	3.10

L.A.C.M. (C.I.T.) Nos.	5244	5245
Length of mandible approx.	36.0	—
Length of diastema	9.5	9.5
Depth of mandible at mental foramen	6.0	—

CITELLUS (OTOSPERMOPHILUS) FRICKI Hibbard

Plate 22, figure 1

Citellus (Pliocitellus) fricki Hibbard, 1942, p. 253, 2 pls.

Type. F:A.M. No. 24627, skull with I, P^3-M^3, lacking squamosal, jugal and bullae; left ramus, lacking angle and M_3; right humerus, radius and ulna, left humerus, radius and ulna, some carpals, left tibia, partial right tibia; various vertebrae.

Hypodigm. Type only.

Horizon and locality. Ogallala Formation, Hemphillian, Pliocene. J. Swayze Quarry, Clark County, Kansas.

Emended diagnosis. Near *C. (Otospermophilus) variegatus* in size; cranium not as inflated as this species; pits for dorsal cheek pouch muscles only slightly developed; P^3 peg-like with no trace of an anterior and lingual cingulum; M^3 short; M_1-M_2 extremely compressed on lingual side.

Hibbard (1942, p. 253) stated that the characters of the subgenus *Pliocitellus* were those of the type species *Citellus fricki.* However, all characters of the species are those of the subgenus *Otospermophilus* with the exception of the extremely simple P^3 and the great buccal compression of M_2. In my opinion these two characters do not warrant subgeneric distinction and *Citellus fricki* is here placed in the subgenus *Otospermophilus.*

Description. The skull resembles that of *C. (Otospermophilus) variegatus* in most respects. The dorsal profile is rounded; the rostrum is relatively long and slender; the cranium is moderately inflated, although not as much so as in the Recent species. The zygomatic plate is fully developed, rising to the dorsal surface of the rostrum. The maxillary root of the zygomatic arch is not as deeply concave as in the Recent species, however. The zygomatic plate is not as steeply inclined, and the zygomatic notch is opposite P^4-M^1 rather than opposite the posterior half of M^1 as in *C. (Otospermophilus) variegatus.* The infraorbital foramen is vertically compressed and slit-like and the masseteric tubercle is large. The cheek-pouch muscle pits are small. The palate is narrow and the alveolar borders are set considerably below it. The paroccipital processes are short and flattened.

The mandibular ramus is slightly smaller than that of *C. (Otospermophilus) variegatus*, but agrees with it in all other respects. The diastema is long and the diastemal depression shallow. The mental foramen lies about halfway between P_4 and the incisor, just below the superior border of the mandible. The masseteric fossa is somewhat constricted anteriorly and ends below the posterior half of P_4. The condyle lies slightly above the alveolar border, as in *C. (Otospermophilus) variegatus,* but differs from that species in having the long axis of the condylar face directed anteroposteriorly rather than transversely.

P^3 resembles that of *Sciurus* more closely than that of *Citellus.* It is a simple peg with no cingulum around the base of the principal cusp, and is smaller than in Recent spermophiles. P^4-M^3 are mesodont and although well worn are clearly very similar to those of *C. (Otospermophilus) variegatus.* P^4-M^2 are roughly triangular, with low lophs, broad anterior cingula, low parastyles, and short, narrow posterior cingula. The metalophs are partially constricted, and metaconules are present. There are no mesostyles. M^3 is broadly triangular with only a slight expansion of the posteroexternal corner. A large mesostyle is present at the base of the paracone. The enamel of the compressed upper incisors is smooth.

Much of the pattern of P_4-M_2 has been obliterated by wear but these teeth nevertheless appear to have been typically otospermophile-like, with the exception of a greater anteroposterior compression of M_1-M_2, and an extreme shortening of lingual length in relation to buccal length. There is no anteroconid on P_4, and the protoconid and metaconid are closely appressed with only a shallow furrow separating them anteriorly. The entoconid corner is angular and the posterolophid low. The buccal valley is shallow on this tooth and on M_1 and M_2. M_1 and M_2 agree in pattern, but M_2 is more compressed lingually. The posterolophids on both pass anterobuccally to the entoconids, which are placed forward near the base of the metaconids. No mesostylids are present.

The limb bones are all somewhat smaller than those of *C. (Otospermophilus) variegatus* but compare with them in most respects. The humeri appear to be identical. The lateral fossa of the ulna is not as deeply excavated as in the Recent species, but the ulna and the radius of *C. fricki* agree in all other respects. The lateral and caudal fossae of the tibia are deeper in *C. fricki,* with the cranial, medial, and interosseous borders sharper and more distinctly elevated than in *C. (O.) variegatus.* In all other characters they agree. Both the scapula and pelvis are too poorly preserved for comparison with the Recent species. The calcaneum and metatarsals agree with those of *C. (O.) variegatus.*

Discussion. Citellus (Otospermophilus) fricki differs markedly from *C. (O.) tephrus* of the Middle Miocene and *Citellus (O.) primitivus* of the Flint Creek in the following characters: (1) a more elongate skull; (2) complete attainment of sciuromorph zygomasseteric structure; (3) somewhat higher crowned cheek teeth; (4) greater anteroposterior compression of P^4-M^2 and M_1-M_2. It is also, of course, much larger than *C. tephrus,* and somewhat larger and of different proportions than the Flint Creek spermophile. The skull of *C. (O.) fricki* differs considerably from *C. matachicensis* in general proportions, being much more elongate and probably not as wide across the zygomatic arches as that species. The cheek teeth in the two also differ on several counts.

The skull of *C. fricki* agrees rather well with that of the Recent *C. (Otospermophilus) variegatus* but is not as advanced as regards the degree of inflation of the cranium, the angle of the zygomatic plate, and the position of the articular surface of the condyle. It is highly specialized in the extreme compression of M_1-M_2 and in the absence of cingula on P^3 and these characters would seem to remove it from the ancestry of the later otospermophiles. On the basis of the compression of M_1-M_2 it may be related to the earlier, Clarendonian, *C. (Otospermophilus)* sp. from the Ingram Creek sites of California.

Measurements

Length of skull	57.2
Width of skull at supraorbital notch	15.5
Width of skull at postorbital notch	16.0
Width across occiput	22.5
Width of rostrum at anterior end of zygomatic plate	11.0
Depth of rostrum at anterior end of zygomatic plate	11.3
Length of diastema I^1-P^3	15.5
Palatal width at M^1	7.5
Alveolar length P^3-M^3	10.5
Length of mandible	39.5
Length of diastema	8.5
Depth below M_1	7.8
Alveolar length P_4-M_3	10.2

	a-p	tr.
I	3.90	1.95
P^3	1.20	1.20
P^4	2.00	2.70
M^1	2.50	3.20
M^2	2.60	3.30
M^3	2.70	3.10
I	3.10	1.75

P_4	2.00	1.75-2.30
M_1	2.20	2.70-2.90
M_2	2.50	3.20-3.10
Length of humerus		37.5
Length of ulna		39.3
Length of radius		31.5
Length of tibia		49.5
Length of calcaneum		11.5

Citellus (Otospermophilus) pattersoni Wilson

Plate 22, figure 2

Citellus pattersoni Wilson, 1949c, p. 170.

Type. L.A.C.M. (C.I.T.) No. 3547, right P^4-M^3.

Hypodigm. Type only.

Horizon and locality. Hemphillian, Pliocene. Yepomera local fauna. California Institute of Technology Vertebrate Paleontology Loc. 296, Arroyo de Los Jises, Matachic, Chihuahua, Mexico.

Diagnosis. Largest known species of genus; metaloph strong on M^3.

Description. The teeth are greatly enlarged and high crowned, but agree in most other respects with those of *C. (Otospermophilus) variegatus;* the only major difference in pattern is the presence of a strong metaloph on M^3 of *C. (O.) pattersoni.* P^4-M^2 are subtriangular in outline with high protocones. The anterior cingulum on P^4 is very low, joining the protocone well down near the base of the cusp. On M^1-M^2 it is low for most of its course but rises to join the protocone about two-thirds of the way up the slope. Parastyles are well developed on all teeth. The protolophs and metalophs are very high on P^4-M^3 and pass directly across the teeth, while the metalophs pass obliquely linguad from the metacones. The metalophs are constricted and large metaconules are present. The posterior cingulum on P^4-M^2 rises to the top of the protocone. Extremely small mesostyles are present. The posteroexternal corner of M^3 is expanded; the metaloph, although strong, is much lower than the protoloph and passes to the base of the protocone.

Discussion. C. (Otospermophilus) pattersoni is easily distinguished from other Tertiary sciurids by its large size combined with a rather primitive otospermophile dentition. As Wilson (1949c) has pointed out, this species resembles *Marmota* only in its large size; the teeth are higher crowned, the protocones are broader, and the metaloph is more constricted at the protocone than in that genus. *C. pattersoni* is smaller than *Paenemarmota.* Also P^4 is smaller than M^1 in *C. pattersoni* while the reverse is true for *Paenemarmota.* There is no special resemblance between *C. pattersoni* and either *Arctomyoides* or *Palaearctomys.* The affinities of *C. pattersoni* seem to be closest to the *Otospermophilus* group of ground squirrels from which it differs only in size and in the presence of a strong metaloph on M^3.

Measurements

	a-p	tr.
P^4	4.10	5.40
M^1	4.30	6.10
M^2	4.50	6.30
M^3	5.10	5.80

CITELLUS (OTOSPERMOPHILUS) sp.

Referred Specimens. U.C.M.P. Nos. 35925, partial left mandible without cheek teeth, 35926, partial left mandible with P_4-M_1, 35928, partial right mandible with P_4-M_1, 35930, incomplete right maxilla with P^4-M^3, 35953, LM^1.

Horizon and locality. Clarendonian, early Pliocene. Ingram Creek Site 2, Loc. V-3952 Stanislaus County, California, and U.C.M.P. No. 35953 Ingram Creek Site 1B, Loc. V-3951.

Description. The maxillary fragment reveals that the major portion of the large masseteric tubercle lies ventral to the infraorbital foramen, which is not greatly compressed, and that the zygomatic notch is opposite the middle of M^1. The mandible is somewhat more lightly built and not as deep as that of the Recent otospermophiles. The diastemal depression is shallow and the diastema long. The major portion of the masseteric fossa ends below the anterior end of M_1, but a large crescentic scar extends forward and dorsal to the main fossa.

P^3 is missing but its presence is indicated by a large alveolus. P^4-M^2 are essentially identical in structure. The protocone is large but the lingual margins of the teeth are narrower than the buccal margins. The anterior and posterior cingula are short and join the protocone in smooth curves on M^1 and M^2. On P^4 the anterior cingulum is low and passes into the base of the protocone. The metaloph is incomplete and a large metaconule is present. The mesostyle is small on M^1-M^2 and lacking on P^4. M^3 is slightly wider than it is long with little expansion of the posterior cingulum; there is no indication of a metaconule and only a small mesostyle.

Only P_4 and M_1 are preserved and in both known specimens they are deeply worn. There is a slight indication of an anteroconid on P_4 of U.C.M.P. No. 35928 but none on U.C.M.P. No. 35926. The protoconid and metaconid are closely appressed, with no trigonid basin intervening and the entoconid angle is rounded. There is no indication of a mesoconid or mesostylid. All detail of crown pattern has been eliminated on M_1. The tooth is quadrate, rather sharply angled at the entoconid corner and much wider than long. The lower incisor is compressed; the anterior and lateral faces are rounded and the enamel extends nearly halfway down the lateral side.

Discussion. This form appears to be a typical, generalized ground squirrel. It is much closer structurally to the *Otospermophilus-Callospermophilus* group of ground squirrels than to other subgenera of the genus but it is impossible to assign it to one or the other of these subgenera on the material available. There is a suggestion of possible relationship to *C. (Otospermophilus) fricki,* especially in the lingual compression of M_1, but in the absence of M_2 in any of this material this relationship cannot be substantiated.

Measurements

		a-p	tr.
U.C.M.P. No. 35930			
	P^4	2.20	2.80
	M^1	2.40	3.00
	M^2	2.40	3.10
	M^3	2.70	2.80
U.C.M.P. No. 35926			
	I	3.10	1.60
	P_4	2.20	2.00-2.50
	M_1	2.50	2.80-3.00
U.C.M.P. No. 35928			
	P_4	2.30	2.00-2.50
	M_1	2.50	2.80- —

CITELLUS MATACHICENSIS Wilson

Plate 22, figure 3

Citellus matachicensis Wilson, 1949, p. 171.

Type. L.A.C.M. (C.I.T.) No. 3551, nearly complete skull, mandible, ulna, radius, pelvis, sacrum, tibia and various foot bones.

Hypodigm. Type only.

Horizon and locality. Hemphillian, middle Pliocene, Yepomera local fauna. California Institute of Technology Vertebrate Paleontology Loc. 299. Matachic, Arroyo de los Pinos, Chihuahua, Mexico.

Emended diagnosis. Rostrum short, of nearly uniform width; zygomatic breadth relatively great; ectopterygoid plates well developed; mesostyles minute; cheek teeth high crowned but lophs and posterolophids low; metaconule on M^3 small; posterlophids low.

Description. The skull resembles that of *C. (Callospermophilus) lateralis* in general proportions, although it is somewhat larger. The rostrum is short and does not taper anteriorly. The interorbital width is greater than that of *C. (Otospermophilus)* and about as in *C. (Callospermophilus)*. The supraorbital notches are large and open laterally, and the postorbital bars are long and slender. The cranium is broad across the posterior zygomatic roots and narrows considerably at the postorbital bars, thus appearing rather globular in outline. The lambdoidal crests are prominent, but this has been accentuated by a slight crushing of the cranium, which has been pushed under the dorsal margin of the occiput.

The nasals extend back beyond the premaxillary-frontal suture, meeting the frontals at the level of the anterior ends of the orbits. The premaxillary-maxillary suture passes anteriorly along the dorsal surface of the skull and then drops straight down at the anterior edge of the zygomatic plate to the ventral surface of the rostrum, where it bends forward to the incisive foramen. The zygomatic plate is fully developed, reaching the dorsal surface of the rostrum where it ends in a distinct pit just behind the premaxillary-maxillary suture. The plate is deeply concave and overhung by an extensive projection of the maxillary root of the zygoma. The infraorbital foramen lies just above and anterior to P^3, and is oval. The masseteric tubercle is large and situated at the lateroventral margin of the foramen. The zygomatic notch lies opposite the posterior end of M^1.

The palate is short and broad, with the tooth rows converging posteriorly. Just behind the incisors there are moderately developed cheek-pouch muscle pits. Opposite M^2 the maxillary-palatine suture passes in a straight line to the middle of the palatine foramina, where it bends posteriorly. The pterygoid fossae are broad, with the pterygoid plates converging posteriorly and the ectopterygoid plates flaring laterally. The buccinator and masticatory foramina are separate.

The posterior zygomatic root extends well out from the cranium, giving the skull a wide zygomatic breadth. The jugal extends to the anterior tip of the orbit behind the maxilla. It is expanded and faces ventrolaterally throughout most of its length. The squamosal extends up the lateral wall of the cranium to a point just below the postorbital bar. The bullae are nearly circular, with their widths almost equaling their lengths. The foramen magnum is elliptical and much wider than in *C. (Callospermophilus) lateralis.* The occiput is also broader in relation to its height than in that species.

The mandible is rather heavy and the diastema short relative to the alveolar length. The diastemal depression is extremely shallow and the mental foramen lies just below the dorsal surface and closer to the incisor than to P_4. The masseteric fossa ends broadly under the posterior end of P_4. The long axis of the condyle is directed transversely rather than anteroposteriorly as in Recent species.

P^3 is small and rises to a steep peak that is supplemented only by a very narrow internal cingulum. P^4-M^3 are high crowned, particularly internally, more so than in Recent species of *Otospermophilus* or *Callospermophilus*, although in pattern they resemble the cheek teeth of these subgenera more closely than they do those of the more specialized ground squirrels of the subgenera *Citellus* and *Ictidomys*. The anterior cingula on P^4-M^2 are short and are set off from the protocones, lying well below the tops of the lophs. The protolophs are moderately high, but lie below the apices of the protocones. The metalophs are set off from the protocones, ending in large metaconules. The posterior cingula rise gently to the apices of the protocones. Small mesostyles are present on all cheek teeth. M^3 is not greatly expanded posteriorly. There is a small metaconule part way down on the buccal slope of the protocone. The anterior cingulum is somewhat larger than on P^4-M^2 and rises to the apex of the protocone. The upper incisors are not as recurved as in Recent species, and their tips are perpendicular to the occlusal surface of the cheek teeth.

The lower molars are high crowned but in pattern are closer to those of the lower crowned *Callospermophilus* than to those of any other group of ground squirrels. The buccal valley on P_4 is broad and shallow and the protoconid and metaconid closely appressed. The posterolophid is low and curves to a small but distinct entoconid. There is no mesoconid or mesostylid on any cheek tooth. M_1-M_2 are rhomboidal, with moderately elevated trigonids and low posterolophids. The entoconid corners are curved and there is a distinct notch between the end of the posterolophid and the base of the metaconid. The trigonid basins are small and completely enclosed by the metalophids. The buccal valleys are constricted and deep. On M_3, the metalophid is weak, joining the metaconid much farther down its posterior slope than is the case on M_1 or M_2. The posterolophid is enlarged and heavy.

The skeletal elements of *C. matachicensis* are similar to those of *C. (Otospermophilus) variegatus* differing primarily in their smaller size and more slender proportions. The lateral fossa of the ulna is not as deeply concave as that of the Recent species and the distal half of the radius is broader in *C. matachicensis.* The proximal third of the right femur and the distal two-thirds of the left tibia also agree with those of *C. (Otospermophilus) variegatus.* The presence of four sacral vertebrae has been mentioned by Wilson. Bryant (1945) found that over 50 per cent of all ground squirrels have four sacrals, but that only in the subgenus *Ictidomys* were four sacrals present in all specimens examined. He points out that the higher number of sacral vertebrae is correlated with increased fossorial specialization. The presence of four sacrals in *C. matachicensis* would indicate that selection for improved fossorial habit had begun at least by the Hemphillian and probably earlier.

Discussion. Citellus matachicensis combines characters which are found in several of the Recent subgenera of *Citellus.* For this reason Wilson (1949c) did not refer it to any of the Recent subgenera and I have followed him in this. The skull resembles that of *Callospermophilus* and to a less extent that of *Citellus* in the narrow, short rostrum, great zygomatic breadth and general proportions. On the other hand, the dentition resembles that of *Otospermophilus,* differing only in that the teeth are much higher crowned in *C. matachicensis.* However, the high crowned dentition differs from that in *Citellus* and *Ictidomys* where the lophs, trigonids, and posterolophids are elevated as sharp lophs while in *C. matachicensis* the lophs, trigonids, and posterolophids are low and rounded and the increase in height has elevated the entire crown of the teeth. *Citellus matachicensis* appears to be most closely allied to either *Otospermophilus* or *Callospermophilus* but its exact subgeneric position is unknown. No descendants of this species are known.

Measurements

Length of skull	47.3
Width of skull at supraorbital notch	11.5

Width of skull at postorbital notch	13.3
Width of skull across posterior zygomatic root	32.0
Width of rostrum at anterior end of zygomatic plate	9.4
Length of palate	23.4
Length of diastema	11.3
Alveolar length P^3-M^3	11.0
Length of mandible	33.4
Length of diastema	6.8
Depth below M_1	6.7
Alveolar length P_4-M_3	10.5

	a-p	tr.
I	2.60	1.70
P^3	1.30	1.20
P^4	2.30	2.90
M^1	2.45	3.25
M^2	2.50	3.25
M^3	2.90	2.90
I	2.50	1.50
P_4	2.10	1.80-2.40
M_1	2.30	2.50-2.70
M_2	2.60	2.90-2.90
M_3	2.70	2.90-2.60

CITELLUS (CITELLUS?) sp.

Plate 22, figure 4

Material. A.M.N.H. No. 8338, incomplete right mandible with I and P_4-M_3.

Horizon and locality. Late Miocene or early Pliocene, "Miocene Loup Fork Formation, *Procamelus* Beds, Nebraska." Information taken from the label. Name of collector and date of collection not given.

Description. The mandible is slender with a long, shallow diastema which lies above the alveolar level at the base of the incisor. Most of the masseteric fossa is missing but anteriorly it extends forward to below the posterior half of P_4. The mental foramen is situated quite far forward at about the midpoint of the anterior portion of the ramus and just below the level of the diastema. Just behind the mental foramen there is a prominent bony knob.

The incisor is compressed, flat medially, and convex laterally. There is no trace of an anteroconid on P_4 and virtually no trigonid basin. The protoconid and metaconid form a continuous high ridge. The buccal valley is deep and bends slightly posteriorly as it passes the hypoconid. The ectolophid is low and there is no trace of a mesoconid. The talonid basin is shallow but completely enclosed. The low posterolophid passes in a gentle curve from the hypoconid around the entoconid corner to the base of the metaconid. There is no indication of an entoconid. M_1 and M_2 are compressed anteroposteriorly and are essentially identical in structure, differing only in size. There is no anteroconid present. The trigonid basins are small, shallow, and completely enclosed in the protoconid-metaconid ridge. The buccal valleys are deep and dammed by low ectolophids without mesoconids. Lingually small mesostylids are present, set off from both the metaconids and entoconids by shallow valleys. The posterolophids are low and merge into indistinct entoconids. M_3 is almost as wide as it is long with very little expansion of the hypoconid and posterolophid. The entoconid is not discernible as a distinct cusp but is submerged in the posterolophid. Neither a mesoconid nor a mesostylid is present. The metalophid is incomplete.

Discussion. This specimen bears some resemblance to the living *Citellus (C.) tridecimalineatus,* the thirteen-lined ground squirrel, and, on the basis of tooth proportions and general shape could be regarded as broadly ancestral to the more specialized ground squirrels of the *Ictidomys-Citellus* group. The protoconid-metaconid ridge is not as greatly elevated as it is in the Recent species although more so than in other contemporary forms. The anteroposterior compression of molars is greater than is generally the case in the *Otospermophilus-Callospermophilus* group or in *Ammospermophilus.* The relatively unexpanded posterior half of M_3 is also closer to the condition found in the subgenus *Citellus* than to that encountered in other ground squirrels. However, all of these characters, while very possibly suggestive of *Citellus (Citellus)* or of *C. (Ictidomys),* are still at so early a stage of development that a positive assignment to that group of ground squirrels is scarcely justified. It is most unfortunate that the age of the specimen is not precisely known; if it is early Pliocene, then the absence of more progressive contemporaneous species would tend to support the view advanced on page 238 that the subgenera *Citellus* and *Ictidomys* did not appear as such until the Hemphillian.

Measurements

Length of diastema		7.6
Alveolar length P_4-M_3		8.5
	a-p	tr.
I	2.50	1.40
P_4	1.70	1.70-2.00
M_1	1.90	2.30-2.50
M_2	2.10	2.60-2.70
M_3	2.60	2.70-2.30

CITELLUS (CITELLUS) MCKAYENSIS Shotwell

Plate 22, figure 5

Citellus (Citellus) mckayensis Shotwell, 1956, p. 728.

Type. U.O.M.N.H. F-3627, left horizontal ramus with M_1-M_3.

Hypodigm. Type and U.O.M.N.H. F-3613 and F-3659, partial mandibles without dentition.

Horizon and locality. Hemphillian, late Pliocene. East bank of McKay Reservoir, 5 miles south of Pendleton, Umatilla County, Oregon.

Diagnosis. "Molars increase in size from M_1-M_3. A species about the size of living *C. (Citellus) columbianus.* Trigonid much higher than talonid on all molars. A distinct notch is present between posterolophid and parametaconid. Metalophid connects progressively farther down on parametaconid from M_1-M_3. M_1 and M_2 are wider than long; M_3 is longer than wide." (Shotwell, 1956, p. 729.)

Description. The two edentulous mandibles are identified as *C. mckayensis* on the basis of the comparatively shallow ramus. Mandibles of *C. (Otospermophilus) wilsoni* from this locality are much deeper and in general more robust than those here referred to *C. (Citellus) mckayensis.* The diastema is relatively short and the diastemal depression extremely shallow. The mental foramen is closer to P_4 than in *C. wilsoni.* The masseteric fossa extends forward to below the posterior end of P_4.

M_1 is slightly smaller than M_2 but agrees with it in every respect except a higher and more complete metalophid. The trigonids are as well developed as in Recent species of the subgenus. The trigonid basin is enclosed on M_1 but open on M_2 and M_3. The buccal valleys of all molars are deep, broad, and closed internally by thin ectolophids; on M_3 two minor tubercles are present at the bottom of the valley. The posterolophids of M_1 and M_2 are higher than the hypoconids. A shallow lingual notch separates the metaconid and posterolophid on M_1-M_3. M_3 is elongate with an expanded posterolophid; the entoconid is not distinct, but a short lophid passes from the entoconid region towards the hypoconid.

Discussion. C. mckayensis is the earliest surely known member of the more highly specialized ground squirrels of the subgenus *Citellus.* It is considerably advanced over *Citellus (Citellus?)* sp. from the "*Procamelus* Beds" having much higher trigonid lophs. The presence of this advanced species in the late Hemphillian suggests either a somewhat longer history for the group than might have been expected, or a very rapid development of these more specialized forms during the Pliocene. I incline toward the latter view, primarily because of the absence of any advanced spermophiles in other Pliocene faunas and because of the great difference between *C. (C.) mckayensis* and *C. (Citellus?)* sp. from the early Pliocene? of Nebraska. *C. (Citellus) mckayensis* resembles *C. (Citellus) cochisei* from the early Pleistocene of Arizona and could well have been ancestral to it.

Measurements

U.O.M.N.H. No. F-3613

Length of diastema	7.5
Depth below M_1	6.6
Alveolar length P_4-M_3	12.8

		a-p	tr.
F-3627	M_1	2.00	2.70-2.70
	M_2	2.30	2.90-2.90
	M_3	3.20	3.00-2.70
F-3613	I	2.40	1.30

AMMOSPERMOPHILUS? sp.[1]

Plate 22, figure 6

Material. U.O.M.N.H. Nos. F-5871 and F-5763, both horizontal right rami with I, P_4-M_3.

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[1] Since this paper was submitted for publication Shotwell's paper on the Juntura Basin faunas has appeared (Shotwell, J.A., et al., 1963. The Juntura Basin: Studies in Earth History and Paleoecology. Trans. Amer. Phil. Soc., n.s., v.53, pt. 1:1-77) in which a new species, *Citellus junturensis,* is described, based upon the material here referred to *Ammospermophilus?* sp. plus some additional material not seen by me. Shotwell (p. 46) points out the resemblance of *C. junturensis* to *Ammospermophilus* but does not refer his species to the latter genus because he believes the resemblances may reflect parallelism rather than direct relationship. This is, of course, possible; however, the suite of characters found in the lower dentition may reflect direct relationship to *Ammospermophilus* as I have indicated above. On the material available this relationship cannot be certainly determined but a tentative reference of this material to *Ammospermophilus* is, I believe, justified.

Horizon and locality. Clarendonian, early Pliocene. About 3 miles SW of Juntura, Oregon.

Description. The ramus is stout in relation to the size of the dentition, more so than in Recent species. The masseteric fossa terminates below the anterior end of M_1 and is pointed anteriorly. It is deeply concave with a sharp ridge bordering it below.

P_4 is much wider posteriorly than anteriorly. There is no indication of an anteroconid. A weak ectolophid closes the broad buccal valley; there is no mesoconid. The posterolophid is moderately high and curves gently forward at the entoconid corner, and the entoconid is completely submerged within it. M_{1-2} are approximately as long as wide. M_1 is smaller than M_2 but otherwise agrees closely with it. The protoconid and hypoconid are of nearly equal size. Neither an anteroconid nor mesoconid is present. The trigonid basin is enclosed anteriorly by a strong cingulum, stronger on M_1 than on M_2 in F-5871, and posteriorly by the metalophid. The degree of development of the metalophid is variable; it is stronger on M_1 than on M_2 in both specimens and more pronounced in F-5763. The posterolophids are elevated and curve gently forward at the entoconid. Small mesostylids are present on M_1 and M_2 of F-5763 but are absent on F-5871. The buccal valleys are broad and the ectolophids weak. The talonid of M_3 is expanded, with a large hypoconid, a heavy posterolophid and an enlarged entoconid area. The metalophid is weak, more so in F-5871 than in F-5763. There is a small mesostylid in F-5763 but not in F-5871. The incisors are compressed and only slightly convex laterally.

Discussion. Reference to *Ammospermophilus?* is based solely on the dentition, and because of this is open to some doubt. The diagnostic characters of *Ammospermophilus* are to be found primarily in the skull (Bryant, 1945, p. 375) and are those of a rather generalized ground squirrel. However, there are a few characters in the dentition, which, when taken together, seem to distinguish *Ammospermophilus* from *Citellus*. These are: (1) small size; (2) teeth low crowned; (3) the lack of anteroposterior compression of M_1-M_2; (4) the straight posterolophid curving only at the lingual border; (5) the equal size of the protoconids and hypoconids on M_1-M_2; (6) shallow and broad buccal valleys; and (7) the almost rectangular outline of M_3. Any one of these characters may of course be found in the subgenera of *Citellus* but I have been unable to find such a combination in any of them. *C. (Callospermophilus)* approaches the condition in *Ammospermophilus* most closely but, nevertheless, differs from it in the construction of the posterolophid, in somewhat higher crowned dentition, and in the larger size of the protoconid relative to the hypoconid on M_1-M_2. *Ammospermophilus?* sp. may therefore stand in an ancestral position for the genus. The mandible is heavier and deeper than in the Recent species but this is to be expected in any early member of the group.

Measurements

		F-5871	F-5763
Alveolar length P_4-M_3		7.00	7.10
P_4	a-p	1.30	1.35
	tr.	1.05-1.45	1.10-1.45
M_1	a-p	1.55	1.50
	tr.	1.60-1.80	1.50-1.80
M_2	a-p	1.75	1.70
	tr.	1.85-1.90	1.80-1.90
M_3	a-p	2.00	1.95
	tr.	1.95-1.90	1.90-1.85

CYNOMYS Rafinesque

Two supposed occurrences of Tertiary prairie dogs have been reported. Matthew (1899) mentioned a specimen of *Cynomys* from the Republican River of Nebraska, and this record has been repeated in later faunal lists (Matthew, 1909; Merriam, 1917; Cook and Cook, 1933; and Bryant, 1945) but I have not come across any material upon which the identification could have been based. Green (1960) has described a new species of *Cynomys, C. spispiza* (S.D.S.M. No. 57100, a mandible with P_4-M_3) from South Dakota, giving the age as either late Miocene or early Pliocene. The material was found on "the spillway of Roosevelt Lake dam, Tripp County, South Dakota" (Green 1960, p. 545), on an exposure of Valentine sand together with a ground squirrel indistinguishable from the Recent *Citellus (Citellus) richardsoni* (S.D.S.M. No. 592, a right mandible with P_4-M_1, and isolated teeth S.D.S.M. Nos. 5934-5936). The prairie dog does not appear to me to be separable from the Recent *Cynomys leucurus*. Since both species found at this locality are indistinguishable from Recent forms, I regard the age assignment as extremely questionable and suspect that the specimens were derived from Pleistocene sediments. I think it fair to state that we do not yet have unequivocal evidence of the existence of *Cynomys* prior to the Pleistocene.

The dentition of *Cynomys* is rather highly specialized being higher crowned than that known for any other North American sciurid. The skeleton is more specialized for fossorial life than that of the spermophiles, less so than that of the marmots (Bryant, 1945). I suspect that the prairie dogs did not branch off from the spermophile line before the later Pliocene.

Sciurid, *incertae sedis*

Sciurid? sp. Wilson, 1934, p. 16.
Sciurid? sp. Bryant, 1945, p. 340.

Material. L.A.C.M. (C.I.T.) No. 1513, a fragment of left mandible with P_4 and partial incisor.

Horizon and locality. Whitneyan late Oligocene. Las Posas Hills, southern part of Ventura County, California.

Description. There is some of the jaw surrounding P_4 and the barest outline of a portion of the alveolus for the incisor, but there is not enough bone present to show anything of the structure of the mandible. The metaconid on P_4 has been broken off and lost as well as some of the enamel on the posterior side of the tooth. The pattern is extremely simple with a large metaconid, protoconid and hypoconid of equal size, and no trace of an entoconid. There is no mesoconid or ectolophid. There does not appear to have been an anteroconid present. The incisor is compressed, and the enamel extends one-third of the way down the lateral side of the tooth.

Discussion. P_4 appears to be that of a sciurid but the material can tell us no more than that.

Measurements

	a-p	tr.
I	2.60	1.10
P_4	1.90	1.70-1.80

PHYLOGENETIC HISTORY

The basic question concerning the evolution of the Sciuridae is the origin of the family. Most American students would derive the Sciuridae from the Paramyidae (e.g. Bryant, 1945; Wilson, 1949b, 1960; Wood, 1955, 1959, 1962). Some European workers, on the other hand, feel that the Sciuridae, at least as regards their dentition, represent the most primitive stage in rodent evolution, and that the Paramyidae are actually more advanced (e.g. Stehlin and Schaub, 1951; Schaub, 1953, 1958; Viret, 1955). This difference of opinion is due primarily to conflicting interpretations of the anterior cusp of the trigonid. Schaub believes this cusp to be a paraconid and accordingly states (1953, p. 9) "parmi tous les Simplicidentés fossiles et récents, les Sciuridés présentent la structure la plus archaïque des molaires." Most American workers, however, interpret this cusp as a neomorph that has arisen from the anterior cingulum, and apply the term anteroconid to it. The

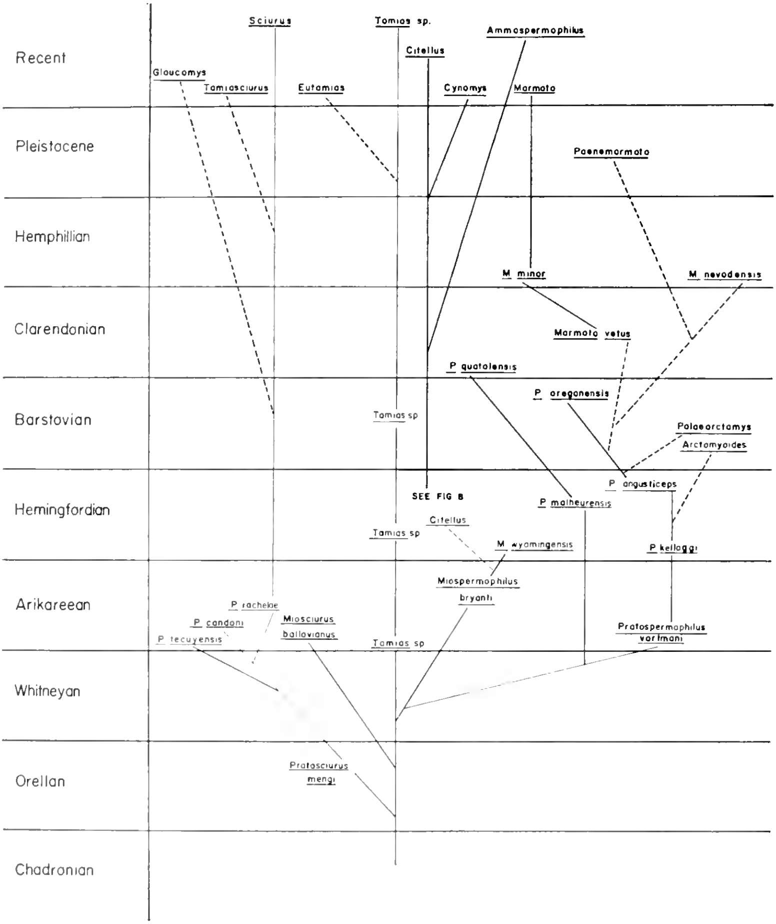

Figure 7. Phylogenetic tree of North American Sciuridae. Solid lines indicate probable relationships, broken lines possible relationships.

paraconid, they believe, was absent in the ancestral stock that gave rise to the order. The early paramyids, especially members of the most generalized subfamily, the Paramyinae, have no cusp in this position at all. This is also true of many Recent sciurids and of many of the Oligocene and early Miocene forms. There is really no concrete evidence whatever that a true paraconid was part of the rodent heritage.

It is evident, I believe, that the ancestors of the Sciuridae, and, ultimately, of all rodent groups, must be looked for within the family Paramyidae, the earliest and most primitive of rodent groups. Wood (1962, p. 116) has described the genus *Uriscus* from the late Eocene of California and believes it to be close to the actual ancestry of the Sciuridae, stating that "the pattern of the molars is so close to that of *Sciurus* that it probably could not be generically separated on tooth structure." He observes that the lower molars of this form are rhomboidal rather than rectangular, the anterior cingulum bears no cusp, the metalophid progressively shortens from M_1 to M_3 and the small trigonid basin opens posteriorly, the posterolophid curves somewhat to the entoconid, which is distinct, small mesostylids and large mesoconids are present, and the hypoconid of M_3 is expanded posteriorly. It is obvious that the dentition of this form is indeed extremely sciurid-like. The similarity ends with molar structure, however. The incisors are not compressed and the masseteric fossa ends below M_2; these characters are definitely those of a true paramyid. Whether this new form is itself directly ancestral to the Sciuridae is, of course, uncertain, but Wood's work makes it very clear that the ancestors of the Sciuridae were members of the Paramyinae.

The Paramyinae were presumably ground living forms with a rather generalized, scampering type of skeleton. In the molars, the protocones were large and the hypocones generally absent or, when present, small. Both protoconules and metaconules were present in the lophs of M^1-M^2 and the upper molars were subquadrate. The lower molars were generally rectangular but, as just mentioned, in at least one genus they were tending towards a more rhomboidal condition. No members of the Paramyinae had anteroconids on the anterior cingulum. The trigonid basins were enclosed by a metalophid posteriorly, which in some cases was incomplete. The hypoconids and entoconids were connected by marginal, somewhat elevated posterolophids. In no members of the subfamily was an entoconid crest present. In one form, *Leptotomus*, there was an indication of a forward migration of the masseter in front of the zygoma. In the mandible, the masseteric fossa ended below M_2 and the diastema was short and straight with no depression.

Just when the ancestral paramyine line reached the sciurid level of organization is at present unknown. However, the transition surely occurred in the latest Eocene or earliest Oligocene. All that was needed to complete the transition was a slight specialization in zygomasseteric structure, the dentition of certain paramyines being already almost completely sciurid-like. Once the *masseter lateralis* had migrated anterodorsally lateral to the infraorbital foramen and the masseteric fossa had shifted forward to a point beneath M_1 the sciurid level had been achieved. Sciurids were definitely present in the mid-Oligocene, and by the early Miocene several distinct lines within the family are recognizable. This would seem to indicate the existence of a rather diversified sciurid fauna in the late Oligocene with the tribal groups probably differentiating at this time. *Protosciurus mengi* of the mid-Oligocene embodies most of the features one would expect in an early sciurid, and it may well be that it is not too far removed from the earliest sciurid stock. If this is the case, an early Oligocene or, at the earliest, a late Eocene origin for the family would seem reasonable.

Several authors have suggested that the ancestry of the sciurids may be found among the Prosciurinae (e.g. Wilson, 1949b, 1960; Galbreath, 1953). Both Galbreath (1953) and Wilson (1960) have stated that *Cedromus* from the middle Oligocene of Colorado, if not a true sciurid, is at least close to the ancestry of the family. Wood (1962, p. 232) places *Cedromus* in the Prosciurinae. The infraorbital foramen and masseter in *Cedromus* and other prosciurines are completely protrogomorph with no squirrel modifications. In view of the occurrence of sciurids in the Oligocene of North America and Europe, it does not seem possible that the masseteric transition could have occurred rapidly enough for any of the known Oligocene prosciurines to have been actual ancestors of the squirrels. Quite apart from this, moreover, there is a further major obstacle to deriving squirrels from prosciurines. The real difficulty lies in the fundamental differences in the morphology of the dentition in the two groups.

All prosciurines, including *Cedromus,* have emphasized the entoconid as a discrete cusp. During the course of prosciurine history, it became progressively isolated from the posterolophid and acquired an independent crest passing into the talonid basin toward the hypoconid. Also, in almost all prosciurines, the lower molars are rectangular and considerably longer than wide. Differences between the upper dentitions of sciurids and prosciurines are less striking, but the molars of prosciurines are generally triangular, with narrow, sharply pointed protocones and rather prominent, buccally projecting mesostyles that tend to make the buccal borders of the teeth appear scalloped. Some prosciurine upper molars are much more reminiscent of those of *Haplomys* and early aplodontids in general than they are of sciurids. These characters are present throughout the history of the Prosciurinae and there is no indication of sciurid tendencies in any of the known forms within the subfamily. In view of these decided differences, I cannot see how the prosciurines can have had anything to do with the origin of the Sciuridae; the ancestry of the family is to be sought in the Paramyinae.

Bryant (1945, p. 365) and Wilson (1960, p. 64) have compiled lists of characters that they suspect were probably present in the early Oligocene sciurids. The following list agrees in most respects with theirs, differing in a few particulars.

Skull: (1) skull roof flat; (2) braincase not expanded; (3) basifacial axis only slightly bent relative to the basicranial; (4) postorbital process short and probably blunt; (5) rostrum short, relatively heavy; (6) broad interorbitally; (7) auditory bullae complete and with two septa; (8) masseter restricted to zygoma and zygomatic plate lateral to infraorbital foramen.

Mandible: (1) diastema short; (2) diastemal depression shallow; (3) masseteric fossa ending behind M_1 with no scar anterior to it; (4) well developed pocket behind M_3 for *temporalis medius* insertion.

Upper cheek teeth: (1) no hypocone; (2) posterior cingulum uniting with protocone at right angle, with slight swelling at union; (3) anterior cingulum expanded, with low parastyle; (4) metaloph and protoloph probably complete; (5) conules present but small.

Lower cheek teeth: (1) M_1-M_2 square to slightly rhomboidal; (2) M_3 elongate; (3) anterior cingulum straight, joining metaconid and protoconid; (4) anteroconid small to absent; (5) metalophid progressively shorter from M_1 to M_3; (6) trigonid basin small; (7) entoconids distinct; (8) posterolophid only slightly elevated and curved; (9) ectolophids weak and submarginal.

Incisors: (1) upper incisors broad, unfurrowed; (2) lower incisors somewhat compressed, probably unfurrowed.

Skeleton: (1) rather generalized scampering type of skeleton, without fossorial adaptations in the limbs or girdles; (2) in general the skeleton probably resembled that of *Tamias;* (3) vertebral column of moderate length with the sacrum composed of three vertebrae; (4) limbs moderately long in relation to the vertebral length, humerus and femur short in relation to the length of the radius-ulna and tibia-fibula; (5) limb bones slender and distal ends of the radius and ulna and tibia and fibula probably narrow.

Habit: forest dwelling, probably semiarboreal, as are the chipmunks and tree squirrels; seed, berry, and nut feeders.

For knowledge of the skeleton we must wait, but so far as the skull and dentition are concerned most of the characters listed above are realized in species of *Protosciurus* from the mid-Oligocene and the early Miocene and in *Miosciurus ballovianus* from the early Miocene. *P. condoni* has evolved beyond the hypothetical ancestral condition in such characters as the long, pointed postorbital process, the deep, abrupt diastemal depression, and the presence of anteroconids. However, such differences as these could have easily been acquired after the origin of the family in the latest Eocene or early Oligocene.

Early and mid-Oligocene microfaunas are well known but for the most part fail to sample forest communities. The absence of squirrels in these faunas is, therefore, not surprising if the assumption that the early members of the family were terrestrial to semiarboreal forest dwellers is accepted. If they were terrestrial and living in open country habitats, it is difficult to explain their absence in these faunas. Late Oligocene microfaunas are very poorly known and it is not surprising that we have no record of the family at that time. In view of the morphological diversity observed in the early Miocene, it is likely that the late Oligocene was a period of rather rapid diversification within the family. This diversification was no doubt profoundly influenced by the changing climatic and vegetational conditions that were taking place in both the Great Basin and Great Plains provinces.

Middle and late Tertiary floras are quite well known for the Great Basin (see Chaney, 1940, and Axelrod, 1950, 1956) but they are poorly represented in the Great Plains. Our knowledge of the vegetation of the Great Plains from the middle Oligocene through the Pliocene is limited to the Florissant flora (some elements of which are certainly plains species while the major portion of the flora indicates an upland habitat [MacGinitie, 1953]), Elias' studies (1932, 1935, 1942) on fossil grasses, and a series of rather limited florules from the Pliocene of Nebraska, Kansas and Oklahoma (Chaney and Elias, 1936).

MacGinitie (1953, pp. 57-59) has suggested that the vegetational picture for the Great Plains during the early and mid-Oligocene was one of mesic forest elements *(Fagopsis, Populus,* *Salix, Zelkova, Chamaecyparis, Sequoia, Acer, Athyana, Bursela, Carpinus, Carya, Cedrela, Dipteronia, Koelreuteria, Lindera, Osmanthus, Rhus, Robinia, Sapindus, Staphylea, Ulmus)* growing along the lake and stream borders with scrub forest and grass predominating away from the stream channels. Through the late Oligocene and the Miocene this vegetational pattern evolved towards a more open plains condition with widespread grasslands developed by the late Miocene. The forest elements were greatly reduced and progressively restricted to the stream banks. This change in the vegetational pattern was brought about by the gradual elevation of the Rocky Mountains and the consequent decrease in annual precipitation which accompanied this uplift. MacGinitie has estimated that the annual rainfall during the mid-Oligocene was near 20 inches just east of the Rocky Mountains, and it probably decreased progressively during the Miocene. By the late Miocene the Great Plains, at least south to southern Kansas and northern Oklahoma, were characterized by a semiarid grassland vegetation *(Platanus, Salix,* and *Fraxinus* along the stream borders). The southern portions of the Great Plains at this time were evidently somewhat more moist (Chaney and Elias, 1936, p. 27) with a more humid type of vegetation (including *Acer, Bumelia, Populus,* and *Ulmus)* along the stream banks.

Such evidence as there is of the Great Plains floras indicates a climate much less humid than that of the Great Basin during the Miocene. Chaney (1940) has stated that the forests of the Great Plains were displaced earlier than those of the Great Basin, with the subsequent development of widespread grassland. During the Miocene the northern Great Basin was dominated by the Arcto-Tertiary flora and a relatively temperate climate with an annual rainfall approaching 50 inches. This flora was composed of hardwood-deciduous and coniferous species. The southern Great Basin and Mohave-Sonoran areas were dominated during the Miocene by the Madro-Tertiary flora composed of live oak, conifers, arid subtropical scrub, chaparral, and plains grasslands. This vegetation was drought resistant and lived under a semiarid climate with 15 to 25 inches of rainfall annually. With the beginnings of the elevation of the Cascade and Sierra Nevada Mountains in the early Pliocene the climate changed drastically. The annual rainfall dropped some 5 to 7 inches during the early Pliocene and Madro-Tertiary floral elements moved into the northern Great Basin as the more mesic elements of the Arcto-Tertiary flora dropped out. In the southern Great Basin the semiarid shrubby species increased while the woodland elements were eliminated.

This general increase in aridity continued through the Hemphillian with a further drop in rainfall, increased temperature extremes, and absence of woodland species. Grasslands probably dominated the Great Basin during the Hemphillian, and it seems likely that the present desert areas in the Great Basin and Mohave-Sonoran areas did not develop until the Pleistocene.[1]

The development of grasslands, the compression and break-up of forest areas, and the increasing aridity must have played a major role in the history of the ground squirrels. The vegetational change could account for the almost complete absence of tree squirrels and chipmunks in the fossil record after the early Miocene.

The compression and gradual elimination of forest areas from the late Oligocene through the Miocene in the Great Plains created a series of new ecological niches while at the same time undoubtedly wiping out many habitats previously occupied by the Oligocene sciurids. This situation presumably led to strong selective pressure for adaptation to an increasingly terrestrial life, and forms capable of making the adaptive shift from forest and forest-edge habitats into the grasslands were favored. Recent chipmunks, in both their morphology and ecology, stand in an intermediate position between the tree squirrels and the ground squirrels. They are capable climbers, and will cache food in trees, but are for the most part terrestrial, living in burrows and foraging on the ground. They inhabit forest to forest-edge environments and are nut, seed, and berry eaters. I visualize the ancestral squirrels as being chipmunk-like. Such animals would be well suited to make the shift into an open grassland habitat as well as being adapted for an arboreal habit.

The transition from a forest habitat to an open plains one probably took place during the late Oligocene. Once this had taken place, several niches within the grasslands zone would be open for exploitation, and the history of the ground squirrels indeed appears to have been one of specialization within such niches.

Soon after the presumed time of appearance of ground squirrels, two distinct evolutionary lines are encountered, the spermophiles and the extinct protospermophiles (Fig. 7). Both first appear in the early Miocene, the former represented by *Miospermophilus bryanti*, the latter by *Protospermophilus vortmani*. The protospermophiles are not met with after the close of Clarendonian time.

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[1] The above account for the middle and late Tertiary climatic and floral conditions in the Great Basin has been taken primarily from Axelrod (1950).

Protospermophilus, because of its widespread distribution and association with the true spermophiles during the Miocene, is believed to be a ground squirrel which lived in the grassland areas but fed on seeds, nuts, and berries. The earliest members of this group are unfortunately poorly represented—two jaws from the John Day and a few isolated teeth from the Martin Canyon Quarry A in Colorado. At this stage, the cheek teeth have more in common with those of *Miospermophilus* than they do with those of any other early Miocene form. This would suggest that the protospermophiles and spermophiles either had a common origin or that the latter diverged from the former shortly after these had arisen from the basal sciurid stock. To the best of my knowledge, no specimens that might belong to the group have been reported from Europe or Asia. In the present state of our knowledge, it is a fair assumption that *Protospermophilus* arose in North America.

The one basic and striking trend within *Protospermophilus* is the development of a heavy, crushing dentition. From *P. vortmani* of the John Day through the Middle Miocene, *P. kelloggi* to *P. angusticeps* of the Deep River, and *P. oregonensis* of the Mascall, the lophs of the upper cheek teeth become heavier and more rounded, the lingual borders of the teeth become more massive through the development of an expanded, almost cusp-like, connection between the protocone and posterior cingulum, and there is a general increase in the overall size of the dentition. Accompanying these changes in the upper dentition, the posterolophid of the lower molars expands; the talonid basins tend to become rugose; and the mesostylid, mesoconid, and ectolophid enlarge. These changes were paralleled for the most part in the Great Basin species *P. malheurensis* and *P. quatalensis*, but in these two species there was no general increase in overall tooth size, although they were of approximately the same overall size as the plains species.

As the dentition changed so also did the zygomasseteric structure. Due to the lack of skull material for the early and mid-Miocene species, there is no way to determine the extent of the zygomatic plate in the early members of the genus. However, in view of the absence of a scar anterior to the masseteric fossa on the jaws of *P. vortmani*, it is not unlikely that the zygomatic plate was small and possibly not yet expanded onto the rostrum. This is the condition seen in the contemporary *Miosciurus* and *Protosciurus*, in which the masseteric fossa ends below M_1 with no indication of any migration of the masseter anterior to this point. By late Hemingfordian time, the masseter had moved well forward onto the rostrum. This is reflected in the anterior movement of the masseteric fossa as well as in the development of the small crescentic scar for a portion of the masseter lateralis anterior to it. Once the zygomasseteric complex had reached this stage there seems to have been little further selection for completing the sciuromorph condition. In the last known species of the genus, *P. quatalensis,* the masseteric fossa was still confluent with the ridge lateral to the incisors on the rostrum, failing to extend to the dorsal surface of the skull.

No postcranial material of *Protospermophilus* is known. The structure of the skull, however, suggests that *Protospermophilus* was terrestrial. Living arboreal forms have a much greater angle between the facial and basicranial axes of the skull and a more convex dorsal profile. In *Protospermophilus,* the skull is only moderately convex in the later forms and the basicranial axis is not bent to any degree relative to the facial. Furthermore, the abundance of these animals and of true spermophiles in deposits of stream channel and flood plain origin argues against their being arboreal.

The disappearance of *Protospermophilus* east of the Rocky Mountains after the middle Miocene may have been at least partially due to the rise of the marmots (Fig. 7) and consequent competition with them. However, it seems likely that further spread of the grassland, retreat of the forest, and removal of scattered woodland patches played a greater part in their extinction. In the Great Basin, increasing aridity and elimination of forest and scrub in that area and in the Mohave-Sonoran region during the early Pliocene were probably the major factors leading to the extinction of the group.

Miospermophilus bryanti, the first of the spermophiles, has a much more advanced zygomasseteric structure than is seen in the protospermophiles. Judging from the masseteric fossa, which is below P_4 in this species, the zygomatic plate was probably almost fully developed. *Miospermophilus* is a small ground squirrel approaching the chipmunks in size, but it differs from them and resembles the later spermophiles in having lower molars that are greatly compressed anteroposteriorly and elevated posterolophids which are rounded at the entoconid corner on M_1-M_2. *Miospermophilus wyomingensis* was undoubtedly descended from *Miospermophilus bryanti.* It is slightly more advanced than that species with smaller entoconids, higher posterolophids, and more prominent metaconules. Later Miocene and early Pliocene ground squirrels are abundant and widely distributed but are at present difficult to identify beyond the generic level. They were probably descended from *Miospermophilus* but the evolutionary sequence is hard to trace (see Fig. 8). Most of these forms are at an otospermophile level of development with low crowned teeth, low lophs, trigonids and posterolophids and rather deep mandibles. Some, such as *Citellus (O.) matthewi*, from the Snake Creek, and *C. (O.) tephrus* from Skull Springs are distinctive, but for the most part one is left with the general impression of a multitude of generalized ground squirrels differing little from locality to locality through the late Miocene and early Pliocene. By the middle Pliocene there appear to be two and possibly three distinct forms of *C. (Otospermophilus)* in the Great Basin. One is represented in the Smiths Valley, Kern River, and Thousand Creek faunas and the

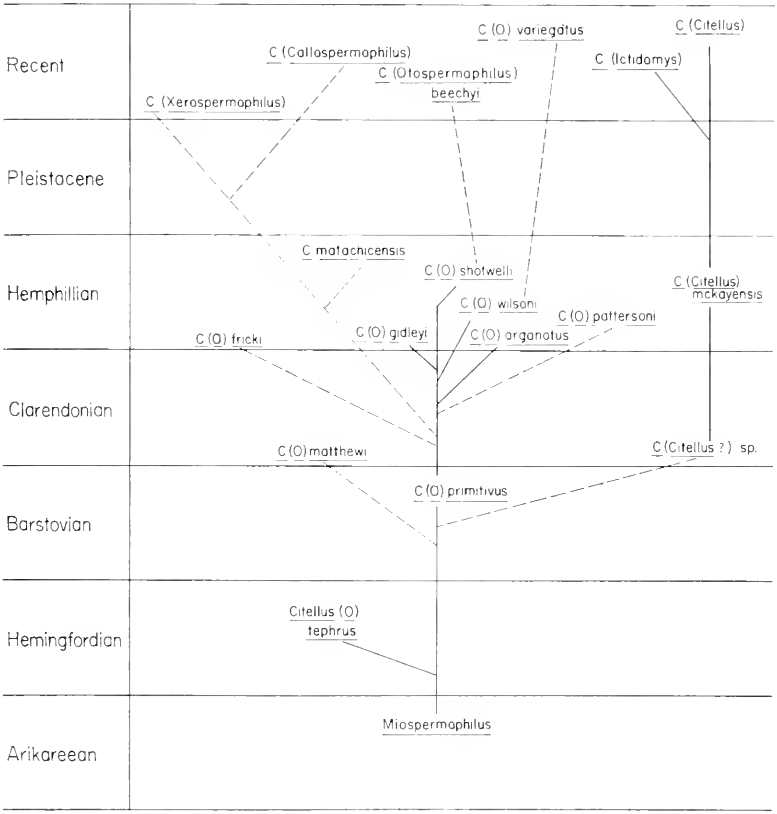

Figure 8. Relationships of subgenera and some species of *Citellus*. Solid lines indicate probable relationships, broken lines possible relationships.

other two in the northern Great Basin. One phyletic line can be traced from the early Pliocene Ellensburg fauna through *C. (Otospermophilus) wilsoni* into the late Hemphillian and may have given rise to the Recent *C. (Otospermophilus) variegatus.* The other northern Great Basin lineage is represented by several populations of *C. (Otospermophilus) shotwelli* and quite probably was ancestral to *C. (Otospermophilus) beechyi.*

Advanced spermophiles of the subgenus *Citellus* make their first appearance in the middle Pliocene. *C. (Citellus) mckayensis* is quite advanced, resembling the Recent species in most respects. (There is one mandible, A.M.N.H. No. 8338, probably of early Pliocene age, which may belong in this subgenus.) These are the only specialized spermophiles known from the Tertiary and this subgenus does not reappear in the fossil record until the early Pleistocene, in the Benson, Curtis Ranch, and Rexroad faunas. The major differentiation of the subgenera *Ictidomys* and *Citellus* would appear therefore to have been a late Pliocene and Pleistocene phenomenon. This conclusion is perhaps supported by the fact that most Recent species of the subgenera of *Citellus* intergrade into a nearly continuous sequence, indicating that differentiation is still in an active phase with no groups clearly delimited today. This fact has led some authors (e.g. Wilson, 1949c) to argue against the recognition of distinct subgenera of spermophiles in the Tertiary. However, the more advanced subgenera, *Citellus* and *Ictidomys*, were undoubtedly derived from the *Otospermophilus* group, probably splitting off in the middle Pliocene. Since this is the case, the recognition of generalized ground squirrels in the late Miocene and early Pliocene and their placement in the subgenus *Otospermophilus* is, I believe, valid.

The genus *Ammospermophilus* may have evolved by the early Pliocene but this is open to some doubt. *Ammospermophilus?* sp. from the early Pliocene of Oregon is known from only two mandibles and, although it resembles *A. leucurus* in many respects, there is not enough material available to be certain of this relationship. The fact that no other specimens referable to the genus are known from the Pliocene might indicate a later date for the origin of *Ammospermophilus.* Prairie dogs are very questionably reported from the Tertiary and it is probable that they did not arise until the late Pliocene. They were undoubtedly descended from ground squirrels of the subgenus *Citellus.*

Sometime during the middle Miocene, the marmots differentiated as a distinct group; they probably evolved from the protospermophile line, although a derivation from the true ground squirrels cannot at present be ruled out. The earliest members of the subtribe are somewhat specialized and appear to be rather far removed from *Marmota*. *Palaearctomys montanus* is of approximately the same size as the Recent *Marmota* but differs strikingly from it in the much smaller size of the cheek teeth and the much larger size of the incisors relative to the size of the skull. In other respects the two genera are similar and *Palaearctomys* was evidently as highly specialized for a fossorial habit as is *Marmota*. *Arctomyoides* is a somewhat smaller form and differs from *Palaearctomys*, *Paenemarmota* and *Marmota* in the shape of its lower molars. *Paenemarmota* is also rather highly specialized as regards its cheek teeth and is also only distantly related to the living marmots. *Marmota vetus* of the early Pliocene is the earliest true marmot so far recognized and was probably ancestral to *M. minor* of the middle Pliocene. The Recent species cannot be traced into the Pliocene but were very probably derived from the *M. vetus*-*M. minor* lineage.

Our knowledge of both tree squirrels and flying squirrels during the later Tertiary is almost nonexistent. Several species of tree squirrels are known from the early Miocene, particularly from the John Day basin. Apart from the primitive nature of the zygomasseteric structure, these species of *Protosciurus* differ surprisingly little from Recent forms. After the early Miocene, the only Tertiary record of tree squirrels consists of a fragmentary specimen from the late Hemingfordian Beatty Buttes local fauna and this, as far as it goes, appears to be completely *Sciurus*-like. No material is known that can be referred with any confidence to the flying squirrels. One mandible, Y.P.M. No. 13602, from the John Day basin has teeth that suggest those of *Glaucomys* but it cannot be placed in the group on the evidence available. In fact, it is extremely doubtful whether flying squirrels, of the *Glaucomys* group at least, could be recognized on anything less than a nearly complete skeleton. Differences between Recent *Glaucomys* and *Sciurus* in the skull, dentition and mandible are slight, and at an earlier stage of divergence they would be even less obvious.

The almost complete absence of tree squirrels, flying squirrels, and chipmunks in the fossil record is not surprising. Forest-living animals are always rare as fossils. What is surprising at first glance is the large number of squirrels known from the John Day basin and the relative abundance of tree squirrels there. However, this accords very well with the floral evidence for the early Miocene of the northern Great Basin, which indicates a region heavily forested over much of its area. Almost all other localities from which squirrels are known were presumably too far away from any large areas of forest to tap tree squirrel populations.

The history of the Sciuridae in North America has been one of short evolutionary spurts and long periods of slow change. This is particularly true for changes in the dentition. The early Miocene tree squirrels have changed remarkably little in their dentition over the last twenty million years. The spermophiles, after their origin in the late Oligocene, evolved very slowly through the Miocene and early Pliocene. The great diversification of ground squirrels is a relatively recent phenomenon that is still in progress, such forms as *Cynomys* having attained their highly specialized dentition over a short period of time, probably no longer than two to three million years. *Marmota* has evolved rather slowly since its probable origin in the late Miocene although it may have undergone a period of rather rapid evolution in the late Pliocene. While the dentition of these several groups was evolving rather rapidly over short periods of time, the zygomasseteric complex was apparently evolving at a rather slow, uniform pace throughout the Miocene and early Pliocene. The evidence reveals that the completely sciuromorph condition of the zygomatic plate was attained independently by the Tamiini, Marmotini and Sciurini. At the time, probably during the late Oligocene, when these three tribes diverged from the basal sciurid stock, the masseter was limited to the masseteric tubercle, the ventral face of the zygoma, and that portion of the anterior zygomatic root lateral to the infraorbital foramen. The masseter had not yet migrated over the infraorbital foramen and onto the rostrum. In the late Miocene, the zygomatic plate was not yet fully developed in the protospermophiles; by the early Pliocene it had reached the present level of development in the spermophiles. When it reached this level in the other lines we do not know due to lack of adequate skull material. Practically nothing can be said about changes in the postcranial skeleton of Tertiary squirrels. By the Hemphillian the spermophile skeleton was completely modern in aspect. What little skeletal material is known for the marmots is also hardly distinguishable from a Recent skeleton. In the other groups no skeletal material is known.

Just where the first squirrels differentiated is unknown. The oldest fossil recorded for the family is from the Orellan of North America but they are also known at only a slightly later date from the Stampian of France. Members of the paramyid subfamily, Paramyinae, here considered as ancestral to the Sciuridae, are known from both the Nearctic and Palearctic regions. Whatever the place of origin, a rapid dispersal, either east or west, must have occurred soon after the family differentiated from the Paramyidae, as all three sciurine tribes are present in the early Miocene of North America, and on the basis of published descriptions and illustrations, this is also true for at least two of the three tribes in Europe. There is some question as to the presence of chipmunks in the European Miocene but spermophiles and tree squirrels are certainly represented there.

Moore (1961) has recently discussed the present distribution of the Sciurinae and has concluded that the major center of dispersal for the various tribes within the Sciurinae was the Palearctic with most migrations passing from west to east across the Bering land bridge. The primary basis for this conclusion is the much greater geographic range of species of *Sciurus, Citellus,* and *Eutamias* in the Palearctic than in the Nearctic and the assumption that dominant species of mammals occupy the largest ranges and can expand their ranges most effectively. This is probably generally true but the present ranges of *Sciurus vulgaris, Citellus undulatus,* and *Eutamias sibiricus* in the Palearctic can be interpreted in a different manner. Moore (*op. cit.,* p. 9) considers the effect of Pleistocene glaciation on the ranges of these species and points out, quite correctly I believe, that each species could have retreated to refugia in Europe and China during the maximum glacial advance and then migrated back into their present extensive ranges as the glacial ice sheets retreated. The present range, then, may merely represent a reoccupation of large areas where no other species were present to offer competition.

During the late Pleistocene there is evidence (Hopkins, 1959) that there was no forest cover across the Bering land bridge. This would have made it almost impossible for species of *Sciurus* to migrate in either direction and left the present range of *S. vulgaris* in the Palearctic completely vacant and open to reoccupation without competition from other members of the genus. Species of *Eutamias* might possibly have been able to cross this bridge but chipmunks generally require at least scrub trees in their habitat. Consequently, here too, the large range now occupied by *E. sibiricus* would have been uncontested. Only species of *Citellus* and *Marmota* could have migrated across the Bering land bridge with any ease and it is only in these two genera that we find more than one species now living in the Palearctic. Therefore, it would appear to me quite possible that the large range of *S. vulgaris* and *E. sibiricus* merely represents a recent occupation of large areas where they were not faced with competition and that their present distribution does not *per se* qualify them as dominant species and, hence, as species which could expand from their ranges most effectively from the Palearctic eastward into the Nearctic. The present distribution of *Eutamias sibiricus* may have resulted from migration west across the Bering land bridge rather than from expansion from a refugium in northeastern China as Moore suggests.

The same dispersal pattern, west to east, would seem even more probable for *Citellus* and *Marmota*. *Citellus undulatus* is found today in both the Nearctic and Palearctic and its present range in Eurasia could be interpreted as resulting from migration west across the Bering land bridge during the Pleistocene as could the occurrence of the other species of *Citellus* in the Palearctic. The major radiation of the ground squirrels certainly appears to have taken place in the New World. Of the twenty-nine Recent species of *Citellus* (from Moore, 1961, p. 4), twenty-three are found in the Nearctic, plus the genera *Ammospermophilus* and *Cynomys,* and five species of *Marmota* occur in the Nearctic while three are found in the Palearctic. On present evidence, migration from this area of major radiation into the Palearctic would seem at least as plausible as the migrations from west to east suggested by Moore.

REMARKS ON OLD WORLD TERTIARY SCIURIDS

Any discussion of the evolution and dispersal of the various phyla within the family Sciuridae, based solely on the fossil record in North America, is, of course, incomplete. Interpretations as to the place and time of origin of certain phyletic lines within the family suffer from a lack of familiarity with the Old World record and this difficulty is compounded by the difference in approach of European and American workers who have dealt with sciurid material. The true relationships of many European species are obscured by a tendency to assign all material to *Sciurus*. Only a complete review of all the Old World fossils can hope to straighten out this confusion and lead to an integration of our knowledge of the family as a whole. A further complication is the lack of a fossil record for various groups that are numerous and widespread in the tropics today.

Among the Tertiary species described by European workers, there are several assigned to the genus *Sciurus* that appear to be more closely related to the spermophiles than to the tree squirrels. Among these are *S. feignouxi, S. fissurae* and *S. bredai.* Wilson (1960, p. 60) has pointed out the similarity of these species to

Miospermophilus bryanti. In general, as in *M. bryanti,* the mandibles appear to be slender, the diastemal depressions shallow, and the entoconids partially or completely submerged in the posterolophids in these species.

From at least the earliest Miocene to the present, the evidence quite clearly indicates the presence of tree squirrels, chipmunks, and ground squirrels in North America and it is becoming clear that this is true for Europe also. It seems likely that the more specialized forms found today in the Oriental, African and tropical American regions are the result of invasions into areas offering greater possibilities for diversification than are to be found in the Holarctic region. These invasions must have occurred at several different times during the history of the family, those into Africa probably occurring at a relatively early date and that from Central into South America only at the end of the Tertiary. Unfortunately, there is only one Tertiary record for the family in Africa (Lavocat, 1956b), and no record in Central America; the only Asian Tertiary sciurids reported (Bohlin, 1946) are much too fragmentary to allow of accurate generic determination.

Dehm (1950) has described *Paracitellus,* from the Burdigalian of Germany and placed it in the Sciuridae. From his illustrations and description it seems evident that *Paracitellus* is not a sciurid. The lower molars are much longer than they are wide, the few upper cheek teeth known show a rather complicated arrangement of lophs with a crest passing from the protocone between the protoconule and metaconule, and the masseteric fossa ends below M_2-M_3. These characters indicate a much closer relationship to the paramyids, particularly to the prosciurines, than to the Sciuridae.

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PLATES

Plate 1

Figure 1. *Tamias* sp. Wounded Knee local fauna, South Dakota. 1a, S.D.S.M. No. 58100-26, LP^4. 1b, S.D.S.M. No. 58100-25, $RM^{1 \text{ or } 2}$. 1c, S.D.S.M. No. 58100-28, LM^3. 1d, S.D.S.M. No. 58100-3, RP_4. 1e, S.D.S.M. No. 58100-2, $LM_{1 \text{ or } 2}$. All ×15. Anterior end to right in 1b and 1d, to left in 1a, 1c, and 1e.

Figure 2. *Tamias* sp. Martin Canyon Quarry A local fauna, Colorado. 2a, K.U. No. 10170, $LM^{1 \text{ or } 2}$, anterior end to left. 2b, K.U. No. 10172, $RM_{1 \text{ or } 2}$, anterior end to right. Both ×15.

Figure 3. *Tamias* sp. Thomas Farm local fauna, Florida. 3a, F.G.S. V-6021, $LM^{1 \text{ or } 2}$. 3b, F.G.S. V-6020, RP_4. 3c, U.F. No. 3873, LM_1. 3d, F.G.S. V-5951, RM_3. All ×20. Anterior end to right in 3b and 3d, to left in 3a and 3c.

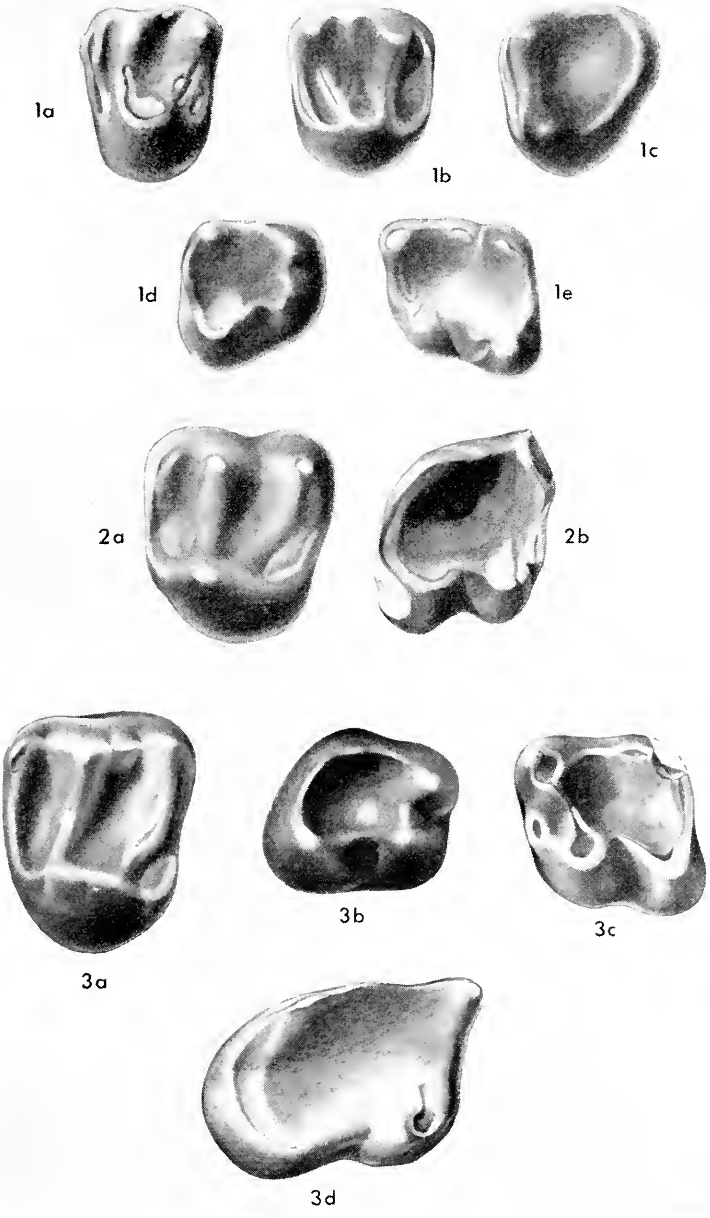


PLATE 1

Plate 2

Figure 1. *Tamias* sp. Split Rock local fauna, Wyoming. U.W. No. 1434, $LM_{1 \text{ or } 2}$, × 15, anterior end to left.

Figure 2. *Tamias ateles*, Barstow, California. 2a, U.C.M.P. No. 28521, Type, RM^1-M^3, × 15, anterior end to right. 2b, L.A.C.M. (C.I.T.) No. 5236a, $RM_{1 \text{ or } 2}$, × 15, anterior end to left. 2c, L.A.C.M. (C.I.T.) No. 5236b, $LM_{1 \text{ or } 2}$, × 15, anterior end to left. 2b and 2c from Tonopah, Nevada.

Figure 3. *Miosciurus ballovianus*. A.M.N.H. No. 6901, Type. 3a, RM_{1-3}. 3b, LM_1. 3c, LM^1. 3d, RM^2. All × 10.

1

2a

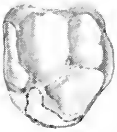
2b

2c

3a

3b

3c



3d

PLATE 2

Plate 3

Figure 1. *Protosciurus condoni* n. gen., n. sp., U.O.M.N.H. F-5171, Type, 1a, 1b, and 1c dorsal, lateral, and ventral views of skull × 1½.

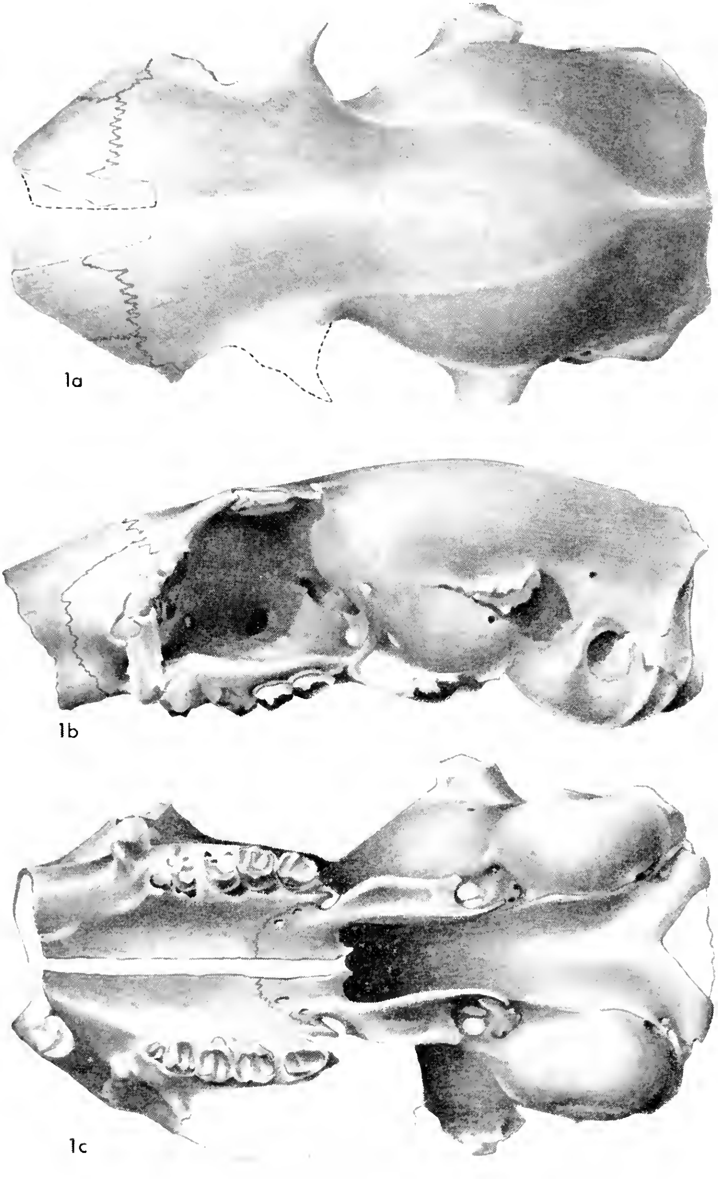


PLATE 3

Plate 4

Figure 1. *Protosciurus condoni*, n. gen., n. sp., U.O.M.N.H. F-5171, Type. 1a, RP^3-M^3, ×6. 1b, Lateral view of right mandible, ×2. 1c, RP_4-M_3, ×7.


1a


1b


1c

PLATE 4

Plate 5

Figure 1. *Protosciurus mengi* n. sp., U.M.M.P. No. 39559, Type. 1a, LP_4-M, × 10. 1b, Lateral view of left mandible, ×5.

Figure 2. *Protosciurus tecuyensis*, U.C.M.P. No. 23611, Type. 2a, RM_1-M_2, ×5. 2b, Lateral view of right mandible, ×3½.

PLATE 5

Plate 6

Figure 1. *Protosciurus rachelae* n. sp., A.M.N.H. No. 7241, Type. 1a, Anterior view of infraorbital foramen and zygomatic plate, ×5. 1b, Ventral view of skull fragment with LM^1-M^3, ×5.

Figure 2. U.O.M.N.H. No. F-5039, RM_1-M_3, ×10.

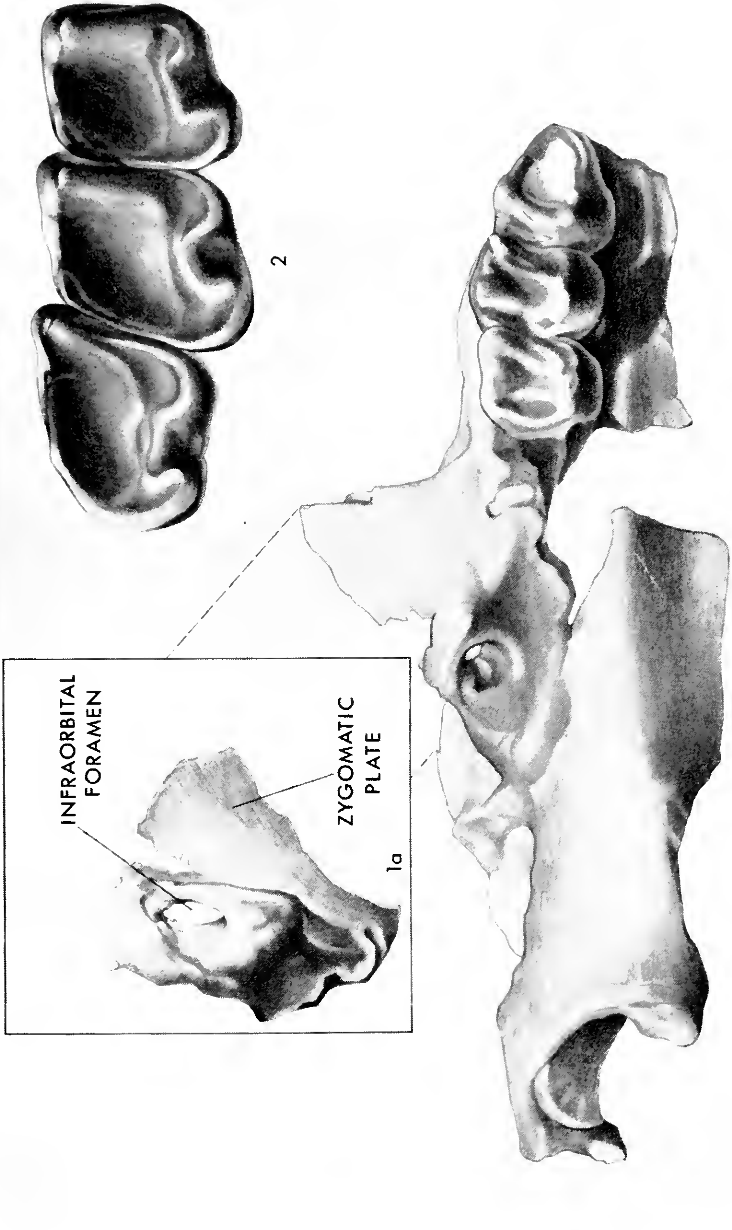


PLATE 6

Plate 7

Figure 1. Genus and species indet., Y.P.M. No. 13602. 1a, Lateral view of right mandible, ×5. 1b, RP_4-M_3, ×10.

Figure 2. *Arctomyoides arctomyoides*, C.M. No. 741, Type. 2a, LP_4-M_3, anterior end to left, ×5. 2b, Lateral view of left mandible, ×1½. 2c, Medial view of right lower incisor, ×5. 2d. RdP^4-M^1, anterior end to right, ×5.

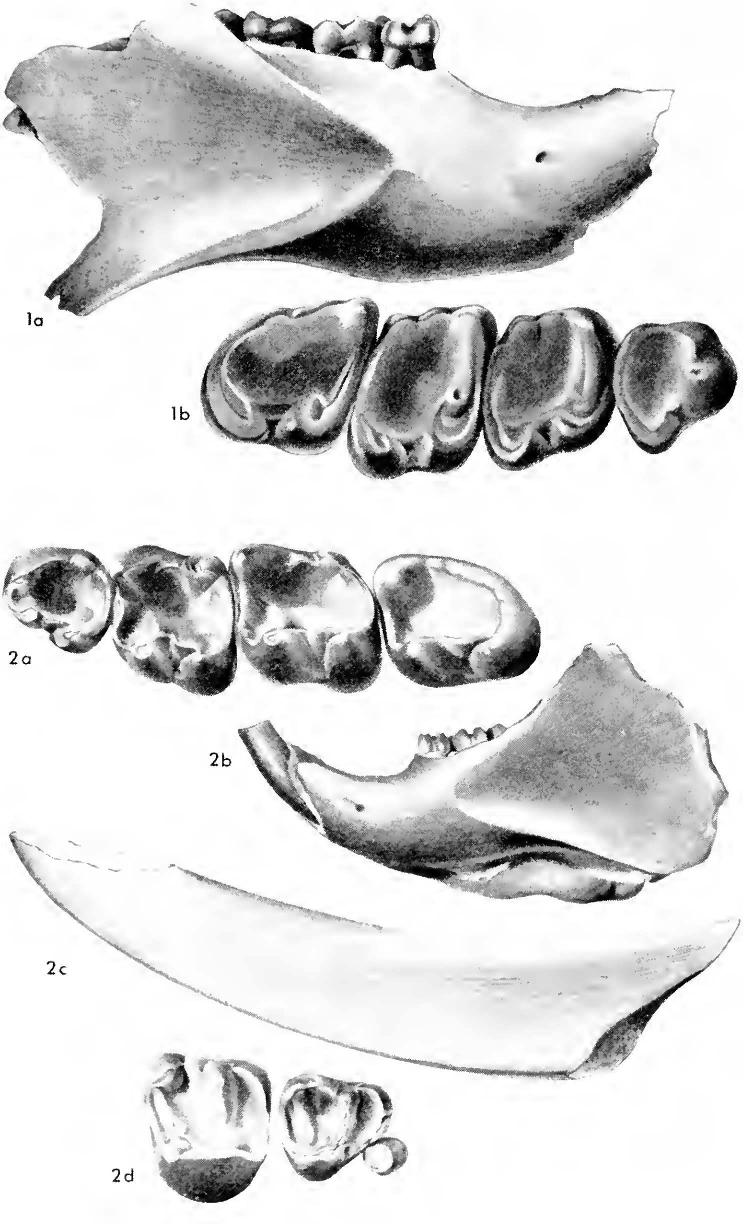
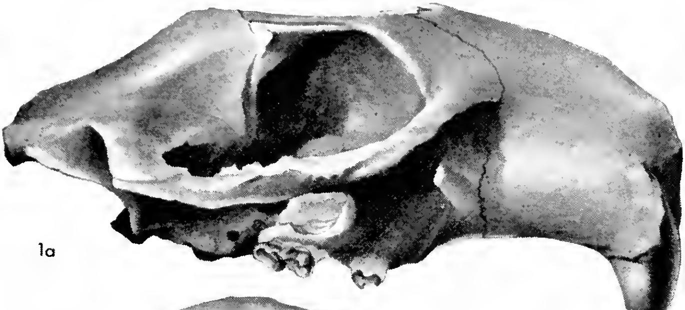


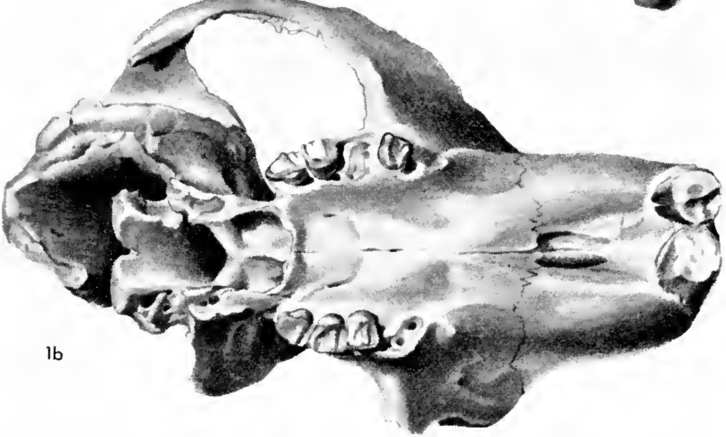
PLATE 7

Plate 8

Figure 1. *Palaearctomys montanus*, C.M. No. 733. 1a, lateral, 1b, ventral, and 1c, dorsal views of skull, *ca.* × 1.



1a



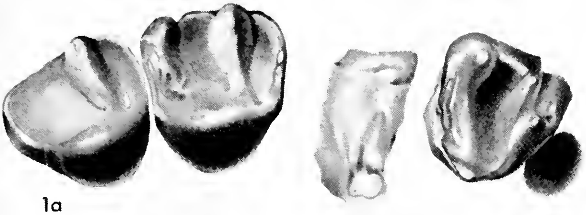
1b

1c

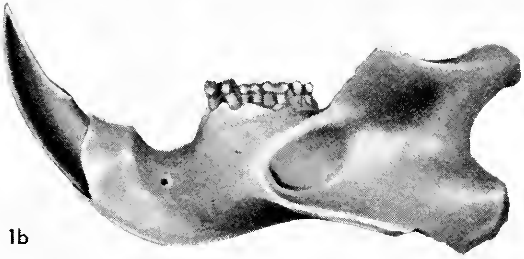
PLATE 8

Plate 9

Figure 1. *Palaearctomys montanus.* 1a, C.M. No. 733, RP^4, M^2-M^3 and LM^1-M^3, anterior end to right, ×5. 1b, C.M. No. 740, Type, lateral view of left mandible, ×1. 1c, Same, LP$_4$-M$_3$, anterior end to left, ×5.



1a



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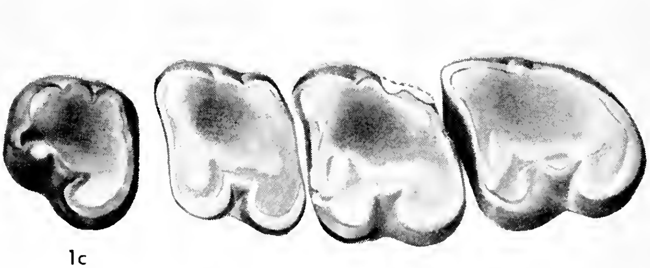


1c

PLATE 9

Plate 10

Figure 1. *Marmota nevadensis,* U.C.M.P. No. 12506, Type. 1a, Lateral view of left mandible, ×1½. 1b, LP_4-M_1, anterior end to left, ×5.

1a

1b

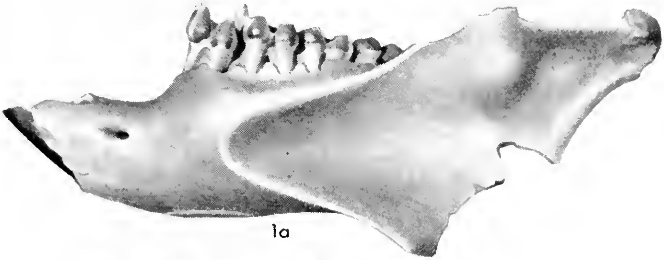
PLATE 10

Plate 11

Figure 1. *Marmota vetus*, Y.P.M. No. 10323, Type. 1a, Lateral view of left mandible, ×2½. 1b, LP$_4$-M$_3$, anterior end to left, ×5.

Figure 2. *Marmota minor*, U.C.M.P. No. 12538, Type. 2a, LP^3-P^4, anterior end to left, ×5. 2b, RM^2-M^3, anterior end to right, ×5. 2c, LM$_2$-M$_3$, anterior end to left, ×5. 2d, RP$_4$-M$_2$, anterior end to right, ×5.

Figure 3. *Marmota monax*, C.M. No. 36298, RP$_4$-M$_3$, ×5.

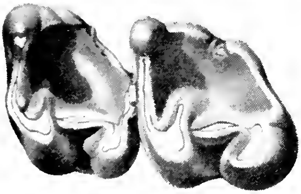


1a

1b

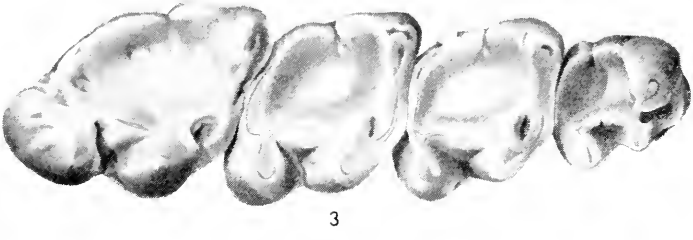
2a

2b



2c

2d



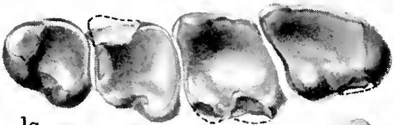
3

PLATE 11

Plate 12

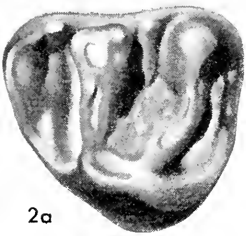
Figure 1. *Protospermophilus vortmani.* A.M.N.H. No. 6960, Type. 1a, LP_4-M_3, anterior end to left, ×5. 1b, Lateral view of left mandible, ×3½.

Figure 2. *Protospermophilus* sp., all *ca.* ×12. 2a, K.U. No. 10163, LdP^4. 2b, K.U. No. 10165, $RM^{1 \text{ or } 2}$. 2c, K.U. No. 10166, $RM^{1 \text{ or } 2}$. 2d, K.U. No. 10168, $RM_{1 \text{ or } 2}$. Anterior end to right except for 2a.



1a

1b



2a

2b

2c

2d

PLATE 12

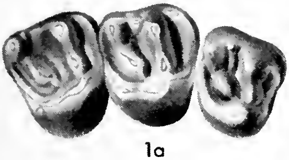
Plate 13

Figure 1. *Protospermophilus angusticeps.* 1a, A.M.N.H. No. 21336, Type, RP^4-M^2, anterior end to right, ×5. 1b, Y.P.M. No. 14032, LM$_1$-M$_3$, anterior end to left, ×5.

Figure 2. *Protospermophilus oregonensis.* U.C.M.P. No. 39093, Type, LP$_4$-M$_3$, anterior end to left, ×5.

Figure 3. *Protospermophilus malheurensis.* L.A.C.M. (C.I.T.) No. 129, Type, RP^4-M^3, anterior and to right, ×5.

Figure 4. *Protospermophilus quatalensis,* L.A.C.M. (C.I.T.) No. 30, Type. 4a, LP$_4$-M$_1$, anterior end to left, ×5. 4b, LP^3-M^2, anterior end to left, ×5. 4c, Lateral view of left mandible, ×3½.



1a

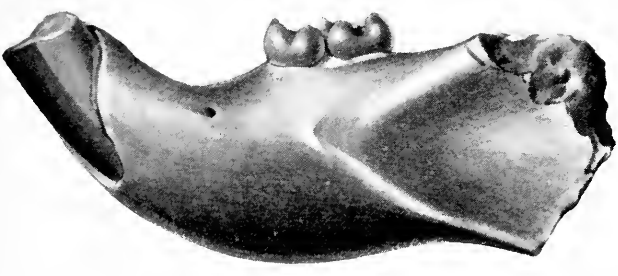
1b

2

3

4a

4b



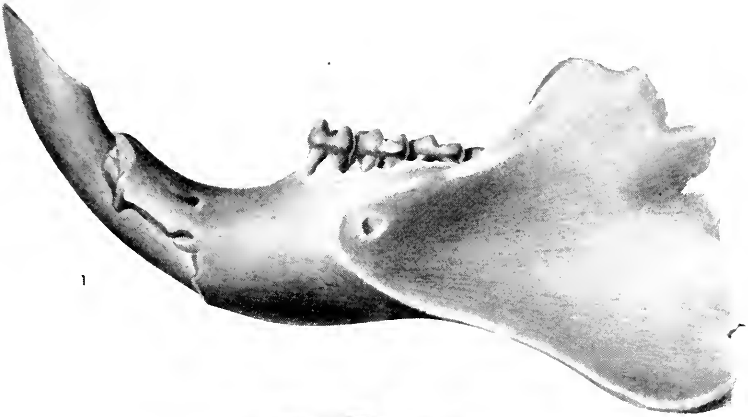
4c

PLATE 13

Plate 14

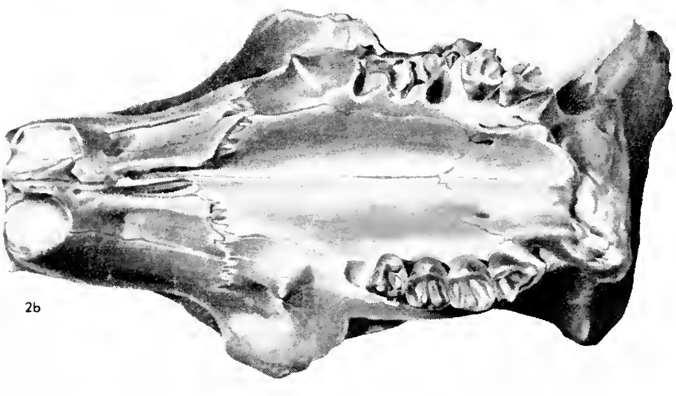
Figure 1. *Protospermophilus oregonensis,* U.C.M.P. No. 39093, Type, lateral view of left mandible, *ca.* ×2.

Figure 2. *Protospermophilus malheurensis,* L.A.C.M. (C.I.T.) No. 129, Type, 2a, lateral and 2b, ventral view of skull, *ca.* ×2.



1

2a



2b

PLATE 14

Plate 15

Figure 1. *Protospermophilus quatalensis*, L.A.C.M. (C.I.T.) No. 30, Type. 1a, lateral, and 1b, ventral views of skull, × 3.

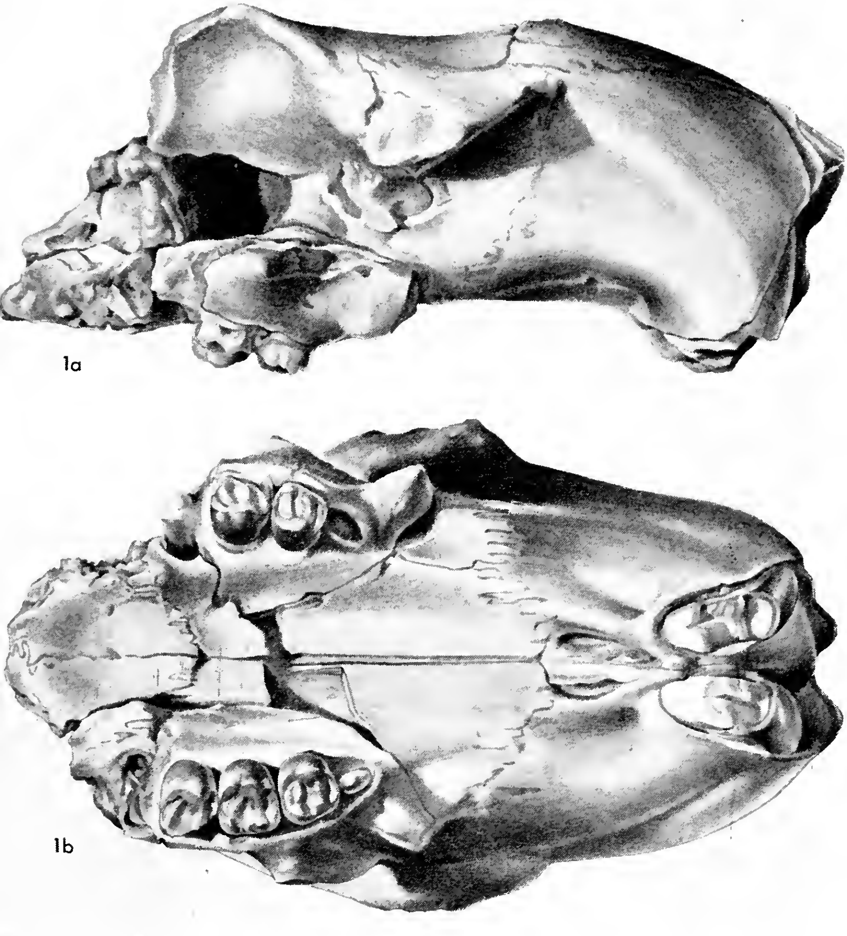


PLATE 15

Plate 16

Figure 1. *Miospermophilus bryanti* n. gen., K.U. No. 10149, Type. 1a, RP_4-M_3, anterior end to right, ×7. 1b, Lateral view of right mandible, ×3½. 1c, K.U. No. 10156, RdP^4, ×15. 1d, K.U. No. 10155, LP^4, ×15. 1e, K.U. No. 10157, $LM^{1 \text{ or } 2}$, ×15. 1f, K.U. No. 10159, $LM^{1 \text{ or } 2}$, ×15. Anterior end to right in 1a, 1b, and 1c, to left in 1d, 1e, and 1f.

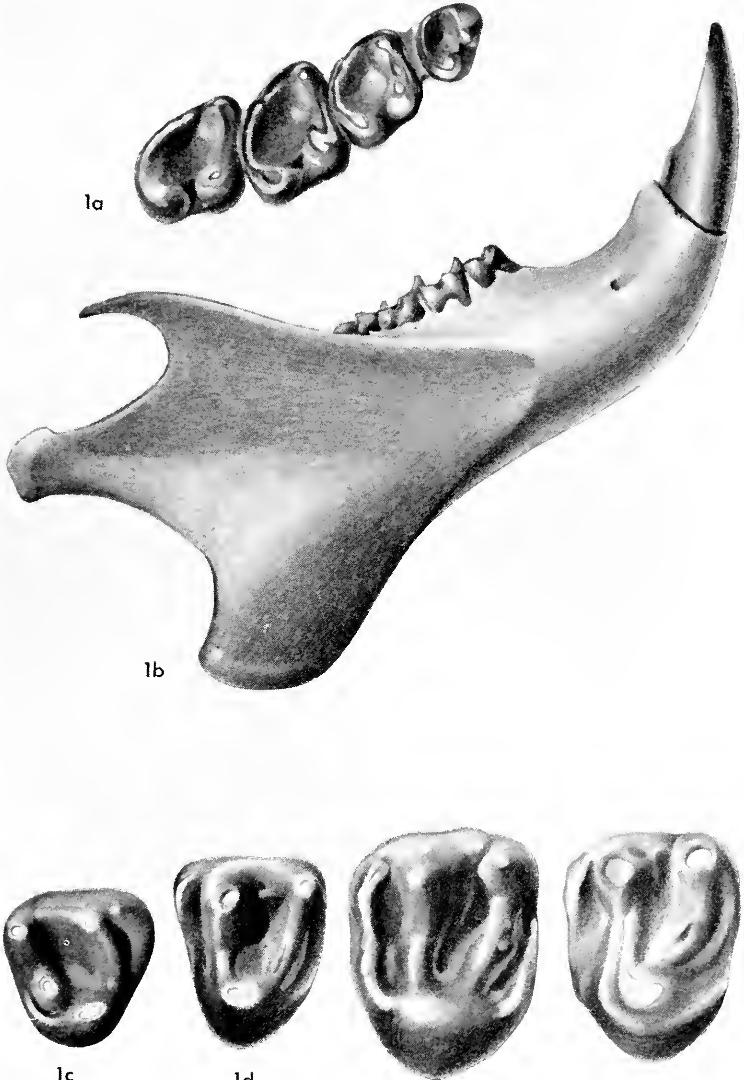
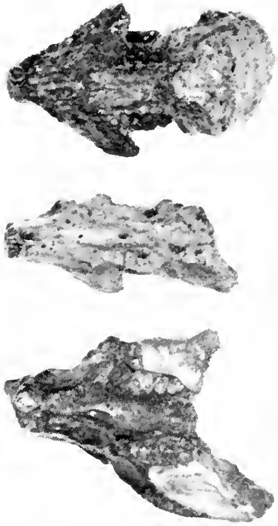


PLATE 16

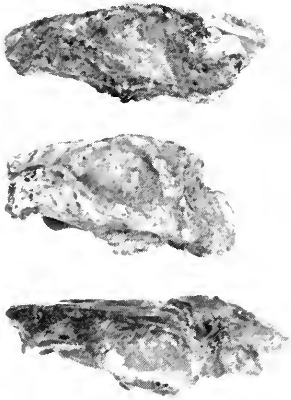
Plate 17

Figure 1. *Citellus (Otospermophilus) tephrus.* 1a-c, Three skulls, from top to bottom: L.A.C.M. (C.I.T.) No. 332, Type, L.A.C.M. (C.I.T.) No. 335, and L.A.C.M. (C.I.T.) No. 334, all ×1. 1a, Dorsal views of the skulls. 1b, Ventral views of same. 1c, Lateral views of same. 1d, L.A.C.M. (C.I.T.) No. 334, RP^4-M^3, ×5. 1e, L.A.C.M. (C.I.T.) No. 332, Type, RP^4-M^3, ×5.

1a



1b



1c

1d

1e

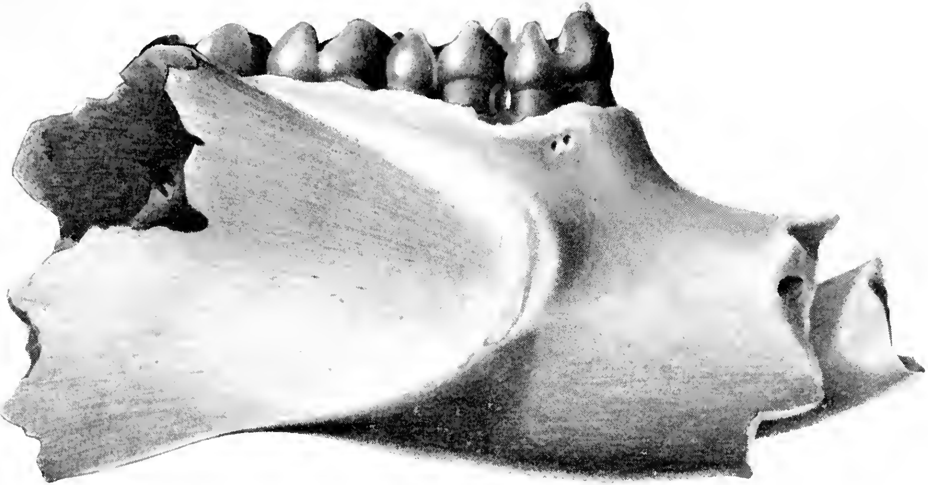
PLATE 17

Plate 18

Figure 1. *Citellus (Otospermophilus) primitivus*, C.M. No. 727, RP_4-M_3, anterior end to right. ×5.

Figure 2. *Citellus (Otospermophilus) matthewi*, n. sp., A.M.N.H. No. 17578, Type. 2a, Lateral view of right mandible, ×5. 2b, RP_4-M_3, anterior end to top, ×5.

1



2a

2b

PLATE 18

Plate 19

Figure 1. *Citellus (Otospermophilus) shotwelli*, n. sp. 1a, U.O.M.N.H. F-3596, Type, lateral view of right mandible, ×3½. 1b, L.A.C.M. (C.I.T.) No. 5243, lateral view of right mandible, ×3½.

1a

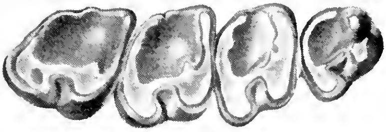
1b

PLATE 19

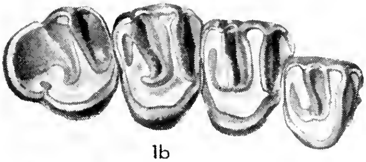
Plate 20

Figure 1. *Citellus (Otospermophilus) shotwelli*, n. sp. 1a-b, U.O.M.N.H. F-3596, Type, RP$_4$-M$_3$, RP^4-M^3, anterior end to right, *ca.* ×5. 1c, U.O.M.N.H. F-7964, LP$_4$-M$_3$, anterior end to left, *ca.* ×5. 1d, L.A.C.M. (C.I.T.) No. 5243, RM$_2$-M$_3$, anterior end to right, *ca.* ×5.

Figure 2. *Citellus (Otospermophilus) gidleyi*, U.C.M.P. No. 26793, Type. 2a, Lateral view of left mandible, ×4. 2b, LP$_4$-M$_3$, anterior end to left, ×10.



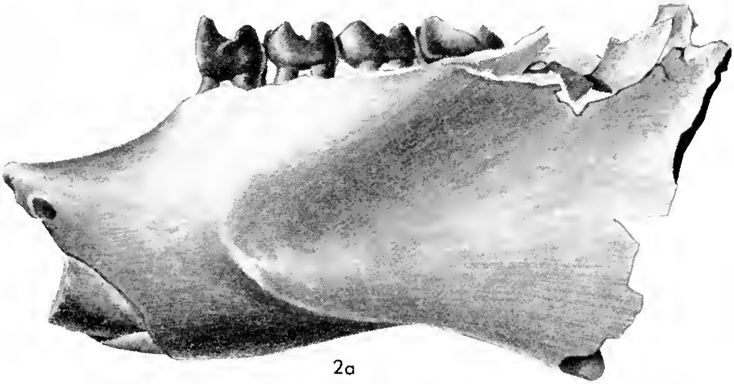
1a



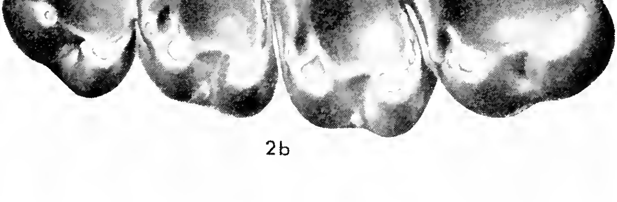
1b

1c

1d



2a

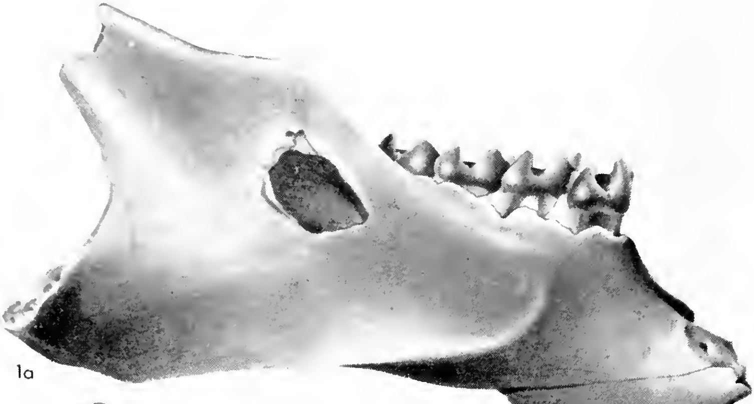


2b

PLATE 20

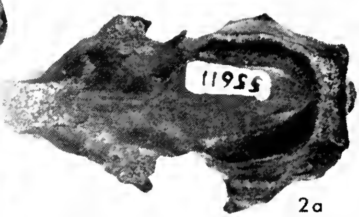
Plate 21

Figures 1-3. *Citellus (Otospermophilus) wilsoni.* la, U.O.M.N.H. F-4097, Type, lateral view of right mandible, *ca.* × 3½. 1b, Same, RP_4-M_3, anterior end to right, *ca.* ×5. 1c, U.O.M.N.H. F-3635, LP^4-M^3, anterior end to left, *ca.* ×5. 2a, 2b, and 2c, U.C.M.P. No. 55611, dorsal, lateral, and ventral views of skull, *ca.* ×1. 3a, L.A.C.M. (C.I.T.) No. 5246, LP^3-M^3, anterior end to left, *ca.* ×5. 3b, L.A.C.M. (C.I.T.) No. 5244, RP_4-M_3, anterior end to right, *ca.* ×5.



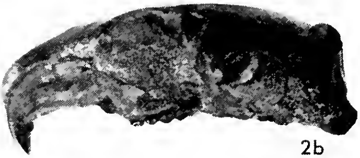
1a

1b



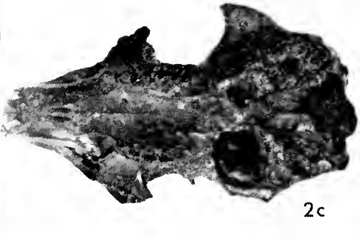
2a

1c

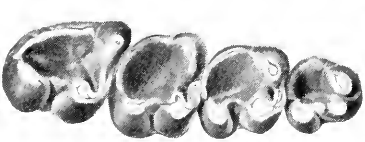


2b

3a



2c



3b

PLATE 21

Plate 22

Figure 1. *Citellus (Otospermophilus) fricki*, F:A.M. No. 24627, Type. 1a, LP^3-M^3, anterior end to left, ×5. 1b, LP$_4$-M$_2$, anterior end to left, ×5.

Figure 2. *Citellus (Otospermophilus) pattersoni*, L.A.C.M. (C.I.T.) No. 3547, Type, RP^4-M^3, anterior end to right, ×5.

Figure 3. *Citellus matachicensis*, L.A.C.M. (C.I.T.) No. 3551, Type. 3a, LP^3-M^3, anterior end to right, ×5. 3b, RP$_4$-M$_3$, anterior end to right, ×5.

Figure 4. *Citellus (Citellus?)* sp., A.M.N.H. No. 8338. 4a, Lateral view of right mandible, ×3½. 4b, RP$_4$-M$_3$, anterior end to top, ×5.

Figure 5. *Citellus (Citellus) mckayensis*, U.O.M.N.H. F-3627, Type, LM$_1$-M$_3$, anterior end to left, *ca.* ×5.

Figure 6. *Ammospermophilus?* sp., U.O.M.N.H. F-5871, RP$_4$-M$_3$, anterior end to right, ×8.

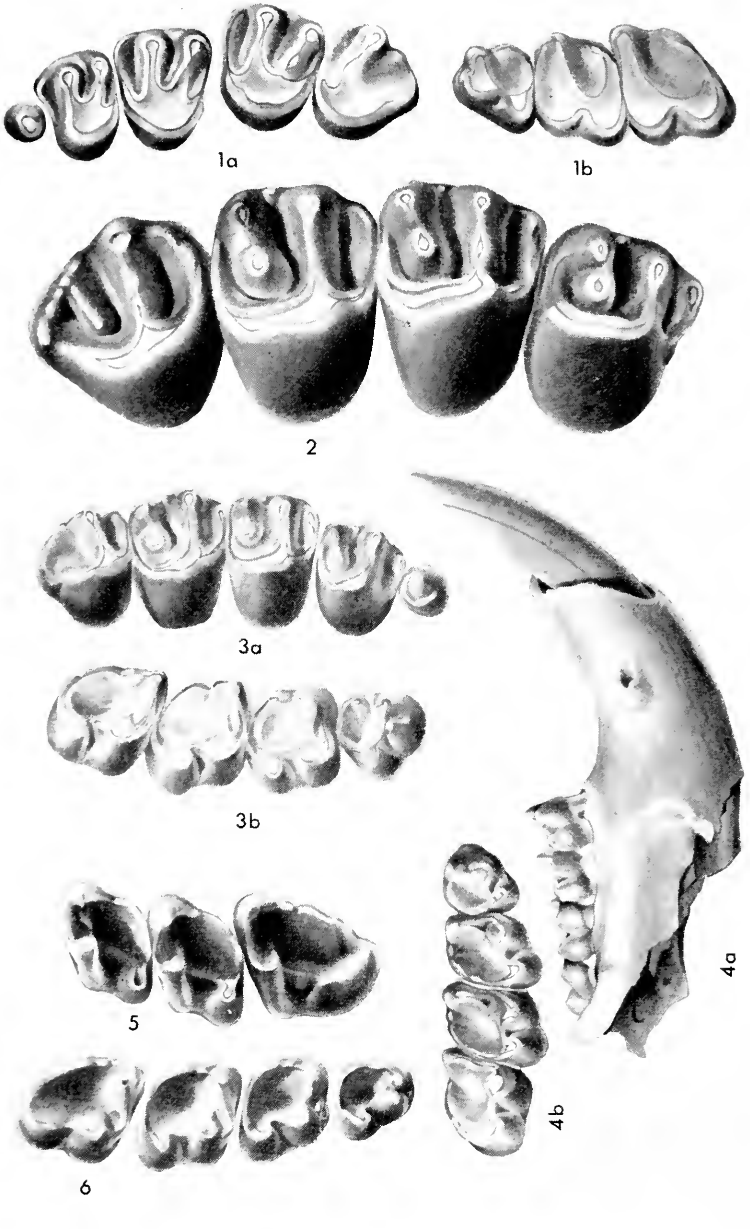


PLATE 22

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 130, No. 4

A REVISION OF THE GENUS APENESIA IN THE AMERICAS (HYMENOPTERA, BETHYLIDAE)

By Howard E. Evans

With Ten Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
December 20, 1963

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Bull. Mus. Comp. Zool., Harvard Univ., **130**(4):249-359 — Dec. 1963

No. 4 — *A Revision of the Genus Apenesia in the Americas (Hymenoptera, Bethylidae)*[1]

By Howard E. Evans

INTRODUCTION

Recent studies of the Pristocerini of North and Central America have resulted in preliminary revisions of the genera *Dissomphalus, Pseudisobrachium,* and *Pristocera* (Evans, 1955, 1961, 1963). After sorting out members of these genera from the Pristocerini, one is still left with an assortment of forms showing a considerable array of characteristics although difficult to sort into clear-cut genera. I have treated a few of the species under the name *Propristocera* (Evans, 1958), pointing out that these forms appear to occupy a central position in the Pristocerini, showing close affinities to the other genera and possibly containing the roots of the phylogenetic lines leading to each of the other three genera. Further study reveals that this group is vastly larger than I had previously supposed, with Kieffer's genera *Cleistepyris* and *Dipristocera* being essentially inseparable from *Propristocera.* These three generic names have all been applied to the male sex only. The females of *Dissomphalus, Pristocera,* and *Pseudisobrachium* are well known, and the residue of female Pristocerini have been placed in Westwood's genus *Apenesia,* known from the female sex only. *Apenesia,* too, exhibits a fairly broad spectrum of characters and also seems to occupy a central position among the genera of Pristocerini. I am convinced that *Apenesia* represents the female sex of *Propristocera* (including also *Cleistepyris* and *Dipristocera*), and since *Apenesia* is much older it is the name which must be used for this complex. In this paper, then, the name *Apenesia* is used in this broad sense, to apply to a rather large, heterogeneous, and protean complex of species, most of which are known from the male sex only. It is possible that some of Kieffer's names can eventually be employed as subgeneric names, but at the present state of our knowledge this does not seem feasible.

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[1] This research was supported by a grant from the National Science Foundation, no. GB-1544. Acknowledgement is also made to the Permanent Science Fund of the American Academy of Arts and Sciences, a grant from which in 1961 made it possible for the author to travel to London to study type specimens in the British Museum (Natural History).

Evidence that this association of sexes is correct may be summarized as follows. The females of *Apenesia* bear much resemblance to those of *Pristocera*, but the propodeum is less strongly constricted, sometimes hardly constricted at all, almost as in *Dissomphalus;* a few species have the abdomen petiolate as in *Dissomphalus*. The eyes are generally smaller than in *Pristocera*, and at least one species has the eyes reduced to a single facet each, a condition characteristic of *Pseudisobrachium*. The males also share some of the characters of each of these genera, and certain males approach these genera very closely indeed. Thus it is morphologically logical that *Apenesia* and *Propristocera* are opposite sexes of one genus.

Evidence of another type is to be found in the coincidence of ranges. Both *Apenesia* and *Propristocera* are distributed throughout the warmer parts of the globe, including the Australian region, which otherwise lacks Pristocerini. In the eastern United States (exclusive of Florida), there is but one species of *Propristocera* and one (previously undescribed) species of *Apenesia;* the two forms are similar in size, and it is logical to conclude that they represent male and female of one species. More conclusive evidence is provided by a reared series of an undescribed species of *Apenesia* from the Bismarck Archipelago in the British Museum (Natural History). This series consists of six females and two males reared from the larvae of *Pantorhytes plutus* Oberthür (Curculionidae) at Kerawak, New Britain, October 1946 (B.A. O'Connor collector). Although the males belong to a species-group not present in the Americas, the females are very similar to those of several American species, including *amazonica*, type of the genus.

There is a second record of these wasps attacking the larvae of weevils. Kieffer (1914) presents a record of *Apenesia parasitica* (Smith) having been reared from *Epiphylax quadricollis* (Fairmaire) (Curculionidae) in Madagascar. The species of *Epiphylax* are said to mine the inner bark of lianas, while *Pantorhytes plutus* is a root-borer. The structure of female *Apenesia* suggests that these wasps spend most of their lives in the soil or in wood, and there are other records to indicate that this is the normal habitat. I have examined three female *A. chontalica* (Westwood) labeled as having been taken "in decayed log," and two female *A. amoena* n. sp. labeled "under loose bark of recently cut down tree." *A. parapolita* (new name for *polita* Evans, preoccupied) has been taken in logs and under bark on several occasions, also "in sweet gum tree crotch," "in debris in hollow sycamore," and "with *Ponera contracta*" (? = *coarctata pennsylvanica* Buckley). The latter is the only record of these insects being associated with ants, and I suspect the association was accidental.

Males of this genus are fully winged and mostly dark in color. Most species fly in the daytime although a few are known to be nocturnal, like many species of *Pseudisobrachium*. The diurnal species are most commonly taken in sweepings from grass, herbs, or the leaves of trees. I have taken a few males at honeydew, but they are much less frequently taken at honeydew than are some of the Epyrini.

ACKNOWLEDGMENTS AND SOURCES OF MATERIAL

Specimens of this genus are uncommon in collections, and I have had to borrow material from many sources. The list below is meant to serve as an acknowledgment to each institution and individual supplying material, as well as an indication of the abbreviation by which each is designated in the text. My own collecting in Mexico and southwestern United States in 1959, when I held a fellowship from the John Simon Guggenheim Memorial Foundation, has been an important source of material. A collection from Barro Colorado Island, Panama, taken by Carl W. and Marian E. Rettenmeyer, has also been extremely valuable. Dr. G. Steinbach, of the Zoologisches Museum der Humboldt-Universität zu Berlin, sent me several Kieffer types for study. Dr. R. L. Doutt, of the University of California at Albany, also sent me several Kieffer types from Pomona College which are currently in his custody. Dr. M. J. Viana, of the Museo Argentino de Ciencias Naturales, Buenos Aires, loaned me the type of *Propristocera boliviensis* Ogloblin. With the assistance of these persons, and with the aid of a grant to study types in England, acknowledged earlier, I have been able to examine the types of all the described American species of this genus.

American Museum of Natural History, New York (AMNH)
British Museum (Natural History), London (BMNH)
California Academy of Sciences, San Francisco (CAS)
California Dept. of Agriculture, Sacramento (CDAS)
California Insect Survey, Berkeley (CIS)
Canadian National Collections, Ottawa (CNC)
Carnegie Museum, Pittsburgh (CM)
Cornell University, Ithaca, N. Y. (CU)

H. K. Townes Collection, Ann Arbor, Mich. (HKT)
Hope Collection, Oxford University, England (HCOU)
Illinois Natural History Survey, Urbana (INHS)
Kansas University, Lawrence (KU)
Museum of Comparative Zoology, Cambridge, Mass. (MCZ)
University of Arizona, Tucson (UA)
University of California, Davis (UCD)
United States National Museum, Washington, D.C. (USNM)

TERMINOLOGY

As in usual in the Pristocerini, sexual dimorphism is so pronounced in this genus that it is convenient to treat the sexes separately both here and in the main body of the text.

Males

Size. — Although total body length is presented for each type specimen, these figures are no more than approximations, as disposition of body parts and telescoping of abdominal segments introduce large errors of measurement. A much more accurately measurable indication of size is length of the fore wing (LFW).

Mandibles. — The mandibular teeth are numbered beginning with the apical, outermost tooth and proceeding toward the inner margin.

Antennae. — Rather than present measurements of all thirteen antennal segments, I have measured the relative length of the first four segments, and the length/maximum width of segments three and eleven. The length of the antennal pubescence is measured (except as otherwise noted) at segment eleven, where the length of the longest setulae is compared with the greatest width of the segment.

Eyes. — In this genus, it is to be assumed that the eyes are bare (or with exceedingly small setae) unless noted otherwise. Height of the eye (HE) is the maximum height as measured in lateral view.

Ocelli. — It is to be assumed that the ocelli are not enlarged unless otherwise noted; where enlargement occurs, the diameter of the anterior ocellus (DAO) is compared to the minimum width of the front (WF). Width of the ocellar triangle (WOT) includes the hind ocelli; the ocello-ocular line (OOL) is simply the distance from the margin of one lateral ocellus to the nearest eye margin. The front angle of the ocellar triangle is measured on the outer sides of the ocelli.

Head dimensions. — Width of the head (WH) is measured at its maximum point, including eyes, in full front view. Length of the head (LH) is measured from the median apical margin of the clypeus to the midpoint of the vertex, also in full frontal view. Width of the front (WF) is the minimum width measurable, often toward the bottoms of the eyes. Distance from eye tops to vertex crest, as compared to HE, is no more than a rough approximation, because of the difficulty in making this measurement (made in lateral view at the same time that HE is measured).

Pronotum. — The dorsal surface, called the pronotal disc, is connected by a sloping anterior face to the flat, anterior collar. Most discussions, and all drawings, pertain only to the disc.

Propodeum. — The term propodeal disc is used for the dorsal surface. Width of the disc is measured at its widest point; length is measured along the midline as far as the transverse carina (or the crest of the declivity, when this carina is absent). A basal, triangular portion of the disc which is often more heavily sculptured than the remainder is termed simply the basal triangle. The disc is margined on each side by lateral carinae, and there may be another pair of longitudinal carinae just mesad of the laterals, called the sublateral carinae. The term transverse carina refers to the carina margining the disc behind. The posterior face (or declivity) is the oblique portion facing the first abdominal tergite, while the side pieces are lateral and more or less vertical.

Mesopleurum. — The term mesopleural callus is applied to a convexity situated on the upper posterior part, often subtended by a groove.

Wing venation. — The discoidal vein (often weakly developed, sometimes absent) is more or less continuous with the median vein, the subdiscoidal vein more or less continuous with the anal vein; the cell between the two, closed on the inner side by the transverse median vein and on the outer side by a deflection of the discoidal vein, is called the discoidal cell. In the modified Comstock-Needham system (Michener, 1944), the median vein is M + Cu, the discoidal vein the outer part of Cu, the subdiscoidal vein plus the anal vein constitute the vannal vein, and the discoidal cell is 2nd Cu.

Abdomen. — The term abdomen is here used to mean the gaster or metasoma (true abdomen minus the propodeum). The abdomen is said to be petiolate if the first tergite does not attain the extreme base of the first segment (as in Figs. 43, 44, 81, 82).

It is said to be sessile if the first tergite reaches the base, even if the segment is slender basally (Figs. 22, 23, 79, 80).

Genitalia. — The lateral, apical structures, termed the parameres, show excellent specific differences and are figured for most species. The volsellae consist of a median cuspis which articulates with the rest of the volsella and is directed laterad, and a more lateral digitus, which in this genus is usually divided into two parts, called the ventral and dorsal arms (shown in lateral view in Figs. 2-7). The ventral arms of the digiti are setose and in some species-groups are strongly separated from the dorsal arms. The aedoeagus is complex, terminating in one to several pairs of apical lobes.

Females

Size. — Total length is difficult to measure accurately as in the males. More significant indications of size are length of the head (LH), and length of the thorax (LT), the latter measured from the anterior margin of the pronotal disc (not including the collar) to the posterior end of the propodeum.

Head shape. — Length of the head (LH) is measured as in the male and is compared to the width of the head (WH), measured at the midpoint of LH.

Pronotum. — Length of the pronotal disc is measured along the midline (excluding collar as usual); width is measured at its greatest, across the prominent shoulder-like posterior corners.

Propodeum. — The propodeum is constricted at or near the spiracles; the width of the constriction (= minimum width) is measured in full dorsal view, as are the width of the portion anterior to the spiracles and the width of the portion behind the spiracles (= maximum width in all but one species). These three measurements presented together constitute the propodeal formula (e.g., 27:16:30 means that the anterior expansion, the constriction, and the posterior expansion present these relative measurements). Length of the propodeum is measured from its extreme anterior end to its extreme posterior end; this figure is slightly greater than the median length, since the anterior margin is concave, embracing the posterior point of the subtriangular mesonotum.

Genus APENESIA Westwood

Apenesia Westwood, 1874, Thesaurus Ent. Oxoniensis, p. 170. [Type species *A. amazonica* Westwood (♀, Brazil); designated by Westwood, 1881.] — Westwood, 1881, Trans. R. Ent. Soc. London, 1881, p. 130. — Kieffer, 1905, *in* André, Spec. Hymen. Eur. Alger., 9: 255. — Kieffer, 1914, Das Tierreich, 41: 391-396.

Aeluroides Tullgren, 1904, Ark. Zool., 1: 428-430. [Type species *A. sjöstedti* Tullgren (♀, Africa); monobasic]. Synonymy by Kieffer, 1914.

Propristocera Kieffer, 1905, *in* André, Spec. Hymen. Eur. Alger., 9: 247. [Type species *P. interrupta* Kieffer (♂, Ceylon); designated by Kieffer, 1914]. — Kieffer, 1914, Das Tierreich, 41: 484-488. — Benoit, 1957, Explor. Parc Nat. Albert, Mission DeWitte, fasc. 88, pp. 37-42. — Evans, 1958, Proc. Ent. Soc. Wash., 59: 289-296. New synonymy.

Cleistepyris Kieffer, 1910, Ann. Soc. Ent. France, 79: 48. [Type species *C. punctatus* Kieffer 1910 (♂, Peru) (*nec Apenesia punctata* Kieffer 1904; = *A. peruana* n. name); designated by Kieffer, 1914]. — Kieffer, 1914, Das Tierreich, 41: 490-494. New synonymy.

Dipristocera Kieffer, 1914, Das Tierreich, 41: 471-472. [Type species *Pristocera microchela* Kieffer (♂, Mexico); monobasic]. New synonymy.

Misepyris Fouts, 1930, Philippine Jour. Sci., 41: 1-10 [*Nec* Kieffer 1913; misidentification].

Neopristocera Benoit, 1957, Explor. Parc Nat. Albert, Mission DeWitte, fasc. 88, pp. 44-46. [Type species *N. triloba* Benoit (♂, Africa); original designation]. Preoccupied by Yasumatsu, 1955, Jour. Fac. Agri. Kyushu Univ., 10: 248. New synonymy.

Generic characters. — *Male.* Mandibles usually with five teeth, occasionally with three or four, in one species-group the basal four teeth fused to form a single cutting edge, leaving only the apical tooth dentiform. Clypeus with a median lobe of very variable shape, but never trapezoidal and narrowly truncate as in *Pseudisobrachium*. Eyes glabrous except in a few species, where there are sparse, short setae. Antennae usually with the pubescence erect or suberect, bristling, and relatively long, but in a few species the pubescence is short and subappressed, these species having some erect setae standing out above the pubescence. Occipital carina complete. Pronotum of variable structure, with or without a transverse groove near posterior margin, only rarely with transverse rugae. Scutellum with a transverse groove at base. Propodeum with basal triangle not marked off by a groove or carina, though usually more heavily sculptured than rest of propodeal disc; disc with or without a transverse margining carina behind. Claws with a single, short, erect tooth in addition to the apical ray. Fore wing with costa extending well past stigma as a strong vein (a few exceptions); discoidal cell partially or fully outlined in most species. Genitalia with parameres simple, sometimes with two apical processes but never deeply divided; digiti divided into ventral and dorsal arms (except in one species-group); inner margin of volsella without a vannus;

aedoeagus complex, without three distinct sets of valves as in *Pristocera*.

Female. Mandibles with from two to four teeth. Clypeus of variable structure. Eyes small, each with from one to about 14 facets. Ocelli absent. Antennae short, flagellar segments not much if any longer than thick, flagellum incrassate in some species. Wings and tegulae completely absent. Mesonotum subtriangular, rounded behind, anterior margin of propodeum slightly extended along sides of mesonotum and arcuately embracing its posterior third. Propodeum weakly to moderately constricted near the spiracles, maximum width from 1.2 to 1.9 X minimum width, sides of propodeum behind the constriction either straight (Fig. 136) or arched (Fig. 134). Mesopleurum with a conspicuous dorsal surface, the thorax much wider here than elsewhere. Femora slightly to strongly swollen and flattened; middle tibiae strongly spinose in most species. Abdomen elongate, with a short to fairly long petiole in some species.

Remarks. — The type species of Kieffer's genera *Cleistepyris* and *Dipristocera* are typical members of this genus and are treated in their proper place in the text (both belong to the *brasiliensis* species-group). The type species of *Dipristocera* does not have paired pits on the scutellum as Kieffer indicated. The type species of *Cleistepyris* does have a transverse carina on the propodeum, as described by Kieffer, but this character is not of generic value in the Pristocerini.

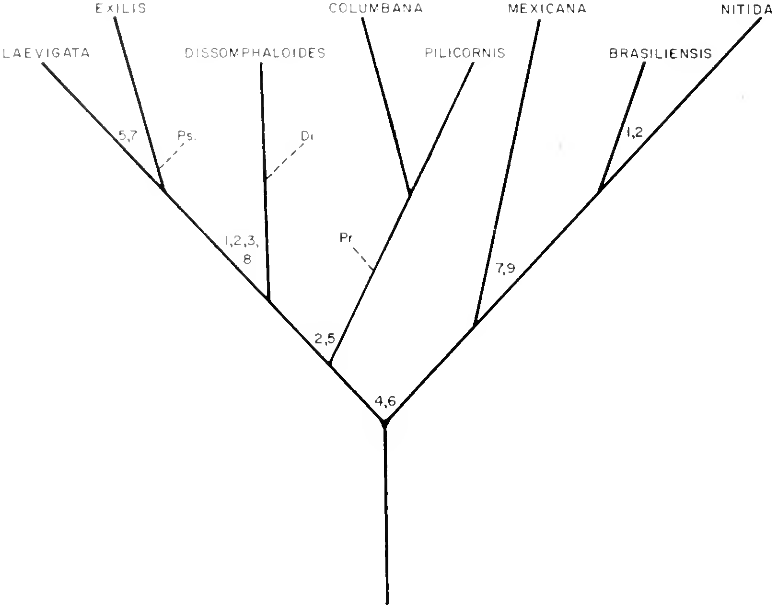
The type species of *Propristocera* is unknown to me, but I have seen several Oriental species which are apparently closely related to it. These species have unidentate mandibles very similar to those of the *nitida* species-group of South America, but they are otherwise not especially close to members of that group. *Apenesia* is represented by an abundance of species in the Orient, Africa, and Australia, and it will eventually be necessary to recognize several additional species-groups to accommodate all of these species.

In the Americas, *Apenesia* is represented by 63 known species, which collectively range from New York, Illinois, Arizona, and southern California to Bolivia and northern Argentina, including the West Indies. Fifty-three of these species are known from males only, 9 from females only, and a single species from both sexes (and even this association has yet to be proved). The males fall into eight well-defined species-groups. The females show considerable structural diversity, but it is difficult to know to what species-groups (as defined in the male sex) the different

TABLE I. CHARACTERS OF THE EIGHT SPECIES-GROUPS OF APENESIA (MALES)

Characters / Species-groups	1 No. of teeth on mandibles	2 Shape of clypeus	3 Eyes weakly hairy	4 Transverse carina pronotum	5 Transverse carina propodeum	6 Middle tibiae spinose	7 Abdomen petiolate	8 Digitus w/setose ventral arm	9 Volsella w/setose inner margin	10 Paramere with mesal lobe
pilicornis	4-5	truncate	—	—	+	—	—	+	—	—
columbana	4-5	truncate	—	—	+	—	—	+	—	+ or —
exilis	5	angulate	—	—	—	—	—	+	—	+ or —
dissomphaloides	3-4	tridentate	+	—	—	—	—	—	—	—
laevigata	5	rounded or angulate	—	—	weakly on sides	—	+	+	—	—
mexicana	3-5	rounded or angulate	— (rarely +)	+	+	+ (rarely -)	—	+	—	+
brasiliensis	5	truncate or angulate	—	+	+	+ (rarely -)	+	+	+	+
nitida	1	angulate or bidentate	—	+	+	+	+	+	+	+

structural types correspond. In the text, I have first treated the eight male species-groups, then treated all the females together at the end. The more important characters of the species-groups of males are summarized in Table I, and the probable relationships of these groups are indicated in Text-figure 1.



Text-figure 1. Diagram showing probable relationships of the eight species-groups of male *Apenesia*. At each branching of the tree I have indicated the important characters which diverge at that point (see Table I for listing of characters by number). I have also indicated the point at which the other three genera of Pristocerini may have arisen from this complex: Pr. = *Pristocera;* Di. = *Dissomphalus;* Ps. = *Pseudisobrachium*. Groups toward the center are assumed to be relatively generalized, those at the extreme right and left to be specialized.

KEY TO SPECIES OF APENESIA

Males

1. Pronotal disc without a transverse carina anteriorly 2
   Pronotal disc with a distinct transverse carina anteriorly . . . 25
2. Abdomen sessile (Figs. 22, 23, 36) 3
   Abdomen with a distinct, moderately long petiole (Figs. 43, 44) (*laevigata* species-group) 23

3. Propodeal disc with a transverse carina behind; relatively large species (LFW at least 3.3 mm.) ... 4
   Propodeal disc without a transverse carina behind; very small species (LFW under 3 mm.) ... 18
4. Antennae with erect setae on the under side which stand out strongly above the short pubescence (most noticeable on segments 4-7); pronotal disc elongate and with the sides (seen from above) slightly concave (Fig. 15) (*pilicornis* species-group) ... 5
   Antennae with erect setae sparse and standing out slightly if at all above the prominent, bristling pubescence; sides of pronotum not concave (Figs. 51-53) (*columbana* species-group) ... 12
5. Transverse carina of propodeum strong, complete; median carina of propodeum reaching the transverse carina, though sometimes weaker behind or represented by a groove or series of small foveae ... 6
   Transverse carina of propodeum obsolete medially, median carina present only on basal two-thirds of disc, not nearly reaching transverse carina ... 10
6. Propodeal disc slightly longer than wide; clypeus weakly rounded apically, with a small median angulation (Fig. 14) (Brazil). ... 5. *elongata* n. sp.
   Propodeal disc slightly wider than long; clypeus more distinctly truncate apically, also usually with a small median tooth (Fig. 13) ... 7
7. Pronotum with punctures absent along a fairly wide median strip; ventral arm of digitus very short (Fig. 3) (Bolivia) ... 4. *angusticeps* n. sp.
   Pronotum more strongly punctate, punctures distributed over most of surface except sometimes a narrow median strip; ventral arm of digitus elongate (Figs. 2, 4, 5) ... 8
8. All trochanters pale straw-colored, contrasting with other basal parts of legs; abdomen weakly suffused with yellowish-brown on apical segment (Brazil) ... 3. *tenebrosa* n. sp.
   Trochanters at least in part brownish or black, not strongly contrasting with remainder of legs; apical two or more segments of abdomen bright rufo-castaneous ... 9
9. Eyes large, WF 1.0-1.2 X HE; scape pale castaneous like the flagellum; LFW under 4.5 mm. (Southern Mexico to Panama and Venezuela) ... 1. *pilicornis* n. sp.
   Eyes small, WF much exceeding HE (1.40-1.52 X HE); scape brownish or blackish; LFW 5.5-6.7 mm. (Brazil) ... 2. *ornata* n. sp.
10. Mandibles with fourth tooth so small as to be scarcely noticeable (Fig. 11); scape blackish; antennal segment eleven 3 X as long as thick (Brazil) ... 6. *reducta* n. sp.
    Mandibles obviously five-toothed (as in Figs. 8, 10); scape castaneous, sometimes suffused with brownish; antennal segment eleven 2.4-2.7 X as long as thick (Central America) ... 11
11. Clypeal carina low, nearly straight in profile; ocelli slightly enlarged, DAO .21 X WF; basal triangle of propodeum reticulate; abdomen

weakly suffused with brownish apically (Mexico) .... 8. *punctata* (Cameron)

Clypeal carina strong, in profile abruptly declivous to apex; ocelli smaller, DAO .16 X WF; basal triangle of propodeum filled with slightly radiating longitudinal carinae; apical two segments of abdomen suffused with orange-brown (Guatemala, El Salvador) .... 7. *guatemalensis* n. sp.

12\. Pronotum either with a strong transverse groove just before the posterior margin, or the whole margin depressed so that there is a constriction between the pro- and mesonota; parameres of genitalia with an angulate process on their outer side (Figs. 16-18) 13

Pronotum with at most a vague indication of a transverse impression, pro- and mesonota forming nearly a smooth plane; parameres slender, not produced on outer side; inner margin of volsella with a finger-like process (Figs. 19-21) 15

13\. Propodeal disc in large part smooth and shining, without transverse striae; pronotum short (Fig. 51), convex, impressed along its posterior margin; inner margin of volsella angularly produced (Fig. 16) (Colombia, Panama) .... 9. *columbana* (Westwood)

Propodeal disc in large part covered with transverse striae; pronotal disc longer (Fig. 52), with a transverse groove just before the posterior margin; inner margin of volsella simple (Figs. 17, 18) . 14

14\. Pronotum smooth except for transverse groove; clypeus narrowly truncate apically, its margin not triangular as seen from below (Fig. 41); apex of parameres and volsella as in Figure 17 (Panama) .... 10. *sulcata* n. sp.

Pronotal disc finely transversely striate anteriorly; clypeus more strongly truncate apically, its margin broadly triangular as seen from below (Fig. 40); apex of parameres and volsella as in Figure 18 (Brazil) .... 11. *striatula* n. sp.

15\. Mandibles and antennae dark brown or nearly black; propodeal disc smooth and polished (except basal triangle), median carina continuous to transverse carina (Brazil) .... 12. *funebris* n. sp.

Mandibles in large part straw-colored; antennae light castaneous or somewhat rufous; median carina of propodeum obsolescent behind, or if complete then the disc somewhat striate on sides and behind 16

16\. Ocelli greatly enlarged, DAO more than .25 X WF, lateral ocelli only 1.25 X their own diameters from eye margin; abdomen in large part rufous; propodeal disc about as long as wide (Argentina) .... 15. *photophila* (Ogloblin)

Ocelli at most slightly enlarged, DAO less than .25 X WF, OOL at least as great as WOT, much greater than diameter of ocelli; abdomen mostly blackish; propodeal disc wider than long ... 17

17\. Mandibles with only four strong teeth (as figured for *columbana*, Fig. 24); antennae relatively shorter and with short pubescence (segment eleven 2.7 X as long as thick, its setulae about one-third as long as width of segment); tegulae and legs fuscous (Bolivia) ....

....13. *flammicornis* n. sp.

Mandibles with five strong teeth (as figured for *funebris*, Fig. 25); antennae elongate, the pubescence long, bristling (segment eleven 3.8 X as long as thick, its setulae nearly as long as width of segment); tegulae and legs (except front coxae) testaceous (Brazil) ....14. *pallidicornis* n. sp.

18\. Clypeus angulate apically (Figs. 34, 35); eyes glabrous; digiti with a setose ventral arm as usual in the genus, aedoeagus without prominent, slender ventral rami (Figs. 26-29) (*exilis* species-group) 19

Clypeus tridentate apically (Fig. 42); eyes with short hairs; digiti in the form of simple, curved rods, without a setose ventral arm; aedoeagus broad and with prominent, very slender ventral rami (Fig 37) (*dissomphaloides* species-group) 22

19\. Head and thorax strongly polished, non-alutaceous; notauli in the form of fairly wide grooves; parameres much broadened apically (Fig. 26) (Arizona) ....16. *pima* n. sp.

Head and thorax rather uniformly alutaceous, less strongly shining than above; notauli linear or obsolescent; parameres slender apically (Figs. 27-29) 20

20\. Notauli distinct, linear; front considerably wider than eye height (WF 1.2 X HE); OOL greater than WOT; antennae and legs dark, nearly black (Arizona) .... 19. *cochise* n. sp.

Notauli barely evident; front narrow (WF subequal to or less than HE); OOL equal to or less than WOT 21

21\. Propodeum elongate, about 1.5 X as long as wide; wing veins light brown; basal parts of legs dark brown (Florida) . 18. *martini* n. sp.

Propodeum shorter, about 1.25 X as long as wide; wing veins nearly colorless, legs light brown to straw-colored (Arizona, California) ....17. *exilis* n. sp.

22\. Mandibles with three teeth (Fig. 48); antennae uniformly light brown, third segment longer than second; OOL subequal to WOT; ocelli slightly enlarged, front angle of ocellar triangle approximately a right angle (Arizona) .... 20. *dissomphaloides* n. sp.

Mandibles with four teeth (Fig. 49); antennae with the basal two segments much paler than the remainder, third segment shorter than second; OOL much greater than POL; ocelli small, front angle of ocellar triangle less than a right angle (Mexico) .... 21. *denticulata* n. name

23\. Discoidal vein arising well down on transverse median vein; head with prominent, bulging eyes, WH 1.07 X LH; spiracles on first two abdominal tergites rather large (Fig. 44); parameres very long and slender (Mexico) .... 24. *laevigata* (Evans)

Discoidal vein absent or interstitial with median vein; head with less bulging eyes, higher than wide, WH .90-.97 X LH; spiracles of first two tergites not notably enlarged 24

24. Propodeum with a strong median carina, posterior part of disc shining; WF 1.17 X HE; LFW 2.1 mm. (Arizona) . . 22. *pallidula* n. sp.
Propodeum without a well-defined median carina, disc weakly and irregularly striate behind; WF 0.9 X HE; LFW 2.4 mm. (Brazil) . . . . 23. *crenulata* (Kieffer)
25. Mandibles with from three to five teeth (Figs. 68-75, 112-116); abdomen sessile or petiolate; subgenital plate and genitalia not as described below 26
Mandibles with only the apical tooth distinct, the remaining teeth fused to form a single cutting edge (Fig. 117); abdomen petiolate; subgenital plate very broadly arcuately emarginate (Fig. 126), revealing the greatly expanded apical lobes of the parameres (Fig. 120); aedoeagus of characteristic form (Figs. 120-123) (*nitida* species-group) 50
26. Abdomen sessile, though sometimes rather slender basally (Figs. 79, 80); mandibles with from three to five teeth; inner margin of volsella at most with a few setae just below the cuspis (Figs. 56-59, 63-67, 76-78) (*mexicana* species-group) 27
Abdomen petiolate, the petiole very short in some species, but the first tergite never reaching the extreme base of the segment (Figs. 81, 82); mandibles with five teeth; inner margin of volsella strongly setose for a considerable distance (Figs. 92-95, 105, 106) (*brasiliensis* species-group) 38
27. Mandibles with five teeth (Figs. 68, 69) 28
Mandibles with three or four teeth (Figs. 70-75) 31
28. Pronotum with a strong transverse groove just before posterior margin; head and thorax strongly shining, non-alutaceous; clypeus more or less rounded apically (Fig. 83) (Panama and Costa Rica) . . . . 25. *bugabensis* (Cameron)
Pronotum with transverse groove absent or vaguely indicated; head and thorax moderately shining, alutaceous; clypeus angulate apically (Fig. 84) 29
29. Eyes with minute, scarcely noticeable setae; discoidal vein very weak, interstitial with median vein; genitalia with inner margin of volsella strongly spined at base of cuspis, striate below (Fig. 59) (Central Mexico) . . . . 28. *malinche* n. sp.
Eyes with short hairs; discoidal vein arising a short distance down on transverse median vein, weak to fairly strong; genitalia with volsellae at most weakly spined at base of cuspis, weakly striate below . . 30
30. Antennae rufo-castaneous, scape and apical part of flagellum infuscated to a variable extent, pubescence dense, pale; subgenital plate rounded apically (Fig. 61); parameres slender, aedoeagus of characteristic form (Fig. 58) (California and Baja California) . 27. *mohave* n. sp.
Antennae brownish, basal flagellar segments usually somewhat lighter, pubescence tending to be coarser and less dense; subgenital plate of most specimens distinctly emarginate (Fig. 60); parameres broad apically, aedoeagus of characteristic form (Fig. 57) (Arizona to

Central Mexico) . . . . 26. *chiricahua* n. sp.

31\. Mandibles with four clearly defined teeth (Figs. 70-72) . . . 32

Mandibles with three teeth (Figs. 74, 75) or in one species actually four-toothed, but the third tooth reduced to a barely visible knob between the basal two teeth (Fig. 73) 34

32\. Flagellum with pubescence subappressed and with erect setae which stand out far above pubescence; front and thoracic dorsum polished, non-alutaceous, with strong punctures (Panama) 29. *peculiaris* n. sp.

Flagellum with erect, bristling pubescence and without erect setae which stand above the pubescence; front and thoracic dorsum uniformly though sometimes weakly alutaceous, punctures of these areas relatively very weak 33

33\. Clypeus denticulate apically, but without a median tooth (Fig. 86); coxae and femora light brown; front and thoracic dorsum weakly alutaceous; propodeal disc slightly longer than broad (Bolivia) . . . . 30. *pando* n. name

Clypeus with a small median tooth, margin also weakly crenulate (Fig. 87); legs wholly bright straw-yellow; front and thoracic dorsum moderately alutaceous; propodeal disc slightly broader than long (Cuba) . . . . 31. *cubensis* n. sp.

34\. Clypeus short, weakly bidentate on the midline apically, median area somewhat elevated but not carinate (Fig. 91); median line of pronotum weakly elevated; parameres subquadrate apically (Fig. 77) (Peru, Ecuador) . . . . 36. *inca* n. sp.

Clypeus not bidentate, with a more or less distinct small to fairly large median tooth (Figs. 88-90); pronotum without a median elevation; parameres not of this form 35

35\. Propodeal disc nearly square, actually very slightly wider than long, posterolateral portions moderately alutaceous, moderately shining; clypeus with a strong median tooth (Fig. 90), median line not carinate; aedoeagus broad and with a complex series of slender, serrate apical processes (Fig. 76) (Brazil, Peru) . . . 35. *neotropica* n. name

Propodeal disc distinctly broader than long (width 1.2-1.35 X median length), posterolateral portions obscurely alutaceous, polished; clypeus with a weak to moderately strong median tooth, median line more or less carinate (Figs. 88, 89); aedoeagus not as above 36

36\. Clypeus subtruncate apically and with a minute median tooth (Fig. 88); ocelli slightly enlarged, DAO about .25 X WF; OOL slightly less than WOT (Panama) . . . . 33. *testaceipes* (Cameron)

Clypeus obtusely angulate apically (Fig. 89); ocelli not notably enlarged, DAO less than .20 X WF; OOL somewhat exceeding WOT 37

37\. Flagellar pubescence very short, longest setulae of antennal segment eleven about .3 as long as width of segment; mandibles actually with four teeth, but third tooth minute, sometimes difficult to see if mandibles are worn (Fig. 73) (Mexico) . . . . 32. *mexicana* (Cameron)

Flagellar pubescence more coarse, longest setulae of antennal segment eleven about half as long as width of segment; mandibles with only three teeth (Fig. 74) (Guatemala) . . . . 34. *maya* n. sp.

38. Median lobe of clypeus roundly or somewhat angularly produced, extending well beyond lateral lobes (Figs. 96-102) 39

Median lobe of clypeus broadly truncate, extending only slightly beyond lateral lobes (Figs. 103, 104) 45

39. Prothorax entirely rufo-castaneous, in contrast to head and to remainder of thorax; ocelli slightly enlarged (DAO .20 X WF); OOL 1.13 X WOT (Brazil) . . . . 43. *fulvicollis* (Westwood)

Prothorax brownish-fuscous or black like head and remainder of thorax 40

40. Median lobe of clypeus narrow, prominent (Fig. 96); surface of propodeum wholly roughened by reticulate ridges; parameres slender throughout, their apices deflected mesad (eastern United States) . . . . 37. *parapolita* n. name

Median lobe of clypeus short and broad (Figs. 97-101); posterolateral parts of propodeal disc often alutaceous, but not covered with reticulate ridges; parameres expanded apically 41

41. Head and thorax uniformly alutaceous, moderately shining; head slightly wider than high; parameres with an angular lateral lobe and slender median lobe (Fig. 93) 42

Head and thorax strongly polished, not or very obscurely alutaceous; head about as wide as high; parameres barely produced laterally, but with a broad median lobe (Figs. 92, 94) 43

42. Front moderately shining, rather weakly alutaceous; median apical lobes of aedoeagus rather large, bearing minute denticles (Fig. 109) (Costa Rica) . . . . 38. *angustata* (Evans)

Front rather dull, strongly alutaceous; median apical lobes of aedoeagus minute, attenuate (Fig. 93) (Tabasco, Veracruz) . . . . 39. *microchela* (Kieffer)

43. Clypeus very short, median lobe extending only slightly beyond lateral lobes (Fig. 100); median apical lobes of aedoeagus forming a point which is nearly or quite as long as lateral lobes (Fig. 94) (Morelos, state of Mexico) . . . . 41. *tlahuicana* n. sp.

Clypeus slightly larger, median lobe extending well beyond lateral lobes (Figs. 99, 101); median apical lobes of aedoeagus much shorter than lateral lobes 44

44. Antennae uniformly dark brown; legs brownish basally; lateral lobes of aedoeagus of moderate size, exceeding the strong, pointed median lobes (Fig. 92) (Michoacan, Chiapas) . . . . 40. *tarascana* n. sp.

Scape and basal parts of flagellum bright yellowish-brown; legs bright testaceous except front coxae weakly infuscated; lateral lobes of aedoeagus unusually large, far exceeding the much reduced median lobes (Fig. 108) (Veracruz) . . . . 42. *olmeca* n. sp.

45. Front alutaceous, with only weak punctures; thoracic dorsum and sides of propodeal disc alutaceous; pronotum with a transverse groove

just before posterior margin; genitalia as in Figure 95 (Venezuela) .... 44. *alutacea* n. sp.

Front polished, barely if at all alutaceous, with distinct punctures; thoracic dorsum and sides of propodeal disc polished, not or barely alutaceous; pronotum at most very indistinctly grooved before posterior margin 46

46. Posterior slope of propodeum smooth and polished, with only some weak striae below, carina margining disc behind standing out strongly; aedoeagus terminating in large, free apical lobes, constricted just below lobes (Fig. 111) (Brazil) .... 48. *brasiliensis* (Kieffer)

Posterior slope of propodeum wholly covered with transverse striae, the carina margining the disc behind barely differentiated from the uppermost of these striae; aedoeagus not of this form 47

47. Mandibles with all the teeth strong and well separated (Fig. 116); greater part of flagellum dull brown, but legs wholly bright testaceous; aedoeagus with apical lobes small, free, not compressed (Fig. 106) (Peru) .... 49. *peruana* n. name

Mandibles with the third and fourth teeth small and close together (Fig. 115); flagellum testaceous or the legs mostly brownish; aedoeagus with large, strongly compressed apical lobes 48

48. Propodeal disc about 1.1 X as wide as long; antennae dull brown; punctures of front rather weak (Ecuador) 45. *zamora* n. sp.

Propodeal disc about 1.3 X as wide as long; antennae bright, pale castaneous or testaceous basally; punctures of front sharply defined although small 49

49. Coxae and femora brownish; apical lobes of aedoeagus elongate, minutely denticulate (Fig. 110) (Brazil) .... 46. *transversa* n. sp.

Legs wholly testaceous; apical lobes of aedoeagus smaller, not denticulate (Fig. 105) (Venezuela) .... 47. *venezuelana* n. sp.

50. Clypeus moderately long, its sides approaching evenly to an obtusely angulate apex (Fig. 125), median carina of clypeus fairly strong (Peru) .... 50. *nitida* (Kieffer)

Clypeus very short, its sides approaching gradually to a bidentate or narrowly truncate apex (Fig. 124), median line weakly elevated 51

51. Head very wide across eyes (WH 1.04-1.07 X LH); ocelli slightly enlarged, lateral ocelli less far removed from eyes (OOL 1.0-1.1 X WOT); flagellar pubescence rather short (Brazil) 54. *laticeps* n. sp.

Head slightly if at all wider than high (WH .99-1.03 X LH); ocelli not enlarged, lateral ocelli far removed from eyes (OOL 1.2-1.6 X WOT) 52

52. Flagellar pubescence short, setulae of segment eleven about half as long as width of segment; transverse pronotal carina very delicate; lateral apical lobes of aedoeagus very slender, not exceeding median lobes (Fig. 121) (Brazil) .... 53. *quadrata* n. sp.

Flagellar pubescence longer, setulae of segment eleven more than half as long as width of segment; transverse pronotal carina strong;

lateral apical lobes of aedoeagus broader and exceeding median lobes (Figs. 120, 123) 53

53. Median carina of propodeum not quite reaching transverse carina; lateral apical lobes of aedoeagus narrow, subacute (Fig. 120) (Brazil, Venezuela) .... 51. *paraensis* (Kieffer)

Median carina of propodeum reaching transverse carina or very nearly so; lateral apical lobes of aedoeagus broad and blunt (Fig. 123) (Bolivia, Peru) .... 52. *truncaticeps* (Kieffer)

Females

1. Clypeus with a relatively narrow, strongly produced median lobe which is rounded or subangulate apically; mandibles with four distinct teeth (Figs. 127, 128) 2

Clypeus broadly truncate or emarginate apically; mandibles with two or three teeth, rarely with weak indication of a fourth tooth (Figs. 129-133) 3

2. Eye consisting of several (3-7) ill-defined facets, distinctly darker than head; propodeal spiracles directed laterad, situated well back from anterior margin of propodeum (Fig. 136); fourth mandibular tooth the smallest (Fig. 127) (eastern United States) 37. *parapolita* n. name

Eye consisting of a single facet, much paler than head; propodeal spiracles fully dorsal, located far forward and preceded by a shallow groove (Fig. 137); third mandibular tooth the smallest (Fig. 128) (Panama) .... 55. *paradoxa* n. sp.

3. Eye unusually large, about .3 as long as distance between eyes, with 14 convex, clearly defined facets; propodeum widest in front of spiracles, behind spiracles narrow and parallel-sided (Fig. 138) (Texas) .... 56. *insolita* n. sp.

Eye small, less than .2 as long as distance between eyes, with a smaller number of ill-defined facets; propodeum at least as wide behind spiracles as in front of spiracles, its sides arcuate behind spiracles (Figs. 134, 135) 4

4. Mandibles with three strong teeth and weak indication of a fourth tooth basad of these (Fig. 129); propodeum as wide in front of spiracles as behind them, and with a weak median impression (Fig. 135) (Dominica in Lesser Antilles) .... 59. *dominica* n. sp.

Mandibles with two strong teeth, with or without some indication of a third tooth (Figs. 130-133); propodeum wider behind spiracles than in front of them and without a median impression (as in Fig. 134) 5

5. Abdomen with an unusually long petiole, the petiole actually .6 as long as the hind tibia; antennae strongly incrassate, segment eleven approximately twice as wide as segment three; length under 3 mm. (Jamaica) .... 57. *delicata* n. sp.

Abdomen with a very short petiole or none at all; antennae slender or weakly incrassate, width of segment eleven not more than 1.5 X width of segment three; length over 4 mm. 6

6. Dorsal and lateral surfaces of mesopleurum separated by a sharp ridge; head relatively elongate, length from 1.08 to 1.17 X width; abdomen distinctly darker than head and thorax 7
   Dorsal surface of mesopleurum rounded gradually onto lateral surface; head almost square, length from .97 to 1.04 X width; body entirely testaceous to castaneous 9
7. Mandibles with third tooth relatively well-defined and located a short distance back along inner margin (as in Fig. 130); a relatively more elongate species, pronotal disc about 1.5 X as long as wide, propodeum 2.1 X as long as its maximum width (Bolivia) . . . . 60. *substriata* (Kieffer)
   Mandibles with third tooth indistinct or absent, when indistinct situated far back along inner margin (Figs. 131, 133); relatively more robust species, pronotal disc not more than 1.4 X as long as wide, propodeum from 1.8 to 2.05 X as long as its maximum width . 8
8. Clypeal emargination rather shallow, not reaching the inter-antennal prominence; inner margin of mandibles simple (Fig. 133) (Costa Rica) . . . . 59. *amoena* n. sp.
   Clypeal emargination strong, reaching the strong, rounded, inter-antennal prominence; inner margin of mandibles subdentate at a considerable distance back from the apex (Fig. 131) . . . . 61. *amazonica* Westwood
9. Head noticeably longer than wide, LH 1.04 X WH; front polished, nonalutaceous (Panama) . . . . 62. *flavipes* Cameron
   Head barely if at all longer than wide, LH .97-1.03 X WH; front polished but in most specimens very weakly alutaceous (Mexico to Costa Rica) . . . . 63. *chontalica* Westwood

PILICORNIS SPECIES-GROUP

This very distinctive group contains eight known species, all very closely related. The antennae are strikingly different from those of any other species group, as the pubescence is short and the under side of the flagellum bears many erect setae. The pronotum is also of characteristic shape, the disc being ecarinate, relatively elongate, and with the sides concave as seen from above. The abdomen is sessile. The genitalia are characterized by truncate, unlobed parameres, by an apical aedoeagal lobe which is directed sharply ventrad at a 45-90° angle with the main part of the aedoeagus, and by having the volsellar cuspis at the end of a process which is deeply separated from the digitus, the latter with the two arms closely associated. There are only very minor differences between the genitalia of the various species. All species are black with more or less castaneous antennae, dark legs, and the abdomen weakly to strongly suffused with rufous or brownish apically. The group ranges from southern Mexico to Bolivia and southern Brazil. See Table II and Plate 1 for summary and illustrations of some of the characters of members of this complex.

TABLE II. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF PILICORNIS GROUP

Species	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	Ant. 11 L/W	Propodeal disc W/L	Reduction in 4th tooth mandibles
1. pilicornis	4.4	0.95	1.05	1.03	3.5	1.10	slight
2. ornata	6.6	0.93	1.45	1.60	3.5	1.10	none
3. tenebrosa	5.4	0.98	1.20	1.35	4.0	1.15	moderate
4. angusticeps	3.3	0.95	1.10	1.30	2.5	1.05	moderate
5. elongata	4.7	0.92	1.07	1.30	3.0	0.90	none
6. reducta	4.0	0.98	1.15	1.25	3.0	1.10	great
7. guatemalensis	4.1	0.95	1.20	1.20	2.7	1.05	slight
8. punctata	3.4	0.95	1.30	1.30	2.4	1.08	moderate

1. APENESIA PILICORNIS new species

Holotype. — ♂, PANAMA: Pacora, Canal Zone, 13 May 1953 (F. S. Blanton) [USNM, No. 66005].

Description of type. — Length 5.9 mm.; LFW 4.4 mm. Head and thorax shining black; first abdominal segment black with pale brown lateral streaks; second segment and base of third piceous, remainder of abdomen bright rufo-castaneous; mandibles castaneous except base infuscated and teeth rufous; palpi straw-colored; antennae wholly castaneous except apical segments weakly infuscated; tegulae testaceous; coxae and middle and hind femora dark reddish-brown, legs otherwise castaneous except tarsi tinged with blackish; wings subhyaline, veins and stigma dark brown. Mandibles with five teeth, third and fourth teeth the smallest, basal tooth rather prominent (Fig. 8). Clypeus moderately long, broadly truncate except for a faint indication of a median tooth (Fig. 13); median carina very strong, abruptly declivous well before margin. First four antennal segments in a ratio of about 23:4:14:13, segment three 2.2 X as long as thick, segment eleven 3.5 X as long as thick; pubescence pale, subappressed, setulae of segment four only about .15 X as long as thickness of segment; erect setae rather sparse except on underside of segments 3-9, to a lesser extent 10 and 11, where these setae are numerous and conspicuous, measuring .3 to .6 as long as width of segments bearing them. Front polished, nonalutaceous, with small though strong punctures which are separated for the most part by less than their own diameters, though more widely spaced above; vertex and temples somewhat more weakly punctate. Head slightly longer than wide, WH .95 X LH; inner orbits subparallel below, front actually very slightly wider at the middle of the eyes than at their bottoms; WF .58 X WH, 1.05 X HE. Vertex extended above eye tops a distance equal to about two-thirds HE; anterior ocellus nearly touching a line drawn between eye tops; posterior ocelli removed from vertex crest by a distance nearly equal to WOT; ocellar triangle compact, OOL very slightly greater than WOT; DAO .18 X WF. Pronotal disc rather elongate, nearly flat, in front obliquely declivous to much lower plane of collar, sides of disc, as seen from above, slightly concave (Fig. 15); disc shining and with strong, well spaced punctures, without sculpturing except for a very shallow transverse impression a short distance before the posterior margin; collar transversely rugose. Mesoscutum shining, sparsely punctate except punctures more crowded along notauli, the latter not quite reaching anterior margin; scutellar disc with small punctures except along median strip. Propodeal disc 1.1 X as wide as long, with strong margining carinae laterally and posteriorly; median carina strong except weakened just before meeting transverse carina; disc with a basal triangle which is slightly depressed and filled with longitudinal, slightly diverging carinae, remainder of disc polished and without sculpturing; side-pieces of propodeum weakly striate, posterior face with only some weak sculpturing. Mesopleurum shining, punctate, callus prominent and without punctures. Fore wing with discoidal cell very weakly outlined by pigmented lines, also with first recurrent vein weakly indicated and subdiscoidal and radial veins weakly continued to wing margin. Subgenital plate arcuately concave apically. Genitalia with the parameres abruptly truncate apically, mesally strongly hollowed out for the reception of the complex volsellar structures; ventral arm of digitus moderately elongate (Figs. 1, 2).[2]

Paratypes. — PANAMA: 1 ♂, Pacora, Canal Zone, same data as type [MCZ]; 1 ♂, Gamboa, Canal Zone, 17 July 1918 (sweeping, H. Dietz & J. Zetek) [USNM]; 2 ♂ ♂, Barro Colorado Island, Canal Zone, 28 March 1955 (C. Rettenmeyer), 22 Dec. 1928 (C. H. Curran) [KU, AMNH]. MEXICO: CHIAPAS: 3 ♂ ♂, Simojovel, 28 Sept. 1961 (F. Pacheco M.) [Escuela Nac. Agri., Chapingo, Mex.]; 1 ♂, 19 km. NE Bochil, 28 Sept. 1961 (F. Pacheco M.) [Escuela Nac. Agri., Chapingo, Mex.]. COSTA

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[2] Description and figure of genitalia based on paratype from Barro Colorado Island (C. H. Curran); the genitalia of the type were not extracted.

RICA: 1 ♂, Port Parker, 4 July 1932 (M. Willows) [CAS]. VENEZUELA: 1 ♂, Los Castillitos, D. F., 27 Feb. 1938 (Vivas Berthier) [HKT].

Variation. — LFW varies from 3.0 to 4.4 mm. There is some variation in the amount of rufous on the tip of the abdomen. The least amount of rufous is present in the Mexican and Costa Rican specimens (only the apical two or three segments). In the Venezuela specimen, the Barro Colorado specimens, and the Gamboa specimen, the entire abdomen is rufous, though the basal tergites are dusky. In some specimens the legs are entirely brown. In the Venezuela specimen the side pieces of the propodeum are completely smooth and the apex of the aedoeagus slightly more expanded. In the Costa Rica and Venezuela specimens the median carina of the propodeum is obsolescent on the posterior fourth of the disc. In the series from Chiapas, Mexico, the front is relatively slightly broader than in the remainder of the series, WF varying from .60-.62 X WH, 1.10-1.20 X HE; OOL varies from 1.12-1.29 X WOT.

2. Apenesia ornata new species

Holotype. — ♂, BRAZIL: Nova Teutonia, Santa Catarina, 2 Nov. 1939 (Fritz Plaumann) [MCZ, No. 30341].

Description of type. — Length 10 mm.; LFW 6.6 mm. Head and thorax shining black; abdomen black except sides of first segment suffused with castaneous and whole abdomen beyond segment four bright rufo-castaneous, the apical segment almost yellow; palpi brownish; mandibles black except apical third somewhat rufous; scape black, second segment somewhat infuscated, rest of antenna bright castaneous except apical segments weakly infuscated; tegulae fuscous; legs black except tarsi dark brown; fore wing lightly tinged with brownish, veins and stigma dark brown, hind wings subhyaline. Mandibles with five strong teeth in an oblique series (Fig. 9). Clypeus broadly truncate except for a weak median tooth; median carina high, arched in profile, abruptly declivous just before margin. First four antennal segments in a ratio of about 30:7:19:17, segment three 2.5 X as long as thick, segment eleven 3.5 X as long as thick; pubescence very fine, pale, appressed; erect setae small and sparse except longer and much more dense on underside of segments 4-7, to a lesser extent 3 and 9-10, these setae mostly somewhat less than half as long as thickness of segments bearing them. Front polished, non-alutaceous, with small but strong punctures which are separated by approximately their own diameters; upper front, vertex, and temples with punctures weaker and more widely separated. Head slightly longer than wide, WH .93 X LH; inner orbits subparallel below, front very slightly wider at middle of eyes than at bottoms; WF .64 X WH, 1.45 X HE. Vertex extended above eye tops a distance about equal to HE; ocellar triangle compact, posterior ocelli removed from vertex crest by a distance greater than WOT; OOL 1.6 X WOT; DAO .13 X WF. Pronotum as described and figured for *pilicornis* (Fig. 15), the transverse subapical depression shallow but well defined. Mesoscutum sparsely punctate, notauli strong and nearly complete; median portion of scutellar disc impunctate. Propodeal disc 1.1 X as wide as long, with strong margining carinae laterally and posteriorly; median carina complete; basal triangle slightly depressed and with a rather irregular network of carinae, remainder of disc smooth except striate laterally; side pieces and declivity somewhat striate. Mesopleurum polished, punctate except for the prominent callus. Fore wing as in *pilicornis* except the discoidal cell somewhat more distinctly outlined, the subdiscoidal vein being especially strong. Subgenital plate broadly truncate apically. Genitalia with the parameres and ventral arm of digitus more elongate than in *pilicornis* (Fig. 4).

Paratypes. — BRAZIL: 8 ♂♂, Nova Teutonia, same data as type except various dates June-Aug., Nov., 1938-61 [MCZ, USNM, BMNH, HKT].

Variation. — LFW varies from 5.5 to 6.7 mm. In some specimens the scape is only moderately infuscated and in some only the basal 3.5 abdominal segments are black, the remainder rufous. WF is relatively constant, varying from 1.40-1.52 X HE. Otherwise little variation can be noted in this series.

3. APENESIA TENEBROSA new species

Holotype. — ♂, BRAZIL: Rio de Janeiro, January 1939 (Yellow fever survey, R. C. Shannon) [USNM, No. 66006].

Description of type. — Length 9.0 mm.; LFW 5.4 mm. Head and thorax shining black, abdomen piceous except apical segment rather weakly suffused with yellowish brown; palpi straw-colored; mandibles black except rufous apically; antennae wholly bright castaneous except apical segments weakly infuscated; tegulae infuscated except pale and translucent on the outer side; coxae piceous; trochanters wholly pale straw-colored; femora dark reddish brown except paler at extreme base and apex; tibiae brownish but paler at base and apex and also paler on inner face, especially the front tibiae; tarsi light brown; wings very lightly tinged with brown, veins and stigma dark brown. Mandibles with five teeth, fourth tooth the smallest, fifth tooth rather broad, reflexed inward (about as in *angusticeps*, Fig. 10). Clypeus broadly truncate apically, with a weak median tooth; median carina moderately strong, in profile nearly straight. First four antennal segments in a ratio of about 28:5:20:18, segment three 2.7 X as long as thick, segment eleven 4 X as long as thick; pubescence pale, short, semi-erect; erect setae sparse and inconspicuous except on underside of segment 3-10, especially 4-6; longest setae of segment four about .4 as long as thickness of segment. Front strongly polished, non-alutaceous, with small but strong, evenly distributed punctures, for the most part separated by approximately their own diameters; vertex and temples somewhat more weakly punctate. Head very slightly longer than wide; inner orbits subparallel below, WF .59 X WH, 1.2 X HE. Vertex extended above eye tops a distance equal to about .7 X HE; diameter of anterior ocellus .16 X WF; OOL 1.35 X WOT; posterior ocelli removed from vertex crest by a distance roughly equal to WOT. Pronotal collar and disc of the usual form in this species-group; transverse depression paralleling posterior margin well developed; surface with strong, evenly distributed punctures. Mesoscutum with punctures slightly more widely spaced; notauli strong and complete; center of scutellar disc impunctate. Propodeal disc 1.15 X as wide as long; lateral and posterior transverse carinae well developed, subfoveolate on their inner sides; median carina weakened behind, barely reaching transverse carina; basal triangle of disc slightly depressed, filled with weakly radiating longitudinal carinae, remainder of disc strongly polished; declivity and side pieces very weakly striate and with a few weak punctures. Mesopleurum strongly and closely punctate, callus very large, impunctate. Fore wing with subdiscoidal vein strong to end of discoidal cell, then continued on weakly to wing margin; discoidal vein arising a short distance down on transverse median vein, weaker than subdiscoidal vein; discoidal cell also closed off apically with a pigmented line, first recurrent vein also weakly indicated. Subgenital plate weakly arcuately concave. Genitalia much like those of *pilicornis*, the parameres slightly more hairy on the outer side (Fig. 5).

Paratype. — BRAZIL: 1 ♂, same data as type except October 1938 [USNM].

Variation. — The paratype is very similar to the type in size, color, and most structural details. The only noticeable difference pertains to the sculpturing of the basal triangle of the propodeum; in the paratype there are several transverse ridges in this area, giving it a much more reticulate appearance.

4. Apenesia angusticeps new species

Holotype. — ♂, BOLIVIA, "Prov. Sara" (= Prov. Gutiérrez, Dept. Santa Cruz) (Steinbach) [MCZ, No. 30433].

Description of type. — Length 5.0 mm.; LFW 3.3 mm. Head and thorax black; abdomen black except apical tergite and apical two sternites suffused with rufo-castaneous; palpi straw-colored; mandibles black, apical third suffused with rufous; antennae uniformly castaneous except scape somewhat infuscated; tegulae testaceous; legs dark brown, tibiae paler at base and apex, tarsi light yellowish brown; wings subhyaline. Mandibles with five teeth, fourth tooth the smallest, basal tooth rather large, reflexed inward (Fig. 10). Clypeus moderately long, truncate apically but with an indistinct, minute median tooth; median carina strong, arched in profile. First four antennal segments in a ratio of about 35:7:22:30, segment three 2.2 X as long as thick, segment eleven about 2.5 X as long as thick; pubescence pale, subappressed; erect setae sparse and small except on underside of segments 4-7, to a lesser extent 3 and 8-10; longest setae on segment four about half as long as thickness of segment. Front polished, punctures strong, rather crowded on midline below, elsewhere separated by about their own diameters except smaller and more widely separated above and on the vertex and temples. Head longer than high, WH .95 X LH; eyes slightly closer together near bottom than at middle; WF .58 X WH, 1.10 X HE. Vertex extended above eye tops a distance equal to about two-thirds HE; ocellar triangle compact, posterior ocelli removed from vertex crest by a distance about equal to WOT; OOL 1.3 X WOT; DAO .16 X WF. Pronotum elongate, its sides concave as seen from above, groove paralleling posterior margin fairly strong; collar transversely rugulose; disc shining, punctures rather small and sparse, completely absent along a wide median strip. Mesoscutum shining, sparsely punctate; notauli strong on posterior .8; scutellar disc shining and impunctate. Propodeal disc very slightly wider than long, smooth and polished except for a basal triangular area filled with longitudinal carinae; median carina reaching the posterior transverse carina although weakened behind; side pieces polished, sculpturing almost absent. Mesopleurum polished, sparsely and rather coarsely punctate, except callus impunctate. Fore wing with subdiscoidal vein fairly strong, continued to wing margin as a faintly pigmented streak; discoidal vein arising a short distance down on the transverse median vein, very weak, discoidal cell also closed on outer side by a very weak pigmented line. Subgenital plate broadly arcuately concave apically. Genitalia with the parameres moderately long, obliquely truncate apically; ventral arm of digitus unusually short (Fig. 3).

Remarks. — This species is known from the type specimen only.

5. APENESIA ELONGATA new species

Holotype. — ♂, BRAZIL: Rio de Janeiro, November (no further data) [USNM, No. 66007].

Description of type. — Length 6.2 mm.; LFW 4.7 mm. Head and thorax shining black; abdomen black except sides of first tergite and all of last tergite suffused with yellowish brown; palpi straw-colored; apical third of mandibles dull rufous; scape moderately infuscated, flagellum light brown, very slightly darker apically than basally; collar dark castaneous; tegulae dusky castaneous; coxae dark brown, trochanters straw-colored, femora dark brown, tibiae and tarsi medium brown, the joints paler; wings subhyaline. Mandibles with five strong teeth (as in Fig. 9). Clypeus produced and rounded apically, with a small median tooth (Fig. 14); median carina strong, in profile nearly straight except roundly declivous well before margin of clypeus. First four antennal segments in a ratio of about 22:5:13:12, segment three 2.6 X as long as thick, segment eleven 3 X as long as thick; pubescence pale, short though semi-erect, erect setae sparse except on underside of segments 3-10, where it is long and abundant, longest setae on segment four about .6 as long as thickness of segment. Front shining, non-alutaceous, with coarse punctures which are separated by about or somewhat less than their own diameters; vertex and temples with punctures much weaker and more widely spaced. Head distinctly longer than wide, WH .92 X LH; inner orbits subparallel below, WF .59 X WH, 1.07 X HE; vertex broadly rounded, distance from eye tops to vertex crest equal to slightly more than half HE. Ocelli of moderate size, DAO .19 X WF, in a compact triangle; OOL 1.3 X WOT; posterior ocelli removed from vertex crest by a distance somewhat less than WOT. Pronotum shaped as in *pilicornis* (Fig. 15);

collar transversely rugose; transverse subapical groove shallow and ill-defined; punctures well spaced, absent from a rather narrow median band. Mesoscutum with strong punctures scattered over most of its surface, more crowded posteriorly and along notauli; center of scutellar disc polished and impunctate. Propodeal disc 0.9 X as wide as long; lateral carinae strong, posterior transverse carina complete, somewhat sinuate; median carina stopping well short of transverse carina but continued on as a weak, subfoveolate impression to the carina; basal triangle rather elongate, filled with several irregular longitudinal ridges and some weaker transverse ridges, margined by shallow depressions; posterior and lateral parts of disc polished and without sculpturing; posterior face of propodeum strongly polished, somewhat convex; side-pieces polished but with some weak striae and punctures. Mesopleurum with scattered punctures except on the callus. Fore wing with discoidal vein starting out a strong stub arising well down on transverse median vein, then abruptly transformed into a very pale pigmented line; subdiscoidal vein more strongly pigmented, outer side of discoidal cell closed off by a very faint brownish streak. Subgenital plate strongly arcuately concave. Genitalia with the parameres moderately long, ventral arm of the digitus elongate and much as in *ornata* (Fig. 6).

Paratypes. — BRAZIL: 1 ♂, Nova Teutonia, Santa Catarina, 13 April 1938 (F. Plaumann) [BMNH]; 1 ♂, same data except Jan. 1963 [MCZ].

Variation. — The paratypes are smaller than the type (LFW 4.0-4.1 mm.) and have the scape, base of the flagellum, and apical two-thirds of the mandibles bright castaneous; however, the trochanters are darker than in the type. Both specimens have the front slightly wider than in the type (WF 1.10 and 1.18 X HE, OOL 1.37 and 1.40 X WOT).

6. Apenesia reducta new species

Holotype. — ♂, BRAZIL: Chapada, January (no further data) [CM].

Description of type. — Length 6.0 mm.; LFW 4.0 mm. Head and thorax shining black, abdomen piceous except apical two segments strongly suffused with rufous; palpi light brown; mandibles black, apical third suffused with rufous; scape black, rest of antennae castaneous except weakly infuscated apically; tegulae testaceous; legs dark brown except paler at joints, tarsi wholly light yellowish-brown; wings subhyaline. Mandibles with fourth tooth reduced to a scarcely noticeable denticle at the base of the notch between the large third and fifth teeth, the mandibles thus essentially 4-toothed (Fig. 11). Clypeus short, broadly truncate, with a small, rounded median tooth; median carina low, straight in profile. First four antennal segments in a ratio of 21:4:12:12, segment three twice as long as thick, segment eleven about 3 X as long as thick; pubescence pale, very short although semi-erect, erect setae sparse except on underside of segments 4-7, to a less extent 3 and 8, longest setae on segment four about half as long as width of segment. Front shining, non-alutaceous, with strong punctures which are separated by about or somewhat less than their own diameters; vertex and temples with punctures more shallow and widely spaced. Head very slightly longer than wide; inner orbits convergent below, WF .57 X WH, 1.15 X HE. Vertex extended above eye tops a distance nearly equal to HE; ocelli in a compact triangle, posterior ocelli removed from vertex crest by a distance about equal to WOT; OOL 1.25 X WOT; DAO .18 X WF. Pronotal disc shaped much as in *pilicornis;* collar with transverse rugae; transverse subapical impression rather weak; disc with strong, rather evenly distributed punctures which are separated by somewhat more than their own diameters. Mesoscutum with strong punctures which are widely spaced except more crowded along notauli; notauli strong except weakened anteriorly and barely reaching anterior margin; center of scutellar disc impunctate. Propodeal disc 1.1 X as wide as long; lateral carinae strong, but posterior transverse carina rather weak, obsolete medially; basal triangle slightly depressed, broad and short, filled with weakly radiating longitudinal carinae, median carina the longest but reaching only .6 the length of the disc; disc behind basal triangle very strongly polished, without any sculpturing whatever; declivity and side pieces polished, obscurely sculptured. Mesopleurum strongly polished, callus large and impunctate, rest of mesopleurum with small, widely spaced punctures. Fore wing as described for *pilicornis.* Subgenital plate broadly arcuately concave apically. Genitalia with the parameres of moderate length; dorsal arm of digitus unusually wide, ventral arm unusually short (Fig. 12).

Remarks. — This species is known only from the type.

7. Apenesia guatemalensis new species

Holotype. — ♂, GUATEMALA: Guatemala City, 9 June 1949 (K. W. Cooper) [USNM, No. 66008].

Description of type. — Length 6.2 mm.; LFW 4.1 mm. Body shining black except apical two segments of abdomen suffused with orange-brown; palpi light brown; apical half of mandibles yellowish brown, teeth rufous; antennae wholly bright castaneous except apical segments somewhat infuscated; tegulae testaceous; front coxae black, remaining coxae and all the femora dark reddish brown except paler at the joints; trochanters brownish except middle pair light yellowish brown; middle and hind tibiae dark brown, paler basally and apically; front tibiae and all tarsi light brown; wings hyaline, stigma, costa, subcosta, and radial vein brown, rest of veins amber. Mandibles with five teeth (about as figured for *pilicornis*, Fig. 8). Clypeus broadly truncate, median tooth barely suggested; median carina strong, in profile straight except abruptly declivous somewhat before apical margin. First four antennal segments in a ratio of about 20:4:12:11, segment three 2.2 X as long as thick, segment eleven 2.7 X as long as thick; pubescence pale, very short though semierect, erect setae sparse except on under side of segments 3-8, especially 4-6, where they are abundant and fairly long; longest setae of segment four about one-third as long as width of segment. Front polished, non-alutaceous, punctures small though strong, separated from one another by about or somewhat less than their own diameters; vertex and temples somewhat more weakly punctate. Head .95 X as wide as high; inner orbits weakly convergent below, WF .62 X WH, 1.2 X HE. Vertex extended above eye tops a distance equal to about .8 X HE; diameter of anterior ocellus .16 X WF; OOL 1.2 X WOT; posterior ocelli removed from vertex crest by a distance nearly as great as WOT. Pronotal collar and disc of the usual form in this species-group; transverse subapical impression rather weak; disc with strong, rather evenly distributed punctures. Mesoscutum sparsely punctate except with punctures crowded along the notauli, the latter rather shallow, not reaching anterior or posterior border; scutellum with small punctures except medially. Propodeal disc very slightly wider than long, lateral carinae strong but transverse carina obsolete medially; basal triangle not notably depressed, broad and short, filled with slightly radiating longitudinal carinae, median carina the longest but not nearly reaching the transverse carina; posterior part of disc smooth, strongly polished; declivity and side-pieces also strongly polished, with only a few weak punctures. Mesopleurum with the punctures smaller and more widely spaced behind than in front, absent from the rather slender callus. Fore wing with veins surrounding discoidal cell above, below, and on outer side all very faintly indicated. Subgenital plate arcuately concave apically, apical tergite rounded apically. Genitalia bearing a close resemblance to those of *pilicornis* and *tenebrosa* (Fig. 7).

Paratype. — EL SALVADOR: 1 ♂, Quezaltepeque, 21 June 1961 (M. E. Irwin) [UCD].

Variation. — The paratype is strikingly similar to the type but is smaller (length 5.0 mm., LFW 3.4 mm.). The antennae are somewhat shorter, segment three measuring 1.7 X as long as thick, segment eleven 2.3 X as long as thick. WF is .58 X WH, 1.12 X HE; OOL is 1.18 X WOT.

8. APENESIA PUNCTATA (Cameron) new combination

Epyris punctatus Cameron, 1888, Mem. Proc. Manchester Lit. Phil. Soc., 1: 174-175. [Type: ♂, MEXICO: VERACRUZ: Orizaba, Dec. 1887 (H. H. Smith) (BMNH)]. — Cameron, 1899, Biol. Centr.-Amer., Hymen. I, Suppl., p. 473. — Kieffer, 1905, Ann. Soc. Sci. Bruxelles, 29:111. — Kieffer, 1914, Das Tierreich, 41: 466.

Description of type. — Length 4.8 mm.; LFW 3.4 mm. Head and thorax piceous, abdomen dark brown, slightly paler basally and apically; palpi straw-colored; mandibles light brown on apical two-thirds; antennae bright, pale castaneous except scape and apical few segments suffused with brownish; legs brown, tibiae very light brown; wings subhyaline, veins and stigma brown. Mandibles with five teeth, fourth tooth smaller than the others (about as figured for *angusticeps*, Fig. 10). Clypeus truncate, with a very weak median tooth, median carina rather low. First four antennal segments in a ratio of about 33:9:18:17, segment three 2.1 X as long as thick, segment eleven 2.4 X as long as thick; pubescence semi-erect, pale, longest setulae of segment eleven .3 as long as width of segment; erect setae abundant on undersides of basal flagellar segments, longest ones about half as long as width of segments. Front polished, non-alutaceous, punctures strong, separated by about their own diameters, even the broad area above the ocelli strongly punctate. WH .95 X LH; inner orbits convergent below, WF .63 X WH, 1.30 X HE. Ocelli in a compact triangle, DAO .21 X WF; OOL 1.3 X WOT. Vertex elevated far above eye tops, broadly rounded; distance from eye tops to vertex crest nearly equal to HE. Pronotum elongate and with concave sides as seen from above; disc shining, strongly punctate except more weakly so along midline. Mesoscutum shining, weakly punctate; scutellar disc impunctate in center. Propodeal disc 1.08 X as wide as long, basal triangle reticulate, but disc otherwise smooth and polished; median carina obsolete behind, not nearly attaining the transverse carina, which is obsolete medially. Mesopleurum shining, with sparse, small punctures. Fore wing with discoidal vein very weakly outlined by pigmented lines; subdiscoidal vein continued nearly to wing margin as a weakly pigmented streak. Apical margin of subgenital plate weakly concave. Genitalia not studied.

Remarks. — This species is known only from the type.

COLUMBANA SPECIES-GROUP

This group of seven relatively large species presents more structural diversity than does the preceding group. The flagellar pubescence is erect and bristling, and only one species (*flammicornis*) has a few setae which extend above the pubescence. The pronotum varies considerably in shape, but the sides are not concave as seen from above. The aedoeagus is rather similar throughout the group and has the apex deflected ventrad as in the preceding species-group. On the basis of the parameres and volsellae the group can be divided into two subgroups. One of these, which includes *columbana, sulcata,* and *striatula,* has the parameres produced subapically along the outer margin and has the inner margin of the volsella simple or weakly produced; in this group the pronotum has an apical or subapical transverse depression. In the remaining four species the parameres are slender and unlobed, and the inner margin of the volsella has a finger-like process; these species all lack a transverse impression on the pronotum. The group ranges from Panama to Bolivia and northern Argentina. See Table III and Plates 2 and 4 for summary and illustrations of some of the characters of this complex.

TABLE III. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF COLUMBANA GROUP

Species	LFW (mm.)	WF/HE	OOL/WOT	Ant. 11 L/W	Propodeal disc W/L	Color mandibles	Reduction in 4th tooth mandibles
9. columbana	5.4	1.15	1.40	5.0	1.15	pale	great
10. sulcata	4.2	0.95	1.40	4.3	1.00	pale	slight
11. striatula	6.0	1.00	1.00	5.0	1.05	pale	great
12. funebris	5.8	1.12	1.25	3.6	1.20	dark	slight
13. flammicornis	5.1	1.07	1.25	2.7	1.35	pale	great
14. pallidicornis	4.2	0.87	1.10	3.8	1.15	pale	slight
15. photophila	6.5	1.06	0.54	4.0	1.00	pale	complete

9. APENESIA COLUMBANA (Westwood) new combination

Pristocera columbana Westwood, 1874, Thesaurus Ent. Oxoniensis, p. 164, pl. XXIX, fig. 5. [Type: ♂, COLOMBIA (no further data) (D. Gaudichaud) (HCOU)]. — Kieffer, 1914, Das Tierreich, 41: 470.

Plesiotype. — ♂, COLOMBIA: Rio Frio, 12 Sept. (G. Salt) [MCZ].[3]

Description of plesiotype. — Length 8 mm.; LFW 5.4 mm. Head and thorax black, abdomen dark reddish brown; palpi brown; mandibles straw-colored except black at extreme base and the teeth rufous; scape black, remainder of antenna dark brown with a weak bluish cast; tegulae brown; coxae nearly black, legs otherwise dark brown, tarsi and joints somewhat paler; wings subhyaline, apical half of fore wing rather distinctly tinged with brownish. Mandibles with four large teeth, the true fourth tooth present as a minute denticle at the base of the notch between the third and fifth teeth (Fig. 24). Clypeus broadly truncate apically, the sides of the truncation subangular (Fig. 39); median ridge high, in profile abruptly, angularly cut off subapically; apical margin, seen from below, broadly triangular, the top of the triangle formed by the median ridge, surface of the triangle actually somewhat concave. First four antennal segments in a ratio of about 22:5:17:17, segment three 3.4 X as long as thick, segment eleven about 5 X as long as thick; pubescence erect, bristling, rather dark in color; setulae of segment eleven slightly longer than width of segment. Front polished, non-alutaceous, with strong punctures which are separated, for the most part, by about their own diameters; punctures of vertex, temples, and under side of head shallower and somewhat more widely spaced. Head very slightly higher than wide; inner orbits converging below, front distinctly wider at middle of eyes than near their bottoms; WF .56 X WH, 1.15 X HE. Vertex broadly rounded off far above eye tops, distance from eye tops to vertex crest equal to about .8 X HE. Ocelli not enlarged, DAO .17 X WF; ocellar triangle compact, far removed from eyes and from vertex crest; OOL 1.4 X WOT; distance from posterior ocelli to vertex crest slightly greater than WOT; anterior ocellus slightly above a line connecting eye tops. Pronotum unusually short (Fig. 51), with smooth contours, rather rounded anteriorly and laterally, distinctly depressed at the

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[3] I have studied the type of this species, but it is somewhat greasy and the pronotum is missing. I therefore prefer to base my description on a specimen compared with the type.

extreme posterior margin so that there is a considerable constriction between the pro- and mesonota; surface of pronotum polished, with strong, well spaced punctures. Mesoscutum polished, with sparse, strong punctures; notauli broad and rather shallow behind, obsolescent in front; scutellar disc polished, with a few punctures. Propodeal disc 1.15 X as wide as long; lateral, sublateral, posterior, and median carinae all strong; disc with a few short longitudinal carinae arising from the base and a few small transverse striae arising from the median carina, but the greater part of the disc smooth and strongly polished; declivity and side-pieces polished and without noteworthy sculpturing. Mesopleurum punctate except on the small, elongate callus. Fore wing with the discoidal cell well outlined by pigmented lines, discoidal vein actually arising a very short distance up the basal vein; subdiscoidal vein visible as a faint line all the way to the wing margin, first recurrent vein also faintly visible. Abdomen sessile although rather slender basally (Fig. 23). Subgenital plate broadly truncate apically. Genitalia (Fig. 16) with the parameres broad apically; digitus with the ventral lobe strong, hairy, dorsal lobe very slender; inner margin of volsella with a small angular projection; aedoeagus with large apical lobes which are directed slightly ventrad.

Other males examined. — PANAMA: 16, Barro Colorado Isl., Canal Zone, Feb.-Oct. (J. Zetek, C. Rettenmeyer) [USNM, KU, MCZ]; 1, Limon Plantation, Chagres River, 14 July 1918 (sweepings around cornfield, Dietz & Zetek) [USNM].

Variation. — Very little variation in size or color can be noted in this series; LFW varies from 4.0 to 5.6 mm., color of the mandibles from light yellowish brown to almost white. Some variation can be noted in the width of the front (WF about 1.1-1.2 X HE). There are minor variations in the details of the sculpturing of the propodeum, but none of the specimens depart strongly from the condition described for the plesiotype.

10. APENESIA SULCATA new species

Holotype. — ♂, PANAMA: Barro Colorado Island, Canal Zone, 30 March 1955 (Carl Rettenmeyer) [KU].

Description of type. — Length 6.0 mm.; LFW 4.2 mm. Head and thorax shining black; abdomen dark brown, suffused with lighter brown on sides of basal segment and at extreme tip; palpi straw-colored; mandibles straw-colored except teeth rufous; antennae dark brown except tip of scape paler, second segment and to a lesser extent third and fourth also lighter brown; tegulae testaceous; front coxae black, remaining coxae and all trochanters straw-colored; femora all with a broad annulus of brown, straw-colored basally and apically; tibiae and tarsi yellowish-brown; wings subhyaline, veins and stigma dark brown. Mandibles with five well defined teeth, the fourth tooth somewhat smaller than the third and fifth (about as figured for *funebris*, Fig. 25). Clypeus slightly more produced and more narrowly truncate than in other species of this group, sides of the truncate portion rounded (Fig. 41); median carina very high, strongly arched in profile. First four antennal segments in a ratio of about 35:6:38:31, segment three unusually long, slightly swollen apically, nearly 5 X as long as its maximum width; segment eleven 4.3 X as long as thick; pubescence golden, erect, bristling, setulae of segment eleven about as long as thickness of segment. Front polished, non-alutaceous, punctures small, separated by from 1.5-3 X their own diameters; vertex, temples, and underside of head with punctures very small and widely separated. Head longer than wide, WH .92 X WH; inner orbits converging below, WF .54 X WH, .95 X HE. Eyes rather long, vertex rounded off a distance above eye tops equal to about .6 X HE; ocelli in a very compact triangle far from eyes and well removed from vertex crest; OOL 1.4 X WOT; DAO .18 X WF. Pronotal disc of moderate length, its sides converging evenly toward the front, the disc crossed by a sharply defined narrow groove just before the posterior margin; disc polished, sparsely punctate, without rugae. Mesoscutum polished, very sparsely punctate, notauli strong, diverging anteriorly; scutellar disc polished and impunctate. Propodeal disc as long as wide, with strong and complete lateral, sublateral, median, and posterior carinae; disc with a pair of basal carinae paralleling the median carina for a short distance, otherwise with rather uniform transverse striations; posterior slope and side-pieces with weak sculpturing. Mesopleurum polished, rather weakly punctate, callus without punctures. Fore wing with the discoidal cell very weakly outlined by pigmented lines. Subgenital plate weakly emarginate apically. Genitalia with aedoeagus as described and figured for *columbana* except the apical lobes slightly smaller and more truncate; lateral elements (Fig. 17) similar to *columbana*, but the parameres more acute and with two very large apical setae, the dorsal arm of the digitus longer and thicker, and the volsella without an angular projection on the inner margin.

Remarks. — This species is known only from the type.

11. Apenesia striatula new species

Holotype. — ♂, BRAZIL: Santarem (no further data) [US NM, No. 66009].

Description of type. — Length 8.5 mm.; LFW 6 mm. Body shining, head and thorax black, abdomen dark reddish brown; palpi light brown; mandibles straw-colored except black at extreme base, the teeth rufous; antennae black, with a faint bluish cast, except second segment and tip of first dark ferruginous; tegulae brown; legs wholly dark brown except tarsi medium brown; wings subhyaline except apical two-thirds of fore wing tinged with brownish, most particularly in and below the radial cell. Mandibles with four large teeth, the true fourth tooth reduced to a small denticle at the base of the incision between the third and fifth teeth (as figured for *columbana*, Fig. 24). Clypeus broadly truncate apically, sides of the truncate portion subangular (Fig. 40); median carina very high, arched in profile, abruptly declivous apically; margin of the clypeus, as seen from below, in the form of a broad triangle, the top of the triangle formed by the median ridge. First four antennal segments in a ratio of about 25:4:18:17, segment three 3.3 X as long as thick, segment eleven 5 X as long as thick; pubescence erect and bristling, longest setulae of segment eleven longer than thickness of segment. Front polished, non-alutaceous, punctures strong, separated from one another by from 1 to 2 X their own diameters; vertex, temples, and underside of head with punctures weaker and more widely spaced. Head longer than wide, WH .95 X LH; inner orbits subparallel below, front about as wide at middle of eyes as below, WF .57 X WH, subequal to HE. Eyes somewhat bulging laterally; vertex rounded off above eye tops a distance equal to about .6 X HE. Ocelli slightly enlarged, DAO about .20 X WF, in a very compact triangle, separated by less than their own maximum diameters; front ocellus well below a line drawn between eye tops, posterior ocelli removed from vertex crest by a distance slightly greater than WOT; WOT and OOL subequal. Pronotal disc moderately long (Fig. 52), anteriorly with a series of fine transverse striae, posteriorly, a short distance before the hind margin, with a strong transverse, round-topped ridge followed by a shallow groove. Mesoscutum polished and with strong, well-spaced punctures; notauli strong on anterior .8, absent behind; scutellar disc sparsely punctate. Propodeal disc 1.05 X as wide as long, with strong lateral, sublateral, posterior, and median carinae; basal half of disc with a pair of strong longitudinal carinae paralleling the median carina and connected with it by some strong ridges; greater part of disc transversely striate, the striations obsolescent on the posterior fourth; posterior slope and side pieces strongly polished, with only a small amount of sculpturing. Mesopleurum with many small punctures except the rather large callus without punctures. Fore wing with the subdiscoidal vein strong, beyond the discoidal cell weaker but reaching wing margin as a faint line; discoidal vein moderately strong, first recurrent vein and vein margining outer side of discoidal cell weakly pigmented. Abdomen sessile although slender basally (Fig. 22). Subgenital plate rounded apically. Genitalia (Fig. 18) much like those of *columbana*, but the parameres much more acute apically, the ventral arm of the digitus very short, and the apical lobes of the aedoeagus apparently wholly wanting, so that the aedoeagus terminates in two slender processes (it is possible that the aedoeagal lobes are broken off, though there is no evidence of a tear).

Paratype. — BRAZIL: 1 ♂ same data as type [USNM].

Variation. — The paratype is slightly smaller, measuring about 7 mm., LFW 5.3 mm. This specimen has the clypeus slightly longer and more narrowly truncate, the front slightly more sparsely punctate, the antennae dark brown rather than black. There is, however, close agreement with the type in head measurements and in the structure of the pronotum; the parameres are also similarly shaped.

12. Apenesia funebris new species

Holotype. — ♂, BRAZIL: Rio de Janeiro, Nov. (no further data) [USNM, No. 66010].

Description of type. — Length 8.4 mm.; LFW 5.8 mm. Body shining, head and thorax black, abdomen dark reddish brown except sides of first tergite and apical half of last tergite yellowish brown; palpi brown; mandibles piceous; antennae wholly dark brown; tegulae dark brown; legs wholly dark brown except front and middle tarsi medium brown; wings uniformly and very lightly tinged with brownish. Mandibles with five strong teeth (Fig. 25). Clypeus broadly truncate apically, actually very weakly concave; median ridge forming a strong tooth subapically (general shape much as in *columbana*, Fig. 93, but apical margin much less distinctly triangularly flattened). First four antennal segments in a ratio of about 25:5:18:16, segment three 2.8 X as long as its maximum width, segment eleven 3.6 X as long as thick; pubescence erect, bristling, brown, setulae of segment eleven about half as long as width of segment. Front strongly polished, non-alutaceous, punctures small, separated from one another by from 1.5 to 3 X their own diameters; vertex and temples with weaker and more widely spaced punctures. Head about as long as wide; inner orbits subparallel below, WF .57 X WH, 1.12 X HE. Vertex very broadly rounded off a distance above the eye tops equal to about two-thirds X HE. Ocelli not notably enlarged, DAO .17 X WF; front ocellus slightly above a line drawn between eye tops, distance from posterior ocelli to vertex crest subequal to WOT; OOL 1.25 X WOT. Pronotum of moderate length (Fig. 53), with smooth contours and without ridges or depressions; disc shining, with strong punctures which are separated by somewhat more than their own diameters. Mesoscutum strongly polished, sparsely punctate, notauli very deep, but not quite attaining anterior or posterior margins; scutellar disc impunctate in the center. Propodeal disc 1.2 X as wide as long; lateral, posterior, and median carinae strong; sublateral carinae absent; basal triangular area with strong, somewhat radiating ridges, disc otherwise smooth and strongly polished; declivity and side pieces strongly polished, obscurely punctate. Mesopleurum strongly polished, with strong punctures except along posterior margin. Venation of fore wing as described for *striatula*. Subgenital plate broadly, weakly emarginate apically. Genitalia with the aedoeagus shaped much as in *columbana* except the apical lobes more complex; parameres (Fig. 20) slender and without an angulation on the outer side; ventral arms of digiti large, strongly setose; inner margin of volsella with a finger-like accessory process.

Paratype. — BRAZIL: 1 ♂, Nova Teutonia, Santa Catarina, 7 April 1937 (F. Plaumann) [BMNH].

Variation. — In the paratype, LFW measures 6.0 mm., WF 1.10 X HE, OOL 1.35 X WOT. The resemblance to the type is very close in every respect.

13. APENESIA FLAMMICORNIS new species

Holotype. — ♂, BOLIVIA: Santa Cruz (J. Steinbach) (no further data) [MCZ, No. 30434].

Description of type. — Length 8 mm.; LFW 5.1 mm. Body shining black except basal two abdominal tergites weakly margined with dark reddish brown; palpi brown; mandibles straw-colored except rufous apically; scape black, flagellum bright rufo-castaneous; tegulae black; coxae black, legs otherwise dark brown except joints and tarsi light brown; wings lightly tinged with brownish, veins and stigma brown. Mandibles as described and figured for *columbana* (Fig. 24), fourth tooth minute and barely noticeable. Clypeus broadly truncate apically, sides of the truncation rounded; margin linear as seen from below, not triangular as in *columbana;* median ridge rather low, subdentate just before apex. First four antennal segments in a ratio of about 21:4:13:12, segment three 2.1 X as long as its maximum width, segment eleven 2.7 X as long as wide; pubescence dense, erect, golden, setulae only about a third as long as width of segments bearing them, flagellum also with a very few hairs which extend slightly above the pubescence. Front polished, non-alutaceous, with moderately strong punctures which are separated by about their own diameters except more widely spaced above and below. Head about as wide as high; inner orbits strongly convergent below, WF .54 X WH, 1.07 X HE. Vertex very broadly rounded off far above eye tops, distance from eye tops to vertex crest equal to about two-thirds X HE. Ocelli not notably enlarged, DAO .19 X WF; OOL 1.25 X WOT. Pronotum considerably longer than in *columbana,* about as in *funebris* (Fig. 53), with smooth contours, not depressed at or near posterior margin; disc polished and with strong punctures. Mesoscutum strongly polished and with only a few punctures; notauli very strongly impressed, not quite reaching the anterior or posterior margins; scutellar disc impunctate in the center. Propodeum very short, disc 1.35 X as broad as long; lateral and posterior carinae fairly strong, median carina obsolescent behind; disc with a number of short, basal longitudinal carinae and with a few short transverse carinae emanating from the median carina, otherwise smooth and polished; declivity and side pieces polished, with a few weak punctures. Mesopleurum with strong punctures except callus convex, impunctate. Fore wing with the discoidal cell very weakly outlined by pigmented lines. Subgenital plate subtruncate apically. Genitalia as shown in Figure 19, differing from those of *funebris* only in having the parameres slightly longer and more strongly bent mesad apically.

Paratype.— BOLIVIA: 1 ♂, Buenavista, near Santa Cruz, 1928 (J. Steinbach) [MCZ].

Variation.— The paratype is very slightly smaller, the fore wing measuring 4.8 mm.; OOL is only 1.15 X WOT. Otherwise there is close agreement with the type in most details. The paratype lacks antennae and all of the abdomen beyond segment two.

14. Apenesia pallidicornis new species

Holotype. — ♂, BRAZIL: Santarem (no further data) [CM].

Description of type. — Length 6.2 mm.; LFW 4.2 mm. Head and thorax black, abdomen dark brown except suffused with lighter brown on sides of basal segment and at extreme tip; palpi straw-colored; mandibles straw-colored except black at extreme base, rufous at apex; antennae light castaneous except scape infuscated on outer side and apical segments of flagellum somewhat infuscated; tegulae testaceous; front coxae black, legs otherwise straw-colored; wings subhyaline, veins and stigma dark brown. Mandibles with five teeth (as figured for *funebris,* Fig. 25). Clypeus broadly truncate apically, sides of truncation rounded; median ridge moderately high, abruptly declivous subapically, forming a very weak median tooth on the margin; margin linear as seen from below, not triangular. First four antennal segments in a ratio of about 18:4:13:12, segment three 2.8 X as long as wide, segment eleven 3.8 X as long as wide; pubescence pale, erect, longest setulae of segment eleven nearly as long as width of segment. Front polished, non-alutaceous, punctures well-defined though rather small, separated for the most part by more than their own diameters. Head about as wide as high; inner orbits strongly convergent below, WF .50 X WH, .87 X HE. Vertex broadly rounded off a short distance above eye tops, distance from eye tops to vertex crest equal to about half HE. Ocelli of moderate size, DAO .21 X WF; anterior ocellus on a line drawn between eye tops; OOL 1.10 X WOT. Pronotum rather long, without depressions or ridges, smooth, polished, punctures rather small and well spaced. Mesoscutum polished, nearly impunctate, notauli very strong, not quite reaching anterior or posterior margins; center of scutellar disc impunctate. Propodeal disc 1.15 X as wide as long; lateral, sublateral, median, and posterior carinae all strong and complete; disc with a basal triangle filled with longitudinal carinae, smooth and polished along sides of triangle, then transversely striate along the sides and posteriorly. Mesopleurum polished, largely impunctate posteriorly and on the large, convex callus. Fore wing with discoidal cell only very faintly indicated by pigmented lines. Subgenital plate broadly truncate. Genitalia (Fig. 21) nearly identical to those of *flammicornis,* differing chiefly in having a more prominently projecting lobe midway along the inner margin of the parameres.

Remarks. — This species is known only from the type.

15. Apenesia photophila (Ogloblin) new combination

Pristocera photophila Ogloblin, 1930, Rev. Soc. Ent. Argentina, 3: 20-23, Figs. 14-22. [Type: ♂, ARGENTINA: Loreto, Misiones, March 1928 (at light, A. Ogloblin) (location not known to writer); paratype: ♂, same data as type (MCZ)].

Description of topotypic paratype.—Length 9 mm.; LFW 6.5 mm. Head and thorax shining black; abdomen rufo-castaneous except first tergite black at base and center, second tergite with small black lateral spots, and apical 2.5 tergites more or less infuscated; mandibles straw-colored, the teeth dark; scape black, flagellum rufo-castaneous, weakly infuscated apically; tegulae dark brown; coxae black, femora dark brown except tips paler, tibiae medium brown except paler apically, tarsi light yellowish brown; wings hyaline, veins and stigma brown. Mandibles with four strong teeth in an oblique series, no evidence of a small tooth between basal two teeth. Clypeus broadly truncate, sides of truncation rounded; median carina strong, arched in profile. First four antennal segments in a ratio of about 23:5:17:17, segment three 2.2 X as long as thick, segment eleven about 4 X as long as thick; pubescence dense, suberect, setulae of segment eleven about half as long as width of segment. Front polished, non-alutaceous, punctures very strong, separated by about or slightly less than their own diameters, more sparse medially and above. Eyes large, bulging from sides of head; head wider than high, WH 1.08 X LH; front narrow, WF .55 X WH, 1.06 X HE. Ocelli very large, ocellar triangle distinctly elevated; DAO .28 X WF; OOL .54 X WOT, only 1.5 X diameter of a lateral ocellus. Vertex broadly rounded off a distance above eye tops equal to slightly more than half HE; an imaginary line drawn between eye tops touching upper margin of anterior ocellus. Pronotum shaped about as in *funebris* (Fig. 53), with only a faint indication of a transverse depression; surface polished, with strong punctures which tend to be smaller and more crowded anteriorly. Mesoscutum polished, sparsely punctate, notauli very deeply impressed; scutellar disc covered with small punctures. Propodeal disc measuring about as wide as its median length, with complete lateral and posterior carinae, but sublaterals absent and median carina indistinct, represented mostly by a very weak elevation crossed by some weak striae, on the posterior fifth entirely absent; disc with a few short basal carinae, but otherwise smooth and strongly polished; declivity and side pieces also smooth and polished. Mesopleurum strongly polished, rather weakly punctate. Fore wing with the discoidal and subdiscoidal veins weakly pigmented, the latter weakly continuous to near wing margin, discoidal cell weakly closed off apically. Subgenital plate slightly emarginate. Genitalia with the parameres almost exactly as figured for *pallidicornis* (Fig. 21), the ventral arm of the digitus broader basally than in that species, subtriangular; inner margin of volsella with a finger-like lobe, as in the preceding three species; aedoeagus much as figured for *flammicornis* except the apical lobes produced laterally rather than mesally (see Ogloblin's fig. 22).

Remarks. — This is a large and striking species. I am much indebted to Dr. Ogloblin for depositing a paratype at the MCZ. The species is closely related to *pallidicornis* and *flammicornis*, but the ocelli, which are very slightly enlarged in those two species, are here enormously enlarged, as in some species of *Pseudisobrachium*.

Exilis species-group

To this group belong four minute species all occurring in southern United States, three of them in the Southwest. All have narrow heads, five-toothed mandibles, a clypeal margin which is weakly to strongly obtusely angulate, and an unmargined propodeal disc. Three of the species have the head and thorax alutaceous and barely punctate, the ocellar triangle broad, the pronotum short, and several other features in common. The fourth species, *pima*, differs in many features from the other three and may represent a link with the preceding two species-groups. Species such as *exilis* are remarkably suggestive of the genus *Pseudisobrachium* in their body form and alutaceous integument, and some of them are nocturnal like many species of that genus. The resemblances may be the result of convergence, as the genitalia are quite different, and there are important differences in the clypeus, eyes, antennae, and occipital carina. See Table IV and Plates 3 and 4 for summary and illustrations of some of the characters of members of this group.

TABLE IV. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF EXILIS, DISSOMPHALOIDES, AND LAEVIGATA GROUPS

Species	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	DAO/WF	Ant. 11 L/W	No. teeth mandibles
16. pima	1.9	0.90	1.35	1.35	.18	2.0	5
17. exilis	1.8	0.89	1.00	0.85	.22	2.5	5
18. martini	2.2	0.87	1.00	1.00	.20	2.5	5
19. cochise	1.8	0.94	1.20	1.15	.16	2.2	5
20. dissomphaloides	2.2	0.98	1.20	0.95	.21	2.0	3
21. denticulata	1.8	1.03	1.20	1.20	.18	1.5	4
22. pallidula	2.1	0.90	1.17	1.25	.21	2.2	5
23. crenulata	2.4	0.97	0.90	1.27	.20	3.0	5
24. laevigata	2.9	1.07	1.30	1.12	.17	1.9	5

16. Apenesia pima new species

Holotype. — ♂ ARIZONA: Tucson, 26 Aug. 1939 (R. H. Crandall) [MCZ, No. 30436].

Description of type. — Length 2.3 mm.; LFW 1.9 mm. Body wholly rich castaneous, shining, head somewhat darker than thorax and abdomen; palpi straw-colored; mandibles dark at base, apical two-thirds yellowish brown; antennae yellowish brown except scape and apical few flagellar segments weakly infuscated; tegulae testaceous; front coxae dark castaneous, legs otherwise light brown except paler at the joints and the front tibiae and all the tarsi almost straw-colored; wings hyaline, with pale setulae, stigma light brown, veins almost colorless. Mandibles with five teeth, fourth tooth smaller than the others (Fig. 31). Apical margin of clypeus convex, actually obtusely subangulate (Fig. 35), median ridge strong, in profile strongly arched, rather abruptly declivous to the margin. First four antennal segments in a ratio of about 14:5:6:6, segment three and segment eleven each about twice as long as thick; pubescence coarse, semi-erect, longest setulae of segment eleven about two-thirds as long as width of segment; erect setae sparse, not standing above the pubescence. Front strongly polished, non-alutaceous, punctures small but well-defined, separated by 3-5 X their own diameters. WH .90 X LH; inner orbits converging below, WF .62 X WH, 1.35 X HE; vertex extended far above eye tops, distance from eye tops to vertex crest subequal to eye height, top of vertex nearly straight across. DAO .18 X WF; front ocellus far above a line drawn between tops of eyes; hind ocelli removed from occipital carina by much more than their own diameters; front angle of ocellar triangle much less than a right angle; OOL 1.35 X WOT, OOL subequal to HE. Pronotum of moderate length (Fig. 54), disc nearly flat, polished and with small but distinct punctures. Mesoscutum rather short, with strong, rather wide notauli which diverge strongly toward the front; surface of scutum and scutellum strongly polished, weakly punctate; groove at base of scutellum gently curved, moderately wide. Propodeum about 1.2 X as long as wide, its dorsal surface somewhat wider than long, but difficult to measure since the disc is not margined behind, but slopes evenly into the declivity; base with several short, irregular longitudinal carinae, the median carina somewhat stronger than the others but extending for only half the length of the disc; posterior part of disc polished, with a few punctures; declivity with weak sculpturing; lateral carinae distinct. Mesopleurum strongly polished, weakly punctate; callus convex, subtended by a large pit. Fore wing with transverse median vein weakly arched, discoidal vein completely absent; basal vein meeting subcosta relatively close to base of stigma. Abdomen slender, sessile (Fig. 36). Subgenital plate shallowly emarginate apically, in general similar to that of *cochise* (Fig. 32). Genitalia (Fig. 26) with the parameres expanded apically on the mesal margin; inner margin of volsella slightly produced just below the cuspis; aedoeagus closely consolidated, with a pair of pointed apical lobes, the apex lacking the pectinations of the other members of this species-group.

Remarks. — The genitalia of this species bear considerable resemblance to those of *columbana*, while the shape of the pronotal disc suggests the *pilicornis* group. It is possible that *pima* represents something of a link between these groups and the more specialized members of the *exilis* group.

17. APENESIA EXILIS new species

Holotype. — ♂, ARIZONA: [Pinal Co., Boyce Thompson Southwestern Arboretum, 4 mi. W. of] Superior, 3 Oct. 1949 (light trap, B. W. Benson) [INHS].

Description of type. — Length 2.2 mm.; LFW 1.8 mm. Head dark brown, thorax and abdomen medium brown; palpi straw-colored; mandibles light brown; antennae wholly and uniformly light brown; tegulae testaceous; legs light brown except tibiae and tarsi straw-colored; wings hyaline, with pale setulae, stigma light brown, veins nearly colorless. Mandibles short, much broadened apically, with five sharp teeth (Fig. 30). Clypeus obtusely angulate apically except medially with a sharp tooth which is formed by an extension of the median carina, the latter very strong, subangulate in profile (Fig. 34). First four antennal segments in a ratio of about 30:9:14:14, segment three 2.1 X as long as thick, segment eleven 2.5 X as long as thick; pubescence coarse, semi-erect, longest setulae of segment eleven slightly more than half as long as width of segment, erect setae sparse, standing somewhat above the pubescence. Front moderately shining, uniformly alutaceous, punctures minute and hardly noticeable. Head longer than wide, WH .89 X LH; inner orbits weakly convergent below, WF .55 X WH, subequal to HE. Ocelli slightly enlarged, DAO .22 X WF; ocelli in a broad triangle, front angle slightly greater than a right angle, OOL .85 X WOT; anterior ocellus far above a line drawn between eye tops, posterior ocelli removed from occipital carina by less than their diameters. Vertex produced above eye tops a distance equal to about .8 X HE. Pronotum short (Fig. 55) sloping up strongly from the collar, without carinae or grooves, somewhat shining although alutaceous, obscurely punctate. Mesonotum also alutaceous, moderately shining, punctures scarcely noticeable; notauli complete although very weakly impressed; parapsidal furrows weak except on posterior .2 of scutum. Propodeum about 1.25 X as long as wide, its dorsal surface about as long as wide although not at all margined behind and therefore difficult to measure accurately; lateral carinae developed, but all other carinae, including median carina, absent; spiracles circular, relatively large, directed laterad. Mesopleurum shining, weakly alutaceous, callus not well differentiated. Middle tibiae not spinose; claws weakly dentate. Fore wing with the transverse median vein arched, the discoidal vein arising well down on it although unpigmented and barely visible; basal vein reaching subcosta far basad of stigma. Abdomen fusiform, depressed, sessile. Subgenital plate rather strongly, arcuately emarginate (Fig. 33). Genitalia (Fig. 28) with the parameres not strongly lobed on the mesal margin, strongly setose; volsellae with the cuspis very slender, the ventral arm of the digitus small; aedoeagus very large, closely consolidated, with some small though strong pectinations at the apex mesally.

Paratypes. — ARIZONA: 4 ♂♂, same data as type except three of them 11 July-5 Aug. 1948 (H. K. Gloyd) [MCZ, INHS, USNM]. CALIFORNIA: 1 ♂, Bard, Imperial Co., 1959 (H. H. Blakemore) [CDAS].

Variation. — The paratypes vary slightly in size (LFW 1.6-2.0 mm.). Some members of the Arizona series are paler than the type, having the entire body light brown, while the California specimen is wholly dark brown, the head nearly black, although with the legs and antennae testaceous. In the California specimen WF is subequal to HE, OOL .82 X WOT. In the Arizona paratypes, WF varies from .90 to 1.0 X HE, OOL from .70 to .85 X WOT.

Remarks. — This species bears a striking similarity to *Pseudisobrachium obscurum* Evans, a sympatric and also a nocturnal species.

18. APENESIA MARTINI new species

Holotype. — ♂, FLORIDA: Manatee Co., Oneco, 21 March 1955 (John C. Martin) [CNC].

Description of type. — Length 2.6 mm.; LFW 2.2 mm. Body dark castaneous, head nearly black; palpi straw-colored; mandibles dark basally, suffused with reddish brown apically; antennae uniformly dark brown except segment two light brown and basal segment light brown basally and apically; tegulae brown; coxae and femora medium brown, legs otherwise light brown; wings hyaline, stigma brown, veins almost colorless. Mandibles with five sharp teeth, as in *exilis* (Fig. 30). Clypeus broadly rounded, weakly obtusely angulate medially, tectiform, the median elevation weakly arched in profile. First four antennal segments in a ratio of about 18:5:8:8, segment three slightly over twice as long as thick, segment eleven 2.5 X as long as thick; pubescence pale, coarse, semi-erect, longest setulae of segment eleven nearly as long as width of segment; fully erect setae numerous, but not extending above the pubescence. Front moderately shining, uniformly alutaceous, punctures so small and sparse as to be scarcely noticeable. Head much longer than wide, WH .87 X LH; front narrow, inner orbits convergent below, WF .54 X WH, subequal to HE. Ocelli enlarged only slightly, DAO .20 X WF; ocellar triangle broad, front angle slightly greater than a right angle; OOL about equal to WOT; anterior ocellus far above eye tops, posterior ocelli separated from occipital carina by less than their own diameters. Vertex produced above eye tops a distance nearly equal to eye height. Pronotum short, though with a narrow anterior median lobe, disc with smooth contours except for a very shallow transverse depression toward the front margin. Surface of pronotum, like that of mesonotum, alutaceous, somewhat shining, obscurely punctate. Notauli very weakly indicated on the posterior half; groove at base of scutellum unusually slender, linear, deflected backward at sides. Propodeum elongate, about 1.5 X as long as broad, dorsal surface about 1.2 X as long as broad; median carina weakly indicated on basal half, disc otherwise polished, weakly alutaceous; declivity weakly transversely striate, the upper striae tending to margin the disc behind weakly; lateral carinae present though weak; spiracles circular, directed laterad, relatively large. Thorax, in lateral view, seen to be strongly depressed; mesopleurum slender, almost horizontal, its features as in the preceding species. Fore wing with discoidal vein indicated as a weak streak arising well down on transverse median vein, the latter strongly arched; basal vein reaching subcosta far basad of stigma. Subgenital plate broadly, arcuately emarginate, about as figured for *exilis* (Fig. 33). Genitalia (Fig. 29) differing from those of *exilis* only in minor details, the ventral arms of the digiti being broader than in that species, the aedoeagus somewhat less robust and with the apical pectinations much weaker.

Remarks. — This species is named for its collector, the late Dr. John C. Martin, a good friend and a fine young hymenopterist.

19. APENESIA COCHISE new species

Type. — ♂, ARIZONA: Cochise Co., Southwestern Research Station, 5 mi. W. Portal, 5400 feet, 13 Sept. 1959 (on honeydew on *Populus*, H. E. Evans) [MCZ, No. 30438].

Description of type. — Length 2.3 mm.; LFW 1.8 mm. Entire body dark brownish-fuscous; palpi brown; mandibles blackish, teeth rufous; antennae wholly dark brownish-fuscous; tegulae dark brown; legs dark brownish-fuscous except tarsi medium brown; wings hyaline, with dark setulae, stigma brown, veins amber-colored. Mandibles short and broad, with five sharp apical teeth (as in *exilis*, Fig. 30). Clypeus obtusely angulate apically, about as described and figured for *exilis* (Fig. 34); median carina weakly arched in profile. First four antennal segments in a ratio of about 14:5:6:6, segment three twice as long as thick, segment eleven about 2.2 X as long as thick; pubescence pale, semi-erect, longest setulae of segment eleven two-thirds as long as width of segment; erect setae numerous, standing somewhat above the pubescence. Front moderately shining, uniformly and rather strongly alutaceous, punctures minute and scarcely noticeable. Head longer than wide, WH .94 X LH; front of moderate width, WF .60 X WH, 1.20 X HE. Ocelli not enlarged, DAO .16 X WF; front angle of ocellar triangle equal to about a right angle; OOL 1.15 X WOT; anterior ocellus far above a line drawn between eye tops, posterior ocelli removed from occipital carina by a distance about equal to their own diameters. Vertex produced above eye tops a distance nearly equal to HE. Pronotum short, disc with smooth contours, narrow in front and much broadened behind. Pronotal disc like that of mesonotum, moderately shining, alutaceous, obscurely punctate. Notauli linear but strongly impressed, diverging in front, running the full length of the mesoscutum. Propodeum 1.25 X as long as wide, its dorsal surface about as wide as long; median carina distinct for about .6 the length of the dorsal surface, paralleled by several rather weak and irregular carinae; lateral carinae strong; major part of disc polished, smooth, weakly alutaceous; declivity transversely striate, the uppermost stria tending to margin the disc behind rather weakly; spiracles circular, directed laterad. Thorax in lateral view rather depressed; mesopleurum elongate, somewhat shining, weakly alutaceous, with a pit in the center but no well defined callus. Fore wing with the transverse median vein strongly arched, the discoidal vein appearing as a very faint streak arising well down on it; basal vein reaching subcosta far basad of stigma, the latter unusually large. Subgenital plate (Fig. 32) shallowly emarginate, the plate itself longer than in *exilis*. Genitalia (Fig. 27) with both parameres and aedoeagus much more slender than in *exilis*, though basically rather similar; apical lobes of aedoeagus directed ventrad, dorsally with some strong pectinations.

Remarks. — This species is very similar to *exilis* in most respects, but differs in having the notauli strong, the propodeum with several delicate median carinae, and the ocelli small and more distant from the eyes.

DISSOMPHALOIDES SPECIES-GROUP

Eyes wholly covered with short hairs; mandibles with three or four teeth; clypeus large, tridentate, shaped much as in *Dissomphalus;* inner orbits weakly convergent below; pronotum with smooth contours, ecarinate; propodeum with a median carina but with no evidence of a transverse carina behind; middle tibiae not spinose; abdomen sessile, rather short and broad; parameres simple, not lobed; digiti simple, not divided or setose; aedoeagus broad, with a pair of slender ventral rami and a pair of very large dorsal apical lobes which are fringed on their inner margins.

The two species assigned here are remarkably *Dissomphalus*-like, but lack the characteristic tergal pits of that genus and also lack a transverse carina on the propodeum. They may well represent a link between the *exilis*-group of *Apenesia* and the genus *Dissomphalus*. The range of the group extends from Arizona to eastern Mexico. See Table IV and Plate 4 for summary and illustrations of some of the characters of this group.

20. APENESIA DISSOMPHALOIDES new species

Holotype. — ♂, ARIZONA: Pinal Co., Superior, 17-24 May 1946 (light trap, H. K. Gloyd) [INHS].

Description of type.—Length about 2.5 mm.; LFW 2.2 mm. Head and thorax dark castaneous, abdomen medium brown, shining; palpi straw-colored; mandibles light brown; antennae uniformly very light brown; legs light brown, like the antennae, except front coxae dark brown; wings hyaline, veins and stigma brownish. Mandibles slender, with three teeth. Clypeus large for the genus, especially laterally, medially with three small, rounded teeth (Fig. 42); median carina well defined but low, not arched in profile. First four antennal segments in a ratio of about 37:11:15:15; segment three and segment eleven each about twice as long as thick; pubescence rather coarse, setulae of segment eleven about .6 as long as width of segment; erect setae fairly numerous, extending well above the pubescence. Front uniformly alutaceous, moderately shining, punctures small, inconspicuous; eyes covered with sparse, short hairs; occipital carina rather weak dorsally. Head very slightly higher than wide, WH .98 X LH; front narrow, inner orbits convergent below, WF .58 X WH, 1.20 X HE; vertex broadly rounded off far above eye tops, distance from eye tops to vertex crest subequal to eye height. DAO .21 X WF; front angle of ocellar triangle approximately a right angle; OOL .95 X WOT. Thoracic dorsum wholly alutaceous like the head, moderately shining, obscurely punctate; pronotum rather short, with smooth contours; notauli distinct on anterior .8 of mesoscutum; basal groove of scutellum slender. Propodeum 1.3 X as long as wide; median carina well defined, basal triangle reticulate; posterior part of disc as well as declivity smooth and polished; transverse carina completely lacking. Mesopleurum wholly alutaceous although somewhat shining, callus not strongly differentiated. Fore wing with basal vein erect, reaching subcosta far basad of stigma; transvere median vein erect, nearly straight; discoidal vein nearly interstitial with median vein, weakly pigmented for a distance about equal to basal vein. Subgenital plate short, truncate apically. Genitalia as shown in Figure 37; parameres strongly curved mesad, slender and not lobed; digiti simple, non-setose, rather large, strongly curved; aedoeagus broad, with large apical lobes which are prominently fringed on their inner margins, also with a pair of elongate, unbranched ventral rami.

21. APENESIA DENTICULATA new name

Propristocera tridentata Evans, 1958, Proc. Ent. Soc. Wash., 59: 292-293. [Type: ♂, MEXICO: VERACRUZ: Cordoba, 21 May (A. Fenyes) (USNM, no. 64115)]. Preoccupied by *Apenesia tridentata* Kieffer, 1910, Ergeb. Zentr.-Afr. Exp., v. 3, fasc. 2, p. 16.

Description of type. — Length about 2 mm.; LFW 1.8 mm. Body uniformly rich castaneous; mandibles and side of clypeus light brown; first two abdominal segments yellowish brown, remainder of antennae dark brown; legs wholly light yellowish brown except front coxae dark brown; wings hyaline, veins and stigma brown. Mandibles broader than in the preceding species, with four apical teeth. Clypeus with three rather sharp teeth medially, median carina strong, in profile almost angulate just before the apex. First four antennal segments in a ratio of about 17:6:4:5, segment three and eleven each about 1.5 X as long as thick; pubescence coarse, pale, semi-erect, setulae of segment eleven .8 as long as width of segment; erect setae numerous, standing well above pubescence. Front alutaceous although rather strongly shining, punctures shallow and inconspicuous; eyes short-haired. Head broader than high, WH 1.03 X LH; inner orbits weakly convergent below, WF .57 X WH, 1.20 X HE; distance from eye tops to vertex crest equal to about two-thirds HE. Ocelli not notably enlarged, DAO .18 X WF; front angle of ocellar triangle slightly less than a right angle; OOL 1.2 X WOT. Thoracic dorsum alutaceous although shining, punctures weak; pronotum of moderate length, with smooth contours; notauli distinct on anterior two-thirds of mesoscutum. Propodeum 1.25 X as long as wide, its features much as in the preceding species. Mesopleurum weakly alutaceous, shining, the callus not strongly differentiated. Fore wing as in *dissomphaloides* except that the discoidal vein is pigmented for a distance distinctly greater than length of basal vein. Subgenital plate weakly arcuately emarginate apically. Genitalia resembling those of *dissomphaloides* in most respects, but the digiti not quite as strong and the ventral rami of the aedoeagus distinctly branched (see fig. 5 in Evans, 1958).

Other males examined. — MEXICO: VERACRUZ: 2, Cordoba, 3 May 1906 and 11 May 1908 (A. Fenyes) [USNM, MCZ].

Variation. — One of these specimens approximates the type in size, while the other is smaller (LFW 1.6 mm). This very small specimen has the head and thorax more weakly alutaceous than in the other two, but all three specimens are alike in color and show only slight variation in structure and standard measurements.

LAEVIGATA SPECIES-GROUP

To this group belong three minute, slender, shining species, all possessing a relatively long abdominal petiole. In all three the propodeal disc is margined behind only on the sides and the ocelli are slightly enlarged. In other respects the group seems to stand close to *exilis* and its allies, although there is little resemblance between the genitalia of the two groups. The three species of this group are each known from a single specimen; one is from Arizona, one from Mexico, and one from Brazil. Some of the characters of the species of this group are illustrated on Plate 4 and tabulated in Table IV.

22. APENESIA PALLIDULA new species

Holotype.— ♂, ARIZONA: Cochise Co., Chiricahua Mts., 3 July 1947 (L. D. Beamer) [KU].

Description of type.—Length 2.5 mm.; LFW 2.1 mm. Head and thorax rich castaneous, shining; abdomen slightly paler than head and thorax, especially basal segments, also shining; apical half of mandibles yellowish brown; antennae wholly yellowish brown; legs straw-colored, coxae and femora suffused with brownish; wings hyaline, veins and stigma light brown. Mandibles with five small teeth in an oblique series (Fig. 50). Clypeus rounded apically, with a median angulation (Fig. 46); median carina strong, arched in profile. First four antennal segments in a ratio of about 15:5:12:10, segment three about 2.5 X as long as thick, segment eleven about 2.2 X as long as thick; pubescence coarse, suberect, longest setulae of segment eleven about .7 X as long as width of segment. Front polished, nonalutaceous, punctures large although shallow, separated by (on the average) about twice their own diameters. Head much higher than wide, WH .90 X LH; eyes weakly convergent below, WF .60 X WH, 1.17 X HE; vertex broadly rounded, distance from eye tops to vertex crest equal to .8 X HE. Ocelli enlarged slightly, DAO .21 X WF; front angle of ocellar triangle less than a right angle; OOL 1.25 X WOT. Pronotum moderately long, with smooth contours except weakly depressed just before posterior margin; disc shining, obscurely punctate. Mesoscutum polished, punctures small, notauli strong and complete; scutellum polished, disc slightly convex, basal groove slightly expanded and directed backward on each side. Propodeum 1.4 X as long as wide; disc without a transverse carina behind except on extreme sides; lateral carinae strong, median carina strong but not reaching edge of declivity; basal triangle of disc filled with irregular carinae which diverge from the median line; posterior part of disc smooth and shining. Mesopleural callus well differentiated, convex and strongly polished. Claws weakly dentate; middle tibiae not spinose. Fore wing with discoidal and subdiscoidal veins absent. Abdominal petiole moderately long (Fig. 43). Subgenital plate truncate apically. Genitalia (Fig. 38) with the parameres slender, angularly bent mesad; ventral arms of digiti short, exceeded by the conspicuous dorsal arms, both arms weakly setose; aedoeagus with large, rather simple apical lobes.

Remarks. — This striking species is known only from the type.

23. APENESIA CRENULATA (Kieffer) new combination

Propristocera crenulata Kieffer, 1910, Ann. Soc. Ent. France, 78: 289-290. [Type: ♂, BRAZIL: Pará (C. F. Baker) (Pomona College, Claremont, Calif.)]. — Kieffer, 1914, Das Tierreich, 41: 486-487.

Description of type. — Length 3.4 mm.; LFW 2.4 mm. Head black, thorax and abdomen shining dark reddish brown, first abdominal tergite margined with paler brown; mandibles rufo-castaneous; scape brown basally, apical third yellowish brown like the following two segments, antenna medium brown beyond segment three; tegulae and legs testaceous, including all coxae; wings hyaline, setulae dark, veins and stigma brown. Mandibles rather slender, terminating in five teeth (much as figured for *pallidula,* Fig. 50). Clypeus with its sides approaching evenly to an obtusely angulate apex, the midpoint very slightly more acute (Fig. 45); median carina very strongly arched in profile. Antennae elongate, first four segments in a ratio of about 23:6:18:17, segment three about 3 X as long as thick, segment eleven also 3 X as long as thick though slightly shorter and more slender than three; flagellar setulae semi-erect to erect, all of one type, setulae of segment eleven .8 X as long as width of segment. Front shining, non-alutaceous, punctures large, separated by somewhat more than their own diameters; vertex rather weakly punctate, median portion of underside of head almost impunctate. Head slightly higher than wide, WH .97 X LH; eyes convergent below, WF .52 X WH, 0.9 X HE; vertex evenly rounded, distance from eye tops to vertex crest equal to somewhat less than half HE. Ocelli somewhat large in relation to width of front, DAO .20 X WF; front ocellus touching a line drawn between eye tops; ocellar triangle compact, front angle less than a right angle; OOL 1.27 X WOT. Pronotum short, smooth and highly polished, without a transverse carina anteriorly, very weakly depressed before posterior margin; disc with weak, well-separated punctures. Mesonotum wholly polished, non-alutaceous, almost impunctate; notauli very strong, diverging evenly toward the front, absent on anterior .05 and posterior .05 of mesoscutum; basal groove of scutellum narrow and deep. Propodeum 1.4 X as long as wide; lateral carinae strong; median basal area strongly reticulate, almost foveolate, but without a well-defined median carina; remainder of disc weakly and irregularly transversely striate, one of the striae on the edge of the declivity stronger than the others (on the sides, at least) and thus weakly margining the disc behind. Mesopleurum polished, non-alutaceous, callus strongly convex, margined below and in front by a broad, foveolate groove. Claws weakly dentate. Fore wing with discoidal vein only very weakly indicated, interstitial with media; transverse median vein straight, erect. Abdomen with a rather long petiole (about as in Fig. 43). Subgenital plate truncate apically. Genitalia not studied.

Remarks. — This species seems closely related to the preceding despite the great geographic gap between them. It is known only from the type.

24. Apenesia laevigata (Evans) new combination

Propristocera laevigata Evans, 1958, Proc. Ent. Soc. Wash., 59: 293. [Type: ♂, MEXICO: VERACRUZ: Cordoba, 21 May (A. Fenyes) (USNM no. 64114)].

Description of type. — Length 3.4 mm.; LFW 2.9 mm. Body entirely castaneous, shining; mandibles testaceous; basal two antennal segments testaceous, rest of antenna medium brown; legs wholly testaceous; wings subhyaline, veins and stigma brownish. Mandibles with five sharp teeth in an oblique series. Clypeus with a prominent median lobe, the sides oblique, the apex weakly notched (Fig. 47); median carina very strong, weakly arched in profile. First four antennal segments in a ratio of about 20:5:8:8, segment three 1.7 X as long as thick, segment eleven nearly twice as long as thick; pubescence pale, semi-erect, longest setulae of segment eleven .7 as long as width of segment; last three segments with dense, short pubescence on under side. Front convex, strongly polished, punctures minute and well separated. Eyes strongly bulging from sides of head, WH 1.07 X LH; WF .60 X WH, 1.3 X HE. Ocelli of moderate size, DAO .17 X WH; OOL 1.12 X POL. Vertex narrowly rounded off far above eye tops. Pronotum short, sloping evenly, smooth and shining. Mesoscutum strongly polished, weakly punctate; notauli complete but weakened anteriorly and posteriorly; scutellar disc strongly polished, lateral foveae unusually large and deep. Propodeal disc about as long as wide, with the median carina replaced by a rather deep median groove which is weakened behind; lateral carinae strong, transverse carina present only on sides; surface of disc polished except weakly sculptured in basal triangle. Mesopleurum strongly polished, the callus ill-defined. Middle tibiae not spinose; claws simple. Fore wing with the discoidal vein arising far down on transverse median vein, fairly strong, but subdiscoidal vein absent (see fig. 4 in Evans, 1958). Abdomen with a relatively long petiole (Fig. 44). Spiracles of first two tergites relatively large, round. Subgenital plate broadly, weakly rounded apically. Genitalia with the parameres very long and slender, nearly straight, with a small accessory lobe at the base laterally; aedoeagus complex, lateral apical lobes directed strongly ventrad (see fig. 8 in Evans, 1958).

Remarks. — This striking species in known only from the type.

MEXICANA SPECIES-GROUP

To this group are assigned twelve species which together range from southwestern United States and Cuba to Brazil and Peru, with more than half the species occurring in Mexico and Central America. In this group the pronotum has a strong transverse carina in front. The abdomen is sessile, rather broadly so in most species, and the genitalia are characterized by broadly expanded parameres. The middle tibiae are spinose except in *bugabensis,* and this species is also unique in having a strong groove just before the posterior margin of the pronotum. The mandibles show much variation in this group and often provide good specific characters. The clypeus also shows much variation, but it is never broadly and abruptly truncate as in some groups.

This group properly occupies a central position in the genus, some species showing relationships to groups already considered, some to the more specialized groups to follow. For example, the grooved pronotum of *bugabensis* suggests certain species of the *columbana* group, the setose antennae of *peculiaris* the *pilicornis* group. On the other hand, the broad head and short, bidentate clypeus of *inca* strongly suggest the *nitida* group, and it must be admitted that the group as a whole can only be rather arbitrarily distinguished from the one which follows, the *brasiliensis* group. Some of the characters of species of this group are summarized in Table V, and some are illustrated in Plates 5, 6, and 7.

TABLE V. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF MEXICANA GROUP

Species	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	Ant. 11 L/W	Propodeal disc W/L	No. teeth mandibles
25. bugabensis	2.7	0.90	1.00	1.45	3.2	1.00	5
26. chiricahua	2.3	0.97	1.33	1.40	2.4	1.30	5
27. mohave	2.7	1.00	1.20	1.07	2.1	1.50	5
28. malinche	2.6	1.02	1.28	1.10	2.0	1.40	5
29. peculiaris	3.6	0.98	1.10	1.30	2.9	1.30	4
30. pando	2.8	1.00	1.06	1.22	3.0	0.95	4
31. cubensis	3.5	0.95	1.20	1.35	3.9	1.15	4
32. mexicana	3.0	1.04	1.10	1.20	2.4	1.35	4
33. testaceipes	3.6	1.03	0.90	0.95	3.0	1.20	3
34. maya	3.4	1.04	1.08	1.12	2.4	1.25	3
35. neotropica	3.7	1.00	1.00	1.13	2.8	1.03	3
36. inca	3.2	1.06	1.17	1.15	2.3	1.05	3

25. APENESIA BUGABENSIS (Cameron) new combination

Epyris bugabensis Cameron, 1888, Biol. Centr.-Amer., Hymen. I, p. 453, pl. 19, fig. 19. [Type: ♂, PANAMA: Bugaba (G. C. Champion) (BMNH)].

Rhabdepyris (Rhabdepyris) bugabensis Kieffer, 1914, Das Tierreich, 41: 362.

Description of type.—Length 3.8 mm.; LFW 2.7 mm. Head and thorax black; abdomen piceous, segments indistinctly annulated with light brown apically (first tergite more distinctly so), apical segment suffused with light brown in its entirety; palpi and mandibles straw-colored, the latter darkened at extreme base and apex; first two antennal segments and base of third yellowish brown, rest of antenna medium brown; tegulae testaceous; front coxae dark brown, legs otherwise light yellowish brown except femora rather strongly suffused with brown and middle and hind coxae weakly suffused with brown; wings subhyaline, veins and stigma brown. Mandibles with five teeth, the basal two partially fused (Fig. 68). Clypeus with a rounded median lobe, with a very weak median tooth which is formed by the end of the very strong, arching median carina (Fig. 83). First four antennal segments in a ratio of about 24:6:17:15, segment three 2.8 X as long as its maximum width, segment eleven 3.2 X as long as wide; pubescence pale, erect, bristling, longest setulae of segment eleven .7 as long as width of segment; there are no other erect setae which extend above the pubescence. Scape strongly curved, antennal scrobes margined by a strong carina passing transversely to the eye margins and strongly arched for the reception of the scape. Head strongly polished, non-alutaceous; front with strong punctures which are separated by about 2-4 X their own diameters; vertex and temples with small, widely spaced punctures. Head higher than wide, WH .90 X LH; inner orbits converging below, WF .57 X WH, 1.00 X HE. Vertex rather narrowly rounded off a distance above eye tops equal to about two-thirds HE; occipital carina strong, visible at top of vertex when head is viewed from in front. Ocelli rather small, DAO .17 X WF; ocelli in a compact triangle, the front angle less than a right angle; anterior ocellus well above a line drawn between eye tops; OOL 1.45 X WOT. Pronotal disc moderately long, its sides slightly concave as seen from above; collar transversely rugulose; disc with a strong transverse carina at anterior margin and a strong transverse groove slightly before the posterior margin; disc polished, rather weakly punctate. Mesoscutum polished, punctures rather strong though well spaced; notauli strong, diverging anteriorly, not quite reaching posterior margin; scutellar disc polished, impunctate in the center. Propodeal disc elongate, about as wide as long, propodeum as a whole about 1.25 X as long as wide; lateral, sublateral, median, and posterior carinae all strong and complete, the posterior carina with a series of irregular foveae both in front of and behind it; disc with some short longitudinal carinae basally besides the median carina, weakly impressed so as to mark off a basal triangular area, otherwise densely transversely striate; declivity polished, weakly sculptured. Mesopleurum polished, weakly punctate, rather irregularly grooved and pitted. Middle tibiae not spinose. Fore wing with the discoidal cell very weakly outlined by pigmented lines. Abdomen slender basally but without a petiole (Fig. 79). Subgenital plate broadly rounded apically. Genitalia (Fig. 56) with the parameres slender, with a prominent mesal lobe apically; ventral arm of digitus margined with strong setae, smaller than the dorsal lobe; aedoeagus rather slender, with large apical lobes which are compressed and deflected ventrad.[4]

Other males examined. — COSTA RICA: 2, Turrialba, 14-16 June 1949 (K. W. Cooper) [USNM]; 1, LaLola, 29 April 1957 (R. D. Shenefelt) [USNM].

Variation. — The Turrialba specimens are very similar to the type in size, color, and structure. The LaLola specimen is

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[4] The description and figure of the genitalia were drawn from a specimen from Turrialba, Costa Rica, compared with the type and found to resemble it very closely. The genitalia of the type were not extracted.

smaller (LFW 2.2 mm.) and has the front more sparsely punctate. In all three Costa Rican specimens the front is very slightly wider than in the type, WF varying from 1.05-1.10 X HE.

26. APENESIA CHIRICAHUA new species

Holotype. — ♂, ARIZONA: Southwestern Research Station, 5 mi. W. of Portal, Cochise Co., 5400 feet, 23 Aug. 1959 (sweeping grass, H. E. Evans) [MCZ, No. 30439].

Description of type. — Length 3.4 mm.; LFW 2.3 mm. Black, margins of first two abdominal segments suffused with brown; palpi light brown; apical half of mandibles rufous; scape black, flagellum medium brown; tegulae brown; front coxae black, remaining coxae and all femora dark brown, legs otherwise light brown; wings subhyaline, veins and stigma brown. Mandibles with five teeth in an oblique series, third and fourth teeth partially connate (Fig. 69). Clypeus forming an obtuse angle apically (Fig. 84), strongly tectiform, median ridge weakly subangulate in profile. First four antennal segments in a ratio of about 19:6:11:10, segment three 2.5 X as long as thick, segment eleven 2.4 X as long as thick; pubescence light brown, semi-erect, setulae of segment eleven about .4 as long as width of segment; erect setae sparse, slightly surpassing pubescence. Front moderately shining, uniformly and fairly strongly alutaceous; punctures shallow, separated by 2-4 X their own diameters. Eyes with some short, weak hairs (about as in *dissomphaloides*). Head slightly longer than high, WH .97 X LH; inner orbits converging below, WF .60 X WH, 1.33 X HE. Ocelli small, DAO .16 X WF; anterior ocellus well above a line drawn between eye tops; OOL 1.4 X WOT. Distance from eye tops to vertex crest nearly equal to HE; vertex very broad. Pronotum of moderate length, its sides approaching evenly toward the front; disc subfoveolate immediately behind the strong transverse carina; disc alutaceous, with shallow, widely-spaced punctures. Mesonotum also alutaceous, moderately shining, with weak, widely scattered punctures; notauli linear, complete. Propodeal disc about 1.3 X as wide as its median length; median carina complete; basal triangle strong reticulate, disc otherwise alutaceous; lateral carinae strong, sublateral carinae irregular; declivity and side-pieces strongly alutaceous. Mesopleurum alutaceous, obscurely punctate. Middle tibiae with a few spines. Fore wing with transverse median vein sloping, discoidal vein weak, arising a short distance down on it; discoidal cell very weakly outlined. Abdomen sessile (Fig. 80). Subgenital plate weakly emarginate (Fig. 60). Genitalia (Fig. 57) with the parameres rather broad apically; ventral arm of digitus expanded and obliquely subtruncate apically; inner margin of volsella simple; aedoeagus slender, with two pairs of apical lobes, the median pair short, semimembranous, clothed with minute spines.

Paratypes. — ARIZONA: 33 ♂♂, same data as type except dates from 7 to 29 August 1959 (all taken sweeping grass in the same small sandy area along Cave Creek) [MCZ, AMNH, CU, USNM, CAS]; 1 ♂, Grand Canyon, 3 Sept. 1921 [AMNH]. MEXICO: MEXICO: 2 ♂♂, Teotihuacan Pyramids, 5 June 1951, 3 July 1959, 7500 feet (H. E. Evans) [MCZ, CU].

Variation. — The 36 paratypes provide an interesting study in variation. The two specimens from central Mexico resemble the type very closely, but the clypeal carina is low and not angulate in profile and the punctures of the front rather strong; the genitalia are much as figured for the type except that the aedoeagus is slightly more slender. The Grand Canyon specimen also has strong punctures on the front, but the clypeal carina is high, although evenly arched rather than subangulate as in the type; in this specimen the ventral arms of the digiti are somewhat more slender than in the type. The topotypic paratypes vary considerably in size (LFW 2.0-2.9 mm.), and in the smaller specimens the antennae are relatively shorter than in the type (third segment 2.2 X as long as thick, eleventh segment about twice as long as thick). There is some variation in the size of the punctures of the front, and in a few cases they are as large as in the Grand Canyon and the Mexican specimens. The clypeal carina may be angulate, strongly arched, or weakly arched in profile. There is much variation in the OOL/WOT ratio, in some specimens this figure approaching 1.0. The discoidal vein of the fore wing varies from fairly strong to almost absent, but in every case it arises a short distance down on the transverse median vein. I examined the genitalia of seven of the topotypic paratypes and found considerable variation. The parameres in six of these specimens are virtually identical to those of the type (Fig. 57), while the other specimen (Fig. 78) has more slender parameres, approaching the condition in *malinche*. Several specimens have very weak striations along the inner margin of the volsellae (much weaker than in *malinche*) and one specimen appears to have a small knob just at the base of the cuspis. Some slight variation can be noted in the shape of the aedoeagus. One topotypic paratype has the subgenital plate rounded apically, much as in *mohave*.

The amount of variation in this series is disconcerting, and it is to be noted that much of the variation is in the direction of *malinche* and *mohave*. It should be noted that the aedoeagus of those two species is of rather different form, and the volsellae have a series of apical spines (at the base of the cuspis) which are strong in *malinche*, weaker in *mohave*.

27. APENESIA MOHAVE new species

Holotype. — ♂, CALIFORNIA: Pine Flats Camp, Indio, 12 July 1941 (E. L. Todd) [KU].

Description of type. — Length 4 mm.; LFW 2.7 mm. Head and thorax black; abdomen dark brown, suffused with light brown on parts of basal segments; palpi straw-colored; mandibles pale castaneous except black at base and rufous at apex; antennae wholly bright, pale castaneous except apical three segments weakly infuscated; tegulae and narrow posterior rim of pronotum light brown; front coxae dark brown, remaining coxae and all femora medium brown, legs otherwise bright yellowish brown; wings subhyaline, veins and stigma brown. Mandibles exactly as in *chiricahua* (Fig. 69). Clypeus obtusely angulate apically, with a very high, strongly arched carina. First four antennal segments in a ratio of about 23:7:11:11, segment three 1.6 X as long as thick, segment eleven 2.1 X as long as thick; pubescence dense, golden, setulae of segment eleven about .4 as long as width of segment; erect setae sparse, inconspicuous. Front moderately shining, strongly alutaceous, punctures fairly strong, separated by from 1.5 to 3 X their own diameters. Eyes weakly hairy, as in *chiricahua*. Head about as wide as high; inner orbits converging below, WF .58 X WH, 1.20 X HE. Ocelli slightly enlarged, DAO .19 X WF; OOL 1.07 X WOT. Vertex broadly rounded, distance from eye tops to vertex crest nearly equal to HE. Characters of thoracic dorsum as described for *chiricahua*. Propodeal disc 1.5 X as wide as long, its characters as described for *chiricahua*. Mesopleurum alutaceous, weakly punctate; middle tibiae spined above. Fore wing with discoidal vein very weak, arising a short distance down on the transverse median vein. Abdomen stout, sessile. Subgenital plate weakly rounded apically, its basal stalk moderately wide (Fig. 61). Genitalia (Fig. 58) with the parameres slender apically; volsellae much as in *chiricahua* but with a somewhat triangular, roughened lobe at base of cuspis; aedoeagus simple, slender except broadened in the middle.

Paratype. — MEXICO: BAJA CALIFORNIA: 1 ♂, 10 mi. NW La Paz, 6 Oct. 1941 (Ross & Bohart) [CAS].

Variation. — The terminalia of the paratype closely resemble those of the type. This specimen is very small (LFW 2 mm.) and has the antennae infuscated beyond segment six, the scape also suffused with brownish. The head is longer than wide, WH .95 X LH; the third antennal segment is about twice as long as thick. In other respects the resemblance to the type is close.

28. APENESIA MALINCHE new species

Holotype. — ♂, MEXICO: PUEBLA: 10 mi. SE of Tehuitzingo, 3900 feet, 3 July 1953 (Univ. Kansas Mexican Exp.) [KU].

Description of type. — Length 3.6 mm.; LFW 2.6 mm. Head and thorax black; abdomen dark brown, first tergite margined posteriorly with light brown, following two tergites more weakly annulated with light brown; palpi brown; mandibles blackish, apical half rufous; scape nearly black, flagellum dark brown, basal segments slightly paler than apical segments; tegulae dark brown; legs dark brown except front tibiae and all the tarsi light brown; wings subhyaline, stigma brown, veins amber. Mandibles with five teeth, basal three teeth small and close together. Clypeus forming an obtuse angle apically, median ridge arched in profile. First four antennal segments in a ratio of about 21:6:10:10, segment three 1.7 X as long as thick, segment eleven twice as long as thick; pubescence light brown, semi-erect, setulae of segment eleven about .4 as long as width of segment; erect setae very sparse, standing somewhat above the pubescence. Front shining although rather strongly alutaceous; punctures fairly large, separated by 3-4 X their own diameters except somewhat more crowded medially. Eyes with setae minute and inconspicuous. Head very slightly wider than high, WH 1.02 X LH; inner orbits converging below, WF .61 X WH, 1.28 X HE. Ocelli small, DAO .16 X WF; front angle of ocellar triangle less than a right angle; OOL 1.10 X WOT. Vertex very broad; distance from eye tops to vertex crest equal to about .8 X HE. Pronotum and mesonotum as in *chiricahua* except slightly more strongly punctate. Propodeal disc 1.4 X as wide as long; disc reticulate medio-basally, behind shining, weakly alutaceous;

median carina complete; posterior margining carina rather weak; lateral carinae well defined but sublaterals absent; declivity strongly alutaceous. Mesopleurum alutaceous, moderately shining, with weak punctures in front. Fore wing with discoidal vein very weak, interstitial with median vein. Middle tibiae with some strong spines above. Subgenital plate weakly emarginate, with a wide basal stalk (Fig. 62). Genitalia (Fig. 59) with the parameres moderately wide, wider than in *mohave* but narrower than in any specimen of *chiricahua* studied; volsella with a group of stout spines just below the cuspis, its mesal margin below somewhat striate; aedoeagus slender, of complex and characteristic structure.

Paratype. — MEXICO: PUEBLA: 1 ♂, same data as type [MCZ].

Variation. — The paratype is very slightly smaller than the type (LFW 2.4 mm.); it is very similar to the type in every respect, including the terminalia.

29. APENESIA PECULIARIS new species

Holotype. — ♂, PANAMA: Barro Colorado Island, Canal Zone, 11 Feb. 1955 (C. Rettenmeyer) [KU].

Description of type. — Length 5.2 mm.; LFW 3.6 mm. Head and thorax black; abdomen brownish, each segment with a somewhat irregular apical annulation of light brown, apical three segments almost wholly light reddish brown; palpi very light brown; mandibles black basally, apical half light brown except teeth rufous; antennae castaneous except basal two-thirds of scape blackish, flagellum gradually infuscated apically; tegulae light brown; front coxae black; middle and hind coxae, front trochanters, and all femora dark brown; middle and hind trochanters and all tibiae and tarsi light brown; wings very lightly tinged with brownish, veins and stigma brown. Mandibles with four strong teeth (Fig. 70). Clypeus broadly rounded, median line weakly obtusely angulate, with a weak tooth formed by the extremity of the median carina, which is very high, in profile subangulate (Fig. 85). First four antennal segments in a ratio of about 30:9:17:15, segment three 2.4 X as long as thick, segment eleven nearly 3 X as long as thick; pubescence short, subappressed, setulae .2-.3 as long as width of segments bearing them; flagellum also with erect setae, slightly more numerous below than above, the longest of these nearly as long as width of segments bearing them. Front strongly polished, nonalutaceous, strongly punctate, the punctures separated for the most part by about their own diameters; temples and vertex with punctures slightly more widely spaced, also very weakly alutaceous. Head very slightly longer than wide, WH .98 X LH; inner orbits convergent below, WF .55 X WH, 1.10 X HE. Vertex broadly rounded off well above eye tops, distance from eye tops to vertex crest equal to about .7 X HE. Ocelli of moderate size, DAO .17 X WF; OOL 1.3 X WOT; anterior ocellus above a line drawn between eye tops, posterior ocelli separated from vertex crest by slightly less than WOT. Pronotum of moderate length, its sides evenly convergent toward the front, anterior margin of disc with a strong transverse carina; disc otherwise smooth, polished, punctures strong, fairly close together except more sparse medially. Mesoscutum polished, with abundant small punctures, except sparsely punctate medially; notauli strong, not quite reaching anterior margin of mesoscutum; scutellar disc rather flat, impunctate medially. Propodeal disc short, 1.3 X as broad as long; lateral, median and posterior carinae strong and complete; sublateral carinae weakly indicated; disc with a basal triangular area filled with strong longitudinal carinae and some weaker transverse carinae, remainder of disc smooth and polished; posterior slope strongly rugulose, side-pieces with only weak sculpturing. Mesopleurum polished, punctate except on the rather large callus. Middle tibiae with a few spines above; claws strongly dentate. Fore wing with discoidal cell very faintly outlined by pigmented lines. Abdomen sessile (about as in *chiricahua*, Fig. 80). Subgenital plate with a broadly V-shaped apical emargination. Genitalia (Fig. 63) with large parameres which are covered with small setae dorsally but bare ventrally except along the margin; ventral arms of digiti large and strongly setose; aedoeagus rather broad, very complex, with two small tufts of setae at the apex.

Remarks.— This unusual species is known only from the type. The conspicuous erect setae on the antennae suggest the *pilicornis* group, with which this species may bear some relationship.

30. APENESIA PANDO new name

Plutobethylus percurrens Kieffer, 1910, Ann. Soc. Ent. France, 79: 52. [Type: ♂, BOLIVIA: Dept. Pando, Mapiri (Staudinger) (no date given) (Berlin Museum, no. 207)].— Kieffer, 1914, Das Tierreich, 41: 489. Preoccupied by *Propristocera percurrens* Kieffer, 1905, Bull. Soc. Metz, 24: 99 (♂, India).

Description of type. — Length 3.6 mm.; fore wing 2.8 mm. Head and thorax piceous, abdomen dark reddish brown except first tergite margined with light brown; mandibles light castaneous, teeth rufous; clypeus brownish; antennae light castaneous basally, gradually infuscated toward the apex; tegulae testaceous; coxae and femora light brown, rest of legs yellowish brown; wings hyaline, veins and stigma brown. Mandibles with four teeth in an oblique series, basal tooth somewhat more rounded than the others (Fig. 72). Clypeus prominent, its margin broadly rounded and with a series of about eight minute teeth, four on each side of the median line (Fig. 86); median carina strong, nearly straight in profile. First four antennal segments in a ratio of about 20:6:13:13, segment three 2.7 X as long as thick, segment eleven 3 X as long as thick; flagellar pubescence erect, bristling, setulae of segment eleven .8 as long as width of segment. Front, vertex, and temples shining, weakly and uniformly alutaceous, punctures very weak, separated by 2-4 X their own diameters. Inner margins of eyes weakly convergent below; WF .55 X WH, 1.06 X HE; vertex evenly rounded off well above eye tops, distance from eye tops to vertex crest about .8 X HE. Front angle of ocellar triangle less than a right angle; OOL 1.22 X WOT; ocelli not enlarged. Pronotum with collar not noticeably striate, but with some strong longitudinal striae on the side pieces; anterior face short, sloping obliquely upward to a strong, sharp transverse carina; disc behind the carina flat, smooth, weakly alutaceous and weakly punctate. Mesonotum also weakly alutaceous and weakly punctate. Propodeum elongate, about 1.3 X as long as broad, disc slightly longer than broad; disc margined with strong carinae laterally and behind and with a strong, complete median carina; disc wholly alutaceous though somewhat more weakly so behind, with some irregular longitudinal carinae at the base, those closest to the median carina extending about half the length of the disc. Mesopleurum wholly alutaceous, callus moderately convex, subtended by a groove which runs anteriorly from the hind margin and gives rise to a branch which extends obliquely upward toward the anterior wing-base. Claws with a weak tooth. Fore wing with discoidal vein arising a short distance down on transverse median vein; discoidal cell weakly outlined. Abdomen slender, sessile; subgenital plate shallowly emarginate. Genitalia not studied.

Remarks. — This species is known only from the type.

31. Apenesia cubensis new species

Holotype. — ♂, CUBA: So. side Pico Turquino, 3000-5000 feet, June 1936 (P. J. Darlington, Jr.) [MCZ, No. 30441].

Description of type. — Length 4 mm.; LFW 3.5 mm. Head and thorax black except pronotum margined with brown; abdomen dark brown, sides of basal segments suffused with light brown; palpi straw-colored; mandibles straw-colored except black at extreme base and the teeth rufous; clypeus rufous apically; antennae straw-colored except weakly infuscated on apical half; tegulae testaceous; legs wholly straw-colored, tarsi tending to be slightly darker than basal parts of legs; wings hyaline, veins and stigma brown. Mandibles with four sharp teeth (Fig. 71). Clypeus rounded apically, the margin minutely crenulate; median line with a small tooth; median carina sharp, weakly arched in profile (Fig. 87). First four antennal segments in a ratio of about 26:6:22:20, segment three 3.3 X as long as thick, segment eleven nearly 4 X as long as thick; pubescence erect and bristling, setulae of segment eleven .7 as long as width of segment; flagellum without erect setae which stand above the pubescence. Front alutaceous, rather weakly shining, with small, shallow punctures which are separated by 2-4 X their own diameters. WH .95 X LH; inner orbits converging below, WF .59 X WH, 1.20 X HE. Head much produced behind eyes, distance from eye tops to vertex crest subequal to HE; anterior ocellus located far above a line drawn between eye tops. Ocelli of moderate size, DAO .20 X WF; OOL 1.35 X WOT. Pronotum of moderate length, with a sharp transverse carina anteriorly but otherwise with smooth contours; entire thoracic dorsum alutaceous, moderately shining, and with weak punctures. Notauli complete, slender and subparallel; groove at base of scutellum slender, scutellar disc rather flat, impunctate. Propodeal disc 1.15 X as wide as long; median carina complete although weakened just before the transverse carina, which is also rather weak; lateral carinae well defined but sublateral carinae indistinct; disc alutaceous, the basal triangle filled with short longitudinal carinae; declivity and side pieces also alutaceous. Mesopleurum wholly alutaceous, obscurely punctate, callus subtended by an arching groove but not very convex. Middle tibiae with the hairs on the upper side only slightly thicker than those on the other tibiae; claws strongly dentate. Fore wing with discoidal vein interstitial with median vein, rather weak. Subgenital plate emarginate apically. Genitalia (Fig. 64) with the lateral elements rather similar to those of *chiricahua,* but the aedoeagus of unusual form, broad at the base, apically with two pairs of simple processes below which is a pair of lateral expansions.

Remarks. — The alutaceous integument of this species suggests *chiricahua* and its allies, as do the genitalia. This unique specimen is the only male *Apenesia* known from the Antilles.

32. APENESIA MEXICANA (Cameron) new combination

Epyris mexicanus Cameron, 1904, Trans. Amer. Ent. Soc., 30: 263. [Type: ♂, MEXICO (no further data) (BMNH)]. — Kieffer, 1914, Das Tierreich, 41: 344.

Description of type. — Length 4.8 mm.; LFW 3.0 mm. Body black except first abdominal tergite margined with light brown; palpi light brown; mandibles yellowish brown except dark at base and apex; scape weakly infuscated, flagellum castaneous basally, gradually infuscated to such an extent that the apical few segments are nearly black; tegulae fuscous; coxae and femora dark brown, legs otherwise yellowish brown; wings hyaline, veins and stigma brown. Mandibles slender, superficially three-toothed, actually with four teeth, third tooth very small (Fig. 73). Clypeus obtusely angulate apically, except sides gently rounded and extreme tip subacute (about as in Fig. 84); median ridge, in profile, weakly arched. First four antennal segments in a ratio of about 13:4:6:6, segment three 1.7 X as long as thick, segment eleven 2.4 X as long as thick; pubescence short, suberect, longest setulae of segment eleven only about .3 as long as width of segment; flagellum also with a few scattered, fully erect setae which stand out slightly above the pubescence. Antennal scrobes not margined; eyes with some short, weak hairs. Front rather uniformly but weakly alutaceous, moderately shining, with fairly strong punctures which are separated, on the average, by 1-2 X their own diameters (more crowded along the midline); vertex and temples alutaceous, rather weakly punctate; front with a shallow median impression. Head wider than high, WH 1.04 X LH; inner orbits converging below, WF .54 X WH, 1.10 X HE; vertex broadly rounded off a distance above eye tops equal to about two-thirds HE. Ocelli small, DAO .17 X WF; ocellar triangle slightly less than a right angle; anterior ocellus barely touching a line drawn between eye tops; OOL 1.2 X WOT. Pronotum moderately long, its sides approaching anteriorly as straight lines, as seen from above; transverse carina strong, weakly arched, disc otherwise smooth except for a very faint indication of a transverse impression near the posterior margin; disc of pro- and mesonota strongly shining, obscurely alutaceous, with moderately strong punctures; notauli slender, complete, weakly diverging anteriorly. Propodeal disc 1.35 X as wide as its median length; lateral, sublateral, and transverse carinae strong; median carina strong but much weakened posteriorly; disc with basal triangular area filled with strong reticulations, elsewhere polished, obscurely alutaceous; declivity and side pieces polished and with weak sculpturing. Mesopleurum alutaceous, with weak punctures anteriorly, callus large but not strongly convex, subtended by a strong groove. Middle tibiae spinose. Fore wing with discoidal cell very weakly outlined by pigmented lines; discoidal vein interstitial with media. Subgenital plate arcuately emarginate apically. Genitalia (Fig. 65) with the parameres large, strongly excavated basally for reception of volsellae; ventral arms of digiti elongate and strongly curved laterad; aedoeagus relatively slender, strongly compressed, apex not deflected ventrad, bearing a few minute lateral setae.

Other males examined. — MEXICO: MORELOS: 1, 4 mi. E. of Cuernavaca, 6000 feet, 23 June 1959 (on honeydew, H. E. Evans) [MCZ]; 1, 5 km. N. of Alpuyeca, 3400 feet, 10 Aug. 1962 (H. E. Evans) [MCZ].

Variation. — The two Morelos specimens resemble the type very closely indeed; LFW varies from 3.0 to 3.7 mm., WF from 1.04 to 1.07 X HE, OOL from 1.15 to 1.18 X WOT.

Remarks. — The short antennal pubescence and the setae on the apical aedoeagal lobes suggest *peculiaris*, although the mandibles approach those of the several species which follow.

33. APENESIA TESTACEIPES (Cameron) new combination

Epyris testaceipes Cameron, 1888, Biol. Centr.-Amer., Hymen. I, p. 452, pl. XIX, fig. 18. [Type: ♂, PANAMA: Bugaba (G. C. Champion) (BMNH)].

Rhabdepyris (*Trichotepyris*) *testaceipes* Kieffer, 1908, Gen. Insect., 76: 32.

Cleistepyris testaceipes Kieffer, 1914, Das Tierreich, 41: 492.

Description of type. — Length 4.8 mm.; LFW 3.6 mm. Head and thorax black; abdomen dark brown, sides of first tergite and apex of last tergite lighter brown; mandibles and clypeus light brown; antennae testaceous except apical half weakly infuscated; legs bright testaceous except coxae very weakly infuscated; wings subhyaline, veins and stigma dark brown. Mandibles slender, with three teeth in an oblique series (about as in *maya*, Fig. 74). Clypeus broadly rounded except median portion truncate and with a minute median tooth which is a continuation of the median carina, this carina weakly arched in profile (Fig. 88). First four antennal segments in a ratio of about 30:10:17:14, segment three 2.7 X as long as thick, segment eleven 3 X as long as thick; pubescence pale, coarse, suberect, longest setulae of segment eleven about half as long as width of segment; erect setae sparse, barely exceeding pubescence. Front uniformly, rather weakly alutaceous, moderately shining, punctures small but well defined, separated by 3-5 X their own diameters. WH 1.03 X LH; inner orbits subparallel below, WF .50 X WH, .90 X HE. Ocelli somewhat enlarged, DAO .25 X WF; front angle of ocellar triangle less than a right angle; OOL .95 X WOT. Vertex evenly rounded off a distance above eye tops equal to slightly more than half HE. Pronotum rather long, with a sharply defined, arching carina in front; disc otherwise rather smooth, alutaceous, moderately shining, punctures strong except along median line. Mesoscutum shining, much less distinctly alutaceous than pronotum; punctures small, closely spaced along notauli but more sparse medially; scutellar disc with a few punctures, its basal groove slender. Propodeal disc 1.2 X as wide as long, with strong lateral and sublateral carinae, median carina strong and attaining the strong transverse carina; basal triangle filled with coarse reticulations; rest of disc polished, very weakly alutaceous; posterior slope alutaceous, with a pair of median carinae. Mesopleurum weakly alutaceous, weakly punctate. Middle tibiae weakly spinose; claws dentate. Fore wing with discoidal cell weakly outlined, discoidal vein arising near top of transverse median vein; basal vein reaching subcosta basad of stigma by about half the length of the stigma. Subgenital plate with a broadly U-shaped emargination. Genitalia with the lateral elements closely resembling those of *maya* (Fig. 67) except ventral arm of digitus more evenly curved; aedoeagus slender, terminating in two pairs of slender, acute processes (Fig. 66).

Remarks. — This species is known only from the type.

34. APENESIA MAYA new species

Holotype. — ♂, GUATEMALA: [San Pedro] Yepocapa, [Dept. Chimaltenango, 4850 feet] May 1948 (H. T. Dalmat) [USNM, No. 66011].

Description of type. — Length 4.5 mm.; LFW 3.4 mm. Head and thorax black; abdomen dark brown, first tergite margin with light brown; palpi and mandibles straw-colored, the latter tipped with dark red; clypeus suffused with rufous apically; antennae bright yellowish brown basally, somewhat infuscated beyond segment five; tegulae testaceous; legs bright yellowish brown except coxae and femora darker brown; wings subhyaline. Mandibles with three teeth in an oblique series (Fig. 74). Clypeus obtusely angulate apically, tectiform, median ridge not arched in profile (Fig. 89). First four antennal segments in a ratio of about 29:8:14:14, segment three 1.9 X as long as thick, segment eleven 2.4 X as long as thick; pubescence semi-erect, longest setulae of segment eleven about half as long as width of segment; erect setae fairly numerous on under side of basal segments, but only slightly exceeding the pubescence. Front moderately shining, wholly but weakly alutaceous, strongly punctate, the punctures rather evenly distributed over the front and vertex, separated by 1-1.5 X their own diameters. WH 1.04 X LH; inner orbits converging below, WF .55 X WH, 1.08 X HE. DAO .18 X WF; front angle of ocellar triangle less than a right angle; OOL 1.12 X WOT. Vertex very broadly rounded, distance from eye tops to vertex crest equal to slightly over half HE. Pronotum of moderate length, seen from above with the sides approaching evenly toward the front, not concave; transverse carina margining the disc in front strong, arcuate; disc strongly shining, barely alutaceous, punctate like the front. Mesoscutum also shining, but with the punctures smaller and more widely separated; notauli complete; scutellar disc shining, with several punctures. Propodeal disc 1.25 X as wide as long, with some rather prominent lateral setae; median carina complete, reaching the posterior carina, which is rather weak and situated just below the crest of the declivity; disc with basal triangle strongly reticulate, otherwise smooth and polished except irregularly sculptured laterally, between the rather ill-defined lateral and sublateral carinae; declivity alutaceous, punctate above and on the sides. Mesopleurum wholly but weakly alutaceous, moderately shining, weakly punctate anteriorly. Middle tibiae spinose above; claws dentate. Fore wing with discoidal vein interstitial with median vein, discoidal cell very weakly outlined. Abdomen sessile, fusiform; subgenital plate broadly truncate. Genitalia (Fig. 67) with the parameres broad apically; ventral arms of digiti strongly bent laterad; aedoeagus with a complex series of apical lobes some of which are prominently fringed, the lateral lobes with some minute setae.

Paratype.— GUATEMALA: 1 ♂, same data as type except December 1948 [USNM]. *Additional specimen* (assigned here tentatively).— PANAMA: 1 ♂, Barro Colorado Island, Canal Zone, 26 March 1924 (J. C. Bradley) [CU].

Variation. — The paratype is smaller than the type (LFW about 3 mm.). The front is slightly less alutaceous and more shining, and the punctures tend to be slightly more widely spaced. Standard measurements are virtually the same as for the type. The Panama specimen is without a head and difficult to place with certainty. The genitalia resemble those of *maya* closely, but the aedoeagus is more conspicuously setose on the sides and the median apical portion differs in details. The pronotum is slightly more elongate than in the type of *maya*, and its surface is much more heavily alutaceous. The propodeum does not differ noticeably from that of the type and paratype of *maya*.

35. APENESIA NEOTROPICA new name

Rhabdepyris paraensis Kieffer, 1910, Ann. Soc. Ent. France, 78: 298-299. [*Holotype:* ♂, BRAZIL: Pará (C. F. Baker) (Pomona College, Claremont, Calif.)]. Preoccupied by *Propristocera paraensis* Kieffer, 1910, *ibid.*, p. 290.

Cleistepyris paraensis Kieffer, 1914, Das Tierreich, 41: 492-493.

Description of type. — Length 5.0 mm.; LFW 3.7 mm. Head and thorax black, abdomen brown, first and second tergites margined laterally and posteriorly with yellowish brown; mandibles yellowish brown, teeth rufous; clypeus margined with rufous; antennae light yellowish brown, apical three segments somewhat infuscated; front coxae nearly black, other coxae and all the femora dark brown, remainder of legs yellowish brown; wings subhyaline, with dark setulae, veins and stigma brown. Mandibles rather slender apically, with three strong teeth in an oblique series (as in *maya*, Fig. 74). Clypeus obtusely produced, with a strong median tooth (Fig. 90); median area weakly elevated, not carinate. Antennae with first four segments in a ratio of about 32:9:18:17, segment three 2.5 X as long as thick, segment eleven 2.8 X as long as thick; pubescence semierect, setulae of segment eleven slightly over half as long as width of segment; also with a few scattered setulae which are fully erect and slightly longer than the others, most noticeable on segments 3-7. Front shining but weakly and uniformly alutaceous, punctures small but well-defined, separated by from 1 to 3 X their own diameters. Head about as wide as high, vertex rather narrowly rounded off a distance above eye tops equal to not much over half HE. Front narrow, inner orbits convergent below, WF .53 X WH, about equal to HE; DAO .19 X WF, ocelli in a compact triangle, front angle less than a right angle, front ocellus barely touching a line drawn between tops of eyes; OOL 1.13 X WOT. Pronotum elongate, sides, seen from above, somewhat concave, disc margined anteriorly with a strong transverse carina; median line of pronotum not elevated; surface of pro- and mesonota shining, weakly and uniformly alutaceous, punctures small but strong, fairly closely spaced except more sparse medially. Propodeal disc almost square (very slightly wider than long) and with strong posterior corners and posterior margining carina; lateral and sublateral carinae strong, median carina strong and reaching transverse carina; disc with strong and irregular reticulations medio-basally, otherwise shining and weakly alutaceous; posterior slope evenly and strongly alutaceous, side pieces somewhat shining, more weakly alutaceous. Mesopleural callus convex, impunctate, shining but weakly and uniformly alutaceous; remainder of mesopleurum alutaceous, rather weakly punctate. Middle tibiae spinose above. Fore wing with discoidal and subdiscoidal veins faintly pigmented, but vein margining outer side of discoidal cell barely indicated; discoidal vein interstitial with median vein; transverse median vein oblique and somewhat curved below. Abdomen sessile; subgenital plate truncate. Genitalia (Fig. 76) with parameres much enlarged apically, shaped somewhat as in *maya* but inner margin less sinuate; ventral arms of digiti erect, inner margin arched; aedoeagus exceeding complex, consisting of numerous slender apical processes all of which are in some measure fringed or serrate.[5]

Additional males examined. — BRAZIL: 1, Santarem [US NM]. PERU: 1, Colonia Perene, 18 mi. NE La Merced, Junin, 3 Jan. 1955 (Schlinger & Ross) [CAS].

Variation. — These two specimens are slightly smaller than the type (LFW 3.2-3.3 mm.) but differ little in color or structure. In the Santarem specimen WF measures .95 X HE, OOL 1.15 X WOT; in the specimen from Peru WF measures .92 X HE, OOL 1.23 X WOT. In both specimens the antennae are slightly shorter than in the type, segment eleven measuring only about 2.5 X as long as thick.

36. APENESIA INCA new species

Holotype. — ♂, PERU: Upper Rio Pachitea, 21 July 1920 (Cornell Univ. Exped.) [CU, No. 3880].

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[5] The description and figure of the genitalia are based on the Santarem specimen, the genitalia of the type not having been extracted.

Description of type. — Length 5 mm.; LFW 3.2 mm. Head and thorax black; abdomen dark brown except basal two segments and apical segment partially suffused with paler brown; palpi straw-colored; mandibles and clypeus ferruginous; first three antennal segments bright yellowish brown, fourth segment suffused with dull brown, remainder of flagellum dull brownish; tegulae light brown; coxae and femora medium brown, remainder of legs yellowish brown; fore wing lightly tinged with brown, veins and stigma dark brown. Mandibles with three teeth in an oblique series, basal tooth rather small (Fig. 75). Clypeus obtusely angulate except the extreme tip weakly concave so as to form two blunt teeth (Fig. 91); median ridge weakly arched in profile. First four antennal segments in a ratio of about 30:8:17:15, segments three and eleven each about 2.3 X as long as thick; pubescence pale, semierect, longest setulae of segment eleven about half as long as width of segment; erect setae sparse, barely exceeding pubescence. Front shining, wholly but rather weakly alutaceous, punctures small, for the most part separated by 2-3 X their own diameters. Eyes covered with short hairs. Head wider than high, WH 1.06 X LH; front of moderate width, inner orbits subparallel below; WF .59 X WH, 1.17 X HE. Vertex broadly rounded, distance from eye tops to vertex crest equal to less than half HE. Ocelli of moderate size, DAO .20 X WF; front angle of ocellar triangle less than a right angle; OOL 1.15 X WOT. Pronotum moderately long, its sides concave as seen from above; carina margining disc anteriorly strong; median line weakly elevated and without punctures, remainder of disc with strong, well spaced punctures; entire thoracic dorsum alutaceous although moderately shining. Mesoscutum with strong punctures which tend to be crowded along the notauli, which are complete. Propodeal disc very slightly wider than long; disc alutaceous, median carina complete and flanked by some shorter carinae on the basal triangle; lateral and sublateral carinae well developed; posterior carina strong and with a series of foveae in front of it; declivity alutaceous. Mesopleurum weakly alutaceous, obscurely punctate, callus large, moderately shining. Middle tibiae spinose above. Fore wing with the discoidal vein arising well down on the transverse median vein, fairly distinct but the discoidal cell otherwise only very weakly outlined. Abdomen sessile, fusiform; subgenital plate broadly truncate. Genitalia (Fig. 77) with the parameres very large, broadly truncate apically; ventral arms of digiti unusually large, broad and subtruncate apically; aedoeagus of much simpler structure than in the preceding several species, and without setae; median apical lobes of aedoeagus rounded.[6]

Paratypes. — PERU: 1 ♂, Dos de Mayo to El Porvenir, Cam. del Pichis, 6 July 1920 (Cornell Univ. Exped.) [CU]. ECUADOR: 1 ♂, Naranjal, Prov. Guayas, Dec. 1955 (Levi-Castillo) [USNM].

Variation. — The paratype from Peru is larger than the type (LFW 4.2 mm.) and has the sculpture of the basal triangle of the propodeum slightly different, the carinae being straighter and fewer in number. The Ecuador paratype approximates the type in size, but the discoidal vein is very weak and is interstitial with the median vein. This specimen also has the third antennal segment no longer than the fourth and only about twice as long as wide; the front is very narrow, WF .55 X WH, 1.05 X HE; the ventral arms of the digiti are rounded apically, as shown in Figure 77. Both paratypes have the clypeus only very indistinctly bidentate.

BRASILIENSIS SPECIES-GROUP

The species of this group differ from those of the preceding group only in having the abdomen short-petiolate and the inner margins of the parameres strongly setose for a considerable distance. The thirteen known species collectively range from New York and central Mexico south to Brazil and Bolivia. The type species of Kieffer's genera *Cleistepyris* and *Dipristocera* belong to this group.

Certain of the species of this group are reasonably distinctive (*fulvicollis, parapolita*), but the remainder form a very closely knit complex. I have found the shape of the clypeus and the characters of the aedoeagus most useful in distinguishing species, but some intraspecific variation occurs in both these features. Furthermore, the clypeus is subject to wear, and the aedoeagus is so complex that it may appear very different when viewed from slightly different angles. At present, all the species of this group are known from one or only a few specimens, and it is probable that much further revision of this group will be necessary when more material is available for study. Some of the specific differences are summarized in Table VI, and some characters are illustrated in Plates 7-9.

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[6] The genitalia figured are those of the Ecuador paratype. Those of the type are very similar except that the ventral arms of the digiti are obliquely subtruncate rather than evenly rounded as figured.

TABLE VI. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF BRASILIENSIS GROUP

Species	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	Ant. 11 L/W	Propodeal disc W/L	Med. lobe clypeus
37. parapolita	2.5	0.95	1.05	1.25	3.2	0.83	produced
38. angustata	2.7	1.05	1.15	1.33	2.9	1.05	produced
39. microchela	3.0	1.03	1.14	1.36	3.8	1.14	produced
40. tarascana	3.4	1.00	1.30	1.30	3.9	1.00	produced
41. tlahuicana	3.2	1.00	1.25	1.50	3.3	1.00	produced
42. olmeca	3.5	1.00	1.10	1.15	3.2	1.20	produced
43. fulvicollis	3.5	1.02	1.04	1.13	--	1.12	produced
44. alutacea	2.8	1.06	1.10	1.50	4.1	1.10	truncate
45. zamora	3.8	1.05	1.05	1.45	3.0	1.10	truncate
46. transversa	4.3	1.07	1.08	1.28	5.0	1.30	truncate
47. venezuelana	4.0	1.06	1.10	1.30	3.4	1.30	truncate
48. brasiliensis	4.8	1.10	1.05	1.25	3.2	1.20	truncate
49. peruana	4.0	1.09	1.12	1.55	3.1	1.25	truncate

37. APENESIA PARAPOLITA new name

Propristocera polita Evans, 1958, Proc. Ent. Soc. Wash., 59: 294-295. [Type: ♂, SOUTH CAROLINA: Columbia, 16 Aug. 1951 (L. & G. Townes) (Coll. H. K. Townes)]. Preoccupied by *Misepyris politus* Fouts 1930 (♂, Philippines) [= *Apenesia polita* (Fouts), new combination].

Description of type. — Length about 3.5 mm.; LFW 2.5 mm. Head black, thorax dark brownish fuscous, abdomen medium brown; mandibles yellowish brown, darker basally and apically; scape and pedicel straw-colored, flagellum gradually darkened to brown at apex; coxae brown, femora light brown, remainder of legs straw-colored; wings hyaline, with dark setulae, stigma brown, veins light brown. Mandibles with five strong sharp teeth in a row. Clypeus with a prominent median lobe the margin of which is rounded with a small median tooth (Fig. 96); median carina very strong, arched in profile. First four antennal segments in a ratio of about 4:1:3:3, segment three 2.7 X as long as thick, segment eleven 3.2 X as long as thick; pubescence erect and bristling, setulae of segment eleven nearly as long as width of segment. Front strongly polished, very obscurely alutaceous, punctures small and widely separated; center of front with a longitudinal impression. WH .95 X LH; WF .53 X WH, 1.05 X HE; ocelli small, well separated, front angle of ocellar triangle less than a right angle; OOL 1.25 X WOT. Front evenly rounded off a distance above eye tops nearly equal to HE; occipital carina very strong. Pronotum crossed anteriorly by a somewhat irregular carina behind which is a foveolate groove; posterior margin of pronotum somewhat depressed. Mesoscutum somewhat alutaceous, punctures very small and widely spaced.

Propodeum elongate, measuring 1.4 X as long as wide in full dorsal view, the disc measuring 1.2 X as long as wide; surface wholly covered with reticulations; median carina distinct, occupying a shallow depression; posterior transverse carina present, but barely distinguishable from the surface sculpturing; declivity and side pieces with strong surface sculpturing. Mesopleurum with the callus convex, weakly alutaceous; remainder of mesopleurum alutaceous, anteriorly rather coarsely sculptured. Middle tibiae not spinose. Fore wing with transverse median vein erect, weakly arched, discoidal and subdiscoidal veins absent. Abdomen with a very short petiole (Fig. 81). Subgenital plate broadly truncate apically. Genitalia with the parameres slender, unlobed, the apices deflected mesad; volsellae with a group of spines at base and another at apex of digitus: aedoeagus complex, terminating in several lobes, the most lateral lobes exceeding the others (see fig. 6 in Evans, 1958).

Other males examined. — SOUTH CAROLINA: 1, Greenville, 31 Aug. 1952 (L. & G. Townes) [Coll. H. K. Townes]. VIRGINIA: 1, Dunn Loring, 11 Sept. 1948 (K. V. Krombein) [Coll. K. V. Krombein]. WEST VIRGINIA: 1, Barbour Co., Philippi, 25 Sept. 1938 (G. E. Wallace) [CM]. NEW JERSEY: 1, Butler, Summer 1955 (R. Dorland) [USNM]. NEW YORK: 1, Ithaca, 14 Sept. 1956 (H. E. Evans) [CU].

Variation. — As noted in the original description, there is an unusual amount of variation in the sculpturing of the pronotum and propodeum in this species. The only additional specimen I have seen since 1958 is the one from West Virginia listed above; this specimen is very similar to the type in sculpturing and in color and size (LFW 2.3 mm.), but has the discoidal and subdiscoidal veins indicated by weakly pigmented streaks. The Ithaca, N. Y., specimen is more darkly colored than the others and has the pronotum somewhat rugulose and the propodeum very strongly reticulate.

Remarks. — This species seems to have no close relatives. Perhaps *angustata* is somewhat related, but that species has spines on the middle tibiae and genitalia of a very different type. This is the only *Apenesia* occurring widely in eastern United States, and the only female known to occur in eastern United States presumably represents the opposite sex of *parapolita*. It is so treated in the final section of this revision, where all females are considered together.

38. APENESIA ANGUSTATA (Evans) new combination

Propristocera angustata Evans, 1958, Proc. Ent. Soc. Wash., 59: 295-296. [Type: ♂, COSTA RICA: San Pedro de Montes de Oca, 3 Feb. 1935 (on *Ipomoea tiliacea,* C. H. Ballou) (USNM, No. 64113)].

Description of type. — Length 3.2 mm.; LFW 2.7 mm. Body dark castaneous, head strongly suffused with blackish; palpi straw-colored; mandibles testaceous; antennae testaceous basally, gradually infuscated beyond segment three, apical segments medium brown; legs entirely straw-yellow; wings subhyaline, veins light brown, stigma dark brown. Mandibles with five teeth which are subequal in size except for the large apical tooth. Clypeus with the median lobe broad, its apex weakly rounded, subdentate medially (Fig. 97). First four antennal segments in a ratio of about 21:6:13:13, segment three 2.5 X as long as thick, segment eleven nearly 3 X as long as thick; pubescence pale, erect, longest setulae of segment eleven about two-thirds as long as width of segment. Front shining, wholly although weakly alutaceous, punctures weak, separated by about 3 X their own diameters. WH 1.05 X LH; inner orbits converging below, WF .58 X WH, 1.15 X HE. Ocelli small, situated far above eye tops, front angle of triangle less than a right angle; OOL 1.33 X WOT. Vertex forming an even arc above eye tops; distance from eye tops to vertex crest equal to about two-thirds X HE. Pronotum with transverse carina moderately strong, situated part way down the anterior face; collar with a median impression; surface of pronotum moderately alutaceous, punctures numerous but rather weak. Mesoscutum and entire scutellar disc alutaceous. Propodeal disc slightly wider than long, weakly margined behind; surface alutaceous, basal triangle with reticulate ridges. Mesopleurum wholly alutaceous, weakly punctate. Middle tibiae weakly spinose. Fore wing with the discoidal cell outlined by weakly pigmented lines; discoidal vein interstitial with median vein. Abdomen with a very short petiole, about as in Figure 81. Subgenital plate broadly truncate apically. Genitalia with the lateral elements about as in *microchela,* shown in Figure 93; aedoeagus (Fig. 109) in general like that of *microchela,* but with larger median apical lobes which bear minute denticles in rows.

Other males examined. — COSTA RICA: 4, same data as type [USNM, CU].

Variation. — In three specimens the thorax and abdomen are dark brownish fuscous, the head black. In some specimens the clypeus appears shorter than figured (perhaps the result of wear) and the median tooth is indistinct. In three specimens the discoidal and median veins are slightly disjointed.

Remarks.— There can be no doubt of the close resemblance of this species to *microchela* (Kieffer). It is possible that when more material is available the two will be found to fall within the range of variation of one species, or at most to be subspecifically distinct.

39. APENESIA MICROCHELA (Kieffer) new combination

Pristocera microchela Kieffer, 1911, Ann. Soc. Sci. Bruxelles, 35: 214. [Type: ♂, MEXICO: TABASCO: Teapa, March (H. H. Smith) (BMNH)].

Dipristocera microchela Kieffer, 1914, Das Tierreich, 41: 471. [Made type of new genus *Dipristocera*, monobasically].

Description of type.— Length 4 mm.; LFW 3 mm. Body piceous except basal abdominal segments suffused with light brown; palpi straw-colored; mandibles light brown, the teeth rufous; antennae testaceous, apical six segments suffused with brown; legs testaceous, front coxae suffused with brown; wings subhyaline, veins and stigma brown. Mandibles with five sharp teeth in an oblique series. Clypeus broadly rounded, with an indistinct median angulation (Fig. 98); median line weakly elevated, not carinate. First four antennal segments in a ratio of about 24:7:17:17, segment three 3 X as long as thick, segment eleven 3.8 X as long as thick; pubescence pale, suberect, longest setulae of segment eleven .6 as long as width of segment. Front strongly alutaceous, weakly shining, punctures small, rather shallow, separated by 3-4 X their own diameters. WH 1.03 X LH; inner orbits converging below, WF .58 X WH, 1.14 X HE. Ocelli not enlarged, forming a triangle well above eye tops, front angle less than a right angle; OOL 1.36 X WOT. Vertex evenly rounded, distance from eye tops to vertex crest equal to about two-thirds X HE. Pronotum moderately long, its transverse carina strong, straight; disc strongly alutaceous, weakly punctate, very weakly depressed close to posterior margin. Mesoscutum alutaceous, with small punctures; notauli complete; scutellar disc weakly alutaceous, basal groove strong, complete. Propodeal disc 1.14 X as wide as long, with strong reticulations in the basal triangle, on the sides behind strongly alutaceous; median carina complete, but transverse carina not sharply differentiated from reticulations bordering the disc behind. Mesopleurum alutaceous, obscurely punctate, callus subtended by a foveolate groove. Middle tibiae spinose; claws weakly toothed. Fore wing with discoidal cell clearly outlined, discoidal vein interstitial with median vein. Abdominal petiole short (Fig. 118). Subgenital plate truncate. Genitalia (Fig. 93) with the parameres slender, with a short lateral and a longer mesal lobe; ventral arms of digiti very long, obliquely truncate apically; aedoeagus bearing a strong resemblance to that of the following three species, with small, sharply pointed median lobes lying between large lateral lobes which considerably exceed them.[7]

Other males examined. — MEXICO: VERACRUZ: 1, Atoyac, May (H. H. Smith) [BMNH].

Variation. — The Atoyac specimen is smaller than the type (LFW 2.8 mm.) and very similar in structure and standard measurements (WF 1.10 X HE, OOL 1.40 X WOT). However, the head is no wider than high and the clypeus evenly arcuate, with no indication of a median angulation.

Remarks. — Kieffer characterized his genus *Dipristocera* as having paired pits on the scutellum. However, this is based on an erroneous observation, as the scutellum of this species has the usual groove at the base.

40. APENESIA TARASCANA new species

Holotype. — ♂, MEXICO: MICHOACAN: Tuxpan, 6000 feet elev., 6 July 1959 (H. E. Evans) [MCZ, No. 30442].

Description of type. — Length 4.4 mm.; LFW 3.4 mm. Body black except sides of first abdominal tergite light brown; palpi brown; mandibles ferruginocastaneous, blackish, at base; antennae uniformly dark brown; tegulae light brown; coxae and femora dark brown, trochanters, tibiae, and tarsi light brown; wings lightly tinged with brownish, veins and stigma brown. Mandibles with five strong teeth (Fig. 112). Clypeus rounded apically, weakly angulate medially; median carina arched in profile (Fig. 99). First four antennal segments in a ratio of about 29:8:23:21, segment three 3 X as long as thick, segment eleven nearly 4 X as long as thick; pubescence erect, bristling, setulae of segment eleven .7 X as long as width of segment; flagellum without erect setae distinguishable from the pubescence. Front strongly shining, very obscurely alutaceous, punctures

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[7] The description and figure of the genitalia are based on the Atoyac specimen, the genitalia of the type not having been extracted.

small, separated by 3-4 X their own diameters. Eyes with numerous very short, inconspicuous setae. Head as wide as high; inner orbits convergent below, WF .62 X WH, 1.3 X HE. Ocelli small, DAO .15 X WF; OOL 1.3 X WOT; front angle of ocellar triangle less than a right angle. Vertex evenly rounded, distance from eye tops to vertex crest equal to about two-thirds HE. Pronotum smooth and polished, with small, widely spaced punctures; transverse carina strong. Mesonotum also strongly polished, non-alutaceous, with small, well spaced punctures; notauli not quite reaching margin of mesoscutum. Propodeal disc about as wide as long; lateral carinae strong, median carina obsolescent behind, posterior transverse carina weak and irregular; disc reticulate at the base, behind alutaceous, somewhat shining. Mesopleurum shining, weakly alutaceous. Middle tibiae with spines above; claws dentate. Fore wing with the discoidal vein fairly strong, arising a short distance down on the transverse median vein; discoidal cell fully outlined by weakly pigmented lines. Abdomen with a very short petiole (about as in Fig. 81). Subgenital plate shallowly emarginate. Genitalia (Fig. 92) with the parameres with a strong mesal lobe; ventral arms of digiti elongate, club shaped; aedoeagus with large, strongly compressed lateral lobes which much exceed the small, sharply pointed median lobes.

Paratypes.—MEXICO: MICHOACAN: 2 ♂♂, same data as type [CU, USNM]; CHIAPAS: 1 ♂, San Cristobal las Casas, 30 July 1957 (Chemsak and Rannells) [CIS].

Variation.—The two topotypic paratypes are smaller than the type (LFW 2.9 and 3.0 mm.), but agree closely in color and in structure. The Chiapas paratype differs in several details. LFW measures 3.3 mm.; the mandibles and antennae are very dark brown, the color otherwise similar to that of the type; the front is very weakly alutaceous. The head is slightly higher than wide, WH measuring .98 X LH. WF is 1.45 X HE, OOL 1.5 X WOT. The propodeum is unusually elongate, the disc .9 as wide as long. The aedoeagus closely resembles that of the type but the ventral arms of the digiti are more slender.

41. Apenesia tlahuicana new species

Holotype.—♂, MEXICO: MORELOS: 4 mi. E. of Cuernavaca, 25 June 1959, 6000 feet (on honeydew, H. E. Evans) [MCZ, No. 30443].

Description of type.—Length 4 mm.; LFW 3.2 mm. Body black except sides of first abdominal tergite light brown; palpi light brown; mandibles yellowish brown except blackish at base and with the teeth rufous; scape and following two antennal segments bright castaneous, antennae beyond third segment gradually infuscated, the apical segments dark brown; tegulae light brown; legs bright castaneous, the coxae and femora darker than the rest; wings subhyaline, veins and stigma brown. Mandibles with five strong teeth. Clypeus short, its apical margin rounded except very weakly produced medially; median line weakly elevated (Fig. 100). First four antennal segments in a ratio of about 28:8:19:18, segment three 2.5 X as long as thick, segment eleven 3.3 X as long as thick; pubescence bristling, setulae of segment eleven .6 as long as width of segment; erect setae no longer than pubescence. Front shining, non-alutaceous, punctures small, separated by 3-4 X their own diameters. Head as wide as high; inner orbits convergent below WF .62 X WH, 1.25 X HE. Ocelli not enlarged, DAO .15 X WF; anterior ocellus situated well above eye tops; OOL 1.5 X WOT. Vertex evenly rounded, distance from eye tops to vertex crest equal to about .7 HE. Pro- and mesonota as described for *tarascana*. Propodeal disc about as wide as long; median basal area strongly reticulate, median carina not reaching transverse carina, which is barely distinguishable among transverse striations along the edge of the declivity; posterior part of disc shining, very weakly alutaceous. Mesopleurum very strongly shining, barely alutaceous. Fore wing and abdominal petiole as in *tarascana*. Subgenital plate truncate apically. Genitalia (Fig. 94) with a large group of small, stout setae at the lower angles of the parameral lobes; ventral arms of digiti elongate, apical part somewhat parallel-sided; aedoeagus with the median apical lobes forming a point which is not notably exceeded by the slender lateral lobes, the latter being twisted mesad.

Paratypes. — MEXICO: MORELOS: 1 ♂, same data as type [CU]; 1 ♂, 30-40 km. NE Cuernavaca, 7-8000 feet, 31 July 1962 (H. E. Evans) [MCZ]. STATE OF MEXICO: 17 ♂♂, 7 km. S. Amecameca, 8000 feet, 12 Aug. 1962 (H. E. Evans) [MCZ, USNM]; 1 ♂, Valle de Bravo, 6500 feet, 3 Aug. 1962 (H. E. Evans) [MCZ].

Variation. — There is little variation in the type series with respect to the clypeus or the aedoeagus, the critical structures by means of which this species may be separated from the closely related species *tarascana* and *olmeca*. There is considerable variation in size (LFW 2.4-3.7 mm.) and some slight variation in the width of the front (WF 1.20-1.35 X HE). Most specimens are very similar to the type in coloration of the antennae and legs, but there is considerable variation in the Ameeameca series; some individuals in this series have the antennae and the coxae and femora wholly dark brown, as in *tarascana*.

42. APENESIA OLMECA new species

Holotype. — ♂, MEXICO: VERACRUZ: 7 mi. SE of Catemaco, 21 April 1953 (R. C. Bechtel & E. I. Schlinger) [CAS].

Description of type. — Length 5 mm.; LFW 3.5 mm. Head and thorax black; abdomen dark castaneous except petiole black, basal segments weakly annulated with light yellowish brown; palpi straw-colored; mandibles yellowish brown except darkened at base and apex; antennae bright yellowish brown except apical five segments weakly infuscated; tegulae testaceous; legs wholly bright testaceous except front coxae weakly infuscated; wings subhyaline, veins and stigma brown. Mandibles with five strong teeth (as in Fig. 112). Clypeus with median lobe of moderate length, longer than in *tlahuicana*, obtusely angulate medially (Fig. 101); median carina low, in profile nearly straight. First four antennal segments in a ratio of about 29:8:19:18, segment three 3 X as long as thick, segment eleven 3.2 X as long as thick; pubescence erect, bristling, longest setulae of segment eleven half as long as width of segment. Front polished, very obscurely alutaceous, punctures small, separated by 3-4 X their own diameters. Head as wide as high; front rather broad, WF .58 X WH, 1.10 X HE. Ocelli slightly enlarged, DAO .19 X WF; OOL 1.15 X WOT. Vertex evenly rounded off a considerable distance above eye tops. Thoracic dorsum polished, punctures numerous but rather small; features as in preceding two species. Propodeal disc 1.2 X as wide as its median length; basal triangle strongly reticulate, rest of disc alutaceous, moderately shining; median carina complete, posterior transverse carina weak and irregular. Mesopleurum polished, weakly punctate, callus large and convex. Middle tibiae weakly spinose above. Fore wing with discoidal cell weakly outlined, discoidal vein arising a short distance down on transverse median vein. Subgenital plate very weakly emarginate. Genitalia with the lateral elements virtually identical to those of *tarascana*, shown in Figure 92, but the aedoeagus (Fig. 108) very different, the lateral apical lobes very much larger and far surpassing the small, acutely pointed median lobes.

Paratypes.—MEXICO: VERACRUZ: 3 ♂♂, same data as type [MCZ, UCD].

Variation.—The three paratypes are all smaller than the type (LFW 2.6 to 2.8 mm.). In all three specimens the antennae are more heavily and extensively infuscated apically and the ocelli barely enlarged (DAO .17 X WF). WF measures 1.08 to 1.22 X HE, OOL 1.29 to 1.35 X WOT. In two specimens the propodeal disc is only about 1.1 X as wide as long and the basal triangle less heavily reticulate than in the type.

43. APENESIA FULVICOLLIS (Westwood) new combination

Pristocera fulvicollis Westwood, 1874, Thesaurus Ent. Oxoniensis, p. 165, pl. 29, fig. 3. [Type: ♂, BRAZIL: Amazonas, 1861 (H. W. Bates) (HCOU)].—Kieffer, 1914, Das Tierreich, 41: 469.

Description of type.—Length 5.8 mm.; LFW 3.5 mm. Head black; thorax black except prothorax wholly bright rufo-castaneous, including notum, collar, and pleura; abdomen medium brown, obscurely banded with darker brown, petiole and most of first tergite blackish; mandibles yellowish brown, the teeth rufous; clypeus yellowish brown except darker medially; antennae light yellowish brown (missing beyond segment three); legs straw-colored except femora very weakly suffused with brownish; wings clear hyaline, veins and stigma brown. Mandibles with five teeth, the teeth rather blunt except for the strong apical tooth (Fig. 114). Clypeus obtusely angulate, the extreme tip rounded (Fig. 102); median line roundly elevated, the elevation weakly arched in profile. First three antennal segments in a ratio of about 15:5:9, segment three 3.5 X as long as thick; pubescence of third segment pale, semi-erect, longest setulae two-thirds as long as width of segment; no erect setae visible. Front very strongly polished, non-alutaceous; punctures small, very widely spaced on the sides but somewhat more crowded medially. WH 1.02 X LH; inner orbits subparallel below, WF .56 X WH, 1.04 X HE. Ocelli slightly enlarged, DAO .20 X WF; ocellar triangle very compact, front angle much less than a right angle; OOL 1.13 X WOT. Vertex broadly rounded; distance from eye tops to vertex crest equal to about two-thirds X HE. Pronotum with a strong, arching transverse carina in front, disc convex behind carina, but without other ridges or grooves; surface strongly polished, non-alutaceous, with weak punctures. Mesoscutum polished, non-alutaceous, weakly punctate, scutellar disc convex, strongly polished. Propodeal disc

1.12 X as wide as long, lateral and sublateral carinae strong, median carina strong, reaching transverse carina, which is also fairly strong; disc with an elongate basal triangle filled with strong reticulations; sides of disc polished. Mesopleurum with the callus strongly convex and polished, subtended by an arcuate groove, remainder of mesopleurum weakly punctate. Middle tibiae strongly spinose. Fore wing with discoidal cell distinctly outlined by pigmented lines; discoidal vein interstitial with median vein; costa extending beyond stigma nearly as far as radial vein. Abdomen with a fairly long petiole (about as in *brasiliensis*, Fig. 82). Subgenital plate weakly emarginate. Genitalia not examined.

Remarks. — This species is known only from the type. The rufous prothorax readily distinguishes it from other known species of *Apenesia*, although this color pattern also occurs in several Brazilian species of *Pseudisobrachium*. It is possible that the blunt mandibular teeth and the lack of a median angulation on the clypeus are the result of wear. The antennae were missing beyond segment three at the time of Westwood's original description.

44. Apenesia alutacea new species

Holotype. — ♂, VENEZUELA: San Esteban, near Puerto Cabello, 1940 (P. J. Anduze) [HKT].

Description of type. — Length 3.7 mm.; LFW 2.8 mm. Head and thorax black, abdomen dark brown except marked with lighter brown on sides of basal segments; palpi and mandibles straw-colored except latter rufous at extreme apex; basal three segments of antennae straw-colored, segments 4-6 gradually infuscated, segments 7-13 rather uniformly medium brown; tegulae, and legs in their entirety, straw-colored; wings hyaline, stigma brown, veins light brown. Mandibles with five sharp teeth in an oblique series (Fig. 113). Clypeus broadly truncate, sides of the truncation rounded (Fig. 104); median line weakly elevated except for a small tooth-like elevation a short distance back from the margin. First four antennal segments in a ratio of about 24:5:20:20, segment three 3.3 X as long as thick, segment eleven more than 4 X as long as thick; pubescence erect, bristling, pale in color, longest setulae of apical several segments about as long as width of segments; there are no erect setae which stand above the pubescence. Front, vertex and temples uniformly and rather weakly alutaceous, shining, with very small punctures which are separated by several times their own diameters. Head wider than high, WH 1.06 X LH; inner orbits convergent below, WF .56 X WH, 1.10 X HE. Vertex evenly rounded off a distance above eye tops equal to somewhat more than half HE. Ocelli small, forming a triangle the front angle of which is less than a right angle; OOL 1.5 X WOT. Thoracic dorsum uniformly and weakly alutaceous like the front, with only minute, barely visible punctures. Pronotum with a subfoveolate transverse impression just before the posterior margin, stronger on the sides than medially; anterior transverse carina strong, arching, disc convex between the anterior carina and the posterior impression. Mesoscutum with the notauli linear, diverging slightly anteriorly and not quite reaching anterior margin. Propodeal disc 1.1 X as wide as long; lateral and median carina rather weak, although complete, transverse carina margining the disc behind weak and barely differentiated from the transverse striae which cover the declivity; sublateral carinae weakly differentiated from the reticulate sculpturing along sides of disc; basal triangular area of disc reticulate, remainder of disc merely alutaceous. Mesopleurum wholly alutaceous, weakly punctate. Middle tibiae weakly spinose above. Fore wing with discoidal cell very weakly outlined by pigmented lines. Abdomen with a short petiole. Subgenital plate weakly emarginate apically. Genitalia (Fig. 95) with the parameres similar to those of *microchela;* ventral arms of digiti broad, truncate apically; aedoeagus broad, its margins subangulate just below the apex.

Remarks. — This species, known only from the type, is immediately separable from related species by the alutaceous head and thorax.

45. APENESIA ZAMORA new species

Holotype. — ♂, ECUADOR: Zamora, 1000 meters, 15 Oct. 1961 (D. B. Laddey) [AMNH].

Description of type. — Length 4.5 mm.; LFW 3.8 mm. Head and thorax black; abdomen dark brown except petiole black and sides of basal segments suffused with light brown; palpi light brown; apical two-thirds of mandibles yellowish brown except teeth rufous; antennae medium brown except second segment and apex of first light brown, flagellum slightly darker toward the apex than basally; tegulae light brown; coxae and femora dark brown, trochanters, tibiae and tarsi light brown; wings hyaline, veins and stigma brown, setulae dark. Mandibles with five teeth, basal three teeth rather small and close together. Clypeus very broadly truncate, sides of the truncation broadly rounded; median carina low, not reaching base or apex. First four antennal segments in a ratio of about 31:8:17:17, segment three and segment eleven each about 3 X as long as thick; pubescence suberect, pale, longest setulae of segment eleven somewhat more than half as long as width of segment; basal segments of flagellum also with a few longer, fully erect setae. Front polished, non-alutaceous, with small punctures which are separated, on the average, by twice their own diameters, more widely spaced than this laterally and above. Head wider than high, WH 1.05 X LH; inner orbits strongly convergent below, WF .56 X WH, 1.05 X HE. Vertex evenly rounded off, distance from eye tops to vertex crest equal to about two-thirds HE. Ocelli small, in a compact triangle well above eye tops; OOL 1.45 X WOT. Pronotal disc short and broad, with a strong transverse carina anteriorly but otherwise smooth, polished, with very small punctures. Mesonotum also strongly polished, non-alutaceous, and with small, well spaced punctures; notauli strong, not quite reaching anterior and posterior margins of mesoscutum. Propodeal disc 1.1 X as wide as long; lateral and sublateral carinae strong, posterior carina developed but not much stronger than the transverse striae which cover the declivity; median carina nearly reaching transverse carina but incomplete basally, flanked by several other rather irregular carinae which fill an elongate basal triangular area; sides of disc smooth and polished. Mesopleurum polished, obscurely punctate, callus large and convex, subtended by a large groove. Middle tibiae spinose above. Fore wing with subdiscoidal vein strong, discoidal vein moderately strong, vein margining outer side of discoidal cell weak. Abdominal petiole relatively long, about as in *brasiliensis* (Fig. 82). Subgenital plate broadly truncate. Genitalia with the mesal lobes of the parameres very large, with numerous rather small setae along the margins; ventral arms of digiti broad, their inner margins rounded (Fig. 107); aedoeagus about as figured for *venezuelana* (Fig. 105) except not quite as broad.

Remarks.—This species is known only from the type.

46. Apenesia transversa new species

Holotype.— ♂, BRAZIL: Rio de Janeiro, July (no further data) [USNM, No. 66012].

Description of type. — Length 6 mm.; LFW 4.3 mm. Body black except basal abdominal segments weakly suffused with brownish; palpi straw-colored; mandibles yellowish brown except teeth rufous; antennae light castaneous except scape suffused with brown and apical segments of flagellum somewhat infuscated; tegulae testaceous; coxae and femora brown, trochanters, tibiae, and tarsi light yellowish brown; wings subhyaline, veins and stigma brown, setulae dark. Mandibles with five teeth, third and fourth teeth smaller than the others, basal tooth rather broad (Fig. 115). Clypeus weakly arcuately concave apically (about as in *brasiliensis*, Fig. 103); median carina low but well-defined, angulate in profile. First four antennal segments in a ratio of about 35:7:25:25, segment three 3 X as long as wide, segment eleven 5 X as long as wide; pubescence erect, bristling, setulae of segment eleven nearly as long as width of segment; flagellum with a few erect setae on the basal segments which stand out slightly above the pubescence. Front polished, non-alutaceous, with small punctures which are separated, for the most part, by more than their own diameters, below and toward the vertex rather widely spaced. Head wider than high, WH 1.07 X LH; inner orbits convergent below, WF .55 X WH, 1.08 X HE. Vertex rounded off a distance above the eye tops equal to somewhat more than half HE. DAO .19 X WF; OOL 1.28 X WOT; anterior ocellus very slightly above a line drawn between eye tops. Pronotal disc short and broad, with a strong transverse carina anteriorly, disc otherwise smooth except for faint impression on the sides just before the posterior margin; surface polished, punctures small but numerous. Mesoscutum polished, punctures small, sparse, somewhat more crowded along notauli, which are complete; center of scutellar disc impunctate. Propodeal disc short, about 1.3 X as wide as long; lateral and median carinae strong, sublateral carinae moderately strong; posterior carina well developed though not standing out strongly above the transverse striae which cover the declivity; disc with basal triangle filled with strong sculpturing, also sculptured on the sides, otherwise smooth and polished. Mesopleurum polished, obscurely punctate, callus large and convex, subtended by a strong groove. Fore wing with subdiscoidal vein strong, reaching wing margin as a faint line; top and outer side of discoidal cell weakly indicated, also the first recurrent vein. Abdomen with a short petiole. Subgenital plate broadly truncate apically. Genitalia with the aedoeagus strongly tapering apically, the apical portion consisting of a pair of strongly compressed lobes which are minutely denticulate on their mesal surfaces (Fig. 110); ventral arms of digiti about as in *peruana*, but more rounded apically; parameres shaped as in *peruana*, somewhat less strongly setose than in that species.

Remarks. — This species is known only from the type.

47. APENESIA VENEZUELANA new species

Holotype. — ♂, VENEZUELA: San Esteban, January 1940 (no further data) [MCZ, No. 30444].

Description of type. — Length 6.3 mm.; LFW 4.0 mm. Head, thorax, and abdominal petiole black; remainder of abdomen dark brown with annulations of paler brown, especially toward the base; palpi straw-colored; mandibles yellowish brown except teeth rufous; scape and base of flagellum straw-colored, apical portion of flagellum gradually darkened to castaneous; tegulae and legs entirely straw-colored; wings subhyaline, veins and stigma brown. Mandibles with five teeth, the third and fourth teeth smaller than the others (as in *transversa*, Fig. 115). Clypeus broadly truncate, sides of truncation rounded; median carina low and even. First four antennal segments in a ratio of about 19:5:10:10, segment three 2.5 X as long as thick, segment eleven 3.4 X as long as thick; pubescence pale, bristling, setulae of segment eleven about two-thirds as long as width of segment; flagellum also with a few erect setae on basal segments which stand somewhat above the pubescence. Front polished, non-alutaceous, punctures fairly strong, somewhat crowded in the middle (about their own diameters apart), below, on the sides, and toward the vertex rather widely spaced. Head wider than high, WH 1.06 X LH; inner orbits convergent below, WF .56 X WH, 1.10 X HE. Vertex rounded off a distance above eye tops equal to about two-thirds HE. DAO .19 X WF; OOL 1.30 X WOT; front ocellus touching a line drawn between eye tops. Pronotal disc smooth and polished, with small punctures; transverse carina strong. Mesoscutum polished and with relatively few punctures, these mostly crowded along the notauli, the latter not quite reaching the anterior or posterior margins; scutellar disc impunctate in the center. Propodeal disc short, about 1.3 X as wide as long; lateral and sublateral carinae strong, posterior transverse carina not strongly differentiated from the transverse striae which cover the declivity; median carina moderately strong, flanked by several other irregular carinae which fill the basal triangular area, disc otherwise smooth and polished.

Mesopleurum with distinct punctures except on the callus, which is large and convex, subtended by a strong groove. Fore wing with discoidal cell faintly outlined, subdiscoidal vein reaching wing margin as a very faint line. Abdomen with a short petiole. Subgenital plate weakly emarginate apically. Genitalia (Fig. 105) with the mesal lobes of the parameres unusually large, the ventral arms of the digiti unusually slender; aedoeagus rather broad, terminating in a pair of compressed lobes, each bearing a finger-like process on its inner side.

Remarks. — This species is known only from the type. The genitalia are very similar to those of *zamora,* from Ecuador, but that species has darker legs and antennae and a more elongate propodeum.

48. APENESIA BRASILIENSIS (Kieffer) new combination

Rhabdepyris brasiliensis Kieffer, 1910, Ann. Soc. Ent. France, 78: 298. [Type: ♂, BRAZIL: Pará (C. F. Baker) (Pomona College, Claremont, Calif.)]

Glenobethylus brasiliensis Kieffer, 1914, Das Tierreich, 41: 495.

Description of type. — Length 6.5 mm.; LFW 4.8 mm. Head and thorax shining black, abdomen piceous except somewhat paler on sides of basal segments and at extreme tip; mandibles yellowish brown, teeth rufous; scape testaceous, flagellum of this color basally, but gradually infuscated to medium brown toward the apex; tegulae testaceous; legs wholly bright yellowish brown; wings subhyaline, veins and stigma dark brown. Mandibles with five teeth, third and fourth small and close together, basal tooth strong, reflexed inward (as in *transversa,* Fig. 115). Clypeus broadly truncate (Fig. 103), somewhat elevated along the midline but without a sharply defined carina here. First four antennal segments in a ratio of about 22:5:12:10, segment three 2.5 X as long as thick, segment eleven slightly over 3 X as long as thick; pubescence semi-erect, bristling, setulae of segment eleven .6 as long as width of segment, basal segments (especially 3-7) also with a few completely erect setae which stand slightly above the others. Front shining, non-alutaceous, punctures strong, separated by slightly more than their own diameters except more crowded medially and anteriorly; vertex with smaller, sparser punctures. Head wider than high, WH 1.1 X LH; inner orbits convergent below, WF .53 X WH, 1.05 X HE; vertex broadly rounded off some distance above eye tops, distance from eye tops to vertex crest equal to about two-thirds HE.

Ocelli of moderate size, DAO .18 X WF; ocellar triangle compact, front angle less than a right angle; OOL 1.25 X WOT. Pronotum with a strong carina margining the disc anteriorly; disc otherwise rather smoothly convex, shining, punctures strong, separated by slightly more than their own diameters. Mesoscutum shining, non-alutaceous, punctures strong but rather scattered, more crowded along notauli; notauli strong, absent on anterior .1 and posterior .05; scutellum strongly shining, center of disc largely impunctate. Propodeum short, barely longer than wide, disc 1.2 X wider than long; disc with strong lateral, sublateral, and posterior transverse carinae, median carina strong but slightly undulate and not quite reaching posterior margining carina; disc with a fairly well-defined basal triangular portion filled with carinae (about seven on each side) which diverge somewhat posteriorly, remainder of disc smooth and polished. Mesopleural callus convex, strongly polished; remainder of mesopleurum polished, weakly punctate. Middle tibiae with stiff, spinose setae; claws strongly dentate. Fore wing with discoidal cell fully outlined by weakly pigmented lines, subdiscoidal vein continued on as a faint brown streak nearly to wing margin, first recurrent vein also weakly indicated. Abdomen petiolate (Fig. 82). Subgenital plate truncate. Genitalia with the lateral elements very similar to those of *peruana* (Fig. 106), aedoeagus also resembling that species but with larger and differently shaped apical lobes (Fig. 111).[8]

Other males examined. — BRAZIL: 1, Santarem (no further data) [USNM].

Variation. — The Santarem specimen is smaller (LFW 4 mm.) but very similar in most respects. The propodeum has fewer carinae (about five on each side of the midline) and these do not diverge behind; the median carina reaches the transverse carina as a weak line. The clypeus is more strongly elevated medially, this elevation appearing angulate in profile. The ocelli are slightly smaller and farther removed from the eyes, OOL being fully 1.5 X WOT.

49. APENESIA PERUANA new name

Cleistepyris punctatus Kieffer, 1910, Ann. Soc. Ent. France, 79:48. [Type: ♂, PERU: Marcapata (Staudinger) (Berlin Museum, No. 196)]. Preoccupied by *Apenesia punctata* Kieffer, 1904 (♀, Africa). — Kieffer, 1914, Das Tierreich, 41: 493.

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[8] The description and figure of the genitalia are based on the Santarem specimen, the genitalia of the type not having been examined.

Description of type. — Length 7 mm.; LFW 4 mm. Head and thorax deep, shining black, abdomen piceous; mandibles yellowish, their apices rufous; scape and base of flagellum yellowish brown, remainder of flagellum dull brown; tegulae testaceous; legs, including coxae, entirely bright yellowish brown; wings completely hyaline, veins and stigma brown. Mandibles with five teeth in a strongly oblique series, the apical two teeth sharp, the others rounded; teeth more evenly spaced and equal in size than in the preceding three species (Fig. 116). Clypeus broadly subtruncate (very weakly arcuately concave) apically (as in *brasiliensis,* Fig. 103). Antennae with the first four segments in a ratio of about 30:8:17:16, segment three 2.8 times as long as thick, segment eleven 3.1 times as long as thick; pubescence of flagellum erect, bristling, the setulae on segment eleven about half as long as width of segment. Front, vertex and temples strongly polished, non-alutaceous, front with punctures small but strong, separated by 2-3 X their own diameters. Eyes converging below, WF .56 X WH, 1.12 X HE; ocelli small, in a small triangle the front angle of which is less than a right angle, OOL 1.55 X WOT. Vertex evenly rounded; distance from posterior ocelli to vertex crest slightly greater than width of ocellar triangle. Pronotum with a strong transverse carina anteriorly; disc strongly shining, with numerous small punctures. Mesoscutum polished, non-alutaceous, with scattered small punctures; notauli strong, nearly attaining posterior margin. Propodeum short, only slightly longer than wide, the disc 1.25 X as wide as long; lateral carinae strong, sublateral carinae absent; median carina strong, not quite reaching the transverse carina; disc also with about 14 additional, somewhat irregular carinae which diverge somewhat from the midline posteriorly, the more lateral ones the shorter; postero-lateral corners of propodeal disc smooth and polished; side pieces of propodeum completely smooth and polished, posterior face transversely striate. Mesopleurum shining, the callus convex and impunctate, remainder of mesopleurum weakly punctate. Fore wing with discoidal vein fairly distinct, the discoidal cell in fact outlined by weakly pigmented veins; first recurrent vein evident as a weakly pigmented streak. First abdominal segment short-petiolate. Subgenital plate truncate. Genitalia (Fig. 106) with the ventral arms of the digiti moderately wide, the aedoeagus slender, with two rather slender apical lobes.[9]

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[9] The genitalia described and figured are those of a specimen from Hacienda San Juan, Peru, those of the type not having been extracted.

Other males examined. — PERU: 3, Hacienda San Juan, Colonia del Perene, Junin, June 1920 (Cornell Univ. Exped.) [CU, MCZ]; 1, El Campamiento, Col. Perene, Junin, 21 June 1920 (Cornell Univ. Exped.) [CU].

Variation. — The available specimens show only a small range in size, LFW varying from 3.9 to 4.4 mm. OOL varies from 1.5 to 1.68 X WOT; other head measurements show almost no variation. There is some variation in propodeal sculpturing, and in all specimens but the type the median carina reaches the transverse carina.

NITIDA SPECIES-GROUP

This group of five closely related species is confined to tropical South America. The mandibles are unlike those of any other American species-group, the inner margin consisting of a blade-like edge which is at most slightly undulate, only the apical tooth being distinct (Fig. 117). The type of *Propristocera* Kieffer, from Ceylon, has mandibles of this type, but the abdomen is sessile and there are several other structural differences from *nitida* and its allies. Hence I doubt if the name *Propristocera* could properly be applied to this group in the event *Apenesia* were divided into subgenera.

Other characters of this group include a short, obtusely angulate clypeus with its apex simple or bidentate; the eyes not convergent below; front polished, non-alutaceous, with minute punctures; propodeal disc wider than long, posteriorly in considerable part polished; middle tibiae spinose; abdomen petiolate, subgenital plate broadly, arcuately emarginate (Fig. 126); parameres greatly expanded apically (Fig. 120); aedoeagus terminating in four slender lobes (Figs. 120-123). Characters of this species-group are illustrated in Plates 9 and 10, and tabulated in Table VII.

TABLE VII. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF NITIDA GROUP

Species	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	Ant. 11 L/W	Flagellar pubescence	Margin clypeus
50. nitida	4.0	1.01	1.18	1.60	3.8	long	angulate
51. paraensis	4.2	1.00	1.10	1.30	3.4	long	bidentate
52. truncaticeps	4.0	1.00	1.30	1.40	3.2	medium	bidentate
53. quadrata	3.6	1.00	1.32	1.50	2.5	short	bidentate
54. laticeps	3.8	1.05	1.22	1.05	2.5	short	bidentate

50. Apenesia nitida (Kieffer) new combination

Cleistepyris nitidus Kieffer, 1910, Ann. Soc. Ent. France, 79: 49. [Type: ♂, PERU: Cosnipata-Ebene, 1000 meters, Dept. Cuzco, 3-12-1900 (Garlepp) (Berlin Museum, No. 197)]. — Kieffer, 1914, Das Tierreich, 41: 493.

Description of type. — Length 5.3 mm.; LFW 4.0 mm. Head and thorax shining black, abdomen dark reddish brown, sides of first tergite suffused with light brown; mandibles light castaneous except somewhat rufous basally and apically; antennae light castaneous except suffused with dull brownish toward the apex; tegulae testaceous; legs wholly bright yellowish brown, femora very slightly darker than rest of legs; wings hyaline, veins and stigma brown. Mandibles of the form typical of the species-group (Fig. 117). Clypeus moderately long and prominent, its sides approaching evenly to an obtuse median angulation (Fig. 125); median carina strong, weakly sloping in profile. First four antennal segments in a ratio of about 33:8:21:20, segment three 3 X as long as thick, segment eleven 3.8 X as long as thick; flagellar pubescence erect, bristling, that of segment eleven about .8 as long as width of segment. Front, vertex, and temples strongly polished, non-alutaceous, punctures minute and inconspicuous, separated by 5 or more X their own diameters. Head very slightly broader than high. Eyes slightly closer together in the middle than below; WF .59 X WH, 1.18 X HE; vertex rather evenly rounded off well above eye tops, distance from eye tops to vertex crest about .8 X HE; occipital carina complete, stronger than in *truncaticeps* and partially visible in full frontal view. Ocelli not enlarged, forming a compact triangle, front angle less than a right angle; OOL 1.60 X WOT. Pronotum as in *truncaticeps* except transverse carina a little weaker and located slightly further forward, part way down the oblique anterior face. Mesonotum polished and virtually impunctate; notauli complete; scutellum with well formed basal groove and lateral foveae. Propodeum slightly longer than wide, but the disc short, wider than long, disc with lateral margining carinae and with an arching transverse carina behind, median carina present but somewhat weakened behind; disc with weak and irregular reticulate sculpturing along the lateral carina and along the median carina, smooth and polished only in relatively narrow streaks on each side, the streaks widened and approaching medially behind. Mesopleurum polished, callus strong, subtended by a groove which anteriorly arches strongly upward. Claws with a very small tooth. Wings not differing noticeably from those of *truncaticeps.* Abdomen with a strong petiole (as in Fig. 119). Subgenital plate arcuately concave apically (as in Fig. 126). Genitalia not studied.

Other males examined. — PERU, 1, same data as type [Berlin Museum].

Variation. — The second specimen is slightly larger (length 5.9 mm., LFW 4.2 mm.). OOL measures 1.45 X WOT. There are no other noticeable structural differences.

51. APENESIA PARAENSIS (Kieffer) new combination

Propristocera paraensis Kieffer, 1910, Ann. Soc. Ent. France, 78: 290-291. [Type: ♂, BRAZIL: Pará (C. F. Baker) (Pomona College, Claremont, Calif.)]. — Kieffer, 1914, Das Tierreich, 41: 486.

Description of type. — Length 5.8 mm.; LFW 4.2 mm. Head black; thorax black except pronotal collar light reddish brown; abdomen dark brown, first tergite margined with light brown and other tergites indistinctly banded with light brown apically; mandibles yellowish brown except apical margin dark rufous; clypeus dark brown; antennae wholly light yellowish-brown except apical five segments gradually infuscated; tegulae pale testaceous; legs wholly bright straw-colored; wings hyaline, setulae dark, veins and stigma brown. Mandibles as in *truncaticeps* (Fig. 117). Clypeus short, rather flat, median carina weak, apex weakly bidentate (as in Fig. 124). Antennae elongate, first four segments in a ratio of about 36:10:17:17, segment three 3.4 X as long as thick, segment eleven also 3.4 X as long as thick although shorter and more slender than three; flagellar pubescence semierect, setulae of segment eleven about .8 as long as width of segment, flagellum also with some setulae which are completely erect and slightly longer than the semierect setulae, some of these erect setae actually slightly longer than the width of the segments bearing them (these erect setae are most noticeable on segments 3-8). Front shining, nonalutaceous, punctures small, separated by 3-5 X their own diameters; occipital carina complete though rather weak dorsally. Head rather broad, subquadrangular, about as wide as high, vertex somewhat squared off well above eye tops, distance from eye tops to vertex crest equal to about .75 X HE. Front of moderate width, inner orbits subparallel on lower two-thirds; WF .57 X WH, 1.10 X HE; ocelli rather small, DAO .17 X WF;

ocellar triangle compact, front angle less than a right angle, anterior ocellus touching a line drawn between eye-tops; OOL 1.3 X WOT. Pronotum with a strong carina margining the disc in front, surface of disc otherwise weakly convex except for a faint transverse depression well before the posterior margin; pronotum, like the mesonotum, strongly shining, non-alutaceous, and only obscurely punctate; notauli deep, diverging anteriorly, extending from posterior margin of mesoscutum nearly to anterior margin; basal groove and lateral foveae of scutellum rather deep. Propodeum short, about 1.2 X as long as wide, disc actually slightly wider than long; lateral and median carinae rather strong, the latter not quite reaching the transverse carina margining the disc behind, this carina moderately strong; basal median area of disc strongly reticulate, disc elsewhere smooth and polished, without sculpturing. Mesopleurum polished, non-alutaceous, weakly punctate, callus prominent. Claws strongly dentate. Fore wing with discoidal cell fully outlined by well pigmented lines, first recurrent vein faintly indicated; discoidal vein interstitial with media, transverse median vein weakly oblique, nearly straight. Abdomen with petiole about as in *truncaticeps* (Fig. 119). Subgenital plate (Fig. 126) broadly, arcuately emarginate apically. Genitalia (Fig. 120) with greatly expanded, bilobed parameres; aedoeagus moderately slender, minutely spinose median lobes.[10]

Other males examined. — BRAZIL: 1, Santarem (no further data) [USNM]; 1, Rio Branco, 1 April 1954 (M. Alvazanga) [Secr. Agri., Dept. Zool., São Paulo, Brazil]. VENEZUELA: 1, Barinitas (P. Anduze) [USNM].

Variation. — The other two Brazilian specimens are smaller than the type (LFW 3.3, 3.6 mm.) and have the median lobe of the clypeus truncate rather than bidentate (probably the result of wear). In these specimens OOL is 1.4-1.5 X WOT. In the Venezuela specimen LFW is 3.3 mm; WF 1.3 X HE, OOL 1.4 X WOT. In this specimen the antennae are somewhat infuscated beginning with segment five. The genitalia of this specimen differ in no noticeable way from those of the Santarem specimen. In both of these specimens, WH is about 1.03 X LH.

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[10] The description and sketch of the genitalia are based on the Santarem specimen. The genitalia of the type were not extracted, but the shape of the parameres agrees perfectly with the Santarem specimen.

52. APENESIA TRUNCATICEPS (Kieffer) new combination

Cleistepyris truncaticeps Kieffer, 1910, Ann. Soc. Ent. France, 79: 50 [Type: ♂, BOLIVIA: Mapiri (Staudinger) (Berlin Museum, no. 198)].

Cleistepyris punctaticeps Kieffer, 1914, Das Tierreich, 41: 494. [Error for *truncaticeps*.]

Propristocera boliviensis Ogloblin, 1938, An. Mus. Arg. Cien. Nat., 40: 44-46. [Type: BOLIVIA: ♂, Dept. Santa Cruz, Prov. Sara, Nov. 1916 (J. Steinbach) (Mus. Arg. Cien. Nat., no. 53.046)]. New synonymy.

Description of type. — Length 5.3 mm.; LFW 4.0 mm. Head and thorax shining black, abdomen dark reddish brown, paler basally and apically; mandibles castaneous; scape light castaneous, flagellum also of this color basally, but becoming gradually suffused with dull brown toward the apex; tegulae testaceous; legs wholly bright yellowish castaneous, spurs somewhat reddish; wings hyaline, stigma brown, veins light brown, Mandibles as in Figure 117. Clypeus rather short, its sides approaching evenly to an obtusely angulate apex which bears two weak teeth (Fig. 124); median carina low and rather ill-defined. First four antennal segments in a ratio of about 17:5:8:8, segment three about 3 X as long as thick, segment eleven about 3.2 X as long as thick; flagellar pubescence erect, bristling, setulae of segment eleven about .7 as long as width of segment. Front, vertex, and temples strongly polished, non-alutaceous, punctures minute and inconspicuous, separated by 5 or more X their own diameters. Head as wide as high; inner margins of eyes subparallel on their lower half; WF .62 X WH, 1.3 X HE; vertex broadly rounded off far above eye tops, distance from eye tops to vertex crest subequal to HE. Ocelli not enlarged, in a compact triangle, the front angle less than a right angle; OOL 1.4 X WOT. Occipital carina complete dorsally, though not visible in frontal view. Pronotum with some transverse rugae on the collar; anterior face oblique, smooth; disc with a transverse carina anteriorly, behind this with a low transverse welt, more noticeable on the sides; surface smooth, polished, non-alutaceous and with only minute punctures. Mesoscutum polished, notauli complete; scutellum polished, very weakly punctate, basal groove and lateral foveae well developed. Propodeum slightly longer than wide, but the disc actually wider than long; disc with complete lateral and median carinae and a complete carina margining the declivity, base with some short, irregular longitudinal carinae which disappear among some irregular transverse striations, sides and posterior third of median area smooth, shining, and without sculpturing. Mesopleurum shining, non-alutaceous, callus convexly elevated, subtended by a groove which reaches the posterior margin. Claws with a well defined tooth. Fore wing with the discoidal vein arising at the junction of the basal and transverse median veins, well pigmented to about the length of the basal vein; subdiscoidal vein also somewhat pigmented, but outer side of discoidal cell very weakly pigmented. Abdomen distinctly petiolate (Fig. 119), rather broad apically, the subgenital plate broadly, arcuately emarginate (as in *paraensis*, Fig. 126). Genitalia with the parameres and volsellae virtually identical to those of *paraensis*, but the aedoeagus (Fig. 123) more parallel-sided and with much broader apical lobes.[11]

Specimens examined. — BOLIVIA: 1 ♂, C. Esperanza, Beni, 1921-22 (W. M. Mann) [USNM]; 1 ♂, Huachi, Beni, Sept. 1921 (W. M. Mann) [USNM]; 1 ♂, Mapiri, Pando (Staudinger) [type, Berlin Mus.]; 1 ♂, Prov. Sara (=Gutiérrez), Dept. Santa Cruz, Nov. 1916 (Steinbach) [type of *boliviensis*, Mus. Arg. Sci. Nat.]; 1 ♂, Las Juntas, Chuquisaca, Dec. 1913 (Steinbach) [CM]. PERU: 1 ♂, Tingo Maria, Huanuco, 22 Jan. 1947, 2200 feet (J. C. Pallister) [AMNH].

Variation. — The available specimens show remarkable uniformity in sculpture, coloration, and body measurements. LFW varies from 3.2 to 4.0, WH/LH from 1.0 to 1.03, WF/HE from 1.16 to 1.33, OOL/WOT from 1.32 to 1.53.

53. APENESIA QUADRATA new species

Holotype. — ♂, BRAZIL: Diamantina, Minas Gerais, 14-18 Nov. 1919 (Cornell Univ. Exped.) [CU, No. 3881].

Description of type. — Length 4 mm.; LFW 3.6 mm. Body dark castaneous, shining, abdomen slightly paler than head and thorax, first tergite margined with light brown; mandibles yellowish brown, the apical margin rufous; basal three antennal segments yellowish brown, antennae gradually infuscated beginning with fourth segment, apical segments dark brown; tegulae testaceous; legs wholly bright yellowish brown, including coxae; wings hyaline, veins and stigma brown. Mandibles broad apically, edentate except for the apical tooth (as in Fig. 117). Clypeus very short and broad, bidentate medially, median

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[11] I did not examine the genitalia of the types of either *truncaticeps* or *boliviensis*. This statement is based on a study of the specimens from C. Esperanza and Huachi, Bolivia, and from Tingo Maria, Peru; the drawing was made from the first-named specimen.

line polished but barely elevated (as in Fig. 124). First four antennal segments in a ratio of about 30:8:13:13, segment three about twice as long as thick, segment eleven 2.5 X as long as thick; flagellar pubescence of moderate length, longest setulae of segment eleven about half as long as width of segment; basal flagellar segments with numerous erect setae which stand well above the pubescence. Front polished, non-alutaceous, punctures minute, separated by 4-6 X their own diameters; occipital carina strong throughout, barely visible when head is viewed from front. LH equal to WH; distance from eye tops to vertex crest actually slightly greater than HE. Front broad, WF .63 X WH, 1.32 X HE; ocelli not enlarged, in a small triangle far removed from eyes; OOL 1.5 X WOT; anterior ocellus well above a line drawn between eye tops. Pronotum with a rather delicate transverse carina behind which the disc is broadly elevated until just before the posterior margin; disc strongly polished and with minute punctures. Mesonotum and mesopleura as in *paraensis*, polished and only very weakly punctate. Propodeum slightly longer than wide, but the disc slightly wider than long; basal triangle of disc filled with delicate carinae which diverge from the median line, median carina nearly reaching the transverse carina, which is very weak; greater part of disc strongly polished, declivity with weak transverse striations which are obsolescent on the sides; spiracles elongate, directed dorsad. Fore wing with discoidal and subdiscoidal veins weak, outer side of discoidal cell closed by a barely pigmented vein. Abdominal petiole rather short. Subgenital plate as figured for *paraensis* (Fig. 126). Genitalia with the lateral elements virtually identical to those of *paraensis*, the aedoeagus (Fig. 121) similar, but the median apical lobes as long as the very slender lateral lobes, apex also with a rather prominent series of pectinations on the dorsal side just below the median lobes.

Remarks. — This species is known only from the type.

54. Apenesia laticeps new species

Holotype. — ♂, BRAZIL: Lassance, Minas Gerais, 9-19 Nov. 1919 (Cornell Univ. Exped.) [CU, No. 3882].

Description of type. — Length 4.5 mm.; LFW 3.8 mm. Head and thorax piceous, abdomen dark castaneous except first tergite margined with light brown; mandibles yellowish brown, apical margin rufous; antennae yellowish brown basally, beyond segment three slightly darkened to a dull, medium brown; tegulae testaceous; legs wholly bright yellowish brown; wings hyaline, veins and stigma brown. Mandibles of the usual form of the species-group (as in Fig. 117); clypeus short, bidentate medially (as in Fig. 124). First four antennal segments in a ratio of about 31:9:15:15, segment three 2.1 X as long as thick, segment eleven 2.5 X as long as thick; flagellar pubescence suberect, moderately long, setulae of segment eleven about half as long as width of segment; erect setae conspicuous on basal segments, standing well above the pubescence. Front shining, non-alutaceous, punctures small although somewhat larger and more abundant than in *paraensis* or *quadrata*, separated from one another by 2-4 X their own diameters. Occipital carina complete, visible at crest of vertex in full frontal view. Head broad, the eyes prominent and somewhat bulging; WH 1.05 X LH; distance from eye tops to vertex crest equal to about .8 X HE. Front of moderate breadth, WF .59 X WH, 1.22 X HE; ocelli slightly enlarged, DAO .18 X WF; anterior ocellus touching a line drawn between eye tops; OOL 1.05 X WOT. Pronotum with a strong, arching transverse carina, behind which the disc is weakly elevated, then depressed just before the posterior margin; disc polished, punctures weak and well separated. Mesoscutum polished, weakly punctate, notauli strong and complete. Propodeum 1.2 X as long as wide, the disc .9 as long as wide; median carina not quite reaching transverse carina, which is fairly strong; disc with irregular sculpturing on both sides of median carina, elsewhere polished. Fore wing with discoidal cell very weakly outlined by pigmented lines. Middle tibiae strongly spinose. Abdominal petiole rather short. Subgenital plate broadly emarginate, as figured for *paraensis* (Fig. 126). Genitalia with the parameres and volsellae essentially as figured for *paraensis* except that the parameres have a larger number of relatively weaker setae; aedoeagus (Fig. 122) with the lateral apical lobes more slender than in *paraensis*, nearly as slender as in *quadrata*, median dorsal portion with a series of pectinations as in *quadrata*, but the median apical lobes shorter than in that species.

Paratypes. — BRAZIL: 3 ♂♂, same data as type [CU, MCZ].

Variation. — The paratypes are all slightly larger than the type (LFW about 4 mm.), but they differ scarcely at all in structure or standard measurements. In one specimen the antennae are very slightly longer, segment eleven measuring 2.8 X as long as thick.

Female Apenesia

As noted in the introductory section, I have grouped together here the nine species known from females only and the one species (*parapolita*) known from both sexes. Under several of the females I have indicated to which species-group they may belong, but at this stage of our knowledge these are no more than rash surmises. Some of the important characters of the females are summarized in Table VIII and some are illustrated in Plate 10.

TABLE VIII. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF FEMALE APENESIA

Species	LH+LT (mm.)	LH/WH	Scape L/W	L Flagellum/ L Scape	Propodeum L/Max W	Propodeum Max W/Min W	Clypeus
37: parapolita	1.43	1.30	2.8	3.2	2.40	1.32	produced
55. paradoxa	1.52	1.15	3.0	2.7	1.65	1.30	produced
56. insolita	1.30	1.37	2.5	3.2	2.40	1.25	truncate
57. delicata	1.28	1.26	2.8	2.7	2.10	1.70	truncate
58. dominica	1.68	1.15	3.4	2.2	2.20	1.50	truncate
59. amoena	2.40	1.15	2.3	2.0	1.90	1.80	emarginate
60. substriata	2.50	1.15	2.3	2.0	2.10	1.90	emarginate
61. amazonica	3.65	1.11	2.8	2.0	1.80	1.60	emarginate
62. flavipes	2.35	1.04	2.8	2.1	2.10	1.65	truncate
63. chontalica	2.70	1.00	2.9	2.0	1.95	1.55	truncate

37. APENESIA PARAPOLITA new name

Propristocera polita Evans, 1958, Proc. Ent. Soc. Wash., 59: 294-295. [Preoccupied; see description of male on an earlier page (*brasiliensis* group)].

Plesiallotype. — ♀, MARYLAND: Bladensburg, 21 July, with *Ponera contracta* (? =*coarctata pennsylvanica*) [USNM].

Description of plesiallotype. — Length 2.5 mm.; LH 0.53 mm.; LT 0.9 mm. Entirely testaceous, including legs and antennae. Body covered sparsely with pale erect setae, legs and basal antennal segments also with short erect or semi-erect setae. Mandibles moderately broad, with four sharp teeth in an oblique series (Fig. 127). Clypeus with a prominent, somewhat trapezoidal median lobe, its apex weakly obtusely angulate; median line carinate. Head 1.30 X as long as wide, its sides gently arcuate so that the head is wider in the middle than elsewhere; vertex slightly concave in anterior view. Eyes very small, nearly circular, with about five ill-defined facets; greatest diameter of eye only about .10 X distance between the eyes. Head wholly although weakly alutaceous, strongly shining; punctures large, separated by 2-3 X their own diameters except absent from a fairly wide median strip. Scape 2.8 X as long as thick, strongly curved but not much flattened; flagellum more than 3 X as long as scape, somewhat incrassate, antennal segment eleven much wider than long, about 1.3 X as wide as segment three. Pronotal disc about 1.4 X as long as wide, its anterior margin evenly rounded, its surface shining although more strongly alutaceous than front; punctures inconspicuous, largely absent medially. Mesonotum .7 as long as wide, weakly alutaceous, weakly punctate. Propodeum (Fig. 136) very long, 1.6 X as long as pronotal disc; propodeal length 2.4 X maximum width, maximum width 1.32 X minimum width, constriction thus weak, well forward, distance from midpoint of constriction to median anterior margin slightly less than width of constriction; propodeal formula 34:25:35; surface of propodeum shining, weakly alutaceous, with a few small punctures on the sides. Mesopleurum with its dorsal surface rounded onto its lateral surface. Middle tibiae with only about six spines, not counting those at apical margin. Abdomen elongate, shining, first segment with a very short petiole.

Other females examined. — Twelve, from the following localities: TENNESSEE: 1, Sinks Canyon, Blount Co., 22 Sept. 1959 (tree crotch, W. Suter) [MCZ]. GEORGIA: 1, Ft. Gordon, Richmond Co., 15 Nov. 1958 (under bark of pine tree stump in swamp, R. R. Snelling) [CDAS]; 1, Columbus, 20 Aug. 1948 (L. W. Cunningham) [INHS]. ALABAMA: 1, Alberta City, Tuscaloosa Co., 1 April 1949 (under bark of fallen pine, B. D. Valentine) [MCZ]. LOUISIANA: 1, Kisatchie Nat. For., near Clarence, 29 June 1950 (Christiansen) [MCZ]. ARKANSAS: 1, Washington Co., 16 Dec. 1941 (M. W. Sanderson) [INHS]. ILLINOIS: 2, Rockford, 3 April 1934 (in old log, T. Horrall) [INHS]; 1, Ware, 3 Feb. 1934 (log in woods, Frison & Mohr) [INHS]; 1, Eichorn, 2 Feb. 1934 (Frison & Mohr) [INHS]; 1, Ursa, 9 Aug. 1945 (debris in hollow sycamore, C. C. Hoff) [INHS]; 1, Antioch, 27 Oct. 1943 (tamarack bog, woody debris, Ross & Sanderson) [INHS].

Variation. — The twelve females listed above vary in size from 2.2 mm. (LH 0.50 mm., LT 0.82 mm.) in the specimen from

Ware, Ill., to 3 mm. (LH 0.63 mm., LT 1.05 mm.) in the specimen from Tuscaloosa Co., Ala. Body color varies from testaceous to rich castaneous, but the legs and antennae are testaceous throughout. LH/WH varies over the narrow range of 1.30-1.39, maximum/minimum width of propodeum over the narrow range of 1.2-1.4. There is somewhat greater variation in the length of the pronotum and propodeum as compared to the width; length/width of pronotal disc varies from 1.28 to 1.47, length/maximum width of propodeum from 2.18 to 2.50. The number of discernible eye facets varies from 3 to 7. None of this variation seems closely associated with geographic distribution.

Remarks. — It will be noted that females have been taken from Alabama and Louisiana north to Illinois, although no males are presently recorded from west of the Appalachians. Nevertheless, I consider this association of sexes a very probable one. Not only are the females of appropriate size for *parapolita,* but the shape of the clypeus and the abdominal petiole suggest the males of this species. The only other alternative would be to assume that the female of *parapolita* has not yet been discovered and to describe the above females as a new species in which the males have not yet been discovered. I have followed what seems to me the more logical and conservative alternative.

55. APENESIA PARADOXA new species

Holotype. — ♀, PANAMA: Barro Colorado Island, Canal Zone, 10 March 1929 (S. W. Frost) [USNM, No. 66013].

Description of type. — Length 3 mm.; LH 0.62 mm.; LT 0.90 mm. Head piceous except somewhat paler along the middle and lower parts of the front; pronotum dark castaneous, almost piceous, except collar and sides light brown; mesonotum dark castaneous; mesopleurum piceous but with a yellowish spot behind; propodeum piceous except paler behind; abdomen bright yellowish brown; mandibles light brown, teeth rufous; clypeus and antennae testaceous; legs wholly bright testaceous. Mandibles relatively broad apically, with a sharp edge above; apex with four teeth, the third tooth very small (Fig. 128). Clypeus somewhat produced medially, its margin rounded, actually weakly subangulate; median carina strong, in profile straight, abruptly declivous just before the apex. Head 1.15 X as long as wide, its sides subparallel except weakly contracted anteriorly and posteriorly; vertex nearly straight. Eyes pale, each consisting of a single facet which is several times the diameter of one of the head punctures. Head strongly shining, not alutaceous or striate, but with strong punctures which are approximately their own diameters apart, except absent along a narrow median strip. Scape about 3 X as long as thick, slightly curved and flattened; flagellum about 2.7 X length of scape, somewhat incrassate, segment eleven wider than long. Pronotal disc 1.2 X as long as its posterior width, surface of pronotum shining, barely alutaceous with strong punctures which are absent from the midline. Mesonotum .6 X as long as wide (not counting part before the transverse depression, i.e., the scutum proper, which is distinct in this specimen); surface impunctate, shining, barely alutaceous. Propodeum (Fig. 137) 1.65 X as long as its maximum width, maximum width 1.3 X minimum width; constriction very weak, far forward, distance from midpoint of constriction to midpoint of anterior margin of propodeum equal to less than half width of constriction; propodeal formula 20:18:23; spiracles fully dorsal in position; disc alutaceous, moderately shining, with punctures toward the sides. Mesopleurum with the dorsal surface rounded onto the lateral surface; sides alutaceous and with a few large punctures. Spines of middle tibiae strong, about 14 in number not counting those at extreme apex; hind tibiae with only weak hairs. Abdomen elongate, sessile.

Remarks. — This striking species is known only from the type.

56. APENESIA INSOLITA new species

Holotype. — ♀, TEXAS: Brownsville, South Texas Garden, 8 Dec. 1910 (taken beating) [INHS].

Description of type. — Estimated total length about 2.2 mm. (abdomen missing); LH 0.50 mm.; LT 0.80 mm. Head and thorax, including antennae and legs, testaceous; eyes fuscous. Head with short, pale, semi-erect setae, but setae of thorax very sparse, short, and inconspicuous. Mandibles slender, with two strong apical teeth and a vestigial third tooth on the inner margin somewhat back from the apex (Fig. 130). Clypeus broadly truncate, actually weakly angularly emarginate, midline keeled. Head 1.37 X as long as wide, its sides strongly arched, the head much wider in the middle than anteriorly or posteriorly; vertex straight across in full frontal view, occipital carina clearly defined and visible for the full width of the vertex when head is viewed from in front. Eye with 14 convex, strongly defined facets; eye elliptical, its height .29 X distance between eyes. Head wholly, rather weakly alutaceous, strongly shining; punctures very shallow and inconspicuous. Scape 2.5 X as long as thick, gently curved but not strongly flattened; flagellum slightly more than 3 X as long as scape, slender, segment eleven only slightly wider than long and only very slightly wider than segment three. Pronotum rather narrow and transversely convex, disc about 1.5 X as long as its posterior width; mesonotum .8 as long as wide; surface of pro- and mesonota shining, very weakly alutaceous, obscurely punctate. Propodeum (Fig. 138) 2.4 as long as its maximum width, which is anterior to the spiracles, 3 X as long as its maximum width behind the spiracles; maximum width 1.25 X minimum width; maximum width behind spiracles slightly less than width at spiracles, the entire posterior two-thirds of propodeum essentially parallel sided except at extreme end; propodeal formula 14:12:11; surface of propodeum wholly alutaceous, moderately shining. Mesopleura strong dorsally, so that the thorax is much wider here than elsewhere; dorsal surface rounded into the broad lateral surface. Femora incrassate; middle femora only 1.6 X as long as thick; middle tibiae smooth, without spines even at apex. Abdomen missing.

Remarks. — I would not describe a unique specimen lacking an abdomen if it did not represent a most unusual species which forms an exception to several of the characters of the genus *Apenesia.* I refer to the large eyes, the non-spinose middle tibiae, and the almost parallel-sided propodeum. Although no other American species are close to *insolita*, the species does appear closely related to *Scleroderma unicolor* Westwood (Morocco) and *S. seychellensis* Kieffer (Seychelle Islands). These species do not by any means belong to *Scleroderma*, but probably to *Parascleroderma* Kieffer, a genus represented by several species in southern Europe and in Africa (the type species of which I have not seen). No males are currently assignable to this complex, but I would expect from the strong mesopleura and the structure of the head of the females that the group belongs in the Pristocerini. It should be noted that non-spinose tibiae occur in many species of *Dissomphalus*, and the propodeum is essentially parallel sided in that genus. As a matter of fact, it seems possible that *insolita* may represent the female sex of one of those species of *Apenesia* that stands very close to *Dissomphalus: dissomphaloides* or *denticulata*. I do not care to make any definite disposition of the name *Parascleroderma* at this time, but I do feel that it belongs in the Pristocerini and may represent only an aberrant species-group of *Apenesia*.

57. APENESIA DELICATA new species

Holotype.— ♀, JAMAICA: Gordontown, 4 Feb. 1937 (Chapin and Blackwelder) [USNM, no. 66014].

Description of type.— Length 2.6 mm.; LH 0.51 mm.; LT 0.77 mm. Entire body straw-colored, shining; mandibles tipped with rufous; antennae and legs pale straw-colored except spines of middle tibiae somewhat rufous. Mandibles slender, with two strong teeth and a weakly defined third tooth (about as figured for *insolita*, Fig. 130). Clypeus broadly truncate, with a strong median carina which is produced slightly beyond the margin as a weak median tooth. Head 1.26 X as long as wide, its sides subparallel except convergent just before the vertex, which is straight. Eyes small, longer than wide, dark rimmed and each with only two grayish facets. Head strongly polished, non-alutaceous, punctures minute and scarcely visible. Scape about 2.8 X as long as thick, flagellum about 2.7 X length of scape, apical segments much wider than basal segments. Pronotal disc 1.12 X as long as its posterior width; disc shining, non-alutaceous, punctures barely visible. Mesonotum about half as long as wide, smooth and shining. Propodeum 2.1 X as long as its maximum width, maximum width 1.7 X minimum width; distance from midpoint of constriction to midpoint of anterior margin of propodeum subequal to minimum width; propodeal formula 28:19:32; disc shining, without punctures or surface sculpturing. Mesopleurum with a small dorsal surface which is rather abruptly rounded to the broad lateral surface. Spines of middle tibia strong; hind tibia with only weak hairs. Abdomen with an unusually long petiole, the length of the petiole .6 the length of the hind tibia.

Remarks.— This species is known only from the type. It resembles closely the several species which follow except for the long abdominal petiole.

58. APENESIA DOMINICA new species

Holotype.— ♀, DOMINICA (LESSER ANTILLES): Roseau (F. Lutz) [MCZ, No. 30445].

Description of type. — Length 3.2 mm.; LH 0.68 mm.; LT 1.00 mm. Head and thorax pale castaneous, shining; mandibles straw-colored, the tips amber; antennae and legs straw-colored; abdomen pale castaneous, the segments indistinctly annulated with paler basally. Mandibles moderately wide, with three strong apical teeth and a very weakly indicated fourth tooth basad of these (Fig. 129). Clypeus weakly emarginate medially, with a high median carina which is declivous before the apical margin. Head 1.15 X as long as wide, its sides subparallel except rounded posteriorly, the vertex weakly rounded. Eyes rather small, longer than wide, each with several rather indistinct grayish facets (apparently about six). Head polished, very weakly alutaceous except along the median strip, which is smooth; punctures shallow and inconspicuous although numerous (except medially), separated for the most part by 2-3 times their own diameters. Scape slender, 3.4 X as long as thick, curved but not strongly flattened; flagellum slightly more than twice length of scape, apical segments much thicker than basal segments. Pronotal disc 1.1 X as long as its posterior width, weakly alutaceous although shining, punctures minute and inconspicuous. Mesonotum .57 X as long as wide, weakly alutaceous like the pronotum. Propodeum (Fig. 135) 2.2 X as long as its maximum width, maximum width 1.5 X minimum width; distance from midpoint of constriction to midpoint of anterior margin of propodeum .75 X minimum width; propodeal formula 20:13:20; disc shining, obscurely alutaceous, with a distinct linear median impression. Mesopleurum with a fairly prominent dorsal surface which is subangularly separated from the broad lateral surface. Spines of middle tibia strong, covering the entire upper surface; hind tibia with only weak hairs. Abdomen with a very short petiole, length of the petiole less than a third the length of the hind tibia.

Remarks. — This species is known only from the type.

59. APENESIA AMOENA new species

Holotype. — ♀, COSTA RICA: Hamburg Farm, Santa Clara Prov., 28 May 1925 (under loose bark of recently cut down tree, F. Nevermann) [USNM, No. 66015].

Description of type. — Length 4.8 mm.; LH 0.95 mm.; LT 1.45 mm. Head and thorax light yellowish brown; antennae and mandibles also of this color except the latter rufous-tipped; legs straw-colored except spines of middle tibia reddish; abdomen medium castaneous, contrasting to the much paler head and thorax. Mandibles slender, with two strong apical teeth (Fig. 133). Clypeus with a broad, arcuately V-shaped emargination, the margin with strong bristles; emargination not reaching the interantennal prominence. Head 1.15 X as long as wide, its sides subparallel except arcuately convergent posteriorly; vertex weakly concave in anterior view, occipital carina obsolescent. Eyes elongate-elliptical, dark, each with about eight small facets, eye height only about .15 X distance between eyes. Head shining, wholly covered with very fine longitudinal striations; punctures small, sparse, separated by 2-5 X their own diameters, somewhat more dense along midline of front than elsewhere. Scape 2.3 X as long as wide, distinctly flattened; flagellum only about twice as long as scape, apical segments only slightly thicker than basal segments. Pronotal disc 1.4 X as long as its posterior width, with a small median anterior notch; disc with fine striae like the front, but these obsolescent medially; punctures small, largely absent medially. Mesonotum about .7 as long as wide, smooth and polished. Propodeum 1.9 X as long as its maximum width, maximum width 1.8 X minimum width; distance from midpoint of constriction to midpoint of anterior margin equal to .8 width of constriction; propodeal formula 28:18:33; disc shining, very weakly alutaceous, with a few small, widely separated punctures. Dorsal surface of mesopleurum separated from broad lateral surface by a distinct ridge; lateral surface strongly alutaceous. Spines of middle tibia very strong. Abdomen with a very short petiole.

Paratype. — COSTA RICA: 1 ♀, same data as type [USNM].

Variation. — The single paratype is smaller than the type (LH .85 mm.; LT 1.30 mm.). This specimen lacks the abdomen, the front leg on the right side, and the middle and hind legs on the left side (in each case beyond the trochanters). LH is 1.17 X WH. Thoracic and propodeal measurements are the same as those presented for the type.

Remarks. — This species is very similar to *substriata* Kieffer, from Bolivia, differing chiefly in its more robust form and slightly different mandibles.

60. APENESIA SUBSTRIATA Kieffer

Apenesia substriata Kieffer, 1904, Ann. Mus. Genova, 41: 365. [Type: ♀, BOLIVIA: Rio Beni, 1891 (Balzan) (Mus. Civ. Stor. Nat. Genova)]. (Studied one of 5 cotypes). — Kieffer, 1914, Das Tierreich, 41: 395.

Description of cotype. — Length 5.1 mm.; LH 0.95 mm.; LT 1.55 mm. Head and thorax pale castaneous, almost straw-colored, abdomen dark castaneous, paler at the tip; mandibles and antennae pale castaneous except the former darker apically; legs straw-colored except the mid-tibial spines rufous. Mandibles slender, with two strong apical teeth and a small third tooth on the inner margin somewhat back from the apex (about as figured for *insolita*, Fig. 130). Clypeus with a strong, broadly V-shaped apical emargination, its median ridge rounded on top. Head 1.15 X as long as wide, its sides subparallel except roundly convergent posteriorly; vertex weakly concave in anterior view. Eyes of moderate size, somewhat darker than head, elliptical, each with eight facets. Head shining, wholly covered with very fine longitudinal striations; punctures small, sparse, rather irregularly distributed, somewhat closer along midline of front than elsewhere. Scape 2.3 X as long as wide, flattened; flagellum not much more than twice length of scape, not notably incrassate. Pronotal disc 1.5 X as long as wide, with a small median anterior notch, rather flat and with fine longitudinal striae much like the front; punctures sparse but fairly strong. Mesonotum .7 as long as wide, shining and with only very weak sculpturing and punctures. Propodeum 2.1 X as long as its maximum width, maximum width 1.9 X minimum width; constriction well forward, distance from midpoint of constriction to midpoint of anterior propodeal margin subequal to width of constriction; propodeal formula 27:16:30; disc of propodeum shining, weakly alutaceous, weakly punctate. Mesopleurum unusually flat, its vertical lateral surface separated from the smaller horizontal dorsal surface by a distinct ridge; side pieces shining though rather strongly alutaceous. Spines of middle tibiae very strong, about 18 in number not counting those at the apex; hind tibiae with only weak hairs. Abdomen elongate, subsessile, fusiform.

Remarks. — This species is known only from the type series. I am indebted to Dr. Delfa Guiglia for lending me a cotype for study.

61. APENESIA AMAZONICA Westwood

Apenesia amazonica Westwood, 1874, Thesaur. Ent. Oxoniensis, p. 171, pl. XXXI, fig. 12 [Type: ♀, BRAZIL: Amazonas (H. W. Bates) (HCOU)]. — Kieffer, 1914, Das Tierreich, 41: 395.

Description of type. — Length 7.5 mm.; LH 1.55 mm.; LT 2.1 mm. Head and thorax pale yellowish brown, abdomen dark castaneous, the segments indistinctly annulated with light brown apically; mandibles pale castaneous, black at apex; eyes blackish; antennae testaceous, flagellum dull, slightly darker than scape; legs wholly testaceous. Mandibles slender, with two strong apical teeth and a weak expansion of the inner margin far back from the apex (Fig. 131). Clypeus broad and short, with a broadly V-shaped apical emargination which is so deep that it reaches the rounded prominence between the antennal bases. Head 1.11 X as long as wide, its sides subparallel to just before the posterior margin, where they are arcuately convergent; vertex very weakly concave in anterior view, occipital carina obsolete. Eyes elongate-elliptical, with about 6-8 ill-defined facets. Front shining, covered with very fine, somewhat irregular longitudinal grooves; punctures small, separated by 3-5 X their own diameters except more crowded both medially and laterally; median line of front weakly depressed. Scape much flattened, 2.8 X as long as wide; flagellum about twice as long as scape, slender, not incrassate, segment eleven barely wider than long and barely wider than segment three. Pronotal disc 1.3 X as long as wide, with a median anterior notch and a very faint median impression on anterior half; punctures moderately strong, surface finely striate like the front. Mesonotum .65 X as long as wide, polished, obscurely alutaceous. Propodeum 1.8 X as long as its maximum width, maximum width 1.6 X minimum width; formula 21:15:24; distance from midpoint of constriction to anterior midpoint .67 X width at constriction; sides of disc, in front of spiracles, rather strongly ridged; surface of disc very weakly alutaceous, shining, punctures small, absent from midline but otherwise well distributed over surface. Mesopleurum with dorsal and lateral surfaces separated by a ridge, lateral surface rather flat, alutaceous. Middle tibiae with about 18 strong spines besides those at apex; front femora 2.2 X as long as wide. Abdomen very short-petiolate, fusiform.

Other females examined. — BRAZIL: 1, same data as type [HCOU]; 7, Ega (some labeled "Smith coll.") [BMNH]; 1, Pará [BMNH]; 11, Benjamin Constant, Amazonas, 18-28 Sept. 1962 (K. Lenko) [Sec. Agri., São Paulo, Brazil].

Variation. — The available specimens show considerable variation in size (length 4.4-7.5 mm.). LH/WH varies from 1.08 to 1.19; propodeal length varies from 1.8 to 2.05 X maximum width, maximum width 1.57 to 1.88 X minimum width. The smaller specimens tend to have the abdomen unbanded, though there is much variation in this regard; the larger specimens, even the type, have the abdomen much less distinctly banded than shown in Westwood's figure.

Remarks. — This species and the two preceding species form a very closely-knit complex, possibly representing females of the *columbana* group.

62. APENESIA FLAVIPES Cameron

Apenesia flavipes Cameron, 1888, Biol. Centr.-Amer., Hymen. I, p. 449, pl. XIX, fig. 11. [Type: ♀, PANAMA: Volcan de Chiriqui, 2-3000 feet (G. C. Champion) (BMNH)]. — Kieffer, 1914, Das Tierreich, 41: 395.

Description of type. — Length 5 mm.; LH 0.90 mm.; LT 1.45 mm. Body entirely light yellowish brown, including legs and antennae. Mandibles slender, bidentate. Clypeus very broadly truncate, with a sharp median carina which is straight in profile. Head 1.04 X as long as wide, sides somewhat bulging, head widest about midway of its length; vertex straight across, occipital carina complete, rather delicate. Eyes elliptical, about 1.8 X as long as wide, each with about 10 indistinct facets covered by a single, flat lens. Front polished, non-alutaceous, with a small pit in the center; punctures minute, widely separated, barely visible. Scape 2.8 X as long as wide; flagellum slightly thickened toward apex, only slightly more than twice as long as scape. Pronotal disc 1.25 X as long as wide, anterior margin with a weak median notch, surface smooth, punctures weak and widely separated. Mesonotum .7 X as long as wide, smooth and obscurely punctate. Propodeum 2.1 X as long as its maximum width, maximum width 1.65 X maximum width; formula 30:19:32; distance from midpoint of constriction to anterior margin slightly less than width of constriction; disc smooth and polished, impunctate. Mesopleurum with dorsal surface rounding gradually to the sides, surface smooth and obscurely punctate. Middle tibiae strongly spinose.

Remarks.— This species is known only from the type. None of the characters cited by Cameron for separating this species from *chontalica* are valid, and the only difference I can find is the slightly longer head (see further discussion under *chontalica*).

63. APENESIA CHONTALICA Westwood

Apenesia chontalica Westwood, 1881, Trans. Ent. Soc. London, 1881, p. 131, pl. 7, fig. 3. [Type: ♀, NICARAGUA: Chontales (HCOU)]. — Cameron, 1888, Biol. Centr.-Amer., Hymen. I, p. 448. — Kieffer, 1914, Das Tierreich, 41: 395.

Description of type. — Length 5 mm.; LH 1.0 mm.; LT 1.7 mm. Entire body rather uniformly light castaneous, shining; mandibles testaceous, darker apically; legs and antennae testaceous. Mandibles slender, bidentate, with a weak undulation on the inner margin (Fig. 132). Clypeus broadly, shallowly emarginate, its median line strongly elevated. Head 1.00 X as long as wide, sides very slightly arching, almost parallel except arcuately converging on posterior third; vertex straight across in anterior view, occipital carina complete, rather delicate. Eyes elliptical, not much darker than head, covered by a single smooth lens beneath which about six facets can barely be made out. Front strongly polished, very obscurely alutaceous, punctures small and sparse, separated by several times their own diameters. Scape 2.9 X as wide as long, distinctly flattened; flagellum about twice as long as scape, slender, only very slightly incrassate; segment eleven considerably wider than long, about 1.2 X as wide as segment three. Pronotal disc 1.3 X as long as wide, with a weak median notch anteriorly; surface polished, non-alutaceous, with a few weak punctures on sides. Mesonotum .65 X as long as wide, smooth and polished. Propodeum (Fig. 134) 1.95 X as long as its maximum width, maximum width 1.55 X minimum width; formula 32:23:36; distance from midpoint of constriction to midpoint of anterior margin .7 X width of constriction; disc strongly polished, non-alutaceous, with scattered weak punctures. Mesopleurum with dorsal surface rounded rather abruptly onto lateral surface, but with no evidence of a ridge at the junction. Middle tibiae with 14 strong spines besides those at the apex; front femora 2.1 X as long as wide. Abdomen subsessile.

Other females examined. — MEXICO: 3, in decayed log intercepted at Laredo, Texas, 20 Dec. 1940 [USNM]. GUATEMALA: 2, Livingston "4-5" (Barber & Schwarz) [MCZ]; 1, San Juan, Vera Paz (G. C. Champion) [BMNH]. COSTA

RICA: 1, Turrialba, 16 June 1949 (K. W. Cooper) [USNM].

Variation. — These specimens vary in length from 4.5 to 6.0 mm. LH varies from .97 to 1.03 X WH; the shorter-headed individuals are from Mexico, the two specimens with the longest heads from Guatemala and Costa Rica (suggesting a cline which might include the Panamanian *flavipes* as one extreme). There is considerable variation in propodeal shape, the length of the propodeum varying from 1.95 to 2.2 X its maximum width, the maximum width from 1.54 to 1.83 X minimum width. In some specimens the front and thoracic dorsum are slightly more evidently alutaceous than in others.

Remarks. — The most probable male of this species is *guatemalensis*, in the *pilicornis* group. It is possible that *pilicornis* is the male of *flavipes*, if in fact that species is distinct from *chontalica*.

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PLATE 1

Characters of the *pilicornis* species-group (males).

Fig. 1. *Apenesia pilicornis* n. sp., paratype, genitalia, ventral aspect

Fig. 2. *A. pilicornis* n. sp., paratype, paramere and digitus, lateral aspect (ventral surface toward right)

Fig. 3. *A. angusticeps* n. sp., holotype, paramere and digitus

Fig. 4. *A. ornata* n. sp., paratype, paramere and digitus

Fig. 5. *A. tenebrosa* n. sp., holotype, paramere and digitus

Fig. 6. *A. elongata* n sp., holotype, paramere and digitus

Fig. 7. *A. guatemalensis* n. sp., holotype, paramere and digitus

Fig. 8. *A. pilicornis* n. sp., holotype, apex of mandible

Fig. 9. *A. ornata* n. sp., holotype, apex of mandible

Fig. 10. *A. angusticeps* n. sp., holotype, apex of mandible

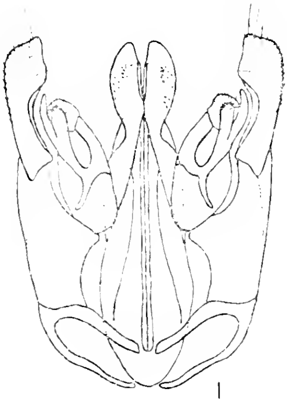
Fig. 11. *A. reducta* n. sp., holotype, apex of mandible

Fig. 12. *A. reducta* n. sp., holotype, paramere and digitus

Fig. 13. *A. pilicornis* n. sp., holotype, clypeus

Fig. 14. *A. elongata* n. sp., holotype, clypeus

Fig. 15. *A. pilicornis* n. sp., holotype, dorsal outline of pronotal disc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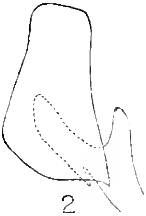
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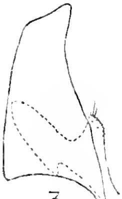
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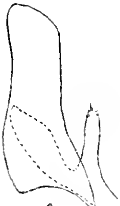
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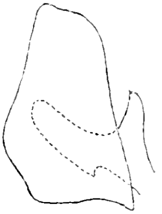
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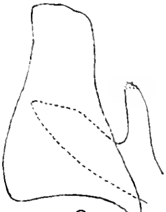
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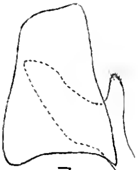
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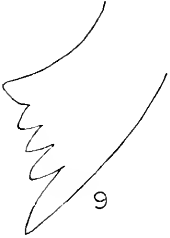
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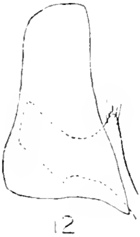
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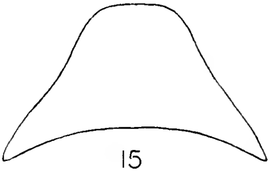
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PLATE 2

Characters of the *columbana* species-group (males)

Fig. 16. *Apenesia columbana* (Westwood), plesiotype, genitalia, ventral aspect.

Fig. 17. *A. sulcata* n. sp., holotype, paramere and volsella, ventral aspect

Fig. 18. *A. striatula* n. sp., holotype, genitalia

Fig. 19. *A. flammicornis* n. sp., holotype, genitalia

Fig. 20. *A. funebris* n. sp., holotype, paramere and volsella

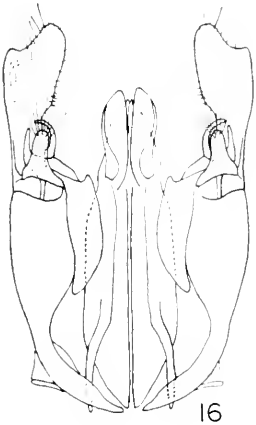
Fig. 21. *A. pallidicornis* n. sp., holotype, paramere and volsella

Fig. 22. *A. striatula* n. sp., holotype, base of abdomen, lateral aspect

Fig. 23. *A. columbana* (Westwood), plesiotype, base of abdomen

Fig. 24. *A. columbana* (Westwood), plesiotype, mandible

Fig. 25. *A. funebris* n. sp., holotype, mandible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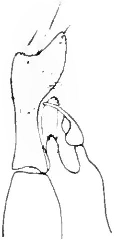
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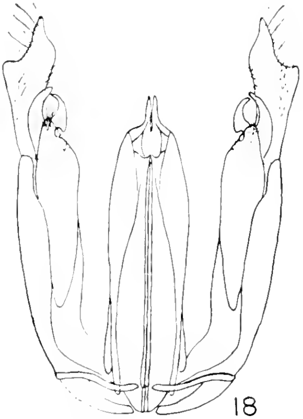
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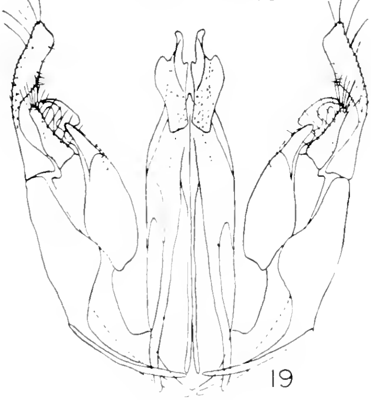
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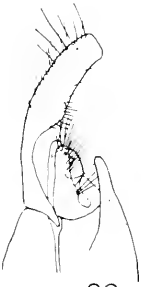
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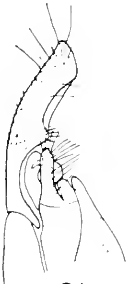
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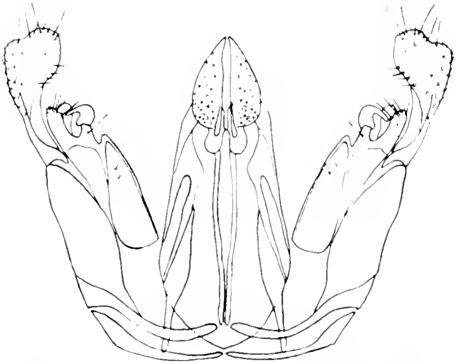
PLATE 3

Characters of the *exilis* species-group (males)

Fig. 26. *Apenesia pima* n. sp., holotype, genitalia, ventral aspect
Fig. 27. *A. cochise* n. sp., holotype, genitalia
Fig. 28. *A. exilis* n. sp., holotype, genitalia
Fig. 29. *A. martini* n. sp., holotype, genitalia
Fig. 30. *A. exilis* n. sp., holotype, apex of mandible
Fig. 31. *A. pima* n. sp., holotype, apex of mandible
Fig. 32. *A. cochise* n. sp., holotype, subgenital plate
Fig. 33. *A. exilis* n. sp., holotype, subgenital plate
Fig. 34. *A. exilis* n. sp., holotype, clypeus
Fig. 35. *A. pima* n. sp., holotype, clypeus
Fig. 36. *A. pima* n. sp., holotype, base of abdomen, lateral aspect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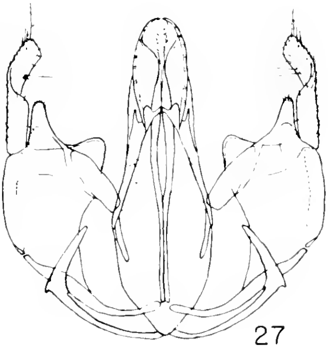
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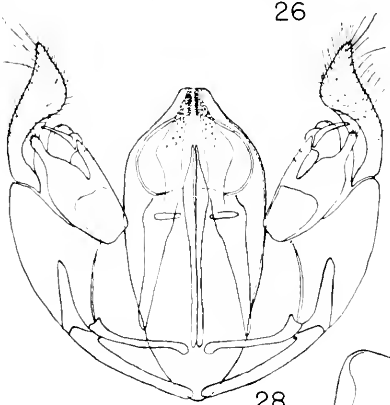
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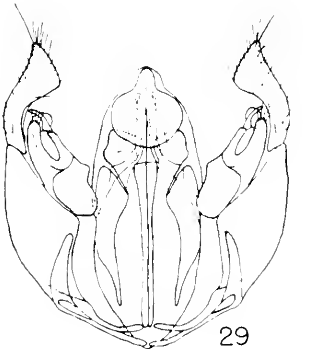
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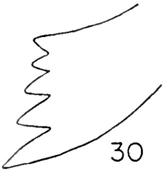
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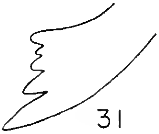
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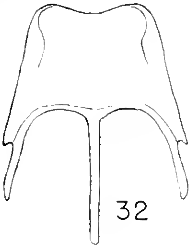
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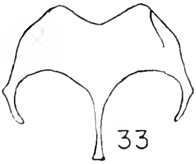
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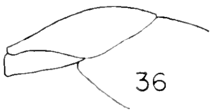
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PLATE 4

Characters of the *dissomphaloides, laevigata, exilis,* and *columbana* species-groups (males).

Fig. 37. *Apenesia dissomphaloides* n. sp., holotype, genitalia, ventral aspect

Fig. 38. *A. pallidula* n. sp., holotype, genitalia

Fig. 39. *A. columbana* (Westwood), plesiotype, clypeus

Fig. 40. *A. striatula* n. sp., holotype, clypeus

Fig. 41. *A. sulcata* n. sp., holotype, clypeus

Fig. 42. *A. dissomphaloides* n. sp., holotype, clypeus

Fig. 43. *A. pallidula* n. sp., holotype, base of abdomen, lateral aspect

Fig. 44. *A. laevigata* (Evans), holotype, base of abdomen

Fig. 45. *A. crenulata* (Kieffer), holotype, clypeus

Fig. 46. *A. pallidula* n. sp., holotype, clypeus

Fig. 47. *A. laevigata* (Evans), holotype, clypeus

Fig. 48. *A. dissomphaloides* n. sp., holotype, apex of mandible

Fig. 49. *A. denticulata* n. name, holotype, apex of mandible

Fig. 50. *A. pallidula* n. sp., holotype, apex of mandible

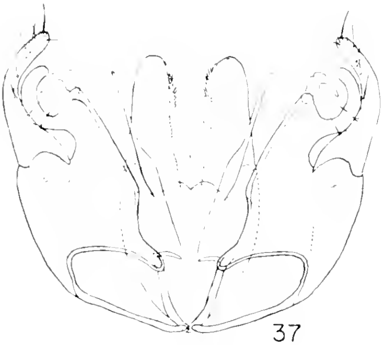
Fig. 51. *A. columbana* (Westwood), plesiotype, dorsal outline of pronotal disc

Fig. 52. *A. striatula* n. sp., holotype, pronotal disc

Fig. 53. *A. funebris* n. sp., holotype, pronotal disc

Fig. 54. *A. pima* n. sp., holotype, pronotal disc

Fig. 55. *A. exilis* n. sp., holotype, pronotal disc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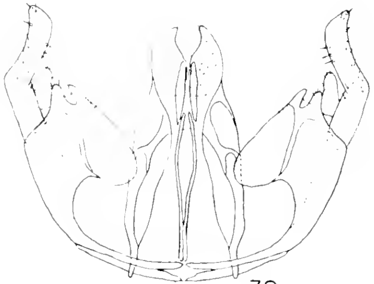
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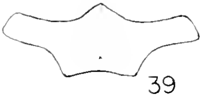
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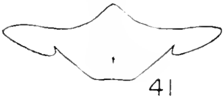
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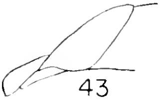
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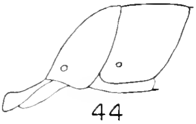
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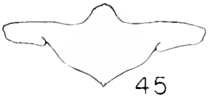
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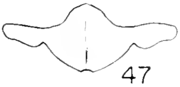
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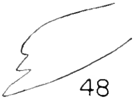
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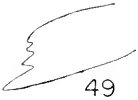
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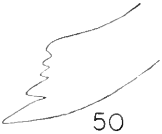
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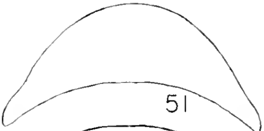
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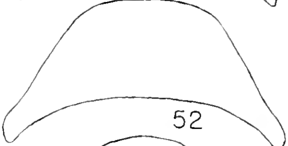
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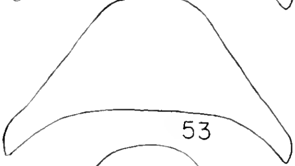
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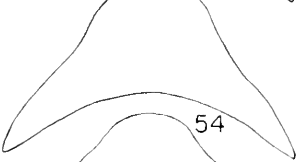
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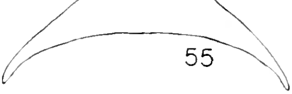
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PLATE 5

Characters of the *mexicana* species-group (males).

Fig. 56. *Apenesia bugabensis* (Cameron), specimen from Turrialba, Costa Rica, genitalia, ventral aspect

Fig. 57. *A. chiricahua* n. sp., holotype, genitalia

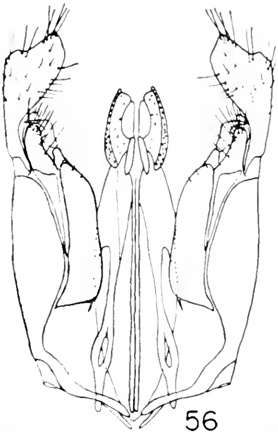
Fig. 58. *A. mohave* n. sp., holotype, genitalia

Fig. 59. *A. malinche* n. sp., holotype, genitalia

Fig. 60. *A. chiricahua* n. sp., paratype, subgenital plate

Fig. 61. *A. mohave* n. sp., holotype, subgenital plate

Fig. 62. *A. malinche* n. sp., holotype, subgenital plate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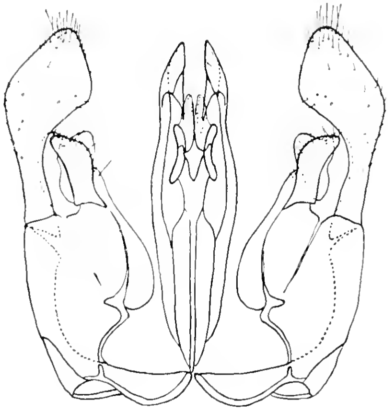
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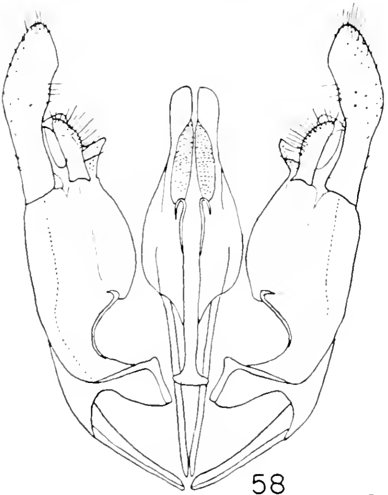
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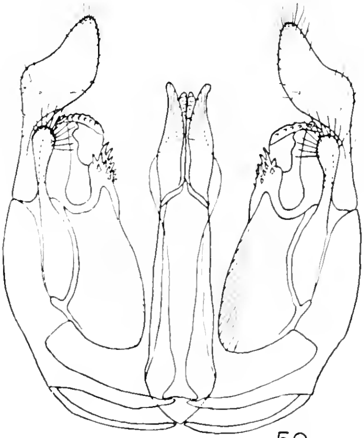
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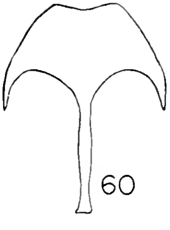
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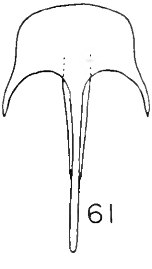
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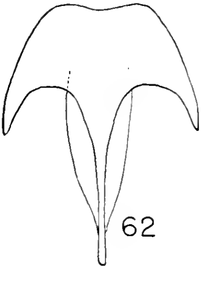
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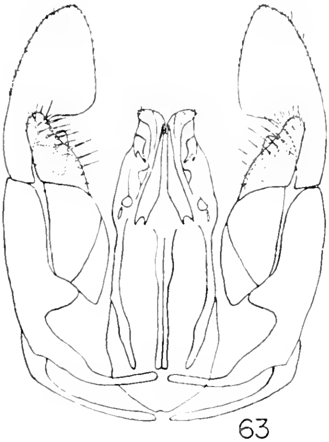
PLATE 6

Characters of the *mexicana* species-group (males).

Fig. 63. *Apenesia peculiaris* n. sp., holotype, genitalia, ventral aspect
Fig. 64. *A. cubensis* n. sp., holotype, genitalia
Fig. 65. *A. mexicana* (Cameron), holotype, genitalia
Fig. 66. *A. testaceipes* (Cameron), holotype, aedoeagus
Fig. 67. *A. maya* n. sp., holotype, genitalia
Fig. 68. *A. bugabensis* (Cameron), holotype, apex of mandible
Fig. 69. *A. chiricahua* n. sp., holotype, apex of mandible
Fig. 70. *A. peculiaris* n. sp., holotype, apex of mandible
Fig. 71. *A. cubensis* n. sp., holotype, apex of mandible
Fig. 72. *A. pando* n. name, holotype, apex of mandible
Fig. 73. *A. mexicana* (Cameron), holotype, apex of mandible
Fig. 74. *A. maya* n. sp., holotype, apex of mandible
Fig. 75. *A. inca* n. sp., holotype, apex of mandible



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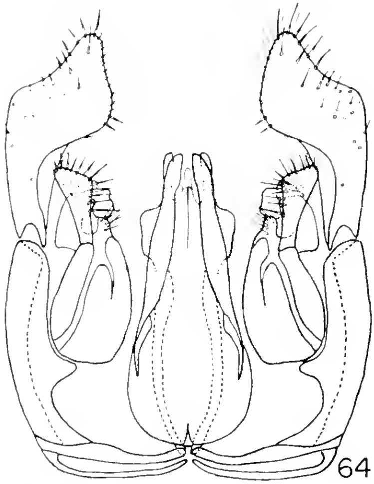

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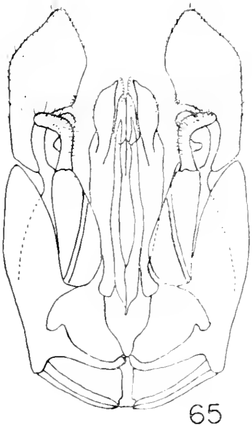

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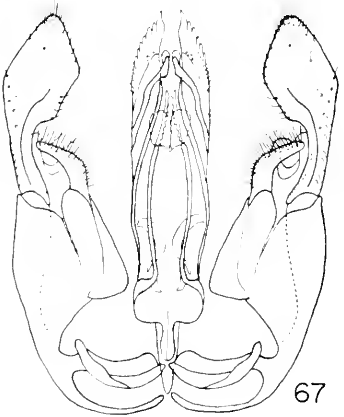

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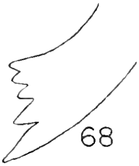

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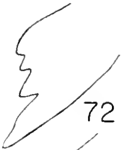

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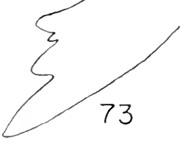

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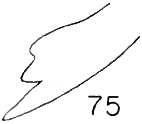

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PLATE 7

Characters of the *mexicana* and *brasiliensis* species-groups (males).

Fig. 76. *Apenesia neotropica* n. name, specimen from Santarem, Brazil, genitalia, ventral aspect

Fig. 77. *A. inca* n. sp., paratype, genitalia

Fig. 78. *A. chiricahua* n. sp., paratype, paramere and volsella

Fig. 79. *A. bugabensis* (Cameron), holotype, base of abdomen, lateral aspect.

Fig. 80. *A. chiricahua* n. sp., holotype, base of abdomen

Fig. 81. *A. parapolita* n. name, paratype, base of abdomen

Fig. 82. *A. brasiliensis* (Kieffer), holotype, base of abdomen

Fig. 83. *A. bugabensis* (Cameron), holotype, clypeus

Fig. 84. *A. chiricahua* n. sp., holotype, clypeus

Fig. 85. *A. peculiaris* n. sp., holotype, clypeus

Fig. 86. *A. pando* n. name, holotype, clypeus

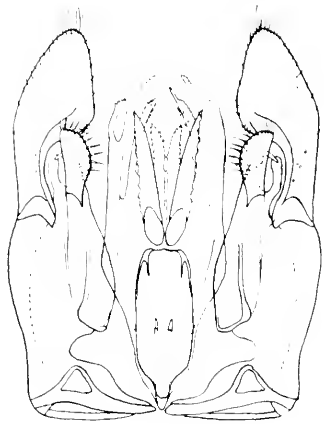
Fig. 87. *A. cubensis* n. sp., holotype, clypeus

Fig. 88. *A. testaceipes* (Cameron), holotype, clypeus

Fig. 89. *A. maya* n. sp., holotype, clypeus

Fig. 90. *A. neotropica* n. name, holotype, clypeus

Fig. 91. *A. inca* n. sp., holotype, clypeus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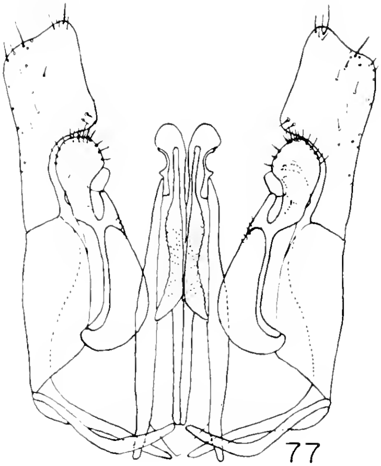
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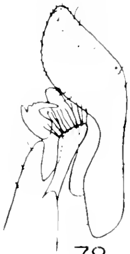
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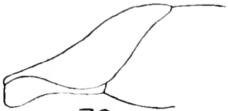
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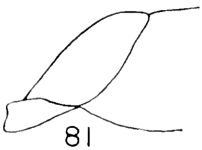
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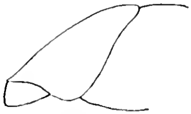
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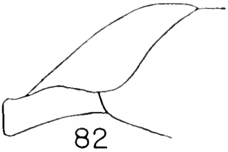
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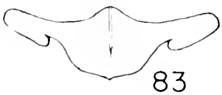
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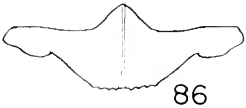
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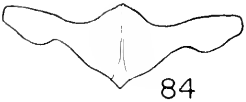
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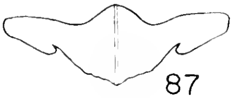
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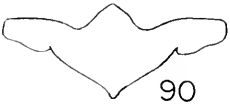
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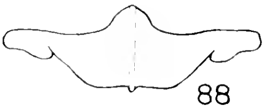
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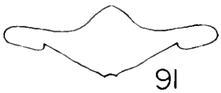
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PLATE 8

Characters of the *brasiliensis* species-group (males)

Fig. 92. *Apenesia tarascana* n. sp., holotype, genitalia, ventral aspect

Fig. 93. *A. microchela* (Kieffer), specimen from Atoyac, Mexico, genitalia

Fig. 94. *A. tlahuicana* n. sp., holotype, genitalia

Fig. 95. *A. alutacea* n. sp., holotype, genitalia

Fig. 96. *A. parapolita* n. name, paratype, clypeus

Fig. 97. *A. angustata* (Evans), holotype, clypeus

Fig. 98. *A. microchela* (Kieffer), holotype, clypeus

Fig. 99. *A. tarascana* n. sp., holotype, clypeus

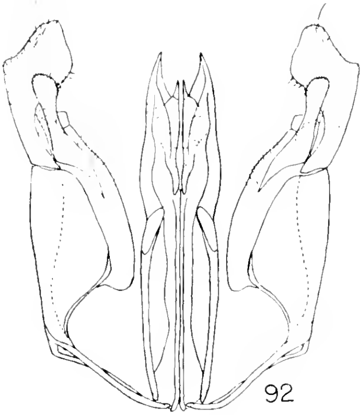
Fig. 100. *A. tlahuicana* n. sp., holotype, clypeus

Fig. 101. *A. olmeca* n. sp., holotype, clypeus

Fig. 102. *A. fulvicollis* (Westwood), holotype, clypeus

Fig. 103. *A. brasiliensis* (Kieffer), holotype, clypeus

Fig. 104. *A. alutacea* n. sp., holotype, clypeus



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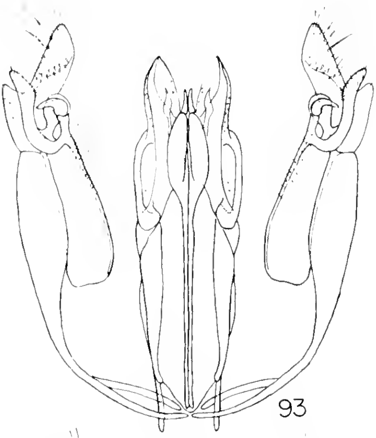

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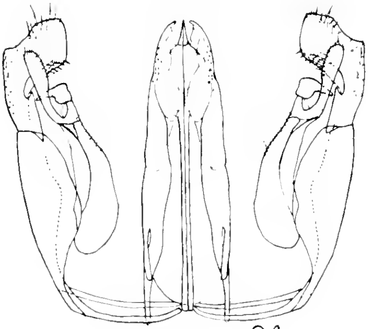

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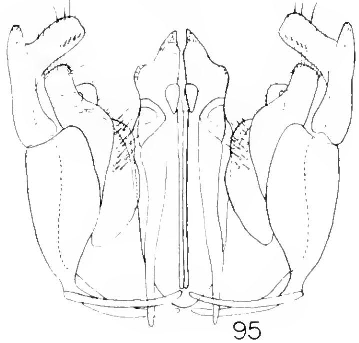

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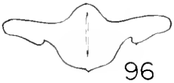

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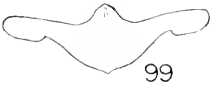

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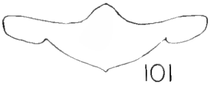

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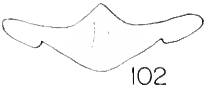

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PLATE 9

Characters of the *brasiliensis* and *nitida* species-groups (males).

Fig. 105. *Apenesia venezuelana* n. sp., holotype, genitalia, ventral aspect

Fig. 106. *A. peruana* n. name, specimen from Hacienda San Juan, Peru, genitalia

Fig. 107. *A. zamora* n. sp., holotype, paramere and volsella

Fig. 108. *A. olmeca* n. sp., holotype, aedoeagus

Fig. 109. *A. angustata* (Evans), paratype, aedoeagus

Fig. 110. *A. transversa* n. sp., holotype, aedoeagus

Fig. 111. *A. brasiliensis* (Kieffer), specimen from Santarem, Brazil, aedoeagus

Fig. 112. *A. tarascana* n. sp., holotype, apex of mandible

Fig. 113. *A. alutacea* n. sp., holotype, apex of mandible

Fig. 114. *A. fulvicollis* (Westwood), holotype, apex of mandible

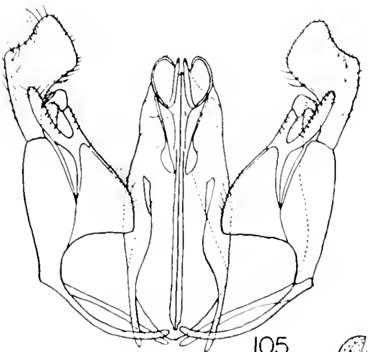
Fig. 115. *A. transversa* n. sp., holotype, apex of mandible

Fig. 116. *A. peruana* n. name, holotype, apex of mandible

Fig. 117. *A. truncaticeps* (Kieffer), holotype, apex of mandible

Fig. 118. *A. microchela* (Kieffer), holotype, base of abdomen, lateral aspect

Fig. 119. *A. truncaticeps* (Kieffer), holotype, base of abdomen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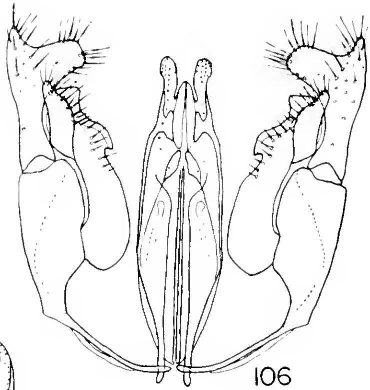
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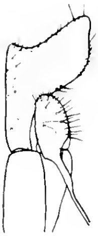
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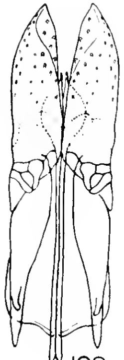
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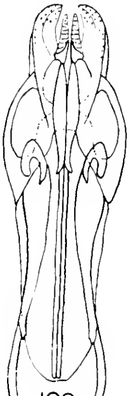
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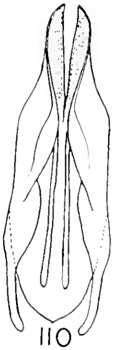
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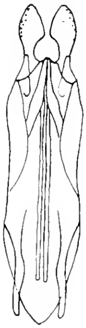
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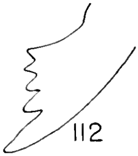
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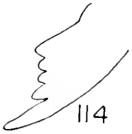
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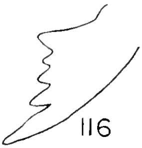
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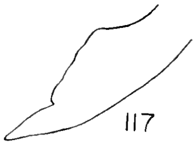
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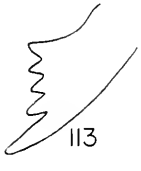
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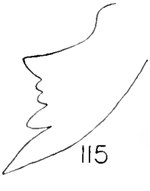
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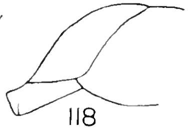
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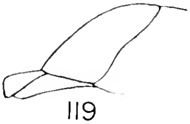
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PLATE 10

Characters of the *nitida* species-group and of female *Apenesia*.

Fig. 120. *Apenesia paraensis* (Kieffer), specimen from Santarem, Brazil, genitalia, ventral aspect

Fig. 121. *A. quadrata* n. sp., holotype, aedoeagus

Fig. 122. *A. laticeps* n. sp., holotype, aedoeagus

Fig. 123. *A. truncaticeps* (Kieffer), specimen from C. Esperanza, Bolivia, aedoeagus

Fig. 124. *A. truncaticeps* (Kieffer), holotype, clypeus

Fig. 125. *A. nitida* (Kieffer), holotype, clypeus

Fig. 126. *A. paraensis* (Kieffer), specimen from Santarem, Brazil, subgenital plate

Fig. 127. *A. parapolita* n. name, plesiallotype, mandible of female

Fig. 128. *A. paradoxa* n. sp., holotype, mandible

Fig. 129. *A. dominica* n. sp., holotype, mandible

Fig. 130. *A. insolita* n. sp., holotype, mandible

Fig. 131. *A. amazonica* Westwood, holotype, mandible

Fig. 132. *A. chontalica* Westwood, holotype, mandible

Fig. 133. *A. amoena* n. sp., holotype, mandible

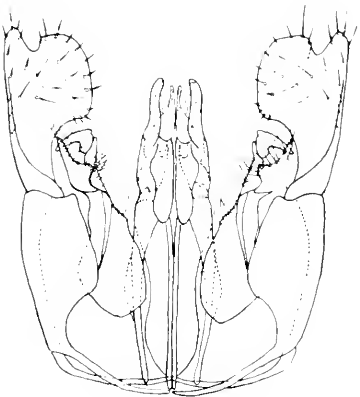
Fig. 134. *A. chontalica* Westwood, holotype, propodeum, dorsal outline

Fig. 135. *A. dominica* n. sp., holotype, propodeum

Fig. 136. *A. parapolita* n. name, plesiallotype, propodeum

Fig. 137. *A. paradoxa* n. sp., holotype, propodeum

Fig. 138. *A. insolita* n. sp., holotype, propodeum



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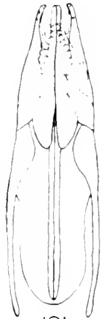

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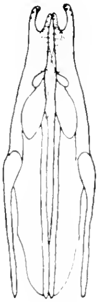

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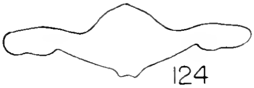

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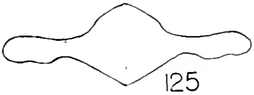

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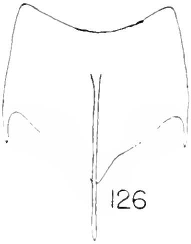

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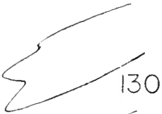

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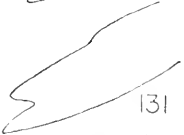

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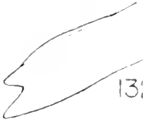

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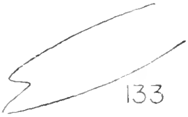

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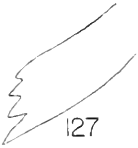

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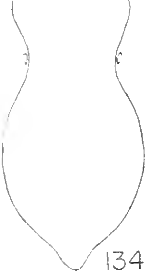

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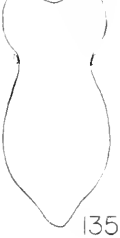

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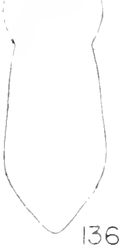

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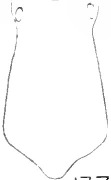

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Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 130, No. 5

RHINOCEROSES FROM THE THOMAS FARM MIOCENE OF FLORIDA

By Horace E. Wood, 2nd
Emeritus Professor of Vertebrate Paleontology,
Rutgers University
and
Research Associate in Fossil Mammals,
American Museum of Natural History

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

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No. 5 *Rhinoceroses from the Thomas Farm Miocene of Florida*

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INTRODUCTION

As long ago as 1941, Dr. Thomas Barbour invited me to study the two forms of rhinoceroses from the Thomas Farm quarry, Gilchrist County, Florida, in the collections of the Museum of Comparative Zoology. I am indebted to the late Dr. Barbour, then Director of the Museum of Comparative Zoology and to Dr. Theodore E. White for the opportunity to describe these forms; to Prof. Bryan Patterson, Dr. A. S. Romer, Mr. Henry Seton, Dr. Donald Baird and my other Harvard friends for hospitable assistance in studying this material. It is appropriate to mention the extended patience during the delay of the completion of this paper. The study was aided by the American Philosophical Society in Philadelphia, and the Rutgers Research Council. The drawings are by Mr. Eugene N. Fischer, supplemented by later ones in 1954 to 1961 by Dr. Florence D. Wood, following additional preparation and the discovery of new material. The preparation and preservation of this fragile material was done by Mr. Russell Olsen.

The abbreviations M.C.Z. and A.M.N.H. refer to the Museum of Comparative Zoology and the American Museum of Natural History, respectively. AP is anteroposterior, Tr is transverse, and e is estimated figure. Measurements throughout the paper are given in millimeters.

White described the geology and the fauna of the Thomas Farm quarry in 1942 (for its history see White, 1942, pp.3-4, and references cited therein), with the exception of the rhinoceros material. He determined the local fauna as early Arikareean or earliest Miocene. Previously, it had been considered early Hemingfordian which is "early middle Miocene" in age (Wood *et al.*, 1941). There is no association in the specimens taken from this quarry and none is established for the rhinoceros collection. However, the rhinoceroses fall into two clearly defined species of the Caenopinae. These two, one a very large animal, the other a small one, are roughly comparable in size to the living black rhinoceros and to *Diceratherium cooki*, respectively. They are so distinctive that anything recognizable as rhinoceros bone or tooth can be allocated between the two. Both are new species and the larger is a new genus.

SYSTEMATIC DESCRIPTIONS

Order PERISSODACTYLA

Family RHINOCEROTIDAE Gray, 1821

Subfamily CAENOPINAE Breuning, 1922

FLORIDACERAS[1] new genus

Type species: F. whitei, new species.

Diagnosis: very large, long-legged, hornless rhinoceros, with small, complete and functional fifth digit in the manus; teeth intermediate in evolutionary progressiveness between *Diceratherium armatum* and *Aphelops*, but without close relationship to either line.

FLORIDACERAS WHITEI[2] new species

Type: M. C. Z. No. 4046, a damaged skull with left P^2-M^3 and right P^3-M^3; *paratype:* M.C.Z. No. 4435, a left mandibular ramus.

Hypodigm: Type and paratype and M.C.Z. Nos. 4047-4053, 7467-7556, including other, less complete skulls and mandibles, most of the girdles and limb bones, and representative parts of the axial skeleton.

Horizon and locality: Thomas Farm local fauna, late Arikareean, eight miles north of Bell, Gilchrist County, Florida.

Diagnosis: a relatively primitive true rhinoceros, but enormous for New World early Miocene age, almost the size of the living black rhinoceros; the skull is hornless and primitive, constricted behind postorbital processes of frontals, with a well developed sagittal crest; occiput deep, not markedly broad; postglenoid process fairly prominent, but much shorter than paroccipital process, which is long spike; dental formula: $I^{?}_{1?}$ $C^{0?}_{0}$ dP^{3}_{3} P^{4}_{4-3} M^{3}_{3}; cheek teeth generally primitive, with ectolophs of upper cheek

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[1] *Florida*, the place of discovery, and *aceras*, without horn.

[2] The specific name acknowledges my indebtedness to Dr. Theodore E. White for his considerable collection from a critical age and region.

teeth more hypsodont than *Diceratherium armatum;* crochets on upper cheek teeth incipient to full size; I_2 large; a small but functional fifth digit in the manus.

DISCUSSION

The late Dr. H. G. Stehlin in the summer of 1927 called my attention to the problem of how to designate the first upper and lower premolars in rhinoceroses. In his opinion there is no replacement of this tooth in rhinoceroses or, for that matter, in perissodactyls in general. When asked if he considered it to belong to the deciduous or to the permanent series, he replied that it was apparently sometimes one, sometimes the other.

Since this hint, my observations on rhinocerotoids have led to the following generalizations:

1. There is no evidence of replacement where the first premolar is concerned.
2. The enamel is heavy as in permanent teeth, unlike the thin enamel of milk teeth.
3. The first upper and lower premolars erupt with the deciduous series, after the second and third, and usually before the fourth deciduous premolar. The first upper premolar continues in use with the permanent series until old age, both in ancestral forms and in later forms which retain reasonably primitive dentitions. The first lower premolar erupts in the same sequence, but continues in function with the permanent series in some primitive forms only; more typically, it is lost with the deciduous series. There is also more individual variation as to the length of time it remains in service than for the upper tooth.

These general inferences apply specifically to *F. whitei* and the teeth in question are regarded as precociously erupting members of the permanent series, and as such are called P^1_1.

Floridaceras whitei has an interesting and contradictory combination of characters. The teeth are entirely too primitive for *Aphelops*, being only slightly more progressive than the *Diceratherium armatum* stage, but having a parallel character of an *Aphelops*-like crochet, incipient on P^3 and increasing to full development on M^2. In becoming more progressive or specialized, rhinoceros molars may increase the cutting surfaces of the fundamental loph pattern in a limited number of ways: by adding crochets, antecrochets and cristae, and by adding corrugations to these in turn. This often results in similar types of parallel dental evolution in groups not closely related. The dentition of the type skull is nearly complete and unbroken but the skull proper is so badly crushed and fragmentary it is not subject to thorough interpretation. In preparation it had been disassembled and remodelled with generous plaster after an *Aphelops* skull, which misleads the observer.

The most astonishing among the numerous primitive characters is the retention of a tetradactyl manus. Previously, *Trigonias* of the lower Oligocene was the latest American true rhinoceros known to have a fifth digit. Among Old World rhinoceroses, the entire *Aceratherium* line has a tetradactyl manus, including its last known representative, *A. incisivum* of the Pliocene. However, it should be pointed out that at least two American forms, of which the manus is unknown, *Amphicaenopus platycephalus* and *Subhyracodon kewi*, are merely presumed to be tridactyl.

DENTITION

In the type dentition of *Floridaceras whitei*, M.C.Z. No. 4046, the cheek teeth only are preserved (Pl. I, fig. 1). The first premolar is double rooted; P^2 is three rooted, the protoloph and metaloph are partly convergent and confluent 11.5 mm. above the complete internal cingulum; P^3 and P^4 are fully molariform in structure, although premolariform in outline. Crochets: bare trace on P^2, small on P^3 and P^4, large but not enormous on M^2, but nowhere as big as any on an *Aphelops* molar; cristae are absent; there is no antecrochet on P^{2-3}, a barely noticeable one on P^4, and there is a moderate swelling on M^{1-2}, less again on M^3; cingula are interrupted internally by the protocones of P^4-M^3. The internal cingulum is complete on P^2; attenuated on the protocone on P^3; in P^3 and P^4 it is strong across the valley and rises to a broad swell opposite the anterior slope of the metaloph; interrupted by the protocone, and barely by the hypocone of P^4; seems present across the valleys of M^{1-2}, weaker across valleys of M^3, not on inner ends of lophs, though there is a very faint suggestion of where it should be.

A partial skull, M.C.Z. No. 4048, very badly crushed, referred to *F. whitei*, is of interest chiefly because right P^{1-4} are present. The restoration of P^1 in the type illustration is from this specimen. P^1 has a well developed metaloph, a protoloph represented only by the crista-like ridge, and a strong low internal cingulum, except around the metaloph, where it is attenuated. A measurement across the occipital condyles, estimated at 148 mm. may be more reliable than that of the type.

The back of a cranium, M.C.Z. No. 4049, referred to *F. whitei*, is crushed, but this specimen is of particular interest since it confirms unmistakably the existence of a real sagittal crest. The crest, as such, extends 165.0 mm. anteriorly from the posterior edge of the center of the lambdoidal crest., i.e., ahead of the occipital surface, before it merges into the smooth brain case.

A crushed face and palate, with well worn teeth, M.C.Z. No. 4047, referred to *F. whitei*, is an older individual than the type. The dentition agrees in essential characters so far as these are not removed by wear, but gives no additional data. The nasals taper off gradually forward and end in a common stubby triangle. The nasal incision extends from the tip of the nasals to a point just above the border of the alveoli between P^2 and P^3, and measures 156.0 mm. in length. The roof of the nasals is partly imbedded in plaster, but as would be expected, there is no evidence of nasal rugosities.

A well-preserved, nearly complete left mandible (Pl. I, figs. 2, 3), M.C.Z. No. 4435, designated as the paratype, has I_2, P_1-$_4$ (of which P_1 is merely an alveolus), and M_1-$_3$. The proportions of the jaw are long and slender, simple and unmodified. The jaw in general and the cheek teeth in particular are strikingly suggestive of *Diceratherium armatum*. The teeth, slightly worn, are relatively simple and unmodified. They are moderately high crowned, being approximately half the depth of the ramus. I_2, not fully erupted, is a large tooth, bluntly triangular in cross section, with a slight upturned flange on the median edge. Its enamel is very heavy laterally and ventrally, but very thin dorsally. The tip is slightly beveled medially with wear. The tooth has been compressed toward the symphysis so that if there had been a very small I_1 or an alveolus it has been destroyed. P_1 is indicated by a single-rooted open alveolus. P_2 has slight cingula on the anterior and posterior ends. Its pattern is simplified secondarily. The trigonid consists largely of the protoconid on which the paraconid forms a good-sized anterior flange, and the metaconid a smaller posterointernal extension. The talonid forms a continual crest from the metaconid region around a centrally enclosed pit. The third and fourth premolars are fully molariform but shorter proportionately, anteroposteriorly, than molars. The third lower premolar has weak cingula on the anterior and posterior ends. An internal extension partly blocks the valley out of the trigonid, but with a slight interruption at the opening of the valley. The fourth lower premolar has cingula on the anterior and posterior ends. The anterior cingulum extends internally to the valley of the trigonid. An internal cingulum crosses the talonid valley. M_1 has slight cingula on the anterior and posterior ends. The anterior cingulum continues internally and stops just beyond the trigonid valley, with a slight interruption at the bottom of the valley. A small cingulum crosses the talonid valley. M_2 has weak cingula on the anterior and posterior ends. The anterior cingulum continues internally to the talonid valley, at the opening of which it is slightly notched, and then ceases. A very slight cingulum crosses the valley of the talonid. M_3 has anterior and posterior cingula, weaker, if anything, than those on M_1 and M_2. The anterior cingulum continues internally to the bottom of the trigonid valley and stops. A weak, brief cingulum crosses the talonid valley.

Another left mandibular ramus, M.C.Z. No. 4050, crushed and distorted, with teeth considerably worn and broken, along with isolated teeth, M.C.Z. No. 4052, are referable to *F. whitei*.

TABLE 1

Skull and tooth measurements of *Floridaceras whitei* and *Diceratherium barbouri*

	F. whitei, type		*F. whitei*, referred			*D. barbouri* type
	M.C.Z. No. 4046		M.C.Z. No. 4047		M.C.Z. No. 4048	M.C.Z. No. 4452
	Right	Left	Right	Left	Right	Right
P^1-M^3	e241.5					
P^2-M^3	e225.0	238.3				
P^{1-4}	e111.3					
P^{2-4}	e 93.7	109.5				
M^{1-3}	140.9	140.6	139.5			e110.0
P^1 AP					23.0	
Tr					19.2	
P^2 AP		e26.3				
Tr		38.2			37.6	
P^3 AP	e34.4	34.5				
Tr	50.3	49.7			41.1	
P^4 AP	39.9	37.3	39.1	38.9		e28.7
Tr	57.0	58.8	e60.7	e60.0	55.2	e40.0
M^1 AP		44.9	42.2	43.7		e34.0
Tr		56.5	62.5			
M^2 AP		48.4	46.4	e46.7		40.2
Tr		61.6	63.2			42.7
M^3 AP		49.7	49.8			e34.8
Tr		56.7	56.4			37.6
Width across zygomata		e324.5				269.5

TABLE 2

Jaw and tooth measurements of *Floridaceras whitei*.
left ramus, paratype, M.C.Z. No. 4435.

Jaw length, symphysis to angle	553.0
Depth, coronoid to ventral border	280.0
Diastema	96.3
P_1-M_3	257.0
P_2-M_3	244.5
P_{1-4}	113.3
P_{2-4}	105.5
M_{1-3}	148.0
P_1 AP	e 9.9 alveolus
P_1 Tr	e 9.9 alveolus
P_2 AP	27.3
P_2 Tr	15.7
P_3 AP	35.6
P_3 Tr	23.0
P_4 AP	37.9
P_4 Tr	26.8
M_1 AP	42.7
M_1 Tr	28.3
M_2 AP	47.2
M_2 Tr	28.3
M_3 AP	58.0
M_3 Tr	27.8
Depth jaw, below P_2	79.6
Depth jaw, below M_2	89.3

A juvenile left mandible, M.C.Z. No. 4051, referable to *F. whitei*, is of particular interest because of the deciduous dentition. The ventral profile of the ramus is slightly bowed. There is a moderate sized alveolus, presumably for dI_2, in the symphyseal region. What is referred to as P_1, discussed earlier, is entirely unworn. It has the protoconid as the main cusp, with the paraconid forming an anterior buttress and with a descending ridge surrounding a small talonid basin. The pattern of dP_{2-4} progressively approaches the molariform level, especially in the asymmetrical talonid crescent. There is typical thin deciduous enamel on dP_{2-4}. A transversely spread protoconid on dP_2 indicates an incipient metaconid; the paraconid is quite distinct and bifurcated anteriorly, incipiently suggesting dP_3; the talonid seems full sized and molariform, which is still more true of dP_{3-4}. The dP_3 has a typical pattern, that is, molariform, except for its great length, and the paraconid region is transversely elongated into a small crescent, which, in this tooth, also has an internal hook recurved to the rear, partly enclosing the trigonid basin as an inner harbor. The dP_4 is molariform; its thin enamel and its position are the chief proofs it is not M_1. External cingula are notably lacking: P_1 has one on the paraconid but it is barely indicated and highly tenuous on the paraconid of dP_2, and altogether absent on dP_{3-4}. Internal cingula are anterointernal on the paraconid of P_1 with a short continuation anteriorly, from the talonid onto the protoconid; they are absent on dP_{2-4}. The anterior and posterior cingula are poorly developed on the deciduous premolars.

Colbert (1932) described and figured worn lower cheek teeth from the Hawthorn Formation of Florida which he assigned to *Aphelops* sp. As they do not agree too well with *Aphelops, sensu stricto,* but are essentially the same size and agree in such characters as are shown with *Floridaceras whitei,* this genus and species seems a reasonable tentative assignment for Colbert's material.

Postcranial skeleton

While the teeth of *Floridaceras whitei,* so far as known, show only average variation, the skeletal elements wherever duplicated show a wider spread in size not related to growth stages. Measurements in tables are arranged in a graduated series so that the unusual variation in a rhinoceros sample of this size becomes apparent at a glance.

The axial skeleton is poorly represented but some information can be distilled out of a few of the better preserved units. The cracked and damaged atlases, M.C.Z. Nos. 7512 and 7513, show that this bone is rhinocerotic, similar to *Trigonias* and *Subhyracodon* but bigger and sturdier. By doubling the measurements of a complete half, the atlas is estimated to measure 340.0 mm. across. The wing is widely expanded and the posteroventral process is blunt but not spiked. There are two axes, M.C.Z. Nos. 7514 and 7515, of which the neural spine forms a heavy keel which broadens posteriorly, presumably to support a heavy head. Neither of the axes are of a size to articulate with the atlases. A robust stubby odontoid process is strongly intruded into the groove in the atlas. A nearly complete anterior thoracic vertebra, M.C.Z. No. 7517, possesses an exceptionally long neural spine, which, although the tip is missing, measures 264.0 mm. anteriorly above the top of the neural canal between the prezygapophyses, and 219.0 mm. posteriorly between the postzygapophyses. A lumbar vertebra, M.C.Z. No. 7519, shows the transverse process rising slightly toward the tips, and a neural spine that is expanded anteroposteriorly, and also thickened at the tip.

TABLE 3

Measurements of the fore limb of *Floridaceras whitei*

Element		Length	Width
Scapula	M.C.Z. No. 7467		
	top to front margin of glenoid	445.0	
	top to glenoid	414.0	
Humerus	M.C.Z. No. 7469	425.0	
	M.C.Z. No. 7470	437.0	
	M.C.Z. No. 7468	440.0	
Ulna	M.C.Z. No. 7477		
	segmental[1]	368.0	
	overall	326.0	
Radius	M.C.Z. No. 7474		
	segmental	368.0	
	M.C.Z. No. 7476		
	segmental	378.0	
Carpus	scaphoid to trapezoid composite	86.4	scaphoid to pisiform 131.5
Metacarpals			Distal
II	M.C.Z. No. 7494	159.3	45.5
III	missing		
IV	M.C.Z. No. 7495	148.1	45.7
	M.C.Z. No. 7496	159.5	51.4
	M.C.Z. No. 7497	159.7	44.1
	M.C.Z. No. 7498	162.7	51.4
V	M.C.Z. No. 7499	77.3	32.1
	M.C.Z. No. 7500	84.3	29.1
	M.C.Z. No. 7501	85.4	27.3
	M.C.Z. No. 7502	86.7	39.3
	M.C.Z. No. 7503	95.5	31.7
	M.C.Z. No. 7504	95.8	32.8
	M.C.Z. No. 7505	97.1	34.6

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[1] Segmental length is measured in the long axis between proximal and distal articular surfaces.

It is interesting to see how well one can picture this remarkable animal in spite of unassociated material. The limb elements about equal the length of those of the black rhinoceros, but are much more slender (Pl. III, fig. 1). The impression persists that it was a very large cursorial beast despite its massiveness. The leg proportions suggest *Trigonias*, or better *Subhyracodon*. There is little similarity to the small slender *Diceratherium cooki* and *Hyracodon* in one direction, and even less to the squat *Teleoceras* in the other, with which it contrasts very sharply. Very few profitable comparisons can be made with any single species as far as limb elements are concerned. The scapula, M.C.Z. No. 7467, is exceedingly long and narrow for an animal of such bulk, but it is also powerful (Fig. 1). There is a fairly close resemblance in outline to that of the Indian rhinoceros. There is no sharp angle between the vertebral and axillary borders, a feature which is so characteristic of rhinoceroses in general. A considerable recurve in the corner between the vertebral and axillary border enlarges the surface for the infraspinatus and especially the teres muscles. The humerus, M.C.Z. Nos. 7468-7472, is like that of *Subhyracodon tridactylus*, much enlarged but stubby. The radius and ulna, M.C.Z. Nos. 7474-7476 and 7477-7483, suggest the equivalents of *Subhyracodon*. They are slender but powerful. These observations indicate that although *Floridaceras* was much bigger, it could run as fast as these lighter weight animals.

The carpus is so complete that it can be reconstructed (Pl. III, fig. 2), lacking only the unciform. This, however, is most unfortunate in that it is impossible to check the articulations with metacarpal V, which is *Floridaceras'* unique character. The carpus was involved in a different weight distribution than in a three-toed manus, is wider than long, with an approximate width across the proximal row of carpals of 131.5 mm., and a length of 86.4 mm., scaphoid to trapezoid. Taken as a functional unit, the carpals compare best with the black rhinoceros but with some dissimilarities in the individual bones in size and modelling. The pisiform resembles that of *Subhyracodon*. The trapezium, a peculiar keeled bone, is unlike rhinoceros trapezia, except in *Aceratherium "gannatense,"* where it appears to agree well with Duvernoy's illustration (1853, pl. VII, fig. 7a). The trapezoid is very large, and the magnum is rather delicate. The carpals as represented are: two left scaphoids, M.C.Z. No. 7485; a left and right lunar, M.C.Z. Nos. 7486 and 7487; a right cuneiform, M.C.Z. No. 7488; two left and one right cuneiforms, M.C.Z. No. 7489; a

Figure 1. *Floridaceras whitei.* M.C.Z. No. 7467, right scapula. × 1/3.

right pisiform, M.C.Z. No. 7490; a left trapezium, M.C.Z. No. 7491; a left trapezoid, M.C.Z. No. 7492; a right magnum, M.C.Z. No. 7493.

Of the metacarpals, the third and largest is missing. Metacarpals II, M.C.Z. No. 7494, and IV, M.C.Z. Nos. 7495-7498, are generally like those of the black rhinoceros, but the proximal end of metacarpal IV resembles that of the white rhinoceros. All of the fourth metacarpals bear a proximal lateral facet for metacarpal V and make a good fit with the corresponding metacarpal V (Pl. III, fig. 2). The second and fourth metacarpals are very similar in size and proportions and even details of structure to those of the fragmentary *Aphelops longipes* (Leidy and Lucas, 1896, pl. 13, figs. 6 and 7) from the Pliocene Alachua Formation of Florida. This resemblance is the closest I have observed, whether in fossil or living rhinoceroses, and together with the geographic location, suggests the possibility of direct descent from *Floridaceras*, in which case *A. longipes* could not be an *Aphelops;* the teeth assigned to *A. longipes* are larger and more advanced.

A remarkable and at first puzzling bone has proved to be metacarpal V of a complete, though relatively short functional digit (Pl. IV, fig. 2a-d). This bone was so unexpected and peculiar as to have suggested the possibilities of other families and even orders. Far-fetched assignments such as chalicothere, big carnivore, *Teleoceras* and even proboscidian were considered and ruled out. It was eliminated from other members of the Thomas Farm fauna on the basis of either size or character or both. Since there are seven complete examples of this metacarpal, and one damaged, M.C.Z. Nos. 7499 - 7506, all alike, it is not an anomaly and therefore must belong to a known member of the fauna. Its size would fit only *Floridaceras,* and yet an early Miocene form with a fifth digit has never been discovered in an American true rhinoceros line. The bone shows obvious resemblances to a tapir metacarpal V, and still more to various extinct tetradactyl rhinoceroses. The Thomas Farm metacarpal V (Pl. IV, fig. 2) has a double proximal facet, forming a right angle, rounded off at the apex, on its proximal and posterior surfaces to articulate with the unciform. There is a hint of this unusual character in metacarpal V of modern tapirs (Kaup, 1859, pl. II, figs. 2 and 2a; A.M.N.H. No. 2592) and in *Protapirus* (A.M.N.H. No. 662; Wortman and Earle, 1893, fig. 4; and Scott, 1941, pl. LXXX, fig. 2). It is better matched, among rhinoceroses, in the fifth metacarpals of *Hyrachyus affinis*, A.M.N.H. No. 12664, in *Aceratherium lemanense* (Duvernoy, 1853, pl. VII, figs. 14a, 14a′, 14a''', *A.* "*gannatense*"), and apparently in *A. depereti* (Borissiak, 1927, pl. 2, fig. 5), and even in the metacarpal V, a mere nubbin, in the white rhinoceros, A.M.N.H. No. 51862.

There are general resemblances between this metacarpal and the unmodified, more primitive metacarpal V of *Trigonias*, shown in the specimens, *T. osborni*, A.M.N.H. No. 9847 (cf. Hatcher, 1901, pl. III; Scott, 1941, pl. LXXXIII, fig. 7), in *T. wellsi*, A.M.N.H. No. 13226C, and in *T.* cf. *gregoryi*, A.M.N.H. No. 13226D (Pl. IV, fig. 1a-d). Finally, the *Floridaceras* bone virtually duplicates in all respects, including size, the metacarpal V of *Aceratherium incisivum* described and figured by Kaup (1834, p. 58, pl. XV, fig. 4; 1859, pp. 163-167, pl. II, figs. 1, 1a, and 4). This resemblance is so close that Kaup's fine illustrations could readily represent M.C.Z. No. 7499 in every respect except the shape of the inner proximal facet for metacarpal IV! Kaup (1834, p. 58) states that this bone was associated with other bones of *A. incisivum*, including a fragment of lower jaw with teeth. He gives the measurements as 80.0 mm. long, 15.0 mm. wide at the proximal articulation and 33.0 mm. at the distal facet, which agrees well with his 1859 illustrations, of which his figures 1 and 1a, although not so stated, are about natural size. These measurements fit neatly into those for the Thomas Farm metacarpal V (see Table 3). The double proximal facet calls for a corresponding concave external distal articular facet on the unciform as is the case in the tapir and white rhinoceros. Since no unciform has come to light in the Florida material, only approximate fits can be made with modern African rhinoceroses.

The transversely narrow proximal end of metacarpal V resembles *Trigonias* (cf. Pl. IV, figs. 1b, 2b), *Aceratherium lemanense*, and, even more exactly, *Aceratherium incisivum*. The ventral 70° bend of the shaft (Pl. IV, fig. 2a,c) is much more extreme than that of *Trigonias* in which it is only 30°. This bend is closer to that of *Aceratherium lemanense* and agrees exactly with *A. incisivum* (Kaup, 1859, pl. II). The significance of this bend is that it permitted the digit to touch the ground, bending over the elastic pad which gives the rhinoceros its characteristic bouncy gait. The heavy rugosities at muscle insertions suggest active use. The foot appears to have been somewhat splayed, perhaps associated with a soft or marshy ground habitat. The bulbous distal ends compare respectably in size with those of metacarpal IV and give the impression of being swollen, with a recess of varying size on the medial surface, just proximal to the trochlea. The trochlea is large and markedly asymmetrical; it is even more on the bias than the distal end, in general, which is broadly comparable to that of *Trigonias* or even of *Metamynodon*. Although no phalanges can be assigned to this digit, the swollen distal end and large trochlea make it certain that the toe was complete (Pl. IV, figs. 1b, 2b), and most probable that it touched the ground however shortened it may have been.

In the posterior limb, the big ilium, M.C.Z. No. 4053-I, is broadly comparable with *Subhyracodon* (Peterson, 1920, fig. 34) but has a more widely expanded blade; it is less excavated anterior to the acetabulum. A right and a left femur, M.C.Z. Nos. 7524 and 7525, are mashed flat, exaggerating the genuine effect of long legs. Surprisingly enough, the closest match among rhinoceros femora is to the elongated femur of *Metamynodon,* though *Floridaceras* lacks the extreme flattening of the former. A scale enlargement of *Diceratherium cooki* would be the next best comparison of the femur. The tibia (M.C.Z. Nos. 7527-7533) is sturdy but slender, suggesting particularly an enlargement of *Subhyracodon tridactylus*. The fibula (M.C.Z. Nos. 7534-7536) is unusually long and slender, differing from most rhinoceroses, but having similarities of proportions to those of *Hyrachyus* and *Hyracodon*.

The pes, not as well represented as the manus, is big and generalized. The tarsals are suggestive of the black rhinoceros but are somewhat smaller. They are stouter and coarser than *Subhyracodon* but also somewhat shorter, relatively. The *Floridaceras* material has large calcanea and astragali, but not as large as in *Trigonias wellsi*. Smaller specimens are close in size to those of *T. gregoryi*, but all have more delicate modelling and a longer tuber calcis. The *Floridaceras* tarsus as a whole is neither squat nor exceptionally long. The calcanea are heavy and coarsely modelled as in the black rhinoceros, but the plantar process is shorter and blunter. It is blunter than that in *T.* cf. *wellsi, T.* cf. *gregoryi, Subhyracodon occidentalis* and *Diceratherium* cf. *annectens*. The naviculars (M.C.Z. No. 7542) are broadly similar to those in rhinoceroses of the same size. A left ectocuneiform (M.C.Z. No. 7545), resembles that of the white rhinoceros in proportions.

The three metatarsals are represented, and while resembling those of the two living African rhinoceroses, do not agree exactly with either. Metatarsal II (M.C.Z. Nos. 7547 - 7549) is noticeably shorter and stouter than the corresponding bone of *Trigonias wellsi* and *gregoryi* though *Floridaceras* was the larger animal. Two of the three specimens of metatarsal II show no facet for the entocuneiform, which was therefore either much reduced, or more probably, somewhat everted. M.C.Z. No. 7549 bears what appears to be a small facet for the entocuneiform in a somewhat more lateral position than usual. Metatarsal III (M.C.Z. Nos. 7550 - 7552), by far the predominant digit, is essentially bilaterally symmetrical in anterior aspect, and is markedly broader than the lateral metatarsals.

There is an assortment of sesamoids and phalanges in the collection which offer nothing constructive. For what little it is worth, a composite of the phalanges of a lateral digit, attributed to the manus, M.C.Z. No. 7511, measures 79.1 mm. in length.

Table 4

Measurements of the hind limb of *Floridaceras whitei*

Element		Length	Width	
Ilium	M.C.Z. No. 4053	384.0 in front of acetabular rim	466.0	
Femur	M.C.Z. No. 7524	580.0 segmental		
Tibia	M.C.Z. No. 7532	337.0 segmental 375.0 overall		
Fibula	M.C.Z. No. 7534	382.0		
Tarsus	astragalus and cuboid composites	112.0	calcaneum and astragalus composite	
		118.0	105.7	
			depth of same 83.2	
Metatarsals			Proximal	Distal
II	M.C.Z. No. 7548	137.7	35.5	41.1
	M.C.Z. No. 7547	148.8	34.0	41.2
	M.C.Z. No. 7549	149.0	36.6	42.2
III	M.C.Z. No. 7550	153.5	56.4	61.5
	M.C.Z. No. 7552	155.6	51.7	58.1
	M.C.Z. No. 7551	168.5	53.6	54.8
IV	M.C.Z. No. 7555	141.4	44.5	39.2
	M.C.Z. No. 7556	142.3	45.1	40.1
	M.C.Z. No. 7554	142.3	46.1	38.7
	M.C.Z. No. 7553	144.7	43.4	35.3

Genus DICERATHERIUM Marsh, 1875

Subgenus MENOCERAS Troxell, 1921

Subgeneric diagnosis: Conforming broadly to the *Diceratherium* pattern; relatively small, slender and long legged; especially prominent paired round knobs on nasals, assumed to be horn supports in males, absent or weakly developed in females; posterior bend of zygomatic arch sharp, essentially a right angle; ectolophs of upper cheek teeth elongated, so as to appear subhypsodont; in correlation, buccal pits and sinuses tend to be deep; strong development of cristae, and especially of crochets.

DICERATHERIUM (MENOCERAS) BARBOURI[1] new species

Type: M.C.Z. No. 4452, a palate, *basis cranii* and occiput.

Hypodigm: The type and M.C.Z. Nos. 4061, 7441-7466, 9328-9329, teeth and isolated bones representing most parts of the skeleton.

Horizon and locality: Thomas Farm local fauna, late Arikareean, eight miles north of Bell, Gilchrist County, Florida.

Diagnosis: Slender, long-legged form, more cursorial than any living rhinoceros, proportions and approximate size of *D. cooki*, but having somewhat longer legs; huge, elongated postglenoid process, completely overshadowing paroccipital process; ectolophs of cheek teeth higher crowned than *D. cooki;* median valleys very deep, close to ectolophs; large sharp crochets with corrugated margins; sharp narrow cristae, protolophs smooth, simple and uncomplicated; internal cusps low; protocones not markedly pinched off; M^2 disproportionately elongated anteroposteriorly.

DISCUSSION

Diceratherium (Menoceras) barbouri shows close resemblance only to *Diceratherium cooki*, among other rhinoceroses. It is a little larger and somewhat longer limbed cursorial form. The cheek teeth have slightly higher crowns and a little more complicated pattern. These differences are such as might reasonably occur in a direct descendant of *D. cooki* found in beds of slightly younger age. Interestingly enough, I received almost precisely similar isolated upper teeth from a local collector, sent me from near Bridgeport, Nebraska, presumably from the Marsland. The

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[1] The specific name is given in recognition of the late Dr. Thomas Barbour.

dentition of *Diceratherium barbouri* shows some few resemblances to that of *Floridaceras whitei* from the same quarry, presumably reflecting partial parallelism. In other respects the two forms are widely different and non-competing. Since the *Diceratherium* line has left no known descendants beyond *barbouri*, it is plausible that the *Parahippus-Merychippus* line eliminated it from the competition just as *Miohippus* perhaps crowded out *Hyracodon* at the end of the Oligocene.

CRANIUM

The type of *D. barbouri,* M.C.Z. No. 4452, a palate, *basis cranii* and occiput is damaged so that only a limited number of cranial characters can be determined. The greatest width across the zygomatic arches, 269.5 mm., is not seriously distorted and it is probably of the right order of magnitude. Posteriorly, the zygomatic arches bend sharply, much as in *D. cooki.* The postglenoid and posttympanic processes, now shoved together, were not fused or appressed, but were probably in contact or thereabouts. A striking character is the huge size and extreme projection of the postglenoid process beyond the glenoid fossa: it projects 89.1 mm. on the right side, and 72.3 mm. on the left, well beyond the corresponding paroccipital processes (80.3 mm. and 54.2 mm.), which are of typical size. Whatever crushing has taken place would tend to reduce these measurements rather than to increase them. The postglenoid process is directed mostly ventrally, somewhat medially, and curves anteriorly at the tip. It also markedly exceeds the length of the well developed postglenoid process of *D. cooki* (35.7 mm.—44.2 mm.), an animal of the same general size.

The measurements of the postglenoids of three *D. cooki* skulls, A.M.N.H. Nos. 14236, 16B (field number), and 14213, gave respectively 35.7 mm., 35.8 mm., and 44.2 mm., as against 74.1 mm. for the same process in *D. barbouri.* Even rhinoceroses with unusually large postglenoid processes, such as *Ceratotherium, Peraceras, Teleoceras,* and especially *Aphelops mutilus,* do not have processes which equal the exaggerated proportions in *D. barbouri.* The sagittal contour line of the occiput is a simple slightly concave curve, as is usually the case in *D. cooki,* instead of the sine curve which is typical of many rhinoceros skulls.

DENTITION

The teeth present in the type skull, M.C.Z. No. 4452, consist of P^4 - M^3 of both sides, and are damaged in varying degrees. The ectolophs are higher than in *D. cooki*, whether viewed laterally or measured from the external deep point of the median valley; there is no corresponding tendency toward hypsodonty in the lingual portion of the teeth. The anteroposterior (mesio-distal) dimension of M^2 is unusually long in proportion to the transverse measurement (Pl. 5). The crochets of P^4 - M^2 are a striking feature; they are unusually long and sharp, with accessory vertical ridges which give a corrugated appearance to the sides of the crochet. Some individuals of *D. cooki* show approaches to this type of crochet in one or more teeth. The crochet of M^3 is a small sharp blade. The cristae of M^{2-3} were sharp blades when unworn, and seem to have been sharp also on P^4 - M^1. The protolophs are smooth and simple, without antecrochets on P^4 and M^{2-3}, and with only a small one on M^1. The protocones are only slightly pinched off: there is a definite anterior groove on M^1, as well as a faint anterior groove on M^2; otherwise the protocones are entirely confluent with the rest of the protolophs. The internal cingula are complete on P^4 - M^3. Altogether, these teeth suggest an exaggeration of the characters of *D. cooki*, such as might be expected in a descendant. The collection of teeth sent to me from Nebraska shows, by all odds, the closest resemblance to *D. barbouri*.

There are fragmentary miscellaneous lower teeth. A right I_2, M.C.Z. No. 7443, has the characteristic shape of the lower tusk (Pl. V, fig. 6); it is generally slender, and well worn at the tip. It might have once had a longer crown than is typical of *D. cooki*. There are right (Pl. V, fig. 3) and left examples of P_2, M.C.Z. No. 7444: they have strong external and internal cingula, and a deep groove buccally, delimiting the talonid from the trigonid. A group of loose broken lower cheek teeth (M.C.Z. No. 7445) suggests fragments from one dentition. The larger pieces include the hypoconid of M_1, most of the external part of M_2, and an entire M_3, with the trigonid crescent slightly worn. This M_3 is generally comparable to corresponding teeth of *D. cooki*, but is somewhat higher crowned (Pl. V, figs. 4, 5).

Axial skeleton

The few vertebrae assignable to *D. barbouri* include an atlas (M.C.Z. No. 4061) and an axis (M.C.Z. No. 7441). The atlas is complete and essentially uncrushed; it is a little larger than in *D. cooki*, measuring 177.0 mm. as opposed to 160.0 mm.

APPENDICULAR SKELETON

A fair number of limb elements are preserved and show that the legs were long and slender. This impression of length characterizes the scapula, M.C.Z. No. 7447, the ulna, M.C.Z. No. 7448, metacarpal III, M.C.Z. No. 7449, the femur, M.C.Z. No. 7450, the fibula, M.C.Z. No. 7451, and metatarsal IV, M.C.Z. No. 7452. The scapula is like that of *D. cooki* with some similarity to *Subhyracodon.*

The only carpals are a left lunar, M.C.Z. No. 7453 and a right pisiform, M.C.Z. No. 7454, both resembling *D. cooki*, with the differences that the lunar is stouter and the pisiform has less neck. Right metacarpal III, M.C.Z. No. 7449, resembles *D. cooki,* but is considerably larger. The bone is crushed but it is clearly longer and stouter. A left metacarpal IV, M.C.Z. No. 7455, agrees closely with *D. cooki,* but is a shorter bone. Comparison with the same bone in *Floridaceras* is striking; the metacarpal IV of *D. barbouri* is 72 per cent as long, but only half of any transverse measurement. A number of phalanges are similar to *D. cooki*, but are a little stouter and more rugose.

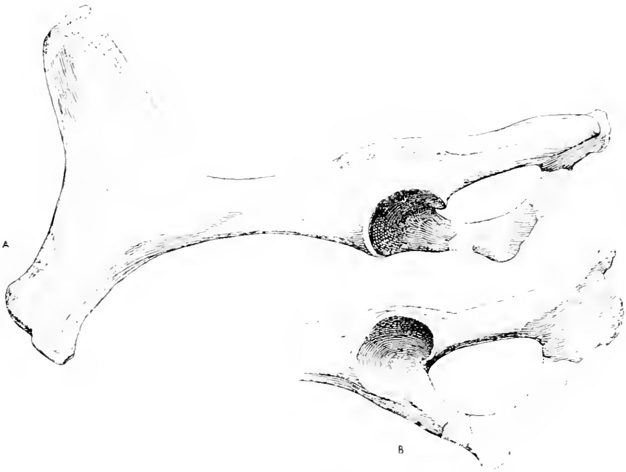

Figure 2. *Diceratherium barbouri.* M.C.Z No. 7456, left half of pelvis. *A*, dorsolateral; *B,* lateral. × ¼.

Enough of the pelvis and hind limb is present to make further comparisons with *D. cooki.* The pelvis, M.C.Z. 7456, is too fragmentary for reliable measurement: what there is of it is small and delicate (Fig. 2). A shaft and distal end of a femur, M.C.Z. No.

7450, is close in character to *D. cooki,* but is proportionately longer. The shaft is just about the same diameter as that in *Subhyracodon occidentalis* but was undoubtedly much longer. The preserved length is 366.0 mm., with an estimate of 390.0 mm. for the whole femur. A left fibula, M.C.Z. No. 7451, measuring 250.0 mm., gives an indication of the length and slenderness of the shank.

The tarsals, a right astragalus, M.C.Z. No. 7457, a left calcaneum, M.C.Z. No. 7458, and a left entocuneiform, M.C.Z. No. 7459, are close to *D. cooki.* The calcaneum and entocuneiform are stouter than in *D. cooki,* and the astragalus is quite noticeably more so.

Like the metacarpals, the metatarsals resemble the corresponding bones of *D. cooki,* but are sturdier. Metatarsals III and IV, and fragments of metatarsal II bear this out (M.C.Z. No. 7452).

TABLE 5

Comparative measurements of *D. barbouri* and *D. cooki.*
Measurements of *D. cooki* from Peterson, 1920.

Element	*Diceratherium barbouri*			*Diceratherium cooki*	
Atlas	M.C.Z. No. 4061	177.0 overall 67.8 condyles		160.0	
		Length	Width	Length	Width
Scapula	M.C.Z. No. 7447	301.0 overall 282.0 segmental		273.0	138.0
Humerus	M.C.Z. No. 7461	293.5 overall e273.0 segmental		250.0	
Radius	M.C.Z. No. 9328	e232.0		250.0	
Ulna	M.C.Z. No. 7448	300.0 overall 232.0 segmental		315.0	
Mc. III	M.C.Z. No. 7449	156.5	37.6 distal 37.9 proximal	138.0	
Mc. IV	M.C.Z. No. 7455	115.4		115.0	
	M.C.Z. No. 9329	130.0			
Femur	M.C.Z. No. 7450	e390.0		323.0	
Fibula	M.C.Z. No. 7451	250.0			
Mt. II				110.0 126.1 A.M.N.H.	
Mt. III	M.C.Z. No. 7452	e140.0		125.0	
Mt. IV	M.C.Z. No. 7452	130.3		110.0 116.5 A.M.N.H.	

CORRELATION AND PALEOGEOGRAPHY

White (1942) apparently regards the Thomas Farm local fauna as a unitary one, representing an essentially contemporaneous assemblage. This is a reasonable interpretation of the evidence, however convenient it might be to split the fossils between two, or even more, faunas of different ages, thereby resolving contradictory indications. He places the Thomas Farm local fauna earlier, in terms of the North American continental scale, than had previously been suggested, considering it as early Lower Miocene (lower Arikareean). The rhinoceroses do not confirm this assignment, and offer some evidence to the contrary. In stage of evolution, without implication of special relationship, the cheek teeth of *Floridaceras* are reminiscent of *Diceratherium armatum* of the John Day, but are somewhat more advanced. The limbs are strikingly long legged, agreeing in this only with *"Aphelops longipes"* of the Mixon bone beds (Alachua fauna) now considered Hemphillian (Middle Pliocene). *Diceratherium barbouri* is a sturdier and more advanced version of *D. cooki*, but is small and slender compared with *F. whitei*, or, for that matter, with most true rhinoceroses. In view of its evolutionary isolation, *Floridaceras whitei* has no precise value in correlation, but is more probably Lower Miocene than either earlier or later. *Diceratherium barbouri*, as a species somewhat more advanced over *D. cooki*, indicates post-Harrison time, i.e., latest Arikareean or possibly earliest Hemingfordian. This agrees with the consensus as to the Thomas Farm local fauna.

I believe that White (1942) attaches too much significance to his phyletic inferences from paleogeographic considerations, and hence his correlation is biased by these considerations. There is no reason to suppose that the Okefenokee Trough was ever more than a shallow trough. Assuming that the former existence of a strait separating a Florida island from the mainland is demonstrated, comparable existing analogies would be with England, Ireland, Newfoundland, or the Behring Straits, rather than with Cuba or Madagascar. Japan, Borneo, Java and even Sumatra are more cut off structurally from the Asiatic mainland than was the "Florida island," yet their faunas do not show the long history of localized evolution inferred by White for Florida but are close to that of the mainland. He believes that intermittent connection by oscillation, bars, etc., can be virtually excluded for a long period of time; but this seems to go far beyond what may be inferred with any confidence from the absence of data. Compare the cases cited above and also dubious evidence cited by White (1942, pp. 36, 37, 41 and 42). Where the peculiar elements in the fauna can represent climatic or other facies differences, the resemblances to Great Plains and Texas faunas are of more significance in correlation than the forms peculiar to the Florida fauna. Bader (1956, p. 70) comes to a similar conclusion in his analysis of the Thomas Farm horse fauna.

White's conclusion as to the fundamental geographic separation of the Florida island fauna from the mainland leads him to the *a priori* improbable hypothesis (1942, p. 42 and implied elsewhere) that a small, isolated southern outlier of the continent gradually developed stock which later invaded the continent when connection was reestablished, and became a considerable element in the later Miocene of the mainland against competition from the pick of a vastly larger area. With all deference to White's special knowledge, I should prefer a more conservative view of the age of this fauna, putting it close to the Arikareean-Hemingfordian boundary. Further evidence could easily shift its position a little, either way. I should also postulate a less complete, perhaps intermittent isolation with elderly phyletic lines surviving in the mild Florida climate, along with bustling northern visitors, so that the latter would give a more dependable check on correlation with the standard sequence. The correlation of mammal-bearing marginal, littoral or marine deposits with the main continental sequence is extremely important; there is no intention to suggest that a definitive correlation has already been reached (whether in Wood, *et al.*, 1941 or elsewhere). If such an idea were entertained, the Quitman, Mississippi, titanothere (Gazin and Sullivan, 1942) would prove the contrary. So detailed a critique is offered because the Thomas Farm local fauna is the most important assemblage of Tertiary land mammals which has yet been discovered in eastern North America.

SUMMARY

1. The Thomas Farm local fauna has yielded two cursorial caenopine rhinoceroses. One is enormous, the other small and delicate.
2. *Floridaceras whitei*, the larger form, dwarfs all its New World contemporaries. It is advanced over Oligocene and Arikareean rhinoceroses, but it is primitive and unmodified compared with Hemingfordian forms and still more so, with later rhinoceroses.
3. *F. whitei* has a tetradactyl manus with a functional fifth digit. This character establishes a distinct line of ancestry back to, say, the early Oligocene *Trigonias*. In view of this evolutionary isolation, it has limited correlative value, but the most reasonable assignment is Lower Miocene.
4. *Diceratherium barbouri*, the smaller form, is slightly more advanced than *D. cooki*, its presumed ancestor. It extends this line, from which there had been no previously reported descendant. Since *D. barbouri* is progressive over the classic

Lower Miocene index fossil, *D. cooki,* it indicates post-Harrison time, i.e., latest Arikareean or possibly earliest Hemingfordian. This agrees with the consensus as to the age of the Thomas Farm local fauna.

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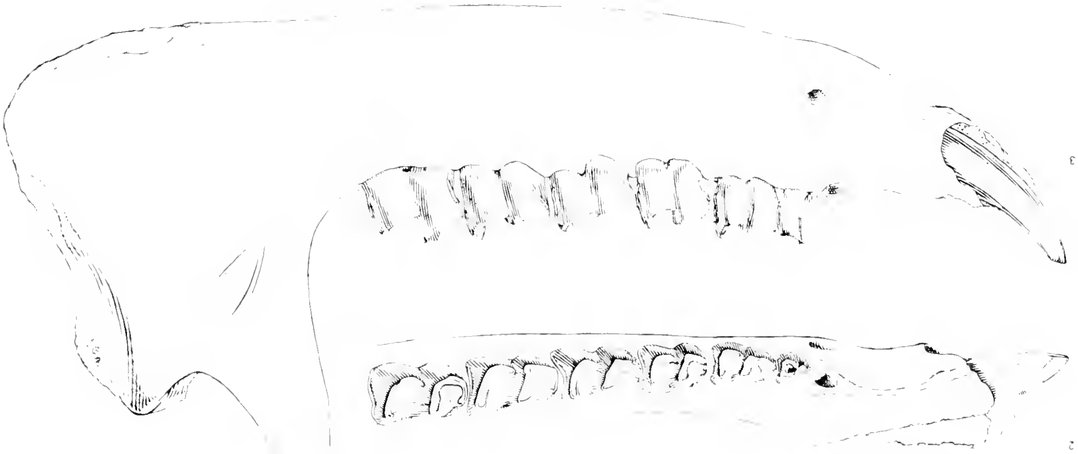
PLATES

PLATE I

Floridaceras whitei

Figure

1. M.C.Z. No. 4046, type, LP^1–M^3, P^1 in outline reversed from RP^1.
2. M.C.Z. No. 4435, paratype, crown view of I_2, P_2–M_3.
3. M.C.Z. No. 4435, paratype, labial view of left mandibular ramus, I_2, P_2–M_3. All × 1¼.



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2

1

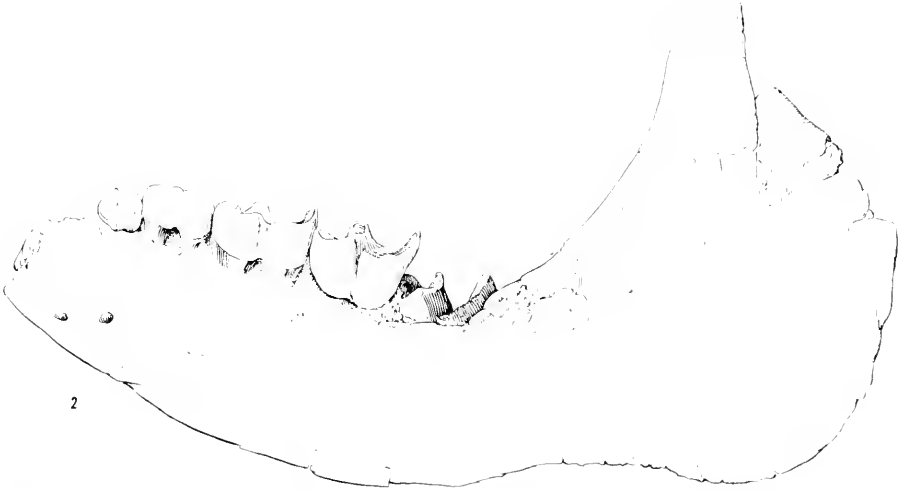
PLATE II

Floridaceras whitei

Figure

1. M.C.Z No. **7473**, I_2, medial view.
2. M.C.Z. No. **4051**, left mandible with dP_{1-4} and M_1 erupting, labial view.
3. M.C.Z. No. **4051**, left mandible with dP_{1-4} and M_1 erupting, crown view. All × 1/3.

1



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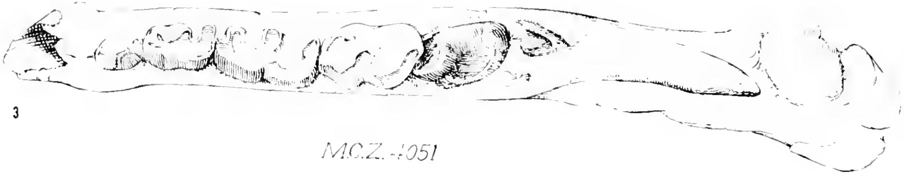

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M.C.Z. 4051

PLATE III

Floridaceras whitei

Figure

1. Composite right upper fore limb: M.C.Z. Nos. **7467**, scapula; 7468, humerus; **7474**, radius; **7477**, ulna.
2. Composite restoration of right manus: M.C.Z. Nos. 7487, pisiform; 7488, cuneiform; **7487**, lunar; **7493**, magnum; 7498, Mc. IV; **7502**, Mc. V; two phalanges, **7507**. All × ¼.

Fig. 1

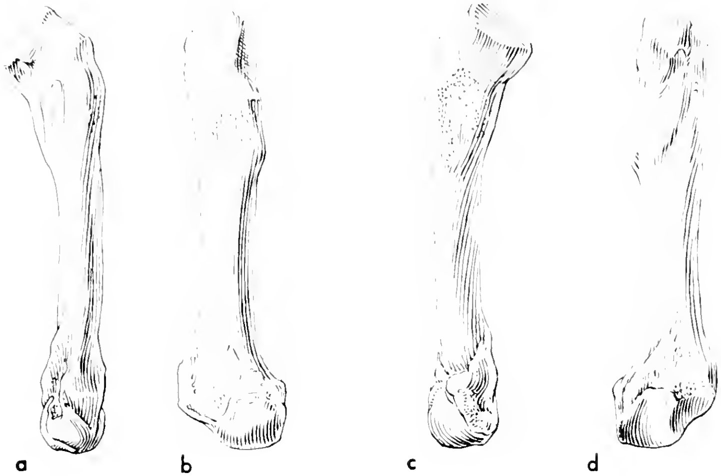

Fig. 2

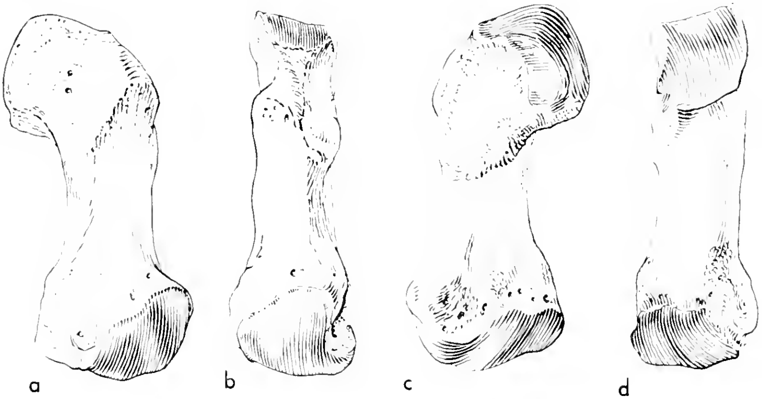

PLATE IV

Figure

1. *Trigonias* cf. *gregoryi*, A.M.N.H. No. 13226D, Mc. V: lateral; *b*, anterior; *c*, medial; *d*, posterior.
2. *Floridaceras whitei*, M.C.Z. No. 7505, Mc. V; *a*, lateral; *b*, anterior; *c*, medial; *d*, posterior. All × ½.

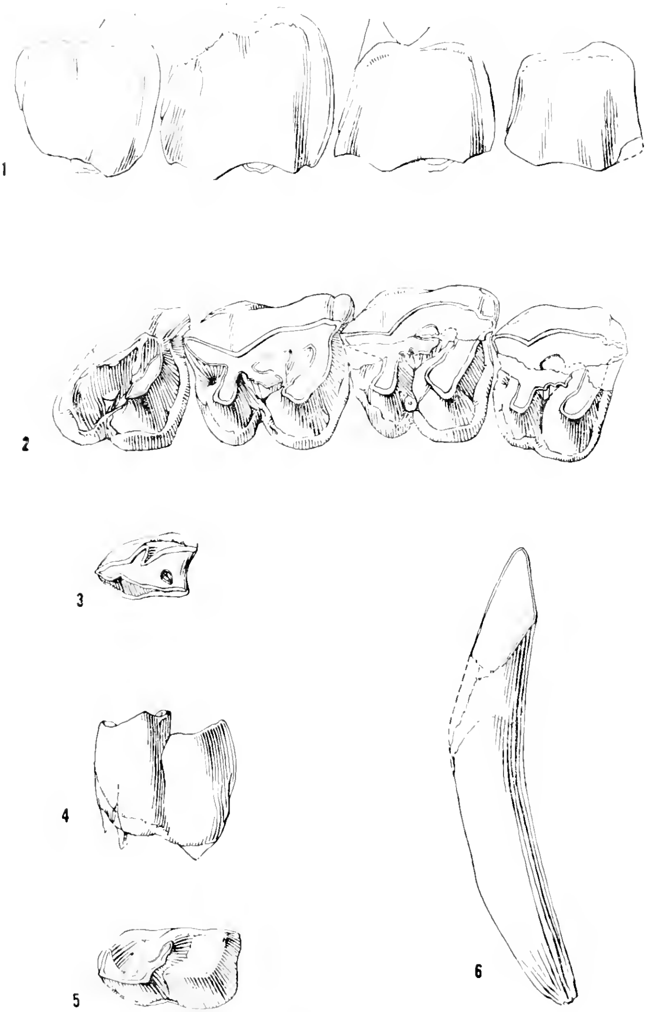

PLATE V

Diceratherium barbouri

Figure

1. M.C.Z. No. 4452, type, external view, RP^4–M^3.
2. M.C.Z. No. 4452, type, crown view, RP^4–M^3.
3. M.C.Z. No. 7444, RP$_2$.
4. M.C.Z. No. 7445, external view LM$_3$.
5. M.C.Z. No. 7445, crown view LM$_3$.
6. M.C.Z. No. 7443, medial view RI$_2$. All × ½.

Bulletin of the Museum of Comparative Zoology
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A REVISION OF THE *PUNCTATUS* GROUP OF AFRICAN *TYPHLOPS* (REPTILIA: SERPENTES)

By R. F. Laurent

CAMBRIDGE, MASS., U.S.A.
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No. 6—*A Revision of the* PUNCTATUS *Group of African* TYPHLOPS *(Reptilia: Serpentes)*

By R. F. Laurent

CONTENTS

INTRODUCTION

For a very long time no herpetologist appears to have been aware that the "nearly panethiopian species," *Typhlops punctatus*, concealed a problem. Only K. P. Schmidt (1923) understood that different forms were being confused under this name; thus he was able to discriminate three different species in Lang and Chapin's beautiful collection. Subsequent authorities, however, especially

Loveridge and Bogert, not only did not follow him but insisted that these forms were only individual or color variants.

However, when I had to study my own snake material (Laurent, 1956), collected in the western Graben (eastern Congo and Ruanda-Urundi), I came to the conclusion that K. P. Schmidt had been perfectly right, and that his only error had been that he distinguished only three species when he had four species in hand. There were indeed nomenclatorial discrepancies, as appears in the comparison below:

Schmidt 1923	Laurent 1956
Typhlops congestus	*Typhlops congestus* *Typhlops punctatus*
Typhlops intermedius	*Typhlops angolensis angolensis*
Typhlops punctatus	*Typhlops boulengeri*

In my 1956 paper, I showed that these species have little geographic variation in the territory of the former Belgian Congo, with the remarkable exception of *T. angolensis* whose savanna and mountain populations are conspicuously differentiated.

The following subspecies of *angolensis* were recognized: *adolfi* Sternfeld in lowland savannas, *dubius* Chabanaud in highland savannas, *symoensi* Laurent in savanna highlands of Itombwe (southern Kivu), *polylepis* Laurent in mountain and transition forest on the western side of the western mountains of the Graben, *irsaci* Laurent in mountain forests of the eastern side of the same highlands and in the Rugege forest (Ruanda).

In 1956, however, I wrongly considered as valid some forms such as *congicus* Peters and *lestradei* Witte, which I have since synonymized, respectively, with *angolensis* Bocage and *dubius* Chabanaud. Those nominal forms were based on specimens whose eyes were hidden under head scales. Loveridge (1942) realized that this character was not necessarily significant and for that reason considered *lestradei* as a subspecies of *blanfordi*. In many species in which the eye is normally distinguishable some specimens may have a lacteous opaque hue and hidden eyes; the proportions of head scales are also different and this correlation has been mistaken for a taxonomic character. In 1960, I suggested that this condition occurred immediately preceding sloughing and can occur in any species.

A revision of the whole *Typhlops* collection in the Musée Royal de l'Afrique Centrale (Tervuren) might have permitted further study of geographical variation in west Africa and increased our knowledge of the distributions towards the west and the south, but I have not had the opportunity to undertake it. On the other hand, the collections of the Museum of Comparative Zoology have offered the possibility of examining the situation in other regions of Africa and this, in fact, is more interesting. This investigation, supplemented by the examination of the pertinent material in the Chicago Natural History Museum (CNHM), the American Museum of Natural History (AMNH), and the United States National Museum (USNM), is the subject of the present paper.

The material studied comprises numerous specimens labeled as *Typhlops punctatus*, *T. p. gierrai*, *T. blanfordi blanfordi*, *T. blanfordi lestradei*, *T. steinhausi*, *T. tettensis tettensis*, *T. tettensis rondoensis*, *T. tettensis obtusus*, *T. mossambicus*, *T. kaimosae*. In place of this arrangement (which is that of Loveridge's 1957 Checklist) I propose the following:

NEW TAXONOMIC ARRANGEMENT

1. *Typhlops punctatus punctatus* (Leach)—Savanna populations in the Sudanese subprovince.

2. *Typhlops punctatus liberiensis* (Hallowell)—Forest populations in the Liberia-Ghana region.

3. *Typhlops congestus* (Duméril and Bibron)—Forest populations of the Cameroon and Congo area.

Typhlops congestus and *T. punctatus* may perhaps be one polytypic species whose terminal races behave, between themselves, like good species. There is, however, at present, no evidence of intergradation between *congestus* and *liberiensis*.

4. *Typhlops boulengeri boulengeri* Bocage—Savanna species with a circum-forest distribution, sympatric with *T. punctatus* in the Sudanese subprovince. The East African material referred to *punctatus* is actually *boulengeri*.

5. *Typhlops boulengeri usambaricus* subsp. n.—A spotted and mountain subspecies of *T. boulengeri*.

6. *Typhlops gierrai* Mocquard—A mountain species sympatric with *usambaricus* which it resembles by its frequently spotted pattern.

7. *Typhlops schmidti schmidti* Laurent—A savanna species from southern Congo, eastern Angola and northern Rhodesia.

8. *Typhlops schmidti tanganicanus* subsp. n.—A recognizable subspecies from southern Tanganyika and northern Mozambique =*T. tettensis tettensis* Loveridge (non Peters).

9. *Typhlops rondoensis* Loveridge—This form described as a subspecies of *tettensis* seems to be a species distinct from *schmidti* and it is entirely different from the true *tettensis* which is a synonym of *fornasinii.*

10. *Typhlops fornasinii* Bianconi—A very distinct species possibly related to *T. angolensis (tettensis* Peters and *mossambicus* Peters appear to be synonyms).

11. *Typhlops obtusus* Peters—A species quite distinct from *tettensis,* and related to *T. angolensis.* Investigation of material from northern Rhodesia and Katanga may yet prove that the whole *angolensis* complex may be conspecific with *obtusus.*

12. *Typhlops steinhausi* Werner—A forest form from Cameroon and Congo.

13. *Typhlops angolensis angolensis* Bocage—A forest form from northern Angola and Congo.

14. *Typhlops angolensis adolfi* Sternfeld—A savanna form from eastern southern Congo and eastern Africa. *T. kaimosae* Loveridge is a synonym based on an individual anomaly.

15. *Typhlops angolensis dubius* Chabanaud—Populations from grassy highlands in Kivu, Uganda, Ituri and Ruanda-Urundi.

16. *Typhlops angolensis symoensi* Laurent—A form derived from *dubius* in southern Itombwe (southern Kivu).

17. *Typhlops angolensis polylepis* Laurent—Western mountain forest in Kivu.

18. *Typhlops angolensis irsaci* Laurent—Eastern mountain forest in Kivu and Ruanda.

19. *Typhlops angolensis blanfordi* Boulenger—Northeastern African highlands.

CHARACTERS EXAMINED[1]

1) *Rows of scales at midbody.* This character has long been recognized as of high diagnostic value. It is often variable within populations but this variability is generally low: 2, 4, 6 and rarely more; the odd numbers are infrequent.

In *T. angolensis,* a positive correlation between the altitude and number of midbody scale rows has been disclosed (Laurent, 1960).

---

[1] Data from the MCZ and AMNH, CNHM, USNM collections and from Laurent (1956, 1960).

The variation for all the forms examined is shown in Table 1 (frequencies given as percentages).

2) *Difference between the number of scale rows at midbody level and behind the head.* (See Table 2.)

3) *Difference in the number of scale rows between the preanal region and the midbody region.* (See Table 3.)

4) *Number of scales between the prefrontal and the end of the tail.* (See Table 4.)

5) *Shape of prefrontal.* This character has already been stressed as an obvious difference between *T. angolensis, sensu lato,* and the *punctatus-boulengeri-schmidti* complex (Laurent, 1956). In the first group it is subhexagonal; in the second, subtrapezoidal. The subhexagonal type exists also in *blanfordi, steinhausi,* and *obtusus,* all forms here considered as subspecies of *T. angolensis* or closely related to this species.

On the other hand, *gierrai* and *tanganicanus* have the subtrapezoidal form described for *schmidti.*

In *T. congestus,* the prefrontal is hexagonal as in *T. angolensis* but flatter (shorter) and wider. In *T. punctatus liberiensis*, a somewhat intermediate condition occurs, tending to the trapezoidal form of *punctatus.* In *rondoensis*, the form is subtrapezoidal, but less angular. It is rounded and very small in *fornasinii.*

6) *Shape of the supraocular.* An almost perfect correlation is obvious between the shape of the prefrontal and the shape of the supraocular. When the prefrontal is subtrapezoidal, the supraocular is band-like and oblique, with its lateral angle inserted between the nasal and the preocular; this condition is seen in *punctatus, boulengeri, usambaricus, gierrai, tanganicanus, schmidti.* When it is subhexagonal, the supraocular is transversely oriented with its lateral angle inserted between the preocular and the ocular; this condition is seen in *T. angolensis* and all its subspecies, as in *obtusus* and *fornasinii. T. congestus* shows almost the same outline but somewhat approaching the oblique band of *punctatus;* in 2 specimens out of 56, the lateral extremity is between the nasal and the preocular. In *T. punctatus liberiensis*, the *punctatus* condition prevails, with some intermediates with the lateral end between the ocular and the preocular (the latter only on 2 sides of 18 Liberian individuals, but in 6 specimens and 2 additional sides of 10 from Ghana—a cline?).

Some exceptions concerning the location of the external end of the supraocular have been observed in *punctatus* (symmetrical in 2 specimens and asymmetrical in 2 others of 14 individuals), in *gierrai* and *boulengeri* (asymmetrical in 4 specimens out of 25). In *T. rondoensis* the supraocular is oblique but more rounded, its external end in contact with the nasal.

7) *Size and location of the eye.* The eye is larger in *punctatus* than in any other form. When the eye is hidden, this condition is generally correlated with a peculiar appearance of the scales and a lacteous hue obscuring any color pattern; this seems to precede sloughing but is striking enough to have been wrongly considered as a taxonomic character. The eye is behind or partly below the ocular-preocular limit in *punctatus, liberiensis, congestus, boulengeri, usambaricus, tanganicanus, schmidti, fornasinii.* It is below the same limit or anterior to it in *T. angolensis,* and clearly before it (below the preocular) in *T. rondoensis.* These relations concern the superficial sutures.

8) *Nasal suture.* The nasal suture generally joins the nostril to the first labial border, but in the eastern populations of *congestus* it generally ends at the rostral limit. It seems that this condition becomes less frequent towards the west; exceptions (i.e. termination at the limit between rostral and first labial) have been more often remarked in specimens from central Congo. In the samples from Cameroon and in *T. punctatus liberiensis,* the "eastern" condition is sometimes seen asymmetrically, and even symmetrically in one case (*Typhlops leprosus* Taylor and Weyer).

In *T. fornasinii,* the suture may go beyond the nostril (type of *tettensis*) or even completely divide the nasal plate (type of *mossambicus*).

9) *Labials touching the preocular* (see Table 5). In *boulengeri,* the frequency of the contact of labials 1 and 2 with the preocular is high in the Congolese and Sudanese samples, and low in east African samples; an internal cline is probable. The absence of contact is effected in two ways: in *gierrai,* a supplementary scale comes between the labials and the preocular; in the type of *kaimosae,* the nasal is in contact with the ocular below the preocular, but this is an abnormal condition—as proven by the existence of sympatric specimens of *adolfi* which differ only by the absence of this peculiarity.

10) *Shape of the contact between the labials and the preocular* (or the intercalary scale in *gierrai*). The shape of this contact has often proven to be taxonomically significant. It may be straight or angular; when it is angular two labials are necessarily involved since a labial never has a concave outline.

The contact is almost always straight in *boulengeri, usambaricus, schmidti, tanganicanus, fornasinii, steinhausi, irsaci, blanfordi*. It is generally so in *rondoensis* and *dubius*.

The contact is angular in *punctatus, gierrai, obtusus, angolensis,* and *symoensi*. It is generally so in *liberiensis, congestus, polylepis,* and *adolfi*.

11) *Color pattern*. The coloration appears in two radically different phases which, oddly enough, rarely occur in the same populations in the former Belgian Congo, but are frequently coexistent outside this area.

One of these phases is spotted or marbled: the pigmentation is so unevenly distributed that some groups of scales are devoid of any pigment, while others are almost black. Two forms have this kind of coloration exclusively: *usambaricus* (but only two specimens of the latter are known to me), and the eastern populations of *T. congestus*.

The same pattern is frequent but not universal in *congestus* (western populations), *punctatus, liberiensis* and *gierrai*. It may occur but rarely in *schmidti, rondoensis* (one specimen), and *boulengeri* (one specimen from Ujiji; I have never seen it in any of the numerous Congolese specimens examined in the past). It seems never to be present in *T. angolensis* and its races. Two aspects are recognizable in this marbled pattern. The belly may be marbled like the back: this is the rule in *T. punctatus punctatus*, and the only spotted specimen of *T. boulengeri* I have seen is similar. In all the other forms with marbled pattern, the belly is always immaculate. The other phase is more evenly pigmented. Each dorsal scale is partly pigmented. Sometimes, the pigment is concentrated on the sides of the scales producing a striped pattern. Sometimes, it forms a transversely elongated blotch leaving a smaller light area in front and a larger behind; this tendency seems to be frequent in the *angolensis* group and *T. obtusus*, but the number of specimens at hand does not permit any generalisation. Sometimes, the black pigment forms a horseshoe pattern on each scale, with the main light area in front; this pattern is seen in *T. punctatus, T. congestus, T. boulengeri, T. schmidti, T. gierrai*. Both patterns occur in *rondoensis*. In either case, a finely punctate appearance is the result of this distribution of pigment. Often the pigment invades the light areas and the scales then become uniformly blackish or nearly so. This happens in the eastern populations of *T. angolensis* and some individuals of *T. punctatus* and *T. boulengeri*.

The greater or lesser development of pigmentation has another aspect. When pigment is relatively scant, the belly is generally

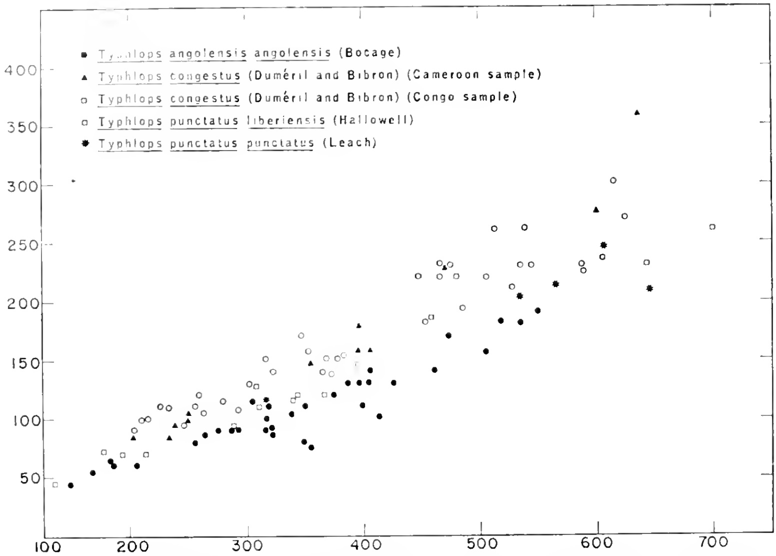


Fig. 1. Scatter diagram of the diameter of the body (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

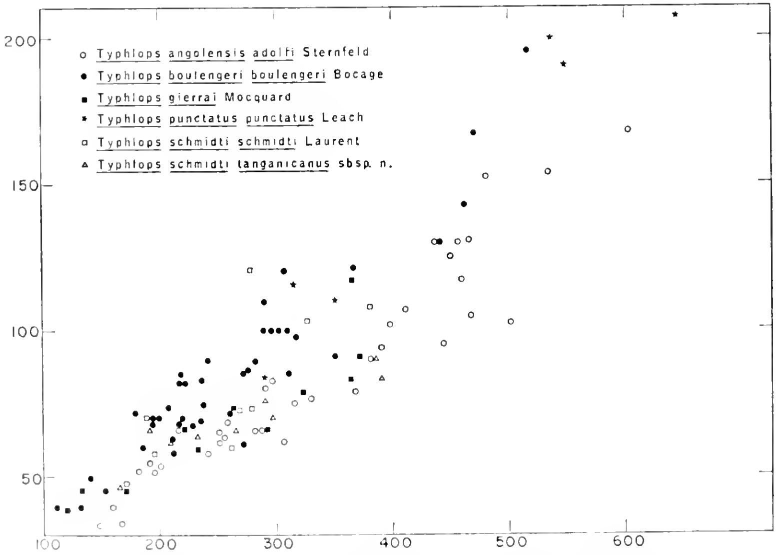


Fig. 2. Scatter diagram of the diameter of the body (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

immaculate; when it is extensive, the number of pigmented scale rows increases until all the ventral rows are affected. Generally there is less pigment ventrally so that even if the dorsal scales are entirely black, the lateral and ventral scales have a light central spot, which is larger in the ventral scales. In this case, we have a dorsoventral gradient of pigmentation. In other cases, there is a sharp difference between the dark back and the light belly, the limit being straight or irregular, lateral or ventral with a narrow light ventral band.

T. fornasinii, very different in its low longitudinal scale count, is also very different in its uniform pigmentation.

12) *Ratio between the length of body and its largest diameter.* This character is unfortunately affected by the physiological condition of the specimen when killed and the state of preservation. However, some species are slender while others are thick. No sexual correlation is apparent in this character. (See Table 6; Figs. 1 and 2.)

13) *Ratio between the length of body and the breadth of the head.* (See Table 7; Figs. 3 and 4.)

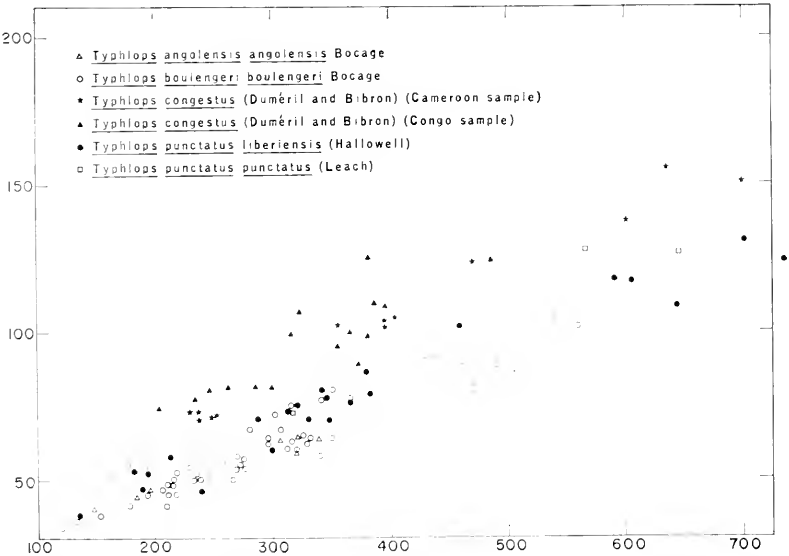


Fig. 3. Scatter diagram of the breadth of the head (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

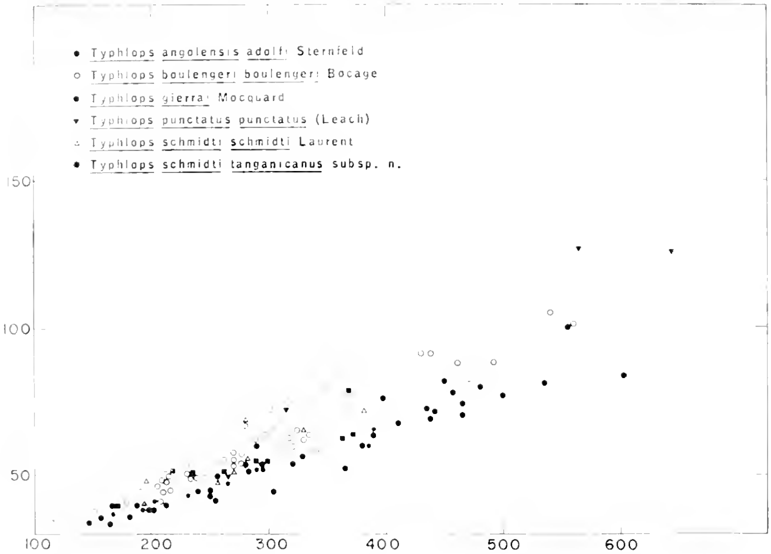


Fig. 4. Scatter diagram of the breadth of the head (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

14) *Relative breadth of the prefrontal.* This character displays a large individual variability and, as such, is not very useful. The percentage values of this measurement in relation to the breadth of the head are given here but only for some samples. An interesting difference appears between *congestus* and *liberiensis*.

Breadth of prefrontal/breadth of head (in per cent)
(Modal condition in bold face)

	26-30	30-34	34-38	38-42	42-46	46-50	50-54	54-58
T. punctatus liberiensis (27)				11	**33**	**33**	12	11
T. congestus congestus (33)	3	6	6	**49**	33	3		
T. boulengeri (38)		3	8	13	24	**26**	13	13
T. gierrai (9)			22	23	**55**			
T. schmidti tanganicanus (9)				11	33	**34**	22	
T. rondoensis (10)			10	30	**50**	10		
T. angolensis subsp. (33)	3	9	18	**43**	15	19		

RECOGNITION OF "NON-DIMENSIONAL" SPECIES

In his outstanding revisionary study of *Dasypeltis*, Gans (1959) began his investigation by the examination of the cases of sympatric differences. No better approach to a difficult taxonomic problem can be conceived and it should be adopted by every taxonomist.

Sympatry of punctatus and congestus. From Sakbayema, Cameroon, the MCZ has four specimens of *congestus* and one specimen of *punctatus.*

The *congestus* individuals have no ventral pigmentation except some lateral encroachments of the dorsal blotches in some of them. On the contrary, the belly is pigmented except in the midventral region in the *punctatus* individual.

The following correlated differences prove that the *"punctatus"* and *"congestus"* specimens could not pertain to the same population.

	congestus	*punctatus*
Supraocular	nearly transverse	definitely oblique
Midbody scale rows	26-28	30
Scale rows in front of anus	19-22	26
Longitudinal number of scales	322-354 (4 ♂ ♂) 341-382 (8 ♀ ♀ from other localities)	376 (♂ from another locality in Cameroon) 428 (♀)
Ratio length/diameter	21.8-29	33
Ratio length/breadth of head	38.3-43.7	53.2

Sympatry of punctatus and boulengeri. I have already recorded the coexistence of these two forms in the northern Congo (Laurent, 1956). Schmidt's data (1923) also prove that these forms are sympatric (at Poko) and thus specifically distinct; however, he confused *punctatus* with *congestus* and gave the name of *punctatus* to *boulengeri.*

The significant data are as follows:

	punctatus	*boulengeri*
Belly	dark or mottled	light
Size	549-605 mm	139-308 mm
Scale rows behind the head	32-34	26-28
Midbody scale rows	30-32	26-28
Shape of the contact between preocular and labials	angular	straight

T. punctatus and *T. boulengeri* are also sympatric in the Sudan. The MCZ has three specimens of *T. boulengeri*, but no *T. punctatus* from this area; however, true Sudanese *punctatus* exist in the collections of the British Museum (Natural History) and the Chicago Museum.

T. boulengeri has the belly nearly as pigmented as *punctatus* in this northern part of its range. It differs however by its lower number of midbody scale rows (28-30 instead of 30-34), and more clearly by the relations between the preocular and the upper labials. The contact is straight and with the 1st and 2nd labials in the three *boulengeri* specimens examined from Sudan, while it is angular and with the 2nd and 3rd labials in *punctatus*. The longitudinal counts of scales of eleven *T. punctatus* are 376-403 (3 ♂) and 399-428 (8 ♀), while the Sudanese *boulengeri* give lower figures: 374 (♂), 391–400 (2 ♀).

Sympatry of congestus and steinhausi. These two forms are so obviously different that their distinctiveness has never been questioned and need not be demonstrated here. They are sympatric in Cameroon.

Sympatry of congestus and angolensis. These two *Typhlops* have been adequately diagnosed by Schmidt (1923) but *angolensis* was called by him *intermedius*. See also Laurent (1956).

	congestus	*angolensis*
Color pattern	blotches	striped (each scale with a yellow spot)
Scale rows behind the head	28-32	24-28
Ratio total length/diameter	19-30	26-41
Ratio total length/breadth of head	27.5-45	37-61
Nasal suture	generally from rostral	from 1st labial
Longitudinal scale counts (in females only)	365-410 (8 ♀♀)	287-364 (8 ♀♀)

Sympatry of punctatus and steinhausi. Schmidt's data (1923) show that *punctatus* and *angolensis* are sympatric in Niangara, but it could be presumed that they are ecologically separated since *punctatus* is an inhabitant of savannas, while *angolensis* lives in the forest. While examining this material in New York I discovered that the "*intermedius*" specimens from Niangara are not *angolensis* but *steinhausi*.

	punctatus	*steinhausi*
Belly	pigmented	not pigmented
Scale rows behind the head	32-34	24-26
Midbody scale rows	30-32	25-26
Scale reduction between midbody and vent level	6	1-2
Prefrontal	trapezoidal and wide	subhexagonal and narrow
Supraocular	oblique, apex generally between nasal and preocular	transverse, apex between preocular and ocular
Eye	large, below ocular	smaller, below preocular
Labials touching preocular	2-3, contact angular	1-2-3, contact straight

Sympatry of boulengeri and adolfi. It was the coexistence of two entirely different "*Typhlops punctatus*" at Uvira, Kivu, and the Mosso region, Urundi, which induced me to question the conception of a wide-ranging and variable species called *T. punctatus*. In fact, this difference has been recognized repeatedly: not only did Schmidt (1923) make a distinction between the two species involved, but Bocage (1893) did also, in describing *T. boulengeri*, and Boulenger (1899) as well, in describing *T. blanfordi*. Loveridge (1942) did the same, recognizing *T. blanfordi lestradei* as distinct from his *T. punctatus*. His concept of *T. punctatus* in East Africa is correct in the sense that it is not a composite as I once believed. Except for two montane specimens apparently referable to a new form, his *T. punctatus* is simply *T. boulengeri*. In this he follows Schmidt. However, his western "*punctatus*" material is a mixture of several species.

The characters which prove that *boulengeri* and *adolfi* are specifically distinct are as follows:

	boulengeri	*adolfi*
Color	lighter	darker
Prefrontal	wide, subtrapezoidal	narrower, subhexagonal
Supraocular	oblique, apex touching the nasal	transverse, apex touching the ocular
Eye	behind the posterior border of preocular	below or before the posterior border of preocular
Contact between preocular and upper labials	straight, predominantly with 2nd labial, often also with 1st or 3rd labial	generally angular, with 2nd and 3rd labials
Midbody scale rows	28, rarely 30	30 or 32, rarely 28
Ratio length/diameter	24-39	25.5-50
Ratio breadth of head/breadth of tail	0.92-1.33	1.22-1.66
Maximum size	50 cm	62 cm

Sympatry of boulengeri and schmidti. T. schmidti is a Katangese species which has been confused with *boulengeri* and *adolfi* under the name of "*punctatus*" (de Witte 1933b, 1953). The complete disentangling of this material is yet to be accomplished, and at the present time the respective distributions of the three species in this area are not known in detail.

At Sandoa, however, the three forms are known to occur together.

The significant differences are the following:

	boulengeri	*schmidti*
Belly	generally pigmented, however slightly	generally not pigmented
Midbody scale rows	28 (rarely 30, sometimes 26)	22-24 (rarely 26)
3rd labial	not often in contact with preocular (25% of sides in Congo specimens)	nearly always in contact with preocular
Reduction in the number of scale rows		
at midbody	rarely more than one	rarely less than two
at anal region	usually more than two	generally two
Longitudinal counts		
♂♂	351-393 (7 spec.)	317-325 (2 spec.)
♀♀	384-400 (8 spec.)	370 (1 spec.)

Sympatry of gierrai and usambaricus. From Amani, Usambara Mountains, the MCZ has a small series of *T. gierrai* and two additional spotted specimens which appear to represent an unrecognized form (both forms are spotted). Loveridge considered *gierrai* as a race of "*punctatus*" (understanding by this what I here consider *boulengeri*). The specimens here described as *usambaricus* were recorded by Loveridge as intermediates between "*punctatus*" and *gierrai*. They are clearly different from *gierrai* and cannot belong to the same population.

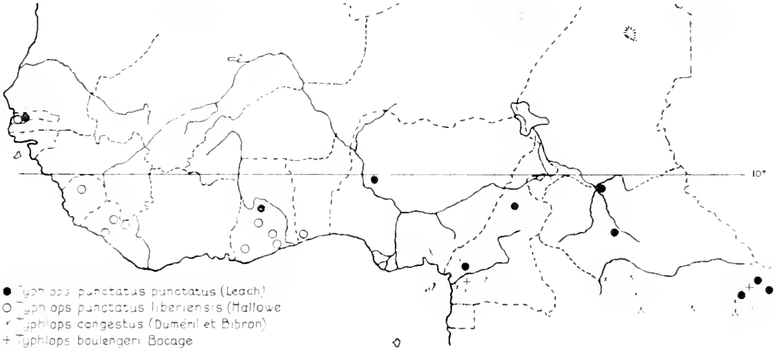
	gierrai	*usambaricus*
Scales outside spots	black bordered	unpigmented
Contact between preocular and labials	inferior part of preocular separated, forming an angular contact with 2nd and 3rd labials	preocular undivided in straight contact with 2nd and 3rd labials
Scale rows in front of the vent	24-26 (23 in one specimen)	22
Eye	under the posterior border of the preocular	behind the posterior border of the preocular

	gierrai	*usambaricus*
Longitudinal count of scales	398-464	344-390
Ratio length/diameter	31.2-44	27-31.1
Ratio length/width of head	42.5-58.4	38.4-42.2

Conclusions. From the foregoing it must be concluded that eight specific gaps, proved by sympatric relationships, are evident in the "*Typhlops punctatus*" complex.

ALLOPATRIC RELATIONSHIPS

The populations of western Africa (Liberia to Ghana). Notwithstanding the number of names which have been based on specimens from this region, there are no apparent grounds for a taxonomic splitting of these populations of *Typhlops*. The characters bridge the gap between true *punctatus* and the Cameroon populations (*congestus*). The color pattern is variable in the three groups, with two phases: the "*punctatus*" phase with each scale bicolored (the amount of black pigment decreasing from the back to the sides or to the belly), and the "blotched" phase.



Map 1. Distribution of species of the *Typhlops punctatus* group in West Africa.

In the savanna populations the ventral pigmentation is strongly developed, i.e. nearly all the ventral scales are partly pigmented, and the blotched phase has spots on the belly. In the two other samples the belly is generally devoid of any pigment except for some punctating or spots on the sides, which may be rather frequent; sometimes the light part of the belly is narrow, but only one specimen from Ghana (Somenya, MCZ 55318) has black spots on most of the ventral scales.

The number of midbody scale rows approaches the *congestus* figures; they are 26 to 28, rarely 30, instead of 30-32 for *punctatus*. The longitudinal scale counts are intermediate, but nearer to *punctatus*.

	punctatus	Liberia-Ghana	*congestus* (Cameroon only)
♂♂	376-403 (n=3) (m=387)	339-385 (n=10) (m=363.2)	322-354 (n=6) (m=339.17)
♀♀	399-428 (n=8) (m=423)	371-435 (n=9) (m=400.78)	341-382 (n=10) (m=364.83)

The shape of the prefrontal is also intermediate. The shape of the supraocular is generally similar to that of *punctatus* but with a definite tendency in eastern populations to the *congestus* condition, i.e. the lateral apex is between the preocular and the ocular in 7 per cent of the cases in Liberia but in 68 per cent in Ghana.

The nasal suture arises from the rostral with a frequency of 22 per cent; such a condition has never been recorded in *punctatus*, but occurs in *congestus*, rarely in Cameroon populations, as a general rule in eastern Congo samples.

The contact of preocular with labials is angular in the three groups with only one symmetrical exception in a Ghana specimen (Somenya, MCZ 55318) and one asymmetric exception in a Cameroon specimen (Lolodorf, MCZ 9241).

The scatter diagram for the relative thickness of the body shows that the Liberia group resembles *punctatus* more than *congestus*; for the relative width of the head, the Liberia group is intermediate.

The relative breadth of the prefrontal, ranging from 41.1 to 55.6 per cent of width of the head (m=47.78), is clearly greater than that of *congestus*, which ranges from 28.2 to 42.9 per cent (m=38.98) but does not differ from that of *punctatus* with a range of 40 to 56.1 (m=46.38).

The characters checked support equally a conspecific relationship with *punctatus* or with *congestus*, or even with both. However, we already know that *congestus* can be sympatric with *punctatus* in at least one locality of Cameroon. Moreover, we have strong evidence that the Congolese populations of *congestus* are not connected to *punctatus* by hybrid populations although they are still not known to be sympatric in any locality; the differences appear too clear-cut in view of the shortness of the distance between the least distant localities (Poko and Akenge).

It is, of course, still possible that *congestus* is subspecifically related to the Liberia populations and by way of these with *punctatus.* But as there exists a distributional gap between the western forest populations and those of Cameroon, we are permitted to postulate that they do not belong to the same species.

The data for the Ghana specimens suggest a short cline between the southern forest populations and the northern savanna ones. Thus, the conditions appear to warrant the recognition of subspecific relationships between these populations.

Western and eastern populations of T. congestus. The spotted forest *Typhlops* of Congo (ex Belgian Congo) have been referred by Schmidt (1923) and Laurent (1956) to *T. congestus.* However, they appear to differ from the Cameroon samples, as shown below.

	Cameroon	Congo
Color pattern	spotted and punctate phase	spotted phase only
Nasal suture	generally from 1st labial	generally from the rostral
Longitudinal counts of scales		
♂ ♂	322-354 (6)	331-378 (12)
♀ ♀	341-382 (10)	381-404 (5)
Relative thickness of body and relative breadth of head	somewhat larger in the Congo specimens (see scatter diagram)	

The populations from Cameroon and eastern Congo are thus fairly different and could perhaps be treated as subspecies; however, the populations of western Congo, which are poorly known, are likely to provide a smooth clinal transition. In consequence, no subspecific distinction is here proposed.

The Usambara Mountains population of T. boulengeri. Two specimens from Amani (MCZ 23099 and 38699) differ from the sympatric *T. gierrai* (see above) and from the allopatric *boulengeri.* I have seen more than 130 specimens of *boulengeri* from the Congo and 25 additional specimens in the MCZ collection; to these figures we may add the 15 specimens examined by Schmidt (1923). One, from Ujiji (MCZ 30037) has a spotted pattern on the belly as well as on the back (a pattern observed elsewhere only in *T. punctatus*). The two Amani individuals, however, are only spotted on the back. Since this pattern is never encountered in typical *T. boulengeri,* it may be assumed that it is characteristic of a montane population which is recognizable as a race.

Typical populations of T. schmidti compared with eastern populations. The material referred by Loveridge to *T. tettensis* (1955,

1956) is so strikingly like *T. schmidti* that I believed, after a first examination, that *schmidti* was simply a synonym of *tettensis*. Some differences exist, however, and justify a subspecific discrimination, pending the ever-possible discovery of a connecting cline. The name of the species must be *schmidti*, since *tettensis* is an entirely different species as explained below:

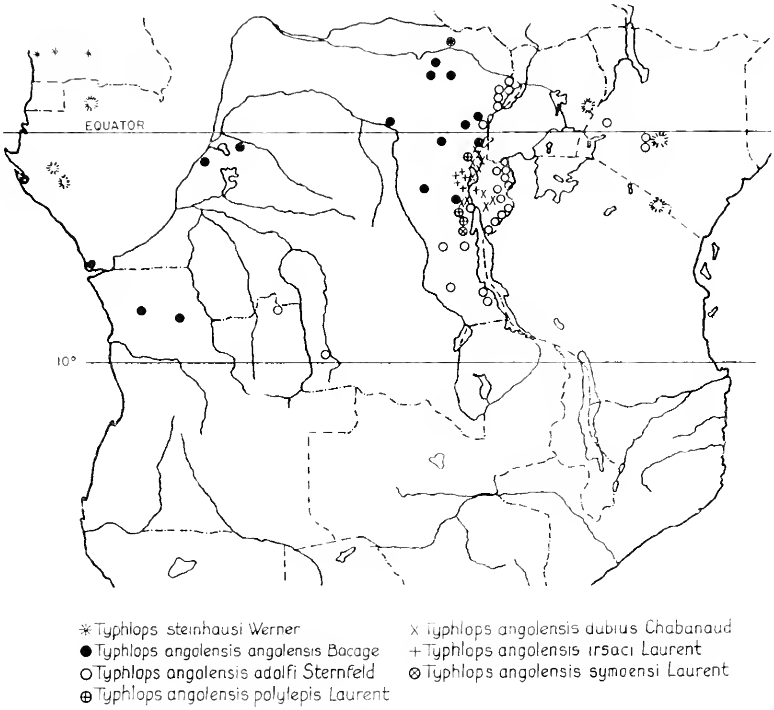
	schmidti	eastern sample (Liwale, Kilwa)
Midbody scale rows	22 to 26 (22 in 32% of specimens, 24 in 63%, 26 in 5%)	21 to 24 (21 in 12%, 22 in 44%, 24 in 44%)
Reduction of scale rows from front part of body to midbody	4, sometimes 2, rarely 0	2 or 0, rarely 3
Longitudinal counts ♂ ♂	317-325 (2)	352-376 (4)
♀ ♀	370	400-425 (6)
Belly	not pigmented	slightly pigmented
Ratio length/diameter	23-42.7 (m=33.58)	29-47 (m=37.82)
Ratio length/width of head	40.6-52.7 (m=48.33)	47-64 (m=54.57)

Allopatric relations of T. angolensis. The subspecific differentiation of *T. angolensis* in the territory of the former Belgian Congo has been described by me (1956, 1960). Loveridge (1942) has correctly pointed out the relationships between *angolensis* mountain populations of Kivu, Ruanda and Uganda (which he called *lestradei*), and *T. blanfordi*. This form is related to *dubius* (= *lestradei*) and to *adolfi*.

The color pattern is similar, but with a mid-belly light zone in some individuals. As I know only two specimens of *blanfordi*, I cannot tell what the frequency of this character is. The difference from *adolfi* is that the contact between the preocular and the labials is straight and not angular.

The longitudinal count of scales is 347-392 in *blanfordi* (2 ♂ ♂), 411-573 in *dubius* (15 specimens which are unsexed because they were eviscerated); these counts are poorly known in the other races, but some indications suggest an altitudinal cline, since one ♀ of *irsaci* has 520 scales and 2 ♂ ♂ have 425 and 485, while 8 ♀ ♀ of the typical lowland form have 287 to 364 scales and 12 ♂ ♂ have 281 to 371 scales.

T. kaimosae differs from *adolfi* in the absence of any contact between the preocular and the labials (nasal and ocular contiguous below the preocular); but this peculiarity is not shared by two other specimens from Kenya, which are referable to *adolfi*, the



Map 2. Distribution of species of the *Typhlops angolensis* group in the region of the Congo.

distribution of which is therefore considerably extended towards the east.

Some relations with southern and southeastern forms like *obtusus*, *fornasinii*, *bibroni* and even *rondoensis* are probable but they are not close enough to warrant any taxonomic recognition.

Relationships between T. angolensis and T. steinhausi. The seven specimens seen of *T. steinhausi* agree with *T. angolensis* in many characters: number of scale rows, color pattern, shape and connections of prefrontal and supraocular, position of eye. *T. steinhausi* differs from *T. angolensis* by the relations of the preocular and the labials: the contact is straight as it is in some highland populations of *T. angolensis (dubius* and *irsaci)*, but with three labials (1st to 3rd) as it is in some individuals of *T. boulengeri*. The longitudinal counts of *T. steinhausi* are considerably higher than in *angolensis* (typical form): 402 to 425 instead of 281 to 371. Lastly, *T. steinhausi* is more slender. The ratio between the total length and the diameter varies from 39.8 to 50. 3 (n=7) (m=43.10), while in the lowland forest *T. angolensis,* the figures are 26.7 to 40.5 (n=33) (m=33.39). Before seeing the collections of the American Museum of Natural History, I was prepared to treat *steinhausi* as a subspecies of *T. angolensis* though it appeared as the most sharply differentiated of all the races of this species. It was plausible as a Cameroon subspecies. I was surprised to discover at the American Museum of Natural History that this form is also present in the northern part of the eastern Congo.[1] Schmidt's series of *T. intermedius* (1923) includes two specimens of *T. steinhausi* from Niangara. This is a quite unexpected extension of range and very unlikely for a subspecies of *T. angolensis.* Sympatry with *angolensis* is not yet proven, but such a proximity of clearly different populations is hardly compatible with a subspecific status when no obvious barrier is involved in the picture.

The relationships of the southeastern forms. The allopatric forms which Loveridge (1942, 1955, 1956) considered as races of a single species and called *T. t. tettensis, T. t. rondoensis,* and *T. t. obtusus,* are not closely related, in my opinion.

Tettensis Loveridge is widely different from *tettensis* Peters, and is a race of *T. schmidti* which deserves a new name; *tanganicanus* subsp. n., *T. tettensis* Peters, and *T. mossambicus* Peters are synonyms of *T. fornasinii* Bianconi.

The differences between these forms are such that it can hardly be doubted they are full species, with the possible exception of *rondoensis.* It could be argued that *rondoensis* is not very different from *tanganicanus,* but it is obvious that *tanganicanus* is more closely related to *schmidti* which is geographically more distant. The location of the eye which is fairly constant in the species of the group is different in *rondoensis,* as well as the more rounded shape of the prefrontal and the supraocular; this suggests that *rondoensis* comes from a much older phylogenetic dichotomy than the *tanganicanus-schmidti* divergence.

The differences between these four forms are tabulated on page 410 (data from the MCZ collection, plus Peters' data from "Reise nach Mossambique").

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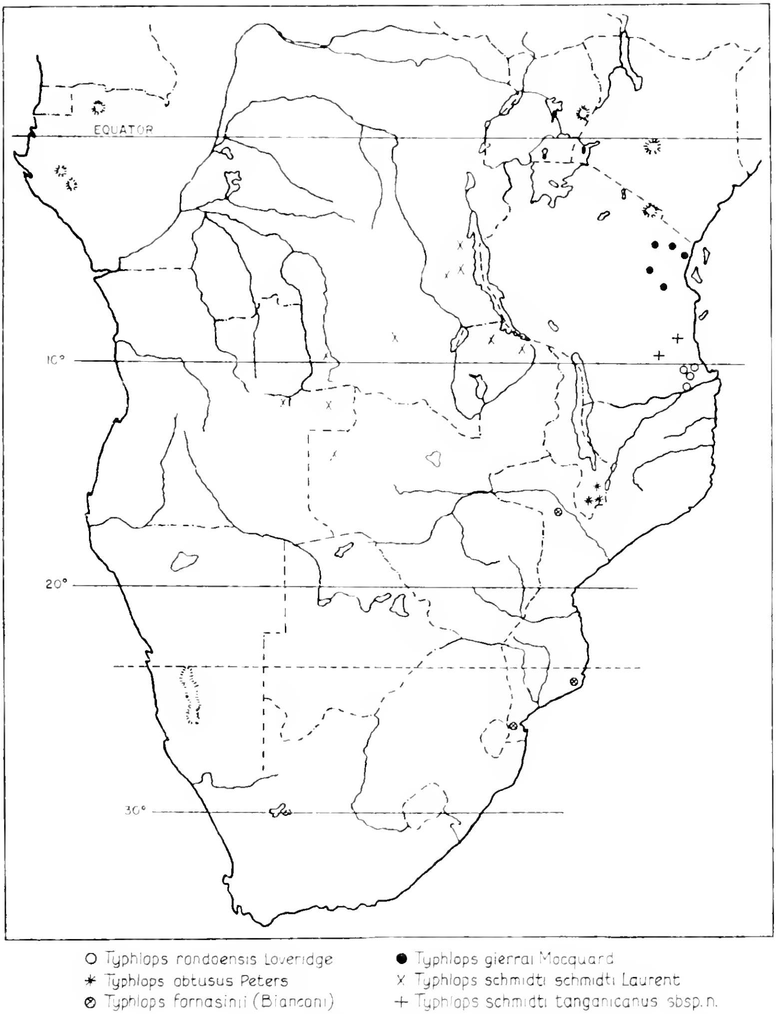
[1] It is very likely that the Museum of Central Africa has many specimens of this species too.



Map 3. Distribution of species of the *Typhlops punctatus* group in southeastern Africa.

	tanganicanus (=*tettensis* Loveridge not Peters)	*rondoensis*	*obtusus*	*fornasinii* (=*tettensis* Peters)
Range	lowlands of south-eastern Tanganyika	Rondo Plateau	Nyasa highlands	Mozambique lowlands
Midbody scale rows	22-24 (rarely 21)	24 (rarely 22)	24 (rarely 25)	22-24-26
Midbody reduction of scale rows	0-2 (rarely 3)	0-2	2-4	-2-0-2
Longitudinal counts	352-425 (10)	314-353 (10)	417-484 (5)	252-272 (9)
Prefrontal	subtrapezoidal	subtrapezoidal but more rounded	subhexagonal	small, rounded
Supraocular	oblique, apex in contact with nasal		transverse, apex in contact with ocular	
Eye	below ocular	below preocular	invisible	below preocular
Contact between preocular and labial	straight, with 2nd and 3rd labials, rarely with 2nd only	straight, with 2nd labial only	angular, with 2nd and 3rd labials (2nd only, 3rd only or 3rd & 4th in some sp. fide Loveridge)	straight, with 2nd labial only
Belly	slightly pigmented	non pigmented	non pigmented	pigmented (unicolor)
Ratio length/diameter	29-47 (m=37.82)	28.8-39 (m=39.83)	51.1-61.1 (m=54.56)	23-36.9 (m=30.77)
Ratio length/breadth of head	46-64 (m=53.73)	41.2-57 (m=50.13)	70-85.5 (m=77.18)	33-48.3 (m=40.12)

SYSTEMATIC ACCOUNT

Typhlops punctatus punctatus (Leach)

1819 *Acontias punctatus* Leach *in* Bowdich, Mission . . . Ashantee, app., p. 493, "Fantee," i.e. Fanti, Ashanti, Ghana.

1844 *Typhlops eschrichti* Schlegel, Abbild. Amph., p. 37, pl. XXXII, figs. 13–16, Ghana.

1893 *Typhlops punctatus:* Boulenger (part)[1], Cat. Snakes Brit. Mus., vol. 1, p. 42, Aa (Fantee, Gambia, Monbuttu, Lado) Ab (Monbuttu).

1923 *Typhlops congestus:* Schmidt (part, non Duméril and Bibron), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 48, Niangara, Poko.

Description. Dark brown above, each scale with a small yellowish spot; each ventral scale yellowish in the center and brown on the borders, or with scattered irregular yellow blotches above and below. Scale rows: 28-30-22 to 34-33-26. Number of scales between the prefrontal and the tip of the tail: 376-403 (3 ♂♂), 399-428 (8 ♀♀). Prefrontal subtrapezoidal, broad. Supraocular oblique, its side apex generally between the nasal and the preocular. Eye large, behind the posterior border of the ocular. Nasal suture arising from the 1st labial. Preocular wedge-shaped below, between the 2nd and 3rd upper labials. Diameter of body 35 to 42 times, and breadth of head 43 to 54 times, in the total length. Size large, up to 650 mm and probably more.

Distribution. From Uganda west to Senegal, through Sudan and northern Congo. The greatest part of the records of *T. punctatus* from the savanna region are probably really referable to this form.

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[1] Some words of explanation seem necessary concerning the usage of the word "part" and its varying position in these citations.

a) When the name of the species is followed directly by the name of an author not the original describer of the species and the author's name is then followed by "part" between parentheses, it means that part of the material referred to in the citation was correctly identified by the author, but that another part was not, and that this citation is for that part of the material which was correctly identified.

Example: *Typhlops congestus*: Schmidt (part) listed in the synonymy of *Typhlops congestus* (Duméril and Bibron).

b) When the name of the species is followed by the name of an author not the original describer and then is followed by "part, *non* name of the original author of the species" between parentheses, it means that part of the material referred to was wrongly identified by the author, but also that another part of this material was not, and that this citation is for that part of the material which was wrongly identified.

Example: *Typhlops congestus*: Schmidt (part, non Duméril and Bibron) listed in the synonymy of *Typhlops punctatus* (Leach).

c) When the name of the species is immediately followed by "*non* name of the original author" between parentheses, then by the name of an author not the original describer, and finally by "part," between parentheses, it means that the whole material was wrongly identified and that the material is also composite; in other words, the several forms were confused and none actually belonged to the species to which they were referred.

Example: 1919 *Typhlops punctatus* (non Leach): Boulenger (part) listed in the synonymy of *Typhlops congestus* (Duméril and Bibron).

Specimens examined. **Ghana.** USNM 56290. **Cameroon.** Sakbayene: MCZ 22828. Boli: MCZ 44101. **Northern Congo.** Niangara: AMNH 11669-70. Poko: AMNH 11671-72. Ekibondo: MCZ 44279. **Tchad.** Fort Archambault: USNM 137761. Fort Crampel: MCZ 55415. **Nigeria.** Marama: USNM 125681. Wushishi: CNHM 42563. **Southern Sudan.** Lipangu: CNHM 58314. **Uganda.** Kaliro, Busoga: AMNH 63768.

TYPHLOPS PUNCTATUS LIBERIENSIS (Hallowell)

1848 *Onychocephalus liberiensis* Hallowell, Proc. Acad. Nat. Sci. Phila., 1848, p. 59, Liberia.

1848 *Onychocephalus nigro-lineatus* Hallowell, Proc. Acad. Nat. Sci. Phila., 1848, p. 60, Liberia.

1864 *Typhlops liberiensis* var. *intermedia* Jan, Icon. Gen. Ophid., p. 24, and vol. 1, livr. 5, pl. V, fig. 2, pl. VI, fig. 2, Liberia.

1864 *Typhlops kraussi* Jan, Icon. Gen. Ophid., p. 26 and vol. 1, livr. 3, pl. VI, fig. 2, Ghana.

1864 *Typhlops lineolatus* Jan, Icon. Gen. Ophid., p. 24 and vol. 1, livr. 9, pl. I, fig. 4, Sierra Leone.

1864 *Typhlops hallowellii* Jan, Icon. Gen. Ophid., p. 29 and vol. 1, livr. 4, pl. IV, fig. 6, pl. V, fig. 6, Ghana.

1893 *Typhlops punctatus:* Boulenger (part, not of Leach), Cat. Snakes, Brit. Mus., vol. 1, p. 42, Ac (West Africa), Bd (Gambia, Oil River), Bs (Accra, Ghana), Be (Ashanti, Sierra Leone).

1920 *Typhlops milleti* Chabanaud, Bull. Mus. Hist. Nat. Paris, vol. 26, p. 463, Togo.

1940 *Typhlops punctatus punctatus* (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Ganta, Liberia.

1958 *Typhlops leprosus* Taylor and Weyer, Univ. Kansas Sci. Bull., vol. 38, p. 1204, Harbel, Liberia.

Description. Dark brown above, each scale with a small yellowish spot, generally uniform yellowish below, sometimes with scattered black points or with brown bordered scales on the sides of the belly, very rarely with all the scales brown bordered as in the typical form. The yellow spots of the dorsal scales can coalesce into longitudinal lines separated by black streaks. A spotted pattern is frequent, but only on the back: black with yellow blotches, or yellow with black blotches. Scale rows: 26-24-20 to 31-30-24. Number of scales between the prefrontal and the tip of the tail: 339-385 (11 ♂♂), 371-435 (14 ♀♀). Prefrontal generally somewhat shorter than in *punctatus*. Supraocular generally as in *punctatus* in western populations, but its apex is more often than not between the ocular and the preocular in the eastern populations (Ghana). Eye as in *punctatus*. Nasal suture arising from the 1st labial, sometimes from the rostral. Preocular generally wedge shaped below, in contact with the 2nd and 3rd labials, very rarely with the 1st and 2nd labials or the 2nd only. Diameter of body 22 to 40 times, width of head 33 to 60 times, in the total length. Size very large, up to 800 mm.

Distribution. Rain forest region and "galleries" from Ghana west to Gambia.

Specimens examined. **Liberia.** Bakratown: MCZ 22490-91. Gbanga: MCZ 22492-96, 51465-66. Ganta: MCZ 43182-87. Harbel, Firestone Plantation: CNHM 58039-41. Mt. Coffee: USNM 24138, 24173. **Ghana.** CNHM 53636. Achimota School: MCZ 53653. Akropong: MCZ 53651. Iafo forest: MCZ 49075-76. Krobo: MCZ 55315-19. Legon Hill: MCZ 53652.

TYPHLOPS CONGESTUS (Duméril and Bibron)

1844 *Onychocephalus congestus* Duméril and Bibron, Herpét, Génér., vol. 6, p. 334, no locality.

1845 *Onychophis barrowii* Gray, Cat. Liz. Brit. Mus., p. 133, no locality.

1893 *Typhlops punctatus:* Boulenger (part, not of Leach), Cat. Snakes Brit. Mus., vol. 1, p. 42, Bb (Cameroon), Bc (Old Calabar), Bd (Old Calabar), Be (Fernando Po).

1919 *Typhlops punctatus* (non Leach): Boulenger (part), Rev. Zool. Afr., vol. 7, p. 18, Moera, northeastern Congo.

1923 *Typhlops congestus:* Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 48, Akenge, Medje, Niapu, northwestern Congo.

1930 *Typhlops punctatus* (non Leach): Barbour and Loveridge, *in* Strong's "African Republic of Liberia and the Belgian Congo," vol. 2, p. 786, Irumu, northeastern Congo.

1933 *Typhlops punctatus* (non Leach): Witte (part). Ann. Mus. Congo, Zool. (1) vol. 3, p. 82, Djamba, northern Congo.

1935 *Typhlops congestus:* Pitman, Uganda Jour., vol. 3, p. 142, pl. I, fig. 4, Budongo Forest, Bugoma Forest, Uganda.

1940 *Typhlops punctatus punctatus* (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Metet, Cameroon; Fataki, northeastern Congo.

1956 *Typhlops congestus:* Laurent, Ann. Mus. Congo, in octavo, Zool., vol. 48, p. 53, figs. 1-2, 11, pl. VII, fig. 1, Meshe, Walikale Road, Djamba, Lubongola, "Bukavu" (in error), eastern and northeastern Congo, p. 348, Hombo, eastern Congo.

1960 *Typhlops congestus:* Laurent, Ann. Mus. Congo, in octavo, Zool., vol. 84, p. 9, Irangi and between Irangi and Hombo, eastern Congo.

Description. Color pattern as in *liberiensis*, but only spotted phase in eastern populations. Scale rows: 28-26-19 to 30-28-22. Number of scales between the prefrontal and the tip of the tail:

322-378 (18 ♂♂), 341-410 (15 ♀♀) (numbers increasing from west to east). Prefrontal subhexagonal but very broad and flat. Supraocular transverse, its apex generally between the preocular and the ocular. Eye behind the anterior border of the ocular, rarely below it. Nasal suture arising from the 1st labial (west), or from the rostral (east). Preocular as in *liberiensis*, in contact with the 2nd and 3rd labials, sometimes in straight contact with them. Diameter of body 17 to 30 times, width of head 27 to 47 times, in the total length. Size large, up to 700 mm.

Distribution. African rain forest from Old Calabar to Lower Congo, east to Kivu and Uganda.

Specimens examined. **Cameroon.** CNHM 58943. Kribi: MCZ 7843, 7860. Kribi River: CNHM 4035. Lolodorf: MCZ 9238-41. Metet: MCZ 13215, 13239. Sakbayeme: MCZ 14983-84, 22826-28. **Northeastern Congo.** Irumu, Ituri: MCZ 26652. Fataki, between Irumu and Beni, Ituri: AMNH 51938. Medje, Uele: AMNH 11646-47. Akenge, Uele: AMNH 11648-63. Niapu, Uele: AMNH 11664-65. **Eastern Congo.** Hombo, Walikale Region, Kivu: MCZ 57458. **Lower Congo.** Leopoldville: USNM 20798. **Western Congo.** Okouma: USNM 62227.

TYPHLOPS BOULENGERI BOULENGERI Bocage

1893 *Typhlops boulengeri* Bocage, Jorn. Sci. Lisboa, (2) vol. 3, p. 117, Quindumbo, Angola.

1893 *Typhlops punctatus:* Boulenger (part, non Leach), Cat. Snakes Brit. Mus., vol. 1, p. 42, Ba (Angola, Mombuttu).

1910 *Typhlops tornieri* Sternfeld, Mitt. Zool. Mus. Berlin, vol. 5, p. 69, Kilimandjaro Mt., Tanganyika.

1923 *Typhlops punctatus:* Schmidt (non Leach), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 45, pl. I, fig. 1, Faradje, Garamba, Poko, northeastern Congo.

1933 *Typhlops punctatus:* Witte (part, not of Leach), Ann. Mus. Congo Zool., (1) vol. 3, p. 82, records mixed with *T. angolensis adolfi.*

1933 *Typhlops boulengeri:* Witte, Ann. Mus. Congo Zool., (1) vol. 3, p. 82, Lukafu, Katanga.

1933 *Typhlops punctatus punctatus:* Loveridge (non Leach), Bull. Mus. Comp. Zool., vol. 74, p. 213, Ujiji, Mwanza, Ukerewe Id. (Tanganyika), Jinja, Mabira Forest (Uganda).

1935 *Typhlops punctatus punctatus:* Pitman, Uganda Journ., vol. 3, p. 141, pl. I, fig. 3, diverse localities from Uganda.

1940 *Typhlops punctatus punctatus* (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Harar, Ethiopia.

1942 *Typhlops punctatus punctatus:* Loveridge (non Leach), Bull. Mus. Comp. Zool., vol. 91, p. 255, Mabira Forest (Uganda), Magrott Mtns. (Tanganyika).

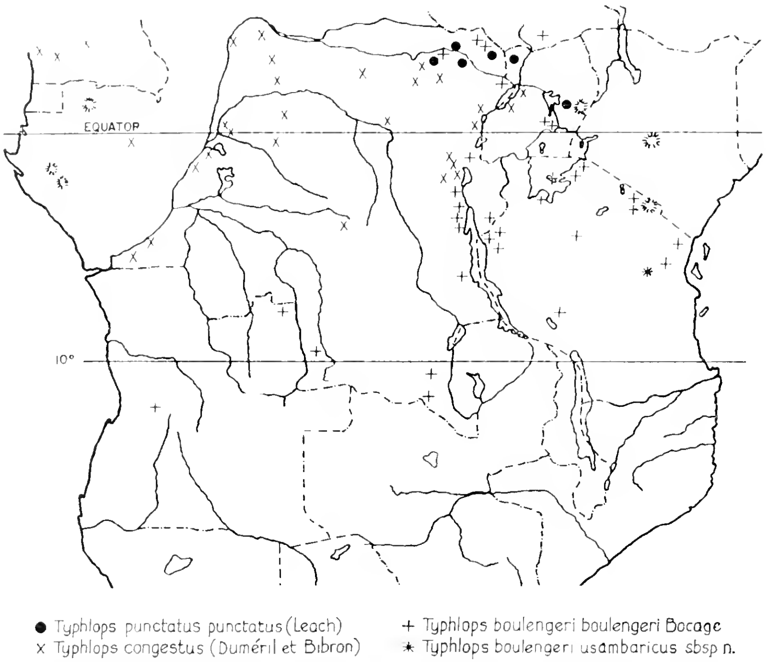
1956 *Typhlops boulengeri:* Laurent, Ann. Mus. Congo., Zool., in octavo, vol. 48, p. 68, figs. 6-7, 11, pl. VIII, fig. 3, Magera, Kiharo (Urundi), Uvira, Rugari, Albertville (eastern Congo).

1960 *Typhlops boulengeri:* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 18, Mahagi (northeastern Congo), Luberizi, Kagando, Runingo, Uvira, Kitutu, Makobola (eastern Congo).

Description. Brown above (generally less dark than in *punctatus*), each scale with a small yellowish spot, each ventral scale yellowish in the center and brown on the borders, with a general shading off from back to belly, some midventral scales sometimes entirely yellowish, forming light scattered spots or an irregular light area. Very rarely, a marbled pattern above and below (one single specimen from Ujiji). Scale rows: 26-24-21 to 32-30-26. Number of scales between the prefrontal and the tip of the tail: 343-401 (343-393 ♂♂, 351-401 ♀♀). Prefrontal broad, subtrapezoidal. Supraocular oblique, its apex generally between the nasal and the preocular. Eye behind the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular in straight contact with the upper labials, often with the 2nd labial only (Congolese populations), less often with the 2nd and 3rd labials (eastern populations), sometimes with the 1st and 2nd labials, rarely with 1st, 2nd and 3rd labials. Diameter of body 24 to 39 times, width of head 29 to 59 times, in the total length. Size moderate, up to 500 mm in Congo and Sudan, to 560 mm in East Africa.

Distribution. Savannas of tropical Africa, from Angola east to Tanganyika, north to Sudan, west to Senegal.

Specimens examined. **Cameroon.** 3 km E of Kribi: MCZ 44238. **Northeastern Congo.** Faradje, Ituri: AMNH 11609-11, 11618. Garamba, Ituri: AMNH 11612, 11614-17. Poko, Uele: AMNH 11621-22. **Eastern Congo.** Luberizi, Kivu: MCZ 57457. **Sudan.** Kagelu: MCZ 45261. Katire: MCZ 53321-22. **Ethiopia.** Harar: AMNH 20339. **Uganda.** Jinja: MCZ 30042. Mabira Forest: MCZ 30040-41, 48059-60. **Tanganyika.** Ujiji: MCZ 30037. Mwanza: MCZ 30038. Ukerewe Id.: MCZ 30039. Kibonoto, Kilimanjaro: MCZ 38684. Magrotto Mtns.: MCZ 48061-65. Senheke: MCZ 49507-08. Lake Rukwa: MCZ 54586. Kasulo: MCZ 54651 Ikiju-Musoma: MCZ 54808. Majita-Musoma: MCZ 54809. Kigoma: MCZ 54810. Handeni-Yamota: MCZ 54811.



Map 4. Distribution of species of the *Typhlops punctatus* group in central Africa.

TYPHLOPS BOULENGERI USAMBARICUS subsp.n.

1928 "*Typhlops* intermediate between *punctatus* and *gierrai*," Barbour and Loveridge, Mem. Mus. Comp. Zool., vol. 50, p. 106, Amani, Usambara Mountains, Tanganyika.

Holotype. MCZ 38699, Amani, Usambara Mtns. (leg. R. E. Moreau 1935).

Paratype. MCZ 23093, same origin (leg. A. Loveridge 1926).

Diagnosis. Mountain subspecies of *T. boulengeri*, differing from it by its color pattern, which is marbled with yellow belly as in *T. congestus*.

Numerical characters

	Scale rows	Labial in contact with preocular	Long. count of scales	Ratio length/ diameter	Ratio length/ width of head
Holotype	28-26-22	2-3	344	27.5	42.2
Paratype	29-28-22	2-3	390	31.1	38.4

Size. Holotype: 380 mm; Paratype: 288 mm.

Distribution. Known only from Amani, Usambara Mountains.

Remarks. The following records may be partly referable to *usambaricus*, partly to *gierrai* Mocquard.

1892 *Typhlops eschrichti* (non Schlegel): Matschie, Sitzb. Ges. Naturf. Freunde, Berlin, p. 110, Derema, Usambara Mountains.

1896 *Typhlops punctatus* (non Leach): Tornier (part), Die Kriechthiere Deutsch Ost-Afrikas, p. 66, Bulba, Usambara Mts., Tanga.

1913 *Typhlops punctatus:* Werner, Denkschr. Akad. Wiss. Wien, vol. 88, p. 717, Amani.

TYPHLOPS GIERRAI Mocquard

1897 *Typhlops gierrai* Mocquard, Bull. Mus. Hist. Nat. Paris, vol. 3, p. 122, Tanga, Tanganyika.

1928 *Typhlops punctatus gierrai:* Barbour and Loveridge, Mem. Mus. Comp. Zool., vol. 50, p. 106, Amani, Bagilo, Mt. Lutindi, Mlalo, Tanganyika.

Description. Dorsal scales yellowish in the center, bordered with black, ventral scales yellowish without any pigmentation. In some specimens, black dorsal blotches in which the scales are entirely black. Scale rows: 26-26-23 to 30-30-26. Number of scales between the prefrontal and the tip of the tail: 398-430 (5 ♂ ♂), 439-464 (2 ♀ ♀). Prefrontal broad and subtrapezoidal. Supraocular generally oblique, its apex between the nasal and the preocular (rarely between the preocular and the ocular). Eye below the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular separated from the labials by a small scale wedged between the 2nd and 3rd labials. Diameter of body 31 to 44 times, width of head 42 to 59 times, in the total length. Size small, up to 380 mm.

Distribution. Mountain forests in Usambara and Uluguru Mountains, Tanganyika.

Specimens examined. **Tanganyika.** Amani: MCZ 23086-90. Mlalo: MCZ 23473. Mt. Lutindi: MCZ 23091. Bagilo: MCZ 23084.

TYPHLOPS SCHMIDTI SCHMIDTI Laurent

1953 *Typhlops boulengeri:* Witte (part, non Bocage), Explor. Parc. Nat. Upemba, vol. 6, p. 138, Kamina, Katanga.

1953 *Typhlops punctatus punctatus* (non Leach): Witte (part), Explor. Parc. Nat. Upemba, vol. 6, p. 139, Lukuga, Katanga.

1956 *Typhlops schmidti* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 71, figs. 9–11, pl. VIII, fig. 4, Nyunzu, Kabila, Lukuga, Sandoa, Kamina, Katanga.

Description. Dorsal scales yellowish in the center, brown on the borders; ventral scales without pigment, except sometimes the lateroventral ones. Spotted pattern in certain individuals. Scale rows: 24-22-20 to 28-26-22. Number of scales between the prefrontal and the tip of the tail: 317-325 (2♂♂), 344-370 (2♀♀). Prefrontal broad and subtrapezoidal. Supraocular oblique, its apex between the nasal and the preocular. Eye behind the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular in straight contact with the 2nd and 3rd labials, rarely with the 2nd only. Diameter of body 23 to 43 times, width of head 40 to 53 times, in the total length. Size small, up to 380 mm.

Distribution. Katanga, northeastern Angola, North Rhodesia.

Specimens examined. **Katanga.** Sandoa: MCZ 57462. **North Rhodesia.** Abercorn: MCZ 55479-80. Edge of Liuwa Plain: CNHM 133036.

TYPHLOPS SCHMIDTI TANGANICANUS subsp.n.

1951 *Typhlops tettensis ?obtusus:* Loveridge (non Peters), Bull. Mus. Comp. Zool., vol. 106, p. 186, Liwale, Tanganyika.

1955 *Typhlops tettensis tettensis:* Loveridge (non Peters), Jour. E. Afr. Nat. Hist. Soc., vol. 22, p. 181, Liwale, Tanganyika.

1956 *Typhlops tettensis tettensis:* Loveridge (non Peters), Tanganyika Notes and Records, 1956, no. 43, p. 10, Kilwa, Tanganyika.

1959 *Typhlops tettensis tettensis* (non Peters): Loveridge (part), Proc. Zool. Soc. London, vol. 133, p. 37, Liwale, Tanganyika.

Holotype. 1 ♀ (MCZ 57439), Liwale, Tanganyika, 11-III-26-IV 1958 (leg. Ionides).

Paratypes. 1 ♂ (MCZ 50066) same locality, 24-I-1948 (Ionides); 1 ♀ (MCZ 55471), same locality, without date (Ionides); 2♂♂, 1♀ (MCZ 55623-25), same locality, 17-II-1951-I-1952 (Ionides); 1♀, 1 specimen the sex of which could not be determined (MCZ 57437-38), same locality (Ionides); 1♂ (MCZ 54509), Kilwa, Tanganyika, IV-1954 (Ionides); 1♀ (CNHM 81011), Liwale, Tanganyika (Ionides).

Diagnosis. Differing from *schmidti* by a higher longitudinal scale count (352-376 instead of 317-325 in males, 400-425 instead of 344-370 in females) and by the fact that the ventral scales are more or less pigmented.

Variation. Scale rows: 24-21-19 to 24-24-20. Preocular in straight contact with the 2nd and 3rd labials, rarely with the

2nd only.[1] Diameter of body 29 to 47 times, width of head 46 to 64 times, in the total length. Size small, up to 390 mm.

Distribution. Southeastern Tanganyika.

TYPHLOPS RONDOENSIS Loveridge

1942 *Typhlops tettensis rondoensis* Loveridge, Bull. Mus. Comp. Zool., vol. 91, p. 256, Nchingidi, Rondo Plateau, southeastern Tanganyika.

1956 *Typhlops tettensis rondoensis* Loveridge, Tanganyika Notes and Records, 1956, No. 43, p. 10, Msimjiri, Rondo Plateau, southeastern Tanganyika.

1959 *Typhlops tettensis rondoensis* Loveridge, Proc. Zool. Soc. London, vol. 133, p. 38, Mtene, Rondo Plateau, southeastern Tanganyika.

1959 *Typhlops tettensis tettensis* (non Peters): Loveridge (part), Proc. Zool. Soc. London, vol. 133, p. 37, Mihuru near Newala, southeastern Tanganyika.

Description. Brown above, with a yellow spot on each scale (generally on the anterior part of the scale, instead of the posterior part as in *tanganicanus*), below uniform yellowish. One specimen with spotted pattern. Scale rows: 24-22-20 to 26-24-22. Number of scales between the preocular and the tip of the tail: 314-353 (without sexual difference). Prefrontal broad, subtrapezoidal but rounded. Supraocular oblique, but with curved external border, its apex between the nasal and the preocular. Eye *in front* of the posterior border of the preocular. Nasal suture proceeding from the 1st labial. Preocular in straight contact with only the 2nd upper labial (however, it is wedged between the 2nd and 3rd labials in the Msinjiri specimen). Ocular wedged between the 2nd and 3rd labials, the lower part sometimes separated. Diameter of body 30 to 39 times, width of head 41 to 57 times, in the total length. Size small, up to 370 mm.

Distribution. Rondo Plateau and Newala region in southeastern Tanganyika.

Specimens examined. **Tanganyika.** Nchingidi, Rondo Plateau: MCZ 48066 (type), 48067-68 (paratypes). Msinjiri: MCZ 54510. Newala: MCZ 57184-86. Mtene: MCZ 57187-88.

Remarks. The Newala specimens previously referred to *tettensis* by Loveridge (1959) have really the *rondoensis* correlation of characters: white belly, same location of the eye, same connections of the preocular and ocular with the labials.

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[1] In this specimen, the ocular is wedged between the 2nd and 3rd labials as in *T. rondoensis*.

TYPHLOPS OBTUSUS Peters

1865 *Typhlops (Onychocephalus) obtusus* Peters, Monatsb. Akad. Wiss. Berlin, p. 260, pl., fig. 2, Shire River, Nyasaland.
1893 *Typhlops obtusus:* Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 38, Shire valley and Nyasaland.
1953 *Typhlops tettensis obtusus:* Loveridge, Bull. Mus. Comp. Zool., vol. 110, p. 243, Cholo Mtn., Mlanje Mtn., Nyasaland.

Description. Dorsal scales brown or blackish, whitish at the base, darker on the sides; lower parts whitish. Scale rows: 24-22-20 to 28-25-22. Number of scales between the prefrontal and the tip of the tail: 417-484 (apparently without sexual difference). Prefrontal rather narrow, subhexagonal. Supraocular transverse, its lateral apex wedged between the preocular and the ocular. Eyes not distinguishable. Preocular wedged between the 2nd and 3rd labials. Nasal suture proceeding from the 1st labial. Diameter of body 48 to 76 times, width of head 70 to 86 times, in the total length. Size small, up to 350 mm (391 mm on freshly killed material, fide Loveridge).

Distribution. Nyasaland.

Specimens examined. **Nyasaland.** Mlanje Mtns.: MCZ 51027-29. Cholo Mtns.: MCZ 51025-26.

Remarks. *T. decorosus* Buchholz and Peters has been claimed (Loveridge, 1953) to be very nearly related to *obtusus.* I have compared the MCZ specimens of *obtusus* with three individuals of *T. decorosus:* two from Sakbayene, Cameroon (MCZ 14994, 22829) and one from Metet, Cameroon (MCZ 13227). Both species are very slender, but they differ widely in other characters; the preocular is in straight contact with the labials in *decorosus* and, what is far more important, the head scale pattern is entirely distinct from what we can see in all the species of the *punctatus* group. In *decorosus*, the supraocular is in very short contact with the ocular and with the nasal. Hence the following ratios are very characteristic of *decorosus*, when compared with all the species examined here:

a) The length of contact of the supraocular and the nasal in per cent of the length of the prefrontal: ± 20 per cent in *decorosus*, 50 to 160 per cent in the others.

b) The contact of the nasal with the prefrontal is more than 1½ times as long (± 180%) as that with supraocular in *decorosus* while it is at most 1½ times as long and often shorter in the other species.

c) The same contact is more than twice as long (230%) as the contact between the supraocular and the ocular in *decorosus*, while it is shorter in the other species.

It seems to me that *T. decorosus* is related to the colorless species group of which *T. coecus* is the oldest known representative.

TYPHLOPS FORNASINII Bianconi

1847 *Typhlops fornasinii* Bianconi, Spec. Zool. Mosamb., p. 13, pl. III, fig. 1, Mozambique.
1854 *Onychocephalus mossambicus* Peters, Monatsb. Akad. Wiss. Berlin, p. 621, Insulae Mozambique and Anjoan.
1854 *Onychocephalus trilobus* Peters, Monatsb. Akad. Wiss. Berlin, p. 621, Inhambane, Mozambique.
1860 *Onychocephalus tettensis* Peters, Monatsb. Akad. Wiss. Berlin, p. 80, Tete, Mozambique.
1882 *Typhlops tettensis:* Peters, Reise nach Mossambique, vol. 3, p. 92, pl. XV, fig. 1.
1882 *Typhlops mossambicus:* Peters, Reise nach Mossambique, vol. 3, p. 93, pl. XV, fig. 2.
1882 *Typhlops fornasinii:* Peters, Reise nach Mossambique, vol. 3, p. 94, pl. XV, fig. 3.

Description. Dark brown, bluish or greyish, often with anal region and lower surface of head yellowish. Scale rows: 26-24-22. Number of scales between the prefrontal and the tip of the tail: 252-272. Prefrontal small, rounded. Supraocular transverse, its lateral apex between the preocular and the ocular. Eyes behind the posterior border of the preocular. Nasal suture proceeding from the 1st labial. Preocular wedged between the 1st and 2nd upper labials. Diameter of body 23 to 38 times, width of head 47.4 times (one cotype of *mossambicus*), in the total length. Size very small, up to 170 mm.

Distribution. Mozambique.

Specimens examined. **Mozambique.** MCZ 21007 (cotype of *mossambicus* Peters). Inhambane: MCZ 21006 (cotype of *trilobus* Peters). Lorenço-Marques: MCZ 41946-49.

Remarks. This species differs from all the forms involved in the *T. punctatus* complex, by its small size, its almost uniformly dark coloration, its small rounded prefrontal and its low number of scales between the prefrontal and the tip of the tail.

It is fortunate that Peters gave the latter figures, since we can now be sure that his *tettensis* has nothing to do with the form to which Loveridge (1942) erroneously gave this name. The alleged differences between *tettensis*, *mossambicus* and *fornasinii* are trifling in comparison with what they have in common, and they are here considered as individual variations.

TYPHLOPS STEINHAUSI Werner

1909 *Typhlops steinhausi* Werner, Mitt. naturh. Mus. Hamburg, vol. 26, p. 209, Kamerun.

1911 *Typhlops batesi* Boulenger, Ann. Mag. Nat. Hist., (8) vol. 8, p. 370, Bitye, Cameroon.

1923 *Typhlops intermedius* (non Jan): Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 47, Niangara, northeastern Congo.

Description. Gray above, with a yellowish spot, corresponding to each scale; venter uniform yellow. Scale rows: 24-25-23 to 26-26-24. Number of scales between the prefrontal and the tip of the tail: 402-425 (without difference between the sexes). Prefrontal small, subhexagonal. Supraocular transverse, its lateral apex between the preocular and the ocular. Eyes below the preocular or indistinct. Nasal suture proceeding from the 1st labial or from its suture with the rostral. Preocular in straight contact with three labials (1st, 2nd and 3rd). Diameter of the body 40 to 51 times, width of head 50 to 62 times, in the total length. Size rather small, up to 410 mm.

Distribution. Northern part of the rain forest from Cameroons to Ituri.

Specimens examined. **Cameroon.** Bitye: MCZ 11294, AMNH 7682-83. Kribi River: CNHM 4034. Lolodorf: MCZ 9242. **Congo.** Niangara, Ituri: AMNH 11630-31.

TYPHLOPS ANGOLENSIS Bocage

This species has been often mistaken for others: *punctatus* and *intermedius* (cf. Schmidt 1923) in the western and southern parts of its range and for *blanfordi* (which is indeed one of its geographical races) in the northeastern part of its range. Its geographical variation is considerable and has added to the past confusion of the group.

It can be easily distinguished from *T. punctatus*, *T. boulengeri*, *T. schmidti*, *T. gierrai*, and *T. rondoensis* by the shape and relations of the prefrontal and the supraocular; the same species (except *rondoensis*) are also different in the location of the eye, as is *T. congestus* which can further be distinguished from *T. angolensis* by its thickness. *T. obtusus* is, on the contrary, more slender than any population of *angolensis*, and *T. fornasinii* is very different in its size and its small longitudinal count of scales.[1] A spotted

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[1] *T. steinhausi* is closely related to *T. angolensis* and must have been the northwestern subspecies of this Rassenkreis in the relatively recent past. The only character by which *T. steinhausi* can be distinguished from all races of *T. angolensis* is the fact that the preocular is in contact (straight) with *three* upper labials (1, 2, 3) instead of *two*.

pattern such as many species have with a varying frequency is never encountered.

Key to the subspecies of *Typhlops angolensis*

1. Belly entirely or almost entirely light colored: color pattern similar in young and adults. Western populations. 2
   Belly brown colored (scales brown on the borders) except, in some forms, for a midventral light band. Young dark colored except for the buccal and anal regions and sometimes for the midventral zone. Oriental races. 4
2. Preocular wedged between the 2nd and 3rd labials. 3
   Preocular in straight contact with the 2nd and 3rd labials; 30 to 36 midbody scale rows. Diameter of body 29 to 47 times, width of head 51 to 68 times, in the total length. Eastern slopes of Mount Kahusi, Bukavu region, Kivu, eastern Congo. Rugege Forest, Ruanda. . . . . *T. angolensis irsaci* Laurent
3. Midbody scale rows, 26 to 32. Diameter of body 26 to 40 times, width of head 37 to 60 times, in the total length. Rain forest and forest galleries in Angola and eastern Congo. . . *T. angolensis angolensis* Bocage
   Midbody scale rows 32 to 36. Diameter of body, 35 to 48 times, width of head 51 to 67 times, in the total length. Mountain forest of Kivu towards the western slope. . . . . *T. angolensis polylepis* Laurent
4. Preocular generally wedged between the 2nd and 3rd labials. . . . 5
   Preocular generally in straight contact with the 2nd and 3rd labials. 6
5. Preocular generally wedged between the 2nd and 3rd labials. No midventral light zone. Midbody scale rows 26 to 32 (generally 30). Lowland in savanna regions from eastern Congo, southeastern Congo, Ruanda Urundi, Kenya and northern Angola. . . . . *T. angolensis adolfi* Sternfeld
   Preocular always wedged between the 2nd and 3rd labials. Central part of the belly light colored. Midbody scale rows 28 to 32 (generally 30). Southern part of Itombwe Mtns., Kivu. . . . . *T. angolensis symoensi* Laurent
6. Preocular generally in straight contact with the 2nd and 3rd labials. No midventral light zone. Scales between the prefrontal and the end of the tail, 411 to 573. Mountain savannas of the eastern Congo, Uganda and Ruanda-Urundi; Rwindi and Ruzizi Valleys. *T. angolensis dubius* Chabanaud[1]
   Preocular in straight contact with 2nd and 3rd labials. Midventral light zone present or absent. Scales between the prefrontal and the end of the tail, 347 to 392. Eritrea and Ethiopia. . . . . *T. angolensis blanfordi* Boulenger

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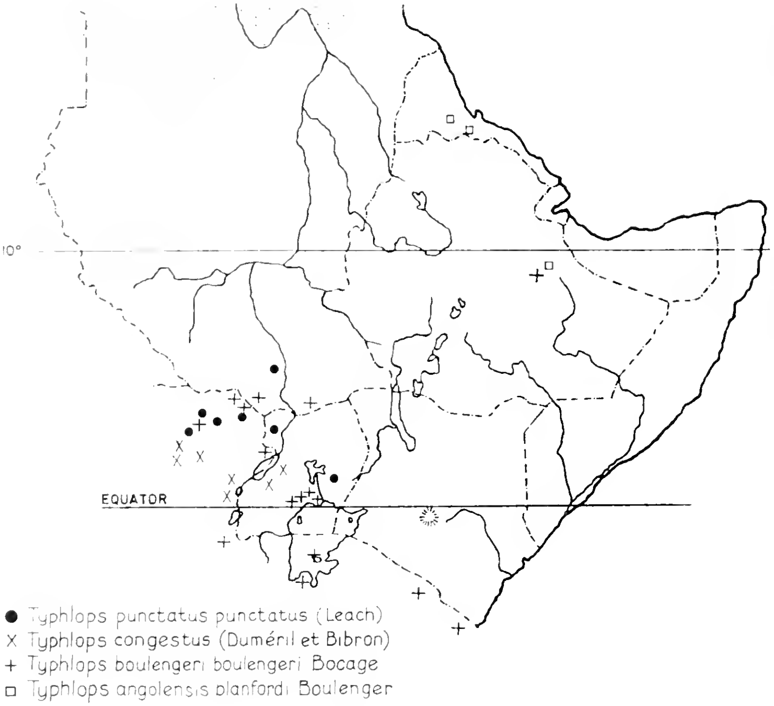
[1] Between *dubius* and *adolfi* the cline in midbody scale rows is smooth enough to make the synonymy of *dubius* an arguable alternative to its recognition. In such a case, however, the striking altitudinal cline must be embodied in the diagnosis of *adolfi; symoensi* could possibly be similarly treated. Likewise, *polylepis* and *irsaci* could be regarded as exemplifying similar orophilous trends and thus could be included with the typical form. However, evidence of a smooth cline is definitely lacking for *irsaci*.



Map 5. Distribution of species of the *Typhlops punctatus* group in northeast Africa.

SUMMARY SYNONYMY OF THE SUBSPECIES OF *T. ANGOLENSIS*

Typhlops angolensis angolensis Bocage[1]

1866 *Onychocephalus angolensis* Bocage, Jorn. Sci. Lisboa, vol. 1, p. 46, p. 65, Duque de Bragança, Angola.

1887 *Typhlops (Onychocephalus) congicus* Boettger, Zool. Anz., vol. 10, p. 650, Povo Netonna, near Banana, Congo.

1923 *Typhlops intermedius* (non Jan): Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 47, west of Fort Beni, Akenge, Medje, Niapu, Stanleyville, Congo.

1923 *Typhlops tornieri* (non Sternfeld): Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 49, p. 50, Stanleyville, Congo.

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[1] Additional specimens: Lukolela, western Congo (AMNH 45912); Omboue, Gaboon (USNM 62146); Canzele, Angola (CNHM 74243).

1940 *Typhlops punctatus punctatus* (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Lukolela, western Congo.

1956 *Typhlops angolensis angolensis:* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 55, Kikungwa, Kamituga, Manguretshipa, Angumu, Kamande, eastern Congo (which see for a more complete synonymy).

TYPHLOPS ANGOLENSIS ADOLFI Sternfeld[1]

1910 *Typhlops adolfi* Sternfeld, Mitt. Zool. Mus. Berlin, vol. 5, p. 70, Fort Beni, Kivu, eastern Congo.

1935 *Typhlops kaimosae* Loveridge, Bull. Mus. Comp. Zool., vol. 79, p. 5, Kaimosi, Kenya.

1940 *Typhlops punctatus punctatus* (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Chogoria, Kenya.

1956 *Typhlops angolensis adolfi:* Laurent, Ann. Mus. Congo, in octavo, vol. 48, pp. 63, 349, figs. 5-6, Beni, Uvira, Nyunzu, "Ituri", Djalasinda, Kilo, Nizi, Geti region, Tembwe, Mpala, Kabambare, Blukwa, eastern Congo; Nyakatare, Ngarama, Rwankuba, Nyarutunga, Lake Tshohoha, Kabuyenge swamps, Mugera Rusengo, Kiharo, Makamba, Gabiro, Chinzowe, Kakitumba, Ruanda-Urundi (which see for a more complete synonymy).

1960 *Typhlops angolensis adolfi:* Laurent, Ann. Mus. Congo, in octavo, vol. 84, p. 15, Kakitumba, Ruanda; Uvira, Lubondja, eastern Congo.

TYPHLOPS ANGOLENSIS DUBIUS Chabanaud

1916 *Typhlops dubius* Chabanaud, Bull. Mus. Hist. Nat., vol. 22, p. 364, figs. 1–3, volcans du Kivori (for Kivu volcanoes).

1933 *Typhlops lestradei* Witte, Rev. Zool. Bot. Afr., vol. 23, p. 207, figs. 1–3, Rubengera, Ruanda.

1935 *Typhlops blanfordii* (non Boulenger): Pitman, Uganda Journal, vol. 3, p. 146, Mushongero, Lake Mulanda, Uganda.

1942 *Typhlops blanfordii lestradei:* Loveridge, Bull. Mus. Comp. Zool., vol. 91, p. 254, pl. 2, Mushongero, Nyakabande, Uganda; Kisenyi, Ruanda; Upper Mulenga, Idjwi Id.

1952 *Typhlops ochraceus:* Laurent, Rev. Zool. Bot. Afr., vol. 46, p. 269, Mulenge, Lulenga, eastern Congo.

1956 *Typhlops angolensis dubius:* Laurent, Ann. Mus. Congo Zool., in octavo, vol. 48, p. 60, Mabenga, Tshanzerwa, Rutshuru, Tshumba, Munagana, Lulenga, between Bobandana and Kisenyi, upper Mulinga, eastern Kivu; Astrida, Ngozi, Murehe, Ruanda-Urundi; p. 349, Malambo, Bushovu, Idjwi Island, eastern Congo (which see for other quotations).

1960 *Typhlops angolensis dubius:* Laurent, Ann. Mus. Congo Zool., in octavo, vol. 84, p. 14, south Idjwi Island, Luvungi, Luberizi, Remera, Runingo, eastern Congo; Astrida, Bubanza, Ruanda-Urundi.

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[1] Additional specimens seen: Mt. Kenya (AMNH 2279); Chigoria, Kenya (AMNH 51939).

TYPHLOPS ANGOLENSIS POLYLEPIS Laurent

1956 *Typhlops angolensis polylepis* Laurent, Ann. Mus. Congo Zool., in octavo, vol. 48, p. 56, fig. 6, pl. VII, fig. 3, Kiandjo, Tubutubu, Kalondo, eastern Congo.

1956 *Typhlops congicus lestradei:* Laurent (part, non Witte), Ann. Mus. Congo Zool., in octavo, vol. 48, p. 74, Burunga, eastern Congo.

1960 *Typhlops angolensis angolensis:* Laurent (non Bocage), Ann. Mus. Congo Zool., in octavo, vol. 84, p. 10, Tshabondo, eastern Congo.

1960 *Typhlops angolensis polylepis:* Laurent, Ann. Mus. Congo Zool., in octavo, vol. 84, p. 13, Luemba, eastern Congo.

TYPHLOPS ANGOLENSIS IRSACI Laurent

1956 *Typhlops angolensis irsaci* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 57, p. 349, figs. 3–4, 6, pl. VII, fig. 4, Lwiro, Mt. Kahusi, Hongo, Bukavu, Katana, Ibanda, eastern Congo; Rwasenkoko, Ruanda.

1956 *Typhlops congicus lestradei:* Laurent (part, non Witte), Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 74, Bukavu, p. 350, Lwiro, eastern Congo.

1960 *Typhlops angolensis irsaci:* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 12, Hombo, Lwiro, eastern Congo.

TYPHLOPS ANGOLENSIS SYMOENSI Laurent

1960 *Typhlops angolensis symoensi* Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 10, Ngovi River, Makobola, Fizi, eastern Congo.

TYPHLOPS ANGOLENSIS BLANFORDI Boulenger

1893 *Typhlops blanfordi* Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 39, pl. II, fig. 5, Senafe, Abyssinia.

PHYLOGENETIC RELATIONSHIPS

The *Typhlops punctatus* group can be defined by the following characters: Scale rows: 22 to 36. Ratio length/diameter 17 to 62. Preocular generally in contact with labials (separated by a small scale in *gierrai*), almost always in contact with 2nd labials, generally with the 3rd also, sometimes even with the 1st. Ocular in contact with labials. No subocular. Snout rounded or with an obtuse angle. Nostrils inferior. Rostral broad (more than a third the width of the head). Nasal cleft proceeding from the first labial, sometimes from the rostral, not extending to the upper surface of the head (individual exceptions to this last character in *T. fornasinii*). Tail broader than long.

We cannot be sure that the group here studied is a truly homogeneous assemblage; some species not considered here, such as *T. bibroni*, may belong here. However, some assumptions can be

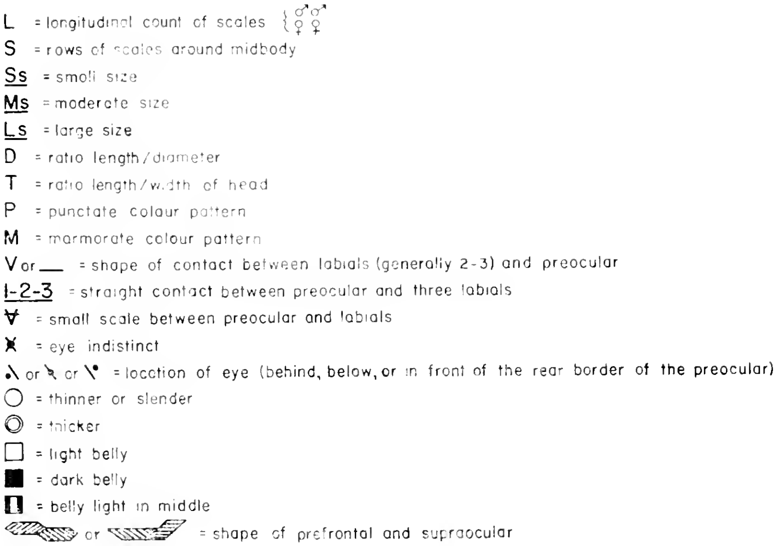

Fig. 5. The symbols listed above apply to Figures 6-9. In addition, certain combinations of symbols are used. Thus MSs means moderate to small size, and M and P combined, one letter larger than the other, indicates that both punctate and marmorate color patterns may exist in the same species, that indicated by the smaller letter being the less frequent. Parentheses around any symbol implies that that condition is exceptional in that species or group.

made. For instance, *T. fornasinii* which is rather different from all other forms, and may even be extraneous to the group, seems to be closely related to *T. boettgeri* from Madagascar; the case is paralleled by other forms, like *Chamaeleon fischeri* and *C. bifidus*. *T. fornasinii* may represent the first dichotomy of the group or an old offshoot of *T. angolensis*. *T. angolensis* must represent a very old speciation also, perhaps having arisen from a first montane differentiation. It seems likely that *T. obtusus* has been a secondary branching from this *angolensis* complex in southeastern Africa, and *T. steinhausi* a more recent one in the northern part of the rain forest.

T. boulengeri appears to result from a more recent splitting (savanna versus forest, or southern savanna versus northern savanna) with two successive montane and local differentiations in the eastern Tanganyika mountains: *T. gierrai*, which has reached specific status, and later *T. b. usambaricus*. Another secondary offshoot of *T. boulengeri* is obviously *T. schmidti* but it is difficult to tell under what conditions the primary geographic differentiation occurred: *T. schmidti* is more southerly in distribution and partly sympatric with *T. boulengeri* but we have no reason whatever for supposing a forest or a montane origin. Much

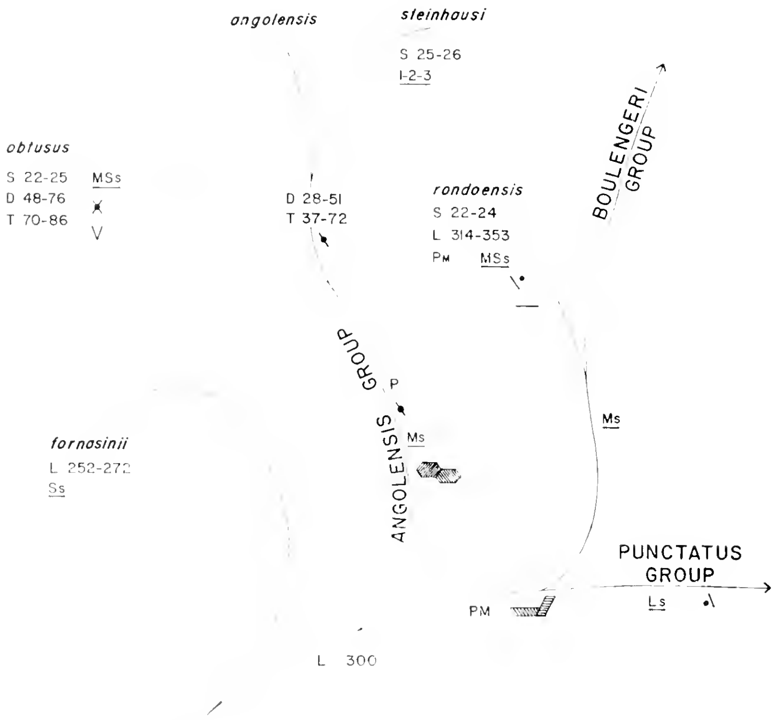

Fig. 6. Dendrogram of the main phylogenetic relationships in the *Typhlops punctatus* group *(sensu lato)*.

more likely is an intrasavanna cline followed by a breakup resulting from the extinction of intermediate populations. The complex comprising *T. punctatus* and *T. congestus* has very likely been a single species with specific isolation between the more distant subspecies, i.e. between *punctatus* and *congestus*, between which *liberiensis* intervenes. Subspecific relationships appear almost certain between *punctatus* and *liberiensis*. Indeed they could exist between *liberiensis* and *congestus* and in this case, *congestus* would have to be considered as a subspecies of *T. punctatus*. But the evidence for species level relationships between *T. congestus* and the *punctatus* savanna populations and of a distributional gap between *congestus* and *liberiensis* suggests a complete specific separation.

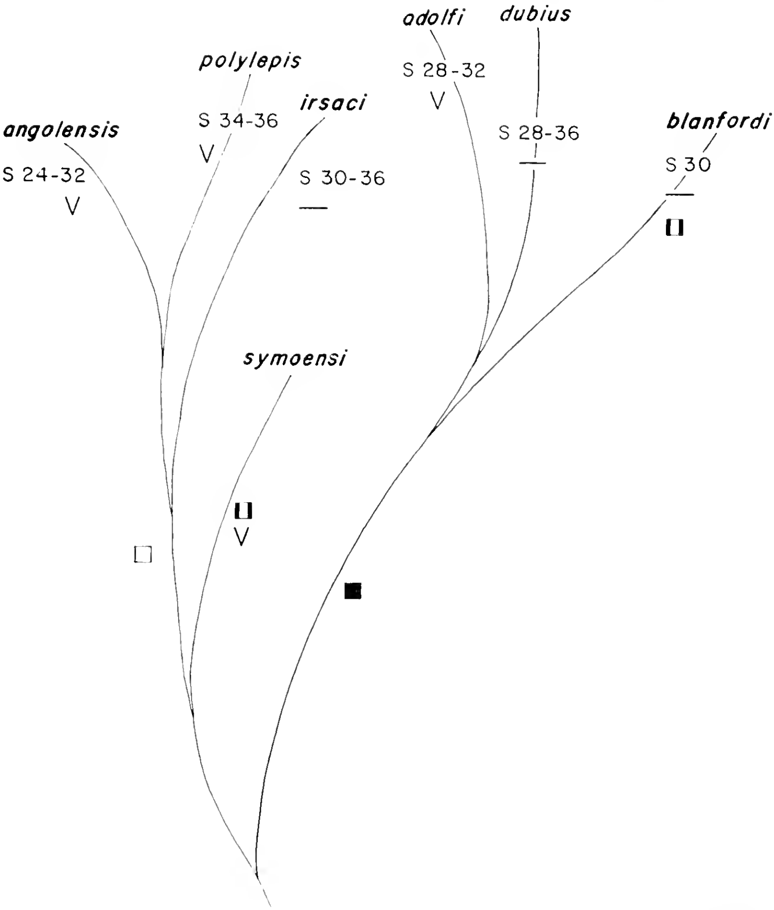

Fig. 7. Dendrogram of the phylogenetic relationships in *Typhlops angolensis*.

However, it is impossible to tell whether the primary factor of speciation has been simple geographic isolation between the two parts of the rain forest, i.e. between *liberiensis* and *congestus*, or geographic plus ecological isolation between savanna *punctatus* and forest *congestus*, or a distance effect between *punctatus* and *congestus* followed by a subsequent extension of range and thus a secondary meeting of these populations along the northern border of the eastern rain forest. Likewise, it is not clear whether this evolution started in a savanna environment (with *punctatus*) or in the forest (with *liberiensis* or *congestus*). Of course, the burrowing habits must have been often initiated as a protection against dryness, and accordingly such adaptations are more frequent in savannas. Hence, there is a slight presumption that *T. punctatus* is more primitive than the three other forms. However, the Typhlopidae, which are now cosmotropical and live in every environment, are so old a group that it is difficult to apply this principle safely to any particular phase of their history.

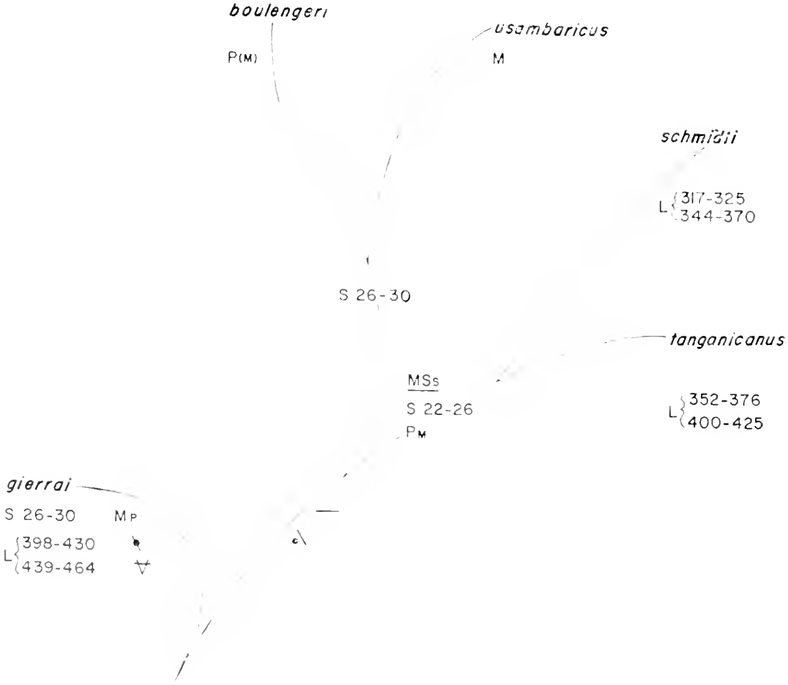

Fig. 8. Dendrogram of the phylogenetic relationships in the *Typhlops boulengeri* group.

The taxonomic characters are hardly useful in this connection because the primitive and secondary conditions cannot be easily distinguished. It may be assumed, however, that the number of scale rows is generally higher in primitive forms, while the longitudinal count is lower; and also that a lengthening of the body is secondary. However, some reversals of these trends are far from excluded, as is indeed obvious in the correlation of higher counts with altitude.

In the present case, eastern *congestus* is probably the most advanced type, since the unusual condition of the nasal suture is apparently secondary and it has only one color phase which, being less frequent than the uniform pattern in *Typhlops*, is probably secondary too. Which is the most primitive among the three forms is a mere guess; moreover it has little meaning, since each of these could have retained one primitive character.

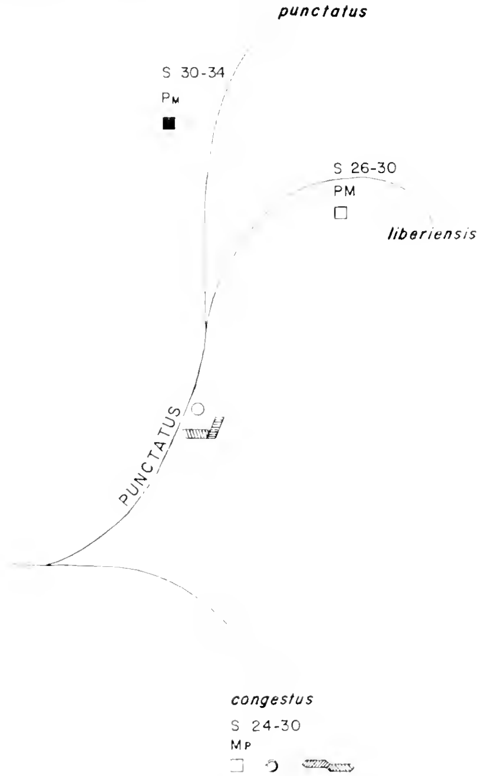

Fig. 9. Dendrogram of the phylogenetic relationships in the *Typhlops punctatus* group *(sensu stricto)*.

ARTIFICIAL KEY TO THE SPECIES OF THE *TYPHLOPS PUNCTATUS* GROUP

1. Less than 280 scales between the prefrontal and tip of the tail. Mozambique. .... *T. fornasinii* Bianconi
   More than 280 scales between the prefrontal and the tip of the tail. 2
2. Less than 26 midbody scale rows.[1] 3
   Midbody scale rows 26 to 36. 9
3. Prefrontal subhexagonal; supraocular generally transverse, its lateral apex between preocular and ocular. 4
   Prefrontal subtrapezoidal; supraocular generally oblique, its lateral apex between nasal and ocular. 7
4. Prefrontal generally broad. Eye under ocular rather than under preocular. Diameter of body 19 to 30, breadth of head 27 to 46, times in body length (see scatter diagrams). Always spotted. Nasal suture generally proceeding from the rostral. Congo. .... Some eastern specimens of *T. congestus* Duméril & Bibron
   Prefrontal generally narrow. Eye under preocular, when visible. Diameter of body 26 to 76 times, breadth of head 37 to 86 times, in body length (see scatter diagrams). No spotted phase. Nasal suture proceeding from the 1st labial. 5
5. Eye visible (except in individuals before sloughing). Diameter of body 26 to 51 times, breadth of head 37 to 72 times, in body length. Between the prefrontal and the tip of the tail, 323 to 425 scales. 6
   Eye always hidden. Diameter of body 48 to 76 times, breadth of head 70 to 86 times, in body length. Scales between the prefrontal and the tip of the tail, 417 to 484. Nyasaland and Mozambique. .... *T. obtusus* Peters
6. Preocular in straight contact with 1st, 2nd and 3rd labials. Diameter of body 40 to 51 times in body length. More than 400 scales between prefrontal and the tip of the tail. Cameroon to northeastern Congo. .... *T. steinhausi* Werner
   Preocular wedged between the 2nd and 3rd labials. Diameter of body 26 to 40 times in body length. Less than 375 scales between the prefrontal and the tip of the tail. Forest in Congo and Angola. .... *T. angolensis angolensis* Bocage
7. Eye below the ocular 8
   Eye below the preocular. Southeastern Tanganyika. .... *T. rondoensis* Loveridge
8. Ventral coloration lighter than dorsal coloration but not sharply delimited. Preocular in contact with 2nd labial, or 2nd and 3rd labials,

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[1] Specimens with 24 midbody scale rows are very rarely encountered in *boulengeri* and in eastern populations of *congestus;* they are infrequent in *T. angolensis angolensis;* in *steinhausi,* two specimens out of seven have 25 midbody scale rows. Generally, all these forms have at least 26 midbody scale rows. In *schmidti,* on the contrary, individuals with 26 midbody scale rows are rare; the normal figures are 22 or 24.

rarely with 3 labials. Scales between the prefrontal and the tip of the tail, 343 to 400 (343–393 ♂♂) (384–400 ♀♀). Generally more than 26 scale rows at midbody. Circum-forest distribution. .... *T. boulengeri boulengeri* Bocage

Ventral coloration lighter than dorsal coloration, but not sharply delimited. Preocular generally in contact with 2d and 3rd labials. Scales between the prefrontal and the tip of the tail, 351 to 376 (♂♂), 400 to 425 (♀♀). Midbody scale rows 22–24. Southeastern Tanganyika (allopatric to *boulengeri*). *T. schmidti tanganicanus* Laurent

Ventral coloration lighter than dorsal coloration and sharply delimited. Preocular generally in contact with 2nd and 3rd labials. Scales between the prefrontal and the tip of the tail: 317–325 (2 ♂♂), 344–370 (2 ♀♀). Midbody scale rows 22–24 (rarely 26). Southeastern Congo, northern Angola and northern Rhodesia. .... *T. schmidti schmidti* Laurent

9. An intercalary scale between the preocular and the 2nd and 3rd labials. Eye below the superficial suture between preocular and ocular. Usambara and Uluguru Mountains. .... *T. gierrai* Mocquard

No such scale between the preocular and the labials. Eye generally below the preocular or the ocular. 10

10. Prefrontal subhexagonal; supraocular generally transverse, its apex between preocular and ocular. 11

Prefrontal subtrapezoidal; supraocular generally oblique, its apex between nasal and preocular (between preocular and ocular however in Ghanean populations of *liberiensis.*) 13

11. Prefrontal generally broad. Eye under ocular rather than under preocular. Diameter of body 17 to 30, breadth of head 27 to 47, times in body length (see scatter diagrams). A spotted phase frequent, even exclusive in eastern populations. Rain forest in Cameroon-Gabon-Congo. .... *T. congestus* Duméril and Bibron

Prefrontal generally narrow. Eye under preocular when visible. Diameter of body 25 to 51 times, breadth of head 37 to 75 times, in body length. No spotted phase. 12

12. Preocular in contact with 2 labials. Nasal in contact with 2nd labial. Angola to Eritrea through Congo and Kenya. .... *T. angolensis* (see key to races on p. 423)

Preocular in contact with 3 labials. Nasal not in contact with 2nd labial. Cameroon to northeastern Congo. ..... *T. steinhausi* Werner

13. Preocular wedged between the 2nd and 3rd labials. Spotted phase frequent. 14

Preocular in straight contact with the labials. Spotted phase infrequent. 15

14. Midbody scale rows 30–34. Belly hardly less dark than the back or spotted like the back. Savanna regions between the Sahara and the rain forest, from Senegal to Sudan. .. *T. punctatus punctatus* (Leach)

Midbody scale rows 26–30. Belly light colored. Western rain forest (Guinea to Ghana). .... *T. punctatus liberiensis* (Hallowell)

15. Scales between prefrontal and tip of tail: 317–325 (♂♂), 344–370 (♀♀). Ventral coloration lighter than dorsal coloration and sharply delimited. Preocular in contact with 2nd and 3rd labials. Rarely 26 midbody scale rows, usually less. A rare spotted phase. Southeastern Congo, northern Angola and Rhodesia. .*T. schmidti schmidti* Laurent
    Scales between prefrontal and tip of tail: 343–393 (♂♂), 384–400 (♀♀). Ventral coloration lighter than dorsal coloration but not sharply delimited. 16

16. Back rarely spotted but, if so, belly spotted also. Preocular in contact with 2nd labial, 1st and 2nd labials, or with 2nd and 3rd labials. Savanna regions around forest from Senegal to Angola through East Africa. .... *T. boulengeri boulengeri* Bocage
    Back spotted and belly light colored. Preocular in contact with 2nd and 3rd labials. Usambara Mountains. .... *T. boulengeri usambaricus* Laurent

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TABLE 1

Number of midbody scale rows in *Typhlops* of the *punctatus* group.
(Modal condition in bold face)

Taxon, and number of specimens in parentheses	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
T.p.punctatus (15)										40		**53**	7			
T.p.liberiensis (27)						24	21	**41**		14						
T.congestus (55)				2		15	7	**65**		11						
T.b.boulengeri (90)				1		15	2	**60**	1	21						
T.b.usambaricus (2)						**50**		**50**								
T.gierrai (9)						**33**	22	**33**		12						
T.s.tanganicanus (10)	10	**40**	10	**40**												
T.s.schmidti (20)		30		**65**		5										
T.rondoensis (10)		10		**90**												
T.fornasinii (6)		16		**50**		17	17									
T.obtusus (5)				**80**	20											
T.steinhausi (7)					29	**71**										
T.a.angolensis (32)				16		**41**	3	25		9		6				
T.a.adolfi (43)								14		**65**		21				
T.a.dubius (64)								1		39		**41**		16		3
T.a.symoensi (8)								12		**63**		25				
T.a.polylepis (5)														10		**60**
T.a.irsaci (44)										41		**52**		5		2
T.a.blanfordi (2)										**100**						

TABLE 2

Difference between the number of scale rows at midbody and behind the head in *Typhlops* of the *punctatus* group.
(Modal condition in bold face)

	Reduction					Increase			
	−4	−3	−2	−1	0	+1	+2	+3	+4
T.p.punctatus (14)			27		27	13	**33**		
T.p.liberiensis (27)	3	4	**41**	15	22	11	4		
T.congestus (55)	27	7	**49**	4	13				
T.b.boulengeri (66)	2	2	18	8	**56**	5	9		
T.b.usambaricus (2)			**50**	**50**					
T.gierrai (9)			22	11	**45**	22			
T.s.tanganicanus (10)		10	**50**		40				
T.s.schmidti (10)	**60**		30		10				
T.rondoensis (10)			40		**60**				
T.fornasinii (6)			17		**50**		33		
T.obtusus (5)	20	20	**60**						
T.steinhausi (7)				14		29	**57**		
T.a.angolensis (32)	3		23	6	**49**	8	11		
T.a.adolfi (40)			5		**63**	3	27		2
T.a.dubius (47)			4	2	**45**	4	34	2	9
T.a.symoensi (5)						20	**80**		
T.a.polylepis (4)					25	25	**50**		
T.a.irsaci (44)			4	7	**67**	20	2		
T.a.blanfordi (2)					**100**				

T. boulengeri is well distinguished by this character from *punctatus*, *liberiensis* and *congestus;* the same is true for *schmidti* compared with *tanganicanus*.

TABLE 3

Difference in the number of scale rows between the preanal region and the midbody region in *Typhlops* of the *punctatus* group. (Modal condition in bold face)

	−9	−8	−7	−6	−5	−4	−3	−2	−1	0
T.p.punctatus (14)		7		**64**		29				
T.p.liberiensis (27)		4	4	15	22	**44**	7	4		
T.congestus (55)	2	4	7	**58**	9	18				
T.b.boulengeri (63)				16	8	**49**	3	22		2
T.b.usambaricus (2)				**50**		**50**				
T.gierrai (9)				11		11	22	**45**	11	
T.s.tanganicanus (10)						20	20	**60**		
T.s.schmidti (10)						40		**60**		
T.rondoensis (10)						30		**60**		10
T.fornasinii (6)						33		**50**		17
T.obtusus (5)							20	**60**		20
T.steinhausi (7)							14	**57**	29	
T.a.angolensis (32)				19	6	**60**	6	9		
T.a.adolfi (40)				17	3	**60**		20		
T.a.dubius (47)		2	2	15		**62**		19		
T.a.symoensi (5)				**80**		20				
T.a.polylepis (4)				25		**50**		25		
T.a.irsaci (44)		2		20	2	**54**	2	20		
T.a.blanfordi (2)				**50**		**50**				

TABLE 4

Number of scales between the prefrontal and the end of the tail.[1]

	Males	Females	Sex Unknown
T.p.punctatus	376–403(3)(m = 392.3)	399–428(8)(m = 415)	363–416(3)
T.p.liberiensis	339–385(11)(m = 362.3)	371–435(14)(m = 392.1)	
T.congestus	322–378(18)(m = 350.3)	341–410(15)(m = 376.1)	331–381(7)
T.b.boulengeri	343–393(11)(m = 368.5)	384–401(11)(m = 391.8)	351–400(15)
T.b.usambaricus	341–390(2)(m = 367)		
T.gierrai	398–430(5)(m = 414.4)	439–464(2)(m = 451.5)	421–435(2)
T.s.tanganicanus	352–376(4)(m = 369.3)	400–425(6)(m = 411.5)	
T.s.schmidti	317–325(2)(m = 321)	344–370(2)(m = 357)	
T.rondoensis	319–353(4)(m = 337.5)	314–350(3)(m = 335.7)	321–345(3)
T.fornasinii		255(1)	252–272(8)(m = 261.9)[2]
T.obtusus	467(1)	465(1)	417–484(3)
T.steinhausi	402–425(3)(m = 415.7)	405–419(4)(m = 412.3)	
T.a.angolensis	281–371(12)(m = 342.1)	287–364(8)(m = 328.4)	347
T.a.dubius	425(1)		411–573(14)(m = 484.7)[3]
T.a.irsaci	425–485(2)(m = 455)	520(1)	
T.a.blanfordi	347–392(2)(m = 369.5)		
T.a.adolfi	381–391(2)(m = 386)		419

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[1] This character has generally been omitted from descriptions and other reports on *Typhlops* because the count is very laborious. However, it is undoubtedly taxonomically useful and even seems to be the only character correlated with sex in most forms. Unfortunately, I can rely here only on the data of material in museums in the United States, but the results are convincing enough.

[2] 252 (type of *tettensis*) -265 (cotype of *mossambicus*) -258 (specimen of *fornasinii* fide Peters 1882 (Reise nach Mossambique).

[3] The variation of *dubius* is particularly striking and suggests an altitudinal cline, as for the number of scale rows.

Table 5

Labials touching the preocular in *Typhlops* of the *punctatus* group, frequency in per cent

	0	1–2	1–2–3	2	2–3	3
T.p.punctatus (14)				4	96	
T.p.liberiensis (27)		2		2	96	
T.congestus (12)					97	3
T.b.boulengeri (57)		29	2	37	32	
T.b.usambaricus (2)					100	
T.gierrai (9)	100					
T.s.schmidti (10)				10	90	
T.s.tangonicanus (10)				10	90	
T.rondoensis (10)				90	10	
T.fornasinii (6)				100		
T.obtusus (5)					100	
T.steinhausi (2)			100			
T.a.angolensis (28)					100	
T.a.adolfi (41)	2				98	
T.a.dubius (47)					100	
T.a.symoensi (5)					100	
T.a.polylepis (4)					100	
T.a.irsaci (46)					100	
T.a.blanfordi (2)	25			25	50	

TABLE 6

Ratio between length of body and its diameter in *Typhlops* of the *punctatus* group.
(Modal condition in bold face)

	16 to 20	20 to 24	24 to 28	28 to 32	32 to 36	36 to 40	40 to 44	41 to 48	48 to 52	52 to 56	56 to 60	60 to 64
T.p.punctatus (14)			**40**	**40**	13		7					
T.p.liberiensis (27)		3	**45**	34	11	7						
T.congestus (54)	15	**41**	37	7								
T.b.boulengeri (76)			31	**36**	24	8	1					
T.b.usambaricus (2)			**50**	**50**								
T.gierrai (9)				11	**34**	22	33					
T.s.schmidti (9)		11	12	**22**	**22**	**22**	11					
T.s.tanganicanus (10)				10	**40**	20	20	10				
T.rondoensis (9)				22	23	**55**						
T.fornasinii (6)			**33**	17	**33**	17						
T.obtusus (5)									**40**	**40**		20
T.steinhausi (7)						**43**	29	14	14			
T.a.angolensis (32)			16	**47**	28	6	3					
T.a.adolfi (47)			2	4	**28**	24	26	12	4			
T.a.dubius (44)				16	23	**36**	20	5				
T.a.symoensi (8)					12	**38**	25	25				
T.a.polylepis (5)				20	20	**40**	20					
T.a.irsaci (44)			2	14	23	**38**	16	5	2			
T.a.blanfordi (2)				**100**								

TABLE 7

Ratio between the length of body and the breadth of the head in *Typhlops* of the *punctatus* group. This character is more reliable than the preceding, since the breadth of the head is not influenced by the physiological condition of the individual. On the other hand, some species have larger heads than others. (Modal condition in bold face)

	20–28	28–36	36–44	44–52	52–60	60–68	68–76	76–84	84–92
T.p.punctatus (12)		8	9	**50**	33				
T.p.liberiensis (27)		3	**50**	27	20				
T.congestus (50)	4	38	**48**	10					
T.boulengeri (63)		9	33	**45**	13				
T.b.usambaricus (2)			**100**						
T.gierrai (9)			22	34	**44**				
T.s.schmidti (9)			23	**44**	33				
T.s.tanganicanus (9)				20	**70**	10			
T.rondoensis (10)		10	20	30	**40**				
T.fornasinii (6)		33	**34**	33					
T.obtusus (5)							**40**	**40**	20
T.steinhausi (7)				14	**72**	14			
T.a.angolensis (28)			22	**48**	26	4			
T.a.adolfi (38)			7	27	**37**	24	5		
T.a.dubius (44)			7	24	**41**	26	2		
T.a.symoensi (8)			13	**50**	37				
T.a.polylepis (4)			25	25	25	25			
T.a.irsaci (44)			7	**43**	27	23			
T.a.blanfordi (2)				**100**					

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THE SPIDER GENUS *THYMOITES* IN AMERICA (ARANEAE: THERIDIIDAE)

BY HERBERT W. LEVI

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No. 7 — *The Spider Genus Thymoites in America* (*Araneae: Theridiidae*)

The small spiders belonging to the genus *Thymoites* have been poorly collected. Of the very few specimens available from South America, most represent new species, but several species that had been misplaced are here redescribed or illustrated for the first time.

The species now placed in *Thymoites* have migrated from genus to genus. First I placed them (1957) in *Paidisca* Bishop and Crosby. Archer established *Tholoceo* for some members of the genus; Bryant established *Thymoella*. In 1959 I thought that *Sphyrotinus* Simon was the correct and oldest name for the group, but also synonymized *Hypobares* Simon, *Philto* Simon, and *Thonastica* Simon, *Hubba* O. P.-Cambridge, *Garricola* Chamberlin, *Spelobion* Chamberlin and Ivie, and *Brontosauriella* Bristowe. Of these genera *Hubba*, *Spelobion* and *Brontosauriella* have type species that are typical members of the genus. Now (Levi and Levi, 1962) we find that *Thymoites* Keyserling is the oldest name for the group. But because the species included are small, and the males are easily mistaken for erigonid spiders, it is possible that a still older name is hidden among the multitude of generic names of the family Linyphiidae (Micryphantidae).

One species of interest from the well-collected northern United States and here described as new is *Thymoites minnesota*. One specimen was on hand in 1957 when I described the United States and Canadian species. Its large size, its similarity to this group, and its uniqueness caused me to postpone description with the thought that it might have been imported from another part of the world. A year later I noticed its striking resemblance to *Theridion oleatum* L. Koch — a Siberian species — but it was still a unique specimen. In 1961 another male was found, this one in a garbage dump in Minnesota, a likely place for an introduced species. Now that I have seen theridiids from all parts of America and other parts of the world, I believe it to be a native species allied to *Thymoites oleatus* (L. Koch), new comb., of Siberia. The female *T. oleatus* resembles *Theridion pretense* Sörensen, suggesting that the two males on hand may be the undescribed males of *T. pretense*, known only from Greenland, the high Rocky Mountains of British Columbia, and Mount Washington in New Hampshire.

I am grateful to the following colleagues for the loan of specimens or for the privilege of examining valuable type specimens: Dr. A. M. Chickering for his theridiid collection now housed in the Museum of Comparative Zoology; Dr. W. J. Gertsch of the American Museum of Natural History (AMNH); Prof. M. Vachon and Mr. J. F. Jézéquel of the Muséum National d'Histoire Naturelle, Paris (MNHN); Dr. A. Collart and Mr. J. Kekenbosch of the Institut Royal des Sciences Naturelles de Belgique (ISNB); Mr. J. Prószyński, Polish Academy of Sciences, Warsaw; Dr. O. Kraus of the Senckenberg Museum, Frankfurt; Dr. G. Owen Evans, Mr. E. Browning, Mr. K. Hyatt and Mr. D. Clark of the British Museum (Natural History); Prof. M. Birabén, director of the Museo Argentino di Ciencas Naturales, for specimens from the La Plata Museum; Mrs. D. L. Frizzell (Dr. H. Exline) for a personal collection and, with Dr. E. S. Ross, for the collection of the California Academy of Sciences; Dr. L. Brundin of the Natural History Museum, Stockholm; and Dr. R. V. Chamberlin for a specimen belonging to the University of Utah (UU). Fr. Chrysanthus checked the Latin specific names. The examination of types in European museums was made possible by a National Science Foundation Grant (G-4317); the completion of the revision was aided by a grant from the National Institutes of Health (AI-01944).

THYMOITES Keyserling

Thymoites Keyserling, 1884, Die Spinnen Amerikas. Theridiidae, 2(1): 161. Type species by monotypy: *T. crassipes* Keyserling, 1884. The name *Thymoites* is masculine in gender.

Note. A description and diagnosis of the genus has been published recently (Levi and Levi, 1962). Species of the United States and Canada, and those of Central America and West Indies were discussed in previous papers (Levi, 1957, 1959); in the keys "fig." in lower case refers to these previous papers. "Figs." capitalized refers to the illustrations in this publication.

Misplaced *Thymoites* species.

Sphyrotinus bimucronatus Simon = *Episinus bimucronatus* (Simon)

S. delfini Simon = probably *Nesticus delfini* (Simon) NESTICIDAE

Thymoites bigibbosus Roewer = *Episinus immundis* (Keyserling)

T. bituberculatus (Keyserling) = *Episinus immundis* (Keyserling)

T. immundis (Keyserling) = *Episinus immundis* (Keyserling)

One species was unavailable: *Thymoites cancellatus* Mello-Leitão, 1943, Rev. Mus., La Plata, n.s. 3:104. Female holotype from Río Atuel, Mendoza, Argentina, in the Museum of La Plata.

Key to female *Thymoites*

1a. Dorsum of abdomen with sclerotized spots 2

1b. Dorsum of abdomen without sclerotized spots 3

2a. Dorsum of abdomen with 15 to 20 sclerotized spots, venter with sclerotized areas (1957, figs. 384, 387); New Mexico, northern Mexico *sclerotis* (Levi)

2b. Abdomen with small spots, the bases of setae; eastern U. S., Mexico *marxi* (Crosby)

3a. Epigynum a knob or a depression with a posterior projecting lip (1957, figs. 405, 406, 409; 1959, fig. 420) 4

3b. Epigynum flat, or if with a depression then without projecting posterior lip 7

4a. Epigynum with a depression and a posterior projecting lip (1959, figs. 420, 422); Mexico to Panama *boquete* (Levi)

4b. Epigynum without depression 5

5a. Tip of knob with dumbbell-shaped dark mark; a loop of duct on each side of knob (1957, figs. 368-370); Utah, Pacific Coast states of U. S. *camano* (Levi)

5b. Epigynum otherwise 6

6a. In ventral view U-shaped dark mark on knob (1957, fig. 404); Florida *sarasota* (Levi)

6b. In ventral view an upside down, dark, V-shaped mark on knob (1957, figs. 408, 412); eastern U. S. *unimaculatus* (Emerton)

7a. Epigynum with a distinct bordered depression (1957, figs. 361, 378; 1959, fig. 428) 8

7b. Epigynum otherwise 10

8a. Depression with a median septum (1957, figs. 360-362); ducts as in 1957, figures 358, 359; U. S. to Venezuela, West Indies *pallidus* (Emerton)

8b. Depression without median septum 9

9a. A dark transverse mark anterior to and slightly wider than depression (1957, fig. 378); connecting ducts very short (1957, fig. 377); Arizona, Pacific Coast of U. S. *pictipes* (Banks)

9b. No transverse mark anterior to depression (1959, fig. 428); connecting ducts longer (1959, fig. 427); Mexico to Peru *confraternus* (Banks)

10a. Epigynum with ducts opening at posterior border; openings often indistinct, often in sclerotized area touching border 30

10b. Epigynum with duct opening in center; openings often in dark spots and indistinct 11

11a. Duct very coiled as seen through epigynum (1959, figs. 390, 391); Trinidad to eastern Brazil *piarco* (Levi)

11b. Duct otherwise 12

12a. A semicircular or curved dark lip anterior to openings (1957, fig. 379; 1959, figs. 405, 412, 418) 13

12b. No such lip present 16

13a. Openings in two contiguous circular dark spots (1959, fig. 412); Panama *notabilis* (Levi)

13b. Openings otherwise 14

14a. Openings in a depression (1957, fig. 379); ducts very short (1957, fig. 377); Arizona, Pacific Coast states *pictipes* (Banks)

14b. Openings otherwise; ducts longer 15

15a. Openings in widely separated dark spots (1959, fig. 418); Panama *bogus* (Levi)

15b. Openings both in a single small central depression (1959, fig. 405); Guatemala to Ecuador *caracasanus* (Simon)

16a. A dark spot anterior to dark area that probably contains openings (Fig. 63); Peru *sanctus* (Chamberlin)

16b. No such dark spot present 17

17a. Ducts leaving openings in a posterior direction (1959, figs. 362, 372; Figs. 64, 65) 18

17b. Ducts leaving openings in a lateral or anterior direction 21

18a. Ducts fused for a short length posterior to single opening; a duct loop visible on each side ventral to seminal receptacles (1959, figs. 361, 362); Mexico to Venezuela *delicatulus* (Levi)

18b. Ducts not fused; no loops visible 19

19a. Ducts opening into a light shallow depression (1957, fig. 417); southeastern U. S.; Mexico, probably West Indies *expulsus* (Gertsch and Mulaik)

19b. Duct openings in a dark spot 20

20a. Posterior rim of epigynum sclerotized (Fig. 65); Colombia *unisignatus* (Simon)

20b. Posterior rim of epigynum not sclerotized (1959, fig. 372); Mexico *bradti* (Levi)

21a. Posterior rim of epigynum sclerotized or dark posterior to openings 22

21b. Rim not sclerotized 28

22a. Ducts leaving openings in an anterior direction, parallel for a short distance (Fig. 45); southern Brazil *aloitus* sp. n.

22b. Ducts otherwise 23

23a. Ducts leaving openings in a lateral direction 24

23b. Ducts leaving openings in a diagonal or anterior direction 25

24a. Duct openings in a pair of dark spots (1959, fig. 368); ducts looping (1959, fig. 367); Mexico *chiapensis* (Levi)

24b. Duct openings in or posterior to a common dark spot (1959, fig. 430); ducts not looping (1959, fig. 429); Costa Rica . . . *vivus* (O. P.-Cambridge)
25a. A pair of dark spots anterior to opening (Fig. 2); Peru *ramon* sp. n.
25b. Without pair of dark spots . . . 26
26a. A small median tongue on posterior margin of epigynum (Fig. 6); Colombia . . . *anserma* sp. n.
26b. Posterior margin of epigynum straight . . . 27
27a. Tarsi longer than metatarsi; leg four longest; Mexico *boneti* (Levi)
27b. Metatarsi longer than tarsi; first leg longest; southeastern U. S. to southern Mexico, probably West Indies . *expulsus* (Gertsch and Mulaik)
28a. Openings in two adjoining black spots, ducts leaving laterally (1959, fig. 388); Panama to Venezuela . *stylifrons* (Simon)
28b. Openings otherwise; ducts leaving toward anterior . . . 29
29a. Ducts with a loop as in Figure 14; Venezuela *struthio* (Simon)
29b. Duct elbowed but without loops as in Figure 28; southeastern Brazil *iritus* sp. n.
30a. Ducts narrow, one-tenth diameter of seminal receptacles; or not visible through epigynum . . . 35
30b. Ducts wide, at their widest point more than one-fifth width of seminal receptacles, visible through epigynum . 31
31a. Ducts with several large coils visible through epigynum (Fig. 68); Trinidad . . . *simla* (Levi)
31b. Duct coils otherwise or absent . . . 32
32a. Openings some distance apart (1959, figs. 375, 376); Panama *reservatus* (Levi)
32b. Openings touching or joined . . . 33
33a. Ducts looping toward anterior margin of seminal receptacles; their entrance into the seminal receptacles visible through the epigynum (1959, figs. 373, 374); Mexico . . . *corus* (Levi)
33b. Ducts without such loops; entrance of duct into seminal receptacles not visible through epigynum . . . 34
34a. Ducts touching for a short distance after leaving openings; a loop of narrower ducts visible posterior to seminal receptacles through epigynum (1959, figs. 377, 378); Central America . *indicatus* (Banks)
34b. Ducts separate after leaving openings; posterior to seminal receptacles a pigmented wide portion of duct loop is visible through epigynum (1957, figs. 420, 421; 1959, figs. 355, 356); Arizona to Panama *maderae* (Gertsch and Archer)
35a. Openings in a squarish sclerotized spot; length of ducts less than radius of seminal receptacles (1957, figs. 380, 381); Texas to Costa Rica . . . *missionensis* (Levi)
35b. Openings otherwise, ducts longer than shorter radius of seminal receptacles . . . 36
36a. Two pairs of small dark spots in center of epigynum; ducts enter seminal receptacles anteriorly (1959, figs. 425, 426; Fig. 58) . 37
36b. Epigynum otherwise; ducts enter seminal receptacles posteriorly 38

37a. Duct looping on each side; opening without septum (Figs. 58, 59); Bolivia ..... *incachaca* sp. n.

37b. Duct without loop on each side; opening with a septum (1959, figs. 425, 426); Panama ..... *prolatus* (Levi)

38a. Eyes with some red pigment; ducts with two pairs of loops (Fig. 47); southern Brazil ..... *ebus* sp. n.

38b. Eyes without red pigment; ducts loop once at most 39

39a. Length of seminal receptacles almost twice width 40

39b. Seminal receptacles subspherical or pear-shaped 42

40a. Duct loops extend on each side beyond seminal receptacles (Figs. 25, 26); southern Brazil, northern Argentina ..... *puer* (Mello-Leitão)

40b. Duct loops not extending laterally 41

41a. Duct short, curved (Figs. 3, 4); Venezuela ..... *maracayensis* sp. n.

41b. Duct longer, with shallow loops (Figs. 32, 33); southeastern Brazil ..... *mirus* sp. n.

42a. Seminal receptacles pear-shaped (Fig. 19) 43

42b. Seminal receptacles subspherical 44

43a. Duct elbowed anterior to openings; entrance of duct into seminal receptacles visible through epigynum as dark spot (1959, figs. 339, 340); Panama ..... *chickeringi* (Levi)

43b. Duct curved; epigynum otherwise (Figs. 19, 20); southeastern Brazil ..... *anicus* sp. n.

44a. Ducts leave openings in an anterior direction, parallel a short distance (1957, figs. 414, 415; 1959, figs. 342, 343); Texas to Panama ..... *illudens* (Gertsch and Mulaik)

44b. Ducts otherwise 45

45a. Ducts with shallow loops (Figs. 37, 40) 40

45b. Ducts straight or curved (1959, figs. 334, 346; Figs. 1, 7) 47

46a. Fertilization ducts and connecting ducts originating together on seminal receptacles (Figs. 37, 38); southeastern Brazil ..... *ilvan* sp. n.

46b. The two ducts originating some distance apart on seminal receptacles (Figs. 40, 41); Paraguay ..... *villarricaensis* sp. n.

47a. Ducts straight 48

47b. Ducts curved 50

48a. Seminal receptacles less than their diameter from posterior margin (1957, fig. 416; 1959, fig. 365); southeastern U. S. to Mexico, probably West Indies ..... *expulsus* (Gertsch and Mulaik)

48b. Seminal receptacles more than their diameter from posterior margin; Peru 49

49a. Ducts narrowing toward openings (Figs. 1, 2) ..... *ramon* sp. n.

49b. Ducts of equal width throughout (Figs. 7, 8) ..... *crassipes* Keyserling

50a. Southeastern Brazil (Fig. 27) ..... *rarus* (Keyserling)

50b. Mexico to Lesser Antilles 51

51a. Total length 1.2 mm (1959, figs. 334, 335); Chiapas, Panama, Lesser Antilles ..... *luculentus* (Simon)

51b. Total length 1.3-1.7 mm (1959, figs. 345-347); Mexico, Greater Antilles ..... *guanicae* (Petrunkevitch)

Key to male *Thymoites*

1a. Clypeus with a transverse seam (1957, fig. 396; 1959, fig. 358) 2
1b. Clypeus without transverse seam 3
2a. Palpal embolus hidden by tegulum (1959, fig. 359); Mexico *verus* (Levi)
2b. Palpal embolus visible in ventral view (1957, fig. 399; 1959, fig. 344); Texas to Panama *illudens* (Gertsch and Mulaik)
3a. Abdomen with a dorsal scutum 4
3b. Abdomen without dorsal scutum 6
4a. Area of posterior median eyes bulging (1959, figs. 395, 396); northern Mexico *matachic* (Levi)
4b. Area of posterior median eyes otherwise 5
5a. Tegulum in ectal half of palpus (1957, fig. 401); eastern U. S., Mexico *marxi* (Crosby)
5b. Tegulum in proximal two-thirds of palpus (1959, fig. 383); Mexico *orilla* (Levi)
6a. Height of carapace in thoracic region two-thirds length, carapace without bulges; clypeus straight (1957, fig. 397) 7
6b. Height of carapace in thoracic region less than one-half length, carapace often with bulges 8
7a. Median apophysis a large prominent sclerite as in 1957, figures 371, 372; Utah to Pacific Coast of U. S. *camano* (Levi)
7b. Median apophysis a very small sclerite, barely visible in ventral view (1957, fig. 398); Arizona to Panama *maderae* (Gertsch and Archer)
8a. Carapace with bulges, grooves, extensions or strong setae in eye region 26
8b. Carapace otherwise, of normal shape 9
9a. Palpus noticeably hairy on ectal (or dorsal) side (1959, fig. 424) 10
9b. Palpus otherwise 11
10a. Base of palpal emoblus large (1959, fig. 424); Panama *prolatus* (Levi)
10b. Base of palpal embolus small (Fig. 60); Bolivia *incachaca* sp. n.
11a. Sclerotized ring around pedicel 12
11b. No sclerotized ring around pedicel 13
12a. Palpal conductor with a narrower stem (Fig. 54); southern Brazil *ipiranga* sp. n.
12b. Palpal conductor a continuation from tegulum, smoothly tapering (1957, fig. 398; 1959, figs. 350-354); Arizona to Panama *maderae* (Gertsch and Archer)
13a. Palpal conductor notched (1959, fig. 382); Mexico to Peru *confraternus* (Banks)
13b. Palpal conductor without notch 14
14a. In ventral view median apophysis extending to proximal end of bulb (Fig. 66); Colombia *unisignatus* (Simon)
14b. Medium apophysis never extending to proximal end of bulb 15

15a. Median apophysis a prominent rectangular sclerite in ventral view, its long axis parallel to cymbium (1959, fig. 419); Mexico to Panama *boquete* (Levi)

15b. Median apophysis otherwise 16

16a. Tegulum showing duct; duct with 90° bend or loop (1959, figs. 348, 349); Mexico, Greater Antilles *guanicae* (Petrunkevitch)

16b. Tegulum otherwise 17

17a. Tip of embolus coiling around conductor (1957, figs. 365, 366); U. S. to Venezuela, West Indies *pallidus* (Emerton)

17b. Tip of embolus straight 18

18a. Distal part of embolus thread-like 19

18b. Embolus not visible or distal parts not thread-like 21

19a. Tegulum showing duct loop (Fig. 49); eyes with red pigment (Fig. 46); southern Brazil *ebus* sp. n.

19b. Tegulum without such duct loop, eyes not reddish 20

20a. Embolus very long; subtegulum not visible in ventral view (1959, fig. 360); Mexico to Venezuela *delicatulus* (Levi)

20b. Embolus shorter, subtegulum visible in ventral view (1957, fig. 388-391); eastern U. S. *unimaculatus* (Emerton)

21a. Embolus hidden by tegulum or conductor in ventral view 22

21b. Embolus partly visible in ventral view 24

22a. Palpus with conductor shaped as in 1957, figure 375; Arizona, Pacific Coast of U. S. *pictipes* (Banks)

22b. Palpal conductor translucent, difficult to see; Panama 23

23a. Long axis of conductor parallel to cymbium (1959, fig. 341) *chickeringi* (Levi)

23b. Long axis of conductor at angle to cymbium (Fig. 43) *amprus* sp. n.

24a. Conductor subspherical, stalked (1959, figs. 336-338); Mexico to Panama; Lesser Antilles *luculentus* (Simon)

24b. Conductor otherwise; if stalked, not subspherical 25

25a. Median apophysis a heavily sclerotized sclerite (1957, figs. 382, 383); Texas to Costa Rica *missionensis* (Levi)

25b. Median apophysis lightly sclerotized (1957, fig. 400); southeastern U. S. to southern Mexico, probably West Indies *expulsus* (Gertsch and Mulaik)

26a. Carapace with anterior projection in eye region; length of carapace anterior to chelicerae more than two-thirds length behind chelicerae 27

26b. Carapace otherwise; if bulging anteriorly, length less than one-half carapace length behind chelicerae 33

27a. Anterior projection with two dorsal "ears" (Fig. 35); southern Brazil *melloleitaoni* (Bristowe)

27b. Anterior projection otherwise 28

28a. Anterior median eyes near or on tip of projection 30

28b. Anterior median eyes near base of projection or half way up projection 29

29a. Tip of projection slightly wider than neck (1959, figs. 385, 386); Panama to Venezuela *stylifrons* (Simon)

29b. Projection evenly tapering to tip (Figs. 17, 18); southeastern Brazil *anicus* sp. n.

30a. Anterior median eyes as far apart as anterior laterals (1959, fig. 402); Trinidad *simla* (Levi)

30b. Anterior median eyes separated by less than anterior laterals 31

31a. Projection truncate in lateral view (Figs. 30, 31); southeastern Brazil *mirus* sp. n.

31b. Projection pointed in lateral view 32

32a. Distance between anterior median eyes and posterior medians less than distance between posterior laterals (1959, fig. 380); Central America *indicatus* (Banks)

32b. Distance between anterior median eyes and posterior medians more than twice distance between posterior laterals (Figs. 12, 13); Venezuela *struthio* (Simon)

33a. A row of strong setae between anterior and posterior median eyes (Figs. 74, 75); carapace longer than 1.0 mm; Minnesota, Michigan *minnesota* sp. n.

33b. No such setae present; carapace less than 0.8 mm total length 34

34a. A bulge above posterior median eye bordered by a seam (1959, figs. 392, 393; Fig. 50); Trinidad to eastern Brazil *piarco* (Levi)

34b. Carapace without such a bulge 35

35a. A transverse seam between anterior and posterior median eyes 36

35b. No transverse seam between anterior and posterior median eyes 40

36a. Anterior median eyes on a truncate projection (Figs. 51, 52); Venezuela *gibbithorax* (Simon)

36b. Eye region otherwise 37

37a. Median eyes on a common short stalk (1959, figs. 406, 413) 38

37b. Eye region otherwise 39

38a. Carapace subcircular (1959, fig. 407); distal prong of median apophysis a flat shield (1959, fig. 409); Guatemala to Ecuador *caracasanus* (Simon)

38b. Carapace pear-shaped (1959, fig. 414); distal prong of median apophysis a narrow finger (1959, fig. 415); Panama *notabilis* (Levi)

39a. Embolus with a long filament (Fig. 57); ectal side of cymbium with few setae; Venezuela *lobifrons* (Simon)

39b. Embolus short without filament (Fig. 24); dense setae on ectal side of cymbium; Peru *lori* sp. n.

40a. A strong spine lateral to each posterior median eye (1959, figs. 398, 399); Dominican Republic *banksi* (Bryant)

40b. No such spine present 41

41a. Embolus without filament (Fig. 9); Peru *crassipes* Keyserling

41b. Embolus with filament 42

42a. A shallow groove between anterior and posterior eye rows (Figs. 51, 52); Venezuela *gibbithorax* (Simon)

42b. No groove between anterior and posterior eye rows 43

43a. Clypeus with a groove below anterior eyes, convex below (Fig. 39); Paraguay *villarricaensis* sp. n.

43b. Clypeus concave (1959, fig. 379); Central America *indicatus* (Banks)

THYMOITES RAMON sp. n.

Figures 1, 2

Type. Female holotype from near Caupañillaya, between Tarma and San Ramón, 2600 m elev., Junín, Peru (W. H. Koepcke), in the Senckenberg Museum. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, legs orange-yellow, patellae slightly lighter. Abdomen whitish without pigment. Anterior median eyes smaller than others and without pigment, others with black and silver pigment. Anterior eyes slightly projecting over clypeus. Anterior median eyes a little more than their diameter apart, one diameter from laterals. Posterior eyes their diameter apart. Total length 2.2 mm. Carapace 0.91 mm long, 0.86 mm wide. First femur, 1.43 mm; patella and tibia, 1.40 mm; metatarsus, 1.04 mm; tarsus, 0.57 mm. Second patella and tibia, 1.10 mm; third, 0.85 mm; fourth, 1.22 mm.

Diagnosis. The genitalia, characterized by spherical seminal receptacles more than their diameter apart, and tapering connecting ducts (Fig. 1), distinguish this species from *T. crassipes.*

THYMOITES MARACAYENSIS sp. n.

Figures 3, 4

Type. Female holotype from Maracay, Aragua, Venezuela, in the Senckenberg Museum (no. RII/9165/1). The specific name is an adjective after the type locality.

Description. Carapace rich brown. Sternum brown. Legs brown with coxae and patellae lighter. Abdomen whitish with sparse dorsal gray pigment and an indistinct gray ring around spinnerets. Anterior median eyes slightly smaller than others, one and one-quarter diameters apart, their radius from laterals. Posterior median eyes three-quarters diameter apart, one diameter from laterals. Total length 1.4 mm. Carapace 0.66 mm long, 0.62 mm wide. First femur, 0.75 mm; patella and tibia, 0.75 mm; metatarsus, 0.50 mm; tarsus, 0.35 mm. Second patella and tibia, 0.60 mm; third, 0.52 mm; fourth, 0.69 mm.

Diagnosis. The long seminal receptacles distinguish this species from most *Thymoites:* the shorter connecting ducts (Figs. 3, 4) distinguish it from *T. mirus.*

THYMOITES ANSERMA sp. n.

Figures 5, 6

Type. Female holotype from 8 km north of Anserma, Caldas, Colombia, 17 March 1955 (E. I. Schlinger, E. S. Ross), in the California Academy of Sciences. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum yellow. Legs red-brown. Abdomen white. Anterior median eyes slightly smaller than others, a little more than their diameter apart, and one diameter from laterals. Posterior median eyes one and one-half diameters apart, one and two-thirds diameters from laterals. Abdomen very soft. Total length 2.0 mm. Carapace 0.71 mm long, 0.68 mm wide. First femur, 1.45 mm; patella and tibia, 1.30 mm; metatarsus, 1.14 mm; tarsus, 0.58 mm. Second patella and tibia, 1.04 mm; third, 0.73 mm; fourth, 1.11 mm.

Diagnosis. The large, spherical seminal receptacles (Fig. 5) and the projecting tongue on the posterior margin of the epigynum (Fig. 6) distinguish this species from *T. boneti* (Levi).

THYMOITES CRASSIPES Keyserling

Figures 7-11

Thymoites crassipes Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 162, pl. 7, fig. 100, ♀, ♂. Male lectotype, here designated, from Pumamarca, [1900 m elev., Junín, prov. Tarma], Peru, in the Polish Academy of Sciences, Warsaw, examined.

Description. Carapace dull orange, light in middle, around margin, and in eye region. Sternum, legs orange. Abdomen whitish without marks. Carapace of male projecting in eye region with two setae at the tip and one seta between anterior median and lateral eyes. Anterior median eyes smaller than laterals. Anterior median eyes of male a little more than their diameter apart; posterior eyes more than their diameter apart. Anterior eyes of female their diameter apart; posterior eyes their diameter apart. Chelicerae probably with two teeth on anterior margin, but this is uncertain. Total length of female 2.1 mm. Carapace 0.94 mm long, 0.87 mm wide. Second patella and tibia, 1.04 mm; third, 0.91 mm. Total length of male 2.0 mm. Carapace 0.91 mm long, 0.83 wide. First femur, 1.36 mm; patella and tibia, 1.52 mm; metatarsus, 0.92 mm; tarsus, 0.52 mm. Second patella and tibia, 1.17 mm; third, 0.91 mm; fourth, 1.45 mm.

The embolus and conductor of the palpus are translucent and difficult to see. Only the radix and median apophysis are sclerotized. The embolus is very short (Fig. 9). The female has the opening of the epigynum invisible and on the posterior margin. The connecting canals are transparent and difficult to see (Fig 7); the fertilization duct shows through the transparent epigynum (Fig. 8).

THYMOITES STRUTHIO (Simon), new combination

Figures 12-16

Theridion struthio Simon, 1894, Histoire Naturelle des Araignées, 1: 542, fig. 555, ♂, *nomen nudum;* 1895, Ann. Soc. ent. France, 64: 142. Male lectotype here designated from Caracas, Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace, sternum, legs dark orange. Abdomen grayish white. Cephalothorax of male with a long projection bearing anterior median eyes near tip (Figs. 12, 13). Anterior median eyes smaller than other eyes in both sexes. Anterior median eyes of female one and one-half diameters apart, their radius from laterals. Posterior median eyes of female slightly less than their diameter apart, two-thirds diameter from laterals. Abdomen of male with a sclerotized ring around spinnerets. Epigynum with ends of ducts showing (Fig. 15), portion of duct ending in seminal receptacles unusually thin and transparent and difficult to see in cleared preparations. Total length of female 1.7 mm. Carapace 0.64 mm long, 0.52 mm wide. First femur, 0.66 mm; patella and tibia, 0.65; metatarsus, 0.45; tarsus, 0.27 mm. Second patella and tibia, 0.49 mm; third, 0.39 mm; fourth, 0.54 mm. Total length of male 1.7 mm. Carapace 1.04 mm long, 0.52 mm wide. First femur, 0.67 mm; patella and tibia, 0.71 mm; metatarsus, 0.53 mm; tarsus, 0.30 mm. Second patella and tibia, 0.58 mm; third, 0.39 mm; fourth, 0.62 mm.

Records. Ten ♂, 4 ♀ paratypes collected with holotype from Caracas, Venezuela.

THYMOITES ANICUS sp. n.

Figures 17-21

Type. Male holotype from Botanical Gardens, São Paulo, Brazil, 13 January 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs yellow. Abdomen whitish. Carapace of male without anterior projection. Diameter of anterior median eyes two-thirds that of posterior medians in male. Anterior median eyes slightly more than their diameter from laterals in males, their diameter apart and slightly more than their diameter from laterals in females. Posterior eyes their radius apart. All eyes of female slightly smaller than those of male and slightly farther apart. Total length of female 1.1 mm. Carapace 0.55 mm long, 0.44 mm wide. First femur, 0.60 mm; patella and tibia, 0.56 mm; metatarsus, 0.36 mm; tarsus, 0.29 mm. Second patella and tibia, 0.42 mm; third, 0.37 mm; fourth, 0.48 mm. Total length of male 1.6 mm. Carapace 0.85 mm long, 0.52 mm wide. First femur, 0.78 mm; patella and tibia, 0.78 mm; metatarsus, 0.41 mm; tarsus, 0.31 mm. Second patella and tibia, 0.65 mm; third, 0.45 mm; fourth, 0.62 mm.

Diagnosis. The palpus (Fig. 21) is very small, has translucent sclerites, and is exceedingly difficult to examine; it is very close to that of *T. stylifrons* (Simon), but differs in some details of sclerites. The species further differs from *T. stylifrons* by its much larger eyes, long setae at the end of the male carapace projection (Figs. 17, 18) and in having the opening of the epigynum located posteriorly (Figs. 20) rather than centrally in the epigynum.

Records. Brazil. São Paulo: ♀ paratype collected with ♂ holotype; Ipiranga, São Paulo, 12 Jan. 1959, ♂ paratype (A. M. Nadler, AMNH).

THYMOITES LORI sp. n.

Figures 22-24

Type. Male holotype from La Merced, Junín, Peru, 1 Jan. 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum orange. Legs grayish orange. Abdomen whitish. Carapace with a swelling in area of anterior median eyes (Figs. 22, 23). Anterior median eyes slightly smaller than others, two diameters apart, one and one-half diameters from laterals. Posterior median eyes one diameter apart, two diameters from laterals. Total length 1.3 mm. Carapace 0.78 mm long, 0.59 mm wide. First femur, 0.68 mm; patella and tibia, 0.66 mm; metatarsus, 0.50 mm; tarsus, 0.36 mm.

Second patella and tibia, 0.59 mm; third, 0.45 mm; fourth, 0.66 mm.

Diagnosis. Like *T. prolatus*, the cymbium has setae on the ectal side (not shown in Fig. 24), and the palpal femur and tibiae are enlarged. It differs, however, from *T. prolatus* in having a shorter embolus (Fig. 24) and having the area of the anterior median eyes of the carapace swollen (Figs. 22, 23).

Record. One ♂ paratype collected with holotype.

THYMOITES PUER (Mello-Leitão), new combination

Figures 25, 26

Theridion puer Mello-Leitão, 1941, Rev. Mus. La Plata, n.s., 2: 211, fig. 15, ♀. Female holotype from Guadalupe, Provincia de Santa Fe, Argentina, in the Museo de la Plata, examined.

This species is very similar to *T. guanicae* (Petrunkevitch), but the ducts loop laterally beyond the seminal receptacles. The species may be the same as *T. rarus* (Keyserling).

Record. Brazil. Santa Catarina: Nova Teutonia, lat 27° 11′S, long 52° 23′W, 300-500 m, May 1957, ♀ (F. Plaumann, ISNB).

THYMOITES RARUS (Keyserling), new combination

Figure 27

Theridium rarum Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):237, pl. 20, fig. 291, ♀. Female holotype from Blumenau, [Santa Catarina], Brazil, in the Polish Academy of Sciences, Warsaw, apparently lost.

This species seems similar to *T. guanicae* (Petrunkevitch). It has a dark longitudinal line on the dorsum.

THYMOITES IRITUS sp. n.

Figures 28, 29

Type. Female holotype from Santa Teresa, Est. Espírito Santo, Brazil, 26 Jan. 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace dark brown. Sternum brown with a slightly rugose texture. Legs lighter brown, coxae lightest. Abdomen whitish. Eyes subequal in size. Anterior median eyes one diameter apart, their radius from laterals. Posterior eyes less than their diameter apart. Total length 1.2 mm. Carapace 0.59 mm long, 0.52 mm wide. First femur, 0.61 mm; patella and tibia, 0.61 mm; metatarsus, 0.43 mm; tarsus, 0.26 mm. Second patella and tibia, 0.50 mm; third, 0.39 mm; fourth, 0.53 mm.

Diagnosis. Unlike *T. struthio*, the connecting ducts of *T. iritus* have only shallow loops (Fig. 28).

THYMOITES MIRUS sp. n.

Figures 30-34

Type. Male holotype from Teresópolis, Est. Rio de Janeiro, 900-1000 m elev., Brazil, March 1946 (H. Sick), in the American Museum of Natural History. The specific name is an adjective meaning wonderful.

Description. Carapace, sternum, legs orange-yellow, some black around eyes and distal segments of legs dusky. Abdomen whitish. Head of male with a blunt anterior projection (Figs. 30, 31). Anterior median eyes slightly smaller than others. Anterior eyes of female one diameter apart, one-quarter diameter from laterals. Posterior median eyes one diameter apart, two-thirds diameter from laterals. Total length of female 1.5 mm. Carapace 0.68 mm long, 0.58 mm wide. First femur, 0.85 mm; patella and tibia, 0.80 mm; metatarsus, 0.58 mm; tarsus, 0.36 mm. Second patella and tibia, 0.68 mm; third, 0.50; fourth, 0.73 mm. Total length of male 1.5 mm. Carapace 0.91 mm long, 0.44 mm wide. First femur, 0.75 mm; patella and tibia, 0.75 mm; metatarsus, 0.49 mm; tarsus, 0.31 mm. Second patella and tibia, 0.55 mm; third, 0.42 mm; fourth, 0.58 mm.

Diagnosis. The shorter projection of the male carapace (Figs. 30, 31) and the structure of the male palpus (Fig. 34) separate this species from *T. struthio*; the longer connecting ducts (Figs. 32, 33) distinguish this species from *T. maracayensis*.

Record. One ♀ paratype collected with ♂ holotype.

THYMOITES MELLOLEITAONI (Bristowe)

Figures 35, 36

Brontosauriella melloleitaoni Bristowe, 1938, Ann. Mag. Nat. Hist., (11) 2: 72, figs. 8-13, ♂. Male holotype from "Santa Catharina," Brazil, in the British Museum, examined.

This species was collected from a termite nest gallery.

THYMOITES ILVAN sp. n.

Figures 37-38

Type. Female holotype from Forest Reservation, São Paulo. Brazil, 16 Jan. 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs yellow-brown. Abdomen whitish. Posterior median eyes slightly larger than others. Anterior median eyes their diameter apart, less than one-quarter diameter from laterals. Posterior median eyes their radius apart, one-quarter diameter from laterals. Total length 1.3 mm. Carapace 0.53 mm long, 0.44 mm wide. First femur, 0.65 mm: patella and tibia, 0.65 mm; metatarsus, 0.43 mm; tarsus, 0.28 mm. Second patella and tibia, 0.52 mm; third, 0.40; fourth, 0.53 mm.

Diagnosis. The shorter legs distinguish this species from *T. rarus*. The fine winding ducts (Fig. 37) distinguish *T. ilvan* from *T. luculentus* and *T. guanicae*. The close origin of fertilization ducts and connecting ducts from the seminal receptacles (Fig. 37) and lack of abdominal spots distinguish the species from *T. villarricaensis*. This may be the female of *T. ipiranga*.

THYMOITES VILLARRICAENSIS sp. n.

Figures 39-42

Type. Male holotype from Villarrica, Guaira, Paraguay (Silvestri), in the Muséum National d'Histoire Naturelle, Paris (no. 22816). The species is named after the type locality.

Description. Carapace orange with a median longitudinal black line; eyes on black spots. Sternum, legs orange-yellow. Abdomen orange-white with five to seven discrete round black spots, four or six on sides of dorsum, one posterior above spinnerets. Genital area on venter of male black. Carapace of male high and slightly projecting in eye region (Fig. 39). Eyes of male subequal in size and quite small. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes two-thirds diameter apart, one and one-half diameters from laterals. Anterior median eyes of female slightly smaller than others, their diameter apart, a little more than their diameter from laterals. Posterior median eyes two-thirds diameter apart, three-quarters diameter from laterals. Total length of female 1.4 mm. Carapace 0.67 mm long, 0.55 mm wide. First femur, 1.12 mm; patella and tibia, 0.87 mm; metatarsus, 0.75 mm;

tarsus, 0.38 mm. Second patella and tibia, 0.65 mm; third, 0.55 mm; fourth, 0.78 mm. Total length of male 1.4 mm. Carapace 0.82 mm long, 0.66 mm wide. First femur, 1.17 mm; patella and tibia, 1.17 mm; metatarsus, 0.91 mm; tarsus, 0.48 mm. Second patella and tibia, 0.95 mm; third, 0.68 mm; fourth, 0.91 mm.

Diagnosis. The black spots on the abdomen, and the separate origin of fertilization and connecting ducts from the seminal receptacles (Fig. 40) distinguish females from *T. ilvan;* the shorter seminal receeptacles distinguish the species from *T. mirus,* and the shorter projeetion of the male carapace (Fig. 39) and the shorter palpal embolus distinguish it from *T. indicatus* (Banks).

Records. One ♀ and 1 ♂ paratype collected with holotype.

THYMOITES AMPRUS sp. n.

Figure 43

Type. Male holotype from Experimental Gardens, Panama Canal Zone, 10-14 July, 1950 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Spider colorless, whitish; only eyes have some black pigment. Carapace not modified. Diameter of anterior median eyes half that of posterior medians. Anterior median eyes a little more than one diameter apart, their radius from laterals. Posterior eyes their diameter apart. Abdomen with a few long setae. Total length 1.1 mm. Carapace 0.62 mm long, 0.53 mm wide. First femur, 0.84 mm; patella and tibia, 0.84 mm; metatarsus, 0.53 mm; tarsus, 0.36 mm. Second patella and tibia 0.60, mm; third, 0.47 mm; fourth, 0.70 mm.

Diagnosis. The small eyes suggest that this species might belong to the genus *Styposis;* however, the palpus indicates that it belongs in *Thymoites* (Fig. 43). The small anterior median eyes and the structure of the palpus distinguish it from other species, particularly from *T. luculentus.*

THYMOITES ALOITUS sp. n.

Figures 44-45

Type. Female holotype from Nova Teutonia, lat 27° 11′S, long 52° 23′W, Santa Catarina, Brazil, Feb. 1956 (F. Plaumann) in the Institut Royal des Sciences Naturelles de Belgique, Brussels. The specific name is an arbitrary combination of letters.

Descripition. The spider is entirely yellow except for a black patch above spinnerets. The posterior median eyes are slightly oval with a long axis parallel to carapace axis. Anterior median eyes much smaller than others, one and one-quarter diameters apart, one-third diameter from laterals. Posterior median eyes two-thirds of their longer diameter apart, their radius from laterals. Total length 1.7 mm. Carapace 0.60 mm long, 0.56 mm wide. First femur, 0.90 mm; patella and tibia, 1.00 mm; metatarsus, 0.60 mm; tarsus, 0.42 mm. Second patella and tibia, 0.80 mm; third, 0.54 mm; fourth, 0.84 mm.

Diagnosis. Thymoites aloitus differs from *T. ebus* by having spherical seminal receptacles (Figs. 44, 45).

Records. Three ♀ paratypes collected with type, 1 ♀ paratype, May 1957 from type locality.

THYMOITES EBUS sp. n.

Figures 46-49

Type. Male holotype from Nova Teutonia, lat 27° 11′S, long 52° 23′W, Santa Catarina, Brazil, May 1957 (F. Plaumann) in the Institut Royal des Sciences Naturelles de Belgique, Brussels. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs yellow. Eyes ringed by some red pigment. Abdomen yellow-white with a black patch above spinnerets in some specimens. Carapace of male without projections (Fig. 46). Anterior median eyes slightly smaller than others, one and one-half diameters apart, their radius from laterals. Posterior eyes about one diameter apart. Abdomen of male quite high (Fig. 46). Total length of female 1.1 mm. Carapace 0.48 mm long, 0.42 mm wide. First femur, 0.56 mm; patella and tibia, 0.53 mm; metatarsus, 0.34 mm; tarsus, 0.32 mm. Second patella and tibia, 0.44 mm; third, 0.38 mm; fourth, 0.54 mm. Total length of male 1.0 mm. Carapace 0.52 mm long, 0.46 mm wide. First femur, 0.62 mm; patella and tibia, 0.60 mm; metatarsus, 0.36 mm; tarsus, 0.32 mm. Second patella and tibia, 0.52 mm; third, 0.32 mm; fourth, 0.54 mm.

Diagnosis. The male of *T. ebus* is distinguished from related Brazilian species by lacking projections on the head (Fig. 46) and by having reddish eyes, and the female can be separated from most species by the long coiled duct and from *T. aloitus* by having oval seminal receptacles (Fig. 47).

Records. Two ♀ collected with type; 2 ♀, 1 ♂ June 1955 from type locality.

THYMOITES PIARCO (Levi), new combination

Figure 50

Sphyrotinus piarco Levi, 1959, Bull. Mus. Comp. Zool., 121: 153, figs. 390-394, ♀, ♂. Male holotype from Trinidad Lesser Antilles, in the American Museum of Natural History.

An additional collection from Brazil indicates that males and females are correctly matched. The carapace shape of the males from Brazil is quite different (Fig. 50) from that of specimens collected in Trinidad; the male genitalia are similar; the duct in the female genitalia may be slightly shorter.

Distribution. Trinidad to eastern Brazil.

Additional record. Brazil. Pará: Belém, Goeldi Museum, Feb. 1959, ♀, ♂ (A. M. Nadler, AMNH).

THYMOITES GIBBITHORAX (Simon), new combination

Figures 51-53

Theridion gibbithorax Simon, 1894, Histoire Naturelle des Araignées, 1: 542, fig. 556, ♂, *nomen nudum;* 1895, Ann. Soc. ent. France, 64: 144. Male holotype from Colonia Tovar, [Aragua], Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined.

THYMOITES IPIRANGA sp. n.

Figure 54

Type. Male holotype from Ipiranga, São Paulo, Brazil, 12 Jan. 1959 (A. M. Nadler), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, legs orange. Abdomen whitish with a black patch above spinnerets (probably a characteristic of the individual specimen). Carapace without bulges or extensions. Anterior median eyes slightly smaller than others, two-thirds diameter apart, one-quarter diameter from laterals. Posterior median eyes their radius apart, two-thirds diameter from laterals. Abdomen with a sclerotized ring around pedicel. Total length 1.3 mm. Carapace 0.65 mm long, 0.52 mm wide. First femur, 0.91 mm; patella and tibia, 1.00 mm; metatarsus, 0.55 mm; tarsus, 0.38 mm. Second patella and tibia, 0.69 mm; third, 0.47 mm; fourth, 0.65 mm.

Diagnosis. The sclerotized ring around the pedicel distinguishes this from most species, the stalked conductor (Fig. 54) from *T. maderae.* This species may be the male of *T. ilvan.*

THYMOITES LOBIFRONS (Simon), new combination
Figures 55-57

Theridion lobifrons Simon, 1894, Histoire Naturelle des Araignées, 1: 542, fig. 558, *nomen nudum;* 1895, Ann. Soc. ent. France, 64: 143. Male holotype from Caracas, [Dist. Fed.], and Colonia Tovar, [Aragua], Venezuela in the Muséum National d'Histoire Naturelle, examined.

Record. Venezuela. Aragua: Rancho Grande, Dec. 1954, ♂ (A. M. Nadler, AMNH).

THYMOITES INCACHACA sp. n.
Figures 58-60

Type. Male holotype from Incachaca, Cochabamba, Bolivia, 31 Aug. 1956 (L. Peña) in the Institut Royal des Sciences Naturelles de Belgique, Brussels. The specific name is a noun in apposition, after the type locality.

Description. Carapace, sternum, legs yellow; abdomen whitish. Carapace of male not modified (without projections in eye region). Anterior median eyes slightly larger than others. Those of male their radius apart, their radius from laterals; posterior eyes their diameter apart. Anterior median eyes of female one diameter apart, their radius from laterals. Posterior median eyes one and one-third diameters apart, one diameter from laterals. Total length of female 1.1 mm. Carapace 0.65 mm long, 0.62 mm wide. First femur, 1.30 mm; patella and tibia, 1.20 mm; metatarsus, 1.04 mm; tarsus, 0.52 mm. Second patella and tibia, 0.93 mm; third, 0.65 mm; fourth, 1.0 mm. Total length of male 1.6 mm. Carapace 0.71 mm long, 0.68 mm wide. First femur, 1.30 mm; patella and tibia, 1.30 mm; metatarsus, 1.10 mm; tarsus, 0.56 mm. Second femur, 1.05 mm; second patella and tibia, 1.05 mm; third, 0.73 mm; fourth, 1.06 mm.

Diagnosis. This species is very close to *T. prolatus* (Levi) and also has fine setae on the ectal side of the palpal cymbium (not shown in Fig. 60). It differs from *T. prolatus* in that the embolus of the male palpus is longer and has a smaller base (Fig. 60), and in that the female connecting ducts (Fig. 58) are longer.

Records. Bolivia. Cochabamba: Incachaca, 31 Aug. 1956, ♀ paratype (L. Peña, ISNB).

THYMOITES SANCTUS (Chamberlin), new combination
Figures 61-63

Garricola sanctus Chamberlin, 1916, Bull. Mus. Comp. Zool., 60: 231, pl. 16, figs. 5, 7, ♀. Female holotype from San Miguel, 2000 m elev., [Ayacucho], Peru, in the Museum of Comparative Zoology, examined.

THYMOITES UNISIGNATUS (Simon)
Figures 64-66

Hypobares unisignatus Simon, 1894, Histoire Naturelle des Araignées, 1: 552, fig. 559. Male holotype from San Esteban, [Carabobo], Venezuela in the Muséum National d'Histoire Naturelle, Paris, examined; 1895, Ann. Soc. ent. France, 64: 144.

The ducts of a female from Colombia are longer. They extend slightly posteriorly, then bend and go anteriorly toward the opening.

Record. Colombia. Magdalena: Aracataca, 21 April 1928, ♀ (P. J. Darlington).

THYMOITES SIMLA (Levi), new combination
Figure 67, 68

Sphyrotinus simla Levi, 1959, Bull. Mus. Comp. Zool., 121: 153, figs. 401-403, ♂. Male holotype from Trinidad, Lesser Antilles, in the American Museum of Natural History.

The genitalia of the female (Figs. 67, 68) are here illustrated for the first time.

Record. Lesser Antilles. Trinidad. Simla near Arima, 26 Feb. 1959, ♀, ♂ (A. M. Nadler, AMNH).

THYMOITES MINNESOTA sp. n.
Figures 74-76

Type. Male holotype from under carton, garbage dump, Albert Lea, Freeborn County, Minnesota, 17 June 1961 (H. Levi) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Description. Carapace yellow with a median longitudinal gray mark. Sternum, legs yellow. Abdomen whitish with two longitudinal rows of black marks on dorsum. Venter with a black mark in epigastric area and a black mark anterior and lateral to spinnerets. A groove between anterior and posterior eyes bearing strong setae (Figs. 74, 76). Eyes subequal in size.

Anterior eyes one and one-half diameters apart, one and one-half diameters from laterals. Posterior eyes separated by slightly more than two diameters. Total length 2.4 mm. Carapace 1.2 mm long, 1.0 mm wide. First femur, 1.7 mm; patella and tibia, 2.1 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm. Second patella and tibia, 1.3 mm; third, 0.8 mm; fourth, 1.3 mm.

Diagnosis. This species is very close to *T. oleatus* (L. Koch) of Siberia (Figs. 69-73) but differs slightly in the palpal sclerites (Fig. 76).

Note. This may well be *Theridion petrense* (Sörensen), of which the male is unknown, and which has been collected in Greenland, Canada and New Hampshire.

Record. Michigan. Marquette Co.: Sauks Head Lake, 2 July 1932. ♂ (R. V. Chamberlin, UU).

THYMOITES CARACASANUS (Simon), new combination

Theridion caracasanus Simon, 1894, Histoire Naturelle des Araignées, 1: 541, 542, fig. 557, ♂, *nomen nudum;* 1895, Ann. Soc. ent. France, 64: 143. Male holotype from Caracas, Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined; 1903, Histoire Naturelle des Araignées, 2: 989.

Hubba insignis O.P.-Cambridge, 1897, Biologia Centrali-Americana, Araneidea, 1: 231, pl. 30, fig. 4, ♂. Male holotype from Guatemala, in the British Museum, probably lost. —Banks, 1929, Bull. Mus. Comp. Zool., 69: 85, figs. 31, 33, 51, ♂.

Sphyrotinus insignis, —Levi, 1959, Bull. Mus. Comp. Zool., 121: 154, figs. 404-410, ♀, ♂.

Note. The holotype of *Theridion caracasanus* was believed lost, but has recently been found in a bottle with unsorted theridiids. Examination of it corroborated Simon's suggestion (1903) that *Hubba insignis* might be a synonym.

Distribution. Guatemala to Venezuela, Ecuador.

Additional records. Ecuador. Pichincha: 35 km NW of Santo Domingo de los Colorados, 22 Dec. 1958, ♀ (A. M. Nadler, AMNH).

THYMOITES CONFRATERNUS (Banks), new combination

Theridium confraternus Banks, 1898, Proc. California Acad. Sci., (3) 1: 236, pl. 14, fig. 11, ♂. Male holotype from Tepic, Mexico, destroyed.

Sphyrotinus confraternus, —Levi, 1959, Bull. Mus. Comp. Zool., 121: 150, fig. 382, ♂.

Sphyrotinus deprus Levi, 1959, *ibid.*, p. 157, figs. 427-428, ♀. Female holotype from Panama Canal Zone, in the Museum of Comparative Zoology, NEW SYNONYMY.

Distribution: Central Mexico to Peru.

Records: Venezuela. Carabobo: San Esteban, 1888, ♀, ♂ (E. Simon, MNHN). *Ecuador: Guayas:* Milagro, July 1943 (H. E., D. L. Frizzell). *El Oro:* Río Jubanes, Pasaje, 23 Oct. 1942. (R. Walls); Quebrada Bejucal, 10 km SW of Arenillas, Oct. 1942 (R. Walls). *Peru. Piura:* Mallares, Río Chira, Dec. 1941 (H. E. Frizzell); 4 km E. of hacienda Meolles, Jan. 1939 (H. E., D. L. Frizzell).

THYMOITES DELICATULUS (Levi), new combination

Sphyrotinus delicatulus Levi, 1959, Bull. Mus. Comp. Zool., 121(3): 146, figs. 360-362, ♀, ♂. Male holotype from Panama Canal Zone in the Museum of Comparative Zoology.

Distribution. Guerrero, Mexico to Venezuela.

Additional record. Venezuela. Carabobo: Valencia, ♀ (MNHN).

THYMOITES EXPULSUS (Gertsch and Mulaik), new combination

Paidisca expulsa, —Levi, 1957, Bull. Amer. Mus. Nat. Hist., 112: 109, figs. 400, 416, 417, ♀, ♂, map 39.

Sphyrotinus expulsus, —Levi, 1959, Bull. Mus. Comp. Zool., 121: 146, figs. 365-366, ♀.

Note. Record from Soledad, Cuba (Levi, 1959), should read from Las Villas province, not Oriente.

Distribution. Southeastern United States, Mexico, probably West Indies.

THYMOITES MADERAE (Gertsch and Archer), new combination

Theridion maderae Gertsch and Archer, 1942, Amer. Mus. Novitates, no. 1171:12, figs. 30, 31, ♀, ♂. Male holotype from Madera Canyon, Santa Rita mtns., Arizona, in the American Museum of Natural History.

Tholocco maderae, —Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30: 16.

Paidisca maderae, —Levi, 1957, Bull. Amer. Mus. Nat. Hist., 112: 106, figs. 397, 398, 420, 421, map 37, ♀, ♂.

Sphyrotinus maderae, —Levi, 1959, Bull. Mus. Comp. Zool., 121: 147, figs. 350-356, ♀, ♂.

Distribution. Arizona to Panama.

Additional record. Honduras. Copán: Copán, sweeping weeds (Roys).

THYMOITES PALLIDUS (Emerton), new combination

Dipoena pallida Emerton, 1913, Trans. Connecticut Acad. Sci., 18: 213, pl. 1, fig. 4, ♂. Male holotype from Buttonwoods, Rhode Island, in the Museum of Comparative Zoology.

Tholloceo pallida, —Archer, 1950, Paper Alabama Mus. Nat. Hist., no 30: 16.

Paidisca pallida, —Levi, 1957, Bull. Amer. Mus. Nat. Hist., 112: 99, figs. 358-366, ♀, ♂; map 35.

Sphyrotinus pallidus, —Levi, 1959, Bull. Mus. Comp. Zool., 121: 158.

Distribution. Massachusetts, Utah, southern California, West Indies to Venezuela.

Additional records. Haiti. Port-au-Prince, 9 Nov. 1959, ♀ (A. M. Nadler, AMNH). *Venezuela. Carabobo.* San Esteban, 1888 (E. Simon, MNHN).

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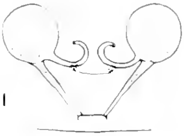
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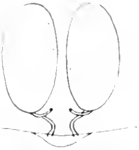
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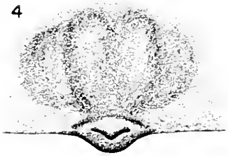
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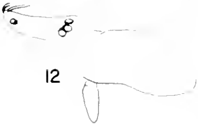
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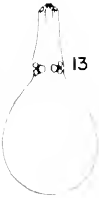
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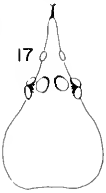
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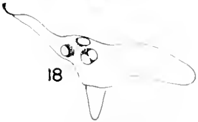
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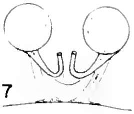
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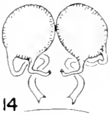
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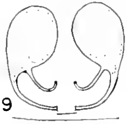
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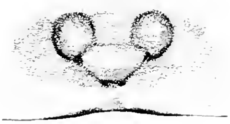
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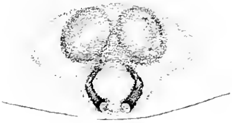
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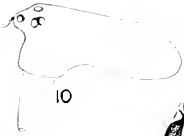
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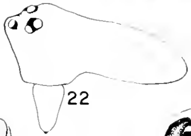
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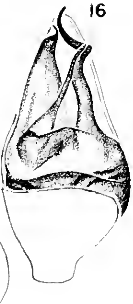
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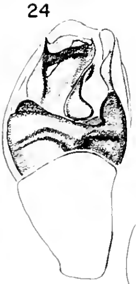
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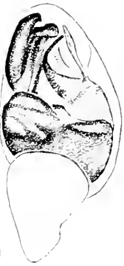
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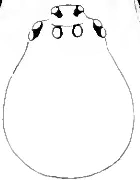
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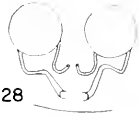
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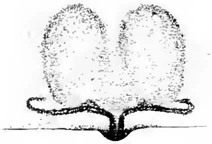
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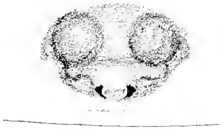
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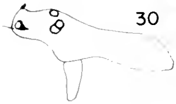
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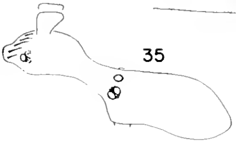
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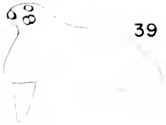
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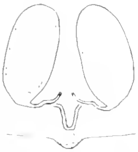
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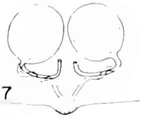
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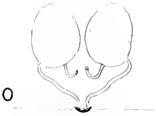
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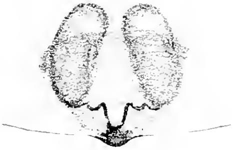
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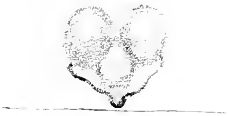
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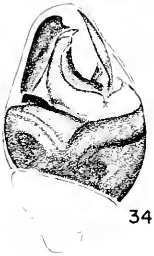
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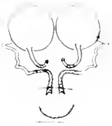

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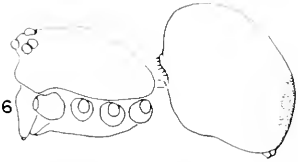

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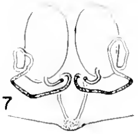

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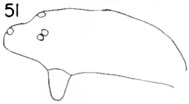

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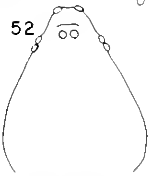

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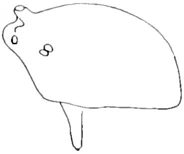

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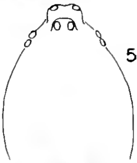

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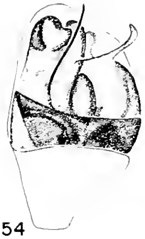

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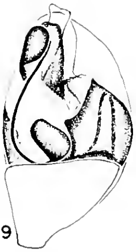

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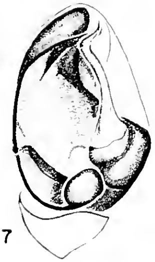

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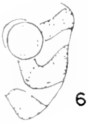
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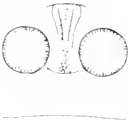
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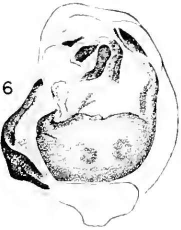
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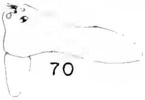
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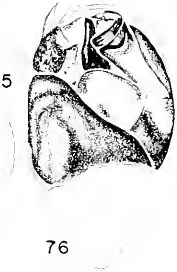
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AN ANNOTATED CHECKLIST AND KEY TO THE ANOLINE LIZARDS OF CUBA

By

Rodolfo Ruibal
Division of Life Sciences
University of California, Riverside

CAMBRIDGE, MASS., U.S.A.
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CONTENTS

INTRODUCTION

In two recent publications (Ruibal and Williams, 1961a, b) the systematics of eight of the Cuban species of the iguanid lizard genus *Anolis* were reviewed in detail. These papers represent the first thorough revision of any of the Cuban anoles since Barbour and Ramsden's "Herpetology of Cuba" published in 1919. The present paper is an attempt to bring up to date our knowledge of the other species of Cuban anoles. In this article no detailed presentation of the morphology and variation of the species will be attempted, but rather a listing of the species with a practical morphological definition, a summary of the distribution, and some indication of the ecology of the various forms. Since Barbour and Ramsden's publication, only three valid new species of Cuban *Anolis* have been described. There has, nevertheless, always existed a certain taxonomic vagueness and biological ignorance about many of the Cuban anoline lizards. This is due in part to Barbour's careless taxonomy and in part to the relatively little herpetological collecting that was done in Cuba until very recently.

A total of twenty-two species of *Anolis* and the monotypic genus *Chamaeleolis* are considered in this checklist. This constitutes the total number of species of anoline lizards on the island and includes the forms previously referred to the genera *Deiroptyx* and *Norops*. Etheridge (1959, unpublished Ph.D. thesis) has reviewed the osteology of *Anolis* and related genera, and has concluded that neither the two species of *Deiroptyx* nor *Norops ophiolepis* merit recognition in separate genera. According to Etheridge, however, the genus *Chamaeleolis*, though related to *Anolis*, appears to be the most distinctive of the anoline genera. Consequently, I follow him in regarding *C. chamaeleonides* as representative of a monotypic genus.

In the checklist that follows, complete synonymies have not been provided. After each species the following is cited: the original description giving the name in the original form, the allocation to the genus *Anolis* (if not placed in that genus originally), Barbour and Ramsden's classification in 1919 and Barbour's in 1937, and any other nomenclatural changes (including the use of trinomials) since 1914. The original type locality is then cited. In some of the cases where no specific type locality was given in the original description, I have restricted the type locality to what appears to be a reasonable site.

A short morphological definition of each species is provided. This contains a description of the color of the animals while alive as well as the more distinctive characters of scalation. In the anoline lizards color and pattern are often a more precise and convenient method of identifying and distinguishing the various species than scalation.

The known distribution of each species is indicated and also the range of any recognized subspecies. The data for the distribution were obtained from specimens in the Museum of Comparative Zoology as well as the American Museum of Natural History, United States National Museum, and University of Michigan Museum of Zoology. Literature citations have also been utilized where I felt that data were reliable or consistent with the museum locality data.

Below are listed the species recognized and the groups that they form. Some species are not included in any group but are placed near the forms that they resemble morphologically.

Genus *Chamaeleolis*

C. chamaeleonides

Genus *Anolis*

A. equestris	
A. porcatus	*carolinensis* group, *sensu lato*
A. allisoni	
A. angusticeps	
A. isolepis	
A. ophiolepis	*homolechis-sagrei* group
A. sagrei	
A. homolechis	
A. mestrei	
A. allogus	
A. ahli	
A. rubribarbus	
A. imias	
A. lucius	*lucius* group
A. argenteolus	
A. loysiana	
A. argillaceus	
A. alutaceus	*alutaceus* group
A. spectrum	
A. cyanopleurus	
A. vermiculatus	*vermiculatus* group
A. bartschi	

The treatment of each species ends with a brief discussion of its ecology under the heading "remarks." Of the twenty-three species included in the checklist, I have observed all but four alive in the field. The species not seen in nature are: *A. bartschi*, *A. vermiculatus*, *A. imias*, and *A. cyanopleurus.*

A key to all twenty-three species is provided. It should be possible with the key and the aid of the additional morphological definitions presented in the text to identify both sexes of all the species. However, the key and descriptions are based primarily on the structure of the adult males; juveniles, as well as female specimens, usually do not demonstrate the diagnostic characters of the species as clearly as the adult males. An attempt has been made to make the key as nearly "natural" as possible and, consequently, the species I believe to be most closely related will key out near each other. In the checklist the related species have also been grouped. However, the sequence of the species in the list or key is not indicative of any supposed relationship.

The species groups are not to be considered definitive. They are based exclusively on the degree of similarity in the external morphology. Consequently, in certain cases, forms that are merely evolutionarily convergent have probably been classed as closely related. The morphological characteristics of these groups are as follows:

carolinensis group, *sensu lato*

Tail round in cross section and the ventrals in transverse rows. Head scales keeled. With the exception of *A. angusticeps* all the species have five scales bordering the rostral posteriorly and have green color phases. All are relatively long-snouted forms.

homolechis-sagrei group

Tail laterally compressed and the ventrals not in transverse rows. Head scales keeled. The supraorbital semicircles are usually not in contact medially. The body scales are small, the head is short snouted, and no green color phase occurs.

lucius group

The supraorbital semicircles are in broad contact medially. The head scales as well as the ventrals are smooth.

alutaceus group

A wide middorsal zone of enlarged keeled scales. Body and limbs elongate.

vermiculatus group

A transverse gular fold, no dewlap present.

COMMON NAMES

The majority of the Cuban species of *Anolis* have no specific common name other than "lagartija" or "lagartijo." This is the name that most Cubans will use when referring to *A. homolechis* or *A. sagrei*, or actually any relatively small lizard. Below are tabulated the names that I have personally heard used or names cited by Barbour and Ramsden (1919) or by Alayo (1955). There is considerable variation between the names used in Oriente and the western end of the island. The same common name may be used for different species in different parts of the island.

caguayo	*A. allisoni* (Camaguey); *A. equestris* (Oriente)
caguayo gris	*C. chamaeleonides* (Oriente)
caguayo verde	*A. equestris* (Oriente)
caiman	*A. vermiculatus*
camaleon	*A. equestris* (western Cuba); *C. chamaeleonides* (Oriente)
chino	*A. sagrei* (Habana)
chipojo	*A. equestris* (Camaguey); *A. porcatus* (Oriente); *C. chamaeleonides*
chipojo blanco	*C. chamaeleonides* (Oriente)
chipojo prieto	*C. chamaeleonides*
chipojo verde	*A. equestris* (Oriente)
coronel	*A. lucius* (Matanzas)
lagartija (o)	*A. sagrei; A. homolechis; A. allogus*, etc.
lagartija de la yerba	*A. ophiolepis*
lagartija de tablado	*A. argenteolus* (Oriente)
lagarto	*A. allisoni* (Camaguey); *A. porcatus*
sabandija	*A. lucius* (Las Villas)

DISTRIBUTION

In Table 1 the distribution of the twenty-three species of Cuban anoline lizards is tabulated. It is evident that all six provinces of the island have a relatively large number of species. Oriente at the extreme eastern end of Cuba has the most varied fauna with 18 of the 23 species represented. Eleven of the species are islandwide in distribution (*sagrei, homolechis, allogus, angusticeps, porcatus, equestris, alutaceus, lucius, loysiana, ophiolepis* and *C. chamaeleonides*). All of the species that are found on Isla de Pinos are islandwide on Cuba. The Isla de Pinos anoline fauna can thus be assumed to be recently derived from Cuba.

TABLE 1

Distribution of anoline species in Cuba

Species	Pinar del Rio	Habana	Matanzas	Las Villas	Camaguey	Oriente	Isla de Pinos
C. chamaeleonides	X	X	X	X	X	X	
A. equestris	X	X	X	X	X	X	X
A. porcatus	X	X	X	X	X	X	X
A. allisoni				X	X	X	
A. angusticeps	X	X	X	X	X	X	X
A. isolepis					X	X	
A. sagrei	X	X	X	X	X	X	X
A. ophiolepis	X	X	X	X	X	X	X
A. homolechis	X	X	X	X	X	X	X
A. allogus	X	X	X ?	X ?	X	X	
A. mestrei	X						
A. ahli				X			
A. rubribarbus						X	
A. imias						X	
A. loysiana	X	X	X	X	X	X	
A. argillaceus		X			X	X	
A. lucius	X	X	X	X	X	X	
A. argenteolus					X	X	
A. alutaceus	X	X	X	X	X	X	X
A. spectrum			X	X			
A. cyanopleurus			?			X	
A. vermiculatus	X						
A. bartschi	X						
Total number of species	14	12	12	14	15	18	7

Within Cuba, the greatest differentiation occurs between the eastern and western ends of the island. Five species are apparently restricted to eastern Cuba (*rubribarbus*, *imias*, *argenteolus*, *isolepis*, and *cyanopleurus*) and three are peculiar to western Cuba (*bartschi*, *vermiculatus* and *mestrei*). A further center of differentiation occurs in central Cuba in the Sierra de Trinidad to which *ahli* and *spectrum* are restricted. The three areas of differentiaton on Cuba are mountainous and each of the areas is isolated from the others by broad regions of flat lowlands. *A. allisoni* has a unique distribution in comparison to all the other Cuban species — it is found in the lowlands of central and eastern Cuba and is limited in Oriente to the flat western portion of the province.

ACCOUNT OF THE SPECIES

CHAMAELEOLIS CHAMAELEONIDES Duméril and Bibron

Anolis chamaeleonides Duméril and Bibron, 1837, p. 168.
Chamaeleolis fernandina Cocteau, 1838, p. 145.
Chamaeleolis chamaeleontides: Barbour, 1914, p. 271; Barbour and Ramsden, 1919, p. 128.
Chamaeleolis chamaeleonides: Barbour, 1937, p. 117.

Type locality. Cuba.

Definition. The dorsum is covered with irregularly dispersed large and small scales. The scales are flat and smooth and the larger scales are circular. There is a middorsal crest composed of a single row of small triangular scales. Head scales are rugose; a very large massive bony head casque overlaps the neck. In the older specimens the orbit is roofed with bone. Two rows of enlarged triangular scales extend from the mental to the anterior border of the dewlap (Fig. 1). There is a small fleshy

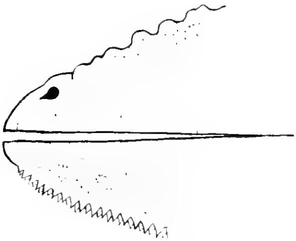

Figure 1. Snout of *C. chamaeleonides* showing the double row of triangular chin scales.

flap above the ear opening. Tail and body are laterally compressed.

The body color is usually grey with streaks and spots of black, brown-tan, and/or dark red. The animal can shift to a dark phase which is brown. The tongue is white and has a black tip. Juveniles lack the head casque but have the same body color as the adults.

There is no sexual dimorphism. Both sexes have a large grey or whitish dewlap; maximum snout to vent length 155 mm.

Distribution. This species is islandwide in its distribution. It has not been reported from Isla de Pinos.

Remarks. It appears that *C. chamaeleonides* is restricted to broadleaf forests and to the shaded portions of the forest. In Oriente it is reputedly common in the coffee groves — these are shaded coffee plantings that grow beneath the canopy of larger trees. Gundlach (1880) observed that it was restricted to forests, and that it was easy to capture. This is true, and its general behavior is chamaeleon-like in its slowness as well as in its ability to move each eye independently. Wilson (1957) has provided a short description of the behavior of a captive specimen. I have caught five of these animals in the forests of Camaguey and Oriente and in every case the lizard failed to make any attempt to escape. The animals are often perched head downward on large tree trunks in the same manner as the small species of *Anolis*.

ANOLIS EQUESTRIS Merrem

Anolis equestris Merrem, 1820, p. 45.
Anolis equestris: Barbour and Ramsden, 1919, p. 133.
Anolis equestris equestris: Barbour and Shreve, 1935, p. 249.
Anolis luteogularis Noble and Hassler, 1935, p. 113.
Anolis equestris luteogularis: Barbour and Shreve, 1935, p. 249.
Anolis equestris luteosignifer Barbour, 1937, p. 118, in error.
Anolis equestris noblei Barbour and Shreve, 1935, p. 250; Barbour, 1937, p. 118.
Anolis equestris hassleri Barbour and Shreve, 1935, p. 251; Barbour, 1937, p. 118.
Anolis equestris thomasi Schwartz, 1958, p. 3.

Type locality. Unknown.

Definition. A middorsal crest of small triangular scales; head scales rugose; body and tail laterally compressed. The canthal crest is thick and bony and there is also a bony nuchal crest and postorbital ridge. There is considerable geographic variation in the size and shape of the scales of the body.

In the light phase the general body color is bright green, and dark brown in the dark phase. The various described subspecies differ in respect to the color pattern of the adults (see Schwartz, 1958). The dewlap varies from yellow or pale orange in Pinar del Rio (*A. equestris luteogularis*) to pink in Oriente (*A. e. noblei*). There is a postorbital light blotch, a labial stripe and a shoulder stripe. These also show geographic variation in coloration and extent.

As has been observed by Barbour and Ramsden (1919) and Alayo (1955), the color pattern of the juveniles is very different from that of the adults. The body of the young specimens of *A. equestris* is marked by four prominent white stripes crossing the body diagonally. There are also prominent white diamonds on the dorsum of the tail.

There is no sexual dimorphism in size or markings. The males and females have large dewlaps; maximum snout to vent length, ♂, 157 mm.

Distribution. The species is found throughout the island and on Isla de Pinos. The distribution of the various subspecies, as mapped by Schwartz (1958), is: *A. e. luteogularis* from Pinar del Rio to Habana; *A. e. equestris* in Habana, Matanzas, Las Villas and western Camaguey; *A. e. thomasi* Camaguey and northwestern Oriente; *A. e. noblei* eastern Oriente; and *A. e. hassleri* on Isla de Pinos.

Remarks. This is the largest of the Cuban anoles, and it is a relatively common and well known species. The giant anole, or "chipojo," is found in agricultural areas, around houses, in gardens, as well as in the forests. It is an aggressive lizard, wary, and difficult to capture. When caught, it is capable of inflicting a painful bite. Many of the Cuban "guajiros" ascribe a poisonous property to the bite of *A. equestris* — this is apparently an old belief since Gundlach (1880) cites this same folklore.

The diet of this species is apparently very varied. It has been observed to eat fruit, tree frogs and insects (Barbour and Ramsden, 1919; Gundlach, 1880). In Camaguey, it has been reportedly observed to feed on birds — nestlings and caged birds. I have observed a half-grown *A. equestris* repeatedly attacked by a "zorzal" (*Minocichla plumbea*) while the lizard slowly backed away along a branch twenty feet from the ground. When threatened, the "chipojo" turns laterally to its attacker and opens its large and cavernous mouth hissing and slowly maneuvering for position.

It lives high in the trees — it is rarely seen less than ten feet from the ground. It sometimes perches head downward on the trunk. The "chipojos" are quick to "freeze" on the approach of man and, consequently, are difficult to observe among the leaves of a tree. They will often slowly circle around a trunk, squirrel-like, keeping just out of sight.

Anolis porcatus Gray

Anolis porcatus Gray, 1840, p. 112.
Anolis porcatus porcatus: Barbour, 1937, p. 119.
Anolis carolinensis porcatus: Oliver, 1948, p. 7.
Anolis porcatus: Ruibal and Williams, 1961a, p. 184.

Type locality. Cuba.

Definition. A long-snouted lizard having the nostril separated from the rostral by three scales. The rostral is bordered posteriorly by five scales (Fig. 2). The ventrals at midbody are in transverse and diagonal rows; ventrals and dorsals slightly keeled; the frontal ridge higher than the canthal ridge in most males. The ear opening is circular, or in some specimens from Pinar del Rio the posterior margin of the ear opening is V-shaped. Body color capable of changing from dark brown to bright green. The color pattern of the body differs between eastern, central, and western populations (see Ruibal and Williams, 1961a). Dewlap reddish or mauve. Females smaller than males and without a dewlap. Maximum snout to vent length, ♂, 73 mm.

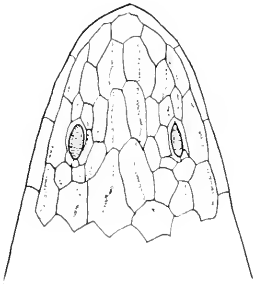

Figure 2. Dorsal view of the tip of the snout of a specimen of *A. porcatus*. The *carolinensis* group characters are shown: five scales bordering the rostral posteriorly and three scales between the rostral and nostril.

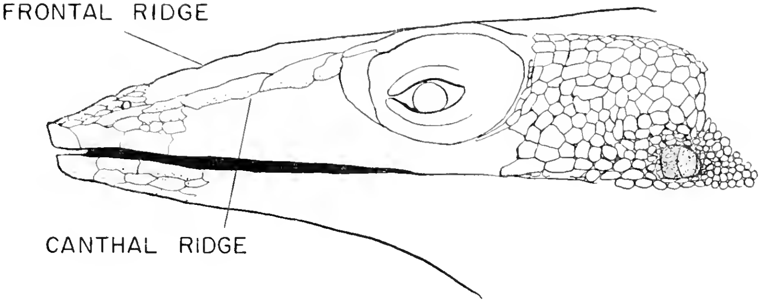

Figure 3. Head of a male *A. porcatus*. The circular ear opening, the high frontal ridges, and the large postorbital scales are shown.

Distribution. This species has an island-wide distribution and is also found on Isla de Pinos. Shaw and Breese (1951) have reported "*A. carolinensis porcatus*" from Honolulu, in the Hawaiian Islands. I have examined some of the specimens on which this report is based. They are males larger than the usual *A. carolinensis* from the southeastern United States. They may represent specimens of *A. porcatus* originally from the area of Habana or *A. carolinensis* from the United States. In any case, their body pattern indicates that the Hawaiian population is not originally derived from Pinar del Rio, central Cuba or eastern Cuba.

The geographic variation of *porcatus* is complex and is discussed in Ruibal and Williams (1961a). *A. porcatus*, as it is recognized, may represent more than one species. With this in mind I have refrained from using the trinomial *A. carolinensis porcatus*. Undoubtedly *A. carolinensis* is closely related to *porcatus;* however, the proper nomenclature will only be clear after the Cuban populations of *porcatus* are better understood.

Remarks. At the western and eastern ends of Cuba, *porcatus* is a very common species found around houses, in gardens, on fences, pastures, and at the outermost edges of the forest. In the provinces of Camaguey and Las Villas (and western Oriente) *porcatus* is sympatric with *A. allisoni* and in these areas it is a relatively rare species.

Collette (1961) has recently provided a detailed study of some aspects of the ecology of *porcatus*. He reports the interesting phenomenon that in Habana during December, specimens of *porcatus* congregate (up to 30 individuals) under palm fronds and exhibit no territoriality.

ANOLIS ALLISONI Barbour

Anolis allisoni Barbour, 1928, p. 58; Ruibal and Williams, 1961a, p. 183.

Type locality. Coxen Hole, Ruatan, Islas de la Bahia, off the north coast of Honduras.

Definition. Similar to *A. porcatus.* However, it differs from that species in having an elongate ear opening, the posterior margin forming a longitudinal depression (Fig. 4). The temporal or postocular scales are smaller than in *A. porcatus.* In males the canthal ridges are higher than the frontal ridges. Males have the head and thorax blue when in the light color phase. Females are all green and show no blue color. Both sexes can change to dark brown. The dewlap is reddish or mauve. Females smaller than males, without a dewlap, and with a light middorsal stripe. Maximum snout to vent length, ♂, 75 mm.

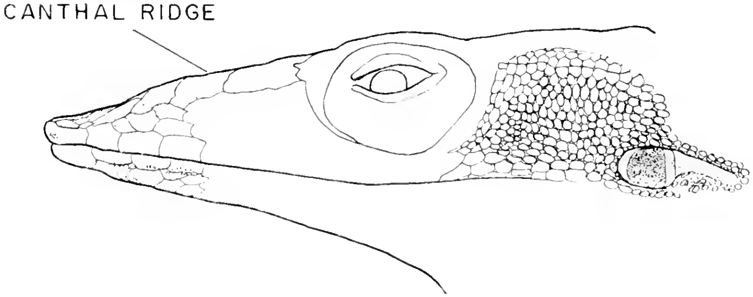

Figure 4. Head of a male *A. allisoni.* The elongate ear opening is shown.

Distribution. Though originally described from the Islas de la Bahia, this is a common species in central Cuba (Las Villas, Camaguey, and western lowland Oriente) and was until recently (Ruibal and Williams, 1961a) confused with and identified as *A. porcatus.* In central Cuba *allisoni* and *porcatus* are sympatric and appear to occupy overlapping ecological niches. Where the two species are sympatric, *allisoni* is always the more abundant species.

Besides being found on Islas de la Bahia, *A. allisoni* has also been collected on Half Moon Cay off the coast of British Honduras.

Remarks. In central Cuba *allisoni* is a very common lizard in the vicinity of human dwellings, in gardens, fence posts, etc. In Camaguey it is very common on the coconut palm and on the royal palm (*Roystonea*). See Ruibal (1961) for further ecological data.

ANOLIS ISOLEPIS COPE

Anolis isolepis Cope, 1861, p. 214; Barbour and Ramsden, 1919; Barbour, 1937, p. 128.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Dorsal surface of head flat; no frontal ridges or depression; head scales large, with wavy longitudinal striations (Fig. 5), flat and generally hexagonal in shape. Single row separating the circumorbital semicircles; five scales bordering the rostral posteriorly; dorsals small, nonimbricate, and may be keeled; the ventrals keeled or smooth and in transverse and diagonal rows; body laterally compressed; tail shows slight lateral compression.

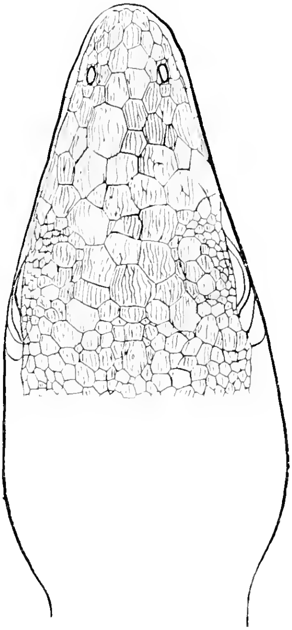

Figure 5. Head scales of *A. isolepis.*

The general body color is bright green. This may change to a purplish shade and dark reticular markings may become evident. Apparently both sexes have a dewlap. The color of the dewlap is apricot yellow, though a female from Camaguey had a yellowish-white dewlap. Males have a thin white line from below the eye to above the forelimb; maximum snout to vent length, ♂, 40 mm.

Distribution. Found only in Oriente and Camaguey.

Remarks. This is probably the rarest of the Cuban anoles. It is a vocal lizard and emits high-pitched squeaks on being captured. Its ability to assume a purple color, its flat head scales, and vocal ability make it one of the most distinctive of the Cuban anoles. It is an aggressive lizard and will bite repeatedly on being captured. This, combined with its relatively large head, laterally compressed body, and green color, cause it to resemble a lilliputian *A. equestris*. This species is restricted to the deep, broadleaf forests of eastern Cuba. The two specimens that I have collected were both obtained at a height of about eight feet in the leaves of the lowest canopy in the forest.

ANOLIS ANGUSTICEPS Hallowell

Anolis angusticeps Hallowell, 1856, p. 228; Barbour and Ramsden, 1919, p. 135.

Anolis angusticeps angusticeps: Barbour, 1937, p. 128; Oliver, 1948, p. 2.

Anolis angusticeps oligaspis: Barbour, 1937, p. 128; Oliver, 1948, p. 2.

Anolis angusticeps chickcharneyi Oliver, 1948, p. 2.

Type locality. Cienfuegos, Las Villas.

Definition. Head scales rugose or striated in males, usually smooth in females; circumorbital semicircles separated by a single row of scales; frontal ridges on the males; usually only two supraoculars. Dorsals and laterals granular, equal in size and smooth; ventrals smooth and in transverse and diagonal rows. Tail round in cross section. Body with slight dorsoventral compression.

General body color can change from greyish to yellowish brown to dark brown. The body pattern is variable and usually shows some longitudinal markings. In the dark phase the body pattern may be obliterated. Ventral surface usually with much yellow pigment and scattered dark markings. The tail may show a cross-banded effect when viewed from above. Three yellow or light spots usually present on the posterior surface of the femoral region. Dewlap peach (yellow-pink) in color. Maximum snout to vent length, ♂, 49.5 mm.

Distribution. Islandwide and on Isla de Pinos. Also in the Bahamas (*A. angusticeps oligaspis*), (*A. angusticeps chickcharneyi*).

Remarks. The characters of scalation distinguishing the subspecies are described by Oliver (1948).

This species is found throughout the island, but it is in most areas a rarely seen form. I have only observed it to be common on small bushes and tree trunks in the pine savanna of the southern coastal plain of Pinar del Rio near Herradura. It is apparently a heliothermic species characteristically found in open habitats: fence posts, rocks, palm trunks, and on *Coccoloba* along the coast (Alayo, 1955). However, Collette (1961) describes it from a forest habitat in Habana.

Barbour (1914) mistakenly described specimens of *allogus* as this species. He corrected this in 1919 in the "Herpetology of Cuba."

ANOLIS OPHIOLEPIS Cope

Anolis (Dracontura) ophiolepis Cope, 1861, p. 211.

Norops ophiolepis: Boulenger, 1885, p. 96; Barbour, 1914, p. 296; Barbour and Ramsden, 1919, p. 164; Barbour, 1937, p. 131.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Head scales longer than wide and each with a single keel; canthus rostralis made up of two scales, the anteriormost scale much the longer; a single suborbital scale; middorsal zone of enlarged, imbricate, lanceolate, keeled scales; lateral scales much smaller but keeled and imbricate; ventrals keeled, pointed, and imbricate and in longitudinal and diagonal rows; limbs with keeled and imbricate scales; tail laterally compressed.

The body color is brown with five longitudinal stripes — a middorsal, two paravertebrals, and two laterals. There is a very small pink to red dewlap that is covered with large keeled scales. Some males have been observed with bluish coloration on the lateral surfaces. Maximum size, ♂, 35 mm.

Distribution. Islandwide and on Isla de Pinos.

Remarks. This is not a rare species; it is merely rarely caught. This is the only truly terrestrial species of the Cuban anoline lizards. This species is found in the pastures and savannas, on the ground, and runs to take refuge in the grass tussocks. I have observed this species at night sleeping on the blades of grass or on the leaves of small bushes.

Contrary to the statement of Barbour (1914, p. 296), this species does possess subdigital lamellae like that of the other species of *Anolis*. The lamellae are fewer in number and relatively narrow.

ANOLIS SAGREI Duméril and Bibron

Anolis sagrei Duméril and Bibron, 1837; Barbour and Ramsden, 1919, p. 143.

Anolis greyi Barbour, 1914, p. 287; Barbour and Ramsden, 1919, p. 144; Barbour, 1937, p. 128.

Anolis bremeri Barbour, 1914, p. 288; Barbour and Ramsden, 1919; Barbour, 1937, p. 129.

Anolis nelsoni Barbour, 1914, p. 287.

Anolis stejnegeri Barbour, 1931, p. 88.

Anolis sagrei sagrei: Barbour, 1937, p. 126; Oliver, 1948, p. 23.

Anolis sagrei ordinatus: Barbour, 1937, p. 126; Oliver, 1948, p. 23.

Anolis sagrei stejnegeri: Oliver, 1948, p. 23; Duellman and Schwartz, 1958, p. 281.

Anolis sagrei mayensis: Smith and Burger, 1949, p. 407.

Type locality. Cuba. It appears reasonable to restrict the type locality to the city of La Habana, Habana.

Definition. In scalation *sagrei* is very similar to *homolechis*. All of the body and head scales are keeled. There is a middorsal zone about six scales wide of slightly enlarged keeled scales, most of which are imbricate. In the other species of the *homolechis* group the middorsal zone of enlarged scales is only about two scales wide, the scales are feebly keeled, and not imbricate. Lateral scales small and granular but showing evidence of keels. Ventrals keeled, imbricate, pointed and in longitudinal and diagonal rows. Supradigital scales multicarinate. Tail laterally compressed and with evidence of a caudal crest in some specimens.

Body color and pattern variable. The general ground color is tan, brown, or very dark brown. The middorsal zone is usually darker than the rest of the body. In some animals the top of the head and top of the neck are reddish brown and the body tan when in the light phase. In the dark phase, yellow vertical stripes and dots are present on the flanks. Dewlap color variable (see below). Maximum body size for Cuban ♂♂, 67 mm. Most adult males are less than 60 mm. (see below).

Distribution. Islandwide and on Isla de Pinos. *A. sagrei* is widely distributed outside of Cuba (Fig. 6): Bahamas (*A. sagrei ordinatus*), Florida (*A. sagrei stejnegeri*), Yucatan, Campeche, British Honduras (*A. sagrei mayensis*), Little Cayman, Jamaica (*A. sagrei sagrei*), and Swan Island (*A. sagrei nelsoni*).

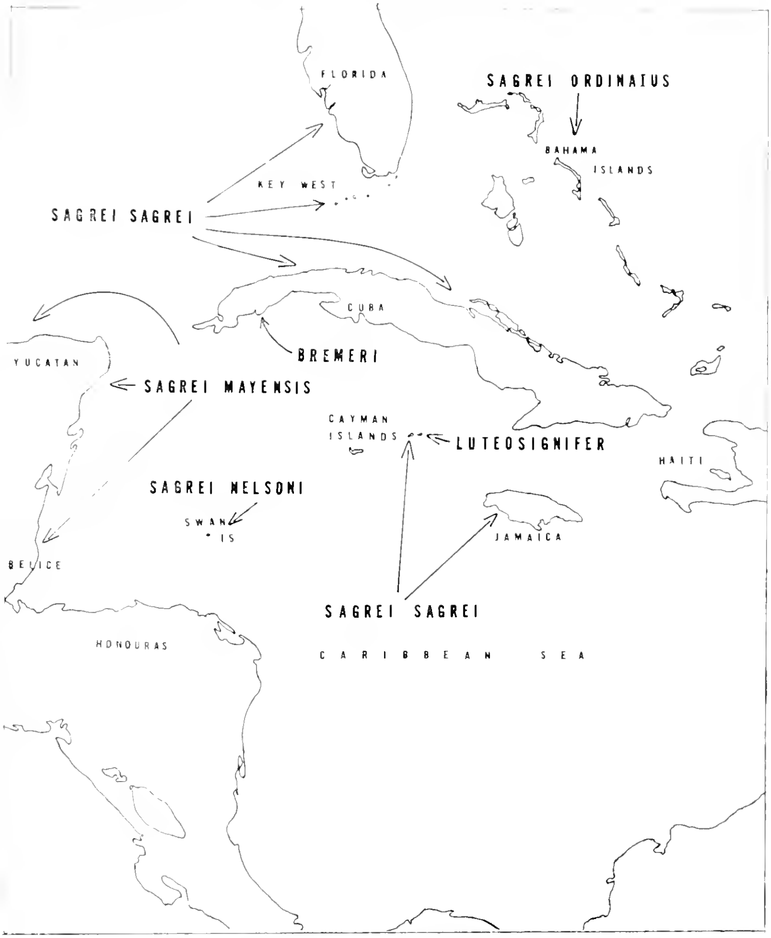

Figure 6. Map of the distribution of *Anolis sagrei* and its close relatives.

Remarks. In 1914 Barbour described *Anolis greyi* from Camaguey as related to *sagrei.* I have examined the type in the Museum of Comparative Zoology and many *sagrei* collected in the vicinity of the city of Camaguey — the type locality of *greyi.* I have found no evidence for considering *greyi* a distinct form and have consequently placed it in the synonymy of *sagrei.*

Barbour also described *Anolis bremeri* from Pinar del Rio as a new species in 1914. This form is readily distinguishable from the "typical" *sagrei*, and furthermore is restricted to the southern coastal plains region of Pinar del Rio. Schwartz (1959) has demonstrated that this area of Cuba has a number of species that are distinct from those on the rest of the island. *A. bremeri* is characterized by having a large and deeply pigmented dewlap. Initially the dewlap appears brownish in color but on closer inspection it is seen to be a deep ochraceous yellow with large deep red (maroon) markings. The margin of the dewlap is the same color as the main portion of the dewlap, and the scales along the margin, as well as on the dewlap itself, are very deeply pigmented with melanin. When the dewlap is folded it appears as a black mark on the throat. The maximum snout to vent length of this lizard is greater than that of most Cuban populations of *sagrei* (see below). This form is morphologically distinct and further study is necessary to determine whether it should be treated as a subspecies or full species.

In 1931 Barbour described another new species, *stejnegeri*, from Key West, Florida, and claimed that it was related to *ahli* and *mestrei* of Cuba. However, Smith (1946), Oliver (1948), and Duellman and Schwartz (1958) have shown that *stejnegeri* is closely related to the Cuban populations of *sagrei* and have indicated this by using the trinominal *A. sagrei stejnegeri*. Duellman and Schwartz studied the Key West and Miami populations of *sagrei* and decided that the two were very similar and should be considered as *A. sagrei stejnegeri*. However, I have been unable to find any valid character to distinguish *sagrei stejnegeri* from the Cuban populations of *sagrei*. Various authors (Smith and Burger, Duellman and Schwartz) have utilized pigmentation and dewlap color of preserved specimens of *s. stejnegeri* and *s. sagrei* to distinguish the two forms. This has led to spurious distinctions being made between Cuban and Floridian populations. The type of preservative (alcohol or formalin) to which specimens are subjected, the time spent in the preservative, and the body color phase at the time of preservation, all affect the color and pattern of the animal. Little reliance can be placed on the dewlap color of a preserved anole. Smith and Burger (1949) describe the dewlap of *sagrei sagrei* as "light brown to light grey." Actually, after preservation, the color of the dewlap in Cuban *sagrei* may range from completely colorless (white) to almost black, and rarely some red pigment will be preserved. In life the dewlap of Cuban *sagrei* shows polymorphism — within the same populations in Camaguey the dewlap may be bright red, dark red, or ochraceous (brownish yellow).

It has been claimed that a further distinction between *stejnegeri* and Cuban *sagrei* is the fact that the midventral throat scales (scales at the edge of the dewlap) are light in the Florida specimens but black or dark grey in Cuban populations. I have been unable to verify this — Cuban specimens usually are devoid of any pigmentation on the throat scales. Some Cuban populations, such as the *bremeri*, do have black throat scales, but this character serves only to distinguish this form from the other Cuban populations.

The distribution of *sagrei* in Florida is discontinuous (Oliver, 1950; Duellman and Schwartz, 1958).[1] Its distribution pattern is that of an introduced species. Thus it exists in ports of entry which trade heavily with Cuba. The Key West population of *sagrei* has probably started to disperse (Duellman and Schwartz record a specimen from Cudjoe Key). However, it is not found in the central keys or in the keys close to the mainland. It is apparently restricted to edificarian habitats. Furthermore, it does not appear to be readily distinguishable in morphology from the Cuban populations of *sagrei*. I am, therefore, of the opinion that *sagrei stejnegeri* does not merit subspecific recognition.

A. sagrei ordinatus from the Bahamas is readily distinguishable from the other populations of *sagrei*. In the Bahaman lizards, in contrast to the other populations, the circumorbital semicircles are usually in contact (Oliver, 1950). Furthermore, the dewlap color and pattern of two specimens of *sagrei ordinatus* that I have seen from Bimini are very distinctive — yellowish or orange-yellow with two or three broken red stripes. Stejneger (1905), in a footnote, describes *sagrei ordinatus* as having, in life, an orange-colored dewlap. However, Rosen (1911) describes specimens from Andros and New Providence as having a yellowish-red dewlap when about 40 mm. in length (snout to vent), and further claims that larger specimens (55-60 mm.), have brown dewlaps with black scales.

Anolis nelsoni Barbour was described in 1914 from Swan Island, and in his description Barbour indicated that it was closely related to *sagrei*. It is distinguished from *sagrei* by having a "deep olive gray" dewlap, a pronounced caudal crest, and a lemon-yellow color to the head. I have here considered it as a subspecies, but it may merit recognition as a full species.

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[1] The localities for *sagrei* in Florida are: St. Petersburg, Tampa, Lake Worth (probably *A. sagrei ordinatus*), Coral Gables, Miami, Key West, Cudjoe Key, and it has recently been found in Fort Myers (Stanley Rand, personal communication).

A. sagrei mayensis was described by Smith and Burger (1949) from Yucatan, and considered distinct from other *sagrei* in its larger size and some supposed scalation and color characters. The majority of specimens of male adult Bahaman and Cuban *sagrei* are between 55 and 60 mm. snout to vent length. The specimens of *bremeri* from Pinar del Rio are larger: the large adult males are over 60 mm. in length (maximum 67 mm.). The mainland *sagrei mayensis* from Mexico and Belice (Neill and Allen, 1959) are about the same size as the Cuban *bremeri*. Specimens of *sagrei nelsoni* from Swan Island are, however, even larger, the males reaching maximum snout to vent length of 70 mm. The Central American, Swan Island, and Mexican mainland forms are thus distinct from the majority of other populations on the basis of size. These various large forms merit further study. The interrelation of these populations is not clear, and their distribution may prove to be much wider than the present data indicate.

As mentioned previously, the dewlap color of the Cuban populations of *sagrei* is a polymorphic character. The majority of specimens have a dewlap of some shade of red — bright red, brick red, orange red, etc. However, within almost every Cuban population of *sagrei* there will be found some specimens with brownish or ochre-colored dewlaps. Off the south coast of Camaguey on the keys of the Laberinto de las Doce Leguas, the majority of the specimens have brown dewlaps. I have observed specimens with these various dewlap colors over prolonged periods of time in captivity. In no instance did the dewlap change color. The dewlap color may become darker or lighter; however, this appears to be a function of the melanophores on the scales and not of the colored skin between the scales.

Throughout most of Cuba *sagrei* is an extremely abundant lizard. It is the characteristic fence-post lizard on farms, in gardens, and in city parks. It is found in savannas, pine, and in coastal regions as well as near the beaches. In the broadleaf forests it is restricted to the large clearings and the open margins of the forest. This species together with *porcatus* and *allisoni* has been the most successful Cuban species to adapt to edificarian habitats (see Ruibal and Williams, 1961a, and Ruibal, 1961, for further discussion of the ecology of *sagrei*).

Alayo (1951) mentions the interesting fact that *sagrei* is not common in patios of Santiago de Cuba. Instead, *argenteolus* together with *porcatus* are the common garden species. This indicates that *sagrei* is a more recent arrival to Oriente than *argenteolus* and that it has not been able to or has not yet entered the edificarian habitat in this area. In Sagua de Tanamo, in northern Oriente, *sagrei* and *homolechis* are found on the same fence posts in farms and gardens. In Camaguey, to the west of Oriente, *homolechis* is never found outside of the forest habitat. *Homolechis* and *sagrei* have identical perching sites but differ in their mean body temperature (Ruibal, *op. cit.*) and presumably would be in direct competition with each other when in the same habitat. The situation at Sagua de Tanamo may thus be a recently created one which will in time yield the same habitat segregation as is exhibited by *sagrei* and *homolechis* in Camaguey.

Anolis luteosignifer Garman from Cayman Brac is a species related but distinct from *sagrei* (Barbour, 1914). I have not studied this species.

ANOLIS HOMOLECHIS Cope

Xiphosurus homolechis Cope, 1864, p. 169.

Anolis homolechis: Boulenger, 1885, p. 28; Barbour, 1914, p. 274; Barbour and Ramsden, 1919, p. 155; Ruibal and Williams, 1961b, p. 228.

Anolis calliurus Ahl, 1924, p. 249.

Anolis muelleri Ahl, 1924, p. 247.

Anolis cubanus Ahl, 1925, p. 87.

Anolis patricius Barbour, 1929, p. 37.

Anolis homolechis homolechis: Barbour, 1937, p. 127; Ruibal and Williams, 1961b, p. 231.

Anolis homolechis patricius: Barbour, 1937, p. 127.

Anolis quadriocellifer Barbour and Ramsden, 1919, p. 158.

Anolis homolechis quadriocellifer: Barbour, 1937, p. 127; Ruibal and Williams, 1961b, p. 231.

Type locality. Here restricted to La Habana, Habana.

Definition. Dorsals small and granular; ventrals smooth and in diagonal and transverse rows. Supraorbital semicircles separated by a single scale; posterior medial margins of the mentals separated by small postmentals (Fig. 7a); supracarpal and supradigital scales usually smooth or with a single keel; a single undivided scale anterior to the nares (Fig. 8); scales along the posterior margin of the interparietal large and sharply demarcated from the dorsals. Tail laterally compressed and with a crest. The general body color ranges from light tan, through reddish brown, brown, and black. Usually there is some evidence of horizontal stripes on the flanks and four dark chevrons on the dorsum. Yellow markings may be present laterally. The dewlap is variable in color (see below). The iris is gold or metallic brown. Maximum snout to vent length, ♂, 56 mm. Females smaller.

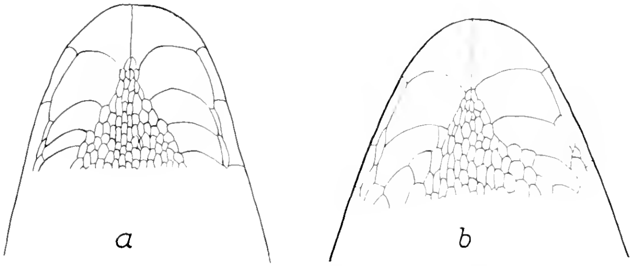

Figure 7. (a) A few small scales separate the posterior medial margins of the mentals in *A. homolechis* and *A. mestrei*. (b) The gulars do not separate the posterior medial margins of the mentals in *A. allogus*, *A. ahli*, *A. rubribarbus*, and *A. imias*.

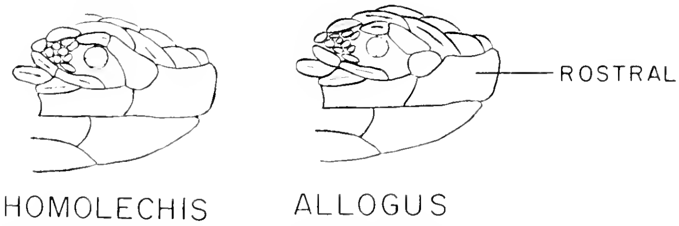

Figure 8. The structure of the scale anterior to the external naris in *A. homolechis* and *A. allogus*.

Distribution. This species has an islandwide distribution and is also found on Isla de Pinos.

Remarks. Numerous populations of this species are characterized by distinctive dewlap colors and patterns — pure white, grey, and yellow. The population of *homolechis* at the extreme western end of the island, Cabo San Antonio, is distinctive enough to warrant recognition as a subspecies, *A. homolechis quadriocellifer* (Barbour and Ramsden). When more data are available, it will be possible to interpret the status of the other color variants of *homolechis*. The morphology and variation of *homolechis* is discussed in detail in Ruibal and Williams (1961b).

A. homolechis quadriocellifer differs from the other populations of *homolechis* in having a yellow dewlap with red stripes and a white margined ocellus above the forelimb.

Throughout the island, *homolechis* is found inhabiting the forest margins and within the more open and sparse forests. It is found from the forests of the Sierra Maestra (from almost 6,000 feet) and the palm-pine savannas of Oriente to the "mogotes" of Pinar del Rio — anywhere that natural forest vegetation has survived. In some localities — Sagua de Tanamo, Oriente — this species has also adapted to the man-made plant associations in gardens, farms, and pastures. The thermal ecology of this species is discussed in Ruibal (1961).

ANOLIS MESTREI Barbour and Ramsden

Anolis mestrei Barbour and Ramsden, 1916, p. 19; Barbour and Ramsden, 1919, p. 161; Ruibal and Williams, 1961b, p. 236.

Anolis allogus mestrei: Barbour, 1937, p. 120.

Type locality. Valle de Luis Lazo, Pinar del Rio.

Definition. The scalation of this species is similar to that of *homolechis* except that the posterior supraciliaries of *mestrei* are small and granular while those of *homolechis* are larger, elongate, and keeled. The ear of *mestrei* is round while that of *homolechis* is higher than wide. The body color ranges from dark to light grey and usually has a greenish cast. Yellow and orange spots are present over the body. The dewlap has a dark red basal spot with two orange-yellow stripes and a broad white margin. The iris is yellowish. Maximum snout to vent length, ♂, 55 mm. Females smaller.

Distribution. Restricted to the broadleaf forests of the limestone "mogotes" and mountains of the Sierra de los Organos and the Sierra del Rosario in Pinar del Rio.

Remarks. This species is sympatric with *allogus* and *homolechis*, species to which it is closely related. *Mestrei* appears to be more terrestrial than either of the other species, and it is usually found on the limestone rocks rather than on tree trunks. It appears to be restricted to the shady portions of the forest.

ANOLIS ALLOGUS Barbour and Ramsden

Anolis allogus Barbour and Ramsden, 1919, p. 159; Ruibal and Williams, 1961b, p. 215.

Anolis abatus Ahl, 1924, p. 248.

Anolis allogus allogus: Barbour, 1937, p. 120.

Type locality. Bueycito, S. of Bayamo, Oriente.

Definition. Dorsals small and granular. Ventrals smooth and in diagonal or transverse rows. Supraorbital semicircles separated by two scales; a transverse suture between the mentals and the postmentals (Fig. 7b); supracarpal and supradigital scales multicarinate and mucronate; scale anterior to the naris divided by a horizontal suture (Fig. 8); scales around the posterior margin of the interparietal small and grading into the dorsals. Tail laterally compressed and usually with a crest. Body color reddish-brown with yellow reticulations. Dewlap ground color ranging from yellow to apricot and with three or four reddish stripes and a white margin. Iris blue. Maximum snout to vent length, ♂, 58 mm. Females smaller.

Distribution. The species is probably islandwide in its distribution; however, it is limited to the deep broadleaf forests and has never been found outside of the forest. It has not been recorded on Isla de Pinos.

There are no records of this species from Matanzas, or Las Villas. However, this is probably the result of the destruction of the natural habitat of this species by agriculture (Ruibal and Williams, 1961b).

Remarks. This species shows little geographic variation outside of minor color and pattern differences of the dewlap.

In the broadleaf forests of Camaguey, Oriente, and Pinar del Rio, this is a common and easily seen lizard. The males perch a few feet from the ground on the trunks of the smaller trees. The dewlap is large and shows up brilliantly against the dark shaded background of the forest. It is a shade-dwelling species and in most parts of its range it is sympatric with *A. lucius.* The thermal ecology of *allogus* and *lucius* is discussed in Ruibal (1961).

ANOLIS AHLI Barbour

Anolis ahli Barbour, 1925, p. 168; Ruibal and Williams, 1961b, p. 221.
Anolis allogus ahli: Barbour, 1937, p. 120.

Type locality. Sierra de Trinidad, Las Villas.

Definition. Scalation like that of *A. allogus.* The males of this species appear to lack a caudal crest. The body color usually shows a greenish cast and the general color may shift from tan to dark brown. A common body pattern is a "salt and pepper" speckling. The dewlap has a large red spot that is surrounded by a broad yellow-white area. The iris is blue. Maximum snout to vent length, ♂, 58 mm. Females smaller.

Distribution. Known only from the Sierra de Trinidad in Las Villas.

Remarks. This is a forest-dwelling species found in the deeply shaded portions of the forest.

ANOLIS RUBRIBARBUS Barbour and Ramsden

Anolis rubribarbus Barbour and Ramsden, 1919, p. 156; Ruibal and Williams, 1961b, p. 222.

Anolis homolechis rubribarbus: Barbour, 1937, p. 127.

Type locality. Puerto de Cananova, near Sagua de Tanamo, Oriente.

Definition. The scalation of this species is like that of *A. allogus* except that the scale anterior to the naris is usually single in *A. rubribarbus*. There is a well developed caudal crest. The body color is usually grey, ranging from a pale grey to almost black. Yellow spots and reticulations may be present on the flanks. The body may show various color and pattern phases ranging from a "salt and pepper" pattern in light grey to a pattern of blackish vertical bands separated by yellowish or grey bands. The dewlap has 4-5 thin red lines on a deep yellow ground color and a white margin. The iris is blue grey. Maximum snout to vent length, ♂, 62 mm. Females smaller.

Distribution. This species is known from the north coast of Oriente from Cananova to Punta Gorda east of Moa. It may extend further east.

Remarks. Like *ahli* this species is very closely related to *allogus*, has a limited distribution, and is allopatric to *allogus*. More detailed information about the populations of *allogus* on the north coast of Oriente will demonstrate whether *rubribarbus* needs to be considered as a subspecies of *allogus*.

This is a forest dwelling species.

ANOLIS IMIAS Ruibal and Williams

Anolis imias Ruibal and Williams, 1961b, p. 237.

Type locality. Imias, south coast of Oriente.

Definition. In scalation similar to *homolechis* but differing in having smooth brachial scales and smooth supraocular scales, and having the postmentals bordering the mental along a transverse border. This species is known only from the type and paratype. The only thing known about its color in life is that the dewlap is brown. Maximum snout to vent length, ♂, 65 mm. Females smaller.

Remarks. This species is known only from the type and paratype. It is the only new species of Cuban *Anolis* described since the publication of Barbour's 1937 checklist.

ANOLIS LUCIUS Duméril and Bibron

Anolis lucius Duméril and Bibron, 1837, p. 105; Barbour and Ramsden, 1919, p. 138; Barbour, 1937, p. 129.

Type locality. Cuba.

Definition. Smooth head scales; circumorbital semicircles in broad contact medially (Fig. 9). Dorsals small and smooth. Ventrals smooth and in transverse and diagonal rows. Three transparent palpebral scales on the lower eyelid. Supraocular scales irregular in shape (not transversely enlarged). Ear opening large and the tympanum completely exposed and the extracolumella visible (Fig. 10).

The overall body color of central and eastern specimens varies from a semi-transparent faint greenish blue to a yellowish tan. The venter is metallic yellow. Four middorsal reddish blotches are sometimes evident. The head and neck is marked by well-defined light stripes that make a chevron-like pattern on the nuchal area. The parietal eye is in the center of a light spot.

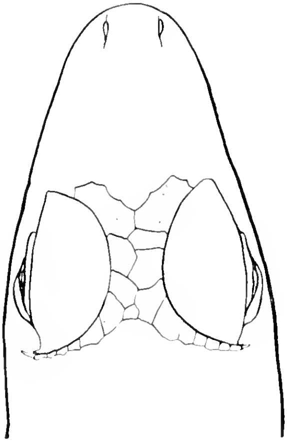

Figure 9. The supraorbital semicircles are in broad contact medially in *loysiana*, *argillaceus*, *lucius*, and *argenteolus*.

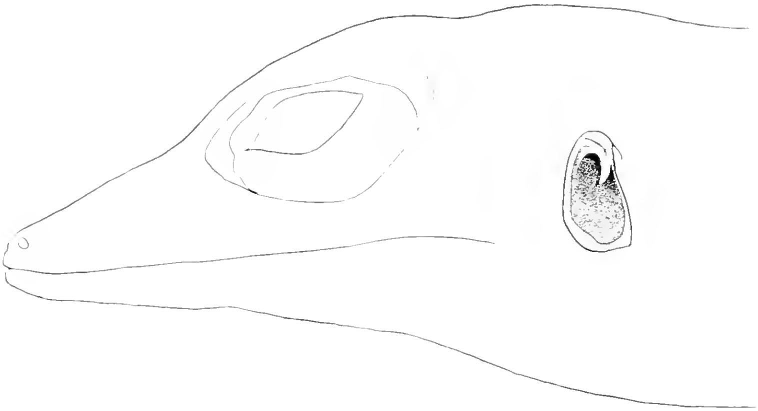

Figure 10. The tympanum of *A. lucius* showing a prominent extra-columella.

The iris is brown. The few specimens of *lucius* from Pinar del Rio that I have observed alive had an overall brilliant blue color and no red dorsal spots.

Dewlap yellowish at the base. A broad white margin having two or three grey stripes. Maximum snout to vent length, ♂, 66 mm. Females smaller than males.

Distribution. From Pinar del Rio to western Oriente. It is apparently absent from the mountainous eastern and southern portions of Oriente. Confined to forested areas.

Remarks. This species has previously been considered to be restricted to limestone areas, and it was thought to select caves and cliffs as its preferred habitat (Barbour and Ramsden, 1919). In lowland forests in Camaguey, where no limestone exists, *lucius* inhabits very large tree trunks (such as the strangler fig, *Ficus*). In the forests of Oriente, Pinar del Rio, Camaguey, and Las Villas, I have seen specimens of this species on every "jagüey" (as the strangler fig is known in Cuba) examined. Apparently *lucius* is specialized in that it is a shade-preferring form (Ruibal, 1961) limited to a substratum of large and intricate surfaces. This type of substratum preference is correlated with the gecko-like, communal egg-laying habits of the species (Dunn, 1926; Hardy, 1957). On limestone caves and cliffs, large numbers of eggs (over 100) are attached to the roofs of certain crevices and hollows in the rock. In the caves, this is usually in the twilight zone of the cave. On the strangler figs, the eggs are deposited in the large interstices made by the contorted growth of the fig, or in the hollows created by the rotting of the parasitized tree. These sites are thus ecologically equivalent to the limestone caves. In Las Villas I have observed *lucius* together with *Tarentola americana* in the hollow of a large mamoncillo (*Melicocca bijuga*). Allen and Neill (1957) report finding these two lizards sympatrically and comment on the gecko-like habits of *A. lucius*.

This species is probably the most vocal of the Cuban anoles. They not only will squeak when captured but can, on occasion, be heard to make the same sound while scurrying about on the vertical surfaces at the entrance of caves. As Barbour and Ramsden (1919) have observed, Cuban peasants ascribe the call of various species of *Eleutherodactylus* to *lucius*.

A further specialization demonstrated by *lucius* is the presence of transparent palpebral scales on the lower eyelid. These scales besides being transparent are bordered by a black, but translucent pigment. Williams and Hecht (1955) have interpreted this condition as an example of "sunglasses": the lizard normally dwelling in deeply shaded areas and protected by its pigmented palpebral scales when it ventures into brightly illuminated areas — the palpebrals acting to reduce the intensity of the light.

Smith and Willis (1955) have described a peculiar variation found in some populations of *lucius:* in the females and juveniles, the tail is always round in cross section, but in the males the tail may vary from round to laterally compressed.

ANOLIS ARGENTEOLUS Cope

Anolis argenteolus Cope, 1861, p. 213; Barbour and Ramsden, 1919, p. 140; Barbour, 1937, p. 129.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Similar to *lucius* in scalation. There are two transparent palpebrals on the lower eyelid of *argenteolus*, while *lucius* usually has three palpebrals. In habitus the specimens of *argenteolus* are thinner and longer limbed than *lucius*, and are also smaller in size.

The general body color of *argenteolus* is brown and lacks the striped head and neck region so characteristic of *lucius*. The body is reticulated with yellow and/or grey. The dewlap in male *argenteolus* has a basal area that is grey or brown while the rest of the dewlap is white. Maximum snout to vent length, ♂, 50 mm. Females smaller.

Distribution. Limited to Oriente and southeastern Camaguey. The Camaguey specimens (M.C.Z.) were collected northeast of Santa Cruz del Sur.

Remarks. I have always observed this species in the shade in broadleaf forests. It inhabits large as well as small tree trunks and does not show the specialization for large surfaces that *lucius* demonstrates. Barbour and Ramsden claim that it is partial to limestone. This is probably true, but I have never had the opportunity to collect *argenteolus* in habitats containing limestone exposures. Barbour and Ramsden as well as Alayo report the species to be common around houses in Santiago. As Barbour and Ramsden have observed, this species appears to be the only shade-dwelling form that has successfully invaded edificarian habitats. Alayo also reports it from forests on the lower portions of the tree trunks.

The report (Cooper, 1958) of *argenteolus* from the *Coccoloba* association on the beach along the south coast of Oriente appears to be in error. The species he observed was probably *angusticeps*.

ANOLIS LOYSIANA Duméril and Bibron

Anolis loysiana: Duméril and Bibron, 1837, p. 100; Boulenger, 1885, p. 42; Barbour and Ramsden, 1919, p. 146; Barbour, 1937, p. 129.
Acantholis loysiana: Cocteau, 1838, p. 141.

Type locality. Cuba.

Definition. Similar to *argillaceus.* The most prominent difference is the presence of large spine-like scales on the body and limbs of *loysiana.* The dorsals between the spine-like scales are small, flat, and smooth. The two species are alike in other scale characters. In *loysiana* the tail is round in cross section and the body is slightly compressed dorsoventrally.

In coloration, *loysiana* has the same greyish to brownish coloring with dark reticular markings. However, it lacks the longitudinal striping often seen in *argillaceus.* When on a grey-barked tree, specimens of *loysiana* are cryptic: the ashgrey color, reticulations, and spines camouflaging the animals. In Camaguey the dewlap color varied from a tan color to pink-tan to pale orange-red. Maximum snout to vent length, ♂, 40 mm. Females smaller.

Distribution. Islandwide. Not recorded from Isla de Pinos.

Remarks. Gundlach (1880) reported this to be an islandwide species and a forest-dwelling form. In Camaguey, where I have collected *loysiana*, it has always been on the trunk of trees in relatively open savanna-like clearings. It has been in areas formerly occupied by forest but partially cleared by agriculture. At the one locality in Camaguey where the species was relatively abundant (15 km. SW of Camaguey), it was usually on the trunk of "guamas" (*Lonchocarpus* sp.).

ANOLIS ARGILLACEUS Cope

Anolis argillaceus Cope, 1862, p. 176; Barbour and Ramsden, 1919, p. 147; Barbour, 1937, p. 129.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Head scales smooth; supraorbital semicircles in broad contact medially; 3 transversely enlarged supraoculars (Fig. 11); ear opening small and the extracolumella not visible. Dorsals smooth, small, and flat. Ventrals smooth with a rounded posterior margin and in diagonal rows; some of the ventrals in longitudinal rows on the anterior part of the venter, others in vague transverse rows. Tail laterally compressed. Males with very large hemipenes (the hemipenial swelling in the tail extending posteriorly to the same level as the heel of the hind foot when adpressed against the tail). Body laterally compressed.

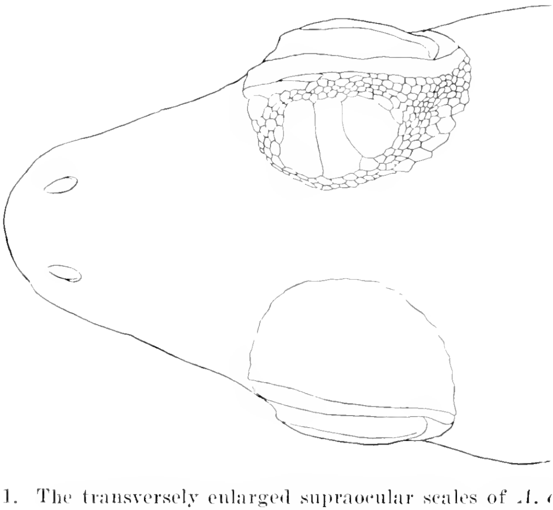

Figure 11. The transversely enlarged supraocular scales of *A. argillaceus*.

General body color greyish. Reticular and longitudinal dark markings over the body. In the light phase the animal is a very pale grey while in the dark phase it becomes brownish. The dewlap is usually very large. In Camaguey, the dewlap colors are variable — I have seen specimens with yellow, orange-yellow, and red dewlaps. Maximum snout to vent length, ♂, 45 mm. Females smaller.

Distribution. Known from Oriente and the eastern half of Camaguey and recently from a single specimen reported from Habana (Collette, 1961).

Remarks. In Camaguey I have found this species to be rare. When collected, it has always been in open savanna-like habitats, the animals being found on the trunks of relatively large trees. The species is apparently very common in some parts of Oriente. Alayo (1951) reports that it is a common fence-post lizard in Santiago; Barbour and Ramsden reported it from coffee groves and on "guásimas" (*Guazuma ulmifolia*) in Oriente. A number of the Camaguey specimens that I collected were also found on the trunks of "guásimas."

Most of the specimens of *argillaceus* show homogeneous dorsal and lateral scales. However, on some specimens a careful examination of the scales under a microscope shows the presence of a few isolated and scattered enlarged scales. These scales are reminiscent of the spine-like scales of *loysiana*. The two species are obviously closely related and are apparently sympatric in Camaguey and Oriente. On one occasion a specimen of *argillaceus* was captured in Camaguey on the same tree trunk that contained a specimen of *loysiana*. In Camaguey both species were always found in comparable ecological situations.

ANOLIS ALUTACEUS Cope

Anolis alutaceus Cope, 1861, p. 212; Barbour and Ramsden, 1919, p. 153.
Anolis clivicolus Barbour and Shreve, 1935, p. 251.
Anolis alutaceus alutaceus: Barbour, 1937, p. 124.
Anolis alutaceus clivicolus: Barbour, 1937, p. 124.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Head scales with longitudinal as well as transverse rugosities (Fig. 12); single row (*a. alutaceus*) or two rows (*a. clivicolus*) of scales between the supraorbital semicircles; supraorbitals separated from the supraorbital semicircle by a row of small scales. A wide middorsal zone of enlarged, keeled scales in longitudinal rows and having the posterior margins truncate (Fig. 13). Ventrals smooth. Limb scales multicarinate. Body laterally compressed and tail round in cross section.

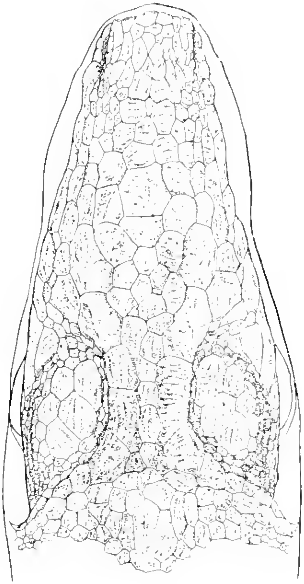

Figure 12. Head scales of *A. alutaceus alutaceus.*

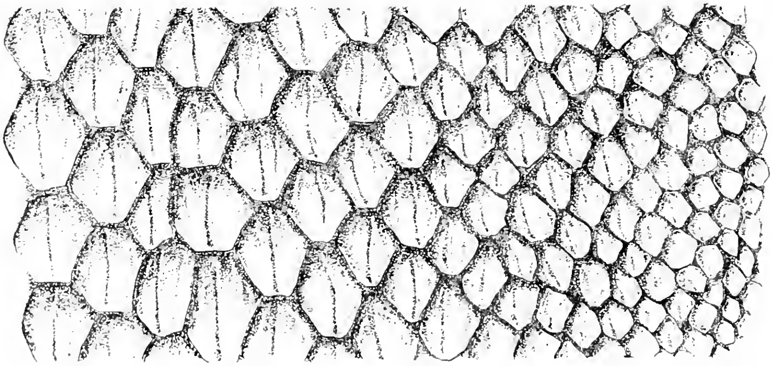

Figure 13. The dorsal and right lateral scales of *A. alutaceus cliricolus.* The dorsals are in longitudinal rows, have truncate posterior margins and are larger than the lateral scales.

In *alutaceus* the general body color is light or dark brown with no particularly prominent pattern; tail with dark crossbars; dewlap large and yellow; iris bright blue; a white stripe from below the eye to the ear is usually prominent. No color data are available from living specimens of *a. clivicolus*. The pattern of preserved specimens appears to resemble *a. alutaceus* except that no prominent white stripe is evident below the eye. Maximum snout to vent length: *a. alutaceus*, ♂, 36 mm.; *a. clivicolus*, ♂, 45 mm.

Distribution. Islandwide and Isla de Pinos. The subspecies *a. clivicolus* is restricted to the higher elevations (4,000 feet) of the Sierra Maestra of Oriente.

Remarks. In 1937 Barbour made *clivicolus* a subspecies of *alutaceus* with the single comment that the two forms seemed to intergrade. The two forms can be distinguished by the characters cited above in the definition and also, and probably most readily, by the body proportions. In *a. alutaceus* the body is thin, the limbs very elongate, the tail remarkably thin, and the head long snouted. In contrast, specimens of *a. clivicolus* are larger, more robust, with a less obvious elongation of the appendages or head. In the series of specimens from the Sierra Maestra (M.C.Z.) all intermediate conditions between *a. alutaceus* and *a. clivicolus* are found. Actually *a. clivicolus* is the only known altitudinal race of lizards in Cuba. This is in contrast to the situation in Puerto Rico where a number of species are segregated by altitudinal difference in habitat (Rand, MS).

A. a. alutaceus is a common lizard in the broadleaf forests of lowland Oriente, and the rest of the island. It is characteristically found on small tree trunks, stems, twigs, grass, and even rocks. The lizards are usually perched about a foot from the ground. In its movement it often progresses by leaping rather than climbing or running. Nothing is known of the ecology of *a. clivicolus*. Collette (1961) describes the ecology of *a. alutaceus* from Habana.

Williams (1961) discusses the evolutionary relationship of the Cuban "grass" anoles (*alutaceus*, *cyanopleurus*, and *spectrum*) with the grass anoles of Hispaniola and Puerto Rico.

ANOLIS SPECTRUM Peters

Anolis spectrum Peters, 1863, p. 136; Barbour and Ramsden, 1919, p. 149; Barbour, 1937, p. 124.

Type locality. Vicinity of Matanzas and Cardenas, Matanzas.

Definition. Head scales with longitudinal striations; supraocular scales medially in direct contact with the supraocular semicircles (Fig. 14); occipitals, nuchals and dorsals confluent, showing no demarcation. A middorsal zone of enlarged scales; the dorsals are keeled and as wide as long and do not have a truncate posterior margin (Fig .15). Laterals smaller, keeled, and imbricate. Ventrals in longitudinal rows that converge toward the midventral line. Limbs with multicarinate scales. Tail round in cross section.

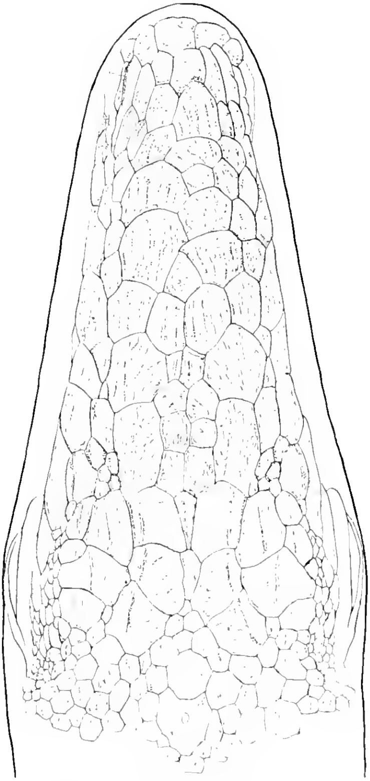

Figure 14. The head scales of *A. spectrum.* The supraocular scales are in direct contact with the supraorbital semicircles.

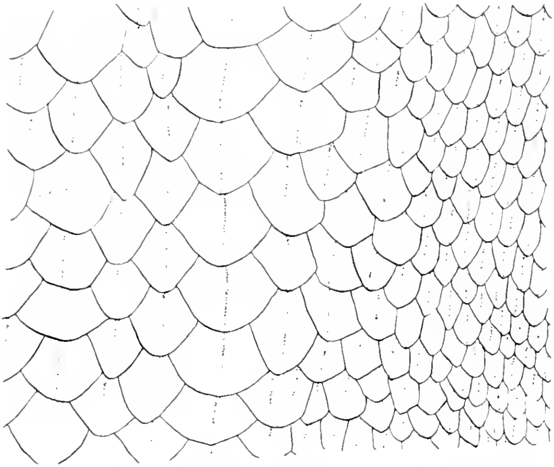

Figure 15. The dorsal and right lateral scales of *A. spectrum*. The lateral scales are imbricate and the dorsals are as wide as long and are not truncate.

In males, the middorsal area is a yellow-cream color, and the lateral surfaces mahogany (red-brown); venter reddish with a midventral streak; chin yellow. Dewlap yellow. In females the middorsal zone is reddish-brown, the lateral surfaces brown, and the venter reddish with a yellow midventral streak from throat to vent. Maximum snout to vent length, ♂, 36 mm. Females smaller.

Distribution. Currently known only from the Sierra de Trinidad in Las Villas. However, the type specimens collected by Gundlach were from Matanzas. The destruction of the forest in most of lowland central Cuba may have destroyed this species in all areas outside of the Sierra de Trinidad.

Remarks. This species is restricted to the broadleaf forests and is found on grass and twigs, along the paths in the forest floor and the dry stream beds. Gundlach recorded it in the forests in the vicinity of Matanzas and Cardenas. Dunn (1926) claimed *spectrum* was rarer in the lowland forests than in the mountain forests of the Sierra de Trinidad. Dunn claimed that in the mountains *spectrum* was as common as *alutaceus*. My collecting experiences in the Sierra de Trinidad confirm Dunn in that both species are equally abundant.

Schwartz and Ogren (1956) record *spectrum* from Santiago de Cuba. This is probably in error.

ANOLIS CYANOPLEURUS Cope

Anolis (Dracontura) cyanopleurus Cope, 1861, p. 211.

Anolis cyanopleurus: Boulenger, 1885, p. 69; Barbour and Ramsden, 1919, p. 150; Barbour, 1937, p. 124.

Type locality. Cafetal Monte Verde, Sierra de Yateras, east of the Bahia de Guantanamo, Oriente.

Definition. Head scales with longitudinal striations (Fig. 16); supraoculars separated from the supraorbital semicircles by a row of small scales. A zone of enlarged, keeled scales in longitudinal rows and having a posterior margin truncate. Dorsals often multicarinate rather than with a single keel. Laterals small, not imbricate. Limb scales multicarinate. Ventrals keeled, the anterior ventrals in longitudinal and diagonal rows, the posterior scales in vague longitudinal or transverse rows. Tail laterally compressed.

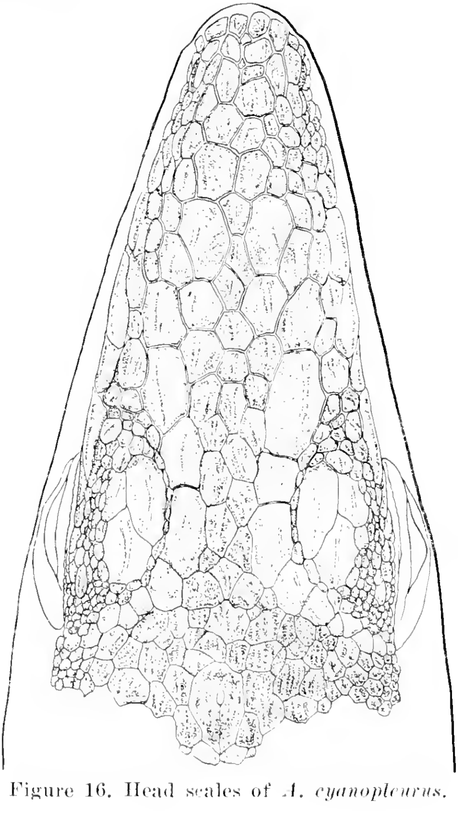

Figure 16. Head scales of *A. cyanopleurus.*

Gundlach (1880) describes a living specimen from the Sierra Maestra as having a blue iris and a general body color of olive-brown. Barbour and Ramsden (1919) describe what may be a living specimen as having a russet dorsal zone and green lateral surfaces and a white belly. They describe the dewlap as ashen-grey in color. Maximum snout to vent length, ♂, 39 mm. Females smaller.

Distribution. Apparently restricted to the mountainous areas of southern Oriente. However, Gundlach records obtaining it in the Sierra Maestra as well as near Cardenas in the province of Matanzas. Since Gundlach knew *spectrum* and *alutaceus*, it seems doubtful that he would confuse a specimen of one of these species with *cyanopleurus*. His description of the color of the Matanzas specimen also fits the Barbour and Ramsden description of *cyanopleurus* since Gundlach cites the animals as having greyish-green and bluish coloration — neither of these colors being found in *alutaceus* or *spectrum*. It is, therefore, very possible that the distribution of *cyanopleurus* is (or was) not limited to Oriente.

Remarks. Gundlach records this as a forest species. Alayo describes it as inhabiting grass. It would appear that *cyanopleurus* is ecologically an eastern equivalent of *spectrum* — a grass anole of the forest floor.

ANOLIS VERMICULATUS Duméril and Bibron

Anolis vermiculatus Duméril and Bibron, 1837, p. 128.

Deiroptyx vermiculatus: Fitzinger, 1843, p. 17; Barbour and Ramsden, 1919, p. 130; Barbour, 1937, p. 117.

Type locality. Restricted to Viñales, Pinar del Rio.

Definition. Two rows of scales between the supraocular semicircles; head scales keeled; suborbitals separated from the supralabials by a row of small scales (Fig. 17); frontal and canthal ridges; pineal in the center of a large light-colored scale. Dorsals keeled and smaller than the ventrals. Ventrals keeled and in diagonal and transverse rows. Digital pads narrow; tail laterally compressed; no dewlap; a transverse gular fold.

Adults variegated in olive green and bluish green. The gular fold is yellowish; iris, blue. The color data are from a living specimen described in detail by Gundlach (1880). Maximum snout to vent length, ♂, 122 mm. Females smaller than the males.

Distribution. Reported only from Pinar del Rio.

Remarks. This large lizard (it is exceeded in size only by *A. equestris* and *C. chamaeleonides*) has the distinction of being a truly aquatic species. Gundlach (*op. cit.*) describes it as inhabiting the trunks and branches of trees along the edges of streams and leaping into the water and hiding under rocks and roots at the bottom of the stream. Neill and Allen (1957) observed the species in its native habitat and described its vocal ability; it produces squeaks and mews. It is apparently an insectivorous species and feeds out of the water. *A. vermiculatus*, like the Central American *Basiliscus*, can also run on its hind legs on the surface of the water.

Most of the localities from which *vermiculatus* has been reported are from the western end of Pinar del Rio. However, Gundlach reports the species from near Taco-Taco which is in the eastern half of the province.

The specimen described by Barbour and Ramsden is an immature male (snout to vent, 70 mm.) and their color description does not fit that of Gundlach, nor the colors of the larger preserved specimens I have examined.

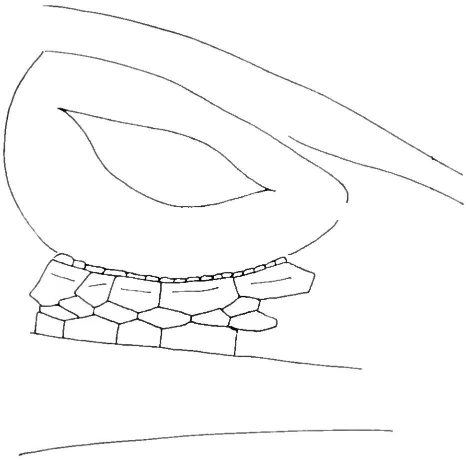

Figure 17. Suborbital scales of *A. vermiculatus*.

ANOLIS BARTSCHI (Cochran)

Deiroptyx bartschi Cochran, 1928, p. 169; Barbour, 1937, p. 118.

Type locality. Baños de San Vicente, Pinar del Rio, Cuba.

Definition. One row of scales between the supraocular semicircles; scales of the snout smooth; suborbitals in contact with supralabials (Fig. 18). Dorsals and ventrals smooth, and the ventrals in transverse and diagonal rows. Digital pad large and dilated. Tail round in cross section. Ear opening very large, the extracolumella visible. No dewlap. A transverse gular fold.

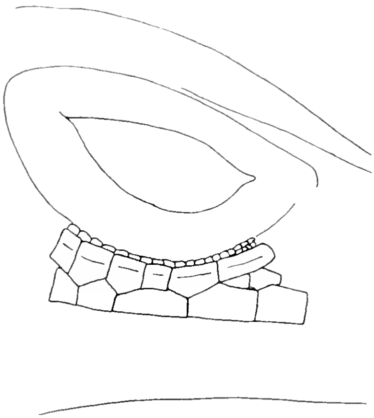

Figure 18. Suborbital scales of *A. bartschi.*

Cochran describes the male type as having yellow vertical wavy stripes edged with black on the sides and a green dorsum, the venter straw yellow and the gular fold deeper yellow. Maximum snout to vent length, ♂, 76 mm. Females smaller than the males.

Distribution. Known only from the western half of Pinar del Rio.

Remarks. This species though originally placed in the genus *Deiroptyx*, (together with *vermiculatus*) does not resemble *vermiculatus* in any character except the presence of a transverse gular fold rather than a dewlap. In many of its external characters, as well as ecology, *bartschi* resembles *lucius* more than any of the other anoline species. *A. bartschi* is not aquatic, but is instead found on the walls of limestone caves and cliffs (Cochran, 1928).

KEY TO THE CUBAN SPECIES OF ANOLINE LIZARDS

1. A middorsal crest of compressed triangular vertical scales 2
   No middorsal crest 3

2\. Row of enlarged triangular scales from mental to anterior border of dewlap (Fig. 1); greyish body color, never green; large head casque overlapping neck in adults *Chamaeleolis chamaeleonides* p. 481

No row of enlarged triangular scales on throat; green or brown in color, never grey; head casque not overlapping the neck *Anolis equestris* p. 482

3\. Transparent scales on lower eyelid 4

No transparent scales on lower eyelid 5

4\. Usually three transparent scales on the lower eyelid; light stripe along upper labials, below eye, and running diagonally through dorsal margin of ear opening to the middorsal line, another light stripe from ventral margin of ear opening to middorsal line; yellow at base of dewlap, maximum snout-vent length = 70 mm *A. lucius* p. 500

Usually two transparent scales on the lower eyelid; head stripes never as above; brown or grey at base of dewlap; maximum snout-vent length = 50 mm *A. argenteolus* p. 502

5\. Three to four transversely enlarged supraoculars (Fig. 11); the supraorbital semicircles in broad contact medially (Fig. 9); ventrals smooth; head scales smooth 6

Supraoculars not transversely enlarged; the supraorbital semicircles not in broad contact medially; ventrals smooth or keeled; head scales smooth, keeled, or rugose 7

6\. Many enlarged spine-like scales on the body and limbs; body dorsoventrally compressed *A. loysiana* p. 503

No enlarged spine-like scales on the body and limbs; body laterally compressed *A. argillaceus* p. 504

7\. Supraocular scales medially in direct contact with the supraorbital semicircles (Fig. 14); dorsals as wide as long; lateral body scales keeled and imbricate (Fig. 15); occipitals, nuchals, and dorsals confluent, showing no demarcation *A. spectrum* p. 507

Not as above 8

8\. A wide middorsal zone of enlarged, keeled, scales having the posterior margin truncate (Fig. 13); scales of the middorsal zone in longitudinal rows and larger than the lateral scales; dorsal head scales are striated 9

No middorsal zone of enlarged, truncate scales; if middorsal scales are enlarged they are keeled, pointed and imbricate; head scales keeled, rugose or striated 10

9\. Ventrals keeled; head scales with longitudinal striations (Fig. 16); middorsal zone of enlarged scales evident on the nape; tail laterally compressed *A. cyanopleurus* p. 510

Ventrals smooth; head scales striated, the scales of the snout with transverse as well as longitudinal rugosities (Fig. 12); tail round in cross section *A. alutaceus* p. 505

10\. A transverse gular fold; no dewlap 11

No transverse gular fold; males with a dewlap; some females with a small dewlap 12

11\. Tail laterally compressed; suborbital scales separated from supralabials by a row of small scales (Fig. 17); digital pad narrow . . . *A. vermiculatus* p. 511
Tail round in cross section; suborbital scales in contact with supralabials (Fig. 18); digital pad large and dilated *A. bartschi* p. 512

12\. Ventral scales in regular transverse rows; tail round in cross section 13
Ventral scales not in transverse rows; in diagonal and/or longitudinal rows; tail laterally compressed 16

13\. More than five scales bordering the rostral posteriorly; the anteriormost sublabials longer than wide; never green in color . . . *A. angusticeps* p. 488
Five scales bordering the rostral posteriorly (Fig. 2); anteriormost sublabials wider than long; color sometimes green 14

14\. Dorsal surface of head flat; dorsal head scales flat and pavement-like with longitudinal striations (Fig. 5); smaller, maximum snout-vent length = 40 mm *A. isolepis* p. 487
Dorsal surface of head not flat, males with well developed frontal ridges, females and young with evidence of a frontal depression; dorsal head scales rugose, keeled, or striated; larger, maximum snout-vent length = 75 mm 15

15\. Ear opening circular; males with frontal ridges higher than the canthal ridges (Fig. 3) *A. porcatus* p. 484
Ear opening with an elongate depressed posterior margin; canthal ridges higher than the frontal ridges (Fig. 4) *A. allisoni* p. 486

16\. Ventrals keeled and with pointed posterior margins 17
Ventrals smooth and with rounded posterior margins 18

17\. A conspicuous zone of enlarged, keeled, pointed scales in longitudinal rows; five longitudinal light stripes on body; a single very elongate suborbital scale . . . *A. ophiolepis* p. 489
No conspicuous middorsal zone of enlarged scales; no longitudinal light stripes on the body; several short suborbital scales *A. sagrei* p. 490

18\. Supraocular and brachial scales smooth and the gulars bordering the mental along a transverse suture; dewlap brown *A. imias* p. 499
Not as above 19

19\. Supracarpal and supradigital scales multicarinate; gulars bordering the mental along a transverse suture (Fig. 7b); two scales separating the supraorbital semicircles . . . 20
Supracarpal and supradigital scales smooth, or with some scales having one or two keels; a few small postmental scales separating the posterior medial margins of the mentals (Fig. 7a); a single scale separating the supraorbital semicircles . . . 22

20\. Body color greyish; dewlap with 4 or 5 stripes of red on a bright yellow background, the edges of the dewlap white *A. rubribarbus* p. 499
Body color not greyish; dewlap not as above 21

21\. Dewlap with a yellowish or tan background color and with 2 or 3 reddish or orange bars; body color reddish-brown . . . *A. allogus* p. 497

Dewlap with a large red basal spot on a yellow background; body color reddish or greenish . . . . *A. ahli* p. 498

22. Small granular posterior supraciliaries; ear opening circular; light grey to greenish body color; dewlap with a large basal red spot with two orange-yellow stripes and a broad white margin *A. mestrei* p. 497

Large, elongate, and keeled posterior supraciliaries; ear opening higher than wide; body color brownish to black; dewlap variable — yellow, white, or grey . . . . *A. homolechis* p. 495

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